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Telenomus Haliday (Hymenoptera, Scelionidae) parasitizing Pentatomidae (Hemiptera) in the Palearctic region

Francesco Tortorici[1], Bianca Orrù[1], Alexander V. Timokhov[2], Alexandre Bout[3], Marie-Claude Bon[4], Luciana Tavella[1], Elijah J. Talamas[5]

1 *Dipartimento di Scienze Agrarie, Forestali e Alimentari (DISAFA), University of Torino, largo P. Braccini 2, 10095 Grugliasco (TO), Italy* **2** *Department of Entomology, Lomonosov Moscow State University, 119234 Moscow, Russia* **3** *INRAE, UMR 1355 Institut Sophia Agrobiotech, CNRS 7254, Université Côté d'Azur, 400 route des Chappes, BP 167, 06903 Sophia Antipolis, France* **4** *European Biological Control Laboratory, Montpellier, France* **5** *Florida Department of Agriculture and Consumer Services, Gainesville, USA*

Corresponding author: Francesco Tortorici (francesco.tortorici@unito.it)

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Abstract

In recent years, the collection of eggs of stink bugs (Pentatomidae) has intensified because of the attention given to egg parasitoids in classical biological control strategies against *Halyomorpha halys* (Stål) in Europe. Several specimens belonging to the genus *Telenomus* Haliday emerged from field-collected pentatomid eggs. Taxonomic knowledge to date has not been sufficient to enable the research community to identify these specimens to species level. Three species of scelionid wasps (Scelionidae) associated with Pentatomidae, *Telenomus gifuensis* Ashmead, *Telenomus truncatus* (Nees von Esenbeck) and *Telenomus turesis* Walker, have been characterized on a morphological basis. A *COI* barcode analysis confirmed the genetic distance between the latter two species. An identification key to the three *Telenomus* species occurring in the Palearctic region associated with stink bugs is provided. *Telenomus heydeni* Mayr is here considered conspecific with *Telenomus truncatus* (Nees von Esenbeck).

Keywords

Biological control, DNA barcoding, identification key, Platygastroidea, species description, taxonomy

Introduction

The subfamily Telenominae (Hymenoptera, Scelionidae), particularly the genera *Trissolcus* Ashmead and *Telenomus* Haliday, have been studied, in part, because of their potential as biological control agents (BCAs) of economically important pests. Species of *Trissolcus* parasitize eggs of stink bugs (Pentatomoidea), particularly Pentatomidae and Scutelleridae, and a few are phoretic on leaf-footed bugs (Coreidae) (Kozlov and Kononova 1983; Johnson 1984a, 1984b, 1987, 1991; Yan et al. 2022). Species of *Telenomus* share these hosts, but also attack a wider range of Heteroptera, as well as Auchenorrhyncha, Lepidoptera, Diptera and Neuroptera (Bin and Johnson 1982; Johnson and Bin 1982; Kozlov and Kononova 1983; Johnson 1984b).

Telenomus is by far the largest genus in the subfamily and includes a considerable number of species that cannot be reliably identified. This taxonomic challenge has its roots in the diversity and size of the genus, and in what Meier et al. (2022) termed the "superficial description impediment". Descriptions for Palearctic taxa, particularly from the early years of European insect taxonomy, are woefully insufficient for species-level identification. Despite these inauspicious beginnings, there have been notable advancements in the classification of telenomine wasps. Kozlov (1967, 1968), Kozlov and Kononova (1983), and Kononova (2014) treated Palearctic species; Johnson (1981) dealt with Nearctic *Telenomus* with keys to identify the species of the *nigricornis* group (Johnson 1981), and *podisi* and *phymatae* groups (Johnson 1984b). After this, the world fauna was catalogued by Johnson (1992). The *podisi* species group, which parasitizes the eggs of Pentatomidae and Scutelleridae, was defined by Johnson (1984b) and includes the species treated here.

The taxonomy of *Telenomus* in the western Palearctic received little attention in the 21st century until the arrival of the brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera, Pentatomidae). The pestiferous nature of this stink bug and the potential risk of dispersal to other countries (Zhu et al. 2012) has led several institutions to deepen the knowledge on biological control strategies (Gariepy et al. 2014b; Maistrello et al. 2017; Bosco et al. 2018; Leskey and Nielsen 2018; Moore et al. 2019). In Integrated Pest Management (IPM) programs, much attention has been given to the ability of BCAs to counter the pest population, and, in the specific case of stink bugs, first to native and then exotic egg parasitoids. To study the diversity of egg parasitoids and their impact on native pentatomid species, egg mass survey programs have been performed in several countries in different habitats (e.g., forests, orchards, urban parks) (Koppel et al. 2009; Dieckhoff et al. 2017; Jones et al. 2017; Moonga et al. 2018; Sabbatini Peverieri et al. 2019; Holthouse et al. 2020; Andreadis et al. 2021; Moraglio et al. 2021b; Japoshvili et al. 2022; Ozdemir et al. 2022). These investigations have expanded knowledge of the distribution and biology of parasitoids attacking stink bugs throughout the western Palearctic and have made significant progress in advancing the species-level taxonomy of Telenominae (Matsuo et al. 2014; Talamas et al. 2015, 2017; Tortorici et al. 2019; Moraglio et al. 2021a).

Trissolcus japonicus (Ashmead) and *Tr. mitsukurii* (Ashmead) (Hymenoptera, Scelionidae) have been shown in Europe to be the most promising BCAs of *H. halys* in terms of habitat suitability (Yonow et al. 2021; Tortorici et al. 2023), exploitation efficiency, and parasitoid impact (Giovannini et al. 2022). These species were quickly recognized because the Palearctic fauna of *Trissolcus* has been well-characterized using morphology, molecular data, and mating experiments to resolve cryptic species (Talamas et al. 2017; Tortorici et al. 2019; Ranjbar et al. 2021). However, the same is not true for *Telenomus*, despite that some species are widespread and are known to attack stink bug eggs.

In Europe, some authors have reported *Te. chloropus* (Thomson) from their surveys (Haye et al. 2015; Roversi et al. 2017) and numerous studies of biological attributes have also used this name (Orr et al. 1985a, b; Orr 1988; Bulezza 1996; Açikgöz and Gözüaçik 2021), but most *Telenomus* species reared from large-scale surveys of stink bug egg parasitism have been indicated as "*Telenomus* spp." (Abram et al. 2017; Moraglio et al. 2020; Bout et al. 2021; Rot et al. 2021; Zapponi et al. 2021; Ozdemir et al. 2022; Ricupero et al. 2022). This reflects the challenge of species-level identification for *Telenomus* and clearly points to the need for better diagnostic tools. Here, we make progress in meeting this need by providing taxonomic treatments of two Palearctic species in the *Te. podisi* group, *Te. truncatus* (Nees von Esenbeck) and *Te. turesis* Walker, which attack stink bugs in the families Pentatomidae and Scutelleridae (Javahery 1968; Voegelé 1969; Kozlov and Kononova 1983; Johnson 1984b; Graham 1988a) and an overview of *Telenomus* species found to parasitize eggs of pentatomids and scutellerids in Europe. *Telenomus gifuensis* Ashmead has been reported as a parasitoid of pentatomids in the eastern Palearctic region. To our knowledge, this species has not been reported from the western Palearctic, but we included it in our identification key because the limits of its distribution are not known and there may be regions where it overlaps with the distributions of *Te. truncatus* and *Te. turesis*.

Our work includes examination of historical type specimens, some of which are nearly 200 years old, which is essential for resolving long-standing ambiguity. An updated morphological diagnosis section provides previously unexplored or unused character systems, and we provide simplified descriptions that focus on diagnostic characters. As other Old-World species of the *Te. podisi* group are treated taxonomically, these descriptions are likely to expand to include characters used for the species group more broadly. We complement our analysis with molecular data that is helpful for establishing which characters are prone to interspecific variation and which are diagnostically stable. For the analyzed species, we provide host associations and biological observations.

Synopsis of Palearctic species in the *Te. podisi* group

The earliest species, described by Nees von Esenbeck (1834), were *Te. truncatus* and *Te. linnei*, originally placed in the genus *Teleas* Latreille. Shortly thereafter, *Te. turesis* was described by Walker (1836). Thomson (1861) described *Te. chloropus* (as *Phanurus*). Mayr described *Te. heydeni* (1879) and *Te. sokolowi* (1897). Mayr (1879) considered *Teleas Zetterstedtii* Ratzeburg to be conspecific with *Te. truncatus* based on a non-type specimen that was identified by Ratzeburg and was reported to emerge from eggs of *Calliteara pudibunda* Linnaeus (Lepidoptera, Erebidae). Ashmead described *Te. gifuensis* (1904) followed by Nixon's species, *Te. tischleri* (1939). Kozlov (1963) considered *Te. mayri* Sokolov a junior synonym of *Te. sokolowi* Mayr and, subsequently, the same author (1967) considered *Te. sokolowi*, *Te. gifuensis* and *Te. tischleri* to be conspecific with *Te. chloropus*. Javahery (1968) provided the most detailed descriptions of *Te. sokolowi* and *Te. truncatus*. Graham (1988a) designated the lectotype of the latter species. Johnson (1984b) analyzed primary types and considered *Te. gifuensis* to be a valid species and removed its synonymy. Mineo (2010) treated *Te. chloropus* and *Te. turesis* as conspecific, with Walker's species name having priority.

