

# Revision of *Therophilus* s.s. (Hymenoptera, Braconidae, Agathidinae) from Thailand

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## Abstract

Based on a phylogenetic analysis, the limits of *Therophilus* (Hymenoptera: Braconidae: Agathidinae) are redefined and restricted to a small proportion of the previously included species. Those species belonging to the world fauna are listed and the species from Thailand are revised. Forty-four species are assigned to the genus including 11 new species, i.e. *T. anuchati*, *T. apichati*, *T. areluckae*, *T. boonthami*, *T. chiang-maiensis*, *T. kwanuiae*, *T. songrami*, *T. sukpengae*, *T. wannai*, *T. wongchahi*, *T. wongwani*. A dichotomous key to species is presented; links to an electronic interactive key and to distribution maps are also included.

## Keywords

Thailand, Insecta, identification key, taxonomy, systematics

## Introduction

Agathidinae is a moderately large subfamily of Braconidae with 1,069 described species worldwide and 246 in the Oriental Region (Yu et al. 2005), though there are an estimated 2,000–3,000 species awaiting description worldwide (Sharkey et al. 2006). The subfamily has a worldwide distribution and members are found in most terrestrial habitats. The history of higher classification of the Agathidinae was summarized by

Sharkey (1992) who also proposed a tribal level classification based on ground-plan coding. Sharkey et al. (2006) conducted phylogenetic analyses based on morphology and the D2–D3 regions of 28S rDNA. The Oriental fauna of Agathidinae were first revised by Bhat and Gupta (1977) and they provided a detailed history of taxonomic research for the area. Sharkey et al. (2009) revised the Oriental genera of Agathidinae. Van Achterberg and Long (2010) revised the Vietnamese agathidine fauna. Sharkey and Clutts (2011) revised the Thai species of *Biroia*, *Braunsia*, *Camptothlipsis*, *Coccygidium*, *Cremnops*, *Cremnoptoides*, *Disophrys*, *Earinus*, *Gyrochus*, *Lytopylus*, and *Troticus*, and included a key to the Agathidinae genera of the Oriental region. Sharkey and Stoelb (in press) revised the Thai species of *Zelodia*. This paper is the third in a series to revise all Thai species of Agathidinae. The genera *Aneurobracon*, *Bassus s.s.*, *Euagathis*, and *Therophilus s.l.* will be dealt with in subsequent publications.

## Methods

As part of the inventory of Thai insects, we ran 3 Malaise traps at each of 30 different localities throughout Thailand from 2007–2010, comprising approximately 90 Malaise traps. The specimens dealt with here are primarily from these traps.

Species concepts are based on morphological data and 28S rDNA data. Regions D2–D3 of 28S rDNA (roughly 560 base pairs) were sequenced using the following primers: 28SD2hymF 5' - AGAGAGAGTTCAAGAGTACGTG - 3' and 28SD-3hymR 5' - TAGTTCACCATCTTTTCGGGTC - 3'. Sequences were edited using Geneious Pro v4.7.5 (Drummond et al. 2009) and aligned based on a secondary structure model for Ichneumonidea developed by Yoder and Gillespie (2004) and Gillespie et al. (2005). Regions of expansion and contraction (RECs), regions of slipped-strand compensation (RSCs), and short regions of alignment ambiguity were further aligned/corrected by eye. Three of these regions (~30 base pairs total) were deleted because they could not be aligned with any confidence, i.e., there were multiple equally supported alignment options.

Phenetic and phylogenetic trees were constructed using neighbor-joining (NJ), maximum parsimony (MP) and Bayesian methods. MP was performed using TNT (Goloboff et al. 2008) [traditional search with 100 random addition sequences followed by branch-swapping, saving 100 trees per replication; 1000 bootstrap replications were used to estimate branch reliability]. The Bayesian analysis was performed using MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003). Best-fitting DNA substitution models were determined using MrModeltest2.2 (Nylander 2004). The general time reversible model of evolution with a parameter for invariant sites and rate heterogeneity modelled under a gamma distribution (GTR+I+G) was determined as the best-fitting model. The Bayesian analysis consisted of two independent Bayesian MCMC runs initiated from different random starting trees. The analysis ran for 5,500,000 generations, reaching a topological similarity criterion of 0.01; trees were sampled every 500 generations. 25% of the trees from each run were removed as burn-in upon topological

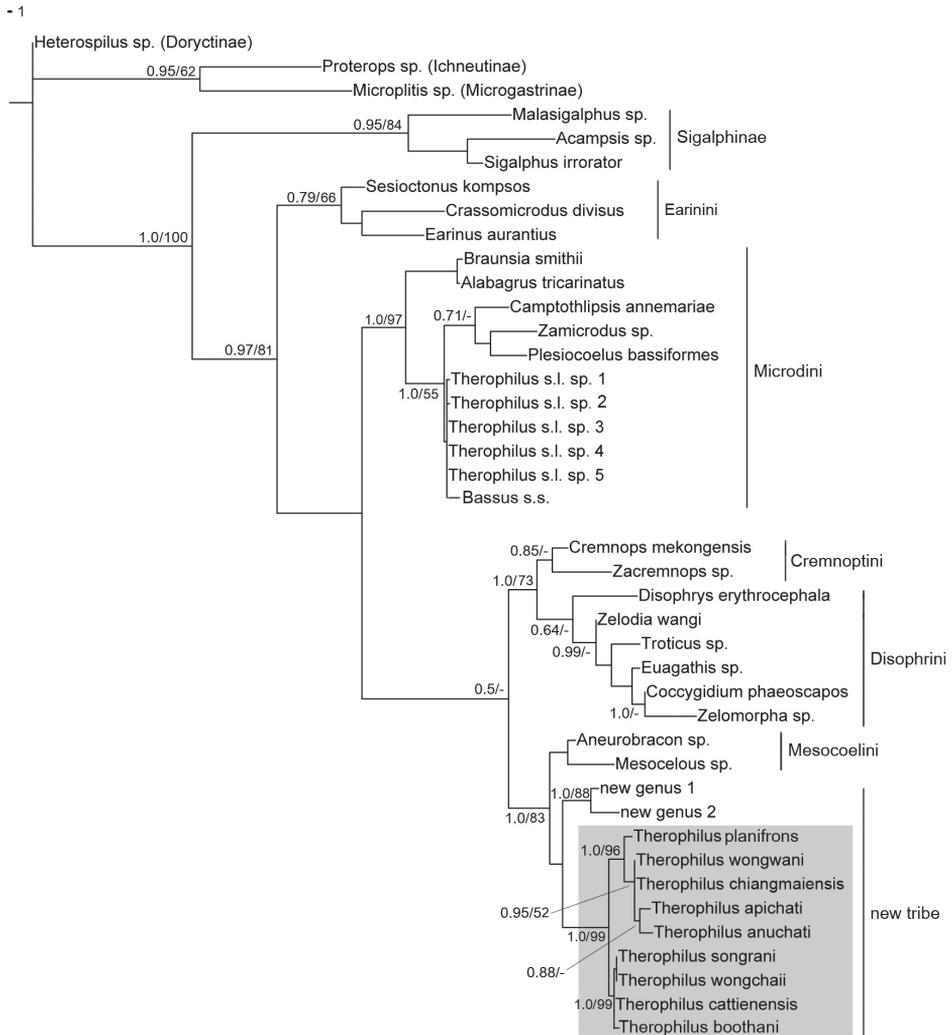


**Figure 1.** Map showing *Therophilus* collection sites in Thailand.

convergence. The NJ tree was produced from PAUP\* (Swofford 2003) using default settings. Figure 2 presents the NJ tree, which was more resolved than the phylogenetic trees produced by MP and Bayesian analyses. We mapped the support values of the Bayesian and MP analyses on the NJ tree.

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

Morphological terms follow Sharkey and Wharton (1997) except for the following: measurements are given for the length and apical width of the first metasomal mediotergite (MT1). Measurement of the apical width is straightforward, however since the base of the tergite is usually hidden from view it is difficult to measure the total length. Instead we measure from the apex of the large tendon that emanates from the propodeum and inserts near the base of the median tergite. Abbreviations used in text: MT1, MT2, MT3...MT7: metasomal mediotergite 1, 2, 3...7.



**Figure 2.** NJ phylogram based on 28S rDNA. Where Bayesian and parsimony analyses agreed with the NJ tree, branch support values are included in the figure, i.e., Bayesian posterior probabilities/parsimony bootstrap (values below 0.5 posterior probability and/or 50% bootstrap support were not recorded on the tree). *Therophilus* s.s. highlighted in grey box.

Morphological terms used in this revision were matched to the Hymenoptera Anatomy Ontology (HAO, Yoder et al. 2010) (Appendix 4). Identifiers (URIs) in the format [http://purl.obolibrary.org/obo/HAO\\_XXXXXXX](http://purl.obolibrary.org/obo/HAO_XXXXXXX) represent anatomical concepts in HAO version <http://purl.obolibrary.org/obo/hao/2011-05-18/hao.owl>. They are provided to enable readers to confirm their understanding of the anatomical structures being referenced. To find out more about a given structure, including, images, references, and other metadata, use the identifier as a web-link, or use the HAO:XXXXXXX (note colon replaces underscore) as a search term at <http://glossary.hymao.org>.

All 14 species found in Thailand are treated with a diagnosis and distributional data. They are illustrated with color photos using a JVC digital camera mounted on a Leica MZ16 microscope and Automontage® stacking software. Distributional data are listed for all species and a Google map via Berkeley Mapper is included for all species. The descriptions are of the holotype and variation is given in parentheses.

The source files for the keys, descriptions, illustrations, DNA sequence and distributional data are all freely available to future researchers who may wish to build on these data. Distribution data, pdf's of non-copywrite references, images, notes, and host and type information can be found by searching Taxabank (a combined specimen and taxonomic database; <http://purl.org/taxabank>). Codes beginning with an "H" and followed by numbers are unique identifiers used for specimens in the Sharkey lab at the University of Kentucky, and in the specimen database TaxaBank (e.g., H235). All sequences have been deposited in the GenBank database.

#### Abbreviations used for specimen depositories are as follows:

- HIC** Hymenoptera Institute Collection, University of Kentucky, Department of Entomology, Lexington, Kentucky, USA.  
**QSBG** Queen Sirikit Botanic Gardens, Chiang Mai, Thailand.  
**RMNH** NCB Naturalis Collection [formerly Rijksmuseum van Natuurlijke Historie], Leiden, Netherlands.  
**IRSNB** Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.

## Results

### Phylogeny

Recently the polyphyletic generic concept, *Bassus*, was divided into four genera, i.e., *Bassus* s.s., a small monophyletic group confined to the Old World, *Lytopylus*, a large monophyletic group with a world-wide distribution, *Neothlipsis*, a small New World genus and *Therophilus*, a polyphyletic dumping ground for the remaining species. Here we refine the concept of *Therophilus* so that it is monophyletic. However, this leaves those species that do not fit the concept without a correct generic placement. We refer to these as *Therophilus* s.l. in this treatment, and they will be treated in a separate publication (Sharkey et al. in prep).

The phylogenetic tree in figure 2 shows that *Therophilus* in the strict sense, and two new genera, are far removed from the majority of the species of *Therophilus sensu lato*. The clade containing *Therophilus* s.s. was referred to as an unnamed new tribe in Sharkey (1996). The monophyly of all agathidine tribes is well supported, though the tribal interrelationships based on 28S remain volatile.

Within *Therophilus* s.s., there are two distinct clades that may deserve generic status when more is known of their biology and diversity. All members of the lower clade,

in figure 2, which includes *T. cattienensis*, are stout and mostly yellow-orange, e.g., all have predominantly yellow-orange heads. *Therophilus conspicuus* Wesmael, the type species, belongs in this group. Members of the clade containing *T. chiangmaiensis* are more gracile and melanic.

### *Therophilus* Wesmael, 1837

<http://species-id.net/wiki/Therophilus>

**Type species.** *Microdus (Therophilus) conspicuus* [Lectotype ♀ IRSNB, examined]

**Diagnosis.** There is neither one character nor a specific combination of characters that distinguishes members of *Therophilus* from all other agathidines. It is easily separated from members of Cremnoptini and Disophrini by the shape of the tarsal claws, i.e., simple with a basal lobe in *Therophilus*, versus cleft claws in members of the two aforementioned tribes. Most members of *Therophilus* have the following combination of diagnostic characters: Apical abscissa of R of fore wing weak at midlength and bent towards apex of wing; interantennal space with two (usually weak and short) longitudinal ridges or with a median keel; postscutellar depression present; cubitus of hind wing strong and tubular, at least basally; subbasal cell of hind wing angled apically at the point from which the cubitus emanates; sclerite between hind coxal cavities and metasomal foramen incomplete or narrow. A combination of characters that distinguishes almost all species of Oriental *Therophilus* is: Interantennal space with longitudinal groove (Figs. 3c, 6c), sometimes weak (Fig. 8c); posteroscutellar depression present (Fig. 8f); notauli sculptured with pits (Fig. 3f).

**Description. Head.** Lateral carina on frons absent (Fig. 3c); interantennal space with longitudinal groove (Fig. 3c, 6c); gena not extended ventroposteriorly into sharp prominence (Fig. 5e); gena lacking sharp angle posteriad eye; labial palpus with three or four segments, third segment much reduced or absent; apical antennomere acute but lacking nipple-like process.

**Mesosoma.** Propleuron lacking a projection at mid height; notauli impressed and pitted, at least in part (Fig. 3f); posteroscutellar depression present (Fig. 8f) (rarely absent); propodeum from rugose to areolate-rugose (Fig. 7g); sclerite between hind coxal cavities and metasomal foramen narrow, sometimes incomplete.

**Legs.** Fore tibia lacking pegs, fore tarsal claws with basal lobe; mid tibia with apical and medial pegs; hind tibia with apical pegs.

**Wings** (Figs. 3b, 4b). Fore wing RS + M vein incomplete; second submarginal cell triangular; fore wing 3RSb decurved, weak at midlength; hind wing r and r-m cross-veins absent; hind wing CUB present and strong, tubular at least basally.

**Metasoma.** MT1 with longitudinal striations, lacking dominant pair of longitudinal carinae (Fig. 4f); MT2 from smooth to striate, usually with some longitudinal striae and weak transverse striae in first transverse depression; MT3 smooth (Fig. 4f); ovipositor as long as or longer than metasoma (Fig. 4a).

**Species diversity.** Including the twelve described here, there are 44 described species known to the senior author. The following 13 species were included in *Therophilus* at the time of this publication: *Therophilus antipoda* Ashmead, 1900, *Therophilus arcuatus* Reinhard, 1867, *Therophilus cattienensis* van Achterberg & Long, 2010, *Therophilus cingulipes* Nees, 1812, *Therophilus clausthalianus* Ratzeburg, 1844, *Therophilus conspicuus* Wesmael, 1837, *T. crenulisulcatus* van Achterberg & Long, 2010, *Therophilus levisoma* van Achterberg & Long, 2010, *Therophilus planifrons* van Achterberg & Long, 2010, *Therophilus rugosiferus* van Achterberg & Long, 2010, *Therophilus similis* (Bhat & Gupta, 1977), *Therophilus stephensae* Stevens, 2011, *Therophilus tumidulus* (Nees, 1812).

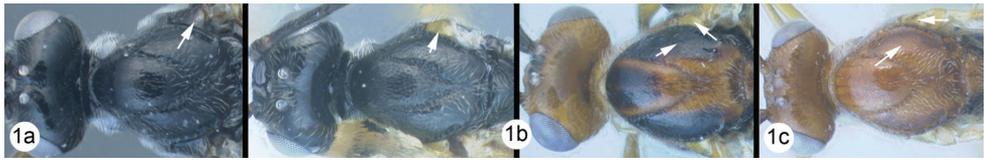
The remainder are here transferred to *Therophilus*: *Bassus arthurellus* Sharkey 1985 = *Therophilus arthurellus* comb. n., *Bassus belokobylskiji* Sharkey, 1998 = *Therophilus belokobylskiji* comb. n., *Agathis bruesi* Shenefelt, 1970 = *Therophilus bruesi* comb. n., *Agathis curvabilis* Bhat & Gupta, 1977 = *Therophilus curvabilis* comb. n., *Agathis cymocles* Nixon, 1950 = *Therophilus cymocles* comb. n., *Agathis flava* Bhat & Gupta, 1977 = *Therophilus flavus* comb. n., *Bassus graecus* Simbolotti & van Achterberg, 1992 = *Therophilus graecus* comb. n., *Agathis hyalinis* Bhat & Gupta, 1977 = *Therophilus hyalinis* comb. n., *Microdus infumatus* Granger, 1949 = *Therophilus infumatus* comb. n., *Microdus insularis* Ashmead = *Therophilus insularis* comb. n., *Bassus lanyuensis* Chou & Sharkey, 1989 = *Therophilus lanyuensis* comb. n., *Microdus nugax* Reinhart, 1867 = *Therophilus nugax* comb. n., *Microdus simillimus* Cresson, 1873 = *Therophilus simillimus* comb. n., *Microdus tautirae* Cheeseman, 1928 = *Therophilus tautirae* comb. n., *Bassus tegularis* Thompson, 1895 = *Therophilus tegularis* comb. n., *Bassus tobiasi* Sharkey, 1998 = *Therophilus tobiasi* comb. n., *Agathis triangularis* Szépligeti = *Therophilus triangularis* comb. n., *Bassus triangulus* Chou & Sharkey, 1989 = *Therophilus triangulus* comb. n., *Microdus postfurcalis* Szépligeti, 1914 = *Therophilus postfurcalis* comb. n., *Microdus zaykovi* Nixon = *Therophilus zaykovi* comb. n. There are many species of Agathidinae currently placed in *Therophilus* and *Bassus* Fabricius which belong to other genera, and many more that are yet to be described.

**Biology.** According to Nixon (1986), *T. conspicuus* attacks larval Tortricidae. Janzen has reared three species of *Therophilus* s.s. in Costa Rica; they are parasitoids of Tortricidae and Elachistidae. See parasitoid DHJPAR voucher numbers 0039084, 0038338, and 0040068 in the “caterpillars of Guanacaste” database at <http://janzen.sas.upenn.edu/caterpillars/database.lasso>

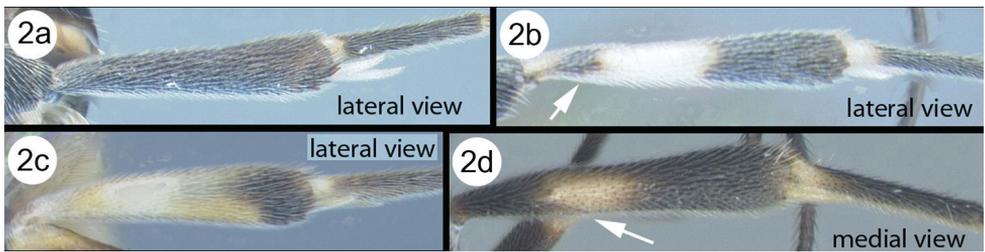
**Distribution.** Worldwide, with more diversity in subtropical and tropical areas.

### Key to Thai species of *Therophilus* s.s.

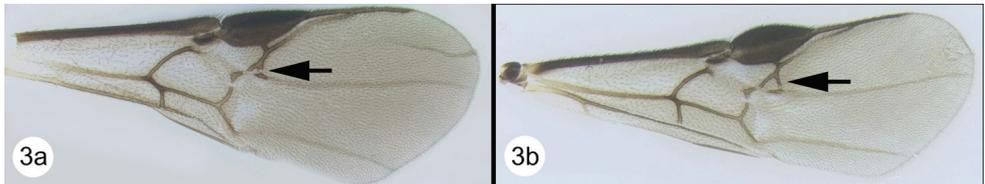
- 1 a. Tegula black, concolorous with mesoscutum..... 2
- b. Tegula yellow, contrasting with predominantly black mesoscutum..... 8
- c. Tegula yellow or orange, similar in color to predominantly orange or yellow mesoscutum ..... 12



- 2(1) a. Hind tibia entirely melanic (check medial surface) ..... *T. anuchati* Sharkey sp. n.
- b. Hind tibia largely pale, melanic apically and with a subbasal melanic band or lateral spot ..... 3
- c. Hind tibia mostly pale, melanic apically only .... *T. kwanuiae* Sharkey sp. n.
- d. Hind tibia mostly melanic with pale coloration at midlength at least medially ..... *T. Chiangmaiensis* Sharkey sp. n.



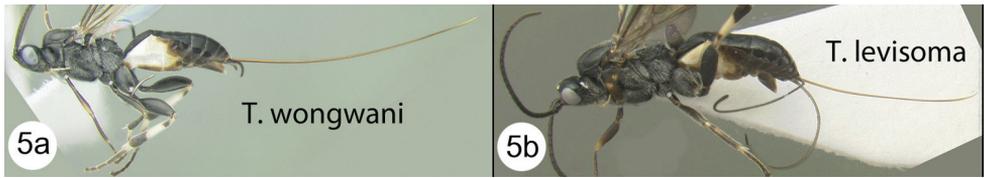
- 3(2) a. 2nd submarginal cell reduced to a small dot, petiole longer than cell is high ..... 4
- b. 2nd submarginal cell larger, cell height subequal to petiole length ..... 6



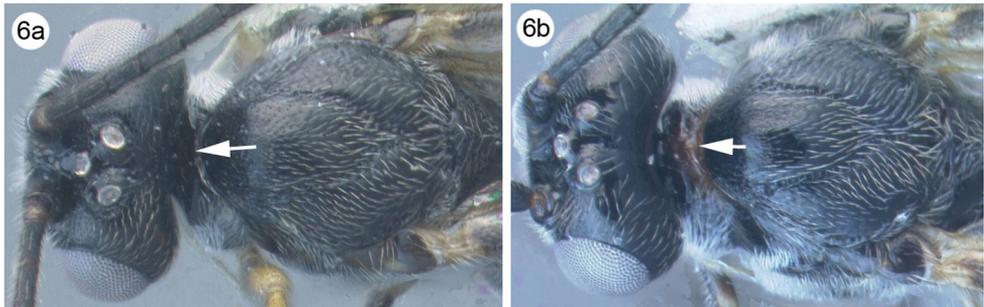
- 4(3) a. Fore tarsus mostly or entirely melanic ..... 5
- b. Fore tarsus mostly or entirely pale ..... *T. kwanuiae* Sharkey sp. n.



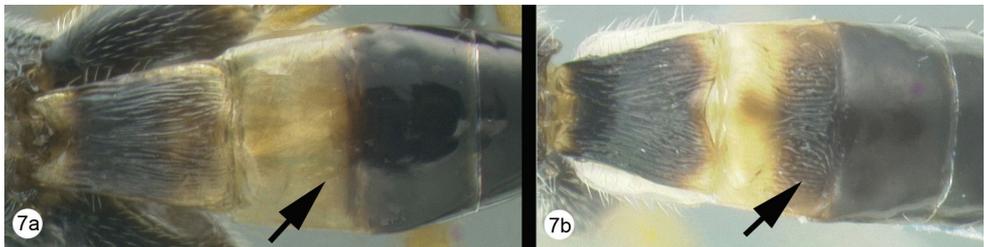
- 5(4) a. Exposed portion of ovipositor distinctly longer than body ..... *T. wongwani* Sharkey sp. n.
- b. Exposed portion of ovipositor slightly shorter than body ..... *T. levisoma* van Achterberg & Long



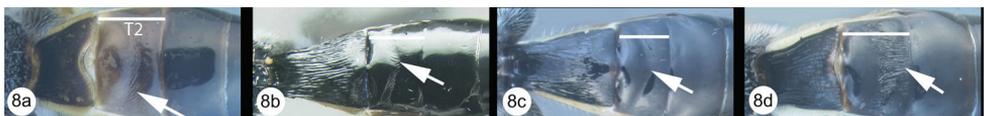
- 6(3) a. Pronotum entirely melanic.....7  
 b. Pronotum mostly melanic but pale dorsomedially.....  
 ..... *T. wannai* Sharkey sp. n.



- 7(6) a. Posterior half of MT2 smooth.....  
 ..... *T. crenulisulcatus* van Achterberg & Long  
 b. Posterior half of MT2 longitudinally striate, at least medially .....  
 ..... *T. sukpengae* Sharkey sp. n.

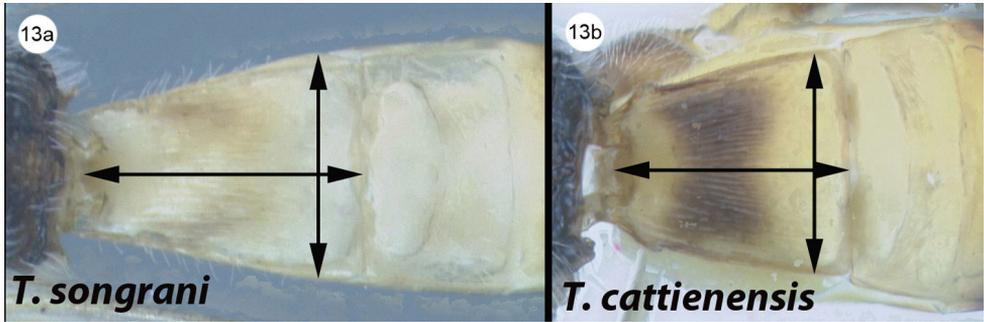


- 8(1) a. MT2 mostly smooth with transverse and/or diagonal striae in and/or near transverse depression..... *T. wongchai* Sharkey sp. n.  
 b. MT2 mostly smooth with short longitudinal striae restricted to transverse depression..... *T. planifrons* van Achterberg & Long  
 c. MT2 entirely smooth.....9  
 d. MT2 smooth in most of anterior half anterior transverse groove, longitudinally striate in transverse groove and area posterior transverse groove, at least medially. .... 10





- 13(12) a. MT1 length distinctly longer than apical width .....  
 ..... *T. songrani* Sharkey sp. n.  
 b. MT1 length only slightly longer than apical width .....  
 ..... *T. cattienensis* van Achterberg & Long



**Species Treatments**

*Therophilus anuchati* Sharkey sp. n.

urn:lsid:zoobank.org:act:134DEB0E-168C-4B81-94C4-A82CC11346DA

[http://species-id.net/wiki/Therophilus\\_anuchati](http://species-id.net/wiki/Therophilus_anuchati)

Figure 3

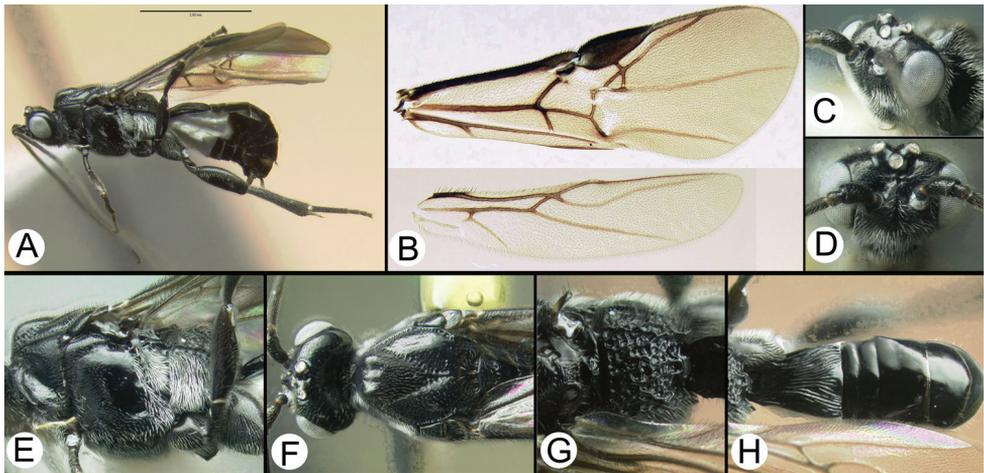
**Diagnosis.** Ocellar triangle melanic, concolorous with remainder of vertex. Hind tibia entirely melanic. Strong transverse carinae between the hind coxal cavities and a wide sclerite between the hind coxal and metasomal foramina. Strong, sharply declivous longitudinal flange between antenna; hind wing CUB strong and long; median lobe of mesoscutum sharply sloping anteriorly.

