

First record of *Celonites osseus* Morawitz, 1888 (Hymenoptera, Vespidae, Masarinae) from Georgia, with notes on its flower association and phylogenetic position

Paul Geisendörfer¹, Volker Mauss², Alexander V. Fateryga³, Manuela Sann^{4,5}

1 Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am Hubland, D-97074 Würzburg, Germany **2** Staatliches Museum für Naturkunde, Abt. Entomologie, Rosenstein 1, D-70191 Stuttgart, Germany **3** T.I. Vjazemsky Karadag Scientific Station – Nature Reserve of RAS – Branch of A.O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Nauki Str. 24, Kurortnoye, 298188 Feodosiya, Russia **4** Naturhistorisches Museum Bern, Bernastrasse 15, CH–3005 Bern, Switzerland **5** University of Bern, Hochschulstrasse 6, CH–3012 Bern, Switzerland

Corresponding author: Volker Mauss (volker.mauss@gmx.de)

Academic editor: Michael Ohl | Received 18 April 2026 | Accepted 7 June 2026 | Published 16 June 2026

<https://zoobank.org/1D8A465A-46D2-40EC-AB45-BB357E121210>

Citation: Geisendörfer P, Mauss V, Fateryga AV, Sann M (2026) First record of *Celonites osseus* Morawitz, 1888 (Hymenoptera, Vespidae, Masarinae) from Georgia, with notes on its flower association and phylogenetic position. Journal of Hymenoptera Research 99: 723–731. <https://doi.org/10.3897/jhr.99.196254>

Abstract

The pollen wasp *Celonites osseus* is recorded for the first time for Georgia from the Vashlovani National Park. It has been observed visiting exclusively flowers of *Heliotropium ellipticum* (Boraginaceae) in a dried rocky riverbed of the Mlashe-Tskali River. The females remove pollen from the concealed anthers with their proboscis performing the same unique and stereotypic behavioural pattern as all other members of the *Celonites cyprius*-group. Flowers of *Heliotropium suaveolens* were not visited by the *C. osseus* females, despite being in bloom. A phylogenetic reconstruction of the mitochondrial cytochrome oxidase I (COI) gene indicates monophyly of the *C. osseus*-complex nested within the *C. cyprius*-group. Based on the COI phylogeny *C. osseus* was identified as sister species to *C. ivanovi*.

Keywords

Barcoding, flower visiting behaviour, oligolecty, Palaearctic, pollen uptake, pollen wasps

Introduction

The pollen wasp *Celonites osseus* Morawitz, 1888 is a member of the *Celonites cyprius*-group (Mauss et al. 2022) that forms a monophyletic clade within the subgenus *Eucelonites* (Mauss et al. 2024). Based on morphological evidence it is closely related to *C. cagrii* Mauss & Yildirim, 2022 and *C. ivanovi* Mauss & Fateryga, 2022, with whom it constitutes the *C. osseus*-complex (Mauss et al. 2022). While *C. cagrii* and *C. ivanovi* are known for being geographically restricted to East Anatolia and the Caucasus, *C. osseus* has a larger distribution area that extends from Armenia over Azerbaijan and Iran to Turkmenistan (Mauss et al. 2022; Fateryga et al. 2025). However, despite its larger distribution range the bionomics of *C. osseus* is still completely unknown, while in other members of the *C. cyprius*-group at least flower visiting behaviour has been extensively studied and described (Mauss et al. 2022, 2024; Fateryga et al. 2025).

The unexpected discovery of a population of *C. osseus* during a visit to the Vashlovani National Park in Georgia by the first author provided the opportunity for field observations of flower visiting behaviour and to collect specimens for morphological determination and DNA barcoding. The national park contains various types of continental steppe habitats and protects flora and fauna of transregional importance for the whole Caucasus region, e.g., one of the last populations of the goitered gazelle, *Gazella subgutturosa* (Güldenstädt, 1780) (Agency of Protected Areas of Georgia 2014). However, to date, the Hymenoptera fauna has been barely studied (Riedel and Japoshvili 2026). Here, we describe the new discovery and ecological observation of *C. osseus* in the Vashlovani National Park and provide initial insights into its phylogenetic placement within the *Celonites cyprius*-group.

