

ARTICLE

# First observations of *Eucera (Cubitalia) breviceps* (FRIESE, 1911) in Italy and France, with updated information on the distribution and ecology of the species (Hymenoptera: Anthophila: Apidae)

Matthieu AUBERT<sup>1</sup>  • Marco BONIFACINO<sup>2</sup>  • David GENOUD<sup>3</sup>  • Vincent LECLERCQ<sup>4</sup>  • Bertrand SCHATZ<sup>5</sup> 

AUBERT, M., M. BONIFACINO, D. GENOUD, V. LECLERCQ & B. SCHATZ (2024). First observations of *Eucera (Cubitalia) breviceps* (FRIESE, 1911) in Italy and France, with updated information on the distribution and ecology of the species (Hymenoptera: Anthophila: Apidae). *Osmia*, 12: 5–18. <https://doi.org/10.47446/OSMIA12.2>

## Abstract

*Eucera (Cubitalia) breviceps* (FRIESE, 1911), hitherto only known from Turkey and Syria, was discovered in the southern part of Massif Central (France), in the "Grands Causses" area, a few years ago. It has been found to be distributed throughout it, also present in the French Alps and Italy (Valle d'Aosta, Abruzzo) as well as in southwestern Bulgaria and northern Greece. Our article presents the corresponding data, originated from field work and examination of material in collections, and gives new data for Turkey from material in the collection of the Oberösterreichisches Landesmuseum, Linz (Austria). Several ecological traits of *E. breviceps* are discussed. We especially highlight the close association between *E. breviceps* and the plant genus *Onosma* L. (Boraginaceae), based on literature and our field observations. Both their ecological requirements and their interactions illustrate the complexity of such relationships and their potential vulnerability in the context of global change. Through this remarkable example of an oligolectic interaction, we aim to promote a better consideration of pollinators, notably bees, and pollinator networks in conservation biology.

**Keywords** | Eucerini • Western Europe • *Onosma* L. • conservation biology • pollinators

**Premières observations d'*Eucera (Cubitalia) breviceps* (FRIESE, 1911) en Italie et en France, avec des informations actualisées sur la répartition et l'écologie de l'espèce (Hymenoptera : Anthophila : Apidae)**

## Résumé

*Eucera (Cubitalia) breviceps* (FRIESE, 1911), jusqu'alors connue de Turquie et de Syrie, a été découverte dans la région des Grands Causses (Massif central) dans le sud de la France il y a quelques années. Elle s'est révélée y être assez largement distribuée, et est également présente dans les Alpes françaises, dans le Val d'Aoste et dans les Abruzzes en Italie, dans le sud-ouest de la Bulgarie et le nord de la Grèce. Notre article présente les données correspondantes provenant de nos prospections de terrain ainsi que de l'examen de spécimens en collection, et apporte de nouvelles données pour la Turquie issues de la révision de matériel au Muséum de Linz en Autriche. Nous y présentons différents éléments de l'écologie d'*E. breviceps* et, en particulier, les interactions étroites qu'elle entretient avec les plantes du genre *Onosma* L. (Boraginaceae), sur la base de la bibliographie et de nos observations *in situ*. Leurs exigences écologiques respectives et leurs interactions illustrent la complexité de telles relations et leur vulnérabilité dans le contexte des changements globaux. À travers la présentation de cet exemple remarquable d'oligolectisme, nous visons une meilleure prise en considération des pollinisateurs, notamment des abeilles, et des réseaux plantes-pollinisateurs dans le champ de la biologie de la conservation.



**Mots-clefs** | Eucerini • Europe de l'Ouest • *Onosma* L. • biologie de la conservation • pollinisateurs



**Reçu • Received** | 04 January 2023 || **Accepté • Accepted** | 07 March 2024 || **Publié (en ligne) • Published (online)** | 08 March 2024  
**Reviewers** | R. CATANIA • D. MICHEZ || <https://zoobank.org/A625D692-9CCB-4AFD-B649-48DD45D000E8>



**Supplementary material (on the website of the journal + archives in Zenodo)** [<https://doi.org/10.47446/OSMIA12.2>]



**Table S1.** Data corresponding to material examined and mentioned in the article [saved at <https://doi.org/10.5281/zenodo.10718775>]

<sup>1</sup> [MA] 4 chemin de la Foux, hameau du Méjanel, F – 34380 Pégairolles-de-Buèges, France • [aubertmatthieu@laposte.net](mailto:aubertmatthieu@laposte.net)  
 <https://orcid.org/0000-0003-2713-9371> •  <https://zoobank.org/8271D8FF-3518-448B-9556-F37A7900129>

<sup>2</sup> [MB] Via Caviglia 8, I – 17047 Vado Ligure, Italy • [mbonifacino2317@gmail.com](mailto:mbonifacino2317@gmail.com)  
 <https://orcid.org/0000-0001-6190-3965> •  <https://zoobank.org/7DCB1D21-A33E-4DAD-B0E4-036555980534>

<sup>3</sup> [DG] 9 rue Hector Berlioz, F – 87240 Ambazac, France • [dge-davidgenoud@orange.fr](mailto:dge-davidgenoud@orange.fr)  
 <https://orcid.org/0000-0001-8564-040X> •  <https://zoobank.org/B9EA26E1-94B2-491E-BE27-1ACE034C777C>

<sup>4</sup> [VL] 5 rue de l'Esplanade, Résidence de l'Arche, Bâtiment Prokofiev, étage 4, F – 13090 Aix-en-Provence, France • [vincent.leclercq44@gmail.com](mailto:vincent.leclercq44@gmail.com)  
 <https://orcid.org/0009-0007-0108-5076> •  <https://zoobank.org/42893A44-22AB-46F4-94AD-A0837EA6860D>

<sup>5</sup> [BS] Centre d'écologie Fonctionnelle et Évolutive (CEFE) (UMR 5175 Univ. Montpellier – CNRS – EPHE – IRD), Campus du CNRS, 1919 route de Mende, F – 34293 Montpellier, France  
• [bertrand.schatz@cefe.cnrs.fr](mailto:bertrand.schatz@cefe.cnrs.fr)  
 <https://orcid.org/0000-0003-0135-8154> •  <https://zoobank.org/A569324C-A857-4911-BA6F-63FBA865DB42>

## INTRODUCTION

The increase in human activities during the past centuries and especially since the Second World War has led to considerable changes in the biosphere and biodiversity. For most taxonomic groups, global change leads to two types of impacts: firstly, the decline in species marked by a decrease in the abundance of individuals, and secondly the simplification (or homogenisation) of species assemblages and their interactions (POTTS *et al.*, 2016; FISCHER *et al.*, 2018). Thus, because of this second type of impact, species that are specialised in their ecology (food preference, habitat preference, short phenology, *etc.*) are more threatened than generalist species, as the latter are more flexible in their ecological requirements and can adapt more easily to environmental variations. Wild bees are not exempted from these two components of biodiversity decline (DROSSART & GÉRARD, 2020; ZATTARA & AIZEN, 2021). While some species are exhibiting stable distributions or are even favoured by global changes, depending on their biology and ecological preferences in specific contexts (GHISBAIN *et al.*, 2021), a lot of species that are ecologically specialised are in decline (BIESMEIJER *et al.*, 2006; BOMMARCO *et al.*, 2012). Indeed, an oligolectic bee species must cope with global changes depending on its own ecology, phenology, and distribution (DUCHENNE *et al.*, 2020) but also in regard to the ecology of the few plants on which it is specialised (flowering phenology, floral attractants, general morphology) and their distribution (HUTCHINGS *et al.*, 2018). Moreover, it must deal with the several interaction dimensions with the host plants (phenological synchronisation, morphological matching, chemical and visual mediation) (GÉRARD *et al.*, 2020). This is why oligolectic bees can be considered as sentinels of the conservation status of the functional diversity of pollinator communities. Given the need to update the conservation status of oligolectic bees in general, and particularly in Southern Europe, this study presents an overview of the information known about one remarkable bee species, *Eucera (Cubitalia) breviceps* FRIESE, 1911, specialised on some species of the genus *Onosma* (Boraginaceae). We aimed to highlight the importance of this association with considerations of conservation.

### General information on *Cubitalia* bees

*Cubitalia* FRIESE, 1911 represents a small palearctic group of longhorn bees in the tribe Eucerini (family Apidae) that have two submarginal cells in the forewing (MICHENER, 2007). It was established and differentiated as a subgenus of *Eucera*, a genus which comprises the rest of the species with two submarginal cells, with *E. breviceps* designated as the type

species (FRIESE, 1911). The taxonomic status of *Cubitalia* has been unstable as that of the genus *Eucera* in general. It has been considered either as a subgenus of *Eucera* (RISCH, 1999) or as a distinct genus (TKALCŮ, 1984; PESENKO & SITDIKOV, 1988, 1990; SITDIKOV & PESENKO, 1988; MICHENER, 2007), and was further divided into an additional two subgenera: *Pseudeucera* TKALCŮ, 1978 and *Opacula* PESENKO & SITDIKOV, 1988. The latter authors even raised these taxa to a generic rank. Based on molecular and morphological phylogenetic analyses, DORCHIN *et al.*, (2018) proposed to include all members of *Cubitalia* among other taxa in a large genus *Eucera*.

