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Hyperparasitoid wasps (Hymenoptera, Trigonalidae) reared from dry forest and rain forest caterpillars of Area de Conservación Guanacaste, Costa Rica

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Abstract

Five species of Trigonalidae, hyperparasitoids of Ichneumonidae (Hymenoptera) and Tachinidae (Diptera) that parasitize caterpillars (Lepidoptera), have been reared during the ongoing caterpillar inventory of Area de Conservación Guanacaste (ACG), Guanacaste Province, northwestern Costa Rica: *Lycogaster apicipennis* (Cameron), *Taeniogonalos woodorum* Smith**, sp. n.**, *Taeniogonalos fasciatipennis* (Cameron), *Trigonalys championi* Cameron, and *Trigonalys maculifrons* Sharp. Morphological and DNA barcoding data support species separation of these generalist hyperparasitoids. *Taeniogonalos gundlachii* (Cresson) is not a widespread, color-variable species as previously treated and is probably confined to eastern North America. The species previously considered as *T. gundlachii* in Costa Rica is regarded as *Taeniogonalos fasciatipennis*, a species found only in ACG dry forest. *Taeniogonalos woodorum* is a similar species but found only in the ACG rain forest. Habitat and host records are given for these five species of trigonalids.

Keywords
Central America, hyperparasitoid host specificity, Lepidoptera, Diptera, DNA barcoding, tropical trophic web

Introduction

Trigonalid wasps are usually hyperparasitoids, parasitizing Ichneumonidae (Hymenoptera) and Tachinidae (Diptera) larvae that parasitize Lepidoptera caterpillars, or they are parasitoids of the larvae of social or possibly solitary wasps (Weinstein and Austin 1991, Carmean 1991, Carmean and Kimsey 1998, Murphy et al. 2009). Some species also have been recorded as primary parasitoids of sawflies in Australia (Raff 1934, Carne 1969, Weinstein and Austin 1995). Trigonalids lay numerous eggs on foliage. For larval development, it is believed the eggs must be consumed by a caterpillar that is already parasitized. The egg hatches in the caterpillar gut, and the first-instar hyperparasitoid finds its way to the primary parasitoid larva inside the caterpillar, in turn developing inside the primary parasitoid larva (Carmean 1991).

Ten species in six genera of Trigonalidae have been recorded from Costa Rica (Carmean and Kimsey 1998). Little has been published on the hosts and biology of these species. Of the ten, five have been reared from parasitoids of caterpillars during the ongoing 34-year caterpillar inventory of Area de Conservación Guanacaste (ACG) in Guanacaste Province in northwestern Costa Rica (Janzen 2000, 2001; Janzen and Hallwachs 2001; Janzen et al. 2009). Although trigonalids are routinely captured in Malaise traps for flying insects, the only known method to obtain host records is through mass rearing of wild-caught caterpillars as is being done by the ACG caterpillar inventory (Janzen et al. 2009). As of 2010, the ACG caterpillar inventory has yielded 246 trigonalid rearings from 490,000 wild-caught caterpillars (0.05% hyperparasitization frequency).

The major identification problem among the reared species is that which appears morphologically to be the color-variable and widespread species *Taeniogonalos gundlachii* (Cresson). This has been considered to be a single species, known from southeastern Canada to Cuba and Central America, following the synonymy by Carmean and Kimsey (1998) of *Taeniogonalos costalis* (Cresson) (eastern Canada and USA) under *T. gundlachii* (described from Cuba). We show that specimens reared in Costa Rica are a distinct species, *Taeniogonalos fasciatipennis* (Cameron), and should not be synonymized with the species known in eastern North America.

Here, we present morphological and DNA analysis evidence for the distinctiveness of the five reared species, one of which is new, and offer rearing records and hosts.

Materials and methods

Images were obtained using an EntoVision Imaging Suite that included a firewire JVC KY-75 3CCD digital camera mounted to a Leica M16 zoom lens via a Leica z-step

microscope stand. Multiple focal planes were merged using Cartograph 5.6.0 (Microvision Instruments, France) software.

Acronyms used are: The Natural History Museum, London, UK (BMNH); Canadian National Collection of Insects, Ottawa (CNC); Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBio), National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM). Other specimens examined in this study were kindly loaned from the Florida State Collection of Arthropods, Gainesville, FL, USA, and the collection of N. M. Schiff, Stoneville, MS, USA.

In the Costa Rican ACG inventory, each reared adult receives one voucher code, and often a second. The invariant voucher code of the form "99-SRNP-4597" (year-Santa Rosa National Park-unique rearing number) is unique for the event of finding and rearing the caterpillar, irrespective of what it produces. The entire rearing record may be obtained by searching with this code at http://janzen.bio.upenn.edu/caterpillars/database.lasso. If a hyperparasitoid wasp is DNA barcoded or otherwise treated as an individual (a "daughter specimen" of the SRNP rearing event) it is assigned a second unique voucher code of the form DHJPAR0034526 which applies only to that individual. This voucher code may be used to obtain the entire caterpillar (and wasp) rearing record from the same website and as described in Janzen (2000, 2001), Janzen et al. (2009), and Burns and Janzen (2001).

When rearing wild-caught caterpillars in the ACG inventory, wasp cocoons and tachinid fly puparia are routinely obtained and held for adult wasp and fly eclosion. There is no way to know if the wild-caught caterpillar has primary parasitoids in it, or if they in turn are hyperparasitized. Usually, primary parasitoids that are uninfected and emerge from a single caterpillar (or pupate in a caterpillar or pupal mummy) eclose during a 1–3 day period after 1–3 weeks (with a few exceptional univoltine species of primary parasitoids remaining dormant for 10–12 months). If the pupae inside these wasp cocoons or fly puparia contain a hyperparasitoid (Trigonalidae, Perilampidae, Eulophidae, or Ichneumonidae), this insect tends to eclose a few days to weeks after the eclosion of the primary parasitoid. This delay necessitates retaining and continuing to observe "dead" primary parasitoid wasp cocoons and tachinid puparia. This is especially the case if there are, for example, five tachinid puparia from one caterpillar and three of them produce tachinid flies; the remaining two are usually dead "of disease" but on rare occasions produce a trigonalid or other hyperparasitoids.

Eclosed trigonalids were killed by freezing, as are other ACG inventory insects, pinned, labeled with the above-described yy-SRNP-xxxxx label, stored frozen, and then oven-dried (40–55°C). In the University of Pennsylvania clearing center, one leg was removed and couriered to the Biodiversity Institute of Ontario (BIO) at the University of Guelph for DNA extraction, barcode amplification, and accessioning in the Barcode of Life Data System (www.boldsystems.org). At this time the leg and the corresponding specimen also received the second above-mentioned DHJPARxxxxxx voucher code, which was used in all DNA barcode analyses of ACG parasites and parasitoids. If the wasp is very small, it may be collected into 95% ethanol for refrigerated storage instead of pinned and oven-dried. This treatment of hyperparasitoids by the

inventory does not differ from that of primary parasitoids, except that more patience is required in waiting longer for hyperparasitoids to eclose.

Field identification (and later corroboration) of the host caterpillar is done by the inventory parataxonomists, later by DHJ and WH as inventory coordinators, using photographs, host remains, food plants, and microgeographic characters of caterpillars. Laboratory identification of the primary parasitoid remains was done by DHJ using intense familiarity and photographs and reference specimens with the parasitoids and their body parts (cocoons, pupae, puparia) as well as ecological information such as the identity of siblings that were not hyperparasitized. Nearly all reared parasitoids were also DNA barcoded to tease out cryptic species complexes (e.g., Smith et al 2006, 2007, 2008). Identification of the hyperparasitoid adults was achieved through all of these methods plus morphological and DNA barcode inspection of the adults by the inventory personnel and by collaborating taxonomists.

DNA extracts for 201 trigonalid specimens were prepared from single legs using a glass fibre protocol (Ivanova et al. 2006). After a re-suspension in 30 µl of dH_2O, a 658-bp region near the 5' terminus of the COI gene was amplified using primers (LepF1–LepR1) following standard (Ivanova et al. 2006) protocols. When initial amplification was not successful, composite sequences were generated using internal primers (300 bp near 5' of barcode region: LepF1/C_ANTMR1D, 400 bp near middle to 3' of barcode region: MLepF1/LepR1 and/or RonMWASPDeg_t1/LepR1). COI sequence divergences were calculated using the K2P distance model and a NJ tree of K2P distance was created to provide a graphic representation of the among-species divergences. Full details of methodology are as in (Smith et al. 2007, Smith et al. 2008). All sequence data are available on BOLD (www.boldsystems.org) in the projects called: "ACG Trigonalidae- in progress" (ASTR) and "ACG Hyperparasitoids compared to North America" (ASHYZ). All sample accessions (DHJPAR sample number, BOLD COI process ID and GenBank Accession) can be found in Supporting Information File 1.

