Revision of New World Helava Masner & Huggert (Platygastridae, Sceliotrachelinae)

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Abstract
Nine new species of Helava are described: H. acutiventris sp. n., H. allomera sp. n., H. aureipes sp. n., H. carinata sp. n., H. microptera sp. n., H. pygmea sp. n., H. reducta sp. n., H. simplex sp. n., and H. samanthae sp. n., and Helava alticola Masner & Huggert is redescribed. New characters are presented to supplement the generic description of Masner and Huggert (1989) and the genus is diagnosed from similar genera in Sceliotrachelinae: Aphanomerus Dodd and Austromerus Masner & Huggert.

Keywords
Parasitoid, taxonomy, Platygastroidea

Introduction
Helava was described by Masner and Huggert in their 1989 treatment of world genera of Sceliotrachelinae. Masner and Huggert separated Helava from Austromerus on the basis of “clavate” antennae in males. We here replace “clavate” with the term “clubbed” to describe the apically enlarged antennomeres in males to maintain strict use of terminology in which clavomeres are defined by the presence of basiconic sensilla. Our revision of Helava reveals that the male antenna is filiform in two species, H. acutiventris and H. allomera, and thus Helava and Austromerus are separable only by the form of
the clava in females: compact in *Helava* and with articulated clavomeres in *Austromerus* (compare Figures 2 and 12; see also figures 168–173 in Masner and Huggert (1989)). *Helava* is also morphologically very close to *Aphanomerus*, from which Masner and Huggert (1989) separated *Helava* by the dense setation on T1–T2 and presence of propodeal foamy structures (compare Figures 1 and 20). In the concept of Masner and Huggert (1989), *Helava* is found in South America, Tasmania and continental Australia, a distribution consistent with a Gondwanan origin. The limits of *Helava*, *Aphanomerus* and *Austromerus* have become blurred following this revision and testing hypotheses about the phylogeography of the genus will require a better understanding of relationships between these three genera. We refrain from describing the Australian species of *Helava* until species-level revision of *Aphanomerus* and *Austromerus* are conducted to provide a full grasp of the morphological diversity of their constituent species. Currently no host data are known for *Helava*.

**Materials and methods**

The numbers prefixed with “CNC” or “OSUC” are unique identifiers for the individual specimens (note the blank space after some acronyms). Details of the data associated with these specimens may be accessed at the following link: http://purl.oclc.org/NET/hymenoptera/hol, and entering the identifier in the form. Persistent URIs for each taxonomic concept were minted by xBio:D in accordance with best practices recommended by Hagedorn et al. (2013). Morphological terms were matched to concepts in the Hymenoptera Anatomy Ontology (Yoder et al. 2010) using the text analyzer function. A table of morphological terms and URI links is provided in Suppl. material 1.

Photographs were captured with a Z16 Leica lens with a JVC KY-F75U digital camera using Cartograph software. Single montage images were produced from image stacks with the program CombineZP. In some cases, multiple montage images were stitched together in Photoshop to produce larger images at high resolution and magnification. Full resolution images are archived at the image database at The Ohio State University (http://purl.oclc.org/NET/hymenoptera/specimage).

Scanning electron micrographs were produced with a Hitachi TM300 Tabletop Microscope. The specimen was disarticulated with a minuten probe and forceps and mounted on 12 mm slotted aluminum mounting stub (EMS Cat. #75220) using carbon adhesive tabs (EMS Cat. #77825-12) by means of a fine paint brush and sputter coated with approximately 70 nm of gold/palladium.

This work is based on specimens deposited in the following repositories with abbreviations used in the text:

ANIC  Australian National Insect Collection, Canberra City, Australia  
CNCI  Canadian National Collection of Insects, Ottawa, Canada  
OSUC  C.A. Triplehorn Collection, The Ohio State University, USA  
USNM  Smithsonian National Museum of Natural History, Washington, DC, USA
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Figure 1. *Aphanomerus* sp. female (USNMENT00916681), head, mesosoma, metasoma, lateral view. Scale bar in millimeters.

Abbreviations and characters annotated in the figures

**apc**  anterior pronotal patch (Figure 16, 50)
**apS2**  anterior setal patch on S2 (Figures 2, 17)
**apT1**  anterior setal patch on T2 (Figure 17)
**fp**  foamy structure on propodeum (Figures 16, 18, 25)
**fS1**  foamy structure on S1 (Figure 17)
**hoc**  hyperoccipital carina (Figures 34, 54)
**mfp**  mesofurcal pit (Figure 14)
**mkT1**  median keel on T1 (Figure 17)
**mkT2**  median keel on T2 (Figures 10, 25)
**not**  notaulus (Figures 10, 25)
**ppc**  posterior pronotal patch (Figure 9)
**sss**  scutoscutellar sulcus (Figure 36)
**tel**  transepisternal line (Figures 3, 35)

**Diagnosis of Helava**


**Key to species (males and females)**

1. Foamy structures on lateral propodeum covering area larger than visible part of metapleuron (Figures 9, 16, 19, 29, 50) ..............................................................
2. Foamy structures on lateral propodeum covering area distinctly smaller than hairy metapleuron (Figures 4, 24, 35, 40, 55) or foamy structures absent (Figure 45) ..............................................................
   5

   2. Lateral pronotum with dorsoventral strip of dense setation posteriorly (Figure 9); notaulus percurrent (Figure 10); male antenna filiform (Figure 13); female antennal clava 3-merous (Figure 2) ..............................................................

   ............................................................................. *H. allomera* Masner & Talamas, sp. n.
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Description. Female body length: 0.99–1.03 mm (n=10). Male body length: 0.90–0.85 mm (n=20). Male antenna: filiform. Number of female clavomeres: 3. Setation of frons anterior to ocellar triangle: present. Setation of vertex posterior to lateral ocel-
Figures 4–8. *Helava acutiventris* 4 female holotype (USNMENT0989201), head, mesosoma, metasoma, lateral view 5 female holotype (USNMENT00989201), head and mesosoma, dorsal view 6 male paratype (USNMENT00989201), metasoma, dorsal view 7 female holotype (USNMENT00989201), head, anterior view 8 male paratype (USNMENT00989202), antenna, ventral view. Scale bars in millimeters.


**Diagnosis.** The ventral protrusion of S2 in *H. acutiventris* separates this species from all other species in *Helava*. In addition to the shape S2, the absence of a transepisternal line on the mesopleuron is shared only with *H. reducta*, which is a starkly different species that can be separated by the absence of ocelli and a scutoscutellar sulcus.

**Etymology.** The epithet “acutiventris” is given to this species in reference to the sharp projection on S2 in both sexes.

**Link to distribution map.** [http://hol.osu.edu/map-large.html?id=354388](http://hol.osu.edu/map-large.html?id=354388)


**Comments.** The diagnostic shape of S2 is found in both males and females, leading us to believe that this is not an adaptation for housing the retracted ovipositor system, as can be found in some species of *Synopeas* Förster and *Platygaster* Latreille.

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**Helava allomera** Masner & Talamas, sp. n.
http://zoobank.org/F786DD15-F5B5-41CB-8910-479F75142D03
http://bioguid.osu.edu/xbiod_concepts/354395
Figures 9–13

Figures 9–12. *Helava allomera* 9 female holotype (USNMENT00989217), head, mesosoma, metasoma, lateral view 10 female holotype (USNMENT00989217), head, mesosoma, metasoma, dorsal view 11 female holotype (USNMENT00989217), head, anterior view 12 female holotype (USNMENT00989217), antenna, dorsal view 13 male paratype (USNMENT00989218), antenna, dorsal view. Scale bars in millimeters.

**Diagnosis.** *Helava allomera* can be differentiated from other species in the genus by the combination of the well-developed hyperoccipital carina, percurrent notauli, and foamy structures on the propodeum that are larger than the visible part of the metapleuron in lateral view. Within *Helava*, this is the only species with a dorsoventral band of dense setae along the posterior margin of the lateral pronotum (Figure 9).
Etymology. The epithet “allomera” is given to this species in reference to the unusual form and segmentation of antennae in both sexes.

Link to distribution map. http://hol.osu.edu/map-large.html?id=354395


Helava alticola Masner & Huggert
http://bioguid.osu.edu/xbiod_concepts/12334
Figures 14–23

Helava alticola Masner & Huggert, 1989: 72 (original description. Species list); Vlug 1995: 26 (cataloged, type information).


Diagnosis. Helava alticola can be separated from species with large propodeal foamy structures by the evenly rounded form of S2 and the pattern of setation on the dorsal head: posterior to the ocelli the posterior vertex is densely setose, and anterior to the ocelli the upper frons is glabrous or with sparse setae only along the inner orbit of the eye.

Link to distribution map. http://hol.osu.edu/map-large.html?id=12334

Figures 14–18. Helave alticola, female (USNMENT00989211) 14 head and mesosoma, ventral view 15 head, dorsal view 16 mesosoma, lateral view 17 metasoma, lateral view 18 mesosoma, posterolateral view. Scale bars in millimeters.


**Helava aureipes** Masner & Talamas, sp. n.
http://zoobank.org/96D177A2-D794-49FF-9B6C-54CBAAF05BCA
http://bioguid.osu.edu/xbiod_concepts/354390
Figures 24–28


**Diagnosis.** *Helava aureipes* and *H. allomera* are the only two South American species with notauli. They can be separated from each other by the transepisternal line, which is absent in *H. allomera* and present as a distinct groove in *H. aureipes*.

**Etymology.** The epithet “aureipes” is given to this species in reference to the golden colour of the legs.

**Link to distribution map.** http://hol.osu.edu/map-large.html?id=354390


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**Helava carinata** Masner & Talamas, sp. n.
http://zoobank.org/1047FBEA-5089-4F07-87FE-E18A1C5BE9E1
http://bioguid.osu.edu/xbiod_concepts/354394
Figures 29–34

**Description.** Female body length: 1.00–1.15 mm (n=19). Male body length: 0.94–1.12 mm (n=20). Male antenna: apically clubbed. Number of antennomeres in male club: 4. Number of female clavomeres: 4. Setation of frons anterior to ocellar triangle: absent or sparsely present only along inner orbit of eye. Setation of vertex posterior to lateral ocellus: very sparse or absent. Hyperoccipital carina: continuous across vertex. Pronotum in dorsal view: present mostly as lateral shoulders. Dorsoventral band of dense setation on posterior part of lateral pronotum: absent. Setation of pronotal cer-

across tergal midline. Lateral patch on T2: present. Foamy structures on S1: present at lateral margin of sternite. Transverse felt field on anterior S2: present. Shape of S2 in lateral view: broadly convex.
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**Diagnosis.** *Helava carinata* belongs to the cluster of species with large propodeal foamy structures that includes *H. alticola*, *H. allomera*, and *H. samanthae*. It can be separated from *H. alticola* and *H. samanthae* by the setation of the upper frons and posterior vertex, which is either absent or very sparse. In *H. alticola* the upper frons is glabrous or nearly so, and then abruptly setose posterior to the ocelli; the dorsal head in *H. samanthae* is setose throughout. *Helava carinata* can be separated from *H. allomera* by the absence of dense setation on the posterior part of the lateral pronotum (compare Figures 9 and 29).

**Etymology.** The Latin adjectival epithet “carinata” refers carinate vertex of the head.

**Link to distribution map.** [http://hol.osu.edu/map-large.html?id=354394]


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**Helava microptera** Masner & Talamas, sp. n.

http://zoobank.org/71FA4BB9-FE32-41AF-8ABF-366AA39BC82A
http://bioguid.osu.edu/xbiod_concepts/354386
Figures 35–39


**Diagnosis.** *Helava microptera* and *H. reducta* are the only species without fully developed wings. They are easily separable by the presence of ocelli, a transepisternal line, and a scutoscutellar sulcus in *H. microptera*, all of which are absent in *H. reducta*.

**Etymology.** The Greek name “microptera” refers to the small size of the wings in males and females of this species.
Figures 35–39. *Helava microptera* 35 female holotype (USNMENT00989197), head, mesosoma, metasoma, lateral view 36 female holotype (USNMENT00989197), head, mesosoma, metasoma, dorsal view 37 female holotype (USNMENT00989197), head, anterior view 38 male paratype (USNMENT00989198), antenna, dorsal view 39 female holotype (USNMENT00989197), antenna, dorsal view. Scale bars in millimeters.

**Link to distribution map.** http://hol.osu.edu/map-large.html?id=354386

**Material examined.** Holotype, female: **ECUADOR:** Napo Prov., paramo, Quito-Baeza Rd., 4200m, 2.III.1979, pan trap, W. R. M. Mason, USNMENT00989197 (deposited in CNCI). Paratypes: **ECUADOR:** 9 females, 2 males, CNC424772, 424774–424782, USNMENT00989198 (CNCI).
**Helava pygmea** Masner & Talamas, sp. n.
http://zoobank.org/A11DC0E8-4C75-4A4C-B4BD-FC67D0374CFC
http://bioguid.osu.edu/xbiod_concepts/354391
Figures 40–44


**Diagnosis.** Helava pygmea is closest to *H. simplex*, with which it shares the presence of small propodeal foamy structures, fully developed wings, and a mesoscutum without notauli. The only character that reliably separates these species is the form of the basal vein (Rs+M) in the fore wing: darkly pigmented in *H. pygmea* and absent in *H. simplex*.

**Etymology.** The species name “pygmea” refers to the small size of the body in this species.

**Link to distribution map.** http://hol.osu.edu/map-large.html?id=354391


**Helava reducta** Masner & Talamas, sp. n.
http://zoobank.org/908D245E-2CF2-495B-B711-87CB4D6AB3EE
http://bioguid.osu.edu/xbiod_concepts/354389
Figures 45–49

**Description.** Female body length: 1.01 mm (n=1). Male body length: 1.04 mm (n=1). Male antenna: apically clubbed. Number of antennomeres in male club: 3. Number of
Figures 45–49. *Helava reducta* 45 female holotype (USNMENT00989203), head, mesosoma, metasoma, lateral view 46 female holotype (USNMENT00989203), head, mesosoma, metasoma, dorsal view 47 female holotype (USNMENT00989203), head, anterior view 48 male paratype (USNMENT00989204), antenna, dorsal view 49 female holotype (USNMENT00989203), antenna dorsal view. Scale bars in millimeters.

Diagnosis. *Helava reducta* can easily be identified by severe microptery, the absence of a scutocutellar sulcus, and the absence of transepisternal line.

Etymology. The Latin adjectival epithet “reducta” is applied to this species for the reduced segmentation of the mesosoma,

Link to distribution map. http://hol.osu.edu/map-large.html?id=354389


*Helava samanthae* Masner & Talamas, sp. n.
http://zoobank.org/33DE4823-9B71-4510-A64E-6E2C2A549E9A
http://bioguid.osu.edu/xbiod_concepts/354387

Figures 50–54


Diagnosis. The form of the hyperoccipital carina as two lateral tubercules on the posterior vertex separates *H. samanthae* from all species except *H. alticola*, in which the form of the hyperoccipital carina is highly variable. These two species can be separated from each other by the setation of the upper frons, which in *H. samanthae* is densely present, and is sparsely present only along the inner orbits of the eye, or entirely absent, in *H. alticola*.

Etymology. This species is named for Samantha Fitzsimmons Schoenberger to thank her for excellent work performed as part of the Smithsonian Internship Program, including most of the photographs presented in this monograph.

Link to distribution map. http://hol.osu.edu/map-large.html?id=354387

Material examined. Holotype, female: CHILE: Bío-Bío Reg., Nuble Prov., Las Trancas Valley, 1300m–1650m, 14.XII–17.XII.1976, S. Peck & H. Howden, USN-
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Figures 50–54. Helava samanthae, female holotype (USNMENT00989199) 50 head, mesosoma, metasoma, lateral view 51 head and mesosoma, dorsal view 52 metasoma, dorsal view 53 head, anterior view 54 head and mesosoma, posterolateral view. Scale bars in millimeters.

Figures 55–60. Helava simplex 55 female holotype (USNMENT00989195) head, mesosoma, metasoma, lateral view 56 female holotype (USNMENT00989195) head and mesosoma, dorsal view 57 female holotype (USNMENT00989195) metasoma, dorsal view 58 female holotype (USNMENT00989195) head, anterior view 59 female holotype (USNMENT00989195) antenna, dorsal view 60 female paratype (USNMENT00989190) fore wing, dorsal view. Scale bars in millimeters.
**Helava simplex** Masner & Talamas, sp. n.
http://zoobank.org/0B8E8E62-CE4F-4652-9C39-AD31F276E659
http://bioguid.osu.edu/xbiod_concepts/354385
Figures 55–60


Diagnosis. *Helava simplex* is the only macropterous species in the genus without a pigmented basal vein in the fore wing (Figure 60).

Etymology. The epithet “simplex” is given to this species in reference to the absence of several character states (notaulus, foamy structures).

Link to distribution map. http://hol.osu.edu/map-large.html?id=354385


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References


Ergatomorph wingless males in *Technomyrmex vitiensis* Mann, 1921 (Hymenoptera: Formicidae)

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Abstract

Ergatomorph wingless males are known in several species of the genus *Technomyrmex* Mayr, 1872. The first record of these males is given in *T. vitiensis* Mann, 1921. In comparison with winged males, wingless males have a smaller thorax and genitalia, but both forms have ocelli and the same size of eyes. Wingless males seem to form a substantial portion (more than 10%) of all adults in examined colony fragments. Wingless males are present in colonies during the whole year, whereas the presence of winged males seems to be limited by season. Wingless males do not participate in the taking care of the brood and active foraging outside the nest. Males of both types possess metapleural gland openings. Beside males with normal straight scapes, strange hockey stick-like scapes have been observed in several males. The cause of this divergence is unclear.

Keywords

Behaviour, biology, greenhouses, *Technomyrmex vitiensis*, wingless ergatomorph males

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Introduction

Two morphs of males evolved independently in several ant genera, such as *Cardiocondyla* Emery, 1869 (Heinze et al. 2013), *Hypoponera* Santschi, 1938 (Bolton and Fisher 2011), *Plagiolepis* Mair, 1861, *Crematogaster* Lund, 1831, *Formicoxenus* Mayr, 1855, *Pheidole* Westwood, 1839 (Heinze and Tsuji 1995) and *Technomyrmex* Mayr, 1872 (Bolton 2007). *Technomyrmex* ants display a unique mode of reproduction. In *Technomyrmex*, wingless intermorphic females are known in more than 25 species and wingless ergatoid males in six species (Bolton 2007). In the well-known species *T. brunneus* Forel, 1895 (Tsuji et al. 1991, Yamauchi et al. 1991, Tsuji and Yamauchi 1994, Ogata et al. 1996), winged queens and males are produced and mate synchronously once a year and each winged female tries to found a new colony independently. Later on, as the colony grows, the foundress is replaced by fertile apterous intermorphic females, which mate with their brothers, apterous ergatoid males. The genitalia of winged reproductives are significantly bigger than the genitalia of apterous individuals. Thus, the copulation between winged and wingless reproductives seems complicated or impossible (Ogata et al. 1996). The colony spreads by budding, forming a huge polycalic colony with thousands of individuals.

*Technomyrmex vitiensis* Mann, 1921 is probably of South-East Asian origin, but recently has been found to be widespread in greenhouses across the whole world (Bolton 2007, Pospischil 2011). Despite its worldwide distribution, its biology is poorly known and it is considered to be similar to its more intensively studied relatives from the *Technomyrmex albipes* species group such as *T. brunneus*, *T. pallipes* (Smith, 1876) and *T. difficilis* Forel, 1892. According to Bolton (2007), *T. vitiensis* nests in various materials and spaces such as in leaf litter, under stones, on vegetation in twigs or under leaves. It tends homopterans for honeydew and preys on small arthropods. Wingless males are not known in *T. vitiensis* although they occur in several related species (Bolton 2007, Oettler and Heinze 2009). Because of the absence of wingless males in studied colonies, Oettler and Heinze (2009) proposed the reproduction of *T. vitiensis* via thelytocous parthenogenesis.

In this paper, the presence of wingless ergatomorph males of *T. vitiensis* is described.