Materials and methods

Reared specimens

Telenomus specimens were reared from naturally laid egg masses (Pentatomidae and Scutelleridae) collected in different sites in Piedmont, Italy, from 2019 to 2022 during surveys to investigate the egg parasitoid populations of native and exotic bugs. Each egg mass was isolated in a plastic Petri dish (6 cm diameter) and reared in a climate-controlled chamber at 24 ± 1 °C, 65 ± 5% r.h., and L16:D8 photoperiod. All egg masses were examined under a stereomicroscope and identified to the species or family level according to Derjanschi and Péricart (2005), Péricart (2010), Ribes and Pagola-Carte (2013). The eggs were visually inspected daily and emerging bug nymphs or parasitoid adults were examined. Parasitoids were stored in 99% ethanol until species identification, as described below. Additional specimens of *Telenomus* were collected on November 26, 2022, in Liguria, Italy, hidden in leaf mines of *Phyllonorycter viburni* (Kumata) (Lepidoptera, Gracillariidae).

Telenomus specimens were also reared from egg masses of *Palomena prasina* (Linnaeus) (Hemiptera, Pentatomidae) or collected by sweeping in their natural habitats in Moscow Province, Russia, in 2016 for a cytogenetic study (Gokhman and Timokhov 2020). Each egg mass was isolated in plastic tubes (5 cm^3) and reared in a thermostatic chamber at 24 ± 1 °C. Female parasitoids (both *Te. truncatus* and *Te. turesis*) were then individually transferred to egg masses of a lab host, *Graphosoma lineatum* Linnaeus (Hemiptera, Pentatomidae), for oviposition. To obtain a proper immature stage of wasps for the cytogenetic study, parasitized host eggs were incubated under thermostatic conditions for a few days (Gokhman and Timokhov 2020).

Morphological analysis

A Wild M5 steromicroscope with 15× oculars and a spotlight were used for biometric diagnosis. Slides were mounted with Eukitt mounting medium (Merck Life Science, Milan, Italy) and examined under a Leitz Dialux 20 EB compound microscope. Male genitalia were prepared by following the protocol of Polaszek and Kimani (1990). Terminology for surface sculpture and morphological terminology follows

Harris (1979), Johnson (1984b), Mikó et al. (2007), and Talamas et al. (2017). The morphological identification was performed independently from keys and once the morphometric analysis of characters was complete and confirmed by molecular analysis, species names were assigned by comparison to primary types.

Imaging

Images of primary type specimens were taken with a Macropod imaging system using 10× and 20× Mitutoyo objective lenses (Mitutoyo Corporation, Kawasaki, Japan) and rendered with Helicon Focus (HeliconSoft Limit., Kharkiv, Ukraine). Photographs of non-type specimens were taken using a Canon 90D camera (Canon Inc., Tokyo, Japan) equipped with an extension tube; 5×, 10×, 20×, and 50× LWD microscope lenses mounted on a macro-rail and illuminated with two speedlight flashes. The frames were merged with Zerene Stacker (PMax algorithm, Zerene Systems LLC, Richland, WA, USA).

The ultrastructures of non-type specimens were examined under a Jeol JSM-6380 scanning electron microscope (SEM) after critical point drying (Hitachi HCP-2) of the specimens and sputter coating with gold (Giko JSM-6380).

Molecular analysis

DNA extraction, amplification, and sequencing were performed at multiple institutions. At the Florida State Collection of Arthropods (FSCA) and the European Biological Control Laboratory (EBCL), this was performed as in Talamas et al. (2021). Cytochrome Oxidase subunit I (*COI*) sequences from French specimens (INRAE UMR ISA) were obtained as in Bout et al. (2021). At the Dipartimento di Scienze Agrarie, Forestali e Alimentari laboratory (DISAFA) of the University of Torino, a non-destructive Chelex DNA extraction method was performed and adapted according to Kaartinen et al. (2010). DNA was extracted from insects by dipping samples in 50 µl of 5% Chelex with 5 µl of 20 mg/ml proteinase K at 37 °C for at least 18 h. The specimens were boiled at 95 °C for 5 min to inactivate proteinase K and then used as templates for PCR. The insects were then removed from the Chelex, washed in 70% ethanol and later mounted on card points. The barcode region of the mitochondrial *COI* was amplified using the universal Folmer primer LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') (Folmer et al. 1994) and the primer HCOout (5'-CCAGGTAAAATTAAAATATAAACTTC-3') (Carpenter 1999). PCR amplifications were performed on a C1000 Touch™ Thermal Cycler (Bio-Rad, CA, USA) in 25 µl volume containing: 2.5 µl of 10 X Buffer and 10 mM dNTPs, 1.25 µl of $MgCl_2$, 0.3 µl of Taq Polymerase, 0.1 µl of 100 µM forward and reverse primer, 16.25 µl of sterile water, and 2 µl of DNA template. Thermocycling conditions were: 95 °C for 15 min, followed by 34 cycles of 95 °C for 30 s, 50 °C for 45 s, and 72 °C for 1 min. After a final extension at 72 °C for 5 min, reactions were held at 4 °C. For the nested PCR, 2 µl of the first PCR was used a template using the reverse primer HCO2189 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') and the forward primer LCO1490, using the same PCR cycling program described above. The fragment size at the end of nested PCR was 700 bp. PCR products were examined by electrophoresis on a 1% agarose gel. Positive samples were purified using a commercial kit (QIAquick PCR Purification Kit, Qiagen, Hilden, Germany), and sequenced by a commercial service (Eurofins Genomics, Germany).

The sequences were compared with the GenBank database using the Basic Local Alignment Search Tool (http://www.ncbi.nlm.nih.gov/BLASTn). All sequences obtained from this study are deposited in GenBank or BOLD (Ratnasingham and Hebert 2007), and all residual DNAs are achieved at DISAFA, FSCA, INRAE UMR ISA or EBCL. Sequences were used to query GenBank (Altschul et al. 1990) and BOLD for similar sequences, which were downloaded from both databases. The *COI* barcodes of *Trissolcus belenus* (Walker) (MN603806) and of *Tr. semistriatus* (Nees von Esenbeck) (MN603800) (Tortorici et al. 2019) were selected as outgroups for the Maximum Likelihood analysis. All sequences were aligned using MUSCLE with default setting as implemented in MegaX (Kumar et al. 2018), and a phylogenetic tree was created by using the Maximum Likelihood method and Tamura-Nei model (Tamura and Nei 1993). Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Joining and BioNJ algorithms to a matrix of pairwise distances estimated using the Tamura-Nei model, and then selecting the topology with superior log likelihood value. The resulting phylogenetic tree was exported and redrawn in the Interactive Tree of Life (iTOL) v5 (Letunic and Bork 2021).

Geographic records of specimens used for molecular and morphological analysis were retrieved from GPS latitude and longitude coordinates and from available data on the GenBank and BOLD dataset as obtained above. A distribution map was created using QGIS.org (2023).

Collections

DISAFA	Dipartimento di Scienze Agrarie, Forestali e Alimentari, University of Torino, Torino, Italy
FSCA	Florida State Collection of Arthropods, Gainesville, United States
INRAE	INRAE UMR Institut Sophia Agrobiotech, Sophia-Antipolis, France
MZLU	Lund Museum of Zoology, Lund University, Lund, Sweden
NHMW	Naturhistorisches Museum Wien, Vienna, Austria
NMINH	National Museum of Ireland - Natural History, Dublin, Ireland
OUMNH	Oxford University Museum of Natural History, Oxford, United Kingdom
ZIN	Zoological Institute, St. Petersburg, Russia
ZMMU	Zoological Museum, Lomonosov Moscow State University, Moscow, Russia

The data for the examined specimens were uploaded onto the BOLD platform (www.barcodinglife.org), and the list of material examined was generated as a supplementary spreadsheet file (Suppl. material 4).

Results and discussion

Taxonomy

Two species were detected in our surveys, *Te. truncatus* and *Te. turesis*, which we identified by comparison to type material (Table 1). Doğanlar (2001) simply described morphological characters of *Te. chloropus*. According to Kozlov and Kononova (1983), the sculpture of the posterior margin of mesoscutum was not clear, and this character is considerably variable in the specimens examined by us. The color of the femora weakly matches with the types of both species, but this is difficult to assess because the types are very old. The description of the shape of A2–A4 of males of both species corresponds with our opinion. The most accurate description for the two species was made by Javahery (1968).

Table 1. Links to images of primary type specimens.

