

European cuckoo bees of the tribe Dioxyini (Hymenoptera, Megachilidae): distribution, annotated checklist and identification key

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Abstract

Altogether, ten species of cuckoo bees of the tribe Dioxyini have been recorded from Europe, with two species distributed widely in the continent while others are restricted in distribution to only one or several countries in southern Europe. These ten representatives are classified into five genera: *Aglaoapis*, *Dioxyis*, *Ensliniana*, *Metadioxys* and *Paradioxys*. *Dioxyis atlanticus* is reclassified from a subspecies to a valid species, and new occurrence records of this species are reported. New synonymy is established for *Dioxyis cinctus* = *D. montana* **syn. nov.** The distribution, morphology, ecology and hosts of all species were reviewed from both published and unpublished sources. New red-list categories for each species were created according to the new records of occurrence. An identification key including all ten species and photographs of their whole bodies and main identification characteristics was prepared, and distribution maps for all species were created.

Keywords

Europe, *Aglaoapis*, *Dioxyis*, *Ensliniana*, *Metadioxys*, *Paradioxys*, maps, ecology, hosts, conservation

Introduction

Bees (Anthophila) form a group of seven families within the monophylum Aculeata inside the highly diversified order Hymenoptera. This group coevolved with flowering plants, whose pollen, nectar and oils serve as the main food sources for both adults

and their brood (Grimaldi and Engel 2005; Michener 2007). There are many nesting strategies for bees that vary according to the placement of the nest, the care of the brood, the level of social behaviour, and the specialisation of the pollen (Klein et al. 2007; Michener 2007; Bogusch et al. 2020a). While the majority of bees create their own nests, there is a group of interspecific nest kleptoparasites known as cuckoo bees, which is distributed across all regions of the world and comprises approximately 15% of all bee species (Batra 1984; Michener 2007; Sless et al. 2022). Cuckoo bees are not a taxonomical group, but rather are ecological groups of phylogenetically unrelated genera across multiple families, whose females lay their eggs into the nests of other bee species. They utilize a variety of strategies for invading host nests and destroying host broods (Michener 2007; Habermannová et al. 2013; Westrich 2018).

Interspecific cuckoo behaviour is known in four families: Colletidae, Halictidae, Megachilidae and Apidae, including the species-rich subfamily Nomadinae of the family Apidae which is comprised of many genera and species (Sless et al. 2022). Within the Megachilidae, several genera with kleptoparasitic behaviour are distributed across more groups of this family, while the tribe Dioxyini represents the least species-rich group of cuckoo bees within Megachilidae (Gonzalez et al. 2012; Westrich 2018). This group of cuckoo bees comprises eight genera of usually rare cuckoo bees, which are distributed in the Old World and in North America (Popov 1936; Michener 2007). Currently, 36 species are known worldwide (Michener 2007). Of this number, ten species in five genera have been recorded from Europe (Warncke 1977; Tkalcu 2001), most of which are very rare and restricted in their distribution to a small area in the south of the continent. Many of these species have their main distribution area in North Africa and/or the Middle East, and their occurrence in Europe represents only the very small, northernmost part of their distribution (Warncke 1977; Baldock et al. 2018; Lhomme et al. 2020; Varnava et al. 2020; Ghisbain et al. 2023).

Warncke (1977) summarised the taxonomy of all species of the western part of the Palearctic region. However, this study is somewhat outdated and does not contain all known species (i.e., *Dioxys lanzarotensis* Tkalcu, 2001, described after the publication of Warncke's (1977) study). The identification key is useful, especially because of the quite simple identification of this group based on very specific differences among the species, but is very different from modern keys that include photographs. Additionally, current surveys in several countries in southern Europe have improved the knowledge of the distribution and ecology of this group.

The goal of this study is to review the taxonomy, distribution, ecology and conservation of all species of tribe Dioxyini recorded from Europe. An identification key for all species is included.

Materials and methods

The specimens for the study were collected by the author from the field or obtained from other collections. A large part of the material studied included pinned specimens from both private and museum collections. Additionally, material from the following

museums and institutions was studied: Národní muzeum, Praha (Czech Republic, curator Jan Macek), Moravské zemské muzeum, Brno (Czech Republic, curator Igor Malenovský), Natural History Museum, London (United Kingdom, curator Joseph Monks), Naturhistorisches Museum, Wien (Austria, curator Manuela Vizek), Biologiezentrum Linz (Austria, curator Esther Öckermüller), Naturhistorisches Museum Berlin (Germany, curator Stefanie Krause), and Naturkundemuseum Bayern Munich (Germany, curator Stefan Schmidt). Several records were obtained from internet sources, especially from photos on Flickr (<https://www.flickr.com/>) and iNaturalist (<https://www.inaturalist.com/>). In this case, only records from specialists or photos enabling identification to the species level were included. However, the goal of this study was not to create detailed maps of distribution, because this work will be done in several European bee projects in the near future and occurrence records from local authorities, taxonomic specialists and museums are still not completely collected and validated.

The author examined only a part of the type material of both valid species and synonyms and all the original descriptions of all species and their synonyms. The type material was not studied in most cases because the description of the species is comprehensive and clear, and/or there was rich material available in private or museum collections for study, so the examination of the original types was not necessary. All of the type material studied by the author is indicated in the taxonomic treatment sections of species.

Morphology was studied using a digital Keyence VHX-700 photographing microscope with measuring tools. Only specimens clearly exhibiting diagnostic features were imaged. The identification keys for females and males are dichotomous, using the following standard abbreviations before the corresponding number: S – metasomal sternum, T – metasomal tergum, and F – flagellomere. Figure abbreviations in brackets (Fig. 1A, Figs 2–4) are used in the text. Head measurements were performed from the labrum base to the occipital ridge at the end of the head. If the same character applied to both females and males, it was photographed only once (in the female). If the species has a restricted range, it is also mentioned in the key in parentheses.

Species distributions were determined using studied material and literary sources on Dioxyini of Europe. Distribution maps were created in QGIS 3.6. The red-list categories from Nieto et al. (2014) are indicated, and updates to conservation status are proposed for several species.

Results

Identification key for the females of European Dioxyini

- 1 Scutellum without lateral projections (Fig. 15C); S6 and T5 elongated, more than three times longer than wide (Fig. 15D) *Ensliniana bidentata* (Spain and Portugal)
- Scutellum with lateral toothlike projections (Fig. 1C), often with medial tooth; S6 usually shorter (Fig. 1D)..... 2

- 2 Head and thorax with dense reddish-brown hair; metasoma without apical bands of whitish hair; metasoma and legs completely reddish (Fig. 3A) ***Dioxys ardens* (Spain and Portugal)**
- Head and thorax hairy or only sparsely haired, colour of hairs whitish or brownish; metasoma and legs usually completely or partly black; metasomal terga usually with narrow but well-developed apical bands of whitish hair (Fig. 7A) **3**
- 3 Forecoxa with a toothlike carina anteriorly (Fig. 1E) **4**
- Forecoxa rounded anteriorly (Fig. 7C) **5**
- 4 Postscutellum with a medial toothlike projection, which is narrow and elongated (Fig. 1C); T6 rounded and flattened medially; S6 slightly emarginate (Fig. 1D); body completely black with whitish hair (Fig. 1A) ***Aglaopis tridentata***
- Postscutellum with a medial toothlike process, which is not elongated (Fig. 17C); T6 not flattened medially; S6 without an emargination (Fig. 17D); legs, metasoma and antennae usually partly reddish (Fig. 17A) ***Metadioxys graeca* (Greece)**
- 5 S6 and T6 sharp and elongated (Fig. 19C); metasomal bands often not well defined; metasoma and legs partly reddish (Fig. 19A) ***Paradioxys pannonicus***
- S6 and T6 not elongated (Fig. 7D); metasomal bands well or ill-visible; body often completely black **6**
- 6 Apex of T6 truncate; S6 very slightly emarginate apically (Fig. 7D); black with whitish hairs and often basal terga of metasoma reddish (Fig. 7A) ***Dioxys cinctus***
- Apex of T6 convex (Fig. 11C); S6 with or without emargination; body completely black or partly reddish; legs can be also partly or completely reddish **7**
- 7 Metasoma completely black (Fig. 5A); small species (5–7 mm) ***Dioxys atlanticus***
- Metasoma partly reddish (Fig. 13A); legs partly reddish or dark; small to larger species **8**
- 8 Legs at least partly reddish (Fig. 13A, D); T6 coarsely, contiguously punctate (Fig. 13C); S2 with medial part slightly protruded (Fig. 13D); head and mesosoma in part with appressed, squamose pubescence ***Dioxys pumilus***
- Legs black (Fig. 11A); T6 finely, densely, but not contiguously, punctate (Fig. 11C); S2 without protruded medial part (Fig. 11E); head and mesosoma with pubescence semi-erect, not squamose ***Dioxys moestus***

Identification key for the males of European Dioxyini

- 1 Scutellum without lateral projections; postscutellum without apical tooth-like process in the middle (Fig. 15C); S7 and T7 with tooth-like processes laterally (Fig. 15E) ***Ensliniana bidentata* (Spain and Portugal)**
- Scutellum with lateral toothlike projections, often with medial tooth-like process (Fig. 1D); S7 and T7 usually without tooth-like processes **2**

