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# A phylogenetic analysis of the genera of Aphelininae (Hymenoptera: Aphelinidae), with a generic key and descriptions of new taxa

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**Abstract.** The genera of Aphelininae (Aphelinidae) are reviewed on a worldwide basis. Identification keys and a phylogenetic hypothesis are presented for 16 genera, of which four are new (*Mashimaro* n.g., *Neophytis* n.g., *Punkaphytis* n.g., *Saengella* n.g.) and *Paraphytis* is resurrected. Newly described species are *Mashimaro hawksii* n.sp., *Mashimaro lasallei* n.sp., *Neophytis myartsevae* n.sp., *Neophytis munroi* n.sp., *Punkaphytis erwini* n.sp. and *Punkaphytis hayati* n.sp. New combinations from *Aphytis* include *Neophytis melanosticus* (Compere) and *N. dealbatus* (Compere), and *Paraphytis acutaspidis* (Rosen & DeBach), *P. angusta* (Compere), *P. anomala* (Compere), *P. argenticorpa* (Rosen & DeBach), *P. australiensis* (DeBach & Rosen), *P. benassyi* (Fabres), *P. breviclavata* (Huang), *P. capillata* (Howard), *P. ciliata* (Dodd), *P. cochereaui* (DeBach & Rosen), *P. costalimai* (Gomes), *P. densiciliata* (Huang), *P. fabresi* (DeBach & Rosen), *P. haywardi* (De Santis), *P. hyalinipennis* (Rosen & DeBach), *P. maculatipennis* (Dozier), *P. maculata* (Shafee), *P. mandalayensis* Rosen & DeBach, *P. nigripes* (Compere), *P. noumeaensis* (Howard), *P. obscura* (DeBach & Rosen), *P. peculiaris* (Girault), *P. perplexa* (Rosen & DeBach), *P. transversa* (Huang), *P. vittata* (Compere) (revived status) and *P. wallumbillae* (Girault). A parsimony analysis of 50 morphological characters for 54 species in 21 genera, including four outgroups (*Coccophagus*, *Eunotiscus*, *Euryishomyia* and *Eriaphytis*), resulted in three equally parsimonious trees supporting monophyly of all genera except *Neophytis*. *Neophytis* was paraphyletic to a monophyletic Aphytini but is monophyletic in unpublished molecular analyses. Three tribes are recognised (Aphelinini, Aphytini and Eutrichosomellini). The questionable inclusion of *Eretmocerus* (Eretmocerini) within Aphelininae is discussed.

## Introduction

Aphelinidae is a diverse group of small-sized (1–2 mm) chalcidoids (Hymenoptera). The World fauna consists of 1156 described species in 32 genera (Noyes, 2011). The number and definitions of some genera have been revised fairly recently (Hayat, 1998). However, the phylogenetic relationships of

the family or subfamilies have not been assessed within a cladistic framework. Monophyly of Aphelinidae is still an open question (Yasnosh, 1976; Woolley, 1988; Gibson, 1989; Heraty *et al.*, 1997; Hayat, 1998; Heraty & Schauff, 1998; Gibson *et al.*, 1999). Gibson (1989) considered Aphelinidae s.s. (excluding Eriaporinae) as paraphyletic with respect to Signiphoridae based on the anterior extension of the metasternum between the mesocoxae. The possible close relationships of Azotinae (Aphelinidae) and Signiphoridae potentially render Aphelinidae paraphyletic with respect to Signiphoridae (Woolley, 1988). Consequently, no single character defines the family Aphelinidae without excluding other families of Chalcidoidea. In addition, molecular data have not supported any higher level groupings in the family, with Aphelininae (excluding

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*Eretmocerus*), Coccophaginae, Calesinae, Azotinae and Eriaphytinae all treated as independent and distantly related to each other (Campbell *et al.*, 2000; Munro *et al.*, 2011).

Despite their morphological diversity and difficulties involved with defining the monophyly of Aphelinidae, understanding their species and relationships is important for their practical use in biological control (Rosen & DeBach, 1979; DeBach & Rosen, 1991; Noyes & Hayat, 1994; Rosen, 1994), as well as understanding the evolution of behavioural characteristics and host associations (Walter, 1983; Williams, 1996; Hunter & Woolley, 2001). For example, the aphelinid genus *Aphytis* has been used in many of the successful classical biological control projects against armoured scale insects (Diaspididae) that illustrate many of the basic concepts and practices of biological control (Rosen, 1973, 1994; Rosen & DeBach, 1973, 1976, 1979; Gulmahamad & DeBach, 1978; DeBach & Rosen, 1991). However, a greater understanding of the generic limits of *Aphytis* and its relationships with its closest relatives can enhance further investigations into their use and effectiveness as biological control agents.

Aphelinidae are endoparasites or ectoparasites and sometimes hyperparasites of sternorrhynchus Hemiptera (aphids, whiteflies, armoured scale insects). However, some attack eggs of Lepidoptera, Hymenoptera, Orthoptera or immature stages of Diptera (Yasnosh, 1979; Viggiani, 1984; Polaszek, 1991; Hayat, 1998). Yasnosh (1979) and Hayat (1998) summarised the many distinct patterns of host utilisation of Aphelinidae. Among 32 genera of Aphelinidae, 10 genera in Aphelininae and Coccophaginae are associated with Diaspididae (Yasnosh, 1979; Hayat, 1998). Host use tends to be similar within each tribe of Aphelininae. Aphelinini, consisting of *Aphelinus* and *Protaphelinus*, solely attack aphids as endoparasites. Eretmocerini (with only *Eretmocerus*) attack whiteflies (Aleyrodoidea). One species of *Eutrichosomella* (Eutrichosomellini) was reared from blattid oothecae (Girault, 1915; Hayat, 1998). However, host associations of Aphytini are different and highly diverse; for example, *Aphytis*, *Marlattia* and *Proaphelinoides* utilise only armoured scale insects (Diaspididae) (Rosen & DeBach, 1979; Yasnosh, 1979; Viggiani, 1984), *Botryoideclava* attack Acleridae, *Centrodora* are egg parasitoids (Viggiani, 1984; Polaszek, 1991) and *Marietta* are hyperparasites. Several reviews of aphelinid biology are available (Rosen & DeBach, 1979; Yasnosh, 1979; Viggiani, 1984; DeBach & Rosen, 1991; Rosen, 1994; Woolley, 1997; Hayat, 1998; Hunter & Woolley, 2001).

#### Subfamily Aphelininae

The Aphelininae currently include 12 genera grouped into 4 tribes (Table 1; Hayat, 1998): Aphelinini, Aphytini, Eutrichosomellini and Eretmocerini, although Noyes (Noyes, 2011) recognises Eretmocerinae following Shafee & Khan (1978). DeSantis (1946) first defined Aphelininae by the presence of a linea calva on the forewing. The subfamily has traditionally been recognised by the following combination of characters: antenna with at most six segments (Fig. 3); anellus generally

**Table 1.** Tribes of Aphelininae (Hayat, 1998).

Tribes of Aphelininae	Genera
Aphelinini Thomson, 1876	<i>Aphelinus</i> Dalman, 1820 <i>Protaphelinus</i> Mackauer, 1972
Aphytini Yasnosh, 1976	<i>Aphytis</i> Howard, 1900 <i>Botryoideclava</i> Subba Rao, 1980 <i>Centrodora</i> Foerster, 1878 <i>Hirtaphelinus</i> Hayat, 1983 <i>Marietta</i> Motschulsky, 1863 <i>Marlattia</i> Howard, 1907 <i>Proaphelinoides</i> Girault, 1917 <i>Samariola</i> Hayat, 1983
Eutrichosomellini Trjapitzin, 1973	<i>Eutrichosomella</i> Girault, 1915
Eretmocerini Shafee & Khan, 1978	<i>Eretmocerus</i> Haldeman, 1850

absent (some *Eretmocerus* and the new genus *Mashimaro* have anelliform funicular segments (fig. 204 in Hayat, 1998; Fig. 125); reduced first funicular segment (Fig. 3, fun); pronotum usually divided into two plates by a dorsal membranous region (Figs 1, 121, no<sub>1</sub>); prepectus usually triangular in lateral view (Fig. 109, pre); mesopleuron usually divided into mesepimeron and mesepisternum (Fig. 109, em<sub>2</sub>, es<sub>2</sub>) (exceptions occur in some genera with an expanded acropleuron); forewing usually with a linea calva (Fig. 8, lc) (*Centrodora* and *Eretmocerus* sometimes lack a complete linea calva, cf. Fig. 196); and male genitalia with well-developed digiti (Fig. 223, dg), but usually without parameres (Yasnosh, 1976; Rosen & DeBach, 1979; Woolley, 1997; Hayat, 1998). However, because of their diverse morphology, many of the described subfamilial characters are not consistent among tribes.

Despite the lack of clear synapomorphies, the monophyly of Aphelininae (excluding Eretmocerini) has been accepted, probably because of a lack of contradictory evidence. Support is based on only a few morphological characters (Hayat, 1994, 1998; Heraty & Schauf, 1998); however, these (e.g. a linea calva and number of tarsal segments) are known to be homoplastic in Chalcidoidea (Hayat, 1998; Heraty & Schauf, 1998). Viggiani & Battaglia (1984) also proposed that support for Aphelininae (= Aphytini + Aphelinini + *Eriaphytis*) could be based on the overall similarity of male genitalia (e.g. absence of parameres and well-developed digiti), but again these features are variable. In addition, the polarity of the loss of parameres is not clear, because outgroups such as *Euryischomyia* also lack parameres. Other putative characters suggested to support the monophyly of Aphelininae, such as a medially divided pronotum (Yasnosh, 1976; Hayat, 1998) and a pair of epicoxal pads (J.B. Woolley, personal communication), have not been tested in a phylogenetic analysis. In a previous molecular study, *Aphelinus* and *Aphytis* (Aphelininae) were supported as monophyletic in the analysis of 28S-D2 rDNA, but *Eretmocerus* was distantly related and placed close to Trichogrammatidae (Campbell *et al.*, 2000).

### Intertribal relationships of Aphelininae

The boundary of Aphelininae has been uncertain especially with regard to the inclusion of *Eriaphytis* and *Eretmocerus*. *Eriaphytis* was originally assigned in Aphelininae (Hayat, 1972, 1978, 1998; Viggiani & Battaglia, 1984); however, it is now accepted as a separate subfamily, Eriaphytinae, based on autapomorphic characters such as antennal structure (1132) and male genitalia (digitus with bar) (Hayat, 1998). Eretmocerinae was suggested for *Eretmocerus* (Shafee & Khan, 1978; Khan & Shafee, 1980; Viggiani & Battaglia, 1984; Yousuf & Shafee, 1987), but Hayat (1998) placed it as a tribe of Aphelininae.

Aphelinini is represented by only two genera, *Aphelinus* and *Protaphelinus*. Because only a single species is known for *Protaphelinus*, the diversity of Aphelinini is mainly represented by *Aphelinus* which consists of 86 described species (Noyes, 2011). The affinity between them has not been disputed, but their relationship has not been thoroughly studied. The prominent hypopygium, aphid-association and mesofurcal structure (fig. 8 in Heraty *et al.*, 1997) are characters supporting their monophyly, and clearly separating them from the Aphytini.

With six genera and 223 described species, Aphytini is the most diverse tribe in Aphelininae, representing about 21% of the described species of aphelinids (Noyes, 1998). The lack of a prominent hypopygium is regarded as the single most important feature for defining the tribe (Hayat, 1998), although based on our study, this condition is likely plesiomorphic. *Hirtaphelinus* Hayat and *Samariola* Hayat were placed in Aphytini (Hayat, 1978, 1994, 1998), although Hayat regards this placement as questionable because both have a prominent hypopygium (reaching the cercal plate but not exceeding it as in *Aphelinus*). Among the eight genera in Aphytini, *Aphytis* is the most diverse including 130 described species in seven species groups of *Aphytis sensu* Hayat (1998).

The tribe Eutrichosomellini included only *Eutrichosomella* prior to this study, with only seven Australian species described (Noyes, 1998). The genus was originally described as an encyrtid, based on the structure of axilla and mesopleuron (Figs 118, 122) (Timberlake, 1941). Hayat (1983) placed *Eutrichosomella* in Aphelinidae as a separate tribe (Hayat, 1998). Based on the expansion of the acropleuron resulting in a swollen mesopleuron (Figs 119, 122) and structure of the transscutal articulation (Figs 128, 126), *Eutrichosomella* is superficially similar to Eupelmidae and Encyrtidae (Girault, 1915; Timberlake, 1941; Trjapitzin, 1973; Gibson, 1989). However, Gibson (1989) suggested several characters separating *Eutrichosomella* from the eupelmid lineage.

Eretmocerini includes only *Eretmocerus* with 71 described species (Noyes, 1998). It was recognised as a separate subfamily of Aphelinidae by Shafee & Khan (1978), but as a tribe of Aphelininae by Hayat (1998). The genus has many distinct morphological features, including having all tarsi four-segmented and two funicular segments with an elongated antennal clava in females. *Eretmocerus* lacks the interfurcal process found in other Aphelininae and has anteriorly directed lateral mesofurcal arms (Heraty *et al.*, 1997). Other unique

characters for *Eretmocerus* are the bifurcate propodeal seta (Hayat, 1998), reduced number of antennal segments, and anteriorly advanced axillae. Yousuf & Shafee (1987) proposed a possible affinity between Trichogrammatidae and *Eretmocerus*, but without presenting characters to support their argument. A relationship between *Eretmocerus*, *Cales* (Calesinae) and Trichogrammatidae was also suggested based on the structure of the mesofurca, having simplified lateral furcal arms without a mesofurcal bridge and no anterior interfurcal process (Heraty *et al.*, 1997). In an analysis of 28S-D2 rDNA, *Eretmocerus* was placed as the sister group of Trichogrammatidae (Campbell *et al.*, 2000). The male genitalia of *Eretmocerus* possess a boat-shaped phallobase and two subdigital stylets (Viggiani & Battaglia, 1984; Hayat, 1998). The subdigital stylets are not found in any other group of Aphelinidae (Viggiani & Battaglia, 1984). Therefore, the inclusion of Eretmocerini in Aphelininae is controversial.

The lack of reliable synapomorphic characters in Aphelininae and its tribes is a considerable problem. Character states involving reduced numbers of antennal and tarsal segments cannot be used alone as supporting characters for intertribal relationships (Hayat, 1998; Heraty & Schauff, 1998). It is commonly accepted that reduction in characters might happen multiple times (Yasnosh, 1976; Hayat, 1994, 1998; Heraty & Schauff, 1998). Therefore, two major studies are imminently necessary: defining Aphelininae and its tribes based on morphological characters and independent molecular data sets. This paper focuses on the relationships of tribes in Aphelininae based on morphology.

### Objectives

Approaches to the study of aphelinid classification are hindered by the lack of detailed studies of comparative morphology and phylogenetic methodology. Polaszek & Hayat (1992) were the first to employ a morphology-based phylogenetic approach to the study of *Encarsia* and *Dirphys* (Coccophaginae), and no such approach had been taken in other aphelinid groups. The objectives of this study are as follows: first, discovering synapomorphic characters for the subfamily Aphelininae; second, delimiting the generic boundary of the known 12 genera in Aphelininae; third, resolving the intertribal relationships of Aphelininae.

### Materials and methods

Species investigated are listed in Table 2. In total, 54 species in 21 genera were included in the phylogenetic analysis (Table 2), and all 16 genera of Aphelininae (now recognised). Holotype and paratype data are recorded exactly as on the labels of the slide specimens and pin-mounted specimens. Measurements of body parts are illustrated in Figs 1–8. Antennal scape, pedicel and flagellar segments are measured in their maximum lengths in lateral view. Ovipositor lengths are as in Hayat (1998, fig. 8).

**Table 2.** Aphelinidae examined for coding of morphological characters.

Subfamily (Tribes)	Genera	Species
Eriaporinae	<i>Eunotiscus</i>	<i>gahani</i> Compere [BMNH]
Euryischiinae	<i>Euryischomyia</i>	sp. 1 [BMNH]
Coccophaginae (Coccophagini)	<i>Coccophagus</i>	sp. 1 [UCRC]
Eriaphytinae	<i>Eriaphytis</i>	<i>chackoi</i> Subba Rao [BMNH]
Aphelininae (Eretmocerini)	<i>Eretmocerus</i>	<i>hayati</i> Zolnerowich & Rose [UCRC], sp. 1* [UCRC]
Aphelininae (Aphelinini)	<i>Aphelinus</i>	<i>albipodus</i> Hayat & Fatima [UCRC], <i>ancer</i> Hayat [BMNH], <i>gossypii</i> Timberlake [UCRC], <i>hongkongensis</i> Hayat [BMNH], <i>lankaensis</i> Hayat [BMNH], <i>nepalensis</i> Hayat [BMNH], <i>polaszeki</i> Hayat [BMNH], <i>sharpae</i> Hayat [BMNH], <i>varipes</i> * Foerster [UCRC]
Aphelininae (Eutrichosomellini)	<i>Protaphelinus</i>	<i>nikolskajae</i> (Yasnosh) [USNM]
	<i>Eutrichosomella</i>	sp. 1 [BMNH], sp. 2 [BMNH], sp. 3* [UCRC], sp. 4* [UCRC], <i>aereiscapus</i> ? Girault [BMNH]
	<i>Mashimaro</i> n.g.	sp. 1 [ANIC], sp. 2 [ANIC], sp. 3 [ANIC], <i>lasallei</i> n.sp. [ANIC], <i>hawksi</i> * n.sp. [ANIC]
	<i>Saengella</i> n.g.	<i>gloria</i> n.sp. [BMNH]
	<i>Samariola</i>	<i>cameroonensis</i> Hayat [BMNH], sp. 1 [CAS], sp. 2* [UCRC]
Aphelininae (Aphytini)	<i>Aphytis</i>	<i>chrysomphali</i> (Mercet) [UCRC], <i>coheni</i> DeBach [UCRC], nr <i>diaspidis</i> sp. 1 [UCRC], <i>mytilaspidis</i> (Le Baron) [UCRC], <i>vandenboschi</i> DeBach & Rosen [UCRC], <i>melinus</i> * DeBach [UCRC], <i>lingnanensis</i> * Compere [UCRC]
	<i>Botryoideclava</i>	<i>bharatiya</i> Subba Rao [BMNH], sp. 1* [UCRC]
	<i>Centrodora</i>	sp. 1 [UCRC], sp. 2 [UCRC], sp. 3* [UCRC], sp. 4* [UCRC], <i>ghorpadei</i> Hayat [BMNH], <i>lineascapa</i> Hayat [BMNH], <i>hexatracha</i> Erdos & Novicky [BMNH]
	<i>Hirtaphelinus</i>	<i>smetanai</i> Hayat [BMNH]
	<i>Marietta</i>	<i>carnesi</i> (Howard) [BMNH], <i>connecta</i> Compere [BMNH], <i>jabensis</i> ? Howard [BMNH], <i>leopardina</i> Motschulsky [BMNH], nr <i>marchali</i> * Mercet [UCRC], <i>montana</i> Myartseva & Ruiz-Cancino [BMNH]
	<i>Marlattia</i>	<i>prima</i> Howard [USNM]
	<i>Neophytis</i> n.g.	<i>myartsevai</i> n.sp. [USNM], <i>munroi</i> n.sp. [USNM]
	<i>Paraphytis</i> n. rev.	<i>maculata</i> (Shafee) [UCRC], <i>vittatus</i> Compere [UCRC], sp. 1 [UCRC], sp. 2 [UCRC], sp. 3 [UCRC], sp. 4 [UCRC], sp. 5* [UCRC], sp. 9 [UCRC]
	<i>Proaphelinoides</i>	<i>elongatiformis</i> Girault [USNM]
	<i>Punkaphytis</i> n.g.	<i>erwini</i> n.sp. [USNM], <i>hayati</i> n.sp. [USNM]

Museum deposition in brackets.

\*Prepared only for SEM.

? after name refers to questionable species determination.

### Specimen examination

Species for card mounts or scanning electron microscopy (SEM) were dried from alcohol using hexamethyldisilazane (Heraty & Hawks, 1998). Some of the card-mounted specimens were later transferred to slides after first removing and mounting the wings. Specimens on slide mounts were prepared by the techniques developed by Noyes (1982) and Platner *et al.* (1999) with some modifications, which were as follows: specimens were warmed in 10% KOH using a heat block for 1–2 h; specimens were flattened between two coverslips; dehydration of specimens was conducted through the series of alcohol concentrations for 15 min for each step. An Emscope ES500 was used for sputter-coating Pd/Au on specimens. SEM pictures were taken using a Phillips XL30-FEG. Specimens were examined under a stereomicroscope (Zeiss Stemi SV6) and a Leica DMRB compound microscope. Line drawings were created using a camera lucida. Pictures of slide-mounted specimens were made using Automontage® (Synscopy) with images captured by a JVC 3-CCD camera mounted on an Axioskop2 compound microscope (Zeiss).

### Acronyms of museums

ANIC – CSIRO, Australian National Insect Collection, Canberra, Australia.

BMNH – Department of Entomology, The Natural History Museum, London, U.K.

BIBM – Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.

CAS – California Academy of Science, San Francisco, U.S.A.

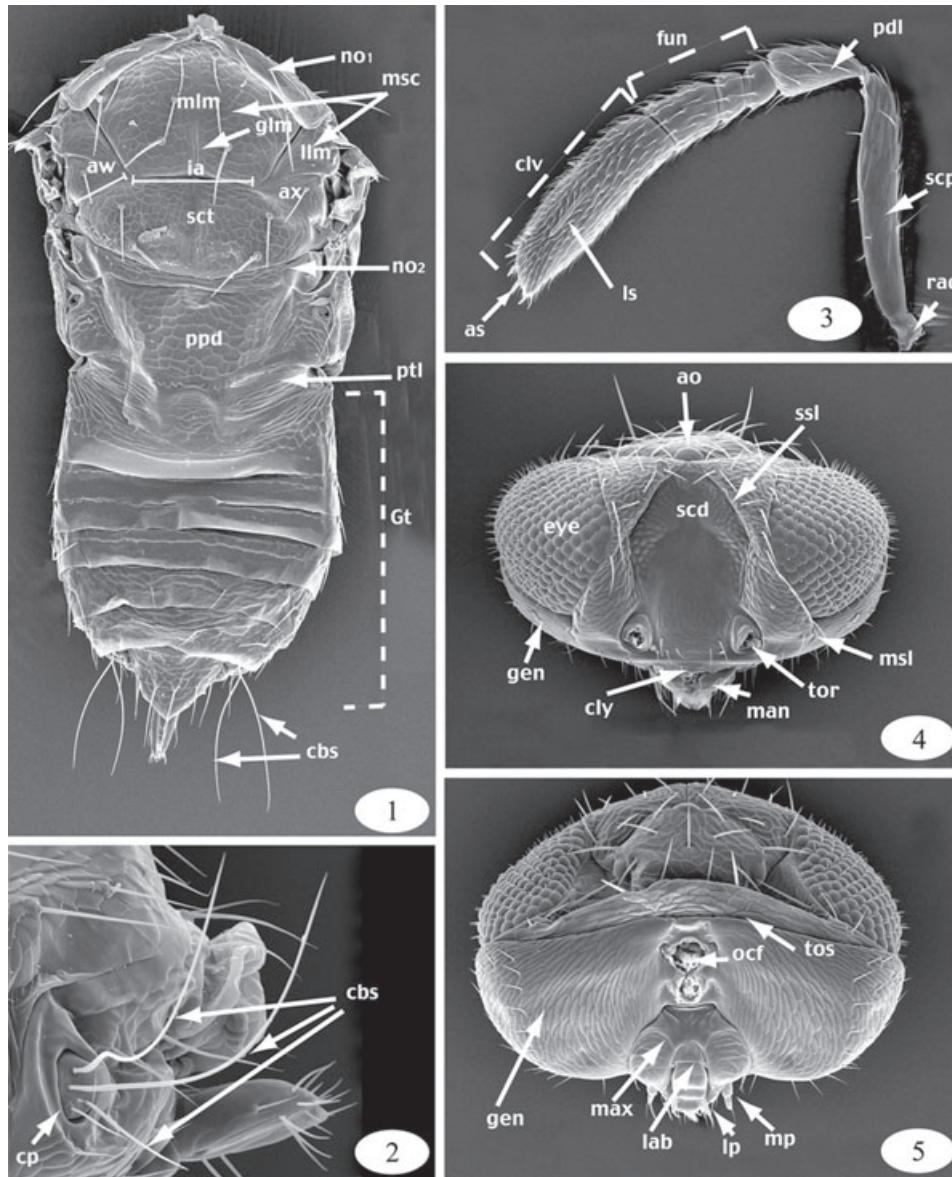
PPRI – Plant Protection Research Institute, Pretoria, Republic of South Africa.

QM – Queensland Museum, South Brisbane, Australia.

UCRC – Department of Entomology, University of California, Riverside, CA, U.S.A.

USNM – U. S. National Museum of Natural History, Washington D.C., U.S.A.

ZDAMU – Department of Zoology, Aligarh Muslim University, Aligarh, India.

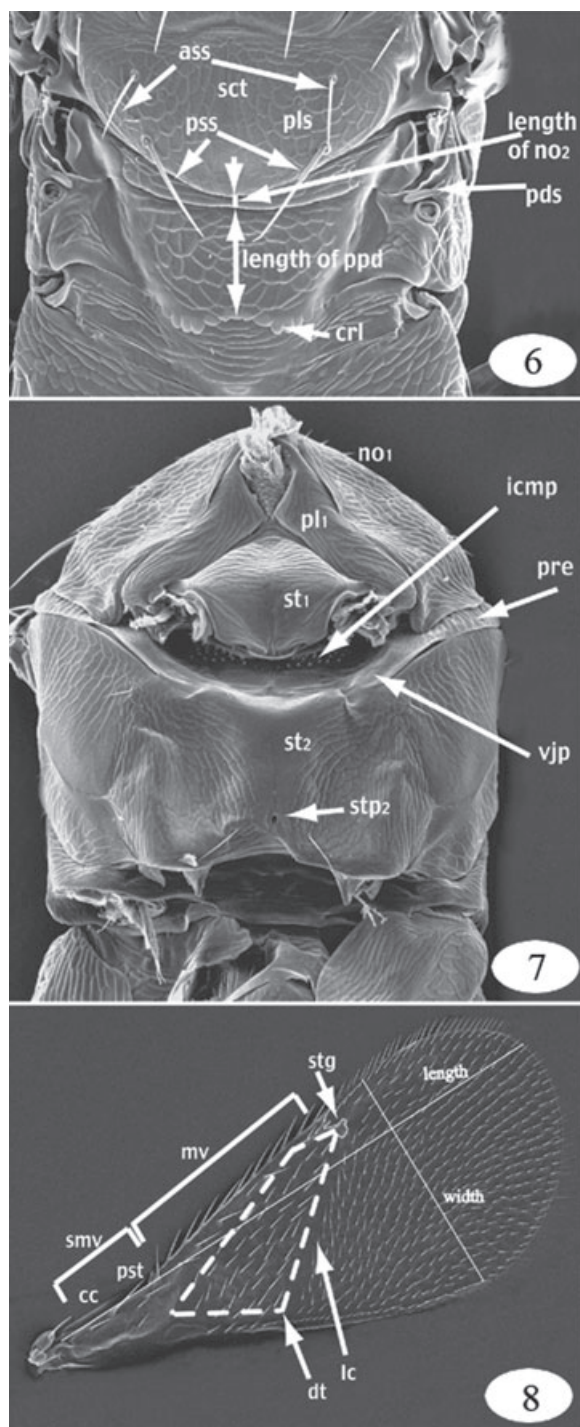


**Figs 1–5.** Explanation of terms and measurements. 1, body (dorsal); 2, cercal plate (lateral); 3, antenna; 4, head (anterior); 5, head (posterior). Abbreviations explained in Table 4.

### Terminology

Terms generally follow Gibson *et al.* (1997) and Gibson (1989) for sternal pit (stp), transscutal articulation (tsa) and mesopleuron, and Hayat (1998) for the rest of body parts, with the following exceptions. Heraty *et al.* (1997) was used for internal structure of the mesosoma. A list of character abbreviations is provided in Table 4. The seta anterior to the propodeal spiracle is termed the propodeal seta (Fig. 6, pds). The epicoxal pads refer to the spiculate membranous areas (Fig. 7, icmp) located posterior to the procoxa and are divided into two separate patches (Rosen & DeBach, 1979; Woolley *et al.*, 1994). A transverse suture on the posterior aspect of the head between

the compound eyes is the transoccipital suture (Fig. 5, tos). In *Aphytis*, *Centrodora* and *Paraphytis*, the mesonotum has a medial longitudinal groove, which is termed the grooved line of the mesosoma (Fig. 1, glm). For *Aphytis*, the shape and number of crenulae (Fig. 6, crl) are important for defining species and species groups (Rosen & DeBach, 1979). The scutellum of the mesosoma has two pairs of setae (Fig. 6, ass, pss) and one pair of sensilla (Fig. 6, pls). The relative location of setae and sensilla on the scutellum were found to be important. The enlarged or swollen mesopleuron (Fig. 122) is the result of an enlargement of the acropleuron obscuring most of the mesepisternum and mesepimeron laterally (Gibson, 1989).



**Figs 6–8.** Explanation of terms and measurements. 6, mesosoma (dorsal); 7, mesosoma (ventral); 8, forewing. Abbreviations explained in Table 4.

Linea calva and speculum have been used interchangeably in the literature. However, Hayat (1983) made a clear distinction between the linea calva (Fig. 8, lc) and the speculum, noting that speculum refers to an area without setae under the

parastigma and posterior to the delta region (fig. 1 in Hayat, 1983). We followed the numbering system for tergites used by Hayat for counting gastral tergites T1–T7 (Fig. 1, Gt<sub>1–7</sub>) (Hayat, 1983, 1998). Male genitalia of Aphelininae were examined in some detail by Yasnosh (1976) and Viggiani & Battaglia (1984). The current study did not include characters of male genitalia because the diversity of male genitalia in Aphelininae is limited (Yasnosh, 1976; Rosen & DeBach, 1979; Viggiani & Battaglia, 1984; Polaszek & Hayat, 1992; Hayat, 1998).

#### *Characters analysis of intertribal relationships of Aphelininae*

Sixty-four characters were initially chosen based on the literature (Yasnosh, 1976; Hayat, 1983, 1998; Viggiani & Battaglia, 1984; Woolley, 1988; Polaszek & Hayat, 1992; Heraty *et al.*, 1997; Babcock *et al.*, 2001). Drs. J.B. Woolley, A. Polaszek, M. Hayat and J. Pinto provided information on potential characters for analysis and insights in to states for certain genera of Aphelininae. Among the characters selected, 14 were excluded after coding because of excessive variation within genera. In total, 50 characters were included in the parsimony analysis (Table 3). All characters are unordered.

#### *Phylogenetic analyses*

The outgroups (*Eumotiscus* Compere, 1928, Eriaporinae; *Euryischomyia* Girault, 1914, Euryishiinae; *Coccophagus* Westwood, 1833, Coccophaginae; *Eriaphytis* Hayat, 1972, Eriaphytinae) were chosen to polarise character states. *Eretmocerus* (Eretmocerini or Eretmocerinae) is included here as a member of Aphelininae.

Parsimony analysis was performed using PAUP v4.0β10 (Swofford, 2002). Searches for most parsimonious trees were performed using an heuristic search with random stepwise addition, 100 replicates and holding 1 tree each step. Tree-Bisection-Reconnection (TBR) was chosen for branch swapping. All characters were unordered and equally weighted. Three characters were parsimony uninformative (characters 9, 12, 14). Some characters could not be coded, either due to the preservational state of the specimens or due to character losses (e.g. *Hirtaphelinus* lacking a metanotum). Successive approximations weighting (SAW) was performed with each iteration being reweighted by the maximum value of the rescaled consistency index and a base weight of 1000, then all the characters were re-weighted to one to compare with the MPTs (Babcock *et al.*, 2001). Both ambiguous and unambiguous characters were mapped on the tree using MacClade v4.05 (Maddison & Maddison, 2002) with a default ACCTRAN (Accelerated Transformation) character optimisation. Bootstrap analyses were conducted with 100 replications with a restriction of the number of arrangements of 1X10<sup>9</sup>. AutoDecay v4.0.2 PPC (Eriksson, 1988) was used to calculate decay indices, and TreeViewPPC (Page, 1996) was used to plot decay values.

