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Notes on the genera *Ammobatoides* and *Melitturga* in Europe (Hymenoptera: Apoidea)

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Abstract. The bee genus *Ammobatoides* Radoszkowski (Apidae) is a species-poor Old World group that predominantly parasitises the pollen-collecting genus *Melitturga* Latreille (Andrenidae). Nine species of *Ammobatoides* are currently recognised, but due to the rarity of most species, four are only known from a single sex. Examination of material from Greece has yielded the previously unknown female of *Ammobatoides okalii* Kocourek, a species previously known only from its male holotype. The suspected host is *Melitturga spinosa* Morawitz. Revised identification keys for *Ammobatoides* and *Melitturga* in Europe are provided, along with a clarification of the statuses and distributions of *Melitturga praestans* Giraud and *Melitturga syriaca* Friese.

INTRODUCTION

Ammobatoides Radoszkowski, 1867 is a morphologically well-defined genus that can confidently be placed in the tribe Ammobatoidini Michener, 1944 along with Schmiedeknechtia Friese, 1896 and Holcopasites Ashmead, 1899 (Michener, 2007; Sless et al., 2022), all three genera exclusively attacking members of the Andrenidae subfamily Panurginae (Morice, 1903; Bischoff, 1923; Popov, 1934; Hurd & Linsley, 1972; Warncke, 1982; Schwarz, 1993; Proshchalykin & Lelej, 2014; Wood, 2023). The fourth genus in Ammobatoidini is the monotypic Aethammobatoides Baker, 1994 (Egypt only), which due to its rarity has never had its ecology studied, but it would seem likely to also be attacking Panurginae based on the principle of host choice conservation.

Ammobatoides species are restricted to the Old World, from the Mediterranean basin east to the Russian Far East and northern China, with one species known from South Africa (Table 1). Ammobatoides therefore closely track the distribution of their hosts, species of the genus Meliturga Latreille, 1809 and Meliturgula Friese, 1903 (Morice, 1903; Bischoff, 1923; Popov, 1934; Warncke, 1982; Rozen, 2001; Proshchalykin & Lelej, 2014; Wood, 2023), which show predominantly the same distribution, although they are present in eastern Africa, not showing the same disjunct distribution on this continent (Michener, 2007; Ascher & Pickering, 2024). Bischoff (1923) lists Meliturgula braunsi Friese, 1903 as the host of Ammobatoides braunsi Bischoff, 1923, not "Meliturgula capensis Friese" (Proshchalykin & Lelej, 2014).

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Table 1. List of species of *Ammobatoides* Radoszkowski with their global distribution, demonstrated or suspected host(s) of *Melitturga* Latreille or *Meliturgula* Friese known sexes, and supporting literature. Countries marked with an * indicate a new record or sex description; ? = uncertain host record.

Species	Distribution	Host	Sex	References
A. abdominalis (Eversmann, 1852)	West and Central Palaearctic	Melitturga clavicornis (Latreille, 1806); Melitturga syriaca Friese, 1899; Melitturga pictipes Morawitz, 1891	₽♂	Popov (1934); Bischoff (1952); Warncke (1982); Rozen (2001); Proshchalykin & Lelej (2014)
A. braunsi Bischoff, 1923	South Africa	Meliturgula braunsi Friese, 1903	Q	Bischoff (1923)
A. luctuosus (Friese, 1911)	North Macedonia, Bulgaria*, Turkey	? Melitturga taurica Friese, 1922	₽ ♂	Warncke (1982), present study
A. okalii Kocourek, 1990	Bulgaria, Greece*	? Melitturga spinosa Morawitz, 1891	₽ ♂*	Kocourek (1990), present study
A. radoszkowskii Proshchalykin & Lelej, 2014	Russia (Eastern Siberia, Far East), China (Hebei)	Melitturga mongolica Alfken, 1936	♀♂	Proshchalykin & Lelej (2014)
A. rubescens (Bischoff, 1923)	Turkey	Unknown	ď	Warncke (1982)
A. schachti Schwarz, 1988	Morocco & Tunisia	Melitturga oraniensis Lepeletier, 1841	ď	Schwarz (1988); Wood (2023)
A. schwarzi Wood, 2023	Morocco	Melitturga albescens Pérez, 1895	♀♂	Wood (2023)
A. scriptus (Gerstäcker, 1869)	Portugal, Spain, France, Morocco, Algeria	Melitturga caudata Pérez, 1879	₽ ♂	Morice (1903); Warncke (1982); Baldock <i>et al.</i> (2018)

Nine species are currently recognised (Proshchalykin & Lelej, 2014; Wood, 2023), but due to the extreme rarity of many *Ammobatoides*, four of the nine species are known only from one sex – *Ammobatoides braunsi* Bischoff, 1923 (female only), *Ammobatoides okalii* Kocourek, 1990 (male only), *Ammobatoides rubescens* (Bischoff, 1923) (male only), and *Ammobatoides schachti* Schwarz, 1988 (male only) (Warncke, 1982; Schwarz, 1988; Kocourek, 1990; Eardley *et al.*, 2010; Proshchalykin & Lelej, 2014; Wood, 2023).

Investigation of undetermined material from the Oskar Vogt collection housed in the Naturalis Biodiversity Center has revealed the unknown female of *A. okalii*. Oskar Vogt (1870–†1959) was a German physician and neurologist, but he also collected, traded, and purchased bees, particularly bumble bees (*Bombus* Latreille; Apidae), on which he published taxonomic works (*e.g.*, Vogt, 1909, 1911). Vogt's collection was acquired by the Zoological Museum of Amsterdam in 1960, and whilst the

bumble bees have received attention, much of the solitary bee material has not yet been investigated. Two specimens from this collection were identified as *A. okalii* by Henny Wiering (1929–†2001) in 2000 when the material was still part of the Zoological Museum, but no details were ever published. The location of the female of *A. okalii* allows for the creation of an updated key to *Ammobatoides* in Europe, as both sexes of all European taxa are now known.