To the present knowledge the subgenus *Cubitalia* (sensu RISCH) includes eight species (TKALCŮ, 1984; RISCH, 1999; ENGEL, 2006), which are distributed in southwestern Asia (Israel, Jordan, Syria, Turkey, Georgia, Russian Caucasus, Iran), with *Eucera (Cubitalia) donatica* (SITDIKOV, 1988 in PESENKO & SITDIKOV, 1988) (= *Cubitalia (Opacula) donatica*) distributed in Central Asia (Uzbekistan) (SITDIKOV & PESENKO, 1990). Two species are known to be present in South-Eastern Europe: *Eucera (Cubitalia) morio* FRIESE, 1922, and *Eucera (Cubitalia) parvicornis* (MOCSÁRY, 1878) (= *Cubitalia (Pseudeucera) parvicornis*) (KUHLMANN *et al.*, 2015).

Recent lists of the Western European fauna of eucerine bees, particularly from France (RASMONT *et al.*, 2017; GARGOMINY *et al.*, 2021) and Italy (PAGLIANO, 1995; STOCH *et al.*, 2003; COMBA, 2019) indicate the presence of *Eucera parvicornis* in Italy (but not in France) and delineate the western boundary of distribution of the subgenus *Cubitalia* in Italy. For example, GRANDI (1931) reported this species in Emilia-Romagna, and COMBA (2019) in Lazio where he caught a single male, whose identity was confirmed by Borek TKALCŮ (M. CORNALBA, *pers. comm.*).

Available observations suggest that females of the subgenus *Cubitalia* exclusively collect pollen from flowers in the plant family Boraginaceae (RISCH, 1999). MÜLLER (1995) contributed details of the pollen collection of *Eucera parvicornis*, showing that this species is specialised in the Boraginaceae and, above all, in *Anchusa* L., strongly preferred genus. DUKAS & DAFNI (1990) reported that *Eucera (Cubitalia) boyadjiani* VACHAL, 1907 (as *C. boyadjiani*) collected the pollen of different species of the genus *Onosma* in Israel. Finally, based on fieldwork conducted in Greece, TEPPNER (1995) indicated that a species of *Cubitalia* was oligolectic to the genus *Onosma*.

## CUBITALIA NEW TO WESTERN EUROPE: HISTORY OF DISCOVERY IN FRANCE AND IN ITALY AND TAXONOMIC CLARIFICATIONS

In the end of June 2010, one of us (MA) participated in fieldwork at the southern department of Lozère, France. It took place specifically on Causse Méjean, a limestone plateau which altitude ranges from 800 m to nearly 1250 m (FONDERFLICK *et al.*, 2010), in an area covered by dry calcareous substeppic grasslands. On this occasion were caught two eucerine bee individuals, one female and one

male while *in copula*. They turned out to correspond to representatives of a *Cubitalia* species, which was neither *E. parvicornis* nor *E. morio*.

This discovery was all the most surprising considering the bee size and robustness (for more details on their identification and habits see taxonomic clarifications in



**Figure 1.** *Eucera breviceps* habitat on Causse Méjean (Lozère, France, 13 June 2016), with large *Onosma tricosperma* subsp. *fastigiata* stand. Photo Matthieu AUBERT.

**Table I.** Locations and years of capture of *Eucera breviceps* in Western Europe

All studied specimen data are presented in online supplementary material (table S1). Administrative units refer to departments in France and provinces in Italy. Abbreviated names of collectors refer to the authors.

Administrative entities		Natural regions	Year(s) of collection	Altitude (m)	Collector(s)
Regions (Country)	Administrative units				
Occitanie (France)	Aveyron	Causse du Larzac	2020	810	MA
	Gard	Causse Noir	2014, 2018, 2021	910–940	MA, DG
		Causse de Blandas	2016, 2017, 2018	700	BS, Marie ZÉLAZNY, Natasha DE MANINCOR
	Hérault	Causse du Larzac	2021	675	BS
	Lozère	Causse Méjean	2010, 2013, 2016, 2018, 2021, 2022	920	MA, DG, BS, Cédric MROCZKO, Rémi RUDELLE
		Causse de Sauveterre	2021	950	DG
PACA (France)	Hautes-Alpes	Serranais-Rosannais	2022	1075	VL
Abruzzo (Italy)	Pescara	Gran Sasso foothills	2022	550	MB
Valle d’Aosta (Italy)	Aosta	Valley base, southern slopes	1977	700–900	Erwin STEINMANN
			2005	650	Gilles CARON

box A). We hypothesized that the species is either very rare, localized, or both, in France. In any case, this finding marked the beginning of further research during the following years. This initially took place in the same area and type of habitat, and in the same season that coincided with the assumed flight period of the species. The supposedly restricted diet of the species also helped to determine following fieldwork. It was assumed that this *Cubitalia* should be associated with Boraginaceae as in other *Cubitalia* species. To improve the chances to find it again, we tried to recognize precisely which plants it could use for pollen collection in such a habitat. We

thought some stenoecious plant would be a good candidate.

One member of the genus *Onosma* caught our attention: *O. tricosperma* subsp. *fastigiata* (BRAUN-BLANQ.) G. LÓPEZ, 1994, which is associated with dry calcareous grassland. It is indeed well represented in open landscapes of Causse Méjean and blooms from May to July (BERNARD 2009; TISON et al., 2014). Moreover, the centre of diversity of *Onosma* is in eastern Turkey and adjacent countries (BINZET et al., 2018) as is the case for the *Cubitalia* bees.



**Box A.** Brief description of *Eucera breviceps* FRIESE, 1911**Size**

- **Female** around 17–18 mm long.
- **Male** around 18–19 mm long.

**Important characters**

- Both sexes have a relatively long tongue (galea length is a little less than 0.4-time body length) and a cubical head.
- The labrum is longer than it is wide, ending in a triangle (it is nearly rhomboidal in males).
- As in other *Cubitalia* representatives (MICHENER, 2007; AUBERT, 2020), the first recurrent vein insertion on the back of second submarginal cell is closer to the second submarginal cross-vein than in other paleartic eucerines with two submarginal cells.

**Pilosity**

- Pilosity is well developed.
- It is particularly dense and long on the head, especially behind the compound eyes, on the genae, labrum and mandibles, as well as on the first femora and thorax sides and underside. In females, it forms a kind of brush on the labrum.
- The pilosity is white on the ventral part of the body, except on the central area of the last sternites where it is black.
- Dorsal part, from the head to the second tergite, is covered with orange pilosity in fresh specimens, set apart on female occiput and forehead where it is black (and even sometimes on the disc of tergite 1).
- Leg pilosity is more or less orange too, mainly on their outer surfaces. Scopa is brownish orange.

**About males**

- Males bear elongated antennas, but less long than in other west-European eucerines (they only reach the back of the thorax, whereas they are as long as body length, reaching abdomen tip in *Eucera nigrescens* PÉREZ, 1879 for example).
- Their mandibles are particularly long, approximately reaching clypeus width. The labrum and the apical two-thirds of clypeus are yellow-coloured. Second and third pairs of metatarsi are modified.

**Differences between *E. breviceps* and *E. tristis***

- Diagnostic characters given by TKALCÚ (1984) to distinguish *E. breviceps* from *E. tristis*, its closest relative, have appeared to us hard to use. Females differ by their vestiture, which is entirely dark in *E. tristis*. Apart from that, differences are not obvious.
- Our difficulties also concern the males. Indeed, the variability we have noticed notably on some genitalia and last sternites details (apex of gonostyli and seventh sternite shapes for example) among the examined series of *E. breviceps* make the proposed criteria difficult to consider. A taxonomic revision concerning the status of these two taxa would certainly be relevant.

**Illustrations**

- Female and male are illustrated respectively in the figures a–b (+ figure 7), and figures c–d.
- Genitalia and last sternites of the latter are illustrated by TKALCÚ (1984).



**Figure a.** *Eucera breviceps* female seen in profile on *Onosma tricosperma* subsp. *fastigiata* flower (Lozère, France, 13 June 2016). Photo Matthieu AUBERT.



**Figure b.** *Eucera breviceps* female seen from the back on *Onosma tricosperma* subsp. *fastigiata* (Lozère, France, 13 June 2016). Photo Matthieu AUBERT.



**Figure c.** *Eucera breviceps* male seen in 3/4 view (Lozère, France, 13 June 2016). Photo Matthieu AUBERT.



**Figure d.** *Eucera breviceps* male held between the fingers, in front view (Lozère, France, 13 June 2016). Photo Matthieu AUBERT.



## French overall distribution

Following the first record, the *Cubitalia* species was indeed regularly found on the southern part of Massif Central. Data was taken on Causse Méjean and again for several comparable limestone plateaus: Causse Noir, Causse de Blandas, Causse du Larzac and Causse de Sauveterre (table I). The species was systematically found on dry grasslands hosting *Onosma* populations, from around 700 m (Causse du Larzac and Causse de Blandas) to 1045 m (Causse de Sauveterre) of altitude (figures 1–2).

In addition, during the June 6<sup>th</sup>, 2022, additional surveys were performed in the French southern Alps. This is because *Eucera breviceps* was suspected to occur there considering the presence of suitable habitats with the host plant *O. tricosperma* subsp. *fastigiata*, and presence of the species in the Italian Alps (following part). It was indeed found by VL in the Serranais-Rosannais area, southwest of Gap (Hautes-Alpes department). Two females were collected on two closed dry grasslands with *O. tricosperma* ssp. *fastigiata*, at an altitude of around 1000 m to 1100 m (figure 3).

