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Life History of the Emerald Jewel Wasp *Ampulex compressa*

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Abstract

The Emerald Jewel Wasp *Ampulex compressa* (Fabricius) is an endoparasitoid of the American cockroach *Periplaneta americana* (Linnaeus). Its host subjugation strategy is unusual in that envenomation is directed into the host central nervous system, eliciting a long-term behavior modification termed hypokinesia, turning stung cockroaches into a lethargic and compliant, but not paralyzed, living food supply for wasp offspring. *A. compressa* manipulates hypokinesic cockroaches into a burrow, where it oviposits a single egg onto a mesothoracic leg, hatching three days later.

Herein we describe the life history and developmental timing of *A. compressa*. Using head capsule measurements and observations of mandibular morphology, we found that the larvae develop through three instars, the first two ectoparasitoid, and the third exclusively endoparasitoid. The first two instars have mandibles sufficient for piercing and cutting the cuticle respectively, while the third instar has a larger and blunter mandibular structure. During ecdysis to the third instar, the larva enters the body cavity of the cockroach, consuming internal tissues selectively, including fat body and skeletal muscle, but sparing the gut and Malpighian tubules. The developmental timing to pupation is similar between males and females, but cocoon volume and mass, and pupation duration are sexually dimorphic. Further, we show that the difference in cocoon mass and volume can be used to predict sex before eclosion, which is valuable for studies in venom pharmacology, as only females produce venom.

Keywords

Instar, Dyar's rule, pupation, development, parasitoid, *Periplaneta americana*

Introduction

The Emerald Jewel Wasp *Ampulex compressa* (Hymenoptera, Ampulicidae) employs a unique strategy to subdue and exploit its host, the American cockroach *Periplaneta americana* (Blattodea, Blattidea). Upon encountering the cockroach, *A. compressa* hunts and aggressively attacks its prey (Keasar et al. 2006). The attack is characterized by two stings: first a swift sting into the thorax resulting in transient paralysis of the prothoracic legs, followed by a sting into the head cavity, targeting both the subesophageal ganglion and brain (Haspel et al. 2003). The head sting is remarkably precise, as the wasp is able to sense the location of cephalic ganglia through mechanosensory inputs from the stinger (Gal et al. 2014). Envenomation of head ganglia induces long-term (7–10 days) behavioral changes characterized by increased escape threshold, decreased escape distance, and decreased spontaneous walking. This modification in behavior, known as hypokinesia, facilitates the parasitization process by rendering the cockroach submissive to manipulation by the wasp (Fouad et al. 1996). After the cockroach is subdued, the wasp clips the antennae at precise locations with buzzsaw actions of its mandibles, then commences to drink hemolymph, using the antennal stumps as straws (Piek et al. 1984) (video 1:45). The wasp leads the stung cockroach into its burrow by grasping the truncated antennae (Veltman and Wilhelm 1991) and proceeds to lay a single egg on a mesothoracic leg of the host, then entombs it by sealing the burrow entrance with miscellaneous debris (Williams 1942). This provides the young wasp larva with a fresh food supply during its development. More recently it has been shown that *A. compressa* larvae secrete antimicrobial compounds into the cockroach as it is being consumed to sanitize and perhaps preserve the host (Herzner et al. 2013; Weiss et al. 2014).

A. compressa larvae hatch approximately three days after oviposition (Fox et al. 2009). The first instar larva pierces the soft cockroach cuticle near the base of the leg to feed on hemolymph. The animal remains in this position through the second instar, continually obtaining nourishment from host hemolymph (Fox et al. 2006). At the end of the second instar, the larva enters the body cavity of the still-living cockroach and begins to consume internal organs in preparation for pupation. Once ready to pupate, the larva spins a cocoon with silk that forms two layers: a hard shell that encases the pupa and a thick, woven silk outer covering that surrounds the shell (Williams 1942). Pupal development time lasts several weeks, after which the adult emerges from the desiccated husk of the cockroach to complete the life cycle.

Herein we describe that *A. compressa* develops through three instars and characterize the unique mandibular structures specific to each instar as well as the developmental time course for both male and female wasps. We report that the third instar larva consumes organs of the host selectively, presumably to preserve its life until development is completed. Lastly, we show that measurements of cocoon volume or mass can be predicative of sex, since females are larger than males.

Materials and methods

Animal husbandry

Ampulex compressa adults were reared in 2 ft^3 plexiglass cages and provided with honey and water ad libitum. One female and two to three males were maintained in each breeding cage. Cockroaches were reared in 55-gallon plastic containers with an 18 volt electric barrier along the perimeter at the top of the container with dry dog food and water *ad libitum*. All insects were maintained at 28 °C and ~50% humidity, on a 16:8 light: dark cycle. Adult female cockroaches were provided to female *A. compressa* for parasitization five times a week but no more than one in 24 hours. Female cockroaches were chosen for parasitization because they contain a significantly larger store of fat body, which provides more energy for the developing larva. Wasp development was completed in French vials in a humidified incubator. Eclosed wasps were placed into gender-specific holding cages.

Larval and pupal development duration

Differences in development times between male and female *A. compressa* were determined relative to the time a cockroach host was introduced into *A. compressa* cages, the time between parasitization and cocoon spinning, and the time between cocoon spinning and eclosion. Sex of the wasp was determined upon emergence. Seven breeding cages were maintained, each containing a single female wasp and one to three males. Cockroaches were introduced once a day, five days a week for approximately one year. When a female wasp would die or lose fecundity, she was replaced with a 10-day posteclosion, virgin female.

Cocoon volume and adult mass

Since pupae of male and female *A. compressa* are visually similar, we distinguished gender prior to eclosion by measuring cocoon volume and mass. To accomplish this, cocoons from thirty parasitized cockroaches were gently removed from the cockroach husk and silk was removed to allow measurements of mass, length and width. Out of the thirty selected, eight were female, 21 were male, and one failed to eclose. Since the cocoon is a prolate spheroid, similar to a parabola revolving about its axis, the following equation was derived to obtain volume as a function of length and width, where l is the long axis of the cocoon, L is length of the cocoon at the longest point and W is the corresponding width. These data were used to generate a binary logistic regression analysis useful for predicting the probability of a female eclosing from a cocoon based on its volume or mass.

Eq. 1 $$Volume \sim \pi \int_0^L [(-W/2)/(L/2)^2(l - L/2)^2 + W/2]^2 \, dl$$

Head capsule measurements

Head capsule measurements were taken from 24 larvae varying in age over a 10-day period. The age of the larva was referenced to time of oviposition. Larval body length and width were measured using a calibrated ruler. Head capsule width was taken as distance between the eyes and length from mandibles to head apex. The product of length and width yielded head capsule area. Head capsule area was used instead of length or width to emphasize differences between instars.

Electron microscopy

For each *A. compressa* larva measured for head capsule size, mandibles were dissected and imaged under a Hitachi TM-1000 tabletop scanning electron microscope at the Microscopy Core at the Institute of Integrative Genome Biology at the University of California, Riverside.

Data analysis and figure generation

Data for Figures 1–3 were analyzed on Prism Graphpad version 7.02. Photoplates in Figures 4–6 were generated with Adobe Photoshop version CS5. Probability of female emergence was determined using logistic regression from cocoon volume and mass data.

Results

Over the course of the study, of 1896 cockroaches introduced to female *A. compressa*, 1656 were parasitized, and 1033 eggs progressed to pupation, of which 962 emerged as adult wasps. Of those, 135 (14%) were female and 818 (80%) were male. We observed no sexual dimorphism in duration of larval development. In contrast, pupal development time, defined as the interval between pupation and adult eclosion, shows significant sexual dimorphism (Fig. 1A). The mass of newly eclosed adult wasps also differs significantly between males and females (Fig. 1B). Given that adult mass and cocoon volume are sexually dimorphic, the probability that a female will emerge from a cocoon can be estimated using cocoon volume (Fig. 2A) or mass (Fig. 2B).

We observed that *A. compressa* develops through three larval instars distinguished by quantum changes in head capsule size over the developmental period of eight days (Fig. 3). Average head capsule length and width by instar are listed in Table 1. We

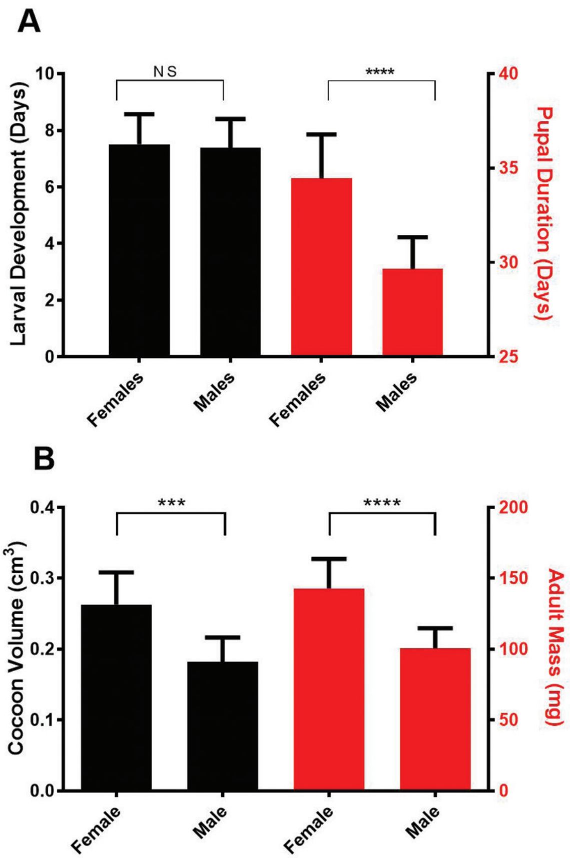

Figure 1. *A. compressa* development time and adult size are sexually dimorphic. **A** Larval development as defined by the duration between egg laying and pupation shows no difference between males and females (black, $p = 0.26$). Pupal duration - time between cocoon spinning and eclosion - is sexually dimorphic (red, $p < 0.0001$). Statistical difference determined by Welch's T test, NS = not significant, **** = $p < 0.0001$. (n = 200, males; n = 135, females) **B** Cocoon volume (black) of females is significantly larger than that of the males. (female n = 8, male n=21). Adult mass (red) is significantly larger for females (Female n = 8, male n=17). (*** = $p < 0.001$, **** = $p < 0.0001$, by Welch's T test). Error bars indicate standard deviation.

observed three distinct mandibular morphologies during larval development (Fig. 4). Mandibles of the first instar are ~100 µm in length. They are slender and pointed, with 2-3 teeth at the end (Fig. 4A). Mandibles of the second instar are ~250 µm long and have a serrated edge (Fig. 4B). Third instar mandibles are larger still at 325 µm and are relatively blunt (Fig. 4C). A comparison between all mandibular morphologies is shown in Fig. 4D.

The first instar hatches within 3 days of oviposition, the second instar appears during the 4th day of development, the third and final instar appears on day 6 with head capsule about double the size of the first instar. First and second instar larvae were observed in all cases to develop outside the cockroach, whereas the third instar is spent

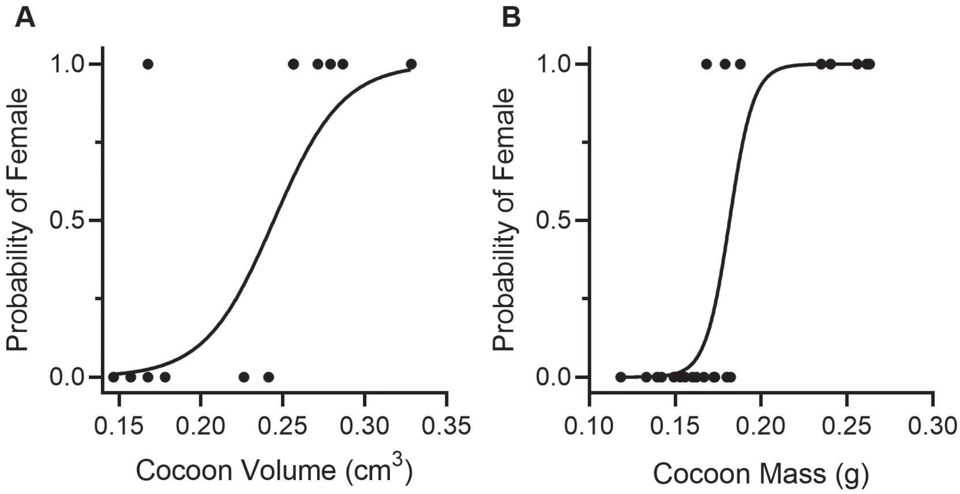

Figure 2. Cocoon mass and volume can be predictors of sex. The probability that a cocoon will emerge as a female is given as **A** a function of pupal volume (p < 0.0001, Chi Square = 16.5), and **B** a function of cocoon mass (p < 0.0001, Chi Square = 19.6)

Table 1. Size of larval body and head capsule by instar. n = 6 for instar 1, n = 5 for instar 2, and n = 13 for instar 3.

	Larva		Head Capsule	
Instar	**Length (mm)**	**Width (mm)**	**Length (µm)**	**Width (µm)**
1	3.53 ± 0.77	1.07 ± 0.18	514 ± 36	561 ± 128
2	10.0 ± 2.88	4.00 ± 0.99	885 ± 88	780 ± 72
3	28.4 ± 7.27	8.79 ± 2.06	1181 ± 104	885 ± 64

exclusively inside of the host. Ecdysis from second to third instar appears to occur upon entry into the cockroach body cavity. This is corroborated by appearance of larval cuticle on the outside of the cockroach near the entry wound (video 4:25). We were not able to observe shedding of cuticle resulting from ecdysis to the second instar, however it has been reported that layers of cuticle appear between larva and host, indicating ecdysis occurs while larvae develop on the outside of the cockroach (Williams 1942).

Once inside the host, the third instar larva consumes all fat body and muscle within its reach, even removing muscle from the coxa and femur of the prothoracic legs. After separating itself from the gut with a layer of silk, the wasp spins a cocoon and pupates inside the cockroach, where it develops into an adult after several weeks and ecloses, ready to mate and hunt, completing the life cycle (Fig. 5). Priority tissues for consumption during the third instar clearly are muscle tissue and fat body, which were first observed to be missing following entry of the larva into the host. Next consumed were the tracheal system, ovaries and accessory glands. The final "meal" was the central nervous system, though a significant portion of the ventral

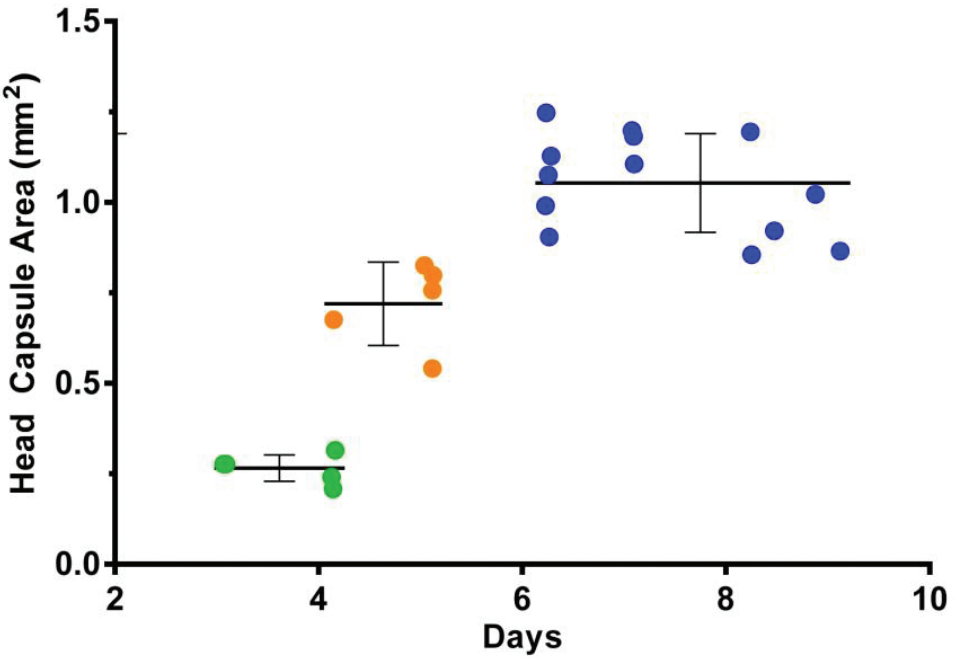

Figure 3. *Ampulex compressa* larvae develop through three instars. The number of instars of *A. compressa* were determined by taking representative larva from different time intervals and plotting the product of the length and width of the head capsule (area) against age of the larva. The data plots as three distinct groups, indicative of three instars (green - first instar, orange - second instar, blue - third instar. Horizontal bars represent average area of the head capsule in each instar and vertical error bars are standard deviation. Each mean head capsule size is significantly different from the others, as indicated by the Kruskal-Wallis test ($p < 0.0001$).

nerve cord remained following wasp pupation. The gut also remains intact following pupation (Fig. 6). Eventually the host desiccates without rotting and the wasp pupa develops in its surrogate womb.

Discussion

Ampulex compressa is a remarkable wasp renowned for its unique host subjugation strategy, in essence turning the cockroach into a "zombie" that becomes a complacent, living source of nourishment for the single offspring (Gal and Libersat 2010). Like all parasitoids, *A. compressa* has evolved an instinctive recognition of its host. We observed that this instinctive familiarity goes beyond just adult behavior, as the larva displays selectivity in its consumption of host tissues. By avoiding the gastrointestinal tract and CNS and focusing instead on fat body, muscle and ovaries, host lifespan may be pro-

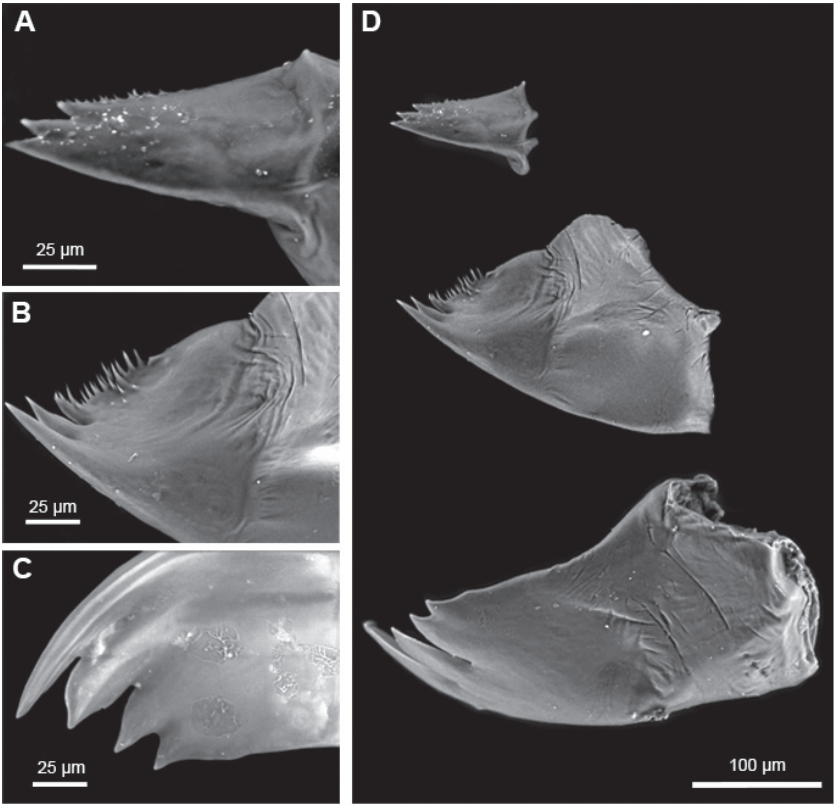

Figure 4. Comparative morphology of mandibles of the three larval instars of *A. compressa*. Mandible morphology is unique to each instar and appears to suit the needs of each stage. **A** First instar mandibles are suitable for piercing the cockroach cuticle and facilitating a steady flow of hemolymph without serious injury to the cockroach **B** The second instar mandible is larger and contains a serrated edge suitable for cutting into the cockroach to facilitate entry into the host **C** Third and last instar mandibles appear after the larva has entered the body cavity of the cockroach to consume fat body and muscle. These mandibles appear to be suited for crushing and macerating the internal tissues **D** All three mandible types together to scale for comparison.

longed until larval development is completed. In fact, *A. compressa* larvae take measures to avoid contact with the host gut by laying down a bed of silk from esophagus to rectum. The cockroach remains alive throughout the first two larval instars and many hours into the third as its organs are consumed selectively.

The wasp larva develops through three instars, the first two outside of the cockroach and the third exclusively inside. This is indicated by distinctive jumps in head capsule size. Dyer's rule asserts that heavily sclerotized body segments such as head capsule and mandibles grow in predictable quantum jumps between instars (Dyar 1890). Dyar's Rule has been applied to many Hymenoptera, where the number of parasitoid wasp instars can vary from two to five (Giannotti 1997; Hansell 1982; Odebiyi and Bokonon-Ganta 1986; Solis et al. 2010; Whitfield et al. 1987). Ad-

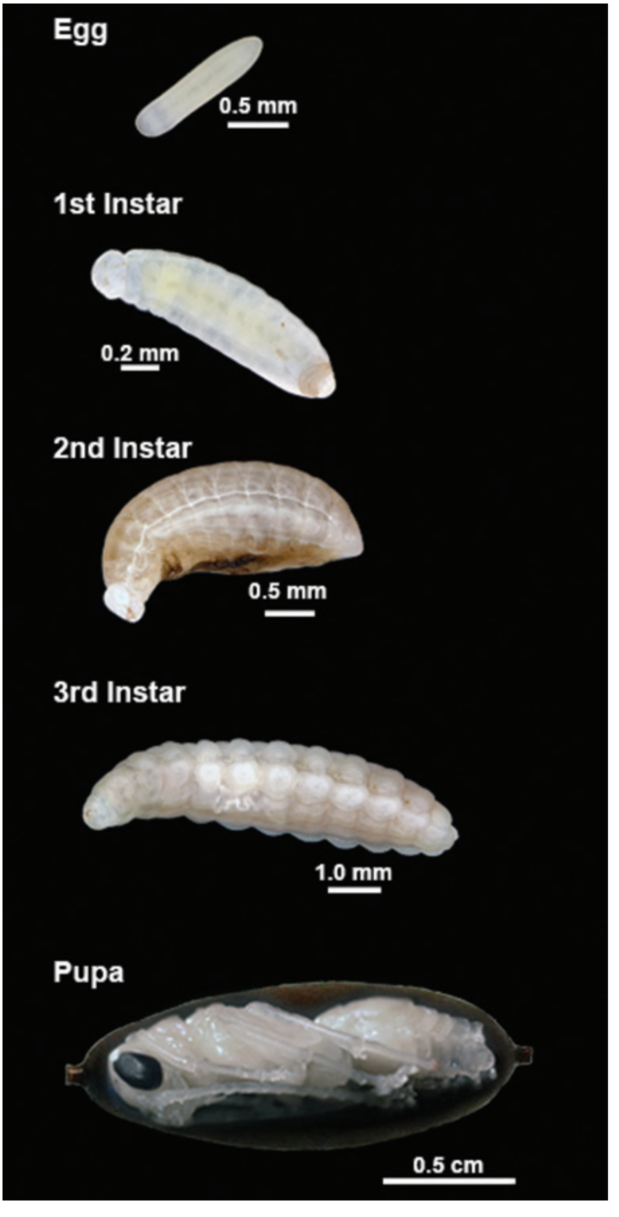

Figure 5. Images of the *Ampulex compressa* life cycle. Life cycle is depicted from egg to pupa.

ditionally, each larval instar is characterized by distinct mandibular morphologies, which appear well-suited to the foraging demands of each instar. The first instar pierces the intersegmental membrane in order to draw hemolymph from the host. The vampiric behavior of the first instar is supported by a circular labium that may be ideal for sucking and ingesting hemolymph (video 3:49). Second instar mandibles are larger, more complex, and serrated, similar to a saw. This may facilitate cutting

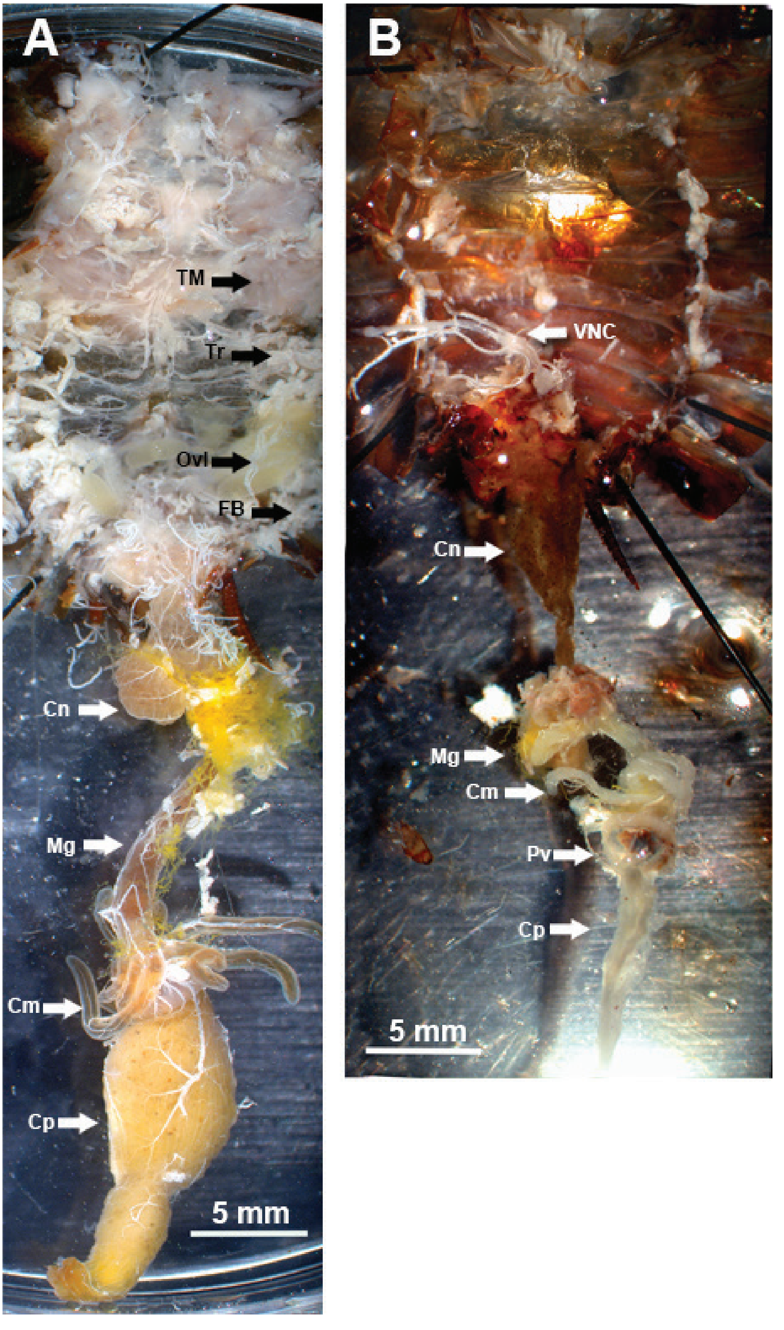

Figure 6. Viscera of *P. americana* before (**A**) and after (**B**) parasitization by *A. compressa*. **A** The entire digestive system has been isolated to more thoroughly illustrate all parts of the gut as well as tissues previously obstructed such as trachea, ovaries, thoracic muscle and fat body **B** Isolated gut from after completion of *A. compressa* larval development. Abbreviations: TM = thoracic muscle, Tr = trachea, Ovl = ovarioles of ovary, FB = fat body, Cn = colon, Mg = midgut, Cm = caeca, Cp = crop, VNC = ventral nerve cord, Pv = proventriculus.

Figure 7. Estimation of pupal size by modeling as a parabola. Shape of the *Ampulex compressa* pupa is a prolate spheroid. Thus, volume of the cocoon can be estimated by modeling it as parabola, rotated about the longitudinal axis, using only length and width measurements.

a hole into the cuticle of the cockroach for entry into the hemocoel. The third and final instar mandibles are larger and have a blunt, crushing surface suitable for maceration and consumption of internal organs.

Development and morphology of *A. compressa* immature stages has been described previously (Fox et al. 2009; Fox et al. 2006; Haspel et al. 2005; Veltman and Wilhelm 1991). Our findings in the present study indicate that developmental timing is more rapid than previously reported, though expected, in that our rearing conditions were 2-3 °C warmer (Fox et al. 2009). Sexual dimorphism also was observed with respect to developmental timing, though this was not found to be statistically significant (Fox et al. 2009). Sexual dimorphism was also suggested as a means to pre-select males from females, though not formally addressed (Veltman and Wilhelm 1991). First and second larval instars are well described as ectoparasitoid (Fox et al. 2006; Haspel et al. 2005). However, we find that, in our colony, the third and last instar, is found exclusively inside the host, which is contradictory to previous reports, despite agreement on body and mandible morphology (Fox et al. 2009; Fox et al. 2006).

Given that female pupae are larger than males, measuring the mass or determining the volume of the cocoon may allow prediction of sex weeks before adult eclosion. *Ampulex compressa* are haplodiploid; females may or may not fertilize their eggs, such that fertilized eggs generate females and non-fertilized eggs generate males. This may result in different numbers of male and female offspring. Only female *A. compressa* envenomate cockroaches and pharmacological research of the envenomation mechanism relies on consistent generation of females. It is therefore useful to predict which pupa will yield female adults and measurement of cocoon mass and volume constitutes a practical way to predict the likelihood that the pupa will develop into a female (Fig. 7).

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Supplementary material 1

Video

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Data type: multimedia

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Three new brachypterous species of *Trimorus* Förster (Hymenoptera, Scelionidae) from Japan

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Abstract

Three new brachypterous species of *Trimorus* Förster, *T. coriaceus* **sp. n.**, *T. granulatus* **sp. n.**, and *T. haniyasu* **sp. n.** were described from Japan. Keys to species of Eastern Palearctic brachypterous *Trimorus* and Japanese male of *Trimorus* are provided.

Keywords

Taxonomy, Teleasinae, East Asia

Introduction

The genus *Trimorus* Förster, 1856 is one of the largest genus in Scelionidae, comprising 389 species (Johnson 2018). Among Scelionidae, the brachypterous females are somewhat common, especially of spider egg parasitoids. Females of *Baeus* Haliday, 1833 are always apterous, although males have developed wings. In *Idris* Föester, 1856, females of some species have shortened wings, however, others species are macropterous. Wing polymorphisms are reported in some heteropterous egg parasitoids (e.g. Gryonini Szabó, 1966 and Telenomini Thomson, 1860 (Kononova and Kozlov 2001)). Brachypteries in these genera are results of adaptation for their habitats; most of them live and seach their host in soils or under litters. Also, among *Trimorus*, egg parasitoids of Carabidae (Masner 1975) and Staphylinidae (Staniec 2005) (Coleoptera), brachyptery is also known in 67 species (Kieffer 1926; Dodd 1930; Nixon 1936; Fouts 1948; Graham 1984; Buhl 1998; Kozlov and Kononova 2007: see also Suppl. material 1). Kieffer (1926) reported 34 brachypterous *Trimorus* (mainly *Hoplogryon* Ashmead at that time) from Europe, North America, and Africa. Dodd (1930) described five brachypterous species from Australia. Kononova and Kozlov (2001) recognized 11 brachypterous species from the Palearctic region mainly in Europe and the Russian Far East. However, no species are recorded from East Asia. In the present study, we describe three new brachypterous species from central Honshu Island and Kyushu Island, Japan.

Methods

Specimens examined in the present study have been deposited in collections of the Entomological Laboratory of Kyushu University, Fukuoka, Japan (ELKU) and Entomological Laboratory of Meijo University, Nagoya, Japan (ELMU). The following abbreviations were used for collecting methods: EmT – emergence trap, MT – Malaise trap, PT – pitfall trap, and YPT – yellow pan trap.

Photos were taken by Canon MP-E65mm micro lens mounted on Canon EOS 60D, combined by CombineZM, and processed in GIMP 2.8.14. SEM images were taken by Hitachi S-3000N.

Morphological terminology and measurements follow Masner (1980), Mikó et al. (2007, 2010), and Komeda et al. (2016). The description of surface sculpture follows Eady (1968) and Harris (1979). Abbreviations used for additional measurements are mainly as Mikó et al. (2010), and some additional abbreviations as : A2–6 – length of female antennomere 2–6, A5L – length of male antennomere 5, A5W – apical width of male antennomere 5, and ty – length of tyloid.

Taxonomy

Trimorus coriaceus **sp. n.**
http://zoobank.org/A6761D41-4A05-486D-B221-46167ADCE361
Figs 1; 4

Diagnosis. Female. Frons coriaceous. A2–4 same length. Mandible tridentate; teeth almost same length. Mesoscutum flat, densely punctate–imbricate. Mesoscutellum flat, imbricate. Postacetabulum imbricate–smooth. Fore and hind wings reaching posterior edge of T1. T1 with slightly developed horn; T3 coriaceous with dense setae.

Description. ***Female*** (n = 3): Length = 0.88–0.90 mm (m = 0.89).

Color (Fig. 1A, B). Body light brown; head and A3–12 dark brown.

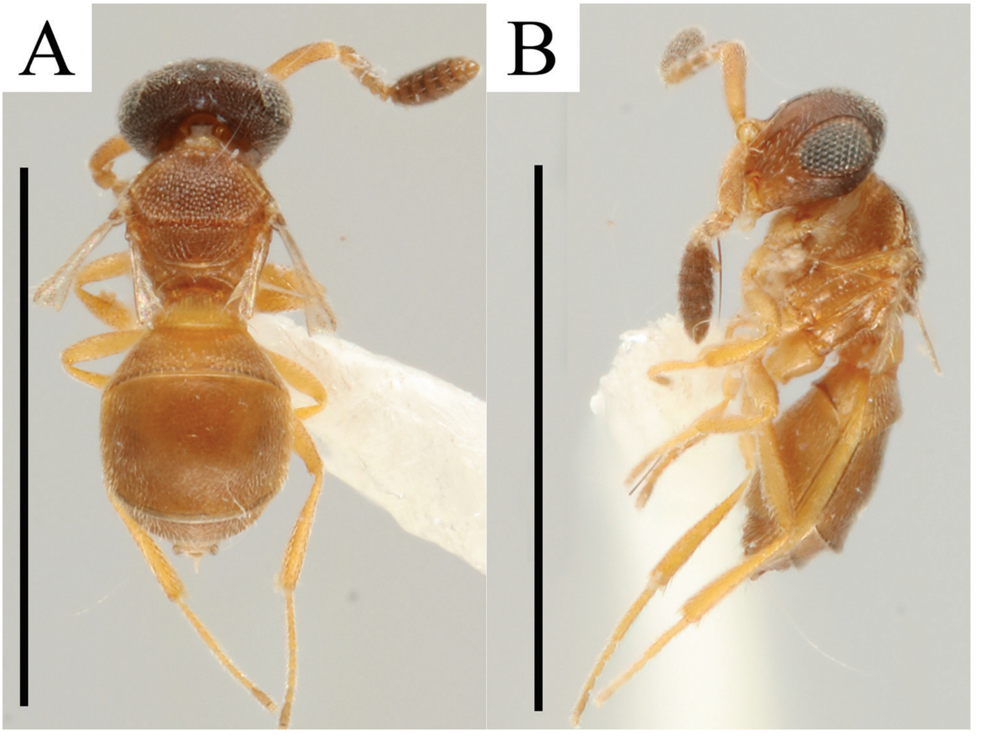

Figure 1. *Trimorus coriaceus* sp. n. **A** female, dorsal view **B** female, lateral view. Scale bars: 1 mm.

Head. FCI = 1.18–1.21 (*m* = 1.19); LCI = 1.50–1.62 (*m* = 1.55); DCI = 1.81–1.90 (*m* = 1.84) HW/IOS = 1.60–1.65 (*m* = 1.62); head about 1.3 times as wide as mesosoma (HW/TSL = 1.27–1.33, *m* = 1.31). Frons (Fig. 4A) coriaceous with dense setae; frontal patch absent; central keel incomplete; antennal scrobe small, smooth, without setae; interantennal process (Fig. 1B) rounded without setae. Vertex coriaceous with dense setae; POL as long as OOL (POL/OOL = 1.00–1.14, *m* = 1.05); OOL 1.5 times as long as LOL (OOL/LOL = 1.40–1.60, *m* = 1.53); hyperoccipital carina absent; vertex patch absent. Eyes with dense setae. Malar region costate; facial striae expanding to bottom of eye; orbital carina extending to top of eye. Gena coriaceous with dense setae; genal patch absent. A1 (Fig. 4B) about 5.7 times as long as radicle (A1/r = 5.50–5.75, *m* = 5.67), about 11.3 times as long as A6 (A1/A6 = 11.00–11.50, *m* = 11.33), as long as clava (A1/cl = 1.00–1.05, *m* = 1.03); A2–4 same length, about 2 times as long as A6 (A2/A6 = 2.00; A3/A6 = 2.00; A4/A6 = 1.50–2.00, *m* = 1.83); A5 as long as A6 (A5/A6 = 1.00). Mandible tridentate; all teeth of mandible almost same length.

Mesosoma. Pronotal suprahumeral sulcus foveolate; epomial carina incompletely present; cervical pronotal area imbricate with dense setae; lateral pronotal area rugulose–smooth. Mesoscutum (Fig. 4C) about 1.8 times as wide as long (TSL/ML = 1.67–1.76, *m* = 1.73), flat, densely punctate–imbricate, with dense setae; mesoscutal suprahumeral sulcus present; mesoscutal humeral sulcus present; antero–admedian line absent; notauli absent. Mesoscutellum about 2.6 times as wide as long (SW/SL = 2.50–2.63, *m* = 2.58), flat, imbricate, with dense setae; scutoscutellar sulcus foveolate; axillular carina present; mesoscutellum without median spine; posterior scutellar sulcus foveolate. Femoral depression (Fig. 4D) smooth; mesopleural carina present; anterior rows of foveae of mesopleural carina present; posterior rows of foveae of mesopleural carina present dorsally; postacetabular sulcus foveolate; postacetabulum imbricate–smooth with dense setae; postacetabular patch absent; sternaulus foveolate; mesepimeral sulcus foveolate; speculum relatively wide, transversely sulcate; prespecular sulcus foveolate; transpleural sulcus foveolate. Metanotal trough foveolate; metascutellum smooth; metascutellar carina unclear; metanotal spine present, short, blunt. Metapleural sulcus foveolate; dorsal metapleural areas smooth; ventral metapleural areas smooth; paracoxal sulcus present; metapleural epicoxal sulcus present; metapleural epicoxal carina completely present; metapleural triangle smooth; prespiracular propodeal area narrow, modified to small teeth; lateral propodeal carina present; lateral propodeal area sulcate; metasomal depression sulcate; plica present posteriorly; posterior propodeal projection modified to shortly curved spine; plical area with dense setae. Legs (Fig. 1A, B) elongate. Fore wing (Fig. 1A, B) short, narrow, reaching posterior edge of T1. Hind wing short, narrow, reaching posterior edge of T1.

Metasoma. T1 about 0.7 times as long as T1+T2 length (T1W/T1+T2L = 0.59–0.87, *m* = 0.70), longitudinally costate; T1 horn slightly producing. T2 longitudinally costate anteriorly, coriaceous with dense setae posteriorly; basal depressions on T2 present; lateral patch of T2 absent; T3 (Fig. 4E) about 1.2 times as wide as long (T3W/T3L = 1.16–1.26, *m* = 1.22), about 1.3 times as wide as mesoscutum (T3W/TSL = 1.23–1.43, *m* = 1.34), coriaceous with dense setae; basal depressions on T3 absent; lateral patch of T3 absent; posterodorsal patch of T3 absent; apical setae on T3 absent. S3 (Fig. 4F) coriaceous with dense setae; basal depressions of S3 absent. T4 coriaceous with dense setae; median patch on T4 absent; lateral patch of T4 absent. T5 coriaceous with dense setae; lateral patch of T5 absent; T6 coriaceous with dense setae; lateral patch of T6 absent.

