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Taxonomic revision of European Rophitinae (Halictidae)

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L’auteur, RIGAUT BLANDINE, atteste avoir respecté les règles éthiques en vigueur, y compris la charte de l’Université relative à l’utilisation de l’Intelligence Artificielle

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P.S.: Yes, Fred, the Rophitinae do exist.

Résumé

Les Rophitinae (Hymenoptera: Halictidae) constituent une sous-famille d'abeilles sauvages qui reste peu étudiée, tant d'un point de vue taxonomique qu'écologique. En Europe, leur faune est relativement bien connue par rapport à d'autres régions où elles sont présentes. Cependant, des confusions taxonomiques persistent et certaines espèces ont encore un des deux sexes à décrire. Hormis les clés d'identification régionales ou basées sur un seul genre, il n'existe actuellement aucune synthèse récente consacrée aux Rophitinae européennes. Ce mémoire vise à actualiser et regrouper les connaissances sur les Rophitinae européennes d'un point de vue taxonomique, écologique et biogéographique. Il vise notamment à clarifier certains problèmes d'identification, synthétiser l'écologie et mettre à jour les cartes de distribution.

D'un point de vue taxonomique, une clé illustrée des 33 espèces européennes de Rophitinae est établie pour la première fois à l'échelle strictement européenne. La femelle de *Rophites thracius* est également décrite dans ce travail. L'inclusion de la femelle de *Rophites thracius* et de *Systropha grandimargo* dans les clés constitue une première, car ces deux espèces n'ont été décrites ou élevées au rang d'espèce que récemment. Certaines espèces, telles que *Dufourea minuta* et *Dufourea halictula*, ont longtemps été confondues; ici, peuvent être clairement distinguées.

D'un point de vue ecologique, ce mémoire clarifie et confirme également les préférences florales de plusieurs espèces, notamment *Dufourea minuta, Dufourea alpina, Dufourea trautmanni* ou encore *Rophites algirus*. La plupart des espèces de *Dufourea* ont été caractérisées comme oligolectiques sur les Campanulaceae, tandis que *Dufourea minuta* est spécialisée sur les Asteraceae. *Rophites algirus* présente un régime différent entre le mâle et la femelle, pouvant s'expliquer notamment par une phénologie légèrement différente ou encore un besoin plus faible de collecter le pollen chez les mâles.

D'un point de vue biogéographique, la distribution des espèces de Rophitinae varie fortement en Europe, avec une diversité plus élevée dans les régions méditerranéennes mais avec des lacunes importantes d'échantillonnage dans les Balkans et l'Europe de l'Est. Le manque de données d'abondance et de connaissances écologiques limite également l'évaluation de leur rareté et de leur vulnérabilité. Cela est accentué par la fragmentation des habitats et leur forte spécialisation alimentaire.

En conclusion, ce travail fournit ainsi une base solide pour la planification future de la conservation à l'échelle européenne.

Summary

Rophitinae (Hymenoptera: Halictidae) constitute a subfamily of wild bees that remains poorly studied, both taxonomically and ecologically. In Europe, their fauna is relatively well known compared to other regions where they are found. However, taxonomic confusion persists, and for some species, one of the two sexes has yet to be described. Excluding regional identification keys or those based on a single genus, there is currently no recent synthesis dedicated to European Rophitinae. This master's thesis offers an update on the taxonomic and ecological knowledge of Rophitinae in Europe. In particular, it aims to clarify certain identification issues, summarize the ecology and update the distribution maps.

From a taxonomic perspective, an illustrated key to the 33 European species of Rophitinae is established for the first time on a strictly European scale. The female of *Rophites thracius* is also described in this work. The inclusion of the female of *Rophites thracius* and *Systropha grandimargo* in the keys is a first, as these two species have only recently been described or classified as a species. Certain species, such as *Dufourea minuta* and *Dufourea halictula*, have long been confused; here, they can be clearly distinguished.

From an ecological perspective, this study also clarifies and confirms the floral preferences of several species, including *Dufourea minuta*, *Dufourea alpina*, *Dufourea trautmanni*, and *Rophites algirus.* Most *Dufourea* species have been characterized as oligolectic on Campanulaceae, while *Dufourea minuta* is specialized on Asteraceae. *Rophites algirus* exhibits a different diet between males and females, which can be explained in particular by slightly different phenology or a lower need for pollen collection in males.

From a biogeography perspective, the distribution of species of Rophitinae varies greatly across Europe, with higher sampling in Mediterranean regions but significant sampling gaps in the Balkans and Eastern Europe. The lack of abundance data and ecological knowledge also limits the assessment of their rarity and vulnerability. This issue is exacerbated by habitat fragmentation and their high food specialization.

In conclusion, this work provides thereby a solid foundation for future conservation planning at the European level.

Abbreviations

FAGX: Collection Gembloux Agro-Bio Tech, Unité d'Entomologie fonctionnelle et évolutive, Université de Liège, Gembloux, Belgium

MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain

MNHN: Muséum National d'Histoire Naturelle, Paris, France

MSDB: Museo di Storia Naturale "Don Bosco", Torino, Italy

MZH: Finnish Museum of Natural History, Helsinki, Finland

NHMUK: Natural History Museum, London, United Kingdom

NHRS: Naturhistoriska riksmuseet, Stockholm, Sweden

NMW: Naturhistorisches Museum, Vienna, Austria

OÖLM: Oberosterreiches Landesmuseum, Linz, Austria

RMNH: Naturalis Biodiversity Center, Leiden, Netherlands

SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main, Germany

UMons: Laboratory of Zoology, University of Mons, Belgium

ZGLC: Natural History Museum, Limassol, Cyprus

ZIN: Russian Academy of Sciences, Zoological Institute, St. Petersburg, Russia

ZMHB: Museum für Naturkunde, Berlin, Germany

1. Introduction

1.1 Biodiversity decline and knowledge gaps

Biodiversity was defined by the United Nations in 1992 as the "variability among living organisms from all sources, including, inter alia, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems". Biodiversity thus comprises genetic diversity, population diversity and ecosystem diversity (Gaggiotti *et al.*, 2018; Pereira *et al.*, 2013; Redford & Richter, 1999; Schmeller *et al.*, 2017). Each of these components can be analyzed along three axes: structural, referring to the physical organization and spatial arrangement of elements within a landscape; compositional, referring to the variety of elements such as different species; and functional, referring to the ecological and evolutionary process of elements such as predation or nutrient cycling (Noss, 1990). These axes provide a framework for assessing pressures such as human impacts on the different dimensions of biodiversity (Redford & Richter, 1999).

A long-term decline in biodiversity has been occurring for approximately 40,000 years, described by some as the sixth mass extinction, even though it is difficult to determine the exact beginning of this phase (Cowie *et al.*, 2022; Dirzo & Raven, 2003; Pievani, 2014). Overhunting is considered the principal driver of the early phase of this decline (Dirzo & Raven, 2003). Over the past 500 years however, the rate of decline has accelerated, largely due to deforestation (Donadio Linares, 2022). Species extinction has been recorded since 1500, with an estimation of 150,000 to 260,000 extinct species, whereas the IUCN has formally documented 935 extinctions (Cowie *et al.*, 2022; IUCN, 2025). However, biodiversity decline does not only include species loss but also reductions of species abundance in geographic distribution (Pereira *et al.*, 2010). Declines in abundance are particularly concerning because they directly affect ecosystem services, such as food provision, climate regulation, and detoxification processes (Daily, 1997). Species loss is irreversible, and especially critical when undescribed species disappear. Centinelan extinction, term for the extinction of undescribed species, is estimated at more than 20% of the total of actual known species (Tedesco *et al.*, 2014; White *et al.*, 2024; Wilson, 1999). In 2025, the Catalog of Life reported 2,068,366 living species including 2,026,405 eukaryotes (Bánki *et al.*, 2025). The estimated total number of species is approximately 8.74 million eukaryotes (Mora *et al.*, 2011), while previous estimations ranged from 5 to 15 million eukaryotes (Stork, 1993). Although the number of described species has doubled in less than 20 years (Bánki *et al.*, 2025; Bisby *et al.*, 2007), knowledge gaps remain.

Insects represent the biggest group within the kingdom Animalia with more than 1 million of described species (Bánki *et al.*, 2025). This class is highly diverse in their ecological habitat and physiological systems including diversity in reproduction systems, degree of sociality or difference of morphology (Gullan & Cranston, 2014; Speight *et al.*, 1999). However, major knowledge gaps persist in this group. The estimated total number of insect species is approximately 5.5 million, suggesting that insect diversity would be 5 times higher than currently described (Stork, 2018). The gap is principally due to undersampling of certain regions, such as tropical regions, making it more difficult to determine and describe species (Gaston & Gauld, 1993; Stork, 2018). Cryptic species further complicate diversity assessments, as they are morphologically indistinguishable and can require genetic methods for ensuring the identification (Stork, 2018).

Knowledge gaps regarding biodiversity, also called "shortfalls", encompass seven different types. A main shortfall is the Linnean shortfall, referring to the gap between currently described species and the true extent of existing biodiversity. Other shortfalls concern insufficient knowledge in distribution (Wallacean shortfall), population dynamics (Prestonian shortfall), species traits (Raunkiaeran shortfall), ecological interactions (Eltonian shortfall), species evolution (Darwinian shortfall), abiotic conditions tolerance (Hutchinsonian shortfall), and high-quality pictures with species characteristic (Keartonian shortfall) (Hortal *et al.*, 2015; Marshall *et al.*, 2024). Shortfalls affect all insect groups, including all pollinator orders such as Hymenoptera, Lepidoptera, Diptera and Coleoptera. Shortfalls are present worldwide but less pronounced in North America and Europe, where sampling biases are lower (Baini & De Biase, 2024; Carvalheiro *et al.*, 2025; Millard *et al.*, 2020; Skaldina & Blande, 2025). The Wallacean shortfall is particularly pronounced where many studies are not in English, limiting accessibility to knowledge (Millard *et al.*, 2020). The Linnean shortfall remains while some domesticated species such as the Western honeybee *Apis mellifera* and the bumblebee *Bombus terrestris* are well studied. Others such as wild bees, many Diptera, Coleoptera and even vertebrate pollinators remain comparatively understudied (Millard *et al.*, 2020; Skaldina & Blande, 2025). The Darwinian shortfall is relevant for pollinators as DNA resources are insufficient to build their phylogenetic histories. For example, Baini & De Biase (2024) mentioned that, in Italy, Lepidoptera are well barcoded but wild bees and forest insects such as Coleoptera are less barcoded; only 41% of bee species from the Italian red list are barcoded. The Prestonian shortfall is also present in Europe, particularly in southern regions, even Linnaean shortfalls are low in these zones (Marshall *et al.*, 2024).

1.2 Bees: decline and conservation

Bees are highly efficient pollinators, permitting highly effective pollination in crops (Klein *et al.*, 2006). Pollination, with other wild pollinators, has a value of hundreds of billions of dollars for worldwide food production (Khalifa *et al.*, 2021; Porto *et al.*, 2020). Beyond pollination, bees provide other ecosystemic services including honey production, medical products derived from hives, food conservation and cultural benefits (Klein *et al.*, 2018; Matias *et al.*, 2017). Some species of bees were domesticated around the world for agriculture such as honeybee while the majority remain wild (Matias *et al.*, 2017). For certain crops and cultures, honeybees are not sufficient to pollinate crops or are just unable to pollinate some of them (Cooley & Vallejo-Marín, 2021; Diller *et al.*, 2022; Page *et al.*, 2021; Vaissière & Vinson, 1994).

Bees have experienced decline for decades due to many pressures (Zattara & Aizen, 2021). The main pressure is the loss of habitat and associated reductions of floral resources impacting not only bees but also all pollinators (Brunet & Fragoso, 2024; LeBuhn & Vargas Luna, 2021; Potts *et al.*, 2010; Winfree *et al.*, 2009). Intensive agriculture and urbanization destroy nesting sites and reduce floral diversity, reducing survival of both adults and larvae (Gekière *et al.*, 2025). Habitat fragmentation further decreases population connectivity (Brunet & Fragoso, 2024; LeBuhn & Vargas Luna, 2021; Winfree *et al.*, 2009). Monocultures can also lead to an underfeeding of bees when they have no access to their typical floral resources (Goulson *et al.*, 2015). Pesticides are another leading pressure on bees (Brunet & Fragoso, 2024; Gekière *et al.*, 2025; Goulson *et al.*, 2015; LeBuhn & Vargas Luna, 2021). Bees are exposed to pesticides during foraging on flowers, either by oral absorption or by direct contact on the flower (Krupke *et al.*, 2012; Main *et al.*, 2020). Pesticides can induce both lethal and sublethal effects, including physiological effects, effects on memory, effects on gene transcription, among other issues (Gekière *et al.*, 2025; Goulson *et al.*, 2015; Raine & Rundlöf, 2024; Tosi *et al.*, 2022). A last important pressure on wild bee populations is domesticated bees such as *Apis mellifera*, *Bombus terrestris* or *Megachile rotundata* (Russo, 2016). Managed bees induce competition with native wild bees for foraging resources, generally being wide generalists (Brunet & Fragoso, 2024; Hudewenz & Klein, 2013; Mallinger *et al.*, 2017). Additionally, pathogen transmission represents a critical risk. Many viruses and parasites infect domesticated species. When they meet wild bees, managed bees may transmit their infections to wild bees, causing several declines in wild bee populations (Goulson *et al.*, 2015; Mallinger *et al.*, 2017; Russo, 2016; Tehel *et al.*, 2016).

Conservation plans aim to protect species, but their effectiveness depends on accurate species identification. While some species are easily identifiable, others require taxonomic expertise to ensure reliable identification (Morrison *et al.*, 2009). Collaboration between taxonomist and ecologist or conservation plan manager is, therefore, essential to build projects such as Red lists (i.e. Michez, Boustani *et al.*, 2026). However, some clades are less studied due to their minor ecological importance or their visual attractivity. That can cause problem in their identification and thus also in their assessment for conservation plans (Hochkirch *et al.*, 2022).

IUCN Red List is the most widely used tool to assess species according to their vulnerability. Five main criteria are used: population reduction, geographic range, small population size and decline, very small populations, and quantitative extinction risk analyses (International Union for Conservation of Nature and Natural Resources, 2001). For now, 48,646 species are threatened, including 2,680 species of Insecta, out of 172,620 species assessed overall, with 13,696 assessed species of Insecta (IUCN, 2025). The Red List functions both as a conservation planning tool and as an instrument for raising public and political awareness (Betts *et al.*, 2020). The Red List is also used to plan concrete action such as the protection of habitats (Bland *et al.*, 2019; Hayward, 2011; Hoffmann *et al.*, 2008). It can be developed at a world range (i.e. Botanic Gardens Conservation International, 2021; Braulik *et al.*, 2023; Pollom *et al.*, 2021), regional range (i.e. Bento Elias *et al.*, 2017; Daniel *et al.*, 2011; Mallon *et al.*, 2023) or national range (i.e. Drossart *et al.*, 2019; Foord *et al.*, 2020; Sotiaux *et al.*, 2007). For example, the European red list of bees assessed 1,928 species of wild bees of which 10 % have an extinction risk (Michez, Boustani *et al.*, 2026).

1.3 Taxonomy of bees

Bees belong to the order of Hymenoptera and to the Aculeata clade with wasps. Bees are distinguished morphologically from wasps by the presence of dense hairs, except for some genera, i.e. *Hylaeus* and *Nomada*. One of the main differences between wasps and bees is the larvae diet: most bees feed their larvae with pollen and nectar while wasps feed their larvae with prey. Bees, also called Apiformes, constitute with Spheciformes the clade Apoidea. Apiformes, also called Anthophila, are differentiated by the presence of plumose and branched hairs in comparison to simple hairs for Spheciformes. Bees comprise seven families: Stenotritidae, Colletidae, Megachilidae, Andrenidae, Mellitidae, Halictidae and Apidae (Michener, 2007). Halictidae is the second largest family of bees after Apidae, comprising currently more than 4,500 species worldwide (Bánki *et al.*, 2025; Michener, 2007). The family of Halictidae is divided into four subfamilies: Halictinae, Nomiinae, Nomioidinae, and Rophitinae. Within Halictidae, only one subfamily has

developed sociality: the Halictinae. Other subfamilies are solitary or build communal nests (Gibbs *et al.*, 2012). Some genera of Halictinae are parasitic, such as *Sphecodes* (Michener, 1978). Diversity is also present in diet within Halictidae. While many bees are polylectic, foraging on a broad range of host plants, others are oligolectic or monolectic, foraging on only one family or one species of plant. Oligolecty is present in the family of Halictidae but mainly in the subfamily of Rophitinae (Astafurova & Pesenko, 2006; Michener, 2007).

1.4 Rophitinae

Rophitinae are solitary bees from the family of Halictidae. They occur in the entire Holarctic region, in the Neotropics and in the south of Africa (Astafurova & Pesenko, 2006; Michener, 2007). Phylogenetic evidence suggests that Rophitinae originated approximately 120 million years ago during the Late Cretaceous (Danforth *et al.*, 2008). Rophitinae was previously called Dufoureinae, comprising all European genera of Rophitinae, and sometimes confused with other Halictidae (Michener, 1944, 2007) or even with Panurginae (Friese, 1923). Robertson (1904) created a new family called Dufoureidae comprising a part of the actual Rophitinae but later this family was grouped with Halictidae (Michener, 1944). 262 species of Rophitinae and 13 genera are currently recognized by Integrated Taxonomic Information System (Integrated Taxonomic Information System (ITIS), 2026). Rophitinae is divided into two recognized tribes: Rophitini and Penipini (Integrated Taxonomic Information System (ITIS), 2026) and two others not recognized by Integrated Taxonomic Information System: Xeralictini and Conanthalictini (Patiny *et al.*, 2008). The 13 genera are *Systropha* Illiger, 1806; *Rophites* Spinola, 1808; *Dufourea* Lepeletier, 1841; *Morawitzia* Friese, 1902; *Conanthalictus* Cockerell, 1901; *Sphecodosoma* Crawford, 1907; *Xeralictus* Cockerell, 1927; *Micralictoides* Timberlake, 1939; *Protodufourea* Timberlake, 1955; *Morawitzella* Popov, 1957; *Penapis* Michener, 1965; *Ceblurgus* Urban & Moure, 1993; *Goeletapis* Rozen, 1997. The genus *Rhophitoides* is not recognized as an official genus by the Integrated Taxonomic Information System (Integrated Taxonomic Information System (ITIS), 2026) even if in recent papers, *Rhophitoides* is considered as a genus (Astafurova & Pesenko, 2006; Ghisbain, Rosa *et al.*, 2025). Phylogenetically, Rophitinae is the most basal subfamily in the family of Halictidae (Danforth *et al.*, 2004, 2008; Patiny *et al.*, 2008; Pesenko, 1999). Rophitinae are morphologically distinct from the other Halictidae by the position of the antennae, which are inserted low on the face below the midline of the eyes and by a short clypeus (Danforth *et al.*, 2008; Michener, 2007; Pesenko, 1999). Rophitinae are all oligolectic and even monolectic for some species. Diet specialization varies between all of the genera and even

within genera (Astafurova & Pesenko, 2006). In Europe, four genera of Rophitinae are present: *Dufourea*, *Rophites*, *Rhophitoides*, and *Systropha*, comprising a total of 33 species (Ghisbain, Rosa *et al.*, 2025).

The Rophitinae remain a relatively understudied group in Europe, with a limited number of specialists. Within the genus *Dufourea*, extensive taxonomic work was conducted by Ebmer across the Western Palaearctic region, encompassing North Africa, Russia and Western Asia. His identification key, originally published in 1984, underwent several revisions, the most recent of which appeared in 2015 (Ebmer 1984, 1987, 1989, 1993, 1999, 2008, 2015). Additional studies focusing on the ecology of *Dufourea* were carried out by van der Meer (2012) for the Netherlands and by Astafurova (2014) in Russia. For the genera *Rophites* and *Rhophitoides*, identification keys for the Western Palaearctic were provided by Ebmer and Schwammberger (1986) and later updated by Ebmer (1993), while Astafurova (2011) produced a key covering the Russian fauna. Ecological studies on these genera were conducted by Astafurova (2014), with a particular focus on Russian species, whereas Radchenko (2015) examined the ecology of *Rhophitoides*. Regarding the genus *Systropha*, important contributions to its taxonomy and biology in Europe were made by Warncke (1979) and Baker (1996).

1.4.1 *Dufourea*

Dufourea Lepeletier, 1841, commonly referred to short-faced bees, comprises 170 described species currently, including 20 European species (Ghisbain, Rosa *et al.*, 2025; Integrated Taxonomic Information System (ITIS), 2026). Some taxonomic problems occurred with *Dufourea*. *Halictoides* was for a long time considered as a genus, now considered as a subgenus of *Dufourea* (Ebmer, 1984). The genus *Dufourea* differ from other European Rophitinae by the absence or sparse hairs on the metasoma, only two submarginal cells and segments of the labial palps that have all the same length. Males do not have a pygidial plate instead of other Rophitinae (Michener, 2007). *Dufourea* occurs in all of the Holarctic region from the Canary Islands to Japan and in North Africa but also in the Nearctic region from Canada to New Mexico. *Dufourea* is the only genus of Rophitinae occurring both in the Holarctic and Nearctic regions (Gibbs *et al.*, 2014; Michener, 2007).

Dufourea are solitary bees although nests may be aggregated in a small area, long of 15 to 20 m. They typically dig in sandy soils, often near forests and frequently in mountainous habitats (Eickwort *et al.*, 1986; Torchio *et al.*, 1967). Excavated soil forms a dome on one side of the nest entrance (Eickwort *et al.*, 1986). The nest consists of a main tunnel with lateral

galleries, each ending in a single brood cell provisioned with pollen and sealed with soil (Eickwort *et al.*, 1986; Torchio *et al.*, 1967). Cells are covered by secretion from the Dufour gland. The end of the nest serves as a reserve of food (Torchio *et al.*, 1967). Larvae are highly mobile due to dorsal tubercles that facilitate movement within the cell. Most species construct a two-layered cocoon, except *D. minuta*, which produces a single layer. Pupae overwinter in the cell until early summer (Eickwort *et al.*, 1986).

