





Review of the bee genus *Eremaphanta* Popov 1940 (Hymenoptera: Melittidae), with the description of a new species

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Abstract

The small central Asian genus *Eremephanta* (Hymenoptera, Apoidea) is poorly known. We provide a catalogue of the eight species included in this genus and an update of the available diagnoses. One new species, *Eremaphanta popovi* **sp. nov.** and the male of *E. fasciata* Popov 1957 are described. A key to species is given and the species ranges are mapped and discussed.

Key words: Melittidae, Central Asia, systematics, biogeography, floral choices, Apoidea, bees

Introduction

According to Engel (2001), the Melittidae are subdivided into four subfamilies: Dasypodainae, Macropidinae, Meganomiinae and Melittinae. These subfamilies consist of 14 genera ranging worldwide, except in Australia and South-America (Michener 1981). Revisions are available for several of these groups, but *Eremaphanta* is still unreviewed (Stage 1966; Michener 1981; Whitehead & Steiner 2001; Michez *et al.* 2004a,b; Michez & Patiny 2005). *Eremephanta* is a well-delimited group of small Dasypodainae (Michener 2000). Morphologically, it is characterised by some unique characters among the Melittidae, such as the presence of extensive yellow markings in both sexes, the stigma as long as the first submarginal cell, the second submarginal cell twice as long as the first and the weak differentiation of the male S7 (Popov 1940; Michener 1981). Likewise, from a biogeographical point of view, *Eremaphanta* is the group of Melittidae endemic to Central Asia, where the diversity of other genera in the family is conspicuously low (Popov 1957; Michez *et al.* 2004b; Michez & Patiny 2005).

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The literature on *Eremaphanta* is particularly scarce. The genus was described by Popov (1940), based on a previously described species: *Rophites vitellinus* Morawitz 1875, transferred as type species of the new genus. In the same work, Popov also transferred *Rophites dispar* Morawitz 1892 to *Eremaphanta* and provided descriptions for *E. convolvuli*. In a second paper, the same author added four more species to the genus: *E. fasciata*, *E. minuta*, *E. turcomanica* and *E. zhelochvtsevi* (Popov 1957). An eighth species, *E. iranica*, was described by Schwammberger (1971). At a higher taxonomic level, Michener (1981) subdivided the genus into two subgenera (*Eremaphanta* s.str. and *Popovapis* Michener 1981) and transferred it to the tribe Dasypodaini (Dasypodainae). More recently, Engel (2005) placed *Eremaphanta* in the subtribe Hesperapina (Dasypodainae) together with *Hesperapis* s.l. This latter proposal is mainly based on two shared morphological characters: the presence of a galeal comb located in front of the maxillary palpus and a patch of keirotrichia on the inner surface of the hind tibia.

The present paper constitutes the first global revision of *Eremaphanta*. We provide a comprehensive catalogue, a key for the identification of the species and descriptions of *E. popovi* **sp.nov.** and the previously unknown male of *E. fasciata*. In addition, the geographic distribution of the taxa are presented and discussed. The available data on the foraging preferences of these bees are discussed.

Material and methods

Type material was obtained from the following institutions: Staatliches Museum für Naturkunde Stuttgart (SMNS, Stuttgart, Germany), Zoological Institute of the Russian Academy of Science (ZISP, Saint Petersburg, Russia), Zoological Museum of the Moscow University (ZMMU, Moscow, Russia) and Snow Entomological Museum of the University of Kansas (SEMK, USA; D.B. Baker's collection). All types were reviewed, except that of *E. zhelochovtsevi*.

Additional material has been studied in the American Museum of Natural History (AMNH, USA), Oberösterreichisches Landesmuseums Linz (OOLL, Austria), Natural History Museum (NHM,UK), SEMK and ZISP.

The maps are based 259 records of specimens. The biogeographical data are available in BDFGM (Banque de données fauniques Gembloux-Mons). Data Fauna Flora 2.0 (Barbier *et al.* 2000) and Carto Fauna Flora 2.0 (Barbier & Rasmont 2000) were used for data storage, management and mapping. A Gall geographic projection was used for mapping of data (Barbier & Rasmont 2000).

The existing partial keys of Michener (1981) and Popov (1940) were reviewed and updated. Terminology is based on Harris (1979) for description of surface sculpturing and Michener (2000) for general morphology. The following abbreviations are used for morphological structures:

A = Antenna segment (A1 = Scape)

Tb = Tibia

F = Femur

Bt = Basitarsus

S = Sternum

T = Tergum

The integumental ultrastructure of *E. dispar* and *E. popovi* were studied using SEM (JEOL JSM-6100) and processed using the software Semafore (JEOL, Sollentuna, Sweden). The resulting pictures allowed the determination of pollen in the scopa of several females of *E. dispar*.

In the differential diagnosis sections, the combination of characters given is diagnostic for the species except in the case of *E. zhelochovtsevi* for which no such diagnosis is possible as specimens were not available to us.

Results

Catalogue of Eremaphanta Popov 1940

Eremaphanta Popov

Eremaphanta Popov 1940: 53-54. Type species: Rophites vitellinus Morawitz 1892.

Differential diagnosis. \$\pi\$ and \$\sigma\$. Eremaphanta are small desert bees (4–7mm) mostly yellow (Fig. 2). Like other Melittidae, Eremaphanta have a short tongue with all segments of the labial palpus similar to one another. Eremaphanta have two sub-marginal cells like others Dasypodainae but it's the only genus with the stigma as long as the first submarginal cell. Like Hesperapis s.l., a patch of keirotrichia is extensively developed on the inner surface of the Tb3 (Fig. 7a–b).

Diagnosis. § and ♂. Yellow areas at least on mandibles, labrum, clypeus and legs. Galea with short hairs on the outer margin (Figs. 8a–b). Galeal fringe present (Fig. 8b). Mandibles without pre-apical tooth. Malar space shorter than A2. Propodeal triangle hairless, longer than metanotum (Fig. 7c). Propodeum in profile with horizontal and vertical faces subequal (Fig. 7c). Basal vein curved (Fig. 3a). First submarginal cell twice as long as the second (Fig. 3a). Stigma large, transparent, about as long as costal margin of marginal cell; more than three times as long as prestigma (Fig. 3a). Second abscissa of Rs straight (Fig. 3a). Jugal lobe of hind wing equal to 2/3–3/4 of the vannal lobe length. Basitibial plate present. Tibial spurs finely serrated (Fig. 7b). § Bt3 narrower than Tb3, longer than the other tarsomeres. Scopa developed on outer face of Tb3 and Bt3 (Fig. 7a). Keirotrichia extensively developed on inner face of Tb3 and Bt3 (Fig. 7a–b). External face



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of Tb3 and Bt3 with small reddish spots at the base of hairs. Pygidial plate, triangular to subtrapezoidal, hairless, transparent, without elevated median area, apex dorsally curved. Prepygidial and pygidial fimbriae absent. & Hind margin of Tb3 with small reddish spots at the base of hairs. Tarsus 3 one and a half times as long as Tb3. Pygidial plate absent. S6 with dense apical pilosity (Figs. 3c, 5a, 8c). S7 without developed latero-apical structure (Figs. 1a, 3d, 4a, 6a, 8d, 9a). S8 with a short and narrow median groove on external side (Figs. 1b, 3e, 4b, 5b, 6b, 8g, 9b). Apical portion of S8 sloping upwards (Figs. 5b, 8f). Gonostylus simple, about as long as gonocoxite, broadly fused to it (Figs. 1c, 3b, 4c, 5e–f, 6c, 9c).

