RESEARCH ARTICLE

Trigonalidae (Hymenoptera) of Thailand, other southeastern Asian records, and a new *Trigonalys* from India

David R. Smith[1], Pierre Tripotin[2]

1 *Research Associate, Department of Entomology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, MRC 168, Washington, DC 20013-7012* **2** *10 Crowther Street, Whitfield Cairns, Queensland 4870, Australia*

Corresponding author: *David R. Smith* (sawfly2@aol.com)

Citation: Smith DR, Tripotin P (2015) Trigonalidae (Hymenoptera) of Thailand, other southeastern Asian records, and a new *Trigonalys* from India. Journal of Hymenoptera Research 44: 1–18. doi: 10.3897/JHR.44.4495

Abstract

Seven species of Trigonalidae are recorded from Thailand, *Lycogaster flavonigrata* Chen, Achterberg, He & Xu, *L. rufiventris* (Magretti), *Taeniogonalos fasciata* (Strand), *T. gestroi* (Schulz), *T. sauteri* Bischoff, *T. tricolor* Chen, and an unidentified species. Four species, *L. flavonigrata*, *T. cordada* Chen, Achterberg, He & Xu, *T. sauteri*, and *T. tricolor* are newly recorded from Laos. Diagnoses, illustrations, and distribution records are given for the Thailand species. *Trigonalys india* Smith, **sp. n.,** is described from southern India for specimens previously misidentified as *T. rufiventris*.

Keywords

Introduction

Trigonalidae is a small, worldwide family with the greatest diversity in the tropical regions. However, there are few records from southeastern Asia, most of which are recorded in Carmean and Kimsey (1998) and Chen et al. (2014). Previously, only two species were known from Thailand, *T. gestroi* (Schulz, 1908) (as *Taeniogonalos thwaitesii* (Westwood, 1874)) and *T. tricolor* Chen, 1949, and only one species from Laos, *T. gestroi*. Here,

we record seven species from Thailand and five species from Laos, provide records of other species examined from southeastern Asia, describe the previously unknown male of *Lycogaster rufiventris* (Magretti, 1897), and describe a new species of *Trigonalys* from India which had been misidentified as *L. rufiventris*.

Materials and methods

The basis and focus for this study are the collections made by the Thailand Biodiversity Inventory, a collaborative project initiated by M. J. Sharkey, University of Kentucky, Lexington, and the Queen Sirikit Botanical Garden and National Parks, Wildlife, and Plant Conservation Department of Thailand. These collections included two species of *Lycogaster* and four species of *Taeniogonalos*. The collections from Laos are from the Oberösterreichische Landes Museen Linz, Linz, Austria. A few additional records are from other collections listed below.

Museum acronyms are as follows: Canadian National Collection of Insects, Ottawa, Canada (CNC); Oberösterreichische Landes Museen Linz, Linz, Austria (OLML); Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZ); Oregon State Arthropod Collection, Department of Zoology, Oregon State University, Corvallis, OR, USA (OSAC); Oxford University Museum of Natural History, Oxford, UK (OXUM); Queen Sirikit Botanical Garden Entomological Collection, Chiang Mai, Thailand (QSBG); National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM); and the collection of Pierre Tripotin, Whitfield Cairns, Australia (PT).

Images were obtained using an EntoVision Imaging Suite that included a firewire JVC KY-75 3CCD digital camera mounted to a Leica M16 zoom lens via a Leica z-step microscope stand. Multiple focal planes were merged using Cartograph 5.6.0 (Microvision Instruments, France) software.

Locality data are given essentially as they appear on the specimen labels. Complete synonymies, except *L. rufiventris*, are found in Chen et al. (2014). A key to genera, descriptions and illustrations of all species, except *L. rufiventris*, and synonymies are given in the treatment of the Trigonalidae of China (Chen et al. 2014).

Results

Lycogaster flavonigrata Chen, Achterberg, He & Xu
Figs 1–3

Lycogaster flavonigrata Chen, Achterberg, He & Xu, 2014: 49, figs 119–129.

Diagnosis. Female. Length 10.5 mm. Antenna, head, and mesosoma black. Legs black with trochanters and small spot at base of each tibia white. Metasoma black; tergite 2

Figures 1–3. *Lycogaster flavonigrata*, female. **1** Lateral. **2** Head, front **3** Apex of second sternite, ventral.

with lateral longitudinal white stripe; tergite 3 with lateral oval white spot; tergite 4 with small lateral white spot, much smaller than that on tergite 3; sternite 2 with apical yellow transverse narrow band. Wings darkly infuscate; lighter toward base; veins and stigma black. Antenna short, flagellum slightly incrassated at center. Medio-apical process present on sternite 2, slightly concave at center.

Male. Unknown.

Specimens examined. LAOS: Prov. Hua Phan, Phou Pan, Umg. Ort Ban Saleui, 20°13'30"N/ 103°59'26"E, 1350–1900 m, 01.05.2012, KJa, leg. C. Holzschuh & locals (1 ♀, OLML), same but 22.04.2012 (1 ♀, OLML); N, 24.IV–16.V.1999, Louang Phrabang Prov., 20°33-4'N, 102°14'E, Ban Song Cha (5 km W), ±1200 m, Vít Kubáň leg (1 ♀ OLML); Khammouan prov., 250 m, Ban Khoun Ngeun, N18°07', E104°29', E. Jendke leg. (1 ♀, OLML). THAILAND: Phetchabun, Nam Nao NP Check point, 16°43.695'N, 101°33.797'E, 921 m, Malaise trap, 28.iv–5.v.2007, Leng Jantaeb leg., T2654 (1 ♀, QSBG).

Distribution. This species was described from China (Fujian, Jiangxi, Yunnan) (Chen et al. 2014). These are the first records from Laos and Thailand.

Comments. The almost completely black color with some yellow markings on the metasoma and the dark wings help distinguish this species.

Lycogaster are fairly rare in collections. From observations by PT, a good number of species of Asian *Lycogaster* seem to parasitize the Eumeninae through caterpillars, somewhat like *Bareogonalos*. At least in Korea this explains their scarcity in collections. They are almost never found in traps set in forest but seem to research more sunny habitats where potter wasps nest, and therefore are likely to have a much better resistance to desiccation than the other Trigonalids.
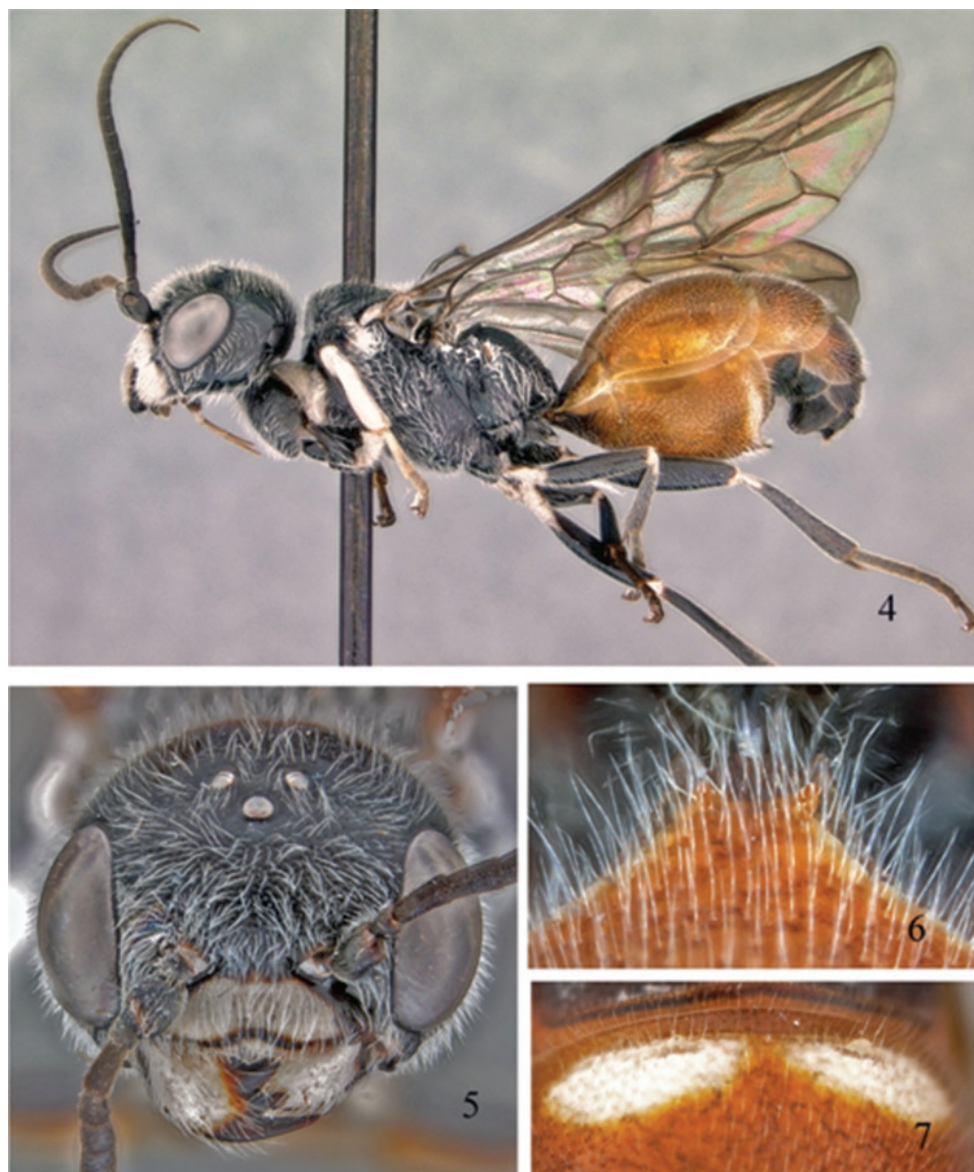
Lycogaster rufiventris (Magretti)
Figs 4–7

Trigonalys rufiventris Magretti 1897: 311, figs 2, 3; Carmean and Kimsey 1998: 70.
Lycogaster rufiventris: Schulz 1908: 28, fig. 2; Bischoff 1938: 10; Weinstein and Austin 1991: 428; Chen et al. 2014: 45.

Diagnosis. Female: Length, 8.0–10.0 mm. Antenna black. Head black with clypeus except for black narrow anterior margin and mandible except black apex white. Mesosoma black with anterior margin of pronotum, spot on posterior lateral corners (near tegula) of pronotum, tegula, small oval spot on posterior-central prescutum, oval spot on anterocentral area of mesoscutellum, and metascutellum white. Legs black with most of trochanters except ventrally, extreme tip at base and apex of femora, outer surface of fore tibia, foretarsus, and extreme bases of mid- and hind tibiae white. Metasoma orange with tergite 5 or 6 to apex, and sterna 3 to apex black; apical broad margin of sternite 2 white. Wings lightly infuscated, a little darker toward apex; veins and stigma black. Head: Antenna with 24–25 antennomeres; flagellum somewhat incrassate at center. Shiny; vertex almost without punctures; frons more densely punctate; covered with fine white hairs. Mesosoma: Shiny, uniformly densely punctate; covered with fine white hairs. Metasoma: Shiny, uniformly densely punctate; covered with fine white hairs. Medio-apical process with small indentation at center on sternite 2 (Figs 4, 6).

Figures 4–7. *Lycogaster rufiventris*. **4** Lateral, female **5** Head, front, female **6** Apex of second sternite of female, ventral **7** Apex of second sternite of male showing paired protuberances.

Male: Length 8.0–9.0 mm. Color similar to female. Antenna without tyloids. Paired protuberances at center near apex of 2nd sternite (Fig. 7).

Specimens examined. THAILAND: Prachuab Khiri, Khan, Khao Sam Roi Yot NP, Sailine wetland/Pa Gwad/N, 12°9.2'N, 99°58.298'E, Malaise trap, 1–8.ii.2009, Yai; Amnad leg., T4191 (1 ♂, QSBG)); Prachaub Khiri, Khan, Khao Sam Yot NP, Saline wetland/Pa Gwad/N, 12.153°N, 99.972°E, MT, 18–26.i.2009, Yai; Amnad, H2648 (1

♀, QSBG); Lampang, Chae Son NP, behind youth camp, 18.831°N, 99.458°E, 445 m, MT, 14–21.ii.2008, B. Kwannui & A. Sukpeng, H2572 (1 ♂, USNM); Loei, Phu Kradueng NP, Mixed deciduous/S Na Noy office, 16.817°N, 101.794°E, 276 m, MT, 7-14.v.2008, Thonghuay Phatai, H2611 (1 ♀, USNM); Sakon Nakhon, Phu Phan NP, stream entrance of Nam Pung substation, 16°54.63'N, 103°54.266'E, 281 m, Malaise trap, 6-12.v.2007, Sailom Tongboonchai leg., T2611 (1 ♀, QSBG); Nakhon Si Thammarat, Namtok Yong NP, Behind campground lavatory, 8°10.434'N, 99°44.508'E, 80 m, Malaise trap, 23-29.vii.2008, U.prai.K. leg, T3082 (1 ♀, PT).

Distribution. Myanmar; Thailand.

Comments. The contrasting red metasoma is not known in any other species of *Lycogaster*. Magretti (1897) described this species from Myanmar. The species was assigned to *Lycogster* by Schultz (1908), Bischoff (1938), and Weinstein and Austin (1991). Carmean and Kimsey (1998) could not locate the holotype and placed it in *Trigonalys* based on similarly colored specimens from central and southern India. We have examined those specimens from India, borrowed from the MCZ and OSAC, and confirm that they are a species *Trigonalys*. However, as explained by Schultz (1908), who redescribed the species from the holotype and corrected the sex to a female, and Chen et al. (2014), Magretti's species is clearly a *Lycogaster*. Our specimens from Thailand agree with Magretti's description of *rufiventris*, and confirm placement in *Lycogaster*. The discovery of the male further confirms placement in *Lycogaster*. The absence of tyloids on the antenna and presence of a pair of protuberances centrally near the apex of sternite 2 (Fig. 7) is typical for the genus. This is the first collection of both sexes of this species since the original description.

Pseudogonalos hahnii (Spinola)

Trigonalys hahnii Spinola 1840: 1.

Specimen examined. CHINA: Yunnan Prov., Lijiang, 1.–19.7.1992, Heishui 35 km N of, 27.13N, 100.19E, lgt. S. Becvar (1 ♀, OLML).

Comments. This is a widespread Palearctic species and is characterized and illustrated by Chen et al. (2014), who recorded it from a number of Chinese provinces. This specimen is the first record from Yunnan.

Taehiogonalos cordata Chen, Achterberg, He & Xu

Taeniogonalos cordata Chen, Achterberg, He & Xu, 2014: 140, figs 317–327.

Diagnosis. Vertex of head black, without V-shaped pale pattern posteriorly; middle mesonotal lobe yellow laterally and orange brown medially, strongly contrasting with black lateral lobes; anterior half of forewing dark brown; mesoscutellum largely or-

ange brown, black only medio-poseriorly and narrowly black laterally; female without medio-apical process on sternite 2.

Specimen examined. LAOS: Prov. Hua Phan, Phou Pan, Umg. Ort. Ban Saleui, 20°18'30"N, 103°59'26"E, 1350–1900 m, 19.04.2012, KJa, leg. C. Holzschuh & locals (1 ♀, OLML).

Comments. This species was described from China (Yunnan), and this specimen from Laos is identical to the description. It is the first record from Laos.

Taeniogonalos fasciata (Strand)
Figs 8–10

Poecilogonalos fasciatus Strand, 1913: 97.

Diagnosis. Female, length, 8.5 mm. Antenna black with basal antennomeres reddish. Head black with inner and outer orbits, antennal tubercles, clypeus, and mandible black. Mesosoma mostly red with sterna black. Legs black and white, trochanters, fore tibia and tarsus, and bases of mid- and hind tibiae white. Metasoma black with broad apical bands on basal two tergites. Wings hyaline with black dorso-apical spot covering most of radial cell. Second sternite without medio-apical projection. Male similar to female.

Specimen examined. CHINA: Huan pr., 30 km N. Yanjiajie from Cayong, 29.5.2005, Ivo Janis lg. (1 ♀, OLML); Sichuan, Shangliang, 14.5–26.5.2005, lg: E. Kucera (1 ♀, OLML). THAILAND: Mae Hong Son, Namtok Mae Surin NP, Visitor's center, 19°21.593'N, 97°59.245'E, 228 m, Malaise trap, 19–26.viii.2007, Manu Namadkum leg., T5872 (1 ♀, QSBG).

Distribution. China, Indonesia, Iran, Japan, Korea, Malaysia, Russia (Primorskii Krai); Taiwan, Thailand. Chen et al. (2014) recorded Japan, Korea, Taiwan, Russia, and 13 provinces in China. Indonesia, Iran, and Malaysia were recorded by Carmean and Kimsey (1998) and may need confirmation.

Comments. This is the only species with a mostly red mesosoma. It is a widespread species in eastern Asia. It is one of the more common species of Trigonalidae in Korea, Japan, and parts of China but seems to be rare in southeastern Asia.

Taeniogonalos gestroi (Schulz)
Figs 11–13

Poecilogonalos pulchella gestroi Schulz 1908: 24, fig. 1.
Taeniogonalos gestroi: Chen et al. 2014: 141 (complete synonymy given).

Diagnosis. Female, Length, mm. Ground color yellow with black maculae, pattern similar to Figs 11–13. Wings hyaline; forewing with black dorso-apical spot covering most of radial cell. Second sternite without medio-apical process. Male similar to female.

Figures 8–10. *Taeniogonalos fasciata*, female. **8** Lateral **9** Head, front **10** Metasoma, lateral.

Specimens examined. INDIA: NE, Assam, 26°45W, 93°N, Pan Bari Res. for, leg. Murzin, XI.97 (1 ♀, OLML). LAOS: south, Ban Houaykong, 18-30.4.99,O. Šauša lgt (1♀, OLML); south, Ban Itou env., 10–18.4.1999, O. Šauša lgt (1♀, OLML); south, Pakse env., 18–30.4.1999, Spevar lgt (1 ♀, OLML); C, 20–29.V.04, Khammouau pr., 250 m, Ban Khoun Ngeun, 18°07'N, 104°29'E, Jendek & Šauša lg (1 ♀, OLML). MALAYSIA: W. Perak, 25 km NE of IPOH, 1200 m, Banjaran Titi Wangsa Mts., KORBU Mt, 11–16.I.1999, P. Čechovský leg. (1 ♀, OLML); Perak, Cameron Highlands,Batu, 19.Vill env, 590 m, N 4°22', E 101°20', Pacholatko lf., 05/09 (1 ♀,

Figures 11–13. *Taeniogonalos gestroi*, female. **11** Lateral. **12** Head, front **13** Metasoma, lateral.

OLML) ; Pahang, 30 km NE Raub, ~300 m, Lata Lembik, IV–V.2002, ET, 3°56'N, 101°38'E, Jendek & O. Šauša leg. (5 ♀, OLML) . THAILAND: Sakon Nakhon, Phu Phan NP, Dry evergreen forest near house at 1567 station, 16.81°N, 103.892°E, 512 m, MT, 9–16.xii.2006, S. Kongnara, H2642 (1 ♀, QSBG); Mae Hong Son, Namtok Mae Surin NP, E/Huai Fai Kor reservoir, 19°20.616'N, 97°59.300'E, Malaise trap, 18–25.v.2008, Kamkoon; A leg., T3518 (1 ♀, QSBG); Mae Hong Son, Namtok Mae Surin NP, Visitor's center, 19.36°N, 97.988°E, 228 m, MT, 23–30. iii.2008, Manu Namadkum, H2679 (1 ♀, QSBG); Nakhon Si Thammarat, Namtok Yong NP, Behind campground lavatory, 8°10.434'N, 99°44.508'E, 95 m, Malaise trap, 15–22.xii.2008, U-prai; K. leg., T4275 (1♀, QSBG); Mae Hong Son, Nantok Mae Surin NP, Nature trail, 19.344°N, 97.988°E, 334 m, MT, 15–22.vii.2007,

Jittrakorn Kaewmanee, H2578 (1 ♀, QSBG); Phetchabun, Nam Nao NP Check point, 16°43.687'N, 101°33.754'E, 924 m, Malaise trap, 19–26.v.2007, Noopean Hongyothi leg., T2662 (3 ♀, QSBG, USNM); Nakhon Si Thammarat, Namtok Yong NP, behind campground lavatory, 8.174°N, 99.742°E, 95 m, MT, 12–19.i.2009, U-prai; K., H2559 (1♀, QSBG); Chiang Mai, Doi Chiang Dao WS Pha Tang unit, 19°24.978'N, 98°54.886'E, 526 m, Malaise trap, 24–31.iii.2008, Songkran & Apichart leg., T3161 (1 ♀, QSBG); Trang NP Khoa Chong Forest Research Stn., 7°33.033'N, 99°47.383'E, 74 m, Malaise trap, 0.xi.2005, D. Lohman leg., T.6372 (1 ♀, QSBG); Chiang Mai, Doi Chiang Dao WS, Pha Tang unit, 19.416°N, 98.915°E, 526 m, MT, 14–21.x.2007, Songkran & Apichart, H2613 (1 ♀, QSBG); Chiang Mai, Queen Sirit Botanic Garden, 18.881°N, 98.862°E, 811 m, MT, 23–30.vi.2009. K. Kaewjanta et al., H2624 (1 ♂, QSBG); Chiang Mai, NP Queen Sirit Botanic Garden, 18°52.845'N, 98°51.705'E, 811 m, Malaise trap, 26.v–2.vi.2009, Kaewjanta & Sawkord leg., T6373 (1 ♀, USNM); Chiang Mai, Queen Sirit Botanic Garden, 18.881°N, 98.862°E, 811 m, MT, 19–26.v.2009, K. Kaewjanta & R. Sawkord, H2595 (1 ♀, PT); Petchaburi, Kaeng Krachan NP, Panernthung/ladies washroom, 12.797°N, 99.456°E, 970 m, MT, 8–15.viii.2008, Sirichai & Chusak, H2583 (1 ♀, QSBG); Nakhon Si Thammarat, Namtok Yong NP, Behind campground lavatory, 8.174°N, 99.742°E, 95 m, MT, 2–9.iii.2009, U-prai; K., H2570 (1 ♀, USNM); Trang, Khoa Pu-Khoa Ya NP, 7°33.038'N, 99°47.369'E, 75 m, Malaise trap, 16–19. vi.2006, M. Sharkey leg., T1954" (1 ♀, QSBG); Loei, Phu Ruea NP, Rong Huay Maklaow, 17.494°N, 101.35°E, 1167 m, MT, 12–19.v.2007, Patikhom Tumtip, H2645 (1 ♀, QSBG); Chiang Dao, 19–21.V.1997, leg. M. Snizek (1 ♀, OLML); Prov. Mae HongSon, WNW Pai, Mo Paeng Wasserfall, Lichtfang, 11.04.2000, 900 m, 19°22'41"N/98°22'34"E (GPS), leg. H. & R. Rausch, 03/2000 (1 ♀, OLML); bor. occ., Soppong (Pai), 28.v.–5.VII.1997, leg.M. Snizek (1 ♀, OLML); Trang Prov., near Nam tok Ton Prov, Khoa Chong Mt., 140 m, 7°32'15"N, 99°47'36"E, iii.2005, D. Lohmai (1 ♀, CNC). Also recorded from Thaleban NP, 200 m (Chen et al. 2014).