Results

General

Five species of trigonalids are recognized from the ACG rearings. DNA barcoding suggests the existence of four entities (Figs 1, 2) of *Taeniogonalos* within the ACG. *Taeniogonalos woodorum*, occurring only in ACG rain forest, is clearly distinct genetically and morphologically from the others and is here described as new. We find *Taeniogonalos fasciatipennis* from the lowland dry forest to be distinct from the eastern North American *T. gundlachii*. Although there is genetic evidence for separation of T. *fasciatipennis* into two species, we treat them here as one, but suggest that further research will reveal that this single name covers two species, here called *T.* fasciatipennisDHJ001 from the driest parts of lowland dry forest and *T.* fasciatipennisDHJ002

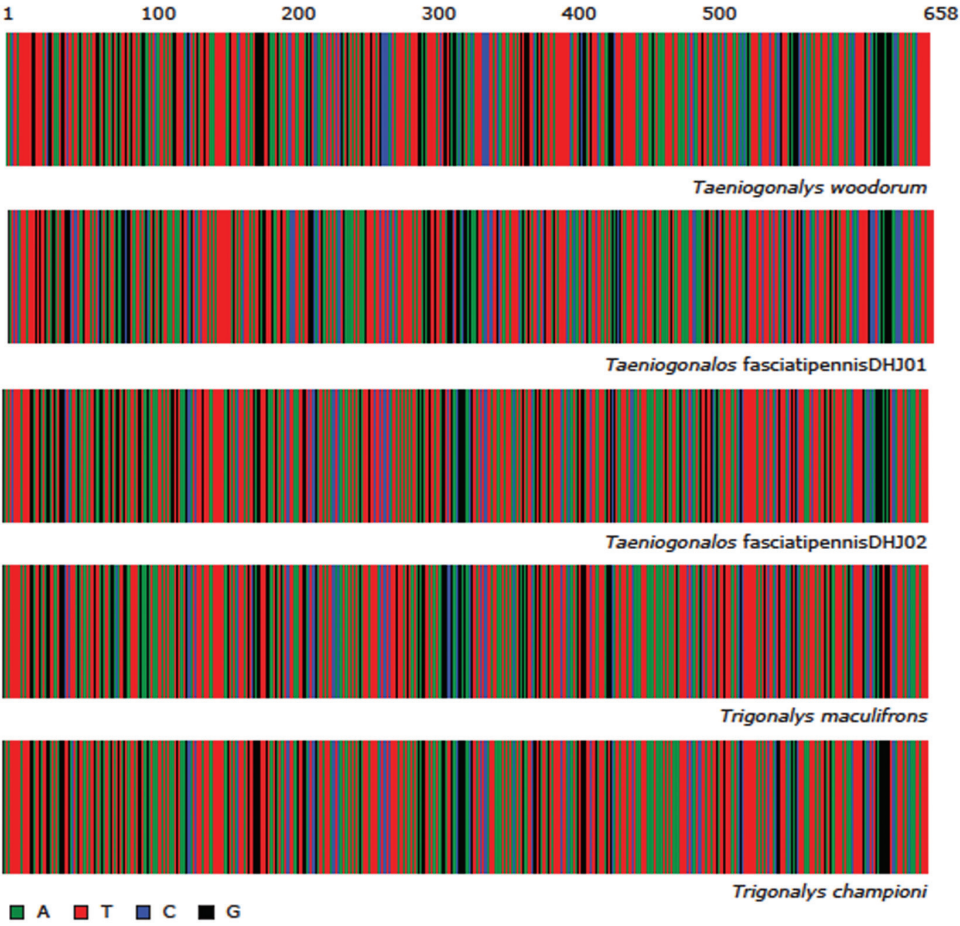

Figure 1. Color representation of the full length (658 base pairs (bp)) DNA barcodes for each of the 5 ACG trigonalid species. Intra-specific variation in the barcode region is represented by vertical bands in the color bar at that position.

from the upper, cooler, and more moist portion of the lowland dry forest (see discussion under *T. fasciatipennis*).

The very low percent yield (0.05%) of trigonalid wasps from wild-caught ACG caterpillars is partly generated by the natural history observation that trigonalids are usually not hyperparasitoids of primary parasitoids of leaf-rolling and leaf-tier caterpillars (Pyralidae, Thyrididae, Crambidae, Elachistidae, Tortricidae, etc.), which make up at least 20% of the caterpillars sampled and largely live their lives inside of leaf rolls. In other words, if just the more exposed caterpillars of the inventory are taken into account, the percent yield of trigonalids increases to (0.07%).

The inventory has to date logged about 47,000 parasitized caterpillars (9.6% parasitization frequency), and 0.59% of these yielded one or more trigonalid wasps. How-

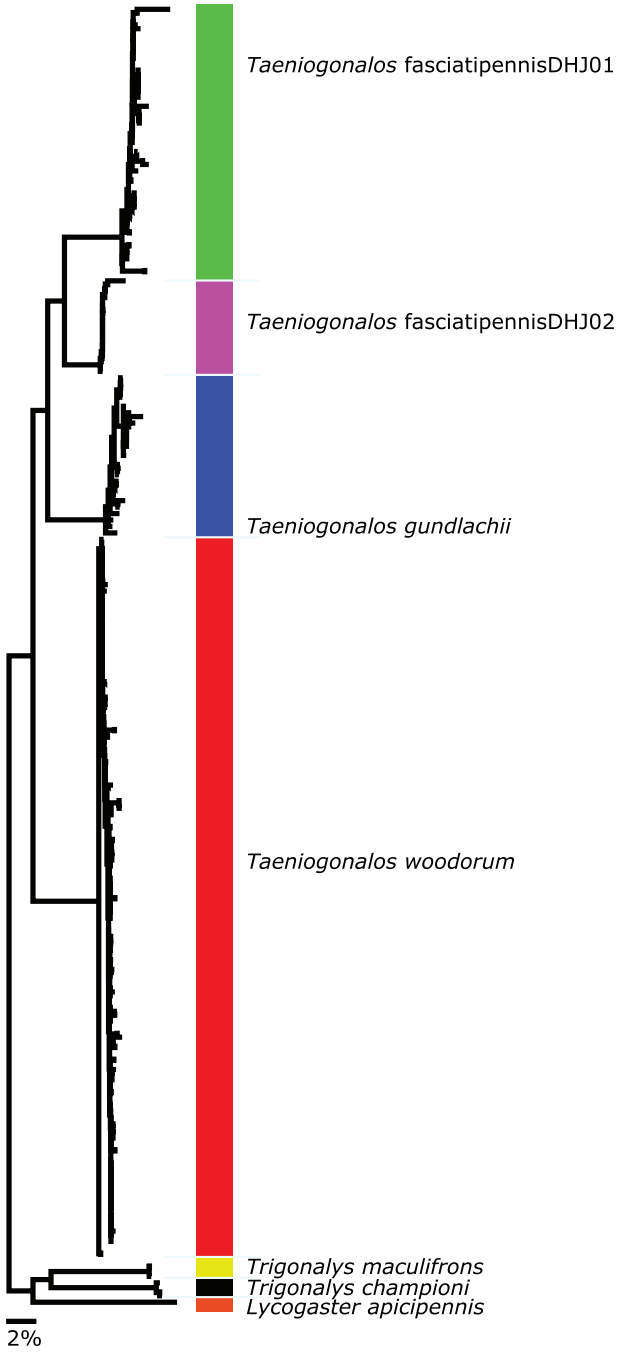

Figure 2. A neighbor-joining tree (NJ) built using Kimura 2 Parameter distance and including 201 sequenced trigonalid specimens from the ACG and North America that have COI sequence greater than 200 bp. Note the divergence between the ACG *Taeniogonalos* and the North American specimens – and within the dry forest *Taeniogonalos* fasciatipennisDHJ01 and *Taeniogonalos* fasciatipennisDHJ02 – all are clearly differentiated by mitochondrial DNA.

ever, 15,000 of these were attacked by Eulophidae and Microgastrinae Braconidae) generally too small to support the much larger trigonalid larva. For the remaining primary parasitoids (Diptera and Hymenoptera), the hyperparasitization frequency was 0.86%.

The Trigonalidae rearing experience to date shows almost no examples of sharing primary parasitoids hosts with other hyperparasitoids (Perilampidae, *Mesochorus* in the Ichneumonidae, Eulophidae, and Chalcididae). That is to say, when a clutch of tachinid puparia or microgastrine braconid cocoons produce a trigonalid wasp(s), that is the only hyperparasitoid that emerges from this clutch of primary parasitoids except in one case of sharing with a perilampid (83-SRNP-1127.2) and one case of sharing with a chalcidid (83-SRNP-1432).

