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A new Nearctic *Scolioneura* (Hymenoptera, Tenthredinidae) mining leaves of *Vaccinium* (Ericaceae)

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Abstract

Scolioneura vaccinii Smith & Eiseman, **sp. n.**, is described. It was reared from blotch mines in *Vaccinium parvifolium* Sm. (Ericaceae) collected in Washington State, USA. This is the first known native species of *Scolioneura* in the Nearctic Region and the first known sawfly leaf miner of *Vaccinium* as well as the order Ericales. Characters are given to separate it from other species of *Scolioneura*, and the life history is presented. One parasitoid, *Shawiana* sp. (Braconidae) was reared from the leaf mines.

Keywords

Sawfly, Symphyta, leaf miner, red huckleberry, parasitoid, Braconidae

Introduction

The four known species of *Scolioneura* Konow (Heterarthrinae: Fenusini) are exclusively Palearctic, one of them being adventive in North America (Taeger et al. 2010). All are leaf miners. Both *S. betuleti* Konow, 1894, and *S. vicina* (Klug, 1816) are on *Betula*, the former also recorded from *Alnus*, and *S. tirolensis* Enslin, 1914, is on *Salix* (Liston, 2007). The host of *S. hyrcana* Benson, 1968, known only from northern Iran,

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is unknown. Here, we describe a new species of *Scolioneura* from Washington State, which represents the apparent first native species of the genus in the Nearctic Region. It also is the only known sawfly leaf miner of *Vaccinium* as well as Ericales.

The two species on *Betula*, *S. betuleti* and *S. vicina*, cannot be distinguished morphologically. Information on phenology is necessary for their identification. Altenhofer and Taeger (1998) chose to keep these species distinct based on phenology, the former a late summer form and the latter a spring form. Although MacQuarrie et al. (2007) found no genetic differences between the two and hypothesized that they constitute a single bivoltine species, they continue to be listed as separated species (Taeger et al. 2010). The early season *S. vicina* is the name applied to the species adventive in North America, and it occurs from eastern Canada to Alberta (Digweed et al. 2009).

Liston (2007) gave notes on the life history and larva of *S. tirolensis*, pointing out some morphological characters to distinguish it from *S. vicina* and *S. betuleti*. Nothing is known about *S. hyrcana* besides the original description (Benson 1968).

Materials and methods

Initial observations and collections were made by CSE and J. A. Blyth during a survey of leaf mining insects throughout western USA, September to November 2012. NDC and SR conducted a targeted search for mines on *Vaccinium* during a visit to the Seattle, WA, area in August 2013.

Leaves containing larvae or parasitoid cocoons were collected in plastic vials, which were checked daily (when possible) until all insects had emerged. Upon emerging, sawfly larvae were placed in small containers partially filled with moistened soil. In 2012, locally available soil from Washington was used; in 2013, a roughly 1:1 mixture of sand and peat was used. These containers were stored in a refrigerator at 1–3 °C from mid-December 2012 to 15 April 2013, and from 6 November 2013 to 25 February 2014. After removal from refrigeration, lids were removed from the containers, which were placed in sealed plastic bags and were checked daily.

Photographs of leaf mines and live specimens (Figs 1, 2, 8–11) were produced using a Canon EOS Rebel XSi SLR digital camera, MP-1 65 mm macro lens, and Macro Twin Lite MT-24EX flash unit. Images of the preserved adult (Figs 3–7) 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.

Results

One adult sawfly and five braconid parasitoids were reared from leaf mines in *Vaccinium* collected containing either larvae or cocoons. The sawfly emerged in April 2014 from a leaf mine collected in August 2013 in Pierce County, Washington. This specimen

represents a distinct new species, and the following characters place this species in *Scolioneura*: Tarsal claw with acute basal lobe and single outer tooth; epicnemium absent; genal carina present; forewing with 2A+3A curved up at its apex; radial cell of both forewing and hind wing closed at apex; hind wing with anal cell. *Scolioneura* was not included in the key to Nearctic Heterarthrinae by Smith (1971). It would go to couplet 11 containing *Metallus* Forbes and *Messa* Leach (now *Fenusella* Enslin). *Scolioneura* is distinguished from both *Metallus* and *Fenusella* by the presence of a genal carina.

***Scolioneura vaccinii* Smith & Eiseman, sp. n.**
http://zoobank.org/CFC012B1-EFFC-4A90-B668-DE0430FC7D29
Figs 1–9

Description. Female: Length, 3.0 mm. Antenna black; ventral surface, especially antennomeres 3–5 paler, dark orange. Head black; mandible reddish brown with apex black; palpi whitish. Thorax black. Legs yellowish with coxae and fore- and midtrochanters black; hind trochanter yellowish apically. Abdomen reddish brown with segments 1–3 and 9 black, tergite 4 slightly darker than 5–8; sheath black. Wings uniformly hyaline, veins and stigma black. Head and body smooth, shiny, without sculpture except for a few punctures at apex of mesoscutellum and very fine meshlike microsculpture on mesonotal lateral lobes. Head and thorax with short, fine white pubescence.

Antennal length 1.3× head width; 3rd antennomere 1.5× length of 4th antennomere and 3.5× longer than apical width; 4th antennomere 2× longer than apical width (Fig.3). Eyes slightly converging below; lower interocular distance about 1.2× eye height (Fig. 4). Distances between eye and hind ocellus, between hind ocelli, and between hind ocellus and posterior margin of head as 1.0: 0.9: 0.7. Postocellar area about 2× broader than long. Genal carina present. Forewing with first cubital cross-vein absent, vein 2A+3A turned up at apex, almost meeting 1A; hind wing with cell R closed, anal cell present, cells Rs and M absent. Cenchri about as far apart as breadth of one. Hind basitarsomere subequal to length of remaining tarsomeres combined. Tarsal claw without inner tooth, with large, acute basal lobe. Tarsal pulvilli absent on hind tarsomeres 1 and 2, present only on hind tarsomeres 3 and 4 (Fig. 6). Sheath in lateral view straight above, rounded below, with long curved hairs (Fig. 7); from above broad, parallel sided and rounded at apex. Entire lancet not examined; apex protruding from sheath (Fig. 7) with rather deep, rounded serrulae.

Male: Unknown.

Prepupa: White to yellowish with slightly darker head and lateral and dorsal lines; eyespot and apex of mandible black (Fig. 8). Abdominal segments apparently with 3 dorsal annulets; apical tergum rounded at apex.

Holotype. Female, labeled "Washington, Pierce Co., Tacoma, Point Defiance, 13.VIII.2013, em. 22.IV.2014, C. S. Eiseman, ex *Vaccinium parvifolium*, #CSE 1092." Altitude ~60 m. Deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC.

Figures 1–7. *Scolioneura vaccinii*. **1** Dorsal **2** Lateral **3** Antenna **4** Head front **5** Head dorsal **6** Hind tarsus **7** Sheath, lateral.

Other specimens. Three specimens were examined that appear identical to *S. vaccinii*, but all have a black abdomen. The color could vary, especially in the western mountains where melanic forms of some species occur, e.g., *Paracharactus montivagus* (Cresson, 1880) and *Lagonis nevadensis* (Cresson, 1880) (Smith 1969). However, we prefer to base the species on the reared specimen and, because of some doubts, not include the darker specimens in the type series. The data are as follows: WASHINGTON: Whatcom Co., Mt. Baker Ski area, VIII.2.1972, W. J. Turner,W. B. Garnett, collectors (altitude ~1,100–1,550 m) (1 ♂), same but additional label "dry ice Malaise

Trap" (1 ♂); Skam. Co., 42 mi S.E. Randle, USFS Rt. N84, VII.29.1972, dry ice Malaise trap, W. J. Turner, W. B. Garnett collectors (altitude ~1,400 m) (1♀). All from the Washington State University collection, Pullman, Washington. The males are similar in color and structure to the female.

Host. Adult reared from leaf mine in red huckleberry, *Vaccinium parvifolium* Sm. (Ericaceae). Sawfly larvae, probably also this species, found in leaf mines of *V. membranaceum* Douglas ex Torr.

Etymology. Based on the genus name of the host plant, *Vaccinium*.

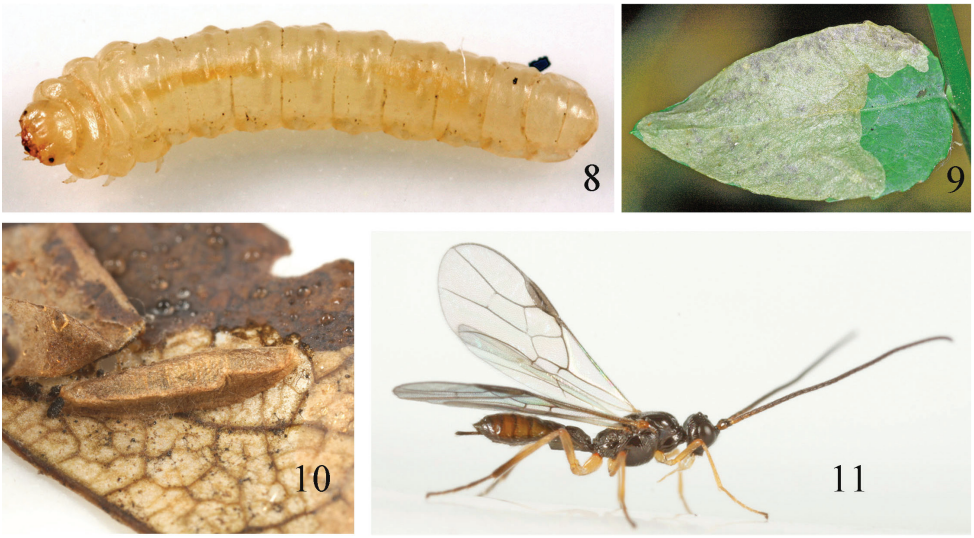
Discussion. This species is characterized by the short antennae, about 1.3× the head width; lower interocular distance slightly longer than eye height; mostly reddish-brown abdomen; absence of the first cubital crossvein in the forewing; presence of pulvilli on only hind tarsomeres 3 and 4; and smooth, shiny mesoscutellum with only a few punctures on the posterior margin.

Liston (2007) separated *S. tirolensis* from *S. betuleti* and *S. vicina* as follows: In *S. tirolensis* the leg color tends to be darker (but highly variable); first cubital crossvein present, though faint; shorter antenna, about 1.5× head width; third antennomere 3.5× as long as apical width; third antennomere about 1.5× as long as fourth. In *S. betuleti* and *S. vicina*, the leg color is lighter; first cubital crossvein absent; antennae longer, 2× the head width; and the third antennomere is 5–6× as long as its apical width and only slightly longer than the fourth. *Scolioneura vaccinii* is closer to *S. tirolensis*, sharing the short antennae, but *S. vaccinii* differs by the absence of the first cubital crossvein, even shorter antennae, presence of pulvilli only on hind basitarsomeres 3 and 4, the smooth, shiny mesoscutellum, and the mostly reddish-brown abdomen. In *S. tirolensis*, the first cubital crossvein is present, pulvilli are present on hind basitarsomeres 1–4, the mesoscutellum is densely punctate with punctures more numerous on the posterior half, and the abdomen is usually black.

Scolioneura hyrcana was not examined, but Benson (1968) separated it from the European species by the enlarged eyes, which are strongly converging below with the lower interocular distance much less than the eye height, and by the presence of tarsal pulvilli only on the two apical tarsomeres. *Scolioneura vaccinii* shares the presence of pulvilli only on hind basitarsomeres 3 and 4, but differs by the smaller eyes which are farther apart than the eye height.

Life history notes. Larvae are solitary and form simple, more or less full-depth blotch mines (Fig. 9), each completing development within a single leaf as is typical of Fenusini. Completed mines occupy 3.5 to 8.5 cm^2, with smaller leaves being entirely mined out. Frass is in the form of discrete, elongate fecal pellets, up to about 0.4 mm by 0.2 mm, which are scattered through the mine at random. When mature, the ~7.0 mm larvae exit their mines and burrow into the ground to overwinter.

Leaf mines on *Vaccinium parvifolium* and *V. membranaceum* containing sawfly larvae were first noted from 4 to 10 October 2012, to the south of Mount Rainier (Pierce Co.) and at several locations on the Olympic Peninsula (Clallam, Jefferson, and Grays Harbor counties). The type specimen was reared from a larva found mining



Figures 8–11. 8 *Scolioneura vaccinii*, prepupa **9** Leaf mine of *S. vaccinii* **10** Cocoon of *Shawiana* sp. in leaf mine of *S. vaccinii* **11** *Shawiana* sp., lateral.

a *V. parvifolium* leaf on 13 August 2013. Since all collected larvae overwintered in soil, there is currently no indication of more than one generation per year. The April emergence date for the type specimen is undoubtedly abnormally early, due to the prepupa having been exposed to artificially warm temperatures. The other known specimens were trapped as adults between 29 July and 2 August, consistent with a single generation emerging in early summer and giving rise to larvae that mine from August to October.

Vaccinium plants were searched in northern Idaho in late September 2012 and in northern California in October 2012, but no leaf mines were found. Similar mines found on *Rhododendron menziesii* Craven (Ericaceae) along Boulder Creek in Bonners Ferry, Idaho on 28 September 2012 possibly were made by the same or a related species. Only a few examples were found, and all were empty.

The 2012 collections yielded four braconid wasps, which emerged 18–27 November 2012 and 4–8 May 2013. The 2013 collection yielded one more, which emerged on 7 September. All had spun elongate, pale brown cocoons, 5 mm long by 1 mm wide, inside the leaf mines (Fig. 10). All five braconids belonged in the genus *Shawiana* van Achterberg (Fig. 11). Two described species in this genus are known from the Nearctic, both in the eastern United States. *Shawiana metalli* (Muesebeck) is a parasitoid of *Metallus rohweri* MacGillivray; *S. phyllotomae* (Muesebeck) was introduced from Europe to control *Heterarthrus nemoratus* (Fallén), and is also recorded from *Fenusa pumila* Leach (Muesebeck 1932, Marsh 1979). All of these hosts, like those of most Palearctic species, are leaf-mining sawflies (Achterberg 1983). Three of our *Shawiana* specimens are deposited in the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario.

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Two new species of the newly recorded subgenus *Tropidodynerus* Blüthgen (Hymenoptera, Vespidae, Eumeninae) from China, with a key to the known species

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Abstract

The genus *Tropidodynerus* Blüthgen is newly recorded from China and two new species of the genus are described and illustrated, namely *Tropidodynerus* (*Tropidodynerus*) *liupanshanensis* **sp. n.** from Ningxia, China and *T.* (*T.*) *concavus* **sp. n.** from Hebei, China. In addition, a key to all known species of the subgenus *Tropidodynerus* is updated. Type specimens of these two new species are deposited in Hebei University and Chongqing Normal University.

Keywords

Hymenoptera, Eumeninae, *Tropidodynerus*, new record, new species, China

Introduction

The genus *Tropidodynerus* includes five species with three subspecies worldwide, belonging to two subgenera, namely *Tropidodynerus* and *Tropidepipona* (van der Vecht and Carpenter 1990; Girish Kumar et al. 2013). So far, the subgenus *Tropidepipona* only occurs in the Oriental Region, and the subgenus *Tropidodynerus* is distributed in the Palearctic Region (Bluthgen 1939; Kurzenko 1977; Giordani Soika 1994; Guse-

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nleitner 1998, 2007a, 2007b; Borsato 2006). No species of the genus was recorded from China. In our study of the eumenine wasps from China, two species of the subgenus *Tropidodynerus* were collected and recognized, which are new to science. In the present paper, these two new species are described and illustrated in detail, and a key to the worldwide species of the subgenus *Tropidodynerus* is updated. The key was produced based on both the examination of specimens and the information extracted from literature.

Materials and methods

The specimens examined are deposited in the Institute of Entomology and Molecular Biology, Chongqing Normal University, Chongqing, China (CQNU) and College of Life Sciences, Hebei University, Baoding (HBU), respectively. Descriptions and measurements were made under a stereomicroscope (Nikon SMZ1500), and all figures were taken with a stereomicroscope (LEICA EZ4HD) attached to a computer using Leica Application Suite version 2.1.0 software. The ratios used throughout the descriptions were measured in the same amplifying multiple of stereomicroscope. All measurements were taken as the maximal length of body parts measured. Body length was measured from the anterior margin of head to the posterior margin of metasomal tergum 2. For the density description of punctures, "sparsely" means that the intervals between are larger than diameter, "moderately" means equal to diameter, and whereas "densely" means less than diameter. The abbreviations used in the text are shown as follows: A1 for antennal segment 1, A2 for antennal segment 2, POD for postocellar distance, OOD for the minimum distance between the compound eye and posterior ocellus; T1 for metasomal tergum 1, T2 for metasomal tergum 2, S1 for metasomal sternum 1, S2 for metasomal sternum 2, and so on. Terminology principally follows Terminology principally follows Carpenter (1982) and Carpenter and Cumming (1985).

Taxonomy

Tropidodynerus Blüthgen, 1939

Tropidodynerus Blüthgen, 1939: 259, 260; Carpenter 1986: 87; van der Vecht and Carpenter 1990: 59; Girish Kumar et al. 2013: 163.

Type species. *Hoplomerus interruptus* (Brullé, 1832) = *H. mandibularis* Morawitz, 1885 (= *Polistes interrupta* Brullé, 1832), by original designation (confirmed by Blüthgen 1941: 306).

Diagnosis. Without cephalic fovea in female; vertex weakly longitudinally rugose; mesosoma and tempora with very fine pubescence, anterior face of pronotum without

foveae; tegula very short and its posterior lobe rounded; parategula elongated and its apex distinctly surpassing the apex of tegula; apical segments of antennae coiled in male; submarginal carina and valvula of propodeum not produced; mid tibia with one spur; forewing with second submarginal cell and not petiolate; metasoma sessile, S3–S7 with conspicuous fringe of setae in male.

Distribution. Oriental and Palearctic Regions.

Key to the subgenera of *Tropidodynerus*

1 Labial palpi 3-segmented; propodeum completely rounded at side, dorsal surface strongly convex; the Oriental Region (Giordani Soika 1994; Girish Kumar 2013) ..... **subgenus *Tropidepipona***

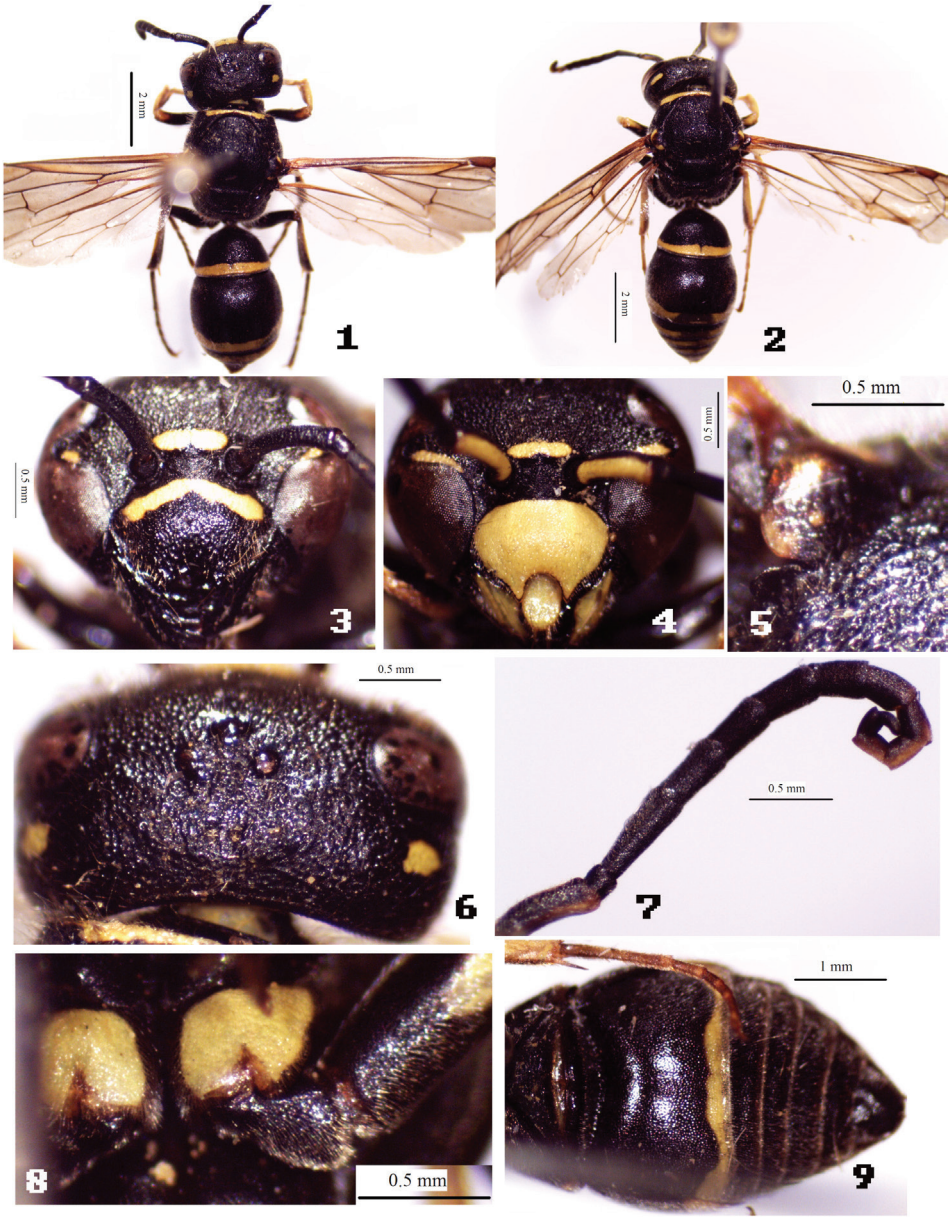
– Labial palpi 4-segmented; propodeum somewhat rounded at side, dorsal surface not convex; the Palearctic Region (Giordani Soika 1994; Girish Kumar 2013) ..... **subgenus *Tropidodynerus***

***Tropidodynerus* (*Tropidodynerus*) *liupanshanensis* Li & Chen, sp. n.**
http://zoobank.org/22BF1014-5536-4EA2-A869-27B6E720BF1D
Figs 1–9

Material examined. Holotype ♀, China, Ningxia Hui Autonomous Region, Guyuan City, Jingyuan County, Liupanshan, Xixia Forest, 35°29'40.22"N, 106°17'42.40"E, 2107m, 27.VI.2008, Feng Yuan, No. 1004046 (HBU). Paratype: 1♂, China, Ningxia Hui Autonomous Region, Guyuan City, Jingyuan County, Liupanshan, Erlong River, 35°21'11.95"N, 106°20'29.28"E, 2300m, 5–6.VII.2009, Hongfan Ran & Shanshan Zhang, No. 1004047 (CQNU).

Description. Female (Figs 1, 3, 5–6): body length 8.0 mm, forewing length 8.5 mm. Black, with the following parts yellow: a basal band of clypeus (Fig. 3), a large transverse interantennal spot, a small mark approaching the middle of inner orbits on the lower side of eye, postocular spot (Fig. 6), a thin band on dorsal surface of pronotum (Fig. 1), small spots on tegula anteriorly and posteriorly, elongated spots on dorsal faces of all tibiae, a broad apical band on each of T1–T4, and a thinner apical band on S2; tibiae except yellow spots and all tarsi dark brown. Wings slightly brownish.

Head. In front view, head much wider than long, its width 1.40× length; clypeus (Fig. 3) somewhat convex, with dense punctures, those on apex mostly so elongated as to forming thin and irregular longitudinal striations, clypeal width 1.60× its length, total width: apical width = 4.0: 1.5, apex deeply emarginated, apical width: depth of emargination = 1.5: 0.7, interantennal space convex, without median carina; punctures on frons thick and reticulate; ocular sinus with sparser punctures; POD: OOD = 12: 21, diameter of anterior ocellus as long as the distance between anterior ocellus and posterior ocelli; vertex punctured, punctures somewhat weaker than those on frons; cephalic fovea obsolete; occipital carina strong only on sides.



Figures 1–9. *Tropidodynerus* (*Tropidodynerus*) *liupanshanensis* sp. n. **1** habitus of holotype (dorsal view), ♀ **2** habitus of one paratype (dorsal view), ♂ **3** clypeus, ♀ **4** clypeus, ♂ **5** parategula (lateral view), ♀ **6** vertex (dorsal view) , ♀ **7** antennae (lateral view), ♂ **8** mid coxa (ventral view), ♂ **9** metasoma (vertral view), ♂.

Mesosoma. Anterior face of pronotum sparsely punctate, pronotal carina obsolete at middle, present and somewhat strong at its shoulder, and stopping abruptly below shoulder, the carina of lateral face well developed, somewhat arced, and not joining the

carina of shoulder; punctures on mesosoma generally larger than those on head and metasoma; posterior face and lateral side of pronotum, mesoscutum, mesopleuron, and scutellum strongly punctured, punctures mostly so elongated as to forming irregular and reticulate striations; punctures on metanotum comparatively sparser; scutellum not convex; metanotum inclined; epicnemial carina of mesopleuron obsolete, present only on the lower side; dorsal surface of propodeum not convex, weakly punctured and with thin reticulate rugae, vertical median area somewhat concave, with thin, wavy, transverse rugae and a median carina, lateral side on the upper half with dense thin, long, and transverse rugae, on the lower half coriaceous and with indistinct rugae; posterior lobe of tegula rounded at the apex; apex of parategula reaching far beyond the apex of tegula (Fig. 5).

Metasoma. In dorsal view, T1 domed, its width 1.89 × length and 0.80 × width of T2, T1 and T2 without apical lamellae; the narrow basal part of S1 coriaceous, posterior area of S1 with reticulate rugae and lateral carina; punctures on metasoma distinctly weaker than those on other portions of the body; punctures on T1 bigger than those of other terga; punctures on T2 at posterior area sparser; punctures on S2 bigger and sparser than those on T2; visible part of T3–T6 and S3–S6 coriaceous and with minute punctures; the apical yellow bands on T3 and T4 not extending to lateral margins, the band on T4 shorter than that of T3.

Male (Figs 2, 4, 7–9). Body length 7.0 mm, forewing length 8.5 mm. Punctures, setae, and coloration similar to female except as follows: clypeus (Fig. 4) entirely, most of mandible on the outside, labrum, ventral surface of antennal scape, all tibiae except ventral sides, dorsal sides of fore and mid tarsi I, ventral side of mid coxa (Fig. 8), apex of mid femur ventrally, and apical bands on T1–T5 yellow; in front view, width of head 1.37× its length; POD: OOD = 13: 22, diameter of anterior ocellus almost equal to the distance between anterior and posterior ocella; clypeus densely punctured, punctures on apex normal and not elongated, width of clypeus 1.38 × length, total width: apical width = 4.5: 1.4, apical emargination deeper than that in female, width: depth of emargination = 1.5: 0.9; antenna (Fig. 7), apical segments coiled; the mark in eye incision (Fig. 4), postocular spot and elongated spots on dorsal faces of all tibia larger than those in female; a small yellow spot on the left upper part of mesepisternum; tarsi except yellow parts ferruginous to brown; in dorsal view, width of T1 2.07 × its length and 0.81 × width of T2; apical bands on T2 and T3 pale and pellucid at the middle, the band on T5 shorter than those on T1–T4; the band on dorsal surface of pronotum wider than that in female; other characters same as those in female.

Recognition. The species resembles *T. fertoni* (Dusmet, 1925) in scutellum and metanotum black, and propodeum without a sharp edge at the transition of dorsal surface to lateral side. It differs from *T. fertoni* and all other members of the genus by the following character combination: clypeal apex deeply emarginated in female, in male clypeal width: apical width = 4.5:1.4, apical width: depth of emargination =1.5:0.9, the band on dorsal surface of pronotum comparatively thinner; T1–T5 and S2 with apical yellow bands, respectively.

Distribution. China (Ningxia).

Etymology. The specific name *liupanshanensis* is the Neolatin adjective, with reference to the region from which the type specimens were collected.

Tropidodynerus (*Tropidodynerus*) *concavus* Li & Chen, sp. n

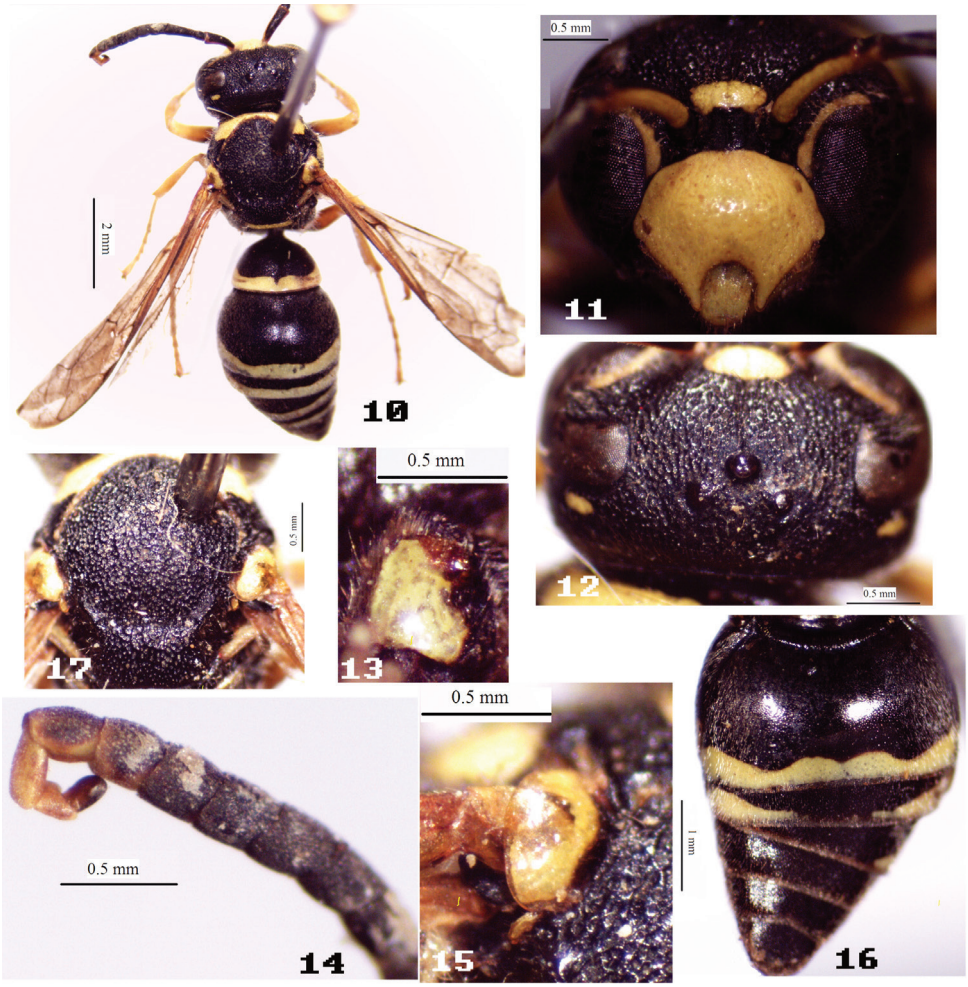
http://zoobank.org/9BE7DFC8-3018-4749-A57E-EEF57CF4386E
Figs 10–17

Material examined. Holotype, ♂, China, Hebei Province, Zhangjiakou City, Zhuolu County, Yangjiaping Forest, 39°58'22.28"N, 115°23'36.38"E, 908m, 6–10.VII.2004, unspecified collector, No. 1004048 (HBU).

Description. Male (Figs 10–16): Body length 7.5 mm, forewing length 7.0 mm. Black, with yellow and ferruginous markings. Yellow markings as follows: entirely clypeus, mandible except apex, labrum, a band along inner orbits on the lower side of eye (Fig. 11), ventral surfaces of antennal scape and pedicel, a large transverse interantennal spot, a small postocular spot (Fig. 12), a broad band on dorsal surface of pronotum (Fig. 10), tegula, a large spot at the upper part of mesepisternum, metanotum, ventral surface of mid coxa, a apical broad band on each of T1–T5 (Fig. 10) and S2, a apical broad interrupted band on S3, and a long transverse spot on lateral side of S4 (Fig. 16); ventral surfaces of A3–A10, whole A11–12, apex of parategula, and apexes of all femora to apical tarsi yellow brown; mid and hind femora except apexes largely ferruginous; Wings slightly brownish.

Head. In front view, head much wider than long, width 1.25 × length; clypeus with sparsely irregular punctures (Fig. 11) and distinctly convex, its apex deeply emarginated and U-shaped, width of clypeus 1.18 × length, apical width: depth of emargination = 1.5: 1.36, width of clypeus: apical width = 4.5: 1.27; antenna (Fig. 14), apical segments coiled; interantennal space slightly convex, with median carina; frons with moderately thick punctures and reticulate; POD: OOD = 20: 22; the diameter of anterior ocellus somewhat smaller than the distance between anterior and posterior ocella; punctures on vertex sparser than those on frons.

Mesosoma. Anterior face of pronotum coriaceous and with minute punctures, pronotal carina complete at the middle and its shoulder, stopping abruptly below shoulder, and its lateral face well developed, somewhat bending, and not joining the carina of shoulder; punctures on pronotum sparser than those on other parts of mesosoma, the distances between punctures almost equal to the diameter, punctures on lateral side of pronotum comparatively denser and stronger; mesoscutum, mesopleuron, and scutellum strongly punctured, punctures distinctly dense and mostly so connected as to forming reticulate striations (Fig. 17); scutellum somewhat convex; metanotum smooth, with sparse punctures and inclined; epicnemial carina of mesopleuron absent on the upper half, present and strong on the lower half; propodeum impunctate, dorsal surface not convex and wholly with dense oblique rugae, vertical median area concave, somewhat deep, and with a median carina; the whole vertical and lateral sides of pro-



Figures 10–17. *Tropidodynerus* (*Tropidodynerus*) *concavus* sp. n. **10** habitus of holotype (dorsal view), ♂ **11** clypeus, ♂ **12** vertex (dorsal view), ♂ **13** mid coxa (ventral view), ♂ **14** antennae (lateral view), ♂ **15** parategula (lateral view), ♂ **16** metasoma (vertral view), ♂ **17** mesoscutum and scutellum (dorsal view).

podeum with densely thin, long and transverse rugae; posterior lobe of tegula rounded at the apex; apex of parategula reaching far beyond the apex of tegula (Fig. 15); mid coxa concave ventrally (Fig. 13).

Metasoma (Fig. 16). In dorsal view, T1 domed, width 2.16 × length and 0.76 × width of T2; T1 and T2 without apical lamellae; S1 coriaceous, posterior area with faint transverse rugae, lateral carina obsolete; punctures on metasoma distinctly minuter and denser than those on other parts of the body; punctures on T1 somewhat bigger and sparser than those on other terga, with interspaces in average as long as the diameter of the punctures; punctures on T2 denser than those on S2, and visible part of T3–T7 and S3–S7 somewhat weaker.

Female. Unknown.

Recognition. The species resembles *T. flavus* (Lepeletier, 1841) in metanotum yellow, propodeum without a sharp edge at the transition of dorsal surface to lateral side, and apical bands on T2 and T3 not interrupted. It differs from *T. flavus* and all other members of the genus by the following character combination: total width of clypeus: apical width = 4.5: 1.27, apical width: depth of apical concavity =1.5: 1.36, scutellum black, and mid coxa concave ventrally.

Distribution. China (Hebei).

Etymology. The specific name is the Latin adjective *concavus*, with reference to mid coxa concave ventrally in male.

Key to the world species of the subgenus *Tropidodynerus* Blüthgen

Males

1 Propodeum with a sharp edge at the transition of dorsal surface to lateral side, extending downwards to metasomal fossa; apical bands on T2 and T3 widely interrupted in the middle, rarely complete (Gusenleitner 1998, 2007) .... ***T.* (*T.*) *interruptus* (Brullé, 1832)**

– Propodeum without a sharp edge at the transition of dorsal surface to lateral side, forming only a dull corner or almost complete; apical bands on T2 and T3 not interrupted or at most pale and pellucid in the middle..... **2**

2 Scutellum and metanotum black **3**

– At least metanotum yellow..... **4**

3 Clypeal total width: apical width = 4.5: 1.4, apical width: depth of apical concavity = 1.5: 0.9; the band on dorsal surface of pronotum thinner; T1–T5 and S2 with apical yellow bands, without lateral spots (Fig. 2)..... ..... ***T.* (*T.*) *liupanshanensis* sp.n.**

– Clypeal total width: apical width = 4.5: 1.9; apical width: depth of apical concavity = 1.5: 0.7; the band on dorsal surface of pronotum broad; T1–T6 with apical yellow bands, S2–S4 with lateral yellow spots (Gusenleitner 2007)..... ..... ***T.* (*T.*) *fertoni* (Dusmet, 1925)**

4 Clypeal total width of clypeus: apical width = 4.5: 1.27, apical width: depth of apical concavity =1.5: 1.36; scutellum black; mid coxa concave ventrally (Fig. 13)..... ***T.* (*T.*) *concavus* sp. n.**

– Clypeal total width: apical width = 4.5:1.5; apical width: depth of apical concavity =1.5: 1.0; scutellum with two large yellow or brown yellow spots; mid coxa normal (Gusenleitner 1998, 2007)..... ***T.* (*T.*) *flavus* (Lepeletier, 1841)**

Females

1 Propodeum with a sharp edge at the transition of dorsal surface to lateral side, extending downwards to metasomal fossa; apical bands on T2 and T3 widely

interrupted in the middle, rarely complete (Gusenleitner 1998, 2007) .... ***T.* (*T.*) *interruptus* (Brullé, 1832)**

– Propodeum without a sharp edge at the transition of dorsal surface to lateral side, forming only a dull corner or almost complete; apical bands on T2 and T3 not interrupted or at most pale and pellucid in the middle..... **2**

2 Scutellum and metanotum with large yellow to brownish yellow spots (Gusenleitner 1998, 2007)..... ***T.* (*T.*) *flavus* (Lepeletier, 1841)**

– Scutellum and metanotum black **3**

3 Clypeal apex deeply emarginated (Fig. 3)..... ***T.* (*T.*) *liupanshanensis* sp.n.**

– Clypeal apex somewhat emarginated (Gusenleitner 1998, 2007) .... ***T.* (*T.*) *fertoni* (Dusmet, 1925)**

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RESEARCH ARTICLE

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Phenological, but not social, variation associated with climate differences in a eusocial sweat bee, *Halictus ligatus*, nesting in southern Ontario

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Abstract

Studies of annual and geographic variation in eusocial bee populations suggest that more stringent environmental conditions result in stronger reproductive skew favouring queens, while moderate conditions favour increasing worker reproduction. To test these predictions, we compared the phenology and colony development of *H. ligatus* nesting in St. Catharines, Ontario, Canada to a previously studied aggregation 90 km north of St. Catharines, in Victoria, Ontario. Despite the close proximity of these two locations, St. Catharines has markedly shorter winters and longer summers. Comparisons between St. Catharines in 2006 and Victoria in the 1980s and 1990s incorporate both geographic differences in climate and temporal differences due to climate change. We predicted that St. Catharines foundress queens should emerge from hibernation and initiate nests earlier in spring, giving them time to produce more workers. Since earlier studies indicated that queens have difficulty suppressing worker reproduction in larger colonies, we also predicted higher rates of worker ovarian development in St. Catharines. In spring and summer 2006, we excavated 65 *H. ligatus* nests, comparing their contents to 713 specimens collected in pan traps. As predicted, nests were initiated about a month earlier in St. Catharines than in Victoria, but contrary to prediction, fewer workers were produced in St. Catharines. St. Catharines workers were just as likely to have developed ovaries as Victoria workers. About 40% of St. Catharines workers were classified as reproductive, and larger reproductive workers tended to have higher ovarian scores. Early queen mortality in the longer nest cycle of St. Catharines bees may have enhanced opportunities for worker reproduction despite their smaller numbers. Novel features of *H. ligatus* sociobiology in St. Catharines included

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evidence that queens can initiate new nests following the loss of their first brood, overlap between worker and gyne production within some nests, and high rates of independent nest founding by worker-sized females, suggesting that many worker-brood females overwinter. Overall, the distinctly warmer climate of St. Catharines compared to Victoria led to earlier nest initiation and lengthening of the flight season, but not to the predicted differences in colony social organisation or queen-worker reproductive skew. A second objective of our study was to assess how well pan trap collections capture important information about demographic and social parameters important in assessing social variability in sweat bees. Nest excavations and pan traps produced similar results, suggesting that pan traps are a good alternative when nest excavations are impossible.