Dufourea have brood parasites. In the Nearctic, the brood parasites are *Neopasites* and *Biastes* (Rozen, 1993; Torchio *et al.*, 1967). In Europe, *Biastes truncatus* is the most current brood parasite but for some species such as *Dufourea halictula* and *Dufourea minuta*, species of *Sphecodes* may parasitize nests (Pesenko *et al.*, 2000; van der Meer, 2012).

Dufourea are oligolectic, primarily on Campanulaceae in Europe, except for *D. minuta* foraging on *Hieracium* and *Leontodon*. Some *Dufourea* such as *D. halictula* are monolectic on *Jasionia montana*, while others, such as *D. paradoxa* tend to be more polylectic (Müller, 2018).

1.4.2 *Rophites*

Rophites Spinola, 1808, known as the bristle-headed bee, has 16 species described currently comprising 7 species in Europe (Ghisbain, Rosa *et al.*, 2025; Integrated Taxonomic Information System (ITIS), 2026). Confusion remains between *Rophites* and *Rhophitoides*. *Rhophitoides* is sometimes classified as a subgenus (Michener, 2007) and sometimes as a genus (Astafurova & Pesenko, 2006). Here, we consider it as a genus as it figured in the new annotated checklist of European bees (Ghisbain, Rosa *et al.*, 2025). The genus *Rophites* differ from other Rophitinae by the presence of two submarginal cells, hair bands on terga well-developed, and first and second labial palp at least five times bigger than the fourth. Females have spines on their foreheads while other Rophitinae do not have spines on their forehead (Astafurova & Pesenko, 2006; Michener, 2007). *Rophites* occur in all of the Holarctic region from Spain to Mongolia and also in North Africa (Michener, 2007).

Rophites species are solitary ground nesters, often forming nest aggregations. They nest in dry meadows, xerothermic grasslands, forest edges, and steppe environments. Females dig nests forming a small cone at the entrance. The main tunnel, approximately 20 cm long, forms an inverted L shape. Lateral galleries of approximately 1 cm long each ending in a single brood cell, except in *Rophites quinquespinosus*, where two cells may occur per gallery. Cells are sealed with soil caps and, unlike *Dufourea*, are not covered with secretions but only smoothed. (Pesenko *et al.*, 2000). The larvae develop during 3 weeks and are strongly attached to the pollen ball.

Larvae develop then a cocoon with 2 layers. Pupae overwinter until early summer (Pesenko *et al.*, 2000; Rozen & Özbek, 2008). *Rophites* also have a brood parasite in Europe: *Biastes emarginatus* (Rozen, 1993; Torchio *et al.*, 1967). *Rophites* are oligolectic on Lamiaceae (Müller, 1996).

1.4.3 *Rhophitoides*

Rhophitoides Schenck, 1861, also called gray bee, has 5 species comprising 2 in Europe although the genus is not recognized as an official genus by ITIS (Ghisbain, Rosa *et al.*, 2025; Integrated Taxonomic Information System (ITIS), 2026). The genus *Rhophitoides* differ from other Rophitinae by the presence of two submarginal cells, hair bands on terga well developed and first and second labial palp maximum two times bigger than the fourth. Females do not have the spines like females of *Rophites* on the forehead (Astafurova & Pesenko, 2006; Michener, 2007). *Rhophitoides* occur from France to Türkiye, in the Caucasus and also Morocco (Michener, 2007; Schwammberger, 1975).

Rhophitoides species are solitary ground nesters, usually forming aggregations in dry, open habitats such as steppes. *Rhophitoides canus* is known to nest in Medicago sativa fields (Ptácek & Rotrekl, 2000; Radchenko, 2015). Nest entrances have a 5–8 mm cone with cemented walls, distinguishing them from other Rophitinae (Pesenko *et al.*, 2000; Radchenko, 2015). The main tunnel is nearly vertical and approximately 25 cm in length, unlike the L-shaped nest of *Rophites*. Lateral galleries, approximately 3 cm long, end with two or three brood cells sealed with soil walls. As in *Rophites*, cells are smoothened but not covered with secretions (Malyshev, 1925; Pesenko *et al.*, 2000; Radchenko, 2015; Rozen & Özbek, 2008). Larvae and pupae have the same development as *Rophites*, being attached to pollen ball and making two layer cocoon. The pupae overwinter from the autumn to the early summer in the cell (Malyshev, 1925; Rozen & Özbek, 2008).

Rhophitoides have a brood parasite in Europe: *Biastes emarginatus* (Rozen, 1993; Torchio *et al.*, 1967).

Rhophitoides canus is oligolectic on *Medicago sativa*, permitting pollination of fields. *Rh. canus* opens the flower permitting efficient pollination. For better efficiency, farmers create nesting bands along the field without watering in this zone (Pesenko *et al.*, 2000; Ptácek & Rotrekl, 2000; Radchenko, 2015).

1.4.4 *Systropha*

Systropha Illiger, 1806, commonly called spiral-horned bee, has 30 recognized species in the world comprising 4 species in Europe (Ghisbain, Rosa *et al.*, 2025; Integrated Taxonomic Information System (ITIS), 2026). Among European *Systropha*, phylogenetic analyses indicate a close relationship between *S. planidens* and *S. curvicornis* (Patiny & Michez, 2006). The genus *Systropha* differs from other European Rophitinae by the presence of 3 submarginal cells and long hairs on metasoma. Males are characterized by a curved flagellum at the end of the antenna, not present for other Rophitinae (Michener, 2007). They occur from Spain to Tajikistan and to the south of Germany. The genus also occurs in the north and in the south of Africa and also in Thailand, Sri Lanka, and China (Michener, 2007; Niu *et al.*, 2005).

Systropha are solitary ground-nesters, although nests frequently occur in aggregations. Habitat preferences vary among species: *Systropha curvicornis* occupies sandy soils, whereas *Systropha planidens* prefers clayey substrates. Females dig nests in the soil, forming a small cone at the entrance. The nest is approximately 25 cm long and generally forms an inverted L shape. Lateral galleries, approximately 1.5 cm in length, branch from the main tunnel and each end with a single brood cell. Cells are sealed with a soil cap and, unlike in *Dufourea*, are not covered with secretions but only smoothed (Pesenko *et al.*, 2000; Rozen & Özbek, 2008). Each brood cell contains a pollen mass on which the larva develops. The larva remains firmly attached to the pollen provision and later spins a two-layered cocoon. Pupae overwinter in the cell from autumn until early summer (Rozen & Özbek, 2008). *Systropha* have a brood parasite: *Biastes* (Torchio *et al.*, 1967). *Systropha* are oligolectic on Convolvulaceae (Amiet *et al.*, 1999).

2. Objectives

The objectives are double and aim to address both taxonomic and ecological shortfalls affecting current knowledge of European Rophitinae.

2.1 Taxonomy

The goal of this work is to clarify and update the taxonomy of European Rophitinae. It will also provide a description of the female *Rophites thracius,* filling a partial Linnean shortfall for *Rophites* in Europe. An updated and illustrated key with all actual Rophitinae species from Europe and diagnoses for all of these species are provided. Given that Rophitinae species are generally rare and remain poorly studied, the development of robust identification tools represents a significant advance for both knowledge acquisition and conservation assessment.

2.2 Ecology

Another goal of this work is to contribute to overcoming the Wallacean shortfall, about distribution, and the Raunkiaeran shortfall, about ecological and functional traits of European Rophitinae. For all species, updated maps are provided. In addition, diet is also investigated for selected species to clarify host-plant associations.

3. Materials and Methods

3.1 Geographical framework

The study area is the same as the one considered for the checklist of European bees and the European Red List of bees (Fig. 1) (Ghisbain *et al.*, 2025; Michez, Boustani *et al.*, 2026). This includes Thrace, the European portion of Türkiye. The eastern boundary of Europe within Russia is delimited by the Ural Mountains and the beginning of the Caucasian region.

The European part of Russia considered in this study includes the following administrative divisions:

- North: Murmansk Province, Arkhangelsk Province, Republic of Karelia, Vologda Province, Republic of Komi;
- Northwest: Kaliningrad Province, Leningrad Province, Pskov Province, Novgorod Province;
- Center: Tver, Yaroslavl, Kostroma, Smolensk, Moscow, Vladimir, Ivanovo, Nizhny Novgorod, Kaluga, Tula, Ryazan Provinces, and the Republic of Mordovia;
- South: Bryansk, Orel, Lipetsk, Tambov, Penza, Kursk, Belgorod, and Voronezh Provinces;
- East: Kirov Province, Udmurt Republic, Mari El Republic;
- West/Central Volga: Chuvash Republic, Republic of Tatarstan, Ulyanovsk Province, Samara Province, Saratov Province;
- Southern Russia: Rostov Province, Volgograd Province, Republic of Kalmykia, and Astrakhan Province.

European island territories are included within the scope of the study, namely Great Britain, Ireland, Iceland, Corsica, Sardinia, Sicily, and Cyprus. In addition, Macaronesian archipelagos belonging to European countries (Azores, Madeira and the Canary Islands) are also considered.

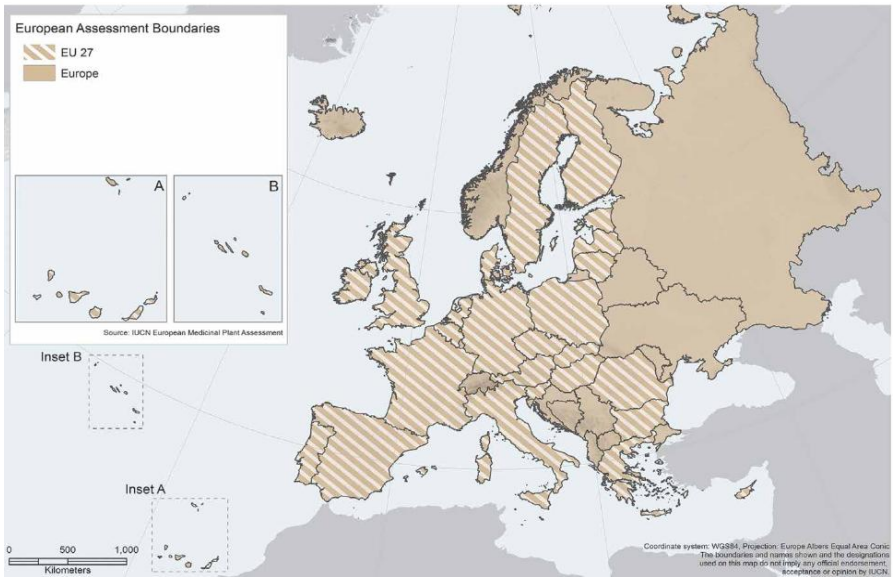

Figure 1: Map of Europe *sensu* IUCN, derived from Michez, Boustani *et al.* (2026).

3.2 Examined material

Examined specimens come from two different institutions: University of Mons, collection of the laboratory of Zoology (UMons) and Naturalis biodiversity center, Leiden (RMNH). All *Dufourea* specimens were redetermined using the key and their addings of Ebmer (1984, 1987, 1989, 1993, 1999, 2008, 2015), Amiet *et al.* (1999) and Astafurova (2014). All *Rophites* and *Rhophitoides* were reidentified using the key of Ebmer & Schwammberger (1986) and Astafurova (2011). All specimen of *Systropha* were reidentified using keys and diagnoses of Amiet *et al.* (1999) and Wood & Le Divelec (2022).

To facilitate the observation of diagnostic characters, specimens should be well prepared. The tongue should be fully extended, the metasoma directed downwards and the wings arranged so as not to cover the tergites. For males, at least one antenna and the sternites should remain visible. For females, an upward orientation of the head is recommended.

Specimens were examined under a stereomicroscope at magnifications ranging from 10x to 40x, depending on the size of the specimen and the analyzed structures. Morphological terminology follows Engel (2001) and Michener (2007). The following abbreviations are used in the species descriptions:

- S1–6(7): Metasomal sterna 1–6 (or 7 for males)
- T1–6(7): Metasomal terga 1–6 (or 7 for males)

- A1–13: Antennal segments
- MP1–6: Maxillary palp segments
- LP1–4: Labial palp segments

Specific terms are defined as follows:

- Rhinaria: The convex part of the antenna in ventral view, usually rugose or punctate.
- Coarse: Broad, impact-like perforation.
- Fine: Narrow, needle-like perforation.

The subgenus concepts applied to the genus *Dufourea* in this study follow the taxonomic frameworks proposed by Ebmer (1984, 1993). Despite the lack of molecular analysis, which prevents confirmation of subgeneric phylogeny, subgenera based on the morphology of the mouthparts are clearly distinct. In this study, we followed this framework for diagnostic purposes. Short diagnoses are provided with the identification key. Complete diagnoses have been included in the appendices due to page limitations (appendix 2).

3.3 Illustrations

Pictures were taken using two different cameras. Habitus were taken with an Olympus E-M1 Mark I with a 60 mm macro lens. Images were stacked using Helicon Focus B (HeliconSoft, Ukraine). Close-up pictures were taken with a Keyence VHX-970F digital microscope equipped with a VHX-7020 camera and a VH-Z20R/Z20T zoom lens, ensuring high-resolution stacking for detailed imaging. All images were post-processed using GIMP (version 2.10.38) to enhance visibility by adjusting minor imperfections such as brightness and contrast, ensuring that features such as punctation are clearly discernible. Pictures for the identification key were placed in the appendices due to page limitations (appendix 1).

3.4 Literature review

A compilation of the literature concerning European Rophitinae was conducted. Publications addressing Nearctic genera that also occur in the Palearctic were also consulted. Literature searches were performed using Google Scholar with the following keywords: “Rophitinae”, “*Dufourea*”, “*Rophites*”, “*Rhophitoides*”, and “*Systropha*”. Additional literature was searched on Zobodat site (Zobodat, n. d.). The literature search was complemented by relevant references suggested by laboratory colleagues.

3.5 Maps

Distribution maps were produced using the dataset of Sentil *et al.* (2026). Only data with "Rophitinae" entry on the subfamily column were used. Every map was done on QGIS version 3.34.12. Base map is derived from ESRI (2026). Due to page limitations, distribution maps for every species were placed in appendices (appendix 3).

3.6 IUCN status

All investigated species were linked to their conservation status according to the International Union for Conservation of Nature (IUCN). The most recent assessment considered in this study was completed in 2026 (Michez, Boustani *et al.*, 2026). For some species, status changed between 2014 (Nieto *et al.,* 2014) and 2026 (Michez, Boustani *et al.*, 2026). In these cases, the two status were mentioned. Status classified species following level of extinction risk which is determined by IUCN criteria. Categories are: EX (Extinct), EW (Extinct in the Wild), CR (Critically Endangered), EN (Endangered), VU (Vulnerable), NT (Near Threatened), LC (Least Concern), DD (Data Deficient), NE (Not Evaluated) and NA (Not Applicable).

3.7 Diet assessments

Pollen samples were collected from all available European Rophitinae specimens from the UMons collection. Pollen was collected on all of the body by touching the specimen with a fushin gel cube. The fuchsin cube was then melted and mounted on a slide (Dafni *et al.*, 2005; Sawyer, 1981; Tourbez *et al.*, 2024). Pollen was identified using a light microscope at magnification 100x to 400x. Identification relied on morphological comparison using reference materials and the online database (Pollen-Wiki, n. d.). The average of each pollen type were calculated and expressed with a percentage.

3.8 Nomenclature used

Species used in the determination key and in the diagnose are the species from Ghisbain, Rosa *et al.* (2025):

- *Dufourea* (*Cephalictoides*) *paradoxa* (Morawitz, 1867)
- *Dufourea* (*Cyprirophites*) *coeruleocephala* Morawitz, 1872
- *Dufourea* (*Cyprirophites*) *cypria* Mavromoustakis, 1952
- *Dufourea* (*Cyprirophites*) *iris* Ebmer, 1987
- *Dufourea* (*Cyprirophites*) *styx* Ebmer, 1976
- *Dufourea* (*Dentirophites*) *gaullei* Vachal, 1897
- *Dufourea* (*Dentirophites*) *lusitanica* Ebmer, 1999
- *Dufourea* (*Dufourea*) *alpina* Morawitz, 1865
- *Dufourea* (*Dufourea*) *balearica* Ebmer, 2015
- *Dufourea* (*Dufourea*) *fortunata* Ebmer, 1993
- *Dufourea* (*Dufourea*) *halictula* (Nylander, 1852)
- *Dufourea* (*Dufourea*) *minuta* Lepeletier, 1841
- *Dufourea* (*Dufourea*) *similis* Friese, 1898
- *Dufourea* (*Dufourea*) *trautmanni* Dusmet, 1935
- *Dufourea* (*Dufourea*) *wolfi* Ebmer, 1989
- *Dufourea* (*Glossadufourea*) *longiglossa* Ebmer, 1993
- *Dufourea* (*Halictoides*) *dentiventris* (Nylander, 1848)
- *Dufourea* (*Halictoides*) *graeca* Ebmer, 1976
- *Dufourea* (*Halictoides*) *inermis* (Nylander, 1848)
- *Dufourea* (*Merrophites*) *merceti* Vachal, 1907
- *Rhophitoides canus* (Eversmann, 1852)
- *Rhophitoides epiroticus* Schwammberger, 1975
- *Rophites algirus* Pérez, 1895
- *Rophites clypealis* Schwammberger, 1976
- *Rophites hartmanni* Friese, 1902
- *Rophites hellenicus* Ebmer, 1984
- *Rophites leclercqi* Schwammberger, 1971
- *Rophites quinquespinosus* Spinola, 1808
- *Rophites thracius* Ebmer, 1993
- *Systropha anatolica* Warncke, 1977
- *Systropha curvicornis* (Scopoli, 1770)
- *Systropha grandimargo* Pérez, 1905
- *Systropha planidens* Giraud, 1861

4. Results

4.1 Literature, distribution, ecology and pollen analyses

4.1.1 *Dufourea* (*Cephalictoides*) *paradoxa* (Morawitz, 1867)

Original description: Morawitz, F. (1867). Ein Beitrag zur Hymenopterenfauna des Ober-Engadins. *Horae Societatis Entomologicae Rossicae,* 5, 39–71.
Available literature with key and/or diagnose for this species: Amiet *et al.* (1999), Astafurova (2014), Ebmer (1984, 1989, 1999), Pesenko *et al.* (2000), Pesenko & Astafurova (2006)
Specimens seen: RMNH, UMons
Holotype location: ZIN (male)
Synonyms: *Halictoides paradoxus* Morawitz, 1867 (synonymization article unknown or nonexistent), *Rhophites atrocoeruleus* Morawitz, 1876 (synonymized by Ebmer, 1984), *Rhophites pamirensis* Morawitz, 1893 (synonymized by Ebmer, 1984),
European IUCN status: LC (Michez, Boustani *et al.*, 2026; Nieto *et al.*, 2014)
Distribution in Europe: Alps (France, Switzerland, Italy, Germany, Austria, Lichtenstein), Pyrenees (France, Spain), south of Spain and around Aegean sea (Greece, Bulgaria) (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: end July- end August (Ebmer, 1984)
Pollen diet based on literature: *Euphrasia rostkoviana, Silene rupestris, Veronica spicata, Thymus serpyllum, Phyteuma scheuchzeri, Hieracium* sp. (Ebmer, 1984), Crassulariaceae, Lamiaceae, Asteraceae (Müller, 2018)
Pollen diet (original data): specimens not available

4.1.2 *Dufourea* (*Cyprirophites*) *coeruleocephala* Morawitz, 1872

Original description: Morawitz, F. (1872). Neue südrussische Bienen. *Horae Societatis Entomologicae Rossicae*, 9, 45–62.
Available literature with key and/or diagnose for this species: Astafurova (2014), Ebmer (1984)
Specimens seen: only seen in pictures (female determined by Friese, 1900 and male determined by Morawitz, ZIN)
Holotype location: ZIN (male)
Synonyms: no synonym
European IUCN status: DD (Michez, Boustani *et al.*, 2026; Nieto *et al.*, 2014)

Distribution in Europe: Russia (Caspian region) (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: found in steppe (Astafurova, 2014)
Phenology: June-end July (Ebmer, 1984; Astafurova, 2014)
Pollen diet based on literature: *Salvia tesquicola* (Astafurova, 2014)
Pollen diet (original data): specimens not available

4.1.3 *Dufourea* (*Cyprirophites*) *cypria* Mavromoustakis, 1952

Original description: Mavromoustakis, G. A. (1952). On the bees (Hymenoptera, Apoidea) of Cyprus—Part III. *Annals and Magazine of Natural History*, Series 12, 5(57), 814–843.
Available literature with key and/or diagnose for this species: Ebmer (1984, 1999)
Specimens seen: UMons, pictures of holotype
Holotype location: ZGLC
Synonyms: *Dufourea caeruleocephala cypria* Mavromoustakis, 1952 (synonymization article unknown or nonexistent)
European IUCN status: DD (Michez, Boustani *et al.*, 2026; Nieto *et al.*, 2014)
Distribution in Europe: Cyprus (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: end April (Ebmer, 1984)
Pollen diet based on literature: *Salvia* sp.(Ebmer, 1984)
Pollen diet (original data): specimens not available

4.1.4 *Dufourea* (*Cyprirophites*) *iris* Ebmer, 1987

Original description: Ebmer, A. W. (1987). Die Westpaläarktischen Arten der Gattung *Dufourea* Lepeletier 1841 mit illustrierten Bestimmungstabellen (Insecta: Hymenoptera: Apoidea: Halictidae: Dufoureinae): Nachtrag. *Linzer biologische Beiträge*, 19(1), 43–56.
Available literature with key and/or diagnose for this species: Ebmer (1987, 1993)
Specimens seen: only seen in pictures (female determined by Ebmer, 1992, OÖLM)
Holotype location: NHMUK
Synonym: no synonym
European IUCN status: DD (Michez, Boustani *et al.*, 2026; Nieto *et al.*, 2014)
Distribution in Europe: North of Greece and South of Bulgaria (Reverté *et al.*, 2023; Sentil *et al.*, 2026).
Habitat: unknown
Phenology: July-August (Ebmer, 1987; 1993)
Pollen diet based on literature: *Acinos alpinus* (Ebmer, 1993)