## Presence in Italy

Conversations with Christophe PRAZ (Neuchâtel, Switzerland) and Andreas MÜLLER (Zürich, Switzerland) about the discovery of a *Cubitalia* species in France highlighted two specimens caught in Aosta Valley in 1977 (Erwin STEINMANN leg.) and 2005 (Gilles CARON leg.) which are preserved in the A. MÜLLER collection. The first one is a male labelled with the following information: “11.7.77 Senin Koel. Stip. 880” (1<sup>st</sup> handwritten label, which means Koelerio-Stipetum, a plant association corresponding to a dry grassland, at 880 m high), “*Eu. curvitaris* ♂” (2<sup>nd</sup> handwritten

label) and “*Eucera breviceps* FRIESE RISCH det. 2011” (3<sup>rd</sup> label, a printed one). The second specimen is a female with one printed label indicating: “Italia: Val d’Aosta Saint-Pierre sur Château Sarre leg. G. CARRON 2.6.2005”. The collection site of the male certainly occurred above Sénin on the southern slopes. The one of the female probably corresponds to a vineyard and dry grassland mosaic that surrounds Castello Reale di Sarre (= “Château Sarre”). Both were carefully sent to MA for comparison with the *Cubitalia* individuals caught in southern France and were found to be conspecific with high likelihood.

More recently, a *Cubitalia* male of the same species was caught in the Abruzzo region, in the southern part of Gran Sasso and Monti della Laga National Park by MB. It was found on May 22<sup>nd</sup>, 2022, at just 550 meters above sea level, in a hilly area characterized by dry meadows interspersed with woods. The specimen, fairly worn, was collected in flight on a grassy slope with some plants of *Onosma echioides* (figure 4).

## Species identification of the specimens from France and Italy

The first two specimens collected in France were sent by MA to Stephan RISCH for identification. They were identified as *Eucera (Cubitalia) breviceps* FRIESE, 1911 and deposited in the MA collection. Later collection events by DG contributed additional reference material that is preserved in his collection. In more recent years, some individuals were also sent to Achik DORCHIN (Mons, Belgium) who agreed with the species identity. The majority of the data presented in this article were confirmed *via* specimen examination by Stephan RISCH, MA or DG. Additional more recently collected specimens were identified only *via* photographs.



Figure 2. *Eucera breviceps* habitat on Causse du Larzac (Aveyron, France), 20 June 2020. Photo Matthieu AUBERT.





**Figure 3.** *Eucera breviceps* habitat in southern Alps (Hautes-Alpes, France). 6 June 2022. Photo Vincent LECLERCQ.



**Figure 4.** *Eucera breviceps* habitat in Abruzzo (Pescara, Italy). 22 May 2022. Photo: Marco BONIFACINO.



Examination of Italian specimens agreed with the species identification of the French specimens. Comparison between French and Italian specimens showed that morphological and anatomical variations can be greater between specimens coming from the same region in France than between specimens that originated in each of the countries. These subtle differences concern cuticular punctuation particularly in females, and the structure of the 7<sup>th</sup> and 8<sup>th</sup> sternites as well as genitalia of males (box A). The *Cubitalia* male caught in Val d'Aosta (Sénin) was initially misidentified as *Eucera curvitaris* MOCSÁRY, 1879. Consequently, the mention of this species in Aosta (STEINMANN, 2002) is erroneous. This east-European and east-Mediterranean *Hetereucera* (*sensu* TKALCŮ, 1978) is currently considered absent from Italy, as STEINMANN's article is the only evidence of the species occurrence there that is cited in COMBA's checklist (2019).

### *Eucera breviceps* overall distribution

FRIESE described *E. breviceps* on the basis of four syntypes, two females and two males. In the framework of a *Cubitalia sensu stricto* revision (including *E. boyadjani*, *E. breviceps*, *E. morio* and *E. tristis* MORAWITZ, 1876), TKALCŮ (1984) examined one male and one female only, which were deposited in Museum für Naturkunde, Berlin. He presumed the two other male and female to be lost. TKALCŮ identified only the male as *Cubitalia* and the female as belonging to another species, and erroneously paired with the male. According to him, it belonged to the subgenus *Hetereucera* (this female was described later and referred to as the holotype of *Eucera maxima* (TKALCŮ, 1987)).

Among the syntypes, the two males and the remaining female – which actually correspond to *E. maxima* – come from the eastern Taurus range in south-central Turkey ("Güleck im Taurus cilic."). The female that is presumably lost came from Syria, potentially from a north-western part of the country as indicated by ENGEL (2006) (it is probable that this specimen was later associated with *E. maxima* as well).

TKALCŮ (1984) provided a map in which he indicated the provenance of the Turkish syntypes (but not that of the Syrian syntype). He illustrated supplementary data from Hatay province, adjacent to Syria (in the Amanus range) which corresponds to a specimen that was deposited in the Oberösterreichisches Landesmuseum (OÖLM), Linz (Austria). In the same article, TKALCŮ mentioned another individual caught in Sertavul (Mersin province), which lies in Central Taurus range in southern Turkey.

A visit at OÖLM in 2019 permitted MA to compile data that concern *E. breviceps* in Turkey from several other provinces: Hakkari and Siirt in south-eastern Turkey (Turkish Kurdistan), the former location including the Cilo-Sat range, on the border of Iran and Iraq, Kars in eastern Turkey, adjacent to Armenia, Cankiri and Ankara in the central northern part of Turkey, and Aydin in the southwestern part of the country, along the Mediterranean Sea. Thus, the distribution of *E. breviceps* in Turkey encompasses a large part of the country, from East to West. Moreover, two *E. breviceps* males taken from southwestern Bulgaria were found at OÖLM, in Maximilian SCHWARZ collection. They were collected there by Miroslaw KOCOUREK and were both

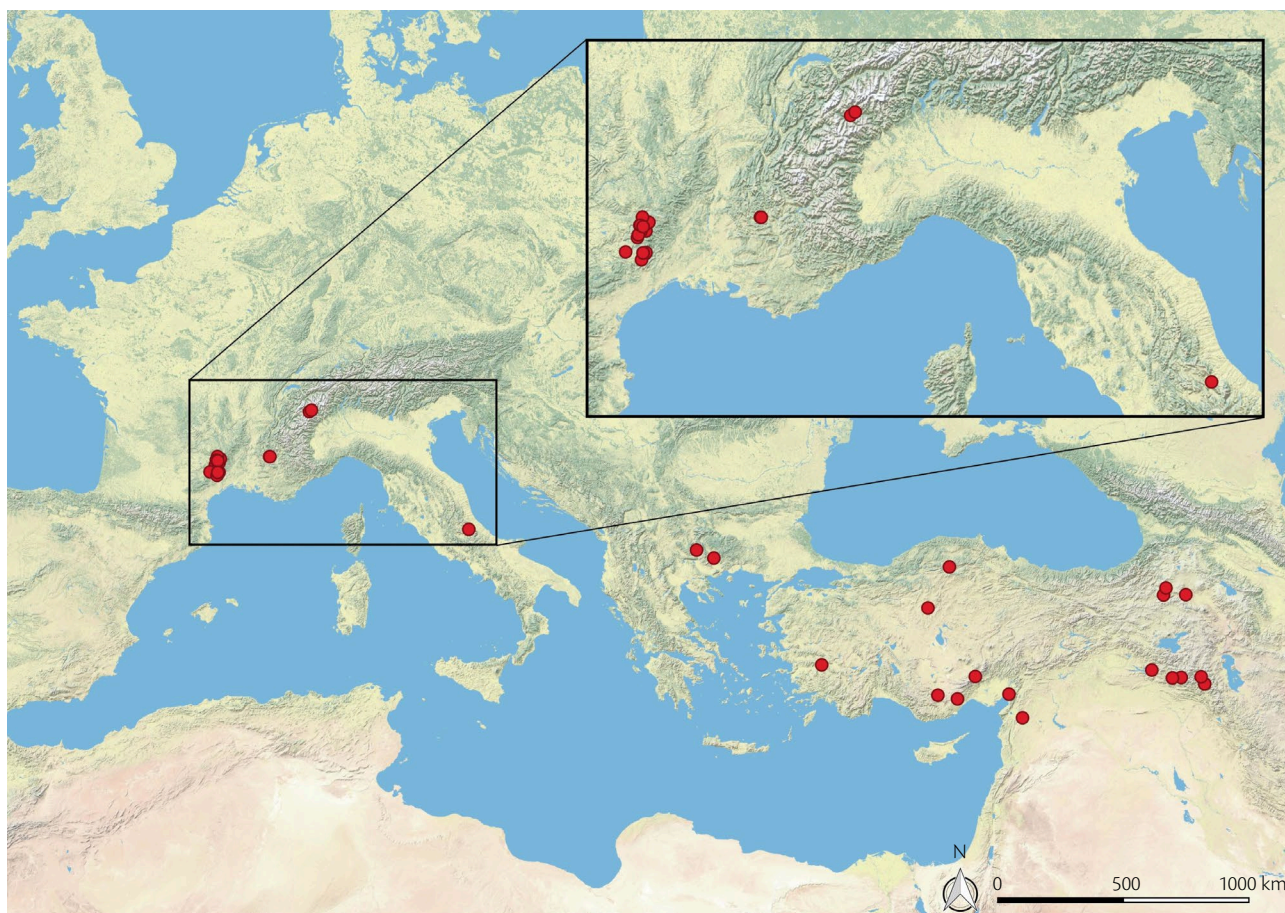


Figure 5. *Eucera breviceps* distribution maps with a focus on South-eastern France and Northern Italy (map generated with QGIS).

labelled as follows: “Sandanski 06/1969” and “*Eucera cf. tristis* MORAWITZ, 1876”.

