

# The genus *Andrena* Fabricius, 1775 in the southern Balkans (Hymenoptera, Andrenidae)

Thomas J. Wood<sup>1</sup>

<sup>1</sup> *Naturalis Biodiversity Center, Darwinweg 2, 2333 CR, Leiden, Netherlands*

Corresponding author: Thomas J. Wood ([thomas.wood@naturalis.nl](mailto:thomas.wood@naturalis.nl))

---

Academic editor: Jack Neff | Received 24 November 2025 | Accepted 23 March 2026 | Published 29 April 2026

<https://zoobank.org/AF5354E6-9BCA-4CEF-8F41-60D4D2E84471>

---

**Citation:** Wood TJ (2026) The genus *Andrena* Fabricius, 1775 in the southern Balkans (Hymenoptera, Andrenidae). *Journal of Hymenoptera Research* 99: 249–604. <https://doi.org/10.3897/jhr.99.179503>

---

## Abstract

The southern Balkans (here comprising the countries of Albania, North Macedonia, Bulgaria, and Greece including the Greek islands) are known for their large bee faunas due to their mixture of Mediterranean, sub-Mediterranean, temperate, and montane habitats. The bee genus *Andrena* is particularly species-rich in this region, but has lacked a comprehensive modern revision. Here the fauna is comprehensively revised, producing a total of 273 species, with national totals of 243 (Greece), 186 (Bulgaria), 153 (North Macedonia), and 116 (Albania). A full identification key is presented to stimulate further work. The following taxonomic changes are necessary after genetic investigation and inspection of type material: *Andrena* (*Graecandrena*) *repressa* Warncke, 1975, **stat. nov.**; *Andrena* (*Limbandrena*) *toelgiana* Friese, 1921, **sp. resurr.**; *Andrena* (*Holandrena*) *decipiens* Schenck, 1861 = *Andrena* (*Holandrena*) *flavilabris* Schenck, 1874, **syn. nov.**, *Andrena* (*Holandrena*) *forsterella* Osytshnjuk, 1978 = *Andrena* (*Holandrena*) *wilhelmi* Schuberth, 1995, **syn. nov.**; *Andrena* (*Lepidandrena*) *caprimulga* Warncke, 1975 = *Andrena* (*Lepidandrena*) *statusa* Gusenleitner, 1998, **syn. nov.**; *Andrena* (*Melandrena*) *creticola* **stat. rev.**; *Andrena* (*Notandrena*) *meridionalis* Dalla Torre & Friese, 1895, **sp. resurr.** = *A.* (*Notandrena*) *langadensis* Warncke, 1965, **syn. nov.**; *Andrena* (*Notandrena*) *albipila* Warncke, 1967, **stat. nov.**; *Andrena* (*Notandrena*) *clanga* Warncke, 1965, **stat. nov.**; *Andrena* (*Notandrena*) *oblonga* Warncke, 1967, **stat. nov.**; *Andrena* (*Ulandrena*) *subglobosa* Dours, 1873, **sp. resurr.** = *A.* (*Ulandrena*) *kriechbaumeri* Schmiedeknecht, 1883, **syn. nov.**; and *Andrena* (*Campylogaster*) *erberi* Morawitz, 1871 = *Andrena* *kozarovi* Nedialkov, 1914, **syn. nov.** Six new species are described: *Andrena* (*Cryptandrena*) *testudo* **sp. nov.** (Greece: Crete), *Andrena* (*Euandrena*) *bulgarica* **sp. nov.** (Bulgaria and Greece), *Andrena* (*Euandrena*) *obscuricrus* **sp. nov.** (Greece: Crete), *Andrena* (*Graecandrena*) *cretica* **sp. nov.** (Greece: Crete), *Andrena* (*Lepidandrena*) *haladai* **sp. nov.** (Greece), and *Andrena* (incertae sedis) *lasithi* **sp. nov.** (Greece: Crete). Finally, *Leucandrena* Haeckel, 1872, a name for a group of sponges, is

considered to be a *nomen oblitum* and *Andrena* subgenus *Leucandrena* Hedicke, 1933 is considered to be a *nomen protectum*. The final regional species total includes 28 endemic species (10.3%), giving the southern Balkans a comparable but slightly lower endemism rate than the Iberian Peninsula (15.7%) and Morocco (12.2%), but with a meaningfully higher species density per unit area, highlighting the southern Balkans as a global hotspot for the genus *Andrena*.

### Keywords

Balkan endemic species, Cryptic species, DNA barcoding, solitary bees, taxonomy

## Table of contents

Introduction.....	251
Methodology.....	252
Species concepts.....	253
Genetic sampling and analysis.....	254
Identification key and geographic scope.....	255
Checklist and “baseline”.....	256
Distribution maps.....	257
Dietary niches of Balkan <i>Andrena</i> species.....	257
Morphological terminology and imaging.....	258
Abbreviations.....	258
Results.....	259
1. Genetic results and taxonomic changes.....	259
Subgenus <i>Aciandrena</i> Warncke, 1968.....	259
Subgenus <i>Campylogaster</i> Dours, 1873.....	262
Subgenus <i>Cryptandrena</i> Pittioni, 1948.....	263
Subgenus <i>Euandrena</i> Hedicke, 1933.....	267
Subgenus <i>Lepidandrena</i> Hedicke, 1933.....	281
Subgenus <i>Leucandrena</i> Hedicke, 1933.....	286
Subgenus <i>Limbandrena</i> Wood, 2023.....	288
Subgenus <i>Graecandrena</i> Warncke, 1968.....	289
Subgenus <i>Holandrena</i> Pérez, 1890.....	294
Subgenus <i>Melandrena</i> Pérez, 1890.....	300
Subgenus <i>Micrandrena</i> Ashmead, 1899.....	304
Subgenus <i>Notandrena</i> Pérez, 1890.....	307
Identification key for females of the <i>meridionalis</i> -group.....	318
Subgenus <i>Orandrena</i> Warncke, 1968.....	318
Subgenus <i>Poecilandrena</i> Hedicke, 1933.....	321
Subgenus <i>Stenomelissa</i> Hirashima & LaBerge, 1965.....	327
Subgenus <i>Taeniandrena</i> Hedicke, 1933.....	329
Subgenus <i>Truncandrena</i> Warncke, 1968.....	333
Subgenus <i>Ulandrena</i> Warncke, 1968.....	339

2. Description of new species .....	346
<i>Andrena</i> ( <i>Cryptandrena</i> ) <i>testudo</i> sp. nov. ....	346
<i>Andrena</i> ( <i>Euandrena</i> ) <i>bulgarica</i> sp. nov. ....	351
<i>Andrena</i> ( <i>Euandrena</i> ) <i>obscuricrus</i> sp. nov. ....	354
<i>Andrena</i> ( <i>Graecandrena</i> ) <i>cretica</i> sp. nov. ....	357
<i>Andrena</i> ( <i>Lepidandrena</i> ) <i>haladai</i> sp. nov. ....	360
<i>Andrena</i> (incertae sedis) <i>lasithi</i> sp. nov. ....	363
3. Updated faunal list .....	368
Species excluded from the fauna of the southern Balkans .....	439
4. Dietary niches of Balkan <i>Andrena</i> species .....	442
5. Identification key to the <i>Andrena</i> of the southern Balkans .....	451
Identification key to females .....	453
Identification key to males .....	522
Discussion .....	585
Acknowledgements .....	590
References .....	590
Suppl. material 1: Checklist of the <i>Andrena</i> of the southern Balkans .....	604
Suppl. material 2: Additional examined <i>Andrena</i> specimens .....	604

## Introduction

The bee genus *Andrena* is hyper-diverse, with 1,738 species known globally as of May 2025 (Gusenleitner and Schwarz 2002; Wood 2025a), but this number is continuously increasing due to the description of new species (e.g. Herrera et al. 2025; Pisanty et al. 2025), as well as the elevation of some of the many subspecific concepts previously favoured by Klaus Warncke, the leading *Andrena* taxonomist of the 20<sup>th</sup> century. Though not quite as species-rich as the bee genus *Lasioglossum* Curtis, 1833, together these bee genera are in the top 10 most species-rich animal genera by number of described species (Wood 2025a), illustrating their ability to colonise both large parts of the world and a diversity of ecological niches.

Our understanding of the evolution of the genus *Andrena* has markedly improved in the last few years. It is now well-established that the genus emerged approximately 25 million years ago (Bossert et al. 2022; Pisanty et al. 2022a), making it relatively young and hence suggesting a rapid rate of speciation. The pattern of evolution and geographical distribution of basal lineages suggests a likely origin in the East Mediterranean, somewhere around Turkey and the Levant, though with a single intriguing species from the Tibetan Plateau in China (Bossert et al. 2022; Pisanty et al. 2022a; Pisanty and Wood 2024). This likely origin in the East Mediterranean has resulted in very species-rich faunas, particularly in Turkey, Israel, and Greece (e.g. Warncke 1965a, 1969a, 1974a, 1975; Scheuchl and Gusenleitner 2009; Pisanty et al. 2018, 2022b, 2025; Wood 2023a, 2024, 2025a), extending also to the western half of Iran (Wood and Monfared 2022).

Although it is well-known that the East Mediterranean has a species-rich *Andrena* fauna, precise works presenting identification keys are currently lacking. The geographically closest keys cover Germany, Switzerland, and Austria (Schmid-Egger and Scheuchl 1997), Ukraine and European Russia (Osytshnjuk 1978), and the Central and Eastern Palaearctic from the Caucasus eastwards (Osytshnjuk et al. 2005, 2008). A prospective bee worker aiming to engage with the Greek fauna therefore has no suitable or practical identification resources available to them; this is problematic when *Andrena* alone represent around 20% of the bee species found in Greece. The current situation is therefore very similar to the case in the Iberian Peninsula, where no comprehensive *Andrena* identification keys were available prior to the work of Wood (2023b).

However, when considering the southern Balkan region within the East Mediterranean (here defined as Albania, North Macedonia, Bulgaria, and Greece), one can see that a reasonable number of taxonomists have worked on this fauna descriptively. The 68 currently valid *Andrena* species with a *locus typicus* in the southern Balkans were described by 11 authors in 17 publications (Brullé 1833; Smith 1853; Morawitz 1871; Dours 1873; Strand 1915, 1921; Friese 1923; Hedicke 1942; Warncke 1965a, 1973, 1975; Grünwaldt 1976; Grünwaldt et al. 2005; Scheuchl 2010; Scheuchl 2011; Wood 2021, 2024a), and additional workers described synonymous taxa (e.g. Kriechbaumer 1873; Alfken 1904; Nedialkov 1914; Friese 1922; Schuberth 1995). Whilst this represents a broader body of study than for Iberia, with only six such publications describing currently valid *Andrena* species before Wood (2023b), it is still only a moderately wide descriptive baseline (particularly in the 19<sup>th</sup> century) when compared to better-studied genera such as *Bombus* Latreille, 1802 (Rasmont et al. 2021).

The purpose of the current work is to revise the *Andrena* fauna of the southern part of the Balkan Peninsula utilising museum specimens (historical and modern collections) and newly available DNA barcodes to clarify the identity of the species present, to continue outstanding and necessary descriptive work (Wood 2021, 2024a), and to produce an up-to-date comprehensive identification key that can be used in the upcoming European Pollinator Monitoring Scheme (EU-PoMS). Novel data on the ecological niches of East Mediterranean *Andrena* species are also presented, hoping to stimulate new ecological study of this diverse lineage of bees.

## Methodology

The layout of the paper follows that of Wood (2023b) as closely as possible for consistency and ease of use for workers who wish to cross-reference the two works. For results, they are presented as 1) the results of the genetic analyses are presented first along with necessary taxonomic changes based on interpretation and type inspection; these results are presented subgenus-by-subgenus; 2) Description of new species; 3) Updated faunal list, with literature references and material support for new country listings; 4) Dietary niche of Balkan *Andrena* species; and 5) Identification key to the *Andrena* of the southern Balkans.

## Species concepts

Given the enormous diversity of the genus, and the variable species concepts that have been applied over time, a brief statement of *Andrena* species concepts is necessary. The concepts presented here follow the philosophy presented in Wood (2023b). Overall, the study of *Andrena* is insufficiently advanced to be able to meaningfully apply biological species concepts, as is the case in the much less species-rich and much better studied genus *Bombus* (e.g. Williams et al. 2020; Rasmont et al. 2021). The scientific community collectively has an extremely limited understanding of their mating systems and pre- and post-zygotic reproductive barriers, with this only being estimated post hoc by quantifying realised gene flow (e.g. McLaughlin et al. 2022).

This is highly relevant as the Balkan Peninsula is known to have acted as a glacial refugium during the Quaternary glaciations (e.g. Ursenbacher et al. 2008; Postolache et al. 2017; Gömöry et al. 2020), but this has been very little studied in bees. As results are presented, a common distribution pattern is seen between closely related *Andrena* species of allopatric distributions, most typically with a “Greek” species present in continental Greece and Albania, extending into central Greece but not typically reaching Thessaloniki, and a “Anatolian” species which can be present on the East Aegean Islands and which enter the continental Balkans in Thrace (south-eastern Bulgaria and north-eastern Greece). Equally, these species do not typically extend beyond Thessaloniki. The region between Thessaloniki and Kavala can broadly be considered a “transition zone” between these two faunal influences, for both *Andrena* as presented here and a great many other vertebrate and invertebrate taxa (Poulakakis et al. 2015). Importantly, these closely related *Andrena* species do not seem to come into contact or form contact zones, as can happen in the *Andrena proxima*-group, for example (McLaughlin et al. 2022). The extent to which they are actually unable to interbreed (i.e. pre- and/or post-zygotic reproductive barriers have formed) or to what degree they have adapted to slightly different climatic conditions and naturally have non-overlapping distributions is unknown.

In this context, given the limitations in our knowledge, conservative species concepts are adopted, specifically that it is best to consider *Andrena* species to be evolutionarily independent lineages (de Queiroz 2007), and that through the application of integrative taxonomy (including genetic, morphological, and ecological data), one can arrive at a robust species concept (Schlick-Steiner et al. 2010). This maintains the greatest consistency with the morphological species concepts developed by previous workers (most clearly Warncke). However, the subspecific concepts used by Warncke are not followed here, and some specific cases are dealt with below in a critical framework aimed at identifying species-species distinctions. Whilst some of Warncke’s Iberian subspecies were pragmatically and functionally retained in the revision of Wood (2023b), they were subsequently treated as good taxa (Wood 2024a), and hence efforts here aim to provide consistent clarity at a specific level.

## Genetic sampling and analysis

As in Wood (2023b), morphological species delineation was complimented by genetic delineation based on the COI barcoding gene. New samples were collected in Greece in May 2023 (Eastern Macedonia and Thrace, Central Macedonia), March/April 2024 (Peloponnese, Central Greece), June 2024 (Western Macedonia, Central Macedonia), and in Bulgaria (Blagoevgrad) in May 2024. Additional specimens from museum and private collections were also sometimes sampled. The BeeCox1F1 primer (Bleidorn and Henze 2021) was always used, but samples were processed differentially. Sequences beginning with the prefix WPATW or ORBIT were sent to the Canadian Center for DNA barcoding (CCDB) in Guelph, Canada, for DNA extraction and sequencing (Ivanova et al. 2006). Specimens were sequenced following standardised high-throughput protocols. Sequences beginning with the prefix “NATBE” were sequenced at the Naturalis Biodiversity Center laboratories using an Oxford Nanopore GridION sequencer. The full methodology is detailed in Wood (2025b).

The newly generated sequences were then complimented with sequences from Genbank, BOLD, and published sources, e.g. Schmidt et al. (2015), Pisanty et al. (2022b), and Wood et al. (2024a). An important source of sequences (prefix “BGENL”) was sequences generated from historical specimens from the Naturalis Biodiversity Center collection (RMNH) as part of the Biodiversity Genomics Europe (<https://portal.boldsystems.org/recordset/DS-BGEMS>). These specimens were revised by myself in order to ensure consistency with the species concepts applied here. Sequences were aligned using MAFFT (Katoh and Standley 2013). Aligned sequences were analysed in Seaview (Gouy et al. 2010) using a maximum likelihood analysis, which was run with 1000 bootstraps. Intra- and interspecific distances were calculated using MEGA-X (Kumar et al. 2018). Outgroups were chosen based on the subgeneric analysis of Pisanty et al. (2022a) in order to ensure that the selected outgroup species is part of a subgenus or species group that diverges earlier in evolutionary time (“basal”) relative to those selected for focused study. Trees were made in FigTree v1.4.4 (Rambaut 2018) and processed in Adobe Illustrator.

As in Wood (2023b), analysis of the COI gene is not the sole basis for making taxonomic decisions. DNA barcodes have a number of important limitations, and an integrative approach is adopted here to take account of multiple lines of evidence, including morphology, phenology, and biogeography. For a more extensive discussion of the limits of DNA barcoding in the context of *Andrena* taxonomy, the reader is asked to refer to Wood (2023b: 246–247). The alpha taxonomy of bees is still strongly based on morphology, and when genetic techniques are used, it is almost always through the use of DNA barcoding. Whilst use of next generation sequencing and inclusion of nuclear DNA would be greatly preferable, molecular species delineation in bees remains highly dependent on DNA barcodes, as is the case even in better studied vertebrates (e.g. Wüster 2025). The use of such techniques remains aspirational and a model to work towards (e.g. McLaughlin et al. 2022).

## Identification key and geographic scope

The geographic scope adopted in this study is somewhat arbitrary. Whilst the Iberian Peninsula is neatly defined by the Pyrenees mountains and the consequent political border between Spain and France, no such division exists in the Balkan Peninsula. Based on the quantity of examined material, the countries of Greece (13,165 examined specimens), Bulgaria (6,254 examined specimens), North Macedonia (319 examined specimens), and Albania (846 examined specimens) were selected, for a total of 20,584 examined specimens. Geographically, these countries cover the southern part of the Balkan Peninsula, and have received the greatest historical study, particularly Greece. Whilst Montenegro, Kosovo, and southern Serbia have an *Andrena* fauna that is very similar to that of these four countries, they were not specifically included in this scope. This is because I have been able to examine only a small handful of specimens from Montenegro, Kosovo, and southern Serbia, and I consider knowledge of this region to be very much a “work in progress”. It is hoped that the publication of the current work will stimulate and facilitate research in, for want of a better term, the “central” Balkans.

Whilst southern Romania is not explicitly included in the geographic scope above, the species *Andrena dacica* Wood, 2024 is included in the key, as it was described from southern Romania and is known from just a few kilometres from the border with Bulgaria (Wood 2024a). The opportunity is also taken to present a few new records for the Romanian fauna for species that just enter the south of this country and which are more characteristic of the fauna of the southern Balkans. The southern portion of Romania in a band reaching at most 100 km north of the Bulgarian border can consequently broadly be considered as part of the southern Balkans due to the presence of southern Balkan *Andrena* faunal elements.

In the context of this geographic scope, the identification key will be useable across much of the Balkans, roughly up to southern Croatia (southern Dalmatia), Montenegro, Kosovo, southern Serbia, and across southern Romania. However, as one begins to move further north, Adriatic (e.g. *Andrena croatica* Friese, 1887; *Andrena korleviciana* Friese, 1887), Pannonian (e.g. *Andrena hungarica* Friese, 1887), and Eurasian steppe elements (e.g. *Andrena comta* Eversmann, 1852; *Andrena nanaeformis* Noskiewicz, 1924; *Andrena pillichii* Noskiewicz, 1939; *Andrena roseipes* Alfken, 1933) begin to appear. The overall species coverage however is high, and the identification key can be used under advisory, in combination with works such as Schmid-Egger and Scheuchl (1997).

For the island of Cyprus, only 51 of the 77 species present are included (66.2%), with naturally no coverage of the nine *Andrena* species endemic to the island. Also missing are 17 species with Turkish and/or Levantine affinities. The key can therefore only be used for a superficial identification, or a “first pass” to potentially recognise the more generic elements of the fauna.

Even more challenging is the use of the key in Turkey. Whilst the key should cover all species in European Turkey (Thrace), it very quickly becomes of limited use even in western Asiatic Turkey (Çanakkale, İzmir, Aydın, Muğla), and the moment one “turns the corner” from the province of Muğla to the province of Antalya or gains altitude and

enters the Anatolian plateau, the *Andrena* worker is assaulted by a wave of Levantine, Anatolian, and Turko-Iranian faunal elements which do not enter the southern Balkans. Of the 273 species included here in the identification key, 210 occur also in Turkey (76.9%). However, for overall coverage of the Turkish *Andrena* fauna (392 species; Wood 2023a, 2024a, 2025a; unpublished data), the key covers only 53.3% of the fauna. The coverage is similar to that of the Lebanese fauna, covering 79 of the 154 species (51.3%, unpublished data). In this regard, the coverage is very similar to the coverage of the Moroccan *Andrena* fauna by the Iberian key of Wood (2023b) at around 50%. Given the enormous size of the Turkish *Andrena* fauna combined with the high number of (often basal) phylogenetic lineages present (Turkey being the centre of *Andrena* diversity along with the Levant; Pisanty et al. 2022a; Pisanty and Wood 2024), a dedicated Turkish key is needed to properly study this fauna. In short, the reader is advised to take care when using this key to identify specimens outside of the southern Balkans, as taxa will either be missing or may present a meaningfully different morphology.

### Checklist and “baseline”

The faunistic study of Balkan *Andrena* has been fragmentary. Warncke (1965a) produced a checklist of the *Andrena* of Greece, listing 136 species. Warncke (1966) reported new records from Albania, and also presented a checklist for Balkan *Andrena*, listing 68 species from Bosnia, 10 from Montenegro, 44 from Serbia, 59 from Macedonia, 45 from Albania, 131 from Greece, and 50 from Bulgaria. Further sporadic records were published in Warncke (1967a, 1969b). Warncke (1973) then worked more synthetically on the Balkan *Andrena* fauna, listing 102 species from “Yugoslavian Macedonia”, 52 species from “Greek Macedonia”, and 56 species from “Bulgarian Macedonia”. Warncke (1988) would publish one further work dealing with Greek *Andrena*, but there was never another formal update to the Greek *Andrena* faunal total.

Further works (e.g. Atanassov 1972; Grünwaldt 1976; Atanassov and Vasileva 1990; Grünwaldt et al. 2005; Scheuchl 2010, 2011; Standfuss et al. 2011) continued to add to our knowledge of the region, but piece by piece and without an integrated perspective. Other than the work of Wood (2021) who revised the Bulgarian *Andrena* fauna, there is no clear baseline (e.g. Ortiz-Sánchez 2011, 2020) from which to judge changes to faunal knowledge in the southern Balkans, as was the case in the revision of Wood (2023b) for the Iberian fauna. For this reason, it is beneficial to produce an updated faunal list for the entire region, citing the most relevant works and presenting examined material where new species are recorded for a country. The literature compiled by Warncke (1965a) for the Greek fauna is not reproduced (other than a few key publications), and workers should examine that work for more comprehensive detail. The same is true for Wood (2021) on the Bulgarian fauna, with necessary updates and corrections indicated below. However, Toshko Ljubomirov (IBER) communicated several important Bulgarian faunal works either published in Bulgarian (Nedialkov 1914; Drenowski 1934, 1936; Atanassov 1962, 1964) or which are generally obscure (Meunier 1897), and which were consequently overlooked during the work of Wood (2021). These are

referenced below, where appropriate. Finally, Gusenleitner and Schwarz (2002) and the distribution maps they present which were created by Warncke (as part of his unpublished West Palaearctic *Andrena* monograph) can be treated as a general distributional resource, and so are only cited where relevant and where discussion is needed.

Given the size of the *Andrena* fauna of the southern Balkans, it is inevitable that some regional works will be unintentionally overlooked, but this current compilation and revision provides an explicit framework by which species are considered present or absent, or for which reasons they are considered newly recorded or excluded. Countries marked with an “\*” denote the first published record from that country. Specimen records are presented where necessary, with an effort to not re-publish recently published records (e.g. Wood 2021). Due to its deep revision of the published literature and collation of additional online resources and specimen databases, the checklist of Ascher and Picking (2025) is also consulted as an independent data source. Reverté et al. (2023) is also consulted in few specific cases, but as it is not primary literature and does not present precise specimen records, it is only referenced occasionally.

A summarised version of the final species checklist and country presence/absence data can be found in Suppl. material 1.

## Distribution maps

Due to the study of Balkan *Andrena* by Klaus Warncke and the distribution maps he produced in the context of a West Palaearctic revision (included in the work of Gusenleitner and Schwarz 2002), as well as the distribution maps produced in the context of the 2<sup>nd</sup> European Red List of Bees (Michez et al. 2026), it is not considered necessary to comprehensively produce distribution maps for all Balkan *Andrena* species. However, where there has been taxonomic confusion, a general lack of clarity, name changes, or few published specimen records, new distribution maps are selectively presented here based on specimens examined during the development of this work and study of *Andrena* collections since 2019. Specimen data used to construct the distribution maps are available in the Suppl. material 2. Maps were made in R version 4.4.2 (R Core Team 2024) using packages “ggplot2” and “rnatuarearth”. Distribution maps are given with the disclaimer that the data they present are not comprehensive, as despite the best efforts, revising all specimens of a species is not possible, and consequently some (hopefully) minor discrepancies will exist.

## Dietary niches of Balkan *Andrena* species

In line with Wood (2023b), pollen was removed from female *Andrena* specimens in order to quantify the pollen foraging niche of understudied Balkan species. Specimens were selected from the Balkans, and sometimes Turkey where appropriate specimens were available. Pollen was removed, processed, and identified following the methodology of Wood and Roberts (2018). Dietary classification (polylecty, mesolecty, oligolecty, narrow oligolecty) follows Müller and Kuhlmann (2008).

## Morphological terminology and imaging

Morphological terminology follows Michener (2007), with the exception of the marginal “zones” of the terga, which are referred to as marginal “areas”, “antennal segments” which are numbered A1–12(13) (rather than scape, pedicel, and antennomeres 1–10(11)), and “nervulus” rather than vein cu-v in the forewing. Specimens were measured from the centre of the clypeus at the front of the head to the apical tip of the metasoma to the nearest 0.5 mm. Photographs were taken using an Olympus E-M1 Mark II with a 60 mm macro lens. Additional close-ups were taken with the addition of a Mitutoyo M Plan Apo 5X infinity corrected objective lens. Photographs were stacked using Helicon Focus B (HeliconSoft, Ukraine) and plates were prepared in GNU Image Manipulation Program (GIMP) 2.10. Post-processing of some images was made in Photoshop Elements (Adobe Systems, USA) in order to improve lighting to highlight specific characters.

The following abbreviations are used in the species descriptions: **A** = antennal segments, **S** = metasomal sterna, and **T** = metasomal terga. Subgeneric concepts follow Pisanty et al. (2022a) with the necessary modifications detailed below. In diagnoses, the defining characters of a species are given, with those of the indicated comparison species given in parentheses. Unless otherwise stated, all specimens were identified by myself. In the case of other listed identifiers (stated in individual specimen entries), inspection and validation was conducted.