Pollen diet (original data): specimens not available

4.1.5 *Dufourea* (*Cyprirophites*) *styx* Ebmer, 1976

Original description: Ebmer, A. W. (1976). Neue westpaläarktische Halictidae IV. (Dufoureinae, Apoidea). *Linzer biologische Beiträge*, 8, 179–203.
Available literature with key and/or diagnose for this species: Ebmer (1984, 1993, 1999)
Specimens seen: only seen in pictures (female determined by Ebmer, 1989, OÖLM and male determined by Ebmer, 2020, OÖLM)
Holotype location: personal collection Ebmer
Synonym: no synonym
European IUCN status: LC (Michez, Boustani *et al.*, 2026), DD (Nieto *et al.*, 2014)
Distribution in Europe: Balkans (from Bosnia to Greece and Bulgaria) (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: end June- early August (Ebmer, 1984)
Pollen diet based on literature: *Acinos alpinus* (Ebmer, 1984)
Pollen diet (original data): specimens not available

4.1.6 *Dufourea* (*Dentirophites*) *gaullei* Vachal, 1897

Original description: Vachal, J. (1897). Éclaircissement sur le genre Scrapter et description d'une espèce nouvelle de *Dufourea* (Hyménoptères). *Bulletin de la Société entomologique de France*, 1897, 61–64.
Available literature with key and/or diagnose for this species: Ebmer (1984)
Specimens seen: RMNH, UMons
Holotype location: MNHN
Synonyms: *Dufourea pumila* Vachal, 1907 (synonymized by Dusmet, 1935)
European IUCN status: LC (Michez, Boustani *et al.*, 2026), DD (Nieto *et al.*, 2014)
Distribution in Europe: Spain and Portugal (Reverté *et al.*, 2023; Sentil *et al.*, 2026).
Habitat: unknown
Phenology: June (Ebmer, 1984)
Pollen diet based on literature: not available
Pollen diet (original data): Male (N=2, location: Camino de Uclès, Spain): 100 % Ranunculaceae

4.1.7 *Dufourea* (*Dentirophites*) *lusitanica* Ebmer, 1999

Original description: Ebmer, A. W. (1999). Die westpaläarktischen Arten der Gattung *Dufourea* Lepeletier 1841 (Insecta: Hymenoptera: Apoidea: Halictidae: Rophitinae): Fünfter Nachtrag. *Linzer biologische Beiträge*.
Available literature with key and/or diagnose for this species: Ebmer (1999, 2008)
Specimens seen: only seen in pictures (female determined by Ebmer, 1998, OÖLM)
Holotype location: OÖLM
Synonym: no synonym
European IUCN status: LC (Michez, Boustani *et al.*, 2026), DD (Nieto *et al.*, 2014)
Distribution in Europe: South of Spain and Portugal (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: sandy area with presence of trees such as Pinaceae, *Fraxinus* sp. and *Quercus* sp.
Phenology: May (Ebmer, 1999; 2008)
Pollen diet based on literature: Asteraceae (Ebmer, 2008)
Pollen diet (original data): specimens not available

4.1.8 *Dufourea* (*Dufourea*) *alpina* Morawitz, 1865

Original description: Morawitz, F. (1865). Über einige Andrenidae aus der Umgegend von St. Petersburg. *Horae Societatis Entomologicae Rossicae*, 3, 61–79.
Available literature with key and/or diagnose for this species: Amiet *et al.* (1999), Ebmer (1984, 1989, 1999)
Specimens seen: RMNH, UMons
Holotype location: ZIN
Synonym: no synonym
European IUCN status: LC (Michez, Boustani *et al.*, 2026; Nieto *et al.*, 2014)
Distribution in Europe: Alps, Pyrenees and Balkans (Reverté *et al.*, 2023; Sentil *et al.*, 2026).
Habitat: present from 1300 m to 2500 m in altitude (Ebmer, 1984)
Phenology: June to end August (Ebmer, 1984)
Pollen diet based on literature: *Phyteuma orbiculare, Hieracium* sp., *Campanula* sp., *Acinos* sp., *Thymus* sp. (Ebmer, 1984). Campanulaceae (Müller, 2018)
Pollen diet (original data): Female (N=2, location: Eyne, France): 100% Campanulaceae

4.1.9 *Dufourea* (*Dufourea*) *balearica* Ebmer, 2015

Original description: Ebmer, A. W. (2015). Die westpaläarktischen Arten der Gattung *Dufourea* Lepeletier 1841 (Hymenoptera: Apoidea: Halictidae: Rophitinae): Sechster Nachtrag. *Linzer biologische Beiträge*, 47, 441–448.
Available literature with key and/or diagnose for this species: Ebmer (2015)
Specimens seen: only seen in pictures (Ebmer, 2015, MNCN)
Holotype location: MNCN
Synonym: no synonym
European IUCN status: VU, threatened by tourism development (Michez, Boustani *et al.*, 2026)
Distribution in Europe: Mallorca (Spain) (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: May-June (Ebmer, 2015)
Pollen diet based on literature: not available
Pollen diet (original data): specimens not available

4.1.10 *Dufourea* (*Dufourea*) *fortunata* Ebmer, 1993

Original description: Ebmer, A. W. (1993). Neue Halictidae von den Kanarischen Inseln mit Bemerkungen zu bereits bekannten Arten (Insecta: Hymenoptera: Apoidea: Halictidae). *Veroeffentlichungen aus dem Übersee Museum Bremen Naturwissenschaften,* 12(2), 767-789.
Available literature with key and/or diagnose for this species: Ebmer (1993)
Specimens seen: only seen in pictures (Ebmer, 1993; 1999, personnal collection Ebmer)
Holotype location: personnal collection Ebmer
Synonym: no synonym
European IUCN status: DD (Michez, Boustani *et al.*, 2026; Nieto *et al.*, 2014)
Distribution in Europe: Canary islands (Spain) (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: unknown
Pollen diet based on literature: not available
Pollen diet (original data): specimens not available

4.1.11 *Dufourea* (*Dufourea*) *halictula* (Nylander, 1852)

Original description: Nylander, W. (1852). Revisio synoptica apum borealium, comparatis speciebus Europae mediae. *Notiser ur Sällskapets pro Fauna et Flora Fennica Förhandlingar*, 2, 235–248.
Available literature with key and/or diagnose for this species: Amiet *et al.* (1999), Astafurova (2014), Ebmer (1984, 1993, 1999, 2008), Pesenko *et al.* (2000)
Specimens seen: RMNH
Holotype location: NHRS
Synonyms: *Rhophites halictulus* Nylander, 1852 (synonymization article unknown or nonexistent)
European IUCN status: VU, threatened by changes in agricultural practice and heat waves (Michez, Boustani *et al.*, 2026), NT (Nieto *et al.*, 2014)
Distribution in Europe: Portugal, Spain, France, Belgium, Germany, Switzerland, Austria, Poland, Italy, Ukraine, Belarus, Russia, Sweden, Denmark and Baltic states (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: sandy area in grassland area (van der Meer, 2012)
Phenology: July (Ebmer, 1984)
Pollen diet based on literature: *Jasione montana* (Ebmer, 1984; 2008)
Pollen diet (original data): specimens not available

4.1.12 *Dufourea* (*Dufourea*) *minuta* Lepeletier, 1841

Original description: Lepeletier, A. (1841). Histoire naturelle des insectes. Hyménoptères (Vol. 2, pp. 227–228). *Librairie Encyclopédique de Roret*.
Available literature with key and/or diagnose for this species: Amiet *et al.* (1999), Astafurova (2014), Ebmer (1984, 1993, 1999), Pesenko *et al.* (2000), Pesenko & Astafurova (2006)
Specimens seen: RMNH, UMons
Holotype location: SMF
Synonym: *Dufourea vulgaris* Schenck, 1861 (synonymized by Baker, 1994)
European IUCN status: VU, threatened by changes in agricultural practice (Michez, Boustani *et al.*, 2026), NT (Nieto *et al.*, 2014)
Distribution in Europe: Spain, France, Belgium, Netherlands, Germany, Switzerland, Austria, Poland, Czech Republic, Italy, Belarus, Russia, Sweden, Finland and Baltic states (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: sandy heatland and forest edges (Radchenko, 2015)
Phenology: end July- early September (Ebmer, 1984)
Pollen diet based on literature: *Hieracium* sp.*, Lactuca* sp.*, Leontodon* sp. (Ebmer, 1984)
Pollen diet (original data): Female (N=9, location: Eyne, France): 100% *Leontodon* sp., Male (N=1): 100% *Leontodon* sp.

4.1.13 *Dufourea* (*Dufourea*) *similis* Friese, 1898

Original description: Friese, H. (1898). Beiträge zur Bienenfauna von Ägypten. *Természetrajzi Füzetek*, 21, 303–313.
Available literature with key and/or diagnose for this species: Ebmer (1984, 1989, 1999)
Specimens seen: RMNH, UMons
Holotype location: ZMHB
Synonym: *Dufourea eatoni* Saunders, 1908 (synonymized by Warncke, 1979)
European IUCN status: NA (Michez, Boustani *et al.*, 2026)
Distribution in Europe: Balearic and Canary Islands (Spain) (Reverté *et al.*, 2023; Sentil *et al.*, 2026).
Habitat: unknown
Phenology: April-May (Ebmer, 1984)
Pollen diet based on literature: not available
Pollen diet (original data): specimens not available

4.1.14 *Dufourea* (*Dufourea*) *trautmanni* Dusmet, 1935

Original description: Dusmet y Alonso, J. M. (1935). Los ápidos de España VIII. Subfamilia Panurginos. *Eos: Revista Española de Entomología*, 11, 117–172.
Available literature with key and/or diagnose for this species: Ebmer (1984, 1999)
Specimens seen: RMNH, UMons
Holotype location: MNCN
Synonym: no synonym
European IUCN status: LC (Michez, Boustani *et al.*, 2026), DD (Nieto *et al.*, 2014)
Distribution in Europe: Spain and Portugal (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: June (Ebmer, 1984)
Pollen diet based on literature: not available
Pollen diet (original data): Female (N=2, location: Pinsapo Escalereta, Spain; Pinto, Spain): 75% Campanulaceae, 25% Cichorioideae.

4.1.15 *Dufourea* (*Dufourea*) *wolfi* Ebmer, 1989

Original description: Ebmer, A. W. (1989). The West Palaearctic species of the genus *Dufourea*, with illustrated keys: Second supplement. *Linzer biologische Beiträge.*
Available literature with key and/or diagnose for this species: Ebmer (1989, 1993, 1999)
Specimens seen: only seen in pictures (female determined by Ebmer, 1998, OÖLM)
Holotype location: personnal collection Ebmer
Synonym: no synonym
European IUCN status: LC (Michez, Boustani *et al.*, 2026), DD (Nieto *et al.*, 2014)
Distribution in Europe: Bulgaria, Greece (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: April-May (Ebmer, 1989;1999)
Pollen diet based on literature: *Campanula* sp. (Ebmer, 1999)
Pollen diet (original data): specimens not available

4.1.16 *Dufourea* (*Glossadufourea*) *longiglossa* Ebmer, 1993

Original description: Andreas, V. P., & Puchenau, W. E. (1993). Die westpaläarktischen Arten der Gattung *Dufourea* Lepeletier 1841 mit illustrierten Bestimmungstabellen (Insecta: Hymenoptera: Apoidea: Halictidae: Rophitinae): Dritter Nachtrag. *Linzer biologische Beiträge*, 25, 15–44.
Available literature with key and/or diagnose for this species: Ebmer (1993)
Specimens seen: only seen in pictures (female determined by Ebmer, 1998, OÖLM)
Holotype location: personnal collection Ebmer
Synonym: no synonym
European IUCN status: DD (Michez, Boustani *et al.*, 2026; Nieto *et al.*, 2014)
Distribution in Europe: Spain (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: June (Ebmer, 1993)
Pollen diet based on literature: Lamiaceae (Ebmer, 1993)
Pollen diet (original data): specimens not available

4.1.17 *Dufourea* (*Halictoides*) *dentiventris* (Nylander, 1848)

Original description: Nylander, W. (1848). Adnotationes in expositionem monographicam apum borealium. *Notiser ur Sällskapets pro Fauna et Flora Fennica Förhandlingar,* 1, 195–205.
Available literature with key and/or diagnose for this species: Amiet *et al.*(1999), Astafurova (2014), Ebmer (1984), Pesenko *et al.*(2000), Pesenko & Astafurova (2006)
Specimens seen: RMNH, UMons
Holotype location: MZH
Synonyms: *Dufourea dejeanii* Lepeletier, 1841 (synonymized by Ebmer, 2001), *Dufourea odontogastra* Ebmer, 1978 (synonymized by Ebmer, 1984), *Dufourea putoniana* Dours, 1873 (synonymized by Warncke, 1979), *Halictoides dentiventris* Nylander, 1848 (synonymization article unknown or nonexistent), *Rophites bispinosa* Eversmann, 1852 (synonymized by Morawitz, 1867)
European IUCN status: NT, threatened by changes in agricultural practice (Michez, Boustani *et al.*, 2026; Nieto *et al.*, 2014)
Distribution in Europe: Spain, France, Belgium, Netherlands, Luxembourg, Germany, Switzerland, Austria, Poland, Czech Republic, Italy, Serbia, Hungary, Slovakia, Slovenia, Belarus, Russia, Sweden, Finland, Norway, Estonia, Latvia (Reverté *et al.*, 2023; Sentil *et al.*, 2026).
Habitat: sandy heatland and forest edges (van der Meer, 2012)
Phenology: July-early September (Ebmer, 1984)
Pollen diet based on literature: *Campanula* sp*., Hieracium pilosella, Dryas octopetala, Calluna* sp. (Ebmer, 1984), Fabaceae, Rosaceae (Astafurova, 2014)
Pollen diet (original data): specimens not available

4.1.18 *Dufourea* (*Halictoides*) *graeca* Ebmer, 1976

Original description: Ebmer, A. W. (1976). Neue westpaläarktische Halictidae IV. (Dufoureinae, Apoidea). *Linzer biologische Beiträge*, 8, 179–203.
Available literature with key and/or diagnose for this species: Astafurova (2014), Ebmer (1984, 1993, 1999)
Specimens seen: UMons
Holotype location: personnal collection Ebmer
Synonym: no synonym
European IUCN status: LC (Michez, Boustani *et al.*, 2026), DD (Nieto *et al.*, 2014)
Distribution in Europe: Greece, Bulgaria (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown

Phenology: July-early August (Ebmer, 1984)
Pollen diet based on literature: *Campanula* sp. (Ebmer, 1984)
Pollen diet (original data): specimens not available

4.1.19 *Dufourea* (*Halictoides*) *inermis* (Nylander, 1848)

Original description: Nylander, W. (1848). Adnotationes in expositionem monographicam apum borealium. *Notiser ur Sällskapets pro Fauna et Flora Fennica Förhandlingar*, 1, 195–205.
Available literature with key and/or diagnose for this species: Amiet *et al.* (1999), Ebmer (1984, 1989, 1999), Pesenko *et al.* (2000)
Specimens seen: RMNH, UMons
Holotype location: MZH (male)
Synonym: *Halictoides inermis* Nylander, 1848 (synonymized by Ebmer, 1976)
European IUCN status: EN, threatened by changes in agricultural practice (Michez, Boustani *et al.*, 2026), NT (Nieto *et al.*, 2014)
Distribution in Europe: Spain, France, Belgium, Netherlands, Germany, Switzerland, Austria, Poland, Czech Republic, Italy, Serbia, Hungary, Slovakia, Romania, Ukraine, Belarus, Russia, Sweden, Finland and Baltic states (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: sandy heatland and forest edges (van der Meer, 2012)
Phenology: July-early September (Ebmer, 1984)
Pollen diet based on literature: *Campanula* sp. (Ebmer, 1984; Astafurova, 2014)
Pollen diet (original data): Female (N= 2, location: Cumparatura, Romania): 100% Campanulaceae, Male (N=1, location: Cumparatura, Romania): 100% Campanulaceae

4.1.20 *Dufourea* (*Merrophites*) *merceti* Vachal, 1907

Original description: Vachal, J. (1907). Sur les *Dufourea* propres à l'Espagne. *Boletín de la Sociedad Española de Historia Natural*, 7, 362–363.
Available literature with key and/or diagnose for this species: Astafurova (2014), Ebmer (1984)
Specimens seen: only seen in pictures (male determined by Warncke, OÖLM)
Holotype location: MNCN
Synonym: no synonym
European IUCN status: DD (Michez, Boustani *et al.*, 2026; Nieto *et al.*, 2014)
Distribution in Europe: Spain (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: unknown
Pollen diet based on literature: not available

Pollen diet (original data): specimens not available

4.1.21 *Rhophitoides canus* (Eversmann, 1852)

Original description: Eversmann, E. (1852). Fauna Hymenopterologica Volgo-Uralensis. *Bulletin de la Société impériale des naturalistes de Moscou*, 25(3), 59–60.
Available literature with key and/or diagnose for this species: Amiet *et al.* (1999), Astafurova (2014), Pesenko *et al.* (2000), Pesenko & Astafurova (2006)
Specimens seen: RMNH, UMons
Holotype location: personnal collection Warncke, OÖLM
Synonyms: *Rophites cana* Eversmann, 1852 (synonymization article unknown or nonexistent), *Rhophites bifoveolatus* Sichel, 1854 (synonymized by Morawitz, 1872), *Rhophitoides distinguendus* Schenck, 1861 (synonymized by Dalla Tore, 1896)
European IUCN status: LC (Michez, Boustani *et al.*, 2026; Nieto *et al.*, 2014)
Distribution in Europe: France, Belgium, Germany, Switzerland, Austria, Poland, Czech Republic, Italy, Serbia, Hungary, Slovakia, Slovenia, Serbia, Bulgaria, Romania, Moldavia, Ukraine, Belarus, Russia, Lithuania (Reverté *et al.*, 2023; Sentil *et al.*, 2026).
Habitat: sandy area, open area with sparse vegetation*, Medicago sativa* crop (Radchenko, 2015), dried or wet meadows, semi-desertic area, forest edges (Astafurova, 2014)
Phenology: June-early September (Pesenko *et al.*, 2000)
Pollen diet based on literature: *Medicago* sp. (Amiet, 1999)
Pollen diet (original data): specimens not available

4.1.22 *Rhophitoides epiroticus* Schwammberger, 1975

Original description: Schwammberger, W. (1976). Zwei neue *Rophites*-Arten aus der Türkei (Hymenoptera: Halictidae). *Entomologische Zeitschrift*, 86, 225–229.
Available literature with key and/or diagnose for this species: Astafurova (2014)
Specimens seen: RMNH
Holotype location: ZMHB
Synonym: no synonym
European IUCN status: LC (Michez, Boustani *et al.*, 2026), DD (Nieto *et al.*, 2014)
Distribution in Europe: Sicily (Italy), Greece, Albania, North Macedonia (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: unknown

Pollen diet based on literature: not available
Pollen diet (original data): specimens not available

4.1.23 *Rophites algirus* Pérez, 1895

Original description: Perez, J. (1895). Espèces nouvelles de mellifères de Barbarie (diagnoses préliminaires) (64 pp.). *Bordeaux: Selbstverlag (Imprimerie G. Gounouilhou)*
Available literature with key and/or diagnose for this species: Astafurova (2011, 2014), Ebmer & Schwammberger (1986), Pesenko *et al.* (2000),
Specimens seen: RMNH, UMons
Holotype location: MNHN
Synonym: no synonym
European IUCN status: LC (Michez, Boustani *et al.*, 2026), DD (Nieto *et al.*, 2014)
Distribution in Europe: Spain, France, Germany, Switzerland, Austria, Poland, Czech Republic, Italy, Serbia, Hungary, Slovakia, Slovenia, Croatia, Serbia, North Macedonia, Greece, Albania, Bulgaria, Romania, Moldavia, Ukraine, Russia (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: steppe (rocky or meadows) (Astafurova, 2011)
Phenology: May-end August (Astafurova, 2011)
Pollen diet based on literature: *Clinopodium vulgare, Stachys recta, Ballota* sp. (Ebmer & Schwammberger, 1986), Lamiaceae (Amiet, 1999; Pesenko *et al.*, 2000)
Pollen diet (original data): Female (N=3, location: Anastasie, Romania; Peyresq, France; Eyne, France): 100% Lamiaceae, Male (N=1, location: Anastasie, Romania): 100% *Campanula* sp.

