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A new species of gregarious *Meteorus* (Hymenoptera: Braconidae) reared from caterpillars of *Venadicodia caneti* (Lepidoptera: Limacodidae) in Costa Rica

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Abstract

A new species of parasitoid wasp, *Meteorus oviedoi* Shaw and Nishida (Hymenoptera: Braconidae), is described from the Central Valley of Costa Rica. The new species is diagnosed and compared to other species in the genus. It was reared from larvae of *Venadicodia caneti* (Lepidoptera: Limacodidae) on leaves of *Licaria triandra* (Lauraceae). The parasitoid is gregarious and modifies the behavior of its host. This is the first record of a *Meteorus* species attacking Limacodidae in Costa Rica.

Resumen

Una nueva especie, *Meteorus oviedoi* Shaw and Nishida (Hymenoptera: Braconidae) es descrita para Valle Central de Costa Rica. La especie es analizada y comparada con otras especies del género. Los especimenes fueron criados de larvas de *Venadicodia caneti* (Lepidoptera: Limacodidae), encontradas en hojas de *Licaria triandra* (Lauraceae). El parasitoide es gregario y modifica comportamiento del hospedero.

Key words: Hymenoptera, Braconidae, Neotropical, parasitoid, Limacodidae, taxonomy, behavior

Introduction

Meteorus Haliday is a large genus with worldwide distribution comprising more than 200 described species (Muesebeck 1923; Nixon 1943; Huddleston 1980, 1983; Maetô 1990;

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Chen & Wu 2000; Zitani & Shaw 2002; Zitani 2003). All are koinobiont endoparasitoids, mostly attacking young exposed-feeding caterpillars but some parasitize beetle larvae (Shaw & Huddleston 1991; Shaw 1995, 1997). *Meteorus* species are noted for their diverse silk-spinning and cocoon-forming behaviors (Zitani & Shaw 2002; Zitani 2003). While most are solitary parasitoids of small caterpillars, several tropical *Meteorus* species are known to be gregarious parasitoids of larger caterpillars (Muesebeck 1939, 1958; Nixon 1943; Zitani *et al*. 1997, 1998; Zitani 2003). Costa Rican *Meteorus* species have been the focus of recent taxonomic studies (Zitani *et al*. 1997, 1998) but many undescribed species still exist in tropical forests. The purpose to this paper is to describe a new species recently found parasitizing caterpillars of *Venadicodia caneti* Corrales and Epstein (Lepidoptera: Limacodidae) on leaves of *Licaria triandra* (Sw.) Kosterm. (Lauraceae). This is the first record of any *Meteorus* parasitizing Limacodidae in Costa Rica. It is also the first record of a hymenopteran parasitoid of *V. caneti*. This same host caterpillar has been extensively studied by Dr. Daniel Janzen in the Area de Conservación Guanacaste (ACG), but until now the only known parasitoid of this species was a tachinid fly, *Austrophorocera* sp. (Corrales & Epstein 1997). This paper is a contribution to studies of caterpillars and their parasitoids in Costa Rica and Ecuador by the senior author. Providing a scientific name for this species is desirable so the taxon can be included in a current study by the senior author, in collaboration with Dr. Donald Quicke (Imperial College) of the molecular phylogeny of *Meteorus* species based on 28S rDNA sequence data.

Methods

Taxonomy: The morphological terminology and characters used in this description follow those of Zitani et al. (1997, 1998). The holotype, associated cocoons, and remains of host larvae are deposited in the University of Wyoming Insect Museum (UWIM). Paratypes are deposited in the University of Wyoming Insect Museum (UWIM), the Imperial College at Silwood Park (ICSP), United States National Museum, Washington D.C. (USNM), the Museum of Comparative Zoology, Harvard University (MCZ), Instituto Nacional de Biodiversidad (INBio), Costa Rica, and la Escuela de Biología, Universidad de Costa Rica (UCR).