Trigonalidae identification by morphology alone is made complicated by as much as 20 times variation in body weight of conspecifics, owing to the body size being determined in great part by the body size of the primary parasitoid host larva. DNA barcoding, however, of the ACG reared trigonalids has demonstrated unambiguously that specimens of this huge size range, from the same place in ACG, are the same species.

In the future, it may be possible to determine the primary parasitoid host of a wild-caught adult trigonalid through DNA barcoding of its gut content (e.g., Rougerie et al. 2011, Hrcek et al. 2011). In this case, specific primers can be designed that will ignore the DNA of the primary and secondary hosts of the hyperparasitoid and amplify the DNA of the hyperparasitoid.

The Costa Rican species of Trigonalidae

Keys to Central American and Neotropical genera of Trigonalidae were provided by Carmean (1995, 2006a, 2006b). The species recorded from Costa Rica are as follows (from Carmean and Kimsey 1998); an asterisk indicates that the species has been reared in ACG.

**Lycogaster apicipennis* (Cameron, 1897).

Nomadina smithii Westwood, 1868. Described from "Amaz." Recorded from Costa Rica by Carmean and Kimsey (1998).

Seminota depressa (DeGeer, 1773). Recorded from Brazil, Bolivia, Peru, Costa Rica by Carmean and Kimsey (1998).

Seminota laeviceps (Cresson, 1879). Described from Mexico. Recorded from Costa Rica, Panama by Carmean and Kimsey (1998).

**Taeniogonalos fasciatipennis* (Cameron, 1897).

**Taeniogonalos woodorum* (described below).

Taeniogonalos ornata (Smith, 1861). Recorded from Mexico and Costa Rica by Carmean and Kimsey (1998).

**Trigonalys championi* Cameron, 1897.

**Trigonalys maculifrons* Sharp, 1895.

Xanthogonalos robertibuyssoni Schulz, 1907. Described from Mexico. Recorded from Costa Rica by Carmean and Kimsey (1998).

Species reared

***Lycogaster apicipennis* (Cameron)**
http://species-id.net/wiki/Lycogaster_apicipennis
Figure 3

Trigonalys apicipennis Cameron, 1897: 269.

Discussion. This is the only species of *Lycogaster* known from Central America. It is distinguished by its spindle-shaped antennae, without tyloids, and with the basal 3 flagellomeres reddish brown (Fig. 3). The head and thorax are mostly black with only the tegula and spot on upper mesopleuron yellow, and the head and body are covered with golden-yellow hairs. The wings are yellowish, darker anteriorly and at apices, with the veins yellowish and stigma black.

Lycogaster apicipennis is between 16–18% different (K2P distance model) from other Trigonalidae in the ACG in the CO1 mtDNA barcode region.

Distribution. Costa Rica, Mexico (Carmean and Kimsey 1998).

Specimens examined. 10, 7 of which are barcoded. Deposited in USNM, INBio.

Hosts and biology. The ACG caterpillar inventory has reared *Lycogaster apicipennis* 10 times (between 1990 and 2008), and always in lowland dry forest. Six rearings have

Figure 3. *Lycogaster apicipennis* female, lateral view.

been from *Enicospilus* flavostigmusDHJ02 (Ichneumonidae) parasitizing *Boriza crossaea* Druce (Notodontidae), once from *Enicospilus flavostigma* Hooker parasitizing *Dicentria* rusticaDHJ05 (Notodontidae), two from *Cubus* validusDHJ03 (Ichneumonidae) parasitizing *Omiodes cuniculalis* Guenée (a large leaf-rolling Crambidae), respectively, and once from *Bassus brooksi* Sharkey (a large solitary Agathidinae Braconidae parasitizing *Epargyreus* in the Hesperiidae). If these primary parasitoid genera are viewed as the possible host universe, 2,377 caterpillars attacked by them yielded 10 *L. apicipennis* (0.42% frequency). Alternatively, if we use the genera of the host caterpillars (*Boriza, Dicentria, Omiodes, Epargyreus*) in the inventory as the available universe, 17,007 reared wild caught caterpillars yielded these ten *L. apicipennis* (0.059% frequency). This is a low density hyperparasitoid. The first six rearings (1990–1995) were all from *Enicospilus* flavostigmusDHJ02 parasitizing *Boriza crossaea* in ACG, and it would have been reasonable to label this wasp as a specialist to this host combination, but subsequent rearings makes it evident that it is at best a specialist on relatively large primary parasitoid wasps (and there is no suggestion that it is a hyperparasitoid of tachinid fly larvae, despite their being commonplace primary parasitoids of *Boriza crossaea*).

***Taeniogonalos woodorum* Smith, sp. n.**
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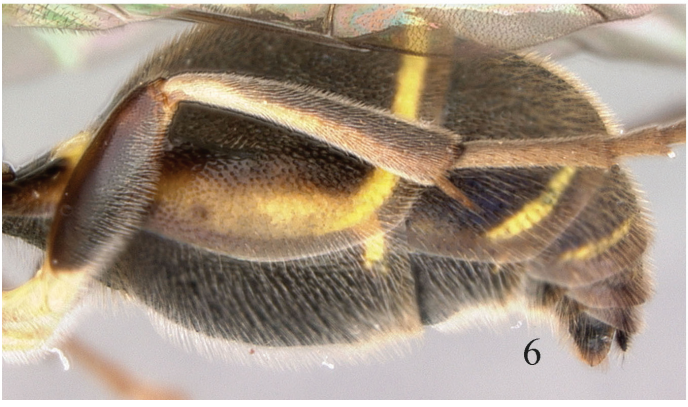
http://species-id.net/wiki/Taeniogonalos_woodorum
Figures 4–7

Diagnosis. Posterior postocellar area with two yellow oblique stripes; mandible mostly yellow, teeth reddish brown; gena mostly yellow, yellow extending dorsally and onto occiput; mesoscutellum with anterior third yellow; second metasomal tergum with narrow yellow band continuous along lateral and posterior margins. Female armature absent. Male with medial flattened area on sternum 2; genitalia with parameres about half as long as gonostipes.

Female. Length, 5.0–12.0 mm (holotype 8.0 mm). Antenna black. Head black, with following yellow (Figs 4. 5): Interantennal area, supraclypeal area, clypeus, labrum, mandible except reddish-brown apex, mouthparts, two oblique stripes at posterior or postocellar area, broad stripe on gena behind eyes extending dorsally onto occiput. Mesosoma black with following yellow markings (Figs 4, 5): anterolateral spot on mesoprescutum, axillae, anterior third of mesoscutellum, metascutellum, stripe on upper pronotum and lower pronotum, broad oblique stripe on mesopleuron, broad oblique stripe on metapleuron, large lateral spots on propodeum. Legs black with inner surfaces of coxae, trochanters, extreme bases of femora, and outer surfaces of tibiae and tarsi yellow. Metasoma black with following yellow markings (Figs 4–6): broad stripe on posterior margin of tergum 1, narrow continuous stripe on posterior and lateral margins of tergum 2; narrow stripe on posterolateral margins of terga 3 and 4, small spot on posterior lateral margin of sternum 2. Wings hyaline, black anterioapically, mostly in radial cell; veins and stigma black. Head and body covered with fine, short,



Figures 4–7. *Taeniogonalos woodorum*. **4** Lateral view, female **5** Dorsal view, female **6** Metasoma, lateral view, female **7** Male genitalia.

white hairs. *Head*: Covered with short, white hairs. Shiny, evenly punctate, punctures mostly separated by rounded ridges, interspaces less than puncture diameters; punctures on gena less dense, farther apart than those on vertex and frons, and with flat shiny

interspaces. Antenna with 24 flagellomeres, length about twice head width. Clypeus with median length about .3× width. Inner margins of eyes subparallel, lower interocular distance 0.7× eye length; malar space about 0.15× eye length. Distance between eye and margin of lateral ocellus about 3.0× distance between inner margins of hind ocelli. Area between torruli slightly concave (Fig.5). Antennal carinae low, sharp. Occipital carina complete. *Mesosoma*: Covered with short, white hairs. Shiny, evenly punctate with punctures similar to those on vertex and frons, most separated by rounded ridges, with interspaces less than puncture diameters; punctures on propleuron farther apart than those on mesonotum and separated by broader, flat interspaces; dorsoposterior section of mesepisternum, posterior downturned margin of mesoscutellum, and metapleuron, except lower margin, almost impunctate; punctures on propodeum small, denser than those on rest of mesosoma. Prescutum elevated above lateral lobes. Notaulus deep, with large punctures posteriorly; transverse row of large punctures anterior to mesoscutellum. Propodeal foramen shallowly concave at center. Hind coxa about as long as wide, with longitudinal carina on outer surface; hind basitarsomere subequal to length of remaining tarsomeres combined. *Metasoma*: Covered with fine, white hairs. Shiny, rather evenly punctate, punctures separated by rounded ridges mostly less than puncture diameters. Tergum 1 depressed at center. Armature absent from sternum 2 (Figs 4, 6). Sheath directed downward, rounded at apex in lateral view.