**Description. Body length.** 5.2 mm.

**Head.** Space between antennal insertions with a well-developed keel that is sharply declivous posteriorly, dorsal surface of keel with a shallow longitudinal groove. Number of flagellomeres 32. Posterior surface of scutellum completely rugose, posterior scutellar depression not distinct.

**Mesosoma.** Number of pegs on mid tibia = 4. Number of pegs on hind tibia = 9. Sclerite between metasoma and hind coxa wide with a high ridge along most or all of its length. Basal lobe of hind tarsal claw longer than high, not sharply declivous. Length-width of hind femur  $1.0/0.342 = 2.9$ . 2nd submarginal cell large, cell height subequal to petiole length. Hind wing vein Cub emanates from near mid length of apical margin of subbasal cell, Cub long and strong. Point of notauli intersection heavily sculptured over a wide area with a median longitudinal ridge. Median lobe of mesoscutum bulging and sharply declivous anteriorly. Metapleuron with dense mat of white setae.

**Metasoma.** MT1 length distinctly longer than apical width. MT1 with widely-spaced longitudinal striae, lacking microsculpture between striae, and with and two pairs of distinctly stronger striae (carinae). MT1 distinctly wider apically than basally.



**Figure 3.** *Therophilus anuchati* sp. n. **a** lateral habitus **b** Wings **c** dorsolateral head **d** anterodorsal head **e** lateral mesosoma **f** dorsal head and mesosoma **g** dorsal propodeum **h** dorsal metasoma.

Ratio of widest point of MT1 to narrowest point  $0.61/0.411 = 1.5$ . Length-width ratio of MT1  $0.8/0.61 = 1.3$ . MT2 entirely smooth.

**Color.** Mostly black or dark melanic except for dense white pilosity on metapleuron and white on anterior lateral tergites and sternites, more apical leg segments lighter, tending towards light brown or dark yellow, all apical spurs white, mandible and palpi mostly yellow, fore wing lightly infuscate, stigma brown with a small pale patch near base. Tegula black, concolorous with mesoscutum. Ocellar triangle melanic, concolorous with remainder of vertex. Hind tibia entirely melanic. MT2 entirely melanic.

**Etymology.** Named in honor of Mr. Anuchat Chaimuangchuen, collector for the TIGER project at Huay Namdung National Park.

**Molecular data.** H099, GenBank Accession: JQ929184.

**Distribution.** Distribution map can be found at <http://purl.org/thaimap/anuchati>

**Material examined.** Holotype ♂. H099 [QSBG] Thailand, Phu Ruea NP, Nature trail, 920m, 17.48°N, 101.354°E, MT, 12–19.i.2007. <http://purl.org/taxabank/T.anuchati>

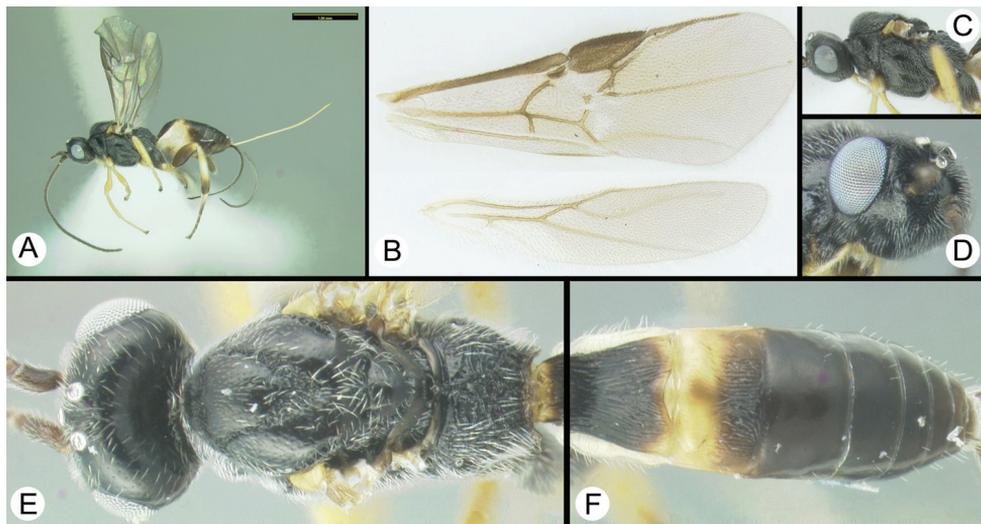
***Therophilus apichati* Sharkey sp. n.**

urn:lsid:zoobank.org:act:5D8F3F04-C77B-482D-A015-4C61204E36F9

[http://species-id.net/wiki/Therophilus\\_apichati](http://species-id.net/wiki/Therophilus_apichati)

Figure 4

**Diagnosis.** MT2 pale in anterior half, melanic posteriorly. Ocellar triangle melanic, concolorous with remainder of vertex.



**Figure 4.** *Therophilus apichati* sp. n. **a** lateral habitus **b** Wings **c** lateral head and mesosoma **d** dorsolateral head **e** dorsal head, mesosoma and propodeum **f** dorsal Metasoma.

**Description. Body length.** 2.6 mm.

**Head.** Space between antennal insertions with a weakly developed bulge that is weakly declivous posteriorly, dorsal surface of bulge with a shallow longitudinal groove. Number of flagellomeres 23. Posterior surface of scutellum mostly smooth, posterior scutellar depression well-defined by two large pits separated by a short longitudinal ridge.

**Mesosoma.** Number of pegs on mid tibia = 5. Number of pegs on hind tibia = 9. Sclerite between metasoma and hind coxa narrow, and lacking a high ridge along its length. Length-width of hind femur  $0.596/0.24 = 2.5$ . 2nd submarginal cell reduced to a small dot, petiole longer than cell is high, or large, cell height subequal to petiole length. Hind wing vein Cub emanates from near mid length of apical margin of sub-basal cell, Cub short and weak. Point of notauli intersection heavily sculptured over a wide area. Median lobe of mesoscutum not bulging and not sharply declivous anteriorly. Metapleuron with scattered white setae.

**Metasoma.** MT1 length distinctly longer than apical width. MT1 with narrowly-spaced longitudinal striae, with some microsculpture between striae, and lacking two pairs of distinctly stronger striae (carinae). MT1 distinctly wider apically than basally. Ratio of widest point of MT1 to narrowest point  $0.32/0.22 = 1.5$ . Length-width ratio of MT1  $0.44/0.32 = 1.4$ . MT2 smooth in most of anterior half anterior transverse groove, longitudinally striate in transverse groove and area posterior transverse groove, at least medially. Ovipositor much longer than metasoma, about as long as body or longer.

**Color.** Body mostly melanic, legs mostly pale; body black except as follows: antenna brown, palpi, labrum and other mouthparts yellow, tegula yellow, fore and mid legs entirely yellow, hind coxa mostly black, hind femur mostly brown, paler apically, hind trochanter, tibia, and tarsus mostly yellow, metasomal mediotergite yellow in an-

terior half or more, anterior metasomal laterotergites and sternites pale yellow. Tegula yellow, contrasting with predominantly black mesoscutum. Ocellar triangle melanic, concolorous with remainder of vertex. Hind tibia mostly pale, melanic apically and with a subbasal melanic band or lateral spot, or mostly pale, melanic apically only. MT2 pale in anterior half, melanic posteriorly.

**Etymology.** Named in honor of Mr. Apichat Watanawanit, collector for the TIGER project at Doi Chiangdao Wildlife Sanctuary.

**Molecular data.** H147, GenBank Accession: JQ929183.

**Distribution.** Distribution map can be found at <http://purl.org/thaimap/apichati>

**Material examined.** Holotype ♀. H147 [QSBG] Thailand, Khao Kho NP, Mixed deciduous forest, 560m, 16.542°N, 101.042°E, MT, 19–26.xii.2006. <http://purl.org/taxabank/T.apichati>

***Therophilus areeluckae* Sharkey sp. n.**

urn:lsid:zoobank.org:act:10482AB4-959F-43A7-8E16-88AE03683437

[http://species-id.net/wiki/Therophilus\\_areeluckae](http://species-id.net/wiki/Therophilus_areeluckae)

Figure 5

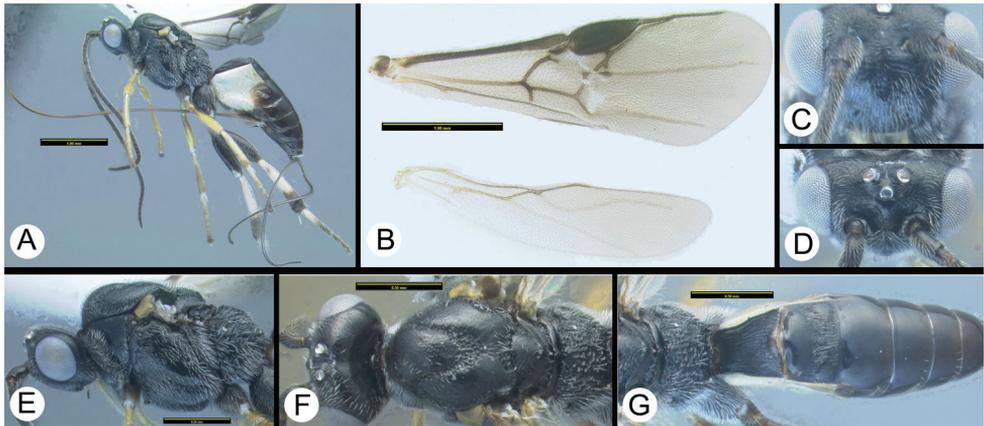
**Diagnosis.** MT2 smooth in most of anterior half antieriad transverse groove, longitudinally striate in transverse groove and area posteriad transverse groove, at least medially. Mid femur mostly pale with a bit of melanic color at extreme base. MT2 entirely melanic. Similar to *Therophilus rugosiferus* but *T. areeluckae* has no transverse ridge on the propodeum, more sculpture on mesoscutum, and the fore and middle legs are paler.

**Description. Body length.** 4.0 mm.

**Head.** Space between antennal insertions with a weakly developed bulge that is weakly declivous posteriorly, dorsal surface of bulge with a shallow longitudinal groove. Number of flagellomeres 28. Posterior surface of scutellum rugose over a semi-circular area that represents the scutellar depression.

**Mesosoma.** Number of pegs on mid tibia = 5. Number of pegs on hind tibia = 9. Sclerite between metasoma and hind coxa wide with a high ridge along most or all of its length. Length-width of hind femur  $0.815/0.256 = 3.2$ . 2nd submarginal cell reduced to a small dot, petiole longer than cell is high, or large, cell height subequal to petiole length. Hind wing vein Cub emanates from near anterior apex of apical margin of subbasal cell, Cub short and weak. Point of notauli intersection heavily sculptured over a wide area. Median lobe of mesoscutum not bulging and not sharply declivous anteriorly.

**Metasoma.** MT1 length distinctly longer than apical width. MT1 with narrowly-spaced longitudinal striae, with some microsculpture between striae, and lacking two pairs of distinctly stronger striae (carinae). MT1 distinctly wider apically than basally. Ratio of widest point of MT1 to narrowest point  $0.414/0.278 = 1.5$ . Length-width ratio of MT1  $0.668/0.414 = 1.6$ . MT2 smooth in most of anterior half antieriad transverse groove, longitudinally striate in transverse groove and area posteriad transverse groove, at least medially. Ovipositor much longer than metasoma, about as long as body or longer.



**Figure 5.** *Therophilus areeluckae* sp. n. **a** lateral habitus **b** Wings **c** anterodorsal head **d** dorsal head **e** lateral head and mesosoma **f** dorsal head and mesosoma **g** dorsal propodeum and Metasoma.

**Color.** Body mostly melanic, legs mostly pale; body black except as follows: antenna brown, palpi, labrum and other mouthparts yellow; tegula yellow; fore and mid legs yellow except for mostly melanic coxae; hind coxa, trochanter, and femur black; hind tibia mostly pale yellow, melanic apically and with a very weak patch of light brown sub-basally; hind basitarsomere mostly yellow, remaining tarsomeres mostly melanic; anterior metasomal laterotergites and sternites pale yellow; fore wing weakly infusate. Scape entirely melanic. Tegula yellow, contrasting with predominantly black mesoscutum. Ocellar triangle melanic, concolorous with remainder of vertex. Hind tibia mostly pale, melanic apically and with a subbasal melanic band or lateral spot, or mostly pale, melanic apically only. Fore tarsus mostly or entirely pale. Pronotum entirely melanic. MT2 entirely melanic.

**Etymology.** Named in honor of Ms. Yuwadee Areeluck, collector for the TIGER project at Doi Inthanon National Park.

**Distribution.** Distribution map can be found at <http://purl.org/thaimap/areeluckae>

**Material examined.** Holotype ♀. H988 [QSBG] Thailand, Chae Son NP, Youth-camp/meeting hall, 476m, 18.831°N, 99.47°E, MT, 22–28.iii.2008. <http://purl.org/taxabank/T.areeluckae>

***Therophilus boonthami* Sharkey sp. n.**

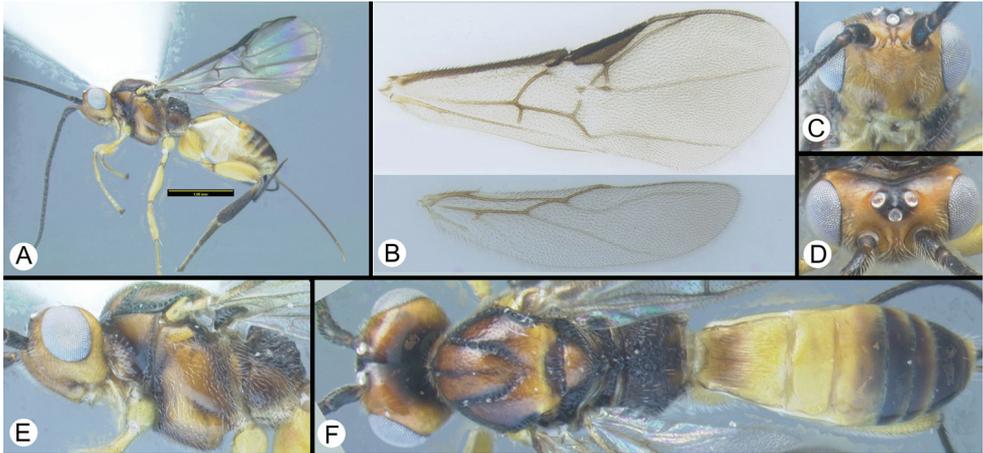
urn:lsid:zoobank.org:act:EC88E916-3270-4275-8333-362B0535B046

[http://species-id.net/wiki/Therophilus\\_boonthami](http://species-id.net/wiki/Therophilus_boonthami)

Figure 6

**Diagnosis.** Ocellar triangle melanic, contrasting with remainder of vertex, which is pale. Hind tibia mostly melanic, pale color restricted to extreme base.

**Description.** **Body length.** 3.3 mm.



**Figure 6.** *Therophilus boonthami* sp. n. **a** lateral habitus **b** Wings **c** anterodorsal head **d** dorsal head **e** lateral head and mesosoma **f** dorsal habitus.

**Head.** Space between antennal insertions with a weakly developed bulge that is weakly declivous posteriorly, dorsal surface of bulge with a shallow longitudinal groove. Number of flagellomeres 28. Posterior surface of scutellum posterior scutellar depression represented by two pits.

**Mesosoma.** Number of pegs on mid tibia = 5. Number of pegs on hind tibia = 9. Sclerite between metasoma and hind coxa narrow, and lacking a high ridge along its length. Length-width of hind femur  $0.755/0.31 = 2.4$ . 2nd submarginal cell large, cell height subequal to petiole length. Hind wing vein Cub emanates from near anterior apex of apical margin of subbasal cell, Cub long and weak. Notauli meeting but sculpture not extending outside of well-defined grooves.

**Metasoma.** MT1 length only slightly longer than apical width. MT1 with narrowly-spaced longitudinal striae, with some microsculpture between striae, and lacking two pairs of distinctly stronger striae (carinae). Ratio of widest point of MT1 to narrowest point  $0.481/0.338 = 1.4$ . Length-width ratio of MT1  $0.55/0.481 = 1.1$ . MT2 entirely smooth. Ovipositor clearly shorter than body, about as long as Metasoma.

**Color.** Mostly yellow or yellow-orange with some brown and black; head yellow or orange except antenna, vertex, and occiput brown; thorax yellow or orange and brown, darker near crenulae and sutures; propodeum mostly dark brown; fore and mid legs yellow; hind leg mostly yellow except most of tibia and tarsus melanic, hind tibial spurs yellow; metasoma mostly yellow; posterior terga mostly brown, MT1 with some weak melanic color on longitudinal striae; fore wing weakly infusate. Tegula yellow, contrasting with predominantly black mesoscutum, or yellow or orange, similar in color to predominantly orange or yellow mesoscutum. Ocellar triangle melanic, contrasting with remainder of vertex. Hind tibia mostly melanic, pale color, if present, restricted to extreme base. MT2 entirely or almost entirely pale.

**Etymology.** Named in honor of Mr. Tawatchai Boontham, collector for the TIGER project at Huay Namdung National Park.

**Molecular data.** H633, GenBank Accession: JQ929201.

**Distribution.** Distribution map can be found at <http://purl.org/thaimap/boonthami>

**Material examined.** Holotype ♀. H633 [QSBG] Thailand, Kaeng Krachan NP, km33/helipad, 735m, 12.836°N, 99.345°E, MT, 18–25.ii.2009. <http://purl.org/taxabank/T.boonthami>

***Therophilus chiangmaiensis* Sharkey sp. n.**

urn:lsid:zoobank.org:act:14069DD0-B68F-4D92-9058-3C20329DDAA7

[http://species-id.net/wiki/Therophilus\\_chiangmaiensis](http://species-id.net/wiki/Therophilus_chiangmaiensis)

Figure 7

**Diagnosis.** Hind tibia mostly melanic with pale coloration restricted to the medial surface at midlength. Wings relatively deeply infusate.

**Description. Body length.** 4.6 mm.

**Head.** Space between antennal insertions with a weakly developed bulge that is weakly declivous posteriorly, dorsal surface of bulge with a shallow longitudinal groove. Number of flagellomeres 28. Posterior surface of scutellum posterior scutellar depression represented by a deep sculptured semicircular pit.

**Mesosoma.** Number of pegs on mid tibia = 5. Number of pegs on hind tibia = 9. Sclerite between metasoma and hind coxa narrow with a high ridge along most or all of its length. Length-width of hind femur  $1.0/0.351 = 2.9$ . 2nd submarginal cell large, cell height subequal to petiole length. Hind wing vein Cub emanates from near anterior apex of apical margin of subbasal cell, Cub long and weak. Point of notauli intersection heavily sculptured over a wide area with a median longitudinal ridge. Metapleuron with white setae of moderate density.

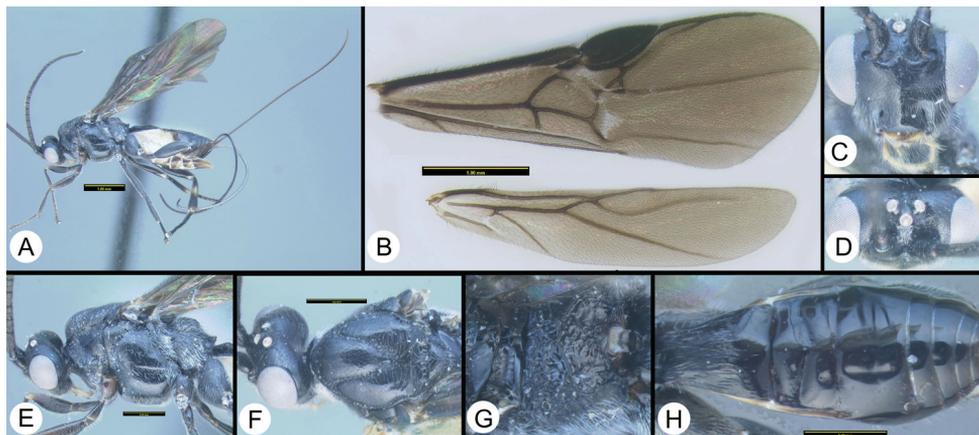
**Metasoma.** MT1 with narrowly-spaced, longitudinal striae, with some microsculpture between striae, and with and two pairs of slightly stronger striae (carinae). MT1 distinctly wider apically than basally. Ratio of widest point of MT1 to narrowest point  $0.6/0.357 = 1.7$ . Length-width ratio of MT1  $0.77/0.6 = 1.3$ . MT2 entirely smooth. Ovipositor much longer than metasoma, about as long as body or longer.

**Color.** Melanic except as follows: mouthparts mostly yellow; mid and hind tibial spurs yellow; hind tibia with a yellow patch medially at mid length; anterior metasomal laterotergites and sternites mostly pale yellow; fore wing infusate, more so than other species in this revision. Tegula black, concolorous with mesoscutum. Ocellar triangle melanic, concolorous with remainder of vertex. Hind tibia mostly melanic with pale coloration at midlength at least medially. MT2 entirely melanic.

**Etymology.** Named after the province in which the type specimen was collected.

**Molecular data.** H1853, GenBank Accession: JQ929190.

**Distribution.** Distribution map can be found at <http://purl.org/thaimaps/chiang-maiensis>.



**Figure 7.** *Therophilus chiangmaiensis* sp. n. **a** lateral habitus **b** Wings **c** anterodorsal head **d** dorsal head **e** lateral head and mesosoma **f** dorsal head and mesosoma **g** dorsal propodeum **h** dorsal Metasoma.

**Material examined.** Holotype ♀. 1853 [QSBG] Thailand, Chiang Mai, Doi Phahompok NP, Kiewlom1: Montane Forest, 20.0575°N, 99.1425°E, MT 7, 14.viii.2007. <http://purl.org/taxabank/T.chiangmaiensis>

***Therophilus cattienensis* van Achterberg & Long**

[http://species-id.net/wiki/Therophilus\\_cattienensis](http://species-id.net/wiki/Therophilus_cattienensis)

Figure 8

*Therophilus cattienensis* van Achterberg and Long 2010 [RMNH, type examined] Vietnam.

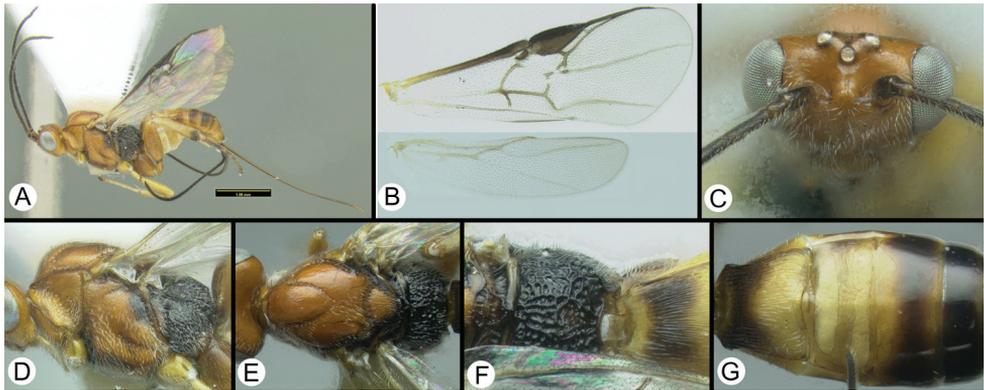
**Diagnosis.** Ocellar triangle pale, concolorous with remainder of vertex. Scape at least partly pale, especially anteriorly.

**Comments.** The Thai specimens differ from the holotype only in the color of the metapleuron which is yellow-brown in the type and melanic in all Thai specimens. This same variation is found in Vietnamese males described by van Achterberg and Long (2010).

**Molecular data.** H024, GenBank Accession: JQ929199; H050, GenBank Accession: JQ929198; H051, GenBank Accession: JQ929197; H059, GenBank Accession: JQ929196; H401, GenBank Accession, JQ929200.

**Distribution.** Distribution map can be found at <http://purl.org/thaimap/cattienensis>

**Material examined.** ♀. Thailand: Doi Inthanon NP: Vachirathan Fall, 700m, 18.539°N, 98.601°E, MT, 9–16.iii.2007: H0024; 16–23.iii.2007: H0051; 29.iv–6.v.2007: H0058, H0059. H058; Doi Inthanon NP: Kew Maepan Trail, 2200m, 18.553°N, 98.48°E, MT, 29.iv–6.v.2007: H0050. Namtok Mae Surin NP, 19.344°N, 97.988°E, MT, 4–11.v.2008: H0318, H0325, H0329, H0330, H0338, H2427, H2429, H2433, H0471; 19.344°N, 97.988°E, 27.iv–4.v.2008: H0401, H0482;



**Figure 8.** *Therophilus cattienensis* van Achterberg and Long **a** lateral habitus **b** Wings **c** anterodorsal head **d** lateral mesosoma **e** dorsal mesosoma **f** dorsal propodeum **g** MT1–MT4.