Biology: The study was conducted during the months of October and November, 2002, and February and November, 2003, in the Reserva Ecológica Leonelo Oviedo (elevation 1150 m; 9º56' N, 84º03' W), which is situated on campus of the University of Costa Rica in Montes de Oca, San Pedro, San José, Costa Rica. The reserve is a 35 year old secondary growth forest, formerly a coffee plantation, which is covering an area of approximately 1 ha. (J. Di Stefano, pers. comm.). The Holdridge life zone is tropical premontane moist forest (Holdridge 1967). Early to late instar larvae of *V. caneti* and cocoons of *M. oviedoi* were collected from 30 cm to 3 m high shrubs of *L. triandra*. These samples were observed and reared in transparent plastic bags in the entomological laboratory of the university (mean room temperature 23 to 24 °C). Adults and cocoons of the *Meteorus* species were preserved in 75% ethanol. Digital images of the early stages were taken with a Nikon Coolpix camera.

Meteorus oviedoi **Shaw & Nishida, NEW SPECIES**
(Figs. 1-14)

Diagnosis: mandible strongly twisted, second tooth directly behind first tooth in lateral view; *ocelli small*, ocello-ocular distance 1.6x ocellar diameter; *occipital carina complete*; wing membrane clear; vein r ½ length of 3RSa; propodeum areolate-rugose; hind coxa finely *rugulose*; first metasomal tergite *without dorsopes*; *ventral borders of first tergite joined completely along basal ½ of segment*; tergum 2 black laterally, medially with *white broad hourglass-shaped figure*.

Description of holotype female:

Body color: body mostly light yellowish brown except head orange, compound eye silver, and other parts of body with dark contrasting markings as follows: flagellum black; scape and pedicel dark orangish brown infused with black; ocellar triangle black; dorsal margin of pronotum with black band; lateral lobes of mesonotum and scutellum black; metanotum and propodeum black; apex of hind coxa and apex of hind tibia black; tarsi of all legs dark brown; wing membrane clear; wing venation dark brown; pterostigma pale yellowish brown medially bordered with dark brown; metasomal tergites 1-3 black dorsally except petiole white basally in dorsal view, petiole entirely white ventrally (Fig. 13), and tergum 2 medially with white broad hourglass-shaped figure (Fig. 14); ovipositor and sheaths dark brown.

Body length: 3.4 mm.

Head: antenna with 30 flagellomeres; flagellar length/width ratios as follows: F1 = 3.1; F2 = 3.1; F3 = 3.0; F26 = 2.4; F27 = 2.2; F28 = 2.0; F29 = 1.8; F30 (apical flagellomere) = 2.6; tip of apical flagellomere acutely pointed (Fig. 7); head 1.2x wider than high, head height 1.4x eye height (Fig. 5); eye small but protuberant, slightly converging ventrally in anterior view (Fig. 5); maximum face width 1.1x minimum face width; minimum face width 1.5x clypeus width; malar space length 1.1x mandible width basally (Fig. 6); ocelli small, ocello-ocular distance 1.6x ocellar diameter; lower margin of clypeus with fine rugulose wrinkles; mandible strongly twisted (Fig. 6); occipital carina complete; vertex, in dorsal view, descending vertically behind lateral ocelli.

Mesosoma: notauli rugulose, not distinct, and mesonotal lobes not well-defined; scutellar furrow with 1 median carina; mesopleuron polished, punctate; sternaulus rugulose, broad but not long; propodeum areolate-rugose, median depression absent.

Legs: hind coxa dull, rugulose (Fig. 8); larger hind tibial spur about ½ as long as hind basitarsus (Fig. 9); tarsal claw with a small blunt basal tooth, strongly curved (Fig. 10).