Male. Length, 4.0–7.5 mm. Color and structure similar to female. Tyloids present, long and narrow, middle tyloids longer than half length of flagellomeres. Male genitalia with parameres about half-length of gonostipes (Fig. 7); sternum 2 with medial flattened area on apical half.

Type material. Holotype female, "Voucher: D. H. Janzen & W. Hallwachs, DB: http://Janzen.sas.upenn.edu, Area de Conservation Guanacaste, Costa Rica," "10-SRNP-22162," "DHJPAR0041177." (USNM). Paratypes: Same data as for holotype except caterpillar rearing code (yy-SRNP-xxxx) and parasitoid individual code (DHJPARxxxxxxx); one specimen for each caterpillar collection and parasitoid rearing code. 98-SRNP-6785, DHJPAR0010613 (♂); 98-SRNP-7262, DHJPAR0016904 (♂); 98-SRNP-7361, DHJPAR0016911 (♀); 98-SRNP-15545, DHJPAR0016916 (♀); 98-SRNP-15545, DHJPAR0016899 (♀); 98-SRNP-15545, DHJPAR0016888 (♂); 99-SRNP-5503, DHJPAR0016895 (♀); 99-SRNP-5508, DHJPAR0016897 (♂); 99-SRNP-12098, DHJPAR0016891 (♀); 99-SRNP-12098, DHJPAR0016892 (♂); 99-SRNP-12098, DHJPAR0016896 (♀); 99-SRNP-12761, DHJPAR0010612 (♀); 99-SRNP-12852, DHJPAR0010604 (♂); 99-SRNP-13819, DHJPAR0010611 (♂); 99-SRNP-13823, DHJPAR0016909 (♀); 01-SRNP-3507, DHJPAR0010598 (♀); 01-SRNP-3507, DHJPAR0010599 (♀); 01-SRNP-5325, DHJPAR0010597 (♂); 01-SRNP-5932, DHJPAR0010605 (♀); 01-SRNP-9359, DHJPAR0010607 (♀); 01-SRNP-25186, DHJPAR0010600 (♂); 02-SRNP-7679, DHJPAR0010596 (♀); 02-SRNP-7978, DHJPAR0010595 (♀); 03-SRNP-6738, DHJPAR0010588 (♂); 03-SRNP-10070, DHJPAR0010585 (♀); 03-SRNP-11855, DHJPAR0010591 (♂); 03-SRNP-11855, DHJPAR0010592 (♂); 03-SRNP-11855, DHJPAR0010593 (♂); 03-SRNP-11855, DHJPAR0010594 (♂); 03-SRNP-20157, DHJPAR0010590

(♀); 03-SRNP-20236, DHJPAR0028047 (♀); 03-SRNP-21817, DHJPAR0010586 (♀); 04-SRNP-30072 [no barcode] (♀); 04-SRNP-41595, DHJPAR0010574 (♂); 04-SRNP-55214, DHJPAR0010571 (♀); 04-SRNP-55214.1, DJHPAR0010572 (♀); 04-SRNP-55215, DHJPAR0010573 (♀); 04-SRNP-56432, DJHPAR0010581 (♀); 04-SRNP-56458, DHJPAR0010582 (♀); 05-SRNP-4939, DHJPAR0010559 (♂); 05-SRNP-7881, DHJPAR0010551 (♂); 05-SRNP-33818, DHJPAR0010569 (♂); 05-SRNP-34358, DHJPAR0010562 (♂); 05-SRNP-42584, DHJPAR0010563 (♂); 05-SRNP-42827, DHJPAR0010570 (♂); 05-SRNP-70122, DHJPAR0010560 (♂); 05-SRNP-70325, DHJPAR0010561 (♀); 06-SRNP-6781, DHJPAR0016876 (♀); 06-SRNP-6781, DHJPAR0016877 (♀); 06-SRNP-6781, DHJPAR0016878 (♂); 06-SRNP-6781, DHJPAR0016884 (♀); 06-SRNP-30294, DHJPPAR0010443 (♂); 06-SRNP-30295, DHJPAR0010554 (♂); 06-SRNP-33412, DHJPAR0016873 (♀); 06-SRNP-34200, DHJPAR0016875 (♀); 06-SRNP-34577, DHJPAR0016886 (♀); 06-SRNP-34579, DHJPAR0016887 (♂); 06-SRNP-42284, DHJPAR0010555 (♀); 06-SRNP-42284, DHJPAR0010556 (♂); 06-SRNP-42284, DHJPAR0010557 (♂); 06-SRNP-42814, DHJPAR0016882 (♀); 06-SRNP-42819, DHJPAR0016883 (♀); 06-SRNP-43560, DHJPAR0016874 (♀); 06-SRNP-65304, DHJPAR0016885 (♂); 08-SRNP-2414, DHJPAR0027762 (♂); 08-SRNP-2414, DHJPAR0027763 (♂); 08-SRNP-6017, DHJPAR0030373 (♂); 08-SRNP-32269, DHJPAR0030377 (♀); 08-SRNP-41835 [no barcode] (♀); 08-SRNP-42172, DHJPAR0030374 (♀); 08-SRNP-42172, DHJPAR0030375 (♀); 08-SRNP-42172, DHJPAR0030376 (♀); 09-SRNP-2888, DHJPAR0036406 (♀); 09-SRNP-5008, DHJPAR0036682 (♀); 09-SRNP-32681, DHJPAR0038544 (♀); 09-SRNP-32752, DHJPAR0038545 (♀); 09-SRNP-32752, DHJPAR0038546 (♀); 09-SRNP-33385, DHJPAR0038543 (♂); 09-SRNP-69541, DHJPAR0036404 (♂); 09-SRNP-70610, DHJPAR0036405 (♀); 09-SRNP-73449, DHJPAR0037846 (♂); 09-SRNP-80526, DHJPAR0037847 (♂); 10-SRNP-1030, DHJPAR0039355 (♀); 10-SRNP-4609, DHJPAR0041181 (♀); 10-SRNP-22641, DHJPAR0041178 (♂); 10-SRNP-32041, DHJPAR0041179 (♂); 10-SRNP-42215, DHJPAR0041180 (♀); 10-SRNP-73124, DHJPAR0041176 (♀); 10-SRNP-73289, DHJPAR0041174 (♀); 10-SRNP-80666, DHJPAR0041175 (♂); 11-SRNP-2784, DHJPAR0045823 (♀); 11-SRNP-2784, DHJPAR0045824 (♂); 11-SRNP-2859, DHJPAR0044983 (♀); 11-SRNP-2911, DHJPAR0045822 (♂); 11-SRNP-71666, DHJPAR0045825 (♂); 11-SRNP-80954, DHJPAR0044984 (♀). Deposited in INBio, USNM, CNC, BMNH.

Other specimens. 03-SRNP-38118, DHJPAR0010587 (metasoma missing); 06-SRNP-6781, DHJPAR0016872 (metasoma missing); 09-SRNP-72860, DHJPAR0040090 (broken).

Specimens examined. 100; 98 submitted for DNA barcoding, 89 of which yielded complete DNA barcodes publically available from BOLD.

Etymology. *Taeniogonalos woodorum* is named in honor of Monty and Grace Wood of Ottawa, Canada in recognition of their three decades of intense and enthusiastic taxonomic and spiritual participation in the tachinid fly inventory of Area de Conservación Guanacaste and in INBio's inventory of the flies of Costa Rica.

Barcode. The DNA barcodes of the 89 *Taeniogonalos woodorum* specimens longer than 400 bp have less than 1% intraspecific divergence (0.702% avg, max 2.523%, min, 0%). They are 9% divergent from the DNA barcodes of *T.* fasciatipennisDHJ01 and *T*. fasciatipennisDHJ02.

