

# A morphological, biological and molecular approach reveals four cryptic species of *Trissolcus* Ashmead (Hymenoptera, Scelionidae), egg parasitoids of Pentatomidae (Hemiptera)

Francesco Tortorici<sup>1</sup>, Elijah J. Talamas<sup>2</sup>, Silvia T. Moraglio<sup>1</sup>, Marco G. Pansa<sup>1</sup>, Maryam Asadi-Farfar<sup>3</sup>, Luciana Tavella<sup>1</sup>, Virgilio Caleca<sup>4</sup>

**1** Dipartimento di Scienze Agrarie, Forestali e Alimentari (DISAFA), Entomologia Generale e Applicata, University of Torino, Largo P. Braccini 2, 10095 Grugliasco (TO), Italy **2** Florida Department of Agriculture and Consumer Service, Division of Plant Industry, Gainesville, Florida, USA **3** Department of Plant Protection, Faculty of Agriculture, Urmia University, Urmia, Iran **4** Department of Agricultural, Food and Forest Sciences, University of Palermo, Edificio 5, Viale delle Scienze, 90128 Palermo, Italy

Corresponding author: Elijah J. Talamas ([talamas.1@osu.edu](mailto:talamas.1@osu.edu))

Academic editor: G. Broad | Received 13 August 2019 | Accepted 1 November 2019 | Published 18 November 2019

<http://zoobank.org/93B22F06-E829-401C-B2E3-1C08169706FB>

**Citation:** Tortorici F, Talamas EJ, Moraglio ST, Pansa MG, Asadi-Farfar M, Tavella L, Caleca V (2019) A morphological, biological and molecular approach reveals four cryptic species of *Trissolcus* Ashmead (Hymenoptera, Scelionidae), egg parasitoids of Pentatomidae (Hemiptera). In: Talamas E (Eds) Advances in the Systematics of Platygastroidea II. Journal of Hymenoptera Research 73: 153–200. <https://doi.org/10.3897/jhr.73.39052>

## Abstract

Accurate identification of parasitoids is crucial for biological control of the invasive brown marmorated stink bug, *Halyomorpha halys* (Stål). A recent work by Talamas et al. (2017) revised the Palearctic fauna of *Trissolcus* Ashmead, egg-parasitoids of stink bugs, and treated numerous species as junior synonyms of *T. semistriatus* (Nees von Esenbeck). In the present paper, we provide a detailed taxonomic history and treatment of *T. semistriatus* and the species treated as its synonyms by Talamas et al. (2017) based on examination of primary types, molecular analyses and mating experiments. *Trissolcus semistriatus*, *T. belenus* (Walker), *T. colemani* (Crawford), and *T. manteroi* (Kieffer) are here recognized as valid and a key to species is provided. The identification tools provided here will facilitate the use of *Trissolcus* wasps as biological control agents and as the subject of ecological studies.

## Keywords

Biological control, taxonomy, brown marmorated stink bug

## Table of contents

Abstract.....	153
Introduction.....	154
Taxonomic history of <i>T. semistriatus</i> and related species.....	155
Material and methods.....	159
Collections.....	159
Geographical distribution and host association.....	160
Cybertaxonomy.....	160
Photography .....	161
Morphology .....	161
Insect collecting and rearing.....	162
Molecular analyses.....	162
Mating tests and reproductive isolation between <i>T. belenus</i> and <i>T. semistriatus</i> ....	163
Results.....	164
Morphological analysis.....	164
Molecular analysis .....	165
Mating tests .....	165
Key to <i>Trissolcus</i> of the Palearctic region (females) .....	167
<i>Trissolcus belenus</i> (Walker).....	170
<i>Trissolcus colemani</i> (Crawford) .....	180
<i>Trissolcus manteroi</i> (Kieffer) .....	184
<i>Trissolcus semistriatus</i> (Nees von Esenbeck) .....	187
Discussion.....	191
Acknowledgements.....	192
References .....	193
Supplementary material 1.....	198
Supplementary material 2.....	199
Supplementary material 3.....	199
Supplementary material 4.....	200
Supplementary material 5.....	200
Supplementary material 6.....	200

## Introduction

Taxonomy of the genus *Trissolcus* Ashmead has received renewed attention in recent years (Talamas et al. 2015, 2017), largely because accurate identification of these wasps is needed to use them as biological control agents against the invasive brown marmorated stink bug (*Halyomorpha halys* (Stål)) in Europe and North America. Morphological similarity, sharing of hosts by various species of *Trissolcus*, and the historical complications presented in Talamas et al. (2017) and Buffington et al. (2018) are some of the challenges faced by taxonomists working with this group.

The revision of Palearctic *Trissolcus* (Talamas et al. 2017) provided keys to species, complete redescriptions, illustrations, and the utilization of new morphological characters. Many new synonymies were presented, including *T. grandis* (Thomson), *T. artus* Kozlov & Lê, *T. colemani* (Crawford), *T. djadetschko* (Rjachovskij), *T. manteroi* (Kieffer), *T. nigripedius* (Nakagawa), *T. pentatoma* (Rondani) and *T. pseudoturesis* (Rjachovskij) as junior synonyms of *T. semistriatus* (Nees von Esenbeck).

In support of studies on the egg-parasitoid complex of European Pentatomoidea, a survey of egg masses was conducted and previously collected specimens were also examined. Using the key to species provided by Talamas et al. (2017), *Trissolcus* specimens that emerged from *Aelia rostrata* Boheman, *Arma custos* (F.), *Carpocoris* spp., *Eurygaster maura* (L.), *Graphosoma lineatum* (L.), *Palomena prasina* (L.) collected between 1996 and 2017 in Piedmont (NW Italy) were identified as *T. semistriatus*. However, some consistent morphological differences were detected among the specimens, which instigated closer examination using multiple methods. The focus of this paper is the morphological and molecular analysis of species synonymized under *T. semistriatus* by Talamas et al. (2017), and the integration of mating tests, when possible, to confirm species delimitation.

## Taxonomic history of *T. semistriatus* and related species

### Species described by Walker

*Telenomus belenus* was described by Walker (1836), then transferred by Kieffer (1912) to *Aphanurus* Kieffer, then transferred to *Microphanurus* Kieffer (Kieffer 1926). Walker (1838) described *Telenomus arminon* but did not provide distinctive characters by which it could be identified or separated from *Telenomus belenus*. Kieffer (1912) transferred *Tē. arminon* to *Allophanurus* Kieffer and provided a redescription. Kieffer did not mention if his treatment was based on type material, and we consider it unlikely that it was. Lectotypes for *Tē. belenus* and *Tē. arminon* were designated by Fergusson (1984, 1983), respectively, from material housed in the National Museum of Ireland, Dublin. Despite their antiquity, and thus priority, these species received no further taxonomic treatment.

### *Trissolcus semistriatus* vs. *T. grandis*

In taxonomic literature, the distinction between *T. semistriatus* and *T. grandis* has long been questioned. Mayr (1879) and Nixon (1939) ascertained *T. semistriatus* to be a highly variable species. Masner (1959) wrote “On base of the check of type of *Asolcus grandis* (Thomson), the latter species was synonymized with *semistriatus*”. However, the meaning of this sentence is unclear because we have not found in the literature previous synonymy of *T. grandis* under *T. semistriatus*, and it is not clear that Masner

sought to synonymize them for the first time. In this paper, Masner addressed characters considered to distinguish *T. grandis* and *T. semistriatus* (rugosity of the frons, leg color, longitudinal sculpture on the posterior mesoscutum, body length) based on the comparison of ~500 reared specimens and stated that these characters were variable within *T. semistriatus*. Viktorov (1967) considered *T. grandis* to be conspecific with *T. semistriatus*, but he did not formally treat it as a junior synonym. Subsequent authors considered *T. semistriatus* and *T. grandis* as different species, but without clearly defining the boundaries between them. Delucchi (1961) provided the first reliable character to distinguish *T. semistriatus* from *T. grandis*: the external surface of the hind femur is almost totally covered by setation in *T. grandis* (Figure 1), and he coupled this character with the color of the tibiae: reddish yellow in *T. semistriatus*, dark or black in *T. grandis*. Most authors continued to distinguish *T. semistriatus* and *T. grandis* by tibial color and ignored setation of the hind femora. This color-based distinction was employed in numerous previous and following papers (Delucchi 1961; Javahery 1968; Kozlov 1968, 1978; Safavi 1968; Voegelé 1969; Fabritius 1972; Kozlov and Lê 1977; Kozlov and Kononova 1983), and no substantial change was indicated in keys to species by Kononova (1995, 2014, 2015). Talamas et al. (2017) did not use tibial setation to differentiate between these species, but listed a new character, the form of the mesoscutal humeral sulcus, and mentioned setation of the first laterotergite, which was first presented as a character for species of *Trissolcus* by Johnson (1987). Although Talamas et al. (2017) treated these characters as variable within *T. semistriatus*, analysis of these characters in light of molecular and mating experiments has allowed us to use them for species delimitation.

In a study on larval stages, Voegelé (1964) provided information about pigmentation of the membrane secreted by the larvae of different *Trissolcus* species reared in eggs of *Eurygaster austriaca* (L.). He distinguished *T. semistriatus* from *T. grandis* by the width of the pigmented band close to the margin of host egg operculum (see fig. 4 in Voegelé 1964). In his key to species, Safavi (1968) coupled color of the hind tibia (instead of mid tibia), and width of the pigmented band in larval membrane shown by Voegelé (1964), also adding different length ratios of the first two flagellomeres in males.

*Trissolcus artus* was distinguished by Kozlov and Kononova (1983) and Kononova (1995) from *T. grandis* (black tibiae) by its reddish-yellow tibiae, and from *T. semistriatus* by having a more elongate clava and infuscation in the fore wing. This last feature is used in the key by Kononova (2014, 2015) to distinguish *T. artus* from both *T. grandis* and *T. semistriatus*.

### ***Trissolcus manteroi***

*Trissolcus manteroi* was described by Kieffer (1909) as having the postmarginal vein (pm) slightly longer than the stigmal vein (st). In Kozlov and Kononova (1983), Koçak and Kilinçer (2003) and Kononova (2014, 2015), *T. manteroi* was distinguished by its postmarginal vein 1.3× as long as the stigmal vein, compared to 1.8× in *Trissolcus rufiventris* (Mayr), and 2× in *T. grandis* (= *T. belenus*) and *T. semistriatus*. Kononova



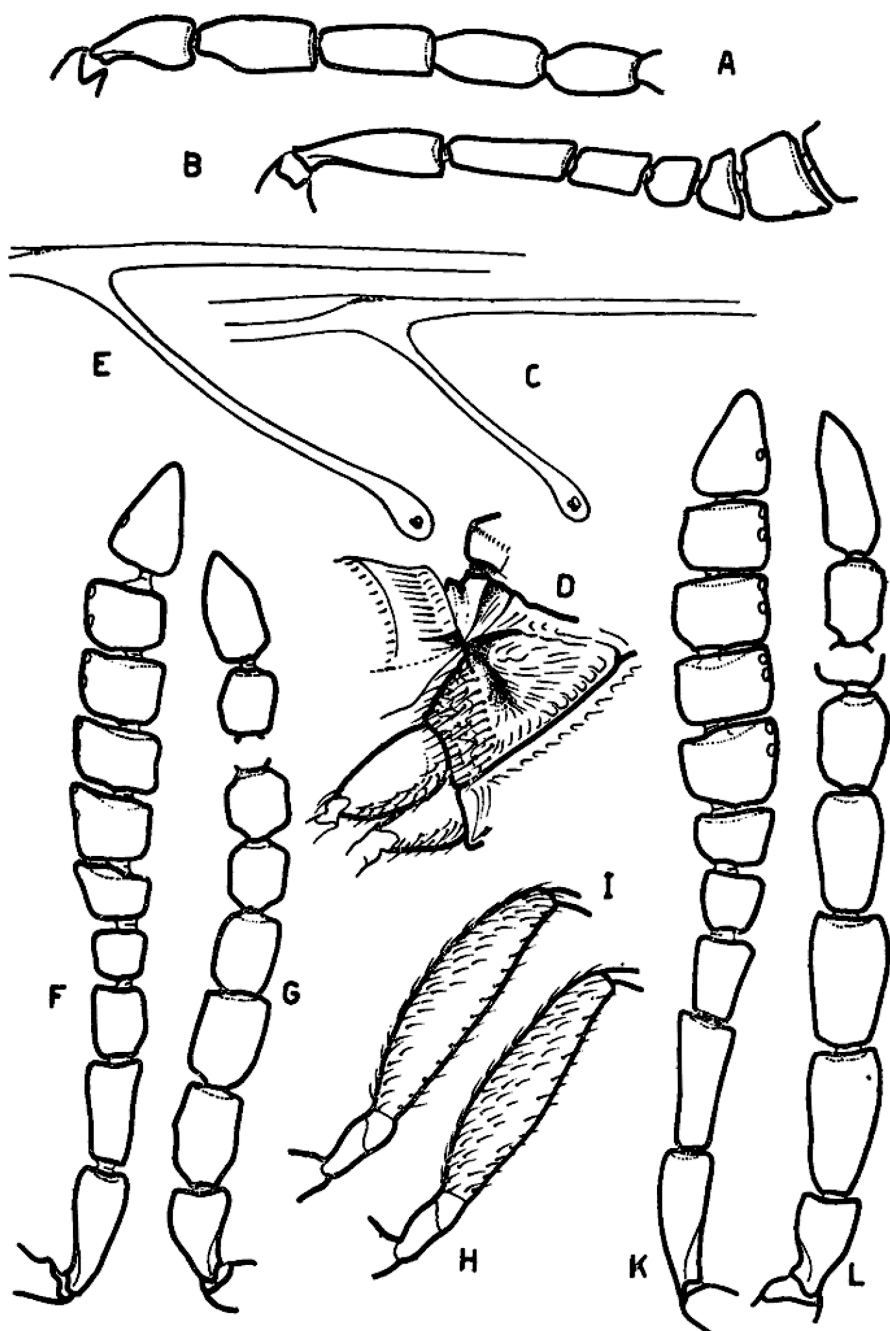


FIG. III — *A. ghorfii* DEL. et VÆG. (A - D), *A. vassilievi* MAYR (E), *A. grandis* THOMSON (F - H) et *A. semistriatus* NEES (I - L). Antennes de la femelle (B, F, K), antennes du mâle (A, G, L). Angle formé par les nervures postmarginale et stigmale de l'aile antérieure (E, C), pubescence de la metapleure (D) et des fémurs postérieurs (H, I).

**Figure 1.** Illustrations published by Delucchi (1961) where differences in the bare area of the external side of hind femora of *Asolcus semistriatus* (Fig III, I) and *A. grandis* (Fig. III, H) are shown.

(2014, 2015) also distinguished *T. manteroi* by the sculpture of T2, in which short longitudinal rugae are arranged medially and do not extend to the posterior half of the tergite, contrasting with longitudinal rugae throughout the anterior two thirds of T2 in *T. belenus* and *T. semistriatus*.

### ***Trissolcus colemani***

Crawford (1912) described *Telenomus colemani* from specimens that emerged from an egg mass of *Dolycoris indicus* Stål, collected in India. Masner and Muesebeck (1968) transferred this species into *Trissolcus* and no other information was recorded until its treatment as a junior synonym of *T. semistriatus* in Talamas et al. (2017).

### ***Trissolcus pseudoturesis* and *T. djadetshko***

The original description of *Microphanurus* (= *Trissolcus*) *pseudoturesis* Rjachovskij (Rjachovskij 1959) distinguished this species from *M. djadetshko* Rjachovskij and *M. semistriatus* by tibial color: completely yellow in *M. pseudoturesis*; reddish or yellow in *M. djadetshko*; almost black in *M. semistriatus*. Viktorov (1964) distinguished *Asolcus* (= *Trissolcus*) *djadetshko* and *A. rufiventris* by the lack of longitudinal striae on the posterior margin of the mesoscutum in contrast to their presence in *A. pseudoturesis* and *A. semistriatus*. Viktorov (1967) then modified his concept, considering the color of the hind tibia as a valid character to distinguish *T. djadetshko* from *T. semistriatus* and the color of femora to distinguish *T. djadetshko* from *T. pseudoturesis*. The keys to species by Kozlov (1968) and Fabritius (1972) distinguished *T. djadetshko* from *T. grandis*, *T. pseudoturesis* and *T. semistriatus* by the absence of longitudinal striation on the posterior mesoscutum and an absence of transverse striation on the frons, and *T. pseudoturesis* from *T. grandis* and *T. semistriatus* by color of the femora. Kozlov and Kononova (1983) separated *T. djadetshko* from both *T. grandis* and *T. semistriatus* by the absence of longitudinal striation on the posterior mesoscutum. Safavi (1968) and Voegelé (1969) separated *T. djadetshko* and *T. pseudoturesis* by their “ochraceous” femora from *T. semistriatus* and *T. grandis* (black femora), and separated *T. djadetshko* from *T. pseudoturesis* by longitudinal striae on the posterior margin of mesoscutum (vs. striate throughout) and the presence of parapsidal furrows. Koçak and Kiliñer (2003) distinguished *T. djadetshko* by its femora being reddish-yellow in contrast with dark brown or black femora in *T. semistriatus* and *T. grandis*, and separated *T. djadetshko* from *T. pseudoturesis* by sculpture on mesoscutum as in Voegelé (1969). Petrov (2013) again distinguished *T. djadetshko* on the basis of the mesoscutum without longitudinal wrinkles, contrasting with the clear longitudinal wrinkles of *T. grandis*, *T. pseudoturesis* and *T. semistriatus*, and he separated *T. pseudoturesis* from *T. grandis* and *T. semistriatus* by the color of femora. Kononova (2014, 2015) differentiated *T. djadetshko* by its yellow legs and mesoscutum without longitudinal rugae posteriorly from *T. semistriatus*

and *T. grandis* having all femora black and mesoscutum with longitudinal rugae posteriorly, and *T. pseudoturesis* from *T. grandis* and *T. semistriatus* as in Kozlov (1968). *Trissolcus djadetschko* and *T. pseudoturesis* were treated as junior synonyms of *T. semistriatus* in Talamas et al. (2017).