Distribution. China (Hainan, Jiangsu, Yunnan), India, Indonesia, Malaysia, Myanmar, Laos, Papua New Guinea, Taiwan, Thailand (Chen et al. 2014). Chen et al. (2014) gave Sri Lanka, but this is probably not correct.

Comments. This was the most commonly collected species and can be distinguished by its yellow and black color pattern and the female lacking a medio-apical process on the second sternite. Chen et al. (2014) discussed the use of the name *gestroi*. This was commonly known as *T. thwaitesii* (Westwood), which was described from Sri Lanka and which Carmean and Kimsey (1998) believed to be a widespread, variable species in Asia. Examination of Westwood's type (OXUM) indicated that *thwaitesii* is different from specimens from southeastern Asia which were previously referred to as *T. thwaitesii*, confirming Schultz's (1908) conclusions. The name *gestroi* is thus available for the Asian populations. So far as we can tell, *T. thwaitesii* is confined to Sri Lanka and possibly southern India. Further studies are needed based on specimens from its entire range.

Taeniogonalos sauteri Bischoff
Figs 14–16

Taeniogonalos sauteri Bischoff 1913: 153.

Diagnosis. Female, length, 8.0 mm. Black with yellow pattern similar to Figs 14–16. Head with yellow markings on occiput, gena, inner orbits, antennal tubercles, and clypeus. Mesosoma with yellow spots at anterior corners of middle lobe and spot on upper pronotum; meso and metascutellum orange. Legs black with hind coxa and bases of tibiae white. Metasoma black with broad apical yellow bands on first and second segments and lateral yellow spots on third to apical tergites. Short, blunt medio-apical process, truncate at apex, on sternite 2 (Figs 14, 16). Male similar to female except for sexual differences.

Specimens examined. LAOS: Hua Phan Prov., Ban Saleui; Phou Pan Mt., 20°13'30"N/ 103°59'26"E GPS, 1350–1900 m, 20.04.2010, leg. C. Holzschuh & locals (1 ♀, OLML), same but 14–18.04.2010 (1 ♀, OLML); Prov. Hua Phan, Phou Pan, Umg. Ort Ban Saleui, 20°13'30"N/ 103°59'26"E, 1350–1900 m, 03.05.2012, KJa, leg. C. Holzschuh & locals (1 ♀, OLML), same but 19.04.2012 (1 ♀, OLML). TAIWAN: Taoyoan Prov., Mingehih env., 1075 m, N24.65°, E121.42°, J. Halada, 9–5.2012 (1 ♀, OLML). TAIWAN: Taeyoan prov., Mingehih env., 1075 m, N 24.65°, E 121.42°, J. Halada, 9.5.2012 (1 ♀, OLML). THAILAND: Petchaburi, Kaeng Krachan NP, Panernthung/km27/water pump, 12°49.151'N, 99°22.483'E, 950 m, Malaise trap, 11–18.vii.2008, Sirichai & Chusak leg., T4334 (1 ♀, QSBG).

Distribution. China (Fujian, Guangxi, Hunan, Shandong, Zhejiang) , Japan, Philippines, Taiwan (Chen et al. 2014). These are the first records for Laos and Thailand.

Comments. These specimens are identical to *T. sauteri* as characterized by Chen et al. (2014).

Taeniogonalos tricolor Chen
Figs 17–19

Poecilogonalos tricolor Chen 1949: 16.

Diagnosis. Female: Length 7.0 mm. Reddish brown and black, with black maculae and color similar to Figs 17–19. Head mostly reddish brown with black on occiput and frons. Mesosoma reddish brown with black maculae on each lobe and most of pleurae and sterna black. Legs reddish brown to black. Metasoma black with broad reddish-brown apical bands on tergites. Metasomal sternite 2 without medio-apical process. Male: Similar to female.

Specimens examined. CHINA: Szechuen [Sichuan], Behluhdin, 6000 ft., VII.25-IX.1.1932, DCGraham (1 ♀, USNM); Szechuen [Sichuan], ShinKaiSi, Mt. Omei, 4400 ft., 8.16–20.34, DCGraham (1 ♀, USNM), same except without date (1
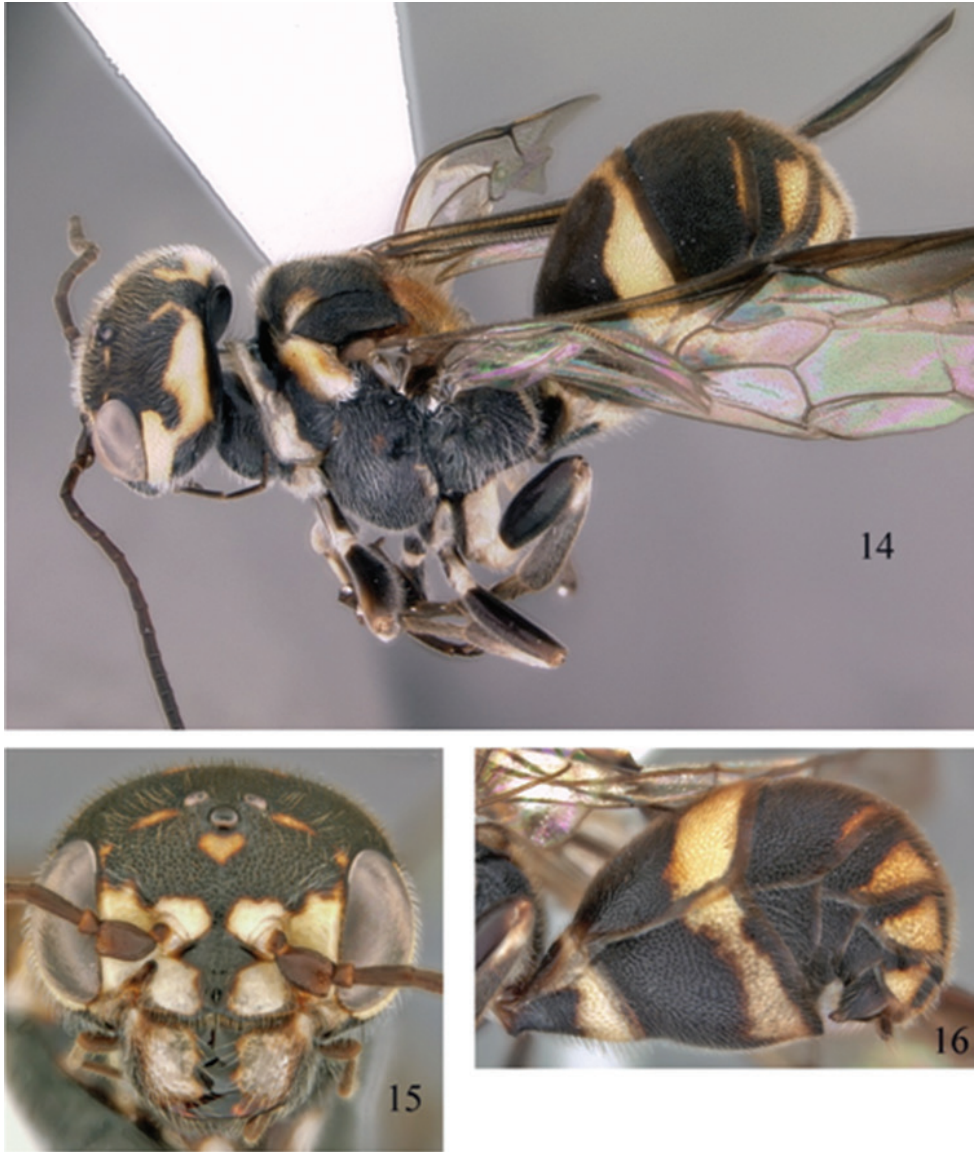
Figures 14–16. *Taeniogonalos sauteri*, female. **14** Lateral **15** Head, front **16** Metasoma, lateral.

♀, USNM); Szechuen [Sichuan], O-Er26mi N Li Fan, 9000 ft., 1933, DCGraham (1 ♀, USNM). LAOS: Phongsaly pr., Phugsaly env., ~1500 m, N21°41', E102°06', Pacholátko lg., 06/2008 (1 ♀, OLML); Hua Phan Prov., Ban Saleui, Phou Pan- Mt., 20°13'30"N, 103°59'26"E, 1350–1900 m, 07.05.2011, leg. C. Holzschuh + locals (1 ♀, OLML), same except 10.05.2001 (1 ♀, OLML), same except 10.04.2010 (1 ♀, OLML). THAILAND: Chiangmai, 4-VI-52 (1 ♀, USNM).

Figures 17–19. *Taeniogonalos tricolor*, female. **17** Lateral **18** Head, front **19** Metasoma, lateral.

Distribution. China, Thailand, Korea (Chen et al. 2014). Recorded from Thailand by Carmean and Kimsey (1998) and Chen et al. (2014), but no localities given. Chen et al. (2013) recorded 11 provinces in China but not Sichuan.

Comments. The largely reddish-brown color and lack of a medio-apical process on the second metasomal sternite will help separate this species. We examined only one specimen from Thailand, but the species seems widespread in Asia.

Taeniogonalos sp.1
Figs 20–22

Specimen examined. THAILAND: Chiang Mai, Queen Sirit Botanic Garden, 18.881°N, 98.862°E, 811 m, MT, 28.iii-3.iv.2009, K. Kaewjanta & R. Sawkord, H2614" (1 ♀, QSBG); Chiang Mai, Doi Phahompok NP, Mae Fang Hotspring, 569 m, 19°57.961'N, 99°9.356'E, Mal. trap, 7–14.III.2008, P. Wongchai, leg. T6286 (1 ♀, QSBG).

   Comments. This is similar to *T. sauteri* but the metasoma is almost completely black and there is a distinct medio-apical process on the second sternite. This process is short and apically truncate. It does not key in Chen et al. (2014) and we do not have enough specimens to evaluate its status.

Taeniogonalos sp.2
Fig. 23

Specimen examined. THAILAND Nan, Doi Phu Kha NP Office 6, 19°12.349'N, 101°4.617'E, 1360 m, Malaise trap, 22–19.iii.2008, Charoen & Nikorn leg., T3326" (1 ♂).

   Comments. This may be male of the unidentified female above. The antenna has elongate tyloids on antennomeres 10–15.

Trigonalys india Smith, sp. n.
http://zoobank.org/B7033A5B-6F42-43DF-A715-2A33DB4DC716
Figs 24–27

Trigonalys rufiventris: Carmean and Kimsey 1998: 70 (misidentification).

Description. Female. Length 8.0 mm. Head black; clypeus and mandibles yellowish except apex of mandible black. Mesosoma black with yellow spot on dorsoposerior pronotum. Legs black with following yellow: apices of coxae, trochanters, extreme bases of femora, apical third of fore femur, outer surfaces of tibiae. Metasoma orange with first segment, and central area of sterna 2 and 3 black. Basal half of wings hyaline, somewhat darkly infuscated at center and apex; veins and stigma black. Head and body with silvery hairs. Head smooth, shiny with very few scattered fine punctures; mesosoma and metasoma uniformly finely punctate. Antenna long, filiform, with 25–26 antennomeres, 2× head width. Malar space narrow, slightly less than diameter of an ocellus. Eyes small, round, inner margins not converging below; lower interocular distance about 1.4× eye height. Lower frons between antennae shelflike or ledgelike, overhanging supraclypeal area. Distance between toruli about equal to distance be-

Figures 20–22. *Taeniogonalos* sp., female. **20** Lateral **21** Head, front **22** Metasoma, lateral.

tween torulus and inner margin of eye. Occipital carina narrow, less than half diameter of an ocellus. Medio-apical process at apex of sternite 3, flangelike, directed backward apically, quadrate.

Male. Length, 7.8 mm. Color similar to female but metasoma mostly black, to darky reddish mostly at base of second tergite. Tyloids present on antennomeres 12–16, round, shiny, diminishing in size toward antennomere 16.

Figure 23. *Taeniogonalos* sp., male, dorsolateral.

Type material. Holotype, female, labeled "Nilgiri Hills, Singara, 3400', So. India, V-48, P. S. Nathan" (MCZ). Paratypes: Same data as for holotype (1 ♀, MCZ); Jabalpur, central India, Sep. 1957, 1600 ft., P. S. Nathan (1 ♀, 1 ♂, OSAC) (female with head missing).

Etymology. Named after the country of origin, a noun in apposition.

Comments. These are the specimens examined and identified as *Trigonalys rufiventris* (Magretti) by Carmean and Kimsey (1998). Generic characters place them in *Trigonalys*, and, although similar to *L. rufiventris* in color, they differ by the placement of the occipital carina, overhanging shelflike interantennal area, presence of tyloids on the antenna of the male, and a medio-apical process on the third sternite of the female.

Most species of *Trigonalys* are Neotropical and Ethiopian. Only one species is recorded from Asia, *T. lachrynosa* Westwood, 1874, described from Mindanao, Philippines. We have examined one female of *T. lachrynosa* from "Surigao, Mindanao" in the USNM, identical to Westwood's illustration (1874, plate 23, fig. 5), the same specimen examined by Carmean and Kimsey (1998). *Trigonalys lachrynosa* is almost entirely black with small yellow spots on the mesosoma. We know of no other species of *Trigonalys* with the color combination of *T. india* – the mostly black head, mesosoma, and legs and a mostly reddish metasoma.

Figures 24–27. *Trigonalys lindia*, holotype female. **24** Lateral **25** Head, front **26** Apex of metasoma, ventral, showing projection on third sternite **27** Metasoma, lateral.

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RESEARCH ARTICLE

Revision of the odd brachycistidine genus *Acanthetropis* Wasbauer, 1958 (Hymenoptera, Tiphiidae, Brachycistidinae)

Lynn S. Kimsey[1], Marius S. Wasbauer[1]

1 *Department of Entomology and Nematology, University of California, Davis, California 95616, USA*

Corresponding author: *Lynn S. Kimsey* (lskimsey@ucdavis.edu)

Abstract

The species of the brachycistidine genus *Acanthetropis* are reviewed. A key to the species is provided along with distribution maps. One species, *A. normalis* Malloch, 1926, is relegated to synonymy under *A. aequalis* (Fox, 1899).

Keywords

Brachycistis, *juncea*, *longula*, *petiolata* group

Introduction

Several species of *Brachycistis* Fox, 1893 were recognized by Bradley (1917) to be closely related as they appeared next to each other in his key. Malloch (1926) grouped these same species (*aequalis* Fox, 1899; *idiotes* Cockerell, 1895; *noctivaga* Bradley,1917, and *normalis* Malloch, 1926) in what he called the *aequalis* group of *Brachycistis*. Wasbauer (1958) in his preliminary studies of the subfamily Brachycistidinae discovered a new species (*lamellatus* Wasbauer, 1958) from Baja California, Mexico, which because of its unique combination of traits was set aside as representing a possible new genus. When this species was compared to others in the genus *Brachycistis*, the species Malloch had

placed in the *aequalis* group were found to share these same traits. To accommodate these species, Wasbauer proposed the genus *Acanthetropis* and included it in his key to the genera known at that time (Wasbauer 1966). The most recent key to genera can be found in Kimsey and Wasbauer (2006).

Materials and methods

Type repositories and specimens studied below are indicated by the following acronyms: ANSP – Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA; BME – Bohart Museum of Entomology, University of California, Davis, USA; CAS – California Academy of Sciences, San Francisco, USA; CDFA – California State Collection of Arthropods, California Department of Food and Agriculture, Sacramento, USA; CUIC – Cornell University Insect Collection, Ithaca, New York, USA; EMEC – Essig Museum, University of California, Berkeley, USA; KSBS – University of Kansas, Lawrence, USA; LACM – Los Angeles County Museum of Natural History, California, USA; MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; UCRC – Entomological Research Museum, University of California, Riverside, USA, and USNM – U.S. National Museum, Washington, D.C., USA.

Morphological terminology follows that of Wasbauer (1966). Of the head, LID = lower interocular distance, the shortest distance between the lower margins of the compound eyes. UID = upper interocular distance, the shortest distance between the upper margins of the compound eyes. The abbreviations L, W and H refer to length, width and height respectively.

Systematics

Genus *Acanthetropis* Wasbauer

Acanthetropis Wasbauer 1958: 139. Type species: *Acanthetropis lamellatus* Wasbauer 1958: 140. Original designation.

Diagnosis. Species of *Acanthetropis* are large, relatively heavy-bodied brachycistidines. The males can be immediately distinguished by the presence of a scrobal sulcus, very long marginal cell of the forewing and metasomal sternum II with a median longitudinal carina or fold. In addition the frons bears a carina above and laterad of the antennal sockets.

Male description. *Body length* 6.5–17.0 mm. *Head.* Rounded, broader than long; ocelli enlarged with a transverse sulcus between their posterior margins; compound eyes slightly convergent below, inner margins broadly emarginate; antennal socket rim with broad carina or thickening beneath small carina above and lateral to antennal

socket; clypeus transverse, not projecting apically, clypeal L/W ratio not exceeding 0.4, central part slightly convex, with narrow, apically projecting ledge; mandibles tridentate, weakly developed external carina extending from mandibular base to point just proximad of inner tooth, obsolescent near its middle; maxillary and labial palpi well-developed, conspicuous, 6 and 4 segmented respectively. *Mesosoma.* Robust, moderately long; pronotum narrow, transverse, nearly vertical, humeral angles rounded, not prominent; mesonotum with parapsidal furrows long, strongly impressed; scutellum with or without median longitudinal sulcus; mesepisternum carinately produced or with low, rounded protuberance anterodorsally, irregularly convex; propodeum with dorsomedian longitudinal sulcus, area laterad of sulcus sloping abruptly posteriorly, dorsal and posterior propodeal faces separated by transverse carina; coxae simple, not carinate ventrally, with well-developed admesal stridulatory area; wings long, venation well-developed, forewing with three submarginal and two discoidal cells, third submarginal cell two-thirds or more length of second, first transverse cubital vein arising beyond basal third of first submarginal cell, marginal cell elongate, costa extending distad of stigma a distance greater than half length of stigma; hindwing with radial and cubital veins well-developed, cubitus arcuate, forming angle with transverse cubital of less than 135°, jugal lobe much shorter than submedian cell. *Metasoma.* Segment I narrower than II in dorsal view, sternum I with median sulcus somewhat expanded posteriorly; sternum II with strong basal median longitudinal carina or fold. *Genital capsule.* Paramere broadest subapically, ventrally rounded to acute apex; aedeagus slender, linear or gradually expanded toward apex; volsella with cuspus broadly rounded, digitus produced apically into short, blunt point in ventral view, inner margin of volsella with several stout spines and slender setae. *Color.* Reddish brown to dark brown.

Female. Unknown, although the female of *Acanthetropis* may well be the "Genus A" described by Kimsey (2005).

Distribution (Figs 15–18). *Acanthetropis* is known from geographically scattered records in the USA: Arizona, California, Idaho, Kansas, Nebraska, Nevada, New Mexico, South Dakota, Utah, and in Mexico: Baja California, Baja California Sur, Sonora, Hidalgo and Zacatecas. Further collecting in intervening areas will probably reveal a more widespread fauna.

