



Redescription of three rare species of *Dasygoda* bees with first description of *D. iberica* and *D. tibialis* females (Hymenoptera, Apoidea, Melittidae)

VLADIMIR G. RADCHENKO¹, GUILLAUME GHISBAIN² & DENIS MICHEZ²

¹Institute for Evolutionary Ecology of the National Academy of Sciences of Ukraine, acad. Lebedev, 37, Kiev 03143, Ukraine.

E-mail: rvg@nas.gov.ua

²Laboratory of Zoology, Institute of Biosciences, University of Mons, Place du Parc 23, B-7000 Mons, Belgium.

E-mail: guillaume.ghisbain@umons.ac.be; denis.michez@umons.ac.be

Abstract

Dasygoda bees are host-specialized solitary species distributed in the Palaearctic Region. In the framework of a global revision of this genus, comprehensive descriptions of three rare species (*D. tibialis* Morawitz, *D. vulpecula* Lebedev and *D. iberica* Warncke) are presented. The detailed morphology of the *D. tibialis* male and both sexes of *D. vulpecula* are given for the first time after a very partial original description. The females of *D. tibialis* and *D. iberica* are described for the first time and additional morphological characters of the male of *D. iberica* are provided. The lectotype of *Dasygoda tibialis* is designated. Host-plants and new localities are also presented.

Key words: Palaearctic Region, taxonomy, host-plant, *Dasygoda vulpecula*

Introduction

The Palaearctic genus *Dasygoda* Latreille, 1802 is one of the most generalized groups of bees (Radchenko 1996; Radchenko & Pesenko 1996; Michener 2007). They are remarkable in their morphology, specifically the well-developed scopae on the hind legs of the females. This genus is relatively diverse, including 39 valid species with 33 species known from both sexes (Michez *et al.* 2004a, b; Michez 2005; Michez & Pauly 2012; Radchenko 2016, 2017). It shows significant sexual dimorphism, which has led to much confusion, as in many cases the males and females of the same species were described under different names. *Dasygoda* species are usually better differentiated in the male sex due to the significant differences seen in the structure of the last abdominal sterna and genitalia. Consequently, some species were described only from males.

Most *Dasygoda* species are strictly specialized to certain groups of plants (e.g., Asteraceae, Cistaceae, and Dipsacaceae) and many species are very rare with a local distribution (Michez *et al.* 2008). In this article, three rare and localized species are redescribed along with designation of *D. tibialis* lectotype and the first description of its female. The first description of the female of *D. iberica* as well as new data on both sexes of *D. vulpecula* are also provided. Among these three species, only one, *Dasygoda iberica*, had a clear subgeneric association (i.e. belonging to the subgenus *Microdasygoda*). The subgeneric status of the two other species remained unclear, since the two existing type specimens of *D. tibialis* were not further investigated after their description by F. Morawitz in 1880, and since all the type material of *D. vulpecula* was probably completely lost with no additional material. We associate for the first time these two species with one of the subgenera (*Dasygoda sensu stricto* and *Megadasygoda*, respectively) considered by Michez *et al.* (2004b).

Material and methods

The specimens examined during this study are deposited in the following collections: Oberösterreichisches Landesmuseum, Linz, Austria (OLL); Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (ZISP);

Laboratory of Zoology, Institute of Biosciences, University of Mons, Belgium (UMONS); American Museum of Natural History, New York, USA (AMNH).

The following abbreviations (after Michener 2007) were used for morphological structures: T1, T2, etc. = first, second, etc., metasomal tergum; S1, S2, etc. = first, second, etc., metasomal sternum. L = length; W = width.

The integument and setae ultrastructures were studied using scanning electron microscopy (JEOL JSM-6100 and JCM 6000) using the software Semafore (JEOL, Sollentuna, Sweden). Color photographs were made using a Canon Mark-II 5D and Canon EOS 5DS R (Canon Inc., Tokyo, Japan) cameras attached to Leica M205C stereomicroscope (Leica Microsystems, Wetzlar, Germany) with Leica LED5000 HDI illuminator under Helicon Remote 3.9.7.w software. Photographs were combined into single image using Helicon Focus 6.8.0 Pro (Helicon Soft Ltd, Kharkiv, Ukraine) automontage software. Quick-Photo Micro v2.3 (PROMICRA, s. r. o., Czech Republic) software was used for measurements. Pollen grains taken from the bee bodies were examined under SEM and upright light microscope Olympus BX51 (Olympus Corp., Tokyo, Japan). All images were prepared in the Institute for Evolutionary Ecology of the NAS of Ukraine (Kiev) except the drawing of hind tibia of *D. vulpecula* [which was copied from Lebedev (1929: 270, Fig. 1)] and 4 SEM pictures of S6–S8 and the hind tibia of *D. tibialis* male (from UMONS).

Results

Dasyпода (Microdasypoda) iberica Warncke, 1973

This species was very briefly described from only two males (Warncke 1973: 119, Fig. 33 on p. 105) collected in Spain (type material stored in OLL, however Blank & Kraus 1994 mentioned three paratypes in the Warncke collection). The females remained unknown prior to the present study. A more detailed description of the males *D. iberica* was given later by Ornosá & Ortiz-Sánchez (2004: 341–342), but these authors also did not pay attention to some essential features (e.g., the presence a small tooth-like prong on the lateral margins of S7; dorso-apical part of S8 has two separated semicircular outgrowths; the presence of longitudinal keel in the middle of T7; peculiarities of the galea and the scutum surface structure, etc.). In addition, we provide the first description of the females of *D. iberica*. These female specimens were collected simultaneously with the males of this species and superficially look similar to them. Both sexes have a similar size and comparable punctures of the body surface, especially on the head and on the scutum; the tibiae of all legs are convex outside and thickened towards the distal part and the tibial spurs are light yellow, almost white; the body pubescence has a similar color, including the yellow-golden hairs on the inner surface of all basitarsi; the T3–T5 on the marginal parts show bands of silver-white hairs and the S3–S5 have yellow-white ones; and many other features described below are similar.

This species shows all the apomorphies of the subgenus *Microdasypoda* (e.g., male with simple gonostylus and the S7 without projection, see discussion) and is similar to *D. cingulata* in its narrow, long penis valves. *D. iberica* can be easily recognized by the inner tooth of the male genitalia (Fig. 25). Moreover, unlike most of other melittids, the tarsal claws of all legs of males and especially females are slightly swollen.

Description. Male (Figs 1, 2). Length: 8.7–10.5 mm. Body black. **Head** (Fig. 3) W = 2.7–2.9 mm, L = 2.3–2.4 mm. Face densely punctured with rough punctures, on clypeus such punctures almost merge, but they poorly visible through long dense pubescence. Cuticle at front and sides of simple eyes shows wide smooth, shiny, non-punctured areas (Fig. 4). Vertex pubescent with relatively short sparse black-brown hair intermixed with long silver-white in middle. Face densely covered with long silver-white hair, except inner margin of parocular area along compound eyes black-brown. Occiput and inner part of genal area show very long curved silver-white hairs intermixed with shorter brown near compound eyes. Malar space (Fig. 5) narrow (L = 0.1 mm), 4.5 times shorter than basal mandibular width. Mandibles black, apical parts red. External basal part of mandibles with short silver-white pubescence and single long hair. Ventral part of mandibles with long silver-white hair, becoming yellow-brown at distal edge. Galea densely covered with flattened oblong tubercles, and apical part roughly wrinkly punctured (Fig. 6). Scape with thick long silver-white hair in front and distal margin strongly intermixed with black hair. Flagellomeres 1–10 (Fig. 7) approximately of same length, except for 3rd, which 8 % longer than others, and 11th which about 25 % longer. 2–10th flagellomeres slightly curved in dorso-ventral side, convexly above and flattened below, densely covered with short gray setae.



FIGURE 1–12. Male of *Dasypoda iberica*: 1—Male in dorsal view; 2—Male in lateral view; 3—Head in frontal view; 4—Vertex; 5—Malar area; 6—Apex of galea; 7—Flagellum; 8—Scutum; 9—Propodeum; 10—Hind tibia and basitarsus; 11—Metasoma in dorsal view; 12—Metasoma in ventral view.

Mesosoma. W (between tegulae) = 2.8 mm, cuticle clearly punctured, distance between points equal to 1–2 point diameters, and center of mesonotum with more scattered punctation (3–4 point diameters) (Fig. 8). Median area of propodeum ribby shagreened in form of shallow fine mesh (Fig. 9). Ventral and lateral parts of thorax with sparse long erected silver-white hairs. Sides of scutum densely punctured with same silver-white hair, mixed with dark brown. Middle of scutum smoothed, very shiny between points, covered with very short sparse dark brown hairs. Tegulae black in front, and translucent yellow-brown at back and lateral sides, transparent along edge, not punctured. Legs black with long, silvery-white hairs, especially long and bent at profemur and protrochanter. Hind tibia convexed outside and thickened towards distal part (Fig. 10). Inner surface of all basitarsi covered with short dense adjacent yellow-ginger hair. Last tarsi slightly lighter brown, with single yellow-golden hairs on top; 5th tarsus on apex before tarsal claws lighter, yellow. Tibial spurs of hind legs light yellow, almost white. Wings transparent, very slightly shaded at top.



FIGURE 13–20. Sterna and genitalia of *Dasypoda iberica* male: 13—Sternum 6; 14—Sternum 7; 15—Apex of sternum 7; 16—Sternum 8; 17—Apex of sternum 8; 18–20—Genitalia. (13–16, 19—ventral view; 17–18—dorsal view; 20—dorso-ventral view, rotated 90 degrees).

Metasoma (Figs 11, 12) short (L = 4.2–5.0 mm, W = 3.1–3.6 mm), ovoid, black. Marginal part of all terga widely enlightened, light yellow, colorless at top, markedly depressed at sides. Horizontal part of T1 very short and limited almost only by depressed enlightened marginal edge. Basal part of terga shagreened, with very short evenly

scattered brown hairs. T4–T7 with coarse wrinkled punctures in middle before marginal part. Marginal parts of T3–T5 with narrow bands of short silver-white hairs, interrupted on T3 in middle. Terga also covered with sparse long silvery-white hairs (especially long on T1—their length equal to hair length on sides of propodeum), erected on sides and semi-adjacent in middle. T7 with longitudinal keel in middle, which poorly visible through semi-adjacent long silvery-white hair covering entire segment. Basal parts of S2–S4 without clear visible punctures, shagreened, covered with very short sparse yellow-brown hairs and sporadic long silver-white hairs. Apex of marginal part semi-transparent, thinly transversely striated and with very narrow bands of short white hairs interrupted in middle. Narrow space in front of apical part smoothed, shiny polished with sparse long hair and denser and longer ones on sides. S5 with very short white hair on basal part and long curved semi-erected ones on marginal part. S6 on top with two bunches of dense silver-white hair divided by smoothed non-pubescent triangular space (Fig. 13). Marginal part of S7 with small tooth-like prong on sides, without long projections (Figs 14, 15). S8 without spinous processes on sides (Fig. 16), its dorso-apical part with two separated semicircular outgrowths (Fig. 17). Genitalia (Figs 18–20, 21–24) with narrow long penis valves, and inner side of gonostyles with long, spiky protuberance (Fig. 25).