### ***Trissolcus waloffae*, *T. nixomartini* and *T. silwoodensis***

Javahery (1968) described and keyed *T. waloffae* (Javahery) using leg color (predominantly brownish to reddish-yellow) and weakly indicated parapsidal furrows to separate it from *T. grandis*, *T. semistriatus*, *T. nixomartini* and *T. silwoodensis*, which he considered to have black femora in both sexes and be without parapsidal furrows. Characters provided to distinguish each of the last four species from each other were black vs. brown front tibiae, presence of infuscation of wings, color of wing venation, ratio between first flagellar segment and pedicel of male, sculpture of the head, distance between lateral ocelli and compound eye, and 'weakly concave' vs. 'somewhat concave' head. *Trissolcus silwoodensis* and *T. nixomartini* were previously treated as synonyms of *T. grandis* by Kozlov and Lê (1977).

### ***Trissolcus crypticus***

During a program for classical biological control of *Nezara viridula* L. in Australia, several 'strains' of different geographical populations of *Trissolcus basalis* (Wollaston) were introduced, starting in the 1930s (Clarke 1990). Of the strains introduced in subsequent years to the interior of Australia, one population imported from Pakistan (1961) was not able to efficiently control *N. viridula* (Clarke 1990). Clarke (1993) demonstrated that this 'strain' was indeed a different species, which he described as *Trissolcus crypticus* Clarke. Comparing *T. crypticus* with *T. basalis*, he considered the complete netirion sulcus (figure 1 in Clarke 1993) as the main diagnostic character for *T. crypticus*. Clarke analyzed specimens of *Trissolcus rungsi* (Voegelé) labelled by Voegelé and deposited in NHMUK and concluded that they were not the same species as *T. crypticus*, but did not present characters to support his hypothesis (Clarke 1993).

## **Material and methods**

### **Collections**

#### **Primary types**

Due to the challenge of historic confusion regarding species close to *T. semistriatus*, we treat only species for which the primary types were directly examined, or the diagnostic characters are clearly visible in photographs.

Images of the primary types of *Telenomus colemani* Crawford, *Microphanurus djadetschko* Rjachovskij, *Trissolcus grandis* Thomson, *Telenomus Manteroi* Kieffer, *Microphanurus pseudoturesis* Rjachovskij and *Teleas semistriatus* Nees von Esenbeck were made available via Specimage (specimage.osu.edu) by Talamas et al. (2017). Images of the lectotype of *Telenomus nigripes* Thomson, syntypes of *Telenomus ovulorum* Thomson, and additional images of the lectotype of *Telenomus grandis* were provided by Dr Hege Vårdal (Naturhistoriska Riksmuseet, Stockholm, Sweden).

#### Institutional acronyms

<b>CNCI</b>	Canadian National Collection of Insects – Ottawa, Canada;
<b>DISAFA</b>	Dipartimento di Scienze Agrarie, Forestali e Alimentari, University of Torino – Torino, Italy;
<b>EIHU</b>	Hokkaido University Museum, Entomology – Sapporo, Japan;
<b>HMIM</b>	Hayk Mirzayans Insect Museum, Plant Pests and Diseases Research Institute – Tehran, Iran;
<b>NHMUK, BMNH</b>	The Natural History Museum – London, United Kingdom;
<b>NHMW</b>	Naturhistorisches Museum Wien – Wien, Austria;
<b>NMID</b>	National Museum of Ireland – Dublin, Ireland;
<b>MSNG, MCSN</b>	Museo Civico di Storia Naturale “Giacomo Doria” – Genoa, Italy;
<b>MZUF</b>	Museo di Storia Naturale di Firenze, Sezione di Zoologia “La Specola”, Università degli Studi di Firenze – Florence, Italy;
<b>NHRS</b>	Naturhistoriska Riksmuseet, Entomology – Stockholm, Sweden;
<b>UCRC</b>	University of California, Riverside – CA, USA;
<b>UNIPA</b>	Dipartimento di Scienze Agrarie, Alimentari e Forestali, Università degli Studi di Palermo – Palermo, Italy;
<b>USNM</b>	National Museum of Natural History, Smithsonian Institution – Washington, DC, USA;
<b>ZIN</b>	Zoological Museum, Academy of Sciences – St. Petersburg, Russia.

#### Geographical distribution and host association

The identification tools of previous literature are not reliable for identifying the species that we treat here. Hence, the geographical distribution and host associations presented in Material Examined sections derive only from specimens examined as part of this study.

#### Cybertaxonomy

Specimens used in this study were assigned collecting unit identifiers (CUIDs) and their associated collection and host association data were deposited in Hymenoptera

Online (hol.osu.edu). In addition to the abbreviated Material examined sections, a DarwinCore archive is provided for each species (Suppl. material: S2–S5). These files contain the totality of specimens for which data is deposited in Hymenoptera Online, including specimens for which updated identification has not yet occurred, which can be assessed by the dates of determination. Taxonomic synopses, descriptions, and material examined sections were generated in the online, matrix-based program vSysLab (vsyslab.osu.edu) with a matrix based on that of Talamas et al. (2017).

## Photography

A Leitz Großfeld-Stereomikroskop TS with magnification up to 160 $\times$ , a Stereomicroscope Wild M3B with oculars 15 $\times$ , and a spot light Leica CLS 150 $\times$  were used for biometric diagnosis. A semi-transparent light shield was used to reduce glare and to diffuse the light. The lectotypes of *T. belenus* and *T. arminon* were photographed with a Macroscopic Solutions Macropod MicroKit with individual slices rendered in Helicon Focus 6. All other images were produced using a Leitz Dialux 20 EB compound microscope with a Leica DFC 290 Camera with LED spot light or dome light based on different points of view after techniques summarized in Buffington et al. (2005), Kerr et al. (2008) and Buffington and Gates (2008). LEICA APPLICATION SUITE V 3.7.0 software was used to manage image acquisition and ZERENE STACKER was used for merging of the image series into a single in-focus image.

## Morphology

Terminology for surface sculpture follows the glossary by Harris (1979), Mikó et al. (2007), Yoder et al. (2010) and Talamas et al. (2017). Measurements of the head, mesosoma, metasoma, total body, and wing venation follow Masner (1980) and Tortorici et al. (2016). In the wing ratio expressed as st:pm:mg, the stigmal vein is treated as the benchmark unit (=1). Morphological terms largely follow Mikó et al. (2007) and were matched to concepts in the Hymenoptera Anatomy Ontology (Yoder et al. 2010) using the text analyzer function and a table of these terms and URI links is provided in Suppl. material: S1.

Additional abbreviations and terminology used in this paper: HL: head length; HW: head width; HH: head height, from vertex to distal end of clypeus; FCI: frontal cephalic index (HW/HH); LCI: lateral cephalic index (HH/HL); OOL:POL:LOL: ocular distance ratio, OOL as the benchmark unit (=1); IOS: interorbital space (Mikó et al. 2010); claval formula: the sequence of sensilla, from the apical antennomere (A11) to the last functional clavomere (Bin 1981), i.e. the last antennomere bearing one or two multiporous gustatory sensilla, as defined by Isidoro et al. (1996); compound eye height and width: measured when eye longitudinal axis is parallel to the focal plane.

## Insect collecting and rearing

A host colony of *E. maura* used for rearing *Trissolcus* was established from adults collected on wheat in Piedmont (NW Italy) and maintained in cages under laboratory conditions (climatized chambers at  $24 \pm 1$  °C,  $65 \pm 5\%$  RH, L:D = 16:8). All eggs laid in the cages were collected and frozen at  $-20$  °C. Because of the short egg-laying period of *E. maura*, freezing the eggs allowed the eggs to be used for a much longer time.

To obtain *Trissolcus* specimens, egg masses of *E. maura* and *P. prasina* were collected in the field in Piedmont (NW Italy) in the spring and summer of 2017. The field-collected egg masses were reared and checked daily. *Trissolcus* specimens that emerged from field-collected egg masses were allowed to mate. Some females were isolated in small plastic boxes ( $64.5 \times 40.9 \times 16$  mm), fed with water and honey, and provided with *E. maura* frozen egg masses to produce progeny for use in subsequent tests.

For interbreeding experiments, specimens were isolated immediately following emergence to prevent mating, and females and males were maintained singly in plastic boxes as described above. When the parasitoids reach the early pupal stage inside the eggs, their red eyes are clearly visible through the transparent operculum of the host egg. Following observation of this feature (Figure 2), the eggs were checked at a frequency of 4–5 times per day to ensure that they were isolated prior to mating.

Some of the progeny from isolated, mated females were selected for preservation, identification and molecular analysis. The remaining progeny were used in breeding experiments.

## Molecular analyses

Molecular analyses were performed to confirm morphological identification and characterize the species. Genomic DNA was extracted from the metasoma of specimens from rearing experiments and pinned collection specimens according to Kaartinen et al. (2010), but doubling the proteinase K dose (5 µl of 20 mg ml<sup>-1</sup> proteinase K). The barcode region of the cytochrome oxidase I (COI) gene was amplified using universal PCR primers for insects LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and HCO2198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer et al. 1994). The PCR was performed in a 50 µl reaction volume: 2 µl of DNA, 37.9 µl molecular grade water, 5 µl 10× Qiagen PCR buffer, 3 µl dNTPs (25 mM each), 1.5 µl MgCl<sub>2</sub>, 0.2 µl of each primer (0.3 µM each), 0.2 µl Taq DNA Polymerase (Qiagen, Hilden, Germany). Thermocycling conditions were optimized to shorten reaction times and included initial denaturation at 94 °C for 300 s, followed by 35 cycles of 94 °C for 30 s, annealing at 52 °C for 45 s and extension at 72 °C for 60 s; then further 600 s at 72 °C for final extension. PCR products were purified using a commercially available kit (QIAquick PCR Purification Kit, Qiagen GmbH, Hilden, Germany) following the manufacturer's instructions, and sequenced by a commercial service (Genechron S.r.l., Rome, Italy). The sequences were compared with the GenBank database and each other using the Basic Local Alignment Search Tool (<http://www.ncbi.nlm>





**Figure 2.** Pupal stage of *Trissolcus* sp. in *Halyomorpha halys* eggs, clearly indicated by the presence of eyes and ocelli, which are visible through the semi-transparent host egg.

[nih.gov/BLASTn](https://www.ncbi.nlm.nih.gov/BLASTn)). All sequences were aligned using ClustalW with default settings as implemented in Mega X. The pairwise nucleotide sequence distances among and within taxa were estimated using the Kimura 2-parameter model (K2P) of substitution (Kimura 1980) using Mega X (Kumar et al. 2018). The sequences generated from this study are deposited in the GenBank database. All residual DNA is archived at DISAFA.

### Mating tests and reproductive isolation between *T. belenus* and *T. semistriatus*

For mating experiments, 1–2-day old virgin females and males were used. Four combinations for mating tests were done: *T. semistriatus* (♀) × *T. belenus* (♂); *T. belenus* (♀) × *T. semistriatus* (♂); *T. semistriatus* (♀) × *T. semistriatus* (♂); *T. belenus* (♀) × *T. belenus* (♂). The total number of interbreeding tests was 24: four replicates for each intraspecific mating combination and eight replicates for each interspecific mating combination. Each pair of wasps was observed at the stereomicroscope until the end of copulation or for 10 minutes if copulation did not occur. The pair then remained together in isolation for 24 hours. After the mating test, an egg mass of *E. maura* was provided to each female wasp for 24 hours of exposure. The egg masses were then moved to other plastic boxes until offspring emergence. Each mating test was considered successful when emerged offspring included females, because in all known *Trissolcus* species, only mated females can produce female offspring. We compared the percentage of mating success among the four combinations and the significance of the results was assessed with a chi-square test.



## Results

### Morphological analysis

The easiest task regarded the distinction of *T. manteroi* from *T. semistriatus*, *T. belenus* and *T. colemani*. *Trissolcus manteroi* clearly has a shorter postmarginal vein, only slightly longer than the stigmal vein; A7 has only one papillary sensillum instead of two in the other three species; and *T. manteroi* has no episternal foveae. The holotype of *T. manteroi* is thus morphologically very close to *T. rufiventris*, from which it can be differentiated by the length of the postmarginal vein.

The distinction of *T. belenus* and *T. colemani* from *T. semistriatus* is more nuanced and required an integrative approach to determine which morphological characters were congruent with the biological and molecular data. The results of this in-depth analysis demonstrate that some of the characters that Talamas et al. (2017) treated as intraspecifically variable have diagnostic power.

The presence or absence of setation on the external face of the hind femur, described in the key and figure III (I) (H) in Delucchi (1961), is a reliable character to distinguish *T. grandis* from *T. semistriatus*. However, in the lectotype of *T. grandis* and neotype of *T. semistriatus* this character is opposite to what was stated by Delucchi (1961). Furthermore, the holotype of *T. colemani* has the external surface of hind femur setose, as in the lectotype of *T. grandis*. The association proposed in Delucchi (1961): ‘external face of hind femora uncovered by hair’ – ‘reddish yellow tibiae’ is the typical combination for *T. colemani*, while Delucchi (1961) proposed it for *T. semistriatus*, and ‘external face of hind femora covered by hair’ – ‘dark or black tibiae’ is the typical combination for *T. semistriatus*. We conclude that this interpretation is contrary to what is found in type material.

#### Synonymy in *T. belenus*

In the analysis of original descriptions and images of lectotype of *T. arminon* and *T. grandis*, no remarkable characters were recognized to distinguish them from *T. belenus*, which we therefore consider it to be their senior synonym. In the analysis of type material of *T. silwoodensis* and *T. nixomartini*, previously considered junior synonym of *T. grandis* (Kozlov & Lê, 1977), we confirmed the findings of previous authors, and thus treat these species as junior synonyms of *T. belenus*. Mayr (1879) considered *Telenomus ovulorum* Thomson to be a junior synonym of *Telenomus semistriatus* Nees von Esenbeck, but through analysis of the photographs of type material of *T. ovulorum* Thomson, we recognized the character states of *T. belenus*, and therefore treat *T. ovulorum* as a junior synonym of *T. belenus*.

#### Synonymy in *T. colemani*

One paratype of *T. djadetshko* and three syntypes of *T. pseudoturesis* were analyzed via photographs and compared with the original description and photographs of the holo-

type of *T. colemani*. The character states of the two first species matched perfectly with those of the latter, leading us to treat *T. colemani* as the senior synonym of *T. djadetshko* and *T. pseudoturesis*. We conclude that the characters of *T. crypticus* match those in the holotype of *T. colemani* based on examination of *T. crypticus* paratypes collected in Pakistan and its original description (see figs 1, 3, 5 in Clarke 1993). We thus treat *T. crypticus* as a junior synonym of *T. colemani*.

Clarke (1993) also reported that “Examination of material of *T. rungsi* labelled by Voegelé (deposited in NHMUK) shows that this species is not the same of *T. crypticus*” but he did not provide any distinguishing characters between the two species. Contrary to what was reported by Clarke (1993), in our analysis of the material deposited at NHMUK, 37 specimens labelled as “*Asolcus rungsi* Voegelé” were identified as *T. colemani* and four specimens labelled as “*rungs* 1965 Voegelé” were identified as *T. basalis*, while other 25 with the same last cumulative label were identified as *T. colemani*. This confirms our interpretation of the description and analysis of figures regarding *A. rungsi* and demonstrates confusion of species in the Moroccan rearing efforts at École Nationale d’Agriculture in Meknès.

The original description of *Asolcus rungsi* mentioned the presence of short traces of notauli (fig. 1, c. in Voegelé 1965); these traces are visible in all specimens *T. colemani* (Figure 23). However, because the location of the holotype of *A. rungsi* is not known, we were unable to examine it and at this time do not treat this species name as a synonym. The morphological analyses of the holotype and paratypes of *T. waloffae* showed the conspecificity of this species with *T. colemani*.

## Molecular analysis

Barcode sequences were obtained from 17 *Trissolcus* specimens (Table 1). The Blast search showed that the sequences of *T. semistriatus* from Italy and from Iran had a 98% sequence identity with the GenBank sequence from *Trissolcus nigripedius* (accession no. [AB971830](#)). The sequences from the two specimens of *T. colemani* showed a 98% identity with a GenBank sequence with a *Platygastridae* sp. (accession no. [KY839581](#)), while the sequences from the specimens of *T. manteroi*, *T. belenus* and *T. rufiventris* showed a lower similarity with GenBank sequences. The final alignment consisted of 548 characters. Pairwise distance values within and among analyzed species are shown in Table 2. The genetic distances between the specimens identified as of the same species (which averaged between  $0.000 \pm 0.000$  and  $0.005 \pm 0.002$ ), were much lower than the mean pairwise distances observed between the specimens identified as of different species (from  $0.105 \pm 0.001$  to  $0.149 \pm 0.000$ ).

## Mating tests

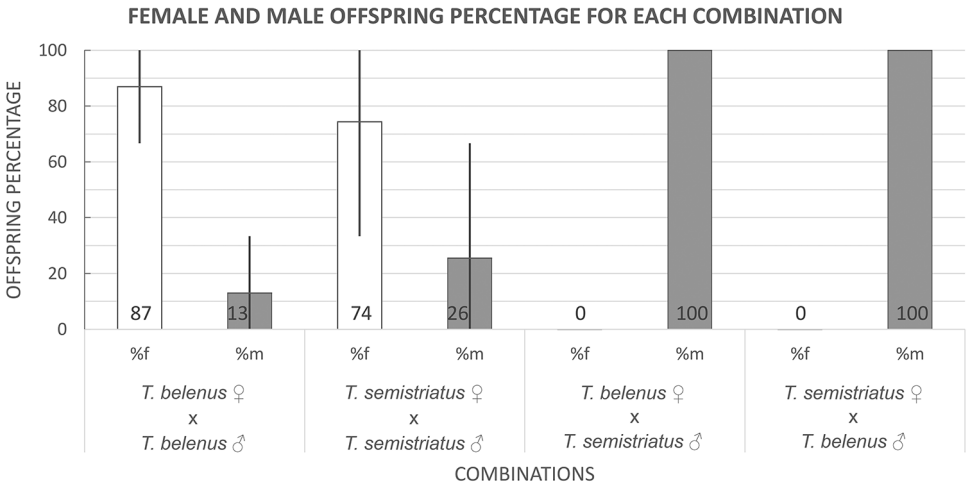
Specimen pairs tested for intraspecific combination mated within ten minutes; pairs tested for interspecific combination did not mate within the 10-minute observation period.