Images of primary type	Original combination	Valid name
https://zenodo.org/record/7846207	*Teleas truncatus* Nees von Esenbeck	*Telenomus truncatus* (Nees von Esenbeck)
https://zenodo.org/record/7622511	*Teleas Linnei* Nees von Esenbeck	*Telenomus truncatus* (Nees von Esenbeck)
https://zenodo.org/record/7846277	*Telenomus Turesis* Walker	*Telenomus turesis* Walker
https://www.flickr.com/photos/127240649@N08/50121706058/in/photostream/	*Phanurus chloropus* Thomson	*Telenomus turesis* Walker
https://zenodo.org/record/7442921	*Telenomus heydeni* Mayr	*Telenomus truncatus* (Nees von Esenbeck)
https://zenodo.org/record/7443068	*Telenomus Sokolowi* Mayr	*Telenomus turesis* Walker

According to Graham (1988a), the most detailed description of *Te. chloropus* was provided by Johnson (1984). Graham, referring to the postocellar furrows behind the lateral ocelli, reported by Johnson (1984), wrote that there are at least two "European forms" of this character: the form, described as *Te. sokolovi* by Javahery (1968) with short, weak postocellar furrows extending inward behind the lateral ocelli, and the form erroneously described as *Te. truncatus* Nees by Javahery (1968) with long, marked postocellar furrows extending inward behind the lateral ocelli. Graham associated the character of eyes densely covered with moderately long hairs and eyes sparsely covered with short hairs, with the two forms, respectively. The two forms described by Graham concur respectively with our concepts of *Te. turesis* and *Te. truncatus*.

The present study reports a similar composition of hosts for *Te. truncatus* and *Te. turesis* as reported by previous authors (Javahery 1968; Kozlov 1968; Samin et al. 2010) but with some new records (Table 2). Some other dubious records from Coleoptera eggs are reported for both species (Kieffer 1926; Samin et al. 2010).

Table 2. Host associations. “X” indicates an association recorded during the present study.

	Stink bugs species	***Telenomus turesis***	***Te. truncatus***
Pentatomidae	*Acrosternum* sp.	X	
	Aelia acuminata (L.)	(Kozlov 1968)	
	Aelia furcula Fieber	(Kozlov 1968)	
	Aelia rostrata Boheman	(Kozlov 1968), X	
	Arma custos (F.)	X	
	Carpocoris sp.	X	X
	Carpocoris fuscispinus (Boheman)	(Kozlov 1968)	
	Dolycoris baccarum (L.)	(Kozlov 1968; Samin et al. 2010), X	X
	Graphosoma lineatum (L.)	(Kozlov 1968)	X
	Halyomorpha halys (Stål)	X	X
	Holcostethus strictus (F.)	X	
	Palomena prasina (L.)	(Kozlov 1968), X	(Kozlov 1968), X
	Palomena viridissima (Poda)	(Kozlov 1968)	(Kozlov 1968)
	Picromerus bidens (L.)	(Javahery 1968)	(Javahery 1968)
	Piezodorus lituratus (F.)	(Javahery 1968), X	(Javahery 1968), X
	Rhaphigaster nebulosa (Poda)		(Kozlov 1968), X
Scutelleridae	*Eurygaster austriaca* (Schrank)	(Kozlov 1968)	
	Eurygaster integriceps Puton	(Javahery 1968; Kozlov 1968; Samin et al. 2010)	(Javahery 1968)
	Eurygaster maura (L.)	(Kozlov 1968), X	
	Eurygaster testudinaria (Geoffroy)	(Samin et al. 2010)	

Diagnosis

We identified specimens of *Te. truncatus* and *Te. turesis* based on characters in the following species treatments:

Telenomus truncatus **(Nees von Esenbeck)**

Figs 1–4, 8A, C, E, 9A, C, E

Teleas truncatus Nees von Esenbeck, 1834: 289 (original description); Graham 1988b: 28 (type information); Graham 1988a: 86 (lectotype designation).

Teleas Linnei Nees von Esenbeck, 1834: 288 (original description); Mayr 1879: 707 (synonym of *Telenomus truncatus* (Nees von Esenbeck)); Graham 1988b: 28 (type information); Johnson 1992: 617 (type information).

Teleas Zetterstedtii Ratzeburg 1844: 185 (original description); Mayr 1879: 707 (synonym of *Telenomus truncatus* (Nees von Esenbeck)).

Telenomus truncatus (Nees von Esenbeck): Mayr 1879: 700, 702, 707 (description, generic transfer, synonymy, keyed); Kieffer 1926: 25, 26, 31(description, keyed); Javahery 1968: 431 (description, keyed); Szabó 1978: 219, 222 (description, neotype designation, keyed); Johnson 1984b: 41 (taxonomic status, neotype information); Johnson 1992: 617 (cataloged, type information); Mineo 2012: 61 (placed in *turesis* group).

Telenomus Heydeni Mayr, 1879: 702, 706 (original description, keyed). syn. nov.

Telenomus Giraudi Kieffer, 1906: 163 (original description).

Prophanurus Giraudi Kieffer: Kieffer 1912: 46, 58 (description, generic transfer).

Prophanurus Heydeni (Mayr): Kieffer 1912: 59 (description, generic transfer).

Prophanurus Truncatus (Nees von Esenbeck): Kieffer 1912: 47, 58 (description, generic transfer).

Telenomus giraudi Kieffer: Kieffer 1926: 25, 26, 31 (description, keyed); Szabó 1978: 221 (junior synonym of *Telenomus heydeni* Mayr).

Telenomus heydeni Mayr: Kieffer 1926: 26, 36 (description, keyed); Kozlov 1967: 360, 364, 372 (description, lectotype designation); Kozlov 1968: 216 (description, keyed); Voegelé 1969: 148 (keyed); Mineo 1977: 84 (description of preimaginal stages); Kozlov 1978: 638, 644 (keyed); Szabó 1978: 219, 221 (description, lectotype designation, keyed); Johnson 1992: 591 (cataloged, type information); Petrov 1994: 276 (keyed); Mineo 2012: 61 (placed in *turesis* group); Timokhov 2019: 55 (cataloged); Gokhman and Timokhov 2020: 216 (karyotype).

Telenomus (*Telenomus*) *heydeni* Mayr: Kozlov and Kononova 1983: 140, 164 (description, subgeneric assignment, keyed); Kononova 2014: 141, 144 (description, keyed).

Teleas linnei Nees von Esenbeck: Graham 1988a: 88 (lectotype designation).

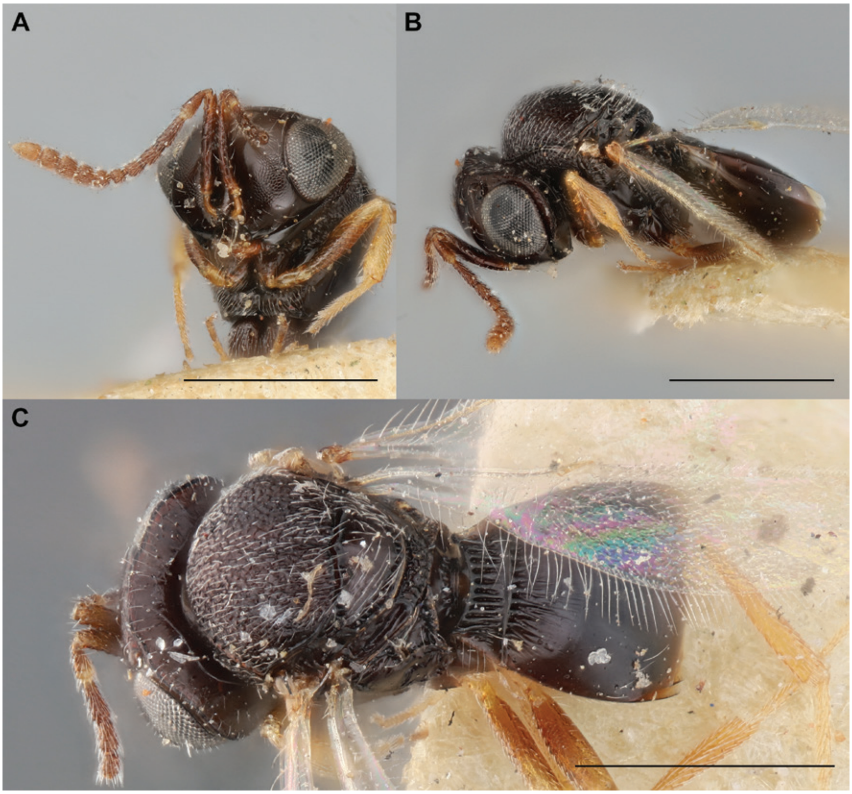

Figure 1. *Telenomus truncatus*. Female lectotype (OXUM 0011): head in frontal view (**A**); habitus in lateral view (**B**); habitus in dorsal view (**C**). Scale bars: 0.5 mm.