19.348°N, 97.985°E, 27.iv-4.v.2008: H0482; 18–25.v.2008: H0435; 19.3482°N, 97.9835°E, H3828, H5514. Doi Chiangdao NP, Headquarter, 19.4046°N, 98.9218°E, MT: H5533. Phu Ruea NP, Pah Lo Noy, 1343m, 17.508°N, 101.348°E, MT, 19–26. ix.2006: H5931, H5933. Khao Sok NP, Headquarter, 115m, 8.915°N, 98.53°E, MT, 25.xi–2.xii.2008: H0319. Chiang Mai Province, Pa Huay Kho, 20–30.vi.1997: H1120. Depository: H1120, H051, H3828, H059, H5533, H050, H024, H401, H5514, H325, H319, H338, H329, H318, H330, H058 [QSBG]; H5933, H5931, H482, H2429, H471, H435, H2427, H2433, H5535 [HIC]. <http://purl.org/taxabank/T.cattienensis>

### *Therophilus crenulisulcatus* van Achterberg & Long

[http://species-id.net/wiki/Therophilus\\_crenulisulcatus](http://species-id.net/wiki/Therophilus_crenulisulcatus)

Figure 9

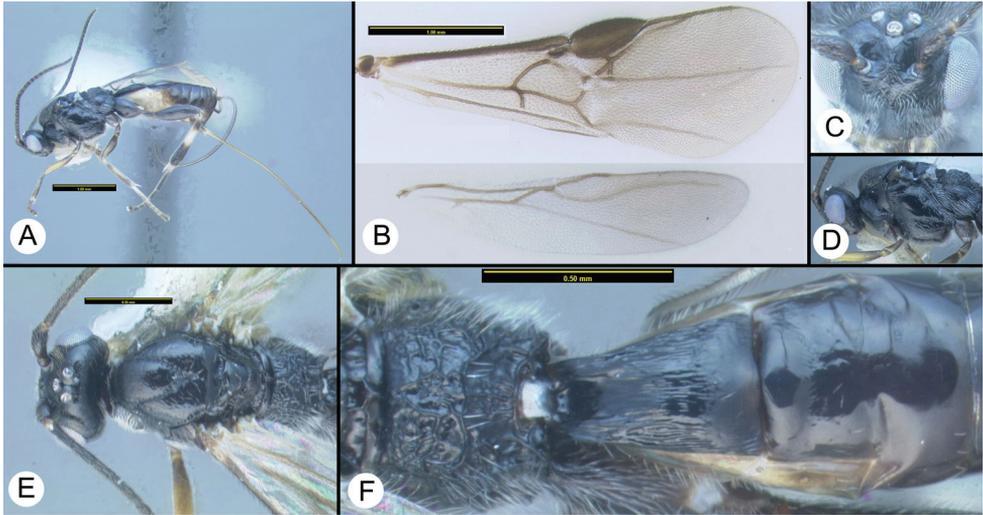
*Therophilus crenulisulcatus* van Achterberg and Long 2010 [RMNH, type examined]  
Vietnam.

**Diagnosis.** Tegula black, concolorous with mesoscutum. 2nd submarginal cell height subequal to petiole length. Hind tibia mostly pale, melanic apically and with a sub-basal melanic band or lateral spot. Pronotum entirely melanic. MT2 with weak short longitudinal striae restricted to transverse depression, or entirely smooth.

**Comments.** The Thai specimen has a slightly longer ovipositor, otherwise very similar to type.

**Distribution.** Distribution map can be found at <http://purl.org/thaimap/crenulisulcatus>

**Material examined.** ♀. 8481 [QSBG] Thailand, Doi Phahompok NP, Kiew-lom1: Montane Forest, 20.0575°N 99.1425°E, MT, 7-14.viii.2007. <http://purl.org/taxabank/T.crenulisulcatus>



**Figure 9.** *Therophilus crenulisulcatus* van Achterberg & Long **a** lateral habitus **b** Wings **c** anterodorsal head **d** lateral head and mesosoma **e** dorsal head and mesosoma **f** dorsal propodeum and MT1–3

***Therophilus kwanuiae* Sharkey sp. n.**

urn:lsid:zoobank.org:act:559CE2A4-FCE2-4EBA-A413-EF983FF0AC1B

[http://species-id.net/wiki/Therophilus\\_kwanuiae](http://species-id.net/wiki/Therophilus_kwanuiae)

Figure 10

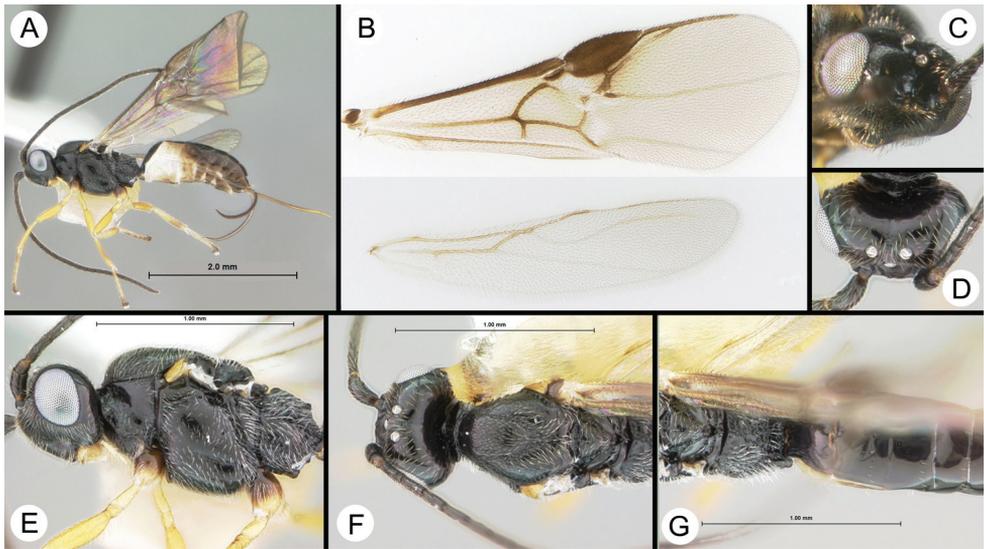
**Diagnosis.** 2nd submarginal cell reduced to a small dot, petiole longer than cell is high. Tegula black, concolorous with mesoscutum. Fore tarsus entirely pale.

**Description. Body length.** 3.8 mm.

**Head.** Space between antennal insertions with a weakly developed bulge that is weakly declivous posteriorly, dorsal surface of bulge with a shallow longitudinal groove. Number of flagellomeres 29. Posterior surface of scutellum posterior scutellar depression represented by several (2–3) pits.

**Mesosoma.** Number of pegs on mid tibia = 5. Number of pegs on hind tibia = 8. Sclerite between metasoma and hind coxa narrow with a high ridge along most or all of its length. Length-width of hind femur  $0.911/0.292 = 3.1$ . 2nd submarginal cell reduced to a small dot, petiole longer than cell is high. Hind wing vein Cub emanates from near anterior apex of apical margin of subbasal cell, Cub short and weak. Notauli meeting but sculpture not extending much outside of well-defined grooves.

**Metasoma.** MT1 length distinctly longer than apical width. MT1 with narrowly-spaced, longitudinal striae, with some microsculpture between striae, and with two pairs of slightly stronger striae (carinae). MT1 distinctly wider apically than ba-



**Figure 10.** *Therophilus kwanuiae* n. sp. **a** lateral habitus **b** wings **c** dorsolateral head **d** dorsal head **e** lateral head and mesosoma **f** dorsal head and mesosoma **g** dorsal propodeum and metasomal terga 1–3.

sally. Ratio of widest point of MT1 to narrowest point  $0.475/0.3 = 1.6$ . Length-width ratio of MT1  $0.695/0.475 = 1.5$ . MT2 entirely smooth. Ovipositor much longer than metasoma, about as long as body or longer.

**Color.** Mostly melanic except as follows: mouthparts yellow except galea melanic; fore and mid legs yellow except coxae, trochanters and base of femora melanic; hind tibia mostly pale, melanic in apical third with a pale, tan, lateral, spot near base; anterior metasomal laterotergites and sternites mostly pale yellow; fore wing weakly infusate. Tegula black, concolorous with mesoscutum. Ocellar triangle melanic, concolorous with remainder of vertex. Hind tibia mostly pale, melanic apically and with a subbasal melanic band or lateral spot, or mostly pale, melanic apically only. Fore tarsus mostly or entirely pale. MT2 entirely melanic.

**Etymology.** Named in honor of Ms. Boonruen Kwanui, collector for the TIGER project at Chae Son National Park

**Distribution.** Distribution map can be found at <http://purl.org/thaimap/kwanuiae>

**Material examined.** Holotype ♀. H927 [QSBG] Thailand, Huai Nam Dang NP, Visitor center, 19.313°N, 98.607°E, MT, 31.iii–7.iv.2008.

Paratype ♀. H5524 [QSBG] Thailand, Chiang Mai, Huai Nam Dang NP, Thung Buatong View Point, 19.2926°N, 98.6004°E, MT, 7–13.ii.2008 <http://purl.org/taxabank/T.kwanuiae>

***Therophilus planifrons* van Achterberg & Long**

[http://species-id.net/wiki/Therophilus\\_planifrons](http://species-id.net/wiki/Therophilus_planifrons)

Figure 11

*Therophilus planifrons* van Achterberg and Long 2010 [RMNH, type examined] Vietnam.

**Diagnosis.** Ovipositor clearly shorter than body, about as long as Metasoma. Hind tibia mostly pale, melanic apically and with a subbasal melanic band or lateral spot.

**Molecular data.** H235, GenBank Accession: JQ929182.

**Distribution.** Distribution map can be found at <http://purl.org/thaimap/planifrons>

**Material examined.** ♀. H235 [QSBG] Thailand, Huai Nam Dang NP, behind visitor house, 1670m, 19.312°N, 98.607°E, MT, 31.vii–7.viii.2007. <http://purl.org/taxabank/T.planifrons>

***Therophilus songrani* Sharkey sp. n.**

urn:lsid:zoobank.org:act:10BACCAA-3356-4484-B8AA-138F5BA8D516

[http://species-id.net/wiki/Therophilus\\_songrani](http://species-id.net/wiki/Therophilus_songrani)

Figure 12

**Diagnosis.** Ocellar triangle pale, concolorous with remainder of vertex. Tegula yellow or orange, similar in color to predominantly orange or yellow mesoscutum. MT1 distinctly longer than apical width.

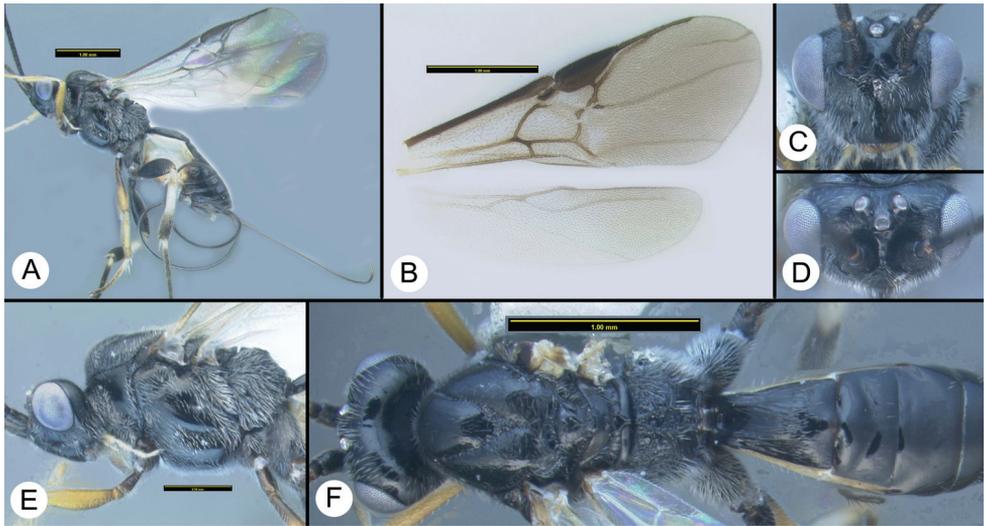
**Description. Body length.** 3.5 mm.

**Head.** Space between antennal insertions with a weakly developed bulge that is weakly declivous posteriorly, dorsal surface of bulge with a shallow longitudinal groove. Number of flagellomeres 29. Posterior surface of scutellum posterior scutellar depression represented by two pits.

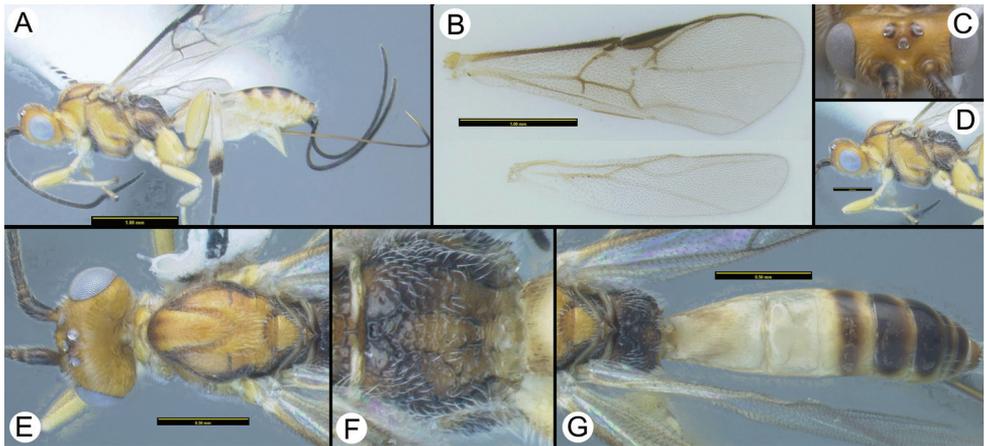
**Mesosoma.** Number of pegs on mid tibia = 6. Number of pegs on hind tibia = 10. Sclerite between metasoma and hind coxa narrow, and lacking a high ridge along its length. Length-width of hind femur  $0.750/0.265 = 2.8$ . 2nd submarginal cell large, cell height subequal to petiole length. Hind wing vein Cub emanates from near anterior apex of apical margin of subbasal cell, Cub long and weak. Notauli barely meeting and sculpture not extending past meeting point.

**Metasoma.** MT1 length distinctly longer than apical width. MT1 with narrowly-spaced longitudinal striae, with some microsculpture between striae, and lacking two pairs of distinctly stronger striae (carinae). MT1 distinctly wider apically than basally. Ratio of widest point of MT1 to narrowest point  $0.367/0.264 = 1.5$ . Length-width ratio of MT1  $0.54/0.387 = 1.4$ . MT2 with transverse and/or diagonal striae in and/or near transverse depression. Ovipositor much longer than metasoma, about as long as body or longer.

**Color.** Yellow or yellow-orange except as follows: antenna melanic; thorax with melanic infusions along crenulae and sutures; propodeum mostly melanic; MT3–MT7



**Figure 11.** *Therophilus planifrons* van Achterberg & Long. **a** lateral habitus **b** Wings **c** dorsolateral head **d** dorsal head **e** lateral head and mesosoma **f** dorsal head and mesosoma **g** dorsal propodeum and MT1–MT3.



**Figure 12.** *Therophilus songrani* sp. n. **a** lateral habitus **b** Wings **c** dorsal head **d** lateral head and mesosoma **e** dorsal head and mesosoma **f** dorsal propodeum **g** dorsal propodeum and Metasoma.

mostly brown; Wings hyaline. Scape entirely melanic. Tegula yellow or orange, similar in color to predominantly orange or yellow mesoscutum. Ocellar triangle pale, concolorous with remainder of vertex. Hind tibia mostly pale, melanic apically only. MT2 entirely or almost entirely pale.

**Etymology.** Named in honor of Mr. Songran Chaksu, collector for the TIGER project at Doi Chiangdao Wildlife Sanctuary.

**Molecular data.** H352, GenBank Accession: JQ929192.

**Distribution.** Distribution map can be found at <http://purl.org/thaimap/songrani>

**Material examined.** Holotype ♀. H352 [QSBG] Thailand, Queen Sirikit Botanic Garden, 811m, 18.881°N, 98.862°E, MT, 30.iv–12.v.2009. <http://purl.org/taxabank/T.songrani>

***Therophilus sukpengae* Sharkey sp. n.**

urn:lsid:zoobank.org:act:F2A17DCC-B414-44FB-80B8-5B1360C28707

[http://species-id.net/wiki/Therophilus\\_sukpengae](http://species-id.net/wiki/Therophilus_sukpengae)

Figure 13

**Diagnosis.** MT2 smooth in most of anterior half anterior transverse groove, longitudinally striate in transverse groove and area posterior transverse groove, at least medially. Tegula black, concolorous with mesoscutum.

**Description. Body length.** 3.9 mm.

**Head.** Space between antennal insertions with a weakly developed bulge that is weakly declivous posteriorly, dorsal surface of bulge with a shallow longitudinal groove. Number of flagellomeres 27. Posterior surface of scutellum posterior scutellar depression represented by two pits.

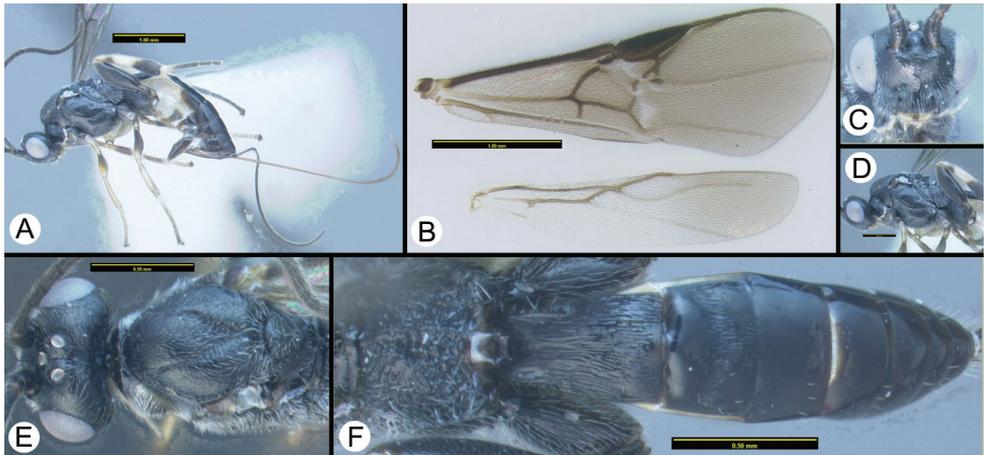
**Mesosoma.** Number of pegs on mid tibia = 4. Number of pegs on hind tibia = 9. Sclerite between metasoma and hind coxa narrow with a high ridge along most or all of its length. Length-width of hind femur  $0.8/0.266 = 3.0$ . 2nd submarginal cell large, cell height subequal to petiole length. Hind wing vein Cub emanates from near anterior apex of apical margin of subbasal cell, Cub long and weak. Point of notauli intersection heavily sculptured over a wide area.

**Metasoma.** MT1 length distinctly longer than apical width. MT1 with narrowly-spaced longitudinal striae, with some microsculpture between striae, and lacking one pair of distinctly stronger striae (carinae). MT1 distinctly wider apically than basally. Ratio of widest point of MT1 to narrowest point  $0.383/0.263 = 1.5$ . Length-width ratio of MT1  $0.61/0.383 = 1.6$ . MT2 smooth in most of anterior half anterior transverse groove, longitudinally striate in transverse groove and area posterior transverse groove, at least medially. Ovipositor much longer than metasoma, about as long as body or longer.

**Color.** Body mostly melanic, legs mostly pale; body melanic except as follows: mouthparts yellow, tegula brown, fore and mid legs mostly yellow except coxae melanic, basal half of femora brown and apex of tibiae and some tarsomeres light brown, hind tibia mostly pale except apex and a light brown subbasal lateral spot, all tibial spurs yellow; anterior metasomal laterotergites and sternites pale yellow; fore wing weakly infuscate. Tegula black, concolorous with mesoscutum. Ocellar triangle melanic, concolorous with remainder of vertex. Hind tibia mostly pale, melanic apically and with a subbasal melanic band or lateral spot. Pronotum entirely melanic. MT2 entirely melanic.

**Etymology.** Named in honor of Ms. Acharaporn Sukpeng collector for the TIGER project at Chae Son National Park.

**Distribution.** Distribution map can be found at <http://purl.org/thaimap/sukpengae>



**Figure 13.** *Therophilus sukpengae* sp. n. **a** lateral habitus **b** Wings **c** anterior head **d** lateral head and mesosoma **e** dorsal head and mesosoma **f** dorsal propodeum and Metasoma.

**Material examined.** Holotype ♀. H998 [QSBG] Thailand Pu Toei NP, Protection unit2/Pu Krathing, 220m, 14.803°N, 99.416°E, MT, 1–7.v.2009. <http://purl.org/taxabank/T.sukpengae>

***Therophilus wannai* Sharkey sp. n.**

urn:lsid:zoobank.org:act:8E959BFE-D614-4100-8123-89A95E0FF0B1

[http://species-id.net/wiki/Therophilus\\_wannai](http://species-id.net/wiki/Therophilus_wannai)

Figure 14

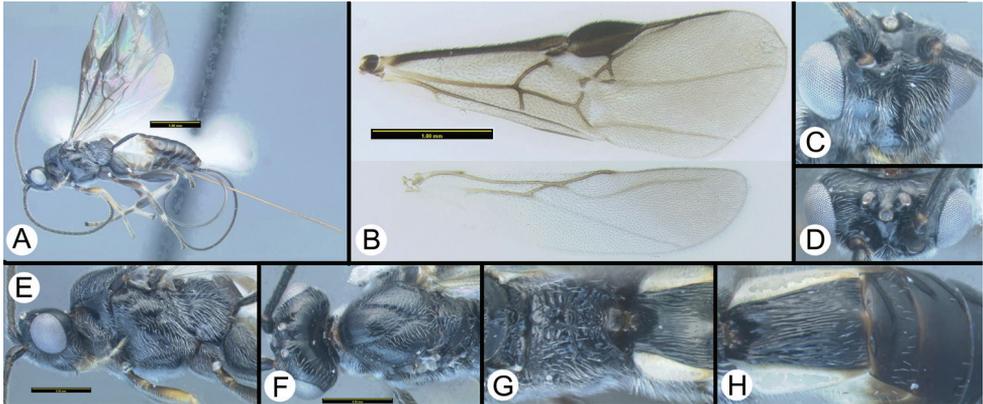
**Diagnosis.** MT2 with short longitudinal striae restricted to transverse depression. Mid femur mostly melanic, pale apically. Fore tarsus mostly pale, melanic basally. Pronotum mostly melanic but with a pale spot dorsomedially.

**Description. Body length.** 3.8 mm.

**Head.** Space between antennal insertions with a weakly developed bulge that is weakly declivous posteriorly, dorsal surface of bulge with a shallow longitudinal groove. Number of flagellomeres 28. Posterior surface of scutellum posterior scutellar depression represented by several pits forming a semicircular area.

**Mesosoma.** Number of pegs on mid tibia = 6. Number of pegs on hind tibia = 8. Sclerite between metasoma and hind coxa narrow with a high ridge along most or all of its length. Length-width of hind femur  $0.823/0.256 = 3.2$ . 2nd submarginal cell large, cell height subequal to petiole length. Hind wing vein Cub emanates from near anterior apex of apical margin of subbasal cell, Cub short and weak. Notauli extending past meeting point but sculpture not extending over a wide area.

**Metasoma.** MT1 length distinctly longer than apical width. MT1 with narrowly-spaced longitudinal striae, with some microsculpture between striae, and lacking two



**Figure 14.** *Therophilus wannai* sp. n. **a** lateral habitus **b** Wings **c** anterior head **d** dorsal head **e** lateral head and mesosoma **f** dorsal head and mesosoma **g** dorsal propodeum **h** dorsal MT1–MT3.

pairs of distinctly stronger striae (carinae). MT1 distinctly wider apically than basally. Ratio of widest point of MT1 to narrowest point  $0.437/0.281 = 1.6$ . Length-width ratio of MT1  $0.702/0.437 = 1.6$ . MT2 with short longitudinal striae restricted to transverse depression. Ovipositor much longer than metasoma, about as long as body or longer.

**Color.** Melanic except as follows: mouthparts mostly yellow; fore and mid femora and tibiae yellow-brown, mid leg noticeably darker than fore leg; hind tibia yellow at mid length and basally, melanic apically and subbasally; anterior metasomal laterotergites and sternites pale yellow; fore wing weakly infusate. Tegula black, concolorous with mesoscutum. Ocellar triangle melanic, concolorous with remainder of vertex. Hind tibia mostly pale, melanic apically and with a subbasal melanic band or lateral spot. Fore tarsus mostly or entirely pale. Pronotum mostly melanic but pale dorsomedially. MT2 entirely melanic.

**Etymology.** Named in honor of Mr. Charoen Wanna, collector for the TIGER project at Doi Phuka National Park.

**Distribution.** Distribution map can be found at <http://purl.org/thaimap/wannai>

**Material examined.** Holotype ♀. H345 [QSBG] Thailand Doi Phu Kha NP, Office 11, 1359m, 19.208°N, 101.081°E, MT, 15–22.xi.2007. <http://purl.org/taxabank/T.wannai>

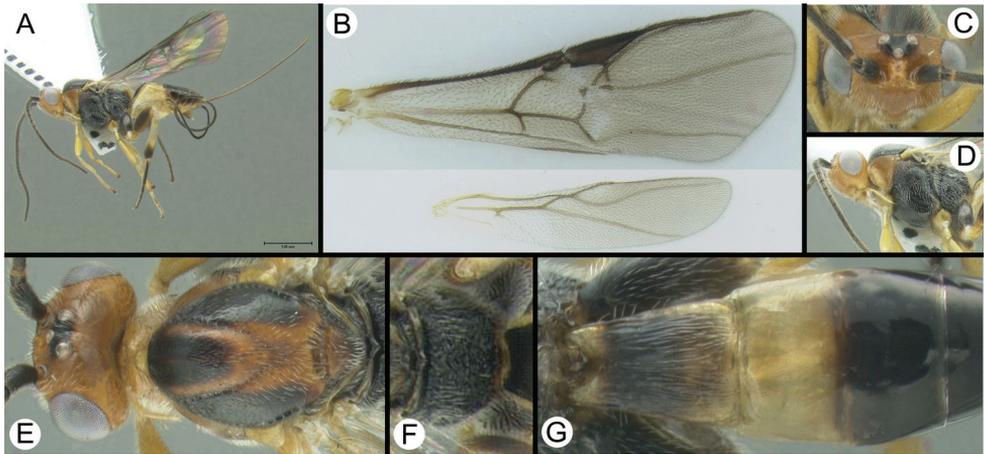
***Therophilus wongchaii* Sharkey sp. n.**

urn:lsid:zoobank.org:act:727FD2FF-CCCD-4090-930D-7DF23FDF71BB

[http://species-id.net/wiki/Therophilus\\_wongchaii](http://species-id.net/wiki/Therophilus_wongchaii)

Figure 15

**Diagnosis.** Ocellar triangle melanic, contrasting with remainder of vertex, or pale, concolorous with remainder of vertex. Tegula yellow, contrasting with black lateral



**Figure 15.** *Therophilus wongchaiti* sp. n. **a** lateral habitus **b** Wings **c** anterodorsal head **d** later head and mesosoma **e** dorsal head and mesosoma **f** dorsal propodeum **g** dorsal MT1–MT3.

lobes of mesoscutum. Hind tibia largely pale, melanic apically and with a subbasal melanic band or lateral spot, or mostly pale, melanic apically only.