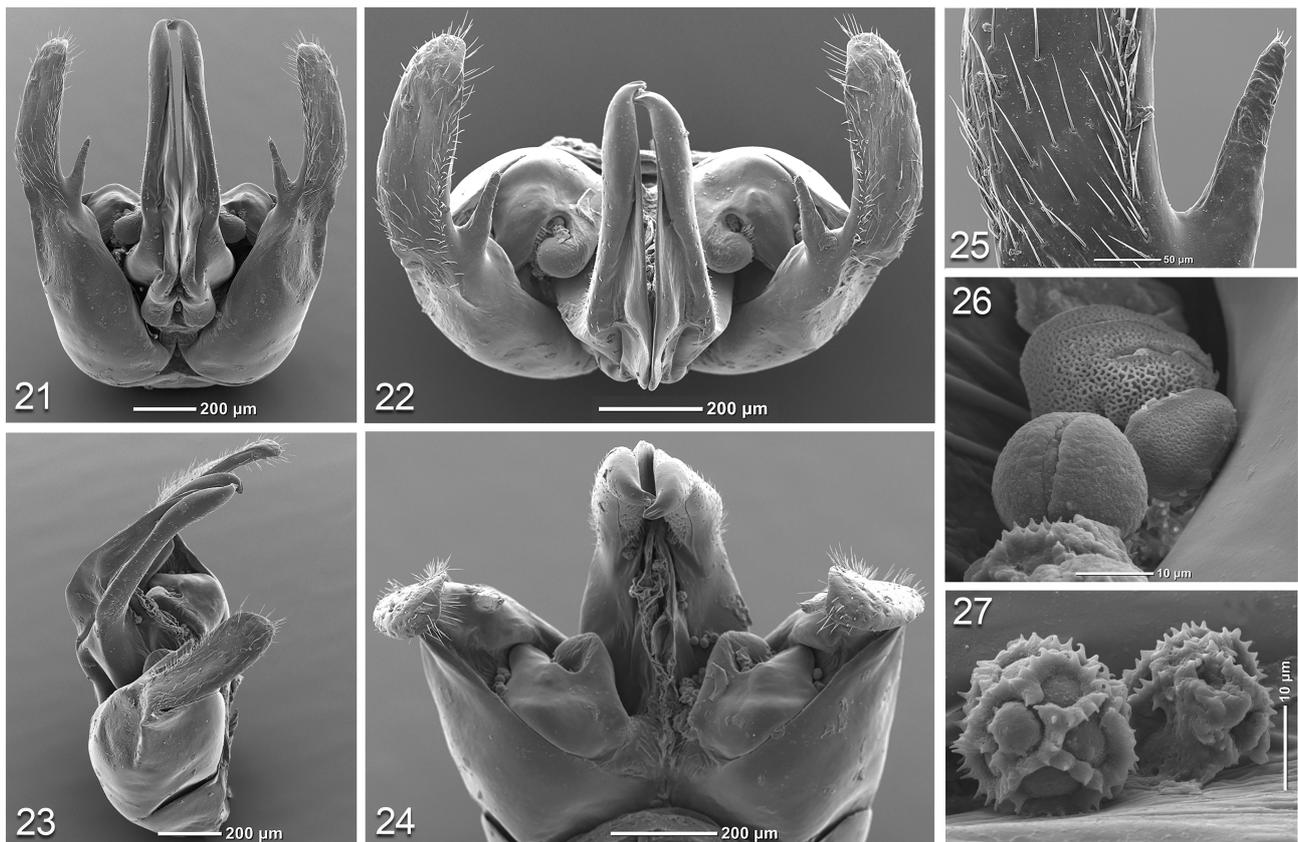


FIGURE 21–27. *Dasyopoda iberica* male genitalia: 21–24—General view of genitalia; 25—Base of gonostylus with protuberance; 26–27—Pollen grains on the genitalia.

Female (Figs 28, 29) **first description.** Length: 11–11.5 mm. Body black. **Head** (Fig. 30) W = 3.1 mm, L = 2.5 mm. Clypeus (Fig. 31) smoothed, polished and not punctured in its median part, while sides and top with scattered points (distance between points equal to 2–5 point diameters), each with one semi-adjacent silver-white hair. Central part of face covered by erect and semi-erect silver-white hairs mixed with sparse black. Parocular area near compound eyes, vertex and upper part of frons with black-brown hair. Malar space (Fig. 32) short (L = 0.08 mm), 7× shorter than mandible width at base. Scape with dense long silver-white hair in front of basal part, these hairs mixed black ones on apex part. Antennae (Fig. 33) slightly thickened towards apex. 1th flagellomer almost twice longer than 2nd. 3rd flagellomer approximately as long as 2nd, and their width equal to length. 4th flagellomer 15 % shorter than 3rd. 5–9th flagellomeres 20–25 % shorter than 3rd, and their width 1.4–1.5× greater than their length. 3–10th flagellomeres cylindrical, marginal parts of their ventral side enlightened, yellow-brown. All flagellomeres evenly covered with very short gray setae. Basal part of mandibles black, apical third red. Galea with same surface as described in males (i.e. densely covered with flattened oblong tubercles and roughly wrinkly punctured on apical

part). Upper distal part of labrum with fringe of intermixed silver and golden hairs, lower part with fringe of dense and slightly darker goldish hairs, longer than ones of upper part.

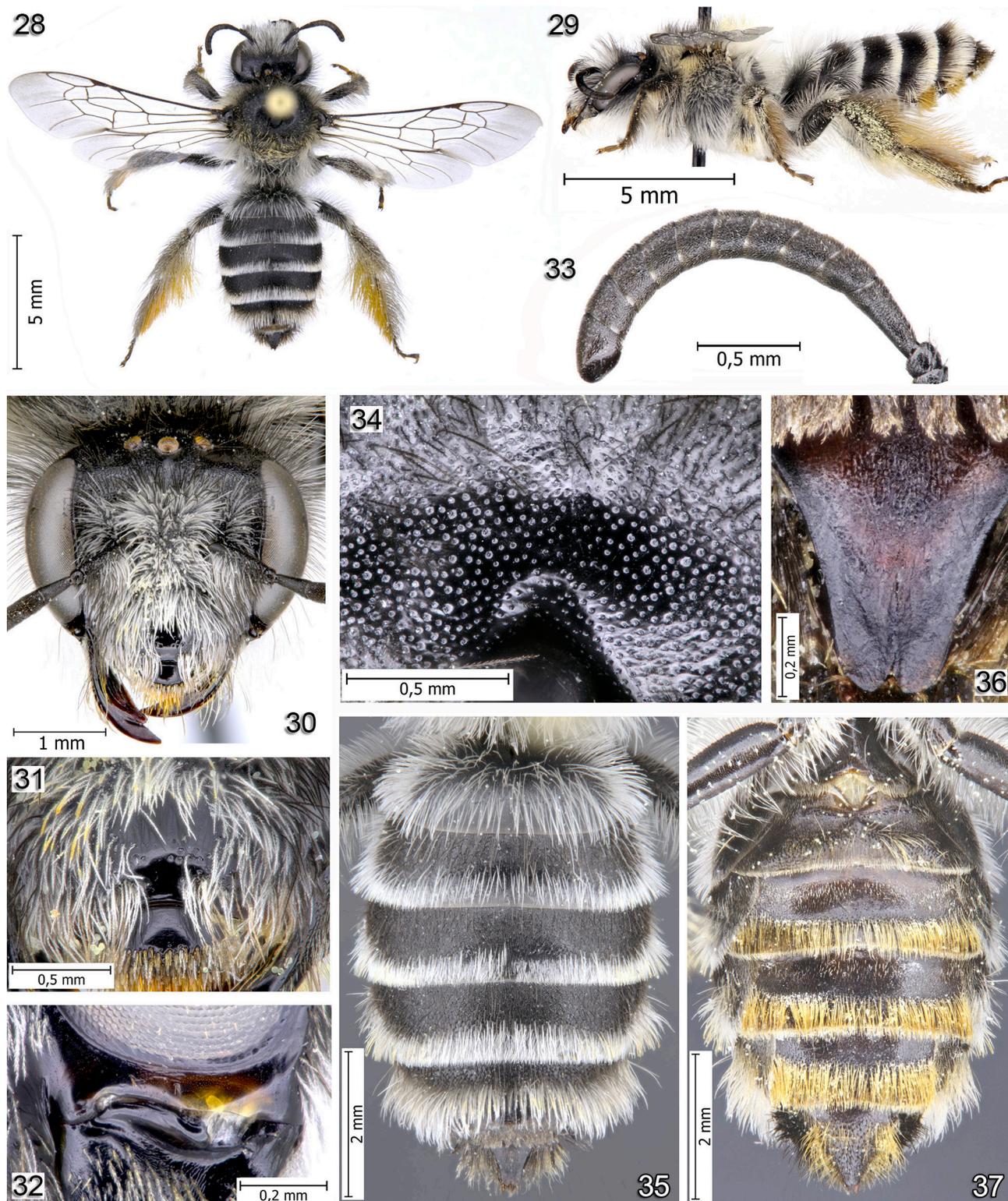


FIGURE 28–37. Female of *Dasyпода iberica*: 28—Female in dorsal view; 29—Female in lateral view; 30—Head in frontal view; 31—Clypeus and labrum; 32—Malar area; 33—Flagellum; 34—Scutum; 35—Metasoma, dorsal view; 36—Pygidial plate; 37—Metasoma, ventral view.

Mesosoma. W (between tegulae) = 2.9 mm. Scutum smoothed, shiny, densely punctured on sides, distance between points equal to their diameter, punctures more sparse in the center (i.e. distances between punctures about 2–3× as long as diameter of 1 puncture) (Fig. 34). Mesosoma mostly covered with long erect silvery-white hair

intermixed with short brown-black ones around scutum edges. Central part of scutum barely pubescent with very sparse short dark brown hair. Apical half of most hair on scutellum with light yellow-ginger color. Propodeum coarsely shagreened, slightly shiny, not pubescent. Tegulae black, strongly shiny, and punctuation present only at its forefront, rest of surface being smooth, not punctured. Wings transparent, almost not darkened. Ventral part of trochanters and basal part of femurs covered with light yellow-golden hair. Outer side of all tibiae and posterior part of basitarsi covered with dark gray hair. Inner surface of basitarsi and distal half of tibiae of all legs with dense brush of golden-yellow hair, and outer part of basitarsi with silver-white ones. Basitarsi black, other tarsomeres dark brown, but apex of last tarsomere (before claws) lighter, yellow-brown. Basal half of claws and arolia more light yellow.