1
2
3
4

FIGURE 1. Mature parasitized caterpillar of *Venadicodia caneti* (lateral view) with *Meteorus oviedoi* larvae just starting to exit. Note dark spots where larvae are chewing exit holes and emerging larva on right. **FIGURE 2.** *Venadicodia caneti* caterpillar (dorso-lateral view) with *Meteorus oviedoi* larvae mostly emerged and in various stages of cocoon-formation. Most of the cocoons are nearly completely spun, but on the upper-right two larvae can be seen spinning silk, while one last larva is exiting the host. **FIGURE 3.** *Venadicodia caneti* host caterpillar (dorsal view) with *Meteorus oviedoi* cocoons nearly completely spun, but cocoon silk not fully hardened and darkened. **FIGURE 4.** *Venadicodia caneti* host caterpillar (dorsal view) with *Meteorus oviedoi* cocoons completely spun, showing final appearance of fully hardened and darkened cocoon silk.

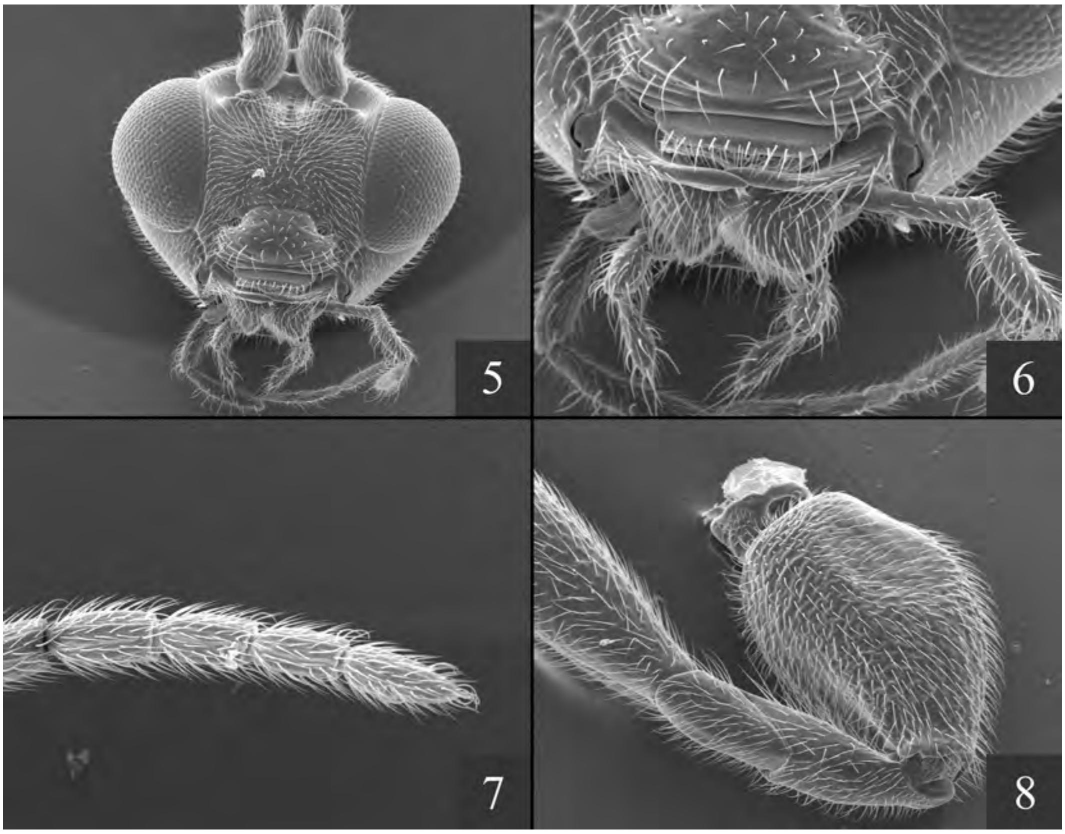

FIGURE 5. Head of *Meteorus oviedoi* female, anterior view. **FIGURE 6.** Close-up of head venter of *Meteorus oviedoi* female, anterior view, showing sculpture of lower clypeal margin, width of malar space, and shape of the mandible. **FIGURE 7.** Apex of antenna of *Meteorus oviedoi* female, lateral view, showing relative sizes of flagellomeres 27 to flagellomere 30 (apical flagellomere) and acutely pointed apex. **FIGURE 8.** Base of hind leg of *Meteorus oviedoi* female, lateral view, showing finely rugulose sculpture on coxa.