Subgenus Eremaphanta Popov

Eremaphanta Popov 1940: 53–54. Type species: *Rophites vitellinus* Morawitz 1892 (original designation).

Diagnosis. See table 1.

TABLE 1. Comparative diagnosis of *Eremaphanta* subgenera. An asterisk denotes the derived state.

Characters	Subgenus Eremaphanta	Subgenus Popovapis
Pronotum, scutellum and metanotum	Yellow*	Black
Head	About as long as wide to wider than long	Twice as long as wide*
Labial palpus	As long as glossa, shorter than prementum	Longer than glossa and prementum*
Vertex	Gently convex, slightly enlarged beyond the summits of eyes	Extending strongly beyond the summits of eyes*
Terga	With or without apical hair bands	With apical hair bands

Eremaphanta (Eremaphanta) convolvuli Popov

Eremaphanta convolvuli Popov 1940: 57–58, ♀/♂.

Type material. & holotype, 1\$\psi/4\$ paratypes, Turkmenistan, Dzhebel [39°38'N 54°14'E], 07.VI.1934, leg. Popov, ZISP; 1\$\sigma\$ paratype, idem, 07.VI.1957, leg. Popov, SEMK; 1\$\psi/1\$\sigma\$ paratypes, idem, 05.VI.1934, leg. Popov, ZISP; 2\$\psi/2\$\sigma\$ paratypes, idem, 03.VI.1934, leg. Popov, ZISP. Original designation of the locus typicus: "railway station Djebel and Molla-Kara, Turkmenia"

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Additional material. 1\(\frac{1}{2}\), Turkmenistan, Mollakara [39\(^33\)3'N 54\(^10\)1'E], 09.VI.1934, leg. Popov, ZISP. 1\(^3\), idem, 09.VI.1934, leg. Popov, SEMK; 1\(^3\), Turkmenistan, Repetek [38\(^35\)3'N 63\(^11\)1'E], leg. Golibek, SEMK.

Differential diagnosis. \mathcal{P} and \mathcal{O} . Close to *E. fasciata*. Body widely yellow. Head about as long as wide. Terga without apical hair bands. Labial palpus longer than maxillary palpus.

Diagnosis (Figs. 1–2). $^{\circ}$ and $^{\circ}$. Length = 5–6mm. Head nearly as long as wide, with sparse white appressed hairs. Labial palpus as long as glossa; longer than maxillary palpus. Galea shiny, with narrowly rounded apex. Maxillary palpus shorter than galea (Lpalpus/Lgalea = 0,5). Labrum yellow and smooth; semicircular, nearly four times as wide as long. Clypeus, face and vertex weakly punctate, smooth and shiny. Flagellum dorsally brownish; ventrally yellowish. Genal area black, covered with white short appressed hairs. Mesoscutum entirely black, weakly punctate, smooth and shiny, with short white appressed hairs. Propodeal triangle minutely rugose; median part elevated and more rugose. Posterior half of propodeum smooth and shiny. Legs 1-3 entirely yellow. Terga glabrous. S1-S2 with emarginate premarginal line. S3-S5 with straight apical margin. \(\varphi \). Clypeus entirely yellow, with scarce white hairs. A3-A12 broader than long. Flagellum twice as long as scape. Pronotum, scutellum and axilla yellow. Mesepisternum dorsally yellow, ventrally black. Propodeum and propodeal triangle yellow. Terga yellowish to brown. J. Clypeus with yellowish apex, covered with short white appressed hairs. A3-A4 broader than long. Pronotum medially brown; margins yellow. Scutellum black with yellow apical margin (entirely yellow in some specimens). Metanotum yellow. Mesepisternum, propodeum and propodeal triangle black. External face of Tb3 and Bt3 with small reddish spots at the base of the hairs; with scopa-like hairs. Bt3 shorter than other tarsomeres. T1 brownish. T2-T6 yellowish to brown. Gonostylus as long as penis valve (Fig. 1). S7-S8 and genitalia as figured in Popov (1940) (Fig. 1).

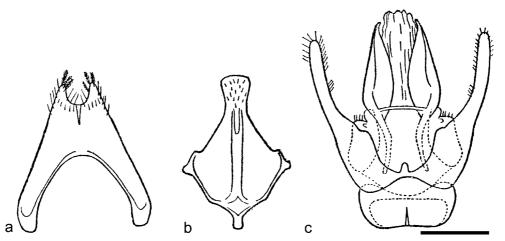


FIGURE 1. *Eremaphanta convolvuli*, male (scale=300μm); a. Sternum 7; b. Sternum 8; c. Dorsal view of genitalia; from Popov (1940).



Distribution (Fig. 11c). Turkmenistan.

Floral choices. Convolvulaceae: *Convolvulus ericaneus* Led. (7º, 11♂; see Popov 1940)

First - last observations. 03.VI-09.VI

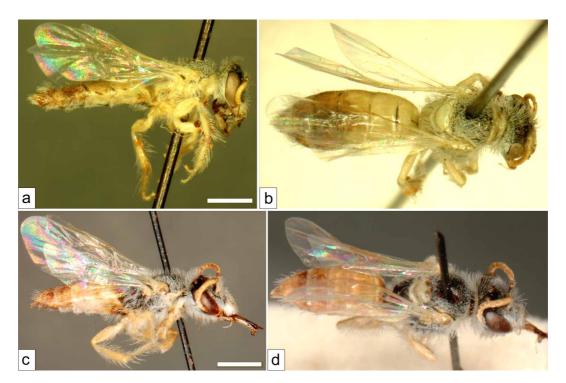


FIGURE 2. *Eremaphanta convolvuli*, a–b: female (scale=1mm); c–d: male (scale=1mm); a. Lateral view of the general habitus of the female; b. Dorsal view of the general habitus of the female; c. Lateral view of the general habitus of the male.

Eremaphanta (Eremaphanta) fasciata Popov

Eremaphanta fasciata Popov 1957: 1705–1706, ♀.

Type material. \$\pi\$ holotype, 13\$\pi\$ paratypes, Turkmenistan, Uch-Adzhi [38\circ{0}5\cdot N 62\circ{4}8\cdot E], 01_03.V.1929, leg. Shestakov, ZISP; 1\$\pi\$ paratype, idem, 01_03.V.1929, leg. Shestakov, SEMC. Original designation of the locus typicus: "Uch-Adzhi (Turkmenia), Bairam-Ali (Turkmenia), Tamdy (Uzbekistan)".