Male. Unknown.

Material examined. Holotype: Aichi pref.: Kita–Shitara dist., Shitara town, Uradani (Beech forest), alt. 900m, 18–24. VII. 1994, K. Yamagishi leg., 1♀ (EmT) [ELMU]. Paratypes: Same locality as the holotype, 9–17. IV. 1994, K. Yamagishi leg., 1♀ (YPT) [ELMU]; 25. IV–1. V. 1994, 1♀ (EmT) [ELMU]; 2–8. V. 1994, 3♀ (YPT) [ELMU]; 9–15. V. 1994, 1♀ (EmT) [ELMU]; 9–15. V. 1994, 1♀ (YPT) [ELMU]; 16–22. V. 1994, 1♀ (EmT) [ELMU]; 23–29. V. 1994, 9♀ (EmT) [ELMU]; 6–12. VI. 1994, 4♀ (YPT) [ELMU]; 13–19. VI. 1994, 23♀ (EmT) [ELMU]; 13–19. VI. 1994, 9♀ (YPT) [ELMU]; 20–26. VI. 1994, 8♀ (EmT) [ELKU]; 20–26. VI. 1994, 1♀ (MT) [ELMU]; 27. VI–3. VII. 1994, 7♀ (EmT) [ELKU]; 27. VI–3. VII. 1994, 2♀ (YPT) [ELMU]; 4–10. VII. 1994, 4♀ (EmT) [ELMU]; 11–17. VII. 1994, 2♀ (EmT) [ELMU]; 15–21. VIII. 1994, T. Kanbe leg., 1♀ (EmT) [ELMU]; 22–28. VIII. 1994, 2♀ (EmT) [ELMU]; 29. VIII–4. XI. 1994, K. Yamagishi leg., 3♀ (EmT) [ELKU]; 5–11. XI. 1994, 2♀ (EmT) [ELMU].

Distribution. Japan (Honshu: Aichi).

Etymology. The species name refers to the sculpture of frons and metasoma.

Remarks. Among eastern Palearctic *Trimorus* species, this species is similar to *T. amesis* Kozlov & Kononova, 2001 and *T. mirandus* Kozlov & Kononova, 2001 in having shortened wings that at most reach posterior margin of mesosoma. However, it differs from *T. amesis* in small body size (*T. coriaceus* about 0.9 mm, whereas *T. amesis* is about 1.4 mm), antenomere length ratio (A2, A3, A4 are same length, A4 is about 2 times longer than A5, A5 and A6 are same length in *T. coriaceus*; A2 and A3 are same length, A4 is about 0.8 times shorter than A3 and 3.4 times longer than A5, A5 and A6 are same length in *T. amesis*) and central keel (not reaching anterior ocellus in *T. coriaseus*; complete in *T. amesis*), and from *T. mirandus* in sculpture of frons, mesoscutellum, and T3 (frons is coriaceous (Fig. 4A), mesoscutellum is imbricate (Fig. 4C), and T3 is densely punctate–imbricate (Fig. 4E) in *T. coriaceus*; all of them are smooth in *T. mirandus*). In addition, this species differs from *T. granulatus* sp. n. in the shape of head (flat in *T. coriaceus* (Fig. 1A, B); globular in *T. granulatus* (Fig. 2A, B)) and sculpture of frons (coriaceous in *T. coriaceus* (Fig. 4A); granulate in *T. granulatus* (Fig. 5A)) and T3 (densely punctate–imbricate in *T. coriaceus* (Fig. 4E); shallowly punctate in *T. granulatus* (Fig. 5E)).

Trimorus granulatus sp. n.

http://zoobank.org/6694BCFA-36A2-4C18-A1D4-13E8381C50F7

Figs 2; 5; 6

Diagnosis. Head globular. Frons granulate. Eyes small. Mandible subtridentate, with anterior and posterior large teeth and median small tooth. Mesoscutum and mesoscutellum flat, granulate. Postacetabulum granulate–smooth. In female, A2 and A3 longest among A2–6; fore and hind wings short, narrow, beyond anterior edge of metasoma; T1 without horn; T3 shallowly punctate with dense setae. In male, A5 about 2.3 times as long as wide, about 1.5 times as long as tyloid; fore and hind wings long, narrow, exceeding to apical metasoma; T3 weakly punctate–smooth.

Description. ***Female*** (n = 3): Length = 0.90–0.95 mm (m = 0.93).

Color (Fig. 2A, B). Body dark brown; A1–2, legs, T1 light brown.

Head globular. FCI = 1.13–1.16 (m = 1.14); LCI = 1.28–1.35 (m = 1.32); DCI = 1.48–1.52 (m = 1.50); HW/IOS = 1.33–1.40 (m = 1.37); head about 1.3 times as wide as mesosoma (HW/TSL = 1.24–1.32, m = 1.29). Frons (Fig. 5A) granulate with dense setae; frontal patch absent; central keel present ventrally; antennal scrobe small, smooth, without setae; interantennal process (Fig. 2B) rounded without setae. Vertex granulate with dense setae; POL as long as OOL (POL/OOL = 0.90–1.11, m = 1.00); OOL about 1.9 times as long as LOL (OOL/LOL = 1.80–2.00, m = 1.87); hyperoccipital carina absent; vertex patch absent. Eyes small with dense setae. Malar region costate; facial striae expanding to bottom level of eye; orbital carina extending to top level of eye. Gena granulate with dense setae; genal patch absent. A1 (Fig. 5B) about

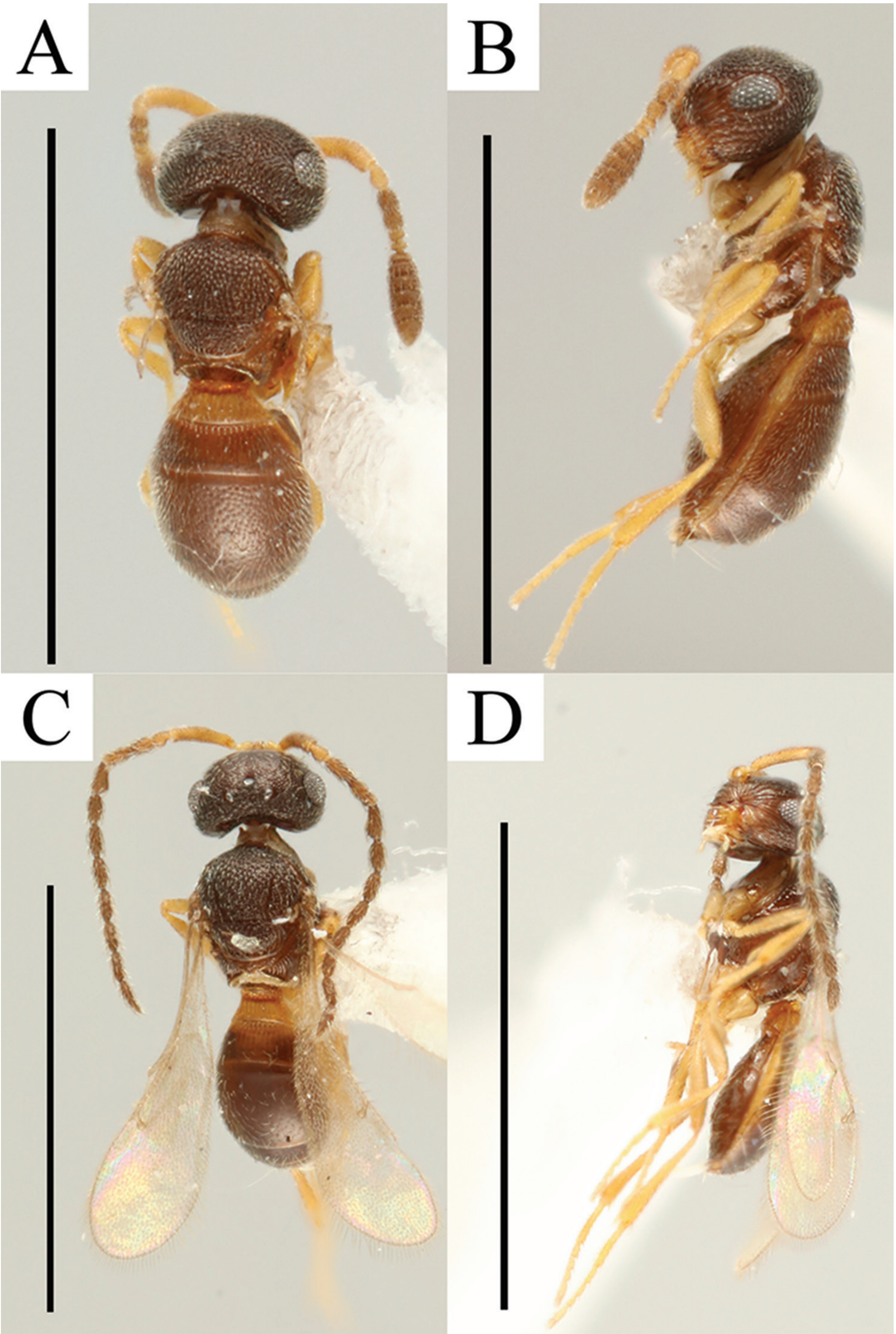

Figure 2. *Trimorus granulatus* sp. n. **A** female, dorsal view **B** female lateral view **C** male, dorsal view **D** male lateral view. Scale bars: 1 mm.

5.6 times as long as radicle (A1/r = 5.50–5.75, *m* = 5.58), about 22.3 times as long as A6 (A1/A6 = 22.00–23.00, *m* = 22.33), about as long as clava (A1/cl = 1.05–1.10, *m* = 1.00); A2–3 same length, 5 times as long as A6 (A2/A6 = 5.00; A3/A6 = 5.00); A4 about 3.3 times as long as A6 (A4/A6 = 3.00–4.00, m = 3.33); A5 as long as A6 (A5/A6 = 1.00). Mandible tridentate; anterior and posterior tooth same length, median tooth shorter.

Mesosoma. Pronotal suprahumeral sulcus sulcate–foveolate; epomial carina weakly present; cervical pronotal area granulate with dense setae; lateral pronotal area smooth. Mesoscutum (Fig. 5C) about 1.6 times as wide as long (TSL/ML = 1.50–1.61, *m* = 1.56), flat, granulate, with dense setae; mesoscutal suprahumeral sulcus weakly present; mesoscutal humeral sulcus weakly present; antero–admedian line absent; notauli weakly present, expanding to half level of mesoscutum; inter notaular area granulate with dense setae; lateral notaular area granulate with dense setae. Mesoscutellum about 2.4 times as wide as long (SW/SL = 2.25–2.50, *m* = 2.36), flat, granulate, with dense setae; scutoscutellar sulcus foveolate; axillular carina present; mesoscutellum without median spine; posterior scutellar sulcus foveolate. Femoral depression (Fig. 5D) smooth; mesopleural carina present; anterior rows of foveae of mesopleural carina present; posterior rows of foveae of mesopleural carina foveolate dorsally; postacetabular sulcus foveolate; postacetabulum granulate–smooth with dense setae; postacetabular patch absent; sternaulus absent; mesepimeral sulcus foveolate; speculum wide, transversely sulcate; prespecular sulcus foveolate; transpleural sulcus absent. Metanotal trough foveolate; metascutellum rugulose–foveolate; metascutellar carina unclear; metanotal spine weakly present, short, blunt. Metapleural sulcus present; dorsal metapleural areas smooth; ventral metapleural areas smooth; paracoxal sulcus foveolate; metapleural epicoxal sulcus present; metapleural epicoxal carina completely present; metapleural triangle smooth; prespiracular propodeal area narrow; lateral propodeal carina present; lateral propodeal area sulcate; metasomal depression sulcate; plica absent; posterior propodeal projection weakly present; plical area narrow, with dense setae. Legs (Fig. 2A, B) elongate. Fore wing (Fig. 2A, B) short, narrow, beyond anterior edge of metasoma. Hind wing short, narrow, beyond anterior edge of metasoma.

Metasoma. T1 about 0.6 times as long as T1+T2 length (T1W/T1+T2L = 0.50–0.59, *m* = 0.55), longitudinally costate. T2 longitudinally costate in anterior, shallowly punctate with dense setae in posterior; basal depressions on T2 present; lateral patch of T2 absent. T3 (Fig. 5E) about 1.2 times as wide as long (T3W/T3L = 1.10–1.22, *m* = 1.16), about 1.2 times as wide as mesoscutum (T3W/TSL = 1.18–1.22, *m* = 1.20), shallowly punctate with dense setae; basal depressions on T3 absent; lateral patch of T3 absent; posterodorsal patch of T3 absent; apical setae on T3 absent. S3 (Fig. 5F) shallowly punctate with dense setae. T4 shallowly punctate with dense setae; median patch on T4 absent; lateral patch of T4 absent. T5 shallowly punctate with dense setae; lateral patch of T5 absent. T6 shallowly punctate with dense setae; lateral patch of T6 absent.

Male (*n* = 3): Length = 0.93–1.00 mm (*m* = 0.95). FCI = 1.17–1.27 (*m* = 1.22); LCI = 1.32–1.36 (*m* = 1.34); DCI = 1.55–1.73 (*m* = 1.64); HW/IOS = 1.42–1.46 (*m* = 1.45); HW/TSL = 1.17–1.27 (*m* = 1.24). Central keel (Fig. 6A) present, incomplete dorsally; antennal scrobe larger than female, smooth, without setae. POL/OOL = 0.89–1.00 (*m*=0.96); OOL/LOL = 1.80–2.25 (*m* = 2.10). Eyes larger than female. Orbital carina extending to bottom level of eye. A1/r = 4.00–4.40 (*m* = 4.20); A5 (Fig. 6B) 2.3 times as long as wide (A5L/A5W = 2.25), about 1.5 times as long as tyloid (A5L/ty = 1.50). TSL/ML = 1.36–1.50 (*m* = 1.44). SW/SL = 2.00–2.20 (*m* = 2.13); notauli (Fig. 6C) present, expanding to 3/4 levels of mesoscutum. Mesoscutellum shallowly punctate–smooth with dense setae. Anterior rows of foveae of mesopleural carina (Fig. 6D) foveolate dorsally, smooth ventrally; postacetabulum granulate–smooth with sparse setae; speculum wide, smooth. Metapleural sulcus absent; paracoxal sulcus foveolate dorsally, absent ventrally; metapleural epicoxal sulcus absent; lateral propodeal area foveolate; metasomal depression foveolate; plica present in posterior; plical area with dense setae. Legs (Fig. 2C, D) elongate. Fore wing (Fig. 2C, D) long, narrow, exceeding to apical metasoma, as wide as mesoscutum (TSL/WW = 0.94–1.04, *m* = 1.00); marginal vain about 3.5 times as long as stigmal vein (m/st = 3.33–3.67, *m* = 3.53). Hind wing long, narrow, exceeding to apical metasoma, 1.5 times as wide as length of marginal cilia at widest point (HWW/HWS = 1.40–1.50, *m* = 1.47). T1W/T1+T2L = 0.60–0.63 (*m* = 0.61). T3W/T3L = 1.11–1.23 (*m* = 1.18); T3 (Fig. 6E) narrower (T3W/TSL = 1.03–1.07, *m* = 1.04), weakly punctate–smooth with sparse setae; posterodorsal patch of T3 present, rugulose. S3 (Fig. 6F) smooth with dense setae; S3 setae sparser than female. T4 smooth with dense setae; T4 setae sparser than female.

Material examined. Holotype: Fukuoka pref.: Fukuoka city, Mt. Tachibana, 2. X. 1993, H. Honda leg., 1♀ (YPT) [ELKU]. Paratypes: Same locality as the holotype, 2. X. 1993, H. Honda leg., 5♂ (YPT) [ELKU]; 16. X. 1993, 7♂2♀ (YPT) [ELKU]; 23. X. 1993, 5♂5♀ (YPT) [ELKU]; 30. X. 1993, 6♂1♀ (YPT) [ELKU]; 6. XI. 1993, 7♂2♀ (YPT) [ELKU]; 14. XI. 1993, 8♂6♀ (YPT) [ELKU]; 20. XI. 1993, 6♂6♀ (YPT) [ELKU]; 27. XI. 1993, 3♂2♀ (YPT) [ELKU].

Distribution. Japan (Kyushu: Fukuoka).

Etymology. The species name refers to the sculpture on frons and mesoscutum.

Remarks. Among eastern Palearctic *Trimorus* species, the female of this species is similar to *T. amesis* Kozlov & Kononova, 2001 and *T. mirandus* Kozlov & Kononova, 2001 in shortened wings at most reaching posterior margin of mesosoma. But it differs from *T. amesis* in small body size (*T. granulatus* about 0.9 mm; *T. amesis* about 1.4 mm) and sculpture of T3 (shallowly punctate in *T. granulatus*, coriaceus in *T. amesis*), and from *T. mirandus* in sculpture of frons, mesoscutellum and T3 (frons and mesoscutellum are granulate (Fig. 5A, C) and T3 is shallowly punctate (Fig. 5E) in *T. granulatus*; all of them are smooth in *T. mirandus*). In addition, this species differs from *T. coriaceus* sp. n. in the shape of head (globular in *T. granulatus* (Fig. 2A, B), flat in *T. coriaceus* (Fig. 1A, B)) and sculpture of frons (granulate in *T. granulatus* (Fig. 5A); coriaceous in *T. coriaceus* (Fig. 4A)) and T3 (shallowly punctate in *T. granulatus* (Fig. 5E); densely punctate–imbricate in *T. coriaceus* (Fig. 4E)). Male of *T. granulatus* is similar to *T. bisulcatus* Kieffer, 1908 in ratio of length and width of antenomeres. The new species differs from *T. bisulcatus* in body size (*T. granulatus* is about 1 mm; *T. bisulcatus* is about 1.7–2 mm) and body sculpture.

Trimorus haniyasu **sp. n.**
http://zoobank.org/52D8DD10-3F9E-41AE-B743-42EF34062BF6
Figs 3; 7; 8

Diagnosis. Frons shallowly punctate. Mandible subtridentate, with anterior and posterior large teeth and median small tooth. Mesoscutum and mesoscutellum densely deeply punctate. Postacetabulum rugulose–densely deeply punctate. T3 deeply punctate. In female, A3 longest among A2–6; mesoscutum and mesoscutellum flat; fore and hind wings reaching apical margin of T3; T1 without horn. In male, A5 about twice as long as wide and about 1.8 times as long as tyloid; mesoscutum and mesoscutellum convex; fore wing far exceeding to apical mesosoma; hind wing exceeding to apical mesosoma.

Description. ***Female*** (n = 2): Length = 1.83–2.00 mm.

Color (Fig. 3A, B). Body mainly black–dark brown; A1–A6 and mandibles brown and legs excluding coxae yellow.

Head. FCI = 1.09–1.13; LCI = 1.62–1.74; DCI = 1.83–1.89; HW/IOS = 1.66–1.76; head about 1.2 times as wide as mesosoma (HW/TSL = 1.18–1.28). Frons (Fig. 7A) shallowly punctate with dense setae; frontal patch absent; central keel completely present; antennal scrobe smooth without setae; interantennal process (Fig. 3B) rounded with sparse setae. Vertex shallowly punctate with dense setae; POL as long as OOL (POL/OOL = 1.00); OOL about 1.6 times as long as LOL (OOL/LOL = 1.50–1.67); hyperoccipital carina absent; vertex patch present, rugulose. Eyes with sparse setae. Malar region costate; facial striae expanding to middle level of eye; orbital carina extending to top level of eye. Gena costate–punctate with dense setae; genal patch absent. A1 (Fig. 7B) about 6.3 times as long as radicle (A1/r = 6.00–6.60), about 10.5 times as long as A6 (A1/A6 = 10.00–11.00), about 1.9 times as long as clava (A1/cl = 1.07–1.10); A2 2.3 times as long as A6 (A2/A6 = 2.33); A3 longest among A2–6, about 2.7 times as long as A6 (A3/A6 = 2.67); A4 about 2.2 times as long as A6 (A4/A6 = 2.00–2.33); A5 as long as A6 (A5/A6 = 1.00). Mandible tridentate, with anterior and posterior large teeth and median small, tubercular tooth.

Mesosoma. Pronotal suprahumeral sulcus foveolate; epomial carina incompletely present; cervical pronotal area rugulose–densely deeply punctate without setae; lateral pronotal area smooth–rugose. Mesoscutum (Fig. 7C) about 1.7 times as wide as long (TSL/ML = 1.60–1.73) flat, densely deeply punctate, with dense setae; mesoscutal suprahumeral sulcus absent; mesoscutal humeral sulcus weakly present; antero–admedian line absent; notauli weakly present. Mesoscutellum about 2.2 times as wide as long (SW/SL = 2.14–2.33); flat, densely deeply punctate with dense setae; scutoscutellar sulcus foveolate; axillular carina present, with weakly tooth; mesoscutellum without median spine; posterior scutellar sulcus foveolate. Femoral depression (Fig. 7D) smooth in upper half, transversely costate in lower half; mesopleural carina present; anterior rows of foveae of mesopleural carina absent; posterior rows of foveae of mesopleural carina absent; postacetabular sulcus absent; postacetabulum rugulose–densely deeply punctate with dense setae; postacetabular patch absent; sternaulus absent; mesepimeral sulcus absent; speculum transversely costate; prespecular sulcus weakly foveo-

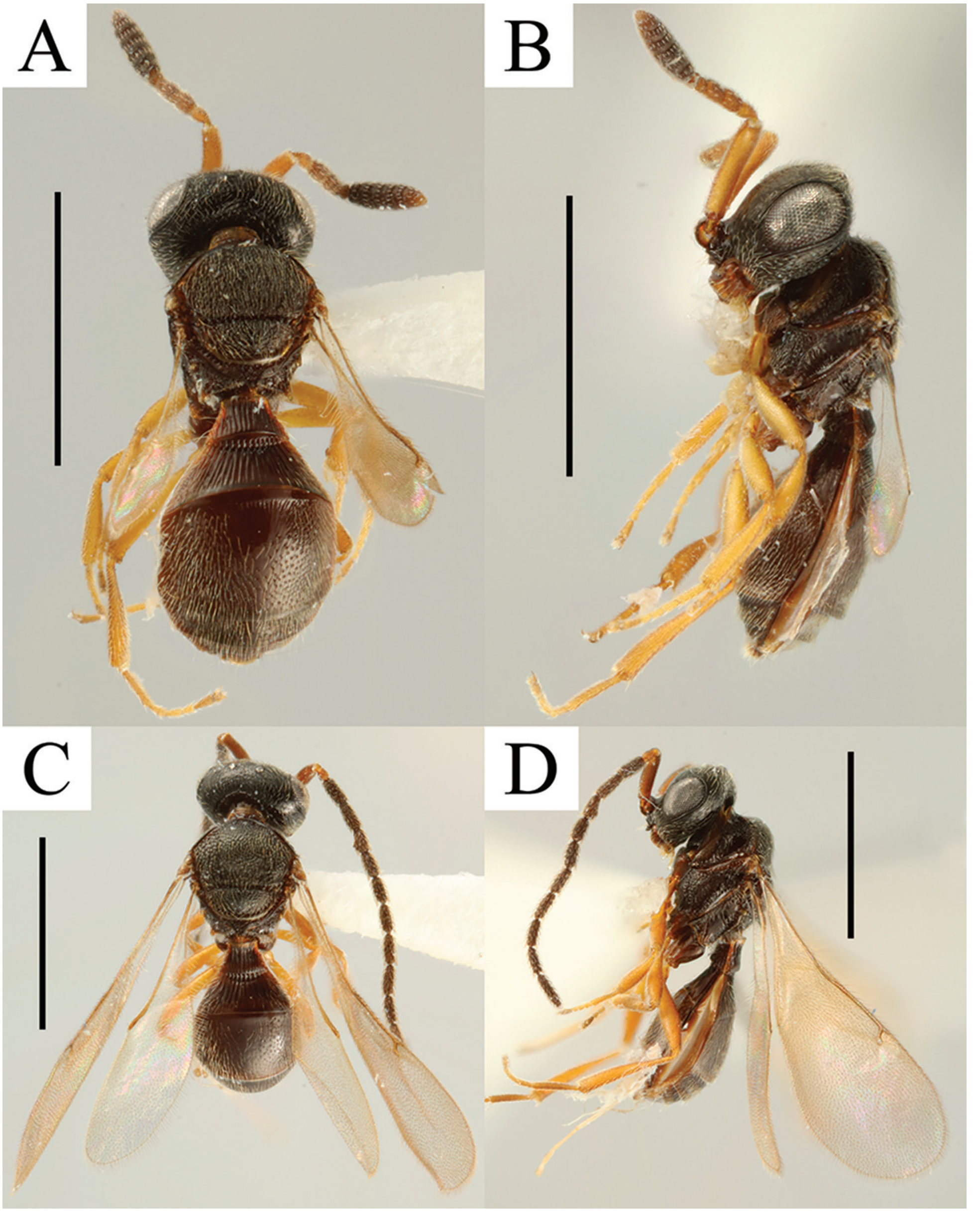

Figure 3. *Trimorus haniyasu* sp. n. **A** female, dorsal view **B** female lateral view **C** male, dorsal view **D** male lateral view. Scale bars: 1 mm.

late; transpleural sulcus absent. Metanotal trough foveolate; metascutellum densely deeply punctate; metascutellar carina present; metanotal spine present, short, blunt. Metapleural sulcus sulcate; dorsal metapleural areas smooth; ventral metapleural areas smooth; paracoxal sulcus present; metapleural epicoxal sulcus weakly present; metapleural epicoxal carina incomplete; metapleural triangle smooth; prespiracular propo-

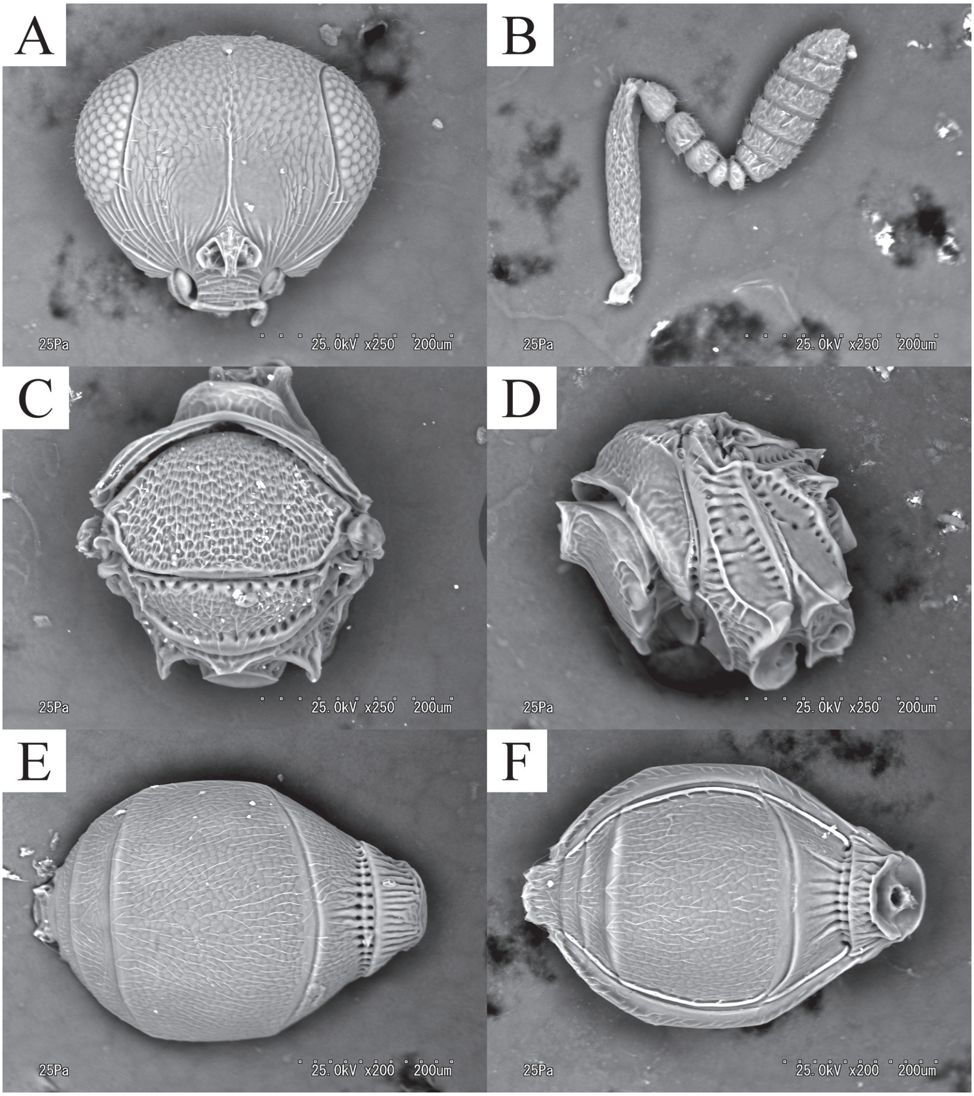

Figure 4. *Trimorus coriaceus* sp. n., female. **A** head, frontal view **B** Antennae **C** mesosoma, dorsal view **D** mesosoma, lateral view **E** metasoma, dorsal view **F** metasoma, ventral view.

deal area narrow, modified to small teeth; lateral propodeal carina present; lateral propodeal area densely deeply punctate; metasomal depression densely deeply punctate; plica present; posterior propodeal projection modified to shortly sharp spine; plical area narrow, densely deeply punctate with dense setae; legs(Fig. 3A, B) elongate. Fore wing (Fig. 3A, B) short, reaching posterior edge of T3, 2 times as wide as mesoscutum (TSL/WW = 2.00–2.05); marginal vein 5 times as long as stigmal vein (m/st = 5.00). Hind wing short, reaching posterior edge of T3, about 4.2 times as wide as length of marginal cilia at widest point (HWW/HWS = 4.00–4.25).

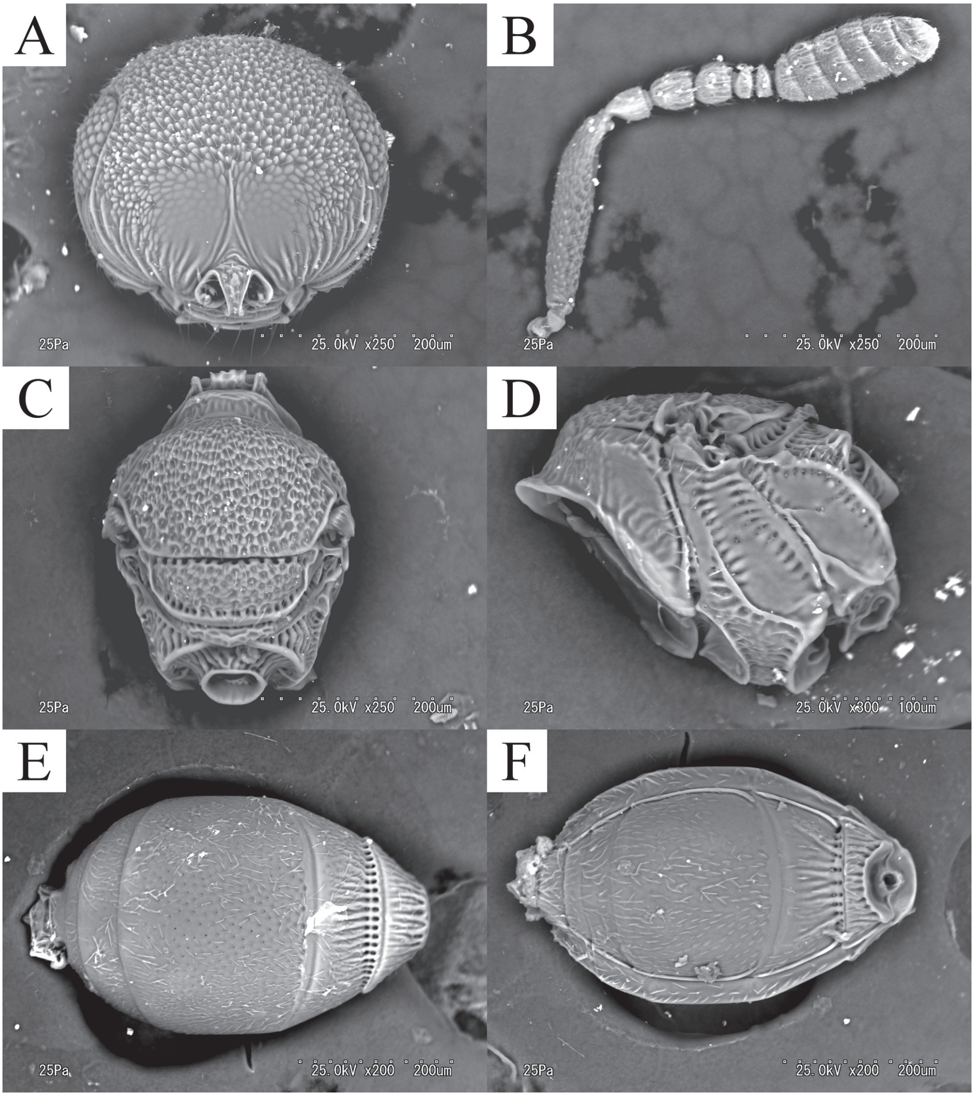

Figure 5. *Trimorus granulatus* sp. n., female. **A** head, frontal view **B** Antennae **C** mesosoma, dorsal view **D** mesosoma, lateral view **E** metasoma, dorsal view **F** metasoma, ventral view.

Metasoma. T1 about 0.6 times as long as T1+T2 length (T1W/T1+T2L = 0.56–0.57), longitudinally costate. T2 longitudinally costate; basal depressions on T2 present; lateral patch of T2 present, with dense setae. T3 (Fig. 7E) about 1.3 times as wide as long (T3W/T3L = 1.26–1.33), about 1.3 times as wide as mesoscutum (T3W/TSL = 1.24–1.33), deeply punctate with dense setae; T3 sculpture sparser medially; basal depressions on T3 absent; lateral patch of T3 absent; posterodorsal patch of T3 absent; apical setae on T3 absent. S3 (Fig. 7F) deeply punctate with dense setae; basal depressions on S3 absent. T4 punctate with dense setae; median patch on T4 absent; lateral patch of T4 absent. T5 punctate with dense

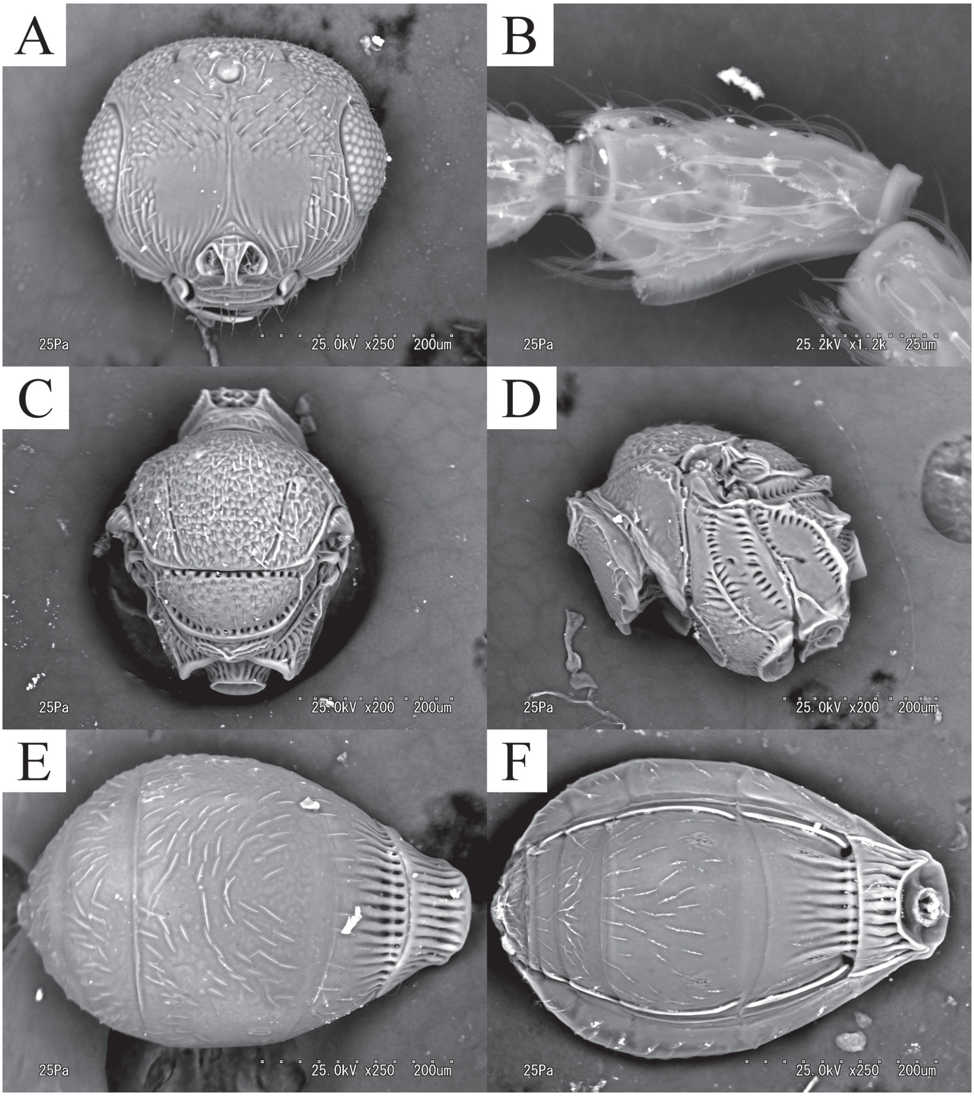

Figure 6. *Trimorus granulatus* sp. n., male. **A** head, frontal view **B** A5, lateral view **C** mesosoma, dorsal view **D** mesosoma, lateral view **E** metasoma, dorsal view **F** metasoma, ventral view.

setae; lateral patch of T5 absent. T6 smooth; lateral patch of T6 present, imbricate, with dense setae.