Wings: forewing length 3.2 mm; vein m-cu postfurcal; second submarginal cell of forewing not strongly narrowed anteriorly; vein r 0.5x length of 3RSa.

Metasoma: first metasomal tergite without dorsopes (Figs. 11-12); ventral borders of first tergite joined completely along basal ½ of segment; first tergite dorsally longitudinally costate on apical half beyond spiracles, costae slightly convergent posteriorly (Fig. 12); ovipositor short, thick at base, 1.8x longer than first tergite (Fig. 11).

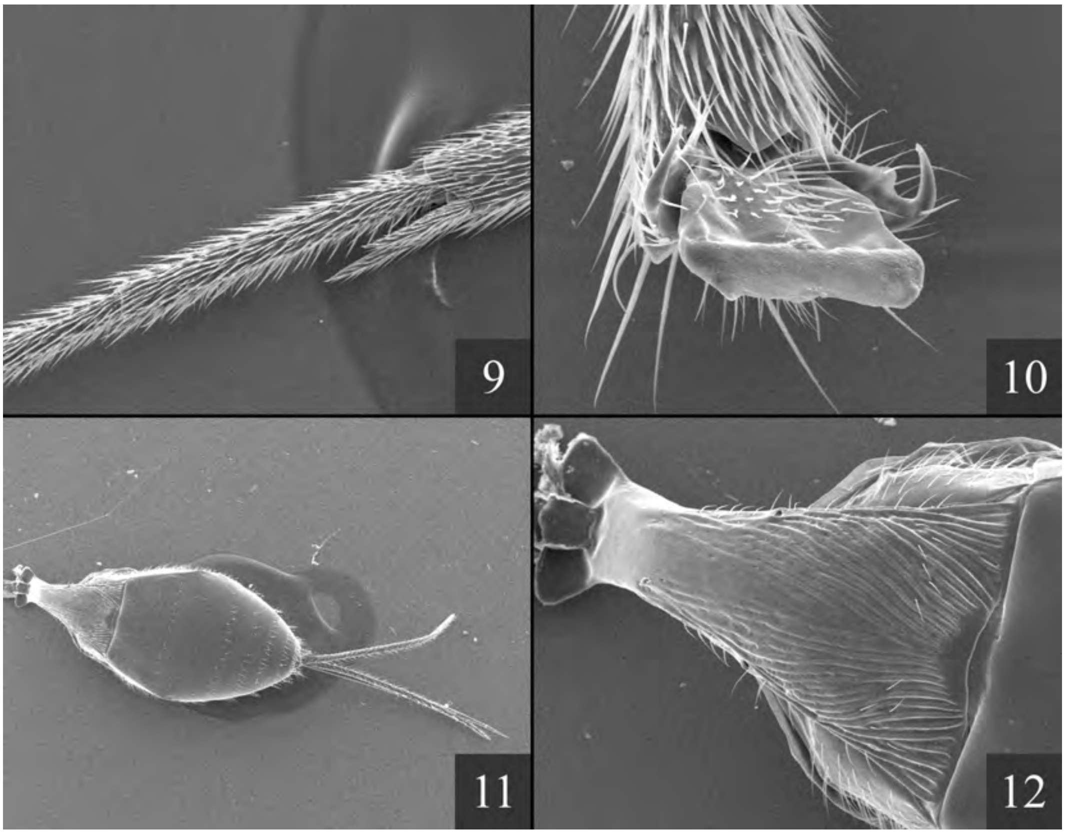

FIGURE 9. Apex of hind tibia and hind basitarsus of *Meteorus oviedoi* female, lateral view, showing size of hind tibial spurs as compared with length of hind basitarsus. **FIGURE 10.** Apex of hind leg of *Meteorus oviedoi* female, ventral view, showing shape of the hind claws with blunt basal tooth. **FIGURE 11.** Entire metasoma of *Meteorus oviedoi* female, dorsal view, showing length of the ovipositor relative to the metasoma. **FIGURE 12.** Metasomal tergite 1 of *Meteorus oviedoi* female, dorsal view, showing longitudinal costae on apical half beyond spiracles and the convergent pattern of costae posteriorly. Note also the absence of dorsopes on the petiole.