Finally, there remains a lack of clarity surrounding the status of two species of *Melitturga* in Europe – *Melitturga praestans* Giraud, 1861 and *Melitturga syriaca* Friese, 1899. As a genus, 16 species of *Melitturga* are known globally, with six species found in Europe (Patiny 2001; Ghisbain & Rosa *et al.*, 2023), including both *M. praestans* and *M. syriaca*. These two taxa were placed in combination (with *M. syriaca* as a subspecies of *M. praestans*) by Warncke (1972). Patiny (2001) returned them to specific rank, but this was not published in the wider literature outside of this PhD thesis. Consequently, some confusion persists surrounding the correct distributions of these two species, as opposed to their broader *sensu lato* distribution in the works of Warncke. The opportunity is taken to present a modified version of the identification key presented in Patiny (2001) to make it more visible, and to inform correct separation of *M. praestans* and *M. syriaca* specifically. Additional data are given for two further species that have a marginal occurrence in Europe, *M. spinosa* Morawitz, 1891 and *M. taurica* Friese, 1922. Collectively, these new keys will hopefully encourage research on this pair of closely linked bee genera.

MATERIAL AND METHODS

Specimens were examined morphologically, building on the species concepts present in the literature (e.g., Warncke, 1982; Kocourek, 1990; Patiny 2001; Proshchalykin & Lelej, 2014). Specimen information is presented for taxa of interest, with a focus on new country records (these are marked with an asterisk "*"). For *Melitturga*, in the interests of brevity, we do not reproduce here the material examined that was published in Patiny & Gaspar (2000). For the map of *M. praestans* and *M. syriaca* distributions, we included *M. praestans sensu stricto* data from Proshchalykin et al. (2016), which is not listed in the "Material examined" section for this species. The publication date of Morawitz (1891) follows Astafurova & Proshchalykin (2024).

Morphological terminology follows Michener (2007). All specimens were either identified by the authors, or existing determinations were validated, in which case the original determiner is included in the specimen information. The following abbreviations are used in the species descriptions or in the identification keys: A = antennal segments, S = metasomal sterna, and T = metasomal terga. Specifically, A1 refers to the scape, A2 to the pedicel, and A3-12/13 refers to the flagellar segments of females and males.

Specimens were measured from the centre of the clypeus at the front of the head to the apical tip of the metasoma and rounded to the nearest 0.5 mm. Photographs were taken using an Olympus E-M1 Mark II with a 60 mm macro lens. Additional close-ups were taken with the addition of a Mitutoyo M Plan Apo 10X infinity corrected objective lens in combination with an Olympus M.Zuiko 2x teleconverter lens, a 10 mm Kenko DG extension tube, and a Meike MK-P-AF3B 10 mm extension tube. Photographs were stacked using Helicon Focus B (HeliconSoft, Ukraine) and plates were prepared in GNU Image Manipulation Program (GIMP) 2.10. Post-processing of some images was

made in Photoshop Elements (Adobe Systems, USA) to improve lighting to highlight specific characters.

Material studied is deposited in the following collections: Bulgarian Academy of Sciences, Institute of Biodiversity and Ecosystem Research, Sofia, Bulgaria (IBER); Oberösterreichisches Landesmuseum, Linz, Austria (OÖLM); Oxford University Museum of Natural History, Oxford, United Kingdom (OUMNH); Naturalis Biodiversity Center, Leiden, the Netherlands (RMNH); Personal collection of S.P.M. Roberts, Salisbury, United Kingdom (SRPC); Personal collection of T.J. Wood, Leiden, the Netherlands (TJWC); Zoologische Staatssammlung München, Munich, Germany (ZSM).

SYSTEMATICS

Ammobatoides abdominalis (Eversmann, 1852)

MATERIAL EXAMINED: **Greec**: 19, Kozani, Siatista Bridge, 19–23 Jun. 1990, J. Tiefenthaler leg. (OÖLM); 19, NW Fea Petra vill., 195 m a.s.l., 2 Jun. 2018, T. Ljubomirov leg. (IBER); 19, Western Macedonia, Anatoliko, 6.3 km E, Church of the Holy Apostles, 1000 m a.s.l., 15 Jun. 2024, T.J. Wood leg. (TJWC); 19, Western Macedonia, Filotas, 3 km N of Antigonos, 600–700 m a.s.l., 11 Jun. 2024, T.J. Wood leg. (TJWC). **North Macedonia**: 10, Jugoslav, Prilep, 1 Jun. 1968, K. Warncke leg., K. Warncke det. (OÖLM); 19, Katlanovska Banja, 9 Jun. 1965, C. v. Heijningen leg. (RMNH; RMNH.INS.1652081).

Remarks: *Ammobatoides abdominalis* is a well-studied and widely distributed species, but surprisingly we could not find any published literature supporting the presence of *A. abdominalis* in Greece, and so the species is newly reported for this country. Warncke (1982) vaguely mentioned a record from North Macedonia, which we reproduce here for clarity.

DISTRIBUTION: Germany, Austria, Italy, Czechia, Slovakia, Hungary, Croatia, Serbia, Albania, North Macedonia, Greece*, Bulgaria, Romania, Moldova, Ukraine, Belarus, Russia (European part, Siberia), Turkey, Cyprus, Syria, Lebanon, Israel, Armenia, Georgia, Azerbaijan, Kazakhstan, Turkmenistan, Uzbekistan, Kyrgyzstan, Tajikistan, and China (Xinjiang) (Warncke, 1982; Kuhlmann *et al.*, 2014; Proshchalykin & Lelej, 2014; Varnava *et al.*, 2020; Reverté *et al.*, 2023)

Ammobatoides luctuosus (Friese, 1911)

Material examined: **Bulgaria:** 1°, 1°, Sandanski, 30 May 1989, B. & O. Tkalců leg. (OÖLM); 1°, N Dolni Pasarel village, 796 m a.s.l., 10 Jun. 2024, T. Trifonov leg., T. Trifonov det. (IBER). **Turkey:** 1°, As. Turk. Sille b. Konya, 9 Jun. 1975, J. Heinrich leg., J. Heinrich det. (ZSM); 1°, Elazig As. Turk. [Elâziğ], 28–29 May 1975, J. Heinrich leg., J. Heinrich det. (ZSM); 1°, As. Turk. Sille b. Konya, 8 Jun. 1972, J. Heinrich leg., J. Heinrich det. (ZSM).