**Description.** **Body length.** 3.5 mm.

**Head.** Space between antennal insertions with a weakly developed bulge that is weakly declivous posteriorly, dorsal surface of bulge with a shallow longitudinal groove. Number of flagellomeres 29. Posterior surface of scutellum posterior scutellar depression represented by two pits.

**Mesosoma.** Number of pegs on mid tibia = 5. Number of pegs on hind tibia = 9. Sclerite between metasoma and hind coxa narrow, and lacking a high ridge along its length. Length-width of hind femur  $0.850/0.298 = 2.9$ . 2nd submarginal cell large, cell height subequal to petiole length. Hind wing vein Cub emanates from near anterior apex of apical margin of subbasal cell, Cub long and weak. Notauli extending past meeting point but sculpture not extending over a wide area.

**Metasoma.** MT1 length distinctly longer than apical width. MT1 with narrowly-spaced longitudinal striae, with some microsculpture between striae, and lacking two pairs of distinctly stronger striae (carinae). MT1 not distinctly wider apically than basally. Ratio of widest point of MT1 to narrowest point  $0.4/0.311 = 1.3$ . Length-width ratio of MT1  $0.642/0.4 = 1.6$ . MT2 with transverse and/or diagonal striae in and/or near transverse depression. Ovipositor much longer than metasoma, about as long as body or longer.

**Color.** Orange, yellow, black, and brown; head mostly orange, ocellar triangle melanic; antenna melanic; mesoscutum mostly pale medially, melanic laterally; prothorax yellow; meso and metapleuron and propodeum melanic; fore and mid legs yellow; hind leg brown except trochanter and most of tibia yellow; metasomal mediotergites mostly melanic except base of MT1 and all of MT2 yellow; anterior metasomal laterotergites and sternites pale yellow, remainder of metasoma melanic; fore wing weakly

infusate. Scape entirely melanic. Tegula yellow, contrasting with predominantly black mesoscutum. Ocellar triangle melanic, contrasting with remainder of vertex, or pale, concolorous with remainder of vertex. Hind tibia mostly pale, melanic apically and with a subbasal melanic band or lateral spot, or mostly pale, melanic apically only. Fore tarsus mostly or entirely pale. MT2 entirely melanic, or pale in anterior half, melanic posteriorly, or entirely or almost entirely pale.

**Etymology.** Named in honor of Mr. Prasit Wongchai, collector for the TIGER project at Doi Phahompok National Park.

**Molecular data.** H314, GenBank Accession: JQ929194; H977, GenBank Accession: JQ929195; H661, GenBank Accession: JQ929193.

**Distribution.** Distribution map can be found at <http://purl.org/thaimap/wongchaii>

**Material examined.** Holotype ♀. H314 [QSBG] Thailand, Kaeng Krachan NP, km33/helipad, 735m, 12.836°N, 99.345°E, MT, 7–14.xi.2008.

Paratypes ♀. Thailand: Kaeng Krachan NP: km33/helipad, 735m, 12.836°N, 99.345°E, MT, 11–18.v.2009: H977; 24.iv–4.v.2009: H661; 17–24.iv.2009: H476; 17–24.iv.2009: H476; 4–11.v.2009: H565, H563; 31.x–7.xi.2008: H604; Pa La-U/waterfall/car park1, 12.536°N, 99.4722°E, pan trap, 2–3.v.2009: H303; 12.536°N, 99.468°E, MT, 4–11.xii.2008: H2439; Panernthung/km30 old lavatory, 970m, 12.825°N, 99.365°E, MT, 11–18.vii.2008: H2404. Depository: H977, H661, H476, H565, H604, [QSBG]; H303, H563, H2439, H2404 [HIC].

<http://purl.org/taxabank/T.wongchaii>

### *Therophilus wongwani* Sharkey sp. n.

urn:lsid:zoobank.org:act:0494CCB9-5FB4-43E1-B807-7E434F43761B

[http://species-id.net/wiki/Therophilus\\_wongwani](http://species-id.net/wiki/Therophilus_wongwani)

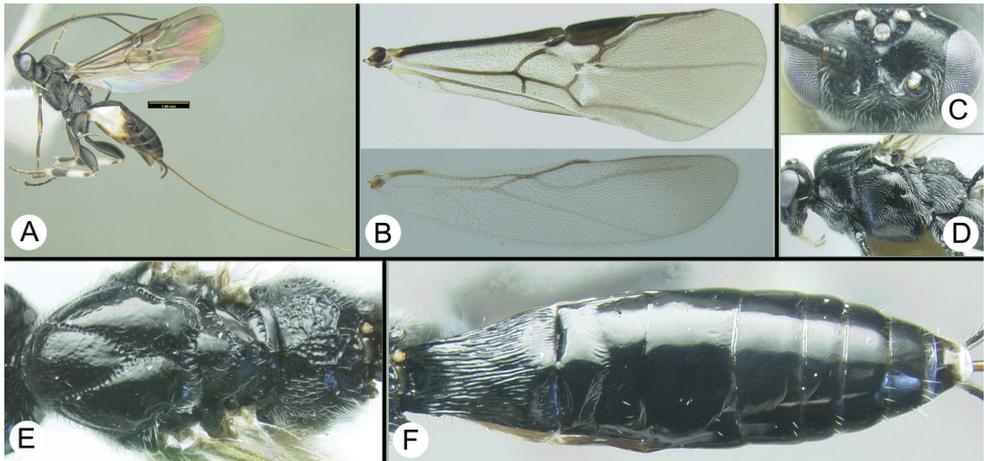
Figure 16

**Diagnosis.** 2nd submarginal cell reduced to a small dot, petiole longer than cell is high. Tegula black, concolorous with mesoscutum. Fore tarsus mostly melanic with some pale color apically. Exposed portion of ovipositor distinctly longer than body.

**Description. Body length.** 4.4 mm.

**Head.** Space between antennal insertions with a weakly developed bulge that is weakly declivous posteriorly, dorsal surface of bulge with a shallow longitudinal groove. Number of flagellomeres 27. Posterior surface of scutellum completely rugose, posterior scutellar depression not distinct.

**Mesosoma.** Number of pegs on mid tibia = 8. Number of pegs on hind tibia = 11. Sclerite between metasoma and hind coxa narrow with a high ridge along most or all of its length. Length-width of hind femur  $0.854/0.263 = 3.3$ . 2nd submarginal cell reduced to a small dot, petiole longer than cell is high. Hind wing vein Cub emanates from near mid length of apical margin of subbasal cell, Cub long and strong. Notauli extending past meeting point but sculpture not extending over a wide area.



**Figure 16.** *Therophilus wongwani* sp. n. **a** lateral habitus **b** Wings **c** anterodorsal head **d** lateral head and mesosoma **e** dorsal mesosoma and propodeum **f** dorsal Metasoma.

**Metasoma.** MT1 length distinctly longer than apical width. MT1 with narrowly-spaced longitudinal striae, with some microsculpture between striae, and lacking two pairs of distinctly stronger striae (carinae). MT1 distinctly wider apically than basally. Ratio of widest point of MT1 to narrowest point  $0.533/0.290 = 1.8$ . Length-width ratio of MT1  $0.717/0.533 = 1.4$ . MT2 with short longitudinal striae restricted to transverse depression. Ovipositor much longer than metasoma, about as long as body or longer. Ovipositor length exposed portion of ovipositor distinctly longer than body.

**Color.** Black except as follows; mouthparts mostly yellow; hind tibia pale yellow except black at apex and subapically; anterior metasomal laterotergites and sternites pale yellow; fore wing weakly infuscate. Tegula black, concolorous with mesoscutum. Ocellar triangle melanic, concolorous with remainder of vertex. Hind tibia mostly pale, melanic apically and with a subbasal melanic band or lateral spot. Fore tarsus mostly or entirely melanic. MT2 entirely melanic.

**Etymology.** Named in honor of Mr. Nikom Wongwan, collector for the TIGER project at Doi Phuka National Park.

**Molecular data.** H028, GenBank Accession: JQ29188; H029, GenBank Accession: HQ929189; H047, GenBank: JQ929186; H048, GenBank Accession: JQ929187; H066, GenBank Accession: JQ929185; H1854, GenBank Accession: JQ929191.

**Distribution.** Distribution map can be found at <http://purl.org/thaimap/wongwani>

**Material examined.** Holotype ♀. H028 [QSBG] Thailand, Doi Inthanon NP, Summit marsh, 2500m, 18.589°N, 98.486°E, MT, 23.iii–1.v.2007.

Paratypes ♀. Doi Inthanon NP, Summit marsh, 2500m, 18.589°N 98.486°E, MT, 8-15.v.2007: H5925, H5926, H5929, H8479, H8480, H066; 23.iii-1.v.2007:

H029; 17-24.xi.2006: H048; 22-29.iv.2007: H047; 1-8.xii.2006: H285; 5-12.i.2007: H5934; 2-10.xi.2006: H1854; Doi Chiangdao NP, water reservoir, 549m, 19.407°N 98.921°E, MT, 18-25.ix.2007: H978, H5510; Doi Phahompok NP, Kiewlom2/ Montane Forest 20.0571°N 99.1425°E: H3803. Depository: H5926, H066, H048, H5510, H285, H5929, H5934 [QSBG]; H029, H5925, H8480, H8479, H978, H1854, H047, H3803 [HIC] <http://purl.org/taxabank/T.wongwani>

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## Appendix 1

DELTA data matrix, images, and other files to the dichotomous key for *Therophilus* s.s. (Hymenoptera: Braconidae: Agathidinae) from Thailand. doi: 10.3897/JHR.27.2832.app1

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**Citation:** Sharkey MJ, Stoelb SAC (2012) Revision of *Therophilus* s.s. (Hymenoptera, Braconidae, Agathidinae) from Thailand. *Journal of Hymenoptera Research* 27: 1–36. doi: 10.3897/JHR.27.2832.app1

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## Appendix 2

DELTA data matrix, images, and other files to species descriptions for *Therophilus* s.s. (Hymenoptera, Braconidae, Agathidinae) from Thailand. doi: 10.3897/JHR.27.2832.app2

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**Citation:** Sharkey MJ, Stoelb SAC (2012) Revision of *Therophilus* s.s. (Hymenoptera, Braconidae, Agathidinae) from Thailand. *Journal of Hymenoptera Research* 27: 1–36. doi: 10.3897/JHR.27.2832.app2

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### Appendix 3

Interactive key, in IntKey format, to *Therophilus* s.s. (Hymenoptera, Braconidae, Agathidinae) from Thailand. doi: 10.3897/JHR.27.2832.app3

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

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

More details on how to use Intkey efficiently are found at [http://florabase.calm.wa.gov.au/help/keys/intkey\\_tutorial.pdf](http://florabase.calm.wa.gov.au/help/keys/intkey_tutorial.pdf)

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**Citation:** Sharkey MJ, Stoelb SAC (2012) Revision of *Therophilus* s.s. (Hymenoptera, Braconidae, Agathidinae) from Thailand. *Journal of Hymenoptera Research* 27: 1–36. doi: 10.3897/JHR.27.2832.app3

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### Appendix 4

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

Term	URI
abscissa	<a href="http://purl.obolibrary.org/obo/HAO_0000076">http://purl.obolibrary.org/obo/HAO_0000076</a>
anatomical structures	<a href="http://purl.obolibrary.org/obo/HAO_0000003">http://purl.obolibrary.org/obo/HAO_0000003</a>
angle	<a href="http://purl.obolibrary.org/obo/HAO_0000285">http://purl.obolibrary.org/obo/HAO_0000285</a>
antenna	<a href="http://purl.obolibrary.org/obo/HAO_0000101">http://purl.obolibrary.org/obo/HAO_0000101</a>
antennal insertions	<a href="http://purl.obolibrary.org/obo/HAO_0001022">http://purl.obolibrary.org/obo/HAO_0001022</a>
antennomere	<a href="http://purl.obolibrary.org/obo/HAO_0000107">http://purl.obolibrary.org/obo/HAO_0000107</a>
area	<a href="http://purl.obolibrary.org/obo/HAO_0000146">http://purl.obolibrary.org/obo/HAO_0000146</a>
band	<a href="http://purl.obolibrary.org/obo/HAO_0000163">http://purl.obolibrary.org/obo/HAO_0000163</a>
basal lobe	<a href="http://purl.obolibrary.org/obo/HAO_0001219">http://purl.obolibrary.org/obo/HAO_0001219</a>
body	<a href="http://purl.obolibrary.org/obo/HAO_0000182">http://purl.obolibrary.org/obo/HAO_0000182</a>
carina	<a href="http://purl.obolibrary.org/obo/HAO_0000188">http://purl.obolibrary.org/obo/HAO_0000188</a>
cell	<a href="http://purl.obolibrary.org/obo/HAO_0001091">http://purl.obolibrary.org/obo/HAO_0001091</a>

Term	URI
costa	<a href="http://purl.obolibrary.org/obo/HAO_0000225">http://purl.obolibrary.org/obo/HAO_0000225</a>
coxa, coxae	<a href="http://purl.obolibrary.org/obo/HAO_0000228">http://purl.obolibrary.org/obo/HAO_0000228</a>
coxal cavities	<a href="http://purl.obolibrary.org/obo/HAO_0000229">http://purl.obolibrary.org/obo/HAO_0000229</a>
crossveins	<a href="http://purl.obolibrary.org/obo/HAO_0000236">http://purl.obolibrary.org/obo/HAO_0000236</a>
cubitus	<a href="http://purl.obolibrary.org/obo/HAO_0000237">http://purl.obolibrary.org/obo/HAO_0000237</a>
depression	<a href="http://purl.obolibrary.org/obo/HAO_0000241">http://purl.obolibrary.org/obo/HAO_0000241</a>
eye	<a href="http://purl.obolibrary.org/obo/HAO_0000217">http://purl.obolibrary.org/obo/HAO_0000217</a>
femur	<a href="http://purl.obolibrary.org/obo/HAO_0000327">http://purl.obolibrary.org/obo/HAO_0000327</a>
flagellomeres	<a href="http://purl.obolibrary.org/obo/HAO_0000342">http://purl.obolibrary.org/obo/HAO_0000342</a>
flange	<a href="http://purl.obolibrary.org/obo/HAO_0000344">http://purl.obolibrary.org/obo/HAO_0000344</a>
metasomal foramen	<a href="http://purl.obolibrary.org/obo/HAO_0000865">http://purl.obolibrary.org/obo/HAO_0000865</a>
fore leg	<a href="http://purl.obolibrary.org/obo/HAO_0000349">http://purl.obolibrary.org/obo/HAO_0000349</a>
fore tarsus	<a href="http://purl.obolibrary.org/obo/HAO_0001125">http://purl.obolibrary.org/obo/HAO_0001125</a>
fore tibia	<a href="http://purl.obolibrary.org/obo/HAO_0000350">http://purl.obolibrary.org/obo/HAO_0000350</a>
fore wing	<a href="http://purl.obolibrary.org/obo/HAO_0000351">http://purl.obolibrary.org/obo/HAO_0000351</a>
frons	<a href="http://purl.obolibrary.org/obo/HAO_0001044">http://purl.obolibrary.org/obo/HAO_0001044</a>
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# A new genus and species of Anomaloninae (Hymenoptera, Ichneumonidae) from China

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† [urn:lsid:zoobank.org:author:3C0EBDB7-26F7-469B-8DB1-5C7B1C6D9B89](https://doi.org/urn:lsid:zoobank.org:author:3C0EBDB7-26F7-469B-8DB1-5C7B1C6D9B89)

‡ [urn:lsid:zoobank.org:author:61913B06-359F-4681-A889-F98613B6A5AF](https://doi.org/urn:lsid:zoobank.org:author:61913B06-359F-4681-A889-F98613B6A5AF)

§ [urn:lsid:zoobank.org:author:974C0354-6118-4EA9-890F-EF5ECE8F257A](https://doi.org/urn:lsid:zoobank.org:author:974C0354-6118-4EA9-890F-EF5ECE8F257A)

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## Abstract

*Elaticarina* Sheng, **gen. n.** and *Elaticarina recava* Sheng, **sp.n.**, belonging to the tribe Gravenhorstiini of subfamily Anomaloninae (Hymenoptera, Ichneumonidae), collected in Jiangxi Province, China, are described. The new genus is placed within existing keys to genera.

## Keywords

Gravenhorstiini, new genus, new species, taxonomy, China

## Introduction

Townes (1971), in his generic revision of the Ichneumonidae, treated the Anomaloninae as comprising four tribes, Anomalonini, Gravenhorstiini, Podogastrini and Theriini. Gauld (1976), in his generic revision, combined the four tribes of Townes (1971) into two, Therionini (= Gravenhorstiini) and Anomalonini. Dasch (1984) subdivided the Anomaloninae into two subfamilies, the Anomaloninae (= tribe Anomalonini *sensu* Gauld, 1976) and the Theriinae (= tribe Therionini *sensu*

Gauld, 1976). Two tribes of Anomaloninae, Gravenhorstiini and Anomalonini were accepted by Gauld et al. (1997). In this paper, the suggestions of Gauld et al. (1997) and Yu et al. (2005) are followed.

The tribe Gravenhorstiini comprises 41 genera (Yu et al. 2005), of which thirteen genera of Gravenhorstiini have been reported in China (Yu et al. 2005; Sheng and Sun 2009). The status of the genera and tribes were elucidated by Townes (1971) and Gauld (1976).

In the last four years the authors have been exploring in six National Natural Reserves: Wuyishan, Lushan, Matoushan, Jiulianshan, Guanshan and Jinggangshan, and mountains in Quannan County in Jiangxi Province, situated in the northern border of the Oriental part of China. New discoveries have been reported (Sheng and Sun 2009; Sheng and Sun 2010a, b; Sheng and Broad 2011; Sheng and Sun 2011; Sheng et al. 2012). Large numbers of anomalonines have been collected there and will be reported successively.

One species, collected in Matoushan National Natural Reserve, Zixi County, and Wuyishan National Natural Reserve, Yanshan County, Jiangxi Province, China, is distinct within the existing phylogenetic framework for the tribe Gravenhorstiini because of its unique combination of characters. For example: apical margin of clypeus evenly convex, without a tooth; lower end of occipital carina joining hypostomal carina distinctly above base of mandible; lower anterior margin of pronotum (Figure 7) symmetrical, rounded, without a tooth or angulation; tarsal claws simple, or fore and middle claws indistinctly pectinate at extreme base; fore wing (Figure 8) vein 2rs-m far distal to 2m-cu, distance between them approximately as long as 2rs-m; fore wing vein 1-Cu (Figure 8) approximately 0.5 times as long as 1m-cu+2-Rs+M; middle tibia with two spurs; epipleuron of tergum 3 not separated by a crease; ovipositor sheath approximately 0.5 times as long as apical depth of metasoma.

This species also exhibits some distinctive autapomorphic characters which are not found in any described genus of the Gravenhorstiini. For example: upper margin of face (Figure 2) extending upwards and partly covering antennal sockets; lower portion of occipital carina (Figure 3) widely and flakily expanded; frons (Figure 4) divided into two portions. Accordingly, based on this combination of character states that preclude the placement of this species in a described genus, we believe this is indeed a previously undescribed genus.

## Materials and methods

Specimens were collected using entomological nets in the forests of Matoushan National Natural Reserve, Zixi County and Wuyishan National Natural Reserve, Yanshan County, Jiangxi Province (CHINA). The forest of Matoushan National Natural Reserve composed of mixed deciduous angiosperms and evergreen conifers, mainly including *Castanea* spp., *Castanopsis fabri* Hance, *Cinnamomum* spp., *Quercus* spp., *Pinus massoniana* (Lamb.). The forest of Wuyishan National Natural Reserve composed of mixed deciduous angiosperms and evergreen conifers, mainly including *Castanea* spp., *Cinnamomum* spp., *Dalbergia hupeana* Hance, *Machilus* spp., *Quercus* spp., *Pinus massoniana* (Lamb.) and Bamboos.

Images of whole bodies were taken using a CANON Power Shot A650 IS. Other images were taken using a Cool SNAP 3CCD attached to a Zeiss Discovery V8 Stereomicroscope and captured with QCapture Pro version 5.1.

The morphological terminology is mostly that of Gauld (1991). Wing vein nomenclature is based on Ross (1936) and the terminology on Mason (1986, 1990).

Type specimens are deposited in the Insect Museum, General Station of Forest Pest Management, State Forestry Administration, People's Republic of China.

## Taxonomy

### *Elaticarina* Sheng, gen. n.

urn:lsid:zoobank.org:act:C6F98C70-C9EE-43B0-AC94-CE4AD5B7C7AF

<http://species-id.net/wiki/Elaticarina>

**Type species.** *Elaticarina recava* Sheng, sp.n.

**Etymology.** The name of the new genus is based on the lower portion of the occipital carina being remarkably wide. The gender is feminine.

**Description.** Fore wing length about 10 to 11 mm. Eye without pubescence, inner margins of eyes distinctly convergent ventrally. Upper margin of face straight, extending upwardly and covering partly over antennal socket. Apical margin of clypeus extending forward and slightly turnup (Figure 2), without a tooth. Upper tooth of mandible distinctly longer than lower tooth. Malar space about 0.5 to 0.6 times as long as basal width of mandible. Frons (Figure 4) divided into two portions: upper portion flat, lower margin with a transverse ridge; lower portion deeply and almost vertically sunken, with a median longitudinal carina. Median portion of flagellum slightly thick. Occipital carina complete, lower portion widely and flakily expanding (Figure 3), lower end joining hypostomal carina distinctly above base of mandible. Lower anterior margin of pronotum (Figure 7) symmetrical, without a tooth or angulation. Epomia indistinct. Mesoscutum evenly convex. Notaulus weak, reaching to subposterior margin of mesoscutum. Scutellum with dorsal profile and hind oblique profile; dorsal profile flat or slightly convex; lateral carina reaching apex. Epicnemial carina almost reaching to mid-height of front margin of mesopleuron, distant from front margin. Fore wing vein (Figure 8) 1cu-a distal of 1/M, distance between them 0.6 to 0.7 times as long as 1cu-a. 2rs-m far distal of 2m-cu, distance between them approximately as long as 2rs-m. 1-Cu approximately 0.5 times as long as 1m-cu+2-Rs+M (distance between 1-Cu and 2m-cu). Hind wing vein 1-cu approximately 0.6 to 0.7 times as long as cu-a; cu-a strongly reclivous. Front coxa without surrounding carina. Middle tibia with two spurs. Claws simple, or fore and middle claws indistinctly pectinate at extreme base. Apical portion of propodeum hardly prolonged. Propodeal spiracle ellipse, situated at basal margin of propodeum. Ovipositor sheath short, 0.5 to 0.6 times as long as apical depth of metasoma. Ovipositor robust (Figure 6), weakly decurved; subapical portion somewhat swollen.

This new genus is similar to *Aphanistes* and *Habronyx* in having the lower anterior margin of the pronotum without a tooth, the posterior transverse carina of the mesosternum interrupted in front of each mid coxa, fore wing vein 1-Cu distinctly shorter than 1m-cu+2-Rs+M (distance between 1-Cu and 2m-cu), etc., but differs in a number of characters from each of them, mainly as following:

- upper margin of face extending upwardly and covering partly over antennal socket; *Aphanistes* and *Habronyx* with the face simple;
- apical margin of clypeus without a tooth; *Aphanistes* and *Habronyx* with a tooth;
- frons divided into two portions: upper portion flat; lower portion deeply and almost vertically sunken; *Aphanistes* and *Habronyx* with frons simple;
- lower portion of occipital carina widely and flakily expanded; *Aphanistes* and *Habronyx* not or slightly widened, not flakily expanded;
- lower end of occipital carina joining hypostomal carina distinctly above base of mandible; *Aphanistes* and *Habronyx* with occipital carina joining base of mandible;
- fore wing vein 2rs-m far distal to 2m-cu, distance between them approximately as long as 2rs-m; *Aphanistes* and *Habronyx* with 2rs-m basal to 2m-cu, or rarely opposite, or *Habronyx* with 2rs-m a little distal;
- fore and middle claws indistinctly pectinate at extreme base, hind claws simple; *Aphanistes* and *Habronyx* with claws mostly distinctly pectinate.

