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Multifemale nests and social behavior in *Euglossa melanotricha* (Hymenoptera, Apidae, Euglossini)

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Abstract

The nesting biology and social behavior of the euglossine bee species *Euglossa melanotricha* was analyzed based on the monitoring of eight nests found in man-made cavities and transferred to observation boxes. *Euglossa melanotricha* females usually construct their nests in cavities in the ground, in buildings, or in mounds. In this study, we present new data on the nesting biology of *E. melanotricha*. The process of reactivation of nests was commonly observed with one to three females participating in the reactivation. The duration of the process of reactivation ranged from 10 to 78 days (n = 31) and were longer during the rainy season. Time spent (in days) for provisioning, oviposition and closing a single cell was higher in reactivations that occurred during the dry period.151 emergences were observed (39 males and 112 females). 90 (80.3%) of the emerged females returned to the natal nest, but only 35 (38.9%) remained and actively participated in the construction and provisioning of cells. The other 55 abandoned the nests after several days without performing any work in the nest. Matrifilial nest structure was regulated by dominance-subordinate aggressive behavior among females, where the dominant female laid almost all eggs. Task allocation was recognized by behavioral characteristics, namely, agonism and oophagy in cells oviposited by other females. *Euglossa melanotricha* is multivoltine and its nesting is asynchronous with respect to season. Our observations suggest a primitively eusocial organization. These observations of *E. melanotricha* provide valuable information for comparison with other species of *Euglossa* in an evolutionary context.

Keywords

Orchid bees, nest structure, nesting behavior

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Introduction

The bees of the tribe Euglossini are the only members of the corbiculate bees that do not form large colonies with a typical queen and worker caste (Soucy et al. 2003). The genus *Euglossa* consists of 129 known species (Nemésio and Rasmussen 2011). These include solitary, communal and social species (Dressler 1982, Young 1985, Roberts and Dodson 1967, Garófalo et al. 1998, Soucy et al. 2003, Otero et al. 2008). The latter include those that form multi-female nests with a division of labor and overlapping generations (Garófalo 1985, Ramírez-Arriaga et al. 1996, Augusto and Garófalo 2004, 2010, Cocom Pech et al. 2008).

A diversity of nesting behavior is observed in the different species of *Euglossa*. Some species construct aerial nests (Roubik and Hanson 2004, Capaldi et al. 2007), while others exploit existing cavities found in both natural substrates, such as the soil (Bodkin 1918, Augusto and Garófalo 2007), termite mounds (Sakagami et al. 1967), bamboo stems (Garófalo et al. 1993), orchid roots (Roberts and Dodson 1967), and abandoned bees nests (Garófalo 1985, 1992), and man-made structures, including walls (Janvier 1955), bait boxes (Vázquez and Aguiar 1990), and abandoned hydraulic installations (Gonzales and Gaiani 1990).

Observations of the intranidal behavior of *Euglossa carolina* females (cited as *E. cordata*) during nest reactivation have clearly demonstrated that the mother or a sister becomes the reproductive female and the other females perform other nest related tasks (Garófalo 1985). This behavior is characterized by two components: reproductive, with the dominant female replacing subordinate's eggs (daughters' or younger sisters' eggs) with her own, and behavioral, with the dominant exhibiting agonistic behavior towards the subordinate. In addition, the dominant female rarely leaves the nest and becomes the main guard bee, while the subordinate females assume the tasks of collecting resin, constructing or reusing cells, and provisioning and ovipositing in them (Garófalo 1985, Augusto and Garófalo 2010).

Similar social organization have been reported by Ramírez-Arriaga et al. (1996) for *Euglossa atroveneta*, Augusto and Garófalo (2009) for *E. fimbriata* and Cocom Pech et al. (2008) for *E. viridissima*. In contrast, in multifemale colonies of *E. townsendi*, all females are reproductively active. Behavioral interactions of dominance and subordination are lacking in this species and all the females were classified as either egg-laying or as forager/egg-laying. In this species reproductive dominance is displayed by an egg-laying female that, after oophagy, replaces the forager/egg layer's eggs with her own. When more than one egg-laying female participates in a reactivation, multiple egg replacements in the same cell may occur (Augusto and Garófalo 2004).

Euglossa melanotricha Moure, 1967 is a medium-sized bee (body length 13 mm) commonly found in open areas of savanna habitat in Brazil and Bolivia. The species is abundant in the Serra do Espinhaço mountain range in the Brazilian states of Minas Gerais and Bahia, but is rare or absent in areas of low altitude or dense forest (Nemésio 2009). Two *E. melanotricha* nests have previously been found in the Brazilian Cerrado (savanna), although the behavior of the females was not monitored. The first was discov-

ered by Sakagami et al. (1967) in an abandoned termite mound. The large number of cells (37) found in the nest, and the fact that two were being provisioned, indicated the reutilization of the site over successive generations. Augusto and Garófalo (2007) found a second nest in a cavity in the ground. Four closed cells and one live female were found in this nest. These observations obviously refer to nests in different phases of development.

This long-term study presents new data on the nesting behavior of *Euglossa melanotricha*, obtained from the monitoring of nests found in man-made cavities at a site in northeastern Brazil.

Material and methods

The present study took place within the urban area of the town of Campo Formoso (10°30'00"S, 40°19'00"W), Bahia, Brazil (MMA 2010) between October, 2008, and October, 2009. The local climate is classified as dry sub-humid tropical, with annual precipitation of 302–1935 mm, and a rainy season between March and August (PERH 2010).

A total of eight *Euglossa melanotricha* nests were found within the study area, including one inside an electrical installation, and seven in the holes in ceramic building blocks. The nests were transferred to wooden boxes (12 × 10 × 8 cm), each with a circular lateral opening of 1 cm in diameter, according to the methodology developed by Garófalo et al. (1993). The wooden boxes were then returned to the original locations of the nests and all females returned to their natal nests following transfer. The number of live females and closed cells per transferred nest varied from one to three females and eight to 22 cells respectively (Table 1). Each box was covered with a glass lid and connected to the exterior by an opening in the wall of blocks. The glass cover was removed for marking of each female on her mesonotum with permanent colored *Opaque Color* pens (a unique mark for each female). When necessary, females were remarked.

The nests were observed under red light between 07:00 h and 18:00 h, with eight hours of observation being conducted three days per week. Nocturnal observations were made once a week between 19:00 and 23:00 h. Quantitative behavioral data were collected using two complementary procedures. All-events records (Altmann 1974) were collected in 460 one-hour sessions, while individual focal samples were conducted at two-minute intervals in 884 one-hour sessions. Overall, 1344 hours of monitoring was conducted over 168 days of data collection.

Nest development was monitored for the collection of data on the following biological and behavioral parameters: (a) cell architecture; (b) nest reactivation and phenology; (c) female foraging behavior; (d) specific aspects of the activity of the females during construction, i.e. reuse of cells, supply, oviposition, cell closure, oophagy, cleaning the nest and the sealing of edges; (e) duration of the period of offspring development; (f) physiological condition of the females (relative fecundity).

Where appropriate, the results were presented as the mean ± standard deviation. The relationship between the number of cells with eggs and the duration of the female activity period was evaluated using Pearson's correlation coefficient, while Mann-

Table 1. Contents of *Euglossa melanotricha* nests collected in the municipality of Campo Formoso, during the period from August to September 2008 (OC- closed cells; UC – open cells; PC –cells being provisioned; F – females live; F † females dead.

Nests	Date of transfer	Contents
N_1	04/08/2008	16 OC; 3 UC; 2 PC; 2 F†; 2 F
N_2	15/08/2008	9 OC; 5 UC; 1 PC; 2 F
N_3	02/09/2008	11 OC; 1 F
N_4	17/09/2008	12 OC; 1 PC; 1 F†; 1 F
N_5	21/09/2008	8 OC; 5 UC; 1 PC; 3 F; 4 F†
N_6	24/09/2008	8 OC; 1 PC; 1 F
N_7	30/09/2008	11 OC; 1 F
N_8	30/09/2008	22 OC; 15 UC; 1 PC; 2 F†; 1 F

Whitney's *U* was used to test differences in the behavior of dominant and subordinate females, and seasonal variation in the duration of behaviors. Analyses were run in the Statistica 7.0 program, with a 5% significance level.

Results

Cell characteristics and arrangement

Cells of *Euglossa melanotricha* were elliptical in shape, with a small apical projection. The cells had a mean height of 11.7±0.71 mm (10.8–14.1 mm, n = 97) and a mean diameter of 7.5±0.21 mm (6.2–7.9 mm, n = 97). Females used resin to construct the cells and seal the nests. The cells were generally aggregated in the same plane on vertical or horizontal substrates, either overlapping or not.

Reactivation and nest phenology

The emergence of 112 females was monitored. Of these, 90 (80.3%) returned to their natal nests, but only 35 (38.9%) remained and actively participated in nest re-use. The other 55 (49.1%) abandoned their natal nests a few days (1–3 days) after their return, without working in the nest. The younger females, more frequently (89.1%, n = 55), abandoned nests days after returning. The great majority (87.1%) of the 31 reactivations observed during the present study involved associations among females.-27 (87.1 %) of these reactivations were performed by more than one female and only four (12.9 %) by one female (Table 2). The reactivation of nests was not synchronized with any specific period of the year. The duration of female activity periods varied from 10 to 78 days (n = 31), and was significantly longer during the rainy season, i.e. between March and August (Table 2: Mann-Whitney, Z = 3.16; $p < 0.008$, n = 31).

Table 2. Number of reactivating females and function assumed in the reactivations occurred in *Euglossa melanotricha* nests, during rainy (March-August) and dry (September-February) seasons.

Nest/ Reactivation	Season		Duration (days)		Number of		
	Rainy	Dry		Associated females	Dominant females	Subordinate Females	Oviposited cells
N_1/R_1	X		54	2	1	1	11
N_1/R_2	X		43	2	1	1	9
N_1/R_3		X	41	2	1	1	13
N_1/R_4		X	28	2	1	1	10
N_1/R_5		X	38	2	1	1	13
N_2/R_1	X		43	2	1	1	9
N_2/R_2	X		52	3	1	2	11
N_2/R_3		X	31	2	1	1	10
N_2/R_4		X	42	1	1	0	13
N_2/R_5		X	22	2	1	1	8
N_3/R_1	X		51	1	1	0	10
N_3/R_2	X		44	2	1	1	9
N_4/R_1	X		53	1	1	0	10
N_4/R_2		X	35	2	1	1	12
N_4/R_3		X	24	2	1	1	8
N_4/R_4		X	37	2	1	1	12
N_4/R_5		X	13	2	1	1	5
N_5/R_1	X		49	2	1	1	10
N_5/R_2	X		10	3	1	2	4
N_5/R_3	X		46	2	1	1	10
N_6/R_1	X		51	1	1	0	10
N_6/R_2	X		23	2	1	1	6
N_6/R_3		X	36	2	1	1	12
N_6/R_4		X	34	2	1	1	11
N_6/R_5		X	26	2	1	1	9
N_7/R_1	X		49	2	1	1	10
N_7/R_2	X		51	2	1	1	11
N_8/R_1	X		78	3	1	2	12
N_8/R_2		X	50	3	1	2	13
N_8/R_3		X	47	3	1	2	12
N_8/R_4		X	38	2	1	1	12

During the intervals between reactivations or during periods of inactivity, the females spent more time inside the nests without engaging in cell construction or provisioning. The number of oviposited cells significantly positively correlated with the duration (in days) of the activity period of the females (Table 2: r = 0.6231; p

< 0.05, n = 31). The time (in days) spent provisioning cells by subordinate females was significantly longer during the dry season (Wet x Dry season: Z = 3.00; p < 0.001, n = 34).

Social structure and female behavior

Foraging behavior: construction or reutilization of cells, provisioning and nectar collection

Subordinate females constructed or reutilized cells using resin deposited in small piles inside the nests. Of the 124 cells which were oviposited in, 92 cells (74.2%) were reutilized, while 32 cells (25.8%) were newly constructed. Females began to collect resin two (n = 39) or three (n = 67) days after emergence, and engaged in this activity throughout the day, but with a higher frequency between 14:00 h and 15:00 h (Fig. 1: n = 90). The mean duration of resin-collection trips was 34.3±6.87 min (range: 22–48 min; n = 96).

Females began to collect and to store food for the larvae four (n = 61) or five days (n = 65) after emergence. The mean duration of food-gathering excursions was 54.4±11.60 min (range: 33–81 min, n = 63), while food storage took 35.1±12.65 s (13–73s, n = 51). Food was gathered primarily in the morning, between 09:00 h and 11:00 h (Fig. 1: n = 99). It took between three and six days for a cell to be provisioned (n = 152).

Females would occasionally return to the nest with neither food nor resin. These excursions were possibly for nectar collection and lasted 27.1±3.58 min (range: 7–68 minutes, n = 78) for dominant females, and 17.5±8.85 min (7–37 min, n = 37) for subordinates. While these trips occurred throughout the day, they were more frequent during the morning (n = 115), primarily between 07:00 h and 08:00 h (Fig. 1).

Specific aspects of the behavior of the females: oviposition and cell operculation, "nest guarding", cell cleaning, hole sealing and oophagy

Subordinate females prepared cells for oviposition by building the collar. Construction of the collar took 28.0±13.44 minutes (range: 11–65 min, n = 97) on average. Once they she had built the collar, a subordinate oviposited in the cell, but a dominant female almost always subsequently substituted her egg for that of the subordinate. The duration of bouts of this activity differed significantly (Z = 8.86; p <0.0001, n = 77) between subordinate (120.8±23.48 s, range: 68–155 s, n = 56) and dominant females (88.1±16.70 s, range: 61–125 s, n = 56). Oviposition (n = 97) took place between 09:00 h and 17:00 h, but was most frequent between 13:00 and 15:00 h (Fig. 2).

The time spent on cell closure also differed significantly between subordinate and dominant females (Z = 6.08; $p < 0.0001$, n = 163). While subordinates averaged 16.3±3.47 min (range: 12–24, n = 96) on this behavior, the mean duration for dominant females was 13.0±1.90 min (range: 10–17, n = 67).

Dominant females spent most of their time inside the nests. This behavior was more frequent (70.4%, n = 366) when the subordinates were foraging The average

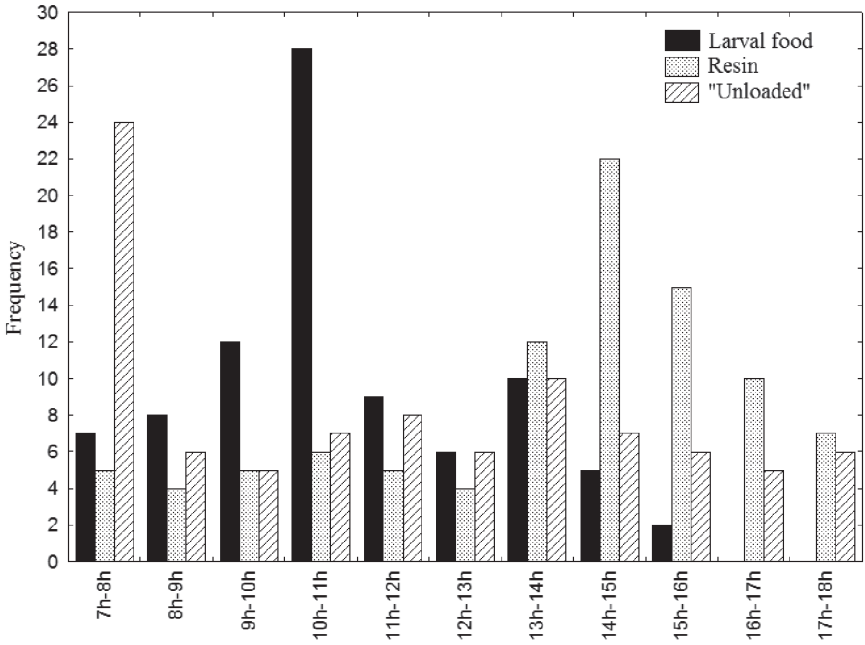

Figure 1. Frequency of excursion from the nest by subordinate female *Euglossa melanotricha* according to excursion type (collection of food, resin, or nectar collection "unloaded") and the time of day.

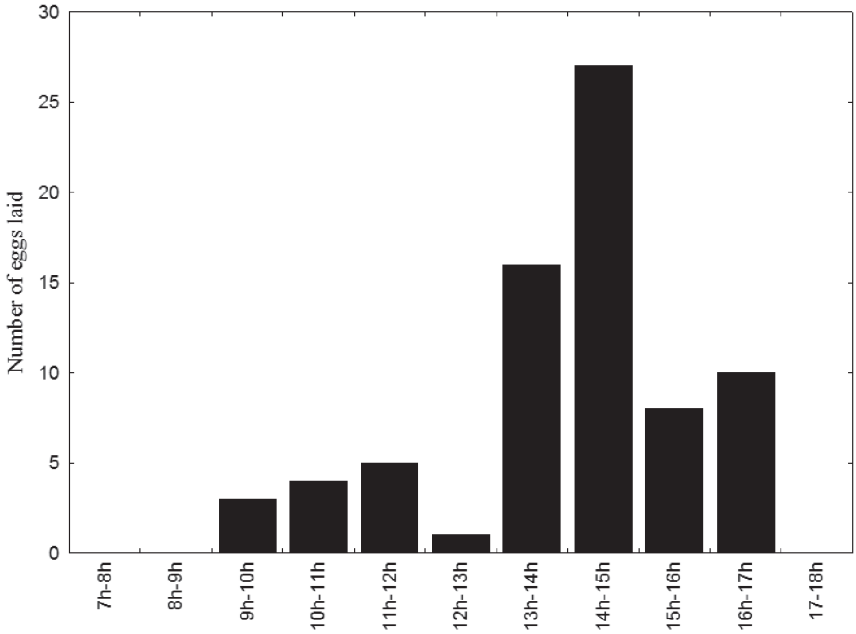

Figure 2. Frequency of oviposition by female *Euglossa melanotricha* (dominant and subordinate) at different times of day.

duration of periods spent by dominant females in the nest guarding position was 13.2±6.13 min (range 6–30, n = 366).

Of the 31 processes reactivations observed, in 14 (45.1%) the dominant females disappeared, died or ceased ovipositing and were replaced by another female. In all cases, the substitute was another female that had emerged in the nest.

Following the emergence of a female and before the reutilization of a cell, the subordinate females cleaned the cell by removing the silk and pieces of the cell closure. This detritus was deposited on the bottom of the box. The mean duration of this behavior was 12.0±5.35 min (range: 2–27, n = 306).

The mean duration of resin work bouts was 10.3±5.0 min (range: 2–29, n = 256) for subordinates, and 9.6±4.18 min (range: 2.5–19.8, n = 126) for dominant females. This difference was not significant (Z = 1.04; $p > 0.05$).

Dominant females opened the closed cells in which subordinates had oviposited after an interval of between 31 and 240.3 min (i.e., more than four hours) after cell closure. Prior to reopening the cells, the dominant females behaved aggressively towards subordinates by biting and pulling them from the closed cell. Opening a cell took an average of 16.7±2.34 min (range: 12.6–21.68 min, n = 62). Following more than half (61% of 141 observed acts) of the subordinate ovipositions, the dominant female ingested the subordinate's egg. Oophagy took between 96 and 248 s (mean = 158.4±45.65 s, n = 86). Oophagy (86 events) occurred between 10:00h and 18:00h, and was most frequent (n = 61) between 14:00h and 18:00h (Fig. 3).

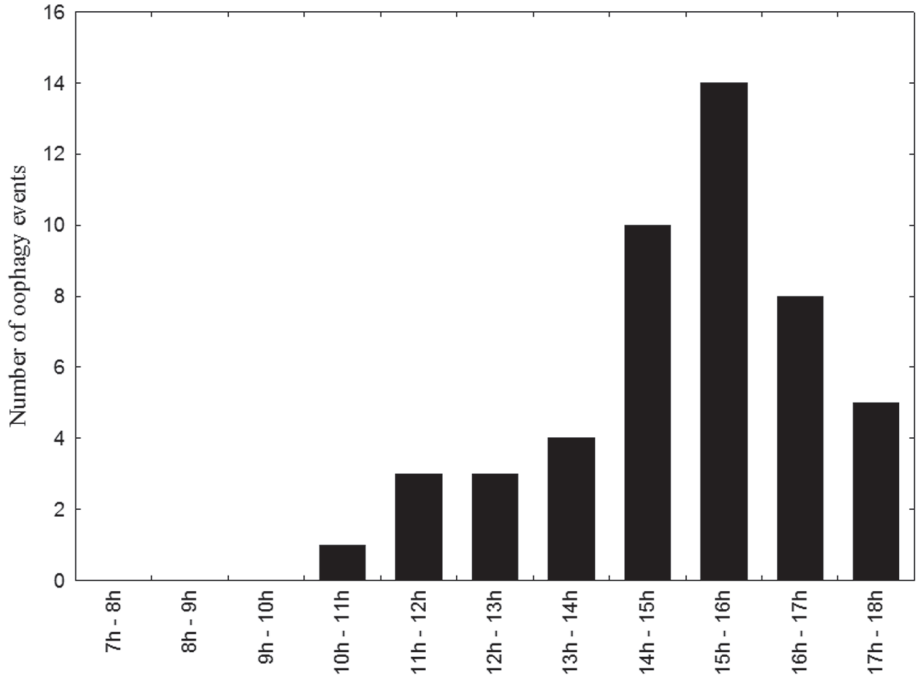

Figure 3. Frequency of oophagy by dominant female *Euglossa melanotricha* at different times of day.

Duration of brood development

The length of brood development was compared between the rainy and dry seasons. The period was significantly longer during the rainy season (rainy season – males: 75.7 ± 3.55 days and females: 82.3 ± 1.92 days; dry season – males: 56.2 ± 0.86 days and females: 61.7 ± 2.44 days; Table 3: Z = 4.21; $p < 0.0001$, n = 26).

Table 3. Duration in days of the development period (egg-adult) of the brood (male and female) of *Euglossa melanotricha* during the dry (September-February) and rainy (March-August) seasons.

	Mean development time (egg-adult) in days during the:			
	Dry season		**Rainy season**	
Nest	**Males**	**Females**	**Males**	**Females**
N_1	55.2	62.3	77.6	79.5
N_2	55.6	59.3	75.4	84.3
N_3	56.1	58.9	-	-
N_4	57.3	63.8	69.8	81.5
N_5	55.8	63.5	-	-
N_6	57.5	58.4	76.4	82.2
N_7	55.4	64.7	-	-
N_8	56.6	62.4	79.1	83.8

Relation between the physiological conditions of the number de females inseminated

The spermathecae of two dominant and three subordinate females were dissected for the analysis of possible differences related to social rank. The analysis revealed long ovarioles with mature or maturing oocytes and all females were inseminated.

Discussion

Cell characteristics and arrangement

The exploitation of pre-existing cavities for the construction of nests observed in *Euglossa melanotricha* is a behavior typical of most *Euglossa* species (Garófalo 1985, Augusto and Garófalo 2004, 2009, 2010), with the exception of those that construct aerial nests, such as *E. hyacinthina*, *E. championi* (Eberhard 1988), *E. turbinifex* (Dressler 1982, Young 1985), and *E. dodsoni* (Riveros et al. 2009).

Reactivation and nest phenology

The replacement of the dominant female by a subordinate female is consistent with the hypothesis of an age-based dominance hierarchy, as occurs in other primitively eusocial bee species (Michener et al. 1971, Kumar 1975, Eickwort 1986, Yanega 1989, Schwarz and O'Keefe 1991, Schwarz and Woods 1994, Arneson and Wcislo 2003, Augusto and Garófalo 2009, 2010).

The reactivation and abandoning of nests by *Euglossa melanotricha* followed an asynchronous pattern, which suggests a lack of any systematic relationship with environmental factors. An important aspect of this asynchrony in tropical bees and wasps is the continuous presence of males in the population. This allows the mating of potentially reproductive females throughout the year (Hunt 1999).

Larval provisioning requires large expenditures of time and energy for *E. melanotricha.* Besides high costs in time and energy, this amount of time away from the nest could increase the risk of brood parasitization or removal of pollen provisions by scavengers. The presence of parasites *Anthrax* spp. (Family Bombyliidae) and *Hoplostelis bivittata* (Megachilidae, Anthidiini) was observed only in nests with a single female in *Euglossa viridissima* (Cocom Pech et al. 2008). An adaptive benefit of multifemale nests may be protection against parasites (Roubik 1990). Further quantitative study may bring to light some of the mechanisms and risks of parasitization, and its potential role in the evolution of nesting behavior.

Social structure and female behavior

Specific aspects of the behavior of the females: oviposition, cell closure, "nest guarding", cell cleaning, hole sealing and oophagy

In associations of *Euglossa carolina*, it has been observed that the oldest female assumes nest dominance (Garófalo 1985). Age and order of eclosion have been reported as determinant factors for task allocation in some species of primitively eusocial bees and wasps (Kumar 1975, Eickwort 1986, Yanega 1989, Schwarz and O'Keefe 1991, Schwarz and Woods 1994, Tsuji and Tsuji 2005), as in some *Euglossa* species.

The high rates of return (80%) and effective reactivation (39%) recorded in *Euglossa melanotricha* were similar to those recorded in *E. cordata, E. townsendi*, and *E. fimbriata* (Garófalo 1985, Augusto and Garófalo 2004, 2009). In three-quarters of the reactivations, associations among females were observed, involving the overlap of generations and interactions of dominance and subordination. The dominant females engage in oophagy, oviposition and closure of the cells provisioned and oviposited in by subordinate females.

Because all nest-mates have developed ovaries, have mated, and do not differ in size, dominant and subordinate females are recognized by their behavioral characteristics. Dominant females exhibited agonistic behaviors towards subordinates and the intensities of these aggressive behaviors where the dominant female had already participated in a reactivation process.

The agonistic interactions observed in *Euglossa melanotricha* can be compared to the behavior of some groups of halictine bees (see Arneson and Wcislo 2003), in which all females are totipotent, as are the females of *Euglossa*, and the differentiation of dominance–subordination relationships is based on behavioral interactions among adults.

Although the agonistic behaviors displayed by dominant females do not prevent oviposition by subordinate females, reproductive dominance, reflected in the monopolization of offspring production, is achieved by the dominant female through the replacement of subordinate female eggs with her own. The monopolization of offspring production leads to the highest reproductive skew, as predicted by the concession-based transactional skew model (Reeve and Keller 1995, 2001), such as that proposed for *Euglossa cordata* and *E. fimbriata* (Augusto and Garófalo 2009). Moreover, permitting oviposition by subordinate females and afterwards performing oophagy would be a prudent selfish strategy by dominant females to avoid group dispersal or lethal fighting among females for nest dominance, and is another prediction of transactional models of reproductive skew (Reeve and Keller 1995, 2001).

If the dominant female of *Euglossa melanotricha* replaces all the eggs laid by subordinates and she mates with only one male, as suggested by Zimmermann et al. (2009) for *Euglossa* species, then a high genetic relatedness between dominant and subordinate females must occur; this favors an optimum reproductive skew, as also predicted by the concession-based transactional skew model (Langer et al. 2004). This condition could help maintain social cohesion in multifemale nests and lead to long-lived colonies through successive reactivation (Augusto and Garófalo 2010), as reported by Garófalo (1987).

In *Euglossa viridissima*, no aggressive behavior was observed by dominant female towards her subordinates when they laid an egg, similar to the findings in *E. townsendi* (Augusto and Garófalo 2004). In contrast, in *E. cordata* (Augusto and Garófalo 1994) the dominant females impose their dominance over reproduction by showing antagonistic (aggressive) behavior towards subordinate females. However, in *E. viridissima* the dominant female showed threatening behavior when the subordinate females tried to touch a cell with her egg, which may be considered physical domination.

Oophagy of some dominant's eggs by subordinates was also observed in *Euglossa viridissima*, however, the dominant cannibalized such eggs and replaced them with her own, confirming her reproductive dominance. The behavior between the dominant and subordinates (associations between mother and daughters) in *E. viridissima* resembles that of a parasitic female that improves her own fitness on detriment of her daughters' reproduction (Stubblefield and Charnov 1986, Garófalo 2006). This seems to be a primitive case of dominant "mother" policing (coercion) on subordinates (her daughters) that may evolve as a result of the mother being twice as related to her offspring as to her daughters offspring (grandoffspring) (Ratnieks and Wenseleers 2007).

The oophagy of subordinate's eggs preceding oviposition by the dominant was also observed in reactivated nests of *Euglossa cordata* (Augusto and Garófalo 1994) and *E. townsendi* (Augusto and Garófalo 2004) but differed from that found in other *Euglossa* species like *E. hyacinthina* where only a communal association was established between non-related females and reproductive division of labor didn't occur (Soucy et al. 2003).

As emphasized by Zimmerman et al. (2009), detailed behavioral observations together with the genetic analysis of brood can help clarify the relationships among all females of an association and the real contribution of each one to the social context of the nest.

Oophagy may have a nutritional function (Crespi 1992), or it may be a reproductive strategy in nests containing more than one reproductive female. This is a characteristic of species with primitively eusocial behavior (Kukuk 1992).

The females of *Euglossa melanotricha* sealed the entrance to the nest during the night and when the weather was rainy. This behavior only occurred once all the females had returned from the field. In *Lasioglossum* (*Evylaeus*) *villosulus*, an essentially solitary species which will occasionally associate with conspecifics, the females seal the entrance to the nest in the absence of the other resident females (Plateaux-Quénu et al. 1989).

Duration of brood development

The development period was similar for males and females, although seasonal variation was influenced by environmental factors, such as the temperature. Higher temperatures may contribute to increased metabolic rates, which may reduce development time considerably (Howe 1967).