Remarks: *Ammobatoides luctuosus* is a rare species recorded predominantly from Turkey. Warncke (1982) was the first to record the species as part of the European fauna, and it can now be newly recorded from Bulgaria. The host is currently unknown, but based on the size, distribution (see examined material below), and flight period (males in late May to early June), *M. taurica* is a suitable candidate. This is currently unconfirmed, but in the absence of evidence to the contrary it forms a good working hypothesis.

It is necessary to discuss the distribution of *A. luctuosus* as this has been confused in secondary sources. Kuhlmann *et al.* (2014) list *A. luctuosus* from Luxembourg, Italy, Malta, North Macedonia, Lithuania, Moldova, Turkey, and Cyprus. This listing from Malta was repeated by Balzan *et al.* (2016), and the listings from Moldova and Malta was repeated by Reverté *et al.* (2023). The listings from Luxembourg, Malta, Lithuania, Moldova, and Cyprus are not credible in isolation and without supporting specimen information. No *Melitturga* species have ever been recorded from Luxembourg or Malta, making the presence of any *Ammobatoides* species highly suspect. We suspect that this listing may be based on an accidental encoding of *Melecta luctuosa* (Scopoli) which is present across these countries (with the exception of Cyprus, although there is a severe taxonomic impediment in this genus which limits understanding of the *luctuosa*-group). Given the few numbers of verified *A. luctuosus* specimens that we could examine, all from south-eastern Europe, we consider European records from outside of this range to be unverified without the provision of the underlying source specimen data.

DISTRIBUTION: North Macedonia, Bulgaria*, and Turkey (Heinrich, 1977; Warncke, 1982).

Ammobatoides okalii Kocourek, 1990 (Figs. 1–6)

MATERIAL EXAMINED: **Greece:** 29, Morea [Peloponnese; no further information], O. Vogt collection (RMNH; ZMA.INS.5103944–ZMA.INS.5103945).

DIAGNOSIS. Ammobatoides okalii can be recognised as an Ammobatoides due to the lack of pollen collecting hairs, long labrum which is around 3 times as long as broad, presence of a pygidial plate (although this is hidden under T5), T5 with a slightly raised and distinct longitudinal ridge medially (Fig. 6), inner margins of compound eyes slightly bowed (compound eyes converging both dorsally and ventrally), marginal cell rounded at the apex and removed from the outer margin of the wing, and body length exceeding 10 mm (Michener, 2007).

Within the genus *Ammobatoides*, *A. okalii* females can be recognised immediately due to their large body size; at 14 mm in length, they are slightly but distinctly larger than comparison species which are typically between 10–12 mm in length. Structurally, *A. okalii* can be recognised by the longitudinal carina on the labrum, and also with the labrum elevated in its basal ½, with the apical ½ flattened in comparison. Moreover, the clypeus has a clear longitudinal ridge placed medially, which is elevated and shiny, contrasting with the densely punctate remaining parts of the clypeus (Fig. 3). Finally, the metasoma is black with strongly contrasting thick white apical hair fringes (Fig. 5); this is similar to the situation in several *Ammobatoides* species, but in the only other species that shows the labrum with a longitudinal carina (*A. abdominalis*), the metasoma is predominantly red. Consequently, *A. okalii* can be unambiguously recognised in the female sex.

Female: Body length: 11 mm (Fig. 2). *Head:* Dark, 1.2 times wider than long. Clypeus domed, densely punctate, punctures essentially confluent with exception of raised longitudinal ridge medially, ridge impunctate, shining, and strongly contrasting remaining clypeal surface (Fig. 3). Labrum 3 times longer than broad, broadest basally, apically slightly narrowing; labral surface elevated in basal ½, apical

 $\frac{1}{3}$ lower in comparison. Basal $\frac{1}{3}$ roughened by presence of ridges and punctures, with longitudinal raised carina running from basal $\frac{1}{3}$ onto apical $\frac{2}{3}$, here reducing in prominence and disappearing into underlying shagreen. Gena approximately 0.6 times as wide as width of compound eye; ocelloccipital distance 4 times diameter of lateral ocellus. Basal part of clypeus, supraclypeal area, paraoccular areas, and space within ocellar triangle with dense white almost adpressed plumose hairs. Antennae brown with orange parts, A3–12 ventrally lightened by presence of grey scales; A3 exceeding A4+5, shorter than A4+5+6.

Mesosoma: Scutum and scutellum densely punctate, punctures separated by <0.5–1 puncture diameter, interspaces when visible shining. Mesepisternum densely punctate, punctures separated by 0.5 puncture diameters, interspaces weakly shining. Mesepisternum in dorsal half entirely covered with dense patch of almost adpressed white plumose hairs. Pronotum laterally with adpressed white hairs, scutellum with small patches of white hairs anterolaterally between pronotum and tegulae, anteromedially and widely separated on either side of scutellar mid-line, and posteriorly adjacent to axillae (Fig. 4). Legs dark, apical tarsal segments lightened orange; pubescence light to dark brown with exception of posterior margin of hind tibiae, these covered with adpressed white hairs. Wings weakly infuscate, stigma and venation orange brown, nervulus postfurcal.

Metasoma: Terga dark, densely punctate, punctures typically separated by 0.5 puncture diameters, slightly sparser on disc, becoming slightly denser on tergal margins. Terga apically with white hair bands, on T1 with lateral parts covered with large patch of white hairs, T2–4 with elongate white hair patches, these 3–5 times wider than long; hairbands broadly separated on T1, becoming progressively less separated, on T4 only narrowly separated (Fig. 5). T5 with a longitudinal rounded median ridge (Fig. 6), surface immediately adjacent to ridge almost impunctate, contrasting lateral parts of disc which are finely and densely punctate, punctures almost confluent. Rounded pygidial plate present under T5.

Remarks: The two specimens are not dated (Fig. 1), but since the Vogt collection was acquired in 1960, it was clearly collected at some point before then, though it is impossible to have certainty as to when. It is not impossible that they were collected in the 19th century. Based on the large size of *A. okalii*, and its late flight period of July (the holotype male was collected 21st July 1966), the most likely host is *M. spinosa*, the largest species of European *Melitturga* (around 15–16 mm in length). In Europe, *M. spinosa* is a species that is only rarely recorded in the southern Balkans. Examination of material from the Kocourek collection (OÖLM, see below for full details) has produced a female specimen of *M. spinosa* from Sandanski (Struma valley, southwestern Bulgaria) that was collected on the 16th July 1966. This matches almost exactly the collecting information for *A. okalii*, which was also collected in Sandanski just five days later in the same year (Kocourek, 1990). This evidence is circumstantial, but also suggestive. As for the tentative host suggestion for *A. luctuosus*, it forms the basis for a good working hypothesis, and if populations of *M. spinosa* can be located, they should be carefully observed for the presence of *A. okalii*.