- 2 Head and thorax with dense reddish-brown hair; metasoma without apical bands of whitish hair, metasoma and legs completely reddish (Fig. 3B).....
..... ***Dioxys ardens* (Spain and Portugal)**
- Head and thorax hirsute or only sparsely haired, colour of hairs whitish or brownish; metasoma and legs usually completely or partly black; metasomal terga usually with narrow but well-developed apical bands of whitish hair (Fig. 7B) **3**
- 3 Forecoxa with a toothlike carina anteriorly (Fig. 1E)..... **4**
- Forecoxa rounded anteriorly (Fig. 7C) **5**
- 4 Postscutellum with a medial toothlike projection, which is narrow and elongate (Fig. 1C); T7 emarginated (Fig. 1F); body completely black with whitish hair (Fig. 1B) ***Aglaoapis tridentata***
- Postscutellum with a medial toothlike process, which is not elongated (Fig. 17C); T7 not flattened medially; last tergum not emarginated (Fig. 17E); legs, metasoma and antennae usually partly reddish (Fig. 17B)
..... ***Metadioxys graeca* (Greece)**
- 5 Metasoma completely reddish with semi-transparent apical parts of terga, without well-visible apical bands (Fig. 19B); apex of S4 with two toothlike processes medially (Fig. 19D, E); T7 with straight apex (Fig. 19F); S7 with lateral teeth (Fig. 19E) ***Paradioxys pannonicus***
- Metasoma black or partly reddish (Fig. 7B); rarely completely reddish but then with well-visible apical bands of whitish or yellowish hair, apex of S4 straight or emarginated but without so prominent toothlike processes, S7 without lateral teeth..... **6**
- 6 Apex of S4 medially swollen, bidentate (Fig. 11F); matt and roughly punctate; T7 shiny with coarse but sparse punctures (Fig. 11G) ***Dioxys moestus***
- Apex of S4 straight (Fig. 13E), emarginated or with small toothlike processes (not as prominent as those of *P. pannonicus*); T7 more densely punctate **7**
- 7 Legs and metasoma partly or completely reddish (Fig. 13B, D); T7 triangular with acute apex (Fig. 13F); apex of S4 waved (Fig. 13E) ***Dioxys pumilus***
- Legs dark, metasoma dark or partly reddish; T7 broad (Fig. 7F); with straight or slightly curved apex; apex of S4 different **8**
- 8 Larger species (7–10 mm); at least part of T1 reddish (Fig. 7B); apex of S4 slightly emarginated (Fig. 7E); T7 coarsely and densely punctate (Fig. 7F) ...
..... ***Dioxys cinctus***
- Smaller species (5–7 mm); completely black (Fig. 5B); apex of S4 with two toothlike processes (Fig. 5E); T7 with shiny interspaces **9**
- 9 Mesonotum, scutellum and T1–T3 densely and deeply punctate, punctures larger; mesosternum medially finely rugose (Fig. 5B, C); emargination between toothlike processes on apex of S4 narrow (Fig. 5E)..... ***Dioxys atlanticus***
- Mesonotum, scutellum and T1–T3 more sparsely and finely punctate, punctures smaller and shallow; mesosternum shiny (Fig. 9B, C); emargination between toothlike processes on apex of S4 wider (Fig. 9D)
..... ***Dioxys lanzarotensis* (Canary Islands: Lanzarote)**

Extralimital species

Altogether, 10 species of five genera of tribe Dioxyini are known to occur in Europe. These are representatives of the genera *Aglaoapis* Cameron, *Ensliniana* Alfken, *Metadioxys* Popov and *Paradioxys* Mocsáry (one species of each genus) and six species of the genus *Dioxys* Lepeletier & Serville.

In the neighbouring regions, representatives of the genera *Allodioxys* Popov, *Eudioxys* Mavromoustakis and *Prodioxys* Friese are recorded, but no species of these genera has ever been recorded from Europe. Representatives of these genera differ from European species by the following characteristics (adopted from Warncke (1977)).

Both sexes of *Allodioxys* have the mesonotum with elongated projections on both sides and postscutellum with a spine-like process medially. Four species occur in the Middle East and/or North Africa (Libya, Algeria, Israel, Syria): *Allodioxys ammobius* (Mavromoustakis), *A. limbifera* Pérez, *A. moricei* (Friese) and *A. schulthessi* Popov (Warncke 1977; Lhomme et al. 2020).

Two species of *Eudioxys* occur in neighbouring regions: *Eudioxys quadridentata* (Friese) in North Africa (Egypt) and *E. schwarzi* Mavromoustakis in the Middle East (Iran) (Warncke 1977; Lhomme et al. 2020). Both sexes of this genus have axillae with two spines laterally and the scutellum with one spine on both sides.

Three species of *Prodioxys* occur in North Africa: *Prodioxys carneus* Gribodo, *P. longiventris* Pérez and *P. rufiventris* Lepeletier (Warncke 1977; Lhomme et al. 2020). All species are generally similar to *Dioxys ardens* with a completely reddish metasoma and legs and brownish hirsute head and mesosoma, females differ by the very long and narrow last tergum and sternum, males have last sternum of different shape than *D. ardens*.

Accounts of European species

Genus *Aglaoapis* Cameron

Aglaoapis Cameron, 1901: 262. Type species: *Aglaoapis brevipennis* Cameron, 1901, monobasic.

Dioxoides Popov, 1947: 89. Type species: *Coelioxys tridentata* Nylander, 1848, by original designation.

Notes. The genus *Aglaoapis* is distributed in Europe, the Middle East, India and South Africa. Three species are known worldwide (Michener 2007), and only one species occurs in Europe (Ghisbain et al. 2023).

Aglaoapis tridentata (Nylander)

Coelioxys tridentata Nylander, 1848 (nec *Apis tridentata* Fabricius, 1775): 254.

Dioxys fasciata Schenck, 1861: 383.

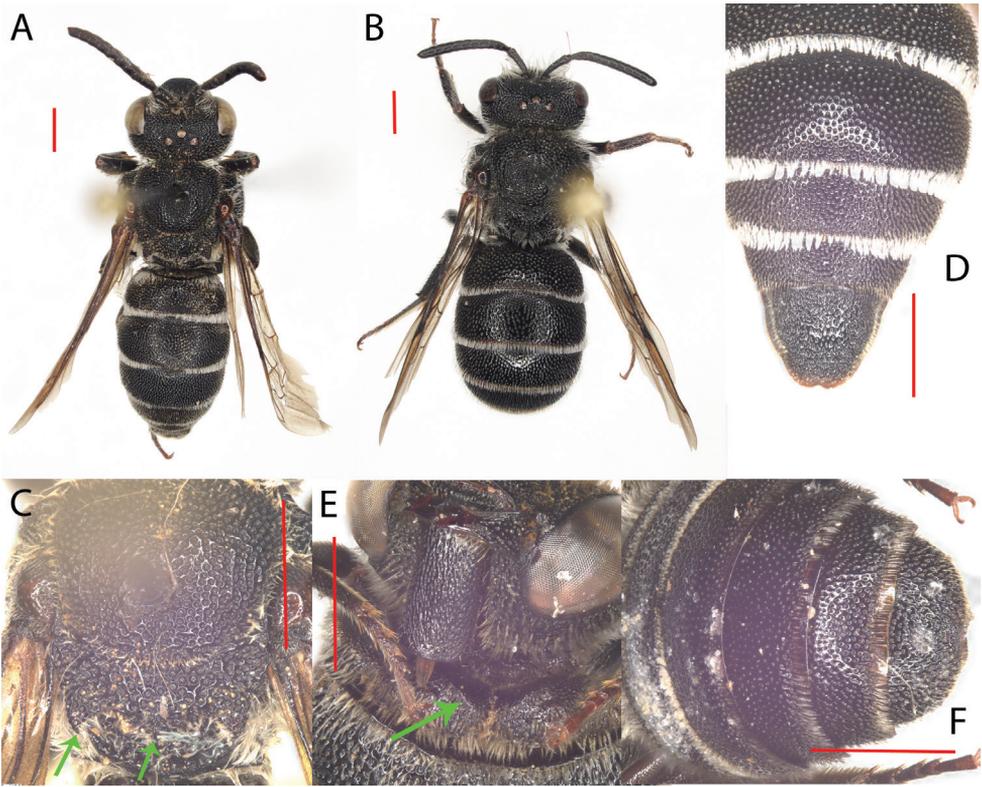


Figure 1. *Aglaoapis tridentata* **A** female, dorsal view **B** male, dorsal view **C** female, mesosoma dorsal view **D** female, metasoma, dorsal view **E** female, fore coxa **F** male, T7, dorsal view. Red scale bars represent the length of 1 mm.

Dioxys kuntzei Noskiewicz, 1940: 99.

Dioxoides tridentata ssp. *limassolica* Mavromoustakis, 1949: 587.

Diagnosis. Larger species (9–12 mm), both sexes are black with well-developed white bands of short hair on metasomal terga (Fig. 1A, B). Both sexes have the fore coxa with a carina anteriorly (Fig. 1E) and a short projection and the scutellum with a medial toothlike projection (Fig. 1C). Females have a longer last tergum than females of the genus *Dioxys* and an emarginated last sternum (Fig. 1D). The last tergum is emarginated for males (Fig. 1F).

Distribution. *Aglaoapis tridentata* is a Palearctic species that occurs in Europe, from Spain in the west to Russia in the east (Fig. 2), and in Asia from the Caucasus, Kyrgyzstan and China, Kazakhstan, Siberia and Russian Far East. This species reaches the farthest north of any species of the tribe, with records from Finland and Sweden (Ornosa et al. 2008; Madsen and Calabuig 2010; Ascher and Pickering 2023).

Biology and hosts: Species recorded especially in steppic formations, sunny slopes, forest steppes and other open or semiopen habitats. Occurs also in abandoned sandpits, spoil

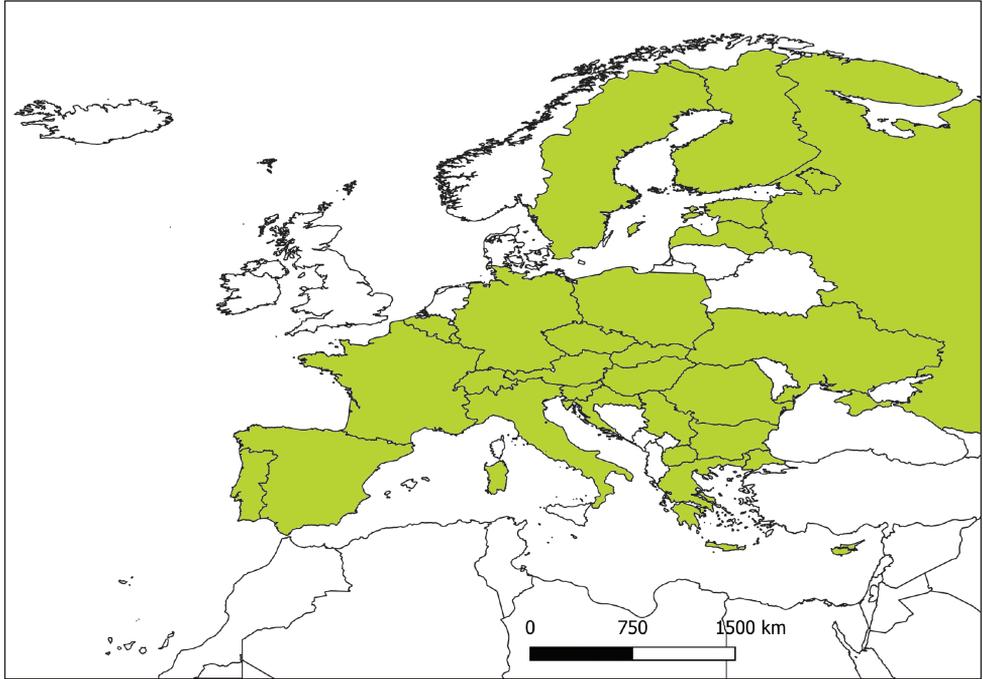


Figure 2. *Aglaopis tridentata*, distribution in Europe.

heaps and other habitats of anthropogenic origin. This species attacks nests of bees of the family Megachilidae, especially those nesting underground or making their own nests near the ground surface. *Hoplitis anthocopoides* (Schenck), *Hoplitis ravouxi* (Pérez), probably also *Hoplitis adunca* (Panzer) and *Megachile pilidens* Alfken, in southern parts of Europe, and also *Chalicodoma parietina* (Geoffroy) were confirmed as hosts of this species (Westrich 2018). Scheuchl and Willner (2016) also listed *Megachile leachella* Curtis as a likely host.