Relation between the physiological conditions of the number de females inseminated

Presumably single females can establish a new nest. Their subordinate status is determined only by the presence of a dominant. These females may be in a state of "sit and waiting" (West-Eberhard 1978) in anticipation of eventually occupying the dominant reproductive position in the nest. As in *Euglossa cordata* (Garófalo 1985) and *E. fimbriata* (Augusto and Garófalo 2009), one of the *E. melanotricha* subordinates eventually replaced the dominant female. Danforth et al. (1996) have suggested that Gadagkar's (1990) hypothesis of assured fitness returns, i.e. indirect care of the offspring by non-dispersing individuals, may best explain the high frequency of nest reactivation.

The nesting behavior of *Euglossa melanotricha* presented in this study provides insights into the social organization of orchid bees. Further studies of the relatedness among individuals will provide data on reproductive partitioning in this species.

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Nest structure and notes on the social behavior of *Augochlora amphitrite* (Schrottky) (Hymenoptera, Halictidae)

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Abstract

The nesting biology of *Augochlora (Augochlora) amphitrite* (Schrottky) in a natural reserve in the Province of Buenos Aires, Argentina, is described. The species nests in decaying wood. Two types of nest architecture were found, which differed according to the substrate where they were built, either soft or hard wood. Nests in soft wood had the cells grouped in clusters surrounded by a cavity, and the clusters were supported by a varying number of pillars. Nests constructed in decomposing portions of cracks in otherwise hard wood had the cells constructed against the walls, without any pillars or surrounding cavity. Cells of both types of nests were oriented in all directions, without any detectable pattern. Measurements and characteristics of the nests are tabulated and compared to those known for other species of *Augochlora s. str*. Behavioral observations of active nests are indicative of a social division of tasks in *A. amphitrite*. Such observations include nests with several females, some of which were never observed outside the nests, females with different degrees of wear and of ovary development, and at least one female that actively collected pollen which had much worn mandibles and wings, and undeveloped ovaries, all characteristics of the worker caste in social halictids.

Keywords

Augochlorini, *Augochlora*, nesting biology, social behavior, Pampean Region, Argentina

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Introduction

The bee tribe Augochlorini has an exclusively New World distribution, with maximal diversity in the Neotropics. This tribe is of particular interest because of the diversity of many of its biological traits, at the genus and species level, as well as within species. The social behavior in this group varies from solitary to primitively eusocial, with various degrees of sociality and transitions, including the origin of solitary behavior from eusocial ancestors (Eickwort 1969, Michener 1990, Danforth and Eickwort 1997, Wcislo and Danforth 1997, Engel 2000, Brady et al. 2006). The structure of the nests also presents ample variation within the tribe (Sakagami and Michener 1962, Eickwort and Sakagami 1979). Although most species nest in the soil, some lineages have shifted to the use of decomposing wood as a nesting substrate. Such behavior has originated repeatedly within the tribe (Engel 2000), and is known in *Augochlora*, *Megalopta*, *Xenochlora*, and some species of *Neocorynura* (Brosi et al. 2006, Wcislo and Gonzalez 2006, Tierney et al. 2008a, b, Tierney et al. 2012).

Augochlora is one of the more diverse genera within the tribe, with nearly 120 named species, classified in two subgenera, *Oxystoglossella* and *Augochlora* s. str. (Moure 2007). The genus ranges from southern Canada to northern Patagonia in Argentina, with most species inhabiting tropical areas. In Argentina the number of species strongly diminishes from north to south, being represented in the temperate Pampean region by only five species (Dalmazzo and Roig-Alsina 2011).

The two subgenera of *Augochlora* are considered as behaviorally divergent (Eickwort 1969, Michener 2007, Engel 2000). The subgenus *Oxystoglossella* includes species that nest in the soil and are primitively eusocial, with caste differentiation (Michener and Lange 1958, Eickwort and Eickwort 1972). Species of *Augochlora* s. str. have been considered solitary species that nest in soft wood (Eickwort 1969, Engel 2000). Their mandibles are modified, robust, with a lower preapical expansion and a well developed preapical tooth, suited for the substrate in which they dig. The behavioral characteristics of both subgenera have been inferred from what is known for a rather reduced number of species. In the case of *Augochlora* s. str., nest structure is known for *A. pura* (Say), *A. hallinani* Michener, *A. sidaefoliae* Cockerell, *A. smaragdina* Friese, *A. esox* (Vachal), *A. isthmii* Schwarz, and *A. alexanderi* Engel (Stockhammer 1966, Eickwort and Eickwort 1973, Zillikens et al. 2001, Wcislo et al. 2003), as well as some comments on a nesting site of *A. amphitrite* (Schrottky) (Sakagami and Moure 1967). The concept that the species of *Augochlora* s. str. are solitary has been challenged by Wcislo et al. (2003), who studied two nests of *A. isthmii* with more than one female. Limited data suggested that the nests might have been functioning as colonies, raising the question of whether the social behavior within the genus may be more variable than previously thought.

This contribution describes the structure of nests of *A. amphitrite*, and presents information on the nesting biology of the species. The data are compared to those known for other species of the subgenus.

Methods

Study site

The nests were studied in the reserve Refugio Natural Educativo "Ribera Norte" (34°28'10"S, 58°29'40"W), San Isidro, province of Buenos Aires, Argentina. This reserve is on the west margin of the Río de La Plata, and preserves a relict of gallery forest with typical riverine vegetation, including trees such as *Ocotea acutifolia* (Nees) Mez (Lauraceae), *Nectandra falcifolia* (Nees) J.A. Castigl. Ex Mart. Crov. & Paccinini (Lauraceae), *Pouteria salicifolia* (Spreng.) Radlk. (Sapotaceae), *Allophylus edulis* (A. St.-Hill., A. Juss. & Cambess.) Hieron. ex Niederl. (Sapindaceae), *Sebastiania brasiliensis* Spreng. (Euphorbiaceae), *Sapium haematospermun* Müll. Arg. (Euphorbiaceae) and *Blepharocalyx tweediei* (Hook, et Arn.) O Berg. (Myrtaceae) (Cabrera and Willink 1973).

Field observations

A nesting site of *A. amphitrite* was discovered in March 2008, near the end of summer. Nests were observed during seven days (35 work hours), from March 12 to April 30, when the nests were excavated. Another nesting site was located the following year in February. It was observed during three days (15 work hours), from February 7 to 14, when the nests were excavated. Although nests were not found in spring, adults flying over flowers (September to November) were collected and kept for dissection.

The activity of the bees was recorded following the methods described by Michener et al. (1955). Nest entrances were marked individually. When possible, females entering and leaving the nests were marked with a two-color code on the mesoscutum using fingernail enamel. One color was used to indicate to which nest a female belonged, and the second one to discriminate between females of the same nest. The length of activity periods, incidence of sunlight, departures and arrivals, and the presence of pollen loads, were recorded.

Nest extraction and description

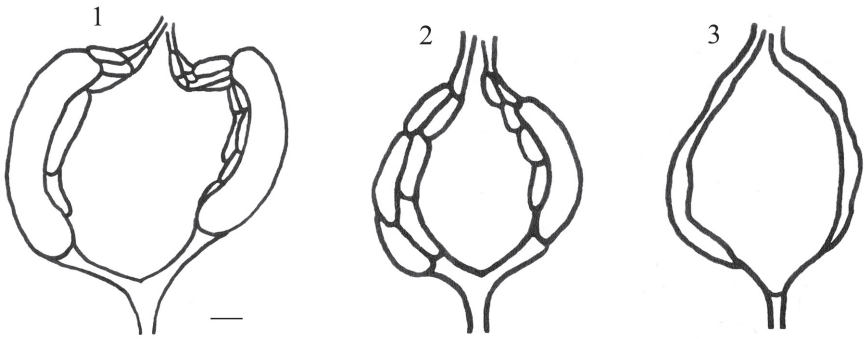
The methodology described by Sakagami and Michener (1962) was followed. Talcum powder was blown through the nest entrance to assist us to follow the nest as it was excavated with the aid of a knife and a sharp point. A caliper was used for field measurements. In the laboratory, observations and measurements were made with a stereomicroscope with an ocular micrometer. Measurements are given in centimeters, with mean values and standard errors. The contents of each cell were recorded. Voucher specimens are deposited in the collections of the Museo Argentino de Ciencias Naturales, Buenos Aires.

Dissections

The day of nest excavation, arriving bees as well as those found within the nest, were fixed in Kahle's solution. Presence of pollen loads, ovarian development, and presence of fat tissue, were recorded. Length of the body, maximum width of the eye and maximum width of the gena were taken. All measurement are in millimeters.

Three groups of females are recognized according to their ovarian development. The classification of Michener and Wille (1961) is followed, but simplified. Group A: ovaries large, well developed, usually with one or two eggs ready to be laid; posterior portions swollen forcing one or both ovaries to bend (Fig. 1). Group B: ovaries developed, but without eggs ready to be laid, so ovaries not as large as those of group A, and not bent (Fig. 2). Group C: ovaries not developed (Fig. 3).

The degree of wear of mandibles and wings is indicated in a scale from 0 (intact mandibles and wings) to 3 (much worn mandibles and tattered wings).



Figs 1–3. Classification of ovaries according to their development. **1** group **A**, developed ovaries with mature eggs ready to be deposited **2** group B, developed ovaries without mature eggs. **3** group **C**, ovaries not developed. Scale line: 0.1 mm.

Results

Nesting site

An aggregation of 18 nests was found in a fallen trunk of *Salix* sp. (Salicaceae) on March 12, 2008. The trunk, 3 m long and 0.8 m in diameter, was in an advanced state of decomposition, with soft wood colonized by fungi and various arthropods. Half of the trunk surface was covered by the plant *Commelina diffusa* Burm. f. (Commelinaceae), but the nests were on the uncovered surface, occupying an area of 0.60 m^2 on the upper and lateral parts. The nest entrances received sunlight from 11:30 to 15:00, being shaded by surrounding trees the rest of the day.

Three nests were found in railroad sleepers made from *Schinopsis* sp. ("quebracho colorado") (Anacardiaceae) on February 7, 2009. The sleepers (1.0 m long, 0.4 m wide, and 0.15 m thick) lay on the ground, forming the visitors trail in the wettest parts of

the reserve. *Schinopsis* wood is well known for its hardness. The nest entrances were located in knots and cracks, where decomposition had begun to soften the wood. The entrances were on the upper and lateral surfaces, occupying an extension of 0.50 m^2, and receiving sunlight from 11:00 to 15:00 hours.

Nest architecture

Nests on *Salix* and on *Schinopsis* differ considerably in their architecture, mainly in the distribution and arrangement of the cells.

Nest entrances on the trunk of *Salix*, separated by a minimum distance of 10 cm, presented a ring of compacted sawdust 0.75–1.00 cm in diameter ($\bar{x}$= 0.85 ± 0.08, n= 8) of the same color of the trunk surface. Active nests sometimes presented loose particles beyond the ring, which came from broken nest plugs. The tunnels, all unbranched, penetrated toward the interior of the trunk. They had a length of 7.00–15.00 cm ($\bar{x}$= 9.67 ± 2.56, n= 8), and a diameter of 0.45–0.50 cm ($\bar{x}$= 0.46 ± 0.03, n= 8); their smoothed walls were lined with substrate particles. Each tunnel led to a cluster of 2–10 cells ($\bar{x}$= 5 ± 2, n= 18), irregularly oriented, supported within a cavity by pillars. Two kinds of pillars were observed, those that were remaining parts of the substrate not excavated, and others, more frequent, made of compacted sawdust. The clusters were retrieved intact (Figs 4–5).

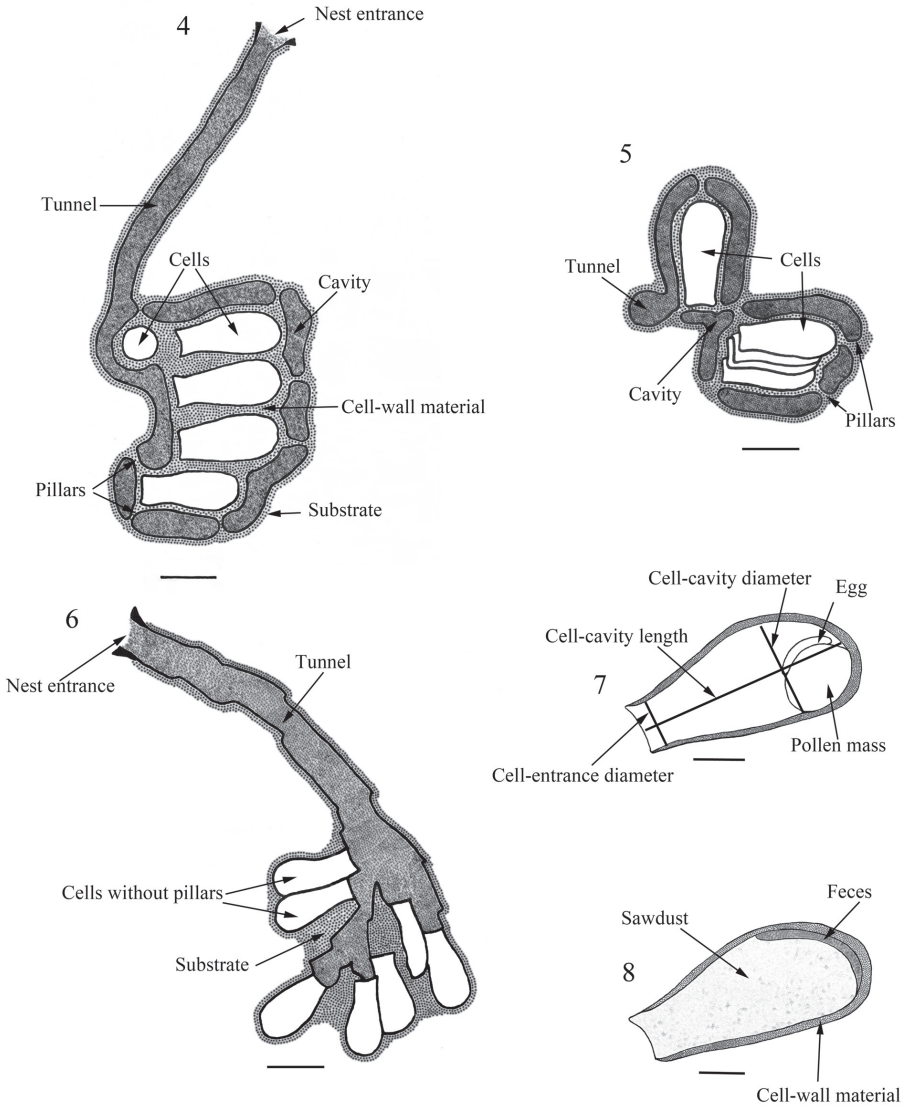
Nests on *Schinopsis* had shorter tunnels, 2.00–5.00 cm long ($\bar{x}$= 3.10 ± 1.36, n= 3). The soft material of the cracks was used for cell construction. The cells were in small groups or isolated, but without any pillars, and lying against the hard wood, with no surrounding cavity, taking advantage of masses of soft substrate within the crack (Fig. 6). Nests had 8–19 cells ($\bar{x}$= 13 ± 5, n= 3).

Cells of all nests were constructed with compacted particles of ground wood. The external surface was irregular, and the internal surface smooth and shiny, lined with a waxy substance. The cells were ovoid, with the lower surface slightly flattened (Fig. 7); the inner cavity was 0.80–1.45 cm long ($\bar{x}$= 1.07 ± 0.13, n= 72), 0.30–0.60 cm in diameter ($\bar{x}$ = 0.46 ± 0.06, n= 72), and 0.25–0.45 cm in cell entrance diameter ($\bar{x}$= 0.36 ± 0.04, n= 72); the cell wall was 0.05–0.30 cm in thickness ($\bar{x}$= 0.09 ± 0.04, n= 72). The cell plugs were made with the same material as the cell walls, 0.15 cm in thickness, dish-shaped, with the outer surface concave. Table 1 summarizes the architectural characteristics of *A. amphitrite*, comparing them to other species of *Augochlora* s. str. known to date.

Cell contents

Nests collected from *Salix* in April had their cells filled with compacted sawdust; they had feces deposited on the posterior portion, oriented toward the bottom of the cell (Fig. 8).

Nests collected from *Schinopsis* in February were active, and the cell contents consisted of pollen masses with eggs, larvae (in various stages of development), pupae, and



Figs 4–8. Nests of *A. amphitrite*. **4–5** nest on *Salix sp.* **4** section of nest in lateral view **5** section of same nest in upper view **6** nest on *Schinopsis sp.*, section of nest in lateral view **7** cell with pollen mass and egg, indicating taken measurements **8** cell filled with feces and sawdust. Scale lines: Figs **4–6**: 10 mm, Figs **7–8**: 5 mm.

a few cells with feces and filled with sawdust (Table 2). The pupae were all males. The pollen mass, placed near the bottom on the flattened surface of the cell, was slightly wider than long (0.40 × 0.35 cm), 0.43 cm high, and rather spherical, except for the flattened resting surface. The whitish egg was deposited on top of the mass, oriented along the longitudinal axis of the cell (Fig. 7).

Table 1. Architechtural characteristics of nests of *Augochlora* s. str. Measurements are given in cm (mean ± SD). Data for species other than *A. amphitrite*, from Wcislo et al. 2003 (*A. isthmii, A. alexanderi*), Zillikens et al. 2001 (*A. esox*), Eickwort and Eickwort 1973 (*A. hallinani, A. sidaefoliae* and *A. smaragdina*), and Stockhammer 1966 (*A. pura*).

	A. amphitrite	***A. isthmii***	***A. alexanderi***	***A. esox***	***A. pura***	***A. hallinani***	***A. sidaefoliae***	***A. smaragdina***
Nest entrance (diameter)	0.85 ± 0.08	0.34 ± 0.04	0.36		0.50			
Tunnel								
Diameter	0.46 ± 0.03	0.64 ± 0.11	0.52			0.80		
Length	9.67 ± 2.56	8.60 ± 0.65	5.60		20	2.50		5.00
Cells								
Arrangement	Clusters supported by pillars. Cells isolated or in groups against substrate without pillars or surrounding cavity	Isolated along the tunnel	Isolated along the tunnel	In groups against substrate without pillars or surrounding cavity	Clusters supported by pillars. Planiform. Along a tunnel. Intermediate forms.	Isolated along the tunnel	Cluster supported by pillars.	In a column along the tunnel
Orientation	Radiated in all directions	Radiated in all directions	Radiated in all directions	Radiated in all directions. Horizontal.	Parallel, sub-horizontal. Radiated in all directions	Horizontal	Horizontal	
Inner length	1.07 ± 0.13	1.39 ± 0.11	0.88	1.2	0.84–1	1.50 (outer dimensions)		
Inner max. diameter	0.46 ± 0.06	0.63 ± 0.06	0.43	0.5	0.4–0.6			
Neck diameter	0.36 ± 0.04	0.48 ± 0.03			0.35– 0.45			
Wall thickness	0.09 ± 0.04				0.1–0.4		0.2	

Table 2. Cell contents of nests of *A. amphitrite*. Po (pollen), E (egg), Lpo (larva with pollen), pdL (pre-defecating larva), Pu (pupa), F,s (Feces, filled with sawdust), f (female), m (male).

	Cell contents						Number of cells	Adults
	Po	**E**	**Lpo**	**pdL**	**Pu**	**F,s**		
Active nests								
Nest 1	7	3	1		4 m		15	5f - 2m
Nest 2	7	1	3	2	3 m	3	19	2f - 1m
Nest 3	4		3			1	8	1 f
Inactive nests						72	72	6 f

Behavioral observations

Females observed leaving and entering nests in March-April did not carry pollen loads. Activity began soon after the sunlight hit the trunk; before that, the entrances were covered with closed tumuli. Flights were inconstant, and up to three females were seen leaving and entering the same nest. The females spent 10–15 minutes perching on the surrounding vegetation, where flying males were also observed. Returning females had erratic flights, and inspected cracks and small holes in the trunk.

The three nests collected in February were active. Foraging activity began 15–20 minutes after the sunlight hit the entrances (around 11:20). A female pushed the plug of sawdust with its hind legs, scattering the particles 2–3 cm around the tumulus. After that the female remained at the entrance, with only its head visible, for 3–5 minutes before departing. After 7–10 minutes the same female came back to the nest laden with pollen. Usually, as soon as a female left the nest, another one showed its head at the entrance. When disturbed, the female turned around, plugging the hole with its metasomal terga. Activity continued for approximately 4 hours until no more sunlight bathed the nests (around 15:00). Nest 1 had five females, four of which were captured when returning to the nest (two with, and two without pollen loads); the fifth female was never observed outside the nest and was captured when it was extracted. Another nest had two females; only one of them was observed collecting pollen. The third nest had a single female. Recently emerged males were found in two nests, and males were seen flying in the surroundings of the nesting area and on flowers of *Ludwigia* (Onagraceae), 50 cm away from the nests.

Dissections

Inactive nests (end of summer). The six fixed females had slender, undeveloped ovaries (group C, Fig. 3) and mandibles and wings without signs of wear (class 0). All specimens had abundant fat tissue, in the form of small, whitish spheres. None carried pollen loads. Measurements (length of body – maximum width of eye – maximum width of gena): 9.0–0.5–0.4; 10.0–0.5–0.4; 10.0–0.5–0.4; 11.0 –0.6–0,6; 8.0–0.6–0.5; 11.0–0.8–0.8.

Active nests (summer)

Nest 1 (5 females). Three females were group A, had unworn mandibles (class 0), and slightly worn wings (class 1); two of them were seen carrying pollen loads to the nest; measurements, 9.0–0.6–0.5; 10.0–0.6–0.8; 9.0–0.6–0.7. One female was group B, with unworn mandibles (class 0), and slightly worn wings (class 1); this female was never observed outside the nest; measurements, 12.0–0.7–0.9. One female was group C, had worn mandibles and wings (class 2); this female carried pollen loads; measurements, 9.5–0.6–0.5. Nest 2 (2 females). Both were group A, with slightly worn mandibles (class 1) and worn wings (class 2); one of them carried pollen loads to the nest. Measurements: 9.5–0.5–0.4; 11.0–0.6–0.7.

Nest 3 (1 female). It was group A, with slightly worn mandibles (class 1) and worn wings (class 2). This female was not observed outside the nest and was captured during excavation. Measurements: 11.0–0.6–0.7.

Spring flying adults. Fourteen females were captured in spring (1, September; 7, October; 6, November). All had developed ovaries (2, group A; 12, group B), and unworn wings and mandibles (class 0). None contained fat tissue. Maximum and minimum values for these females were: length of body, 8.0–12.5, width of eye, 0.5–0.7, and width of gena, 0.5–0.9.

Discussion and conclusions

The nests of *A. amphitrite* presented two types of nest architecture according to the substrate where they were built. Common features to both types were the entrance surrounded by a ring of compacted sawdust, and the unbranched tunnels leading to the cells. Cells of all nests had the same structure, and similar proportions to those of other species of *Augochlora* s. str. (Table 1).

Nests constructed in the thick trunk of *Salix*, with a large mass soft wood, had the cells grouped in clusters surrounded by a gallery of similar diameter to that of the tunnel, and supported by a varying number of pillars. Nests constructed in the decomposing parts of the cracks and knots of the hard wood of *Schinopsis* had the cells toward the end of the tunnel, constructed against the hard walls, without any pillars or surrounding cavity. In both cases the number of cells was variable and the orientation of the cells irregularly radiated.

Cluster nests are known for *A. pura* and *A. sidaefoliae*, while studied nests of *A. isthmii, A. alexanderi, A. hallinani* and *A. smaragdina* had tunnel nests with sessile cells distributed along the tunnel, and *A. essox* had nests with grouped cells, but not forming clusters (Table 1) (Stockhammer 1966, Eickwort and Eickwort 1973, Zillikens et al. 2001, Wcislo et al. 2003). A nest with a cluster of cells supported by pillars within a cavity is the predominant and probably plesiomorphic type of nest within the tribe Augochlorini (Eickwort and Sakagami 1979, Danforth and Eickwort 1997, Engel 2000), and it is the plesiomorphic condition for the monophyletic *Augochlora*

genus-group (Engel 2000, Coelho 2004), indicating that departures from the cluster type of nest are derived conditions within *Augochlora*. Although the nests of few species of *Augochlora* s. str. have been studied, their structure is highly variable. The two types of nests found in the present study indicate that this variation can be intraspecific, coincidently with the variation found by Stockhammer (1966) for *A. pura*, which had tunnel, planiform, and cluster nests, with some intermediate forms. This variation observed within *Augochlora* s. str., greater than in other genera of Augochlorini, would result from the irregularity of the nesting substrate. Species that nest in the soil, may be less constrained by the substrate, and can fully express their behavioral capabilities. Species of *Augochlora* nest on the substrate offered by diverse plants, usually trees, but also bromeliads (Zillikens et al. 2001), which offer a heterogeneous supply regarding the size, shape and degree of decomposition of the nesting sites. Probably all species of *Augochlora* s. str. can construct well defined clusters when an unconstrained substrate is available, as is the case in *A. pura* and *A. amphitrite*.

The daily activity pattern of the females was limited by the forest environment where the bees were studied. Females left the nests to collect pollen during a period of 3.5–4 hours, while the sunlight hit the nesting site.

The annual cycle in the study area was typical of the cycle of most halictids in temperate regions, although the winters in the study area are mild and the temperatures in July are rarely freezing. Activity begins in spring (September-October), when posthibernating females begin to visit flowers. Females captured at this time showed well developed ovaries and would be the foundresses of the first nests. The activity continues until mid March, when the nests become inactive and females of the last generation are looking for hibernacula. Females captured at this time had undeveloped ovaries and abundant fat tissue.

Nests studied in summer (February) contained larvae in various stages of development, male adults, male pupae, and adult females, which correspond at least to the first brood of the foundress (Table 2). Although possible, we are not certain whether more generations are bred between spring and mid-summer. A further brood is produced by the end of summer, so at least two broods are produced during the activity cycle. Although most females collected in February had developed ovaries, one female, from nest 1, had the ovaries undeveloped and actively collected pollen. It also had worn mandibles and wings, all characteristics of the worker caste in social halictids (Michener et al. 1955). Also, the presence within the excavated nests of females that were never observed outside the nest, is indicative of a social division of tasks.

Values taken from the fixed females show size variation among females with enlarged ovaries. The female that was never observed outside the nest in multi-female nest 1 was distinctly larger than the others in the same nest. It also had an allometrically enlarged head, with a broad gena. Females of *A. amphitrite* have distinct cephalic polymorphism (Dalmazzo and Roig-Alsina 2011), which can be indicated by the maximum width of the eye - maximum width of the gena coefficient. A few other females of nests 1–3 had moderately enlarged heads.

Although the number of studied nests is very low, the information recovered is suggestive of social behavior in *A. amphitrite*. Wcislo et al. (2003) reached similar conclusions for *A. isthmii*, pointing out that social behavior within *Augochlora s.str.* is more variable than previously thought, since members of the subgenus had been considered as solitary and derived from an eusocial ancestor (Eickwort 1969, Michener 1990, Danforth and Eickwort 1997, Wcislo and Danforth 1997, Engel 2000, Brady et al. 2006). Further studies are needed, both in the field and laboratory, to understand the degree of sociality in *Augochlora*, and whether its occurrence is widespread in the subgenus.

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Revision of *Zelodia* (Hymenoptera, Braconidae, Agathidinae) from Thailand

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Abstract

The species of Thai *Zelodia* (Hymenoptera: Braconidae: Agathidinae) are revised. Twenty-one species are treated, 19 new species are described, i.e. *Zelodia charoeni*, *Zelodia chongkraii*, *Zelodia cholathorni*, *Zelodia idrisi*, *Zelodia nikomi*, *Zelodia nopadoli*, *Zelodia pahangensis*, *Zelodia panyaii*, *Zelodia poonsathii*, *Zelodia ratanae*, *Zelodia saksiti*, *Zelodia surachaii*, *Zelodia suyaneeae*, *Zelodia toyae*, *Zelodia uthaii*, *Zelodia wangi*, *Zelodia wichaii*, *Zelodia wirati*, *Zelodia wirotei*. A dichotomous key to species is presented; links to electronic interactive keys and to distribution maps are also included.

Keywords

Thailand, Insecta, identification key, taxonomy, systematics

Introduction

Agathidinae is a moderately large subfamily of Braconidae with 1,061 described species worldwide and 238 in the Oriental Region (Yu et al. 2005) though there are an estimated 2,000–3,000 species awaiting description worldwide (Sharkey et al.

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Figure 1. Map showing collection sites in Thailand.

2006). The subfamily has a worldwide distribution and members are found in most terrestrial habitats. The history of higher classification of the Agathidinae was summarized by Sharkey (1992) who also proposed a tribal level classification based on ground-plan coding. Sharkey et al. (2006) conducted phylogenetic analyses based on morphology and the D2–3 regions of 28S rDNA. The Oriental fauna of Agathidinae was first revised by Bhat and Gupta (1977) and they provided a detailed history of taxonomic research for the area. Sharkey et al. (2009) revised the Oriental genera of Agathidinae. Achterberg and Long (2010) revised the Vietnamese agathidine fauna, erected the genus *Zelodia*, described 5 new species of *Zelodia* and transferred 20 species to *Zelodia*, mostly from *Coccygidium* and *Zelomorpha*. Sharkey and Clutts (2011) revised the Thai species of *Biroia, Braunsia*, *Camptothlipsis, Coccygidium, Cremnops, Cremnoptoides, Disophrys, Earinus, Gyrochus, Lytopylus*, and *Troticus,* and included a key to the Agathidinae genera of the Oriental region. This paper is the second in a series to revise all Thai species of Agathidinae. The genera *Aneurobracon, Bassus, Euagathis*, and *Therophilus* will be dealt with in subsequent publications.

Methods

As part of the inventory of Thai insects, we ran three Malaise traps at 30 different localities throughout Thailand from 2007-2010, comprising approximately 90 Malaise trap years. The specimens dealt with here are primarily from these traps.