**Table 3.** Character matrix for phylogenetic analysis.

Taxon	Characters														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Eumotiscus gahani</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Euryischomyia</i> sp. 1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coccophagus</i> sp. 1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eriaphytis chackoi</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eretmocerus hayati</i>	2	2	1	0	1	1	1	1	0	2	2	1	0	2	1
<i>Aphelinus albipodus</i>	2	1	2	0	1	0	1	1	1	2	1	0	1	2	0
<i>Aphelinus ancer</i>	2	1	1	0	1	0	1	1	1	2	1	0	1	2	0
<i>Aphelinus gossypii</i>	2	1	2	0	1	0	1	1	1	2	1	0	1	2	0
<i>Aphelinus hongkongensis</i>	2	1	1	0	1	0	1	1	1	2	1	0	1	2	0
<i>Aphelinus lankaensis</i>	2	1	1	0	1	0	1	1	1	2	1	0	1	2	0
<i>Aphelinus nepalensis</i>	2	1	1	0	1	0	1	1	1	2	1	0	1	2	0
<i>Aphelinus polaszeki</i>	2	1	2	0	1	0	1	1	1	2	1	0	1	2	0
<i>Aphelinus sharpae</i>	2	1	1	0	1	0	1	1	1	2	1	0	1	2	0
<i>Protaphelinus nikolskajae</i>	2	1	2	0	1	0	1	1	1	2	1	0	1	2	0
<i>Eutrichosomella aereiscapus?</i>	2	1	1	0	1	0	1	1	1	2	1	0	1	2	0
<i>Eutrichosomella</i> sp. 1	2	1	1	0	1	0	1	1	1	2	1	0	1	2	0
<i>Eutrichosomella</i> sp. 2	2	1	1	0	1	0	1	1	1	2	1	0	1	2	0
<i>Hirtaphelinus smetanai</i>	2	1	2	0	1	0	1	1	1	2	1	0	1	2	0
<i>Mashimaro lasallei</i>	2	1	0	1	0	1	1	1	1	2	1	0	1	2	0
<i>Mashimaro</i> sp. 1	2	1	0	1	0	1	1	1	1	2	1	0	1	2	0
<i>Mashimaro</i> sp. 2	2	1	0	1	0	1	1	1	1	2	1	0	1	2	0
<i>Mashimaro</i> sp. 3	2	1	0	1	0	1	1	1	1	2	1	0	1	2	0
<i>Saengella gloria</i>	2	1	0	1	0	1	1	1	1	2	1	0	1	2	0
<i>Samariola cameronensis</i>	2	1	1	2	0	1	0	1	1	1	1	1	0	1	1
<i>Samariola</i> sp. 1	2	1	1	2	0	1	0	1	1	1	1	1	0	1	1
<i>Aphytis chrysomphali</i>	2	1	2	0	1	0	1	1	1	2	1	0	1	2	0
<i>Aphytis coheni</i>	2	1	2	0	1	0	1	1	1	2	1	0	1	2	0
<i>Aphytis nr diaspidis</i> sp. 1	2	1	2	0	1	0	1	1	1	2	1	0	1	2	0
<i>Aphytis mytilaspidis</i>	2	1	2	0	1	0	1	1	1	2	1	0	1	2	0
<i>Aphytis vandenboschi</i>	2	1	2	0	1	0	1	1	1	2	1	0	1	2	0
<i>Botryoideclava bharatiya</i>	2	1	2	0	1	0	1	1	1	2	1	0	1	2	0
<i>Centrodora ghorpadei</i>	2	1	1	1	0	0	0	1	1	2	1	0	1	2	0
<i>Centrodora hexatracha</i>	2	1	2	0	1	1	1	1	1	2	1	0	1	2	0
<i>Centrodora lineascapa</i>	2	1	2	0	1	1	1	1	1	2	1	0	1	2	0
<i>Centrodora</i> sp. 1	2	1	2	0	1	1	1	1	1	2	1	0	1	2	0
<i>Centrodora</i> sp. 2	2	1	2	0	1	1	1	1	1	2	1	0	1	2	0
<i>Marietta carnesi</i>	2	1	2	0	1	0	0	1	1	2	1	0	1	2	0
<i>Marietta connecta</i>	2	1	2	0	1	0	0	1	1	2	1	0	1	2	0
<i>Marietta jabensis?</i>	2	1	2	0	1	0	0	1	1	2	1	0	1	2	0
<i>Marietta leopardina</i>	2	1	2	0	1	0	0	1	1	2	1	0	1	2	0
<i>Marietta montana</i>	2	1	2	0	1	0	0	1	1	2	1	0	1	2	0
<i>Marlattella prima</i>	2	3	1	0	1	0	0	1	1	2	1	0	1	2	0
<i>Neophytis munroi</i>	2	1	2	0	1	0	0	1	1	2	1	0	1	2	0
<i>Neophytis myartsevai</i>	2	1	2	0	1	0	0	1	1	2	1	0	1	2	0
<i>Proaphelinoides elongatiformis</i>	2	1	2	0	1	0	1	1	1	2	1	0	1	2	0
<i>Paraphytis maculata</i>	2	2	1	0	0	0	1	1	1	2	1	0	1	2	0
<i>Paraphytis vittatus</i>	2	1	2	0	1	0	0	1	1	2	1	0	1	2	0
<i>Paraphytis</i> sp. 1	2	1	2	0	1	0	0	1	1	2	1	0	1	2	0
<i>Paraphytis</i> sp. 2	2	1	2	0	1	0	0	1	1	2	1	0	1	2	0
<i>Paraphytis</i> sp. 3	2	1	2	0	1	0	0	1	1	2	1	0	1	2	0
<i>Paraphytis</i> sp. 4	2	1	2	0	1	0	0	1	1	2	1	0	1	2	0
<i>Paraphytis</i> sp. 9	2	1	2	0	1	0	0	1	1	2	1	0	1	2	0
<i>Punkaphytis erwini</i>	2	1	1	0	1	0	0	1	1	2	1	0	1	2	0
<i>Punkaphytis hayati</i>	2	1	1	0	1	0	0	1	1	2	1	0	1	2	0

Question marks denote missing data.



**Table 4.** List of abbreviations used in the text and for figures.

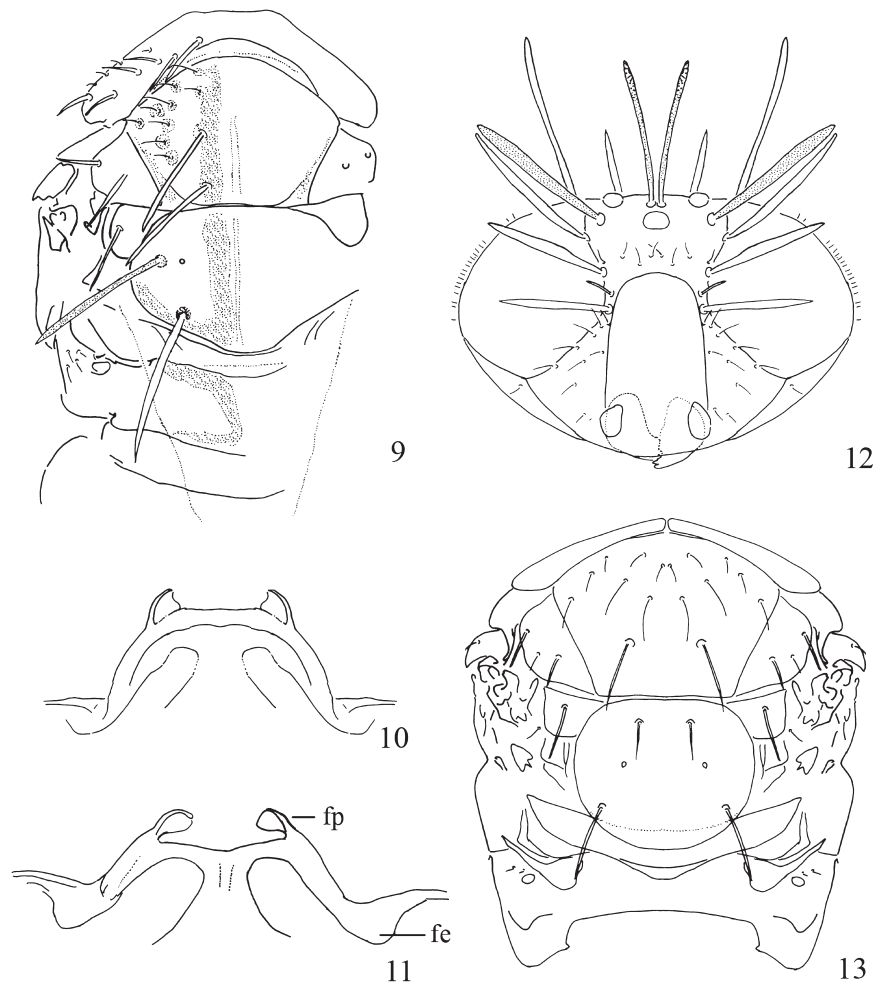
ao	anterior ocellus	max	maxilla
anl	anellus	mlm	midlobe of mesoscutum
ass	anterior scutellum setae	mp	maxillary palpus
aw	axillar width	msc	mesoscutum
ax	axilla	msl	malar sulcus
cbs	cercal bristles	mv	marginal vein
cc	costal cell	no <sub>1-3</sub>	notum (pro, meso, meta)
clv	clava	ocf	occipital foramen
cly	clypeus	pdl	pedicel
cp	cercal plate	pds	propodeal seta
crl	crenulae	pgb	postgenal bridge
csl	cubital setal line	pl <sub>1-3</sub>	pleuron (pro, meso, meta)
dt	delta	pls	placoid sensillum
eps	epistomal suture	ppd	propodeum
es <sub>2</sub>	mesepisternum	pre	prepectus
em <sub>2</sub>	mesepimeron	ps	propodeal seta
fe	posterior interfurcal process of mesofurca	pss	posterior scutellum seta
fmd	femoral depression	pst	parastigma
fp	anterior interfurcal process of mesofurca	pt	posterior tentorial pits
Fu <sub>1-3</sub>	funicular segments	ptl	petiole
gen	gena	rad	radicle
glm	grooved line in middle of mesosoma	scd	scrobal depression
Gt <sub>1-7</sub>	gastral tergum	scp	scape
hsb	hypostomal bridge	sct	scutellum
hyp	hypopygium	smv	submarginal vein
ia	interaxillar width	ssa	specialised sensilla on club apex
icmp	intercoxal membrane pad (epicoxal pad)	ssl	scrobal sulcus
lab	labium	st <sub>1-2</sub>	sternum (pro and meso)
lc	linea calva	stg	stigma
lgb	length of genal bridge	stp <sub>1-2</sub>	sternal pit (pro and meso)
llm	lateral lobe of mesoscutum	tfl	transfacial line
lp	labial palpus	tor	torulus
lr	lateral ridge on face	tos	transoccipital suture
ls	longitudinal sensilla	tsa	transcutal articulation
man	mandible	vp	ventral prepectus

### Character and state definitions

**1. Number of distinct claval segments of female. 0:** Three segments (Fig. 57). **1:** two segments (Fig. 72). **2:** unsegmented (Fig. 100). A three-segmented clava (State 0; Fig. 57) is plesiomorphic, with increasing fusion to a single fused claval segment, which is considered apomorphic (Figs 100, 113, 128). Even when fused, each differentiated claval segment usually has a relatively even row of linear sensilla. The clava is usually distinguished from the funicular segments by a distinct line of separation and difference in segment width (Fig. 57); however, in some cases this separation is not so clear (Figs 30, 128, 200). If the sensilla are absent or scattered and the distinction not so clear, only the degree of separation is useful in differentiating the funicle from the clava. Hayat (1998) considered *Botryoideclava* to have a two-segmented clava; however, the two apical segments are distinctly separated (Fig. 171), and the subapical segment is more likely homologous with the third funicular segment (Fu<sub>3</sub>). In some *Marietta*, the clava appears two-segmented, with both segments of roughly equal proportion and enlarged in relation to the

basal funicular segments (Fig. 200), but again, the clear line of separation (articulation) would suggest that the basal segment is the third funicular segment. Only females of some *Paraphytis* s.s. (Fig. 38), males of *Marietta* and males and females of *Eretmocerus* have the third funicular segment fused with the clava, and usually associated with a funicle comprised of two or fewer segments.

**2. Number of funicular segments of female. 0:** four. **1:** three. **2:** two. **3:** unsegmented. Three or more funicular segments (Figs 3, 39, 257), excluding the anellus, are plesiomorphic for Aphelinidae. A distinct four-segmented funicle occurs only in Eriaporinae, *Eumotiscus* and *Promuscidea* (cf. fig. 833 in Hayat, 1998); therefore, having four funicular segments was coded as State 0. However, Euryischiinae (including *Euryischia*, *Euryischomyia* and *Myiocnema*) has a three-segmented funicular segment with one or more anelli (Hayat, 1998). The definition of funicular segments in Aphelininae is often problematic. All Aphelininae were considered to have at most three funicular segments. One minute anellar segment (Figs 72, 125) may be present, but in all Aphelininae these are in addition to a three-segmented



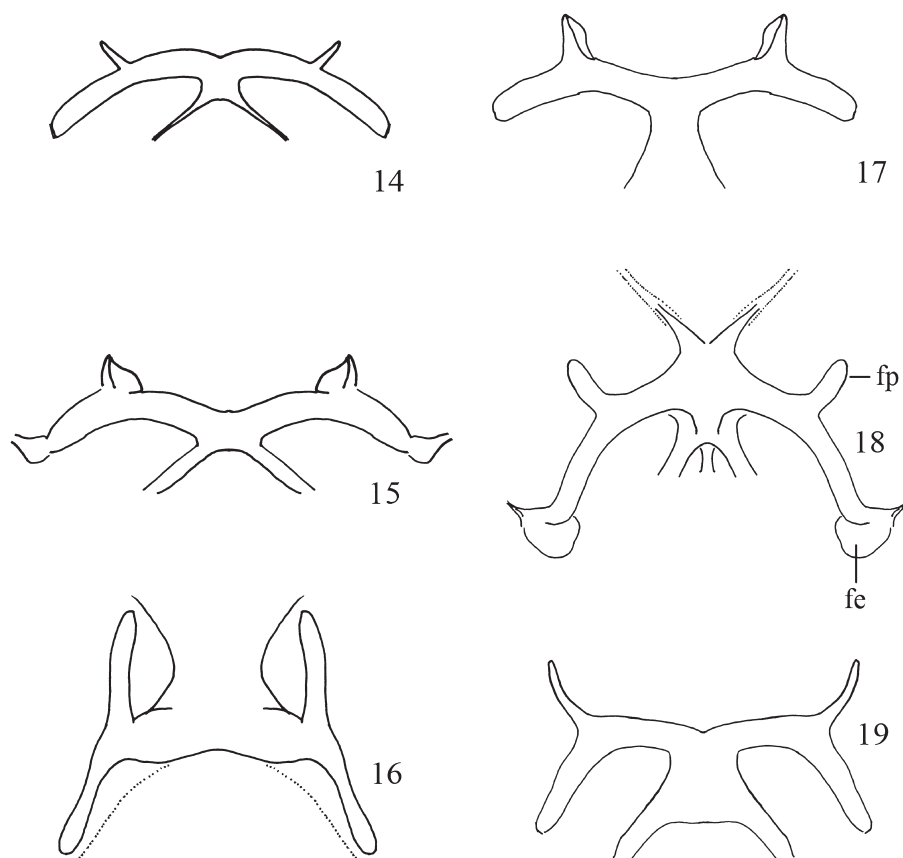
**Figs 9–13.** 9–10, *Punkaphytis erwini* n.sp. (female): 9, mesosoma (dorsal); 10, mesofurca (dorsal). 11–12, *P. hayati* n.sp. (female): 11, mesofurca (dorsal); 12, head (anterior). 13, *Saengella gloria* n.sp. (female), mesosoma (dorsal).

funicle. Exceptionally, *Paraphytis* sp. 1 has the two basal funicular segments greatly reduced and ring-like (Fig. 42), but these two segments are clearly homologous with the basal two funicular segments of other *Paraphytis* and similar in structure to *Eretmocerus* (fig. 204 in Hayat, 1998). *Paraphytis* and *Punkaphytis* also have a small wedge-shaped basal funicular segment (Figs 38, 40, 246), but in both cases this segment appears to be homologous to the basal funicular segment.

The groundplan antennal formula for Aphelininae is 1-1-3-3, as in *Coccophagus* (Fig. 57), with an apparent tendency for fusion of all three claval segments. There is some confusion surrounding *Eriaphytis* (Fig. 72) as to whether the apparent anellus should be counted as an extra funicular segment with the two apical segments representing the clava segments (antenna formula 1-1-4-2; 1-1-3-2, if the anellus is not counted), or if the three longer segments are funicular, and the apical three segments are an unfused clava (antenna formula 1-1-3-3, if anellus counted as the first funicular segment). However, choosing an

antenna formula for *Eriaphytis* as 1-1-3-3 instead of 1-1-3-2 did not affect the tree topology. Therefore, the antenna formula of *Eriaphytis* was coded as 1-1-3-2, and the funicular segments coded as State 1.

**3. Anellar segments of female. 0:** present. **1:** absent. A distinct anellus, defined as a narrow ring segment more than  $4.5\times$  times broader than long and without any multiporous plate sensilla, is present in Eriaporinae, Euryischiinae, *Eriaphytis* (with a wedge-shaped anellus) and most species of *Coccophagus* (figs 348, 353, 361 in Hayat, 1998). An additional minute partial segment occurs between the anellus and basal funicular segment of some Euryischiinae and Eriaporinae, but this is autapomorphic and is not considered here. An anellus is considered to be absent in all Aphelininae except for *Mashimaro* (Fig. 125, anl), which has a minute, incomplete wedge-shaped segment (State 0) at the base of the flagellum in addition to the three funicular segments. Some *Eretmocerus* have a very minute transverse ring-like segment, but this is considered



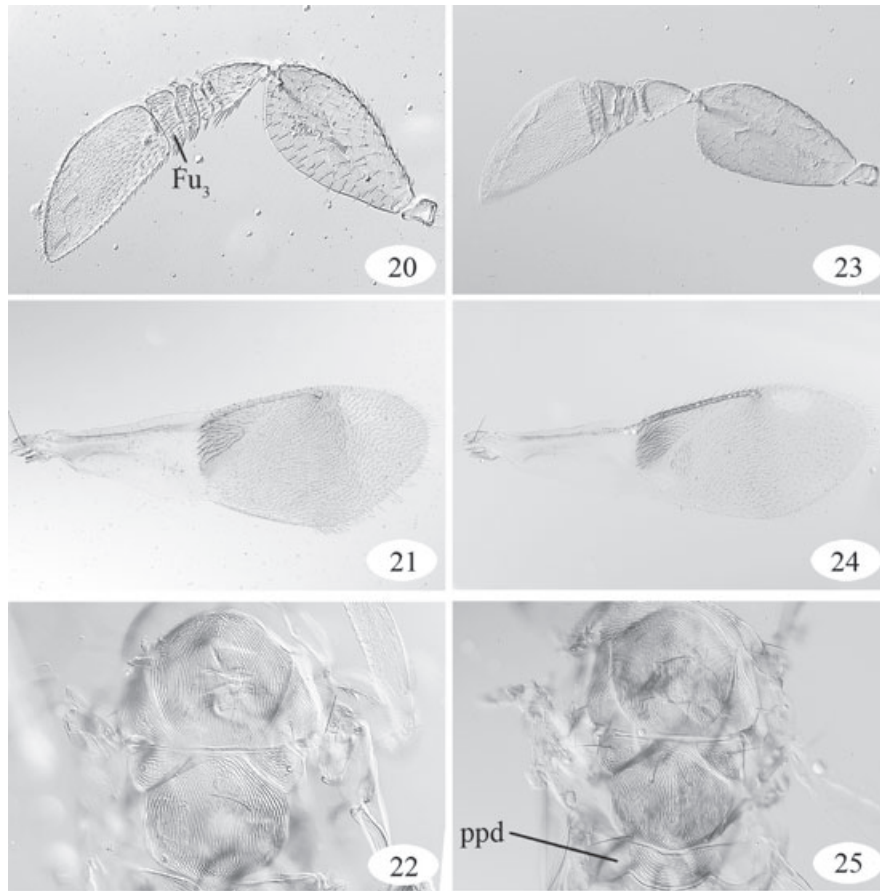
**Figs 14–19.** Mesofurca. 14, *Paraphytis* sp. 3; 15, *Neophytis munroi*; 16, *Saengella gloria*; 17, *Paraphytis* sp. 1; 18, *Mashimaro hawksi*; 19, *Samariola* sp. 1.

homologous to one of the two quadrate funicular segments found in other species of *Eretmocerus* (Hayat, 1998).

- 4. Relative ratio of funicular segment  $Fu_3$  to  $Fu_1 + Fu_2$  in female.** **0:**  $Fu_3$  less than  $Fu_1 + Fu_2$  (all segments subequal). **1:** 1.0–1.2 $\times$  as long as  $Fu_1 + Fu_2$ . **2:** more than 1.2 $\times$   $Fu_1 + Fu_2$ .
- 5. Clava length in female.** **0:** 2.5–5 $\times$  as long as wide (usually 2.5–3.5 $\times$ ). **1:** more than 5 $\times$  as long as wide. **2:** less than 2.5 $\times$  as long as wide. *Eretmocerus* and *Punkaphytis* have a long and slender antennal club with parallel sides (Figs 44, 47, 246). Most genera in Aphelininae have an antennal club that is 2.5–3.5 $\times$  as long as broad, with lateral sides somewhat expanded. *Samariola* has a short and stout antennal club (State 0; at most 2.3 $\times$  as long as wide).
- 6. Shape of claval apex in female.** **0:** rounded or truncated. **1:** pointed and asymmetrically tapered (Fig. 184). This is an apomorphic character for most *Centrodora* (Fig. 184), but not for all species (Fig. 180).
- 7. Transfacial line (tfl).** **0:** present (Figs 56, 71, 86, tfl). **1:** absent (Figs 99, 142, 154). The transfacial line (figs 866, 872 in Hayat, 1998) is a distinct horizontal suture across the scrobes in *Eriaphytis*, *Eretmocerus* and *Coccophagus*. A minute transfacial line is also found in some *Encarsia* (cf. fig. 868 of Hayat, 1998) and a similar line is

present in some Mymaridae, Eulophidae, Trichogrammatidae and Pteromalidae. The transfacial line of *Eriaphytis* and *Eretmocerus* is  $\wedge$ -shaped and has a medial vertical extension to the anterior ocellus (Figs 71, 86). These features were coded as absent or present as two additional characters. Inclusion or exclusion of these additional characters did not affect tree topology; therefore, the transfacial line was coded as a single character.

- 8. Epistomal sulcus.** **0:** absent. **1:** present (Fig. 181, eps). The sulcus is autapomorphic for *Centrodora*. Homology of this sulcus with the true epistomal sulcus (eps) is uncertain because it is dorsal to the tentorial pits, and laterally, the sulcus is continuous with the malar sulcus (Fig. 181).
- 9. Position of posterior tentorial pits.** **0:** pits ventral to foramen magnum (Fig. 69, pt). **1:** pits lateral to foramen (Fig. 102, pt). In the plesiomorphic state, the tentorial pits are located on the hypostomal area, and positioned ventrally under the foramen magnum. In Aphelininae and *Eriaphytis*, the tentorial pits are positioned lateral to the foramen, and associated with a well-developed and fused genal bridge (Figs 74, 102).
- 10. Vertical length of genal bridge.** **0:** long, more than 1.2 $\times$  as long as the width of lower foramen (Fig. 74, lgb). **1:** short, at most less than 1.0 $\times$  of width of lower foramen



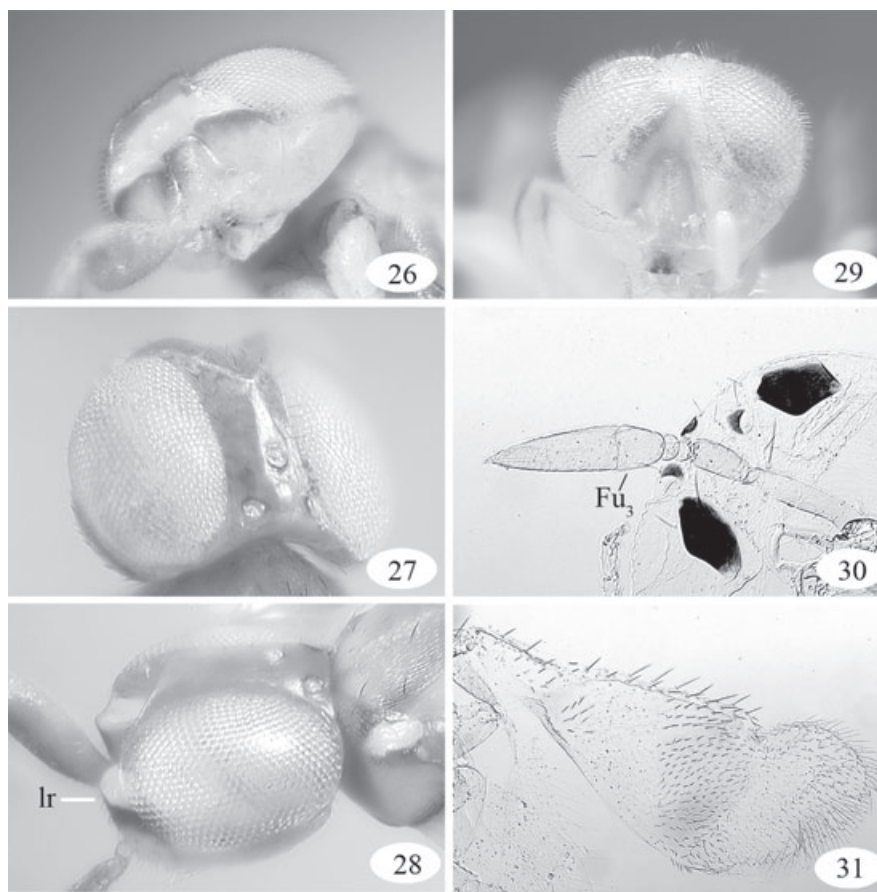
**Figs 20–25.** *Mashimaro* (holotypes). 20–22, *M. hawksii* n.sp. (female): 20, antenna; 21, forewing; 22, mesosoma (dorsal view). 23–25, *M. lasallei* n.sp. (female): 23, antenna; 24, forewing; 25, mesosoma.

(Figs 89, 157). If a genal bridge is absent as in *Coccophagus*, then the length was the distance between the lower margin of the foramen and the oral fossa.

11. **Number of mandibular teeth.** **0:** bidentate with a truncation. **1:** tridentate. **2:** tetradentate. **3:** rudimentary.
12. **Number of maxillary palp segments.** **0:** three-segmented. **1:** two-segmented. **2:** unsegmented (Polaszek & Hayat, 1992; Babcock *et al.*, 2001). Only *Euryischia* (Euryischiinae) and *Promuscidea* (Eriaporinae) have a three-segmented maxillary palp (Hayat, 1998). Within Coccophaginae, only some *Encarsia* (Coccophaginae) have an unsegmented palp, while the palps of most other Aphelinidae are two-segmented (Hayat, 1998).
13. **Number of labial palp segments.** **0:** two-segmented. **1:** unsegmented.
14. **Malar sulcus.** **0:** present. **1:** absent. The malar sulcus is absent in the outgroups Euryischiinae and Eriaporinae (Hayat, 1998). However, the majority of Chalcidoidea have a malar sulcus and therefore its presence is considered plesiomorphic.
15. **Transoccipital suture (tos) on posterior aspect of head.** **0:** absent (Figs 145, 201). **1:** present (Figs 79, 89, 102, 115, tos). This is one of the characters first discussed for

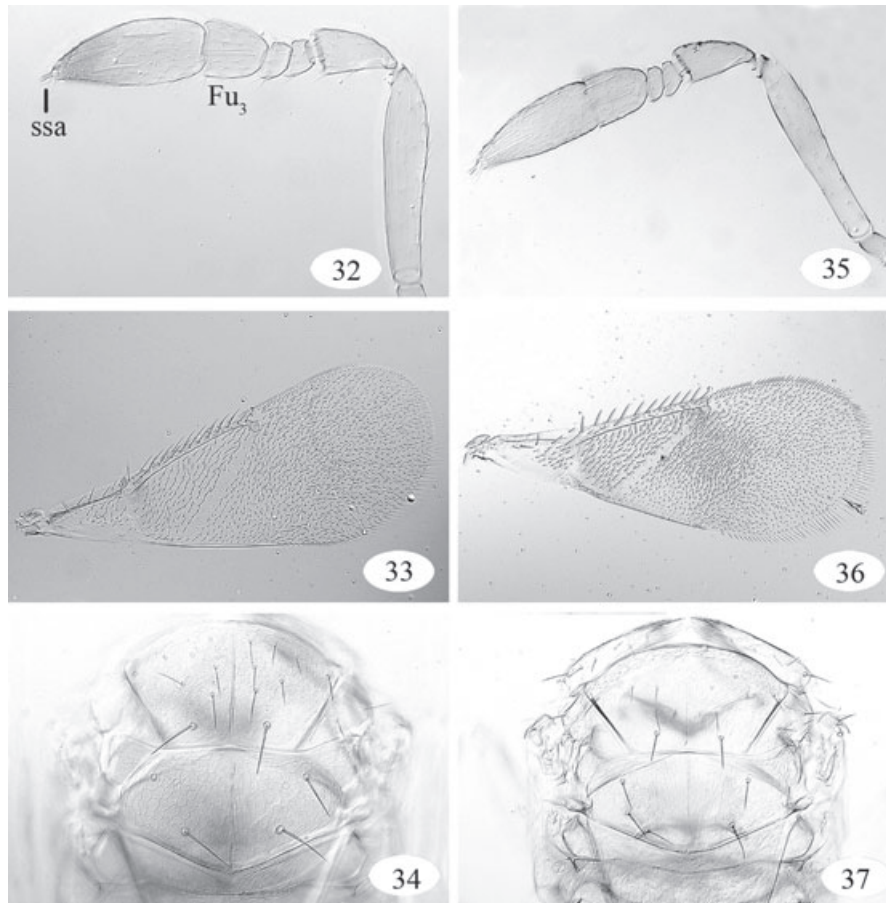
delimiting species groups of *Pteroptrix* (Prinsloo & Nesar, 1990). The structure of this transverse suture is different in *Pteroptrix* and Aphelininae. The former has a transverse suture meeting the occipital foramen medially (figs 1–3, Prinsloo & Nesar, 1990), while in Aphelininae the transoccipital suture does not meet the occipital foramen (Fig. 89). However, *Marietta*, *Samariola* and *Punkaphytis* in Aphelininae (Figs 145, 201, 248) lack the transoccipital suture. Both *Eriaphytis* (Fig. 74) and Calesinae have a vertical occipital sulcus meeting the tos medially, but this is autapomorphic for this analysis, and this aspect of the character was not considered.

16. **Pronotum divided medially.** **0:** one plate (fused medially with no indication of separation) (Fig. 80, 204, 205, no<sub>1</sub>). **1:** two plates broadly or narrowly separated by a membranous connection medially (Figs 37, 121, 130, no<sub>1</sub>). Both a divided and undivided pronotum occur in Coccophaginae (Hayat, 1998) and Aphelininae. Within Coccophaginae, the Pteroptricini have a divided pronotum, while Coccophagini have a continuous pronotum (Hayat, 1998). *Marietta*, *Punkaphytis* and some *Paraphytis* lack a median separation (Figs 205, 239, 252, pn<sub>1</sub>).



**Figs 26–31.** *Mashimaro* and *Neophytis* (female). 26–27, *M. hawksi*: 26, head (anterior); 27, head (dorsal). 28, *M. lasallei* n.sp., head (lateral). 29, *Eutrichosomella* sp. (unidentified), head (anterior). 30–31, *N. dealbatus*: 30, antenna; 31, forewing.

- 17. Visibility of pronotum in dorsal view.** **0:** visible (Fig. 80). **1:** hidden (Figs 105, 118).
- 18. Midventral width of prepectus.** **0:** broad, ventral width more than  $1\times$  as wide as maximum lateral width (Fig. 66, vp). **1:** narrow, with ventral width less than  $0.8\times$  as wide as lateral width, usually much narrower (Figs 94, 108, 127, 133, vp). *Coccophagus* have a broad ventral prepectus (fig. 7 in Hayat, 1998); however, sometimes a suture is not clear between the posterior ventral prepectus and mesosternum (Fig. 66). The ventral prepectus is narrow in all Aphelininae and the width of the prepectus is narrowed immediately when it meets ventrally (Figs 94, 163, 194).
- 19. Posterior margin of ventral prepectus.** **0:** distinctly separated medially and laterally from mesepisternum (Figs 108, 127, 133, 152). **1:** ventral margin partially or completely fused medially with mesepisternum (Figs 94, 163, 210, 220, 235). **2:** fused ventrolaterally but not medially to mesepisternum (Fig. 242). Yasnosh (1976) first used the shape of prepectus as a supporting character for subfamilies in combination with other characters. Hayat (1998) also commented that the structure of a continuous prepectus along the ventral margin was an important character for Aphelininae.
- 20. Pronotum overlapping prepectus ventrolaterally.** **0:** pronotum not overlapping prepectus ventrolaterally (Figs 62, 96, 122, 189, 207, 220, 241, 251). **1:** pronotum overlapping prepectus, obscuring the ventrolateral region of prepectus (Figs 109, 151).
- 21. Number of setae on midlobe of mesoscutum.** **0:** more than 24 (Figs 65, 105). **1:** 12–24 (Figs 160, 204). **2:** six to ten. **3:** less than six (Fig. 95) (Polaszek & Hayat, 1992; Babcock *et al.*, 2001).
- 22. Number of setae on side lobe of mesoscutum.** **0:** three or four, or rarely more than four (Fig. 80). **1:** two (Fig. 105). The number of setae on the side lobe of the mesoscutum varies in some genera, for example, *Coccophagus* have four or more and *Eriaphytis* have four to eight (Hayat, 1998); therefore, more than three setae were treated as one state.
- 23. Number of setae on axilla.** **0:** more than one (Figs 65, 80). **1:** one (Figs 95, 105). **2:** absent (Figs 217, 236) (Polaszek & Hayat, 1992).
- 24. Number of setae on scutellum.** **0:** more than four (Fig. 80). **1:** four (Figs 95, 105, 118) (Polaszek & Hayat, 1992).
- 25. Relative length of propodeum to metanotum.** **0:** less than  $0.8\times$  (usually  $0.8\text{--}0.9\times$ ) (Figs 64, 79). **1:**



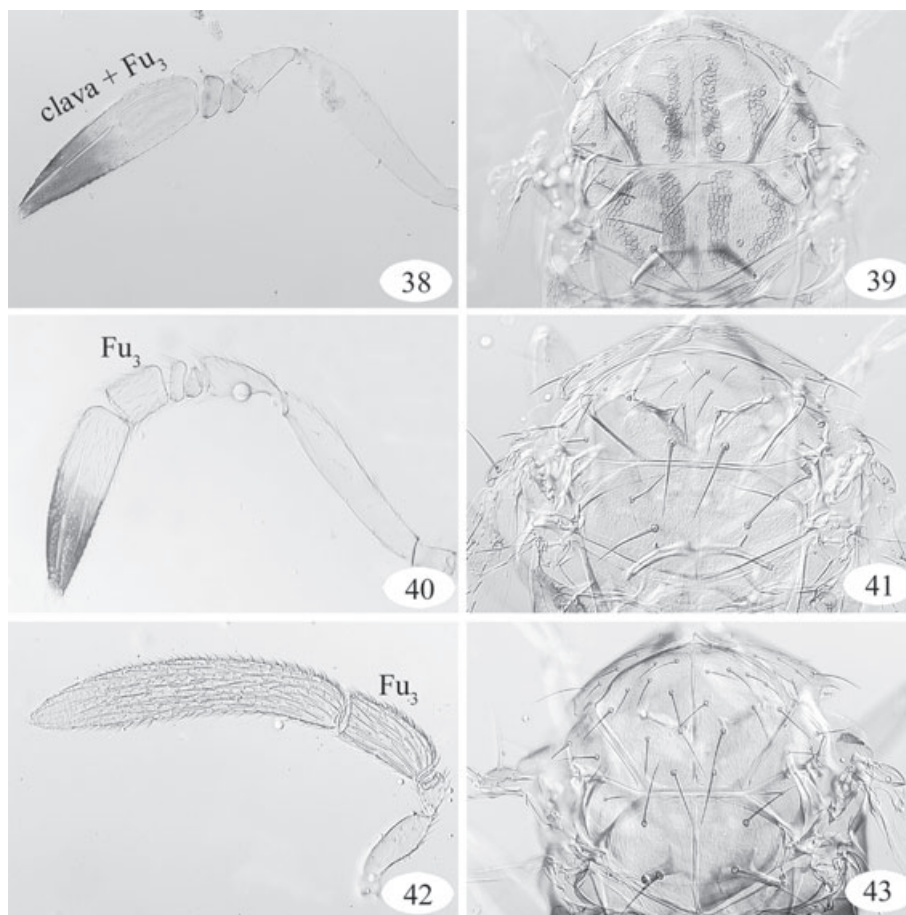
**Figs 32–37.** *Neophytis*. 32–34, *N. myartsvai* n.sp. (female): 32, antenna; 33, forewing; 34, mesosoma (dorsal). 35–37, *N. munroi* n.sp. (female): 35, antenna; 36, forewing; 37, mesosoma (dorsal).