**Distribution.** There is a single Chinese species, described below.

**In Townes’ (1971) key to genera, the new genus can be inserted as follows:**

- 8 Mesoscutum in profile with a distinct concavity just before its front end, so that its front end is like a small shelf. Frons usually with a median compressed tooth. Tarsal claws pectinate to the apex. Almost worldwide ..... **3 *Aphanistes* (p.131)**
- Mesoscutum in profile with an evenly convex curve to the front end or with a slight flattening (but not a distinct concavity) just before the front end. Frons without a median compressed tooth. Tarsal claws usually not pectinate to the apex ..... **9**
- 9 Notaulus distinct, reaching at least to center of mesoscutum. Upper end of prepectal (epicnemial) carina usually reaching above lower 0.15 of hind margin of pronotum and approaching front edge of mesopleurum (mesopleuron) ..... **9a**
- Notaulus absent. Upper end of prepectal (epicnemial) carina not reaching lower 0.15 of hind margin of pronotum ..... **10**

- 9a Lower portion of occipital carina widely and flakily expanded (Figure 3), lower end joining hypostomal carina distinctly above base of mandible. Apex of clypeus (Figure 2) evenly convex, without a tooth. Frons divided into two portions (Figure 4), lower potion deeply and almost vertically concave. Forewing 2rs-m far distal of 2m-cu, distance between them approximately as long as 2rs-m ..... ***Elaticarina* Sheng, gen. n.**
- Lower portion of occipital carina not or slightly expanding, lower end joining base of mandible. Apex of clypeus with a median tooth. Frons not divided into two portions, not particularly concave. Forewing 2rs-m basal of 2m-cu, sometimes opposite or a little distal.....***Habronyx* (p.130)**

**In Gauld’s key to genera and subgenera (1976), the new genus can be inserted as follows:**

- 20(19) Mesoscutum in profile anteriorly evenly round (Text–fig. 209); notauli entirely absent, not even represented by an area of coarse sculpture. Lower corner of pronotum simply acute (Text–fig. 204); claws of ♂ long, weakly curved, pectinate only at extreme base (Text–fig. 215–218), those of ♀ shorter, moderately curved, pectinate to, or just beyond, the centre; ♂ with apex of aedeagus with a dorsal lobe. (Cosmopolitan) ..... **Gravenhorstia subgenus *Erigorgus* Foerster (p.60)**
- Mesoscutum in profile weakly to strongly abruptly round (Text–fig. 206); notauli present, strongly impressed, rarely quite weakly impressed but then discernible by being strongly rugose..... **20a**
- 20a Lower end of occipital carina joining hypostomal carina distinctly above base of mandible. Frons divided into two portions, lower potion deeply and almost vertically concave. Apex of clypeus (Figure 2) evenly convex, without a tooth..... ***Elaticarina* Sheng, gen. n.**
- Lower end of occipital carina joining base of mandible. Frons not divided into two portions, lower potion normal, not particularly concave. Apex of clypeus always with a median tooth ..... **21**

In Gauld’s key to genera and subgenera (1976), if *Elaticarina* specimens are run to couplet 7 (which they should not), then there are resemblances to the genus *Therion* in that the posterior transverse carina of the mesosternum is interrupted before each mid coxa and the clypeus lacks a median apical tooth. *Elaticarina* differs from *Therion* in the lower end of the occipital carina joining the hypostomal carina distinctly above the mandible base, fore wing vein 2rs-m far distal to 2m-cu, distance between them approximately as long as 2rs-m, 1-Cu approximately 0.5 times as long as 1m-cu+2-Rs+M.

***Elaticarina recava* Sheng, sp.n.**

urn:lsid:zoobank.org:act:1DE099EC-68E4-4467-9913-D15F4226592F

[http://species-id.net/wiki/Elaticarina\\_recava](http://species-id.net/wiki/Elaticarina_recava)

Figures 1–8

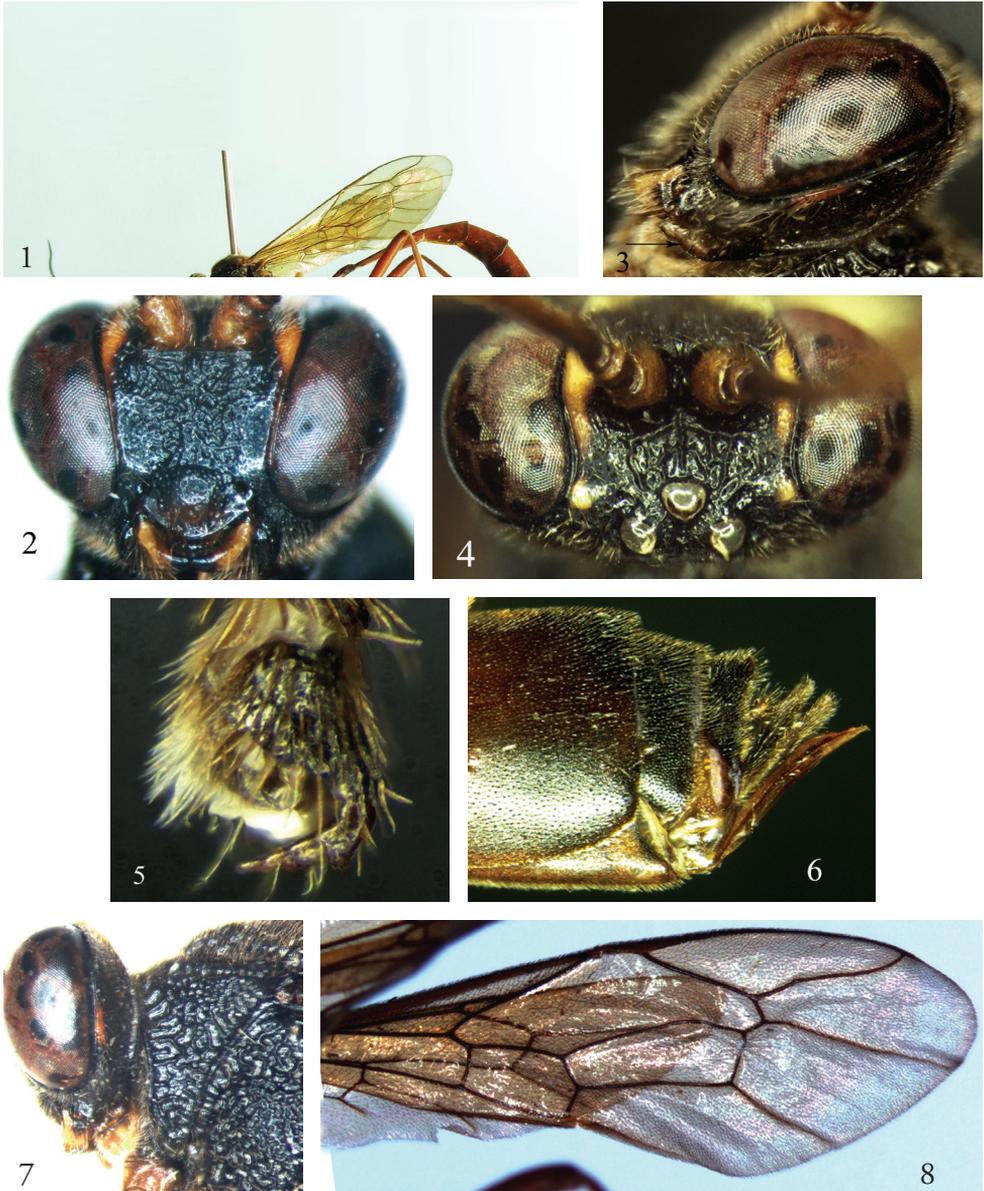
**Etymology.** The name of the new species is based on the lower portion of frons being deeply concave.

**Type material.** *Holotype*, Female, CHINA: Matoushan National Natural Reserve, 400m, Zixi County, Jiangxi Province, 8 May 2009, leg. Mei-Juan Lou. *Paratypes*: 1 female, same data as holotype except 1 May 2009. 1 female, CHINA: Wuyishan National Natural Reserve, 1160m, Yanshan County, Jiangxi Province, 15 June 2009, leg. Zhi-Yu Zhong.

**Description.** Female. Body length 16.0 to 18.0 mm. Fore wing length 10.5 to 11.0 mm. Ovipositor sheath length about 1.2 mm.

**Head.** Face approximately 1.1 times as wide as long, median portion slightly concave, with irregular wrinkles; lateral margin finely punctate; upper-lateral portion nearby antennal socket with irregular transverse wrinkles; upper margin with a small median tubercle. Clypeal suture weak. Clypeus (Figure 2) approximately 1.6 times as wide as long, evenly and evidently convex; basal portion with sparse, distinct and fine punctures; apical portion almost impunctate. Mandible short, basal portion with weak and indistinct punctures and brown hairs. Cheek slightly concave, with fine coriaceous texture. Malar space 0.48 to 0.63 times as long as basal width of mandible. Gena with distinct dense punctures and long brown hairs; straightly convergent backwardly. Vertex smooth, with fine and weak punctures. Postocellar line approximately 0.8 times as long as ocular-ocellar line. Interocellar area with wrinkles and a deep median longitudinal groove. Dorsal profile of frons rough, weakly concave centrally, with irregular wrinkles; lateral portion almost smooth. Antenna with 52 to 54 flagellomeres.

**Mesosoma.** Pronotum (Figure 7) rough, anterior portion with distinct transverse wrinkles, hind margin with oblique transverse wrinkles; upper-posterior portion with indistinct fine transverse wrinkles; lower portion with distinct reticulate wrinkles; subanterior margin with a strong longitudinal ridge (Figure 7). Mesoscutum with dense, indistinct and fine punctures, hind margin with fine transverse wrinkles; nearby hind margin irregularly rough. Scutellum and postscutellum with dense wrinkles. Mesopleuron rough, upper-anterior portion with fine oblique longitudinal wrinkles; lower portion with distinct reticulate wrinkles. Without speculum, the place with oblique lines. Posterior transverse carina of mesosternum not complete, broken before middle coxa. Metapleuron evidently convex, with rough and dense reticular wrinkles. Anterior portion of submetapleural carina strongly convex, posterior portion weak and indistinct. Wing (Figure 8) grey-brownish hyaline. Fore wing vein 1cu-a distal of 1/M, distance between them about 0.65 times length of 1cu-a. Vein 2-Cu approximately as long as 2cu-a. Hind wing vein cu-a strongly reclivous, 1-cu 0.6 to 0.7 times as long as cu-a. Legs comparatively slender. Hind coxa with distinct fine punctures; dorso-apical margin of first trochanter



**Figures 1–8.** *Elaticarina recava* Sheng, sp.n. Holotype **1** Body, lateral view **2** Head, anterior view **3** Head, lateral view **4** Frons **5** Claw **6** Apical portion of metasoma, lateral view **7** Head and pronotum, lateral view **8** Fore wing.

produced as a tooth. Fore and middle claws indistinctly pectinate at extreme base. Hind claws simple, strongly curved approximate at right-angle. Ratio of length of hind tarsomeres 10.0:3.7:2.0:1.0:1.7. Propodeum with dense and rough reticular wrinkles and a shallow median longitudinal concavity.

**Metasoma.** Hind portion from second tergum strongly compressed. Apical margin of first sternum reaching to level of spiracle. Second tergum approximately 1.25 times as long as first tergum, 1.9 times as long as third tergum. Ovipositor sheath approximately 0.5 times as long as apical depth of metasoma.

**Color** (Figure 1). Head and mesosoma black, except the following: inner orbits, median portions of gena orbits and scape yellowish brown; apical portion of pedicel, basal half of flagellum except base of first flagellomere, coxae except black bases, trochanters and femora reddish brown; apical portion of flagellum blackish brown; fore and middle tibiae and tarsi except fifth segments, brownish yellow; basal 0.7 to 0.8 of hind tibia darkish brown; tegulae blackish brown to reddish brown; median portion of mandible and hind tarsi except fifth segment, yellow. Terga, except dorsal portion of second tergum and main portions of seventh and eighth terga brownish black, reddish brown. Stigma brown. Veins brownish black.

**Variation.** The specimen from Wuyishan National Natural Reserve, Yanshan County, Jiangxi Province, has the fore and middle legs almost entirely yellow.

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# Nectary use for gaining access to an ant host by the parasitoid *Orasema simulatrix* (Hymenoptera, Eucharitidae)

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## Abstract

Eucharitidae is the only family of insects known to specialize as parasitoids of ant brood. Eggs are laid away from the host onto or in plant tissue, and the minute first-instars (planidia) are responsible for gaining access to the host through some form of phoretic attachment to the host ant or possibly through an intermediate host such as thrips. *Orasema simulatrix* (Eucharitidae: Oraseminae) are shown to deposit their eggs into incisions made on leaves of *Chilopsis linearis* (Bignoniaceae) in association with extrafloral nectaries (EFN). Nectary condition varies from fluid-filled on the newest leaves, to wet or dry nectaries on older leaves. Filled nectaries were about one third as common as dry nectaries, but were three times as likely to have recent oviposition. Larger numbers of undeveloped eggs, or eggs with mature planidia inside, were associated with filled and wet EFN. For emerged planidia, the distribution was shifted from a concentration at filled nectaries to an even greater concentration at wet nectaries. More planidia were found in EFN ( $9.50 \pm 2.85$ ) than outside EFN ( $1.00 \pm 0.60$ ). Planidia were tested for their attachment to adult and larval ants and to adult and immature thrips (potential intermediate host), but the results do not support simple attachment as a viable means for transfer and successful parasitism. *Pheidole desertorum* was identified as the host ant, and at night is the dominant ant in the tree canopy of *C. linearis*. Feeding at the EFN by the host ant, and the direct association with planidia near to or in the EFN, is interpreted as a novel means of accessing the host brood.

## Keywords

Parasitoid, ant, extrafloral nectaries, Chalcidoidea, Formicidae, Pheidole

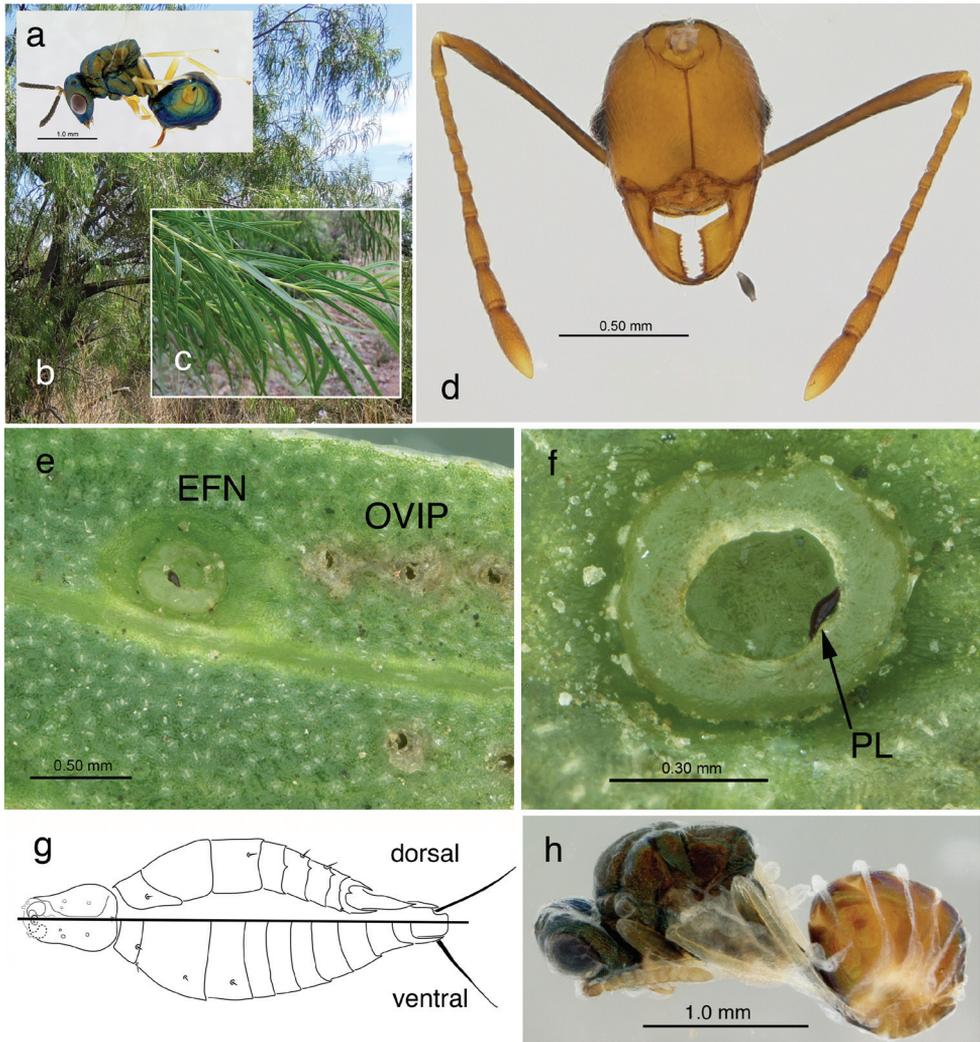
## Introduction

As with other Eucharitidae, *Orasema* (Hymenoptera: Eucharitidae: Oraseminae) deposit their eggs away from the host, and the active first-instar larvae (planidia) are responsible for gaining access to the larval ant host (Clausen 1941; Heraty 2000). Although commonly collected in the arid regions of the southwestern United States, little is known of their biology. The ant hosts for *Orasema* are usually Myrmicinae (*Lepthorax*, *Monomorium*, *Pheidole*, *Solenopsis* and *Wasmannia*) (Das 1963; Gahan 1940; Heraty 1994a; Johnson et al. 1986; Kerrich 1963; Reichensperger 1913; Snelling and George 1969; Van Pelt 1950; Wheeler and Wheeler 1937; Wheeler 1907), but with one North American record from *Formica nitens* Creighton (Formicinae) (Johnson et al. 1986). How they gain access to their larval ant host is unclear.

Females of *Orasema* oviposit into a variety of plant structures, with eggs deposited into punctures made by the scimitar-shaped ovipositor (cf. Fig. 1a) (Clausen 1940b; Heraty 1994b; Johnson et al. 1986). When deposited into flowering structures, the emerging planidia are often associated with thrips larvae (Thysanoptera), possibly as accidental associations, food sources, or intermediate hosts for gaining access to the ant colony (Ananthakrishnan 1984; Beshear 1974; Heraty 1994a; 2000; Heraty et al. 1993; Johnson et al. 1986; Wilson and Cooley 1972). In the latter scenario, the thrips presumably act as a transport mechanism for the attached planidium to reach the brood of the host ant when the worker returns with the infested prey. However, eggs are sometimes deposited into green leaf tissue (leaves or young shoots), and no thrips association is evident. In this case, planidia are proposed to attach to the bodies of foraging ant workers and then get transported back to the ant nest. Transfers by thrips-intermediate prey items or directly by adult ants to the host brood have never been confirmed by direct observation.

The *Orasema simulatrix* group is morphologically distinct and consists of seven species distributed throughout the southwestern US and temperate regions of Mexico (Heraty 2000). Little has been published on species within the group apart from collection records and an identification key that includes only three of these species (Gahan 1940). Within the complex, *O. simulatrix* Gahan is commonly collected and found in Arizona, southern California, New Mexico and western Texas. It is almost exclusively associated with desert willow, *Chilopsis linearis* Cav. (Bignoniaceae).

Bignoniaceae has approximately 100 genera worldwide, but only a few are native to temperate North America (Jones Jr. and Luchsinger 1986). *Chilopsis* is a typical member of the family for both habitat type and morphology of its flowers and fruit. Common to the family is the presence of extrafloral nectaries (EFN, Fig. 1e) over much of the plant (Elias 1983). EFN are specialized tissues that secrete nectar, which is a heterogenous liquid mixture of carbohydrates, amino acids, proteins, and other compounds (Elias 1983). The structures found on *C. linearis* closely match the description of nectaries of most Bignoniaceae, in which nectaries are non-vascularized and cupular or disc-shaped (Elias 1983). Our observations suggest that *O. simulatrix* oviposit almost exclusively in the near vicinity of these extrafloral nectaries.



**Figure 1.** **a** female of *Orasema simulatrix* **b** *Chilopsis linearis*, habitat **c** leaf shoot **d** head of *Pheidole desertorum* with planidium of *O. simulatrix* **e** extrafloral nectary (EFN) with planidium inside nectary and oviposition punctures (OVIP) along leaf **f** EFN with planidium (PL) **g** planidium with dorsal and ventral view divided by bar **h** male pupa of *O. simulatrix*.

The *simulatrix* species group is postulated as being a derived clade among other Nearctic species groups that include species with documented thrips associations (Heraty 2000). No such thrips associations have been observed for any member of the *simulatrix* group. Instead, the adults not only preferentially oviposit around the leaf nectaries, but the planidia were observed to migrate into the fluid-filled nectaries that are likely acting as a food source for their host ant. This research describes the peculiar oviposition habits and host association of *O. simulatrix* in Arizona and southwestern New Mexico, and documents the first case of a parasitoid using a nectary food source to gain access to the brood of its ant host.

## Materials and methods

### Study site descriptions and material examined

**Geographic Area of Investigation.** Data collections, observations, and ant baiting experiments were conducted at four sites near the Southwestern Research Station (SWRS) near Portal, AZ. Ambient temperatures over the year range from night time lows near 5°C in early spring or late autumn to daytime highs of 40°C during summer. Additional sampling and casual observations of *O. simulatrix* on *Chilopsis* were made at several other localities in California, Texas and New Mexico, at sites ranging from sea level to nearly 2500 meters.

**Study Sites.** Site 1 (31°52'36"N, 109°03'32"W) was in a stand of six trees (maximum height about 4 m) of *C. linearis* in Arizona in the foothills of the Chiricahua Mountains, approximately 8 km east of Foothills Road on Portal Road (leading to San Simon). The habitat was high desert, dominated by sparse trees of *Larrea tridentata* Coville (Zygophyllaceae), *Acacia constricta* Benth. (Fabaceae) and *Prosopis* sp. (Fabaceae), a variety of shrubs including *Yucca* (Agavaceae), *Fouquieria splendens* Engelman (Fouquieriaceae), *Opuntia* spp. (Cactaceae), and annual herbs in the genera *Parthenium*, *Baileya*, *Senecio*, *Gutierrezia* (all Asteraceae) and *Sphaeralcea* (Malvaceae). Site 2 (31°56'14"N, 108°57'59"W) consisted of seven trees in New Mexico in the Peloncillo Mountains, 7 km east of US Highway 80 on New Mexico Highway 9. Site 2 was less vegetated than Site 1, with *L. tridentata* and *C. linearis* being the dominant tree species. Shrubs and annuals were also less abundant and diverse. Site 3 (31°55'14"N, 109°42"W) consisted of five trees approximately 0.8 km north of the intersection of Foothills Road and Portal Road. Site 3 was rocky, and the dominant vegetation a mix of *L. tridentata*, *A. constricta* and *Prosopis* sp. Site 4 (31°54'50"N, 109°07'42"W) consisted of 5 trees and began at the intersection of the above-mentioned roads, and extended south and east along Portal Road. The trees were spread over a distance of 0.25 km alongside the road, within 50m of the road edge. The dominant tree species were the same as for Site 3. In 1999, Sites 1 and 2 were abandoned for study because of low activity of *O. simulatrix*. At Site 2, the area was in extreme drought, and no wasps were recovered. Site 1 was abandoned because the Arizona Department of Highways chose to improve the shoulders of Portal Road and leveled the entire stand of *C. linearis*. Therefore, in 1999, studies were shifted to Sites 3 and 4, which were approximately 1 km apart. Sites 3 and 4 were revisited in September 2011 for additional collections of leaves, immature stages of eucharitids, and foraging ants.

**Insect and Plant Identifications.** Museum collections examined were University of California, Riverside, CA (UCRC), Texas A&M University, College Station, TX (TAMU), University of Arizona, Tucson, AZ (UAZC), and the Southwestern Research Station, Portal, AZ (SWRS). Voucher specimens of wasps, ants and thrips were deposited in the UCR Entomology Research Museum (UCRC) (voucher code BC1). Ants were determined or verified by S. Cover (Museum of Comparative Zoology) or R. Snelling (Los Angeles County Museum). Slide mounted thrips were identified by L.

Mound (Commonwealth Scientific and Industrial Research Organization, Australia). Host plant vouchers were deposited in the UCRC Herbarium, with identifications provided by A. Sanders (UCRC).

## Terminology

**Host Plant.** Terminal growing shoots were used for sampling, with a growing shoot defined as any single branch without subtending shoot growth and having at least 20 leaves and some extrafloral nectaries (EFN). Typically, leaves at the tip are less than 4 cm long, while mature leaves are about 10 cm long (Fig. 1c). Shoot-tip leaves can have EFN, but these are usually inaccessible to wasps because they are grouped in a tight cluster. Three qualitative conditions of EFN were identified: “filled” when the nectary had a distinct convex meniscus of fluid, “wet” when the quantity of fluid did not equal or exceed the perimeter of the nectary, and “dry” when it contained no obvious fluid. EFN are reabsorbed on older leaves, and oviposition activity was not observed on older shoots that lacked any nectaries. Examination of shoots included up to 60 leaves from, but not including, the clustered shoot-tip leaves. Leaves were grouped into categories of ten consecutive leaves, with Category I containing the youngest leaves, 1-10, and so on through leaf 60. This allowed for the number and condition of EFN to be correlated with the relative age of the growing shoot. EFN are also found on the subtending bracts of flowers and sepals; these were also examined for oviposition, but these were rare events.

**Immature *Orasema*.** Immature stages of *Orasema* observed on leaves were categorized as undeveloped eggs, developed eggs, and planidia. Undeveloped eggs were white in color, indicative of recent oviposition. Developed eggs were dark brown to black in color, with the developing planidium visible inside the egg. Emerged first-instar larvae (planidia) were dark brown to black and could be seen crawling, maggot-like, along plant parts or congregated in nectaries.

## Oviposition habits of *Orasema*

The distribution of oviposition punctures on plant structures of *C. linearis* did not appear to be random, so a series of experiments was designed to test for a preference for plant structure, concentration of oviposition on particular structures, and choice along shoots.

**Oviposition Pattern and Abundance.** In 1998, each site was sampled three times (July 30, August 20, August 27). Five shoots were removed from each of two trees and returned to SWRS for analysis. Samples were stored in paper sacs within Ziploc<sup>®</sup> plastic bags and refrigerated at 4°C. Each leaf or flower was removed sequentially from the apex of the shoot to the base and examined using a Leica Wild M5 stereomicroscope for presence of nectaries and distribution of oviposition punctures. Measurements of nectary size and the maximum distance of punctures from the associated nectary were made using an ocular micrometer (0.01 mm divisions). Females of *Orasema* deposit

single eggs into a linear series of punctures formed in the plant tissue by the ovipositor (Heraty 1994b; 2000). The number of punctures (eggs), puncture series and punctures per series surrounding each nectary were recorded. The distribution of punctures and nectaries were recorded for position on the adaxial or abaxial leaf surface, and for the punctures, whether they were on the same side of the vein as the nectary or on the opposite side. Leaf surface alone (adaxial or abaxial) was recorded for the few punctures not placed close to an EFN. Leaves and flowers were counted separately, and for flowers, sepals and bracts were treated separately. Sepals were counted in “pairs” because the five calyx parts are fused in Bignoniaceae (Jones Jr. and Luchsinger 1986). Nectaries or egg condition was not recorded for these flower samples.