Additional material. 2\(\frac{9}{2}\), Turkmenistan, Jebel [39\(^38\)'N 54\(^14\)'E], 28.IV.1993, leg. Denes, OOLL; 1\(^14\), Turkmenistan, Nebitdag [39\(^33\)'N 54\(^22\)'E], 01.V.1993, leg. Denes, OOLL; 1\(^14\), Turkmenistan, Bairam-Ali [37\(^33\)'N 62\(^10\)'E], 28.V.1929, leg. Shestakov, ZISP; 1\(^14\), Uzbekistan, Tamdy [41\(^09\)'N 67\(^44\)'E], 19.V.1935, leg. Andrushko, ZISP; 1\(^14\),

Turkmenistan, Akhcha-Kuyma [39°21'N 55°10'E], 12–15.V.1977, leg. Pesenko, ZISP.

Popov (1957) described only the female of *E. fasciata*. We give here the first description for the male, based on two specimens from Turkmenistan: Orta-Kuyu [40°42'N 57°30'E], 29.V.1953, M. Arens, ZISP. Although there is no female associated with these males, the specimens are morphologically very close to the Popov species, and this leads us to describe them as the unknown sex of *E. fasciata*. Mouthparts are not described because they are hidden in the specimens.

Differential diagnosis. \mathcal{L} and \mathcal{L} . Close to E. convolvuli. Body widely yellow. Head about as long as wide. Terga without apical hair bands. Labial palpus shorter than maxillary palpus.

Diagnosis (Fig. 3). \(\frac{1}{2} \) and \(\sigma^2 \). Labrum semicircular. Flagellum dorsally brownish, ventrally yellow. Pronotum brown in the middle; margins yellow. Mesoscutum black, with few short erect white hairs. Mesepisternum black. Propodeum black, smooth and shiny. Anterior part of propodeum weakly rugose; with a minute median groove. Propodeal triangle with smooth and shiny apical area. Discs of T1-T5 glabrous. 9. Head entirely black (clypeus apex yellow in some specimens), weakly punctate, cuticle smooth, with few white erect hairs, mainly around antennal sockets. Labial palpus as long as glossa, half as long as maxillary palpus. Galea tapering; surface smooth and shiny, weakly punctate; distance between punctures wider than puncture diameter. Maxillary palpus as long as galea. Clypeus hairless. Flagellum twice as long as scape. Genal area black covered with white short appressed hairs. Scutellum and axilla yellow. F1-F3 yellow with brown spots. Discs of T1-T5 yellow on basal half; brown on apical half. S3-S5 with straight premarginal line. J. Clypeus, face and vertex with white erect hairs. Mesoscutum, propodeum and propodeal triangle black. External face of Tb3 and Bt3 with small reddish spots at the base of hairs. T1-T6 with a median black stripe; basal and apical margins yellow. Gonostyli longer than penis valve. S6-S8 and genitalia as in Figs. 3b-e.

Description (Fig. 3). & Length (vertex-T7) = 5,2mm. Head. Length = 1,4mm. Maximal width = 1,6mm. Head integument black but yellow on mandible base, labrum, malar area and apex of clypeus. Flagellum dorsally brown, ventrally yellow. Labrum with long white apical hairs. Clypeus, face and vertex with white erect hairs. Genal area covered with white short appressed hairs. Face and vertex smooth and shiny, with few weak punctures. Flagellum three times as long as scape. A3 shorter than A4. A3 and A4 broader than long. A5-A12 as long as wide. Mesosoma. Length = 1,9mm. Maximal width = 1,3mm. Integument black; yellow on apical margin of pronotum, apical half of scutellum and metanotum. Mesoscutum and mesepisternum with white short appressed hairs. Scutellum and metanotum glabrous. Propodeum with white erect hairs. Propodeal triangle hairless. Mesoscutum, mesepisternum, scutellum and metanotum smooth and shiny, with few weak punctures. Propodeum in profile with horizontal and vertical surfaces subequal. Propodeal triangle very wide, shiny; rugose basally, apex and lateral margins smooth, with minute median groove. Legs. Integument entirely yellow with long white setae; without

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differentiated structures such as in some species of *Capicola* and *Dasypoda*. External face and external margin of Tb3 and Bt3 with small reddish spots at base of hairs. Tarsal claws simple. Basitarsus narrower than femur. Wings. Tegula yellow but transparent. First submarginal cell twice as long as second (Fig. 3a). Stigma large, transparent, approximately as long as costal margin of marginal cell and more than three times as long as prestigma (Fig. 3a). Second abscissa of Rs straight. Jugal lobe equal to 2/3 to over 3/4 of vannal lobe length. Metasoma. Length = 2,8mm. Maximal width = 1,5mm. T1-T6 with a transverse black stripe, basal and apical margins yellow. Sterna yellow. Disc of T1 with some erect white hairs. Discs of T2-T5 glabrous. S1-S5 with premarginal line slightly emarginate. S1-S5 with whitish apical hair band. S6-S8 and genitalia as in Figs. 3b—e.

Distribution (Fig. 11b). Turkmenistan and Uzbekistan.

Floral choices. Unknown.

First - last observations. 15.IV-29.V

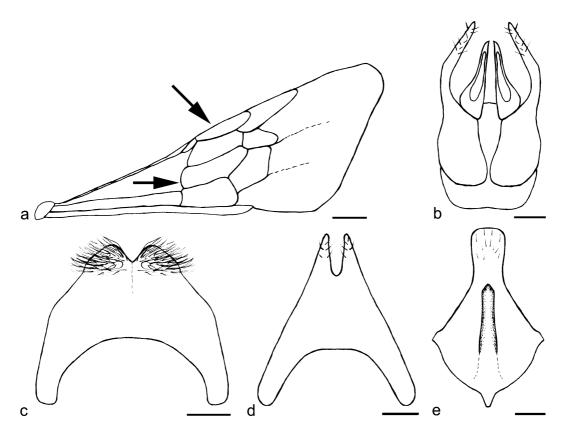


FIGURE 3. *Eremaphanta fasciata*, male (scale=200μ); a. Anterior wing, basal vein curved (left arrow), stigma (right arrow); b. Dorsal view of genitalia; c. Sternum 6; d. Sternum 7; e. Sternum 8.

Eremaphanta iranica Schwammberger 1971: 1, &.

Type material. ♂ holotype, 3♂ paratypes, Iran, Tiz bei Chahbar [25°18'N 60°38'E], 25.III.1954, leg. R.U. Schäuffele, SMNS. Original designation of the locus typicus: "*Tiz bei Chahbar, Iran*".

Additional material. 1 °, Oman, Ruwi [23°35'N 58°32'E], III. 1976, leg. Guichard, NHM.

Differential diagnosis. $^{\circ}$ and $_{\circ}$. Body mainly black. Head about as long as wide. Terga without apical hair bands. Marginal zone of T1-T4 with few appressed hair on lateral margins.