Metasoma (Figs 35, 37). L = 6.3 mm, W = 3.9 mm, wide-oval. Marginal parts of terga slightly depressed, enlightened yellow-brown, discolored on edge. Basal part of T1 with erect and semi-erect hair each of them rising from oblique backward-directed arcuate raised puncture. Basal part of T2–T4 thinly shagreened, with densely, almost felt, very short branched black-brown hair and in same color very sparse scattered longer ones, extending from almost imperceptible small dots. Apical part of T2–T4 with bands of white, densely adjoined short hair (band on T2 narrowly triangularly interrupted in apical part), over which overhanging long semi-erect silvery-white hair that more erected at sides. Basal part of T5 distinctly punctured and covered with long erect black-brown hair, its marginal part with band of densely adjoined dark-brown hair, over which also overhanging long semi-erect silvery-white ones. Sides of T6, around pygidial plate, covered with long, semi-adjoined brown hair. Pygidial plate strongly depressed (Fig. 36), dark purple at sides and lightened red-yellow in middle, its apical part narrowly elongated and bifurcated. Surface of all sterna thinly shagreened, their basal part with very short silvery-white hairs. Marginal parts of sterna weakly punctuated, their edge with narrow fringe of very short adjoined silvery-white hairs. Basal parts of S3–S6 enlightened, yellow-brown, its marginal part with wide bands of long semi-adjoined golden-yellow hair (Fig. 37). S6 with sparse erect hair of same color, more densely hairy at sides, narrowly semicircularly emarginated at center of apex.

Flight period. May–June.

Host-plants. Herrera (1988) mentioned that this species visits flowers of *Cistus libanotis*, and Lara Ruiz (2013) mostly (64 %) noted it on flowers of *Cistus laurifolius*, but also on different species of Asteraceae. Among studied material, one male specimen was collected on *Helianthemum* and one female on *Malva*. The scopae of the females were mainly filled by pollen of *Helianthemum* (Cistaceae) with several pollen grains of *Malva* (Malvaceae) and Cichorioideae (Asteraceae). On the male body, we observed pollen of Cichorioideae (Asteraceae), *Onosma* (Boraginaceae) and Lamiaceae (Figs 26–27).

Distribution (Fig. 110). As far as known, *Dasypoda iberica* is endemic to Spain. **Published data.** Cádiz [36.5336,-6.29944]; Cádiar [36.949,-3.1845]; Madrid [40.4,-3.68333] (Warncke 1973; Ornos & Ortiz-Sánchez 2004; Asher & Pickering 2018). **Additional material.** Spain, El Espinar, SG[Segovia] 500, 05.vi.2010 [40.704944,-4.348833] on *Helianthemum* 1♂, leg. D. Michez; Naval Peral [40.597, -4.412], 05.vi.2010, 1♀ on *Malva*, leg. D. Michez; Sevilla reg., La Rocina (Doñana National Park) [37.123206, -6.507239], 14.v.2018, 2♀, 2♂, leg. C. Molina.

***Dasypoda (Dasypoda) tibialis* Morawitz, 1880**

Dasypoda tibialis was briefly described from two males collected by N. M. Przhivalsky and M. A. Pyl'tsov from Inner Mongolia (Morawitz 1880: 358; type material stored in ZISP). The females remained unknown prior to the present study. Both type specimens are very bedraggled and partly damaged. However, this species is characterized by very clear and unique features for the genus *Dasypoda*. First, the structure of the apical part of the male hind tibia is unique (Fig. 46). A similar structure was found on the hind tibia of another species of this genus, *D. (Dasypoda) riftensis* Michez & Pauly, 2012, but the shape is very different. The S7 of *D. tibialis* male has two long latero-apical processes (Fig. 49, 57–58), as most of the other species of subgenus *Dasypoda* s.str. (Michez *et al.* 2004b; Radchenko 2016). The genitalia have three-lobed gonostylus (Fig. 51–53, 60–65) like *D. (Dasypoda) tubera* Warncke, 1973 and *D. (Dasypoda) pyriformis* Radoszkowski, 1887, but the pilosity differs. While the gonostyli of the two latter species are hairless on their external lobe, *D. tibialis* has pubescence and the medial lobe showing longer hairs on the apical part.

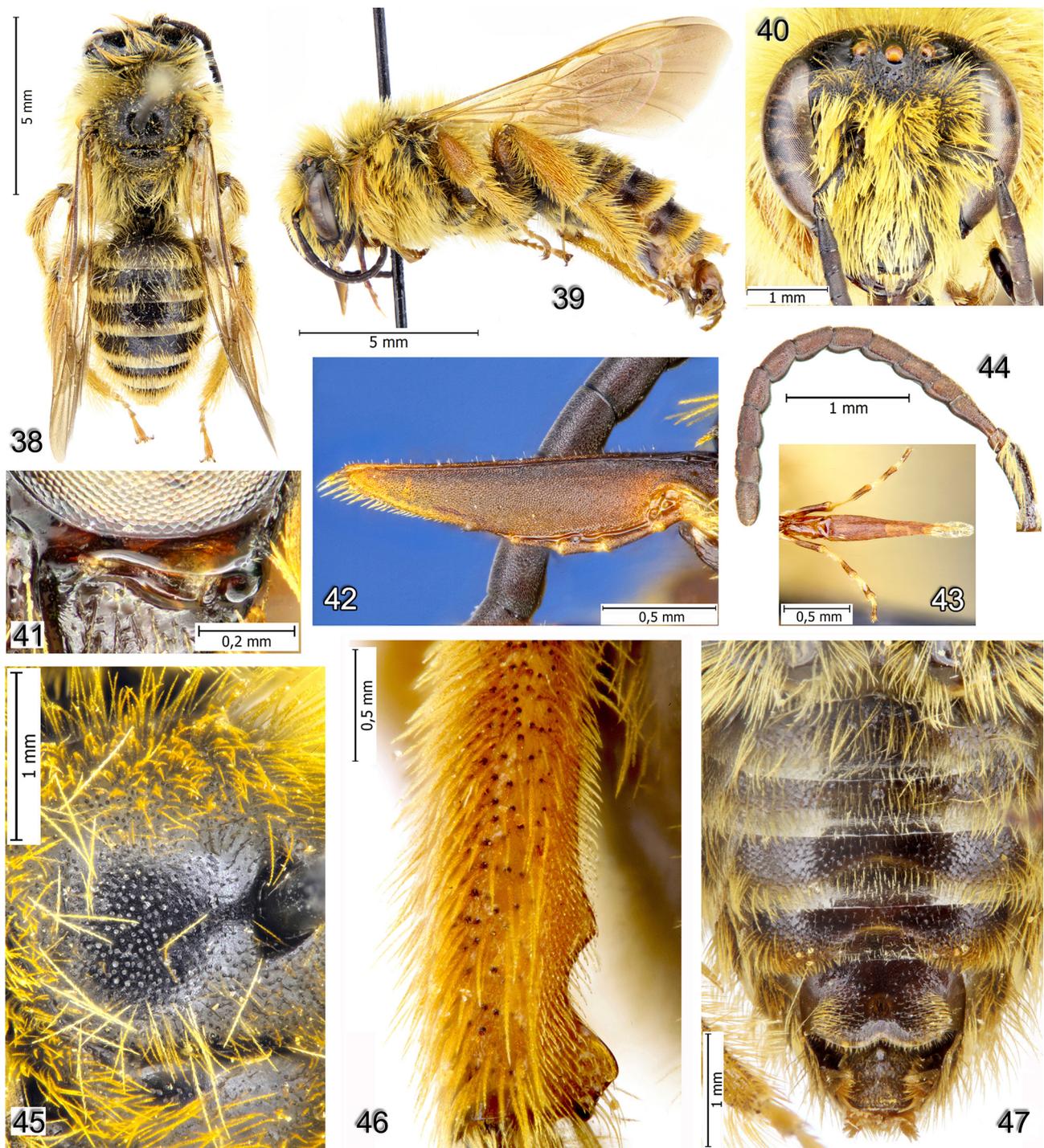


FIGURE 38–47. Male of *Dasypoda tibialis*: 38—Male in dorsal view; 39—Male in lateral view; 40—Head in frontal view; 41—Malar area; 42—Galea; 43—Glossa; 44—Flagellum; 45—Scutum and scutellum; 46—Hind tibia; 47—Metasoma, ventral view.

In the OOL collection, we found 79 males and four females of *D. tibialis* collected by J. Halada in Mongolia (Gobi Desert). Based on this large quantity of material, we provide a detailed redescription of this species and, for the first time, to describe the female. These females were collected simultaneously with the *D. tibialis* males and superficially look similar to them. Both sexes have a similar size and equivalent punctures on the different parts of the body surface, as well as a comparable color of pubescence. In addition, the tibiae and the tarsi of all legs in both sexes have the same yellow-red color. Females and males of this species are also similar in a number of other features that are described below and in the discussion.

Description. Male (Fig. 38, 39). Body black, L = 9–12 mm. **Head** wide (Fig. 40), W = 2.8–3.3 mm, L =

2.5–2.9 mm. Frons, supraclypeal and paracocular areas characterized by cuticle very densely punctured by points that almost merge, and by pubescent with dense, long erect light-yellow hair that mixed on apical part of frons with shorter brown ones. Lateral parts of vertex, between ocellus and compound eye, smoothed and not punctured, with very short sparse brown setae (trichia); posterior part of vertex and areas between ocelli densely punctured and covered with long erect light-yellow hair. Clypeus smoothed, shining, with scattered punctuation, which poorly visible through dense adjacent pubescence of long light-yellow hair. Genae (behind compound eyes) smoothed, polished and shiny, with fine sparse punctuation, in short semi-adjacent light-yellow pubescence that turns into longer, dense erect hair in its posterior part. Malar area very short (Fig. 41), $L = 0.04\text{--}0.05$ mm, ten times shorter than mandible base width ($W = 0.4\text{--}0.5$ mm). Mandibles on apical half part hairless, enlightened and red; basal part with long light-yellow hair on external and ventral sides, these hairs becoming shorter and semi-adjacent on basal part of mandibles. Galea completely covered with small tubercles (Fig. 42). Glossa short and narrow (Fig. 43). Front of scape with semi-erect long light-yellow hair, shorter near apex. Pedicel and flagellum black or lighter, maroon (Fig. 44). Flagellomeres semi-cylindrical from above, densely covered with very short gray-yellow setae, and convexly curved from below, not pubescent, smooth with slightly noticeable fine punctures. 1st flagellomere one quarter shorter than next two combined together.