Discussion. The mostly black color with yellow maculation, as described and illustrated, and lack of female armature on metasomal sternum 2 help distinguish this species from most other New World species of *Taeniogonalos*. The females of *T. fasciatipennis*, *T. gundlachii*, *T. lugubris* (Westwood), and *T. ornata* (Smith) have distinct armature on sternum 2, and the latter three are mostly yellow or reddish-brown with black maculation. The females of *T. enderleini* (De Santis) and *T. jucunda* (Westwood) from South America lack female armature. *Taeniogonalos enderleini* occurs in southeastern Brazil, is mostly black with some yellow maculation, but the posterior lower part of the mesopleuron and the metapleuron are reddish brown and the postocellar area lacks yellow marks. *Taeniogonalos jucunda* (Westwood) was described from "Amaz.", and the color was described as mostly reddish brown, head yellow, and the scutellum black, all of which differ from the color of *T. woodorum*.

Hosts and biology. *Taeniogonalos woodorum* is the most frequently reared of the ACG Trigonalidae, known only from ACG rain forest, and superficially resembles *Taeniogonalos fasciatipennis* and *Taeniogonalos gundlachii* (see below). It is the only species of trigonalid that has been reared from the sample of more than 220,000 wild-caught ACG rain forest caterpillars. This microgeographic and ecosystem separation from the parapatric and adjacent ACG dry forest of *Taeniogonalos fasciatipennis* (see below) allows first-pass species-level identification of *Taeniogonalos woodorum* even if key morphological traits are invisible and DNA barcodes have not been obtained from the specimen, such as when the reared wasp escapes or the abdomen is broken off and lost or consumed in analysis. This method of ecology-based identification cannot, however, be used for specimens from the narrow ecotone between ACG dry forest and rain forest, where both species of *Taeniogonalos* have been reared from caterpillars found in the same hectare. The presence of *Taeniogonalos woodorum* was first noticed in 2006 by its strikingly different (15%) DNA barcode from that of *Taeniogonalos fasciatipennis* (also called *Taeniogonalos gundlachii* at that time). Adult *Taeniogonalos woodorum*, as is the case with the other ACG *Taeniogonalos*, is a Batesian and Mullerian mimic of *Polybia* wasps (Vespidae; abundant in ACG) in body size, color pattern, and flight/walking behavior.

Taeniogonalos woodorum has been reared 97 times from 14 caterpillar families (Arctiidae, Crambidae, Elachistidae, Geometridae, Hesperiidae, Lasiocampidae, Noctuidae, Notodontidae, Nymphalidae, Pyralidae, Saturniidae, Sphingidae, Thyrididae, Uraniidae), parasitized by Braconidae (*Bassus, Dolichogenidea, Glyptapanteles, Meteorus, Stantonia, Zelomorpha*), Ichneumonidae (*Agrypon, Charops, Dusona, Eiphosoma, Hyposoter, Leurus, Microcharops, Xiphosomella, Zaglyptomorpha*) and Tachinidae (at least *Anoxynops, Agryrochaetona, Argyrophylax, Belvosia, Calolydella, Campylochaeta, Chrysotachina, Drino, Eucelatoria, Eujuriniodes, Eumea, Genea, Houghia, Hyphatrophaga, Lespesia, Patelloa, Phytomyptera, Winthemia*). The host caterpillars of these primary parasitoids may all be characterized as exposed leaf feeders (even these par-

ticular species of leaf rollers and tiers, Crambidae, Elachistidae, Pyralidae, Thyrididae, venture out of their leaf-silk nests to feed on fully exposed leaf blades), and no one species dominates this diverse list. While it is evident that *Taeniogonalos woodorum* can develop in a very wide variety of host caterpillars and primary parasitoids, experience with other apparent "generalists" in the ACG inventory warns that when much larger sample sizes have accumulated, it may become evident that certain taxa and ecologies are either being avoided by ovipositing wasps or the eggs/larvae do not survive their tour in the host or primary parasitoid.

It remains a mystery as to why this hyperparasitoid remains microgeographically restricted to ACG rain forest and does not venture into the extensive adjacent dry forest with its many thousands of species of potential caterpillar and primary parasitoid hosts only a few hundred meters away. Indeed, there is a single record of *Taeniogonalos woodorum* (DHJPAR0016846) well into the microgeographic distribution of *Taeniogonalos* fasciatipennisDHJ02 (see below), emphasizing the parapatric nature of the distribution of these two species of *Taeniogonalos.* However, in remaining restricted to rain forest, it is representative of the thousands of other species of ACG Lepidoptera, Hymenoptera, and Diptera which are faithful to their respective ecosystems, even at the time when the intense six month rainy season turns the adjacent dry forest in a very wet ecosystem.

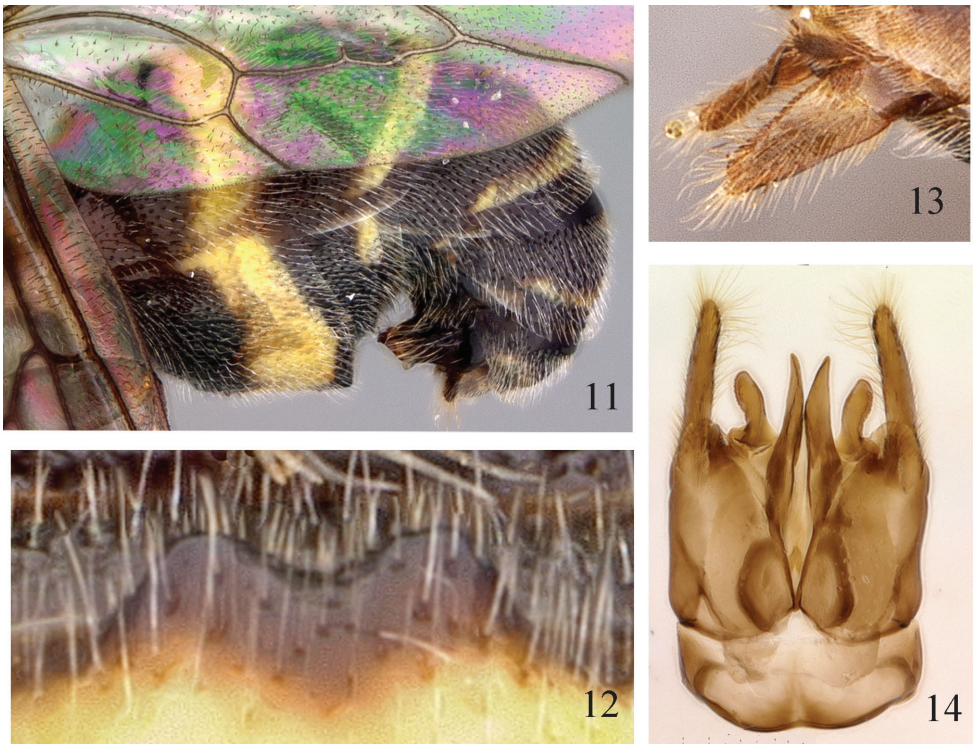
***Taeniogonalos fasciatipennis* (Cameron)**
http://species-id.net/wiki/Taeniogonalos_fasciatipennis
Figures 8–14

Trigonalys fasciatipennis Cameron, 1897: 271.
Taeniogonalos gundlachii (in part): Carmean and Kimsey 1998: 67.

Discussion. This species is distinguished as follows: vertex black; mandible outer surface black, upper surface yellow, teeth reddish brown; clypeus with large yellow spot on each side; narrow yellow line on gena on hind orbit (Figs 8, 10); mesoscutellum entirely yellow or with thin medial black stripe; second metasomal tergum with broad posterior transverse band, not extended laterally (Figs 8, 10). Female armature present, in ventral view with lobes short and with shallow central depression (Fig. 12), in lateral view, posterior and ventral sides perpendicular, not directed downward at apex (Figs 8, 11); male genitalia with paramere long, about three-quarters length of gonostipes (Fig. 14); paramere in lateral view with dorsal margin straight (Fig. 13), without slight depression.

Taeniogonalos fasciatipennis was described by Cameron (1897) from two Mexican specimens, a female from "Atoyac in Vera Cruz" and a male from "Venta de Zopilote in Guerrero." The male from the State of Guerrero was chosen as the lectotype by Carmean and Kimsey (1998). This lectotype (BMNH, examined) is morphologically identical to males reared as this species from ACG. It is noteworthy that the region around the type locality in Mexico is ecologically the same kind of tropical dry for-

Figures 8–10. *Taeniogonalos fasciatipennis,* female. **8** *T*. fasciatipennisDHJ01, lateral view **9** *T*. fasciatipennisDHH01, dorsal view **10** *T*. fasciatipennisDHJ02, lateral view.



Figures 11–14. *Taeniogonalos* fasciatipennis DHJ01. **11** Metasoma, lateral view, female **12** Female armature, sternum 2, ventral view **13** Male paramere, lateral view **14** Male genitalia.

est ecosystem as is the dry forest of ACG and shares a very large number of species of plants and insects with it.