Methods

Two populations of *T. vitiensis* were discovered in the Czech Republic in the autumn of 2014: one in the greenhouse of the botanical garden of Charles University (Czech Republic, Praha, 50°4’N, 14°25’E; 8.10.2014, lgt., det. et coll. P. Pech, revid. et coll. B. Bolton) and another in the greenhouse of the Prague Zoo (Czech Republic, Praha, 50°7’N, 14°24’E; 23.9.2014; lgt., det. et coll. P. Pech). Collections of individuals and observations of the behavior of ants in the greenhouse of the botanical garden were carried out from the beginning of October 2014 to November 2015. Two colony fragments were collected and preserved in pure ethanol, one in the botanical garden in November 2014 and the other in zoological garden in November 2015.
The morphology of ants was examined using a JEOL JSM-7401F electron microscope and a binocular microscope with 40× magnification. Differences in morphometry between winged and wingless males were analyzed using the Mann-Whitney U test and the correlation between thorax length and width of genitalia was tested by Spearman rank-order correlation. Six winged and 12 wingless males were examined. The following characteristics were measured:

- **HW**: Head width; maximum width of cephalic capsule with eyes, measured in full-face view;
- **HL**: Maximum length of head; length of cephalic capsule measured in full-face view in midline from anterior margin of clypeus to posterior head margin;
- **MH**: Mesosoma height; maximum height of mesosoma from ventral margin of mesopleuron to dorsal margin of metanotum, measured in lateral view;
- **ML**: Mesosoma length; maximum length measured from anterior margin of pronotum to posterior margin of propodeum, measured in lateral view;
- **SL**: Scape length; maximum length of single scape, measured along outer edge;
- **EL**: Eye length; maximum length of single eye;
- **EW**: Eye width; maximum width of single eye perpendicular to EL;
- **GW**: Genitalia width; maximum width of genital capsule (sensu Boudinot 2013), measured in dorsal view.

To observe behavior and reproduction, one colony fragment was collected in the botanical garden and reared in captivity at room temperature and with a natural photoperiod from November 2014, first in a plastic box (30×20×10 cm) and later in a petri dish (10 cm in diameter). The walls of both containers were coated in baby oil to prevent escape. The ants were fed with honey and pieces of insects. Another colony fragment was collected in the zoological garden in November 2015. It was reared under the same temperature and photoperiod, but kept in a glass terrarium (30×20×20 cm) situated in a flat plastic container with water. These ants were fed by Bhatkar and Whitcomb (1970) diet.

**Results**

**Morphology**

Beside the presence or absence of wings, the architecture of the thorax is the most obvious difference between males of both types (Tab. 1). The thorax of a winged male is high and large due to the presence of wing muscles whereas the smaller thorax of the wingless male resembles a worker (Fig. 1A, B) at first sight. Moreover, thoraces of winged males are longer. Males of both types have ocelli and similar head morphology (Fig. 1C; Tab. 1). The width of male genitalia is positively correlated with the length of the thorax (n = 18, R = 0.82, p<0.01).
Figure 1. Lateral (A), dorsal (B) and frontal (C) view of wingless *T. vitiensis* male.
Ergatomorph wingless males in *Techomyrmex vitiensis* ...

**Figure 2.** Metapleural gland opening of wingless *T. vitiensis* male.

**Table 1.** Means (in mm) and standard deviations of selected characteristics of *T. vitiensis* males with the significance of differences between winged and wingless morphs. Significant differences between winged and wingless forms are highlighted.

<table>
<thead>
<tr>
<th>Character</th>
<th>Winged males (n=6)</th>
<th>Wingless males (n=12)</th>
<th>p</th>
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</tbody>
</table>
Metapleural gland openings are present in females as well as both winged and wingless males (Figs 2, 3).

Three wingless males show curious scape morphology: whereas normal scapes are straight, their scapes have a bulge on the distal end; thus, the whole scape resembles a hockey stick. Two males have modified both scapes and the third male has one normal and one modified scape (Fig. 4). The other morphological traits of these males do not seem to differ from males with normal scapes.

**Behavior**

In the botanical garden, apterous males were found during all visits (October, November, February, June). Winged males were captured only in the fall (one male was found in October and the other in November 2014 and another one in November 2015).

The preserved colony fragment from the botanical garden contained 67 workers, three intermorphic females and 14 wingless males. Additionally, several males, including two winged ones, were collected directly from the greenhouse and several lived in
the reared colony fragment. The preserved colony fragment from the zoological garden contained 499 workers, 80 intermorphic females (79 apterous and one brachypterous), eight winged queens and 24 males (21 winged and three wingless).

The reared colony fragment from the botanical garden contained about 100 apterous females and four apterous males with an amount of eggs, larvae and pupae at the time of collection. The colony fragment from the zoological garden contained about 30 apterous females and one apterous male with some brood. The ants from the botanical garden (fed by honey and pieces of insects) stopped breeding shortly after the collection and the brood disappeared in three weeks: female pupae matured but larvae and male pupae were probably eaten. Although eggs were present during six months of breeding, only one larva appeared but vanished soon.

During the breeding in captivity, no more than five males lived simultaneously in this colony fragment from the botanical garden. Males were not observed to carry or tend eggs or other juveniles. No aggressive interactions among these males were observed. Males behaved more actively than females and explored the arena more frequently. This behavior led to high male mortality, because two of them got stuck in the oil cover on the walls and one in the honey; no worker died in this way. All wingless
males died within two weeks after capturing the colony fragment or emerging from pupae, whereas the mortality of females was much lower (1–2 dead individuals per week). Also, during the search in the botanical garden, several wingless males were observed outside nests, walking on leaves and the ground.

Ants from the zoological garden (fed by Bhatkar and Whitcomb diet), four months since the start of breeding, still have brood of all stages but no new males are produced.

Discussion

Interestingly, the loss of wings is not connected with an absence of ocelli. The development of flight muscles and the size of the genitalia seem to be the main differences between the two types of males. In *T. brunneus*, mating between wingless and winged sexuals is probably impossible due to the big difference in the size of the genitalia (Ogata et al. 1996) – the average width of the genitalia of wingless males is almost two times smaller than that of winged males. A similar difference occurs in the genitalia width between winged and wingless females. Also in *T. vitiensis*, the difference in size of the genitalia of males of both types is significant. Because no winged females were measured, it is unclear whether female genitalia share the same pattern. However, the male genitalia size seems to be linked with the body size.

Both winged and wingless males have developed metapleural gland openings. Antimicrobial and antifungal metapleural gland secretion is an important component of ant immunity, but several other functions of these glands are also suggested (Yek and Mueller 2011). Metapleural glands are usually present in females but rarely in male ants, possibly because of the usually short life of ant males in the adult stage (Hölldobler and Engel-Siegel 1984, Yek and Mueller 2011). Until now, metapleural glands have been observed in males of only two species – *Dorymyrmex tener donisthorpei* (Santschi, 1936) and *Iridomyrmex purpureus* (Smith, 1858) – out of more than 700 species of the subfamily Dolichoderinae (Yek and Mueller 2011). It should be noted that the presence of metapleural gland openings does not imply the existence of a functional metapleural gland. The functionality and structure of metapleural glands in *T. vitiensis* are currently being studied (Billen and Pech, in prep.). Because *T. vitiensis* males (especially alate) seem not to live very long, the adaptive function of their metapleural glands, if present, is not clear (beside the high pressure of fungal and bacterial parasites in wet tropical habitats in general; but that would apply for many other tropical ant species as well). As the function of metapleural gland is poorly understood, all potential hypotheses are speculations.

The existence of two types of scapes in males is very interesting. Further research is needed to resolve whether there is a separate caste of male or teratological form.

Apterous males are probably present in colonies during the whole year, whereas the occurrence of winged males seems to be limited seasonally. The question is: If the amount of males can reach more than 10% of all adults in a nest, why have apterous
males not been observed until now? First, wingless males are very similar to females at first sight. Second, according to Yamauchi et al. (1991), the variation in the number of apterous males both inter-colonial and intra-colonial (among nests of the same polydomous colony) in *T. brunneus* is high and these males appear in the relatively small proportion of colonies in the field. The differences in the number of apterous males in our samples from the botanical and zoological gardens show that it is reality also in populations of *T. vitiensis*. Wingless males are clearly not always abundant. The diet of ants in the captivity could be another reason because ants are often fed by honey and dead insects as in case of Oettler and Heinze (2009) research of *T. vitiensis*. Using this diet, adults of *T. vitiensis* survive but do not breed.

Our observation supports the absence of aggressive male-to-male interaction in *Technomyrmex*. In contrast to wingless males in *Cardiocondyla* (e.g., Heinze and Hölldobler 1993) and *Hypoponera* (e.g., Bolton and Fisher 2011), which struggle with each other in an attempt to monopolize mating, *Technomyrmex* males were not observed Fighting with each other (Yamauchi et al. 1991). Interestingly, six wingless and one winged male with amputated legs and antennae were discovered during the research in the botanical garden, located in one leaf about 1 m above the ground (3.xi.2014). All were immobilized but some of them were still alive. Additionally, at the other site, a *T. vitiensis* female was observed carrying and tossing away a badly injured apterous male. As male-to-male aggression is probably absent in *Technomyrmex*, the injuring and death of these males were most probably caused by intercolonial aggression. Fights among ants from different colonies are mentioned by Tsuji and Yamauchi (1994) in *T. brunneus*. One expects *T. vitiensis* to form one huge polydomous colony in the same greenhouse, but if several live individuals from another nest (captured at the same time in a banana tree about 4 m distant from the original site of the reared colony fragment) were added to the reared colony fragment, aggressive interactions among members of both nests were observed. This behavior (jerky lunges with open mandibles and pulling at appendages) ceased within two days. Thus, the males were probably killed by members of a more distant nest in the greenhouse.

The walking of wingless males outside nests implies the possibility of their extranidal mating with intermorphic females from another nest or colony and can weaken the intracolonial inbreeding in *Technomyrmex* colonies.

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References


Review of the genus *Leptopilina* (Hymenoptera, Cynipoidea, Figitidae, Eucoilinae) from the Eastern United States, including three newly described species

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Abstract

The genus *Leptopilina* has historically been a poorly understood group. However, some species of *Leptopilina* are among the best-known model organisms for studying host-parasitoid interactions. As there is no identification system for *Leptopilina* in any part of the United States, we review species that were collected throughout their range in Eastern North America and those commonly used in laboratories. We provide a key for seven species, *L. boulardi*, *L. heterotoma*, *L. clavipes*, *L. victoriae*, *L. decemflagella* sp. n., *L. maia* sp. n., and *L. leipsi* sp. n., the last three of which are newly described here. This study is the first of its kind for *Leptopilina* species in North America, as our review and key were developed by examining a large number of specimens collected across broad chronological and geographic scales. This allowed us to account for the phenotypic variation within species, and helped us discover diagnostic characters. The geographic distribution and taxonomic information from this review provides a solid foundation for future research on *Leptopilina*.

Keywords

Parasitoid wasps, *Drosophila*, Nearctic Region, geographic distribution, DNA barcoding
Introduction

Parasitoid wasps (Hymenoptera: Apocrita) are a particularly speciose group of insects, potentially accounting for over 20% of all insect species (LaSalle and Gauld 1993). However, in some groups, more than 50% of the extant species still remain undescribed (Aguiar et al. 2013, Rodriguez et al. 2013). A primary reason for this lack of taxonomic information is the extensive amount of cryptic morphological variation among the species, and general lack of expertise focused on researching this group. One such group are species of *Leptopilina* Förster, 1869 (Cynipoidea: Figitidae: Eucoilinae). This is somewhat of an anachronism in entomological research, because on one hand, some species of *Leptopilina* are among the best-known model organisms for studying host-parasitoid interactions, and are easily cultivated in a laboratory setting. Species such as *Leptopilina boulardi* (Barbotin, Carton & Kelner-Pillault, 1979), *L. heterotoma* (Thomson, 1862), and *L. clavipes* (Hartig, 1841), are commonly reared koinobiont endoparasitoids of *Drosophila melanogaster* (Meigen, 1830) and *D. simulans* (Sturtevant, 1919) (Carton 1986). However, the overall taxonomic scope of this genus is rather cloudy to the non-specialist, leading several species belonging to this genus to be identified in other genera such as *Cothonaspis* and *Ganaspis*. Moreover, many species names within this genus, and their identity, are poorly known (Forshage et al. 2013).

The genus *Leptopilina* has historically been a poorly understood group, and it was not until the relatively recent revision by Nordlander (1980) that any species of *Leptopilina* could be identified with any degree of certainty. Nordlander’s revision is the first and only complete study of this genus on a world-wide scale that included redescriptions, a key to European *Leptopilina* species and identified several type-species in other genera that were confused with *Leptopilina*. Later, Schilthuizen et al. (1998) used 23 morphological characteristics and DNA sequences of the ITS2 gene fragment to analyze the phylogenetic relationships among ten *Leptopilina* species from laboratory cultures. Their study provided much needed insight by interpreting the historical distribution of species as well as ecological and behavioral traits. A follow up study, Allemand et al. (2002) used morphological descriptions, crossing experiments, ITS2 sequences and RFLP data to describe the geographic distribution of six *Leptopilina* species in the Afrotropical region. Continuing this research, Novkovic et al. (2011) combined molecular evidence from, CO1, ITS1, and ITS2 sequences with hybridization experiments and morphological data to describe the taxonomic and phylogenetic relationships of five *Leptopilina* species attacking frugivorous *Drosophila* in Japan. Most recently, Wachi et al. (2015) reported three putative thelytokous species with two newly described species in central Japan and Tshushima Island in Japan.

Some species of *Leptopilina* are cosmopolitan and are present on all continents except Antarctica (Allemand et al. 2002, Buffington pers. obsv., Fontal-Cazalla et al. 1997). There are 29 *Leptopilina* species that have been described, mainly from the Neotropical, Afrotropical and Palearctic regions (Allemand et al. 2002, Nordlander
1980, Novkovic et al. 2011, Wachi et al. 2015). While this increased research on species of *Leptopilina* is desperately needed, similar research on the biogeographic and taxonomic concepts of Nearctic species are limited. Moreover, few North American specimens have been identified past the level of genus, and there is no key available for the identification of North American *Leptopilina* (nor for Eucoilinae, even at the generic level) (Forshage et al. 2013). We are aided, however, by Forshage et al. (2013), which provide a catalogue of *Leptopilina* species in North America, a good starting point for understanding the diversity of *Leptopilina* in North America. With this in mind, the present study aims to describe and clarify the identity of *Leptopilina* species that are routinely collected on the East Coast of the United States.

**Materials and methods**

**Specimens**

Specimens of *Leptopilina* for this study were obtained from two main resources. One was from freshly collected specimens by Lue and the other was from the extensive insect collections of the USNM (National Museum of Natural History, the Smithsonian Institution, Washington DC, United States). During the breeding season of *Drosophila* hosts in 2012 and 2013, seasonal surveys of *Leptopilina* species in Eastern North America were carried out. Samples were collected in various regions of North America (listed in the examined materials). Sites were chosen to obtain samples from a broad geographic distribution and cover most of the range of these species in the eastern U.S. Each site was sampled two to three times a year spanning the early to late portion of the *Drosophila* breeding season at each location. We obtained a large number of specimens from many locations throughout their geographic range, helping to ensure that the characters we used were of diagnostic value for a given species.

Parasitoids were collected in the field using yellow pan traps, or by hand-held electric vacuum from traps that were baited with fermented peaches. Wasps were collected two times per day (early a.m. and late p.m.) when wasps were most active/present on the baits. Samples of the fruit baits were placed in 25mm × 95mm polystyrene vials and returned to the laboratory. Additional wasps were collected as they emerged from hosts that had been parasitized in the field. All insects were placed in 95% ethanol either immediately upon collection from the vacuum and laboratory reared samples or within 12 hours from when the yellow pan traps were first set out. Parasitoids were dry mounted on acid-free cards for examination. To morphologically circumscribe species, we included individuals from field collections as well as, all the North American *Leptopilina* specimens housed at the USNM, and many North American species housed at MNHN (Natural History Museum, Paris, France), and BMNH (The Natural History Museum, London, United Kingdom).
Specimen examination and description

Specimens used in this study were dry mounted for long-term preservation and examined in the Hymenoptera Unit at the USNM. Morphological structures of insects were observed using a binocular stereomicroscope (using a Leica MZ9.5, M10 or M205c stereomicroscope) with incandescent and fluorescent light sources. Diagnostic characters for each species were illustrated by using a scanning electron microscope (Hitachi™ TM3000) and an EntoVision™ multiple-focus imaging system. Images were produced from image stack software with the program ComineZP™. Techniques and methods for generating photographs follow those in Buffington et al. (2005), Buffington and van Noort (2009), Buffington and Gates (2009), and Kerr et al. (2009). For SEM images, samples were mounted to SEM stubs and sputter-coated with gold-palladium for three 30s intervals resulting in 25–30 nm of gold-palladium alloy (using a Cressington™ 108 autosputtercoater).

Morphological terminology follows Fontal-Cazalla et al. (2002), Nordlander (1982), and Ronquist and Nordlander (1989). The description of species was generated using vSyslab (http://vsyslab.osu.edu/). The Leptopilina genus description was generated by modifying the 186 morphological characters of Figitidae housed in vSyslab curated by Buffington. Characters that were common to all seven Leptopilina species in this study were filtered out in the species level descriptions and are not repeated. This filtering resulted in 34 characters useful for species-level description/redescription (7 of which were newly created for this project). The geographic distribution and collecting event data of the examined specimens (1015 individuals) are available in HOL (Hymenoptera Online: http://hol.osu.edu/). All examined specimens and SEM stubs are deposited at the USNM. Most of the type specimens of the newly described species in this study also yielded DNA sequence data.

Molecular sequencing

The barcoding region of the mitochondrial cytochrome-c oxidase subunit I (CO1) was sequenced for this study (Suppl. material 1). DNA was extracted from three legs of each sequenced individual using the AutoGenPrep phenol-chloroform automated extractor (AutoGen) after digestion overnight in buffer containing proteinase-k. Amplification of CO1 was carried out using the primer pairs LCO1490/HCO2198 (Folmer et al. 1994) or LepF1/LepR1 (Hebert et al. 2004). A 10 µL reaction mix contained 2.5 mM MgCl₂, 0.3 µM of each primer, 0.5 mM dNTPs, and 5 units of Biolase DNA polymerase (Bioline). Annealing temperatures ranged from 48-50 °C. PCR products were cleaned with ExoSAP-IT (Affymetrix), sequenced using Big Dyes (Life Technologies) and run on a 3730xl DNA sequencer (Applied Biosystems). Sequences were examined using the Sequencher 5.01 (Gene Codes) and Geneious 9.0. All information for the sequences of each individual in this study are deposited as DNA barcodes in GenBank. All voucher specimens for the CO1 database are housed at the USNM.
Results

Characterization of Leptopilina

Leptopilina Förster, 1869


**Diagnosis.** *Leptopilina* are typically small wasps, less than 2mm in length, rather stout when compared with other eucoiline taxa, and have a worldwide distribution. Many species within this genus are easily confused with those in other genera, such as *Ganaspis*, *Kleidotoma*, *Rhoptromeris*, and *Trybliographa*. However, *Leptopilina* possess some unique morphological characteristics that allow them to be distinguished from other eucoiline genera. Generally speaking, in *Leptopilina*, the head narrows ventrally at the bottom of the eyes and forms a triangle. The petiole is enlarged posteriorly, and the broad posterior rim has varying sculptural patterns. The hairy ring at the base of the metasoma is more or less reduced in density with various lengths of setae, but there is no connection dorsally, leading to the common state of ‘hairy ring broken’. The mesoscutum lacks notauli, and the subalar pits are moderately developed.

In *Leptopilina*, as in all other Eucoilinae, the scutellum is surmounted by a disc with a glandular pit close to the posterior margin of the disc. The posterior margin of the scutellum is usually rounded with punctate sculpture, reticulate sculpture, striate sculpture or a combination of these three. In some species of *Leptopilina*, the scutellum has ridges radiating from the scutellar disc; this state is similar to some species of *Hexacola* Förster, but these *Leptopilina* can be differentiated by having an incomplete hairy ring on the metasoma (complete hairy ring in most *Hexacola*) and a glabrous postero-lateral corner of the metapleuron (setose postero-lateral corner of metapleuron in *Hexacola*). Compared to *Rhoptromeris*, the basal part of the pronotal plate of *Leptopilina* is distinct and foveae on the pronotal plate are open laterally; by contrast, in *Rhoptromeris*, but the lateral foveae are closed. Compared to *Ganaspis*, males have the antennal F1 distinctly modified, whereas the F1 of *Leptopilina* is shorter than the F2, and F2 is distinctly modified by being curved outward and elongate. This flagellomere character is one of the main characteristics used to separate *Leptopilina* from *Ganaspis*. Another important characteristic used to distinguish between *Leptopilina* and *Ganaspis* is their metapleural corners: in *Leptopilina*, the corner is hairless (glabrous), and in *Ga-
naspid, the corner is hairy (setose). Wing morphology can also be helpful in separating other genera from *Leptopilina*. *Leptopilina* wings are always covered with short hair, rounded apically, and typically have a long hair fringe on wing tip; the marginal cell is quadrangular in shape and may or may not be closed completely along the anterior margin. In *Rhoptromeris* the cell is always closed, and more triangular in shape: in *Kleidotoma* the cell is always open and apical margin is typically emarginate.