Keywords

Halictinae, social evolution, geographic variation, pan trap, worker reproduction

Introduction

Eusociality is the most frequent, caste-based form of colony social organisation in sweat bees (Halictidae) (Michener 2007). In sweat bees, eusociality is characterized by the behavioural totipotency of all adult females, such that any newly eclosed female is potentially capable of taking on either the queen or worker role (Yanega 1989, 1990). The flexibility inherent in the behaviour of individual females is also observed at the level of entire colonies or populations, as there is considerable evidence for both intra- and inter-population variation in colony social organisation, especially in response to local climatic conditions (Yanega 1993, Miyanaga et al. 1999, Hirata et al. 2005, Kocher and Paxton 2014). Ultimately, variation in colony social organisation seems to reflect colony or population-typical outcomes of conflict between queens and workers over control of reproduction, the conflict being moderated by the environmental conditions experienced by individual bees and colonies.

Halictus ligatus Say is one of the most widespread eusocial bees in North America, and together with its closely related and morphologically cryptic sister species, *H. poeyi* Lepeletier, represents a spectrum of queen-worker reproductive skew from high skew at high latitudes to low skew at lower latitudes (Michener and Bennett 1977, Packer and Knerer 1986, 1987, Dunn et al. 1998). Studies of annual variation within populations and geographic variation among populations suggest that more stringent environmental conditions result in stronger reproductive skew favouring queens, whereas moderate conditions favour increasing worker reproduction (Richards and Packer 1995, 1996, Richards et al. 1995, Richards 2004). At a nesting aggregation in Victoria, Ontario (northwest of Toronto), variation in colony social behaviour was ultimately due to extreme annual variation in local rainfall and temperature patterns, that led to dynamic changes in queen-worker behavioural interactions. In 1990, poor weather conditions (higher than normal rainfall) limited queen foraging time, leading to the production of workers with relatively small body sizes. The wet conditions also led to high levels of juvenile mortality, so worker brood survival was low. As a result, queens had to contend with relatively few, relatively small workers in 1990, which

provisioned relatively small gynes. In contrast, the summer of 1991 was unusually warm, with normal rainfall levels. That year, the small queens born in 1990, experienced excellent conditions during the worker brood provisioning phase and raised relatively large numbers of large-bodied workers. The weather variation that directly led to differences in worker body size and numbers indirectly led to significant social variation. In 1990, large queens had to contend with relatively few, small workers, and were more successful in preventing worker oviposition, whereas in 1991, small queens had large numbers of large workers, and workers increased their contribution to oviposition of Brood 2.

The social variation observed within a single population of *H. ligatus* in response to temporal variation in local environmental conditions, supports the view that much or most social variation is due to phenotypic plasticity. Temperature and breeding season length are among the most important factors influencing colony social variation, because almost all eusocial halictines must produce at least two broods per year, whereas solitary halictines need produce only one brood per year (Kocher et al. 2014). Studies in several species of facultatively social *Halictus* and *Lasioglossum* indicate that colonies develop socially when foundresses can initiate nests early, but develop solitarily when nest initiation is delayed (Packer 1990, Yanega 1993, Hirata and Higashi 2008, Field et al. 2012). Warmer soil temperatures can also speed up colony development, which can lead to production of more workers or extra worker broods (Weissel et al. 2006, Hirata and Higashi 2008). Direct environmental effects such as these can be amplified by indirect effects of longer breeding seasons. For instance, production of extra workers can lead to increased production of reproductive brood (gynes and workers) or may result in declines in reproductive skew, as increased colony size often is associated with increased rates of worker ovarian development (Packer et al. 1989, Richards et al. 1995, Strohm and Bordon-Hauser 2003).

In the current study, we examined the phenology and colony development of *H. ligatus* at a nesting aggregation in St. Catharines, in the Niagara region of southern Ontario in 2006. St. Catharines is about 90 km south of Victoria, Ontario, but has markedly shorter and milder winters and longer summers (Table 1). Moreover, examination of temperature records for southern Ontario (based on data from the "St. Catharines A" and "Orangeville" stations, available at climate.weather.gc.ca) demonstrates that from 2000–2006, average monthly temperatures were higher than they had been in the 1980s (summarized in Table 1). This suggests that comparisons of bees nesting in Victoria in the 1980s and 1990s and St. Catharines in 2006 incorporate both geographic variation in climate and temporal differences due to climate change. Accordingly, we predicted that the longer spring and summer seasons in Niagara in 2006, compared to Victoria 15–22 years earlier, should be associated with differences in colony phenology that translate into differences in colony social organisation. In Niagara, foundress queens should emerge from hibernation and initiate nests earlier in spring than in Victoria, and start provisioning the worker brood earlier. This would give them time to produce more workers and thus larger colonies by mid-summer. Larger colony sizes, in turn, would lead to relatively high rates of worker egg-laying, as queens would be less able to

Table 1. Geographic variation in temperature and precipitation patterns in St. Catharines and Victoria, as indicated by climate normals for the period 1981–2010. Climate data were obtained from for the St. Catharines A and Orangeville stations (http://climate.weather.gc.ca/climate_normals). Bees nesting in St. Catharines experience considerably shorter winters and longer flight seasons and higher temperatures, especially during the spring. Precipitation patterns are very similar at the two sites. Degree-days represent the number of days per year in which the temperature exceeds the given average temperature. Note that *H. ligatus* foragers cannot fly at temperatures below 14 °C (M.H. Richards, pers. obs.).

Event, 1981–2010	St. Catharines	Victoria (Orangeville)
Average date of last spring frost	24 April	20 May
Average date of first autumn frost	21 October	30 September
Average length of frost-free period (days)	179	132
Days with minimum temperature above 0 °C	238.1	194.6
Degree-days above 15 °C	656.2	403.5
Degree-days above 18 °C	334.9	169.2
Rainfall (mm)	754.2	750.1
Snowfall (cm)	137.1	151.5
Total precipitation (mm)	880.1	901.5
Days with precipitation >0.2mm, April–September	71.6	66.7

suppress worker oviposition (Richards et al. 1995). Longer breeding seasons might also be associated with an increased likelihood that queens die prior to completion of Brood 2, promoting worker oviposition, especially by the youngest workers which might often emerge into nests without large foundress queens. The early initiation of spring might not be the only factor influencing bee behaviour; the shorter, milder winters in Niagara compared to Victoria might also have an influence. Most females that found nests are gynes (large, fat females produced in Brood 2 of the previous year). However, workers (small, skinny females produced in Brood 1 of the current year) also attempt to nest independently or to overwinter and become foundresses the following spring (Rehan et al. 2013; Richards and Packer 1994). Worker-sized females might be more likely to survive hibernation in areas with milder winters. This would increase the number of small foundresses in spring, possibly influencing rates of pleometrotic (multi-foundress) nest-founding if worker-sized females are more likely to become subordinate females rather than founding their own nests (Packer 1986a).

Collecting detailed field observations of colonises is very important in studies of demographic and social variation among sweat bee nesting aggregations, but nesting aggregations can be difficult to locate, a serious impediment to extensive comparisons among populations. An alternative source of demographic data, season-long collections of bees in pan traps, is widespread, but mostly aimed at assessing variation in abundance and diversity of entire bee communities (e.g. Richards et al. 2011). To date, only one study has evaluated the social status of a halictine species based solely on pan trap data. Packer et al. (2007) used dissection and measurement data of pan trapped specimens to show that *H. tripartitus* is eusocial in California. A second objective of our study was to assess how well pan trap collections capture important information about demographic and social parameters important in assessing social variability in sweat bees.

Methods

Nest excavations

Nest excavation techniques for *H. ligatus* nesting in St. Catharines, were as previously described (Rehan et al. 2013). Briefly, 65 *Halictus ligatus* nests, including four previously described nests founded by workers in mid-summer (Rehan et al. 2013) were excavated over the period from late May to late August 2006 from a temporary pile of dirt created by landscaping activities on the Brock University campus, St. Catharines, Ontario, Canada (N 42°07'11", W 79°14'57"). We aimed to excavate five nests per week, weather permitting. Nests were excavated early in the morning or late in the day to ensure that all occupants were inside. Talcum powder was blown down nest entrances to enhance visibility prior to nest excavation. Adults, young larvae and injured specimens were collected directly into 95% ethanol, while older larvae and pupae were collected in paraffin-lined petri dishes to be raised to adulthood in the lab. In classifying the life stages of brood, prepupae (post-defecatory larvae) were classified as larvae, while newly eclosed bees still in their brood cells (sometimes referred to as imagoes) were classified as adults.

Pan trapping

Pan trapping techniques and locations were as previously described (Richards et al. 2011). In brief, pan trap lines were set out weekly at six sites (406, BrNW, BrS, Esc, Pon, and StD) on the Brock University campus and the nearby Glenridge Quarry Naturalization Site, within 1–2 km of the nesting aggregation described below. Pan trapping was carried out from the last week of April (week 1) until late September (week 23). A total of 713 *H. ligatus* specimens were pinned and identified, and used to assess flight patterns of adult males and females, thus revealing breeding season phenology (Richards et al. 2010). A subset of pan-trapped females, selected from the peak collecting periods, was measured and dissected as described below.

Status of adult females

All adult females (N = 171) collected from nests were measured and dissected to determine head width, wing length, mandibular wear, wing wear, ovarian development, and whether they had mated. In addition, 133 females collected from nests as larvae or pupae and reared to pupation or adulthood, were measured. We also measured head width and wing wear and dissected 153 of the 463 females collected in pans. Most of these dissected specimens were queens collected in mid-May (week 4), workers in mid-July to mid-August (weeks 13–16), and a mix of workers and early gynes in late August (week 19). The procedures for dissections and measurements followed those used in previous studies (e.g. Richards et al. 2010). Briefly, mandibular wear (nest bees

only) and wing wear (both nest and pan bees) were each scored from 0 (unworn) to 5 (extremely worn) and then added together to give a total wear score (TW). Ovarian development (OD) was assessed by assigning to each developing oocyte a fraction indicating its size relative to a fully developed oocyte (1, ¾, ½, or ¼) and summing. OD provides a cardinal measure of each female's total volume of developing oocytes. An OD value of 0.1 was assigned to females with thickened ovaries but no developing oocytes, and 0 was assigned to females with thread-like ovaries.

In eusocial sweat bees, caste is associated with differences in behaviour, body size, wear, and ovarian development (Schwarz et al. 2007). In general, queens fly and provision brood in spring, remain in the nest in summer, are larger than their own workers, become quite worn by mid-summer, are mated, and have high rates of ovarian development. Workers emerge and provision brood in summer, are almost always smaller than queens, become progressively more worn by late summer, are often mated, and may or may not have developed ovaries (Packer and Knerer 1985, Packer 1986a, Richards 2001, Richards et al. 2010). Therefore, we used the following criteria for categorizing females collected in nest excavations. Adult females collected before week 10, when Brood 1 had not yet begun to emerge as adults, were categorized as queens, regardless of size. From week 10 onward, we used the median head width for all females (median HW = 2.82 mm) to categorize females are large (above the median) or small (below the median). From weeks 10–16, small (HW < 2.82) adult females were designated as workers. Two worker-sized females collected in nests excavated in weeks 16 and 17, were categorized as foundresses rather than workers, because their unusually high wear scores (TW = 10) suggested that they had been foraging for much longer than the workers in their own nests. After week 16, large, very worn (TW > 5) females were designated as queens, small, worn females (TW > 1) were designated as workers, and large, unworn females (TW ≤ 1) were designated as gynes. Females that did not fit these criteria were not assigned to caste. Note that the term 'gyne' is used here to describe females that overwinter prior to reproduction, whereas 'reproductive workers' are Brood 1 females that attempt to breed shortly after eclosion.

Assignment of caste to females caught in pan traps was also based on the above criteria, as well as comparisons to the colony development phenology inferred from nest excavations. Adult females collected before week 10 were categorized as queens. From weeks 10–16 onwards, all females caught in pan traps were designated as workers because gynes had not yet eclosed in excavated nests. It is possible that some of the small, worn females captured at this time were not workers, but very late-foraging small queens or subordinate foundresses that continued foraging after worker emergence (Packer 1986b). From week 17 onwards, females with head width above the median (2.82 mm), low wing wear (WW ≤ 1), and no ovarian development were designated as gynes, while those with head width below the median and worn wings (WW > 1) were designated as workers. Females that did not fit these criteria were designated as caste unknown.

Statistical analyses

We checked our initial caste assignments in two ways. We used Principal Components Analysis (PCA) to examine differentiation among queens, workers, and gynes. Bees collected in nests and pans were analysed separately. For nest bees, the PCA was based on head width, total wear, and ovarian development, whereas for pan-trapped bees, the PCA was based on head width, wing wear, and ovarian development. The PCA analyses were carried out using the princomp function on the rescaled variables in R version 2.15.0. Visual inspection of the principal components plots indicated general separation of the castes. We also used Discriminant Functions Analysis (DFA) to examine the caste classifications of individual females using the lda and predict functions (R, library MASS). For 171 queens, workers, and gynes collected in nest excavations, a DFA based on head width, wing length, and wear (TW) (but not ovarian development) produced a list of 22 females that were re-classified to a different caste. Of these, 12 reclassifications were wholly implausible given the time of collection (queens collected before worker emergence cannot reasonably be reclassified as workers or gynes), but 10 reclassifications of females collected from week 16 onward (workers that might have been gynes, and vice versa) were incorporated into the data set. We then combined the nest and pan trap bees for a second DFA to classify females collected from week 16 onward (based on HW, WW, and TOD), as these were the most difficult to assign. Females whose caste was initially assigned as 'unknown' and which were still unclassifiable after the DFA, were excluded from statistical analyses in which caste was a factor.

In eusocial sweat bees, size differentiation between castes is often measured by proportional differences between queens and workers. We calculated queen-worker differences as [(queen value – worker value) / queen value] × 100. Proportional differences were compared for queens and daughters from their own nests or using the average queen and worker trait values within the nest and pan-trapped individuals separately.

Where parametric statistics are presented, these were based on model statements which generated error terms with normal distributions. The response variables in general linear models were cardinal variables (e.g. head width, ovarian development). Where it was not possible to achieve normally distributed error terms using standard data transformations and where ordinal variables (e.g. wing wear) were analysed, we used non-parametric statistics. All analyses were carried in R-Studio, using R, version 2.15.1. Except where otherwise noted, degrees of freedom (df) = 1.

Data resources

The data underpinning the analyses reported in this paper are deposited in the Dryad Data Repository at doi: 10.5061/dryad.vm11c.

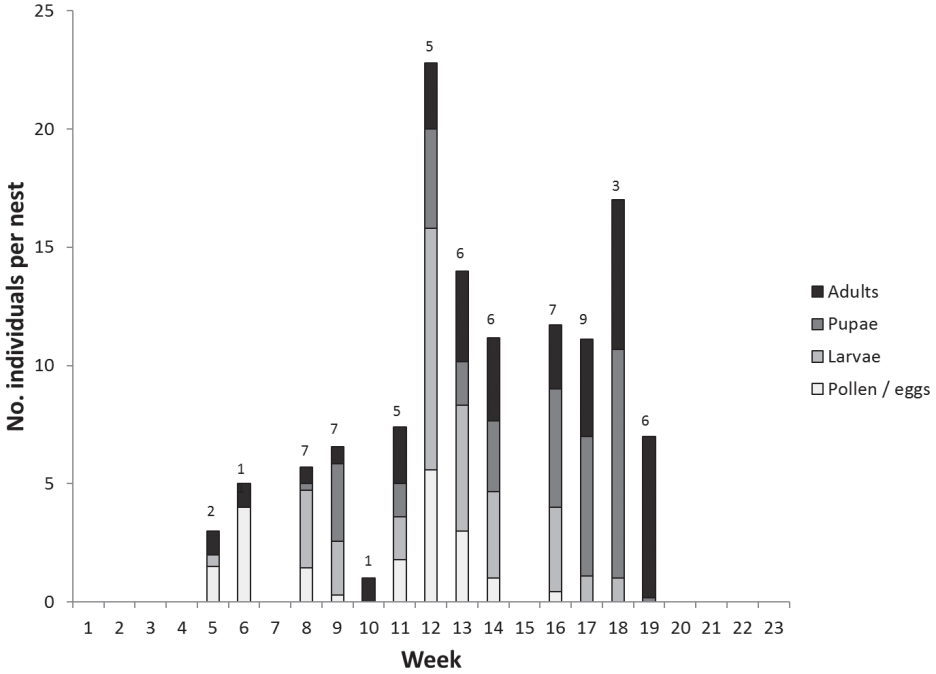

Figure 1. Timing of brood production and development in *Halictus ligatus* nests excavated at Brock University in St. Catharines, Ontario in 2006. Week 1 was the last week of April, and week 11 was the first week of July. Numbers above each bar are the numbers of nests excavated each week.

Results

Brood and colony development based on nest excavations

We excavated 67 nests excavated in St. Catharines from May to August 2006 (weeks 5 to 19). The contents of excavated nests were used to infer the timing of brood production and development (Figure 1).

Nests excavated in weeks 5–6 contained pollen masses, eggs, and small larvae. Pupae were first detected in week 8, and by week 9 very few Brood 1 provision masses were being constructed, so worker brood provisioning was mostly complete. In weeks 8 and 9, the apparent peak of Brood 1 production, nests contained an average of 5.5 ± 3.2 (SD) brood (range = 1 to 10, n = 14 nests). Based on 21 sexable pupae collected during this 2-week period, 9.5% of brood were males (n = 2).

Nests excavated from week 11 onward contained juveniles representing both broods. Pollen masses attributed to Brood 2 were collected from weeks 11–16. Gyne provision masses, which are identifiable by their distinctive saddle shape (Boomsma and Eickwort 1993), were collected from weeks 11–14, suggesting that Brood 2 was protogynous. The first gyne pupae were collected in week 14 and newly eclosed gynes (still in the brood cell) were collected in week 17. During weeks 16–18 (mid to late

Table 2. Evidence for simultaneous production of workers and gynes in three nests of *Halictus ligatus* based on ages of pupae, which indicate that some worker pupae were younger than gyne pupae in the same nest. Caste was assigned based on head width; the sizes of adult workers from the same nests are shown for comparison. Individuals born "out of order" are indicated in boldface.

Week	Date	Nest	Developmental stage when collected (oldest to youngest)	Head width (mm)	Caste
14	25-Jul-06	45	Adult	2.75	W
			Adult	2.45	W
			Black-eyed pupa	2.35	W
			Brown-eyed pupa	**3.20**	**G**
			Red-eyed pupa	2.68	W
			Pink-eyed pupa	2.73	W
			White-eyed pupa	3.20	G
			Prepupa	3.01	G
			Prepupa	3.15	G
17	14-Aug-06	271	Adult	2.59	W
			Adult	2.54	W
			Adult	2.85	W
			Adult	2.85	W
			Adult	2.87	W
			¾-pigmented pupa	3.29	G
			Black-eyed pupa	3.15	G
			Brown-eyed pupa	**2.82**	**W**
			White-eyed pupa	2.96	G
17	15-Aug-06	278	Adult	2.73	W
			Adult	3.15	G
			Black-eyed pupa	3.01	G
			Brown-eyed pupa	**2.45**	**W**

August), 56/96 (58%) female larvae and pupae that could be measured, were gyne-sized. In most nests, juvenile females identified as workers were clearly older than those identified as gynes. However, in three nests, the ages of pupae of distinctly different sizes suggested that workers and gynes had been produced at about the same time (Table 2). For instance, in nest 45 (Table 2), a gyne-sized, brown-eyed pupa was evidently older than the next two female offspring, which were distinctly smaller and worker-sized.

The fact that many nests excavated from week 11 onward contained juveniles representing both broods, as well as the extended period of brood development, complicates evaluation of the number of offspring in Brood 2. That most juveniles found in nests during weeks 16–18 were probably members of Brood 2 is supported by the observation that provision masses were not found after week 16 and the earliest (oldest) individuals of Brood 2 began to eclose in week 17. During weeks 16–18, the average number of brood per nest was 9.9 ± 6.0 (range = 1–23, n = 19 nests), and 36 of 117 sexable pupae (31.0%) were male. The number of brood per nest began to decline around week 19 (Figure 1), suggesting that reproductive brood were completing their development and dispersing.

Ten of 14 nests excavated in weeks 8 and 9 contained a queen, while 4 of 5 nests contained a queen in week 11. This suggests that up to 80% of queens survived to worker emergence. Only five of 16 nests excavated in weeks 16–18 contained queens, suggesting that only 31% survived to the end of Brood 2 egg-laying. Both these survival rates are likely over-estimates as we do not include nests that failed early in the season and therefore were not marked. During weeks 11 and 12, the first two weeks of the worker foraging period, excavated nests contained an average of 1.8 ± 1.6 adult workers (range 0–6, n = 10 nests). Later, during weeks 16–18, the average was 1.5 ± 1.6 (range 0–6, n = 19 nests), which was not significantly different (Kruskal-Wallis X^2 = 0.615, df = 1, n.s.).

Rates of pleometrosis were inferred from demographic data. Only one nest contained two foundress queens; however, this nest was excavated on 5 July after *Astata* wasps had begun excavating burrows among the bee nests (Rehan et al. 2013), and the resulting soil disruption may have caused two separate nests to be joined. A nest excavated on 14 July (week 12) contained only a single adult with HW = 2.44 mm and TW = 6. The oldest brood in this nest were pigmented pupae and the youngest were larvae, so this female could have been a small subordinate that outlived the dominant foundress in a pleometrotic association. A nest excavated on 8 August (week 16) contained a highly worn, worker-sized female (HW = 2.59 mm and TW = 10) and six workers, all of them larger and none of them with TW > 4. Similarly, a nest excavated on 15 August (week 17), contained a highly worn, worker-sized female (HW = 2.54 mm and TW = 10) and a larger worker with little wear (TW = 2). In a fifth nest, excavated on 22 June (week 9), the only indication of pleometrosis was that the worker pupae were all slightly larger than the nest queen. In all these nests, the highly worn, small females were either tiny haplometrotic queens or subordinate foundresses that had outlived larger dominants. Since preliminary analyses based on microsatellite DNA genotyping suggested high rates of pleometrosis (A. Giroux and M.H. Richards, unpub. data), we estimate the rate of pleometrosis was as high as 5/65 excavated nests (7.1%).

Two nests suggest the possibility that queens occasionally start new nests after losing the first one. A nest excavated in week 10 (29 June) contained only a large, worn female (HW = 2.92 mm, WW = 0, MW = 5) but no brood cells, so the nest may have been newly founded. A nest excavated in week 11 contained a worn adult female of intermediate size (HW = 2.82, WW = 2, MW = 5), as well as an unfinished provision mass, a provision mass with an egg, and two larvae, but no workers or empty brood cells.

Flight activity and phenology based on pan trapping

The numbers of bees caught in weekly pan trap collections were used to infer the timing of important events in the colony cycle of *Halictus ligatus* in 2006 (Figure 2). Spring foundresses (queens whose workers have not yet emerged) were trapped from 3 May (week 2) to mid-June (week 8), suggesting a queen foraging period about 6 weeks in duration. However, the peak foraging period was in mid-May (weeks 4 and 5).

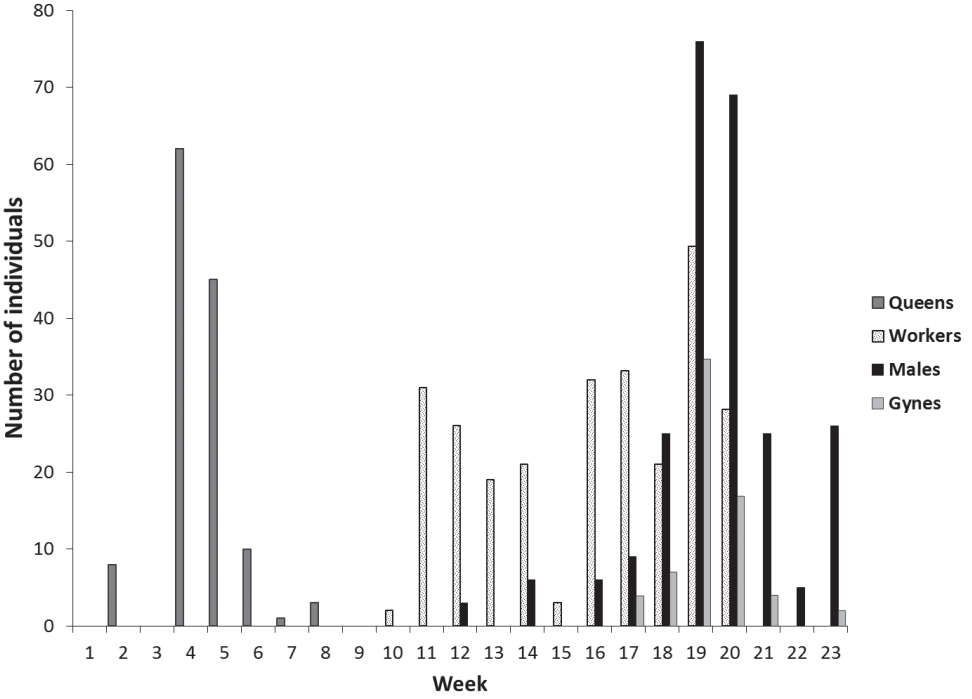

Figure 2. Seasonal phenology of *Halictus ligatus* inferred from weekly pan trap samples at six sites at Brock University and the adjacent Glenridge Quarry Naturalization Site in 2006. Week 1 was the last week of April, and week 11 was the first week of July.

Unworn workers were trapped from late June to late July, suggesting that in most nests, Brood 1 completed development as adults during weeks 10–14, about 7 weeks after provisioning by queens. Worn workers were collected until the last week of trapping in early September (week 20), except for an apparent hiatus during week 15, suggesting that population-wide, the worker foraging period was at least 10 weeks in duration. Males trapped during weeks 10–14 were likely produced in Brood 1; based on the proportional representation of males and workers in pan traps during weeks 10–14, about 8.3% of Brood 1 were males and 91.7% were workers. The first gynes were trapped in mid-August (week 17), signalling the beginning of Brood 2 emergence 6–7 weeks after initiation of worker provisioning. The largest numbers of gynes and males were caught in late August and early September (weeks 19–20), suggesting that most of Brood 2 eclosed as adults around this time. Males and gynes were caught as late as the end of September (week 23), when pan-trapping ceased. During weeks 16–18, the period for which the Brood 2 sex ratio was estimated from nest data based on pupae, the majority (40 / 44) of females trapped were workers; since most gynes were still pupae, this period was too early to estimate the Brood 2 sex ratio from pan trap collections. During weeks 19–21, gynes represented 42.8% (24/56) of dissected females, indicating that they were emerging in large numbers. Applying this propor-

tion to the total 404 females caught in weeks 19–21, we collected about 173 gynes and 324 males, suggesting that the Brood 2 sex ratio was about 65%.

Characteristics of adult females

PCA outcomes for females collected in nests and pans are presented in Figure 3. In both data sets, the PCA suggests three clusters of females congruent with our caste assignments. In nest bees, there was better separation of queens, workers and gynes, likely because more information was available for nest bees (mandibular wear scores and demographics of whole colonies) than for pan trap bees.

More detailed comparisons of body size, wing wear, and ovarian development of queens, workers, and gynes collected from nests and pan traps are presented in Figure 4. Queens collected by the two methods were similar in size and ovarian development (Kruskal-Wallis tests: HW $X^2 = 0.12$, n.s.; WW: $X^2 = 2.87$, n.s. ; TOD: $X^2 = 0.21$, n.s.). Workers from nests were significantly smaller ($X^2 = 11.03$, $p < 0.001$), less worn ($X^2 = 26.15$, $p < 0.0001$), and had more ovarian development ($X^2 = 25.10$, $p < 0.0001$) than those from pan traps. Gynes from nests were significantly larger ($X^2 = 5.87$, $p < 0.05$) than those from pan traps. One nest contained a queen that was about 2.8% smaller than her worker pupae (the possible pleometrotic queen described above). In the remaining nests, queens were from 1.5 to 29.7% larger than their own workers (mean based on one randomly chosen worker per nest = 16.5%). Using the aggregate average sizes of all nest queens and workers, the size difference was 11.8% (Kruskal-Wallis $X^2 = 9.56$, $p < 0.01$), while the difference was 8.4% in the pan-trapped bees (Kruskal-Wallis $X^2 = 27.90$, $p < 0.0001$). Despite these differences in average body size, there was still considerable overlap in the size distributions of queens and workers; in particular, many queens that were active before worker emergence, were actually worker-sized.

Figures 3 and 4 demonstrate that many workers had developing ovaries. We further classified workers as non-reproductives (OD = 0 or 0.1) or as reproductives (OD ≥ 0.25). Among 80 nest workers dissected, 47 (59%) were reproductive and 33 (41%) were non-reproductive. Among 97 pan trap workers dissected, 27 (28%) were reproductive and 70 (72%) were non-reproductive. These proportions were significantly different ($X^2 = 17.223$, df = 1, $p < 0.0001$ with Yates correction), indicating a higher proportion of reproductive workers among nest bees. Among workers in which the spermatheca could be clearly seen upon dissection (nest and pan trapped specimens pooled), a significantly greater proportion of reproductive workers were mated (26/51 = 51%) compared to non-reproductive workers (9/38 = 24%; Yates $X^2 = 5.704$, df = 1, $p = 0.017$).

We then compared both head width and wing wear for nest and pan trapped bees combined, as well as mandibular wear for nest bees (Figure 5). Overall, non-reproductive and reproductive workers did not differ in size (Kruskal-Wallis $X^2 = 0.56$, ns.). However, there was a body size effect on ovarian development among reproductive

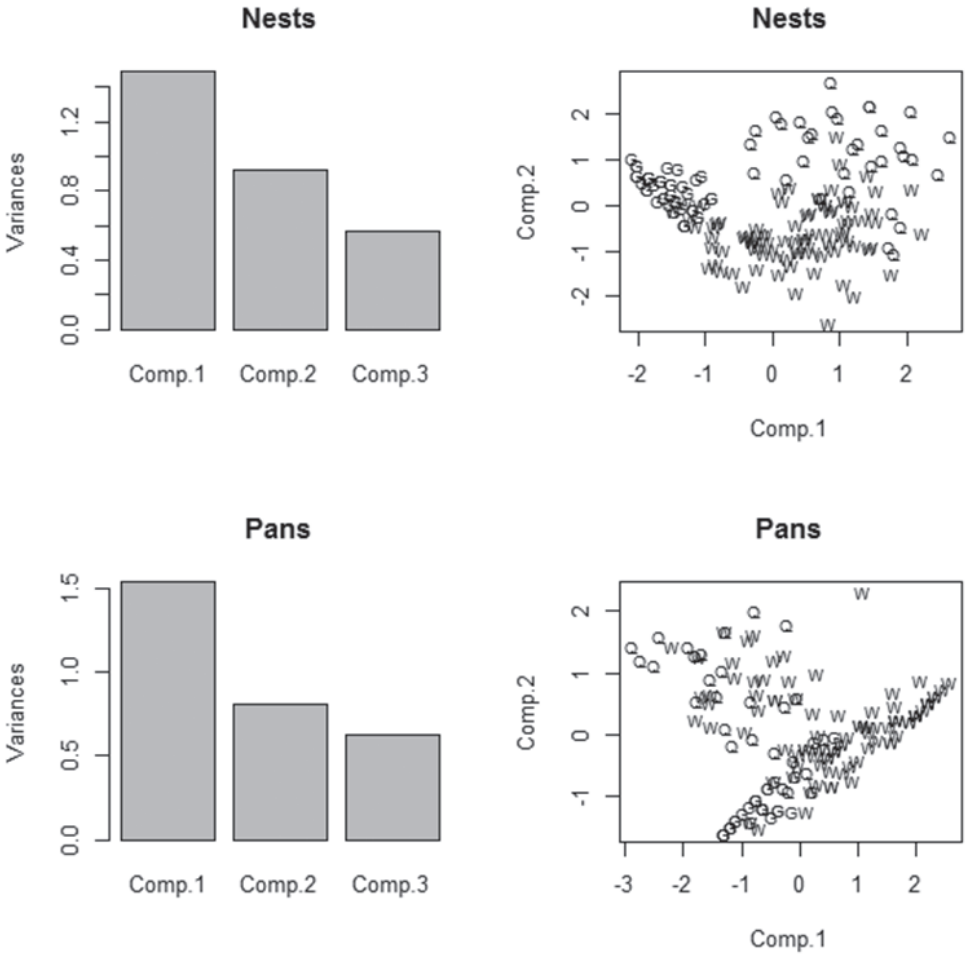

Figure 3. Principal components analyses (PCA) indicating caste differentiation and supporting caste classifications of female *Halictus ligatus* collected in nests and pan traps. The histograms are scree plots indicating the significance of the first three prinicipal components for each analysis. The scatterplots indicate the relationship between the first two principal components for each analysis. PCA for nest bees was based on head width, total wear, and ovarian development, while that for pan trap bees was based on head width, wing wear, and ovarian development. Note the greater separation among queens (Q), workers (W), and gynes (G) in the nest sample.

workers, with larger females having significantly higher ovarian scores than smaller females ($F = 18.32$, $df = 1,72$, $p < 0.0001$).

Non-reproductive workers exhibited significantly higher wing wear scores, indicating that they flew more than reproductive workers (Kruskal-Wallis $X^2 = 42.11$, $p < 0.0001$). However, they did not have significantly different mandibular wear scores (Kruskal-Wallis: $X^2 = 0.77$, n.s.), suggesting that both non-reproductive and reproductive workers excavated brood cells and nest tunnels.

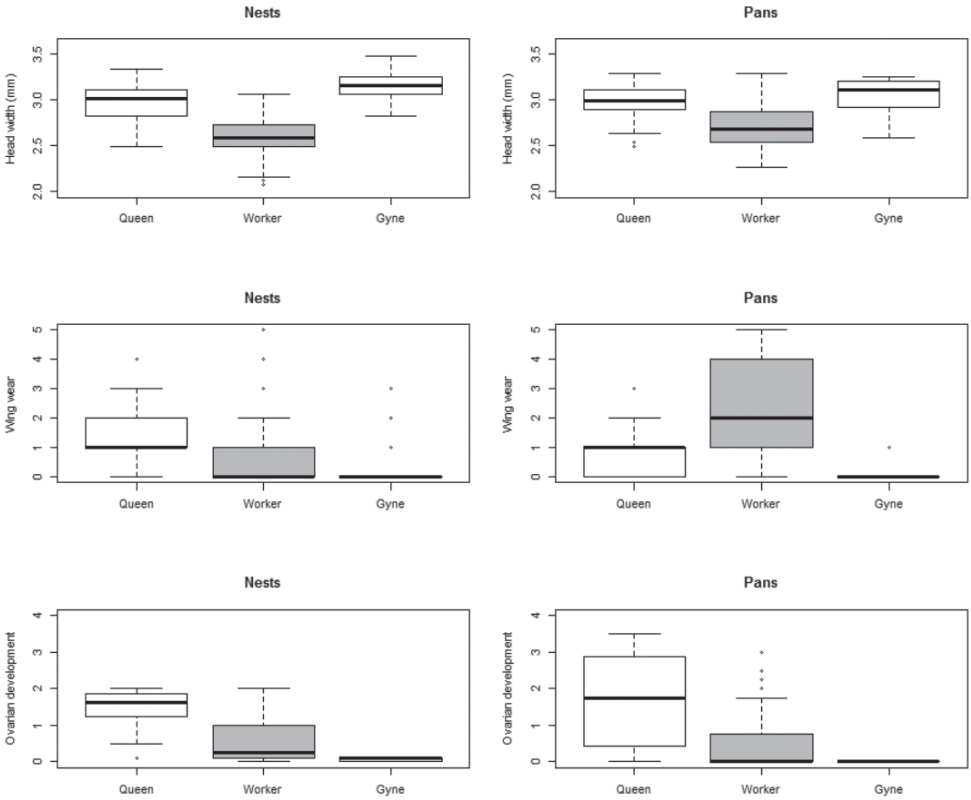

Figure 4. Variation in head width, wing wear, and ovarian development among *H. ligatus* queens, workers, and gynes collected in nest excavations and pan traps in 2006. Box plots represent means and quartiles, with unfilled circles indicating outliers. Gynes were classified by their lack of wear or ovarian development (as well as by time of emergence), and are included here to emphasize the phenotypic differences among the three groups of females.

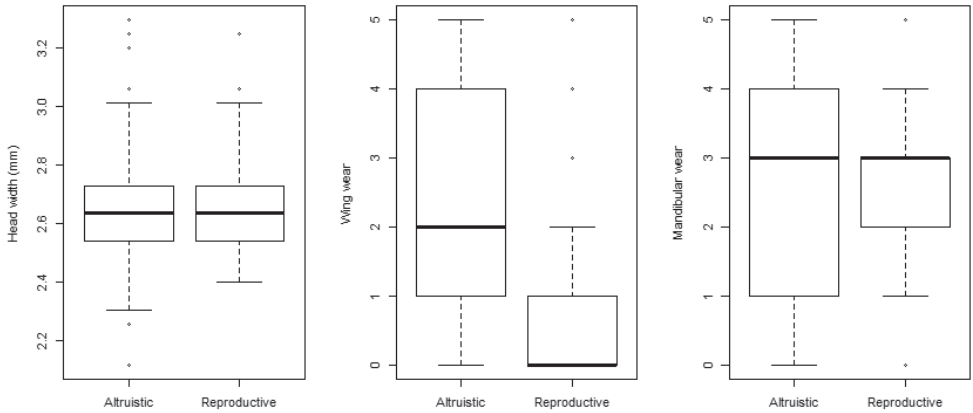

Figure 5. Size and wear distributions compared between altruistic, non-reproductive (OD = 0 or 0.1) and reproductive workers (OD ≥ 0.25).

Discussion

Phenological and social variation in *Halictus ligatus*

The colony cycle of *Halictus ligatus* was typical for this species and most temperate, eusocial halictids (Litte 1977, Packer 1986a, Richards and Packer 1995). Foundress queens established nests in spring, provisioned Brood 1, then remained inside their nests for the remainder of the breeding season. Across the population, Brood 1 comprised 90% workers and 10% males. After emerging as adults, workers provisioned a brood of gynes and more males, which mated prior to the onset of gyne hibernation in late summer and early autumn.

Table 3 summarizes phenological and colony traits of the St. Catharines and Victoria populations. The most obvious differences between the populations are phenological. As predicted, foundress queens in the St. Catharines population initiated reproductive activities, including nest construction and brood provisioning, considerably earlier than in Victoria. In St. Catharines, the first foraging queens were pan trapped on 1 May in 2006, and this is not unusual at our study sites- in 2012, we collected a *Halictus ligatus* queen on 22 March, during an unusually early warm spell when many bees left their hibernacula (R. Kutby and M. Richards, unpub. data).

We predicted that earlier initiation of brood production in St. Catharines would result in a longer Brood 1 provisioning period, allowing queens time to produce more workers, eventually resulting in larger colony sizes. Spring nest initiation and brood provisioning by foundress queens, as well as worker emergence, were indeed considerably earlier in St. Catharines than in Victoria. In 2006, St. Catharines temperatures were warmer than average from January to July, which likely encouraged foundresses to initiate even earlier than usual. However, the nest excavation data indicated that contrary to prediction, Brood 1 was somewhat smaller in St. Catharines (Table 3). Since St. Catharines queens started and finished provisioning the worker brood earlier than in Victoria, but ended up with fewer brood, the length of spring may not be the proximate factor influencing brood size. More likely, spring resource (pollen and nectar) availability, mediated by local weather conditions, dictates annual brood size. Another possibility is that the average number of workers is more or less set within a population, such that queens produce enough workers to ensure eventual production of a reproductive brood. This has been suggested for another obligately eusocial sweat bee, *Lasioglossum malachurum*, in which average size of the first worker brood is remarkably similar in much of Europe (Knerer 1992). Moreover, differences in temperature induce intra-population variation in *L. malachurum* nesting phenology (warmer nests are earlier), but not intra-population variation in colony size (i.e. number of workers in Brood 1; Strohm and Bordon-Hauser 2003). Perhaps variation in the numbers of workers produced has more to do with the local availability of pollen and nectar resources, than with the timing of nest initiation.