Species concepts are based on morphological data and cytochrome *c* oxidase (COI) data. Phenetic and phylogenetic trees, using 558 base pairs of COI data, were constructed using neighbor-joining (NJ), maximum parsimony (MP) and Bayesian methods. MP was performed using TNT (Goloboff et. al, 2008) [traditional search with 100 random addition sequences followed by branch-swapping, saving 100 trees per replication; 1000 bootstrap replications were used to estimate branch reliability]. The Bayesian analysis was performed using MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003). Best-fitting DNA substitution models were determined using MrModeltest2.2 (Nylander 2004). The general time reversible model of evolution with a parameter for invariant sites and rate heterogeneity modeled under a gamma distribution (GTR+I+G) was determined as the best-fitting model. The Bayesian analysis consisted of two independent Bayesian MCMC runs initiated from different random starting trees. The analysis ran for 2,000,000 generations, reaching a topological similarity criterion of 0.01; trees were sampled every 500 generations. 25% of the trees from each run were removed as burn-in upon topological convergence. The NJ tree was produced from PAUP* (Swofford 2002) using default settings. Figure 2 presents the NJ tree, which was much more resolved than were the phylogenetic trees produced by MP and Bayesian analyses. We mapped the support values of the Bayesian and MP analyses on the NJ tree. Branches without values are those that collapsed in the phylogenetic analyses.

The dichotomous key, descriptions, and the interactive key (Appendices 1–3) were generated using DELTA Editor Dallwitz et al. (1999), DELTA Dallwitz et al. (1993), and Intkey Dallwitz et al. (1995).

Morphological terms follow Sharkey and Wharton (1997) except for the following: measurements are given for the length and apical width of the first metasomal mediotergite (MT1). Measurement of the apical width is straightforward, however since the base of the tergite is usually hidden from view it is difficult to measure the total length. Instead we measure from the apex of the large tendon that emanates from the propodeum and inserts near the base of the median tergite. Abbreviations used in text: S1, S2, S3; metasomal mediosternite 1, 2, 3; MT1, MT2, MT3: metasomal mediotergite 1, 2, 3; LT1, LT2, LT3: metasomal laterotergite 1, 2, 3.

Morphological terms used in this revision were matched to the Hymenoptera Anatomy Ontology (HAO, Yoder et al. 2010) (Appendix 4). Identifiers (URIs) in the format http://purl.obolibrary.org/obo/HAO_XXXXXXX represent anatomical concepts in HAO version http://purl.obolibrary.org/obo/hao/2011-05-18/hao.owl. They are provided to enable readers to confirm their understanding of the anatomical structures

being referenced. To find out more about a given structure, including, images, references, and other metadata, use the identifier as a web-link, or use the HAO:XXXXXXX (note colon replaces underscore) as a search term at http://glossary.hymao.org.

All 19 species are treated with a diagnosis and distributional data. They are illustrated with color photos using a JVC digital camera mounted on a Leica MZ16 microscope and Automontage® stacking software. Distributional data are listed for all species and a Google map via Berkeley Mapper is included for all species. The descriptions are of the holotype and variation is given in parentheses.

The source files for the keys, descriptions, illustrations, DNA sequence and distributional data are all freely available to future researchers who may wish to build on this beginning. DNA trace files and primer information are available through the Barcode of Life Data system (BOLD) [Ratnasingham and Hebert 2007] at http://www.boldsystems.org. Sixteen of the twenty five *Zelodia* COI sequences were generated by BOLD (project ASTRK Revisions of Thai Agathidinae Braconids), the remaining nine were generated in the Sharkey lab. All sequences have been deposited in GenBank database (JQ763436–JQ763460). All twenty five *Zelodia* COI sequences are characterized by a -1 frameshift mutation. A majority of Agathidinae CO1 sequences are distinguished by a series of 1 bp deletions which are not restricted to one portion of the barcode region. Codon composition in sequences with 1bp deletions remains highly biased towards AT and substitutions remain biased towards 3rd codon position (M. Alex Smith pers. comm.). It is suggested that the genes are correctly decoded by a programmed frameshift during translation (Beckenbach et al. 2005) and are functional.

Distribution data, pdf's of non-copyright references, images, notes, and host and type information can be found by searching TaxaBank (a combined specimen and taxonomic database; http://purl.org/taxabank). Codes beginning with an "H" and followed by numbers are unique identifiers used for specimens in the Sharkey lab at the University of Kentucky, and in the specimen database TaxaBank (e.g., H647).

Abbreviations used for specimen depositories are as follows:

BMNH	The Natural History Museum, London, England.
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, USA.
HIC	Hymenoptera Institute Collection, University of Kentucky, Department of Entomology, Lexington, Kentucky, USA.
QSBG	Queen Sirikit Botanic Gardens, Chiang Mai, Thailand.
RMNH	NCB Naturalis Collection [formerly Rijksmuseum van Natuurlijke Historie], Leiden, Netherlands.
UKM	Universiti Kebangsaan, Bangi, Selangor, Malaysia.

Results

Refer to the tree in Sharkey and Clutts (2010) for generic level placement. The host lepidopterans of the genus are unknown. The neighbor joining branching diagram in Figure 2, based on COI mtDNA, was used to help in determining species limits although we did not devise any cutoff threshold to delimit species. We conducted Bayesian and parsimony analyses and where these agreed with the NJ tree the support values are given in Figure 2. An examination of this figure shows that the NJ diagram

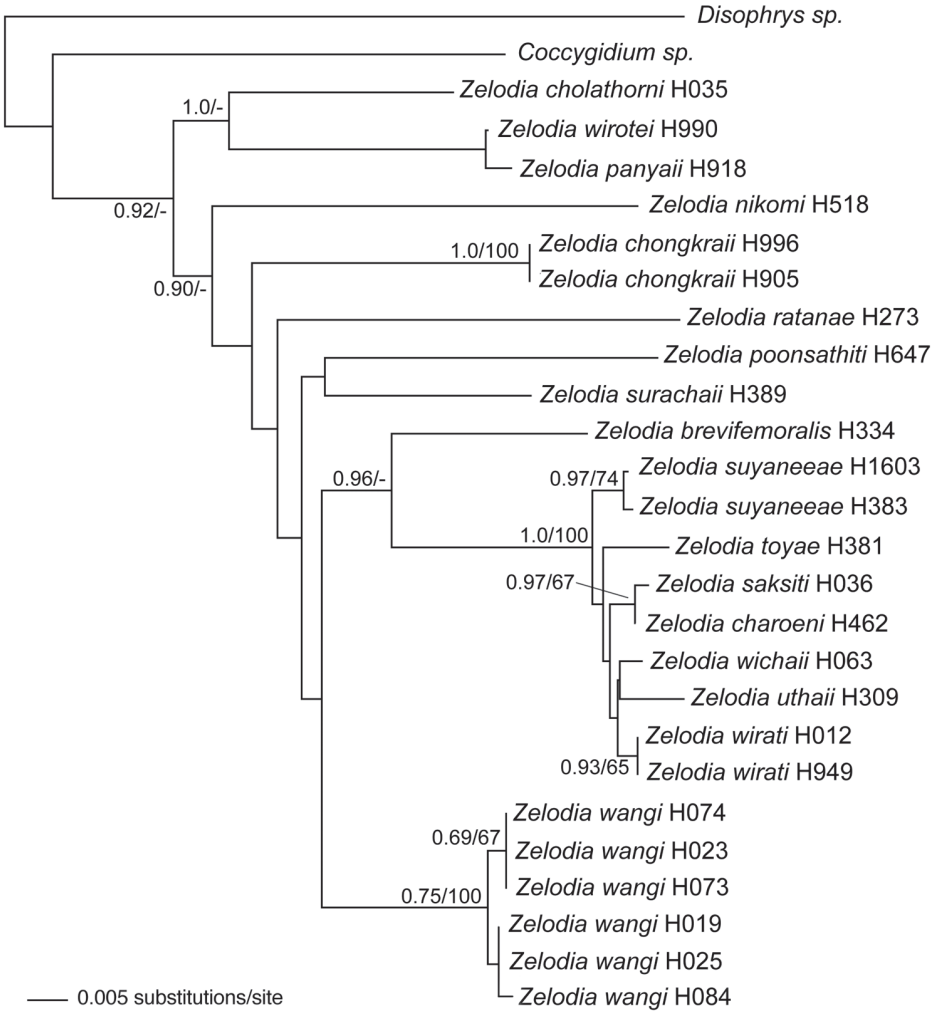


Figure 2. NJ phylogram of the COI barcode region for 17 of the 21 *Zelodia* species treated here. Wherever Bayesian and parsimony analyses agreed with the NJ tree branch support values are included in the figure i.e., Bayesian posterior probabilities / parsimony bootstrap (bootstrap values less than 60 are not illustrated).

and the phylogenetic analyses were in close agreement. We also used morphological differences to delimit species. For example, *Z. saksiti* and *Z. charoeni* are very similar (1/558 bp difference) in COI sequences but are very different morphologically. Contrastingly, *Zelodia wangi* is a widespread species and COI sequences show some variation (2/558 bp difference), however we could find no morphological differences. The complex may represent several species.

Taxonomy

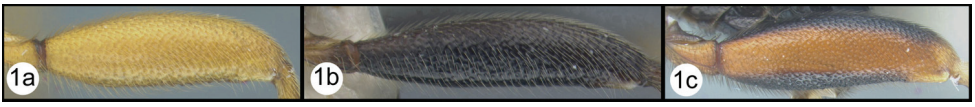
Diagnosis

Members of *Zelodia* may be distinguished from all other Agathidinae with the following combination of characters: ovipositor short, shorter than length of metasoma; tarsal claws cleft; hind trochantellus with 2 longitudinal carinae; frons lacking lateral carinae between antennae and lateral ocelli.

Key to Thai species of *Zelodia*

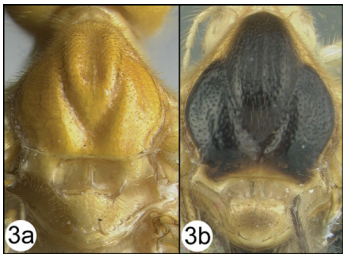
(Note: there are often more than 2 alternatives in each couplet)

1 a. Hind femur all pale **2**
b. Hind femur all melanic **7**
c. Hind femur melanic dorsally and ventrally, orange laterally and medially ..... ***Z. ratanae*** **Sharkey sp.n.**

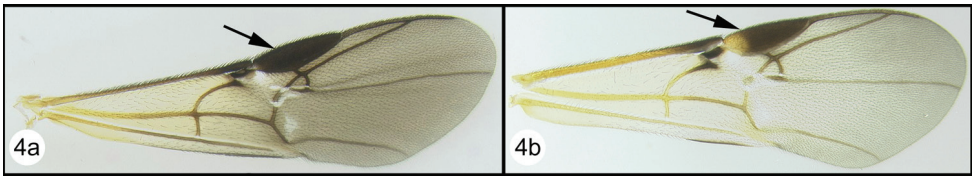


2(1) a. Hind leg including tarsus entirely pale ..... ***Z. brevifemoralis*** **Achterberg & Long**
b. Hind leg melanic and pale, often mostly pale with tarsus melanic **3**

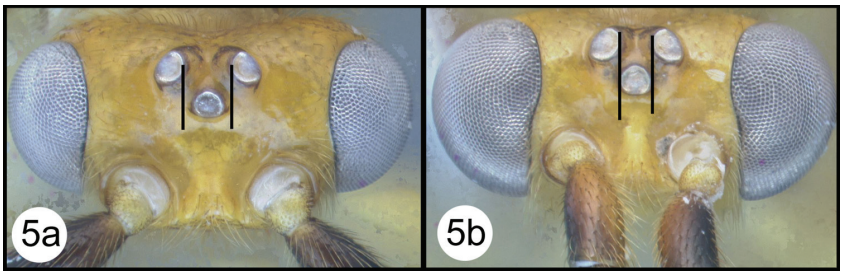
3(2) a. Mesoscutum entirely pale **4**
b. Mesoscutum mostly melanic except margins pale ... ***Z. idrisi*** **Sharkey sp.n.**



4(3) a. Stigma entirely melanic ..... ***Z. nikomi*** **Sharkey sp.n.**
b. Stigma partly or entirely yellow **5**

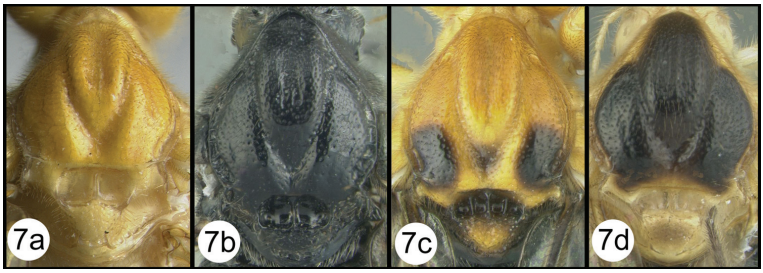


5(4) a. Median ocellus distinctly narrower than space between lateral ocelli **6**
b. Median ocellus about as widen as space between lateral ocelli .....
..... ***Z. toyae*** **Sharkey sp.n.**

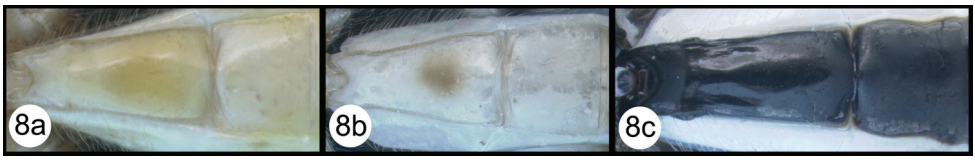


6(5) a. Hind femur more than 4× longer than wide (average 4.2×) .....
..... ***Z. suyaneeae*** **Sharkey sp.n.**
b. Hind femur less than 4× longer than wide (average 3.5×) .....
..... ***Z. wichaii*** **Sharkey sp.n.**

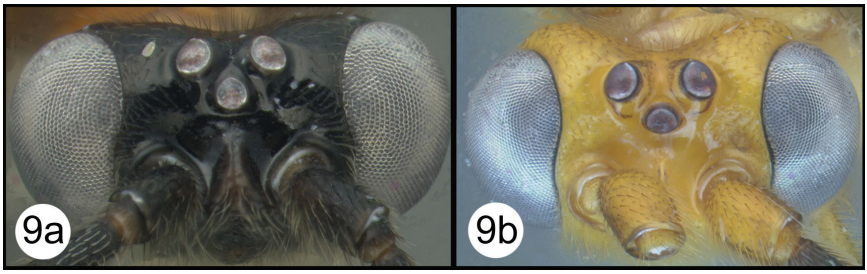
7(1) a. Mesoscutum entirely pale **8**
b. Mesoscutum entirely melanic **10**
c. Mesoscutum mostly pale with melanic spots posteriorly ..... ***Z. chongkraii*** **Sharkey sp.n.**
d. Mesoscutum mostly melanic except on margins pale **12**



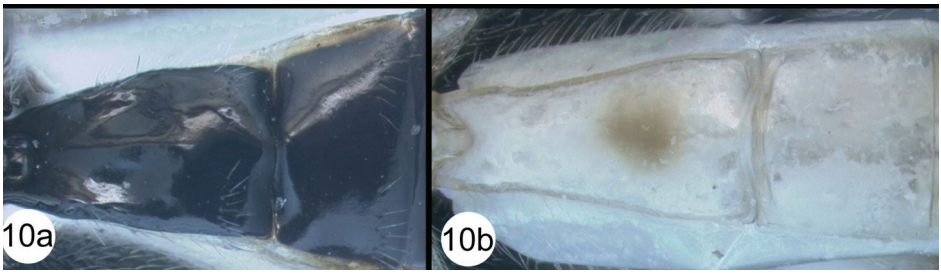
8(7) a. Median tergite 1 mostly yellow **15**
b. Median tergite 1 all white or cream colored, sometimes with a bit of melanic color subapically ..... ***Z. wirotei*** **Sharkey sp.n.**
c. Median tergite 1 all black **9**



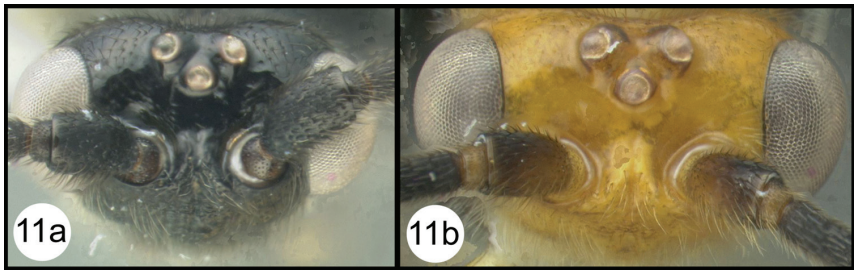
9(8) a. Head (not including mouthparts or antenna) mostly or entirely pale ..... ***Z. longidorsata*** **(Bhat & Gupta)**
b. Head (not including mouthparts or antenna) mostly or entirely melanic .. ***Z. panyaii*** **Sharkey sp.n.**



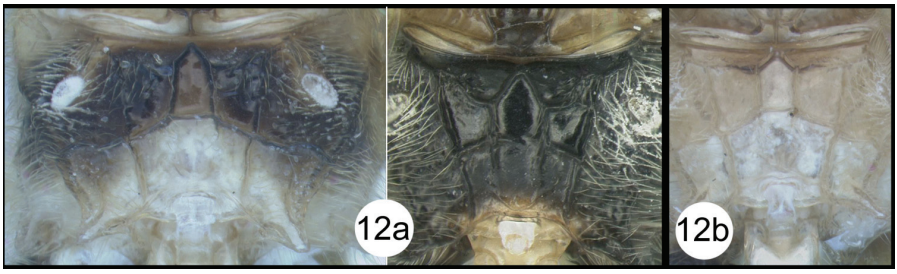
10(7) a. Median tergite 1 all black ..... ***Z. cholathorni*** **Sharkey sp.n.**
b. Median tergite 1 all white or cream colored or sometimes with a bit of melanic color subapically **11**



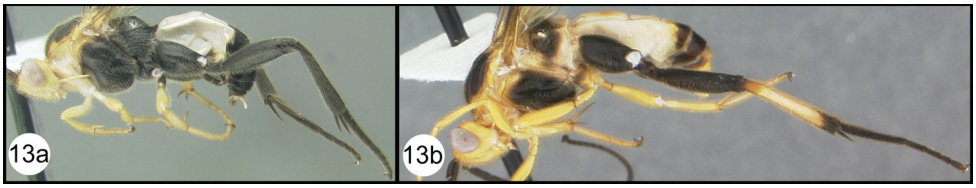
11(10) a. Head (not including mouthparts or antenna) mostly or entirely melanic... ..... ***Z. surachaii*** **Sharkey sp.n.**
b. Head (not including mouthparts or antenna) mostly or entirely pale..... ..... ***Z. nopadoli*** **Sharkey sp.n.**



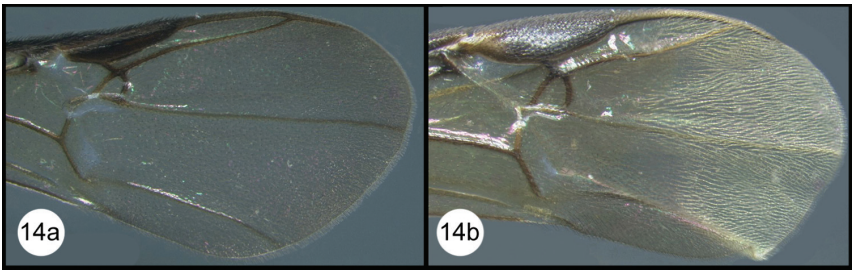
12(7) a. Propodeum melanic in anterior half or more.....**13**
b. Propodeum entirely pale **14**



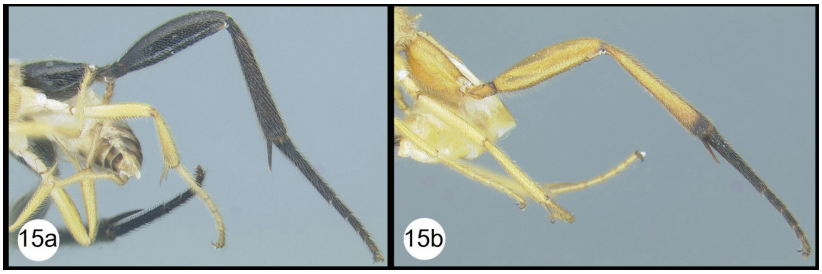
13(12) a. Hind leg entirely melanic..... ***Z. poonsathii*** **Sharkey sp.n.**
b. Hind leg melanic except tibia mostly pale..... ***Z. saksiti*** **Sharkey sp.n.**



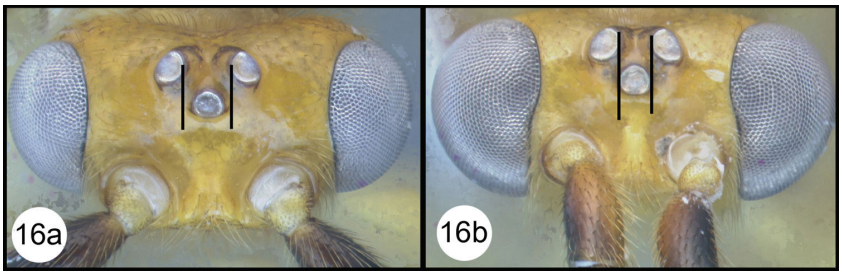
14(12) a. Fore wing not lighter apically than subapically, lacking white setae apically ..... ***Z. uthaii*** **Sharkey sp.n.**
b. Fore wing lighter apically than subapically, with extensive white setae apically ..... ***Z. pahangensis*** **Sharkey sp.n.**



15(8) a. Hind tibia entirely melanic..... ***Z. wangi*** **Sharkey sp.n.**
b. Hind tibia mostly pale **16**



16(15) a. Median ocellus distinctly narrower than space between lateral ocelli..... ..... ***Z. charoeni*** **Sharkey sp.n.**
b. Median ocellus about as wide as space between lateral ocelli .... ***Z. wirati*** **Sharkey sp.n.**



Species Treatments

Zelodia brevifemoralis Achterberg & Long

http://species-id.net/wiki/Zelodia_brevifemoralis
Fig. 3

Zelodia brevifemoralis Achterberg and Long, 2010 [Holotype ♀ (RMNH) examined]

Diagnosis. Hind leg, including tarsus (except apical tarsomere), entirely pale.

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H334/ATRMK197-11/JQ763436.

Distribution. Recorded from Vietnam and central Thailand. Distribution map of the sole Thai locality can be found at http://purl.org/thaimap/brevifemoralis

Material examined. H0334 [QSBG] ♀, Thailand, Phu Kradueng NP, 420, 16.844°N, 101.692°E, MT, 1–7.vii.2008.

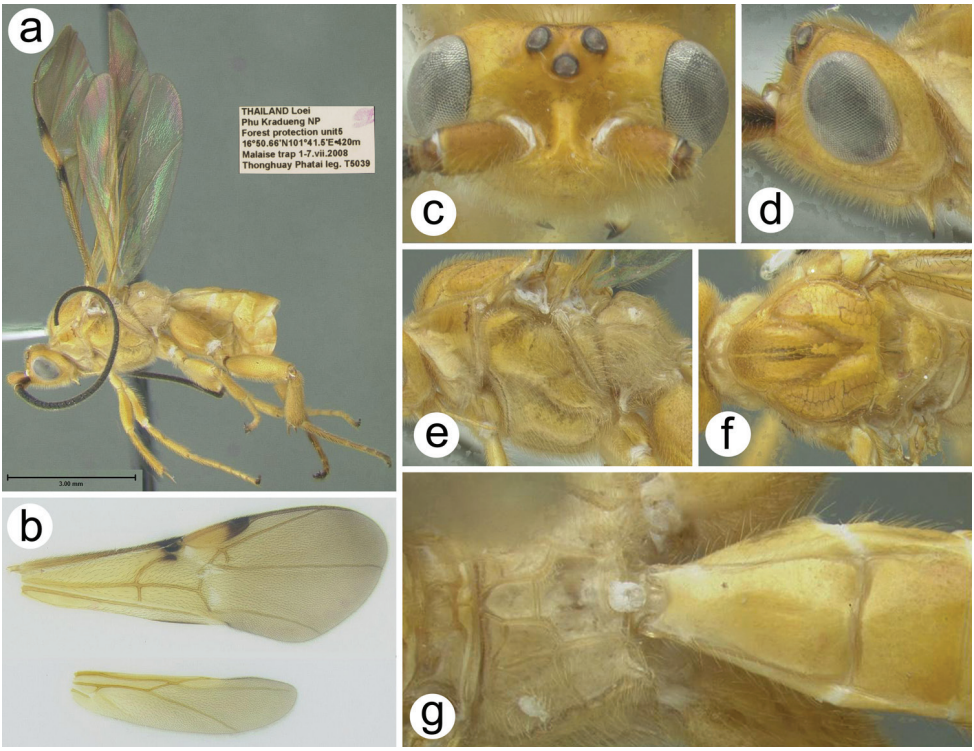


Figure 3. *Zelodia brevifemoralis* Achterberg and Long **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum and MT1–MT2.

Zelodia charoeni **Sharkey sp.n.**
urn:lsid:zoobank.org:act:85D50740-7E31-4F89-AB31-B8689CC225CF
http://species-id.net/wiki/Zelodia_charoeni
Fig. 4

Diagnosis. Hind tibia pale except apex black; hind femur melanic; mesoscutum pale; median ocellus distinctly narrower than space between lateral ocelli.

Description. Body length 7.4 mm (7.2–7.4). **Head.** 41 (39–41) flagellomeres. Median ocellus diameter narrower than space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli partly smooth, otherwise with weak punctures. Metapleuron sparsely covered with setae. Fore wing cells hyaline basally, weakly infuscate apically, veins yellow basally except costa mostly melanic, melanic apically and around parastigma, stigma yellow in basal fifth. Hind tarsal claw bifid. Length/width of hind femur 2.22/0.552 = 3.9 (3.9–4.1). Lateral surface of hind femur punctate. **Metasoma.** Length/width ratio of MT1, 1.257/0.539 = 2.3. Ratio of widest point of MT1 to narrowest point 0.539/0.35 = 1.5 (1.4–1.5). **Color.** Mostly yellow; black as follows: antenna except scape brown medially, hind leg except basal 4/5 of tibia yellow. Median area of mesopleuron yellow (to mostly brown).

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H462/ATRMK214-11/JQ763437.

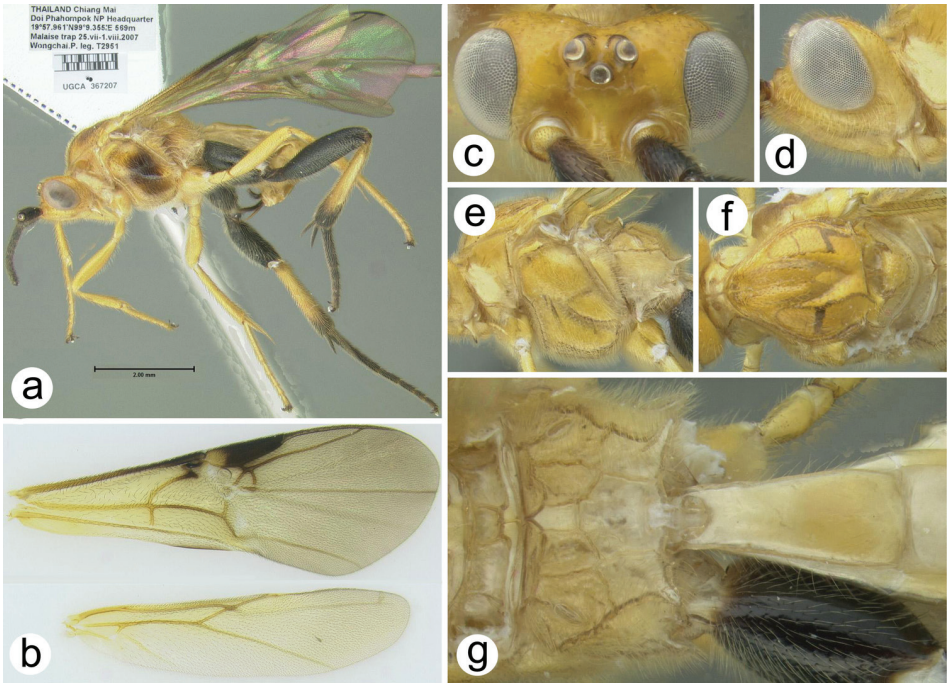


Figure 4. *Zelodia charoeni* sp.n. **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum and MT1.

Distribution. Found only in northern Thailand. Distribution map can be found at http://purl.org/thaimap/charoeni

Etymology. Dedicated to Mr. Charoen Wanna, collector at Doi Phuka National Park.

Material examined. Holotype ♀. H5905 [QSBG], Thailand, Doi Phahompok NP Headquarters, 569, 19.966°N, 99.156°E, MT, 25.vii–1.viii.2007.

Paratypes. Thailand: ♀, Nam Nao NP, Check point, 921m, 16.728°N, 101.563°E, MT, 28.iv–5.v.2007: H0461 [HIC]; ♂, Doi Phahompak Office, 569m, 20.191°N, 99.248°E , MT, 28.v–7.vi.2008: H0462 [QSBG].

Zelodia cholathorni Sharkey sp.n.

urn:lsid:zoobank.org:act:655F182B-8A0E-4EC7-A530-0188F26B0926
http://species-id.net/wiki/Zelodia_cholathorni
Fig. 5

Diagnosis. Mesoscutum entirely melanic; hind tibia all melanic; head melanic; MT1 black.