Mesosoma. W (between tegulae) = 2.1–2.8 mm. Scutum (except its central part), pronotum and mesepisternum densely punctured, distance between points equal to their diameter, completely covered with long erect white-yellow hair. Center of mesonotum smoothed, shining, with sparser punctuation (distance between points equal to 2–3 times their diameter), with short, very sparse yellow-brown hair (Fig. 45). Scutellum smooth, not punctured on narrow anterior part; rest of scutellum and metanotum roughly coarsely punctured with long erect white-yellow hair. Basal area of propodeum not punctured but shagreened, with longitudinal furrow-like depression in middle; shagreening with shape of thin long dashes on side. Lateral parts of propodeum with sparse punctuation and long erect white-yellow hair. Tegulae light-yellow, almost transparent. Wings slightly darkened light-brown. Tibiae and tarsi of all legs and apical part of hind femur rust-yellow and covered with semi-adjacent long light-yellow hairs, with basal black point scattered on surface (distance between points equal 2–5 their diameters). Inner surface of hind tibia covered with dense cilia of short thin yellow hairs. Apical part of hind tibia with deep notch on inner side (Figs 46, 55).



FIGURE 48–54. Male of *Dasygoda tibialis*. 48–53—Sterna and genitalia: 48—Apex of sternum 6; 49—Sternum 7 on the base of sternum 8; 50—Apex of sternum 8 under the base of genitalia; 51–53—Genitalia in dorsal (51), lateral (52) and latero-ventral (54) view; 54—Lables of *Dasygoda tibialis* lectotype.

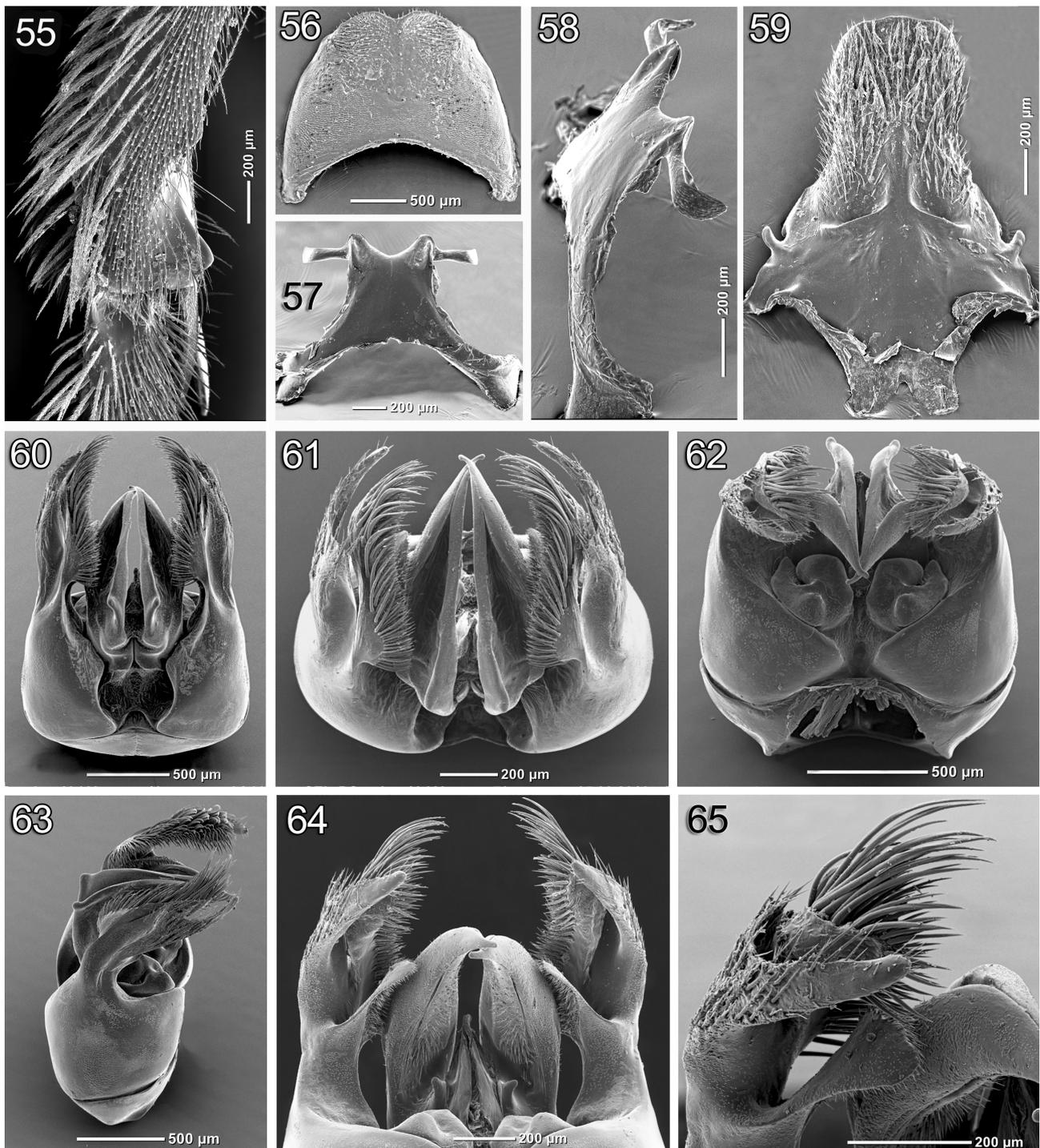


FIGURE 55–65. Structure of *Dasygaster tibialis* male body: 55—Hind tibia; 56—Sternum 6; 57–58—Sternum 7 in ventral (57) and lateral (58) view; 59—Sternum 8; 60–64—Genitalia in dorsal (60), dorso-ventral (61), ventral (62, 64) and lateral (63) view; 65—Gonostylus in ventral view.

Metasoma (Fig. 47) W = 2.7–3.4 mm, L = 4.8–6.2 mm. Basal parts of terga slightly shagreened, oily shiny, in sparse punctuation, distance between points equal 1–3 point diameters; covered with sparse semi-erect long yellow hair, longer on T1. Marginal parts of T1–T6 enlightened, light yellow, translucent, pressed on sides. T2–T6 with bands of very short adjacent white hairs, on T1 such band weakly marked, in sparse hair, on T2 narrowed in center, and on T7 only in sparse long semi-erect thick yellow hair. Wide marginal parts of S1–S4 depressed and semi-circularly widened in center, strongly enlightened, light yellow, translucent, with slightly noticeable sparse punctures. Their basal parts smoothed and shiny, more clearly, but also sparsely punctured. Central apical part of S6 semi-cir-

cularly emarginated, with short sparse yellow hair on sides, centered shiny not punctuated and hairless (Figs 48, 56). S7 with two long latero-apical processes (Figs 49, 57–58). S8 with one spine-like outgrowth at each side (Figs 49, 59), apical part of S8 broad and rounded, with two separated teeth on its dorsal side (Fig. 50). Genitalia with three-lobed gonostylus (Figs 51–53, 60–65), medial lobe showing long pubescence, longer on its apical part.

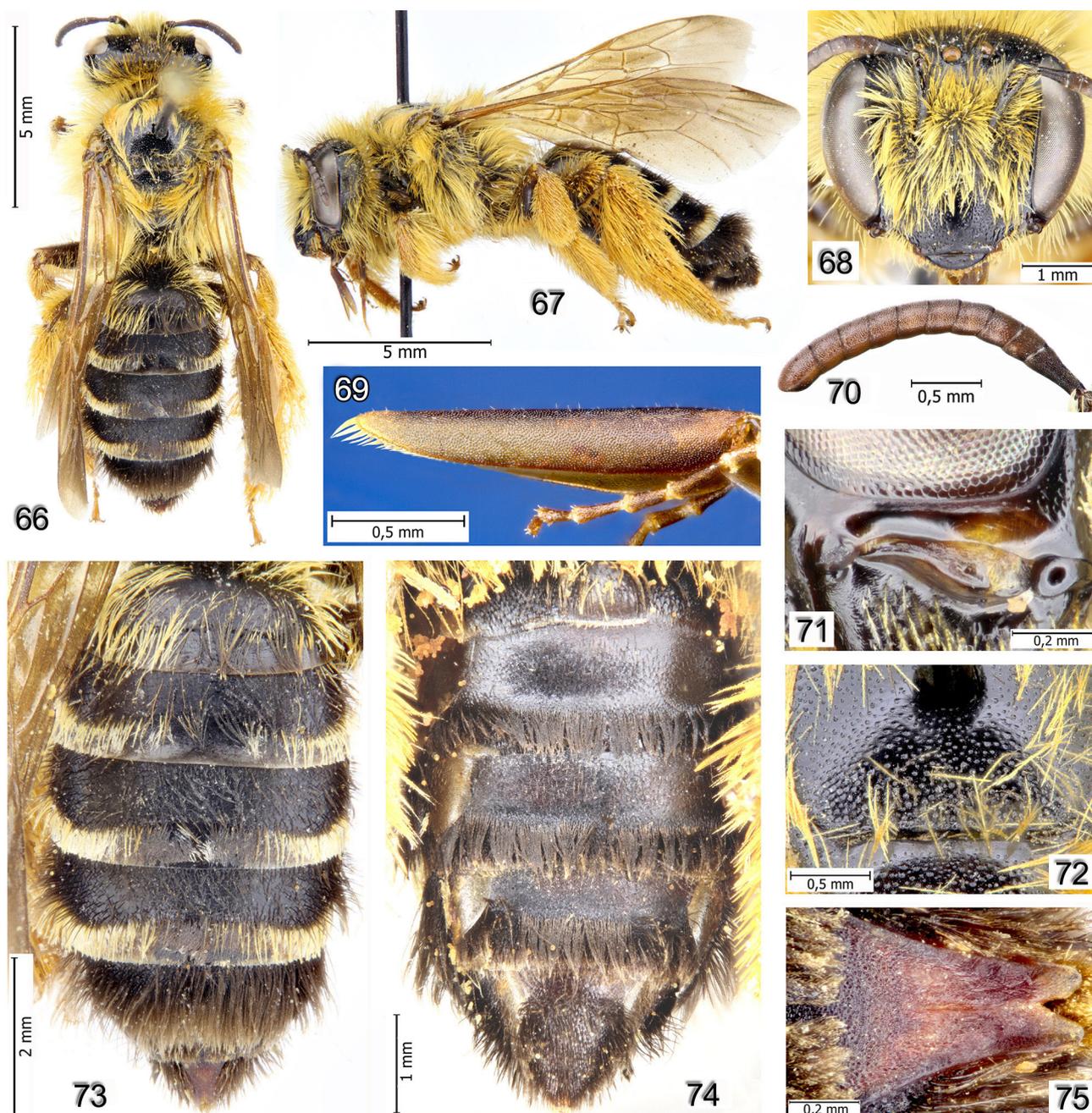


FIGURE 66–75. Female of *Dasygoda tibialis*: 66—Female in dorsal view; 67—Female in lateral view; 68—Head in frontal view; 69—Galea; 70—Flagellum; 71—Malar area; 72—Scutum and scutellum; 73—Metasoma, dorsal view; 74—Metasoma, ventral view; 75—Pygidial plate.