Finally, TEPPNER (1995) reported field observations of visitors of *Onosma*. His studies were performed in northern Greece, notably the Falakron area. One of them concerns a *Cubitalia* species visiting *Onosma stajanoffi* (TURRIL) TEPPNER. A female specimen was collected and identified as *Eucera morio* FRIESE (referred to as *Cubitalia morio* (FRIESE)). The article comprises some black and white pictures of limited resolution, but the appearance of the specimen does not seem to us to match the species concept of *E. morio* as we understand it. Indeed, as indicated in TKALCÚ’s revision (1984), *E. morio* has darkened wings and nearly entirely dark pilosity, while the pilosity of the Falakron female, especially on the thorax, is light. We therefore inquired with H. TEPPNER, who has kindly provided us with higher resolution colour photographs of the same specimen, which confirm it doesn’t

match with *E. morio*. In addition to the coloration, an important diagnostic feature of the first tergite allows to exclude this species. We couldn’t examine the Falakron specimen under the dissecting microscope, but we are convinced that it belongs to *E. breviceps*. It differs merely in the colour of the pilosity of the first and second tergites. While the tergal hair pilosity is commonly light as that of the thorax, it is mostly darker in the specimen studied by TEPPNER, with some intermixed pale hairs limited to the sides of first tergite. We think that this specimen only presents a morphological variation of *E. breviceps*, that may be typical to higher elevations as the specimen in question was caught at an altitude of 1400 m.

All the mentioned data are mapped in the figure 5. All studied specimen data are presented in table S1 (online supplementary materials).

## ELEMENTS OF ECOLOGY

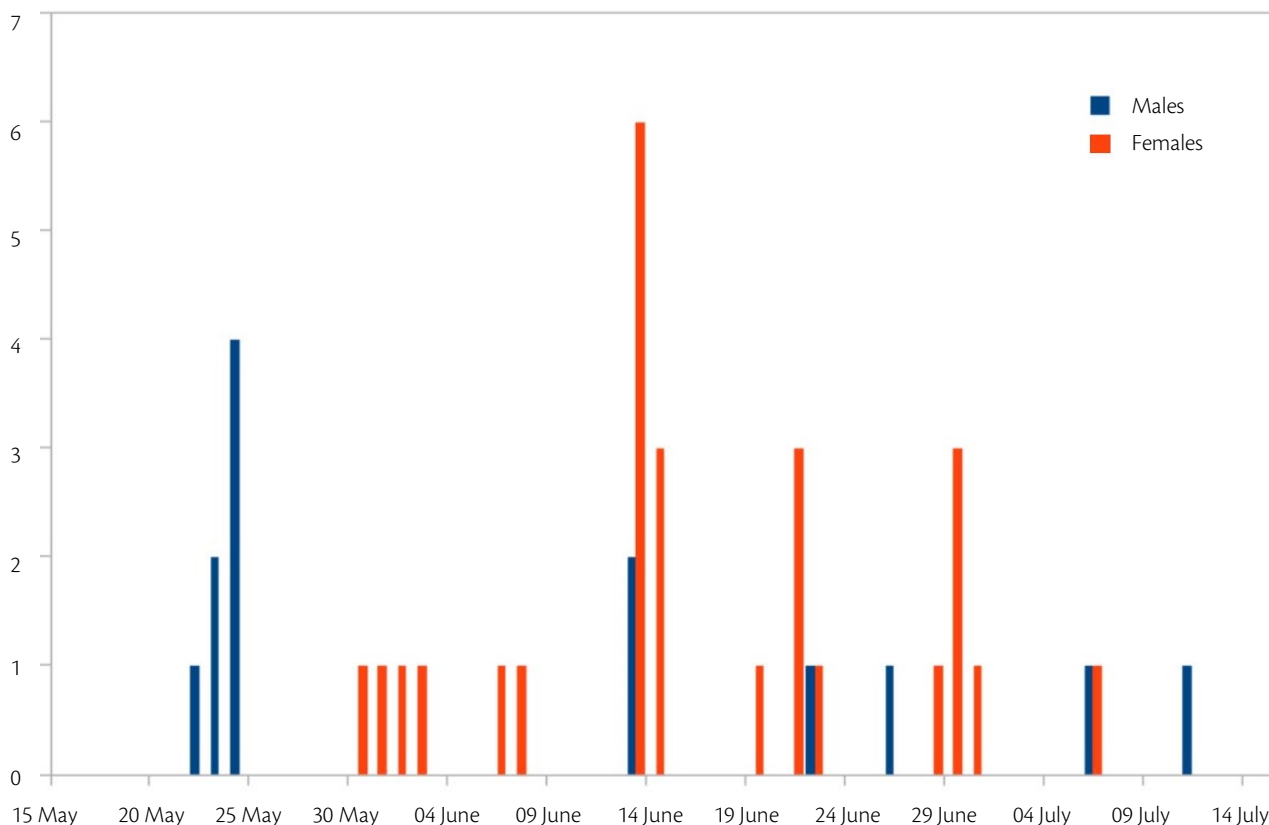
### Flight period, relative abundance and rareness

*E. breviceps* is clearly univoltine: its flight period is probably short, no longer than three or four weeks for the majority of individuals in a given generation. In Italy and France, it was contacted from last decade of May to the first decade of July, with a peak in June (figure 6).

Concerning abundance, still considering only Italy and France, 23 of the 30 occurrences (*i.e.* collection or observation of the species at one place and one date, that is one fieldwork) correspond to only 1 specimen. Two

occurrences correspond to 2 specimens, four occurrences correspond to 3 or 4 specimens and one occurrence corresponds at least to 8 specimens (males and females).

Besides, as indicated earlier, several surveys conducted in France led to no contacts. Indeed, between 2013 and 2019, especially on the Larzac plateau (La Couvertoirade, Saint-Maurice-Navacelle, Saint-Michel), as well as in 2022 on the northwest border of Var department (in the vicinity of Trigance village), some focused field research in suitable habitats did not lead to *E. breviceps* collection or observation. In most cases, it was noticed that *Onosma*



**Figure 6.** Number of females and males collected or observed in France and Italy per 5-day periods between mid-May to mid-July from 1977 to 2022.



flowering peak was over, though some flowers remained. Moreover, on most occasions (except near Trigance), no high *Onosma* densities but only sparse individual plants were found (often about ten or a little more, distributed over hundreds to thousands of square metres, as it could be observed). Some *Cubitalia* specimens were found under comparable flower densities, but only by applying a rather important time of survey (for example it took around one hour for each female caught in the Hautes-Alpes department in France).

The absence of observations does not mean systematically the absence of bees in these studied areas, but either an insufficient study design in regard to the bee density or an inappropriate study date. However, it is likely that there is a threshold in terms of the number and density of *Onosma* that allows the detection and above all the sufficient feeding of *E. breviceps*.

Other ecological factors may explain the absence of the species. Indeed, the altitudinal distribution of *E. breviceps* appears to be relatively restricted in France and Italy (table 1), though large populations of *Onosma* are also present at high altitudes in southern Alps, up to 2300 m. Repeated field research undertaken by MA and colleagues at several locations around 2000 m in this area did not permit to find the species.

Since the species was only recently discovered and its apparent low abundance in most sites, it can be assumed that *E. breviceps* is indeed generally scarce. That said, research efficiency could certainly be optimized by focusing fieldwork efforts during the blooming peak of *Onosma*, and perhaps during the first part of the day when pollen may be more abundant in the flowers. As suggested earlier, that parameter could influence female behaviour and detectability.

The exceptional observations, with three, four and eight specimens observed at the same time and place may be explained by a combination of good timing (peak of flight period) and the existence of particularly suitable habitat with high *Onosma* densities. Four of the five most prolific observation events are those of the Causse Méjean and one at the Causse du Larzac in France. In each case, especially the one where at least eight specimens were observed, the density and abundance of *O. tricosperma* ssp. *fastigiata* were visibly high with dozens of plants distributed within a few hundreds of squared meters.

### About close links between *E. breviceps* and *Onosma* flowers

Among the data we compiled in France, at thirteen different locations we caught or observed at least one female, that was visiting or foraging on *Onosma* flowers (as indicated previously, in some cases, the number of females observed on *Onosma* was higher). The only other visitation data concerns one female caught on *Salvia pratensis* L. (Lamiaceae).

Concerning the data gathered for Italy, the observation in the Abruzzo included an *Onosma echioides* population. The collecting period in Aosta also theoretically corresponds

with the blooming period of that genus. A. MÜLLER analysed pollen grains taken from three *Cubitalia* females, including two that originated from France, and one from Aosta (Italy). His results are the following: 100 % pear-shaped Boraginaceae pollen grains, with many typical *Onosma* grains. Nevertheless, it cannot be excluded that a certain proportion of *Echium* grains were mixed among them (MÜLLER, *pers. comm.*). We do not have direct observation information on specimens collected in Turkey, but the genus *Onosma* is abundant there and it is therefore likely that the species is associated with *Onosma* also in Turkey. It cannot be excluded however that in its eastern range of distribution, the species uses pollen from other close relatives of *Onosma*, which do not occur in its western distribution range (like *Podonosma* BOISS.).

### Sonication and pollen collection

One more interesting observation on the relation between females of *E. breviceps* and *Onosma* flowers can be developed, namely floral sonication, which is observed in many bees, notably in the family Apidae, including generalists (bumblebees and some anthophorine bees) as well as specialist species.

Also known as “buzzing” or vibratory pollen collection, it is a behaviour that involves flight muscles to vibrate the flowers and extract the pollen. It produces a quite loud sound, audible from several meters. It is particularly adapted to flowers with mostly closed anthers, with only small apertures, as short slits, valves or pores (BUCHMANN, 1983; CARDINAL *et al.*, 2018; TEPPNER, 2018). In *Onosma* flowers, anthers are bent towards the style (the established term is introrse) and partly or completely connected to each other, hence forming a cone at the base inside the tubular corolla (TEPPNER, 2011). Consequently, *Onosma* pollen is enclosed and not directly accessible to bees.