**Description.** Coloration with head, mesosoma, metasoma black to dark brown, legs light brown. Sculpture on vertex, lateral surface of pronotum and mesoscutum absent, surface smooth.


Apical segment of maxillary palp with pubescence, consisting one long erect setae. Apical seta on apical segment of maxillary palp longer than twice length of second longest apical seta. Maxillary palp composed of four segments. Last two segments of maxillary palp (in normal repose) straight. Apical segment of maxillary palp more than 1.5 times or 1-1.5 times as long as preceding segment.

Terminal flagellomere with one to three basiconic sensillae. Basiconic sensillae present between F5-F11 and also on F1, F2 in *L. maia*. Articulation between flagellomeres in antenna moniliform, segments distinctly separated by narrow neck-like articulation. Female antenna composed of 11 flagellomeres, 10 flagellomeres in *L.
Review of the genus Leptopilina (Hymenoptera, Cynipoidea, Figitidae, Eucoilinae)...

*decemflagella*. Male antenna composed of 13 flagellomeres. Female F1 longer than F2. Flagellomeres of female antenna cylindrical, distinctly widened towards apex, semiclavate. Placoidal sensilla present between F5-11. Last antennal flagellomeres of female antenna not conspicuously enlarged compared to adjacent flagellomeres.

Macrosculpture on lateral surface of pronotum absent dorsally and laterally, in *L. decemflagella* with longitudinal ridge ventrally. Anteroventral inflection of pronotum narrow. Pubescence on lateral surface of pronotum present, sparse long hair. Number of ridges on pronotal plate in lateral view between 2 to 4. Anterior flange of pronotal plate distinctly protruding anteriorly, transversely striate. Ridges extending posteriorly from lateral margin of pronotal plate distinct but short, not extending to the dorsal margin of pronotum; present. Lateral pronotum carina absent. Crest of pronotal plate absent. Dorsal margin of pronotal plate (in anterior view) spatulate. Submedian pronotal depressions open laterally, deep. Lateral margin of pronotal plate defined all the way to the dorsal margin of the pronotum. Width of pronotal plate narrow, not nearly as wide as head.


Mesopleuron entirely smooth. Subpleuron entirely smooth, glabrous. Lower pleuron entirely smooth, glabrous. Epicnemial carina absent. Lateroventral mesopleural carina present, not marking abrupt change of slope of mesopectus. Mesopleural triangle absent. Subalar pit present, located under subalar area obscure to see. Speculum absent. Mesopleural carina present, complete, composed of one complete, uninterrupted carina. Anterior end of mesopleural carina inserting above notch in anterior margin of mesopleuron.

Dorsal surface of scutellum foveate-areolet, areolet - rugulose or irregularly striate. Circumscutellar carina present, complete, delimiting dorsal and ventral halves of scutellum, or incomplete, posteriorly. Posterior margin of axillula marked by distinct ledge, axillula distinctly impressed adjacent to ledge. Latero-ventral margin of scutellum posterior to axillula, smooth or with weakly rugulose. Dorsoposterior part of scutellum rounded. Transverse median carina on scutellar plate absent. Dorsal part of scutellum entirely rugose, foveate, or areolate. Scutellar plate, in dorsal view, medium sized, exposing about half of scutellum. Scutellar fovea present, two, distinctly margined posteriorly. Longitudinal scutellar carinae absent. Single longitudinal carina separating scutellar foveae present, short, ending at posterior margin of foveae. Postero-lateral margin of scutellum rounded. Lateral bar smooth, narrow.

Posterior impression of metepimeron absent or present. Metapectal cavity antero-dorsal to metacoxal base present, well-defined. Anterior margin of metapectal-propodeal complex meeting mesopleuron at same level at point corresponding to anterior end of metapleural carina. Posteroventral corner of metapleuron (in lateral view) not extended posteriorly. Anterior impression of metepimeron absent. Posterior margin of metapleural carinae present, separating metapleural from propodeum. Subalar area broad-
ened anteriorly, narrowed posteriorly. Prespiracular process present, blunt, lobe-like, polished. Dorsellum absent. Anterior impression of metepisternum, immediately beneath anterior end of metapleural carina, present. Pubescence consisting of few hairs on posterior part of metepisternum, few or dense hair on propodeum.

Pubescence posterolaterally on metacoxa, present, small, rounded, with adjacent sparse pubescence. Microsculpture on hind coxa absent. Longitudinal ridge on the posterior surface of metatibia absent. Metafemoral tooth present, elongate, with adjacent serrate ridge posteriorly. Ratio of first metatarsal segment to remaining 4 segments greater than 1.0.

Wing vein M absent or present but not well defined. Pubescence of fore wing present, long, dense on most of surface. Apical margin of female fore wing rounded. Rs+M of forewing defined but nebulous at point of origin from basal vein at posterior third. Mesal end of Rs+M vein situated closer to anterior margin of wing, directed towards middle of basalis. Vein R1 forming marginal cell completely. Basal abscissa of R1 (the abscissa between 2r and the wing margin) of fore wing as broad as adjacent wing veins. Coloration of wing absent, entire wing hyaline. Marginal cell of fore wing membranous, similar to other wing cells. Areolet absent. Hair fringe along apical margin of fore wing present, long or very long.

Propodeal spurs absent. Lateral propodeal carinae present, not reaching scutellum. Ventral end of lateral propodeal carina reaching nucha, carinae separated from each other. Inter propodeal carinae space lightly setose, or too dense to see underlying surface, in *L. boulardi* with a horizontal carina. Petiolar rim of uniform width along entire circumference. Petiolar foramen removed from metacoxae, directed posteriorly. Horizontal carina running anteriorly from lateral propodeal carina present, or not visible, setae too dense. Lateral propodeal carina, straight, sub-parallel, in *L. boulardi* distinctly angled. Calyptra, in lateral view, rounded. Propodeum neck-like, drawn out posteriorly. Calyptra, in posterior view, dorsoventrally elongate or rounded.

Petiole about as long as wide. Surface of petiole longitudinally costate, ventral keel absent. Posterior part of female petiole abruptly widened. Ventral and lateral parts of petiolar rim broad.

Setal band (hairy ring) at base of tergum 3 present, interrupted dorsally, ventrally. Tergum 3 indistinct, fused with syntergum. Posterior margin of tergum 3 indistinct, fused with tergum 4 in syntergum. Posterior margin of tergum 4 evenly rounded. Sternum 3 encompassed by syntergum. Sculpture on metasomal terga absent. Syntergum present with terga 3 to 5 fused, ventral margin rounded. Peglike setae on T6–T7 absent. Postero-ventral cavities of female metasoma T7 present, glabrous save for few, long setae. Female postero-ventral margin of T6–T7 straight, parallel. Terebrum and hypopygium (in lateral view) curved, pointing upward. Ovipositor clip, present.

Comments. It was difficult to locate type specimens before the revision of Nordlander (1980). Only one European species of *Leptopilina* (*Cothonaspis longipes* Hartig, 1841) was placed in this genus by Weld (1952). Nordlander (1980) suggested *Cothonaspis longipes* (Hartig, 1841) should be maintained as type species, and included a taxonomic history of *Leptopilina*. Many species belonging to this genus have also been treated
under various generic names for decades. Meanwhile, the true *Leptopilina* species had been assigned to other genera such as *Erisphagia* and *Cothonaspis* (Nordlander 1980).

**Distribution.** This genus has a worldwide distribution and is known from Europe, Africa, Asia, Australia, North America and South America.

**Key to Eastern North American *Leptopilina* species**

1. Female with 10 flagellomeres on the antenna (Fig. 1); vertical carina present adjacent to ventral margin of antenna socket (arrow, Fig. 2); hypopygium pointing ventrally in lateral view (arrow, Fig. 3) ................................................................. *Leptopilina decemflagella* Lue & Buffington, sp. n.

2. Female with 11 flagellomeres (Fig. 4); no obvious carina adjacent to margin of antenna socket (Fig. 5); hypopygium pointing dorsally (arrow, Fig. 6) ...

![Image 1](image1.png)

![Image 2](image2.png)

![Image 3](image3.png)

![Image 4](image4.png)

![Image 5](image5.png)

![Image 6](image6.png)
2 Mesoscutal hair absent (Figs 7–8) ...............................................................3
– Mesoscutal hair present, sometimes reduced (arrow, Figs 9–10) ..............5

3 Scutellum with semi-parallel to slightly radiating ridges running the length of
the dorsal surface of the scutellum, totally lacking foveate-areolet or rugulose
pattern (Fig. 11); metasomal hairy ring scarce and only has few long hairs
(arrow, Fig. 12); propodeal carinae angled and with horizontal carinae in
between (when viewed from postero-dorsal angle) (arrow, Fig. 13)..............
...........Leptopilina boulardi (Barbotin, Carton & Kelner-Pillault, 1979)
– Scutellum with foveate-areolet or rugulose pattern on the dorsal surface of
the scutellum (Fig. 14); metasomal hairy ring dense (Fig. 15); propodeal cari-
nae sub-parallel and without a horizontal carina in between propodeal cari-
nae (when viewed from postero-dorsal angle) (arrow, Fig. 16)...............4
4 Scutellar cup large, covering most of the surface of the scutellum, rhomboid shaped (arrow, Figs 17–18); metasomal hairy ring dense and long (Fig. 19) .............................................................................................................. *Leptopilina heterotoma* (Thomson, 1862)

– Scutellar cup smaller, exposing more than half of the dorsal surface of the scutellum, tear-drop in shape (Figs 20–21); metasomal hairy ring thinner, hairs shorter, composed by one or two rows of hairs, narrowly broken dorsally (Fig. 22) ........................................................................... *Leptopilina victoriae* Nordlander, 1980

5 Metapleuron, posteriorly, with a deep depression that is continuous with propodeum (arrow, Fig. 23); wing vein M without clear trace line on fore wing (Fig. 24) ......................................................................................... *Leptopilina clavipes* (Hartig, 1841)

– Metapleuron, posteriorly, not continuous with propodeum but with distinct posterior border (arrow, Fig. 25); wing vein M with or without a clear trace line on fore wing (Figs 27, 26) .........................................................................................
Metapleuron, posteriorly, without a deep depression (arrow, Fig. 28); in flagellomeres F5-F10, the length is twice the width of each flagellomere (Fig. 29); hairy ring is widely broken dorsally, not directly connected to anterior margin of metasoma (arrow A, Fig. 30), dense and long ventrally (arrow B, Fig. 30); wing vein M without a clear trace line (Fig. 26) .................................................................

\textit{Leptopilina leipsi} Lue & Buffington, sp. n.

Metapleuron, posteriorly, with a deep depression (arrow, Fig. 31); in flagellomeres F5-F10, the length is 1 to 1.5 times longer than width of each flagellomere (Fig. 32); hairy ring is widely or slightly broken dorsally, and all hairs are about equal in length, directly attached to anterior margin of metasoma (arrow, Fig. 33); wing vein M present, with a clear trace line (arrow, Fig. 27) ................................................................. \textit{Le{"o}}pitilina maia Lue & Buffington, sp. n.
Taxonomic treatment of species

**Leptopilina boulardi** (Barbotin, Carton & Kelner-Pillault, 1979)

*Charips mahensis* Kieffer, 1911: 312 (original description); Forshage, Nordlander & Buffington, 2013: 233 (synonym of *Leptopilina boulardi* (Barbotin, Carton & Kelner-Pillault), type information).

*Erisphagia mahensis* Kieffer, 1911: 312 (original description).

*Cothonaspis (Cothonaspis) boulardi* Barbotin, Carton & Kelner-Pillault, 1979: 22 (original description).

*Leptopilina boulardi* (Barbotin, Carton & Kelner-Pillault): Nordlander, 1980: 432 (generic transfer); Paretas-Martínez, Forshage, Buffington, Fisher, La Salle & Pujade-Villar, 2013: 80 (new distribution record for Australia, listed); Forshage, Nordlander & Buffington, 2013: 233 (cataloged, type information, synonymy); van Noort, Buffington & Forshage, 2015: 92 (listed).

**Diagnosis.** *Leptopilina boulardi* (Figs 34–35) is the most common species in our collections. This species is distinguishable by the patterns on the scutellum that are smooth in the background with irregular striae (Fig. 11), whereas the scutellar patterns of many other *Leptopilina* species are entirely foveollate or areollate (Fig. 14). Most of *Leptopilina* species have a dense hairy ring on the metasoma (Fig. 15), but the hairy ring in *L. boulardi* is thin, consisting of scarce hairs (Fig. 12). The propodeal carina from the lateral view are distinctly angled and with horizontal carinae between them (Fig. 13). This differs from the propodeal carina in other species which are straight, sub-parallel and without a horizontal carina between them (Fig. 16).


Review of the genus Leptopilina (Hymenoptera, Cynipoidea, Figitidae, Eucoilinae)...

Review of the genus Leptopilina (Hymenoptera, Cynipoidea, Figitidae, Eucoilinae)...


Leptopilina clavipes (Hartig, 1841)

Cothonaspis clavipes Hartig, 1841: 357 (original description); Nordlander, 1978: 50 (lectotype designation).

Leptopilina clavipes (Hartig): Nordlander, 1980: 430 (generic transfer, description); van Alphen, Nordlander & Eijs, 1991: 325 (diagnosis); Forshage, Nordlander & Buffington, 2013: 233 (cataloged, type information).

Diagnosis. Leptopilina clavipes (Figs 36–37) could be easily misidentified as L. maia or L. leipsi. L. clavipes differs from these species by having a strong impression on the lower posterior metepimeron that is continuous with the propodeum (Fig. 23). By contrast, the metapleural impression on L. maia (Fig. 31) and L. leipsi (Fig. 28) separates the metepimeron from the propodeum. The other character that can be used to distinguish L. clavipes is that the M-vein trace line is absent, and 2r-m vein is short (Fig. 24).
Figure 36–37. Leptopilina clavipes.


Material examined. United States. FL, Leon Co., 30.580557°N 84.277435°W, Tallahassee Site, 12.VI-17.VI.2013, yellow pan trap, C.-H. Lue (2 females, USNMENT01022195, 01022765 (USNM)). FL, Leon Co., 30.580557°N 84.277435°W, Tallahassee Site, 29.V.2012, yellow pan trap, C.-H. Lue (1 female, USNMENT01022740 (USNM)). FL, Leon Co., 30.580557°N 84.277435°W, Tallahassee Site, no date, C.-H. Lue (1 female, USNMENT01022243 (USNM)). VA, Falls Church, 15-VI (1 female, USNMENT01197513 (NMNH)). VA, Falls Church, 17-VI (1 female, USNMENT01119194 (NMNH)). VA, Falls Church, 28.V.1927
Review of the genus Leptopilina (Hymenoptera, Cynipoidea, Figitidae, Eucoilinae)... 55

Leptopilina decemflagella Lue & Buffington, sp. n.
http://zoobank.org/6486319D-5290-430D-97D7-D21ED355BB86

**Diagnosis.** Female *Leptopilina decemflagella* (Figs 38–39) are immediately distinguishable from other North Eastern US *Leptopilina* females by having 10 flagellomeres (Fig. 1). There are also several additional characters that separate this species from other *Leptopilina*; this species has an obvious vertical carina adjacent to the ventral margin of the antennal socket (Fig. 2); this character is not found in other *Leptopilina* species in the Eastern US. Finally in the lateral view, the hypopygium of *L. decemflagella* is pointing ventrally (Fig. 3); in other *Leptopilina* species their hypopygium is pointing upwards (Fig. 6). Male diagnostic characters are lacking as males for this species are as of yet unrecorded.

**Description.** Coloration with head, mesosoma, metasoma black, legs light brown. Vertical carina adjacent to ventral margin of antennal socket present. Malar sulcus present. Apical segment of maxillary palp more than 1.5 times as long as preceding segment. Terminal flagellomere with three basiconic sensillae. Basiconic sensilla present on F5-F10. Female antenna composed of 10 flagellomeres. Placoidal sensilla present on F6-10. Number of ridges on pronotal plate in lateral view 3. Sculpture on mesoscutum absent, entire surface smooth, shiny. Subpleuron entire smooth, anteriorly with transversely striate. Dorsal surface of scutellum foveate-areolet. Circumsutellar carina present, incomplete, laterally delimiting dorsal and ventral halves of scutellum, not present posteriorly. Latero-ventral margin of scutellum posterior to axillula entirely smooth. Dorsal part of scutellum entirely areolate. Scutellar plate, in dorsal view, medium sized, exposing about half of scutellum. Posterior impression of metapleuron absent. Anterior impression of metapleterum, immediately beneath anterior end of metapleural carina, absent. Wing vein M present but not well defined. Inter propodeal carinae space setose, too dense to see underlying surface. Horizontal carina running anteriorly from lateral propodeal carina, present. Surface of petiole longitudinally costate,
ventral keel absent. Setal band (hairy ring) at base of tergum 3 present ventrolaterally, absent dorsally and ventrally. Terebrum and hypopygium (in lateral view) curved, pointing ventrally.

**Distribution in Eastern North America.** Florida. [http://hol.osu.edu/map-full.html?id=410492]

**Etymology.** The name *Leptopilina decemflagella* is based on the 10 flagellomeres of the female antenna. This feature is unique among female North American *Leptopilina* which all have 11 flagellomeres. We treat this name as a noun in apposition.

**Comments.** *Leptopilina decemflagella*, shares some unique morphological characters with *L. tsushimaensis* Wachi and Kimura, 2015, a species described from Japan. These characters include an antenna with only 10 flagellomeres, and the presence of a vertical carina adjacent to the ventral margin of the antenna socket. However, the vertical carinae adjacent to the toruli in *L. decemflagella* do not extend to the mid-point of the eye (when viewed anteriorly); in *L. tsushimaensis*, the carinae extend to the mid-point of the eye. Furthermore, the clava in *L. decemflagella* is clearly five segmented, and the claval segments are about as long as wide; in *L. tsushimaensis*, the clava is six segmented, and each segment is longer than wide. Flagellomere 5 in *L. decemflagella* is the transition flagellomere between claval and non-claval portions of the antenna, and results in rather gradually defined clava; in *L. tsushimaensis*, flagellomere 5 is the first full claval segment, and there is no transitional segment, resulting in an abruptly defined clava. Finally, the COI barcode region was sequenced for *L. tsushimaensis*, and this data suggests more than a 5% divergence from *L. decemflagella* (data not presented). Ergo, we feel we have ample evidence to describe *L. decemflagella* as a distinct species from *L. tsushimaensis*.

Review of the genus Leptopilina (Hymenoptera, Cynipoidea, Figitidae, Eucoilinae)...


**Leucoila heterotoma** (Thomson, 1862)

*Eucoila heterotoma* Thomson, 1862: 403 (original description); Nordlander, 1978: 50 (lectotype designation).

*Ganaspis subnuda* Kieffer, 1904: 64 (original description); Forshage, Nordlander & Buffington, 2013: 233 (junior synonym of *Leptopilina heterotoma* (Thomson), type information).

*Ganaspis monilicornis* Kieffer, 1905: 623 (original description); Weld, 1952: 228 (junior synonym of *Ganaspis musti*).


*Cothonaspis (Erisphagia) philippinensis* (Kieffer): Weld, 1952: 244 (generic transfer).


*Leptopilina monilicornis* (Kieffer): Nordlander, 1980: 430 (removed from synonymy with *G. musti* and entered into synonymy with *Leptopilina heterotoma*).


*Leptopilina subnuda* (Kieffer): Nordlander, 1980: 430 (junior synonym of *Leptopilina heterotoma*).

Leptopilina heterotoma (Thomson): Nordlander, 1980: 430 (generic transfer); Paretas-Martínez, Forshage, Buffington, Fisher, La Salle & Pujade-Villar, 2013: 80 (new distribution record for Australia, listed); Forshage, Nordlander & Buffington, 2013: 233 (cataloged, type information, synonymy); Ward, 2014: 575 (keyed); van Noort, Buffington & Forshage, 2015: 92 (listed).

**Diagnosis.** *Leptopilina heterotoma* (Figs 40–41) is immediately distinguishable from other *Leptopilina* by their large and rhombus shaped scutellar plate (Fig. 17); other species have a smaller scutellar plate that is shaped like a tear drop (Fig. 20), and exposing at least half of the scutellum (in dorsal view).

laterally, shagreen dorsally. Setal band (hairy ring) at base of tergum 3 present, interrupted dorsally, ventrally, dense hair.