The female syntype (not examined) from Veracruz was treated by Carmean and Kimsey (1998) as the "same" as *Taeniogonalos gundlachii*. It may not be the same species as the lectotype, and some of the specimens treated as *T. fasciatipennis* by Carmean and Kimsey (1998) are probably the species we here describe as *T. woodorum*.

This and the species from North America and Cuba have long been regarded as the "*gundlachii*" group, the members of which are distinguished from others by having similar color and the presence of distinctive female armature. However, *Taeniogonalos fasciatipennis* can be distinguished from North American *Taeniogonalos gundlachii* by the female armature and male parameres as described above. *Taeniogonalos fasciatipennis* is morphologically separable from *Taeniogonalos woodorum* by the former having the female armature present and the male paramere short in relation to the gonostipes.

The DNA barcodes of *Taeniogonalos fasciatipennis*DHJ01 and *T. fasciatipennis*-DHJ02 are 5.66% divergent from each other in the COI barcode region and both are 9% divergent from *T. woodorum.*

Distribution. Mexico and Costa Rica.

Specimens examined. *T.* fasciatipennisDHJ01 53, 42 barcoded; *T.* fasciatipennisDHJ02 15, 13 barcoded. Deposited in USNM, INBio, CNC, BMNH.

Hosts and biology. In the absence of genetic information, *Taeniogonalos fasciatipennis* appears to be one morphologically distinctive species that occurs throughout ACG dry forest (85 m to about 1300 m elevation) and does not occur in adjacent ACG rain forest or cloud forest. It is a hyperparasitoid of a wide variety of caterpillar and primary host species (see below). However, DNA barcoding has revealed that this morphologically-distinct species is divided into two distinct mitochondrial types in the ACG dry forest. One, baptized here as *Taeniogonalos* fasciatipennisDHJ01 (Figs 8, 9, 11–14) is an interim name in the inventory website database (http://janzen.bio.upenn.edu/caterpillars/database.lasso) and occurs throughout the ACG dry forest (85 to 700 m elevation). The other, interim name *Taeniogonalos* fasciatipennisDHJ02 (Fig. 10), has a very distinctive microgeographic distribution. Twelve of the 13 records are from the intermediate elevation southwest facing slope of the volcanic massif of Rincon de la Vieja (325–1276 m elevation in Sector Mundo Nuevo of ACG). The single other rearing record (two individuals from tachinid fly puparia from the same caterpillar) is from a site that is an ecogeographic analogue in biota, elevation, and climate to the Sector Mundo Nuevo site (600 m on the southwest facing slope of Volcan Cacao in Sector Cacao of ACG). *Taeniogonalos* fasciatipennisDHJ01 is probably the same as the lectotype from western (dry forest) Mexico, but since there is no present way to know for certain, both *T.* fasciatipennisDHJ01 and *T.* fasciatipennisDHJ02 have to be treated as interim names, and are therefore not italicized (and see below).

In general terms, *T.* fasciatipennisDHJ01 conspicuously ranges from the driest parts of ACG dry forest to its intermediate-elevation intersection with cloud forest and rain forest, and *T.* fasciatipennisDHJ02 is restricted to the upper, cooler, moister portion of this range. To emphasize the cooler and moister aspect of this very small range, there is even a single specimen (DHJPAR0016846) of the rain forest specialist, *Taeniogonalos woodorum,* from the very center of the range of *T.* fasciatipennisDHJ02. While *T.* fasciatipennisDHJ01 has not been found in the Sector Mundo Nuevo exact site occupied by *T.* fasciatipennisDHJ02, and thus they are parapatric, *T.* fasciatipennisDHJ01 is absolutely sympatric with the single record of *T. fasciatipennis*DHJ02 on the southwestern slopes of Volcan Cacao.

This situation creates two different taxonomic problems. First, since the two apparent ACG species within what appears morphologically to be *Taeniogonalos fasciatipennis* currently cannot be distinguished by any morphological trait, there is no way to know which of the two matches the lectotype from the State of Guerrero, Mexico. It is also possible that neither does. Second, the presence of two sympatric/parapatric species of "*Taeniogonalos fasciatipennis*" in the small area of ACG raises the spectre that this species of wasp may be a complex of sibling (cryptic) species. In contrast to parallel cases with extremely host-specific Microgastrinae Braconidae (e.g., Smith et al. 2008)

or Tachinidae (Smith et al. 2007), the unambiguously generalist host-selection and/or larval-survival ability of *Taeniogonalos fasciatipennis* excludes the use of host records as a way to verify or predict the presence of cryptic species.

If *T.* fasciatipennisDHJ02 were not distinctive by barcode from *T.* fasciatipennisDHJ01 (Fig. 2), it would not have been noticed. *Taeniogonalos* fasciatipennisDHJ01 and *T.* fasciatipennisDHJ02 have the same extremely varied lists of caterpillar and primary parasitoid hosts. In brief, *T.* fasciatipennisDHJ01 has been reared and barcoded 48 times from nine Lepidoptera families: Crambidae, Hesperiidae, Megalopygidae, Noctuidae, Nymphalidae, Papilionidae, Saturniidae, Sphingidae, and Uraniidae. While 53 more specimens of *T. fasciatipennis* have been raised, until (and if) those specimens are successfully barcoded, we cannot categorize them as *T.* fasciatipennisDHJ01 or *T.* fasciatipennisDHJ02.

In all cases, the primary parasitoid host was Tachinidae: *Acantholespesia, Belvosia, Blepharipa, Calolydella, Carcelia, Chetogena, Drino, Eucelatoria, Hemisturmia, Houghia, Hyphantrophaga, Leschenaultia, Lespesia, Patelloa, Winthemia,* and *Zizyphomyia.* If we add to this the other specimens of "*T. fasciatipennis*" that were not successfully barcoded but occupy the ACG ecosystem occupied by *T.* fasciatipennisDHJ01 a few more Lepidoptera families and tachinid genera are added to these lists, as well as three large-bodied genera in the Ichneumonidae (*Enicospilus, Pedinopelte, Trogus)*.

Taeniogonalos fasciatipennisDHJ02 has been reared 13 times from parasitoids of Crambidae, Hesperiidae, Noctuidae, Notodontidae, Nymphalidae, Riodinidae, Saturniidae, and Sphingidae. The primary host genera are Tachinidae (*Blepharipa, Drino, Houghia, Lespesia, Patelloa*), Ichneumonidae (*Enicospilus*) and Braconidae (Macrocentrinae).

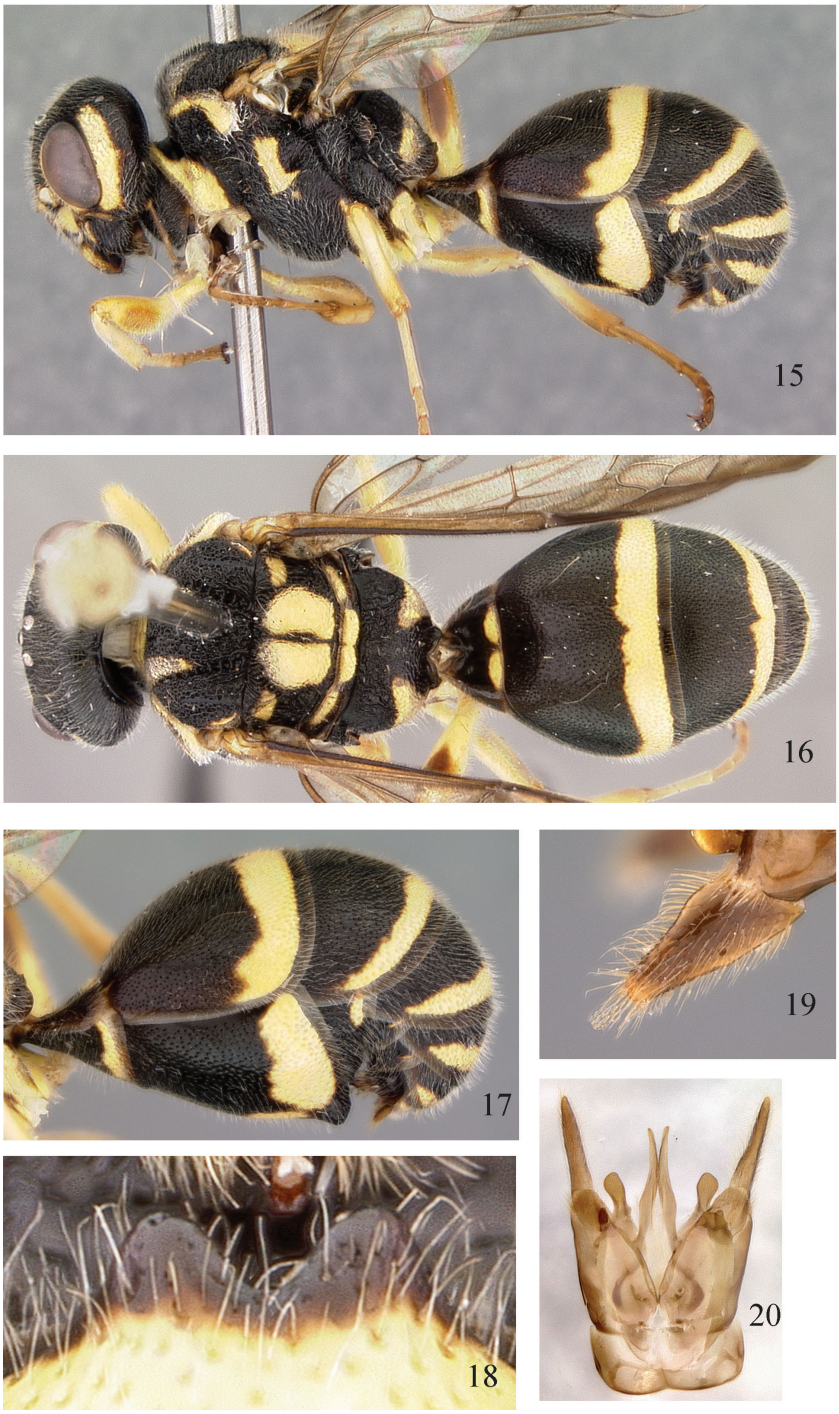
Taeniogonalos gundlachii (Cresson)