**Table 1.** Specimen information and GenBank Accession Number for the sequences generated by this study.

Species	Sex	Country	Year of collection	GenBank accession number	Collecting unit identifier
<i>Trissolcus manteroi</i>	f	ITALY	2010	MK906047	DISAFA-draw1465-HYM-0424
	f	ITALY	2010	MN603796	DISAFA-draw1465-HYM-0425
<i>Trissolcus semistriatus</i>	f	ITALY	2017	MK906048	DISAFA-draw1465-HYM-0233
	f	IRAN	2015	MK906049	USNMENT01223088
	f	ITALY	2017	MN603799	DISAFA-draw1465-HYM-0238
	f	ITALY	2017	MN603800	DISAFA-draw1465-HYM-0240
	f	ITALY	2016	MN603798	DISAFA-draw1465-HYM-0242
	f	ITALY	2016	MN603797	DISAFA-draw1465-HYM-0283
<i>Trissolcus belenus</i>	f	ITALY	2017	MK906050	DISAFA-draw1465-HYM-0014
	f	ITALY	2017	MN603802	DISAFA-draw1465-HYM-0012
	f	ITALY	2017	MN603803	DISAFA-draw1465-HYM-0013
	f	ITALY	2017	MN603804	DISAFA-draw1465-HYM-0016
	f	ITALY	2017	MN603806	DISAFA-draw1465-HYM-0018
	f	ITALY	2017	MN603805	DISAFA-draw1465-HYM-0019
<i>Trissolcus colemani</i>	f	IRAN	2015	MK906051	USNMENT01223460
	f	IRAN	2015	MN603801	USNMENT01223455
<i>Trissolcus rufiventris</i>	f	IRAN	2015	MN603807	UNIPA-HYM-S01347

**Table 2.** Barcode mean pairwise genetic distances ( $\pm$  SE) between *T. manteroi*, *T. semistriatus*, *T. belenus*, *T. colemani* and *T. rufiventris* (under the diagonal), and within taxa (along the diagonal). n = number of sequences.

	<i>T. manteroi</i> (n = 2)	<i>T. semistriatus</i> (n = 6)	<i>T. belenus</i> (n = 6)	<i>T. colemani</i> (n = 2)
<i>T. manteroi</i> (n = 2)	0.000	–	–	–
<i>T. semistriatus</i> (n = 6)	0.139 $\pm$ 0.000	0.005 $\pm$ 0.002	–	–
<i>T. belenus</i> (n = 6)	0.139 $\pm$ 0.000	0.109 $\pm$ 0.000	0.000 $\pm$ 0.000	–
<i>T. colemani</i> (n = 2)	0.138 $\pm$ 0.000	0.105 $\pm$ 0.001	0.107 $\pm$ 0.000	0.000
<i>T. rufiventris</i> (n = 1)	0.144 $\pm$ 0.000	0.141 $\pm$ 0.001	0.149 $\pm$ 0.000	0.133 $\pm$ 0.00



**Figure 3.** Sex ratio of emerged specimens. Combinations: *T. belenus* (♀  $\times$  ♂), n = 4; *T. semistriatus* (♀  $\times$  ♂), n = 4; *T. belenus* (♀)  $\times$  *T. semistriatus* (♂), n = 8; *T. semistriatus* (♀)  $\times$  *T. belenus* (♂), n = 8. Bars indicate standard deviation.

All females used for the two intraspecific combinations successfully produced female offspring (Figure 3); as expected the sex ratio was similar, in *T. belenus* (♀ × ♂) combination 31 females and 5 males emerged, and in *T. semistriatus* (♀ × ♂) 21 females and 4 males emerged. Females used for the two interspecific combinations produced only male offspring, 78 males in the *T. belenus* (♀) × *T. semistriatus* (♂) combination, and 65 males in the *T. semistriatus* (♀) × *T. belenus* (♂) combination. A total of 3 females failed to reproduce, producing no offspring in either the intraspecific or interspecific combinations.

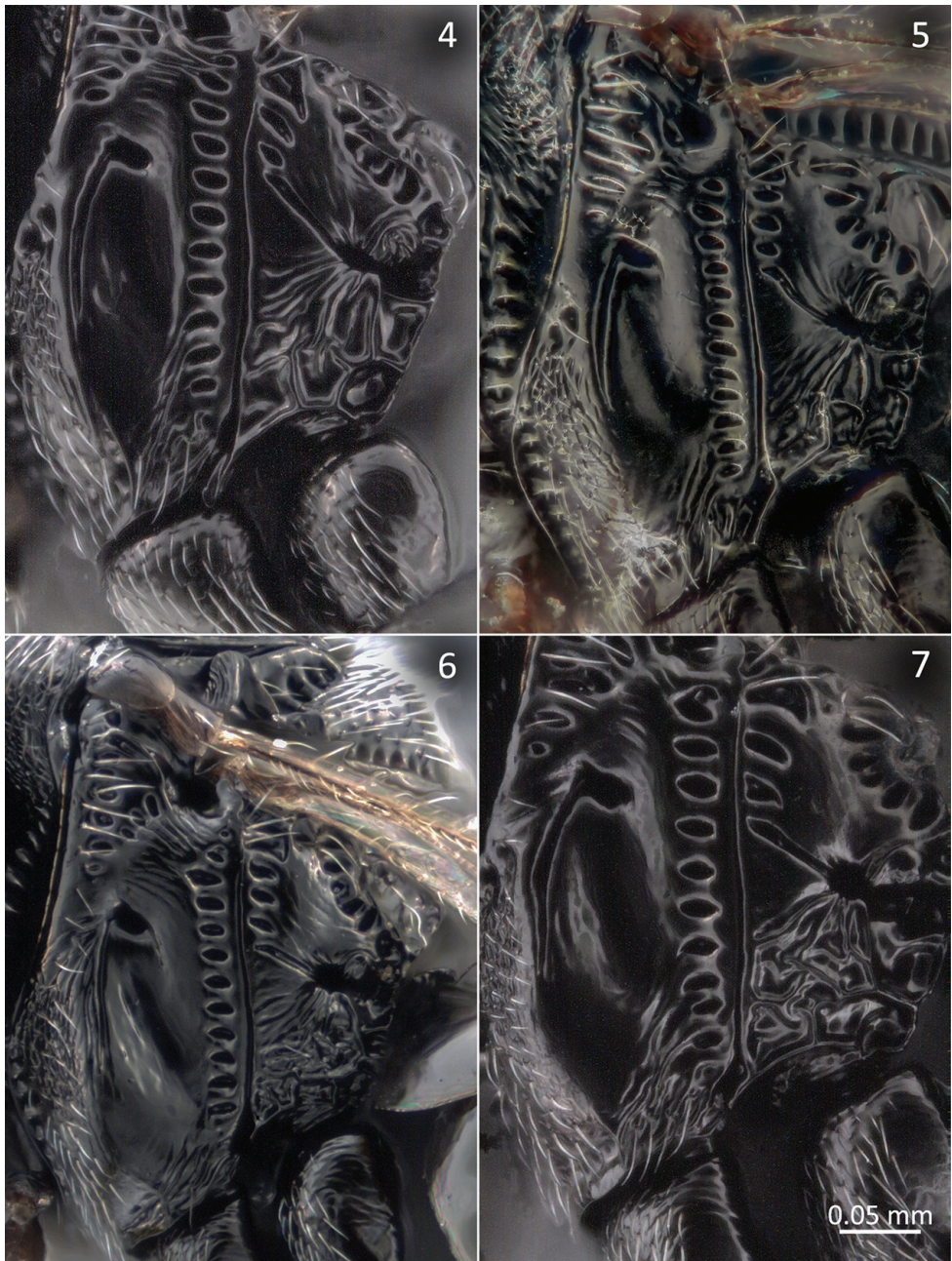
### Key to *Trissolcus* of the Palearctic region (females)

Modified couplets for the Key to *Trissolcus* of the Palearctic region (females) in Talamas et al. (2017)

- 29      Ventral mesopleuron distinctly bulging; mesocoxa oriented parallel to long axis of body; dorsal frons with sculpture effaced, sometimes entirely smooth and shining; A7 with two papillary (basiconic) sensilla (figures 128–132 in Talamas et al. 2017)..... ***Trissolcus perepelovi* (Kozlov)**
- Ventral mesopleuron not distinctly bulging; mesocoxa oriented at an angle of ~45° relative to long axis of body (Figure 6); dorsal frons evenly and densely covered in microsculpture; A7 with one papillary (basiconic) sensillum (Figure 10)..... **29A**
- 29A      Postmarginal vein in fore wing about twice as long as stigmal vein (Figure 14); metasoma yellow to dark brown, typically reddish-brown..... ***Trissolcus rufiventris* (Mayr)**
- Postmarginal vein only slightly longer than stigmal vein (Figure 13); metasoma dark brown to black (Figure 18)..... ***Trissolcus manteroi* (Kieffer)**
- 32      Lateral mesoscutum with mesoscutal humeral sulcus present as a smooth furrow (Figure 25)..... **32A**
- Lateral mesoscutum with mesoscutal humeral sulcus comprised of distinct foveae (Figures 20–23)..... **32B**
- 32A      Lateral pronotum with netrion sulcus incomplete dorsally, netrion often poorly defined; medial part of occipital carina rounded in dorsal view..... ***Trissolcus basalis* (Wollaston)**
- Lateral pronotum with netrion sulcus complete dorsally (Figures 5, 50, 53, 55, 60), netrion distinct; medial part of occipital carina angled (Figure 36), vertex of angle with short carina directed toward median ocellus..... ***Trissolcus semistriatus* (Nees von Esenbeck)**
- 32B      Laterotergite 1 with line of 3 setae (Figures 30, 45)..... ***Trissolcus belenus* (Walker)**
- Laterotergite 1 without setae (Figure 32)..... ***Trissolcus colemani* (Crawford)**

A matrix of the diagnostic characters used in this key is provided in Suppl. material: S6.



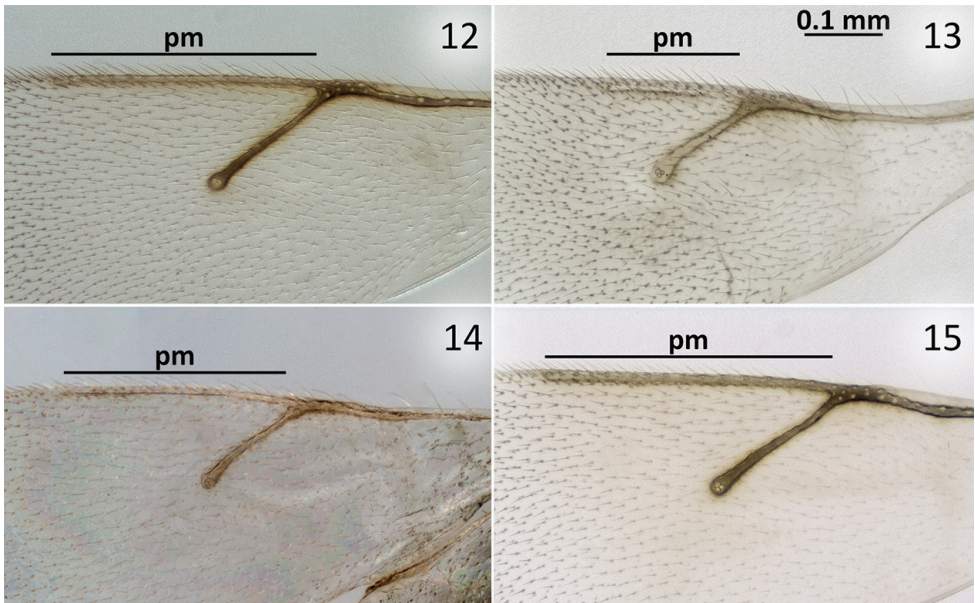


**Figures 4–7.** EPS, metapleural epicoxal sulcus, anterolateral extension of metapleuron: **4** *Trissolcus belenus* [DISAFA-draw1465-HYM-0009] **5** *T. colemani* [DISAFA-draw1466-HYM-0484] **6** *T. maneroi* [DISAFA-draw1465-HYM-0430] **7** *T. semistriatus* [DISAFA-draw1465-HYM-0227].

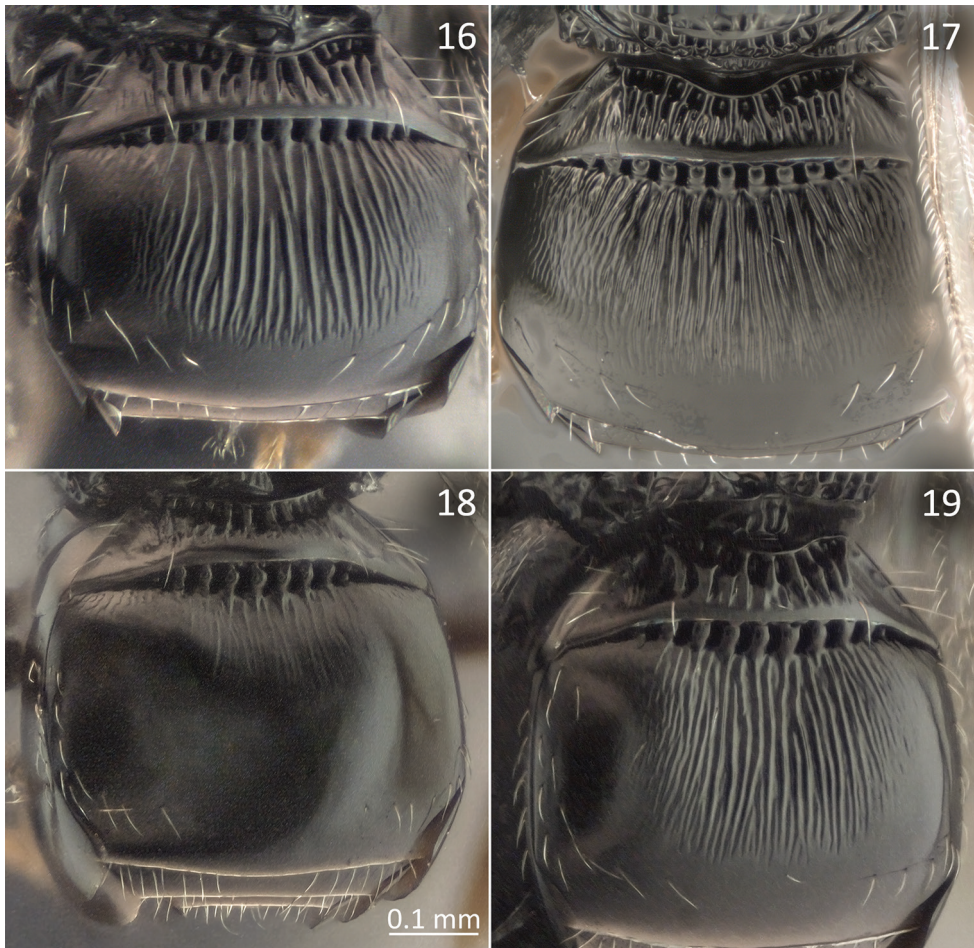




**Figures 8–11.** Basiconic sensilla, indicated by arrows, in the ventral surface of female antennal clava: **8** *Trissolcus belenus* [DISAFA-draw1465-HYM-0009] **9** *T. colemani* [DISAFA-draw1466-HYM-0484] **10** *T. manteroi* [DISAFA-draw1465-HYM-0430] **11** *T. semistriatus* [DISAFA-draw1465-HYM-0227].



**Figures 12–15.** Fore wing venations: **12** *Trissolcus belenus* [DISAFA-draw1465-0010] **13** *T. manteroi* [DISAFA-draw1465-0430] **14** *T. rufiventris* [USNMENT01223145] **15** *T. semistriatus* [DISAFA-draw1465-0229].



**Figures 16–19.** Metasomal tergites: **16** *Trissolcus belenus* [DISAFA-draw1465-HYM-0009] **17** *T. colemani* [DISAFA-draw1466-HYM-0484] **18** *T. manteroi* [DISAFA-draw1465-HYM-0430] **19** *T. semistriatus* [DISAFA-draw1465-HYM-0227].

### ***Trissolcus belenus* (Walker)**

[https://bioguid.osu.edu/xbiod\\_concepts/3190](https://bioguid.osu.edu/xbiod_concepts/3190)

Figures 4, 8, 12, 16, 20, 21, 26, 30, 33, 37, 41, 45–51.

*Telenomus Belenus* Walker, 1836: 352 (original description).