Material and methods

The pollen wasps were found during a one-week expedition in the Vashlovani National Park, Georgia. They were observed for 1.5 hours on 10 August 2025. The observation period was from 9:45 am to 11:15 am (UTC+4). Nine females were collected after the observation period as physical records, two of which were immediately pinned and dried for DNA barcoding. Specimens were morphologically identified using the identification key by Mauss et al. (2022). All collections were carried out in accordance with the local guidelines for protected areas and in close collaboration to the local conservation agencies. Plant species of the genus *Heliotropium* Tourn. ex L. were photographed in the field. The pictures were uploaded to [www.inaturalist.org](https://www.inaturalist.org/observations/323226145) (<https://www.inaturalist.org/observations/323226145> and <https://www.inaturalist.org/observations/323226190>) and identified using the characters given in the identification key by Grossheim (1967).

For the photographic documentation, a digital mirrorless camera system was used. Specifically, the camera body employed was the Sony Alpha 6100, equipped with a Sony FE 90 mm f/2.8 Macro G OSS lens. Illumination was supported by an external flash unit (Neewer TT560 Electronic Flash Speedlite), and the camera was fitted with a Pope

Shield Magnetic System diffusor and Pope Shield Roof to ensure soft and even light distribution under variable daylight conditions. Contrast and brightness of the images were adjusted with Adobe Photoshop 2026. Wasp activity and flower visiting behaviour were observed with the naked eye or using the electronic viewfinder of the camera.

DNA barcoding was accomplished by AIM – Advanced Identification Methods GmbH, Leipzig following in-house protocols for DNA extraction, polymerase chain reaction (PCR) amplification of the mitochondrial COI gene region and subsequent Sanger Sequencing. For the extraction of genomic DNA a single leg from each dry specimen or specimens collected and preserved in 96% pure ethanol was provided. DNA barcode sequences were generated for the two newly collected *C. osseus* females and combined with previously generated barcodes from 32 *Celonites* specimens collected in the Mediterranean region and the Middle East (Suppl. material 1). Thus, a total of 34 raw nucleotide sequences were uploaded to the BOLD database (www.BOLDsystem.org). Further, we added another nine COI sequences from *Celonites* specimens that were obtained from the BCHYM- and GBACU-Project of Christian Schmid-Egger and Stefan Schmidt (†) (Suppl. material 1). All specimens were identified morphologically a priori.

Phylogenetic reconstruction was performed using the Molecular Evolutionary Genetics Analysis (MEGA) software v. 12.1.2 (Kumar et al. 2024) comprising 37 nucleotide sequences of the *Celonites cyprius*-group, one from *Celonites crenulatus* Morawitz, 1888 and five from *Celonites jousseaumei* du Buysson, 1906 as outgroup species. All barcode DNA sequences were quality checked and translated into amino acids to check for stop codons. Subsequently, all nucleotide sequences were aligned in MEGA using the Muscle algorithm (Edgar 2004). Phylogenetic reconstruction was performed using the Maximum Likelihood (ML) method and the Kimura (1980) 2-parameter model of nucleotide substitutions and 1000 bootstrap replicates (Felsenstein 1985). The partial deletion option was applied to eliminate all positions with less than 95% site coverage resulting in a final data set comprising 536 positions.

Results and discussion

Records and habitat

Celonites osseus was found in the central eastern area of the Vashlovani National Park in Georgia. This is the first record of the species from Georgia, which is already known to occur in Armenia, Azerbaijan (Nakhchivan Autonomous Republic), Iran, and Turkmenistan (Mauss et al. 2022; Fateryga et al. 2025).