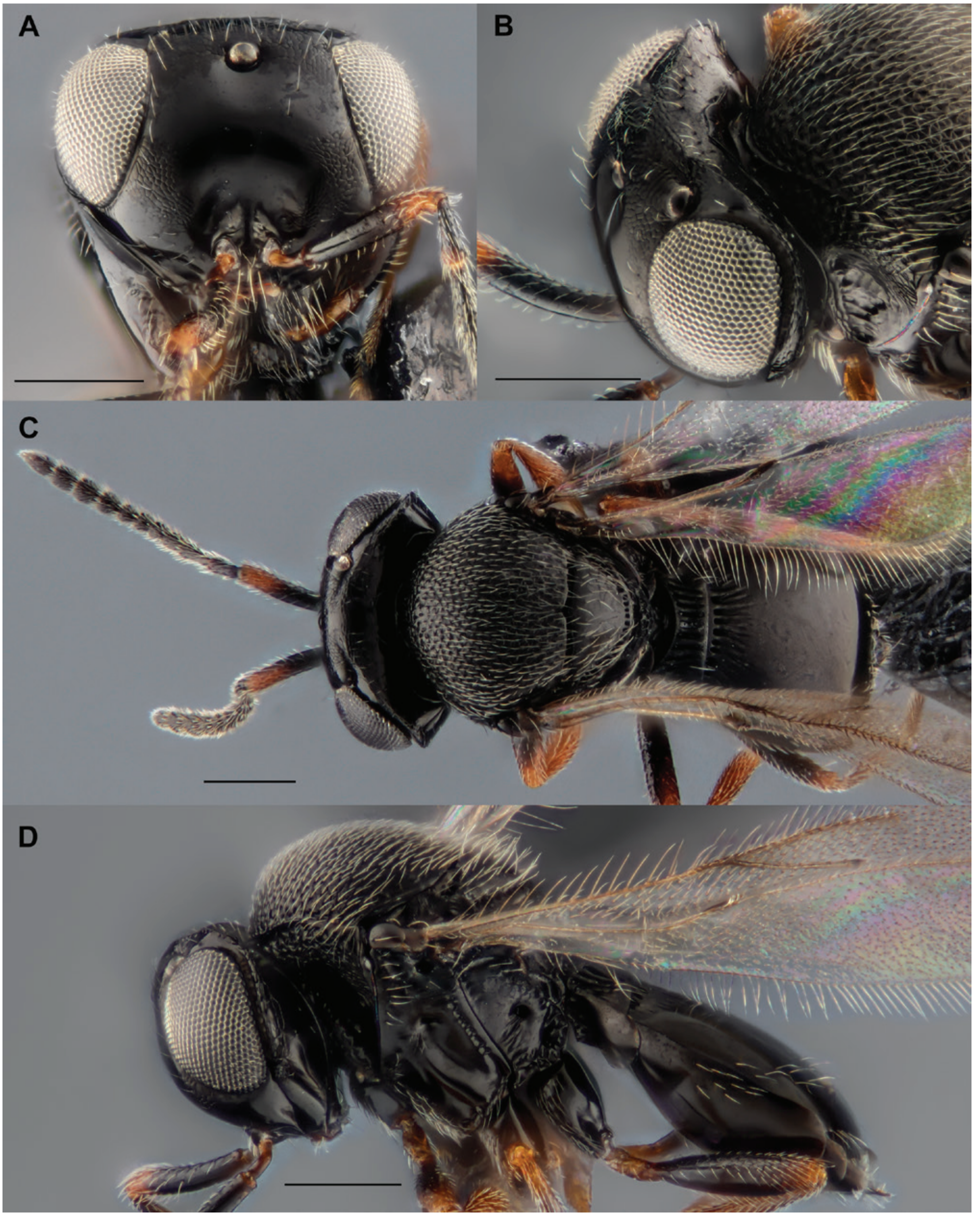

Figure 2. *Telenomus truncatus*. Female (DISAFA-FT HYM-0519): head in frontal view (**A**); head in dorso-lateral view (**B**); habitus in dorsal view (**C**); habitus in lateral view (**D**). Scale bars: 0.2 mm.

Diagnostic characters. Female. ***Head*:** compound eye with sparse and short setation throughout (Figs 1A, 2B, 3B, 4A, 8C); vertex shallowly and evenly granulate (Figs 1C, 2B, 3B, 4A, 8C); occipital carina complete (Fig. 8A); hyperoccipital carina present directly behind the lateral ocellus, carina sharp and well defined, sculpture smooth along

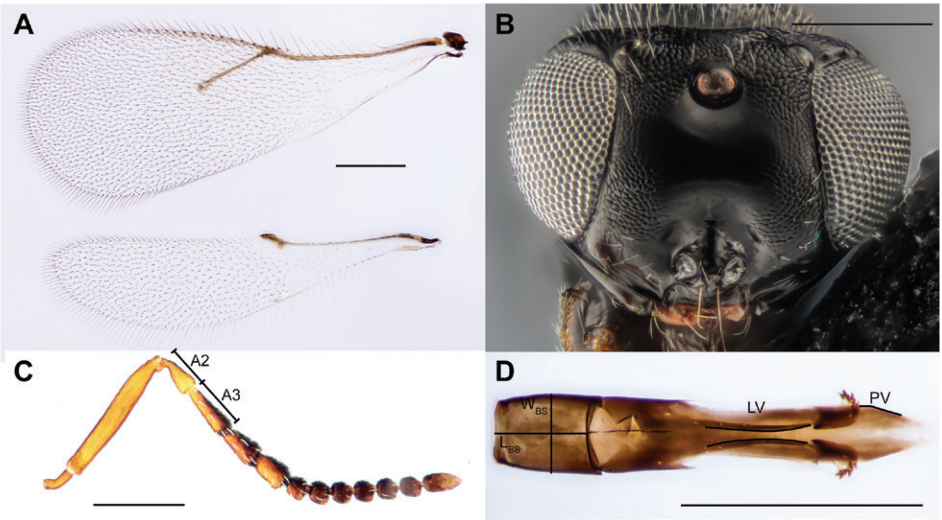

Figure 3. *Telenomus truncatus*. Female (DISAFA-FT HYM-0650): fore and hind wings (**A**). Male (DISAFA-FT HYM-0516): head in frontal view (**B**); antenna (**C**); genitalia (**D**). Scale bars: 0.2 mm.

posterior margin of carina (Fig. 8C); outer orbital furrow wide (2–2.5 times as wide as an ommatidium) (Fig. 8C); clypeal sensillum present above the line connecting the medial and lateral clypeal setae (Fig. 8E).

***Mesosoma*:** mesoscutal humeral sulcus (mshs) present as a smooth furrow (Figs 1B, 2D, 9A); metapleural carina in antero-dorsal area of metapleuron (pdms, between metapleural arm and propodeal spiracle) complete, distinct and strong (Fig. 9A); surface of the furrow between metanotal trough and metascutellar arm (msn) usually crenulate (Fig. 9A); mesoscutum longitudinally strigose posteriorly (Fig. 9C); median mesoscutal sulcus present in largest specimens, barely visible in smaller ones. Fore wing postmarginal (pm) and stigmal (st) veins length ratio: pm:st = 1.9:1 (n=20) (Fig. 3A). Hind femora dark brown with yellowish tips (Fig. 2C, D).

***Metasoma*:** first metasomal tergite with one or rarely two pairs of sublateral setae (ss) (Figs 1C, 2C, 9E).

Male. *Head*: antennal length ratio A3:A2 = 1.2:1 (n=20), antennomeres A6–A11 bead-like, subequal (Fig. 3C). Genitalia: basal ring ratio: Length: Width = 6:5; minimum distance between inner margin of laminae volsellares: narrow (laminae volsellares lyre-shaped); external margin of penis valve more intensely sclerotized curved and distally converging (Fig. 3D). Hind femora yellow to pale brown. Other morphological characters as in female.

From the analysis of the lectotype of *Te. heydeni* (NHMW-HYM#0005387), the combination of morphological characters (Fig. 4) coincides with the characters of the lectotype of *Te. truncatus* (OXUM 0011), and the length ratio between the A3 and A2 antennomeres (Fig. 4A) matches with that of the male of *Te. truncatus* (Fig. 3C). Therefore, *Te. heydeni* is here considered a junior synonym of *Te. truncatus*.