Description. Body length 6.0 mm. **Head.** 38 flagellomeres. Median ocellus diameter narrower than space between lateral ocelli. Vertex densely and heavily punctate. **Mesosoma.** Notauli mostly or entirely crenulate. Metapleuron densely covered with setae. Fore wing cells weakly infuscate, more so apically, veins brown to black. Hind

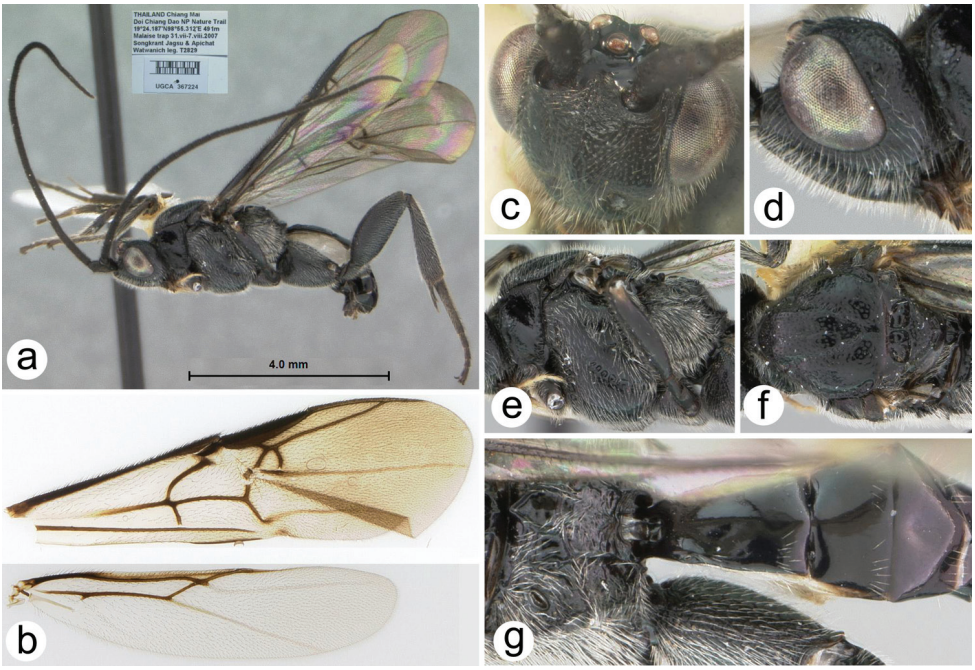


Figure 5. *Zelodia cholathorni* sp.n. **a** lateral habitus **b** wings **c** anterodorsal head **d** lateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum and MT1–MT3.

tarsal claw with elongate basal tooth. Length/width of hind femur 1.8/0.7 = 2.7. Lateral surface of hind femur aciculate. **Metasoma.** Length/width ratio of MT1, 0.91/0.659 = 1.37. Ratio of widest point of MT1 to narrowest point 0.7/0.4 = 1.5. **Color.** Black except palpi mostly yellow and metasomal laterotergites and S1–S3.

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H035/ATRMK141-09/JQ763438.

Distribution. Found only at the type locality in northern Thailand. Distribution map can be found at http://purl.org/thaimaps/cholathorni

Etymology. Dedicated to Mr. Cholathorn Chamnanthip, chief of Doi Phahompok National Park, one of our collecting sites.

Material examined. Holotype ♂. H0035 [QSBG], Thailand, Doi Chiang Dao WS, Nature Trail, 491m, 19.403°N, 98.922°E, MT, 31.vii–7.viii.2007.

Paratypes. ♂ Thailand, Doi Chiangdao NP, Headquarters, 491m, 19.405°N, 98.922°E, MT, 21–28.viii.2007: H4597 [QSGB], H4593 [HIC].

Zelodia chongkraii **Sharkey sp.n.**
urn:lsid:zoobank.org:act:9D77F05D-907C-4643-AD41-FFA1E12A74C9
http://species-id.net/wiki/Zelodia_chongkraii
Fig. 6

Diagnosis. Mesoscutum mostly pale with melanic spots posteriorly.

Description. Body length 7.3 mm (7.1–7.3). **Head.** 41 (40–41) flagellomeres. Median ocellus diameter narrower than space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli mostly or entirely crenulate. Metapleuron sparsely covered with setae. Fore wing cells all weakly infuscate, more so apically, veins melanic. Hind tarsal claw bifid. Length/width of hind femur 2.169/0.506 = 4.3. Lateral surface of hind femur aciculate. **Metasoma.** Length/width ratio of MT1, 1.258/0.458 = 2.3 (2.2–2.3). Ratio of widest point of MT1 to narrowest point 0.543/0.405 = 1.3 (1.3–1.4). **Color.** Yellow, black, and white; metasomal segments 1 and 2, LT3 and S3 all white; yellow as follows: head except antenna, prothorax, most of mesoscutum and scutellar disc, fore leg, mid leg except coxa, trochanter, trochantellus, and base of femur partly melanic; remaining body parts black.

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H905/ATRMK260-11/JQ763439; H996/ATRMK273-11/JQ763440.

Distribution. Eastern and northeastern Thailand. Distribution map can be found at http://purl.org/thaimap/chongkraii

Etymology. Dedicated to Mr. Chongkrai Worapongthorn, chief of Doi Inthanon National Park, one of our collecting sites.

Material examined. Holotype ♀. H0996 [QSBG], Thailand, Huai Nam Dang NP, Thung Buatong, 19.293°N, 98.6°E, MT, 21–28.iv.2008.

Paratype. ♀, Thailand, Kaeng Krachan NP, Panernthung/km27, 950m, 12.8217°N, 99.371°E, MT, 8–15.vi.2009, H0905 [HIC].

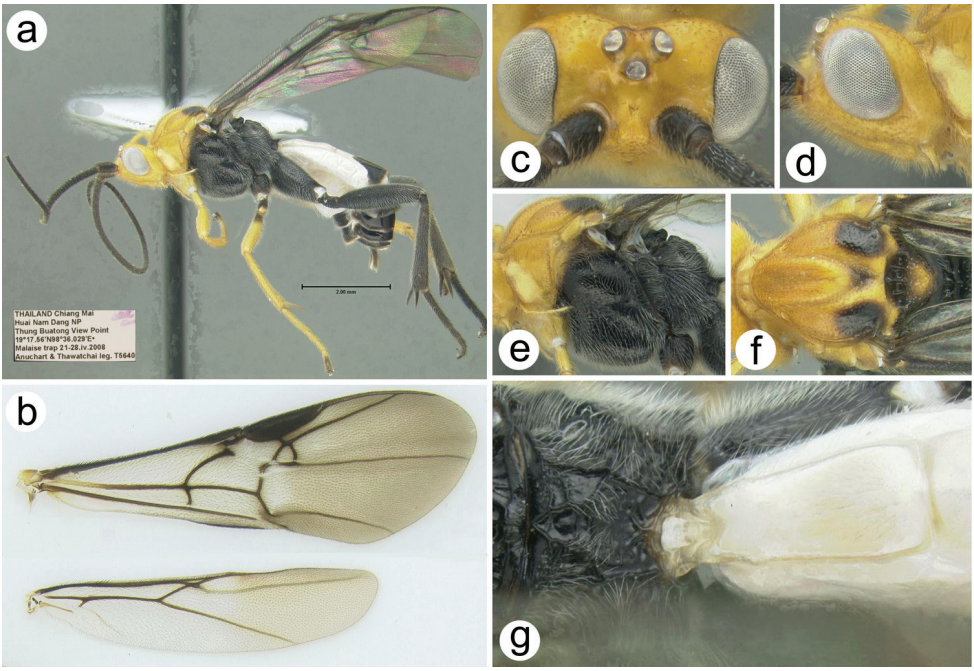


Figure 6. *Zelodia chongkraii* sp.n. **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum and MT1.

Zelodia idrisi **Sharkey sp.n.**
urn:lsid:zoobank.org:act:F01DB087-985E-4475-8E3D-D0F50A398CB6
http://species-id.net/wiki/Zelodia_idrisi
Fig. 7

Diagnosis. Head melanic dorsally and posteriorly, pale ventrally and anteriorly; hind femur all pale.

Description. Body length 9.0 mm (7.6–9.0). **Head.** 43 (42–43) flagellomeres. Median ocellus diameter equal to the space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli partly smooth, otherwise with weak punctures. Metapleuron sparsely covered with setae. Fore wing cells yellowish basally, infuscate in distal 3rd fourth and clear in apical fourth with white setae, veins yellow basally and apically, brown at midlength, stigma yellow in basal fourth, otherwise dark brown. Hind tarsal claw bifid. Length/width of hind femur 2.63/0.75 = 3.5 (3.5–3.7). Lateral surface of hind femur punctate. **Metasoma.** Length/width ratio of MT1, 1.60/0.82 = 2.0 (1.9–2.0). Ratio of widest point of MT1 to narrowest point 0.82/0.49 = 1.7 (1.5–1.7). **Color.** Mottled yellow, brown, orange, cream-colored, and black.

Distribution. Widespread in western Malaysia and likely present in southern Thailand. Distribution map can be found at http://purl.org/thaimap/idrisi

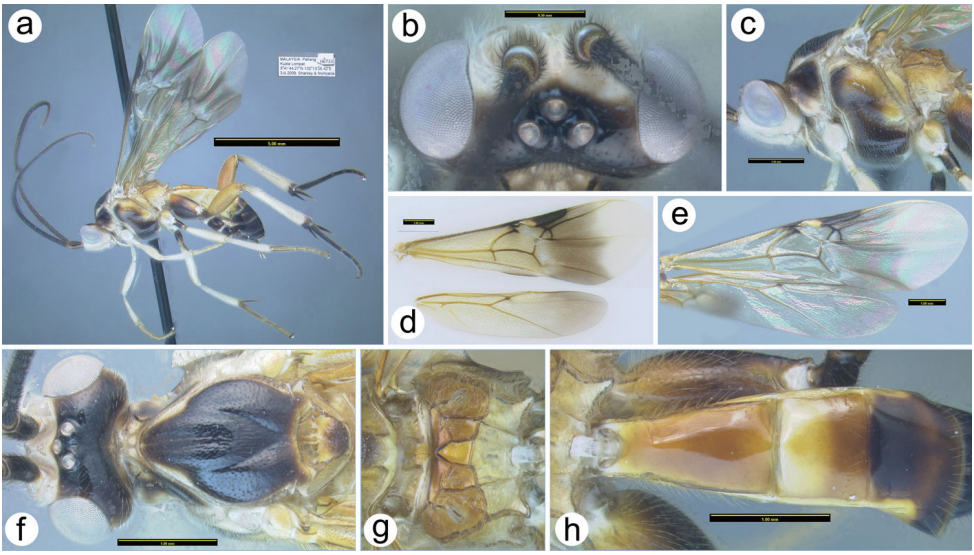


Figure 7. *Zelodia idrisi* sp.n. **a** lateral habitus **b** dorsal head **c** lateral head and mesosoma **d** wings with buffered light source **e** wings with normal light source **f** dorsal head and mesosoma **g** dorsal propodeum **h** dorsal MT1–MT3.

Etymology. Dedicated to Prof. Idris Abd. Ghani, professor at the School of Environmental and Natural Resource Science, Universiti Kebangsaan, Malaysia.

Material examined. Holotype ♀. H6733 [UKM], Malaysia, Kuala Lompat, Pahang, 3.695°N, 102.224°E, 3.iii.2009.

Paratypes. ♀, Malaysia: Kampung PETA, Johor, 2.541°N, 103.418°E, viii.2008: H8467 [QSBG]; Kuala Lompat, Pahang, 3.695°N, 102.224°E, 3.iii.2009:H8468 [QSBG]; Wang Kelian, Perlis, 6.678°N, 100.19°E, xi.2008: H8469 [HIC], H8466 [UKM]; Pasoh Forest Reserve, 23.x.2002: H8470 [HIC].

Zelodia longidorsata (Bhat & Gupta)

http://species-id.net/wiki/Zelodia_longidorsata
Fig. 8

Zelodia longidorsata (Bhat and Gupta) 1977 [Holotype, ♀ (CNC) examined]

Diagnosis. Hind tibia all melanic; mesoscutum entirely pale; stigma entirely melanic; head, except antenna, pale; propodeum mostly or entirely pale; median ocellus diameter equal to the space between lateral ocelli; MT1 long and narrow, not much wider apically than basally

Distribution. Recorded from southern India and a locality east of Bangkok, undoubtedly more widespread. Distribution map of Thai locality can be found at http://purl.org/thaimap/longidorsata

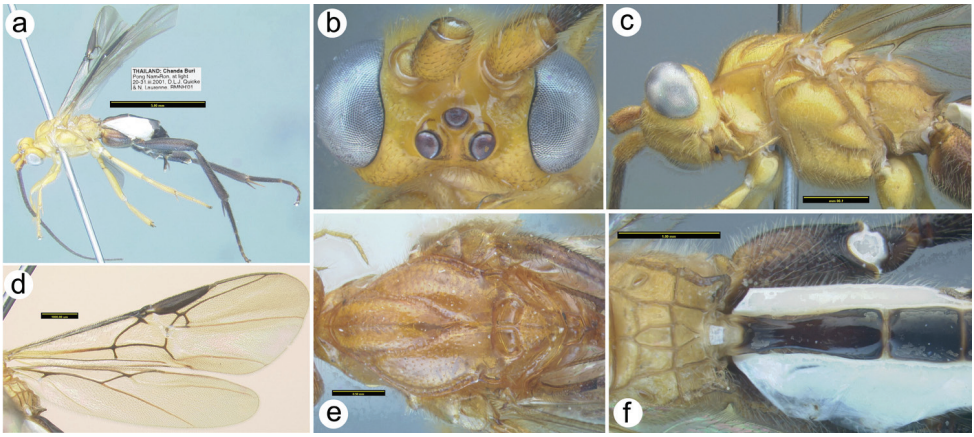


Figure 8. *Zelodia longidorsata* **a** lateral habitus **b** dorsal head **c** lateral head and mesosoma **d** wings **e** dorsal mesosoma **f** dorsal propodeum and metasomal terga 1 and 2.

Material examined. ♀, Thailand, Chanda Buri, Pong Nam Ron, 12.908°N, 102.262°E, MT, 20-31.iii.2001: H8471 [RMNH].

Zelodia nikomi **Sharkey sp.n.**
urn:lsid:zoobank.org:act:906199C7-511C-4D3E-A709-74059891E100
http://species-id.net/wiki/Zelodia_nikomi
Fig. 9

Diagnosis. Hind femur all pale; stigma entirely melanic; MT1 long and narrow, only slightly wider apically than basally.

Description. Body length 5.5 mm. **Head.** 35 flagellomeres. Median ocellus diameter narrower than space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli mostly or entirely crenulate. Metapleuron sparsely covered with setae. Fore wing cells with a yellowish hue basally, infuscate apically, veins yellow basally, melanic apically, stigma entirely melanic. Hind tarsal claw bifid. Length/width of hind femur 1.83/5.0 = 3.7. Lateral surface of hind femur aciculate. **Metasoma.** Length/width ratio of MT1, 0.95/0.585 = 1.6. Ratio of widest point of MT1 to narrowest point 0.585/0.394 = 1.5. **Color.** Mostly yellow except as melanic as follows: flagellum, lateral surface of scape, hind tarsus, apex of hind tibia.

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H518/ATRMK220-11/JQ763441.

Distribution. Known only from the type locality in central Thailand. Distribution map can be found at http://purl.org/thaimap/nikomi

Etymology. Dedicated to Mr. Nikom Wongwan, collector at Phuka National Park.

Material examined. Holotype ♀. H0518 [QSBG], Thailand, Phu Kradueng NP, 420m, 16.844°N, 101.692°E, MT, 9–16.iii.2009.

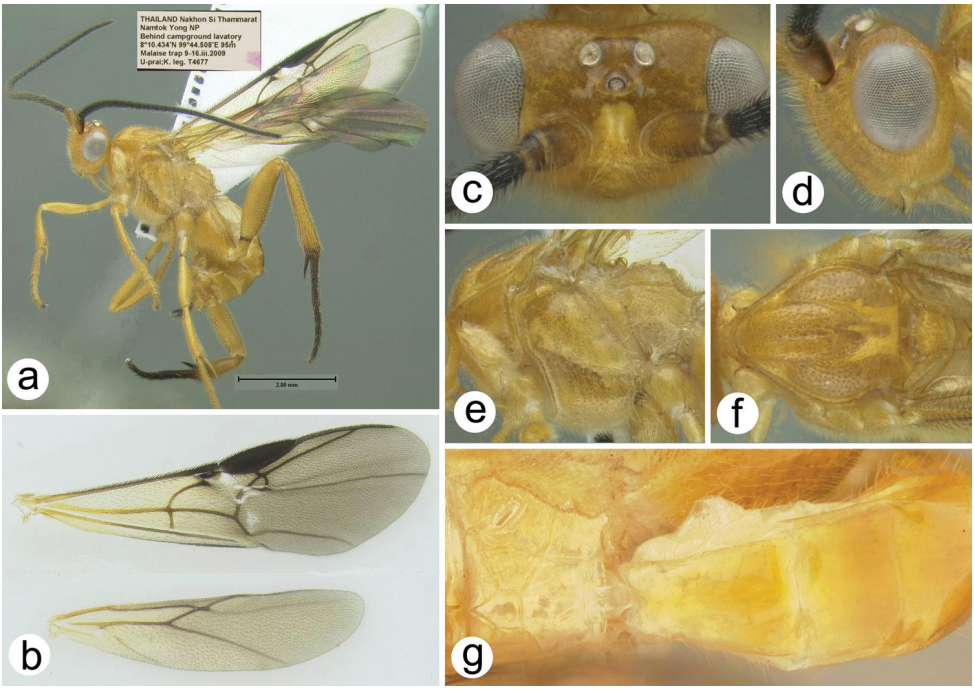


Figure 9. *Zelodia nikomi* sp.n. **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum and MT1-MT3.

Zelodia nopadoli **Sharkey sp.n.**
urn:lsid:zoobank.org:act:CDC346AF-61D7-4CA3-88A6-33318DA2939E
http://species-id.net/wiki/Zelodia_nopadoli
Fig. 10

Diagnosis. Mesoscutum entirely melanic; head, except antenna, pale.

Description. Body length 7.7 mm (6.2–7.7). **Head.** (37–41) flagellomeres (both flagella broken in holotype). Median ocellus diameter equal to the space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli mostly or entirely crenulate. Metapleuron with moderately dense setae. Fore wing cells hyaline basally, infuscate distally, veins including stigma melanic. Hind tarsal claw bifid. Length/width of hind femur 2.059/0.551 = 3.8 (3.5–4.8). Lateral surface of hind femur aciculate. **Metasoma.** Length/width ratio of MT1, 1.231/0.583 = 2.1 (2.1–2.3). Ratio of widest point of MT1 to narrowest point 0.583/0.376 = 1.6 (1.2–1.6). **Color.** Mostly black with yellow, white and cream color; head yellow, scape brown, flagellum black, prothorax yellow; fore leg and mid leg, except parts of coxa, yellow; MT1 and MT2 cream colored; basal laterotergites and sterna white; remainder of body black.

Distribution. Recorded from southeastern and northwestern Thailand. Distribution map can be found at http://purl.org/thaimap/nopadoli

Etymology. Dedicated to Mr. Nopadol Nachin, chief of Tad Tone National Park.

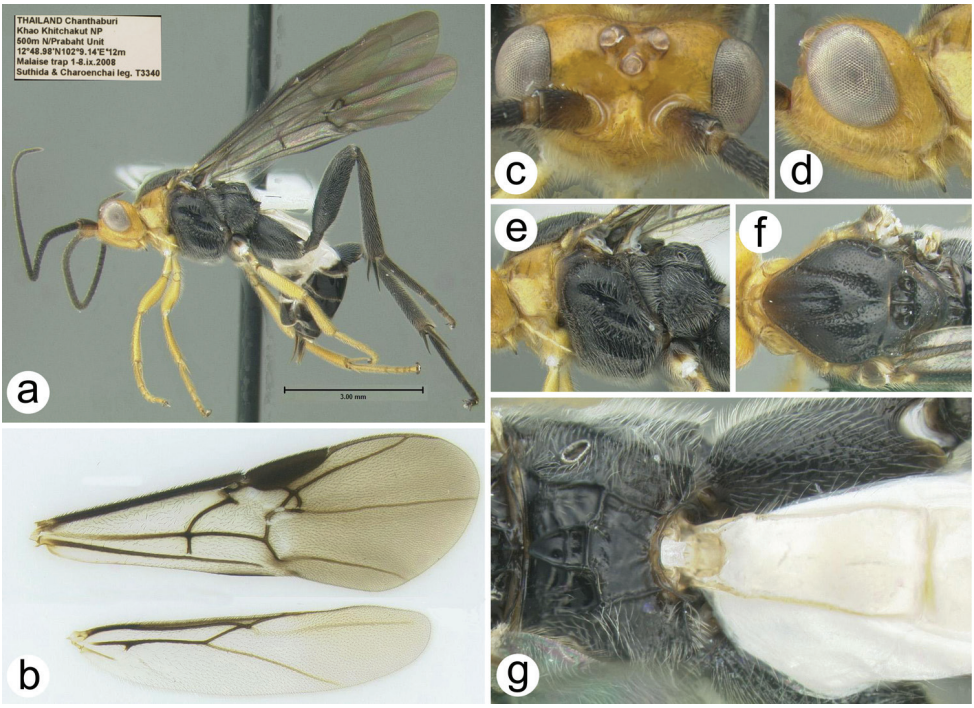


Figure 10. *Zelodia nopadoli* sp.n. **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum and MT1.

Material examined. Holotype ♀. H0323 [QSBG], Thailand, Khao Khitchakut NP, N/Prabaht Unit, 500m, 12.816°N, 102.152°E , MT, 1–8.ix.2008.

Paratypes. ♀, Thailand: Doi Inthanon NP, Chiang Mai, 1700m, 18.544°N, 98.525°E, MT, 3-12.v.1900: H8491[HIC]; Doi Chiangdao NP, Pha Tang substation, 526m, 19.416°N, 98.9147°E, MT, 28.viii–4.ix.2007: H0948 [QSBG].

Zelodia pahangensis Sharkey sp.n.

urn:lsid:zoobank.org:act:C2307CCB-C04A-46EF-8244-B83DCD4899EE
http://species-id.net/wiki/Zelodia_pahangensis
Fig. 11

Diagnosis. Mesoscutum mostly melanic except margins pale; hind tibia mostly pale except apex and extreme base black; hind femur melanic; apex of fore wing hyaline with white setae.

Description. Body length 7.8 mm (7.4–7.8). **Head.** 39 (39–42) flagellomeres. Median ocellus diameter equal to the space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli mostly or entirely crenulate. Metapleuron sparsely covered with setae. Fore wing cells weakly infuscate, veins mostly brown, lighter

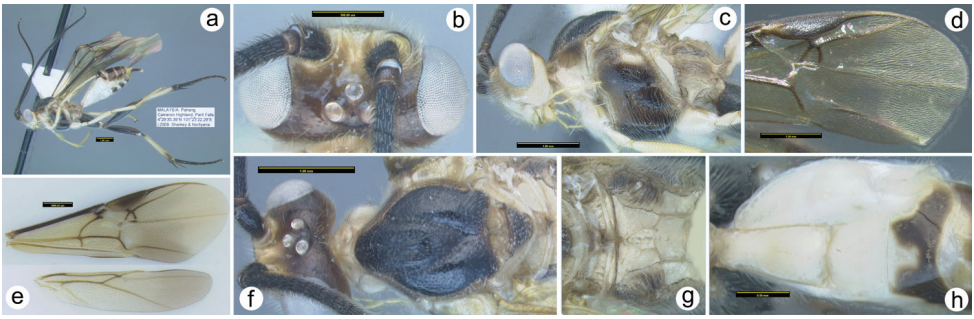


Figure 11. *Zelodia pahangensis* sp.n. **a** lateral habitus **b** dorsal head **c** lateral head and mesosoma **d** apex of fore wing **e** wings **f** dorsal head and mesosoma **g** dorsal propodeum **h** dorsal MT1–MT3.

basally and apically, stigma yellowish brown in basal 1/3, apex of wing with white setae, making it appear lighter. Hind tarsal claw bifid. Length/width of hind femur 2.32/0.5 = 4.6 (4.5–4.6). Lateral surface of hind femur aciculate. **Metasoma.** Length/width ratio of MT1, 1.3/0.59 = 2.2 (2.1–2.2). Ratio of widest point of MT1 to narrowest point 0.59/0.38 = 1.6 (1.5–1.6). **Color.** Mottled yellow, cream-colored and black; head yellow except vertex brown and antenna black, hind leg black except most of tibia pale.

Distribution. Known only from the type locality in western Malaysia but likely to be found in peninsular Thailand. Distribution map can be found at http://purl.org/thaimap/pahangensis

Etymology. The name is in reference to the Malaysian state, Pahang, in which the specimens were collected

Material examined. Holotype ♀, H8489 [UKM], Malaysia, Pahang, Cameron Highland, Parit Falls, 4.493°N, 101.389°E, MT, i.2009.

Paratypes. ♂ Malaysia, Pahang, Cameron Highland: Jasa, 4.493°N, 101.389°E, MT, 28.ii.2009: H8482 [HIC], H8484 [HIC], H8485 [QSBG], H8488 [UKM]; Parit Falls, 4.493°N, 101.389°E, MT, i.2009: H8486 [QSBG], H8487 [QSBG], H8483 [HIC], H8465 [UKM].

***Zelodia panyaii* Sharkey sp.n.**
urn:lsid:zoobank.org:act:CAE2FCB9-74C6-4B1B-B4A8-35216ACA9154
http://species-id.net/wiki/Zelodia_panyaii
Fig. 12

Diagnosis. Head (not including mouthparts) melanic; mesoscutum entirely pale.

Description. Body length 7.5 mm. **Head.** 39 flagellomeres. Median ocellus diameter equal to the space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli mostly or entirely crenulate. Metapleuron densely covered with setae. Fore wing cells weakly infuscate, more so apically, veins melanic. Hind tarsal claw bifid. Length/width of hind femur 2.117/0.539 = 3.9. Lateral surface of hind femur aciculate. **Metasoma.** Length/width ratio of MT1, 1.234/0.505 = 2.4. Ratio

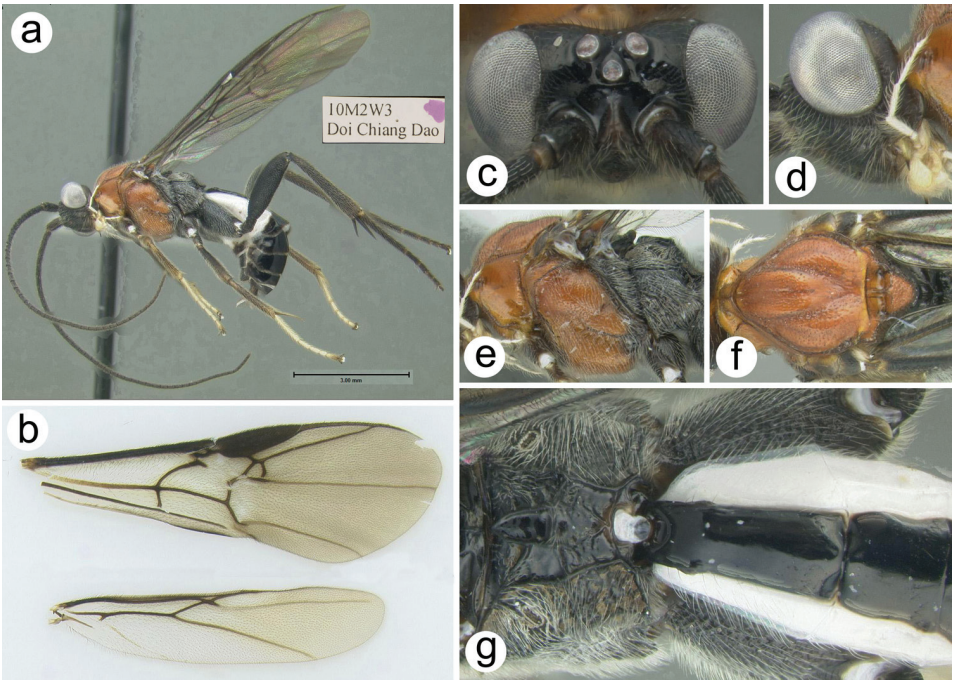


Figure 12. *Zelodia panyaii* sp.n. **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum and MT1 and MT2.

of widest point of MT1 to narrowest point 0.505/0.421 = 1.2. **Color.** Black, reddish orange, brown, cream colored and white: mostly black, reddish orange as follows: pro and mesothorax, most of fore leg; mid leg mostly brown; fore and mid tarsi yellow; mouthparts cream colored and yellow, anterior laterotergites and sterna white.

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H918/ATRMK263-11/JQ763442.

Distribution. Known only from the type locality in northwestern Thailand. Distribution map can be found at http://purl.org/thaimap/panyaii

Etymology. Dedicated to Mr. Panya Kotesanlee, chief of Phuphan National Park.

Material examined. Holotype ♀ H0918 [QSBG], Thailand, Doi Chiangdao NP, Pha Tang substation, 19.416°N, 98.9147°E, MT, 15-21.v.2008.

Zelodia poonsathiti **Sharkey sp.n.**
urn:lsid:zoobank.org:act:B98E3538-0386-430E-9681-50360DD1CD74
http://species-id.net/wiki/Zelodia_poonsathiti
Fig. 13

Diagnosis. Mesoscutum mostly melanic except margins pale; hind tibia all melanic.

Description. Body length. 7.2 mm. **Head.** 39 flagellomeres. Median ocellus diameter equal to the space between lateral ocelli. Vertex sparsely and weakly punctate.