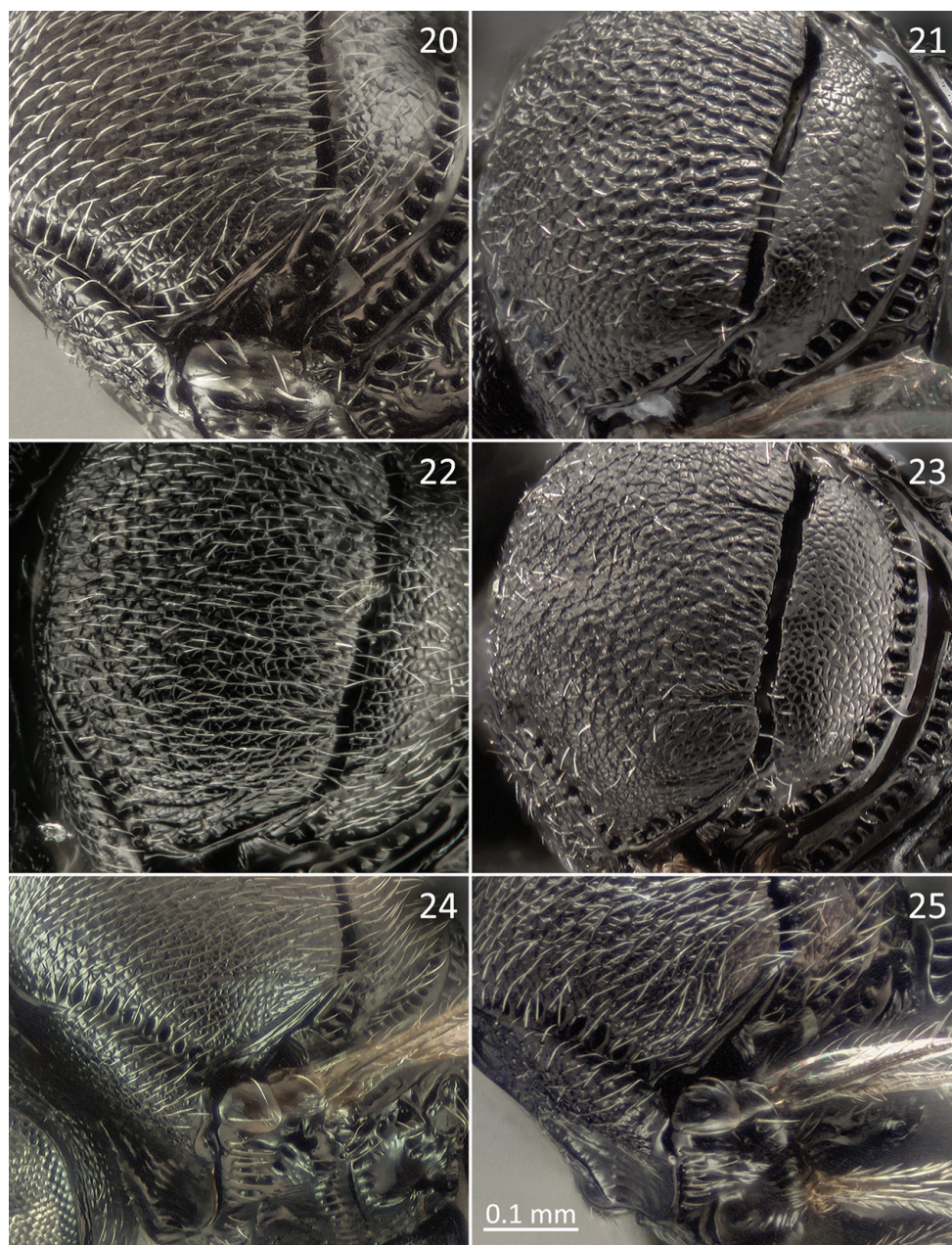
*Telenomus arminon* Walker, 1838: 457 (original description).

*Telenomus Nigrita* Thomson, 1860: 172 (original description, synonymized by Kozlov (1968)); Kozlov 1968: 214 (junior synonym of *Trissolcus grandis* (Thomson)).

*Telenomus frontalis* Thomson, 1860: 170 (original description, synonymized by Kozlov (1968)); Kozlov 1968: 214 (junior synonym of *Trissolcus grandis* (Thomson)).

*Telenomus grandis* Thomson, 1860: 169 (original description).





**Figures 20–25.** Mesonotum; mshs and traces of notauli: **20** *Trissolcus belenus* [DISAFA-draw1465-HYM-0009] **21** *T. belenus* [DISAFA...] after treatment in potassa solution to remove setae **22** *T. colemani* [DISAFA-draw1466-HYM-0484] **23** *T. colemani* [DISAFA-draw1466-HYM-0483] after treatment in potassa solution to remove setae **24** *T. manteroi* [DISAFA-draw1465-HYM-0430] **25** *T. semistriatus* [DISAFA-draw1465-HYM-0227].



**Figures 26–29.** Hind femur: **26** *Trissolcus belenus* [DISAFA-draw1465-HYM-0009] **27** *T. colemani* [DISAFA-draw1466-HYM-0484] **28** *T. mantero* [DISAFA-draw1465-HYM-0430] **29** *T. semistriatus* [DISAFA-draw1465-HYM-0227].

*Telenomus nigripes* Thomson, 1860: 170 (original description, synonymized by Kozlov (1968)); Kozlov 1968: 214 (junior synonym of *Trissolcus grandis* (Thomson)); Fergusson 1984: 230 (lectotype designation); Johnson 1992: 629 (type information).

*Telenomus ovulorum* Thomson, 1860: 171 (original description, synonymized by Mayr (1879)); Mayr 1879: 704 (junior synonym of *Telenomus semistriatus* (Nees von Esenbeck)).

*Teleas* (?) *Pentatomae* Rondani: Rondani, 1874: 135 (nomen nudum).

*Teleas pentatomae* Rondani, 1877: 199 (original description).

*Telenomus ovulorum* Thomson: Mayr 1879: 704. Junior synonym of *Telenomus semistriatus* (Nees von Esenbeck)

*Telenomus nigritus* Thomson: Dalla Torre 1898: 517 (emendation).

*Telenomus pentatomae* (Rondani): Dalla Torre, 1898: 518 (generic transfer).

*Allophanurus Arminon* (Walker): Kieffer, 1912: 12 (description, generic transfer).

*Aphanurus Belenus* (Walker): Kieffer, 1912: 83 (description, generic transfer).

*Aphanurus Frontalis* (Thomson): Kieffer, 1912: 81 (description, generic transfer).

*Aphanurus Grandis* (Thomson): Kieffer, 1912: 76 (description, generic transfer).

*Aphanurus Nigrita* (Thomson): Kieffer, 1912: 79 (description, generic transfer).

*Aphanurus nigripes* (Thomson): Kieffer, 1912: 75 (description, generic transfer).

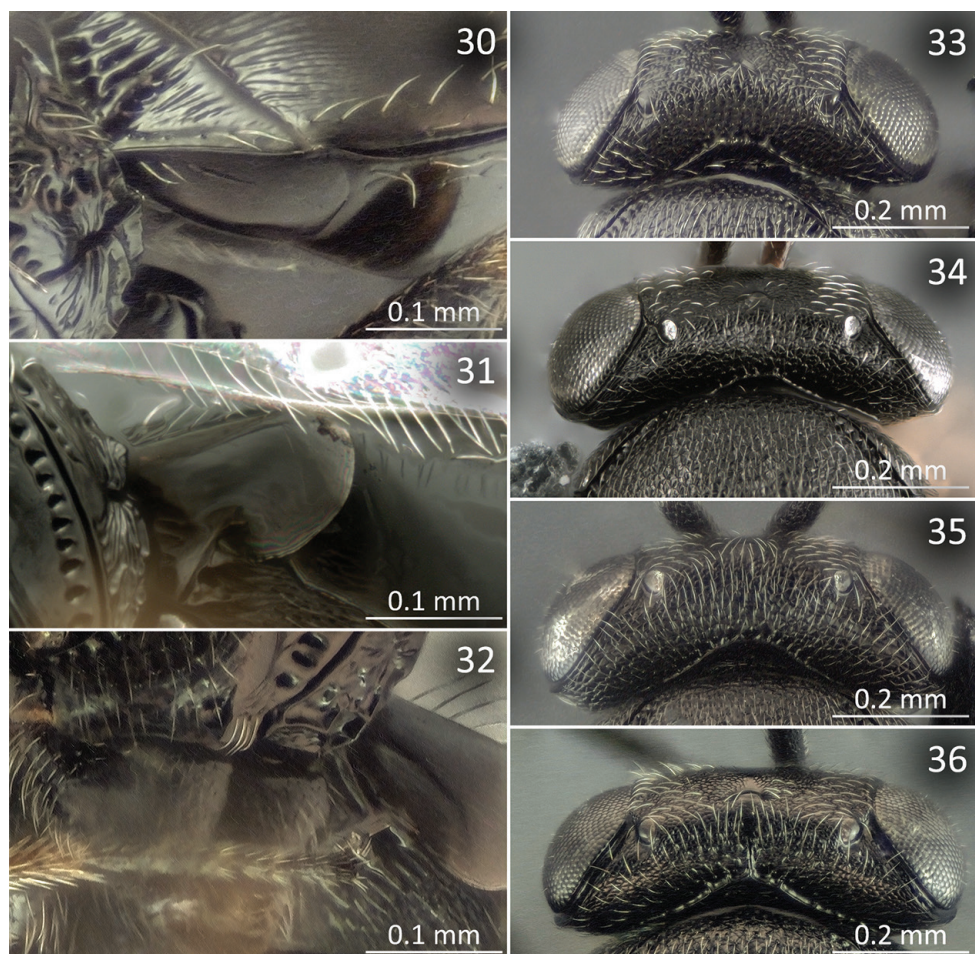
*Liophanurus Pentatomae* (Rondani): Kieffer, 1912: 69 (description, generic transfer).

*Allophanurus arminon* (Walker): Kieffer, 1926: 23 (description, keyed).

*Liophanurus pentatomae* (Rondani): Kieffer, 1926: 71 (description).

*Microphanurus belenus* (Walker): Kieffer, 1926: 91, 102 (description, generic transfer, keyed).





**Figures 30–36.** 30–32 Laterotergite 1 30 *Trissolcus belenus* [DISAFA-draw1465-HYM-0009] 31 *T. colemani* [DISAFA-draw1466-HYM-0484] 32 *T. semistriatus* [DISAFA-draw1465-HYM-0227] 33–36 Occipital carina 33 *Trissolcus belenus* [DISAFA-draw1465-HYM-0009] 34 *T. colemani* [DISAFA-draw1466-HYM-0484] 35 *T. manteroi* [DISAFA-draw1465-HYM-0430] 36 *T. semistriatus* [DISAFA-draw1465-HYM-0227].

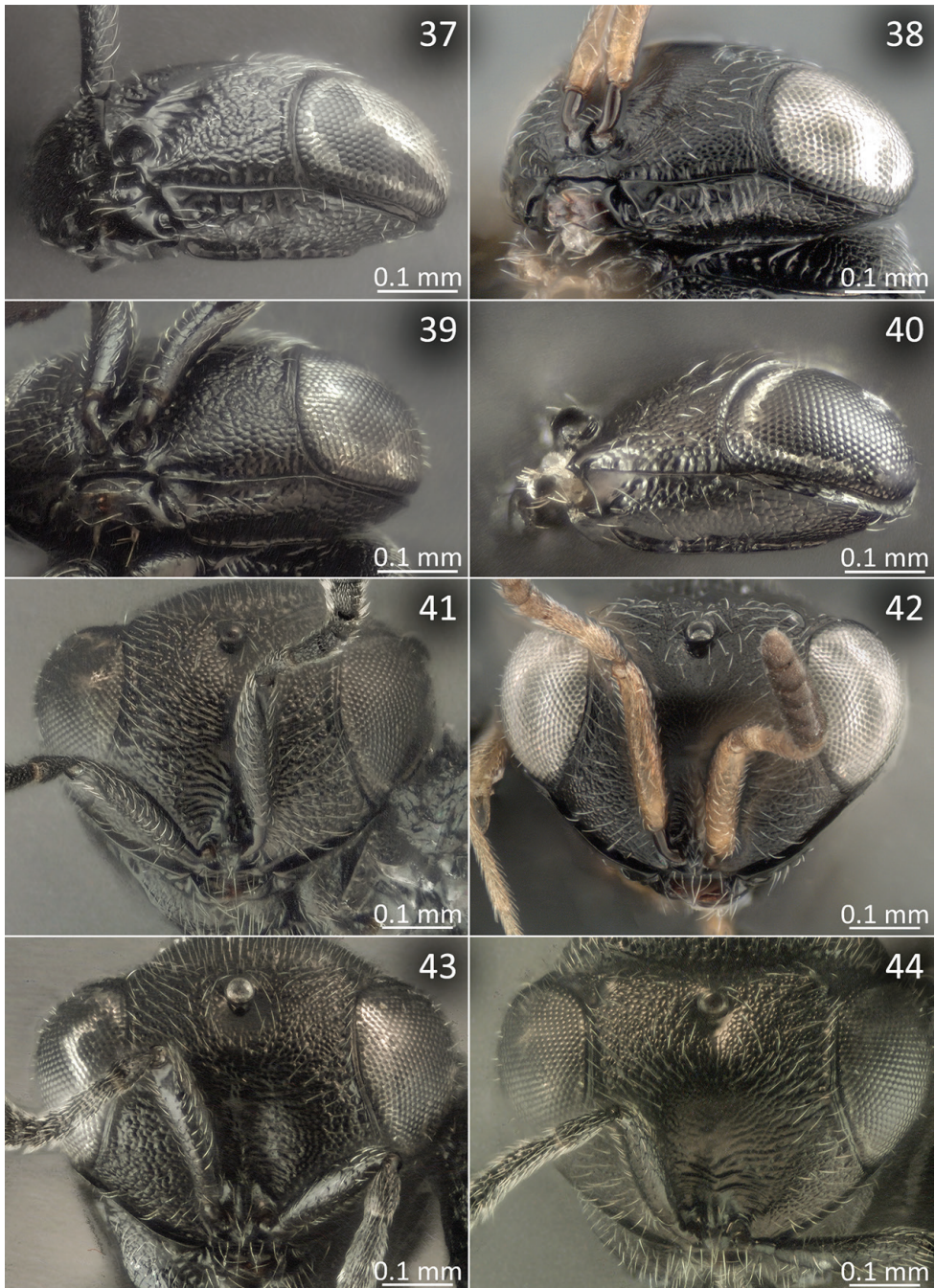
*Microphanurus frontalis* (Thomson): Kieffer, 1926: 91, 103 (description, generic transfer, keyed).

*Microphanurus grandis* (Thomson): Kieffer, 1926: 91, 99 (description, generic transfer, keyed); Debauche 1947: 256 (description).

*Microphanurus nigripes* (Thomson): Kieffer, 1926: 91, 98 (description, generic transfer, keyed).

*Microphanurus nigritus* (Thomson): Kieffer, 1926: 91, 100 (description, generic transfer, keyed).





**Figures 37–44.** 37–40 Head; malar area and gena **37** *Trissolcus belenus* [DISAFA-draw1465-HYM-0009] **38** *T. colemani* [DISAFA-draw1466-HYM-0484] **39** *T. manteroi* [DISAFA-draw1465-HYM-0430] **40** *T. semistriatus* [DISAFA-draw1465-HYM-0227] **41–44** Head in frontal view **41** *Trissolcus belenus* [DISAFA-draw1465-HYM-0009] **42** *T. colemani* [DISAFA-draw1466-HYM-0484] **43** *T. manteroi* [DISAFA-draw1465-HYM-0430] **44** *T. semistriatus* [DISAFA-draw1465-HYM-0227].

- Asolcus grandis* (Thomson): Masner, 1959: 376. (diagnosis, variation); Delucchi 1961: 44, 60 (description, keyed); Voegelé 1964: 28 (keyed); Javahery 1968: 419 (keyed); Voegelé 1969: 150 (keyed).
- Trissolcus grandis* (Thomson) syn. nov.: Viktorov, 1967: 91 (generic transfer, keyed); Safavi 1968: 416 (keyed); Kozlov 1968: 200, 214 (description, lectotype designation, synonymy, keyed); Fabritius 1972: 32, 35. (keyed; host catalogue; distribution); Viggiani and Mineo 1974: 156, 160, 161 (description, keyed); Kozlov and Lê 1977: 512 (synonymy, keyed); Kozlov 1978: 636 (description); Kozlov 1981: 187 (keyed); Kozlov and Kononova 1983: 110 (description); Johnson 1992: 629 (cataloged, type information); Kononova 1995: 96 (keyed); Doganlar 2001: 112 (description); Koçak and Kilinçer 2003: 302, 307 (keyed, description); Fabritius and Popovici 2007: 158 (host informations, distribution); Buhl & O'Connor, 2010: 154 (distribution); Ali 2011: 10 (keyed); Ghahari et al. 2011: 596 (host association, listed); Guz et al. 2013: 87 (description, phylogenetic relationships); Petrov 2013: 326 (keyed); Kononova 2014: 1424 (keyed); Kononova 2015: 262 (keyed); Talamas et al. 2017: 129, 135 (junior synonym of *Trissolcus semistriatus* (Nees von Esenbeck), type information).
- Asolcus nixomartini* Javahery, 1968: 419, 429 (original description, keyed, synonymized by Kozlov and Lê (1977)); Kozlov and Lê 1977: 512 (junior synonym of *Trissolcus grandis* (Thomson)); Johnson 1992: 629 (type information).
- Asolcus silwoodensis* Javahery, 1968: 419, 425 (original description, keyed, synonymized by Kozlov and Lê (1977)); Kozlov and Lê 1977: 512 (junior synonym of *Trissolcus grandis* (Thomson)); Johnson 1992: 629 (type information).
- Trissolcus pentatoma* (Rondani) syn. nov.: Bin, 1974: 463 (generic transfer, lectotype designation); Johnson 1992: 634 (cataloged, type information); Talamas et al. 2017: 130, 135 (junior synonym of *Trissolcus semistriatus* (Nees von Esenbeck), type information).
- Trissolcus belenus* (Walker): Fergusson, 1978: 120 (generic transfer); Fergusson 1984: 230 (lectotype designation); Johnson 1992: 623 (cataloged, type information); Kononova 2014: 1426 (possibly in *Telenomus*); Kononova 2015: 264 (possibly in *Telenomus*).
- Trissolcus nigripes* (Thomson) syn. nov.: Fergusson, 1978: 120 (generic transfer).
- Trissolcus nixomartini* (Javahery) syn. nov.: Fergusson, 1978: 120 (generic transfer); Fergusson 1984: 230 (type information).
- Trissolcus silwoodensis* (Javahery) syn. nov.: Fergusson, 1978: 120 (generic transfer); Fergusson 1984: 230 (type information).
- Trissolcus arminon* (Walker) syn. nov.: Fergusson 1983: 208 (generic transfer, description, lectotype designation); Fergusson 1984: 230 (type information); Johnson 1992: 622 (cataloged, type information).
- Trissolcus ovulorum* (Thomson) comb. nov., syn. nov.

