






The ectoparasitoid wasp *Heterospilus sicanus* (Marshall, 1888) (Hymenoptera, Braconidae, Doryctinae) as a natural enemy of *Gastrallus pubens* Fairmaire, 1875 (Coleoptera, Ptinidae) in Italy

Sergey A. Belokobylskij¹, Salvatore Guarino², Sara Savoldelli³, Costanza Jucker³, Ezio Peri⁴, Gavin R. Broad⁵, Giuliano Cerasa⁴

1 Zoological Institute of the Russian Academy of Sciences, St Petersburg 199034, Russia

2 Institute of Biosciences and Bioresources (IBBR), National Research Council of Italy (CNR), Corso Calatafimi 414, 90129 Palermo, Italy

3 DeFENS – Department of Food, Environmental and Nutritional Sciences, University of Milan, Via G. Celoria 2, 20133 Milan, Italy

4 Department of Agriculture, Food and Forest Sciences, University of Palermo, Viale delle Scienze, Building 5, 90128 Palermo, Italy

5 Natural History Museum, Cromwell Road, London SW7 5BD, UK

Corresponding author: Salvatore Guarino (salvatore.guarino@cnr.it)



Academic editor: Kees van Achterberg

Received: 10 January 2024

Accepted: 17 February 2024

Published: 14 May 2024

ZooBank: <https://zoobank.org/901583F6-332C-473D-88B3-E96187BA5FAC>

Citation: Belokobylskij SA, Guarino S, Savoldelli S, Jucker C, Peri E, Broad GR, Cerasa G (2024) The ectoparasitoid wasp *Heterospilus sicanus* (Marshall, 1888) (Hymenoptera, Braconidae, Doryctinae) as a natural enemy of *Gastrallus pubens* Fairmaire, 1875 (Coleoptera, Ptinidae) in Italy. ZooKeys 1201: 233–253. <https://doi.org/10.3897/zookeys.1201.118549>

Copyright: © Sergey A. Belokobylskij et al. This is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International – CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).

Abstract

Heterospilus sicanus (Marshall, 1888) is redescribed and illustrated based on the holotype of *Dendrosoter sicanus* Marshall, 1888 and on recently collected material from its type locality (Sicily, Italy). Previous host records for this species are unreliable. Here, the host of *H. sicanus*, the rare ptinid beetle *Gastrallus pubens* Fairmaire, 1875, is recorded for the first time, having been reared in a historic library in Palermo, Italy. *Heterospilus sicanus* is compared with the similar species *Telebolus* (= *Heterospilus*) *corsicus* Marshall, 1888, which was described in the same monograph from Corsica (France), and it is also redescribed and illustrated. *Atoreuteus ceballosi* Docavo Alberti, 1960, **syn. nov.** is synonymised under *Heterospilus sicanus* (Marshall, 1888), and *Hormiopteris* (= *Rhaconotus*) *ollivieri* Giraud var. *flava* Fahringer, 1931, **syn. nov.** is a junior synonym of *Heterospilus cephi* Rohwer, 1925. A key for determination of the Western Palaearctic *Heterospilus* species with a striate vertex is provided and the distributions of *H. sicanus* and *H. corsicus* are discussed.

Key words: Bookworm, diagnosis, Ichneumonoidea, parasitoid, redescrptions, taxonomy

Introduction

The family Braconidae is a vast group within the order Hymenoptera, comprising more than 20,000 recognised species (Yu et al. 2016). Together with the family Ichneumonidae it constitutes one of two recent families of Ichneumonoidea, the vast majority of which are parasitoids (Wharton 1993).

The braconid subfamily Doryctinae is renowned for its exceptional genera and species richness and diversity, including more than 2000 described species distributed globally across almost 200 genera (Shenefelt and Marsh 1976; Marsh 1993, 2002; Belokobylskij et al. 2004a, 2004b; Belokobylskij and Maetô 2009; Yu et al. 2016). Doryctines, for the most part, are idiobiont ectoparasitoids on

the larvae of xylophagous and bark-boring Coleoptera. Some members of this group also parasitise the larvae of Lepidoptera and Hymenoptera (Symphyta), while a few genera are known to be phytophagous (Ramírez and Marsh 1996; Wharton and Hanson 2005; Zaldívar-Riverón et al. 2007, 2014). Additionally, in certain cases, they function as parasitoids (perhaps endoparasitoids) of adult Embioptera or have been observed inhabiting termite nests (Shaw and Edgerly 1985; Wharton 1993; Kistner et al. 2000; Belokobylskij 2002).

Within this subfamily, the genus *Heterospilus* Haliday, 1836, belonging to the tribe Heterospilini, stands out as one of the largest and most hyperdiverse braconid genera, with already more than 400 species described and many more to be described (Marsh et al. 2013; Yu et al. 2016; Ghahari et al. 2022). In total, 21 species of *Heterospilus* of 45 Palaearctic species are known in Europe, while more than 340 species have been described from the New World (Nearctic and mainly Neotropics) and 37 species from the Oriental region; only one species has been described from Australia and none from the Afrotropical region (Yu et al. 2016; Belokobylskij and Ku 2021).

Species of *Heterospilus* are idiobiont ectoparasitoids known for their exceptionally diverse range of primarily endophytic hosts (Belokobylskij and Maeto 2009; Yu et al. 2016), primarily targeting stem-boring Coleoptera of various families, including Anobiidae, Buprestidae, Cerambycidae, Chrysomelidae (mainly Bruchinae), Curculionidae (including Scolytinae), Languriidae, Mordellidae, and Ptinidae. Additionally, they also parasitise Lepidoptera species of the families Cosmopterigidae, Gelechiidae, Prodoxidae and Pyralidae, and even stem-boring Hymenoptera of the family Cephidae. In addition, a few species have been reared from nests of Crabronidae (Hymenoptera) (Marsh 1982; Shaw 1995; Marsh and Melo 1999; Cabrera et al. 2002).

In this study we provide an illustrated redescription and updated diagnosis of *Heterospilus sicanus* (Marshall, 1888), discovered in the frass, holes, and tunnels created by *Gastrallus pubens* Fairmaire, 1875 (Coleoptera: Ptinidae) in books seriously infested by this book-boring beetle during inspections in the “Ottavio Ziino” Law History Library of the Law Department at the University of Palermo (Sicily, Italy). *Heterospilus sicanus* is compared with the congeneric *Telebolus* (= *Heterospilus*) *corsicus* Marshall, 1888, which is also redescribed and illustrated, and *Atoreuteus ceballosi* Docavo Alberti, 1960 is here synonymised under *H. sicanus* (Marshall, 1888). Finally, a key for the determination of the Western Palaearctic *Heterospilus* species with a striate vertex is included and the distributions of *H. sicanus* and *H. corsicus* are discussed.

Materials and methods

The terminology employed in this work for the morphological features, measurements, and wing venation nomenclature follows Belokobylskij and Maeto (2009), with the terminology for wing venation by van Achterberg (1993) shown in parentheses. Images were taken using a Leica DM series compound microscope (Leica, Benzheim, Germany) and a Leica DFC series mounted camera with Leica Application Suite software (LAS EZ 3.4.0, Leica, Switzerland), and with a Canon SLR EOS 5DSR with either a 65 mm macro lens or a Mitutoyo 10× lens in combination with a 70–130 mm macro lens, mounted on a stand

with an automated Z-stepper (the Natural History Museum, London, UK). All insect photos were integrated using the freeware CombineZP (Hadley 2011) or Helicon Focus and processed in Adobe Photoshop CS4.

Abbreviations of specimen depositories

The specimens (including types) examined in this study have been deposited in the following collections.

HNHM	Hungarian Natural History Museum, Budapest, Hungary;
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain;
NHMUK	the Natural History Museum, London, UK;
NHMW	Naturhistorisches Museum, Wien, Austria;
SAAF-UNIPA	Department of Agricultural, Food and Forest Science, University of Palermo, Palermo, Italy;
ZISP	Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia.

Taxonomy

Class Hexapoda Blainville, 1816

Order Hymenoptera Linnaeus, 1758

Family Braconidae Nees, 1811

Subfamily Doryctinae Foerster, 1863

Tribe Heterospilini Fischer, 1981

Genus *Heterospilus* Haliday, 1836

The original description of *Dendrosoter sicanus* Marshall, 1888: 242, translated from French, is as follows:

“Head transverse, largely dark brown as well as the thorax; the rest of the body tawny; abdomen black towards the tip. Vertex high, gibbous, without frontal protuberances, finely wrinkled crosswise; eye and stemmaticum smooth. Ocelli sunk in the head, the front one placed on the slope of the forehead. Frontal excavation very shallow and poorly determined. Orbits and genae fawn. Antennae as long as the body, slender, blackish with ferruginous base, with 20 antennal segments. Thorax granular, slightly shiny. Mesonotum dark brown; its crenulated furrows converging towards a deep, rough dimple. Metanotum fawn, slightly shiny, granular irregularly streaked lengthwise on its anterior part, roughly reticulated in rear, with several high lines which cross in all directions. Wings slightly smoky, veins and stigma brown; second cubital cell receiving the recurrent vein; vein posterior non-interstitial. Legs fairly short and thick, testaceous. Abdomen as long as the head and thorax, and wider than the latter, tawny, becoming more and more blackish towards the end, last segment pale; first segment in truncated triangle, twice wider at the tip than at the base, bicarinated and high in the middle, depressed on the side edges, leathery, dull, longitudinally streaked. Second suture erased, even on the sides. Second segment very linearly wrinkled at the base, smooth and shiny on the rest of its surface, as well as all the following ones. Ovipositor as long as the abdomen. Male unknown. Long. 2–3.5 mm.”