## Abbreviations

<b>ADC</b>	Personal collection of Achik Dorchin, Brussels, Belgium
<b>CEGX</b>	Conservatoire entomologique de Gembloux, Gembloux Agro-Bio Tech, Gembloux, Belgium
<b>CSE</b>	Personal collection of Christian Schmid-Egger, Berlin, Germany
<b>DEI</b>	Deutsches Entomologisches Institut, Eberswalde, Germany
<b>EBDC</b>	Estación Biológica de Doñana, CSIC, Sevilla, Spain
<b>IBER</b>	Bulgarian Academy of Sciences, Institute of Biodiversity and Ecosystem Research, Sofia, Bulgaria
<b>IUZC</b>	University of Istanbul Zoology Collection, Istanbul, Turkey
<b>JSPC</b>	Personal collection of Jakub Straka, Prague, Czechia
<b>KJCB</b>	Personal collection of Kobe Janssen, Zonhoven, Belgium
<b>LBCM</b>	Personal collection of Leander Bertsch, Munich, Germany
<b>MHNN</b>	Muséum d'histoire naturelle de la ville de Neuchâtel, Switzerland
<b>MNHN</b>	Muséum national d'Histoire naturelle, Paris, France
<b>MSNG</b>	Museo Civico di Storia Naturale “Giacomo Doria”, Genoa, Italy
<b>MSVI</b>	Personal collection of Marco Selis, Viterbo, Italy
<b>MZH</b>	Finnish Museum of Natural History, Helsinki, Finland
<b>MZUR</b>	Museo di Zoologia, Sapienza Università di Roma, Rome, Italy
<b>NHMW</b>	Naturhistorisches Museum Wien, Vienna, Austria
<b>NMNHs</b>	National Museum of Natural History, Sofia, Bulgaria
<b>NMPC</b>	National Museum Natural History, Prague, Czechia

<b>NHMUK</b>	Natural History Museum, London, United Kingdom
<b>NZMS</b>	National Museum of Natural History, Sofia, Bulgaria
<b>OÖLM</b>	Oberösterreichs Landesmuseum, Linz, Austria
<b>OUMNH</b>	Oxford University Museum of Natural History, Oxford, United Kingdom
<b>RBINS</b>	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
<b>RLDC</b>	Personal collection of Romain Le Divelec, Mons, Belgium
<b>RMNH</b>	Naturalis Biodiversity Center, Leiden, the Netherlands
<b>SFC</b>	Personal collection of Simone Flaminio, Mons, Belgium
<b>SIZK</b>	Scientific Collections of the Schmalhausen Institute of Zoology, Kyiv, Ukraine
<b>SMFD</b>	Naturmuseum Senckenberg, Frankfurt am Main, Germany
<b>SPMRC</b>	Personal collection of Stuart P.M. Roberts, Salisbury, United Kingdom
<b>SMNH</b>	Steinhardt Museum of Natural History, Tel-Aviv University, Tel-Aviv, Israel
<b>TJWC</b>	Personal collection of Thomas J. Wood, Leiden, the Netherlands
<b>TUZ</b>	Zoological Museum of the University of Tartu, Tartu, Estonia
<b>UMONS</b>	Laboratory of Zoology collection, University of Mons, Mons, Belgium
<b>VLC</b>	Personal collection of Vincent Leclercq, Dijon, France
<b>WHLC</b>	Personal collection of Wolf-Harald Liebig, Bad Muskau, Germany
<b>WML</b>	World Museum, Liverpool, United Kingdom
<b>WVC</b>	Personal collection of Win Vertommen, Diest, Belgium
<b>ZMHB</b>	Museum für Naturkunde, Berlin, Germany
<b>ZSM</b>	Zoologische Staatssammlung München, Germany

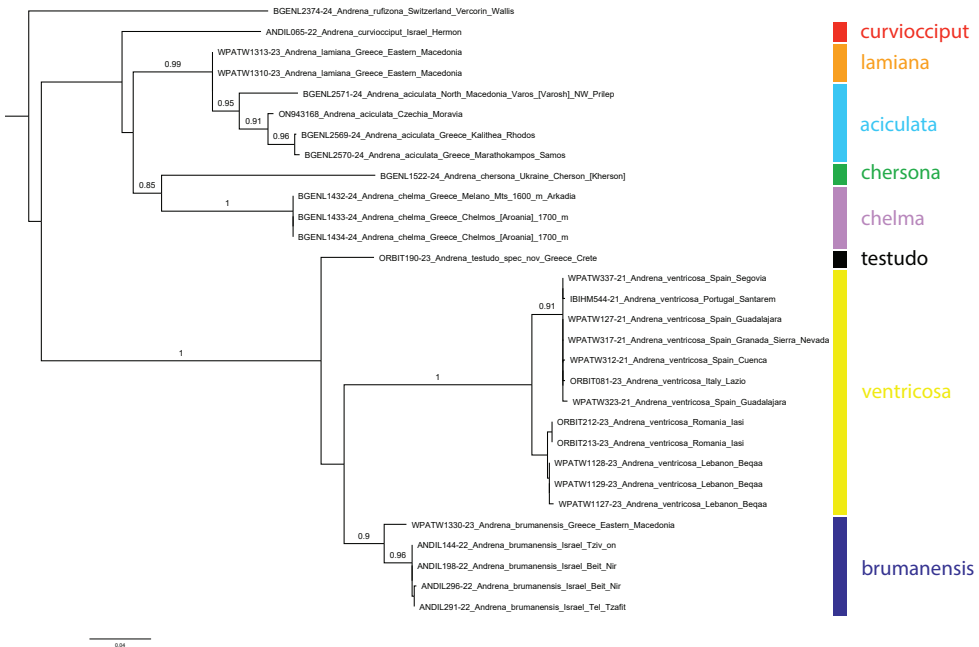
## Results

### 1. Genetic results and taxonomic changes

#### Subgenus *Aciandrena* Warncke, 1968

**Genetics.** The subgenus *Aciandrena* is taxonomically complex, and difficult to characterise both morphologically and genetically using barcodes. Some taxa placed in the subgenus such as *Andrena janthina* Warncke, 1975 (see Gusenleitner and Schwarz 2002) actually represent undescribed subgenera (Pisanty et al. 2022a, 2022b), and are not considered here, as all constituent species are Levantine (S. Bossert, G. Pisanty, T.J. Wood, unpublished data). Even in a narrow sense, *Aciandrena* s. str. seems particularly prone to the generation of NUMTs (Nuclear Mitochondrial DNA sequences) based on results from nanopore sequencing which can produce multiple different sequences from the same individual (unpublished data). As such, individual unusual sequences must be treated with great care to avoid the overdescription of taxa, particularly since females are often impossible to separate with confidence morphologically.

A particularly troublesome species pair are *Andrena aciculata* Morawitz, 1886 and *Andrena lamiana* Warncke, 1965. Males are separable after dissection and examination of the apex of sternum 8 (truncate in *A. aciculata*, narrowly pointed in *A. lamiana*,



**Figure 1.** Phylogenetic tree (maximum likelihood) of *Andrena* subgenera *Aciandrena* Warncke, 1968 and *Cryptandrena* Pittioni, 1948 based on the mitochondrial COI gene. *Andrena (Lepidandrena) rufizona* Imhoff, 1834 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

see male identification key), but females are much more challenging if not impossible to separate morphologically. Genetically, sequences of *A. aciculata* were available from Czechia, North Macedonia, and Greece (Samos, Rhodes), and sequences of *A. lamiana* were available from Greece (East Macedonia; Fig. 1). *Andrena aciculata* showed moderate intraspecific variation of 3.37% (range 0.45–6.28%) but formed a ladder of sequences towards *A. lamiana*. The two *A. lamiana* sequences were identical, and were separated from *A. aciculata* by an average genetic distance of 3.76% (range 0.86–5.05%). Resolution of these two taxa remains obscure, and it is very possible that many specimens are misidentified in the female sex. Identification continues to rely on dissection of males. Additional focused study of this subgenus using additional molecular tools including nuclear DNA is necessary to resolve species boundaries across the East Mediterranean and Middle East.

### *Andrena (Aciandrena) chelma* Warncke, 1975

*Andrena (Aciandrena) chelma* Warncke, 1975: 66, ♀ [Greece, OÖLM, examined]

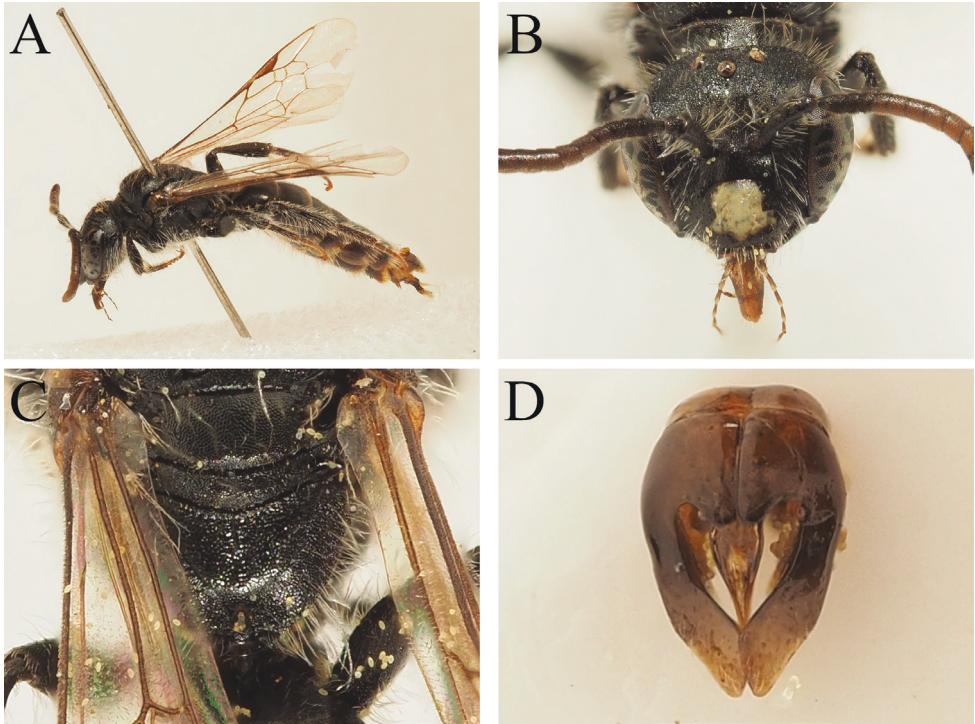
**Material examined.** GREECE • 2♀; Chelmos, Peloponnese; 4 Jun. 1962; M. Schwarz leg.; OÖLM (**holotype** and **paratype**) • 1♀; Chelmos, Peloponnese; 4 Jun. 1962; M.

Schwarz leg.; OÖLM (**paratype** of *Andrena pulicaria* Warncke, 1975) • 1♀; Chelmos, Peloponnes; 1900 m a.s.l.; 4 Jun. 1962; M. Schwarz leg.; OÖLM (not part of type series; originally determined as *Andrena tenuis* Morawitz, 1877 by Warncke) • 1♂, 1♀; Chelmos [Aroania]; 1700 m a.s.l.; 27–29 May 1987; H. Teunissen leg.; RMNH • 1♀; Melano Mts (Arkadia); 1600 m a.s.l.; 27 May 1986; H. Teunissen leg.; RMNH • 2♀; Pelop. Tripolis 30 km Sparta; 870 m a.s.l.; 23 Apr. 2014; K. Deneš leg.; OÖLM • 4♂, 1♀; Peloponnes, Mount Maenalon, 4.5 km NW Kardaras; 1600 m a.s.l.; 4 Apr. 2024; T.J. Wood leg.; TJWC • 19♂, 2♀; Central Greece, Mt. Parnassos, 4.4 km NNW of Kalyvia Livadiou Arachovas; 1250 m a.s.l.; 9 Apr. 2024; T.J. Wood leg.; TJWC.

**Notes.** Warncke (1975) introduced a complicated situation when describing *A. chelma*. On page 66 he described *A. chelma* in the female sex only (male newly diagnosed below) with the holotype coming from Chelmos in the Peloponnes (Mount Aroania). Then, on page 68 he described *A. pulicaria* in both the female and male sexes, with a female holotype coming from Ürgüp in central Anatolia in Turkey. Additional paratypes came from Yeşilhisar and Konya (Warncke 1974a: 100). However, in Warncke (1975: 69) he writes “außerdem Griechenland: Chelmos”. Indeed, in the Warncke collection there is a female paratype of *A. pulicaria* from the exact same collecting event (4 Jun. 1962) as the type series of *A. chelma*. The two species are very similar in the female sex due to the elongate head with the process of the labrum extremely small, narrowly triangular and pointed (see also *Andrena afghana* Warncke, 1974).

Furthermore, a specimen in Warncke’s boxes of “in progress” material (i.e. outside of the main catalogued Warncke collection) contained another specimen from the same collecting event which was determined by Warncke as *A. tenuis*, a species that does not occur in Greece. As Warncke never dated his determination labels (e.g. see Ebmer 1999: 183), it is not possible to reconstruct a timeline as to how his species concepts developed. Examination of the specimens from Chelmos (determined by Warncke as *A. chelma*, “*A. pulicaria*”, and “*A. tenuis*”), as well as additional specimens collected by Teunissen and contemporary collections suggests that there is just a single taxon in Greece that can be referred to as *A. chelma*. Morphological differentiation in female *Aciandrena* species is extremely challenging, but the newly recognised males can be diagnosed with reference to their genital capsule. New sequences of *A. chelma* have been generated from Chelmos and the Melano mountains (Fig. 1); additional sequencing from Turkey is required to understand genetic differentiation from *A. pulicaria*.

**Diagnosis.** The male of *A. chelma* can be recognised as an *Aciandrena* due to its small body size (Fig. 2A), overall dark integument with the exception of a partially yellow-marked clypeus (Fig. 2B), finely granulose propodeal triangle (Fig. 2C; lacking lateral or internal rugae), and “typical” genital capsule which has gonocoxae teeth and elongate gonostyli (Fig. 2D; not as in *Graecandrena* Warncke, 1968 with the gonostyli short and stubby and without gonocoxal teeth). The genital capsule is elongate, which allows separation from *Andrena aciculata* Morawitz, 1886 and *Andrena lamiana* Warncke, 1965 (see photographs in the identification key below), placing *A. chelma* close to *A. pulicaria*. The two species can be separated due to the genital capsule. In *A. chelma*, the inner margins of the gonostyli are raised but smooth, without a kink



**Figure 2.** *Andrena (Aciandrena) chelma* Warncke, 1975 male. **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Propodeum, dorsal view; **D.** Genital capsule, dorsal view.

(in *A. pulicaria* with the inner margins of the gonostyli raised and showing a distinct kink medially), and the penis valves at their base have the outer margins slightly raised, penis valves broadest slightly before the gonocoxal teeth (in *A. pulicaria* with the penis valves laterally lacking raised margins, penis valves continuing to broaden as they meet the gonocoxal teeth). Overall, these characters are slight, but are typical for species-level differences in *Aciandrena*. Given the small nature of the differences, a formal description of the male of *A. chelma* is not considered to be necessary, especially as it is integrated into the identification key below. In this context, *A. chelma* is best considered to be an isolated species restricted to southern Greece and geographically separated from populations of *A. pulicaria* in Anatolian Turkey.

**Distribution.** Greece (Peloponnese and south-central Greece on Mount Parnassus).

### Subgenus *Campylogaster* Dours, 1873

#### *Andrena (Campylogaster) erberi* Morawitz, 1871

*Andrena erberi* Morawitz, 1871: 222, ♀♂ [Greece, ZISP, examined by photograph]  
*Andrena kozarowi* Nedialkov, 1914: 189, ♀ [Bulgaria, type lost] syn. nov.

**Material examined.** ALBANIA • 1♂; Xhafaj; 15 Jul. 2017; K. Janssen leg.; KJCB; BULGARIA • 1♂; Blagoevgrad, Dolno Spanchevo, 500 m S, sandy/calcareous grassland; 150 m a.s.l.; 16 May 2024; T.J. Wood leg.; TJWC • 2♀; Kresna [Кресна]; 9 Jul. 1990; B. & O. Tkalčū leg.; OÖLM • 2♂; Kresna [Кресна]; 12 Jul. 1990; B. & O. Tkalčū leg.; OÖLM • 1♀; S Sinitovo vill; 310 m a.s.l.; 8 May 2023; T. Trifonov leg.; IBER • 1♀; Struma, Valkovo, Sandanski; 3 Jul. 2019; M. Halada leg.; OÖLM • 2♀; údolí řeky [river valley] Lebnice; 1 Jul. 2000; J. Straka leg.; JSPC

**Notes.** Nedialkov (1914) described *Andrena kozarowi* based on an unknown number of female specimens from Stara Zagora collected in July (*Mense Iulio*). The name was not included in the catalogue of Warncke (1967b), but it was indicated as a possible synonym of *A. erberi* by Gusenleitner and Schwarz (2002: 252). Given this regional revision, it is appropriate to deal with it more definitively here.

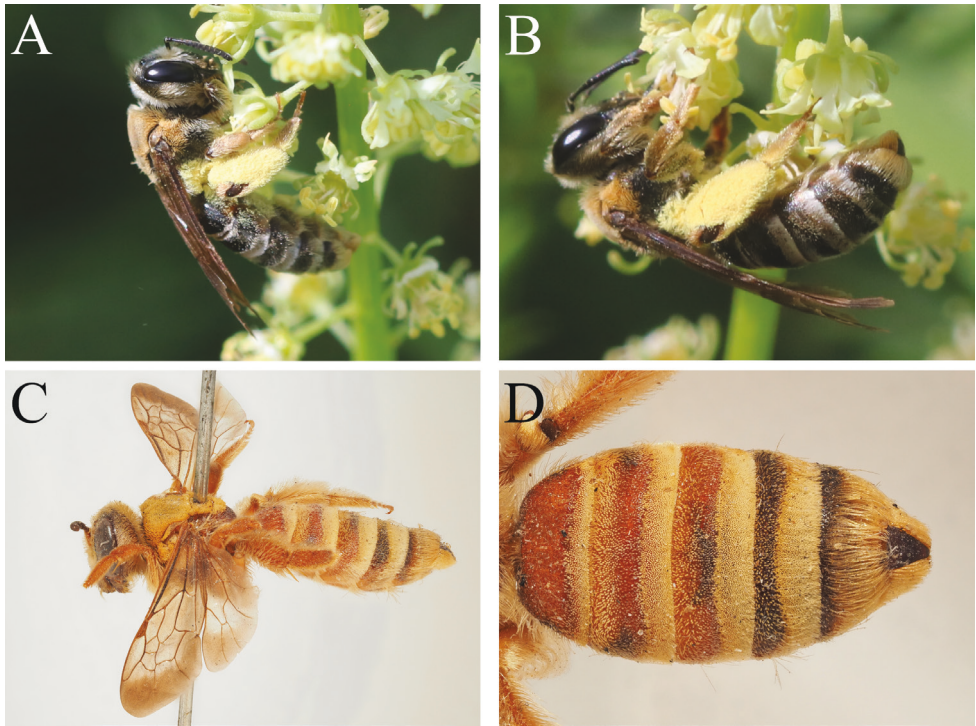
The species name is written using the Latin alphabet, and the original description is written in Latin and then duplicated and translated into Bulgarian; the name is consequently available, as it fulfils ICZN (1999) requirements. It is diagnosed as “*Andrena erberi Mor similis*”, indicating close proximity to Morawitz’s species. The description presents a bee that conforms to the key aspects of *A. erberi*, including the scutum, scutellum, and metapostnotum densely covered with ferruginous squamous hairs (*thorax superne (etiam scutellum et postscutellum) densissime ferrugineo squamosus, lateribus albido villosus*), metasoma elongate, convex, and dull, subtly punctate and with T1–2 laterally weakly reddish (*Abdomen elongatum, convexiusculum, opacum, subtilissime punctatum; segmenta 1 et 2 lateribus subttus rufescentia*), the tergal margins with ochraceous squamous hair bands (*segmenta 1–4 apice densissime ochraceo squamosa (late fasciata)*), and body length of 13 mm.

The overall bee is described as black (*nigra*), and *A. erberi* can present dark specimens such as the type (Astafurova et al. 2021) and contemporary specimens caught in Bulgaria and northern Greece (Fig. 3A, B), as well as specimens extensively lightened red (Fig. 3C, D) as in *Andrena amasia* Radoszkowski, 1876 (a junior synonym described from Amasya in northern Turkey; the specimen illustrated is the possible holotype in the ZMHB collection). Concerning *A. kozarowi*, searches in the NZMS unfortunately could not locate Nedialkov’s material (T. Ljubomirov, pers. comm.), but it is not considered necessary to create a neotype, as the identity of the taxon appears clear based on the description. It is formally synonymised under *A. erberi* syn. nov.; the species continues to be present in southern Bulgaria.

**Distribution.** Albania\*, North Macedonia, Greece, Bulgaria, Romania, Ukraine, Crimea, Turkey, Syria, ?Egypt [unclear; based on the known distribution, *A. erberi* is a species of warm and humid East Mediterranean habitats, but not of dry desert habitats], Georgia, Armenia, Azerbaijan, Iran (Fig. 4; Gusenleitner and Schwarz 2002; Osytsnjuk et al. 2005; Astafurova et al. 2021).

### Subgenus *Cryptandrena* Pittioni, 1948

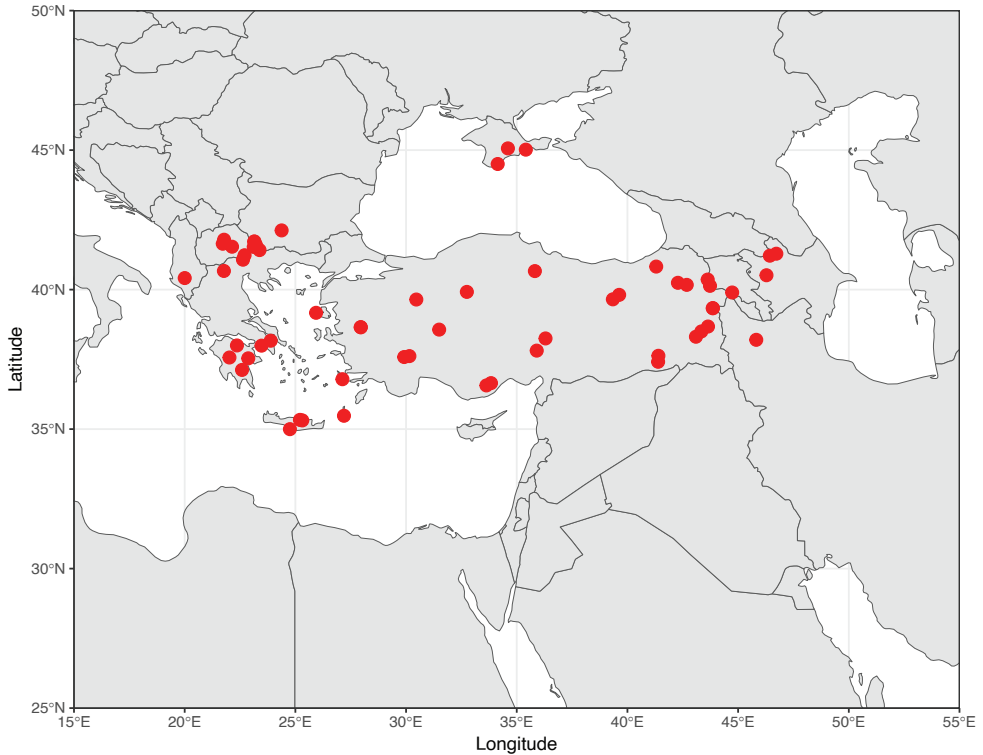
**Genetics.** Sequences of *Andrena ventricosa* Dours, 1873 were available from Portugal, Spain, Italy, Romania, and Lebanon, and sequences of *Andrena brumanensis* Friese,



**Figure 3.** *Andrena (Campylogaster) erberi* Morawitz, 1871 female. **A, B.** Dark specimen foraging at *Reseda* (Greece: Western Macedonia, June 2024); **C, D.** Light specimen from Amasya, Turkey (ZMHB).

1899 were available from Greece and Israel (Fig. 1). A single sequence from Crete that was tentatively identified as *A. brumanensis* was separated from *A. ventricosa* by an average genetic distance of 10.29% (range 9.76–10.56%) and from *A. brumanensis* by an average genetic distance of 7.07% (range 6.89–7.20%). Within *A. ventricosa*, two clades were seen, a western clade (Portugal, Spain, Italy) and an eastern clade (Romania and Lebanon). Overall intraspecific variation was 1.80% (range 0.00–3.34%) with the greatest separation (3.34%) seen between the Romanian sequences and three identical sequences from Portugal, Spain, and Italy. Variation within the western clade was 0.21% (range 0.00–0.47%) and within the eastern clade was 0.40% (0.00–0.76%). Although two clades are formed, the lack of morphological differentiation suggests that this is simply isolation by distance, and the current broad concept of *A. ventricosa* is maintained. In *A. brumanensis*, intraspecific variation was 1.43% (range 0.00–3.50%). Due to the strong genetic isolation combined with morphological differences, the Cretan taxon is therefore newly described below as *Andrena testudo* sp. nov.

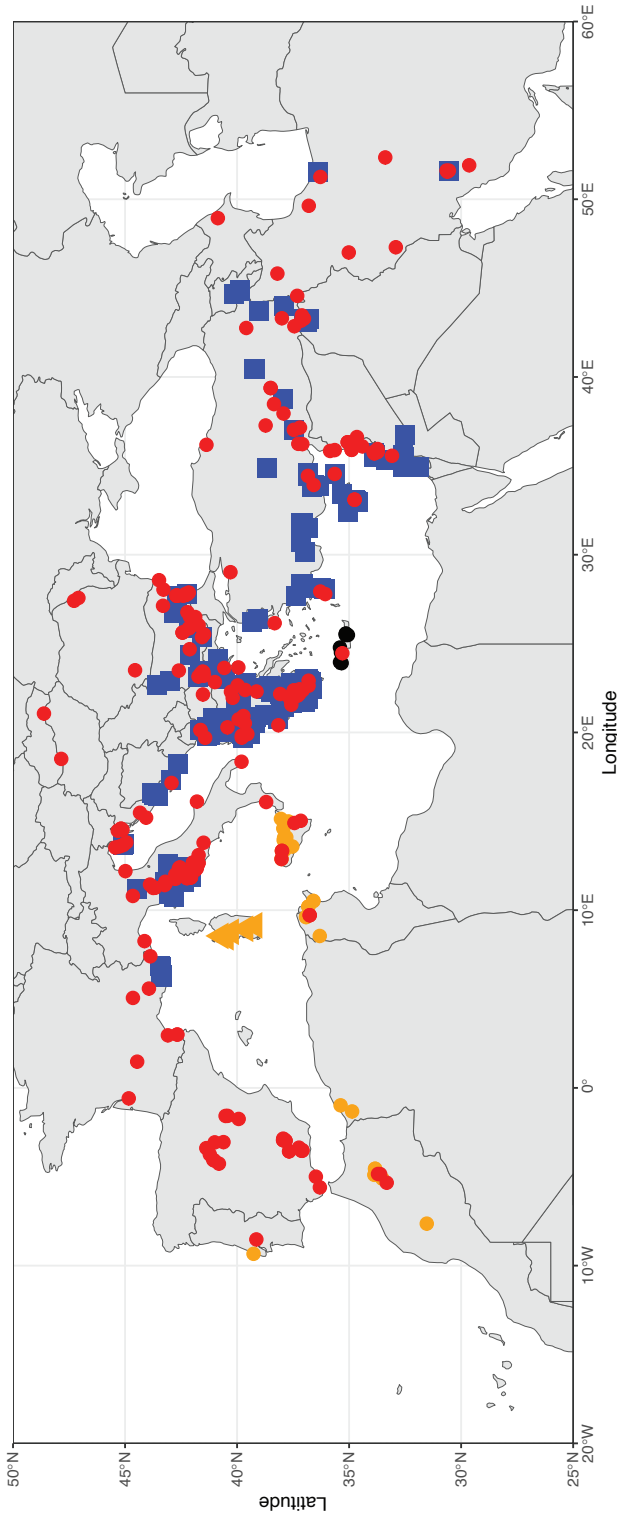
More broadly, revision of *Cryptandrena* material from the West Palaearctic (see Suppl. material 2) revealed an interesting pattern by the four members of this subgenus (Fig. 5). In all cases, no more than two *Cryptandrena* species ever seem to be found in sympatry, these being *Andrena rotundata* Pérez, 1895 and *A. ventricosa* in Portugal



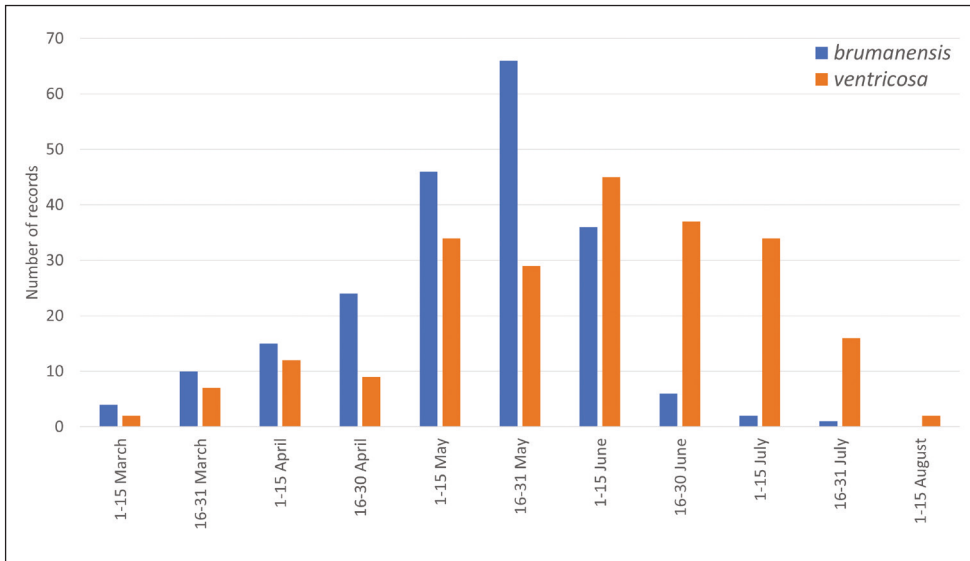
**Figure 4.** *Andrena (Campylogaster) erberi* Morawitz, 1871 global distribution map based on examined specimens. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

(see Gaspar et al. 2025), north-west Africa, and Sicily, *A. brumanensis* and *A. ventricosa* from south-eastern France to Iran, and *A. testudo* and *A. ventricosa* on Crete. *Andrena ventricosa* therefore appears to be able to co-exist with the other members of the sub-genus, but the others do not. This is reminiscent of the situation in the *proxima*-group (McLaughlin et al. 2022) where *Andrena proxima* (Kirby, 1802) and *Andrena ampla* Warncke, 1967 cannot exist in sympatry, but the slightly later flying *Andrena alutacea* Stöckert, 1942 can be found at the same sites as *A. proxima*. McLaughlin et al. (2022) concluded that phenological and *Wolbachia*-induced mating incompatibilities may maintain species boundaries in this species group.