**Oviposition choice.** Sampling was conducted to determine preference for oviposition along the branch or next to nectaries. In 1999, five trees at Site 3 and 4 were sampled sequentially from July 7–13 and from July 18–30, respectively. Two shoots were sampled per day from one tree at each site and processed within 18 hours of removal. Samples were processed in a similar manner to the 1998 sampling. Counts focused on the condition of nectaries and immature stages (eggs and planidia) along shoots. Nectaries were assessed for quality (filled, wet or dry) and eggs within each puncture were assessed for condition (undeveloped, developed or emerged) by dissecting oviposition punctures using a number 3 insect pin. The condition of eggs within a series could not always be accurately identified because of difficulties with dissection of an egg from a puncture. Because all eggs within a series are deposited at a single oviposition, the condition of any egg within a series was considered representative of the entire series. Therefore, the number of eggs is an estimate, not necessarily an accurate count of the condition of each individual egg. Counts were also made of the number of planidia crawling free on the leaf surface or within nectaries. The distributions of EFN and of immature stages were compared by partitioning leaves into categories as described above. The distribution of oviposition sites among leaves or EFN was compared with a Chi square test for homogeneity (using Excel 1997). Differences in the distribution of undeveloped eggs and planidia at filled, wet, and dry nectaries were analyzed by Kruskal-Wallis rank test using Statview 4.02 (Abacus Concepts 1992). Significance for all statistical analyses was  $\alpha=0.05$ .

Regrowth can occur after damage (e.g., by grazing ruminants) and can result in a large flush of new growth. Regrowth branches are fundamentally different in that filled nectaries are distributed over the entire length, rather than concentrated at the anterior end of a shoot. In two samples, this resulted in an apparent oviposition bias, and these samples were excluded.

## Ant Associations

Earlier discussion focused on interactions between *Orasema* and *C. linearis*. We were interested in the distribution of potential ant hosts on the plant and foraging activities that might place them into direct contact with planidia of *O. simulatrix*. Investigations

consisted of nest excavations of potential ant hosts in the near vicinity of wasp-infested *Chilopsis* (based on assessment of foraging activity to baits on the ground and tree), and observations of arboreal foraging in the absence of baits.

**Host Record.** Broods of several species of ants were excavated in the vicinity of infested *Chilopsis* at the four study sites. Numerous excavations also were made at other locations; these results are not reported but were similar to the results from the study sites. Brood and workers were collected and preserved in 75% EtOH and then examined for parasitism using a Leica Wild M5 stereomicroscope. Excavated soil containing brood from nests of *Solenopsis* or *Pheidole* was placed into Fluon-lined plastic containers (60 cm × 50 cm). Over two days, brood, ants, and any parasites were sorted out of the soil with forceps, a hand trowel, thin paintbrushes, and an aspirator. Brood was examined for parasitoids, and then either preserved in EtOH or maintained in a live colony.

Live colonies were maintained in artificial humidity chambers made of a plaster-filled plastic petri dish (90 mm × 15 mm) with three 3 mm holes drilled laterally and one 3 mm hole in the lid of the dish as entrances. Each chamber was covered by red plastic film to act as a light filter. Chambers were placed into larger polyethylene containers (various sizes) in which the sides were coated with Fluon to prevent ants from escaping. Water was offered in cotton-stoppered glass vials. Food consisted of peanut butter and sugar water offered continuously and freshly killed insects occasionally.

**Host Foraging.** In addition to investigations of ant nest distribution, observations were conducted in 1998 to determine the foraging patterns of ants near or on *C. linearis* infested with *O. simulatrix*. The expectation was that one or more myrmicine ant species, such as *Pheidole desertorum*, would be present and foraging. Ant distribution was characterized either by infrequent monitoring, or using peanut butter bait stations that preferentially attract Myrmicinae (Snelling and George 1969). At Sites 1 (August 1, 1998) and 2 (August 14, 1998), two trees were observed over a 24 hour period using baits. Approximately one teaspoon of Safeway brand peanut butter was put into a plastic hexagonal weigh dish (2", Fisher brand) taped to 3" by 5" index cards. Baits were placed in the trees and/or ground. Five baits were scattered indiscriminately within a 10 m<sup>2</sup> plot on the ground, thus within a 3 m radius of the base of the trunk of selected trees. In trees, five tree baits were placed at random on branches not touching the ground. One bait station was placed per branch. The frequency of occurrence for each species of ant was measured at the five ground and tree bait stations. Each tree was inspected hourly for 24 hours, with observations of one minute for each of the ten baits.

### **Insect-Planidium Associations**

From 1997–1999, tests were conducted to determine if first-instar larvae (planidia) of *O. simulatrix* will attach to adult ants, larval ants or immature thrips. Using a minuten pin, insect pin, or thin paintbrush, individual planidia were placed into clear plastic tubes (ca. 10 mm × 5 mm), with each end of the tube plugged with cotton. After insects were introduced, the tubes were taped to index cards and placed into a closed

polyethylene container (132 cm × 21.5 cm × 22 cm) over a saturated salt solution to maintain a relative humidity of 75%, and in a growth chamber at 21°C and 14 L:10 D photoperiod cycle. Two types of associations were tested. In a non-contact association, a planidium was placed into the vial first, and an associate (thrips, immature ant or adult) introduced nearby within the vial, but not contacting the planidium. In a contact association, a planidium was placed directly onto the associate. For each trial, the planidium and associate were checked intermittently over a 36 hour period, or until one of the two insects died. At each observation, planidia were monitored as to whether they were unattached, attached externally, or if they had burrowed into the associate.

Combinations with the planidia placed near, but not on the host, were conducted only with immature thrips (n = 12). Combinations with planidia placed onto the insect associate were: a) planidia on immature thrips (n = 45), b) planidia on mature ant larvae (*Solenopsis* n = 8, *Pheidole desertorum* n = 8), c) planidia on an adult worker (*Solenopsis* n = 12, *Pheidole desertorum* n = 10, *Pheidole tucsonica* n = 8). Individual ant workers were also combined with sections of leaf that included a single nectary with one or more planidia within the nectary (n = 12).

In 2011, 250 workers of *P. desertorum* were sampled by either sweeping or aspirating *C. linearis* at night over a 6 hour period. Numerous planidia were present both on the leaves and within EFN on the trees sampled. Foraging ants were examined both externally and internally (mouthparts) for planidia.

## Results

### Collections and Host Range

*Orasema simulatrix* has been collected from numerous localities in southern California, Arizona, New Mexico and western Texas (locality information available on request). Museum records include collections from several different plant families, including Apocynaceae, Asteraceae, Bignoniaceae, Fabaceae and Malvaceae. This apparent diversity is likely misleading, as most records for *O. simulatrix* are from only one or two specimens collected for each plant species. All of these records are from random sweep-net samples, and no cases of oviposition were recorded. Although different angiosperms were sampled as part of this study, only two specimens of *O. simulatrix*, one male and one female, were ever sampled from another plant, *Acacia constricta* Benth. (Fabaceae) (Site 4). Oviposition was observed only on *Chilopsis linearis*.

### Oviposition Choice

Using their scimitar-shaped ovipositor, females of *O. simulatrix* oviposit into leaves of *C. linearis*, with the single egg inserted parallel to the leaf surface. Females oviposit in a linear series of 1–27 eggs, with an average of 3.27 eggs per series. Females pref-

erentially deposited their eggs into leaves with extrafloral nectaries (Table 1). Of 310 leaves sampled in 1998, 57% (176) had one or more EFN, and 76% of these (134) had oviposition punctures (Table 1). Only three of the 134 leaves without EFN (2%) had oviposition punctures. Leaves with EFN had a total of 509 extrafloral nectaries, averaging  $2.89 \pm 1.41$  (SE) EFN per leaf. There were a total of 2599 punctures, of which 2546 occurred on leaves with EFN. Of 798 leaves sampled in 1999, a smaller proportion of leaves (327; 41%) had EFN, but these included the majority of leaves with oviposition punctures (268) and a total of 5,790 punctures (Table 1). There was a marked difference between sites, as Site 3 had 1,940 punctures next to 270 EFN on leaves and Site 4 had 4,151 punctures next to 381 EFN on leaves. Only 12 of the 471 leaves without EFN (2%) had oviposition. In contrast to leaves, 47 flowers contained only 13 oviposition punctures (Table 1). Extrafloral nectaries (EFN) were found on both bracts and sepals. Eggs deposited next to EFN on bracts or sepals were placed in close proximity to EFN, as they were on leaves, although because of the small size of the bracts and sepals, it is possible that eggs were deposited randomly.

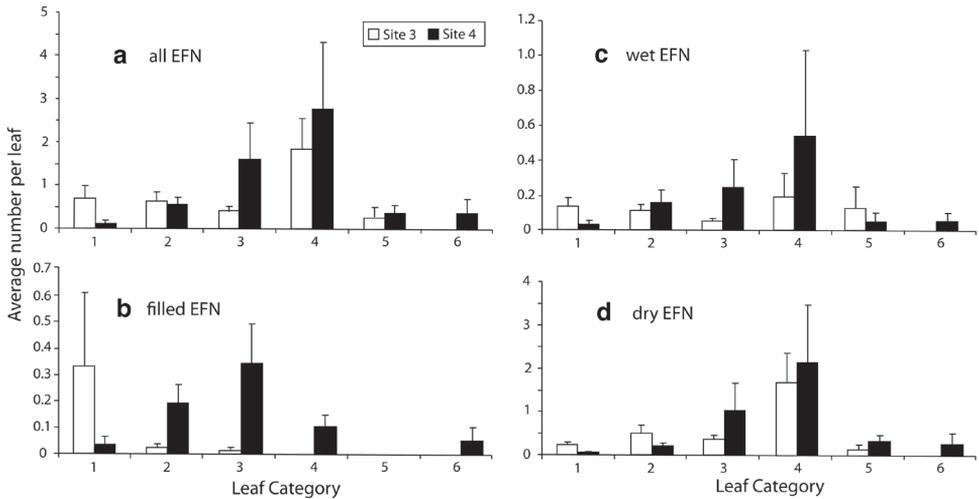
Females deposited eggs in close association with the EFN. The average distance of oviposition marks from the edge of an EFN was  $2.38 \pm 0.20$  mm based on 14 shoots, 61 leaves, and 140 nectaries. Leaves were approximately 10 cm long, and the average nectary diameter was  $0.26 \pm 0.01$  mm. Oviposition marks could be on both sides of the leaf. However, the number of adaxial oviposition punctures per leaf was  $1.05 \pm 0.34$ , as compared to  $7.15 \pm 1.09$  abaxial ovipositions per leaf. The average number of ovipositions per EFN on the same side of the leaf midrib as the EFN was  $5.88 \pm 0.42$ , with  $4.67 \pm 0.35$  across the midrib from the nearest EFN.

**Table 1.** Distribution of oviposition punctures on *Chilopsis linearis* for 1998/1999. No flowers (sepals or floral bracts) were sampled in 1998.

	Leaves with EFN	Leaves without EFN	Sepals	Floral bracts
number examined	176 / 327	134 / 471	- / 47	- / 113
number with punctures	134 / 268	3 / 12	- / 2	- / 3
total number of punctures	2546 / 5790	53 / 301	- / 4	- / 9
% with punctures	76 / 82	2 / 3	- / 4	- / 3

## Distribution of Nectaries and Immatures along Shoots

**Distribution of nectaries.** *Chilopsis linearis* shoots averaged 39.9 leaves for the twenty shoots sampled. Because of differences in shoot length, not all shoots had a full complement of 10 leaves in the more basal categories (4, 5 and 6). The distribution of nectaries along shoots of *C. linearis* was not uniform across leaf categories (Fig. 2). Nectaries were most abundant on leaves in Category 4 (leaves 31-40 distal to branch tip), with an average of  $2.37 \pm 1.90$  nectaries (Fig. 2a). Most nectaries were dry (Fig. 2d), suggesting they were no longer a potential food source for ants. For Category 4 leaves, the proportion of wet nectaries was much greater than filled, but much less than

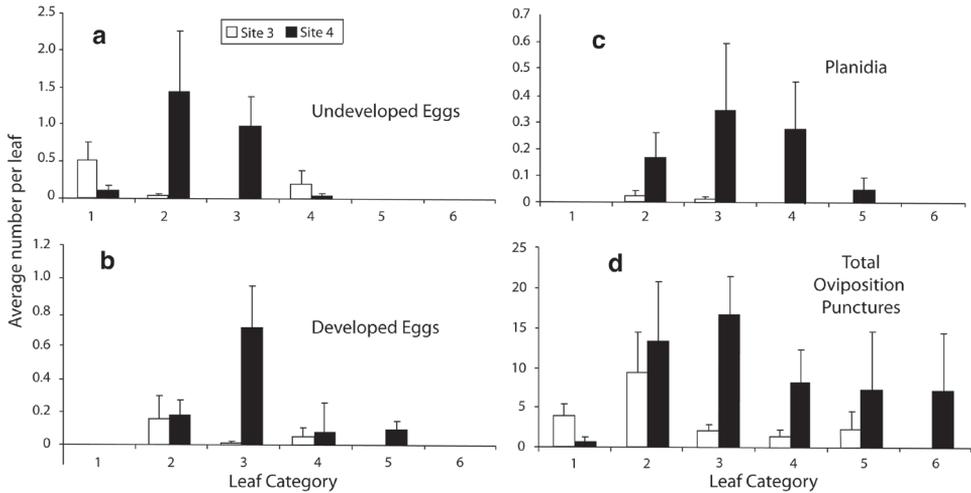


**Figure 2.** Distribution of extrafloral nectaries (EFN) on shoots of *Chilopsis linearis* in AZ, 1999. Shoot defined as branch with new growth and leaves with EFN. **a** all EFN **b** filled EFN **c** wet EFN **d** dry EFN.

the dry or senescing nectaries. The number of nectaries per leaf declined dramatically in Categories 5 and 6 (Figs 2a–d). This decline is probably a result of reabsorption of the nectaries on these older leaves, although it could also represent fewer nectaries present on these leaves when initially formed.

**Distribution of Immatures.** The condition of eggs was used to gauge the relative time since oviposition by females, with white or undeveloped eggs indicating recent oviposition, and dark or developed eggs indicating earlier oviposition. Assuming that planidia did not wander far from the oviposition site, especially to different leaves or different leaf groups, their presence corresponds with an even earlier oviposition event. Empty punctures could be the result of previous cohorts of *Orasema* and were not used as indicators of activity. The distribution of immature stages was not uniform for the typical growth shoots and there was a significant difference in the distribution of immature stages at the two sites ( $X^2 = 5.59$ ) (Fig. 3).

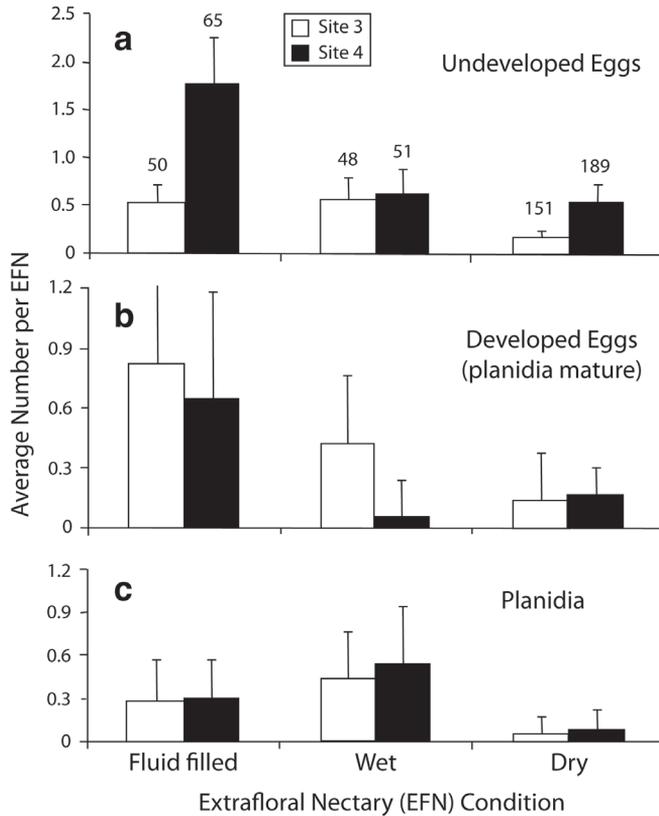
There was a progression from younger to older immature stages from the apical leaf groups to the more basal leaf groups (Fig. 3a–c). The distribution of immatures was very different between sites, likely representing different peaks of activity, with Site 1 having both fewer eggs, and a much higher proportion of empty (emerged) punctures (Fig. 3a–d). The number of undeveloped eggs varied from  $0.51 \pm 0.25$  in Category 1 for Site 3 to  $1.44 \pm 0.82$  in Category 2 for Site 4 (Fig. 3a). No undeveloped eggs were found on the older Category 5 and 6 leaves at either site. Developed eggs (planidia ready to emerge) were found only on leaves from Categories 2 through 5, and most numerous in Category 2 for Site 3, with  $0.15 \pm 0.14$  eggs, and in Category 3 for Site 4, with  $0.71 \pm 0.38$  (Fig. 3b). Planidia were not found in the Category 1 leaves at either site. Planidia were mostly distributed medially on a shoot, with the highest number



**Figure 3.** a–c Distribution of immature stages of *Orasema simulatrix* among leaf categories on *Chilopsis linearis* in AZ, 1999 d total number of oviposition punctures on *C. linearis*. Regrowth samples excluded (see text for details).

in leaf Category 3 for Site 4 ( $0.34 \pm 0.25$ ), while planidia were scarce, but highest in Category 2 for Site 3 ( $0.02 \pm 0.02$ ; Fig. 3c). The distribution among immature stages was not correlated with the distribution of total number of nectaries along the branch; however, the distribution of undeveloped eggs (most recent oviposition events) could be roughly correlated with the larger number of filled and wet nectaries in Categories 1 to 3. More undeveloped eggs were found to be associated with filled nectaries than wet nectaries, although neither distribution was significant (Spearman Rank correlation coefficient  $P = 0.586$  and  $p = 0.19$  and  $P = 0.757$  and  $p = 0.09$ , respectively).

**Association by EFN type.** Overall, 85% of EFN had associated oviposition marks (554 of 651). The greatest number of undeveloped eggs per EFN ( $1.78 \pm 0.48$ ) was associated with fluid-filled nectaries at Site 4 (Fig. 4a). The least number of undeveloped eggs were associated with dry nectaries, even though dry nectaries were numerically more abundant at sites 3 and 4 (Fig. 3). Although filled nectaries were about one third as common as dry nectaries, they were three times as likely to have undeveloped eggs indicating recent oviposition. Larger numbers of the undeveloped eggs were associated with filled and wet EFN; this pattern was significant at Site 4 (Kruskal-Wallis  $H_2 = 30.65$ ,  $p = 0.0001$ ), but not Site 3 (Kruskal-Wallis  $H_2 = 4.98$ ,  $p = 0.08$ ). Developed eggs followed a similar pattern to that of undeveloped eggs, with the greatest concentration at filled EFN, with  $0.82 \pm 0.86$  and  $0.65 \pm 0.54$  for Site 3 and 4, respectively (Fig. 4b). For planidia, the distribution was shifted from a concentration at filled nectaries to an even greater concentration at wet nectaries (Fig. 4c). The three EFN conditions were tested for differences in number of planidia and were significantly different at Site 1 (Kruskal-Wallis  $H_2 = 9.891$ ;  $p = 0.0071$ ). For both sites, more planidia were in the EFN ( $9.50 \pm 2.85$ ) than outside EFN ( $1.00 \pm 0.60$ ). Additionally, planidia were most uncommon at wet nectaries at Site 4 ( $0.06 \pm 0.17$ ).



**Figure 4.** Distribution of immature stages among the three conditions of extrafloral nectaries (EFN) in AZ, 1999. **a** undeveloped eggs **b** developed eggs with mature planidia **c** planidia. Regrowth samples excluded.

## Ant Associations

**Host Record.** A single nest of *Pheidole desertorum* was excavated that contained larvae and pupae of *O. simulatrix* (Fig. 1h). Of 30 excavated nests of various ant species nesting near *C. linearis*, only one *P. desertorum* nest contained *O. simulatrix* (Table 2). This is the first host record for any member of the *O. simulatrix* species group. Of 229 ant larvae, 97 (42%) had a total of 119 planidia. Planidia were either surface-attached or embedded (c.f. Wheeler 1907), even on the same ant larva. When burrowed, the anterior end of a planidium penetrates the body of the larva, and the posterior end remains exposed. Twelve second-instar ant larvae had two or three planidia each, three third-instar ant larvae had two or three planidia, and three fourth-instar larvae had two or three planidia each. No first-instar larva had more than one planidium attached. Although cases of multiple parasitization by planidia were common, only a single second or third instar of *O. simulatrix* were found on individual *P. desertorum* pupae. These latter instars were located on the thoracic sternites of the ant pupae. In the lab colony, *O. simulatrix* pupae nearing eclosion were removed from the brood pile by worker ants and

**Table 2.** Ant nests excavated within two metres of *Chilopsis linearis* (1997–1999).

Ant Species	Colonies with Brood	Colonies without Brood	Number of Nests Parasitized
<i>Aphaenogaster cockerelli</i> Andre	1	0	0
<i>Camponotus festinatus</i> Buckley	0	3	0
<i>Crematogaster</i> sp.	0	1	0
<i>Forelius pruinosus</i> Roger	1	0	0
<i>Formica</i> sp.	1	4	0
<i>Monomorium</i> sp.	1	1	0
<i>Myrmecocystus mimicus</i> Wheeler	0	3	0
<i>Pheidole desertorum</i> Wheeler	2	2	1
<i>Pheidole tusconica</i> Wheeler	1	1	0
<i>Solenopsis aurea</i> Wheeler	1	1	0
<i>Solenopsis xyloni</i> McCook	2	2	0
<i>Tetramorium hispidum</i> Wheeler	1	1	0

placed in one of several refuse piles inside the humidity chambers. A total of 35 second and third instar larvae, and 32 pupae of *O. simulatrix* were found in the nest. *Orasema* do not kill the host pupa but leave behind a living but deformed ant pupa, as described by Wheeler (1907). The number of worker caste affected (128 phthisergates) was far greater than the number of alate castes (three phthisogynes and no phthisaners). These parasitized pupae represented only 13% of the 974 ant pupae recovered.

**Morphology of Immature Stages of *Orasema*.** *Egg.* The undeveloped eggs of *O. simulatrix*, as found in plant tissue, are white, elliptical in shape, and stalked, as described for nearly all eucharitids (Heraty 1994b; 2000). *Planidia* (Fig. 1e–g). These are similar to *O. xanthopus* (Heraty et al. 1993), but with the caudal cerci as long as the terminal three segments. *Second Instar.* The bodies of second instar larvae are white and weakly sclerotized, with the dorsal surface covered by minute pustulate lumps and one spherical tubercle occurring laterally on the thorax. *Third Instar.* The bodies are white and weakly sclerotized, with the dorsal surface covered by minute pustulate lumps, and one spherical tubercle occurring laterally on the thorax. *Pupa* (Fig. 1h). The pupa contains three swollen nodules along the petiolar region, and one prominent lateral nodule near the mesothoracic spiracles. These characteristics are consistent with other pupae of *Oraseminae* (Heraty 1994b; 2000; Heraty et al. 1993).

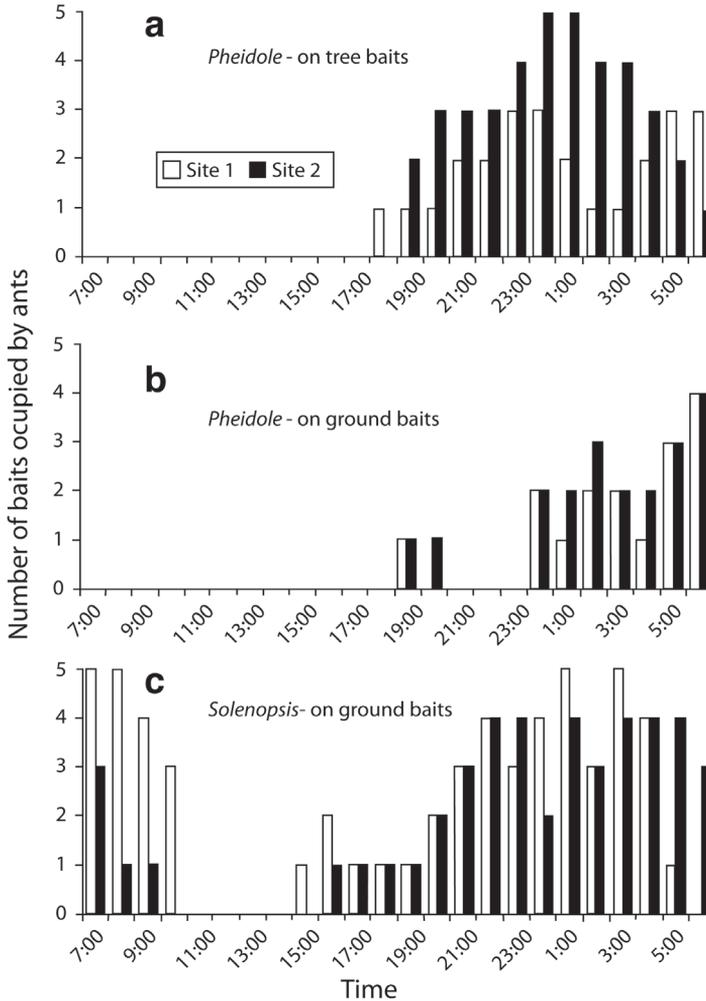
**Ant Presence and Activity.** Twelve species of ants were found nesting within two meters of *Chilopsis linearis* from which adult *O. simulatrix* had been swept (Table 2). Of these, *Pheidole* (2 spp.) and *Solenopsis* (2 spp.) are known hosts for *Orasema* (Heraty 1994a). Only *P. desertorum* has been previously recorded as a host for another species, *Orasema occidentalis* Ashmead (Snelling and George 1969). Many more nests were casually observed, but Table 2 provides data only for nests excavated near the host trees. Of the encountered nests, only *Myrmecocystus mimicus* Wheeler, *Solenopsis xyloni*

McCook and *Pheidole desertorum*, including the one parasitized colony, nested near the base of *C. linearis*.