**Distribution in Eastern North America.** Maryland and Virginia. [http://hol.osu.edu/map-full.html?id=323709]


**Leptopilina leipsi** Lue & Buffington, sp. n.
http://zoobank.org/A764DAAE-F90F-4A91-A540-77F239A00C36

**Diagnosis.** *Leptopilina leipsi* (Figs 42–43) is distinguishable by flagellomeres F5-F10, in that the length is more than twice long as width of each flagellomere (Fig. 29). In *L. clavipes* and *L. maia* the length is 1–1.5 times the width of the flagellomere (Fig. 32). Moreover, the hairy ring is wide broken dorsally, and long and dense ventrally in *L. leipsi* (Fig. 30). This differs from other *Leptopilina* species in which the hairy ring is equally dense and of equal length (Fig. 33).

**Description.** Coloration with head, mesosoma, metasoma black to dark brown, legs light brown. Malar sulcus present. Apical segment of maxillary palp 1–1.5 times as long as preceding segment. Terminal flagellomere with one basiconic sensillum. Basiconic sensillae present on F5–F11. Placoidal sensilla present on F5-11. Number of ridges on pronotal plate in lateral view 2. Sculpture on mesoscutum absent, with sparse long hairs. Dorsal surface of scutellum foveate-areoletate. Circumscutellar carina present, incomplete, laterally delimiting dorsal and ventral halves of scutellum, not present posteriorly. Latero-ventral margin of scutellum posterior to axillula smooth ventrally, weakly rugulose dorsally. Dorsal part of scutellum entirely foveate. Scutellar plate, in dorsal view, small to medium sized, exposing small part of scutellum. Posterior impression of metepimeron present but not well defined. Anterior impression of metepisternum, immediately beneath anterior end of metapleural carina, present, small and narrow. Wing vein M absent. Inter propodeal carinae space setose, too dense to see underlying surface. Horizontal carina running anteriorly from lateral propodeal carina not visible, setae too dense. Surface of petiole longitudinally costate, ventral keel absent. Setal band (hairy ring) at base of tergum 3 present, interrupted dorsally, ventrally, longer hairs at ventral part.
Figure 42–43. *Leptopilina leipsi*.


**Etymology.** *Leptopilina leipsi* is named in honor of Dr. Jeff Leips (the PhD advisor of Lue) in appreciation for his support of her dissertation project.

Review of the genus Leptopilina (Hymenoptera, Cynipoidea, Figitidae, Eucoilinae)...

Leptopilina maia Lue & Buffington, sp. n.

Diagnosis. Leptopilina maia (Figs 44–45) is the second most common species in our collections and shares similar morphological characters with both L. clavipes and L. leipsi. In L. maia, the M vein is represented by a relatively clear trace vein that can be seen on the wing (arrow, Fig. 27). In L. clavipes and L. leipsi this trace vein is absent (Figs 24, 26). Leptopilina maia (Fig. 31) also has a deep impression on posterior margin of the metapleuron like L. clavipes (Fig. 23) but the edge of posterior metapleuron is clear and the impression not connected to the propodeum.

present but not well defined. Anterior impression of metepisternum, immediately beneath anterior end of metapleural carina, present, small and narrow. Wing vein M present but not well defined. Inter propodeal carinae space setose, too dense to see underlying surface. Horizontal carina running anteriorly from lateral propodeal carina not visible, setae too dense. Surface of petiole longitudinally costate, ventral keel absent. Setal band (hairy ring) at base of tergum 3 present, interrupted dorsally, ventrally, dense hair.


**Etymology.** *Leptopilina maia* is named in honor of the mother of the first author. The name *maia* means ‘mother’ in Greek form. Here we also use *maia* is to show our appreciation for Mother Nature and also the women who nurtured us growing up. Moreover, parasitoids, in general, are good mothers that have amazing strategies to find suitable hosts for their offspring. This name is a noun in apposition.

Review of the genus Leptopilina (Hymenoptera, Cynipoidea, Figitidae, Eucoilinae)...

Review of the genus Leptopilina (Hymenoptera, Cynipoidea, Figitidae, Eucoilinae)...

M. NORDLANDER, 1980

Diagnosis. The shape of antenna and metasoma of Leptopilina victoriae is similar to L. boulardi. However, the two species can be easily separate by the patterns of the scutellum (Figs 11, 20). In general, the hairy ring in L. victoriae (Figs 46–47) is dense and relatively shorter than other Leptopilina species (Fig. 22). This species also has a long horizontal ridge across middle of the metapleuron (arrow, Fig. 22). The ridge is parallel to the upper ridge of metapleura and that different from other Leptopilina species the ridge is not display parallel.


Distribution in Eastern North America. Of the seven species in our identification key, L. victoriae did not appear in our field collections. However, because this species is commonly used in laboratory experiments we include this species in the identification key to assist with diagnosis of other Leptopilina species that are also commonly used as laboratory strains (e.g., L. boulardi, L. heterotoma and L. clavipes).
**Figure 46–47. Leptopilina victoriae.**


**Discussion**

Species of *Leptopilina* have been studied as *Drosophila* parasitoids for over five decades. However, knowledge of their natural history and taxonomic information remains limited for most species. None of this is too surprising when one considers the difficulties associated with identifying *Leptopilina* species. The cryptic morphological features among species, combined with geographic variation within species, could lead to the misidentification or description of species in this genus. Here we provide a key for identifying seven North American *Leptopilina* species associated with frugivorous hosts and within this group, describe three new species: *Leptopilina decemflagella* sp. n., *L. maia* sp. n., and *L. leipsi* n.sp. In addition to describing morphological characters that can be used for diagnosis, we also provide sequence data on CO1 for each species, in part to evaluate to what extent morphological divergence is reflected at the sequence level.

Molecular markers can be useful for distinguishing operational taxonomic units, especially for very small organisms that are difficult to separate morphologically due to their cryptic nature, or when species exhibit extensive intraspecific morphological variation. However, the high-efficiency associated with gathering sequence data poses a possible trade-off in accuracy for species that lack diagnostic data and/or lack trained taxonomists to develop character-based analysis to verify the molecular signal (Goldstein and DeSalle 2010, Smith et al. 2013). This situation was made apparent...
in the current study. In *Leptopilina*, the DNA sequences downloadable from public databases such as GenBank, are lacking specific epithets or labeled as unknown species. Furthermore, many named species in Genbank are possibly mis-identified, as there is no solid identification system in place for *Leptopilina*. Perhaps most alarming are many sequences that are not backed up by morphological studies or voucher specimens. For this reason, it is difficult to find good reference specimens for the species in our study, and raises questions about whether the species name associated with the sequence provided in the online database is correct.

The ideal use of DNA barcoding for species identification is to complement the sequence data with other sources of information (Goldstein and DeSalle 2010). Also, in the process of delimiting or discovering an organism, the species needs a formal description. As such it is crucial to consider both molecular and morphological diagnostic criteria in these kinds of study. In the current study, sequences receiving the tag ”DNA Barcode” in the Genbank database are associated with specified voucher specimens and specimen metadata, such as collection locality. These are ideally suited for use as reference sequences for future studies. Our sequences and associated information have been submitted to Genbank as DNA Barcodes. Deposited in GenBank with the accession numbers KY077389-KY077436.

Although the large size of our collection captures variation and allows us to identify diagnostic characters for most groups, difficulties delimiting cryptic species are still present in this study. In our collections some morphological characteristics (e.g., body size, scutellum size and ridge patterns on the metapleura) show high intraspecific variation but low interspecific divergence, and as a consequence, fail to consistently delimit species. For example, three *Leptopilina* species share similar morphological characters and habitats in this study, *L. clavipes*, *L. maia* and *L. leipsi* and the scutellum pattern, body size, and morphological characters that we commonly used to delimit other *Leptopilina* species, fail to discriminate *L. maia* from *L. leipsi*. We had to complement the consistent morphological characters (see results) with 5% genetic divergence in the CO1 sequence to be confident in assigning them to different species.

Two complicating factors often make it difficult to discriminate species in this group. First, parasitoid wasps often have limited ranges and small population size. As a result, parasitic life style can accelerate the rate of mitochondrial genetic divergence (Dowton and Austin 1999, Castro et al. 2002). If groups are undergoing rapid speciation, there may have not been sufficient time to accumulate differences in morphological traits among species (Kankare et al. 2005, Smith et al. 2008), yet biologically, these species might be quite isolated. This is where determining levels of sequence divergence among groups can be helpful in identifying OTUs. Second, is the reproductive mode of some parasitoids. Arrhenotoky (haplodiploid-diploid) and thelytoky (all haplodiploid eggs develop into females) are common reproductive modes in Hymenoptera species. The clone reproductive mode (thelytoky) could decrease the genetic diversity within a population and increase the genetic distance among different populations of the same species. As a result, populations of the same species might exhibit significant divergence at the molecular and morphological level and potentially mislead species determina-
tion. In addition, infection by *Wolbachia*, a common maternally transmitted bacteria in arthropods (Smith et al. 2012), can alter the reproductive mode from arrhenotoky to thelytoky in *L. clavipes*. Interestingly, this reproductive mode displays geographic variation in Europe (Pannebakker et al. 2004) and so the presence or absence of *Wolbachia* infection may also affect the degree of genetic and morphological divergence among populations, further complicating efforts to delimit parasitoid species.

**Conclusion**

This study is the first of its kind in North America, and in three ways, the first of its kind for *Leptopilina*. First, historically important museum specimens were augmented by specimens comprehensively collected across the *Drosophila* host breeding season and also across a broad geographic scale. Sampling across this geographic scale, and obtaining a large sample of individuals at each location throughout the breeding season, allowed us to account for intraspecific variation among *Leptopilina* when delimiting the species, something not possible when using a smaller pool of specimens. Consequently, we are able to describe morphological variation at the lowest taxonomic level. This is important because phenotypic variation is one of the main factors that reflects rapid evolution of parasitoid wasps. Within the framework of this new collecting paradigm, we also collected potential hosts at the same time we collected parasitoid wasps (Lue et al. in preparation). Secondly, sorting bulk, passively collected samples for *Leptopilina*, as well as direct rearing, allowed us to discover three new species. Finally, we consider this study especially critical at the present time, as the invasive Spotted Wing Drosophila (SWD; *Drosophila suzukii* Matsumura) has spread rapidly on the east coast of the US (Gabarra et al. 2015, Miller et al. 2015, Walsh et al. 2015), and *Leptopilina* spp. are routinely collected associated with this pest fly (Lue and Buffington, per. obsv.). As there had previously been no identification system for *Leptopilina* in any part of the United States, we hope that this review of the species and identification key for eastern North American species, will assist in future *Leptopilina* research in the United States.

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UMBC. All the molecular laboratory work was conducted in and with the support of the L.A.B. facilities of the National Museum of Natural History. This study has been supported by a USNM graduate student fellowship to CHL, and UMBC (University of Maryland Baltimore County). Drs. Jose-Luis Nieves-Aldrey, George Melika, Mattias Forshage and Matthew Yoder reviewed and helped greatly improve this paper. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information does not imply recommendation or endorsement by the USDA. USDA is an equal opportunity provider and employer.

References


Supplementary material 1

Percent sequence difference among *Leptopilina* species.
Authors: Chia-Hua Lue, Amy C. Driskell, Jeff Leips, Matthew L. Buffington
Data type: measurement
Explanation note: Percent sequence difference among species at the barcode region of the cytochrome oxidase subunit I gene. Values in bold are the percent sequence difference within each species. Sample sizes are in parentheses in the left-most column. The asterisk indicates the newly described species of *Leptopilina*.
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New *Dryocosmus* Giraud species associated with *Cyclobalanopsis* and non-*Quercus* host plants from the Eastern Palaearctic (Hymenoptera, Cynipidae, Cynipini)

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http://zoobank.org/989B7FE4-1F50-48A7-8414-8D0AF4F4C064


Abstract

Our knowledge about gall wasps associated with the diverse East Asian oaks, *Castanopsis* and *Cyclobalanopsis*, is limited due to the lack of extensive field studies. Here, we describe twelve new oak gall wasp species, *Dryocosmus cannoni* Schwéger & Tang, *D. caputgrusi* Tang & Schwéger, *D. crinitus* Schwéger & Tang, *D. harrisonae* Melika & Tang, *D. hearni* Melika & Tang, *D. hualieni* Schwéger & Tang, *D. konradi* Tang & Melika, *D. liyingi* Melika & Tang, *D. moriius* Tang & Melika, *D. quadripetiolus* Schwéger & Tang, *D. salicinai* Schwéger & Tang, and *D. taitungensis* Tang & Melika, from Taiwan and mainland China. Seven newly described species induce galls on *Quercus* subgenus *Cyclobalanopsis* and five on other Fagaceae genus, *Castanopsis*. All of the new species concepts are supported by morphological and molecular data. We provide descriptions, diagnoses, host associations for the new species and an illustrated identification key to Eastern Palaearctic *Dryocosmus* species. We represent natural language phenotypes in a semantic format supported by biomedical ontologies to increase the accessibility of morphological data.
Keywords
Cynipidae, Dryocosmus, Plagiotrochus, Cyclobalanopsis, Castanopsis, Lithocarpus, Castanea, biology, morphology

Introduction
Oak gallwasps (Hymenoptera: Cynipidae: Cynipini), with about 1000 species, are the most species-rich cynipid lineage (Csóka et al. 2005). Most cynipine species are associated with oaks of the Quercus L. subgenus Quercus L. in the Western Palaearctic and Nearctic (Stone et al. 2002, 2009, Abe et al. 2007). Although the other Quercus subgenus, the Asian Cyclobalanopsis (Oersted) C. K. Schneider, is represented by 76 species (Govaerts and Frodin 1998, Manos and Stanford 2001), our knowledge about Cyclobalanopsis associated cynipines is restricted to a few, recently described taxa (Abe et al. 2014a, b, Ide et al. 2010, 2012, 2013, Melika et al. 2011, 2013, Tang et al. 2011a, b, 2016a, b).

Similarly to Cyclobalanopsis, East Asia is also a diversity center for three other Fagaceae genera. The tropical and subtropical Castanopsis Miller is represented with 134 species in Asia and Malesia; the 325 species of Lithocarpus Blume (=Pasionia (Miq.)) occur almost entirely in Asia and Malesia (one species in the western North America), and the 8 species of Castanea Miller are distributed in the Northern Hemisphere (Govaerts and Frodin 1998). Associations between East Asian representatives of these Fagaceae genera and Cynipini have been revealed only very recently (Tang et al. 2011a and Tang et al. 2016a).

Of the ten Eastern Palaearctic Dryocosmus species, D. sakureiensis Ide, Wachi & Abe, D. sefuriensis Ide, Wachi & Abe, are associated with Cyclobalanopsis, four species, D. carlesiae Tang & Melika, D. pentagonalis Melika & Tang, D. testisimilis Tang & Melika, D. triangularis Melika & Tang, with Castanopsis, two species, D. kuriphilus (Yasumatsu), and D. zhuili Liu & Zhu, with Castanea. Hosts of Dryocosmus nanlingensis Abe, Ide, & Odagiri and D. okajimai Abe, Ide, Konishi & Ueno are unknown (Abe et al. 2014a, b, Ide et al. 2010, 2012, 2013, Melika et al. 2011, 2013, Tang et al. 2011a, b, Zhu et al. 2015). Ide and Abe (2015) described a new cynipine species, Dryocosmus kunugiphagus, from a section Cerris oak, Quercus acutissima Carruth, as the first Dryocosmus species developing on section Cerris oaks in the Eastern Palaeartic. This species shares numerous diagnostic features with Plagiotrochus and lack key character states of Dryocosmus (e.g. in D. kunugiphagus the mesoscutum is rugose, with dense setae, the mesopleuron rugose and the apical setae of the ventral spine of hypopygium do not form a truncate apical tuft; Melika et al. 2010, Ide and Abe 2015), thus we did not treat Dryocosmus kunugiphagus in the present paper.

In this study we double the number of Dryocosmus species associated with non-subgenus Quercus oaks and describe twelve new Dryocosmus species from Taiwan and four from mainland China. Seven of these, Dryocosmus crinitus Schwéger & Tang, D. hualieni Schwéger & Tang, D. konradi Tang & Melika, D. liyingi Melika & Tang, D. moriius Tang & Melika, D. salicinai Schwéger & Tang, and D. taitungensis Tang

**Materials and methods**

Galls were collected from *Castanopsis* and *Quercus* subgenus *Cyclobalanopsis* species in Taiwan and China in March 2011 and 2012 from the following localities: Taiwan: *Castanopsis carlesii* (Hemsley) Hayata and *C. uraiana* (Hayata) Kaneh. & Hatus at Taoyuan and Taitung Counties; *Q. glauca* Thunb. in Murray at Hualien and Nantou Co., *Q. morii* Hayata and *Q. longinux* Hayata at Nantou Co., *Q. hypophaea* Hayata at Taitung Co., *Q. salicina* Blume at Taichung Co., *Q. sessilifolia* Blume at New Taipei City, China: *Castanopsis echinocarpa* Miq. at Yunnan Province, Xishuangbanna Lan Cang County and Xishuangbanna, Yunnan Province; *Castanopsis* sp.4 at Lan Cang County, Yunnan Province. Galls were kept at room temperature in plastic containers with openings on the lids that were covered with meshes to keep ventilation. Emerged adult wasps were preserved in 99% ethanol.

The type material is deposited in the following institutions: NMNS, National Museum of Natural Science, Taichung, Taiwan (curator M.L. Jeng); PHMB, Plant Health and Molecular Biology Laboratory, National Food Chain Safety Office, Budapest, Hungary (curator G. Melika); NCHU, Department of Entomology, National Chung Hsing University, Taichung, Taiwan (curator M.-M. Yang); USNM, U.S. National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. (curator M. Buffington).

Bright field images of adults and galls were produced with a digital Leica DC500 camera attached to a Leica DM2700M compound microscope using the LAS Store&Recall software, followed by processing in Adobe Photoshop 6.0. High resolution plates are available from Figshare (https://dx.doi.org/10.6084/m9.figshare.3837915.v1).

Anatomical terms were matched to concepts in the Hymenoptera Anatomy Ontology (Yoder et al. 2010) and a URI table (Suppl. material 1) containing morphological terms, definitions and Uniform Resource Identifiers resolved at http://hymao.org were generated using the text analyzer function (Seltmann et al. 2013, http://portal.hymao.org/projects/32/public/ontology/).

Matrix-based descriptions were generated using mx (http://purl.org/NET/mx-database). Terminology of morphological statements used in descriptions, identification key and diagnoses are mapped to relevant biomedical ontologies (Hymenoptera Anatomy Ontology (HAO), Phenotypic Quality Ontology (PATO), Biospatial Ontology (BSPO), Common Anatomy Reference Ontology (CARO); available at http://obofoundry.org/).

We represent natural language phenotypes in an Entity: Quality (EQ) format: Entity attribute: value. Semantic statements of natural language phenotypes (Suppl. material 2) were composed in Protégé 5.0 (http://protege.stanford.edu/) using the OWL Manchester syntax (http://www.w3.org/TR/owl2-manchester-syntax/) following Balhoff et al. (2013) and Mikó et al. (2014).
The full data set, represented in OWL (Web Ontology Language; http://www.w3.org/TR/owl2-overview/ last accessed February 4, 2014), was deposited as a Resource Description Framework (RDF)-XML file (http://www.w3.org/TR/REC-rdf-syntax/ in Github (https://github.com/hymao/hymao-data/blob/master/Tang_et_al_dryocosmus_merged.owl). The phenotypic descriptors “glossy and matte” (http://purl.obolibrary.org/obo/PATO_0001373), refer to the reflectance quality of the cuticle. These relation phenotypes can only be observed under direct light (without light diffusers) and might correlate to the cuticular hydrocarbon profile (Hora et al. 2007, 2010).

The phenotypic descriptor “smooth” refers to the sculpture quality of a cuticular region that lacks “leathery” microsculpture (Ball 1985). Hexagonal sculptural elements (scutes, http://purl.obolibrary.org/obo/HAO_0002430) of this microsculpture type most likely correspond to epidermal cells (Hinton 1970, Moretto 2015). Sculptures with convex scutes surfaces are referred here as “coriaceous” while that of flat scute surfaces are named “alutaceous”.