Diagnosis (Fig. 4). §. Unknown. J. Tb1-Tb3 and tarsi yellow; other parts of the body entirely black. Head nearly as long as wide. Antennae dorsally brownish, ventrally yellowish. Propodeal triangle dull and rugose. Disc of terga with short brown appressed hairs. Marginal zone of T1-T4 with few appressed hair on lateral margins. Premarginal line of S1-S5 slightly emarginate or straight. S7-S8 and genitalia as figured by Schwammberger (1971) (Fig. 4).

Distribution (Fig. 11b). Iran and Oman.

Floral choices and phenology. Unknown.

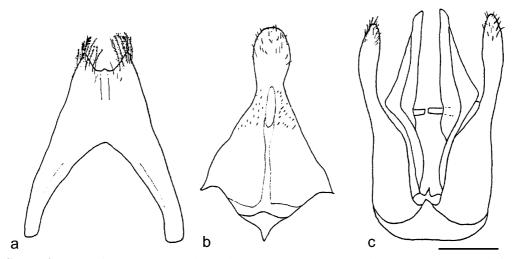


FIGURE 4. *Eremaphanta iranica*, male (scale=300µm); a. Sternum 7; b. Sternum 8; c. Dorsal view of genitalia; from Schwammberger (1971).

Eremaphanta (Eremaphanta) minuta Popov

Eremaphanta minuta Popov 1957: 1706–1707, ♀.

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Type material. ♀ holotype, Turkmenistan, Repetek [38°35'N 63°11'E], leg. Pazhitnova, ZISP. Original designation of the locus typicus: "*Repetek, Turkmenia*".

Only one specimen of *E. minuta* is currently known (ZISP). Unfortunately, the mouthparts are hidden.

Additional material. None.

Diagnosis. \mathcal{L} . Similar to *E. popovi* but slightly smaller. Length = 4mm. Body mainly yellow. Propodeal triangle and legs yellow. T1-T4 with short apical yellowish hair bands. \mathcal{L} , Unknown.

Distribution (Fig. 11c). Turkmenistan.

Floral choices and phenology. Unknown.

Eremaphanta popovi Michez sp.nov.

Type Material. 1 & holotype, 6 & paratypes, Turkmenistan, Orta-Kuyu [40°42'N 57°30'E], 23.V.1953, leg. Arens, ZISP. Original labelling (label with black ink printed on white paper): Orta-Kuyu 23.V.1953 Arens [in Cyrillic].

Additional material. 1 °, Turkmenistan, Orta-Kuyu [40°42'N 57°30'E], 23.V.1953, leg. Arens, SEMK. 1 °, Kazakhstan, desert of Kysylkum, Dyusebay [42°24'N 66°58'E], determined as *E. vitellina* by Morawitz, ZISP. The head of the specimen is missing. However, several morphological characters support its identification as *E. popovi*. Both sexes have a yellow metasoma and terga with apical hair bands (see diagnosis and description). This combination of characters is unique in *Eremaphanta*.

Etymology. Named in honour of V. V. Popov who described the genus.

Differential diagnosis. \mathcal{P} and \mathcal{P} . Close to *E. minuta*. Body mainly yellow. Head about as long as wide. Terga with apical hair bands.

Diagnosis (Fig. 5). ♀ and ♂. Legs yellow. T1-T5 yellow, with white apical hair bands. ♀. Mesepisternum with upper part yellow, lower part black. Mesoscutum black. Pronotum yellow. ♂. Head nearly as long as broad. Genal area, dorsal half of face and propodeum yellow. Flagellum dorsally brownish, ventrally yellowish. Pronotum brown in the middle; margins yellow. Hind margin of Bt3 and F3 with small reddish spots at the base of hairs.

Description. §. Head. Unknown. Mesosoma. Length = 2,3mm. Maximal width = 1,5mm. Pronotum, upper part of mesepisternum, scutellum, metanotum and propodeum yellow; Mesoscutum and lower part of mesepisternum black. Mesoscutum and mesepisternum with short white appressed hairs. Scutellum, metanotum and propodeum with white erect hairs. Propodeal triangle hairless. Mesoscutum, scutellum and metanotum smooth, shiny, weakly punctate. Propodeum in profile with horizontal and vertical surfaces subequal. Propodeal triangle minutely rugose with a median groove. Legs. Integument yellow. Scopa on outer surface of Tb3 and Bt3; with conspicuous reddish spots at the base of hairs. Keirotrichia on inner surface of Tb3 and Bt3. Wings. Tegula yellow and transparent. First submarginal cell twice as long as the second. Stigma large,



transparent, about as long as costal margin of marginal cell; up to three times as long as prestigma. Second abscissa of Rs straight. Jugal lobe 2/3 to 3/4 as long as vannal lobe. Metasoma. Length = 3,3mm. Maximal width = 1,6mm. Terga yellow; disc glabrous, T1-T5 with white apical hair bands. Sterna glabrous. Margin of terga and sterna straight. Pygidial plate flat, hairless, transparent, triangular; apex briefly truncated and dorsally curved. Prepygidial and pygidial fimbria absent. ♂ (Fig. 5). Length (vertex-T7): 5,3mm. ♂. Head. Length = 1,5mm. Maximal width = 1,8mm. Integument black, but mandible base, labrum, malar area and clypeus yellow. Flagellum dorsally brown, ventrally yellow. Labrum with long white apical hairs. Clypeus, face and genal area covered with white short appressed hairs. Vertex with white erect hairs. Labial palpus as long as glossa; shorter than prementum, maxillary palpus and galea. Galea with short setae on the outer margin, tapering, narrowly rounded. Mandibles without pre-apical tooth. Malar space shorter than A2. Face and vertex smooth and shiny, with few weak punctures. Flagellum four times as long as scape. A3 shorter than A4. A3 broader than long. A4 as long as broad. A5-A12 longer than wide. Mesosoma. Length = 2mm. Maximal width = 1,6mm. Mesoscutum, mesepisternum, propodeum and propodeal triangle black. Pronotum, apical and basal margin of scutellum and metanotum yellow. Mesoscutum and mesepisternum with white short appressed hairs. Scutellum and metanotum glabrous. Propodeum with white erect hairs. Propodeal triangle hairless. Mesoscutum, mesepisternum, scutellum and metanotum smooth and shiny, with few weak punctures. Propodeum in profile with horizontal and vertical surfaces subequal. Propodeal triangle large, shiny, minutely rugose with a median groove; apical area smooth. Legs. Integument yellow, with long white setae. External margin of Bt3 and F3 with small reddish spots at the base of hairs. Tarsal claw simple. Basitarsus narrower than femur. Wings. Venation similar to that of female. Metasoma. Length = 2,8mm. Maximal width = 1,5mm. Terga yellow except basal half of T1 brownish. T1 with few white erect hairs basally. Disc of T2-T5 glabrous. T1-T5 with white apical hair bands. S1-S5 with white apical hair bands, longer medially. S1-S4 with premarginal line strongly emarginate. S6-S8 and genitalia as in Fig. 5.