DISTRIBUTION: Bulgaria and Greece* (Kocourek, 1990).



Figures 1–6. *Ammobatoides okalii* Kocourek, 1990 female. **1.** Label details. **2.** Habitus, lateral view. **3.** Clypeus, frontal view. **4.** Vertex and scutum, dorsal view. **5.** Terga, dorsal view. **6.** Tergum 5, dorsal view detail.

Identification key for European Ammobatoides species

A total of four species of *Ammobatoides* are found in Europe (Ghisbain & Rosa *et al.*, 2023). Following the description of the female of *A. okalii*, all four species are known in both sexes. The key of Warncke (1982) is translated from German, updated, and modified for ease of use.

1. Females; 12 antennal segments, five visible terga plus pygidial plate.....2

 2(1).	Males; 13 antennal segments, six visible terga plus pygidial plate
- .	Ventral surface of labrum often with bristles that partially obscure the underlying surface, but without longitudinal ridge, instead with two raised
3(2).	bumps placed more or less medially
- .	Metasoma entirely black, without a trace of red. T1–4 with strong and thick white hairbands that strongly contrast the underlying dark integument; hairbands broadly interrupted on T1, progressively less interrupted on subsequent terga, almost complete on T4. Labrum with basal ½ slightly elevated, apical ½ flat. Larger, 14 mm in length. Bulgaria and Greece only A. okalii Kocourek
4(2).	Ocelloccipital distance relatively short, 1.5 times the diameter of a lateral ocellus. Terga densely punctate, this most evident on T3–4, on T4 punctures almost touching medially and therefore the surface appears dull due to reduction in the size of the interspaces. White hair bands on T3–4 narrow, elongate, more than five times as long as wide. Found in south-western Europe (Portugal, Spain, France)
	Ocelloccipital distance relatively long, 3 times the diameter of a lateral ocellus. Terga with relatively sparse punctures, on T3–4 with punctures separated by 1–2 puncture diameters. White hair bands on T3–4 less elongate, more or less rectangular, twice as long as wide. Found in south-eastern Europe (North Macedonia, Bulgaria)
5(1).	Labrum medially with a longitudinal carina of variable length; surface of labrum with only weak and obscure hairs, surface clearly visible
- .	Labrum without a longitudinal carina, instead with two raised bumps placed more or less medially; surface of labrum often partially obscured by presence of dense bristles
6(5).	Labrum divided in two by presence of a transverse bulge in the basal third, with the flattened apical part occupying the apical two-thirds. Labrum medially with a longitudinal carina that runs from the base of the labrum towards the apex. Clypeus strongly domed, with a strongly pronounced longitudinal ridge medially (most strongly developed basally). A13 slightly but distinctly broadened, wider than the preceding segments. Space between lateral ocellus and inner margin of the compound eye equalling the diameter of a lateral ocellus. Bulgaria and Greece only
	Labrum not divided in two, uniformly flattened. Labrum medially with a longitudinal carina, but this does not reach the base of the labrum. Clypeus not domed and with the surface uniform, lacking a longitudinal ridge. A13 not broadened, as wide as the preceding segments. Space between lateral ocellus and inner margin of the compound eye ½ the diameter of a lateral ocellus. Widespread, from Central Europe (Italian Alps and east Germany) eastwards

- Space between lateral ocellus and inner margin of the compound eye subequal
 to the diameter of a lateral ocellus. Terga with lateral hair patches elongate,
 five times wider than long. Found in south-western Europe (Portugal, Spain,
 France)

Melitturga praestans Giraud, 1861 (Figs. 7, 8)