Conservation status. Nieto et al. (2014) classified this species as LC – data deficient. This species is relatively rare throughout its range. Its distribution in Europe is the largest of any species, and it is still being recorded in most countries – it was reported to be regionally extinct only in Belgium and Finland (Ghisbain et al. 2023). It should therefore be classified as LC.

***Dioxys* Lepeletier & Serville**

Dioxys Lepeletier & Serville, 1825: 109, type species: *Trachusa cincta* Jurine, 1807, monobasic.

Hoplospites Ashmead, 1898: 284, type species: *Phileremus productus* Cresson, 1879, by original designation.

Chrysopheon Titus, 1901: 256, type species: *Chrysopheon aurifuscus* Titus, 1901, monobasic.

Notes. *Dioxys* is a Holarctic genus distributed in most of Europe and North Africa to central Asia in the east and the southwestern USA and adjacent Mexico in the western hemisphere (Hurd 1958; Michener 2007). Five species occur in North America, and approximately 13 occur in the Palaearctic region (Warncke 1977; Ghisbain et al. 2023). Six species occur in Europe.

Dioxys ardens Gerstaecker

Dioxys ardens Gerstaecker, 1869: 161.

Dioxys rufispina Pérez, 1895:26.

Diagnosis. Larger species, body length 8–10 mm. In both sexes, typical in its colouration, the metasoma is completely reddish without terminal or basal bands, and the legs and flagellum are reddish (Fig. 3A, B). T6 of females is elongated and narrowed posteriorly, with a rounded apex. The mesosoma is ferruginously hirsute. Axillae with teeth and postscutellum with short but sharp tooth in the middle. The same characteristics are also typical for males.

Distribution. Spain, Portugal (Fig. 4) and North Africa (Morocco to Libya).

Biology and hosts. Species recorded from semideserts and other arid open habitats. Hosts unknown.

Conservation status. This species is known only from several records from southern parts of Spain and one record from Portugal. Nieto et al. (2014) listed this species as DD – data deficient. According to the distribution records, it can be VU-vulnerable because of its long-lasting rarity. However, we know only a little about the populations and occurrence of this species in recent years.

Note. In general, a similar species, *Dioxys chalicoda* Lucas, was recorded from North Africa (Algeria and Libya). One very old record is from Gibraltar, but this specimen was erroneously identified and belongs to *D. ardens* (coll. Biologiezentrum Linz, Austria). This species differs in the colouration of the metasoma, which has black colouration of at least the last three segments. Females have mandibles with lateral tubercles, and males have ends of S4 with an emargination and S5 and S6 convex.

Dioxys atlanticus Saunders, 1904, stat. nov.

Dioxys atlanticus Saunders, 1904: 232.

Diagnosis. This species is small (5–7 mm in total length) and completely black with well-developed apical bands on metasomal terga (Fig. 5A, B). It is generally similar to *Dioxys lanzarotensis*, from which it can be identified by denser punctation on metasomal terga (Fig. 5C) and clypeus. It is morphologically similar to *D. moestus*, which is probably its near relative, rather than to *D. cinctus*, into which it was previously classified as a subspecies (Warncke 1977). The dark colouration of tibial spurs reported

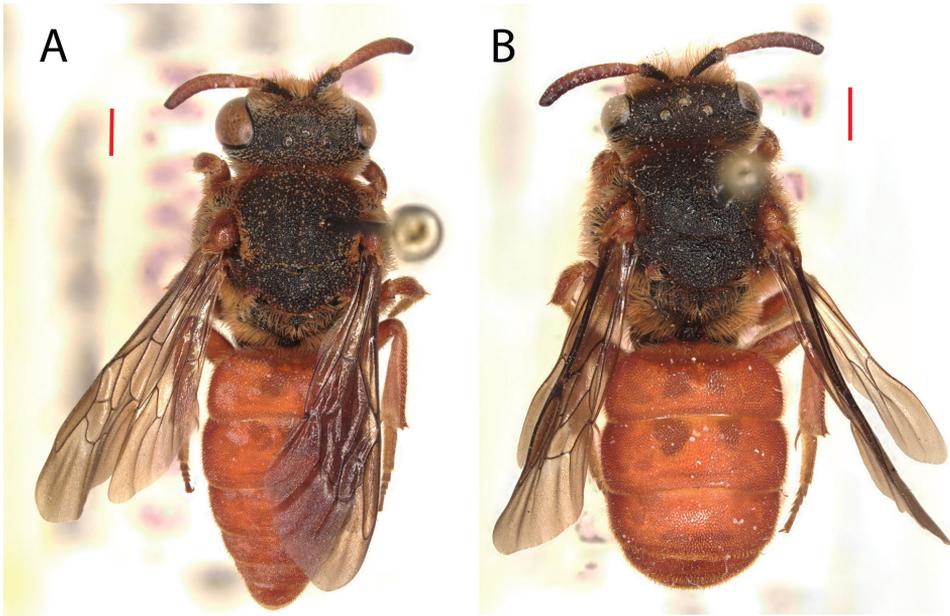


Figure 3. *Dioxys ardens* **A** female, dorsal view **B** male, dorsal view.



Figure 4. *Dioxys ardens*, distribution in Europe.

by Warncke (1977) was not observed in any specimen I have studied (Fig. 5D). Based on the morphology and distribution, it is clearly a separate species. Syntypes (a male and a female from Santa Cruz, Tenerife) from the Natural History Museum London were studied.

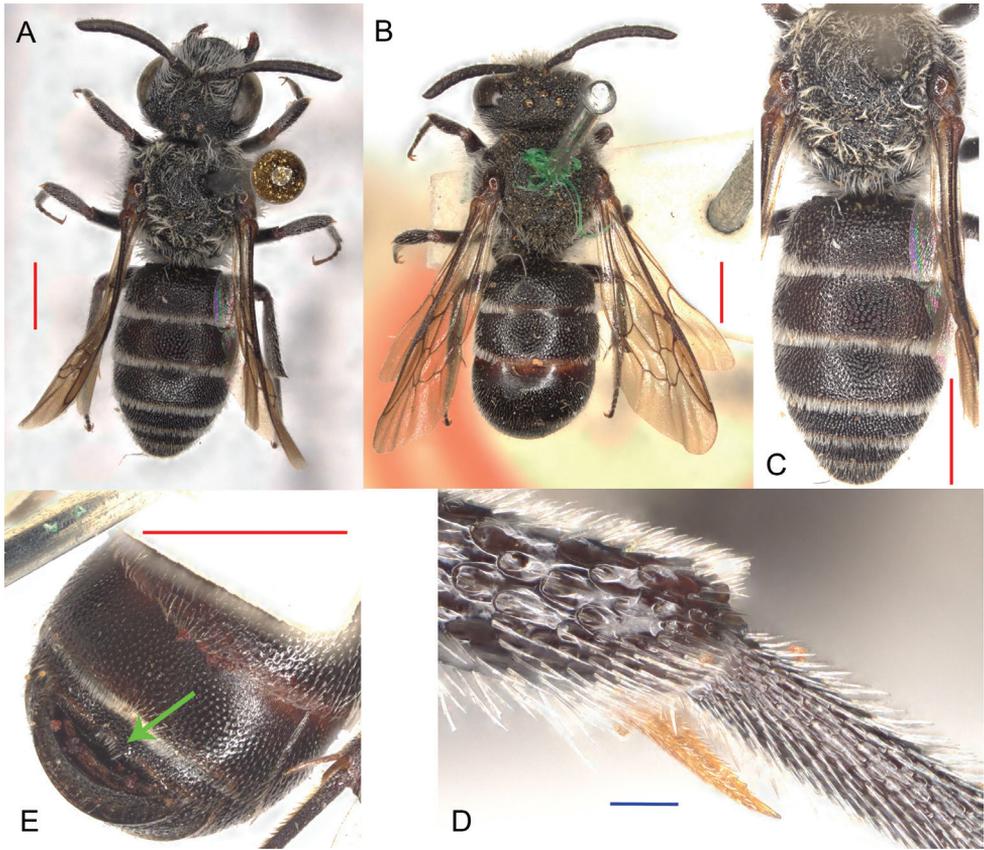


Figure 5. *Dioxys atlanticus* **A** female, dorsal view **B** male, dorsal view **C** female, mesosoma dorsal view **D** female, tibial spur on fore leg **E** male, last metasomal segments, ventral view. Red scale bars represent the length of 1 mm, blue scale bars 100 μm .

Distribution. This species was described from a male and a female from the Canary Islands (Tenerife), where it was also recorded on two other islands – Lanzarote and Gran Canaria (Hohmann et al. 1993) (Fig. 6). It was also recorded in Egypt (Warncke 1977) and currently in Sardinia (Orroli, 02.vi.2011, 6 ♀♀, G. Pagliano lgt., P. Bogusch det., coll. Biologiezentrum Linz, Austria). Based on the records, the species occurs in the Canary Islands and several parts of North Africa, South Europe and perhaps the Middle East, but it is very rare and hard to find. Specimens from Sardinia correspond in size, morphology and colouration with those of the Canary Islands and with both syntypes.

Biology and hosts. The species occurs in open habitats – steppes, semideserts, in rocky areas with shrubby vegetation. Little is known about its biology. Hosts unknown.

Conservation status: Nieto et al. (2014) listed this species as DD – data deficient. There are quite recent records from the Canary Islands and new records from Sardinia (Italy). In my opinion, it should be VU – vulnerable because of its restricted distribution area.

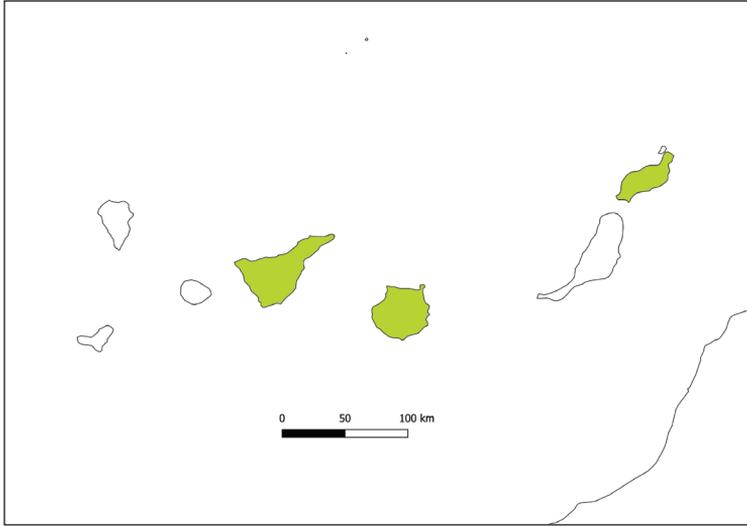


Figure 6. *Dioxys atlanticus*, distribution in Canary Islands.