1.0×–1.3×. **2:** 1.5×–2.9×. **3:** 3.1×–4.8×. **4:** more than 5×. **5:** propodeum long and metanotum absent (cf. fig. 36 of Hayat, 1983).

- 26. Shape of posterior margin of metanotum.** **0:** transverse or broadly rounded (Figs 64, 79). **1:** with a median projection, forming a triangular shape (Fig. 150). The projection is a feature of some *Aphelinus* and *Samariola*.
- 27. Shape of posterior margin of propodeum.** **0:** transverse (Fig. 64). **1:** with acute process medially (Fig. 111). **2:** with rounded, triangularly elevated process medially (Fig. 204). **3:** bilobed (Fig. 161). **4:** broadly rounded (Fig. 252).
- 28. Crenulae.** **0:** absent. **1:** present (Fig. 161, crl). The structure of crenulae was believed to be a unique derived character for *Aphytis* by Rosen & DeBach (1979), although it occurs in some species of *Centrodora* (Rosen & DeBach, 1979), *Neophytis* (Figs 218, 237) and *Paraphytis* (Fig. 243).
- 29. Epicoxal pad.** **0:** absent. **1:** present (Fig. 94, icmp). The epicoxal pads are a pair of spiculate areas located on the intercoxal membrane posterior to the procoxa (Rosen & DeBach, 1979; Woolley *et al.*, 1994). One undetermined

species of *Coccophagus* has a similar structure, but the homology with Aphelininae is not clear (J.B. Woolley and A. Polaszek, personal communication). In another species of *Coccophagus*, the spiculate membranous area is present but the area is continuous, not forming a pair of distinct and separated patches.

- 30. Mesopleuron.** **0:** acropleuron small, mesopleuron usually divided by pleural suture or femoral depression (Fig. 109). **1:** enlarged and convex, acropleuron displacing most of the mesepimeron and mesepisternum in lateral view (Fig. 129) (Gibson, 1989).
- 31. Axillar width relative to interaxillar distance.** **0:** 0.7–1× as long as interaxillar distance (Figs 118, 138). **1:** 0.45–0.5× as long as interaxillar distance (Fig. 105). **2:** 0.3–0.4× as long as interaxillar distance (Polaszek & Hayat, 1992).
- 32. Axilla anterior margin.** **0:** not advanced, thus the anterior apex of axilla is transverse and even with anterior margin of scutellum along the transscutal articulation (Figs 118, 126, 130, tsa). **1:** slightly but distinctly advanced; however, the anterior margin of the axilla does not extend beyond one third of length of side lobe (Fig. 160). **2:**



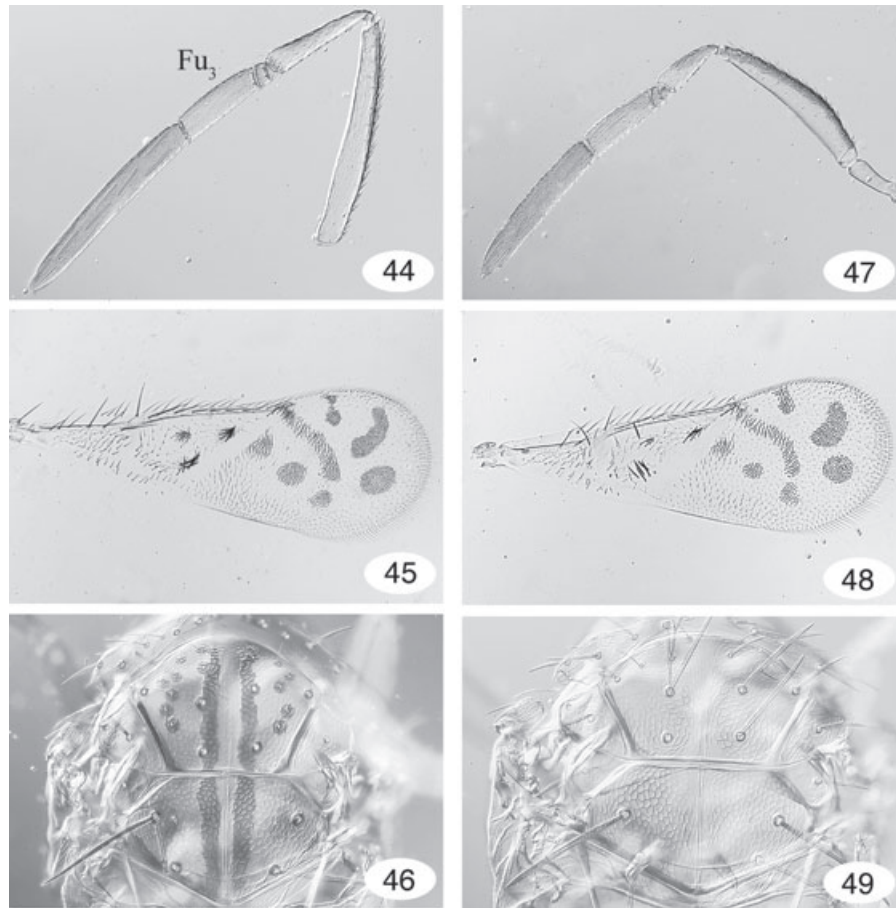
**Figs 38–43.** *Paraphytis*. 38–39, *P. maculata* (female): 38, antenna; 39, mesosoma (dorsal). 40–41, *P. sp. 3* (female): 40, antenna; 41, mesosoma (dorsal). 42–43, *P. sp. 1* (female): 42, antenna; 43, mesosoma (dorsal).

advanced by more than one third the length of side lobe of mesoscutum (Fig. 105). The axillae of genera with an enlarged mesopleuron (e.g. *Eutrichosomella* and *Samariola*) are not advanced and are in line with the anterior margin of the scutellum along the transscutal articulation (State 2, Fig. 130, tsa), which is apomorphic in Aphelininae. However, the plesiomorphic state of axilla in Chalcidoidea is likely in having a nonadvanced axilla (State 0).

- 33. Axillar width to length.** **0:** 1.0–1.8× as broad as long. **1:** 0.5–0.95× as broad as long. Axillar width (aw) was measured along the posterior margin of the axilla where it meets the scutellum and compared with the length of the anterior scutellar margin (ia) where the sclerite meets the mesoscutal midlobe (Fig. 1).
- 34. Scutellum shape.** **0:** ovate and wider than long (Fig. 160). **1:** ovate and longer than wide. **2:** pentagonal or hexagonal (Figs 22, 25, 138). **3:** heptagonal (Fig. 252). The shape of scutellum is often specific and typical for each genus. *Eutrichosomella* has a hexagonal scutellum (State 2) because the relatively round posterior margin of the scutellum was counted as one-sided, compared to *Punkaphytis*

with a V-shaped posterior margin (heptagonal). *Samariola* sp. 1 has a scutellum that is slightly wider than long (State 0); a character that can be used to separate it from *Samariola cameroonensis*. *Paraphytis* has a heptagonal scutellum. However, *Paraphytis* sp. 3 (Fig. 41) has a rounded posterior margin. Nevertheless, the shape of scutellum was coded as a variation of State 3. In *Euryischomyia* and *Hirtaphelinus*, the scutellum is wider than long (considered as variation of State 0), but trapezoid rather than oval.

- 35. Modification of seta adjacent to propodeal spiracle.** **0:** unmodified single seta (Figs 67, 83). **1:** single short and thick seta (Figs 222, 231). **2:** single bifurcated seta (Fig. 97). **3:** single leaf-like seta (Fig. 164). *Eretomocerus* has a bifurcated seta, which was considered autapomorphic (Hayat, 1998). However, one undetermined species of *Centrodora* also had a bifurcated seta, while in other *Centrodora* it was simple. *Aphytis* s.s. have a flattened, leaf-like seta (State 3; Fig. 164), which is distinct from the cylindrical thickened seta of species in *Punkaphytis* and *Paraphytis* (Fig. 222).
- 36. Number of setae on lateral propodeum.** **0:** more than two (Figs 107, 120, 134, 140, 153). **1:** two, including seta



**Figs 44–49.** *Punkaphytis* (holotypes). 44–46, *P. erwini* n.sp. (female): 44, antenna; 45, forewing; 46, mesosoma (dorsal). *P. hayati* n.sp. (female): 47, antenna; 48, forewing; 49, mesosoma (dorsal).

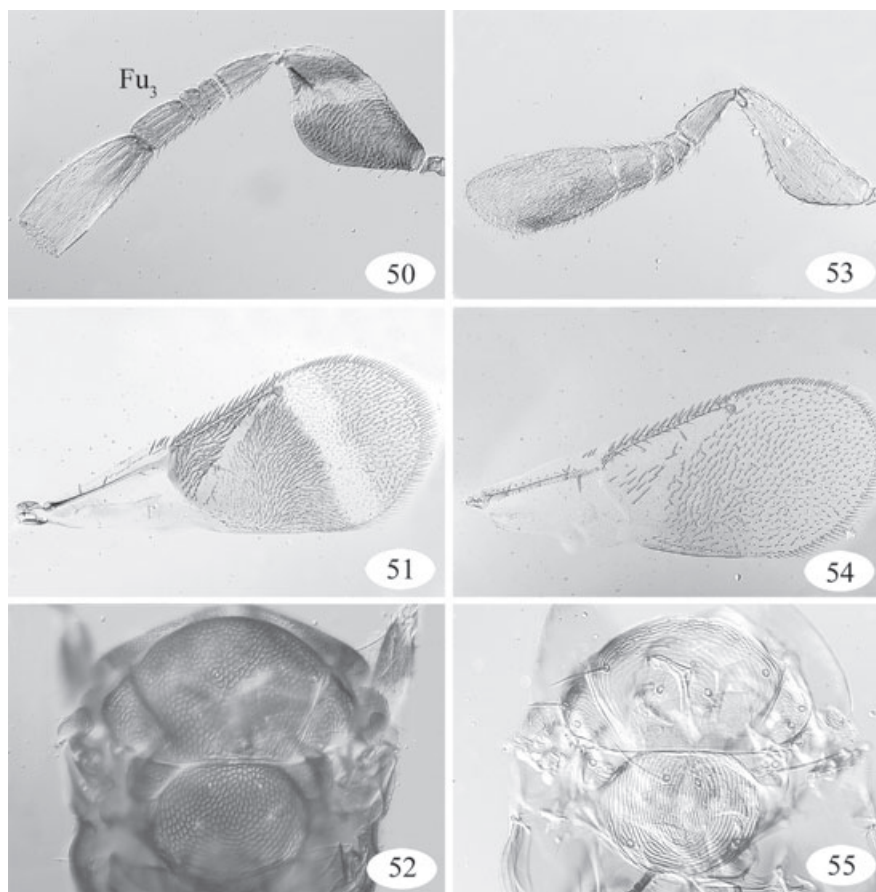
near propodeal spiracle (Figs 164, 190, 208) (Polaszek & Hayat, 1992).

- 37. Longitudinal medial groove of mesoscutum.** **0:** absent (Figs 95, 204). **1:** present (Figs 160, 185, 217, 232, 252). The groove almost always continues onto the scutellum.
- 38. Relative position of anterior and posterior scutellar setae.** **0:** anterior pair farther apart than posterior pair (Fig. 161). **1:** anterior pair in line with posterior pair. **2:** posterior pair farther apart than anterior pair (Fig. 105).
- 39. Mesofurcal bridge.** **0:** present. **1:** bridge absent and lateral furcal arms with process that has a medial flange (Figs 10, 11). **2:** bridge absent, furcal process without a flange (Figs 16, 18). **3:** bridge and furcal process absent. The putative outgroups, Eriaporinae and Eriaphytinae, have a complete mesofurcal bridge (fig. 6 in Heraty *et al.*, 1997), as does *Eriaphytis* (Eriaphytinae) (Heraty *et al.*, 1997). A mesofurcal structure having an anterior interfurcal process is one of the few characters supporting monophyly of the subfamily Aphelininae, excluding Eretmocerini. *Eretmocerus* (Eretmocerini) has a very unique mesofurcal structure that is similar to *Cales* and Trichogrammatidae (Heraty *et al.*,

1997). The typical structure of the mesofurca in Aphelininae is differentiated, and has a lateral arm with a furcal process and a flange (Fig. 10) (Heraty *et al.*, 1997). The similarity of the mesofurca and its attached muscles support the proposed hypothesis of [(Aphelinini + Aphytini + Eutrichosomellini) + Azotinae] (Heraty *et al.*, 1997). The anterior interfurcal processes of *Ablerus* are distinct from Aphelininae by lacking a medially produced flange (Heraty *et al.*, 1997).

- 40. Lateral furcal arm (lf) of mesofurca.** **0:** lateral furcal arm directed laterally. **1:** lateral arms deflected posteriorly (Figs 16, 18, 19). The posterior projection of the lyre-shaped lateral furcal arms occurs in *Eutrichosomella* (fig. 10 in Heraty *et al.*, 1997).
- 41. Posterior interfurcal process of mesofurca.** **0:** absent (Figs 14, 17). **1:** present (Figs 10, 11, 18). The lobe is well developed in *Eutrichosomella* and *Mashimaro* with some variation in its size and shape. Absence of a posterior interfurcal process was considered to be plesiomorphic (Heraty *et al.*, 1997).
- 42. Relative length of marginal vein to costal cell.** **0:** 0.40–1.07× as long as costal cell. **1:** 1.09–1.70× as long

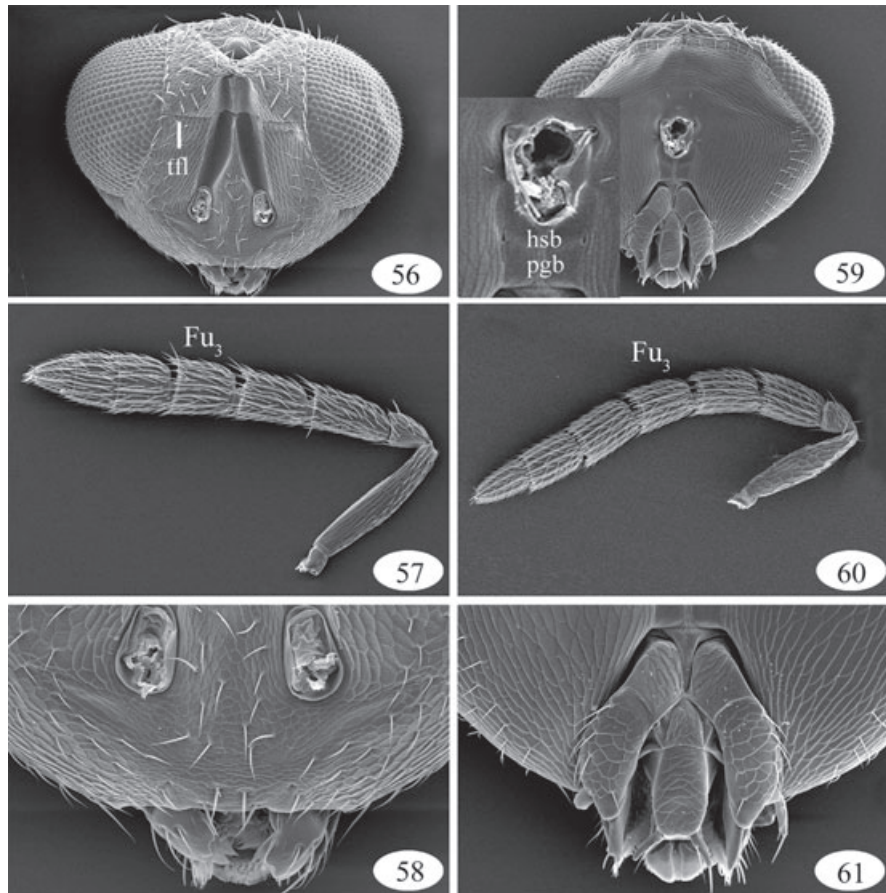




**Figs 50–55.** *Saengella* (holotype) and *Samariola*. 50–52, *Saengella gloria* n.sp. (female): 50, antenna; 51, forewing; 52, mesosoma (dorsal). 53–55, *Samariola* sp. 1 (female): 53, antenna; 54, forewing; 55, mesosoma (dorsal).

as costal cell. The length of the costal cell (rather than the submarginal vein) is considered to be more accurate for comparison with the marginal vein (Hayat, 1983).

- 43. Sensilla on parastigma of forewing.** **0:** two sensilla (rarely three in a group). **1:** one sensillum. *Centrodora* have two distinctly separated sensilla or two adjacent sensilla. The latter state is not found in other Aphelininae. Therefore, the juxtaposed two sensilla is an autapomorphic feature within *Centrodora*.
- 44. Arrangement of stigmal sensilla.** **0:** three or four sensilla grouped in a cluster. **1:** four sensilla grouped in two clusters of two and two. **2:** three or four sensilla arranged linearly. **3:** three sensilla grouped and one distant sensillum. The arrangement of sensilla in each genus is usually typical. For example, *Coccobius* has a characteristic stigmal vein and sensilla arrangement (Hayat, 1998). The linear arrangement of sensilla found in *Centrodora* is unique in Aphelininae. *Eretmocerus* also has the unique pattern of three grouped sensilla and one separated sensillum (Hayat, 1998).
- 45. Number of stigmal sensilla.** **0:** three. **1:** four.
- 46. Linea calva.** **0:** absent (Fig. 68). **1:** present (Figs 85, 159) (Polaszek & Hayat, 1992).
- 47. Setae on delta area.** **0:** delta not defined and evenly setose. **1:** setose with well-defined bare margins. **2:** setose with bare spot, slightly bare (90% setose), or somewhat bare (30% < area < 50%). **3:** mostly bare, usually forming a row of setae (less than 10–20% of setae in delta). State 1 is a distinct feature but may include taxa with few setae covering the entire delta area. For example, *Aphelinus nepalensis* Hayat has very few long and thick setae; however, the delta area remains well defined (variation of State 1, e.g. Fig. 147).
- 48. Hypopygium structure.** **0:** hypopygium not reaching cercal plates (Figs 70, 117, 177, 197). **1:** hypopygium prominent, reaching at most to cercal plates (Figs 78, 106, 132, 141, 254). **2:** hypopygium prominent, reaching apex of gaster. This is the conventional character for dividing Aphytini and Aphelinini (Hayat, 1998). *Aphelinus* has a prominent hypopygium extending beyond the cercal plates, while other genera (e.g. *Eriaphytis* and *Marlatiella*) have a prominent hypopygium reaching only to the cercal plates.
- 49. Relative lengths of cercal bristles.** **0:** formula of 3 + 1 (Fig. 135). **1:** formula of 2 + 1 (Figs 110, 165). **2:** formula of 2 + 2 (Fig. 254). **3:** formula of 3 + 0. **4:** formula



**Figs 56–61.** *Coccophagus* sp. 1 (female unless otherwise noted): 56, head (anterior); 57, antenna; 58, face (anterior); 59, head (posterior); 60, antenna (male); 61, mouthparts (posterior).

of 2 + 0. State 0 may have three equally long setae and one short one; however, if the third seta is shorter than the other two longest ones, then the formula was coded as 2 + 2 (State 2).

**50. Specialised sensilla on apex of clava.** 0: absent. 1: present (Fig. 3, as).

## Results

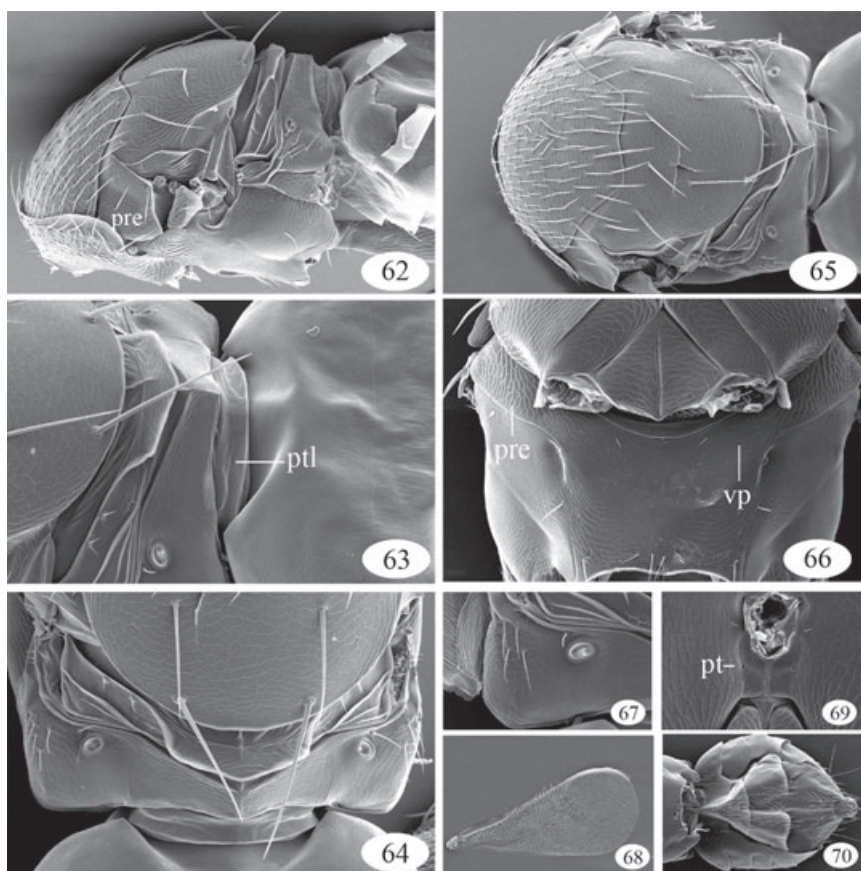
### *Phylogenetic analysis of intertribal relationships*

The parsimony analysis produced one island (*sensu* Maddison, 1991) of three most parsimonious trees (Fig. 257, Length = 253, CI = 0.34, RI = 0.71). The strict consensus tree supports all genera as monophyletic except *Neophytis*, which was paraphyletic (Fig. 257). However, *Neophytis* is supported as monophyletic in unpublished morphological and molecular analyses (J.-W. Kim and J. Heraty, unpublished data). Successive approximations character weighting (SAW) was stable, resulting in the same three MPTs after three iterations. Morphological character support was plotted on the simplified tree, represented by only generic terminals (Fig. 258).

Bootstrap values are fairly low for all clades, with the highest value of 67% for *Eutrichosomella* and most clades having less than 50% support (Fig. 257). Decay indices also are low, with the majority of nodes having values of 1 or 2 (Fig. 257).

Prior to discussing this tree, it is important to note that these results differ substantially in the placement of some taxa when molecular data are included (J.-W. Kim and J. Heraty, in preparation). In particular, *Eretmocerus* are placed outside of Aphelinidae, and *Hirtaphelinus*, *Neophytis*, *Punkaphytis* and *Paraphytis* (*vittatus* species group) are all placed in the Eutrichosomellini clade. Our discussion below is based only in the context of the morphology-based tree and will need to be revised after the molecular data are published.

Aphelininae has been defined by a combination of characters: in particular, the possession of fewer than six antennal segments and a linea calva on the forewing (Hayat, 1998). In the parsimony analysis, Aphelininae was supported by eight characters, including four unambiguous synapomorphic characters (3:1, 23:1, 24:1, 39:1; Fig. 258). Absence of an anellar segment on the antenna (3:1) was a supporting character for Aphelininae, with a reversal in *Mashimaro*. Other characters include a single seta on axilla (23:1), four setae on scutellum (24:1) and a laterally oriented mesofurcal arm with



**Figs 62–70.** *Coccophagus* sp. 1: 62, mesosoma (lateral); 63, propodeum (dorsolateral); 64, scutellum (dorsal); 65, mesosoma (dorsal); 66, mesosoma (ventral); 67, propodeal setae (dorsal); 68, forewing; 69, posterior tentorial pit; 70, gaster (ventral).

anterior interfurcal process (39:1). Four additional ambiguous characters, optimised to favour reversals (ACCTRAN), are as follows: three-segmented funicle (1:2), absence of a transfacial line (7:1), medially divided pronotum (16:1), and third funicular segment less than  $1.0\times$  or more than  $1.2\times$  first and second funicular segments (4:0/2). The absence of a transfacial line (7:1) is ambiguous on the morphology tree because of the inclusion of *Eretmocerus*; when removed in the combined analysis, this becomes an unambiguous character state change. The polarity of a medially divided pronotum (16:1) is uncertain, because it is divided in Pteroptricini (*Coccophaginae*), and entire in some Aphelininae (e.g. *Marietta*).

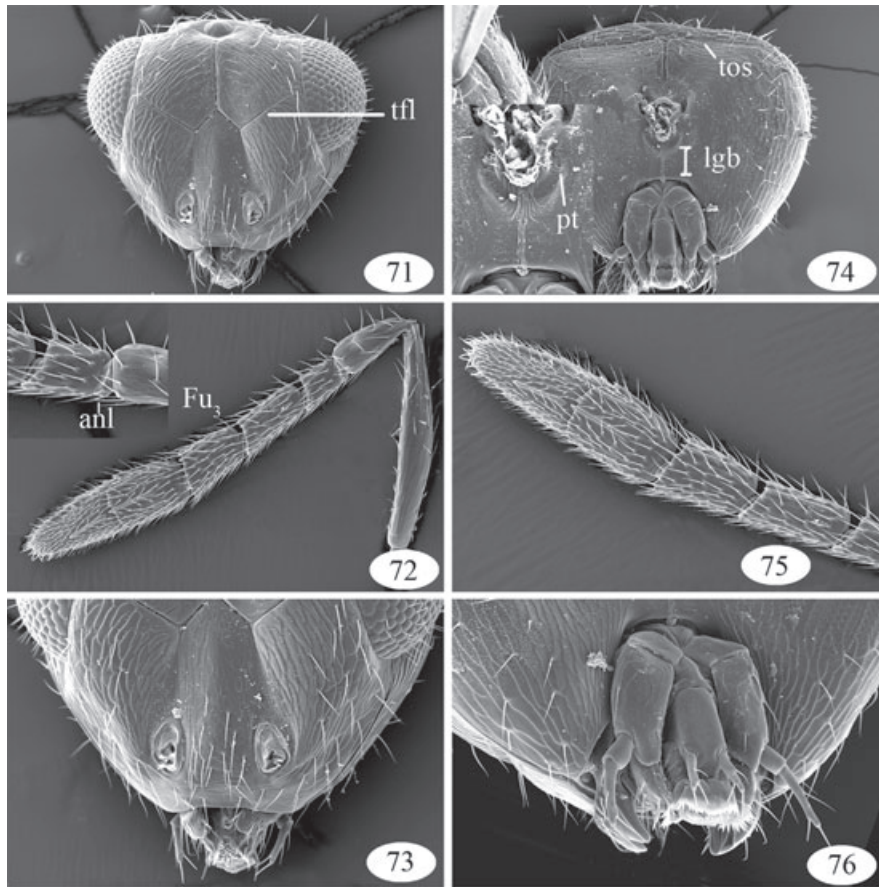
#### *Eretmocerini*

*Eretmocerini*, represented by *Eretmocerus*, was supported by 14 different characters including 11 unambiguous characters. Its placement renders Aphytini paraphyletic (Figs 257, 258). *Eretmocerus* was placed as sister group to *Marlattella* based on four unambiguous characters (Fig. 258): extremely long clava (5:1), triangular shape of the posterior margin of the metanotum (27:2), small axilla (31:2), and one sensillum on the parastigma (43:1). The facial line and two mediofrontal lines

(Fig. 86, tfl) found in *Eretmocerus* are absent in other tribes of Aphelininae, but are present in *Eriaphytis* (Fig. 71, tfl). *Eretmocerus* is highly autapomorphic, having some significant features such as the W-shaped transfacial line, anteriorly directed mesofurcal arms, and four-segmented tarsi, which might support a more basal placement or a more distant relationship to Aphelininae.

#### *Aphelinini*

Aphelinini, represented by *Aphelinus* and *Protaphelinus*, was rendered paraphyletic by *Hirtaphelinus*. Aphelinini including *Hirtaphelinus* was supported by six characters including two unambiguous characters: dorsally hidden pronotum (17:1) and hypopygium prominent, reaching the apex of the gaster (48:2). Ambiguous support for the clade is provided by the following characters: pronotum overlapping prepectus (20:0/1), midlobe with more than 24 setae (21:0), an acute process on posterior propodeum (27:0/1), and a short marginal vein of the forewing (less than  $1.1\times$  as long as costal cell, 42:0). The inclusion of *Hirtaphelinus* within Aphelinini may be an artifact because of 17 missing characters based on the lack of forewings (only vestigial flap-like structure; fig 36 in Hayat,



**Figs 71–76.** *Eriaphytis orientalis* (female): 71, head (frontal); 72, head (posterior); 73, antenna and anellus; 74, claval segment; 75, face (anterior); 76, mouthparts (posterior).

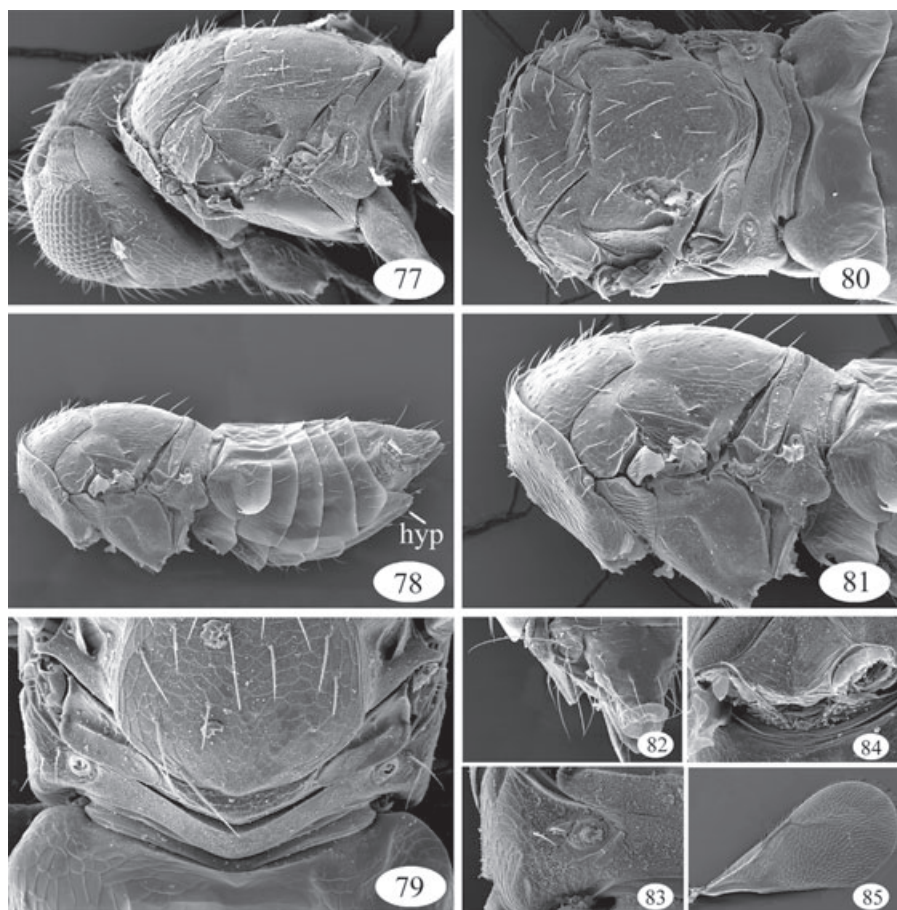
1983) and reduced metanotum. *Hirtaphelinus* is somewhat similar to *Samariola* in the structure of the mesosoma, and was placed in the Aphytini with some doubt by Hayat (1998). In our morphological analysis (Figs 257, 258), *Hirtaphelinus* was the sister group to *Aphelinus* based on a separated ventral prepectus (19:0) and a 2 + 2 formula of cercal bristles (49:2). The relationship with Aphelinini was supported by four unambiguous characters: pronotal shape (17:1), separated prepectus (19:0), projecting hypopygium (48:2) and cercal formula (49:2). Aphelinini (*Aphelinus* + *Protaphelinus*; without *Hirtaphelinus*) is supported by six characters including four unambiguous characters: dorsally hidden pronotum (17:1), metanotum triangular (26:1), an acute process on propodeum (27:1), and a prominent hypopygium reaching the apex of gaster (48:2). These are all substantial characters that support the monophyly of Aphelinini, without *Hirtaphelinus*.