Distribution (Fig. 11c). Kazakhstan and Turkmenistan.

Floral choices and phenology. Unknown.

Eremaphanta (Eremaphanta) turcomanica Popov

Eremaphanta turcomanica Popov 1940: 1704–1705, ♀.

Type material. ♀ holotype, Turkmenistan, 1895, leg. Ahnger, ZISP. Original designation of the locus typicus: "*Turkmenia*".

Additional material. None.

Differential diagnosis. \mathcal{P} and \mathcal{P} . Close to *E. vitellina*. Body yellow. Head one and half times wider than long. Mesoscutum mostly yellow. Terga without apical hair bands.

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Diagnosis. \(\frac{9}{2} \). Length = 6,5mm. Body almost entirely yellow, except black spots along inner margins of eyes, median portion of mesoscutum and bases of S1-S5. Galea yellow. Face and clypeus glabrous. Vertex with dense white erect hairs. Genal area yellow, with white short erect hairs. Head shiny and weakly punctate. Clypeus three times broader than long. Flagellum short, one and a half times as long as scape. A3-A12 broader than long. Propodeal triangle yellow, minutely rugose, with a median groove. T1-T5 glabrous, without apical hair bands. Premarginal line of sterna emarginate. \(\sigma \). Unknown.

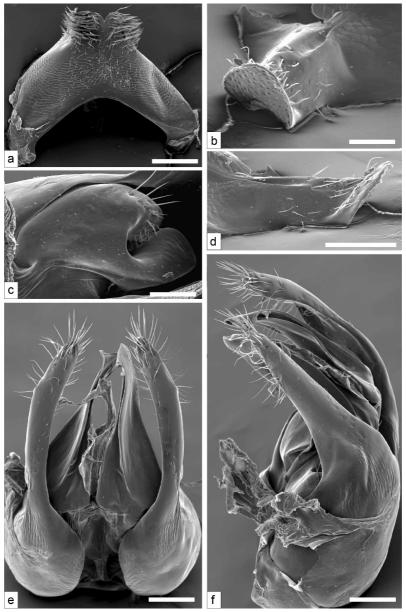


FIGURE 5. *Eremaphanta popovi* sp. nov., male; a. Sternum 6 (scale= $200\mu m$); b. Apical view of sternum 8 (scale= $40\mu m$); c. Volsella (scale= $40\mu m$); d. Lateral view of sternum 8 (scale= $100\mu m$); e. Dorsal view of gonostylus (scale = $100\mu m$); f. Lateral view of genitalia (scale = $100\mu m$).

Eremaphanta (Eremaphanta) vitellina (Morawitz)

Rophites vitellinus Morawitz 1875: 72–73, ♀/♂.

Type material. 1♀ and 4♂ syntypes, Kazakhstan, desert of Kysylkum, Dyusebay [42°24'N 66°58'E], leg. Morawitz, designation of type by Popov, ZISP. Original designation of the locus typicus: "*Derserto Kisilkum, Okolo Kolodtsa Dyusebaj*".

Only one female is known (ZISP), its head is missing.

Additional material. None.

Differential diagnosis. \mathcal{P} and \mathcal{O} . Close to *E. turcomanica*. Body mainly yellow. Head one and half times wider than long. Mesoscutum mostly black. Terga without apical hair bands.

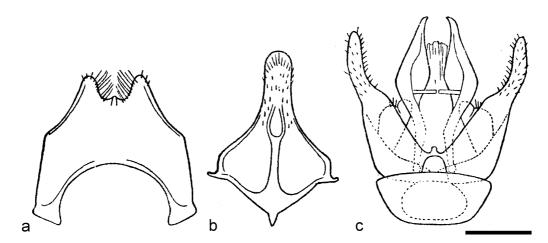


FIGURE 6. *Eremaphanta vitellina*, male (scale=300µm); a. Sternum 7; b. Sternum 8; c. Dorsal view of genitalia; from Popov (1940).

Diagnosis (Fig. 6). ♀. Length = 5–6mm. Pronotum, margins of mesoscutum, mesepisternum, scutellum, metanotum, propodeum and propodeal triangle yellow. Propodeal triangle rugose, with median groove. Legs and metasoma yellow. T1-T5 with glabrous disc, without apical hair bands. S2-S3 with emarginate premarginal line. ♂. Head one and a half times wider than long. Face with ventral half (including clypeus) and genal area yellow. Clypeus, face and vertex with white short erect hairs. Flagellum yellow. Galea yellow, tapering, apex narrowly rounded. Maxillary palpus longer than galea. A3-A5 broader than long. Pronotum, margin of mesoscutum, mesepisternum, axilla, metanotum and propodeum yellow. Scutellum partly yellow, at least on margins. Propodeal triangle

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brown. Mesosoma with few white erect hairs. Propodeal triangle hairless. Legs yellow. F3 with few long white hairs. Tarsus 3 longer than Tb3. Bt3 as long as other segments. Metasoma yellow. Discs of T1-T5 glabrous, without apical hair bands. S7-S8 and genitalia as figured in Popov (1940) (Fig. 6).

Distribution (Fig. 11b). Kazakhstan.

Floral choices and phenology. Unknown.

Subgenus Popovapis Michener

Eremaphanta (*Popovapis*) Michener 1981: 80. Type species: *Rophites dispar* Morawitz 1892 (original designation).

Diagnosis. See table 1.

Eremaphanta (Popovapis) dispar (Morawitz)

Rophites dispar Morawitz 1892: 139–141, ♀/♂.

Type material (designated here). ♂ lectotype, 1♂ and 2♀ paralectotypes, Turkmenistan, Dort-Kuyu [37°38'N 61°18'E], 05.V.1888, leg. Semenov, ZISP. Original designation of the locus typicus: "*Dort-kuju*".

Lectotype & (ZISP), labels: 1st, handwritten with black ink on white paper "Dort-kuju 5.V.88 Semenow" (in Cyrillic); 2nd printed on white paper "K.. F. Morawitz" (in Cyrillic); 3rd handwritten with black ink on white paper "Rophites dispar & F. Mor."; 4th handwritten with black ink on red paper "Lectotype Rophites dispar Mor. Design Michez D. 2005". Paralectotypes & (ZISP), labels: 1st, handwritten with black ink on white paper "Dort-kuju 5.V.88 Semenow" (in Cyrillic); 2nd printed on white paper "K. F. Morawitz" (in russian Cyrillic); 3rd handwritten with black ink on white paper "Rophites dispar & F. Mor."; 4th handwritten with black ink on red paper "Paralectotype Rophites dispar Mor. Design Michez D. 2005". 2 \(\frac{1}{2}} \) (ZISP); labels: 1st, handwritten with black ink on white paper "K. F. Morawitz" (in Cyrillic); 3rd handwritten with black ink on white paper "Rophites dispar \(F. Mor."; 4th handwritten with black ink on red paper "Paralectotype Rophites dispar \(F. Mor."; 4th handwritten with black ink on red paper "Paralectotype Rophites dispar Mor. Design Michez D. 2005".