A possible consequence of the longer breeding season in St. Catharines was lower survival of queens past the peak of reproductive brood (Brood 2) production in August

Table 3. Colony social parameters compared between *Halictus ligatus* aggregations in St. Catharines, Ontario (current study) and Victoria, Ontario (Packer 1986; Richards et al. 1995; Richards and Packer 1995, 1998). All values are based on specimens collected in nest excavations.

Phenological or social trait	St. Catharines 2006	Victoria 1984, 1990–91
Earliest spring foragers (queens)	1 May	21 May
Earliest summer foragers (workers)	14 June	8 July
Queen survival to peak production of Brood 2	31% (maximum)	45–65%
Proportion of pleometrotic nests	7.1%	10%
Size of Brood 1 (n)	5.1	5.8–9.0
Sex ratio of Brood 1 (% males)	9.5%	5–15%
Number of Brood 1 females (n)	4.7	5.2–8.5
Average no. of adult workers in summer	3.9	≤4.5
Size of Brood 2 (n)	7.9	12–15
Sex ratio of Brood 2 (% males)	31%	45%
Queen–worker size difference[1]	16.5%	11.4–15.8%
Proportion of nest workers mated	39%	42–52%
Proportion of nest workers with developing ovaries[2]	59%	60%

[1] Comparing queens to the workers in their own nests.

[2] Worker OD ≥0.25.

than observed in Victoria (Table 3). Lower survival of queens may explain why the proportions of mated nest workers with developing ovaries were so similar in the two populations. Although the queen-worker size difference was larger in St. Catharines, the relatively early deaths of many queens would have led to increased opportunities for workers to lay eggs that would have produced males and gynes in Brood 2. Thus the prediction that milder environmental conditions in St. Catharines would be associated with increased worker reproduction is supported, but not for the reasons predicted, namely increased colony sizes and a concomitant decline in queen control of worker behaviour. Rather, early queen mortality makes it possible for relatively large numbers of workers to become the primary reproductives in colonies, especially late in summer.

The frequency of pleometrotic nest-founding varies intra-specifically in *Halictus ligatus*. In the current study, the rate inferred from inspection of nest contents in St. Catharines was about 7%, while in Victoria, the average was similar and varied considerably from year to year (Richards and Packer 1998). We found only one nest that contained two live foundresses, but strong circumstantial evidence for pleometrosis in others. In *H. ligatus*, pleometrosis is probably an accidental by-product of overwintering behaviour; gynes hibernate beneath their natal nests, often in the same tunnel, and likely encounter each other in spring (Richards and Packer 1998). When associations form between gynes that are quite different in size, the large one becomes dominant and behaves like a queen, while the smaller ones become subordinates that behave like workers (Packer 1986b). The frequency of pleometrosis may be influenced by environmental factors that influence whether worker-sized females successfully overwinter. In St. Catharines, the relatively early mortality of queens may afford females produced

in Brood 1, especially late-emerging ones, more frequent opportunities to enter hibernation. First brood females with fewer fat stores than second brood females may be less likely to survive hibernation (Richards and Packer 1994), but their overwintering survival might be higher in places like St. Catharines with milder winters.

Production of gynes in the first brood is well documented in the facultatively eusocial sweat bee, *Halictus rubicundus* (Yanega 1989), but in obligately eusocial bees production of large gynes before small workers within a single nest appears to be rare. This phenomenon has not previously been reported for *H. ligatus*, but has been observed in another obligately eusocial species, *Lasioglossum malachurum* (Wyman and Richards 2003). Although it is always possible that undetected errors in nest excavation underlie such observations, there are plausible behavioural explanations. First, egg-layers may occasionally make mistakes about the sex of the offspring for which a provision mass has been provided. Although *H. ligatus* provision masses for gynes and males differ in both size and shape (Boomsma and Eickwort 1993), females may sometimes deposit diploid eggs on male provision masses, and the resulting female would be worker-sized. Such errors might be relatively frequent in colonies where conflict over oviposition between queens and reproductive workers may result in one female substituting her own egg for another, increasing the likelihood that a female egg is mistakenly laid on a male provision mass. Another possibility is that production of late workers is adaptive in areas where foraging seasons are long, particularly where they are longer than the average lifespan of queens. Queen production of late workers could be an insurance strategy that extends both brood care and brood production as long as provisions can be gathered.

Are there two kinds of workers in *Halictus ligatus*?

In eusocial halictids, the potential for worker reproduction is well known, and in almost all known eusocial species, dissections of workers or genetic studies of relatedness suggest the potential for worker reproduction (Packer and Knerer 1985, Packer and Owen 1994, Paxton et al. 2002, Yagi and Hasegawa 2012). Several of these studies indicate that relatively large numbers of workers have developing ovaries but that queens are often highly successful at preventing worker maternity, probably because they remove most worker-laid eggs by eating them (Michener and Brothers 1974). In both the Victoria and St. Catharines populations of *H. ligatus*, almost two-thirds of workers had developing ovaries and some workers had as much ovarian development as queens. Moreover, in the current study, reproductive workers were more frequent among nest bees, which include both foragers and non-foragers. Workers with no ovarian development, some of which must have been altruistic workers provisioning brood for queens, were proportionately more frequent among pan trapped bees, which are foragers. Body size did not predict which workers would have developed ovaries, but among workers with ovarian development, larger individuals had more and larger oocytes, a pattern also observed in *H. tripartitus* (Packer et al. 2007a). Also, workers with

ovarian development were less worn and more likely to be mated than those with no ovarian development. What determines which *H. ligatus* workers will become altruistic or reproductive? Body size is not a good predictor (Richards and Packer 1996). Queen viability is also not a good predictor, as we find reproductive workers in nests with viable queens, as well as in queenless nests. We propose that production of both altruistic and reproductive workers is actually a strategy by queens to maximize colony brood production.

Worker reproduction in eusocial sweat bees and other social insects is often conceptualized in terms of queen-worker reproductive conflict, with worker reproduction resulting from the failure of queens to completely suppress worker oviposition (Schwarz et al. 2007). However, worker egg-laying might actually be favoured by queens when queens cannot produce eggs fast enough to utilize all the brood provisions brought to nests by workers. Most halictid queens probably cannot lay more than two eggs per day; we have dissected many hundreds of individual females of several species (*Halictus ligatus*, *Halictus confusus*, *Halictus sexcinctus*, and *Lasioglossum malachurum*) and have never observed one with more than two fully developed oocytes (M. Richards, pers. obs.). Egg limitation may mean that queens are unable to utilize all available brood provisions, at times when these are being brought to the nest at a rate allowing more than two eggs per day to be provisioned. Under these circumstances, queen fitness is actually enhanced by worker reproduction. On the other hand, it is certainly in a queen's interest that at least some of her daughters behave as altruistic workers, as queens can produce far more reproductive offspring with worker help than without it (Strohm and Bordon-Hauser 2003, Richards et al. 2005). How a *H. ligatus* queen could bias the developmental programs of her worker-brood daughters is unclear, but in the facultatively eusocial sweat bee, *Megalopta genalis*, there seem to be inherent differences among workers that will become altruistic helpers versus those that have the potential to become egg-layers (Kapheim et al. 2012). Possibly, *H. ligatus* queens nutritionally bias the developmental programs of worker-brood females such that some larvae are more likely to develop into "reproductively suppressable", altruistic workers that will help raise the queen's reproductive brood, while others are more likely to develop their ovaries when circumstances favour worker egg-laying (Richards and Packer 1994, Kapheim et al. 2011). Under such a scenario, higher rates of worker reproduction would be expected when queens cannot or do not suppress worker reproductivity.

Halictus poeyi is the morphologically cryptic sister species of *Halictus ligatus*. It has a much more southerly distribution, including subtropical and tropical regions (Dunn et al. 1998). Mature colonies of *H. poeyi* reach sizes much larger than those of *H. ligatus* colonies in southern Ontario (Michener and Bennett 1977, Packer and Knerer 1986). Workers are also larger, so queen-worker size dimorphism is relatively low. Predictably, rates of worker reproductivity in *H. poeyi* are high (Michener and Bennett 1977). Thus both *H. ligatus* and *H. poeyi* share the behavioural tendency for some workers to become egg-layers when colonies outstrip the ability of queens to monopolize oviposition.

Nest excavations versus pan traps

The second major objective of this paper was to use pan trap collections as a source of information about demographic and social parameters important in assessing intra-specific social variation. Clearly, the best option for sociobiological data collection is to observe nest occupants in order to quantify behavioural interactions among nestmates and the nature of colony social organization. Unfortunately, nesting aggregations of eusocial sweat bees are difficult to find even where the bees are very common, so nest-based study is often impossible. The alternative is to collect bees outside their nests. For instance, Dunn et al. (1998) compared several sociobiologically important traits of *Halictus ligatus* and *H. poeyi* in their zone of sympatry, using bees netted on a biweekly schedule throughout the flight season. This allowed Dunn et al. to infer the phenology of colony development (e.g. when females fly, when males emerge, etc.) and to collect females for dissection and body size measurements. Pan trapping presents the possibility for a further refinement of this approach, because it is less time-consuming and more or less eliminates collector bias. Pan trapping data have been used to supplement nest excavation data in several behavioural studies of *Halictus confusus* (Richards et al. 2010) and *Ceratina* (Rehan and Richards 2010, Vickruck et al. 2011), and were the sole source of data in a study on *H. tripartitus* (Packer et al. 2007a).

To what extent can we rely on pan trap data when nest data are completely unavailable? Some sociobiologically important information, namely data on colony sizes, numbers of workers, colony-specific sex ratios, and nestmate relatedness, simply cannot be obtained from specimens collected with pan traps; observations and collections from colonies are required. In our study, there was very close agreement between pan traps and nest collections in the timing of major events in colony development, such as Brood 1 provisioning by queens, Brood 2 provisioning by workers, and emergence of male and female brood. Our previous studies also showed good phenological agreement based on nest and pan data (Richards et al. 2010, Rehan and Richards 2010, Vickruck et al. 2011). The advantage of the pan traps was that sample sizes were larger and collection effort was much less. However, in the current study, nest excavations suggested that brood provisioning was over by about week 19, whereas we collected foraging workers until week 23. This discrepancy could indicate that many bees continue foraging for themselves even after brood provisioning has ceased, but is more likely a sample size effect: we excavated relatively few nests per week (e.g. 6 in week 19) and from a single aggregation, whereas the pan traps were likely sampling bees from a wider area. Foraging workers from very late nests might be relatively rare, but given the large sampling area covered (trapping sites were up to a km apart) might be quite likely to be collected in pan traps. This suggests that the traps provided more precise information about timing of bee flight activity. Some subtle effects, such as the correlation between body size and ovarian status in reproductive workers detected in this study and in *H. tripartitus* (Packer et al. 2007b) may only be detectable with the very large sample sizes often collected in pan traps.

Other sociobiologically important parameters critical for comparing colony social organisation among populations or species, such as the proportion of mated workers, the proportion of workers with ovarian development, caste size dimorphism, and the Brood 1 sex ratio can also be obtained from pan trapped specimens. A second sociobiologically important parameter that is rarely estimated is Brood 2 sex ratio, which is difficult to measure because nest excavations rarely obtain complete second broods. We obtained good agreement between the Brood 1 sex ratio derived from nests (proportion of males, 9.5%) and that derived from pan traps (8.3%). However, the Brood 2 sex ratios derived from nests (31% males) and pan traps (65% males) were quite disparate, and it is difficult to determine which sex ratio is more accurate. The nest estimate may be biased by broods that were not complete at the time of excavation, either because the youngest brood had not yet been produced or because the oldest had already emerged and dispersed. However, both pan trapping and sweep netting probably underestimate the numbers of gynes in the population, because gynes enter hibernation shortly after emergence, whereas males spend the rest of their lives searching for flowers and females and thus are more likely to be trapped. In the current study, the Brood 2 sex ratio of 65% males based on pan traps was likely an over-estimate, because individual males had more chances to be caught.

For some kinds of demographic information, the pan trap data were arguably superior to the nest excavation data, because the use of a standardized pan trap protocol makes it possible to infer relative abundances of different groups of individuals across years or species. For instance, we can compare the pan trapping patterns and phenology of different species caught in the same pan traps, as this may reveal sociobiologically relevant, interspecific variation for species living in close proximity. To illustrate, we compare *Halictus ligatus* to *Halictus confusus* (Figure 6), another eusocial sweat bee that we studied at the same sites in 2006 (Richards et al. 2010). Comparison of pan trap collections reveals contrasting patterns in the two species. In *H. ligatus*, many queens were caught in spring, relatively few workers were caught in summer, and then many gynes were caught in late summer. In *H. confusus*, relatively few queens were caught in spring, many workers were caught in summer, and few gynes were caught in late summer. Although seasonal differences in floral abundance might influence the relative trappability of queens and workers within species (see below), it is unlikely that the overall differences in the patterns illustrated in Figure 6 are due simply to trappability bias caused by caste and species-specific responses to pan traps. More likely, the differences in pan trap "syndromes" reflect real differences in demography and colony social organization. For *H. ligatus*, the large numbers of queens followed by small numbers of workers suggest high rates of queen mortality and nest failure. For *H. confusus*, the large peak in female abundance at the time of worker provisioning of Brood 2, followed by a low abundance of gynes later in the summer, suggests the possibility of differential diapause by Brood 1 females, which instead of helping to raise Brood 2, begin hibernation in mid-summer, preparatory to founding nests the following spring (Yanega 1988, 1989).

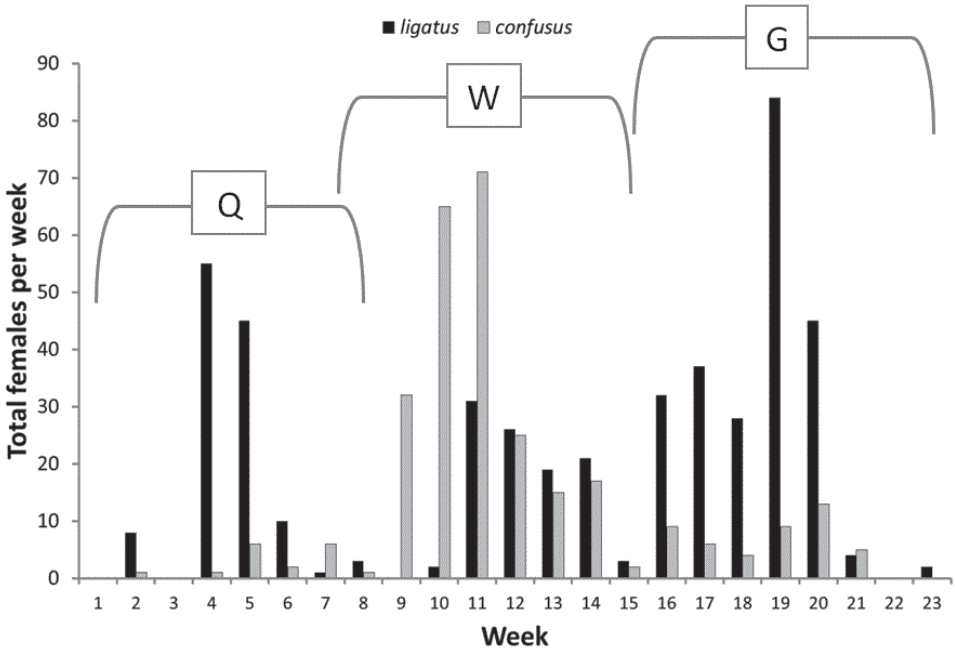

Figure 6. Comparison of pan trapping phenologies of *Halictus ligatus* and *H. confusus* collected at the same sites in 2006. The three main flight periods are indicated, for queens (**Q**), workers (**W**), and the late summer mix of workers and gynes (**G**). Note the differences between species. In *H. ligatus*, more females were caught towards the end of the flight season (the gyne flight period), whereas in *H. confusus*, more females were caught in the middle of the flight season, during the worker foraging period. Week 1 was the last week of April, and week 11 was the first week of July.

A disadvantage of pan traps is that their attractiveness to bees seems to be inversely proportional to blossom availability (Cane et al. 2000, Baum and Wallen 2011). In our study sites, flowers were much less abundant before week 6 than after, so early-foraging queens may have been more attracted to pan traps than late queens or workers. It is also possible that early and late workers were differentially trappable. However, biases caused by differential trappability over time would mainly bias temporal analyses of abundance, which were not a part of this study. In fact, differences in trappability among different sets of individuals may sometimes be informative, as in the contrasting proportions of non-reproductive workers among nest and pan trapped samples, which supported the contention that non-reproductives are altruistic workers that were more likely to forage (and be trapped) than reproductive workers.

Conclusions

Based on previous studies of geographical and annual variation in colony social organisation of *Halictus ligatus*, and evidence that this was due to local climatic variation,

we predicted that in St. Catharines, the longer flight season would translate into earlier nest initiation, larger colony sizes and lower reproductive skew. Although earlier springs in St. Catharines clearly resulted in early nest initiation, the result seems to have been to shift the entire first phase of colony development forward, with no more workers being produced than if nests had been initiated a month later, as they were in Victoria. One reason for this may be that earlier onset of spring in St. Catharines is not associated with an increase in floral resources; ultimately the number of brood that a foundress queen produces may have more to do pollen and nectar availability than with temperatures. Within sites, warmer temperatures may be associated with increased floral resources, as seems to have been true in Victoria (Richards 2004), but this relationship is not necessarily true for comparisons between sites.

Earlier colony initiation in St. Catharines does not seem to have resulted in early completion of flight and nesting activity, so overall, the bee activity season was considerably longer than in Victoria. The longer colony season helps to explain why measures of queen-worker interactions and reproduction, such as the proportions of reproductive workers, were similar in the two sites and time periods, despite the phenological differences. This does not mean there were no behavioural differences between the sites. In St. Catharines, queens had fewer workers to contend with but died relatively sooner in the colony cycle, and the net result was rates of worker reproductivity as high as in Victoria. Another possible behavioural difference may be indicated by the observation that many St. Catharines queens were worker-sized. It is possible that extended flight seasons coupled with milder winters allow a greater proportion of worker-sized females to overwinter and found nests the following spring. Interestingly, the observed rate of pleometrosis was no higher in St. Catharines than in Victoria so higher overwintering survival for small females did not translate into higher rates of subordinacy in spring multifoundress assemblages. Global climate change will likely mean that nesting seasons for temperate bee populations become even more extended, affording late workers even more opportunities for reproduction.

We found that pan trapping bees throughout the breeding season was a useful complement to collections based on nest excavations. There was good phenological agreement between nest data and trap data, while pan trap data provided much larger sample sizes for assessing caste-related variation in size, wear and ovarian development. Nest-based studies (e.g. Yanega 1989, 1990) provide a "gold standard" for revealing many crucial aspects of social behaviour in insects, because they allow us to infer colony social organisation and the consequences of interactions among nestmates. But when nests are difficult to find in large enough numbers to justify excavating and destroying them, sociobiological studies based on pan trapped specimens generate inferences about colony social organization and female reproductive behaviour that are a viable alternative. The study of *Halictus tripartitus* by Packer et al. (2007), which was based solely on pan-trapped specimens, is an excellent example of how our understanding of bee social behaviour can be advanced even when colonies cannot be found. We hope that the increasing use of pan trapping studies, including those aimed primarily at assessments of bee community abundance and diversity, will generate additional

specimens that can be used for studies of intra- and inter-specific social variation in what is arguably the most critical taxon for understanding the origins and extinctions of sociality in insects.

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Key to Nearctic species of *Trissolcus* Ashmead (Hymenoptera, Scelionidae), natural enemies of native and invasive stink bugs (Hemiptera, Pentatomidae)

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Abstract

Trissolcus japonicus (Ashmead) and *T. cultratus* (Mayr), **comb. rev.** are under study as classical biological agents to control the brown marmorated stink bug *Halyomorpha halys* (Stål) in North America. Here we present diagnoses for all Nearctic species of *Trissolcus*, including *T. japonicus* and *T. cultratus* **comb. rev.**, and identification keys to enable separation of these species from the existing fauna. *Trissolcus cultratus* **comb. rev.** is removed from synonymy with *T. flavipes*. Two new species are described, *Trissolcus valkyria* **sp. n.** and *T. zakotos* **sp. n.** A neotype is designated for *T. brochymenae* and a lectotype is designated for *T. basalis*.

Keywords

Trissolcus japonicus, *Trissolcus cultratus*, *Trissolcus flavipes*, *Halyomorpha halys*, *Trissolcus*, Scelionidae, biological control, identification key, egg parasitoid

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Introduction

A decade after its introduction into the United States in 1999, the economically destructive brown marmorated stink bug (BMSB), *Halyomorpha halys* Stål (Heteroptera: Pentatomidae), has been detected in 39 US states and the District of Columbia, as well as Canada, Switzerland, Germany, France, and Italy, and has been intercepted in New Zealand (Xu et al. 2013). BMSB has an extraordinarily wide host range in both its native range (Asia) and invaded countries where it feeds on over 200 species of tree fruits, vegetables, field crops, ornamental plants, and native vegetation (Hoebeke and Carter 2003; Leskey et al. 2012). Some notable crops attacked include fruit trees (especially apples and pears), corn, wheat, soybean, and grape. In the US in 2010, $37 million in losses to mid-Atlantic apples was recorded; in some pear orchards 100% loss was observed (Leskey et al. 2012). Further, BMSB is a well-known nuisance species, invading homes and businesses in the mid-Atlantic region, with over 25,000 individuals being recorded from a single household (Inkley 2012).

BMSB is difficult to manage with pesticides because it feeds on interior plant tissues via its proboscis, bypassing ingestion of pesticides that are deposited on the surfaces of plant tissues. As a result, increased pesticide applications to combat BMSB disrupt ecosystem services, resulting in secondary pest outbreaks (Leskey et al. 2012). Xu et al. (2013) determined that a single introduction to North America from the Beijing area of China, with secondary migration to the West Coast, is responsible for the presence of this destructive pest. Due to the difficulty and potential non-target effects of controlling this pest with pesticides, foreign exploration of natural enemies of BMSB began in earnest in 2008, with the Beijing area of China as a focal point of collections, followed by additional collecting in South Korea and Japan (Xu et al. 2013). These collections have identified two species with potential as classical biological control agents. Both species were initially referred to by incorrect names, and through the examination of primary type specimens, we have identified them as *Trissolcus japonicus* (Ashmead) and *Trissolcus cultratus* (Mayr), comb. rev. A community of extension agents, field scientists, and ARS scientists (at the Beneficial Insects Introduction Research Unit and Systematic Entomology Laboratory), are presently studying the host preferences of *T. japonicus*, *T. cultratus*, and native species of *Trissolcus*, and the ability of these species to successfully develop in BMSB eggs. However, such studies are ineffective unless the species can be distinguished reliably – a task that may be challenging for non-experts due to the small size of these insects and their defining characters, as well as historical taxonomic confusion of species.

This paper is presented as an updated synthesis of the works of Norman Johnson (1984, 1985a,b) with the addition of four species, *T. japonicus*, *T. cultratus* comb. rev., *T. valkyria* sp. n. and *T. zakotos* sp. n., and previously unexplored or unutilized character systems. Following the keys to species, an updated and expanded diagnosis section provides more nuanced discussions on sexual dimorphism and phenotypic plasticity. The authors hope that this publication will demonstrate the long-term relevance of primary taxonomic research. The concepts of the previously described spe-

cies presented here are based primarily on the works of Johnson (1984, 1985a,b), as are many of the characters used in the identification keys and character data reported in the diagnoses. Without these publications, preparation for the introduction of an exotic species would require revision of the Nearctic fauna to establish the characters by which the introduced species could be recognized. Production of the identification tools provided here would not have been possible within the time frame of the USDA-ARS biocontrol release project, nor is there sufficient funding for revisionary work on *Trissolcus* in *both* the Nearctic and the Eastern Palearctic, from which *T. japonicus* and *T. cultratus* comb. rev. originate. The revision of the latter is underway.

Although it may be impossible to fully predict which species will become introduced pests, educated decisions can be made about which species have the greatest potential, and similarly, which species have potential as biological control agents. While this paper was in review, a wild population of *T. japonicus* was discovered in Beltsville, Maryland (Talamas et al 2015), which we were able to rapidly identify with the tools we produced for exactly this purpose. We believe that this emphasizes the utility of alpha taxonomy and the need for continued revisionary work in Platygastroidea.

The identification keys of Johnson (1984, 1985a,b) remain relevant for the Nearctic species and the dichotomous key presented here largely follows their structure. The goals of this publication are to document the Nearctic fauna as completely as possible, and to provide identification tools with high resolution color illustrations that should greatly facilitate species-level identification. Two formats for this identification key are given: a traditional dichotomous key, and a multi-choice Lucid key[1].

The contributions of the authors are as follows: E.J. Talamas: character definition and coding, imaging, manuscript preparation; N.F. Johnson: character definition and coding, manuscript preparation; M. Buffington: manuscript preparation, project coordination.

Materials and methods

The locality data reported for primary types are not literal transcriptions of the labels: some abbreviations are expanded; additional data from the collectors are also included. The numbers prefixed with "USNMENT" or "OSUC " are unique identifiers for the individual specimens (note the blank space after some acronyms). Details on the data associated with these specimens may be accessed at the following link, http://purl.oclc.org/NET/hymenoptera/hol, and entering the identifier in the form. The taxonomic synopsis was generated by the Hymenoptera Online Database (http://hol.osu.edu).

Persistent URIs for each taxonomic concept were minted by xBio:D in accordance with best practices recommend by Hagedorn et al (2013).

Morphological terms were matched to concepts in the Hymenoptera Anatomy Ontology using the text analyzer function. A table of morphological terms and URI links is provided in Suppl. material 1.

Photographs were captured with a Z16 Leica®™ lens with a JVC KY-F75U digital camera using Cartograph®™ software, or a Leica®™ DMRB compound microscope with a GT-

Vision®™ Lw11057C-SCI digital camera attached. In both systems, lighting was achieved using techniques summarized in Buffington et al. (2005), Kerr et al. (2009) and Buffington and Gates (2009). Single montage images were produced from image stacks with the program CombineZP®™. In some cases, multiple montage images were stitched together in Photoshop®™ to produce larger images at high resolution and magnification. Full resolution images are archived at the image database at The Ohio State University (http://purl.oclc.org/NET/hymenoptera/specimage), MorphBank (http://www.morphbank.net), and Hymenoptera Holotypes of the Smithsonian Institution (http://usnmhymtypes.com).

High quality optics and bright, diffuse lighting are critical for observing the characters in this key. The authors recommend fluorescent desk lamps, or fiber optic lamps with mylar sleeves affixed to the tips of the light pipes, or a mylar 'shield' between the tip of the light pipes and the specimen. Direct illumination of the specimen should be avoided. Additionally, some characters are better observed with appendages moved (especially the legs in couplet 5 and the wings in couplet 6 of the *Trissolcus* species key). Fine forceps or a minuten pin achieve this effectively.

Collections

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

BMNH	Natural History Museum, London, England
CNCI	Canadian National Collection of Insects, Ottawa, Canada
NHMW	Naturhistorisches Museum Wien, Vienna, Austria
NHRS	Naturhistoriska riksmuseet, Stockholm, Sweden
OSUC	C.A. Triplehorn Insect Collection, Columbus, USA
USNM	Smithsonian National Museum of Natural History, Washington DC, USA
UANL	Facultad de Ciencias Forestales, Linares, Mexico
LACM	Los Angeles County Museum of Natural History, Los Angeles, USA
UCRC	Entomology Research Museum, Riverside, USA
MEMU	Mississippi State University
MSWC	M.S. Wasbauer Collection, Sacramento, USA
ANIC	Australian National Insect Collection, Canberra City, Australia
RMCA	Musee Royal de l'Afrique Centrale, Tervuren, Belgium
FSCA	Florida State Collection of Arthropods, Gainesville, USA

Character discussion

Axillar crescent

We coin this term to refer to the structure formed by the transaxillar, axillar, and axillular carinae located posterodorsal to the wing base (see Figs 1, 17, 19–20, 60, 62). The

transaxillar and axillar carinae are fused in *Trissolcus* and form the anterodorsal part of the axillar crescent. The axillular carina forms the posterior and ventral portion. Proper examination of this character may require removal or adjustment of the wings.

Clypeal setae

In the Nearctic fauna, species in the *basalis* and *thyantae* species groups have 6 clypeal setae (Fig. 27). *Trissolcus cultratus* and native species of the *flavipes* group have 2 (Fig. 23), making it easy to separate *T. japonicus*, which has 4 clypeal setae (Fig. 25). Rarely, and usually in males, superfluous clypeal setae exist. These are typically much smaller and arise near the base of one of the "true" clypeal setae. We consider the number of these setae to be extremely useful for identification of *T. japonicus*, but this character is variable.

Episternal foveae

The episternal foveae of the *thyantae* group are clearly defined; they extend from the dorsal limit of the acetabular carina to the mesopleural pit and are typically antero-posteriorly elongate. In the *basalis* group, the episternal foveae are often distinctly separate from the mesopleural pit, and with the exception of some *T. cosmopeplae*, are distinctly separate from the dorsal limit of the postacetabular sulcus. Nearctic species of the *flavipes* group tend to be variable in the external expression of this character. In most cases, the foveae are irregularly shaped and are at varying distances from both the mesopleural pit and acetabular carina. In the Eastern Palearctic species of the *flavipes* group the episternal foveae often appear as a continuation of the postacetabular sulcus and extend dorsally to the mesopleural pit as in *T. japonicus* (Fig. 70) and *T. cultratus*.

Facial striae

The presence of striae on the frons is typically weakly indicated or entirely absent, with a few exceptions. In some species the striae are present as shallowly incised short lines arising from the anterior articulation of the mandible (eg. *T. cultratus*, Fig. 54), and in a few, *T. radix*, *T. solocis* and *T. zakotos*, the striae exist as rugulae that extend further toward the compound eye (Fig. 112).

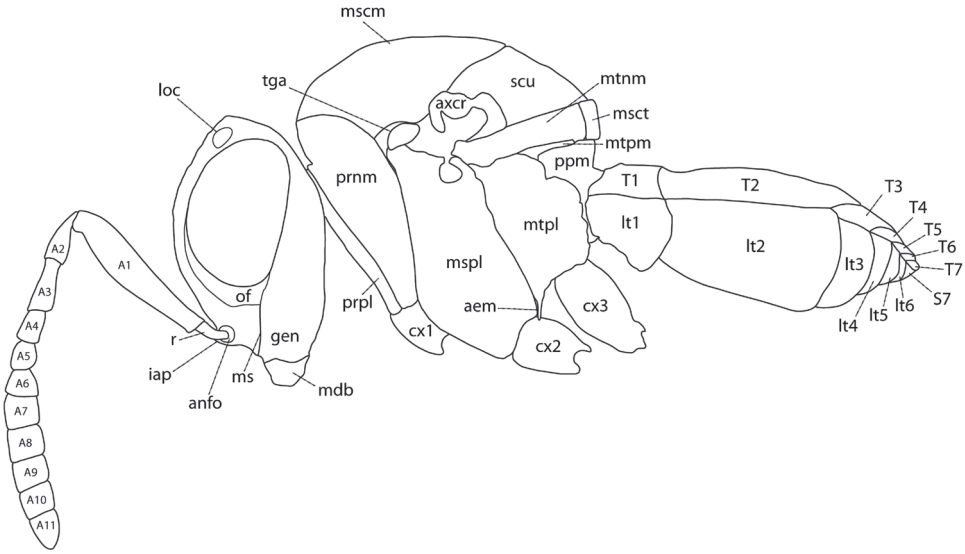
Mesopleural carina

The mesopleural carina was used more extensively for species identification in the key of Johnson (1984) than it is here. Specifically, we observed that in *T. edessae* this carina may be present (Fig. 58) and we no longer use its absence to separate this species. In the *thyantae* and *basalis* groups this character exhibits far less intraspecific variability than in the *flavipes* group and we use it for the identification and delimitation of *T. valkyria*.

Mesoscutal humeral sulcus

Among the published descriptions and diagnoses, we have not encountered previous use of this character for species-level delimitation in *Trissolcus*. In all but one species,

T. cosmopeplae, the form of this character is fixed. As stated by Johnson (1985), *T. cosmopeplae*, as currenly understood, is a highly variable species. We point out that most specimens of *T. cosmopeplae* examined for this key have a mesoscutal humeral sulcus present as a smooth furrow, and that in the holotype specimen this sulcus is comprised of distinct cells.



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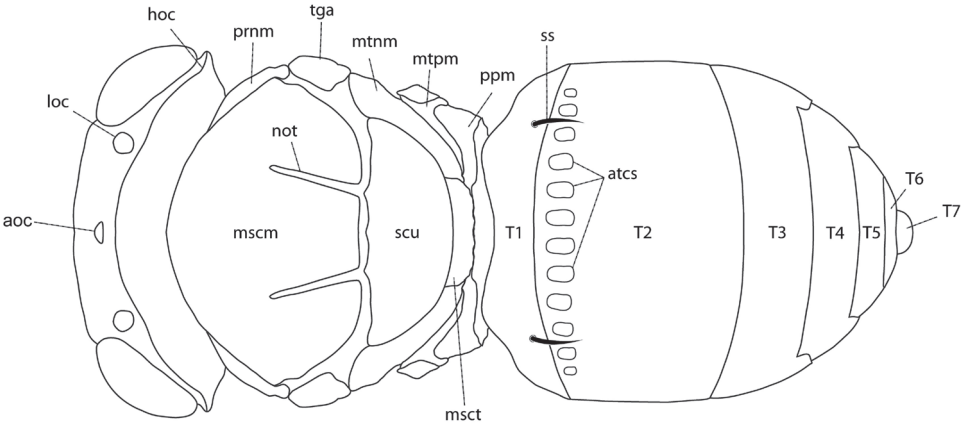

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Figures 1–2. 1 *Trissolcus*, lateral view **2** *Trissolcus*, dorsal view.

Characters annotations

A1–12	antennomeres 1–12 (Fig. 1)
ac	acetabular carina (Figs 43–44, 70)
aem	anteroventral extension of metapleuron (Figs 1, 43, 58, 82, 88)
anfo	antennal foramen (Fig. 1)
aoc	anterior ocellus (Fig. 2)
as	antennal scrobe (Figs 13, 26, 54)
atcs	antecostal sulcus (Figs 2, 29, 61)
ats	postacetabular sulcus (Figs 42, 70, 82)
axcr	axillar crescent (Figs 1, 17, 19–20, 60, 62)
bs	basiconic sensilla (Figs 8–9)
cs	clypeal setae (Fig. 23, 25, 27)
ctk	central keel (Figs 7, 10, 79)
cx1	procoxa (Fig. 1)
cx2	mesocoxa (Fig. 1)
cx3	metacoxa (Fig. 1)
eps	episternal foveae (Figs 35, 43, 48, 70, 82)
fs	facial striae (Figs 7, 10, 54, 112)
gc	genal carina (Figs 48, 112)
gen	gena (Fig. 1)
hoc	hyperoccipital carina (Figs 2, 19, 29)
iap	interantennal process (Fig. 1)
loc	lateral ocellus (Figs 1–2)
lt(s)	laterotergite(s) (Figs 2, 11–12)
mc	mesopleural carina (Fig. 43, 45, 58, 107)
mdb	mandible (Fig 1)
mmc	median mesoscutal carina (Fig. 39, 63)
mms	median mesoscutal sulcus (Fig. 93)
mpp	mesopleural pit (Figs 35, 43, 82)
ms	malar sulcus (Figs 1, 24, 26, 28)
mscm	mesoscutum (Figs 1–2)
msct	metascutellum (Figs 1–2, 21–22)
mshs	mesoscutal humeral sulcus (Figs 29, 30, 46, 49)
mspl	mesopleuron (Fig. 1)
mtnm	metanotum (Figs 1–2, 21–22)
mtpl	metapleuron (Fig. 1)
mtpm	metapostnotum (Figs 1–2, 21–22)
nes	netrion sulcus (Figs 44, 48)
not	notaulus (Figs 2, 29)
of	orbital furrow (Figs 1, 24, 26, 28–29, 71)
pcxs	paracoxal sulcus (Figs 82, 109)

ppm	propodeum (Figs 1–2, 21–22)
prnm	pronotum (Figs 1–2)
prpl	propleuron (Fig. 1)
pvm	posteroventral portion of metapleuron (Figs 17, 18, 20, 74, 106)
r	radicle (Figs 1, 37, 80, 112)
scu	mesoscutellum (Figs 1–2)
ss	sublateral seta (Figs 2, 30, 89)
T1–6	mediotergite (Figs 1–2)
tga	tegula (Figs 1–2)

Key to genera of Nearctic Platygastroidea known to attack pentatomoid eggs

The following key includes platygastroids with host records indicating emergence from pentatomoid eggs. More associations are certain to exist, particularly in *Telenomus*, which contains many species with undocumented biology, and many undescribed species.

1 Metasoma with laterotergites tightly appressed to sternites, forming a sharply angled lateral margin (Fig. 11); female antenna with 12 antennomeres (Fig. 11)..... ***Gryon obesum*** **Masner**

– Metasoma with laterotergites wide and loosely attached to sternites, metasoma without sharp lateral margin (Fig. 12); female antenna with 10 or 11 antennomeres **2**

2 Frons with central keel extending from interantennal process to anterior ocellus (Figs 7, 10); frons with facial striae distinct, striae often extending along inner orbit of compound eye (Figs 7, 10)..... **3**

– Frons without central keel or keel short, not extending to anterior ocellus (Figs 54, 79); frons without facial striae or, if present, sinuate and usually attenuating before reaching inner orbit of compound eye (Figs 54, 112) **4**

3 Mesoscutum with notauli (Fig. 5); base of metasoma usually yellow-orange and contrasting with dark color of posterior metasoma (Figs 3, 5); in lateral view, procoxa distinctly separated from mesocoxa (Fig. 3) .... ***Paratelenomus saccharalis*** **(Dodd)**

– Mesoscutum without notauli (Fig. 6); base of metasoma never yellow-orange (Fig. 4); in lateral view, procoxa contiguous with mesocoxa (Fig. 4) .... ***Psix tunetanus*** **(Mineo & Szabó)**

4 T2 longer than wide (Fig. 14); frons predominantly smooth and shining (Fig. 13); female antenna with basiconic sensilla on apical 4 (rarely 5 or 6) antennomeres (Fig. 9)..... ***Telenomus*** **(*T. astrictus*, *T. calvus*, *T. goliathus*, *T. grenadensis*, *T. persimilis*, *T. podisi*, *T. sanctiventris*, *T. scaber*)**

– T2 wider than long (Fig. 16); frons with microsculpture throughout, often superimposed on coarse surface sculpture (Fig. 15); female antenna with basiconic sensilla on apical 5 antennomeres (Fig. 8) ..... ***Trissolcus***

Figures 3–4. [21] **3** *Paratelenomus saccharalis*, female (USNMENT00896342), head, mesosoma, metasoma, lateral view **4** *Psix tunetanus* (USNMENT00989625), head, mesosoma, metasoma, lateral view. Scale bars in millimeters.