Marshall (1897: 127) additionally noted (here translated from French), “This species [*D. sicanus*], like the others, is variable as to the size and the colours. I received from Genoa two ♀ which are much darker than the type, and one of which is only half the size indicated. In other aspects their features agree with those of *D. sicanus*. Homeland: add, Italy (Genoa), sent from Mr Mantero.”

Mantero (1904: 28) elaborated on the Italian specimens (here translated from Italian): “Belvedere, July 1891 (Solari). The Ligurian specimens, also cited by Marshall (1897) have a darker colour than the type.”

***Heterospilus sicanus* (Marshall, 1888)**

Figs 1–5

Dendrosoter sicanus Marshall, 1888: 243.

Heterospilus sicanus: Tobias 1971: 194; 1976: 35; Shenefelt and Marsh 1976: 1312; Yu et al. 2016.

Atoreuteus ceballosi Docavo Alberti, 1960: 33, syn. nov.

Heterospilus ceballosi: Shenefelt and Marsh 1976: 1302; Yu et al. 2016.

Type material examined. Holotype of *Dendrosoter sicanus*: female, Italy, “Type” (round with red border), “*sicanus* Marsh. (Sicily)” (handwriting), “Marshall coll. 1904–120”, “Almost certainly type of *Dendrosoter sicanus* Msh., G. Nixon, 25.I.38” (handwriting by G. Nixon), “This is definitely type of *Dendrosoter sicanus* Marshall. Paul M. Marsh, VI–17–71” (handwriting by P. Marsh), “B.M. Type Hym. 3c.1751”, “NHMUK 010880780” (NHMUK, London). **Holotype of *Atoreuteus ceballosi*:** female, Spain, “Tenerife, Bajamar, 8.V.1901”, “♀”, “*Atoreuteus ceballosi* Docavo n. sp.”, “Tipo”, “*Heterospilus* ♀ *ceballosi* Doc., det. Papp J., 1983”, “MNCN Cat. Typos N 11.246” (MNCN, Madrid).

Additional material examined. Italy: Sicily, “Ottavio Ziino” Law History Library of the Law Department of the University of Palermo, 5.VI.2023 (E. Peri, S. Savoldelli, C. Jucker and S. Guarino), 18 females, 15 males (SAAF-UNIPA); Sicily, Vittoria, IX – X.1899 (G. Mantero), 1 female (ZISP). Russia: Crimea, Sebastopol, 5.V.1917 (W. Pliginski), 8 females with the same label of the latter (ZISP).

Redescription. Female (holotype). Body length 2.6 mm; fore wing length 2.3 mm.

Head. Head not depressed, its width 1.6× median length, 1.1× width of mesoscutum. Head behind eyes weakly convex anteriorly, evenly and roundly narrowed posteriorly. Transverse diameter of eye 1.2× longer than temple (dorsal view). Ocelli small, in almost equilateral triangle. POL 1.3× Od, 0.35× OOL. Diameter of antennal socket equal to distance between sockets, twice distance between socket and eye. Eye with sparse and short setae, without emargination opposite antennal sockets, 1.2× as high as broad. Malar space 0.7× height of eye, 1.2× basal width of mandible. Face convex, its width 1.2× height of eye and almost equal to height of face and clypeus combined. Malar suture absent. Clypeus with distinct lower flange. [Hypoclypeal depression covered by glue.] Occipital carina complete dorsally, ventrally joining hypostomal carina distant from base of mandible. Head below eyes (front view) roundly narrowed. Hypostomal flange distinct but narrow.

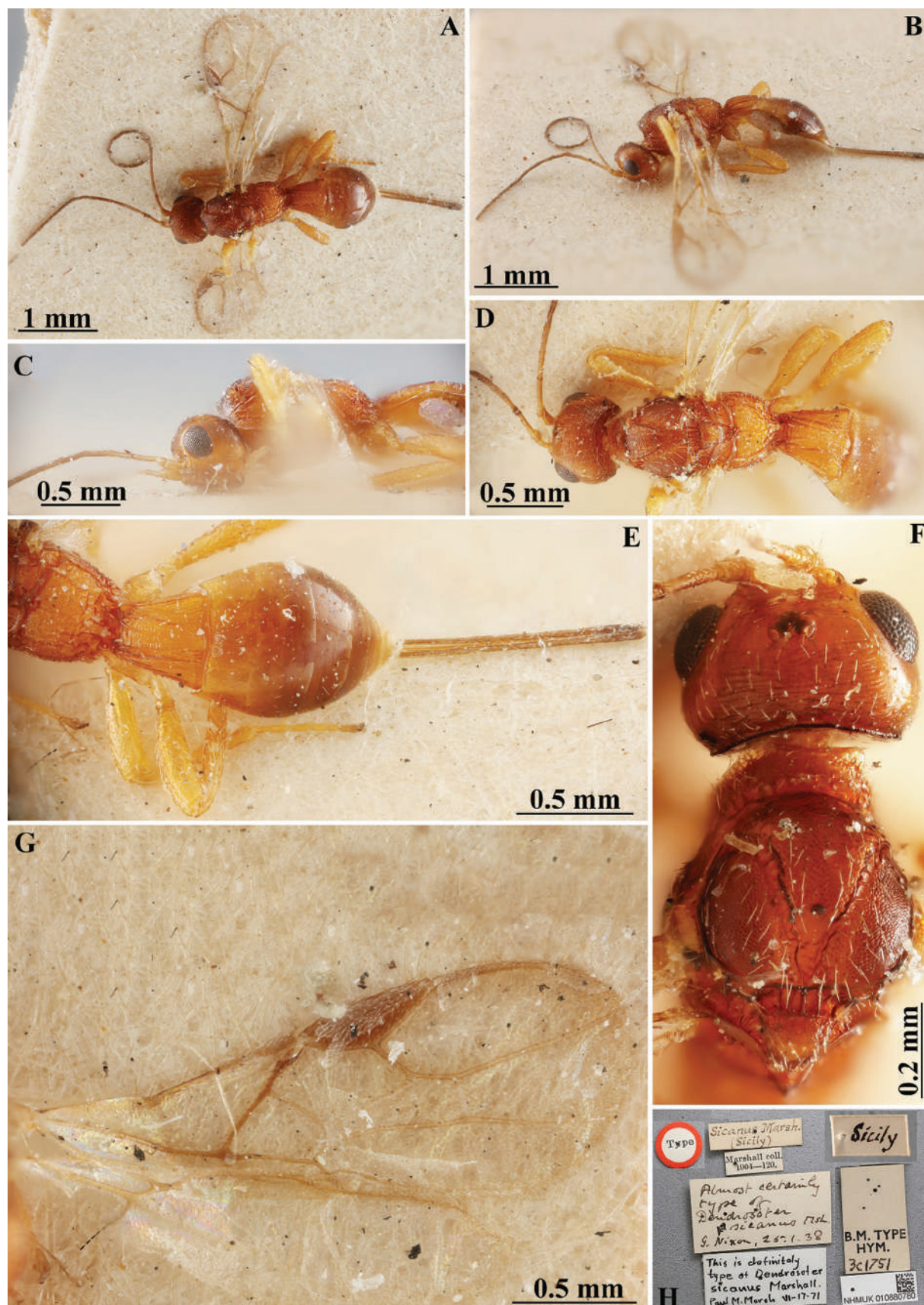


Figure 1. *Heterospilus sicanus* (Marshall, 1888) (female, holotype) **A** habitus, dorsal view **B** habitus, lateral view **C** head, mesosoma and base of metasoma, lateral view **D** head, mesosoma and base of metasoma, dorsal view **E** propodeum, metasoma and ovipositor, dorsal view **F** head and mesoscutum, dorsal view **G** wings **H** labels.