Male (*n* = 3): Length=1.88–1.98 mm (*m* = 1.93); A1–2 (Fig. 3C, D) brown. Head wider than female (FCI = 1.17–1.26, *m* = 1.22); LCI = 1.56–1.70 (*m* = 1.62); DCI = 1.96–2.00 (*m* = 1.97); HW/IOS = 1.55–1.64 (*m* = 1.60); HW/TSL = 1.16–1.23 (*m* = 1.20). Frons (Fig. 8A) punctate with dense setae: antennal scrobe smooth–costate without setae. Vertex costate–punctate with dense setae; OOL longer (POL/OOL = 0.91–1.00, *m* = 0.94; OOL/LOL = 2.00–2.75, *m* = 2.32); vertex patch absent. Ocelli more developed than female. Facial striae expanding to 3/4 of eye. Gena costate with dense setae. A1/r =

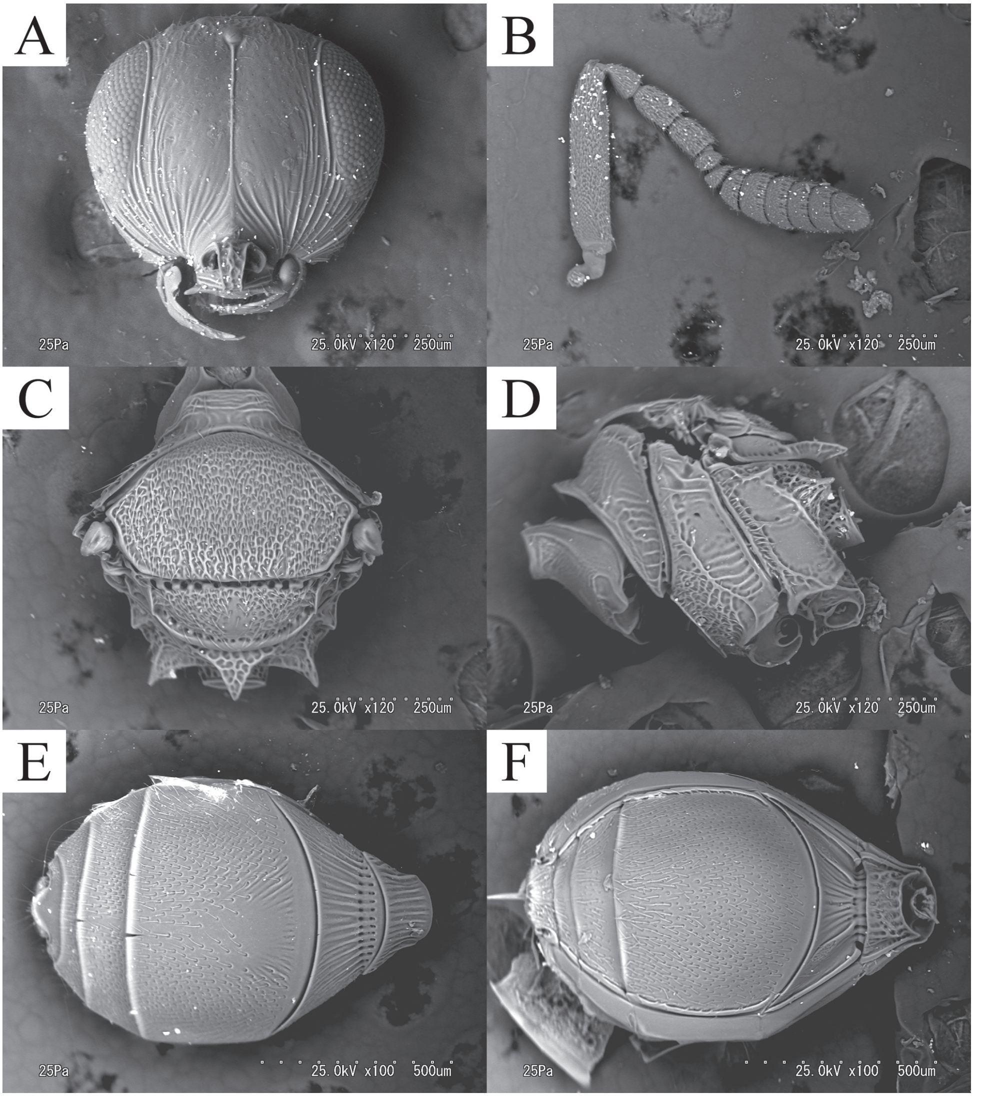

Figure 7. *Trimorus haniyasu* sp. n., female. **A** head, frontal view **B** Antennae **C** mesosoma, dorsal view **D** mesosoma, lateral view **E** metasoma, dorsal view **F** metasoma, ventral view.

4.50–5.00 (m = 4.67); A5 (Fig. 8B) about twice as long as wide (A5L/A5W = 1.83–2.20, m = 2.01); A5 about 1.9 times as long as tyloid (A5L/ty = 1.83–2.00, m = 1.89). Cervical pronotal area rugulose without setae. Mesoscutum (Fig. 8C) longer (TSL/ML = 1.41–1.48, m = 1.44), convex; notauli incompletely present. Mesoscutellum longer (SW/SL = 2.00–2.14, m = 2.07), convex, densely deeply punctate with dense setae. Paracoxal sulcus (Fig. 8D) sulcate–foveolate; metapleural epicoxal sulcus sulcate; metapleural epicoxal carina completely present; prespiracular propodeal area larger than female, modified to small teeth. Fore wing (Figs 3C, D) long, far exceeding to apical mesosoma, wider than mesoscutum (TSL/WW = 0.71–0.73, m = 0.72); marginal vein about 4.2 times as long

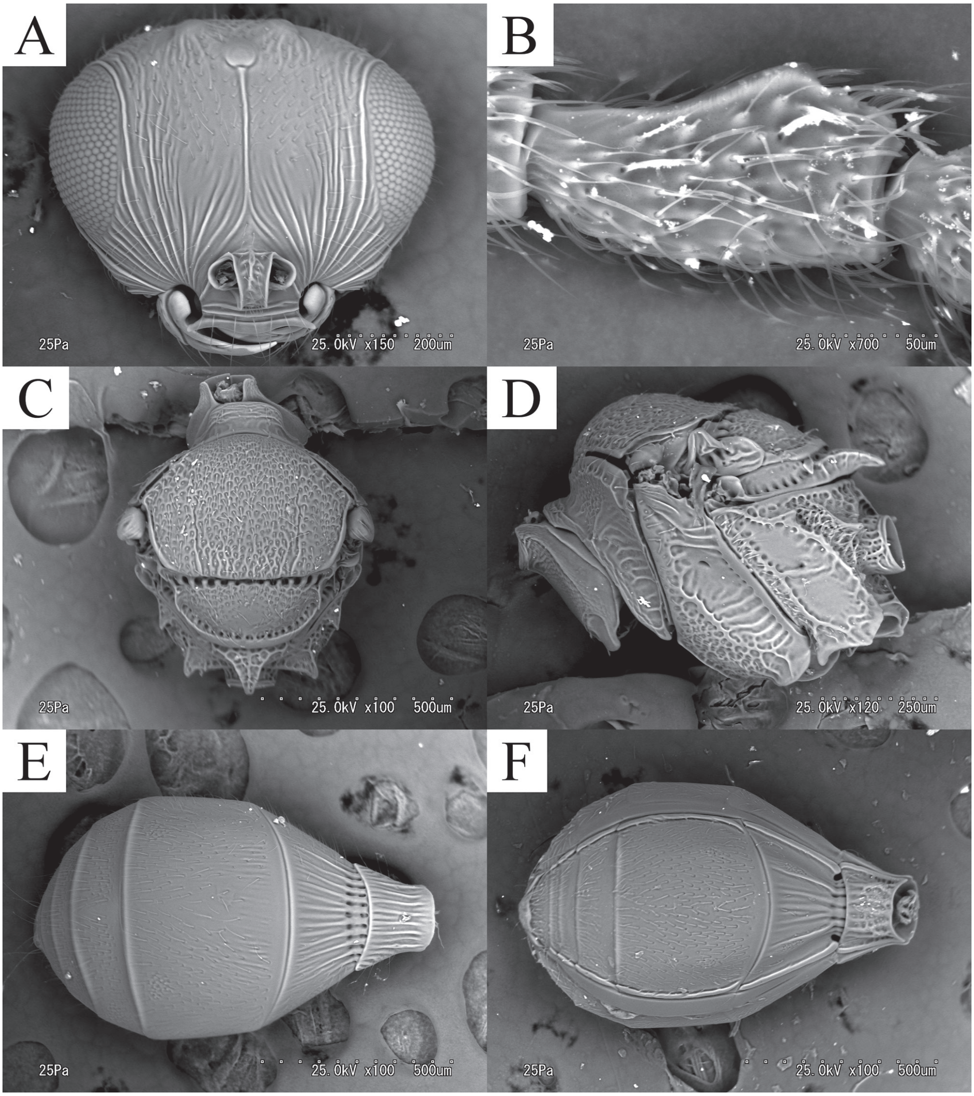

Figure 8. *Trimorus haniyasu* sp. n., male. **A** head, frontal view **B** A5, lateral view **C** mesosoma, dorsal view **D** mesosoma, lateral view **E** metasoma, dorsal view **F** metasoma, ventral view.

as stigmal vein (m/st = 4.00–4.44, *m* = 4.19). Hind wing long, exceeding to apical mesosoma, about 6.4 times as wide as length of marginal cilia at widest point (HWW/HWS = 6.20–6.60, *m* = 6.40). T1W/T1+T2L = 0.44–0.45 (*m* = 0.45); T2 longitudinally costate with dense setae laterally; lateral patch of T2 present, imbricate. T3W/T3L = 1.31–1.36 (*m* = 1.33); T3 narrower (T3W/TSL = 1.07–1.09, *m* = 1.08); sculpture of T3 (Fig. 8E) sparser than female; posterodorsal patch of T3 present, imbricate. S3 (Fig. 8F) deeply punctate with dense setae. Lateral patch of T4 present, imbricate.

Material examined. Holotype: Aichi pref.: Kita–Shitara dist., Shitara town, Uradani (Beech forest), alt. 900m, 13–19. VI. 1994, K. Yamagishi leg., 1♀ (YPT)

[ELMU]. Paratypes: Same locality as the holotype, 16–22. V. 1994, K. Yamagishi leg., 1♂ (EmT) [ELMU]; 6–12. VI. 1994, 2♂ (YPT) [ELKU]; 6–12. VI. 1994, 1♂ (MT) [ELMU]; 13–19. VI. 1994, 1♀ (YPT) [ELKU]; 10–16. X. 1994, 1♂ (PT) [ELMU].

Distribution. Japan (Honshu: Aichi).

Etymology. The species named after Haniyasu, a Japanese god of the soil.

Remarks. Among eastern Palearctic *Trimorus* species, the female of this species is similar to *T. mirificus* Kozlov & Kononova, 2000 and *T. angulator* Kozlov & Kononova, 2000 in shortened wings that reach T3. However, it differs from both species in sculpture of frons (shallowly punctate in *T. haniyasu*; along to central keel smooth and other part costate in *T. mirificus*; dorsally reticulate, ventrally smooth *T. angulator*), mesoscutum (densely and deeply punctate in *T. haniyasu*; reticulate in *T. mirificus* and *T. angulator*) and T3 (deeply punctate in *T. haniyasu*; costate and granulate in *T. mirificus*; reticulate in *T. angulator*). In male, antenomeres about twice as long as wide in *T. haniyasu*, but about 5 times as long as wide in *T. mirificus*.

Key to species of brachypterous female of the Eastern Palearctic *Trimorus*

(“Brachypterous” means shortened wing reaching or not beyond posterior margin of T3 in this key.)

1	Body length more than 1.7 mm; wings reaching T3	**2**
–	Body length less than 1.4 mm; wings shorter, at most reaching posterior margin of mesosoma	**4**
2	Frons (Fig. 7A) shallowly punctate; mesoscutum (Fig. 7C) densely and deeply punctate; T3 (Fig. 7E) deeply punctate	***T. haniyasu* sp. n.**
–	Sculptures of frons and T3 different from above; mesoscutum reticulate	**3**
3	T1 horn present; frons and T3 strigate	***T. mirificus* Kozlov & Kononova, 2000**
–	T1 horn absent; frons and T3 reticulate	***T. angulator* Kozlov & Kononova, 2000**
4	Central keel completely present, reaching anterior ocellus	***T. amesis* Kozlov & Kononova, 2000**
–	Central keel incomplete, not reaching anterior ocellus	5
5	Frons, mesoscutellum, and T3 smooth; mesoscutellum wide: SW/SL about 3.3; T3 wider: T3W/T3L about 1.5	***T.mirandus* Kozlov & Kononova, 2000**
–	Frons, mesoscutellum and T3 sculptured; mesoscutellum not so wide: SW/SL less than 2.6; T3W/T3L about 1.2	**6**
6	Head (Fig. 1B) flat: LCI about 1.5, DCI about 1.8; eyes large; frons (Fig. 4A) and T3 (Fig. 4E) coriaceous; mesoscutum (Fig. 4C) densely punctate–imbricate; T1 horn weakly present	***T. coriaceus* sp. n.**
–	Head (Fig. 2B) globular: LCI about 1.3, DCI less than 1.5; eyes small; frons (Fig. 5A) and mesoscutum (Fig. 5C) granulate; T3 (Fig. 5E) shallowly punctate; T1 horn absent	***T. granulatus* sp. n.**

Key to males of species of Japanese *Trimorus*

(Male of *T. butus* Kononova & Kozlov, 2001, *T. calvus* Miyazaki, 1979, *T. coriaceus*, *T. fulviclavatus* Miyazaki, 1979, *T. nasutus* Kononova & Kozlov, 2001, *T. nipponensis* Masner & Muesebeck, 1968, *T. striatissimus* Miyazaki, 1979 and *T. viktori* Kononova, 2001 are unknown.)

1 Mandible tridentate, with almost same length teeth (body mainly black-dark brown; notaulus present, expanding to half level of mesoscutum; T3 weakly coriaceous).. ***T. nigrigaster* Miyazaki, 1979**

– Mandible subtridentate, with anterior and posterior large teeth and median small tooth (or bump)..**2**

2 Antennomeres elongated: A5L more than 3.5 times as long as A5W............ .... ***T. laticlypeatus* Miyazaki, 1979**

– Antennomeres shortened: A5L less than 2.5 times as long as A5W **3**

3 Body length less than 1 mm. (frons (Fig. 6A) and mesoscutum (Fig. 4C) granulate; postacetabulum (Fig. 6D) granulate–smooth) ....***T. granulatus* sp. n.**

– Body length greater than 1.8 mm. (frons (Fig. 8A) punctate; mesoscutum (Fig. 8C) deeply punctate with densely locates punctures; postacetabulum (Fig. 8D) rugulose–deeply punctate with densely locates punctures)............ .... ***T. haniyasu* sp. n.**

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Supplementary material 1

Checklist of brachypterous *Trimorus*

Authors: Yoto Komeda, Toshiharu Mita, Kenzo Yamagishi

Data type: species data

Link: https://doi.org/10.3897/jhr.63.23671.suppl1

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RESEARCH ARTICLE

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Host acceptance by three native braconid parasitoid species attacking larvae of the Mexican fruit fly, *Anastrepha ludens* (Diptera, Tephritidae)

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Abstract

We studied the oviposition and host acceptance behavior of three braconid parasitoid species native to Mexico, *Doryctobracon crawfordi* (Viereck), *Opius hirtus* (Fischer), and *Utetes anastrephae* (Viereck), with potential to be considered as biocontrol agents against tephritid fruit fly pests in the Neotropics. Third instar larvae of *Anastrepha ludens* (Loew), with and without previous parasitization by conspecifics, were simultaneously offered to females of each species, and the individual behavior was video recorded to construct oviposition flow diagrams. The patterns of foraging and host acceptance were similar in the studied species; all rejected mostly parasitized hosts suggesting that this strategy is common in the guild of larval parasitoids attacking *Anastrepha* spp. The complete searching and host acceptance process took 2.2 ± 0.1 min (mean ± SE) in *D. crawfordi*, 1.7 ± 0.1 s in *U. anastrephae* and 1.5 ± 0.1 s in *O. hirtus*. Notably, because of toxins injected by parasitoid females during oviposition, the parasitized hosts experienced a transient paralysis of variable duration. Hosts attacked by *U. anastrephae* remained immobile for the shortest time (12.5 ± 1 min) (mean±SE), followed by *D. crawfordi* (20.5 ± 3.4 min) and *O. hirtus* (24.1 ± 2 min). Our data revealed a notable discrimination ability in all three species, and that behavioral differences lay mainly in the time of parasitization and in the duration of paralysis experienced by attacked hosts. This suggest that the three species could be valuable as biocontrol agents, but additional studies are necessary to better understand the advantages and limitations of each one as natural enemies of fruit fly pests.

Keywords

Host discrimination, transient host paralysis, biocontrol agents, *Doryctobracon crawfordi*, *Opius hirtus*, *Utetes anastrephae*

Introduction

Fruit flies (Diptera: Tephritidae) are considered one of the main fruit pests worldwide (Enkerlin 2005). To reduce pest populations, various control tactics have been developed among which the augmentative release of parasitoids has arisen as one sound and well oriented strategy against these pests (Sivinski et al. 1996, Montoya et al. 2007).

Parasitoids are insects whose larvae develop by feeding in or on the body of other arthropods, usually insects; larval feeding almost always results in the death of the host (Godfray 1994). Parasitoids are immersed in a multitrophic context (Hassell and Waage 1984, Vet and Dicke 1992), where foraging for nutrients and hosts is performed at different scales (Kramer 2001, Gingras et al. 2002). In general, it is the female parasitoid that locates a suitable host. Because parasitoid development is dependent on limited resources (the host), adult preference and larval performance should be correlated to maximize fitness (Harvey et al. 2015) and the host acceptance procedure is considered the definitive step in host searching behavior (Vinson 1984). The hosts are often hidden in the interior of stems, leaves or fruits (Richerson and Borden 1972), consequently parasitoid females must detect and respond to a number of indirect signals where chemical-sensorial information plays a fundamental role (Vinson 1976, 1998, van Alphen and Vet 1986, Vet and Dicke 1992). In addition to chemical stimuli, parasitoids are also capable of identifying vibrations emitted by their hosts through the substrates in which they develop (van Alphen and Janssen 1982, Vet and van Alphen 1985, Meyhöfer et al. 1997).

Once female parasitoids have located their hosts, they have the capacity to distinguish between parasitized and not parasitized hosts, a strategy known as discrimination ability (van Alphen and Visser 1990). This ability can occur at three levels: (1) self-discrimination, (2) conspecific discrimination and (3) heterospecific discrimination (Mackauer 1990). This ability has been observed in many species of hymenoptera parasitoids (Vinson 1976), and is particularly important in the case of potential biocontrol agents, since these are expected to be efficient in host searching and to have the ability to discriminate between parasitized and non-parasitized hosts (van Lenteren et al. 1978). The latter helps females to avoid superparasitism, reducing the time and energy spent in searching behavior (Mackauer 1990, Godfray 1994).

Host location and host acceptance behavior has been widely studied in the generalist fruit fly parasitoid *Diachasmimorpha longicaudata* (Ashmead) (Greany et al. 1977, Lawrence 1981, Carrasco et al. 2005). This species is exotic in the Americas where it has been successfully reared for augmentative biological control of *Anastrepha* (Schiner) fruit flies in Mexico (Montoya et al. 2000, 2007) and in Florida USA (Sivinski et al. 1996); and for *Ceratitis capitata* (Wiedemann) in Argentina (Sanchez et al. 2016). However, there is a guild of native opiine braconid parasitoids (Sivinski et al. 2000, 2001) with potential as biocontrol agents, for which little information exists regarding their foraging and host acceptance behavior. This is the case of *Doryctobracon crawfordi* (Viereck), *Utetes anastrephae* (Viereck) and *Opius hirtus* (Fischer), all of which are solitary, larval-pupal endoparasitoids of *Anastrepha* spp. (López et al. 1999), that coexist in different regions of America (Sivinski et al. 2000). It has been postulated that differences in ovipositor size, as well as specific foraging behaviors, serve to prevent direct competition among these species (Ovruski et al. 2000, Sivinski et al. 2000). Under laboratory conditions, the three species can develop in the third instar larvae of *Anastrepha ludens* (Diptera: Tephritidae) (Aluja et al. 2009).

Doryctobracon crawfordi is native in habitats above 600 masl from Mexico to Argentina (Ovruski et al. 2005); possess a long ovipositor 5.39 ± 0.08 mm and attacks *Anastrepha* spp. mainly in citrus fruits and is sensitive to both high temperature and low humidity (Sivinski et al. 2000). *Utetes anastrephae* is characterized by a short ovipositor (1.57 ± 0.04 mm, Sivinski et al. 1997, 2001) and can be found associated with small fruits such as those of *Spondias* spp. (Anacardiaceae), with 2-5 cm of diam and 4 to 33 g weight (Avitia 2000). *Opius hirtus* is a more specialized parasitoid being recovered from *Anastrepha obliqua* (Macquart) in *Spondias mombin* L. and from *Anastrepha alveata* (Stone) infesting *Ximenia americana* L. (Olacaceae) (Sivinski et al. 2000). The three species are synovigenic (Sivinski et al. 2001).

The purpose of this study was to compare the foraging and host acceptance behaviors of the parasitoid species *D. crawfordi*, *U. anastrephae* and *O. hirtus* on previously parasitized and non-parasitized larvae of *A. ludens,* using video recording equipment under laboratory conditions. This knowledge should allow an improved understanding of the oviposition performance and potential of these parasitoid species as biocontrol agents against fruit fly pest species.

Material and methods

Study site and biological material

The experiments were conducted in the Biological Control laboratory of the Moscafrut Program SAGARPA-IICA, located in Metapa de Dominguez, Chiapas, Mexico. The parasitoid colonies were initiated from field infested fruits and maintained at 25±1 °C, 70±5% HR with a photoperiod of 12:12 (L:D) h. Eight-day-old larvae of *A. ludens* mixed with artificial diet were provided as host by the Moscafrut facility, where this species is mass reared as described by Orozco-Davila et al. (2017). Adult parasitoids of the species *D. crawfordi*, *U. anastrephae* and *O. hirtus* were reared according to Aluja et al. (2009).

Preparation of host larvae

Parasitized host larvae were obtained by exposing groups of approximately 100 host larvae for two hours to 100 females and 50 males of each species separately. Larvae with three or more oviposition scars were considered as being successfully parasitized (Montoya et al. 2000, 2003). Host larvae without previous parasitization were allocated to the "not parasitized host group".

Preparation of the parasitoids

Copulated females, 5–6 day old with previous experience of oviposition were used. To gain this experience, groups of ~150 recently emerged adults (1female: 1male) were confined in aluminum frame acrylic cages (30 × 30 × 30 cm) and provided with water and honey as a source of food. Twenty-four hours before conducting the bioassays, ~200 *A. ludens* larvae mixed with larval diet were offered to these parasitoids in a Petri dish oviposition unit, for 2 h.

Host acceptance test

The host searching and acceptance performance of individual parasitoid females was observed with two different types of *A. ludens* host larvae that were exposed simultaneously: 1) larvae previously parasitized (24 h earlier) by conspecifics, and 2) larvae with no previous parasitization. Bioassays were conducted in oviposition units consisting of Petri dishes (55 mm in diameter × 9 mm in depth) with the edges reduced to five mm in depth and a central division of 5 mm to separate the two type of larvae. Five previously parasitized *A. ludens* larvae were placed in one of the two sides, and five non-parasitized larvae, of the same age, were placed in the other side. The oviposition unit was covered with an organza elastic cloth and secured with a rubber band in order to prevent larval escape. This cloth was semi-transparent making possible the observation of the host larvae through it. Guava juice was added on the surface of the cloth in order to attract the females and keep them on the parasitization units until larval detection.

Video recording procedure

The oviposition sequences of thirty females per species were observed and video recordings made with a Samsung KREUZNACH video camera (f = 2.3–78.2 mm; F:1.6; ø30.5). One female was released onto the surface of the oviposition unit in each observation. The larvae and females were replaced after each observation, as well as the cloth and the oviposition unit. Environmental conditions were 25 ± 1 °C and 75 ± 5%

RH. Bioassays were conducted between 8:30 and 15:00 and the time of observation was ~1 h per female. If the female presented null activity for the first five minutes, it was replaced. Time of latency (defined here as "time that elapsed between two ovipositions"), the number of ovipositions, oviposition attempts, duration of oviposition and duration of host paralysis following oviposition (from the moment the stung larva remained immobile, to the moment it resumed crawling), were recorded for both host types. Video recordings were independently analyzed using the *Movie Maker* software version 2.6.4037.0, in order to obtain the sequences and transition frequencies of the different behaviors.

Statistical analysis

The number of ovipositions and oviposition attempts on the two larval types were compared using the *t* test for each parasitoid species. In order to compare the time spent on the different activities observed among the three species, a one-way analysis of variance with the Tukey-HSD test was conducted. Prior to analysis, a Box -Cox transformation of the data was conducted. For all analyses we used the JMP Starter software version 7.0.1 (SAS Institute 2007).

Results

The general behavioral sequences of the three parasitoid species on the two host types were identified. The operational definitions for the observed behaviors are presented in Table 1. The most common sequence for any of the three-braconid species included: 1. Walking (W), 2. Searching for a host (S), 3. Detection of a host (D), 4. Oviposition attempt (OP), 5. Oviposition (O), 6. Rejection (RE), and 7. Failure (F) with some variants occurring depending on species (Figs 1a, b; 2a, b; 3a, b).

Searching and oviposition behavior

In general, the females walked on the surface of the oviposition unit with their antennae in close contact with the surface of the oviposition unit. Once the females detected a larva, they attempted to establish contact with the host by introducing their ovipositor and began a movement of abdominal vibration (associated with the descent of the egg (Montoya et al. 2009); they then moved the antenna and extracted the ovipositor. Even though the three species maintained a similar pattern of oviposition behavior, *U. anastrephae* was often observed to perform a wing movement when inserting its ovipositor into a host. *D. crawfordi* rotated on its axis once contact was established with the larva. These specific behavioral acts led to successful ovipositions (Figs 1, 2 and 3).

Table 1. Definitions of the different behaviors exhibited by *Utetes anastrephae*, *Doryctobracon crawfordi* and *Opius hirtus* while foraging for host larvae.

Behavior	Description
1. Walking	Female walking on the oviposition unit surface, antennae not directed to the substrate
2. Searching for a host	While walking the female touches the surface of the oviposition unit with the antennae
3. Detection of a host	The female stays immobile over a host larva
4. Oviposition attempt	Insertion of the ovipositor in order to have contact with the host. The latter is very mobile
5. Oviposition	Oviposition, the female remains immobile during a certain period of time with the ovipositor inserted in the interior of the host larva
6. Rejection	The female inserts the ovipositor in the host for a few seconds, but withdraws the ovipositor without actually laying an egg.
7. Failure	When the female inserts the ovipositor in the oviposition unit without having contact with some host, mainly by the escape of the larvae

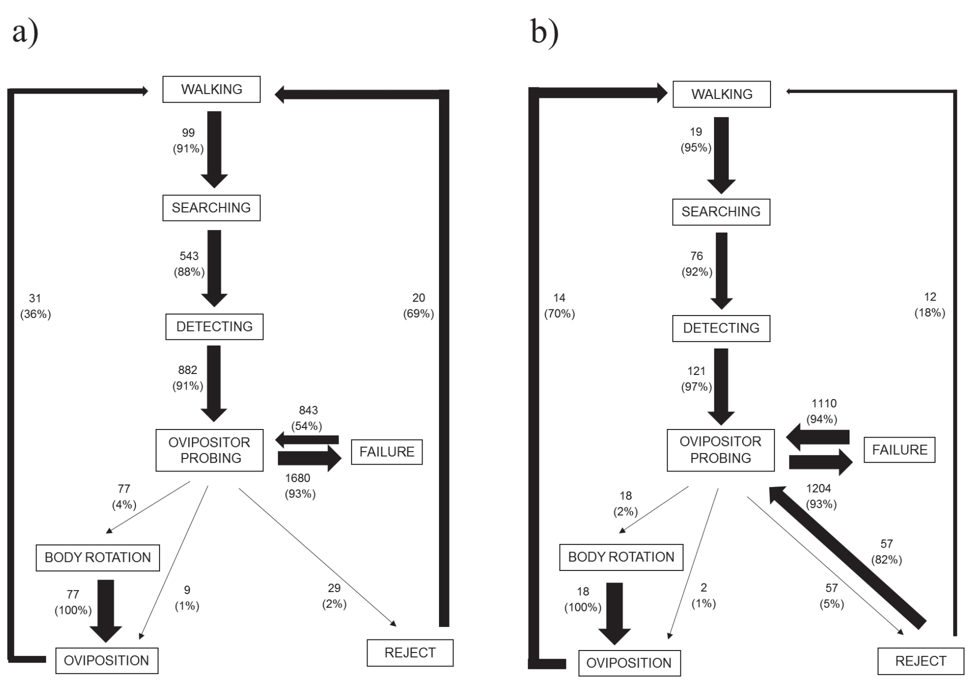

Figure 1. Ethogram of oviposition of females of *Doryctobracon crawfordi* on non-parasitized larvae (**a**) and larvae previously parasitized by conspecifics (**b**) under laboratory conditions. The width of the arrow is proportional to the relative frequency of transition. The numbers associated with the arrows represent the observed frequencies of the successive behaviors of a complex sequence of behavior (proportions are indicated in parentheses).

No marked differences in the flow diagrams were observed between non-parasitized hosts and parasitized hosts for any of the braconids studied here. However, females significantly rejected hosts previously parasitized by conspecifics following insertion of the

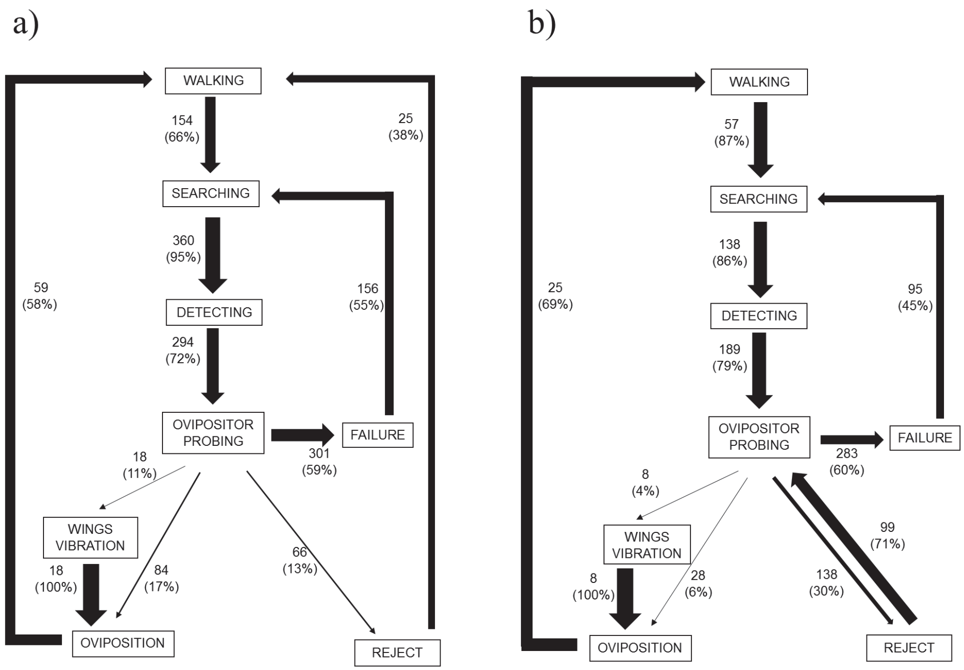

Figure 2. Ethogram of oviposition of females of *Utetes anastrephae* on non-parasitized larvae (**a**) and larvae previously parasitized by conspecifics (**b**) under laboratory conditions. The width of the arrow is proportional to the relative frequency of transition. The numbers associated with the arrows represent the observed frequencies of the successive behaviors of a complex sequence of behavior (proportions are indicated in parentheses).

ovipositor compared to those not parasitized (F = 2.35; df = 2, P < 0.001). Overall, *U. anastrephae* females rejected 79% of parasitized hosts, *D. crawfordi* 74% and *O. hirtus* 62%. Furthermore, a more intensive searching was observed when a failure (because the host moved away) occurred when attacking non-parasitized hosts than when attacking parasitized hosts. The complete process of searching and host acceptance (from the beginning of the observation until ovipositor removal) was completed in 2.2 ± 0.8 min (mean ± SE) in *D. crawfordi*, 1.7 ± 0.75 min in *U. anastrephae* and 1.52 ± 0.75 min in *O. hirtus*.

Latency

The time elapsed between ovipositions differed significantly between *U. anastrephae* and the other two species when the hosts had previously been parasitized ($F = 0.5$, df = 2, $P < 0.05$; N = 30). Regarding the time of latency with non-parasitized larvae, *U. anastrephae* presented the shortest time (3.25 ± 0.3 min) (mean ± SE) (Fig. 4) ($F = 10.6$, df = 2, $P < 0.001$), compared to that of the other two species (*D. crawfordi* = 4.88 ± 0.48 min and *O. hirtus* = 5.65 ± 0.75 min) (mean ± SE).

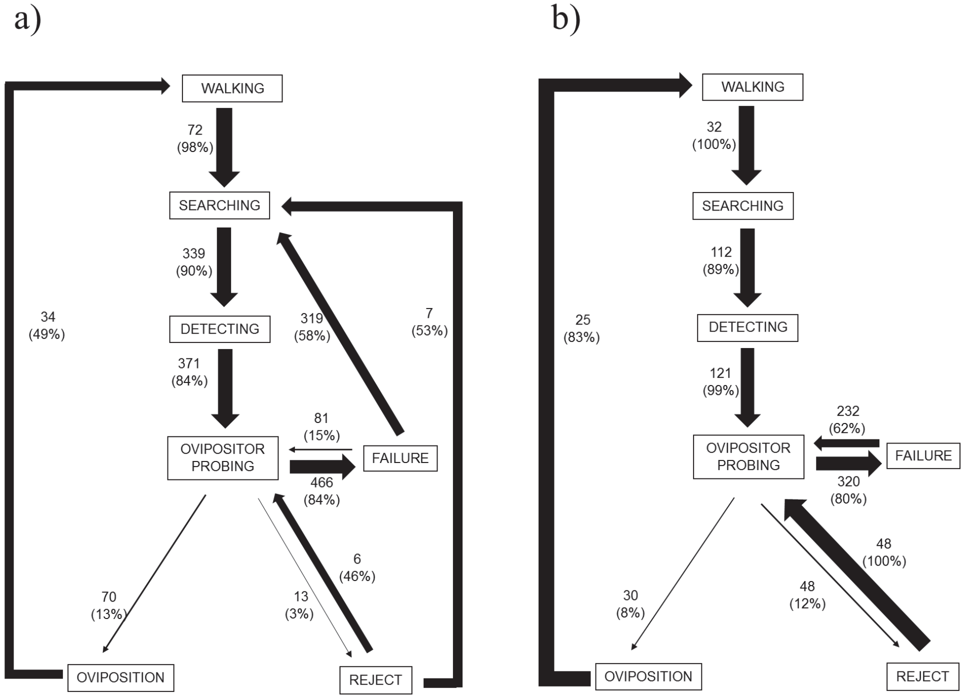

Figure 3. Ethogram of oviposition of females of *Opius hirtus* on non-parasitized larvae (**a**) and larvae previously parasitized by conspecifics (**b**) under laboratory conditions. The width of the arrow is proportional to the relative frequency of transition. The numbers associated with the arrows represent the observed frequencies of the successive behaviors of a complex sequence of behavior (proportions are indicated in parentheses).

Discrimination ability

The first host choice in the three parasitoid species corresponded mostly to the non-parasitized larvae (*D. crawfordi* 22/30; *U. anastrephae* 18/30 and *O. hirtus* 19/30). *Utetes anastrephae* parasitized a significantly (F = 3.39, df = 2, P = 0.03) higher quantity of non-parasitized hosts (3.3 ± 0.25) compared to the other two species (*D. crawfordi* 2.7 ± 0.23 and *O. hirtus* 2.3 ± 0.32). *Doryctobracon crawfordi* performed a greater number of oviposition attempts than *U. anastrephae* and *O. hirtus* in both types of larvae (Table 2).

The time of ovipositor insertion on previously parasitized larvae differed significantly (F = 4.7, df = 2, P = 0.001) among species, with *D. crawfordi* spending more time with the ovipositor inserted, and *O. hirtus* the shortest one (Table 3). The time of ovipositor insertion of *O. hirtus* was significantly shorter in previously parasitized larvae compared to that in non-parasitized larvae (t = 2.67, df = 67, P = 0.0094, Table 3), while in the other two species no significant difference was found between the two host types. No significant differences were found between the two types of larvae in the duration of abdomen vibration and duration of the host paralysis after the attack by each parasitoid species. However, the duration of paralysis of the host differed among

Table 2. Average values (±SE) of number of ovipositions and attempts at oviposition on host larvae parasitized by conspecifics and non-parasitized host larvae.

Species of parasitoid	Number of ovipositions		Number of oviposition attempts (rejections)		N
	Non-parasitized larvae	Parasitized larvae	Non-parasitized larvae	Parasitized larvae	
Doryctobracon crawfordi	2.7±0.23[ab]	0.6±0.15*	56.9±5.1[a]	42.4±7.5[a]	30
Utetes anastrephae	3.3±0.25[a]	1.3±0.23*	12.2±2.1[b]	14.7±2.2[b]	30
Opius hirtus	2.3±0.32[b]	1±0.16*	15.9±2.2[b]	12.26±2.3[b]	30

Different letters indicate statistically significant differences (Anova, α=0.05) between species of parasitoids. *Indicates a statistically significant difference between parasitized and non-parasitized hosts.

Table 3. Average values (±SE) of duration of oviposition, vibration of the abdomen of the females, and immobility of the host after stinging (all in minutes) in non-parasitized and parasitized host larvae of *A. ludens*.

Species	Duration of oviposition		Vibration of the abdomen		Host immobility		N
	Unparasitized host	Parasitized host	Unparasitized host	Parasitized host	Unparasitized host	Parasitized host	
Doryctobracon crawfordi	2.2±0.1[a]	2.2±0.1	0.35±0.01[a]	0.35±0.03	21.3±1.2[a]	20.5±3.4	30
Utetes anastrephae	1.6±0.1[b]	1.9±0.1	0.28±0.01[ab]	0.26±0.01	13.4±0.6[b]	12.1±1	30
Opius hirtus	1.5±0.1[b]	1.2±0.1*	0.26±0.01[b]	0.3±0.01	23.8±1.2[a]	24.5±2	30

Different letters indicate a statistically significant difference per columns for each parameter (ANOVA, α=0.05). *Indicates a statistically significant difference between parasitized and non-parasitized hosts for each species per parameter.

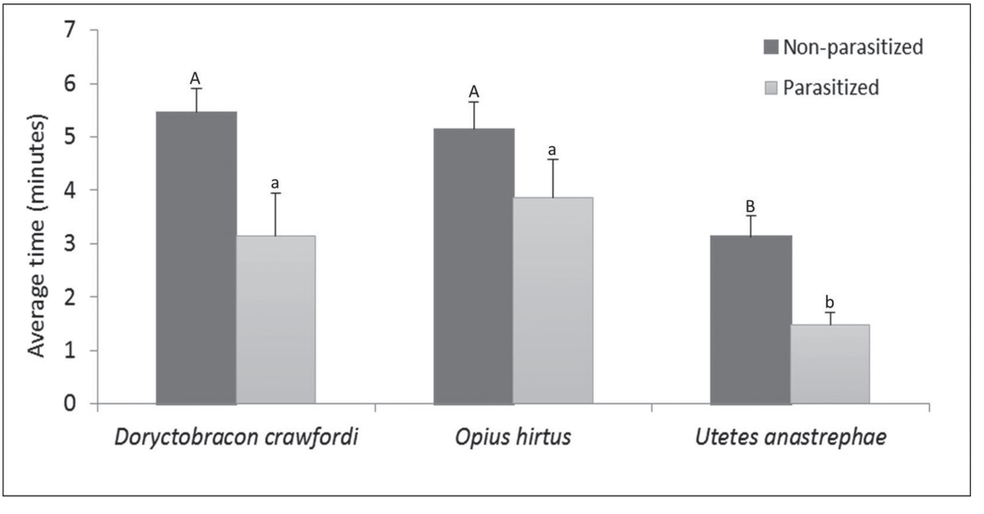

Figure 4. Latency (average ± SE, in minutes) between ovipositions of three native opine parasitoids attacking non-parasitized and previously parasitized *Anastrepha ludens* larvae. Different capital letters indicate statistically significant difference between the bars. Different letters, indicate statistically significant difference between the bars. Different lower case letters, indicate statistically significant difference between species.

the three species (parasitized hosts, $F = 12.8$, df = 2, $P = 0.00001$; non-parasitized hosts, $F = 29.5$, df = 2, $P = 0.000001$). All hosts successfully stung showed temporary paralysis: *D. crawfordi* = 21.3 ± 1.2 min, *O. hirtus* = 23.8 ± 1.2 min and *U. anastrephae* = 13.4 ± 0.6 min) (mean ± SE) (Table 3).

Discussion

Knowledge on host acceptance behavior in insect parasitoids is fundamental to improve our understanding on the plant-herbivore-natural enemy tritrophic relations (Vet and Dicke 1992), as well as the population dynamics and their possible implications in pest biological control programs (Minkenberg et al. 1992).

Several studies have indicated that responses of natural enemies are mediated mainly by chemical signals detected in the environment (Vinson 1998, Vet and Dicke 1992, van Alphen and Visser 1990), by host-generated vibrations in its microhabitat (Meyhöfer et al. 1997, Vet and van Alphen 1985), and by the individual learning experiences of foraging females. Its stated that parasitoids perceive stimuli about host quality once direct contact has been made with the host, influencing the host acceptance process (Brodeur and Boivin 2004, Wajnberg et al. 2008). Here we established the patterns of host acceptance by *D. crawfordi*, *U. anastrephae* and *O. hirtus* in the presence of both non-parasitized and previously parasitized hosts. We further characterized the time spent in different behaviors, and the duration of the paralysis induced through parasitism.