Phenologically, *A. brumanensis* and *A. ventricosa* are only weakly differentiated (Fig. 6), with *A. brumanensis* peaking between 16–31 May, and *A. ventricosa* between 1–15 June. However, both have overall long activity periods from March to the end of July or early August; there may be partial or facultative bivoltinism in parts of the range. Restricting the analysis to just the southern Balkans (815 specimens compared to 1,543 specimens in the full analysis), *A. brumanensis* peaks at the same period of 16–31 May and *A. ventricosa* between 1–15 June, suggesting no difference from the overall pattern or any clear evidence of consistent bivoltinism in this region. The small



**Figure 5.** *Andrena* (*Cryptandrena*) Pittoni, 1948 global distributions. Orange circles = *Andrena rotundata* Pérez, 1895; Red circles = *Andrena ventricosa* Dours, 1873; Black circles = *Andrena testudo* sp. nov.; Blue squares = *Andrena brunnensis* Friese, 1899. Displayed distributions are not comprehensive. Specimen details in Suppl. material 2.



**Figure 6.** Phenological plot of *Andrena brumanensis* Friese, 1899 and *Andrena ventricosa* Dours, 1873 based on recorded flight date of examined pinned specimens.

number of available records for *A. rotundata* make comparisons difficult; the greatest number of records (nine) occur in the 16–30 June period, but records occur between the beginning of March and the end of July. Overall, some factor is maintaining species boundaries between *A. brumanensis* and *A. ventricosa*, and interactions between *brumanensis-rotundata-testudo* require further study. The status of *A. rotundata* ssp. *diomedea* Warncke, 1975 (endemic to Sardinia) also requires further study. It may well deserve species-status.

### Subgenus *Euandrena* Hedicke, 1933

**Genetics.** The subgenus *Euandrena* is very young by *Andrena* standards (Pisanty et al. 2022a), and contains a swarm of morphologically variable and challenging to characterise taxa. The situation is particularly acute in the East Mediterranean, where multiple faunas meet. There are also many mountainous areas; these landscape features create many areas with phenologically distinct microclimates, and seem to support high *Euandrena* species richness when considered at a global scale (Osytshnjuk et al. 2008; Praz et al. 2019; Wood et al. 2021; Wood 2021, 2023b, 2023c, 2024a).

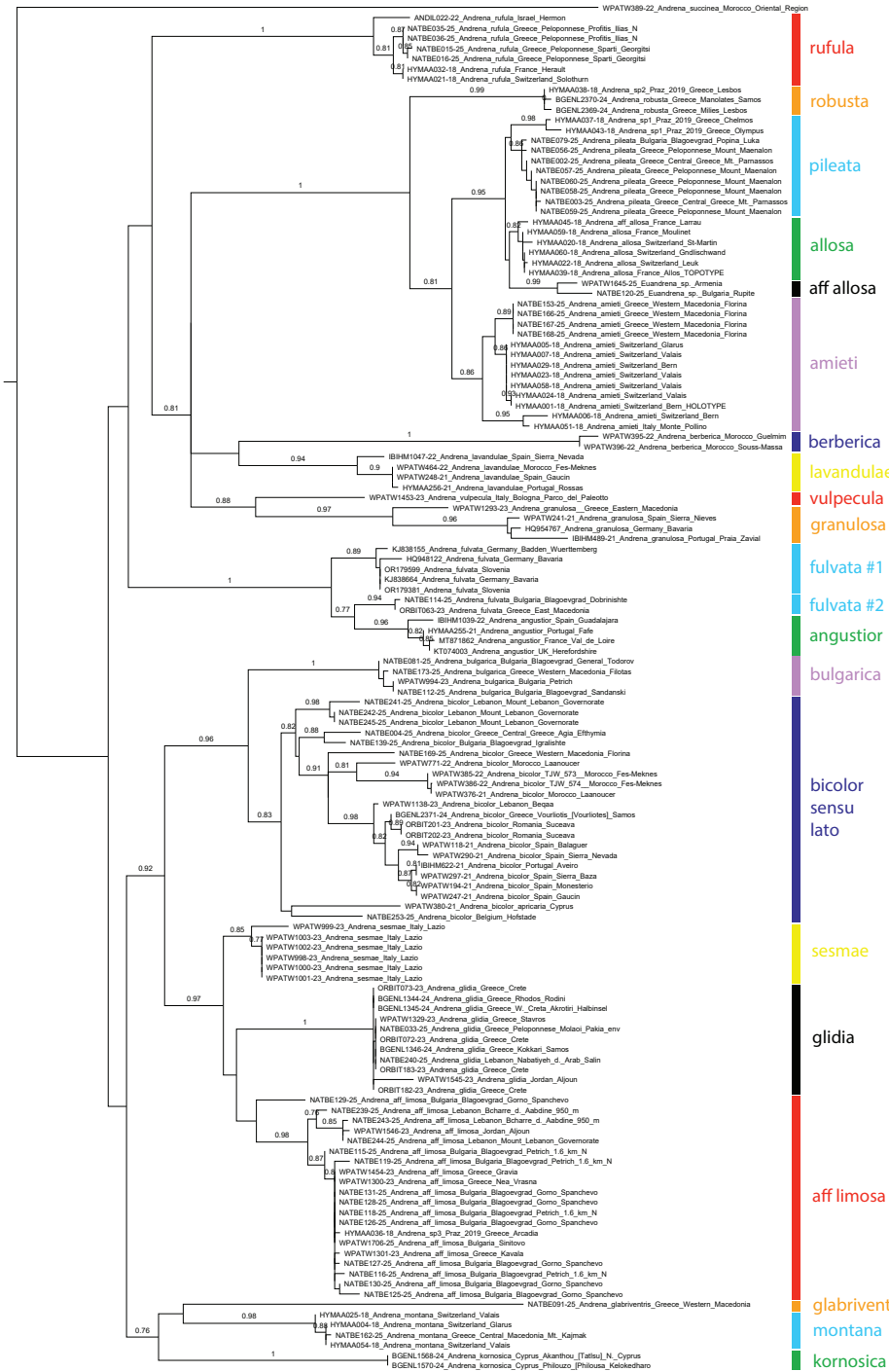
Since the work of Praz et al. (2019) which resolved taxon delineation issues in Central European *Euandrena*, a large number of sequences have now become available from the East Mediterranean. This is pertinent, as Praz et al. left a number of questions open; whilst elevating *Andrena pileata* Warncke, 1975 and treating it distinct from *Andrena allosa* Warncke, 1975 (Spain, France, Switzerland). *Andrena pileata* was

described from Chelmos mountain in the Peloponnese, and Praz et al. considered the described paratype male not to be conspecific with the holotype male. They also identified three uncertain taxa supported by DNA barcodes which could not at the time be named; sp. 1, sp. 2, and sp. 3. Analysis of DNA barcodes, including the most pertinent barcodes of Praz et al., provides resolution to these open questions (Fig. 7). To begin with, sp. 2 *sensu* Praz et al. ([HYMAA038-18](#)) comes from the island of Lesbos, and almost perfectly matches sequences of *Andrena robusta* Warncke, 1975 from Lesbos and Samos (separated by 0.26%); the species was originally described from the island of Rhodes. This question at least is straightforward to answer.

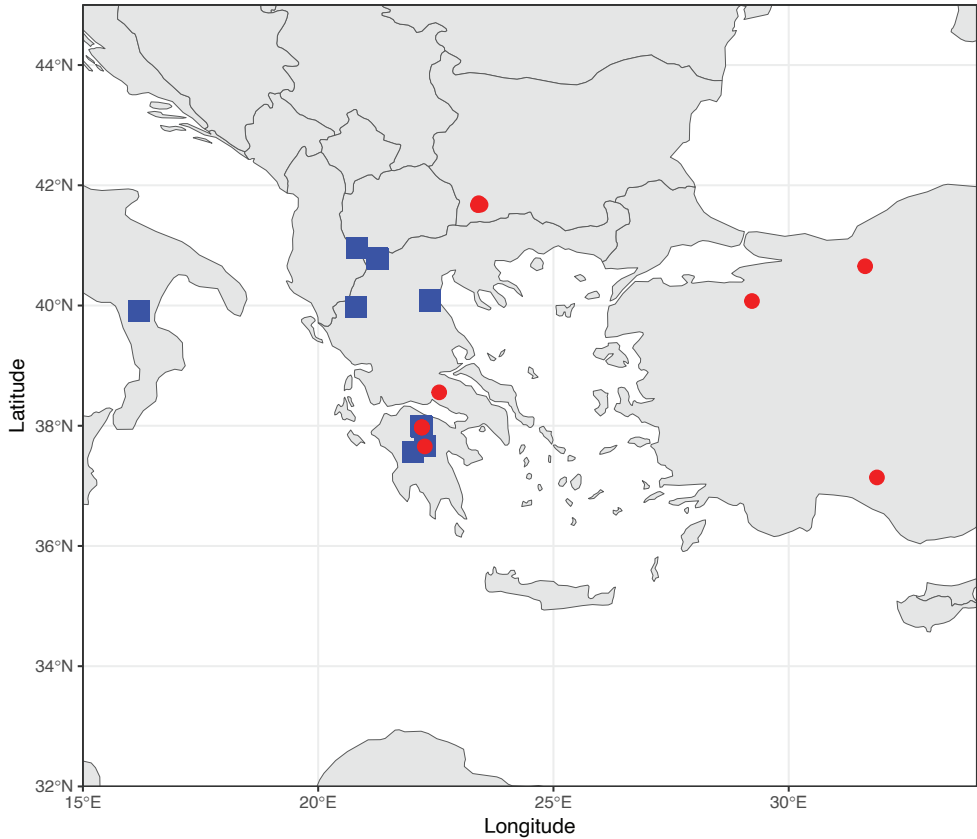
More challenging is sp. 1 *sensu* Praz et al.; sequences from Chelmos and Mount Olympus ([HYMAA037-18](#); [HYMAA043-18](#)) placed adjacent to a long series of sequences of *A. pileata* from Mount Maenalon (Peloponnese), Mount Parnassus (south Central Greece), and the Pirin Mountains (south-western Bulgaria) (Fig. 8), separated by an average genetic distance of 2.02% (range 1.67–2.44%). As in the analysis of Praz et al., sp. 1 was placed close to *A. allosa*, but the addition of new Balkan sequences has resulted in a topology where clades of *A. pileata* and *A. allosa* are reciprocally monophyletic, although bootstrap support is relatively low, potentially indicating an unstable topology. Taking *A. pileata* (inclusive of sp. 1), it was separated from *A. allosa* by an average genetic distance of 1.46% (range 0.95–2.28%); excluding sp. 1, *A. pileata* was separated by an average genetic distance of 1.35% (range 0.95–1.67%). sp. 1 alone was separated from *A. allosa* by an average genetic distance of 1.89% (range 1.55–2.28%).

Adjacent to *A. allosa* are two sequences, [NATBE120-25](#) which is a female *Euan-drena* from Petrich (Bulgaria) on low altitude grassland at the Rupite mineral baths (20 May 2024) and [WPATW1645-25](#) which is a male *Euandrena* from Armenia. They were separated from *A. allosa* by an average genetic distance of 2.22% (range 1.27–3.19%). The male specimen is badly abraded and essentially uncharacterisable given the challenges associated with identification of isolated male *Euandrena* specimens. The female specimen shows the densely plumose scutal hairs typical of *allosa+pileata*, but the clypeus is comparatively slightly shorter and the terga are shinier than in *A. pileata*. Moreover, it was collected at an altitude of 90 m a.s.l., when the one available sequenced specimen of *A. pileata* from Bulgaria was collected at an altitude of approximately 2,000 m a.s.l. (3.5 km NNE of Popina Luka).

Given what is known about *Euandrena* and their ecological and altitudinal niches, and the likely break in gene flow between low and high altitude in this group, it is difficult to imagine these being conspecific. In this context, it is best to currently consider *A. allosa* and *A. pileata* (inclusive of sp. 1) as distinct following Praz et al. (2019), and to consider the Bulgarian+Armenian sequences of uncertain identity at the present time until more data become available. Praz et al. (2019) also considered that Warncke's paratype male of *A. allosa* ssp. *pileata* was not conspecific with the holotype (even though they were collected in sympatry, just two days apart), but based on the examination of a barcoded male of *A. pileata* ([NATBE056-25](#); Fig. 9), it seems to match Warncke's specimen in all aspects including the shape of the genital capsule, and so Warncke's existing male paratype is considered to have been correctly associated.

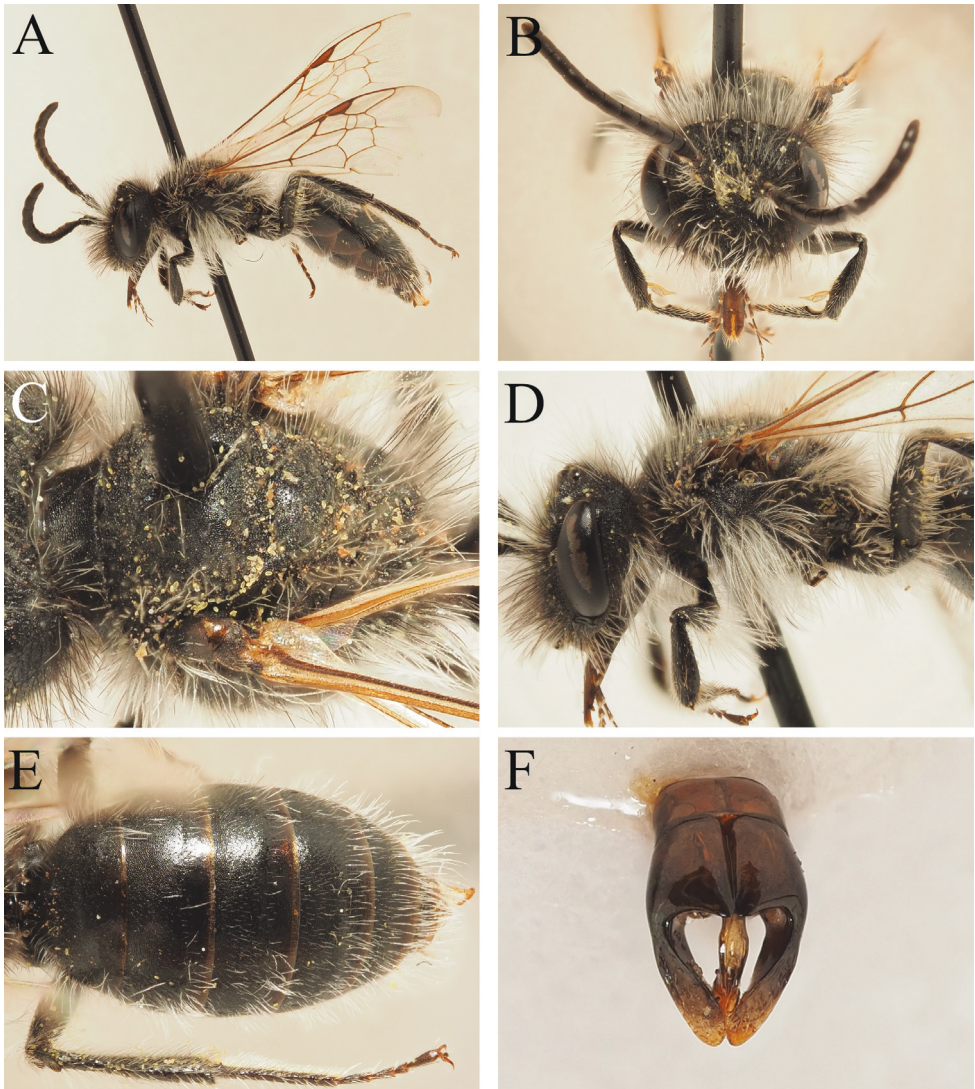


**Figure 7.** Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Euandrena* Hedicke, 1933 based on the mitochondrial COI gene. *Andrena (Pruinosandrena) succinea* Dours, 1872 is used as the outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).



**Figure 8.** Distribution map of *Andrena (Euandrena) amieti* Praz, Müller & Genoud, 2019 (blue squares) and *Andrena (Euandrena) pileata* Warncke, 1975 (red circles) in the southern Balkans based on examined specimens. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

Before moving to sp. 3 *sensu* Praz et al., it is also necessary to report *Andrena amieti* Praz, Müller & Genoud, 2019 as new for the southern Balkans. Four sequences were available from northern Greece collected at an altitude of 1800–1900 m a.s.l. which were separated from *A. amieti* group 1 (Switzerland, including the holotype; bootstrap support of 86) sequences by an average genetic distance of 0.96% (range 0.91–1.07%) and from *A. amieti* group 2 (Switzerland and Italy; bootstrap support of 95) by an average genetic distance of 2.45% (range 2.31–2.58%). Compared to the analysis of Praz et al. (2019: 16), all *Andrena amieti* sequences formed a monophyletic clade with bootstrap support of 86, rather than fall into two distinct clades which were interrupted by the clade of *A. allosa*. The Greek clade of *A. amieti* received bootstrap support of 89, and overall seems to have helped resolve the topology, grouping all three clades together with bootstrap support of 86. Although there is slight population structuring, the morphology of *A. amieti* remains recognisable over this range. Examination of 111 *A. amieti* specimens from Greece and North Macedonia (see Suppl. material 2) shows activity between 12 May and 25

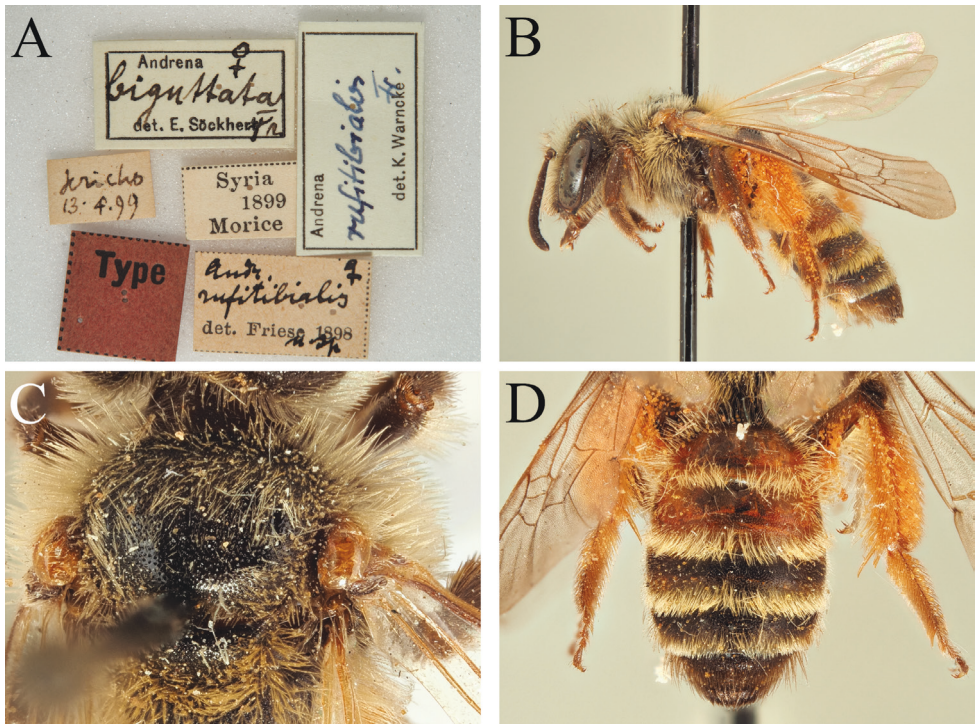


**Figure 9.** *Andrena (Euandrena) pileata* Warncke, 1975 male. **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Scutum, dorsolateral view; **D.** Mesepisternum, lateral view; **E.** Metasoma, dorsal view; **F.** Genital capsule, dorsal view.

August, supporting the bivoltine behaviour reported in Switzerland by Praz et al. (2019). In this context, *A. amieti* can be considered a species found in high mountains in the Alps, southern Apennines, and southern Balkans (Fig. 8). Collectively, covering all three clades, a low average intraspecific genetic distance of 1.04% (range 0.00–2.74%) was observed. The distribution is not unlike that of *Andrena montana* Warncke, 1973; the one available sequence from northern Greece (Mount Kajmakčalan) clustered with sequences from Switzerland, showing minimal average genetic differentiation of 0.25% (range 0.15–0.46%).

For sp. 3 *sensu* Praz et al. (HYMAA036-18), the sequence clustered with a long series of sequences from Bulgaria, Greece, Lebanon, and Jordan. This group of sequences requires discussion, and an analysis of what Warncke referred to as *Andrena rufitibialis* Friese, 1899 in a broad sense. Friese (1899: 342) described *A. rufitibialis* from two female specimens from 13 Apr. 1899 collected at Jericho by Francis Morice. Gusenleitner and Schwarz (2002: 647) give ZMHB or OUMNH as the possible type repositories. Examination of these collections produced three female specimens (Figs 10, 11), but only the specimen in the ZMHB was actually labelled by Friese with one of his red type labels. Friese's type material is often difficult to interpret (see Rasmussen and Ascher 2008); although the OUMNH material may well be syntypic, it is best to treat as only possibly syntypic, and the female in the ZMHB collection illustrated here is designated as the lectotype. It was later redetermined as *Andrena biguttata* Friese, 1923 by Stöckhert for inexplicable reasons, given that this name is younger, regardless of specimen morphology.

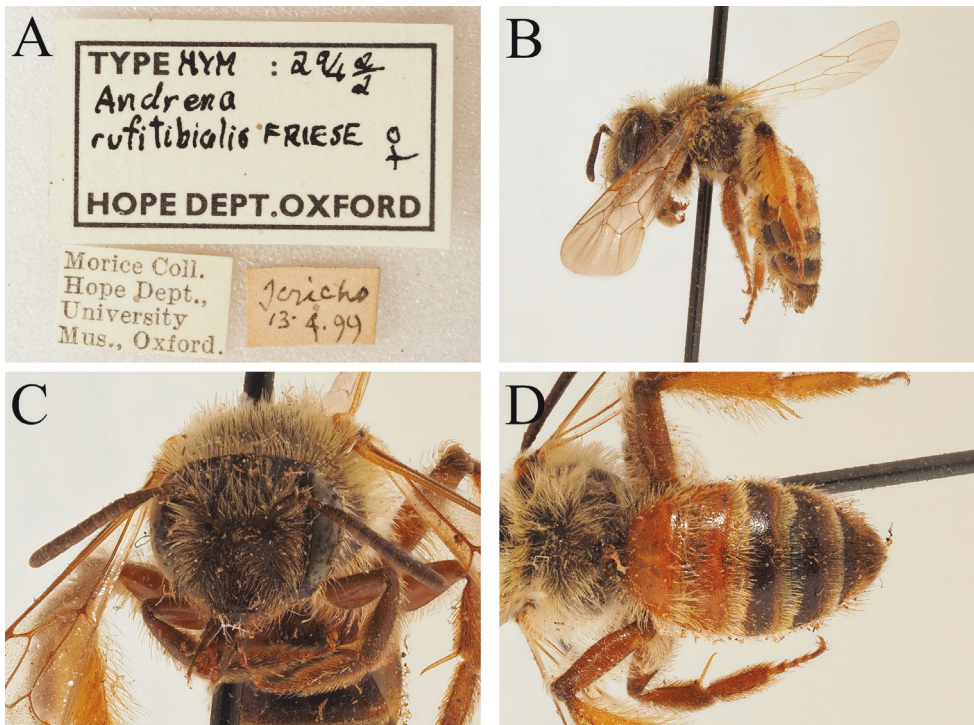
Warncke (1969a) listed *A. rufitibialis*, and then described *Andrena rufitibialis* ssp. *limosa* Warncke, 1969 from Turkey (*locus typicus*), Syria, and Israel which is darker, with the metasoma entirely dark, but still with partial reddish colouration of the hind tibiae (Fig. 12). This reddish colouration of the hind tibiae is absent on many “dark” specimens that can be collected in the southern Balkans and the Levant. Rasmont et al.



**Figure 10.** *Andrena* (*Euandrena*) *rufitibialis* Friese, 1899 lectotype female (ZMHB). **A.** Label information; **B.** Habitus, lateral view; **C.** Scutum, dorsal view; **D.** Metasoma, dorsal view.

(2017: 18) elevated *Andrena rufitibialis* ssp. *limosa* to species status based on personal communication from Erwin Scheuchl and reported it as new for Greece based on specimens from the East Aegean Islands. No species concept was discussed, or global range indicated, for example whether Turkish material is conspecific with dark material from the southern Balkans and Levant. However, this elevation is justified due to their differing morphologies combined with the ecological affinities of the taxa; *A. rufitibialis* s. str. is a very rarely collected species of arid habitats (see Material examined below), and is completely absent from the Mediterranean zone in the Levant whereas darker specimens (lacking extensive red tergal markings, *A. limosa sensu lato*) are common throughout the Mediterranean zone (G. Pisanty, pers. comm.).

In the current analysis, it has not been possible to generate a barcode from either i) a specimen with orange hind tibiae and abundant red markings on the terga (*A. rufitibialis* s. str.) or ii) a generally dark specimen still displaying partially orange hind tibiae (*A. limosa*), but many sequences are available from entirely dark specimens which form a broad clade from southern Bulgaria to Lebanon and north-western Jordan (Fig. 7). It is necessary to highlight the sequence [NATBE129-25](#) which was generated from a specimen that was part of a long series of dark specimens collected from *Campanula* (Campanulaceae) flowers near Gorno Spanchevo in south-western Bulgaria. It shows no morphological differentiation from other specimens from the same collecting



**Figure 11.** *Andrena* (*Euandrena*) *rufitibialis* Friese, 1899 possible syntype female (OUMNH). **A.** Label information; **B.** Habitus, lateral view; **C.** Face, frontal view; **D.** Mesosoma, dorsal view.

event (e.g. [NATBE128-25](#), [NATBE131-25](#)), but shows a level of genetic differentiation from all remaining dark specimen sequences of 3.38% (range 2.93–3.67%). It is unclear if this is variation or if the sequence has problems, for example, if it was generated from nuclear mitochondrial DNA (a NUMT), sequences that are notoriously difficult to differentiate from genuine mitochondrial fragments (e.g. Williams et al. 2020, 2024). If it is excluded, the clade receives bootstrap support of 98 and the average intraspecific variation is 0.82% (range 0.00–2.69%), and if included then average intraspecific variation is 1.08% (range 0.00–3.67%). In any case, inclusion or exclusion does not affect the overall topology of the clade. Based on the morphology of these specimens, including their dark legs, it is not clear if they actually correspond to *A. limosa*. Until it is possible to generate a sequence from a specimen displaying at least partially orange legs (ideally from Turkey), to be as cautious as possible these sequences are referred to as *A. aff limosa* (Fig. 7). Based on the available sequences, *A. aff limosa* is still well-differentiated from its nearest neighbour *Andrena glidia* Warncke, 1965 by an average genetic distance of 5.69% (range 4.84–6.23%). The two species are in principle easy to separate in the male sex (at least in the southern Balkans) due to the male head morphology, but it is unclear if these characters are stable (see comments in the *Andrena glidia* section below) and females can be challenging; differences are given in the identification key below.



**Figure 12.** *Andrena* (*Euandrena*) *rufitibialis* ssp. *limosa* Warncke, 1969 holotype female (OÖLM). **A.** Label information; **B.** Dorsum, dorsal view; **C.** Head, frontal view; **D.** Metasoma, dorsal view.

The very widespread and common species *Andrena bicolor* Fabricius, 1775 is one of the most challenging *Andrena* species in the West Palaearctic due to its abundance, widespread distribution, and variable morphology, particularly pubescence colouration. It has been described many times from across its range (Gusenleitner and Schwarz 2002), and has acted as something of a waste bin for difficult to characterise or place *Euandrena* taxa. Warncke lumped many names under a broad *A. bicolor* concept, and the process of revalidating valid species or confirming existing synonymies from this “waste bin” concept is ongoing (Praz et al. 2019; Wood 2023b, 2023c). Generation of *A. bicolor* sequences from the East Mediterranean confirms the presence of a broad *A. bicolor* taxon across the southern Balkans and into the Levant (Fig. 7). No comparative pattern of two moderately separated clades as seen in the analysis of Praz et al. (2019) was found, with complex structuring observed, though a focused analysis including all available sequences would be necessary to investigate this possible pattern further. One sequence of *Andrena bicolor* ssp. *apricaria* Warncke, 1975 from Cyprus was placed as the base of the *bicolor*-clade, but was grouped with a sequence (NATBE253-25) of a morphologically ambiguous specimen from Belgium. The status of ssp. *apricaria* must wait for a future analysis. Taking a broad concept of *A. bicolor* inclusive of the Cypriot and Belgian sequences show an average intraspecific genetic distance of 3.37% (range 0.00–6.01%). The greatest distance of 6.01% was seen between the specimen from Cyprus and a specimen from the Sierra Nevada mountain in southern Spain (WPATW290-21).

What can be resolved here is that sequences were available from a *Euandrena* taxon from southern Bulgaria and northern Greece which is noticeably larger and shinier than typical *A. bicolor* specimens in the southern Balkans. Four sequences were generated which were consistently placed at the base of a broad *bicolor*-clade with bootstrap support of 100. They were separated from the *bicolor*-clade by an average genetic distance of 5.99% (range 5.22–6.91%). Based on this consistent genetic differentiation and observed differences in size, integument sculpture, and existence in sympatry with *A. bicolor* s. str., they are described below as *Andrena bulgarica* sp. nov.