Additional material. 69/2\$\sigma\$, Kazakhstan, Aksuek [44°45'N 74°21'E], 29.VI.1979, on *Cousinia shestopter* (Asteraceae), leg. Pesenko, ZISP; 6\$\sigma\$, idem, 27.VI.1979, on *Cousinia shestopter* (Asteraceae), leg. Pesenko, ZISP; 1\$\circ\$, Pakistan, Pishin [30°35'N 67°00'E], 23.V.1984, leg. Rozen, AMNH; 1\$\circ\$, idem, 27.V.1984, leg. Rozen, AMNH; 1\$\circ\$, idem, 27.V.1984, leg. Rozen, SEMK; 106\$\sigma\$, Turkmenistan, Badkhyz [35°34'N 62°00'E],

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05.VI.1976, on *Cousinia shestopter* (Asteraceae), leg. Pesenko, ZISP; 3\$/1\$ σ , Turkmenistan, Imambaba [36°45'N 62°28'E], 1932, ZISP; 2\$ σ , idem, 08.V.1912, ZISP; 2\$ σ , Turkmenistan, Mary [37°38'N 61°50'E], 28.V.1976, on *Statice* sp. (Plumbaginaceae), leg. Pesenko, ZISP; 9\$ σ , Turkmenistan, Orta-Kuyu [40°42'N 57°30'E], 29.V.1953, ZISP; 3\$ σ , Turkmenistan, Tash-Kepri [36°03'N 62°43'E], 14.V.1954, ZISP; 1\$ σ , idem, 14.V.1954, SEMK; 12\$ σ , idem, 28.V.1954, ZISP; 1\$ σ /4\$ σ , idem, 28.V.1954, ZISP; 2\$ σ /4\$ σ , idem, 01.VI.1954, SEMK; 1\$ σ , idem, 01.VI.1954, AMNH; 10\$ σ , idem, 04.VI.1954, ZISP; 1\$ σ , idem, 04.VI.1954, SEMK; 1\$ σ , idem, 08.VI.1954, ZISP; 1\$ σ /6\$ σ 0, Uzbekistan, Mubarek [39°16'N 65°09'E], 15.V.1978, on *Convolvulus* sp. (Convolvulaceae), leg. Pesenko, ZISP.

Differential diagnosis. \mathcal{P} and \mathcal{P} . Close to *E. zhelochovtsevi*. Body mainly black. Head twice as long as wide. Terga with apical hair bands. Labrum twice as wide as long.

Diagnosis (Figs. 7–8). $\,^{\circ}$ and $\,^{\circ}$. Length = 5mm. Head black, twice as long as broad; few white erect hairs on vertex and around antennal sockets. Labial palpus elongated, longer than glossa, twice as long as maxillary palpus (Figs. 8a–b). Galea shiny, semicircular, tapering narrowly rounded (Figs. 8a–b). Labrum long, smooth and shiny (Fig. 8a). Clypeus with yellow apical margin. Genal area black, covered with white short appressed hairs. Mesosoma black, with white short appressed hairs. T1-T5 with apical hair bands. Disc of T1-T5 glabrous. $\,^{\circ}$. Flagellum twice as long as scape. Flagellum dorsally brown, ventrally reddish. F1 yellow, black at the base. Legs 2–3 yellow. Metasoma brownish. S1-S4 with premarginal line weakly emarginate. $\,^{\circ}$. Flagellum three times as long as scape. Flagellum dorsally brown, ventrally reddish. F1-F3 black. Tb1-Tb3 black with yellow apex. Tarsi 1–3 yellow. Metasoma black. T2-T4 with lateral patches of short appressed hairs. S6-S8 see Figs. 7c–g. Genitalia as figured in Popov (1940).

Distribution (Fig. 11a). Kazakhstan, Pakistan, Turkmenistan and Uzbekistan.

Floral choices. Asteraceae, *Cousinia shestopter* $(6^{\circ}, 114^{\circ})$; Convolvulaceae, *Convolvulus* sp. $(1^{\circ}, 6^{\circ})$; Plumbaginaceae, *Statice* sp. (2°) . Moreover, tricolporate pollen (very similar to the *Convolvulus* one) are observed on the pictures of scopae (Figs. 7a–b) of the females collected on Asteraceae.

First - last observations. 08.V-29.VI

Eremaphanta (Popovapis) zhelochovtsevi Popov

Eremaphanta zhelochovtsevi Popov 1957: 1707–1708, ♂.

Type material. & holotype, Tajikistan, Aivadzh [36°59'N 68°02'E], 15.IX.1934, leg. Zhelochovtsev, ZMMU. Original designation of the locus typicus: "Aivadzh, Tadjikistan". Additional material. None.

Diagnosis (Fig. 9). ♂. Length = 6mm. Clypeus protruding. Labrum twice as wide as long (see Popov 1957).

Distribution (Fig. 11a). Tajikistan. Floral choices and phenology. Unknown.

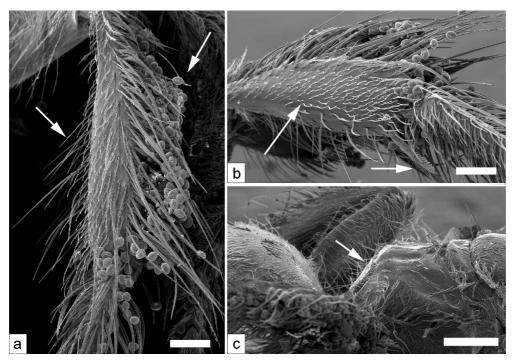


FIGURE 7. *Eremaphanta dispar* female; a. Tibia 3, inner surface with keirotrichia (left arrow), outer surface with scopa and tricolporate pollen (right arrow) (scale=100μm); b. Tibia 3, facial view of keirotrichia (left arrow), spur finely serrated (right arrow) (scale=100μm); c. Propodeum in profile view, half horizontal and half vertical (arrow) (scale=300μm).