4.1.24 *Rophites clypealis* Schwammberger, 1976

Original description: Schwammberger, F. (1976). Zwei neue *Rophites*-Arten aus der Türkei (Hym., Halictidae). *Entomologische Zeitschrift*, 86, 225–229.
Available literature with key and/or diagnose for this species: Astafurova (2011, 2014), Ebmer & Schwammberger (1986)
Specimens seen: RMNH
Holotype location: SMF
Synonym: no synonym
European IUCN status: NA (Michez, Boustani *et al.*, 2026), DD (Nieto *et al.*, 2014)
Distribution in Europe: Ukraine, Russia (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: steppe (Astafurova, 2011)

Phenology: June-July (Astafurova, 2011; 2014)
Pollen diet based on literature: not available
Pollen diet (original data): specimens not available

4.1.25 *Rophites hartmanni* Friese, 1902

Original description: Friese, H. (1902). Zwei neue Rhophites-Arten (Hym.). *Zeitschrift für systematische Hymenopterologie und Dipterologie*, 2, 380–381.
Available literature with key and/or diagnose for this species: Astafurova (2011, 2014), Ebmer & Schwammberger (1986), Pesenko *et al.*(2000)
Specimens seen: RMNH, UMons
Holotype location: NMW
Synonym: *Rhophites bistrispinosus* Lebedev, 1931 (synonymized by Schwammberger, 1971)
European IUCN status: LC (Michez, Boustani *et al.*, 2026), DD (Nieto *et al.*, 2014)
Distribution in Europe: from Austria and Poland to Greece and Russia (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: steppes,meadows, forest edges, waste grounds (Astafurova, 2011)
Phenology: end May-early September (Ebmer & Schwammberger, 1986; Astafurova, 2011)
Pollen diet based on literature: *Origanum* sp*., Ballota nigra, Melilotus albus, Nepeta* sp*., Lamium album* (Ebmer & Schwammberger, 1986)
Pollen diet (original data): specimens not available

4.1.26 *Rophites hellenicus* Ebmer, 1984

Original description: Ebmer, A. W. (1984). *Rophites hellenicus* n. sp., eine montane Art aus Griechenland (Hymenoptera, Halictidae). Entomologische Zeitschrift, 94(4), 46–48.
Available literature with key and/or diagnose for this species: Astafurova (2011, 2014), Ebmer & Schwammberger (1986)
Specimens seen: RMNH
Holotype location: personnal collection Ebmer
Synonym: no synonym
European IUCN status: LC (Michez, Boustani *et al.*, 2026), DD (Nieto *et al.*, 2014)
Distribution in Europe: Bulgaria, Greece (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: not available
Pollen diet based on literature: not available
Pollen diet (original data): specimens not available

4.1.27 *Rophites leclercqi* Schwammberger, 1971

Original description: Schwammberger, K. H. (1971). Beitrag zur Kenntnis der Bienengattung Rhophites Spinola (Hymenoptera, Apoidea, Halictidae). *Bulletin des Recherches Agronomiques de Gembloux (Nouvelle Série)*, 6, 578–584.
Available literature with key and/or diagnose for this species: Astafurova (2011, 2014), Ebmer & Schwammberger (1986)
Specimens seen: only seen in pictures
Holotype location: FAGX (female)
European IUCN status: DD (Michez, Boustani *et al.*, 2026; Nieto *et al.*, 2014)
Distribution in Europe: Greece, Bulgaria, Türkyie (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: July (Ebmer & Schwammberger, 1986)
Pollen diet based on literature: not available
Pollen diet (original data): specimen not available

4.1.28 *Rophites quinquespinosus* Spinola, 1808

Original description: Spinola, M. (1808). Insectorum Liguriae species novae aut rariores, quas in agro Ligustico nuper detexit (Vol. 2, Fasc. 2, pp. 1–81). *Genuae: Yves Gravier*.
Available literature with key and/or diagnose for this species: Amiet *et al.* (1999), Astafurova (2011, 2014), Ebmer & Schwammberger (1986), Pesenko *et al.* (2000), Pesenko & Astafurova (2006)
Specimens seen: RMNH, UMons
Holotype location: MSBD
Synonyms: *Rophites bluethgeni* Benedek, 1973 (synonymized by Warncke, 1980), *Rhophites moeschleri* Schwammberger, 1971 (synonymized by Warncke, 1980), *Rhophites pilichi* Móczár, 1967 (synonymized by Warncke, 1980)
European IUCN status: VU, threatened by changes in agricultural practice (Michez, Boustani *et al.*, 2026), NT (Nieto *et al.*, 2014)
Distribution in Europe: from Austria and Poland to greece and Russia (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: steppes, meadows, forest edges, urban area (Astafurova, 2011)
Phenology: May-August (Ebmer & Schwammberger, 1986; Astafurova, 2011)
Pollen diet based on literature: *Ballota nigra, Bettonica officinalis, Stachys recta* (Ebmer & Schwammberger, 1986)
Pollen diet (original data): specimens not available

4.1.29 *Rophites thracius* Ebmer, 1993

Original description: Ebmer, A. W. (1993). The bee genus *Rophites* Spinola, 1808: First supplement. Linzer biologische Beiträge, 25(1), 3–14.
Available literature with key and/or diagnose for this species: Astafurova (2011, 2014), Ebmer (1993)
Specimens seen: UMons
Holotype location: personal collection Ebmer
Synonym: no synonym
European IUCN status: DD (Michez, Boustani *et al.*, 2026; Nieto *et al.*, 2014)
Distribution in Europe: Bulgaria (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: June (Ebmer & Schwammberger, 1986)
Pollen diet based on literature: not available
Pollen diet (original data): specimens not available

4.1.30 *Systropha anatolica* Warncke, 1977

Original description: Warncke, K. (1977). Missione Giordani Soika in Iran 1965. 6. Beitrag zur Bienenfauna des Iran: 2. Die Gattung *Systropha* III. *Bollettino del Museo Civico di Storia Naturale di Venezia*, 28, 93–97.
Available literature with key and/or diagnose for this species: Wood & Le Divelec (2022)
Specimens seen: seen only in pictures (Wood & Le Divelec, 2022, OÖLM)
Holotype location: OÖLM
Synonyms: *Systropha planidens anatolica* Warncke, 1977 (synonymized by Wood & Le Divelec, 2022)
European IUCN status: not available
Distribution in Europe: Türkyie (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: May-June (Wood & Le Divelec, 2022)
Pollen diet based on literature: not available
Pollen diet (original data): specimens not available

4.1.31 *Systropha curvicornis* (Scopoli, 1770)

Original description: not available
Available literature with key and/or diagnose for this species: Amiet *et al.* (1999), Astafurova (2014), Pesenko *et al.* (2000), Wood & Le Divelec (2022),
Specimens seen: RMNH, UMons
Holotype location: MNHN
Synonyms: *Andrena labrosa* Eversmann,1852 (synonymized by Dalla Torre, 1896), *Andrena spiralis* Olivier, 1789 (synonymized by Dalla Torre, 1896),

Eucera *curvicornis* Scopoli, 1770 (synonymized by Baker, 1996), *Tenthredo convolvuli* Pallas, 1773 (synonymized by Baker, 1996)
European IUCN status: LC (Michez, Boustani *et al.*, 2026), NT (Nieto *et al.*, 2014)
Distribution in Europe: from Germany to Russia and Greece, south of France and Spain (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: not available
Phenology: May-August (Pesenko *et al.*, 2000)
Pollen diet based on literature*: Convolvulus arvensis* (female) (Pesenko *et al.*, 2000; Amiet *et al.*, 1999), *Cichorium intybus* (male) (Amiet *et al.*, 1999)
Pollen diet (original data): specimens not available

4.1.32 *Systropha grandimargo* Pérez, 1905

Original description: Pérez, J. (1905). Espèces nouvelles d'Hymenoptera de Catalogne*. Butlletí de la Institució Catalana d'Història Natural*, 5, 81–88.
Available literature with key and/or diagnose for this species: Wood & Le Divelec (2022)
Specimens seen: UMons
Holotype location: MNHN
Synonym: *Systropha chrysura* Pérez, 1905 (synonymized by Wood & Le Divelec, 2022)
European IUCN status: LC (Michez, Boustani *et al.*, 2026)
Distribution in Europe: Portugal, Spain, France (South and Corsica) (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: unknown
Phenology: May-June (Wood & Le Divelec, 2022)
Pollen diet based on literature: not available
Pollen diet (original data): Male (N=1, location: Greece): 50 % Convolvulaceae, 35 % *Lamium* sp., 15% Fabaceae

4.1.33 *Systropha planidens* Giraud, 1861

Original description: Giraud, J. (1861). Fragments entomologiques. I. Description de plusieurs Apides nouvelles et observations sur quelques espèces connues*. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien*, 11, 447–470.
Available literature with key and/or diagnose for this species: Amiet *et al.* (1999), Astafurova (2014), Pesenko *et al.* (2000), Wood & Le Divelec (2022)
Specimens seen: RMNH, UMons
Holotype location: MNHN
Synonym: not available

European IUCN status: LC (Michez, Boustani *et al.*, 2026), VU (Nieto *et al.*, 2014)
Distribution in Europe: from Germany to Russia and Greece, South of France (Reverté *et al.*, 2023; Sentil *et al.*, 2026)
Habitat: Open and sunny area (Pesenko *et al.*, 2000)
Phenology: June-August (Pesenko *et al.*, 2000)
Pollen diet based on literature: *Convolvulus arvensis* (female) (Pesenko *et al.*, 2000; Amiet *et al.*, 1999), *Cichorium intybus* (male) (Amiet *et al.*, 1999)
Pollen diet (original data): Male (N=1, location: Greece): 50% Fabaceae, 50 % Convolvulaceae

4.2 Description of the female of *Rophites thracius*

Material examined. 1 ♀, Bulgaria SW, Blagoevgrad, Melnik env., 4.VII.2019, leg. M. Halada. ITD: 2.9 mm, length: 7.4 mm

The attribution of the female to this species was supported by the overlap with the known distribution of *Rophites thracius* male, as well as by similiraty in predicted morphological features such as spines coloration by Ebmer (1993). In addition, the arrangement of the spines differs strongly from the patterns known in other European Rophitinae.

4.2.1 Head

Dark brown, 1.2 times longer than wide. Mandibule red to brown, bidentate, rounded. Labrum black, rectangular, striated. Clypeus brown to black, three times larger than long, convex, finely reticulate without puncture, hairs yellow on the apical part, spines from the clypeus to middle of the frons; spines on clypeus larger than those on frons, inclined at 30°, more visible on the clypeus than on frons. Paraocular area black, densely punctuated (interspace less than 0.1 times interspace), appresed white hairs. Scape and pedicel brown, sparsely short yellow hairs. Ventral part of flagellum yellow, shagrined, short yellow hairs. Dorsal part of flagellum brown, short yellow hairs. Frons with spines positioned in a clear V-shaped, forming two parallel rows with shagrined interspace. Some spines at the base of the "V" forming a third row and not well arranged like the two other rows; spines separated from each other by less than one spine diameter; spines not reaching the upper edge of the eyes. Frons densely punctuate (interspace less than 0.1 puncture diameter), shiny between punctures, appresed white hairs. Distance between the upper middle spines and the middle ocelli equal or larger to an ocellus. Vertex dark brown, rectangular, finely and densely punctuated (interspace less than 0.5 punctures), shiny between punctures, white hairs. Vertex upper edge slightly rounded. OVL (upper vertex length, from the upper edge of the middle ocellus to the vertex) (Ebmer,1986) two times the diameter of the middle ocellus. Gena dark brown, densely punctuated (interspace less than 0.5 punctures), shiny between punctures, white hairs (Fig. 2, C, D)

4.2.2 Mesosoma

Mesosoma brown, entierly covered with white hairs. Scutum dark brown, short beige hairs, punctation dense (interspace less than 0.5 times point diameter) and coarse, interspace smooth and shiny. Scutellum and metanotum dark brown, punctation dense (interspace less than 0.5 times point diameter) and coarse, interspace smooth and shiny, long beige hairs

(Fig. 2, E). Propodeal enclosure dark brown, triangular to elliptic, reticulate on the base and shagrined on apical part. Propodeum side dark brown, densely and finely punctuate (interspace less than 0.5 point diameter), long beige hairs (Fig. 2, F). Mesopleura dark brown, finely and densely punctured (interspace less than 0.5 times point diameter), underlying surface shiny, dense and long feathery white hairs. Wings slightly smoked, venation dark yellow to brown. Legs brown with dense white hairs on tibia and femora, tarsus orange without hairs.

4.2.3 Metasoma

Metasoma brown, ellipictic, white hairs. Apical part of terga light brown with a fringe of white hairs. T1 with dense punctures on the disc (interspace less than 0.5 puncture diameter), sparser and finer puncture on apical part (interspace egal or bigger than 1 puncture diameter), underlaying surface shiny, appressed white hairs on apical part and interrupted on the middle. T2 with dense punctures on the disc (interspace less than 0.5 puncture diameter), sparser and finer puncture on apical part (interspace egal or bigger than 1 puncture diameter), underlaying surface shiny, appressed continuous white hairs on apical part. T3 punctured with an interspace egal or bigger than 1 puncture diameter, underlaying surface shiny, appressed continuous white hairs on apical part, sparser white hairs on disc. T4, T5 and T6 punctured with an interspace egal or bigger than 1 puncture diameter, underlaying surface shiny, appressed continuous white hairs on apical part, dense long white hairs covering the tergites (Fig. 2, G).

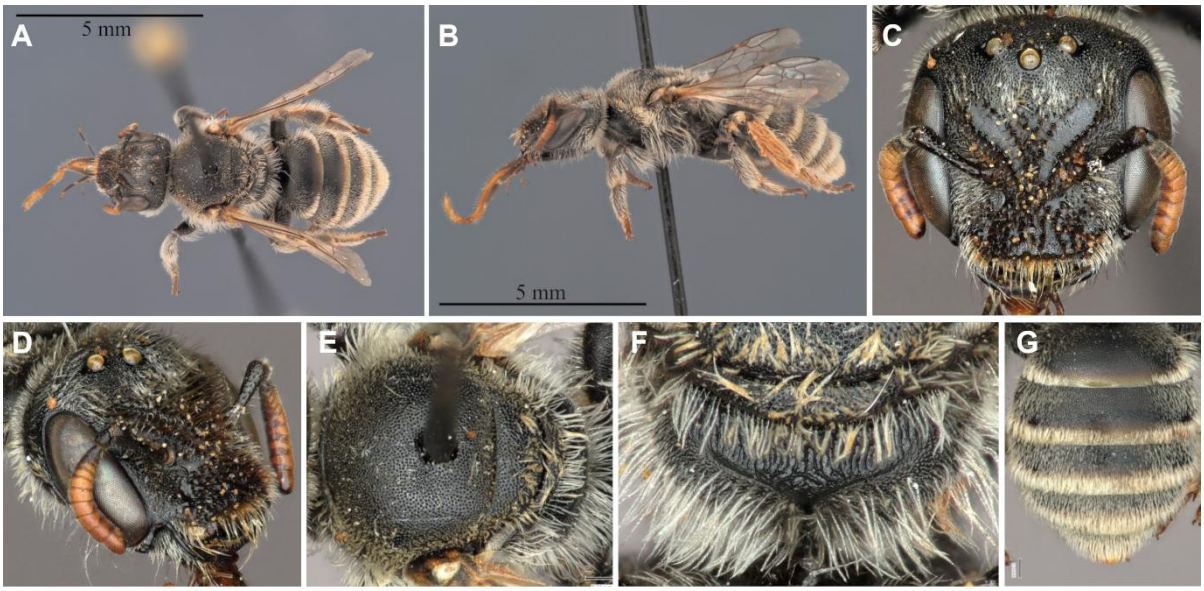

Figure 2: Newly described female sex in *Rophites thracius* A. Dorsal view B. Lateral view C. Head (frontal view) D. Head (lateral view) E. Mesosoma (dorsal view) F. Propodeum (dorsal view) G. Metasoma (dorsal view)

4.3 Key to the European species of Rophitinae

1. 7 tergite segments; presence of genital capsule……2.

- 6 tergite segments; presence of sting apparatus……32.

2. Three submarginal cells (Fig. 5, C); end of antenna curved, spiral shaped (A9 to A11-12); 11 or 12 antennal segments (Fig. 5, A) (***Systropha***)……3.

- Two submarginal cells; end of antenna linear or slightly curved; 13 antennal segments ……6.

3. Sharp teeth on S2 and S3 (Fig. 5, B); S7 with concave end……***Systropha curvicornis*** **(Scopoli, 1770)**

- Truncated tooth on S2, S3 with protuberance but not sharp tooth (Fig. 5, G); S7 with convex end ……4.

4. Second submarginal cell longer than wide (Fig. 5, C); apical part of S8 forming a trapeze on ventral view (Fig. 5, D) ……***Systropha grandimargo*** **Pérez, 1905**

- Second submarginal cell as long as wide (Fig. 5, E); apical part of S8 forming another shape on ventral view (Fig. 5, F, H)……5.

5. Tergite hairs brown (well visible on T4-6)(Fig. 5, G); apical part of S8 forming hemicircular or elliptic shape on ventral view (Fig. 5, F) ……***Systropha planidens*** **Giraud, 1861**

- Tergite hairs yellow; apical part of S8 forming rectangular shape on ventral view (Fig. 5, H)……***Systropha anatolica*** **Warncke, 1977**

6. All segments of labial palp with same length; absence of hairs or sparse hairs on metasoma; no pygidial plate (***Dufourea***)……7.

- First and second labial palp bigger than other segments; dense hairs on metasoma; presence of pygidial plate ……25.

7. S6 with swellings (tubercles) or a carina (Fig. 5, L, N, O)…… 8.

- S6 without swellings or carina ……15.

8. Head and thorax with greenish reflections (Fig. 5, I, J); S6 with carina beginning on basal part and ending in the middle of S6 ……..***Dufourea alpina*** **Morawitz, 1865**

- Head and thorax without greenish reflections; S6 sometimes with carina but beginning in the middle of S6……..9.

9. Rhinaria barely visible (Fig. 5, K); S6 with only a carina, no real swellings (Fig. 5, L)……..***Dufourea styx*** **Ebmer, 1976**

- Rhinaria clearly visible; S6 with swellings and sometimes a carina (Fig. 5, N)(swellings visible in profile)……..10.

10. S5 with a terminal tooth on each side (Fig. 5, M) ……..***Dufourea dentiventris*** **(Nylander, 1848)**

- S5 without terminal teeth ……..11.

11. S6 with a sharp terminal carina forming a spine, exceeding the apical margin of S6 (Fig. 5, N)……..***Dufourea graeca*** **Ebmer, 1976**

- S6 without sharp carina exceeding the apical margin of S6……..12.

12. S6 forming a triangle with a central keel-like swelling (Fig. 5, O) ……..***Dufourea fortunata*** **Ebmer, 1993**

- S6 differently shaped……..13.

13. Apical part of S6 hyaline (Fig. 5, Q), forming a chitinous-like membrane; big species……..***Dufourea inermis*** **(Nylander, 1848)**

- S6 not hyaline; smaller species ……..14.

14. Basal part of antenna yellow; vertex angulate and raised, forming a square face (Fig. 5, R); T1 with very dense punctation, interlaced medially (Fig. 5, S)……..***Dufourea cypria*** **Mavromoustakis, 1952**

- Basal part of antenna brown; face elongated, vertex not angulate; T1 without interlaced punctation……..***Dufourea iris*** **Ebmer, 1987**

15. Rhinaria concave extending over almost the entire length of the segment (Fig. 5, P); median and hind femora swollen and flattened (Fig. 5, T); hind tibia enlarged, leaf-like (Fig. 5, U); S4 with a triangular hair brush (Fig. 5, V)……..***Dufourea paradoxa*** **Morawitz, 1867**

- Rhinaria concave or flat extending over less than the full length of the antennal segment; median and hind femora not swollen, of the same thickness as other legs; hind tibia not enlarged; S4 without hair brush .....16.

16. Head with strong green reflects; apical part of tergites red ……..……..***Dufourea lusitanica*** **Ebmer, 1999**

- Head without green reflects; apical part of tergites black, brown or translucent……17.

17. Long glossa, reaching the end of the body; vertex angulated and raised (more than 2 times ocelli), forming a square face (Fig. 5, W) ……***Dufourea longiglossa*** **Ebmer, 1993**

-Glossa short or not elongated; head without raised angulated vertex.. 18.

18. Basal part of antenna yellow; squared vertex; inflated propodeum (seen in lateral view)……***Dufourea coeruleocephala*** **Morawitz, 1872**

- Basal part of antenna yellow or with another color; rounded vertex; propodeum not inflated (seen in lateral view)…… 19.

19. Hairs on head and thorax totally brown (see between antenna)(Fig. 4, A)……***Dufourea trautmanni*** **Dusmet, 1935**

- Hairs of another colour on head and thorax ……20.

20. Last antennal segment swollen and flattened, forming a leaf-like shape (Fig. 5, X)……..……***Dufourea merceti*** **Vachal, 1907**

- All antennal segments normal shaped …… 21.

21. Second and third antennal segments strongly convex, forming a tooth-like shape (Fig. 4, B); temporal tooth present (Fig. 4, C) ……***Dufourea gaullei*** **Vachal, 1897**

- Second antennal segment normal or slightly convex; no temporal tooth ……22.

22. Antenna with rhinaria covering all of the antenna without depression (Fig. 4, D)……***Dufourea halictula*** **(Nylander, 1852)**

- Antenna with rhinaria covering more than half of the segment length on apical segments……23.

- Antenna with rhinaria covering about one-third of the segment length on apical segments ……..…….. 24.

23. Head wider than long; rhinaria beginning on A7 (Fig. 4, E) ……..……..……***Dufourea balearica*** **Ebmer, 2015**

- Head as wide as long; rhinaria beginning on A5 (Fig. 4, F) ……***Dufourea minuta*** **Lepeletier, 1841**

24. Frons distinctly elongated (Fig. 4, G); punctation on T2 coarser than on T1; apical part of tergites not hyaline (Fig. 4, H) ……..……***Dufourea wolfi*** **Ebmer, 1989**

- Frons not distinctly elongated (Fig. 4, I); punctation on T2 not coarser than on T1; apical part of tergites hyaline (Fig. 4, J) ……..……***Dufourea similis*** **Friese, 1898**

25. First and second labial palp at least five times bigger than the fourth (***Rophites***)(Fig. 4, M)…….……26.

- First and second labial palp two times or less bigger than the fourth (***Rhophitoides***)(Fig. 4, Q)……..……..32.

26. Long hairs on end of S6 (Fig. 4, K)……..……27.

- Short hairs on end of S6 ……..……29.

27. Clypeus convex……***Rophites clypealis*** **Schwammberger, 1976**

- Clypeus flat……..……..28.

28. Vertex rounded (Fig. 4, L); S6 with finer middle brush, spines on S6 placed lower on apical part forming a rounded end, interspace between space egal to the brush length (Fig. 4, K) ……..……***Rophites quinquespinosus*** **Spinola, 1808**

- Vertex squared (Fig. 4, M); S6 with denser middle brush, spines on S6 placed higher on apical part forming an acute end, interspace between space inferior or superior to the brush length (Fig. 4, N) ……..……***Rophites algirus*** **Pérez, 1895**

29. Vertex elevated, distance between middle ocelli and upper margin of vertex egal 2 times dimeter of middle ocelli (Fig. 4, O) ……..……***Rophites hartmanni*** **Friese, 1902**

- Vertex not elevated, distance between middle ocelli and upper margin of vertex egal less than 2 times dimeter of middle ocelli……30.