***Dioxys cinctus* (Jurine)**

Trachusa cincta Jurine, 1807: 253.

Dioxys pyrenaica Lepeletier, 1841: 515.

Dioxys maura Lepeletier, 1841: 516.

Dioxys cruenta Gerstaecker, 1869: 166.

Dioxys spinigera Pérez, 1884: 299.

Dioxys cincta var. *jucunda* Mocsáry, 1894: 36.

Dioxys cincta ab. *friederikae* Mader, 1933: 125.

Dioxys montana Heinrich 1977: 11–12, syn. nov.

Notes. Type specimens of this species and the description were studied in Biologiezentrum Linz, Austria. Both type specimens (a male and a female from the Sertavul Pass in Turkey) do not morphologically differ from typical specimens of *D. cinctus*.

Diagnosis. Larger species, body length variable between 5–12 mm, probably depending on the host. In both sexes, the body is black with the first two metasomal terga entirely or partly reddish and narrow apical bands of whitish short appressed hair (Fig. 7A, B). In several cases, red colouration is present on T3–T4. Mesosoma bears long whitish hair, apex of T6 of females straight and only shortly elongated, shorter than in similar species (Fig. 7D). The legs and antennae are black. This species has a very large distribution area and is connected with many host species. It causes variability in size (5–12 mm), while populations from southern Europe and North Africa are often smaller. The colouration is very variable, too – normally both sexes have first metasomal terga entirely reddish but usually populations from the north of the distribution area are darker and sometimes are entirely black with no reddish pattern.

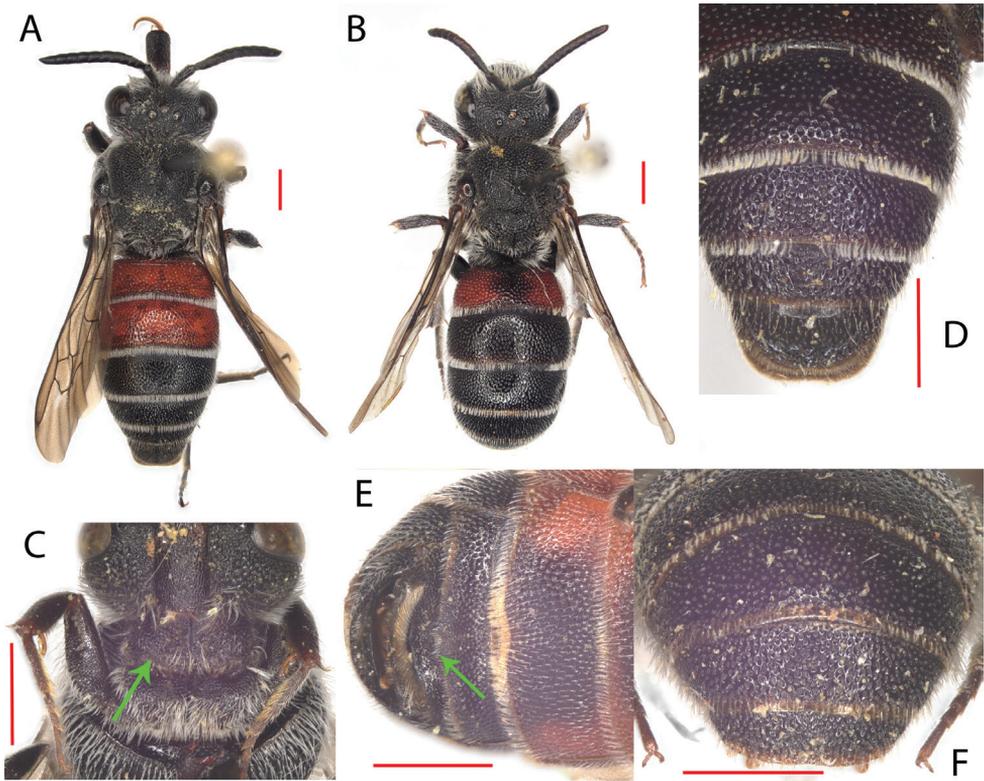


Figure 7. *Dioxyx cinctus* **A** female, dorsal view **B** male, dorsal view **C** female, fore coxa **D** female, mesosoma dorsal view **E** male, last metasomal segments, ventral view **F** male, T4–T6, dorsal view. Red scale bars represent the length of 1 mm.

Distribution. A species with a western Palaearctic distribution known from central and southern Europe from Portugal to Greece and Romania (Fig. 8). Outside of Europe, it is found in North Africa, Israel and as far east as the Caucasus (Dusmet 1921; Popov 1936; Warncke 1977; Standfuss et al. 2003; Ornos et al. 2008; Ascher and Pickering 2023).

Biology and hosts. Species occurring in a variety of open and semi-open habitats: steppe, semideserts, forest steppes and many others. It was also recorded in sites of anthropogenic origin – former sandpits, quarries, spoil heaps and military exercising areas. This species has more host species in its large distribution area: *Chalicodoma parietina*, *Chalicodoma pyrenaica* Lepeletier, *Hoplitis adunca* and *Hoplitis anthocopoides* were confirmed (Scheuchl and Willner 2016). Its hosts nest underground, create nests of mud or resin, or nest in various types of cavities above the ground. Parasitising females of this species were often recorded around bee hotels associated with nests of *H. adunca* in the Czech Republic (P. Bogusch, unpublished records). The actual number of hosts is certainly higher, and the preferred host species differ among the localities within the large distribution area.

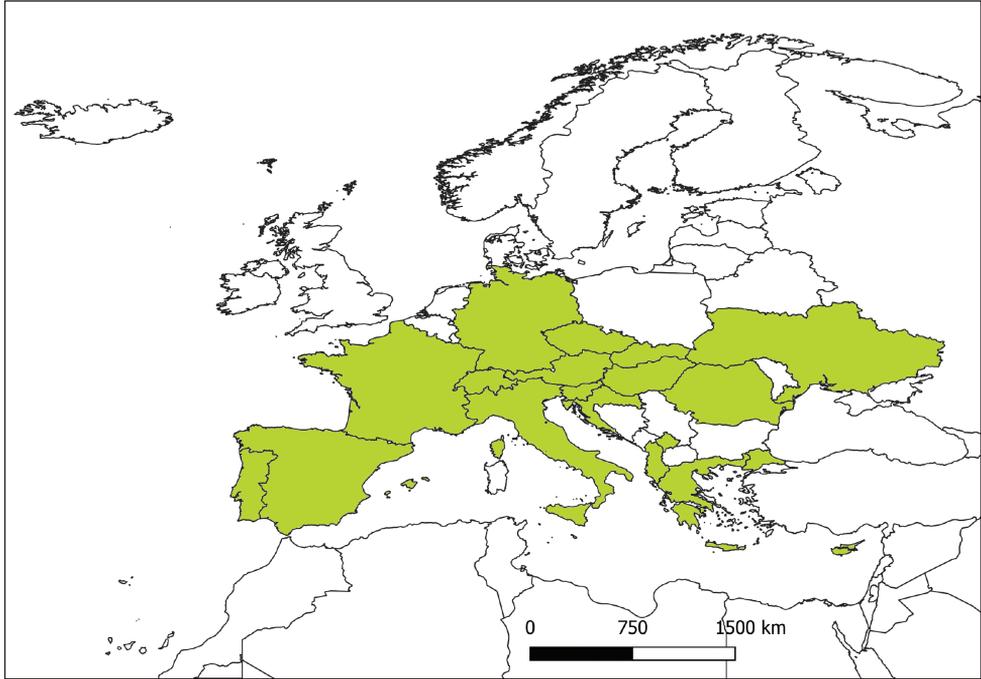


Figure 8. *Dioxys cinctus*, distribution in Europe.

Conservation status. Nieto et al. (2014) classified this species as LC – least concern. It is distributed in most of southern and central Europe, with the northern distribution border in France, Germany, the Czech Republic and Ukraine. In many countries, it is not rare, and the numbers of recorded individuals are even higher than those of *A. tridentata*. In the Czech Republic, the species has spread in the last 20 years (Straka and Bogusch 2017). Thus, it should stay in the category LC.

Dioxys lanzarotensis Tkalcu

Dioxys lanzarotensis Tkalcu, 2001: 49–50.

Diagnosis. Small species very similar in morphology to *D. atlanticus* (Fig. 9A) but differs by sparser punctures on metasomal terga (Fig. 9B) and on clypeus. Only a single male (holotype) was recorded from the island Lanzarote of the Canary Islands (Spain) (Tkalcu 2001). The holotype should be deposited in Übersee-Museum Bremen, Germany, but was discovered in the collection of Francisco La Roche in San Cristóbal de La Laguna, Tenerife, Spain. According to the studies of the holotype, this species is very similar to males of *D. atlanticus* but differs by the above reported characteristics, as well as several others (length and position of toothlike processes on S4 (Fig. 9D), shape of head). It is certainly a separate species; however, its distribution area is restricted to one island.

Distribution. Lanzarote, Canary Islands, Spain (Fig. 10) (Tkalcu 2001).

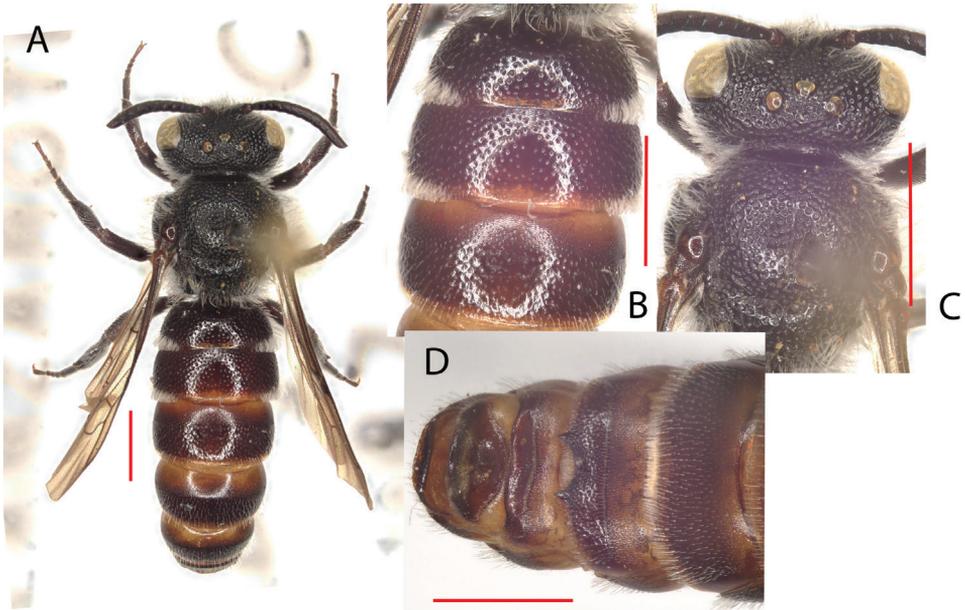


Figure 9. *Dioxys lanzarotensis* **A** male, dorsal view **B** male, metasoma, dorsal view **C** male, mesosoma dorsal view **D** male, last metasomal segments, ventral view. Red scale bars represent the length of 1 mm.