*Andrena fulvata* Stöckert, 1930 sequences from Greece and Bulgaria currently do not have strong genetic support, being more closely placed next to *Andrena angustior* (Kirby, 1802) sequences than *A. fulvata* sequences from Germany and Slovenia (Fig. 7). Based on their observed morphology and knowledge of the western- and eastern-biased distribution of the two taxa, respectively (Wood et al. 2021), assignment to *A. fulvata* is made without doubts. Greek and Bulgarian sequences were separated from German and Slovenian sequences by an average genetic distance of 3.45% (range 3.16–3.99%), and from *A. angustior* by an average genetic distance of 3.17% (range 2.80–3.53%). Alignment with either clades is therefore somewhat arbitrary purely based on genetic distance and without consideration of specimen morphology. It may well be the case that additional sampling in countries such as Serbia and Romania produces intermediate sequences and results in a change in the topology of the tree, and a monophyletic *A. fulvata* is formed. Currently, bootstrap support for Greek and Bulgarian *A. fulvata* + *A. angustior* is moderate at 77. Additional study is required, and the current morphological concept of *A. fulvata* is maintained (Schmid-Egger and Scheuchl 1997; Wood et al. 2021).

Finally, specimen [NATBE091-25](#) is a female *Euandrena* from near to Anatoliko in West Macedonia (Greece) collected in fields at an altitude of 750 m a.s.l. (15 Jun. 2024). It was strongly separated from all other *Euandrena* taxa studied here, and matched a sequence of *Andrena glabriventris* Alfken, 1935 from Turkey (G. Pisanty, *unpublished data*). It morphologically corresponds to that species, and is therefore newly reported from Greece and Europe; it is treated below.

### *Andrena (Euandrena) amieti* Praz, Müller & Genoud, 2019

*Andrena (Euandrena) amieti* Praz, Müller & Genoud, 2019: 20, ♀♂ [Switzerland, MHNN, not examined]

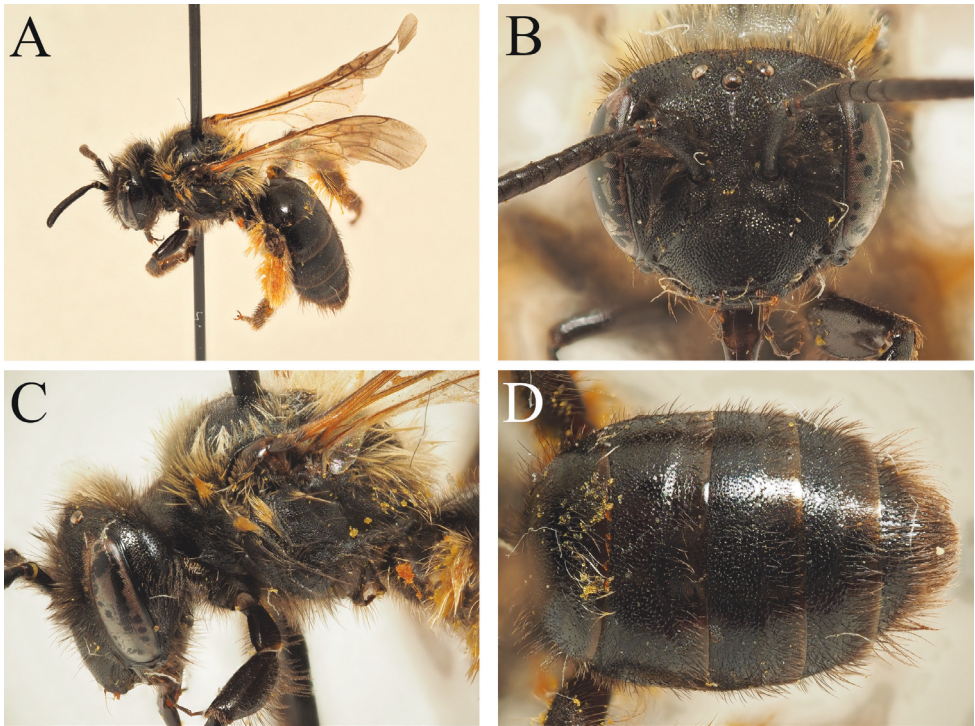
**Material examined.** GREECE • 1♀; [Peloponnese] top ski center Kalavrita, Ahaia [Achaia]; 20 Jun. 2022; K. Janssen leg.; TJWC • 2♀; Chelmos [Aroania]; 1700 m a.s.l.; 27 May 1987; H. Teunissen leg.; RMNH • 2♀; Chelmos, Peloponnes; 2250 m a.s.l.; 25 Aug. 1987; K. Warncke leg.; OÖLM • 74♀; Peloponnese, Melano Mountains; 1500 m a.s.l.; 12 May 1987; H. Teunissen leg.; RMNH • 2♀; Mt. Olymp. Ost-flanke; 2200–2500 m a.s.l.; 19 Sep. 1989; D. Lange & T. Osten leg.; OÖLM • 3♀; Mt. Tymfi / Pindos; 18–2000 m a.s.l.; K. Warncke leg.; OÖLM • 1♂; Olymp, Agios Antonis; 2500 m a.s.l.; 2 Aug. 1985; L. Blank leg.; OÖLM • 1♀; Olymp, Balkoni N; 1900 m a.s.l.; 31 Jul. 1985; L. Blank leg.; OÖLM • 1♀; Olymp.; 2000 m a.s.l.; 24 Aug. 1981; K. Warncke leg.; OÖLM • 2♀; Olymp.; 2000–2200 m a.s.l.; 18 Aug. 1978; K. Warncke leg.; OÖLM • 3♀; Peloponn., Menalo Mts., Kardaras NW; 1450 m a.s.l.; 20 Apr. 1999; Blank & Kutzscher leg.; DEI • 7♂, 1♀; Western Macedonia, Florina, 3 km N of Vigla; 1800–1900 m a.s.l.; 13 Jun. 2024; T.J. Wood leg.; TJWC • 1♂; Western Macedonia, Florina, immediately north of Vigla; 1500 m a.s.l.; 9 Jun. 2024; T.J. Wood leg.; TJWC; NORTH MACEDONIA • 1♀; Galicia Mt.; 29 Jun. 1985; J. Hladil leg.; OÖLM • 1♀; Ochrid, Calicica-Geb, 0.6 km E Livada-Pass; 1595–1650 m a.s.l.; 8 Jul. 2023; E. & J. Hüttinger leg.; LBCM.

**Notes.** The first confirmed records from the southern Balkans. As in the Alps, where altitudinal data are available, the species is found at high altitude above 1400 m up to 2500 m. Most records are from the second summer generation, but some specimens from April and May have also been collected.

### *Andrena (Euandrena) glabriventris* Alfken, 1935

*Andrena glabriventris* Alfken, 1935: 158, ♀ [Turkey, SMFD, examined]

**Material examined.** GREECE • 1♀; Western Macedonia, Anatoliko, 2.8 km E, fields; 750 m a.s.l.; 15 Jun. 2024; T.J. Wood leg.; RMNH, RMNH.INS.1152469; TURKEY • 4♀; 10 May 1934; A. Seitz leg.; SMFD (**holotype** and **paratypes**) • 1♀; 20 km E Karakurt/Arastal; 12 Jun. 1977; K. Warncke leg.; OÖLM • 1♀; Acigel [Acıgöl]; 19



**Figure 13.** *Andrena (Euandrena) glabriventris* Alfken, 1935 female from Greece. **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Mesepisternum, lateral view; **D.** Metasoma, dorsal view.

May 1999; K. Deneš leg.; TJWC • 1♀; Kars, 15 km E Karakurt; 1460 m a.s.l.; 2 Jun. 1988; K. Warncke leg.; OÖLM • 1♀; Kulu/Konya; 1000 m a.s.l.; 3 Jun. 1978; M. Kraus leg.; OÖLM • 3♂, 4♀; N Güzelsu/Van; 9 Jun. 1977; K. Warncke leg.; OÖLM • 1♀; Şereflikoçhisar; 24 May 1972; K. Warncke leg.; K. Warncke det.; OÖLM.

**Notes.** *Andrena glabriventris* strongly resembles *A. bicolor* in its colour pattern with orange-brown hairs on the mesosoma dorsally (Fig. 13A), becoming black on the mesepisternum (Fig. 13C), dark facial hairs (Fig. 13B), and with orange tibial scopae. However, it can be recognised due to the irregular tergal punctation, with punctures separated by 1–3 puncture diameters and with polished and shining interspaces (Fig. 13D). In *A. bicolor*, the tergal punctation is much more regular, with interspaces typically not exceeding the diameter of a puncture on average. The sculpture of the interspaces is variable, but polished shining interspaces are typically not visible.

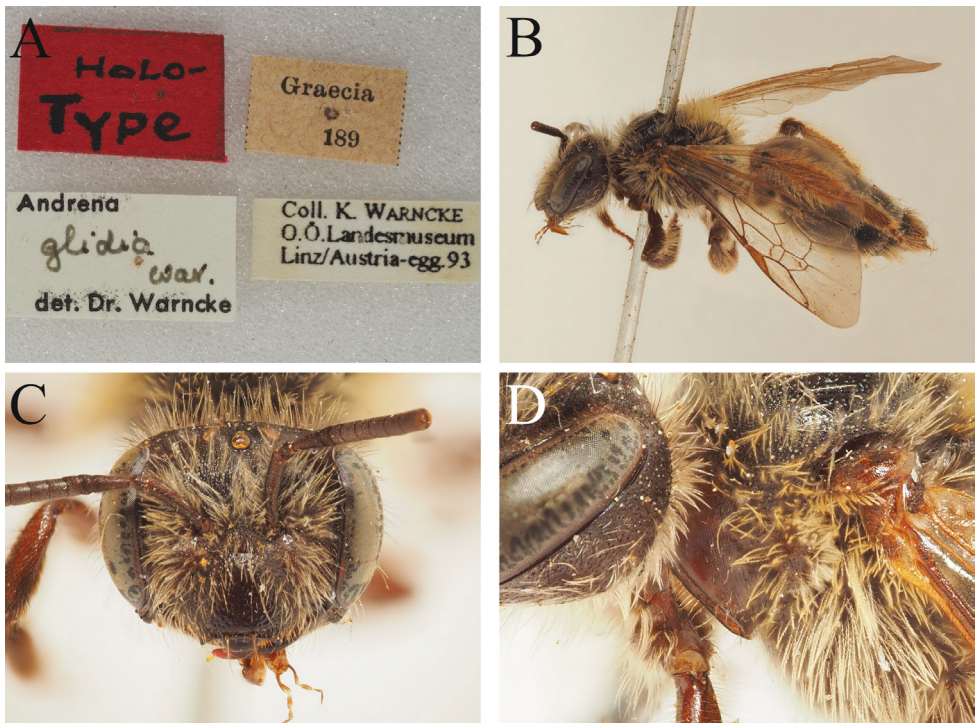
**Distribution.** Greece\* and Turkey (Alfken 1935; Warncke 1974a; Pisanty et al. 2022b).

### *Andrena (Euandrena) glidia* Warncke, 1965

*Andrena glidia* Warncke, 1965a: 49, ♀♂ [Greece, OÖLM, examined] (Fig. 14)

**Material examined.** GREECE • 1♀; Graecia [no further information]; OÖLM (**holotype**). See Suppl. material 2 for additional examined material.

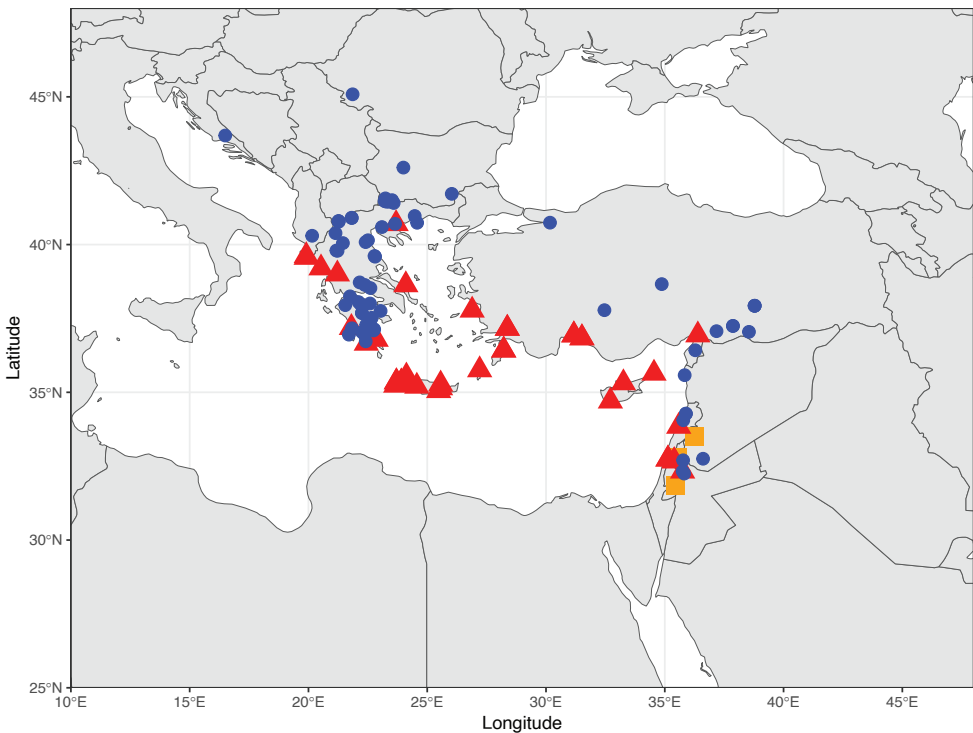
**Notes.** Warncke unhelpfully selected the oldest possible specimen to serve as holotype, as was sometimes his wont. *Andrena glidia* has traditionally been considered a species of south-eastern Europe and Turkey, but the available DNA barcodes and examined specimens support an extension of its range south into the Levant (Fig. 15). Warncke (1968: 87) placed *A. glidia* in the subgenus *Ptilandrena* Robertson, 1902 (currently restricted to North American species only, see Pisanty et al. 2022a) due to the presence of a pronotal angle (in both sexes) and a broadened gena that exceeded the width of the compound eye (males only). However, some specimens in the original type series have weak to absent pronotal angles, and specimens from the Levant are much more challenging and ambiguous. Specimens from Israel lack pronotal angles, and display a dull scutum compared to specimens from the southern Balkans (G. Pisanty, pers. comm.). At the present time, a full understanding of this morphological variation is not possible, even though the species appears to be very well characterised genetically. Whilst the classical morphological characters as used by Warncke are here included in the identification key, this substantial caveat is here emphasised and users of the key are urged to treat carefully in this challenging group.



**Figure 14.** *Andrena (Euandrena) glidia* Warncke, 1965 holotype female (OÖLM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Pronotum, lateral view.

This caveat notwithstanding, *A. glidia* has an unusual pattern of activity; it appears to be bivoltine, with a generation in the spring and another generation in the autumn to early winter. Warncke (1974a: 113) gives activity in April, with additional November activity based on a single female specimen. Based on specimens examined here, the activity period can be described as March (Cyprus, Greece;  $n$  specimens = 3), April (Cyprus, Greece, Greece: Crete, Israel, Jordan, Lebanon, Turkey;  $n$  = 25), May (Greece, Greece: Crete, Israel, Turkey;  $n$  = 18), June (Greece, Greece: Crete, Turkey;  $n$  = 6), October (Greece: Crete;  $n$  = 17), and December (Cyprus, Israel;  $n$  = 11). This would appear to support a broad spring generation centred on April and a poorly characterised autumn-early winter generation.

**Distribution.** ?Croatia, Greece, Turkey, Cyprus, Lebanon\*, Israel\*, Jordan\* (Warncke 1965a, 1974a; Gusenleitner and Schwarz 2002; Fig. 15). The Croatia listing comes from a single dot on the Warncke distribution maps presented by Gusenleitner and Schwarz (2002: 1052). It has not been possible to examine any specimens from this country; it is not impossible that it actually refers to a specimen of *A. aff. limosa* (see below).



**Figure 15.** Distribution map of *Andrena (Euandrena) rufitibialis* Friese, 1899 (orange squares), *Andrena (Euandrena) glidia* Warncke, 1965 (red triangles), and *Andrena (Euandrena) limosa* Warncke, 1969 *sensu lato* (including *A. aff. limosa*) (blue circles) in the East Mediterranean based on examined specimens. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

***Andrena (Euandrena) limosa* Warncke, 1969**

*Andrena (Euandrena) rufotibialis* [sic] ssp. *limosa* Warncke, 1969a: 408, ♀♂ [Turkey, OÖLM, examined] (Fig. 12)

**Material examined (*Andrena limosa*).** **TURKEY** • 1♀; Konya; 15 Jun. 1965; M. Schwarz leg.; OÖLM (**holotype**); **SYRIA** • 1♂; N. Syria, Ladikye [Latakia]; 1–31 May 1885; E. Leuthner leg.; OÖLM (**paratype**).

(*Andrena* aff *limosa*, indicative). **ALBANIA** • 1♀; Gjirokastër [SW of Këlcyrë]; 1 Jun. 2024; W. Vertommen leg.; WVC; **BULGARIA** • 1♀; 30 km SW Svilengrad; 550 m a.s.l.; 21 Jun. 2008; M. & Z. Halada leg.; OÖLM • 1♀; S Petrich vill. [near Sofia]; 593 m a.s.l.; 20 May 2016; T. Ljubomirov leg.; IBER; **CROATIA** • 2♀; Split, Gornji Muc, MT [malaise trap]; 500 m a.s.l.; 14 May – 8 Jun. 2014; B. Kokan leg.; OÖLM; **JORDAN** • 3♀; 15 km W Jerash, Dibbin; 2 May 2006; K. Deneš leg.; TJWC • 1♀; Aljoun; 28 Apr. 2012; M. Kafka leg.; TJWC • 1♀; Irbid, Saham vill; 25 Apr. 2003; I. Pljushtch leg.; TJWC; **LEBANON** • 2♀; Bcharre d., Aabdine; 950 m a.s.l.; 12 May 2003; V. Soon leg.; TUZ, TUZ346124 • 1♀; Mount Lebanon Governorate, Jabal Moussa Biosphere Res.; 1400 m a.s.l.; 14 May 2023; V. Soon leg.; TUZ, TUZ341652; **ROMANIA** • 1♀; SW, Resita, Anina; 4 Jun. 2000; M. Snížek leg.; OÖLM. See Suppl. material 2 for additional examined specimens.

**Notes.** Following the discussion above, *A. limosa* is treated as a species distinct from *A. rufitibialis*, but doubts are expressed as to whether the commonly encountered species with dark legs that is found in the southern Balkans and represented here in the genetic sampling is actually conspecific with it. These records are presented as *A. aff limosa*, and are subject to change following future study of populations in Turkey and the Levant.

**Distribution.** Croatia\*, Romania\*, Albania\*, Bulgaria\*, Greece, Turkey, Syria, Lebanon\*, Israel & West Bank, Jordan\* (Fig. 15; Warncke 1969a, 1974a; Gusenleitner and Schwarz 2002; Rasmont et al. 2017, inclusive of *A. aff limosa*).

***Andrena (Euandrena) pileata* Warncke, 1975**

*Andrena (Euandrena) allosa* ssp. *pileata* Warncke, 1975: 85, ♀♂ [Greece, OÖLM, examined]

*Andrena (Euandrena) allosa* ssp. *canigica* Warncke, 1975: 86, ♀ [Turkey, OÖLM, examined] (see Wood 2024a)

**Material examined.** **BULGARIA** • 1♀; Blagoevgrad, Popina Luka, 3.5 km NNE, path to Spano Pole hut; 1800–2000 m a.s.l.; 18 May 2024; T.J. Wood leg.; RMNH, RMNH.INS.1152448 • 1♀; Pirin, Kozia dolina [valley]; 2000 m a.s.l.; 30 May 1999; J. Straka leg.; JSPC • 1♀; Pirin, Popina Luka [Попина Лъка]; 1800 m a.s.l.; 14 Jul. 1966; M. Kocourek leg.; OÖLM; **GREECE** • 1♀; Chelmos, Peloponnes; 1900 m a.s.l.; 2 Jun. 1962; M. Schwarz leg.; OÖLM (**holotype** of *Andrena allosa* ssp. *pileata*) • 1♂;

Chelmos, Peloponnes; 1900 m a.s.l.; 1 Jun. 1962; M. Schwarz leg.; OÖLM (**paratype** of *Andrena allosa* ssp. *pileata*) • 1♀; Chelmos, Peloponnes; 1900 m a.s.l.; 1 Jun. 1962; M. Schwarz leg.; TJWC • 6♀; Central Greece, Mt. Parnassos, immediately NW of ski centre; 1750 m a.s.l.; 9 Apr. 2024; T.J. Wood leg.; RMNH/TJWC • 2♀; Chelmos [Aroania]; 1700 m a.s.l.; 27 May 1987; H. Teunissen leg.; RMNH, RMNH.INS.1264657 • 1♂, 4♀; Peloponnese, Mount Maenalon, 4.5 km NW Kardaras; 1600 m a.s.l.; 4 Apr. 2024; T.J. Wood leg.; RMNH, RMNH.INS.1152409. See Wood (2024: 95) for examined material from Turkey.

**Notes.** The dot maps of Warncke (Gusenleitner and Schwarz 2002) indicate the presence of *A. pileata* (as *Andrena allosa* ssp. *pileata*) in southern Bulgaria. This can be confirmed with modern samples from the Pirin Mountains (Fig. 8).

**Distribution.** Bulgaria, Greece, Turkey (Warncke 1974a, 1975; Praz et al. 2019; Wood 2024a).

### *Andrena (Euandrena) rufitibialis* Friese, 1899

*Andrena rufitibialis* Friese, 1899: 342, ♀ [West Bank, ZMHB, lectotype by present designation] (Fig. 10)

**Material examined.** ISRAEL • 1♀; Kinereth [Sea of Galilee]; 13 Apr. 1959; SM-NHTAU, SMNH-TAUI 331515; SYRIA • 1♂; Damascus; [probably 1899]; O. Schmedeknecht leg.; K. Warncke det.; OÖLM; WEST BANK • 1♀; Jericho; 13 Apr. 1899; F. Morice leg.; ZMHB (**lectotype** by present designation) • 1♀; Jericho; 13 Apr. 1899; F. Morice leg.; OUMNH; ENT-HYME294-01 (possible **syntype**) • 1♀; Jericho; 13 Apr. 1899; F. Morice leg.; OUMNH; ENT-HYME294-02 (possible **syntype**).

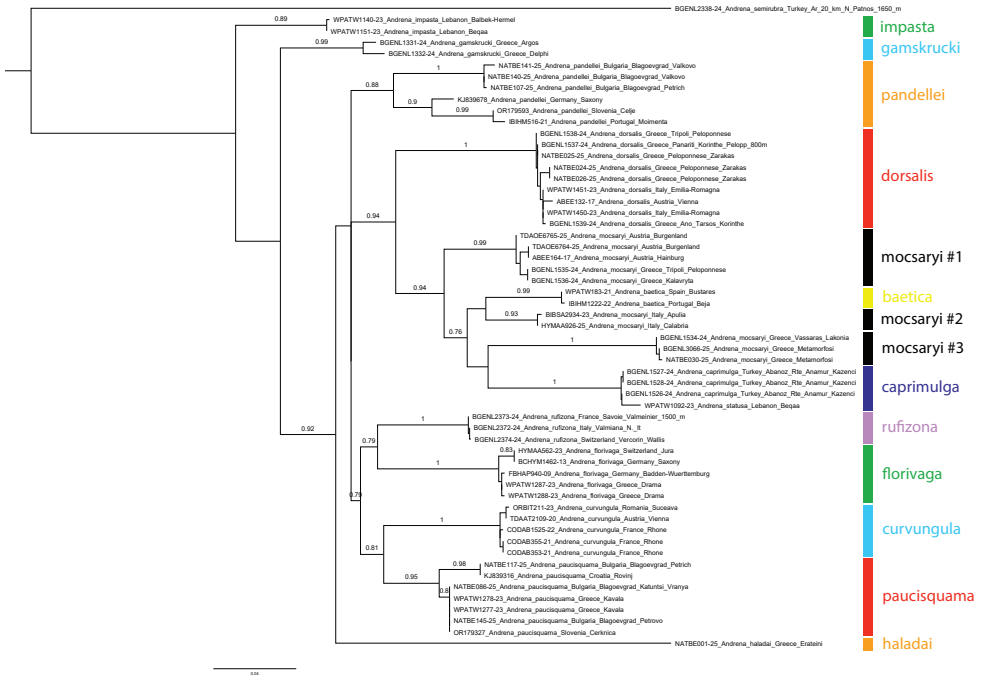
**Notes.** Following the discussion above, *A. rufitibialis* is considered in a narrow sense (only specimens matching the lectotype), giving it a small distribution in drier parts of the Levant.

**Distribution.** Syria, Israel & West Bank (Fig. 15; Friese 1899; Warncke 1969a).

### Subgenus *Lepidandrena* Hedicke, 1933

**Genetics.** Many sequences were available covering all species of the southern Balkans. Most species were well-resolved with high bootstrap support of >95 for species such as *Andrena rufizona* Imhoff, 1834, *Andrena dorsalis* Brullé, 1833, *Andrena florivaga* Evermann, 1852, *Andrena curvungula* Thomson, 1870, and *Andrena paucisquama* Noskiewicz, 1924. However, other species require discussion (Fig. 16).

*Andrena pandellei* Pérez, 1895 formed a monophyletic clade with bootstrap support of 88, but showed moderate average intraspecific genetic variation of 4.80% (range 0.15–8.05%). Three sequences from Bulgaria clustered together with bootstrap support of 100, with three sequences from Portugal, Germany, and Slovenia grouped together



**Figure 16.** Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Lepidandrena* Hedicke, 1933 based on the mitochondrial COI gene. *Andrena (Poecilandrena) semirubra* Morawitz, 1875 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

with bootstrap support of 90. *Andrena pandellei* was originally described from Algeria (lectotype: Theniet el Had) from a cedar forest in the Tell Atlas mountain range. The species is very rare in North Africa, and Warncke (1967b: 215) described *Andrena pandellei* sp. *europaea* Warncke, 1967 for the much more abundant, widespread, and commonly encountered European population. No authors have recognised population structuring within Europe, and hence a broad concept of *A. pandellei* is maintained for the time being.

Warncke adopted a broad species concept for *Andrena gamskrucki* Warncke, 1965 (*locus typicus*: Greece, Larisa), later describing *Andrena gamskrucki* ssp. *eburnea* Warncke, 1975 (*locus typicus*: Turkey, Ayvalik) and *Andrena gamskrucki* ssp. *impasta* Warncke, 1975 (*locus typicus*: Turkey, Bircik). Subsequent authors have treated these as distinct taxa (Dubitzky et al. 2010), and DNA barcodes support this distinction, at least for the two sampled taxa. Sequences of *A. gamskrucki* from mainland Greece were separated from sequences of *A. impasta* from Lebanon by an average genetic distance of 7.52% (range 7.29–7.75%). Unfortunately no barcodes are available for *A. eburnea*, but based on the morphological differences (see identification key), the conclusions of Dubitzky et al. (2010) can be followed. *Andrena gamskrucki* is treated here in a narrow sense as a species endemic to the southern Balkans. See species entry in the Updated Faunal List for discussion of *A. eburnea* on the East Aegean Islands. One additional morphologically-unrelated *Lepidandrena* sequence from southern Greece, NATBE001-25, was

placed as sister to *A. gamskrucki* and *A. impasta*, and was strongly isolated from all other *Lepidandrena* sequences by an average genetic distance of 12.18% (range 10.97–13.23%). It shows a genital and sternal morphology with aspects of *A. pandellei* and *A. paucisquama*, and is newly described below as *Andrena haladai* sp. nov.

The greatest problems come in the *mocsaryi*-group of species. These seem to be taxa strongly associated with *Ornithogalum* (Asparagaceae) (e.g. Westrich 2010). It contains *Andrena mocsaryi* Schmiedeknecht, 1884 (types lost, but described from Hungary), *Andrena baetica* Wood, 2020 (*locus typicus*: Portugal, Portalegre), *Andrena caprimulga* Warncke, 1975 (*locus typicus*: Turkey, Horasan), and probably *Andrena elisaria* Gusenleitner, 1998 (*locus typicus*: Turkey, Hakkâri: Uludere) and *Andrena statusa* Gusenleitner, 1998 (*locus typicus*: Turkey, Hakkâri: Uludere). This group can be recognised due to the combination of the outer surface of the female galea which is strongly roughened and dull and the male sternum 8 which is flat and not divided into horizontal and vertical parts (as is the case in the *florivaga*-group *sensu* Schmid-Egger and Scheuchl 1997).