30. Antenna serriated, black on the end and rounded (Fig. 4, P) ……***Rophites hellenicus*** **Ebmer, 1984**

- Antenna not serriated, end of the same color of the antenna and elongated ……***Rophites thracius*** **Ebmer, 1993**

31. Ventral part of antenna orange without rhinaria or slightly visible rhinaria; apical part of tergites with dense light hairs ……***Rhophitoides canus*** **(Eversmann, 1852)**

- Ventral part of antenna black with rhinaria (Fig. 4, Q); apical part of tergites with sparse light hairs (Fig. 4, R) ……***Rhophitoides epiroticus*** **Schwammberger, 1975**

32. Three submarginal cells (Fig. 5, C); tergites with long hairs (Fig. 4, S) (***Systropha***)……33.

- Two submarginal cells; tergites with short hairs……36.

33. A3 as long as A4 and A5; T1-2 with grey or dark hairs (Fig. 4, S) ……***Systropha curvicornis*** **(Scopoli, 1770)**

- A3 longer than A4 and A5; T1-2 with brown hairs……34.

34. Second submarginal cell longer than wide (Fig. 4, C); double punctation on tergites; appearance of tergite dark (Fig. 4, T) ……***Systropha grandimargo*** **Pérez, 1905**

- Second submarginal cell as long as wide; simple punctation on tergites; appearance of tergite light (Fig. 4, U)……35.

35. Punctation on the frons dense and coarse (Fig. 4, V) ……***Systropha planidens*** **Giraud, 1861**

- Punctation on the frons sparse and fine (Fig. 4, W) ……***Systropha anatolica*** **Warncke, 1977**

36. All segments of labial palp with same length; absence of hairs or sparse hairs on metasoma (***Dufourea***)……37.

- First and second labial palp bigger than other segments; dense hairs on metasoma……55.

37. Scutum with sparse punctation in the central part of the scutum (more than 2 punctures diameter interspace) (Fig. 4, X) .....38.

- Scutum with dense punctation (less than 2 punctures diameter interspace) in the central part of the scutum (Fig. 6, D)……..……..40.

38. Apical part of tergites translucent (Fig. 4, Y); interantennal part convex form like a carena converging on the frons (Fig. 6, A) ……*Dufourea similis* **Friese, 1898**

- Apical part of tergites not translucent or slightly translucent; frons without bulge or just small bugle ……..…….. 39.

39. Clypeus with U shape; labrum squared (Fig. 6, B); basal part of propodeum with sparse wrinkles, lateral part chagrinated (Fig. 6, C) ……..……..*Dufourea minuta* **Lepeletier, 1841**

- Clypeus without U shape; labrum rounded; basal part of propodeum with dense wrinkles, lateral part like a mirror ……..*Dufourea balearica* **Ebmer, 2015**

40. T1 with coarse punctures (Fig. 6, E)……..41.

- T1 with fine punctures (Fig. 7, G)……..…….48.

41. Elongated face, longer than wide (Fig. 6, F) ……*Dufourea cypria* **Mavromoustakis, 1952**

- Face not slightly elongated……..……..……42.

42. T1 with even punctures (Fig. 6, E)……*Dufourea wolfi* **Ebmer, 1989**

- T1 with irregular punctures ……43.

43. Scutum with fine and coarse punctures (Fig. 6, G) ……..*Dufourea styx* **Ebmer, 1976**

- Scutum with one type of punctures only ……..44.

44. Apical part of tergites hyaline (Fig. 6, H)……..45.

- Apical part of tergites not hyaline……..47.

45. Head with strong green reflects……*Dufourea lusitanica* **Ebmer, 1999**

- Head without green reflects ……..46.

46. Head wider than long; frons very irregularly and sparsely punctuated (Fig. 6, I); basal part of propodeum tesselate; T1 punctuated with 0.5-1 puncture interspace ……..***Dufourea gaullei*** **Vachal, 1897**

- Head rounded; frons evenly punctuated (Fig. 6, J); basal part of propodeum shiny (Fig. 6, K); T1 sparsely punctuated with 1 or more puncture interspace ……..***Dufourea halictula*** **(Nylander, 1852)**

47. Basal part of propodeum wide as 2 times mesoscutum; ridge on basal part of propodeum reticulate (Fig. 6, L) ……..***Dufourea inermis*** **(Nylander, 1848)**

- Basal part of propodeum wider than 2 times mesoscutum; ridge on basal part of propodeum linear without ramification (Fig. 6, M) ……..***Dufourea coeruleocephala*** **Morawitz, 1872**

48. Head hair black (Fig. 6, N); median femora enlarged like a leaf on ventral view; median tibia concave (Fig. 6, O) ……***Dufourea paradoxa*** **(Morawitz, 1867)**

- Head hair not black; tibia and femora with usual shape …….. 49.

49. Vertex angulated forming a squared head (Fig. 6, P) ……***Dufourea longiglossa*** **Ebmer, 1993**

- Vertex rounded ……50.

50. Elongated head, longer than wide (Fig. 6, Q) ……***Dufourea iris*** **Ebmer, 1987**

- No elongated head……51.

51. Green reflects on head and scutum (Fig. 6, R) ……..***Dufourea alpina*** **Morawitz, 1865**

- No green reflects on head and scutum ……52.

52. Barely no puncture on T1, extremely fine for the ones on T1 (Fig. 6, S) ……..***Dufourea dentiventris*** **(Nylander, 1848)**

- Punctures fine but well present on T1……53.

53. Superior part of the clypeus forming like a U without puncture (Fig. 6, T)……..***Dufourea trautmanni*** **Dusmet, 1935**

- Superior part of the clypeus without U shape with puncture……54.

54. Clypeus with sparse punctures; tergite black to brown (Fig. 6, U) ……***Dufourea graeca*** **Ebmer, 1976**

- Clypeus with dense punctures; tergite light red ……***Dufourea fortunata*** **Ebmer, 1993**

55. First and second labial palp at least five times bigger than the fourth (***Rophites***) (Fig. 7, B)……56.

- First and second labial palp two times or less bigger than the fourth (***Rhophitoides***) (Fig. 7, E)……62.

56. 6 spines on the frons, forming 2 rows, upper spines of the frons grouped by two; head two times larger than long (Fig. 6, V) ……***Rophites hartmanni*** **Friese, 1902**

- At least 10 spines on the frons ……57.

57. Spines positioned above the median ocellus and irregularly arranged; vertex not elevated, less than 1 ocelli high (Fig. 6, W) …… ***Rophites hellenicus*** **Ebmer, 1984**

- Spines positioned below the median ocelus; vertex elevated, 1 ocelli or higher ……58.

58. Spines regularly arranged in two rows, forming a clear V-shaped structure and strongly implanted in clypeus; spines red to brown-black (Fig. 7, A)……***Rophites thracius*** **Ebmer, 1993**

- Spines not arranged in clear V-shape in two rows and not strongly implanted in the clypeus; spines black or white ……59.

59. Clypeus elevated in the middle; spines arranged in a V-shaped in three rows (Fig. 7, B); scutum and scutellum scarcely punctuated ……***Rophites clypealis*** **Schwammberger, 1976**

- Clypeus flat, not elevated. More than 20 spines on the frons. Scutum and scutellum densely punctuated……60.

60. Bugle on the frons; spines separated from each other by less than one spine diameter; vertex rounded.***Rophites leclercqi*** **Schwammberger, 1971**

- Flat frons; spines separated from each other by more than one spine diameter; vertex rectangular……61.

61. Clypeus with dense red-brown hairs, sculptures on the clypeus are not visible due to the hairs density (Fig. 7, C) ……..***Rophites quinquespinosus*** **Spinola, 1808**

- Clypeus with loose yellow hairs, sculptures on the clypeus are visible (Fig. 7, D)……..***Rophites algirus*** **Pérez 1895**

62. Frons concave and shiny without punctation; yellow hairs (Fig. 7, E) ……..***Rhophitoides epiroticus*** **Schwammberger, 1975**

- Frons without depression and chagrinated; hairs white (Fig. 7, F) .....***Rhophitoides canus*** **(Eversmann, 1852)**

4.4 Map of sampled Rophitinae in Europe

The map of European Rophitinae (Fig. 3) highlights significant sampling density, particularly across Central and Western Europe. The map also reveal regional gaps in Eastern Europe, Balkans, Italy, Western France and Nothern Germany.

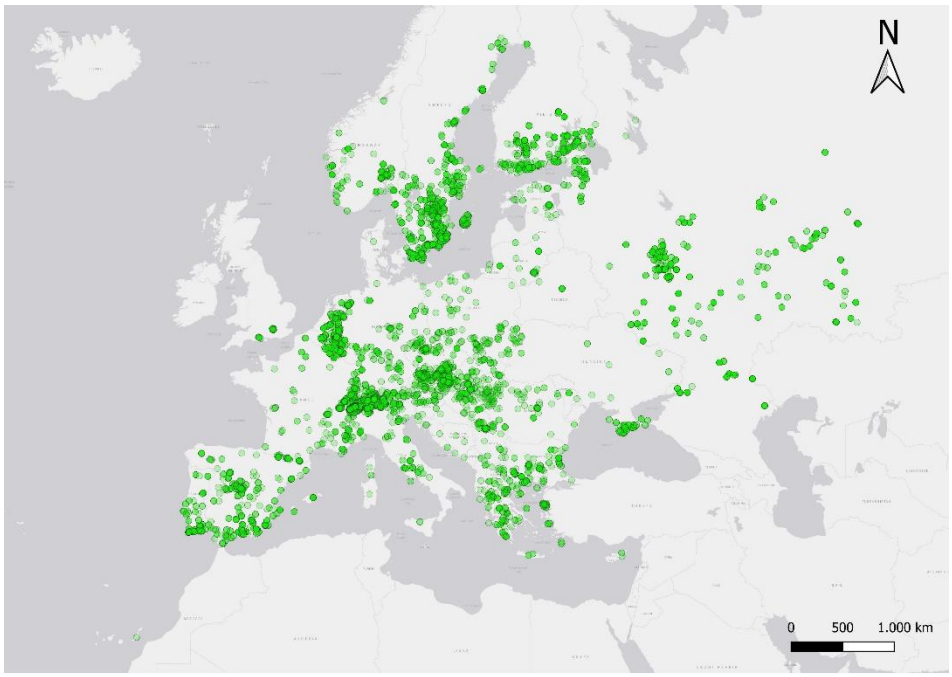

Figure 3: Map of sampled Rophitinae from Sentil *et al.*, 2026. Each point represents 1 specimen. 11017 specimens, collected between 1877 and 2022, are mapped.

5. Discussion and conclusion

5.1 Taxonomy

The lack of identification tools and a clear taxonomy represents a major issue for insect conservation (Cardoso et al., 2011). A strong taxonomic framework is required to address the different biodiversity shortfalls. Without reliable species identification, it is impossible to establish conservation plans targeting specific taxa. An illustrated key to European Rophitinae, together with diagnoses, is provided in this study in order to facilitate identification. Several keys already exist for particular genera (i.e. Ebmer, 1984; Astafurova, 2011) or for specific regions (i.e.: Amiet, 1999; Astafurova, 2014), but no recent synthesis has been produced at a European scale. Taxonomic uncertainties also affect ecological and conservation studies, as invalid identifications may lead to incorrect distribution records, incorrect host-plant associations and unreliable conservation assessments (Vázquez-Ramírez et al., 2025; Vogel Ely et al., 2017).

Basic taxonomic knowledge remains incomplete for several taxa for European Rophitinae. Some species are still known from only one sex or with unresolved taxonomic boundaries. Such deficiencies contribute directly to the Linnean shortfall. The description of the female of *Rophites thracius* partially resolves the Linnean shortfall in Europe. The only species showing a similar spine pattern is *Rophites gruenwaldti*, which occurs in eastern Russia, Mongolia, and China (Astafurova, 2011). Discovery and description of unknown sexes remain crucial in bee taxonomy. Particularly, in poorly studied groups, sexual dimorphism may complicate species identification.

Despite this description, important gaps remain within European Rophitinae. The male of *Rophites leclerqi* is still undescribed. Further investigations need to be done in museum collection but also on the field, especially in Greece, Bulgaria, Türkiye, where the female was found. The investigations for the male in the field have to be done in July or a little bit before, as male emerge before female. The host plant to target is principally Campanulaceae but male could forage other plant. Further investigations on several subspecies are also required to confirm their taxonomic status. The Darwinian shortfall is one of important shortfall for the group. Molecular data, and particularly DNA barcoding, are needed to delimit species and subspecies and associate sex into a same species (Sheffield *et al.*, 2009). Currently, European Rophitinae are severely underrepresented in genetic databases such as BOLD. Subgeneric delimitations also require confirmation through molecular analyses, as they are currently based on the morphology

of the labial palps (Ebmer, 1984). However, barcoding alone is not sufficient for species discovery without detailed morphological expertise (Schmidt *et al.*, 2015). Integrative taxonomy combining morphology, molecular data and ecology will thus be necessary to resolve species boundaries for European Rophitinae.

5.2 Ecology

The Eltonian shortfall is one of the least critical shortfall for European Rophitinae. Host plant preferences are quite well documented and confirmed in this study. Following criteria about lectisim of Müller & Kuhlmann (2008), several Rophitinae species exhibit oligolectic behaviour. *Dufourea alpina, Dufourea inermis*, and males of *Rophites algirus* are oligolectic on Campanulaceae. Females of *Rophites algirus* are oligolectic on Lamiaceae. *Dufourea trautmanni* appears polylectic, although it shows a strong preference for Campanulaceae, whereas *Dufourea minuta* displays oligolecty on *Leontodon* species. *Dufourea gaullei* males are oligolecticon Ranunculaceae. *Systropha grandimargo* and *Systropha planidens* is polylectic, with approximately 50% of its pollen spectrum composed of Convolvulaceae. Except for males of *Rophites algirus* and *Dufourea gaullei*, the obtained data were consistent with the host plants previously reported for these species.

The pollen collection observed in males of *Rophites algirus* and *Dufourea gaullei* should nevertheless be interpreted cautiously. Unlike females, males do not actively collect pollen for larval provisioning and mainly forage for nectar (Roswell et al., 2019). Consequently, the pollen found on their bodies is acquired accidentally during nectar foraging or while resting inside flowers. Brennan et al. (2026) showed that male bees tend to carry a more diverse pollen diversity because they are not allogroomed by workers after resting periods. Phenological differences between sexes may also contribute to these difference. Males generally emerge earlier than females and therefore may not have access to the same floral resources (Roswell et al., 2019). In addition, males tend to visit a wider diversity of flowers and forage over bigger distances than females, collecting therfore more diverse pollen (Smith et al., 2019; Tang et al., 2019). These differences between males and females highlight the importance of considering difference between sex in ecological behaviours when defining floral specialization in bees.

The extent of the Wallacean shortfall varies between regions in Europe: some are well sampled when other are undersampled. Several cluster of sampling, with high species diversity, were identified, particularly in the Alps, Greece, and the Iberian Peninsula. These results are consistent with the general distribution pattern of wild bee diversity in Europe, which show

higher diversity levels in southern and Mediterranean regions (Leclercq et al., 2023). Mediterranean regions are recognized as major centers of bee diversity due to their climatic heterogeneity, topographic complexity, and high plant diversity, which may explain the high richness of Rophitinae observed in these areas (Martín-Vélez & Abellán, 2022; Médail & Quezél, 1999). The Wallacean shortfall appears to be particularly pronounced in the Balkans and Eastern Europe, mainly because of sampling biases. Multiple factors may explain these biases. Geopolitical instability can strongly limit field sampling efforts and access to suitable habitats. In addition, the lack of collectors and regional taxonomic experts may contribute to these knowledge gaps (Guéorguiev & Ljubomirov, 2009; Patiny et al., 2009; Reverté et al., 2023; Wetzel et al., 2018). Regional specialists are particularly important because they possess knowledge about suitable habitats and local fauna, facilitating targeted sampling efforts (Cardoso et al., 2011). Countries with stronger financial support for biodiversity research also tend to benefit from more intensive and efficient sampling programs (Leclercq et al., 2023). Another factor influencing the apparent rarity of Rophitinae is their morphology and size. With the exception of *Systropha* and some *Dufourea*, most European Rophitinae are represented by fewer than 100 occurrence records. These bees are generally small, usually less than one centimetre long, and mostly dark-coloured. They can easily be confused with genera such as *Lasioglossum* or *Panurgus*, which may result in misidentifications or specimens being ignored during field collections. In general, small wild bees are more poorly sampled than bigger bees (Cardoso et al., 2011). As a consequence, the current distribution maps of many Rophitinae reflect uneven sampling effort rather than their true distribution. In addition to distribution gaps, the Prestonian shortfall also remains important for Rophitinae. Abundance data are unavailable for most species. Consequently, it remains difficult to determine whether species are rare or simply undersampled.

The rarity of several Rophitinae species may also be linked to the availability of suitable habitats. Most species nest in sandy habitats located near forests or in steppe-like environments. These habitats are becoming increasingly fragmented and are declining throughout Europe, reducing nesting opportunities for Rophitinae and other ground-nesting bees (Exeler et al., 2009; Kajtoch et al., 2016; Markl et al., 2022). As many Rophitinae species are also floral specialists, habitat degradation may simultaneously affect nesting resources and food availability, increasing their vulnerability to environmental changes (Bogusch et al., 2020).

The IUCN status of several species has changed between 2014 and 2026 (Michez et al., 2026; Nieto et al., 2014). Many species are now considered more threatened than previously estimated due to improved knowledge and increased sampling efforts. Conversely, the improved understanding of

Systropha species has resulted in a reassessment of their conservation status from Vulnerable to Least Concern. More generally, pollen specialists are considered particularly vulnerable to environmental perturbations, especially in cases of phenological mismatches with their host plants (Weaver & Mallinger, 2022). Monolectic species, such as *Dufourea halictula*, are especially vulnerable because they depend on a single floral resource to feed larvae. As specialist bees depend on a limited number of plants, any decline affecting these resources may rapidly impact their long-term population viability.

The Hutchinsonian shortfall is also present for Rophitinae and for all of non-domesticated bees species. In fact, only domesticated species of bees were deeply studied for tolerance for abiotic and biotic. conditions (Marshall *et al.*, 2024). Most of wild bees being ground nesting, gap of knowledge are present about their maintenance in artificial nest in laboratory and thus their abiotic tolerence (Leonard & Harmon-Threatt, 2019).

Finally, the Keartonian shortfall appears to be more pronounced for rare species, for which the limited availability of material constrains the production of high-quality images. In insect taxonomy, rare taxa are often represented by only a few specimens, sometimes distributed across institutions or accessible only through specialist collections (Marshall *et al.*, 2024). Moreover, although taxonomists sometimes provide photographs of specimens from their collections, image quality or angle of capture may not allow diagnostic characters to be reliably distinguished.

The availability of specimens, and particularly of holotypes, remains a major challenge for ensuring the quality and reliability of taxonomic research on poorly known groups. The retention of holotypes in private collections is increasingly difficult to justify in the context of modern open science practices. Broad access to type material is essential for the verification of taxonomic hypotheses, the reproducibility of scientific studies and the advancement of knowledge. Facilitating access to specimens and associated data is therefore a necessary step toward developing effective research and conservation actions for biodiversity.

Beyond European Rophitinae, highlighted biodiversity shortfalls illustrate broader challenges affecting the conservation of wild bees and insects. Taxonomic uncertainties, gap in ecological knowledge or uneven sampling effort remain widespread limitations for many non-domesticated pollinators (Marshall *et al.*, 2024). Improving taxonomic expertise and ecological monitoring should be considered a priority for conservation biology due to the importance of pollinators. More integrative approaches will be essential for conservation strategies for wild bees.

Future studies should combine standardized sampling, molecular analyses and monitoring. That will permit in to improve our understanding of species distributions, floral specialization and population dynamics. Overall, this study highlights the importance to combine taxonomy, ecology and biogeography to improve our understanding of wild bees for supporting future conservation strategies.