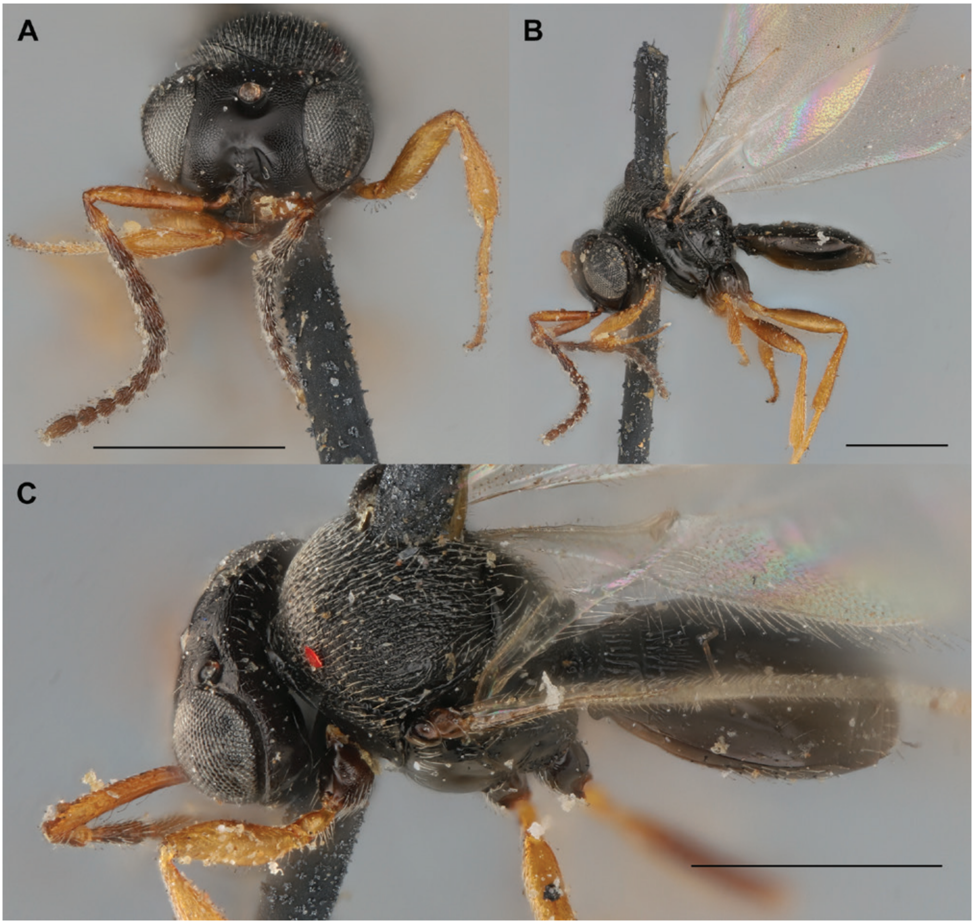

Figure 4. *Telenomus heydeni*. Male lectotype (NHMW-HYM#0005387): head in frontal view (**A**); habitus in lateral view (**B**); habitus in dorso-lateral view (**C**). Scale bars: 0.5 mm.

Biological information. Host species associated: Table 2. The specimen DISAFA-FT HYM-0657 - OQ466097 was found overwintering in November in *Viburnum* leaf mines created by *P. viburni*; the specimens AVT001908 and AVT001909 were found already dead in egg-mass of *Lymantria monacha* (Linnaeus) (Lepidoptera, Erebidae), presumably after wintering.

DNA barcoding. Barcode sequences were obtained from 49 specimens of *Te. truncatus*. Pairwise distance values within species are shown in Suppl. material 3. The genetic distances between the insects identified as the same species were between 0.000 and 0.074 (mean 0.013 +/- 0.003). The analysis of *COI* sequences discovered that *Te. truncatus* includes the specimen OL631282, previously identified as *Telenomus* sp. (Ricupero et al., 2022) (Suppl. material 1).

Distribution. Suppl. material 2

Material examined. Suppl. material 4.

Telenomus turesis Walker

Figs 5–7, 8B, D, F, 9B, D, F

Telenomus Turesis Walker, 1836: 353 (original description).

Phanurus chloropus Thomson, 1861: 173 (original description).

Telenomus turesis Walker: Mayr 1879: 699, 705 (description, keyed). Fergusson 1984: 232 (lectotype designation); Mineo et al. 2010: 116 (synonymy, type information, new distribution record for Ireland); Johnson 1992: 617 (cataloged, type information); Timokhov 2019: 55 (cataloged); Gokhman and Timokhov 2020: 216 (karyotype).

Telenomus Sokolowi Mayr, 1897: 442 (original description); Johnson 1992: 579 (type information).

Telenomus Mayri Sokolov, 1904: 29 (original description).

Aphanurus Turesis (Walker): Kieffer 1912: 75 (description, generic transfer).

Prophanurus Sokolowi (Mayr): Kieffer 1912: 53, 60 (description, generic transfer)

Microphanurus turesis (Walker): Kieffer 1926: 92, 98 (description, generic transfer, keyed).

Telenomus chloropus (Thomson): Kieffer 1926: 25, 29 (description, keyed); Kozlov 1967: 361, 364, 371 (lectotype designation, keyed); Kozlov 1968: 216, 217 (description, keyed); Boldaruyev 1969: 161, 170 (description, keyed); Voegelé 1969: 148 (keyed); Kozlov 1978: 638, 643 (keyed); Johnson 1984b: 39, 65 (description, keyed); Graham 1988a: 86 (taxonomic status); Johnson 1992: 579 (cataloged, type information); Petrov 1994: 276 (keyed); Doğanlar 2001: 112 (description); O'Connor and Mineo 2009: 106 (distribution); Mineo et al. 2010: 116 (junior synonym of *Telenomus turesis* Walker, possible type information).

Telenomus sokolowi Mayr: Kieffer 1926: 25, 26, 34 (description, keyed).

Telenomus tischleri Nixon, 1939: 129 (original description); Kozlov 1967: 364 (junior synonym of *Telenomus chloropus* (Thomson)); Johnson 1992: 580 (type information).

Telenomus sokolovi Mayr: Meier 1940: 79, 80 (description, keyed); Rjachovskij 1959: 82 (keyed); Kozlov 1963: 295 (synonymy); Viktorov 1967: 91 (keyed); Kozlov 1967: 361, 364 (lectotype designation, junior synonym of *Telenomus chloropus* (Thomson)); Javahery 1968: 431, 434 (description, keyed).

Telenomus mayri Sokolov: Kozlov 1963: 295, 296 (junior synonoym of *Telenomus sokolovi* Mayr).

Trissolcus turesis (Walker): Fergusson 1978: 120 (generic transfer).

Telenomus (*Telenomus*) *chloropus* (Thomson): Kozlov and Kononova 1983: 140, 161 (keyed, description, subgeneric assignment); Kononova 1995: 100 (keyed); Kononova and Proshchalykin 2012: 135 (cataloged); Kononova 2014: 141, 142 (description, keyed).

Diagnostic characters. Female. ***Head*:** dense setation on compound eyes (Figs 6A, 7B, 8D); granulate sculpture on the vertex (Figs 5C, 6B, 8D); occipital carina incomplete (Fig. 8B); hyperoccipital carina directly behind the lateral ocelli weakly indicated (almost absent in smaller specimens) (Figs 5C, 6B, 8D); outer orbital furrow narrow, (1–1.5 times as wide as an ommatidium) (Fig. 8D); clypeal sensillum present below the line connecting the medial and lateral clypeal setae (Fig. 8F).

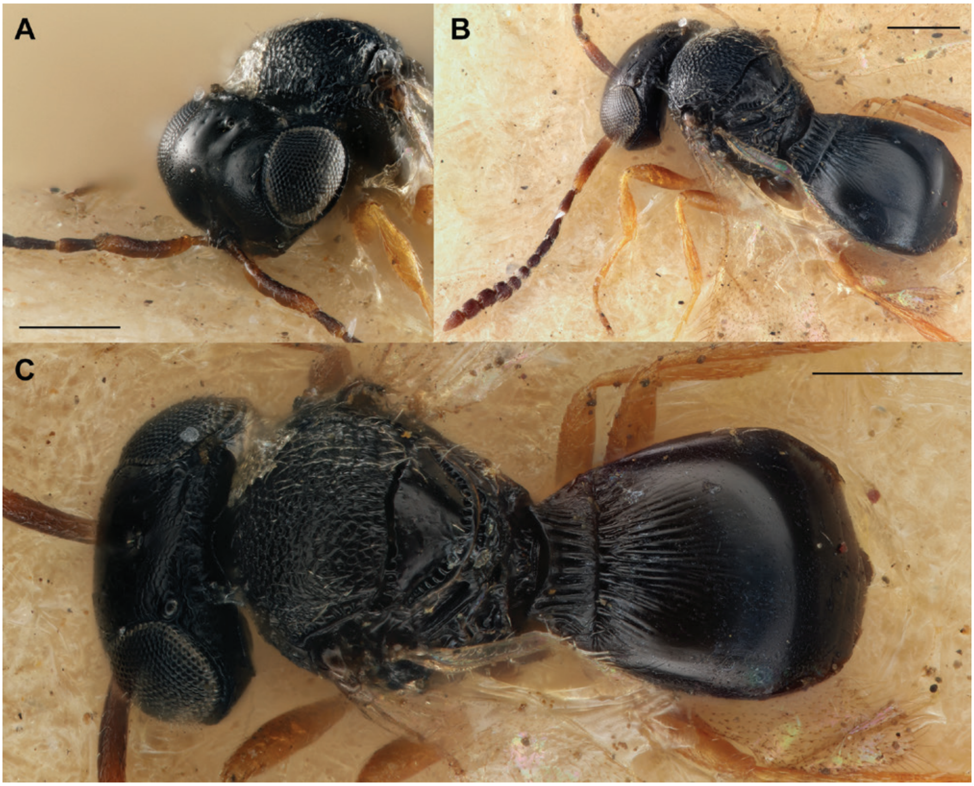

Figure 5. *Telenomus turesis*. Female lectotype (NMINH:2018:11:54): head in latero-frontal view (**A**); habitus in dorso-lateral view (**B**); habitus in dorsal view (**C**). Scale bars: 0.2 mm.