http://species-id.net/wiki/Taeniogonalos_gundlachii
Figs 15–20

Trigonalys Gundlachii Cresson, 1865: 10.
Trigonalys (*Lycogaster*) *costalis* Cresson, 1867: 352.
Trigonalis sulcatus Davis, 1898: 349

Discussion. This species is noted here because Costa Rican specimens of *Taeniogonalos* have been previously identified as belonging to this species. Carmean and Kimsey (1998) regarded *T. gundlachii* as a widespread, color-variable species occurring from Canada to Central America. They stated that "Specimens of '*T. costalis*' from North and Central America have less extensive yellow markings than *T. gundlachii* from Cuba, but specimens from Florida are intermediate." All specimens we have seen from Costa Rica are *Taeniogonalos woodorum* and *Taeniogonalos fasciatipennis*, both of which are separated from *T. gundlachii* of North America by morphology and DNA barcoding.

The color of *T. gundlachii* (Figs 15–17) is very similar to *T. fasciatipennis* (Figs 8–10) from Costa Rica, but we noted several morphological differences which appear



Figures 15–20. *Taeniogonalos gundlachii*. **15** Lateral view, female **16** Dorsal view, female **17** Metasoma, lateral view, female **18** Female armature, sternum 2, ventral view **19** Male paramere, lateral view **20** Male genitalia.

consistent in specimens examined: lobes on female armature on sternum 2 in ventral view much longer and central emargination deeper (Fig. 18) than in *T. fasciatipennis* (Fig. 12); female armature in lateral view more rounded, and slightly protruding ventrally (Fig. 17) than the squared appearance in *T. fasciatipennis* (Fig. 11); male paramere slightly indented dorsally (Fig. 19) rather than straight in *T. fasciatipennis* (Fig. 13).

Specimens from the northern parts of the range of *T. gundlachii*, northeastern United States and Canada, are relatively uniform in color, black with yellow maculation as in Figs 15–17. Specimens from Cuba, Florida, Louisiana, and Texas have a broader yellow band on the inner and outer orbits; legs all yellow with only coxae black; male with one yellow band on the metasoma, and female with 3–4 yellow bands. We have not seen specimens from the area between Texas and Guerrero, Mexico, and have seen only the type of *T. fasciatipennis* from Mexico and one specimen from El Salvador which appears to be *T. fasciatipennis*.

It is not our intent here to resolve the entire taxonomic problem and there is not enough material available from Cuba and intermediate ranges. Therefore, we continue to apply the name *T. gundlachii* to the specimens from Canada to Cuba, while suspecting that those from Canada and eastern U. S. eventually will again be called *T. costalis*. Though we cannot deny the possible presence of *T. gundlachii* in Costa Rica, the ACG dry forest specimens reared in this study are different from those from North America, and thus we refer them to *T. fasciatipennis*.

The DNA barcode for specimens from Virginia, West Virginia, and Mississippi is 8.6% divergent from *T. woodorum* and 7.49–7.75% divergent from *T.* fasciatipennis-DHJ02 *and T.* fasciatipennisDHJ01, respectively.

Distribution. Canada to Cuba, and west to Wisconsin and Texas.

Specimens examined. 200+; 25 DNA barcoded. Deposited in USNM.

Hosts and biology. See Smith 1996, Carmean and Kimsey 1998, and Krauth and Williams 2006.

Key to *Taeniogonalos* species in Costa Rica

1 Predominately yellow with black maculations ..... ***T. ornata***

– Predominately black with yellow markings (as in Figs 4–6, 8–10)..... **2**

2 Vertex with two oblique yellow stripes; yellow on gena broad, extending dorsally to occiput (Figs 4, 5); anterior half or third of mesoscutellum yellow (Fig. 5); mandible mostly yellow; female armature absent (Fig. 6); male parameres short, about half length of gonostipes (Fig. 7); ACG rain forest ..... ***T. woodorum***

– Vertex black; yellow on gena confined to narrow stripe on hind orbit (Figs 8, 10); metascutellum mostly yellow; mandible mostly black; female armature present (Figs 11, 12); male parameres longer, about ¾ length of gonostipes (Fig. 14); ACG dry forest..... ..... ***T.* fasciatipennisDHJ01 and *T.* fasciatipennisDHJ02**

***Trigonalys championi* Cameron**
http://species-id.net/wiki/Trigonalys_championi
Figures 21, 22

Trigonalys championi Cameron, 1897: 273.

Discussion. This strikingly large species is mostly black, shiny, with the propodeum and first metasomal segment contrastingly white; the forewing is darkly infuscated with only the extreme apex and posterior margin somewhat lighter (Figs 21, 22).

The *Trigonalys championi* DNA barcode is 13–17 % different from other Trigonalidae in the ACG.

Distribution. Guatemala, Costa Rica (Carmean and Kimsey 1998).

Specimens examined. 5; 5 barcoded. Deposited in USNM, INBio.

Hosts and biology. This species has been reared just four times, always from ACG dry forest and its ecotone with rain forest, and always from the large primary parasitoid wasp *Enicospilus monticola* (Cameron) (Ichneumonidae, Ophioninae) parasitizing *Oraesia* and *Gonodonta* spp. (Noctuidae) feeding on *Piper* (Piperaceae), *Annona* (Annonaceae), or *Cissampelos* (Menispermaceae).

***Trigonalys maculifrons* Sharp**
http://species-id.net/wiki/Trigonalys_maculifrons
Figure 23

Trigonalys maculifrons Sharp, 1895: 564, fig. 371.

Discussion. This species is mostly yellow with various black maculations on the head and body (Fig. 23). The specimens reared from Costa Rica resemble this species with very similar black markings on the head and mesosoma. The black on the metasoma, however, differs. It is possible this is species-level variation, but we do not have enough specimens to evaluate this, and it does not seem to justify the description of a new species. *Trigonalys flavescens* Bischoff 1951, described from Mexico, is similar, but it differs by the more weakly striped metasoma and lack of a triangular mark at the top of the gena.

As explained by Carmean and Kimsey (1998), Sharp (1895) illustrated *Trigonalys maculifrons* with the caption "*Trigonalys maculifrons* Cam., i.l. Mexico" prior to Cameron's (1897) description of the species. The illustration clearly depicts the holotype specimen described in Cameron, and Sharp is therefore the author of the species.

The *Trigonalys maculifrons* DNA barcode is 13–17% different from other ACG Trigonalidae.

Distribution. Costa Rica, Guatemala, Honduras, Mexico (Carmean and Kimsey 1998).

Figures 21–22. *Trigonalys championi*, female. **21** Lateral view **22** Dorsal view.

Specimens examined. 4; 4 DNA barcoded. Deposited in USNM, INBio.

Hosts and biology. This striking species has been reared just three times, all in 2001 and in ACG dry forest (Sector Santa Rosa), from caterpillars of *Euscirrhopterus poeyi* Grote (Noctuidae) feeding on *Pisonia aculeata* L. (Nyctaginaceae) and primary parasitized by *Lespesia* posticaDHJ01 (Tachinidae).