Five clades were observed, all with bootstrap support >93 (Fig. 16). One contained *A. baetica* (Spain and Portugal), one contained *A. caprimulga* from Turkey plus *A. statusa* from Lebanon, one contained *A. mocsaryi* from Austria and Greece (Peloponnese) (*mocsaryi* #1), one contained *A. mocsaryi* from Italy (*mocsaryi* #2; see also Mendicino et al. 2026), and one contained *A. mocsaryi* from the Peloponnese only (*mocsaryi* #3). The three clades of “*A. mocsaryi*” were all strongly separated. *mocsaryi* #1 was separated from *mocsaryi* #2 by an average genetic distance of 5.86% (range 4.88–6.33%) and from *mocsaryi* #3 by an average genetic distance of 9.87% (range 8.61–10.70%). *mocsaryi* #2 was separated from *mocsaryi* #3 by an average genetic distance of 8.83% (range 8.51–9.17%). The situation is particularly confusing because the two *mocsaryi* lineages that can be found in sympatry in the Peloponnese (nos. #1 and #3) show the greatest observed separation of 10.70% (sequences [NATBE030-25](#) and [BGENL1535-24](#)). This genetic distance is substantial, and may indicate the presence of a cryptic species. Unfortunately, all of the barcoded Greek specimens of “*A. mocsaryi*” are female (all selected males failed), and in general it has only been possible to examine two male specimens from Greece compared to 36 female specimens. It seems that most collectors travel to Greece slightly too late to encounter males. If a cryptic species truly is present, then it is *mocsaryi* #1 that represents the true *A. mocsaryi* since this clade contains a specimen from Austria, close to the *terra typica* of Hungary. More male material is required to understand what is happening in these different mitochondrial lineages of *A. mocsaryi*.

More broadly, the three *mocsaryi* lineages do not form a monophyletic clade. *Andrena baetica* was nested within, but was strongly separated from *mocsaryi* #1 (5.66%, range 4.88–6.43%), *mocsaryi* #2 (5.75%, range 4.95–6.55%), and *mocsaryi* #3 (9.71%, range 9.58–9.88%). Morphologically, in principle there is no strong barrier to including *A. baetica* within a broad concept of *A. mocsaryi* as a geographically isolated population (differences are mostly related to female scutal hair length and structure and male clypeus colour), but the topology of the tree does not allow this given the strong genetic separation of *A. caprimulga* which is also nested within the broad *A. mocsaryi sensu lato* clade, in addition to the differences in the structure of the male S8.

The inclusion of sequences of *A. caprimulga* is important to exclude the possibility that one of the “lineages” of *A. mocsaryi* in the Peloponnese is actually *A. caprimulga*. However, *A. caprimulga* sequences were strongly separated from the lineages present in the Peloponnese, namely *mocsaryi* #1 (7.47%, range 6.43–8.16%) and *mocsaryi* #3 (9.74%, range 8.87–10.35%). Morphologically, *A. caprimulga* is differentiated from *A. mocsaryi* by a small but distinct difference; it was not well-expressed by Warncke in his writing, but he did illustrate the key difference which is that the 8<sup>th</sup> sternum is produced into three distinct points in *A. caprimulga*, and is rounded with a tiny apical point in *A. mocsaryi* (illustrated Warncke 1975: 95; see also Schmid-Egger and Scheuchl 1997: 156 for the character state of *A. mocsaryi*). None of the examined males from the southern Balkans have shown this distinctive *A. caprimulga* structure of the 8<sup>th</sup> sternum. This difference has been slightly obscured because in the OÖLM collection, although Blank and Kraus (1994) indicated two female (holotype and paratype) and one male (paratype) specimens in the collection of Warncke during its accession, only the two female specimens are currently present. Moreover, the female paratype is stylotipised and displays intersex features (e.g. a partially yellow-marked clypeus; Fig. 17).

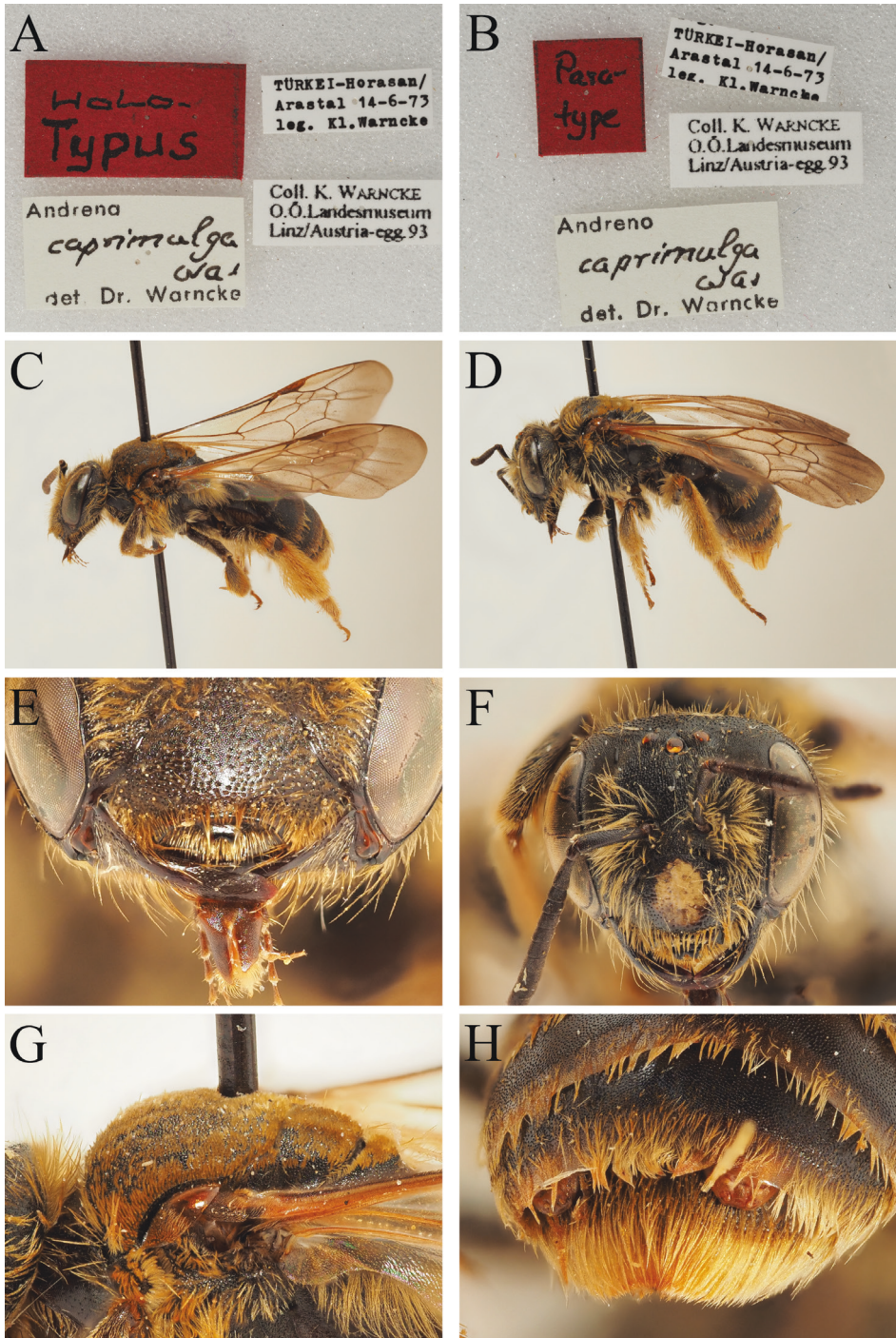
The sequence of *A. statusa* from Lebanon is separated from the Turkish sequences by an average of 1.01% (range 0.91–1.07%), but the topology indicates that it is nested between them. Examination of a paratype male from Israel (directly; photographs also available on zobodat.at) indicate that the 8<sup>th</sup> sternum shows the typical *A. caprimulga* shape, with three distinct points. This is consistent between Levantine specimens, newly examined and sequenced specimens from the Taurus mountains (RMNH), and Warncke’s original type series from Horasan (as illustrated by Warncke 1975). Consequently, *A. statusa* is formally synonymised under *A. caprimulga* below. Finally, Pisanty et al. (2018) already expressed doubts about the nominal differences described between *A. elisaria* and *A. statusa* based on co-occurrence of the taxa in Israel, concluding that they may simply be dark and red-marked specimens of *A. statusa* (= *A. caprimulga*). Some male *Lepidandrena* specimens from south-eastern Turkey (OÖLM/TJWC) with extensive red maculations show a S8 that is laterally rounded – these may represent *A. elisaria*, but the description combined with the holotype designated in the female sex is currently limiting. No taxonomic action for *A. elisaria* is taken at the present time, awaiting the generation of additional genetic sequences from Turkey.

### *Andrena (Lepidandrena) caprimulga* Warncke, 1975

*Andrena (Lepidandrena) caprimulga* Warncke, 1975: 94, ♀♂ [Turkey, OÖLM, examined] (Fig. 17)

*Andrena (Lepidandrena) statusa* Gusenleitner, 1998: 119, ♀♂ [Turkey, OÖLM, examined] syn. nov.

**Material examined. LEBANON** • 1♂; Beqaa, Beqaa valley, Qaraoun dam; 850 m a.s.l.; 4 Apr. 2023; T.J. Wood leg.; TJWC • 1♂; Tannourine el Tahta, Wadi Ain al Raha; 936 m a.s.l.; 11 Apr. 2017; M. Boustani leg.; TJWC; **ISRAEL** • 1♂; 850 m S Bet



**Figure 17.** *Andrena* (*Lepidandrena*) *caprimulga* Warncke, 1975 holotype female (**A**; **C**; **E**; **G**) and paratype female (**B**; **D**; **F**; **H**) (both OÖLM). **A.** Label information; **B.** Label information; **C.** Habitus, lateral view; **D.** Habitus, lateral view; **E.** Clypeus and process of labrum, frontal view; **F.** Head, frontal view; **G.** Scutum and scutellum, lateral view; **H.** Metasomal apex, posterior view.

Oren; 256 m a.s.l.; 31 Mar. 2012; A. Dorchin leg.; ADC • 1♂, 1♀; Galilea, 10 km E of Nahariyya; 9 Apr. 1988; R. Leys leg.; RMNH • 5♂, 16♀; Hasharon, Zikhron Ya'aqov, Ramas Hanadiv; 12 Mar. 1990; R. Leys leg.; RMNH/TJWC • 1♂, 3♀; Hasharon, Zikhron Ya'aqov, Ramas Hanadiv; 25 Mar. 1990; R. Leys leg.; RMNH • 1♂; Jerusalem env; 7 Apr. 1946; Bytinski-Salz leg.; OÖLM (**paratype** of *Andrena statusa*) • 3♀; Mt Carmel, Denia; 8 Apr. 1999; S.P.M. Roberts leg.; SPMRC • 3♀; Mt. Gilboa, Merav [Meirav], 0.33 km W; 353 m a.s.l.; 20 Mar. 2021; A. Dorchin leg.; ADC • 1♂; Tiberias; 26 Mar. 1996; H. Wolf leg.; OÖLM; **TURKEY** • 2♀; Horasan, Arastal; 14 Jun. 1973; K. Warncke leg.; OÖLM (**holotype** and styloipised **paratype** of *Andrena caprimulga*) • 4♂, 3♀; Abanoz (Rte Anamur Kazenci), Taurus; 1200 m a.s.l.; 10 May 1991; H. Teunissen leg.; RMNH • 3♀; Tanin-Tanin-Pass; 1700 m a.s.l.; 12 Jun. 1984; K. Warncke leg.; OÖLM/TJWC • 14♀; E of Şirnak/Siirt; 4 Jun. 1977; K. Warncke leg.; OÖLM (**paratypes** of *Andrena statusa*) • 1♀; Uludere, Hakkari; 5 Jun. 1977; K. Warncke leg.; OÖLM (**holotype** of *Andrena statusa*); **WEST BANK** • 1♂; Judea, Har Gilo; 6 Apr. 1988; R. Leys leg.; RMNH.

**Distribution.** Crimea, Turkey, Lebanon, Israel & West Bank (Fig. 18; Warncke 1974a, 1975; Osytshnjuk et al. 2008; Pisanty et al. 2018, as *A. statusa*; Wood et al. 2020, as *A. statusa*). Although the key presented by Osytshnjuk et al. (2008: 142) includes only the female sex and not the distinctive male, the listing from Crimea can be confirmed through personal correspondence from Erwin Scheuchl:

“I own one female and three genitalized males from Crimea:

1♂, 18.06.1997 \ Crimea, Balaklava District \ W. Cholodorov leg.

1♂, 18.06.1997 \ Crimea, Balaklava Area, Chernorech \ W. Cholodorov leg.

1♀, 09.06.1997 \ Crimea, Balaklava Area, Chernorech \ W. Cholodorov leg.

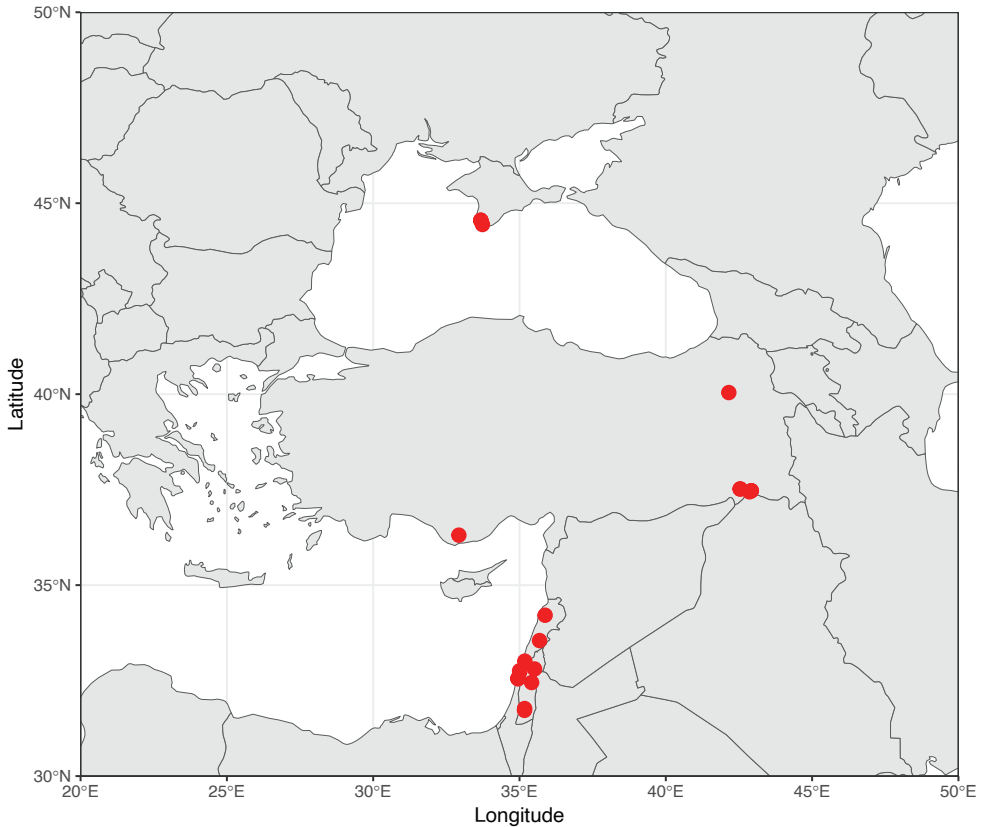
1♂, 06.06.1997 \ Ukraine, Crimea, Area Tylovoje Village \ Ivanov leg.

[Chernorechye = Chernorechye, 44.55°N, 33.68°E, Tylovoje Village = Tylove Village.

Osytshnjuk actually first encountered the male of *A. caprimulga* in 1997 during her stay in Munich at the Grünwaldt Collection. The female from Alushta, which Osytshnjuk used to include it in the Central and Eastern Palaearctic Key, was confirmed by Grünwaldt as *A. caprimulga*”.

### Subgenus *Leucandrena* Hedicke, 1933

**Notes.** Hedicke (1933: 215) described the subgenus *Leucandrena* with the type species of *Apis sericea* Christ, 1791 nec. Forster, 1771 = *Andrena barbilabris* (Kirby, 1802). This name has been used widely at a subgeneric level in the classification of *Andrena* since its original description. However, it has been discovered (Doug Yanega, pers. comm.) that Haeckel (1872: Band II: 172) created the name *Leucandrena* Haeckel, 1872 “in cohors” (sub-subgenus) within the genus *Leucandra* Haeckel, 1872 subgenus *Leucogypsa* Haeckel, 1872. This name is considered to be available under Article 10.4 (ICZN 1999) as even



**Figure 18.** *Andrena (Lepidandrena) caprimulga* Warncke, 1975 global distribution map based on examined specimens. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

though it was created as a tertiary division of a genus, it was accompanied by the term “cohors” which can be considered equivalent to a term such as “section” or “division”.

There is no evidence that *Leucandrena* Haeckel has ever been used in any subsequent publications, and its recognition would result in subgeneric instability within *Andrena*, a challenging enough issue given the difficulties associated with applying and delineating *Leucandrena* Hedicke (see Pisanty et al. 2022a). For this reason, the application of the Principle of Priority should be set aside and I here invoke reversal of precedence in accordance with Article 23.9.1 of the Code (ICZN 1999). The senior homonym *Leucandrena* Haeckel has not been used as a valid name after 1899, and the junior homonym *Leucandrena* Hedicke has been used in at least 25 works published by at least 10 different authors in the last 50 years and encompassing a span of not less than 10 years (LaBerge 1987; Schmid-Egger and Scheuchl 1997; Xu and Tadauchi 1997, 2009; Guseleitner and Schwarz 2002; Guseleitner et al. 2005; Grünwaldt et al. 2005; Dubitzky 2006; Michener 2007; Osytshnjuk et al. 2008; Dubitzky et al. 2010; Ortiz-Sánchez 2011, 2022; Hazir et al. 2014; Scheuchl and Willner 2016; Álvarez Fidalgo et al. 2021;

Astafurova et al. 2021; Bossert et al. 2022; Pisanty et al. 2022a; Wood and Monfared 2022; Wood 2021, 2023b, 2024a, 2025a; Ghisbain et al. 2023; Gautam et al. 2024).

Therefore, I establish the reversal of precedence according to Article 23.9.1 giving the senior homonym *Leucandrena* Haeckel, 1872 the status of *nomen oblitum* and the junior homonym *Leucandrena* Hedicke, 1933 the status of *nomen protectum*.

### Subgenus *Limbandrena* Wood, 2023

#### *Andrena* (*Limbandrena*) *toelgiana* Friese, 1921, sp. resurr.

*Andrena toelgiana* Friese in Fahringer & Friese, 1921: 171, ♀ [Turkey, DEI, examined] (Fig. 19)

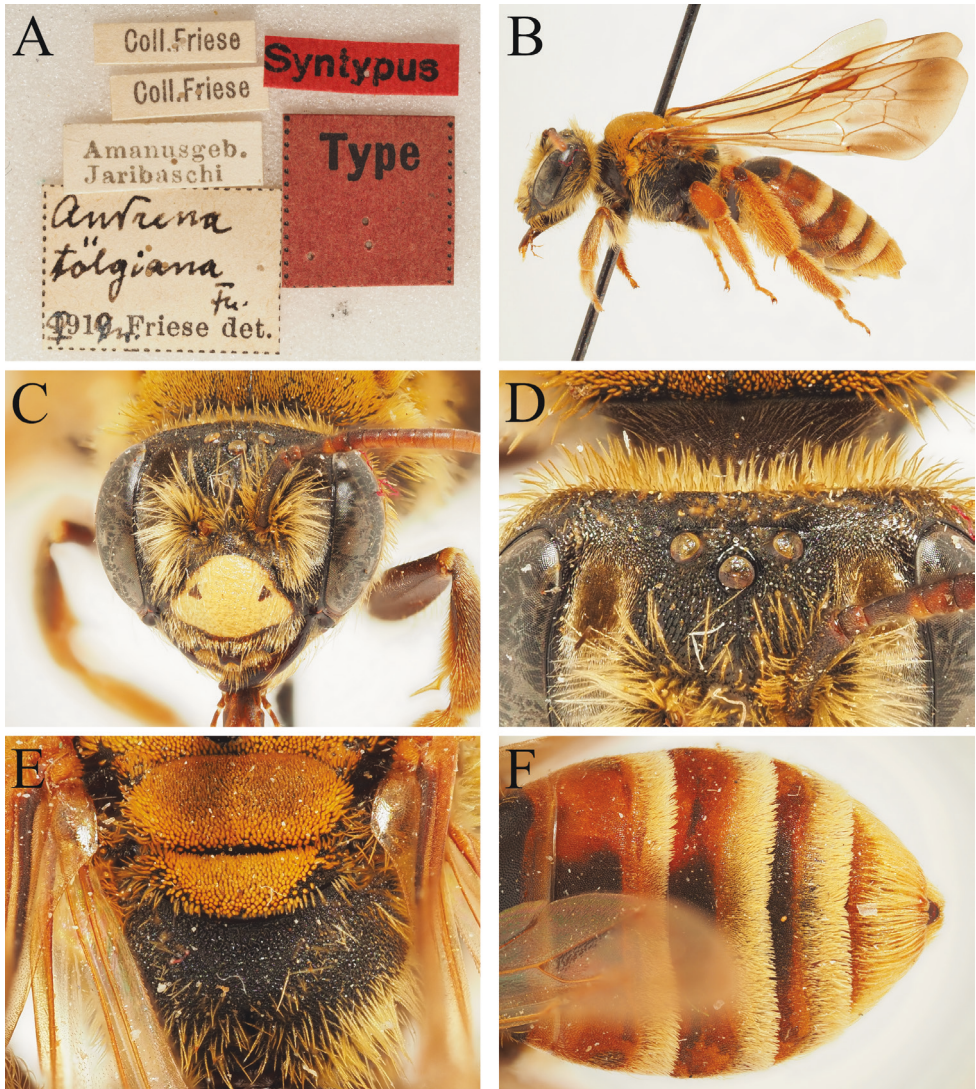
**Material examined.** GREECE • 3♀; Lesbos, Agiassos; 658 m a.s.l.; 5 Jun. 2009; M. Hull leg.; WML; TURKEY • 1♀; Amanusgeb [Amanus mountains], Jaribaschi; DEI (probable **holotype**) • 1♀; Akyaka, Yeşilova; 20 Jun. 2016; M. Kasperek leg.; OÖLM • 1♀; Ayvalik; 13 Apr. 1965; K. Warncke leg.; K. Warncke det.; OÖLM • 1♀; Diyarbakır; 15 Apr. 1972; Bytinski-Salz leg.; K. Warncke det.; OÖLM • 1♀; Side; 23 Apr. 1973; K. Warncke leg.; K. Warncke det.; OÖLM • 4♀; Side; 10 Apr. 1974; K. Warncke leg.; K. Warncke det.; OÖLM • 2♀; Antalya, Gençler; 341 m a.s.l.; 23 Apr. 2025; Ghisbain, Michez, Santerre leg.; TJWC/UMONS • 2♀; Çanakkale; 2024; L. Efil leg.; IUZC.

**Notes.** A single specimen of *A. toelgiana* is preserved in the DEI collection; it is almost certainly the holotype, as Friese simply writes “♀ von Jaribaschi im Amanusgebirge, 7. Mai”, whereas for other species he specifies the number of specimens, suggesting that only a single specimen was considered.

Wood (2023b: 325) synonymised *A. toelgiana* under the widespread *A. limbata* Eversmann, 1852 due to the inconsistent and variable nature of the “key” discriminative character provided in the literature, namely the yellow-marked clypeus (Gusenleitner and Schwarz 2002). However, what was not clear from the literature is that this character is not at all important for identification; what is instead key is the short ocellocipital distance which only slightly exceeds the diameter of a lateral ocellus (Fig. 19D; 1–1.5 times), whereas in *A. limbata* this distance equals three times the diameter of a lateral ocellus. That the clypeus is yellow marked is incidental given the partial expression of this character in some specimens of *A. limbata* (see photographs in Wood 2023b). In this context, *A. toelgiana* sp. resurr. is restored to species status, as the original synonymy was unjustified without the inspection of the original type material. The male remains unknown and undescribed.

In the southern Balkans, it is known only from the island of Lesbos (Grace 2010); this can be confirmed through new specimen examination. It has also been possible to examine specimens from Ayvalık and Çanakkale from the adjacent parts of nearby Turkey.

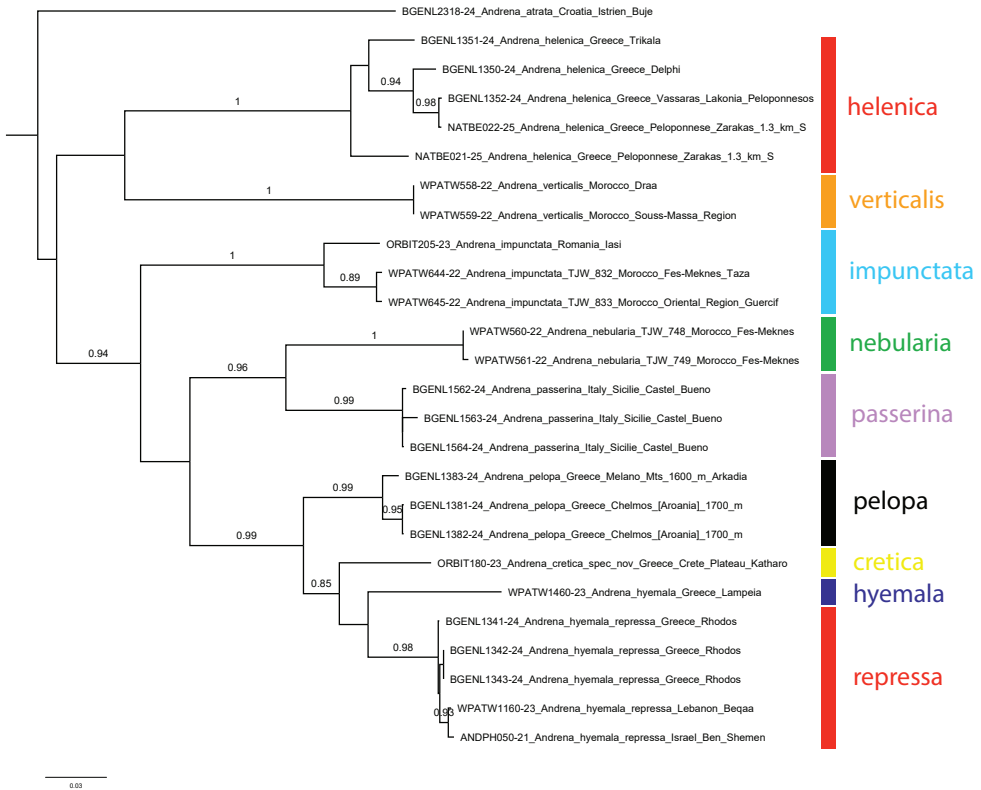
**Distribution.** Greece (Lesbos) and Turkey descending into the Levant (Syria and northern Israel; Gusenleitner and Schwarz 2002) but ideally Levantine material should be located and validated.



**Figure 19.** *Andrena (Limbandrena) toelgiana* Friese, 1921 probable holotype female (DEI). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Vertex, dorsal view; **E.** Propodeum, dorsal view; **F.** Metasoma, dorsal view.