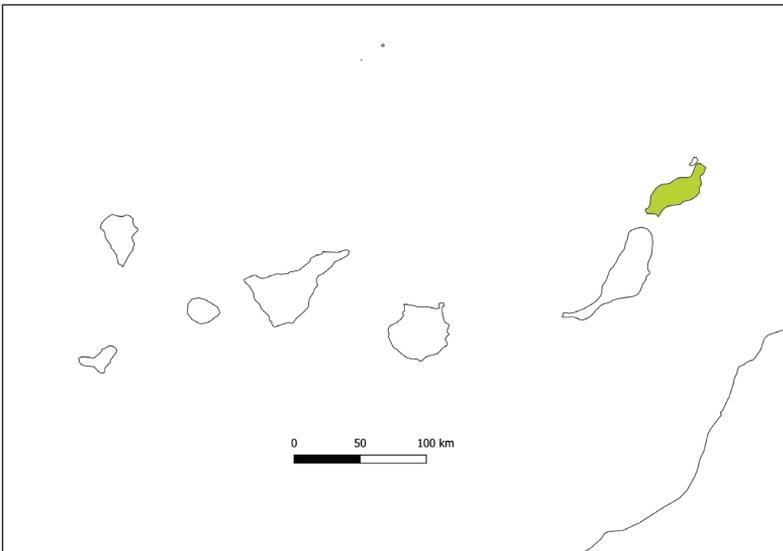


Figure 10. *Dioxys lanzarotensis*, distribution in Canary Islands.

Biology and hosts. Unknown.

Conservation status. Nieto et al. (2014) classified this species as DD – data deficient. It is the only category in which this species can be classified because we know only one specimen, the type.

Dioxys moestus Costa*Dioxys moesta* Costa, 1883: 96.*Dioxys rotundata* Pérez, 1883: 300.

Diagnosis. Middle-sized species, body length 5–8 mm. Species with typical general appearance for this genus, black with first 2–3 metasomal terga entirely or partly reddish, with narrow apical bands of whitish short appressed hair (Fig. 11A, B). Mesosoma with long whitish hair, apex of metasomal T6 rounded (Fig. 11C). The legs and antennae are black. The last metasomal terga in males was not as narrow as that in *D. cinctus*. In general, similar to *D. cinctus* but differs by several characteristics: it is usually smaller and the reddish colouration is more distributed (usually on T1–3, in *D. cinctus* on T1–T2). Females of *D. cinctus* have a straight apex of T6, while females of *D. moestus* have a round apex of T6. Males of *D. moestus* have two

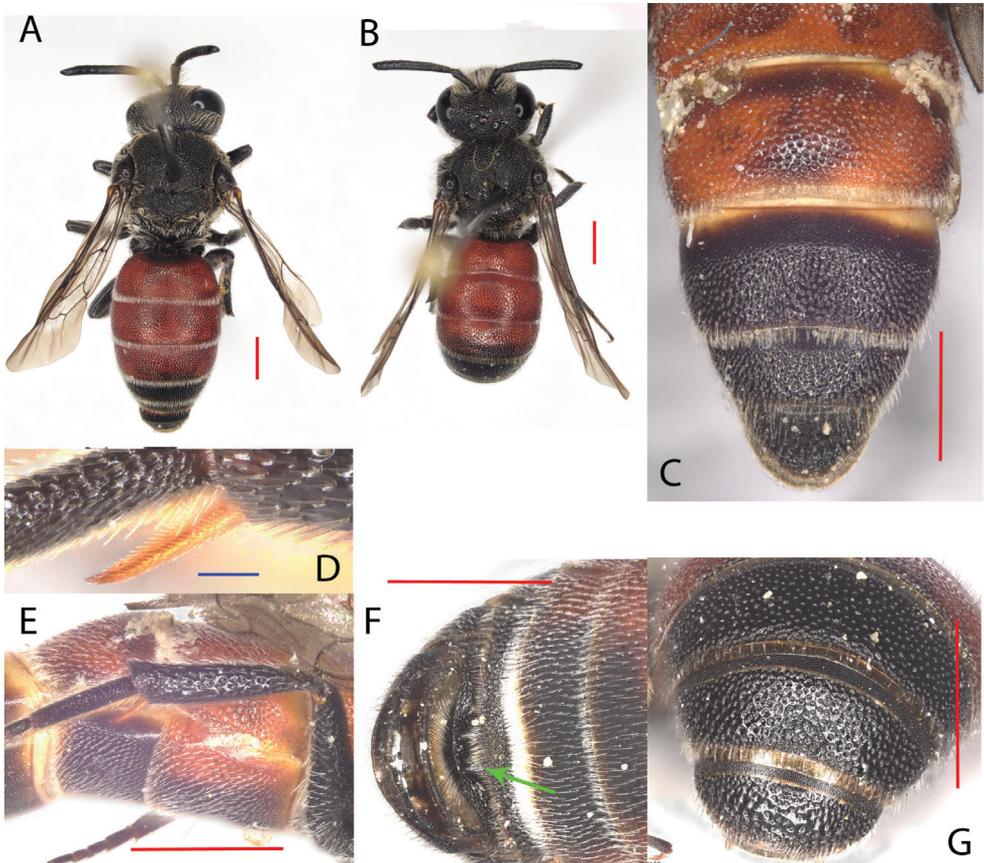


Figure 11. *Dioxys moestus* **A** female, dorsal view **B** male, dorsal view **C** female, mesosoma dorsal view **D** female, metasoma, dorsal view **E** female, metasoma lateral **F** male, last metasomal segments, ventral view **G** male, T4–T6, dorsal view. Red scale bars represent the length of 1 mm, blue scale bars 100 μm .

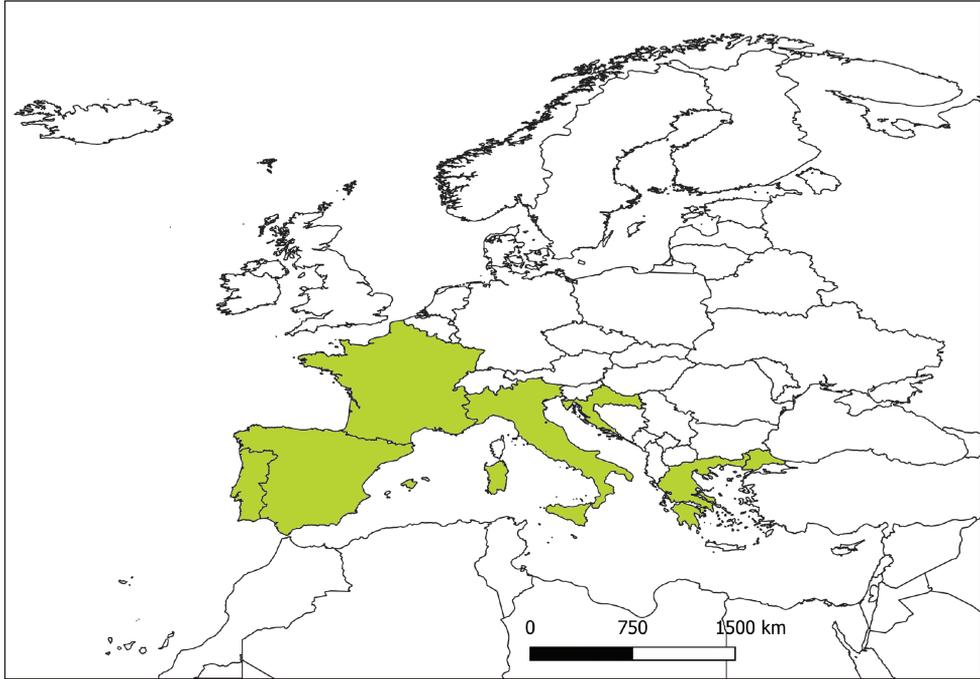


Figure 12. *Dioxyys moestus*, distribution in Europe.

tooth-like processes on S4 medio-posteriorly (Fig. 11F), and males of *D. cinctus* lack this characteristic. Punctuation of T2–T3 of *D. moestus* is finer and sparser than in *D. cinctus*.

Distribution. Mediterranean species described from Sardinia. Recorded from Portugal to Greece (Fig. 12). Outside of Europe, it is recorded in North Africa, from Morocco to Tunisia, and Israel (Warncke 1977; Ornos et al. 2008).

Biology and hosts. This species occurs in open habitats. It was collected in open habitats with shrubby vegetation, steppic formations or rocky landscapes with almond orchards. Hosts are *Hoplitis benoisti* (Alfken), *Hoplitis fertoni* (Pérez) and *Hoplitis zandeni* (Teunissen & van Achterberg) (Bogusch et al. 2020b), probably also *Hoplitis ochraceicornis* (Ferton) (I. Cross, unpublished record). Several specimens were reared from nests of *H. fertoni* placed inside snail shells (Bogusch et al. 2020b).

Conservation status. Nieto et al. (2014) classified this species as DD – data deficient. This species occurs in most of southern Europe, where it is rare but still frequently recorded. It can be classified as LC – least concern.

Note. *Dioxyys heinrichi* Warncke occurs in North Africa (Morocco and Algeria) and is similar to *D. moestus*. Female *D. heinrichi* have a longer F2 and more convex clypeus, and males do not have a swollen end of S4 and lack the two small teeth. The end of S5 is slightly emarginated.

Dioxys pumilus* GerstaeckerDioxys pumilus* Gerstaecker, 1869: 167.*Dioxys varipes* De Stefani, 1887: 113.*Dioxys maroccana* Popov, 1936: 16.*Dioxys cypriaca* Popov, 1944: 121.