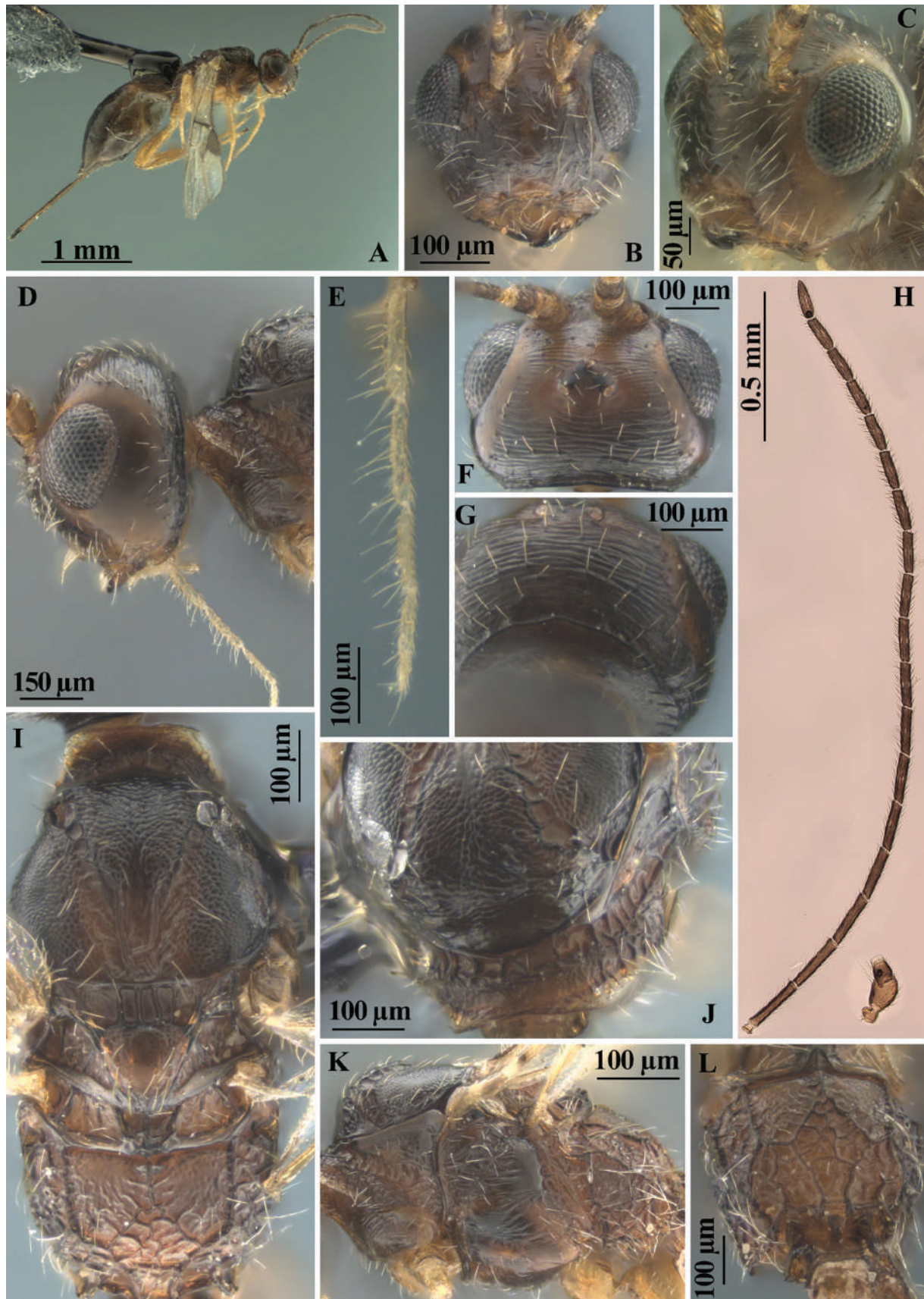


Figure 2. *Heterospilus sicanus* (Marshall, 1888) (female) **A** habitus, lateral view **B–D** head, frontal, antero-lateral and lateral view **E** maxillary palp **F, G** head, dorsal and postero-dorsal view **H** antenna **I** mesosoma, dorsal view **J** pronotum, antero-dorsal view **K** mesosoma, lateral view **L** propodeum, dorsal view.

Antennae. Antenna slender, filiform, 20-segmented, almost as long as body. Scape rather short and thick, 1.5× longer than its maximum width. First flagellar segment slender, almost straight, subcylindrical, 5.5× longer than apical width, almost as long as second segment. Penultimate segment 3.3× longer than wide, 0.6× as long as first segment, 0.9× as long as apical segment; the latter pointed apically and without spine.

Mesosoma. Mesosoma not depressed dorso-ventrally, its length 1.6× maximum height. Pronotal neck rather long, dorsally without convex lobe, with rather distinct submedial pronotal carina; side of pronotum with distinct, almost straight, and rather wide submedial oblique crenulate furrow. Mesoscutum highly and perpendicularly elevated above pronotum, maximum width of mesoscutum 1.3× its median length. Median lobe of mesoscutum (dorsal view) protruding forwards, weakly convex anteriorly, with distinct and almost pointed anterolateral corners. Notauli wide, rather deep, densely and coarsely crenulate. Prescutellar depression deep, wide, with 4 carinae, finely sculptured between carinae, ~ 0.3× as long as wide, 0.45× as long as scutellum. Scutellum convex, with fine lateral carinae, its width 1.1× median length. Subalar depression rather deep, wide, sparsely and coarsely rugose-striate. Precoxal sulcus deep, almost straight, rugulose, running along anterior 0.6 of lower part of mesopleuron. Metanotal tooth (lateral view) relatively long, wide, distinctly pointed apically. Metapleural lobe rather large, more or less wide, rounded posteriorly. Propodeum (lateral view) regularly convex-roundly slanted from base to apex, without lateral tubercles; propodeal spiracle small.

Wings. Fore wing 3.0× longer than its maximum width, 0.9× as long as body. Pterostigma 3.0× longer than wide. Radial vein (r) arising before middle of pterostigma, distance from base of pterostigma to radial vein (r) 0.85× distance from radial vein (r) to apex of pterostigma. Radial (marginal) cell not shortened. Metacarp (1-R1) 1.2× longer than pterostigma. First radial abscissa (r) almost as long as maximum width. Second radial abscissa (3-SR) as long as first abscissa (r), 0.25× as long as the straight third abscissa (SR1), 0.5× as long as trace of first radiomedial vein (2-SR). Trace of first radiomedial vein (2-SR) 2.3× longer than second radiomedial vein (r-m), 4.0× longer than recurrent vein (m-cu). Recurrent vein (m-cu) distinctly postfurcal. First medial abscissa (1-SR+M) curved. Discoidal (discal) cell 1.6× longer than its width. Distance (1-CU1) from nervulus (cu-a) to basal vein (1-M) ~ 0.5 of nervulus (cu-a) length; nervulus (cu-a) straight and almost perpendicular to longitudinal anal vein (1-1A). Mediocubital vein (M+CU1) almost straight. Parallel vein (CU1a) distinctly curved subbasally. Brachial (subdiscal) cell widely open distally, brachial vein (CU1b) absent. Hind wing 4.2× longer than wide. First abscissa of costal vein (C+SC+R) 1.2× longer than second abscissa (1-SC+R); second abscissa (1-SC+R) strongly sclerotised. Last costal abscissa (SC+R1) 0.8× as long as first (C+SC+R) and second (1-SC+R) abscissae combined. Radial vein (SR) strongly desclerotised. Medial (basal) cell narrow, almost parallel-sided in its apical half, its length ~ 11.0× maximum width, almost 0.3× length of wing. First abscissa of mediocubital vein (M+CU) 0.8× as long as second abscissa (1-M). Recurrent vein (m-cu) unsclerotised, almost interstitial, straight, very weakly oblique toward base of wing.

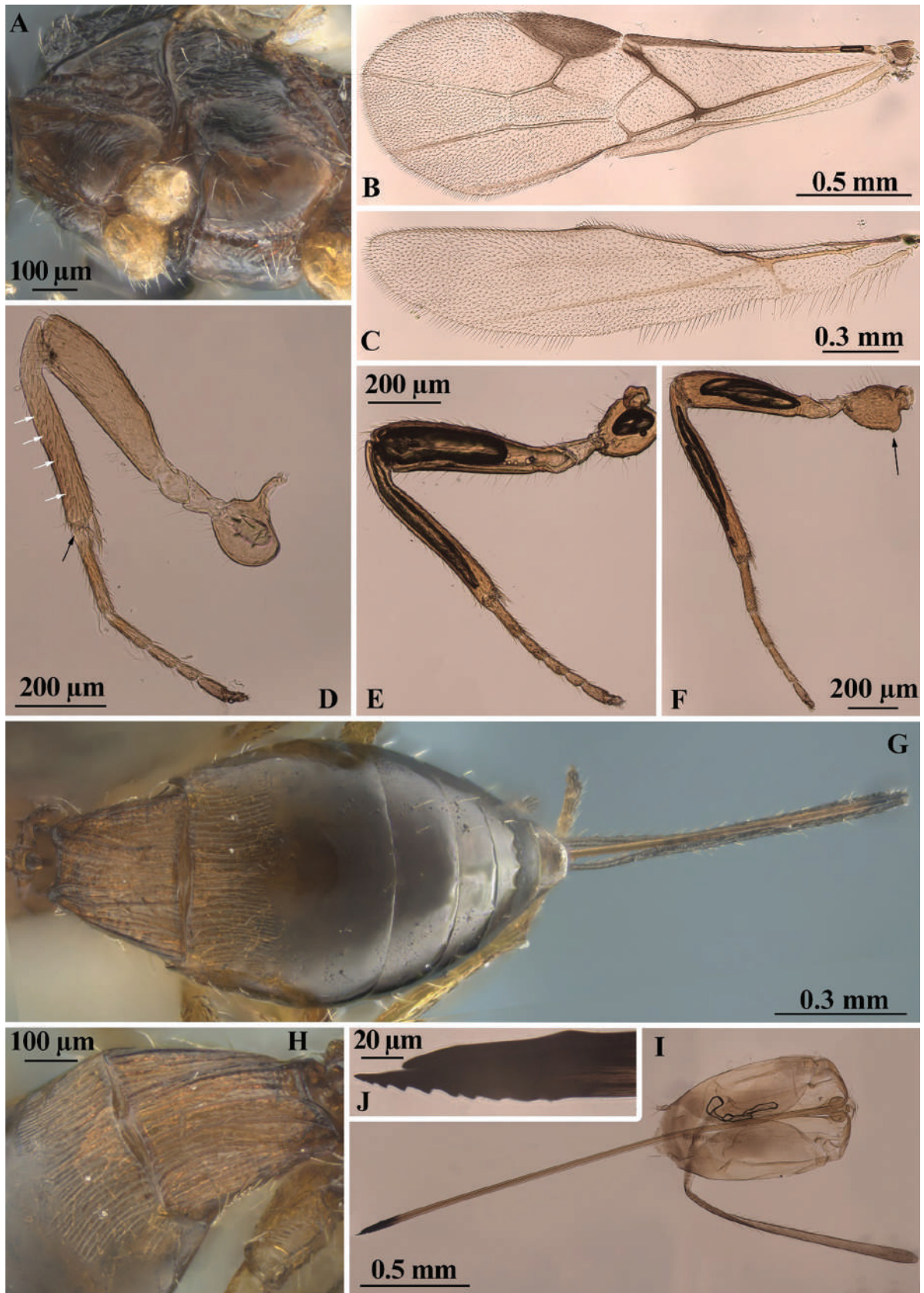


Figure 3. *Heterospilus sicanus* (Marshall, 1888) (female) **A** mesosoma, ventro-lateral view **B** fore wing **C** hind wing **D** fore leg (white arrows indicate short stout spines on its front tibia surface and black arrow those on the apical part) **E** middle leg **F** hind leg (black arrow indicates a distinct antero-ventral basal tubercle on the coxa) **G** metasoma, dorsal view **H** first tergite, dorso-lateral view **I** ovipositor and one of its sheaths **J** ovipositor apex.