### Subgenus *Graecandrena* Warncke, 1968

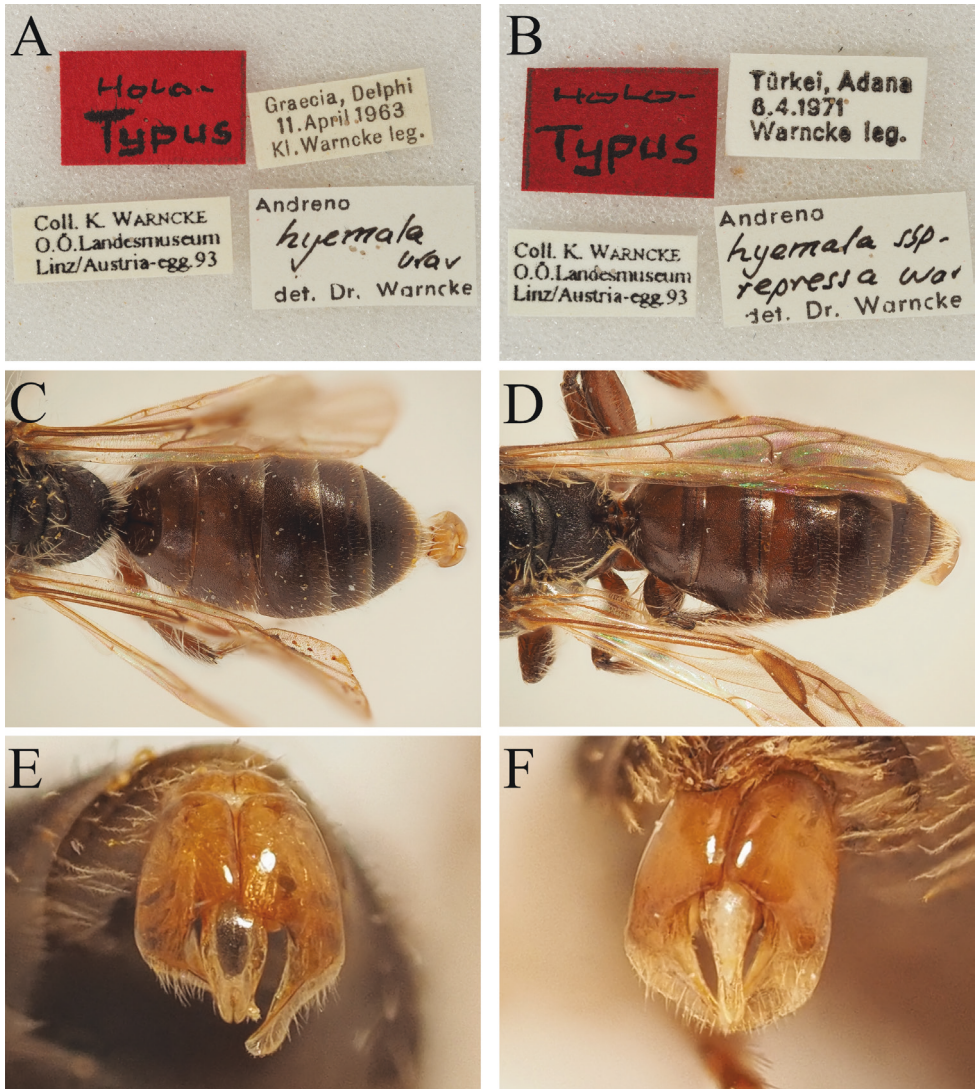
**Genetics.** Sequences of *Andrena hyemala* Warncke, 1973 were available from continental Greece (Peloponnese) and Crete, and sequences of *A. hyemala* ssp. *repressa* Warncke, 1975 were available from Rhodes, Lebanon, and Israel (Fig. 20). However, the sequence from Crete was surprisingly strongly separated from that of continental Greece. Whilst *A. hyemala* s. str. from continental Greece was separated from *A. h. repressa* by



**Figure 20.** Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Graecandrena* Warncke, 1968 based on the mitochondrial COI gene. *Andrena* (*Parandrenella*) *atrata* Friese, 1887 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

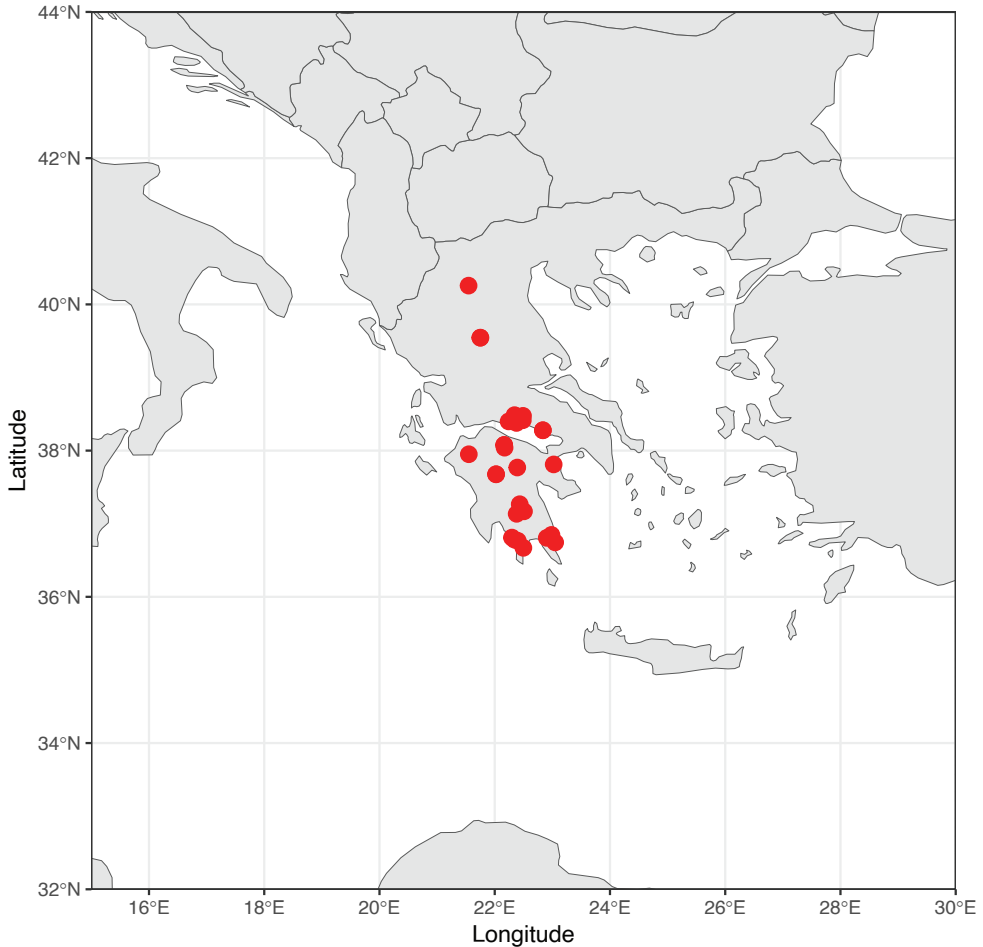
an average genetic distance of 8.09% (range 7.75–8.36%), it was also separated from the Cretan sequence by 8.89%. The separation between the Cretan “*A. hyemala*” and *A. h. repressa* was also high at an average genetic distance of 7.08% (range 6.95–7.27%). These strong genetic distances combined with morphological differences mean that it is appropriate for *A. repressa* stat. nov. to be treated at a specific level, and for Cretan specimens to be described as *Andrena cretica* sp. nov. Morphologically, *A. repressa* can most easily be recognised in the male sex through comparison of the genital capsule and specifically the width of the penis valves (Fig. 21), broader in *A. hyemala* (Fig. 21E) and narrower in *A. repressa* (Fig. 21F); full diagnosis is made through the identification key below which includes *A. hyemala*, *A. repressa*, and *A. cretica*, as well as the diagnosis section in the description of *A. cretica*. Formal elevation is carried out below.

Additionally, comment is necessary on the placement of *Andrena helenica* Warncke, 1965. Warncke (1968: 58) placed *A. helenica* in the subgenus *Graecandrena*, but *A. helenica* does not show the typical genital capsule form seen in most members of the group, and the female has very narrow facial foveae which could be indicative of



**Figure 21.** *Andrena (Graecandrena) hyemala* Warncke, 1973 holotype male (**A**; **C**; **E**) and *Andrena (Graecandrena) hyemala* ssp. *repressa* Warncke, 1975 holotype male (**B**; **D**; **F**) (both OÖLM). **A.** Label information; **B.** Label information; **C.** Metasoma, dorsal view; **D.** Metasoma, dorsal view; **E.** Genital capsule, dorsal view; **F.** Genital capsule, dorsal view.

the *Distandrena* Warncke, 1968 group (= *Micrandrena* Ashmead, 1899). Doubts also existed about *Andrena verticalis* Pérez, 1895 which was only tentatively placed in the *Graecandrena* until Pisanty et al. (2022a) confirmed this placement. *Andrena helenica* sequences placed most closely to *A. verticalis* (Fig. 20), and whilst this is weak evidence, it is enough to maintain its current subgeneric placement. *Andrena helenica* remains endemic to Greece, extending north to Siatista and Trikala (Warncke 1965a; Fig. 22).



**Figure 22.** *Andrena (Graecandrena) helenica* Warncke, 1965 global distribution map. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

***Andrena (Graecandrena) repressa* Warncke, 1975, stat. nov.**

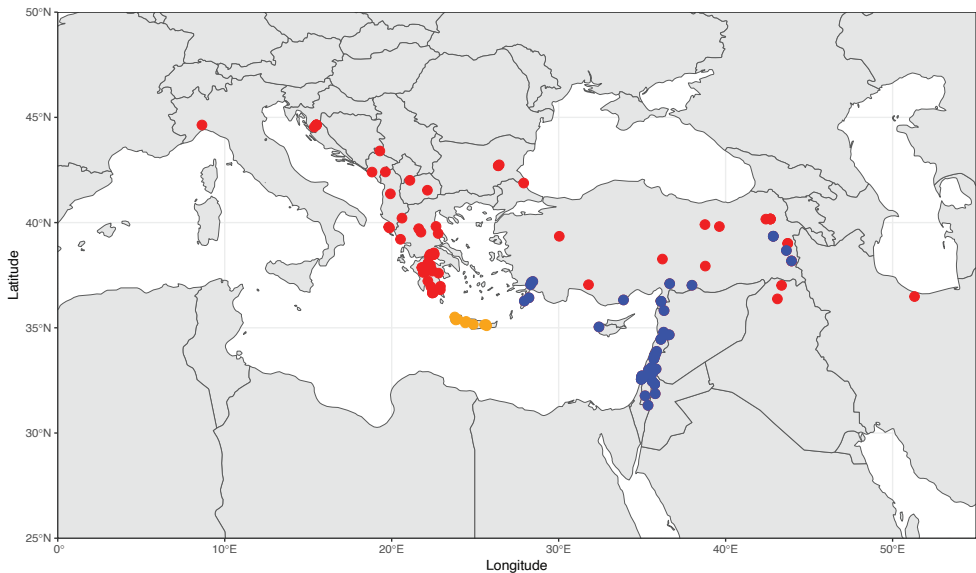
*Andrena hyemala* ssp. *repressa* Warncke, 1975: 62, ♀♂ [Turkey, OÖLM, examined]  
Figs 21B, D, F.

**Material examined (illustrative).** **CYPRUS** • 1♀; Paphos, Polis, Chrysochous; 10 m a.s.l.; 1 Jun. 2023; P. Rosa leg.; UMONS; **GREECE** • 1♂, 4♀; Rhodos; 23 Apr. 1976; K. Vegeter leg.; RMNH • 1♂; 23 Apr. 1970; v. Oostroom leg.; RMNH; **ISRAEL** • 2♀; Mas'ada [Masada]; 19 Apr. 1988; M. Kraus leg.; OÖLM • 6♂, 1♀; Mt. Carmel, En Hod; 4 Apr. 1999; S.P.M. Roberts leg.; SPMRC • 10♂, 3♀;

Hasharon, Zikhron Ya'aqov, Ramas Hanadiv; 25 Mar. 1990; R. Leys leg.; RMNH; **JORDAN** • 1♀; 20 km N Amman; 620 m a.s.l.; 23 Apr. 2006; K. Deneš leg.; OÖLM • 3♀; 30 km NW Ajlun [Aj'loun]; 600 m a.s.l.; 29 Apr. 2006; K. Deneš leg.; OÖLM/TJWC • 4♀; Ajlun [Aj'loun] env; 840 m a.s.l.; 1 May 2006; K. Deneš leg.; OÖLM/TJWC **LEBANON** • 3♀; Beqaa, Beqaa valley, Mansourah, Aammiq wetland preserve; 850 m a.s.l.; T.J. Wood leg.; TJWC • 2♂; Beqaa, Beqaa valley, Mansourah, Kafraiya village; 1000 m a.s.l.; T.J. Wood leg.; TJWC • 5♀; Beqaa, Beqaa valley, Qaraoun, 3.5 km W of Madjal Balhis; 900 m a.s.l.; T.J. Wood leg.; TJWC • 2♂; Mount Lebanon, Hazerta; c. 1400 m a.s.l.; 6 May 1996; C.G. Roche leg.; OUMNH; **SYRIA** • 1♀; Jisr al-Shughur [written as Jisr-esh-Shughur], Syria; 18 Apr. 1992; K. Warncke leg.; OÖLM • 1♀; occ. An Nasrah env [Al-Nasrah]; 8–13 Apr. 2005; J. Saki leg.; OÖLM • 1♂, 11♀; Orontes, 30 km SW Homs; 500 m a.s.l.; 15 Apr. 1992; K. Warncke leg.; OÖLM • 1♀; Stausee [Dam], 500 m, 10 km SW Homs; 15 Apr. 1992; K. Warncke leg.; OÖLM **TURKEY** • 1♂, 1♀; Adana; 6 Apr. 1971; K. Warncke leg.; OÖLM (male **holotype**, female **paratype**).

**Notes.** *Andrena repressa* was originally described from Turkey (Adana), with additional material from Greece (Rhodes), and Israel (Ramla). A selection of records is presented above; full details can be found in the Suppl. material 2.

**Distribution.** Greece (Rhodes), Turkey, Cyprus\*, Syria\*, Lebanon\*, Israel, Jordan\* (Fig. 23; Warncke 1975, as *A. hyemala* ssp. *represa*).



**Figure 23.** Distribution map of *Andrena* (*Graecandrena*) Warncke, 1968 species. *Andrena* (*G.*) *hyemala* Warncke, 1973 (red circles); *A. (G.) cretica* sp. nov. (orange circles); *A. (G.) repressa* Warncke, 1975 (blue circles). Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

### Subgenus *Holandrena* Pérez, 1890

**Genetics.** There are two major issues within this subgenus which must be resolved, specifically the statuses of the two pairs of nominally univoltine taxa which fly in the spring and summer, respectively, these being *Andrena flavilabris* Schenck, 1874 – *Andrena decipiens* Schenck, 1861 and *Andrena wilhelmi* Schubert, 1995 – *Andrena forsterella* Osytshnjuk, 1978. Whilst Warncke (1967b, 1974a, 1974b) treated both “pairs” as bivoltine species, but variable treatments have been produced since them which are dissected below.

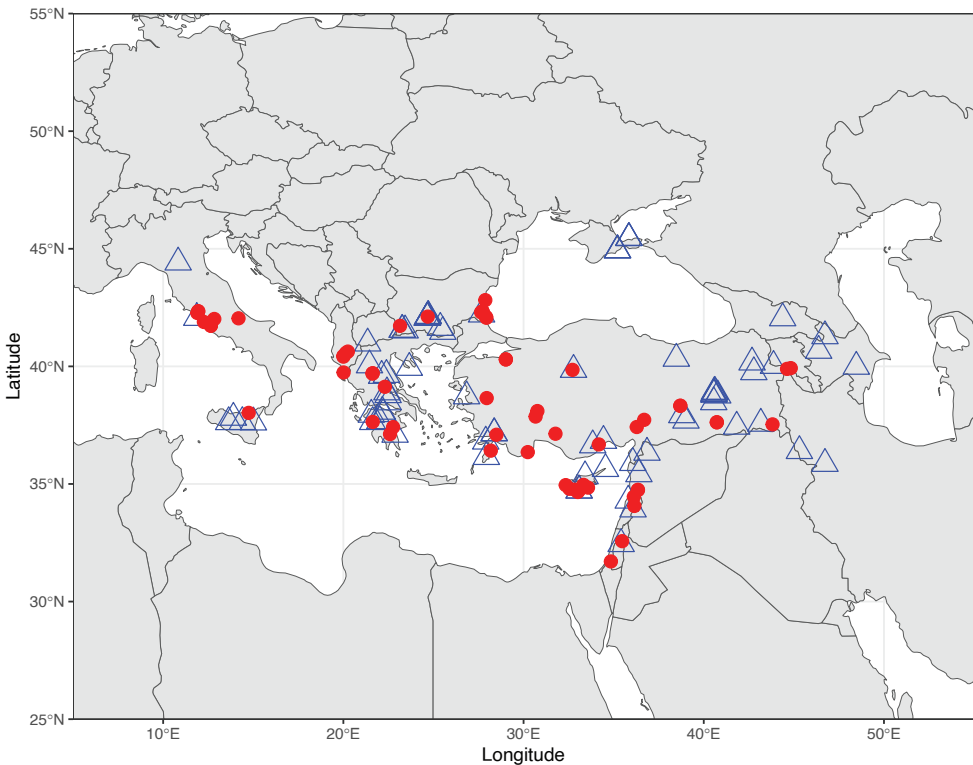
*Andrena forsterella* is discussed first, as the creation of this name has been complex, requiring an understanding of changing concepts presented by Warncke (1965a, 1967b). A summary was presented by Schönitzer et al. (1995), but in short, *Andrena forsterella* Warncke, 1967 is an invalid name as it does not meet ICZN (1964, 1985, 1999) standards. Under Article 13.1.3, a name created after 1930 must be proposed expressly as a new replacement name (*nomen novum*) for an available name – *Andrena forsterella* Warncke, 1967 was proposed as a replacement name for a *sensu auctorum*, i.e. not an available name. The correct authority is *Andrena forsterella* Osytshnjuk, 1978.

This background is important to note, as *A. forsterella* is a problematic taxon; originally considered to be bivoltine, the “first” generation was described as a new species by Schuberth (1995) as *Andrena wilhelmi* Schubert, 1995. The separation of *A. wilhelmi* from *A. forsterella* is morphologically challenging in females if the collecting date information has been removed. Schuberth cites primarily the slightly smaller size, darker colouration, longer hairs, less strongly developed tergal hairbands, and yellow facial markings in the male restricted to the clypeus (and not extending onto the lower paraocular areas). However, these are characters which are subject to intergenerational variation due to developing and flying in different seasons; the different generations of *Andrena variabilis* Smith, 1853 also display these types of colouration and pubescence differences. For structural differences, Schuberth cites slightly sparser tergal punctation, the slightly more strongly upturned fore margin of the male clypeus, and more strongly striate gena. However, slight differences in sculpture are also subject to intergenerational variation, as can be seen in *Andrena (Micrandrena)* Ashmead, 1899 such as in the widely accepted to be bivoltine *Andrena minutula* (Kirby, 1802) and *Andrena minutuloides* Perkins, 1914. Schuberth asserts that the characters are clear, and that they cannot be subject to seasonal variation, but evidence to support this claim is required given the pattern of morphological intergenerational variation often seen in bivoltine *Andrena*.

Schuberth (1995: 818) noted that the two taxa seemed to avoid occupying the same sites, at least at a small geographic scale (*Der Vergleich der Verbreitungskarten der beiden Arten erweckt vielmehr den Anschein, als würden sich die beiden Arten zumindest kleinflächig meiden*). However, examination of 123 specimens of *A. wilhelmi* and 127 specimens of *A. forsterella* from across their known ranges (see Suppl. material 2 for full details) make it difficult to believe this idea (Fig. 24). Whilst only a small quantity of summer-flying material from the Caucasus has been examined and none from Crimea, Schönitzer et al. (1995) presented material from Azerbaijan (including the lectotype

designation of *A. forsterella*) and northern Iran along the Caspian Sea, and Osytshnjuk (1978) cited the presence of *A. forsterella* in Crimea. Therefore, combining the specimen records presented here and by Schuberth (1995) and Schönitzer et al. (1995), *A. wilhelmi* and *A. forsterella* are considered to have completely overlapping ranges. The consistent northern boundary of both taxa can be seen, for example, across Bulgaria, and both taxa extend consistently into the Levant (Fig. 24).

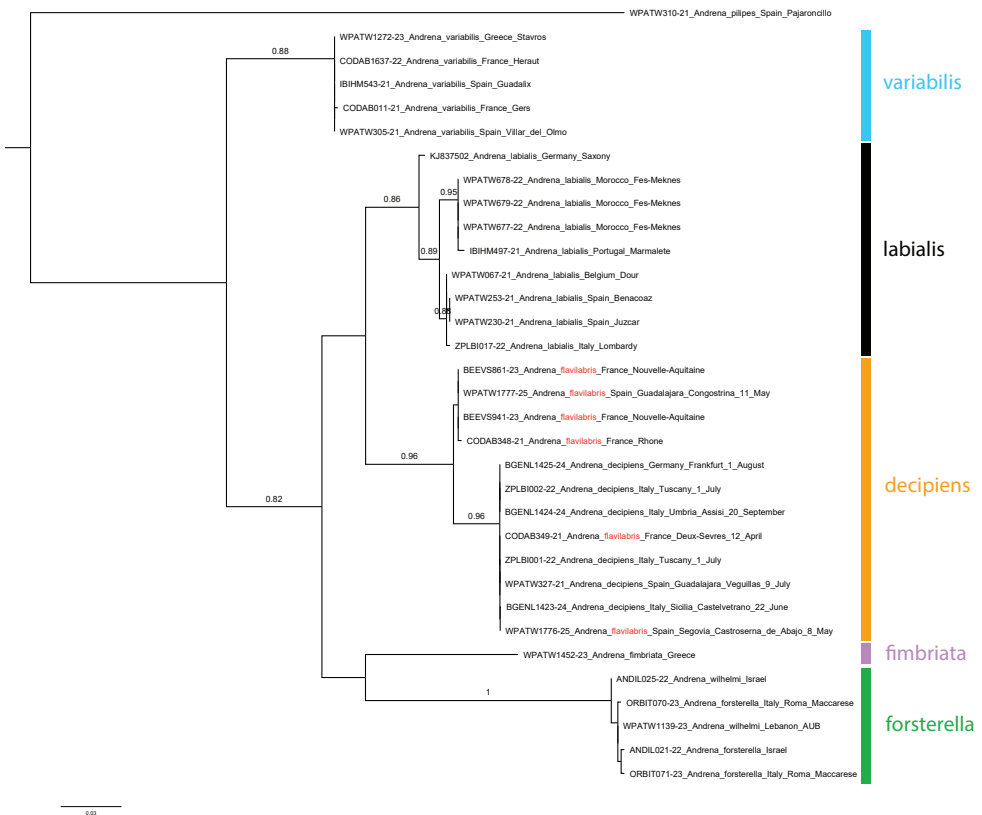
Genetic evidence provides a level of clarity (Fig. 25). Spring-flying sequences were available from Israel and Lebanon ( $n = 2$ ), and summer-flying sequences were available from Italy and Israel ( $n = 3$ ). All sequences were grouped together with bootstrap support of 100. If treating the taxa as distinct, average intraspecific distance for *A. wilhelmi* was 0.30%, and average intraspecific distance for *A. forsterella* was 0.41% (range 0.30–0.46%). Average “interspecific” genetic distance was 0.41% (range 0.15–0.61%). Treating them as a single species showed average intraspecific variation of 0.40% (range 0.15–0.61%). Unsurprisingly, these very low genetic distances strongly support just a single species that is bivoltine. When compared to other *Holandrena* species, high interspecific distances are seen, such as an average of 9.12% (range 8.03–9.58%) between *Andrena labialis* (Kirby, 1802) and *Andrena variabilis*. Consequently,



**Figure 24.** Global distribution map of *Andrena (Holandrena) forsterella* Osytshnjuk, 1978. Spring generation (*Andrena wilhelmi* Schuberth, 1995) (blue open triangles); summer generation (*Andrena forsterella*) (red circles). Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

*A. wilhelmi* syn. nov. is synonymised under *A. forsterella*; this change is formalised below, and *A. forsterella* is integrated into the identification key as a bivoltine species.

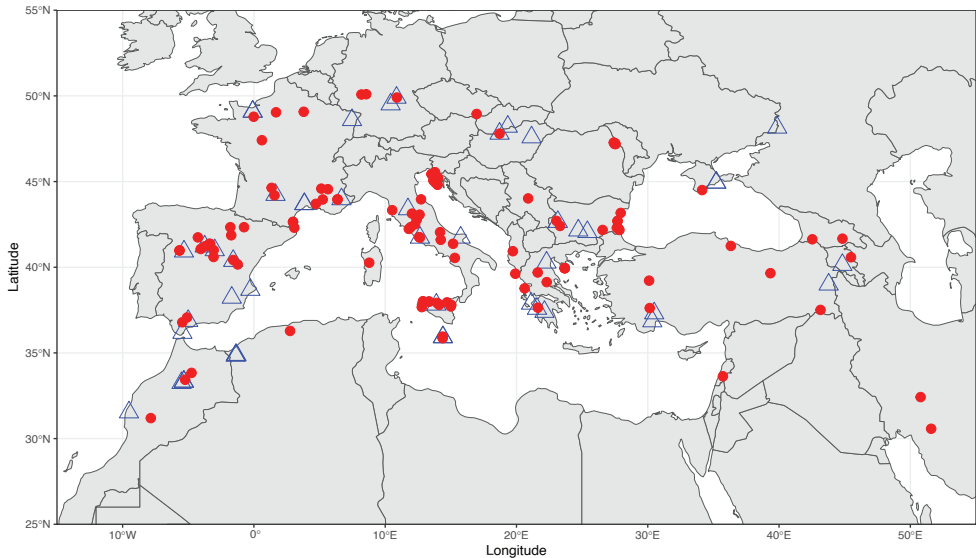
Finally, it is appropriate to discuss the status of *Andrena flavilabris* Schenck, 1874 as distinct from *Andrena decipiens* Schenck, 1861. Long considered (with a degree of uncertainty) to be just the spring generation of *A. decipiens* (e.g. Schönitzer et al. 1995; Schuberth 1995), Mandery et al. (2008) returned *A. flavilabris* to species status based on morphological and 16S ribosomal DNA genetic data, specifically divergence of 3% between *A. decipiens* and *A. flavilabris*. Using the different COI marker, two clades were detected in a contemporary analysis. One contained four sequences identified as *A. flavilabris* which showed average intraspecific variation of 0.08% (range 0.00–0.16%). The second clade was composed of eight sequences showing intraspecific variation of 0.00% (range 0.00–0.00%). The two clades were separated by an average genetic distance of 1.99% (range 1.11–2.51%), and consequently appeared visually well-separated, although the clade with four sequences only received bootstrap support of 56 compared to 96 for the clade with eight sequences (Fig. 25).



**Figure 25.** Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Holandrena* Pérez, 1890 based on the mitochondrial COI gene. *Andrena (Plastandrena) pilipes* Fabricius, 1781 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

However, the clade of eight sequences contained six specimens identified as *A. decipiens* and two sequences (CODAB349-21 and WPATW1776-25) identified as *A. flavilabris*. The specimen CODAB349-21 was caught on 16 Apr. 2012 in France, and WPATW1776-25 was caught on 8 May 2025 in central Spain. The issue is illustrated by specimens from central Spain. WPATW1776-25 (a female specimen) and WPATW1777-25 (a male specimen) were identified as *A. flavilabris* and were caught a few days apart in May 2025 in the provinces of Segovia and Guadalajara, but showed a genetic difference of 1.11%. They consequently fell into the two observed clades. Specimen WPATW1776-25 was caught just 6 kilometers east of sequence WPATW327-21 that was caught on 9 Jul. 2021, and the two sequences were identical.

There is therefore a lack of congruence between the morphology, the observed flight date, and the genetic analysis. Looking at other lines of evidence, in Germany, both *A. decipiens* and *A. flavilabris* have reappeared simultaneously at several sites in recent years after decades without evidence of their presence, and *A. flavilabris* in the spring flies to the same nesting sites as *A. decipiens* in the summer (E. Scheuchl, pers. comm.). This strongly suggests that they are the same bivoltine species. Inspection of museum material illustrates that *A. decipiens* and *A. flavilabris* have completely overlapping ranges (Fig. 26), as is the case in the bivoltine *A. forsterella*. The two taxa share the same northern and western limit, and the south-eastern limit is a little blurry but is limited by the availability of museum specimens representing spring sampling in Lebanon and Iran. For the barcoding results, as the mitochondrial genome is inherited matrilineally, there is no recombination and these mixed results could be as a



**Figure 26.** Global distribution map of *Andrena (Holandrena) decipiens* Schenck, 1861. Spring generation (*Andrena flavilabris* Schenck, 1874) (blue open triangles); summer generation (*Andrena decipiens*) (red circles). Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

result of incomplete lineage sorting. The fact that specimens flying at the same time in close geographical proximity (central Spain, May 2025) showed barcodes from the two clades, and that specimens flying in both spring and summer in near sympatry (central Spain, July 2021 and May 2025) showed identical barcodes strongly suggests that the observed genetic distance is not biologically meaningful. Consequently, the broad concept of a bivoltine *A. decipiens* (as used by Schönitzer et al. 1995; Schuberth 1995; Osytsnjuk et al. 2008) is returned to, and the change is formalised below.

### *Andrena (Holandrena) decipiens* Schenck, 1861

?*Apis albifrons* Christ, 1791: 191 [Germany, type lost] nec. Forster, 1771 and Rossi, 1790.

*Andrena decipiens* Schenck, 1861: 250, ♀♂ [Germany, SMFD, examined]

*Andrena fonscolombii* Dours, 1872: 357, ♀♂ [Greece: Corfu, MSNG, examined]

?*Andrena insolita* Dours, 1872: 422, ♀♂ [Spain, Algeria, possibly MNHN, not examined]

?*Andrena strigosa* Dours, 1872: 428, ♀♂ [France, types lost]

*Andrena flavilabris* Schenck, 1874: 170 [Germany, SMFD, examined] syn. nov.

*Andrena deceptor* Schmiedeknecht, 1884: 745, ♀♂ [France, types lost]

*Andrena fimbriata* var. *paganettii* Alfken, 1904: 294, ♀♂ [Greece: Corfu, ZMHB, not examined]

*Andrena decipiens* ssp. *capta* Warncke, 1974b: 46, ♀♂ [Morocco, OÖLM, examined]

**Material examined.** **ALBANIA** • 1♀; Fier region, Lushnje env., pastures and steppes; 177 m a.s.l.; 29 Jun. 2018; D. Benda leg.; JSPC; **GERMANY** • 1♀; Wiesbaden; Schenck collection; SMFD (**syntype** of *Andrena decipiens*) • 1♀; Bamberg; Schenck collection; SMFD (**syntype** of *Andrena flavilabris*); **GREECE** • 1♂, 1♀; Corfu; Gri-bodo collection; MSNG (male **lectotype** and female **paralectotype** of *Andrena fonscolombii*); **LEBANON** • 1♂; Kherbet Kanafar [Kherbet Qanafar], Bekaa; 16 Jun. 1953; G. Schmidt leg.; OÖLM; **MOROCCO** • 1♀; El Hajeb; 22 Jul. 1932; Ad. Nadig leg.; OÖLM (**holotype** of *Andrena decipiens* ssp. *capta*) • 1♂; Ifrane; 30 May 1973; H. Teunissen leg.; OÖLM (**paratype** of *Andrena decipiens* ssp. *capta*). See Suppl. material 2 for additional examined material.