Buzzing behaviour on *Onosma* flowers was already reported by DUKAS & DAFNI (1990) and TEPPNER (1995), involving several species of the plant genus and several bee species (see below). In the case of *O. tricosperma* spp. *fastigiata* and *E. breviceps* in southern France, sonication was regularly noticed in the field and even allow the bee to be heard and detected within 10–20 meters before it is seen. Its size and its pilosity appear to be arranged to optimize falling pollen capture while buzzing. The corolla size and shape of *Onosma* flowers, and the presence of an exerted style, allow *E. breviceps* to enter only its head and forelegs into the floral tube. But in doing so, it nearly entirely closes the corolla opening with the front part of the head and thorax. The effect of the ‘buzz’ action releases pollen, the majority falls onto the body of the bee, especially on its ventral side.

During examination under dissecting microscope, sparse pollen grains are visible on the pilosity of the fore region of the female: head, underneath and sides of the thorax as well as the forelegs (where the pilosity is especially dense and long). Some cuticular areas at the base of the genae and hair fringes of the first femora show some pollen deposits. In the field, between buzzing sequences, we observed the bees hanging at the tip of the corolla by the hind legs and grooming its front body parts with its forelegs. The pollen is then actively accumulated by the bee on the third tibiae, mixed with little nectar (figure 7).



**Figure 7.** *Eucera breviceps* female seen in profile on *Onosma tricosperma* subsp. *fastigiata* flower (Lozère, France, 13 June 2016). Photo Matthieu AUBERT.

Unfortunately, we didn't pay enough attention on the use of the glossa. As part of the bee is hidden inside the corolla for harvesting the pollen, it is difficult to directly watch this body part at this moment. We observed the glossa was deployed several times during the grooming sequence, and it is quite possible that it is used inside the corolla to collect nectar before and after sonication, as specific sequences may be required.

The eventual use of mandibles inside the corolla is not clear either. Some bumblebees were reported to « milk » the anthers to optimize the pollen extraction along with sonication (BUCHMANN, 1983). 'Milking' means here extracting pollen by pressing the anthers with their mandibles. It is a terminology used in literature while referring to poricidal anthers and it may not be relevant for anther cones. One example is known on *Onosma* flowers, which is referred to as 'leg shaking': *Osmia apicata* SMITH, 1853, oligolectic on Boraginaceae with a strong preference for *Onosma* flowers, uses its first legs to shake the anther cone to harvest pollen, without the use of flight muscles (GOGALA & SURINA, 2011). The figure 3 of their article shows a female hanging upside down under an *Onosma* corolla, that has its ventral side white with pollen. It suggests that this method could be efficient.

Yet, evolution has led to another strategy to effectively exploit the pollen of narrow corolla flowers, notably in Boraginaceae. It involves modified bristles (mostly with a hooked tip) on mouthparts or front legs, in combination with scraping behaviour (MÜLLER, 1995; SEDIVY *et al.*, 2013). But *E. breviceps* females lack such hooked bristles on their mouthparts or front legs.

We did not systematically count the number of buzzing instances per visited flower, nor measured their duration. Some of our observations suggest that females could sonicate each flower during one long period of time or, more rarely, two or three periods of times with repositioning in between. It is most probable that females adapt sonication modalities throughout the day, depending on the amount of pollen available in the flowers (BUCHMANN, 1983).

We have not talked much about males so far because we did not notice a lot about them except that they actively patrol between *Onosma* plants or patches close to the ground. Some have been observed higher up. They are less easy detected probably because they land less often. The long tongues certainly permit them, as well as females, to take up the nectar concentrated at the bottom of the flowers of *Onosma*.

### ***Onosma* ecology in relation to *E. breviceps***

*Onosma* flowers are present on limestone and alluvial soil and individuals are generally located and very scattered. Some populations can be relatively concentrated, on some hundred square meters, even with 20-30 ind. by 2-3 square meters, but such concentration is rare and exceptional (*pers. obs.*).

In the Occitanie region (France), *Onosma* populations are present in steppe-like grasslands typical of the limestone plateaus of the Grands Causses region. In French Alps, they are found locally in calcareous grasslands, from 850 m in Pre-Alps up to 2300 m in Haute-Ubaye Region (*pers. obs.*). In Aosta (Italy), they exist in mosaics of substeppic habitats



where it is represented by *Onosma pseudoarenaria* SCHUR where this species is the only representative of the genus (BARTOLUCCI *et al.*, 2018; MARTELLOS & NIMIS, 2022). In Turkey, the genus *Onosma* is extremely diverse (comprising dozens of species), and largely distributed (BINZET *et al.*, 2018; TEPPNER, 2011). The representatives of this plant genus are characterised by partitioned flowering, where flowers of

individuals do not flower at the same time but spread out over time (BERNARD 2009; TISON *et al.*, 2014). The downward orientation of these so-called pendulous flowers also ensures that the pollen is always well protected from rain and radiation that could alter the nutritional qualities and volume of the available pollen and nectar.

## CONSERVATION ISSUES

The relation between *E. breviceps* and *Onosma* species involve several key facts about their ecology and their actual interaction. On the *E. breviceps* side, we note (1) a foraging behaviour that allows the bees to detect their host plants from a long distance, (2) a sonication behaviour allowing to optimize pollen collection, and we hypothesize (3) a relatively large flight distance (probably up to 1 km around the nest) as suggested by the large size of the individuals (GATHMANN & TSCHARNTKE, 2002). On the *Onosma* side, it is important to note (4) a floral colour and a height of the stems that allow remote detection by the bees, (5) a flowering partitioning through time, (6) large flowers directed downwards, allowing the abundant pollen to remain dry and efficient for pollination and (7) a pollination also ensured by other large bees which increase the chances of fertilization and reproduction. Finally, on the interaction side, (8) the emergence period of *E. breviceps* is synchronized with the flowering period of *Onosma* and can withstand interannual variations (this particularly can be extended to all specialist bees), and (9) an open and calcareous semi-natural habitat suitable for both species. Thus, this interaction is weakened by the low density of *Onosma* populations and the rather large distances between populations. It has been shown that increasing distances between nesting and foraging sites reduce the offspring production of bee species (ZURBUCHEN *et al.*, 2010). Because of its big size, *E. breviceps* certainly requires high amounts of *Onosma* pollen to breed new individuals, which can partly explain the relative rarity of *E. breviceps* individuals in most cases.

At least in southern France (and probably in Aosta too), the conservation of open grasslands with high *Onosma* densities in areas where both the plant and *Cubitalia* are present is certainly key to preserve the bee. This conservation directly relies on that as a whole, which can be considered at landscape scale. The grasslands and mosaics they are part of provide remarkable landscapes of high interest and are recognized as such, in the actual context. They are the results of ancestral interactions between traditional human activities and the local environment (LEPART *et al.*, 2011). In the case of French Massif Central and its southern limestone plateaus, in addition to the creation of the “Parc Naturel Régional des Grands Causses” and the “Parc National des Cévennes”, the landscape justified the inscription of the area to UNESCO world heritage list with the name “The Causses and the Cévennes, Mediterranean agro-pastoral Cultural

Landscape”. It is interesting to observe that all southern Massif Central *E. breviceps* data are included in this perimeter.

Since the nineteenth century, the landscape has become largely woodland within it, as well as in a large part of Mediterranean area, although in a heterogenous way. This reforestation is largely spontaneous due to land abandonment and may be accelerated by coniferous plantations. This increasing trend, even in areas where agropastoralism is still well developed as in « causses » context (especially in Lozère department), shows that maintaining extensive farming is not sufficient to conserve open habitats (LEPART *et al.*, 2011). The evolution of the agricultural management, in particular farm enlargements and concentrations and the resulting changes in practices (more fodder crops and less grazing), allows a more nuanced explanation. The main driver of these changes is economic and lies in the agricultural and rural policies, notably the Common Agricultural Policy (FONDERFLICK *et al.*, 2010a, 2010b). To change this trend and to combine the existence of a dynamic agriculture with the preservation of biodiversity through the maintenance of grasslands and mainly open landscapes, public grants must be conditional on the implementation of appropriate practices (FONDERFLICK *et al.*, 2010b).

Of course, global changes may have important effects on the composition of these grasslands too and could directly or indirectly affect *E. breviceps*. Many factors may influence the future of its populations, such as spring droughts which could affect both the bee, the plant and their interaction.

It would be relevant to inventory the relatively high-density populations of *Onosma* and to promote the conditions for their conservation. This attention also corresponds to the strong and growing interest in conserving ancient natural grasslands (FONDERFLICK *et al.*, 2010a, 2010b; LEPART *et al.*, 2011). Meanwhile, we encourage the monitoring of changes in use of substeppe areas, the documentation of the effects of overgrazing or the abandonment of grazing – extensive or intensive – and to provide spatial information on the reallocation of these areas towards intensive livestock farming (sheep, goat, horses and sometimes pig farming) and towards natural or anthropogenic reforestation. Areas with a regulatory status, those that are protected, could be relevant territories in this respect.