***Mesosoma*:** mesoscutal humeral sulcus (mshs) indicated by cells (Figs 6B, 9B); metapleural carinain antero-dorsal area of metapleuron (pdms, between metapleural arm and propodeal spiracle) incomplete, irregular (Fig. 9B); surface of the furrow between metanotal trough and metascutellar arm (mns) smooth (Fig. 9B); macrosculpture of mesoscutum imbricate (Fig. 9D). Fore wing postmarginal (pm) and stigmal (st) veins length ratio: pm:st = 1.9:1 (n=20) (Fig. 7A). Hind femora yellow to pale brown (Figs 5C, 6D).

***Metasoma*:** first metasomal tergite with one or rarely two pairs of sublateral setae (ss) (Figs 6C, D, 9F).

Male. Antennal length ratio A3:A2 = 2:1 (n=20), antennomeres A6–A11 elongate, uniform in length (Fig. 7C). Genitalia: basal ring (BS) ratio: Length:Width = 7:4; minimum distance between inner margin of laminae volsellares (LV): wide; external margin of penis valve (PV) more intensely sclerotized and parallel rods (Fig. 7D). Other morphological characters as in female.

Biological information. Host species associated: Table 2. Three specimens (DISAFA-FT HYM-0667, HYM-0666 - OQ466110, and HYM-0662 - OQ466105) were found overwintering in November in the mines of *P. viburni* in *Viburnum* leaves.

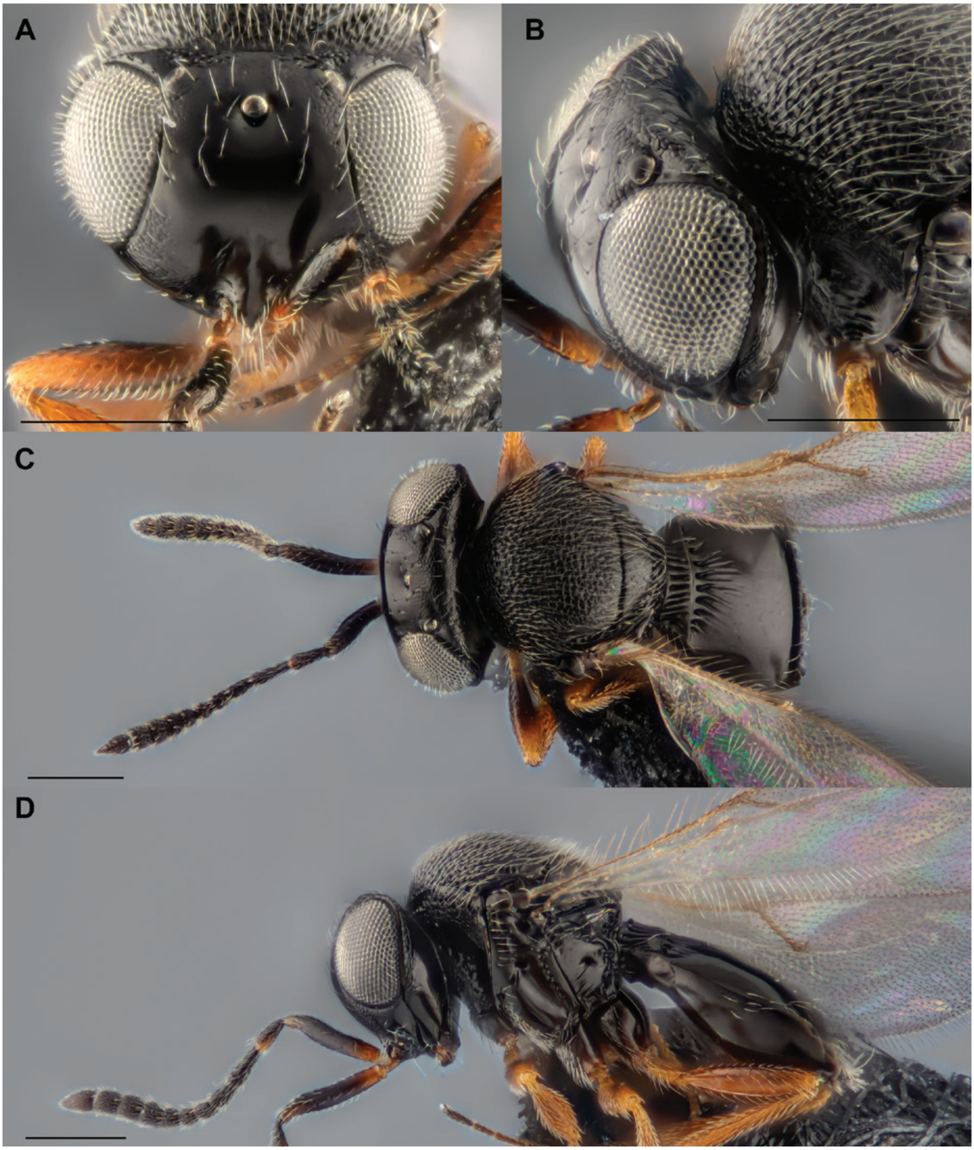

Figure 6. *Telenomus turesis*. Female (DISAFA-FT HYM-0536): head in frontal view (**A**); head in dorsolateral view (**B**); habitus in dorsal view (**C**); habitus in lateral view (**D**). Scale bars: 0.2 mm.

DNA barcoding. Barcode sequences were obtained from 46 specimens of *Te. turesis*. Pairwise distance values within species are shown in Suppl. material 3. The genetic distances between the insects identified as the same species were between 0.000 and 0.096 (mean 0.015 +/- 0.004).

The analysis of *COI* sequences discovered that *Te. turesis* includes samples KY843528 (Ashfaq et al. 2022); the specimens BIOUG55155-D12, BIOUG16220-G06,

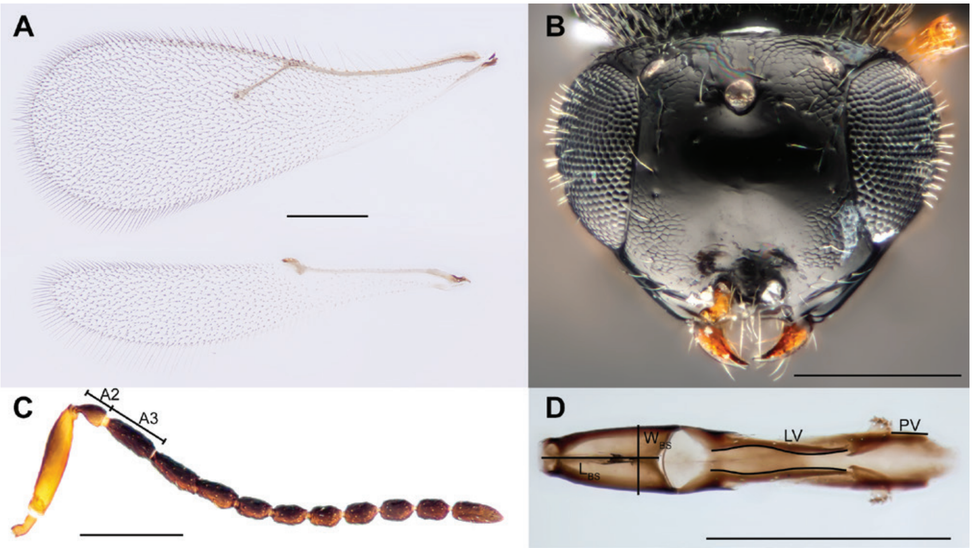

Figure 7. *Telenomus turesis*. Female (DISAFA-FT HYM-0625): fore and hind wings (**A**). Male (DISAFA-FT HYM-0532): head in frontal view (**B**); antenna (**C**); genitalia (**D**). Scale bars: 0.2 mm.

BIOUG15112-C08, BIOUG36831-G01, BIOUG27850-E03, and KF303516 (Gariepy et al. 2014a), previously identified as *Te. chloropus*, and the sample OK562072 (Ozdemir et al. 2022) (Suppl. material 1).

Distribution. Suppl. material 2.

Material examined. Suppl. material 4.

Telenomus gifuensis Ashmead

Fig. 1A–C

Diagnosis. The distance between the inner margin of the compound eyes is smaller than the width of the compound eyes in frontal view (Fig. 10A), and the presence of two sublateral setae on the first tergite (Fig. 10B) separate this species from *Te. truncatus* (figs 1–45), and *Te. turesis* (Figs 5–7). In addition, *Te. gifuensis* can be distinguished from *Te. turesis* by the presence of a median mesoscutal line (mml) on the posterior margin of the mesoscutum (Fig. 10C). Mahmoud and Lim (2008) reported this species as a solitary parasitoid of *D. baccarum*, *Piezodorus hybneri* (Gmelin), *Riptortus clavatus* (Thunberg), and *Nezara antennata* Scott. We also add *Piezodorus rubrofasciatus* (Fabricius) to the list of species as a new associated host (specimen AVT002233). Apart from this last record from Korea and the original description from Japan (Ashmead 1904), there are no further reports outside of the eastern Palearctic region.