The three studied species presented typical behavior of antennal contact with the surface of the oviposition unit during the process of searching for the host larvae, which is an important step for host detection (Leyva et al. 1991, Gonzalez et al. 2010). All of the species presented a similar foraging pattern, beginning the search for the host by walking and touching the oviposition surface with the antennae. Once a larva was detected, the females adopted an alert position that consisted of remaining immobile for some seconds with the antennae extended to the front, skimming the surface of the parasitization unit. On locating a larva, the females performed small turns on their axis until positioning their first pair of legs towards the front and arranging their ovipositor to form a 90° angle to the contact surface. On initiating the process of oviposition in the parasitization unit, as reported for *D. longicaudata* (Montoya et al. 2003), the females make various attempts to insert the ovipositor until contact was made with a host, which then was accepted or rejected.

According to our results, the three parasitoid species have a high discrimination ability in the form defined by van Alphen and Visser (1990), given that females rejected most of the previously parasitized hosts compared to those with no previous parasitization. However, *U. anastrephae* notoriously presented the highest frequency of rejection of parasitized hosts (79%). This suggests that this species possesses a high performance avoiding superparasitism and saving time and energy when foraging for their hosts (Godfray 1994, Mackauer 1990). This corroborate previous findings by Aluja et al. (2013), who showed that this species avoids ovipositing on previously parasitized hosts under conspecific and heterospecific situations, although it also has been noted that superparasitized hosts yielded relatively more daughters (Alvarenga et al. 2016), as referred for *D. longicaudata* (Montoya et al. 2011). The host acceptance behavior presented by the three species was similar to that reported for *D. longicaudata* by Montoya et al. (2003), who observed that the previously parasitized hosts experienced a lower number of ovipositions than the hosts with no previous parasitization.

Doryctobracon crawfordi presented the longest time spent on oviposition compared to the other two species. Host acceptance may depend on extrinsic factors such as host availability and quality, as well as intrinsic factors such as the quantity of eggs in the females, the age and their nutritional state (Vet et al. 2002, Bernstein and Jervis 2008). In the case of *D. crawfordi,* availability of eggs in the females can be an important limiting factor (Iwasa et al. 1984). Females of this species may tend to be more selective, avoiding oviposition on previously parasitized hosts or those considered to be of poor quality (Rosenheim 1996, Ayala et al. 2014). This could explain the large numbers of oviposition attempts (host probing) observed and the greater time on selection of non-parasitized hosts. The native parasitoids *D. crawfordi*, *U. anastrephae* and *O. hirtus* invest more time in the process of oviposition (2.2 ± 0.8, 1.7 ± 0.1 and 1.52 ± 0.75 min, respectively) than exotic species such as *D. longicaudata* (0.49 ± 0.2 min; Montoya et al. 2003) and *D. tryoni* (0.69 ± 0.065 min; Ramadan et al. 1994) under laboratory conditions. This could be related to the level of host discrimination ability, since *D. longicaudata* has a strong tendency to superparasitize (Montoya et al. 2003) while the native species here studied seem to avoid superparasitism. In *O. hirtus*, the duration of oviposition when parasitizing previously parasitized hosts was significantly smaller (1.2 ± 0.1 min) than with non-parasitized l hosts (1.6 ± 0.1). The time invested in oviposition can vary according to the particular species and host size (Rivero 2000). In our study, females with experience that had contact with previously parasitized hosts, proved to be the most insistent and inserted their ovipositor a second time in order to conduct contact (*D. crawfordi* 16/30, *U. anastrephae* 22/30 and *O. hirtus* 16/30).

Though koinobionts do not arrest host development, some species can induce transient host paralysis (temporary paralysis after being stung by the female wasp; e.g. Desneux et al. 2009, Chau and Maeto 2009). Our data show that the three braconids studied here temporarily paralyzed their hosts, with 100 percent of hosts undergoing transient paralysis. Interestingly, the duration of paralysis was species specific. Larvae parasitized by *U. anastrephae* remained immobile for 13 ± 1 minutes, and thus presented this state for the shortest time, compared to the immobility presented by host larvae parasitized by *D. crawfordi* and *O. hirtus* (20.9 ± 1.1 and 23.8 ± 1 min, respectively). The duration of immobility caused by oviposition of the native parasitoids exceeds the time of immobility experienced by larvae parasitized by *D. longicaudata* (4.8 ± 27 min; Montoya et al. 2003).

The factors associated with host immobility are toxic substances in a mixture such as venom, as well as polydnaviruses (PDVs) that function as regulatory elements and disrupt the host metabolism (Moreau and Guillot 2005, Kaeslin et al. 2010), affecting the immune system (Richards and Parkinson 2000, Cai et al. 2004). Two hypothesis have been advanced to explain the adaptive value of transient host paralysis: 1) facilitation of oviposition by interfering with host defensive behaviors; and 2) self-superparasitism avoidance. Support for the latter hypothesis comes from the work of Desneux et al. (2009) with two species of aphidiine braconids of the genus *Binodoxys* that attack aphids, and from the work of Chau and Maeto (2009) with *Meteorus pulchricornis* also a braconid (Euphorinae) that attacks a wide range of lepidopteran larvae. Transient paralysis caused by *Binodoxys* spp. lasted up to 15 min and paralyzed aphids were accepted at a significantly lower rate than control aphids (Desneux et al. 2009). Likewise, in *M. pulchricornis*, host movements remained at a low level for approximately 1h after oviposition, and additional ovipositions on paralyzed hosts were not observed (Chau and Maeto 2009). We further hypothesize that transient host paralysis may also be a means to avoid host detection by conspecifics and heterospecific competitors, reducing the risk of larval competition not only from superparasitism but also from multiparasitism. In solitary endoparasitoids only one adult emerges per host, all other larvae are eliminated through direct (intrinsic) competition. Intrinsic competition in the guild of opine braconids that attack *Anastrepha* spp. has been demonstrated in *U. anastrephae* and *D. areolatus,* with the first instar larva of *U. anastrephae* being a superior competitor (Aluja et al. 2013). The duration of paralysis of the host in the three species studied here may allow some advantage to the developing embryo, delaying additional attacks. The first eclosed first instar larva might have more chances to win when competing with second laid individuals.

There are few studies regarding the oviposition behavior of opiine parasitoid species native to the Neotropical region, which makes our data of valuable importance. Our study reveals that behavioral differences among the studied parasitoid species lay mainly in the time of parasitization and in the time for which the parasitized hosts remained immobile, which could delay or minimize superparasitism. The three species were significantly capable of discriminating previously parasitized hosts, suggesting that this strategy is commonly present in the guild of fruit fly parasitoids attacking larvae in the Neotropics. Finally, our data also suggest that the studied species have the potential to be considered as suitable biological control agents. However, more studies are necessary to better understand the advantages and limitations that each one presents as natural enemies of fruit fly pests under field conditions.

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RESEARCH ARTICLE

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Neotype designation for *Anaphes brevis* Walker (Hymenoptera, Mymaridae)

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Abstract

A neotype for *Anaphes brevis* Walker (Hymenoptera: Mymaridae) is designated from among specimens reared in a laboratory culture on *Lygus* sp. (Hemiptera: Miridae). Based on specimens examined, the distribution of *A. brevis* extends west-east from UK (Wales) apparently as far as China and north-south from Germany to Morocco. The species also apparently occurs in North America.

Keywords

France, *Anaphes brevis*, neotype, species description

Introduction

Walker (1846) described *Anaphes brevis* as "*A. fuscipenni* affinis, alis limpidis latioribus". This was one of seven species he described or redescribed and placed under *Anaphes* Haliday, and the only one mentioned as having been collected in France, in this case from the Forest of Fontainebleau (about 55 km south-south-east of Paris). Graham (1982) briefly discussed the species but could not locate any type material. Walker's short description included only the fore wing feature, i.e., the clear, wider [than in *fuscipennis*] wings. This distinctive feature fits few species of *Anaphes*, as mentioned by Graham who determined that Walker's specimen(s?) had been collected in late July, 1830 and noted that the species fits rather well the specimens misidentified by Debauche (1948) as *A. fuscipennis* Haliday. Consequently Graham listed *A. fuscipennis sensu* Debauche under *A.* ?*brevis*. Huber and Thuróczy (2018) illustrated specimens they identified as *A. brevis* that had been reared from *Lygus* sp. (Hemiptera: Miridae) in Spain, and placed 8 other nominal species in synonymy under it. One of them was described originally from California, USA, and the remainder from four countries in Europe (Austria, Germany, Italy and Romania). *Anaphes brevis* clearly belongs to subgenus *Patasson* Walker on the basis of the 2-segmented clava. As understood by Huber and Thuróczy (2018) and assuming their synonymy is correct the species is evidently quite widespread in Europe and is almost certainly an accidental introduction into North America. Because specimens of *A. brevis* have definitely been reared from at least one species of *Lygus* Hahn, which contains economically important pests in many crops (Schwartz and Foottit 1998), it is potentially important for biological control. Despite this, relatively few references mentioning the species name *brevis* exist because no one knew how to recognize the species. Because of its potential importance, a neotype is designated below to fix the name *A. brevis* objectively and with the express purpose of clarifying the taxonomic status of the species. If the original material is ever discovered, which is unlikely given Graham's (1982) inability to find it despite his meticulous study of the Haliday (and Walker) collections, Article 75.8 of the International Code of Zoological Nomenclature applies.

Several corrections to Huber and Thuróczy (2018) are given here: P. 4, line 13 add a colon after "the names under 3 valid genera"; P. 4, line 23 should read "The great majority of *Anaphes* species were described from Europe"; P. 8, caption to Figure 2 should read "European type localities of *Anaphes*. See Tables ..."; P. 12, lines 8, 9, and 10, and P. 16, lines 11, 12 and 13, delete parentheses around Soyka and replace *Synanaphes*, *Mymar* and *Ferrierella* with *Anaphes*; P. 25, line 6, should read *crassipennis* Soyka, 1946a: 41 (*Anaphes*); P. 26, line 3 from bottom should read *medius* Soyka, 1946a: 40 (*Anaphes*); P. 27, line 13 should read *ovipositor* Soyka, 1946a: 41 (*Anaphes*); P. 27, lines 37 and 38 should be moved to just after line 19; P. 27, lines 39 and 40 should be moved to just after line 33; P. 68, caption to figure 33 should read "arrow indicates occipital groove".

Methods

Specimens preserved in ethanol were obtained from the European Parasite Laboratory, ARS, USDA, Orgerus-Béhoust, Yvelines, France. The specimens, including the neotype, had been reared from *Lygus* sp. in a laboratory culture. The original host and host plant, based on label data, apparently was *Lygus* sp. on stems of *Matricaria* sp. Several specimens were cleared and slide mounted in Canada balsam for photography. The remainder were card mounted after critical point drying. Slide-mounted specimens were photographed with a ProgRes C14^{plus} digital camera attached to a Nikon Eclipse E800 compound microscope, and the resulting layers were combined electronically using Zerene Stacker and the images enhanced as needed with Adobe Photoshop (no re-touching of the neotype was done). The neotype was measured at 100× magnification using a Leitz stereoscope fitted with an ocular micrometer. Measurements are given in micrometers. The specimens examined are deposited in two institutions:

BMNH Natural History Museum, London, England;
CNC Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada.

Taxonomy

Anaphes brevis Walker, 1846

Figs 1–11

Anaphes brevis Walker, 1846: 52 (original description); Graham 1982: 214 (diagnosis, discussion [as *Anaphes ?brevis*]); Huber and Thuróczy 2018: 28 (catalogue), 46 (key).

Type material. Neotype ♀ (BMNH) here designated to avoid ambiguity about the identity of this species, whose type material is lost (Graham 1982). The neotype (Fig. 1) is card mounted and in good condition but faded to brown, with 4 labels: 1. "FRANCE Yvelines Behoust vi.1987". 2. "D. Coutinot Vial 2. F3 lab. culture". 3. "ex Lygus eggs. CIE A19211". 4. "NEOTYPE ♀ Anaphes brevis Walker".

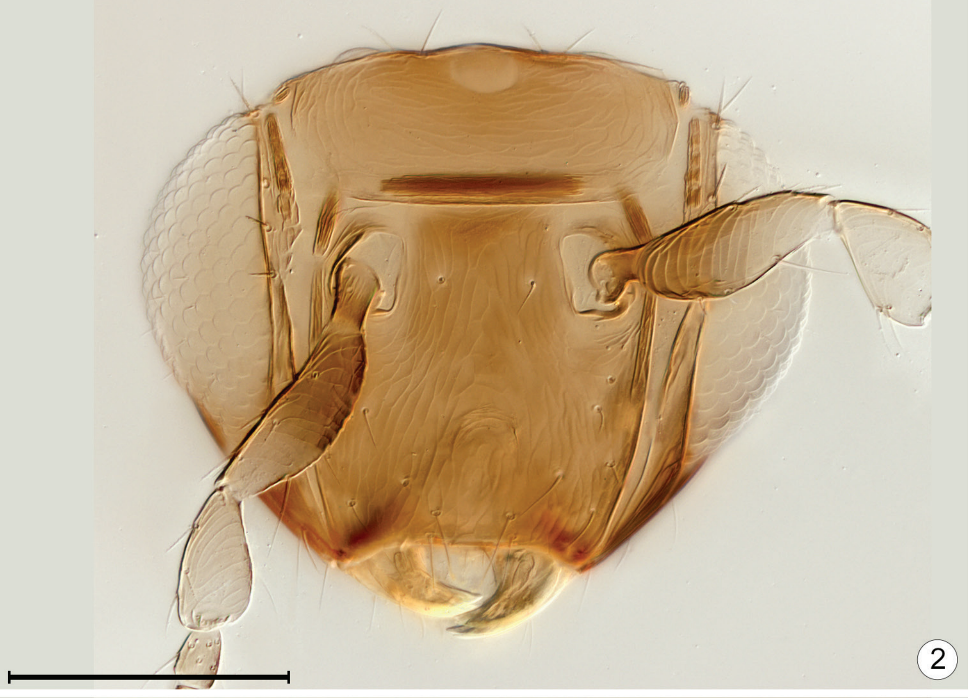
Type locality. France, Yvelines, Béhoust, which is about 100 km from Walker's original collecting locality (Fontainbleau Forest). The neotype is designated from among specimens near the type locality rather than from among specimens reared in Spain (illustrated in Huber and Thuróczy 2018, figs 32–49), relatively far from the type locality. It is deposited in the institution (BMNH) where many of Walker's primary types of Chalcidoidea are located. The slide mounted specimens illustrated (Figs 2–11) came from the same laboratory culture as the neotype.

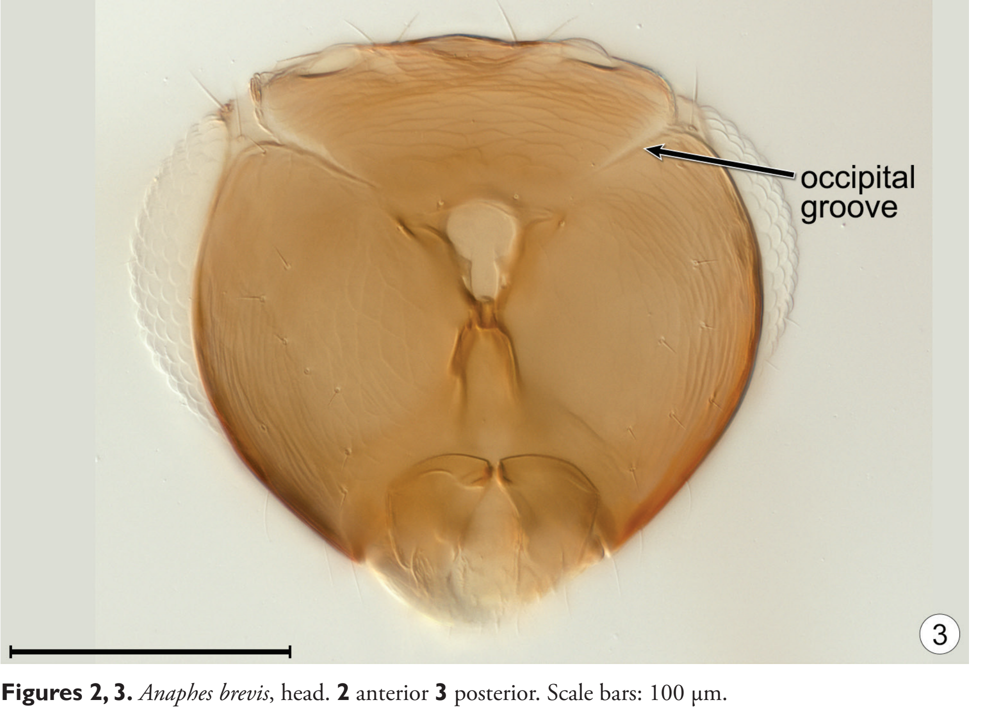
Species diagnosis. In Europe, *A.* (*Patasson*) *brevis* belongs to a small group of species with occipital groove directed medially towards occipital foramen, thus forming an angle with supraorbital trabecula and strongly diverging away from posterior margin of eye (Fig. 3), and with fore wing hyaline (Fig. 7, top arrow), its posterior margin with a short hyaline section subapically separating distal dark margin from proximal slightly darker margin (Fig. 7, left arrow), and cubital line of seta distinctly separated by a gap from posterior margin of fore wing (Fig. 7, bottom arrow). It is distinguished from the most similar species, *A. collinus* Walker, 1846 (type locality: Northern Ireland, Belfast, Cavehill) and *A. inexpectatus* Huber & Prinsloo, 1990 (introduced from Australia into Portugal and established there) by the following combination of features: length/width of fl_2–fl_5 each at least 3.1 in most specimens (Fig. 5) and with 2 mps (Figs 1, 5), though sometimes fl_4 with 1 or 0 mps (Fig. 6), the segments without or with 1 mps usually shorter and slightly narrower than remaining funicle segments (rarely, the same specimen may have different numbers of mps on fl_4); fore wing relatively wide (length/width 3.66–4.61) cubital row of setae separated from posterior margin of fore

Figure 1. *Anaphes brevis*, neotype, habitus. Scale bar: 500 µm.

wing by a noticeable gap (Figs 1, 7); ovipositor at most about 1.5 as long as metatibia, extending anteriorly under mesosoma at most to level of mesocoxa (Fig. 11).

Female (neotype). Body length 645 µm. Antenna brown, with apex of scape and pedicel except narrowly along their dorsal surfaces lighter brown; body and legs dark brown (presumably black if neotype were fresh) except trochantellus and apex of femora, base and apex of tibia, and tarsomeres 1–3 white. Antenna with length measurements





Figures 2, 3. *Anaphes brevis*, head. **2** anterior **3** posterior. Scale bars: 100 µm.

as follows: scape (not measurable, its base hidden by collapsed face), pedicel 50, fl_1 20, fl_2 50, fl_3 70, fl_4 60, fl_5 60, fl_6 50, clava 110. Fore wing length/width 3.95 (790/200); ovipositor/metatibia length 1.49 (395/265), the ovipositor sac extending to base of mesocoxa. Metatarsomere 1 distinctly shorter than metatarsomere 2.

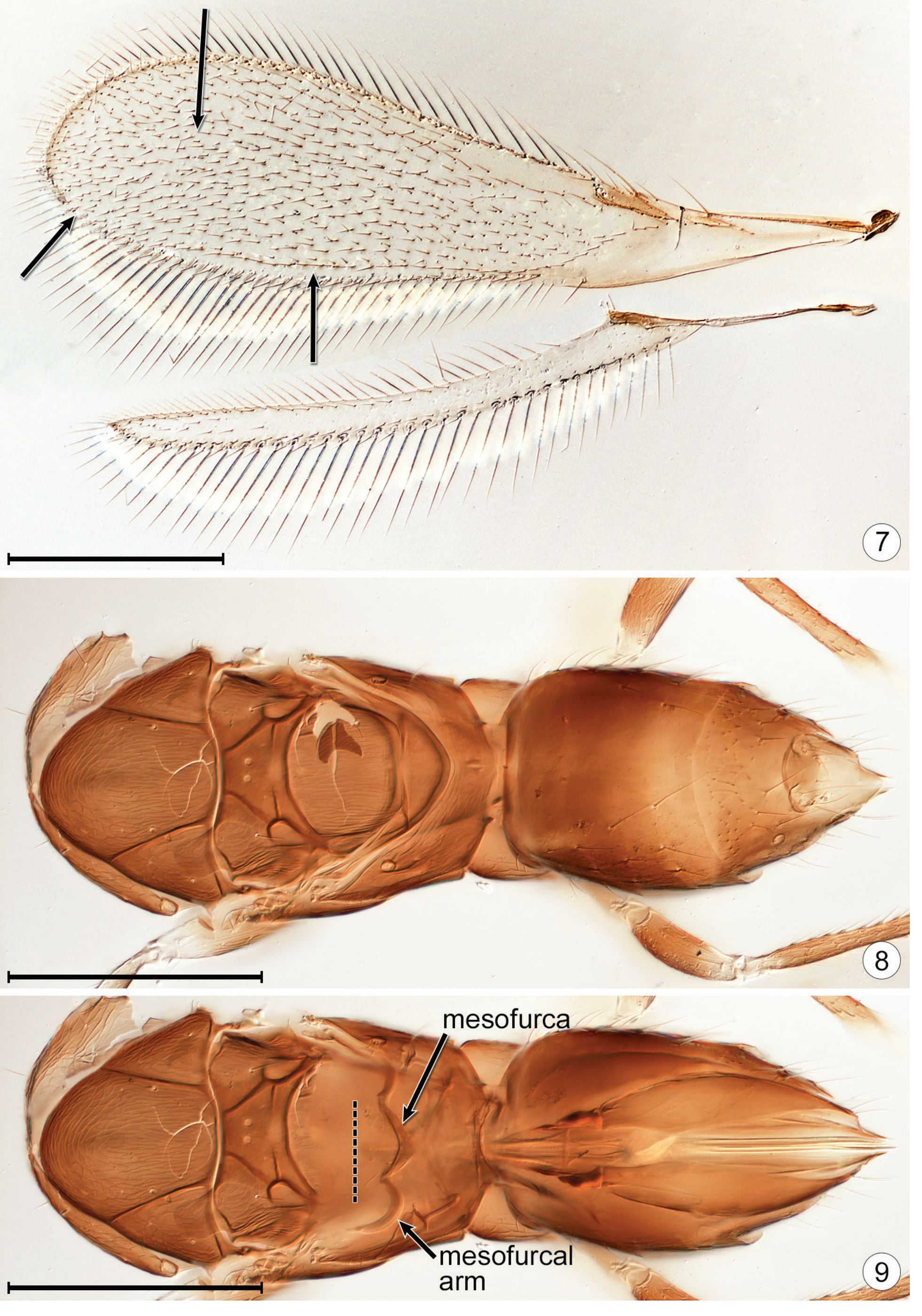
Additional material examined. CHINA. **Hebei**. Beijing, Mentougou, 1140-1250m, 19.v.2002, Zhu C.-d. (1 ♀ on slide, CNC). **Shaanxi**. Zhouzhi, 25.vi.1999, Zhu C.-d. (1 ♀, 1 ♂ on points, 1 ♀ on slide, CNC); Foping, 1750–2150m, 28.vi.1999, Zhu C.-d. (1 ♀ on slide, CNC). **Tibet**. Riwoqê, 3920 m, 17.viii.2001, Zhu C.-d. (1 ♂ on slide, CNC). FRANCE. **Yvelines**. Béhoust, 30.vii.1986, ex *Lygus* sp. in stems of *Matricaria* and in laboratory culture on *Lygus*, F1 and F3 generations, vi.1987, D. Coutinot, CIE A19211 (5 ♀, 3 ♂ on cards; 9 ♀, 4 ♂ on slides, CNC). MOROCCO. **Marrakech**. Ouirgane, 1000 m, 4–10.ix, 10-22.ix, 29.x–4.xi.1996, C. Kassebeer (2 ♀, 1 ♂, CNC). SPAIN. **Gerona**. Navata, emerged 21.ix.2000 ex. *Lygus* eggs on *Chenopodium* in cages, 14–21.ix.2000, D. Coutinot & J. Lopez (17 ♀, 6 ♂ on cards; 3 ♀, 2 ♂ on slides, CNC). UNITED KINGDOM. **England**. Berkshire, Ascot, Silwood Park, 11 & 12.vi.1994, J.S. Noyes (4 ♀ on cards, CNC). **Wales**. Wrexham, 10 km SW Llangollen, Llamon Dyffryn Ceiriog, 31.vii.1999, J.S Noyes (1♀, CNC).

Discussion. *Anaphes* (*Patasson*) *collinus* Walker, described on the same page but before *A. brevis*, presents an interesting problem. It is very similar to *A. brevis* in wing colour and antennal features, but fl_4 almost always has no mps (Huber & Thuróczy 2018, figs 90b, c). Otherwise, *A. collinus* is smaller, with a longer, trombone-shaped ovipositor extending as far as base of procoxa.

In Europe, specimens of *A. collinus* were reared from stems of *Cardraria draba* containing eggs of *Ceutorhynchus cardraria* Korotyaev (Coleoptera: Curculionidae) from Romania, Valea Lupului, with various collecting/emergence dates in iv & v.2010, A. Diaconu (16 ♀ & 15 ♂ on cards, 2 ♀ on slides, CNC) and a similar, possibly undescribed species with generally longer funicle segments has been reared from *Rhinocyllus conicus* (Frölich) (Curculionidae) on *Carduus nutans* and *Silybum marianum* from France, Bouches-du-Rhône, St. Martin de Crau, 10.v.1988, J.-P. Aeschlimann (2 ♀, CNC) and Hérault, La Vacquerie-et-Saint-Martin-de-Castries, 19.vii.1985, J.-P. Aeschlimann (1 ♀, CNC). Whether these specimens actually represent *A. brevis* (or are indeed *A. collinus*, if priority of position on page is accepted) or yet another species, with the variation due to rearing from a different host order or different species is unknown. Since both named species parasitize hosts that are economically important or potentially so it might be worth determining their species status and host range.

In North America, *A. conotracheli* (Girault, 1905) is also extremely similar to *A. brevis*. Huber (2006) compared and contrasted *A. conotracheli* with *A. pallipes* (Ashmead, 1887) that Huber and Thuróczy (2018) placed in synonymy under *A. collinus*. The neotype fits very well Walker's (1846) short description of *brevis* quoted above but depending on the specimen it also more or less fits his equally short description of *collinus*: "Fem. Antennarum articulis a 4° inde alternis minoribus" and could also fit specimens of *A. conotracheli*. Because the relative size of fl_4 may vary, even between the antennae of the same specimen, and all three species have very similar fore wings, the

Figures 4–6. *Anaphes brevis*. **4** head + base of antennae **5** antenna, outer surface **6** antenna, inner surface. Note difference in fl_4 and cross striations on inner surface of scape (striations very faint and more longitudinal on outer surface). Scale bars: 200 µm.



Figures 7–9. *Anaphes brevis*. **7** wings (see text for discussion) **8** body, dorsal **9** with frenum-gaster internal (more ventral) to show mesofurca and ovipositor through gaster; dashed line indicates anterior extension of ovipositor. Scale bars: 200 μm.

Figures 10, 11. *Anaphes brevis*, body, lateral. **10** outer surface **11** median view of gaster showing ovipositor. Scale bars: 200 µm.

neotype designation for *A. brevis* is even more important. Body length and, possibly, relative length of ovipositor (compared to metatibia length) may also vary depending on host though this needs to be verified. Breeding experiments among individuals and their progeny reared on different hosts (*Lygus* spp. versus various Curculionidae) and rearing F1 progeny on the alternate host to their parents, as was done with *Anaphes iole* Girault, 1911 (Huber and Rajakulendran 1988) or several species of *Anaphes* reared from carrot weevil, *Listronotus oregonensis* (LeConte) (Curculionidae) (Huber et al. 1997), might elucidate whether only one or several biological species are involved.

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RESEARCH ARTICLE

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First record of the genera *Diaparsis* Förster and *Phradis* Förster (Hymenoptera, Ichneumonidae, Tersilochinae) from Mexico

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Abstract

In this paper, one species of *Diaparsis* Förster (*D. splendens* Horstmann) is recorded and two species of *Phradis* Förster (*P. bufalosus* **sp. n.** and *P. nanacamilpus* **sp. n.**) are described from Mexico. Both genera are extremely rare in the Mexican fauna, being represented by single specimens from a large amount of ichneumonids examined in many Mexican and USA collections. A partial identification key to North American species of *Phradis* is given. Colour photographs and morphological remarks on *D. splendens* are provided.

Resumen

Se registran para México una especie de *Diaparsis* Förster (*D. splendens* Horstmann) y se describen dos especies nuevas de *Phradis* Förster (*P. bufalosus* **sp. n.** and *P. nanacamilpus* **sp. n.**) de México. Ambos géneros son extremadamente raros en la fauna mexicana, siendo representados por especímenes únicos entre una gran cantidad de ichneumónidos examinados en varias colecciones mexicanas y de Estados Unidos. Se elaboró una clave parcial para la identificación de las especies norteamericanas de *Phradis*. Se incluyen fotografías a color y comentarios sobre la morfología de *D. splendens*.

Keywords

Baja California, Tlaxcala, Nearctic region, North America, fauna, new species, taxonomy, parasitoids, key

Introduction

Tersilochinae is a moderately large subfamily of parasitoid wasps (Hymenoptera: Ichneumonidae) distributed worldwide and represented by about 500 described species in 23 genera (Yu et al. 2016, Khalaim pers. obs.). The majority of host records of tersilochine species are from beetle larvae (Yu et al. 2016) but some taxa are known as parasitoids of non-coleopteran hosts, e.g. mining larvae of Eriocraniidae (Lepidoptera) (Jordan 1998), larvae of xyelid sawflies (Hymenoptera: Xyelidae) in staminate pine cones (Khalaim and Blank 2011, Horstmann 2013a) and gall-forming *Pontania* spp. on willows and leaf-folder sawfly of the genus *Phyllocolpa* Benson (Hymenoptera: Tenthredinidae) (Kopelke 1994, 2011).

The Mexican fauna of Tersilochinae is poorly known, in spite of several recent studies comprising records of the genera *Allophrys* Förster (Horstmann 2010), *Aneuclis* Förster (reported as *Sathropterus* Förster in Khalaim et al. 2015, synonymized by Khalaim 2018), *Barycnemis* Förster (Khalaim 2002a), *Gelanes* Horstmann (Khalaim and Ruíz-Cancino 2017), *Labilochus* Khalaim (Khalaim et al. 2017) and *Stethantyx* Townes (Khalaim and Ruíz-Cancino 2013) from Mexico. All these genera are represented in the Mexican fauna by single or several species, except for the large Neotropical genus *Stethantyx* which comprises at least 11 species in Mexico (Khalaim and Ruíz-Cancino 2013, Khalaim unpubl.).

The aim of this work is to describe two Mexican species of *Phradis* and report one species of *Diaparsis*, representing first record of these genera from Mexico. A portion of the identification key to North American species of *Phradis* is also provided.

Material and methods

Among a large number of ichneumonids examined in many Mexican (Universidad Autónoma de Tamaulipas, Cd. Victoria; Instituto de Biología, Universidad Nacional Autónoma de México, D.F., further **UNAM**; Universidad Autónoma de Nuevo León, Monterrey; Universidad Autónoma de Estado Morelos, Cuernavaca; Instituto Politécnico Nacional, Oaxaca; Universidad Veracruzana, Xalapa, Veracruz) and some United States collections (Essig Museum of Entomology, University of California, Berkeley, further **EMEC**; Texas A&M University, College Station, Texas; the Townes collection, recently moved to the Utah State University, Logan, Utah; Florida State Collection, Gainesville, Florida), only one specimen of *Diaparsis* and two specimens of *Phradis* were found.

Types of 17 Nearctic species of *Phradis* described by Horstmann (2013b) were examined by the senior author during his visit to the Zoologische Staatssammlung (Munich, Germany) in May 2016, and compared with the two Mexican species described in this paper.

Morphological terminology follows that of Townes (1969) with changes according to Khalaim (2011). Photographs were taken in the Zoological Institute RAS (St. Petersburg, Russia), with a Canon EOS 70D digital camera attached to an Olympus SZX10 stereomicroscope. Images were assembled with Helicon Focus 6 Pro software.

Taxonomy

Genus *Diaparsis* Förster, 1869

Type species. *Ophion nutritor* Fabricius, 1804.

Large genus of almost worldwide distribution (unknown only from the Neotropical region). Comprises 12 species in the Nearctic region, including 11 native species and one introduced from Europe into the United States and established there (Horstmann 2012).

The genus lacks examined materials from Mexico except for one rare species described from California by Horstmann (2012) and recorded here from a low-mountainous region in Northwest Mexico.

Diaparsis (*Diaparsis*) *splendens* Horstmann, 2012

Figs 1–6

Remarks. The female from Mexico corresponds well with the original description and illustrations of this species (Horstmann 2012: 137). A brief description of the specimen from Mexico is provided below. Colour photographs of this species are provided for the first time.

Female (Mexico): body length 4.0 mm, fore wing length 3.25 mm; flagellum (Fig. 1) slightly clavate, with 17 flagellomeres, proportions of flagellomeres as in original description; head strongly rounded posterior to eyes (Fig. 1); temple 0.8 times as long as eye width; clypeus (Fig. 2) 3.4 times as broad as long, separated from face by very shallow impression mediodorsally and by quite distinct furrow laterally; propodeum mediodorsally (Fig. 3) without distinct basal keel, with weak longitudinal wrinkles, basal part of propodeum half as long as apical area; first abscissa of radius (Rs+2r) 1.15 as long as width of pterostigma; first tergite dorsally polished, 2.2 times as long as posteriorly broad; glymma large and deep, situated more or less in centre of first tergite (Fig. 4); second tergite slightly transverse, 0.95 as long as anteriorly broad (Fig. 5); ovipositor slender, weakly and evenly bent upwards over its total length, with conspicuous nodus apically (Fig. 6, arrow), its sheath 2.5 times as long as first tergite.

This species resembles the Holarctic genus *Gelanes* Horstmann as it has a smooth or shallowly sculptured head and mesosoma, dorsally polished first metasomal tergite with a broad postpetiole, deep glymma in the centre of the first tergite, transverse thyridial depressions, lacks a foveate groove on the mesopleuron, and was collected in the spring. Nevertheles, it possesses an isolated glymma, i.e. not joining by a furrow to the ventral part (Fig. 4), while the remaining characters also occur in the genus *Diaparsis*.

Material examined. 1 female (EMEC), Mexico, Baja California Norte [Baja California], Jaraguay Summit [29.33°N, 114.5°W, NW of Agua León], ex flowers Yucca peninsularis, 27 March 1973, coll. Doyen, “U.C. Berkeley EMEC 203, 505”.

Figures 1–6. *Diaparsis splendens*, female (Mexico). **1** head with antenna and mesoscutum, dorsal view **2** head, front view **3** mesosoma, dorsal view **4** propodeum and metasoma, lateral view **5** postpetiole and second tergite, dorsal view **6** apex of ovipositor, lateral view.

Distribution. Southwestern USA (California), Northwestern Mexico (Baja California). First record of genus and species from Mexico.

Biology. Reared or collected from flowers of *Hesperoyucca whipplei* (Torr.) Baker ex Trel. [=*Yucca peninsularis*] (Agavaceae) in Mexico.

Genus *Phradis* Förster, 1869

Type species. *Thersilochus* (*Phradis*) *brevis* Brischke, 1880.

A moderately large genus with a predominantly Holarctic distribution and a few species known from the Afrotropical (Khalaim 2007) and Neotropical regions (Khalaim and Bordera 2012) and Australia (Khalaim 2017). About 40 species are known to occur in the Palaearctic region (Yu et al. 2016) and 18 species in the Nearctic region (Horstmann 2013b). Two undescribed species of *Phradis* were found in material from the State of Tlaxcala in Central Mexico. This is the first record of the genus from Mexico.

Phradis is found to be extremely rare in Mexico, being represented by two species, both known from a single female, collected from the same locality at 2830–2900 m in pine-oak forest. The two Mexican species easily differ from the 18 species occurring in the USA and Canada by the very long second metasomal tergite (see the key below).

Portion of the key to North American species of *Phradis*

1 Second metasomal tergite, in dorsal view, very long, 2.8–3.6 times as long as anteriorly broad. Central Mexico **2**

– Second metasomal tergite, in dorsal view, transverse to moderately long, 0.8–2.0 times as long as anteriorly broad. USA and Canada ....**18 species** (see identification key in Horstmann 2013b)

2 Second antennal flagellomere 2.5 times as long as broad (Fig. 8). Apical area of propodeum flat (Fig. 11). Second metasomal tergite 2.8 times as long as anteriorly broad (Fig. 12). Ovipositor with apex needle-shaped, without dorsal notch (Fig. 13); sheath 1.1 times as long as first tergite ......***P. bufalosus* sp. n.**

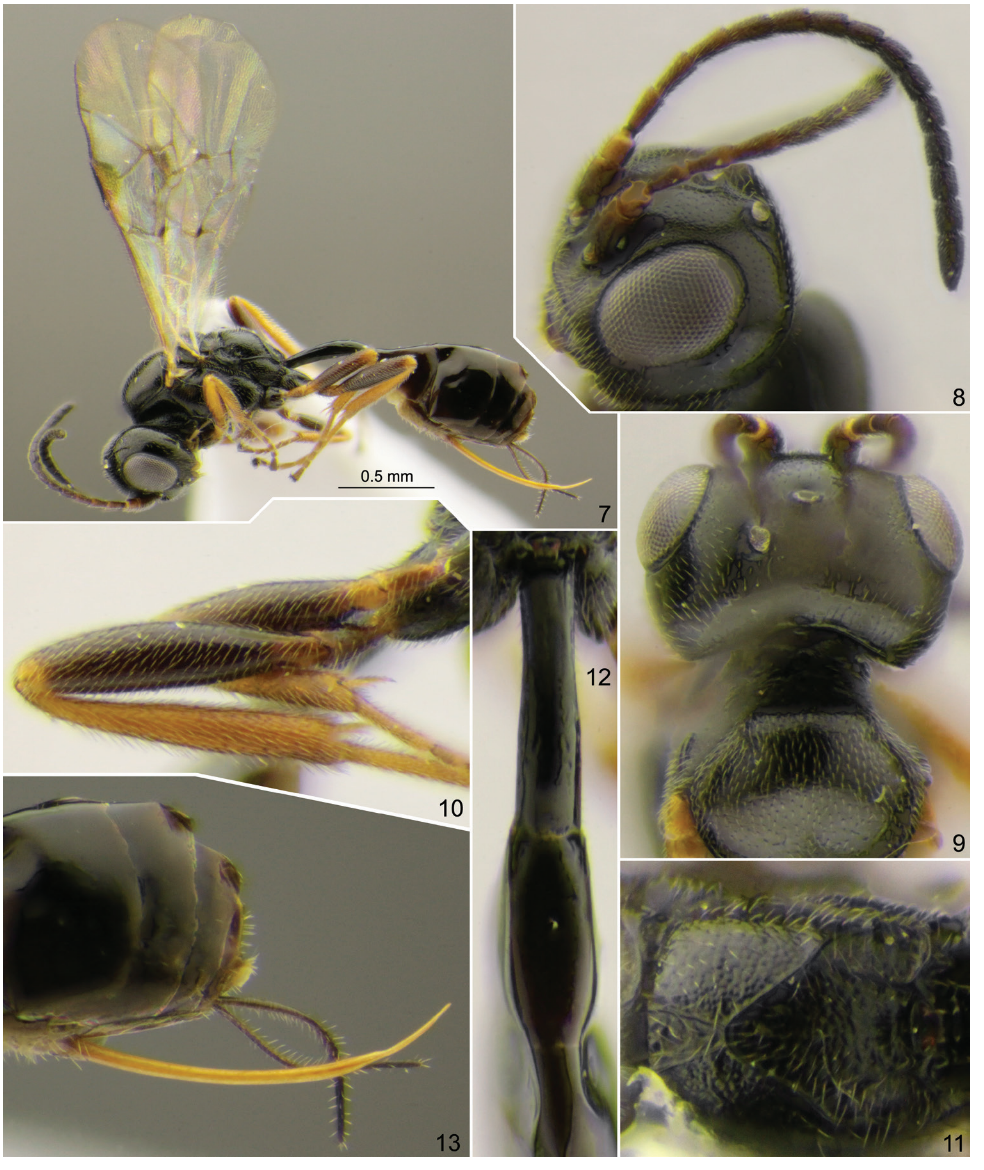
– Second antennal flagellomere 3.5 times as long as broad (Fig. 15). Apical area of propodeum impressed along midline (Fig. 20). Second metasomal tergite 3.6 times as long as anteriorly broad. Ovipositor evenly tapered apically, with weak but distinct dorsal subapical notch (Fig. 21); sheath 1.4 times as long as first tergite ....***P. nanacamilpus* sp. n.**

Phradis bufalosus Khalaim & Ruíz-Cancino, sp. n.

http://zoobank.org/2FD83281-5DDA-4BB5-9968-7AD188630EA7

Figs 7–13

Comparison. In the key to the Nearctic species of *Phradis* (Horstmann 2013b), *P. bufalosus* runs to *P. flavicoxa* Horstmann in couplet 9 but may be distinguished from this species by the head being weakly constricted behind the eyes (Fig. 9), dark legs (Fig. 10), smooth first metasomal tergite, long second tergite (Fig. 12) and a needle-shaped ovipositor apex (Fig. 13).