Variation: Other females as in holotype except body length 3.2-3.5 mm; forewing length 3.1-3.2 mm; antennae with 30-32 flagellomeres.

Males: Similar to females except body size smaller, body length 2.8-3.2 mm. Antenna with 28-30 flagellomeres. Body color generally much lighter than in females with less extensive black markings particularly noticeable on the ocellar triangle (diffuse black markings), mesonotum (black almost absent except at corners), propodeum (diffuse black markings), and tergum 2 (lateral black markings much smaller than in female). The white medial pattern on tergum 2 still present in males, but much broader and more variable in shape.

Holotype: Female (point-mounted), COSTA RICA: San José, San Pedro, UCR campus, Reserva Ecológica Leonelo Oviedo, 1150 m, 15-16 November 2002, collected and reared by Kenji Nishida, host: 5th instar larva of *Venadicodia caneti* (Limacodidae) on *Licaria triandra* (Lauraceae), host collected 30 October 2002, feeding on leaves, host not moving 4 November 2002, black spots on the host 4 November 2002, *Meteorus* larvae (26) came out 4 November 2002 (evening) (pictures associated), the host larva became aggressive after 3-4 larvae came out, immediately the larvae started spinning cocoons (pictures associated): 5:18 pm. Deposited in UWIM.

Paratypes: 9 females, 16 males, same data as holotype. 10 females, 3 males, same data as holotype except 13 cocoons hanging collected 27 October 2002 (pictures associated), wasps emerged 4 November 2002. 8 females, 2 males, same data as holotype except *Meteorus* larvae (10) emerged 4 November 2002 (evening) (pictures associated), host larva died 6 November 2002. 5 females, 3 males, same data as holotype except host larva and wasp cocoons collected 23 October 2002, wasps emerged 28 October 2002. 10 females, 1 male, same data except from penultimate larva collected on 28 October 2002, molted to final instar 4 November, host larva stopped feeding 19 November, 16 *Meteorus* larvae emerged and spun cocoons 21 November, host larva died and fell off leaf 24 November 2002, adult wasps emerged 30-31 November 2002 (some adults did not emerge from cocoons). 7 males, same data except larvae came out 25 October 2002, adult wasps emerged 2 November 2002. 8 females, 7 males, same data except collected from cocoons found attached to a *L. triandra* leaf on 11 October 2003, adult wasps emerged 20 October 2003. 5 females, 3 males, same data except adult wasps emerged 15 October 2003. Deposited in UWIM, ICSP, USNM, MCZ, INBio, and UCR.

Mature larva exiting and spinning cocoon: 3 to 4 mm long, translucent to creamy white showing pinkish-red color of interior body. Head translucent to creamy white with mouth parts dark brown (Figs. 1-2).

Cocoon: spindle-shaped, brown with loosely spun exterior silk appearing whitish. Cocoon suspending thread attached to host plant, about 5 mm in length (Figs. 2-4).

Comments: *Meteorus oviedoi* is most similar to *Meteorus uno* Zitani. Both species have a bright orange head (more brightly colored in females) and extensive black markings. In the key to Costa Rican *Meteorus* species by Zitani *et al*. (1998) *M. oviedoi* keys to couplet 8 (near *M. uno*) but it can easily be distinguished from *M. uno* by the complete occipital carina. Also, there are several obvious color differences between these two species. The mesonotum of *M. uno* is uniformly orange, while the mesonotum of *M. oviedoi* has black lateral lobes. The hind coxa is entirely black in *M. uno* but only black apically in *M. oviedoi*. Only the dorsal surface of the propodeum is black in *M. uno*, while the propodeum is entirely black in *M. oviedoi*. Metasomal tergum 2 is entirely black in *M. uno*, while in *M. oviedoi* tergum 2 is white medially, black laterally, forming a somewhat broad hourglass-shaped figure medially. Although the shape of this white pattern is somewhat variable, especially in the males, it is still quite distinctive.