Species concepts of the present paper were also examined using genetic data. Part of the mitochondrial cytochrome b (cyt b) gene was amplified from extractions of whole genomic DNA from between one and four individuals per species using the primers CB1/ CB2 or CB1/CP2, following protocols in Nicholls et al. (2010). PCR products were cleaned up using a standard SAP/ExoI protocol, then sequenced in both directions using BigDye v3.1 terminator chemistry and run on an ABI3730 capillary sequencer. Base calls were confirmed by eye using Sequencer version 4.10.1 (Gene Codes Corporation 1995). Sequence data for the corresponding fragment were also obtained for two or three individuals of four previously described Dryocosmus species: D. carlesiae, D. pentagonalis, D. testisimilis, D. triangularis. Pairwise distances between all individuals were determined in PAUP* v4.0b10 (Swofford 1998) using a HKY model of sequence evolution, then average within- and between-species distances were calculated for each species-level comparison.

**Results**

**Molecular markers**

A 433 base-pair fragment of the cyt b gene was successfully amplified for between one and six individuals of each species; in total 49 sequences were obtained from 17 species (GenBank accession numbers KU760807–KU760855). Variation within species was minimal, ranging from 0 to 1.6% (Table 1, values on diagonal). Variation between all species, both new ones described herein and previously described taxa, was greater than 6.9% for all comparisons except the one between D. harrisonae and D. cannoni (2.0%), and in some instances was greater than 20% (Table 1). These values are consistent with those expected for within- and between-species variation both in gall wasps (Nicholls et al. 2012) and among insects in general (Hebert et al. 2003), supporting the distinctiveness of the newly described Dryocosmus species.
Table 1. Pairwise genetic distances between 17 *Dryocosmus* species, based upon 433 base pairs of the cytochrome *b* gene using a HKY correction. Values on the diagonal indicate variation levels among individuals of the same species; off-diagonal values indicate between-species distances.

|             | *D. cannoni* | *D. caputgrusi* | *D. crinitus* | *D. harrisonae* | *D. hearni* | *D. hualieni* | *D. konradi* | *D. liyingi* | *D. morius* | *D. quadripetiolus* | *D. salicinai* | *D. taitungensis* | *D. carlesiae* | *D. kuriphilus* | *D. pentagonalis* | *D. testisimilis* | *D. triangularis* |
|-------------|--------------|----------------|--------------|----------------|-------------|--------------|-------------|-------------|-------------|---------------------|----------------|----------------|----------------|---------------|----------------|----------------|----------------|----------------|----------------|
| *D. cannoni* | 0.00         |                |              |                |             |              |             |             |             |                     |                |                |                |               |                |                |                |                |                |
| *D. caputgrusi* | 0.09        | -              |              |                |             |              |             |             |             |                     |                |                |                |               |                |                |                |                |                |
| *D. crinitus* | 0.20         | 0.18           | 0.01         |                |             |              |             |             |             |                     |                |                |                |               |                |                |                |                |                |
| *D. harrisonae* | 0.02         | 0.09           | 0.19         | 0.00          |             |              |             |             |             |                     |                |                |                |               |                |                |                |                |                |
| *D. hearni* | 0.28         | 0.29           | 0.28         | 0.30          | 0.00        |              |             |             |             |                     |                |                |                |               |                |                |                |                |                |
| *D. hualieni* | 0.26         | 0.25           | 0.24         | 0.25          | 0.29        | 0.00         |             |             |             |                     |                |                |                |               |                |                |                |                |                |
| *D. konradi* | 0.17         | 0.16           | 0.19         | 0.18          | 0.27        | 0.18         | 0.01        |             |             |                     |                |                |                |               |                |                |                |                |                |
| *D. liyingi* | 0.21         | 0.21           | 0.25         | 0.22          | 0.33        | 0.26         | 0.20        | 0.02        |             |                     |                |                |                |               |                |                |                |                |                |
| *D. morius* | 0.19         | 0.16           | 0.18         | 0.19          | 0.27        | 0.20         | 0.16        | 0.22        | 0.01        |                     |                |                |                |               |                |                |                |                |                |
| *D. quadripetiolus* | 0.09        | 0.07           | 0.19         | 0.09          | 0.29        | 0.27         | 0.14        | 0.22        | 0.18        | 0.00              |                |                |                |               |                |                |                |                |                |
| *D. salicinai* | 0.20         | 0.21           | 0.21         | 0.19          | 0.29        | 0.22         | 0.17        | 0.24        | 0.11        | 0.19              | 0.00            |                |                |               |                |                |                |                |                |
| *D. taitungensis* | 0.18        | 0.13           | 0.20         | 0.18          | 0.29        | 0.26         | 0.16        | 0.23        | 0.21        | 0.15              | 0.21            | 0.01           |                |               |                |                |                |                |                |
| *D. carlesiae* | 0.15         | 0.15           | 0.22         | 0.16          | 0.29        | 0.24         | 0.19        | 0.25        | 0.19        | 0.16              | 0.16            | 0.15           | 0.00           |               |                |                |                |                |                |
| *D. kuriphilus* | 0.17         | 0.14           | 0.24         | 0.16          | 0.29        | 0.23         | 0.16        | 0.22        | 0.20        | 0.15              | 0.18            | 0.18           | 0.00           | 0.00          |                |                |                |                |                |
| *D. pentagonalis* | 0.11         | 0.08           | 0.19         | 0.12          | 0.27        | 0.23         | 0.15        | 0.20        | 0.19        | 0.11              | 0.20            | 0.16           | 0.17           | 0.14         | 0.00           |                |                |                |                |
| *D. testisimilis* | 0.17         | 0.18           | 0.28         | 0.18          | 0.28        | 0.24         | 0.22        | 0.20        | 0.23        | 0.20              | 0.19            | 0.19           | 0.20           | 0.19         | 0.00           | 0.00            |                |                |                |
| *D. triangularis* | 0.11         | 0.10           | 0.18         | 0.11          | 0.26        | 0.23         | 0.16        | 0.19        | 0.18        | 0.12              | 0.18            | 0.17           | 0.17           | 0.15         | 0.07           | 0.19            | 0.00           |                |                |
Morphology

*Dryocosmus* Giraud, 1859

**Description.** Clypeus ventral margin shape: straight; Malar striae count: present; Malar striae dorsal limit: torulus-eye line on lower face and lower eye margin on malar area; Malar area: alutaceous; Malar sulcus: absent; Impression around central ocellus: present; Postgenal bridge / length of oral foramen: <1.

Transversepronotal sulcus depth: deep; Notaulus limits: well-impressed, posterior end adjacent to posterior margin of mesoscutum, anterior end adjacent to anterior margin of mesoscutum; Mesoscutum sculpture: smooth or delicately alutaceous; Mesoscutum reflectivity: glossy; Metanotal trough sculpture: smooth; Metanotal trough reflectivity: glossy; Metascutellum sculpture: coriaceous; Scutellar foveae count: present; Foveal septum count: present or absent; Dorsomedian area of mesoscutellar-axillar complex (disc of mesoscutellum+axillar foveae) shape: trapezoid or quadrangular. Subaxillular bar sculpture: smooth; Subaxillular bar reflectivity: glossy; Mesoscutellar axillar complex posterior margin vs metanotum: overhanging; Mesopleuron sculpture: smooth, mostly glossy, only partially coriaceous; Speculum sculpture: smooth, mostly glossy, only partially coriaceous; Lateral propodeal carinae count: present; Central propodeal area reflectivity: glabrous; Lateral propodeal area pilosity: present; Nucha sculpture: with delicate longitudinal rugae dorsally and laterally; Wings fully developed; Marginal cilia: long; R1 distal end vs wing margin: adjacent to wing margin; Rs distal end vs wing margin: adjacent to wing margin.

Metasoma lateral height / metasoma lateral length: <1; Metasoma length / head+mesosoma length: <1; Second metasomal tergite sculpture: smooth; Metasomal tergites 3-6 reflectivity: glossy; Distal end of ventral spine of hypopygium shape: acute or rounded distally apically; Prominent part of ventral part of hypopygium length / width: < 3.5; ventral part of hypopygium seta length: short.

**Diagnosis.** Most similar to *Plagiotrochus* Mayr by sharing the following character states: lower face with striae radiating from clypeus to inner margin of eye (sometimes indistinct because of short malar space), malar sulcus absent; lateral propodeal carinae curved outwards, median longitudinal carina sometimes present; central propodeal area with rugae; metasoma strongly compressed laterally; ventral spine of hypopygium short, acute or rounded apically, with or without a dense truncate tuft, prominent part < 3.5 times as long as broad (Melika et al. 2010).

*Dryocosmus:* mesoscutum smooth or alutaceous; ventral spine of hypopygium with setae forming a truncate apical tuft.

*Plagiotrochus:* mesoscutum entirely coriaceous or rugose; ventral spine of hypopygium with setae not forming a truncate apical tuft.
New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...

**Key to Dryocosmus species**

1. Mesosoma orange-yellow, metasoma light brown, female head orange-yellow to light brown, male head orange-yellow to dark brown .......................... 2
   - Body dark brown to black, with some minute, light brown areas ............. 3

2. Notaulus posterior region width / notaulus anterior region width = 5 (not: Fig. 73); posterior height of subaxillular bar / height of metanotal trough = 0.25 (sab, mtr: Fig. 72); central propodeal area with transverse carina (trc: Fig. 74) in dorsal 1/3rd and with longitudinal parallel rugae between transverse carina and nucha (Fig. 74) .................................................................
   - Notaulus anterior region width / notaulus posterior region width = 1 (not: Fig. 181); posterior height of subaxillular bar / height of metanotal trough > 1.00; central propodeal area without transverse carina in dorsal 1/3rd and with irregular rugae between dorsal propodeal margin and nucha (Fig. 180) ........

3. Basal lobe on metatarsal claw present .................................................... 4
   - Basal lobe on metatarsal claw absent .................................................. 5

4. Number of flagellomeres (female): 12; eye height / malar distance = 2.6; intertorular distance / eye torulus distance = 0.70; radial cell length / radial cell width = 3.40; 2nd metasomal tergite length dorsal view / length of metasoma dorsal view ≥ 0.50; prominent part of ventral spine of hypopygium length ventral view / prominent part of ventral spine of hypopygium width ventral view = 2.2 ................ Dryocosmus sakureiensis Ide, Wachi & Abe, 2013
   - Number of flagellomeres (female): 13 (Fig. 126); eye height / malar distance = 2.0; intertorular distance / eye torulus distance = 0.40 (Fig. 122); radial cell length / radial cell width = 4.50 (rad: Fig. 129); 2nd metasomal tergite length dorsal view / length of metasoma dorsal view = 0.33; prominent part of ventral spine of hypopygium length ventral view / prominent part of ventral spine of hypopygium width ventral view = 1.3 (vsh: Fig. 132) ........

5. Dense setae present on lateral mesopleural surface ventral to transepisternal line (tel: Fig. 142) .... Dryocosmus quadripetiolus Schwéger & Tang, sp. n.
   - Mesopleuron glabrous or few setae present along posteroventral margin of lateral mesopleural surface (Figs 24, 40, 72, 166) ........................................

6. Striae marking transepisternal line extends 3/4 of mesopleuron length (tel: Fig. 24) ....................................................................................... 7
   - Striae marking transepisternal line absent (Fig. 99) or not extends 1/2 of mesopleuron length (tel: Figs 84) .................................................... 10

7. Speculum striate (spe: Fig. 24) ..................................................... Dryocosmus zhuili Liu & Zhu, 2015
   - Speculum without striae ..........................
8 Female POL/OOL = 1.40 (Fig. 2); male eye height / malar distance = 8.1; male eye height / transfacial distance = 1.2 (Fig. 5); male pedicel length / scape length < 1 (Fig. 10). 

9 Female POL/OOL = 1.80 (Fig. 176); male eye height / malar distance = 8.70; male eye height / transfacial distance = 1.40 (Fig. 177), male pedicel / scape = 1. 

\textit{Dryocosmus triangularis} Tang & Melika, 2011 

9 Disc of mesoscutellum glossy and smooth at least in anterior half (dms: Figs 25, 26). 

\textit{Dryocosmus caputgrusi} Tang & Schwéger, sp. n. 

– Disc of mesoscutellum entirely rugose, matt (dms: Fig. 178). 

\textit{Dryocosmus pentagonalis} Tang & Melika, 2011 

10 Mesopleuron and speculum matt, uniformly coriaceous, without striae. 

\textit{Dryocosmus salicinai} Schwéger & Tang, sp. n. 

– Mesopleuron glossy, smooth without striae (Fig. 99) or with few delicate indistinct striae marking transepisternal line (tel: Figs 84). 

11 Mesopleuron and speculum smooth, without striae (Fig. 113). 

– Mesopleuron with few delicate indistinct striae marking transepisternal line (tel: Figs 166, 182, 184). 

12 Second metasomal tergite with multiple setae laterally (Fig. 87). 

– Second metasomal tergite without or few setae laterally (Fig. 119). 

13 Scutellar foveae without longitudinal striae (scf: Fig. 100); female F1 / F2 = 1.00; female F1 / pedicel = 2.7; placoid sensilla present on F1–F12 (Fig. 97). 

\textit{Dryocosmus konradi} Tang & Melika, sp. n. 

– Scutellar foveae with longitudinal striae (scf: Fig. 83); female F1 / F2 < 1; Female F1 / pedicel = 1.6; placoid sensilla present on F2–F12 (Fig. 81). 

\textit{Dryocosmus hualieni} Schwéger & Tang, sp. n. 

14 Scutellar fovea minimum diameter / foveal septum width = 3.00; anterior pits of foveal septum present. 

\textit{Dryocosmus okayimai} Abe, Ide, Konishi & Ueno, 2014 

– Scutellar fovea minimum diameter / foveal septum width = 6.00–10.00; anterior pits on foveal septum absent (Fig. 183). 

15 Disc of mesoscutellum with irregular rugae (dms: Fig. 183). 

\textit{Dryocosmus carlesiae} Tang & Melika, 2011 

– Disc of mesoscutellum without irregular rugae (dms: Fig. 116). 

16 Transverse pronotal sulcus not foveolate (tps: Fig. 40); pronotum posterolaterally with few short rugae as long as or shorter than diameter of anterior thoracic spiracle (Fig. 40). 

– Transverse pronotal sulcus foveolate (tps: Fig. 113); pronotum posterolaterally with numerous long rugae 2–3 times as long as diameter of anterior thoracic spiracle (Fig. 113). 

\textit{Dryocosmus liyingi} Melika & Tang, sp. n. 

– Central propodeal area with 1–2 delicate longitudinal lateral rugae (cpa: Fig. 42). 

\textit{Dryocosmus crinitus} Schwéger & Tang, sp. n. 

– Central propodeal area with numerous irregular longitudinal and transverse lateral and medial rugae. 

\textit{Dryocosmus nanlingensis} Abe, Ide & Odagiri, 2014
New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...

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<table>
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<tbody>
<tr>
<td>18</td>
<td>Speculum striate dorsally (spe: Fig. 166)</td>
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<tr>
<td></td>
<td>Speculum without striae (spe: Figs 11, 55, 184)</td>
</tr>
<tr>
<td>19</td>
<td>Triangular mesopleural furrow present; frons, interocellar area, vertex glossy, smooth, if frons alutaceous than only in lateral part, along compound eye...</td>
</tr>
<tr>
<td></td>
<td>Triangular mesopleural furrow absent; frons, interocellar area, vertex alutaceous or coriaceous (Figs 184–185)</td>
</tr>
<tr>
<td>20</td>
<td>Head width / head height &gt;1; gena broadened behind eye, visible in frontal view along entire lateral eye margin (gen: Fig. 186)</td>
</tr>
<tr>
<td></td>
<td>Head width / head height = 1; gena not or very slightly broadened behind eye, not visible in frontal view or only visible along ventral region of lateral eye margin (gen: Figs 1, 48)</td>
</tr>
<tr>
<td>21</td>
<td>Parapsidal line and median mesoscutal line present (pl, mml: Fig. 12)</td>
</tr>
<tr>
<td></td>
<td>Parapsidal line and median mesoscutal line absent (Fig. 56)</td>
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**Dryocosmus cannoni** Schwéger & Tang, sp. n.
http://zoobank.org/1466DED3-5B57-474D-89FA-20A2B1A4356F
Figures 1–17


The female holotype and the male paratype are deposited in PHMB.

**Etymology.** Named after Prof. Chuck Cannon (Xishuangbanna Tropical Botanical Garden, Yunnan, China).

**Diagnosis.** *Dryocosmus cannoni*, *D. harrisonae*, *D. sefuriensis* and *D. kuriphilus* belong to the group of species in which the area dorsal to the transepisternal line is delicately striate anteriorly and the speculum lacks striae.

*Dryocosmus cannoni* is most similar to *Dryocosmus harrisonae*, sharing the presence of a slightly broadened gena visible only ventrally along the lateral eye margin.

*Dryocosmus cannoni*: parapsidal line and median mesoscutal line present (Fig. 12); placoid sensilla present on female F4–F12 (Fig. 9); scutellar foveae semilunar, with longitudinal parallel rugae; foveal septum absent (Fig. 13).
**Figures 1–10.** *Dryocosmus cannoni* sp. n. 1–4 head, female: 1 frontal view 2 dorsal view 3 posterior view 4 lateral view 5–8 head, male: 5 frontal view 6 dorsal view 7 posterior view 8 lateral view 9–10 antenna: 9 female 10 male (gen=gena).

*Dryocosmus harrisonae*: parapsidal line and median mesoscutal line absent (Fig. 56); placoid sensilla present on female F2–F12 (Fig. 53); scutellar foveae transversely ovate, without rugae; foveal septum present (Fig. 57).
Description. Sexual female: Head color: brown; mandibles, maxillary and labial palps yellowish; scape and pedicel yellow, flagellomeres progressively darker. Meso-soma and metasoma color: dark brown to reddish brown, except for lighter tegula, propodeum, and posterior half of metasoma, legs yellow.

Figures 11–15. *Dryocosmus cannoni*, female, sp. n. 11 mesosoma, lateral view 12 mesoscutum, dorsal view 13 mesocutellum, dorsal view 14 metascutellum and propodeum, posterodorsal view 15 fore wing, part (mml=median mesoscutal line, pl=parapsidal line, spe=speculum).

New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...


Body length: 2.30 mm (n=1).


Gall (Fig. 17): The main body of the gall is located on a long, thin stalk, 1.5–2.1 mm long, growing from the base of the petiole or midrib of the leaf. The gall body contains a spherical part 6.0–8.1 mm in diameter and a needle-like projection at the top of the gall body nearly the same length as the gall diameter. The gall is green, surface smooth; parenchyma is green and succulent. Unilocular, with a centrally
New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...

Biology. Only the sexual generation is known. Galls were collected from Castanopsis echinocarpa in April; adults emerge from galls under laboratory conditions immediately after field collection.

Distribution. China: Yunnan Province (Xishuangbanna).

Dryocosmus caputgrusi Tang & Schwéger, sp. n.
http://zoobank.org/BE520902-9F48-41F3-97DC-0152ADEB90E9
Figures 18–32


The female holotype and 1 female paratype are deposited in NMNS, 1 female paratype in PHMB, 1 female paratype in NCHU.

Etymology. The Latin “caput” means “head”, and “Grus” is a common crane genus name. The name reflects the shape of the gall which looks like a crane head.

Diagnosis. Dryocosmus caputgrusi, D. pentagonalis and D. triangularis belong to the group of species in which striae marking the transepisternal line extend at least ¾ of the mesopleuron length and the speculum is delicately striate (Fig. 24).

In Dryocosmus triangularis the female POL/OOL = 1.8 (Fig. 176); the male eye height / malar distance = 8.70; the male eye height / transfacial distance = 1.40 (Fig. 177); male pedicel nearly as long as the scape.

In Dryocosmus caputgrusi and D. pentagonalis the female POL/OOL = 1.4 (Figs 20, 174); male eye height / malar distance = 8.1; male eye height / transfacial distance = 1.20 (Fig. 175); the male pedicel / scape<1.

Dryocosmus caputgrusi: the disc of the mesoscutellum is glabrous, smooth, at least in anterior half (Fig. 25).

Dryocosmus pentagonalis: the disc of the mesoscutellum is entirely rugose, matt (Fig. 178).

Description. Sexual female: Head color: brown; mandibles, maxillary and labial palps yellowish; scape and pedicel yellow, flagellomeres progressively darker. Mesosoma and metasoma color: dark brown, except for lighter tegula, propodeum and posterior half of metasoma, legs yellowish.
Figures 18–23. *Dryocosmus capitatus*, female, sp. n. 18–21, head: 18 frontal view 19 posterior view 20 dorsal view 21 lateral view 22 antenna 23 pronotum and propleuron, frontal view.

New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...