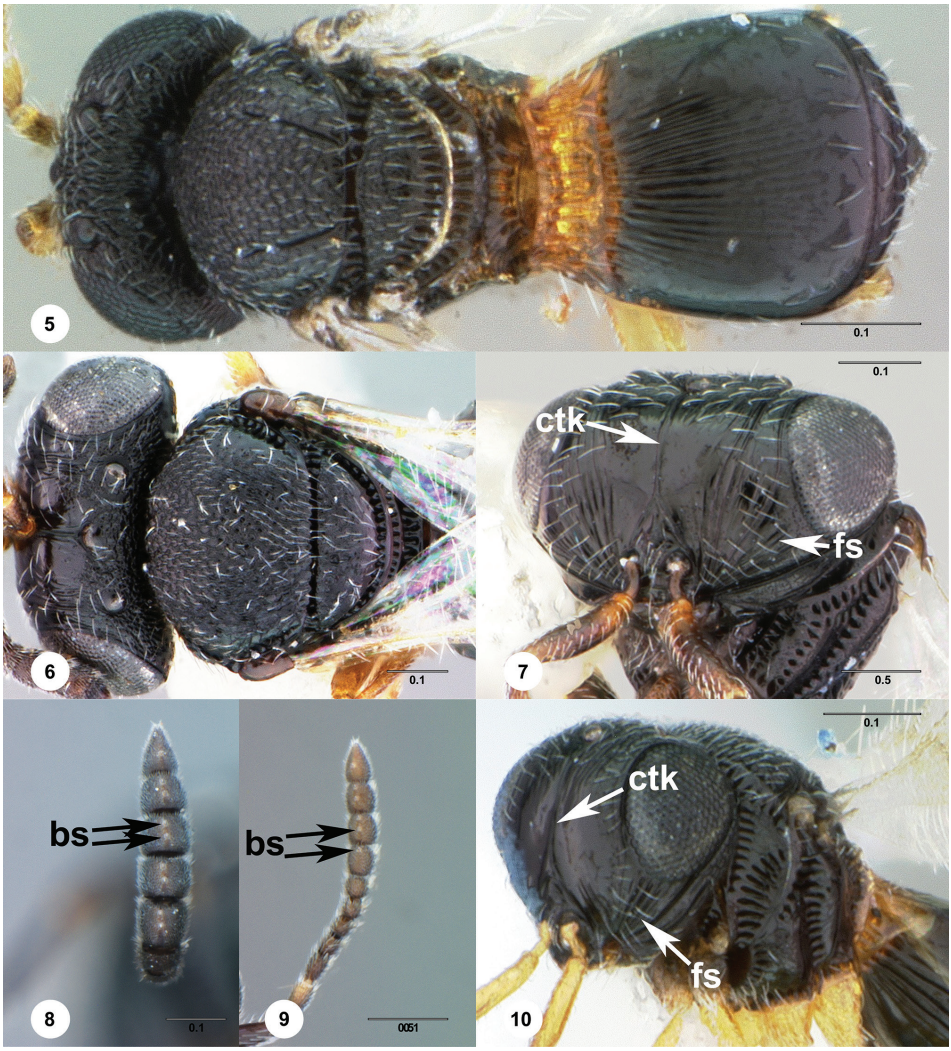
Key to species of Nearctic *Trissolcus* (males and females)

1 Metapleuron with posteroventral portion glabrous (Figs 17, 19–20).....**2**

– Metapleuron with posteroventral portion setose (Figs 18, 73–74, 76, 106)... .....(*thyantae* group) **15**

2 Vertex with hyperoccipital carina (Figs 19, 29, 64); mesoscutum with notauli (Figs 21, 29); clypeus with 4 or fewer setae (Figs 23, 25); inner margin of eye with orbital furrow not uniform in width, usually expanded near malar sulcus (Figs 1, 12, 15, 28) ..... (*flavipes* group) **3**

– Vertex without hyperoccipital carina (Fig. 30); mesoscutum usually without notauli (Fig. 30); clypeus with 6 setae (Fig. 27); inner margin of eye with



Figures 5–10. [22] **5** *Paratelenomus saccharalis*, female (USNMENT00896342), female, head, mesosoma, metasoma, dorsal view **6** *Psix tunetanus*, female (USNMENT00989625), head and mesosoma, dorsal view **7** *Psix tunetanus*, female (USNMENT00877258), head, anterior view **8** *Trissolcus strabus*, female (USNMENT00954423), antennal clava, ventral view **9** *Telenomus* sp., female (OSUC 523925), antennal clava, ventral view **10** *Paratelenomus saccharalis*, female (USNMENT00896364), head and mesosoma, anterolateral view. Scale bars in millimeters.

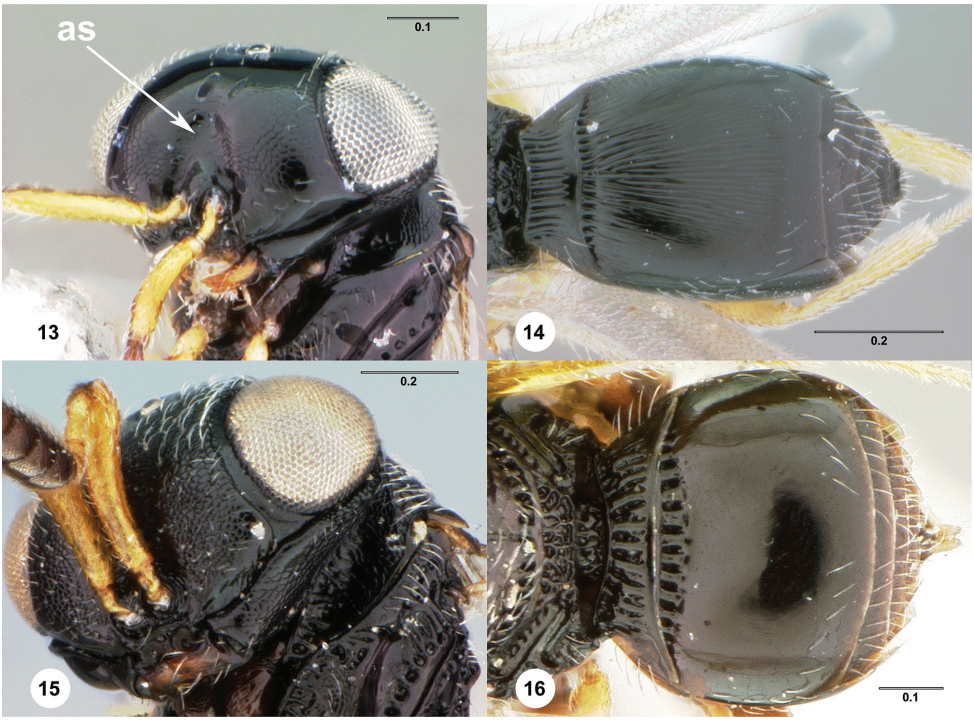
orbital furrow uniform in width, not expanded near malar sulcus (Fig. 24) .. ..(*basalis* group) **8**

3 Frons between antennal scrobe and anterior ocellus with parallel, arched rugae (Figs 52, 54) ..... ***T. cultratus* (Mayr), comb. rev.**

– Frons between antennal scrobe and anterior ocellus smooth or with rugae that are not parallel and arched (Figs 26, 40, 55, 59, 65) **4**

Figures 11–12.[23] **11** *Gryon obesum*, female paratype (USNMENT00989078), head, mesosoma, metasoma, anterolateral view 1**2** *Trissolcus euschisti*, female (OSUC 404912), head, mesosoma, metasoma, ventrolateral view. Scale bars in millimeters.

4 Inner margin of eye with orbital furrow constricted ventrally (Fig. 26); mesoscutellum rugose, at least laterally and usually throughout (Fig. 32); first laterotergite usually with setae (Fig. 92); mesoscutum often with median mesoscutal sulcus (Fig. 93) ..... ***T. strabus*** **Johnson**



Figures 13–16.[24] **13** *Telenomus* sp., female (USNMENT00872628), head, anterolateral view **14** *Telenomus* sp., female (USNMENT00903997), metasoma, dorsal view **15** *Trissolcus urichi*, female holotype (USNMENT00989070), head, anterolateral view **16** *Trissolcus urichi*, female (USNMENT00896405), metasoma, dorsal view. Scale bars in millimeters.

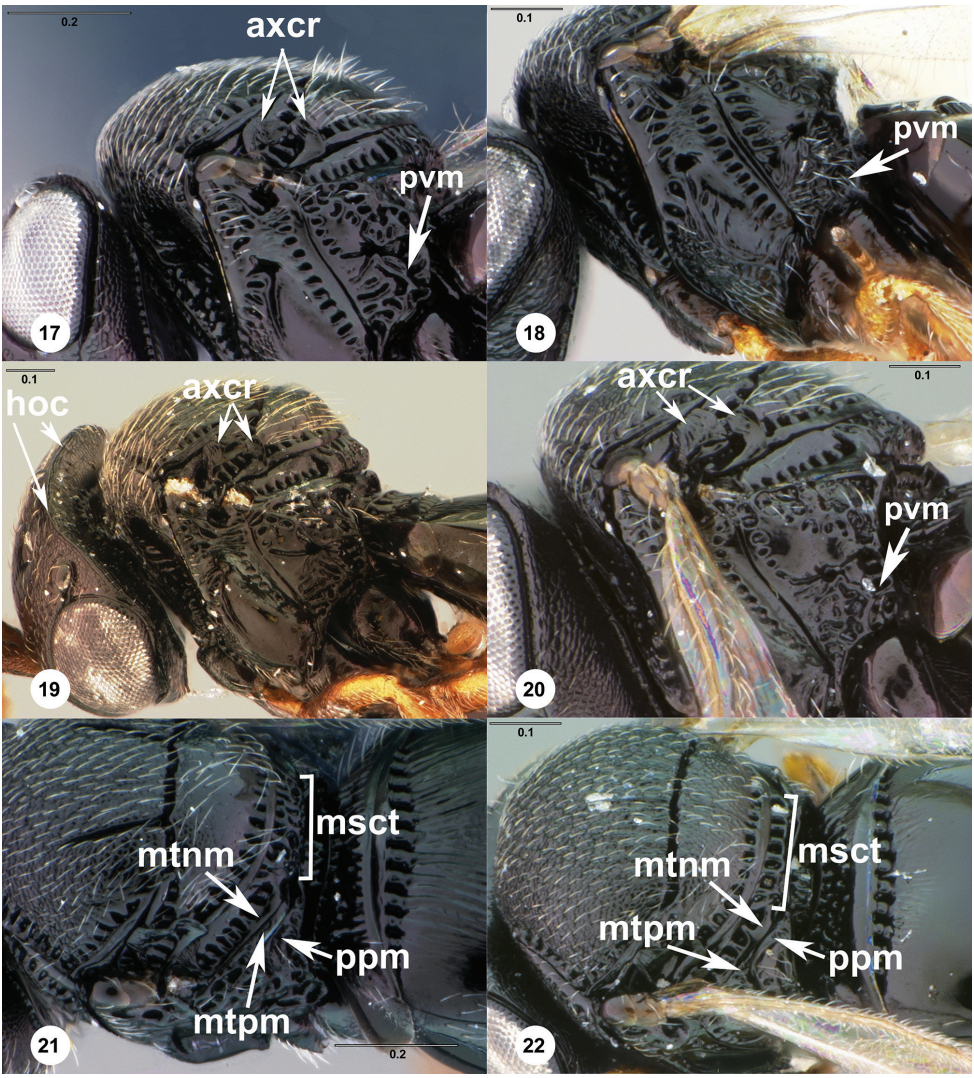
– Inner margin of eye with orbital furrow expanded near intersection with malar sulcus (Figs 12, 15, 28); mesoscutellum smooth (Fig. 34) or with coriaceous microsculpture (Fig. 33); first laterotergite without setae (Figs 62, 68); mesoscutum without median mesoscutal sulcus Fig. 69) **5**

5 Clypeus with 4 setae (Fig. 25); mesopleuron with episternal foveae well-defined and deep, forming a continuous line of cells from postacetabular sulcus to mesopleural pit (Fig. 70); mesoscutum without median mesoscutal carina (Fig. 69) ..... ***T. japonicus* (Ashmead)**

– Clypeus with 2 setae (Fig. 23); mesopleuron with episternal foveae poorly defined, often shallow, irregular (Figs 42–45) and typically distant from postacetabular sulcus; mesoscutum often with median mesoscutal carina (Figs 39, 63) **6**

6 Female with antennal flagellum distinctly bicolored: A3–A6 yellow, A7–A11 dark brown (Fig. 59, as in Fig. 68); area bounded by axillar crescent (axcr Fig. 1) striate (as in Figs 17, 19) ..... ***T. edessae* Fouts**

– Female with antennal flagellum (A3–A11) infuscate throughout (Fig. 38); area bounded by axillar crescent (axcr Fig. 1) with cells visible only along dorsal margin (Figs 20, 62) 7

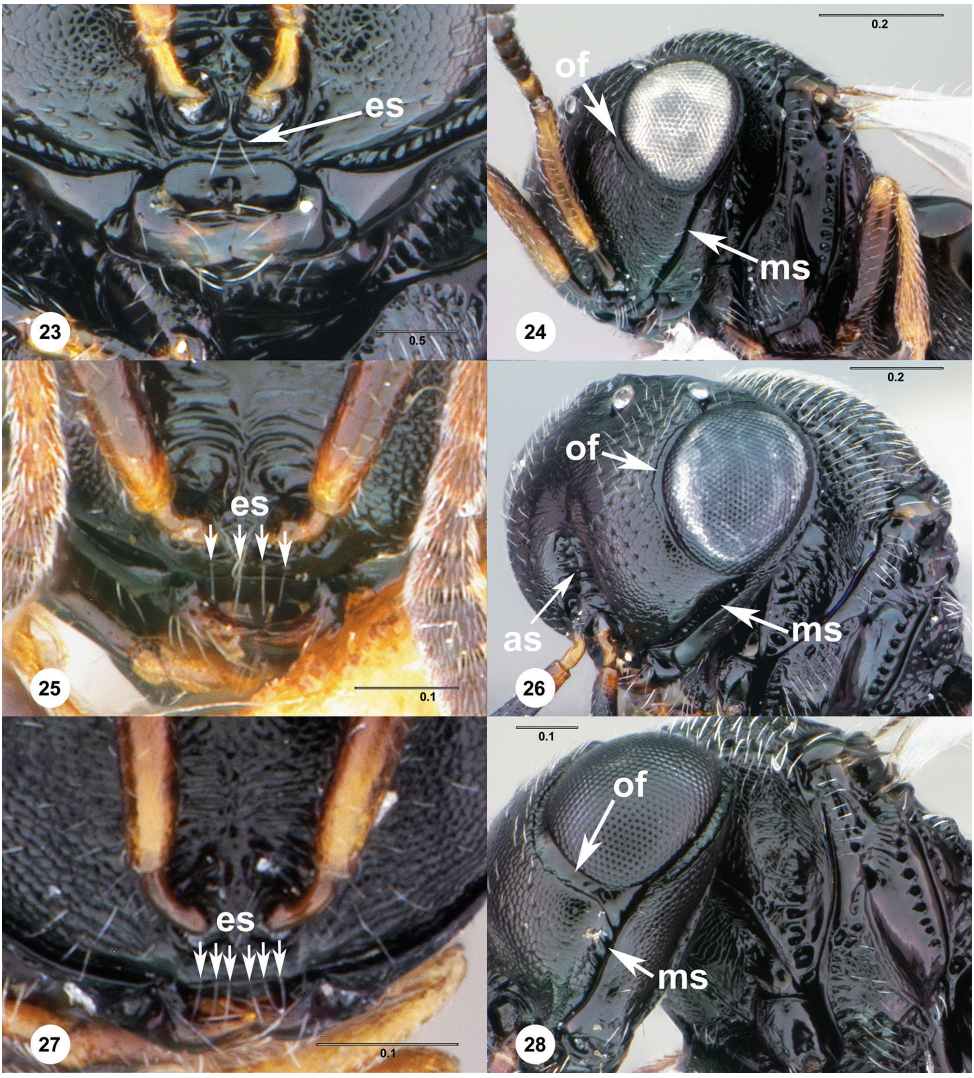


Figures 17–22. [25] **17** *T. japonicus*, female (USNMENT00675989), mesosoma, lateral view **18** *T. occiduus*, female (USNMENT00764995), mesosoma, lateral view **19** *Trissolcus cultratus*, female (USNMENT00764850), head and mesosoma, dorsolateral view **20** *T. euschisti*, female (OSUC 523871), mesosoma, lateral view **21** *T. japonicus*, female (USNMENT00675989), mesosoma, posterolateral view **22** *T. hullensis*, female (OSUC 523881), mesosoma, dorsolateral view. Scale bars in millimeters.

7 Mesopleuron with anteroventral portion rugulose (Figs 41, 44–45)..... ..... ***T. brochymenae*** **(Ashmead)**

– Mesopleuron with anteroventral portion smooth or with shallowly impressed microsculpture (Figs 12, 42–43)..... ***T. euschisti*** **(Ashmead)**

8 Mesoscutellum coarsely rugose (Figs 80–81, 90); vertex sharply angled onto occiput (Fig. 81)..... **9**

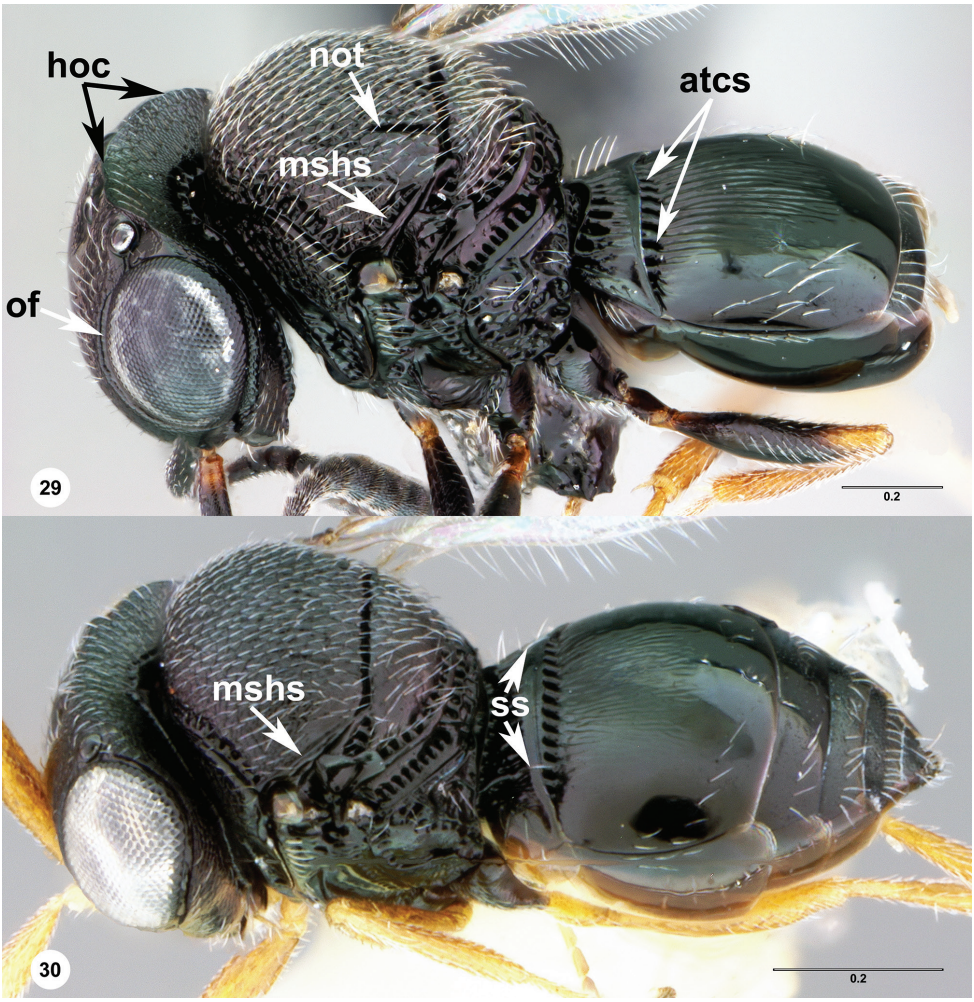


Figures 23–28. [26] **23** *T. strabus*, female (BMSB 1203), mouthparts, anterior view **24** *T. hullensis*, female, (OSUC 523881), head and mesosoma, anterolateral view **25** *T. japonicus*, female holotype, (USNMENT00831865), mouthparts, anterior view **26** *T. strabus*, female, (BMSB 1202), head mesosoma, anterolateral view **27** *T. erugatus*, female, (OSUC 523929), head mesosoma, anterolateral view **28** *T. euschisti*, female, (BMSB 1223), head mesosoma, anterolateral view. Scale bars in millimeters.

– Mesoscutellum smooth or with coriaceous microsculpture (Figs 33–34); vertex rounded onto occiput (Figs 30, 66) **10**

9 Radicle yellow (Fig. 80, 83); metapleuron with paracoxal sulcus indicated by line of distinct foveae in ventral half (Fig. 82) ..... ***T. radix* Johnson**

– Radicle dark brown to black (Fig. 91); metapleuron with paracoxal sulcus absent or obscured by rugae in ventral half (Fig. 88) ..... ***T. solocis* Johnson**



Figures 29–30. [27] **29** *T. strabus*, female (BMSB 1202), head mesosoma, metasoma, dorsolateral view **30** *T. basalis*, female, (USNMENT00954022), head, mesosoma, metasoma, dorsolateral view. Scale bars in millimeters.

10 Metapleuron with paracoxal sulcus visible in ventral half (Fig. 109); frons with facial striae extending as rugulae from anterior mandibular articulation toward compound eye (Fig. 112) ..... ***T. zakotos* Talamas, sp. n.**

– Metapleuron with paracoxal sulcus absent or obscured by coarse rugae in ventral half (Figs 35, 46, 67); frons without facial striae (Fig. 37) **11**

11 T2 smooth or with faintly impressed striation posterior to antecostal sulcus (Figs 61, 66) **12**

– T2 with pronounced striae posterior to antecostal sulcus (Figs 30, 51, 101).... **13**

12 Metapostnotum invaginated near propodeal spiracle, not separating propodeum from metanotum near metascutellum (Figs 22, 66) ..... ***T. hullensis* (Harrington)**

– Metapostnotum invaginated near metascutellum, separating propodeum from metanotum near metascutellum (as in Fig. 21).... ***T. erugatus* Johnson**

13 Mesoscutellum with distinct coriaceous microsculpture and setal bases usually pustulate (Fig. 31); mesopleuron with episternal foveae shallowly impressed and distinctly separated from mesopleural pit (Fig. 35); netrion sulcus incomplete (as in Fig. 44)..... ***T. basalis* (Wollaston)**

– Mesoscutellum entirely smooth and setal bases not strongly raised (Fig. 34); mesopleuron with episternal foveae extending dorsally to proximity of mesopleural pit (Fig. 48); netrion sulcus complete (Fig. 48) **14**

14 Gena in lateral view bulging (Fig. 102), without genal carina (Fig. 102); mesoscutum without notauli (Fig. 100); anteroventral extension of metapleuron short, not extending to mesocoxa in lateral view (Fig. 102); lateral mesoscutum with mesoscutal humeral sulcus present as a smooth furrow (as in Fig. 30).....***T. utahensis* (Ashmead)**

– Gena in lateral view narrow, often with genal carina extending dorsally from base of mandible (Fig. 48); mesoscutum with notauli sometimes indicated; anteroventral extension of metapleuron usually long and extending to base of mesocoxa in lateral view (Fig. 46, as in Fig. 43); lateral mesoscutum with mesoscutal humeral sulcus present as a smooth furrow (Fig. 49) or comprised of cells (Fig. 46) .....***T. cosmopeplae* (Gahan)**

15 Mesoscutellum covered with shallowly impressed coriaceous microsculpture (Fig. 33).....**16**

– Mesoscutellum entirely smooth, without microsculpture (Fig. 34) **17**

16 Frons outside of antennal scrobes with raised, irregular rugulae (Fig. 86); mesoscutum between notauli often with longitudinal rugulae (Fig. 87) .... ***T. ruidus* Johnson**

– Frons outside of antennal scrobes coriaceous, without raised rugulae but with more or less well-defined setigerous punctures, (Fig. 79); mesoscutum without longitudinal elements in sculpture (Fig. 77)..... ***T. parma* Johnson**

17 Gena in lateral view bulging (Fig. 74) .....***T. occiduus* Johnson**

– Gena in lateral view narrow (Figs 95, 106) **18**

18 Mesopleural carina absent ventrally (Fig. 97)..... ***T. thyantae* Ashmead**

– Mesopleural carina complete (Fig. 107) .... ***T. valkyria* Johnson & Talamas, sp. n.**

Multi-choice Lucid key

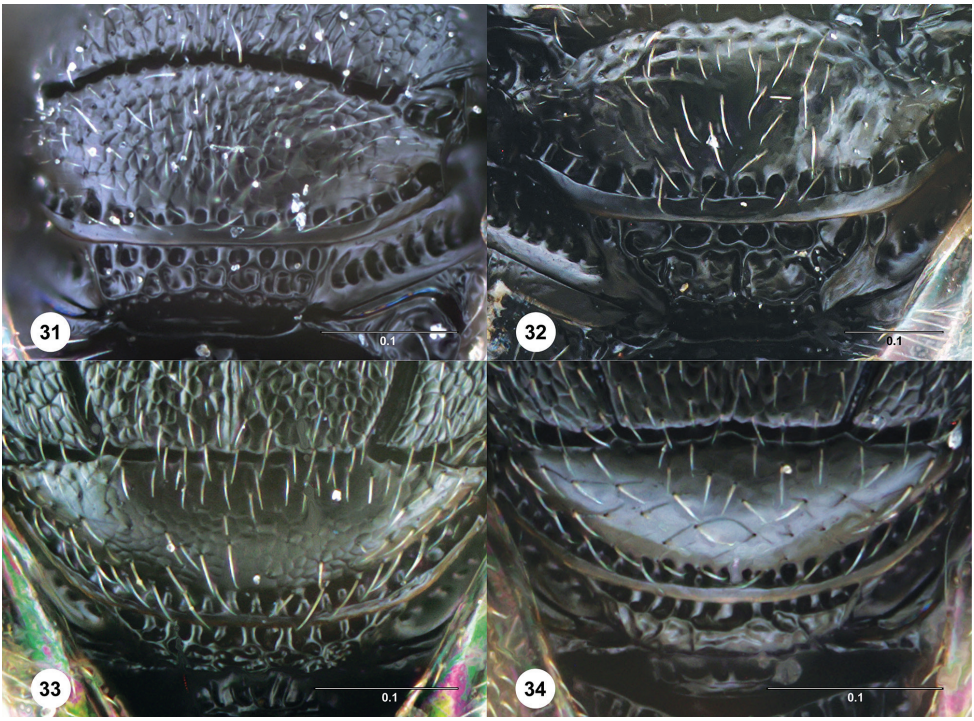
Lucid Key Server edition (only web browser required):
http://keys.lucidcentral.org/key-server/key.jsp?keyId=127
Applet edition (requires installation of Java Runtime Environment):
http://keys.lucidcentral.org/keys/v3/Nearctic_Trissolcus/

Taxonomy

***Trissolcus basalis* (Wollaston)**
http://bioguid.osu.edu/osuc_concepts/3189
Figures 30–31, 35–37; Morphbank[2]

Telenomus Maderensis Wollaston, 1858: 25 (original description, synonymized by Nixon (1935)).
Telenomus basalis Wollaston, 1858: 25 (original description); Kieffer 1926: 39 (description).
Telenomus megacephalus Ashmead, 1894: 203, 212 (original description, synonymized by Nixon (1935)); Ashmead 1896: 790 (keyed); Ashmead 1900: 326 (distribution); Nixon 1935: 100 (junior synonym of *Microphanurus basalis* (Wollaston)).
Telenomus megalocephalus Schulz: Schulz 1906: 152 (emendation).
Telenomus piceipes Dodd, 1920: 354 (original description, synonymized by Nixon (1935)); Nixon 1935: 100 (junior synonym of *Microphanurus basalis* (Wollaston)).
Liophanurus megacephalus (Ashmead): Kieffer 1926: 65, 76 (description, generic transfer, keyed).
Telenomus maderensis Wollaston: Kieffer 1926: 39 (description); Nixon 1935: 100 (junior synonym of *Microphanurus basalis* (Wollaston)).
Microphanurus basalis (Wollaston): Nixon 1935: 96, 100 (description, generic transfer, synonymy, keyed); Nixon 1943: 138 (keyed); Risbec 1950: 570, 571 (variation, keyed).
Asolcus basalis (Wollaston): Delucchi 1961: 44, 57 (description, keyed); Voegelé 1962: 155 (variation, diagnosis); Voegelé 1964: 28 (keyed); Voegelé 1965: 96, 108 (variation, diagnosis, keyed); Voegelé 1969: 151 (keyed).
Trissolcus basalis (Wollaston): Masner 1965: 125 (type information, generic transfer); Safavi 1968: 415 (keyed); Fabritius 1972: 31 (keyed); Kozlov and Lê 1977: 516 (keyed); Kozlov 1978: 637 (description); Kozlov and Kononova 1983: 121 (description); Graham 1984: 100 (variation); Johnson 1985b: 432, 434 (description, keyed); Johnson 1991: 212, 213, 214, 216 (diagnosis, keyed); Ghahari, Buhl and Kocak 2011: 594 (listed); Mao, Valerio, Austin, Dowton and Johnson 2012: 194 (presentation of mitochondrial genome, phylogenetic position); Fusu, Bin and Popovici 2013: 263 (description of chromosomes).
Trissolcus maderensis (Wollaston): Masner 1965: 126 (type information, generic transfer).
Trissolcus piceipes (Dodd): Masner 1965: 127 (type information, generic transfer).
Trissolcus megacephalus (Ashmead): Johnson 1983: 448 (type information).

Lectotype designation. Masner (1965) did not mention the type status of the specimen labeled "Type H.T." in his treatment of the types in BMNH, and Johnson (1985) referred to this specimen of the holotype, although it was originally part of a syntype series. Consequently, a lectotype was not actually designated for *T. basalis*. We here designate the specimen mentioned by Masner (1965) (B.M. TYPE HYM. 9.304) as the lectotype of this species.



Figures 31–34. [28] **31** *T. basalis*, female (USNMENT00954023), mesoscutellum, dorsal view **32** *T. strabus*, female (OSUC 523850), mesoscutellum, dorsal view **33** *T. ruidus*, (OSUC 76431), mesoscutellum, dorsal view **34** *T. occiduus*, female (OSUC 76430), mesoscutellum, dorsal view. Scale bars in millimeters.

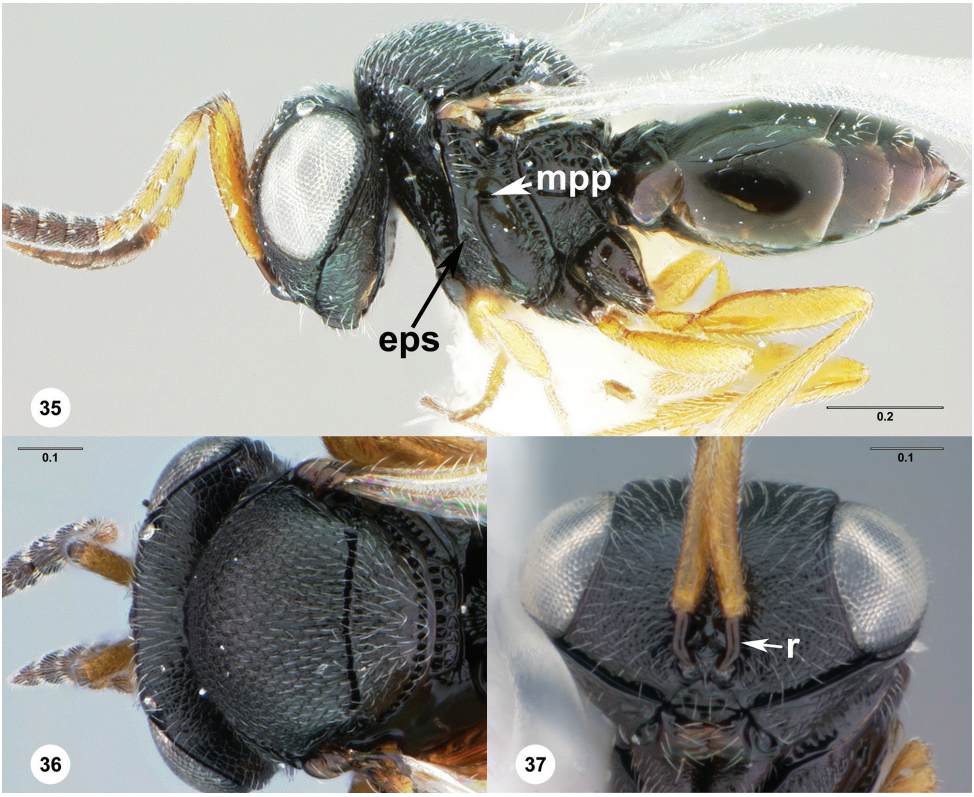
Diagnosis. Within the New World species of the *basalis* group, the combination of the broadly rounded vertex, wide gena, and rugose T2 is found only in *T. basalis* and *T. utahensis*. *Trissolcus basalis* may be distinguished by its coriaceous mesoscutellum, incomplete netrion sulcus and weakly developed episternal foveae. *Trissolcus basalis* may be dark in color, but typically can be distinguished by the yellow scape (sharply contrasting in color with the dark radicle) and abruptly bicolored antennae.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3189]

Associations. Emerged from egg of *Aelia* Fabricius: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Aelia acuminata* (Linnaeus): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Aelia cognata* Fieber: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Aelia germari* Küster: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Agonoscelis rutila* (Fabricius): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Asopinae* Spinola: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Calidea* Laporte: [Hemiptera: Heteroptera: Pentatomoidea: Scutelleridae]; emerged from egg of *Calidea dregeii* Germar: [Hemiptera: Heteroptera: Pentatomoidea: Scutelleridae]; emerged from egg of *Carpocoris fuscispinus* (Boheman): [Hemiptera: Heteroptera: Pentato-

moidea: Pentatomidae]; emerged from egg of *Coleotichus blackburniae*: [Hemiptera: Heteroptera: Pentatomoidea: Scutelleridae]; emerged from egg of *Cuspicona simplex* Walker: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Dolicoris baccharum* (Linnaeus): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Dolycoris baccarum* (Linnaeus): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of*Eurydema ornata* (Linnaeus): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Eurygaster austriaca* (Schrank): [Hemiptera: Heteroptera: Pentatomoidea: Scutelleridae]; emerged from egg of *Eurygaster integriceps* Puton: [Hemiptera: Heteroptera: Pentatomoidea: Scutelleridae]; emerged from egg of *Euschistus* Dallas: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; solitary egg parasitoid of *Euschistus servus* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; solitary egg parasitoid of *Euthyrhynchus floridanus* (Linnaeus): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Graphosoma semipunctata* (Fabricius): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Halyomorpha annulicornis* (Signoret): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Nezara* Amyot & Serville: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; solitary egg parasitoid of *Nezara* Amyot & Serville: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; egg parasite of *Nezara viridula* (Linnaeus): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from *Nezara viridula* (Linnaeus): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Nezara viridula* (Linnaeus): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; parasite of *Nezara viridula* (Linnaeus): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; solitary egg parasitoid of *Nezara viridula* (Linnaeus): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; solitary egg parasitoid of *Nezara viridula* (Linnaeus): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Odontotarsus grammicus* (Linnaeus): [Hemiptera: Heteroptera: Pentatomoidea: Scutelleridae]; egg ectoparasite of *Oechalia* Stål: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Oechalia schellenbergi* Guérin-Méneville: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Pentatomidae*: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; solitary egg parasitoid of *Pentatomidae*: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Piezodorus hybneri* (Gmelin): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Plautia affinis* (Dallas): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Raphigaster* Laporte: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; collected on *Solanum nigrum* L.: [Solanales: Solanaceae]; collected on bokhara: [Fabales: Fabaceae]; collected on buchan: [Capparales: Brassicaceae]; collected on cotton: [Malvales: Malvaceae]; collected on hore: [Lamiales: Lamiaceae]; collected on mint: [Lamiales: Lamiaceae]; collected on mung: [Fabales: Fabaceae]; collected in drilled soybean: [Fabales: Fabaceae]; collected on soybean: [Fabales: Fabaceae]

Material examined. Lectotype, female, *T. basalis*: **PORTUGAL**: Madeira Reg. Autó., Madeira Island, VII–1855, Wollaston, B.M. TYPE HYM. 9.304 (deposited in



Figures 35–37. [29] *Trissolcus basalis* **35** female (USNMENT00903007), head, mesosoma, metasoma, lateral view **36** female (USNMENT00872109), head and mesosoma, dorsal view **37** female (OSUC 75271), head, anterior view. Scale bars in millimeters.

BMNH). Holotype, female, *T. megacephalus*: **SAINT VINCENT AND THE GRENADINES**: Saint Vincent Island, no date, H. H. Smith, USNM Type No. 2525 (deposited in USNM). *Other material*: (58 females, 15 males, 393 sex unrecorded) **AUSTRALIA**: 8 females, 4 males, 149 sex unrecorded, ANIC DB 32-020991, 32-020992, 32-020993, 32-020994, 32-020996–32-020999 (ANIC); OSUC 17738 (BMNH); OSUC 75398–75424 (OSUC); OSUC 145814, 78027–78147 (QDPC); USNMENT00872088, USNMENT00872089, USNMENT00872090, USNMENT00903007 (USNM). **BRAZIL**: 67 sex unrecorded, OSUC 75299–75365 (OSUC). **CHINA**: 10 sex unrecorded, OSUC 75366, 75389–75397 (OSUC).**DEMOCRATIC REPUBLIC OF THE CONGO**: 3 females, OSUC 182081–182083 (RMCA). **DOMINICAN REPUBLIC**: 3 sex unrecorded, OSUC 398658–398659, 398667 (CNCI). **EGYPT**: 2 females, 4 sex unrecorded, OSUC 144795–144796, USNMENT00872006, USNMENT00872007, USNMENT00872008, USNMENT00872009 (USNM). **ERITREA**: 1 female, OSUC 17736 (BMNH). **FIJI**: 16 sex unrecorded, OSUC 77661–77676 (BPBM). **FRENCH POLYNESIA**: 2 sex unrecorded, OSUC 77659–77660 (BPBM). **GREECE**: 1 sex unrecorded, OSUC 398669 (CNCI). **IRAN**: 1 sex unre-

corded, OSUC 144797 (CNCI). **ITALY**: 2 females, 1 male, OSUC 173847–173849 (OSUC). **JAMAICA**: 2 sex unrecorded, OSUC 398660–398661 (CNCI). **JAPAN**: 1 sex unrecorded, OSUC 144391 (CNCI). **MONTSERRAT**: 12 sex unrecorded, OSUC 398662 (CNCI); OSUC 145281 (FSCA); OSUC 75289–75298 (OSUC). **MOROCCO**: 1 sex unrecorded, OSUC 17743 (BMNH). **NEW CALEDONIA**: 1 sex unrecorded, OSUC 77624 (BPBM). **OCEANIA**: 5 sex unrecorded, OSUC 77625–77628 (BPBM); OSUC 75425 (OSUC). **SAINT VINCENT AND THE GRENADINES**: 3 sex unrecorded, OSUC 143816–143818 (LACM). **SENEGAL**: 1 female, OSUC 17737 (BMNH). **SOUTH AFRICA**: 6 sex unrecorded, OSUC 145553, 75384–75388 (OSUC). **TANZANIA**: 1 sex unrecorded, OSUC 17741 (BMNH). **TONGA**: 31 sex unrecorded, OSUC 77629–77658 (BPBM); OSUC 75427 (OSUC). **TRINIDAD AND TOBAGO**: 2 sex unrecorded, USNMENT00764950, USNMENT00764951 (USNM). **TURKEY**: 3 females, OSUC 17739–17740, 17742 (BMNH). **UNITED STATES**: 38 females, 9 males, 49 sex unrecorded, ANIC DB 32-020995 (ANIC); OSUC 398668 (CNCI); OSUC 131149–131186, 154353, 157486–157487, 157542–157549, 157563–157566, 7339, 75256–75288 (OSUC); USNMENT00872103, USNMENT00872104, USNMENT00872105, USNMENT00872106, USNMENT00872107, USNMENT00872108, USNMENT00872109 (USNM). **VANUATU**: 1 male, 1 sex unrecorded, ANIC DB 32-020997 (ANIC); OSUC 75426 (OSUC). **ZIMBABWE**: 17 sex unrecorded, OSUC 75367–75383 (OSUC).