Key to the species of *Acanthetropis*

1	Mesepisternal prominence high and sharp, often appearing carinate in certain lights (as in Figs 5, 6, 10); mesepisternal carina present; dorsolateral areas of propodeum sharply, carina-margined posteriorly, separated from posterior transverse carina by pronounced sulcus **2**
–	Mesepisternal prominence low, rounded, not appearing carinate; mesepisternal carinae absent; dorsolateral areas of propodeum sometimes with a distinct posterior margin but never sharp and carinate **3**
2	Second metasomal sternum with a median longitudinal elevation, terminating in a spine (Figs 5, 10); gular carina sharply elevated anteriorly, forming

a tooth visible behind the posterior mandibular condyle in full lateral view (Figs 3, 4) ....***noctivaga* (Bradley)**

–   Second metasomal sternum with a longitudinal broad median basal ridge terminating at a transverse ledge (Fig. 6); gular carina low, not visible in full lateral view.. *lamellata* **Wasbauer**

3   Flagellomere I at least 3.5× as long as greatest width (Fig. 8); metasomal segment I long and petiolate, L/H 2.5 or more (Fig. 9) ....***idiotes* (Cockerell)**

–   Flagellomere I less than 3.0× as long as greatest width (Fig. 7); first metasomal segment shorter, L/H 2.0 or less.....................................***aequalis* (Fox)**

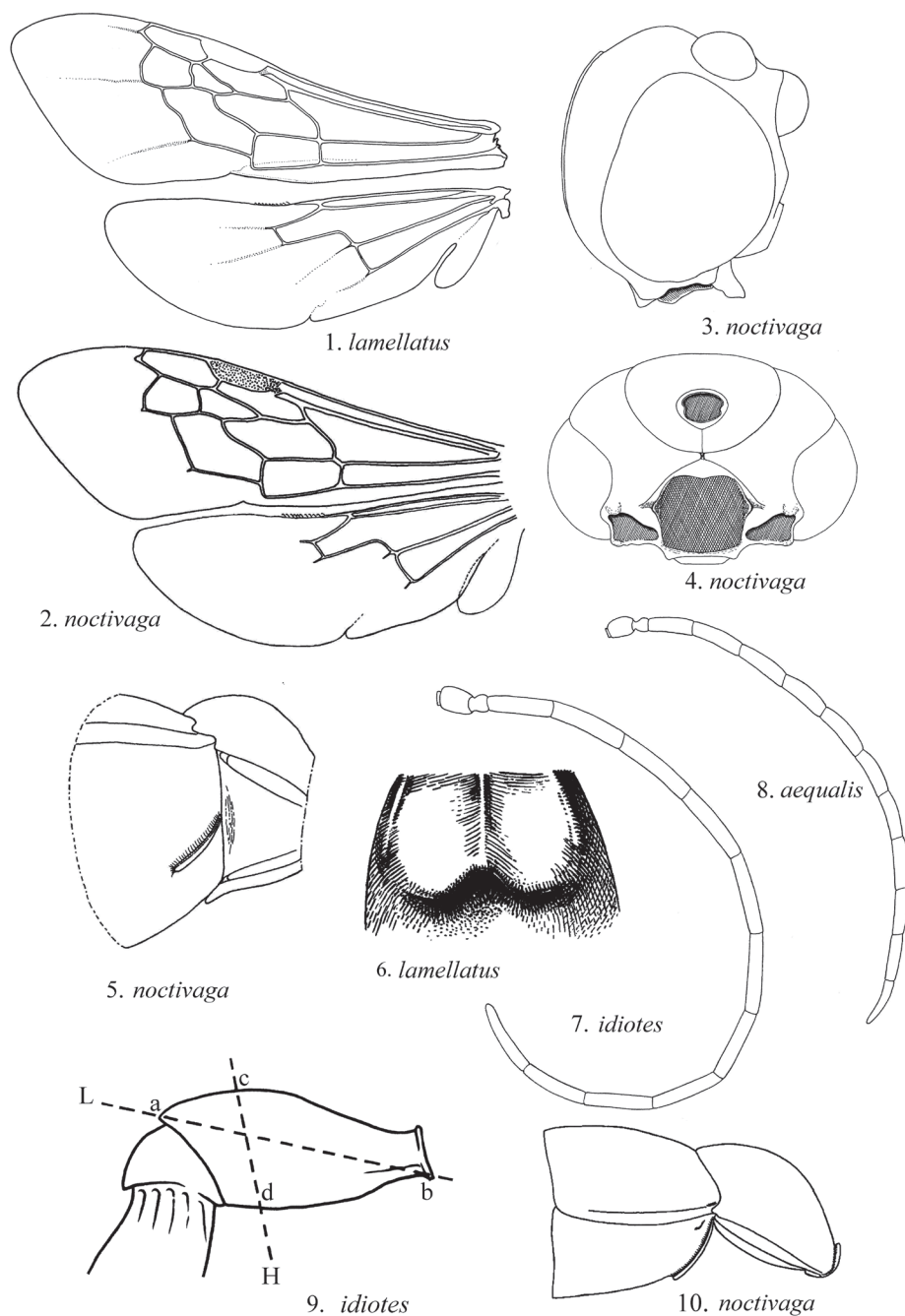## *Acanthetropis aequalis* (Fox)
Figs 7, 11, 15

Brachycistis aequalis Fox 1899: 284. Syntype males; Nevada (ANSP).
Brachycistis normalis Malloch 1926: 8. Holotype male; USA: South Dakota, Jackson
    Co., Cedar Pass (USNM). **New synonymy**.

Diagnosis. This species most closely resembles *A. idiotes*. It can be distinguished by the shorter antennomeres, mesepisternum without vertical or transverse ridge, the shorter first metasomal segment and sharp median longitudinal ridge of metasomal sternum I.

Male description. *Body length* 6.5–13.0 mm. *Head*. Flagellum with appressed yellow pubescence; L/W ratio of flagellomere I 2.4–2.9 (Fig. 7); lower rim of antennal socket produced into distinct vertical carina beneath; clypeus with scattered punctures, becoming larger and irregular apically; gular carina elevated for most of length but not produced into an anterior tooth. *Mesosoma*. Pronotum with small punctures medially, larger, coarser laterally; mesepisternum with a low, rounded prominence anteriorly, not carinately produced, mesonotum with small, scattered punctures; propodeum with dorsum finely reticulate, impunctate, dorsal sulcus with edges scarcely or not appearing carinate, posterior transverse sulcus absent or poorly defined, without or with anterior ill-defined carina; posterior transverse carina often incomplete. *Metasoma*. Segment I short and stout, L/H 1.3–1.5 sternum with longitudinal sulcus expanded and deepened posteriorly, tergum heavily punctate; tergum II moderately to lightly punctate, punctures small and shallow; terga III-VII with punctures small, shallow except for row of larger, deeper punctures before apex; sternum II with median basal longitudinal ridge terminating in blunt spine (as in Fig. 6). *Genital capsule* (Fig. 11). *Color*. Uniform medium brown. Entire body clothed with long, golden setae.

Distribution (Fig. 15). MEXICO: **Baja California:** Hamilton Ranch (4 km n Punta Gorda); **Baja California Sur**: 15 mi n El Rosario; **Zacatecas**: 10 mi n Fresnillo. USA: **Arizona**: Apache Co.: 14 km nnw Salina; Coconino Co.: Tuba City; **California**: Imperial Co.: Bard; Inyo Co.: Tinemaha Reservoir; Kern Co.: Randsburg; Mono Co.: Benton; Riverside Co.: Chino Canyon; San Bernardino Co.: Zzyzx Springs; Tulare Co.: White River; **Idaho**: Cassia Co.: 5 mi ne Malta; Elmore Co.: Glenns Ferry;

1. *lamellatus*

3. *noctivaga*

2. *noctivaga*

4. *noctivaga*

5. *noctivaga*

6. *lamellatus*

8. *aequalis*

7. *idiotes*

L — a — c

d

H

b

9. *idiotes*

10. *noctivaga*

Figures 1–10. 1–2 Forewing and hindwing **3** Side view of head, antennae removed **4** Ventral view of head, mouthparts and mandibles removed **5** Oblique ventral view of metasomal sterna I and II **6** Ventral view of metasomal sternum II **7, 8** Antenna **9** Lateral view of metasomal segment I showing measurement points, H = height between points c and d, L = length, between points a and b **10** Lateral view of metasomal segments I and II.

Kansas: Cheyenne Co. (no locality given); Decator Co.: 5 mi e. Cedar Bluff; Morton Co. (no locality given); Seward Co. (no locality given); Stanton Co. (no locality given); **Nebraska:** Garden Co.: 8 mi ne Oshkosh: Sioux Co.: Agate; **Nevada**: Churchill Co.: Sand Mountain, 35 km se, 8 mi n Fallon; Blow Sand Mountains, San Mountain, 12 mi ne Stillwater; Elko Co.: Deeth; Esmeralda Co.: Clayton Valley dunes; Eureka Co.: 27.5 and 44 km w Carlin; Humboldt Co.: Golconda Summit, Winnemucca, 10 mi n Winnemucca; Nye Co.: Duckwater; Peavine Cyn.; Pershing Co.: Woolsey; Washoe Co., Fallon, south end Pyramid Lake, 3 mi n Nixon; White Pines Co.: 5 mi w Baker; **New Mexico:** Bernalillo Co.: Albuquerque; Chaves Co. (no locality given); Dona Ana Co.: Las Cruces; Otero Co.; Tularosa, 5 mi w Tularosa, White Sands; San Juan Co.: Chaco Cyn. Nat. Mon.; Taos Co.: Ojo Caliente; Torrance Co. (no locality given); **Oregon**: Malheur Co.: 12 mi s Blue Mt. Pass; **South Dakota**: Jackson Co., Cedar Pass; **Utah**: Emery Co.: Buckskin Springs, n. Goblin Valley; Grand Co.: Arches National Monument; San Juan Co.: Monticello; Weber Co.: Ogden; **Wyoming**: Converse Co.: Douglas; Platt Co.: Ft. Laramie; 723 males were examined including the holotype (BME, CAS, KSBS).

Seasonal distribution. This is a summer species, collected from June through September.

Discussion. When Malloch proposed *A. normalis* as a new species in *Brachycistis*, he had only seen one specimen of *Brachycistis aequalis* Fox and thus was unaware of the amount of structural variation seen in that species. The differences he perceived in the dimensions of the first metasomal segment proved to fall within the normal range of variation of this trait in *A. aequalis*.

## *Acanthetropis idiotes* (Cockerell)
Figs 8, 9, 12, 16

Brachycistis idiotes Cockerell 1895a: 63. Holotype male; USA: New Mexico (Repository unknown).

Diagnosis. *Acanthetropis idiotes* is separable from other species in the genus by the rounded, unridged mesepisternum, lack of a gular elevation, long antennae, and long, slender body.

Male Description. *Body length* 12–17 mm. *Head*, with few short to moderately long setae, clypeus and mandibles with more numerous, longer setae; scape with shorter setae; flagellum with tiny, scattered setae, flagellomere I L/W 3.9–4.2 (Fig. 8); lower rim of antennal socket with low carina beneath; clypeus with uniformly scattered punctures; gular carina slightly elevated but not produced into tooth anteriorly. *Mesosoma*. Pronotum with scattered, small punctures medially, larger, denser punctures laterally; mesepisternum with large, scattered punctures, becoming nearly impunctate posteriorly, with low, rounded prominence anteriorly, not carinately produced; mesonotum and scutellum with large, scattered punctures; propodeal dorsum impunctate,

11. *aequalis*

12. *idiotes*

13. *lamellatus*

14. *noctivaga*
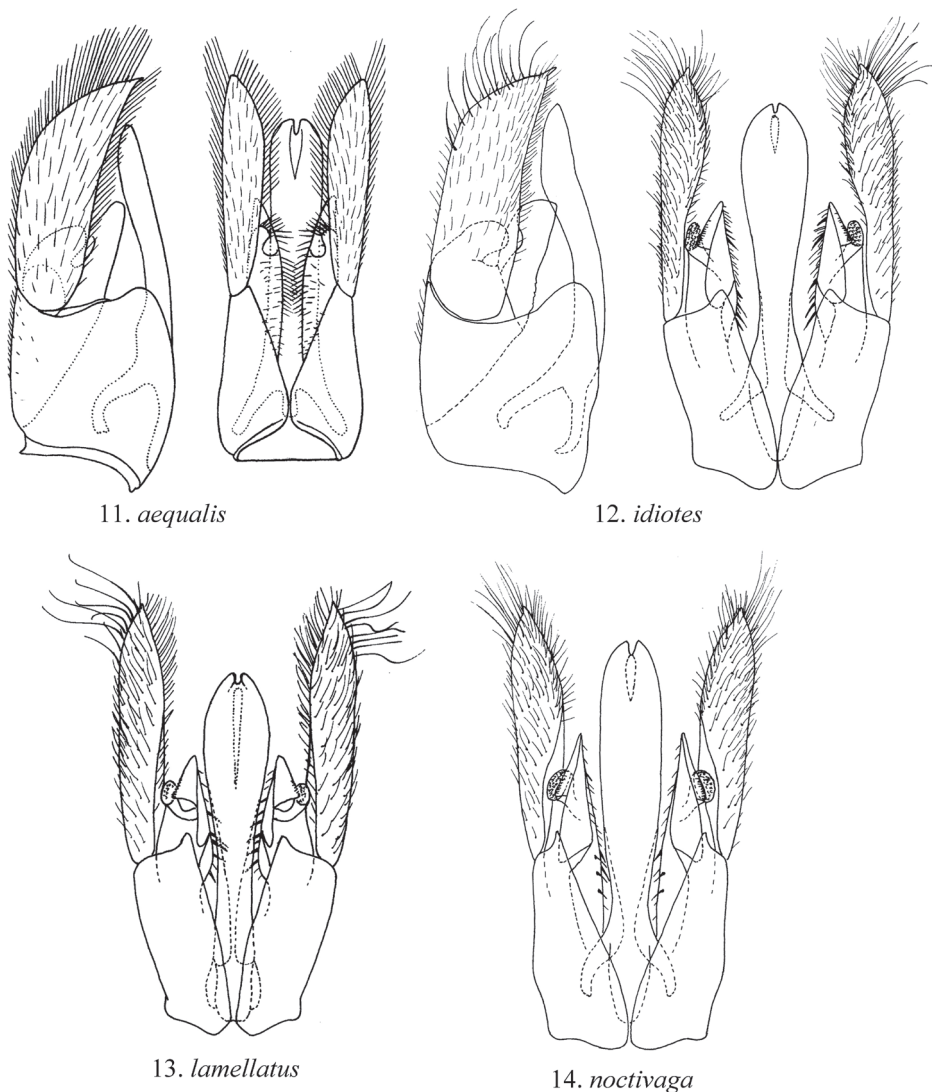
Figures 11–14. Male genital capsule. **11, 12** lateral view (left), ventral view (right) **13, 14** Ventral view.

dorsal sulcus not usually carina margined, areas laterad of sulcus poorly defined, posterior transverse sulcus absent or ill-defined without anterior carina, posterior transverse carina complete. *Metasoma*. First segment long and slender, L/H 2.5–4.0 (Fig. 10), sternum with longitudinal sulcus narrow, slightly widened posteriorly; tergum I slightly rugose, with small, irregular punctures laterally; tergum I with small, scattered punctures; terga III-VII nearly impunctate, except for row of shallow, setose punctures apically; sternum II with a median basal longitudinal ridge terminating in blunt spine (as in fig. 9). *Genital capsule* (Fig. 12). *Color.* Uniform medium to chestnut brown, entire body shining, clothed with long golden setae.

Distribution (Fig. 17). MEXICO: **Baja California**: 23 mi w Punta Prieta; **Baja California Sur**: 2 mi ne El Rosario, 3.5 mi se San Augustin; **Hidalgo**: Jacala; USA: **Arizona**: Mojave Co.: Oatman; Pima Co.: Growler Valley; **California**: Imperial Co.: Bard, Glamis; Algodones Dunes; Inyo Co.: Saline Valley; Riverside Co: Cochella, Indian Wells; San Diego Co.: Borrego Springs; **New Mexico**: Dona Ana Co.: Las Cruces; Quay Co.: House; 92 specimens were examined (BME, CAS, CDFA).

Seasonal distribution. Specimens of this species have been collected only during the winter months (November through January).

Discussion. Collection of desert insects during the winter in temperate areas of the western U.S. has been largely ignored because of assumptions about seasonality. However, a unique fauna of brachycistidine wasps has developed with adult males appearing during the winter. In addition to *Acanthetropis idiotes,* two species of *Brachycistis*, *juncea* Wasbauer, 1966, and *longula* Wasbauer, 1966, in the *petiolata* group are known only from winter collection dates (November and January) (Wasbauer 1966). Interestingly, the habitus of males of these two species is similar to that of *A. idiotes* males. They are longer and more slender than males of other species in their respective groups.

Acanthetropis lamellatus Wasbauer
Figs 1, 6, 13, 17

Acanthetropis lamellatus Wasbauer 1958: 140. Holotype male; Mexico: Baja California Sur, La Paz (CAS).

Diagnosis. The most distinctive feature of *lamellatus* is the elevated transverse ledge on metasomal sternum II. Additional diagnostic features include the high sharp mesepisternal prominence and gular carina not elevated or dentate.

Male description. *Body length* 11–14 mm. *Head.* Face shining with few scattered punctures, punctures stronger between lateral ocelli and on occiput; scape with few long, erect setae ventrally; flagellomere I L/W 2.5–3.1; lower rim of antennal socket not sharp or carinate below; basal half of clypeus shining, impunctate, apical half with several irregularly spaced, broad, shallow punctures and long apically directed setae; gular carina not abruptly raised anteriorly, not visible below mandibular condyle in full lateral view; mandibles with several long, stout amber-colored setae on outer surface. *Mesosoma.* Strongly punctured, sparsely clothed with medium to long erect or suberect setae; anterior face of pronotum shining medially, nearly impunctae, lateral surface strongly punctate; mesonotum with punctures smaller, more closely set anteriorly; mesepisternum with strongly raised, ridge-like elevation below anterodorsal protuberance; propodeum with dorsal sulcus strongly impressed, shining, raised area laterad of sulcus finely reticulate, impunctate except for small lateral area, posterior declivity sharp, carinate, sulcus between declivity and posterior transverse carina smooth, shining; posterior propodeal face separated from lateral face by lateral diagonal carina meeting posterior carina dorsally, obsolete before posterior rim. *Metasoma.* Segment
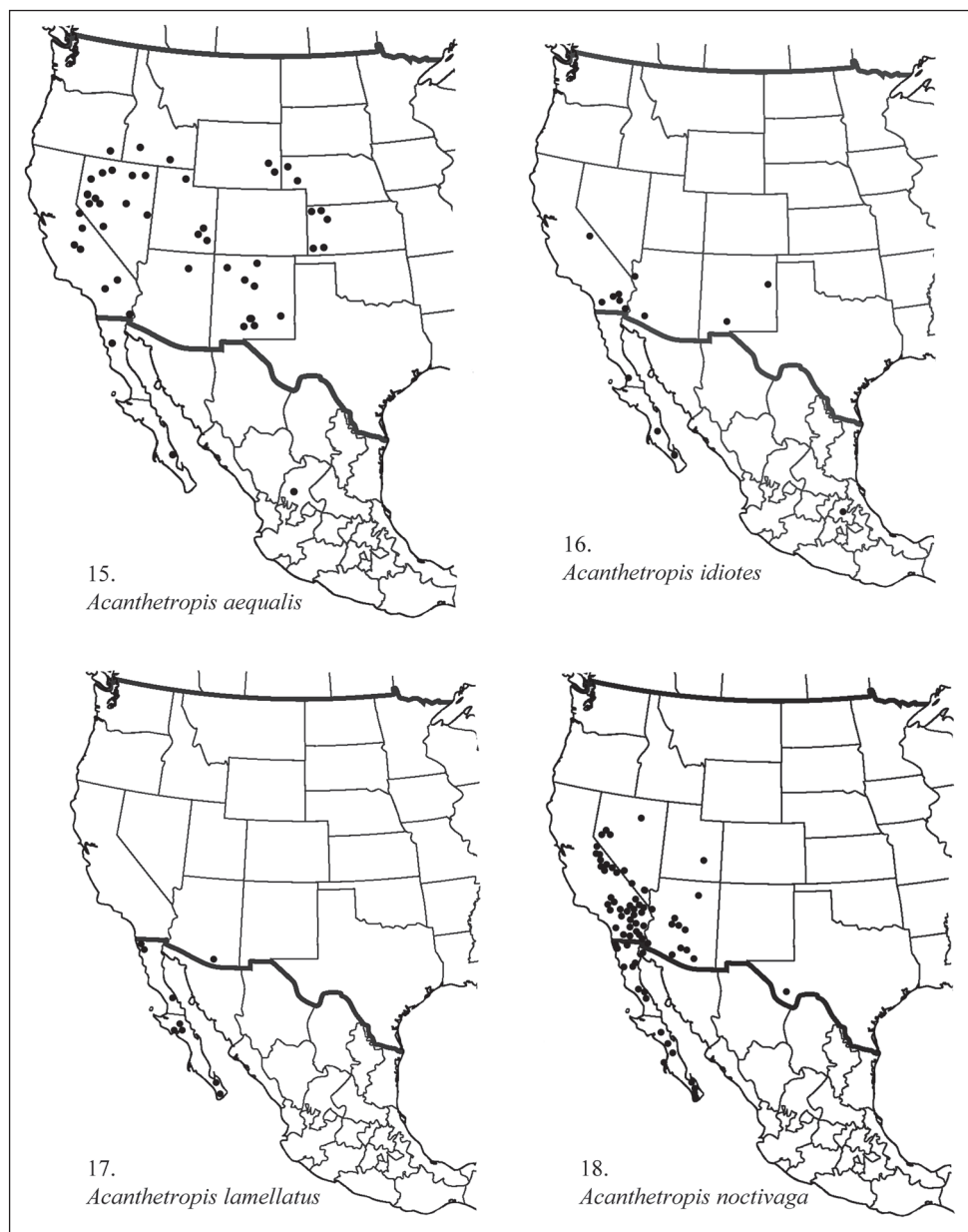
Figures 15–18. Distribution maps.