The discovery of a new *Meteorus* attacking Limacodidae in Costa Rica is of interest because use of this host family was not previously known from the region, however a gregarious African species (*Meteorus komensis* Wilkinson) is known to attack Limacodidae (Nixon 1943). According to Zitani (2003) all the gregarious species of *Meteorus* can be assigned to a single monophyletic lineage. Although the gregarious New World species attacking large Sphingidae are more common and better known (Zitani *et al*. 1998), it appears that the use of smaller clumped-feeding Limacodidae may be another important target for the gregarious lineage of *Meteorus*.

Etymology: This new species in named after Sr. Leonelo Oviedo. All the type specimens were collected in the Leonelo Oviedo Ecological Reserve. Sr. Oviedo was a professor in the School of Biology at the University of Costa Rica during the 1960s and 1970s. During that time he worked on starting the ecological reserve, and he contributed more towards its development than anyone else. The ecological reserve was later named in honor of Leonelo Oviedo by Luis Fornier in recognition of Sr. Oviedo's contributions to the development of the ecological study site.

Distribution: Costa Rica. All the type specimens are reared from *V. caneti* larvae collected in the ecological reserve on campus of the University of Costa Rica, Montes de Oca, San Pedro, San José. This is the only location where the species has been found, although the host is more widely distributed.

Biology and rearing records

The hosts are late instar caterpillars of *V. caneti* feeding on *L. triandra*. Limacodidae is a new host family record for Meteorinae in Costa Rica. *V. caneti* is recorded from southern Mexico to central and northern Costa Rica (Corrales and Epstein 1997). The mature larva of *V. caneti* is semi-hard and smooth. The general color is emerald green with two yellow stripes on the latero-dorsum and a median dark reddish-brown dot on each stripe (Fig. 1). The caterpillars are solitary, feeding and resting attached to the underside of host plant leaves (Corrales and Epstein 1997). The caterpillars were only found feeding on *L. triandra*, which is commonly found in secondary growth forest (Missouri Botanical Garden 2003). In Costa Rica, the tree is found from elevations between 40 m and 1350 m on both Atlantic and Pacific slopes (INBio data 1997).

Meteorus oviedoi is a gregarious koinobiont endoparasitoid. The number of individuals that emerged per host ranged from 7 to 26 (mean = 12.5, n = 8). The ratio of females to males emerging was variable (10:16, 10:3, 10:1, 8:7, 8:2, 5:3, 5:3, 0:7).

It seems likely that the females oviposit into late instar host larvae because no *M. oviedoi* larvae emerged from host larvae collected in their early instars. On the contrary, *M. oviedoi* did emerge from host larvae collected in their last instar. There was one case where the larvae did emerge from the last instar host, which was collected at the penultimate instar. Cocoons were found hanging from underside leaves of the host plant. The *M. oviedoi* larvae spun their cocoons adjacent to the host larva, which stayed at the same spot and remained alive for two days (n=2) after the emergence of *M. oviedoi* larvae.