***Trissolcus brochymenae* (Ashmead)**
http://bioguid.osu.edu/osuc_concepts:3195
Figures 38–41, 44–45; Morphbank[3]

Telenomus Crochymenae Ashmead, 1881: 181 (original description, spelling error).
Telenomus brochymenae Ashmead: Ashmead 1887: 118 (emendation).
Trissolcus brochymenae (Ashmead): Ashmead 1893: 162, 164 (generic transfer, description, keyed); Brues 1916: 549, 550 (description, keyed); Kieffer 1926: 127, 129 (description, keyed); Masner 1964: 146 (variation); Masner and Muesebeck 1968: 72 (lectotype designation); Johnson 1984: 799 (description, synonymy, keyed); Johnson 1987: 289, 298 (diagnosis, variation, synonymy, keyed).
Trissolcus murgantiae Ashmead, 1893: 162, 163 (original description, keyed, synonymized by Johnson (1984)); Brues 1916: 549, 550 (description, keyed); Kieffer 1926: 127, 128 (description, keyed); Masner and Muesebeck 1968: 73 (lectotype designation); Johnson 1984: 799 (junior synonym of *Trissolcus brochymenae* (Ashmead)).
Trissolcus rufiscapus Ashmead, 1893: 162, 163 (original description, keyed, synonymized by Johnson (1984)); Kieffer 1926: 127, 129 (description, keyed); Masner and Muesebeck 1968: 73 (type information); Johnson 1984: 799 (junior synonym of *Trissolcus brochymenae* (Ashmead)).
Trissolcus laticeps Ashmead, 1894: 212 (original description, synonymized by Johnson (1987)); Ashmead 1900: 326 (distribution); Kieffer 1926: 127, 130 (descrip-

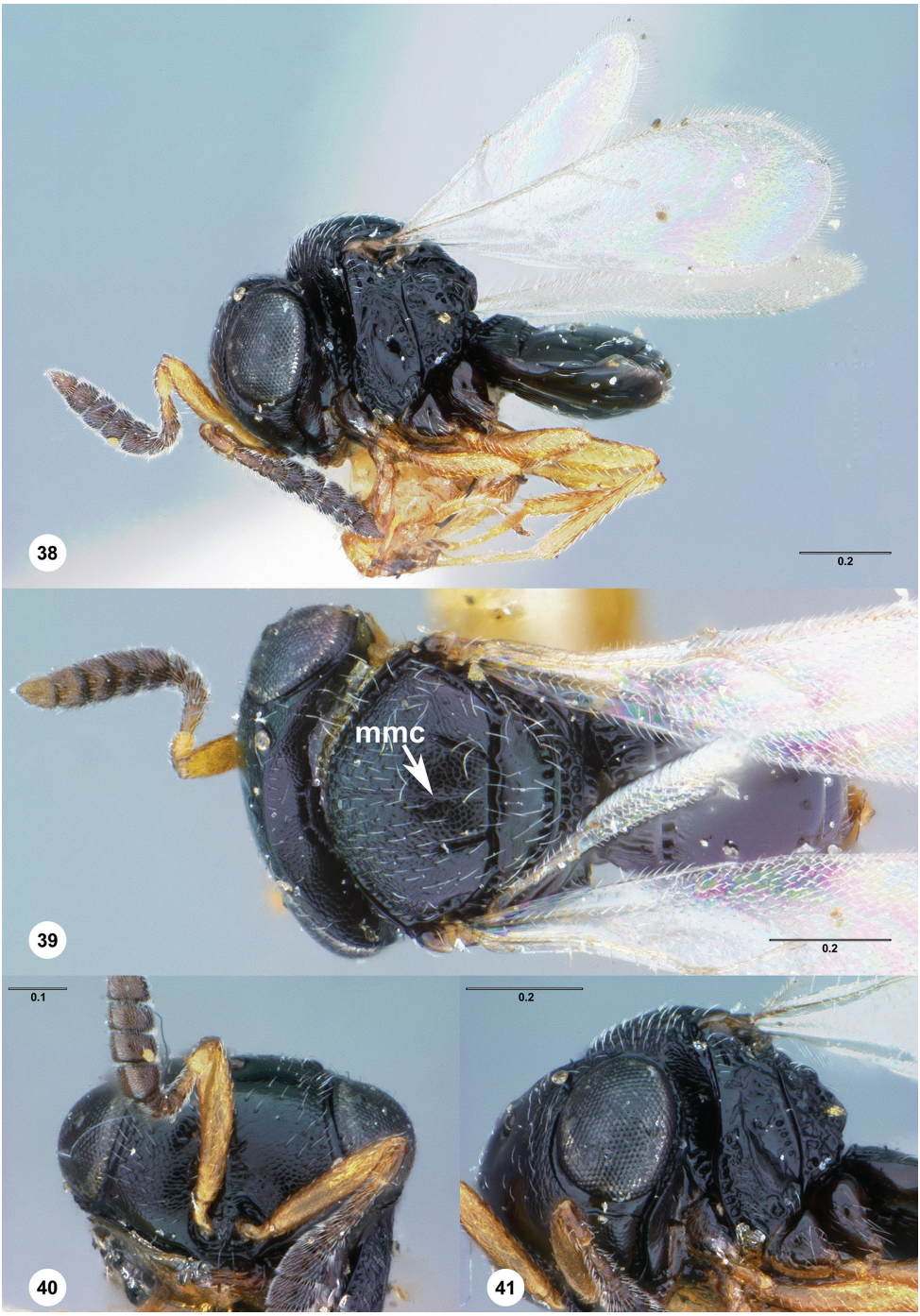
tion, keyed); Masner 1965: 126 (type information); Johnson 1983: 448 (lectotype designation); Johnson 1987: 298 (junior synonym of *Trissolcus brochymenae* (Ashmead)).

Neotype designation. The last known examination of the lectotype of *T. brochymenae* was by Johnson (1984) in his revision of the *flavipes* species group. The specimen was returned to USNM intact but presently consists of a pin, labels, and an empty point. *Trissolcus brochymenae* is the type species of *Trissolcus* and we consider the designation of a neotype to be important for the stability of both the genus and species names. Additionally, *T. brochymenae* is a morphologically variable species with a geographic distribution that spans the United States. A case study of cryptic species within *Trissolcus* was recently presented by Matsuo et al. (2014) and a similar phenomenon may exist in other species, including *T. brochymenae*. *Trissolcus brochymenae* is morphologically very close to *T. euschisti,* separable by only a few characters, and in our opinion this increases the need for an objective neotype. The specimen selected for this purpose was originally a syntype, reared from the same egg mass as the lectotype and is consistent with Ashmead's original description and the most thorough treatment of the species (Johnson 1984). In accordance with article 75 of The Code we hereby designate specimen USNMENT00965611 (Figs 38–41) as the neotype of *Trissolcus brochymenae*, deposited in the insect collection of the National Musuem of Natural History (USNM).

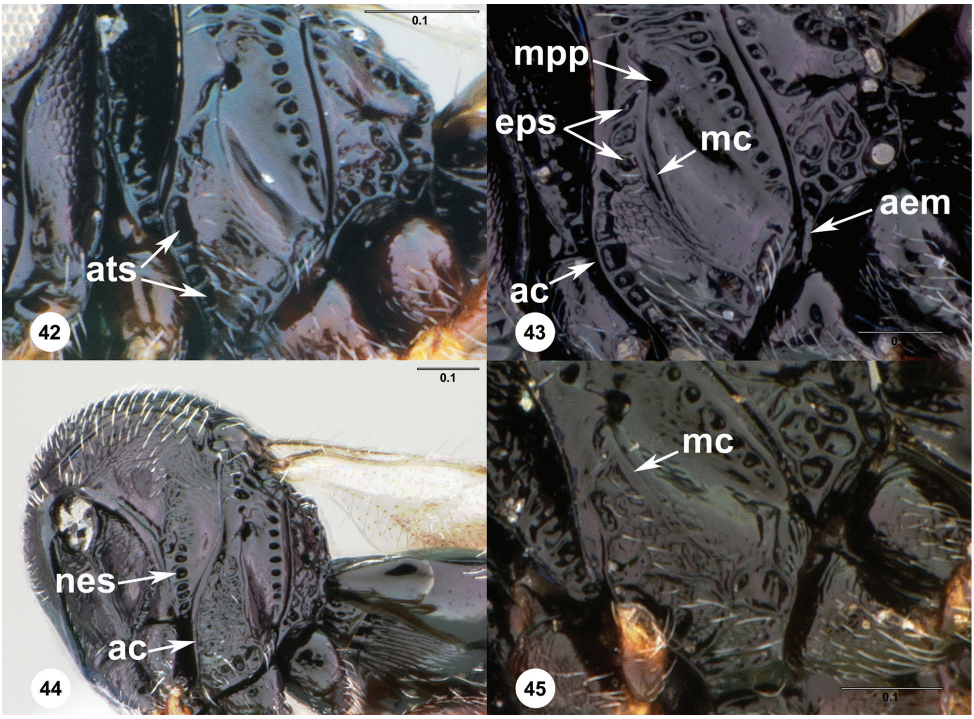
Diagnosis. *Trissolcus brochymenae* is most similar to *T. euschisti* and may be distinguished from it by the strongly rugulose ventral portion of the mesepisternum anterior to the mesopleural carina (Figs 44–45). This species is also similar to *T. euschisti* in that it shows a great deal of variability, presumably in association with its wide geographic distribution and host range.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3195]

Associations. emerged from *Acrosternum hilare* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Acrosternum impicticorne* (Stål): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Brochymena arborea* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; collected on *Hydrangea* L.: [Rosales: Hydrangeaceae]; emerged from *Murgantia histrionica* (Hahn): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Murgantia histrionica* (Hahn): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Piezodorus guildini* (Westwood): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Piezodorus guildinii* (Westwood): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from sentinel egg mass of *Podisus maculiventris* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Podisus nigrolimbatus* (Spinola): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; collected on *Prosopis* L.: [Fabales: Fabaceae]; collected on cotton: [Malvales: Malvaceae]; collected on rose: [Rosales: Rosaceae]; collected on soybean: [Fabales: Fabaceae]; living in soybean: [Fabales: Fabaceae]; emerged from egg of stink bug: [Hemiptera: Heteroptera: Pentatomoidea:



Figures 38–41. [30] *Trissolcus brochymenae*, female neotype (USNMENT00954611) **38** lateral habitus **39** dorsal habitus **40** head, anterior view **41** head and mesosoma, anterolateral view. Scale bars in millimeters.



Figures 42–45. [31] **42** *T. euschisti* female (OSUC 523902), mesosoma, ventrolateral view **43** *T. euschisti* female (OSUC 404912), mesosoma, ventrolateral view **44** *T. brochymenae* (BMSB 1216), mesosoma, anterolateral view **45** *T. brochymenae* (USNMENT00896401), mesosoma, ventrolateral view. Scale bars in millimeters.

Pentatomidae]; collected on turnip greens: [Capparales: Brassicaceae]; collected on wax myrtle: [Myricales: Myricaceae]

Material examined. Neotype, female, *T. brochymenae*: **UNITED STATES**: FL, Duval Co., Jacksonville, no date, reared from egg, W. H. Ashmead, USNMENT00965611 (deposited in USNM). Lectotype, female, *T. laticeps*: **SAINT VINCENT AND THE GRENADINES**: Saint Vincent Island, no date, H. H. Smith, USNM Type No. 2526 (deposited in USNM). Lectotype, female, *T. murgantiae*: **UNITED STATES**: LA, East Baton Rouge Parish, Baton Rouge, no date, reared from egg, H. A. Morgan, USNMENT00989032 (deposited in USNM). Holotype, female, *T. rufiscapus*: **UNITED STATES**: Washington, 12.IV.1885, USNMENT00989047 (deposited in USNM). *Paralectotype*: **UNITED STATES**: 1 female, USNM Type No. 2231 PLT (USNM). *Other material*: (71 females, 2 males, 236 sex unrecorded) **BRAZIL**: 159 sex unrecorded, OSUC 398724–398725 (CNCI); OSUC 373344–373345, 495206–495305, 75445–75499 (OSUC). **COLOMBIA**: 1 sex unrecorded, OSUC 398719 (CNCI). **COSTA RICA**: 7 sex unrecorded, OSUC 398702–398703, 398714 (CNCI); OSUC 142482–142485 (OSUC). **DOMINICAN REPUBLIC**: 4 sex unrecorded, OSUC 398710–398712,

398716 (CNCI). **GUATEMALA**: 1 sex unrecorded, OSUC 398718 (CNCI). **HONDURAS**: 1 sex unrecorded, OSUC 398717 (CNCI). **JAMAICA**: 3 sex unrecorded, OSUC 398708–398709, 398713 (CNCI). **TRINIDAD AND TOBAGO**: 2 sex unrecorded, OSUC 398706–398707 (CNCI). **UNITED STATES**: 71 females, 2 males, 45 sex unrecorded, OSUC 17821 (BMNH); OSUC 398679–398688 (CNCI); OSUC 436701 (LACM); OSUC 145555, 157494–157503, 266797, 413700–413703, 413709–413713, 523852–523855, 523857–523861, 523864–523865, 523904–523923, 523931, 523933, 523935–523937, 523940, 523942, 523944, 542440, 542442, 542445, 542450, 542453–542454, 62796, 70464–70465, 75434–75444, 76425–76426 (OSUC); BMSB 1216–1217, OSUC 145648, USNMENT00872091, USNMENT00872092–USNMENT00872095, USNMENT00989146–USNMENT00989149, USNMENT00989160–USNMENT00989170, USNMENT00989173 (USNM). **VENEZUELA**: 5 sex unrecorded, OSUC 398704, 398720–398723 (CNCI). **VIRGIN ISLANDS**: 2 sex unrecorded, OSUC 398705, 398715 (CNCI).

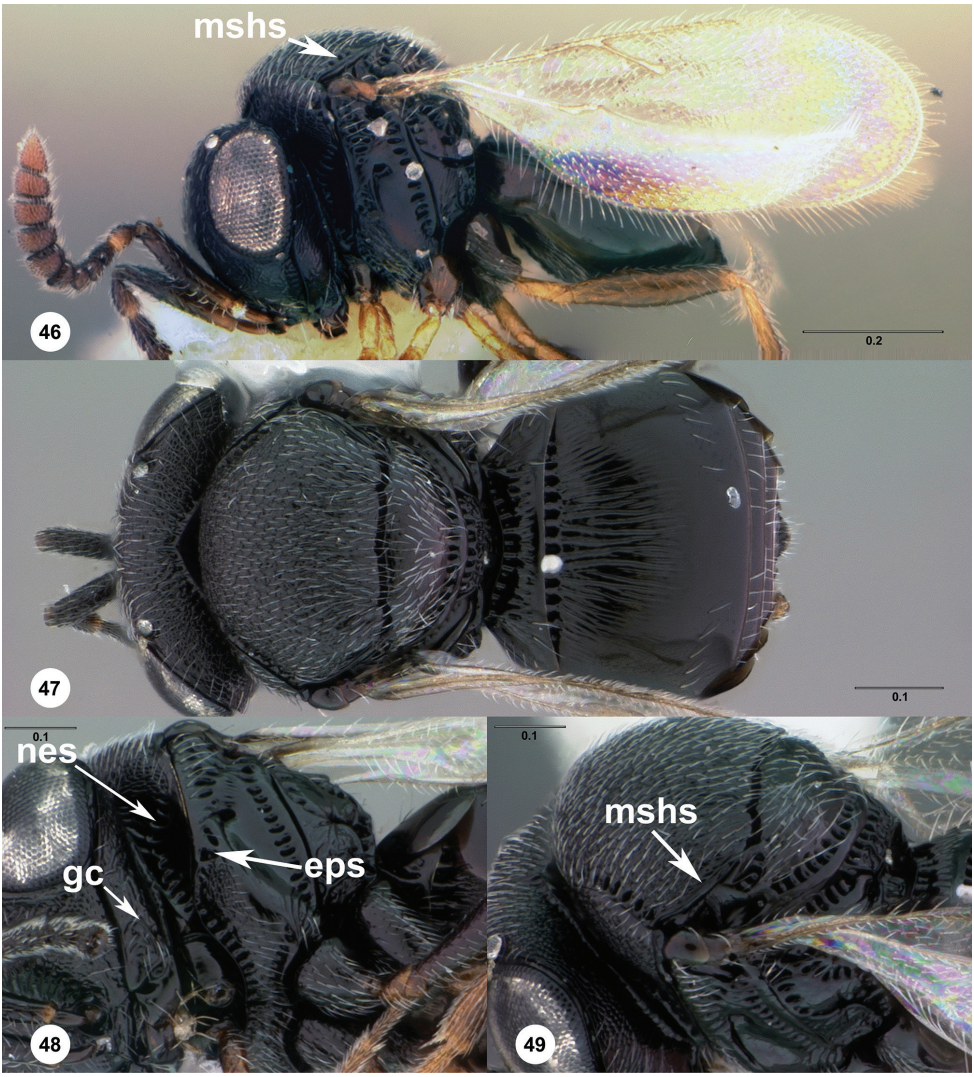
Trissolcus cosmopeplae **(Gahan)**
http://bioguid.osu.edu/osuc_concepts:3206
Figures 46–49; Morphbank[4]

Telenomus cosmopeplae Gahan, 1926: 67 (original description).
Trissolcus cosmopeplae (Gahan): Krombein and Burks 1967: 297 (generic transfer); Masner and Muesebeck 1968: 72 (type information); Johnson 1985b: 432, 436 (description, keyed).

Diagnosis. *Trissolcus cosmopeplae* may be distinguished from other species that have sublateral setae and a narrow gena (*T. erugatus*, *T. hullensis*, *T. radix*, *T. solocis*, and *T. zakotos*) by the presence of extensive rugulae on T2 and the mesoscutellum without macrosculpture. This is also the only New World species outside the *thyantae* and *flavipes* groups in which notauli may be visible. All other species with sublateral setae and a narrow gena usually have the posterior region of the mesoscutum longitudinally rugulose and the notauli, if present, are thus obscured.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3206]

Associations. Emerged from egg of *Cosmopepla bimaculata* (Thomas): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Euschistus conspersus* Uhler: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Pentatomidae*: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Perillus bioculatus* (Fabricius): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; collected on alfalfa: [Fabales: Fabaceae]; collected on bitterbrush: [Rosales: Rosaceae]; collected on blackberry: [Rosales: Rosaceae]; collected on brome: [Cyperales: Poaceae]; collected on red-osier dogwood: [Cornales: Cornaceae]



Figures 46–49.[32] *Trissolcus cosmopeplae* **46** female holotype (USNMENT00989096), head, mesosoma, metasoma, lateral view **47** female (OSUC 77129), head, mesosoma, metasoma, dorsal view **48** female (OSUC 77129), head and mesosoma, ventrolateral view **49** female (OSUC 77129), head and mesosoma, dorsolateral view. Scale bars in millimeters.

Material examined. Holotype, female, *T. cosmopeplae*: **UNITED STATES**: IL, Champaign Co., Urbana, 8.VIII.1925, reared from egg, USNMENT00989096 (deposited in USNM). *Other material*: (9 females, 1 male, 74 sex unrecorded) **CANADA**: 16 sex unrecorded, OSUC 145181, 398732–398743 (CNCI); OSUC 145556, 75612–75613 (OSUC). **UNITED STATES**: 9 females, 1 male, 58 sex unrecorded, OSUC 398744–398747 (CNCI); OSUC 413941, 75606–75611, 76429, 77122–77177 (OSUC).

***Trissolcus cultratus* (Mayr), comb. rev.**
http://bioguid.osu.edu/osuc_concepts:13182
Figures 19, 50–52, 54; Morphbank[5]

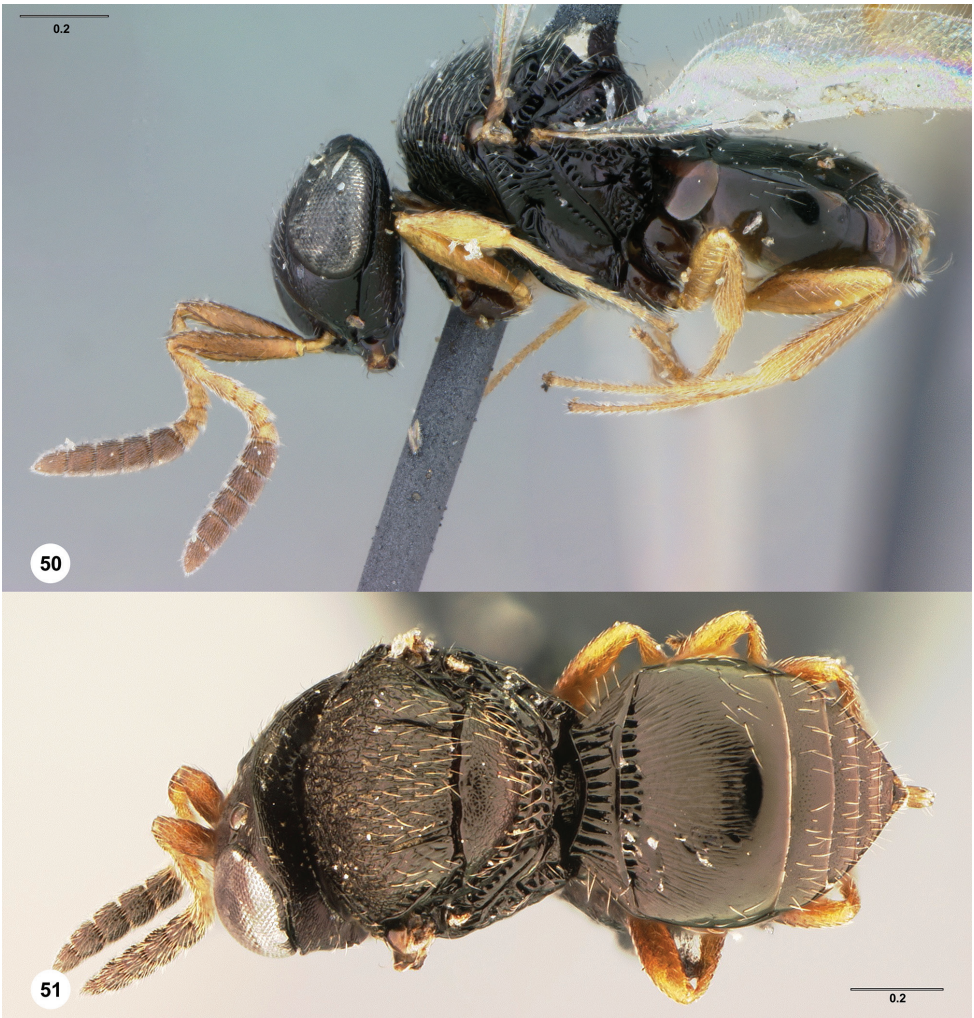
Telenomus cultratus Mayr, 1879: 699, 701, 703 (original description, keyed, synonymized by Kozlov (1968)); Kozlov 1968: 200 (junior synonym of *Trissolcus flavipes* (Thomson)).
Aphanurus Cultratus (Mayr): Kieffer 1912: 70 (description, generic transfer).
Microphanurus cultratus (Mayr): Kieffer 1926: 91, 95 (description, generic transfer, keyed); Nixon 1939: 130, 133 (description, keyed); Rjachovsky 1959: 83 (keyed).
Asolcus cultratus (Mayr): Masner 1959: 378 (diagnosis, variation); Delucchi 1961: 44, 51 (description, keyed).
Trissolcus cultratus (Mayr): Safavi 1968: 414 (keyed); Szabó 1975: 266, 267 (description, lectotype designation, keyed).

Diagnosis. *Trissolcus cultratus* is easily distinguished from other members of the *flavipes* group treated here by the parallel arched rugae on the frons between the anterior ocellus and the antennal scrobe. This species also lacks a well-developed orbital furrow near the malar sulcus, and by this character it may be separated from *T. brochymenae*, *T. edessae*, *T. euschisti*, and *T. japonicus*.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=13182]

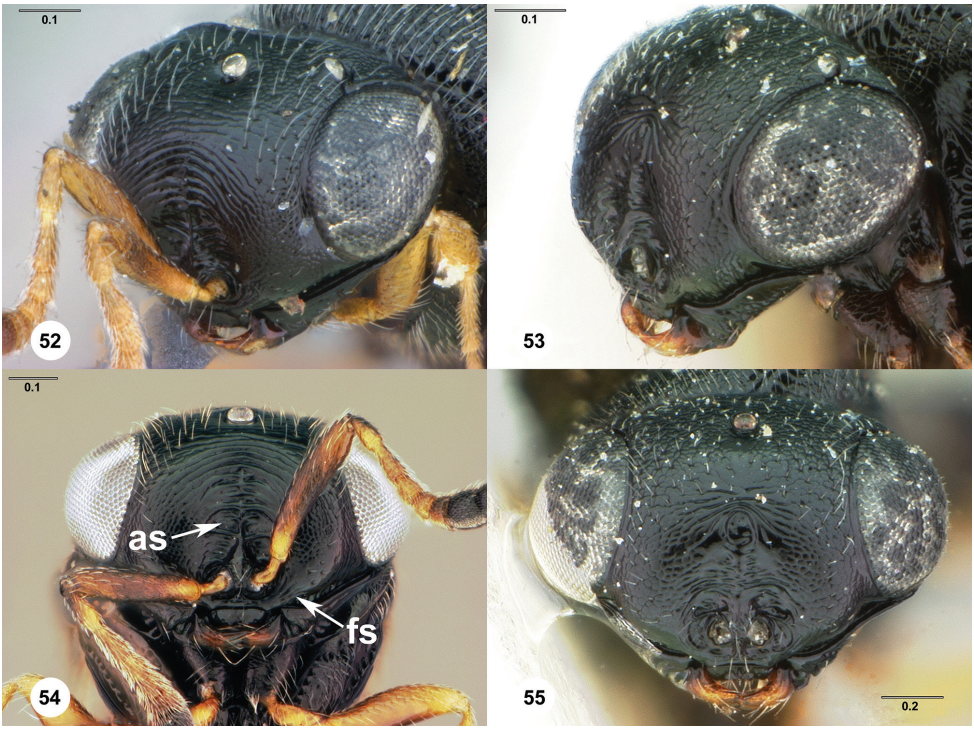
Associations. Emerged from egg of *Carpocoris pudicus* (Poda): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Eurygaster* Laporte: [Hemiptera: Heteroptera: Pentatomoidea: Scutelleridae]; collected near eggs of *Raphigaster nebulosa* (Poda): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Raphigaster nebulosa* (Poda): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; on leaf of maple: [Sapindales: Aceraceae]; collected near mulberry: [Urticales: Moraceae]

Material examined. Lectotype, female: *Other material*: (122 females, 13 males, 4 sex unrecorded) **AUSTRIA**: 5 females, 2 sex unrecorded, USNMENT00979612, USNMENT00979613 (CUIC); OSUC 75765–75767 (OSUC); USNMENT00675943, USNMENT00675944 (USNM). **CHINA**: 2 females, UCRC ENT 142635, 143817 (UCRC). **CZECH REPUBLIC**: 1 female, 3 males, USNMENT00896311, USNMENT00896312, USNMENT00896313, USNMENT00896314 (CNCI). **FRANCE**: 4 females, OSUC 75753–75756 (OSUC). **HUNGARY**: 3 females, 1 sex unrecorded, OSUC 75771–75773, 75783 (OSUC). **JAPAN**: 32 females, 5 males, OSUC 144472–144480, 542363, 542374, 542412, 542415, USNMENT00896136, USNMENT00896138, USNMENT00896140, USNMENT00896305, USNMENT00896307–USNMENT00896309, USNMENT00896315, USNMENT00896339, USNMENT00896341 (CNCI); OSUC 75784, 75786–75788 (OSUC); UCRC ENT 297012 (UCRC); USNMENT00675730–USNMENT00675737, USNMENT00764849 (USNM). **RUSSIA**: 34 females, USNMENT00896048, USNMENT00896049, USNMENT00896050–USNMENT00896054,



Figures 50–51. [33] *Trissolcus cultratus* **50** female lectotype (NHMW 0008A), head, mesosoma, metasoma, lateral view **51** female (USNMENT00764850), head, mesosoma, metasoma, dorsal view. Scale bars in millimeters.

USNMENT00896074, USNMENT00896075, USNMENT00979282–USNMENT00979286, USNMENT00979289 (CNCI); UCRC ENT 110944, 110951, 110963, 110983, 110985, 110992, 111001–111003, 111009, 111011, 111066, 111078, 133622, 297001–297003, 297009, 297013 (UCRC). **SOUTH KOREA**: 29 females, 3 males, OSUC 144470–144471, USNMENT00896011, USNMENT00896015, USNMENT00896016, USNMENT00896018, USNMENT00896019, USNMENT00896029, USNMENT00896032, USNMENT00896044 – USNMENT00896046, USNMENT00896112, USNMENT00896113 – USNMENT00896116, USNMENT00896118, USNMENT00896119, USNMENT00896121, USNMENT00896122, USNMENT00896134,



Figures 52–55.[34] **52** *T. cultratus*, female lectotype (NHMW 0008A), head, anterolateral view **53** *T. flavipes*, female lectotype (NHRS-HEVA 000002617), head, anterolateral view **54** *T. cultratus*, female (USNMENT00675734), head, anterior view **55** *T. flavipes*, female lectotype (NHRS-HEVA 000002617), head, anterior view. Scale bars in millimeters.

USNMENT00896135, USNMENT00896157, USNMENT00979237, USNMENT-00979246–USNMENT00979250, USNMENT00979253, USNMENT00979280 (CNCI). **SWITZERLAND**: 4 females, 1 male, USNMENT00979222–USNMENT00979226 (CNCI). **TAIWAN**: 1 female, UCRC ENT 112210 (UCRC). **UNITED KINGDOM**: 1 female, USNMENT00916251 (BMNH).

Comments. Kozlov (1968) designated a lectotype for *T. flavipes* and simultaneously treated *T. cultratus* as a junior synonym. However, the concept of *T. flavipes* presented in the key and description of his publication was that of *T. cultratus*, and not of *T. flavipes*, which in our assessment is a distinctly different species; the two may easily be separated by the presence of parallel arched rugae on the frons of *T. cultratus*, contrasting with absence of large rugae and presence of a circular impression on the frons of *T. flavipes* (see Figs 52–55). The arched rugae on the frons of *T. cultratus* make the species particularly easy to identify, and the erroneous use of this character to identify *T. flavipes* was propagated throughout subsequent literature because Kozlov's treatment was followed, and the primary type of *T. cultratus* was not re-examined. An unfortunate consequence of this error is that undoubtedly most, if not all, specimens of *T. cultratus* and *T. flavipes* have been misidentified.

***Trissolcus edessae* Fouts**
http://bioguid.osu.edu/osuc_concepts:3221
Figures 56–59; Morphbank[6]

Trissolcus edessae Fouts, 1920: 65 (original description); Masner and Muesebeck 1968: 72 (type information); Johnson 1984: 799, 801 (description, keyed); Johnson 1987: 289, 300 (diagnosis, keyed).

Diagnosis. *Trissolcus edessae* may be distinguished from the native species of Nearctic *Trissolcus* in the *flavipes* group (*T. brochymenae*, *T. euschisti*, and *T. strabus*) by the abruptly bicolored female antennae. It may be separated from *T. japonicus* by the presence of 2 clypeal setae and the episternal foveae that do not form a continuous line from the postacetabular sulcus to the mesopleural pit. It may be separated from *T. cultratus* by the absence of parallel arched rugae on the frons. In *T. edessae* a median mesoscutal carina is often present, and this is absent in *T. cultratus* and *T. japonicus*.

Johnson (1984) used the absence of a mesopleural carina in *T. edessae* as a diagnostic character. Our examination included a specimen in which the mesopleural carina is present (Fig. 58) and thus we prefer not to use this character for identification. A result of this is that unambiguous identification of male specimens may require movement or removal of the wings to properly evaluate the surface sculpture within the axillar crescent.

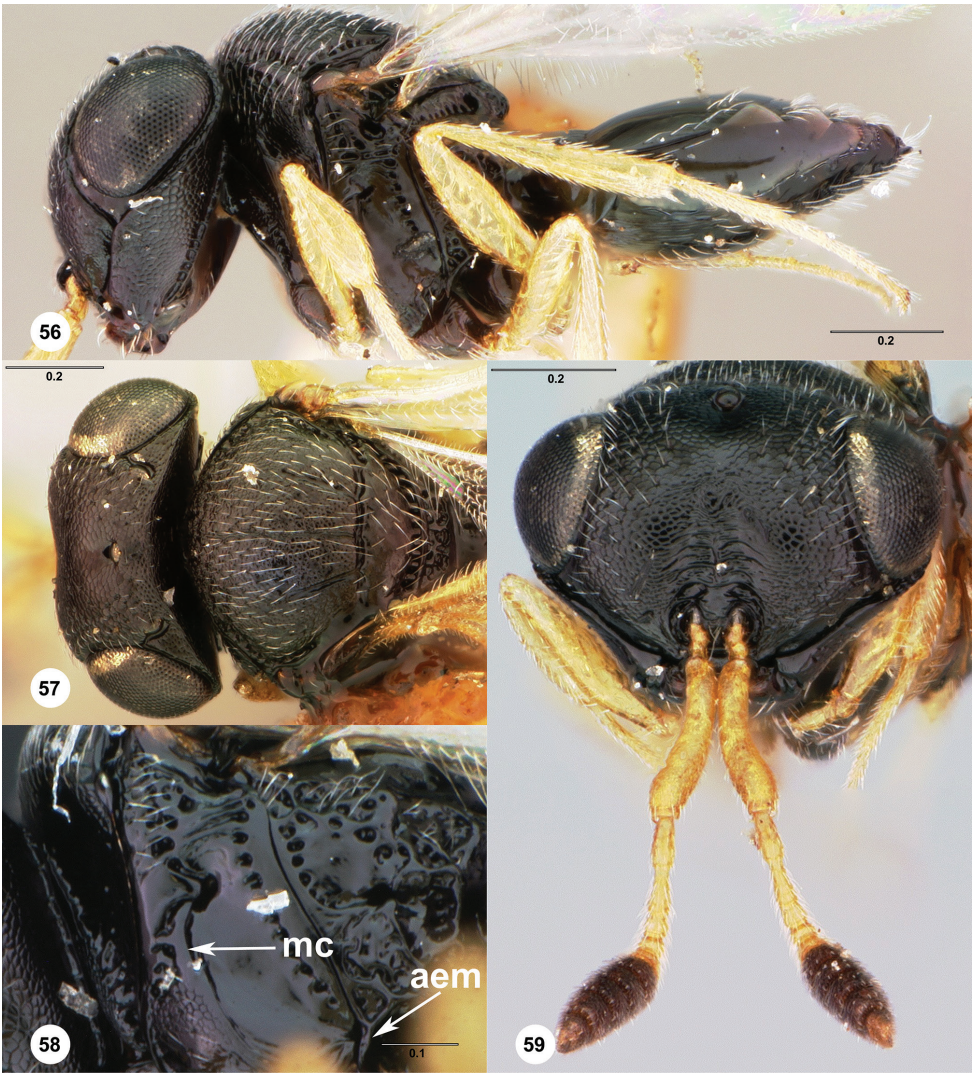
Link to distribution map. [http://hol.osu.edu/map-large.html?id=3221]

Associations. Emerged from egg of *Acrosternum hilare* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Edessa bifida* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; parasite of *Edessa bifida* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Euschistus* Dallas: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from *Pachycoris torridus* (Scopoli): [Hemiptera: Heteroptera: Pentatomoidea: Scutelleridae]

Material examined. Holotype, female: **UNITED STATES**: LA, Orleans Parish, New Orleans, 23.VII.1919, C. E. Smith, USNMENT00872412 (deposited in USNM). *Other material*: (2 females, 1 male, 29 sex unrecorded) **EL SALVADOR**: 3 sex unrecorded, USNMENT00764980, USNMENT00764981, USNMENT00764993 (USNM). **NICARAGUA**: 2 sex unrecorded, OSUC 398762–398763 (CNCI). **UNITED STATES**: 2 females, 1 male, 24 sex unrecorded, OSUC 17814 (BMNH); OSUC 398760–398761 (CNCI); OSUC 523872 (MEMU); OSUC 145559, 542444, 75617–75636 (OSUC); OSUC 145649 (USNM).

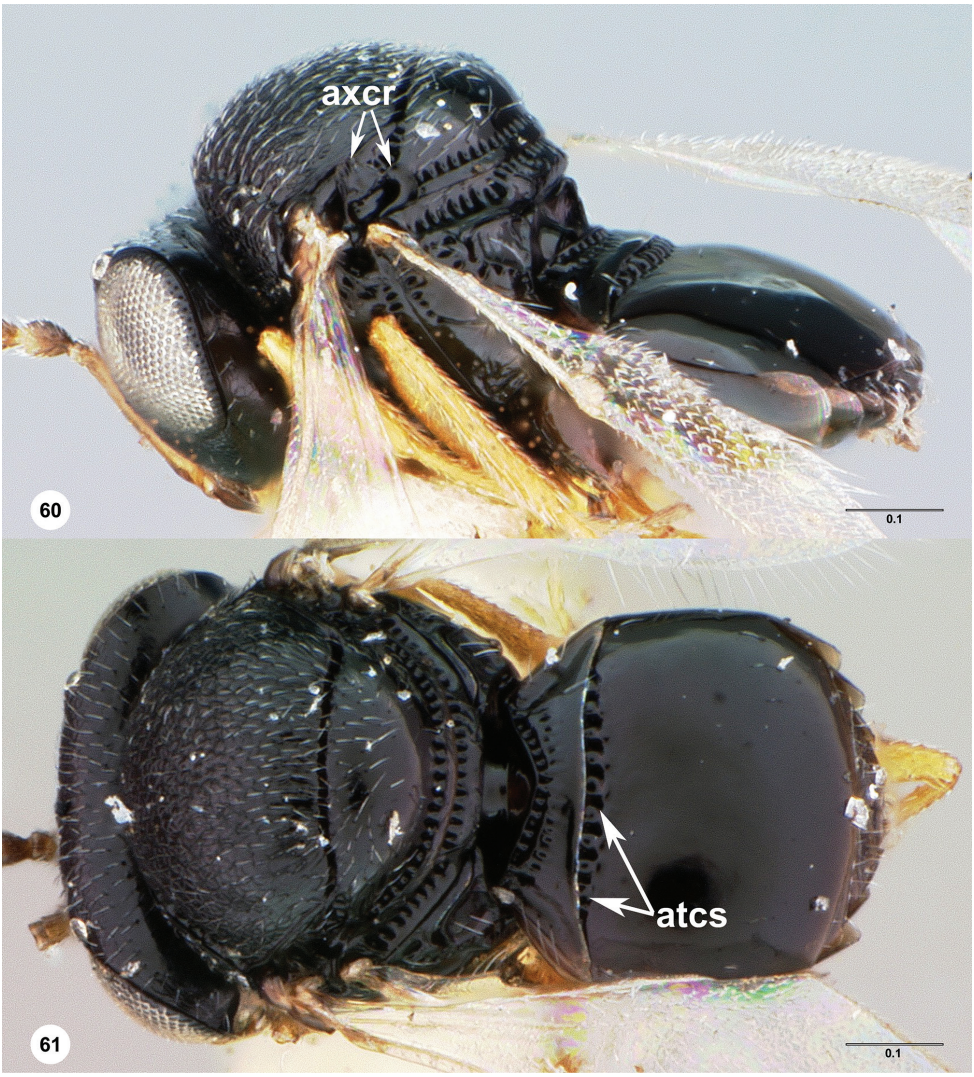
***Trissolcus erugatus* Johnson**
http://bioguid.osu.edu/osuc_concepts:3228
Figures 27, 60–61; Morphbank[7]

Trissolcus erugatus Johnson, 1985b: 433, 436 (original description, keyed); Sarazin 1986: 980 (type information).



Figures 56–59.[35] *Trissolcus edessae* **56** female holotype (USNMENT00872412) head, mesosoma, metasoma, lateral view **57** female holotype (USNMENT00872412) head, mesosoma, dorsal view **58** (USNMENT00764981), mesopleuron, metapleuron, lateral view **59** female holotype (USNMENT00872412), head, anterior view. Scale bars in millimeters.

Diagnosis. *Trissolcus erugatus* may be distinguished from the most common Southwestern species of *Trissolcus* discussed here, *T. utahensis*, by its strongly narrowed gena, angulate vertex, and the lack of rugulae on T2 (occasionally rugulae are present, but these are very short in comparison with those of *T. utahensis*). It may be distinguished from *T. hullensis* by the following characters: metapostnotum invaginated near metascutellum and separating metanotum from propodeum, anterior extension of metapleuron short, not reaching mesocoxa, mandibular teeth shallowly incised; mesopleural



Figures 60–61. [36] *Trissolcus erugatus* female paratype (USNMENT00903009) **60** head, mesosoma, metasoma, lateral view **61** head, mesosoma, metasoma, dorsal view. Scale bars in millimeters.

carina absent; legs and A1–A6 usually yellow. *Trissolcus cosmopeplae* may usually be separated from *T. erugatus* by the strong development of rugulae on T2 and the long anteroventral extension of the metapleuron toward the mesocoxa in the former species.