Material examined: **Armenia:** 1σ, 8 km SE Shumuch [probably Shurnukh], 10 May 2003, Mučka leg. (OOLM). Austria: 1º, Bisambg [Bisamberg], 7 Jul. 1889, K. Warncke det. (OÖLM); 29, Bisambg [Bisamberg], 23 Jun. 1889, K. Warncke det. (OÖLM); 19, Bisambg [Bisamberg], 25 Jul. 1884, K. Warncke det. (OÖLM); 10, Pitten, N.O. [Niederösterreich], 16 Jun. 1889, K. Warncke det. (OÖLM). Azerbaijan: 1&, 1\, 1\, A3. CCP [Azeri SSR] Талыш [Talysh] Диабар. Котл [Diabag. Cauldron], 7 Jun. 1967, A. Osytshnjuk leg., A. Osytshnjuk det. (ZSM); 19, Talysch, Zuwand Plateau, Gosmolojan [Qosmalyan], 1600 m a.s.l., 21 May 2001, Dolin & Andreewa leg. (ZSM). Bulgaria: 10, 39, Bulgaria, Blagoevgrad, Katuntsi, 2.6 km ESE of Katuntsi, 300 m a.s.l., 25 May 2024, T.J. Wood leg. (TJWC); 1σ, Bulgaria, Blagoevgrad, Petrovo, 5.3 km SE of Petrovo, 700 m a.s.l., 27 May 2024, T.J. Wood leg. (TJWC); 19, Kresno, 12 May 1979, M. Kocourek leg., M. Kocourek det. (OÖLM); 1σ, Nessebr [Nessebar], 27 Jun. 1982, M. Kocourek leg., M. Kocourek det. (OÖLM); 1&, Sandanski, 1–8 Jun. 1967, M. Kocourek leg., M. Kocourek det. (OÖLM). Czechia: 1ơ, 1º, Pouzdřany, 18 Jun. 1966, B. Tkalců leg. (OÖLM). Iran: 2ơ, Tehran, 10 km N Karaj, 22 May 1976, C. Holzschuh leg., K. Warncke det. (OÖLM). North Macedonia: 19, Ohrid, 29 May – 10 Jun. 1972, H. Teunissen leg. (RMNH; RMNH. INS.1652057); 2o, Varos [Varosh], NW Prilep, 1 Jun. 1972, H. Teunissen leg. (RMNH; RMNH.INS.1652058–RMNH.INS.1652059). Russia: 10, 19, Bashkiria, Chishmy, 28 May 1957, Nikiforuk leg. (OÖLM); 19, Bashkiria, Chishmy, 24 Jul. 1960, Nikiforuk leg. (OÖLM). Slovakia: 1º, Dev. Koblya [Devínska Kobyla], 19 Jun. 1969, M. Kocourek det. (OÖLM); 1ơ, 19, Gbelce, 1–30 Jun. 1973, M. Kocourek leg. (OÖLM); 1ơ, 19, M. Karpaty, Dev. Koblya [Devínska Kobyla], 29 Jun. 1977, J. Lukáš leg., M. Kocourek det. (OÖLM); 2ơ, M. Karpaty, Dev. Koblya [Devínska Kobyla], 28 Jun. 1978, J. Lukáš leg., M. Kocourek det. (OÖLM). Turkey: 10, 10 km S Ankara, 5 Jun. 1988, K. Warncke leg., K. Warncke det. (OÖLM); 19, 30 km N Kutahya [Kütahya], 13 Jun. 2000, M. Halada leg. (OÖLM); 1 o, 4 p, 50 km S Kars, Pasli, 1 Jul. 1997, Ma. Halada leg. (OÖLM); 1 p, Ankara, 3 Jun. 1972, K. Warncke leg., K. Warncke det. (OÖLM); 1&, Ankara, 80 km SE Cogun Lake [Çoğun Barajı], 22 Jun. 1993, K. Deneš leg. (OÖLM); 19, Bolu, 17 km S of Seben, 17 Jun. 1998, J. Halada leg. (OÖLM); 19, Elazig [Elâzığ], 29 May 1968, J. Gusenleitner leg., K. Warncke det. (OÖLM); 5ơ, 3೪, Ercek [Erçek]/Van, 9–10 Jun. 1977, K. Warncke leg., K. Warncke det. (OÖLM); 1º, Erzurum, 9 Jun. 1970, H. Özbek leg., K. Warncke det. (OÖLM); 1_o, Göreme, 2₃ Jun. 1993, K. Deneš leg. (OÖLM); 1_o, Horasan/Arastal, 16 Jun. 1973, K. Warncke leg., K. Warncke det. (OÖLM); 29, Madensehir [Madenşehri], Konya, 6 Jun. 1971, K. Warncke leg., K. Warncke det. (OÖLM); 1&, Muradiye env., 2000m, 120 km NE Van, 5 Jun. 2001, K. Deneš leg. (OÖLM); 1º, Sille, Konya, 21 Jun. 1973, K. Warncke leg., K. Warncke det. (OÖLM); 1^o, Sivas, Şarkışla, 1⁵ Jun. 1977, K.

Warncke leg., K. Warncke det. (OÖLM); 1&, Zor Dagi [Zor Dağ], Sulucan env., 25 Jun. 1993, K. Deneš leg. (OÖLM).

Remarks: Following the characters given in the key (below), *M. praestans* and *M. syriaca* can be consistently and unambiguously separated across their ranges. To date, we have not been able to examine the two species occurring together in sympatry. *Melitturga praestans* has a distribution across warm grasslands such as in the Pannonian basin or steppe in Central Turkey, whereas *M. syriaca* is a species found in true Mediterranean habitats extending to the sub-Mediterranean habitats of Hakkâri in south-eastern Turkey and the Zagros mountains in south-western Iran (Fig. 7). The distribution of *M. praestans* relative to *M. syriaca* is strongly reminiscent of the distribution of *Systropha planidens* Giraud relative to *Systropha anatolica* Warncke (Wood & Le Divelec, 2022). In both cases, there is a species distributed from Central Europe across Turkey to northern Iran (the two taxa coincidentally described by Giraud in the same publication), which is mirrored by a more recently described species found in southern Turkey and that descends into the Levant. There is a visible tension between central Turkey (which supports the widespread Eurasian taxa) and southern Turkey (which supports the Mediterranean/Middle Eastern taxa).

In Central Europe, the population trend of *M. praestans* is strongly negative. We have not comprehensively revised Central European collections, but based on the material we have checked, the last records from Austria (1889), Czechia (1966), and Slovakia (1978) suggest that populations are in trouble. We stress that we have not examined modern collections from Czechia and Slovakia, but in Czechia the species was listed as Critical Endangered in 2005 and is now considered regionally extinct (Farkač *et al.*, 2005; Hejda *et al.*, 2017), supporting a position of no modern records. Establishing the status of Central European populations is needed to understand if the species persists here, in contrast to the southern Balkans where the species was recorded in the Struma valley as recently as 2024.

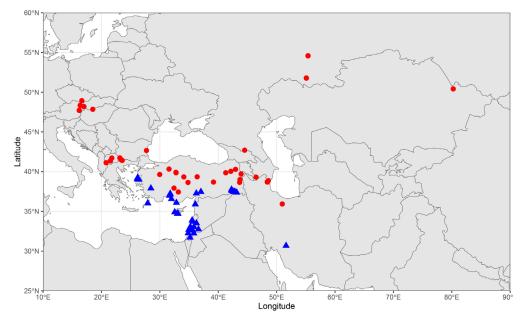


Figure 7. Distribution map of *Melitturga praestans* Giraud, 1861 (red circles) and *Melitturga syriaca* Friese, 1899 (blue triangles).

DISTRIBUTION: Austria, Czechia, Slovakia, Romania, North Macedonia, Greece, Bulgaria, Turkey, Georgia, Armenia, Azerbaijan*, Russia (Bashkiria, Orenburg), Iran, and Kazakhstan (Patiny, 2012; Kuhlmann et al., 2014; Proshchalykin et al., 2016) (Fig. 7).

Melitturga spinosa Morawitz, 1891 (Fig. 13)

Material examined: **Bulgaria**; 19, Sandanski, 16 Jul. 1966, M. Kocourek leg. (OÖLM); **Greece**: 19, 40 km N Lamia, Domokos, 1 Jul. 1996, Ma. Halada leg. (OÖLM); 1σ, Korinth, 25 Jul. 1937, N.G. Gejvall leg. (RMNH; RMNH.INS.1652065); 19, Peloponnese, 20 km E Sparta, Ag. Anagiri, 5 Jul. 1996, Ma. Halada leg. (OÖLM). **North Macedonia**: 29, Lake Dojran, 10 Jul. 1968, Z. Pádr leg. (OÖLM); 1σ, Stip [Shtip], 2–4 Jul. 1938, Zwick-Roehl leg. (OÖLM).