I short, stout, L/W 1.7–2.3 in lateral view; sternum II with basal longitudinal fold, terminating at raised, transverse lamella (Fig. 6). *Genital capsule* (Fig. 13). Aedeagus widest near subapically, narrowed to bluntly pointed apex. *Color.* Uniform medium to chestnut brown, entire body shining, clothed with long golden setae; flagellum sparsely clothed with minute appressed whitish pubescence.

Distribution (Fig. 17). Mexico: **Baja California Sur**: 23 mi s San Miguel de Commondu, El Pescadero (Playa Los Cerritos), San Ignacio (15, 20 mi s, 13 mi n, 13 mi e), Palmarito, La Paz, 13 mi w La Paz, Isla Espiritu Santo (Bahia San Gabriel), 26 mi s El Arco; USA: **Arizona**: Santa Cruz Co.: Madera Canyon; 22 specimens were examined including the holotype (BME, CAS, UCR).

Seasonal distribution. This is a summer species, collected from June through September.

Acanthetropis noctivaga (Bradley)
Figs 2–5, 10, 14, 18

Brachycistis noctivaga Bradley 1917: 272. Holotype male; USA: Nevada, Clark Co., Las Vegas (CUIC).

Diagnosis. This species can be distinguished by the rugose ridged mesepisternum, presence of an anterior tooth on the gular carina, medially carinate metasomal sternum II, and short stout body.

Male description. *Body length* 12.0–15.4 mm. *Head* (Figs 3, 4), with relatively sparse, short setae, mainly on clypeus and outer surface of mandibles, longest on occiput, scape and inter-antennal area with moderately long setae; clypeus with large, irregular punctures, flagellomere I L/W 3.0–3.5; lower rim of antennal socket with broad carina or swelling beneath; clypeus with large, irregular punctures; gular carina produced into prominent tooth visible below posterior mandibular condyle. *Mesosoma*. Pronotum anterior face with very small punctures, humeral angles and lateral face with large, closely set, irregular punctures; mesepisternum heavily punctate, punctures large, close set, irregular; mesepisternal prominence high and sharp, appearing carinate in certain angles; mesepisternal carina present; mesonotum and scutellum with scattered punctures, scutellum usually with median longitudinal sulcus extending from anterior to posterior margins; propodeal dorsum impunctate, dorsal longitudinal sulcus carinately margined, areas laterad of sulcus well-defined, margins usually appearing carinate, posterior transverse sulcus impunctate, often traversed by longitudinal ridges, posterior transverse carina well-developed, complete. *Metasoma* (Figs 5, 10). Segment I short and stout, L/H 1.5–1.9, sternum I with longitudinal sulcus gradually expanded and deepened posteriorly; tergum I heavily punctate, punctures large, often irregular; terga II-VII with scattered large and small punctures and row of setose punctures before apex of each segment; sternum II with median basal longitudinal ridge terminating in blunt spine (Fig. 5). *Genital capsule* (Fig. 14). *Color*. Uniform medium to dark brown, body shining, heavily punctate, entirely clothed with shiny white to straw-colored setae; flagellum with tiny erect to appressed golden setae.

Distribution (Fig. 18). MEXICO: **Baja California**: Bahia de Los Angeles, 2 km s Bahia de Los Angeles, 11 km e Chapala, 10.3 mi sw Los Medanos, San Felipe, 16 mi s San Felipe, 4 mi nw Rancho San Juan, 2 mi n El Porvenir, 1.5 mi n Puertocito, 16

mi e. La Rumorosa, 3 mi n Gonzaga Bay; **Baja California Sur**: La Paz, 13 mi w La Paz, 7 mi sw La Paz, 4.5 mi se La Paz, 3 mi w San Miguel de Commondu, Isla Partida dunes, Sierra Placeres, Bahia Concepcion, El Pescadero (Playa Los Cerritos), Puerto Escondido, 20 mi s San Ignacio, El Rosario; **Sonora**: 6 mi n El Golfo; USA: **Arizona**: Coconino Co.: 2 mi s Moenkopi, Maricopa Co.: 3 mi nw Wickenburg, Ness, Pleasant Lake, Coon's Bluff, Mesa; Mojave Co.: Topock; Pima Co.: Organ Pipe Nat. Mon. (Quitobaquito), Sabino Canyon; Pinal Co.: 4 mi se, 24 mi w Casa Grande, Picacho, Picacho Pass, Picacho Peak, 5 mi w Stanfield; Yavapai Co.: 2 mi ne Congress; Yuma Co. 30 mi ne Yuma; Nevada: Churchill Co.: Blow Sand Mountains, Sand Mountain; Nye Co.; **California**: Contra Costa Co.: Brentwood; Imperial Co.: Plaster City, 3 mi n Glamis, 3 mi nw Glamis, Heber; Kane Spring; Inyo Co.: Bishop, Inyo, 8 mi e Big Pine, 5 mi w Bishop, Death Valley Nat. Mon., Deep Springs, Eureka Valley dunes, s side Owens Vly., Stovepipe Wells, dunes e Tinemaha Res., Panamint dunes; Kern Co.: Mojave (4 mi e, 0.5 mi ne), Picacho St. Park; Mono Co.: Swall Meadows, 5 mi w Bishop, 3 mi s Benton Insp. Sta.; Riverside Co.: 1 mi w Blythe, Cathedral City, Corn Springs, Dead Indian Creek, Deep Canyon, Desert Center, 16 km e Desert Center, Indian Wells, Indio, Joshua Tree Nat. Mon. (Pinto Wash), Painted Canyon, nr. Mecca, 2 mi s Thermal, 1 mi w Blythe, 3 mi n Mecca, Whitewater Canyon; San Bernardino Co.: Adelanto, 2 km s Afton, Cadiz dunes, Halloran Spring, Kelso dunes, Kramer Junction, Zzyzx Springs, Needles, Adelanto, 10 mi e 29 Palms, 6 mi n Lake Baldwin, Ivanpah; San Diego Co.: Hidden Springs, 1 mi s, 6 mi se Ocotillo Wells; **Nevada:** Churchill Co.: Horse Creek; Sand Mountain dunes; Clark Co., Las Vegas; Nye Co.: Beatty; Lincoln Co.: Game Range dunes, Pahrump; **Utah**: Emery Co.: Buckskin Spring n Goblin Valley; **Texas**: Brewster Co.: Alpine; 620 specimens were examined including the holotype (BME, CAS, CUIC, EMEC, UCR).

Seasonal distribution. This species has been collected in the months from February through November. The March and November records are from Mexico (Baja California Sur).

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DATA PAPER

Geographic distribution of *Labidus coecus* (Latr.) (Hymenoptera, Formicidae), a subterranean army ant

James K. Wetterer[1], Gordon C. Snelling[1]

1 *Wilkes Honors College, Florida Atlantic University, 5353 Parkside Drive, Jupiter, Florida 33458 USA*

Corresponding author: *James K. Wetterer* (wetterer@fau.edu)

Abstract

Labidus coecus (Latreille) (Hymenoptera, Formicidae) is a New World subterranean army ant with an extensive geographic range. We compiled and mapped >650 site records for *L. coecus*, documenting the earliest known report for 27 geographic areas (countries, US states, and major West Indian islands), including three for which there are no previously published records: Margarita, Tobago, and Trinidad. With the new records, *L. coecus* has now been reported from 20 countries in Central and South America (all except Chile), three West Indian islands (Margarita, Trinidad, and Tobago), and four US states (Arkansas, Louisiana, Oklahoma, and Texas). The range of *L. coecus* appears to be essentially continuous, from Buenos Aires, Argentina in the south (~34.6°S) to Delaware County, Oklahoma in the north (~36.6°N). The three West Indian islands with *L. coecus* populations are all continental shelf islands that were connected to South America during periods of lower sea levels a few thousand years ago, so *L. coecus* populations on these islands have only recently become isolated. *Labidus coecus* commonly nests in caves, a microhabitat that may allow it to live in regions with otherwise inhospitable climates. Although recent papers listed *L. coecus* as an exotic species in North America, we found no evidence that *L. coecus* is exotic to any part of its known range.

Keywords

Introduction

Labidus coecus (Latreille) (Hymenoptera, Formicidae) is a widespread New World subterranean army ant. Longino (2007) wrote that *L. coecus*: "is one of the most remarkable of all army ant species. It has an extremely broad ecological tolerance. It occurs across a great latitudinal range, from the equator to the subtropics of both North and South America. It occurs in dry forest and wet forest, in primary forest and in second growth, in coffee farms and pastures, and in suburban yards. It occurs from sea level to high montane regions. The highest ant record I have for Costa Rica, a collection at 3000 m near Villa Mills, is *Labidus coecus*. The species is almost entirely subterranean, sometimes at considerable depth... In the study of army ants, most of the attention has focused on the large epigaeus species in the genus *Eciton*. But the highest density and most ecologically important army ants may turn out to be *L. coecus*." Crawley (1916) noted this underappreciation, writing that *L. coecus* in Guyana is "a common species, but owing to its habit of burrowing beneath the surface of the soil it is not frequently observed."

Smith (1965) wrote that *L. coecus*: "is a native and widely distributed species, ranging from Oklahoma and Arkansas to Texas and Louisiana, and south to Argentina." Recently, however, Wittenborn and Jeschke (2011) included *L. coecus* on their list of exotic ant species established in North America. Here, we examine the biogeography of *L. coecus*. We were particularly interested in evaluating evidence concerning whether or not *L. coecus* has established any exotic populations in North America or elsewhere.

Taxonomy

Latreille (1802) described *Formica coeca* (= *L. coecus*) from Central America. Junior synonyms of *L. coecus* include *Formica omnivora* Olivier, *Labidus latreillii* Jurine, *Labidus latreillii jurine* Shuckard, *Labidus servillei* Westwood, *Mutilla fulvescens* Blanchard, *Labidus saji* Haldeman, *Labidus panzeri* Smith, *Labidus atriceps* Smith, *Labidus pilosus* Smith, *Eciton vastator* Smith, *Eciton erratica* Smith, *Myrmica rubra* Buckley, *Pseudodichthadia incerta* André, *Eciton smithi* Dalla Torre, *Eciton coecum kulowi* Forel, *Eciton coecum biloba* Emery, *Eciton nigrita* Emery, *Eciton selysi* Forel, *Eciton grassator* Forel, *Eciton coecum servillei hostilis* Santschi, *Eciton coecum opacifrons* Wheeler, *Eciton coecum elsbethae* Forel, and *Eciton serpentis* Weber.

Material and methods

Using published and unpublished records, we documented the known range of *L. coecus*. We obtained unpublished site records from museum specimens in the collections of Louisiana State Arthropod Museum (LSAM); the Museum of Comparative Zoology (MCZ), and the Smithsonian Institution (SI). We obtained unpublished site

records of *L. coecus* from C. Sanabria (Colombia), A.J. Pérez-Sánchez (Margarita), and E. Mendoza (El Salvador). In addition, we used on-line databases with collection information on specimens by the Field Museum, Antweb (www.antweb.org), and the Global Biodiversity Information Facility (www.gbif.org). JKW collected *L. coecus* in Tobago and El Salvador.

We obtained geo-coordinates for collection sites from published references, specimen labels, maps, or geography web sites (e.g., earth.google.com, www.tageo.com, and www.fallingrain.com). Published records usually included collection dates. In a number of cases, publications did not include the collection dates for specimens, but we were able to determine the approximate date based on information on the collector's travel dates. For example, Forel (1899a) reported *L. coecus* from Colombia collected by Princess Theresa of Bavaria, who took part in a scientific expedition to South America in 1898.

Results

We compiled and mapped >650 site records (Fig. 1), documenting the earliest known record for 27 geographic areas (countries, US states, and major West Indian islands), including three for which there are no previously published records: Margarita, Tobago, and Trinidad (Table 1).

In the US, the vast majority of *L. coecus* records came from Texas. O'Keefe et al. (2000) listed records of *L. coecus* from 67 counties in Texas. We found records from six additional counties in Texas, primarily from caves: Burnet, Coryell, Medina, Menard, Montague, and Val Verde (Reddell and Cokendolpher 2001, Calixto 2008, Cokendolpher et al. 2009, antweb).

Watkins (1976) included a distribution map for *L. coecus* showing continuous range from Buenos Aires, Argentina to Oklahoma, Arkansas, and Louisiana with gaps around Uruguay and (inexplicably) Nicaragua.

We found no published site records for *L. coecus* in Oklahoma. Smith (1935) wrote that in Oklahoma, *L. coecus* "may range into the extreme southern part of the state." Later, Smith (1947) listed *L. coecus* as occurring in Louisiana, Oklahoma, and Texas, but gave no site information. Smith (1965, 1979) then listed *L. coecus* from Arkansas, Louisiana, Oklahoma, and Texas. We found only one *L. coecus* specimen from Oklahoma, collected at a black light in Delaware County (1971; C. M. Smith; LSAM).

We found no specific site records for *L. coecus* in Uruguay. Fernández and Sendoya (2004) listed *L. coecus* in Uruguay citing Borgmeier (1955), Watkins (1976), and Palacio (1999) as their source of information on this species, but none of these references recorded *L. coecus* in Uruguay. Zolessi et al. (1989) did not include *L. coecus* in their summary of the ants of Uruguay. Nonetheless, we mapped the Uruguay record to Artigas in northern Uruguay, near records in southern Brazil. It seems almost certain that *L. coecus* does occur in Uruguay, given its presence in surrounding parts of Brazil and Argentina.

Figure 1. Site records of *Labidus coecus.*

Problematic records

Antbase coded one *L. coecus* record as from Espiritu Santo, Vanuatu, but the specimen was actually from Espiritu Santo, Brazil. Antbase previously listed a record of *L. coecus* from New Mexico, but this turned out to be a misidentification (C. Moreau, pers. comm.).

Discussion

Labidus coecus has now been reported from 27 geographic areas, including 20 countries in Central and South America (all except Chile), three West Indian islands (Margarita, Tobago, and Trinidad), and four US states (Arkansas, Louisiana, Oklahoma, and Texas). The range of *L. coecus* appears to be essentially continuous, from Buenos Aires, Argentina (~34.6°S; Borgmeier 1955) in the south to Delaware County, Oklahoma (~36.6°N; see Results) in the north. The three West Indian islands with *L. coecus* populations are all continental shelf islands that were connected to South America during

Table 1. Earliest known records for *Labidus coecus*. + = no previously published records. FM = Field Museum; UWI = University of the West Indies (Trinidad); MCZ = Museum of Comparative Zoology.

	Earliest record
French Guiana	≤1791 (Olivier 1791 as *Formica omnivora*)
Central America	≤1802 (Latreille 1802)
Surinam	≤1807 (Jurine 1807 as *Labidus latreillii*)
Brazil	1830 (Westwood 1842 as *Labidus servillei*)
Guyana	≤1840 (Shuckard 1840 as *Labidus jurinii*)
Texas	≤1852 (Haldeman 1852 as *Labidus saji*)
Colombia	≤1859 (Smith 1859 as *Labidus panzeri*)
Guatemala	1878–1883 (Forel 1899b)
Mexico	≤1885 (André 1885 as *Pseudodichthadia incerta*)
Costa Rica	1889 (Emery 1890)
Venezuela	≤1890 (Emery 1890)
Belize	1870-1890 (Forel 1899b)
Paraguay	≤1894 (Emery 1894)
Nicaragua	≤1899 (Forel 1899b)
Panama	≤1899 (Forel 1899b)
Argentina	1898–1900 (Emery 1906)
Ecuador	≤1901 (Emery 1901 as *Eciton coecum biloba*)
Bolivia	1911 (Mann 1916)
Honduras	1920 (Mann 1922)
+Trinidad	1924 (AE Emerson, FM): Blue Basin
Louisiana	≤1947 (Smith 1947)
Oklahoma	≤1947 (Smith 1947)
Peru	≤1955 (Borgmeier 1955)
El Salvador	≤1957 (Berry and Salazar 1957)
Arkansas	≤1965 (Smith 1965)
+Tobago	1993 (SK Starr, UWI): Charlotteville
Uruguay	≤2004 (Fernández and Sendoya 2004)
+Margarita	2008 (AJ Pérez-Sánchez, pers. comm.): Cerro Macanao

periods of lower sea levels a few thousand years ago, so *L. coecus* populations on these islands have only recently become isolated. *Labidus coecus* has been recorded from numerous caves in Texas (53), Mexico (4), Venezuela (1), and Peru (1) (Kempf 1961, Reddell and Cokendolpher 2001, Cokendolpher et al. 2009). The more stable microclimate of caves may allow *L. coecus* to extend its range into regions with otherwise inhospitable climates. Given its extremely broad ecological tolerance, it is unclear why *L. coecus* populations in the southeast US are not known east of Louisiana, when there would appear to be suitable habitat for this species below 31°N all along the Gulf coast of Alabama and Mississippi and into Florida.

Wittenborn and Jeschke (2011) included *L. coecus* in a list of 93 exotic ant species established in North America. The populations of *L. coecus*, however, appear to be continuously distributed from Argentina to the southern US. We know of no evidence

that even suggests that *L. coecus* has any exotic populations. In addition to *L. coecus*, Wittenborn and Jeschke (2011) appear to have misclassified as exotics numerous other ant species that are actually native to North America. For example, *Gnamptogenys hartmani* (Wheeler), *Leptogenys elongata* (Buckley), and *Pachycondyla harpax* (Fabricius) all have distributions in the southern US that appear to be the northern end of continuous native ranges and give no indication that these species are exotic to North America. Other species that Wittenborn and Jeschke (2011) most likely misclassified as exotics include *Cephalotes varians* (Smith), a widespread arboreal species known from Cuba, the Bahamas, and Florida (de Andrade and Baroni Urbani 1999) and *Leptogenys manni* (Wheeler), a species endemic to Florida (Trager and Johnson 1988). For more than 20 additional ant species, Wittenborn and Jeschke's (2011) classification as exotic in North America is questionable. It seems hazardous research protocol to list species as exotic without documenting the source of this classification. In addition, there is some danger that if native species are erroneously considered to be exotics, they may be treated as such and exterminated, rather than valued and protected.

Acknowledgments

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RESEARCH ARTICLE

Studies of Laboulbeniales (Fungi, Ascomycota) on *Myrmica* ants: *Rickia wasmannii* in the Netherlands

Danny Haelewaters[1], Peter Boer[2], Jinze Noordijk[3]

1 *Department of Organismic and Evolutionary Biology, Harvard University, 22 Divinity Avenue, Cambridge, MA 02138, United States* **2** *Gemene Bos 12, 1861 HG Bergen, The Netherlands* **3** *European Invertebrate Survey (EIS) / Naturalis Biodiversity Center, PO Box 9517, 2300 RA Leiden, The Netherlands*

Corresponding author: *Danny Haelewaters* (dhaelewaters@fas.harvard.edu)

Abstract

An important group of fungal insect parasites is the Laboulbeniales (Ascomycota). These are microscopic in size and live attached to the cuticle of their arthropod hosts. *Rickia wasmannii* is a common European species limited to the ant genus *Myrmica* (Hymenoptera, Formicidae). We present new records of *R. wasmannii* in the Netherlands on three host species: *Myrmica ruginodis*, *M. sabuleti*, and *M. scabrinodis*. Our data show a mass infection of *M. sabuleti* by *R. wasmannii*. The average parasite prevalence is 38% (n = 3,876). The prevalence was much lower on the other *Myrmica* species. So far, *R. wasmannii* infections have been found only on *Myrmica* species in the *rubra*-group and the *scabrinodis*-group. We provide possible explanations for this observation. To date, *Rickia wasmannii* is known on nine *Myrmica* species in sixteen European countries; an overview is included in tabulated form.

Keywords

Ant-associated fungi, ectoparasites, Formicidae, host shift, Laboulbeniales, parasite prevalence

Introduction

The order Laboulbeniales (Ascomycota: Laboulbeniomycetes) consists of microscopic ectoparasites of Arthropoda, mostly true insects. Within the subphylum Hexapoda representatives of nine orders are known as hosts (Weir and Hammond 1997): Blattodea, Coleoptera, Dermaptera, Diptera, Hemiptera, Hymenoptera, Mallophaga, Orthoptera, and Thysanoptera. [Note that the termites, previously ranked in the order Isoptera, were recently included in the order Blattodea, based on phylogenetic data (Beccaloni and Eggleton 2013).] In addition, Acari (subphylum Cheliceriformes) and Diplopoda (subphylum Myriapoda) are known to host Laboulbeniales (Haelewaters et al. 2012, Weir and Hammond 1997). Laboulbeniales are unusual in their determinate growth pattern and lack of hyphae. Diversity in the group is largely underexplored and many questions related to the taxonomy and biology of these fungi remain unresolved.

Within the order Hymenoptera, only ants (family Formicidae) host Laboulbeniales. To date, six species have been reported from ants: *Dimorphomyces formicicola* (Speg.) I.I. Tav., *Laboulbenia camponoti* S.W.T. Batra, *Laboulbenia ecitonis* G. Blum, *Laboulbenia formicarum* Thaxt., *Rickia wasmannii* Cavara, and the recently described *Rickia lenoirii* Santam. (for a short review, see Santamaría and Espadaler 2014; fungal names updated to meet most recent revisions).