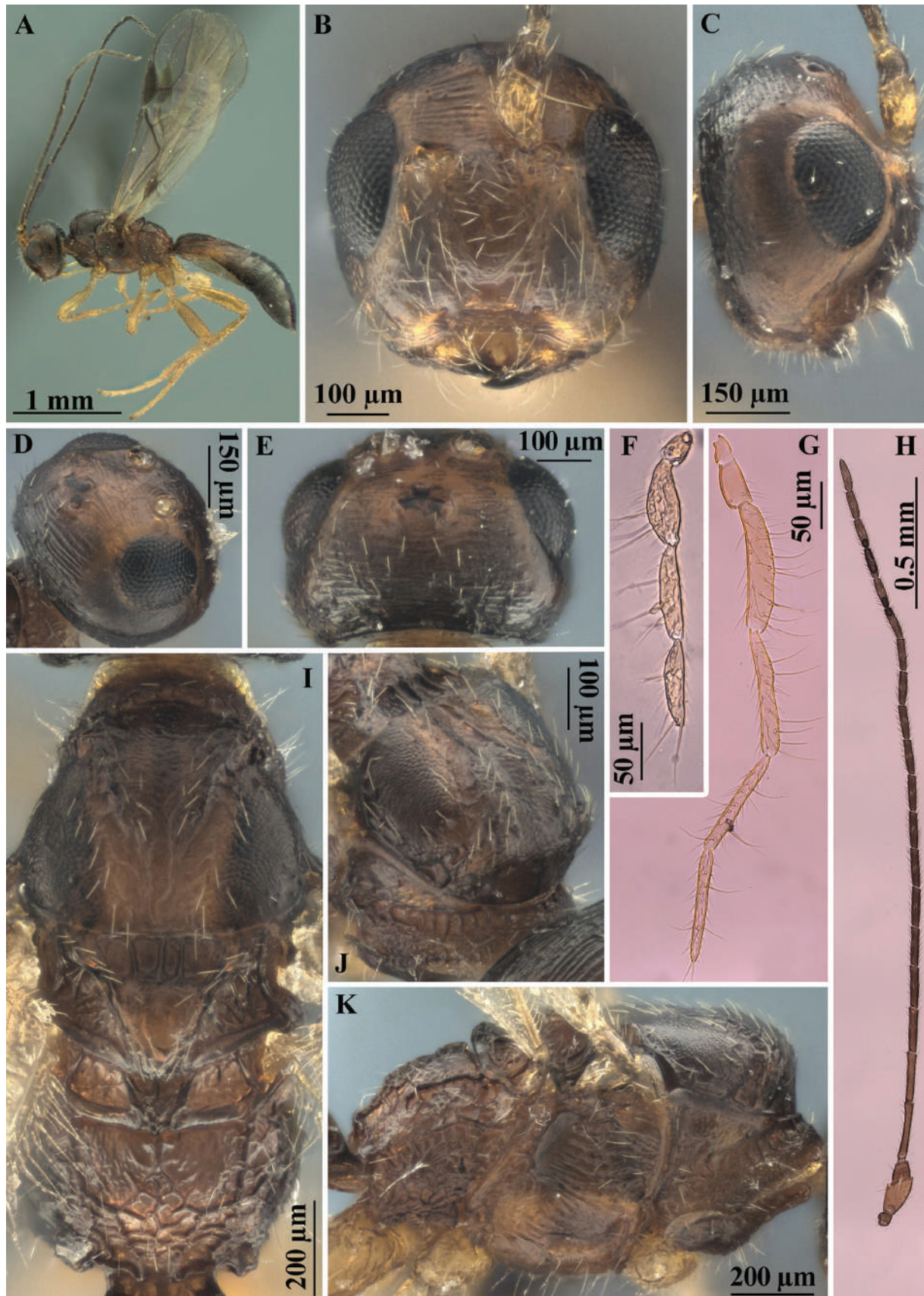


Figure 4. *Heterospilus sicanus* (Marshall, 1888) (male) **A** habitus, lateral view **B** head, front view **C** head, lateral view **D** head dorso-lateral view **E** head dorsal view **F** labial palpus **G** maxillary palpus **H** antenna **I** mesosoma, dorsal view **J** pronotum, antero-dorsal view **K** mesosoma, lateral view.

Legs. Fore tibia with several rather slender spines arranged in longitudinal line. Hind coxa with basoventral tubercle, 1.3× longer than its maximum width. Hind femur rather wide, without dorsal protuberance, 3.5× longer than wide. Hind tarsus 0.9× as long as hind tibia. Basitarsus not thickened, without ventral keel, 0.5× as long as second–fifth segments combined. Second tarsal segment 0.7× as long as basitarsus, 1.6× longer than fifth segment (without pretarsus).

Metasoma. Metasoma 0.9× as long as head and mesosoma combined, 1.8× longer than its maximum width. First segment with short acrosternite. First tergite with not high but rather distinct and wide median area, with distinct dorsope, without spiracular tubercles; tergite distinctly and almost linearly widened from base to apex. Length of first tergite equal to its apical width, 1.4× length of propodeum; maximum width of tergite ~ 2.0× its minimum width. Median length of second tergite 0.45× its basal width, 0.8× length of third tergite. Combined length of second and third tergites 0.9× basal width of second tergite, 0.7× their maximum width. Second suture present, but fine, usually weakly curved laterally. Third tergite without transverse furrow. Ovipositor sheath rather slender, 0.8× as long as metasoma, 1.1× longer than mesosoma, 0.4× as long as body, 0.5× as long as fore wing.

Sculpture and pubescence. Vertex entirely distinctly and rather densely transversely striate, partly with very fine additional reticulation between striae; frons entirely densely and distinctly transversely striate [face covered in glue]; temple smooth. Mesoscutum densely and distinctly granulate, medioposteriorly with two posteriorly convergent carinae. Scutellum granulate. Mesopleuron entirely rugose-striate. Metapleuron entirely distinctly rugose-reticulate. Propodeum with rather wide, short and finely granulate-coriaceous basolateral areas, weakly delineated by carinae; areola finely delineated; basal carina 0.8× as long as anterior fork of areola; posterior 0.7 of propodeum irregularly rugose-reticulate. Hind coxa densely granulate, transversely striate dorsally. Hind femur finely and densely granulate-coriaceous. First tergite with rather distinct and posteriorly convergent dorsal carinae, densely and distinctly longitudinally striate, with fine and dense additional reticulation between striae. Second tergite mostly distinctly longitudinally striate, laterally smooth over rather wide area, rugulose postero-medially. Remaining tergites smooth. Vertex almost entirely with rather dense, short and semi-erect setae arranged in rows. Mesoscutum with rather dense, relatively long and semi-erect pale setae at wide area along notauli and scattered across lobes, all lobes narrowly glabrous medially. Hind tibia dorsally with short, sparse, semi-erect setae; length of these setae ~ 0.3× maximum width of hind tibia.

Colour. Body reddish brown, vertex, mesonotum, and posterior half of metasoma dark reddish brown. Antenna dark brown, four basal segments pale brown. Palpi yellow. Legs entirely pale brown. Ovipositor sheath mainly brown, black apically. Fore wing very faintly infusate. Pterostigma almost entirely brown.

Variation. Head width 1.4–1.6× median length. Transverse diameter of eye 1.1–1.3× longer than temple (dorsal view). Malar space 0.6–0.7× height of eye. Hypoclypeal depression round, its width 0.7–0.8× distance from margin of depression to margin of eye, 0.4–0.5× width of face. Face mainly smooth. Antennae 20-segmented. First flagellar segment 4.5–5.5× longer than its apical width. Penultimate segment 3.0–3.3× longer than wide. Mesosoma length