Female (Figs 66, 67) **first description.** Body black, L = 12.8–13.4 mm. **Head** wide (Fig. 68). W = 3.6 mm, L = 3.2 mm. Frons, supraclypeal and inner part of paraocular areas densely punctured (points almost merge) and with dense, long erect yellow hairs. Supraclypeal area in middle with an elevated longitudinal keel on top of which is situated a thin groove. External part of paraocular areas, along compound eyes, not punctured and shiny. Clypeus densely punctured, except in median longitudinal stripe and thin line at base and apical parts. Half basal part of clypeus with long semi-erect yellow hair; other parts hairless, although possible that studied specimens lost hairs. Vertex with sparse erect brown hairs, intermixed with yellow ones in middle part. Malar area short (L = 0.09 mm),

eight times shorter than mandible base width ($W = 0.7$ mm) (Fig. 71). Apical part of mandibles slightly enlightened, red-brown; external basal part with short semi-adjointed yellow hairs with long erected ones in middle. Galea yellow-brown, completely covered with small tubercles (Fig. 69). Glossa like described for male, but lighter, yellow. Front part of scape with long semi-erect yellow hair mixed with very short ones. 1st flagellomere black, 10 % longer than next two combined together (Fig. 70). 2nd–10th flagellomeres light-brown, only slightly curved below; punctuation similar to that of male, densely punctured, but punctures larger, and covered with very short gray-yellow setae from above and not pubescent, smooth with slightly noticeable fine punctures from below.

Mesosoma. W (between tegulae) = 2.9 mm. Scutum (except at its central part), pronotum and mesepisternum densely punctured by deep points; surface between punctures smoothed, shiny; distance between points equal to their diameter; each puncture with one long erect yellow plumose hair. Morphological structure of hairs varies in different parts of mesosoma. Pilosity on its ventral part with spherical extension on apex of hair branches (see Fig. 79), and hair branches on other parts of mesosoma pointed and thin on top (see Fig. 78). Central part of scutum smoothed and shining between small and sparse punctuation (Fig. 72); distance between points equal 2–3 times their diameter; some of these points hold short yellow-brown hair (hairs probably lost in other points in examined specimen). Scutellum like described for male but narrow anterior part smoothed shiny, not punctured; rest of scutellum and metanotum roughly coarsely punctured, with long erect yellow hair. Basal area of propodeum not punctured, shagreened; and with shallow pits-like depression in middle. Tegulae light-yellow, transparent but with thin black basal part. Wings light-brown. Tibiae and tarsi of all legs rust-yellow, covered with semi-adjointed long golden-yellow dense hair, each of which situated in separate scattered black points. Scopa on hind tibia and hind basitarsus with similar plumose hairs than ventral part of mesosoma (i.e. spherical extension on apex of each branch of hair, Fig. 79), whereas hairs of front and middle tibiae and basitarsi with pointed tops (Fig. 78).

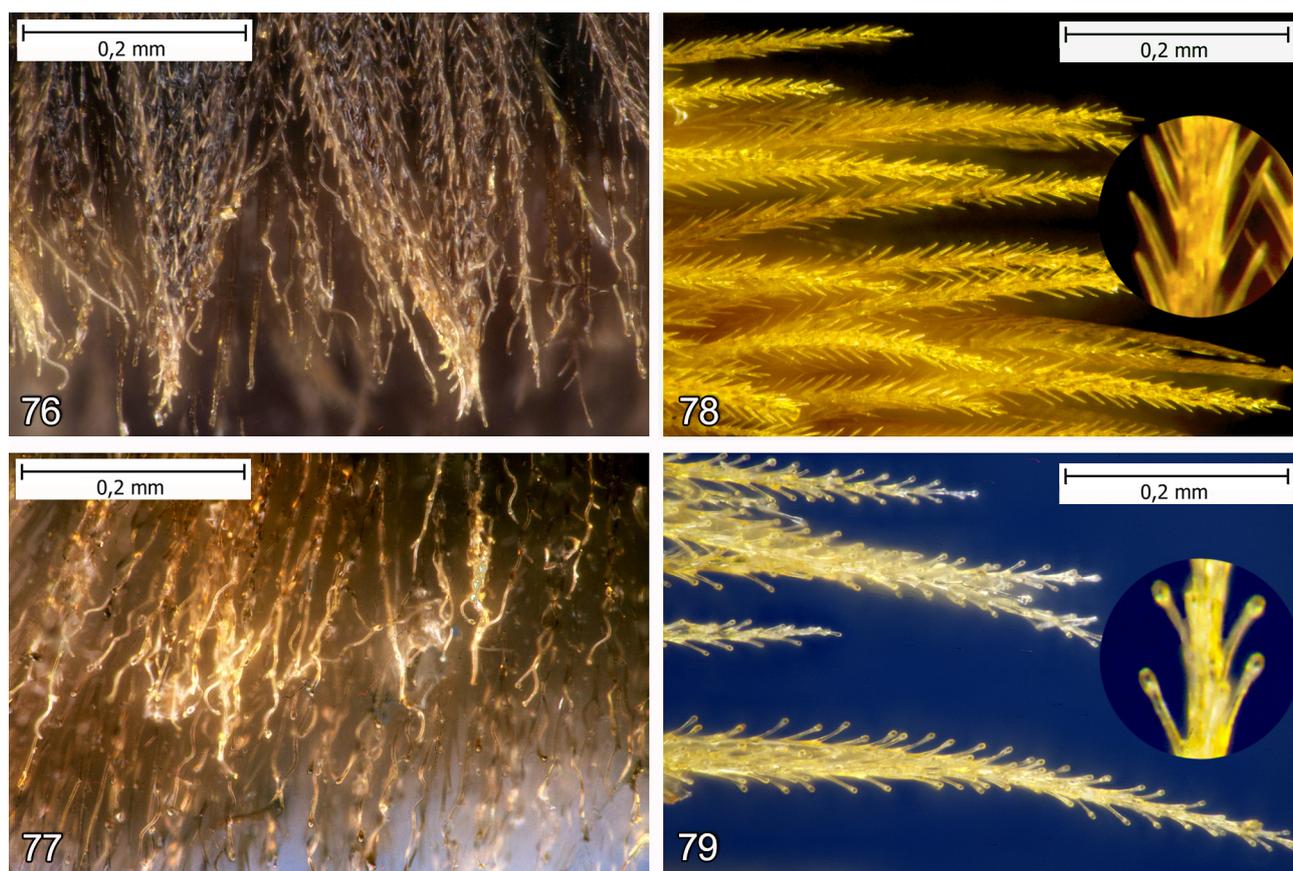


FIGURE 76–79. Hairs of *Dasygaster tibialis* female: 76—Hair on sternum 4; 77—Hair on sternum 5; 78—Hair on middle tibia; 79—Hair of hind tibia scopa (78–79—diameter of the circles with enlarged parts of the hair = 0.05 mm).

Metasoma (Figs 73, 74). $W = 3.7$ mm, $L = 6.8$ mm. Basal parts of terga very thinly shagreened. Marginal parts of terga wide, semitransparent, slightly depressed, especially on sides. T1 sparsely punctured with long semi-erect yellow hair on its vertical part and semi-adjointed hairs on its horizontal part. T2–T4 with almost invisible sparse

punctures, and very short thin erect brown hair on their sides and semi-adjacent ones in their middle. Basal part of T5 densely punctured with long semi-erect dark brown hair that more lightened in their apical half. T2–T4 with apical bands of tightly adjacent short dense white hairs that covered from above by semi-adjacent long sparse white-yellow hair (Fig. 73). Band on T2 interrupted in middle. Marginal part of T5 thickly covered with long adjacent brown hair. Lateral ventral parts of terga enlightened, yellow. Pygidial plate thin, deeply forked at apex, red-yellow, and its basal part darker with dense mesh-ribbed structure (Fig. 75). Sides of T6 near pygidial plate covered by long dense semi-erect brown hair (Fig. 75). Basal part of S1 densely punctured with long semi-adjacent brown hair at sides, and in middle with yellow ones; marginal part of this tergum shagreened, semi-circularly widened backwards in middle and hairless. Narrow apical margin enlightened translucent, yellow on all sterna. Basal parts of S2–S4 shagreened and not punctured, with very short thin semi-adjacent brown hairs. Marginal parts of S2–S4 with entire wide bands of dense semi-erect long dark-brown branched hairs which curly at their apical half (Fig. 76). S5 light-brown, densely punctured, with same long erect hairs (Fig. 77).

Lectotypus designavi here, male: 1st label—a small circle of golden color; 2nd label handwritten “76·592.”; 3rd label handwritten—“ю[го].в[осточная]. Монголия, май и первая половина июня 1871, Пржевальск[ий]. и Пыльцов” [SE Mongolia [China, Inner Mongolia], May and the first half of June 1871, [leg.] [N.M.] Przhevalsk[y] et [M.A.] Pyl'tsov”; 4th label handwritten by F.Morawitz—“tibialis. Mor. Typ.”; 5th printed label “Lectotypus *Dasygoda tibialis* F. Mor. design. V. Radchenko, 2012” (Fig. 54).

Paralectotypus, male: 1st label “76·692.”; 2nd label handwriting—“[SE Mongolia [China, Inner Mongolia]] ridge *Muni-Ula*, 2nd part of June 1871; [leg.] [N. M.] Przhevalsk[y] et [M.A.] Pyl'tsov”; 3rd label handwriting by F.Morawitz—“tibialis. Mor. Typ.”; 4th printed label “Paralectotypus *Dasygoda tibialis* F. Mor. design. V. Radchenko, 2012”.

Flight period. May–June.