Diagnosis. Smaller species, total body length 4–6 mm. Species with typical general appearance for this genus, black with first 2–4 metasomal terga entirely or partly reddish, with narrow apical bands of whitish short appressed hair (Fig. 13A, B). Mesosoma with long whitish hair, apex of metasomal T6 rounded (Fig. 13C). The legs and antennae are at least partly reddish. Last metasomal terga in males not as narrowed as in *D. cinctus*, last tergum more curved than in *D. moestus* and *D. cinctus*. Species in general similar to smaller individuals of *D. moestus* and *D. cinctus* differ by reddish legs and flagellum. Females have a T6 that is longer than it is wide (distinctly longer than the T6 of both

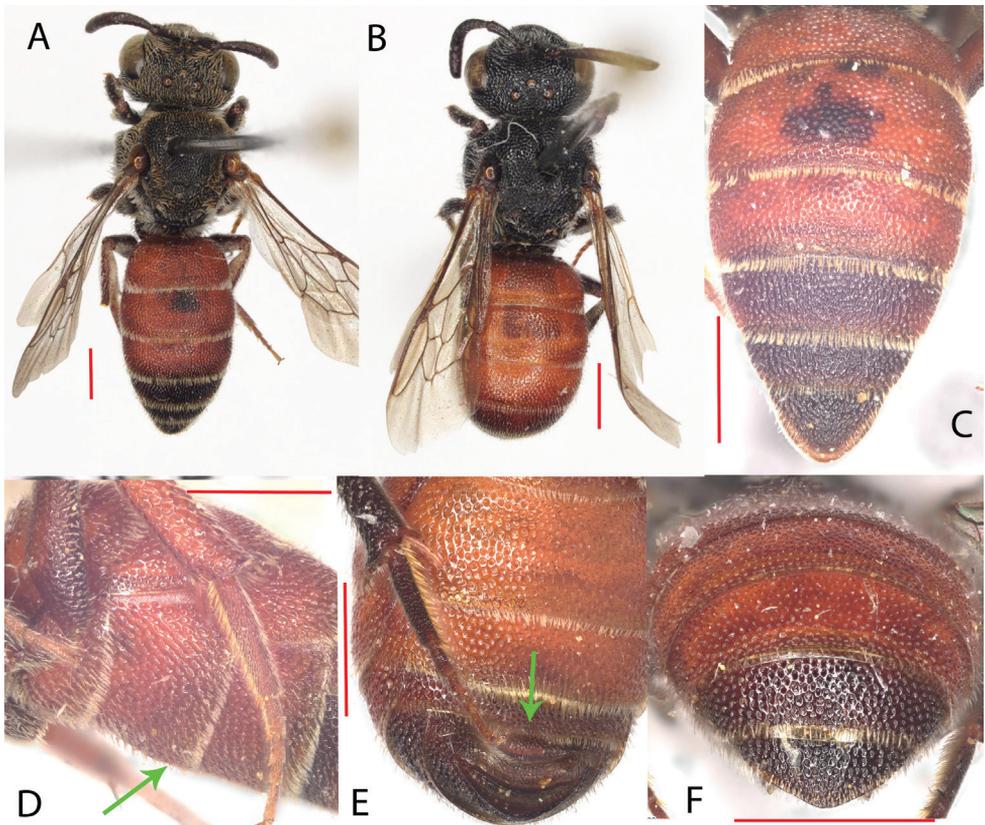


Figure 13. *Dioxys pumilus* **A** female, dorsal view **B** male, dorsal view **C** female, metasoma, dorsal view **D** female, metasoma lateral **E** male, last metasomal segments, ventral view **F** male, last metasomal segments, dorsal view. Red scale bars represent the length of 1 mm.

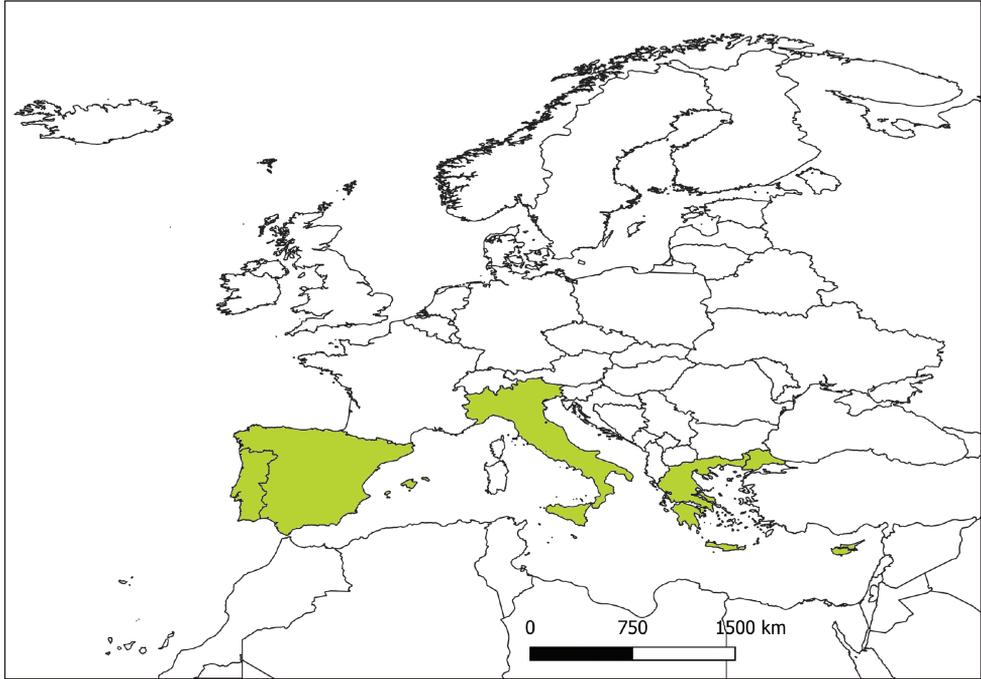


Figure 14. *Dioxys pumilus*, distribution in Europe.

similar species), males do not have a sharp medio-posterior projection on S4 (present in *D. moestus*) but the apex of S4 is waved, not straight as in *D. cinctus* (Fig. 13E). Punctuation of T2–T3 is coarser and denser than in *D. moestus* and *D. cinctus*. Specimens from Cyprus (described by Popov, 1944 as a separate species) look Smore colourful at first view but do not differ in their morphology, and the diagnostic characteristics of *D. cypriaca* are variable and form a continuous line to *D. pumilus*. Thus, *D. cypriaca* is currently supposed to be a synonym of *D. pumilus*.

Distribution. This is a western Palearctic species. The nominate subspecies occurs in the eastern Mediterranean basin (Greece, Cyprus, Turkey) (Fig. 14) and spreads towards Asia Minor (Israel, Syria) and Iran. The subspecies *D. p. varipes* occurs in the western Mediterranean basin (Sicily, Spain, Morocco, Algeria, Tunisia). The taxonomic statuses of these subspecies are unclear, but they do not differ in morphology, other than the specimens from western parts of the distribution area often being darker than those from the east.

Biology and hosts. This species was recorded in a variety of open and semi-open habitats – steppes, forest steppes, semideserts, open landscapes with shrubby vegetation and many others. *Heriades crenulatus* Nylander was reported as a likely host of this species in Cyprus (Mavromoustakis 1959). In Portugal, it was recorded in association with *Hoplitis annulata* Latreille (Baldock et al. 2018). Small species of *Osmiini* are also supposed to be host species of *D. pumilus*.

Conservation status. Nieto et al. (2014) classified this species as DD – data deficient. This species occurs in many countries in southern Europe, while in several localities, it has been recorded in large series. It is more local than *D. moestus* but probably more numerous at the localities. It can be classified as LC – least concern.

Ensliniana Alfken

Ensliniana Alfken, 1938: 431, type species: *Ensliniana cuspidata* Alfken, 1938 = *Stelis bidentata* Friese, 1899, by original designation.

Dioxoides Popov, 1947: 89. Type species: *Coelioxys tridentata* Nylander, 1848, by original designation.

Notes. This genus is distributed in North Africa and the Middle East, from Morocco in the west to Turkmenistan in the east. Three species were described, one of which was reported from Europe – Portugal and Spain (Popov 1936, 1953; Michener 2007).

Ensliniana bidentata (Friese)

Stelis bidentata Friese, 1899: 285.

Paradoxys pannonica var. *rufipes* Friese, 1899: 285.

Dioxys richaensis Friese, 1911: 139.

Dioxys bidentata Friese in Schulthess, 1924: 319.

Ensliniana cuspidata Alfken, 1938: 431.

Diagnosis. Larger species, body length 7–10 mm. The only species of the genus recorded from Europe. It is typical by the characteristics of the genus; both sexes are generally similar to *Dioxys* species (Fig. 15A, B) but lack axillar teeth (Fig. 15C). T5 of females is shiny, and T6 and S6 are elongated with two lateral teeth, similar to *Paradoxys pannonica* (Fig. 15D). *P. pannonica* differs in the black or dark brown colour of the entire body, with a reddish pattern only on the first three metasomal terga and distinct apical bands of whitish short appressed hair on the metasomal terga.

Distribution. In Europe, only several specimens are known from Spain and Portugal (Ornosa and Ortiz-Sánchez 2014; Torres 2020; Ascher and Pickering 2023) (Fig. 16). It was described from Israel (Jericho and Oran). Outside of Europe, it is known from Morocco, Algeria, Tunisia, Turkey, Syria, Israel and Jordan (Grace 2010).

Biology and hosts. This species probably occurs in open habitats – steppic grasslands, rocky slopes, semideserts and other habitats. Baldock et al. (2018) listed *Hoplitis zaianorum* (Benoist) as a likely host of this species.

Conservation status. Nieto et al. (2014) classified this species as DD – data deficient. This species is known in Europe only from Spain and Portugal, where it was recorded both in the past and in recent years. It can be classified as VU – vulnerable because of its restricted distribution area in Europe.