The wasps were observed in a dried riverbed of the seasonal Mlashe-Tskali River, which also partially functioned as access road in the national park (41.1694°N, 46.5678°E, WGS 84; 286 m a.s.l.). The riverbed consisted of coarse gravel with a few higher islands of gravel and washed-up material, such as small tree trunks. Two species of *Heliotropium* were recorded from these seasonal islands, *Heliotropium suaveolens* M. Bieb. and *H. ellipticum* Ledeb. Along a 200 m transect in the riverbed, approximately

30 individuals of *C. osseus* could be observed on those small islands. Due to time constraints, the riverbed was not further assessed, and comparable habitats in the park could also not be monitored. A distribution of *C. osseus* along seasonal riverbeds throughout the national park seems likely.

All observed individuals of *C. osseus* were females that were mainly recorded during flower visits. On a single occasion a female was observed to clean her body, wings and legs, while she was standing on a dried fecal pellet near a small aggregation of *Heliotropium* plants (Fig. 1a). This cleaning behaviour lasted for around 45 seconds.

Flower association

Females of *Celonites osseus* were exclusively observed to visit flowers of *Heliotropium ellipticum*. This indicates that *C. osseus* is probably narrowly oligolectic (*sensu* Müller and Kuhlmann 2008) on the plant genus *Heliotropium*, like all other species of the *C. cyprius*-group for which flower association is known (Mauss et al. 2022, 2024). Visits to flowers of *H. ellipticum* were also observed in the closely related *Celonites cagarii* (Mauss et al. 2022). 37.5% of the photo documented visits of *C. osseus* ($n = 16$) occurred at flowers of *H. ellipticum* that were in a very early stage of anthesis, with their corolla still nearly closed (Fig. 1c, d). This phenomenon was also reported for *C. cyprius* Saussure, 1854 at *H. europaeum* L. and *H. dolosum* De Not. flowers (Mauss et al. 2024) and also observed in *C. ivanovi* at flowers of *H. styligerum* Trautv. (A. Fateryga pers. obs.). It can be assumed that flowers in a very early stage of anthesis offer higher pollen rewards than older flowers, which would explain the common observation of visits to these flowers (Mauss et al. 2024). The females of *C. osseus* were not observed to visit flowers of *H. suaveolens*, even though they were in bloom. This could be the result of differences in flower morphology between *H. ellipticum* and *H. suaveolens* (cf. Riedl 1966) that may prevent the females of *C. osseus* to exploit the flowers of *H. suaveolens*.

The females of *Celonites osseus* removed pollen from the concealed anthers of the *H. ellipticum* flowers with the proboscis. The photo series revealed that pollen uptake is performed by a mostly stereotypic behavioural sequence similar to that of *C. jousseumei* and all members of the *C. cyprius*-group, for which pollen uptake behaviour is known, i.e. *C. rugiceps* Bischoff, 1928, *C. cyprius* and *C. ivanovi* (Mauss et al. 2022, 2024). This behavioural sequence consists of three sections: pollen removal, pollen transfer to the foretarsi and pollen ingestion (for further details see Mauss et al. 2024).

At the beginning of pollen removal, a *C. osseus* female held on to the flower or adjacent parts of the inflorescence with her mid- and hindlegs, while her head was situated above the corolla opening and her foretarsi were positioned on the level surface of the corolla postero-laterally to the sides of her head (Fig. 1b). She then rapidly protruded the proboscis and inserted it into the corolla tube (Fig. 1c),



Figure 1. Behaviour of *Celonites osseus* females at flowers of *Heliotropium ellipticum*. **a** resting and cleaning on feces pellet on the ground close to *Heliotropium* plants **b** protraction of proboscis into the corolla opening at the beginning of pollen removal **c** pollen removal from the corolla tube with the proboscis **d** parallel downward movement of the forelegs along the simultaneously retracting proboscis during pollen transfer **e** pollen removal with proboscis inserted into the corolla tube **f** transition at the end of pollen transfer to next proboscis cycle **g** pollen ingestion from the foretarsi.