*Camponotus festinatus* (Buckley), *M. mimicus* and *P. desertorum* were nocturnal species that foraged at and drank from extrafloral nectaries on *C. linearis*. Similar foraging and drinking activities at the nectaries were observed for diurnal ants such as *Forelius pruinosus* (Roger) (commonly, but in low numbers) and *Monomorium* (rarely and only a few individuals). *Forelius* was commonly sampled at bait stations, but the other diurnal ants were only rarely sampled at baits (less than 15 individuals in all studies). *Pheidole desertorum* was the most commonly seen ant in baits in the tree at night (Fig. 5a). *Pheidole tucsonica* Wheeler and *Solenopsis* sp. were not observed at baits in the canopy of *C. linearis*. *Pheidole desertorum* was common at ground bait stations (Fig. 5b), but was largely superseded by *S. xyloni* (Fig. 5c). Foraging activity by *Pheidole* was similar at both sites and time periods sampled, beginning close to sunset (6:00 P.M.) and ending by sunrise (7:00 A.M.) with peak activity through the night. *Solenopsis xyloni* had a much longer period of foraging, being present at 3:00 P.M. through 11:00 A.M. the following morning. At the ground bait station, both *P. desertorum* and *S. xyloni* could be found together, but only when there were less than 10 individuals of either species. Besides the dominant, ground-foraging *S. xyloni*, other species that were moderately active at baits on ground included other myrmicines such as *Aphaenogaster cockerelli*, *Pogonomyrmex rugosus*, and *Pogonomyrmex barbatus*, and several non-myrmicines such as *Formica*, *Myrmecocystus* and *Forelius*. Rarely observed ant species that foraged at ground baits included *Tetramorium hispidum*, *Crematogaster* sp., and *Pheidole tucsonica*.

**Thrips and Ant Interactions.** *Neohydatothrips* sp. (Thripidae) was the only thrips found associated with *C. linearis*. This is a polyphagous, flower-loving genus, found in the Nearctic and widely distributed in the Neotropics (L. Mound, pers. comm.). Immature and adult thrips were observed mostly in flowers or on leaves in the terminal growing tip of branches of *C. linearis*, but only rarely were adults or immatures found on mature leaves (Categories 1–6), and none were observed in direct association with leaf nectaries. None of the adult thrips were observed to harbor planidia. Of 143 immature thrips observed from field samples (all plant structures), none had an attached planidium.

To explore the interaction between planidia and immature thrips, single planidium were placed close to but not on a single immature thrips (12 trials), and directly on the immature thrips (45 trials). After at least four hours, only 4% (2/45) of the planidia remained on the immature thrips. Of these, one planidium remained attached to the surface of the thrips, while the other burrowed through the cuticle of the immature thrips as has been reported for other species of *Orasema* (Das 1963; Heraty 2000; Johnson et al. 1986; Wheeler and Wheeler 1937). None of the planidia that were remote from the thrips attached to a thrips. Throughout this study, similar trials were conducted with *O. occidentalis*, a species that is more typically associated with immature thrips. In contrast to the results for the *simulatrix* group, planidia of this species were commonly found attached to immature thrips in flowers of *Acacia constricta*. Similar laboratory trials for this species had approximately 32% (18/56) of the planidia remain attached to thrips, including both superficial and burrowed attachment.



**Figure 5.** Ant abundance at baits on or near *Chilopsis linearis* in AZ, 1998. **a** *Pheidole desertorum* on tree **b** *P. desertorum* on ground **c** *Solenopsis xyloni* on ground. Only *P. desertorum* was recovered at baits in the tree.

Other experiments with *O. simulatrix* investigated several behavioral components of the planidia, including the attachment of planidia to adults of three ant species. One of eight planidia remained on workers of *P. tucsonica*. Of 10 planidia placed on workers of *P. desertorum*, none remained attached after a similar time period. Two of 12 planidia remained attached to workers of *S. xyloni*. Thus, only three of 30 planidia (10%) placed on workers remained attached after four hours. These planidia remained where they were placed on the ant host and did not migrate to what might be considered as appropriate places for transfer to the larval host, such as the mouthparts. Planidia were placed on eight mature larvae of *P. desertorum* and eight mature larvae of *S. xyloni*; no planidia remained on the host for more than four hours. In 1999, 83

foraging ant workers were collected from leaves and branches of *C. linearis* at Sites 3 and 4; none had attached planidia. Twelve trials were set up in which one to five ants were placed in petri dishes with leaves of *Chilopsis* that had filled or wet nectaries and planidia. Ants did not show any particular interest in the nectaries, possibly as a result of the artificial setup, and overnight, no planidia were found attached to the included ant workers. Ants offered thrips with and without attached planidia were not observed to prey on or carry thrips alone, or thrips with planidia placed on their bodies. Of 250 adult workers of *P. desertorum* collected in 2011 from *C. linearis* (near Site 3) infested with planidia of *O. simulatrix*, none of the workers had planidia attached externally or, after dissection, embedded within their mouthparts. Thus, to date no direct observations have been made of the planidia being transferred by the ant host to the nest.

## Discussion

Planidia of several species of *Orasema* representing most New World species groups and one Old World species group are postulated as being dependent on an interaction with intermediate hosts to move from their plant hosts to the nest of their ant hosts (Clausen 1940a; b; Das 1963; Heraty 1990; 1994b; 2000; Kerrich 1963; Wheeler and Wheeler 1937). Presumably, planidia encounter and attach to immature thrips or immature cicadellids on plants, and are later carried by predaceous or scavenging ants back to the nest where they are placed in direct contact with the larval host (Clausen 1940a; b; 1941; Das 1963; Heraty 1994a; 2000). *Orasema simulatrix* is one of the few New World species that does not appear to have a thrips association. The *simulatrix* group is considered to be a derived group within *Orasema* (Heraty 2000), and is nested within a clade of species usually associated with a thrips intermediate host. Based on their position, a similar pattern of behavior would be expected from planidia of the *O. simulatrix* group. Our new data concerning planidia of *O. simulatrix* indicate unique behaviors that allow the planidia to gain transport from the host plant to the interior of the ant nest. First, females oviposit immediately adjacent to moist nectaries on leaves of the host plant. Second, planidia do not attach to intermediate hosts, but instead migrate to nectaries, where they are likely to encounter foraging workers of *Pheidole desertorum*. We have not been able to prove this final step, but the association is extremely strong, especially as *Pheidole* are the dominant ant foragers on *Chilopsis* they have been observed feeding at nectaries, and they are the only documented host association.

The distribution of planidia observed in nectaries on leaves of *Chilopsis* may be due to one or several interacting factors. Both total number and qualitative condition of nectaries change along shoots of *C. linearis* (Fig. 2). The distribution of immature stages of *O. simulatrix* was not uniform along the branch, and although wasps preferred to oviposit next to nectaries, there was no correlation between eggs laid and total number of nectaries (Figs 2, 3). However, the most recent oviposition events, based on the presence of white, undeveloped eggs, were biased toward nectaries filled with

fluid or at least wet (Fig. 5a). Older dry nectaries were generally least favored (Fig. 5a,b). Planidia, as indicators of old oviposition, were not present in the apical 1-10 leaves and the growing tip, except in the regrowth sample. There was a general progression of development of *O. simulatrix* along the branch, from undeveloped (light) to developed (dark) to planidia. Planidia were mostly found on older Category 3 and 4 leaves. In general, the more basal leaves had fewer nectaries, and on typical growth branches, these were mostly dry. Most nectaries were in Category 4 (31-40 leaves from growing tip), but this was the least favored area for oviposition. When nectary condition was more evenly distributed, as in the two regrowth samples, oviposition events were also more evenly distributed along branches. The placement of eggs appears to be biased toward the fresher leaves with the most fluid-filled nectaries, with planidia emerging near EFN that are most likely either fluid filled or wet. This would maximize encounters with foraging ant workers feeding at the nectaries. A direct association with the nectary, either on the rim of the nectary or within the fluid of the nectary, likely maximizes the chances for the planidia to be orally transferred along with the nectar/food by trophylaxis to the ant larvae within the nest.

Overall, the evolution and behavior of *O. simulatrix* are tied to its ant host, with the wasp dependent on the host plant. This wasp is closely associated with a common desert plant that can harbor populations of an ant host such as *P. desertorum*. Furthermore, both adult female wasps and planidia exhibit behaviors that increase the chances of encounter between planidia and their ant hosts. The use of extrafloral nectaries has not been documented for any ant parasitoid. A direct food-source interaction is known only for eucharitid parasitoids of camponotine ants, which lay their eggs into fruit attractive to the ants (Heraty and Barber 1990). With the vast diversity of foraging behaviors, food sources, and plant associations of ants, these factors may allow a broader avenue of opportunity for adaptations by the wasps to their particular ant hosts.

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# A hymenopterists' guide to the Hymenoptera Anatomy Ontology: utility, clarification, and future directions

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## Abstract

Hymenoptera exhibit an incredible diversity of phenotypes, the result of ~240 million years of evolution and the primary subject of more than 250 years of research. Here we describe the history, development, and utility of the Hymenoptera Anatomy Ontology (HAO) and its associated applications. These resources are designed to facilitate accessible and extensible research on hymenopteran phenotypes. Outreach with the hymenopterist community is of utmost importance to the HAO project, and this paper is a direct response to questions that arose from project workshops. In a concerted attempt to surmount barriers of understanding, especially regarding the format, utility, and development of the HAO, we discuss the roles of homology, “preferred terms”, and “structural equivalency”. We also outline the use of Universal Resource Identifiers (URIs) and posit that they are a key element necessary for increasing the objectivity and repeatability of science that references hymenopteran anatomy. Pragmatically, we detail a mechanism (the “URI table”) by which authors can use URIs to link their published text to the HAO, and we describe an associated tool (the “Analyzer”) to derive these tables. These tools, and others, are available through the HAO Portal website (<http://portal.hymao.org>). We conclude by discussing the future of the HAO with respect to digital publication, cross-taxon ontology alignment, the advent of semantic phenotypes, and community-based curation.

## Keywords

URI, morphology, biodiversity informatics

## Background

Hymenopterists share a common interest, in part, because their research almost invariably requires the study of or reference to hymenopteran anatomy. Which morphological characters are diagnostic or phylogenetically informative? How is behavior manifested morphologically? In what part of the body are certain genes expressed or certain odors detected? Our collective knowledge of this complex data source, however,

remained decentralized, resulting in a corpus of observations that remained relatively disconnected and dispersed in the literature.

There have been numerous attempts to clarify relevant anatomy, spanning from comprehensive anatomical treatments of character systems across Hymenoptera (e.g., Oeser 1961 for the ovipositor system, Gibson 1985 and Vilhelmsen et al. 2010 for thoracic structures, Vilhelmsen 1996 for preoral cavity in lower Hymenoptera, Schulmeister 2001 for male genitalia), to more focused taxonomic treatments that cover anatomy at a relatively small scale (e.g., Sharkey and Wharton 1997 for Braconidae, Gibson 1997 and Gibson et al. 1998 for Chalcidoidea, Bolton 1994 for Formicidae, and Michener 2000 for Anthophila). There has been proportionally little effort, however, to unify our collective knowledge of hymenopteran anatomy in a way that is both deeply anatomical and broadly taxonomic (but see Richards 1977, Vilhelmsen et al. 2010). Clarification of anatomical terminology is only one benefit of an ontology. As described by Deans et al. (2012), incorporating concepts from an anatomy ontology into our descriptions allows them to be useful for the greater scientific community and creates a corpus of semantic statements about biodiversity. Simply speaking, applying ontology to taxonomy makes our descriptive statements relevant and utilizable by many scientific disciplines, from new prospective students of Hymenoptera to genomic discovery, to many purposes not yet conceptualized.

In 2006, at the 6<sup>th</sup> International Congress of Hymenopterists meeting in South Africa, a proposal was made to develop a new mechanism for clarifying hymenopteran anatomy: the Hymenoptera Anatomy Ontology (HAO; Deans and Ronquist 2006). Preliminary data and a prototype collaborative ontology editing interface was developed shortly thereafter primarily by ARD and MJY. In 2008, MJY and ARD used these efforts as leverage to secure funding from the United States National Science Foundation's Advances in Biological Informatics program. The applications and approaches described herein, alongside the ontology itself, are products of the ongoing project.

The HAO has since grown into the largest, best illustrated, and most documented multi-species arthropod anatomy ontology and now includes 2055 anatomical concepts and 3622 terms for these concepts, which are extensively annotated (2880 image-based, sub annotated with 2912 figure annotations; 5686 text-based), with 269 references linking terms to concepts (see Table 1 for definitions of concept/term). These data are derived from existing publications (the HAO database contains >1000) and ongoing research by HAO curators and other contributors.

Yoder et al. (2010) described the general development and structure of the HAO and outlined some of the core problems we seek to address through the development and application of an anatomy ontology, including homonymy (same term for different structures), synonymy (different terms for the same structure), and concept drift (application of a term to an increasingly diverse set of structures over time). General ontological issues, specific anatomical challenges and potential applications of the HAO have been discussed at several meetings (2009–2011 Entomological Society of America meetings, 7<sup>th</sup> International Congress of Hymenopterists) and at workshops

**Table 1.** Glossary of ontology-related terminology.

Word	Definition
Class	A synonym of <i>concept</i> , in the context of the HAO.
Concept	The idea (primarily the definition and related annotations) that circumscribes our understanding of an anatomical feature, as denoted by its structural properties. For example, “The tagma that is located anterior to the thorax” defines the concept commonly referenced by the <i>term</i> “head”.
Concept Drift	The application of a term to an increasingly diverse set of structures over time.
Genus-differentia	A type of definition structured so as to first describe a more inclusive class of <i>concepts</i> (genus) and then the characteristics differentiating ( <i>differentia</i> ) it from other children of that concept. Definitions in this format typically follow the pattern “The <i>x</i> that is <i>y</i> .” Biologists will recognize this as the way Linnaeus structured scientific names.
Homonym	A term that is used for two or more <i>concepts</i> .
Instance	A real-life exemplar of the <i>concept</i> . For example, the actual physical head of a specific specimen, perhaps one of many collected by Lubo Masner, is an instance of the HAO <i>class</i> identified by the <i>URI</i> <a href="http://purl.obolibrary.org/obo/HAO_0000397">http://purl.obolibrary.org/obo/HAO_0000397</a> .
Label	The HAO has in the past used <i>label</i> and <i>term</i> interchangeably; here we use <i>term</i> to reflect the broader use of the latter.
Ontology	A set of <i>concepts</i> and <i>relationships</i> (properties) pertaining to a particular domain of knowledge (e.g. hymenopteran anatomy). Ontology is a mechanism of classification. In the case of the HAO, a goal is to allow a user to classify anatomical structures within a logically consistent framework.
Obsolete Concept	Once an HAO identifier (e.g. HAO:0000397) is assigned to an anatomical concept, that <i>concept</i> will not be altered except for misspellings or obvious grammatical errors. If there is a fundamental problem with a <i>concept</i> definition (and therefore its <i>URI</i> ) that <i>concept</i> is made obsolete but remains resolvable.
Relationship	A property (or attribute) shared between two <i>instances</i> (e.g., “mouthparts part_of head”). Within the HAO, relationships are recorded as linking two <i>concepts</i> , however when the ontology is applied to real-life examples, the relationships apply to instances of those <i>concepts</i> . For example, “the eye is not part of the head” (as recorded in the ontology), but rather “my eye is part of my head”.
Semantic Phenotype	Structured annotations that represent observations of the phenome (see Deans et al. 2012). A semantic phenotype is a descriptive statement that can be used in computation, or some logical inference.
Sensu	A data construct that is a combination of a <i>concept</i> , <i>term</i> , and an associated reference. For example, Snodgrass (1941) used the <i>term</i> “phallobase” in combination with the <i>concept</i> <a href="http://purl.obolibrary.org/obo/HAO_0000713">http://purl.obolibrary.org/obo/HAO_0000713</a> (“The anatomical cluster that is composed of the cupulae, gonostipites and volsellae.”). See discussion and definition in Yoder et al. (2010).
Structural Equivalence	Topographical sameness of structures.
Synonyms	Two or more <i>terms</i> used to reference the same <i>concept</i> . For example, both <i>terms</i> “phallobase” and “paramere” have been used to reference the <i>concept</i> <a href="http://purl.obolibrary.org/obo/HAO_0000713">http://purl.obolibrary.org/obo/HAO_0000713</a> .
Term	A name (e.g., word, phrase, acronym) representing a <i>concept</i> to a human user. For example, “head”. (compare <i>label</i> )
URI	In the context of the HAO, a unique identifier for a <i>concept</i> . HAO URIs are resolvable, i.e., if used in a web browser additional information will be provided to the person or agent (other computer) that made the request. For example, <a href="http://purl.obolibrary.org/obo/HAO_0000713">http://purl.obolibrary.org/obo/HAO_0000713</a> is the <i>URI</i> for the <i>concept</i> “The anatomical cluster that is composed of the cupulae, gonostipites and volsellae.”

hosted at North Carolina State University (2010), the Swedish Malaise Trap Project's 3rd Hymenoptera Workshop in Öland, Sweden (2011), and the HAO email list. Based largely on the dialog generated through these interactions we offer here a hymenopterist-centric reintroduction to the HAO, which focuses on describing new tools and on clarifying some frequently asked questions. The topics addressed herein came up in discussion as points of confusion about ontology and were identified as road blocks to fully understand the reasoning behind how the HAO is created and how it would benefit the community beyond a glossary of terms. We attempt to address ontology-related jargon here through our own glossary (Table 1), rather than avoiding the terminology altogether. We also describe how to contribute to the ongoing development of this community resource.

## **The Hymenoptera Anatomy Ontology Project**

The HAO is more than a simple glossary, as it is formally structured and follows rules of logic (Yoder et al. 2010). The HAO also serves as the core element of a larger “ecosystem” of digital tools designed to facilitate a more rigorous approach to the study of, and reference to, hymenopteran anatomy. In addition to the discussion provided here on format, archiving, and use, readers are encouraged to learn (and share) more about the HAO on the HAO Wiki (<http://hymao.org>).

### **Format of the HAO**

The raw, archived representation of an ontology, such as the HAO, is an explicitly formatted and defined text file. Typically these files are in Web Ontology Language (OWL; <http://www.w3.org/TR/owl-features>) or Open Biomedical Ontology (OBO; <http://www.geneontology.org/GO.format.shtml>) format. The OWL family of languages is a general-purpose means of representing knowledge on the Web, and their development is supported by the World Wide Web Consortium (W3C; <http://www.w3.org/>). OBO specifications are much more narrowly focused and technically simpler, their purpose being to serve the specific needs of biologists who use ontologies. With some exceptions not yet pertinent to the HAO, tools exist to losslessly (i.e., without loss of data/meaning) translate between OWL- and OBO-formatted ontologies, and the HAO can be downloaded in either format (OWL: <http://purl.obolibrary.org/obo/hao.owl> or OBO: <http://purl.obolibrary.org/obo/hao.obo>).

### **Where to find the HAO**

Hymenopterists will most likely access the HAO through the HAO Portal website (<http://portal.hymao.org/>; see below), but the ontology itself is accessible through

several widely used biomedical databases. For example, the HAO is one of many ontologies archived by the Open Biomedical Ontology (OBO) Foundry (<http://www.obofoundry.org>). The OBO Foundry supports archiving and development of OWL and OBO formats as part of an effort to maintain and promote the use of biological ontologies across biological and medical domains. The OBO Foundry also facilitates ontology dissemination and use, and ontologies archived there are automatically made available through other portals such BioPortal and Ontobee (for the HAO versions see <http://bioportal.bioontology.org/ontologies/1362> and <http://www.ontobee.org/browser/index.php?o=HAO> respectively). Our association with the greater biomedical ontology community, especially the National Center for Biomedical Ontology (<http://www.bioontology.org/>), ensures that the HAO will be archived for long-term sustainability and distributed for broad use in other domains.

### **The HAO in the broader community**

Protocols for ontology construction are produced by a large community of ontologists (HAO curators included), some of whom work with anatomy ontologies in practical ways and others who are more theoretical and primarily concerned with the logic inherent in the structure of ontologies. It is important for the HAO, as it is for any anatomy ontology, to be integrated into larger ontology initiatives. As contributors to the larger anatomy ontology community, the collective HAO is naturally incorporated into a field of research that embraces many biological disciplines and taxa. We benefit from, and contribute to, the efforts of the entire ontology community, including their infrastructure and software advances. By working within larger initiatives we ensure that the HAO is positioned to take advantage of ongoing initiatives (e.g. integration with the genomics community).

### **The HAO “ecosystem”**

The principal product of the HAO Project is the ontology itself, but the process of development has also resulted in multiple applications, built upon the ontology, that facilitate Hymenoptera research. HAO developers are responsible for creating human-usable Web interfaces and applications that make the text-file ontology into tools for the biological community, and to encourage an ontology-based approach to morphology. The primary application is the Hymenoptera Anatomy Ontology Portal (formerly the “Hymenoptera Glossary”). The HAO Portal displays data contained within the Hymenoptera Anatomy Ontology, as well as other information useful for Hymenoptera research including annotated images, alternative definitions, comments from users, ontology visualization tools, an extensive bibliography, and the “analyzer” tool (described below).

## **Unique identifiers for anatomical concepts**

Most hymenopterists are familiar with the process of submitting sequences to GenBank and receiving unique identifiers (i.e., GenBank accession numbers) that serve as published references to their data. The HAO serves a similar function for anatomy by providing unique identifiers for anatomical concepts. The identifiers used by the HAO are Uniform Resource Identifiers (URIs) that consist of a Persistent Uniform Resource Locator (PURL: <http://purl.obolibrary.org/obo/>) plus an HAO identifier in OBO format (e.g. HAO:0000397). The latter is a combination of the namespace used in the OBO Foundry (“HAO”) and a unique seven-digit number (e.g. “0000397”). The “:” in the identifier is replaced with an “\_” in the URL form. Any given URI points to only a single concept within the HAO (e.g. [http://purl.obolibrary.org/obo/HAO\\_0000397](http://purl.obolibrary.org/obo/HAO_0000397) = “The tagma that is located anterior to the thorax” = head).

## **The virtue of URIs**

The concept of the URI is important because it allows the HAO to be utilized in multiple contexts. Within Web browsers (e.g. Firefox, Google Chrome, Internet Explorer) many URIs (including the HAO’s) may be used in the same manner as URLs (Uniform Resource Locators) for webpages. URIs, in combination with Web-server configurations, allow for different responses, based on who is making the request. For example, a request from a Web browser—a person clicking on a link in a journal article or website—would return content that a human can interpret (e.g., a webpage), whereas requests from computational sources would receive responses that the application can understand (leaving out the human-readable components). This core functionality is at the heart of the long-term use and application of HAO URIs within publications, websites, applications and analyses. The challenge then is to facilitate the production, use, and publication of URIs (see below).

## **Referencing the HAO in publications**

### **The URI Table**

Materials and methods sections within papers that reference hymenopteran anatomy frequently point to concepts published elsewhere (e.g., “Morphological terminology largely follows Mikó et al. 2007” in Talamas et al. 2011). New or revised anatomical concepts are typically paragraphical, with terms highlighted and a definition or discussion following (e.g. Yoder 2004). Here we introduce an alternative, table-based format that facilitates reference to existing anatomical concepts within the HAO. Examples exist in Johnson and Musetti 2011, Mikó et al. 2012, and Talamas et al. 2011. In its simplest format the table only requires two columns: a term and a URI. The format,

including its required elements and additional optional extensions (up to six total columns), is exemplified in Table 2. An explanation of the columns follows:

1. **Term:** The literal text (string of letters) used in the paper for the anatomical concept. It is important to reference anatomical terms used within the table exactly throughout a paper, to eliminate ambiguity. Simplification of terms within a document, without including these simplifications in the table, reduces the effectiveness of a table intended to clarify terminology. For example, if “abdominal tergum 3” is in the table, the structure should be fully referenced throughout the document as “abdominal tergum 3” and not simplified to “the tergum” anywhere.
2. **URI:** The unique, resolvable, identifier for the anatomical concept. HAO curators create these identifiers, which can be found by accessing the HAO Portal.
3. **Definition:** A verbatim replication of the definition in the HAO, which are written as genus-differentia (see Smith 2005).
4. **Definition source:** A citation from which the concept/definition was derived; within the HAO
5. **HAO preferred term:** The present preferred term for the concept denoted by the URI in the HAO (see below for explanation). This term is provided only when it does not match the term the author uses in his or her publication. This option provides authors the freedom to reference anatomy in any manner he or she sees fit.
6. **Comment:** Comments may pertain to any or all of the columns for a given concept. For example they can be used to clarify subtleties or provide taxon-specific discussion.

**Table 2.** An example URI table. Starred (\*) columns are required. See discussion for details.

<b>Term*</b>	<b>URI*</b>	<b>Definition</b>	<b>Definition Source</b>	<b>HAO Preferred term</b>	<b>Comment</b>
head	<a href="http://purl.obolibrary.org/obo/HAO_0000397">http://purl.obolibrary.org/obo/HAO_0000397</a>	The tagma that is located anterior to the thorax.	Snodgrass, R. E. 1935.		
paramere	<a href="http://purl.obolibrary.org/obo/HAO_0000395">http://purl.obolibrary.org/obo/HAO_0000395</a>	The sclerite that is connected distally to the gonostipes.	Crampton, G. C. 1919.	<i>harpe</i>	
propodeum	<a href="http://purl.obolibrary.org/obo/HAO_0001249">http://purl.obolibrary.org/obo/HAO_0001249</a>	The area that is located posterior to the metapleural carina.	Mikó, I., L. Vilhelmsen, N. F. Johnson, L. Masner, and Z. Péntzes. 2007		The propodeum here is also part_of the metapectal-propodeal complex- this further bounds the somewhat generalized definition.

## Creating a URI table

URI tables are created (Fig. 1) prior to submission of a manuscript, usually in close conjunction with an HAO curator, though they can also be built independently. The goal of building a URI table is to find or help create a URI that represents the anatomical structures referenced in a paper (though a URI table that only references a subset is still useful; see Wharton et al. 2010). The highest priority candidates for a URI table are those structures that have historically been poorly defined, new concepts, or those that have synonymous and/or homonymous terms. Authors will typically reference more than one anatomical character or feature (= “pool of anatomical concepts” in Fig. 1:1) in a manuscript. This pool typically comes from the description and diagnosis sections of a manuscript.

The first step in building a URI table involves discovering available URIs (Fig 1:2), using tools available at the HAO Portal site: the simple Portal search tool, the “analyzer tool” (described in detail below), or by requesting help from the HAO e-mail list. If URIs are found they can be added to the table (Fig 1:3) after the user is satisfied with the HAO concept, citation, and labels provided. If a match is not found, or the author is not satisfied with a present concept, an HAO curator will work with the author to create a new URI (Fig 1:4). HAO curators can be contacted through the feedback form online (links from <http://portal.hymao.org>), through email directly to an HAO curator, or through contacting the broader HAO community on the listserv (<http://purl.oclc.org/NET/hymontology/listserv>). Authors are cautioned when reviewing concepts to watch for homonymy and synonymy, and not to assume that if a term match is returned that the definition will also match the authors notion of its meaning in the manuscript (Fig 1:5). In other words, authors should carefully review term definitions before adding them to the URI table. Tables can be included in Materials and Methods sections or as appendices, preferably as part of the manuscript rather than supplementary documents (Fig 1:6). While URI tables can be developed independently it is recommended that you pass along your table to the HAO curators to review prior to submission for publication. The entire process is iterative (Fig 1:7) and may be repeated multiple times as a manuscript develops.