Notaulus posterior region width / anterior region width: NOT CODED. Mesoscutal suprahumeral sulcus anterior end vs notaulus anterior end: adjacent. Mesoscutal suprahumeral sulcus sculpture: NOT CODED. Median mesoscutal line: absent. Median mesoscutal line shape: NOT CODED. Parapsidal line: absent. Parapsidal line distinctness: NOT CODED. Antero-admedian line: present. Antero-admedian line length / mesoscutum median length: 0.2. Dorsomedian area of mesoscutellar-axillar complex (disc of mesoscutellum-axillar foveae): smooth anteromedially, ru-
New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...

Body length: 2.60 mm (n=2).

Male: unknown

Gall (Figs 31–32): The gall is unilocular, spindle-shaped and is attached with a long stalk to the leaf. The gall is 8.0–12.7 mm long, 1.5–1.8 mm wide (n=4), with a stalk varying in length from 6.4 mm to 8.1 mm. The swollen part of the spindle-shaped gall indicates the position of the larval chamber. The gall is green at both young and mature stages, with a smooth surface when growing and delicately rugose when mature. Galls were found also on male catkins (Fig. 32). In this case, the gall is greenish and pubescent. The main body of the gall is spindle-shaped with a stalk; the spindle-shaped part is 5.3–6.0 mm long, and 1.1–1.4 mm wide (n=5). The length of the stalk varies from 4.9 mm to 6.8 mm (n=5).

**Biology.** Although only females were collected, the emergence of adults in May and the female morphology suggest that this is a sexual generation. Galls appear on
young leaves of *Castanopsis uraiana* in March; adults emerged in late May. The catkin
galls (TWTc1, TWT601) were found on *Castanopsis carlesii* in late March; adults
emerged in the first half of April.

**Distribution.** Taiwan: Taoyuan and Taitung Counties.

*Dryocosmus crinitus* Schwéger & Tang, sp. n.
http://zoobank.org/EA49CB22-6819-4BA6-9134-E39C7BD63D3C

**Figures 33–47**


New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...


The female holotype, 20 female paratypes are deposited in NMNS, 20 female paratypes in PHMB, 10 female paratypes in USNM, and 19 female paratypes in NCHU.

Etymology. Named after the dense pilosity covering the gall surface. The Latin “crinitus” means “fluffy”.

Diagnosis. Dryocosmus crinitus, D. nanlingensis and D. liyingi belong to the group of species in which the disc of the mesoscutellum lacks irregular rugae (Fig. 116), the scutellar fovea minimum diameter / foveal septum width = 6.0–10.0 and the anterior pits of foveal septum are absent (Fig. 116).

The central propodeal area has numerous distinct medial and lateral rugae in Dryocosmus nanlingensis and with 1–2 indistinct, delicate, longitudinal, lateral wrinkles in D. crinitus (Fig. 42). Dryocosmus liyingi: the transverse pronotal sulcus is foveolate; the pronotum posterolaterally has numerous long rugae which are 2–3 times as long as the diameter of the anterior thoracic spiracle (Fig. 113); the head is dark brown except yellowish brown malar region; the eye height / malar distance = 2.32; the transfacial distance / eye height = 1.44; the diameter of torulus / intertorular distance = 0.8 (Fig. 105); the POL/OOL = 1.06; the OOL / diameter of lateral ocellus = 2.1; the OOL / LOL = 2.05 (Fig. 106); the antenna is with 13 flagellomeres (Fig. 111).

Dryocosmus crinitus: the transverse pronotal sulcus is not foveolate; the pronotum posterolaterally has few short rugae as long as the diameter of the anterior thoracic spiracle (Fig. 40); the cranium is reddish brown anteriorly, dark brown dorsally and posteriorly, the eye height / malar distance = 4.54; the transfacial distance / eye height = 0.9; the diameter of torulus / intertorular distance = 1.8; the POL / OOL = 1.6; the OOL / diameter of lateral ocellus = 1.36; OOL / LOL = 1.36; the antenna is with 12 flagellomeres (Fig. 37).

Description. Asexual female: Head color: reddish brown, except for dark brown to black postgena, occiput, vertex; mandibles, maxillary and labial palps yellowish; scape, pedicel, F1 and F2 yellow, subsequent flagellomeres progressively darker. Meso-soma and metasoma color: black or dark brown, except for lighter tegula, propodeum, propuleuron and mesopleuron, legs yellowish.

New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...


Body length: 1.80–2.10 mm (n=10).

Gall (Figs 46–47): The multilocular gall comprises 3–20 gall chambers in one cluster (n = 20). Each larval chamber is ovate at the base. The gall is attached to the leaf
midrib by a short stalk. A tuft of dense, dark brown hairs covers the larval cells. The gall is 10.7–15.5 mm long, and 8.1–13.3 mm wide (n=6).

**Biology.** The gall matures in late autumn, when the larval chambers drop off from the galls and the larvae overwinter in the leaf litter; adults emerge in the next spring suggesting that the asexual generation is described here. The sexual generation remains unknown. This species induces galls on *Quercus morii* and *Q. sessilifolia*.

**Distribution.** Taiwan: Renai Township, Nantou County; Jianshih Township, Hsinchu County; Shishding Township, New Taipei City; Datung Township, Ilan County.

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**Dryocosmus harrisonae** Melika & Tang, sp. n.

http://zoobank.org/796EC89B-9267-464E-B2B3-C888AEC76CFC

Figures 48–63


The female holotype and 1 male paratype are deposited in NMNS, 2 females and 1 male paratypes in PHMB, and 2 female paratypes in NCHU.

**Etymology.** Named in honour of Ms Warin Harrison (Xishuangbanna Tropical Botanical Garden, Yunnan, China), who was our guide during the collecting trip in China in 2011.

**Diagnosis.** See the diagnosis for *Dryocosmus cannoni*.

**Description.** Sexual female: Head color: dark brown, except for lighter clypeus; mandibles, maxillary and labial palps yellowish; scape and pedicel yellow, flagellomeres
progressively darker. Mesosoma and metasoma color: dark brown, except for lighter tegula and propodeum, legs yellowish.

New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...


Figures 56–60. *Dryocosmus harrisonae*, female sp. n. 56 mesoscutum, dorsal view 57 mesoscutellum, dorsal view 58 pronotum and propleuron, frontal view 59 metascutellum and propodeum, posterodorsal view 60 fore wing, part.

mesoscuteellum+axillar foveae) pilosity color: white. Dorsomedian area of mesoscuteellum-
axillar complex (disc of mesoscuteellum+axillar foveae) pilosity density: rare. Mesoscuteellum-
axillar complex posterior margin vs metanotum: overhanging. Mesoscuteellum-axillar
complex length / mesoscuteellum disc width: >1. Disc of mesoscuteellum sculpture: rugose.
Disc of mesoscuteellum maximum width: in posterior 1/3. Scutellar fovea sculpture:
smooth without longitudinal rugae. Scutellar fovea shape: transversely ovate. Scutellar
fovea reflectivity: glossy. Foveal septum: narrow. Anterior pits on foveal septum: NOT
CODED. Scutellar fovea maximum diameter / scutellar fovea minimum diameter: 1.7.
Scutellar fovea minimum diameter / foveal septum width: NOT CODED. Postacetabular
suclus count: NOT CODED. Mesopleuron sculpture: smooth transepisternal line is
marked by few delicate sulci, area dorsal to transepisternal line smooth except few short
transverse anterior striae . Mesopleuron reflectivity: matt; glossy. Mesopleuron pilosity:
glabrous. Speculum sculpture: wrinkled. Speculum reflectivity: NOT CODED. Mesop-
leural triangle sculpture: smooth. Mesopleural triangle reflectivity: glossy. Mesopleural
triangle pilosity: present. Mesopleural triangle pilosity color: NOT CODED. Mesop-
leural triangle pilosity density: NOT CODED. Dorsoaxillar area sculpture: alutaceous
with few rugae. Dorsoaxillar area reflectivity: NOT CODED. Dorsoaxillar area pilosity
color: NOT CODED. Dorsoaxillar area pilosity density: NOT CODED. Lateroaxillar
area sculpture: alutaceous with few rugae. Lateroaxillar area reflectivity: NOT
CODED. Dorsoaxillar area pilosity color: NOT CODED. Dorsoaxillar area pilosity
density: NOT CODED. Lateroaxillar area sculpture: alutaceous with few rugae. Lateroaxillar area reflectivity: NOT
CODED. Dorsoaxillar area pilosity color: NOT CODED. Dorsoaxillar area pilosity
density: NOT CODED. Lateroaxillar area sculpture: alutaceous with few rugae. Lateroaxillar area reflectivity: NOT
CODED. Dorsoaxillar area pilosity color: NOT CODED. Dorsoaxillar area pilosity
density: NOT CODED. Lateroaxillar area sculpture: alutaceous with few rugae. Lateroaxillar area reflectivity: NOT
CODED. Dorsoaxillar area pilosity color: NOT CODED. Dorsoaxillar area pilosity
density: NOT CODED. Lateroaxillar area sculpture: alutaceous with few rugae. Lateroaxillar area reflectivity: NOT
CODED. Dorsoaxillar area pilosity color: NOT CODED. Dorsoaxillar area pilosity
density: NOT CODED. Lateroaxillar area sculpture: alutaceous with few rugae. Lateroaxillar area reflectivity: NOT
CODED. Dorsoaxillar area pilosity color: NOT CODED. Dorsoaxillar area pilosity
density: NOT CODED. Lateroaxillar area sculpture: alutaceous with few rugae. Lateroaxillar area reflectivity: NOT
Metasomal tergites 3–6 pilosity: absent. Prominent part of ventral spine of hypopygium length ventral view / Prominent part of ventral spine of hypopygium width ventral view: 1.16. Hypopygial setae apical end: not extending beyond posterior end of ventral spine of hypopygium.

Body length: 1.90–2.10 mm (n = 3).


Gall (Figs 62–63): Galls are located on axillary buds or young leaves on young shoots. The cross-section of the gall is triangular, with a short stalk connected to the host-plant. The gall is greenish, with a brownish tip and a greenish-brown central region, 3.9–4.6 mm long and 1.7–2.0 mm broad (n=2).

**Biology.** Only the sexual generation is known. Galls are on young shoots of *Castanopsis echinocarpa*. Galls were collected in April; adults emerged from galls under laboratory conditions immediately after field collection.

**Distribution.** China: Yunnan Province.
**Dryocosmus hearni** Melika & Tang, sp. n.
http://zoobank.org/3E8127B2-15D1-4180-A727-E63DCA523064
Figures 64–76


The female holotype, 4 female and 7 male paratypes are deposited in NMNS, 5 female and 7 male paratypes in PHMB, 2 female and 4 male paratypes in USNM, 4 female and 9 male paratypes in NCHU.

**Etymology.** Named in honour of Dr. Jack Hearn (Institute of Evolutionary Biology, University of Edinburgh, Scotland), whose help was crucial in the organization of the collecting trip to China in 2011.

**Diagnosis.** Most similar to *Dryocosmus testisimilis*.

*Dryocosmus hearni*: the head and mesosoma of females and males are orange-yellow (Figs 64–69, 72–73), the metasoma is dark brown. The notaulus posterior region width / anterior region width = 5 (Fig. 73); posterior height of subaxilllar bar / height of metanotal trough = 0.25 (Fig. 72); the central propodeal area is with a transverse carina in dorsal 1/3rd (Fig. 74).
Dryocosmus testisimilis: in females the head and mesosoma are light brown, the mesoscutum, mesopleuron, metapleuron and propodeum are darker, the metasoma dark brown (Figs 180–181).

The body dark brown in males.

The notaulus posterior region width / anterior region width = 1 (Fig. 181), posterior height of subaxilllar bar / height of metanotal trough >1; the central propodeal area without a transverse carina in dorsal 1/3rd (Fig. 179).
**Description.** Sexual female: Head color: orange-yellow, except for darker mandibles, scape, pedicel, F1–F5 yellowish brown, subsequent flagellomeres progressively darker. Mesosoma and metasoma color: mesosoma orange-yellow, except for legs yellowish, except tibia and first tarsomere dark brown, metasoma dark brown.

Figures 72–76. *Dryocosmus hearni* sp. n. 72–75 female: 72 mesosoma, lateral view 73 mesosoma, dorsal view 74 metascutellum and propodeum, posterodorsal view 75 fore wing, part. 76 gall (photo by C.-T. Tang) (not=notaulus, trc=transverse carina on central propodeal area, sab=subaxillular bar, mtr=metanotal trough).

New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...


Body length: 2.80–3.10mm (n = 5).


Gall (Fig. 76): Galls are integrated leaf swellings, usually located at the base of leaves, and are concolorous with the leaves. The galls are 22.4–24.3 mm long, 18.2–19.0 mm wide (n=3).

Biology. Only the sexual generation is known. Galls were collected from young leaves of Castanopsis sp. in April and adults emerged from galls under laboratory conditions immediately after field collection.

Distribution. China: Yunnan Province

Comments. The pairwise genetic distances from other Dryocosmus species, based upon 433 base pairs of the cytochrome b gene (Table 1) and some morphological characters (the very broad notaulus in the posterior half, large scutellar foveae, the unique pattern of carinae on the central propodeal area, the uniformly orange-yellow body) make this species peculiar among all other Eastern Palaearctic Dryocosmus species which are associated with Cyclobalanopsis or Castanopsis.
New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...

**Dryocosmus hualieni** Schwéger & Tang, sp. n.
http://zoobank.org/658C175E-8C34-44CA-B9C4-F3E6B07D3290
Figures 77–90

**Type material.** Holotype female: TAIWAN, Hualien Co., 152K, Central-Cross Island Highway, Xiulin township, ex twig swellings on *Quercus glauca* (spTWs2); 24.204171N, 121.443636E, 1162m, gall collected 14.II.2012 (TWT546), adult emerged 1.V.2012, leg. Chang-Ti Tang. 6 female PARATYPES: TAIWAN, Hualien Co., 152K, Central-Cross Island Highway, Xiulin township, ex twig swellings on *Quercus glauca* (spTWs2); 24.204171N, 121.443636E, 1162m, gall collected 14.II.2012 (TWT546), adult cut out 28.IX.2012, leg. Chang-Ti Tang.

The holotype female, 2 female paratypes are deposited in NMNS, 2 female paratypes in PHMB, 1 female paratype in USNM and 1 female paratype in NCHU.

**Etymology.** Named after Hualien County, Taiwan where the species was collected.

**Diagnosis.** Asexual females of *Dryocosmus hualieni* resemble the asexual females of *D. taitungensis* and the sexual females of *D. konradi*. All three species are known from Taiwan only and are associated with *Cyclobalanopsis* species. *Dryocosmus hualieni* and *D. taitungensis* induce stem swelling-like galls, while *D. konradi* induces bud galls.

In *Dryocosmus hualieni* and *D. konradi* the second metasomal tergite has multiple setae laterally (Fig. 87), while in *D. taitungensis* the second metasomal tergite has only few setae laterally (Fig. 171). In *Dryocosmus konradi*: the bottom of scutellar foveae without rugae (Fig. 100); the female F1 / F2 = 1; female F1 / pedicel = 2.7; placoid sensilla are present on F1–F12 (Fig. 97).

**Dryocosmus hualieni**: the bottom of scutellar foveae with numerous longitudinal rugae (Fig. 83); female F1 / F2<1; the female F1 / pedicel = 1.6; placoid sensilla are present on F2–F12 (Fig. 81); the frons is alutaceous; the acetabular sulcus absent, the speculum is without striae (Fig. 84), the mesoscutellum rounded, anterior part without rugae, glabrous (Fig. 83).

**Dryocosmus taitungensis**: the frons is coriaceous, with numerous transverse striae above toruli; the acetabular carina present; the speculum with striae (Fig. 166); the mesoscutellum trapezoid, uniformly rugose, matt (Fig. 167).

**Description.** Asexual female: Head color: black, except lighter clypeus, central part of lower face and area around toruli; mandibles, maxillary and labial palps yellowish; scape and pedicel yellow, flagellomeres progressively darker. Mesosoma and metasoma color: dark brown to black, except for lighter tegula, propleuron, propodeum; legs yellowish.

Figures 77–83. *Dryocosmus hualieni*, female, sp. n. 77–80 head: 77 frontal view 78 dorsal view 79 posterior view 80 lateral view. 81 antenna 82 mesosoma, dorsal view 83 mesoscutellum, dorsal view.

New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...


Figures 84–87. *Dryocosmus hualieni*, female, sp. n. 84 mesosoma, lateral view 85 pronotum and propleuron, frontal view 86 metascutellum and propodeum, posterior view 87 metasoma, lateral view (tel=transepisternal line).

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Body length: 2.30–2.50 mm (n=6).

Gall (Figs 89–90): The gall is a multilocular stem swelling, similar to the asexual galls of Dryocosmus taitungensis. The gall is dehiscent when mature, larval cells drop off from the gall (stem swelling) during the winter and they overwinter in the leaf litter. The mature gall is 3.78–5.38 cm in length, and 1.05–1.28 cm in width (n=2). The larval cell is oblong, 4.78–5.68 mm long, and 1.74–2.13 mm wide (n=5).
Biology. The gall maturation in late autumn and the emergence of adults in spring, suggests that the asexual generation is described here. The sexual generation remains unknown. The host-plant is *Q. glauca*.

Distribution. Taiwan: Hualien County, Xiulin Township.

**Dryocosmus konradi** Tang & Melik, sp. n.
http://zoobank.org/AFA7387F-1ABC-4885-BB4A-D8ED1637B279
Figures 91–104

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120.981033°E, 1270m, ex small oval yellow gall towards base of young buds, (AGWP-Morpho28), em. 27.III.2011, leg. C. T. Tang, F. Sinclair, J. Hearn, K. Lohse; 1 female paratype: TAIWAN: Nantou Co., road to Lingxiao Temple, Renai Township, ex Quercus glauca, 26.IV.2011 (TWT499), 24°59'48.08"N, 121°00'51.52"E, 774m, ex oval-shaped gall at bud base (AGWP-Morpho28), adult em. 28.IV.2011, leg. Chang-Ti Tang; 1 male and 1 female paratypes: TAIWAN: Nantou Co., road to Lingxiao Temple, Renai Township, ex Quercus glauca, 26.IV.2011 (TWT499), 24°59'48.08"N, 121°00'51.52"E, 774m, ex oval-shaped gall at bud base (AGWP-


The female holotype, 2 female and 1 male paratypes are deposited in NMNS, 4 female and 2 male paratypes in PHMB, 4 female and 1 male paratypes in NCHU.

**Etymology.** In recognition of the continuous contribution of Dr. Konrad Lohse (Institute of Evolutionary Biology, University of Edinburgh, Scotland) in related studies on oak gall wasps.

**Diagnosis.** See diagnosis for Dryocosmus hualieni.

**Description.** Sexual female: Head color: black to dark brown, clypeus lighter; mandibles, maxillary and labial palps yellowish; scape, pedicel and F1 light brown, subsequent flagellomeres progressively darker. Mesosoma and metasoma color: dark brown, except lighter tegula; legs yellow.
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length / F11 length: NOT CODED. F12 length / F11 length: 1.76. F13 length / F12 length: NOT CODED. Placoid sensilla present on: F1–F12.


Body length: 2.10–2.30 mm (n=3).


Gall (Figs 103–104): The gall is single-chambered and ovate, greenish with a yellowish central area, 2.3–2.8 mm in length, 1.3–2.1 mm in width (n=5). Galls are located at the base of young shoots, covered by bud scales and are cryptic unless bud scales are removed.

Biology. Only the sexual generation is known. Galls were collected from late March through April on Q. glauca and Q. longinux; adults emerge from galls under laboratory conditions immediately after field collection.

Distribution. Taiwan: Renai Township, Nantou County. Quercus glauca is widespread from India through China to Japan; it is possible that this Dryocosmus species occurs in these regions as well.

Comments. Some specimens reared from galls on Quercus longinux slightly differ from those reared from galls on Q. glauca (the description given above): the head and mesosoma have weaker coriaceous sculpture, the head, mesosoma, and metasoma are more glossy; the mesoscutum narrower; F1 in females slightly shorter.
Dryocosmus liyingi Melika & Tang, sp. n.
http://zoobank.org/1CFE5699-CBF1-4901-B799-785B5872FE5B
Figures 105–121


The female holotype, 5 female and 3 male paratypes are deposited in NMNS, 5 female and 7 male paratypes in PHMB, 3 female and 3 male paratypes in USNM, 5 female and 3 male paratypes in NCHU.

Etymology. Named after Liying Mountain in Renai Township, Nantou Co., Taiwan, where it was first recorded.

Diagnosis. Dryocosmus liyingi resembles D. crinitus, see Diagnosis for D. crinitus. The species is also similar to Dryocosmus sakureiensis. In Dryocosmus liyingi the mesopleuron lacks striae and in D. sefuriensis the mesopleuron is striate anteromedially.

Description. Sexual female:
New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...