## FURTHER PROSPECTS

In any event, *E. breviceps* deserves to be studied further to better know its distribution and population dynamics and to

better understand its biology and ecology. Key features like actual foraging ranges or ecological requirements would be

worth studying. It would be interesting to determine whether the distribution of this species is limited by the existence of high-density populations within the distribution of its host plant (<https://www.tela-botanica.org/bdtfx-nn-45009-repartition> and [https://inpn.mnhn.fr/espece/cd\\_nom/138244/tab/carte](https://inpn.mnhn.fr/espece/cd_nom/138244/tab/carte)) [accessed 21 April 2022]. One alternative hypothesis is that *E. breviceps* is under-sampled in other areas where this plant or a related species such as *Onosma pseudoarenaria* occurs. The answers to these questions can be provided by targeted campaigns on this remarkable bee where it has not been searched for in *Onosma* populations, as well as by assessments of *Onosma* density in sites of presence/absence of this bee.

The key factors in this close relationship could be analysed in more detail, such as the visual and olfactory mediation

linked to the interaction, but also the ecology of this plant, so as to explain the low density of these populations. The identification of threats to the reproduction of this plant, which is not very common on a national scale in France, would certainly provide information to promote its conservation.

Beyond the case of *E. breviceps* and *Onosma* species, this study also provides a conceptual framework for the study of close interactions involving other rare oligolectic bee species and host plants. This point is particularly important in the current context of the start of the establishment of the national red list of wild bees in metropolitan France. Finally, our ambition here is also to raise awareness in protected areas and conservation stakeholders of the conservation issues of these species and of these remarkable interactions.

---

## ACKNOWLEDGMENTS

A special thanks goes to Andreas MÜLLER who kindly provided specimens from Aosta and who identified some pollen samples for us. The Aostan specimens were caught by the late Erwin STEINMANN and Gilles CARRON to whom we pay tribute here. A second special thanks go to Stephan RISCH and Achik DORCHIN who helped with the identification of the *Cubitalia* from Western Europe and proposed many improvements of the article. We give a great deal of thanks to all the contributors to the data compiled in the article: Natasha DE MANINCOR, Marie ZÉLAZNY (who benefited with BS from the ANR ARSENIC grant no. 14-CE02-0012), Rémi RUDELLE and Cédric MROCZKO. All of them also provided complementary information. BS and DG benefited from capture authorisation 2022-0148 and the grant n° 90555174 from the Cévennes National Park. BS benefited from the Hérault Departmental Council grant n°175578 and from the program *Pollimed* from OSU-OREME. MA and DG are very grateful to the Observatoire des Abeilles for paying for a trip to Linz to work on the extensive and essential collection of the OÖLM. We thank Esther ÖCKERMÜLLER, Martin SCHWARZ and Fritz GUSENLEITNER for the warm welcome there and their help, including the sending of pictures of *Eucera morio*. And we thank Christophe PRAZ for the organization! We also thank the following persons for their contributions. Herwig TEPPNER provided several articles and permitted us to get recent pictures of Falakron female. Bernard VAISSIÈRE kindly sent us an essential bibliographical reference. Jocelyn FONDERFLICK (Cévennes National Park) sent us several other essential articles and also mission facilities and contract for DG. Maurizio CORNALBA permitted MB's participation in the article. Amy Lily HURDISS helped us with English translation. Last but not least, we are grateful to Roberto CATANIA, Denis MICHEZ & Achik DORCHIN (once again!) for their proofreading and comments on the manuscript.