Rickia wasmannii is widely distributed in Europe, with reports from Austria, Bulgaria, Czech Republic, France, Germany, Hungary, Italy, Luxembourg, Romania, Slovakia, Slovenia, Spain, Switzerland, the United Kingdom (Espadaler and Santamaría 2012), and from the Netherlands (Haelewaters 2012) and most recently Poland (Witek et al. 2014). It was originally described from Germany on *Myrmica rubra* (Linnaeus, 1758) [as *Myrmica laevinodis*], and is also known to infect eight other species of *Myrmica*, i.e. *M. gallienii* Bondroit, 1920; *M. ruginodis* Nylander, 1846; *M. sabuleti* Meinert, 1861; *M. scabrinodis* Nylander, 1846, *M. slovaca* Sadil, 1952; *M. specioides* Bondroit, 1918; *M. spinosior* Santschi, 1931; and *M. vandeli* Bondroit, 1920 (Csata et al. 2013, Espadaler and Santamaría 2012).

In the Netherlands, a single worker of *Myrmica sabuleti* Meinert, 1861 (as *M. scabrinodis*) infected with *Rickia wasmannii* is known (Haelewaters 2012). Its discovery has initiated the search for Laboulbeniales on ants in this country. For this research project, ants were collected with many pitfall traps and subsequently screened for the presence of *R. wasmannii*.

Methods

The study site spans somewhat less than 1 km^2, situated east of Maastricht (Limburg, the Netherlands) near the border with Belgium. This area has a rolling landscape and calcareous soil. Many different habitats were sampled: calcareous grassland, thicket, moist forest, forest edge, felling area, agricultural field edge, and hollow road.
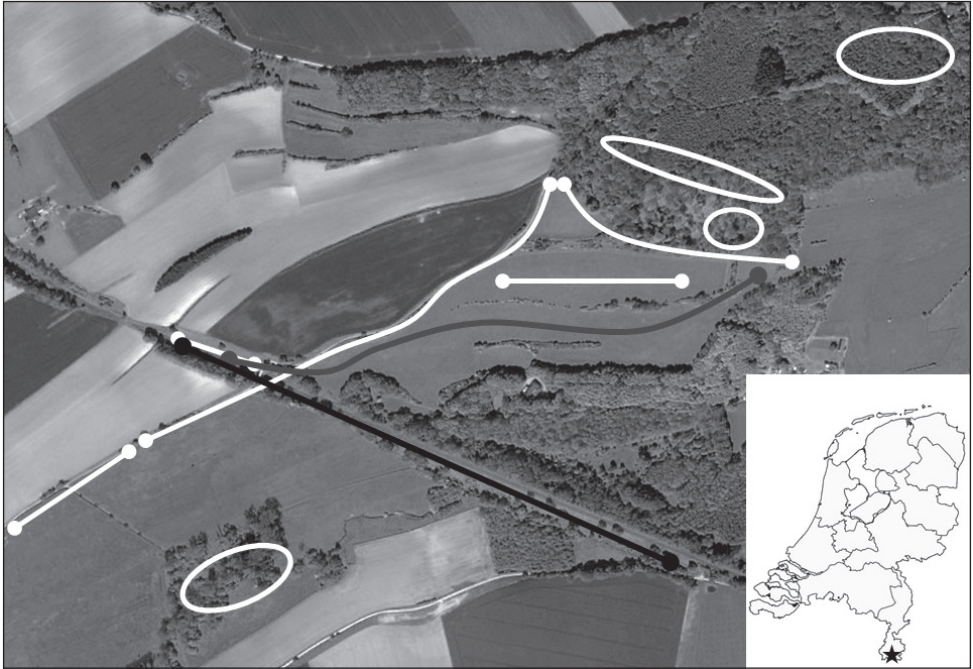
Figure 1. The study site with all the sampling localities indicated. Trajectories (lines) and areas (circles) were sampled with pitfall traps during three inventories. The separate inventories that are mentioned in the text are given: (i) in black (45 pitfall traps in nine series), (ii) in white (55 pitfall traps in eleven series), and (iii) in grey (324 pitfall traps in nine series). Inset: map of the Netherlands with location of the study site in Limburg.

Pitfall traps were filled with a formol solution (3%) or with a saturated salt solution. A lid was placed above each trap to exclude rainfall. Pitfall trapping was performed during three inventories for which in total 424 pitfall traps were placed in 29 series: (i) a year-round inventory of the insect fauna with nine trap series (each with five pitfall traps) at a railroad verge with semi-natural grassland and thicket, (ii) a two-month-long inventory with eleven trap series (each with five pitfall traps) of the arthropod fauna of a nature restoration parcel with a species-rich hay-meadow (dominated by *Arrhenatheretum elatioris* Braun-Blanq.), and (iii) a four-day-long inventory of nine different habitats (nine traps series, one series per habitat, each with 36 pitfall traps) during a student course. For an overview of the study area, see Figure 1.

Screening for thalli of Laboulbeniales was done at 45× magnification with a Euromex Z-1740H stereomicroscope (Arnhem, the Netherlands). Infected ants were sent to Harvard University for study of their associated fungi. Thalli were carefully removed from the host integument using a Minuten Pin (BioQuip #1208SA) and embedded in Amann solution (Benjamin 1971) or PVA Mounting Medium (BioQuip #6371A). Cover slips were ringed with transparent nail varnish. Morphological analyses, measurements, and identifications were done using an Olympus BX40 light microscope

with Olympus XC50 digital camera and MicroSuite Special Edition software 3.1 (Soft Imaging Solutions GmbH). Voucher specimens are deposited at the Farlow Herbarium, Harvard University (FH).

Chi-square tests were performed to analyze whether infection rate of the infected ant species was different from a hypothesized even distribution of *Rickia wasmannii* presence over the infected species. In social insects, it sometimes seems better to analyze the number of infected nests instead of the number of infected workers. However, the infected *Myrmica* species are very abundant in our study area, are polygynous and occur in clusters of mini-populations. They are hardly territorial and contact between workers of different nests is likely (Garnas et al. 2007, Wilson 1971). Each pitfall trap (and trap series) thus likely samples ants from many nests. Our sampling effort with 424 pitfall traps is so widespread over the study area and combines workers from so many nests, that we performed our test on worker individuals.

Results

Twenty-seven ant species were recorded during this study (Table 1). Only three species in the genus *Myrmica* bore thalli of *Rickia wasmannii*.

Within the current study, the highest parasite prevalence was found on *Myrmica sabuleti*: 38% (n = 3,876; Figure 2). For the other two species, parasite prevalence was considerably lower: 11% on *M. scabrinodis* (n = 643) and 0.55% on *M. ruginodis* (n = 182). These infection rates differ significantly when an even proportional distribution of *Rickia* over the three species is presumed, with *M. sabuleti* a significantly higher infection rate as would be expected by chance (observed number of infected ants: 1479; expected: 1279; χ^2=46.82, df=2, *p*<0,001), and a significantly lower infection rate for both *M. scabrinodis* (observed number of infected ants: 71; expected: 212; χ^2=140.11, df=2, *p*<0,001) and *M. ruginodis* (observed number of infected ants: 1; expected: 60; χ^2=68.64, df=2, *p*<0,001). When we look at *Rickia* prevalence over the 29 traps series instead of at the level of individual workers, the same pattern emerges: infected *M. sabuleti* workers in 15 series, infected *M. scabrinodis* in five series, and infected *M. ruginodis* in only one series.

Only workers were found infected; neither gynes nor males were found infected, not even in the highly infected *Myrmica sabuleti*. *Myrmica ruginodis* and *M. scabrinodis* are reported as hosts of *Rickia wasmannii* in the Netherlands for the first time.

Discussion

Rickia wasmannii is mentioned in the literature in the literature to occur on nine host species (Table 2), most of which are widespread across Europe (Radchenko and Elmes 2010). It is reported from sixteen European countries, and expected to occur in Belgium, Denmark, Ireland, and Portugal (Espadaler and Santamaría 2012, Haelewaters 2012, Witek et al. 2014).

Table 1. Total number of ant species studied for infection with *R. wasmannii*, over all three series of pitfall traps.

Genus	Species	Author, Year	Workers			Sexuals	
			Total	Infected	Parasite prevalence	Gynes	Males
Formica	*cunicularia*	Latreille, 1798	589	0	0	0	0
Formica	*fusca*	Latreille, 1798	193	0	0	0	0
Formica	*polyctena*	Foerster, 1850	0	0	0	1	0
Formica	*rufibarbis*	Fabricius, 1793	92	0	0	0	0
Lasius	*brunneus*	(Latreille, 1798)	148	0	0	0	0
Lasius	*flavus*	(Fabricius, 1782)	983	0	0	22	8
Lasius	*fuliginosus*	(Latreille, 1798)	267	0	0	19	0
Lasius	*mixtus*	(Nylander, 1846)	6	0	0	8	0
Lasius	*niger*	(Linnaeus, 1758)	> 3,400	0	0	5	0
Lasius	*platythorax*	Seifert, 1991	39	0	0	0	0
Lasius	*sabularum*	(Bondroit, 1918)	0	0	0	4	0
Lasius	*umbratus*	(Nylander, 1846)	1	0	0	5	0
Myrmecina	*graminicola*	(Latreille, 1802)	328	0	0	13	0
Myrmica	*rubra*	(Linnaeus, 1758)	974	0	0	1	3
Myrmica	*ruginodis*	Nylander, 1846	182	1	0.55	0	1
Myrmica	*rugulosa*	Nylander, 1849	7	0	0	0	0
Myrmica	*sabuleti*	Meinert, 1861	3,876	1,479	38	41	3
Myrmica	*scabrinodis*	Nylander, 1846	643	71	11	11	0
Myrmica	*schencki*	Viereck, 1903	632	0	0	63	1
Ponera	*coarctata*	(Latreille, 1802)	2	0	0	0	0
Solenopsis	*fugax*	(Latreille, 1798)	1	0	0	0	0
Stenamma	*debile*	Foerster, 1850	236	0	0	6	1
Stenamma	*westwoodi*	Westwood, 1840	0	0	0	1	0
Tapinoma	*erraticum*	(Latreille, 1798)	12	0	0	0	0
Temnothorax	*affinis*	(Mayr, 1855)	3	0	0	0	0
Temnothorax	*nylanderi*	(Foerster, 1850)	25	0	0	1	0
Tetramorium	*caespitum*	(Linnaeus, 1758)	33	0	0	0	0
		Total *Myrmica*	**6,314**	**1,551**		**116**	**8**
		Total ants	**> 12,675**	**1,551**		**201**	**17**

Ant species with *Rickia* infection

Santamaría and Espadaler (2014) mention the "high host phylogenetic specificity" of Laboulbeniales, but caution is needed when interpreting support for this assertion. Although specific to the genus *Myrmica*, host species of *Rickia wasmannii* belong to two clades or so-called species groups that are not phylogenetically closely related: *rubra*-group and *scabrinodis*-group (Jansen et al. 2010).

The Palearctic species in the genus *Myrmica* are classified into 17 taxonomic species groups based on their morphology (Radchenko and Elmes 2010), three of which are represented in our study: the *rubra*-group, encompassing *M. rubra* and *M. ruginodis*; the *scabrinodis*-group, with *M. rugulosa*, *M. sabuleti*, and *M. scabrinodis*; and the *schencki*-group, to which (in most parts of Europe) only *M. schencki* belongs. The

Figure 2. A worker of *M. sabuleti*, heavily infected with *R. wasmannii* on all body parts. Photograph: Theodoor Heijerman.

monophyly of these morphological species groups was confirmed using molecular data (Jansen et al. 2010). So far, only species of the *rubra*-group and *scabrinodis*-group have been found with *Rickia wasmannii* infection.

Our research confirms this finding: although six *Myrmica* species were screened (n = 6,314), *Rickia wasmannii* was only present on *M. ruginodis*, *M. sabuleti*, and *M. scabrinodis* (Table 1). Several researchers screened multiple species of *Myrmica* in Hungary/Romania (Tartally et al. 2007), Slovakia (Bezděčka and Bezděčkova 2011), and the Czech Republic (Bezděčkova and Bezděčka 2011), but found only species in the *scabrinodis*-group infected by *R. wasmannii*. In addition, our study in the Netherlands revealed a single lightly infested worker in the *rubra*-group (*M. ruginodis*). In all four studies, *R. wasmannii* was found only in the *rubra*- and *scabrinodis*-groups.

Inadequate sampling of potential hosts may (partly) explain this pattern, although recently in Europe several studies have been conducted on Laboulbeniales on *Myrmica*, including various studies in which different species groups were sampled and screened. To avoid taxon-sampling errors in these kinds of observation, we suggest that systematic collections in natural history museums be screened for *Rickia wasmannii* on *Myrmica*. Screening museum collections previously has yielded important contributions on patterns of host utilization (Weir and Hammond 1997: 80,000 insects screened) and the distribution of *Hesperomyces virescens* Thaxt. (Haelewaters et al. 2014: 4,000 ladybirds screened).

Host shift could be another explanation for the restricted presence of *R. wasmannii* on two species groups that are not sister clades. Host shifts have been suggested for morphologically similar *Laboulbenia* species between Cicindelinae and other Car-

Table 2. All published records of *R. wasmannii* on different *Myrmica* hosts (Bezděčka and Bezděčkova 2011; Bezděčkova and Bezděčka 2011; Csata et al. 2013; Espadaler and Santamaría 2012; Haelewaters 2012; Tartally et al. 2007; Witek et al. 2014), completed with the current findings from the Netherlands. *In Hungary and Romania, *M. scabrinodis* is the most common host of *R. wasmannii* (Csata et al. 2014; Tartally et al. 2007). In our study area in the Netherlands, *M. sabuleti* is the most commonly infected host species.

Country	rubra-group		scabrinodis-group						
	M. rubra	*M. ruginodis*	*M. gallienii*	*M. sabuleti*	*M. scabrinodis*	*M. slovaca*	*M. specioides*	*M. spinosior*	*M. vandeli*
Austria	X				X				
Bulgaria					X				
Czech Republic					X	X			
France					X				
Germany	X								
Hungary*					X	X	X		X
Italy					X				
Luxembourg	X								
The Netherlands		X		X	X				
Poland					X				
Romania*	X	X	X		X	X			
Slovakia					X				
Slovenia				X					
Spain							X	X	
Switzerland	X								
United Kingdom				X					

abidae living in the same habitat (Arndt et al. 2003, Rossi 2011), and De Kesel and Haelewaters (2014) provide morphological and ecological data to support the hypothesis that a species of *Laboulbenia* shifted between Carabidae and Staphylinidae. To explain the extremely small size of *Rickia lenoirii* on *Messor* spp. ants (Hymenoptera, Formicidae), Santamaría and Espadaler (2014) suggest that Laboulbeniales can shift between myrmecophilous Acari and their ant hosts.

Geographical variation

Parasite prevalence (= infection frequency) is often used to quantify differences in populations of Laboulbeniales in a given host community (De Kesel 2011, Haelewaters et al. 2012). It is beyond doubt that in our study area *Myrmica sabuleti* is the main host of *Rickia wasmannii*, considering the actual prevalence of *R. wasmannii* on *M. sabuleti* workers infected, compared to the low parasite prevalence on *M. ruginodis* and *M. scabrinodis* (Table 1).

In our study site, parasite prevalence was high in the *scabrinodis*-group (Table 1). *Myrmica sabuleti* and *M. scabrinodis* occur in other habitats; the former species gener-

ally lives in drier areas than the latter. While in our study area in the province Limburg both species live in sympatry, we observed noticeable differences in occurrence and parasite prevalence. In the *rubra*-group, only one specimen of *M. ruginodis* was found with *Rickia wasmannii*. The fact that we did not find any infected *M. rubra* out of 974 workers raises questions, since this species is the second-most commonly found infected species in Europe after *M. scabrinodis*, with examples in Austria, Germany, Luxembourg, Romania, and Switzerland (Espadaler and Santamaría 2012, Table 2).

Also in Romania, so far, infection by *Rickia wasmannii* only occurs in the *rubra*-group and *scabrinodis*-group (Csata et al. 2013, Tartally et al. 2007). In Romania, *Myrmica scabrinodis* often is the only or main host; in a single population *R. wasmannii* was found only on *M. rubra*, although thalli were also observed in populations of *M. scabrinodis* and *M. slovaca*; *M. gallienii* and *M. rubra*; and *M. ruginodis* (Csata et al. 2013).

Myrmica scabrinodis is the main host in Romania (studied areas, Csata et al. 2013), as is *M. sabuleti* in our studied site in the Netherlands. These observations suggest (1) that *R. wasmannii* has a considerable host choice plasticity within the genus *Myrmica* and (2) that infection rates of *Rickia wasmannii* show geographical variation, potentially with different dominant host species across regions. It is not known what factors cause this geographical variation. Future research in the Netherlands is needed to confirm that *M. sabuleti* is the main host in a wider region.

Acknowledgments

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SHORT COMMUNICATION

Prey carriage varies with prey size in *Cerceris fumipennis* (Hymenoptera, Crabronidae)

Christine A. Nalepa[1], Whitney G. Swink[1]

I *North Carolina Department of Agriculture and Consumer Services, Beneficial Insects Laboratory, 1060 Mail Service Center, Raleigh, NC 27699-1060 U.S.A.*

Corresponding author: *Christine A. Nalepa* (christine.nalepa@ncagr.gov)

Citation: Nalepa CA, Swink WG (2015) Prey carriage varies with prey size in *Cerceris fumipennis* (Hymenoptera, Crabronidae). Journal of Hymenoptera Research 44: 49–55. doi: 10.3897/JHR.44.5158

Abstract

Exploitation of the hunting behavior of the solitary wasp *Cerceris fumipennis* is proving to be a useful method for detecting pest Buprestidae as well as for documenting buprestid diversity in eastern North America. Here we review prey carriage mechanisms in the species, and conclude that variation in prey carriage is correlated with the spectacular size range of their buprestid prey (4.9–22.3 mm length). Small prey items, including *Agrilus* species, are transported with the aid of a specialized morphological structure on the fifth metasomal sternite ("buprestid clamp"), resulting in a distinct curved posture during flight. Analysis of prey items from *C. fumipennis* in North Carolina in 2014 indicates that 30% of collected *Agrilus* spp. were not paralyzed prior to wasp arrival at the nest, and suggests that the buprestid clamp may function to prevent the escape of active small prey. Recognition that the curved flight posture of a female approaching her nest is a signal that she may be carrying a beetle in the genus *Agrilus* can improve efficiency of biosurveillance for pest Buprestidae.

Keywords

Introduction

The solitary, ground-dwelling wasp *Cerceris fumipennis* Say currently is being employed as a tool for biosurveillance of pest Buprestidae in eastern North America as well as for the documentation of regional buprestid diversity (reviewed by Swink et al. 2013, Careless et al. 2014). Any observations that contribute to more efficiently using this unique system is therefore of interest and value. Here we focus on prey carriage and paralysis by the wasp.

Current literature offers mixed reports of prey carriage by *Cerceris fumipennis*. Although there is general agreement that the beetle is carried in the wasps' mandibles with its head forward and venter facing up, where the beetle is grasped, and the involvement of the wasp legs in supporting the prey varies. Mueller et al. (1992) indicate that *C. fumipennis* appears to use just legs to hold larger buprestids while in flight, but Careless (2009) reports that an antenna of large beetle prey is grasped in the mandibles, with the wasp fore- and mid-legs embracing the body. Available images of *C. fumipennis* with prey are of little help, because they typically show the wasp perched on vegetation or the ground, or on final approach with her landing gear down. There are a few exceptions. Careless et al. (2009: fig. 23) picture a female in flight carrying a prey item about half her length. The wasp metasoma is extended, the thorax of the prey beetle is under her head, and the fore and middle legs are supporting the prey with the hind legs flexed and uninvolved. In video footage of a wasp hovering near her nest entrance with a large prey item (Walton 2011), it is fairly clear that all three sets of legs embrace the prey, but involvement of the mandibles is not visible.

Mueller et al. (1992) reported that smaller beetle species, including those in the genus *Agrilus,* are clasped about the mid-thorax with the wasp mandibles. In the course of six seasons of working with *Cerceris fumipennis*, however, the authors (CAN and WGS) independently noted that females coming back to the nest carrying small, *Agrilus*-sized beetles often can be recognized in flight by the curvature of the wasp's metasoma (Fig. 1d). Investigation into the basis of this flight posture led us to Krombein (1981), who described a "buprestid clamp" on the fifth metasomal sternite of *Cerceris* females in the *bupresticida* group, including *C. fumipennis*. He described it as a median concavity with an erect lamella at the posterior margin (Fig. 1a–c). He goes on to state that the female "grasps the head of the buprestid in her mandibles, curves the tip of her abdomen beneath and forward so that the abdominal apex of the buprestid rests in the concavity and is prevented from slipping by the erect flange. This clamp functions only with long slender buprestids such as *Agrilus* species." He found it a pleasing example of the correlation between structure and function.