#### *Eutrichosomellini*

The *Eutrichosomella* clade included *Eutrichosomella* + [*Saengella* + (*Samariola* + *Mashimaro*)] (Fig. 258). *Eutrichosomellini* s.l. was supported by three unambiguous

characters: axilla not advanced (32:0), posteriorly directed lateral arm of mesofurca (40:1) and cercal formula of 3 + 1 (49:0). Three other ambiguous characters supported the clade, including the third funicular segment less than 1× as long as the first and second funicular segments (4:0), divided pronotum (16:1) and propodeum with numerous setae (36:0). Hayat (1998) commented that the relationship of *Eutrichosomella* is not clear because of the similarity to the mesopleuron and axillae of Encyrtidae and other genera of Aphelinidae, such as *Marietta*, *Samariola* and *Coccobius* (Hayat, 1998). *Marietta* was placed as a sister group to the *Eutrichosomellini* clade based on an enlarged acropleuron (30:1) and well-defined delta area of the forewing (47:1). This relationship is suspect because of possible homoplasy of the two characters (Gibson, 1989; Hayat, 1998). The enlarged acropleuron (30:1) is also a feature of *Punkaphytis* and *Paraphytis*, which are here placed with the other Aphytini. Additionally, a posterior interfurcal process (41:1) is present in *Eutrichosomella*, *Mashimaro* (Fig. 18, fe) and *Punkaphytis* (Figs 10, 11).

*Samariola* was placed in Aphytini by Hayat (1998). It is a unique genus with unknown affinity to other groups (Hayat, 1983), even though it can be easily recognised by a poorly defined delta area of the forewing (Fig. 54), short antennal



**Figs 77–85.** *Eriaphytis orientalis* (female): 77, head and mesosoma (dorsolateral); 78, body (lateral); 79, scutellum and propodeum (dorsal); 80, mesosoma (dorsal); 81, mesosoma, (lateral); 82, cercal bristles (dorsal); 83, propodeal setae (dorsal); 84, icmp (ventral); 85, forewing.

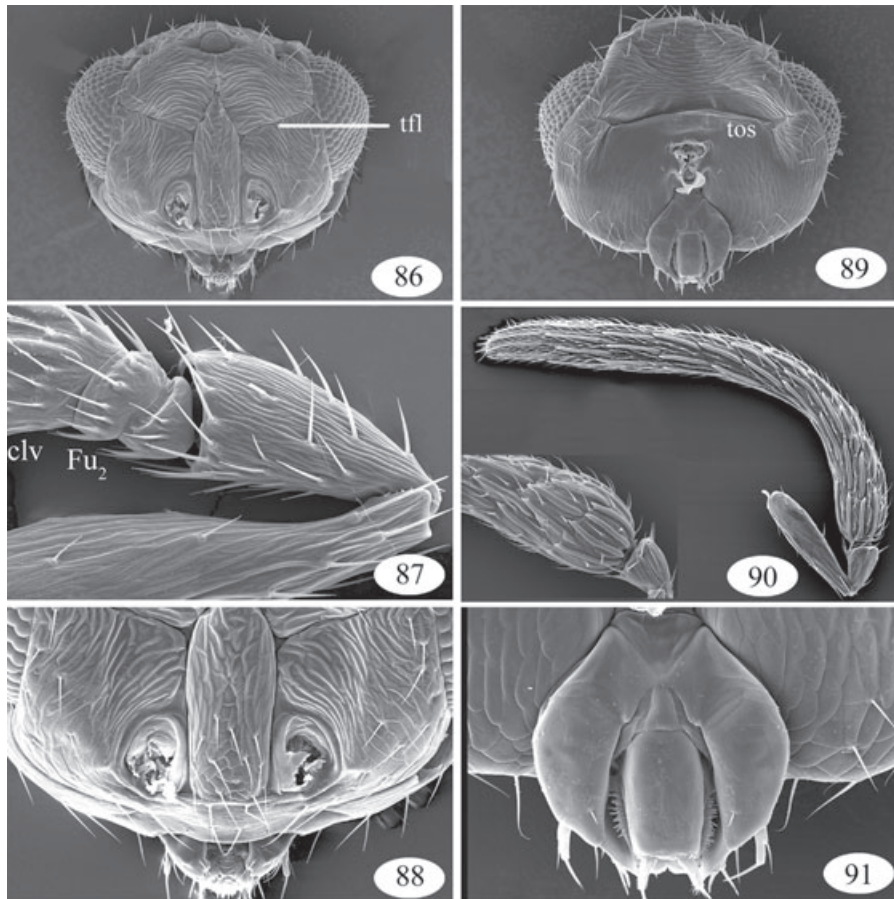
clava (Fig. 53), an enlarged acropleuron (30:1; Fig. 151) and nonadvanced axillae (32:0; Fig. 55). *Samariola* also has relatively smaller axilla (Fig. 55) than *Mashimaro* or *Eutrichosomella*. A medially separated and broadly connected pronotum (Fig. 148) and numerous setae laterally on the propodeum (Fig. 153) are also characteristic of *Samariola*. The pronotum of *Samariola* (Fig. 151) overlaps the prepectus as in *Aphelinus* (Fig. 109), and a medially projected posterior metanotum (26:1) also suggests a possible relationship between *Samariola* (Fig. 150) and some *Aphelinus*. However, the placement of *Samariola* with *Mashimaro* n.g. was well supported in the parsimony analysis by four characters, including two unambiguous characters: clava less than 2.5× as long as wide (5:2) and one sensillum on the parastigma of the forewing (43:1). The same relationships of *Saengella*, *Samariola* and *Mashimaro* are recovered in molecular analyses.

#### *Aphytini*

*Aphytini* was not monophyletic, and scattered across the MPT (Figs 257, 258). *Marietta* was placed with the

*Eutrichosomellini* clade, and *Aphytini* excluding *Marietta*, was still paraphyletic because of the placement of *Eretmocerus* (Fig. 258). Morphologically, the odd placement of *Marietta* might have been expected, as the genus was even suggested to be put in a tribe of its own based on having an undivided pronotum (Shafee & Khan, 1978). *Aphytini* excluding *Marietta* and including *Eretmocerus*, was supported by a single unambiguous character – that of having a grooved line on the mesosoma (37:1); however, this state is reversed in *Eretmocerus* (37:0). Three additional ambiguous characters for *Aphytini* including *Eretmocerus* are as follows: midlobe with six to ten setae (21:2), two setae on lateral propodeum (36:1), and marginal vein 1.1–1.7× as long as costal cell (42:1).

*Aphytis* s.s. (excluding the *vittatus* group, = *Paraphytis* + *Neophytis*) was monophyletic, with a sister group relationship to *Neophytis*, *Paraphytis* and *Punkaphytis* (Fig. 257). *Aphytis* s.s. was supported by one unambiguous character, that is, two setae on the side lobe of the mesoscutum (22:1), and two ambiguous characters: a short postgenal bridge length (10:1) and the leaf-like modified seta near the propodeal spiracle (35:3). The leaf-like seta on the propodeum (Fig. 164) is



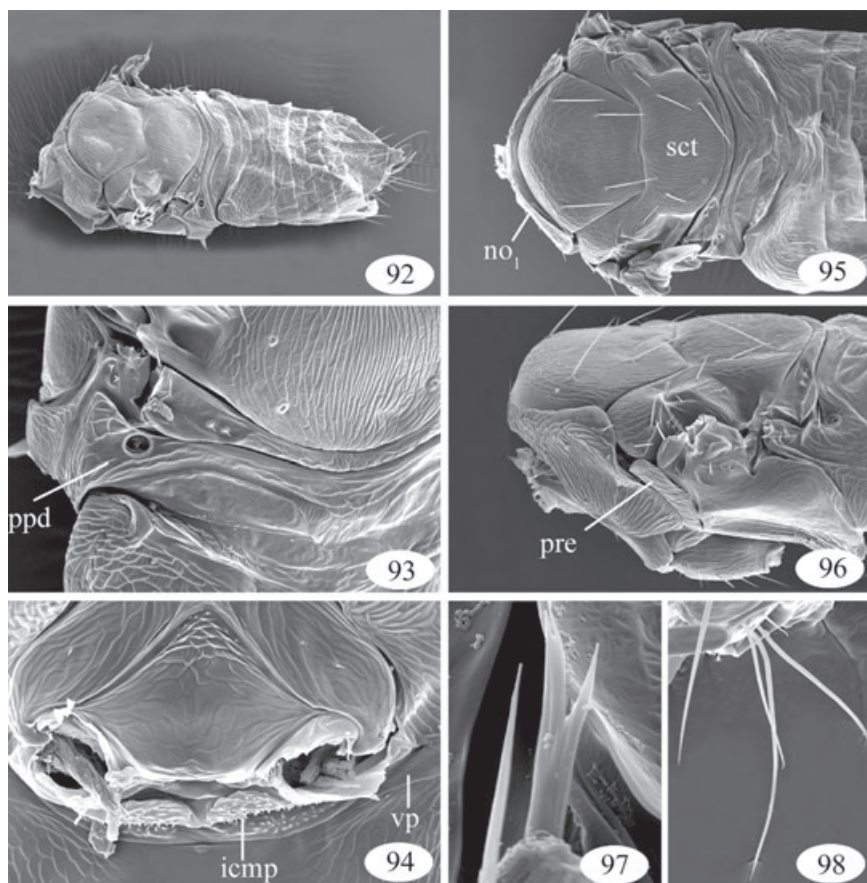
**Figs 86–91.** *Eretmocerus* sp. 1 (female unless otherwise noted): 86, head (anterior); 87, antenna; 88, face (anterior); 89, head (posterior); 90, antenna (male); 91, mouthparts (posterior).

an autapomorphic feature of *Aphytis* s.s.; however, the polarity of this character is uncertain because of the ambiguous states in other Aphelininae. *Aphytis* s.l. (*Aphytis sensu* Hayat which would include the *vittatus* group) has traditionally been well supported with two putative synapomorphic characters, presence of crenulae (28:1) and a relatively long propodeum (25:3). Our decision not to include the *vittatus* group and to recognise the three other genera, is based primarily on the highly supported results of our unpublished molecular and combined analyses, which instead group *Neophytis*, *Paraphytis* and *Punkaphytis* with Eutrichosomellatini.

**Key to genera of Aphelininae**

An identification key to the genera of Aphelininae is provided, largely based on previous keys by Hayat (1983, 1998). The following key assumes that Aphelininae s.l. (including *Eretmocerus*) are already recognized: antenna at most with six segments, forewing usually with a linea calva, protibial spur curved and bifid, broad connection of mesosoma and metasoma and a nonmetallic yellow or brown body.

- 1 Female ..... 2
- Male ..... 21
- 2 (1) Tarsi four-segmented; forewing without a linea calva, but if present then poorly defined; face with transfacial line (Fig. 86) ..... *Eretmocerus* Haldeman
- Tarsi five-segmented; forewing usually with a linea calva; face without transfacial line ..... 3
- 3 (2) Antenna four-segmented, formula 1-1-1-1; antennal clava elongated, more than 5× as long as wide ..... 4
- Antenna five- or six-segmented, formula 1-1-2-1 or 1-1-3-1, antennal clava stout, less than 4.9× as long as wide (Figs 100, 155) ..... 5
- 4 (3) Propodeum with crenulae (Fig. 6, crl), and more than 4× as long as metanotum; forewing usually with at least a dark mark under stigma and not noticeably elongated; malar sulcus of head and body usually with some dark markings ..... *Aphytis* Howard (Chilensis species group) (part)
- Propodeum without crenulae, and less than 2× as long as metanotum; forewing clear and elongated; head and body without dark markings ..... *Marlattella* Howard



**Figs 92–98.** *Eretmocerus* sp. (female): 92, body (dorsal lateral); 93, propodeum; 94, icmp; 95, mesosoma (dorsal); 96, mesosoma (lateral); 97, propodeal seta (lateral); 98, cercal bristles (lateral).

5 (3) Antenna five-segmented, 1-1-2-1; mandible reduced with only one tooth or truncate .. *Aphytis* Howard (the Funicularis species group) (part)

– Antenna six-segmented, 1-1-3-1 or 1-1-2-2 (Fig. 3); mandible well developed with two teeth with a truncation, sometimes three or four teeth; if antenna five-segmented, then mandible with two teeth and mesosoma with four longitudinal dark bands (Fig. 39) .. 6

6 (5) Mesopleuron convex, large and undivided (Figs 114, 122); forewing with at least one dark spot, often patterned with several markings (Figs 21, 24, 45, 48, 51), body yellow, orange or brown, sometimes with cross bands on gaster; if forewing clear then delta poorly defined or clava with a specialised sensilla (Fig. 32) or forewing venation less than 0.5× length of forewing, forewing rarely brachypterous .. 7

– Mesopleuron concave and divided by an oblique suture into a mesepimeron and mesepisternum (Figs 62, 81, 109); forewing never patterned, but sometimes slightly darker under stigma; body yellow or orange usually without dark bands on gaster, if present only lateral marks distinct .. 16

7 (6) Axilla not exceeding anterior line of scutellum (Fig. 118); forewing never mottled but sometimes with a broad dark band

across forewing (Figs 21, 24, 51); scape usually expanded ventrally, if not expanded then antennal clava 3× as long as wide or metanotum absent .. 8

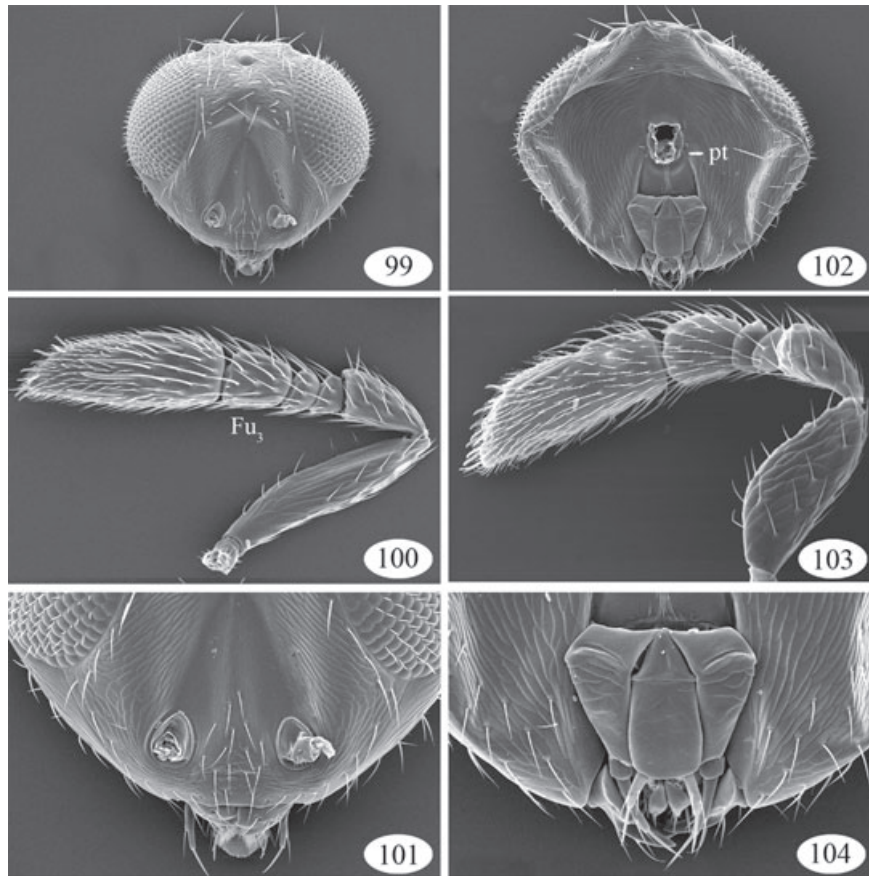
– Axilla slightly but distinctly advanced and distinctly exceeding anterior line of scutellum (Figs 160, 188, 204); forewing usually mottled and patterned (Figs 45, 48), sometimes with only faint marking under stigma (Figs 33, 36); scape usually not expanded, if expanded then forewing distinctly mottled .. 12

8 (7) Axilla large, width of axilla as long as anterior margin of scutellum (Figs 118, 126) .. 9

– Axilla small, width of axilla at most 1/2 as long as anterior margin of scutellum (Fig. 252) .. 10

9 (8) Antennal clava more than 2.5× as long as wide (Fig. 113), at least third funicular segment longer than wide, anellus absent (Fig. 113); scape not ventrally expanded; head not posteriorly carinate in dorsal view, face laterally rounded (Fig. 112) .. *Eutrichosomella* Girault

– Antennal clava 2.2–2.3× as long as wide (Figs 128, 139), all funicular segments wider than long, anellus present (Fig. 125, anl); scape ventrally expanded (Figs 20, 23); head posteriorly



**Figs 99–104.** *Aphelinus varipes* (female unless otherwise noted): 99, head (anterior); 100, antenna; 101, face (anterior); 102, head (posterior); 103, antenna (male); 104, mouthparts (posterior).

carinate in dorsal view (Fig. 27, 28); face with lateral ridge (Fig. 28, lr) ..... *Mashimaro* n.g.

10 (8) Brachypterous; scutellum posteriorly truncated; metanotum absent ..... *Hirtaphelinus* Hayat  
 – Macropterous; scutellum posteriorly rounded (Figs 52, 55); metanotum present ..... 11

11 (10) Forewing without distinct markings, delta loosely setose (Fig. 54); antennal clava less than 2.1× as long as wide, Fu<sub>1</sub> trapezoid with one short side (Fig. 53) .....  
 ..... *Samariola* Hayat  
 – Forewing usually with a broad brown band, delta densely setose (Fig. 51); antennal clava 2.5× as long as wide, Fu<sub>1</sub> rectangular (Fig. 50) ..... *Saengella* n.g.

12 (7) Forewing clear, usually more than 3× as long as wide, with wing venation usually at most less than 0.5× length of forewing; body usually elongate (Fig. 197), rarely with distinct colour pattern; epistomal suture present (Fig. 181, es) .....  
 ..... *Centrodora* Foerster  
 – Forewing with some colour markings, usually mottled, at least with a marking under stigma, forewing broad, usually less than 3× as long as wide, with venation always

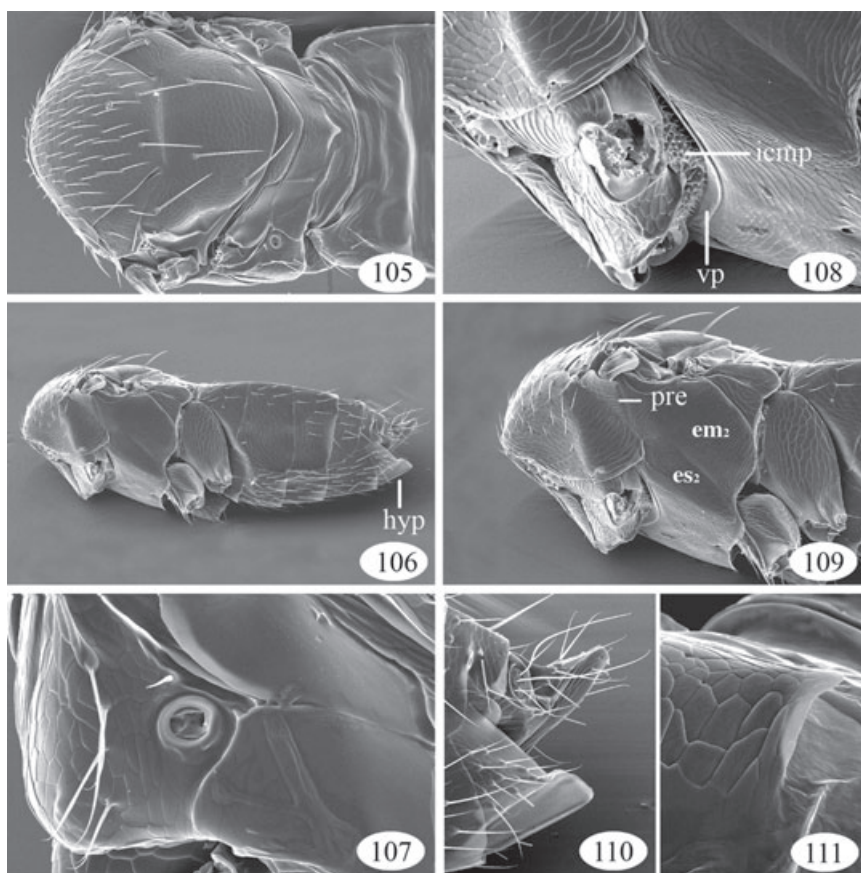
exceeding 0.5× length of forewing; body not elongate, generally some dark markings or bands; epistomal suture absent ..... 13

13 (12) Head and mesosoma with long-flattened setae, setae at least as long as length of compound eye (Figs 12, 245); antennal clava more than 6× as long as wide .....  
 ..... *Punkaphytis* n.g.  
 – Head and mesosoma without long-flattened setae; antennal clava less than 5× as long as wide ..... 14

14 (13) Propodeum at most 1× as long as metanotum; posterior end of propodeum never with crenulae; forewing usually with mottled pattern formed by dark membrane .....  
 ..... *Marietta* Motschulsky  
 – Propodeum more than 2× as long as metanotum; posterior end of propodeum always with crenulae; forewing sometimes with mottled pattern, formed by dark setae ..... 15

15 (14) Axilla with seta (Figs 39, 41, 43, 241); antennal clava without a thick special sensillum at apex, suture between clava and third funicular segment usually distinct (Fig. 40) .....  
 ..... *Paraphytis* Compere  
 – Axilla without seta (Figs 217, 232); antennal clava with a thick special sensillum at apex (Fig. 32, ssa), suture between





**Figs 105–111.** *Aphelinus albipodus* (female): 105, mesosoma (dorsal); 106, body (lateral); 107, propodeum (dorsal); 108, icmp (ventral); 109, mesosoma (lateral); 110, cercal plate (lateral); 111, posterior end of propodeum (dorsolateral).

clava and third funicular segment usually not distinct (Figs 30, 35) ..... *Neophytis* n.g.

16 (6) Hypopygium prominent, extending to apex of gaster or beyond (Figs 106, 132); propodeum less than 2.9× as long as metanotum; middle lobe of mesoscutum with more than 24 setae; parasites of aphids ..... 17  
 – Hypopygium not extending to apex of gaster (Figs 162, 197); propodeum usually more than 3.1× as long as metanotum; middle lobe of mesoscutum usually with less than 24 setae; parasites of coccoids or insect eggs ..... 18

17 (16) Axillae slightly advanced anteriorly, reaching less than 0.3 length of side lobe of mesoscutum, posteriorly barely reaching the anterior scutellar setae (fig. 90 in Hayat, 1998); anterior scutellar setae lateral to posterior pair; hypopygium densely setose apically (fig. 90 in Hayat, 1998); tarsal claws unequal length (fig. 88 in Hayat, 1998); labial palp two-segmented; epicoxal pad absent ..... *Protaphelinus* Mackauer

– Axillae strongly advanced anteriorly, reaching usually more than 0.3 length of side lobe of mesoscutum, posteriorly reaching beyond the anterior scutellar setae (Fig. 105); anterior scutellar setae medial to posterior pair; hypopygium not

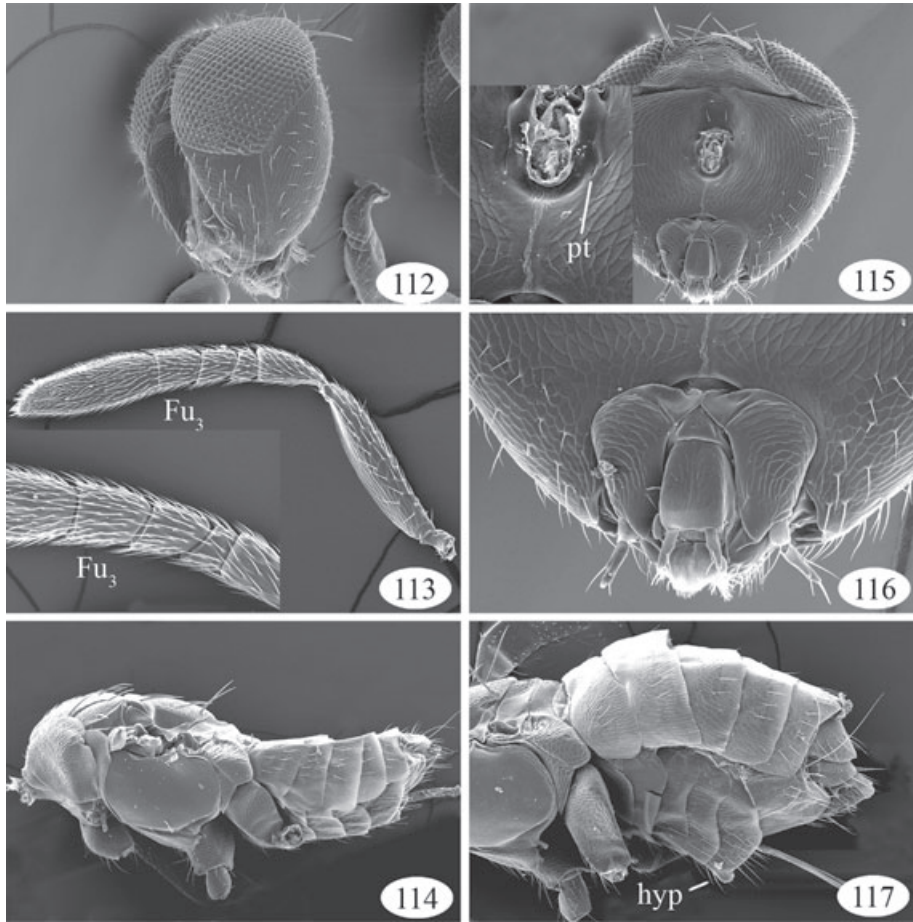
densely setose apically; tarsal claws equal length; labial palp unsegmented; epicoxal pad present (Fig. 108, icmp) ..... *Aphelinus* Dalman

18 (16) Bristles of cercal plate 2 + 2; forewing more than 3× as long as wide, with venation usually not exceeding half of forewing length (Fig. 196); body elongated (Fig. 197); apex of clava usually strongly tapered ventrally (Fig. 184); epistomal suture present (Fig. 181, es) ..... *Centrodora* Foerster

– Bristles of cercal plate 2 + 1 (Fig. 165); forewing less than 3× as long as wide, (Fig. 8) with venation exceeding the half of forewing length; body not elongate; clava never strongly tapered at apex (Fig. 3); epistomal suture absent ..... 19

19 (18) Eye small, 0.1× as long as vertex; temple well developed (fig. 140 in Hayat 1998); Fu<sub>3</sub> expanded, as wide as clava (Fig. 171); antennal clava with numerous elongate oval sensilla (fig. 141 in Hayat, 1998); forewing without a distinct linea calva ..... *Botryoideclava* Subba Rao

– Eye normal, about 0.2× as long as vertex; temple not developed; Fu<sub>3</sub> not expanded; antennal clava at most with a few elongate slender longitudinal sensilla; forewing with a distinct linea calva ..... 20



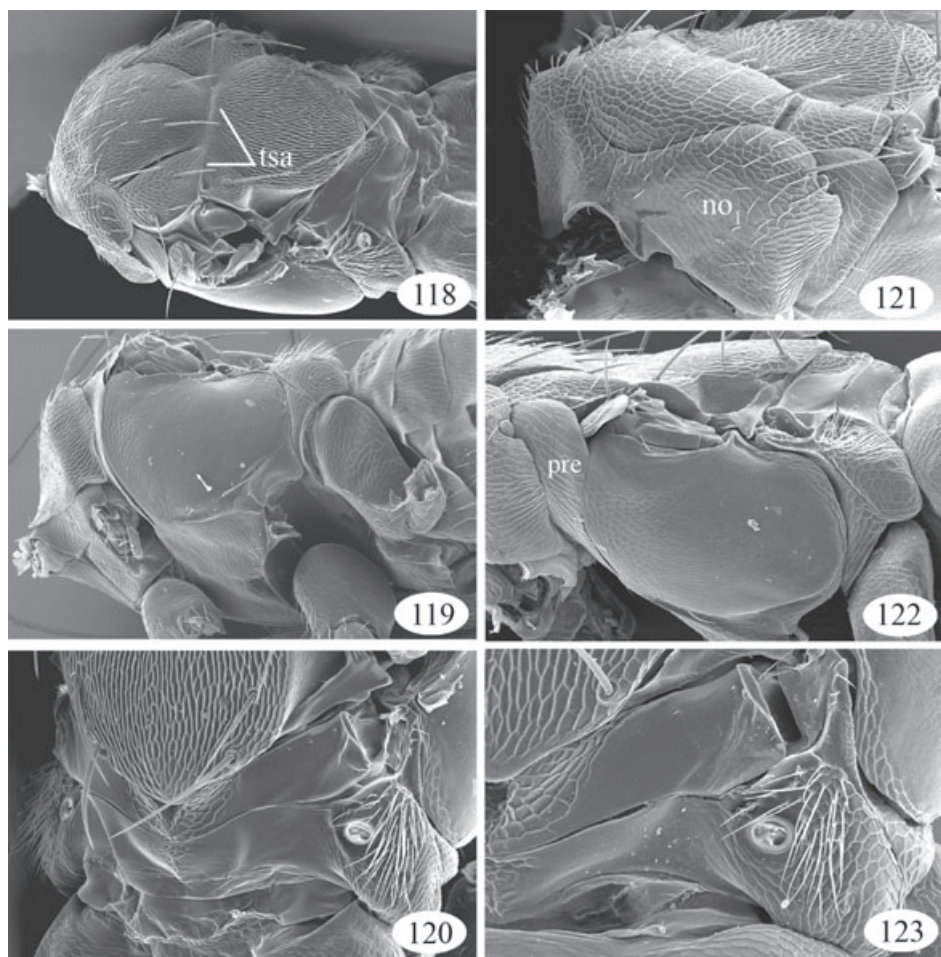
**Figs 112–117.** *Eutrichosomella* (female). 112–116, *Eutrichosomella* sp. 3: 112, head (lateral); 113, antenna; 114, body (lateral); 115, head (posterior); 116, mouthparts (posterior). 117, *Eutrichosomella* sp. 4: gaster (lateral).

20 (19) Crenulae absent, posterior end of propodeum transverse, propodeal seta simple; body flattened and elongated; ovipositor long and exerted (figs 146 and 150 in Hayat, 1998); pronotum long, 0.5× as long as midlobe of mesosoma (fig. 147 in Hayat, 1998) ..... *Proaphelinoides* Girault  
 – Crenulae present (Fig. 161), posterior end of propodeum usually bilobed, propodeal seta leaf-like (Fig. 165); body not flattened; ovipositor usually not long and exerted; pronotum short, 0.15× as long as midlobe of mesosoma (Fig. 160) ...  
 ..... *Aphytis* Howard

*Key to males:*

21 (1) Tarsi four-segmented; antennal formula 1101, clava 6× as long as wide ..... *Eretmocerus* Haldeman  
 – Tarsi five-segmented; antennal formula variable, clava less than 5.5× as long as wide ..... 22  
 22 (21) Antenna three-segmented, formula 1-1-0-1 .....  
 ..... *Marlattella* Howard  
 – Antenna four to six-segmented, formula 1-1-1-1, 1-1-2-1, 1-1-3-1 ..... 23

23 (22) Antenna four-segmented; crenulae present .....  
 ..... *Aphytis* Howard  
 – Antenna five- or six-segmented; crenulae present or absent ..... 24  
 24 (23) Mesopleuron convex and enlarged; forewing usually with dark bands or mottled pattern; linea calva usually well defined, if not, then wings clear and head with temple well developed (Fig. 145) ..... 25  
 – Mesopleuron concave with femoral depression; forewing usually clear with never mottled marks; linea calva not well defined or, if well defined then crenulae present or axilla strongly advanced ..... 28  
 25 (24) Forewing usually mottled; propodeum at most as long as metanotum, propodeal setae one simple one and only one more simple extra seta; antenna formula usually 1121 .....  
 ..... *Marietta* Motschulsky  
 – Forewing at most with a brown marking, never mottled; propodeum more than 1× as long as metanotum, propodeal setae variable, one simple and one thick seta or numerous simple setae; antennal formula 1-1-3-1 ..... 26



**Figs 118–123.** *Eutrichosomella* (female). 118–120, *Eutrichosomella* sp. 3: 118, mesosoma (dorsolateral); 119, mesosoma (ventrolateral); 120, propodeum (dorsal). 121–123, *Eutrichosomella* sp. 4: 121, pronotum (anterior lateral); 122, mesopleuron (lateral); 123, propodeum (dorsal).