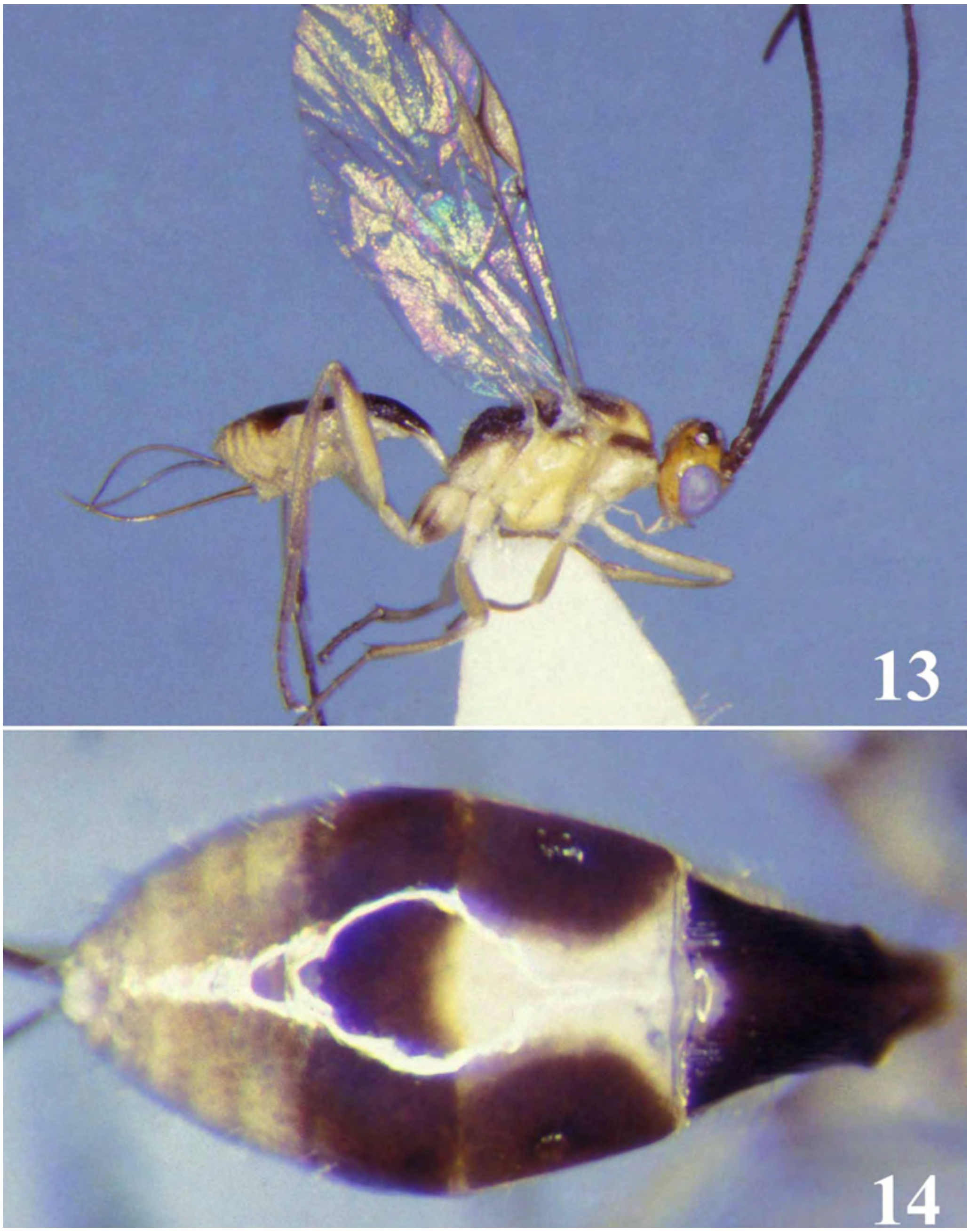

FIGURE 13. Habitus of *Meteorus oviedoi* female, lateral view, showing color patterns. **FIGURE 14.** Metasomal tergite 2 of *Meteorus oviedoi* female, dorsal view, showing median white broad hourglass-shaped pattern.