Trissolcus erugatus seems to be a rather isolated species within the New World fauna of the genus. The narrowed gena allies it with *T. hullensis*, *T. solocis*, *T. radix*, and *T. cosmopeplae*, but the condition of the metapostnotum, mandibular teeth, and metapleural extension usually distinguish it quite clearly. Specimens from the Southwest are easily identifiable, but variation in color and sculpture in the northern part of its range may result in confusion between this species and *T. cosmopeplae*.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3228]

Associations. collected on *Larrea tridentata* (Sessé & Moc. ex DC.) Coville: [Sapindales: Zygophyllaceae]; emerged from egg of *Thyanta custator* (Fabricius): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; collected on alfalfa: [Fabales: Fabaceae]; collected on lodgepole pine: [Pinales: Pinaceae]

Material examined. *Paratypes*: (1 female, 1 male, 11 sex unrecorded) **CANADA**: 1 female, OSUC 17813 (BMNH). **UNITED STATES**: 1 male, 11 sex unrecorded, OSUC 398779–398780 (CNCI); OSUC 77860–77862 (MSWC); OSUC 145560, 75668–75672 (OSUC); USNMENT00903009 (USNM). *Other material*: (3 females, 2 males, 9 sex unrecorded) **CANADA**: 4 sex unrecorded, OSUC 398784–398787 (CNCI). **UNITED STATES**: 3 females, 2 males, 5 sex unrecorded, OSUC 398781–398783, 398788 (CNCI); OSUC 436700 (LACM); OSUC 413943, 523926–523927, 523929, 75667 (OSUC).

***Trissolcus euschisti* (Ashmead)**
http://bioguid.osu.edu/osuc_concepts:3232
Figures 12, 20, 28, 42–43, 62–65; Morphbank[8]

Telenomus euschristus Ashmead, 1888: ii (original description, spelling error).

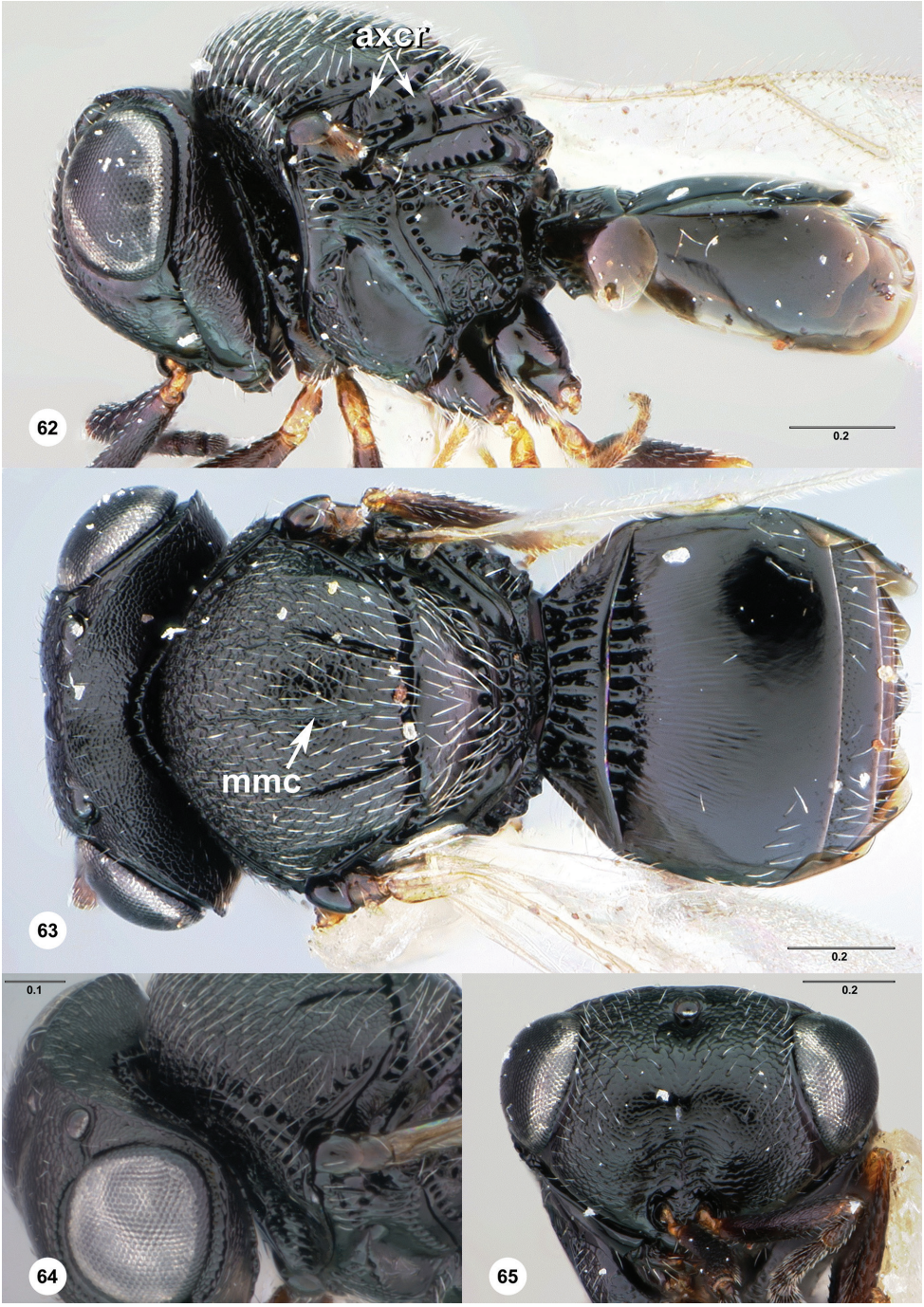
Trissolcus euschisti (Ashmead): Ashmead 1893: 161, 162 (emendation, description, generic transfer, keyed); Harrington 1900: 183 (variation); Brues 1916: 549, 550 (description, keyed); Kieffer 1926: 127, 129 (description, keyed); Johnson 1984: 799, 801 (lectotype designation, synonymy, description, keyed); Johnson 1987: 289, 301 (diagnosis, keyed).

Trissolcus podisi Ashmead, 1893: 161, 162 (original description, keyed, synonymized by Johnson (1984)); Brues 1916: 550 (description, keyed); Kieffer 1926: 127, 129 (description, keyed); Masner and Muesebeck 1968: 73 (lectotype designation); Johnson 1984: 801 (junior synonym of *Trissolcus euschisti* (Ashmead)).

Trissolcus rufitarsis Kieffer, 1906: 262 (original description, synonymized by Johnson (1984)); Kieffer 1926: 127, 128 (description, keyed); Hoebeke 1980: 27 (type information); Johnson 1984: 801, 803 (lectotype designation, junior synonym of *Trissolcus euschisti* (Ashmead)); Zuparko and Hamai 1994: 314 (type information).

Trissolcus euchisti (Ashmead): Brues 1908: 11 (emendation); Golin, Loiácono, Margaría and Aquino 2011: 618 (host association).

Diagnosis. *Trissolcus euschisti* may be distinguished from the similar *T. brochymenae* by the smooth or shallowly impressed sculpture on the ventral portion of the mesopleuron anterior to the mesopleural carina. The smaller specimens of *T. euschisti* are often quite distinct from the larger ones in the following characters: number of lateral setae on T1, extent of fine wrinkles on T2, extent of rugae on S2, extent of S1 setation, number of setae on the mesopleuron above the mesocoxa, sculpture of the upper



Figures 62–65.[37] *Trissolcus euschisti* **62** female (USNMENT00872098), head, mesosoma, metasoma, lateral view. **63** female (USNMENT00872098), head, mesosoma, metasoma, dorsal view **64** female (OSUC 334007), head and mesosoma, dorsolateral view **65** female (USNMENT00872098), head, anterior view. Scale bars in millimeters.

portion of the frons, extent of transverse striae within the antennal scrobe, and the presence of a shallow groove below the anterior ocellus.

The separation of *T. euschisti* and *T. brochymenae* may be difficult with specimens that exhibit an intermediate state of faint rugosity on the anteroventral mesopleuron. These specimens are not common in our experience and the situation reflects the need for molecular data to further test the hypotheses of species delimitation presented here and in the revisions of Nearctic *Trissolcus* by Johnson (1984, 1985a,b).

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3232]

Associations. Collected on *Acer saccharum* Marshall: [Sapindales: Aceraceae]; emerged from egg of *Acrosternum hilare* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; on leaf of *Catalpa* Scop.: [Scrophulariales: Bignoniaceae]; emerged from egg of *Edessa meditabunda* (Fabricius): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of / host egg of *Euschistus* Dallas: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Euschistus conspersus* Uhler: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Pentatomidae*: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of / host egg of *Pentatomidae*: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; unspecified association *Pentatomidae*: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Podisus maculiventris* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from sentinel egg mass of *Podisus maculiventris* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; parasite of *Podisus maculiventris* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; unspecified association *Podisus maculiventris* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Podisus serieventris* Uhler: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Podisus spinosus* (Dallas): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; collected on *Quercus agrifolia* Nee.: [Fagales: Fagaceae]; emerged from sentinel egg mass of *Thyanta accerra custator* (Fabricius): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; collected on alder: [Fagales: Betulaceae]; on young maple: [Sapindales: Aceraceae]; collected on pecan: [Juglandales: Juglandaceae]; collected on red pine: [Pinales: Pinaceae]; collected on wax myrtle: [Myricales: Myricaceae]

Material examined. Lectotype, female, *T. euschristus*: **UNITED STATES**: Riley Co., VI, Marlatt, OSUC 256926 (deposited in OSUC). Lectotype, female, *T. rufitarsis*: **UNITED STATES**: Ormsby Co., VII, Baker, Cornell U. No. 388.1 (deposited in CUIC). Lectotype, female, *T. rufitarsis*: **UNITED STATES**: Ormsby Co., VII, Baker, USNMENT00979614 (deposited in CUIC). Lectotype, female, *T. podisi*: **UNITED STATES**: PA, Philadelphia Co., Philadelphia, no date, Cresson, USNMENT00989033 (deposited in USNM). *Paratypes*: **UNITED STATES**: 2 sex unrecorded, OSUC 398789, 398823 (CNCI). *Other material*: (71 females, 10 males, 243 sex unrecorded) **BRAZIL**: 3 sex unrecorded, OSUC 75746–75748 (OSUC). **CANADA**: 1 female, 1 male, 32 sex unrecorded, OSUC 145426–145427, 398793–398798, 398800–398803, 398805–398817, 398836–398840, 398844–398847 (CNCI). **FRENCH GUIANA**:

1 sex unrecorded, OSUC 248138 (OSUC). **MEXICO**: 1 sex unrecorded, OSUC 75745 (OSUC). **NORTH AMERICA**: 1 female, OSUC 398799 (CNCI). **UNITED STATES**: 69 females, 9 males, 201 sex unrecorded, OSUC 17808 (BMNH); OSUC 145178, 145409–145410, 398790–398792, 398818–398822, 398824–398835, 398841–398843 (CNCI); USNMENT00979600, USNMENT00979603, USNMENT00979605 (CUIC); OSUC 436702 (LACM); OSUC 523870–523871, 523874 (MEMU); OSUC 145411–145418, 145421–145425 (MSWC); IRREC 1794, IRREC834, OSUC 143837, OSUC 143838–OSUC 143850, OSUC 145177, OSUC 145561, OSUC 157488–OSUC 157493, OSUC 181546, OSUC 248134, OSUC 248139, OSUC 334007, OSUC 402728, OSUC 404912, OSUC 409995, OSUC 413680, OSUC 413681, OSUC 413682–OSUC 413699, OSUC 413729–OSUC 413748, OSUC 413940, OSUC 523862, OSUC 523863, OSUC 523866–OSUC 523868, OSUC 523883–OSUC 523903, OSUC 523924, OSUC 523928, OSUC 523934, OSUC 523939, OSUC 523941, OSUC 542439, OSUC 542441, OSUC 542443, OSUC 70463, OSUC 75678–OSUC 77202, OSUC 79805 (OSUC); OSUC 145419–145420 (UCRC); BMSB 1218, 1220–1230, 1232, OSUC 523851, USNMENT00872096–USNMENT00872102, USNMENT00989171, USNMENT00989172, USNMENT00989174–USNMENT00989179 (USNM).

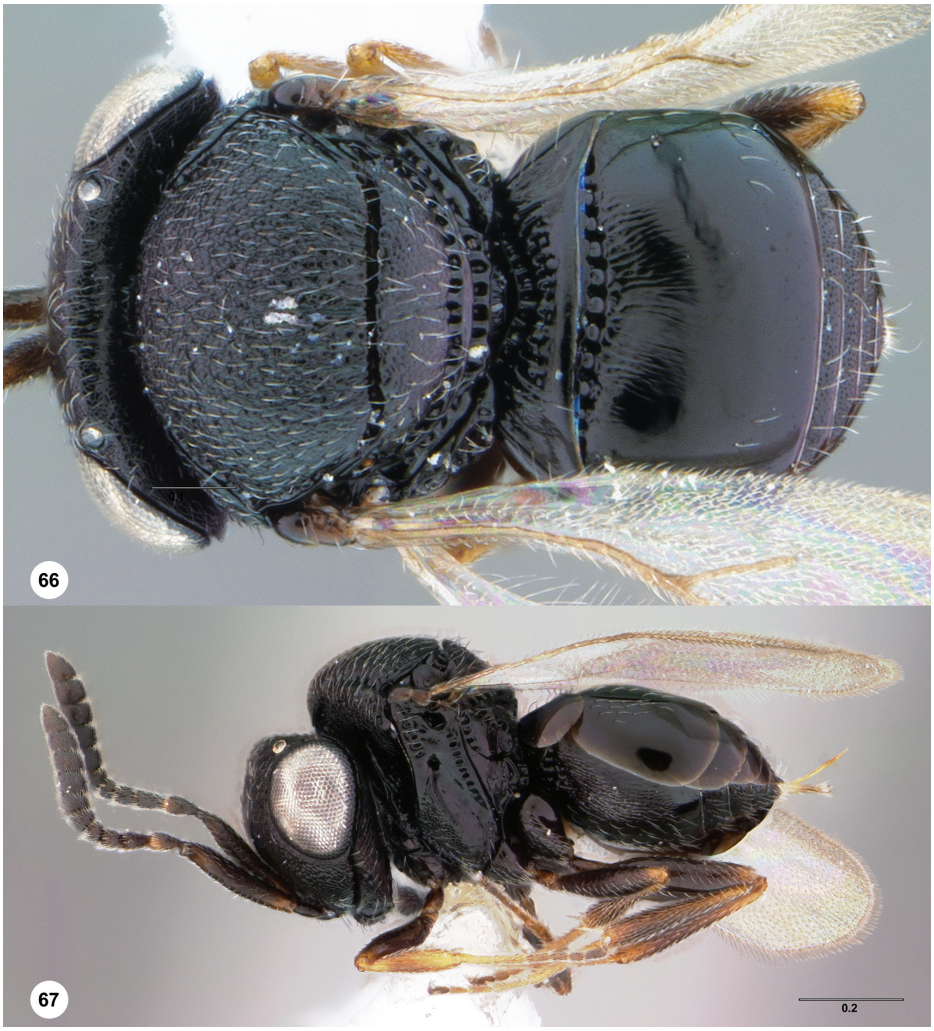
***Trissolcus hullensis* (Harrington)**
http://bioguid.osu.edu/osuc_concepts:3244
Figures 22, 24, 66–67; Morphbank[9]

Telenomus hullensis Harrington, 1900: 182 (original description); Kieffer 1926: 27, 40 (description, keyed).
Trissolcus hullensis (Harrington): Johnson 1984: 10 (generic transfer); Johnson 1985b: 433, 438 (description, keyed); Sarazin 1986: 981 (type information).

Diagnosis. *Trissolcus hullensis* is most closely related to *T. solocis*, *T. radix* and *T. zakotos*. *Trissolcus hullensis* may be distinguished from these by the anteriorly invaginated metapostnotum. Additional characters useful for identification are: the paracoxal sulcus in the ventral half of the metapleuron, absent in *T. hullensis*, present in *T. radix* and *T. zakotos*; sculpture of the mesoscutellum, coriaceous or smooth in southern specimens of *T. hullensis*, coarsely areolate in *T. solocis* and *T. radix*; the color of the radicle, black in *T. hullensis*, *T. zakotos* and *T. solocis*, yellow in *T. radix*; and the rounded vertex, sharply angled in *T. radix* and *T. solocis*.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3244]

Associations. Emerged from *Euschistus servus* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Pentatomidae*: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Podisus maculiventris* (Say): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from *Recurvaria milleri* Busck: [Lepidoptera: Glossata: Gelechioidea: Gelechiidae].



Figures 66–67.[38] *Trissolcus hullensis* **66** female (OSUC 523881), head, mesosoma, metasoma, dorsal view **67** female (USNMENT00903008), head, mesosoma, metasoma, lateral view. Scale bars in millimeters.

Material examined. *Non-type*: **UNITED STATES**: 1 female, OSUC 266782 (OSUC). *Other material*: (17 females, 1 male, 64 sex unrecorded) **CANADA**: 1 female, 5 sex unrecorded, OSUC 17815 (BMNH); OSUC 145179, 145392–145393, 398853 (CNCI); OSUC 75837 (OSUC). **MEXICO**: 11 sex unrecorded, OSUC 398854 (CNCI); OSUC 77870–77877 (MSWC); OSUC 75838–75839 (OSUC). **UNITED STATES**: 16 females, 1 male, 48 sex unrecorded, OSUC 145391, 398855–398857, 542438 (CNCI); OSUC 523873, 523875–523882 (MEMU); OSUC 77865–77869 (MSWC); OSUC 142487–142491, 143851, 145369–145373, 145389, 145562, 523856, 523946, 542456, 62453, 70529, 75826–75836, 76427–76428 (OSUC); OSUC 145374–145378, 145380–145388, 145390 (UCRC).

***Trissolcus japonicus* (Ashmead)**
http://bioguid.osu.edu/osuc_concepts:3249
Figures 17, 21, 25, 68–71; Morphbank[10]

Dissolcus japonicus Ashmead, 1904: 73 (original description); Kieffer 1926: 124, 125 (description, keyed).

Trissolcus japonicus (Ashmead): Masner and Muesebeck 1968: 72 (type information, generic transfer); Hirashima and Yamagishi 1981: 153 (description, synonymy); Ryu and Hirashima 1984: 37, 43 (description, keyed); Talamas, Buffington and Hoelmer 2013: 114 (description, synonymy, type information).

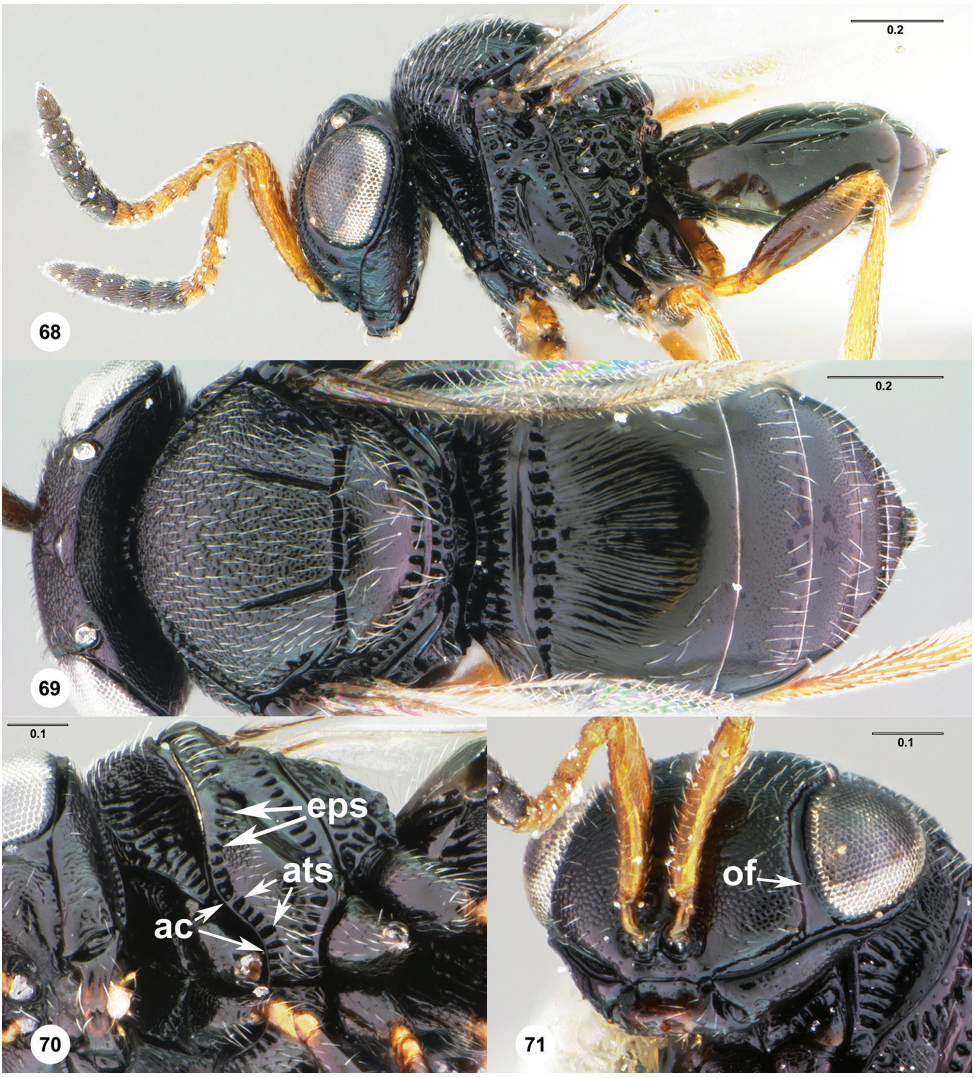
Trissolcus halyomorphae Yang: Qiu, Yang and Tao 2007: 62 (unavailable: nomen nudum); Yang, Yao, Qiu and Li 2009: 40 (original description); Talamas, Buffington and Hoelmer 2013: 114 (junior synonym of *Trissolcus japonicus* (Ashmead)).

Diagnosis. As previous authors have stated (Yang et al. 2009), *T. japonicus* belongs to the *flavipes* species group, first recognized by Kozlov and Lê (1976) and refined by Johnson (1984). *Trissolcus japonicus* may be separated from other species of the *flavipes* group *Trissolcus* in the Nearctic by the following characters: orbital furrow expanded near intersection with malar sulcus; postacetabular and mesopleural epicoxal sulci formed by lines of closed cells (Fig. 70); episternal foveae extending from dorsal apex of postacetabular carina to mesopleural pit (Fig. 68); 4 clypeal setae (Fig. 25).

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3249]

Associations. Emerged from egg of *Halyomorpha halys* (Stål): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from *Plautia stali* Scott: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; collected on mulberry: [Urticales: Moraceae]; emerged from stink bug: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of stink bug: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]

Material examined. Holotype, female, *D. japonicus*: **JAPAN**: Kanagawa Pref., Ashigarashimo Dist., Hakone Town, no date, Koebele, USNMENT00831865 (deposited in USNM). *Paratypes*: **CHINA**: 2 females, USNMENT00872401, USNMENT00872402 (USNM). *Other material*: (44 females, 16 males, 12 sex unrecorded) **CHINA**: 32 females, 11 males, 1 sex unrecorded, USNMENT00979190, USNMENT00979191, USNMENT00979192–USNMENT00979198, USNMENT00979200, USNMENT00979201–USNMENT00979221 (CNCI); USNMENT00675704, USNMENT00675738, USNMENT00675739, USNMENT00675743, USNMENT00675747, USNMENT00675925, USNMENT00764940, USNMENT00764941, USNMENT00764944, USNMENT00764948, USNMENT00764949, USNMENT00764984, USNMENT00916255 (USNM). **JAPAN**: 8 females, 4 males, 10 sex unrecorded, OSUC 144481–144482, 398858, USNMENT00896340 (CNCI); OSUC 145632, 75843–75848 (OSUC); US-



Figures 68–71. [39] *Trissolcus japonicus* **68** female (USNMENT00872402), head, mesosoma, metasoma, lateral view **69** female (USNMENT00675989), head, mesosoma, metasoma, dorsal view 7**0** female (USNMENT00675989), head, mesosoma, ventral view **71** female (USNMENT00872402), head, anterolateral view. Scale bars in millimeters.

NMENT00675755, USNMENT00675770, USNMENT00872125–USNMENT00872133 (USNM). **RUSSIA**: 1 female, USNMENT00979287 (CNCI). **SOUTH KOREA**: 3 females, 1 male, USNMENT00979251, USNMENT00979254 (CNCI); USNMENT00675705, USNMENT00675708 (USNM).

***Trissolcus occiduus* Johnson**
http://bioguid.osu.edu/osuc_concepts:3275
Figures 18, 34, 72–75; Morphbank[11]

Trissolcus occiduus Johnson, 1985a: 109, 111 (original description, keyed).

Diagnosis. This species may be distinguished from other species in the *thyantae* group by the expanded gena. It may also be separated from *T. thyantae* by the complete mesopleural carina, and from *T. parma* and *T. ruidus* by the entirely smooth mesoscutellum and absence of a genal carina.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3275]

Associations. Collected on *Abronia maritima* Nutt. ex S.Watson: [Caryophyllales: Nyctaginaceae]; emerged from egg of *Chlorochroa norlandorum* Buxton & Thomas: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Chlorochroa sayi* (Stål): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from *Pentatoma sayii* (Stål): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]

Material examined. Holotype, female: **UNITED STATES**: CA, Ventura Co., area 2, Point Mugu Naval Air Station, 31.VII–24.VIII.1981, C. D. Nagano & J. N. Hogue, CNCI 0004 (deposited in CNCI). *Paratypes*: **UNITED STATES**: 4 females, 5 sex unrecorded, OSUC 17811 (BMNH); OSUC 145180 (CNCI); OSUC 143814 (LACM); OSUC 77864 (MSWC); OSUC 145564, 76216–76217 (OSUC); USNMENT00764995, USNMENT00877675 (USNM). *Other material*: **UNITED STATES**: 3 females, 1 male, 1 sex unrecorded, OSUC 145365, 76430 (OSUC); USNMENT00954754, USNMENT00979294, USNMENT00979295 (USNM).

***Trissolcus parma* Johnson**
http://bioguid.osu.edu/osuc_concepts:3284
Figures 76–79; Morphbank[12]

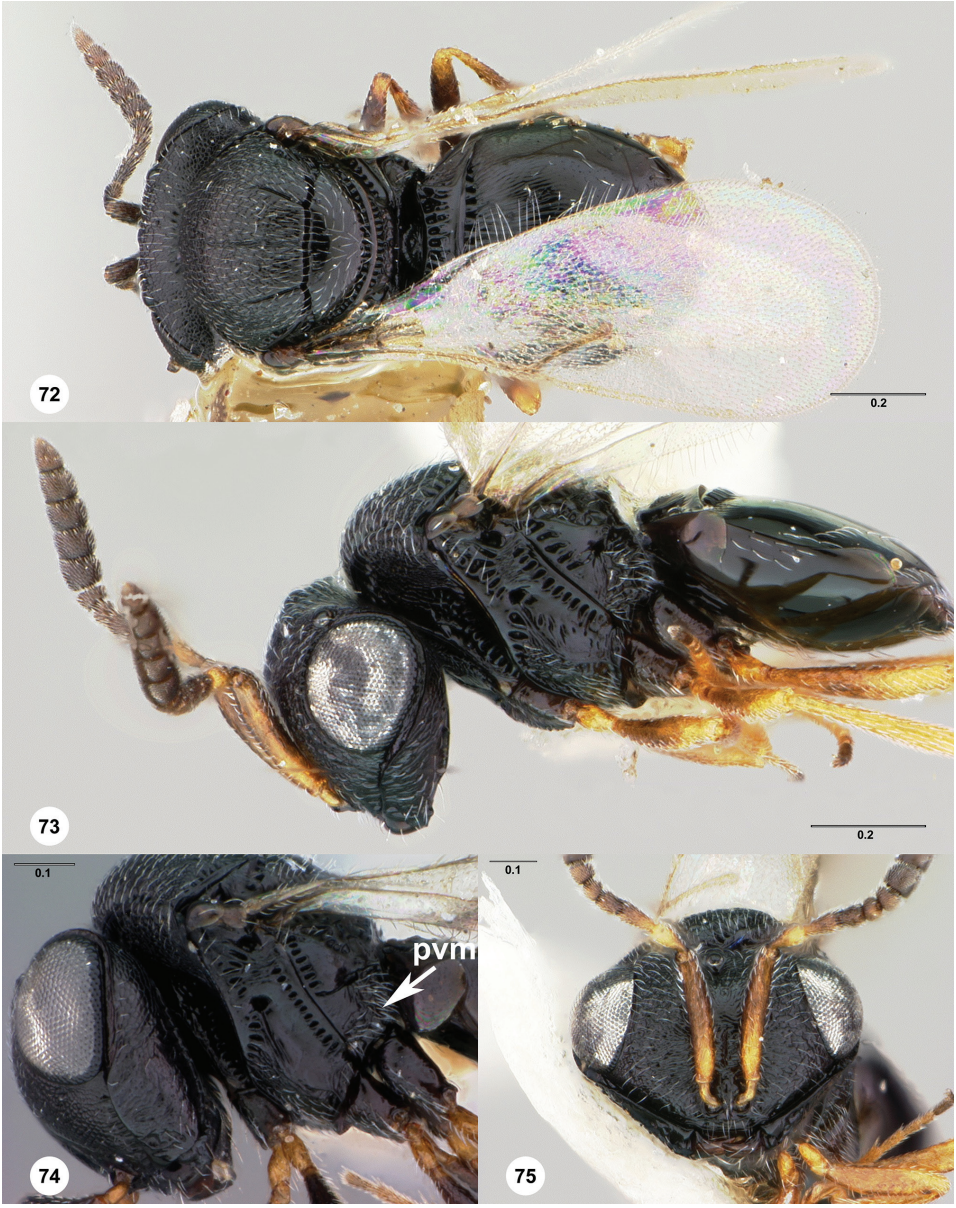
Trissolcus parma Johnson, 1985a: 110, 111 (original description, keyed); Sarazin 1986: 981 (type information).

Diagnosis. *Trissolcus parma* may be distinguished from *T. ruidus* by the lack of rugulae outside of the antennal scrobe and the lack of longitudinal elements in the sculpture of the posterior portion of the mesoscutum. It may be separated from the other members of the *thyantae* group by the presence of microsculpture on the mesoscutellum.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3284]

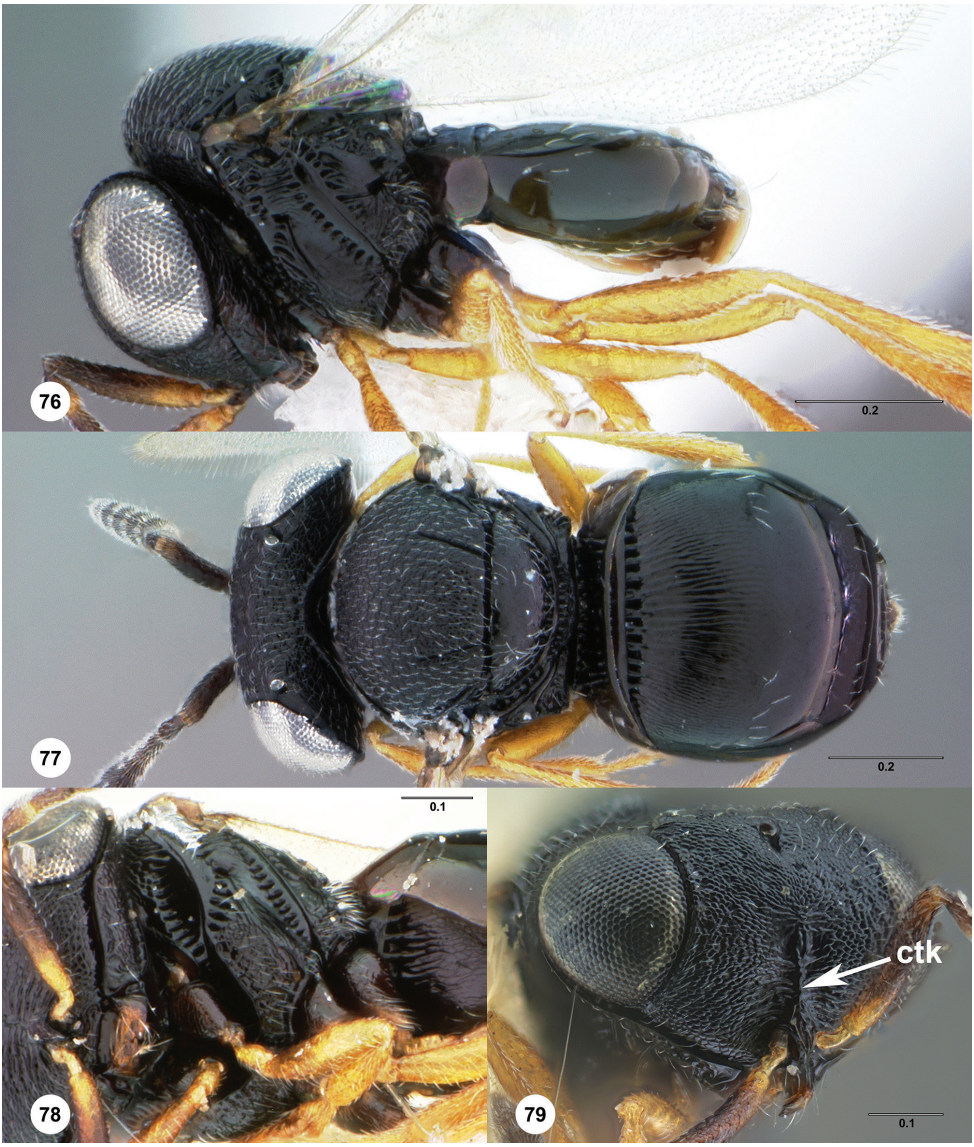
Associations. Collected on *Medicago sativa* L.: [Fabales: Fabaceae]; collected under *Vaccinium uliginosum* L.: [Ericales: Ericaceae]

Material examined. Holotype, female: **CANADA**: AB, Scandia, 2.VII.1956, sweeping, O. Peck, CNC No. 18339 (deposited in CNCI). *Paratypes*: (1 female, 1 male, 1 sex unrecorded)**CANADA**: 1 female, 1 sex unrecorded, OSUC 17809 (BMNH);



Figures 72–75. [40] *Trissolcus occiduus* **72** female (USNMENT00877675), head, mesosoma, metasoma, dorsal view **73** female (USNMENT00764995), head, mesosoma, metasoma, lateral view **74** female (OSUC 76126), head and mesosoma, lateral view **75** female (USNMENT00764995), head, anterior view. Scale bars in millimeters.

OSUC 145565 (OSUC). **UNITED STATES**: 1 male, USNMENT00764990 (USNM). *Other material*: (2 females) **CANADA**: 1 female, OSUC 76264 (OSUC). **UNITED STATES**: 1 female, OSUC 62481 (OSUC).



Figures 76–79.[41] *Trissolcus parma* **76** female (OSUC 76432), head, mesosoma, metasoma, lateral view **77** female (OSUC 62481), head, mesosoma, metasoma, dorsal view **78** female (USNMENT00765990), head and mesosoma, ventral view **79** female (USNMENT00765990), head, anterior view. Scale bars in millimeters.

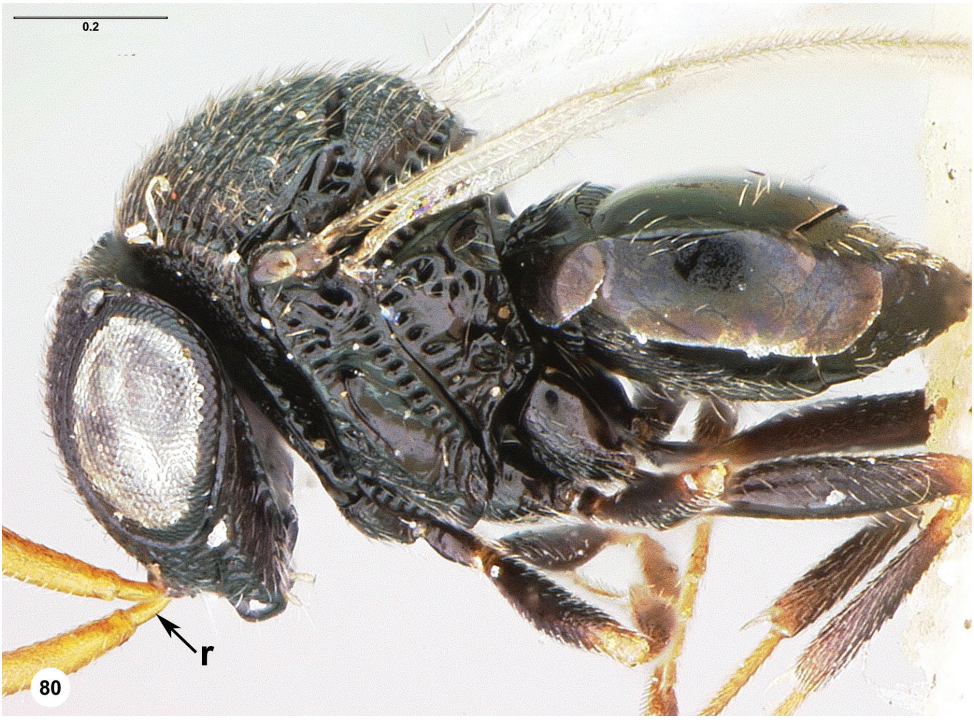


Figure 80. [42] *Trissolcus radix* female (USNMENT00764955), head, mesosoma, metasoma, lateral view. Scale bar in millimeters.

***Trissolcus radix* Johnson**
http://bioguid.osu.edu/osuc_concepts:3295
Figures 80–83; Morphbank[13]

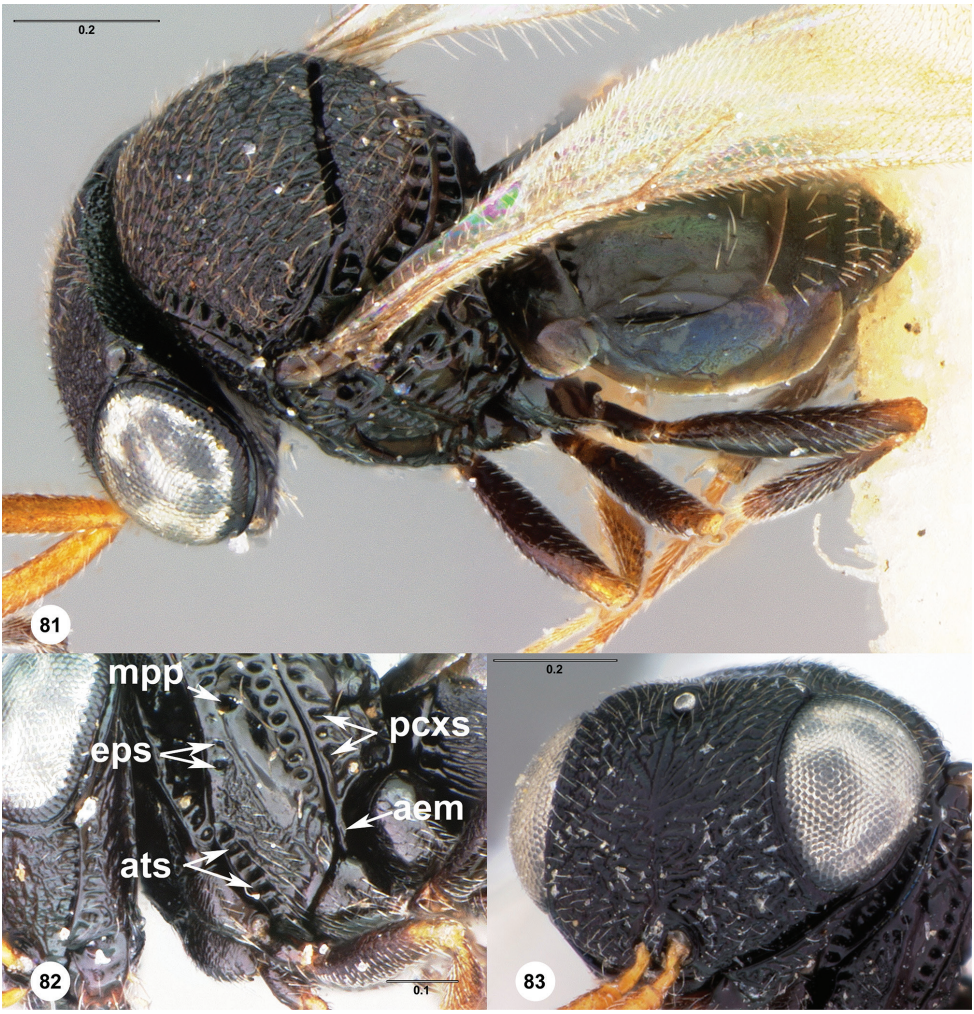
Trissolcus radix Johnson, 1985b: 432, 440 (original description, keyed).