**Diagnosis.** The presence of setae on the first laterotergite (Figures 30, 45) allows *T. belenus* to be easily diagnosed, as only two other Palearctic species share this character: *T. saakowi* and *T. mitsukurii* (Ashmead). Both of these species have distinct notauli,

which are absent in *T. belenus* (Figures 20, 22). Additionally, the hyperoccipital carina is entirely absent in *T. belenus* (Figures 33, 47, 49), whereas it is complete in *T. saakowi* and present posterior to the lateral ocellus in *T. mitsukurii*.

**Description.** Body length: 1.03–1.1 mm, median = 1.06 mm, SD = 0.02, n = 20. Body color: head, mesosoma, and metasoma black.

**Head.** FCI = 1.4; LCI = 1.9; IOS = 0.3 mm; OOL:POL:LOL = 1:12:5.8. Color of radicle: dark brown. Length of radicle: about equal to width of clypeus. Color of A1–A6 in female: distal A2 yellow to light brown, otherwise black. Color of A7–A11 in female: black. Number of papillary sensilla on A6: 0. Number of papillary sensilla on A7: 2. Facial striae: absent. Number of clypeal setae: 6. Shape of gena in lateral view: narrow. Genal carina: present only at base of mandible. Malar striae: absent. Sculpture of malar sulcus: distinctly and sparsely striate. Orbital furrow: uniform in width between midpoint of eye and malar sulcus. Macrosculpture of frons directly dorsal to the antennal scrobe: coarsely rugose. Preocellar pit: present. Setation of lateral frons: sparse; moderately dense. Punctuation of lateral frons: sparse. Sculpture directly ventral to preocellar pit: dorsoventrally fluted. Rugae on lateral frons: weakly developed to absent. OOL: less than one ocellar diameter. Hyperoccipital carina: absent. Macrosculpture of posterior vertex: absent. Microsculpture on posterior vertex along occipital carina: granulate. Anterior margin of occipital carina: crenulate. Medial part of occipital carina in dorsal view: rounded.

**Mesosoma.** Epomial carina: present. Macrosculpture of lateral pronotum directly anterior to netrion: finely rugulose. Netrion sulcus: complete. Pronotal suprahumeral sulcus in posterior half of pronotum: undifferentiated from sculpture of dorsal pronotum. Number of episternal foveae: 2. Course of episternal foveae ventrally: distinctly separate from postacetabular sulcus. Course of episternal foveae dorsally: distinctly separate from mesopleural pit. Subacropleurul sulcus: present. Speculum: transversely strigose. Mesopleural pit: extending ventrally into dorsoventral furrow parallel to mesopleural carina. Mesopleural carina: well defined anteriorly, poorly defined to absent posteriorly. Sculpture of femoral depression: smooth. Patch of striae at posteroventral end of femoral depression: present, striae oblique to long axis of femoral depression. Setal patch at posteroventral end of femoral depression: present as a line of setae. Microsculpture of anteroventral mesopleuron: present throughout. Macrosculpture of anteroventral mesopleuron: absent. Postacetabular sulcus: comprised of large cells. Mesopleural epicoxal sulcus: comprised of cells. Setation of posteroventral metapleuron: absent. Sculpture of dorsal metapleurul area: absent. Posterodorsal metapleurul sulcus: present as a line of foveae. Paracoxal sulcus in ventral half of metapleuron: indistinguishable from sculpture. Length of anteroventral extension of metapleuron: elongate, extending to base of mesocoxa. Apex of anteroventral extension of metapleuron: rounded. Metapleurul epicoxal sulcus: present as coarse rugae. Mesoscutal humeral sulcus: comprised of cells. Median mesoscutal carina: absent. Microsculpture of mesoscutum: imbricate-punctate anteriorly, becoming longitudinally imbricate-strigate posteriorly. Mesoscutal suprahumeral sulcus: comprised of cells. Length of mesoscutal suprahumeral sulcus: two-thirds the length of anterolateral edge of mesoscutum. Parapsidal line: absent. Notaulus: absent. Median protuberance on anterior



margin of mesoscutellum: absent. Shape of dorsal margin of anterior lobe of axillar crescent: acute. Sculpture of anterior lobe of axillar crescent: dorsoventrally strigose. Area bound by axillar crescent: smooth. Macrosculpture of mesoscutellum: absent. Microsculpture on mesoscutellum: imbricate-punctate laterally to granulate medially. Median mesoscutellar carina: absent. Setation of posterior scutellar sulcus: present. Form of metascutellum: single row of cells. Metanotal trough: foveate, foveae occupying more than half of metanotal height. Metapostnotum: invaginated near lateral edge of metascutellum. Length of postmarginal vein: about twice as long as stigmal vein. Color of legs: coxae dark brown to black, femora and tibia dark brown with yellowish tips, trochanters and tarsi yellow to pale brown. Anteroventral area of hind femora: not covered by setae. Anteromedial portion of metasomal depression: smooth.

**Metasoma.** Width of metasoma: about equal to width of mesosoma. Longitudinal striae on T1 posterior to basal costae: pair of longitudinal submedial carinae separate a lateral smooth area from an internal area where striate sculpture starts with basal grooves. Number of sublateral setae (on one side): 1. Setation of laterotergite 1: present. Length of striation on T2: extending two-thirds the length of the tergite. Setation of T2: present in a transverse line and along lateral margin. Setation of laterotergite 2: present.

**Host associations.** Pentatomidae: *Aelia rostrata*; *Arma custos*; *Carpocoris* sp.; *Dolycoris* sp.; *Graphosoma italicum* Müller; *Palomena prasina*; *Picromerus bidens* (L.); *Piezodorus* sp.; sentinel frozen eggs of *Halyomorpha halys*. Scutelleridae: *Eurygaster integriceps* Puton; *Eurygaster maura*.

**Link to distribution map.** [<https://hol.osu.edu/map-large.html?id=3190>]

**Material examined.** Lectotype, male *Telenomus Belenus*: ENGLAND and WESTERN EUROPE: no date, NMINH\_2018\_11\_49 (deposited in NMID); Lectotype, female, *Telenomus arminon*: UNITED KINGDOM: England, Dorset County, Lyme Regis, no date, NMINH\_2018\_11\_46 (deposited in NMID); Holotype, female, *Asolcus nixomartini*: UNITED KINGDOM: England, Windsor and Maidenhead Unit. Auth., Silwood Park, 1966, reared from egg, M. Javahery, B.M. TYPE HYM. 9.798 (deposited in BMNH); Paratypes of *Asolcus nixomartini*: UNITED KINGDOM: 1 female, 2 males, UNIPA-HYM-S01317–S01318 (BMNH); OSUC 17734 (BMNH); Holotype, female, *Asolcus silwoodensis*: UNITED KINGDOM: England, Windsor and Maidenhead Unit. Auth., Silwood Park, 1966, reared from egg, M. Javahery, B.M. TYPE HYM. 9.797 (deposited in BMNH); Paratypes of *Asolcus silwoodensis*: UNITED KINGDOM: 4 females, 4 males, UNIPA-HYM-S01309–S01316 (BMNH). Syntype males, *Telenomus ovulorum* Thomson: SWEDEN: no date, Boheman, NHRS-HEVA 000006872 (deposited in NHRS). Lectotype, female, *Telenomus nigripes*: SWEDEN: Västra Götaland, no date, Boheman, NHRS-HEVA 000006873 (deposited in NHRS). Paratype of *T. nixomartini*: UNITED KINGDOM: 1 male, OSUC 17734 (BMNH). *Other material*: (437 females, 67 males, 21 pins with multiple specimens). CHINA: 1 female, OSUC 571231 (OSUC). IRAN: 16 females, HMIM-HYM-05–06, 08–09, 011–012, 014, 027, 039 (HMIM); USNMENT01223080–01223082, 01223425, 01223430, 01223435, 01223440 (UNIPA). ITALY: 366 females, 63 males, 17 pins with multiple specimens, DISAFA-draw1465-HYM-0006–0219 (DISAFA); MSG -HYM-0001–0004, USNMENT01223249–01223258 (MCSN); USNMENT01223090–01223130, 01223132–01223139, 01223230–01223246 (UNIPA).





**Figures 45–48.** Holotype of *Trissolcus belemus* [NMINH\_2018\_11\_49]: **45** mesoscutal humeral sulcus and laterotergite 1 in lateral view **46** body in lateral view **47** body in antero-lateral view **48** body in dorsal view.





**Figures 49–51.** Holotype of *Trissolcus arminon* [NMINH\_2018\_11\_46]: **49** body in dorsal view **50** head and mesosoma in antero-lateral view **51** body in postero-lateral view.

MOROCCO: 24 female, 1 pin with multiple specimens, OSUC 17729 (BMNH); USNMENT01223131 (UNIPA). PORTUGAL: 6 females, 1 male, 1 pin with multiple specimens, USNMENT00916191, 00916210–00916213, 00916217 (BMNH). RUSSIA: 4 females, 2 males, 2 pins with multiple specimens, OSUC 17796–17797 (BMNH).

SWEDEN: 12 females, 2 males, UNIPA-HYM-S01306–S01307, USNMENT00916047, USNMENT00916051, USNMENT00916052, USNMENT00916070, USNMENT00916302–00916309 (BMNH). SWITZERLAND: 6 females, DISAFA-draw1465-HYM-0001–0005 (DISAFA); USNMENT01109059 (USNM). TANZANIA: 1 female, USNMENT01223480 (MZUF). UNITED KINGDOM: 1 female, 1 male, UNIPA-HYM-S01308 (BMNH); USNMENT00896318 (CNCI).

***Trissolcus colemani* (Crawford)**

[https://bioguid.osu.edu/xbiod\\_concepts/3203](https://bioguid.osu.edu/xbiod_concepts/3203)

Figures 5, 9, 17, 22, 23, 27, 31, 34, 38, 42, 52–55

*Telenomus colemani* Crawford, 1912: 2 (original description).

*Microphanurus djadetshko* Ryakhovskii, 1959: 84, 87 (original description, keyed).

*Microphanurus pseudoturesis* Ryakhovskii, 1959: 83, 85 (original description, keyed).

*Microphanurus rossicus* Ryakhovskii, 1959: 83, 86 (original description, keyed, synonymized by Viktorov (1964)); Viktorov 1964: 1021 (junior synonym of *Trissolcus pseudoturesis* (Ryakhovskii)); Johnson 1992: 635 (type information).

*Asolcus nigribasalis* Voegelé, 1962: 155 (original description); Voegelé 1964: 28 (keyed); Voegelé 1965: 96, 108 (variation, diagnosis, keyed); Voegelé 1969: 151 (junior synonym of *Asolcus djadetshko* (Ryakhovskii)).

*Asolcus djadetshko* (Ryakhovskii): Viktorov, 1964: 1015, 1021 (description, generic transfer, removed from synonymy with *Telenomus scutellaris* Thomson, keyed); Voegelé 1969: 151 (synonymy, keyed, spelling error).

*Asolcus pseudoturesis* (Ryakhovskii): Viktorov, 1964: 1013, 1021 (description, generic transfer, synonymy, keyed); Voegelé 1969: 151 (synonymy, keyed).

*Asolcus bennisi* Voegelé, 1964: 119 (original description); Voegelé 1965: 96, 108 (variation, diagnosis, keyed); Voegelé 1969: 151 (junior synonym of *Asolcus pseudoturesis* (Ryakhovskii)).

*Trissolcus djadetshko* (Ryakhovskii) syn. nov.: Viktorov, 1967: 91 (generic transfer, keyed); Safavi 1968: 415 (keyed); Kozlov 1968: 200 (keyed); Fabritius 1972: 31 (keyed); Kozlov and Lê 1977: 512 (keyed); Kozlov 1978: 636 (description); Kozlov 1981: 187 (keyed); Kozlov and Kononova 1983: 115 (description); Johnson 1992: 626 (cataloged, type information); Kononova 1995: 96 (keyed); Koçak and Kilinçer 2000: 171 (description, diagnosis, new distribution record for Turkey); Koçak and Kilinçer 2003: 303, 313 (keyed, description); Fabritius and Popovici 2007: 159 (checklist, host information, distribution); Ghahari et al. 2011: 595 (listed); Petrov 2013: 326 (keyed); Kononova 2014: 1425 (keyed); Kononova 2015: 263 (keyed); Talamas et al. 2017: 129 (junior synonym of *Trissolcus semistriatus* (Nees von Esenbeck)).

*Trissolcus pseudoturesis* (Ryakhovskii) syn. nov.: Viktorov, 1967: 91 (generic transfer, keyed); Safavi 1968: 415 (keyed); Kozlov 1968: 200 (keyed); Fabritius 1972: 31 (keyed); Kozlov and Lê 1977: 512 (keyed); Kozlov 1978: 636 (description); Kozlov and Kononova 1983: 114 (description); Johnson 1992: 635 (cataloged, type

- information); Kononova 1995: 96 (keyed); Koçak and Kiliñer 2003: 302, 310 (keyed, description); Ghahari et al. 2011: 596 (listed); Petrov 2013: 326 (keyed); Kononova 2014: 1425 (keyed); Kononova 2015: 263 (keyed).
- Trissolcus colemani* (Crawford): Masner and Muesebeck 1968: 72 (type information, generic transfer); Johnson 1992: 625 (cataloged, type information).
- Asolcus waloffae* Javahery, 1968: 419 (original description, keyed).
- Asolcus djadestshko* (Ryakhovskii): Voegelé, 1969: 151 (synonymy, keyed, spelling error).
- Trissolcus bennisi* (Voegelé): Kozlov and Lê 1977: 516 (generic transfer, keyed); Kozlov 1978: 637 (description); Kozlov and Kononova 1983: 122 (description); Johnson 1992: 623 (cataloged, type information); Kononova 2014: 1425 (keyed); Kononova 2015: 263 (keyed).
- Trissolcus nigribasalis* (Voegelé): Kozlov and Lê 1977: 518 (keyed); Kozlov 1978: 637 (description); Kozlov and Kononova 1983: 124 (description); Johnson 1992: 633 (cataloged, type information); Kononova 2014: 1425 (keyed); Kononova 2015: 263 (keyed).
- Trissolcus waloffae* (Javahery) syn. nov.: Kozlov and Lê 1977: 516 (keyed, generic transfer); Kozlov 1978: 637 (description); Kozlov and Kononova 1983: 123 (description); Fergusson 1984: 231 (type information); Johnson 1992: 640 (cataloged, type information); Kononova 2014: 1425 (keyed); Kononova 2015: 263 (keyed).
- Trissolcus crypticus* Clarke syn. nov., 1993: 524 (original description); Ghahari et al. 2011: 595 (new distribution record for Iran, host association, listed); Kononova 2014: 1426 (status unknown (not examined)); Kononova 2015: 264 (status unknown (not examined)).

**Diagnosis.** *Trissolcus colemani* is identified by a combination of characters more than by the presence of a distinct feature. The foveate mesoscutal humeral sulcus (Figures 21, 23) separates it from all the species treated here with the exception of *T. belenus* (Figures 20, 22). *Trissolcus colemani* and *T. belenus* are very similar in general appearance and these two species can be separated most reliably by setation of laterotergite 1: present in *T. belenus* (Figures 30, 45) and absent in *T. colemani* (Figure 31, 53). The anteroventral extension of the metapleuron reaches the mesocoxa in lateral view in both *T. belenus* and *T. colemani* and exhibits difference in the shape of its apex between these species. In *T. colemani*, the anteroventral extension of the metapleuron is very slender (Figure 5) compared to *T. belenus*, in which it is thicker, and the apex is rounded (Figure 4).

**Description.** Body length: 0.96–1.10 mm,  $m = 1.01$  mm,  $SD = 0.03$ ,  $n = 22$ . Body color: head, mesosoma, and metasoma black.

**Head.** FCI = 1.5; LCI = 1.7; IOS = 0.31 mm; OOL:POL:LOL = 1:13:5.9. Color of radicle: brown. Length of radicle: about equal to width of clypeus. Color of A1–A6 in female: variably yellow to brown. Color of A7–A11 in female: brown to black. Number of papillary sensilla on A6: 0. Number of papillary sensilla on A7: 2. Facial striae: absent. Number of clypeal setae: 6. Shape of gena in lateral view: narrow. Genal carina: present only at base of mandible. Malar striae: absent. Sculpture of malar sulcus: distinctly and sparsely striate. Orbital furrow: uniform in width between midpoint of eye and malar sulcus. Macrosculpture of frons directly



dorsal to the antennal scrobe: weakly rugose. Preocellar pit: present. Setation of lateral frons: sparse; moderately dense. Punctuation of lateral frons: sparse. Sculpture directly ventral to preocellar pit: dorsoventrally fluted. Rugae on lateral frons: coarse. OOL: less than one ocellar diameter. Hyperoccipital carina: absent. Macrosculpture of posterior vertex: absent. Microsculpture on posterior vertex along occipital carina: granulate. Anterior margin of occipital carina: crenulate. Medial part of occipital carina in dorsal view: rounded.