26 (25) Two propodeal setae with one simple and one thick setae, propodeum more than 3× as long as metanotum; crenulae present; forewing delta setae dense, delta well defined ..... *Paraphytis* Compere  
 – Numerous propodeal setae simple, propodeum 1–2.5× as long as metanotum; crenulae absent; forewing delta well defined, if not well-defined delta then with sparse setae .. 27

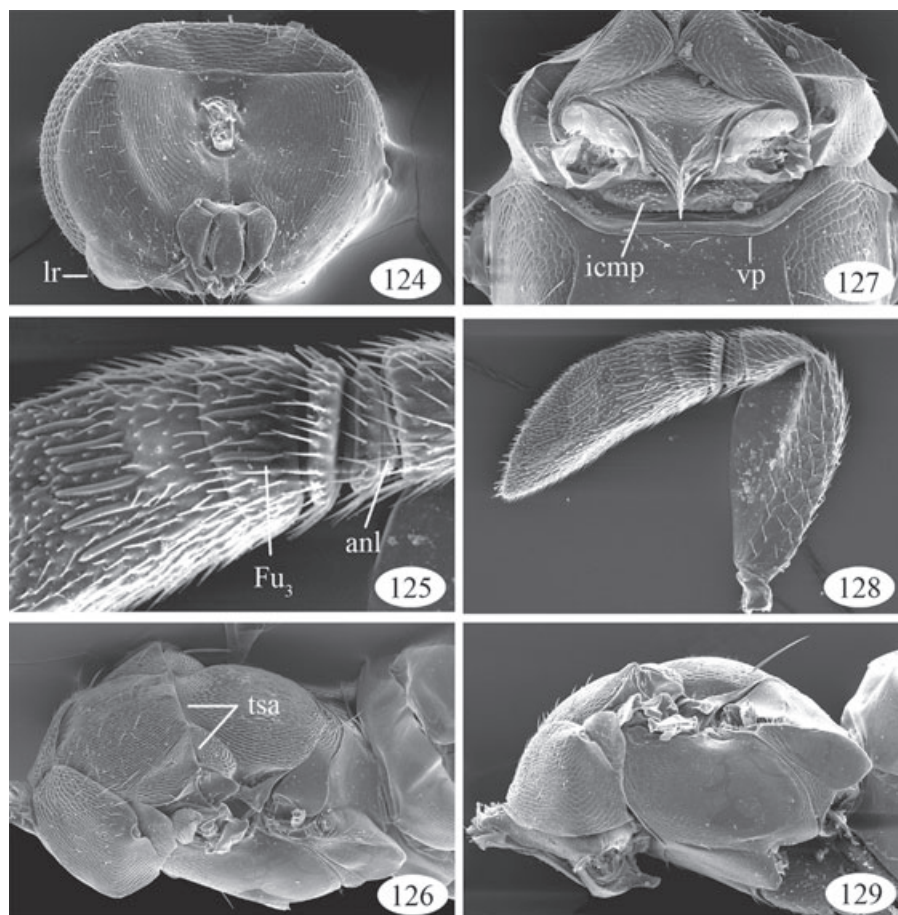
27 (26) Forewing delta loosely setose, not well defined; propodeum less than 1.1× as long as metanotum .....  
 ..... *Samariola* Hayat  
 – Forewing delta densely setose and well defined; propodeum more than 2× as long as metanotum ..... *Mashimaro* n.g.

28 (24) Propodeal seta leaf-like; crenulae present; forewing with a linea calva; parasites of Diaspididae .....  
 ..... *Aphytis* Howard  
 – Propodeal seta simple; crenulae absent; forewing with or without a linea calva; parasites of aclerdids, or aphids or eggs.....30

30 Marginal vein less than 1× as long as costal cell, wing venation usually less than 0.5× as long as forewing, linea calva usually absent; usually parasites of eggs .....  
 ..... *Centrodora* Foerster  
 – Marginal vein longer than costal cell, wing venation more than 0.5× as long as forewing, linea calva present or incomplete; parasites of aclerdids or aphids .....31

31 Pronotum long, 0.5× as long as midlobe of mesoscutum; antennal clava less than 3× as long as wide; sensilla on antennal scape randomly arranged (fig. 141 a in Hayat, 1998); parasitoids of aclerdids .....  
 ..... *Botryoideclava* Subba Rao  
 – Pronotum short, less than 0.2× as long as midlobe of mesoscutum; antennal clava more than 3.4× as long as wide; sensilla on antennal scape, if present, linearly arranged; parasitoids of aphids .....32

32 Anterior scutellar setae outer to posterior pair; tarsal claws unequal in length .....  
 ..... *Protaphelinus* Mackauer  
 – Anterior scutellar setae inner or equal to posterior pair; tarsal claws equal in length ..... *Aphelinus* Dalman



**Figs 124–129.** *Mashimaro hawksi* n.sp.: 124, head (posterior); 125, funicular segments of antenna; 126, mesosoma (dorsolateral); 127, mesosoma (ventral); 128, antenna; 129, mesosoma (lateral).

### Descriptions

#### *Mashimaro* new genus

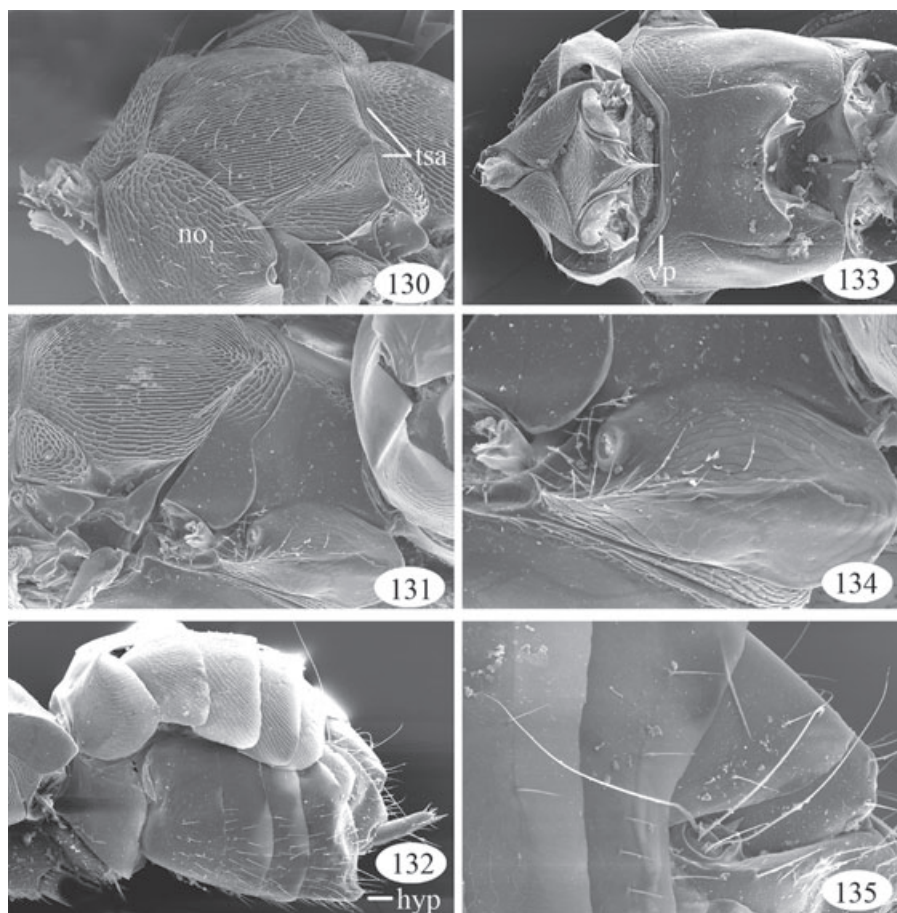
(Figs 20–28, 124–141)

*Type species.* *Mashimaro hawksi* new species.

**Diagnosis.** Recognised by relatively large body size (1.3 mm), orange body colour, enlarged mesopleuron (Figs 129, 137), with combination of a stout antennal clava, transverse funicular segments and forward extending vertex of head (Fig. 27). Scrobal depression is well defined and with lateral ridge on upper face (Fig. 28, lr). The lateral ridge and presence of one incomplete wedge-shaped anellus (Fig. 125, anl) are autapomorphic, and are different from all other genera in Aphelininae. Posterior head with a transverse occipital suture (Figs 124, 136, tos), which a related genus *Samariola* (Fig. 146) lacks. The axillae are relatively larger (as wide as anterior margin of scutellum) and not advanced beyond transscutal articulation (tsa) (Figs 22, 25, 126, 138), which can be used with combination of a swollen mesopleuron (= enlarged

acropleuron) to recognise this genus; however, these structures are similar among members of Eutrichosomellini.

**Description.** Body yellow to orange. Scape of antenna orange, funicular segments of antenna orange or brown, antennal clava yellow to white; mesosoma dorsally bright orange, metasoma yellow to brown; forewing apical 3/5 dusky brown, sometimes with apical 1/5 lighter colour creating a broad band under the marginal vein (Fig. 21). **Head.** Head ovate, somewhat laterally expanded (Fig. 26). Vertex extended forward (Figs 27, 28). Mandible with two teeth. Antennal torulus near clypeus, distinctly lower than lower eye margin (Fig. 26). Each side of face with ridge (Fig. 28, lr) and well-defined scrobal depression area. Posterior margin of head carinate in dorsal view (Fig. 27). Posterior aspect of head with transoccipital suture (Figs 124, 136, tos). **Antenna.** Antenna with six segments (1131) (Figs 128, 139). Scape 2.0× as long as wide, anellus incomplete and wedge-shaped (Fig. 125, anl),  $Fu_1$  and  $Fu_2$  5.5–6.6× as wide as long, clava 2.2–2.3× as long as wide. **Mesosoma.** Pronotum broadened medially and divided into two plates (Figs 130, 138). Axillae not advanced, width almost as wide as anterior margin of scutellum;

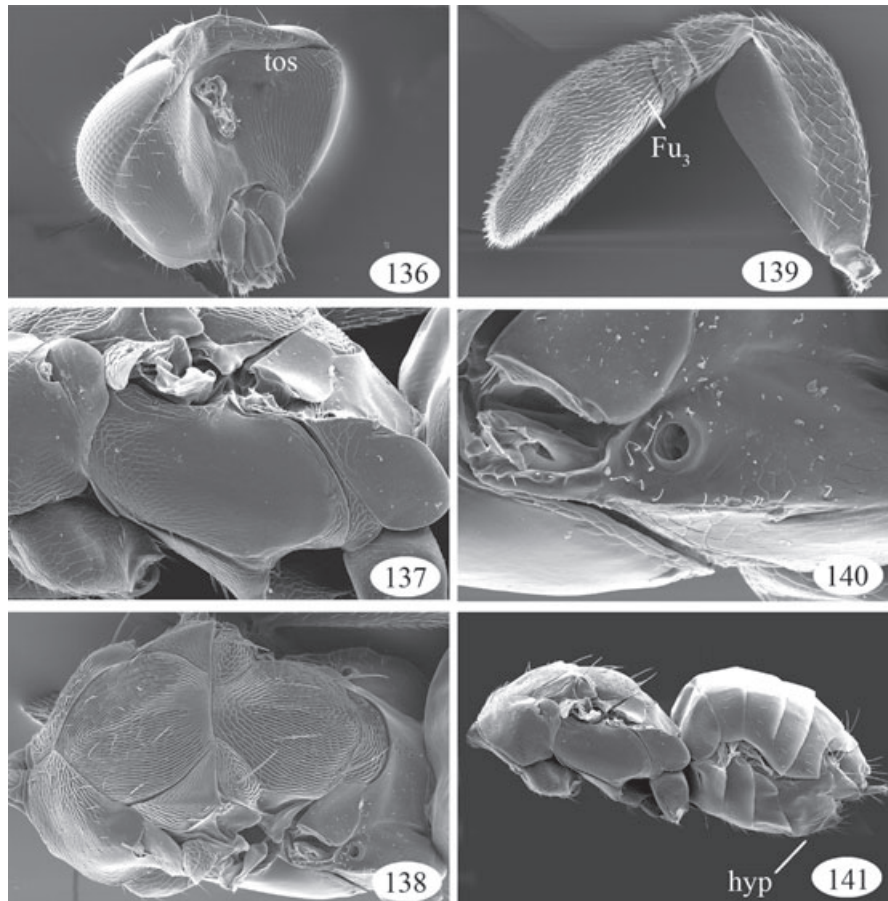


**Figs 130–135.** *Mashimaro hawksi* n.sp.: 130, mesosoma (dorsolateral); 131, scutellum and propodeum (dorsolateral); 132, metasoma (lateral); 133, mesosoma (ventral); 134, propodeum (dorsal); 135, cercal plate (lateral).

axillae with one seta. Scutellum hexagonal (posterior end of scutellum counted as one sided in contrast to the heptagonal scutellum of *Punkaphytis* as in Fig. 252). Scutellum with two pairs of setae; posterior scutellar seta farther apart than anterior ones (Figs 22, 25). Scutellar sensilla between two pairs of scutellar setae. Mesopleuron swollen (Figs 129, 141). Ventral prepectus narrowly connected medially (Fig. 127) and separated completely from mesepisternum. Posterior margin of metanotum transverse (Figs 131, 138). Propodeum without crenulae at posterior end; median sculpture cellulose otherwise smooth. Callus and area around spiracle of propodeum with several small setae (Figs 134, 140). Propodeum 1.28–2.3× as long as metanotum. *Wings.* Forewing with linea calva and well-defined delta area; forewing with broad band under marginal vein, proximal 2/5 clear and distal 1/5 relatively lighter colour than band. Mesofurca with posteriorly oriented mesofurcal lateral arm, anterior interfurcal process (Fig. 18, fp) and posterior interfurcal process (Fig. 18, fe). *Metasoma.* Cercal plates with bristles 3 + 1 (Fig. 135). Cercal plate positioned anteriorly (Figs 135, 141). Hypopygium prominent (Figs 132, 141), at least reaching cercal plate. Ovipositor 0.9× as long as mesotibia.

*Phylogenetic affinities.* The monophyly of *Mashimaro* is supported by three unambiguous synapomorphic characters (Fig. 258): presence of a wedge-shaped anellus (3:0), hexagonal scutellum (34:2), and presence of posterior interfurcal process (41:1). Three additional ambiguous characters that support the genus are: propodeum 1.0–1.3× as long as metanotum (25:1), presence of epicoxal pad (29:1) and mesofurcal arm with an anterior interfurcal process missing the flange (39:2). *Mashimaro* are related to *Samariola* based on four characters (Fig. 258): clava length less than 2.5X (5:2), relative length of propodeum to metanotum (25:0/1), one sensilla on parastigma (43:1) and dense or loose setae defining a delta area (47:1/3).

*Eutrichosomella* superficially resemble *Mashimaro* in body colour and mesosomal structure based on having a swollen mesopleuron and the shape of the transscutal articulation (Figs 114, 118, 121). However, *Eutrichosomella* were distantly related to *Mashimaro* (Fig. 258), and *Eutrichosomella* were strongly supported as monophyletic by five characters: dorsally hidden pronotum (17:1, Fig. 118), axillar width 0.4–0.5× as long as interaxillar distance (31:1), hexagonal scutellum (34:2), presence of posterior interfurcal process (41:1), and marginal vein 1.1–1.7× as long as costal cell (42:1). The



**Figs 136–141.** *Mashimaro lasallei* n.sp.: 136, head (posterior); 137, mesosoma (lateral); 138, mesosoma (dorsal); 139, antenna; 140, propodeal seta (dorsal); 141, body (lateral).

clade that includes *Mashimaro* and *Eutrichosomella* share six synapomorphic characters including three ambiguous characters (Fig. 258):  $Fu_3$  less than  $1.0\times$  as long as  $Fu_1 + Fu_2$  (4:0), divided pronotum (16:1), nonadvanced axilla (32:0), several setae on propodeum (36:0), posteriorly directed lateral arms of mesofurca (40:1) and hypopygium reaching cercal plate (49:0).

*Distribution.* Australian: Australia.

*Host.* Unknown.

*Discussion.* Two species are described in *Mashimaro*, but two more undescribed species were examined. The undescribed species were different in relative length of propodeum (to metanotum), antenna colour and wing colour; however, those were not described because of the limited number of available specimens.

**Key to species**

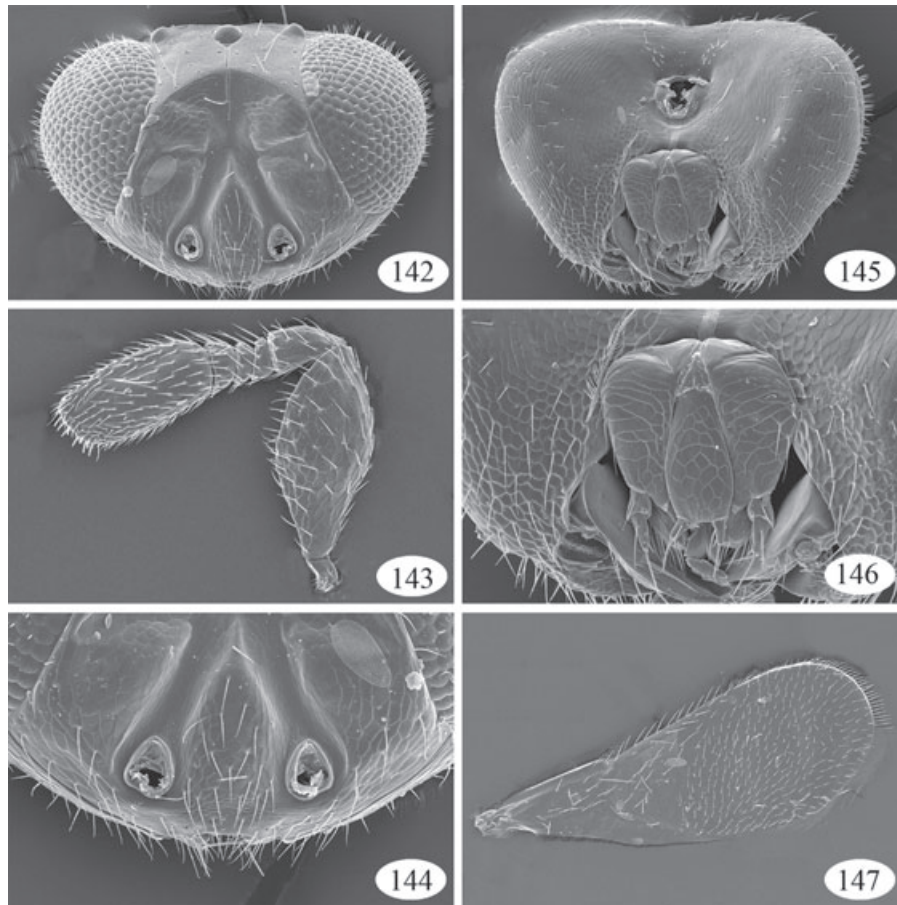
1 Antennal scape orange without black mark on ventral side (Fig. 20), funicle orange and clava yellow. Side lobe of

mesoscutum with one dorsal seta and two lateral setae; scutellum slightly overhanging metanotum (Fig. 131), metanotum sculpture smoothly disappearing laterally (Fig. 131); propodeum  $2.3\times$  as long as metanotum ..... *M. hawksi* n.sp.  
 ..... *M. hawksi* n.sp.  
 – Antenna scape orange with black marginal mark along ventral side (Fig. 23), scape and pedicle orange, funicle brown, clava yellow. Side lobe of mesoscutum with only two lateral setae; scutellum not overhanging metanotum (Figs 137, 138), metanotum sculpture abruptly ended on lateral side, with distinct line defining the cellulate area (Fig. 138); propodeum  $1.3\times$  as long as metanotum ..... *M. lasallei* n.sp.

***Mashimaro hawksi* new species**

(Figs 18, 20–22, 124–135)

*Diagnosis.* This species can be recognised by the uniform orange to dusky orange colour of the antenna and a whitish yellow clava, one dorsal seta and two lateral setae on the side lobe of mesoscutum, and the propodeum  $2.3\times$  as long as metanotum.



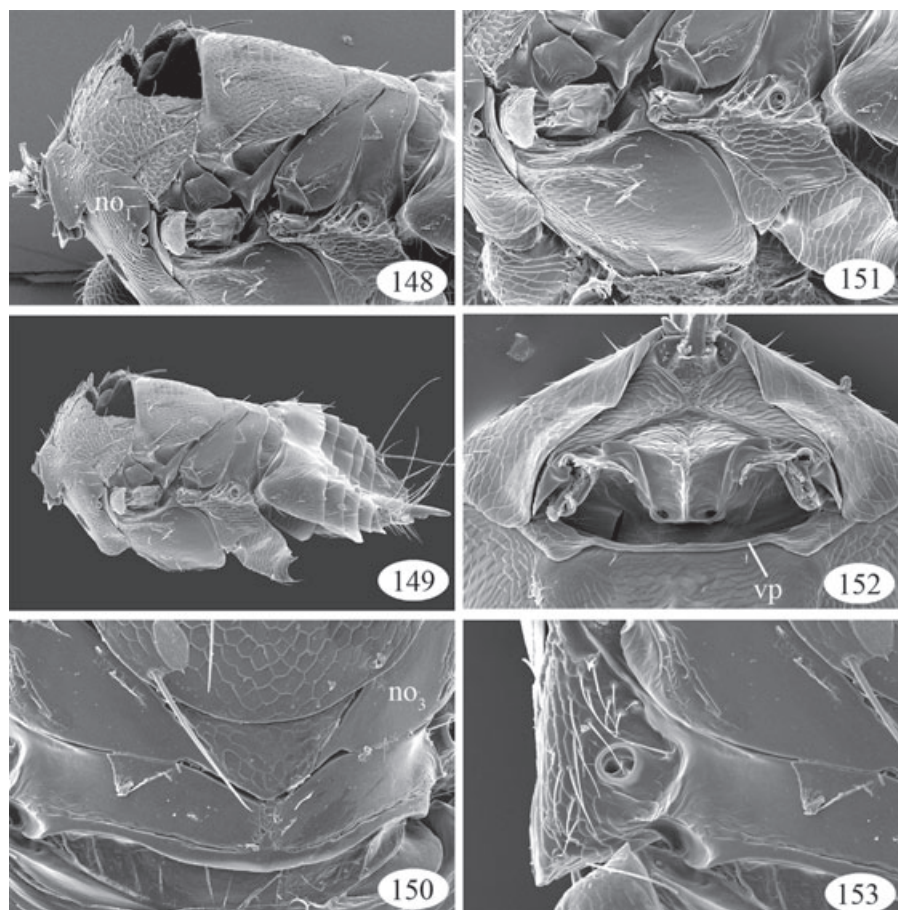
**Figs 142–147.** *Samariola* sp. 2 (male): 142, head (anterior); 143, antenna; 144, face (anterior); 145, head (posterior); 146, mouthparts (posterior); 147, forewing.

**Description.** *Female* (holotype). Length, 1.3 mm. Body dorsally orange, laterally and ventrally yellow with the following parts brown; lower mesopleuron, prosternum, mesosternum, and irregular parts of metasoma. Vertex of head orange, face yellow with broad white and narrow brown stripe (Fig. 26). Antennal scape and  $Fu_{1-3}$  orange, clava yellow. Mesosoma orange with the following yellow or pale orange; pronotum, axilla and anterior margin of scutellum. Each lateral side of pronotum with a white round marking surrounded by brown. Forewing clear under submarginal vein, delta dusky brown; forewing with apical 3/5 brown, apical 1/5 light brown. Legs yellow or white except mid coxa and apex of metatibia brown. **Head.** Head width  $2.1\times$  as wide as frontvertex width. **Antenna** (Figs 20, 125, 128). Scape  $2.2\times$  as long as wide; pedicel  $1.0\times$  as long as wide; pedicel  $1.3\times$  as long as three funicular segments combined;  $Fu_1$  and  $Fu_2$   $0.5\times$  length of  $Fu_3$ ;  $Fu_1$   $1.0\times$  as long as  $Fu_2$ ;  $Fu_2$   $0.2\times$  as long as wide;  $Fu_2$   $0.2\times$  as long as  $Fu_3$ ;  $Fu_3$   $0.5\times$  as long as wide; clava one-segmented,  $2.5\times$  as long as wide. **Mesosoma** (Figs 126, 129). Pronotum aciculate with numerous setae. Midlobe of mesoscutum aciculate, with 14 setae; side lobe of mesoscutum with one dorsal seta and two lateral setae. Metanotum aciculate, medially distinct and

gradually disappearing laterally (Fig. 131). Propodeum  $2.3\times$  as long as metanotum (Fig. 131); propodeal seta numerous, located around spiracle and callus (Fig. 134). **Wings** (Fig. 21). Forewing  $3\times$  as long as broad; all setae on forewing subequal in length; submarginal vein with 8 short setae; costal cell with three setae; marginal vein  $0.7\times$  length of costal cell, with more than 12 small dorsal setae and 8 small anterior setae on marginal vein. Parastigma with one sensillum; stigma with three sensilla. Hind wing  $3.8\times$  as long as broad, marginal fringe  $0.2\times$  as long as hind wing width. **Legs.** Mesotibial spur  $0.7\times$  length of basitarsus. Metatibia  $1.1\times$  as long as mesotibia. **Metasoma.** Petiole and gaster  $1.0\times$  as long as mesosoma. Ovipositor  $0.9\times$  as long as mesotibia. Second valvifer  $1.6\times$  as long as third valvula.

**Male.** Similar to female in colour. Scape less widened and metanotum shorter than female.

**Type material.** Holotype female. Australia: QLD, Heathlands, 25.vii–18.viii.1992, P. Zborowski & J. Cardale, 11.45S 142.35E, Malaise trap, deposited in ANIC (slide). **Paratypes** (all in ANIC): three females and one male with same



**Figs 148–153.** *Samariola* sp. 2 (male): 148, mesosoma (dorsolateral); 149, body (dorsolateral); 150, metanotum and propodeum (dorsal); 151, mesosoma (lateral); 152, prosternum (ventral); 153, propodeal setae (dorsal).

data as holotype; QLD, Batavia Downs, 22.vi–23.viii.1992, P. Zborowski & J. Cardale (three females); QLD, 2 km N Rokeby, 13.ix–26.x.1993, P. Zborowski & D. Rentz (one male); QLD, Cockatoo Creek, 12.viii–10.ix.1993, P. Zborowski & S. Shattuck (one female); QLD, 3 km W Batavia Downs, 16.ix–24.x.1992, P. Zborowski & T. Weir (one female).

*Distribution.* Australia.

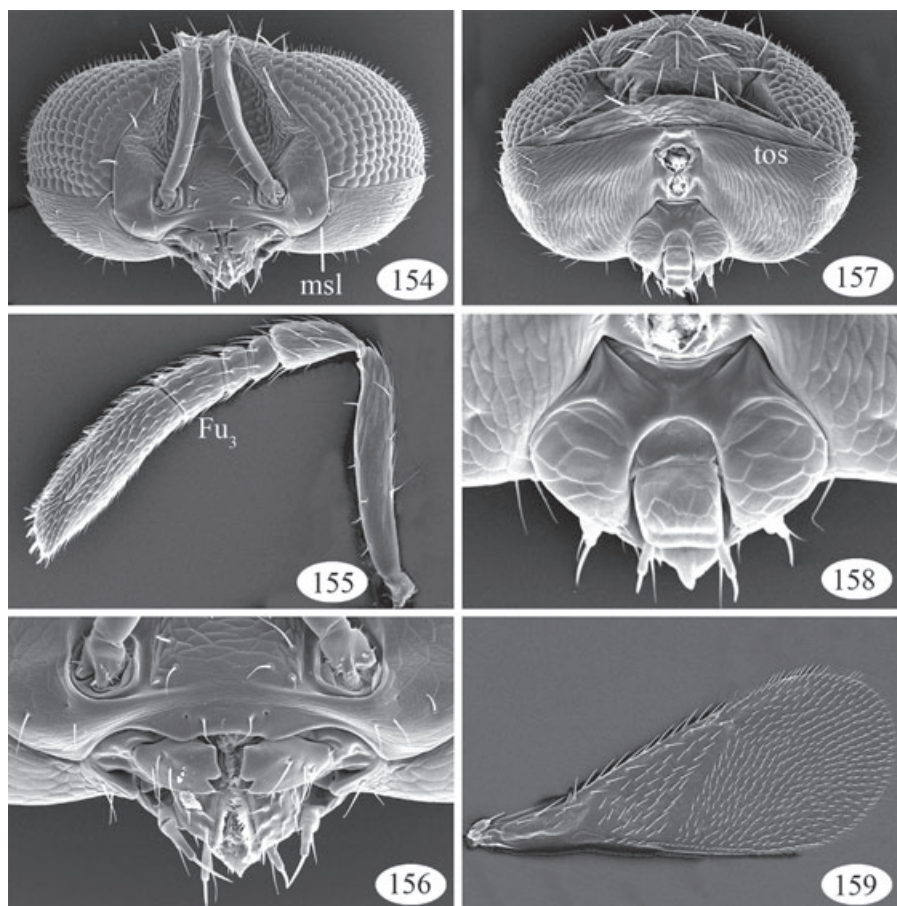
#### ***Mashimaro lasallei* new species**

(Figs 23–25, 28, 136–141)

*Diagnosis.* Recognised by the colour of antenna, having scape and pedicle orange, funicle brown, clava yellow to white. The antennal scape also has a black marginal marking on ventral apex (Fig. 23). The side lobe of mesoscutum has two lateral setae, and lacking a dorsal seta. The anterior scutellar setae placed closer than *M. hawksii*. The metanotum is relatively longer than *M. hawksii*. The propodeum is 1.28× as long as metanotum.

*Description. Female* (holotype). Length, 1.3 mm. Body colours are very close to *M. hawksii* except colour of antenna and metafemur. Vertex of head orange, face yellow with white band. Antennal scape and pedicel orange with brown marking, funicles brown, clava yellow to white. Mesosoma orange with the following light yellow; pronotum, axilla, and anterior margin of scutellum. Forewing beyond delta area brown, clear spot apically next to stigma. Legs yellow, metafemur with apical 1/4 brown. *Head.* Head width 1.83× as wide as frontvertex width. *Antenna* (Figs 23, 139). Scape 2.0× as long as wide; pedicle 1.2× as long as wide; pedicel 1.5× as long as three funicles combined;  $Fu_1$  and  $Fu_2$  0.9× length of  $Fu_3$ ;  $Fu_1$  as long as  $Fu_2$ ;  $Fu_2$  0.2× as long as wide;  $Fu_2$  0.4× as long as  $Fu_3$ ;  $Fu_3$  0.3× as long as wide; clava one-segmented, 1.9× as long as wide. *Mesosoma* (Figs 25, 138). Pronotum aciculate. Midlobe of mesoscutum vertically cellulate, with 14 setae; side lobe of mesoscutum with two lateral setae. Metanotum cellulate sculpture in middle, abruptly ended with suture at lateral side. Propodeum 1.3× as long as metanotum; propodeal seta numerous, located around spiracle and callus. *Wings* (Fig. 24). Forewing 3× as long as broad; all setae on forewing subequal length; submarginal vein with three setae;





**Figs 154–159.** *Aphytis* (female). 154–156, 158–159, *A. melinus*: 154, head (anterior); 155, antenna; 156, face (anterior); 158, mouthparts (posterior); 159, forewing. 157, *A. lingnanensis*: head (posterior).

costal cell without setae; marginal vein  $0.8\times$  length of costal cell, numerous setae on dorsal side of marginal vein and 11 setae on anterior edge of marginal vein. Parastigma with one sensillum; stigma with three sensilla. *Legs*. Mesotibial spur  $0.7\times$  length of basitarsus. Metatibia  $1.1\times$  as long as mesotibia. *Metasoma*. Petiole and gaster  $1.2\times$  longer than mesosoma. Ovipositor  $1.0\times$  as long as mesotibia. Second valvifer  $1.0\times$  as long as third valvula.

*Male*. Unknown.

*Type material*. Holotype female. Australia: Mitchell Plateau, 'The Crusher' CALM site 9/1, 4 km S by W Mining Camp, 2–6.vi.1988, T. A. Wier, 14.52S 125.50E, deposited in ANIC. *Paratypes* (all in ANIC): Australia: Mitchell Plateau, 4 km S by W Mining Camp, 'The Crusher' CALM site 9/1, 2–6.vi.1988, I. D. Naumann (two females); 4 km W of King Cascade W. A., CALM site 28/3, 12–16.vi.1988, T. A. Weir (three females); Prince Frederick Harbour, 'Marun' CALM site 8/4, 11.vi.1988, I. D. Naumann (two females); 14 km SbyE Kalumburu Mission W. A. CALM site 4/3, 3–6.vi.1988, T. A. Weir (two females).