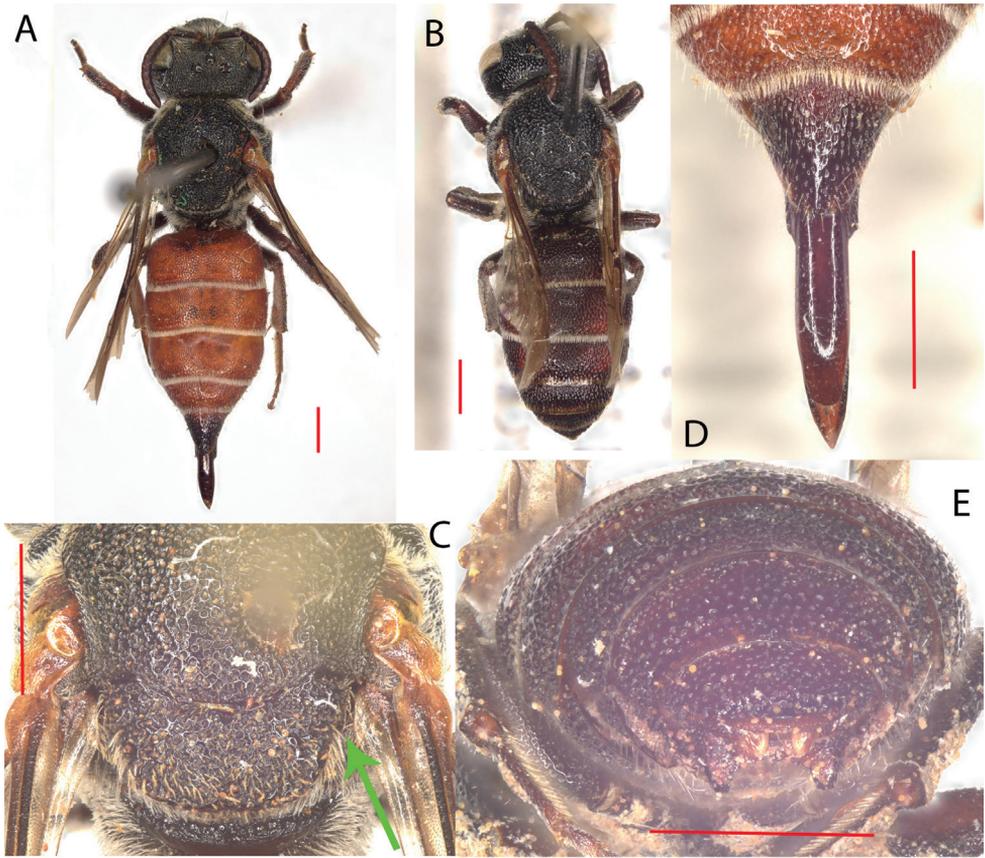


Figure 15. *Ensliniana bidentata* **A** female, dorsal view **B** male, dorsal view **C** female, last metasomal segments, dorsal view **D** female, mesosoma, dorsal view **E** male, last metasomal segments, dorsal view. Red scale bars represent the length of 1 mm.

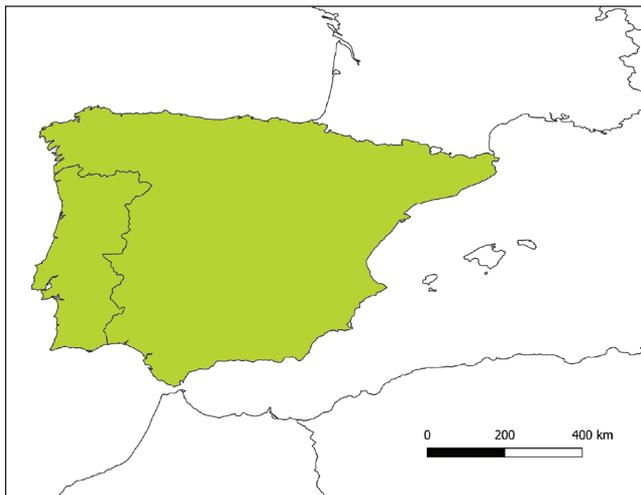


Figure 16. *Ensliniana bidentata*, distribution in Europe.

Metadioxys Popov

Metadioxys Popov, 1947: 88, type species: *Dioxys formosa* Morawitz, 1875, by original designation.

Notes. This genus has a similar distribution to the previous genera in North Africa and the Middle East, from Morocco in the west to Uzbekistan in the east. Three species were described, one of which was reported from Europe – Greece (Popov 1936, 1953; Michener 2007).

Metadioxys graeca (Mavromoustakis)

Dioxys formosa graeca Mavromoustakis, 1963: 696.

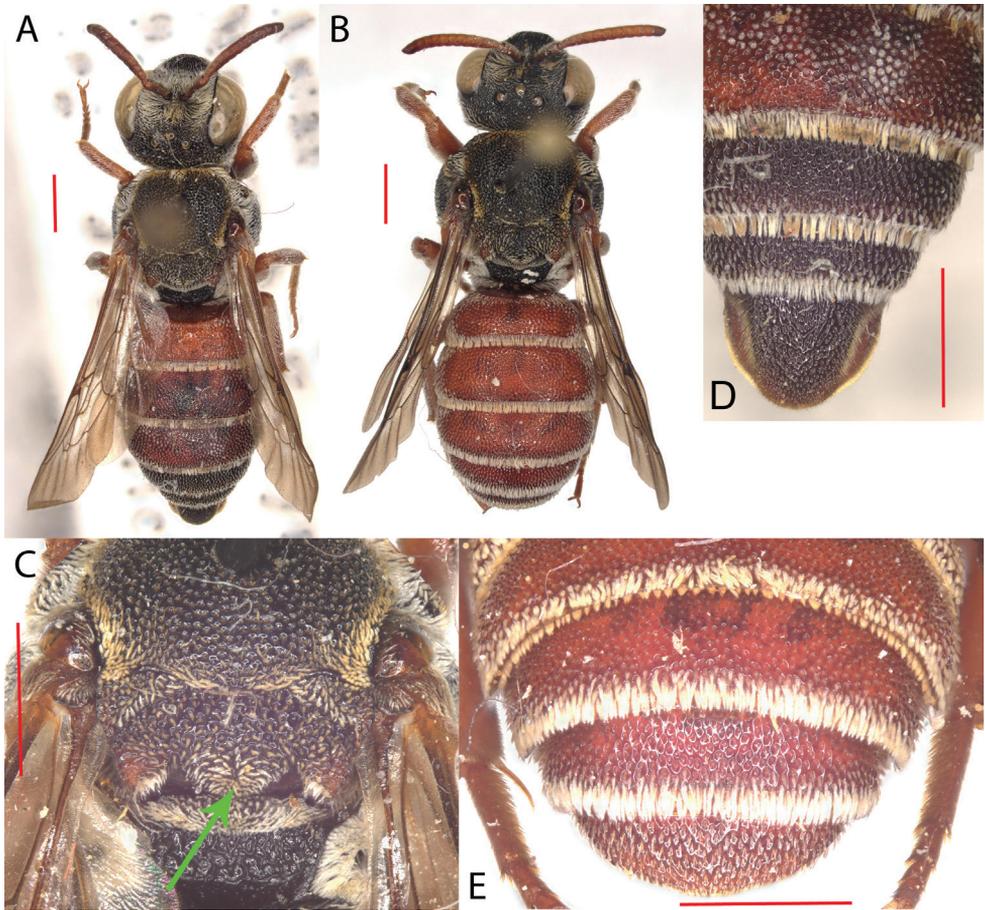


Figure 17. *Metadioxys graeca* **A** female, dorsal view **B** male, dorsal view **C** female, mesosoma dorsal view **D** female, metasoma, dorsal view **E** male, last metasomal segments, dorsal view. Red scale bars represent the length of 1 mm.

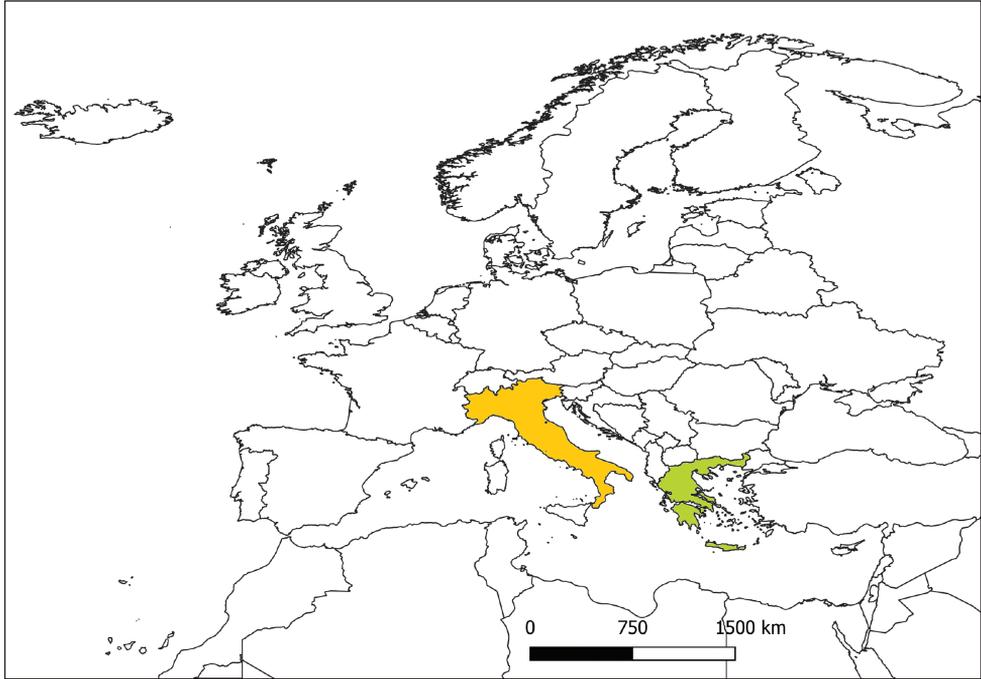


Figure 18. *Metadioxys graeca*, distribution in Europe. Doubtful record from Italy in orange.

Diagnosis. Larger species, body length 8–10 mm. Species generally very similar to those of the genus *Dioxys*, black with first 2–4 metasomal terga entirely or partly reddish (rarely whole metasoma reddish and other body parts reddish), with narrow apical bands of whitish short appressed hair (Fig. 17A, B). Whole body with scale-like whitish short appressed hair, similar to those of *Epeolus* species. Apex of metasomal T6 more elongated than in *Dioxys* and *Aglaopis*, rounded (Fig. 17D). The legs and antennae are at least partly reddish. Typical with sharp carina on coxa of front leg laterally, postscutellum without teeth medioapically, only with an ill-visible tubercle (Fig. 17C). In both sexes, T6 was without emargination (Fig. 17D, E).

Distribution. In the European region, this species is known from Greece (Thessaly and Crete) (Fig. 18). Its range extends out of the European region to Asiatic Turkey, Morocco and Israel (Warncke 1977; Grace 2010; Ascher and Pickering 2023; Kuhlmann et al. 2023).

Biology and hosts. This species probably occurs in open habitats – steppic grasslands, rocky slopes, semideserts and other habitats. Hosts unknown.

Conservation status. Nieto et al. (2014) classified this species as DD – data deficient. There are only old records from Greece and one doubtful record from Italy (certainly this species but probably wrongly labelled), and no recent finds are known. Because of its unknown population trend, we must leave this species in category DD – data deficient.

Note. *Metadioxys formosa* Morawitz occurs in North Africa (Morocco) and the Middle East (Israel and Turkmenistan). It is smaller than *M. graeca* (6–8 mm), and

both sexes have scale-like whitish short appressed hair distributed on more parts of the body than *M. graeca*. Female has last tergum broadened laterally; male has deeply emarginated last sternite.