Figures 7–13. *Phradis bufalosus* sp. n., holotype female. **7** habitus, lateral view **8** head with antenna, lateral view **9** head and mesoscutum, lateral view **10** hind legs, lateral view **11** propodeum, dorsal view **12** base of metasoma, dorsal view **13** apex of metasoma with ovipositor, lateral view.

Morphologically and in colouration, *P. bufalosus* is very similar to *P. coriaceus* Horstmann, from which it differs by the temple being finely punctate on a smooth background (granulate, impunctate and dull in *P. coriaceus*) and longer second metasomal tergite (2.8 times as long as anteriorly broad in *P. bufalosus* and 1.8 times in *P. coriaceus* [measured from Fig. 21 in Horstmann 2013b: 73]).

Description. *Female*. Body length 2.5 mm. Fore wing length 1.85 mm.

Head, in dorsal view, 1.65 times as broad as long, weakly constricted and rounded posterior to eyes (Fig. 9); temple 0.8 times as long as eye width (Fig. 9). Eyes with short and rather dense setae. Clypeus lenticular in anterior view, 3.4 times as broad as long, weakly convex in lateral view, smooth, separated from face by sharp furrow, with fine scattered punctures in upper 0.3. Mandible weakly tapered at base, with upper and lower margins subparallel in apical 0.8; upper tooth distinctly longer than the lower. Malar space almost as long as basal mandibular width. Antennal flagellum (Fig. 8) with 14 flagellomeres, basally slender; second and third flagellomere 2.3–2.5 times and subapical flagellomeres 1.2–1.3 times as long as broad. Face with elongate median prominence in upper part. Face very finely punctate (punctures vanishing on medial prominence and laterally next to eyes and malar spaces), smooth between punctures and shining centrally, and very finely granulate and dull laterally. Frons very finely punctate on very finely granulate background (punctures partly hardly discernible because of granulation), weakly shining to dull. Vertex and temple with very fine but distinct punctures on smooth and shining background. Occipital carina complete, somewhat dipped mediodorsally.

Mesosoma predominantly finely granulate, impunctate, weakly shining to dull, except for mesoscutum which is very finely punctate on more or less smooth and shining background. Notaulus discernible as weak and short wrinkle on anterolateral side of mesoscutum. Scutellum with lateral longitudinal carinae at basal 0.2. Foveate groove absent, mesopleuron centrally almost smooth. Propodeal spiracle very small, separated from pleural carina by about 3.0 times diameter of spiracle. Propodeum with basal area strongly widened anteriorly, about 3.0 times broader anteriorly than posteriorly and almost half as long as apical area (Fig. 11); basal longitudinal carinae weak but distinct. Apical area flat, rounded anteriorly (Fig. 11); apical longitudinal carinae distinct posteriorly and weak anteriorly, not reaching transverse carina anteriorly.

Fore wing with second recurrent vein (2m-cu) interstitial. Intercubitus (2rs-m) long. First abscissa of radius (Rs+2r) slightly arcuate, longer than width of pterostigma. First and second abscissae of radius (Rs+2r and Rs) meeting at slightly acute angle (less than 90°). Metacarpus (R1) short, not reaching apex of fore wing (Fig. 7). Second abscissa of postnervulus represented by a short protrusion, thus brachial cell is widely open posteriorly. Hind wing with nervellus (cu1&cu-a) slightly reclivous.

Legs slender. Hind femur 4.3 times as long as broad and 0.9 times as long as tibia (Fig. 10). Tarsal claws not pectinate.

First tergite slender, 4.2 times as long as posteriorly broad (Fig. 8), smooth, with shallow striae laterally; tergite round in cross-section centrally, with lateral sides subparallel and petiole not separated from postpetiole in dorsal view (Fig. 12). Glymma absent. Second tergite about 2.8 times as long as anteriorly broad (Fig. 8). Thyridial depression almost 3.0 times as long as broad, with narrow groove extending from posterior end of thyridial depression along lateral margin of second tergite and reaching nearly its midlength. Ovipositor slender, weakly and nearly evenly bent upwards over its total length, with abruptly narrowed needle-shaped apex (Fig. 13); sheath 1.1 times as long as first tergite.

Head, mesosoma and first metasomal segment black. Palpi, mandible (teeth dark reddish brown), lower 0.7 of clypeus and tegula yellow to yellow-brown. Scape of antenna dark brown with narrow yellowish ring on distal end; pedicel yellow-brown; flagellum gradually darkening from brownish basally to black apically. Pterostigma brown. Fore leg brownish yellow with fore coxa dark brown and femur basally on dorsal side darkened with brown. Mid and hind legs with coxae brownish black, first and second trochanters brownish yellow (first trochanter darkened with brown), femora dark brown with extreme apex brownish yellow (Fig. 10), and tarsi brownish yellow. Metasoma posterior to first tergite and ovipositor sheath brownish black.

Male. Unknown.

Etymology. The species is named after the type locality, [Los] Búfalos.

Material examined. Holotype female (UNAM), Mexico, Tlaxcala, Nanacamilpa, Ejido Los Búfalos, N19°28', W98°35', bosque Pino-Encino, 2830–2900 m, Malaise trap, 4 April–3 May 2016, coll. Y. Marquez & A. Contreras.

Distribution. Central Mexico (Tlaxcala).

Phradis nanacamilpus **Khalaim & Ruíz-Cancino, sp. n.**

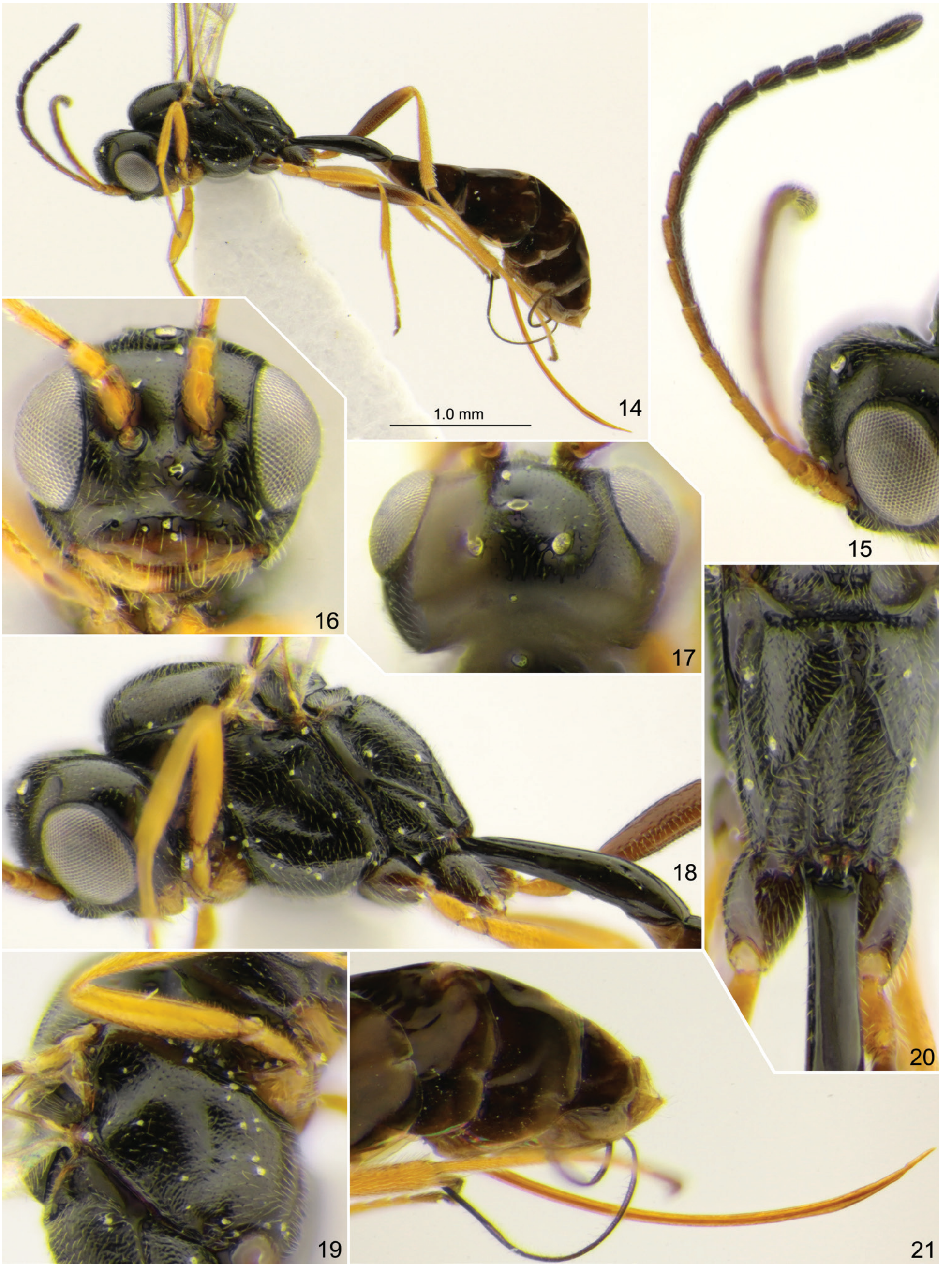
http://zoobank.org/6047BF50-51DB-4229-90D2-62FB2162F068

Figs 14–21

Comparison. In the key to the Nearctic species of *Phradis* (Horstmann 2013b), *P. nanacamilpus* runs to couplet 10 but does not correspond with either side of the couplet as it has the mesopleuron very finely and sparsely punctate on a smooth background centrally, shallowly granulate peripherally (Fig. 19), dorsolateral area of propodeum without irregular wrinkles (Figs 18, 20), and ovipositor sheath 1.4 times as long as first tergite.

Description. *Female*. Body length 3.8 mm. Fore wing length almost 2.5 mm.

Head, in dorsal view, almost 1.7 times as broad as long, weakly constricted and weakly rounded posterior to eyes (Fig. 17); temple 0.7 times as long as eye width (Fig. 17). Eyes with short and rather dense setae. Clypeus (Fig. 16) lenticular in anterior view, 3.5 times as broad as long, almost flat in lateral view, smooth, separated from face by sharp furrow, with a few fine punctures next to upper and lower margins. Mandible weakly tapered at base, with upper and lower margins subparallel in apical 0.8; upper tooth distinctly longer than the lower. Malar space slightly shorter than basal mandibular width. Antennal flagellum (Fig. 15) with 14 flagellomeres, basally very slender; second and third flagellomere 3.0–3.5 times and subapical flagellomeres 1.4–1.6 times as long as broad. Face with weak median prominence in upper part. Face with very fine inconspicuous punctures (medial prominence impunctate), smooth between punctures and shining centrally, and very finely granulate and weakly shining laterally. Frons smooth and very fine punctate, laterally (next to eye orbits) very finely



Figures 14–21. *Phradis nanacamilpus* sp. n., holotype female. **14** habitus (without wings), lateral view **15** antenna, lateral view **16** head, front view **17** head, dorsal view **18** head, mesosoma and base of metasoma, lateral view **19** mesopleuron, postero-lateral view **20** propodeum, dorsal view **21** apex of metasoma with ovipositor, lateral view.

granulate and dull. Vertex and temple with very fine punctures on smooth and shining background. Occipital carina complete, flattened mediodorsally.

Mesosoma predominantly finely granulate, impunctate, dull; mesoscutum evenly finely punctate smooth and shining background; mesopleuron centrally more or less smooth and shining, with fine and sparse punctures, peripherally shallowly granulate and weakly shining to dull. Notaulus as a rather strong wrinkle on anterolateral side of mesoscutum. Scutellum with lateral longitudinal carinae at extreme base. Foveate groove weak and narrow, situated in centre of mesopleuron, slightly oblique, with fine and short transverse wrinkles (Fig. 19). Propodeal spiracle small, separated from pleural carina by about 4.0 times diameter of spiracle. Propodeum with basal area weakly widened anteriorly, twice broader anteriorly than posteriorly and almost 0.4 times as long as apical area (Fig. 20); basal longitudinal carinae weak but distinct. Apical area impressed along midline, rounded anteriorly (Fig. 20); apical longitudinal carinae distinct, reaching transverse carina anteriorly.

Fore and hind wing venation very similar to that in *P. bufalosus*. Fore wing with second recurrent vein (2m-cu) interstitial. Intercubitus (2rs-m) long. First abscissa of radius (Rs+2r) slightly arcuate, longer than width of pterostigma. First and second abscissae of radius (Rs+2r and Rs) meeting at slightly acute angle (less than 90°). Metacarpus (R1) short, not reaching apex of fore wing. Second abscissa of postnervulus incomplete, partly enclosing brachial cell posteriorly. Hind wing with nervellus (cu1&cu-a) weakly reclivous.

Legs slender. Hind femur 4.8 times as long as broad and 0.85 times as long as tibia. Tarsal claws not pectinate.

First tergite slender, almost 5.0 times as long as posteriorly broad, smooth, with very weak striae ventrolaterally; tergite round in cross-section centrally, with lateral sides subparallel and petiole not separated from postpetiole in dorsal view. Glymma absent. Second tergite 3.6 times as long as anteriorly broad. Thyridial depression very long and narrow, pointed posteriorly, extending in basal 0.4 of tergite. Ovipositor slender, weakly and nearly evenly bent upwards over its total length, evenly tapered apically, with weak but distinct dorsal subapical notch (Fig. 21); sheath 1.4 times as long as first tergite.

Head, mesosoma and first metasomal segment black. Palpi, mandible (teeth dark reddish brown) and tegula brownish yellow. Lower 0.7 of clypeus yellow-brown. Antenna brownish yellow basally to brownish black apically (Fig. 15). Pterostigma brown. Leg brownish yellow; mid and hind coxae darkened with brown; hind femur brown except base and apex. Metasoma posterior to first tergite dark brown.

Male. Unknown.

Etymology. The species is named after the type locality, Nanacamilpa.

Material examined. Holotype female (UNAM), Mexico, Tlaxcala, Nanacamilpa, Ejido Los Búfalos, N19°28', W98°35', bosque Pino-Encino, 2830–2900 m, Malaise trap, 3–30 June 2016, coll. Y. Marquez & A. Contreras.

Distribution. Central Mexico (Tlaxcala).

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Taxonomic revision of the genus *Oodera* Westwood, 1874 (Hymenoptera, Chalcidoidea, Pteromalidae, Cleonyminae), with description of ten new species

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Abstract

The world species of *Oodera* Westwood, 1874 (Chalcidoidea: Pteromalidae: Cleonyminae: Ooderini) are revised. We examined 115 specimens of this rarely collected genus and based on morphological characters assign 110 specimens to 20 recognised species, of which the following ten are described as new: *Oodera circularicollis* **sp. n.** (Morocco), *O. felix* **sp. n.** (Central African Republic), *O. fidelis* **sp. n.** (Vietnam), *O. florea* **sp. n.** (Thailand), *O. heikewernerae* **sp. n.** (Botswana and South Africa), *O. leibnizi* **sp. n.** (Papua New Guinea, Malaysia and Phillippines), *O. mkomaziensis* **sp. n.** (Tanzania), *O. namibiensis* **sp. n.** (Namibia), *O. niehuisorum* **sp. n.** (Egypt and Israel), and *O. srilankiensis* **sp. n.** (Sri Lanka). *Oodera monstrum* Nikol'skaya, 1952, syn. n., is synonymised under *O. formosa* (Giraud, 1863). Five specimens could not be assigned to species and are treated as *Oodera* sp. Redescriptions are provided for all previously described valid species. *Oodera albopilosa* Crosby, 1909 is excluded from *Oodera* and transferred to *Eupelmus* Dalman, 1820 (Eupelmidae) as *E. albopilosa* (Crosby, 1909) n. comb. *Oodera rufimana* Westwood, 1874 and *O. obscura* Westwood, 1874 are treated as *nomina dubia* because we were unable to locate type specimens and the original descriptions are not sufficiently informative to clarify the taxonomic status of these names. Several specimens from North America are identified as introduced specimens of the European species *O. formosa*. We provide images and diagnostic characters for all 20 included species and an identification key to species.

Keywords

Taxonomy, parasitoid wasps, identification key, new species

Introduction

Oodera Westwood, 1874 is a morphologically extraordinary and conspicuous genus in Chalcidoidea. The group is currently classified as the monotypic tribe Ooderini in the Cleonyminae, a subfamily of the polyphyletic Pteromalidae (Heraty et al. 2013).

It included 14 species prior to this revision. Gibson (2003) provides a detailed generic description and a key to differentiate *Oodera* from other Cleonyminae. Individuals of *Oodera* have modified front legs with enlarged profemora and modified tibiae, and a long pronotum. The mesothorax of *Oodera* has a membranous area ventrally anterior to each mesocoxa (Gibson 1989, fig. 105) similar to that of individuals of Calosotine and females of Eupelminae (Eupelmidae) (Gibson 1989, figs 99–103). Individuals also have a unique mesonotal structure in which the mesoscutum and the mesoscutellar-axillar complex are fused and the axillae are strongly advanced such that a flexible, transverse transscutal articulation is lacking, and V-like, sulcate notauli extend to the base of the mesoscutellum (Fig. 5). Individuals are generally comparatively large-bodied (>5 mm).

The phylogenetic position and proper classification of *Oodera* remain unclear. When Bouček (1958) transferred *Oodera* from Eupelmidae to Pteromalidae he established the tribe Ooderini for it and suggested that it formed a 'bridge' to Eupelmidae, though he also stated that some species of *Heydenia* suggest a close relationship with *Oodera*. Graham (1969) suggested that *Oodera* formed a 'link' with Eupelmidae, whereas Gibson (1989) suggested that based on the structure of its middle legs *Oodera* might be the sister group of Eupelmidae or some part of it. Current molecular-data-only studies were unable to robustly place the genus in the phylogenetic Chalcidoidea tree (Munro et al. 2011), or placed it as sister group of Leucospidae, yet with a very limited taxon sampling (Peters et al. 2018). Using morphological evidence only, Heraty et al. (2013) retrieved *Oodera* as part of a polytomy along with Eupelmidae, Encyrtidae and Tanaostigmatidae (Heraty et al. 2013, fig. 8), but using combined morphological and molecular data either as nested within Calosotinae (Heraty et al. 2013, fig. 9) or as the sister group of Neanastatinae + Calosotinae (Heraty et al. 2013, fig. 10). Future molecular analyses will likely provide more reliable relationships.

All *Oodera* species are thought to be parasitoids of woodboring beetles (mainly Buprestidae and Scolytinae) but only very few host-parasitoid records are actually verified or even vouchered (Noyes 2017). Other details on their biology are unknown. They are only rarely collected, especially with the usual collecting methods of Chalcidoidea specialists, i.e., Malaise trap, sweep net, and pan trap. Accordingly, the function of such conspicuous morphological characteristics as front legs resembling raptorial legs and prolonged pronotum, that give *Oodera* specimens a praying-mantis-like habitus, remains unknown. Gibson (2003) hypothesised that these features and the ability to rotate the mesocoxae forward so that the middle legs can extend straight forward all formed a functional complex for grasping and manipulating whatever was caught. However, Gates (2004) offered small insects to a female *Oodera* in a Petri dish and observed no such actions. The conspicuous crest-like parascrobal areas of the head, each of which we call the 'corona', are most probably used to clear the tunnels of their woodboring host larva from frass and debris after emergence, analogous to other hymenopterans with similar structures that are wood borers (e.g., Stephanidae, Orussidae, some Calosotinae).

The genus has never been taxonomically revised. Of the 14 valid species described prior to this revision, all were described in isolation or with just another species. The only taxonomic actions so far, apart from new combinations to transfer species to *Oodera*, were by Fusu et al. (2015) who excluded *Oodera dakarensis* Risbec, 1957 from *Oodera* and transferred it to *Eupelmus*, and by Bouček (1958) and Bouček et al. (1978), who synonymised *Oodera bestia* Nikol'skaya, 1952 with *O. formosa* (Giraud, 1863) and *Oodera ornata* Gahan, 1925 with *O. longicollis* (Cameron, 1903). In fact, *O. formosa* and *O. longicollis* are both extraordinary, with *O. formosa* being the first described species and the only species from central Europe, and *O. longicollis* from East Asia being rather unusual in body length, ovipositor length, and colouration. In addition to these two species, there is one species described from the European part of Russia, four species described from Africa, and seven additional species described from Asia. No species are found in Australia or the New World except for one presumably introduced species in North America (Bouček and Heydon 1997). The latter was suspected to be *O. formosa* (Gibson 2003) but the identity of this species was not previously confirmed. Generally, *Oodera* species are recorded from warm to temperate areas.

Oodera are rarely collected and are, accordingly, also rare in scientific collections. The taxonomic revision presented here is based on 115 specimens. Most specimens are old (>10 years), dry-pinned material that does not allow routine DNA extraction and molecular sequencing. Our revision is based solely on morphological characters. We made high-resolution images of all relevant available type and non-type material and used a variety of qualitative features as well as morphometric ratios that describe body proportions as diagnostic characters to differentiate between species. Based on this, we describe new species, clarify the status of previously described species and redescribe them, and provide an identification key to all species considered valid after the taxonomic revision.

Methods

This study is based on material borrowed from the following museums (with abbreviations used in the text):

BMNH Natural History Museum, London, UK;
CNC Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada;
DECU Department of Entomology, Cornell University, Ithaca, New York, USA;
MFNB Museum für Naturkunde Berlin, Berlin, Germany;
MHNG Naturkunde Museum Genf, Geneva, Switzerland;

MNHN Muséum national d'Historie naturelle, Paris, France;
NHMW Naturhistorisches Museum Wien, Vienna, Austria;
NMBE Naturhistorisches Museum Bern, Bern, Switzerland;
NMP Národní Muzeum, Prague, Czech Republic;
SAMC Iziko Museums of Cape Town, Cape Town, South Africa;
USNM Smithsonian National Museum of Natural History, Washington D.C., USA;
ZFMK Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany;
ZIRAS Zoological Institute of Russian Acedemy of Science, St. Petersburg, Russia.

The terminology in this study follows Gibson (1997, 2003) and Bouček (1988). Terms for surface sculpture follow Harris (1979). The term 'corona' is newly used for the crest-like parascrobal area on the frons dorsally between each inner orbit and scrobal depression. The following four types of corona are characterised (in dorso-frontal view): 'interrupted': all horizontal crests either connected by one, occasionally two vertical crests or interrupted by vertical crevices (Fig. 1a); 'continuous': none or only some horizontal crests connected by vertical crests or interrupted by vertical crevices, median areas between horizontal crests distinctly rectangular (Fig. 1b); 'square': horizontal crests neither interrupted by vertical crevices nor connected by vertical crests, median areas between horizontal crests almost square (Fig. 1c); and 'three- to four-part': all horizontal crests connected by two or three vertical crests (Fig. 1d).

Both sexes were used for description of all characters, except for shape and size of the metasoma and the size of the ovipositor. Detailed character definitions are given in Table 1.

Table 1. List of characters used in this study, with character definition and abbreviation as also used in Suppl. material 1 (character definitions follow Graham (1969), Baur (2015) and Janšta et al. (2016)).

Abbreviation	Character	Definition
bdy.l	Body length	Length of body, excluding the ovipositor in females, dorsal view
hea.h	Head height	Distance between lower edge of clypeus and lower edge of anterior ocellus, frontal view
hea.l	Head length	Maximum length of head, lateral view
hea.w	Head width	Maximum width of head, frontal view
eye.h	Eye height	Height of eye, lateral view
eye.l	Eye length	Length of eye, lateral view
msp.l	Malar space	Distance between the points where malar sulcus touches mouth margin and lower edge of eye, lateral view
lof.h	Lower face height	Distance between lower margin of torulus and margin of clypeus
eya.d	Eye to antennal toruli	Distance between the lower margin of eye and lateral margin of antennal toruli, frontal view
tor.d	Distance antennal toruli	Distance between the inner margins of the toruli, frontal view
eye.d	Eye distance	Shortest distance between eyes, dorsal view
pol.l	POL	Shortest distance between posterior ocelli, dorsal view

Abbreviation	Character	Definition
ool.l	OOL	Shortest distance between posterior ocellus and eye margin, dorsal view
cor.l	Corona length	Maximum length of corona, frontal view
cor.w	Corona width	Maximum width of corona, frontal view
scp.l	Scape length	Length of scape exclusive of radicle, outer aspect
pdl.l	Pedicel length	Length of pedicel, outer aspect
flg.l	Flagellum length	Length of all flagellomers
fun.l	Funicule length	Length of flagellum excluding clava
clv.l	Clava length	Length of clava, outer aspect
no.l	Pronotum length	Length of pronotum along median line, dorsal view
no.w	Pronotum width	Maximum width of pronotum, dorsal view
msn.l	Mesonotum length	Length of mesonotum along median line from anterior edge of mesoscutum to posterior edge of mesoscutellum, dorsal view
msc.w	Mesoscutum width	Maximum width of mesoscutum just anterior to tegulae, equals mesonotum width, dorsal view
msc.l	Mesoscutum length	Length of mesoscutum along median line from posterior edge of pronotum to posterior edge of mesoscutum, dorsal view
sct.l	Mesoscutellum length	Length of mesoscutellum along median line from posterior edge of mesoscutum to posterior edge of scutellum, dorsal view
sct.w	Mesoscutellum width	Maximum width of mesoscutellum, dorsal view
sam.l	Mesoscutellum anterior margin	Length of part of mesoscutellum from anterior margin of mesoscutellum to imaginary transverse line connecting posterior margins of axillae, measured along median line, dorsal view
ppd.l	Propodeum length	Length of propodeum measured along median line from anterior edge of propodeum to posterior edge of nucha, dorsal view
ppd.w	Propodeum width	Maximum width of propodeum, dorsal view
tb1.l	Protibia length	Length of protibia along median line, outer aspect
fm1.l	Profemur length	Length of profemur, from distal end of trochanter to tip of profemur, measured along median line, outer aspect
fm1.w	Profemur width	Maximum width of profemur, outer aspect
fwi.l	Fore wing length	Maximum length of fore wing, measured from end of humeral plate to tip of wing
fwi.w	Fore wing width	Maximum width of fore wing
cc.l	Costal cell length	Length of the costal cell, 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
mav.l	Marginal vein length	Length of marginal vein, distance between the point at which the submarginal vein touches the leading edge of the wing and the point at which stigmal vein and postmarginal vein unite
pmv.l	Postmarginal vein length	Length of postmarginal vein, distance between the point at which stigmal vein and postmarginal vein unite, apically to where the vein appears to end
stv.l	Stigmal vein length	Length of stigmal vein, distance between the point at which stigmal vein and postmarginal vein unite apically, and the distal end of the stigma
mts.l	Metasoma length	Length of metasoma along median line, from end of nucha to tip of metasoma, excluding ovipositor, dorsal view
mts.w	Metasoma width	Maximum width of metasoma, dorsal view
ovp.l	Ovipositor length	Length of the visible part of ovipositor, dorsal view

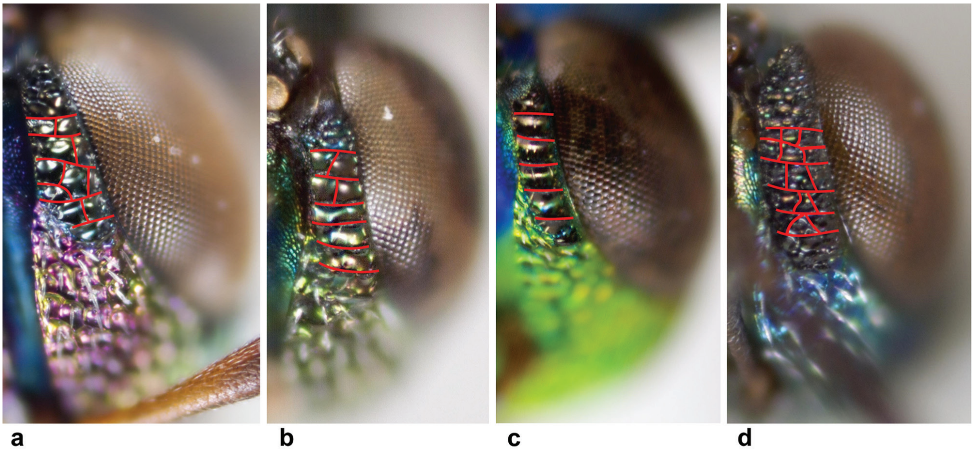

Figure 1. Four different types of corona structure in *Oodera*, in dorso-frontal view. Antennal scrobes are left of corona, eye is right of corona; **a** interrupted (exemplar species imaged: *O. namibiensis* sp. n.) **b** continuous (exemplar species imaged: *O. formosa*) **c** square (exemplar species imaged: *O. longicollis*) **d** three- to four-part (exemplar species imaged: *O. leibnizi* sp. n.). For additional definitions of corona types see main text.

We calculated a number of ratio characters to describe shape and dimensions of body parts, and assigned ratios to categories to allow easier diagnosis and use in the identification key. These ratios and categories – used throughout the text – are given in Table 2.

For morphological examination and measurements we used an Olympus SZX12-ILLK stereomicroscope with an eyepiece micrometer (1 mm divided in 100 units). Magnification ranged from 11.2× (16× eyepiece, 0.7× objective) to 144× (16× eyepiece, 9× objective). For photographs, we used a BK Lab Imaging system (Dun, Inc. 2016).

Photos were taken with a Canon EOS 7D, serially in 30 to 40 different focal distances. The camera was equipped with a Tamron Tele-Converter SP AF 1.4X, a Canon AC Adapter Kit ACK E6-(CBCB) and with different objectives (CF1B, CF2, CF3, CF4 or micro/macro-objective) that were selected depending on specimen or character size. For the lighting, the camera's own flash light and three movable light sources were used. A dull Plexiglas tube was placed over the specimen to avoid reflection from direct light.

Adobe Lightroom 5 was used for initial evaluation and for storing the photos. Then, the photos were stacked with Zerene Stacker and Helicon Focus and modified with GIMP 2.8.14 and Adobe Photoshop CS6. For scaling, photos of a 1 mm scale were made with all used objectives.

The image plates were made with PowerPoint 2010.

We examined a total of 115 specimens (24 males, 85 females, four of undetermined sex due to missing metasoma (= 113) plus two females examined from images). All 113 examined and measured specimens were given a unique code number referring to this study, composed of a species name abbreviation (e.g., OFo for *O. formosa*) and a consecutive number that was added to the specimen on a separate label. All measurements and calculated ratios for each specimen are given in Suppl. material 1.

Table 2. Characters and categories used in the text, with respective ranges of measured ratios.

Character	Categories and Ranges		
Body shape (mesonotum length/mesonotum width = mesoscutum width)	**robust**	**medium**	**slender**
	<1.4	1.4–1.44	>1.44
Head shape in lateral view (head height/head length)	**round**	**oval**	**elongated**
	<1.45	1.45–1.6	>1.6
Eye size (eye height/head height)	**small**		**large**
	<0.6		≥0.6
Corona shape (corona length/corona width)	**thick**	**medium**	**slim**
	<4.1	4.1–7.0	>7.0
Mesoscutellum shape (mesoscutellum length/mesoscutellum width)	**normal**		**slender**
	<0.75		≥0.75
Mesoscutellum anterior margin (part anterior to virtual transverse line between posterior margins of axillae/mesoscutellum length)	**hardly convex**		**convex**
	≤0.33		>0.33
Propodeum size (propodeum length/mesoscutum length)	**small**	**medium**	**large**
	<0.08	0.08–0.15	>0.15
Profemur shape (profemur length/profemur width)	**robust**	**medium**	**elongated**
	<1.99	2.0–2.2	>2.2
Marginal vein length (marginal vein length/postmarginal vein length)	**short**	**medium**	**long**
	<0.9	0.9–1.10	>1.10
Metasoma length (metasoma length/body length)	**short**	**medium**	**long**
	<0.46	0.46–0.5	>0.5
Ovipositor length (ovipositor length/metasoma length)	**short**		**rather long**
	<0.16		≥0.16
Body length (in mm)	**small**	**medium**	**large**
	<7.0	7.0–9.0	>9.0

Results

Oodera Westwood, 1874

Diagnosis. BOTH SEXES. Comparatively large-bodied (3.6–17 mm). Parascrobal area of head raised and with crest-like structure (= corona) (Fig. 1). Pronotum long and in dorsal view separated from mesothorax by distinct constriction, semicircularly strigulate (Figs 11–13). Mesonotum with mesoscutum and mesoscutellar-axillar complex fused, without flexible, transverse transscutal articulation; mesoscutum with notauli V-like sulcate and extending to base of mesoscutellum; axillae strongly advanced laterally (Figs 11–13). Mesothorax ventrally with membranous region anterior to each mesocoxa, enabling mesocoxae to rotate anteriorly. Profemur enlarged (Figs 2–4) and ventrally with comb of small teeth and strong black bristles.

FEMALE. Always with exserted part of ovipositor visible in dorsal view (Figs 2–4).

Description. For a detailed description of the genus see Gibson (2003). Only few characters given there need to be redescribed based on the material examined in this study:

Mesosoma. Pronotum in dorsal view appearing somewhat pentagonal or almost circular. Mesoscutellum sculpture variable dorsally, always with longitudinally strigose parts, with smoother, coriaceous apical rim distinguished by furrow or carina.

Wings. Postmarginal vein slightly shorter to slightly longer than marginal vein.

Metasoma. Length of ovipositor sheaths varying from less than 10% of metasoma length to 110% of metasoma length.

Note that some of the characters given by Gibson (2003) were not studied for all species because they were not visible in some specimens, including types, specifically ventral views of mesosoma.

Key to *Oodera* species

Note: If combinations of characters are given, connected with **and** and separated by comma (not semicolon), then **all** characters have to be present; in the alternative path at least one of the characters has to be different.

1 Ovipositor longer than 0.25× metasoma length; with bright blue or green colour on mesosoma (Fig. 3a, e)....**2**

– Ovipositor distinctly shorter than 0.25× metasoma length; mesosoma not brightly coloured **3**

2(1) Ovipositor longer than metasoma; corona structure three- to four-part; body length >15 mm (Fig. 3a).... ***O. gracilis* Westwood** (Indonesia)

– Ovipositor shorter than metasoma; corona structure square; body length <15 mm (Fig. 3e).... ***O. longicollis* (Cameron)** (China, Indonesia, Malaysia, Myanmar, Philippines, Vietnam)

3(1) Head width about 7× eye distance (Fig. 3d); large-sized (>9.0 mm) .... ***O. madegassa* Bouček** (Madagascar)

– Head width at most 4.38× eye distance; usually small- to medium-sized (≤9.0 mm) **4**

4(3) Eyes small (eye height <0.6× head height), **and** head oval (head height 1.45–1.6× head length), **and** small-sized (<7.0 mm) **5**

– Different combination of characters....**6**

5(4) Pronotum virtually round; profemur robust (profemur length <1.99× width) (Fig. 2b).... ***O. circularicollis* sp. n.** (Morocco)

– Pronotum pentagonal, with broadest part before midlength; profemur medium (profemur length 2.15× width) (Fig. 4f)...... ***O. pumilae* Yang** (China)

6(4) Head round (height <1.45× length), **and** marginal vein long (marginal vein length >1.10× postmarginal vein length), **and** small-sized (<7.0 mm) **7**

– Different combination of characters....**10**

7(6) Profemur elongated (profemur length >2.2× width); fore wing at least weakly infumate in part **8**

– Profemur medium (profemur length 2.0–2.2× width); fore wing hyaline (Fig. 2e) .... ***O. florea* sp. n.** (Thailand)

8(7) Anterior margin of mesoscutellum convex (part anterior to imaginary transverse line connecting posterior margins of axillae more than 1/3 mesoscutellum length, 0.37–0.39); mesoscutellum completely lineate; pronotum pentagonal with posterior part hardly narrowing towards mesoscutum (Figs 2d, 14d) .... ***O. fidelis* sp. n.** (Vietnam)

– Anterior margin of mesoscutellum hardly convex (part anterior to imaginary transverse line connecting posterior margins of axillae at most 1/3 mesoscutellum length, 0.17–0.33); mesoscutellum lineate only in anterior two thirds; pronotum oval or pentagonal, if pentagonal then with posterior part distinctly narrowing towards mesoscutum **9**

9(8) Pronotum oval (Fig. 4i); corona structure continuous (Figs 1b, 7i) .... ***O. tenuicollis* (Walker)** (Indonesia)

– Pronotum pentagonal with posterior part distinctly narrowing towards mesoscutum (Fig. 3d); corona structure three- to four-part (Fig. 1d) .... ***O. leibnizi* sp. n.** (Malaysia, Papua New Guinea, Philippines)

10(6) Body slender (mesonotum length 1.45× mesonotum width), **and** eyes large (eye height 0.64× head height), **and** marginal vein long (marginal vein length 1.17× postmarginal vein length) (Figs 2c, 8c) .... ***O. felix* sp. n.** (Central African Republic)

– Different combination of characters **11**

11(10) Medium- to large-sized (≥7.0 mm), **and** either uniformly dark-coloured, or if not uniformly dark-coloured then fore wing hyaline **12**

– Small-sized (<7.0 mm) or if medium-sized (7.0–9.0 mm) then in part with distinct dark green or coppery colour and fore wing partly infumate **14**

12(11) Body robust or medium (mesonotum length ≤1.44× width) (Figs 4d, 13d); fore wing partly infumate (Fig. 4d) .... ***O. namibiensis* sp. n.** (Namibia)

– Body slender (mesonotum length >1.44× width) (Figs 4b, 13b); fore wing hyaline (Fig. 4b) **13**

13(12) Head and mesosoma uniformly black with tinges of dark green and purple (Figs 4b, 7b, 10b, 13b); head oval (head height 1.56× length); eyes large (eye height 0.63× head height) (Fig. 10b) .... ***O. mkomaziensis* sp. n.** (Tanzania)

– Head and mesosoma dark blue and green-blue (Figs 2a, 5a, 8a, 11a); head round (head height 1.41× length); eyes small (eye height 0.57× head height) (Fig. 8a) .... ***O. ahoma* (Mani & Kaul)** (India)

14(11) Head round (head height <1.45× length) or if oval (head height 1.45–1.6× length) then either mesoscutellum only partially lineate **and** fore wing partly infumate (some *O. formosa*) or mesoscutellum only partially lineate **and** with distinct blue on head and mesosoma (*O. srilankiensis* males) **15**

– Head oval or elongated (head height ≥1.45× length) and without other character combination **16**

15(14) Propodeum large (propodeum length >0.15× mesoscutum length) (Fig. 16h); fore wing hyaline (Fig. 4h); head and mesosoma blue or blue-green (Figs 7h, 10h, 13h) .... ***O. srilankiensis* sp. n.** (Sri Lanka)

– Propodeum usually medium (propodeum length 0.08–0.15× mesoscutum length) (Fig. 14f); fore wing partly infumate (Fig. 2f); head and mesosoma dark green and coppery, without significant blue or blueish colour (Figs 5f, 8f, 11f) .... ***O. formosa* (Giraud)** (Southern and Central Europe, Russia, eastern USA (introduced))

16(14) Marginal vein short (marginal vein length <0.9× postmarginal vein length), **and** propodeum medium to large (propodeum length ≥0.08× mesoscutum length), **and** fore wing hyaline, **and** mesoscutellum at least partly areolate or rugolose **17**

– Different combination of characters.. **18**

17(16) Mesoscutellum densely lineate in anterior half to two-thirds and areolate in posterior one-third to half (Fig. 16e); pronotum with broadest part before midlength (Fig. 13e) .... ***O. niehuisorum* sp. n.** (Egypt, Israel)

– Mesoscutellum lineate in anterior two-thirds and rugulose in posterior one-third (Fig. 15c); pronotum broadest at midlength (Fig. 12c)........................ .... ***O. hoggarensis* Hedqvist** (Algeria)

18(16) Marginal vein long (marginal vein length 1.19× postmarginal vein length); corona short (corona length 0.45× eye height) (Fig. 7g).. ***O. regiae* Yang** (China)

– Marginal vein short to medium (marginal vein length <1.07× postmarginal vein length); corona longer (corona length always >0.52× eye height)....... **19**

19(18) Fore wing hyaline (Fig. 3b); mesoscutellum completely densely lineate (Fig. 15b)................................ ***O. heikewernerae* sp. n.** (Botswana, South Africa)

– Fore wing partly infumate (Fig. 4a); mesoscutellum completely rippledly lineate (Fig. 16a) .... ***O. magnifica* (Risbec)** (Senegal)

***Oodera ahoma* (Mani & Kaul, 1973)**

Figs 2a, 5a, 8a, 11a, 14a

Lycisca ahoma Mani & Kaul, 1973: 53–55.
Oodera ahoma; Bouček et al. 1978: 448.