where it was partially pro- and retracted in a high frequency, accompanied by up and down movements of the head (Fig. 1e). Directly thereafter, pollen was transferred from the proboscis to the foretarsi by moving the forelegs characteristically parallel downwards from the lower part of the head towards the corolla opening along the simultaneously retracting proboscis (Fig. 1d, f). Then she placed her forelegs back on the surface of the petals, postero-laterally to the sides of her head, protruded her proboscis again into the corolla tube, and the whole sequence was repeated. After a few cycles of pollen removal and transfer to the foretarsi (proboscis-cycles *sensu* Mauss et al. 2024), she switched over to pollen ingestion. For this, the foretarsi were placed parallel to the sides of the head (Fig. 1g). Then the distal ends of the forelegs were alternately drawn backwards through the opened mandibles, from the proximal end of the tibiae towards the distal end of the tarsi. In the process, she consumed the pollen that had accumulated on the forelegs during the preceding proboscis cycles with the mouthparts (Fig. 1g).

Owing to the high similarity of this complex behavioural sequence of the *C. osseus* females with the pollen uptake behaviour performed by the other members of the *C. cyprius*-group and *C. jousseaumei*, it is probably homologous (cf. Mauss et al. 2024). It evolved only once in the stem-line of [*C. jousseaumei* + *C. cyprius*-group] (Mauss et al. 2024) and was probably adopted from the ground-pattern of this clade in *C. osseus*.

Position of *C. osseus* and *C. crenulatus* within the *C. cyprius*-group

The phylogenetic tree reconstruction of the mitochondrial COI gene region indicates that *C. osseus* is deeply nested within the *C. cyprius*-group (Fig. 2). This result is in congruence with the morphological investigations by Mauss et al. (2022) and Fateryga et al. (2025). The identified monophyletic clade comprising *C. cagarii*, *C. ivanovi*, and *C. osseus*, previously described as *C. osseus*-complex by Mauss et al. (2022), is also in congruence with identified similarities in most morphological characters including the apomorphic structure of sternum VIII of the males. Within the *C. osseus*-complex *C. osseus* is more closely related to *C. ivanovi* than to *C. cagarii* (Fig. 2).

The phylogenetic reconstruction further indicates that *C. crenulatus* is nested within the *C. cyprius*-group as the sister group to *C. rugiceps* (Fig. 2). This supports the hypothesis by Mauss et al. (2026) that the *C. crenulatus*-clade might be closer related to the *C. cyprius*-group than to *C. jousseaumei*. This assumption is based on the synapomorphic structure of the harpides of the male genitalia and the structure of the mesosoma (cf. Mauss et al. 2022, 2026). Moreover, the morphological investigation by Mauss et al. (2026) showed that the *C. crenulatus*-clade is probably a basal lineage within the *C. cyprius*-group, since sternum VIII of the males is posteriorly not or only a little convexly produced, which is a plesiomorphic condition (cf. Richards 1962; Mauss et al. 2022). However, to achieve a more detailed resolution of phylogenetic relationships, it remains essential to include nuclear marker genes and a greater number of individuals.