Distribution (Fig. 110). China (Inner Mongolia), Mongolia (Ömnögovı Aimag). **Additional material.** 79 males, four females: “Mongolia-Gobi, Dalanzadgad env. [43.558, 104.375], 24–26.vi.2003, J. Halada leg.”.

***Dasygoda (Megadasypoda) vulpecula* Lebedev, 1929**

This species was described by Lebedev based on material including about 30 specimens of males and females collected from Kazakhstan: [coast of river] Usek near Jarkent [44.186, 79.974], former prov. Semirechye [or Jetyssu; now Panfilov District of Almaty Region] (Lebedev 1929: 269–271). This type material was deposited in Kiev (Institute of Zoology, Academy of Sciences of Ukraine), but probably was lost during World War II. Besides this first description, *D. vulpecula* has been listed by Popov (1957), who referred to a single female collected from Shohimardon [39.984, 71.799]—an exclave of Uzbekistan, surrounded by Kyrgyzstan, in a valley in the Alai mountains, but this specimen was probably also lost. Finally, the species has been mentioned without any reference in the Red Book of Kyrgyz Republic (Davletkeldiev 2006: p. 293) as a species that required special attention for its conservation.

We found two females and one male of *D. vulpecula* among undetermined material stored in different collections that allowed us to make a redescription of both sexes and to clarify the subgeneric assignment of the species. One of the females was collected relatively close to the *locus typicus* (300 km from the same Almaty region) but this specimen was significantly damaged by a *Dermestes* larva. The second female was collected 230 km from the *locus typicus*, but this point is located in another country (in Kyrgyzstan). The male was also collected from Kazakhstan, however at a distance of about 2,000 km from the type locality. It shows a very clear, unique diagnostic feature, namely a large beak-shaped protrusion on the distal part of hind tibia (Figs 88, 91). This trait was shown on the figure along with the original description of this species (Lebedev, 1929: 270, Fig. 1) that excludes possible misidentification, in contrast with original description of females, which do not have such unique features. Moreover, *Dasygoda vulpecula* shows the characteristic structure of the genitalia of the subgenus *Megadasypoda*. According to the structure of S6–S8 and genitals, *D. vulpecula* is most similar to *D. (Megadasypoda) friesana* Schletterer, 1890 but this species does not show the particular structure on the hind tibia.

Description. Male (Figs 80, 81). Length: 14 mm. **Head:** W = 3.4 mm; L = 3.7 mm; black elongated and narrowed downwards (Fig. 82). Clypeus (W = 1.9 mm, L = 1.3 mm) strongly convex, with hidden punctures under pubescence; its central part with shape of slightly protruding vertical keel, smooth, not punctured and hairless. Face, vertex and gena covered with long light-ginger hair intermixed with short brown on vertex. Frons and paraocular

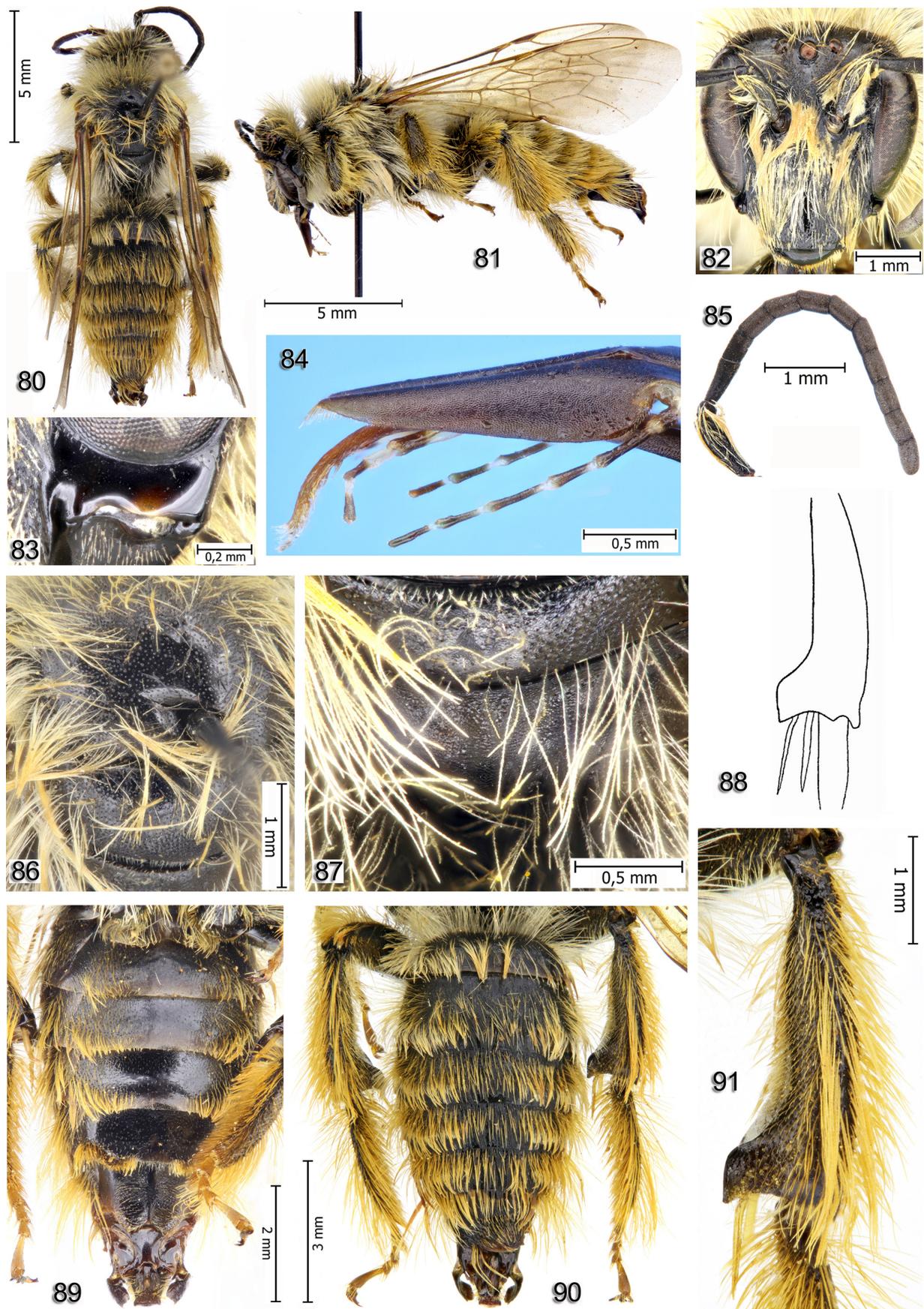


FIGURE 80–91. Male of *Dasydoda vulpecula*: 80—Male in dorsal view; 81—Male in lateral view; 82—Head in frontal view; 83—Malar area; 84—Galea; 85—Antenna; 86—Scutum; 87—Metanotum and propodeum; 88, 91—Hind tibia (88—from Lebedev 1929: 270, fig. 1); 89—Metasoma in ventral view; 90—Metasoma in dorsal view.

areas densely punctured; area around ocelli smoothed, shiny and not punctured. Malar area relatively long ($L = 0.2$ mm), almost one-half of mandible width at base ($W = 0.47$ mm); cuticle overall black, smooth and shining, but lighter and semitranslucent at its middle apical part (Fig. 83). Mandible black, narrower than for female, with lighter yellow-red ring in middle and red at apex part. Galea brown, densely covered with flattened oblong and circular tubercles (Fig. 84). Flagellum black on inner side, light brown on external side (Fig. 85). 1st flagellomere 1.6 times longer than 2nd. 2nd–10th flagellomeres cylindrical, almost of same length (difference between separate segments less than 7%), ratio of their width to length about 1 : 1.6.

Mesosoma. W (between tegulae) = 2.8 mm. Dorsal side covered by long blond yellow-gray hair; lateral, posterior and ventral sides with more light gray-white ones. Scutum smoothed, shiny, densely punctured, punctures more scattered in middle (distance between points equal to 1.5–2 point diameters) (Fig. 86). Propodeum with thin little ribs forming dense mesh (Fig. 87). Tegulae yellow, translucent. Legs black except 2–5 tarsomeres, which yellow-brown. Legs with long blond yellow-ginger hair, longer on rear, lighter yellow-gray on forelegs. Inner distal part of hind tibia with large beak-shaped protrusion (Figs 88, 91). Wings slightly darkened, light brown.

Metasoma (Figs 89, 90) black, oblong. $L = 7$ mm, W (in widest part) = 3.8 mm. All terga with yellow-ginger long hair erected or semi-erected on T1–T2 and more appressed on other ones except on their sides. Each hair rising from oblique backward-directed puncture. Distance between two punctures about 2–4 times as long as diameter of punctures. Marginal parts of each tergum semi-translucent, not punctured, hairless and lighter than apical parts. Sterna hairy, with short yellow-ginger hair only on sides of basal part and longer at margin, rest of sterna with very short sparse setae. Central apical part of S6 widely concave (Fig. 92). Distal part of S7 with long latero-apical processes (Figs 93, 96). S8 with long spike-like outgrowths at each side (Fig. 93); its apical part with two separated long teeth on dorsal side (Fig. 94). Gonostylus 3-lobed (Figs 96–98), distal half part of external lobe widened; its ventral part extended into rounded tooth on apex (Figs 95–97); inner ventral and dorsal lobes of gonostyles widened and with long hair on apex (Fig. 98).