Diagnosis. FEMALE (N = 1). Medium-sized (8.40 mm). Head and mesosoma dark blue to green-blue. Fore wing hyaline. Body slender (mesonotum 1.51× as long as wide). Head round (1.41× as high as long). Eyes small (0.57× as high as head) (Fig. 8a). Corona medium (5.20× as long as wide), structure continuous (Fig. 5a). Pronotum pentagonal with posterior part distinctly narrowing towards mesoscutum, with broadest part before midlength (Fig. 11a). Mesoscutellum normal (0.70× as long as wide), anterior margin convex (part anterior to imaginary transverse line connecting posterior margins of axillae more than 1/3 of mesoscutellum length; 0.42), mesoscutellum lineate in anterior third to half, rugulose in posterior half or two thirds (Fig. 14a). Propodeum medium (0.13× as long as mesoscutum) (Fig. 14a). Profemur medium (2.04× as long as wide). Marginal vein long (1.13× as long as postmarginal vein). Metasoma medium (0.47× as long as body). Ovipositor short (0.11× as long as metasoma) (Fig. 2a).

Redescription. FEMALE. *Colour* (Figs 2a, 5a, 8a, 11a, 14a). Scape brown, darkening apically, rest of antenna dark brown. Procoxa dark brown, profemur dark green and blue, meso- and metafemur dark brown, tibiae light brown, tarsi yellow, except for brown last tarsal segments. Metasoma dark brown.

Head (Figs 5a, 8a). Face completely reticulate. Head 1.39× as wide as long. Head width 3.57× eye distance. Malar space 0.43× head height. Corona 0.71× as long as eye height. POL 0.75× OOL. Scape 2.31× as long as pedicel. Clava length to funicule length not available. Flagellum length to head width not available.

Mesosoma (Figs 11a, 14a). Pronotum 1.03× as long as wide. Pronotum 0.51× as long as mesonotum. Mesonotum 1.35× as long as mesoscutum. Mesoscutum 1.12× as long as wide. Mesoscutellum 0.35× as long as mesoscutum. Profemur 1.34× as long as protibia.

Wings (Fig. 2a). Fore wing 3.00× as long as wide. Costal cell 0.38× as long as fore wing. Marginal vein 0.20× as long as fore wing. Marginal vein 3.10× as long as stigmal vein. Postmarginal vein 2.76× as long as stigmal vein.

MALE. Unknown.

Material examined. ASIA. **India:** female holotype, Lumding, Assam, leg. R.O., 25.05.1942, det. Mani and Kaul as *Lycisca ahoma* (USNM) (OAh01).

Biology. Hosts may be *Agrilus* sp. (Buprestidae) (Noyes 2017) (unverified host record).

Distribution. India.

Oodera circularicollis sp. n.

http://zoobank.org/37D7A5DC-D3ED-430F-8A99-9CEA23091F7C

Figs 2b, 5b, 8b, 11b, 14b

Diagnosis. FEMALE (N = 3). Small-sized (5.88–6.48 mm). Head and mesosoma blackish with dark green, purple and yellow parts. Fore wing partly infumate. Body robust to medium (mesonotum 1.22–1.43× as long as wide). Head oval (1.45–1.51× as high as long). Eyes small (0.54–0.56× as high as head) (Fig. 8b). Corona thick (3.64–4.0× as long as wide), structure interrupted (Fig. 5b). Pronotum virtually round (Fig. 11b). Mesoscutellum normal to slender (0.64–0.76× as long as wide), anterior margin hardly convex or convex (part anterior to imaginary transverse line connecting posterior margins of axillae slightly less or more than 1/3 of mesoscutellum length; 0.32–0.35), mesoscutellum lineate in anterior two thirds, rugulose in posterior third (Fig. 14b). Propodeum medium (0.13–0.14× as long as mesoscutum) (Fig. 14b). Profemur robust (1.78–1.91× as long as wide). Marginal vein short to medium (0.88–0.94× as long as postmarginal vein). Metasoma medium (0.45–0.48× as long as body). Ovipositor short (0.12–0.15× as long as metasoma) (Fig. 2b).

Figure 2. Habitus (dorsal) I **a** *O. ahoma* (Mani & Kaul) (imaged specimen: OAh01, holotype) **b** *O. circularicollis* sp. n. (OCi01, holotype), **c** *O. felix* sp. n. (OFe01, holotype) **d** *O. fidelis* sp. n. (OFi01, holotype) **e** *O. florea* sp. n. (OFl01, holotype) **f** *O. formosa* (Giraud) (OFo13). Scale bars: 1 mm.

Figure 3. Habitus (dorsal) II **a** *O. gracilis* Westwood (imaged specimen: OGr01; ovipositor not visible in full length) **b** *O. heikewernerae* sp. n. (OHe01, holotype) **c** *O. hoggarensis* Hedqvist (OHo02, paratype) **d** *O. leibnizi* sp. n. (OLe01, holotype) **e** *O. longicollis* (Cameron) (OLo01) **f** *O. madegassa* Bouček (OMad01, holotype). Scale bars: 1 mm.

Description. FEMALE. *Colour* (Figs 2b, 5b, 8b, 11b, 14b). Scape yellow, darkening apically, rest of antenna dark brown. Procoxa and profemur light to dark green, all other parts of legs yellow to light brown. Metasoma black.

Head (Figs 5b, 8b). Face completely reticulate. Head 1.46–1.51× as wide as long. Head width 3.4× eye distance. Malar space 0.44–0.47× head height. Corona 0.62–0.71× as long as eye height. POL equal to OOL. Scape 2.52–2.86× as long as pedicel. Clava length to funicle length not available. Flagellum length to head width not available.

Mesosoma (Figs 11b, 14b). Pronotum 0.91× as long as wide. Pronotum 0.49–0.55× as long as mesonotum. Mesonotum 1.42–1.45× as long as mesoscutum. Mesoscutum

Figure 4. Habitus (dorsal) III **a** *O. magnifica* (Risbec) (imaged specimen: OMag01, holotype) **b** *O. mkomaziensis* sp. n. (OMk01, holotype) **c** *O. monstrum* syn. n. (OFo12, paratype) **d** *O. namibiensis* sp. n. (ONa01, holotype) **e** *O. niehuisorum* sp. n. (ONi01, holotype) **f** *O. pumilae* Yang (OPu01, paratype) **g** *O. regiae* Yang (ORe01, paratype) **h** *O. srilankiensis* sp. n. (OSr01, holotype) **i** *O. tenuicollis* (Walker) (OTe01, holotype). Scale bars: 1 mm.

0.86–0.98× as long as wide. Mesoscutellum 0.42–0.45× as long as mesoscutum. Profemur 1.21–1.29× as long as protibia.

Wings (Fig. 2b). Fore wing 2.67–2.89× as long as wide. Costal cell 0.35–0.38× as long as fore wing. Marginal vein 0.17–0.20× as long as fore wing. Marginal vein 2.5–3.53× as long as stigmal vein. Postmarginal vein 2.83–3.76× as long as stigmal vein.

MALE. Unknown.

Material examined. AFRICA. **Morocco**: female holotype, Granja del Muluya, Kebdana-Marruecos, leg. P. Alcaide VII. 1953, ex larva 'unreadable word' Punica, ex coll. V. Delucchi (NMBE) (OCi01); two female paratypes with same data (NMBE) (OCi02), (ZFMK) (OCi03).

Biology. Unknown. The label data point towards an association with *Punica* (pomegranate).

Distribution. Morocco.

Etymology. Named for its unusual, round pronotum.

***Oodera felix* sp. n.**
http://zoobank.org/2475099E-8892-4C89-8243-72FE741F76C9
Figs 2c, 5c, 8c, 11c, 14c

Diagnosis. FEMALE (N = 1). Medium-sized (7.20 mm). Head and mesosoma mostly blackish and dark greenish. Fore wing partly infumate. Body slender (mesonotum 1.45× as long as wide). Head oval (1.59× as high as long). Eyes large (0.64× as high as head) (Fig. 8c). Corona medium (4.80× as long as wide), structure continuous (Fig. 5c). Pronotum pentagonal with posterior part distinctly narrowing towards mesoscutum, roof-like, with broadest part behind midlength (Fig. 11c). Mesoscutellum slender (0.80× as long as wide), anterior margin convex (part anterior to imaginary transverse line connecting posterior margins of axillae more than 1/3 of mesoscutellum length; 0.38), mesoscutellum lineate in anterior two thirds, finely areolate in posterior third (Fig. 14c). Propodeum medium (0.14× as long as mesoscutum) (Fig. 14c). Profemur medium (2.08× as long as wide). Marginal vein long (1.17× as long as postmarginal vein). Metasoma short (0.43× as long as body). Ovipositor short (0.10× as long as metasoma) (Fig. 2c).

Description. FEMALE. *Colour* (Figs 2c, 5c, 8c, 11c, 14c). Scape, pedicel and first funicle segment yellow, darkening apically, rest of antenna dark brown. Procoxa and profemur black, all other parts of legs light brown with yellow joints, tarsi yellow, except for brown last tarsal segments. Metasoma brown.

Head (Figs 5c, 8c). Face completely reticulate. Head 1.54× as wide as long. Head width 3.72× eye distance. Malar space 0.36× head height. Corona 0.68× as long as eye height. POL 1.20× OOL. Scape 2.41× as long as pedicel. Clava 0.18× as long as funicle. Flagellum 1.47× as long as head width.

Mesosoma (Figs 11c, 14c). Pronotum as long as wide. Pronotum 0.55× as long as mesonotum. Mesonotum 1.80× as long as mesoscutum. Mesoscutum 1.05× as long as wide. Mesoscutellum 0.38× as long as mesoscutum. Profemur 1.28× as long as protibia.

Wings (Fig. 2c). Fore wing 3.20× as long as wide. Costal cell 0.34× as long as fore wing. Marginal vein 0.22× as long as fore wing. Marginal vein 3.50× as long as stigmal vein. Postmarginal vein 3.0× as long as stigmal vein.

MALE. Unknown.

Material examined. AFRICA. **Central African Republic**: female holotype, Prefecture Sangha-Mbaéré, Parc Ntional de Dzanga-Ndoki, 38.6 km 173 °S Lidjombo, leg. S. van Noort, 26–27.05.2001 (SAMC) (OFe01).

Biology. Unknown.

Distribution. Central African Republic.

Etymology. Named after the Latin adjective *felix*, meaning lucky.

Taxonomic remarks. Unfortunately, the holotype was damaged during examination for this study (metasoma detached from body). The images show the still undamaged specimen.

***Oodera fidelis* sp. n.**
http://zoobank.org/80A1EAF4-0C4C-4685-8A0A-399CA3CD9169
Figs 2d, 5d, 8d, 11d, 14d

Diagnosis. BOTH SEXES (N = 3). Small-sized (6.48–6.80 mm). Head and mesosoma dark green to blue. Fore wing partly infumate. Body robust to slender (mesonotum 1.29–1.47× as long as wide). Head round (1.33–1.41× as high as long). Eyes large (0.61–0.67× as high as head) (Fig. 8d). Corona medium to thick (4.00–6.00× as long as wide), structure continuous (Fig. 4d). Pronotum pentagonal with posterior part hardly narrowing towards mesoscutum, with broadest part before midlength (Fig. 11d). Mesoscutellum slender (0.75–0.87× as long as wide), anterior margin convex (part anterior to imaginary transverse line connecting posterior margins of axillae more than 1/3 of mesoscutellum length; 0.37–0.39), mesoscutellum completely lineate, with median lines converging (Fig. 14d). Propodeum large (0.19–0.20× as long as mesoscutum) (Fig. 14d). Profemur elongated (2.23–2.51× as long as wide). Marginal vein long (1.11–1.19× as long as postmarginal vein).

FEMALE. Metasoma medium (0.45–0.46× as long as body). Ovipositor short (0.13–0.13× as long as metasoma) (Fig. 2d).

Description. BOTH SEXES. *Colour* (Figs 2d, 5d, 8d, 11d, 14d). Scape yellow, darkening apically, rest of antenna dark brown. Procoxa and profemur dark green, all other parts of legs dark yellow, except for brown meso- and metafemur. Metasoma brown.

Head (Figs 5d, 8d). Face completely reticulate. Head 1.39–1.45× as wide as long. Head width 3.18–3.66× eye distance. Malar space 0.33–0.37× head height. Corona 0.57–0.76× as long as eye height. POL 0.6–1.00× OOL. Scape 2.18–2.86× as long as pedicel. Clava 0.14–0.18× as long as funicle. Flagellum 1.29–1.50× as long as head width.

Mesosoma (Figs 11d, 14d). Pronotum 0.83–1.10× as long as wide. Pronotum 0.44–0.64× as long as mesonotum. Mesonotum 1.44–1.47× as long as mesoscutum. Mesoscutum 0.89–1.02× as long as wide. Mesoscutellum 0.44–0.47× as long as mesoscutum. Profemur 1.27–1.43× as long as protibia.

Wings (Fig. 2d). Fore wing 2.80–2.97× as long as wide. Costal cell 0.35–0.40× as long as fore wing. Marginal vein 0.20–0.21× as long as fore wing. Marginal vein 2.95–3.64× as long as stigmal vein. Postmarginal vein 2.11–3.27× as long as stigmal vein.

Material examined. ASIA. **Vietnam**: female holotype, Ha Tinh Huong son, 900 m, 18°22'N/105°13'E, leg. L. Herman, MT, 05.05.1998 (CNC) (OFi01); two male paratypes, Ha Tinh Huong son, 900 m, 18°22'N/105°13'E, leg. L. Herman, MT, 18.–28.5.1998 (CNC) (OFi02), (ZFMK) (OFi03).

Biology. Unknown.

Distribution. Vietnam.

Etymology. Named after the latin adjective *fidelis*, meaning faithful, because of the distinct blueish colour of head and mesosoma and blue being the symbolic colour of trust.

Figure 5. Head (frontal) I **a** *O. ahoma* (Mani & Kaul) (imaged specimen: OAh01, holotype) **b** *O. circularicollis* sp. n. (OCi01, holotype) **c** *O. felix* sp. n. (OFe01, holotype) **d** *O. fidelis* sp. n. (OFi01, holotype) **e** *O. florea* sp. n. (OFl01, holotype) **f** *O. formosa* (Giraud) (OFo03). Scale bars: 1 mm.

Oodera florea sp. n.

http://zoobank.org/65A161CA-A576-4882-BE2F-E45327ED51A6

Figs 2e, 5e, 8e, 11e, 14e

Diagnosis. FEMALE (N = 1). Small-sized (4.80 mm). Head and mesosoma dark green and green-blue. Fore wing hyaline. Body robust (mesonotum 1.32× as long as wide). Head round (1.41× as high as long). Eyes large (0.66× as high as head) (Fig. 8e). Corona medium (5.83× as long as wide), structure continuous (Fig. 5e). Pronotum oval and wider than long, with broadest part at midlength (Fig. 11e). Mesoscutellum normal (0.72× as long as wide), anterior margin hardly convex (part anterior to imaginary transverse line connecting posterior margins of axillae less than 1/3 of mesoscutellum length; 0.28), mesoscutellum lineate in anterior third, areolate in posterior two thirds (Fig. 14e). Propodeum large (0.18× as long as mesoscutum) (Fig. 14e). Profemur medium (2.08× as long as wide). Marginal vein long (1.25× as long as postmarginal vein). Metasoma medium (0.49× as long as body). Ovipositor short (0.12× as long as metasoma) (Fig. 2e).

Description. FEMALE. *Colour* (Figs 2e, 5e, 8e, 11e, 14e). Scape yellow, darkening apically, rest of antenna dark brown. Procoxa and profemur light green, all other parts of legs dark brown with yellow joints and tarsi, except for brown last tarsal segments. Metasoma dark brown.

Figure 6. Head (frontal) II **a** *O. gracilis* Westwood (imaged specimen: OGr01) **b** *O. heikewernerae* sp. n. (OHe01, holotype) **c** *O. hoggarensis* Hedqvist (OHo02, paratype) **d** *O. leibnizi* sp. n. (OLe03, paratype) **e** *O. longicollis* (Cameron) (OLo01) **f** *O. madegassa* Bouček (OMad01, holotype). Scale bars: 1 mm.

Head (Figs 5e, 8e). Face completely reticulate. Head 1.41× as wide as long. Head width 3.76× eye distance. Malar space 0.34× head height. Corona 0.67× as long as eye height. POL 1.67× OOL. Scape 2.43× as long as pedicel. Clava length to funicle length not available. Flagellum length to head width not available.

Mesosoma (Figs 11e, 14e). Pronotum 0.92× as long as wide. Pronotum 0.52× as long as mesonotum. Mesonotum 1.45× as long as mesoscutum. Mesoscutum 0.91× as long as wide. Mesoscutellum 0.45× as long as mesoscutum. Profemur 1.37× as long as protibia.

Wings (Fig. 2e). Fore wing 3.33× as long as wide. Costal cell 0.36× as long as fore wing. Marginal vein 0.21× as long as fore wing. Marginal vein 3.16× as long as stigmal vein. Postmarginal vein 2.53× as long as stigmal vein.

MALE. Unknown.

Material examined. ASIA. **Thailand:** female holotype, Loei, Phu Kradueng NP, labelled "Deciduous", leg. S. Glong-lasae, 02–10.10.2006 (CNC) (OFl01).

Biology. Unknown.

Distribution. Thailand.

Etymology. Named after the latin adjective *florea*, meaning flowery. The species is, in our subjective view, particularly beautiful and flimsy, like a flower.

***Oodera formosa* (Giraud, 1863)**
Figs 2f, 5f, 8f, 11f, 14f

Heydenia formosa Giraud, 1863: 21–22.
Stellophora formosa; Hedqvist 1957: 44–46.
Oodera formosa; Bouček 1958: 375.
Oodera bestia Nikol'skaya, 1952: 487–488. Synonymy by Bouček 1958: 375–380.
Oodera monstrum Nikol'skaya, 1952: 487–488, **syn. n.** (Figs 4c, 7c, 10c, 13c, 16c)

Diagnosis. BOTH SEXES (N = 35). Usually small-sized (3.60–7.12 mm, with only 1 of 27 medium-sized). Head and mesosoma dark green and coppery. Fore wing partly infumate. Body robust to slender (mesonotum 1.19–1.47× as long as wide). Head usually round (1.30–1.48× as high as long, with only 3 of 32 with head oval). Eyes usually large (0.55–0.68× as high as head, with only 4 of 32 with eyes small) (Fig. 8f). Corona thick to medium (3.20–6.67× as long as wide), structure continuous (Fig. 5f). Pronotum pentagonal with posterior part distinctly narrowing towards mesoscutum, with broadest part at midlength (Fig. 11f). Mesoscutellum normal to slender (0.63–0.95× as long as wide), anterior margin usually convex (part anterior to imaginary transverse line connecting posterior margins of axillae more than 1/3 mesoscutellum length; 0.24–0.47, with only 8 of 32 with anterior margin of mesoscutellum hardly convex), mesoscutellum lineate in anterior half to anterior two-thirds, with median lines converging, rugulose in posterior half or third (Fig. 14f). Propodeum usually medium (0.08–0.18× as long as mesoscutum, with only 5 of 28 with propodeum large) (Fig. 14f). Profemur usually medium to elongated (1.94–2.33× as long as wide, with only 5 of 31 with profemur robust). Marginal vein short to medium (0.85–1.00× as long as postmarginal vein).

FEMALE. Metasoma short to long (0.43–0.55× as long as body). Ovipositor usually short (0.09–0.17× as long as metasoma, with only 2 of 26 with metasoma rather long) (Fig. 2f).

Redescription. BOTH SEXES. *Colour* (Figs 2f, 5f, 8f, 11f, 14f). Scape yellow, darkening apically, rest of antenna dark brown. Procoxa and profemur dark green, all other parts of legs dark brown, except for brown last tarsal segments. Metasoma brown to black.

Head (Figs 5f, 8f). Face completely reticulate. Head 1.29–1.73× as wide as long. Head width 3.00–3.78× eye distance. Malar space 0.33–0.45× head height. Corona 0.56–0.84× as long as eye height. POL 0.5–1.33× OOL. Scape 1.95–3.16× as long as pedicel. Clava 0.13–0.20× as long as funicle. Flagellum 1.12–1.66× as long as head width.

Mesosoma (Figs 11f, 14f). Pronotum 0.86–1.05× as long as wide. Pronotum 0.49–0.64× as long as mesonotum. Mesonotum 1.38–1.55× as long as mesoscutum. Mesoscutum 0.82–1.02× as long as wide. Mesoscutellum 0.38–0.55× as long as mesoscutum. Profemur 1.19–1.71× as long as protibia.

Wings (Fig. 2f). Fore wing 2.56–3.86× as long as wide. Costal cell 0.28–0.39× as long as fore wing. Marginal vein 0.17–0.21× as long as fore wing. Marginal vein

2.24–4.25× (2.24–3.29× if two outliers with very short stigmal vein are removed) as long as stigmal vein. Postmarginal vein 2.40–4.50× (2.40–3.29× if two outliers with very short stigmal vein are excluded) as long as stigmal vein.

Material examined. EUROPE. **Bulgaria**: male, Slencev Brjag, leg. Kocourek, 26.07.1968, det. Z. Bouček 1976 (BMNH) (OFo04). **France**: female, Landes, leg. Reinhard, det. Z. Bouček 1958 (MFNB) (OFo03). **Germany**: three females, MTB 6315 Flörsheim-Dalsheim, Rheinland-Pfalz, BRD RP 49°39'16"N–8°12'51"E, „Garten am Haus“, leg. G. Reder, 11.06, 19.06 and 04.07.2014 (ZFMK) (OFo33-35). **Romania**: female, Herculeana, leg. T.E. Leiler, 1921 (BMNH) (OFo07). **Russia**: male paratype *O. monstrum*, Taganrog, leg. K. Anger, 20.06.1929, det. N. Nikol'skaya (BMNH) (OFo12); female holotype *O. monstrum*, USSR, VI.1935 (ZIRAS, examined from photographs); female syntype *O. bestia*, Ul'yanovsk Aksinin, 19.04.1905 (ZIRAS, examined from photographs); female, USSR, Adigea, Soci, leg. K. Pospisil, 23.06.1957, det. Z. Bouček 1958 (BMNH) (OFo13). **Slovenia**: two males, one ? sex, Vipava, Carniolia, Wippach, leg. Handl, 16.07.1986, det. Z. Bouček 1958 (NHMW) (OFo09-11). **Spain**: female, Villaviciosa, 8.1969 (BMNH) (OFo08). **Switzerland**: female, Genève, Miolan, leg. C. Besuchet, 07.08.1991, det. H. Baur 1994 (NMBE) (OFo03). **Turkey**: female, G.antep, Gaziantep, leg. M Yasar Celik, 14.07.1971 (MNP) (OFo32). Former **Yugoslavia**: two females, leg. T.E. Leiler, 1955 (BMNH) (OFo05-06); **without location**: female holotype *O. formosa*, labelled "*Heydenia formosa* Gir." (plus unreadable addition) (MNHN) (OFo01). NORTH AMERICA. **Canada**: Ontario: female, Ottawa, Fletcher Garden, 45°23'11.58"N, 75°42'12.84"W, Boudreault, Goulet &Ferdandez, 28.VII–18.VIII.2016, MT (CNC) (collected subsequent to study, not included in diagnosis and description, no specimen ID assigned). **USA:** Kentucky: female, Owen County, Herndorn Farm, Hym Institute, 22.06–08.07.2009 (CNC) (OFo31). New Jersey: 11 females, one ? sex, Camden County, Merchantville, leg. H.A. Hespenheide, 1969 (CNC) (OFo19-30). Virginia: five females, Clarke County, Univ. Va. Blandy Exptl. Farm 2 miD Boyce, leg. D.R. Smith, 17.–30.06.1993, 01.–14.07.1993, 25.06–05.07.1994 and 25.07.–08.08.1995 (CNC) (OFo14-18).

Biology. Hosts: Buprestidae (*Agrilus* sp., *A. graminis*, *A. suvorovi*, *A. viridis*, *Capnodis* sp.), Cleridae (*Tillus unifaciatus*), Ptinidae (*Ptinus germanus*), Scolytinae (*Hylesinus* sp.); Plant associates: Fabaceae (*Robinia* sp.). The host and associates records are taken from Noyes (2017) (and references therein) and are not verified.

Distribution. Southern and Central Europe, northernmost location in Germany, Rhineland-Palatinate, representing first record from Germany; Russia. Introduced to the eastern United States (Kentucky, Virginia, New Jersey) and recently found in eastern Canada (Ontario).

Taxonomic remarks. Comparison of the female holotype (examined from images) and the male paratype of *O. monstrum* (Figs 4c, 7c, 10c, 13c, 16c) with the holotype of *O. formosa* indicates the specimens are conspecific, resulting in the new synonymy of *O. monstrum* under *O. formosa*. The characters used by Nikol'skaja (1952) to separate *O. monstrum* and *O. formosa* (as *O. bestia*) cannot be confirmed as valid. The first diagnostic character used to differentiate *O. monstrum* from *O.*

Figure 7. Head (frontal) III **a** *O. magnifica* (Risbec) (imaged specimen: OMag01, holotype) **b** *O. mkomaziensis* sp. n. (OMk01, holotype) **c** *O. monstrum* syn. n. (OFo12, paratype) **d** *O. namibiensis* sp. n. (ONa01, holotype) **e** *O. niehuisorum* sp. n. (ONi01, holotype) **f** *O. pumilae* Yang (OPu01, paratype) **g** *O. regiae* Yang (ORe01, paratype) **h** *O. srilankiensis* sp. n. (OSr01, holotype) **i** *O. tenuicollis* (Walker) (OTe01, holotype). Scale bars: 1 mm.

formosa was "pedicel length of first funicular segment" (interpreted as pedicel being as long as first funicular segment) versus "pedicel slightly longer than first funicular segment". This variation is characteristic of almost all *Oodera* species. The second character, "ovipositor shorter than first hind tarsal segment" versus "equal in length to first hind tarsal segment" is equally variable in *O. formosa*. Other differences between the two putative species included colour differences of the body, metasoma, antennae and legs. We found the rather slight differences in colouration to be within the variation of what we interpret as *O. formosa*. In general, differences in intensity or hue of colour, especially in the weaker sclerotised parts such as legs, antennae, and metasoma, are mostly unsuitable to differentiate between species in

Figure 8. Head (lateral) I **a** *O. ahoma* (Mani & Kaul) (imaged specimen: OAh01, holotype) **b** *O. circularicollis* sp. n. (OCi01, holotype) **c** *O. felix* sp. n. (OFe01, holotype) **d** *O. fidelis* sp. n. (OFi01, holotype) **e** *O. florea* sp. n. (OFl01, holotype) **f** *O. formosa* (Giraud) (OFo06). Scale bars: 1 mm.

Chalcidoidea (e.g., Peters and Baur 2011), though differences in colour pattern of different structures can be important. Bouček (1958) provided some more characters to differentiate *O. monstrum*, which he considered a valid species, and *O. formosa*. These differences, mainly of the surface sculpture of the head and mesoscutellum are accurate when examining the respective type specimens. However, we consider the differences to constitute intraspecific variation when taking into account all specimens we include in *O. formosa*. In all additional diagnostic characters we use in this revision, there is no difference between *O. monstrum* and *O. formosa*. The synonymy of *O. bestia* Nikol'skaja, 1952 under *O. formosa* by Bouček (1958) is confirmed after examination of one of the syntypes.

The specimens from North America were assumed to be *O. formosa* by Gibson (2003). Our examination of a number of specimens from North America and comparison with European *O. formosa*, including the holotype, revealed that the North American specimens are in fact introduced *O. formosa*.

In general, we found distinguishing *O. formosa* from many other species of *Oodera* to be rather difficult. This is mainly due to the fact that *O. formosa* is the only species of *Oodera* represented by a significant number of specimens from several series (except for *O. longicollis* (Cameron) which is, however, very easily distinguished from all other *Oodera* species). The specimens show intraspecific variation that can be quite staggering for some characters. Only examination of this larger series allowed us to recognise the variation as intraspecific. For many other species, only single or a few specimens were available or (small) uniform series that originate from the same host or region. The variation of *O. formosa* is reflected in several diagnostic characters for which we add the term "usually" if the vast majority of examined specimens exhibits this character but a minority does not. We made these additions (also in the diagnoses of few other species) to make diagnoses and key more easily applicable for the reader. With a combination of characters, *O. formosa* is well separated from all other species.

***Oodera gracilis* Westwood, 1874**

Figs 3a, 6a, 9a, 12a, 15a

Oodera gracilis Westwood, 1874: 145.

Diagnosis. FEMALE (N = 1). Large-sized (17.00 mm). Head and mesosoma bright dark blue and green-blue with blackish parts. Fore wing partly infumate. Body slender (mesonotum 1.45× as long as wide). Head elongated (1.67× as high as long). Eyes large (0.60× as high as head) (Fig. 9a). Corona thick (3.32× as long as wide), structure three- to four-part (Fig. 6a). Pronotum oval and longer than wide, with broadest part at midlength (Fig. 12a). Mesoscutellum slender (0.82× as long as wide), anterior margin convex (part anterior to imaginary transverse line connecting posterior margins of axillae more than 1/3 of mesoscutellum length; 0.37), mesoscutellum completely rugose without clear structure, medial part shiny (Fig. 15a). Propodeum medium (0.08× as long as mesoscutum) (Fig. 15a). Profemur elongated (2.31× as long as wide). Marginal vein short (0.67× as long as postmarginal vein). Metasoma long (0.56× as long as body). Ovipositor very long (1.16× as long as metasoma) (Fig. 3a).

Redescription. FEMALE. *Colour* (Figs 3a, 6a, 9a, 12a, 15a). Scape with first half yellow and second half dark brown, rest of antenna dark brown. Procoxa and profemur blue, middle leg completely black, hind leg black with proximal 4/5 of femur orange. Metasoma black and blue.

Head (Figs 6a, 9a). Face transversely striate from parascrobal area at lower third of eye height to clypeus margin. Head width to length not available. Head width to eye distance not available. Malar space 0.40× head height. Corona 0.60× as long as eye height. POL 0.77× OOL. Scape 2.90× as long as pedicel. Clava length to funicle length not available. Flagellum length to head width not available.

Mesosoma (Figs 12a, 15a). Pronotum 0.86× as long as wide. Pronotum 0.42× as long as mesonotum. Mesonotum 1.43× as long as mesoscutum. Mesoscutum 1.02× as long as wide. Mesoscutellum 0.43× as long as mesoscutum. Profemur 1.30× as long as protibia.

Wings (Fig. 3a). Fore wing 3.27× as long as wide. Costal cell 0.39× as long as fore wing. Marginal vein 0.16× as long as fore wing. Marginal vein 3.50× as long as stigmal vein. Postmarginal vein 5.25× as long as stigmal vein.

MALE. Unknown.

Material examined. ASIA. **Indonesia** (North Sulawesi): female, Indonesia, Sulawesi Utara, Dumoga-Bone N.P., leg. G. Else, 09.06.1985, det. Z. Bouček (compared with holotype in Oxford Museum) (BMNH) (OGr01).

Biology. Unknown.

Distribution. Indonesia (Sulawesi), West Papua.

Taxonomic remarks. We did not examine the type (described from West Papua). However, the uniqueness of the species and the fact that we examined a specimen compared to the type by Bouček allow us to include this species in the taxonomic revision.

***Oodera heikewernerae* sp. n.**
http://zoobank.org/CB445D43-EB36-4A23-BF8B-88F7325FF125
Figs 3b, 6b, 9b, 12b, 15b

Diagnosis. BOTH SEXES (N = 12). Head and mesosoma mostly blackish with blue and coppery parts. Fore wing hyaline. Body robust to medium (mesonotum 1.22–1.40× as long as wide). Head usually oval (1.45–1.65× as high as long, with only 3 of 12 with head elongated). Eyes small to large (0.58–0.67× as high as head) (Fig. 9b). Corona thick to medium (3.80–5.33× as long as wide), structure continuous (Fig. 6b). Pronotum pentagonal with posterior part distinctly narrowing towards mesoscutum, with broadest part before midlength (Fig. 12b). Mesoscutellum normal to slender (0.58–0.77× as long as wide), anterior margin usually convex (part anterior to imaginary transverse line connecting posterior margins of axillae more than 1/3 of mesoscutellum length; 0.26–0.47, with only 2 of 12 with anterior margin hardly convex), mesoscutellum completely densely lineate (Fig. 15b). Propodeum small to medium (0.05–0.14× as long as mesoscutum) (Fig. 15b). Marginal vein usually medium (0.83–1.06× as long as postmarginal vein, with only 1 of 12 with short marginal vein).

FEMALE. Small-sized (5.31–6.64 mm). Profemur robust to medium (1.71–2.04× as long as wide). Metasoma short to medium (0.39–0.47× as long as body). Ovipositor short to rather long (0.12–0.18× as long as metasoma) (Fig. 3b).

MALE. Body length not available. Profemur elongated (2.29× as long as wide).

Description. BOTH SEXES. *Colour* (Figs 3b, 6b, 9b, 12b, 15b). Scape yellow, darkening apically, rest of antenna dark brown. Procoxa and profemur black with tinge of blue, all other parts of legs yellow to brown. Metasoma brown.

Figure 9. Head (lateral) II **a** *O. gracilis* Westwood (imaged specimen: OGr01) **b** *O. heikewernerae* sp. n. (OHe01, holotype) **c** *O. hoggarensis* Hedqvist (OHo02, paratype) **d** *O. leibnizi* sp. n. (OLe03, paratype) **e** *O. longicollis* (Cameron) (OLo01) **f** *O. madegassa* Bouček (OMad01, holotype). Scale bars: 1 mm.

Head (Figs 6b, 9b). Face completely reticulate. Head 1.45–1.75× as wide as long. Head width 3.13–4.00× eye distance. Malar space 0.34–0.42× head height. Corona 0.53–0.67× as long as eye height. POL 0.75–1.6× OOL. Scape 2.33–3.32× as long as pedicel. Clava 0.13–0.20× as long as funicle. Flagellum 1.3–1.51× as long as head width.

Mesosoma (Figs 12b, 15b). Pronotum 0.77–1.07× as long as wide. Pronotum 0.50–0.59× as long as mesonotum. Mesonotum 1.33–1.46× as long as mesoscutum. Mesoscutum 0.87–1.05× as long as wide. Mesoscutellum 0.33–0.46× as long as mesoscutum. Profemur 1.17–1.4× as long as protibia.

Wings (Fig. 3b). Fore wing 2.67–3.52× as long as wide. Costal cell 0.31–0.4× as long as fore wing. Marginal vein 0.15–0.20× as long as fore wing. Marginal vein 2.5–4.00× as long as stigmal vein. Postmarginal vein 2.67–4.21× as long as stigmal vein.

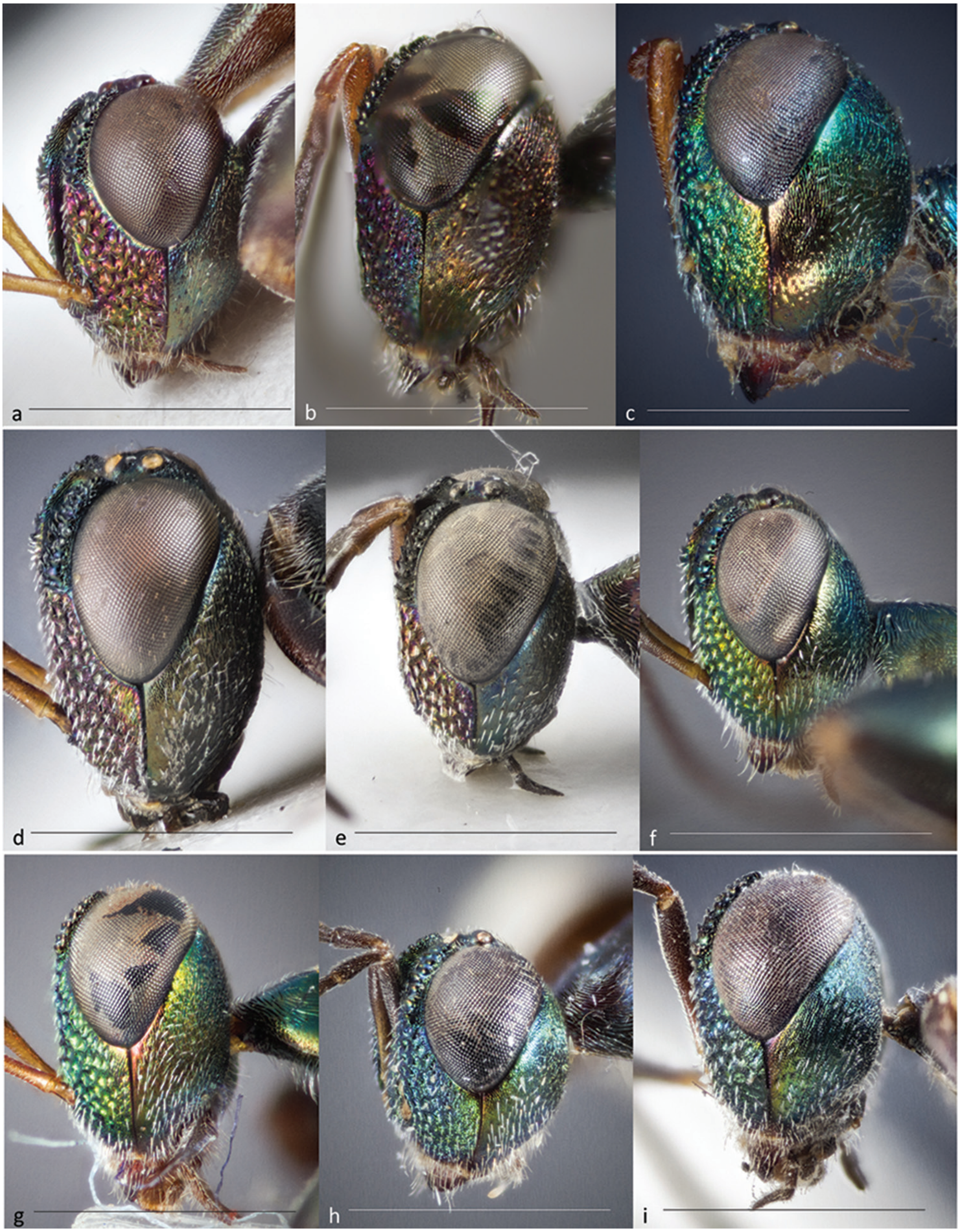

Figure 10. Head (lateral) III **a** *O. magnifica* (Risbec) (imaged specimen: OMag01, holotype) **b** *O. mkomaziensis* sp. n. (OMk01, holotype) **c** *O. monstrum* syn. n. (OFo12, paratype) **d** *O. namibiensis* sp. n. (ONa01, holotype) **e** *O. niehuisorum* sp. n. (ONi01, holotype) **f** *O. pumilae* Yang (OPu01, paratype) **g** *O. regiae* Yang (ORe01, paratype) **h** *O. srilankiensis* sp. n. (OSr01, holotype) **i** *O. tenuicollis* (Walker) (OTe01, holotype). Scale bars: 1 mm.