Diagnosis. *Trissolcus radix* is most closely related to *T. hullensis*, *T. solocis*, and *T. zakotos*, from which it may be distinguished by the bright yellow radicle. The well defined paracoxal sulcus in the ventral half of the metapleuron serves to separate this species from *T. hullensis* and *T. solocis*, and the rugose sculpture of the mesoscutellum will separate it from *T. hullensis* and *T. zakotos*.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3295]

Associations. Emerged from egg of *Euthyrhynchus floridanus* (Linnaeus): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; collected on coffee: [Rubiales: Rubiaceae]

Material examined. *Paratypes*: (1 female, 4 sex unrecorded) **COSTA RICA**: 1 sex unrecorded, OSUC 76272 (OSUC). **GUATEMALA**: 1 sex unrecorded, USNMENT00764955 (USNM). **UNITED STATES**: 1 female, 2 sex unrecorded, OSUC 145567, 76270–76271 (OSUC). *Other material*: **MEXICO**: 2 sex unrecorded, USNMENT00896395, USNMENT00896396 (UANL).



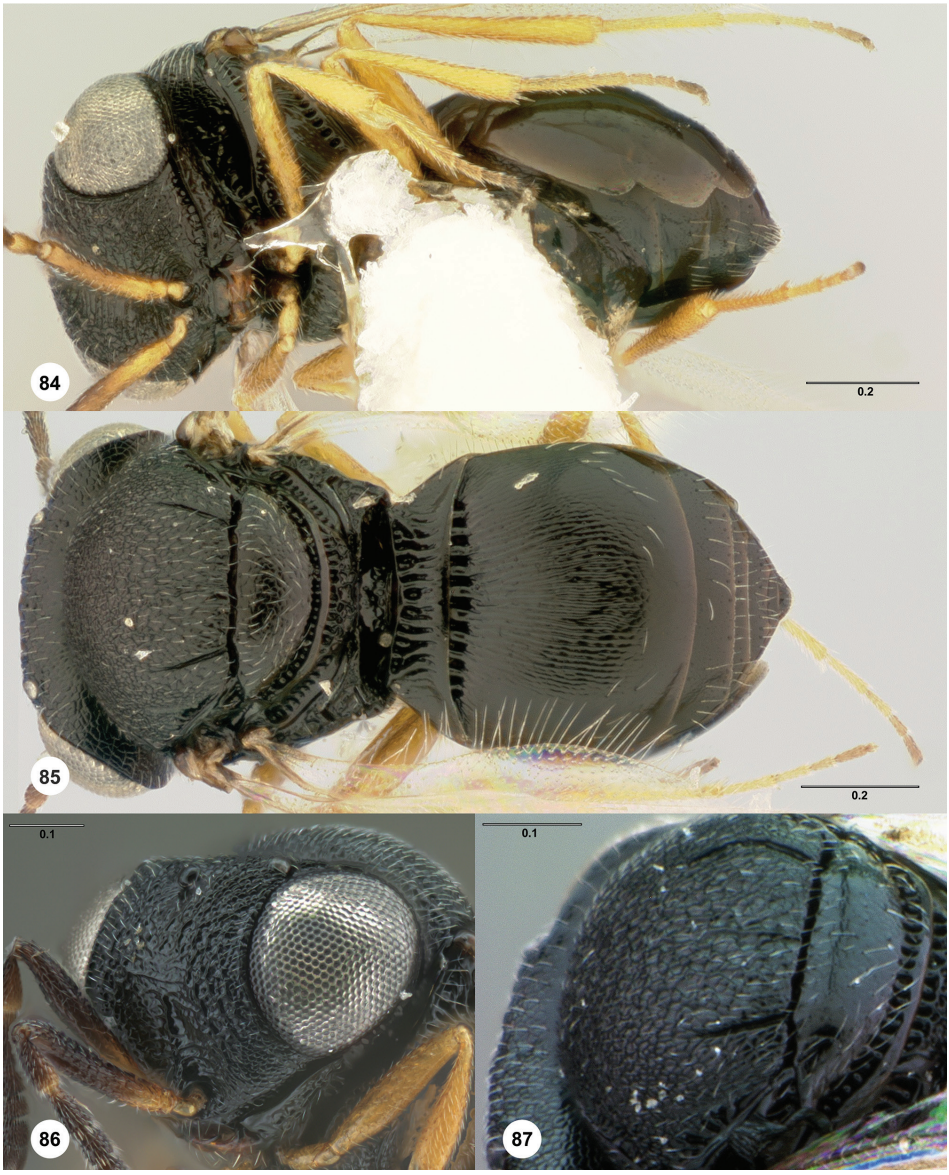
Figures 81–83.[43] *Trissolcus radix* **81** female paratype (USNMENT00764955), head, mesosoma, metasoma, dorsal view **82** female (USNMENT00764955), head and mesosoma, lateral view **83** female (OSUC 76271), head, anterolateral view. Scale bars in millimeters.

Trissolcus ruidus Johnson

http://bioguid.osu.edu/osuc_concepts:3299
Figures 33, 84–87; Morphbank[14]

Trissolcus ruidus Johnson, 1985a: 111 (original description, keyed); Sarazin 1986: 981 (type information).

Diagnosis. *Trissolcus ruidus* may be separated from *T. parma* by the presence of rugae on the lateral frons (Fig. 86) and longitudinal elements that are often present in the sculpture of the mesoscutum between the notauli. Like *T. parma*, it may be separated



Figures 84–87. [44] *Trissolcus ruidus* female paratype (OSUC 145568) **84** head, mesosoma, metasoma, ventrolateral view **85** head, mesosoma, metasoma, dorsal view **86** head mesosoma, anterolateral view **87** head, anterior view. Scale bars in millimeters.

from the other members of the *thyantae* group by the presence of microsculpture on the mesoscutellum.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3299]

Material examined. Holotype, female: **UNITED STATES**: AZ, Cochise Co., Portal, Southwestern Research Station (SWRS), 19.X.1978, Masner & Gibson, CNC

No. 18341 (deposited in CNCI). *Paratype*: **UNITED STATES**: 1 sex unrecorded, OSUC 145568 (OSUC). *Other material*: **UNITED STATES**: 2 females, 1 male, OSUC 76431–76432 (OSUC); OSUC 144847 (USNM).

Trissolcus solocis **Johnson**
http://bioguid.osu.edu/osuc_concepts:3311
Figures 88–91; Morphbank[15]

Trissolcus solocis Johnson, 1985b: 433, 441 (original description, keyed).

Diagnosis. *Trissolcus solocis* may be distinguished from the closely related *T. hullensis* and *T. zakotos* by the coarse sculpture of the mesoscutellum. From *T. radix* it may be most easily separated by its black radicle and the absence of a well-defined paracoxal sulcus in the ventral half of the metapleuron.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3311]

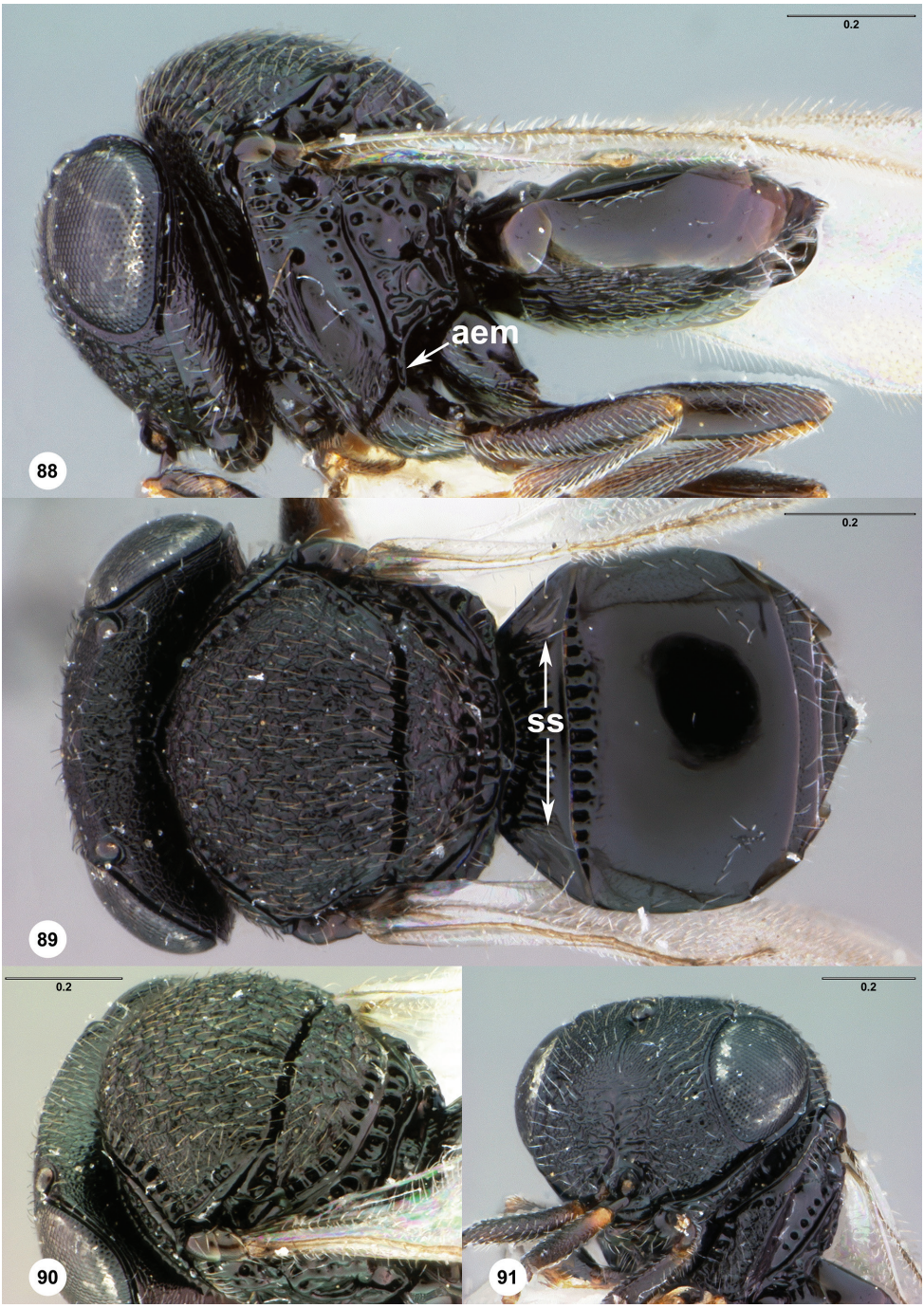
Associations. Emerged from egg of *Acrosternum marginatum* (Palisot): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Alcaeorrhynchus grandis* (Dallas): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Hemiptera*: [Hemiptera]

Material examined. *Paratypes*: (1 female, 1 male, 9 sex unrecorded) **MEXICO**: 4 sex unrecorded, USNMENT00764956, USNMENT00764957, USNMENT00764958, USNMENT00764959 (USNM). **UNITED STATES**: 1 female, 1 male, 5 sex unrecorded, OSUC 398866 (CNCI); OSUC 145569, 76309–76313 (OSUC).

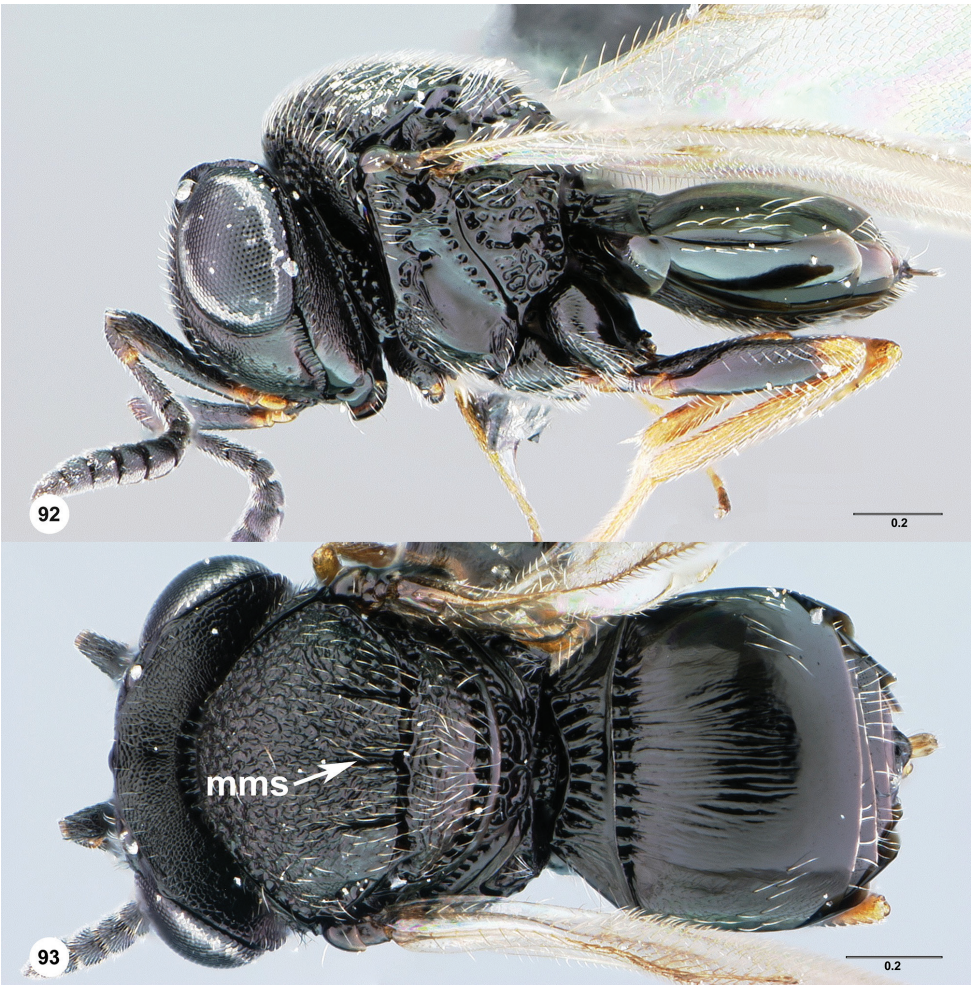
Trissolcus strabus **Johnson**
http://bioguid.osu.edu/osuc_concepts:3313
Figures 8, 23, 26, 29, 32, 92–93; Morphbank[16]

Trissolcus strabus Johnson, 1984: 798, 806 (original description, keyed); Sarazin 1986: 981 (type information); Johnson 1987: 286, 296 (diagnosis, keyed).

Diagnosis. *Trissolcus strabus* may be distinguished from species of the *flavipes* group in the Nearctic by the ventral constriction of the orbital furrow and the relatively coarse sculpture of the mesoscutellum. Most specimens have setae present on the first laterotergite, a character found among some *flavipes* group species of the Neotropics, but not elsewhere in the Nearctic. The rugose mesoscutellum can be used as a diagnostic character in most cases, but the degree of rugosity is variable. In some specimens the mesoscutellum is almost completely smooth with faint hints of rugae along the anterior margin. In others, the rugosity is confined to the lateral portions of the sclerite. In the latter case, rugose sculpture exists where there is setation, and in specimens



Figures 88–91.[45] *Trissolcus solocis* female paratype (OSUC 76312) **88** head, mesosoma, metasoma, lateral view **89** head, mesosoma, metasoma, dorsal view **90** head and mesosoma, dorsolateral view **91** head, anterolateral view. Scale bars in millimeters.



Figures 92–93. [46] *Trissolcus strabus*, female (BMSB 1203) **92** head, mesosoma, metasoma, lateral view **93** head, mesosoma, metasoma, dorsal view. Scale bars in millimeters.

with an entirely rugose mesoscutellum, the entire surface is setose. This leads us to hypothesize that, at least on the mesoscutellum of *T. strabus*, the rugose sculpture and setation are linked. The specimens with reduced macrosculpture on the mesoscutellum also have reduced sculpture on the lateral mesoscutum (lateral of the notaulus), revealing coriaceous microsculpture.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3313]

Associations. Emerged from egg of / host egg of *Brochymena* Amyot & Serville: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; on leaf of apple: [Rosales: Rosaceae]

Material examined. Holotype, female: **CANADA**: ON, Hamilton, 31.VII.1980, malaise trap, M. Sanborne, CNC No. 18342 (deposited in CNCI). *Paratypes*: (1 female, 3 sex unrecorded) **CANADA**: 1 sex unrecorded, OSUC 145570 (OSUC). **UNITED STATES**: 1 female, 2 sex unrecorded, OSUC 17810 (BMNH); OSUC 76314 (OSUC); USNMENT00764998 (USNM). *Non-type*: **UNITED STATES**: 1 female, OSUC 248187 (OSUC). *Other material*: (14 females, 1 male, 13 sex unrecorded) **UNITED STATES**: 14 females, 1 male, 12 sex unrecorded, IRREC 1469–1470, 1472, 1521, 1587, 1595, 1787, 1789, 1797, IRREC1582, IRREC1584 (OSUC); BMSB 1202–1215, OSUC 145650, OSUC 523850 (USNM).

***Trissolcus thyantae* Ashmead**
http://bioguid.osu.edu/osuc_concepts:3321
Figures 94–98; Morphbank[17]

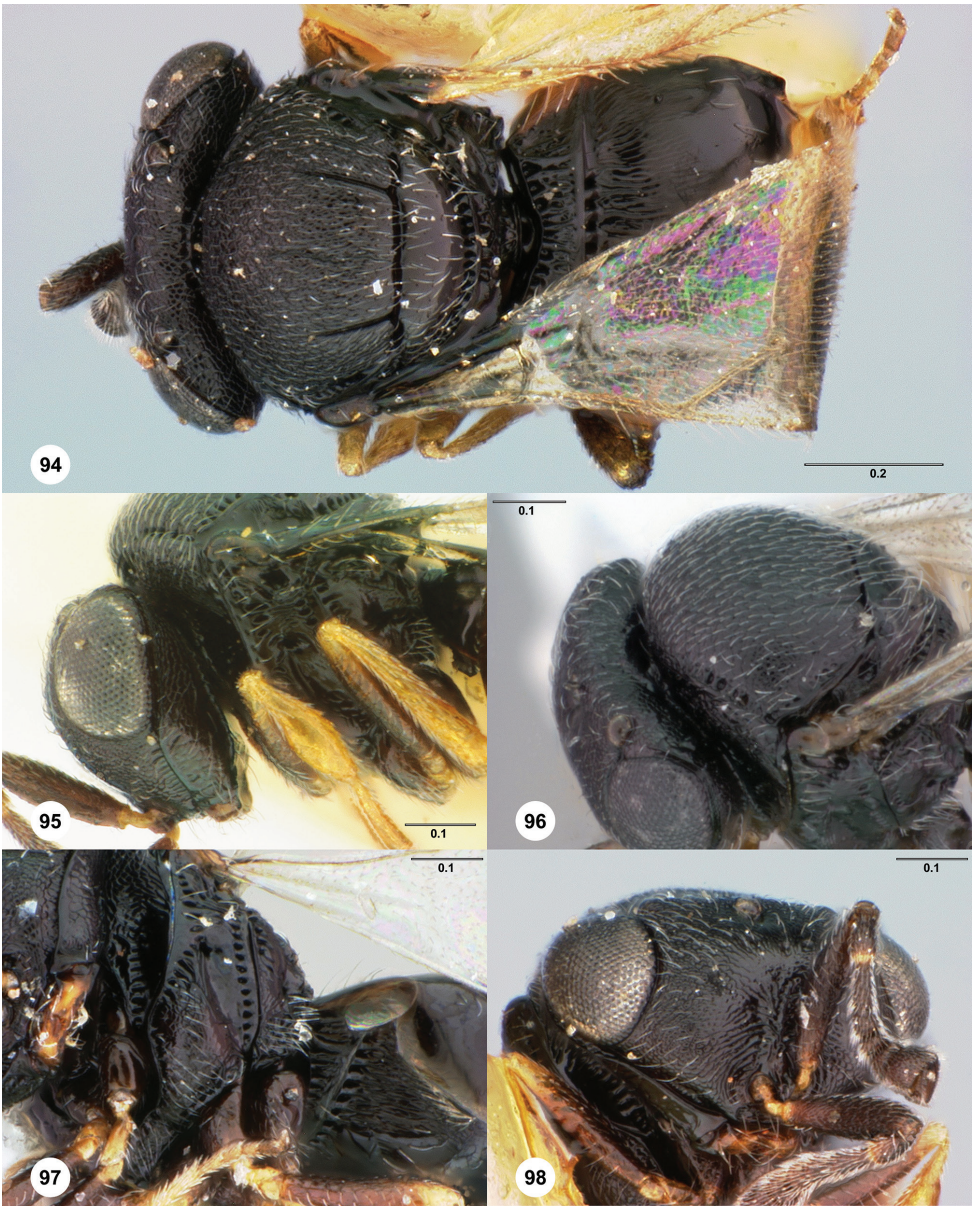
Trissolcus thyantae Ashmead, 1893: 162, 163 (original description, keyed); Brues 1916: 550 (description, keyed); Kieffer 1926: 127, 128 (description, keyed); Masner and Muesebeck 1968: 74 (lectotype designation); Johnson 1985a: 108, 111 (description, keyed).

Diagnosis. *Trissolcus thyantae* is most similar to *T. occiduus* and *T. valkyria*. It may be separated from *T. occiduus* by the narrow malar region and from both by the lack of a complete mesopleural carina.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3321]

Associations. Emerged from egg of *Euschistus* Dallas: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Euschistus variolarius* (Palisot de Beauvois): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Panthea furcilla* (Packard): [Lepidoptera: Glossata: Noctuoidea: Noctuidae]; emerged from egg of *Pentatomidae*: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Pinaceae*: [Pinales: Pinaceae]; emerged from egg of *Thyanta custator* (Fabricius): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; collected on pine: [Pinales: Pinaceae]; emerged from egg of pine: [Pinales: Pinaceae]; collected on soybean: [Fabales: Fabaceae]

Material examined. Lectotype, female: **UNITED STATES**: AL, Dallas Co., Selma, IX-1880, reared from egg, E. A. Schwarz, USNMENT00989048 (deposited in USNM). *Non-type*: **UNITED STATES**: 1 female, OSUC 266773 (OSUC). *Other material*: (2 females, 27 sex unrecorded) **CANADA**: 1 female, 6 sex unrecorded, OSUC 17812 (BMNH); OSUC 145196, 145368, 398870–398871 (CNCI); OSUC 145572, 76328 (OSUC). **UNITED STATES**: 1 female, 21 sex unrecorded, OSUC 157505–157506, 157512–157520, 76320–76327 (OSUC); USNMENT00764991, USNMENT00764994, USNMENT00979296 (USNM).



Figures 94–98. [47] *Trissolcus thyantae* **94** female holotype (USNMENT00989048), head, mesosoma, metasoma, dorsal view **95** female holotype (USNMENT00989048), head, mesosoma, lateral view **96** female (OSUC 76325), head and mesosoma, dorsolateral view **97** female (USNMENT00764991), mesosoma, ventrolateral view **98** female holotype (USNMENT00989048), head, anterolateral view. Scale bars in millimeters.

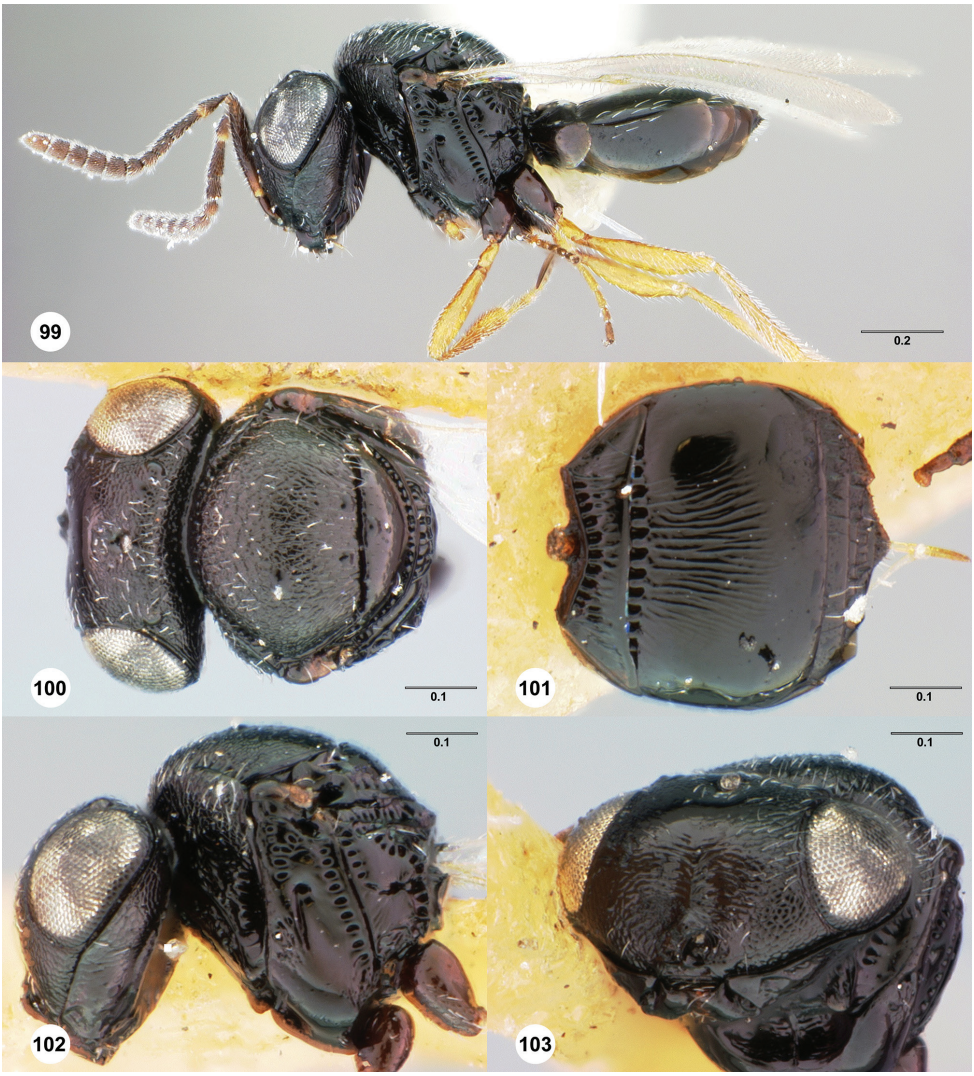
***Trissolcus utahensis* (Ashmead)**
http://bioguid.osu.edu/osuc_concepts:3327
Figures 99–103; Morphbank[18]

Telenomus utahensis Ashmead, 1893: 143, 145, 148 (original description, keyed).
Hadronotus mesillae Cockerell, 1897: 25 (original description, synonymized by Muesebeck & Walkley (1951)); Brues 1910: 47 (keyed); Kieffer 1926: 454, 464 (description, keyed); Muesebeck and Walkley 1951: 694 (junior synonym of *Telenomus utahensis* Ashmead).
Telenomus ashmeadi Morrill, 1907: 419 (original description, synonymized with *Telenomus mesillae* (Cockerell) by Gahan (1932)); Kieffer 1926: 27, 48 (description, keyed); Gahan 1932: 757 (junior synonym of *Telenomus mesillae* (Cockerell)); Mani 1936: 335 (description of misidentified Indian specimen).
Liophanurus utahensis (Ashmead): Kieffer 1926: 65, 73 (description, generic transfer, keyed).
Telenomus mesillae (Cockerell): Gahan 1932: 757 (generic transfer, synonymy).
Trissolcus utahensis (Ashmead): Krombein and Burks 1967: 297 (generic transfer); Masner and Muesebeck 1968: 74 (type information); Johnson 1985b: 432, 441 (description, keyed).
Trissolcus ashmeadi (Morrill): Masner and Muesebeck 1968: 71 (lectotype designation).
Trissolcus mesillae (Cockerell): Masner and Muesebeck 1968: 73 (type information).

Diagnosis. *Trissolcus utahensis* is a relatively dark-colored species, though some specimens from the southern part of its range have lighter-colored appendages. In the Nearctic region it is most similar to *T. basalis*. The two may be distinguished by the color of A1, usually dark, concolorous with the radicle in *T. utahensis,* and yellow, sharply contrasting with the dark radicle in *T. basalis*; and the mesoscutellar sculpture, smooth in *T. utahensis*, coriaceous in *T. basalis*.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=3327]

Associations. Emerged from *Chlorochroa sayi* (Stål): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Chlorochroa sayi* (Stål): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from *Chlorochroa uhleri* (Stål): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; collected on *Fremontia* Torr.: [Malvales: Malvaceae]; emerged from egg of *Pentatoma ligata* Say: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from *Pentatoma sayii* (Stål): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; egg parasite of *Pentatomidae*: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from *Pentatomidae*: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; emerged from egg of *Pentatomidae*: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; unspecified association *Pentatomidae*: [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; collected on *Pinus ponderosa* P. & C. Lawson: [Pinales: Pinaceae]; collected on *Prosopis* L.: [Fabales: Fabaceae]; living with *Rhyacionia neomexicana* (Dyar): [Lepidoptera: Glossata: Tortricoidea: Tortricidae]; collected on Russian thistle: [Caryophyllales: Chenopodi-



Figures 99–103. [48] *Trissolcus utahensis* **99** female (USNMENT00872111), head, mesosoma, metasoma, lateral view **100** female lectotype (USNMENT00), head and mesosoma, dorsal view **101** lectotype female (USNMENT00989049), metasoma, dorsal view **102** female lectotype (USNMENT00989049), head and mesosoma, lateral view **103** female lectotype(USNMENT00989049), head and mesosoma, anterolateral view. Scale bars in millimeters.

aceae]; emerged from *Thyanta pallidovirens* (Stål): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]; collected on tomato: [Solanales: Solanaceae]; on leaf of tomato: [Solanales: Solanaceae]; collected on wild carrot: [Apiales: Apiaceae].

Material examined. Lectotype, female, *T. utahensis*: **UNITED STATES**: Wasatch Range, 27.VI.1891, E. A. Schwarz, USNMENT00989049 (deposited in USNM). *Paralectotype*: **UNITED STATES**: 1 male, USNMENT00764992 (USNM). Lecto-

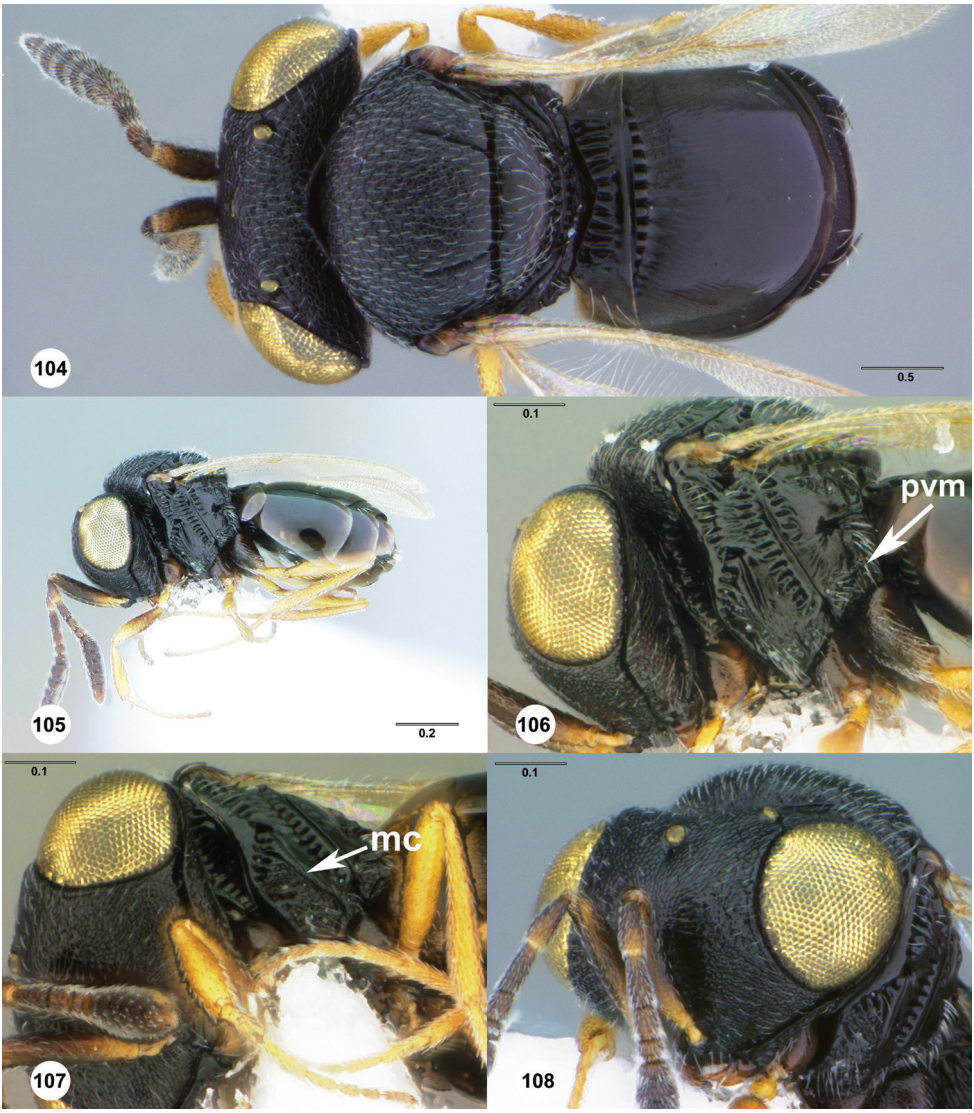
type, female, *T. ashmeadi*: **UNITED STATES**: TX, Ward Co., Barstow, 12.IX.1905, reared from egg, A. W. Morrill, USNM Type No. 10364 (deposited in USNM). Holotype, female, *H. mesillae*: **UNITED STATES**: NM, Doña Ana Co., Las Cruces, no date, reared from egg, T. D. A. Cockerell, USNM Type No. 3696 (deposited in USNM). *Other material*: (10 females, 3 males, 142 sex unrecorded) **CANADA**: 5 sex unrecorded, OSUC 145192–145193, 398862 (CNCI); OSUC 76416–76417 (OSUC). **UNITED STATES**: 10 females, 3 males, 136 sex unrecorded, OSUC 17807 (BMNH); OSUC 143819–143823, 436690–436699 (LACM); OSUC 77878–77930 (MSWC); OSUC 145230–145252, 145635, 405748, 413942, 542448–542449, 542451–542452, 542455, 76383–76415, 77203–77212 (OSUC); OSUC 205760 (UCDC); USNMENT00872110–USNMENT00872114 (USNM).

***Trissolcus valkyria* Johnson & Talamas, sp. n.**
http://zoobank.org/4DB6B48B-9DA2-47E0-98A5-A28103C42C15
http://bioguid.osu.edu/osuc_concepts:344497
Figures 104–108; Morphbank[19]

Description. Female body length: 0.97–1.11 mm (n=6). Color of radicle: yellow; brown; pale brown. Number of mandibular teeth: three. Number of clypeal setae: 6. Facial striae: absent. Shape of gena in lateral view: receding posteriorly. Genal carina: extending dorsally from base of mandible. Macrosculpture of frons outside of antennal scrobe: absent; irregularly rugose. Orbital furrow: narrow to absent near malar sulcus. Hyperoccipital carina: absent. Preocellar pit: present.

Epomial carina: present. Netrion sulcus: complete. Mesoscutal suprahumeral sulcus: indicated by cells. Mesoscutal humeral sulcus: indicated by cells. Pattern of mesoscutal microsculpture: antero-posteriorly uniform. Macrosculpture of mesoscutum: coriacious. Area bounded by axillar crescent: smooth. Parapsidal line: absent. Notaulus: present. Median mesoscutal carina: absent; present. Median mesoscutal sulcus: absent.

Sculpture of mesoscutellum: smooth. Postacetabular sulcus: comprised of cells. Shape of episternal foveae: round; antero-posteriorly elongate. Number of episternal foveae: 3–5. Course of episternal foveae ventrally: abutting cells of postacetabular sulcus. Course of episternal foveae dorsally: extending dorsally to mesopleural pit. Sculpture of anterior mesepisternum: smooth or with shallowly impressed microsculpture. Mesopleural epicoxal sulcus: comprised of cells. Mesopleural carina: complete. Speculum: transversely striate. Paracoxal sulcus in ventral half of metapleuron: absent or indistinguishable from sculpture. Anteroventral extension of metapleuron: short, not reaching mesocoxa. Line of pits along metapleural carina: present. Setation of metapleuron: present. Metapostnotum: invaginated near edge of metascutellum and separating metanoum from propodeum. Color of legs beyond coxae: yellow; femora brown, otherwise variably yellow to brown. Metasomal depression: punctate or crenulate dorsally.



Figures 104–108. [49] *Trissolcus valkyria*, female holotype (OSUC 542457) **104** head, mesosoma, metasoma, dorsal view **105** lateral habitus **106** head and mesosoma, lateral view **107** head and mesosoma, ventrolateral view **108** head, anterolateral view. Scale bars in millimeters.

Sublateral setae on T1: absent. Setation of laterotergite 1: absent. Sculpture of T2 posterior to antecostal sulcus: smooth or with very faintly impressed striation; distinctly striate posterior to basal costae.

Diagnosis. *Trissolcus valkyria* is most similar to *T. thyantae* with which it shares a mesoscutellum without microsculpture and a narrow gena. *Trissolcus valkyria* may be separated *T. thyantae* and *T. occiduus* by the presence of a complete and well defined mesopleural carina. From *T. occiduus* it may also be separated by the narrow gena.