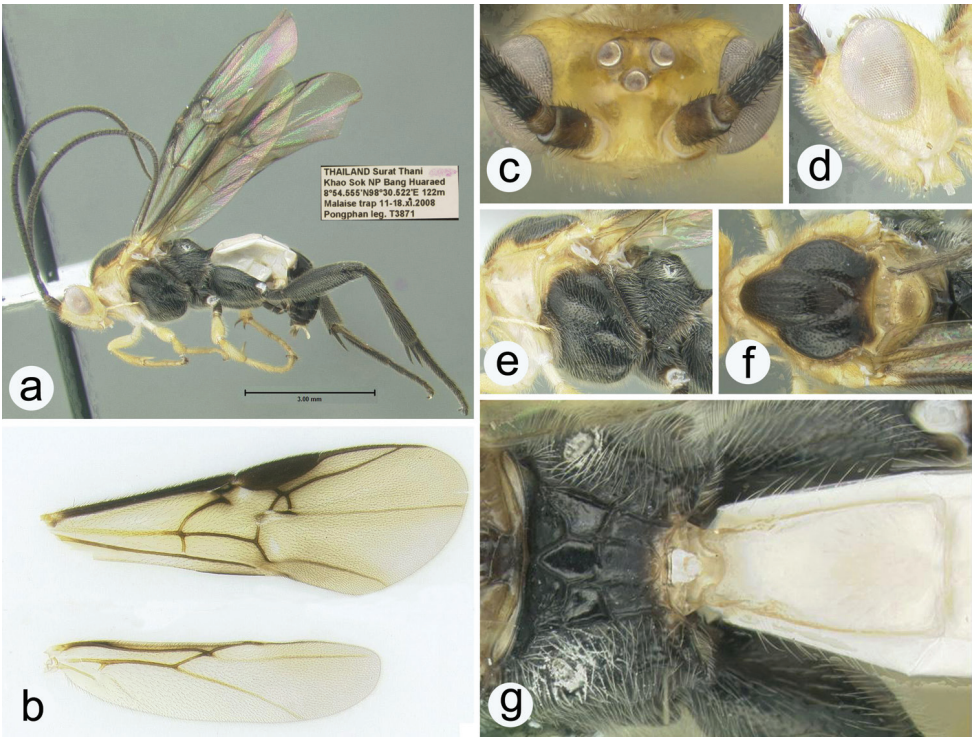


Figure 13. *Zelodia poonsathiti* sp.n. **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum and MT1.

Mesosoma. Notauli mostly or entirely crenulate. Metapleuron sparsely covered with setae. Fore wing cells weakly infuscate, veins mostly brown to black, M+Cu yellow. Hind tarsal claw bifid. Length/width of hind femur 2.059/0.586 = 3.5. **Metasoma.** Length/width ratio of MT1, 1.273/0.656 = 1.9. Ratio of widest point of MT1 to narrowest point 0.656/0.436 = 1.5. **Color.** Mottled yellow, cream-colored and black, head yellow except flagellum black and scape brown, hind leg black, MT1 and MT2 cream colored.

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H647/ATRMK231-11/JQ763443.

Distribution. Found only at the type locality in southern peninsular Thailand. Distribution map can be found at http://purl.org/thaimap/poonsathiti

Etymology. Dedicated to Mr. Poonsathit Wongsawat, chief of Doi Phuka National Park.

Material examined. Holotype ♂ H0647 [QSBG], Thailand, Khao Sok NP, Bang Huaraed, 122m, 8.909°N, 98.509°E, MT, 11-18.xi.2008.

Zelodia ratanae **Sharkey sp.n.**
urn:lsid:zoobank.org:act:2738BC9E-B243-45EE-B970-90AE358BBDB7
http://species-id.net/wiki/Zelodia_ratanae
Fig. 14

Diagnosis. Hind tibia mostly pale, extreme base cream, apex black, most of dorsal and ventral surfaces black, otherwise orange.

Description. Body length 7.6 mm. **Head.** 42 flagellomeres. Median ocellus diameter equal to the space between lateral ocelli. Vertex densely and heavily punctate. **Mesosoma.** Notauli mostly or entirely crenulate. Metapleuron sparsely covered with setae. Fore wing cells and veins melanic in basal 3/5, cells hyaline basally with white setae, veins R1, RS, r-m, and M yellow distally, stigma yellow in apical third. Hind tarsal claw bifid. Length/width of hind femur 2.4/0.8 = 3.2. Lateral surface of hind femur punctate. **Metasoma.** Length/width ratio of MT1, 1.112/1.245 = 0.88. Ratio of widest point of MT1 to narrowest point 1.2/0.4. **Color.** Black except as follows; scape yellow, margins of prothorax cream colored to yellow, legs with extensive orange and/or yellow, scutellar sulcus, lateral and posterior areas of scutellum, and much of metapectal-propodeal complex, yellowish orange, anterior laterotergites and sterna pale brown.

Molecular data. TaxaBank#/Genbank Accession: H273 /JQ763452.

Distribution. Found only at the type locality in southern peninsular Thailand. Distribution map can be found at http://purl.org/thaimap/ratanae

Etymology. Dedicated to Ms. Ratana Luckanawarakul. She is currently the director of the Recreation and Interpretation Division of the Thai Department of National Parks. Ratana was of great assistance to us on numerous field trips and was always the best of company.

Material examined. Holotype ♂. H0273 [QSBG], Thailand, Khao Pu-Khao Ya NP, 75m, 7.551°N, 99.789°E, MT, 8–10.v.2006.

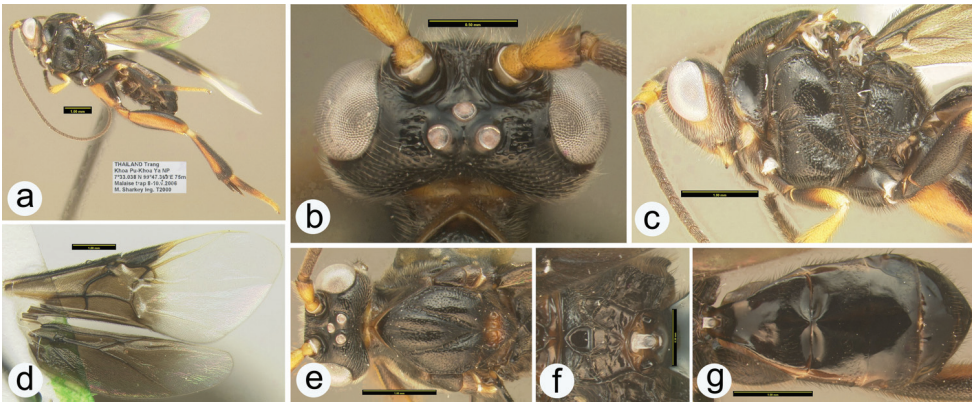


Figure 14. *Zelodia ratanae* sp.n. **a** lateral habitus **b** dorsal head **c** lateral head and mesosoma **d** wings **e** dorsal head and mesosoma **f** dorsal propodeum **g** dorsal metasoma.

Zelodia saksiti **Sharkey sp.n.**
urn:lsid:zoobank.org:act:AE7C81C4-5E9B-477E-87A0-D80FC221940F
http://species-id.net/wiki/Zelodia_sakstii
Fig. 15

Diagnosis. Mesoscutum mostly melanic except margins pale; hind tibia mostly pale except apex black; propodeum color mostly or entirely melanic.

Description. Body length 8.4 mm (7.2–8.4). **Head.** 41 (40–41) flagellomeres. Median ocellus diameter narrower than space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli partly smooth, otherwise with weak punctures. Metapleuron sparsely covered with setae. Fore wing cells weakly infuscate, veins melanic. Hind tarsal claw bifid. Length/width of hind femur 2.007/0.533 = 3.8 (3.8–4.0). Lateral surface of hind femur aciculate. **Metasoma.** Length/width ratio of MT1, 1.318/0.62 = 2.1 (2.0–2.1). Ratio of widest point of MT1 to narrowest point 0.620/0.389 = 1.6 (1.6–1.7). **Color.** Mottled yellow, orange, cream-colored and black, head yellow except antenna black, hind leg black except most of tibia pale.

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H036/ATRMK142-09/JQ763444.

Distribution. Widespread throughout western Thailand. Distribution map can be found at http://purl.org/thaimap/saksiti

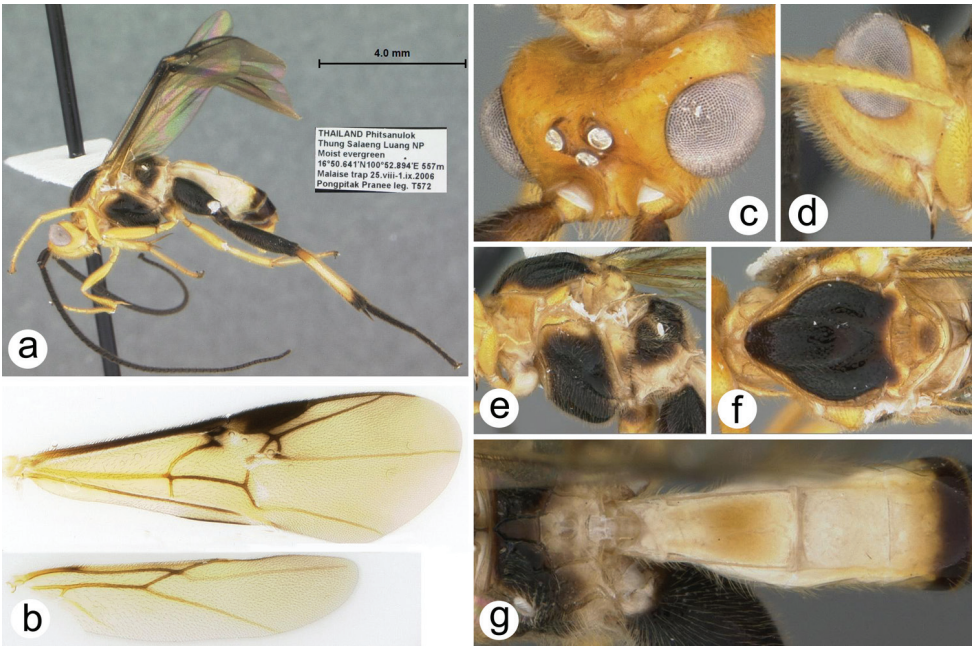


Figure 15. *Zelodia saksiti* sp.n. **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum and MT1-MT3.

Etymology. Dedicated to Saksit Poonsapsiri, one of the chiefs of Phataem National Park.

Material examined. Holotype ♀. H0324 [QSBG], Thailand, Khao Sok NP, Head quarters, 115m, 8.915°N, 98.53°E, MT, 12-19.v.2009.

Paratypes. ♂, Thailand: Salaeng Luang NP: 557m, 16.844°N, 100.882°E, MT, 25.viii–1.ix.2006: H0036 [QSBG], H8464 [UKM]; 479m, 16.839°N, 100.863°E, MT, 11–18.viii.2006: H5996 [QSBG]; ♀, Khao Sok NP, Headquarters, 155m, 8.915°N, 98.53°E, MT, 9–16.vi.2009: H0663 [HIC]; ♂, evergreen forest, MT, 1988: H8490[BMNH]; ♀, Kaeng Krachan NP, km16/road/stream2, 320m, 12.802°N, 99.444°E, MT, 25.v–1.vi.2009: H0920 [HIC]; ♀, Doi Chiangdao NP: Headquarters, 491m, 19.405°N, 98.922°E, MT, 18–25.ix.2007: H4108 [QSBG]; Pha Tang substation, 526m, 19.416°N, 98.915°E, MT, 28.viii–4.ix.2007: H5967 [UKM].

Zelodia surachaii **Sharkey sp.n.**
urn:lsid:zoobank.org:act:D1619B8D-BE53-440D-A637-B1A40338B4A7
http://species-id.net/wiki/Zelodia_surachaii
Fig. 16

Diagnosis. Mesoscutum entirely melanic; hind tibia all melanic; head (not including mouthparts or antenna) melanic; apex of flagellum pale, contrasting with melanic base. Median tergite 1 white or cream colored.

Description. Body length 6.6 mm (6.6–8.3). **Head.** 41 flagellomeres. Median ocellus diameter narrower than space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli mostly or entirely crenulate. Metapleuron with moderately dense setae. Fore wing cells weakly infuscate, veins and stigma melanic. Hind tarsal claw bifid. Length/width of hind femur 2.019/0.511 = 4.0 (4.0–4.7). Lateral surface of hind femur aciculate. **Metasoma.** Length/width ratio of MT1, 1.117/0.518 = 2.2 (2.2–2.3). Ratio of widest point of MT1 to narrowest point 0.518/0.427 = 1.2 (1.2–1.4). **Color.** Black except mouthparts yellow, apical 12 flagellomeres yellowish brown, MT1 cream colored, L1 and L2 and basal sterna white.

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H389/ATRMK207-11/JQ763445.

Distribution. Taiwan, peninsular Malaysia and Thailand. Distribution map can be found at http://purl.org/thaimap/surachaii

Etymology. Dedicated to Mr. Surachai Pransil, chief of Khao Kitchagoot National Park.

Material examined. Holotype ♀. H0389 [QSBG] Thailand, Kaeng Krachan NP, Panernthung/km27, 950m, 12.819°N, 99.375°E, MT, 18–25.vii.2008.

Paratypes. ♀, Malaysia, Cameron Highlands, Tanah Rata, 4.475°N, 101.38°E, MT, iii–iv.2001: H1122 [UKM]; ♂, Taiwan, Taipei Co., Chuntou, 9.iv.1999: H8492 [FSCA].

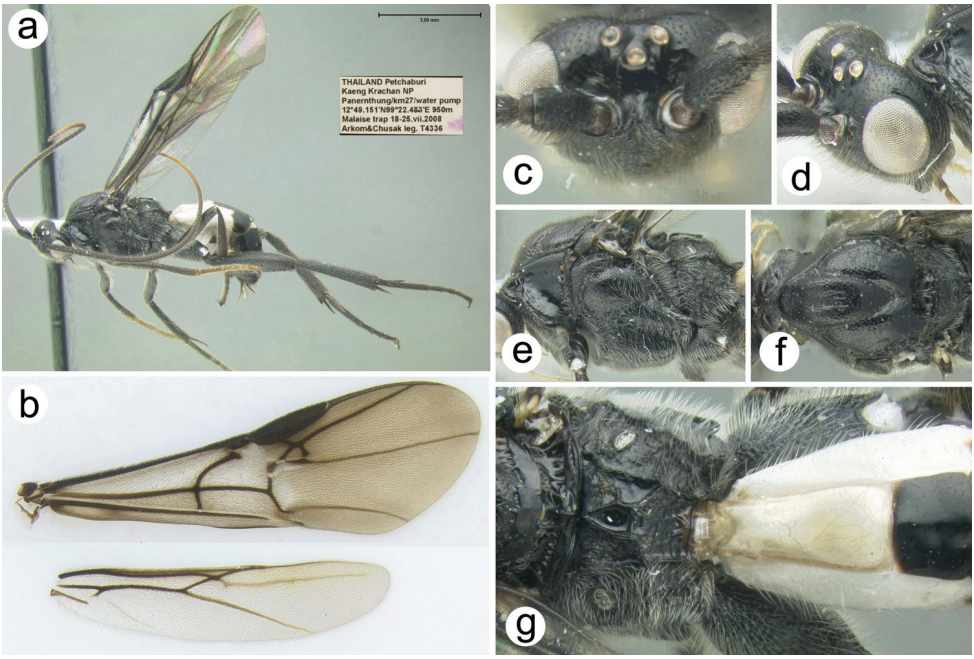


Figure 16. *Zelodia surachaii* sp.n. **a** lateral habitus **b** wings **c** dorsal head **d** dorsolateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum and MT1-MT2.

Zelodia suyaneeae **Sharkey sp.n.**
urn:lsid:zoobank.org:act:5B1641DD-9A03-4B56-B7B7-8A1749AE17FE
http://species-id.net/wiki/Zelodia_suyaneeae
Fig. 17

Diagnosis. Hind femur all pale; mesoscutum entirely pale; hind tibia mostly pale except apex and sometimes extreme base black; stigma partly or entirely yellow; median ocellus distinctly narrower than space between lateral ocelli; lateral surface of hind femur sparsely punctate, spaces between punctures wider than diameter of punctures.

Description. Body length 5.7 mm (5.7–6.4). **Head.** 40 (40–45) flagellomeres. Median ocellus diameter narrower than space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli partly smooth, otherwise with weak punctures. Metapleuron sparsely covered with setae. Fore wing cells hyaline basally, weakly infuscate apically, veins yellow basally, melanic apically and around parastigma, stigma yellow in basal third. Hind tarsal claw bifid. Length/width of hind femur 1.856/0.531 = 3.5 (3.4–4.4). Lateral surface of hind femur punctate. **Metasoma.** Length/width ratio of MT1, 0.87/0.434 = 2.0 (2.0–2.5). Ratio of widest point of MT1 to narrowest point 0.434/0.269 = 1.3 (1.3 – 1.4).

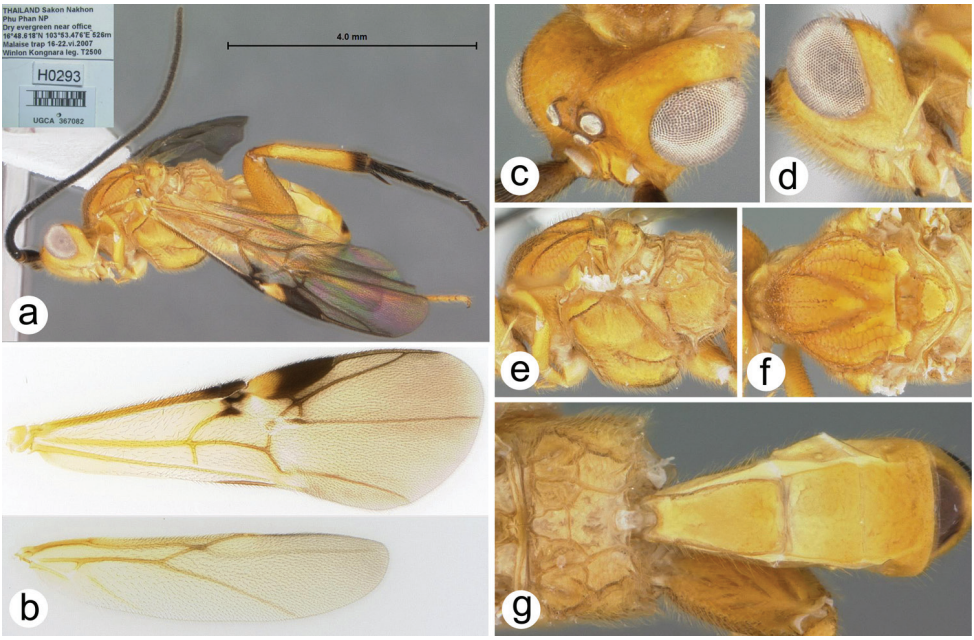


Figure 17. *Zelodia suyaneeae* sp.n. **a** lateral habitus **b** wings **c** dorsal head **d** dorsolateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum and metasoma.

Color. Yellow except as follows: flagellum melanic, lateral surface of scape brown, apex of hind tibia and entire tarsus melanic.

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H1603/ATRMK321-11/JQ763446; H383/ATRMK206-11/JQ763447.

Distribution. Widespread in northern and central Thailand. Distribution map can be found at http://purl.org/thaimap/suyaneeae

Etymology. Dedicated to Dr. Suyanee Vessabutr. She was the deputy director of QSBG and was of great assistance to us in providing space and resources at the museum.

Material examined. Holotype ♀. H1603 [QSBG], Thailand, Chae Son NP, Visitor center, 18.836°N, 99.4739°E, MT, 15-22.ix.2007.

Paratypes. ♀, Thailand, Khuean Srinagarindra NP, 210m, 14.5°N, 98.884°E, MT, 26.iii-2.iv.2009: H0355 [QSBG], H0359 [QSBG]; 22–29.i.2009: H0383 [HIC]; Chae Son NP, Nature Trail; 507m, 18.836°N, 99.473°E, MT, 14–21.x.2007: H4103 [HIC]; 1–8.x.2007: H4119 [HIC]; Doi Chiangdao NP, Headquarters, 491m, 19.405°N, 98.922°E, MT: 18–25.ix.2007: H4113 [HIC]; 19.404°N, 98.9218°E, MT, 21–27.v.2008: H0891 [UKM]; Phu Kradueng NP, 274m, 16.942°N, 101.694°E, MT, 26.iv–3.v.2008: H0572 [UKM]; Kaeng Krachan NP,km16/road/stream2, 320m, 12.802°N, 99.444°E, MT, 25.v–1.vi.2009: H0921 [UKM]; ♂, Phu Phan NP, 526m, 16.81°N, 103.891°E, MT, 16–22.vi.2007: H0293 [QSBG].

Zelodia toyae **Sharkey sp.n.**
urn:lsid:zoobank.org:act:26B4E73C-65B5-4589-AB1D-BBD907DE0FDA
http://species-id.net/wiki/Zelodia_toyae
Fig. 18

Diagnosis. Hind femur all pale; mesoscutum entirely pale; hind tibia mostly pale except apex black; median ocellus about as wide as or wider than space between lateral ocelli; stigma partly yellow.

Description. Body length 7.6 mm. **Head.** 41 flagellomeres. Median ocellus diameter equal to the space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli partly smooth, otherwise with weak punctures. Metapleuron sparsely covered with setae. Fore wing cells hyaline basally, weakly infuscate apically, veins yellow basally except costa mostly melanic, veins melanic apically and around parastigma, stigma yellow in basal third. Hind tarsal claw bifid. Length/width of hind femur 2.25/0.54 = 4.2. Lateral surface of hind femur punctate. **Metasoma.** Length/width ratio of MT1, 1.28/0.59 = 2.2. Ratio of widest point of MT1 to narrowest point 0.59/0.325 = 1.8. **Color.** Yellow except as follows: flagellum melanic, lateral surface of scape brown, apex of hind tibia and entire tarsus melanic.

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H381/ATRMK205-11/JQ763448.

Distribution. Known only from the type locality in northwestern Thailand. Distribution map can be found at http://purl.org/thaimap/toyae

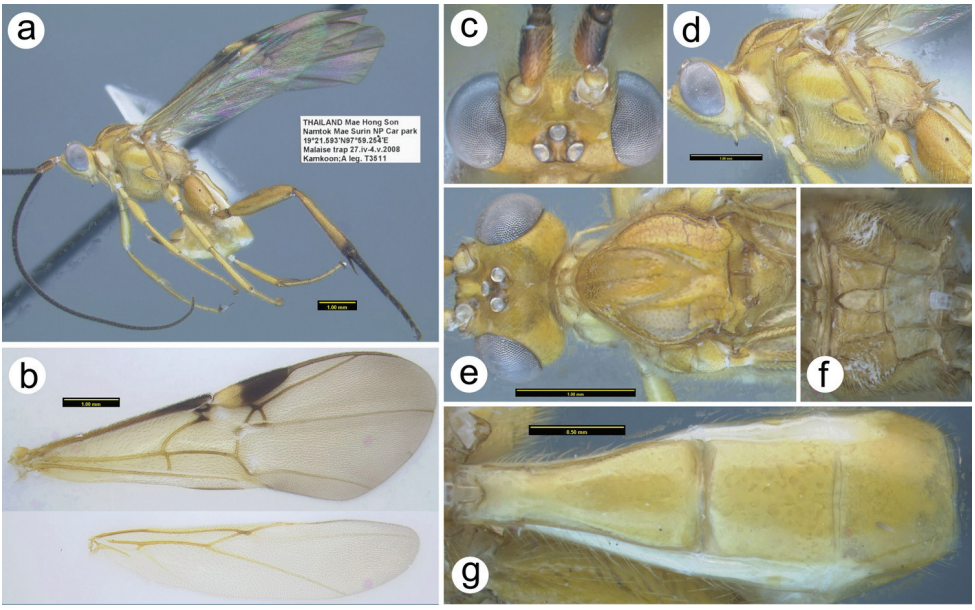


Figure 18. *Zelodia toyae* sp.n. **a** lateral habitus **b** wings **c** dorsal head **d** lateral head and mesosoma **e** dorsal head and mesosoma **f** dorsal propodeum **g** dorsal metasoma.

Etymology. Dedicated to Ms. Chayanit (Toy) Satatha. Toy was the sorter of Diptera for the TIGER project and is currently a technician at QSBG. The species name reflects her nick-name, Toy.

Material examined. Holotype ♀. H0381 [QSBG], Thailand, Namtok Mae Surin NP, Car park, 19.36°N, 97.988°E , MT, 27.iv–4.v.2008.

Zelodia uthaii Sharkey sp.n.

urn:lsid:zoobank.org:act:1BE5192A-344A-4A1D-9959-0255A5A9976A
http://species-id.net/wiki/Zelodia_uthaii
Fig. 19

Diagnosis. Mesoscutum mostly melanic except margins pale; hind tibia mostly pale except apex and extreme base black; hind femur all melanic; apical half of wing not noticeably more infuscate than base.

Description. Body length. 6.1 mm. **Head.** 42 flagellomeres. Median ocellus diameter equal to the space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli mostly or entirely crenulate. Metapleuron sparsely covered with setae. Fore wing cells hyaline basally, weakly infuscate distally, veins yellow basally except costa black, veins melanic distally, stigma melanic. Hind tarsal claw bifid.

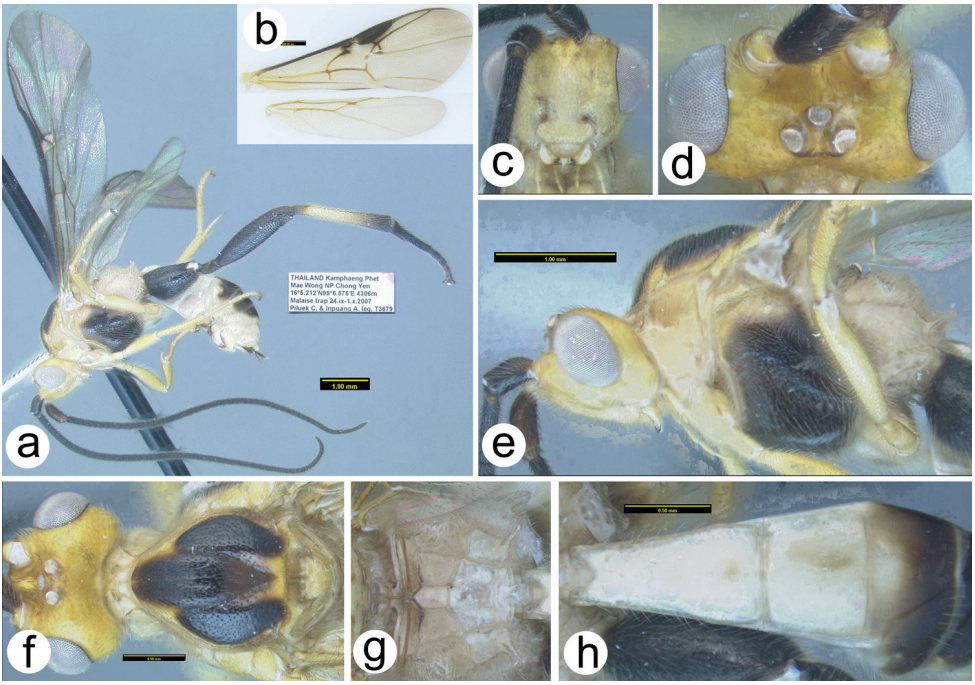


Figure 19. *Zelodia uthaii* sp.n. **a** lateral habitus **b** wings **c** anterior head **d** dorsal head **e** lateral head and mesosoma **f** dorsal head and mesosoma **g** dorsal propodeum **h** dorsal MT1–MT3.

Length/width of hind femur 2.05/0.54 = 3.8. Lateral surface of hind femur aciculate. **Metasoma.** Length/width ratio of MT1, 1.13/0.61 = 1.9. Ratio of widest point of MT1 to narrowest point 0.61/0.38 = 1.6. **Color.** Mottled yellow, cream-colored and black, head yellow except antenna black, hind leg black except most of tibia pale.

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H309/ATRMK450-11/JQ763449.

Distribution. Known only from the type locality in western Thailand. Distribution map can be found at http://purl.org/thaimap/uthaii

Etymology. Dedicated to Mr. Uthai Promnaree, one of the chiefs of Phataem National Park.

Material examined. Holotype ♀. H0309 [QSBG], Thailand, Mae Wong NP, Chong Yen, 1306m, 16.087°N, 99.11°E, MT, 24.ix–1.x.2007.

Zelodia wangi **Sharkey sp.n.**
urn:lsid:zoobank.org:act:14DE5D59-9589-46DA-AE41-D0530F98EB1C
http://species-id.net/wiki/Zelodia_wangi
Fig. 20

Diagnosis. Scutum and MT1 yellow; hind leg, including tibia, melanic.

Description. Body length 6.7 mm (6.5–7.1). **Head.** 43 (41–45) flagellomeres. Median ocellus diameter equal to the space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli partly smooth, otherwise with weak punctures. Metapleuron sparsely covered with setae. Fore wing cells very weakly infuscate with a yellowish tinge basally, veins yellow basally, melanic in apical half, stigma yellow in basal fourth (or entirely melanic). Hind tarsal claw bifid. Length/width of hind femur 2.0/0.5 = 3.9 (3.7–3.9). Lateral surface of hind femur punctate. **Metasoma.** Length/width ratio of MT1, 1.156/0.481 = 2.4 (2.4–2.5). Ratio of widest point of MT1 to narrowest point 0.481/0.349 = 1.4 (1.4). **Color.** Yellow except as follows: scape and pedicel pale brown, flagellum brown, hind leg mostly brown in females with areas near joints and most of tibia pale brown to yellow, anterior metasomal laterotergites and sterna cream-colored, median tergites entirely yellow in holotype (but some female paratypes have pale brown markings on apical tergites; males as in females but with hind leg mostly to entirely black, and apical terga and sterna extensively black).

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H074/JQ763457; H023/JQ763455; H073/JQ763456; H019/JQ763458; H025/JQ763460; H084/JQ763459.

Distribution. Widespread throughout Thailand. Distribution map can be found at http://purl.org/thaimap/wangi

Etymology. Dedicated to Mr. Wang Saeyang, who was the sorter for Hymenoptera for the TIGER project.