Key to species

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	pletely black5
4.	Mesoscutum mainly black, yellow on marginal parts. S2-S4 yellow with a dark medio-
	basal spot. Premarginal line of S2-S3 emarginate
-	Mesoscutum mainly yellow with two median black spots. S2-S4 yellow with numer-
	ous small black spots on basal part. Premarginal line of S2-S3 straight. E. turcomanica
5.	Terga with apical hair bands6
_	Terga without hair band
6.	Body length < 4mm
_	Body length round 6mm
7.	Clypeus black (apical margin yellow in some specimens) and glabrous. Pronotum
	brown on median part, yellow on margins. Propodeum black. Basis of F1-F3 brown
	T1-T5 yellow anteriorly, brown distally. Labial palpus shorter than maxillary palpus;
	maxillary palpus as long as galea. Apex of galea pointed
_	Clypeus yellow, with white erect hairs. Pronotum, propodeum and femora yellow
	(Figs. 2a–b). T1-T5 anterior part yellowish to brown. Labial palpus longer than maxil-
	lary palpus. Maxillary palpus half as long as galea; Apex of galea narrowly rounded
	E. convolvuli
8.	Head nearly one and a half times wider than long. Antennae and pronotum entirely
	yellow. Cuticle coloration notably bright
-	Head nearly as long as wide. Antennae dorsally brownish, ventrally yellowish. Prono-
	tum medially black or brown, yellow or black on margins. Cuticle coloration
	yellow pale9
9.	Terga with continuous apical hair bands. Clypeus entirely yellow. Premarginal line of
	S1-S5 strongly emarginate
-	Terga without continuous apical hair bands. Clypeus with base yellow or entirely
	black. Premarginal line of S1-S5 slightly emarginate or straight
10.	Labrum, F1-F3 and terga entirely black. Marginal zone of T1-T4 with few appressed
	hairs on lateral margins. Disc of terga with short brown appressed hairs E. iranica
-	Labrum, F1-F3 and terga entirely yellow. Marginal zone of T1-T4 glabrous. Disc of
	terga glabrous
11.	T1-T6 mostly black, with yellow basal and apical margins. Propodeal triangle without
	median elevated area; lateral parts smooth. Clypeus with white erect hairs. Gonostyli
	longer than penis valves (Fig. 3b)
-	T1-T6 entirely yellowish or brownish (Figs. 2c-d). Propodeal triangle with a median
	convexity more rugose; lateral parts rugose. Clypeus covered with short white
	appressed hairs. Gonostyli as long as penis valves (Fig. 1c) E. convolvula
12.	Clypeus protruding. Labrum twice as wide as long E. dispar
-	Clypeus flat. Labrum more than twice as wide as long E. zhelochovtseva

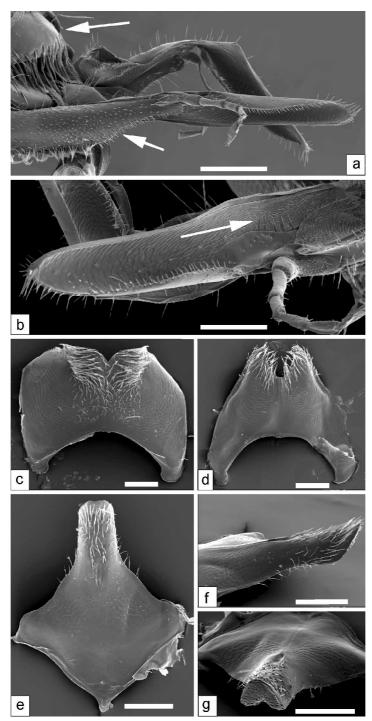


FIGURE 8. Eremaphanta dispar, male; a. Labrum (left arrow), external view of tongue, maxillary stipes with large concavity in posterior margin (right arrow) (scale= $200\mu m$); b. Inner view of galea with a fring (arrow) (scale= $100\mu m$); c. Sternum 6 (scale= $100\mu m$); d. Sternum 7 (scale= $100\mu m$); e. Dorsal view of sternum 8 (scale= $100\mu m$); f. Lateral view of sternum 8 (scale= $100\mu m$); g. Apical view of sternum 8 (scale= $100\mu m$).

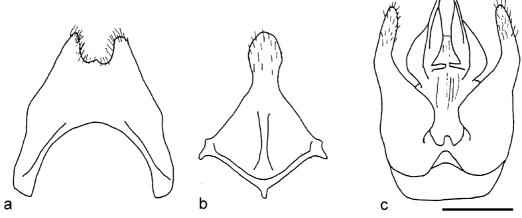


FIGURE 9. *Eremaphanta zhelochovtsevi*, male (scale=300μm); a. Sternum 7; b. Sternum 8; c. Dorsal view of genitalia; from Popov (1957).

Discussion

Morphology and taxonomy

Several important features: the ratio between palpi and glossa lengths; the development of apical bands on terga and the appearance (sculpture, coloration) of the propodeal triangle, allow the characterisation of most species in the genus. The coloration patterns of the integument are also specific. On the contrary, the morphology of the genitalia and hidden sterna (S6-S8) is almost uniform among species. Whereas these structures are diagnostic in most groups of Apoidea, notably in other Melittidae (Michener 2000; Michez *et al.* 2004a,b; Michez & Patiny 2005).

The yellow markings are one main characteristic of *Eremaphanta*. In most species, the integument coloration provides evidence for the association of the sexes. In the five species for which both sexes are described: *E. convolvuli*, *E. dispar*, *E. fasciata*, *E. popovi* and *E. vitellinus*, the coloration patterns are quite similar in males and females. The above description of the unknown male in *E. fasciata* is based on this usual resemblance in the male and female habitus. We have to emphasize that, contrary to the situation in other Melittidae (*Macropis*, Meganomiinae and *Promelitta*), these markings are generally wider in females of *Eremaphanta* than in males (Michener 1981; Michez & Patiny 2005).

Numerous characters supporting the subdivision of the genus into *Eremaphanta* s.str. and *Popovapis* are listed in the previous subgeneric diagnoses (table 1). However, the absence of apical hair bands on the terga, used by Michener (1981) as a diagnostic character for subgenera, is obviously not typical to the subgenus *Eremaphanta* s.str. Such apical hair bands are present in *E.* (*Eremaphanta*) popovi and *E.* (*Eremaphanta*) minuta.

At a higher taxonomic level, while *Eremaphanta* is presently grouped with *Hesperapis* within the Hesperapina (Engel 2005), the conformation of their S6-S8 and genitalia closely resemble the subgenus *Dasypoda* (*Microdasypoda*) (Michez *et al.* 2004b). The



phylogenetic relationships of *Eremaphanta* need to be re-evaluated based through a global phylogenetic analysis of Dasypodainae.

Biogeography

Eremaphanta species are almost endemic and sympatric in the xeric part of Turkestan (Kazakhstan, Tajikistan, Turkmenistan, Uzbekistan; see Terzo & Rasmont (2004) for the description of this geographical area) (Fig. 10b; Popov 1955). Two species were recorded outside these limits: *E. iranica* in the south of Iran and the north of Oman (Fig. 11b) and *E. dispar* in Pakistani Baluchistan (Fig. 11a). This range contrasts strongly with the general rarity of other Melittidae in this xeric part of the Palaearctic (Michez *et al.*, 2004; Michez & Patiny, 2005).

In addition, while in most Apoidea, faunal affinities between Central Asia and the Mediterranean basin are obvious (Terzo & Rasmont, 2004), the endemism of *Eremaphanta* is a notable exception. The phylogenetic relationships among genera in Dasypodaini being still poorly known, drafting a phylogeographical hypothesis for the biogeographic history of *Eremaphanta* species is not possible. The strong geographical concentration of all the described species and their nearly complete allopatry with other Melittidae, suggest that *Eremaphanta* could be a relict genus with a long period of isolation in Central Asia.