Etymology. The epithet "valkyria" is Old Norse for "chooser of the slain" and refers to the female figures in Norse mythology that selected which soldiers would die in battle. The name is to be treated as a noun in apposition.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=344497]

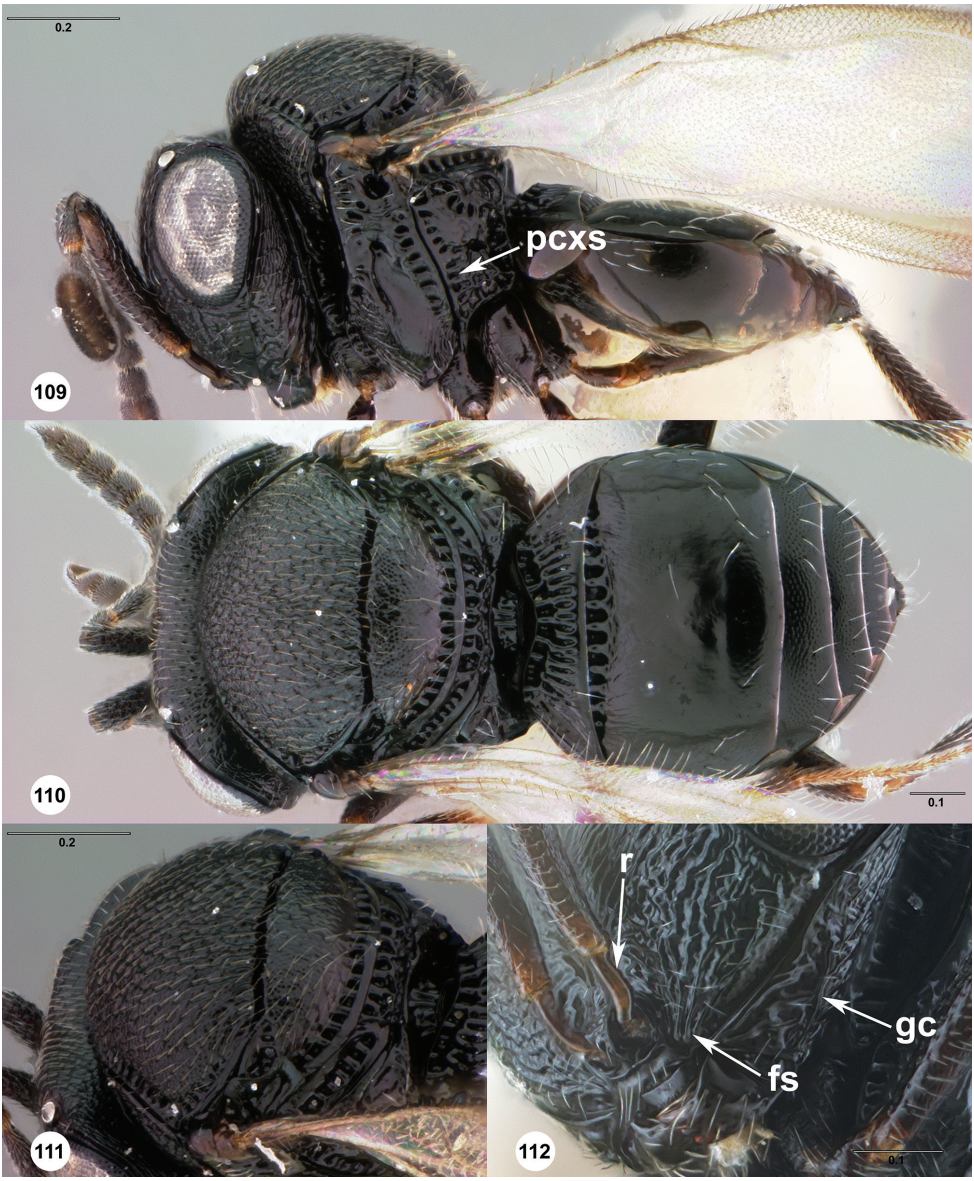
Material examined. Holotype, female: **UNITED STATES**: WI, Juneau Co., North Rynearson site, Necedah National Wildlife Refuge, 21.VI–11.VII.1996, flight intercept trap, R. H. Williams, OSUC 542457 (deposited in OSUC). *Paratypes*: **UNITED STATES**: 5 females, OSUC 405747, 76433 (OSUC); OSUC 144848–144849, 145646 (USNM).

Comments. *Trissolcus valkyria*, was previously recognized by Johnson but remained undescribed due to a dearth of specimens. A small number of additional specimens are now known, providing in our opinion a sufficient basis for the description of this species.

***Trissolcus zakotos* Talamas, sp. n.**
http://zoobank.org/4E138794-6517-42FE-9AC7-B7D92CDB04B6
http://bioguid.osu.edu/osuc_concepts:345034
Figures 109–112; Morphbank[20]

Description. Female body length: 1.28–1.41 mm (n=20). Male body length: 1.18 mm (n=1). Color of radicle: brown. Number of mandibular teeth: three. Number of clypeal setae: 6. Facial striae: present as 3 or more rugulae extending onto lateral frons. Shape of gena in lateral view: receding posteriorly. Genal carina: extending dorsally from base of mandible. Macrosculpture of frons outside of antennal scrobe: irregularly rugose. Orbital furrow: narrow to absent near malar sulcus. Hyperoccipital carina: absent. Preocellar pit: present.

Epomial carina: present. Netrion sulcus: complete. Mesoscutal suprahumeral sulcus: indicated by cells. Mesoscutal humeral sulcus: indicated by cells. Pattern of mesoscutal microsculpture: antero-posteriorly uniform. Macrosculpture of mesoscutum: reticulate anteriorly, longitudinally rugulose posteriorly. Area bounded by axillar crescent: smooth. Parapsidal line: absent. Notaulus: absent. Median mesoscutal carina: absent. Median mesoscutal sulcus: absent. Sculpture of mesoscutellum: coriaceous. Postacetabular sulcus: comprised of cells. Shape of episternal foveae: irregular; round. Number of episternal foveae: 1–2. Course of episternal foveae ventrally: distinctly separate from postacetabular sulcus. Course of episternal foveae dorsally: distinctly separated from mesopleural pit. Sculpture of anterior mesepisternum: faintly rugulose; finely reticulate. Mesopleural epicoxal sulcus: present as a smooth furrow; comprised of cells. Mesopleural carina: complete; well defined in anterior half, posterior half poorly defined to absent. Speculum: transversely striate. Paracoxal sulcus in ventral half of metapleuron: indicated by a line of distinct foveae. Anteroventral extension of metapleuron: long, extending to mesocoxa. Line of pits along metapleural carina: present. Setation of metapleuron: absent. Metapostnotum: invaginated near edge of metascutellum and separating metanoum from



Figures 109–112. [50] *Trissolcus zakotos* **109** female paratype (USNMENT00954596), head, mesosoma, metasoma, lateral view **110** female holotype (USNMENT00903008), head, mesosoma, metasoma, dorsal view **111** female holotype (USNMENT00903008), mesosoma, dorsolateral view **112** female paratype (USNMENT00954600), head, anterolateral view. Scale bars in millimeters. [50]

propodeum. Color of legs beyond coxae: femora and tibiae brown, otherwise variably yellow to brown. Metasomal depression: punctate or crenulate dorsally.

Sublateral setae on T1: absent; present. Setation of laterotergite 1: absent. Sculpture of T2 posterior to antecostal sulcus: smooth or with very faintly impressed striation.

Diagnosis. *Trissolcus zakotos* is closest to *T. radix*, with which it shares a well defined paracoxal sulcus. The two may be separated by the presence of of bright yellow radicle and coarse sculpture of the mesoscutellum in *T. radix*. In *T. zakotos* the radicle is brown and the mesoscutellum is covered by microsculpture, but without additional rugae. Additionally, *T. zakotos* has numerous (3–5) rugae radiating from the lateral edge of the clypeus. This character is present is both *T. radix* and *T. solocis* but is less pronounced and the number of rugae is smaller (1–2).

Etymology. The epithet "zakotos" is Greek for "angry" and is applied to this species because of the appearance of its frons. The name is treated as an appositional noun.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=345034]

Associations. Emerged from *Apateticus bracteatus* (Fitch): [Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae]

Material examined. Holotype, female: **UNITED STATES**: MT, Ravalli Co., Hamilton, V-1972, W. L. Jellison, USNMENT00903008 (deposited in USNM). *Paratypes*: **UNITED STATES**: 22 females, 1 male, USNMENT00954588–USNMENT00954589 (CNCI); USNMENT00954586–USNMENT00954587 (OSUC); USNMENT00903005, USNMENT00903006, USNMENT00954590–USNMENT00954606 (USNM).

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Endnotes

1 http://keys.lucidcentral.org/keys/v3/Nearctic_Trissolcus/
2 http://morphbank.net/?id=836557
3 http://morphbank.net/?id=836441
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Supplementary material 1

URI table of HAO morphological terms

Authors: Elijah J. Talamas, Norman F. Johnson, Matthew Buffington

Data type: Microsoft Excel Spreadsheet (.xls)

Explanation note: This table lists the morphological terms used in this publication and their associated concepts in the Hymenoptera Anatomy Ontology.

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RESEARCH ARTICLE

JOURNAL OF Hymenoptera RESEARCH
A peer-reviewed open-access journal
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Synonymy of *Kozlotelenomus* Mineo, O'Connor & Ashe

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Abstract

Kozlotelenomus Mineo, O'Connor & Ashe, **syn. n.** is treated as junior synonym of *Trissolcus* Ashmead; *Trissolcus mopsus* (Nixon), **comb. rev.** is transferred from *Kozlotelenomus*.

Keywords

Trissolcus mopsus, *Trissolcus*, *Kozlotelenomus*, synonymy, Platygastroidea, Telenominae

Introduction

Numerous monotypic genera exist in Platygastroidea that were created for placement of autapomorphic species. A cladistic perspective on classification emphasizes shared characteristics for taxonomic placement, not derived characters found in a single species. However, many of these genera were erected with little regard for natural classification and did not include phylogenetic analyses to determine if these genera represent independent evolutionary lineages or a cladistic perspective. In the interest of generating a classification system based on monophyletic groups, and minimizing polyphyly, we examined the holotype specimen of *T. mopsus* to determine if its characters were unique within Telenominae, as posited by Mineo et al. (2009), and therefore indicative of a lineage separate from *Trissolcus*.

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The contributions of the authors are as follows: E.J. Talamas: specimen examination, imaging, manuscript preparation; M. Buffington: manuscript preparation.

Materials and methods

The locality data reported for primary types are not literal transcriptions of the labels: some abbreviations are expanded; additional data from the collectors are also included. The numbers prefixed with "USNMENT" or "B.M. TYPE HYM. " are unique identifiers for the individual specimens (note the blank space after some acronyms). Details on the data associated with these specimens may be accessed at the following link, http://purl.oclc.org/NET/hymenoptera/hol, and entering the identifier in the form. The taxonomic synopses were generated by the Hymenoptera Online Database (http://hol.osu.edu).

Photographs were captured with a Z16 Leica® lens with a JVC KY-F75U digital camera using Cartograph® software, or from a Leica® DMRB compound microscope with a GT-Vision® Lw11057C-SCI digital camera attached. In both systems, lighting was achieved using techniques summarized in Buffington et al. (2005), Kerr et al. (2009) and Buffington and Gates (2009). Single montage images were produced from image stacks with the program CombineZP®. In some cases, multiple montage images were stitched together in Photoshop to produce larger images at high resolution and magnification. Scanning electron micrographs were produced with a Hitachi® TM3000 desktop scanning electron microscope, and gold/palladium coated specimens were imaged at 'analysis' voltage, running in 'compo' mode. Full resolution images are archived at the image database at The Ohio State University (http://purl.oclc.org/NET/hymenoptera/specimage) and MorphBank (http://www.morphbank.net).

Collections

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

BMNH Natural History Museum, London, England
OSUC C.A. Triplehorn Insect Collection, Columbus, USA
USNM Smithsonian National Museum of Natural History, Washington DC, USA

Results

***Trissolcus* Ashmead**
http://bioguid.osu.edu/osuc_concepts:606

***Kozlotelenomus* Mineo, O'Connor & Ashe, syn. n.**
http://bioguid.osu.edu/osuc_concepts:259495

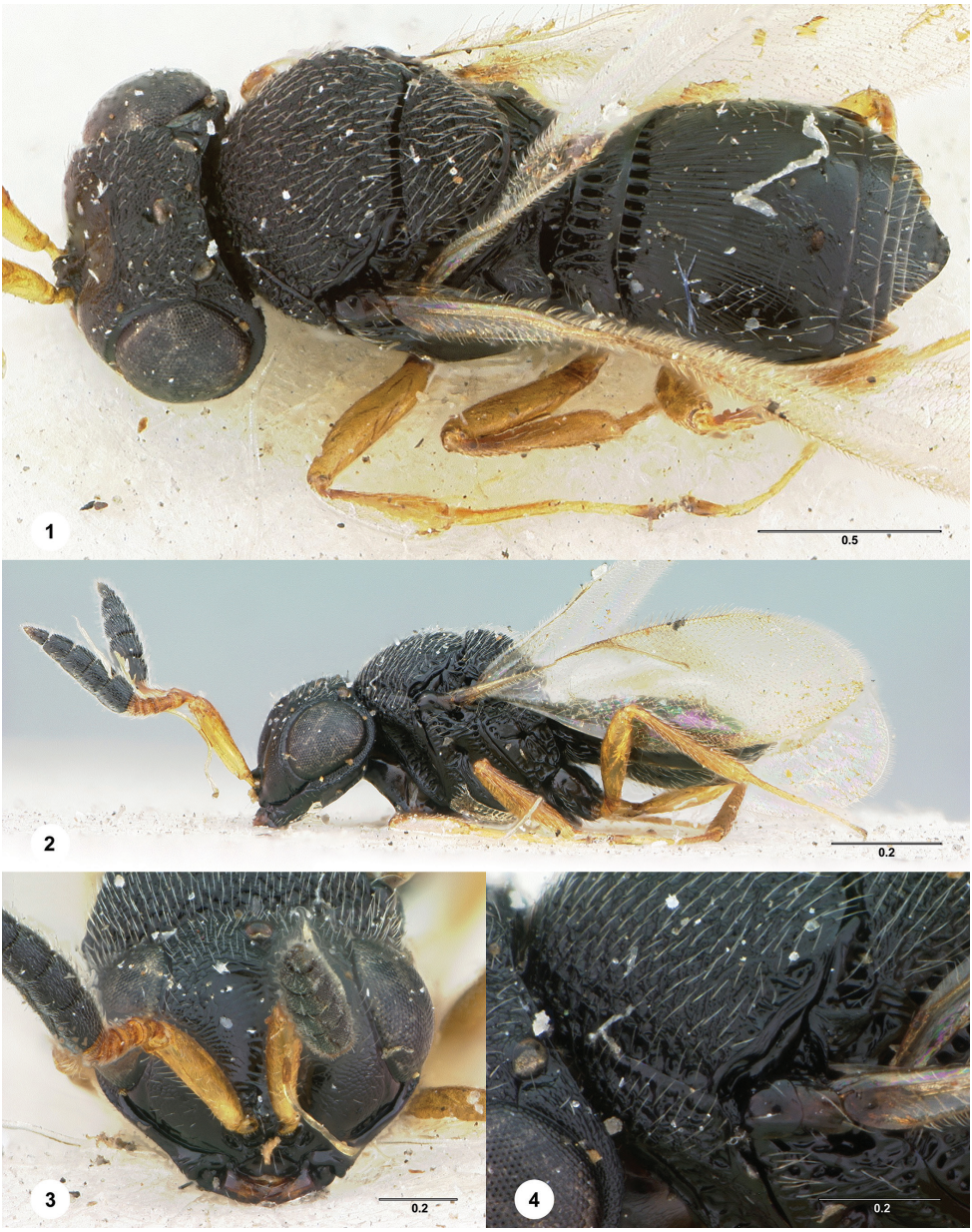
Kozlotelenomus Mineo, O'Connor & Ashe, 2009: 193 (original description. Type: *Microphanurus mopsus* Nixon, by monotypy and original designation).

***Trissolcus mopsus* (Nixon), comb. rev.**
http://bioguid.osu.edu/osuc_concepts:259496
Figures 1–5

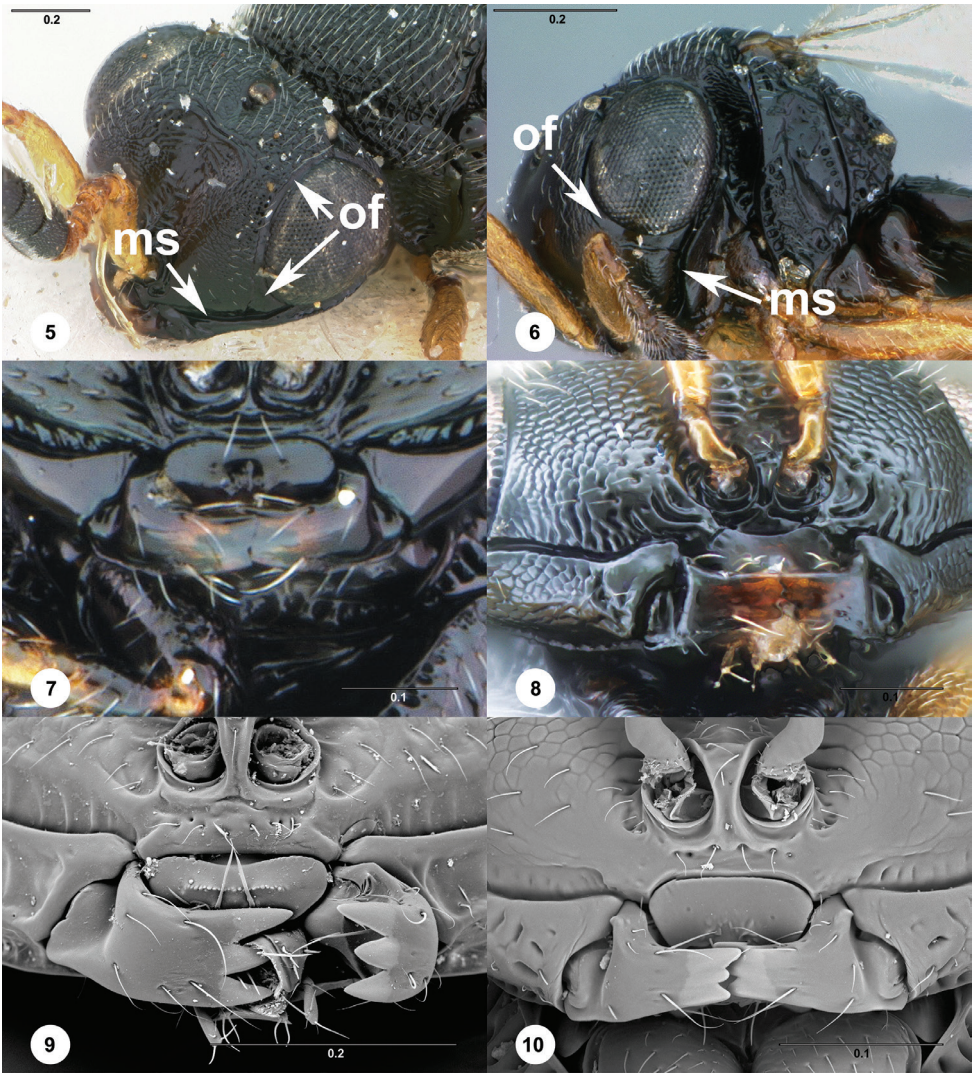
Microphanurus mopsus Nixon, 1935: 96, 97 (original description, keyed); Nixon 1943: 137, 139 (diagnosis, keyed); Risbec 1950: 569, 636 (description, keyed); Risbec 1955: 196 (variation).
Trissolcus mopsus (Nixon): Masner 1965: 127 (type information, generic transfer).
Kozlotelenomus mopsus (Nixon): Mineo, O'Connor and Ashe 2009: 193 (description, generic transfer, distribution, host association).

Material examined. Holotype, female, *M. mopsus*: **SOUTH AFRICA**: Eastern Cape Prov., Pondoland, Port Saint John's, 1.VII–9.VII.1923, R. E. Turner, B.M. TYPE HYM. 9.309 (deposited in BMNH)

Results. Mineo, O'Connor and Ashe (2009) created the genus *Kozlotelenomus* on the basis of three characters in *Trissolcus mopsus* (Nixon) that in their estimation were not found elsewhere in Telenominae: an orbital furrow expanded at its intersection with the malar sulcus (Fig. 5, tear-drop collector sensu Mineo et al 2009), a "drill-shape mandible", and a 3-2 palpal formula. We contend that these characters do not warrant placement in a separate genus for the following reasons: The ventrally expanded orbital furrow is known to occur in *Trissolcus*, particularly in the *flavipes* species group, and is present in the type species of *Trissolcus*, *T. brochymenae* (Fig. 6). The "drill-shape mandible" illustrated in Mineo et al (2009) has multiple teeth. The shape of mandibular teeth varies between species of *Trissolcus* (Figs 7–10) and we do not consider this variation to indicate a separate lineage at the generic level. Lastly, the drawing of the maxillo-labial complex in Mineo et al (2009) illustrates a 2-1 palpal formala with incorrect designation of the base of the palpi as segments. Consequently, all of the characters used to separate *Kozlotelenomus* from *Trissolcus* are found in *Trissolcus*.



Figures 1–4. *Trissolcus mopsus*, female holotype (B.M. TYPE HYM. 9.309) **1** head, mesosoma, metasoma, dorsal view **2** lateral habitus **3** head, anterior view **4** mesosoma, dorsolateral view. Scale bars in millimeters.



Figures 5–10. 5 *Trissolcus mopsus*, female holotype (B.M. TYPE HYM. 9.309), head, dorsolateral view **6** *T. brochymenae*, female neotype (USNMENT00954611), head and mesosoma, lateral view **7** *T. strabus*, female (BMSB 1203), mouthparts, ventral view **8** *T. gonopsidis*, female (OSUC 542413), mouthparts, ventral view **9** *Trissolcus* sp. female (USNMENT00872666), mouthparts, ventral view **10** *T. japonicus* female (USNMENT00896000), mouthparts, ventral view. Scale bars in millimeters. Abbreviations: of, orbital furrow; ms, malar sulcus.

Acknowledgements

We are grateful to David Notton (BMNH) for the loan of the holotype of *T. mopsus*, to Luciana Musetti (OSUC) for the loan of *T. gonopsidis*, to Dylan Johnston-Jordan for SEM imaging, and to Norman Johnson and Joe Cora (OSUC) for database support and making taxonomic literature available. This work was made possible by funding from the Systematic Entomology Lab, USDA-ARS, and the Beneficial Insect Introduction Research Laboratory. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA. USDA is an equal opportunity employer.

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Endnotes

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SHORT COMMUNICATION

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Trissolcus japonicus (Ashmead) (Hymenoptera, Scelionidae) emerges in North America

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Abstract

Trissolcus japonicus (Ashmead) is an Asian egg parasitoid of the brown marmorated stink bug, *Halyomorpha halys* (Stål). It has been under study in U.S. quarantine facilities since 2007 to evaluate its efficacy as a candidate classical biological control agent and its host specificity with regard to the pentatomid fauna native to the United States. A survey of resident egg parasitoids conducted in 2014 with sentinel egg masses of *H. halys* revealed that *T. japonicus* was already present in the wild in Beltsville, MD. Seven parasitized egg masses were recovered, of which six yielded live *T. japonicus* adults. All of these were in a wooded habitat, whereas egg masses placed in nearby soybean fields and an abandoned apple orchard showed no *T. japonicus* parasitism. How *T. japonicus* came to that site is unknown and presumed accidental.

Keywords

Trissolcus japonicus, *Halyomorpha halys*, *Trissolcus*, Scelionidae, biological control, egg parasitoid

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Introduction

The invasive brown marmorated stink bug, *Halyomorpha halys* Stål (Heteroptera: Pentatomidae), first identified in the U.S. in the Allentown area, Pennsylvania, in 2001 (Hoebeke and Carter 2003), has spread from the east to the west coast and has now been found in 41 states, with 13 states on both coasts reporting significant agricultural damage in addition to its nuisance status as an invader of buildings during the coldest months of the year (Northeastern IPM Center 2014a). The species is native to northeastern Asia where it is widespread in China, Taiwan, South Korea, and Japan (Lee et al. 2013). In its native and introduced ranges *H. halys* feeds on a wide variety of economically important fruit crops (Lee et al. 2013), and not surprisingly it has become a significant agricultural pest in the U.S. (Leskey et al. 2012). Over 120 different host plants in numerous families have been recorded in Asia and North America (Lee et al. 2013, Northeastern IPM Center 2014b). In Asia, *H. halys* feeds on many tree fruit species, soybeans, and numerous woody tree and shrub hosts (Lee et al. 2013), although its importance as a pest tends to be sporadic and regionally localized. In the U.S., however, chemical control strategies have not prevented it from causing economic damage in fruit and vegetable crops (Rice et al 2014).

Several species of *Trissolcus* (Hymenoptera: Scelionidae) are reported to attack eggs of *H. halys* in Asia (Arakawa and Namura 2002, Yang et al. 2009), with high rates of parasitism noted (Yang et al. 2009). Beginning in 2007, collections of *Trissolcus* by the USDA/ARS Beneficial Insect Introduction Research Unit (ARS/BIIRU) from China, South Korea and Japan were brought to quarantine laboratories in the U.S. for evaluation as potential biological control agents of *H. halys* in North America. Taxonomic studies and genetic characterization of these collections determined that two species, *T. japonicus* (Ashmead) and *T. cultratus* (Mayr) predominated in the Asian collections obtained from *H. halys* (authors' unpublished data).

Materials and methods

A sentinel egg mass study to assess indigenous egg parasitoids of *H. halys* was conducted in three field habitats during summer 2014 on the Beltsville Agricultural Research Station (BARC) North Farm in Beltsville, MD. All *H. halys* eggs used in this experiment came from a colony established at the USDA/ARS Invasive Insect Biocontrol and Behavior Laboratory (ARS/IIBBL) in 2011 with *H. halys* adults collected in Beltsville, MD. Insects in this colony are reared in growth chambers at 25 °C, 40–60% humidity and a 16L:8D light cycle. They are provided with certified organic green beans, hulled sunflower seed, whole buckwheat seed, and water *ad libitum*. Sentinel egg mass treatments, fresh and frozen in identical numbers, were deployed weekly in three different habitat types, as follows.

Sentinel egg mass treatments

"Fresh" egg masses (≤ 24-hours-old) were laid by colony insects on paper towels. "Frozen" egg masses were identical to "fresh" but were then immediately frozen at -80 °C for 2 minutes. Frozen eggs were included to assess parasitism by species that would oviposit in *H. halys* but be killed by defenses of living fresh eggs (personal communication, Tim Haye, CABI Bioscience, Delémont, Switzerland). Both types of egg masses were then pinned, with the underlying piece of paper towel, to the underside of leaves of various vegetation via a sewing pin, at each of the three sites.

Habitat characteristics

To gain insight into the effect of habitat on parasitoids of *H. halys*, we stationed each type of egg mass in each of three contrasting habitats: soybean field, apple orchard, and second-growth woods, on the BARC North Farm, Beltsville, MD.

Soybean field: Two adjacent soybean (*Glycine max* (L.) Merr.) fields were used, the first one a 2.2 ha certified organic field (39°01'47"N, 76°55'41"W) with abundant pigweed (*Amaranthus* sp.) used before 5 August 2014, and the second a 1.1 ha conventional soybean field (39°02'01"N, 76°55'39"W) used thereafter.

Orchard: The orchard site (39°01'28"N, 76°56'22"W) was an abandoned apple (*Malus domestica* Borkh.) orchard, 40 m by 43 m, with apple trees ~6 m tall, row spacing of 5 m, alleys mowed ~2× per year, with native and non-native grasses, and additional woody vegetation growing in with the apple trees, primarily Japanese honeysuckle (*Lonicera japonica* Thunb.), bush honeysuckle (*Lonicera* sp.), feral Callery pear (*Pyrus calleryana* Decne.), blackberry (*Rubus* sp.), and multiflora rose (*Rosa multiflora* Thunb. ex Murr.). Overall canopy cover was <50%. To the east and north were mowed hayfields, to the south, soybeans, and to the west, a gravel road bounded by a windbreak of arborvitae (*Thuja* sp.) and bush honeysuckle (*Lonicera* sp.).

Woods: The woods site was an open second-growth woods adjacent (within 20m) to the west bank of the channelized Little Paint Branch creek (39°01'42"N, 76°55'47"W). Vegetation was native and nonnative, planted and invasive, with over 20 woody species within 10 m, dominated by basswood (*Tilia americana* L.), American holly (*Ilex opaca* Aiton), red maple (*Acer rubrum* L.), arborvitae (*Thuja* sp.), sycamore (*Platanus occidentalis* L.), mulberry (*Morus rubra* L.), Norway maple (*Acer platanoides* L.) tree of heaven (*Ailanthus altissima* (Mill.) Swingle), black cherry (*Prunus serotina* Ehrh.), feral Callery pear, Japanese honeysuckle (*Lonicera japonica*), bush honeysuckle (*Lonicera* sp.), grape (*Vitis* sp.), poison ivy (*Toxicodendron radicans* (L.) Kuntze), and dewberry (*Rubus hispidus* L.), with an herb layer including grasses, mugwort (*Artemisia vulgaris* L.) and yellow rocket (*Barbarea vulgaris* R.Br.).

Egg deployment, collection, and evaluation

From 18 July through 15 September 2014, weekly, egg masses were exposed in their respective habitats for 72 hours, at which time they were returned to the laboratory and held to determine survival and rates of parasitism. Field exposures comprised a total of 39 egg masses per treatment (fresh or frozen) per habitat, for a total of 234 egg masses with 5864 individual *H. halys* eggs. All field-exposed egg masses were reared in plastic zip top bags in a growth chamber set at 25 °C, 40–60% humidity and a 16L:8D light cycle, and checked daily for emergence of *H. halys* or parasitoids. Any parasitoids that emerged were placed in 95% ethanol for identification. Parasitoid adults that were unable to emerge from the host eggs were extracted for identification. If this dissection was required, the egg mass was placed in a Petri dish, covered with gel hand sanitizer (62% ethanol, HDX®™, Atlanta, GA) to prevent live wasps from flying or the eggs from bouncing away during dissection. Dissected wasps were then placed in 95% ethanol to await identification.

Fresh sentinel egg masses were placed in two other nearby locations (personal communications, M. Cornelius and M. Greenstone, ARS/IIBBL). One involved vegetable fields (<500 m from both our woods and soybean sites; summer squash and bell pepper, and additionally, tomato in 2014) during 4 June through 27 September, 2013, and 10 June through 26 September, 2014, with a total of 124 and 263 egg masses in these years respectively. A second site was sampled with 183 fresh sentinel egg masses from 4 June to 12 September, 2014, in experimental plots of ornamental trees and shrubs at the U.S. National Arboretum (located in Washington, DC, ca. 13 km SSW of the BARC recovery site). The Arboretum plots had a similar canopy structure to the BARC orchard plots. Deployment for the vegetable and ornamental habitats was for 72 hours and the egg masses were sourced from the ARS/IIBBL rearing as above.

Statistical analysis

Differences for parasitism between egg treatments (fresh and frozen) and among the three habitats were assessed at the egg mass level (since this presumably reflects the choices of individual ovipositing females) using Fisher's exact probability tests for frequency (Lowry 2015).

Species Identification

Species of *Trissolcus* were determined using the characters and identification key of Talamas et al. (2015). Images of *T. japonicus* collected in Beltsville, MD, are presented in Figures 1–5. To confirm morphological identifications, genomic DNA was extracted from the legs of 4 females, and one whole female specimen, using techniques summarized in Buffington et al. (2012). The 'barcode' region of cytochrome oxidase I (*COI*) and the internal transcribed spacer region 2 (*ITS2*) regions were amplified and

Figure 1. *Trissolcus japonicus*, female (USNMENT01059357), specimen preserved during emergence from BMSB egg. Scale bar in millimeters.[1]

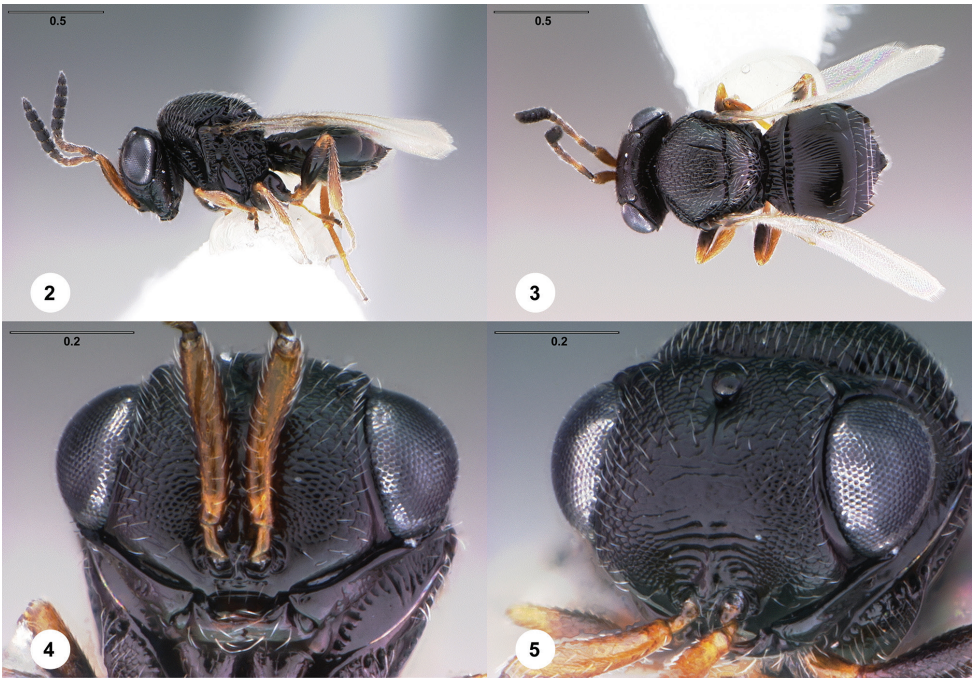
sequenced in the Scheffer Laboratory (USDA/ARS, Systematic Entomology Laboratory) and compared with sequences obtained from populations of previously identified Asian *Trissolcus* from Asian field surveys (Bon et al., unpublished). Voucher specimens for all molecular data are deposited in the National Insect Collection of the National Museum of Natural History, Smithsonian Institution, Washington, DC.

Photography

Images were captured using a Z16 Leica®™ lens with a JVC KY-F75U digital camera and Cartograph®™ software. Montage images were produced from image stacks with the program CombineZP®™. Full resolution images are archived at the image database at The Ohio State University (http://purl.oclc.org/NET/hymenoptera/specimage) and MorphBank (http://www.morphbank.net).

Results

The specimens of *T. japonicus* collected in Beltsville fall well within the concept of this species developed by EJT and MLB in their ongoing revision of *Trissolcus* from the



Figures 2–5. *Trissolcus japonicus*, female (USNMENT01059359) **2** lateral habitus **3** dorsal habitus **4** head, anterior view **5** head, anterodorsal view. Scale bars in millimeters.[2]

Palearctic. They exhibit no morphological anomalies that would complicate confirmation of species identity based on morphology alone. The *COI* and *ITS2* sequences were identical among specimens sampled from the US population, and to sequences generated from *T. japonicus* populations from China, Japan, and South Korea. A complete molecular analysis of *Trissolcus* species is beyond the scope of this note, and will be published in a forthcoming paper (Bon et al., in prep.)

Of the 234 egg masses and 5864 total *H. halys* eggs deployed, 47 egg masses and 994 eggs (17.0%) were parasitized, and 35 egg masses yielded 756 fully-developed adults, but only 389 of these adults (51.5%) successfully emerged from the host eggs, for a total of 6.6% successful parasitism from all eggs exposed. *Trissolcus japonicus* parasitized a total of 7 egg masses, 6 successfully, yielding a total of 159 adults, 131 (82.4%) of which emerged successfully from host eggs, with an approximate 19:1 female:male ratio. *Trissolcus japonicus* parasitized 2 egg masses on 28 July (both fresh), 3 on 2 September (1 fresh and 2 frozen), and 2 on 9 September (both fresh). The other parasitoids recovered consisted of 3 scelionids native to North America, *Telenomus podisi* Ashmead, *Trissolcus euschisti* (Ashmead) and *Trissolcus brochymenae* Ashmead, and 1 species of *Anastatus* Motschulsky (Eupelmidae).

Trissolcus japonicus was found only in host eggs deployed in the woods habitat, and this pattern of occurrence was a significant departure from the null hypothesis of equal likelihood for parasitism in the three habitats (Fisher's exact test, Freeman-

Halton extension (2×3), parasitized versus unparasitized by *T. japonicus* in three habitats: P_A=0.00114; total n=234). Two of the 7 parasitized egg masses were in the frozen treatment (total of 43 adults, of which 39 emerged alive), and the remaining 5 from fresh egg masses (total of 116 adults, of which 92 emerged alive); this represents no significant difference between fresh versus frozen egg masses for *T. japonicus* (Fisher's exact test $P_{1\text{-tail}}$=0.215, NS (2×2 fresh versus frozen and parasitized versus unparasitized by *T. japonicus*, total n=78, woods habitat only)). The native parasitoids, as a group, also exhibited a significant habitat preference, with 14 of 29 parasitized egg masses occurring in the woods habitat (Fisher's exact test, Freeman-Halton extension (2×3), parasitized versus unparasitized by all native species in three habitats: P_A=0.035; total n=234). Natives were far more likely to develop to adulthood in frozen egg masses (26 egg masses with total 425 adults, of which 253 emerged alive), compared to the fresh hosts (only 3 egg masses with a total of 5 adults, all of which emerged alive); this frozen/fresh difference was highly significant (Fisher's exact test $P_{1\text{-tail}}$=0.0000022, (2×2 fresh versus frozen and parasitized versus unparasitized by all native species, total n=234, all habitats)).

Trissolcus japonicus made up 159 (27.0%) of the 589 parasitoid adults in all habitats, and 33.7% of emerged live adult parasitoids in all habitats. Within the woods habitat, the 159 *T. japonicus* were 41.4% of parasitoid adults recovered, and 42.5% of emerged live parasitoids. Among fresh egg masses only, a more realistic treatment for field performance than the frozen treatment, 5 of the 8 parasitized egg masses in the woods habitat were parasitized by *T. japonicus*, and 4 of them yielded a total of 92 live adults (96.8% of live parasitoids for fresh eggs in the woods habitat), as compared to only 5 live adults emerged for native parasitoids.

Sentinel fresh egg masses on nearby vegetables, and at the Arboretum site in Washington, DC, yielded 98 and 38 parasitized egg masses, respectively. Egg parasitoid recoveries (including females that were guarding egg masses) from the vegetable and Arboretum sites described above, and surveys in seven adjacent states collected during 2013 and 2014, were identified at ARS/BIIRU in Newark, DE, with no evidence of the presence of *T. japonicus*.

Discussion

Although we do not know how *T. japonicus* arrived in Maryland (populations imported for laboratory evaluation have not yet been released from quarantine facilities pending completion of studies and issuance of permits), we may speculate that parasitized egg masses of *H. halys* could easily be transported long distances by air cargo (two busy international airports and a major maritime port are located within the Baltimore-Washington area) on the foliage of many different species of plants shipped from Asia to the U.S. Furthermore, *T. japonicus* is recorded from several other Asian pentatomids with wide host plant ranges, and those species and their host plants could also have been the source. It is not known how adult *T. japonicus* overwinter, but they

are capable of living for several months and it is conceivable that they survive host-free periods under bark or in soil litter, and could have arrived in this manner.

Should the occurrence of *T. japonicus* at a single site in Maryland be regarded as an established population? It is probably premature for this conclusion, as the identified samples were obtained only during a single field season in 2014, and numerous additional samples from other nearby and more distant sites have not yet evidenced any *T. japonicus*.

Surveys in subsequent years at this site and at progressively more distant locations will demonstrate whether *T. japonicus* has successfully overwintered in temperate North America and begun to disperse over a wider range. Of particular interest will be the habitats that are colonized if establishment occurs. Among the habitats selected for sentinel deployment at Beltsville, occurrence of *T. japonicus* was limited to the woods, where it was by far the most successful parasitoid in terms of emergence of live adults from fresh *H. halys* eggs. Does the initial discovery only in host eggs in wooded areas but not in nearby soybeans, vegetables, and an apple orchard, indicate a habitat preference? Again, it is probably too soon to be certain given the limited time frame and lack of knowledge regarding how *T. japonicus* arrived.

The host range of classical biological control candidates must first be evaluated and a high degree of host specificity (narrow host range) demonstrated in order to obtain regulatory permission for field release in the U.S. Release permits are unlikely to be obtained if there is significant risk of non-target impact. Information on physiological host range (ability to successfully develop in a host) is ideally accompanied by knowledge of ecological (realized) host range and parasitoid behavior, because maximum-challenge laboratory conditions often overestimate the likely impact and host range in the field (e.g., Haye et al. 2005, Jenner et al. 2014). Given that hundreds of pentatomid species occur in the U.S., some of which are predatory species, extensive host range testing of Asian *Trissolcus*, including *T. japonicus*, as candidate agents for *H. halys* has been in progress but is not yet completed.

Many species and/or geographic populations of non-target Pentatomoidea have been examined using no-choice (only non-target species offered) and choice (*H. halys* and non-target offered simultaneously) tests in quarantine facilities. Thus far, *T. japonicus* (Beijing, China, population) has shown an inability to attack or develop in some species tested, whereas other non-target species were attacked to varying degrees (authors' unpublished data, CD and KH). Results from both no-choice and choice tests have shown that *H. halys* is a preferred or superior host based on higher parasitism rates. Further laboratory studies are in progress to examine the influence of environment (e.g., host habitat) and parasitoid behavior on host selection.

It is possible that the Beltsville population of *T. japonicus* differs from populations under study in quarantine in some characteristics that influence their impact on *H. halys* and on other hosts. The introduction of *T. japonicus*, if it proves to have established and spreads beyond the Maryland site, will provide an opportunity to compare laboratory evaluation studies of host selection and specificity with performance in the field.

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Endnotes

1 www.morphbank.net/?id=852700
2 www.morphbank.net/?id=852708