Krombein supplied the foundation for the unique flight posture we observed, but it seemed unusual that a female transporting a small paralyzed beetle in her mandibles had need to stabilize such a light load by means of a morphological structure specific to the purpose. Here we suggest that the basis of specialized carriage of small prey by *Cerceris fumipennis* is that small beetles, including most *Agrilus* species, often are not successfully paralyzed at their collection site.
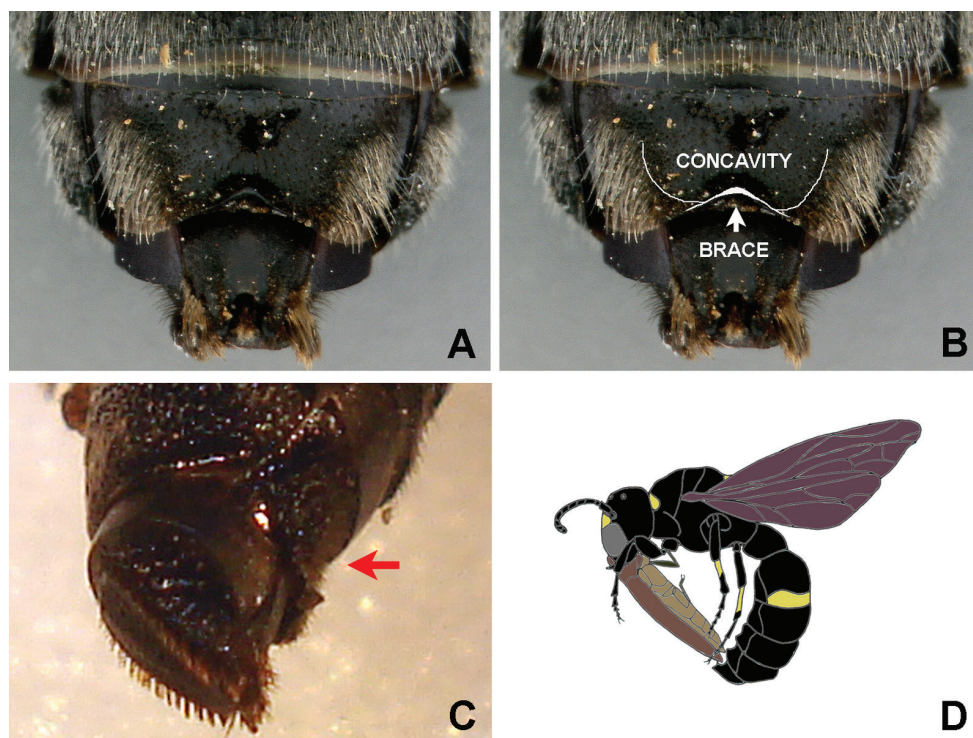
Figure 1. Buprestid clamp in *Cerceris fumipennis*. (**a, b**) Ventral view of broadly concave median area of ventral fifth metasomal segment with an erect, cuticular process at the posterior margin acting as a brace (= buprestid clamp); (**c**) Ventrolateral view of buprestid clamp, showing the concavity (arrow) and brace; (**d**) Curved, in-flight posture of female *Cerceris fumipennis* using the buprestid clamp. Drawing by WGS.

Methods

During biosurveillance with *Cerceris fumipennis* in North Carolina during 2014, a subset of wasps captured with prey from seven widely scattered nesting aggregations were analyzed. A total of 258 females carrying prey were captured in a sweep net and the activity level of the prey item rated as paralyzed (incapable of locomotion) or not paralyzed (capable of escape). The beetle prey were then transported on ice to the laboratory where body length was measured using digital calipers (Mitutoyo Absolute Digimatic caliper – 0.01mm). Individual beetles were measured 3×, and the average recorded. Beetles were identified by W.G. Swink and J.P. Basham (Tennessee State University).

Results

Nine of the 258 beetles taken by *Cerceris fumipennis* females (3.5%) were active and capable of escape, i.e., not paralyzed when captured. Eight of the non-paralyzed beetles were in the genus *Agrilus*: *A. bilineatus* (Weber), *A. difficilis* Gory, *A. ruficollis* (F.), and

Table 1. Body length and state of paralysis of 27 specimens of *Agrilus* (nine species) from seven locations (six counties) in North Carolina during 2014.

Agrilus species	Length (mm)	Paralysis?	Site	County	Latitude	Longitude
A. arcuatus (Say)	6.71	+	Faith Christian Acad.	Wayne	35.399°N	78.012°W
A. arcuatus	8.00	+	Franklinton Park	Franklin	36.108°N	78.437°W
A. arcuatus	7.04	+	Lake Lynn Park	Wake	35.889°N	78.698°W
A. arcuatus	8.26	+	Vance Elementary	Buncombe	35.577°N	82.600°W
A. arcuatus	7.82	+	Vance Elementary			
A. arcuatus	8.08	+	Vance Elementary			
A. bilineatus (Weber)	9.16	+	Franklinton Park			
A. bilineatus	8.10	+	Lake Lynn Park			
A. bilineatus	7.52	-	Lake Lynn Park			
A. bilineatus	9.08	-	Lake Lynn Park			
A. bilineatus	6.50	-	Vance Elementary			
A. bilineatus	7.87	-	Vance Elementary			
A. bilineatus	6.58	+	Vance Elementary			
A. bilineatus	7.95	-	Vance Elementary			
A. bilineatus	7.61	+	Vance Elementary			
A. bilineatus	6.16	+	Vance Elementary			
A. bilineatus	7.93	+	Vance Elementary			
A. bilineatus	8.40	+	Vance Elementary			
A. cliftoni Knull	5.86	+	Vance Elementary			
A. difficilis Gory	10.72	+	Luddy Park	Franklin	36.022°N	78.483°W
A. difficilis	9.25	-	Luddy Park			
A. ferrisi Dury	10.17	+	Luddy Park			
A. pensus Horn	9.33	-	Meadowview MS	Surry	36.481°N	80.652°W
A. quadriimpressus Ziegler	10.56	+	Faith Christian Acad.			
A. ruficollis (F.)	6.39	-	McCray Recreation	Alamance	36.171°N	79.386°W
A. ruficollis	6.03	+	McCray Recreation			
A. subrobustus Saunders	4.86	+	Vance Elementary			

A. pensus Horn. The single non-paralyzed, non-*Agrilus* species captured was *Brachys ovatus* (Weber).

Overall, 27 *Agrilus* (nine species) were captured; in three species, both paralyzed and active individuals were collected from foraging wasps (Table 1). Just one individual of *A. pensus* was collected overall, and it was active when collected. The 27 *Agrilus* captured ranged from 4.9 mm in length (*A. subrobustus*) to 10.7 mm (*A. ferrisi*). There was no significant difference in the length of *Agrilus* that were paralyzed vs. those that were not ($t = 0.31$, $P = 0.76$; two-sample t-test). It is notable that the smallest *Agrilus* captured (*A. subrobustus* Saunders) was paralyzed. The single active *Brachys ovatus* measured 5.4 mm.

Discussion

Krombein's (1981) proposal that the buprestid clamp on *Cerceris fumipennis* is specialized for the transport of *Agrilus*, combined with the inconsistent paralysis of *Agrilus*

spp. reported here suggests that the two are related. Stinging behavior as well as "the state of the stung" is known to vary considerably with context (Steiner 1986), and it is likely difficult for *C. fumipennis* to manipulate small buprestids into a suitable position for stinging at the capture site. All Buprestidae are well sclerotized, and the vulnerable coxal membranes (Careless et al. 2009) of small beetles offer a miniscule target for insertion of the stinger. All buprestids furthermore exhibit death feigning (thanatosis) as a defense mechanism; they typically respond to disturbance by retracting their appendages and becoming quiescent. This allows the wasp to carry a compact and motionless beetle into its nest, even if stinging was unsuccessful (Careless 2009). We suggest that the buprestid clamp in *C. fumipennis* functions primarily to prevent the elytra from opening in small prey that may or may not be successfully paralyzed. This applies to those in the genus *Agrilus* (as suggested by Krombein 1981), as well as to other small species with an abdominal tip narrow enough to fit in the concavity of the clamp, such as *Brachys ovatus* and perhaps the alternative prey *Neochlamismus bebbianae* Brown (Chrysomelidae) (references in Careless et al. 2014). The latter is a small, heavily sclerotized beetle that has been taken nine times from *C. fumipennis* in North Carolina, and none to date have been paralyzed (WGS, pers. obs.).

Medium to large beetles also may be less than completely paralyzed prior to transport, but the leg embrace by the wasp assures their immobility during flight. Once in the nest, the wasp is free to assure paralysis of the prey at her leisure. Prey temporarily stored in the main burrow, prior to placement in the brood cells, continue to vary in their degree of paralysis; an *Agrilus bilineatus* was observed crawling out of the nest by Hook and Evans (1991). However, beetles are stung (or re-stung) prior to final placement in the brood chamber (Careless et al. 2009; Hook and Evans 1991), and prey collected from *Cerceris fumipennis* brood cells are always "rather thoroughly paralyzed" (Kurczewski 1984, Hook and Evans 1991).

Prey carriage plasticity in *Cerceris fumipennis* is related to the remarkable range of both size and shape of their buprestid prey. Careless (2009) reported that the beetles he collected were 4.9–22.3 mm in length, and those taken from *C. fumipennis* in North Carolina in 2014 exhibit a similar range (4.9–21.3 mm; n=258; Nalepa and Swink, unpublished data); shape varies from the elongate, parallel-sided *Agrilus* to the broadly oval species of *Buprestis*. In medium to large beetle prey, an anterior body part of the beetle is clasped by the wasp mandibles and the number of legs involved in load support likely depends on prey length, their weight in relation to the center of gravity during wasp flight, and perhaps the degree of beetle paralysis. The load needs to be not only secure, but balanced during transport. Small prey are grasped with the mandibles, and secured via the buprestid clamp. As a whole, then, *C. fumipennis* falls into two established categories of prey carriage mechanisms depending on prey size: Mandibular 3, where the prey is held in mandibles and supported in flight with the legs, and Abdominal 2, with prey carried in flight supported by structural modifications of the apical metasomal segment (Evans 1962, O'Neill 2001: table 3–10).

Species composition of the buprestid prey of *Cerceris fumipennis* varies with geographic location and the plant species composition surrounding nesting aggregations.

For example, of the 310 beetles taken from *C. fumipennis* nests by Evans (1971) in New York State, 84.5% were *Agrilus* spp., while just 8.2% of the 466 beetles collected from *C. fumipennis* in the Goldsboro area of North Carolina over four years were in that genus (Swink et al. 2014). Nonetheless, *C. fumipennis* has specific morphological and behavioral adaptations to secure and transport *Agrilus*, suggesting that this buprestid genus is an evolutionarily significant prey item of the wasp. Such specific adaptations to prey transport are exhibited by additional *Cerceris* species that hunt Buprestidae (Krombein 1981), as well as by the weevil hunting *C. halone* (Byers 1978).

Conclusions

The genus *Agrilus* contains mostly small, elongate species (4–13 mm – Paiero et al. 2012), many of which are economically important and thus the primary target of biosurveillance programs. Collections from *Cerceris fumipennis* can be biased against *Agrilus*, however, not only because of the speed of females laden with small prey, but also because of their ability to pass though, unimpeded, the plastic "Careless collars" designed to slow or stop females carrying larger beetles (see Careless et al. 2014: Fig. 1b). The latter drawback can be overcome, at least in part, by placing the hole in the collar slightly askew over the burrow entrance (Careless et al. 2014). Here we suggest that the bias can be further mitigated by expanding the search image for prey-laden incoming wasps. *Cerceris fumipennis* females carrying *Agrilus* and other small buprestid species can be recognized by their characteristic curved posture while in flight, even if the prey item is not visible. Attempts to capture these females in a sweep net prior to their arrival at the nest can help fine tune the biosurveillance system and increase the odds of detecting pest Buprestidae.

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RESEARCH ARTICLE

Colemanus keeleyorum (Braconidae, Ichneutinae s. l.): a new genus and species of Eocene wasp from the Green River Formation of western North America

J. Ray Fisher[1], Erika M. Tucker[2], Michael J. Sharkey[2]

1 *Department of Entomology, University of Arkansas, Fayetteville, AR 72701, USA* **2** *Department of Entomology, University of Kentucky, Lexington, KY 40546, USA*

Corresponding author: *J. Ray Fisher* (jrfisher@uark.edu)

Citation: Fisher JR, Tucker EM, Sharkey MJ (2015) *Colemanus keeleyorum* (Braconidae, Ichneutinae s. l.): a new genus and species of Eocene wasp from the Green River Formation of western North America. Journal of Hymenoptera Research 44: 57–67. doi: 10.3897/JHR.44.4727

Abstract

A new genus and species of Ichneutinae s. l., *Colemanus keeleyorum* Fisher, is described from the Eocene Green River Formation in Colorado, USA. *Colemanus* was placed on a phylogenetic hypothesis using morphological data. Using a parsimony criterion, *Colemanus* is placed within Proteropini (Ichneutinae s. l.). Reconstructions of well-preserved regions (mesosomal dorsum and wings) are included. A previously described species from lower Oligocene Baltic amber is transferred to *Colemanus*, resulting in the new combination *C. contortus* (Brues, 1933).

Introduction

Herein we describe *Colemanus keeleyorum* gen. n. et sp. n. (Braconidae: Ichneutinae s. l.) from the Eocene Green River Formation in the western United States. The Green River Formation represents one of the best documented ancient lake systems and has offered a particularly well preserved window into Eocene fauna. The formation is best known for fossil fish (Conrad et al. 2007), but other key discoveries include the oldest known bats: *Icaronycteris index* Jepsen, 1966 and *Onychonycteris finneyi* Simmons et al., 2008.

Recent collecting efforts by David Kohls (Colorado Mountain College) and colleagues have accumulated more than 120,000 specimens, including more than 2,000 insects. One specimen, a wasp collected in 2005 in the Parachute Member of the Piceance Creek Basin (northwestern Colorado), caught the attention of Jim Whitfield (University of Illinois) due to its resemblance to members of a large braconid assemblage called the microgastroid complex.

The microgastroid complex is a well-supported rapid radiation (e.g., Whitfield and Lockhart 2007, Whitfield and Kjer 2008, Murphy et al. 2008, Sharanowski et al. 2011) well-known for its association with host-immunosuppressing polydnaviruses (e.g., Whitfield 2000). Overall, the relationships of subfamilies within the complex are poorly understood due to the rapid nature of their diversification (Whitfield and Lockhart 2007, Whitfield and Kjer 2008), but two relationships are clear. First, Cheloninae is sister to all other subfamilies (Whitfield 1997, Dowton and Austin 1998, Dowton et al. 1998, Belshaw et al. 2000, Banks and Whitfield 2006, Murphy et al. 2008, Sharanowski et al. 2011). Second, Ichneutinae s. l., usually excluded from the microgastroid complex because members are not known to contain polydnaviruses, is sister to the microgastroid complex (Quicke and van Achterberg 1990, Belshaw et al. 2000, Belshaw and Quicke 2002, Dowton et al. 2002, Murphy et al. 2008, Sharanowski et al. 2011).

Ichneutinae has received considerable attention and endured a chaotic taxonomic history, despite its relatively small size of approximately 100 species (Sharkey 1994, Yu et al. 2005). Three lineages are recognized and traditionally assigned to the tribal level (Proteropini, Ichneutini, and Muesebeckiini); however, tribal designation has been disputed Sharkey 1994, 1996). Although normally treated as a single subfamily, phylogenetic analysis often renders Ichneutinae paraphyletic (e.g., Quicke and van Achterberg 1990, Belshaw et al. 2000, Dowton et al. 2002, Sharanowski et al. 2011). The most rigorous of these analyses, which investigated multiple ribosomal and nuclear genes, recovered Proteropini as sister to microgastroids and Ichneutini as sister to that complex (Sharanowski et al. 2011). The affinities of the highly-derived muesebeckiines remain unknown as they were excluded from that analysis.

Placing the fossil within the Ichneutinae s. l. + microgastroid complex is difficult due to its resemblance to several lineages. Specifically, the fossil resembles Cardiochilinae because the last abscissa of the fore wing radial sector (3RSb) is recurved, although unlike many cardiochilines this vein remains tubular as it reaches the wing margin; and it resembles Proteropini (Ichneutinae s. l.) because the first abscissa of the fore wing media (1M) is evenly curved. Some Cheloninae also share these characters, but are readily differentiated by the presence of a metasomal carapace.

To determine the fossil's affinity, we placed it on a phylogenetic hypothesis for Braconidae (Sharanowski et al. 2011) using a parsimony criterion (tree length) of morphological characters. The dataset was expanded by adding taxa superficially resembling the fossil (*Bohayella* and *Schoenlandella* (Cardiochilinae); *Helconichia* (Proteropini)). The method implemented herein has the benefit over a standard analysis of easily comparing alternative placements of the fossil.

Materials and methods

The photographs of *Colemanus* gen. n. (Fig. 1) were taken with a JVC KY-F75 3CCD digital camera and prepared with Archimed™ by Microvision Instruments. Reconstructions (Fig. 2) were created by tracing these photographs in Adobe Illustrator CS4, and by editing in Adobe Photoshop CS4. Unfortunately, the metasoma and legs did not preserve during fossilization (or are obscured by the rock matrix), and the head is crushed, offering no codable characters for these regions. The wings are remarkably preserved, complete with wing setae, whereas the dorsal mesosoma and antennae are moderately well preserved.

Thirteen characters (Table 1) were selected from Sharkey and Wharton (1994, with corrections in Sharkey 1996), Sharkey (1997), and Dangerfield et al. (1999), and were modified to reflect characters discernible in the fossil.

Table 1. Description of characters and character states. Sources: 1) Sharkey and Wharton (1994, with corrections in Sharkey 1996); 2) Sharkey (1997); 3) Dangerfield et al. (1999).

Characters	States	Code	Source
1. Fore wing 3RSb	recurved	0	2, 3
	straight	1	
2. Fore wing 3RSb	reaching wing margin as tubular vein	0	2, 3
	not reaching wing margin as tubular vein	1	
3. Fore wing 2RS	strongly curved	0	2
	straight	1	
4. Fore wing (RS+M)b	longer than its width	0	2
	equal to, or shorter than its width	1	
5. Fore wing 1cu-a origin	nearly in line with M	0	2
	not in line with and often far distal to M	1	
6. Fore wing 1cu-a angle	toward apex	0	1
	not toward apex	1	
7. Fore wing 1M	straight or slightly curved	0	2
	evenly curved or bent at mid-length	1	
	apically bent toward wing tip	2	
8. Fore wing 1a	present	0	2
	absent	1	
9. Hind wing M+Cu length	≥ 1st abscissa of M	0	2
	< 1st abscissa of M	1	
10. Hind wing crossvein r	present	0	2
	absent	1	
11. Hind wing M+Cu position	posterior half of wing	0	1, 3
	anterior half of wing	1	
12. Notauli	deep, wide, meeting posteromedially	0	1
	relatively reduced	1	
13. Propodeum	with areolate sculpture	0	2
	without areolate sculpture	1	

Table 2. Character matrix.

Taxa	Characters: 1234567890123
Meteorideinae (*Meteoridea*)	1010100101111
Agathidinae (*Earinus*)	1010000101111
Ichneutini (*Ichneutes*)	1010012001110
Proteropini (*Proterops*)	1000111001111
Proteropini (*Muesonia*)	1011011001100
Proteropini (*Helconichia*)	1001011001100
Cheloninae (*Phanerotoma*)	1010100101110
Mendesellinae (*Epsilogaster*)	1100100101110
Khoikhoiinae (*Khoikhoia*)	0110100000111
Cardiochilinae (*Heteropteron*)	0110110110111
Cardiochilinae (*Bohayella*)	0110100010100
Cardiochilinae (*Cardiochiles*)	0110110110110
Cardiochilinae (*Schoenlandella*)	0110110111100
Microgastrinae (*Snellenius*)	1110100100100
Microgastrinae (*Microplitis*)	1110100101101
Colemanus gen. n.	0001101001000

Taxa included (Table 2) were based upon the molecular analysis of Braconidae presented by Sharanowski et al. (2011) with the following modifications: 1) highly derived groups were excluded (e.g., Miracinae); 2) sampling of Cardiochilinae was increased given the superficial resemblance of certain genera to *Colemanus* (*Bohayella* and *Schoenlandella*); 3) *Heteropteron* was added due to its basal placement within Cardiochilinae (Dangerfield et al. 1999); 4) although Sharanowski et al. (2011) included only two of the five proteropine genera (*Proterops* and *Muesonia*), we added *Helconichia* due to its resemblance to the fossil.

Fossil placement was investigated with Mesquite 3.01, which allows for quick repositioning of branches while calculating the number of character substitutions (tree length) (Madison and Madison 2014). Tree topology was constrained to the relationships elucidated in previous studies (Sharanowski et al. 2011, Dangerfield et al. 1999). To analyze the matrix on the constrained topology, the fossil was placed at every node and tree lengths were compared to assess the most parsimonious placement. Given the uncertain relationships among Proteropini, our analyses were carried out with each possible relationship of the three included genera (Fig. 3A–C). Figures were created with Adobe Illustrator CS6.

Results

Morphology: Reconstruction of the whole body was not possible, given the poorly preserved head, legs, and metasoma (Fig. 1). Additionally, although the mesosoma contained sections preserved in excellent detail, the overall quality prevented complete reconstruction. Nevertheless, a nearly complete reconstruction of the dorsal mesosoma was possible (Fig. 2A). Some interpretations should be considered "best guesses", as

they were poorly preserved. These characters are as follows: the degree of notauli sculpturing posteriorly, the medial carina on the lateral scutellum, and the carinae on the lateral metanotum.

