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

Elijah J. Talamas¹, Norman F. Johnson², Matthew Buffington¹

¹ Systematic Entomology Laboratory, USDA/ARS c/o NMNH, Smithsonian Institution, Washington DC, USA
² Department of Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, OH 43212, USA

Corresponding author: Elijah J. Talamas (elijah.talamas@ars.usda.gov)

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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
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.

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, axillary, and axillar 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 anteroposteriorly 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 currently 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.

### Characters annotations

<table>
<thead>
<tr>
<th>Code</th>
<th>Description</th>
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<tr>
<td>A1–12</td>
<td>antennomeres 1–12 (Fig. 1)</td>
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<tr>
<td>ac</td>
<td>acetabular carina (Figs 43–44, 70)</td>
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<tr>
<td>aem</td>
<td>anteroventral extension of metapleuron (Figs 1, 43, 58, 82, 88)</td>
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<td>anfo</td>
<td>antennal foramen (Fig. 1)</td>
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<td>anterior ocellus (Fig. 2)</td>
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<td>as</td>
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<td>ats</td>
<td>postacetabular sulcus (Figs 42, 70, 82)</td>
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<td>pcxs</td>
<td>paracoxal sulcus (Figs 82, 109)</td>
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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) .............

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*
Key to Nearctic species of Trissolcus Ashmead (Hymenoptera, Scelionidae)...

Figures 3–4. 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
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 5–10. 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.
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**
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

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

Female with antennal flagellum distinctly bicolored: A3–A6 yellow, A7–A11 dark brown (Fig. 59, as in Fig. 68); area bounded by axillary 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 axillary crescent (axcr Fig. 1) with cells visible only along dorsal margin (Figs 20, 62)................................................................. 7
Key to Nearctic species of *Trissolcus* Ashmead (Hymenoptera, Scelionidae)...

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7 Mesopleuron with anteroventral portion rugose (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

---

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

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

Radicle dark brown to black (Fig. 91); metapleuron with paracoaxal sulcus absent or obscured by rugae in ventral half (Fig. 88) ....... $T.\ solocis$ Johnson
Key to Nearctic species of Trissolcus Ashmead (Hymenoptera, Scelionidae)

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 striae 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. bullensis (Harrington)

Figures 29–30. 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.
Metapostnotum invaginated near metascutellum, separating propodeum from metanotum near metascutellum (as in Fig. 21).... **T. erugatus Johnson**

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

**13**

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 mesocutal 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 mesocutal 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; Morphbank²

_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 megalopecephalus_ 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)).


_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).


_Trissoicus basalis_ (Wollaston): Masner 1965: 125 (type information, generic transfer); Safavi 1968: 415 (keyed); Fabritius 1972: 31 (keyed); Kozlov and Lé 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).

_Trissoicus maderensis_ (Wollaston): Masner 1965: 126 (type information, generic transfer).

_Trissoicus piceipes_ (Dodd): Masner 1965: 127 (type information, generic transfer).


**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.
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]


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 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). **VA-nuatu:** 1 male, 1 sex unrecorded, ANIC DB 32-020997 (ANIC); OSUC 75426 (OSUC). **ZIMBABWE:** 17 sex unrecorded, OSUC 75367–75383 (OSUC).

**Trissolcus brochymena**e (Ashmead)

http://bioguid.osu.edu/osuc_concepts:3195

Figures 38–41, 44–45; Morphbank³

*Trissolcus* brochymena*ce* Ashmead, 1881: 181 (original description, spelling error).

*Telenomus* Crochymena*ce* Ashmead: Ashmead 1887: 118 (emendation).


*Trissolcus mergantea*ce* 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 brochymena*ce* (Ashmead)).

*Trissolcus rufiscapu*us 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 brochymena*ce* (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 Museum 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](http://hol.osu.edu/map-large.html?id=3195)

Key to Nearctic species of Trissolcus Ashmead (Hymenoptera, Scelionidae)...


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

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]

Material examined. Holotype, female, \textit{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

*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).