Material examined. Suppl. material 4.

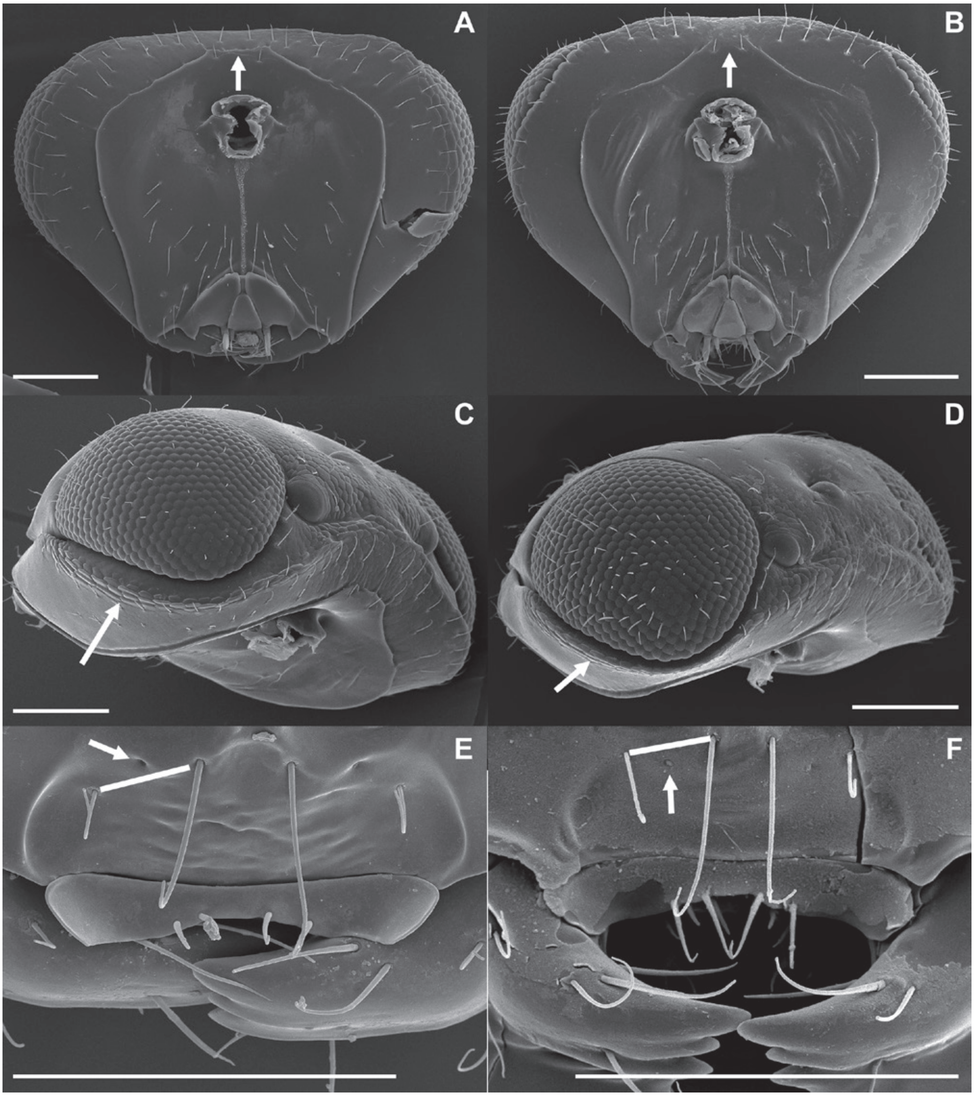

Figure 8. Head in posterior view: *Telenomus truncatus* (**A**) and *Te. turesis* (**B**); head in dorso-lateral view: *Te. truncatus* (**C**) and *Te. turesis* (**D**); clypeus: *Te. truncatus* (**E**) and *Te. turesis* (**F**). Scale bars: 0.1 mm.

Key to species

1 Metasomal tergite 1 with two pairs of sublateral setae (Fig. 10B); frons narrow, minimum distance between inner margin of compound eyes less than eye width in frontal view (Fig. 10A) .... ***Telenomus gifuensis*** **Ashmead**

– Metasomal tergite 1 with one pair of sublateral setae (Fig. 9E, F); frons wide, minimum distance between inner margin of compound eyes more than eye width in frontal view (Figs 2A, 3B, 6A, 7B) **2**

2 Female **3**

– Male **4**

3 Compound eyes with sparse, short setation throughout (Figs 1A, 2B, 3B, 4A, 8C); hyperoccipital carina present directly posterior to the lateral ocellus; hyperoccipital carina sharp and smooth anteriorly, and sculpture on the surface behind the vertex smooth (Figs 2B, 8C); median and posterior femora dark brown with yellowish tips (Fig. 2D) .... ***Telenomus truncatus*** **(Nees von Esenbeck)**

– Compound eyes with dense setation throughout (Figs 6A, 7B, 8D); hyperoccipital carina present directly posterior to the lateral ocellus but weakly sharp, and sculpture on the surface behind the vertex imbricate (Figs 5C, 6B, 8D); median and posterior femora yellow to pale brown (Figs 5C, 6D).................... ***Telenomus turesis*** **Walker**

4 Compound eyes with sparse and short setation throughout (Fig. 4B); antennal length ratio A3:A2 = 1.2:1 (Fig. 3C)... ***Telenomus truncatus*** **(Nees von Esenbeck)**

– Compound eyes with dense setation throughout (Fig. 7B); antennal length ratio A3:A2 = 2:1 (Fig. 7C) .... ***Telenomus turesis*** **Walker**

Molecular analysis

The analysis involved 105 nucleotide sequences. All positions with less than 95% site coverage were eliminated, i.e., fewer than 5% alignment gaps, missing data, and ambiguous bases were allowed at any position (partial deletion option). There was a total of 492 positions in the final dataset. Barcode sequences were obtained from 95 *Telenomus* specimens (Suppl. material 1) from the Palearctic Region. They were compared with eight sequences of specimens from the Nearctic Region identified as *Te. cristatus* Johnson (n: 4), *Te. persimilis* Ashmead (n: 3), and *Te. sanctivincenti* Ashmead (n: 1). The mean pairwise distances between the samples identified as the same species were much lower than those observed between the samples identified as different species (Suppl. material 3), as expected. The average of the pairwise evolutionary divergence (ED) between Palearctic and Nearctic *Telenomus* is 0.418 +/- 0.6671 (respectively, n: 95 and n: 8, 1000 replicates). The ED average in the two Palearctic species is 0.431 +/- 1.106 (*Te. truncatus* n: 49 and *Te. turesis* n: 46, 1000 replicates). The Blast search showed that the sequences of *Te. truncatus* have a 99.67% sequence identity with the GenBank sequence from *Telenomus* sp. (accession no. OL631282). The sequences from *Te. turesis* showed a 99.58% identity with a *Te. turesis* GenBank sequence (accession no. KY843528), a 99.38% identity with the GenBank and BOLD sequences from *Te. chloropus* (accession no. KF303516, BIOUG55155-D12, BIOUG16220-G06, BIOUG15112-C08, BIOUG36831-G01, BIOUG27850-E03), and a 99.84% identity with a *Te. turesis* GenBank sequence (accession no. OK562072). The ED average between sequences is 0.013 +/- 0.0028 (n. 49, 1000 replicates) within *Te. truncatus* and 0.241 +/- 0.0015 (n: 46, 1000 replicates) within *Te. turesis* (Suppl. material 3). The presence of different haplotypes in each species (Suppl. material 1) suggests that it may be necessary to sequence multiple molecular markers to investigate the different clades for both species.