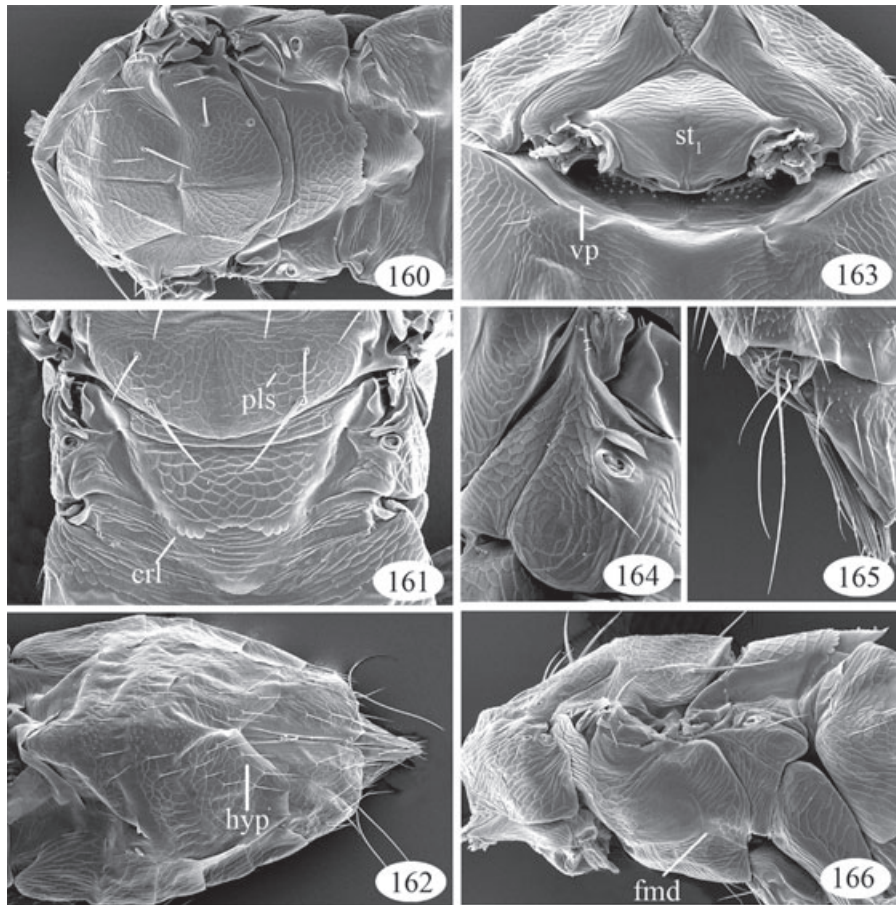
*Distribution*. Australia.

#### *Neophytis* new genus

(Figs 15, 32–37, 211–237)

*Type species*. *Neophytis myartsevae* new species.

*Diagnosis*. Moderate body size (0.7–1.1 mm). Apex of antennal clava in female has a specialised prominent sensillum. The sensillum is thicker than other sensilla on apex of clava (Fig. 32), which is a unique character only shared with *Punkaphytis*. Except for *N. myartsevae* **n.sp.**, females of *Neophytis* lack a constriction between the clava and  $Fu_3$  (Figs 30, 32, 35). *Neophytis* has a thick cylindrical propodeal seta associated with spiracle and one additional simple seta (Figs 222, 231) (as compared with a flattened seta in *Aphytis*, Fig. 164). The lack of axilla setae separates *Neophytis* from all other genera of Aphelininae (Figs 217, 236). The presence of crenulae and bilobed posterior propodeal margin of *Neophytis* is different from *Punkaphytis* which has a broadly round posterior propodeal margin without crenulae. *Neophytis* is very

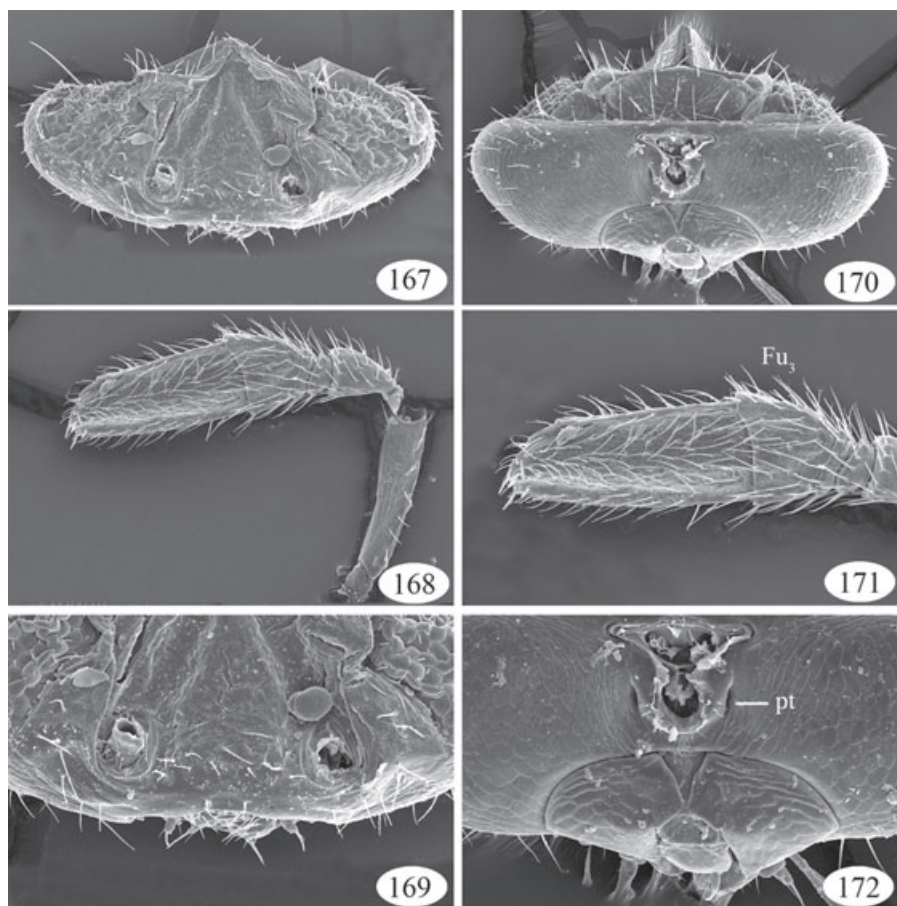


**Figs 160–166.** *Aphytis* (female). 160–165, *A. melinus*: 160, mesosoma (dorsal); 161, propodeum (dorsal); 162, metasoma (ventral); 163, prosternum (ventral); 164, propodeal seta (dorsolateral); 165, cercal bristles (dorsolateral). 166, *A. lingnanensis*: mesosoma (lateral).

similar to *Paraphytis*, having a thick cylindrical propodeal seta; however, *Paraphytis* always have one seta on axilla and a constriction between the clava and  $Fu_3$ . *Neophytis* has long vertical length of genal bridge (10:1, Fig. 214), which is different from *Aphytis* (10:2, Fig. 157). *Aphytis* s. s. has modified seta near the propodeal spiracle (Fig. 164); however, *Neophytis* has a simplified seta (Fig. 222) in the area.

**Description.** Body usually yellow, dorsally orange to yellow. Scape of antenna yellow, funicular segments of antenna yellow, antennal clava yellow or apical 1/3 dark. Mesosoma yellow to orange, metasoma yellow to orange with gaster tergites T1 to T5 ( $Gt_{1-5}$ ) with lateral brown markings. Forewing of female with dusky mark under stigma and parastigma, or cross bands in case of *N. dealbatus*. **Head.** Head round, slightly longer laterally. Vertex normal, not extended. Mandible bidentate with truncation. Antennal torulus near clypeus (Fig. 211). Side of face smooth. Posterior margin of head smooth. Posterior margin of head with transoccipital suture (Figs 214, 225). **Antenna.** Antenna with six segments (1131). Scape 5.0–6.1× as long as wide, anellus absent,  $Fu_2$  0.4–0.5× as long as wide,  $Fu_3$  1.1–1.2× as long as wide, clava 2.4–2.6× as long as

wide. Antennal clava of female with a prominent sensillum at apex (Fig. 32). Clava and  $Fu_3$  connected without constriction except *N. myartsevae*. **Mesosoma.** Pronotum medially divided (Fig. 229). Axilla slightly, but distinctly advanced (Figs 217, 232); axilla without seta. Scutellum heptagonal or triangular with round posterior end (Figs 217, 236). Scutellum with two pairs of setae; anterior scutellar setae lateral to posterior scutellar setae (Figs 219, 236). Scutellar sensilla between the pairs of scutellar setae (Figs 219, 236). Mesopleuron swollen, acropleuron enlarged but not reaching posterior margin of mesopleuron (Figs 221, 234–235). Ventral prepectus narrowly connected and entirely fused with mesepisternum. Posterior margin of metanotum transverse. Propodeum with crenulae (Figs 218, 237). Callus and area around spiracle of propodeum one simple and one thick seta near spiracle (Figs 222, 231). Propodeum 3–4× as long as metanotum. **Wings.** Forewing with a linea calva and well-defined delta area (Figs 33, 36); forewing sometimes with dusky mark or a band under stigma (Figs 31, 36). Mesofurca with anterior interfurcal process and small posterior interfurcal process (Fig. 15); furcal arm laterally orientated and short (Fig. 15). **Metasoma.** Cercal plates with 2 + 2 cerci (Fig. 224). Cercal plate posteriorly positioned



**Figs 167–172.** *Botryoideclava* sp. 1 (female): 167, head (anterior); 168, antenna; 169, face (anterior); 170, head (posterior); 171, antennal club; 172, mouthparts (posterior).

(Fig. 224). Hypopygium not prominent. Ovipositor 1.2–1.5× as long as midtibia.

**Phylogenetic affinities.** Both of the previously described species, *N. dealbatus* and *N. melanosticus*, were originally assigned to *Aphytis* and later determined to be members of the *vittatus* species group of *Aphytis* (Rosen & DeBach, 1979). Rosen & DeBach (1979) commented that *N. dealbatus* and *N. melanosticus* were related to *Marietta* based on the nonconstricted connection of the clava and  $Fu_3$ ; therefore, these two species were suggested as a possible link between *Aphytis* and *Marietta*. In the morphology analysis, *Neophytis* was not monophyletic (Fig. 257), but an unpublished combined analysis of morphology and molecules supported the monophyly of *Neophytis*, which was placed as the sister group of *Punkaphytis* + *Paraphytis*. In the combined analysis, the monophyly of *Neophytis* was supported by two characters: two setae on the side lobe of mesoscutum (22:1) and an absence of setae on the axilla (23:2). In the morphological analysis (Fig. 258), the absence of axillar seta ambiguously supported each species of *Neophytis*, but no other characters supported the genus as monophyletic.

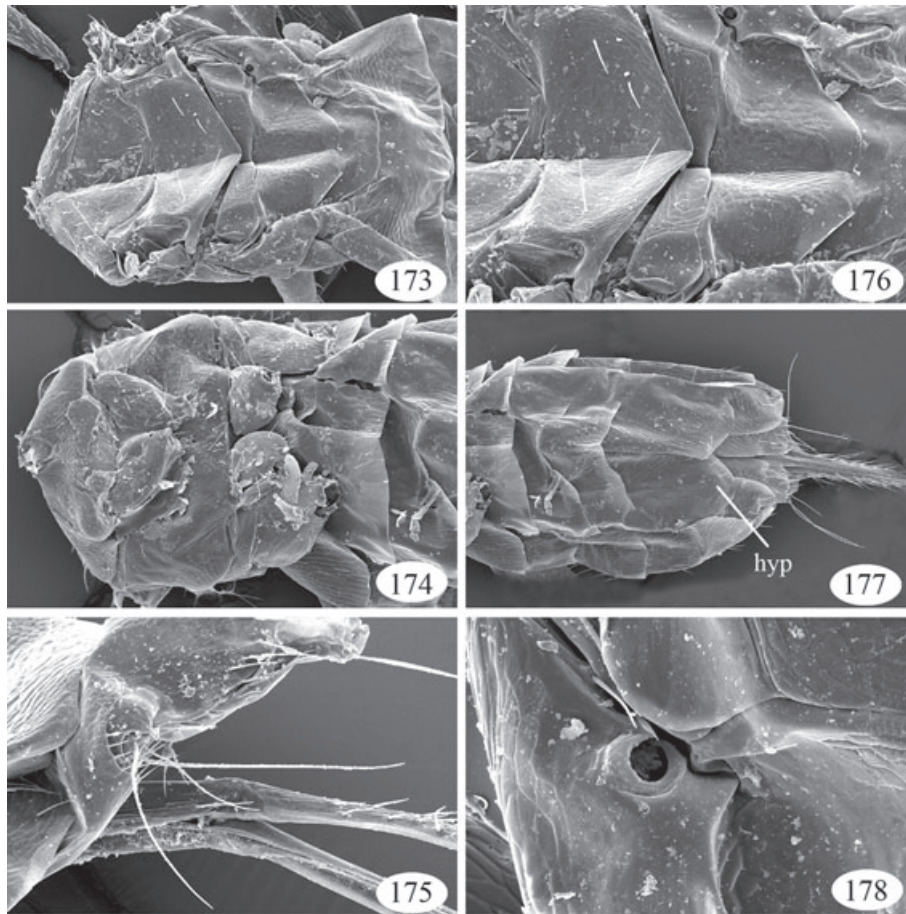
**Distribution.** Nearctic: U.S.A. and Mexico.

**Host.** Diaspididae (Rosen & DeBach, 1979).

**Discussion.** All four described species are from the Nearctic region, which indicates that this genus may be restricted geographically.

**Key to species**

- 1 Malar sulcus without black mark; propodeum less than 3.8× as long as metanotum; clava and  $Fu_3$  connected without constriction (Fig. 30) ..... 2
- Malar sulcus with black mark; propodeum more than 4× as long as metanotum; constriction of clava and  $Fu_3$  variable (Figs 32, 35) ..... 3
- 2. Clava with fuscus tip; forewing clear with dusky marking under stigma and parastigma; male tibia with apical 1/5 black; male scape sensilla located 3/4 of the length of the scape from its apex ..... *N. melanosticus*



**Figs 173–178.** *Botryoideclava* sp. 2 (female): 173, mesosoma (dorsal); 174, mesosoma (ventral); 175, cercal plate (lateral); 176, scutellum and propodeum (dorsal); 177, metasoma (ventral); 178, propodeal seta (dorsal).

– Clava without fuscus tip (Fig. 30); forewing with two crossbands interrupted by transparent setae, bands under apical 1/2 marginal vein and apex of forewing (Fig. 31); male tibia without mark at apex; male scape sensilla located about half-way along the length of the scape ..... *N. dealbatus*

3. Clava with apical 1/3 black (Fig. 32), clava and  $Fu_3$  connected with constriction (Fig. 32); spur of midtibia 0.83× as long as mesobasitarsus; scutellum posteriorly triangular (Fig. 219); crenulae elongated or triangular shape (Fig. 218); forewing uniformly clear (Fig. 33) ..... *N. myartsevae* **n.sp.**

– Clava without black mark, clava and  $Fu_3$  connected without constriction; spur of midtibia 0.72× as long as mesobasitarsus; scutellum posteriorly round (Fig. 236); crenulae wavy, not elongated (Fig. 237); forewing dusky under stigma and parastigma (Fig. 36) ..... *N. munroi* **n.sp.**

#### *Neophytis dealbatus* (Compere) new combination

*Aphytis dealbatus* Compere, 1955, 286–287.

*Aphytis dealbatus*; redescription by Rosen and DeBach, 1979: 290–291.

**Diagnosis.** The antennal clava and malar sulcus are yellow without black markings, separating this species from the other three species. The clava and  $Fu_3$  are separated only by a suture (Fig. 30). The head is immaculate. The propodeum is relatively short, 3.0× as long as metanotum. The forewing has two fuscate cross bands alternating from distal half of marginal vein to posterior forewing margin (Fig. 31). The mesotibia of the male does not have apical black marks.

**Description.** Female: see Rosen and DeBach, 1979.

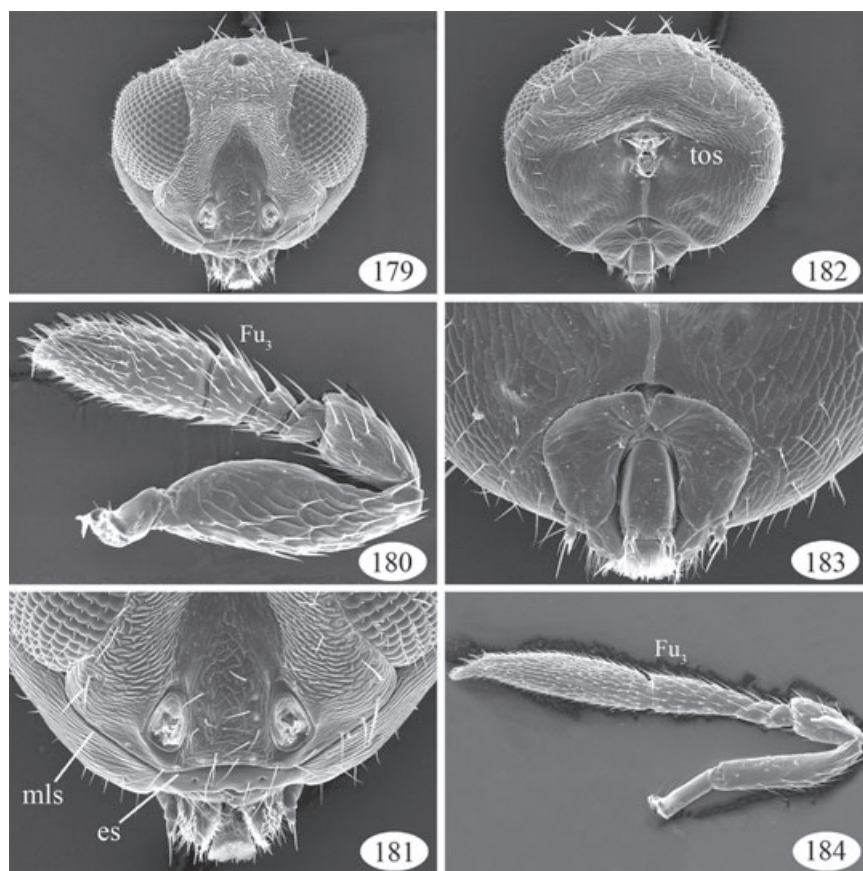
**Male.** Male is similar to female.

**Distribution.** Nearctic: U.S.A.

#### *Neophytis melanosticus* (Compere) new combination

*Aphytis melanosticus* Compere, 1955, 287.

*Aphytis melanosticus*; redescription by Rosen and DeBach, 1979: 291–294.



**Figs 179–184.** *Centrodora* sp. 3 (female): 179, head (anterior); 180, antenna; 181, face (anterior); 182, head (posterior); 183, mouthparts (posterior). 184, *Centrodora* sp. 4: antenna.

**Diagnosis.** The antennal clava has a black mark at the tip (fig. 452 in Rosen & DeBach, 1979). The clava and  $Fu_3$  are separated only by a suture. The head is immaculate. The propodeum is 3–3.5 $\times$  as long as metanotum. The forewing has a distinct dusky marking just posterior to the stigma and parastigma. The male midtibia has a black mark covering the apical 1/4 (fig. 464 in Rosen & DeBach, 1979). The male scape has two sensilla located at apical 3/4 of the scape (fig. 462 in Rosen & DeBach, 1979).

**Description.** Female: See Rosen and DeBach, 1979.

**Male.** See Rosen and DeBach, 1979.

**Distribution.** Nearctic: U.S.A. and Mexico.

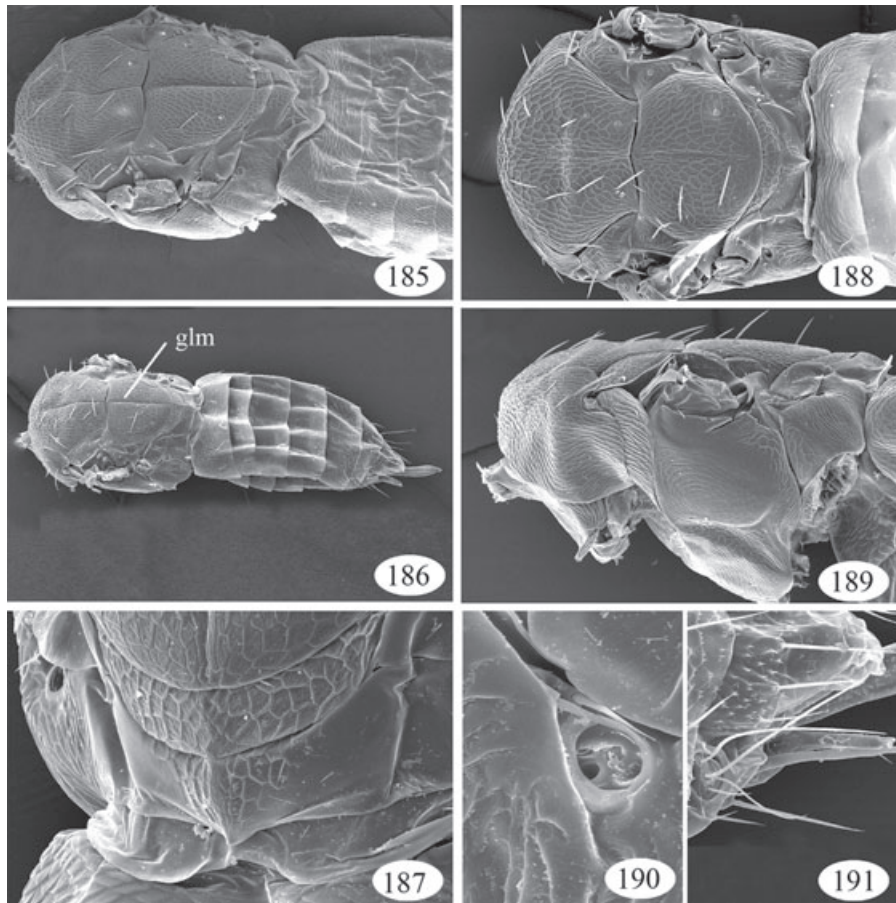
#### *Neophytis munroi* new species

(Figs 15, 35–37, 225–237)

**Diagnosis.** The antennal clava is yellow. The malar sulcus and its vicinity of head is brown. The clava and  $Fu_3$  are separated only by a suture (Fig. 35). The crenulae are small

and wavy, which is distinctly different from *N. melanosticus* (fig. 455 in Rosen & DeBach, 1979) and *N. myartsevae* n.sp. The relative length of mesotibial spur to mesobasitarsus is 0.72 $\times$ . The propodeum is 4 $\times$  as long as metanotum. The forewing has a light brown mark under the stigma and the parastigma. The male has a black marking on the apical 1/4 of the midtibia.

**Description.** Female (holotype). Length, 0.8 mm. Body yellow to orange. Vertex of head orange, face yellow with black malar sulcus and the area below the sulcus is light brown. Antennal scape and  $Fu_{1-3}$  yellow, antennal clava yellow with a dusky yellow tip. Mesosoma orange, with the following yellow; pronotum, metanotum, and propodeum. Metasoma yellow, lateral side of gastral tergites of  $Gt_{1-5}$  with brown marking. Forewing with brown cross bands below stigma and parastigma. Legs yellow to orange, except midtibia with two light brown marking at basal 2/5 and apical 4/5, hindtibia with basal half light brown. **Head.** Head width 3.6 $\times$  as wide as frontvertex width; eye length 1.0 $\times$  as long as malar space. **Antenna** (Fig. 35). Scape 6.1 $\times$  as long as wide; pedicel 1.9 $\times$  as long as wide; pedicel 0.7 $\times$  as long as three funicles combined;  $Fu_1$  and  $Fu_2$  0.5 $\times$  length



**Figs 185–191.** *Centrorodora* sp. 3 (female): 185, mesosoma (dorsolateral); 186, body (dorsal); 187, propodeum (dorsal); 188, mesosoma (dorsal); 189, mesosoma (lateral); 190, propodeal setae (dorsal); 191, cercal bristles (lateral).

of  $Fu_3$ ;  $Fu_1$  1.4× as long as  $Fu_2$ ;  $Fu_2$  0.4× as long as wide;  $Fu_2$  0.2× as long as  $Fu_3$ ;  $Fu_3$  1.2× as long as wide; clava one-segmented, 2.6× as long as wide. *Mesosoma* (Figs 37, 232–233). Pronotum cellulate with numerous setae. Midlobe of mesoscutum cellulate, with ten setae; side lobe of mesoscutum with three setae (Fig. 232). Scutellum anteriorly three-sided and posteriorly evenly rounded (Fig. 236) (coded as variation of heptagonal, 34:3); anterior scutellar setae lateral to posterior scutellar setae (Fig. 236). Scutellar sensilla medial to scutellar setae. Metanotum with cellulate sculpture on median 3/4. Propodeum 4× as long as metanotum (Fig. 237); one propodeal seta near spiracle. *Wings* (Fig. 36). Forewing 2.6× as long as broad; submarginal vein with five setae; costal cell with one seta; marginal vein 1.5× length of costal cell, with ten setae on dorsal marginal vein and ten setae on anterior marginal vein. Parastigma with two sensilla; stigma with four sensilla. Hind wing 5.9× as long as broad, marginal fringe 0.6× as long as hind wing width. *Legs*. Mesotibial spur 0.7× length of basitarsus. Metatibia 1.3× as long as mesotibia. *Metasoma*. Petiole and gaster 1.1× longer than mesosoma. Ovipositor 1.5× as long as mesotibia. Second valvifer 3.1× as long as third valvula.

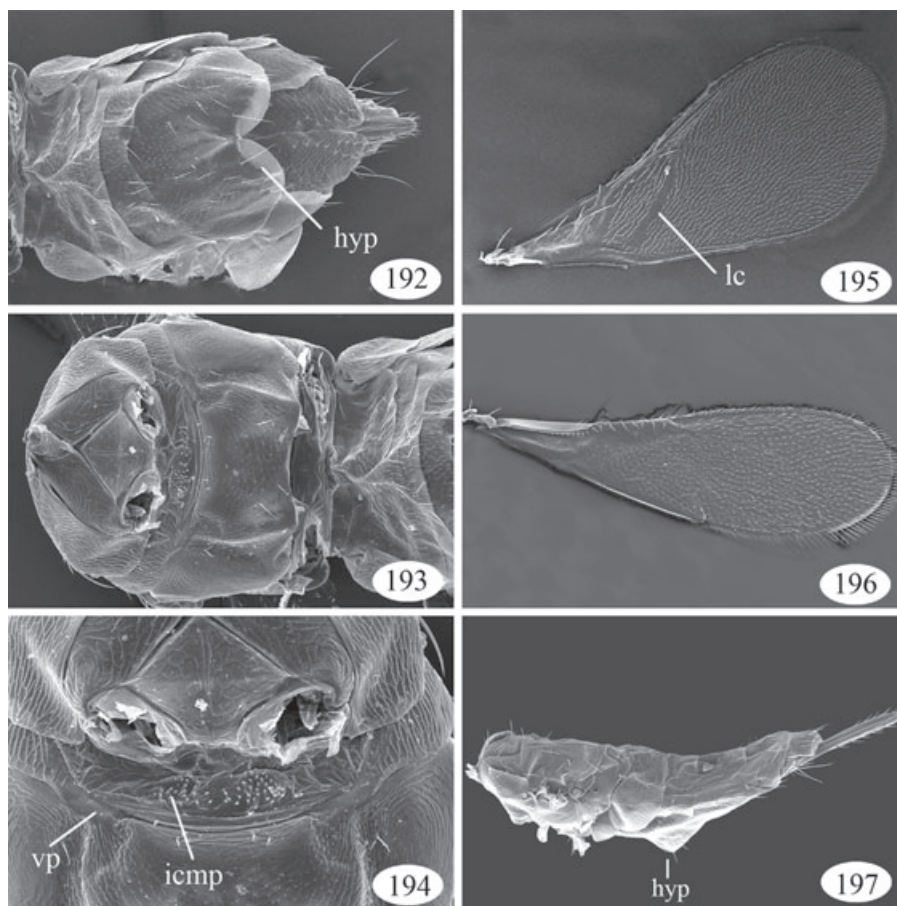
*Male*. Similar to female with the following colour differences: body yellow, vertex of head and body entirely orange except dorsal median 3/4 of metanotum and propodeum yellow, antennal clava and malar sulcus yellow, midtibia with ventral apical 1/4 black and dorsally dusky yellow. Male scape with two sensilla on apical 3/4.

*Type material*. Holotype female. U.S.A.: Nebraska: Lincoln Co., University of Nebraska, Lincoln, 15.v.2002, J. Munro, ex. Diaspididae on *Quercus* sp., around Architecture Hall, deposited in USNM. *Paratypes*: one female and one male with same data as holotype, deposited in UCRC.

*Distribution*. U.S.A.

***Neophytis myartsevae* new species**  
(Figs 32–34, 211–224)

*Diagnosis*. The clava of female has black colouration in the apical 1/3 (Fig. 32). The connection between clava and  $Fu_3$  has a distinct constriction (Fig. 32). The propodeum is 4.1×



**Figs 192–197.** *Centrodora* sp. 3 (female): 192, metasoma (ventral); 193, mesosoma (ventral); 194, prosternum (ventral); 195, forewing. 196–197, *Centrodora* sp. 4: 196, forewing; 197, body (lateral).

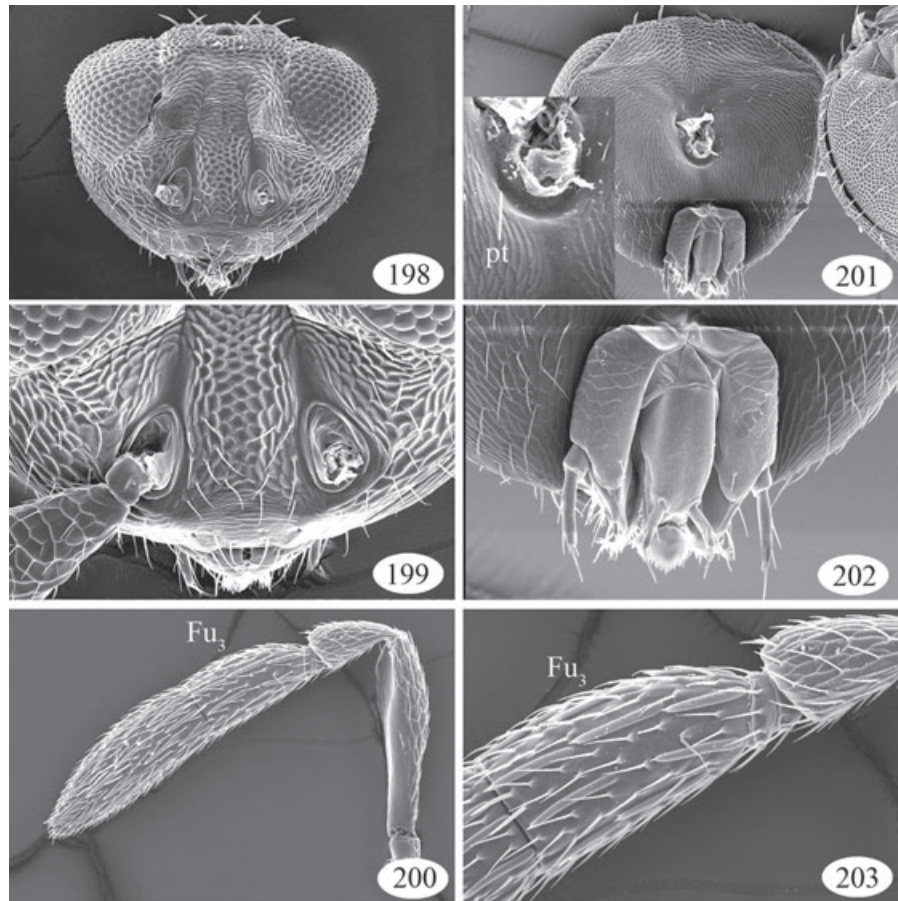
as long as metanotum. The relative length of mesotibial spur to mesobasitarsus is  $0.8\times$ . The forewing is clear.

**Description.** *Female* (holotype). Length, 0.7 mm. Body dorsally orange, laterally and ventrally white to yellow. Vertex of head orange, face yellow with lower 1/2 of malar sulcus black. Antennal scape and  $Fu_{1-3}$  yellow, clava yellow with distal 1/3 to 1/2 black. Mesosoma dorsally orange. Lateral gastral tergites of  $Gt_{1-5}$  with brown marking. Forewing clear with slight dark under parastigma. Legs yellow except tibia and tarsus dusky yellow. **Head** (Fig. 211). Head width  $2.6\times$  as wide as front vertex width; eye length  $1.5\times$  as long as malar space. **Antenna** (Fig. 32). Scape  $5.0\times$  as long as wide; pedicle  $1.6\times$  as long as wide; pedicel  $0.68\times$  as long as three funicles combined;  $Fu_1$  and  $Fu_2$   $0.7\times$  length of  $Fu_3$ ;  $Fu_1$   $1.29\times$  as long as  $Fu_2$ ;  $Fu_2$   $0.5\times$  as long as wide;  $Fu_2$   $0.3\times$  as long as  $Fu_3$ ;  $Fu_3$   $1.2\times$  as long as wide; clava one segment,  $2.4\times$  as long as wide. **Mesosoma** (Fig. 34). Pronotum cellulate with numerous setae. Midlobe of mesoscutum cellulate, with 16 setae; side lobe of mesoscutum with two setae. Scutellum heptagonal. Scutellum with two pairs of setae, anterior scutellar setae lateral to posterior scutellar setae. Scutellar sensilla medial to scutellar

setae. Metanotum with cellulate sculpture on median 3/4. Propodeum  $4.1\times$  as long as metanotum; one propodeal seta near spiracle. **Wings** (Figs 33, 216). Forewing  $2.51\times$  as long as broad; submarginal vein with four setae; costal cell with two setae; marginal vein  $1.36\times$  length of costal cell, with 13 setae on dorsal area of marginal vein and nine setae on anterior edge of marginal vein. Parastigma with two sensilla; stigma with four sensilla. **Legs.** Mesotibial spur  $0.84\times$  length of basitarsus. Metatibia  $1.3\times$  as long as mesotibia. **Metasoma.** Petiole and gaster  $1.42\times$  longer than mesosoma. Ovipositor  $1.12\times$  as long as mesotibia. Second valvifer  $3.5\times$  as long as third valvula.

**Male.** Similar to female with differences in colour as follows: Antennal clava yellow without distinct black apex, malar sulcus with lower 1/2 dusky, pronotum brown medially, mesosoma yellow to orange dorsally, metasoma orange without lateral markings.