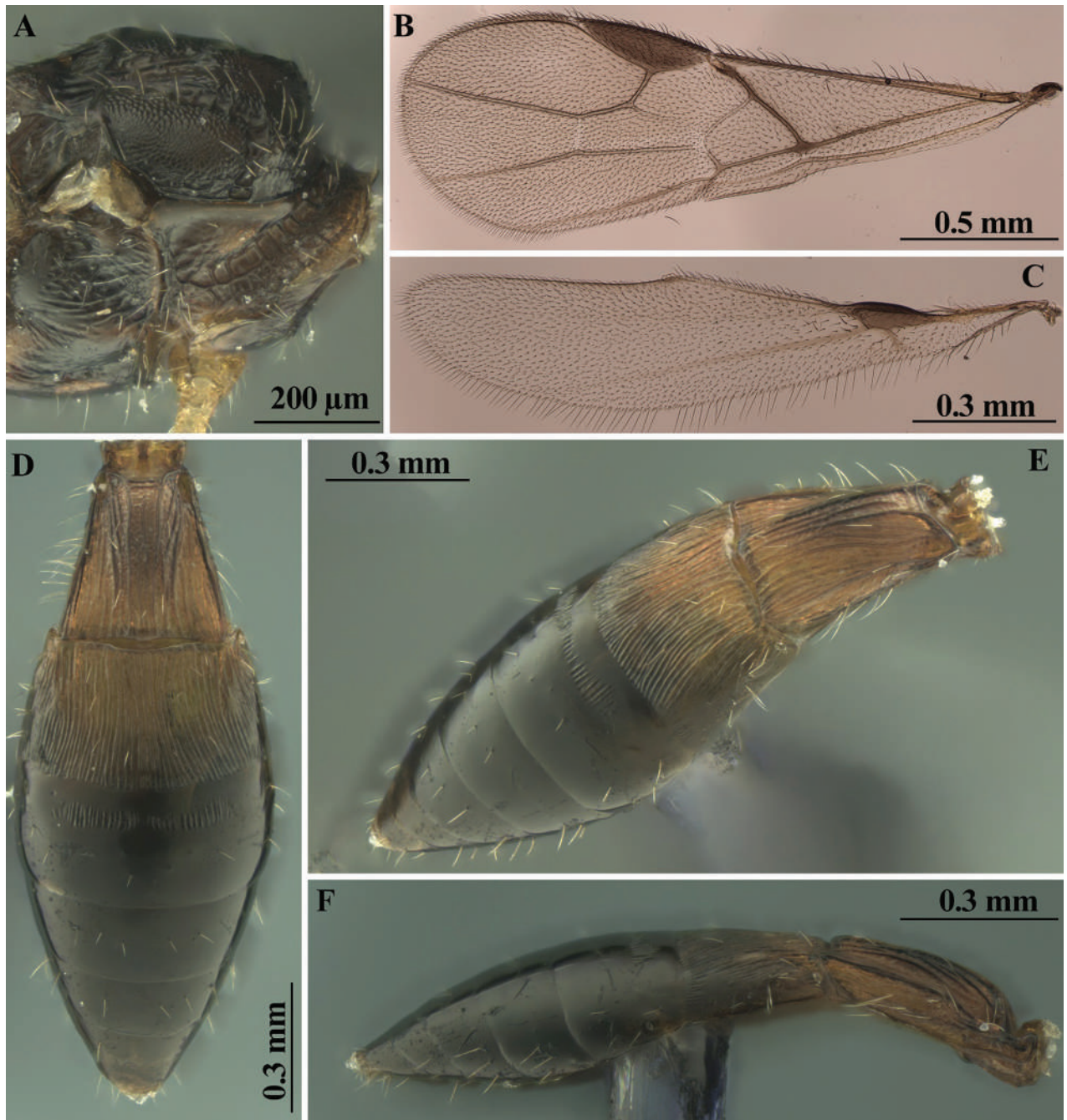


Figure 5. *Heterospilus sicanus* (Marshall, 1888) (male) **A** pronotum and propleuron, dorso-lateral view **B** fore wing **C** hind wing **D** metasoma, dorsal view **E** metasoma dorso-lateral view **F** metasoma, lateral view.

1.6–1.7× maximum height. Maximum width of mesoscutum 1.2–1.3× its median length. Mesopleuron sometimes smooth in small submedial area. Basal carina of propodeum 0.8–1.0× as long as areola anterior fork. Wings. Pterostigma 2.8–3.6× longer than wide. Second radial abscissa (3-SR) 1.0–1.3× as long as first abscissa (r), 0.25–0.30× as long as third abscissa (SR1), 0.5–0.7× as long as trace of first radiomedial vein (2-SR). Discoidal (discal) cell 1.6–1.8× longer than its width. Legs. Hind femur 3.5–3.8× longer than wide. Hind tibia dorsal setae 0.3–0.4× maximum width of hind tibia. First metasomal tergite 1.3–1.4× longer than propodeum. Median length of second tergite 0.40–0.45× its basal width, 0.7–0.8× length of third tergite. Ovipositor sheaths 0.7–0.9× as

long as metasoma, 1.1–1.2× longer than mesosoma. Body mainly dark reddish brown, sometimes ventrally distinctly paler. Legs entirely pale brown or yellow, anterior half of metasoma often yellow or pale reddish brown. Fore wing very faintly infusate. Pterostigma brown or pale brown.

Male. Body length 2.6–2.8 mm; fore wing length 2.1 mm. Antennae slender, filiform, 21-segmented, approximately as long as body. Hind wing with relatively small, complex, brown stigma-like enlargement, its length 0.7–0.8× distance from base of wing to base of enlargement. Length of first metasomal tergite 1.1× its apical width. Second tergite entirely striate. Median length of second tergite 0.75× its anterior width, 1.2× length of third tergite. Third tergite with shallow and crenulate transverse furrow in anterior one-third. Body mainly brown to dark brown, anterior third of metasoma paler. Otherwise similar to female.

Host. Until recently, the only reported host of this species was *Cryphalus piceae* (Ratzeburg, 1837) (Coleoptera, Curculionidae, Scolytinae) (Tobias 1971; Kenis et al. 2004; Wegensteiner et al. 2015). However, the first author checked material assigned to this species deposited in the collection of the Zoological Institute RAS (St Petersburg, Russia) determined by Dr V. I. Tobias as *H. sicanus* (Marshall) (Tobias 1971). This sample comprised seven females and ten males with the label: “Teberda, Sev. Kavkaz [North Caucasus, Karachay-Cherkess Republic], on *Cryphalus piceae*, T. Guryanova [leg], 24 VI [19]64”, “*Dendrosotinus sicanus* Marsh., Tobias det. 1965”. Our redetermination of these specimens showed that they actually belong to another genus and species, *Dendrosotinus (Gildoria) similis* Boucek, 1955. Thus, the host of *H. sicanus* was unknown before this study and *Gastrallus pubens* Fairmaire, 1875 (Coleoptera, Anobiidae) is the first and only known host of *H. sicanus*.

Distribution. According to Taxapad, the world catalogue of Ichneumonoidea (Yu et al. 2016), besides Italy (Sicily), *H. sicanus* has also been recorded in Spain (Falco Gari et al. 1993), Croatia (Papp 1977), Serbia (Brajkovic 1989), and Hungary (Papp 1984); however, at least some of these records require confirmation. In Russia, this species has only been found in Crimea (new record; see ‘Additional material examined’), whereas its records from the North Caucasus of Russia (Tobias 1971, 1976) were erroneous (for details see ‘Remarks’ under the ‘Hosts’ section).

Comparative diagnosis. *Heterospilus sicanus* (Marshall) is very similar to *H. corsicus* (Marshall, 1888), but differs from the latter by having the head behind the eyes convex anteriorly and roundly narrowed posteriorly (evenly roundly narrowed posteriorly in *H. corsicus*), eyes setose, transverse diameter in dorsal view 1.1–1.3× length of temple (glabrous, transverse diameter 1.5–1.6× length of temple in *H. corsicus*), antenna slender (thickened in *H. corsicus*), mesosoma 1.6–1.7× longer than its height (1.8× in *H. corsicus*), medial lobe of mesoscutum without pointed anterolateral corners (with pointed corners in *H. corsicus*), radial vein (r) of fore wing arising slightly before middle of pterostigma (almost from or behind middle in *H. corsicus*), setae on dorsal side of hind tibia short, ~ 0.3× as long as maximum width of tibia (long, 0.5–0.7× in *H. corsicus*), and pterostigma almost entirely brown (yellow in *H. corsicus*).

Western Palaearctic *Heterospilus* species with an almost entirely sculptured vertex can be differentiated using the key below.

***Heterospilus corsicus* (Marshall, 1888)**

Fig. 6

Telebolus corsicus Marshall, 1888: 202.

Heterospilus corsicus: Shenefelt and Marsh 1976: 1303; Yu et al. 2016.

Caenophanes cingulatus Szépligeti, 1900: 213.

Heterospilus cingulatus: Shenefelt and Marsh 1976: 1302; Belokobylskij and Tobias 1986: 33 (as synonym); Yu et al. 2016.

Type material examined. *Holotype of Telebolus corsicus*: female, France (Corsica), "Type" (round with red border), "Corsica", "B.M. Type Hym. 3c.188", "*corsicus* Marsh.", "Marshall coll. 1904–120.", "B.M. Type Hym. *Telebolus corsicus* Marshall 1888". "NHMUK010880788" (NHMUK, London). *Holotype of Caenophanes cingulatus*: female, "Szóváta, Csiki", "Transsylvania", "Holotypus ♀ *Caenophanes cingulatus* Szép., 1900 sp. n. / des/ Papp J. 1967", "Hym. Typ. N 598. Museum Budapest", "*Heterospilus cingulatus* Sz., det. Papp J., 1983" (HNHM).

Redescription. Female (holotype). Body length 2.6 mm; fore wing length 1.8 mm.

Head. Head not depressed, its width 1.5× median length, 1.3× width of mesoscutum. Head behind eyes evenly and roundly narrowed. Transverse diameter of eye 1.6× longer than temple (dorsal view). Ocelli small, in almost equilateral triangle. POL almost equal to Od, 0.4× OOL. Diameter of antennal socket 1.3× distance between sockets, 1.8× distance between socket and eye. Eye without setae, with shallow emargination opposite antennal sockets, 1.2× as high as broad. Malar space 0.5× height of eye, 1.3× basal width of mandible. Face convex, its width 1.15× height of eye and 1.3× height of face and clypeus combined. Malar suture absent. Clypeus with short lower flange. Hypoclypeal depression rather small and suboval, its width 0.7× distance from edge of depression to eye, 0.35× width of face. Occipital carina complete dorsally, joining hypostomal carina ventrally distant from upper base of mandible. Head below eyes distinctly and weakly-roundly narrowed. Hypostomal flange distinct but narrow.

Antenna. Antenna weakly thickened, filiform, 21-segmented, slightly longer than body. Scape rather long and thick, 1.5× longer than its maximum width. First flagellar segment weakly thickened, weakly curved, subcylindrical, 4.5× longer than its apical width, almost as long as second segment. Penultimate segment 2.7× longer than wide, 0.6× as long as first segment, 0.9× as long as apical segment; the latter pointed apically and without spine.