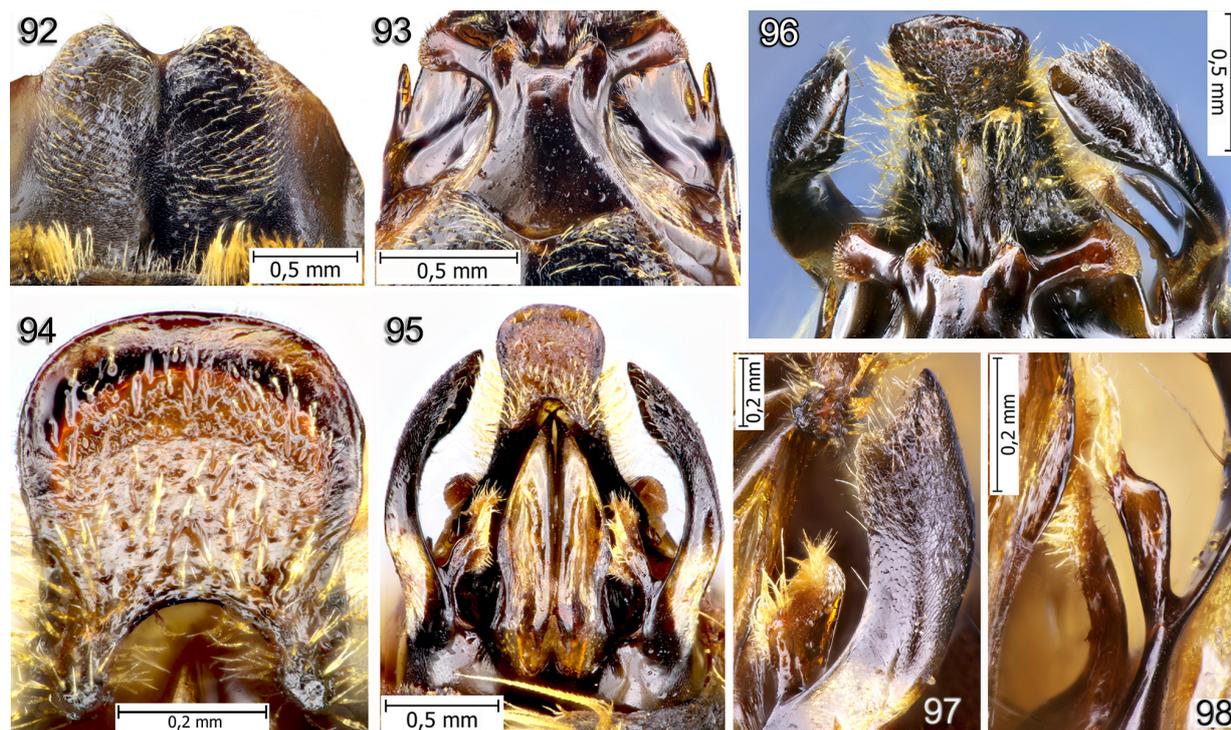


FIGURE 92–98. Sterna and genitalia of *Dasygoda vulpecula* male: 92—Sternum 6; 93—Sternum 7 on the base of sternum 8 with two basal hooks on the sides; 94—Apex of sternum 8; 95—Genitalia in dorsal view; 96—Genitalia in ventral view; 97—Gonostylus in dorsal view; 98—Two inner lobes of gonostylus.

Female (Figs 99, 100). Length: 15–16.5 mm. **Head** (Fig. 101): $W = 4.26$ mm; $L = 4.07$ mm. Clypeus ($W = 2$ mm, $L = 1.5$ mm) black and densely punctured with deep oblique dots, except on relatively wide median line impunctate, smooth and shiny, which not reach margin. In front of central ocellus and on outer sides of lateral ones, presence of shiny impunctate surface. Oculo-ocellar space shiny, but still with very shallow punctures. Surface behind central ocella with tuft of shaggy brown and ginger hair. Vertex (behind ocelli), frons and paraocular areas (near

compound eyes) with brown hair; central part of face covered with lighter ginger intermixed with very few brown ones. Malar area long ($L = 0.27$ mm), length at center equal to one-third width of mandible at base ($W = 0.8$ mm); cuticle dark brown, smooth and shiny, but orange on surface above condyles (Fig. 102). Scape with relatively scarce long ginger hair. Basal half of mandible with sparse long light-yellow hair on external part. Occiput near vertex and genae with dense long brown pilosity intermixed with ginger hairs. Proximal part of mandible black, shiny and finely (but densely) punctured; medial part black with red ring in middle, shiny, with strong but scarce punctation; distal part lighter, reddish, mat and very finely punctured, carrying very short ginger-gold branched hair; proximal and medial parts with ginger hair on their lower and upper edges. Dorso-distal part of labrum with fringe of goldish ginger hair; basal part with fringe of thick and slightly darker orange-brown hair, shorter than ones of distal part. Galea dark brown, lighter in its apical part, completely covered with small flat circular and oblong tubercles, with apical fringe of yellow hair, most distal piles longest (Fig. 103). Maxillary palpa brown, with proximal segments (including first one carrying few erect hair) darker than distal ones. Glossa with shaggy yellow hair and presenting lighter coloration than rest of mouth parts (Fig. 105). 1st flagellomere long (only 15 % shorter than three next ones taken together) (Fig. 104). 3rd–9th flagellomeres almost same length, 2nd—10 % shorter and 10th—30 % longer.



FIGURE 99–109. Female of *Dasypoda vulpecula*: 99—Female in dorsal view; 100—Female in lateral view; 101—Head in frontal view; 102—Malar area; 103—Galea; 104—Flagellum; 105—Glossa and labial palpus; 106—Apex of hind tibia; 107—Metasoma, ventral view; 108—Marginal band on sternum 4; 109—Pygidial plate.

Mesosoma W (between tegulae) = 4 mm. Scutum shiny and evenly punctured by small fine points. Full mesosoma with ginger hair, which darker auburn on center of scutum. Tegulae orange and transparent. Ventral part of mesosoma monochrome, with long shaggy ginger hair. Front leg with monochrome ginger hair; profemur, protibia and probasitarsus with longer hair on their posterior part than on their anterior part, posterior fringes longer than largest part of articles. Distal articles of legs with lighter cuticle than proximal ones. Hind legs with long monochrome ginger hair, slightly darker than ones of other legs; metafemur with orange hair; metatibia covered by orange scopa, posterior hairs slightly longer and denser than anterior ones; distal part of metatibia extended posteriorly (Fig. 106). Wings slightly dark, light brown.

Metasoma (Fig. 107). Cuticle of terga black, with more or less dense very small punctures on basal part. Basal parts of T1–T2 with sparse long semi-erect ginger hair, intermixed with brown ones on T2, marginal part of T1 very wide and hairless. Marginal parts of T1–T3 not punctured (this character not visible through pubescence on other terga), very thinly transversely striated. T2–T4 covered from above with very thick tight white hair, forming entire wide bands. T5 with dark brown band. Basal parts of T3–T4 with long sparse brown hair, and T5–T6 with dense dark brown pilosity intermixed with ginger and blond hairs on sides. Pygidial plate elongated at apex, with uplifted margins, dark brown to black (turning lighter red-brown to orange in middle), mat, glabrous and more densely and roughly punctuated in centre than discs of terga (Fig. 109). 3th–5th sterna with long hair at their apical margins which forms wide entire red-orange bands (Fig. 107), and basal part of these sterna covered with short brown hairs (Fig. 108). 1st–2nd and 6th sterna with scarcer erected ginger pilosity.

Flight period. From May (Lebedev, 1929) to end of June.

Distribution (Fig. 110). Kazakhstan, Uzbekistan and Kyrgyzstan, rising to 2660 m in the mountains. **Published data.** Kazakhstan, river Usek near Jarkent [44.186, 79.974] (Lebedev 1929); Uzbekistan, Shohimardon [39.984, 71.799], 1 ♀ collected.

Additional material. Kazakhstan, 20 km SE Aksay env. [West Kazakhstan Region] [51.06, 53.25], 16.–19.vi.1992, 1 ♂, leg. J. Halada [OLL]; Kazakhstan mer., Fabritchny 40 km E. [W?] Alma Ata [43.147, 76.428], 23.vi.[19]92, 1 ♀, leg. M. Halada [OLL]; Kyrgyzstan, Naryn, S. slope, Moldo-Too ridge, E. Kara-Go Pass, 41°30'22"N, 74°44'11"E [41.5061, 74.7364], 2660 m, 30.vi.1999, 1 ♀, leg. J. G. Rozen, J. K. Bouseman, #74 [AMNH].

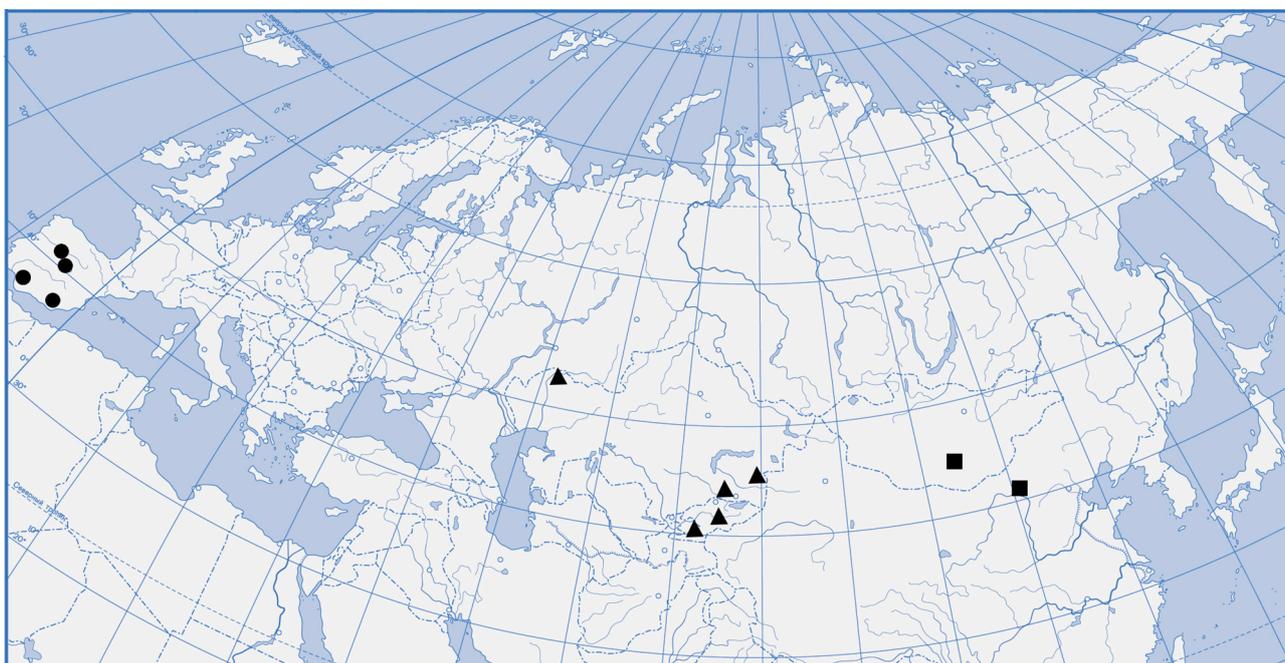


FIGURE 110. Distribution map of *Dasyroda iberica*, *D. tibialis* and *D. vulpecula*: ●—*D. iberica*; ▲—*D. vulpecula*; ■—*D. tibialis*.

Discussion

The taxonomy of the genus *Dasyroda* has been substantially improved as a result of the present work. From the

currently known 39 valid species of *Dasypoda*, only four species [i.e. *D. (Dasypoda) gusenleitneri* Michez, 2004, *D. (Dasypoda) syriensis* Michez, 2004, *D. (Heterodasypoda) michezi* Radchenko, 2017 and *D. (Megadasypoda) intermedia* Michez, 2005] remain with an unknown female.