Material examined. Holotype ♀. H0057 [QSBG], Thailand, Khoa Chong, Forest Research Stn., 75m, 7.551°N, 99.789°E, MT, vii–xi.2005.

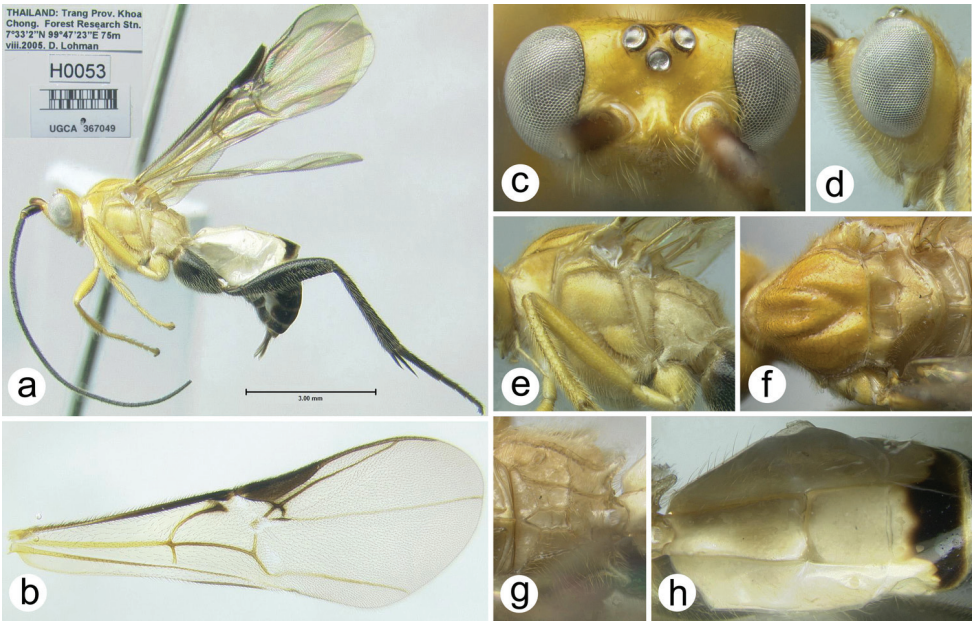


Figure 20. *Zelodia wangi* sp. n. **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum **h** dorsal MT1–MT3.

Paratypes. ♀, Thailand: Khoa Chong, Forest Research Stn., 75m, 7.551°N, 99.789°E, MT, xi.2005: H0019 [QSBG], H5990 [UKM], H0084 [HIC]; x.2005: H0023 [QSBG]; viii.2005: H0054 [QSBG], H5906 [UKM], H5988 [UKM], H5991 [UKM], H5994 [UKM], H0061 [UKM]; ♂, x.2005: H5992 [UKM]; viii.2005: H5986 [UKM]; ♀, Thailand, Nayong Khaochong, 75m, 7.561°N, 99.886°E, MT, 24–27.vi.2005: H0025 [QSBG], H0034 [QSBG]; ♀, Nayong Khaochong, 75m, 7.561°N, 99.886°E, MT, 15–18.vi.2005: H0074 [HIC]; 6-8.vii.2005: H0076 [HIC]; ♂, 26–30.vii.2005: H0073 [HIC]; ♀, Khao Sok NP, Headquarters, 115m, 8.915°N, 98.53°E, MT, 12–19.v.2009: H0391 [QSBG]; 17–24.iii.2009: H0475 [QSBG]; 8–15.ix.2008: H0477 [QSBG]; ♂, 28.x–4.xi.2008: H0304 [QSBG]; 25.xi-2.xii.2008: H0310 [QSBG]; 28.iv–5.v.2009: H0332 [QSBG]; 21-28.iv.2009: H0592 [UKM]; 9–16.xii.2008: H0673 [HIC]; 18–25.xi.2008: H0675 [HIC]; 24-31.iii.2009: H0683 [HIC]; 31.viii–8.ix.2008: H0758 [HIC]; 9–16.vi.2009: H0972 [HIC], H0691 [HIC], H0666 [UKM]; ♂, Namtok Yong NP, 95m, 8.174°N, 99.742°E, MT, 9–16.ii.2009: H0351 [QSBG]; Namtok Mae Surin NP, Near Visitor Ctr, 228m, 19.358°N, 97.988°E, MT, 8–15.vii.2007: H5987 [UKM], H0617 [UKM], H0620 [UKM]; Namtok Mae Surin NP, 334m, 19.344°N, 97.988°E, MT, 26.viii–2.ix.2007: H5980 [HIC]; ♂, Namtok Yong NP, 80m, 8.174°N, 99.742°E, MT, 23–30.ix.2008: H0979 [HIC]; Mae Surin near visitor center, 228m, 19.489°N, 98.056°E, MT. 15–22.vii.2007: H0442 [QSBG], H0443 [QSBG]; ♀, Khao Pu-Khao Ya NP, 75m, 7.551°N, 99.789°E, MT, 28–30.v.2006: H5989 [UKM], H5995 [UKM]; 10–13.ii.2006:

H5993 [UKM]; Tat Tone NP, 250m, 15.984°N, 102.035°E, litter, 23–26.vi.2006: H5997 [UKM]; Kaeng Krachan NP, km33/helipad, 735m, 12.836°N, 99.345°E, MT, 18–25.ii.2009: H0623 [UKM]; ♂, Doi Chiangdao NP, Pha Tang substation, 526m, 19.4163°N, 98.9147°E, MT, 3–10.xii.2007: H0926 [HIC].

Zelodia wichaii **Sharkey sp.n.**
urn:lsid:zoobank.org:act:3FF67B83-DB04-4CB8-A339-47B60BB77C10
http://species-id.net/wiki/Zelodia_wichaii
Fig. 21

Diagnosis. Hind femur all pale; mesoscutum entirely pale; hind tibia mostly pale except apex black; stigma partly or entirely yellow; ocelli median ocellus distinctly narrower than space between lateral ocelli; lateral surface of hind femur densely punctate to aciculate, spaces between punctures not wider than diameter of punctures.

Description. Body length 6.3 mm (6.0–6.4). **Head.** 40 flagellomeres. Median ocellus diameter narrower than space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli partly smooth, otherwise with weak punctures. Metapleuron sparsely covered with setae. Fore wing cells hyaline basally, weakly

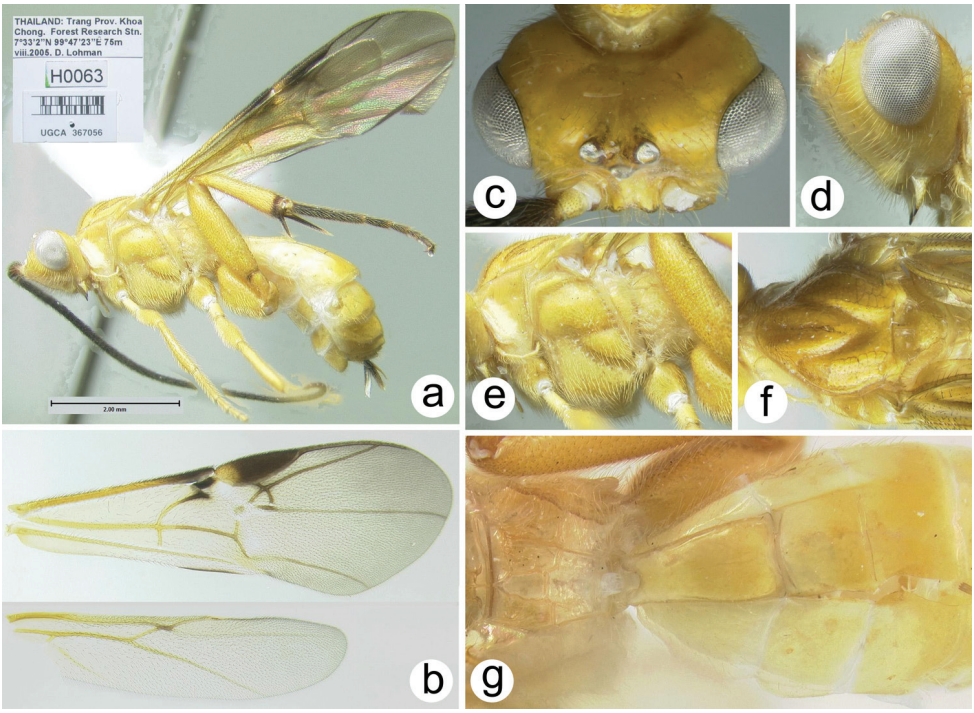


Figure 21. *Zelodia wichaii* sp.n. **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum and MT1–MT3.

infuscate apically, veins yellow basally, melanic apically and around parastigma, stigma yellow in basal third. Hind tarsal claw bifid. Length/width of hind femur 1.027/0.519 = 3.7 (3.4–3.7). Lateral surface of hind femur aciculate. **Metasoma.** Length/width ratio of MT1, 1.038/0.49 = 2.1 (2.0–2.1). Ratio of widest point of MT1 to narrowest point 0.49/0.313 = 1.6. **Color.** Yellow except as follows: antenna melanic, apex of hind tibia and entire tarsus melanic.

Molecular data. TaxaBank#/Genbank Accession: H063/JQ763453.

Distribution. Recorded from two localities in peninsular Thailand. Distribution map can be found at http://purl.org/thaimap/wichaii

Etymology. Dedicated to Mr. Wichai Srisuka, the curator of insects at QSBG.

Material examined. Holotype ♀. H0063 [QSBG], Thailand, Khoa Chong, Trang, 75m, 7.551°N 99.789°E, MT, viii.2005.

Paratype. ♀, Thailand, Namtok Yon NP, Klong Jang Waterfall, 154m, 8.338°N, 99.827°E, MT, 12–19.v.2009: H0594 [HIC].

Zelodia wirati **Sharkey sp.n.**
urn:lsid:zoobank.org:act:73E375A4-5D6C-4668-9A49-95F6BB6B1E5A
http://species-id.net/wiki/Zelodia_wirati
Fig. 22

Diagnosis. Hind tibia mostly pale except apex black; hind femur all melanic; mesoscutum entirely pale; median ocellus about as wide as or wider than space between lateral ocelli.

Description. Body length 6.9 mm (male 5.8 – 6.7 mm). **Head.** 41 flagellomeres (41–43 males). Median ocellus diameter equal to the space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli partly smooth, otherwise with weak punctures. Metapleuron sparsely covered with setae. Fore wing cells hyaline basally, weakly infuscate apically, veins yellow basally, except costa mostly melanic, melanic apically and around parastigma, stigma yellow in basal fifth. Hind tarsal claw bifid. Length/width of hind femur 2.28/.58 = 3.9 (3.45 – 3.52 males). Lateral surface of hind femur punctate. **Metasoma.** Length/width ratio of MT1, 1.22/.633 = 1.93. Ratio of widest point of MT1 to narrowest point .633/.385 = 1.6 (1.4–1.6). **Color.** Mostly yellow, black as follows: antenna except scape brown medially, hind leg except basal 4/5 of tibia yellow.

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H012/JQ763454; H949/ATRMK451-11/JQ763450.

Distribution. Recorded from three localities in northwestern Thailand. Distribution map can be found at http://purl.org/thaimap/wirati

Etymology. Dedicated to Mr. Wirat Sukho, collector for the TIGER project at Khao Yai National Park.

Material examined. Holotype ♀. H0981 [QSBG], Thailand, Doi Phahompok NP, 569m, 19.966°N, 99.156°E, MT, 28.viii–4.ix.2007.

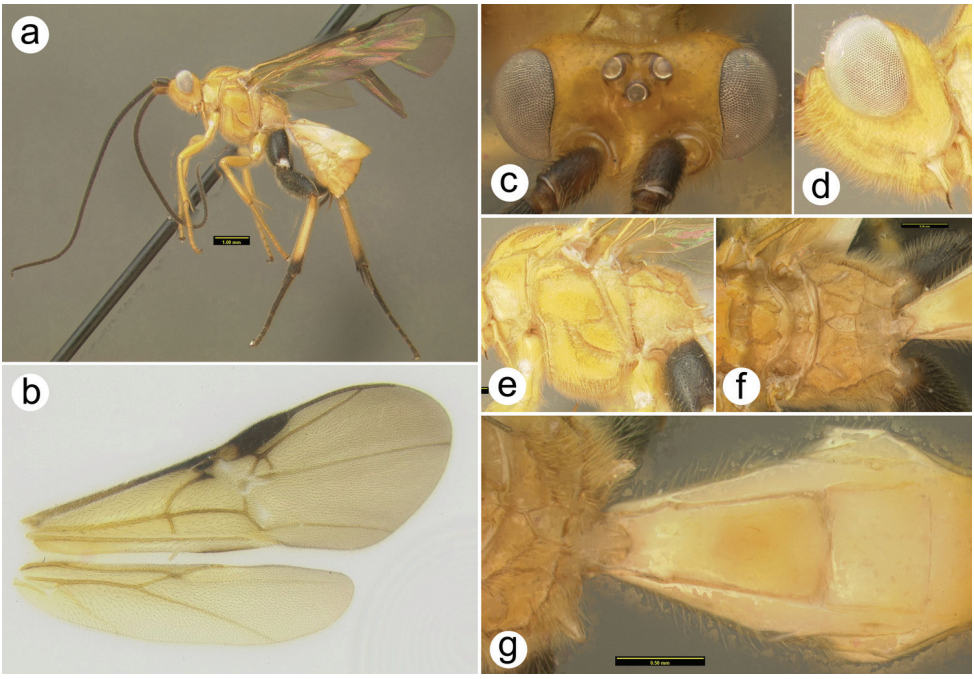


Figure 22. *Zelodia wirati* sp.n. **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal propodeum **g** dorsal MT1–MT2.

Paratypes. ♂ Thailand: Doi Inthanon NP, campground pond, 1200m, 18.544°N, 98.525°E, MT, 16–24.viii.2006: H0012 [QSBG]; Doi Chiangdao NP, Headquarters, 491m, 19.404°N, 98.9218°E, MT, 15–22.iv.2008: H0909 [HIC]; Chae Son NP, Doi Laan, 1528m, 18.825°N, 99.411°E, MT, 22–28.iii.2008: H949 [UKM].

***Zelodia wirotei* Sharkey sp.n.**
urn:lsid:zoobank.org:act:8895B38A-E94B-42C3-82E8-77E10978141D
http://species-id.net/wiki/Zelodia_wirotei
Fig. 23

Diagnosis. Hind tibia all melanic; mesoscutum entirely pale; MT1 all white or cream colored, sometimes with a bit of melanic color subapically.

Description. Body length 5.9 mm. **Head.** 35 (35–37) flagellomeres. Median ocellus diameter equal to the space between lateral ocelli. Vertex sparsely and weakly punctate. **Mesosoma.** Notauli mostly or entirely crenulate. Metapleuron densely covered with setae. Fore wing cells all weakly infuscate, veins all melanic. Hind tarsal claw bifid. Length/width of hind femur 1.714/0.475 = 3.5 (3.5–3.7).

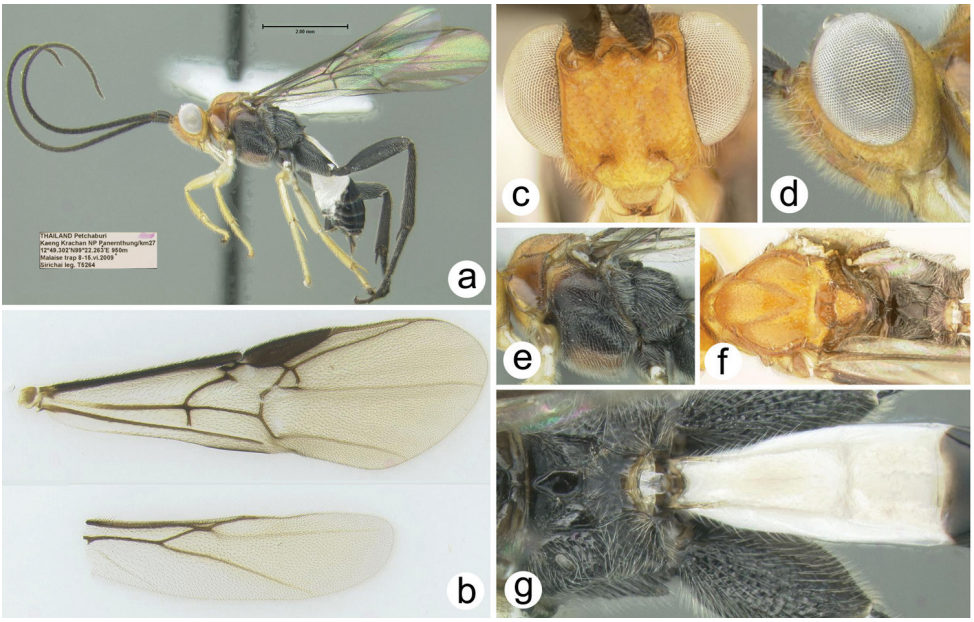


Figure 23. *Zelodia wirotei* sp.n. **a** lateral habitus **b** wings **c** anterior head **d** lateral head **e** lateral mesosoma **f** dorsal mesosoma **g** dorsal propodeum and MT1–MT2.

Lateral surface of hind femur aciculate. **Metasoma.** Length/width ratio of MT1, 3.978/0.350 = 2.8 (2.8–3.0). Ratio of widest point of MT1 to narrowest point 0.350/0.248 = 1.4. **Color.** Mostly black with orange, white, brown and cream color; head mostly orange, except area around ocelli slightly darker and antenna black; prothorax orange to brown; mesoscutum orange; scutellum brown, mesopleuron mostly black but orange-brown dorsally; fore leg yellow to cream colored; mid leg yellow to cream colored except coxa mostly melanic; MT1, M2 and part of MT3 cream colored (MT1 sometimes with a tan area posteromedially); anterior laterotergites and sterna white.

Molecular data. TaxaBank#/BOLD Process ID/Genbank Accession: H990/ATRMK272-11/JQ763451.

Distribution. Recorded only from the type locality south-west of Bangkok**.** Distribution map can be found at http://purl.org/thaimap/wirotei

Etymology. Dedicated to Mr. Wirote Naknan, chief of Namnao National Park.

Material examined. Holotype ♀. H0634 [QSBG], Thailand, Kaeng Krachan NP, km33/helipad, 735m, 12.836°N, 99.345°E, MT, 11–18.v.2009.

Paratype. ♀, Thailand, Kaeng Krachan NP, Panernthung/km27, 950m, 12.822°N, 99.371°E, MT, 8–15.vi.2009: H0990 [HIC].

Acknowledgements

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Appendix 1

DELTA data matrix, images, and other files to the dichotomous key for *Zelodia* (Hymenoptera: Braconidae: Agathidinae) from Thailand. doi: 10.3897/JHR.26.2527.app1

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Citation: Sharkey MJ, Stoelb SAC (2012) Revision of *Zelodia* (Hymenoptera, Braconidae, Agathidinae) from Thailand. Journal of Hymenoptera Research 26: 31–71. doi: 10.3897/JHR.26.2527.app1

Appendix 2

DELTA data matrix, images, and other files to species descriptions for *Zelodia* (Hymenoptera: Braconidae: Agathidinae) from Thailand. doi: 10.3897/JHR.26.2527.app2

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Citation: Sharkey MJ, Stoelb SAC (2012) Revision of *Zelodia* (Hymenoptera, Braconidae, Agathidinae) from Thailand. Journal of Hymenoptera Research 26: 31–71. doi: 10.3897/JHR.26.2527.app2

Appendix 3

Interactive key, in IntKey format, to *Zelodia* (Hymenoptera: Braconidae: Agathidinae) from Thailand. doi: 10.3897/JHR.26.2527.app3

Explanation note: To run the identification key, you will need Windows 95/NT or a later version.

You also need to download Intkey software and reboot your computer, if it is not already installed. The software package, Intkey, can be downloaded from http://delta-intkey.com/www/programs.htm. Once Intkey is installed you need only click on the .ink file (below) and the key will open. Click on any character on the left to begin.

More details on how to use Intkey efficiently are found at http://florabase.calm.wa.gov.au/help/keys/intkey_tutorial.pdf

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Citation: Sharkey MJ, Stoelb SAC (2012) Revision of *Zelodia* (Hymenoptera, Braconidae, Agathidinae) from Thailand. Journal of Hymenoptera Research 26: 31–71. doi: 10.3897/JHR.26.2527.app3

Appendix 4

Morphological terms matched to the Hymenoptera Anatomy Ontology. Identifiers (URIs) represent anatomical concepts in HAO version http://purl.obolibrary.org/obo/hao/2011-05-18/hao.owl

Abbreviations		URI
LT3	abdominal laterotergite 3	http://purl.obolibrary.org/obo/HAO_0001456
MT1	abdominal mediotergite 1	http://purl.obolibrary.org/obo/HAO_0001463
MT2	abdominal mediotergite 2	http://purl.obolibrary.org/obo/HAO_0001150
MT3	abdominal mediotergite 3	http://purl.obolibrary.org/obo/HAO_0001147
	antenna	http://purl.obolibrary.org/obo/HAO_0000101
	apical tarsomere	http://purl.obolibrary.org/obo/HAO_0000994
	area	http://purl.obolibrary.org/obo/HAO_0000146
	body	http://purl.obolibrary.org/obo/HAO_0000182
	carina	http://purl.obolibrary.org/obo/HAO_0000188
	costa	http://purl.obolibrary.org/obo/HAO_0000225
	coxa	http://purl.obolibrary.org/obo/HAO_0000228
	femur	http://purl.obolibrary.org/obo/HAO_0000327

Abbreviations		URI
	flagellomere	http://purl.obolibrary.org/obo/HAO_0000342
	flagellum, flagella	http://purl.obolibrary.org/obo/HAO_0000343
	fore leg	http://purl.obolibrary.org/obo/HAO_0000349
	fore wing	http://purl.obolibrary.org/obo/HAO_0000351
	frons	http://purl.obolibrary.org/obo/HAO_0001044
	head	http://purl.obolibrary.org/obo/HAO_0000397
	hind femur	http://purl.obolibrary.org/obo/HAO_0001140
	hind leg	http://purl.obolibrary.org/obo/HAO_0000399
	hind tarsus	http://purl.obolibrary.org/obo/HAO_0001141
	hind tibia	http://purl.obolibrary.org/obo/HAO_0000631
	lateral ocelli	http://purl.obolibrary.org/obo/HAO_0000481
	laterotergite	http://purl.obolibrary.org/obo/HAO_0001861
	leg	http://purl.obolibrary.org/obo/HAO_0000494
	median ocellus	http://purl.obolibrary.org/obo/HAO_0000526
	mediosternite	http://purl.obolibrary.org/obo/HAO_0001654
S2	mediosternite 2	http://purl.obolibrary.org/obo/HAO_0001829
S3	mediosternite 3	http://purl.obolibrary.org/obo/HAO_0001830
	mediotergite	http://purl.obolibrary.org/obo/HAO_0001860
	mesopleuron	http://purl.obolibrary.org/obo/HAO_0000566
	mesoscutum	http://purl.obolibrary.org/obo/HAO_0001490
	mesosoma	http://purl.obolibrary.org/obo/HAO_0000576
	mesothorax	http://purl.obolibrary.org/obo/HAO_0000583
	metapleuron	http://purl.obolibrary.org/obo/HAO_0001869
	metasoma	http://purl.obolibrary.org/obo/HAO_0000626
	metapectal-propodeal complex	http://purl.obolibrary.org/obo/HAO_0000604
	mid leg	http://purl.obolibrary.org/obo/HAO_0000636
	mouthparts	http://purl.obolibrary.org/obo/HAO_0000639
	notaulus	http://purl.obolibrary.org/obo/HAO_0000647
	ocellus	http://purl.obolibrary.org/obo/HAO_0000661
	ovipositor	http://purl.obolibrary.org/obo/HAO_0001004
	palpi	http://purl.obolibrary.org/obo/HAO_0000683
	pedicel	http://purl.obolibrary.org/obo/HAO_0000706
	propodeum	http://purl.obolibrary.org/obo/HAO_0001249
	prothorax	http://purl.obolibrary.org/obo/HAO_0000874
	puncture	http://purl.obolibrary.org/obo/HAO_0000885
	scape	http://purl.obolibrary.org/obo/HAO_0000908
	scutellar disc	http://purl.obolibrary.org/obo/HAO_0000915
	scutellar sulcus	http://purl.obolibrary.org/obo/HAO_0000917
	scutellum	http://purl.obolibrary.org/obo/HAO_0000572
	scutum	http://purl.obolibrary.org/obo/HAO_0000575
	metasomal segment	http://purl.obolibrary.org/obo/HAO_0001969
	seta	http://purl.obolibrary.org/obo/HAO_0000935
	sternite	http://purl.obolibrary.org/obo/HAO_0000955
	stigma	http://purl.obolibrary.org/obo/HAO_0000957
	tarsal claw	http://purl.obolibrary.org/obo/HAO_0000989

Abbreviations		**URI**
	tarsomere	http://purl.obolibrary.org/obo/HAO_0000991
	tarsus	http://purl.obolibrary.org/obo/HAO_0000992
	tendon	http://purl.obolibrary.org/obo/HAO_0000996
	terga	http://purl.obolibrary.org/obo/HAO_0001006
	tergite	http://purl.obolibrary.org/obo/HAO_0001005
	basal tooth	http://purl.obolibrary.org/obo/HAO_0001219
	trochantellus	http://purl.obolibrary.org/obo/HAO_0001033
	trochanter	http://purl.obolibrary.org/obo/HAO_0001034
	vein	http://purl.obolibrary.org/obo/HAO_0001095
	vertex	http://purl.obolibrary.org/obo/HAO_0001077
	wing	http://purl.obolibrary.org/obo/HAO_0001089
	wing cell	http://purl.obolibrary.org/obo/HAO_0001091

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RESEARCH ARTICLE

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An identification key to species in the *mali* complex of *Aphelinus* (Hymenoptera, Chalcidoidea) with descriptions of three new species

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Abstract

The *Aphelinus mali* complex consists of eleven described species. Monophyly of this complex is well supported by a combination of traits: (1) a single complete row of setae proximal to the linea calva of the fore wing, with a few additional setae in the angle between this row and the marginal vein; (2) linea calva open (no setae at its posterior edge); (3) head and body dark except for parts of the metasoma; (4) meso- and metacoxae dark; (5) metafemur pale, (6) metatibia dark. Species within the complex have been distinguished by color and shape of antennal segments (particularly the third funicular segment), color of legs and metasoma, and relative length of ovipositor versus mesotibia. We provide a key for identifying species in the *mali* complex, and describe three new species, *Aphelinus glycinis* **sp. n.**, *Aphelinus rhamni* **sp. n.**, and *Aphelinus coreae* **sp. n.** from material in laboratory cultures originally reared from soybean aphid in China and Korea as candidates for biological control of soybean aphid, *Aphis glycines*.

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Keywords
cryptic species, taxonomy, biological control

Introduction

The genus *Aphelinus* (Hymenoptera: Aphelinidae) comprises 84 recognized species (Noyes 2011), all of which are internal parasitoids of aphids. There are several complexes of closely related species in the genus, and identification of species within these complexes has been problematic (Heraty et al. 2007), leading to a confused literature on host specificity. The *Aphelinus mali* complex comprises 11 described species (Ashmead 1888; Evans et al. 1995; Gahan 1924; Girault 1913; Haldeman 1851; Hayat 1998; Prinsloo and Neser 1994; Timberlake 1924; Yasnosh 1963; Zehavi and Rosen 1988), and there are 6 other closely related species (Carver 1980; Hayat 1998; Howard 1917; Kurdjumov 1913; Walker 1839; Yasnosh 1963) that differ from the members of the complex in one or two traits (Table 1). The species within the complex have diverged little in morphology so the taxonomy within the complex has been confused, and many specimens have been identified as *A. mali* (Haldemann) or *A. gossypii* Timberlake that are likely different species based on differences in the aphid host species and geographical regions from which they were collected. We provide a key to identification of species in the *A. mali* complex based on 19 traits coded primarily from species descriptions. We describe three new species that were collected in China and Korea during exploration for natural enemies of the soybean aphid, *Aphis glycines* Matsumura, all of which are candidates for biological control of this important pest.

The genus *Aphelinus* consists of several complexes of cryptic species including the *mali* complex, the *varipes* complex (Heraty et al. 2007), the *asychis* complex (Kazmer et al. 1995, 1996), the *perpallidus* complex (unpublished data), and possibly others. Cryptic species are closely related species that differ little in the morphological features used for taxonomy, but differ critically in physiological, behavioral and ecological traits, such as climatic adaptation and host range (Darling and Werren 1990; DeBach 1969). Recent evidence from molecular studies suggests that cryptic species of hymenopteran parasitoids may be far more common than previously realized (Campbell et al. 1993; Clarke and Walter 1995; Darling and Werren 1990; Kankare et al. 2005a; Kankare et al. 2005b; Kazmer et al. 1996; Molbo et al. 2003; Rincon et al. 2006; Stouthamer et al. 2000; Stouthamer et al. 1999). The success of biological control programs depends on accurate species-level identifications of hosts and natural enemies, but choosing the best parasitoids for biological control programs is complicated by cryptic species (Rosen 1986; Wharton et al. 1990). Because cryptic species are difficult to recognize, studies on host ranges of parasitoids have often confounded more than one parasitoid species (Clarke and Walter 1995; Hopper et al. 1993), making analysis and prediction of host range difficult. Heightened concern about potential impacts of introduced parasitoids on non-target species makes accurate prediction of host range crucial to biological control introductions.