Paradioxys Mocsáry

Paradioxys Mocsáry, 1894: 35, type species: *Dioxys pannonica* Mocsáry, 1877, monobasic.

Notes. This genus is reported from southeastern Europe and the Middle East. Its occurrence ranges from Austria in the west to Iran in the east. Two species are known, one of which occurs in Europe (Popov 1936; Michener 2007).

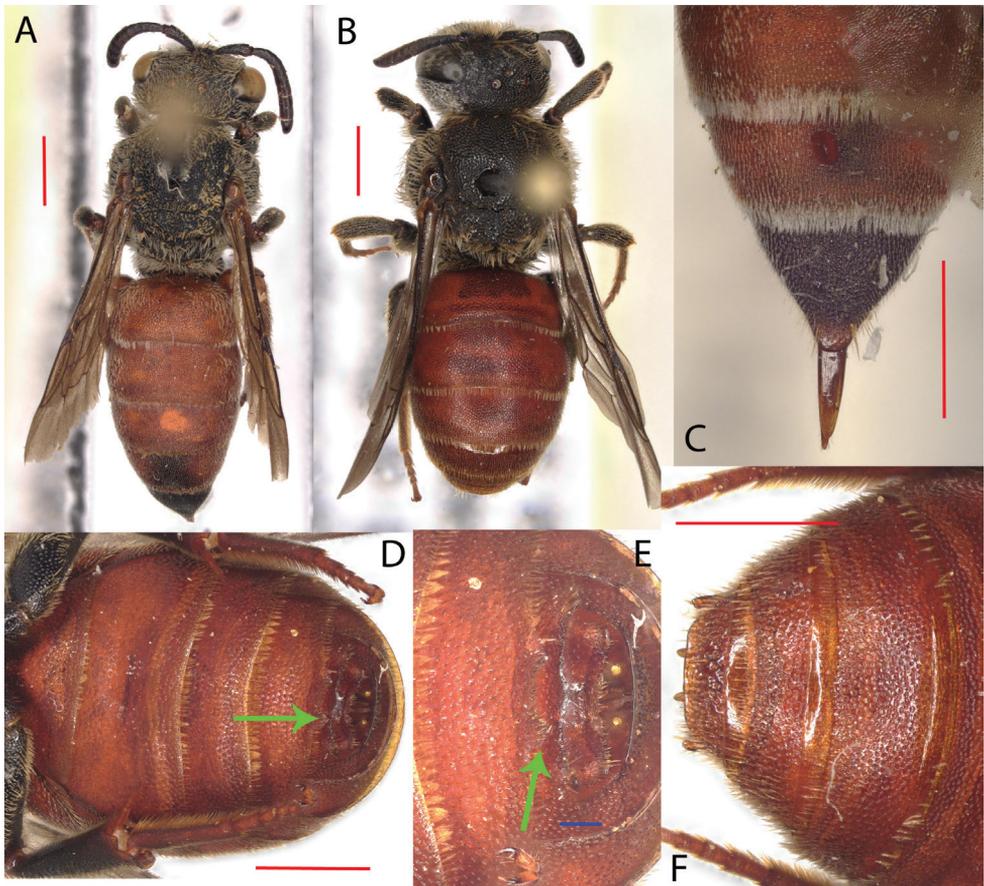


Figure 19. *Paradioxys pannonicus* **A** female, dorsal view **B** male, dorsal view **C** female, last metasomal segments, dorsal view **D** male, metasoma, ventral view **E** male, last metasomal segments, ventral view **F** male, last metasomal segments, dorsal view. Red scale bars represent the length of 1 mm, blue scale bars 100 μ m.

Paradioxys pannonicus (Mocsáry)

Paradioxys pannonica Mocsáry, 1894: 35.

Diagnosis. Middle-sized species, body length 7–10 mm. The only species of the genus within Europe. Typical by the characteristics of the genus, similar to species of the genus *Dioxys*. It is uniform in appearance, females black with first four metasomal terga entirely reddish and males' whole metasoma reddish. Legs are also reddish (Fig. 19A, B). Metasoma of females have narrow apical bands of whitish short appressed hair; similar hairs are also distributed on the first metasomal terga laterally. The metasoma of males have bands of whitish short appressed hair that are sparse and barely visible. The male body has a tomentum-like light brown or yellowish hair. Females have a narrowed T6 and a very long and sharp S6, projecting behind the T6 (Fig. 19C). In males, the end of the metasoma is straight, not curved (Fig. 19F), and the apex of S4 has two prominent toothlike projections, which are larger than in males of *Dioxys* (Fig. 19D, E).

Distribution. This species was described from Hungary and is a Euro-Asiatic species that occurs from central Europe to the north-eastern Mediterranean (Fig. 20) and outside of Europe towards the Middle East and Iran (Popov 1936; Warncke 1977; Bogusch et al. 2007; Gusenleitner et al. 2012; Ascher and Pickering 2023).

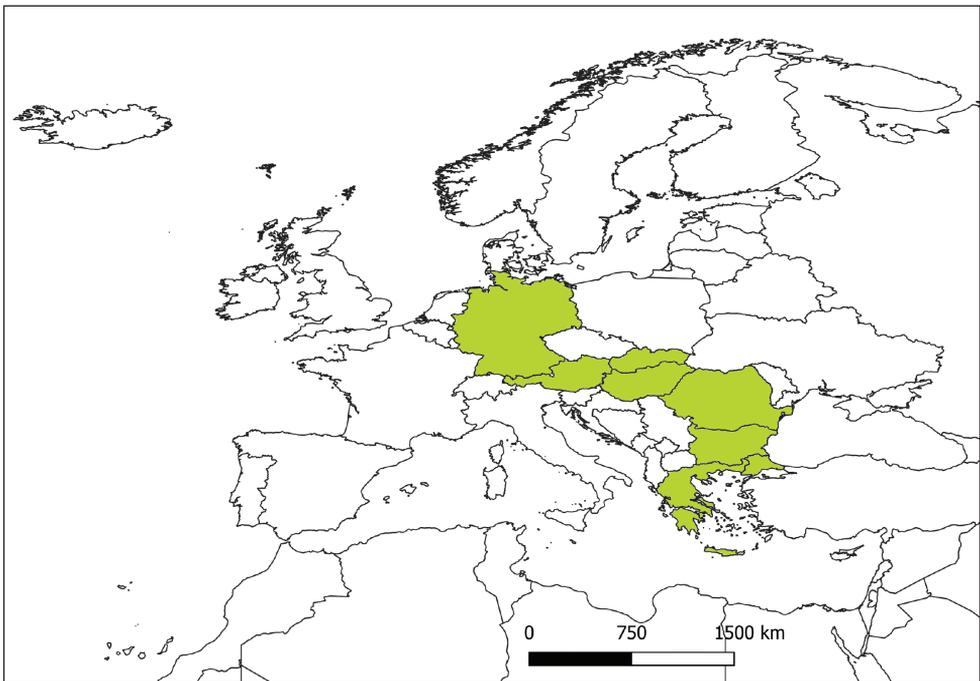


Figure 20. *Paradioxys pannonicus*, distribution in Europe.

Biology and hosts. This species attacks nests of species of the family Megachilidae. Scheuchl and Willner (2016) reported *Chalicodoma hungarica* (Mocsáry) as its main host, and Gusenleitner et al. (2012) included *C. parietina* as its host.

Conservation status. Nieto et al. (2014) classified this species as DD – data deficient. This is a typical Pannonian species occurring in the Pannonian basin. However, there is a lack of records from recent years, and the most recent finds are from the 1970s and 1980s. We suppose this species is CR – critically endangered in Europe.

Discussion

Cuckoo bees of the tribe Dioxyini are represented by ten species in Europe. These cuckoo bees are usually rare, and sightings are not common. Only two species occur in a large part of the continent. *Aglaopis tridentata* is a relatively rare species of steppic habitats whose distribution covers large parts of Europe, including Scandinavia (Sweden and Finland) and Russia. *Dioxys cinctus* occurs in most of southern and central Europe, where it spreads towards the north – the first record from the northwestern part of the Czech Republic (Bohemia) comes from 2012 (Straka et al. 2015) and from Germany from 2019 (Saure and Petrischak 2020). Other species occur only in southern Europe, while two of them were recorded from a larger part of this region. *Dioxys moestus* has a larger distribution but is usually recorded in small numbers of individuals, in contrast to *D. pumilus*, which has a smaller distribution but numerous series of individuals from multiple localities. *Paradioxys pannonicus* is known from central and southeastern Europe historically but there are no recent records on the occurrence of this species in Europe (the latest record I have revised is from Bulgaria from 1983). Two species occur in North Africa and reach their distribution area to Spain and Portugal. *Ensliniana bidentata* was recorded and observed several times after 2000 (Baldock et al. 2018), but for *Dioxys ardens* the latest record from Spain dates back to 1976. A similar case is seen in *Metadioxys graeca*, which occurs in the Middle East and in Greece in Europe, where it was recently recorded only in Crete. *Dioxys atlanticus* and *D. lanzarotensis* were thought to be endemic to the Canary Islands. *Dioxys lanzarotensis* is known only from a single male from Lanzarote, in contrast, *D. atlanticus* was collected on Lanzarote, Gran Canaria and Tenerife, while several specimens were collected on Gran Canaria around the year 2020 (P. Bogusch, own observations). But *D. atlanticus* was also recorded from Egypt (Warncke 1977) and recently from Sardinia.

Several other species were recorded in North Africa or the Middle East. All these species are rare, and their occurrence in Europe is unlikely. The record of *Dioxys chalicoda* from Gibraltar belongs to *D. ardens* (P. Bogusch revised). Thus, in future, studies on the distribution of *D. atlanticus* in southern Europe (if the species will be discovered elsewhere than in Sardinia and Egypt) and attempts to find specimens or populations of *P. pannonica* would be interesting. Although this species has not recorded for a long time, it is likely to occur in Slovakia, Hungary, Bulgaria, Greece or Romania.

Dioxyini are cuckoo bees. This means that discovering these bees is more complicated than discovering nesting bee species. Their hosts are bees of the family Megachilidae, which usually do not nest in aggregations, and thus their nests are harder to find. However, several species have quite visible nests made of mud (genus *Chalicodoma*) or can be recorded in bee hotels (hosts of *D. cinctus* as well as this cuckoo bee species). Furthermore, nests of *Hoplitis fertoni* parasitised by *D. moestus* were reported from empty snail shells in Spain (Bogusch et al. 2020b).

To preserve the fauna of this tribe of cuckoo bees, it is necessary to take care of their habitats. Most species were recorded mainly in open habitats of steppic or semi-desert characteristic. Conservation of these habitats across Europe can go hand in hand with the conservation of the hosts and be helpful for these rare, beautiful and interesting cuckoo bees.

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