**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]


**Material examined.** Lectotype, female: Other material: (122 females, 13 males, 4 sex unrecorded) AUSTRIA: 5 females, 2 sex unrecorded, USNMENHT00979612, USNMENHT00979613 (CUIC); OSUC 75765–75767 (OSUC); USNMENHT00675943, USNMENHT00675944 (USNM). CHINA: 2 females, UCRC ENT 142635, 143817 (UCRC). CZECH REPUBLIC: 1 female, 3 males, USNMENHT00896311, USNMENHT00896312, USNMENHT00896313, USNMENHT00896314 (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, USNMENHT00896136, USNMENHT00896138, USNMENHT00896140, USNMENHT00896305, USNMENHT00896307–USNMENHT00896309, USNMENHT00896315, USNMENHT00896339, USNMENHT00896341 (CNCI); OSUC 75784, 75786–75788 (OSUC); UCRC ENT 297012 (UCRC); USNMENHT00675730–USNMENHT00675737, USNMENHT00764849 (USNM). RUSSIA: 34 females, USNMENHT00896048, USNMENHT00896049, USNMENHT00896050–USNMENHT00896054,
Figures 50–51. *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,
Key to Nearctic species of Trissolcus Ashmead (Hymenoptera, Scelionidae)...

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](http://bioguid.osu.edu/osuc_concepts:3221)  
Figures 56–59; Morphbank

*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](http://hol.osu.edu/map-large.html?id=3221)


**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](http://bioguid.osu.edu/osuc_concepts:3228)  
Figures 27, 60–61; Morphbank

*Trissolcus erugatus* Johnson, 1985b: 433, 436 (original description, keyed); Sarazin 1986: 980 (type information).
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 metasternum and separating metanotum from propodeum, anterior extension of metapleuron short, not reaching mesocoxa, mandibular teeth shallowly incised; mesopleural
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 anterovelar extension of the metapleuron toward the mesoaxa 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 South-west 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.*

Figures 60–61. *Trissolcus erugatus* female paratype (USMNT00903009) 60 head, mesosoma, metasoma, lateral view 61 head, mesosoma, metasoma, dorsal view. Scale bars in millimeters.
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: Pentatomomoidea: 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

*Telamonius 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)).


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
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. brochymena* 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](http://hol.osu.edu/map-large.html?id=3232)


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); USMENT00979600, USMENT00979603, USMENT00979605 (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 523941, OSUC 542443, OSUC 70463, OSUC 75678–OSUC 77202, OSUC 79805 (OSUC); OSUC 145419–145420 (UCRC); BMSB 1218, 1220–1230, 1232, OSUC 523851, USMENT00872096–USMENT00872102, USMENT00989171, USMENT00989172, USMENT00989174–USMENT00989179 (USNM).

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

*Telungmus 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]

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](http://hol.osu.edu/map-large.html?id=3249)


**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. *Trissolcus japonicus* 68 female (USNMENT00872402), head, mesosoma, metasoma, lateral view 69 female (USNMENT00675989), head, mesosoma, metasoma, dorsal view 70 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

*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).

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**Trissolcus parma** Johnson

http://bioguid.osu.edu/osuc_concepts:3284

Figures 76–79; Morphbank

*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. *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. *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.
Key to Nearctic species of Trissolcus Ashmead (Hymenoptera, Scelionidae)...

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

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: Pentatomoida: 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, USNM. UNITED STATES: 1 female, 2 sex unrecorded, OSUC 145567, 76270–76271 (OSUC). Other material: MEXICO: 2 sex unrecorded, USNM700896395, USNM700896396 (UANL).
Figures 81–83. *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; Morphbank14

*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
Key to Nearctic species of *Trissolcus* Ashmead (*Hymenoptera, Scelionidae*)...

from the other members of the *thyanta* 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

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 *Alcaeorhynchus 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

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. *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.
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

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]


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. *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

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).
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]

Figures 99–103. *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 (depomitted 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; Morphbank19


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]


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; Morphbank20


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.

Figures 109–112. 50 *Trissolcus zakotoi* 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
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 in 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: Pentatomomidea: 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); USNMENT00954585, USNMENT00903005, USNMENT00903006, USNMENT00954590–USNMENT00954606 (USNM).

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Endnotes

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33. http://morphbank.net/?id=836728
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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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