## REFERENCES

- AUBERT, M. (2020). *Proposition de clé d'identification des Eucerini (Hymenoptera: Anthophila) de France continentale. Version provisoire*. Observatoire des Abeilles, Flines-lez-Râches (France), 45 pp. <https://oabeilles.net/projets/eucerini> [accessed 21 April 2022]
- BALITEAU, L., S. ISERBYT, G. MAHÉ, P. RASMONT, G. LE GOFF, A. PAULY & E. SCHEUCHL (2013). Contribution à l'inventaire des Abeilles sauvages du département de l'Aveyron (France) (Hymenoptera, Apoidea). *Bulletin de la Société entomologique de France*, **118**(3): 343–362. <https://doi.org/10.3406/bsef.2013.3116>
- BARTOLUCCI, F., L. PERUZZI, G. GALASSO, A. ALBANO, A. ALESSANDRINI, N. M. G. ARDENGHI, G. ASTUTI, G. BACCETTA, S. BALLELLI, E. BANFI, G. BARBERIS, L. BERNARDO, D. BOUVET, M. BOVIO, L. CECCHI, R. DI PIETRO, G. DOMINA, S. FASCETTI, G. FENU, F. FESTI, B. FOGGI, L. GALLO, G. GOTTSCHLICH, L. GUBELLINI, D. IAMONICO, M. IBERITE, P. JIMÉNEZ-MEJÍAS, E. LATTANZI, D. MARCHETTI, E. MARTINETTO, R. R. MASIN, P. MEDAGLI, N. G. PASSALACQUA, S. PECCENINI, R. PENNESI, B. PIERINI, L. POLDINI, F. PROSSER, F. M. RAIMONDO, F. ROMA-MARZIO, L. ROSATI, A. SANTANGELO, A. SCOPPOLA, S. SCORTEGAGNA, A. SELVAGGI, F. SELVI, A. SOLDANO, A. STINCA, R. P. WAGENKOMMER, T. WILHALM & F. CONTI (2018). An updated checklist of the vascular flora native to Italy. *Plant Biosystems*, **152**(2): 179–303. <https://doi.org/10.1080/11263504.2017.1419996>
- BERNARD, C. (2009). *Fleurs et paysages des Causses*. Éditions du Rouergue, Arles (France), 398 pp.
- BIESMEIJER, J. C., S. P. ROBERTS, M. REEMER, R. OHLEMÜLLER, M. EDWARDS, T. PEETERS, A. P. SCHAFFERS, S. G. POTTS, R. KLEUKERS, C. D. THOMAS, J. SETTELE & W. E. KUNIN (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**(5785): 351–354. <http://doi.org/10.1126/science.1127863>
- BINZET, R., I. KANDEMIR & N. ORCAN (2018). Numerical taxonomic study of the genus *Onosma* L. (Boraginaceae) from eastern mediterranean region in Turkey. *Pakistan Journal of Botany*, **50**(2): 561–573. <https://www.pakbs.org/pjbot/papers/1518733663.pdf> [accessed 21 April 2022]
- BOMMARCO, R., O. LUNDIN, H. G. SMITH & M. RUNDLÖF (2012). Drastic historic shifts in bumble-bee community composition in Sweden. *Proceedings of the Royal Society B: Biological Sciences*, **279**(1727): 309–315. <http://doi.org/10.1098/rspb.2011.0647>
- BUCHMANN, S. (1983). Buzz pollination in angiosperms, pp. 73–113. In: C. E. JONES & R. J. LITTLE (eds.). *Handbook of experimental pollination biology*. Scientific and Academic Editions, van Nostrand Reinhold, New York (NY, USA), 558 pp.
- CARDINAL, S., S. BUCHMANN & A. L. RUSSEL (2018). The evolution of floral sonication, a pollen foraging behavior used by bees (Anthophila). *Evolution*, **72**(3): 590–600. <https://doi.org/10.1111/evo.13446>
- COMBA, M. (2019). *Hymenoptera: Apoidea: Anthophila of Italy*. <http://digilander.libero.it/mario.comba> [accessed 21 April 2022]
- DELMAS, R. (1976). Contribution à l'étude de la faune française des Bombidae (Hymenoptera, Apoidea, Bombidae). *Annales de la Société entomologique de France (N.S.)*, **12**(2): 247–290. <https://doi.org/10.1080/21686351.1976.12278571>
- DORCHIN, A., M. M. LÓPEZ-URIBE, C. J. PRAZ, T. GRISWOLD & B. N. DANFORTH (2018). Phylogeny, new generic-level classification, and historical biogeography of the *Eucera* complex (Hymenoptera: Apidae). *Molecular Phylogenetics and Evolution*, **119**: 81–92. <https://doi.org/10.1016/j.ympev.2017.10.007>
- DROSSART, M. & M. GÉRARD (2020). Beyond the Decline of Wild Bees: Optimizing Conservation Measures and Bringing Together the Actors. *Insects*, **11**(9): 649. <https://doi.org/10.3390/insects11090649>
- DUCHENNE, F., E. THÉBAULT, D. MICHEZ, M. ELIAS, M. DRAKE, M. PERSSON, J.-S. ROUSSEAU-PIOT, M. POLLET, P. VANORMELINGEN & C. FONTAINE (2020). Phenological shifts alter the seasonal structure of pollinator assemblages in Europe. *Nature Ecology & Evolution*, **4**(1): 115–121. <https://doi.org/10.1038/s41559-019-1062-4>
- DUKAS, R. & A. DAFNI (1990). Buzz-pollination in three nectariferous Boraginaceae and possible evolution of buzz-pollinated flowers. *Plant Systematics and Evolution*, **169**: 65–68. <https://link.springer.com/article/10.1007/BF00935985>
- ENGEL, M. S. (2006). A new bee of the genus *Cubitalia* in Israel. *Beiträge zur Entomologie*, **56**(1): 61–67. <https://doi.org/10.21248/contr.entomol.56.1.61-67>
- FONDERFLICK, J., P. CAPLAT, F. LOVATY, M. THÉVENOT & R. PRODON (2010a). Avifauna trends following changes in a Mediterranean upland pastoral system. *Agriculture, Ecosystems & Environment*, **137** (3–4): 337–347. <https://doi.org/10.1016/j.agee.2010.03.004>
- FONDERFLICK, J., J. LEPART, P. CAPLAT, M. DEBUSSCHE & P. MARTY (2010b). Managing agricultural change for biodiversity conservation in a Mediterranean upland. *Biological Conservation*, **143**(3): 737–746. <https://doi.org/10.1016/j.biocon.2009.12.014>
- FRIESE, H. (1911). Neue Bienen-Arten der paläarktischen Region (Hym.). *Archiv für Naturgeschichte*, **77**(1/2): 135–143. [https://www.zobodat.at/pdf/Archiv-Naturgeschichte\\_77-1\\_2\\_0135-0143.pdf](https://www.zobodat.at/pdf/Archiv-Naturgeschichte_77-1_2_0135-0143.pdf) [accessed 21 April 2022]
- GARGOMINY, O., S. TERCERIE, C. RÉGNIER, T. RAMAGE, P. DUPONT, P. DASZKIEWICZ & L. PONCET (2021). *TAXREF v15. Référentiel taxonomique pour la France : méthodologie, mise en œuvre et diffusion*. Rapport UMS PatriNat (OFB-CNRS-MNHN). Muséum national d'Histoire naturelle, Paris, 63 pp. <https://inpn.mnhn.fr/telechargement/referentielEspece/taxref/15.0/men u> [accessed 21 April 2022]
- GATHMANN, A. & T. TSCHARNTKE (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, **71**(5): 757–764. <https://doi.org/10.1046/j.1365-2656.2002.00641.x>
- GENOUD, D. & J. FONDERFLICK (2021). *Liste commentée des Hyménoptères Apiformes (Anthophila) du Parc national des Cévennes*. Parc national des Cévennes, Florac-Trois-Rivières (France), 97 pp. [https://www.cevennes-parcnational.fr/sites/cevennes-parcnational.fr/files/available\\_docs/liste\\_commentee\\_apiformes\\_2021\\_pnc\\_def.pdf](https://www.cevennes-parcnational.fr/sites/cevennes-parcnational.fr/files/available_docs/liste_commentee_apiformes_2021_pnc_def.pdf) [accessed 21 April 2022]
- GÉRARD, M., M. VANDERPLANCK, T. WOOD & D. MICHEZ (2020). Global warming and plant-pollinator mismatches. *Emerging topics in Life Sciences*, **4**(1): 77–86. <https://doi.org/10.1042/ETLS20190139>
- GHISBAIN, G., M. GÉRARD, T. J. WOOD, H. M. HINES & D. MICHEZ (2021). Expanding insect pollinators in the Anthropocene. *Biological Reviews*, **96**(6): 2755–2770. <https://doi.org/10.1111/brv.12777>
- GOGALA, A. & B. SURINA (2011). Foraging behaviour of the bee *Osmia apicata* SMITH, 1853 (Hymenoptera: Megachilidae). *Acta entomologica slovenica (Ljubljana)*, **19**(2): 139–144. <https://www.dlib.si/stream/URN:NBN:SI:doc-5SMU8IST/61b9eae-e0f8-4330-b85d-06353b164c09/PDF> [accessed 21 April 2022]
- GRANDI, G. (1931). Contributi alla conoscenza biologica e morfologica degli Imenotteri melliferi e predatori. XII. *Bollettino dell'Istituto di Entomologia dell'Università di Bologna*, **4**: 19–72. <http://www.bullettinofinsectology.org/pdfarticles/vol04-1931-019-072grandi.pdf>
- HUTCHINGS, M. J., K. M. ROBBIRT, D. L. ROBERTS & A. J. DAVY (2018). Vulnerability of a specialized pollination mechanism to climate change revealed by a 356-year analysis. *Botanical Journal of the Linnean Society*, **186**(4): 498–509. <https://doi.org/10.1093/botlinnean/box086>
- POTTS, S. G., V. L. IMPERATRIZ-FONSECA & H. T. NGO (eds.) (2016). Summary for policymakers of the assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. IPBES secretariat, Bonn (Germany), 40 pp. <https://www.ipbes.net/assessment-reports/pollinators> [accessed 21 April 2022] or <https://doi.org/10.5281/zenodo.2616458>
- FISCHER, M., M. ROUNSEVELL, A. TORRE-MARIN RANDO, A. MADER, A. CHURCH, M. ELBAKIDZE, V. ELIAS, T. HAHN, P. A. HARRISON, J. HAUCK, B. MARTÍN-LÓPEZ, I. RING, C. SANDSTRÖM, I. SOUSA PINTO, P. VISCONTI, N. E. ZIMMERMANN & M. CHRISTIE (eds.) (2018). Summary for policymakers of the regional assessment report on biodiversity and ecosystem services for Europe and Central Asia. IPBES secretariat, Bonn (Germany), 52 pp. <https://www.ipbes.net/assessment-reports/eca> [accessed 21 April 2022] or <https://doi.org/10.5281/zenodo.3237468>
- KUHLMANN, M. (ed.), H. H. DATHE, A. W. EBMER, P. HARTMANN, D. MICHEZ, A. MÜLLER, S. PATINY, A. PAULY, C. PRAZ, P. RASMONT, S. RISCH, E. SCHEUCHL, M. SCHWARZ, M. TERZO, P. H. WILLIAMS, F. AMIET, D. BALDOCK, Ø. BERG, P. BOGUSCH, I. CALABUIG, B. CEDERBERG, A. GOGALA, F. GUSENLEITNER, Z. JOSAN, H. B. MADSEN, A. NILSSON, F. ØDEGAARD, F.-J. ORTIZ-SÁNCHEZ, J. PAUKKUNEN, T. PAWLKOWSKI, M. QUARANTA, S. P. M. ROBERTS, M. SÁROPATAKI, H.-R. SCHWENNINGER, J. SMIT, G. SÖDERMAN, B. TOMOZEI & J. ASCHER (2015). *Checklist of the Western Palaearctic Bees (Hymenoptera: Apoidea: Anthophila)*. <http://westpalbees.myspecies.info> [accessed 21 April 2022]
- MICHENER, C. D. (2007). *The bees of the world*. Second edition. The John Hopkins University Press, Baltimore (MA, USA), xvi + [i] + 953 pp. + 20 pls.
- MÜLLER, A. (1995). Morphological specializations in Central European bees for the uptake of pollen from flowers with anthers hidden in narrow corolla tubes (Hymenoptera: Apoidea). *Entomologia Generalis*, **20**(1–2): 43–57. <https://doi.org/10.1127/entom.gen/20/1995/43>
- LE DRIANT, F. (2013). *Onosma fastigiata* (BRAUN-BLANQ.) BRAUN-BLANQ. ex LACAITA, 1924 – Oscanette fastigiée. *Base de données floristique participative du département des Hautes-Alpes. Version 1.30*. France. [https://www.bdflore05.org/zoom\\_espece.php?recherche\\_station\\_espece=4530200](https://www.bdflore05.org/zoom_espece.php?recherche_station_espece=4530200) [accessed 21 April 2022]
- LE DRIANT, F. (2022). Oscanette fastigiée – *Onosma tricosperma* subsp. *fastigiata* (BRAUN-BLANQ.) G. LÓPEZ, 1994. *FloreAlpes*. France.