Modification of host larval behavior was observed as follows: Prior to parasitoid larval emergence, the host remained still in one spot (abaxial of a host plant leaf) without feeding for approximately half a day. After parasitoid emergence, when the host was molested (e.g. touched by a twig manually or an ant walking on top of it), it demonstrated "rocking" behavior. The larva moved the anterior 2/3 of the body upward vigorously, approximately 40 to 45 degrees from the leaf, then down, using the posterior part of the abdominal sucker as a pivot. The up and down process took about one second, and up to 14 successive movements by one contact was observed. Some of the up/down movements were somewhat less vigorous (the larva reacted more vigorously the moment right after it was molested). Also, when selected *M. oviedoi* cocoons (those in direct contact with the plant surface) or plant surface near the *V. caneti* larva were touched by a twig manually, the larva reacted in the same way as if it was directly molested. This "rocking" behavior of the host larva was not observed in molested unparasitized larvae or in molested parasitized larvae of which none of the *M. oviedoi* larvae had yet emerged. After the emergence of the third or fourth parasitoid larva the host larva started to respond to forceps-pokes by "rocking."

Observations on emergence of *M. oviedoi* larvae from the host were as follows. About 16 minutes prior to the emergence of the first larva, pinkish color and more than a dozen brownish spots were observed on the lower part of the lateral wall of the host caterpillar. Immediately before the emergence, grayish-brown spots (head and mandibles of the parasitoid larvae) were visible on lateral sides of the host larva, and through the remaining cuticle (Fig. 1). Then each larva chewed an exit hole and protruded 1/2 to 3/4 of its body, and immediately started spinning silk by attaching silk strands to the plant substrate. The amount the larval body was protruded depended on the distance between the emergence spot and the plant surface. Larvae attempted to secure a silk strand to the plant surface before emerging entirely from the host. After securing a silk line, larvae completely exited the host by bending their body towards the host and pushing against the host cuticle with their head. These exiting larvae continually ejected silk as they emerged. Upon dropping to the substrate, they immediately scooted over approximately 5 mm while wiggling and ejecting silk, and then commenced spinning cocoons.

Emergence of the larvae took approximately 2 hours and 45 minutes from the time the first larva emerged until the last larva emerged (n=1, 26 larvae/host). When the host larva was poked by forceps, the emergence of the larvae appeared to stop for a few minutes (possibly prolonging the overall emergence time).

The recently-emerged larvae spun cocoons using the apex of the last abdominal segment with the mouthparts dexterously by bending and rotating the body, head downwards. Pupation always was in the same position: head downwards (facing away from end with suspending thread), and with the meconium and last larval exuvium above (packed in the end nearest the suspending thread). The adult wasp emerged from the cocoon by cutting a circular emergence hole at the tip of the cocoon (lower end opposite suspending thread). The cocoon cap usually remained attached to the rest of the cocoon.

Peaks of the presence of mature host larvae were in the months of September, October, and November in 2002 and 2003 (M. Epstein and K. Nishida, unpublished data), and this coincided with the encounter of *M. oviedoi* cocoons hanging from the plants.

A solitary species of hyperparasitoid, *Conura* sp. (Chalcididae), was reared from field-collected *M. oviedoi* cocoons. This hyperparasitoid made a circular emergence hole laterally near the lower end of the *Meteorus* cocoon.

Discussion

As reported by Corrales and Epstein (1997), *V. caneti* was previously known in Costa Rica only from the dry forest at Santa Rosa National Park (ACG), where limacodid caterpillars have been extensively reared by D. H. Janzen (http://janzen.sas.upenn.edu/). A massive survey of Santa Rosa caterpillars was conducted from 1978-1994, during which 394 limacodid caterpillars, on 82 host plants, were reared. Of these, 15 caterpillars were *V. caneti* feeding on the lauraceous understory small tree, *Ocotea veraguensis* (Meisn.) Mez. No *M. oviedoi* were reared in the ACG from these caterpillars, but about 33% of the larvae were parasitized by a tachinid fly (*Austrophorocera* sp.). The reason for the apparent absence of *M. oviedoi* in the ACG is not known, but it could be due to climate differences between the mid-elevation site where *M. oviedoi* is found and the lowland sites in the ACG, or it could be due to differences in the host plants of the caterpillars in these areas. In Santa Rosa, *V. caneti* is restricted to feeding on *O. veraguensis*, the only native species of Lauraceae in this dry forest.

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