**Notes.** Wood and Bossert (2025: 287) located type material of *A. fonscolombii*, which was actually described from Corfu and was not a junior synonym of *A. variabilis* as inferred by Warncke (1967b: 272).

**Distribution.** Morocco, Algeria, Spain, Andorra, France, Switzerland, Germany, Austria, Czechia, Slovakia, Hungary, Italy, Malta, Slovenia, Croatia, Bosnia & Herzegovina, Serbia, Romania, Poland, Belarus, Ukraine, Russia (European part), Montenegro, Albania\*, Greece, Bulgaria, Turkey, Lebanon\*, Georgia, Armenia, Azerbaijan, Iran (Dours 1872, as *A. fonscolombii*; Warncke 1965a, 1974a, 1974b; Gusenleitner and Schwarz 2002; Osytsnjuk et al. 2008; Standfuss et al. 2011; Wood 2021, 2023c, as *A. flavilabris*; Wood and Bossert 2025). Records from Tajikistan and Uzbekistan presented by Wood and Monfared (2022: 74) are here considered to be misidentifications of *A. labialis*, rendering *A. decipiens* a strictly West Palaearctic species.

***Andrena (Holandrena) forsterella* Osytshnjuk, 1978**

*Andrena fimbriata* Brullé, 1833 *sensu auctorum* (Warncke 1965a: 57, ♀♂)

*Andrena forsterella* Warncke, 1967b: 205–206 nom. nov. pro. *Andrena fimbriata sensu auctorum* (*nomen nudum*)

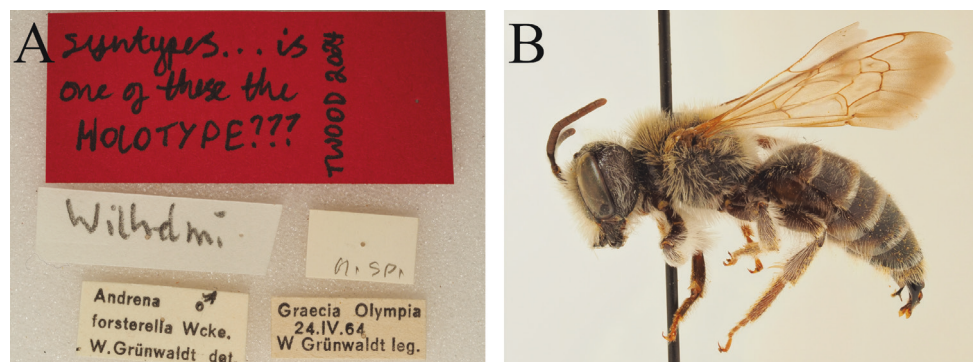
*Andrena forsterella* Osytshnjuk, 1978: 318, 321, 337, 350, ♀♂ [Azerbaijan, lectotype designated by Schönitzer et al. 1995: 829, SIZK, not examined]

*Andrena wilhelmi* Schuberth, 1995: 808, ♀♂ [Greece, ZSM, partially examined] syn. nov.

**Material examined.** ALBANIA • 1♂; Butrint NP; 2 Jul. 2021; M. Jacobs leg.; KJCB • 2♂, 1♀; Buz [Buzë]; 16 Jul. 2017; K. Janssen leg.; KJCB • 1♀; Novaj [3 km N Therepelë]; 18 Jul. 2017; K. Janssen leg.; KJCB • 1♀; rivier Gjerbës; 21 Jul. 2017; K. Janssen leg.; KJCB • 3♂; Xhafaj; 15 Jul. 2017; K. Janssen leg.; KJCB; AZERBAIJAN • 1♂; Sabirabad; 5 May 1969; ZSM (labelled as **paratype** of *A. wilhelmi*); GREECE • 1♂; Olympia; 24 Apr. 1964; W. Grünwaldt leg.; ZSM (labelled as “n.sp.”, probable **paratype** of *A. wilhelmi*) • 1♂; Olympia; 24 Apr. 1964; W. Grünwaldt leg.; ZSM (labelled as “n.sp.”, probable **paratype** of *A. wilhelmi*) • 1♂; Olympia; 24 Apr. 1964; W. Grünwaldt leg.; ZSM (labelled as **paratype** of *A. wilhelmi*). See Suppl. material 2 for additional examined material.

**Notes.** Concerning the type material of *A. wilhelmi*, the holotype male from Olympia (24 Apr. 1964) is supposed to be deposited in the ZSM, but examination of this collection could only produce three males from this collecting event (Fig. 27), only one of which was labelled as paratype. Three paratype males from this collection event are listed by Schuberth (1995: 816), and so they are likely simply all paratypes, but the precise location of the holotype is currently unclear. Regardless, they are representative of the taxon and there is no doubt as to what the name applies to.

**Distribution.** Italy, Croatia, Albania\*, North Macedonia, Bulgaria, Greece, Turkey, Ukraine, Crimea, Cyprus, Syria, Lebanon, Israel & West Bank, Georgia, Armenia, Azerbaijan, Iran (Fig. 24; Schuberth 1995; Schönitzer et al. 1995; Osytshnjuk et al. 2008).



**Figure 27.** *Andrena (Holandrena) wilhelmi* Schuberth, 1995 probable paratype male (ZSM). **A.** Label information; **B.** Habitus, lateral view.

### Subgenus *Melandrena* Pérez, 1890

**Genetics.** The subgenus *Melandrena* remains challenging to resolve using barcodes (e.g. *nitida-limata-thoracica* complex), and the widespread species *Andrena morio* Brullé, 1833 (originally described from Greece) is currently incompletely characterised with seemingly multiple mitochondrial lineages (Wood 2023b). These two groups are not presented in the current phylogenetic analysis, as the subgenus would benefit from a revision utilising nuclear markers. Their statuses remain open questions, and for now the typical Warncke concepts (as modified by Wood 2023b) are used here. One further reason for this is that the sequences of *Andrena hungarica* Friese, 1887 and *Andrena quadrimaculata* Friese, 1921 presented here are strongly intermixed with sequences of the *nitida-limata-thoracica* complex. Those of *A. hungarica* fall into BIN [BOLD:AGU5376](#) which contains sequences of *A. nitida* (Müller, 1776) and *A. limata* Smith, 1853, and those of *A. quadrimaculata* fall into BIN [BOLD:AAE1815](#) which contains sequences of *A. nitida*, *A. limata*, and *A. thoracica* (Kirby, 1802), as well as a likely mis-identification of *A. assimilis* Radoszkowski, 1876. This group of species requires molecular revision using nuclear DNA to understand current levels of gene flow; their exclusion from the current barcode tree represents the challenging use of this marker in the subgenus *Melandrena*, and a desire for higher-quality data, rather than an attempt to avoid dealing with this complex issue.

Concerning the taxa that are included here, many East Mediterranean taxa are represented by DNA barcodes for the first time (Fig. 28). Members of the subgenus showed sometimes strange patterns of very low genetic divergence, with species like *Andrena flavipes* Panzer, 1799 (Portugal to India; 3.85%), *Andrena albopunctata* (Rossi, 1792) (Italy to Kyrgyzstan; 0.30%), *A. assimilis* (Morocco to Kyrgyzstan; 0.95%) separated by low percentages considering the geographic distances involved. Equally, some geographically close sequences showed moderate divergence, specifically between Levantine and Cypriot sequences of *Andrena pyrozonata* Friese, 1921 (average 3.16%; range 2.74–3.93%) and *Andrena elmaria* Gusenleitner, 1998 (average 4.46%; range 4.41–4.56%). Surprisingly, sequences of *Andrena discors* Erichson, 1841 from Portugal and Israel were very strongly separated from sequences from Crete (ssp. *creticola* Strand, 1915) by an average genetic distance of 8.85% (range 8.81–8.97%). This resulted in a major topographical separation, placing *creticola* much closer to *Andrena gravida* Imhoff, 1832, *Andrena korleviciana* Friese, 1887, and *Andrena vulcana* Dours, 1873. This case is discussed here.

#### *Andrena* (*Melandrena*) *creticola* Strand, 1915, stat. rev.

*Andrena cretica* Strand, 1915: 150, ♀♂ [Greece: Crete, DEI, examined]

*Andrena cretica* var. *antennalis* Strand, 1915: 151, ♂ [Greece: Crete, DEI, examined]

*Andrena strigifrontalis* Strand, 1921: 281, ♂ [Greece: Crete, DEI, examined]

*Andrena pectoralis* var. *cretensis* Friese, 1922: 211, ♀ [Greece: Crete, ZMHB, not examined]

**Material examined.** GREECE • 1♂, 4♀; Canea [Chania] (Crete); 1 Mar. – 30 Jun. 1914; Paganetti leg.; DEI (**syntypes** of *Andrena cretica*) • 1♂; Canea [Chania] (Crete);



Friese, 1887 (Adriatic region), *Andrena vulcana* Dours, 1873 (Iberia, north-west Africa, and the Canaries in a broad sense), and *Andrena gravida* (Europe and Turkey).

Morphologically, there are few differences from *A. discors*, leading to Warncke's original combination (as *A. vachali*). In the female sex the tibial scopae are black (orange-red in *A. discors*), the scutal pubescence is entirely brown (variable, from foxy red to orange brown in *A. discors* but always with some short black hairs intermixed medially), and the pattern of punctures on the clypeus only weakly suggests the presence of longitudinal wrinkles (in *A. discors*, with a comparatively stronger pattern of longitudinal wrinkles on the clypeus, in North African specimens with almost shining interspaces). Males are structurally identical. Despite these very slight morphological differences, based on the known *Andrena* fauna of Crete, it does not have North African *Andrena* elements. With the revisions presented here, all of the species present are either very widely distributed pan-Mediterranean, European, or Cretan endemic species with the closest relative present in mainland Greece (e.g. *Andrena pelagica* Warncke, 1975 – *Andrena rugothorace* Warncke, 1965; *Andrena incustodita* Wood, 2024 – *Andrena abbreviata* Dours, 1873; *Andrena lediveleci* Wood, 2024 – *Andrena sandanskia* Warncke, 1973; *Andrena testudo* – *Andrena brumanensis*; *Andrena cretica* – *Andrena hyemala*). Based on this pattern, and the pattern suggested by the DNA barcodes, *A. cretica* stat. rev. is considered to be an isolated lineage (Fig. 29) descended from a European ancestor which due to colouration and the typical minimal morphological differentiation observed within members of the *flavipes*-group (here defined as corresponding to the former subgenus *Zonandrena* Hedicke, 1933, see Pisanty et al. 2022a) simply resembles *A. discors*. A similar pattern can be found in the subgenus *Taeniandrena* Hedicke, 1933 (Praz et al. 2022) where structurally similar but differently coloured and partially geographically isolated species are strongly differentiated by DNA barcodes (*Andrena russula* Lepelletier, 1841; *Andrena croceiventris* Morawitz, 1871; *Andrena antonellae* Praz & Genoud, 2022).

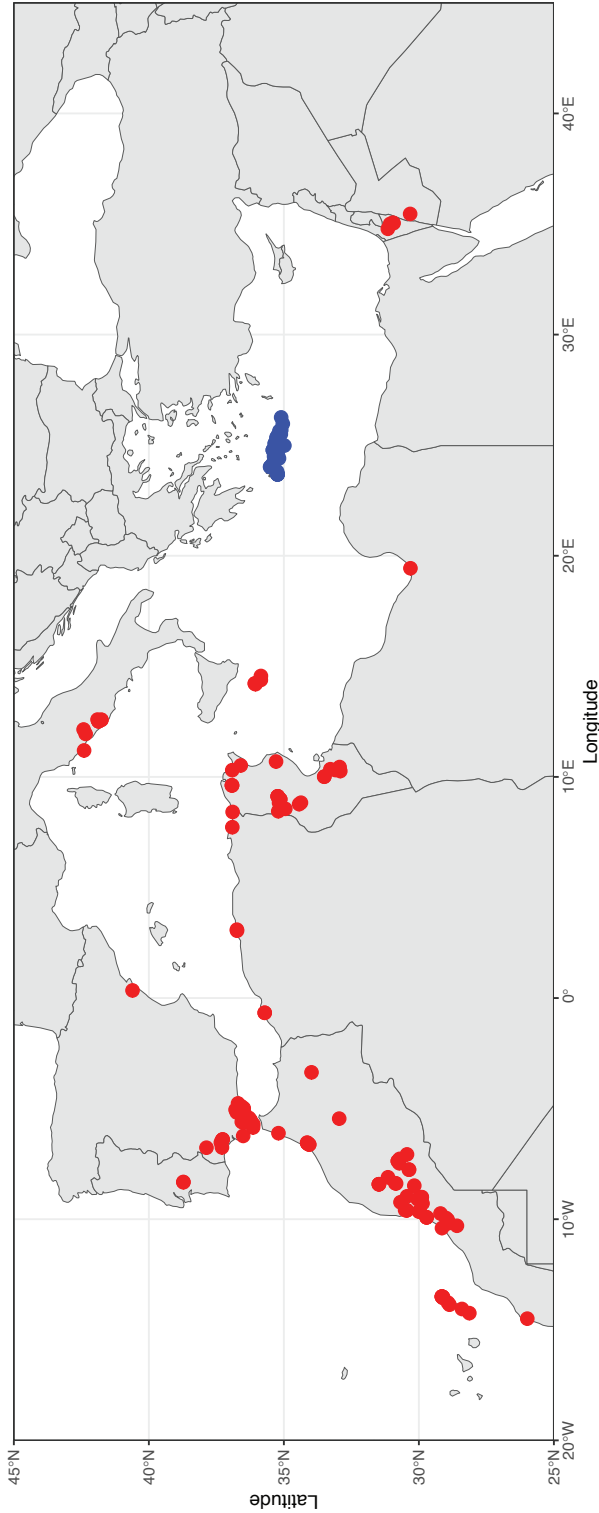
**Distribution.** Greece (Crete) (Fig. 29).

### *Andrena (Melandrena) pyropygia* Kriechbaumer, 1873

*Andrena pyropygia* Kriechbaumer, 1873: 52, ♀ [“Palestine”, ZSM, lectotype by present designation] (Fig. 30)

**Material examined.** ISRAEL • 1♀; “Palästina” [actually Jerusalem]; Dr. Roth leg.; ZSM (lectotype by present designation).

**Notes.** The locations of types described by Kriechbaumer are not always clear, so it is beneficial to designate the one remaining specimen in the ZSM collection as the lectotype (Fig. 30). The species was originally described from two females from “Palästina”, with Kriechbaumer noting in the publication that specimens were collected in Jerusalem. Friese labelled the specimen as “*morio* v. *pyropygia*”, indicating a level of scepticism as to the status of *A. pyropygia*, and indeed there are minimal structural differences between the two taxa. Warncke (1965a, 1967b) treated *A. pyropygia* as a



**Figure 29.** Global distribution map of *Andrena (Melandrena) cretica* Strand, 1915 (blue circles) and *Andrena (Melandrena) discors* Erichson, 1841 (red circles). Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.



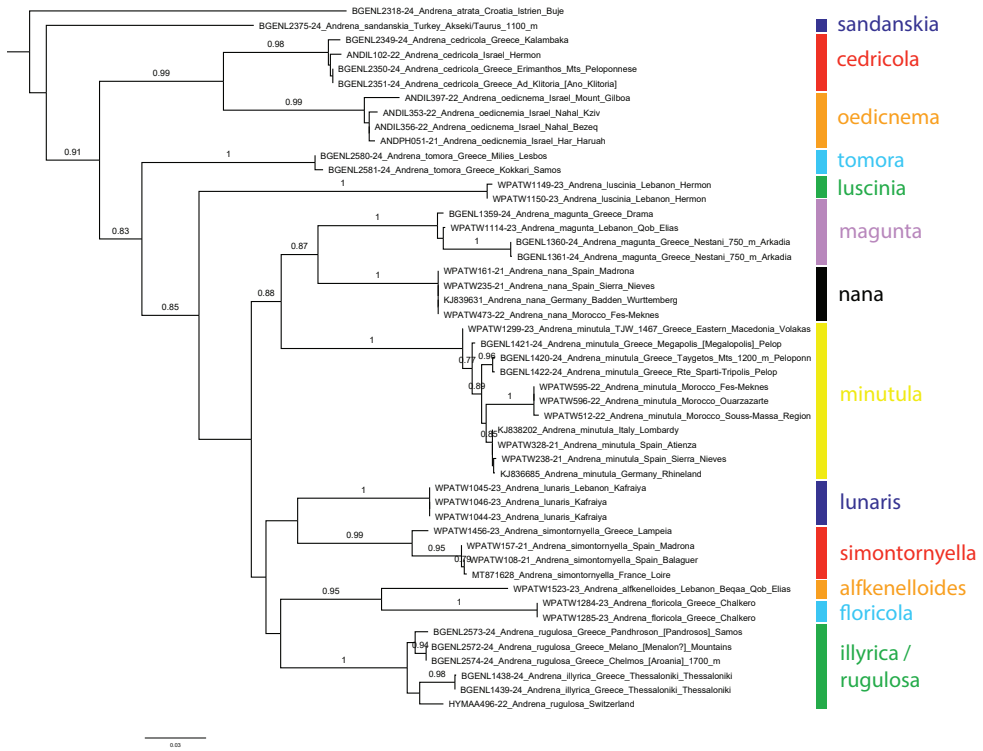
**Figure 30.** *Andrena (Melandrena) pyropygia* Kriechbaumer, 1873 lectotype female (ZSM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Metasoma, dorsal view.

valid species, and in the southern Balkans it can only be found in Greece. For now, *A. pyropygia* is maintained as a species in the sense of Warncke.

**Distribution.** Greece, Crimea, Russia (European part), Turkey, Georgia, Armenia, Cyprus, Syria, Lebanon, Israel & West Bank (Warncke 1974a; Gusenleitner and Schwarz 2002; Osytshnjuk et al. 2008).

### Subgenus *Micrandrena* Ashmead, 1899

**Genetics.** Before discussing the genetics, it is necessary to highlight two taxonomic actions. The first is that *Andrena corpana* Warncke, 1965 (described from Larisa in Greece) is currently treated as a junior synonym of *Andrena simontornyella* Noskiewicz, 1939 (Gusenleitner and Schwarz 2002: 701). The second is that Pisanty et al. (2025) synonymised *Andrena dargia* Warncke, 1965 (described from Delphi in Greece) with *Andrena minutula* (Kirby, 1802); barcodes of “*Andrena dargia*” from the Peloponnese are presented here; these were also used in the analysis of Pisanty et al. (2025; Fig. 31). New barcodes of eastern *Micrandrena* are presented here, and the presence of *Andrena oedicnema* Warncke, 1975 in Greece is here discussed. There was some complexity seen with *Andrena rugulosa* Stöckert, 1935 and *Andrena illyrica* Warncke, 1975, with *A. illyrica* intermixed between sequences of *A. rugulosa*. The *rugulosa*-group of species



**Figure 31.** Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Micrandrena* Ashmead, 1899 based on the mitochondrial COI gene. *Andrena (Parandrenella) atrata* Friese, 1887 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

is taxonomically challenging with cryptic and only recently described Levantine species of high mountains (Pisanty et al. 2025), and the topology of this group is unstable; detailed analysis with additional samples is needed for clarity, and no action is taken here. Morphologically, the two taxa are separable, as indicated in the identification key.

***Andrena (Micrandrena) cedricola* Wood, 2020**

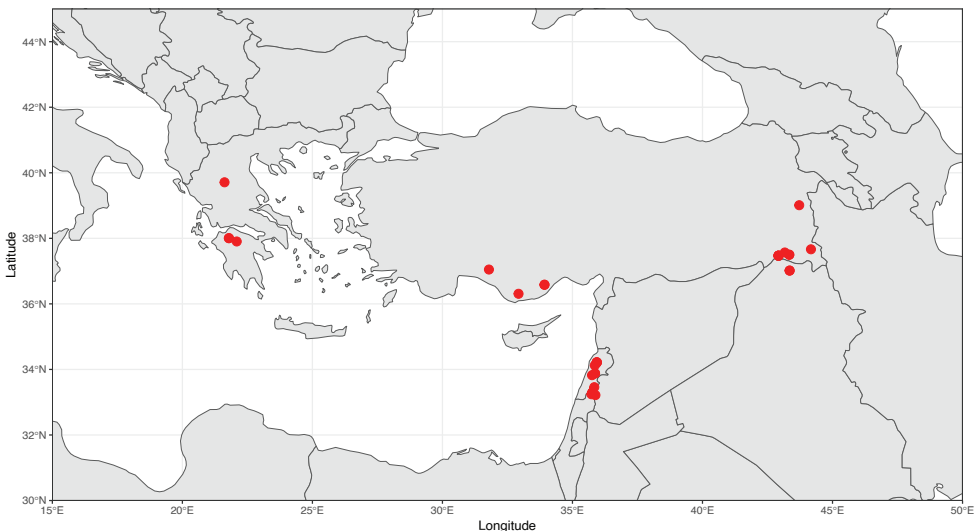
*Andrena* (incertae sedis) *cedricola* Wood in Wood et al. 2020: 10, ♀♂ [Lebanon, RBINS, examined]

**Material examined.** GREECE • 1♀; Ad Klitoria [Ano Klitoria]-Kalavrita (Pelop.); 21 May 1987; H. Teunissen leg.; RMNH • 5♀; Erimanthos Mts (Peloponn); 28 May 1987; H. Teunissen leg.; RMNH • 2♀; Erimanthos Mts (Peloponn); 2 Jun. 1987; H. Teunissen leg.; RMNH • 2♀; Kalambaka; 17 May 1978; H. Teunissen leg.; RMNH; TURKEY • 1♀; Abanoz (Rte Anamur), Kazanci; 11–1200 m a.s.l.; 11 May 1991; H. Teunissen leg.; RMNH • 1♀; Akseki; 1000 m a.s.l.; 5 May 1991; H. Teunissen leg.; RMNH • 6♀; Uzuncaburç, 30 km N of Silifke; 28 May 1996; Mi. Halada leg.; OÖLM/TJWC.

**Notes.** Rasmont et al. (2017) reported *Andrena oediconema* Warncke, 1975 (described from Turkey) for Europe based on the dot maps of Warncke (Gusenleitner and Schwarz 2002) which show a point in central Greece. No precise details for this specimen or specimens have ever been located. Examination of Teunissen material from the RMNH collection unexpectedly produced several specimens of *Andrena cedricola*, a species that is closely morphologically related to *A. oediconema*. This identification is also supported by DNA barcode data (Fig. 31). The sequences from Greece were clustered with a sequence from northern Israel (Mount Hermon), separated by an average genetic distance of 1.32% (range 0.91–2.13%). Collectively, the Greek and Israeli sequences of *A. cedricola* were separated from four Israeli sequences of *A. oediconema* by an average genetic distance of 10.37% (range 8.42–14.42%). Consequently, due to this high interspecific genetic distance, *A. cedricola* received bootstrap support of 98 and *A. oediconema* received bootstrap support of 99.

After its original description from high-altitude sites in Lebanon and Syria, *A. cedricola* was recorded from Israel, Turkey, and northern Iraq (see Pisanty et al. 2022b; Wood et al. 2024 for specimen details). Since then, additional Turkish specimens from central Taurus mountains have been discovered. The records from Greece come from the northern Peloponnese and central Greece, mountainous areas with a faunal affinity with the Taurus mountains (Fig. 32). In this context, the Warncke dot of “*Andrena oediconema*” from central Greece is considered to belong to *A. cedricola* which replaces it on the Greek and European list. The precise specimen examined by Warncke may have been one of Teunissen’s specimens from Kalambaka, but this cannot currently be traced or demonstrated.

**Distribution.** Greece\*, Turkey, Lebanon, Syria, Israel, Iraq (Fig. 32; Wood et al. 2020, 2024; Pisanty et al. 2022b).



**Figure 32.** Global distribution map of *Andrena (Micrandrena) cedricola* Wood, 2020. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

**Subgenus *Notandrena* Pérez, 1890**

***Andrena (Notandrena) meridionalis* Dalla Torre & Friese, 1895, sp. resurr.**

*Andrena gravida* Dours, 1872: 429, ♀♂ [Greece, MSGN, lectotype by present designation] nec. Imhoff, 1832 and Eversmann 1852 (Fig. 33)

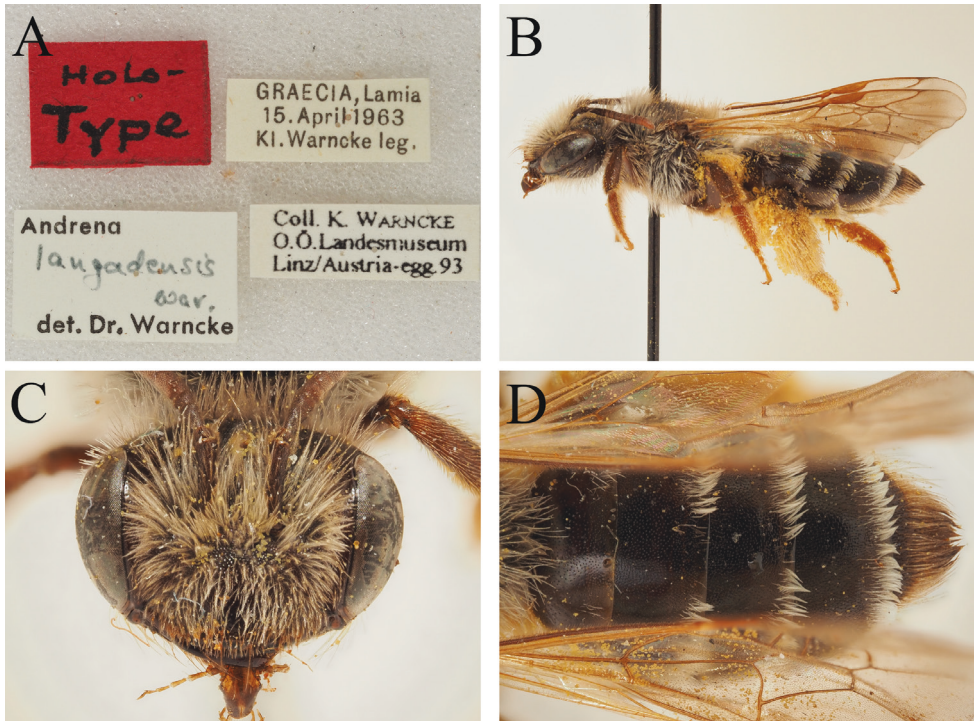
*Andrena meridionalis* Dalla Torre & Friese, 1895: 46, nom. nov. *pro Andrena gravida*  
*Andrena commutata* Schulz, 1906: 241, unnecessary replacement name.



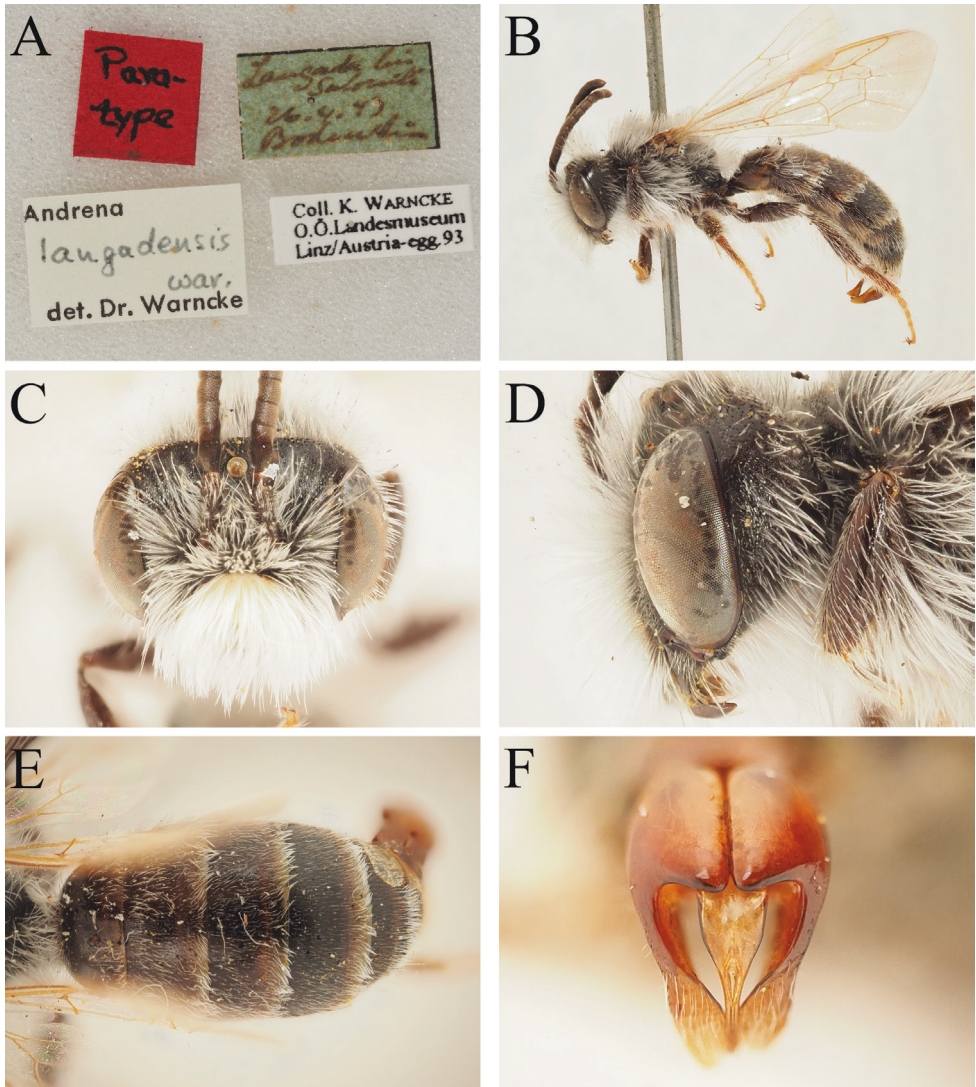
**Figure 33.** *Andrena (Notandrena) gravida* Dours, 1873 nec. Eversmann = *Andrena (Notandrena) meridionalis* Dalla Torre & Friese, 1895 lectotype female (MSGN). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Scutum, dorsal view; **E.** Hind leg, lateral view; **F.** Metasoma, dorsal view.