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Appendices

Appendix 1: Figures of the identification key

Figure 4: Diagnostic characters used in identification key of European Rophitinae. **A.** Head of *D. traumanni* male **B.** Antenna of *D. gaullei* male **C.** Head of *D. gaullei* male **D.** Antenna of *D. halictula* male **E.** Antenna of *D. balearica* male (derived from Ebmer, 2015) **F.** Antenna of *D. minuta* male **G.** Head of *D. wolfi* male **H.** Tergites of *D. wolfi* male **I.** Head of *D. similis* male **J.** Tergites of *D. similis* male **K.** Head of *R. quinquespinous* male **L.** S6 of *R. quinquespinous* male **M.** Head of *R. algirus* male **N.** S6 of *R. algirus* male **O.** Head of *R. hartmanni* male **P.** Antenna of *R. hellenicus* male **Q.** Antenna of *Rh. epiroticus* male **R.** Tergite of *Rh. epiroticus* male **S.** Tergites of *S. curvicornis* female **T.** Tergites of *S. grandimargo* female **U.** Tergites of *S. planidens* female **V.** Head of *S. planidens* female **W.** Head of *S. anatolica* female **X.** Scutum of *D. similis* female **Y.** Tergites of *D. similis* female

Figure 5: Diagnostic characters used in identification key of European Rophitinae. **A.** Antenna of *S. curvicornis* male **B.** Sternites of *S. curvicornis* male **C.** Wing of *S. grandimargo* male **D.** S8 of *S. grandimargo* male **E.** Wing of *S. planidens* male **F.** S8 of *S. planidens* male **G.** Sternites of *S. planidens* male **H.** S8 of *S. anatolica* male **I.** Head of *D. alpina* male **J.** Propodeum of *D. alpina* male **K.** Antenna of *D. styx* male (derived from Ebmer, 1984) **L.** S6 of *D. styx* male (derived from Ebmer, 1984) **M.** S5 of *D. dentiventris* male **N.** S6 of *D. graeca* male **O.** S6 of *D. fortunata* male (derived from Ebmer, 1993)**P.** Antenna of *D. paradoxa* male **Q.** S6 of *D. inermis* male **R.** Head of *D. cypria* male **S.** T1 of *D. cypria* male **T.** Femur of *D. paradoxa* male **U.** Tibia of *D. paradoxa* male **V.** S4 of *D. paradoxa* male **W.** Head of *D. longiglossa* male **X.** Antenna of *D. merceti* male

Figure 6: Diagnostic characters used in identification key of European Rophitinae. **A.** Head of *D. similis* female **B.** Head of *D. minuta* female **C.** Propodeum of *D. minuta* female **D.** Scutum of *D. wolfi* female **E.** T1 of *D. wolfi* female **F.** Head of *D. cypria* female **G.** Scutum of *D. styx* female **H.** Tergites of *D. halictula* female **I.** Head of *D. gaullei* female **J.** Head of *D. halictula* female **K.** Propodeum of *D. halictula* female **L.** Propodeum of *D. inermis* female **M.** Propodeum of *D. coeruleocephala* female **N.** Head of *D. paradoxa* female **O.** Tibia of *D. paradoxa* female **P.** Vertex of *D. longiglossa* female **Q.** Head of *D. iris* female **R.** Head and scutum of *D. alpina* female **S.** T1 of *D. dentiventris* female **T.** Head of *D. trautmanni* female **U.** Head of *D. graeca* female **V.** Head of *R. hartmanni* female **W.** Head of *R. hellenicus* female

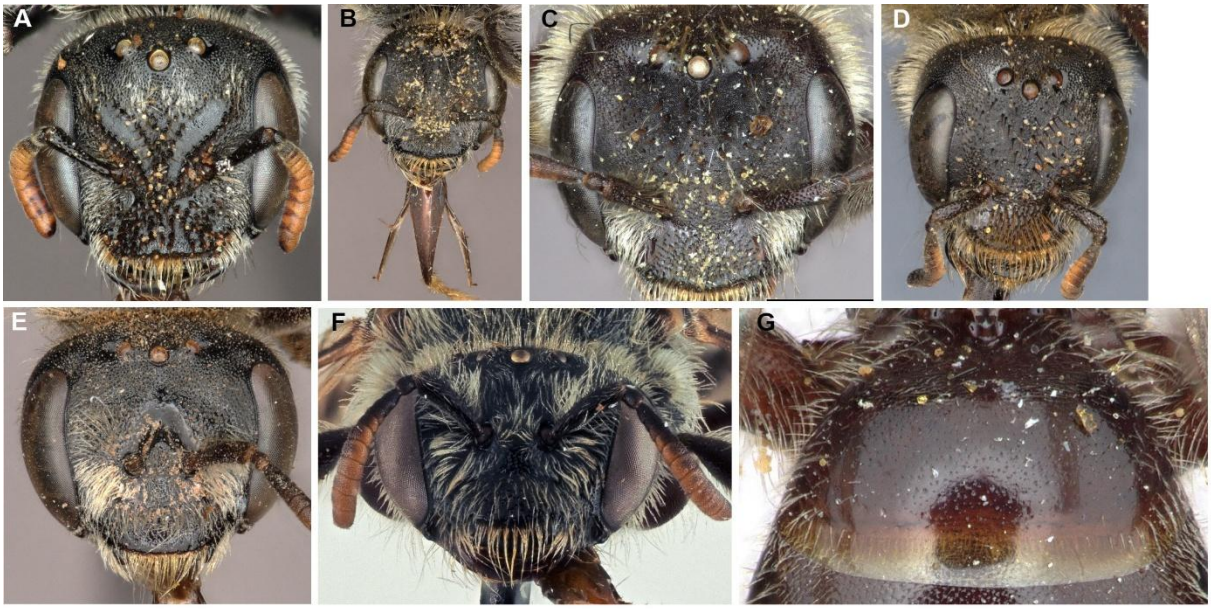

Figure 7: Diagnostic characters used in identification key of European Rophitinae. **A.** Head of *R. thracius* female **B.** Head of *R. clypealis* female **C.** Head of *R. quinquespinosus* female **D.** Head of *R. algirus* female **E.** Head of *Rh. epiroticus* female **F.** Head of *R. canus* female **G.** T1 of *D. alpina* female

Appendix 2: Diagnoses

Dufourea (*Cephalictoides*) *paradoxa* (Morawitz, 1867)

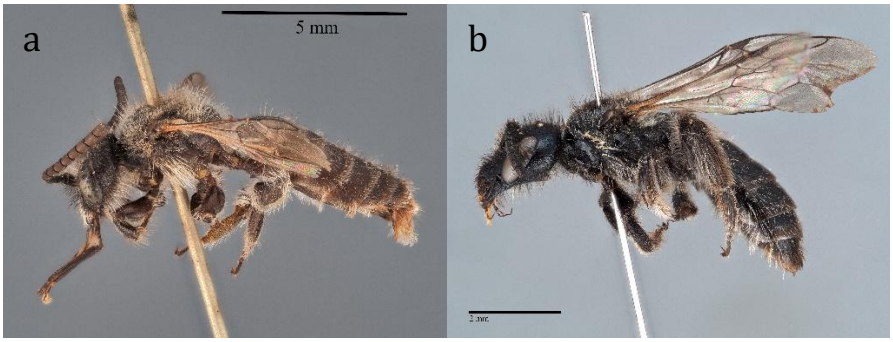

Figure 8. Habitus *Dufourea* (*Cephalictoides*) *paradoxa* a) male. b) female.

Male: *Dufourea paradoxa* belongs to the subgenus *Cephalictoides*, as indicated by its enlarged median tibia, hind and median femora. Another trait that distinguishes *D. paradoxa* from other European *Dufourea* species is the presence of well concave rhinaria along the entire length of the antennal segments.

Female: *Dufourea paradoxa* belongs to the subgenus *Cephalictoides,* as indicated by its concave tibia. Additionally, *D. paradoxa* have black hairs on the head.

Dufourea (*Cyprirophites*) *coeruleocephala* Morawitz, 1872

Male: *Dufourea coeruleocephala* belongs to the subgenus *Cyprirophites*, as indicated by its long maxillary palps, which exceed the length of the apex of the glossa. It can be distinguished from other *Cyprirophites* species by its sparse punctation on scutum, with interspaces larger than two punctures diameter, and its distinct hyaline coloration of the apical part of the tergites, resulting in a nearly translucent margin.

Female: *Dufourea coeruleocephala* belongs to the subgenus *Cyprirophites*, as indicated by its long maxillary palps exceeding the apex of the glossa. It can be distinguished from *D. styx* by its even size of the punctures on the scutum. Furthermore, *D. coeruleocephala* is differentiated from *D. iris* by the presence of coarse punctation on T1, and from *D. cypria* by a clear median line on the basal part of the scutum that extends nearly to its center.

Dufourea (*Cyprirophites*) *cypria* Mavromoustakis, 1952

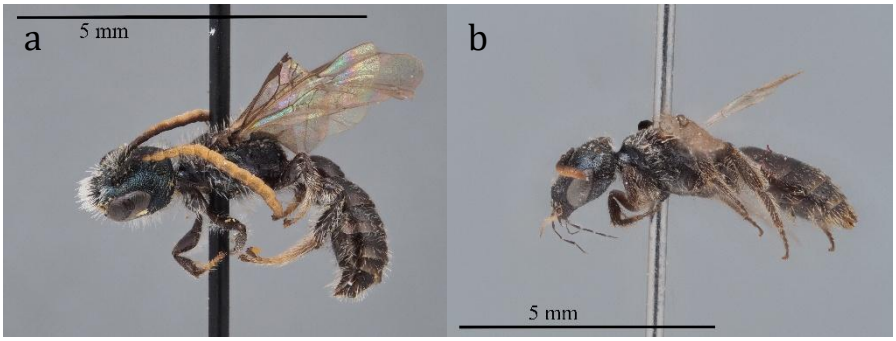

Figure 9. Habitus *Dufourea* (*Cyprirophites*) *cypria* a) male b) female.

Male: *Dufourea cypria* belongs to the subgenus *Cyprirophites*, as indicated by its long maxillary palps, which exceed the length of the apex of the glossa. It can be distinguished from other *Cyprirophites* species by its raised vertex, measuring more than two times the diameter of the middle ocellus and by the interlaced punctation on T1 and T2.

Female: *Dufourea cypria* belongs to the subgenus *Cyprirophites*, as indicated by its long maxillary palps exceeding the apex of the glossa. It can be distinguished from other *Cyprirophites* species by its raised vertex, more than two times the diameter of the middle ocellus and by the presence of interlaced punctation on T1 and T2.

Dufourea (*Cyprirophites*) *iris* Ebmer, 1987

Figure 10. Habitus *Dufourea* (*Cyprirophites*) *iris* female

Male: *Dufourea iris* belongs to the subgenus *Cyprirophites*, as indicated by its long maxillary palps, which exceed the length of the apex of the glossa. It can be distinguished from *D. coeruleocephala* and *D. styx* by the presence of dense punctation on the scutum, with interspace less than one puncture. *Dufourea iris* is differentiated of *D.cypria* by brown antenna on the two sides and without interlaced punctations on T1.

Female: *Dufourea iris* belongs to the subgenus *Cyprirophites*, as indicated by its long maxillary palps exceeding the length of the apex of the glossa. It can be distinguished from other *Cyprirophites* by the presence of a carina in the middle of the frons and very fine punctation on T1.

Dufourea (*Cyprirophites*) *styx* Ebmer, 1976

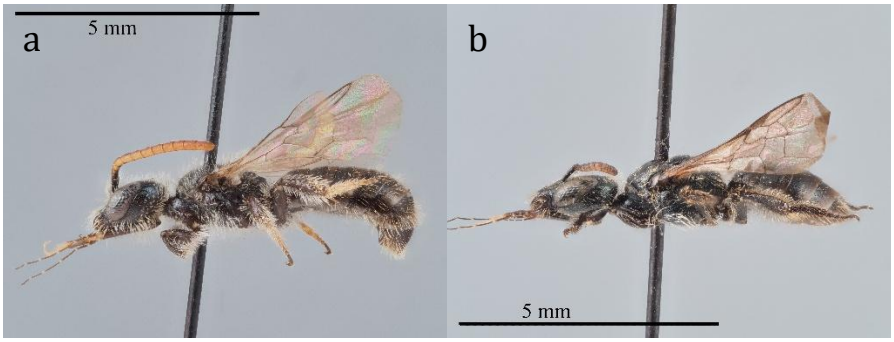

Figure 11. Habitus *Dufourea* (*Cyprirophites*) *styx* a) male b) female.

Male: *Dufourea styx* belongs to the subgenus *Cyprirophites*, as indicated by its long maxillary palps, which exceed the length of the apex of the glossa. It can be distinguished from *D. coeruleocephala* by its densely punctuate scutum, with interspaces between punctures measuring less than two diameters and its uniform coloration of the tergites. *Dufourea styx* is differentiated from *D. iris* by its barely visible rhinaria and the absence of swellings on S6. Furthermore, it is distinct from *D. cypria* by a vertex not elevated, measuring less than two times the diameter of the middle ocellus, and by the well-separated punctures on T1 and T2.

Female: *Dufourea styx* belongs to the subgenus *Cyprirophites*, as indicated by its extremely long maxillary palps exceeding the apex of the glossa. It can be distinguished from other *Cyprirophites* by the presence of two distinct sizes of punctation on the scutum.

Dufourea (*Dentirophites*) *gaullei* Vachal, 1897

Figure 12. Habitus *Dufourea* (*Dentirophites*) *gaullei* male.

Male: *Dufourea gaullei* belongs to the subgenus *Dentirophites*, as indicated by its very short mouthparts, particularly the labial palps which are enlarged and flattened. As with other males of *Dentirophites*, it also possesses a temporal tooth. *Dufourea gaullei* is distinct from *D. lusitanica* by the presence of a tooth on A4-5 and by having tergites that are entirely brown.

Female: *Dufourea gaullei* belongs to the subgenus *Dentirophites*, as indicated by its very short mouthparts and the enlarged, flattened labial palps. It can be distinguished from *D. lusitanica* by the presence of wrinkles on the apical part of the propodeal triangle and by the entirely brown coloration of the tergites.

Dufourea (*Dentirophites*) *lusitanica* Ebmer, 1999

Figure 13. Habitus *Dufourea* (*Dentirophites*) *lusitanica* female.

Male: *Dufourea lusitanica* belongs to the subgenus *Dentirophites*, as indicated by its very short mouthparts, specifically the enlarged and flattened labial palps. As with other males of *Dentirophites*, it possesses a temporal tooth. *Dufourea lusitanica* is distinct from *D. gaullei* by the absence of a tooth on A4-5, the presence of green reflections on the head and its red coloration on the basal part of the tergites.

Female: *Dufourea lusitanica* belongs to the subgenus *Dentirophites*, as indicated by its very short mouthparts and the enlarged, flattened labial palps. It can be distinguished from *D. gaullei* by the green reflections on the head, a smooth apical part of the propodeal triangle and its reddish coloration of the tergites.

Dufourea (*Dufourea*) *alpina* Morawitz, 1865

Figure 14. Habitus *Dufourea* (*Dufourea*) *alpina* a) male b) female

Male: *Dufourea alpina* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. It is distinct from other species of the subgenus by the presence of a carina on the basal part of S6 and green coloration on its frons.

Female: *Dufourea alpina* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. It is distinct from *D. minuta*, *D. balearica*, and *D. similis* by its green reflections on the head and a scutum with dense punctation, where interspaces are less than two punctures. It can be distinguished from *D. halictula* and *D. wolfi* by its green reflections on the head and the fine punctation on T1. Furthermore, *D. alpina* is distinct from *D. fortunata* and *D. trautmanni* by its green reflections on the head and the uniform brown to black coloration of the tergites, without hyaline coloration on the apical part.

Dufourea (*Dufourea*) *balearica* Ebmer, 2015

Male: *Dufourea balearica* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. It is distinct from *D. alpina*, *D. fortunata*, *D. halictula*, *D. similis*, *D. trautmanni*, and *D. wolfi* by its rhinaria reaching half of the antennal segment. Furthermore, *D. balearica* is distinct from *D. minuta* by having a head wider than it is long and by its rhinaria beginning on A7.

Female: *Dufourea balearica* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. It is distinct from *D. alpina*, *D. fortunata*, *D. halictula*, *D. trautmanni*, and *D. wolfi* by a scutum with sparse punctation, where interspaces exceed two punctures. It is further distinguished from *D. minuta* by the absence of a U-shape on the clypeus and the presence of a strong carina on the frons. Additionally, *D. balearica* is distinct from *D. similis* by having a linear carina on the frons that does not form a V-shape from the antennal sockets to the middle of the frons.

Dufourea (*Dufourea*) *fortunata* Ebmer, 1993

Male: *Dufourea fortunata* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. *D. fortunata* is differentiated from other species within the subgenus *Dufourea* by the presence of a keel-shaped swelling on S6.

Female: *Dufourea fortunata* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. It is distinct from *D. minuta*, *D. balearica*, and *D. similis* by its dense punctation on the scutum, where interspaces measure less than two punctures. It can be distinguished from *D. halictula* and *D. wolfi* by its fine punctation on T1. Furthermore, *D. fortunata* is distinct from *D. alpina* and *D. trautmanni* by its reddish coloration present on T1 through T3.

Dufourea (*Dufourea*) *halictula* (Nylander, 1852)

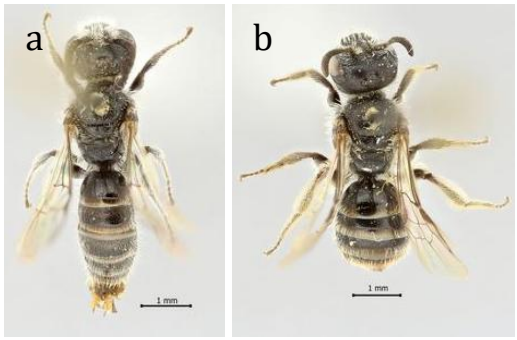

Figure 15. Habitus *Dufourea* (*Dufourea*) *halictula* a) male b) female

Male: *Dufourea halictula* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. *Dufourea halictula* differs from other species of the subgenus *Dufourea* by the presence of flat rhinaria covering the entire length of the antennal segments.

Female: *Dufourea halictula* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. It is distinct from *D. minuta*, *D. balearica*, and *D. similis* by its dense punctation on the scutum, where interspaces measure less than two punctures. It can be distinguished from *D. alpina*, *D. fortunata*, and *D. trautmanni* by its coarse punctation on T1. Furthermore, *D. halictula* is distinct from *D. wolfi* by the sparsely punctate frons and the tergites, which are hyaline and smooth on the apical part.

Dufourea (*Dufourea*) *minuta* Lepeletier, 1841

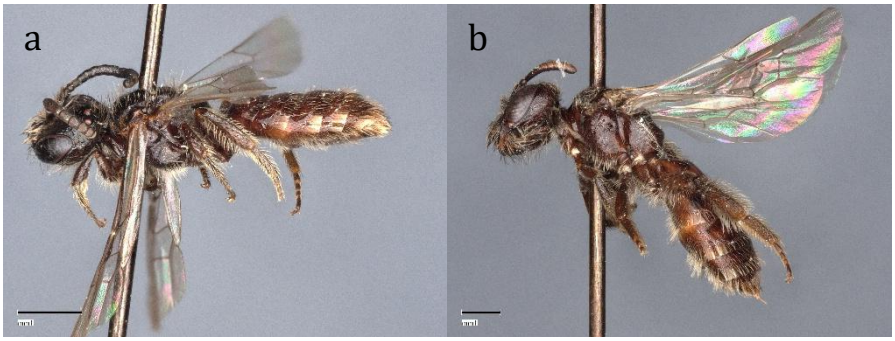

Figure 16. Habitus *Dufourea* (*Dufourea*) *minuta* a) male b) female

Male: *Dufourea minuta* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. It is distinct from *D. alpina*, *D. fortunata*, *D. halictula*, *D. similis*, *D. trautmanni*, and *D. wolfi* by its rhinaria reaching half of the antennal segment. Furthermore, *D. minuta* is distinct from *D. balearica* by having a head that is as long as it is wide and by the rhinaria beginning on A5.

Female: *Dufourea minuta* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. It is distinct from *D. alpina*, *D. fortunata*, *D. halictula*, *D. trautmanni*, and *D. wolfi* by a scutum with sparse punctation, where interspaces measure more than two punctures. Additionally, *D. minuta* is distinct from *D. balearica* and *D. similis* by the presence of a U-shape on the clypeus and the absence of a carina on the frons.

Dufourea (*Dufourea*) *similis* Friese, 1898

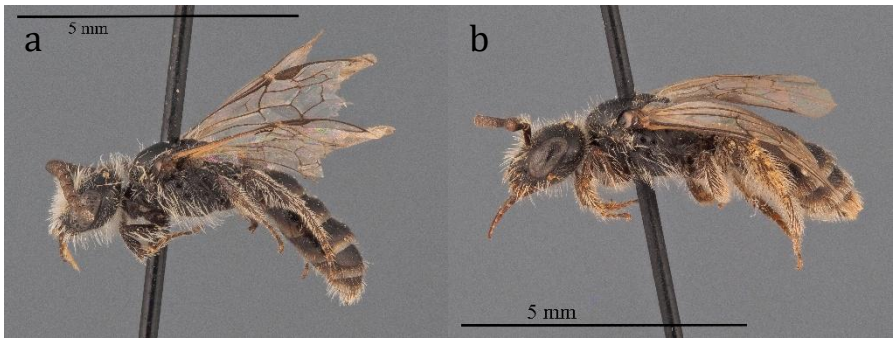

Figure 17. Habitus *Dufourea* (*Dufourea*) *similis* a) male b) female

Male: *Dufourea similis* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. *D. similis* differs from other species within the subgenus *Dufourea* by its hyaline coloration of the apical part of the tergites, which are nearly translucent.

Female: *Dufourea similis* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. It is distinct from *D. alpina*, *D. fortunata*, *D. halictula*, *D. trautmanni* and *D. wolfi* by a scutum with sparse punctation, where interspaces measure more than two punctures. It is further distinguished from *D. minuta* by the absence of a U-shape on the clypeus and the presence of a strong carina on the frons. Additionally, *D. similis* is distinct from *D. balearica* by a carina that forms a V-shape extending from the antennal sockets to the middle of the frons.

Dufourea (*Dufourea*) *trautmanni* Dusmet, 1935

Figure 18. Habitus *Dufourea* (*Dufourea*) *trautmanni* a) male b) female

Male: *Dufourea trautmanni* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. *Dufourea trautmanni* is different from the other bees of the subgenus *Dufourea* by the presence of brown hairs, especially on the head.

Female: *Dufourea trautmanni* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. It is distinct from *D. minuta*, *D. balearica*, and *D. similis* by its dense punctation on the scutum, where interspaces measure less than two punctures. It can be distinguished from *D. halictula* and *D. wolfi* by its fine punctation on T1. Furthermore, *D. trautmanni* is distinct from *D. alpina* and *D. fortunata* by the presence of brown hairs on the head and a U-shaped margin on the clypeus.

Dufourea (*Dufourea*) *wolfi* Ebmer, 1989

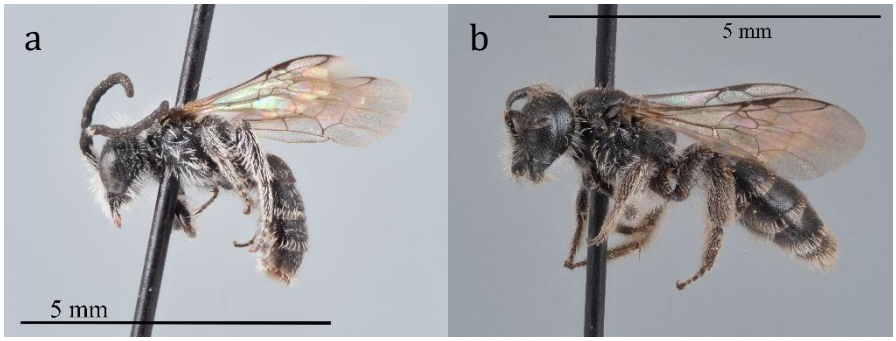

Figure 19. Habitus *Dufourea* (*Dufourea*) *wolfi* a) male b) female

Male: *Dufourea wolfi* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. *Dufourea wolfi* is different from the other bees of the subgenus *Dufourea* by its raised vertex, measuring two times middle ocellus diameter, and its oval-shaped head.