**Mesosoma.** Epomial carina: present. Macrosculpture of lateral pronotum directly anterior to netrion: finely rugulose. Netrion sulcus: complete. Pronotal suprahumeral sulcus in posterior half of pronotum: undifferentiated from sculpture of dorsal pronotum. Number of episternal foveae: 2; 3. Course of episternal foveae ventrally: distinctly separate from postacetabular sulcus. Course of episternal foveae dorsally: distinctly separate from mesopleural pit. Subacroleural sulcus: present. Speculum: transversely strigose. Mesopleural pit: extending ventrally into dorsoventral furrow parallel to mesopleural carina. Mesopleural carina: well defined anteriorly, poorly defined to absent posteriorly. Sculpture of femoral depression: smooth. Patch of striae at posteroventral end of femoral depression: present, striae oblique to long axis of femoral depression. Setal patch at posteroventral end of femoral depression: present. Microsculpture of anteroventral mesopleuron: present throughout. Macrosculpture of anteroventral mesopleuron: absent. Postacetabular sulcus: comprised of large cells. Mesopleural epicoxal sulcus: comprised of cells. Setation of posteroventral metapleuron: absent. Sculpture of dorsal metapleural area: absent. Posterodorsal metapleural sulcus: present as a line of foveae. Paracoxal sulcus in ventral half of metapleuron: indistinguishable from sculpture. Length of anteroventral extension of metapleuron: elongate, extending to base of mesocoxa. Apex of anteroventral extension of metapleuron: acute. Metapleural epicoxal sulcus: present as coarse rugae. Mesoscutal humeral sulcus: comprised of cells. Median mesoscutal carina: absent. Microsculpture of mesoscutum: imbricate-punctate anteriorly, becoming longitudinally imbricate-strigate posteriorly. Mesoscutal suprahumeral sulcus: comprised of cells. Length of mesoscutal suprahumeral sulcus: two-thirds the length of anterolateral edge of mesoscutum. Parapsidal line: absent. Notaulus: presence of short traces. Median protuberance on anterior margin of mesoscutellum: absent. Shape of dorsal margin of anterior lobe of axillar crescent: acute. Sculpture of anterior lobe of axillar crescent: dorsoventrally strigose. Area bound by axillar crescent: smooth. Macrosculpture of mesoscutellum: absent. Microsculpture on mesoscutellum: imbricate-punctate. Median mesoscutellar carina: absent. Setation of posterior scutellar sulcus: present. Form of metascutellum: single row of cells. Metanotal trough: foveate, foveae occupying more than half of metanotal height. Metapostnotum: invaginated near lateral edge of metascutellum. Length of postmarginal vein: about twice as long as stigmal vein. Color of legs: coxae dark brown to black, femora yellow to light brown with yellowish tips, tibia trochanters and tarsi yellow to pale brown. Anteroventral area of hind femora: not covered by setae. Anteromedial portion of metasomal depression: smooth.



**Figures 52–55.** Holotype of *Trissolcus colemani* [USNMENT00989063]: **52** body in dorsal view **53** body in lateral view **54** head in frontal view **55** head in ventral view and mesosoma in lateral view.

**Metasoma.** Width of metasoma: about equal to width of mesosoma. Longitudinal striae on T1 posterior to basal costae: pair of longitudinal submedial carinae separate a lateral smooth area from an internal area where striate sculpture starts with basal grooves. Number of sublateral setae (on one side): 1. Setation of laterotergite 1: absent. Length of striation on T2: extending two-thirds the length of the tergite. Setation of T2: present in a transverse line and along lateral margin. Setation of laterotergite 2: present.

**Host associations.** Pentatomidae: *Dolycoris indicus* (Type host); *Aelia acuminata* L.; *Aelia* sp.; *Brachynema germarii* (Kolenati); *Dolycoris* sp.; *Graphosoma semipunctatum* (F.); *Graphosoma* sp. Scutelleridae: *Eurygaster integriceps*; *Eurygaster maura*.

**Link to distribution map.** [<https://hol.osu.edu/map-large.html?id=3203>]

**Material examined.** Holotype, female, *Telenomus colemani*: INDIA: Karnataka St., Hongashenhalli (Hunsmanalli), 6.II.1909, L. C. Coleman, USNMENT00989063 (deposited in USNM). Syntype, female, *Microphanurus pseudoturesis*: UKRAINE: Donetsk (Stalinskaya) Reg., V-1952/1953–VII-1952/1953, V. Rjachovsky, USNMENT00954008 (deposited in ZIN). Syntype, female, *Microphanurus pseudoturesis*: UKRAINE: Donetsk (Stalinskaya) Reg., V-1952/1953–VII-1952/1953, V. Rjachovsky, USNMENT00954010. Holotype, female, *A. waloffae*: UNITED KINGDOM: England, Windsor and Maidenhead Unit. Auth., Silwood Park, VI-1965, reared, B.M. TYPE HYM. 9.795 (deposited in BMNH). Paratypes of *Trissolcus crypticus*: PAKISTAN: 3 females, 3 males, OSUC 17744, UNIPA-HYM-S01319–S01323 (BMNH). Paratype of *Microphanurus djadetskho*: UKRAINE: 1 female, USNMENT00954012 (ZIN). Paratypes of *Asolcus waloffae*: UNITED KINGDOM: 11 females, 11 males, 1 pin with multiple specimens, OSUC 17731, UNIPA-HYM-S01324, USNMENT0119671–0119674 (BMNH).

**Other material:** (144 females, 52 males, 6 pins with multiple specimens) CHINA: 1 female, UCRC ENT 142649 (UCRC). FRANCE: 1 female, USNMENT00896254 (CNCI). GREECE: 1 female, USNMENT00896062 (CNCI). IRAN: 17 females, HMIM-HYM-015, 017–018, 020–021, 025, 028, 031, 036, 042 (HMIM); USNMENT01223445, 01223450, 01223455, 01223460, 01223465, 01223470, 01223475 (UNIPA). ITALY: 82 females, 19 males, 2 pins with multiple specimens, DISAFA-draw1466-HYM-0483–0488 (DISAFA); USNMENT01223144, 01223146–01223221, 01223481 (UNIPA). MOROCCO: 39 females, 31 males, 3 pins with multiple specimens, OSUC 17728, 17743 (BMNH); UNIPA-HYM-S01325 (BMNH). RUSSIA: 3 females, 1 pin with multiple specimens, USNMENT01223222–01223223 (MCSN). SWEDEN: 2 males, USNMENT00916067–00916068 (BMNH).

### ***Trissolcus manteroi* (Kieffer)**

[https://bioguid.osu.edu/biod\\_concepts/3260](https://bioguid.osu.edu/biod_concepts/3260)

Figures 6, 10, 13, 18, 24, 28, 35, 39, 43, 56–58

*Telenomus Manteroi* Kieffer, 1909: 268 (original description).

*Aphanurus Manteroi* (Kieffer): Kieffer 1912: 84 (description, generic transfer).

*Microphanurus manteroi* (Kieffer): Kieffer 1926: 91, 102. (description, generic transfer, keyed); Boldaruyev 1969: 163, 170 (description, keyed)



*Trissolcus manteroi* (Kieffer): Kozlov 1968: 199 (keyed); Fabritius 1972: 31 (keyed); Bin 1974: 462 (type information); Kozlov and Lê 1977: 514 (keyed); Kozlov 1978: 636 (description); Kozlov and Kononova 1983: 117 (description); Johnson 1992: 631 (cataloged, type information); Koçak and Kiliñer 2000: 174 (description, diagnosis, new distribution record for Turkey); Koçak and Kiliñer 2003: 302, 310 (keyed, description of female); Koçak and Kodan 2006: 41 (description of male); Fabritius and Popovici 2007: 159. (host information, distribution); Ghahari et al. 2011: 596 (listed); Kononova 2014: 1424 (keyed); Kononova 2015: 262 (keyed); Talamas et al. 2017: 129, 135 (junior synonym of *Trissolcus semistriatus* (Nees von Esenbeck), type information).

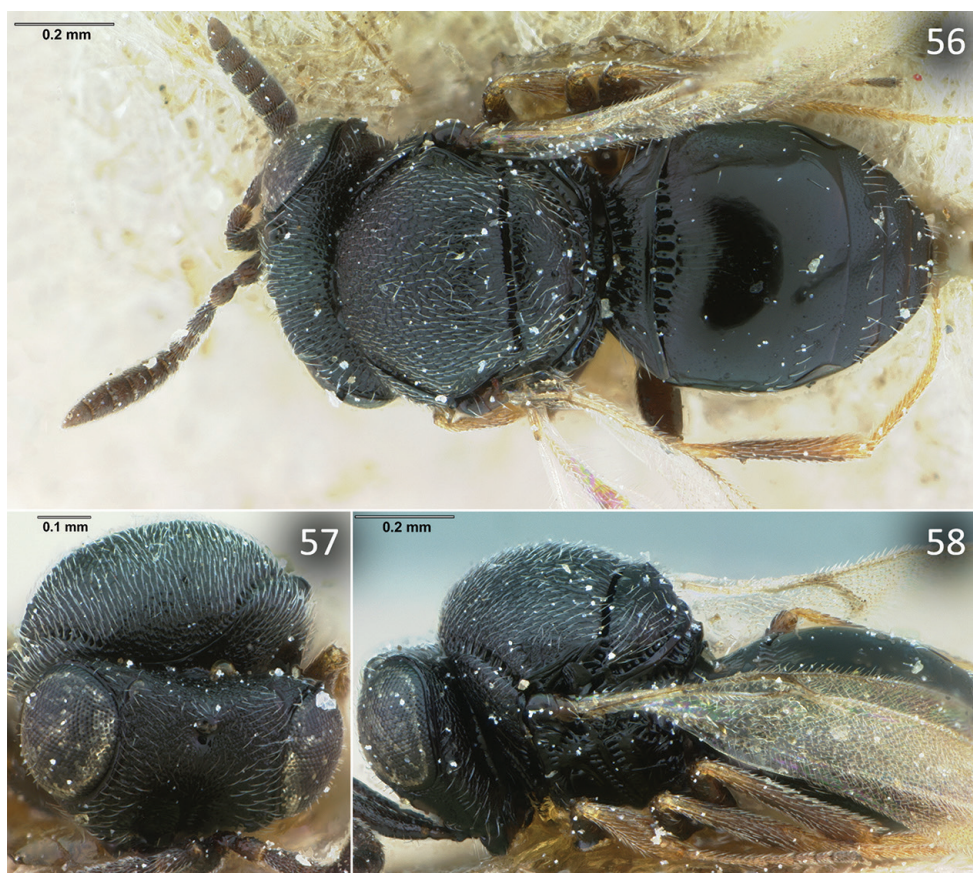
**Diagnosis.** *Trissolcus manteroi* and *T. rufiventris* are the only two species of Palearctic *Trissolcus* in which females exhibit a 1-2-2-2-1 claval formula (Figure 10). These two can be separated from each other by the length of the postmarginal vein in the fore wing: slightly longer than the stigmal vein in *T. manteroi* (Figure 13) and about twice as long as the stigmal vein in *T. rufiventris* (Figure 14). These two species can also be separated from each other by the form of the mesopleural epicoxal sulcus, which is comprised of cells in *T. manteroi* and is a smooth furrow in *T. rufiventris*.

**Description.** Female body length: 0.99–1.09 mm,  $m = 1.04$  mm,  $SD = 0.02$ ,  $n = 16$ . Body color: head, mesosoma, and metasoma black.

**Head.** FCI = 1.4; LCI = 1.8; IOS = 0.3 mm; OOL:POL:LOL = 1:12:5.3. Color of radicle: dark brown. Length of radicle: less than width of clypeus. Color of A1–A6 in female: distal A2 yellow to light brown, otherwise black. Color of A7–A11 in female: black. Number of papillary sensilla on A6: 0. Number of papillary sensilla on A7: 1. Facial striae: absent. Number of clypeal setae: 6. Shape of gena in lateral view: narrow. Genal carina: present only at base of mandible. Malar striae: absent. Sculpture of malar sulcus: weakly and densely striate. Orbital furrow: uniform in width between midpoint of eye and malar sulcus. Macrosculpture of frons directly dorsal to the anterior ocellus: weakly rugose. Preocellar pit: present. Setation of lateral frons: sparse; moderately dense. Punctuation of lateral frons: sparse. Sculpture directly ventral to preocellar pit: dorsoventrally fluted. Rugae on lateral frons: weakly developed to absent. OOL: less than one ocellar diameter. Hyperoccipital carina: absent. Macrosculpture of posterior vertex: absent. Microsculpture on posterior vertex along occipital carina: granulate. Anterior margin of occipital carina: crenulate. Medial part of occipital carina in dorsal view: rounded.

**Mesosoma.** Epomial carina: present. Macrosculpture of lateral pronotum directly anterior to netrion: finely rugulose. Netrion sulcus: complete. Pronotal suprahumeral sulcus in posterior half of pronotum: undifferentiated from sculpture of dorsal pronotum. Number of episternal foveae: 0. Subacroleural sulcus: present. Speculum: transversely strigose. Mesopleural pit: extending ventrally into dorsoventral furrow parallel to mesopleural carina. Mesopleural carina: well defined anteriorly, poorly defined to absent posteriorly. Sculpture of femoral depression: smooth. Patch of striae at posteroventral end of femoral depression: present, striae oblique to long axis of femoral depression. Setal patch at posteroventral end of femoral depression: absent. Microsculpture of anteroventral mesopleuron: present throughout. Macrosculpture of anter-

oventral mesopleuron: absent. Postacetabular sulcus: comprised of large cells. Mesopleural epicoxal sulcus: comprised of cells. Setation of posteroventral metapleuron: absent. Sculpture of dorsal metapleural area: absent. Posterodorsal metapleural sulcus: present as a line of foveae. Paracoxal sulcus in ventral half of metapleuron: indistinguishable from sculpture. Length of anteroventral extension of metapleuron: short, not extending to base of mesocoxa. Metapleural epicoxal sulcus: present as coarse rugae. Mesoscutal humeral sulcus: present as a simple furrow. Median mesoscutal carina: absent. Microsculpture of mesoscutum: imbricate-punctate anteriorly, becoming longitudinally imbricate-strigate posteriorly. Mesoscutal suprahumeral sulcus: comprised of cells. Length of mesoscutal suprahumeral sulcus: two-thirds the length of anterolateral edge of mesoscutum. Parapsidal line: absent. Notaulus: absent. Median protuberance on anterior margin of mesoscutellum: absent. Shape of dorsal margin of anterior lobe of axillar crescent: acute. Sculpture of anterior lobe of axillar crescent: dorsoventrally strigose. Area bound by axillar crescent: smooth. Macrosculpture of mesoscutellum:



**Figures 56–58.** Holotype of *Trissolcus manteroi* [MCSN 0013]: **56** body in dorsal view **57** head in antero-lateral view **58** body in lateral view.

absent. Microsculpture on mesoscutellum: imbricate-punctate laterally to granulate medially. Median mesoscutellar carina: absent. Setation of posterior scutellar sulcus: present. Form of metascutellum: single row of cells. Metanotal trough: foveate, foveae occupying more than half of metanotal height. Metapostnotum: invaginated near lateral edge of metascutellum. Length of postmarginal vein: 1.1–1.2 times as long as stigmal vein. Color of legs: coxae dark brown to black, femora and tibia dark brown with yellowish tips, trochanters and tarsi yellow to pale brown. Anteroventral area of hind femora: not covered by setae. Anteromedial portion of metasomal depression: smooth.

**Metasoma.** Width of metasoma: about equal to width of mesosoma. Longitudinal striae on T1 posterior to basal costae: pair of longitudinal submedial carinae separate a lateral smooth area from an internal area where striate sculpture starts with basal grooves. Number of sublateral setae (on one side): 1. Setation of laterotergite 1: absent. Length of striation on T2: extending one-third the length of the tergite. Setation of T2: present in a transverse line and along lateral margin. Setation of laterotergite 2: present.

**Host associations.** Pentatomidae: *Carpocoris* sp. (Type host); *Aelia rostrata* Boheman; *Dolycoris* sp.

**Link to distribution map.** [<https://hol.osu.edu/map-large.html?id=13225>]

**Material examined.** Holotype, female, *T. Manteroi*: ITALY: Liguria, Genoa, 9.VIII.1997, G. Mantero, MCSN 0013 (deposited in MCSN). *Paratypes*: ITALY: 5 females, 1 male, 1 pin with multiple specimens, UNIPA-HYM-S01327, S01328 (MCSN). *Other material*: (20 females, 2 males, 1 pin with multiple specimens) ARMENIA: 3 females, 1 pin with multiple specimens, USNMENT00979995, 00979997 (ZIN). IRAN: 4 females, USNMENT01223224–01223227 (MCSN). ITALY: 13 females, 2 males, DISAFA-draw1465-HYM-0424–0438 (DISAFA).

### *Trissolcus semistriatus* (Nees von Esenbeck)

[https://bioguid.osu.edu/xbiod\\_concepts/3305](https://bioguid.osu.edu/xbiod_concepts/3305)

Figures 7, 11, 15, 19, 25, 29, 32, 36, 40, 44, 59, 60.

*Teleas semistriatus* Nees von Esenbeck, 1834: 290 (original description); Ratzeburg 1852: 182 (description); Johnson 1992: 519 (cataloged).

*Telenomus semistriatus* (Nees von Esenbeck): Thomson, 1860: 171 (description, generic transfer); Mayr 1879: 699, 701, 704 (description, synonymy, keyed).

*Asolcus nigripedius* Nakagawa, 1900: 17 (original description); Watanabe 1951: 21, 25 (description, type information, keyed); Watanabe 1954: 22 (keyed).

*Aphanurus Semistriatus* (Nees von Esenbeck): Kieffer, 1912: 74 (description, generic transfer).

*Microphanurus semistriatus* (Nees von Esenbeck): Kieffer, 1926: 91, 97 (description, generic transfer, keyed); Nixon 1939: 131, 134 (description, keyed); Meier 1940: 80 (description, keyed); Ryakhovskii 1959: 84 (keyed).

*Microphanurus alexeevi* Meier, 1949: 114 (original description, not seen: reference from Kozlov (1963), synonymized with *Asolcus semistriatus* (Nees von Esenbeck)

by Kozlov (1963)); Ryakhovskii 1959: 83 (keyed); Kozlov 1963: 295 (junior synonym of *Asolcus semistriatus* (Nees von Esenbeck)).

*Microphanurus schtepetelnikovae* Meier, 1949: 114 (original description, not seen: reference from Kozlov (1963), synonymized with *Asolcus semistriatus* (Nees von Esenbeck) by Kozlov (1963)); Kozlov 1963: 295 (junior synonym of *Asolcus semistriatus* (Nees von Esenbeck)).

*Asolcus semistriatus* (Nees von Esenbeck): Masner 1959: 376 (diagnosis, variation); Delucchi 1961: 44, 59 (diagnosis, taxonomic status, keyed); Kozlov 1963: 295 (synonymy); Viktorov 1964: 1013, 1020 (variation, keyed); Kochetova 1966: 558 (description of immature stages); Javahery 1968: 419 (keyed); Voegelé 1969: 150 (keyed); Szabó 1976: 176, 178 (description, neotype designation, keyed).

*Microphanurus stscheptilnicovae* Meier: Ryakhovskii, 1959: 83 (keyed, spelling error).