Table 1. Species in *Aphelinus mali* complex and related species

Group	Species	Original description
mali complex	*basilicus*	Hayat 1998
	campestris	Yasnosh 1963
	coreae sp. n. [1]	
	engaeus	Prinsloo and Neser 1994
	ficusae	Prinsloo and Neser 1994
	glycinis sp. n. [1]	
	gossypii	Timberlake 1924
	mali	Haldeman 1851
	niger [2]	Girault 1913
	paramali	Zehavi & Rosen 1989
	rhamni sp. n. [1]	
	sanborniae	Gahan 1924
	siphonophorae [2]	Ashmead 1888
	spiraecolae	Evans et al. 1995
related species	*chaonia* [3]	Walker 1839
	prociphili[3]	Carver 1980
	sharpae [3]	Hayat 1998
	brunneus [4]	Yasnosh 1963
	daucicola [4]	Kurdjumov 1913
	lapisligni [4]	Howard 1917

1 new species described in this paper
2 insufficient description to be included in tree or key
3 difference from *mali* complex: more than 1 line of setae in delta region
4 difference from *mali* complex: posterior femur dark

Methods

Three new species in the *A. mali* complex were collected from *Aphis glycines* in the Peoples Republic of China near Beijing and Xiuyan (Liaoning Province) and in the Republic of South Korea near Miryang (Gyeongsangnam Province) and maintained as laboratory cultures at the Beneficial Insects Introduction Research Unit, USDA-ARS, Newark, DE. All of the specimens described below were taken from lab cultures, killed in 95% ethanol, and most were critical-point-dried and card-mounted. Selected specimens were then slide-mounted in Canada balsam. Specimens photographed for coloration (Figs 1–6,15–20, and 29–34) were killed in ethanol and photographed as soon as possible, by placing specimens on a layer of KY® jelly in a small watch glass, submerging the specimen in ethanol, and photographing using a Leica MZ 16 stereomicroscope, fiber optic illumination, a Zeiss Axiomat MRc5 camera, and Helicon Pro image-stacking software. Slide-mounted specimens were photographed using differential interference contrast optics (DIC) with an Olympus BH2 compound microscope, and the same camera and software. Final modifications to images were made using Adobe Photoshop, Adobe Lightroom, and Adobe InDe-

sign. Type material and other specimens examined have been deposited as indicated in the species descriptions. The label data for each specimen has been digitized and all specimens bear individual accession numbers for Texas A&M University Insect Collection (e.g. TAMU x0616203), as well as a machine-readable bar-code. In the verbatim label data provided for holotypes, a single | symbol indicates a new line on a label, and the || symbol indicates a second or third label. Vouchers are maintained at -20°C in molecular grade ethanol at the Beneficial Insect Introduction Research Unit, Newark, Delaware, and at the Department of Entomology, Texas A&M University, College Station, Texas.

We tabulated and coded 19 traits for species in the *A. mali* complex, using the original species descriptions for the most part. These traits included color of scape, pedicel, club, coxae, femora, tibiae, tarsi, and metasoma, as well as shape of third funicle and club (length:width) and length of ovipositor relative to mesotibia. For some traits, males and females differed (e.g., F3 shape, procoxae color) and the values were scored separately. When trait data were lacking from original descriptions, we used data from later descriptions. Trait values for the new species in the complex were taken from specimens freshly killed in ethanol and slide-mounted specimens. These traits were used to construct an on-line, interactive, multiple entry identification key to the *mali* complex which is available on request. Of the 19 traits, 12 proved to be most consistent and useful in distinguishing species, and these are presented in Table 2.

Table 3 is a list of anatomical terms used in the paper followed by URI values (uniform resource identifiers), that will link the terms to precise definitions and illustrations in the Hymenoptera Anatomy Ontology project (see http://portal.hymao.org and http://hymao.org for more information on this initiative). Additional information on morphological terminology in Chalcidoidea is available in Gibson (1997) and http://www.canacoll.org/Hym/Staff/Gibson/apss/chglintr.htm.

The ventral surface of the antennal scape refers to the surface that is ventral when the antennae are deployed, or anterior when the antennae are folded on the face. F1, F2 and F3 refer to the first, second and third segments of the funicle of the antennal flagellum, respectively. T1, T2 etc. refer to metasomal terga. We use the term ovipositor to refer to the anatomical cluster consisting of the first valvula, second valvula, third valvula, first valvifer and second valvifer. Length of the ovipositor is the measurement (generally of a slide-mounted specimen) from the anterior margin of the second valvifer to the posterior (distal) end of the third valvula.

Measurements were made with an eyepiece reticle in a Leica MZ16 microscope or Zeiss standard 16 compound microscope, or from digital images captured using the methods described above. As with any species of *Aphelinus*, users will require series of high quality specimens, both male and female, and both card- or point-mounted and slide-mounted specimens, to obtain confident identifications. Noyes (1982) remains the best guide to techniques for preparing specimens of Chalcidoidea, and we have largely followed his recommendations for card-mounting and slide-mounting specimens.

Table 2. Traits coded for species in *mali* complex of *Aphelinus*.

Species	F3 female[1]	F3 male[2]	Club female[3]	Club male[4]	Procoxa color[5]	Profemur color[6]	Mesofemur color[7]	Protibia color[8]	Mesotibia color[9]	Metatibia color[10]	Metasoma color[11]	Ovipositor to mesotibia[12]
basilicus	1	2	2	2	1	1	1	1	2	1	1	1
campestris	1	1	1	1	1	2	1	1	2	1	2	?
coreae sp. n.	1	1	2	2	1	4	1	3	5	3	2	2
engaeus	1	2	2	2	2	3	4	2	4	3	5	2
ficusae	2	3	2	2	2	3	3	2	3	3	1	1
glycinis sp. n.	2	3	2	2	3	3	4	3	2	3	6	2
gossypii	1	1	1	1	1	2	1	1	1	1	2	2
mali	1	2	2	2	1	2	5	2	1	1	1	3
paramali	2	2	2	2	1	5	2	2	2	2	3	1
rhamni sp. n.	1	1	2	2	1	2	1	1	2	3	2	2
sanborniae	2	3	?	?	1	1	1	4	2	1	4	?
spiraecolae	1	1	1	1	1	3	4	2	4	1	1	3

1- F3 female: 1 = subquadrate, 2 = at least 1.2× longer than wide

2- F3 male: 1 = subquadrate, 2 = 1.2 to 2.0× longer than wide, 3 = more than 2.0× longer than wide

3- Club female: 1 = less than 2.5× as long as wide, 2 = at least 2.5× as long as wide

4- Club male: 1 = less than 3× as long as wide, 2 = at least 3× as long as wide

5- Procoxae: 1 = dark, 2 = yellow, 3 = pale in females, dark grey in males

6- Profemora: 1 = dark, 2 = dark with apex pale, 3 = yellow or pale, 4 = yellow in females, middle part fuscous in males

7- Mesofemora: 1 = dark, 2 = dark with apex pale, 3 = yellowish white, 4 = yellow in females, middle part fuscous in males, 5 = middle part dark brown in both sexes

8- Protibia: 1 = pale brownish yellow with basal half dark brown, 2 = white, yellow or pale, 3 = pale to grey, 4 = pale yellow, often with middle part darker

9- Mesotibia: 1 = black with apex brownish yellow, 2 =- middle part dark, base and apex lighter, 3 = yellow or yellowish white, 4 = pale yellow, middle part dark, 5 = dark with distal half pale

10- Metatibia: 1 = dark brown or black, 2 = dark with apex pale, 3 = black or brown with base white, 4 = pale yellow, often with middle part darker

11- Metasoma: 1 = T1 or T1&T2 yellow, 2 = T1 or T1&T2 and apex pale, 3 = T1-T3 yellow, 4 = dark, black, 5 = female yellow with brown dorsum, except T1&T2, male dark with pale base, 6 = female yellow with brown dorsum except T1&T2, male base and apex pale

12- Ovipositor / mesotibia: 1 = less than 1.2, 2 = 1.3–1.5, 3 = more than 1.5

Table 3. List of anatomical terms and links to URI locations in the Hymenoptera Anatomy Ontology portal.

Term	Definition	URI
antenna	The anatomical cluster that is composed of the scape, pedicel and flagellum.	http://purl.obolibrary.org/obo/HAO_0000101
apical denticle	The spur that is located distally on the gonossiculus.	http://purl.obolibrary.org/obo/HAO_0001574
base	The tergum that is located on abdominal segment 2 AND The tergum that is located on the abdominal segment 3.	http://purl.obolibrary.org/obo/HAO_0000053 and http://purl.obolibrary.org/obo/HAO_0000056
body	The anatomical cluster that is composed of the whole organism but which excludes the antennae, legs and wings.	http://purl.obolibrary.org/obo/HAO_0000182
club	The anatomical cluster composed of the apical flagellomeres that are differentiated by size from the basal flagellomeres.	http://purl.obolibrary.org/obo/HAO_0001185
compound eye	The compound organ that is composed of ommatidia.	http://purl.obolibrary.org/obo/HAO_0000217
costal cell	The membranous region of the forewing anterior to the submarginal vein, measured from the basal constriction that delimits the apex of the humeral plate of the wing to the point at which the submarginal vein touches the leading edge of the wing.	http://purl.obolibrary.org/obo/HAO_0000226
coxa	The leg segment that is connected to the body and to the trochanter via conjunctivae and muscles.	http://purl.obolibrary.org/obo/HAO_0000228
digitus	The sclerite that is located distally on the parossiculus.	http://purl.obolibrary.org/obo/HAO_0000385
edge	The margin that extends along the border of two areas that are oriented differently.	http://purl.obolibrary.org/obo/HAO_0000285
eye margin	The margin of the compound eye.	http://purl.obolibrary.org/obo/HAO_0000672
F1	The flagellomere that is proximally attached to the pedicel.	http://purl.obolibrary.org/obo/HAO_0001148
F2	The flagellomere that is located distal to the first flagellomere.	http://purl.obolibrary.org/obo/HAO_0001883
F3	The flagellomere that is located immediately distal to the second flagellomere.	http://purl.obolibrary.org/obo/HAO_0001895
femur	The leg segment that is distal to the trochanter and proximal to the tibia.	http://purl.obolibrary.org/obo/HAO_0000327
fore wing	The wing that is located on the mesothorax.	http://purl.obolibrary.org/obo/HAO_0000351
frontovertex	The anatomical cluster that is composed of the vertex and the dorsal area of the upper face dorsal to the frontofacial ridge.	http://purl.obolibrary.org/obo/HAO_0001823
genitalia	The anatomical cluster that is composed of the cupula, gonostyle, volsella and the aedeagus.	http://purl.obolibrary.org/obo/HAO_0000312
head	The tagma that is located anterior to the thorax.	http://purl.obolibrary.org/obo/HAO_0000397
hind wing	The wing that is located on the metathorax.	http://purl.obolibrary.org/obo/HAO_0000400
leg	The anatomical cluster that is composed of the coxa and all distal leg segments and is connected to the pectus.	http://purl.obolibrary.org/obo/HAO_0000494

Term	Definition	URI
longitudinal sensillum	The multiporous plate sensillum that is elongate.	http://purl.obolibrary.org/obo/HAO_0001936
mandible	The sclerite that is connected to the cranium along the anterior margin of the oral foramen via the anterior and posterior cranio-mandibular articulations.	http://purl.obolibrary.org/obo/HAO_0000506
margin	The line that delimits the periphery of an area.	http://purl.obolibrary.org/obo/HAO_0000510
marginal vein	The abscissa that is located along the anterior margin of the fore wing and is thought to correspond to the anterior abscissa of the radius (R1).	http://purl.obolibrary.org/obo/HAO_0000512
mesobasitarsus	The basitarsus that is located in the mid leg.	http://purl.obolibrary.org/obo/HAO_0001133
mesocoxa	The coxa that is located on the mid leg.	http://purl.obolibrary.org/obo/HAO_0000635
mesofemur	The femur that is located on the mid leg.	http://purl.obolibrary.org/obo/HAO_0001131
mesoscutum	The area that is located anterior to the transscutal articulation.	http://purl.obolibrary.org/obo/HAO_0001490
mesosoma	The anatomical cluster that is composed of the prothorax, mesothorax and the metapectal-propodeal complex.	http://purl.obolibrary.org/obo/HAO_0000576
mesotibia	The tibia that is located on the mid leg.	http://purl.obolibrary.org/obo/HAO_0001351
mesotibial spur	The tibial spur that is located on the mesotibia.	http://purl.obolibrary.org/obo/HAO_0001120
metabasitarsus	The basitarsus that is located on the hind leg.	http://purl.obolibrary.org/obo/HAO_0001142
metabasitarsus	The basitarsus that is located on the hind leg.	http://purl.obolibrary.org/obo/HAO_0001142
metacoxa	The coxa that is located on the hind leg.	http://purl.obolibrary.org/obo/HAO_0000587
metasoma	The tagma that is connected anteriorly to the metapectal-propodeal complex at the propodeal foramen and consists of abdominal segments.	http://purl.obolibrary.org/obo/HAO_0000626
metatibia	The tibia that is located on the hind leg.	http://purl.obolibrary.org/obo/HAO_0000631
metatibial spur	The tibial spur that is located on the metatibia.	http://purl.obolibrary.org/obo/HAO_0001121
mid lobe of mesoscutum	The area that is located between the notauli.	http://purl.obolibrary.org/obo/HAO_0000520
occipital margin	The edge that separates the occiput from the vertex.	http://purl.obolibrary.org/obo/HAO_0001963
ocellus	The multi-tissue structure that is located on the top of the head, composed of the corneal lens, pigment cell, rhabdoms and synaptic plexus.	http://purl.obolibrary.org/obo/HAO_0000661
ovipositor	The anatomical cluster that is composed of the first valvulae, second valvulae, third valvulae, first valvifers and second valvifers .	http://purl.obolibrary.org/obo/HAO_0000679
pedicel	The antennal segment that is the second segment of the antenna and is connected proximally with the scape and distally with the flagellum.	http://purl.obolibrary.org/obo/HAO_0000706

Term	Definition	URI
phallobase	The anatomical cluster that is composed of the cupulae, gonostipites and volsellae.	http://purl.obolibrary.org/obo/HAO_0000713
posterior ocellus	The ocellus that is paired.	http://purl.obolibrary.org/obo/HAO_0000481
procoxa	The coxa that is located on the fore leg.	http://purl.obolibrary.org/obo/HAO_0001122
profemur	The femur that is located on the fore leg.	http://purl.obolibrary.org/obo/HAO_0001124
protibia	The tibia that is located on the fore leg.	http://purl.obolibrary.org/obo/HAO_0000350
row	The anatomical cluster that is composed of repeated units of anatomical structures.	http://purl.obolibrary.org/obo/HAO_0000901
scape	The antennal segment that is proximal to the pedicel and is connected with the head via the radicle.	http://purl.obolibrary.org/obo/HAO_0000908
sculpture	The area that is located on the sclerite and that is composed of repetitive anatomical structures.	http://purl.obolibrary.org/obo/HAO_0000913
scutellar sensillum	The campaniform sensillum that is paired and is located submedially on the mesoscutellum.	http://purl.obolibrary.org/obo/HAO_0001965
scutellum	The area that is located posteriorly of the transscutal line and is composed of the axillae and the mesoscutellum.	http://purl.obolibrary.org/obo/HAO_0000572
secretory pore	The anatomical space that corresponds to the distal end of an exocrine gland.	http://purl.obolibrary.org/obo/HAO_0001966
seta	The sensillum that is multicellular and consists of trichogen, tormogen, and sense cells.	http://purl.obolibrary.org/obo/HAO_0000935
side lobe	The area that is located between the notaulus and the parascutal carina.	http://purl.obolibrary.org/obo/HAO_0000466
stigma	The patch on the wing that is sclerotized and is located on the anterior margin of the fore wing.	http://purl.obolibrary.org/obo/HAO_0000957
submarginal vein	Basal-most portion of the forewing vein complex that occurs behind the costal cell; measured from the constriction that delimits the humeral plate to the point at which the vein touches the leading edge of the wing apically.	http://purl.obolibrary.org/obo/HAO_0000972
T1	The tergum that is located on abdominal segment 2.	http://purl.obolibrary.org/obo/HAO_0000053
T2	The tergum that is located on the abdominal segment 3.	http://purl.obolibrary.org/obo/HAO_0000056
tarsus	The leg segment that is apical to the tibia.	http://purl.obolibrary.org/obo/HAO_0000992
third valvula	The sclerite that is located posterior to the second valvifer and is connected to the second valvifer via conjuntiva.	http://purl.obolibrary.org/obo/HAO_0001012
tooth	The projection that is located distally on the mandible.	http://purl.obolibrary.org/obo/HAO_0001019
wing	The wing that is located on the mesothorax.	http://purl.obolibrary.org/obo/HAO_0000351

Results and discussion

Following the work of Zehavi and Rosen (1988), we consider the following traits to be diagnostic for the *A. mali* complex: (1) head and body dark except for parts of the metasoma; (2) metafemur pale, (3) a single complete row of setae proximal to the linea calva of the fore wing, with a few additional setae in the angle between this row and the marginal vein; (4) linea calva open (no setae at its posterior edge); (5) meso- and metacoxae dark; (6) metatibia more or less dark. The *A. mali* complex consists of eleven described species, and there are six similar species with either a dark metafemur or more than one line of setae proximal to the linea calva (Table 1). Species within the complex have been distinguished by color and shape of antennal segments (particularly the third funicular segment), color of legs and metasoma, and relative length of ovipositor versus mesotibia (Ashmead 1888; Evans et al. 1995; Gahan 1924; Girault 1913; Haldeman 1851; Hayat 1998; Prinsloo and Neser 1994; Timberlake 1924; Yasnosh 1963; Zehavi and Rosen 1988).

Key to species in the *Aphelinus mali* complex

1 Female: procoxa white or yellowish-white, male: procoxa yellowish-white or grey, both sexes: meso- and metacoxae dark **2**

– All coxae dark in both sexes **4**

2(1) F3 more than twice as long as broad in male, subquadrate in female.... ***engaeus***

– F3 less than twice as long as broad in male and from subquadrate to more than 1.4× as long as broad in female. **3**

3(2) Procoxa yellowish white in male; metatibia yellowish white; metabasitarsus pale; club light brown in male; metasoma dark with base yellow in female and slightly pale in male; ovipositor less than 1.2× middle tibia ..... ***ficusae***

– Procoxa grey in male, particularly on anterior surface; metatibia dark in center; metabasitarsus greyish brown; club yellow in male; metasoma dark with T1&2, venter, and apex yellow in female and base and apex yellow in male; ovipositor more than 1.2× mesotibia..... *glycinis* sp. n.

4(1) F3 longer than broad in male and subquadrate to longer than broad in female; metasoma dark or dark with pale base, but with apex dark **5**

– F3 subquadrate in both male and female; metasoma dark with pale base or pale base and apex..... **8**

5(4) Pro- and metafemur dark; protibia dark or dark with yellow apex; metasoma dark or dark with pale base **6**

– Pro- and metafemur partly yellow; protibia yellow; metasoma dark with pale base..... **7**

6(5) Scape yellow to pale brown with apical third yellow; pedicel and club infuscate brown; metabasitarsus dark; F3 subquadrate in female and 1.2–2× as long as broad in male; metasoma dark with pale base ..... ***basilicus***

– Scape dark brown to black; pedicel yellow in female and yellow to dusky in male; club yellow; metabasitarsus yellow; F3 longer than broad in female and more than 2× as long as broad in male; metasoma dark. ..... ***sanborniae***

7(6) Pro- and mesofemur dark with base and apex pale; protibia dark with pale base and apex, metatibia dark with pale apex; F3 1.2–1.5 as long as broad in female and 1.2–2× as long as broad in males; ovipositor equal to metatibia; metasoma dark with T1–T3 yellow ..... ***paramali***

– Pro- and mesofemur dark with apex pale; protibia dark with brownish yellow apex, metatibia dark; F3 subquadrate in female and 1.2–2× as long as broad in male; ovipositor more than 1.5× mesotibia; metasoma dark with T1 or T1&2 yellow. ..... ***mali***

8(4) Profemur pale yellow, mesofemur pale yellow in female, dark brown in male; metabasitarsus yellow; metasoma dark with base yellow ..... ***spiraecolae***

– Profemur dark with apex pale yellow, mesofemur dark in both sexes; metabasitarsus dark; metasoma dark with base and apex yellow. **9**

9(8) Club more than 2× as long as broad in female; metatibia dark with pale base... **11**

– Club 2× as long as broad in females; metatibia all dark. **10**

10(9) Club and pedicel light brown in female and darker in males; mesofemur dark; mesotibia dark with pale base and apex ..... ***campestris***

– Club pale yellow in female and male; pedicel dusky yellow in female and light brown in male; mesotibia dark with brownish yellow apex ..... ***gossypii***

11(9) Club more than 3× as long as broad in males; scape yellowish white in female and infuscate brown in male; mesotibia dark with base and apex pale .... ***rhamni*** **sp. n.**

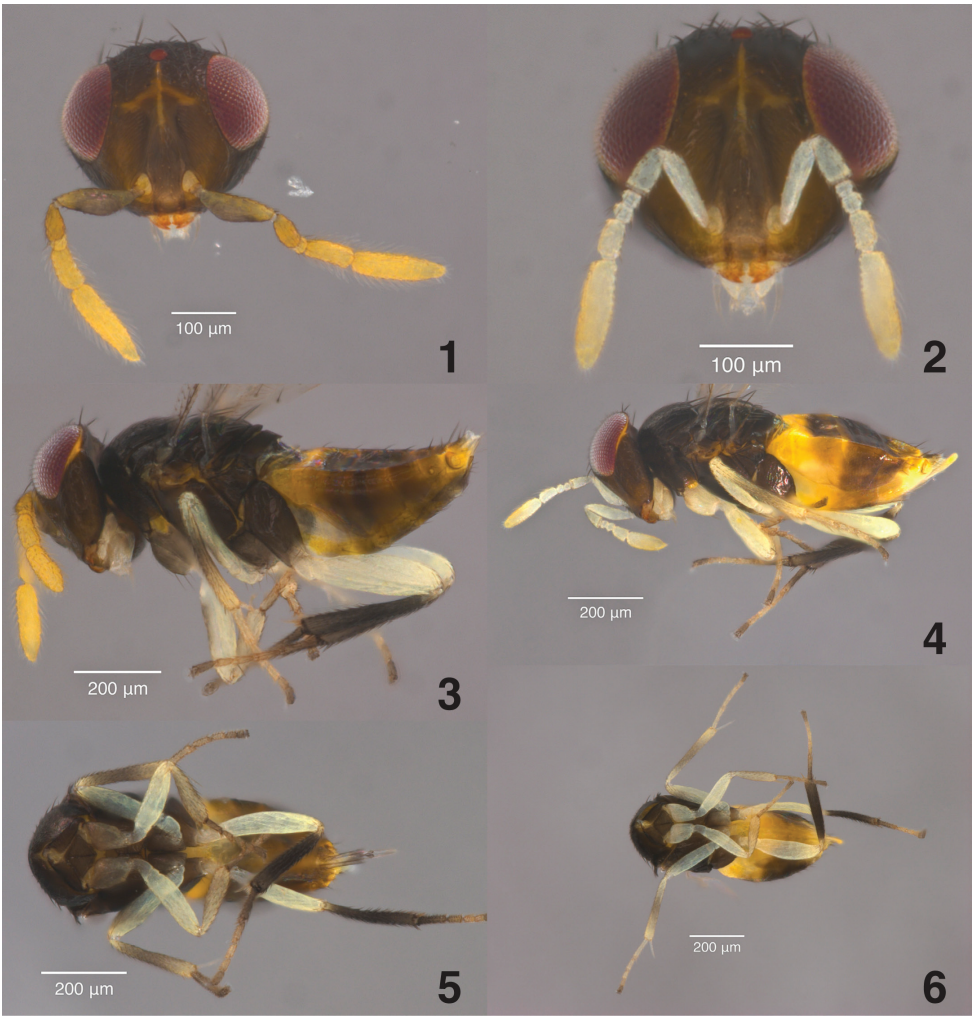
– Club less than 3× as long as broad in males; scape dark brown with distal half yellow in both sexes; mesotibia dark with distal half yellow ..... ***coreae*** **sp. n.**

Taxonomy

Aphelinus glycinis **Hopper & Woolley, sp. n.**
urn:lsid:zoobank.org:act:1132B1E4-8F2E-4FF3-9E6B-30FAFD497EA1
http://species-id.net/wiki/Aphelinus_glycinis

Figs 1–14

Diagnosis. Female. Head and mesosoma dark brown to black; legs with procoxa yellowish white, meso- and metacoxae dark brown to black, femora yellowish white, protibia yellowish white, mesotibia yellowish white with center greyish, metatibia dark grey to black with base pale; metasoma with base, apex, and venter yellow, remainder brown; antenna white to yellowish white; F3 1.3–1.7 times as long as broad; club 3.2 times as long as broad. **Male** similar except procoxa grey; pro- and mesofemur sometimes with darkened center; metasoma brown with base and apex yellow; scape dark greyish brown with greyish yellow distal tip, swollen in center, maximum width 3× distal end width, with three to five



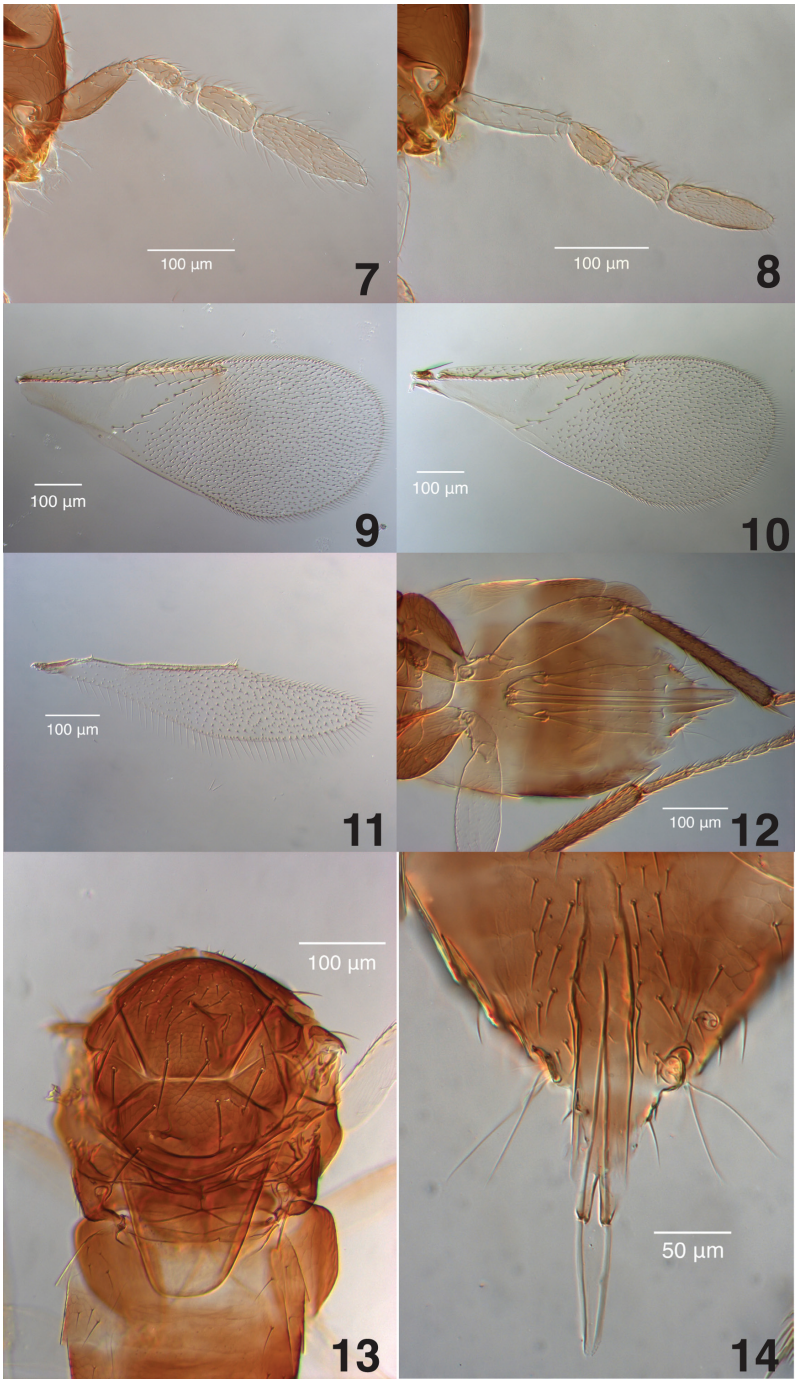
Figures 1–6. *Aphelinus glycinis* sp. n. paratype specimens in 95% ethanol. **1** male antennae and face **2** female antennae and face **3** male, lateral view **4** female, lateral view **5** male, ventral view **6** female, ventral view.

volcano-shaped secretory pores in a single line on ventral surface, pedicel greyish yellow, third funicle more than 2 times as long as broad, club 3.9 times as long as broad.

Description. Female (Figs 2, 4, 6, 8, 10, 11, 12, 13).

Body length. 0.77–0.93 (Holotype 0.90 mm).

Head. (Figs 2, 8) Head 1.3× as broad as high in frontal view, about as broad as mesosoma; frontovertex width 0.4× of head width, 1.2× as long as broad, and 0.8× as broad as scape length; posterior ocelli 1.0× their diameter from eye margin, 3× their diameter from one another, and 0.33× their diameter from occipital margin; mandible with 2 acute teeth and a broad truncate surface below the teeth, antenna as in Fig. 8 with scape 4.8× as long as broad, pedicel 2.2× as long as broad, F1 anneliform, 1.7× as



Figures 7–14. *Aphelinus glycinis* sp. n., slide-mounted paratypes. **7** male antenna (TAMU x0616203) **8** female antenna (TAMU x0616201) **9** male fore wing (TAMU x0616206) **10** female fore wing (TAMU x0616201) **11** female hind wing (TAMU x0616204) **12** female metasoma (TAMU x0616204) **13** female mesosoma (TAMU x0616211) **14** male genitalia (TAMU x0616206).

wide as long, F2 1.2× as broad as long, F3 1.6–1.7× as long as broad, club 3.2× as long as broad, 2.7× times as long as F3, and with 6–7 longitudinal sensilla.