**Type material.** Holotype female. Mexico: Tamaulipas, Miguinua, 1.iv.2001, S. Myartseva, ex. Diaspididae on *Agave*, deposited in USNM. **Paratypes:** four females and seven males



**Figs 198–203.** *Marietta* (female). 198–199, *M. montana*: 198, head (anterior); 199, face (anterior). 200–203, *M. nrmarchali*: 200, antenna; 201, head (posterior); 202, mouthparts (posterior); 203, funicular segments.

with same data as holotype, deposited in BMNH, USNM and UCRC.

*Distribution.* Mexico.

#### ***Punkaphytis* new genus**

(Figs 44–49, 245–256)

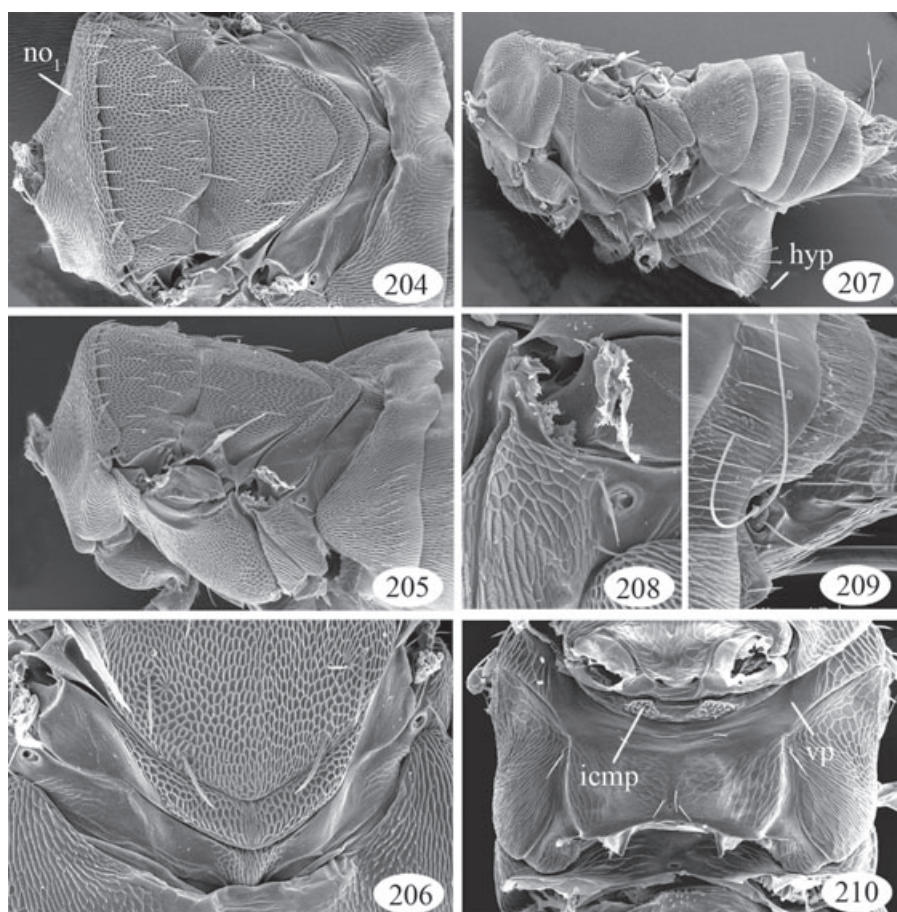
*Type species.* *Punkaphytis hayati* new species.

*Diagnosis.* Recognised by the long and flattened setae on the dorsal aspects of the head and mesosoma (setae longer or as long as frontovertex width) (Figs 12, 245), which are not present in other genera of Aphelinidae (*Ablerus* may have long, but never flattened setae, see fig. 239 in Hayat, 1998). The shape of head is subtriangular in frontal view (Fig. 245). The clava of antenna is long and slender (6.4–7.4× as long as wide, Figs 44, 47, 246), which separates this genus from all other aphelinid genera except *Eretmocerus*. The forewing is mottled with dark colour attributed to both the setae and integument (Figs 45, 58). The pigmentation of both setae and the forewing

is an autapomorphic feature, as the colouration and pattern of the forewing is formed by dark setae in *Paraphytis* but by the integument in *Marietta*.

*Description.* Body white or yellow. Scape and pedicel of antenna brown dorsally, funicular segments of antenna with some brown, antennal clava with some brown; mesosoma with or without markings, if patterned, then midlobe of mesosoma and scutellum with two submedian brown lines (Figs 9, 46); metasoma with at least brown markings on Gt<sub>6</sub>, if transverse cross bands on Gt<sub>1</sub>, then Gt<sub>1–4</sub> with distinct cross bands; forewing mottled (Figs 45, 48). *Head.* Head triangular in frontal view. Head with long, flattened setae dorsally (Figs 245, 249); three located on face near eye margin, one long black seta lateral to anterior ocellus, a pair of black setae between posterior ocellus, one long and one short seta on vertex lateral to posterior ocellus (Fig. 12). Vertex normal without forward extension. Mandible with two teeth and a truncation. Top margin of antennal torulus lower or inline with lower margin of eyes. Posterior margin of head smooth. Posterior aspect of head without transoccipital suture (Fig. 248). *Antenna.* Antenna six-segmented (1131)



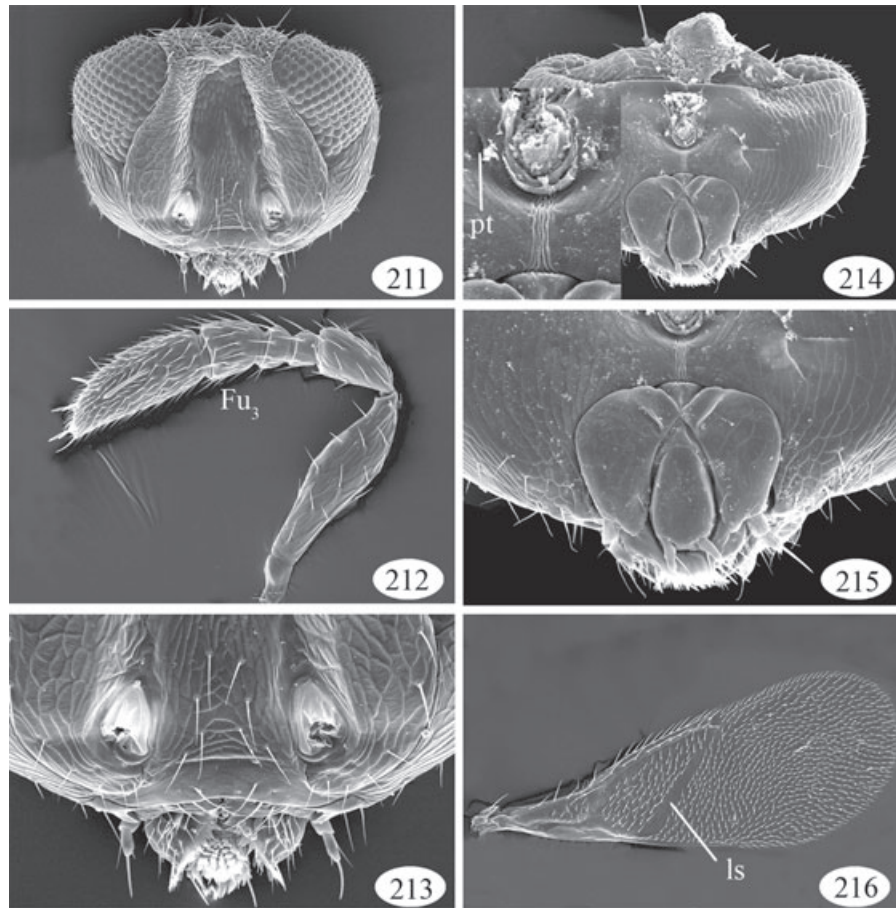


**Figs 204–210.** *Marietta* (female). 204–209, *M. nr marchali*: 204, mesosoma (dorsal); 205, mesosoma (lateral); 206, scutellum and metanotum (dorsal); 207, body (lateral); 208, propodeal setae (dorsal); 209, cercal bristles (lateral). 210, *M. montana*: mesosoma (ventral).

(Figs 44, 47, 246). Scape 1.0–1.1× as long as clava, anellus absent,  $Fu_1$  triangular (Fig. 246,  $Fu_1$ ),  $Fu_2$  and  $Fu_3$  wider than long,  $Fu_1 + Fu_2$  0.2–0.4× as long as  $Fu_3$ ; clava 5.7–7.4× as long as wide, with specialised sensilla on apex of clava (Fig. 246, ssa). *Mesosoma*. Pronotum entire. Axillae hardly advanced beyond line of anterior margin of scutellum (if advanced, then they are advanced less than 1/3 length of inner side of side lobe of mesoscutum); axillae with one seta. Scutellum heptagonal. Scutellum with four setae; anterior scutellar setae farther apart than posterior pair. Scutella sensilla lateral to anterior scutellar setae. Mesopleuron swollen (Figs 251, 256). Ventral prepectus connected narrowly and medially fused with mesepisternum. Posterior margin of metanotum transverse. Propodeum without crenulae at posterior end (Fig. 253). Callus and area around spiracle of propodeum with several setae (Fig. 253). Propodeum 4.0–4.3× as long as metanotum (Fig. 253). *Wings*. Forewing (Figs 45, 48) with linea calva; delta area loosely defined with three patches of thick setae; forewing mottled with thick setae and integument infusate with seven marks. Mesofurca (Figs 10, 11) without mesofurcal bridge, but with anterior interfurcal process and posterior interfurcal process.

*Metasoma*. Cercal plates with bristles of 2 + 2 (Fig. 254). Cercal plates positioned anteriorly, close to same plane as that of the spiracle. Hypopygium prominent (Fig. 254), at least reaching to cercal plate. Ovipositor 3.0× as long as mesotibia.

*Phylogenetic affinities*. Monophyly of the genus was well supported by eight unambiguous characters (Fig. 258). The following characters also support the monophyly of the genus, but are shared with other genera. An elongated antennal clava (5:1) is shared with *Eretmocerus*. The absence of a transocipital suture (16:0) occurs in *Samariola* and *Marietta*, and the absence of crenulae (28:0) is a character for all Aphelininae except *Aphytis*, *Neophytis* and *Paraphytis*. However, the flattened setae on the body and elongated clava make *Punkaphytis* distinctive among all Aphelinidae. Interestingly, the features of mesofurcal arm are a combination of Eutrichosomellini and Aphytini: the posterior interfurcal process is present (41:1) as in *Eutrichosomella* (fig. 10 in Heraty *et al.*, 1997) and *Mashimaro* (Figs 10, 11), and the laterally orientated mesofurcal arm and the anterior interfurcal process with a flange are similar to those of Aphelininae (figs 8–10 in Heraty *et al.*, 1997). The hypopygium reaches only to the cercal



**Figs 211–216.** *Neophytis myartsevae* n.sp. (female unless otherwise noted): 211, head (anterior); 212, antenna (male); 213, face (anterior); 214, head (posterior); 215, mouthparts (posterior); 216, forewing.

plate (48:1), as in *Mashimaro* and *Samariola*. The absence of epicoxal pads (29:0) is shared with a number of genera in Aphelininae, such as *Proaphelinooides*, *Protaphelinus*, *Saengella* n.g. and *Samariola*. The specialised sensillum on the clava (Fig. 246) was also found in *Neophytis* (Fig. 32); therefore, the character may suggest an affinity between two genera.

Morphological analysis placed *Neophytis* as a paraphyletic sister group to *Paraphytis* + *Punkaphytis* (Fig. 257). The sister group relationship of *Paraphytis* + *Punkaphytis* was supported both in morphology (Fig. 257) and in an unpublished combined analysis.

*Distribution.* Neotropical: Ecuador.

*Host.* Unknown.

*Discussion.* Two species are currently described, both from Ecuador. However, many vials of unsorted material are not yet processed and additional species were noticed during the ongoing sorting effort. There is one other undescribed species with entirely white body and white setae. The body colour

is believed to be a reliable character for species; therefore, the two new species can be separated from other undescribed species based on colour of body and shape of antennal scape. The two described species were the most common.

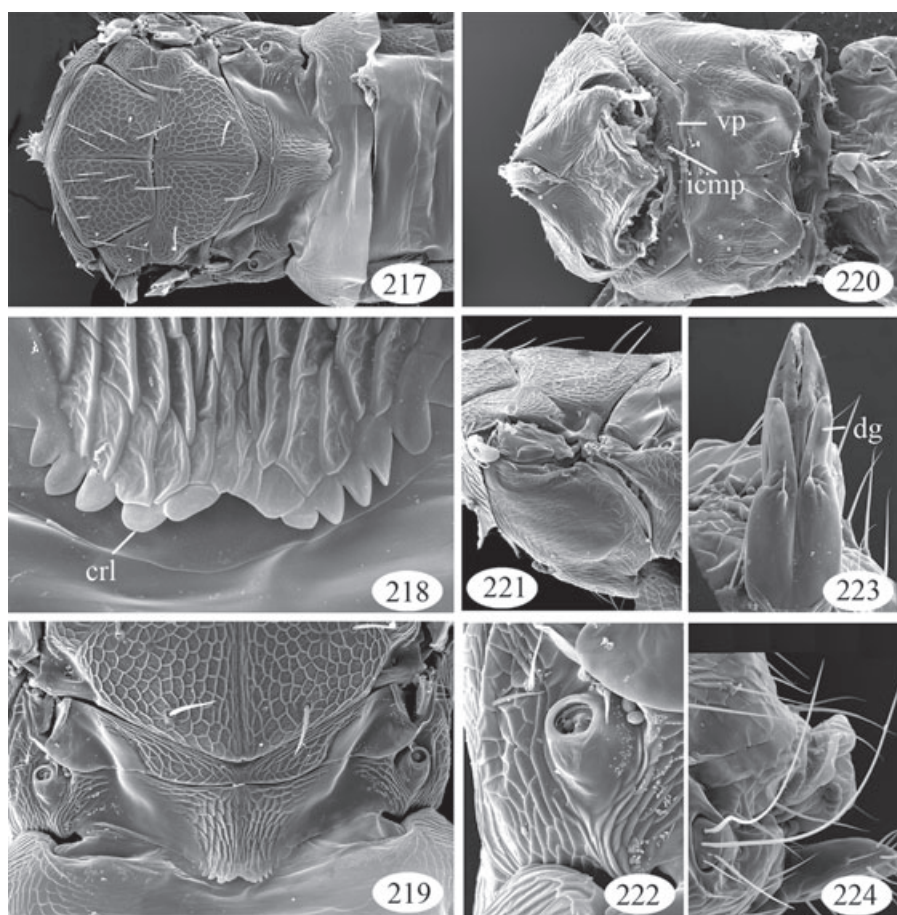
#### Key to species

- 1 Mesosoma with two submedian longitudinal stripes (Fig. 46); gastral tergites 1–4 (Gt<sub>1–4</sub>) with transverse cross bands; antennal scape 8.7× as long as wide . . . . . *P. erwini* n.sp.  
 – Mesosoma without longitudinal stripes (Fig. 49); Gt<sub>1–4</sub> without transverse cross bands, at best terga seven with markings; antennal scape 5.8× as long as wide . . . . .  
 . . . . . *P. hayati* n.sp.

#### *Punkaphytis erwini* new species

(Figs 9–10, 44–46)

*Diagnosis.* Differs from *P. hayati* n.sp. by having longitudinal stripes on the mesosoma and transverse bands on the gastral terga dorsally. The relatively longer antenna is also a

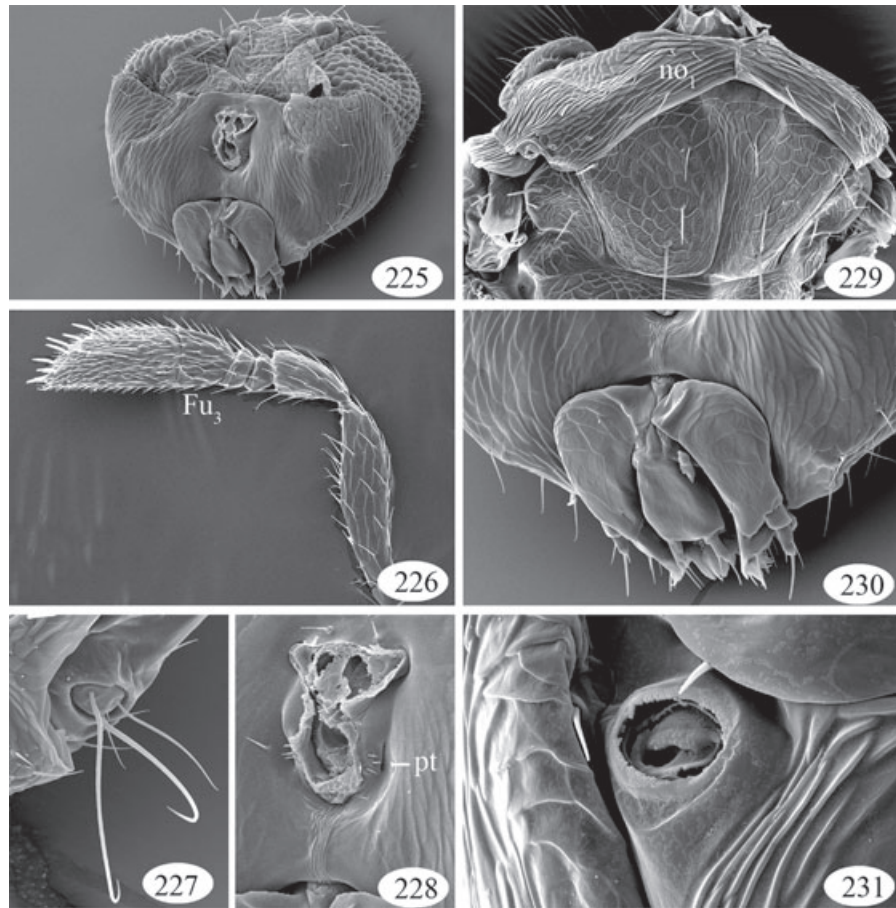


**Figs 217–224.** *Neophytis myartsevae* n.sp. (female otherwise noted): 217, mesosoma (dorsal); 218, crenulae (dorsal); 219, propodeum (dorsal); 220, mesosoma (ventral); 221, mesopleuron (lateral); 222, propodeal setae (dorsal); 223, genitalia (male); 224, cercal bristles (lateral).

notable feature; for example, the antennal clava is  $7.4\times$  as long as wide and the scape is  $8.7\times$  as long as wide.

**Description.** *Female* (holotype). Length, 1.0 mm. Body and appendages yellow. Vertex of head and face yellow with sockets surrounding setae on head brown; setae on head yellow except for the two black setae on the head. Antennal scape and pedicel dorsally light brown, clava uniformly dusker than funicular segments. Mesosoma yellow, midlobe with two brown submedian longitudinal lines and brown lateral lines along each lateral margin (Fig. 46), sockets surrounding setae on mesosoma brown; setae on mesosoma yellow except for two black setae on the scutellum. Scutellum with two submedian brown lines and a marking on posterolateral margin; propodeum with an anteriorly median brown transverse line, interrupted medially. Forewing patterned, delta area with three thick patches of setae, linea calva distinct. Blade (distal to linea calva) with seven irregular patches formed by thick setae and integumentary infuscation (Fig. 45); three round patches diagonally arranged beginning from linea calva; one long patch of setae starting from stigma about  $3/5$  of the way diagonally across blade; one small patch near anterior margin

of forewing blade; one C-shaped and one round patch at apex of forewing. Legs yellow, except midtarsi and metatarsi light brown (dusky yellow). Gastral terga with posterior margin of  $G_{1-4}$  with a brown transverse band,  $G_7$  with a median brown marking. **Head.** Head  $2.2\times$  as wide as frontvertex; eye length  $1.7\times$  as long as malar space; distance from torulus to eye margin  $1.8\times$  width of torulus. **Antenna** (Fig. 44). Scape  $8.7\times$  as long as wide; pedicel  $4.6\times$  as long as wide; pedicel as long as three funicular segments combined;  $Fu_1$  and  $Fu_2$   $0.2\times$  length of  $Fu_3$ ;  $Fu_1$   $0.8\times$  of  $Fu_2$ ;  $Fu_2$   $0.5\times$  as long as wide;  $Fu_2$   $0.1\times$  as long as  $Fu_3$ ;  $Fu_3$   $3.1\times$  as long as wide; clava one-segmented,  $7.4\times$  as long as wide. **Mesosoma** (Figs 9, 46). Pronotum entire, with imbricate sculpture, each side with two long medial and four short lateral flattened setae, and numerous short thin setae (Figs 9, 46). Mesoscutum and scutellum with cellulate reticulation. Midlobe of mesoscutum with asymmetric pairs of setae (Figs 9, 46); side lobe of mesoscutum with three setae. Axilla slightly projected forward into side lobe of mesoscutum, with one flattened seta. Posterior scutellar setae medial to anterior setae. Scutellar sensilla lateral to anterior scutellar setae. Metanotum cellulate. Propodeum medially cellulate, otherwise smooth. Propodeum  $4.3\times$  as long



**Figs 225–231.** *Neophytis munroi* n.sp. (female unless otherwise noted): 225, head (posterior); 226, antenna (male); 227, cercal bristle; 228, occipital foramen (posterior); 229, pronotum; 230, mouthparts; 231, propodeal setae.

as metanotum; four to five propodeal setae located around spiracle and callus. *Wings* (Fig. 45). Forewing  $2.8\times$  as long as broad; submarginal vein with five setae including a long seta at apex of submarginal vein; costal cell with four long setae distally and numerous short setae proximally; marginal vein  $1.5\times$  length of costal cell, with eight setae on vein dorsally and 16 small setae on anterior margin. Hind wing  $4.1\times$  as long as broad; marginal fringe  $0.2\times$  as long as wing width. *Legs*. Mesotibial spur  $0.8\times$  as long as basitarsus. Hindtibia  $1.3\times$  as long as midtibia. *Metasoma*. Petiole and gaster  $1.7\times$  longer than mesosoma. Ovipositor  $3.0\times$  as long as mesotibia. Second valvifer  $2.1\times$  as long as third valvula.

*Male*. Unknown.

*Type material*. Holotype female. Ecuador: Napo, Res. Eth. Waorani,  $00^{\circ}39'S$   $76^{\circ}26'W$ , 4–8.x.1995, 220 m canopy fog, lot#1263, T. L. Erwin *et al.* BM2000-22, deposited in USNM (slide). *Paratype*: Ecuador: Orellana, S. Onkone, Onkone Gare Camp 216.3 m, 3.x.2000,  $00^{\circ}39'25.7''S$ ,  $076^{\circ}27'10.8''W$ , T. L. Erwin *et al.*, lot # 1707 (one female on card deposited in USNM).

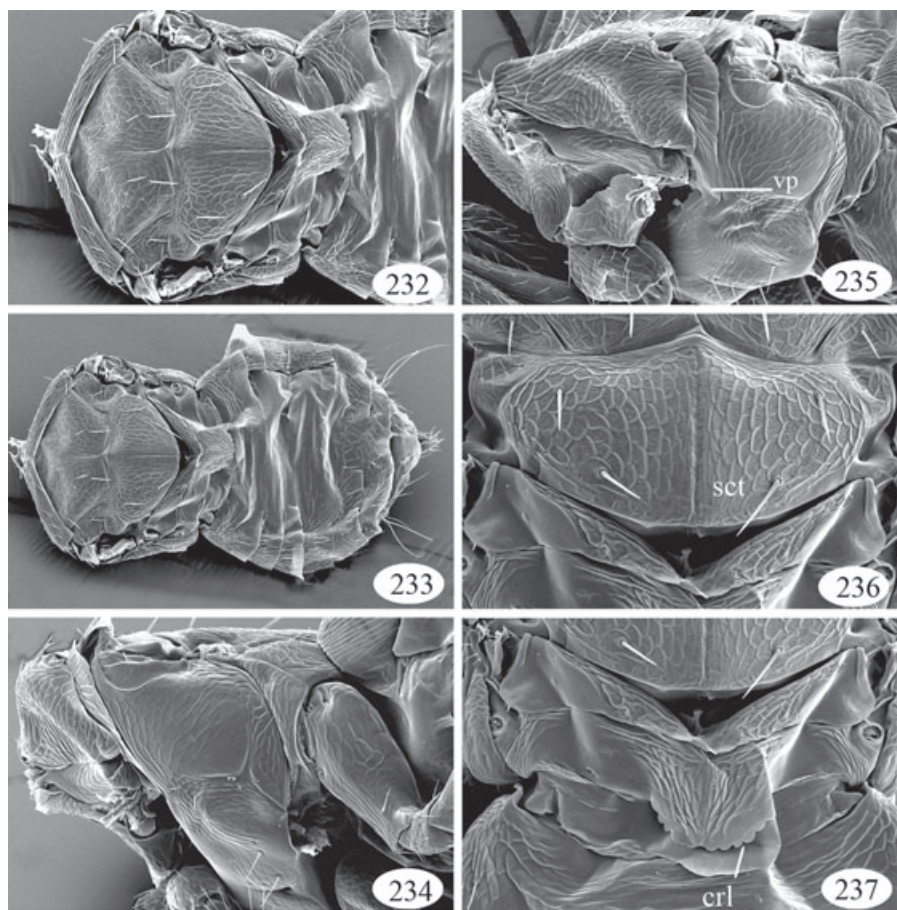
*Distribution*. Known only from type locality.

#### *Punkaphytis hayati* new species

(Figs 11–12, 47–49, 245–256)

*Diagnosis*. Recognised by the absence of markings on dorsum of mesosoma and metasoma except  $Gt_7$ . The forewing colour pattern is different from *P. erwini*, having fewer setae forming three groups of patches on delta of forewing (Fig. 48). The antennal scape is relatively short ( $5.8\times$  as long as wide).

*Description*. *Female* (holotype). Length, 1.0 mm. Body and appendages whitish yellow. Vertex of head and face whitish yellow, setae on head yellow except two pairs. Antennal scape and pedicel dorsally dark brown,  $Fu_{1-3}$  dusky yellow, clava uniformly dusker. Mesosoma whitish yellow, midlobe with thin brown lateral lines along each lateral margin; anterior scutellar seta brown. Forewing lightly patterned, blade of forewing with seven irregular patches similar to *P. erwini* (Fig. 48). Legs yellow, pro-, meso-, and metatarsi dusky yellow.  $Gt_7$  with median brown marking. *Head*



**Figs 232–237.** *Neophytis munroi* n.sp. (female): 232, mesosoma (dorsal); 233, body (dorsal); 234, mesosoma (lateral); 235, mesosoma (ventrolateral); 236, scutellum (dorsal); 237, propodeum (dorsal).

(Figs 12, 245). Head  $2.7\times$  as broad as the width of frontvertex; eye length  $2.4\times$  as long as malar space; distance from torulus to eye margin  $3.1\times$  width of torulus. *Antenna* (Fig. 47). Scape  $5.8\times$  as long as wide; pedicel  $2.8\times$  as long as wide; pedicel as long as three funicles combined;  $Fu_1$  and  $Fu_2$   $0.4\times$  length of  $Fu_3$ ;  $Fu_1$   $1\times$  as long as  $Fu_2$ ;  $Fu_2$   $0.5\times$  as long as wide;  $Fu_2$   $0.1\times$  as long as  $Fu_3$ ;  $Fu_3$   $3.1\times$  as long as wide; clava one segment,  $5.7\times$  as long as wide. *Mesosoma* (Figs 49, 251–252). Pronotum entire, with cellulate sculpture, each side with five flattened setae and numerous short thin setae (Fig. 49). Mesoscutum and scutellum with cellulate reticulation. Midlobe of mesoscutum with six pairs setae (Fig. 49); side lobe of mesoscutum with two flattened setae. *Wings* (Fig. 48). Forewing  $2.6\times$  as long as broad; submarginal vein with five seta (one long seta at apex of submarginal vein); costal cell with three long setae distally and numerous short setae proximally; marginal vein  $1.6\times$  length of costal cell, with eight setae on dorsum of vein and 12 small setae on anterior margin. Delta area with three weakly developed patches of setae, linea calva distinct. Hind wing  $4.5\times$  as long as broad; marginal fringe  $0.2\times$  as long as wing width. *Legs*. Mesotibial spur  $0.9\times$  as long as basitarsus. Metatibia  $1.1\times$  as

long as mesotibia. *Metasoma*. Petiole and gaster  $1.9\times$  longer than mesosoma. Ovipositor  $3.0\times$  as long as mesotibia. Second valvifer  $2.1\times$  as long as third valvula.

*Male*. Unknown.

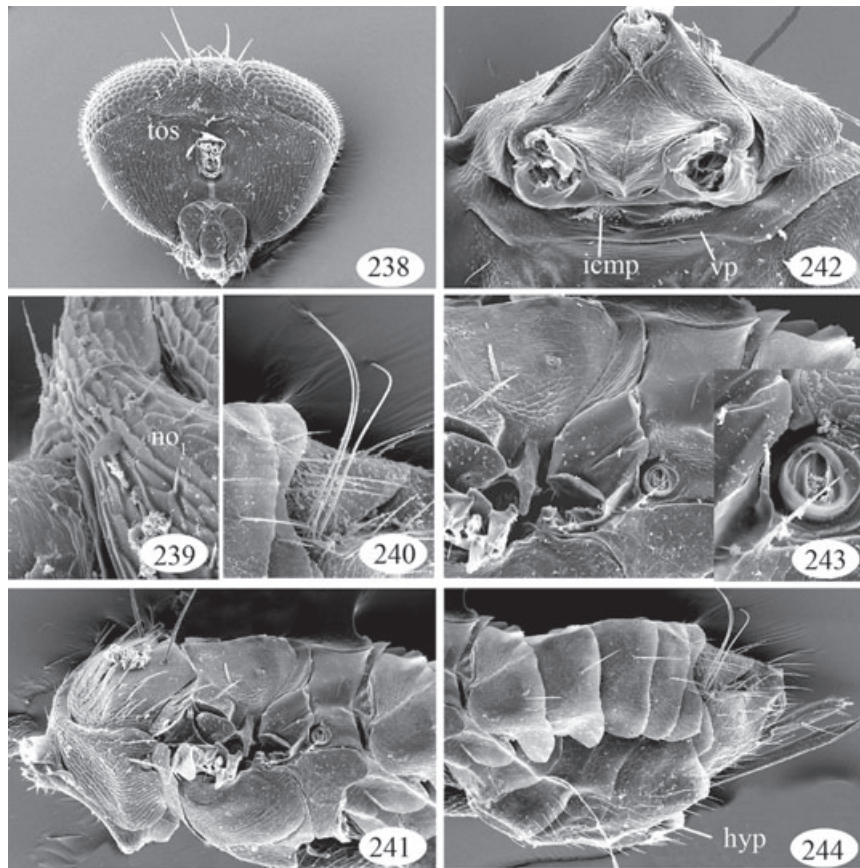
*Type material*. Holotype female. Ecuador: Napo, Res. Eth. Waorani,  $00^{\circ}39'S$   $76^{\circ}26'W$  4–8.x.1995, 229 m canopy fog, lot#1261, T. L. Erwin *et al.* BM2000-22, deposited in USNM (slide). *Paratypes*: Ecuador: Orellana, Tiputini Biodiversity Station nr Yasuni National Park, 220–250 m, 6.ii.2003, W, T. L. Erwin *et al.* lot # 2083 (two females with identical collection data, one female on SEM stub deposited in UCRC and one female on card deposited in USNM).

*Distribution*. Known only from type locality.

#### ***Saengella* new genus**

(Figs 13, 16, 50–52)

*Type species*. *Saengella gloria* new species.



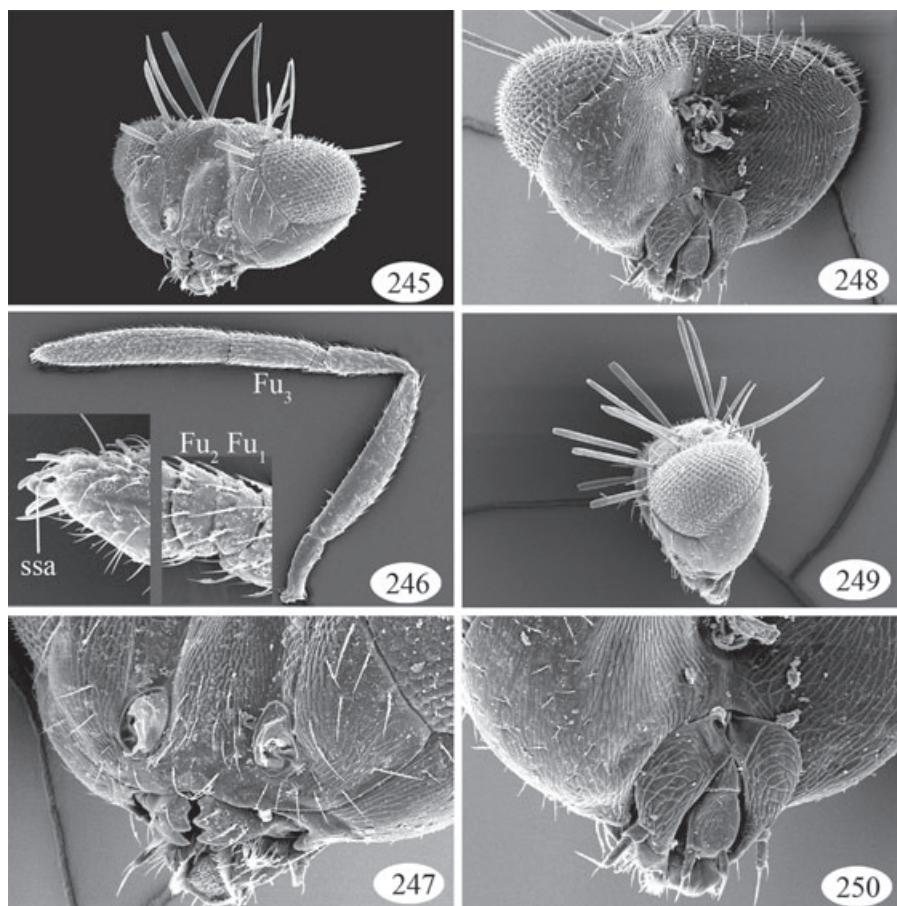
**Figs 238–244.** *Paraphytis* sp. 5 (female): 238, head (posterior); 239, pronotum (dorsolateral); 240, cercal bristles (lateral); 241, mesosoma (lateral); 242, prosternum (ventral); 243, propodeum and propodeal setae (lateral); 244, metasoma (lateral).