The remarkably preserved wings provided most detail and were the principle units used in morphology. Both wings showed some bending, so both wings were used to create a composite hypothesis for wing veins (Fig. 2B). Areas of the wing where unbiased reconstruction were impossible include the apparently non-tubular region surrounding (RS+M) b (Fig. 1C), the apical non-tubular limits of the fore wing media and cubitus, and the apical non-tubular limits of the hind wing radial sector and media. Noteworthy is that (RS+M) b appears to be vertical, which is a rare character for all braconids, although this region is difficult to interpret. Also, the last abscissa of the radial sector (3RSb) is recurved, lending the resemblance to Cardiochilinae and some Cheloninae, although 3RSb in cardiochilines is not tubular as it reaches the wing margin and chelonines have a metasomal carapace.

Despite the great condition of the antennae, no characters could be extracted except flagellomere number (33–34), which itself is inconclusive due to the indiscernible basal antennomeres. Regardless, there are more antennomeres than in other described proteropines (24–31). However, given the variability of this character across Ichneutinae s. l. (12–38), this difference is not considered informative at the level of our analyses and is not included in the matrix.

***Morphological phylogenetics*:** Tree lengths representing placement of *Colemanus* at each possible node can be viewed in Figure 3, across the three possible relationships of Proteropini (A–C). Without the addition of *Colemanus*, total tree lengths varied (33–35) depending on the arrangement of Proteropini (boxed values in Fig. 3). Adding *Colemanus* raises total tree lengths to a minimum of 36 (when placed sister to *Helconichia*+*Muesonia*, given the topology in Fig. 3A) and a maximum of 44 (when placed sister to *Cardiochiles*, given the topology in Fig. 3C). For each topology, the most parsimonious placement of *Colemanus* is within Proteropini.

We conclude from these findings that *Colemanus* should be placed within Proteropini, although given the uncertainty of proteropine relationships, exact placement within this group is not yet feasible. The fossil contains character states that do not fit within any current genus. Therefore, we suggest placement within a new genus, *Colemanus*.
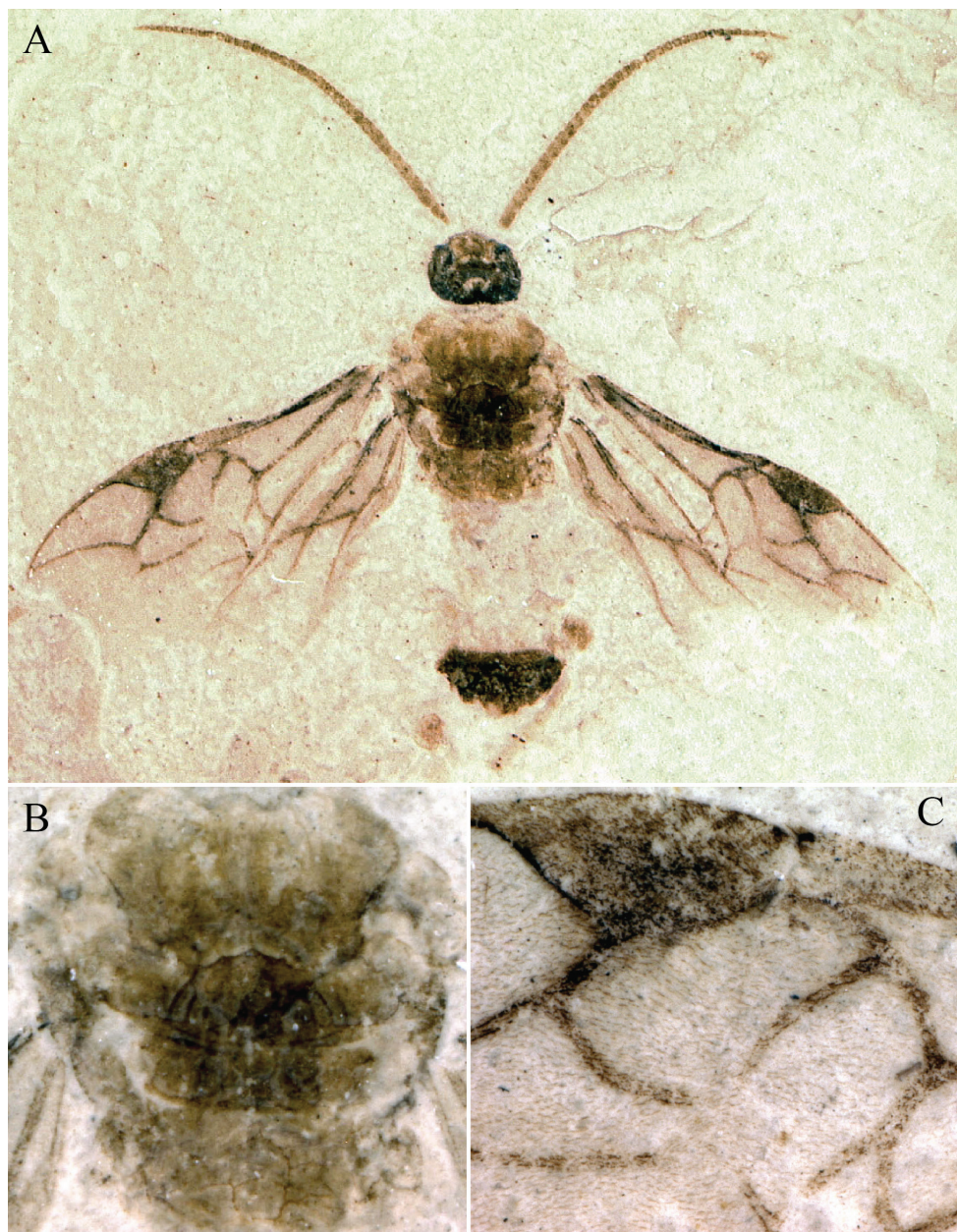
Taxonomy

Braconidae Stephens, 1829
Ichneutinae Förster, 1862

***Colemanus* Fisher, gen. n.**
http://zoobank.org/DBB8F27A-3FB4-4740-8719-FF760BC6E150
Figs 1–3

Type species. *Colemanus keeleyorum* Fisher, sp. n.

Figure 1. Fossil of *Colemanus keeleyorum* sp. n.: **A** whole fossil **B** close-up of mesosoma **C** close-up of left pterostigma, note preserved microtrichia.

Diagnosis. There are several similarities between *Colemanus* and other braconids, specifically Cardiochilinae and Cheloninae. Like *Colemanus*, some Cheloninae have a recurved 3RSb and an evenly curved 1M. However, chelonines possess a metasomal

carapace. *Colemanus contortus* comb. n. lacks a carapace (Brues 1933) and although the metasoma of *C. keeleyorum* sp. n. is not completely visible, it seems apparent that it also lacks a metasomal carapace (Fig. 1A). Thus, the lack of a metasomal carapace distinguishes *Colemanus* from Cheloninae. *Colemanus* also resembles many Cardiochilinae in having a recuved 3RSb and heavily sculptured mesosoma, but can be readily distinguished by 3RSb remaining tubular as it reaches the wing margin.

Colemanus can be distinguished from other Ichneutinae s. l. by the presence of a curved 3RSb; fore wing 1cu-a curved downward, not angled toward wing margin; hind wing M+Cu positioned in the posterior half of the wing; and a heavily sculptured mesosoma.

Etymology. Named for bodybuilder Ronnie Coleman, who was famous for his back; referring to the robust and sculptured nature of the mesosomal dorsum.

Colemanus keeleyorum Fisher, sp. n.
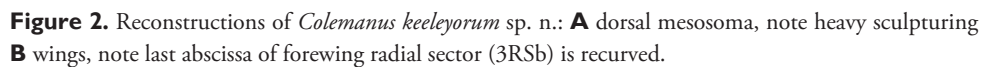http://zoobank.org/AC0F5EA3-4526-43FD-85F3-4544FFC0EF5E
Figs 1–2

Diagnosis. *Colemanus keeleyorum* can be distinguished from *C. contortus* (Brues, 1933) (new combination; see below) by having curved (RS+M)a and 2RS veins in the fore wing (straight in *C. contortus*). Also, *C. keeleyorum* is only known from the western United States (Eocene) and *C. contortus* is only known from the Baltic region (lower Oligocene).

Description. Holotype (n = 1): body length 9 mm (estimated due to incomplete metasoma); sex unknown. **Head** (Fig. 1A) 1.4 mm long and 1.7 mm wide. Antenna 7.2 mm long with 33–34 flagellomeres. **Mesosoma** (Figs 1B, 2A) 3.8 mm long and 3.3 mm wide; robust and heavily sculptured; notauli deeply crenulate; scutellum with crenulate depression medio-posteriorly; side of scutellum deeply hollowed with crenulate carinae and bordered by prominent carinae; metanotum with median, raised, rectangular tubercle having radiating carinae; scutellar sulcus with carinae; propodeum with areolate sculpturing. **Wings** (Figs 1A,C, 2B) with last abscissa of fore wing radial sector (3RSb) recurved and tubular as it reaches the wing margin; (RS+M)b short, nearly vertical; 1cu-a originating far distal to M and curving downward, thus not angling toward wing apex; fore wing M curved; tubular portion of 1a long; C+SC and R closely fused; second abscissa of RS strongly curved; parastigma well-developed; hind wing M+Cu longer than first abscissa of M; hind wing r-crossvein absent; hind wing M+Cu in posterior half of wing; 1A strongly developed.

Biology. Unknown. However, placement within Proteropini is suggestive of shared biology, koinobiont endoparasitoids of sawflies.

Remarks. Wings, antennae, and dorsal mesosoma are overall well-preserved; metasoma and legs either did not completely fossilize or are obscured by the rock matrix; head is crushed.

Figure 2. Reconstructions of *Colemanus keeleyorum* sp. n.: **A** dorsal mesosoma, note heavy sculpturing **B** wings, note last abscissa of forewing radial sector (3RSb) is recurved.

Etymology. Named for Dr. Jack and Flo Keeley, who, together with their daughter and her husband (first author's mother & father), were largely responsible for the first author's pursuit of the natural sciences.
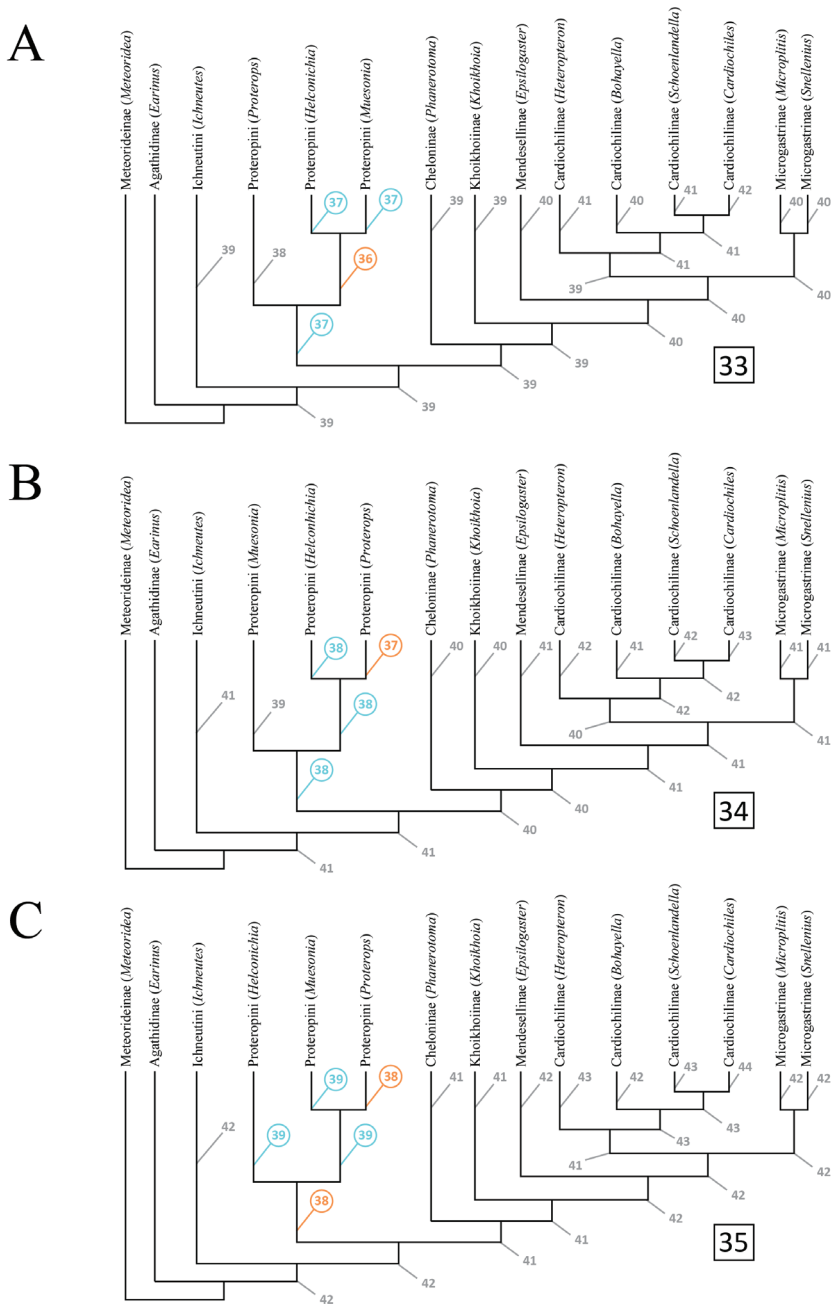
Figure 3. Placement of *Colemanus* gen. n. with known relationships of extant taxa: **A–C** represent the three possible relationships between included Proteropini. Numbers on branches represent total tree length when *Colemanus* is placed at that location. Circled numbers are most parsimonious placements (most parsimonious in orange; second-most in blue). Number boxes are total tree lengths of that topology when *Colemanus* is excluded. Note that lowest tree lengths are always achieved when *Colemanus* is placed within Proteropini.

Material examined. HOLOTYPE: USA, Colorado, Piceance Creek Basin, Parachute Member, 2005. Deposited with the David Kohls collection in the Smithsonian Institution, Museum of Natural History, Washington D.C.

Colemanus contortus (Brues, 1933), comb. n.

Remarks. Two other fossil ichneutines have been described, both from Baltic amber of the lower Oligocene (Brues 1933): *Ichneutes stigmaticus* and *I. contortus*. The illustration of *I. stigmaticus* (Brues 1933: pl. 10 fig. 58) is not similar to *Colemanus*. However, the description for *I. contortus* (Brues 1933: pg. 89–90; pl. 10 fig. 50) is consistent with *Colemanus* in having "coarsely crenulated" notauli (pg. 90) and a fore wing (pl. 10 fig. 50) with recurved 3RSb and nearly vertical (RS+M)b. Further, fore wing 3RSb appears to be tubular as it reaches the wing margin (unlike Cardiochilinae); a carapace is absent (unlike Cheloninae); and 1M is evenly curved (consistent with Proteropini). Therefore, we suggest the new combination *Colemanus contortus* (Brues, 1933).

The material Brues (1933) examined is part of the Königsberg collection. Most of this collection was rescued and is housed at the Geowissenschaftliches Museum (Göttingen, Germany), though some of Brues's collection, which included some of the Königsberg collection, remains at Harvard University, his old institution. However, neither the Museum of Comparative Anatomy (Harvard), nor the Geowissenschaftliches Museum could locate Brues's 1933 material, including *Ichneutes contortus*. The problem is exacerbated by the fact that Brues did not include catalog numbers in his description or any other information regarding deposition. Therefore, the holotype of *I. contortus* should be considered lost.

Key to *Colemanus* gen. n.

1   Fore wing (RS+M)a and 2RS straight; Palaearctic........... ***C. contortus* comb. n.**
–   Fore wing (RS+M)a and 2RS curved; Nearctic .... ***C. keeleyorum* sp. n.**

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RESEARCH ARTICLE

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A new species of *Labania* Hedqvist (Braconidae, Doryctinae) from Costa Rica, reared from aerial root galls of *Ficus obtusifolia* Kunth

Sergey A. Belokobylskij[1,2], Miguel Artavia Solís[3],
Paul E. Hanson[3], Alejandro Zaldívar-Riverón[4]

1 *Zoological Institute of the Russian Academy of Sciences, Universitetskaya naberezhnaya 1, St Petersburg 199034, Russia* **2** *Museum and Institute of Zoology of the Polish Academy of Sciences, Wilcza 64, 00–679 Warsaw, Poland* **3** *Escuela de Biología, Universidad de Costa Rica, San Pedro de Montes de Oca, Costa Rica* **4** *Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autónoma de México, 3er. circuito exterior s/n, Cd. Universitaria, Copilco, Coyoacán, A. P. 70–233, C. P. 04510, D. F., México*

Corresponding author: *Alejandro Zaldívar-Riverón* (azaldivar@ib.unam.mx)

Citation: Belokobylskij SA, Solís MA, Hanson PE, Zaldívar-Riverón A (2015) A new species of *Labania* Hedqvist (Braconidae, Doryctinae) from Costa Rica, reared from aerial root galls of *Ficus obtusifolia* Kunth. Journal of Hymenoptera Research 44: 69–78. doi: 10.3897/JHR.44.4722

Abstract

A new species of the Doryctinae genus *Labania* Hedqvist, *L. ficophaga* **sp. n.** from Costa Rica is described. This new species was reared from aerial root galls of *Ficus obtusifolia* Kunth. An updated key to the five described species of *Labania* and digital pictures of *L. ficophaga* **sp. n.** and *L. minuta* Marsh are provided.

Keywords

Ichneumonoidea, Neotropics, gall-association, Hymenoptera

Introduction

The genus *Labania* Hedqvist is a small doryctine group restricted to the Neotropical region and is currently composed of four species. This genus was erected by Hedqvist (1963) based on a single species from Honduras, *L. straminea* Hedqvist. In the description, *Labania* was placed within the morphologically heterogeneous subfamily Hormiinae, but it was subsequently transferred to the Doryctinae in a tribal reclassi-

fication of this subfamily (Belokobylskij 1992). To date, only three additional species of *Labania* have been described from Costa Rica (Marsh 2002), *L. hansoni* Marsh, *L. minuta* Marsh and *L. prolata* Marsh, with the first two being reared from aerial root galls on *Ficus citrifolia* Mill. and leaf galls on *F. colubrinae* Strandl., respectively.

In his tribal reclassification of the Doryctinae, Belokobylskij (1992) placed *Labania* as the single member of the tribe Labaniini based on several putative apomorphic features. More recently, however, three molecular phylogenetic studies consistently recovered a clade exclusively composed of genera whose species are associated with galls from different plant families, including *Labania* (Zaldivar-Riveron et al. 2007, 2008, 2014). In the most recent of these studies (Zaldívar-Riverón et al. 2014), the authors described three new gall-associated doryctine genera whose species with rearing records were all associated with *Ficus* species. One of them, *Ficobolus* Belokobylskij & Zaldívar-Riverón, was recovered as sister to *Labania*; the latter genus was represented in that study by an undescribed species from Costa Rica.

In this work, this new species of *Labania*, which was reared from aerial roots on *F. obtusifolia* Kunth is described, and observations that suggest that this new species is phytophagous are provided. An updated key (adapted from Marsh 2002) to the five described species of *Labania* is given.

Material and methods

All specimens of the new species of *Labania* described here were reared from a single tree of *F. obtusifolia* (see details below). Specimens belonging to two of the remaining species of the genus were also examined, as well as digital photographs of the holotype of *L. straminea*, deposited at National Museum of Natural History (Washington, D.C., USA). The type material of the new species is deposited in the following collections: Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autónoma de México (CNIN IB-UNAM); Museo de Zoología, University of Costa Rica, San José, Costa Rica (MZCR); Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZISP); and National Museum of Natural History, Washington, DC (NMNH).

The terminology employed in this work for the morphological features and measurements follows Belokobylskij and Maetô (2009). The wing venation nomenclature follows Belokobylskij and Maetô (2009) and Sharkey and Wharton (1997) in parentheses. Photographs were taken with a Leica IC 3D digital camera mounted on a Leica® MZ16 microscope and using the Leica Application Suite® imaging system.

Other examined material

Labania straminea. Holotype: female, Honduras, La Ceiba. *Labania minuta*: 5 females, 5 males. Costa Rica, Turriatlico, Turrialba, ex leaf-ball gall of *Ficus colubrinae*, IX-2013, K. Nishida col. *Labania hansoni*: 2 females, 1 male. "Costa Rica: DNA Hym- 46".

Results

Taxonomy

Labania ficophaga **Belokobylskij & Zaldívar-Riverón, sp. n.**
http://zoobank.org/7A4A0738-1F19-46C8-B8AA-1C9788785478
Figs 1; 2A–B

Diagnosis. This new species is morphologically similar to *L. hansoni* Marsh; however, *L. ficophaga* can be distinguished from the latter species by the following features: 1) greater diameter of eye 2.0–2.2 times wider than temple (1.4–1.7 times in *L. hansoni*); 2) eye covered by short and sparse setae (long and very dense setae in *L. hansoni*); 3) malar space 0.35–0.4 times height of eye (0.4–0.5 times in *L. hansoni*); 4) propodeum mainly rugose-striate, smooth only in basolateral areas (mainly smooth, rugose only medially in *L. hansoni*); 5) discoidal (first discal) cell distinctly sessile anteriorly (petiolate anteriorly in *L. hansoni*); 6) dorsal carinae of the first metasomal tergite almost complete (incomplete in *L. hansoni*); 7) vertex and frons light reddish brown or brownish yellow (reddish brown to black in *L. hansoni*); 8) basal antennal segments black or almost black (yellow or brownish yellow in *L. hansoni*); 9) hind femur and tibia of female dark reddish brown to reddish brown (yellow or brownish yellow in *L. hansoni*).