The very first description of *D. iberica* females confirmed its accordance with subgenus *Microdasypoda* as described by Michez *et al.* (2004b). Like the other species of the subgenus, *D. iberica* shows (i) a bicolored scopa (i.e. dark gray-brown and yellow-golden), (ii) a clypeus with a smooth, shiny, impunctate zone (but *D. iberica* has the area almost round, not reaching the base of the clypeus only 1/4 of its height, which is much larger than at the other members of the subgenus, for other species see Michez *et al.* 2004b), (iii) a T2 with straight apical edge, (iv) a glabrous pygidial plate, (v) a galea relatively short, (vi) a malar space shorter than the pedicel, and (vii) the nervulus antefurcal. An additional study of *D. iberica* males allowed us to complete the description of the morphology of the subgenus *Microdasypoda*: (i) the S7 can have a short latero-apical structure (but still shorter than the structure of *Dasypoda* s.str. and *Heterodasypoda*), (ii) the apical pubescence of the S6 is not only brown but can be also white, and (iii) the inner apical side of S8 can have two distinct semicircular keels. In addition, we should note that Warncke (1973) erroneously pointed the absence of bands on the terga in the description, although he indicated their presence in the determination key of the same article. In this identification key, he also mistakenly refers this species to a group in which the 2nd segment of the flagellum (1st flagellomere) is much longer than the 3rd (2nd flagellomere), although these segments are approximately of the same length. Moreover, Warncke's schematic figure of the *D. iberica* genital gonobase, represented as narrowly rectangular (Warncke, 1973, Fig. 33 on p. 105), does not correspond to its real structure, on what Baker (2002) had already drawn the attention.

The examination of the type material of *D. tibialis*, as well as additional new specimens (including the females newly described here), revealed that this species belongs to the subgenus *Dasypoda* s.str. as described by Michez *et al.* (2004b). Males and females show: (i) a malar space shorter than pedicel, (ii) a 2/3 length ratio between the maxillary palpus and galea, (iii) a galea densely covered with small tubercles, (iv) a ventral margin of the galea with setae only on the apical part, and (v) an antefurcal nervulus. The males have additional specific characters: (i) an apex of S6 with short, light, and sparse pubescence, (ii) an apex of S7 with two long narrow and fully sclerotized latero-apical processes, (iii) a dorso-apical side of S8 with two distinct teeth that do not reach the lateral edges, and (iv) the basal part of S8 with two lateral hooks directed backwards. Likewise, the females present: (i) a clypeus with a median impunctate strip, (ii) a hind tibia with monochrome pubescence (scopa fully golden-yellow), (iii) a T2 with straight apical margin, (iv) a pygidial plate glabrous. Based on this new revision, we can propose one additional synapomorphy for the subgenus *Dasypoda* s.str., the special structure of the hairs on marginal parts of the S2–S4 that form entire wide bands of dense semi-erect long branched hairs, which are corkscrew-shaped at half apical part (Fig. 77). While most other members of this subgenus have bilobed gonostylus (see for example *Dasypoda morawitzi* Radchenko, 2016), the males of *D. tibialis* have genitalia with three-lobed gonostyles like *D. tubera* and *D. pyriformis*.

Finally, *D. vulpecula* most likely belongs to the subgenus *Megadasypoda*. In support of this hypothesis, the following characters are shared with all the other species of the subgenus: (i) a large body size, (ii) a malar area longer than the pedicel, (iii) male genitalia with a three-lobed gonostylus, (iv) inner lobes of gonostylus have sub-equal size, much smaller than the outer lobe, (v) an inner side of S8 apical part with two distinct long ridges, (vi) a scopa with monochrome ginger hair, and (vii) a ventral margin of the galea only with some bristles at the apex. However, unlike other representatives of the subgenus *Megadasypoda*, *D. vulpecula* shows the ratio of the length of the maxillary palpus and the galea is above 0.5 (about 0.75), the apex of S7 with two long narrow and fully sclerotized latero-apical processes, and the basal part of S8 with two straight lateral hooks.

Acknowledgements

We thank the collection curator who provided access the studied material: J.G. Rozen Jr. and J.S. Ascher (AMNH); Yu.A. Astafurova (ZISP) and M. Schwarz (OOL) and the collectors of the material: J. & M. Halada and C. Molina. We would like also to thank P. Rasmont (UMons), who contributed to the organization of this study in Mons, and D. Evrard (UMons) for technical assistance. We thank T.J. Wood (UMons) for comments on the English. We are also grateful to two anonymous reviewers and Jason Gibbs for their corrections to the text and constructive comments that improved this manuscript. The research leading to this publication has received funding from the “Fonds

de la Recherche Scientifique—FNRS” and “The support of the priority research areas development of Ukraine, KPKVK 6541230”. Guillaume Ghisbain was supported by a FRS-FNRS Ph-D grant “Aspirant”.

Literature

- Ascher, J.S. & Pickering, J. (2018) Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Available from: http://www.discoverlife.org/mp/20q?guide=Apoidea_species (accessed 1 June 2019)
- Baker, D.B. (2002) A provisional annotated list of the nominal taxa assigned to the genus *Dasygaster* Latreille, 1802, with the description of an additional species (Hymenoptera, Apoidea, Melittidae). *Deutsche entomologische Zeitschrift*, 49, 89–103. <https://doi.org/10.1002/mmnd.20020490107>
- Blank, S.M. & Kraus, M. (1994) The nominal taxa described by K. Warncke and their types (Insecta, Hymenoptera, Apoidea). *Linzer biologische Beiträge*, 26 (2), 665–761.
- Davletkeldiev, A.A. (ed.) (2006) *Red Data Book of Kyrgyz Republic. 2 Edition*. State agency on environment protection and forestry under the Government of Kyrgyz Republic, Institute for Biology and Pedology of National Academy of Sciences of Kyrgyz Republic, Ecological Movement “Aleine” of Kyrgyzstan, Bishkek, 544 pp.
- Herrera, J. (1988) Pollination relationships in southern Spanish Mediterranean shrublands. *Journal of Ecology*, 76, 274–287. <https://doi.org/10.2307/2260469>
- Lara Ruiz, J. (2013) Fuentes alimenticias de los Melittidae ibéricos. *Micobotánica-Jaén*, 8 (3), 18–22.
- Latreille, P.A. (1802) *Histoire naturelle des fourmis, et recueil de mémoires et d'observations sur les abeilles, les araignées, les faucheurs, et autres insectes*. Théophile Barrois père, Paris, xvi + 445 pp., xii pls. <https://doi.org/10.5962/bhl.title.65810>
- Lebedev, A.G. (1929) Neue Bienen-Arten aus S.S.S.R. *Konowia*, 8 (3), 268–272.
- Michener, C.D. (2007) *The bees of the world, second edition*. The Johns Hopkins University Press, Baltimore, xvi + [i] + 953 pp., 20 pls.
- Michez, D. (2005) *Dasygaster (Megadasygaster) intermedia* sp. nov. (Hymenoptera, Apoidea, Melittidae), new species from Iran. *Zoologische Mededelingen*, 79 (6), 123–127.
- Michez, D., Patiny, S., Rasmont, P., Timmermann, K. & Vereecken, N. (2008) Phylogeny and host-plant evolution in Melittidae s.l. (Hymenoptera: Apoidea). *Apidologie*, 39 (1), 146–162. <https://doi.org/10.1051/apido:2007048>
- Michez, D. & Pauly, A. (2012) A new species of the palaeartic genus *Dasygaster* Latreille 1802 (Hymenoptera: Dasygasteridae) from the Great Rift Valley in Ethiopia. *Zootaxa*, 3181 (1), 63–68. <https://doi.org/10.11646/zootaxa.3181.1.5>
- Michez, D., Terzo, M. & Rasmont, P. (2004a) Révision des espèces ouest-paléarctiques du genre *Dasygaster* Latreille 1802 (Hymenoptera, Apoidea, Melittidae). *Linzer biologische Beiträge*, 36 (2), 847–900.
- Michez, D., Terzo, M. & Rasmont, P. (2004b) Phylogénie, biogéographie et choix floraux des abeilles oligolectiques du genre *Dasygaster* Latreille 1802 (Hymenoptera: Apoidea: Melittidae). *Annales de la Société Entomologique de France, New Series*, 40 (3–4), 421–435. <https://doi.org/10.1080/00379271.2004.10697431>
- Morawitz, F.F. (1880) Ein Beitrag zur Bienen-Fauna Mittel-Asiens. *Bulletin de l'Académie Impériale des Sciences de St.-Petersbourg*, 26 (22/36), 337–389.
- Ornosa, C. & Ortiz-Sánchez, F.J. (1998) Contribución al conocimiento de los melítidos ibéricos (Hymenoptera, Apoidea, Melittidae). *Boletín de la asociación española de Entomología*, 22 (3–4), 181–202.
- Ornosa, C. & Ortiz-Sánchez, F.J. (2004) Hymenoptera, Apoidea I. In: Ramos, M.A., Alba, J., Bellés, X., Gonsálbes, J., Guerra, A., Macpherson, E., Martín, F., Serrano, J. & Templado, J. (Eds.), *Fauna Ibérica. Vol. 23*. Museo Nacional de Ciencias Naturales, CSIC, Madrid, 556 pp.
- Popov, V.B. (1957) New species and the geographical distribution of the bee genus *Eremaphanta* Popov (Hymenoptera, Melittidae). *Zoologicheskyy Zhurnal*, 36 (11), 1706–1716. [in Russian]
- Radchenko, V.G. (1996) Evolution of nest building in bees (Hymenoptera, Apoidea). *Entomological Review*, 75 (6), 20–32.
- Radchenko, V.G. (2016) A new widespread European bee species of the genus *Dasygaster* Latreille (Hymenoptera, Apoidea). *Zootaxa*, 4184 (3), 491–504. <https://doi.org/10.11646/zootaxa.4184.3.4>
- Radchenko V.G. (2017) A new bee species of the genus *Dasygaster* Latreille (Hymenoptera, Apoidea) from Portugal with comparative remarks on the subgenus *Heterodasygaster* Michez. *Zootaxa*, 4350 (1), 164–176. <https://doi.org/10.11646/zootaxa.4350.1.10>
- Radchenko, V.G. & Pesenko, Yu.A. (1996) “Protobee” and its nests: a new hypothesis concerning the early evolution of Apoidea (Hymenoptera). *Entomological Review*, 75 (2), 140–162.
- Warncke, K. (1973) Die westpaläarktischen Arten der Bienenfamilie Melittidae (Hymenoptera). *Polskie Pismo Entomologiczne*, 43 (1), 97–126.