*Trissolcus nigripedius* (Nakagawa): Masner, 1964: 146 (generic transfer); Ryu and Hirashima 1984: 37, 56 (description, keyed); Johnson 1992: 633 (cataloged); He, Chen, Fan, Li, Liu, Lou, Ma, Wang, Wu, Xu et al. 2004: 321 (description); Fabritius and Popovici 2007: 157 (host informations, distribution); Kononova 2014: 1424 (keyed); Kononova 2015: 261 (keyed); Talamas et al. 2017: 130 (junior synonym of *Trissolcus semistriatus* (Nees von Esenbeck), neotype designation).

*Trissolcus semistriatus* (Nees von Esenbeck): Safavi, 1968: 416 (keyed); Kozlov 1968: 200 (keyed); Fabritius 1972: 32, 34 (keyed, host catalogue; distribution); Kozlov and Lê 1977: 512 (keyed); Kozlov 1978: 636 (description); Kozlov and Kononova 1983: 113 (description); Graham 1984: 92 (variation); Johnson 1992: 636 (cataloged, type information); Kononova 1995: 96 (keyed); Koçak and Kilinçer 2003: 302, 305 (keyed, description); Ali 2011: 10 (keyed); Ghahari et al. 2011: 597 (listed); Guz et al. 2013: 87 (description, phylogenetic relationships); Petrov 2013: 326 (keyed); Kononova 2014: 1425 (keyed); Kononova 2015: 262 (keyed); Talamas et al. 2017: 20, 25, 128 (description, keyed, synonymy, type information, distribution).

*Trissolcus artus* Kozlov and Lê 1977: 512, 519 (original description, keyed); Kozlov 1978: 636 (description); Kozlov and Kononova 1983: 112 (description); Johnson 1992: 622 (cataloged, type information); Kononova 1995: 96 (keyed); Kononova 2014: 1424 (keyed); Kononova 2015: 262 (keyed); Talamas et al. 2017: 128, 135 (junior synonym of *Trissolcus semistriatus* (Nees von Esenbeck), type information).

**Diagnosis.** *Trissolcus semistriatus* is most similar to *T. belenus* and *T. colemani*, with which it overlaps in distribution and host range. It can be separated from both by the mesoscutal humeral sulcus present as a smooth furrow (Figure 25) and the short anteroventral extension of the mesopleuron, which does not extend to the base mesocoxa (Figure 7). Additionally, the angular form of the occipital carina in dorsal view, with a short carina extending toward the median ocellus, is found only in this species (Figure 36). The anteroventral area of the hind femur that is covered by setae (Figure 29) is



useful when separating *T. semistriatus* from *T. belenus* (Figure 26), *T. colemani* (Figure 27) and *T. manteroi* (Figure 28).

**Description.** Body length: 1.07–1.11 mm, median = 1.08 mm, SD = 0.01, n = 20. Body color: head, mesosoma, and metasoma black.

**Head.** FCI = 1.4; LCI = 1.9; IOS = 0.33 mm; OOL:POL:LOL = 1:12:5.4. Length of radicle: less than width of clypeus. Color of A1–A6 in female: distal A2 yellow to light brown, otherwise black. Color of A7–A11 in female: black. Number of papillary sensilla on A6: 0. Number of papillary sensilla on A7: 2. Facial striae: absent. Number of clypeal setae: 6. Shape of gena in lateral view: narrow. Genal carina: present only at base of mandible. Malar striae: absent. Sculpture of malar sulcus: weakly and densely striate. Orbital furrow: uniform in width between midpoint of eye and malar sulcus. Macrosculpture of frons directly dorsal to the antennal scrobe: coarsely rugose. Preocellar pit: present. Setation of lateral frons: sparse; moderately dense. Punctuation of lateral frons: sparse. Sculpture directly ventral to preocellar pit: dorsoventrally fluted. Rugae on lateral frons: weakly developed to absent. OOL: less than one ocellar diameter. Hyperoccipital carina: absent. Macrosculpture of posterior vertex: absent. Microsculpture on posterior vertex along occipital carina: granulate. Anterior margin of occipital carina: crenulate. Medial part of occipital carina in dorsal view: angled, vertex of angle with short carina directed toward median ocellus.

**Mesosoma.** Epomial carina: present. Macrosculpture of lateral pronotum directly anterior to netrion: finely rugulose. Netrion sulcus: complete. Pronotal suprahumeral sulcus in posterior half of pronotum: undifferentiated from sculpture of dorsal pronotum. Number of episternal foveae: 2. Course of episternal foveae ventrally: distinctly separate from postacetabular sulcus. Course of episternal foveae dorsally: distinctly separate from mesopleural pit. Subacroleptal sulcus: present. Speculum: transversely strigose. Mesopleural pit: extending ventrally into dorsoventral furrow parallel to mesopleural carina. Mesopleural carina: well defined anteriorly, poorly defined to absent posteriorly. Sculpture of femoral depression: smooth. Patch of striae at posteroventral end of femoral depression: present, striae oblique to long axis of femoral depression. Setal patch at posteroventral end of femoral depression: absent. Microsculpture of anteroventral mesopleuron: present throughout. Macrosculpture of anteroventral mesopleuron: absent. Postacetabular sulcus: comprised of large cells. Mesopleural epicoxal sulcus: comprised of cells. Setation of posteroventral metapleuron: absent. Sculpture of dorsal metapleuron: absent. Posterodorsal metapleuron sulcus: present as a line of foveae. Paracoxal sulcus in ventral half of metapleuron: indistinguishable from sculpture. Length of anteroventral extension of metapleuron: short, not extending to base of mesocoxa. Metapleuron epicoxal sulcus: present as coarse rugae. Mesoscutal humeral sulcus: present as a simple furrow. Median mesoscutal carina: absent. Microsculpture of mesoscutum: imbricate-punctate anteriorly, becoming longitudinally imbricate-striate posteriorly. Mesoscutal suprahumeral sulcus: comprised of cells. Length of mesoscutal suprahumeral sulcus: two-thirds the length of anterolateral edge of mesoscutum. Parapsidal line: absent. Notaulus: absent. Median protuberance on anterior margin of mesoscutellum: absent. Shape of dorsal margin of anterior lobe of axillar crescent:

acute. Sculpture of anterior lobe of axillar crescent: dorsoventrally strigose. Area bound by axillar crescent: smooth. Macrosculpture of mesoscutellum: absent. Microsculpture on mesoscutellum: imbricate-punctate laterally to smooth medially. Median mesoscutellar carina: absent. Setation of posterior scutellar sulcus: present. Form of metascutel-



**Figures 59, 60.** *Trissolcus semistriatus* [DISAFA-draw1465-HYM-0227]: **59** body in dorsal view **60** body in lateral view.



lum: single row of cells. Metanotal trough: foveate, foveae occupying more than half of metanotal height. Metapostnotum: invaginated near lateral edge of metascutellum. Length of postmarginal vein: about twice as long as stigmal vein. Color of legs: coxae dark brown to black, femora and tibia dark brown with yellowish tips, trochanters and tarsi yellow to pale brown. Anteroventral area of hind femora: covered by setae. Anteromedial portion of metasomal depression: smooth.

**Metasoma.** Width of metasoma: about equal to width of mesosoma. Longitudinal striae on T1 posterior to basal costae: pair of longitudinal submedial carinae separate a lateral smooth area from an internal area where striate sculpture starts with basal grooves. Number of sublateral setae (on one side): 1. Setation of laterotergite 1: absent. Length of striation on T2: extending two-thirds the length of the tergite. Setation of T2: present in a transverse line and along lateral margin. Setation of laterotergite 2: present.

**Host associations.** Pentatomidae: *Aelia rostrata*; *Brachynema germarii* (Kolenati); *Carpocoris* sp.; *Dolycoris baccarum* (L.); *Graphosoma semipunctatum*; *Rhaphigaster* sp.; Scutelleridae: *Eurygaster maura*.

**Link to distribution map.** [<https://hol.osu.edu/map-large.html?id=3305>]

**Material examined.** Neotype, female, *Teleas semistriatus*: PALEARCTIC: no date, NHMW 0007A (deposited in NHMW). Paratype of *Trissolcus artus*: RUSSIA: 1 female, USNMENT00916276 (ZIN). Neoparatype: PALEARCTIC: 1 female, NHMW 0007B (NHMW).

**Other material:** (183 females, 50 males, 2 pins with multiple specimens) IRAN: 11 females, HMIM-HYM-022, 038 (HMIM); USNMENT01223083–01223089 (UNIPA); USNMENT01223228–01223229 (MCSN). ITALY: 189 females, 54 males, 2 pins with multiple specimen, DISAFA-draw1465-HYM-0226–0240, 0242–0423 (DISAFA); MSNG-HYM-0005–0013 (MCSN); UNIPA-HYM-S01329–01346, USNMENT01223140–01223142, 01223482 (UNIPA). JAPAN: 1 female, EIHU 0003 (EIHU). MOROCCO: 1 female, USNMENT01223143 (UNIPA). PORTUGAL: 3 females, USNMENT00916201–00916202, 00916236 (BMNH). SWEDEN: 1 female, UNIPA-HYM-S01326 (BMNH). SWITZERLAND: 1 female, DISAFA-draw1465-HYM-0241 (DISAFA).

## Discussion

More than 180 years have passed between the original descriptions of *T. semistriatus* and *T. belenus* and the development of identification tools that can reliably distinguish them. This can be viewed as a glacial rate of progress, but also as an indication that modern methods can resolve long-standing taxonomic challenges. The taxonomy of *Trissolcus* illustrates that the examination of primary types and detailed comparison of specimens across a broad geographical range is necessary to advance the field, and that further refinement may be required even when these practices are implemented. Talamas et al. (2017) significantly advanced the taxonomy of Palearctic *Trissolcus* but additional analysis was needed to distill diagnostic characters from those that were treated as intraspecifically variable. Specifically, setation on the first laterotergite, the form of the mesoscutal humeral sulcus, and the length of the anteroventral extension of the

metapleuron were treated as variable within *T. semistriatus*. Although the utility of these characters for separating *T. belenus* and *T. colemani* was not recognized, Talamas et al. (2017) did bring attention to them, as they had not yet been used in the taxonomy of Palearctic *Trissolcus*. Setation of the hind femora, not mentioned by Talamas et al. (2017), represents a case in which a diagnostic character was previously recognized, but incorrectly associated with a taxon name (Delucchi 1961), and is now treated as useful for identifying *T. belenus*. *Trissolcus manteroii* is a different matter, in which reexamination of the type specimen was needed for its diagnostic characters (wing venation, claval formula, absence of episternal foveae) to be correctly characterized. These features place *T. manteroii* closer to *T. rufiventris* than to *T. semistriatus*, *T. belenus* or *T. colemani*.

The trail of photographic evidence provided by Talamas et al. (2017) enabled junior synonyms of *T. semistriatus* to be rapidly redistributed among *T. belenus* and *T. colemani* once the characters that delimit these species were identified, as well as the resurrection of *T. manteroii*. Given that producing a natural classification is an iterative process, explicit presentation of data that underlies taxonomic decisions accelerates further refinement. This is perhaps the only means by which the various quagmires of inadequate species descriptions in Platygastroidea can be transformed into a useful classification.

The need for reliable identification can be clearly seen in examples where quality taxonomy was absent. In the early part of the 20<sup>th</sup> century, *Trissolcus* specimens identified as *T. semistriatus* or *T. grandis* were reared and released in Russia and Iran as classical biological control agents against *Eurygaster* (Alexandrov 1947; Saakov 1903; Vaezi 1950; Vassiliev 1913; Zomorodi 1959). Some of these authors did not indicate how they identified the species, and in any case, the characters that reliably separate these species were not established. It is only by retroactively identifying voucher specimens, if they exist, that the results of these efforts can be interpreted in a meaningful way. The presence of *H. halys* in Europe has created a similar situation, with the same species involved in studies of its biological control. The refined species concepts presented here are thus of immediate relevance, given that *T. belenus* was recorded from frozen sentinel eggs of *H. halys* in Europe, and was previously identified as *T. semistriatus*.

Finally, it should be noted that independent testing of species concepts, ideally using multiple methods, is the best means by which they can be verified or improved. This study employed such an approach, using morphology, mating studies and molecular analysis to resolve four species from the concept of *T. semistriatus* provided in Talamas et al. (2017). In a manner conforming with this perspective, our results have been confirmed by a concomitant study by Talamas et al. (2019), in which a phylogeny of *Trissolcus* based on five molecular markers retrieved *T. belenus*, *T. colemani* and *T. semistriatus* as distinct entities.

## Acknowledgements

We are grateful to: Dr. Hege Vårdal (NHRS) for photographing a number of Thomson types: *Telenomus frontalis*, *Telenomus nigripes*, *Telenomus nigrita*, *Telenomus ovulorum* and *Trissolcus grandis*; Dr. Matthew Buffington (USNM, USDA/SEL) for providing supplemental images of the holotype of *Telenomus colemani*; Valentina Guerini for

transliteration from Cyrillic to Latin alphabet of labels; David Notton (BMNH), who hosted a visit of Virgilio Caleca; Dr. Paolo Visconti, who hosted a visit of Elijah Talamas to NMID which enabled the lectotypes of *T. belenus* and *T. arminon* to be studied and photographed and Dr. Norman Johnson (The Ohio State University), for maintaining Hymenoptera Online and vSysLab and assisting with data processing. Elijah Talamas was supported in part by a cooperative agreement with Kim Hoelmer (USDA/BIIRU) and by the Florida Department of Agriculture and Consumer Services- Division of Plant Industry. This research was funded by Fondazione Cassa di Risparmio di Cuneo (project HALY-END) and Regione Piemonte (project BIOHALY).

## References

- Alexandrov N (1947) *Eurygaster integriceps* Put. a Varamine et ses parasites. Entomologie et Phytopathologie Appliquees 5: 29–41.
- Ali WH (2011) The level of sunn pest oophagous parasitoids (Hymenoptera: Scelionidae) in infested wheat fields of northern governorate in Iraq with an identification key of *Trissolcus* species. Bulletin of the Iraq Natural History Museum 11: 7–15.
- Bin F (1974) The types of Scelionidae [Hymenoptera: Proctotrupoidea] in some Italian collections (Museums of Genoa and Florence, Institute of Portici). Entomophaga 19: 453–466. <https://doi.org/10.1007/BF02372781>
- Bin F (1981) Definition of female antennal clava based on its plate sensilla in Hymenoptera Scelionidae Telenominae. Redia 64: 245–261.
- Boldaruyev VO (1969) [Egg parasites of the subfamily Telenominae (Hymenoptera, Scelionidae), reared from the eggs of harmful insects.]. Trudy Buryatskogo Instituta Estestvennykh Nauk Buryatskii Filial Siirskogo Otdeleniya Akademii Nauk USSR 7: 156–171.
- Buffington ML, Burks RA, McNeil LA (2005) Advanced techniques for imaging parasitic Hymenoptera (Insecta). American Entomologist 51: 50–54. <https://doi.org/10.1093/ae/51.1.50>
- Buffington ML, Gates M (2008) Advanced Imaging Techniques II: Using a Compound Microscope for Photographing Point-Mount Specimens. American Entomologist 54: 222–224. <https://doi.org/10.1093/ae/54.4.222>
- Buffington ML, Talamas EJ, Hoelmer KA (2018) Team *Trissolcus*: Integrating Taxonomy and Biological Control to Combat the Brown Marmorated Stink Bug. American Entomologist 64: 224–232. <https://doi.org/10.1093/ae/tmy057>
- Buhl PN, O'Connor JP (2010) Five species of Ceraphronidae and Scelionidae (Hymenoptera) new to Ireland. Entomologists Monthly Magazine 146: 1–154.
- Clarke AR (1990) The Control of *Nezara viridula* L. with Introduced Egg Parasitoids in Australia. A Review of a “Landmark” Example of Classical Biological Control. Australian Journal of Agricultural Research 41: 1127–1146. <https://doi.org/10.1071/AR9901127>
- Clarke AR (1993) A new *Trissolcus* Ashmead species (Hymenoptera: Scelionidae) from Pakistan: Species description and its role as a biological control agent. Bulletin of Entomological Research 83: 523–527. <https://doi.org/10.1017/S0007485300039948>
- Crawford JC (1912) Descriptions of new Hymenoptera. No. 4. Proceedings of the United States National Museum 42: 1–10. <https://doi.org/10.5479/si.00963801.42-1880.1>



- Dalla Torre CG de (1898) *Catalogus Hymenopterorum Hucusque Descriptionum Systematicus et Synonymicus* (Vol. V). Chalcididae et Proctotrupoidea. Sumptibus Guilelmi Engelmann, Lipsiae, 598 pp.
- Debauche (1947) Scelionidae de la faune belge (Hymenoptera Parasitica). Bulletin et Annales de la Société Entomologique de Belge 83: 255–285.
- Delucchi VL (1961) Le complexe des *Asolcus* Nakagawa (*Microphanurus* Kieffer) (Hymenoptera, Proctotrupoidea) parasites oophages des punaises des cereales au Maroc et au Moyen-Orient. Cahiers de la Recherche Agronomique 14: 41–67.
- Doganlar M (2001) Egg parasitoids of *Rhaphigaster nebulosa* (Poda) (Hemiptera; Pentatomidae) with description of a new species of *Trissolcus* Ashmead (Hymenoptera: Scelionidae). Turkish Journal of Entomology 25: 109–114.
- Fabritius K (1972) Genul *Trissolcus* Ashmead 1893 (Hymenoptera, Scelionidae) în România și perspectivele utilizării acestui gen de entomofagi în combaterea biologică și integrată a ploșnițelor cerealelor. Lucrări Științifice – Zoologie, Constanța 1972: 27–42.
- Fabritius K, Popovici OA (2007) A Catalogue of Scelionidae from Romania (Hymenoptera, Platygastridae). Entomologica Romanica 12: 133–161.
- Fergusson NDM (1978) Proctotrupoidea and Ceraphonoidea. Pages 110–126 in Fitton, Graham, Boucek, Fergusson, Huddleston, Quinlan & Richards. 1978. A check list of British insects by George Sidney Kloet and the late Walter Douglas Hincks, second edition (completely revised). Pa. Handbooks for the Identification of British Insects 11: 1–159.
- Fergusson NDM (1983) The status of the genus *Allophanurus* Kieffer (Hymenoptera: Proctotrupoidea, Scelionidae). Entomologist's Monthly Magazine 119: 207–209.
- Fergusson NDM (1984) The type-specimens and identity of the British species of *Trissolcus* Ashmead (Hym., Proctotrupoidea, Scelionidae). Entomologist's Monthly Magazine 120: 229–232.
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.
- Ghahari H, Buhl PN, Koçak E (2011) Checklist of Iranian *Trissolcus* Ashmead (Hymenoptera: Platygastridae: Scelionidae: Telenominae). International Journal of Environmental Studies 68: 593–601. <https://doi.org/10.1080/00207233.2011.617531>
- Graham MWR de V (1984) Madeira insects, mainly Hymenoptera Proctotrupoidea, Ceraphonoidea, and Bethyloidea. Boletim do Museu Municipal do Funchal 36: 83–110.
- Guz N, Kocak E, Kilincer N (2013) Molecular phylogeny of *Trissolcus* species (Hymenoptera: Scelionidae). Biochemical Systematics and Ecology 48: 85–91. <https://doi.org/10.1016/j.bse.2012.12.010>
- Harris RA (1979) A Glossary of Surface Sculpturing. California Department of Food and Agriculture Division of Plant Industry Laboratory Services 28: 1–31.
- He J-H, Chen X-X, Fan J-J, Li Q, Liu C-M, Lou X-M, Ma Y, Wang S-F, Wu Y-R, Xu Z-H, Xu Z-F, Yao J (2004) [Hymenopteran Insect Fauna of Zhejiang.] Science Press, Beijing. 1373 pp.
- Isidoro N, Bin F, Colazza S, Vinson SD (1996) Morphology of antennal gustatory sensilla and glands in some parasitoids Hymenoptera with hypothesis on their role in sex and host recognition. Journal of Hymenoptera Research 5: 206–239.