- [https://www.florealpes.com/fiche\\_onosmafastigiata.php](https://www.florealpes.com/fiche_onosmafastigiata.php) [accessed 21 April 2022]
- LEPART, J., P. MARTY & J. FONDERFLINCK (2011). Dynamique des paysages agro-pastoraux des Causses et biodiversité. *Fourrages*, **208**: 343–352. <https://afpf-asso.fr/article/dynamique-des-paysages-agro-pastoraux-des-causses-et-biodiversite> [accessed 21 April 2022]
- MANINCOR, N. DE (2019). *Écologie des plantes et des pollinisateurs dans les prairies calcaires le long d'un gradient latitudinal en France : diversité des espèces et structure des réseaux d'interaction plantes-pollinisateurs*. PhD thesis, University of Lille (France), 369 pp. [https://pepite-depot.univ-lille.fr/LIBRE/EDSMRE/2019/50376-2019-De\\_Manincor.pdf](https://pepite-depot.univ-lille.fr/LIBRE/EDSMRE/2019/50376-2019-De_Manincor.pdf) [accessed 21 April 2022]
- MARTELLOS, S. & P. L. NIMIS [eds.] (2022). *Portale della Flora d'Italia*. Italy. <https://dryades.units.it/floritaly> [accessed 31 October 2022]
- MNHN & OFB [ed.] (2003-2022). *Onosme à graines à trois cornes, Orcanette à graines à trois cornes Onosma tricosperma LAG., 1816*. Inventaire national du patrimoine naturel (INPN), Paris. [https://inpn.mnhn.fr/espece/cd\\_nom/110298](https://inpn.mnhn.fr/espece/cd_nom/110298) [accessed 31 October 2022]
- NASROLLAHI, F., S. KAZEMPOUR-OSALOO, N. SAADATI, V. MOZAFFARIAN & H. ZARE-MAIVAN (2019). Molecular phylogeny and divergence times of *Onosma* (Boraginaceae s.s.) based on nrDNA ITS and plastid *rpl32-trnL(UAG)* and *trnH-psbA* sequences. *Nordic Journal of Botany*, **37**(1): e02060. <https://doi.org/10.1111/njb.02060>
- PAGLIANO, G. (1994). Catalogo degli Imenotteri italiani. IV (Apoidea: Colletidae, Andrenidae, Megachilidae, Anthophoridae, Apidae). *Memorie della Società Entomologica Italiana*, **72**(1993): 331–467. [https://www.researchgate.net/publication/316587903\\_Catalogo\\_degli\\_Imenotteri\\_italiani\\_IV\\_Apoidea\\_Colletidae\\_Andrenidae\\_Megachilidae\\_Anthophoridae\\_Apidae](https://www.researchgate.net/publication/316587903_Catalogo_degli_Imenotteri_italiani_IV_Apoidea_Colletidae_Andrenidae_Megachilidae_Anthophoridae_Apidae) [accessed 31 October 2022]
- PAGLIANO, G. (1995). Hymenoptera Apoidea. In: A. MINELLI, S. RUFFO & S. LA POSTA (ed.). *Check-list delle specie della fauna Italiana*. **106**. Calderini, Bologna, 25 pp. [https://www.researchgate.net/publication/322978045\\_Hymenoptera\\_Apoidea](https://www.researchgate.net/publication/322978045_Hymenoptera_Apoidea) [accessed 31 October 2022]
- PATINY, S. (1995). *Biogéographie et écologie des Bourdons (Hymenoptera, Apidae) des départements de Lozère et d'Aveyron (France, Massif central)*. Mémoire de fin d'études, University of Mons-Hainaut, Mons (Belgium), 84 + 8 pp. [http://www.atlashymenoptera.net/biblio/01000/Patiny\\_1995\\_Ecologie\\_Bourdons\\_Aveyron\\_TFE.pdf](http://www.atlashymenoptera.net/biblio/01000/Patiny_1995_Ecologie_Bourdons_Aveyron_TFE.pdf) [accessed 21 April 2022]
- RASMONT, P. (1988). Monographie écologique et zoogéographique des Bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae). PhD Thesis, Faculté des Sciences agronomiques de Gembloux (Belgium), 309 + LXII pp. [http://www.atlashymenoptera.net/biblio/00500/Rasmont\\_1988\\_PhD\\_fuII.pdf](http://www.atlashymenoptera.net/biblio/00500/Rasmont_1988_PhD_fuII.pdf) [accessed 21 April 2022]
- RASMONT, P., D. GENOUD, S. GADOUM, M. AUBERT, É. DUFR[É]NE, G. LE GOFF, G. MAHÉ & A. PAULY (2017). *Hymenoptera Apoidea Gallica : liste des abeilles sauvages de Belgique, France, Luxembourg et Suisse*. Atlas Hymenoptera, University of Mons (Belgium), 15 pp. [http://www.atlashymenoptera.net/biblio/01500/414\\_Rasmont\\_et\\_al\\_2017\\_Hymenoptera\\_Apoidea\\_Gallica\\_2017\\_02\\_16.pdf](http://www.atlashymenoptera.net/biblio/01500/414_Rasmont_et_al_2017_Hymenoptera_Apoidea_Gallica_2017_02_16.pdf) [accessed 21 April 2022]
- RISCH, S. (1999). Neue und wenig bekannte Arten der Gattung *Eucera* SCOPOLI 1770 (Hymenoptera, Apidae). *Linzer biologische Beiträge*, **31**(1): 115–145. [https://www.zobodat.at/pdf/LBB\\_0031\\_1\\_0115-0145.pdf](https://www.zobodat.at/pdf/LBB_0031_1_0115-0145.pdf) [accessed 21 April 2022]
- SEDIVY, C., S. DORN, A. WIDMER & A. MÜLLER (2013). Host range evolution in a selected group of osmiine bees (Hymenoptera: Megachilidae): the Boraginaceae-Fabaceae paradox. *Biological Journal of the Linnean Society*, **108**(1): 35–54. <https://doi.org/10.1111/j.1095-8312.2012.02013.x>
- PESENKO, Y. A. & A. A. SITDIKOV (1988). [Classification and phylogenetic Relationships of the genera of the tribe Eucerini (Hymenoptera, Anthophoridae) with two submarginal cells]. *Entomologicheskoye Obozreniye*, **67**(4): 846–860. [in Russian]
- PESENKO, Y. A. & A. A. SITDIKOV (1990). Classification and Phylogenetic Relationships Between Genera of the Tribe Eucerini (Hymenoptera, Anthophoridae) with Two Submarginal Cells. *Entomological Review*, **69**(1): 88–104. [English translation of PESENKO & SITDIKOV, 1988] [http://www.atlashymenoptera.net/biblio/01500/Pesenko\\_&\\_Sitdikov\\_1990\\_Eucerini\\_with\\_two\\_submarginal\\_cells\\_full.pdf](http://www.atlashymenoptera.net/biblio/01500/Pesenko_&_Sitdikov_1990_Eucerini_with_two_submarginal_cells_full.pdf) [accessed 21 April 2022]
- SITDIKOV, A. A. & Y. A. PESENKO (1988). [The subgeneric classification of bees of the genus *Eucera* SCOPOLI (Hymenoptera, Anthophoridae), with a scheme of the phylogenetic relationships between the subgenera]. *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR*, **175**: 75–101. [in Russian]
- STEINMANN, E. (2002). Die Wildbienen (Apidae, Hymenoptera) einiger inneralpiner Trockentäler. *Jahresbericht der Naturforschenden Gesellschaft Graubünden*, **111**(2002): 5–26. <https://doi.org/10.5169/seals-594636>
- STOCH, F. (ed.) (2003). *Checklist of the species of the Italian Fauna*. <https://faunaitalia.it/checklist> [accessed 21 April 2022]
- TEPPNER, H. (1995). Blüten und Blütenbesucher bei *Onosma* (Boraginaceae – Lithospermeae). *Feddes Repertorium*, **106**(5–8): 525–532. <https://doi.org/10.1002/fedr.19961060522>
- TEPPNER, H. (2011). Flowers of Boraginaceae (*Symphytum*, *Onosma*, *Cerinth*) and *Andrena symphyti* (Hymenoptera – Andrenidae): Morphology, Pollen-Portioning, Vibratory Pollen Collection, Nectar Robbing. *Phyton, Annales Rei Botanicae*, **50**(2): 145–180. [https://www.zobodat.at/pdf/PHY\\_50\\_2\\_0145-0180.pdf](https://www.zobodat.at/pdf/PHY_50_2_0145-0180.pdf) [accessed 21 April 2022]
- TEPPNER, H. (2017). The first records of vibratory pollen-collection by bees. *Phyton, Annales Rei Botanicae*, **57**(1–2): 129–135. <http://doi.org/10.12905/0380.phyton57-2018-0129> or [https://static.uni-graz.at/fileadmin/\\_Persoenliche\\_Webseite/teppner\\_herwig/Publicationen/Phyton-57-1-18\\_12-Teppner\\_VPC.pdf](https://static.uni-graz.at/fileadmin/_Persoenliche_Webseite/teppner_herwig/Publicationen/Phyton-57-1-18_12-Teppner_VPC.pdf) [accessed 21 April 2022]
- TISON, J.-M., P. JAUZEIN & H. MICHAUD (2014). *Flore de la France Méditerranéenne*. Naturalia publications, Turriers (France), 2078 pp.
- TKALCÚ, B. (1978). Beiträge zur Kenntnis der Fauna Afghanistans (Sammelergebnisse von O. JAKEŠ 1963–64, D. POVOLNÝ 1965, D. POVOLNÝ & Fr. TENORA 1966, J. ŠIMEK 1965–66, D. POVOLNÝ, J. GAISLER, Z. SEBEK & Fr. TENORA 1967). *Melliturga LATR., Eucera SCOP., Apidae; Lithurge LATR., Stelis Pz., Creightonella COCKILL, Megachilidae, Apoidea, Hym. Časopis Moravského musea v Brně Vědy společenské – Acta Musei Moraviae, Scientiae naturales*, **63**: 153–181.
- TKALCÚ, B. (1984). Revision der Gattung *Cubitalia* FRIESE, 1911 (Hymenoptera, Apoidea). *Annotationes zoologicae et botanicae*, **161**: 1–15. [http://www.atlashymenoptera.net/biblio/01500/Tkalcu\\_1984\\_Revision\\_Gattung\\_Cubitalia\\_full.pdf](http://www.atlashymenoptera.net/biblio/01500/Tkalcu_1984_Revision_Gattung_Cubitalia_full.pdf) [accessed 21 April 2022]
- TKALCÚ, B. (1987). Eine neue Art der Gattung *Eucera* SCOP. aus Kleinasien (Hymenoptera, Apoidea). *Entomologische Nachrichten und Berichte*, **31**(5): 225–227. [https://www.zobodat.at/pdf/EntBer\\_31\\_0225-0227.pdf](https://www.zobodat.at/pdf/EntBer_31_0225-0227.pdf) [accessed 21 April 2022]
- VACHAL, J. (1907). Quelques *Eucera* nouvelles ou peu connues du contour de la Méditerranée [Hym.]. *Annales de la Société entomologique de France*, **76**: 371–378. [http://www.atlashymenoptera.net/biblio/01500/Vachal\\_1907\\_Quelques\\_Eucera\\_nouvelles\\_Mediterranee\\_full.pdf](http://www.atlashymenoptera.net/biblio/01500/Vachal_1907_Quelques_Eucera_nouvelles_Mediterranee_full.pdf) [accessed 21 April 2022]
- ZATTARA, E. E. & M. A. AIZEN (2021). Worldwide occurrence records suggest a global decline in bee species richness. *One Earth*, **4**(1): 114–123. <https://doi.org/10.1016/j.oneear.2020.12.005>
- ZURBUCHEN, A., S. CHEESMAN, J. KLAIBER, A. MÜLLER, S. HEIN & S. DORN (2010). Long foraging distances impose high costs on offspring production in solitary bees. *Journal of Animal Ecology*, **79**(3): 674–681. <https://doi.org/10.1111/j.1365-2656.2010.01675.x>