Labania ficophaga is also morphologically similar to *L. minuta*, but differs from this species by having: 1) a larger body length, from 3.6 to 4.1 mm (1.0 to 1.8 mm in *L. minuta*; Fig. 3A); 2) antenna 23–26-segmented (less than 20 antennomeres in *L. minuta*; Fig. 3A); 3) notauli joining at the end of mesoscutum in a wide longitudinally striate-rugose area (joining at the end of mesoscutum in narrow rugose area in *L. minuta*; Fig. 3B); 4) head light reddish brown or yellowish brownish (face and temple honey yellow to brown, frons and vertex black in *L. minuta*; Figs 3A–C); and 5) entirely smooth second metasomal tergite (with mediobasal longitudinal striae in *L. minuta*; Fig. 3E).

Description. Female. Body length 3.6–4.1 mm; fore wing length 3.1–3.2 mm.

Head: width 1.8–1.9 times its median length, 1.15–1.20 times width of mesoscutum. Head behind eyes (dorsal view) distinctly roundly narrowed. Transverse diameter of eye 2.0–2.2 times wider than temple. Ocelli medium-sized, arranged in triangle with base 1.2–1.3 times its sides. POL 0.8–1.0 times Od, 0.30–0.35 times OOL. Frons excavation deep, not wide, not extending beyond antennal sockets, with shallow or very shallow median furrow. Eye without emargination opposite antennal socket, 1.3 times as high as broad. Malar space 0.35–0.40 times height of eye, 0.8–1.0 times basal width of mandible. Face slightly convex, its width 0.9 times height of eye and 0.9–1.0 times height of face and clypeus combined. Clypeus convex, about twice as wide as high. Width of hypoclypeal depression almost equal to distance from edge of depression to eye, 0.5–0.6 times width of face. Hypostomal flange narrow. Occipital carina not fused with hypostomal carina and obliterated ventrally. Palpi short, maxillary palpus 5-segmented, labial palpus 2-segmented.
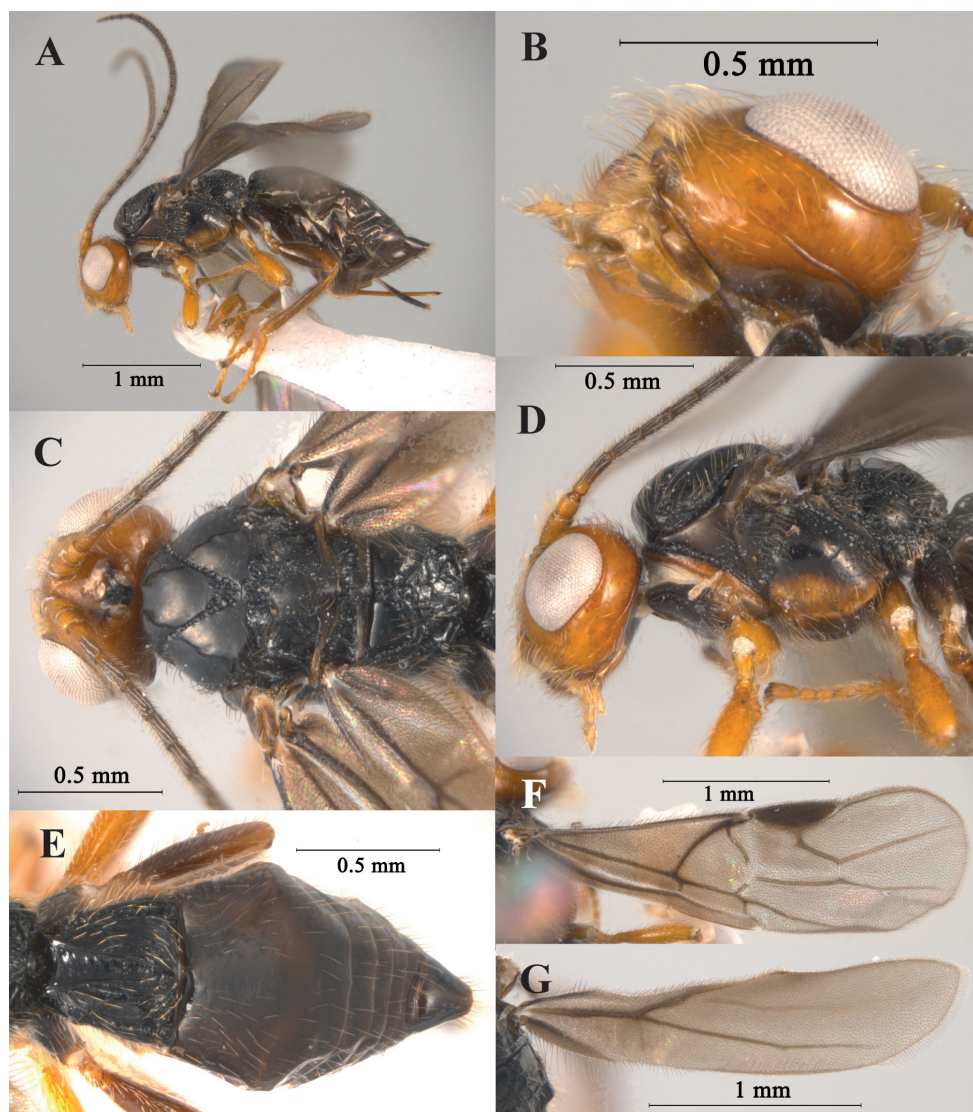
Figure 1. *Labania ficophaga* sp. n. (female, paratype): **A** habitus, lateral view **B** head and palpi, ventro-latero-posterior view **C** head and mesosoma, dorsal view **D** head and mesosoma, lateral view **E** metasoma, dorsal view **F** fore wing **G** hind wing.

Antenna: thickened, weakly setiform, covered by dense and dark setae, 23–26-segmented. Scape 1.5–1.6 times longer than its maximum width, almost twice as long as pedicel. First flagellar segment 4.0–4.5 times longer than its apical width, 1.2–1.3 times longer than second segment. Penultimate segment 2.2–2.3 times longer than its width, 0.7–0.8 times as long as apical segment; the latter pointed apically.

Mesosoma: length 1.6–1.7 times its height. Median lobe of mesoscutum distinctly and highly convex (lateral view), slightly protruding forward and rounded

anteriorly (dorsal view). Oblique submedian furrow on side of pronotum narrow and densely crenulated. Notauli complete, deep, narrow and densely crenulated, joining at the end of mesoscutum in a longitudinally striate-rugose area. Prescutellar depression long, deep, with several more or less high carinae, densely and distinctly reticulate-striate between carinae, 0.25–0.35 times as long as scutellum. Scutellum 1.2 times longer than maximum anterior width. Scuto-scutterlar suture absent. Precoxal sulcus almost absent or very weak, short. Metanotal tooth low (lateral view). Metapleural flange quite short and wide, almost indistinct. Propodeal lateral tubercles large and wide.

Wings: fore wing 2.7–3.0 times longer than its maximum width. Pterostigma 2.9–3.5 times longer than width. Metacarp (R1) 1.2–1.3 times longer than pterostigma. Radial (marginal) cell long, open apically after strong desclerotisation of apical part of third radial abscissa (3RSb). First (r) and second (3RSa) radial abscissae forming an obtuse angle. Second radial abscissa (3RSa) 4.0–4.3 times longer than first abscissa (r), 0.35–0.40 times as long as the straight third abscissa (3RSb). First radiomedial vein (2RS) mainly or completely absent, rarely present and short, or (exceptionally) with elongate anterior part of abscissa. Second radiomedial (second submarginal) cell fused with first radiomedial (first submarginal) cell, slightly narrowed apically. First medial abscissa ((RS+M)a) distinctly sinuate. Discoidal (first discal) cell sessile. Recurrent vein (1m-cu) 0.3–0.4 times as long as basal vein (1M); these veins parallel. Distance from nervulus (1cu-a) to basal (1M) vein 0.7–0.8 times nervulus (1cu-a) length. Brachial (first subdiscal) cell long, wide, opened apico-posteriorly after strong desclerotisation of second abscissa of longitudinal anal vein (2-1A). Brachial vein (2cu-a) long and mainly pigmented. Hind wing 4.0–4.1 times longer than its maximum width. Hamuli 3–4. Medial (basal) cell apically widely open after strong desclerotisation of second abscissa of costal vein (SC+R). Nervellus (cu-a) absent; submedial (subbasal) cell widely open apically. Recurrent vein (m-cu) distinct or fine, straight or slightly curved, more or less inclivous, interstitial, distinctly or sometimes faintly pigmented.

Legs: hind coxa without basoventral corner and tubercle, 1.4–1.5 times longer than maximum width, about 0.8 times as long as propodeum. Hind femur 2.8–3.1 times longer than width. Hind tarsus 0.8–0.9 times as long as hind tibia. Basitarsus of hind tarsus 0.55–0.60 times as long as second to fifth segments combined. Second segment of hind tarsus 0.5 times as long as basitarsus, 0.9 times as long as fifth segment (without pretarsus). Claws large.

Metasoma: 1.0–1.1 times longer than head and mesosoma combined. First tergite distinctly and almost linearly widened from base to apex, with slightly impressed spiracular tubercles in basal third, with distinct, almost complete and slightly convergent posterior dorsal carinae. Maximum width of first tergite about 2.0 times its minimum width; length 0.9–1.0 times its apical width, 1.4–1.5 times length of propodeum. Suture between second and third tergites quite shallow and almost complete. Median length of second and third tergites 1.1–1.2 times basal width of second tergite, 0.8–0.9 times maximum width of these tergites. Ovipositor short, its sheath about as
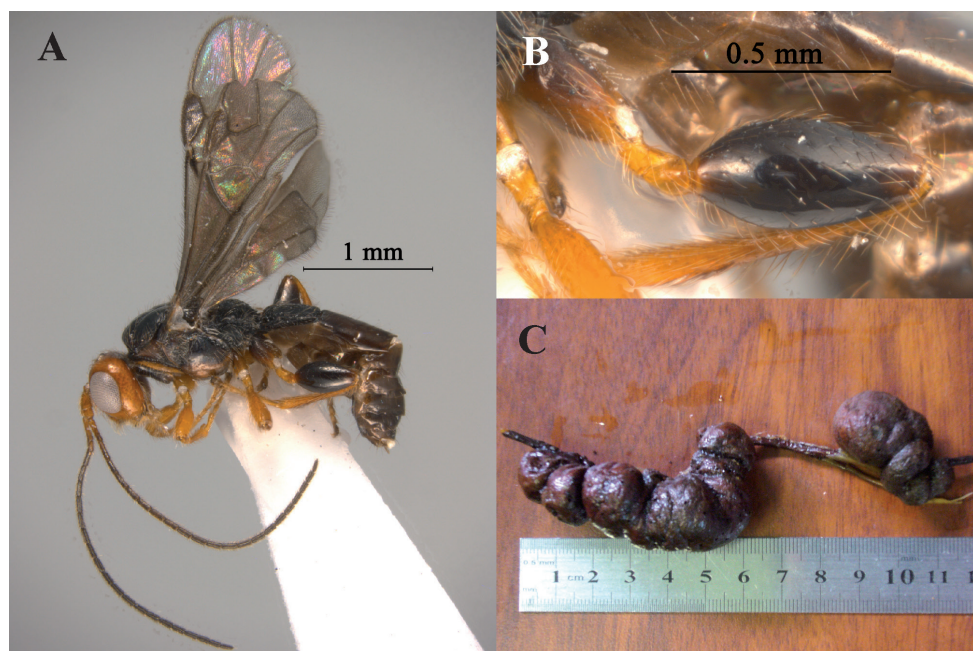
Figure 2. *Labania ficophaga* sp. n. (male, paratype): **A** habitus, lateral view **B** hind femur **C** Aerial root galls on *F. obtusifolia* Kunth where specimens of *L. ficophaga* were reared.

long as first tergite of metasoma, 0.40–0.45 times as long as mesosoma, 0.18–0.22 times as long as fore wing.

Sculpture and pubescence: head entirely smooth, sometimes frons near antennal sockets with several curved striae. Mesoscutum smooth, with rugulosity in short and small medioposterior area. Scutellum mainly smooth, finely striate laterally. Mesopleuron mostly smooth. Propodeum widely rugose-striate, with all areas distinctly delineated by carinae; basolateral areas short, semi-rounded, mainly smooth; areola wide, about as long as maximum width; basal carina 0.2–0.3 times as long as basal fork of areola. Hind coxa and femur smooth. First tergite mainly striate with rugosities, finely reticulate to almost smooth between dorsal carinae. Remaining tergites entirely smooth. Vertex with numerous, dense and semi-erect pale setae. Mesoscutum mainly glabrous, with dense and erect pale setae arranged in almost single lines along notauli and laterally. Mesopleuron medially rather widely glabrous. Hind tibia dorsally with dense, relatively long and semi-erect pale setae, its length 0.5–0.8 times maximum width of hind tibia.

Colour: head entirely light reddish brown or sometimes yellowish brownish, ocellar triangle often black. Antenna black, dark reddish brown basally, two basal segments yellowish brown. Palpi pale brown. Mesosoma almost reddish black, with light brown on narrow stripe along lower margin of pronotal sides and along area of precoxal sulcus. Metasoma mainly dark reddish brown, dorsal basal and apical parts black. Fore and mid-

dle legs light reddish brown to yellowish brown. Hind leg mainly dark reddish brown, tibia faintly paler and light reddish brown basally and apically, hind tarsus entirely light reddish brown. Ovipositor sheath almost black. Fore and hind wings distinctly and evenly darkened, veins dark brown. Pterostigma black, slightly paler apically.

Male. Body length 2.9–3.9 mm; fore wing length 2.5–2.7 mm. Antenna slender, filiform or narrow basally and weakly thickened apically, 20–22-segmented. First flagellar segment 4.5–4.8 times longer than its apical width. Hind femur strongly widened, 1.9–2.1 times longer than width, dark brown or dark reddish brown. Hind tibia almost entirely light reddish brown. Metasoma 0.9–1.0 times as long as head and mesosoma combined. Length of first tergite 1.1 times its apical width, 1.2–1.5 times length of propodeum. Otherwise similar to female.

Distribution. Known only from Costa Rica.

Type material. *Holotype*: female, "Costa Rica: San Jose, Reserva el Rodeo, root galls on *Ficus obtusifolia*, IV.2011, Col. Miguel Artavia (IB-UNAM). *Paratypes*: 30 females (9 in alcohol), 16 males (4 in alcohol), the same label as holotype (IB-UNAM, MZCR, ZISP, NMNH); 1 female, same data as holotype, DNA voucher number CNIN1078 (IB-UNAM), GenBank accession numbers KJ586713 (COI), KJ586690 (*wingless*) and KJ586780 (28S) (Zaldívar-Riverón et al. 2014) (IB-UNAM).

Biology. All examined specimens of *L. ficophaga* were reared from aerial root galls on a single *F. obtusifolia* tree. Each gall (Fig. 2C) was approximately 1.5 cm in diameter and contained multiple larval chambers. Galls were frequently grouped together forming a mass that measured up to 6 cm in diameter and 12 cm in length. A photograph of these galls is shown in Zaldívar-Riverón et al. (2014; Fig. 1B). They are similar to the galls induced by *L. hansoni* Marsh on *F. citrifolia*, as reported by Marsh (2002). It should be noted that the identification of the *F. citrifolia* requires verification; it is possible that the correct identity is *F. eximia* Schott.

Galls of *L. ficophaga* were tracked on the host tree during a two years period (2011–2012), during which time the tree was visited every month. All wasps, including four additional species that are probably parasitoids, emerged during April and May. No wasps emerged during any other month. New galls began appearing in May and June and became full-sized in August.

Two lines of evidence suggest that *L. ficophaga* is the gall inducer. First, it is larger than the other four species emerging from these galls (parasitoids are expected to be slightly smaller, unless they feed on gall tissue). Second, of the five species of hymenopterans reared from these galls (no other insects were reared), *L. ficophaga* was the only species that was present in all the samples and in most samples it was also the most numerous species. For example, eight galls collected in April 2011 yielded 389 *Labania*, 89 Eurytomidae (probably *Phylloxeroxenus* Ashmead) species #1, and 28 Eurytomidae (probably *Phylloxeroxenus* Ashmead) species #2. Two galls collected in April 2012 yielded 45 *Labania* and 4 Eurytomidae species #2. One gall collected in May 2012 yielded 10 *Labania*, 17 *Torymus* Dalman (Torymidae), 1 Eurytomidae species #1, and 2 Platygastridae.
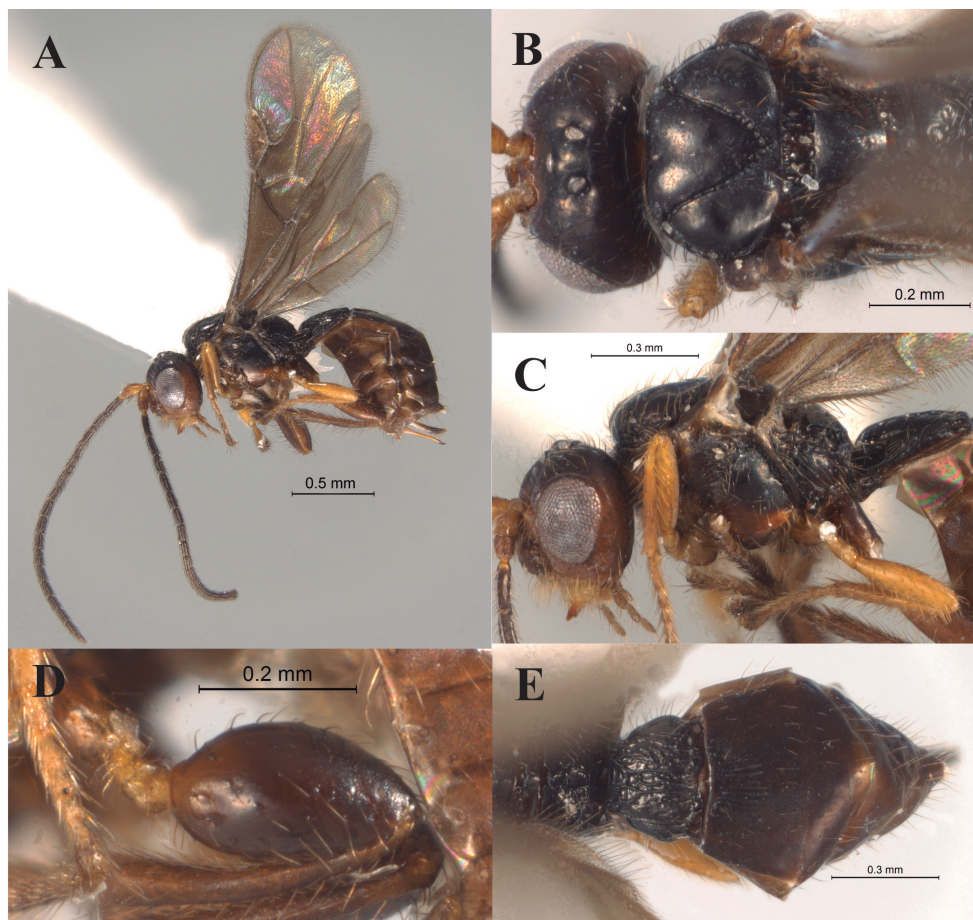
Figure 3. *Labania minuta* Marsh (female **A–C, E**; male **D**): **A** habitus, lateral view **B** head and mesosoma, dorsal view **C** head and mesosoma, lateral view **D** hind femur **E** metasoma, dorsal view.

Updated key to species of *Labania* (after Marsh 2002)

1   Body length 1.0–1.8 mm (Fig. 3A). Antenna with less than 20 segments ....*L. minuta* **Marsh** (Fig. 3A–E).
–   Body length 2.5–4.1 mm (Fig. 1A). Antenna with more than 20 segments..... **2**
2   Second metasomal tergite completely smooth (Fig. 1E). Mesosoma and metasoma mainly or entirely black or dark reddish brown (Figs 1A, C, D, E). Wings distinctly darkened (Figs 1A, F, G, 2A) **3**
–   Second metasomal tergite longitudinally striate basally. Mesosoma and meta- soma at least partly brown. Wings mainly subhyaline **4**
3   Transverse diameter of eye 1.4–1.7 times wider than temple. Eye covered with long and very dense setae. Malar space 0.4–0.5 times height of eye. Propodeum mainly smooth, rugose only medially. Discoidal (first discal) cell

petiolate. Dorsal carinae of first metasomal tergite incomplete. Vertex and frons dark reddish brown to black.................................... **L. hansoni Marsh**

– Transverse diameter of eye 2.0–2.2 times wider than temple (Fig. 1C). Eye covered with short and sparse setae. Malar space 0.35–0.40 times height of eye (Fig. 1D). Propodeum mainly rugose-striate, smooth only in basolateral areas (Fig. 1C). Discoidal (first discal) cell sessile (Fig. 1F). Dorsal carinae of first metasomal tergite almost complete (Fig. 1E). Vertex and frons light reddish brown or brownish yellow.. **L. ficophaga sp. n.**

4 Ovipositor extending beyond apex of mesosoma by length of hind basitarsus. First metasomal tergite parallel-sided, its length greater than apical width. Body length 3.0–3.5 mm.. **L. prolata Marsh**

– Ovipositor usually not extending beyond apex of mesosoma, rarely only very weakly and much less than length of hind basitarsus. First metasomal tergite distinctly widened apically, its length about equal to posterior width. Body length 2.5–4.0 mm .... **L. straminea Hedqvist**

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