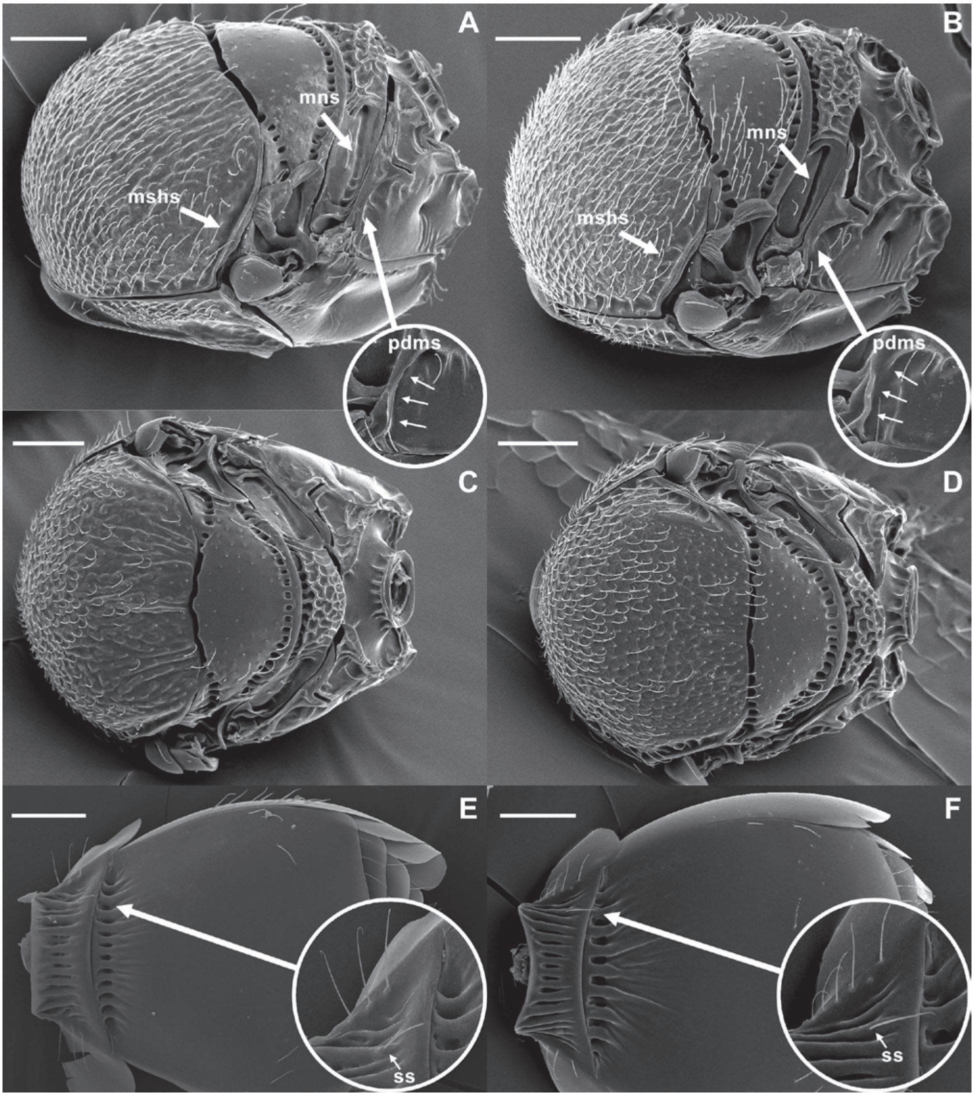

Figure 9. Thorax in dorso-lateral view: *Telenomus truncatus* (**A**) and *Te. turesis* (**B**); thorax in dorsal view: *Te. truncatus* (**C**) and *Te. turesis* (**D**); abdomen in dorsal view (ss: sublateral setae): *Te. truncatus* (**E**) and *Te. turesis* (**F**). Scale bars: 0.1 mm.

Conclusion

In recent years, researchers have limited the identification of *Telenomus* to genus level or grouped all of the specimens, referring only to *Te. chloropus* when they emerged from eggs of pentatomids in western Palearctic region. Despite the setbacks of these misidentifications, the taxonomy of Palearctic species of *Telenomus* associated with stink bugs has advanced, and we here provide a more solid foundation for continued

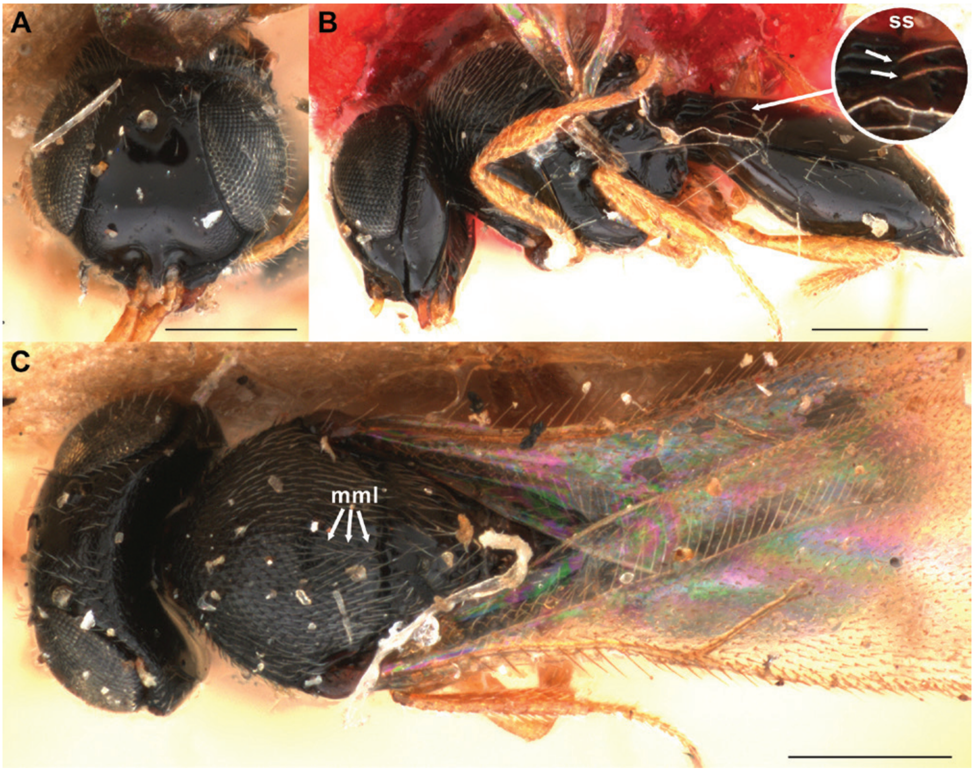

Figure 10. *Telenomus gifuensis*. Female paralectotype (USNMENT01109267): head in frontal view (**A**); female lectotype (USNMENT01109265): habitus in lateral view (**B**); female paralectotype (USNMENT01109266): habitus in dorsal view (**C**). Scale bars: 0.2 mm.

research. For the first time, the West Palearctic species of the *Te. podisi* species group associated with the Pentatomidae can be reliably identified, with diagnostic tools based on multiple lines of evidence. The logical next test of our species concepts would be interbreeding studies, as were performed for cryptic species of the genus *Trissolcus* (Matsuo et al. 2014; Tortorici et al. 2019; Moraglio et al. 2021a). The identification of European *Telenomus* species that attack stink bugs also provides new prospects for a detailed study of their biology, which may lead to improved pest management. Furthermore, identification of the wasps from new localities and hosts will expand the distributional and biological knowledge that is available from specimens in collections.

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Supplementary material 1

Phylogeny reconstruction of COI of *Telenomus truncatus* and *Te. turesis*

Authors: Francesco Tortorici

Data type: tif

Explanation note: The tree of life was inferred by using the Maximum Likelihood method and Tamura-Nei model with an interior branch test and 1000 bootstrap replications. The percentage of trees in which the associated taxa clustered together is shown next to the branches. This analysis involved 97 nucleotide sequences. There was a total of 492 positions in the final dataset. Star (*) indicates sequences mined from online datasets.

Link: https://doi.org/10.3897/jhr.97.127112.suppl1

Supplementary material 2

Distribution map

Authors: Francesco Tortorici

Data type: tif

Explanation note: Distribution map indicating the points for *Telenomus truncatus* (blue spots) and for *Te. turesis* (red spots) retrieved from material examined and from BOLD barcodes.

Link: https://doi.org/10.3897/jhr.97.127112.suppl2

Supplementary material 3

Estimates of Evolutionary Divergence between Sequences

Authors: Francesco Tortorici

Data type: xlsx

Explanation note: The number of base substitutions per site from between sequences are shown. Analyses were conducted using the Maximum Composite Likelihood model (Tamura and Kumar 2004). The rate variation among sites was modeled with a gamma distribution (shape parameter = 1). This analysis involved 105 nucleotide sequences. All ambiguous positions were removed for each sequence pair (pairwise deletion option). There were a total of 861 positions in the final dataset. Evolutionary analyses were conducted in MEGA X (Kumar et al. 2018). Kumar S., Stecher G., Li M., Knyaz C., and Tamura K. (2018). MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. Molecular Biology and Evolution 35: 1547–1549. Tamura K., Nei M., and Kumar S. (2004). Prospects for inferring very large phylogenies by using the neighbor-joining method. Proceedings of the National Academy of Sciences (USA) 101:11030–11035.

Link: https://doi.org/10.3897/jhr.97.127112.suppl3

Supplementary material 4

List of the specimens examined

Authors: Francesco Tortorici, Bianca Orrù, Alexander V. Timokhov, Alexandre Bout, Marie-Claude Bon, Luciana Tavella, Elijah J. Talamas

Data type: xlsx

Explanation note: Images and sequence data for species of *Telenomus* that are classified in the podisi species group (sensu Johnson 1984).

Link: https://doi.org/10.3897/jhr.97.127112.suppl4