- Javahery M (1968) The egg parasite complex of British Pentatomoidea (Hemiptera): taxonomy of Telenominae (Hymenoptera: Scelionidae). Transactions of the Royal Entomological Society of London 120: 417–436. <https://doi.org/10.1111/j.1365-2311.1968.tb00345.x>
- Johnson NF (1987) Systematics of New World *Trissolcus*, a genus of pentatomid egg-parasites (Hymenoptera: Scelionidae): Neotropical species of the *flavipes* group. Journal of Natural History 21: 285–304. <https://doi.org/10.1080/00222938700771021>
- Johnson NF (1992) Catalog of world Proctotrupoidea excluding Platygastriidae. Memoirs of the American Entomological Institute 51: 1–825.
- Kaartinen R, Stone G, Hearn J, Lohse K, Roslin T (2010) Revealing secret liaisons: DNA barcoding changes our understanding of food webs. Ecological Entomology 35: 623–638. <https://doi.org/10.1111/j.1365-2311.2010.01224.x>
- Kerr PH, Fisher EM, Buffington ML (2008) Dome lighting for <https://doi.org/10.1093/ae/54.4.198> insect imaging under a microscope. American Entomologist 54: 198–200.
- Kieffer JJ (1909) Description de quelques nouveaux Scelionides d'Europe (Hym.). Bulletin de la Société Entomologique de France 15: 268–271. <https://doi.org/10.5962/bhl.part.13507>
- Kieffer JJ (1912) Proctotrypidae (3e partie). Species des Hyménoptères d'Europe et d'Algérie. 11: 1–160.
- Kieffer JJ (1926) Scelionidae. Das Tierreich (Vol. 48). Walter de Gruyter & Co., Berlin, 885 pp.
- Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of molecular evolution 16(2): 111–120. <https://doi.org/10.1007/BF01731581>
- Koçak E, Kilinçer N (2000) Türkiye faydalı faunası için yeni kayıt *Trissolcus* (Hym.: Scelionidae) türleri. Bitki Koruma Bülteni 40: 169–177.
- Koçak E, Kilinçer N (2003) Taxonomic studies on *Trissolcus* sp. (Hymenoptera: Scelionidae), egg parasitoids of the sunn pest (Hemiptera: Scutelleridae: *Eurygaster* sp.), in Turkey. Turkish Journal of Zoology 27: 301–317.
- Koçak E, Kodan M (2006) *Trissolcus manteroi* (Kieffer, 1909) (Hymenoptera, Scelionidae): male nov. with new host from Turkey. Journal of Pest Science 79: 41–42. <https://doi.org/10.1007/s10340-005-0101-x>
- Kochetova NI (1966) [Development of *Asolcus semistriatus* Nees (Hymenoptera, Scelionidae) – egg parasite of the little tortoise bug and other Pentatomoidea (Hemiptera).]. Zoologicheskii Zhurnal 45: 558–567.
- Kononova SV (1995) [25. Fam. Scelionidae.]. In: Lehr PA (Ed.) Key to Insects of Russian Far East in Six Volume (Vol. 4). Neuropteroidea, Mecoptera, Hymenoptera. Part 2. Hymenoptera.]. Dal'nauka, Vladivostok, 57–121.
- Kononova SV (2014) Egg-parasitoids of the genus *Trissolcus* (Hymenoptera, Scelionidae, Telenominae) from the Palaearctic fauna (the *flavipes* morphological group). 1. New species of the genus *Trissolcus*. Zoologicheskii Zhurnal 93: 1420–1426. <https://doi.org/10.1134/S0013873814070112>
- Kononova SV (2015) Egg-parasitoids of the genus *Trissolcus* (Hymenoptera, Scelionidae, Telenominae) from the Palaearctic region. The *flavipes* morphological group: 2. A key to the species of the *flavipes* group. Entomological Review 95: 257–264. <https://doi.org/10.1134/S0013873815020086>

- Kozlov MA (1963) [New synonyms of species of the genus *Asolcus* Nak., *Gryon* Hal. and *Telenomus* Hal. (Hymenoptera, Scelionidae), egg parasites of *Eurygaster integriceps* Put.]. Zoologicheskii Zhurnal 63: 294–296.
- Kozlov MA (1968) Telenomines (Hymenoptera, Scelionidae, Telenominae) of the Caucasus – egg parasites of the sun pest (*Eurygaster integriceps* Put.) and other grain bugs. Trudy Vsesoyuznogo Entomologicheskogo Obshchestva 52: 188–223.
- Kozlov MA (1978) [Superfamily Proctotrupoidea]. In: Medvedev GS (Ed.) [Determination of Insects of the European Portion of the USSR.]. Nauka, Leningrad, 538–664.
- Kozlov MA (1981) The system and zoogeography of scelionids (Hymenoptera, Scelionidae). Entomologicheskoe Obozrenie 60: 174–182.
- Kozlov MA, Kononova SV (1983) [Telenominae of the Fauna of the USSR.]. Nauka, Leningrad.
- Kozlov MA, Lê XH (1977) Palearctic species of egg parasites of the genus *Trissolcus* Ashmead, 1893 (Hymenoptera, Scelionidae, Telenominae). Insects of Mongolia 5: 500–525.
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. Molecular biology and evolution 35(6): 1547–1549. <https://doi.org/10.1093/molbev/msy096>
- Masner L (1959) Some problems of the taxonomy of the subfamily Telenominae (Hym. Scelionidae). Transactions of the 1<sup>st</sup> International Conference on Insect Pathology and Biological Control, Prague 1958: 375–382.
- Masner L (1964) A comparison of some Nearctic and Palearctic genera of Proctotrupoidea (Hymenoptera) with revisional notes. Casopis Československé Společnosti Entomologické 61: 123–155.
- Masner L (1980) Key to genera of Scelionidae of the Holarctic Region, with descriptions of new genera and species (Hymenoptera: Proctotrupoidea). Memoirs of the Entomological Society of Canada 112: 1–54. <https://doi.org/10.4039/entm112113fv>
- Masner L, Muesebeck CFW (1968) The types of Proctotrupoidea (Hymenoptera) in the United States National Museum. Bulletin of the United States National Museum 270: 1–143. <https://doi.org/10.5479/si.03629236.270>
- Mayr G (1879) Ueber die Schlupfwespengattung *Telenomus*. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 29: 697–714.
- Meier NF (1940) [Parasites reared in the USSR in 1938–1939 from eggs of the corn-bug (*Eurygaster integriceps* Osch.).]. Vestnik Zashchita Rastenii 3: 79–82.
- Meier NF (1949) [Toward knowledge of the species of egg-parasites of bugs found in recent years in the USSR.]. Trudy Vsesoyuznogo Instituta Zashchity Rastenii 2: 114–116.
- Mikó I, Masner L, Deans AR (2010) World revision of *Xenomonus* Walker (Hymenoptera: Platygastroidea, Platygastriidae). Zootaxa 2708: 1–73. <https://doi.org/10.11646/zootaxa.2708.1.1>
- Mikó I, Vilhelmsen L, Johnson NF, Masner L, Péntzes Z (2007) Skeletomusculature of Scelionidae (Hymenoptera: Platygastroidea): Head and mesosoma. Zootaxa 1571: 1–78. <https://doi.org/10.11646/zootaxa.1571.1.1>
- Nakagawa H (1900) [Illustrations of some Japanese Hymenoptera parasitic on insect eggs. I.]. Special Report of the Agricultural Experiment Station, Tokyo 6: 1–26.



- Nees von Esenbeck CG (1834) Hymenopterorum Ichneumonibus Affinium Monographiae, Genera Europaea et Species Illustrantes (Vol. 2). J. G. Cotta, Stuttgart, 448 pp. <https://doi.org/10.5962/bhl.title.26555>
- Nixon GEJ (1939) Parasites of hemipterous grain-pests in Europe (Hymenoptera: Proctotrupoidea). Arbeiten über Morphologische und Taxonomische Entomologie aus Berlin-Dahlem 6: 129–136.
- Petrov S (2013) Three new species of *Trissolcus* Ashmead (Hymenoptera: Platygastroidea: Scelionidae) from Bulgaria. Biologia (Bratislava) 68: 324–329. <https://doi.org/10.2478/s11756-013-0151-0>
- Ratzeburg JTC (1852) Die Ichneumoniden der Forstinsecten in Forstlicher und Entomologischer Beziehung (Vol. 3). Nicolaischen Buchhandlung, Berlin, 272 pp.
- Rjachovskij VV (1959) [Egg parasites of the sunn pest in the Ukrainian SSR.]. Ukrainskii Nauchno-Issledovatel'skii Institut Zashchity Rastenii 8: 76–88.
- Rondani C (1874) Nuove osservazioni sugli insetti fitofagi e sui loro parassiti. Bullettino della Società Entomologica Italiana 6: 130–136.
- Rondani C (1877) Vesparia parasita no vel minus cognita observata et descripta. Bullettino della Società Entomologica Italiana 9: 166–213.
- Ryu J, Hirashima Y (1984) Taxonomic studies on the genus *Trissolcus* Ashmead of Japan and Korea (Hymenoptera, Scelionidae). Journal of the Faculty of Agriculture, Kyushu University 29: 35–58.
- Saakov AI (1903) [The artificial breeding of egg parasites of the bread bug.]. Trudy Byuro po Entomologii 4: 1–12.
- Safavi M (1968) Etude biologique et ecologique des hymenopteres parasites des oeufs des punaises de cereales. Entomophaga 13: 381–495.
- Szabó JB (1976) Neue Daten zur Kenntnis der Gattung *Asolcus* Nakagawa, 1900 (Hymenoptera: Proctotrupoidea, Scelionidae). Folia Entomologica Hungarica 29: 175–191.
- Talamas EJ, Johnson NF, Buffington ML (2015) Key to Nearctic species of *Trissolcus* Ashmead (Hymenoptera, Scelionidae), natural enemies of native and invasive stink bugs (Hemiptera, Pentatomidae). Journal of Hymenoptera Research 43: 45–110. <https://doi.org/10.3897/JHR.43.8560>
- Talamas EJ, Buffington ML, Hoelmer K (2017) Revision of Palearctic *Trissolcus* Ashmead (Hymenoptera, Scelionidae). Journal of Hymenoptera Research 56: 3–185. <https://doi.org/10.3897/jhr.56.10158>
- Talamas EJ, Bon M-C, Hoelmer KA, Buffington ML (2019) Molecular phylogeny of *Trissolcus* wasps (Hymenoptera, Scelionidae) associated with *Halyomorpha halys* (Hemiptera, Pentatomidae). In: Talamas E (Eds) Advances in the Systematics of Platygastroidea II. Journal of Hymenoptera Research 73: 201–217. <https://doi.org/10.3897/jhr.73.39563>
- Thomson CG (1860) Sverges Proctotruper. Tribus IX. Telenomini. Tribus X. Dryinini. Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar 17: 169–181.
- Tortorici F, Caleca V, van Noort S, Masner L (2016) Revision of Afrotropical *Dyscritobaeus* Perkins, 1910 (Hymenoptera: Scelionidae). Zootaxa 4178: 1–59. <https://doi.org/10.11646/zootaxa.4178.1.1>

- Vaezi M (1950) Rapport du laboratoire d'élevage des parasites d'*Eurygaster integriceps* Put. Entomologie et Phytopathologie Appliquées 11: 27–41.
- Vassiliev JV (1913) [*Eurygaster integriceps* Put. and New Methods of Fighting it by the Aid of Parasites]. St. Petersburg, 81 pp.
- Viggiani G, Mineo G (1974) Identificazione dei parassitoidi del *Gonocerus acuteangulatus* (Goeze). Bollettino dell'Istituto di Entomologia Agraria e dell'Osservatorio di Fitopatologia di Palermo 8: 143–163.
- Viktorov GA (1964) [Food specialization of egg parasites of *Eurygaster integriceps* Put. and the role of this specialization for the diagnostics of species in the genus *Asolcus* Nakagawa (*Microphanurus* Kieffer) (Hymenoptera, Scelionidae).]. Zoologicheskii Zhurnal 43: 1011–1025.
- Viktorov GA (1967) [Problems in Insect Population Dynamics with Reference to the Sunn Pest.] Nauka, Moscow, 271 pp.
- Voegelé J (1962) Isolement d'une espèce jumelle d'*Asolcus basalis* Wollaston (Hymenoptera, Proctotrupoidea). Al Awamia 4: 155–161.
- Voegelé J (1964) Contribution à la connaissance des stades larvaires des espèces du genre *Asolcus* Nakagawa (*Microphanurus* Kieffer) (Hymenoptera, Proctotrupoidea). Al Awamia 10: 19–31.
- Voegelé J (1965) Nouvelle méthode d'étude systématique des espèces du genre *Asolcus*. Cas d'*Asolcus rungsi*. Al Awamia 14: 95–113.
- Voegelé J (1969) Les hyménoptères parasites oophages des *Aelia*. Al Awamia 31: 137–323.
- Walker F (1836) On the species of *Teleas*, &c. Entomological Magazine 3: 341–370.
- Walker F (1838) Descriptions of some Oxyuri. Entomological Magazine 5: 453–458.
- Watanabe C (1951) On five scelionid egg-parasites of some pentatomid and coreid bugs from Shikoku, Japan (Hymenoptera: Proctotrupoidea). Transactions of the Shikoku Entomological Society 2: 17–26.
- Watanabe C (1954) Discovery of four new species of Telenominae, egg parasites of pentatomid and plataspid bugs, in Shikoku, Japan. Transactions of the Shikoku Entomological Society 4: 17–22.
- Yoder MJ, Mikó I, Seltmann KC, Bertone MA, Deans AR (2010) A gross anatomy ontology for Hymenoptera. PLoS ONE 5(12). e15991. <https://doi.org/10.1371/journal.pone.0015991>
- Zomorodi A (1959) La lutte biologique contre la Punaise du blé *Eurygaster integriceps* Put. Part *Microphanurus semistriatus* Nees en Iran. Anzeiger Für Schadlingskunde 3: 167–175.

## Supplementary material I

### URI table of HAO morphological terms

Authors: Francesco Tortorici, Elijah J. Talamas, Silvia T. Moraglio, Marco G. Pansa, Maryam Asadi-Farfar, Luciana Tavella, Virgilio Caleca

Data type: species data

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

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License

(ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.73.39052.suppl1>

## Supplementary material 2

### *Trissolcus belenus* occurrence data

Authors: Francesco Tortorici, Elijah J. Talamas, Silvia T. Moraglio, Marco G. Pansa, Maryam Asadi-Farfar, Luciana Tavella, Virgilio Caleca

Data type: species data

Explanation note: This table provides a DarwinCore archive of occurrence records for *Trissolcus belenus*.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.73.39052.suppl2>

## Supplementary material 3

### *Trissolcus colemani* occurrence data

Authors: Francesco Tortorici, Elijah J. Talamas, Silvia T. Moraglio, Marco G. Pansa, Maryam Asadi-Farfar, Luciana Tavella, Virgilio Caleca

Data type: species data

Explanation note: This table provides a DarwinCore archive of occurrence records for *Trissolcus colemani*.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.73.39052.suppl3>



## Supplementary material 4

### ***Trissolcus manteroi* occurrence data**

Authors: Francesco Tortorici, Elijah J. Talamas, Silvia T. Moraglio, Marco G. Pansa, Maryam Asadi-Farfar, Luciana Tavella, Virgilio Caleca

Data type: species data

Explanation note: DarwinCore archive of occurrence records for *T. manteroi*.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.73.39052.suppl4>

## Supplementary material 5

### ***Trissolcus semistriatus* occurrence data**

Authors: Francesco Tortorici, Elijah J. Talamas, Silvia T. Moraglio, Marco G. Pansa, Maryam Asadi-Farfar, Luciana Tavella, Virgilio Caleca

Data type: species data

Explanation note: DarwinCore archive of occurrence records for *Trissolcus semistriatus*.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.73.39052.suppl5>

## Supplementary material 6

### **Matrix of diagnostic characters**

Authors: Francesco Tortorici, Elijah J. Talamas, Silvia T. Moraglio, Marco G. Pansa, Maryam Asadi-Farfar, Luciana Tavella, Virgilio Caleca

Data type: species data

Explanation note: This table provides a matrix of diagnostic characters to separate Palearctic species that are morphologically close to *Trissolcus semistriatus*.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.73.39052.suppl6>