Pronotum sculpture: alutaceous with some rugae laterally. Pronotal dorsal row of setae count: present. Transverse pronotal sulcus depth: deep. Transverse pronotal sulcus
New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...

Figures 113–117. *Dryocosmus liyingi*, female, sp. n. 113 mesosoma, lateral view 114 pronotum and propleuron, frontal view 115 mesoscutum, dorsal view 116 mesoscutellum, dorsal view 117 metascutellum and propodeum, posterior view (tps=transverse pronotal sulcus, dms=disc of mesoscutellum).


New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...

um length ventral view / Prominent part of ventral spine of hypopygium width ventral view: NOT CODED. Hypopygial setae apical end: extending beyond posterior end of ventral spine of hypopygium.

Body length: 2.10–2.20 mm (n=5).


Gall (Fig. 121): The gall resembles the sexual galls of *Dryocosmus sefuriensis*. The gall is a cluster of multiple larval chambers, and covered by bud scales and young leaves in a bud. The infected bud becomes thicker and the young shoot will not develop, providing a clue to search for galls on the host-plant. The mature gall is yellowish-white.

**Biology.** Only the sexual generation is known. Galls were collected from late March to late April. Adults emerged from galls in the laboratory immediately after collection. Galls are on *Q. morii* and *Q. sessilifolia*.

**Distribution.** Taiwan: Renai Township, Nantou County.

*Dryocosmus moriius* Tang & Melika, sp. n.

http://zoobank.org/9C8A4DD6-E635-4B7A-A8EB-02646151D521

Figures 122–135

New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...


2217m, ovipositing female on young leaves of host plant, leg. Chang-Ti Tang; 2 male and 1 female paratypes: TAIWAN: Nantou Co., near Cuifeng, Renai Township, ex *Quercus morii*, 25.IV.2011 (TWT498), 24°06'06.63"N, 121°11'24.47"E, 2285m, ex small green oval bud gall cover by bud-scales (TWTb13), em. 1.V.2011, leg. Chang-Ti Tang; 1 male and 3 female paratypes: TAIWAN: Nantou Co., near Cuifeng, Renai Township, ex *Quercus morii*, 25.IV.2011 (TWT498), 24°06'06.63"N, 121°11'24.47"E, 2285m, ex small green oval bud gall cover by bud-scales (TWTb13), em. 2.V.2011,

The female holotype, 9 female and 2 male paratypes are deposited in NMNS, 9 female and 3 male paratypes in PHMB, 3 female and 1 male paratypes in USNM, 10 female and 2 male paratypes in NCHU.

**Etymology.** Named after the host plant, *Q. morii*.

**Diagnosis.** *Dryocosmus moriius* is most similar to *D. sakureiensis*, both sharing the presence of a basal lobe on the metatarsal claw.

*D. sakureiensis*: Female antenna with 12 flagellomeres; eye height / malar distance = 2.62; intertorular distance / eye torulus distance = 0.67; radial cell length / radial cell width = 3.43; 2nd metasomal tergite length dorsal view / length of metasoma dorsal view > 0.50; prominent part of ventral spine of hypopygium length ventral view / prominent part of ventral spine of hypopygium width ventral view = 2.20.

*D. moriius*: Female antenna with 13 flagellomeres, eye height / malar distance = 2.0; intertorular distance / eye torulus distance = 0.36; radial cell length / radial cell width = 4.5; 2nd metasomal tergite length dorsal view / length of metasoma dorsal view = 0.33; prominent part of ventral spine of hypopygium length ventral view / prominent part of ventral spine of hypopygium width ventral view = 1.3.

**Description.** Sexual female: Head color: Head black, except for light brown clypeus; mandibles, maxillary and labial palps yellowish; scape, pedicel, F1–F4 light
New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...

Brown, subsequent flagellomeres progressively darker. Mesosoma and metasoma color: mesosoma black, except for lighter tegula; metasoma dark brown; legs yellowish.


Body length: 2.60–2.80 mm (n=5).


Gall (Figs 134–135): The gall closely resembles the sexual galls of Dryocosmus saku-reiensis. The gall is unilocular, ovate, 2.8–3.4 mm long and 1.8–2.1 mm wide (n=5). Galls are at the base of young shoots, usually by bud scales. Galls are green and yellowish white in the central area.

Biology. Only the sexual generation is known. Galls are induced on young shoots on Quercus morii. Galls were collected in April and adults emerged from galls under laboratory conditions immediately after field collection.

Distribution. Taiwan: Renai Township, Nantou County. Quercus morii is endemic to Taiwan, suggesting that Dryocosmus morii is also endemic to Taiwan.

Dryocosmus quadripetiolus Schwéger & Tang, sp. n.
http://zoobank.org/C09DF087-BC26-466E-8A08-712688D50FF4
Figures 136–148

Type material. HOLOTYPE female: CHINA: Yunnan Prov., Lan Cang Co., Foufang quarry, ex Castanopsis echinocarpa, 11.IV.2011 (CHI38), 22.593300°N, 99.982633°E, 1625m, ex bird head shaped gall with ridges (AGWP-Morpho74), em. 11.IV.2011,
New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...

The female holotype is deposited in NMNS, the female paratype in PHMB.

**Etymology.** Named after the shape of the gall, which has four petiole-like ridges.

**Diagnosis.** In *Dryocosmus quadripetiolus* the mesopleuron is densely setose ventral to the transepisternal line (Fig. 142), while in all other species the mesopleuron is glabrous or with few setae present along the margin of the lateral mesopleural face (Figs 24, 40, 72, 166).

Figures 136–141. Dryocosmus quadripetiolus, female, sp. n. 136–139 head: 136 frontal view 137 dorsal view 138 posterior view 139 lateral view 140 antenna 141 pronotum and propleuron, frontal view.

New Dryocosmus *Giraud* species associated with *Cyclobalanopsis* and non-*Quercus* host...


Figures 142–146. *Dryocosmus quadripetiolus*, female, sp. n. 142 mesosoma, lateral view 143 mesosoma, dorsal view 144 mesoscutellum, dorsal view 145 metascutellum and propodeum, posterodorsal view 146 metasoma, lateral view (tel=transepisternal line).

New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...


Body length: 2.45 mm (n=2).

Male: Unknown.

Gall (Fig. 148): Galls develop from buds, detachable. The body of the gall contains a subglobose part and a needle-like projection; the subglobose part is 5.0–6.0 mm in diameter, 6.0–7.0 in height; the needle-like projection at the top of the gall body nearly as long as or slightly longer than the height of the subglobose part. The gall body is marked

with four longitudinal ribs, pubescent. The mature gall is brownish, similar to the color of the twig. The larval chamber is centrally located at the subglobose part, unilocular.

**Biology.** Based on the morphology, gall maturation and emergence period of adults, the described females represent the sexual generation. Galls are in buds on *Cassanopsis echinocarpa*. Galls were collected in April and adults emerged from galls under laboratory conditions immediately after field collection.

**Distribution.** China: Yunnan Province (Lan Cang County).

**Dryocosmus salicinai** Schwéger & Tang, sp. n.  
http://zoobank.org/5D21585D-E7F1-4C5A-A23F-5A4350206028  
Figures 149–161

**Type material.** HOLOTYPE female: TAIWAN: Taichung City, 104.5 K, Central Cross Island Highway, Heping Dist., ex monolocular bud gall on *Quercus salicina* (TWTb16), 24°12′44.4″N, 121°18′20.2″E, 2437m, gall collected 19.III.2012 (TWT583), adult emerged 4.IV.2012, leg. Chang-Ti Tang. Three female and four male PARATYPES: 4 male paratypes with the same labels as the holotype: 3 female paratypes: TAIWAN: Taichung City, 104.5 K, Central Cross Island Highway, Heping Dist., ex unilocular bud gall on *Quercus salicina* (TWTb16), 24°12′44.4″N, 121°18′20.2″E, 2437m, gall collected 19.III.2012 (TWT583), adult emerged 5.IV.2012, leg. Chang-Ti Tang.  

The holotype female, 1 female and 2 male paratypes are deposited in NMNS, 1 female and 1 male paratypes in PHMB, 1 female and 1 male paratypes in NCHU.

**Etymology.** The species is named after the host plant, *Quercus salicina*.

**Diagnosis.** *Dryocosmus salicinai* is the only *Dryocosmus* species in which the mesopleuron and speculum are matt, uniformly coriaceous, without striae. In all other *Dryocosmus* species the mesopleuron and/or speculum are glossy and smooth. Albeit the structure of the mesopleuron is somewhat similar to that of *Plagiotrochus*, based on the a presence of the truncate apical tuft on the ventral spine of hypopygium and the smooth and glossy mesoscutum we treat this species as *Dryocosmus*.

**Description.** Sexual female: Head color: black or dark brown, except for lighter clypeus; mandibles, maxillary and labial palps yellowish; scape and pedicel yellowish or light brown, flagellomeres progressively darker till last one. Mesosoma and metasoma color: mesosoma dark brown to black, except for lighter tegula; metasoma dark brown; legs uniformly brown.

New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...


New Dryocosmus Giraud species associated with Cyclobalanopsis and non-Quercus host...


Body length: 2.30 mm (n=1).


Gall (Figs 160–161): The unilocular gall is pink and ovate. One or two galls are embedded in one bud, which is usually flat and short. The gall is 2.1–2.6 mm long and 1.3–1.6 mm wide (n=5). The presence of the gall interrupts the development of the shoot.

Biology. Only the sexual generation is known. Mature galls were collected in March and adults emerged from the galls under laboratory conditions in early April. This species induces galls on *Quercus salicina*.

Distribution. Taiwan: Heping District, Taichung City, and Renai Township, Nantou County. The distribution of *Quercus salicina* (Govaerts & Frodin, 1998) suggests the potential occurrence of this gallwasp species in Japan.
**Dryocosmus taitungensis** Tang & Melika, sp. n.

http://zoobank.org/B3BACB7F-F575-4E79-AA44-21ED50585781

Figures 162–173


The holotype female, 6 female paratypes are deposited in NMNS, 7 female paratypes in PHMB, 4 female paratypes in USNM, 7 female paratypes in NCHU.

**Etymology.** Named after Taitung County, Taiwan.

**Diagnosis.** *Dryocosmus taitungensis* resembles *D. liyingi*.

*Dryocosmus taitungensis*: female head black; POL / OOL = 1.6; OOL / diameter of lateral ocellus = 1.58; OOL / LOL = 1.37 (Fig. 162); central propodeal area with longitudinal rugae; lateral propodeal carina slightly curved outward in mid-height (Fig. 169).

*Dryocosmus liyingi*: female head dark brown, with a light brown lower face, POL / OOL = 1.06; OOL / diameter of lateral ocellus = 2.1; OOL / LOL = 2.05 (Fig. 105); central propodeal area with distinct longitudinal rugae; lateral propodeal carina
strongly curved outwards in the mid-height (Fig. 117). *Dryocosmus taitungensis* is also similar to *D. hualieni*, see diagnosis to *D. hualieni*.

**Description.** Asexual female: Head color: black, except for mandibles, maxillary and labial palps yellowish; scape, pedicel and F1 dark brown, F2–F12 darker. Mesosoma and metasoma color: black, except for lighter tegula; legs yellowish.


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Body length: 2.20–2.40 mm (n=5).

Gall (Figs 172–173): The multilocular gall is a stem swelling on the current year shoot. The gall is 8.4–29.2 mm long and 3.6–7.7 mm wide (n=7). Galls are located proximally on the branches, never apically, and are concolorous with the bark. The gall is brownish-red if the external layer peels off from the gall surface. The tissue of the mature gall is hard and lignified. During the winter the larval chambers fall to the ground, and the larvae overwinter in the leaf litter. Sometimes the larvae remain in the galls. Larval chambers are 2.5–3.3 mm long and 1.4–1.8 mm wide (n=10).

**Biology.** The period of the gall maturation, the absence of males, and the adult morphology suggest that the asexual generation is described here. Mature galls were found in January and adults emerged under laboratory conditions in March and April in the next spring.

**Distribution.** Taiwan: Taitung County, Beinan Township. *Quercus hypophaea* is an endemic of Taiwan (Govaerts & Frodin 1989), thus the described species might be also endemic to Taiwan.

**Discussion**

East Asia harbours more than 70 species of the *Quercus* subgenus *Cyclobalanopsis* (Govaerts & Frodin, 1998). Despite this relatively high species richness, little was known about cynipine galls on *Cyclobalanopsis* until the recent description of the genera *Cycloneuroterus* Melika & Tang, 2011 and *Cyclocynips* Melika, Tang, & Sinclair, 2013 and new species of *Plagiotrochus* (Ide et al. 2010, 2012, 2013; Melika et al. 2013; Tang et al. 2011a, b, 2016a,b). Only one cynipine species, *Cycloneuroterus wangi* Abe, Ide, & Odagiri, 2014, has been reported to oviposit on *Cyclobalanopsis* outside Japan, Taiwan and Vietnam despite the wide Asian distribution (Abe et al. 2014) of this *Quercus* subgenus. Although *Dryocosmus* species have been collected in Yunnan province of southern China (Abe et al. 2014b) and in the Indochina region (Abe et al. 2014a), their host associations are unknown. Although all *Cyclobalanopsis* associated *Dryocosmus* species—including the five new species of the present paper—are known from Taiwan (Table 2), we can not confirm or deny if this restricted distribution is due to sampling bias.

While *Cyclocynips* and *Cycloneuroterus* are associated with *Castanea*, *Lithocarpus* and *Cyclobalanopsis*, the sole cynipine genus of *Castanopsis* is *Dryocosmus*. Our study doubled the number of *Dryocosmus* species associated with *Castanopsis*. With this new information, we can now clearly say that of all known Eastern Palaearctic *Dryocosmus*, almost half (n=9) are associated with *Castanopsis* (Table 2). Eastern Palaearctic species of *Dryocosmus* is known yet to associate with large and species rich *Quercus* subgenus *Quercus*.
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Most oak gallwasps are cyclically parthenogenetic, with obligate alternation between a sexual and an asexual (unisexual) generation. Males and females of the sexual generation usually occur at the same time as the flush of new growth on host plants in the spring, while the parthenogenetic females of the asexual generation occur in the winter (Csóka et al. 2005, Abe et al. 2014b). Of the 22 described Eastern Palaearctic Dryocosmus, no species are known to have alternate sexual and asexual generations; asexual specimens are known for four and sexual for 18 species (Table 2). Likewise, a significant proportion of other Holarctic cynipine species are known from only one of the two generations (Melika 2006). Stone et al. (2008) confirmed that many of these species actually do have a sexual generation (Stone et al. 2008) and it is likely that alternate generation of many East Asian Dryocosmus species are yet to be described.

### Table 2. Eastern Palaearctic Dryocosmus species, their host plants, life cycles (sexual=known only from sexual generation; asexual=known only from asexual generation) and distributions.

<table>
<thead>
<tr>
<th>Dryocosmus species</th>
<th>Host species</th>
<th>Life cycle</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. cannoni Schwéger &amp; Tang, sp. n.</td>
<td>Castanopsis echinocarpa</td>
<td>sexual</td>
<td>China</td>
</tr>
<tr>
<td>D. caputgrusi Tang &amp; Schwéger, sp. n.</td>
<td>Castanopsis uraiana</td>
<td>sexual</td>
<td>Taiwan</td>
</tr>
<tr>
<td>D. carlesiae Tang &amp; Melika</td>
<td>Castanopsis carlesii</td>
<td>sexual</td>
<td>Taiwan</td>
</tr>
<tr>
<td>D. crinitus Schwéger &amp; Tang, sp. n.</td>
<td>Quercus (Cyclobalanopsis) morii, Q.(C.) sessilifolia</td>
<td>sexual</td>
<td>Taiwan</td>
</tr>
<tr>
<td>D. harrisonae Melika &amp; Tang, sp. n.</td>
<td>Castanopsis echinocarpa</td>
<td>sexual</td>
<td>China</td>
</tr>
<tr>
<td>D. hualieni Schwéger &amp; Tang, sp. n.</td>
<td>Castanopsis sp.</td>
<td>sexual</td>
<td>China</td>
</tr>
<tr>
<td>D. konradi Tang &amp; Melika, sp. n.</td>
<td>Quercus (Cyclobalanopsis) glauca</td>
<td>asexual</td>
<td>Taiwan</td>
</tr>
<tr>
<td>D. liyingi Melika &amp;Tang, sp. n.</td>
<td>Quercus (Cyclobalanopsis) longinux</td>
<td>sexual</td>
<td>Taiwan</td>
</tr>
<tr>
<td>D. moritus Tang &amp; Melika, sp. n.</td>
<td>Quercus (Cyclobalanopsis) morii</td>
<td>sexual</td>
<td>Taiwan</td>
</tr>
<tr>
<td>D. nanlingensis Abe, Ide, &amp; Odagiri</td>
<td>unknown</td>
<td>sexual</td>
<td>China</td>
</tr>
<tr>
<td>D. okajimai Abe, Ide, Konishi &amp; Ueno</td>
<td>unknown</td>
<td>sexual</td>
<td>Vietnam</td>
</tr>
<tr>
<td>D. pentagonalis Melika &amp; Tang</td>
<td>Castanopsis carlesii</td>
<td>sexual</td>
<td>Taiwan</td>
</tr>
<tr>
<td>D. quadripetiolus Schwéger &amp; Tang, sp. n.</td>
<td>Castanopsis echinocarpa</td>
<td>sexual</td>
<td>China</td>
</tr>
<tr>
<td>D. salicinai Schwéger &amp; Tang, sp. n.</td>
<td>Quercus (Cyclobalanopsis) salicina</td>
<td>sexual</td>
<td>Taiwan</td>
</tr>
<tr>
<td>D. sefuriensis Ide, Wachi &amp; Abe</td>
<td>Quercus (Cyclobalanopsis) acuta</td>
<td>sexual</td>
<td>Japan</td>
</tr>
<tr>
<td>D. taitungensis Tang &amp; Melika, sp. n.</td>
<td>Quercus (Cyclobalanopsis) hypophaea</td>
<td>asexual</td>
<td>Taiwan</td>
</tr>
<tr>
<td>D. testisimilis Tang &amp; Melika</td>
<td>Castanopsis uraiana</td>
<td>sexual</td>
<td>Taiwan</td>
</tr>
<tr>
<td>D. triangularis Melika &amp; Tang</td>
<td>Castanopsis carlesii</td>
<td>sexual</td>
<td>Taiwan</td>
</tr>
<tr>
<td>D. kuriphilus (Yasumatsu)</td>
<td>Castanea crenata, C. henryi, C. mollissima, C. seguinii, C. dentata, C. sativa</td>
<td>asexual</td>
<td>Holarctic</td>
</tr>
<tr>
<td>D. zhuli Liu &amp; Zhu</td>
<td>Castanea henryi</td>
<td>sexual</td>
<td>China</td>
</tr>
</tbody>
</table>
The above mentioned uncertainties about the distribution, host association and biology of Eastern Palaearctic *Dryocosmus* species demonstrate that research on this taxon is still in its infancy. Further studies applying refined morphological and molecular methods on freshly collected Eastern Asian specimens is needed to galvanize life into the non-functional systematics of the likely polyphyletic *Dryocosmus* (Melika et al. 2010).

**Acknowledgement**

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**References**


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Supplementary material 1

URI table (Seltmann et al. 2013) containing anatomical terms, definitions and uniform resource identifiers of Hymenoptera specific classes in the Hymenoptera Anatomy Ontology (http://hymao.org).

Authors: Chang-Ti Tang, István Mikó, James A. Nicholls, Szabina Schwéger, Man-Miao Yang, Graham N. Stone, Frazer Sinclair, Miklós Bozsó, George Melika, Zsolt Pénzes

Data type: PDF file


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Supplementary material 2

Semantic statements of natural language phenotypes composed in Protégé 5.0 (http://protege.stanford.edu/) using the OWL Manchester syntax.

Authors: Chang-Ti Tang, István Mikó, James A. Nicholls, Szabina Schwéger, Man-Miao Yang, Graham N. Stone, Frazer Sinclair, Miklós Bozsó, George Melika, Zsolt Pénzes

Data type: PDF file

Explanation note: Semantic statements of natural language phenotypes composed in Protégé 5.0 (http://protege.stanford.edu/) using the OWL Manchester syntax.

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Two unusual new species of *Aulacus* Jurine (Hymenoptera, Aulacidae) from South America

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Abstract

*Aulacus flavus* Smith, *sp. n.* from Brazil and *Aulacus subflavus* Smith, *sp. n.* from Brazil, French Guiana, and Guyana are described. These two species are separated from other *Aulacus* by the enlarged genae, flat mesoscutum, enlarged pronotum, and presence of small tubercles on the mesoprescutum, axillae, and mesoscutellum.