Mesosoma. Mesosoma not depressed, its length 1.8× maximum height. Pronotal neck rather long, dorsally weakly convex, but without convex lobe and pronotal carina; side of pronotum with rather shallow, weakly curved and wide submedian oblique and sparsely crenulate furrow. Mesoscutum highly and roundly elevated above pronotum (lateral view), maximum width of mesoscutum 1.3× its length (dorsal view). Median lobe of mesoscutum (dorsal view) weakly protruding forwards, without anterolateral corners, distinctly convex anteriorly. Notauli rather narrow, deep, sparsely and finely crenulate. Prescutellar depression deep, long, with median carina, finely and irregularly sculptured, 0.5× as long as wide, 0.55× as long as scutellum. Scutellum convex, with fine lateral carinae, its basal width almost equal to median length. Subalar depression rather deep, wide, sparsely and coarsely striate. Precoxal sulcus rather deep, almost

straight, distinctly crenulate, running along anterior 0.6 of lower part of mesopleuron. Metanotal tooth (lateral view) rather long, wide, more or less pointed apically. Metapleural lobe rather long, more or less wide, rounded apically. Propodeum (lateral view) regularly convex-roundly slanted from base to apex, without lateral tubercles; propodeal spiracle small.

Wings. Fore wing 3.5× longer than its maximum width, 0.7× as long as body. Pterostigma 3.5× longer than wide. Radial vein (r) arising almost from middle of pterostigma, distance from base of pterostigma to radial vein (r) almost equal to distance from radial vein (r) to apex of pterostigma. Radial (marginal) cell not shortened. Metacarp (1-R1) 1.3× longer than pterostigma. First radial abscissa (r) 0.75× as long as maximum width of pterostigma. Second radial abscissa (3-SR) twice longer than first abscissa (r), 0.35× as long as the straight third abscissa (SR1), 0.7× as long as the trace of first radiomedial vein (2-SR). Trace of first radiomedial vein (2-SR) 2.2× longer than second radiomedial vein (r-m), 2.2× longer than recurrent vein (m-cu). Recurrent vein (m-cu) postfurcal. First medial abscissa (1-SR+M) almost straight. Discoidal (discal) cell 1.6× longer than wide. Nervulus (cu-a) almost interstitial, straight and subperpendicular. Mediocubital vein (M+CU1) almost straight. Parallel vein (CU1a) very weakly curved subbasally. Brachial (subdiscal) cell widely open distally, brachial vein (CU1b) absent. Hind wing with 5.5× longer than wide. First abscissa of costal vein (C+SC+R) 1.5× longer than second abscissa (1-SC+R); second abscissa (1-SC+R) strongly sclerotised. Last costal abscissa (SC+R) 0.75× as long as first (C+SC+R) and second (1-SC+R) abscissae combined. Radial vein (SR) very strongly desclerotised. Medial (basal) cell narrow, almost parallel-sided to weakly narrowed in apical half, its length 8.5× maximum width, ~ 0.3× length of wing. First abscissa of mediocubital vein (M+CU) almost as long as second abscissa (1-M). Recurrent vein (m-cu) unsclerotised, almost interstitial, straight, distinctly oblique toward base of wing.

Legs. Fore tibia with several slender spines arranged in narrow stripe. Hind coxa with basoventral tubercle, ~ 1.4× longer than its maximum width. Hind femur relatively narrow, without dorsal protuberance, 4.0× longer than wide. Hind tarsus 0.9× as long as hind tibia. Basitarsus not thickened, without ventral keel, 0.5× as long as second–fifth segments combined. Second tarsal segment 0.7× as long as basitarsus, 1.3× longer than fifth segment (without pretarsus).

Metasoma. Metasoma 0.9× as long as head and mesosoma combined, almost twice as long as its maximum width. First tergite with rather high and wide median area, with small dorsope, without spiracular tubercles; tergite strongly and almost linearly widened from anterior to posterior apex. Length of first tergite 0.85× its apical width, a little larger than length of propodeum; maximum width of tergite 2.5× its minimum width. Median length of second tergite 0.4× basal width of second tergite, 0.7× length of third tergite. Combined length of second and third tergites 0.9× basal width of second tergite, 0.7× their maximum width. Second suture distinct, distinctly curved laterally. Third tergite without sculptured transverse furrow. Ovipositor sheaths 0.8× as long as metasoma, 1.1× longer than mesosoma, 0.4× as long as body, 0.6× as long as fore wing.

Sculpture and pubescence. Vertex rather finely and densely transversely striate with additional rugulosity between striae; frons mostly finely and densely transversely striate. Face mainly smooth, rugose medially; temple finely striate above, but mostly smooth. Mesoscutum densely and rather finely granulate, with two carinae medioposteriorly. Scutellum finely granulate. Mesopleuron entirely finely

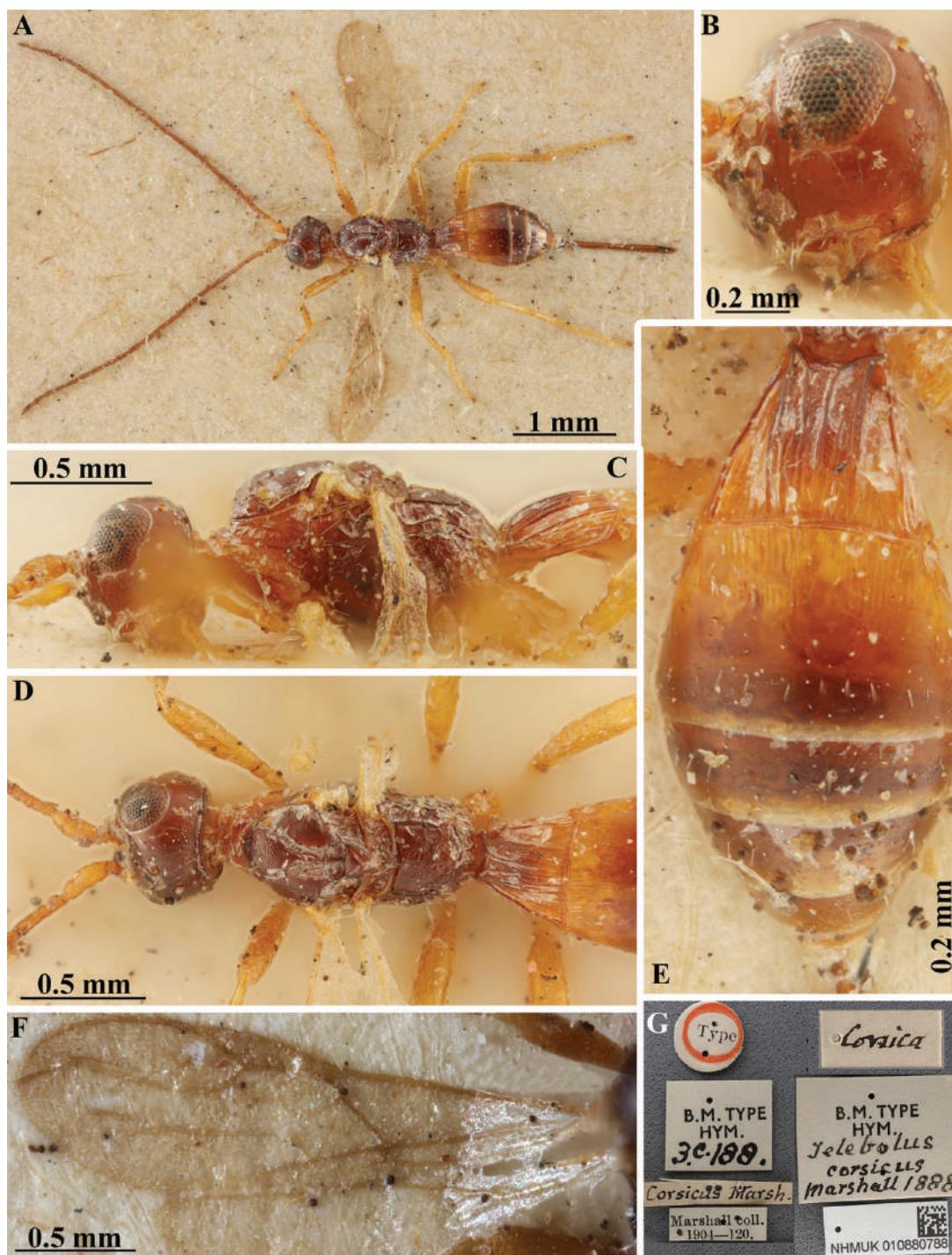


Figure 6. *Heterospilus corsicus* (Marshall, 1888) (female, holotype) **A** habitus, dorsal view **B** head, lateral view **C** head, mesosoma and base of metasoma, lateral view **D** head, mesosoma and base of metasoma, dorsal view **E** metasoma, dorsal view **F** wings **G** labels.

reticulate-granulate. Metapleuron entirely and rather distinctly rugose-reticulate. Propodeum with rather wide and finely granulate-coriaceous basolateral areas, distinctly delineated by carinae; areola indistinctly delineated by carinae; basal carina relatively long, 0.8× as long as anterior fork of areola; posterior 0.7 of propodeum coarsely and irregularly rugose-reticulate. Hind coxa densely granulate, coarsely transversely striate dorsally. Hind femur finely coriaceous. First tergite with rather distinct and convergent posteriorly dorsal carinae, distinctly longitudinally striate,

with very fine, partly indistinct ground sculpture. Second tergite entirely densely and distinctly longitudinally striate. Remaining tergites smooth. Vertex partly with rather sparse and relatively long setae, almost glabrous medially. Mesoscutum with sparse, rather long and semi-erect pale setae arranged almost in one line along notauli and marginally, all lobes widely glabrous medially. Metapleuron widely glabrous medially. Hind tibia dorsally with relatively long, sparse and semi-erect setae; length of these setae 0.5–0.7× maximum width of hind tibia.