Female: *Dufourea wolfi* belongs to the subgenus *Dufourea*, as indicated by its labial palps reaching MP3. It is distinct from *D. minuta*, *D. balearica*, and *D. similis* by its dense punctation on the scutum, where interspaces measure less than two punctures. It can be distinguished from *D. alpina*, *D. fortunata*, and *D. trautmanni* by its coarse punctation on T1. Furthermore, *D. wolfi* is distinct from *D. halictula* by its densely punctate frons and the tergites, which are uniformly colored and chagrined on the apical part.

Dufourea (*Glossadufourea*) *longiglossa* Ebmer, 1993

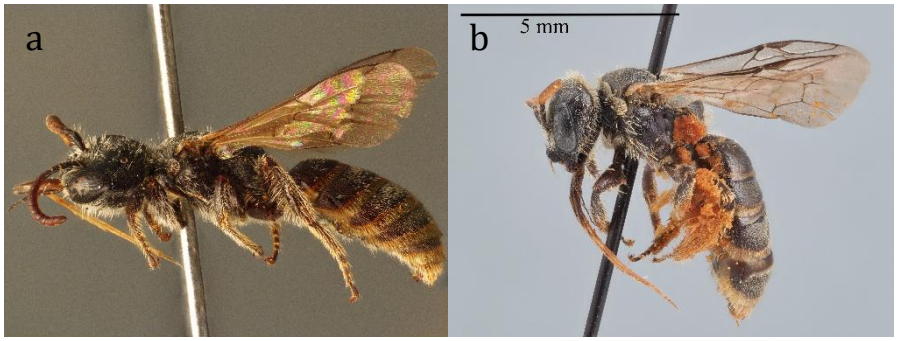

Figure 20. Habitus *Dufourea* (*Glossadufourea*) *longiglossa* a) male b) female

Male: *Dufourea longiglossa* belongs to the subgenus *Glossadufourea*, as indicated by its extremely long glossa paired with shorter palps. Another trait that distinguishes *D. longiglossa* from other European *Dufourea* species is its squared and raised vertex, measuring two times the diameter of the middle ocellus.

Female: *Dufourea longiglossa* belongs to the subgenus *Glossadufourea*, as indicated by its extremely long glossa paired with shorter palps. Another trait that distinguishes *D. longiglossa* from other European *Dufourea* species is its squared and raised vertex, measuring two times the diameter of the middle ocellus.

Dufourea (*Halictoides*) *dentiventris* (Nylander, 1848)

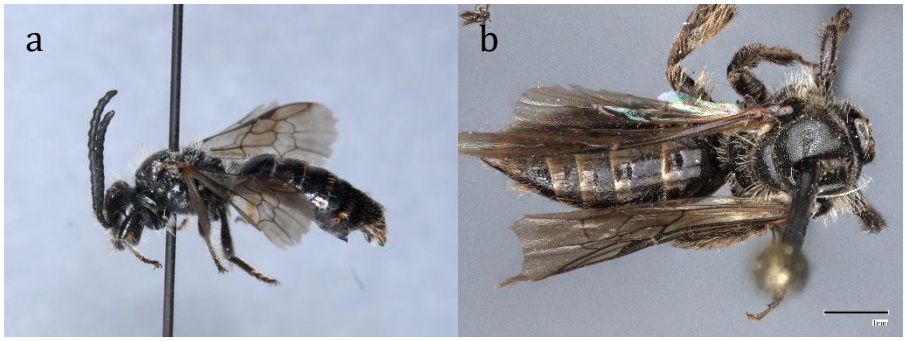

Figure 21. Habitus *Dufourea* (*Halictoides*) *dentiventris* a) male b) female

Male: *Dufourea dentiventris* belongs to the subgenus *Halictoides*, as indicated by LP2 being shorter than LP3-4. *Dufourea dentiventris* is distinct from other *Halictoides* species by the presence of a tooth on the apical part of S5.

Female: *Dufourea dentiventris* belongs to the subgenus *Halictoides*, as indicated by LP2 being shorter than LP 3-4. *Dufourea dentiventris* is distinct from other *Halictoides* by the near absence of punctation on T1.

Dufourea (*Halictoides*) *graeca graeca* Ebmer, 1976

Figure 22. Habitus *Dufourea* (*Halictoides*) *graeca graeca* female

Male: *Dufourea graeca graeca* belongs to the subgenus *Halictoides*, as indicated by LP2 being shorter than the LP3-4. *Dufourea graeca* is distinct from other *Halictoides* species by the absence of a tooth on S5 and the absence of hairs on the middle of S6.

Female: *Dufourea graeca graeca* belongs to the subgenus *Halictoides*, as indicated by LP2 being shorter than the LP3-4. *Dufourea graeca* is distinct from other *Halictoides* by a concave frons and fine punctation that is barely visible on T1.

Dufourea (*Halictoides*) *inermis* (Nylander, 1848)

Figure 23. Habitus *Dufourea* (*Halictoides*) *inermis* female

Male: *Dufourea inermis* belongs to the subgenus *Halictoides*, as indicated by LP2 being shorter than the LP3-4. *Dufourea inermis* is distinct from other *Halictoides* species by the presence of dense hair and the hyaline coloration of the apical part on S6.

Female: *Dufourea inermis* belongs to the subgenus *Halictoides*, as indicated by LP2 being shorter than the LP3-4. *Dufourea inermis* is distinct from other *Halictoides* by its very dense punctation of the frons (with interspaces measuring less than 0.5 punctures) and its well-defined punctation on T1.

Dufourea (*Merrophites*) *merceti* Vachal, 1907

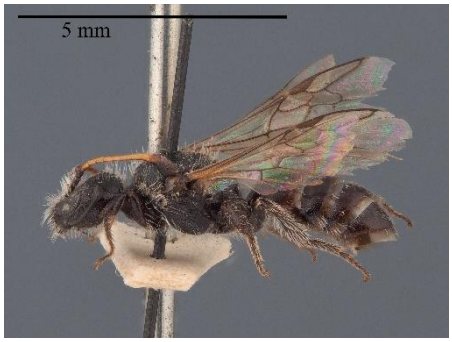

Figure 24. *Dufourea* (*Merrophites*) *merceti* male

Male: *Dufourea merceti* belongs to the subgenus *Merrophites*, as indicated by its extremely long glossa paired with shorter palps. It can be easily distinguished from other *Dufourea* males by the presence of a flattened and enlarged last antennal segment.

Rhophitoides canus (Eversmann, 1852)

Figure 25. *Rhophitoides canus* female

Male: *Rhophitoides canus* is distinguished from *Rhophitoides epiroticus* by its orange coloration of the ventral part of its antennae and the presence of dense hairs on the tergites.

Female: *Rhophitoides canus* is distinguished from *Rhophitoides epiroticus* by a concave frons featuring chagrination and the presence of white hairs.

Rhophitoides epiroticus Schwammberger, 1975

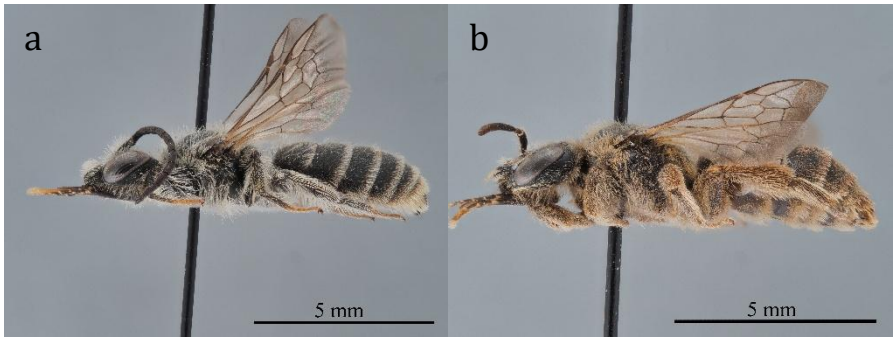

Figure 26. *Rhophitoides epiroticus:* a) male b) female

Male: *Rhophitoides epiroticus* is distinguished from *Rhophitoides canus* by its dark coloration of the ventral part of its antennae and the presence of sparse hairs on the tergites.

Female: *Rhophitoides epiroticus* is distinguished from *Rhophitoides canus* by a flat frons without chagrination and the presence of yellow hairs.

Rophites algirus Pérez, 1895

Figure 27. *Rophites algirus* a) male b) female

Male: *Rophites algirus* is distinguished from *Rophites hellenicus* by the presence of spines on S6. It is distinct from *R. hartmanni* and *R. thracius* by the presence of long hair on the apical part of S6. *Rophites algirus* is further distinguished from *R. clypealis* by a flat clypeus, and from *R. quinquespinosus* by the trapezoidal shape of the apical end of S6. Additionally, it differs from *R. leclerqi* by the absence of two circular lines of hairs on the basal part of S6.

Female: *Rophites algirus* is distinguished from other European *Rophites* species by the presence of dense, fine yellow hairs on the clypeus and three rows of spines forming a weak V-shape on the forehead. It is further characterized by a raised vertex measuring 2.5 times the diameter of the middle ocellus and a linear posterior margin of the vertex.

Rophites clypealis Schwammberger, 1976

Figure 28. *Rophites clypealis* female

Male: *Rophites clypealis* is distinguished from other European *Rophites* species by the presence of a convex clypeus.

Female: *Rophites clypealis* is distinguished from other European *Rophites* by an elevated clypeus that lacks spines and a raised vertex measuring two times the diameter of the middle ocellus.

Rophites hartmanni Friese, 1902

Figure 29. *Rophites hartmanni* a) male b) female

Male: *Rophites hartmanni* is distinguished from *Rophites hellenicus* by the presence of spines on S6. It is distinct from *R. algirus*, *R. clypealis*, *R. quinquespinosus*, and *R. leclerqi* by the presence of short hair on the apical part of S6. Furthermore, *R. hartmanni* is distinguished from *R. thracius* by the absence of two patches of short hair on the basal part of S6.

Female: *Rophites hartmanni* is distinguished from other European *Rophites* species by the absence of spines on the clypeus and the presence of fewer than 10 spines on the head, with these being arranged in two groups of two spines on the frons.

Rophites hellenicus Ebmer, 1984

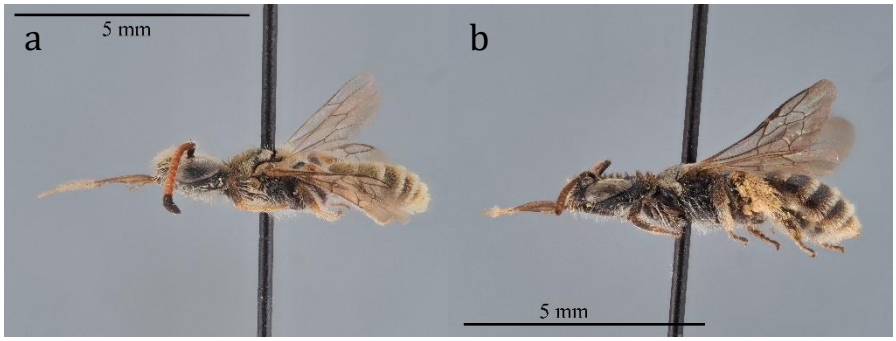

Figure 30. *Rophites hellenicus* a) male b) female

Male: *Rophites hellenicus* is distinguished from other European *Rophites* species by the absence of spines on S6.

Female: *Rophites hellenicus* is distinguished from other European *Rophites* by the presence of more than 40 spines on its frons, which extend upward to reach the middle ocellus.

Rophites leclercqi Schwammberger, 1971

Female: *Rophites leclerqi* is distinguished from other European *Rophites* species by the presence of more than 20 spines on its frons, featuring two specific groups of four spines.

Rophites quinquespinosus Spinola, 1808

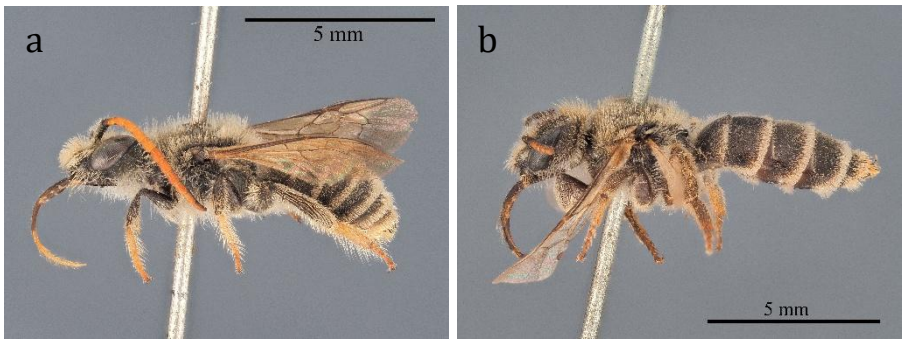

Figure 31. *Rophites quinquespinosus* a) male b) female

Male: *Rophites quinquespinosus* is distinguished from *Rophites hellenicus* by the presence of spines on S6. It is distinct from *R. hartmanni* and *R. thracius* by the presence of long hair on the apical part of S6. It is further distinguished from *R. clypealis* by a flat clypeus and from *R. algirus* by the rounded shape of the apical end of S6. Additionally, *R. quinquespinosus* differs from *R. leclerqi* by the absence of two circular lines of hairs on the basal part of S6.

Female: *Rophites quinquespinosus* is distinguished from other European *Rophites* species by the presence of dense brown hairs on the clypeus and more than 40 spines on the frons.

Rophites thracius Ebmer, 1993

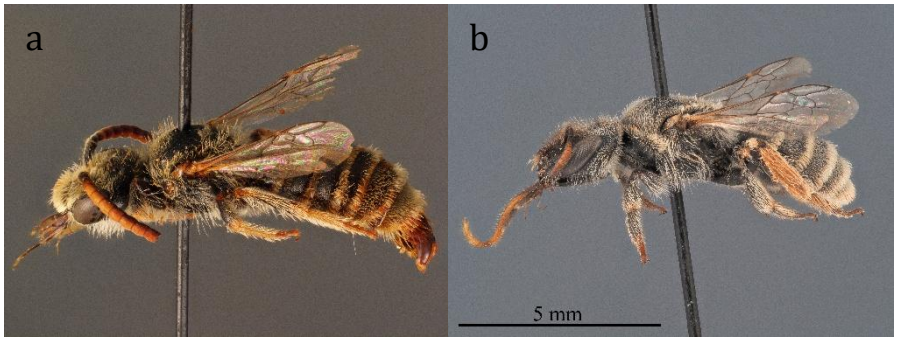

Figure 32. *Rophites thracius* a) male b) female

Male: *Rophites thracius* is distinguished from *Rophites hellenicus* by the presence of spines on S6. It is distinct from *R. algirus*, *R. clypealis*, *R. quinquespinosus*, and *R. leclerqi* by the presence of short hair on the apical part of S6. Additionally, *R. thracius* is distinct from *R. hartmanni* by the presence of two patches of short hair on the basal part of S6.

Female: *Rophites thracius* is distinguished from other European *Rophites* species by the presence of strong brown to red spines on its clypeus and spines arranged in three rows forming a V-shape on the frons.

Systropha anatolica Warncke, 1977

Male: *Systropha anatolica* is distinguished from *Systropha curvicornis* by the presence of truncated teeth on S2, a protuberance on S3, and an S7 with a convex end. *Systropha anatolica* differs from *S. grandimargo* by having a second submarginal cell that is as long as it is wide and the apical part of S8 forming a half-circle. It is further distinguished from *S. planidens* by the presence of yellow hairs on the tergites and a rectangular shape on the apical part of S8.

Female: *Systropha anatolica* is distinguished from *Systropha curvicornis* by having A3 longer than A4 and A5, and brown hairs on T1-2. *Systropha anatolica* differs from *S. grandimargo* by a second submarginal cell that is as long as it is wide, a single size of punctation on the tergites, and a light appearance of the tergites. It is distinguished from *S. planidens* by the sparse and fine punctation on the frons.

Systropha curvicornis (Scopoli, 1770)

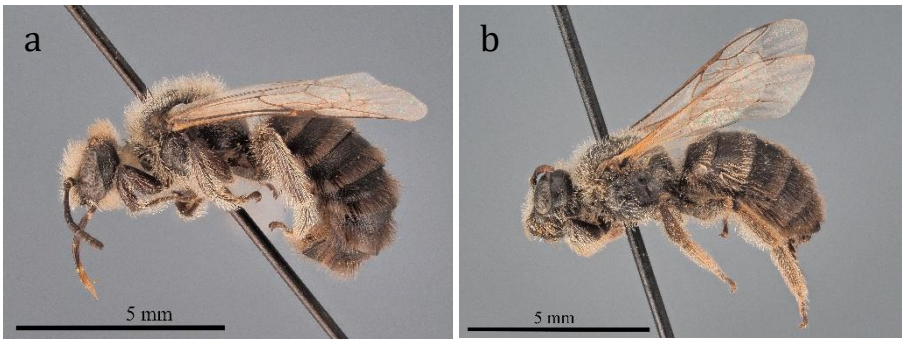

Figure 33. *Systropha curvicornis* a) male b) female

Male: *Systropha curvicornis* is distinguished from other European *Systropha* species by the presence of sharp teeth on S2 and S3, and an S7 with a concave end.

Female: *Systropha curvicornis* is distinguished from other European *Systropha* by having A3 as long as A4 and A5 combined, and the presence of grey or dark hairs on T1-2.

Systropha grandimargo Pérez, 1905

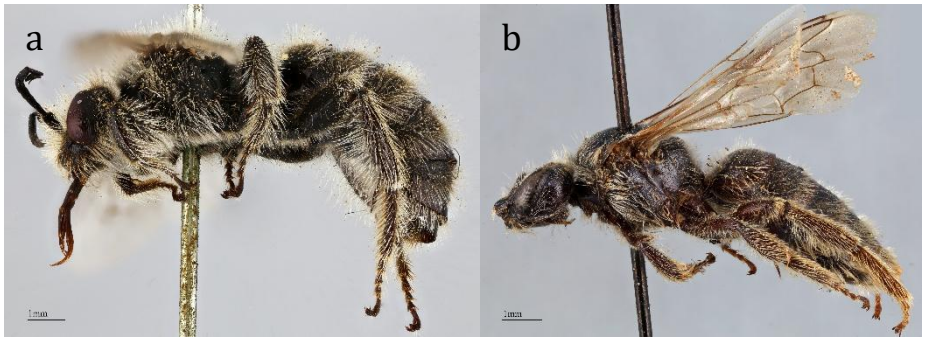

Figure 34. *Systropha grandimargo* a) male b) female

Male: *Systropha grandimargo* is distinguished from *Systropha curvicornis* by the presence of truncated teeth on S2, a protuberance on S3, and an S7 with a convex end. It differs from *S. anatolica* and *S. planidens* by having a second submarginal cell that is longer than it is wide and an apical part of S8 that forms a trapezoid in ventral view.

Female: *Systropha grandimargo* is distinguished from *Systropha curvicornis* by having A3 longer than A4 and A5, and the presence of brown hairs on T1-2. It is further distinguished from *S. anatolica* and *S. planidens* by a second submarginal cell that is longer than wide, two distinct sizes of punctation on the tergites, and a dark appearance of the tergites.

Systropha planidens Giraud, 1861

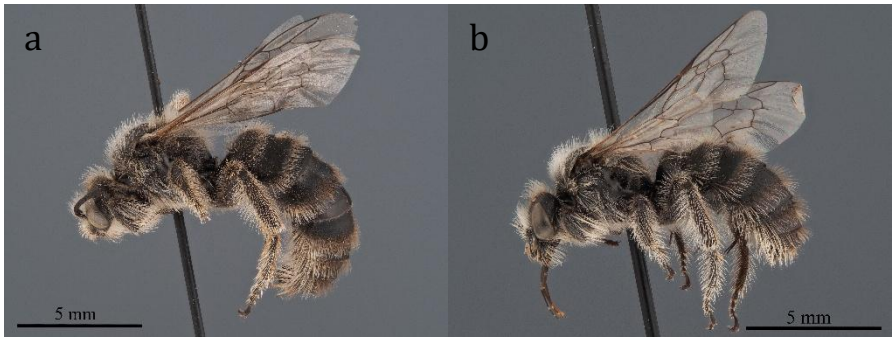

Figure 35. *Systropha planidens* a) male b) female

Male: *Systropha planidens* is distinguished from *Systropha curvicornis* by the presence of truncated teeth on S2, a protuberance on S3, and an S7 with a convex end. It differs from *S. grandimargo* by having a second submarginal cell that is as long as it is wide and the apical part of S8 forming a half-circle. Furthermore, *S. planidens* is distinguished from *S. anatolica* by the presence of brown hairs on the tergites and the half-circle shape of the apical end of S8.

Female: *Systropha planidens* is distinguished from *Systropha curvicornis* by having A3 longer than A4 and A5, and brown hairs on T1-2. It differs from *S. grandimargo* by a second submarginal cell that is as long as it is wide, a single size of punctation on the tergites, and a light appearance of the tergites. *Systropha planidens* is distinguished from *S. anatolica* by the dense and coarse punctation on the frons.