Keywords

parasitoids, South America

Introduction

Both genera of Aulacidae, *Pristaulacus* Kieffer and *Aulacus* Jurine, are widespread in the Neotropics. Twelve Neotropical species of *Aulacus* were listed by Smith (2001). Subsequently, 13 species have been added (Smith 2005a, 2005b, 2008; Smith and Carvalho 2010). Here, I describe two species very different from other *Aulacus* species.

Hosts are not known, but elsewhere aulacids are parasitoids of wood-boring Hymenoptera (Xiphydriidae) and Coleoptera (mainly Buprestidae and Cerambycidae) (Smith 2001, Jennings and Austin 2004).
Materials and methods

Abbreviations: AEI, American Entomological Institute, Gainesville, FL; RBINS, Royal Belgian Institute of Natural Sciences, Bruxelles; CNC, Canadian National Collection of Insects, Ottawa, Ontario, Canada; MCZ, Museum of Comparative Zoology, Cambridge, MA; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC.

Images were acquired through an EntoVision micro-imaging system. This system included a Leica M16 or Leica DRMB compound microscope with a JVC KY-75U 3-CCD digital video camera or a GT-Vision Lw11057C-SCI digital camera attached that fed image data to a notebook or desktop computer. The program Cartograph 6.6.0 was then used to merge an image series into a single in-focus image.

Terminology follows Huber and Sharkey (1993) and Smith (2008). Descriptions are based on the female holotypes. The species used for comparison (Figs 1–3) is Aulacus costulatus (Kieffer), which occurs in Brazil. The specimen illustrated is from Santa Catarina, Nova Teutonia, 27°11’S, 52°23’W, 300–500 m, Nov. 1966, Fritz Plaumann.

Results

The two species described below belong to Aulacus as currently defined (e.g., Smith 2001, 2008; Turrisi et al. 2009). They are distinguished from other Aulacus species in the first couplet in the key below. No other species of Aulacus share the flat mesoscutum, tubercles on the mesonotum, axillae, and scutellum, enlarged pronotum, and enlarged genae. The exact relationship with other species of Aulacus is unknown. Turrisi et al. (2009) considered the genus paraphyletic, and the phylogenetic classification remains unresolved. A study of world Aulacus on a much more comprehensive basis is needed to determine relationships of the two species described here.

Key to species

1 Mesonotum (Figs 2, 3) rounded, convex, without tubercles; pronotum in lateral view short, about as long as high and almost triangular (Fig. 2), hardly visible in dorsal view (Fig. 3); head in lateral view with gena not enlarged below, distance between eye and hind margin of head greater dorsally (Fig. 1) .... other Aulacus
– Mesonotum (Figs 4, 8, 9, 10, 14, 15) flat, with a short tubercle on each anterolateral corner of mesoscutum, one on each axilla (shown best in Fig. 15), and one on posterior mesoscutellum; pronotum enlarged, in lateral view about 2x longer than high almost rectangular (Figs 9, 15), clearly visible in dorsal view (Figs 8, 14); head in lateral view with gena enlarged ventrally, distance between eye and hind margin of head greater ventrally than dorsally (Figs 5, 11) .................................................................................................2
Two unusual new species of Aulacus Jurine (Hymenoptera, Aulacidae) from South America

2 Eyes smaller, lower interocular distance subequal to eye height (Fig. 7); head in lateral view with greatest width of gena more than half width of eye (Fig. 5); head behind eyes in dorsal view slightly convex (Fig. 6); pronotum entirely yellow (Figs 4, 9) ...........................................................................flavus

– Eyes larger, lower interocular distance 0.8× eye height (Fig. 13; head in lateral view with greatest width of gena half or less width of eye (Fig. 12); head behind eyes in dorsal view almost straight (Fig. 12); pronotum usually with dorsal half yellow, ventral half black (Figs 10, 15) ......................subflavus

Aulacus flavus Smith, sp. n.
http://zoobank.org/DD80199E-A9A6-44B9-8CF3-785C832A2A52
Figs 4–9

Description. Female (holotype). Length, 9.5 mm; forewing 7.0 mm; ovipositor 4.5 mm. Antenna black; scape yellow. Head yellow with frons and ocellar area and vertex
black; lower inner orbits, area below antennae, genae and upper inner orbits with spot extending behind each lateral ocellus yellow. Mesosoma with propleuron black; pronotum yellow, pleurae black with orange spot on lower part of mesepisternum, and mesoscutum, metanotum, and propodeum black. Fore and midlegs orange; apical 1 or 2 tarsomeres dark; hind leg black with extreme apex of coxae, both trochanteral segments, extreme apex of femur and extreme base of tibia and tarsus except for apical tarsomere black. Metasoma orange with tergum 1 black dorsally interrupted by transverse orange band at center, terga 2 to apex each with central black spot, appearing as a longitudinal black stripe; sheath black. Wings hyaline with apex black; veins and stigma black. Head (Figs 5–7): Shiny; clypeus and supraclypeal area rugose, with scattered pits separated by flat shiny interspaces several times diameter of an ocellus; pits densest on frons. Antennal length about 3.0× head width; first antennomere longer than broad, second antennomere about as long as broad, third and fourth antennomeres subequal in length. Lower interocular distance subequal to eye height. Malar space about 0.25× eye length. Head behind eyes from above slightly convex behind eyes; in lateral view, lower gena markedly produced with greatest width of gena more than half width of eye. Mesosoma (Figs 4, 8, 9): Shiny with fine white hairs; longs hairs laterally and ventrally on propleuron. Propleuron with dorsolateral longitudinal carina; area above carina slightly dulled, microsculptured; area below carina punctured with flat interspaces equal to or slightly more than puncture diameters. Pronotum shiny with widely scattered punctures; vertical scrobiculate line near posterior margin; front and lower margins flangelike. Mesoscutum shiny, with pair of tubercles on anterior margin, area anterior to tubercles punctate, posterior to tubercles with about 10 strong widely spaced transverse carinae; notauli meeting transscutal articulation at separate points; axilla with one or two transverse carinae, each with small tubercle; mesoscutellum with 3 or 4 transverse carinae, with small tubercle near posterior margin, area lateral to mesoscutellum rugulose. Meso- and metapleurae finely punctate, with small shiny impunctate area on upper halves. Propodeum coarsely rugulose. Tarsal claws simple. Hind coxa about 2.2× longer than broad, shiny, punctate, punctures denser and somewhat more rugulose on sides and venter; without projecting ventral lobe; ovipositor guide a very shallow, almost indiscernible oblique groove near apex on inner surface. Hind tarsus about 1.2× length of hind tibia; hind basitarsus subequal in length to remaining tarsomeres combined. Forewing with 2-Rs+M long, longer than first discal cell. Hind wing with 3 hamuli. Metasoma: Shiny with short, fine white hairs, densest on apical 3 segments. Ovipositor about 0.7 length of forewing.

Male. Length, 8.5 mm. Color and structure similar to Female.

Two unusual new species of *Aulacus* Jurine (Hymenoptera, Aulacidae) from South America

Figures 4–9. *Aulacus flavus*. 4 Lateral (scale bar = 1.0 mm) 5 Head, lateral 6 Head, dorsal 7 Head, front 8 Mesosoma dorsal 9 Mesosoma, lateral.


**Distribution.** Brazil: Bahia, Mato Grosso do Sul, Paraná, Santa Catarina. Apparently most common in southern Brazil.

**Etymology.** From Latin meaning yellow, with reference to the entirely yellow pronotum.

**Remarks.** There are slight variations in color, especially the amount of orange on the mesonotum and size of black marks on the metasoma. The entirely yellow pronotum seems to be constant in the specimens examined. Size is relatively stable, the length varying only by ±1.0 mm; proportions of the ovipositor and forewing remain the same regardless of length.

---

**Aulacus subflavus Smith, sp. n.**

http://zoobank.org/C3AE80D9-6DB6-4ACF-B6E5-D48383DAA3B4

Figs 10–15

**Description.** Female (holotype). Length, 8.0 mm; forewing 6.0 mm; ovipositor 4.2 mm. Similar to *A. flavus* except for the following differences: Pronotum white on dorsal half, black on ventral half (Figs 10, 15). Head (Figs 11–13) with eyes larger; lower interocular distance 0.8× eye height; in dorsal view straight behind eyes; in lateral view lower gena less produced with greatest width of gena half or less width of eye.

Male. Length, 7.5 mm. Color and structure similar to female.


**Distribution.** Brazil: Mato Grosso; French Guiana; Guyana.

**Etymology.** From the Latin partly yellow, referring to the usual half yellow and half black pronotum.

**Remarks.** The “other specimens” are structurally like this species but the mesosoma is entirely yellow orange and I prefer not to include them in the type series. The
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Figures 10–15. *Aulacus subflavus*. 10 Lateral (scale bar = 1.0 mm) 11 Head, lateral 12 Head, dorsal 13 Head, front 14 Mesosoma, dorsal 15 Mesosoma, lateral (tubercle on axilla is shown immediately above base of wing).

Bicolored pronotum seems to be a helpful character, though several specimens have an entirely yellow pronotum. The side lobes of the mesonotum may be entirely black or partly orange. The length varies only by about ±0.7 mm; the proportions of the ovipositor and forewing remain the same regardless of size.
Acknowledgments

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References


A new species of *Aulacus* (Hymenoptera, Aulacidae) from Hokkaido, Japan

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Abstract

*Aulacus machaerophorus* sp. n. is described from females collected in Sapporo, Hokkaido, Japan. This new species has some interesting characteristics such as a very short ovipositor, absence of a ventral lobe and ovipositor guide on hind coxa, and smooth and shiny axillula, and is considered to be closely related to Nearctic species, *A. schiffi*. A key to three Japanese species of *Aulacus* is given.

Keywords

Aulacidæ, *Aulacus*, Evanioidea, Hymenoptera, new species, taxonomy

Introduction

*Aulacus* Jurine, 1807 is composed of 78 extant species and has been recorded from all biogeographical regions except Antarctica and the Afrotropical (Chen et al. 2016). Wasps of this family are koinobiont endoparasitoids and use Xiphydriidae (Hymenoptera) and Buprestidae and Cerambycidae (Coleoptera) as hosts (Chen et al. 2016; Jennings and Austin 2004; Smith 2001). Aulacidae consists of two genera, *Aulacus* and *Pristaulacus*. *Aulacus* is distinguished from *Pristaulacus* by the following features: occipital carina absent; tarsal claw with a basal tooth or none; pronotum without a dentiform process.
along latero-ventral margin; petiole slender, at least 2.5 times as long as wide. *Aulacus* is considered to be a paraphyletic group with respect to *Pristaulacus* (Turrisi et al. 2009).

Seven species of *Aulacus* have been recorded from the Palaearctic Region, with two from Japan, *A. japonicus* Konishi, 1990 from Iwate, Tohoku and *A. uchidai* Turrisi and Konishi 2011 from Hokkaido (Konishi 1990; Turrisi and Konishi 2011). Recently, we collected *Aulacus* specimens from Sapporo, Hokkaido, and found that they have distinctive and peculiar characteristics separate them the known species. Here we describe a new species based on these specimens.

### Materials and methods

Specimens used in this study are dried except one which is preserved in 99% ethanol. They are deposited as follow: Hokkaido University Museum, Sapporo, Japan (SEHU); the Ehime University Museum, Matsuyama, Japan (EUM); and National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM). Morphological technical terms follow Huber and Sharkey (1993) and surface sculpture follows Eady (1968). The methods of measurements follow Konishi (1990) and Smith (2008), and measured traits are shown in Fig. 1. In this paper, we use the following abbreviations: **OOL** = distance between outer margin of posterior ocellus and eye; **POL** = distance between inner margins of posterior ocelli. Most photographs (Figs 1–14) were obtained at the Laboratory of Environmental Entomology, Ehime University, using a Nikon Digital Sight DS-Fi1 camera attached to a Leica S8APO stereomicroscope. Fig. 15 was taken under a digital microscope.

**Figure 1.** Methods for measurements of wing venation: a *Rs* between 1*R* and 1*Rs+M* b *M* between 1*Rs+M* and *M+Cu*.
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HiROX KH-1300 and the image captured with the 2D measurement software SHX-13M ver. 2.9.0. Several partially focused images were combined and post-processed using Adobe Photoshop® CS6.

Taxonomy

Genus Aulacus Jurine

Aulacus Jurine, 1807: 89.

Type species. Aulacus striatus Jurine, 1807. By monotypy.

See Smith (2001) for complete synonymy.

Aulacus machaerophorus sp. n.

http://zoobank.org/EFF61306-4EC9-4387-B841-7DC2BB562BD3

Figs 2–15


Description of female.

Length: 4.1–6.5 mm

Color: Black; median portion of mandible yellowish brown; apical 1/3 to entire scape yellowish brown; apical portion of pedicel yellowish brown; trochanter yellowish brown to black; basal and apical portions of femora yellowish brown; fore tibia yellowish brown; mid tibia yellowish brown, sometimes black with basal and apical portions yellowish brown; hind tibia with basal and apical portions yellowish brown; fore and middle tarsi yellowish brown to light yellowish brown; hind tarsus yellowish brown, sometimes dark yellowish brown; wings hyaline, stigma and veins black; setae silver, setae on mandible gold.

Head glossy (Figs 3–7), 0.6–0.7 times as long as wide; lower area of gena coriaceus; malar space 0.4–0.5 times as long as eye height; head length behind eye in dorsal view 0.4–0.5 times as long as eye height; lower interocular distance 1.2–1.4 times as long as eye height; posterior margin of head weakly concave in dorsal view; occiput and postocciput smooth with dense setae and punctures; temple smooth; vertex smooth, with setae and sparse punctures, coriaceus between eye and posterior ocellus; OOL:POL=1:1; frons coriaceus and sparsely punctate with setae; antennal socket situated at about lower level of eye, separated from anterior tentorial pit by its own diam-
eter; face densely punctate with setae and coriaceous-granulate; clypeus granulate and densely punctate with setae, with a protuberance situated at middle of apical margin; punctures on face and clypeus much stronger and denser than on temple; mandible smooth, basal area and upper half with some setae; antenna (Fig. 7) with fine hairs, 3.1–4.4 times as long as head length; pedicel 1.4–1.9 times as long as wide; 1st flagel-lomere 3.0–4.0 time as long as wide, 0.6–0.7 time as long as 2nd.

Mesosoma glossy (Fig. 8 & Fig. 10), punctate with setae; propleuron reticulate rugose along dorsal edge, antero-dorsal portion reticulate rugose, canaliculate along ventral edge; upper pronotum with subtriangular smooth area surrounded by crenulate furrows, lower pronotum with punctures and dense setae; mesoscutum transversely strigate; notauli moderately narrow and canaliculate, meeting at posterior margin of mesoscutum; scutellum transversely strigate; axillula smooth, shiny; mesopleuron canaliculated-reticulate, epicnemium smooth, with some punctures and setae; mesosternum with dense setae and punctures, reticulate rugose; metanotum smooth, anterior half with canaliculate furrow except median 1/3 with longitudinal ridges; metapleuron reticulate rugose and sparsely punctate with setae; propodeum with dorsal surface rugose and anterior 1/4 with transverse canaliculate furrow, with lateral surface and posterior surface reticulate rugose.
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Legs: Coxae setose and trans-strigate; hind coxa (Fig. 11) 1.9–2.3 times as long as wide, without ventral lobe and ovipositor guide; tibiae with dense setae and puncture; tarsi with dense spines and punctures; hind basitarsus 1.1–1.4 times as long as length of remaining tarsomeres combined; hind tarsal claw with a basal tooth.

Figures 3–7. *Aulacus machaerophorus* sp. n. 3 head, dorsal view 4 frons, frontal view 5 face, frontal view 6 head, lateral view 7 antenna, dorsal view. Scale bars: 0.5 mm (3–6), 1.0 mm (7).
Figures 8–12. *Aulacus machaerophoruss* sp. n. 8 mesosoma, lateral view 9 metasoma, dorsal view 10 mesosoma, dorsal view 11 hind coxa, lateral view 12 ovipositor. Scale bars: 1.0 mm.
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Figures 13–14. *Aulacus machaerophorus* sp. n. 13 fore wing 14 hind wing. Scale bars: 0.5 mm.

Wings: Fore wing (Fig. 13) 3.1–5.1 mm long and 2.6–3.4 times as long as wide; stigma 2.3–3.8 times as long as wide, length of stigma basad *r-rs* 1.2–1.4 times as long as length of stigma distad *r-rs*; *M+Cu* with distal tubular portion as long as basal non-tubular portion; cell *M* 1.9–3.0 times as long as wide; cell *1R* 1.5–1.9 times as long as wide; *Rs* between *1R* and *Rs+M* 1.7–2.8 times as long as *M* between *Rs+M* and *M+Cu* (Fig. 1); *r-rs* 0.7–1.0 times as long as stigma width; anteriorly 2/5 and posteriorly 1/10 of 2*r-m* distinct; *Cu* curved downward; hind wing (Fig. 14) weakly tapering toward rounded apex, 3.3–3.9 times as long as wide and with 3 hamuli; *M* of apical portion colored.

Metasoma glossy (Fig. 10); petiole 2.1–3.2 times as long as wide; 1st sternum with strong longitudinal furrows; 2nd to 5th terga coriaceus and 2nd tergite without setae and punctures, 3rd to 7th terga with sparse setae and punctures; 2nd to 5th sterna coriaceus; ovipositor 0.8–1.1 mm long and 0.2–0.3 times as long as fore wing, 1.1–1.7 times as long as hind coxa; ovipositor (Fig. 12) strongly upcurved near apex and with some setae on dorsal valve near apex (Fig. 15); ovipositor sheath with dense short hairs; second gonocoxa with setae and punctures; apical portion of ovipositor sheath weakly enlarged and rounded.

**Male.** Unknown.

**Distribution.** Japan (Hokkaido).
**Biology.** All specimens used in this study were collected on the tree trunk of a blighted broad leaf tree in a broad-leaved forest.

**Etymology.** From the Latin *machaerophorus*, meaning bearing a short sword. This new species has a short ovipositor like a short sword.

**Remarks.** This new species possesses the following peculiar features: frons without transverse carina and rugulose sculpture; axillula smooth, shiny; hind coxa without ventral lobe and ovipositor guide; ovipositor very short (0.2–0.3 times as long as fore wing); apical portion of ovipositor with some short setae.

In *Aulacus* species so far described, a Nearctic species, *A. schiffi* Smith, 1996 is considered to be most closely related to *A. machaerophorus*. They share the short ovipositor; hind coxa without projecting ventral lobe and ovipositor guide; smooth frons without transverse carina; and ovipositor with setae (Smith, personal communication). Among these characteristics, the presence or absence of setae on ovipositor has not been reported in other *Aulacus* species and therefore needs further examination. *Aulacus machaerophorus* can be separated from *A. schiffi* by the absence of diagonal carinae on the axillula, the shorter ovipositor (ovipositor is 0.5 times as long as fore wing in *A. schiffi*) and wing venation (*A. schiffi* has a longer discal cell, $2R_3+M$ between the discal and submarginal cells is much shorter, and $2r-m$ is absent). This relationship of *A. machaerophorus* and *A. schiffi* suggest close relationships of some of the fauna and flora of eastern Asia and eastern North America. For example, relationship of North American and eastern Asian species of *Stronglygaster* (Tenthredinidae) (Smith and Naito 1995) and example of the flora see Tiffney (1985).

Other Palaearctic species have rugulose frons with transverse carina judging from figures in Chen et al. (2016) and Sundukov and Lelej (2015). On the other hand, Australian and Nearctic *Aulacus* species have the frons with or without transverse carinae.
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and the hind coxa with or without a ventral lobe and ovipositor guide (Jennings et al. 2004; Smith 2008).

This new species can be distinguished from two Japanese species by the following key.

**Key to Japanese species – females**

1. Frons without transverse carina, smooth (Fig. 5); axillula smooth (Fig. 10); fore wing with anterior part of 2r-m (Fig. 1); hind coxa without ventral lobe and ovipositor guide (Fig. 11) .................. *A. machaerophorus, sp. n.*

   – Frons with transverse carinae, rugulose-foveolate or rugulose; axillula reticulate rugose; fore wing without anterior part of 2r-m; hind coxa with ventral lobe............................................................................................................2

2. Ovipositor 0.6–0.9 times as long as fore wing length; frons less extensively sculptured and weakly rugulose-foveolate ..... *A. uchidai Turrisi & Konishi*

   – Ovipositor 0.4 times as long as fore wing length; frons rugulose ..................

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   *A. japonicus Konishi*

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**References**