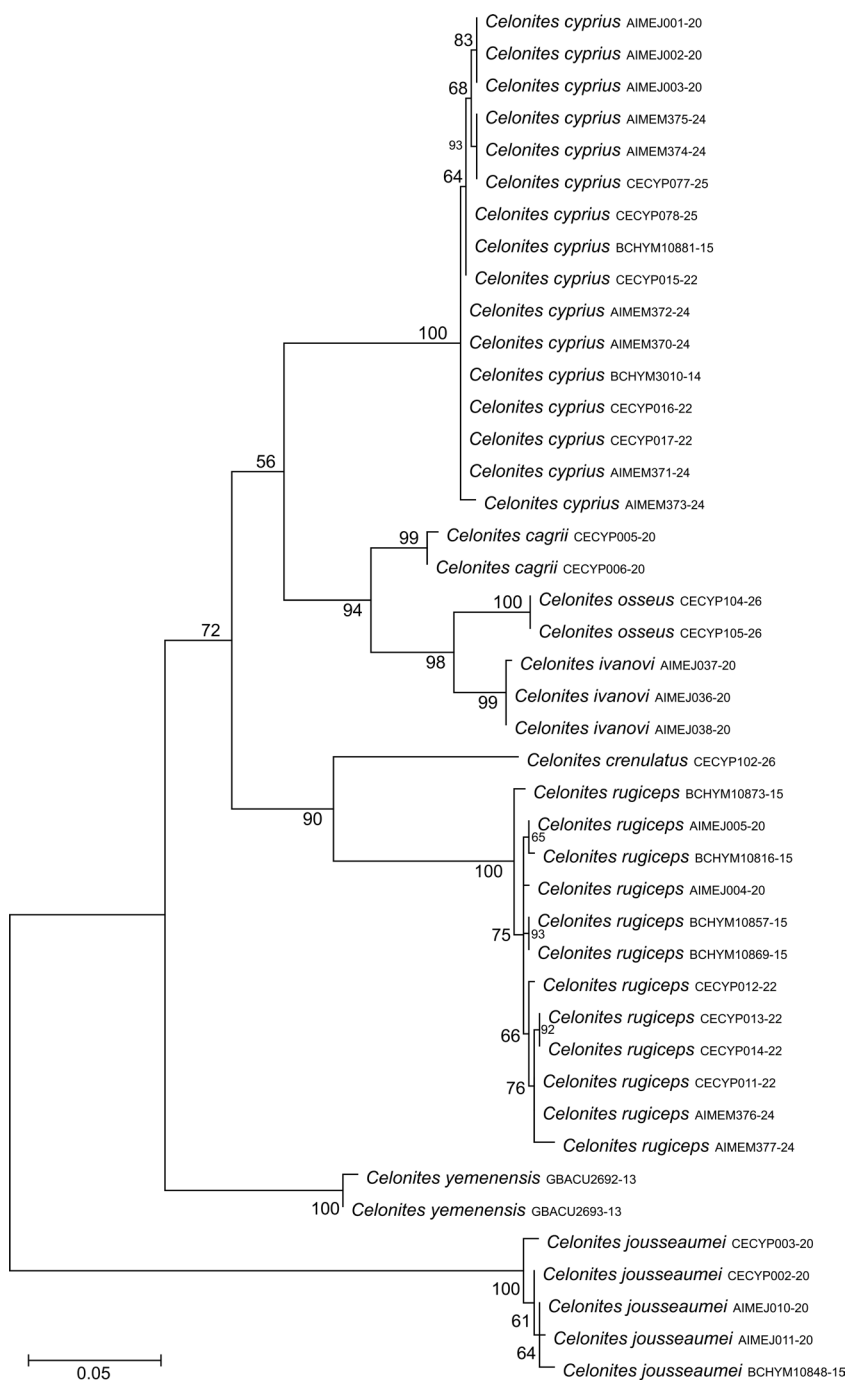


Figure 2. Phylogenetic tree of the *Celonites cyprius*-group. The phylogeny is based on maximum likelihood analysis of 43 COI barcode sequences with *C. jousseaumei* defined as outgroup species. Specimens were assigned to species a priori by morphological characters and are individually marked by BOLD process ID; numbers next to branches indicate statistical support in percent based on 1000 replicates.

Acknowledgements

We deeply want to thank Giorgi Mamadashvili (LEPL Agency of Protected Areas of Georgia) for enabling this expedition to the Vashlovani National Park. Our thanks also go to Christian Schmid-Egger and Stefan Schmidt (†) who provided COI sequences of nine specimens of the *C. cyprius*-group for phylogenetic data analysis. We thank the staff of AIM – Advanced Identification Methods, Leipzig for their good and careful custom service. The work of A. Fateryga was carried out within the state assignment No. 124030100098-0.