Material examined. AFRICA. **Botswana**: female holotype, Serowe, Farmer's Brigade, leg. P. Forchhammer, MT, XII. 1987 (CNC) (OHe01); three female paratypes, Serowe, Farmer's Brigade, leg. P. Forchhammer, MT, XII. 1992 (CNC) (OHe03-04), (ZFMK) (OHe09); female paratype, Serowe, Farmer's Brigade, leg. P. Forchhammer, MT, I. 1993 (CNC) (OHe08); female paratype, Serowe, Farmer's Brigade, leg. P. Forchhammer, MT, XII. 1987 (CNC) (OHe10); female paratype, Botswana (B9) Lake Ngami 2900 12 m. NE Sehitwa, 17.04.1972 (NMP) (OHe11); **Republic of South Africa**: male paratype, E. Transvaal 15km NW Klaserie Guernsey Farm M. FITs, Woodland, leg. S. & J. Peck, 19–31.07.1985 (CNC) (OHe02); female paratype, E. Transvaal, 15km NW Klaserie, Guernsey Farm, M. FITs, leg. W. Mason, 19–31.12.1985 (CNC) (OHe05); female paratype, Cape Prov. Roaring Sands Resort nr. Witsand, leg. J. Londt, 17–18.08.1982 (CNC) (OHe06); female paratype, E. Transvaal, 15km NW Klaserie, yellow, leg. M. Sandborne, 19–31.12.1985 (CNC) (OHe07); female paratype, Natal. Weenen., H.P. Thomasset, 11.1925–3.1929 (NMP) (OHe12).

Biology. Unknown.

Distribution. Botswana and South Africa.

Etymology. Named in memory of Heike Werner, the mother of the first author, who sadly passed away during completion of this revision.

Oodera hoggarensis **Hedqvist, 1967**

Figs 3c, 6c, 9c, 12c, 15c

Oodera hoggarensis Hedqvist, 1967: 186

Diagnosis. FEMALE (N = 2). Exact body length not available (both specimens are fragmented), roughly small-sized. Head and mesosoma blackish with light green, purple and yellow parts. Fore wing hyaline. Body robust (mesonotum 1.16–1.2× as long as wide). Head oval (1.52–1.54× as high as long). Eyes small to large (0.59–0.64× as high as head) (Fig. 9c). Corona thick (4.10–4.75× as long as wide), structure continuous (Fig. 6c). Pronotum pentagonal with posterior part distinctly narrowing towards mesoscutum, with broadest part at midlength (Fig. 12c). Mesoscutellum normal (0.55–0.57× as long as wide), anterior margin hardly convex (part anterior to imaginary transverse line connecting posterior margins of axillae less than 1/3 of mesoscutellum length; 0.28–0.29), lineate in anterior two thirds, rugulose in posterior third (Fig. 15c). Propodeum medium to large (0.14–0.18× as long as mesoscutum) (Fig. 15c). Profemur robust (1.79–1.97× as long as wide). Marginal vein short (0.86–0.88× as long as postmarginal vein). Metasoma length not available. Ovipositor short (0.14× as long as metasoma) (Fig. 3c).

Redescription. FEMALE. *Colour* (Figs 3c, 6c, 9c, 12c, 15c). Scape and pedicel yellow, rest of antenna dark brown. Procoxa dark green, profemur dark green and yellow, all other parts of legs yellow, except for tarsi brown. Metasoma dark brown, with lateral green regions on tergites 3 and 4.

Head (Figs 6c, 9c). Face completely reticulate. Head 1.46–1.52× as wide as long. Head width 3.52× eye distance. Malar space 0.35–0.41× head height. Corona 0.63–0.69× as long as eye height. POL 1.20× OOL. Scape 2.73–2.81× as long as pedicel. Clava length to funicle length not available. Flagellum length to head width not available.

Mesosoma (Figs 12c, 15c). Pronotum 0.88× as long as wide. Pronotum 0.59× as long as mesonotum. Mesonotum 1.40–1.46× as long as mesoscutum. Mesoscutum 0.80–0.86× as long as wide. Mesoscutellum 0.40–0.46× as long as mesoscutum. Profemur 1.23–1.33× as long as protibia.

Wings (Fig. 3c). Fore wing 2.83–3.13× as long as wide. Costal cell 0.34–0.36× as long as fore wing. Marginal vein 0.18–0.19× as long as fore wing. Marginal vein 2.82–3.29× as long as stigmal vein. Postmarginal vein 3.29–3.76× as long as stigmal vein.

MALE. Unknown.

Material examined. AFRICA. **Algeria:** female holotype, Timesdelssine, Hoggar, leg. J. Mateu, 23.05.1962, det. K-J. Hedqvist (1966) (MHNG) (OHo01); female paratype, Qued Teredjine, Hoggar Sahara, leg. J. Mateu, 15.05.1965, det. K-J Hedqvist (1966) (BMNH) (OHo02).

Biology. Noyes (2017) lists an association with *Acacia* sp. This association with *Acacia* trees is unverified and likely refers to *O. hoggarensis* hosts reared from *Acacia*.

Distribution. Algeria (Hoggar Mountains).

Taxonomic remarks. The species description of *O. hoggarensis* by Hedqvist (1967) includes a detailed characterisation of the colour of the different body parts, but only few measurements, shape or structure information. Accordingly, we provide a redescription and diagnosis with more character ratios that are necessary to differentiate all *Oodera* species.

Oodera leibnizi **sp. n.**

http://zoobank.org/849CBD26-ACFF-428A-A0C4-AFE627C78F99

Figs 3d, 6d, 9d, 12d, 15d

Diagnosis. BOTH SEXES (N = 4). Small-sized (5.31–6.06 mm). Head and mesosoma dark green to blue-green. Fore wing partly weakly infumate. Body robust to medium (mesonotum 1.34–1.42× as long as wide). Head round (1.29–1.42× as high as long). Eyes large (0.60–0.66× as high as head) (Fig. 9d). Corona structure three- to four-part (Fig. 6d). Pronotum pentagonal with posterior part distinctly narrowing towards mesoscutum, with broadest part before midlength (Fig. 12d). Mesoscutellum normal to slender (0.69–0.83× as long as wide), anterior margin hardly convex (part anterior to imaginary transverse line connecting posterior margins of axillae less than or exactly 1/3 of mesoscutellum length; 0.26–0.33), mesoscutellum lineate in anterior two thirds, rugose in posterior third (Fig. 15d). Propodeum medium to large (0.14–0.24× as long as mesoscutum) (Fig. 15d). Profemur usually elongated (2.02–2.43× as long as wide, with only 1 of 4 with profemur medium). Marginal vein long (1.21–1.27× as long as postmarginal vein).

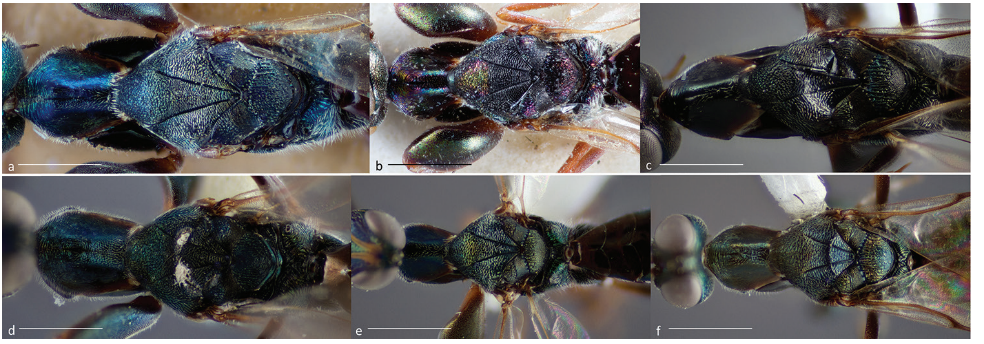

Figure 11. Mesosoma (dorsal) I **a** *O. ahoma* (Mani & Kaul) (imaged specimen: OAh01, holotype) **b** *O. circularicollis* sp. n. (OCi01, holotype), **c** *O. felix* sp. n. (OFe01, holotype) **d** *O. fidelis* sp. n. (OFi01, holotype) **e** *O. florea* sp. n. (OFl01, holotype) **f** *O. formosa* (Giraud) (OFo03). Scale bars: 1 mm.

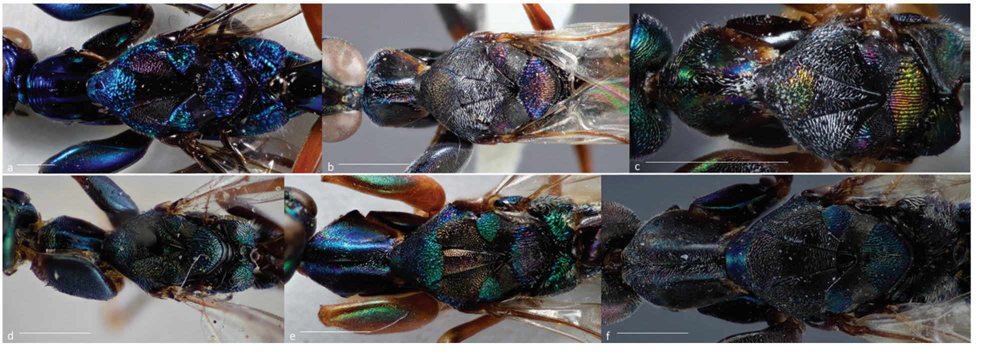

Figure 12. Mesosoma (dorsal) II **a** *O. gracilis* Westwood (imaged specimen: OGr01) **b** *O. heikewernerae* sp. n. (OHe01, holotype) **c** *O. hoggarensis* Hedqvist (OHo02, paratype) **d** *O. leibnizi* sp. n. (OLe01, holotype) **e** *O. longicollis* (Cameron) (OLo01) **f** *O. madegassa* Bouček (OMad01, holotype). Scale bars: 1 mm.

FEMALE. Corona thick (3.64–4.00× as long as wide). Metasoma short (0.45–0.45× as long as body). Ovipositor short (0.08–0.10× as long as metasoma) (Fig. 3d).

MALE. Corona medium (4.36× as long as wide).

Description. BOTH SEXES. *Colour* (Figs 3d, 6d, 9d, 12d, 15d). Antenna dark brown. Procoxa and profemur light to dark green, all other parts of legs dark brown, except for yellow last tarsal segments. Metasoma dark brown.

Head (Figs 6d, 9d). Face completely reticulate. Head 1.24–1.42× as wide as long. Head width 3.28–3.63× eye distance. Malar space 0.34–0.41× head height. Corona 0.52–0.59× as long as eye height. POL 1.00–1.67× OOL. Scape 2.48–2.63× as long as pedicel. Clava 0.21× as long as funicle. Flagellum 1.34× as long as head width.

Mesosoma (Figs 12d, 15d). Pronotum 0.99–1.00× as long as wide. Pronotum 0.95–1.11× as long as mesonotum. Mesonotum 1.40–1.50× as long as mesoscutum. Mesoscutum 0.91–0.96× as long as wide. Mesoscutellum 0.40–0.50× as long as mesoscutum. Profemur 1.29–1.47× as long as protibia.

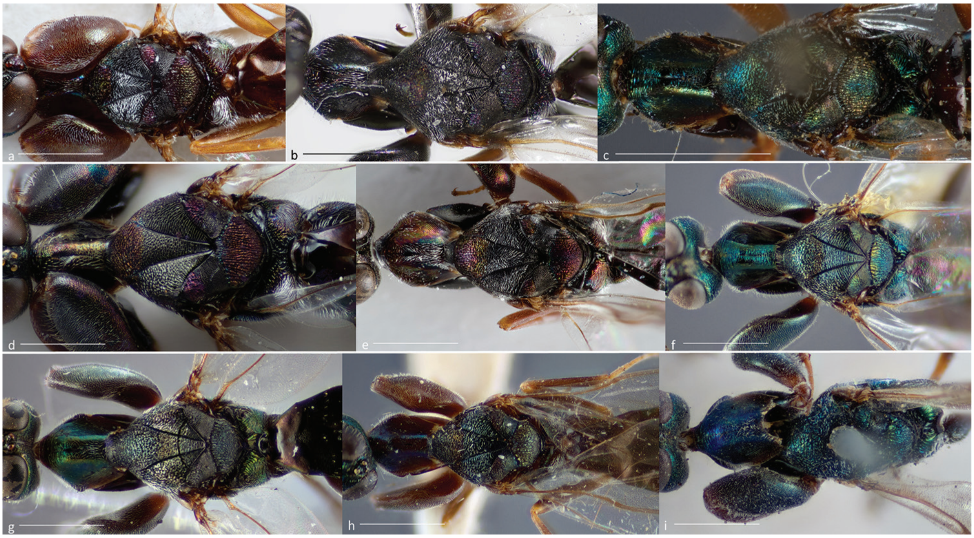

Figure 13. Mesosoma (dorsal) III **a** *O. magnifica* (Risbec) (imaged specimen: OMag01, holotype) **b** *O. mkomaziensis* sp. n. (OMk01, holotype) **c** *O. monstrum* syn. n. (OFo12, paratype) **d** *O. namibiensis* sp. n. (ONa01, holotype) **e** *O. niehuisorum* sp. n. (ONi01, holotype) **f** *O. pumilae* Yang (OPu01, paratype) **g** *O. regiae* Yang (ORe01, paratype) **h** *O. srilankiensis* sp. n. (OSr01, holotype) **i** *O. tenuicollis* (Walker) (OTe01, holotype). Scale bars: 1 mm.

Wings (Fig. 3d). Fore wing 2.99–3.78× as long as wide. Costal cell 0.37–0.39× as long as fore wing. Marginal vein 0.18–0.20× as long as fore wing. Marginal vein 2.72–3.17× as long as stigmal vein. Postmarginal vein 2.24–2.53× as long as stigmal vein.

Material examined. ASIA. **Philippines**: female holotype, S.O. Luzon, determined as *O. ornata* by anonymous (BMNH) (OLe01); **Malaysia**: female paratype, Perak, leg. K. Staudinger, identified as *Oodera* by Bouček, later as *O. ornata* by anonymous (BMNH) (OLe02); **Papua New Guinea**: male paratype, Bulolo, Manki, leg. H. Roberts, 30.07.1981, identified as *O. gracilis* by Bouček (1984), crossed out by anonymous (BMNH) (OLe03); male paratype, Bulolo, Manki, leg. H. Roberts, 30.07.1981 (BMNH) (OLe04).

Biology. Unknown.

Distribution. Malaysia, Philippines (both Oriental part of Asia), Papua New Guinea (Australasian part of Asia).

Etymology. Named in honour of Gottfried Wilhelm Leibniz (1646–1716) on the occasion of his 300th death day. The Zoologisches Forschungsmuseum Alexander Koenig in which this study was done is part of the Leibniz Association, named after Leibniz.

Taxonomic remarks. The two specimens from Malaysia and the Philippines were originally identified as *O. ornata* (valid species name *O. longicollis*), one of the specimens from Papua New Guinea was identified by Bouček as *O. gracilis* in 1984, later crossed out by an unknown person. The new species is rather easily distinguished from *O. longicollis* and *O. gracilis*, as *O. longicollis* and *O. gracilis* exhibit exceptionally long ovipositors and bright metallic colours on head and mesosoma while *O. leibnizi* sp. n. does not.

***Oodera longicollis* (Cameron, 1903)**
Figs 3e, 6e, 9e, 12e, 15e

Epistenia longicollis Cameron, 1903: 98.
Oodera longicollis; Hedqvist 1961: 97.
Oodera ornata Gahan, 1925: 97. Synonymy with *Oodera longicollis* and lectotype designation by Bouček et al. (1978: 448–449).

Diagnosis. BOTH SEXES (N = 14). Head and mesosoma bright green to blue and blackish. Fore wing partly infumate. Body robust to slender (mesonotum 1.28–1.45× as long as wide). Head oval to elongated (1.57–1.72× as high as long). Eyes large (0.60–0.65× as high as head) (Fig. 9e). Corona medium to slim (5.33–7.38× as long as wide), structure square (Fig. 6e). Pronotum pentagonal with posterior part distinctly narrowing towards mesoscutum, with broadest part at midlength (Fig. 12e). Mesoscutellum normal to slender (0.68–0.80× as long as wide), anterior margin usually convex (part anterior to imaginary transverse line connecting posterior margins of axillae more than 1/3 of mesoscutellum length; 0.29–0.45, with only 3 of 13 with anterior margin hardly convex), mesoscutellum completely lineate, with median lines converging (Fig. 15e). Profemur usually elongated (2.14–2.58× as long as wide, with only 1 of 14 with profemur medium). Marginal vein medium to long (1.05–1.18× as long as postmarginal vein).

FEMALE. Medium- to large-sized (8.80–12.60 mm). Propodeum medium to large (0.12–0.22× as long as mesoscutum) (Fig. 15e). Metasoma short to long (0.44–0.54× as long as body). Ovipositor long (0.26–035× as long as metasoma) (Fig. 3e).

MALE. Small- to medium-sized (5.38–9.6 mm). Propodeum very large (0.26 to 0.34× as long as mesoscutum).

Redescription. BOTH SEXES. *Colour* (Figs 3e, 6e, 9e, 12e, 15e). Scape green, rest of antenna dark brown. Procoxa yellow, profemur yellow and green, all other parts of legs irregularly dark brown and yellow. Metasoma dark brown.

Head (Figs 6e, 9e). Face transversely striate from parascrobal area at lower third of eye height to clypeus margin. Head 1.59–1.79× as wide as long. Head width 4.00–5.19× eye distance. Malar space 0.34–0.40× head height. Corona 0.52–0.59× as long as eye height. POL 1.0–1.67× OOL. Scape 1.69–2.78× as long as pedicel. Clava 0.10–0.25× as long as funicle. Flagellum 1.31–1.85× as long as head width.

Mesosoma (Figs 12e, 15e). Pronotum 0.95–1.11× as long as wide. Pronotum 0.52–0.69× as long as mesonotum. Mesonotum 1.36–1.47× as long as mesoscutum. Mesoscutum 0.92–1.05× as long as wide. Mesoscutellum 0.36–0.48× as long as mesoscutum. Profemur 1.25–1.50× as long as protibia.

Wings (Fig. 3e). Fore wing 2.85–3.78× as long as wide. Costal cell 0.33–0.38× as long as fore wing. Marginal vein 0.19–0.21× as long as fore wing. Marginal vein 2.98–4.19× as long as stigmal vein. Postmarginal vein 2.60–3.70× as long as stigmal vein.

Material examined. ASIA. **China**: female, Matang Rd, 18.05.1920, det. C. R. Vardy (1962) (BMNH) (OLo10); **Malaysia**: female, Sandakan, det. Z. Bouček (1980) (BMNH) (OLo01); female, Quop, Sarawak, leg. G.E. Bryant, 06.03.1914, det. Z. Bouček (1976) (BMNH) (OLo04); female, Perak, leg. K. Staudinger, det. Z. Bouček

(1976) (BMNH) (OLo05); female, Bettotan near Sandakan, 20.08.1927, det. Z. Bouček (1976) (BMNH) (OLo09); female, Perak, det. Z. Bouček (1960) as *Oodera* sp., later as *O. ornata* by anonymous (BMNH) (OLo13); male, Negeri, Sembilan Pasoh Forest, leg. E. Jendek & O. Sausa, 10–21.06.2013 (CNC) (OLo02); **Myanmar**: ? sex, Burma, Bilumyo Res., Mytikyina, leg. D.J. Atkinson, 31.05.1928, det. Z. Bouček (1976) (BMNH) (OLo06); male, Manymar, Yeni Res. Pyinmana, leg. D.H. Desai, 29.06.1934, det. Z. Bouček (1980) (BMNH) (OLo07); **Philippines**: female holotype *O. ornata*, Davao on Island Mindanao, leg. Baker (examined from images provided by the USNM, http://usnmhymtypes.com/default.asp?Action=Show_Types&Single_Type=True&TypeID=7233, accessed 20/01/2017); female, Davao in Island Mindanao, leg. Baker, det. Ch. Ferriere as *O. ornata* (BMNH) (OLo03); female, Surigao, Mindanao, det. as *O. ornata* by anonymous (BMNH) (OLo11); male, Island of Basilan, det. as *O. ornata* by anonymous (BMNH) (OLo12); **Vietnam**: male, Tonkin, Hoabinh, leg. R.V.de Salvaza, 8.1918, det. Ch. Ferriere as *Heydenia longicollis*, second location label says “Indo China” (BMNH) (OLo08).

Biology. Associated with teak (*Tectona grandis*) (Verbenaceae), presumably as habitat for the parasitoids’ host (unverified record taken from Noyes (2017)).

Distribution. China (Oriental part), Malaysia, Myanmar, Philippines, Vietnam.

Taxonomic remarks. *Oodera ornata* was synonymised with *O. longicollis* by Bouček et al. (1978); this was confirmed by us after examining the images of *O. ornata* available online (for exact reference see examined material).

Gahan (1925) compared *O. ornata* and *O. gracilis* and declared them similar, except for the different ovipositor lengths and some colour differences (*O. ornata* “can be distinguished from that species [*Oodera gracilis*] at once by the much shorter ovipositor and the differently coloured legs“). After examining material of both species we found many more distinguishing characters (see diagnoses and key).

The species description of *O. ornata* by Gahan (1925: 97) points out that *O. ornata* (= *O. longicollis*) is a species of “rather variable size“. He characterised a specimen from Borneo as the smallest (body length: 7 mm) and a specimen from Mindanao (Phillipines) as the largest specimen (body length: 12 mm). We confirm the large size differences after examining the available material from various countries (smallest: 5.38 mm, largest: 12.6 mm). We see these large intraspecific size differences in both *Oodera* species for which we were able to examine a considerable number of specimens not originating from the same series and with both sexes available (i.e., *O. formosa* and *O. longicollis*). Comparable differences might also be found for other species of *Oodera* if more specimens are examined. Because of this we use body length in the diagnoses and key but avoid using it as an exclusive character. This still holds a certain risk that users of the key will have difficulties to identify specimens of extreme body length. However, we think that body length is such an obvious character that it should be mentioned in identification keys. If the key might fail in rare cases, all specimens should be assignable to a certain species with the diagnoses provided.

Note that we located one additional specimen in the Australian National Insect Collection in Canberra (ANIC). It originated from the same series as specimens already included here (from Philippines, Davao/Mindanao). *O. longicollis* is a well-defined species and we did not borrow and include this additional specimen.

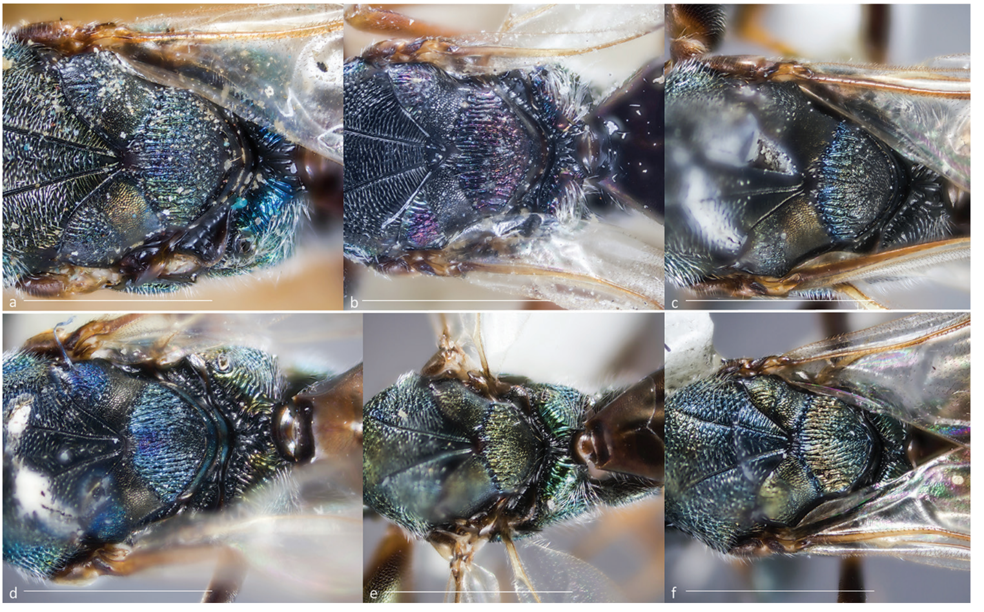

Figure 14. Mesoscutellum and propodeum (dorsal) I **a** *O. ahoma* (Mani & Kaul) (imaged specimen: OAh01, holotype) **b** *O. circularicollis* sp. n. (OCi01, holotype) **c** *O. felix* sp. n. (OFe01, holotype) **d** *O. fidelis* sp. n. (OFi01, holotype) **e** *O. florea* sp. n. (OFl01, holotype), **f** *O. formosa* (Giraud) (OFo14). Scale bars: 1 mm.

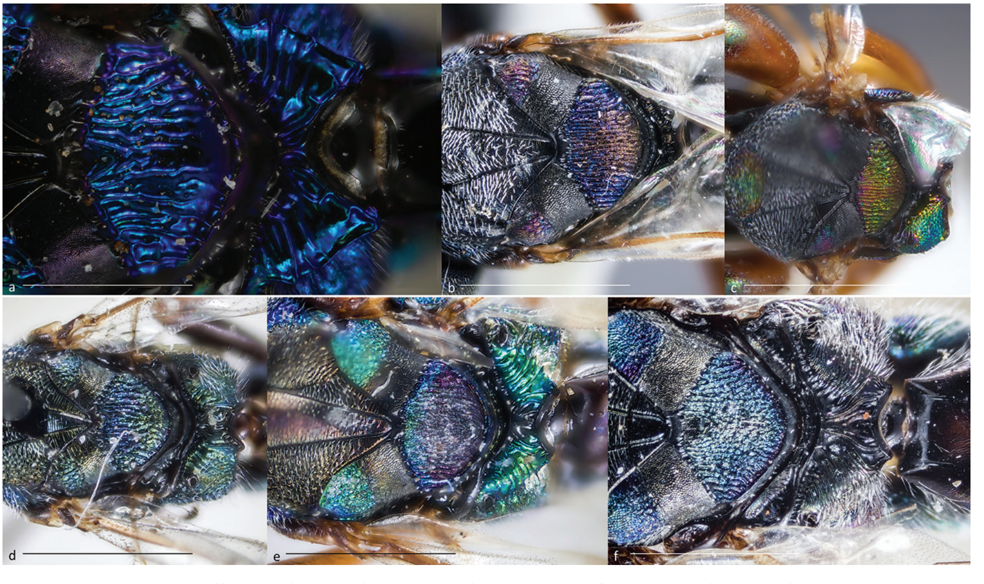

Figure 15. Mesoscutellum and propodeum (dorsal) II **a** *O. gracilis* Westwood (imaged specimen: OGr01) **b** *O. heikewernerae* sp. n. (OHe01, holotype) **c** *O. hoggarensis* Hedqvist (OHo02, paratype) **d** *O. leibnizi* sp. n. (OLe03, paratype) **e** *O. longicollis* (Cameron) (OLo01) **f** *O. madegassa* Bouček (OMad01, holotype). Scale bars: 1 mm.

***Oodera madegassa* Bouček, 1958**

Figs 3f, 6f, 9f, 12f, 15f

Oodera madegassa Bouček, 1958: 376.

Diagnosis. FEMALE (N = 1). Large-sized (10.30 mm). Head and mesosoma dark blue to blackish. Fore wing partly infumate. Body slender (mesonotum 1.52× as long as wide). Head elongated (1.77× as high as long). Eyes large (0.63× as high as head) (Fig. 9f). Eye distance very short, head width 7.09× eye distance. Corona slim (7.13× as long as wide), structure continuous (Fig. 6f). Pronotum oval and wider than long, with broadest part at midlength (Fig. 12f). Mesoscutellum slender (0.85× as long as wide), anterior margin convex (part anterior to imaginary transverse line connecting posterior margins of axillae more than 1/3 of mesoscutellum length; 0.44), mesoscutellum almost lineate in anterior third, longitudinally rugose in posterior two thirds (Fig. 15f). Propodeum large (0.20× as long as mesoscutum) (Fig. 15f). Profemur elongated (2.38× as long as wide). Marginal vein long (1.19× as long as postmarginal vein). Metasoma medium (0.48× as long as body). Ovipositor rather long (0.17× as long as metasoma) (Fig. 3f).

Redescription. FEMALE. *Colour* (Figs 3f, 6f, 9f, 12f, 15f). Scape brown, slightly brightening apically, rest of antenna dark brown. Procoxa dark blue to blackish, profemur dark brown, all other parts of legs brown. Metasoma black, with greenish spots laterally on tergites 2 to 5.

Head (Figs 6f, 9f). Face completely reticulate. Head 1.86× as wide as long. Head width 7.09× eye distance. Malar space 0.38× head height. Corona 0.61× as long as eye height. POL 2× OOL. Scape length not available. Clava 0.10× as long as funicle. Flagellum 1.53× as long as head width.

Mesosoma (Figs 12f, 15f). Pronotum 0.95× as long as wide. Pronotum 0.51× as long as mesonotum. Mesonotum 1.43× as long as mesoscutum. Mesoscutum 1.06× as long as wide. Mesoscutellum 0.43× as long as mesoscutum. Profemur 1.33× as long as protibia.

Wings (Fig. 3f). Fore wing 3.40× as long as wide. Costal cell 0.35× as long as fore wing. Marginal vein 0.22× as long as fore wing. Marginal vein 4.41× as long as stigmal vein. Postmarginal vein 3.70× as long as stigmal vein.

MALE. Unknown.

Material examined. AFRICA. **Madagascar**: female holotype, Haute-Vallée de Sambirano, det. Z. Bouček (1958) (NMP) (OMad01).

Biology. Unknown.

Distribution. Madagascar.

***Oodera magnifica* (Risbec, 1951)**

Figs 4a, 7a, 10a, 13a, 16a

Stellophora magnifica Risbec, 1951: 239–243.
Oodera magnifica; Bouček 1958: 375.

Diagnosis. FEMALE (N = 1). Small-sized (5.75 mm). Head and mesosoma blackish, coppery and reddish. Fore wing partly infumate. Body robust (mesonotum 1.25× as long as wide). Head oval (1.51× as high as long). Eyes large (0.65× as high as head) (Fig. 10a). Corona medium (5.50× as long as wide), structure continuous (Fig. 7a). Pronotum shape not available (pronotum is partly covered by the legs) (Fig. 13a). Mesoscutellum normal (0.66× as long as wide), anterior margin hardly convex (part anterior to imaginary transverse line connecting posterior margins of axillae less than 1/3 of mesoscutellum length; 0.29), mesoscutellum completely rippledly lineate (Fig. 16a). Propodeum medium (0.15× as long as mesoscutum) (Fig. 16a). Profemur robust (1.90× as long as wide). Marginal vein medium (1.0× as long as postmarginal vein). Metasoma medium (0.47× as long as body). Ovipositor short (0.14× as long as metasoma) (Fig. 4a).

Redescription. FEMALE. *Colour* (Figs 4a, 7a, 10a, 13a, 16a). Scape yellow, darkening apically, rest of antenna brown. Procoxa and profemur dark brown, all other parts of legs yellow. Metasoma brown.

Head (Figs 7a, 10a). Face completely reticulate. Head 1.54× as wide as long. Head width 3.89× eye distance. Malar space 0.36× head height. Corona 0.66× as long as eye height. POL 1.20× OOL. Scape 2.60× as long as pedicel. Clava 0.16× as long as funicle. Flagellum 1.30× as long as head width.

Mesosoma (Figs 13a, 16a). Pronotum length to width not available. Mesonotum 1.44× as long as mesoscutum. Mesoscutum 0.87× as long as wide. Mesoscutellum 0.44× as long as mesoscutum. Profemur 1.34× as long as protibia.

Wings (Fig. 4a). Fore wing 2.59× as long as wide. Costal cell 0.36× as long as fore wing. Marginal vein 0.20× as long as fore wing. Marginal vein 3.16× as long as stigmal vein. Postmarginal vein 3.16× as long as stigmal vein.

MALE. Unknown.

Material examined. AFRICA. **Senegal**: female holotype, M'Bambey, leg. A. Wane, 13.11.1945, det. J.Y. Rasplus (1990) (MNHN) (OMag01).

Biology. Unknown.

Distribution. Senegal.

Taxonomic remarks. The description of *O. magnifica* by Risbec (1951) is very detailed but misses some characters that we found to be of diagnostic value. Therefore, our redescription should be considered an addition to Risbec's work and not a replacement.

Oodera mkomaziensis **sp. n.**

http://zoobank.org/E054C035-9265-46ED-910F-F6C038DC06A3

Figs 4b, 7b, 10b, 13b, 16b

Diagnosis. FEMALE (N = 1). Medium-sized (7.20 mm). Head and mesosoma black, with tinges of dark green and purple. Fore wing hyaline. Body slender (mesonotum 1.50× as long as wide). Head oval (1.56× as high as long). Eyes large (0.63× as high as head) (Fig. 10b). Corona thick (3.92× as long as wide), structure interrupted (Fig. 7b).

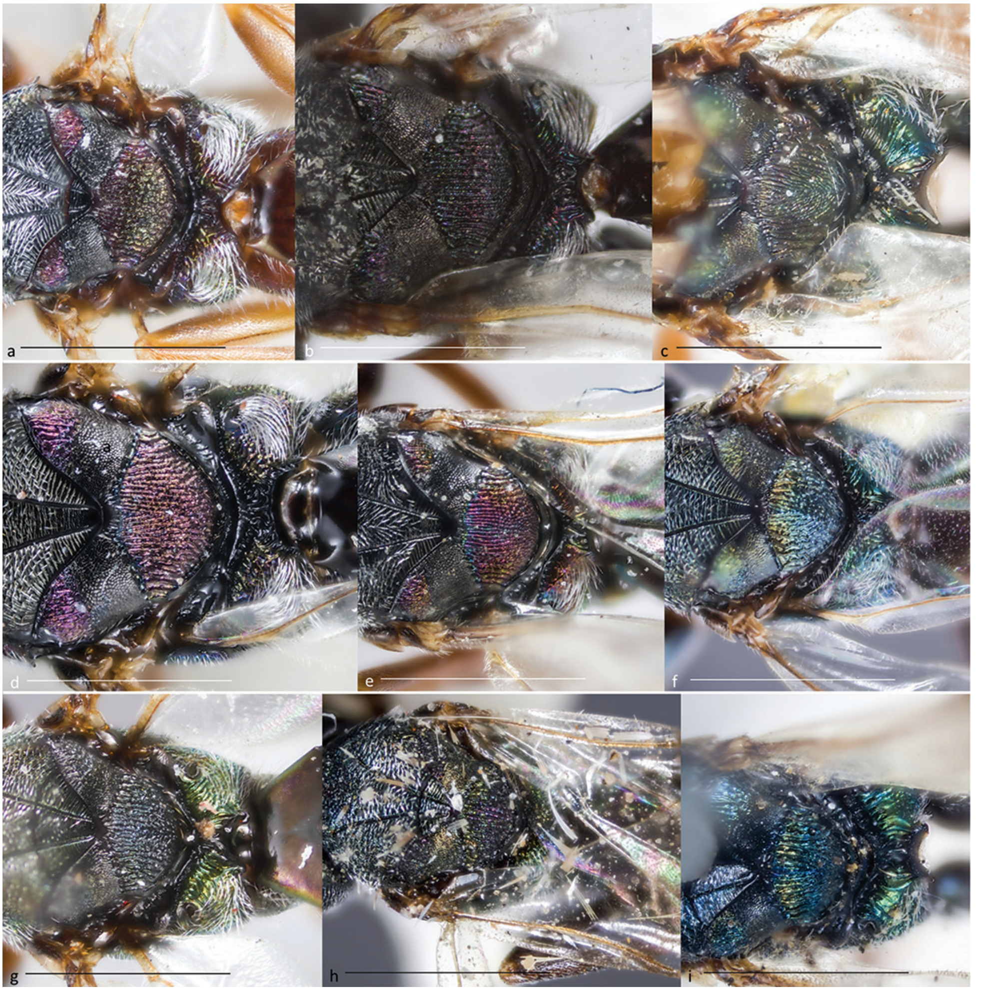

Figure 16. Mesoscutellum and propodeum (dorsal) III **a** *O. magnifica* (Risbec) (imaged specimen: OMag01, holotype) **b** *O. mkomaziensis* sp. n. (OMk01, holotype) **c** *O. monstrum* syn. n. (OFo12, paratype) **d** *O. namibiensis* sp. n. (ONa01, holotype) **e** *O. niehuisorum* sp. n. (ONi01, holotype) **f** *O. pumilae* Yang (OPu01, paratype) **g** *O. regiae* Yang (ORe01, paratype) **h** *O. srilankiensis* sp. n. (OSr01, holotype) **i** *O. tenuicollis* (Walker) (OTe01, holotype). Scale bars: 1 mm.

Pronotum oval, with broadest part at midlength (Fig. 13b). Mesoscutellum normal to slender (0.68× as long as wide), anterior margin convex (part anterior to imaginary transverse line connecting posterior margins of axillae 1/3 of mesoscutellum length; 0.33), mesoscutellum lineate in anterior two thirds, finely areolate in posterior third (Fig. 16b). Propodeum medium (0.09× as long as mesoscutum) (Fig. 16b). Profemur robust (1.31× as long as wide). Marginal vein short (0.85× as long as postmarginal vein). Metasoma long (0.52× as long as body). Ovipositor short (0.14× as long as metasoma) (Fig. 4b).

Redescription. FEMALE. *Colour* (Figs 4b, 7b, 10b, 13b, 16b). Scape and pedicel light brown, rest of antenna dark brown. Procoxa and profemur black, all other parts of legs yellow to brown. Metasoma black.

Head (Figs 7b, 10b). Face completely reticulate. Head 2.21× as wide as long. Head width 4.13× eye distance. Malar space 0.37× head height. Corona 0.73× as long as eye height. POL 1.33× OOL. Scape 3.19× as long as pedicel. Clava 0.11× as long as funicle. Flagellum 1.39× as long as head width.

Mesosoma (Figs 13b, 16b). Pronotum 0.80× as long as wide. Pronotum 0.41× as long as mesonotum. Mesonotum 1.50× as long as mesoscutum. Mesoscutum 1.11× as long as wide. Mesoscutellum 0.68× as long as mesoscutum. Profemur 1.21× as long as protibia.