Remarks: *Melitturga spinosa* was recorded from Europe based on three records from Greece, Bulgaria, and North Macedonia (Patiny & Gaspar, 2000; Patiny, 2012). The details of the Bulgarian record were not included in Patiny & Gaspar (2000), as the specimen was not examined until after the publication of this work, and so precise information from this country has not previously been published. Examination of museum material has revealed a few additional specimens of *M. spinosa* from Europe, though it remains a very infrequently recorded species. As noted above, *M. spinosa* was caught with *A. okalii* at Sandanski in July 1966, and since both are the largest members of their respective genera, a host association is here inferred. The relatively late flight period (for a Mediterranean *Melitturga*) of July may partially explain the small number of records.

DISTRIBUTION: North Macedonia, Bulgaria, Greece, Turkey, Azerbaijan, and Israel (Warncke 1972; Patiny & Gaspar, 2000; Patiny, 2012; Kuhlmann *et al.*, 2014; Proshchalykin *et al.*, 2016; Astafurova & Proshchalykin, 2024).

Melitturga syriaca Friese, 1899 (Figs. 7, 9)

Material examined: Cyprus: 3o, Agios Dimitrianos N Pafos, 630 m a.s.l., 3 Mar. 2000, Vogtenh & Hentscholek leg. (OÖLM); 2&, 19, Akrounda [Akrounta], 23 Mar. 1937, G.A. Mavromoustakis leg. (OÖLM); 4&, 5\, Limassol, 1-30 Apr. 1937, G.A. Mavromoustakis leg. (RMNH; RMNH.INS.1652008); 19, Limassol, 17 Apr. 1956, G.A. Mavromoustakis leg. (OÖLM); 19, Mesa Geitonia, 24 Apr. 1935, G.A. Mavromoustakis leg. (OÖLM); 1&, Yerasa, 6 Apr. 1978, H. Teunissen leg. (RMNH; RMNH.INS.1652063); 4σ, 19, Yermosoyia, 3 Apr. 1978, H. Teunissen leg. (RMNH; RMNH.INS.1652060). Greece: 1σ, Lesbos, 0.5 km S of Stavros, 10 Apr. 2001, S.P.M. Roberts leg. (SRPC); 5σ, 19, Lesbos, 1 km N of Stavros, 10 Apr. 2001, S.P.M. Roberts leg. (SRPC/TJWC); 20, Lesbos, 2 km W of Vatera, 17 Apr. 2001, S.P.M. Roberts leg. (SRPC); 3°, Lesbos, Kalloni saltworks, 18 Apr. 2001, S.P.M. Roberts leg. (SRPC); 3\sigma, Lesbos, Vatera, seashore, 5 Apr. 2001, S.P.M. Roberts leg. (SRPC); 11\u00f3, 7\u00a7, Milies, Lesbos, 21 May 1980, H. Teunissen leg. (RMNH; RMNH.INS.1652006); 109, Parakila (Lesbos), 14 May 1980, H. Teunissen leg. (RMNH; RMNH.INS.1652000–RMNH.INS.1652005); 1\u03c3, 1\u27, Rhodos, Genadion [Gennadi], 22 Apr. 1970, v. Oostroom leg. (RMNH; RMNH.INS.1266241, RMNH. INS.1652055). Iran: 1\u00f3, Ostan Boyr Ahmadi, Yasuj, Abshar, 2050 m a.s.l., 5 May 1977, W.K. Blom leg. (RMNH; RMNH.INS.1652035). Israel: 1\u03c4, Elon [Eilon], Bytinski-Salz

leg. (OÖLM); 1σ, 49, Mt. Carmel, En Hod, 4 Apr. 1999, S.P.M. Roberts leg. (SRPC); 8σ, 39, Mt. Carmel, En Hod, 2–16 Apr. 2000, S.P.M. Roberts leg. (SRPC/TJWC); 20, 19, Mt. Carmel, Etzbah, 5 Apr. 1999, S.P.M. Roberts leg. (SRPC); 70, 19, Mt. Carmel, Etzbah, 3 Apr. 1999, S.P.M. Roberts leg. (SRPC/TJWC); 29, Mt. Carmel, Kedumim, 10 Apr. 2000, S.P.M. Roberts leg. (SRPC). Jordan: 19, N. Shuna env, 29–30 Apr. 1996, Mi. Halada leg. (OÖLM); 1°, SW Jerash, Alhuna, 12 Apr. 2009, M. Snižek leg. (OÖLM). Lebanon: 1°, (Chouf), El Barak [Barouk], c. 1100 m a.s.l., 12 Jun. 1995, C.G. Roche leg. (OUMNH). Syria: 39, Damascus, O. Schmiedeknecht leg. (OÖLM); 10, 19, Ganawat [Qanawat], 16 May 1995, K. Deneš leg. (OÖLM). **Turkey:** 1*o*, 12/30 km N Akseki, 1400 m a.s.l., 12 Jul. 1981, H. & Th. v. Oorschot & H. v. d. Brink leg. (RMNH; RMNH.INS.1652056); 10, 19, Adiyaman, Kuyucak, 8 Jun. 1998, Ma. Halada leg. (OÖLM); 2σ, 19, Alanya/Antalya, 23 Apr. 1984, K. Warncke leg. (OÖLM); 5ơ, Anamuryam [Anamur]/İçel [Mersin], 22 Apr.1984, K. Warncke leg. (OÖLM); 29, E of Şırnak/Siirt, 4 Jun. 1977, K. Warncke leg. (OÖLM); 12σ, 29, Hakkari, 22 km S Beytüşşebap, 1300 m a.s.l., 2 Jun. 1980, K. Warncke leg. (OÖLM); 3ơ, Hakkari, 5 km N Uludere, 1100 m a.s.l., 4 Jun. 1980, K. Warncke leg. (OÖLM); 1^o, Hakkari: 10 km W Uludere, 1000 m a.s.l., 4 Jun. 1980, K. Warncke leg. (OÖLM); 19, Kahramanmaras, 40 km SE, 10 Jun. 1998, Ma. Halada leg. (OÖLM); 30, Karatepe/Adana, 17 Apr. 1984, K. Warncke leg. (OÖLM); 1&, Kiremithaneler nr Antalya [location unclear], 22 Apr. 1959, Exp. Turkey 1959 leg. (RMNH; RMNH.INS.1652031); 1σ, 1♀, N of Akseki, 19 Jun. 1998, Ma. Halada leg. (OÖLM); 2σ, Siirt, 5 km E Eruh, 1000 m a.s.l., 26 May 1983, K. Warncke leg. (OÖLM); 1 or, Siirt: 20 km NW Sirnak, 1500 m a.s.l., 5 Jun. 1980, K. Warncke leg. (OÖLM); 19, Taskesigi [Taşkesiği], 100 km E Antalya, 25 May 1998, Ma. Halada leg. (OÖLM); 29, Yayladagi [Yayladağı], 11 Jun. 1998, Ma. Halada leg. (OÖLM). West Bank: 1&, 1\, Har Gilo, 5 km SW Jerusalem, 850 m a.s.l., 27 Apr. 1988, C. O'Toole leg. (OUMNH).