References

- Agency of Protected Areas of Georgia (2014) Vashlovani Protected Areas Administration. <http://apa.gov.ge/en/> [Accessed March 31, 2026]
- Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32(5): 1792–1797. <https://doi.org/10.1093/nar/gkh340>
- Fateryga AV, Mauss V, Proshchalykin MYu, Maharramov MM (2025) Taxonomic review of the pollen wasps (Hymenoptera: Vespidae: Masarinae) from the Caucasus, with the description of two new species, new nest and flower-visiting records, and a key to the species. *Zootaxa* 5716(4): 514–540. <https://doi.org/10.11646/zootaxa.5716.4.3>
- Felsenstein J (1985) Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39(4): 783–791. <https://doi.org/10.2307/2408678>
- Grossheim AA (1967) *Flora Kavkaza* [Flora of the Caucasus]. 2nd edn. Volume VII. Nauka, Leningrad, 894 pp. [In Russian]
- Kimura M (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 111–120. <https://doi.org/10.1007/BF01731581>
- Kumar S, Stecher G, Suleski M, Sanderford M, Sharma S, Tamura K (2024) MEGA12: Molecular Evolutionary Genetics Analysis version 12 for adaptive and green computing. *Molecular Biology and Evolution* 41(12): msae263. <https://doi.org/10.1093/molbev/msae263>
- Mauss V, Fateryga AV, Carpenter JM (2026) Identity and distribution of *Celonites crenulatus* Morawitz, 1888 (Hymenoptera: Vespidae: Masarinae) and *Celonites kurzenkoi*, a new species from Turkmenistan. *American Museum Novitates* 4054: 1–24. <https://doi.org/10.1206/4054.1>
- Mauss V, Fateryga AV, Praz C, Zimmermann D, Mauss H, Prosi R (2024) Evolution of different adaptations for pollen uptake from flowers of *Heliotropium* (Boraginaceae) with narrow corolla tube in pollen wasps of the genus *Celonites* (Hymenoptera: Vespidae: Masarinae). *Zoological Journal of the Linnean Society* 202(4): zlae155. <https://doi.org/10.1093/zoolinnean/zlae155>
- Mauss V, Fateryga AV, Yildirim E, Carpenter JM (2022) Contribution to the taxonomy, biometrics and distribution of the Palaearctic *Celonites cyprius*-group (Hymenoptera, Vespidae, Masarinae) with the description of two new species from the North Caucasus and East Anatolia. *Journal of Hymenoptera Research* 89: 109–155. <https://doi.org/10.3897/jhr.89.79832>

- Müller A, Kuhlmann M (2008) Pollen hosts of western palaearctic bees of the genus *Colletes* (Hymenoptera: Colletidae): the Asteraceae paradox. *Biological Journal of the Linnean Society* 95(4): 719–733. <https://doi.org/10.1111/j.1095-8312.2008.01113.x>
- Richards OW (1962) A revisional study of the masarid wasps (Hymenoptera, Vespoidea). *British Museum (Natural History)*, London, [vi +] 294 pp.
- Riedel M, Japoshvili G (2026) New contribution to the Darwin wasps (Hymenoptera: Ichneumonidae) from Vashlovani National Park, Georgia (Sakartvelo), with description of two new species. *Journal of Insect Biodiversity and Systematics* 12(2): 337–356.
- Riedl H (1966) Die Gattung *Heliotropium* in Europa. *Annalen des Naturhistorischen Museums in Wien* 69: 81–93.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.

No AI tools were used in the preparation of this manuscript.

Funding

No funding was reported.

Author contributions

All authors have contributed equally.

Author ORCIDs

P. Geisendörfer  <https://orcid.org/0009-0001-6493-5337>

V. Mauss  <https://orcid.org/0009-0009-9023-2684>

A.V. Fateryga  <https://orcid.org/0000-0002-5346-3477>

M. Sann  <https://orcid.org/0000-0002-5932-6799>

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

Supplementary material I

Further Information on the specimens used for barcoding

Authors: Paul Geisendörfer, Volker Mauss, Alexander V. Fateryga, Manuela Sann

Data type: xlsx

Explanation note: Details of DNA-barcoded specimens used in the maximum likelihood analysis.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.196254.suppl1>