**Diagnosis.** The genus can be recognised in the key couplet 23 of Hayat (1983) and by the following characters. The combination of characters of the ventrally expanded scape, nonadvanced axillae (in line with anterior margin of scutellum) and swollen mesopleuron exclude all other genera of Aphelininae except closely related genera, such as *Eutrichosomella*, *Mashimaro* and *Samariola*. Absence of epicoxal pads separates this genus from *Eutrichosomella* and *Mashimaro*, with an exception of *Samariola*. *Samariola* is distinct by having a sparse delta area of the forewing (Fig. 54). The structure of the mesofurca of *Saengella* is unique for Aphelininae, with the anterior mesofurcal process long and extended forward without a flange (Fig. 16).

**Description.** Body brown, sometimes mesosoma yellowish white. Scape of antenna brown, sometimes with a white crossing band, funicular segments brown, antennal clava entirely white or apical 3/4 white. Mesosoma brown or yellow, metasoma brown dorsally, sometimes ventrally white. Forewing with brown markings under a marginal vein, forming a broad crossing band. **Head.** Head round. Mandible with two teeth. Antennal torulus located below lower margin of eyes. Each side of face smoothly round. Posterior margin of head smoothly

round. Transoccipital suture present. **Antenna.** Six-segmented (1131) (Fig. 50). Scape with ventrally expansion  $1.9\times$  as long as wide, anellus absent,  $Fu_1$  and  $Fu_2$  wider than long,  $Fu_3$  longer than wide, clava  $2.8\times$  as long as wide. **Mesosoma.** Pronotum medially divided. Axilla not advanced in line with anterior margin of scutellum,  $0.47\times$  as wide as anterior margin of scutellum; axilla with one seta. Scutellum oval, posterior margin of scutellum rounded (Figs 13, 55). Scutellum with two pairs of setae; anterior pair medial to posterior pair. Scutella sensilla with one seta. Mesopleuron swollen. Ventral prepectus narrowly connected and separated from mesepisternum. Posterior end of metanotum transverse. Callus and area around spiracle of propodeum with two lateral setae (Fig. 13). Propodeum  $0.8\times$  as long as metanotum. **Wings.** Forewing with linea calva and well-defined delta area (Fig. 51). Mesofurca with long interfurcal process projecting forward on both sides of furcal arm (Fig. 16); lateral arm orientated backward, therefore the entire mesofurca structure H-shaped. **Metasoma.** Cercal plate with bristles  $2 + 2$ . Hypopygium prominent reaching cercal plate. Ovipositor  $1.1\times$  as long as midtibia.

**Phylogenetic affinities.** *Saengella* was first discussed as ‘Genus A’ by Hayat (1983) in his generic key of the



**Figs 245–250.** *Punkaphytis hayati* n.sp. (female): 245, head (anterior); 246, antenna 247, face (anterior); 248, head (posterior); 249, head (lateral); 250, mouthparts (posterior).

world. With his permission, this new genus based on the same specimens is described. *Saengella* are close to *Mashimaro* + *Samariola* based on four synapomorphic characters including two unambiguous characters: clava less than  $2.5\times$  as long as wide (5:2), propodeum less than  $1.3\times$  as long as metanotum (25:0/1), parastigma of forewing with one sensilla (43:1) and delta of forewing well defined or mostly bare (47:1/3). In the unpublished combined analysis, different sets of characters supported a sister group relationship between *Saengella* and *Mashimaro* + *Samariola*. The characters are as follows: setae on midlobe of mesoscutum 12–24 (21:1), propodeum less than  $0.8\times$  as long as metanotum (25:0), absence of a flange of anterior interfurcal process of mesofurca (39:2), marginal vein less than  $1.07\times$  as long as costal cell (42:0), and hypopygium prominent reaching cercal plate (48:1). The absence of a flange on the anterior interfurcal process of mesofurca was previously only reported for Azotinae (Heraty *et al.*, 1997), but now two more genera lack the flange (Figs 16, 18); therefore, the polarity of the character is uncertain within Aphelininae.

*Distribution.* Indo-Pacific: Brunei.

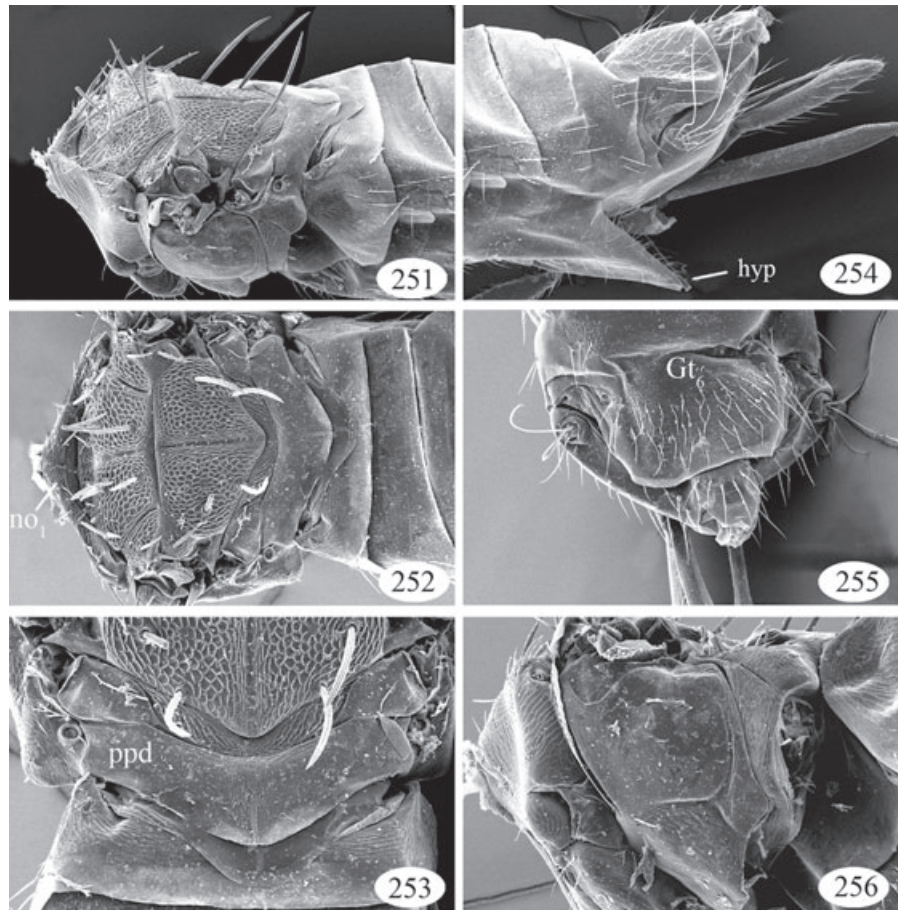
*Host.* Unknown.

*Discussion.* This genus is currently based on only a single specimen. The diversity of this genus needs further investigation. Two more specimens were identified as ‘Genus A’ by Hayat (A. Polaszek, personal communication); however, only one of three specimens designated as ‘Genus A’ could be used to make a slide preparation. It is not clear if the other two species belong to this same genus, *Saengella*. The two additional specimens appear to have a similarly shaped scutellum (posterior margin rounded) and nonadvanced axillae with similar transscutal articulation (tsa). However, one unidentified specimen has a smaller axilla than the others. The H-shaped mesofurca is unique among aphelinids; therefore examination of internal structure will help to determine if all three indeed belong to one genus.

#### *Saengella gloria* new species

(Figs 13, 16, 50–55)

*Diagnosis.* Recognised by the entirely brown body except the following white structures; clava, some parts of legs



**Figs 251–256.** *Punkaphytis hayati* n.sp. (female): 251, mesosoma (dorsolateral); 252, mesosoma (dorsal); 253, propodeum (dorsal); 254, metasoma (lateral); 255,  $Gt_{6-7}$  (dorsal); 256, mesosoma (ventrolateral).

and anterior ventral metasoma. Scape is brown with a white transverse band starting medial dorsal margin and ending apical a fourth of ventral margin (Fig. 50). Forewing has a clear cross band starting at the apex of stigma (Fig. 51). Forewing has a broad brown band under marginal vein and distal 1/5 of forewing lighter brown (Fig. 51).

**Description.** *Female* (holotype). Length, 1.0 mm. Body brown with the following parts white; posterior lateral lobe of propodeum and anterior ventral metasoma. Vertex of head and face brown. Antennal scape brown with white apical dorsal margin and diagonal medial strip (Fig. 50),  $Fu_{1-3}$  brown, antennal clava brown. Mesosoma brown with posterior lateral lobe of propodeum white. Forewing clear with a broad brown band (Fig. 51). Legs brown with the following parts white to light brown; ventral middle 1/3 of pro-, meso- and metafemur, proximal base of meso- and metatibia, meso- and metatarsus. **Head.** Head width  $2.3\times$  as wide as frontvertex width. **Antenna** (Fig. 50). Scape  $1.9\times$  as long as wide; pedicle  $2.2\times$  as long as wide; pedicel  $0.7\times$  as long as three funicles combined;  $Fu_1$  and  $Fu_2$   $0.6\times$  length of  $Fu_3$ ;  $Fu_1$   $1\times$  as long as  $Fu_2$ ;  $Fu_2$   $0.6\times$  as long as wide;  $Fu_2$   $0.3\times$  as long as  $Fu_3$ ;  $Fu_3$   $1.7\times$

as long as wide; clava one-segmented,  $2.8\times$  as long as wide. **Mesosoma** (Figs 13, 52). Pronotum cellulate with numerous setae. Midlobe of mesoscutum cellulate, with 18 setae; side lobe of mesoscutum with two long and one short setae. Scutellum protruding over metanotum (Fig. 13). Metanotum with cellulate sculpture in middle, abruptly ended with a suture. Propodeum  $0.8\times$  as long as metanotum; propodeum with two setae near spiracle. **Wings** (Fig. 51). Forewing  $2.3\times$  as long as broad; submarginal vein with two setae; costal cell with 21 setae (16 thin setae and five thick setae); marginal vein  $0.8\times$  length of costal cell. Hind wing  $3.5\times$  as long as broad, marginal fringe  $0.2\times$  as long as hind wing width.

**Legs.** Mesotibial spur  $0.7\times$  length of basitarsus. Metatibia  $1.1\times$  as long as mesotibia. **Metasoma.** Petiole and gaster  $1.1\times$  longer than mesosoma. Ovipositor  $1.1\times$  as long as mesotibia. Second valvifer  $2.3\times$  as long as third valvula.

**Male.** Unknown.

**Type material.** Holotype female. Brunei: Ulu, Temburong, 300 m, ii–iii.1982, M. Day, deposited in BMNH (slide).



*Distribution.* Known only from type locality.

***Paraphytis* Compere nom.rev.**

(Figs 14, 17, 38–43, 238–244)

*Paraphytis* Compere, 1925, 129. Type species: *Paraphytis vittata* Compere. Monotypy.

Synonymy under *Marietta* by Compere, 1936, 311; under *Aphytis* by Rosen and DeBach, 1976: 541.

*Syediella* Shafee, 1970: 144. Type species: *Syediella maculata* Shafee. Original designation. Synonymy under *Aphytis* by Hayat, 1982: 169.

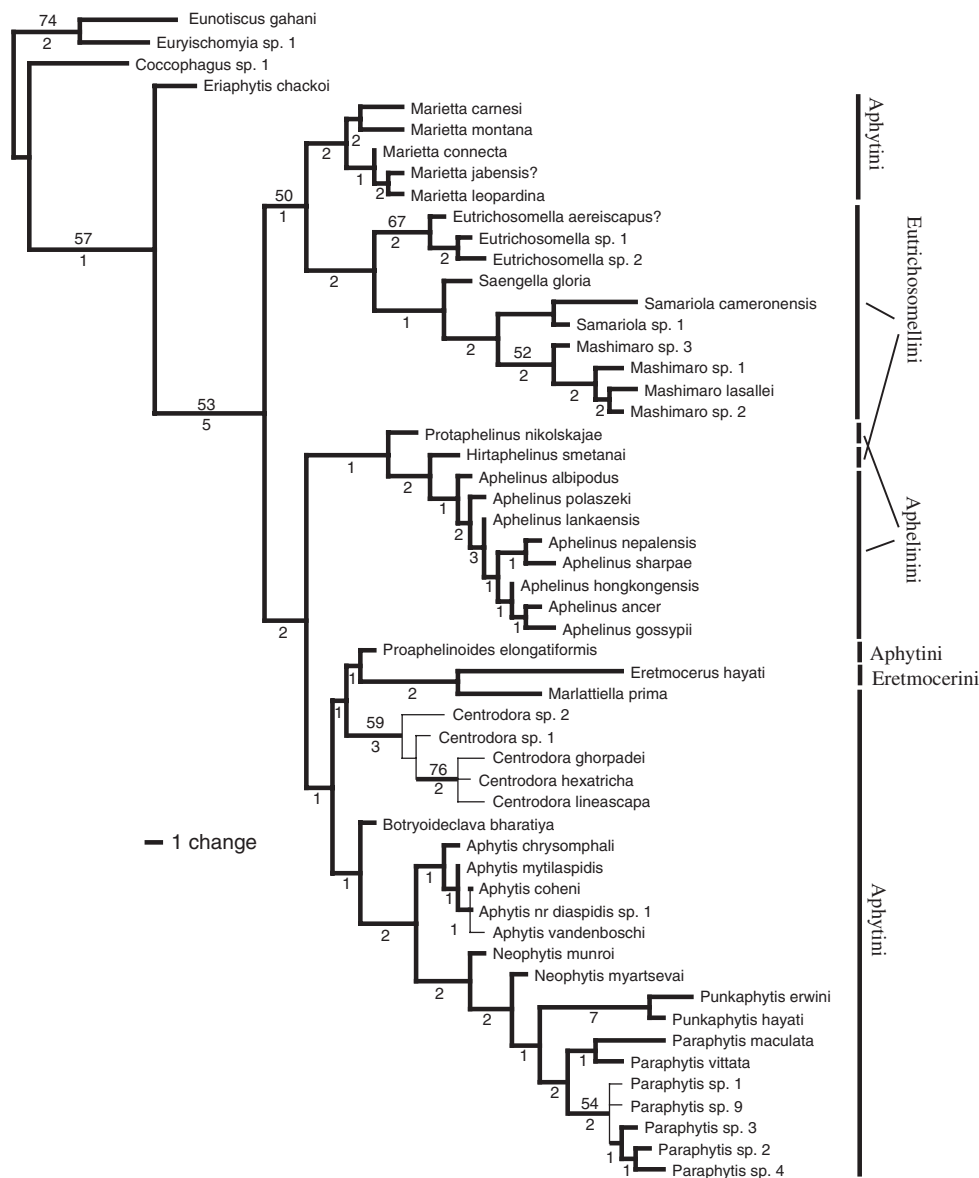
*Diagnosis.* General characters of *Paraphytis* (the *vittatus* species group of *Aphytis*), including body and wing colouration, were summarised by Rosen & DeBach (1979). *Paraphytis* can be separated from other genera, based on the ventral prepectus medially separated from mesepisternum and absence of specialised sensilla on clava. *Paraphytis* has long vertical length of genal bridge (10:1, Fig. 238), which is different from *Aphytis* (10:2, Fig. 157). *Aphytis* s. s. has modified seta near the propodeal spiracle (Fig. 164); however, *Paraphytis* has a simplified seta (Fig. 243) in the area.

*Paraphytis* is *Marietta*-like, having distinctly mottled forewings and usually heavily pigmented mesosoma (Fig. 39), metasoma and legs. However, *Paraphytis* has a strong constriction between the antennal clava and  $Fu_3$  (Fig. 40) and the forewing mottling pattern is formed by dark setae. By contrast, *Marietta* has a less constricted connection of clava and  $Fu_3$  (Fig. 200) and mottled forewing formed by darkened areas of wing cuticle. *Paraphytis* may have similar body colouration as *Punkaphytis*; however, *Punkaphytis* are distinct in having long and flattened setae on the head and mesosoma (Figs 9, 12, 245, 251) and a prominent hypopygium (Fig. 254).

*Description.* Body yellow to orange usually with dark crossing bands. Scape yellow to orange, funicular segments of antenna orange or brown, antennal clava yellow to white, sometimes apex with black mark (Figs 38, 40) or clava entirely black; mesosoma dorsally bright orange with or without longitudinal dark bands, metasoma yellow to brown, usually gastral tergum with dark bands, or at least laterally brown markings; forewing mottled by dark setae, sometimes only with dark spot under stigma. *Head.* Head round in frontal view. Vertex roundly curved. Mandible with two teeth with or without truncation. Antennal torulus near clypeus, distinctly lower than lower eye margin. Each side of face round. Posterior margin of head round. Posterior aspect of head with transoccipital suture (Fig. 238, tos). *Antenna.* Antenna six-segmented (1131) (Fig. 40), rarely five-segmented (Fig. 38), or first two funicular segments ring-shaped (Fig. 42). Scape usually 5–6× as long as wide, sometimes 2.8× as long as wide (Fig. 42); anellus absent;  $Fu_1$  triangular or anelli-form,

usually 1–2× as wide as long;  $Fu_2$  2.2–2.6× as wide as long; clava usually 3–4× as long as wide, sometimes 6.3× as long as wide (Fig. 42). *Mesosoma.* Pronotum medially divided or not (Fig. 239). Axillae slightly but distinctly advanced, axillar width 1.8–2.1× as wide as anterior margin of scutellum; axilla with one seta. Scutellum hexagonal (posterior end of scutellum counted as one sided in contrast to the heptagonal scutellum of *Punkaphytis* as in Fig. 252). Scutellum with two pairs of setae; anterior scutellar seta farther apart than posterior ones (Figs 39, 41, 43). Scutellar sensilla between two pairs of scutellar setae. Mesopleuron swollen (Fig. 241). Ventral prepectus narrowly connected laterally (Fig. 242) and separated completely from mesepisternum medially. Posterior margin of metanotum transverse. Propodeum with crenulae at posterior end, but crenulae shape and structure variable (e.g. medially protruding propodeum slightly bilobed with crenulae on each side, fig. 301 in Rosen & DeBach, 1979; median protrusion rectangular with indistinct crenulae, fig. 404 in Rosen & DeBach, 1979; median protrusion triangular with elongated crenulae on each side, fig. 334 in Rosen & DeBach, 1979); median sculpture cellulate but otherwise smooth. Callus and around spiracle of propodeum with one thick and one simple setae (Fig. 243). Propodeum 2.0–3.6× as long as metanotum. *Wings.* Forewing with a linea calva and delta area sometimes with different setae forming a marking; forewing usually with mottled markings (Figs 268, 291, 303, 316 in Rosen & DeBach, 1979). Mesofurca with laterally oriented mesofurcal lateral arm (Figs 14, 17), anterior interfurcal process with or without flange. *Metasoma.* Cercal plates with bristles of 3 + 1 (Fig. 240) or 2 + 2 or 2 + 1. Cercal plate positioned anteriorly (Fig. 244). Hypopygium not prominent (Fig. 244). Ovipositor 1.6–2.4× as long as mesotibia.

*Phylogenetic affinities.* This *Marietta*-looking group of species was suggested as a distinct species group in *Aphytis* (DeBach & Rosen, 1976; Rosen & DeBach, 1979). Females usually have mottled wings and patterned body and legs (figs 268, 303, 322 in Rosen & DeBach, 1979). Rosen and DeBach proposed that the long propodeum and crenulae at the posterior end of the propodeum were reliable characters separating *Aphytis* (including the *vittatus* species group, VSG) from *Marietta* and other related genera. Hayat (1994) further suggested that a medially membranous pronotum would be a useful character for separating *Aphytis* from *Marietta*. Rosen & DeBach (1979) proposed six species groups of *Aphytis* based on pattern of forewings and body colour, commenting that the VSG may be polyphyletic. Nevertheless, based on morphology (Figs 257) and unpublished combined molecular analysis, the VSG (labelled as *Paraphytis* in the analyses) was supported as monophyletic. However, in the combined analysis, *Paraphytis* were placed in the Eutrichosomellini and distantly related to *Aphytis* s.s.; therefore, species of the VSG were transferred from *Aphytis* to *Paraphytis*, except for two species described as a new genus, *Neophytis*. Previously 18 species and 6 related species were recorded in the *vittatus* species group (= *Paraphytis*) (Rosen & DeBach, 1979). Currently, there



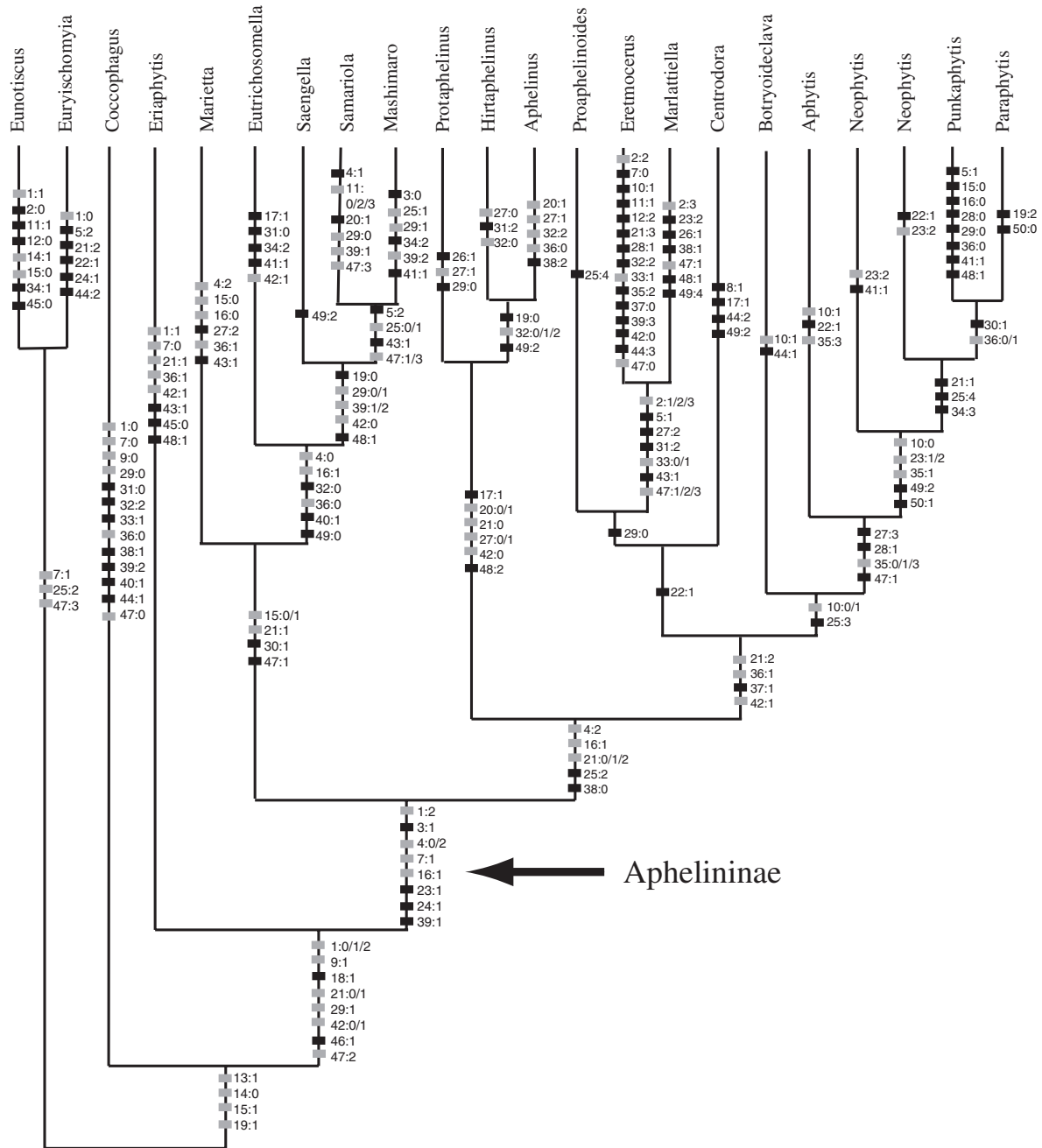
**Fig. 257.** One of three most parsimonious trees from morphology analysis; thin branches collapse in consensus tree. Length 253, CI 0.34, RI 0.71. Bootstrap values greater than 50% are shown on the above branches and decay indices below branches.

are 23 species and 5 related species described (Shafee, 1970; Fabres, 1978; Huang, 1994). In the morphological study and unpublished combined analysis, *Paraphytis* (Fig. 258) were supported by two unambiguous characters: ventral prepectus medially separated from mesepisternum (19:2, Fig. 242) and absence of specialised sensilla on clava (50:0). *Punkaphytis* and *Paraphytis* both have a swollen mesopleuron (30:1), which is also shared among genera of *Eutrichosomella* clade (Fig. 258). The sister group relationships of *Paraphytis* and *Punkaphytis* were supported in the unpublished combined analysis based on a single character of 2 + 2 cercal bristles (49:2), which is likely unreliable because it is variable within the genus.

*Distribution.* Australian: Australia, New Caledonia. Oriental: China, India. Neotropical: Argentina, Brazil, Ecuador, Haiti.

*Host.* Diaspididae.

*Discussion.* *Paraphytis* are usually easy to recognise based on mottled forewing and body colour with a combination of long propodeum and presence of crenulae. When assigning a species group, authors describing a species can confidently place it in the *vittatus* species group, unlike *Aphytis stepanovi* and *A. landii*, which are considered as intermediates of the *Mytilaspidis* and the *Chrysomphali* species group. Many of



**Fig. 258.** Characters mapped on one of three most parsimonious trees from morphology analysis. Multiple terminal taxa represented only by generic names. Length 253, CI 0.34, RI 0.71. Unambiguous character state changes black, while ambiguous state changes gray. Characters mapped on tree using MacClade v4.05 with ACCTRAN character optimisation.

the species in the *vittatus* species group can be verified for species group placement based on literature and figures. The characteristics of *Paraphytis* including dozens of undescribed species are extremely diverse. Though the genus was well supported as monophyletic by morphology (Fig. 257) and in the unpublished combined analysis, a major revision of *Paraphytis* is necessary to define the boundaries of its morphological diversity.

**Species list of *Paraphytis***

(\*for types examined by JWK)

1. *Paraphytis acutaspidis* (Rosen & DeBach)\* **new combination**  
*Aphytis acutaspidis* Rosen & DeBach, 1979: 248. Type depository: UCRC. Distribution: Neotropical: Brazil.

2. *Paraphytis angusta* (Compere) **new combination**  
*Aphytis angustus* Compere, 1955, 286. Type depository: USNM. Distribution: Oriental: China.
3. *Paraphytis anomala* (Compere) **new combination**  
*Aphytis anomalus* Compere, 1955, 286. Type depository: UCRC. Distribution: Neotropical: Brazil.
4. *Paraphytis argenticorpa* (Rosen & DeBach) **new combination**  
*Aphytis argenticorpus* Rosen & DeBach, 1979: 257. Type depository: QM. Distribution: Australian: Queensland.
5. *Paraphytis australiensis* (DeBach & Rosen) **new combination**  
*Aphytis australiensis* DeBach & Rosen, 1976: 542. Type depository: UCRC. Distribution: Australian: Australia.
6. *Paraphytis benassyi* (Fabres) **new combination**  
*Aphytis benassyi* Fabres, 1978: 164–167. Type depository: Muséum National d'Histoire Naturelle de Paris. Distribution: Indo-Pacific: Solomon Islands.
7. *Paraphytis breviclavata* (Huang) **new combination**  
*Aphytis breviclavatus* Huang, 1994: 51–53. Type depository: Fujian Agricultural University, Fujian, China. Distribution: Oriental: China.
8. *Paraphytis capillata* (Howard) **new combination**  
*Perrissopterus capillatus* Howard, 1907, 87. Type depository: USNM. Distribution: Australian: Australia.  
*Aphytis capillatus* (Howard): DeBach and Rosen, 1976: 542.
9. *Paraphytis ciliata* (Dodd) **new combination**  
*Aphelinus ciliatus* Dodd, 1917, 353. Type depository: QM. Distribution: Australian: Australia.  
*Marietta ciliatus* (Dodd): Compere, 1936, 307, 311.  
*Aphytis ciliatus* (Dodd): DeBach and Rosen, 1976: 542.
10. *Paraphytis cochereaui* (DeBach & Rosen) **new combination**  
*Aphytis cochereaui* DeBach & Rosen, 1976: 541–542. Type depository: UCRC. Distribution: Australian: New Caledonia.
11. *Paraphytis costalimai* (Gomes) **new combination**  
*Marietta costalimai* Gomes, 1942, 23–25. Type depository: Escola Nacional de Agronomia and the Divisão de Defesa Sanitária Vegetal, Rio de Janeiro. Distribution: Neotropical: Brazil.  
*Aphytis costalimai* (Gomes): DeBach, 1963, 35–38.
12. *Paraphytis densiciliata* (Huang) **new combination**  
*Aphytis densiciliatus* Huang, 1994: 49–51. Type depository: Fujian Agricultural University, Fujian, China. Distribution: Oriental: China.
13. *Paraphytis fabresi* (DeBach & Rosen) **new combination**  
*Aphytis fabresi* DeBach & Rosen, 1976: 542. Type depository: UCRC. Distribution: Australian: New Caledonia.
14. *Paraphytis haywardi* (De Santis) **new combination**  
*Marietta haywardi* De Santis, 1948, 146–149. Type depository: Instituto de Patologia Vegetal, I.N.T.A., Castelar, Buenos Aires, Argentina. Distribution: Neotropical: Argentina.  
*Aphytis haywardi* (De Santis): DeBach and Rosen, 1976: 541.
15. *Paraphytis hyalinipennis* (Rosen & DeBach) **new combination**  
*Aphytis hyalinipennis* Rosen & DeBach, 1979: 285–287. Type depository: UCRC. Distribution: Australian: New Caledonia.
16. *Paraphytis maculatipennis* (Dozier)\* **new combination**  
*Marietta maculatipennis* Dozier, 1933, 88–89. Type depository: USNM. Distribution: Neotropical: Haiti.  
*Aphytis maculatipennis* (Dozier): Rosen and DeBach, 1979: 241–244.
17. *Paraphytis maculata* (Shafee)\* **new combination**  
*Syediella maculata* Shafee, 1970. Type depository: ZDAMU. Distribution: Oriental: India.  
*Aphytis malayensis* Rosen and DeBach, 1979: 295.  
*Aphytis maculatus* (Shafee): Hayat, 1982: 169–170.
18. *Paraphytis mandalayensis* Rosen & DeBach **new combination**  
*Aphytis mandalayensis* Rosen & DeBach, 1979: 296–299. Type depository: UCRC. Distribution: Indo-Pacific: Burma.
19. *Paraphytis nigripes* (Compere)\* **new combination**  
*Marietta nigripes* Compere, 1936, 312. Type depository: USNM. Distribution: Australian: Australia.  
*Aphytis nigripes* (Compere): DeBach and Rosen, 1976: 542.
20. *Paraphytis noumeaensis* (Howard)\* **new combination**  
*Perrissopterus noumeaensis* Howard, 1907, 87. Type depository: USNM. Distribution: Australian: New Caledonia.  
*Marietta noumeaensis* (Howard): Compere, 1936, 312.  
*Aphytis noumeaensis* (Howard): DeBach and Rosen, 1976: 541.
21. *Paraphytis obscura* (DeBach & Rosen) **new combination**  
*Aphytis obscurus* DeBach & Rosen, 1976: 541. Type depository: UCRC. Distribution: Neotropical: Argentina.
22. *Paraphytis peculiaris* (Girault) **new combination**  
*Marietta peculiaris* Girault, 1932, 2. Type depository: Department of Agriculture, South Perth, Western Australia. Distribution: Oriental: China.  
*Aphytis peculiaris* (Girault): Rosen and DeBach, 1979: 238–241.
23. *Paraphytis perplexa* (Rosen & DeBach)\* **new combination**  
*Aphytis perplexus* Rosen & DeBach, 1979: 249. Type depository: UCRC. Distribution: Neotropical: Brazil.
24. *Paraphytis transversa* (Huang) **new combination**  
*Aphytis transversus* Huang, 1994: 53–55. Type depository: Fujian Agricultural University, Fujian, China. Distribution: Oriental: China.
25. *Paraphytis vittata* (Compere) **revised status**  
*Paraphytis vittata* Compere, 1925, 129–133. Type depository: USNM. Distribution: Oriental: China.  
*Marietta vittata* (Compere): Compere, 1936, 311.  
*Aphytis vittatus* (Compere): DeBach and Rosen, 1976: 541.

26. *Paraphytis wallumbillae* (Girault) **new combination**  
*Aphelinus wallumbillae* Girault, 1924, 4. Type depository: QM. Distribution: Australian: Australia.  
*Aphytis wollumbillae* (Girault): Mercet, 1932, 355.

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