Appendix 3: Maps

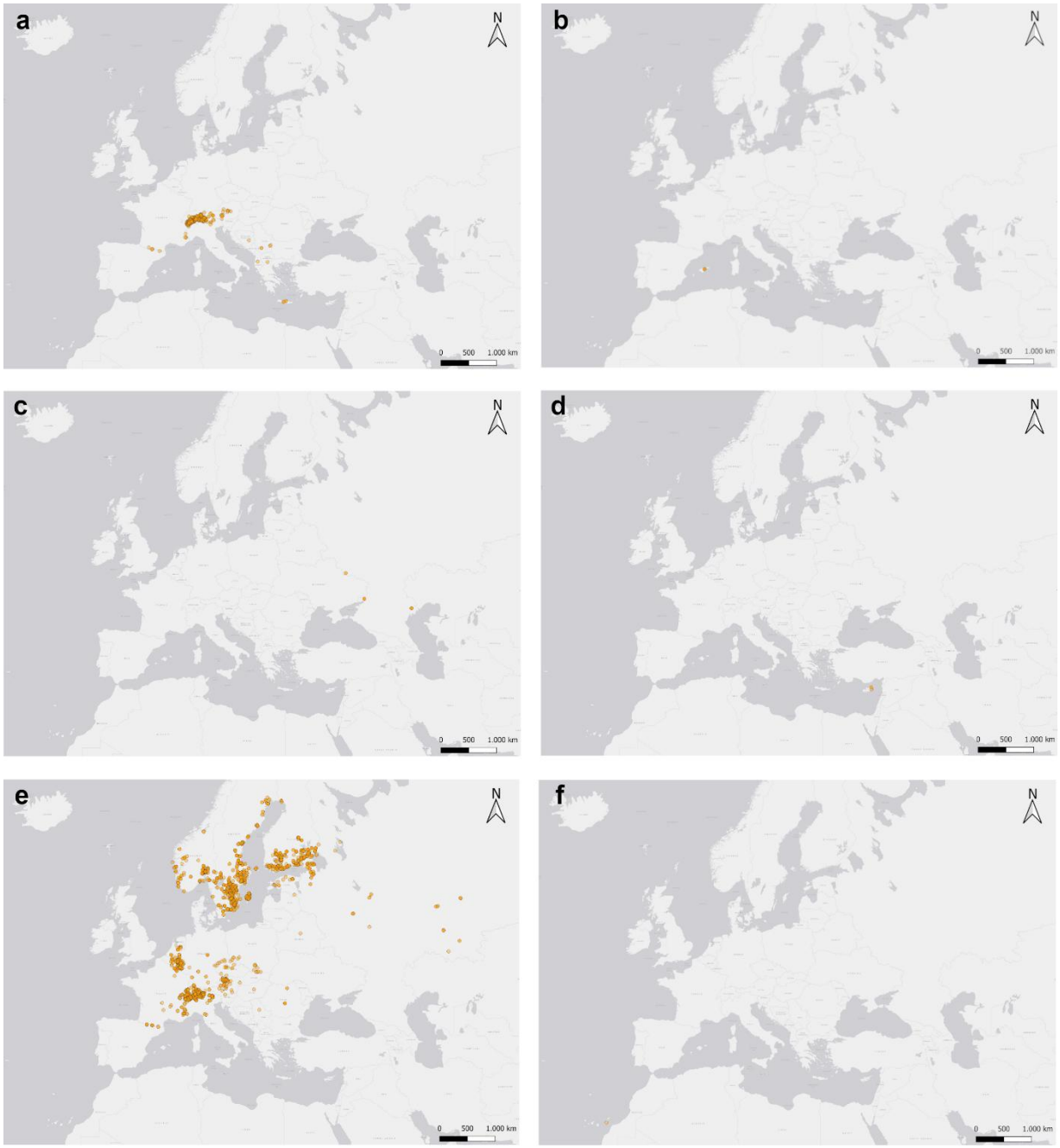

Figure 36: Maps of sampled Rophitinae from Sentil *et al.* (2026). Each point represents 1 specimen. a) *Dufourea alpina* b) *Dufourea balearica* c) *Dufourea coeruleocephala* d) *Dufourea cypria* e) *Dufourea dentiventris* f) *Dufourea fortunata*

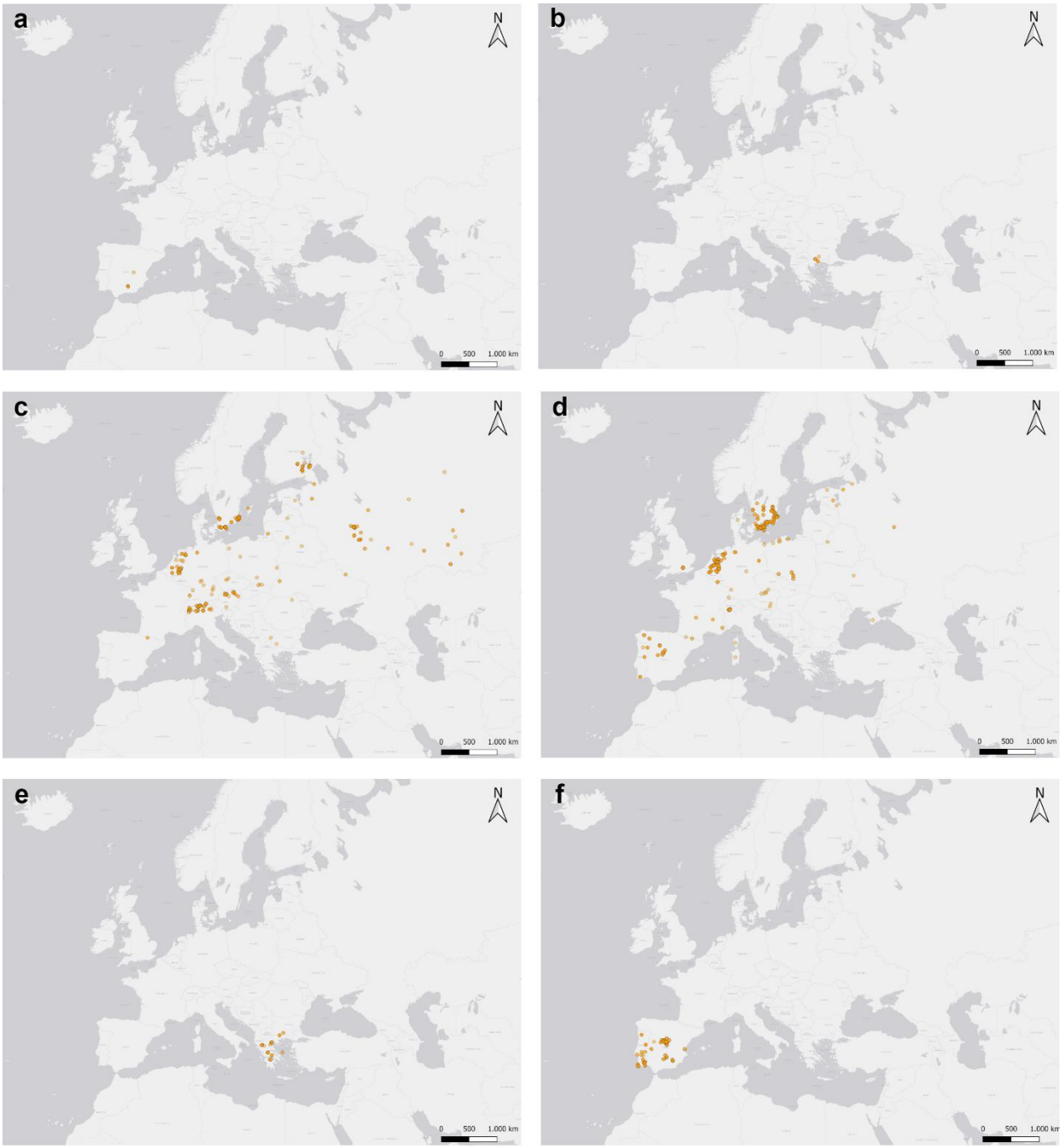

Figure 37: Maps of sampled Rophitinae from Sentil *et al.* (2026). Each point represents 1 specimen. a) *Dufourea longiglossa* b) *Dufourea iris* c) *Dufourea inermis* d) *Dufourea halictula* e) *Dufourea graeca* f) *Dufourea gaullei*

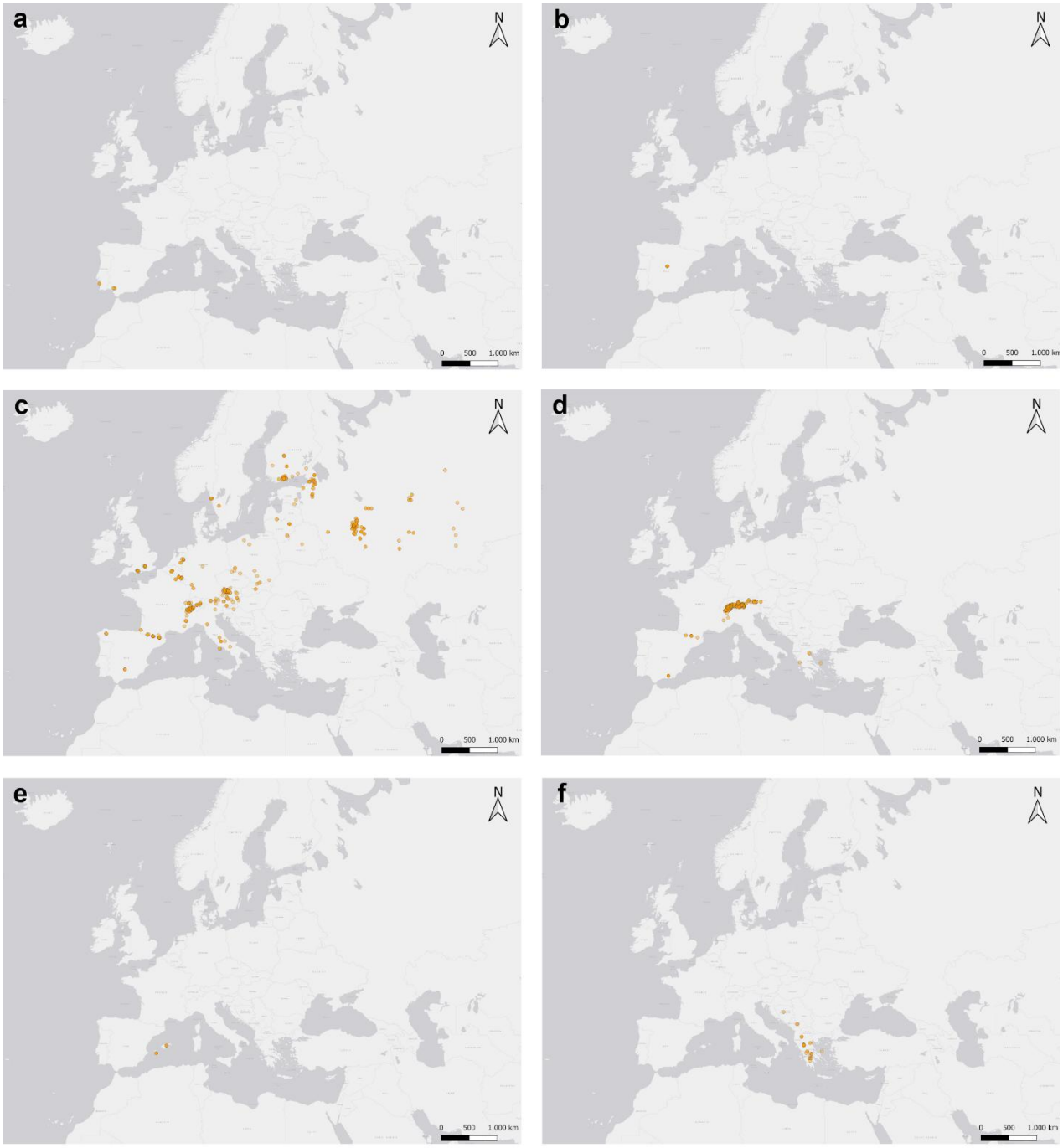

Figure 38: Maps of sampled Rophitinae from Sentil *et al.* (2026). Each point represents 1 specimen. a) *Dufourea lusitanica* b) *Dufourea merceti* c) *Dufourea minuta* d) *Dufourea paradoxa* e) *Dufourea similis* f) *Dufourea styx*

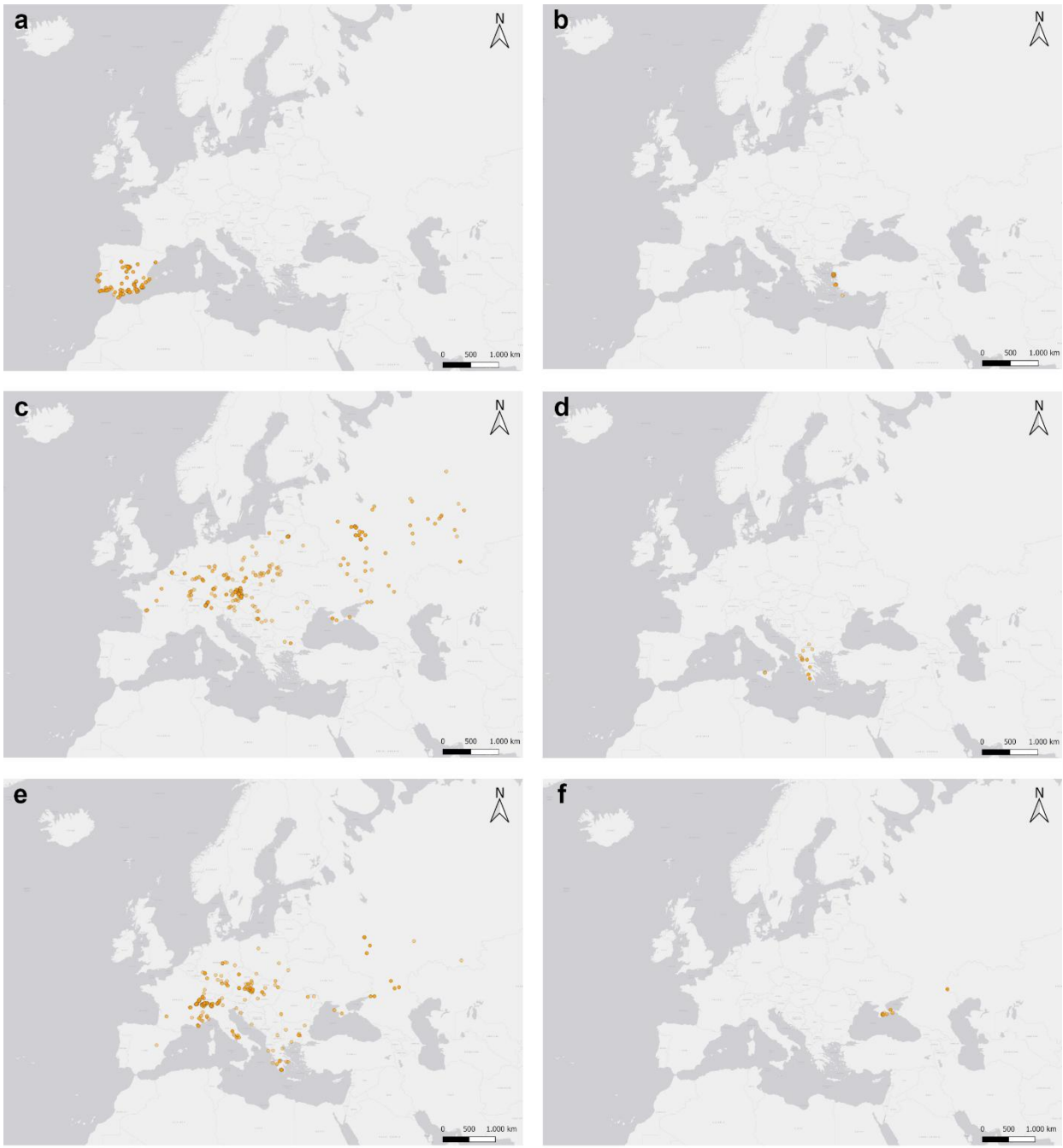

Figure 39: Maps of sampled Rophitinae from Sentil *et al.* (2026). Each point represents 1 specimen. a) *Dufourea trautmanni* b) *Dufourea wolfi* c) *Rhophitoides canus* d) *Rhophitoides epiroticus* e) *Rophites algirus* f) *Rophites clypealis*

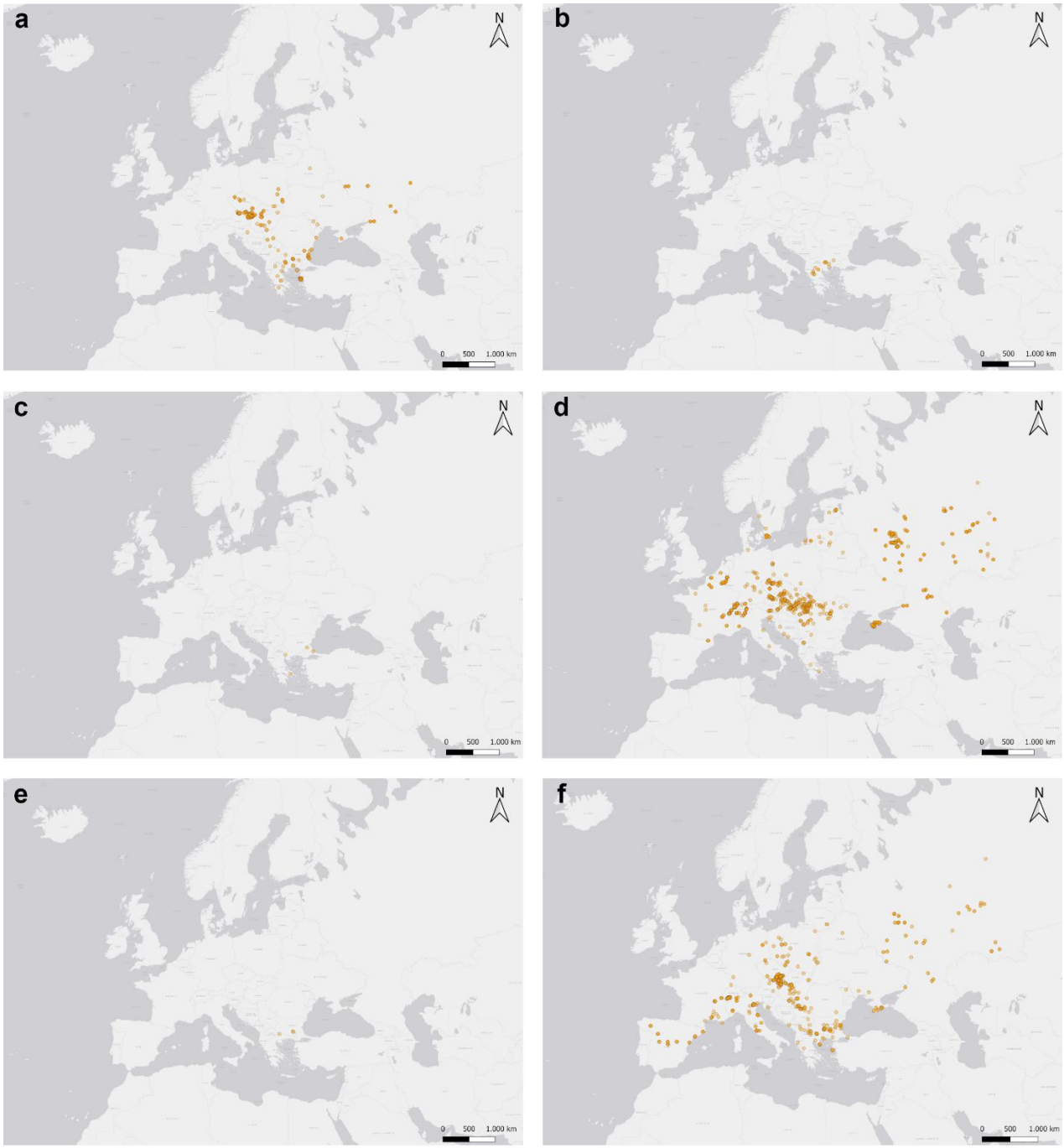

Figure 40: Maps of sampled Rophitinae from Sentil *et al.* (2026). Each point represents 1 specimen. a) *Rophites hartmanni* b) *Rophites hellenicus* c) *Rophites leclerqi* d) *Rophites quinquespinosus* e) *Rophites thracius* f) *Systropha curvicornis*

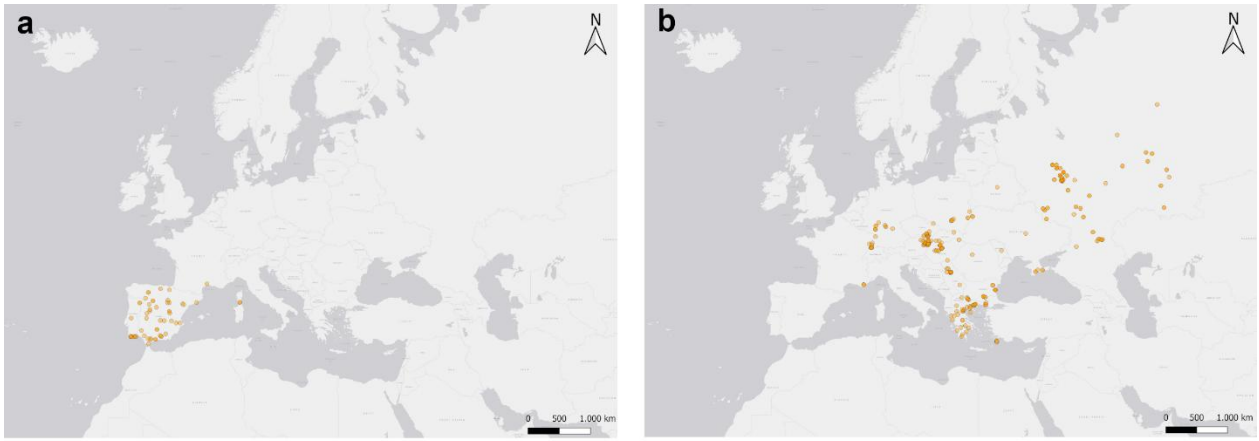

Figure 41: Maps of sampled Rophitinae from Sentil *et al.* (2026). Each point represents 1 specimen. a) *Systropha grandimargo* b) *Systropha planidens*