Mesosoma. (Figs 4, 6, 13) Mesoscutum and scutellum with fine reticulate sculpture, longest diameter of reticulations approximately twice the diameter of the scutellar sensilla, interior of reticulations with fine, granulate surface (visible only in slide-mounts under high magnification); mid-lobe of mesoscutum with 2 pairs of long setae and about 40 short setae, side lobes each with 2 long and 1 short setae; scutellum with 2 pairs of long setae and two sensilla directly posterior to the anterior pair of setae, scutellar sensilla slightly posterior to middle of scutellum; mesotibial spur 0.8× mesobasitarsus; metatibial spur 0.6× metabasitarsus.

Fore wing. (Fig. 10) 2.3× as long as broad; costal cell with 1 complete row of dorsal setae and 2 rows of ventral setae, the posterior row extending from under the proximal end of the marginal vein almost to stigma, costal cell 1.2× longer than marginal vein; submarginal vein with 5–6 setae; marginal vein with 10 setae along the margin; stigmal vein short with stigma rounded; delta region proximal to linea calva with one complete line of 13–15 setae and 2–6 additional setae in angle with marginal vein, linea calva with no dorsal setae at its posterior edge; wing distal to linea calva with dense, evenly spaced, dorsal setae and much smaller ventral setae.

Hind wing. (Fig. 11) 4.3× as long as broad, marginal fringe 0.26× wing width.

Metasoma. (Figs 4, 6, 12) 1.2× as long as mesosoma; ovipositor inserted at middle of metasoma, slightly exerted distally, 1.3× as long as meso- and metatibiae; third valvula one-third length of ovipositor.

Color. (Figs 2, 4, 6) Head and mesosoma dark brown to black; legs with procoxa yellowish white, meso- and metacoxae dark brown to black, femora yellowish white, protibia yellowish white, mesotibia yellowish white with center greyish, metatibia dark grey to black base pale, tarsi pale brown with tips and metabasitarsus greyish brown; metasoma with base (T1 and T2), apex, and venter yellow, remainder brown; antennae yellowish white; compound eyes burgundy, and ocelli red in life, both silver-colored in dried specimens.

Male (Figs 1, 3, 5, 7, 9, 14). Similar to female except:

Head. (Figs 1, 7) Antenna with scape swollen in middle, 3.4 as long as broad, maximum width 3× distal end width, with 3–5 volcano-shaped secretory pores in line on ventral surface, pedicel 2.1× as long as broad, F1 anneliform, 1.8× as wide as long, F2 1.5× as broad as long, F3 2.0× as long as broad, club 3.9× as long as broad, 2.1× as long as F3, and with 4–6 longitudinal sensilla.

Metasoma. (Figs 3, 5, 14) About the same length as mesosoma, phallobase of genitalia including digiti 4.5× longer than broad, digiti about twice longer than broad and with two apical denticles.

Color. (Figs 1, 3, 5) Legs with procoxa grey, pro- and mesofemora sometimes with darkened centers; metasoma brown with base and apex yellow; scape dark greyish brown with greyish yellow distal tip, pedicel greyish yellow.

Holotype female (card-mounted, deposited in USNM, USNM ENT 00703637). "China: Liaoning, Xiuyan | 40°18'N, 123°14'E | 11.vii.2007, K. Hoelmer || ex: *Aphis*

glycines | on: soybean | plots 1/3, 2007/007 || From Lab Culture | USDA-ARS-BIIRU | Newark, Delaware"

Paratypes (USNM, TAMU, BMNH)**.** 30 card-mounted and 4 slide-mounted ♀♀, 14 card-mounted and 4 slide-mounted ♂♂ with same data as holotype. 13 card-mounted and 4 slide-mounted ♀♀ and 9 card-mounted and 3 slide-mounted females: **China**, Liaoning, Xiuyan, 40˚20'N 116˚6'E, 12.vii.2007, K. Hoelmer, ex: *Aphis glycines* on: soybean, plot 2, 2008/008, from Lab Culture, USDA-ARS-BIIRU, Newark, Delaware, all bearing TAMU accession numbers.

Hosts. In the field, *Aphis glycines* is the only known host. In laboratory experiments, *A. glycinis* parasitizes *A. glycines* and closely related species in the genus *Aphis*.

Etymology. This species is named for the host from which it was collected. The species epithet is a noun in genitive case.

Relationships. *Aphelinus glycinis* is closest to *A. engaeus* and *A. ficusae* Prinsloo and Neser based on our matrix of traits (Table 2). *Aphelinus glycinis* differs from *A. engaeus* in having elongated third funicle segments in males and females, and it differs from *A. ficusae* in having an ovipositor more than 1.2× as long as the mesotibia and grey procoxa in males. It also differs from these species in its aphid hosts and geographical distribution. *Aphelinus glycinis* is a specialist on *Aphis* species close to *Aphis glycines*, but *A. engaeus* is reported from *Schizaphis graminum* (Rondani) and *Sitobion ochnearum* (Eastop) and *A. ficusae* was reared from an undetermined aphid on *Ficus sycomorus* (Prinsloo and Neser 1994). Furthermore, *Aphelinus glycinis* was collected in northeastern China, whereas *A. engaeus* and *A. ficusae* have been reported only from South Africa.

Aphelinus rhamni Hopper & Woolley, sp. n.

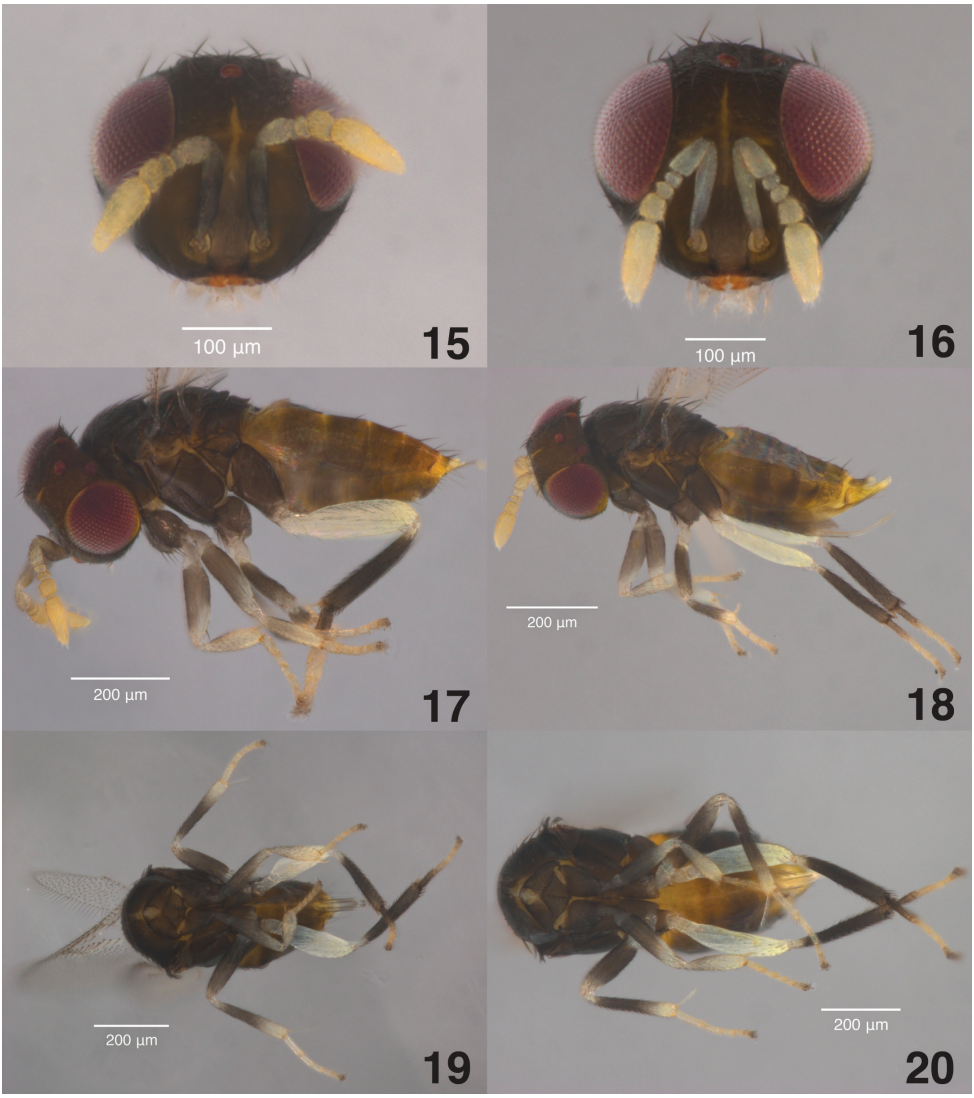
urn:lsid:zoobank.org:act:1132B1E4-8F2E-4FF3-9E6B-30FAFD497EA1
http://species-id.net/Aphelinus_rhamni
Figs 15–28

Diagnosis. Females. Head and mesosoma dark brown to black; legs with coxae dark brown to black, profemur dark grey with pale apex, mesofemur dark grey to black, metafemur white, protibia white with pale greyish base, mesotibia dark grey to black with pale base and apex, and metatibia dark grey to black with pale base; metasoma yellowish brown with base and apex yellow; antennae yellow with basal half of scape and pedicel sometimes greyish; F3 quadrate; club 2.8 times as long as broad. **Males** similar except scape swollen in middle, 3× broader in middle than at distal end, with 2 or 3 volcano-shaped secretory pores; scape dark yellowish grey, pedicel pale greyish yellow; club 3.3 times as long as broad.

Description. Female (Figs 16, 18, 20, 22, 24, 25, 26, 27).

Body length. 0.75–0.94 (Holotype 0.87 mm).

Head. (Figs 16, 22) Head 1.2× as broad as high in frontal view, about as broad as mesosoma; frontovertex 0.4× head width and as broad as scape length; posterior ocelli



Figures 15–20. *Aphelinus rhamni* sp. n., paratype specimens in 95% ethanol. **15** male antennae and face **16** female antennae and face **17** male, lateral view **18** female, lateral view **19** male, ventral view **20** female, ventral view.

0.5× their diameter from eye margin, 3.0× their diameter from one another, and 0.33× their diameter from occipital margin; mandible with 2 acute teeth and a broad truncate surface below the teeth; antennae as in Fig. 21 with scape 4.8 longer than broad, pedicel 1.8× as long as broad, F1 anneliform, F2 1.5× as broad as long, F3 quadrate, club 2.8× as long as broad and 3.3× times longer than F3, with 4–6 longitudinal sensilla.

Mesosoma. (Figs 18, 20, 27) Mesoscutum and scutellum with fine reticulate sculpture, longest diameter of reticulations approximately twice the diameter of scutellar

Figures 21–28. *Aphelinus rhamni* sp. n., slide-mounted paratypes. **21** male antenna (TAMU x0616221) **22** female antenna (TAMU x0616215) **23** male fore wing (TAMU x0616217) **24** female fore wing (TAMU x0616215) **25** female hind wing (TAMU x0616129) **26** female metasoma (TAMU x0616214) **27** female mesosoma (TAMU x0616129) **28** male genitalia (TAMU x0616217).

sensilla, interior of reticulations with fine, granulate surface (visible only in slide-mounts under high magnification); mid-lobe of mesoscutum with 2 pairs of long setae and 35–40 short setae, side lobes each with 2 long and 1 short seta; scutellum with 2 pairs of long setae, pair of scutellar sensilla directly posterior to the anterior pair of setae and slightly posterior to middle of scutellum; mesotibial spur equal in length to mesobasitarsus; metatibial spur 0.5× metabasitarsus.

Fore wing. (Fig. 24) 2.2× as long as broad ; costal cell with 1 row of dorsal setae and two rows of ventral setae, the posterior row extending from under the proximal end of the marginal vein almost to stigma, costal cell 1.1× as long as marginal vein; submarginal vein with 5 setae, marginal vein with 10 setae along the anterior margin; stigmal vein short with stigma rounded; delta region proximal to linea calva with one complete line of 13–15 setae and 2–6 additional setae in angle with marginal vein, linea calva with no setae at its posterior edge; wing distal to linea calva with evenly spaced, dense dorsal setae and much smaller ventral setae.

Hind wing. (Fig. 25) 3.9× longer than broad, marginal fringe 0.23× wing width.

Metasoma. (Figs 18, 20, 26) 1.4× as long as mesosoma; ovipositor inserted at middle of metasoma, slightly exerted distally, 1.3× longer than metatibia and mesotibia; third valvulae one-third the length of ovipositor.

Color. (Figs 16, 18, 20) Head and mesosoma dark brown to black; legs with coxae dark brown to black, profemur dark grey with pale apex, mesofemur dark grey to black, metafemur white, protibia white with pale greyish base, mesotibia dark grey to black with pale base and apex, and metatibia dark grey to black with pale base; metasoma yellowish brown with venter of T1 and apex yellow; antennae yellow sometimes with basal half of scape and pedicel greyish yellow; compound eyes dark burgundy and ocelli red in life, both silver-colored in dried specimens.

Male (Figs 15, 17, 19, 21, 23, 28). Similar to female except:

Body length. 0.66–0.78 mm.

Head. (Figs 15, 21) Antenna with scape swollen in center, 3.1× as long as broad, maximum width 3× width at distal end, with 2–3 volcano-shaped secretory pores in single line on ventral surface, pedicel 1.8× as long as broad, F1 subquadrate, 1.1× as broad as long, F2 shorter, 1.4× as broad as long, F3 trapezoidal, 1.1× longer than width at apex, 1.5× as long as wide at base, club 3.3× as long as broad, with 4 longitudinal sensilla.

Metasoma. 0.7× length of mesoma

Color. (Figs 15, 17, 19) Scape dark yellowish grey, pedicel pale greyish yellow, base of metasoma pale brown and with yellow region at apex smaller.

Holotype female (card-mounted, deposited in USNM, USNM ENT 00763638)**.** "China, Daxing (Beijing) | 39˚48'N, 116˚28'E | 10.ix.2005, K. Hoelmer || ex: *Aphis glycines* | on: *Rhamnus* sp. | 2005/005 || From Lab Culture | USDA-ARS-BIIRU | Newark, Delaware"

Paratypes (USNM, TAMU, BMNH)**.** 33 card-mounted and 6 slide-mounted females, 19 card-mounted and 3 slide-mounted males with same data as holotype. 9 card-mounted and 2 slide-mounted females, 6 card-mounted and 2 slide-mounted males: **China**: Daxing (Beijing), 39˚48'N 116˚28'E, 10.iv.2004, W. Meikle coll.,

ex: *Aphis glycines* on *Rhamnus* sp., 2004/008, from lab culture, USDA-ARS-BIIRU, Newark, Delaware.

Host. In the field, *Aphis glycines* is the only known host. In laboratory experiments, *A. rhamni* parasitizes *A. glycines* and closely related species in the genus *Aphis*, and rarely *Rhopalosiphum padi* L. and *Schizaphis graminum*.

Etymology. This species is named for the primary host plant of the aphid species from which it was collected. The species epithet is a noun in genitive case.

Relationships. *Aphelinus campestris* and *Aphelinus gossypii* are the closest described species to *A. rhamni* based on our matrix of traits (Table 2). *Aphelinus rhamni* differs from both species in having a more elongate club and in coloration of the metatibia. *Aphelinus rhamni* has a much narrower host range than *A. gossypii*, which is reported from at least 18 species of aphids in 10 genera and two tribes, including species which *A. rhamni* does not parasitize in laboratory experiments.

***Aphelinus coreae* sp. n.**

urn:lsid:zoobank.org:act:F4B3A880-2136-474C-815C-13406F2A48A0
http://species-id.net/Aphelinus_coreae
Figs 29–42

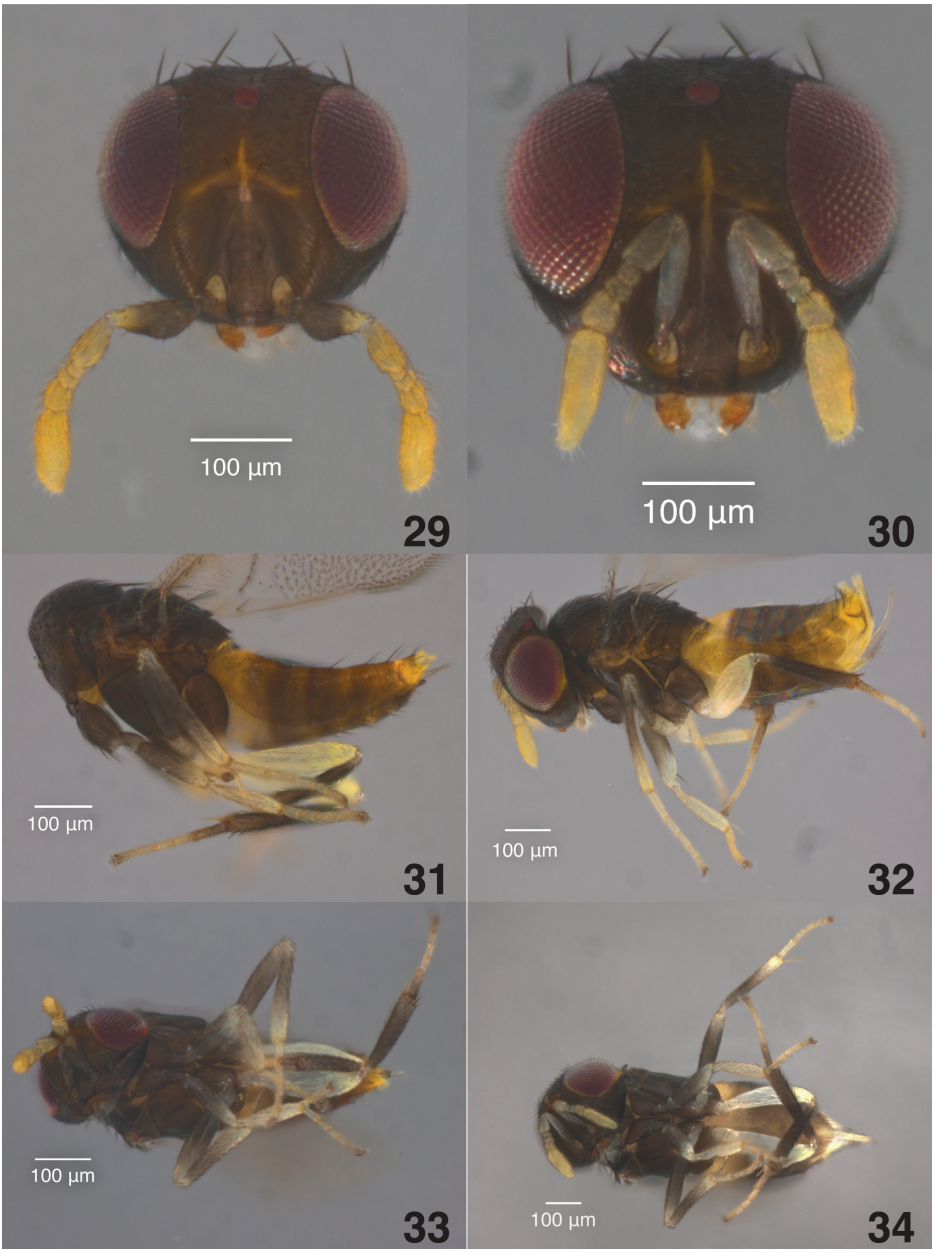
Diagnosis. Females. Head and thorax dark brown to black; legs with coxae dark brown to black, profemur dark grey with distal half pale, mesofemur dark grey to black, metafemur pale yellowish white, protibia pale yellowish white to somewhat fuscous, mesotibia dark grey to black with distal half pale, and metatibia dark grey to black with pale base; metasoma dark brown with base and apex yellow; antennae yellow; F3 quadrate. **Males** similar except scape swollen in middle, 2.0× as broad in middle than at distal end, with two or occasionally three circular secretory pores in the middle of a shallow depression on ventral surface, scape dark yellowish grey with distal half yellow, pedicel greyish yellow.

Description. Female (Figs 30, 32, 34, 36, 38, 39, 40, 41).

Body length. 0.80–0.93 (Holotype 0.93 mm).

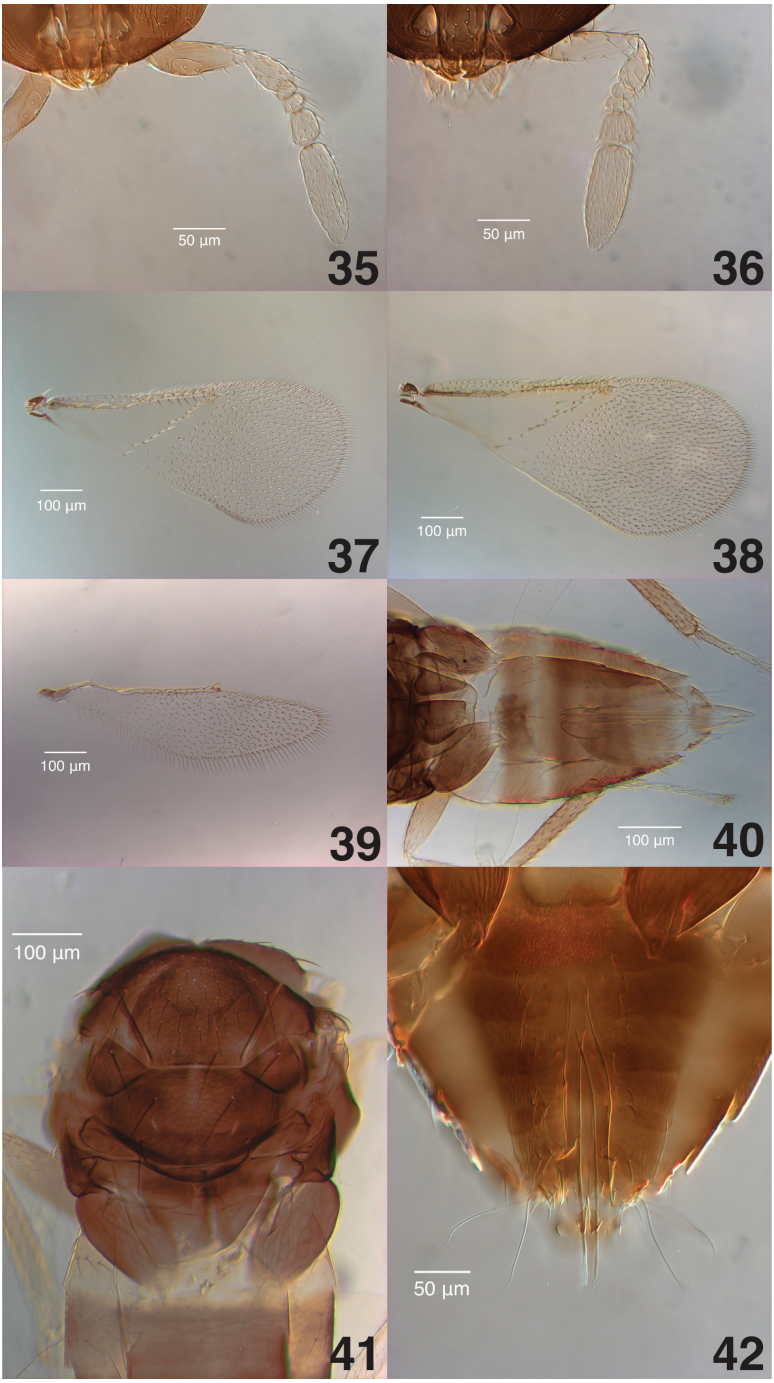
Head. (Figs 30, 36) Head 1.3× as broad as high in frontal view, about as broad as mesosoma; frontovertex 0.4× head width and as broad as scape length; posterior ocelli approximately their own diameter from eye margin, 5× their diameter from one another, and 0.5× their diameter from occipital margin; mandible with two acute teeth and a broad truncate surface below the teeth, ventral tooth sometimes not distinct; antennae as in Figs 30 and 36 with scape 4.0× as long as broad, pedicel 1.6× as long as broad, F1 anneliform, F2 1.4× as broad as long, F3 subquadrate or very slightly broader than long, club 3.75× as long as broad and 3.5× longer than F3, with 7–8 linear sensilla.

Mesosoma. (Figs 32, 34, 41) Mesosoma and scutellum with fine reticulate sculpture, longest diameter of reticulations approximately 2–3× diameter of scutellar sensilla; interior of reticulations with fine, granulate surface (visible only in slide-mounts under high magnification), mid-lobe of mesoscutum with 2 pairs of long setae and about 40–60



Figures 29–34. *Aphelinus coreae* sp. n., paratype specimens in 95% ethanol. **29** male antennae and face **30** female antennae and face **31** male, lateral view **32** female, lateral view **33** male, ventral view **34** female, ventral view.

short setae, side lobes each with 2 long and 1–2 short setae; scutellum with 2 pairs of long setae; pair of scutellar sensilla approximately equidistant from anterior and posterior pairs of long setae; mesotibial spur 1.1× mesobasitarsus; metatibial spur 0.6× metabasitarsus.



Figures 35–42. *Aphelinus coreae* sp. n., slide-mounted paratypes. **35** male antenna (TAMU x0616221) **36** female antenna (TAMU x0616215) **37** male fore wing (TAMU x0616217) **38** female fore wing (TAMU x0616215) **39** female hind wing (TAMU x0616129) **40** female metasoma (TAMU x0616214) **41** female mesosoma (TAMU x0616129) **42** male genitalia (TAMU x0616217).

Fore wing. (Fig. 38) 2.2× as long as broad; costal cell with 1 row of dorsal setae and 2 rows of ventral setae, the posterior row extending from under the distal end of the submarginal vein almost to stigma, costal cell 1.3× as long as marginal vein; submarginal vein with 5 setae; marginal vein with 12 setae along the anterior margin; stigmal vein short with stigma rounded; delta region proximal to linea calva with one complete line of 12–13 setae and 2–5 additional setae in angle with marginal vein, linea calva with no setae at its posterior edge; wing distal to linea calva with evenly spaced, dense dorsal setae and much smaller ventral setae.

Hind wing. (Fig. 39) 3.9× as long as broad, marginal fringe 0.26× wing width.

Metasoma. (Figs 32, 34, 40) 1.1× as long as mesosoma; ovipositor inserted at basal third of metasoma, slightly exerted distally, 1.4× as long as metatibia or mesotibia; third valvula 0.28× length of ovipositor.

Color. (Figs 30, 32, 34) Head and mesosoma dark brown to black; legs with coxae dark brown to black, profemur dark grey with distal half pale, mesofemur dark grey to black, metafemur pale yellowish white, protibia pale yellowish white to somewhat fuscous, mesotibia dark grey to black with distal half pale, and metatibia dark grey to black with pale base; metasoma dark brown with base and apex yellow; antennae yellow; compound eyes dark burgundy, ocelli red in life, both silver-colored in dried specimens.

Male (Figs 29, 31, 33, 35, 37, 42). Similar to female except:

Body length. 0.68–0.81 mm.

Head. (Figs 29, 35) Antenna with scape swollen in center, 3.3× as long as broad, maximum width 2× distal width, with 2 or 3 circular, secretory pores in the middle of a shallow depression on ventral surface, pedicel 2.0× longer than broad, F1 and F2 1.4× broader than long, F3 rectangular, 1.3× as long as wide at apex, club 3.2× as long as broad, with 3–4 longitudinal sensilla.

Metasoma. (Figs 31, 33, 42) 1.5× length of mesoma.

Color. (Figs 29, 31, 33) Scape dark yellowish grey with distal half yellow, pedicel greyish yellow.

Holotype female (card-mounted, deposited in USNM, USNM ENTO 00763639)**.** "Korea, Gyeongsangnam Province, Miryang |35°30'N, 128°44'E | 11.viii.2009, K. Hoelmer || ex: *Aphis glycines* | on: soybean | 2009/011 || From Lab Culture | USDA-ARS-BIIRU | Newark, Delaware"

Paratypes (USNM, TAMU, BMNH)**.** 13 card-mounted and 3 slide-mounted ♀♀ and 9 card-mounted and 5 slide-mounted ♂♂ with same data as holotype.

Other material examined. None.

Host. In the field, *Aphis glycines* is the only known host. In laboratory experiments, *A. coreae* parasitizes *A. glycines* and other species in the genus *Aphis*, and occasionally *Rhopalosiphum padi* and *Schizaphis graminum*.

Etymology. This species is named for its country of origin. The species epithet is a noun in genitive case.

Relationships. *Aphelinus campestris* and *Aphelinus gossypii* are the closest described species *A. coreae* based on our matrix of traits (Table 2). *Aphelinus coreae* differs from both species in having a more elongate club in females and in coloration of the scape

and mesotibia. Like *A. rhamni*, *A. coreae* has a much narrower host range than *A. gossypii*. *Aphelinus coreae* is very close to *A. rhamni*, but male *A. coreae* have shorter clubs and, as noted in the key, the two species differ in coloration of scape and mesotibia. Although difficult to distinguish, these species are reproductively isolated in laboratory crosses. Their DNA differs by 2130 fixed substitutions and 293 indels across 1.8 megabases of homologous DNA sequence. They also differ in host specificity: *A. coreae* parasitizes species of *Aphis*, e.g. *A. nerii* Boyer de Fonscolombe and *A. rumicis* L., not parasitized by *A. rhamni* in laboratory experiments.

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Alyssa Mann, undergraduate student at Texas A&M University, helped with digital imaging and preparation of figures. Kathryn Lanier, USDA-ARS, Newark, Delaware, reared the cultures of *A. coreae*, *A. glycinis* and *A. rhamni*. We thank István Miko for his generous help in reading the ms and helping us to standardize our terminology according to the Hymenoptera Anatomy Ontology project, and for providing the table of uri's for anatomical terms used in the paper. We thank the editors and two anonymous reviewers for their suggestions. This research was supported in part by funding from the North Central Soybean Research Program (KRH) and NSF award DEB 0730616 (JBW).

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