Figure 23. *Trigonalys maculifrons*, female, dorsal view.

Key to *Trigonalys* species in Costa Rica

1 Black, propodeum and first metasomal tergum yellow (Figs 21, 22); forewing darkly infuscate, especially anteriorly; pronotal collar not raised... ***T. championi***

– Predominately yellow with black maculations on head and body (Fig. 23); wings uniformly hyaline; pronotal collar abruptly raised..... ***T. maculifrons***

Acknowledgments

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References

Burns JM, Janzen DH (2001) Biodiversity of pyrrhopygine skipper butterflies (Hesperidae) in the Area de Conservación Guanacaste, Costa Rica. Journal of the Lepidopterists' Society 55: 15–43.

Cameron P (1897) New species of Hymenoptera from Central America. Annals and Magazine of Natural History 6(19): 261–276. doi: 10.1080/00222939708680536

Carmean D (1991) Biology of the Trigonalyidae (Hymenoptera), with notes on the vespine parasitoid *Bareogonalos canadensis*. New Zealand Journal of Zoology 18: 209–214.

Carmean D (1995) Trigonalyidae. In: Hanson PE, Gauld ID (Eds) The Hymenoptera of Costa Rica. Oxford University Press, 187–192.

Carmean D (2006a) Trigonalidae. In: Hanson PE, Gauld ID (Eds) Hymenoptera de la Región Neotropical. Memoirs of the American Entomological Institute, vol. 77, 212–216.

Carmean D (2006b) Superfamilia Trigonalioidea y familia Trigonalide. In: Fernández F, Sharkey MJ (Eds) Introducción a los Hymenoptera de la Región Neotropical. Sociedad Colombiana de Entomología y Universidad National de Colombia, Bogotá DC, 279–281.

Carmean D, Kimsey L (1998) Phylogenetic revision of the parasitoid wasp family Trigonalidae (Hymenoptera). Systematic Entomology 23: 35–76. doi: 10.1046/j.1365-3113.1998.00042.x

Carne PB (1969) On the population dynamics of the Eucalyptus-defoliating sawfly *Perga afinis affinis* Kirby (Hymenoptera). Australian Journal of Zoology 17: 113–141. doi: 10.1071/ZO9690113

Cresson ET (1865) On the Hymenoptera of Cuba. Proceedings of the Entomological Society of Philadelphia 4: 1–200.

Cresson ET (1867) Synopsis of the families and genera of the Hymenoptera of America, north of Mexico, together with a catalogue of the described species and bibliography. Transactions of the American Entomological Society Suppl. 14: 1–350.

Cresson ET (1879) [Descriptions of three new species of *Trigonalys*.] Proceedings of the Monthly Meetings of the Entomological Section of the Academy of Natural Sciences, Philadelphia. Transactions of the American Entomological Society 7: VII.

Davis GC (1898 [1897]) Descriptions of new species of Trigonalidae, Stephanidae, and Ichneumonidae. Transactions of the American Entomological Society 24: 349–372.

De Geer C (1773) Mémoires pour servir à l'histoire des insectes. 3. Pierre Hosselberg, Stockholm.

Hrcek J, Miller S, Quicke DJ, Smith MA (2011) Molecular detection of trophic links in a complex insect host-parasitoid food web. Molecular Ecology Resources 11:786–794. doi: 10.1111/j.1755-0998.2011.03016.x

Ivanova NV, Dewaard JR, Hebert PDN (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. Molecular Ecology Notes 6: 998–1002. doi: 10.1111/j.1471-8286.2006.01428.x

Janzen DH (2000) Costa Rica's Area de Conservación Guanacaste: a long march to survival through non-damaging biodevelopment. Biodiversity 1: 7–20. doi: 10.1080/14888386.2000.9712501

Janzen DH (2001) Ecology of dry forest wildland insects in the Area de Conservación Guanacaste, northwestern Costa Rica. In: Frankie GW, Mata A, Vinson SB (Eds) Biodiversity Conservation in Costa Rica: learning the lessons in seasonal dry forest. University of California Press, Berkeley, 1–44.

Janzen DH, Hallwachs W (2011) Joining inventory by parataxonomists with DNA barcoding of a large complex tropical conserved wildland in northwestern Costa Rica. PLoS ONE 6(8): e18123. doi: 10.1371/journal.pone.0018123

Janzen DH, Hallwachs W, Blandin P, Burns JM, Cadiou J, Chacon I, Dapkey T, Deans AR, Epstein ME, Espinoza B, Franclemont JG, Haber WA, Hajibabaei M, Hall JPW, Hebert PDN, Gauld ID, Harvey DJ, Hausmann A, Kitching I, Lafontaine D, Landry J, Lemaire C, Miller JY, Miller JS, Miller L, Miller SE, Montero J, Munroe E, Rab Green S, Ratnasingham S, Rawlins JE, Robbins RK, Rodriguez JJ, Rougerie R, Sharkey MJ, Smith MA, Solis MA, Sullivan JB, Thiaucourt P, Wahl DB, Weller SJ, Whitfield JB, Willmott KR, Wood DM, Woodley NE, Wilson JJ (2009) Integration of DNA barcoding into an ongoing inventory of complex tropical biodiversity. Molecular Ecology Resources 9(1):1–26. doi: 10.1111/j.1755-0998.2009.02628.x

Krauth SJ, Williams AH (2006) Notes on *Taeniogonalos gundlachii* (Hymenoptera: Trigonalidae) from Wisconsin. The Great Lakes Entomologist 39: 54–58.

Murphy SM, Lil JT, Smith DR (2009) A scattershot approach to host location: Uncovering the unique life history of the trigonalid hyperparasitoid *Orthogonalys pulchella* (Cresson). American Entomologist 55: 82–87.

Raff JW (1934) Observations on saw-flies of the genus *Perga*, with notes on some reared primary parasites of the families Trigonalidae, Ichneumonidae, and Tachinidae. Proceedings of the Royal Society of Victoria 47: 54–77.

Rougerie R, Smith MA, Fernandez-Triana J, Lopez-Vaamonde C, Ratnasingham S, Hebert PDN (2011) Molecular analysis of parasitoid linkages (MAPL): gut contents of adult parasitoid wasps reveal larval host. Molecular Ecology 20: 179– 186. doi: 10.1111/j.1365-294X.2010.04918.x

Schulz WW (1907) Fam. Trigonaloidae. In: Wytsman P (Ed.) Genera Insectorum. Desmet-Verteneul, Bruxelles. 61, 24 pp, 3 pls.

Sharp D (1895) Insects. In: Harmer SF, Shipley AE (Eds) Cambridge Natural History, Vol. 5. MacMillan & Co., London, 83–584.

Smith DR (1996) Trigonalyidae (Hymenoptera) in the eastern United States: Seasonal flight activity, distributions, hosts. Proceedings of the Entomological Society of Washington 98: 109–118.

Smith F (1861 [1860]). Descriptions of new genera and species of exotic Hymenoptera. Journal of Entomology 1: 65–84, 146–155.

Smith MA, Woodley NE, Janzen DH, Hallwachs W, Hebert PDN (2006) DNA barcodes reveal cryptic host-specificity within the presumed polyphagous members of a genus of parasitoid flies (Diptera: Tachinidae). Proceedings of the National Academy of Sciences 103: 3657–3662. doi: 10.1073/pnas.0511318103

Smith MA, Wood DM, Janzen DH, Hallwachs W, Hebert PDN (2007) DNA barcodes affirm that 16 species of apparently generalist tropical parasitoid flies (Diptera, Tachinidae) are not all generalists. Proceedings of the National Academy of Sciences 104: 4967–4972. doi: 10.1073/pnas.0700050104

Smith MA, Rodriguez JJ, Whitfield JB, Deans AR, Janzen DH, Hallwachs W, Hebert PDN (2008) Extreme diversity of tropical parasitoid wasps exposed by iterative integration of natural history, DNA barcoding, morphology, and collections. Proceedings of the National Academy of Sciences 105:12359–12364. doi: 10.1073/pnas.0805319105

Weinstein P, Austin AD (1991) The host relationships of trigonalid wasps (Hymenoptera: Trigonalyidae), with a review of their biology and catalogue to world species. Journal of Natural History 25(2): 399–433. doi: 10.1080/00222939100770281

Weinstein P, Austin AD (1995) Primary parasitism, development and adult biology in the wasp *Taeniogonalos venatoria* Riek (Hymenoptera: Trigonalyidae). Australian Journal of Zoology 43: 541–555. doi: 10.1071/ZO9950541

Westwood JO (1868) Descriptions of new genera and species of exotic Hymenoptera. Transactions of the Entomological Society of London: 327–332.