Colour. Body dark reddish brown, almost black; pronotum pale reddish brown; first (except its dark medio-anterior half), second and anterior half of third metasomal tergites pale brown with reddish tint. Antenna dark reddish brown, paler basally. Palpi yellow. Legs pale brown. Ovipositor sheath almost black. Fore wing faintly infusate. Pterostigma yellow.

Distribution. France (Corsica), Italy, Hungary, Romania, Bulgaria, Moldova, Crimea (Yu et al. 2016).

Remarks. The records of this species for Lithuania, Kazakhstan, Korea, and the Russian Far East by Belokobylskij and Tobias (1986) were erroneous due to the unclear understanding of this species before the study of the holotype.

Host. Unknown.

Key to the Western Palaearctic species of *Heterospilus* with distinctly sculptured vertex

- 1 Metasoma behind third tergite striate anteriorly on fourth or fourth and fifth tergites **2**
- Metasoma entirely smooth behind third tergite; often third tergite also smooth **6**
- 2 Fore wing strongly shortened, reaching at maximum to middle of metasoma; wing venation in distal half of fore wing strongly reduced. [Europe (rarely), Turkey, Iran, Mongolia] **3**
- Fore wing not shortened, complete, prolonged behind posterior end of metasoma; wing venation in distal half of fore wing complete as usual for *Heterospilus* **3**
- 3 First metasomal tergite relatively long, its length not less than posterior width. Often only fourth tergite striate anteriorly. Vertex often less distinctly striate. Body slender and slim **4**
- First metasomal tergite short, its length distinctly shorter than posterior width. Fourth and fifth tergites always striate anteriorly. Vertex distinctly and coarsely transversely striate. Body robust **5**
- 4 Second tergite shorter, its medial length ~ 0.3× anterior width. Sculpture of first two tergites distinctly striate, less infilled with rugosity. Ovipositor projecting just more than 0.6× length of metasoma, just more than 1.1× length of hind tibia. Body predominantly reddish brown. [Europe, Russia (widely), western and central Asia, China, Korea, Japan] ***H. leptosoma* Fischer, 1960**
- Second tergite longer, its medial length ~ 0.4× anterior width. Sculpture of first two tergites less regular, more rugulose. Ovipositor shorter, projecting 0.3–0.5× length of metasoma, 0.7–1.1× length of hind tibia. Body usually extensively dark. [UK, Sweden, China (?)] ***H. fuscexilis* M. Shaw, 1997**

- 5 Ovipositor sheaths distinctly shorter than metasoma, 0.4–0.6× as long as metasoma. Body often predominantly brownish yellow or light reddish brown. [Holarctic]
***H. cephi* Rohwer, 1925 (*H. testaceus* Telenga, 1941; *H. rubicundus* Fischer, 1960; *Rhaconotus ollivieri* (Giraud) var. *flava* Fahringer 1931, syn. nov.)**
- Ovipositor sheaths slightly shorter than or almost equal to metasoma, 0.7–1.0× as long as metasoma. Body often predominantly reddish brown to light reddish brown with often dark propodeum and first metasomal tergite. [Europe, Russia (widely), Turkey, Israel, Iran, Kazakhstan, Mongolia, China, Korea, Japan].....
 ***H. tauricus* Telenga, 1941 (*H. graeffei* Fischer, 1960)**
- 6 Second metasomal tergite striate only on its anterior one-third or quarter. Suture between second and third tergites absent. Mesopleuron smooth over wide median area. [Portugal (Madeira), Israel, Russia (Crimea)].....
 ***H. divisus* (Wollaston, 1858)**
- Second metasomal tergite striate or striate-rugulose over anterior fourth-fifths or entirely. Suture between second and third tergites present but sometimes rather weak. Mesopleuron usually rugose-reticulate over wide median area **7**
- 7 Head behind eyes (dorsal view) weakly convex in anterior half and roundly narrowed in posterior half; transverse diameter of eye 1.1–1.3× longer than temple. Mesosoma 1.5–1.6× longer than maximum height. Medial lobe of mesoscutum without or with indistinct anterolateral corners. Radial vein (r) of fore wing arising before middle of pterostigma. [Spain, Italy, Croatia, Hungary, Russia (Crimea)] ***H. sicanus* (Marshall, 1888) (*Atoreuteus ceballosi* Docavo Alberti, 1960, syn. nov.)**
- Head behind eyes (dorsal view) evenly and rather distinctly roundly narrowed; transverse diameter of eye 1.5–2.0× longer than temple. Mesosoma 1.8–2.0× longer than maximum height. Medial lobe of mesoscutum usually with distinct pointed anterolateral corners. Radial vein (r) of fore wing arising from or slightly behind middle of pterostigma..... **8**
- 8 Malar space 0.5–0.6× height of eye, 1.2–1.3× basal width of mandible. Occipital carina ventrally joining hypostomal carina. Precoxal sulcus distinctly crenulate. Second segment of hind tarsus 1.3–1.5× longer than fifth segment (without pretarsus). Third metasomal tergite without transverse furrow. Mesopleuron entirely reticulate-granulate. Basal carina of propodeum relatively long. Pterostigma yellow or light brown. [France (Corsica), Italy, Hungary, Romania, Bulgaria, Moldova, Ukraine] ***H. corsicus* (Marshall, 1888) (*Caenophanes cingulatus* Szépligeti, 1900)**
- Malar space 0.4× height of eye, equal to basal width of mandible. Occipital carina obliterated below and not joining hypostomal carina ventrally. Precoxal sulcus smooth. Second segment of hind tarsus almost 2.0× longer than fifth segment (without pretarsus). Third metasomal tergite with crenulate transverse furrow in anterior one-third. Mesopleuron smooth over lower three-fifths. Basal carina of propodeum very short. Pterostigma brown. [Spain] ***H. marchi* (Docavo Albert, 1960)**

Discussion

The species *Dendrosoter sicanus* Marshall, 1888 and *Telebolus corsicus* Marshall, 1888 both actually belonging to the genus *Heterospilus*, were described in the same year and in the same book (Marshall 1888) and have never subsequently been redescribed or compared with each other. The diagnostic characters of these species were relatively badly designated and the reliable determination of these taxa as well as stable differences between the species subsequently caused certain difficulties. This study with illustrated redescrptions of the type material, together with the preparation of a key for determination of the European *Heterospilus* species with a sculptured vertex, should help to avoid errors in their identification.

The holotype (female) of *Atoreuteus ceballosi* Docavo Albert, 1960, studied by the first co-author in MNCN (Madrid, Spain), is morphologically very similar to *H. sicanus* (Marshall, 1888), which allowed us to synonymise the first name under the second as a new synonym. Also in the same Museum (MNCN), the holotype of *Atoreuteus* (= *Heterospilus*) *marchi* Docavo Albert, 1960, described from Spain (female, with labels "Barcelona, 27.V.1896", "♀", "*Atoreuteus marchi* Docavo n. sp.", "Holotip", "*Heterospilus* ? *tauricus* Tel., det. Papp J., 1983", "MNCN Cat. Typos N 11.489"), was examined, which helped us to evaluate the status of this species as closely related to *H. corsicus* (Marshall, 1888). The first co-author has also studied the single specimen (female) in NHMW (Wien, Austria) of the form *Hormiopterus* (= *Rhaconotus*) *ollivieri* Giraud var. *flava* Fahringer 1931 (Fahringer 1931; Shenefelt and Marsh 1976) (with labels: "*Hormiopterus ollivieri* (sic!) Gr. var *flava* m." (handwriting by Fahringer), "*ollivieri* (sic!) Fer. (sic!), det. Fahringer", but without any geographic information), which turned out to be a new junior synonym of *Heterospilus cephi* Rohwer, 1925.

The discovery of *H. sicanus* in the frass, holes, and tunnels of rare books damaged by *Gastrallus pubens* Fairmaire (Coleoptera: Ptinidae), with its illustrated redescription and updated diagnosis, and its comparison with the morphologically similar *H. corsicus* sheds light on these rare and barely studied doryctine species. The inclusion of digital photographs and the key for determination of the Western Palaearctic species of *Heterospilus* with distinctly sculptured vertex have also helped to improve the precise species identification of these taxa. This accurate identification of parasitoids is crucial for effective and sustainable pest management programmes. In fact, *Heterospilus sicanus* could be a potential biological control agent against *G. pubens*, which is an emerging threat to librarians and archivists in Italy and across Europe given the destructive larval activity of the beetles, which causes serious damages to books, especially ancient.

Acknowledgments

The authors are very thankful to Dr Alejandro Zaldívar-Riverón (México City, México), Dr Konstantin G. Samartsev (St Petersburg, Russia) and Dr Avunjikkattu Parambil Ranjith (Bangalore, India) for their useful suggestions and comments of this manuscript. The authors also would express their gratitude to Dr. Mark Shaw, Department of Natural Sciences, National Museums of Scotland, Edinburgh, UK, for his invaluable assistance in establishing connections

between our the research groups that collaborated to the study. The authors are thankful to Professor Mario Varvaro, Delegate appointed by the Rector to the University of Palermo Historical Archive for his precious support.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was performed as part of the Russian State Research Project No. 122031100272–3 for SAB.

Author contributions

Conceptualization: EP, CJ, GC, SS, SAB, SG, GRRB. Data curation: SAB. Investigation: GC, GRRB, SAB, CJ, SG, SS, EP. Methodology: EP, SS, SG, GRRB, GC, SAB. Supervision: SS, CJ. Writing - original draft: GC, SAB, SG. Writing - review and editing: GRRB, SS, CJ, EP.

Author ORCIDs

Sergey A. Belokobylskij  <https://orcid.org/0000-0002-3646-3459>

Salvatore Guarino  <https://orcid.org/0000-0001-6670-3997>

Sara Savoldelli  <https://orcid.org/0000-0003-2689-4252>

Costanza Jucker  <https://orcid.org/0000-0001-5052-3705>

Ezio Peri  <https://orcid.org/0000-0002-1095-7258>

Gavin R. Broad  <https://orcid.org/0000-0001-7223-5333>

Giuliano Cerasa  <https://orcid.org/0000-0003-1837-4302>

Data availability

All of the data that support the findings of this study are available in the main text.