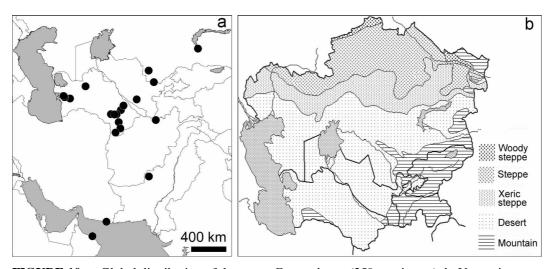


FIGURE 10. a. Global distribution of the genus *Eremaphanta* (259 specimens); b. Vegetation map of Turkestan (according to Terzo and Rasmont, 2004).

Ecology

Eremaphanta, like several groups ranging in subdesertic areas (such as Camptopoeum Spinola (Andrenidae), Nomioides Schenk (Halictidae), Capicola Friese (Melittidae) or Pararophites Friese (Fideliinae)) show convergence in some morphological features: small size, yellow (or whitish) marks and short appressed whitish hairs (Patiny 2001;

Pesenko & Pauly 2005). We can hypothesise that these characters are, at least partially, adaptations to thermoregulation in xeric conditions and for camouflage against desert sands.

Like most genera in the Melittidae, *Eremaphanta* species are oligolectic on some groups of plants (Eickwort & Ginsberg 1980; Popov 1940, 1957; Stage 1966; Michez *et al.* 2004b; Michez & Patiny 2005). The literature overview and our studies of the available series suggest a strong orientation of floral choices toward some plant taxa in Euasteridae. *Convolvulus* and *Cousinia* seem to be resources for *E. convolvuli* and *E. dispar* respectively. Tricolporate pollen (*Convolvulus* sp. like) has been determined in the scopa of several specimens of *E. dispar* (Figs. 7a–b).

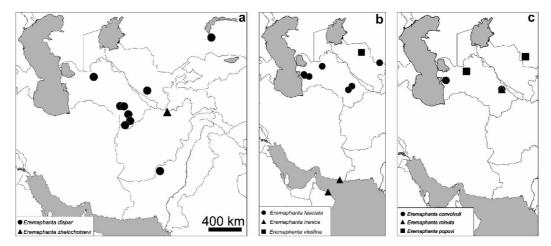


FIGURE 11. Specific distribution; a. Distribution of *Eremaphanta dispar* and *E. zhelochovtsevi*; b. Distribution of *E. fasciata*, *E. iranica* and *E. vitellina*; c. Distribution of *E. convolvuli*, *E. minuta* and *E. popovi*.

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References



- Barbier, Y. & Rasmont, P. (2000) *Carto Fauna-Flora 2.0. Guide d'utilisation*, Université de Mons-Hainaut, Mons (Belgium), 59 pp.
- Barbier, Y., Rasmont, P., Dufrne, M. & Sibert, J.M. (2000) *Data Fauna-Flora. Guide d'utilisation*, Université de Mons-Hainaut, Mons (Belgium), 107 pp.
- Eickwort, G. C. & Ginsberg, H. S. (1980) Foraging and mating behavior in Apoidea. Annual Review of Entomology, 25, 421–446.
- Engel, M.S. (2001) A monograph of the Baltic Amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History*, 259, 1–192.
- Engel, M.S. (2005) Family-Group Names for Bees (Hymenoptera: Apoidea). *American Museum Novitates*, 3476, 1–33.
- Harris, R.A. (1979) A Glossary of Surface sculpturing. Occasional Papers in Entomology, 28, 1–31.
- Michener, C.D. (1981) Classification of the bee family Melittidae with a review of species of Meganomiinae. *Contribution of the American Entomological Institute*, 18, 1–135.
- Michener, C.D. (2000) The bees of the world, The Johns Hopkins University Press, Baltimore, 913 pp.
- Michez, D., Terzo, M. & Rasmont, P. (2004a) Révision des espèces ouest-paléarctiques du genre *Dasypoda* Latreille 1802 (Hymenoptera, Apoidea, Melittidae). *Linzer biologische Beiträge*, 36, 847–900.
- Michez, D., Terzo, M. & Rasmont, P. (2004b) Phylogénie, biogéographie et choix floraux des abeilles oligolectiques du genre *Dasypoda* Latreille 1802 (Hymenoptera, Apoidea, Melittidae). *Annales de la Société entomologique de France (n.s.)*, 40, 421–435.
- Michez, D. & Patiny, S. (2005) World revision of the oil-collecting bee genus *Macropis* Panzer 1809 (Hymenoptera, Apoidea, Melittidae) with a description of a new species from Laos. *Annales de la Société entomologique de France* (n.s.), 41, 15–28.
- Morawitz, F. (1875) Bees (Mellifera). [I. Apidae genuinae]. *In*: von Kaufmann, K. P., *Travel to Turkestan by A. P. Fedtschenko*, Society of Naturalists Anthropologists and Etnographists, Moscow, pp. 1–160 pp.
- Morawitz, F. (1892) Hymenoptera Aculeata Rossica Nova. Horae Societatis Entomologicae Rossicae, 26, 132–181.
- Patiny, S. (2001) *Monographie des Panurginae de l'ancien monde (Hymenoptera: Apoidea, Andrenidae)*, Ph-D, Faculté universitaire des Sciences agronomiques de Gembloux, Gembloux (Belgium), 266 pp.
- Pesenko, Y.A. & Pauly, A. (2005) Monograph of the Bees of the Subfamily Nomioidinae (Hymenoptera: Apoidea) of Africa (excluding Madagascard). *Annales de la Société entomologique de France (n.s.)*, 41, 129–236.
- Popov, V.V. (1940) A new genus of bees from Turkestan (Hymenoptera, Panurgidae). *Travaux de l'Institut Zoologique de l'Académie des Sciences de l'U.R.S.S.*, 6, 53–59. [in english and russian]
- Popov, V. V. (1955). The zoogeography of the genus *Eremaphanta* (Hymenoptera, Melittidae). *Dokladya Akademin Nauk CCCP*, 101, 569–572. [in Russian]
- Popov, V.V. (1957) New species and the geographical distribution of the genus *Eremaphanta*. *Zoologicheskii Zhurnal*, 36, 1706–1716. [in russian with english abstract]
- Schwammberger, K.-H. (1971) Zwei neue Bienen-Arten aus dem Iran (Hymenoptera, Apoidea). *Stuttgarter Beitrge zur Naturkunde*, 225, 1–4.
- Stage, G.I. (1966) Biology and systematics of the American species of the genus Hesperapis Cockerell, Ph-D, University of Berkley, New-York, 464 pp.
- Terzo, M. & Rasmont, P. (2004) Biogéographie et systématique des abeilles rubicoles du genre *Ceratina* Latreille au Turkestan (Hymenoptera, Apoidea, Xylocopinae). *Annales de la Société entomologique de France (n.s.)*, 40, 109–130.
- Whitehead, V.B. & Steiner, K.E. (2001) Oil-Collecting Bees of the Winter Rainfall Area of South Africa (Melittidae, *Rediviva*). *Annals of the South African Museum*, 108, 143–277.