Remarks: To our knowledge, *M. syriaca* has not previously been recorded from Jordan or Iran within this narrower species concept.

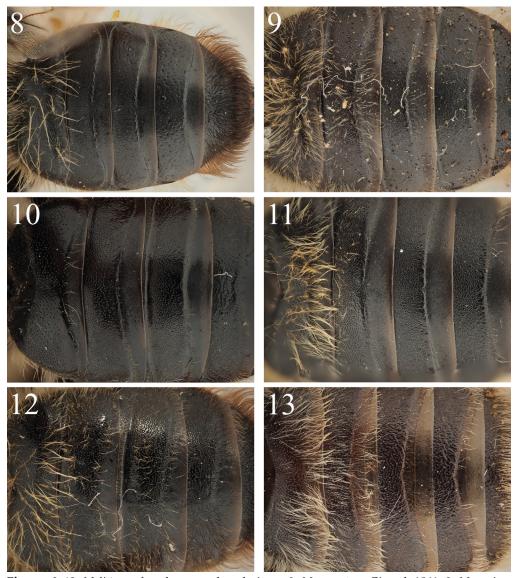
DISTRIBUTION: Greece (East Aegean Islands), Turkey, Cyprus, Syria, Lebanon, Israel & West Bank, Jordan*, and Iran* (Friese, 1899; Patiny, 2012; Kuhlmann *et al.*, 2014) (Fig. 7).

Melitturga taurica Friese, 1922 (Fig. 10)

Material examined: Bulgaria: 20, 19, Blagoevgrad, Katuntsi, 2.6 km ESE of Katuntsi, 300 m a.s.l., 25 May 2024, T.J. Wood leg. (TJWC); 7o, Blagoevgrad, Sandanski, 1.4 km SW Ploski, 400 m a.s.l., 24 May 2024, T.J. Wood leg. (TJWC); 10, 59, Daboviza, Rodopi, 18 Jun. 1969, N. Atanassov leg., T. Ljubomirov det. (IBER); 19, Mandriza [Mandritsa], Rodopi, 19 Jun. 1969, N. Atanassov leg., T. Ljubomirov det. (IBER); 19, Sw. Wratsch [Sweti Wratsch = Sandanski], 12 Jun. 1938, N. Atanassov leg., T. Ljubomirov det. (IBER); 19, NW Zemen, 2 Jul. 2024, T. Trifonov leg., T. Trifonov det. (IBER). Greece: 39, N, SE of Grevena, 500 m a.s.l., 24 May 2016, M. Halada & L. Bica leg. (OÖLM/TJWC); 19, NW Fea Petra vill., 178 m a.s.l., 4 May 2018, T. Ljubomirov leg. (IBER); 1σ, Western Macedonia, Anatoliko, 6.3 km E, Church of the Holy Apostles, 1000 m a.s.l., 15 Jun. 2024, T.J. Wood leg. (TJWC); 18, Western Macedonia, Filotas, 2.8 km N of Antigonos, 600 m a.s.l., 8 Jun. 2024, T.J. Wood leg. (TJWC); 29, Western Macedonia, Filotas, 3 km N of Antigonos, 600-700 m a.s.l., 11 Jun. 2024, T.J. Wood leg. (TJWC); 19, Western Macedonia, Petres, 2.5 km SE of Kella, 670 m a.s.l., 14 Jun. 2024, T.J. Wood leg. (TJWC); 19, Western Macedonia, Petres, 2.8 km S of Kella, 670 m a.s.l., 12 Jun. 2024, T.J. Wood leg. (TJWC).

Remarks: The occurrence of *M. taurica* in Europe is marginal, and was previously supported by only three records (Patiny & Gaspar, 2000; Patiny, 2012). New expeditions and examination of additional museum material reveals that *M. taurica* is more widespread in Greece and Bulgaria than previously reported. This species was frequently collected in Greece (Western Macedonia) in June 2024, usually on *Onobrychis* Mill. (Fabaceae). Given the records of the species in north-western Greece and western Bulgaria, *M. taurica* could be present also in Albania, North Macedonia, and possibly even south-eastern Serbia, but this must be supported with specimens.

DISTRIBUTION: Bulgaria, Greece, Turkey, Georgia, Azerbaijan, Iran, and Kyrgyzstan (Warncke, 1972; Patiny & Gaspar, 2000; Patiny, 2012; Kuhlmann *et al.*, 2014; Proshchalykin *et al.*, 2016).



Figures 8–13. *Melitturga* female terga, dorsal views. **8.** *M. praestans* Giraud, 1861. **9.** *M. syriaca* Friese, 1899. **10.** *M. taurica* Friese, 1922. **11.** *M. clavicornis* (Latreille, 1806). **12.** *M. caudata* Pérez, 1879. **13.** *M. spinosa* Morawitz, 1891.