References

- Belokobylskij SA (2002) Two new Oriental genera of Doryctinae (Hymenoptera, Braconidae) from termite nests. *Journal of Natural History* 36(8): 953–962. <https://doi.org/10.1080/00222930110048927>
- Belokobylskij SA, Ku D-S (2021) Review of species of the genus *Heterospilus* Haliday, 1836 (Hymenoptera, Braconidae, Doryctinae) from the Korean Peninsula. *ZooKeys* 1079: 35–88. <https://doi.org/10.3897/zookeys.1079.73701>
- Belokobylskij SA, Maetô K (2009) Doryctinae (Hymenoptera: Braconidae) of Japan. *Natura optima dux Foundation*, Warsaw, Poland, 806 pp.
- Belokobylskij SA, Tobias VI (1986) Subfam. Doryctinae. In: Medvedev GS (Ed.) *Keys to insects of the USSR European part*. Vol. 3. Hymenoptera. Pt. 4. Nauka, Leningrad, 21–72. [In Russian]
- Belokobylskij SA, Iqbal M, Austin AD (2004a) Systematics, distribution and diversity of the Australasian doryctine wasps (Hymenoptera, Braconidae, Doryctinae). *Records of the South Australian Museum. Monograph Series* 8: 1–150.

- Belokobylskij SA, Zaldívar-Riverón A, Quicke DLJ (2004b) Phylogeny of the genera of the parasitic wasps subfamily Doryctinae (Hymenoptera: Braconidae) based on morphological evidence. *Zoological Journal of the Linnean Society* 142: 369–404. <https://doi.org/10.1111/j.1096-3642.2004.00133.x>
- Brajkovic MM (1989) Knowledge of the Braconidae (Hymenoptera) fauna in Yugoslavia. *Glasnik Prirodnjackog Muzeja I Beogradu, Seriya B Bioloske Nauke* B43/44: 127–138. [In Serbian with English summary]
- Cabrera BJ, Marsh PM, Lewis VR, Seybold SJ (2002) A new species of *Heterospilus* (Hymenoptera: Braconidae) associated with the deathwatch beetle, *Hemicoelus gibbicollis* (LeConte) (Coleoptera: Anobiidae). *The Pan-Pacific Entomologist* 78: 7–16.
- Docavo Alberti I (1960) Especies nuevas de Braconinae de España (Hym. Braconidae). *Eos. Revista Espanola de Entomologia* 36: 25–39.
- Fahringer J (1931) Palaearktische Region. Bd II. Braconinae (Cyclostomi Aut.). Cheloniinae (Cryptogastres Aut.). *Opuscula braconologica*. Bd III. Lieferung 3: 163–242.
- Falco Gari JV, Moreno J, Jiménez R (1993) Datos sobre Ciclostominos españoles: 2. Doryctinae (Hymenoptera: Braconidae). *Boletín de la Asociación Espanola de Entomologia* 17(2): 65–75.
- Ghahari H, Belokobylskij SA, Gadallah NS, Quicke DLJ, Shaw SR (2022) Subfamily Doryctinae Foerster, 1863. In: Gadallah NS, Ghahari H, Shaw S R (Eds) *Braconidae of the Middle East (Hymenoptera)*, 294–312. <https://doi.org/10.1016/B978-0-323-96099-1.00029-7>
- Hadley A (2011) CombineZP-Free image stacking software for depth of field correction. <http://www.hadleyweb.pwp.blueyonder.co.uk/CZM/combinezm.htm> [Access in 21.IX 2011]
- Kenis M, Wermelinger B, Grégoire JC (2004) Research on parasitoids and predators of Scolytidae – a review. In: Lieutier F, Day KR, Battisti A, Grégoire JC, Evans HF (Eds) *Bark and wood boring insects in living trees in Europe, a synthesis*. Kluwer Academic Publishers, Dordrecht (Germany), 237–290. https://doi.org/10.1007/1-4020-2241-7_11
- Kistner DH, Jacobson RJ, Elliot DE (2000) Some interesting Braconidae that live with termites and their behavior (Hymenoptera; Isoptera: Termitidae, Nasutitermitinae). *Sociobiology* 36: 257–264.
- Mantero G (1904) Res Ligusticae XXXIII. Materiali per un catalogo degli Imenotteri Liguri. Parte III, Braconidi. *Annali del Museo Civico di Storia Naturale di Genova* 41: 14–51.
- Marsh PM (1982) Two new species of *Heterospilus* (Hymenoptera: Braconidae) from Mexico being introduced against the cotton boll weevil, *Anthonomus grandis* (Coleoptera: Curculionidae). *Proceedings of the Entomological Society of Washington* 84: 849–854.
- Marsh PM (1993) Descriptions of new Western Hemisphere genera of the subfamily Doryctinae (Hymenoptera: Braconidae). *Contributions of the American Entomological Institute* 28: 1–58.
- Marsh PM (2002) The Doryctinae of Costa Rica (excluding the genus *Heterospilus*). *Memoirs of the American Entomological Institute* 70: 1–319.
- Marsh PM, Melo GAR (1999) Biology and systematics of New World *Heterospilus* (Hymenoptera: Braconidae) attacking Pemphredoninae (Hymenoptera: Sphecidae). *Journal of Hymenoptera Research* 8: 13–22.
- Marsh PM, Wild AL, Whitfield JB (2013) The Doryctinae (Braconidae) of Costa Rica: Genera and species of the tribe Heterospilini. *ZooKeys* 347: 1–474. <https://doi.org/10.3897/zookeys.347.6002>

- Marshall TA (1888) Les Braconides. In: Andre E (Ed.) Species des Hymenopteres d'Europe et d'Algerie Tome 4, 609 pp.
- Marshall TA (1897) Les Braconides (3e partie-Supplément). In: Andre E (Ed.) Species des Hyméneptères d'Europe & d'Algérie Tome 5^{bis}: 373 + 82 pp.
- Papp J (1977) Contributions to the Braconid fauna of Yugoslavia. III. Folia Entomologica Hungarica 30: 105–117.
- Papp J (1984) Contributions to the braconid fauna of Hungary, V. Doryctinae. (Hymenoptera: Braconidae). Folia Entomologica Hungarica 45: 173–185.
- Ramírez BW, Marsh PM (1996) A review of the genus *Psenobolus* (Hymenoptera: Braconidae) from Costa Rica, an inquiline fig wasp with brachypterous males, with descriptions of two new species. Journal of Hymenoptera Research 5: 64–72.
- Shaw SR (1995) Braconidae. In: Hanson P, Gauld I (Eds) The Hymenoptera of Costa Rica. Oxford University Press, UK, 431–463.
- Shaw SR, Edgerly JS (1985) A new braconid genus (Hymenoptera) parasitising web-spinners (Embiidina) in Trinidad. Psyche (Cambridge, Massachusetts) 92(4): 505–512. <https://doi.org/10.1155/1985/54285>
- Shenefelt RD, Marsh PM (1976) Braconidae 9. Doryctinae. In: van der Vecht J, Shenefelt RD (Eds) Hymenopterorum Catalogus. Pars 13, Dr W. Junk, Gravenhage, 1263–1424.
- Szépliget G (1900) Neue Braconiden aus Ungarn. Természetrázi Füzetek 23: 213–219.
- Tobias VI (1971) A review of the Braconidae (Hymenoptera) of the USSR. Trudy Vsesoyuznogo Entomologicheskogo Obshchestva 54: 156–268. [In Russian] [English translation by Amerind, 1975. New Delhi]
- Tobias VI (1976) Braconids of Caucasus (Hymenoptera, Braconidae). Nauka, Leningrad, 286 pp. [In Russian]
- van Achterberg C (1993) Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). Zoölogische Verhandelingen 283: 1–189.
- Wegensteiner R, Wermelinger B, Herrmann M (2015) Natural enemies of bark beetles: predators, parasitoids, pathogens, and nematodes. In: Vega FE, Hofstetter RW (Eds) Bark beetles: biology and ecology of native and invasive species, Elsevier Academic Press, Cambridge, UK, 247–304. <https://doi.org/10.1016/B978-0-12-4171156-5.00007-1>
- Wharton RA (1993) Bionomics of the Braconidae. Annual Review of Entomology 38(1): 121–143. <https://doi.org/10.1146/annurev.en.38.010193.001005>
- Wharton RA, Hanson PE (2005) Gall wasps in the family Braconidae (Hymenoptera). In: Raman A, Schaefer WC, Whithers TM (Eds) Biology, ecology, and evolution of gall-inducing arthropods. Enfield, NH, USA, 495–505.
- Yu DS, van Achterberg C, Horstmann K (2016) Taxapad 2016. Ichneumonoidea 2015. Nepean, Ottawa, Ontario. [Database on flash-drive]
- Zaldívar-Riverón A, Belokobylskij SA, León-Regagnon V, Martínez JJ, Briceño R, Quicke DLJ (2007) A single origin of gall association in a group of parasitic wasps with disparate morphologies. Molecular Phylogenetics and Evolution 44(3): 981–992. <https://doi.org/10.1016/j.ympev.2007.05.016>
- Zaldívar-Riverón A, Martínez JJ, Belokobylskij SA, Pedraza-Lara C, Shaw SR, Hanson PE, Carela-Hernandez F (2014) Systematics and evolution of gall formation in the plant-associated genera of the wasp subfamily Doryctinae (Hymenoptera: Braconidae). Systematic Entomology 39(4): 633–659. <https://doi.org/10.1111/syen.12078>