Wings (Fig. 4b). Fore wing 2.78× as long as wide. Costal cell 0.36× as long as fore wing. Marginal vein 0.19× as long as fore wing. Marginal vein 3.40 as long as stigmal vein. Postmarginal vein 4.00× as long as stigmal vein.

MALE. Unknown.

Material examined. AFRICA. **Tanzania**: female, Mkomazi Game Reserve (now Mkomazi National Park), Ibaya Hill, 3°58.40'S 37°47.13'E, leg. S. van Noort, 15.–30.04.1996 (SAM) (OMk01)

Biology. Unknown.

Distribution. Tanzania.

Etymology. Named after the type locality, the Mkomazi National Park in north-eastern Tanzania.

Oodera namibiensis **sp. n.**

http://zoobank.org/409663D3-3FE9-4E0B-A020-A6DBBB72EF9E

Figs 4d, 7d, 10d, 13d, 16d

Diagnosis. FEMALE (N = 8). Medium- to large-sized (7.36–9.10 mm). Head and mesosoma dark, mostly blackish and reddish. Fore wing partly infumate. Body robust to medium (mesonotum 1.01–1.40× as long as wide). Head round to oval (1.42–1.59× as high as long). Eyes large (0.6–0.66× as high as head) (Fig. 10d). Corona thick to medium (4.0–6.38× as long as wide), structure interrupted (Fig. 7d). Pronotum pentagonal with posterior part distinctly narrowing towards mesoscutum, with broadest part at midlength (Fig. 13d). Mesoscutellum normal (0.60–0.75× as long as wide), anterior margin hardly convex to convex (part anterior to imaginary transverse line connecting posterior margins of axillae less than or more than 1/3 of mesoscutellum length; 0.28–0.35), mesoscutellum completely densely lineate (Fig. 16d). Propodeum small to medium (0.07–0.14× as long as mesoscutum) (Fig. 16d). Profemur medium (2.02–2.15× as long as wide). Marginal vein medium to long (0.9–1.13× as long as postmarginal vein). Metasoma medium to long (0.49–0.55× as long as body). Ovipositor rather long (0.16–0.2× as long as metasoma) (Fig. 4d).

Description. FEMALE. *Colour* (Figs 4d, 7d, 10d, 13d, 16d). Scape yellow, darkening apically, rest of antenna dark brown. Procoxa and profemur black, all other parts of legs light dark brown, except for yellow last tarsal segments. Metasoma black.

Head (Figs 7d, 10d). Face completely reticulate. Head 1.51–1.61× as wide as long. Head width 3.71–4.38× eye distance. Malar space 0.34–0.41× head height. Corona 0.57–0.70× as long as eye height. POL 0.75–1.6× OOL. Scape 2.33–3.17× as long as pedicel. Clava 0.18–0.21× as long as funicle. Flagellum 1.12–1.34× as long as head width.

Mesosoma (Figs 13d, 16d). Pronotum 0.87–0.90× as long as wide. Pronotum 0.47–0.64× as long as mesonotum. Mesonotum 1.0–1.49× as long as mesoscutum. Mesoscutum 0.69–1.40× as long as wide. Mesoscutellum 0.28–0.49× as long as mesoscutum. Profemur 1.23–1.34× as long as protibia.

Wings (Fig. 4d). Fore wing 2.88–3.21× as long as wide. Costal cell 0.32–0.40× as long as fore wing. Marginal vein 0.19–0.21× as long as fore wing. Marginal vein 2.93–3.40× as long as stigmal vein. Postmarginal vein 2.67–3.50× as long as stigmal vein.

MALE. Unknown.

Material examined. AFRICA. **Namibia**: female holotype, ca. 1500 m (above sea level), ca. 140 km N Okanhandja, 20°50.85'S/16°47.77'E, Holzeintrag (= from wood), leg. M. & O. Niehuis, 01.04.1997 (ZFMK) (ONa01); two female paratypes, same data (BNMH) (ONa04), (CNC) (ONa05); ? sex paratype, same data (NMBE) (ONa06); female paratype, 2000 m Khomas, highland, 22°42.26'S/16°31.24'E, Holzeintrag (= from wood), leg. M. & O. Niehuis, 4.4. e.l. M.5 1998 (ZFMK) (ONa02); female paratype, 1000 m NN e.l., 140 km N Okahandja, 20°50.85'S/16°47.77'E, Holzeintrag (= from wood), leg. M. & O. Niehuis, 01.04.1997 (ZFMK) (ONa03); female paratype, Waterberg ca. 1500 m (above sea level), 20°36.58'S/17°10.43'E, Holzeintrag (= from wood), ex larva, leg. M. & O. Niehuis, 01.04.1997 (USNM) (ONa07); female paratype, S. W. Africa, leg. R.E. Turner, 8–30.11.1929, labelled "*Oodera obscura cf.*" (NMP) (ONa08).

Biology. Reared from wood, exact tree species unknown.

Distribution. Namibia.

Etymology. Named after the type series' origin from Namibia.

Oodera niehuisorum sp. n.

http://zoobank.org/81C69EDF-F739-46FE-88B0-5A04DA79D745

Figs 4e, 7e, 10e, 13e, 16e

Diagnosis. BOTH SEXES (N = 13). Small-sized (4.50–6.48 mm). Head and mesosoma blackish and coppery, with small dark green parts, never with blue. Fore wing hyaline. Head usually oval (1.42–1.59× as high as long, with only 2 of 13 with head round). Eyes large (0.60–0.74× as high as head) (Fig. 10e). Corona usually medium (3.8–6.0× as long as wide, with only 1 of 10 with corona thick), structure continuous (Fig. 7e). Pronotum pentagonal with posterior part distinctly narrowing towards mesoscutum, with broadest part before midlength (Fig. 13e). Mesoscutellum normal to slender (0.55–0.85× as long as wide), anterior margin hardly convex to convex (part anterior to imaginary transverse line connecting posterior margins of axillae less than or more than 1/3 of mesoscutellum length; 0.3–0.45), mesoscutellum densely lineate in anterior half to anterior two thirds, areolate in posterior half or third (Fig. 16e).

Propodeum medium to large (0.12–0.21× as long as mesoscutum) (Fig. 16e). Profemur robust to medium (1.82–2.15× as long as wide). Marginal vein short (0.78–0.89× as long as postmarginal vein).

FEMALE. Body robust to medium (mesonotum 1.29–1.41× as long as wide). Metasoma short (0.40–0.45× as long as body). Ovipositor short to rather long (0.14–0.18× as long as metasoma) (Fig. 4e).

MALE. Body robust to slender (mesonotum 1.27–1.47× as long as wide).

Description. BOTH SEXES. *Colour* (Figs 4e, 7e, 10e, 13e, 16e). Scape yellow, pedicel yellow, darkening apically, rest of antenna dark brown. Procoxa and profemur yellow to coppery, all other parts of legs mid brown with yellow joints, except for darker brown last tarsal segments. Metasoma black.

Head (Figs 7e, 10e). Face completely reticulate. Head 1.42–1.59× as wide as long. Head width 3.13–4.0× eye distance. Malar space 0.26–0.39× head height. Corona 0.53–0.67× as long as eye height. POL 1.0–1.20× OOL. Scape 2.29–2.83× as long as pedicel. Clava 0.14–0.21× as long as funicle. Flagellum 1.09–1.31× as long as head width.

Mesosoma (Figs 13e, 16e). Pronotum 0.88–1.0× as long as wide. Pronotum 0.50–0.59× as long as mesonotum. Mesonotum 1.28–1.53× as long as mesoscutum. Mesoscutum 0.84–1.10× as long as wide. Mesoscutellum 0.28–0.53× as long as mesoscutum. Profemur 1.19–1.37× as long as protibia.

Wings (Fig. 4e). Fore wing 2.68–3.11× as long as wide. Costal cell 0.28–0.37× as long as fore wing. Marginal vein 0.15–0.20× as long as fore wing. Marginal vein 1.90–2.91× as long as stigmal vein. Postmarginal vein 2.29–3.43× as long as stigmal vein.

Material examined. AFRICA. **Egypt**: female holotype, Sinai, Nuweiba, ex *Acacia* sp. tree, 29°01.17'N/34°40.52'E, leg. O. Niehuis, 11.03.2001, 10 m amsl (= above sea level) (ZFMK) (ONi01); seven female and four male paratypes, same data (ZFMK) (ONi02-05, ONi06-08, ONi10), (CNC) (ONi05), (BHMN) (ONi09), (NMBE) (ONi11), (USNM) (ONi12). ASIA, MIDDLE EAST. **Israel**: female paratype, Yeroham 329 m ü. NN (= above sea level), 30°57'9"N/35°4'51"E, e. l. ex *Acacia* Holzeintrag (= from wood), leg. M. & O. Niehuis, 24.04.2013 (ZFMK) (ONi13).

Biology. Reared from *Acacia* wood, which is likely the habitat of the *O. niehuisorum* host.

Distribution. Egypt and Israel.

Etymology. Named after Manfred and Oliver Niehuis, who collected the specimens of the type series.

Oodera pumilae Yang, 1996

Figs 4f, 7f, 10f, 13f, 16f

Oodera pumilae Yang, 1996: 100, 311.

Diagnosis. FEMALE (N = 1). Small-sized (5.81 mm). Head and mesosoma dark green to blue-green. Fore wing partly weakly infumate. Body robust (mesonotum 1.25× as long as wide). Head oval (1.46× as high as long). Eyes small (0.59× as high as head) (Fig.

10f). Corona medium (4.13× as long as wide), structure continuous (Fig. 7f). Pronotum pentagonal with posterior part distinctly narrowing towards mesoscutum, with broadest part before midlength (Fig. 13f). Mesoscutellum normal (0.71× as long as wide), anterior margin hardly convex (part anterior to imaginary transverse line connecting posterior margins of axillae less than 1/3 of mesoscutellum length; 0.30), mesoscutellum lineate in anterior third, rugulose in posterior two thirds (Fig. 16f). Propodeum large (0.16× as long as mesoscutum) (Fig. 16f). Profemur medium (2.15× as long as wide). Marginal vein medium (1.07× as long as postmarginal vein). Metasoma medium (0.46× as long as body). Ovipositor rather long (0.16× as long as metasoma) (Fig. 4f).

Redescription. FEMALE. *Colour* (Figs 4f, 7f, 10f, 13f, 16f). Scape yellow, darkening apically, rest of antenna dark brown. Procoxa and profemur dark green, all other parts of legs dark brown with yellow joints and tarsi. Metasoma dark brown.

Head (Figs 7f, 10f). Face completely reticulate. Head 1.51× as wide as long. Head width 3.28× eye distance. Malar space 0.41× head height. Corona 0.61× as long as eye height. POL equal to OOL. Scape 2.57× as long as pedicel. Clava 0.16× as long as funicle. Flagellum 1.25× as long as head width.

Mesosoma (Figs 13f, 16f). Pronotum 0.93× as long as wide. Pronotum 0.55× as long as mesonotum. Mesonotum 1.44× as long as mesoscutum. Mesoscutum 0.87× as long as wide. Mesoscutellum 0.44× as long as mesoscutum. Profemur 1.29× as long as protibia.

Wings (Fig. 4f). Fore wing 2.96× as long as wide. Costal cell 0.38× as long as fore wing. Marginal vein 0.20× as long as fore wing. Marginal vein 3.37× as long as stigmal vein. Postmarginal vein 3.16× as long as stigmal vein.

MALE. Unknown.

Material examined. ASIA. **China**: female paratype, leg. Z.Q. Yang, 02.07.1989, rest of label in Chinese, det. Z.Q. Yang 1995 (CNC) (OPu01).

Biology. Probably parasitic on *Scolytus* spp. on elm (*Ulmus*) trees (Yang 1996).

Distribution. China (Province: Heilongjiang; Palaearctic part of China) (Yang 1996).

Taxonomic remarks. We were unable to examine the holotype. Given that the paratype we examined is from the same series as the holotype and that it perfectly matches the (short) description, we decided to include the species in our revision, diagnoses and key without examination of the primary type. Yang (1996) gives some characters to differ between *O. pumilae* and *O. regiae* in the English summary. Yet, without full translation of the Chinese descriptions these characters cannot be understood and checked. They are not mandatory though as there are several other characters to differentiate the two species (see diagnoses and key).

Oodera regiae **Yang, 1996**

Figs 4g, 7g, 10g, 13g, 16g

Oodera regiae Yang, 1996: 98, 310.

Diagnosis. FEMALE (N = 1). Small-sized (6.25 mm). Head and mesosoma dark green to green. Fore wing hyaline. Body robust (mesonotum 1.25× as long as wide).

Head oval (1.58× as high as long). Eyes large (0.69× as high as head) (Fig. 10g). Corona very short (0.45× as long as eye height), thick (4.0× as long as wide), structure continuous (Fig. 7g). Pronotum pentagonal with posterior part distinctly narrowing towards mesoscutum, with broadest part at midlength (Fig. 13g). Mesoscutellum normal (0.63× as long as wide), anterior margin hardly convex (part anterior to imaginary transverse line connecting posterior margins of axillae less than 1/3 of mesoscutellum length; 0.26), mesoscutellum densely lineate in anterior half, rugulose in posterior half (Fig. 16g). Propodeum large (0.18× as long as mesoscutum) (Fig. 16g). Profemur elongated (2.25× as long as wide). Marginal vein long (1.19× as long as postmarginal vein). Metasoma medium (0.49× as long as body). Ovipositor rather long (0.16× as long as metasoma) (Fig. 4g).

Redescription. FEMALE. *Colour* (Figs 4g, 7g, 10g, 13g, 16g). Scape yellow, darkening apically, rest of antenna dark brown. Procoxa and profemur dark green, all other parts of legs dark brown with yellow joints and tarsi. Metasoma dark brown.

Head (Figs 7g, 10g). Face completely reticulate. Head 1.58× as wide as long. Head width 3.55× eye distance. Malar space 0.31× head height. Corona 0.45× as long as eye height. POL 1.20× OOL. Scape 2.41× as long as pedicel. Clava 0.16× as long as funicle. Flagellum 1.31× as long as head width.

Mesosoma (Figs 13g, 16g). Pronotum 0.95× as long as wide. Pronotum 0.54× as long as mesonotum. Mesonotum 1.38× as long as mesoscutum. Mesoscutum 0.91× as long as wide. Mesoscutellum 0.38× as long as mesoscutum. Profemur 1.31× as long as protibia.

Wings (Fig. 4g). Fore wing 2.65× as long as wide. Costal cell 0.37× as long as fore wing. Marginal vein 0.21× as long as fore wing. Marginal vein 3.17× as long as stigmal vein. Postmarginal vein 2.67× as long as stigmal vein.

MALE. Unknown.

Material examined. ASIA. **China**: female paratype *Oodera regiae*, 12.1994, det. Z.Q. Yang 1995, rest of labels in Chinese (CNC) (ORe01).

Biology. Parasitic on the larvae of *Xyeloborus* sp. (Curculionidae) and *Agrilus* sp. (Buprestidae) on a walnut (*Juglans regiae*) tree (Yang, 1996).

Distribution. China (Province: Shaanxi; Palaearctic part of China) (Yang 1996).

Taxonomic remarks. The species is characterised by a very short corona (measured as corona length to eye height). In all other species the corona is distinctly longer, with no diagnostically useful differences among them.

We were unable to examine the holotype. Given that the paratype we examined is from the same series as the holotype and that it perfectly matches the (short) description, we decided to include the species in our revision, diagnoses and key without examination of the primary type.

The description of *O. regiae* Yang, 1996 lists four characters to distinguish this species from *O. formosa*. First, *O. regiae* does not have dense hairs on the basal tergite (interpreted as the first gastral tergite), arranged circularly, while *O. formosa* does. This was not confirmed. The distribution of gastral hairs is identical between the examined *O. regiae* and specimens of *O. formosa*. Second, *O. regiae* is described to have "eyes having sparse pubescence“ (Yang 1996). However, this character is shared among all examined *Oodera* species. Third, *O. regiae* should have “not radiately striated crests on propodeum“ (Yang 1996), implying that *O. formosa* has radiately striated crests on the propodeum. We found the propodeal structures to be rather variable intraspecifically and decided not to use them as diagnostic characters. Fourth, “notauli not touch each other posteriorly” in *O. regiae* (Yang, 1996), implying that they do in *O. formosa*. In fact, the notauli never touch in *Oodera* species. In summary, the diagnostic characters for *O. regiae* listed in the description by Yang (1996) are not useful. However, we found other characters to differentiate the two species (see diagnoses and key).

***Oodera srilankiensis* sp. n.**
http://zoobank.org/6ABF2E1E-F336-431C-AD68-1D9DC0E0D2B3
Figs 4h, 7h, 10h, 13h, 16h

Diagnosis. BOTH SEXES (N = 5). Small-sized (4.00–5.75 mm). Head and mesosoma dark blue to blue-green. Fore wing hyaline. Body robust (mesonotum 1.26–1.33× as long as wide). Eyes large (0.60–0.67× as high as head) (Fig. 10h). Corona thick to medium (3.70–4.75× as long as wide), structure continuous (Fig. 7h). Pronotum pentagonal with posterior part distinctly narrowing towards mesoscutum, with broadest part before midlength (Fig. 13h). Mesoscutellum normal to slender (0.64–0.80× as long as wide), anterior margin hardly convex to convex (part anterior to imaginary transverse line connecting posterior margins of axillae less than or more than 1/3 of mesoscutellum length; 0.28–0.39), meoscutellum lineate in anterior third to half, rugulose in posterior half or two thirds (Fig. 16h). Propodeum large (0.18–0.23× as long as mesoscutum) (Fig. 16h). Profemur usually medium to elongated (1.98–2.33× as long as wide, only only 1 of 5 with profemur robust). Marginal vein medium (0.93–1.07× as long as postmarginal vein).

FEMALE. Head round (1.30–1.41× as high as long). Metasoma medium (0.47× as long as body). Ovipositor short (0.13–0.14× as long as metasoma) (Fig. 4h).

MALE. Head oval (1.53–1.54× as high as long).

Description. BOTH SEXES. *Colour* (Figs 4h, 7h, 10h, 13h, 16h). Scape brown, darkening apically, rest of antenna dark brown. Procoxa and profemur dark brown, meso- and metafemur dark brown, tibiae light brown, joints and tarsi yellow, except for brown last tarsal segments. Metasoma dark brown.

Head (Figs 7h, 10h). Face completely reticulate. Head 1.28–1.48× as wide as long. Head width 3.44–3.83× eye distance. Malar space 0.33–0.40× head height. Corona 0.59–0.73× as long as eye height. POL 1.00–2.00× OOL. Scape 2.38–3.16× as long as pedicel. Clava 0.15–0.21× as long as funicle. Flagellum 1.23–1.29× as long as head width.

Mesosoma (Figs 13h, 16h). Pronotum 0.90–1.00× as long as wide. Pronotum 0.52–0.55× as long as mesonotum. Mesonotum 1.40–1.49× as long as mesoscutum. Mesoscutum 0.87–0.92× as long as wide. Mesoscutellum 0.40–0.49× as long as mesoscutum. Profemur 1.25–1.41× as long as protibia.

Wings (Fig. 4h). Fore wing 2.69–3.20× as long as wide. Costal cell 0.31–0.39× as long as fore wing. Marginal vein 0.18–0.20× as long as fore wing. Marginal vein 2.50–4.00× as long as stigmal vein. Postmarginal vein 2.33–4.25× as long as stigmal vein.

Material examined. ASIA. **Sri Lanka**: female holotype, Mate. Dist. Kibissa, 0,5 mi West of Sigiriya, Jungle, leg. K.V. Krombein, 28.06–04.07.1978 (USNM) (OSr01); male paratype, Anu. Dist. Hunuwilagama, near Wilpatta, 200 feet, leg. G.F. Hevel, 28.10–03.11.1976 (USNM) (OSr02); male paratype, Anu. Dist. Hunuwilagama, near Wilpatta, 200 feet, leg. G.F. Hevel, 28.10–03.11.1976 (USNM) (OSr04); female paratype, Tri. Dist. China Bay Ridge Bungalow, 0–50 feet, leg. K.V. Krombein, 24–25.07.1978 (ZFMK) (OSr03); female paratype, Gal. Dist. Udugama, Kanneliya, 400 feet, Jungle, leg. K.V. Krombein, 06–12.10.1973 (1978), det. Oodera ahoma by Z. Bouček 1978 (USNM) (OSr05).

Biology. Unknown.

Distribution. Sri Lanka.

Etymology. Named after the geographic origin of the type series from Sri Lanka.

Taxonomic remarks. Some (or maybe all) specimens described here as *O. srilankiensis* were probably those examined and mentioned by Bouček et al. (1978) and considered as *O. ahoma*. After careful examination they can be distinguished from the holotype of *O. ahoma* by several characters, for example, the very different body length (medium in *O. ahoma*, small in *O. srilankiensis*), the body shape (slender in *O. ahoma*, robust in *O. srilankiensis*), and the eye size (small in *O. ahoma*, large in *O. srilankiensis*). Bouček et al. (1978) also mentioned the close resemblance of some specimens (including one from Pakistan that we were unable to locate) with "a European species", i.e., *O. formosa*. In fact, the new species is rather similar to *O. formosa* but can be distinguished from this by some characters, for example, fore wing hyaline (*O. srilankiensis*) vs. partly infumate (*O. formosa*), and propodeum large (*O. srilankiensis*) vs. propodeum usually medium (*O. formosa*) (see also diagnoses and key).

Oodera tenuicollis **(Walker, 1872)**

Figs 4i, 7i, 10i, 13i, 16i

Eupelmus tenuicollis Walker, 1872: 86.
Oodera tenuicollis; Hedqvist 1961: 98.

Diagnosis. FEMALE (N = 1). Exact body length not available (the only specimen available is missing metasoma), if metasoma is not uniquely long, then small-sized. Head and mesosoma dark blue to green-blue. Fore wing partly infumate. Body slender (mesonotum 1.45× as long as wide). Head round (1.40× as high as long). Eyes large (0.67× as high as head) (Fig. 10i). Corona medium (4.40× as long as wide), structure continuous (Fig. 7i). Pronotum oval and longer than wide, with broadest part at midlength (Fig. 13i). Mesoscutellum slender (0.82× as long as wide), anterior margin hardly convex (part anterior to imaginary transverse line connecting posterior margins of axillae less than 1/3 of mesoscutellum length; 0.17), mesoscutellum lineate in anterior two thirds, with median lines converging, rimose in posterior third (Fig. 16i). Propodeum large (0.18× as long as mesoscutum) (Fig. 16i). Profemur elongated (2.34× as long as wide). Marginal vein long (1.13× as long as postmarginal vein). Metasoma length not available. Ovipositor length not available (Fig. 4i).

Redescription. FEMALE. *Colour* (Figs 4i, 7i, 10i, 13i, 16i). Scape brown, darkening apically, rest of antenna dark brown. Procoxa dark brown, profemur dark green, all other parts of legs brown with yellow joints, tarsi yellow, except for brown last segments. Metasoma colour unknown.

Head (Figs 7i, 10i). Face completely reticulate. Head 1.37× as wide as long. Head width 4.00× eye distance. Malar space 0.32× head height. Corona 0.65× as long as eye height. POL 1.20× OOL. Scape 2.63× as long as pedicel. Clava length to funicle length not available. Flagellum length to head breadth not available.

Mesosoma (Figs 13i, 16i). Pronotum 1.05× as long as wide. Pronotum 0.52× as long as mesonotum. Mesonotum 1.40× as long as mesoscutum. Mesoscutum 1.04× as long as wide. Mesoscutellum 0.40× as long as mesoscutum. Profemur 1.30× as long as protibia.

Wings (Fig. 4i). Fore wing 3.04× as long as wide. Costal cell 0.35× as long as fore wing. Marginal vein 0.20× as long as fore wing. Marginal vein 2.72× as long as stigmal vein. Postmarginal vein 2.40× as long as stigmal vein.

MALE. Unknown.

Material examined. ASIA. **Indonesia**: female type (probably holotype), *Eupelmus tenuicollis* Walker Notes on Chalcidide 5:86.1872, Type female checked RDE 1955 (1955), det. *Oodera* sp. by R. D. Eady, BMNH(E) #1414764, labelled "Mysol" (?) (might be Misool, an Island in Indonesia, South Moluccas, see also Gibson (2003) who gives the same locality information) (BMNH) (OTe01).

Biology. Unknown.

Distribution. Indonesia.

Taxonomic remarks. This species is a bit problematic, because only the single type specimen without metasoma is available. However, the rest of the body provides some good diagnostic characters that allow differentiation from all other species of *Oodera*.

Nomina dubia and species removed from *Oodera*

Oodera obscura Westwood, 1874, nomen dubium

Oodera obscura Westwood, 1874: 146.

Distribution. Maybe Indonesia. This information is given by Gibson (2003) and Noyes (2017), yet the original description does not give information about the type locality.

Taxonomic remarks. Gibson (2003) states that the location of the holotype is uncertain. Based on the information in the original description we expected the holotype to be in Oxford as part of the W. W. Saunders collection. However, even after extensive search at Oxford and London (where other parts of the Saunders collection are located) by the respective curators the type could not be located. The species description by Westwood includes only a short description of colouration pattern and body length, both unspecific. The description does not provide sufficient information to clarify the taxonomic status of this species. We therefore consider it as a nomen dubium.

Oodera rufimana Westwood, 1874, nomen dubium

Oodera rufimana Westwood, 1874: 146.

Distribution. Cambodia.

Taxonomic remarks. As for *O. obscura* (see above), we expected the holotype to be in Oxford as part of the W. W. Saunders collection (both species were described in the same publication). However, even after extensive search at Oxford and London (where other parts of the Saunders collection are located) by the respective curators the type could not be located. The species description is not conclusive and specific. We therefore considered it as a nomen dubium.

Eupelmus (Eupelmus) albopilosa (Crosby, 1909), comb. n.

Oodera albo-pilosa Crosby, 1909: 86.

Remarks. This new combination is by authority of G. Delvare (CSIRO, Montpellier), J. Werner and R. S. Peters.

Material examined. Female holotype, labelled "Eupelmidae?" by Bouček 1958 (examined from two images (head frontal, body lateral), kindly provided by J. Liebherr, DECU).

Biology. Parasite of an unknown gall-forming fly on branches of *Combretum olivaceum* (Crosby, 1909).

Distribution. The species is listed from South Africa and Zambia in Noyes (2017). The record from Zambia is taken from the description; the record from South Africa is assigned to Bouček (1958). However, Bouček (1958) actually names South-East-Africa ("Südostafrika" in the German orginal) as a geographic region, which includes Zambia, and he does not refer to a record that is different from the original description, i.e., the record from South Africa in Noyes (2017) is not correct.

Taxonomic remarks. We only examined images of the holotype. However, the female type is clearly a specimen belonging to the subfamily Eupelminae (Eupelmidae), not an *Oodera*. The species is therefore removed from *Oodera* and transferred to *Eupelmus*. The tentative assignment to Eupelmidae was already done by Bouček (1958) (see also the label of the holotype). The species belongs to the *Eupelmus orientalis* species group, and might be a senior synonym of *E. orientalis* (Crawford, 1913) or *E.*

vuilleti (Crawford, 1913) (Delvare pers. comm.) but the decision on the identity of this species should be left for a future *Eupelmus*-related work. This is the first record of *Eupelmus* from Zambia (Noyes 2017).

Oodera sp.

Note. Five specimens could not be assigned to any of the previously or newly described species (specimens OSp01 (ZFMK), OSp02 (BMNH) and OSp03-05 (SAMC)). All do not match the characters used in the key and diagnoses for the species included herein. All are single specimens and all are found in countries from which already one or more species have been described or are described in this study. We deliberately refrain from describing these five single specimens as five additional new species, because they are apparently close to but not identical with other species (for details see below), they show overlap in distribution with other species and we have no information about the variation of the potential new species. Most species of *Oodera* are fairly similar, and reliable diagnostic characters are hard to find and describe, especially because most type series are small in this rarely collected group. Describing the additional five specimens as five new species would potentially cause significant confusion. We decided to list these specimens in this revision so that they can easily be located for future studies, and include all measurements in Suppl. material 1. We hope for additional material collected in the future, ideally also including ethanol preserved material for an integrative study, to formulate robust species hypotheses. Note that we describe three species from single specimens (i.e., *O. felix* sp. n., *O. florea* sp. n., and *O. mkomaziensis* sp. n.), but these are much more easily separated morphologically and are also geographically isolated from all other species.

Oodera sp. 1

Material examined. AFRICA. **Namibia**: female, Waterberg ca. 1500 m (above sea level), 20°36.58'S/17°10.43'E, Holzeintrag (= from wood), ex larva, leg. M. & O. Niehuis, 01.04.1997 (ZFMK) (OSp01).

Remarks. This specimen has the same collecting data as one of the paratypes of *O. namibiensis* sp. n. and was at first included as paratype of this species. Yet, it does not belong to this species because it is, for example, not uniformly dark-coloured on head and mesosoma but has some distinct dark green parts, and the fore wing is not partly infumate but hyaline.

Oodera sp. 2

Material examined. ASIA. **Indonesia**: male, Sumatra: Tep. Tingi, standing over: *Oodera ornata* in Hedqvist coll. BMNH(E) 2011-27 (BMNH) (OSp02).

Remarks. It is a single male specimen. It was collected in Indonesia, yet very distant from the only other species from Indonesia *O. tenuicollis*. It was standing as *Oodera ornata* (now *O. longicollis*) in the Hedqvist collection at the BMNH but clearly differs from *O. longicollis* by, for example, the absence of bright colours on the head, a continuous corona (square in *O. longicollis*), and a different mesoscutellum sculpture (completely lineate in *O. longicollis*, lineate only in anterior half in this specimen). We first intuitively assigned it to *O. tenuicollis* but it is also different from this species, not only by geographic distribution, but also by, for example, an elongated head (round in *O. tenuicollis*), and a pentagonal pronotum (oval in *O. tenuicollis*).

Oodera sp. 3

Material examined. AFRICA. **Republic of South Africa**: female, Western Cape, Gamkaberg Nature Reserve, 33°39.941'S/21°53.505'E, 315 m, 21.03.–05.05.2009, leg. S. van Noort (SAMC) (OSp03).

Remarks. This specimen has very few conspicuous characteristics that might allow placing it close to any other species. It differs from the other South African species *O. heikewernerae* sp. n. by, for example, a distinctly larger body length (7.7 mm compared to maximum of 6.64 mm in *O. heikewernerae*), a slightly different corona (no horizontal crests connected by vertical crests vs. some horizontal crests connected by vertical crests in *O. heikewernerae*), and a different scutellum sculpture (only partially lineate vs. completely lineate in *O. heikewernerae*). It is tentatively close to *O. felix* (from Central African Republic), but differs also from this species by, for example, hyaline fore wings (partly infumate in *O. felix*), small eyes (large in *O. felix*), and a partly blueish mesosoma (dark green in *O. felix*).

Oodera sp. 4

Material examined. AFRICA. **Tanzania**: female. Mkomazi Game Reserve (now Mkomazi National Park), Kisima Plot, 4°06.06'S/38°05.58'E, Acacia/Commiphora bushland, 25.11.–08.12.1995, leg. S. van Noort (SAMC) (OSp04).

Remarks. The specimen was collected in the same National park in Tanzania as *O. mkomaziensis* sp. n. but is different from this species by, for example, distinct light green colour on the head (dark in *O. mkomaziensis*), partly infumate fore wings (hyaline in *O. mkomaziensis*), and being distinctly smaller (this specimen: 5.56 mm, *O. mkomaziensis*: 7.20 mm).

Oodera sp. 5

Material examined. AFRICA. **Republic of South Africa**: female, Merweville, Laingsburg Distr., leg. H. Zinn (SAMC) (OSp05).

Remarks. The specimen is not too different from the other South African species *O. heikewernerae* sp. n., yet cannot be assigned to this species because of a few rather subtle differences, for example, the colour of the head and mesosoma (light green on head and reddish parts on mesosoma, both not present in *O. heikewernerae*), and the head shape (round in this specimen, usually oval in *O. heikewernerae*).

Discussion

This taxonomic revision of *Oodera* is based on a comparatively small number of specimens (115) and on morphological data only. Several of the new and previously described species are known from only a single specimen. This is inevitable because of the rarity of specimens in scientific collections. The samples we used were borrowed from 13 different museums, but more museums in Germany and abroad (e.g., Bavarian State Collection for Zoology Munich, Senckenberg Museum Frankfurt, Senckenberg Deutsches Entomologisches Institut Müncheberg, University of Oxford Hope Collection, National Museum of Natural History Stuttgart, Zoological Museum of the University of Zurich, Zoologisches Museum Hamburg, Australian National Insect Collection) were investigated for specimens of *Oodera* but do not have any (except for one specimen of *O. longicollis* in Canberra, see part on *O. longicollis*). Apart from the specimens gathered for this revision that are deposited at the ZFMK (Bonn), only a single specimen of *Oodera* was found in all major German scientific collections (a specimen of *O. formosa* in MFNB). Furthermore, 15,000 unidentified Chalcidoidea specimens were examined at the Royal Museum of Central Africa in Tervuren, Belgium but none of them was identified as a species of *Oodera*. We were restrained from taking a more integrative approach and including nucleotide sequence data due to an overall lack of specimens and the considerable age of most of the available material.

Species of *Oodera* seemingly prefer warmer to temperate regions (Fig. 17). There are no records from north of 50. parallel north. The absence from more northern regions of Asia, however, might well be an artifact as the fauna of many areas is not well-studied. So far, there are no records from Australia. Given that there is at least one species in Papua New Guinea, we might assume that the absence from Australia is a sampling artifact. However, the genus is very conspicuous – yet rarely collected – and is not likely to be overlooked easily. Generally, we found that the rarity of this genus in Chalcidoidea collections might be related to the sampling habits of chalcidoid workers. They prefer to use sweep nets, Malaise or colour pan traps. However, some of the new species (and also the new record of *O. formosa* from Germany) are based on material from hand collecting on wood or from rearings from wood. The latter is done in large scale, for example, by beetle specialists. Accordingly, teaming up with beetle workers or collecting wood and rearing specimens could rapidly increase the number of *Oodera* specimens known and potentially also the number of species known, possibly allowing for an integrative taxonomic approach.

After comprehensive examination of all available material of this genus, we would like to add some speculation on the function of the modified front legs that are pre-

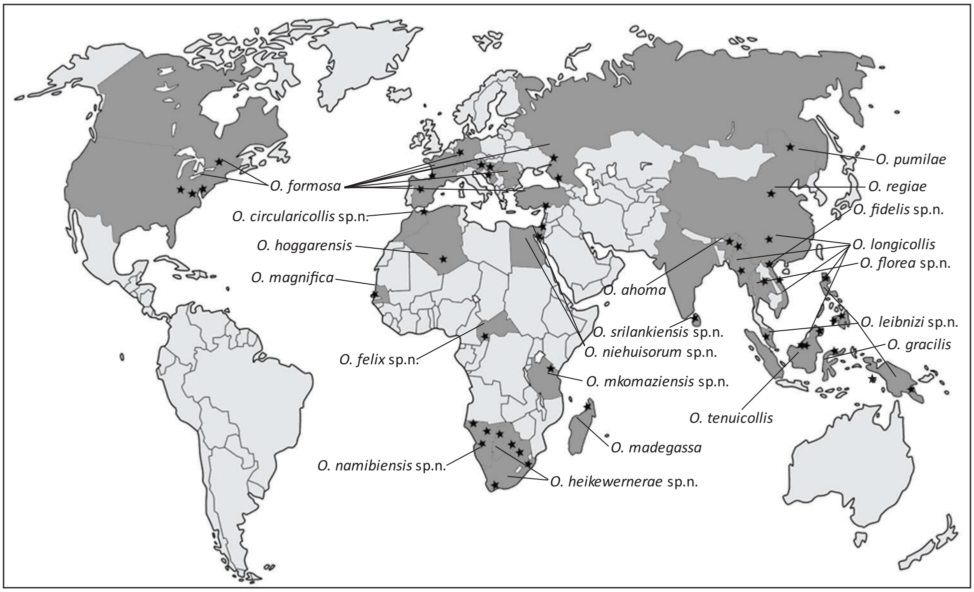

Figure 17. Geographic distribution of the genus *Oodera*. Countries from which *Oodera* was recorded are highlighted in dark grey. Stars indicate record localities. Record localities of *O. pumilae* Yang and *O. regiae* Yang are not exact but placed in the centre of the respective Chinese province from which the species was recorded.

sent in both sexes in striking conspiciousness. Raptorial function is highly unlikely. Although *Oodera* is an extraordinary chalcidoid in many ways, its mouth parts, head shape, etc. are typical for Chalcidoidea, and no other chalcidoid has been reported to be raptorial and carnivorous in the adult stage. Also, the anecdotal descriptions of Gates (2004) do not support raptorial function. A function in mating or courtship is unlikely, given that both sexes exhibit the character. This holds also for a function in catching host specimens, similar to Dryinidae females (in addition, host specimens are not free living but concealed in wood). Instead, we suspect a function in the clearing of wooden tunnels by the escaping newly emerged adult specimens. The legs are equipped with some strong bristles and pegs, but not with teeth or spines. Furthermore, the profemora are very massive and broad, much different from insects with raptorial front legs. They resemble shovels or rakes rather than a predator's instruments. Also, the long pronotum enables much greater moveability of the head, presumably allowing the specimens to use the coronated head to dig through narrow, frass- or debris-filled tunnels. Species of *Heydenia* (Cleonyminae: Heydeniini) have similar structures, and apparently also a comparable biology. However, verification of this function is still to be done by observations in the field or the lab.

We hope that this first revision of the group and the included identification key will foster studies on this beautiful and intriguing group of chalcids that will eventually lead to at least some basic knowledge about the species' biology and evolution.

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Supplementary material 1

Table S1. Measurements (in mm) and ratios for all specimens examined

Authors: Jennifer Werner, Ralph S. Peters

Data type: measurement

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Corrigenda: North-Western Palaearctic species of *Pristiphora* (Hymenoptera, Tenthredinidae). Journal of Hymenoptera Research 59: 1–190. https://doi.org/10.3897/jhr.59.12656

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It has come to our attention that we used the term "scopa" incorrectly throughout our revision of north-west Palaearctic *Pristiphora* species (Prous et al. 2017, p. 12 *et seq*.), and in the associated electronic identification key available at figshare (http://dx.doi.org/10.6084/m9.figshare.5235805). The term is in frequent use for assemblages of stiff hairs, on the legs or abdominal sterna, used for transporting pollen in bees (Huber and Sharkey 1993). Our intention, in sawflies, was to denote an invagination or concavity at the tip of the sawsheath (e.g. Figs 75, 104–107, 111, 115, 121 in Prous et al. 2017) that distinguishes such sawsheaths from unmodified ones (e.g. Figs 98–99 in Prous et al. 2017), or from those having a "carina" (e.g. Figs 66–69 in Prous et al. 2017). The meaning of "scopa" (from Latin "broom") in the context of Symphyta, consistent with most recent literature, is a paired, latero-posteriorly projecting structure at the tip of the sawsheath (Ross 1937: 76, Smith 1988: 229, 1992: 4). The "scopa" of sawflies sometimes bears a clearly defined setose area, often conspicuous in Diprionidae, termed "scopal pad" by Ross (1955) and Smith (1988). A potential source of further confusion is the use by some authors of "scopa" for the scopal pad alone (e.g. Hara and Shinohara 2015). In future, it might be preferable to restrict the use of the word scopa to the bees, and refer to the respective structures of sawfly sawsheaths as "latero-posterior projections" and "setose fields".

On page 82, under *Pristiphora parva* (Hartig, 1837) we incorrectly designated a specimen (DEI-GISHym31699) as the lectotype of *Lygaeonematus ambiguus* var. *flavater* Enslin, 1916. We overlooked the collection date of the specimen (1918-05-03). The specimen was therefore not a syntype, and the lectotype designation is thus invalid (ICZN 1999, Article 74.2). No syntype specimen is known. Accordingly, the sentence "Lectotypes are designated for 43 taxa" in the abstract should read "Lectotypes are designated for 42 taxa".

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