Identification key for European Melitturga species

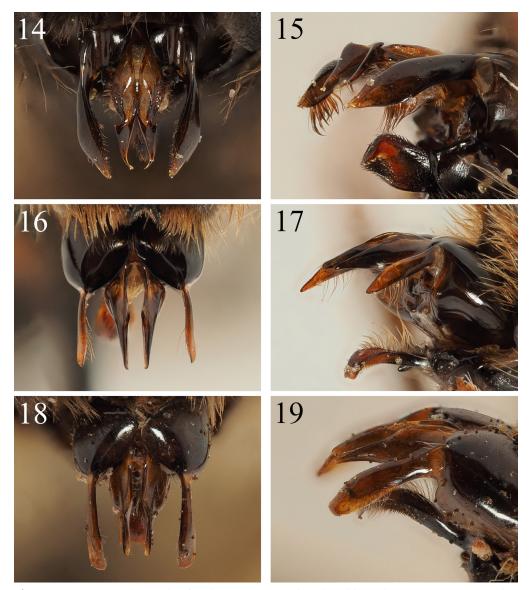
1. 2(1).	Females; 12 antennal segments, six visible terga
3(2).	Clypeus entirely dark. Mesonotum medially with an area of sparse punctures, punctures separated by 3–4 puncture diameters compared to 0.5–1 puncture diameter laterally, the underlying surface here strongly polished and shining. Disc of T2 with punctures sparse, separated by 2–3 puncture diameters (Fig. 8).
	Found in temperate to steppic grasslands from Central Europe to Turkey and further east (not in strongly Mediterranean habitats)
4(2).	not so strongly disappearing into the underlying sculpture (Fig. 9). Found in Mediterranean habitats from the East Aegean islands to the Levant, southern Turkey, and southern Iran
	never with a large patch of punctures placed medially which are consistently separated by 0.5 puncture diameters. Tergal discs polished and shining, disc of T1 with punctures separated by 0.5–2 puncture diameters, punctures not extending onto the tergal margin which is covered with fine latitudinal reticulation (Fig. 10). Body with pubescence reduced, even in fresh specimens with only a few scattered hairs on the scutum, never with dense and abundant scutal hairs. Found in south-eastern Europe only (Bulgaria and Greece)
	Scutum and scutellum with comparatively denser punctation; scutellum with majority of surface (particularly medially) covered with large patch of punctures separated by 0.5 puncture diameters. Tergal discs with sculpture variable (Figs. 11–13), shagreened to shining, but disc of T1 with punctures extending at least partially onto the marginal area, this area therefore not so strongly contrasting the tergal disc. Body with more abundant pubescence, in fresh specimens with abundant and dense hairs on the scutum. Distribution variable
5(4).	Clypeus almost entirely marked with yellow. Terga with distinctive sculpture, tergal discs densely punctate but with impunctate area immediately before

	tergal margins, tergal margins clearly depressed relative to the discs, step-like, and tergal margins with fine granular shagreen, surface dark and concolourous with tergal discs (Fig. 11). Galea with outer surface finely sculptured, matt and dull. Terminal fringe golden-orange. Widespread across Europe
	Clypeus entirely dark, never yellow-marked. Terga different, either with marginal areas only weakly depressed without forming step-like structure between discs and margins (Fig. 12), or without impunctate area on discs immediately adjacent to marginal area, or tergal margins lightened hyaline and not concolourous with the discs (Fig. 13). Galea with outer surface shiny. Terminal fringe variable. Found in either south-western or south-eastern
6(5).	Europe, but not in Central Europe
	Large species, 15–16 mm. Terminal fringe golden-white. Mesosoma and first tergal segments with shorter and sparser grey pubescence, face with short greyish pubescence. Process of labrum only weakly constricted, width of truncate apex ½ to ¾ of maximum basal width. Tergal margins lightened yellowish-brown, contrasting the tergal discs (Fig. 13). Found in south-eastern Europe (North Macedonia, Bulgaria, Greece) M. spinosa Morawitz
7(1). 8(7).	Antennal scape marked with yellow
	Body with abundant orange-brown pubescence, including the metasoma in fresh specimens. S3–4 with the apical margins medially emarginate. Genital capsule with gonostyli more or less parallel-sided, only slightly tapering apically. Gonocoxae with dorsal surfaces smooth, without any kind of longitudinal impression. Slightly smaller, 13–14 mm in length. Distribution variable
9(8).	Supraclypeal area yellow-marked. Margin of S5 medially with a slightly raised carina forming a ventrally projecting tooth, structurally differing from S3–4 which are medially emarginate. S6 with strongly pronounced longitudinal carina, this carina joining a raised transverse carina along the apical margin of S6, this transverse carina strongly raised relative to the disc of S6 and medially produced into a clear point. Widespread across Europe

- —. S2 flat, the apical margin showing no sign of being thickened or elevated above the remaining parts of the disc; posterior margin of S2 straight. Genital capsule with gonostyli in profile view almost parallel-sided, only slightly broadened subapically; gonocoxae with dorsal surfaces smooth, without any longitudinal impressions; outer surface of gonostyli with weak hairs subapically that do not form a dense tuft (Figs. 16–19). Found in Central and south-eastern Europe

DISCUSSION

This contribution and clarification highlight the importance of the southern Balkans (North Macedonia, Bulgaria, and Greece) as a hotspot of *Ammobatoides-Melitturga* diversity. Three of the nine (33.3%) global *Ammobatoides* and five of the 16 (31.3%) global *Melitturga* species can be found here, increasing to four (44.4%) and six (37.5%), respectively, when including neighbouring Turkey. The importance of the southern Balkans for *Melitturga* diversity was previously highlighted by Patiny & Gaspar (2000), and it is logical that this region would therefore also be important for *Ammobatoides*, since this genus is dependent upon its *Melitturga* hosts. The importance of the southern Balkans as a centre of bee diversity is known for other groups such as *Dasypoda* (*Megadasypoda*) (Michez *et al.*, 2004), though none are quite as striking as the pattern seen for *Melitturga* + *Ammobatoides*.



Figures 14–19. Genital capsule of *Melitturga* species, dorsal and lateral views. **14–15.** *M. caudata* Pérez, 1879. **16–17.** *M. praestans* Giraud, 1861. **18–19.** *M. syriaca* Friese, 1899.

Focussed field study is required to test the host-parasite hypotheses proposed here, and to identify the true status of these very uncommonly encountered parasitic bees. Additional searches in museum collections are also needed, to ensure that previously collected *Ammobatoides* and *Melitturga* are found, identified, and records are made available to more accurately understand the distribution and statuses of these interlinked bee genera.

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