## Using the “analyzer” tool

The goal of the analyzer tool (Fig 1:2) is to facilitate the adoption of URIs in publications and digital applications. The mechanism created to accomplish this is a simple interface (Fig. 2) for submitting an author’s anatomy-related text. The provided text is broken down into individual and groups of words, and these are compared against the terms in the HAO for matches by an internal algorithm. Terms are matched letter-for-letter, i.e., “forewing” will not match “fore wing”. No “fuzzy” matching attempts are made, i.e., the software does not try to predict what anatomical concepts the author is referring to. Matching terms are summarized by the anatomical concept to which they are attached (Fig. 2D). URIs for each matching concept are also provided. To use the analyzer follow these steps and see the online help (Fig. 2A, “What is this?”):

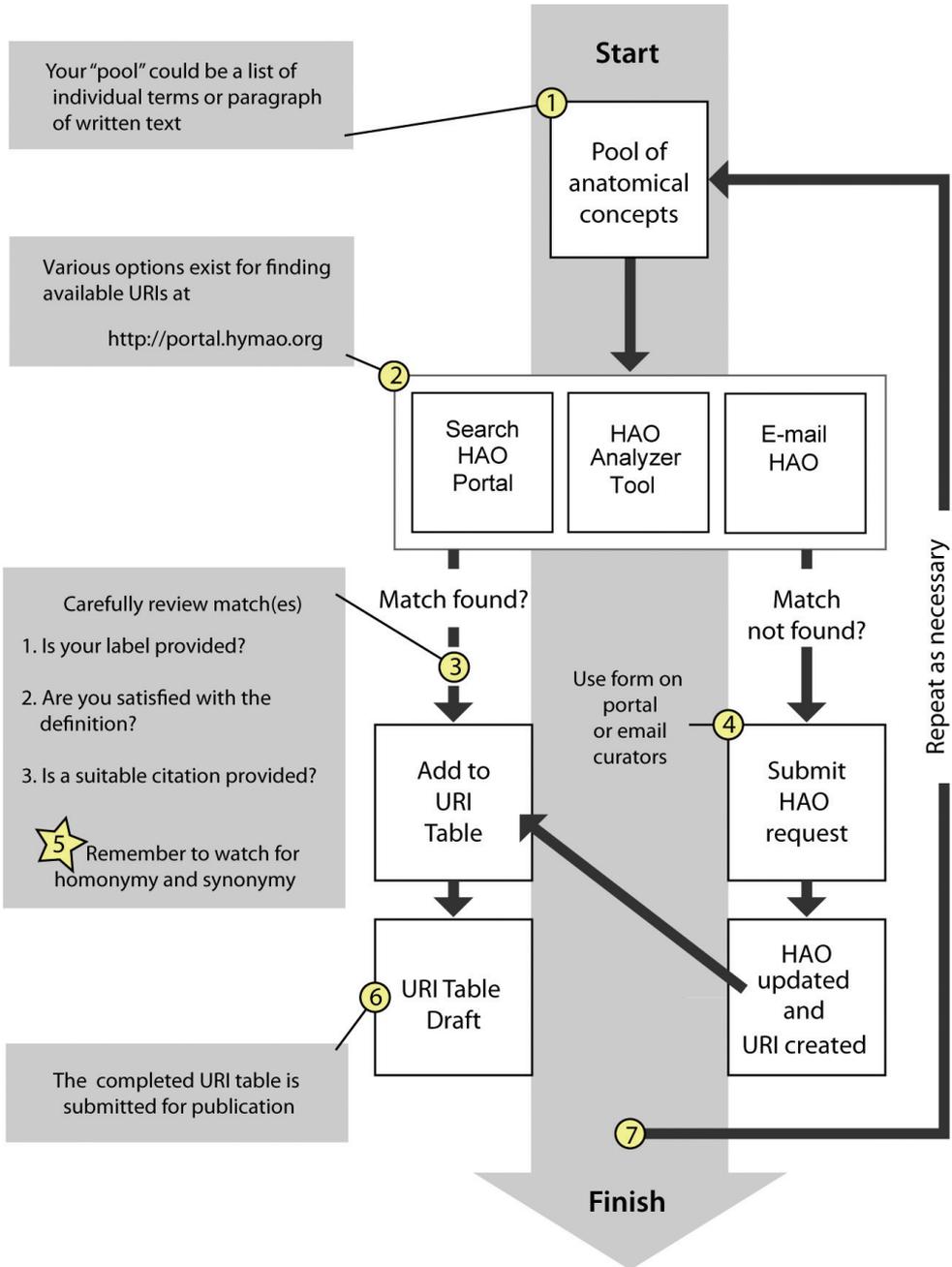


Figure 1. Workflow for drafting a URI table.

1. Provide your text: Copy and paste your text, or type directly into the text box (Fig. 2B). Try to limit the text in the box to that which is pertinent to the underlying ontology being analyzed (e.g., do not include specimen examined sections from

taxonomic descriptions, but rather the description alone). You can paste sentences, entire paragraphs from a manuscript description or diagnosis, comma-delimited lists, or any combination thereof. Typically, this would include a description and diagnosis from the manuscript.

2. Prove you are human: To discourage spammers and other troublemakers the analyzer form includes a “CAPTCHA” (<http://www.captcha.net/>) (Fig. 2C). Type the two words shown into the text box. If you need help click the small “?” on the form. Each time you click the submit button you will have to re-complete the CAPTCHA, even after you have successfully filled one out the first time.
3. Submit: Click Submit and wait (you will see a spinner turning). You might have to wait for a few seconds depending on the amount of text submitted.
4. Examine results: Results are displayed in a table (Fig. 2D) below the form. Be aware that if a term is not in the HAO it will not appear in the results list. Use the “Match Map” from the Detailed Breakdown Report (see Fig. 3) to check if all of your terms are included. References (Fig. 2, “References”) represent citations wherein the term was used in conjunction with the definition/concept as interpreted by an HAO curator. Carefully reviewing each conceptual match is critical; do not assume that the result is using the term you have provided in the manner you mean. Feedback based on missing terms, problems with definitions, etc. can be provided as outlined in Fig. 1 (and see *Curators and Curation* below). An additional breakdown of the results (Fig. 1F; Fig. 2) provides more details.
5. Download results: Download the result by clicking the “Download” button (Fig. 1E). The downloaded file is a tab-delimited file that can be opened directly in a spreadsheet program (e.g., Microsoft Excel) or a text editor.
6. Edit the results: If multiple concepts (definitions) are available for a given term choose the one that matches your concept. If you need help determining which concept to select use a feedback mechanism (Fig. 1). Delete the other rows. Repeat for all the terms in the table.
7. See more: For additional details click on “Detailed breakdown” (Fig. 1F; Fig. 3). This report can be used to visually inspect for misformatted terms, alternate spellings or usages of a term, or potentially new additions to the HAO. The report includes:
  - a. Analyzed Text: Use this to confirm that your text was submitted correctly. The analyzer may truncate your text if it is too long, or if other problems are encountered.
  - b. Match Map: The words that were matched and returned are highlighted in the context of the text here. Green highlights indicate a 1:1 mapping (i.e., there is only one concept present for the given term). Pink highlights indicate that there are multiple concepts for a given term.
  - c. Matched Terms: A simple comma separated list of the terms that were found.
  - d. Matched Classes: A list of the concepts that were matched.
  - e. Homonymous Terms: Matched terms that are homonyms.
  - f. Synonymous Terms: Matched terms that are synonyms.

## Analyze

For an explanation see [What is this?](#)

Type or paste text to analyze and complete the captcha

propodeum, head, labium

ORR. *Scienti*

Type the two words:

Submit

Result

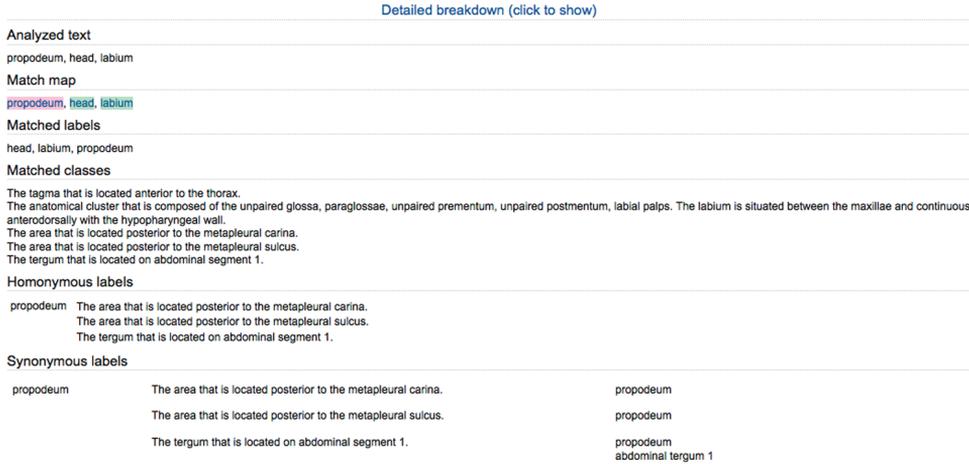
Term	Definition	URI	References	Preferred Term
head	The tagma that is located anterior to the thorax.	<a href="http://purl.obolibrary.org/obo/HAO_0000397">http://purl.obolibrary.org/obo/HAO_0000397</a>	Snodgrass, R. E. 1935.; Deans, A. R. 2009.	head
labium	The anatomical cluster that is composed of the unpaired glossa, paraglossae, unpaired prementum, unpaired postmentum, labial palps. The labium is situated between the maxillae and continuous anterodorsally with the hypopharyngeal wall.	<a href="http://purl.obolibrary.org/obo/HAO_0000453">http://purl.obolibrary.org/obo/HAO_0000453</a>	Deans, A. R. 2009.	labium
propodeum	The area that is located posterior to the metapleural carina.	<a href="http://purl.obolibrary.org/obo/HAO_0001249">http://purl.obolibrary.org/obo/HAO_0001249</a>	Miko, I. 2009.; Mikó, I., L. Vilhelmsen, N. F. Johnson, L. Masner, and Z. Péntzes. 2007.; Johnson, N. F. 1984.	propodeum
	The area that is located posterior to the metapleural sulcus.	<a href="http://purl.obolibrary.org/obo/HAO_0001248">http://purl.obolibrary.org/obo/HAO_0001248</a>	Miko, I. 2009.; Vilhelmsen, L. B. 2000.; Vilhelmsen, L. B., I. Miko, and L. Krogmann. 2010.	propodeum
	The tergum that is located on abdominal segment 1.	<a href="http://purl.obolibrary.org/obo/HAO_0000051">http://purl.obolibrary.org/obo/HAO_0000051</a>	Snodgrass, R. E. 1935.	abdominal tergum 1

[Detailed breakdown \(click to show\)](#)

**Figure 2.** Using and interpreting results from the analyzer. See Using the “analyzer” tool for explanation. **A** Help link **B** Input field **C** CAPTCHA test **D** Result table **E** Download link; and **F** Detailed breakdown link.

## Recurrent Issues

The HAO project is exemplary in its close connection to domain experts (hymenopterists), and its success depends on broad community support. During its short life, the potential utility of the HAO has already begun to emerge (e.g., Mikó et al. 2012, Johnson and Musetti 2011, Kawada 2011, Talamas et al. 2011, Mikó et al. 2010, Vilhelmsen et al. 2010, Mikó and Deans 2009, Deans and Kawada 2008, Yoder 2007). Here we attempt to clarify recurrent issues, with the goal of facilitating continued adoption of the HAO. The topics listed here result from input from many of the authors of this paper. These interactions, facilitated by the HAO email listserv, HAO Portal feedback form, workshops, and personal interactions, guided the structure of this manuscript, as well as the development of the “analyzer” tool. Integration and reference to the HAO should not be interpreted as “additional work” but rather as “due diligence”. Simply put, when an author references anatomical concepts s/he needs to ensure that those references will be consistently interpreted. Utilizing the HAO can help ensure this goal is realized.



**Figure 3.** The detailed breakdown report from an analyzer report. See Using the “analyzer” tool for explanation.

### Homology and the HAO

Understanding the criteria for defining HAO concepts is important for understanding the decision-making process for constructing the HAO and how it can be useful as a tool for referencing and aligning anatomical concepts. Fundamentally, the HAO project rests on recognizing different instances of a topographically-defined concept as “the same” (e.g., the fore wing of taxon A is the same structure as the fore wing of taxon B) (topographical homology of Jardine 1969 and Rieppel 1980; topographical correspondence of Rieppel 1988 and De Pinna 1991; topographical identity of Brower and Schawaroch 1996; homology of Owen 1843 and Remane 1952). The HAO employs the principle of “structural equivalence” to discuss topographical sameness. In biology, however, homology is often more explicit, referring to a more profound “sameness”, because it expresses a theory about structures sharing a common evolutionary origin even if they appear structurally dissimilar (homology of Patterson 1982, Nixon and Carpenter 2011, secondary homology of de Pinna 1991, Brower and Schawaroch 1996, historical homology of Wagner 1989, taxic homology of Haszprunar 1992, Scotland 2000, Wiley and Lieberman 2011, homogeneity of Lankester 1870, “Darwinian homology”). Homology in this evolutionary context is often dynamic, and may be controversial or involve conflicting hypotheses or quickly changing views. The dynamic nature of homology hypotheses conflicts with the HAO’s goal of unambiguous circumscription of anatomical concepts, and, as such, overt reference to homology hypotheses are avoided in constructing HAO definitions.

The HAO provides structure-based anatomical concepts, from which homology hypotheses can be developed and subsequently tested. This strategy derives from the premise that statements of homology, in the absence of phylogenetic tests, should be avoided. This is not to say that the construction of the HAO is not influenced by (and can influence) phylogeny-based homology hypotheses. New concepts can be derived as necessary, but these concepts will be rooted in what can be observed, not in what is hypothesized. One of the HAO's greatest strengths is that it forces the careful introspection necessary for generating strong primary homology hypotheses by forcing users to reconcile a localized understanding (e.g. an author's unwritten understanding of the anatomical nuances) with a broader conceptual framework. Many HAO concepts are sufficient for the basis of evolutionary homology hypotheses; however this is not always the case.

One example of how a structurally equivalent concept might not be homologous pertains to processes ([http://purl.obolibrary.org/obo/HAO\\_0000822](http://purl.obolibrary.org/obo/HAO_0000822)). Many distantly related hymenopterans have similarly located (i.e. structurally equivalent) pronotal spines. These spines would correspond to the same concept in the HAO, i.e., they are analogous but are not necessarily homologous.

### **Classifying anatomical structures using structural equivalency**

Structural equivalency allows clustering of anatomical structures described in the literature, based on clear, repeatable criteria—i.e. the criteria are observable, not hypothesized. Because of the structural equivalency criterion, the match between ontology concept and author concept of a term does not need to be exact but rather only structurally equivalent. HAO definitions, then, do not include all of the nuances of a concept; only the author can articulate those. When an author's concept of a term (based on observations pertaining to its structure) differs from that of the definition in the HAO (including its properties) a new concept should be created.

If an author intends to state that a particular anatomical concept was observed in some instance of a hymenopteran then that author must ensure that they observed all of the components of the anatomical concept provided in the HAO for that concept. For example, in many HAO concepts points of muscle attachment are used (an important line of evidence for topographical definitions). The author must have observed these muscles and their points of attachment to state that the class in question was present in their hymenopteran instance. Careful attention must also be made to the relationships a particular anatomical concept has to other concepts; these relationships must also be observed by the author.

There is, however, one circumstance in which anatomical concepts in the HAO might be “loosely referenced” (e.g., referencing an anatomical concept that includes, in part, reference to muscle arrangements when said muscle arrangements have not been observed). This is during the formulation or discussion of *hypotheses*, often pertaining to character evolution. For example, a paleontologist studying two fossils may wish to

discuss them in the context of anatomical concepts in the HAO: “I hypothesize that fossil one bears anatomical concept HAO 1234 *except for feature A* (which I cannot observe based on preservation), and fossil two bears anatomical concept HAO 1234 *except for feature B* (which I believe is absent, but I would like to see more specimens)”. In this hypothetical scenario minting two new HAO URIs (i.e., HAO 1234 minus feature A, HAO 1234 minus feature B), gains us little (and may be positively misleading based on the uncertainty of the observer), in the absence of additional observations. The referencing to HAO 1234, however, provides an anchor to a discussion of the evolution of an anatomical concept, something potentially of use to future researchers.

### **Separation of terms and concepts**

Terms and concepts are treated separately, and only concepts are given unique identifiers. Terms in the HAO are considered to be simply strings of letters that are used to reference concepts, associated together because they are structurally equivalent anatomical structures. Concepts encapsulate meaningful anatomical observations. Different observers looking at the same anatomical structure can have the same conceptualization of it, where it is located on the body, and the circumscription of area around it. Yet even with this similarity, they may still use different terms for the observed anatomical structure (synonymy). Different observers may use the same term yet have different understandings of when and how that term is applicable (the “sensu” construct of Yoder et al. 2010), or the same term may be used for different anatomical concepts (homonymy). The separation of concept from term is important for understanding how the HAO is useful for clarification of terminology.

### **Preferred terms**

Because there are no international rules of anatomical nomenclature, as there are for zoological nomenclature, anyone can use any terms they want to refer to an anatomical concept of interest. The HAO stands as a robust mechanism (through URIs) to clarify diverse concepts. Given the dual legacies of published literature and training histories, we envision a community where personalized lexicons continue to be refined and accommodated. Many hymenopterists, however, including a group at the 7th International Congress of Hymenopterists (Kőszeg, Hungary; June 2010), have called for the HAO Project to serve as an instrument for deciding upon preferred terms for concepts. Preferred terms facilitate accurate communication by simplifying concordance of terms with concepts, and they are required by potential HAO users in biomedicine.

Terms in a manuscript are strings of letters that may or not have meaning to a reader depending on his or her knowledge. A reader experienced enough with the terminology typically used to describe a certain taxon will not necessarily need to check the attached URI table to understand the meaning of a term. For a non-expert reader, unfamiliar

with terms in a manuscript, preferred terms may be meaningless (or even misleading). However, preferred terms are very important for experts, who use “short” terms to encompass a hidden mountain of unexpressed background information. Preferred terms also are of use to taxonomists in the early stages of developing a vocabulary for their taxa, as the set is much smaller than the total number of possibilities. If an aspiring taxonomist can navigate directly to this set they potentially become more efficient in its use and less confused by the historical baggage carried by a larger set of overlapping terms.

The HAO now has an accessible listserv (<http://purl.oclc.org/net/hymontology/listserv>) for preferred term voting. Preferred term choices are emailed to the list once or twice a week and the votes are collected with the term obtaining the most votes moved into the “preferred” position on the HAO Portal webpages. All other terms are then considered synonyms. The “term of the week” is selected based on the frequency of term usage found in past issues of the *Journal of Hymenoptera Research*. As of this writing, listserv members have voted on about 60 preferred terms, all of which may be revisited by calling for a new discussion on the listserv.

### **Why not simply include definitions in one’s paper?**

Ontologies have structure, and concept definitions therefore inherit the definitions of all the concepts contained within the definition and the concepts it is related to. Authors themselves cannot easily explicitly define all the terms used in a publication, as their definitions will inevitably include terms that must also be defined. To precisely define one concept requires an entire ontology and one that is internally consistent (i.e. only uses terms that are also defined in the ontology). In addition, the HAO project provides a wealth of additional information. By linking to concepts in the HAO authors not only explicitly define terms in their publications, but the reader also gets other information about the concept, such as which major publications used the concept, its synonyms, homonyms, annotated images, and additional comments from the HAO curators.

### **Persistence**

Our ideas of concepts may change over time, but the original concepts will never disappear in HAO. Once an HAO identifier (e.g. HAO:0000397) is assigned to an anatomical concept, that concept will not be altered except for misspellings or obvious grammatical errors. If there is a fundamental problem with a concept definition (and therefore its URI) that concept is made obsolete. Links to the obsolete concept persist, however, so that published URIs will always resolve, regardless of their standing in the current HAO. Obsolete classes in the HAO require statements as to why they were made obsolete and links to the newly derived concepts where pertinent. The obsolescence mechanism, in conjunction with a pluralistic approach to providing concepts (i.e., it is not a problem to create subtly different concepts), are strategies to minimize concept drift.

## Web-browsers

Some functionality of the HAO Portal currently does not work for some Web browsers. The HAO Project strongly recommends using Firefox (<http://firefox.org>) to view the HAO Portal pages in order to assure the proper rendering of annotated images. The HAO Portal utilizes cutting-edge functionality that some browsers (e.g., Internet Explorer, IE) presently do not support. However, if a person accesses a webpage in IE a warning message will appear directing the user to open the page in Firefox. Because free, standards-compliant browsers are available we do not see this requirement as a critical limitation. We anticipate that advances in browser capabilities related to the advent of the HTML5 standard will ensure that the HAO Portal will shortly truly become cross-browser compatible.

## The Future of the HAO

The HAO is a resource based on a foundation of explicitly defined anatomical concepts and a straightforward mechanism for dereferencing these concepts (URIs). This resource is intended for any and all users who reference Hymenoptera anatomy. The HAO, like other biological ontology efforts, is rapidly evolving, both in its underlying data and its application. Its adoption depends first and foremost on the support of the hymenopterist community. The HAO is poised to succeed thanks, in part, to technological advances in publication, ontology alignment, and the burgeoning potential of semantic phenotypes (Deans et al. 2012).

## HAO in Publications

Publications that precisely illustrate morphology routinely become the most cited and useful papers for future hymenopterists. The *Journal of Hymenoptera Research (JHR)* serves many experts and is well positioned to benefit from the rapidly growing publishing tool kit. The open-access model adopted by the *JHR* embraces the Web, pushing publications out of the traditional print-only format. Additionally, the *JHR* is published by Pensoft Press, which uses the TaxPub XML schema (Catapano 2010) to mark-up manuscripts and subsequently transform them through semantic enhancements (Penev et al. 2010). There is amazing potential for hymenopterists created by the connection of these elements and those introduced by the HAO Project. As demonstrated multiple times from output of the vSysLab workbench (<http://vsyslab.osu.edu>; Johnson 2010), TaxPub marked-up text for descriptions can be generated directly from a database, without additional formatting headaches. The resulting XML already explicitly identifies which sections of a publication are the descriptions of new taxa. Names are automatically sent to ZooBank (the International Commission on Zoological Nomenclature name-registration service), sequence data to the National Center for

Biotechnology Information (GenBank), and information is aggregated from marked-up publications by the Global Biodiversity Information Facility (GBIF) and the Encyclopedia of Life (EOL). HAO and TaxPub developers are working to integrate the URI links into the schema; thus not only will the portions of the text be identified as the description but also the terminology used in that block of text can be explicitly defined.

## Alignment

As ontologies continue to be adopted beyond the model-organism community they will be increasingly cross-referenced. Precisely defined concepts for hymenopteran anatomy, for example, can be connected to anatomical concepts in other domains that also have an ontology (e.g. Diptera). These alignments have the potential to facilitate novel evolutionary developmental biology hypotheses and hypotheses of homology. For example, while aligning the muscles in the FlyBase anatomy ontology (*Drosophila*; <http://flybase.org/>) with those concepts in the HAO, HAO developers noticed that the muscle patterns of the hymenopteran meso- and metathorax share similarities with the metathorax of different *Drosophila Ultrabithorax (Ubx)* mutants (see Rivlin et al. 2001). This approach is extensible to numerous other genotype-phenotype comparisons, and knowledge derived from *Drosophila* (or other model-organism) mutant phenotypes stands to shed light on Hymenoptera evolution. This avenue of discovery, building on the well-founded work in other model-organism communities, is made possible with well-aligned anatomy ontologies.

The process of alignment and integration across ontologies is itself an intellectually challenging endeavor. Work facilitated by the Phenotype RCN (<http://www.phenotypercn.org>), which includes several HAO developers, is supporting the development of new arthropod-specific ontologies (e.g. one each for Coleoptera, Neuroptera, and Arthropoda). Work of this nature and scope is novel and will undoubtedly lead to big discoveries and new interpretations.

## Semantic phenotypes

Deans et al. (2012) recently expressed the opinion that taxonomic diagnoses and descriptions (and perhaps other prosaic descriptions of phenotypes) should be transformed by new approaches to derive semantic phenotype (Table 1) statements. Their premise was that taxonomic descriptions (the actual descriptive text found in a taxon description or diagnosis text) are essentially inaccessible in their current form. If these data are recorded in a semantic format, however, referencing the HAO and other phenotype-relevant ontologies, they would be accessible to researchers in other domains in what is clearly an increasingly digital world. Pragmatically speaking, we are not quite prepared to complete this transformation, but hymenopterists are well positioned to

be on the cutting edge of this endeavor thanks, in part, to the existence of a robust, domain-specific anatomy ontology.

### **Curators and curation**

No formal organization currently governs the HAO, but the International Society of Hymenopterists has extended their support in making sure its future is secure. An ontology working group was formed (see ISH newsletter, March 2006), and the Society has offered to host HAO resources through their website should that service be desired by the community. The *de facto* curators (IM, MJY, ARD, KCS, MAB) strongly support community input and governance and will work with stakeholders to develop mechanisms for recruiting other curators and for facilitating decisions about ontology development (which must follow the recommendations of the broader ontology community, mainly the National Center for Biomedical Ontology and the OBO Foundry principles, to ensure robustness and broad use).

### **Conclusion**

In addition to increasing the repeatability of our research, references to well-defined and illustrated anatomical concepts will open up their interpretation and use to a much broader array of users than just highly specialized scientists. Biodiversity, host-parasite biology, collections digitization, genomics, ecology, evolutionary developmental biology (evo-devo), invasive species evaluation, agro-ecosystem management and biological control (to name just a few) as well as those aspects of society impacted by these all rely on the correct interpretation of anatomical structures (e.g., Mikó et al. 2012). The core mechanism by which one can reference the HAO, URIs, is implementable now via simple URI tables. Much more needs to be done to transparently and seamlessly integrate the HAO into the scientists' workflow for maximum benefit of scientists and the users of their science, but the basic mechanism, URIs, will be central to these emerging methods. As we move forward into an exciting period of exploding new technologies and exploration we ask that the hymenopterist community continue to participate in the growth, refinement, and evolution of the HAO.

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