*Andrena langadensis* Warncke, 1965a: 51, ♀♂ [Greece, OÖLM, examined] syn. nov.  
(Figs 34, 35)

**Material examined.** ALBANIA • 1♀; Ksamil bij Butrinti; 24 May 2017; M. Jacobs leg.; KJCB; GREECE • 1♀; “Al.” [=Algeria, considered mislabelled]; MSNG (**lecto-type**) • 1♀; Corfu, Acharavi; 26 Apr. 1994; M. Koponen leg.; MZH • 1♂, 3♀; Corfu, Agios Spiridon; 7–17 May 1978; M. Viitasaari leg.; MZH • 1♂; Corfu, Sidari; 5 May 1978; H. Teunissen leg.; TJWC • 1♂; Crete, Kato Zakros; 11 Apr. 1988; M. Archer leg.; M. Archer Colln. • 1♂, 1♀; Crete: Lassithi, Goudouras; 11 Apr. 1992; S.P.M. Roberts leg.; SPMRC • 5♀; Hellas, Evros, Evros Deltagebiet; 4 May 2004; J. v. d. Nieuwegiessen leg.; RMNH • 1♀; Lamia; 15 Apr. 1963; K. Warncke leg.; OÖLM (**holotype** of *Andrena langadensis*) • 1♂, 1♀; Langada b. Saloniki; 26 May 1945; Bodenstein leg.; OÖLM (**paratypes** of *Andrena langadensis*) • 3♀; Messinia, Agios Nikolaos; 26 May 1998; H. & J.E. Wiering leg.; RMNH/TJWC • 2♀; Messinia, Gialova; 16 May 1998; H. & J.E. Wiering leg.; RMNH • 1♀; Messinia, Petrochori; 17 May 1998; H. & J.E. Wiering leg.; RMNH • 1♀; O. Creta, Gournia; 21 Apr. 1973; H. Teunissen leg.; OÖLM • 1♀; Peloponnese NE, N of Astros, Vernenon beach; 24 Mar. 2016; M. Snížek leg.; OÖLM • 1♀; Saloniki, Thessalien; 1–30 May 1942; Babiý leg.; OÖLM (**paratype** of *Andrena langadensis*) • 1♀; Syra [Syros]; OÖLM • 26♀; W, N of Amfilochia, Bukka [Mpoukka]; 1 Apr. 2016; M. Snížek leg.; OÖLM/TJWC.



**Figure 34.** *Andrena (Notandrena) langadensis* Warncke, 1965 holotype female (OÖLM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Metasoma, dorsal view.

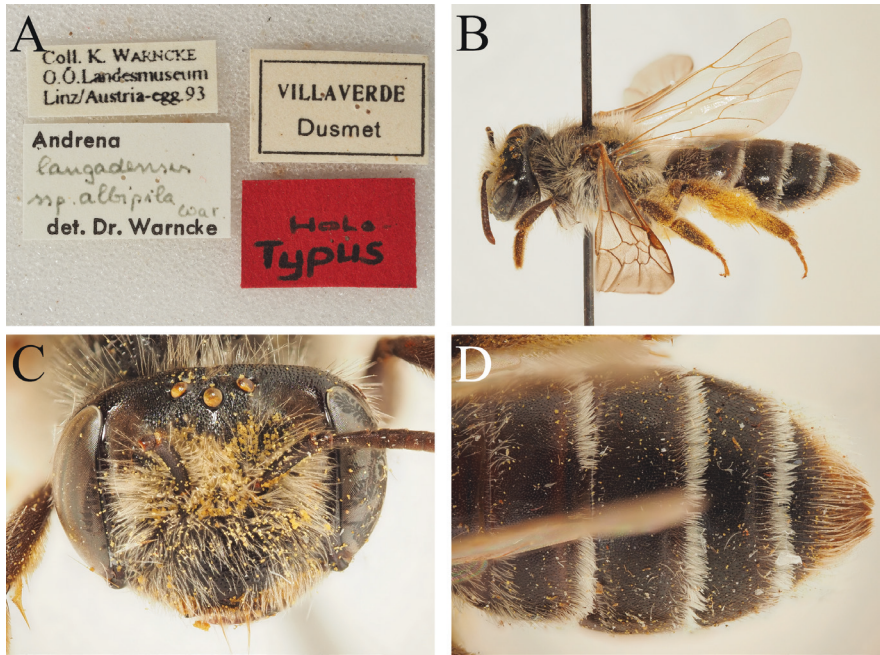


**Figure 35.** *Andrena (Notandrena) langadensis* Warncke, 1965 paratype male (OÖLM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Head, lateral view; **E.** Metasoma, dorsal view; **F.** Genital capsule, dorsal view.

*Andrena (Notandrena) albipila* Warncke, 1967, stat. nov.

*Andrena langadensis* ssp. *albipila* Warncke, 1967b: 237, ♀♂ [Spain, OÖLM, examined] (Figs 36, 37)

**Material examined.** MOROCCO • 1♀; Agadir; 2–8 Apr. 1999; M. Hrodsky leg.; TJWC • 2♀; High Atlas, Aoulouz; 28 May 1995; J. Macek leg.; NMPC; SPAIN • 1♀; Cádiz, Finca WWF (Trebujera); 19 Feb. 2022; Á.P. Gómez leg.; Á.P. Gómez Colln • 1♂; Caracoles



**Figure 36.** *Andrena (Notandrena) langadensis* ssp. *albipila* Warncke, 1967 holotype female (OÖLM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Metasoma, dorsal view.



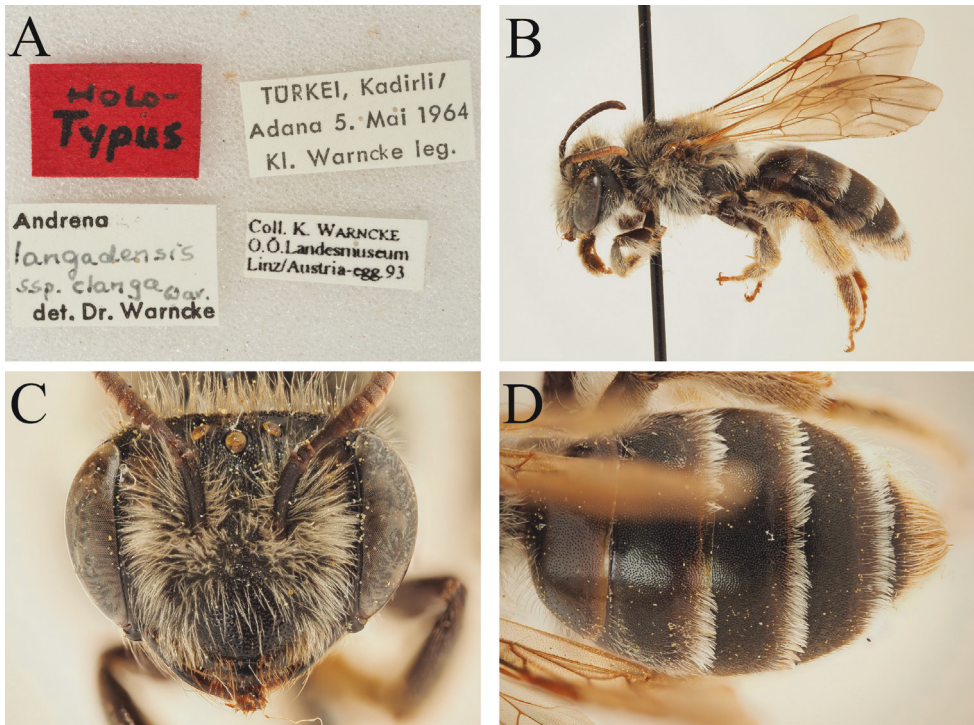
**Figure 37.** *Andrena (Notandrena) langadensis* ssp. *albipila* Warncke, 1967 paratype male (OÖLM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Genital capsule, dorsal view.

(P.N. Doñana); 7 Apr. 2018; C. Molina leg.; EBDC • 1♀; Caracoles (P.N. Doñana); 19 Apr. 2021; C. Molina leg.; EBDC • 1♀; Convento de la Luz (P.N. Doñana); 8 Mar. 2017; C. Molina leg.; EBDC • 1♀; Granada, Cerro del Chupa, 1200 m [10 km NNW Otivar]; 4 Jun. 1986; W. Perraudin leg.; OÖLM • 1♀; Huelva, Isla Mayor; 17 Mar. 2012; I. Cross leg.; I. Cross Colln. • 1♂; Pozuelo de Ca. [Pozuelo de Calatrava]; La Fuente leg.; OÖLM (**paratype** of *Andrena langadensis* ssp. *albipila*) • 1♀; Villaverde; 6 Jun. 1909; J.M. Dusmet y Alonso leg.; OÖLM (**holotype** of *Andrena langadensis* ssp. *albipila*).

*Andrena (Notandrena) clanga* Warncke, 1965, **stat. nov.**

*Andrena langadensis* ssp. *clanga* Warncke, 1965b: 259, ♀♂ [Turkey, OÖLM, examined] (Figs 38, 39)

**Material examined.** **CYPRUS** • 1♀; North Cyprus, 15 km E Diakarpaz, Golden Sands; 10 Apr. 2007; C. Schmid-Egger leg.; CSE • 2♀; Sov. Base Area, Akrotiri, marsh; 1 m a.s.l.; 4 Apr. 2024; R. Santerre leg.; TJWC/UMONS; **GREECE** • 1♀; Lesbos, Parakila; 14–17 May 1980; H. Teunissen leg.; RMNH, RMNH.INS.1716257; **ISRAEL** • 1♂; Akko [Acre], swamp; 1 Apr. 2012; A. Freidberg leg.; SMNHTAU; **JORDAN** • 1♀; Irbid,



**Figure 38.** *Andrena (Notandrena) langadensis* ssp. *clanga* Warncke, 1965 holotype female (OÖLM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Metasoma, dorsal view.



**Figure 39.** *Andrena* (*Notandrena*) *langadensis* ssp. *clanga* Warncke, 1965 paratype male (OÖLM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Head, lateral view; **E.** Meta-soma, dorsal view; **F.** Genital capsule, dorsal view.

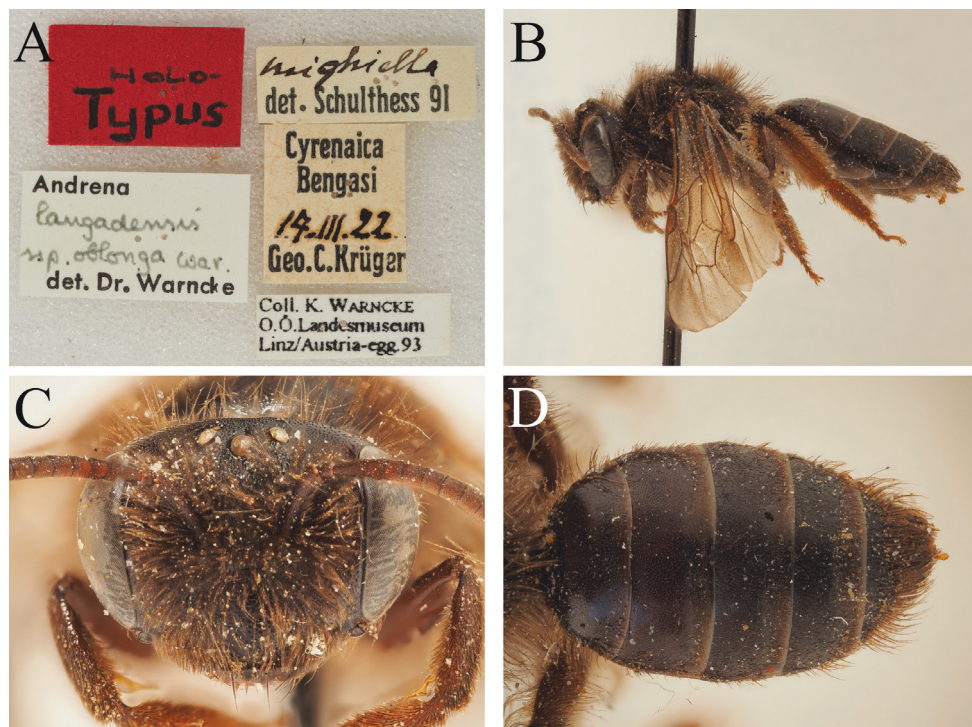
Saham vill; 19 Apr. 2003; I. Pljushtch leg.; OÖLM; **SYRIA** • 1♂; Ras al Basit; 19 May. 1995; K. Deneš leg.; OÖLM; **TURKEY** • 5♂, 1♀; Adana; 25 Mar. 1967; K. Warncke leg.; OÖLM • 1♀; Ceyhan/Adana; 4 May 1964; K. Warncke leg.; OÖLM (**paratypes** of *Andrena langadensis* ssp. *clanga*) • 1♂; Dalyan, salty meadow [2 km S Dalyan]; 30 Apr. 2016; Barták & Kubik leg.; OÖLM • 1♀; Hakkari, 5 km N Oramar [river]; 1450 m a.s.l.; 11 Jun. 1981; M. Kraus leg.; OÖLM • 1♀; Kadirli/Adana; 5 May 1964; K. Warncke leg.; OÖLM (**holotype** of *Andrena langadensis* ssp. *clanga*) • 8♀; Karatas [Karataş]/Adana; 29

Apr. 1964; K. Warncke leg.; OÖLM (**paratypes** of *Andrena langadensis* ssp. *clanga*) • 1♂; Milet/Aydin [Milet Antik Kenti]; 22 Apr. 1981; K. Warncke leg.; OÖLM • 1♀; Tanin-Tanin-Pass; 2300–2600 m a.s.l.; 3 Jun. 1980; M. Schwarz leg.; OÖLM.

***Andrena (Notandrena) oblonga* Warncke, 1967, stat. nov.**

*Andrena langadensis* ssp. *oblonga* Warncke, 1967b: 236, ♀♂ [Libya, OÖLM, examined] (Figs 40, 41)

**Material examined.** EGYPT • 1♀; Dekhela [Ad Dakhilah]; 20 Feb. 1917; Storey leg.; OÖLM (**paratype** of *Andrena langadensis* ssp. *oblonga*); LIBYA • 2♀; Cirenaica, Ras El Hilal [Ra's Al Hilal]; 26 Apr. 1967; G. Dellacasa & P. Maifredi leg.; MSNG/TJWC • 1♀; Cyrenaica, Bengasi; 14 Mar. 1922; G.C. Krüger leg.; OÖLM (**holotype** of *Andrena langadensis* ssp. *oblonga*) • 1♀; Cyrenaica, R. U. Agrario; 1 Jun. 1925; G.C. Krüger leg.; OÖLM (**paratype** of *Andrena langadensis* ssp. *oblonga*) • 1♀; Cyrenaica, R. U. Agrario; 17 Mar. 1929; G.C. Krüger leg.; OÖLM (**paratype** of *Andrena langadensis* ssp. *oblonga*) • 1♀; Cyrenaica, R.U. Agrario, Bu Teija; G.C. Krüger leg.; MSNG • 1♂, 1♀; Cyrenaica, Mars el Brega; 8–11 Feb. 1942; Kirchberg leg.; OÖLM



**Figure 40.** *Andrena (Notandrena) langadensis* ssp. *oblonga* Warncke, 1967 holotype female (OÖLM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Metasoma, dorsal view.

(**paratype** of *Andrena langadensis* ssp. *oblonga*) • 1♀; Libia occ., u. Ramla; 1–31 Mar. 1938; G.C. Krüger leg.; MSNG.

**Notes.** This group of species was treated by Warncke (1965a, 1965b, 1967b) as a pan-Mediterranean taxon under the name *A. langadensis*. However, Warncke (1967b) made several incorrect treatments and assessments of *Notandrena* species, leading to confusion and requiring taxonomic action to stabilise names and concepts (Gusenleitner and Schwarz 2002; Wood and Monfared 2022; Wood 2023b). One stabilised species is *Andrena (Notandrena) griseobalteata* Dours, 1872. Although the modern concept of this species is clear, there is one remaining issue which is that Warncke (1967b: 288) treated *A. meridionalis* as a junior synonym (as *A. erythrocnemis* auctorum), and this remains the current placement of the taxon (Gusenleitner and Schwarz 2002: 323); this treatment requires dissection.

*Andrena meridionalis* is a replacement name for *Andrena gravida* Dours which is a junior primary homonym of *A. gravida* Imhoff, 1832 (and also *A. gravida* Eversmann, 1852). Dours described the species from “Iles de l’archipel grec. Algérie”. Whilst *A. griseobalteata* is common in Greece, it is not known from North Africa (Wood 2023b); it is not clear if the original type series contained multiple taxa, or has been misinterpreted. A neotype was designated from southern France, and *A. griseobalteata* was considered to be a North Mediterranean species distributed from Spain to Turkey (Wood 2023b). The identity of *A. griseobalteata* and *A. meridionalis* has always been



**Figure 41.** *Andrena (Notandrena) langadensis* ssp. *oblonga* Warncke, 1967 paratype male (OÖLM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Genital capsule, dorsal view.

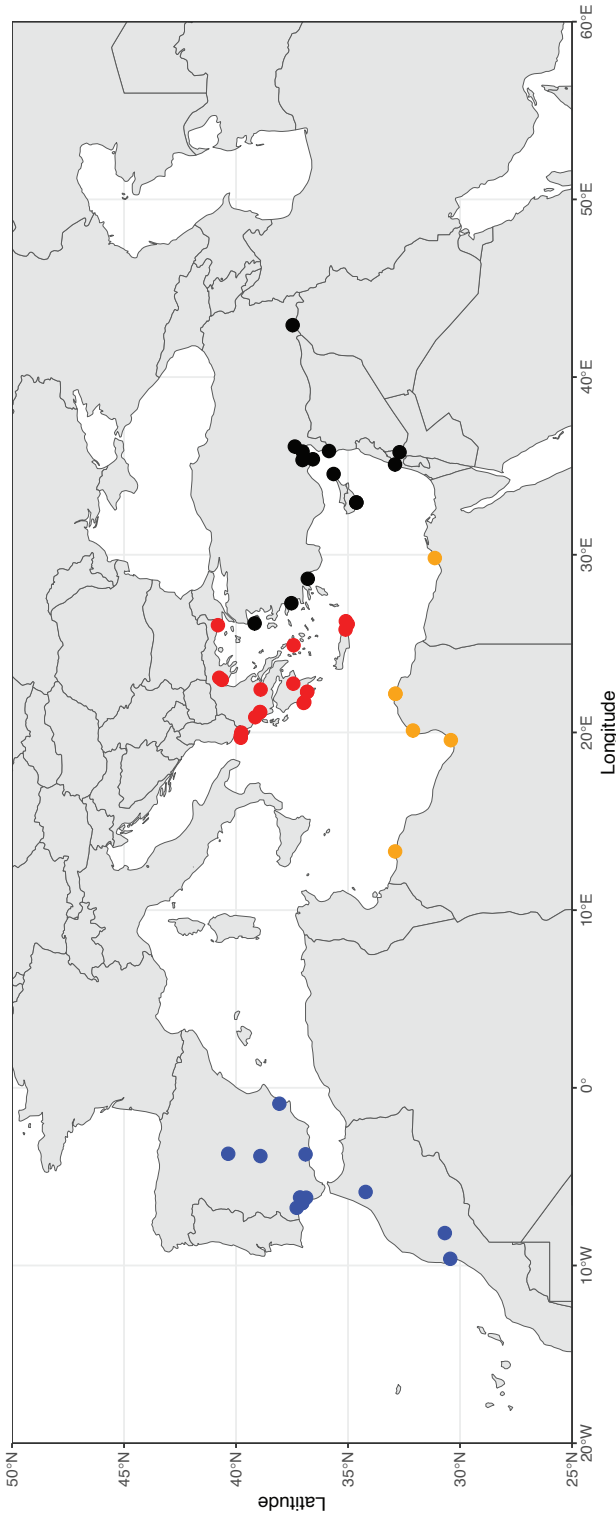
unclear and confused because the collection of Dours was destroyed in the bombing of Amiens in the First World War (e.g. see Wood 2023b); this is what necessitated the neotype designation for *A. griseobalteata*. However, what is less known is that some of Dours' type material survived as specimens were traded with other hymenopterists such as Giovanni Gribodo (1846–†1924), and a number of syntypes for taxa described by Dours have been located in the MSNG collection (see Wood and Bossert 2025).

Examination of the Gribodo collection produced a female specimen labelled as “*Andrena gravida* Typus Dours” and nominally coming from Algeria (Fig. 33). Due to the short and broad head, pronotum with a humeral angle, and densely punctate terga, it can be placed into the subgenus *Notandrena*, as is expected. However, the punctuation of the scutum is dense, but not as dense as in *A. griseobalteata* (punctures in this species almost confluent), and instead conform to those seen in *A. langadensis sensu lato*. It is beneficial to reproduce the female description here:

“♀. Noire; antennes noires; mandibules ferrugineuses au bout. Tête arrondie, ponctuée; les poils cendré roux. Corselet assez fortement ponctué, les poils en dessus roux, plus pâles sur les côtés et en dessous. Abdomen elliptique très-élargi au niveau des 2<sup>e</sup> et 3<sup>e</sup> segments, nu, assez fortement ponctué. Bord inférieure des 2<sup>e</sup>, 3<sup>e</sup>, 4<sup>e</sup> segments cilié de poils couchés, courtes, d'un blanc de neige. Les poils du 5<sup>e</sup> segment et de l'anus sont roux doré. En dessous, le bord des segments est cilié de longs poils cendrés. Pattes noires. Tibias intermédiaires et postérieurs ferrugineux hérissées de poils blancs frisés, brosse cendré roux. Ailes assez limpides; point calleux testacé, noire au centre; côte, nervures brunes”.

The description matches the specimen in key aspects, specifically the quite strongly punctured scutum, the hairs above red-brown (the probable meaning of *roux* in this case), those on the mesepisternum paler, metasoma with the discs of T2–3 quite densely punctate, apical margins of T2–4 with short hairbands of snow-white hair, and legs dark with the mid and hind tibiae ferruginous. Given these consistencies, and the known presence of Dours material in the MSNG collection (Wood and Bossert 2025), the specimen is hereby designated as the lectotype, and considered not to be conspecific with *A. griseobalteata* due to this sparser scutal punctuation. As *A. meridionalis* is the oldest name in the *langadensis*-group of species, the challenge becomes 2) Where precisely was *A. meridionalis* described from? 2) Should all taxa in this group be lumped under the name *A. meridionalis*? and 3) Are multiple good species involved?

Examination of the relevant type material (MSNG; OÖLM) shows that the MSNG lectotype of *A. meridionalis* is morphologically most similar to *A. langadensis* due to the relatively long tergal hairbands that are poorly defined and laterally exceed the length of the marginal areas before continuing onto the base of the following tergum (Figs 33F, 34D), the brownish pubescence of the head and (to a lesser extent) mesosoma (Figs 33B, C, 34B, C), and moderately dense tergal punctuation and brown terminal fringe (Figs 33F, 34D). The problem is that *A. langadensis* s. str. is only known from the southern Balkan Peninsula, and the taxon found in the West Mediterranean (ssp. *albipila*) has never been confidently recorded from Algeria, only Spain and Morocco (Gusenleitner and Schwarz 2002; Fig. 42).



**Figure 42.** Distribution map of *Andrena* (*Notandrena*) species in the group of *A. meridionalis* Dalla Torre & Friese, 1895. *Andrena* (*N. meridionalis*) (red circles); *A. (N.) clanga* Warncke, 1965 (black circles); *A. (N.) oblonga* Warncke, 1967 (yellow circles); *A. (N.) albipila* Warncke, 1967 (blue circles). Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

There is therefore an incongruence between the reported collecting locality and the morphology presented by the lectotype of *A. meridionalis*. Given that Dours reported the species from “Iles de l’archipel grec. Algérie”, numerous *Andrena* species he described from “Iles de l’archipel grec” were based on material from Corfu (see Wood and Bossert 2025, section on Subgenus *Ulandrena* Warncke, 1968 below), and *A. langadensis* s. str. is known from Corfu based on material from multiple collectors (see Suppl. material 2), it is entirely plausible that this specimen is actually from Corfu (or at least Greece) and is simply mislabelled as coming from Algeria. Given this combined evidence, the position is taken that *A. meridionalis* was described from Greece as fixed by lectotype designation, and that it is senior to *A. langadensis* syn. nov.

The issue now becomes, what is the status of the taxa described as subspecies of *A. langadensis*? Examination of material from Lesbos has produced a female specimen which is referable to *A. langadensis* ssp. *clanga*. It shows the characters given by Warncke (1965b), namely the bright orange antennae (Fig. 38B; ventral surface), narrow tergal hairbands, and more strongly punctate terga (Fig. 38D). When considering *A. meridionalis* and *A. langadensis* ssp. *clanga*, the density of the tergal punctation consistently differs, suggesting specific status for each taxon. When including *A. langadensis* ssp. *oblonga* (melanic, lacking tergal hairbands) and *A. langadensis* ssp. *albipila* (tergal hairbands consistently narrower and pubescence brighter, terga less densely punctate than *A. langadensis* ssp. *clanga*), as well as considering their non-overlapping geographic distributions (Fig. 42), the conclusion is that four distinct allopatric species are involved. Consequently, *A. albipila* stat. nov., *A. clanga* stat. nov., and *A. oblonga* stat. nov. are all elevated to species-status. An identification key for the females is presented below; males are currently insufficiently characterised, but can be identified through geographic provenance and co-occurrence with females.

Finally, it is necessary to discuss the species *Andrena* (*Notandrena*) *stellaris* Warncke, 1965. This species was described from Aksaray in Anatolian Turkey, and the published distribution is Central Anatolia (Aksaray, Niğde, Ürgüp, Yeşilhisar, Sultanhani/Kayseri; Warncke 1974a; Gusenleitner and Schwarz 2002). This species was reported from Lesbos by Grace (2010) without any further information or precise specimen details, and then in Rasmont et al. (2017) with personal communication from Erwin Scheuchl. For Anatolian *Andrena* species, unless they are very widespread (and hence are present in Anatolia as only a small part of their range), they do not typically descend to the Mediterranean coast. The presence of *A. stellaris*, a species with a small distribution range on the high Central Anatolian steppe, on Mediterranean Lesbos is considered implausible given the complete lack of published records or examined specimens from Mediterranean Turkey. Given the presence of *A. clanga* on Lesbos, it is strongly suspected that these listings of *A. stellaris* are in fact misidentifications of *A. clanga*. The two species are quite similar, but in the female sex *A. clanga* can be recognised due to the denser scutal punctures which are separated by 0.5–1 puncture diameters (in *A. stellaris* with scutal punctures separated by 1–3 puncture diameters) and the denser tergal punctures, on the disc of T2 with punctures separated by <0.5–1 puncture diameters (in *A. stellaris* with the punctures of the disc of T2 separated by 1–2 puncture

diameters). Since no actual evidence of *A. stellaris* on Lesbos has ever been published, it is here excluded from the *Andrena* fauna of the Balkans pending publication of precise information including diagnosis against *A. clanga*; *Quod gratis asseritur, gratis negatur*.

**Distributions (Fig. 42).** *Andrena meridionalis*: Albania and Greece (including Crete); *Andrena albipila*: Spain and Morocco; *Andrena clanga*: Greece (East Aegean Islands), Turkey, Cyprus, Syria, Israel, and Jordan; *Andrena oblonga*: Libya and Egypt.

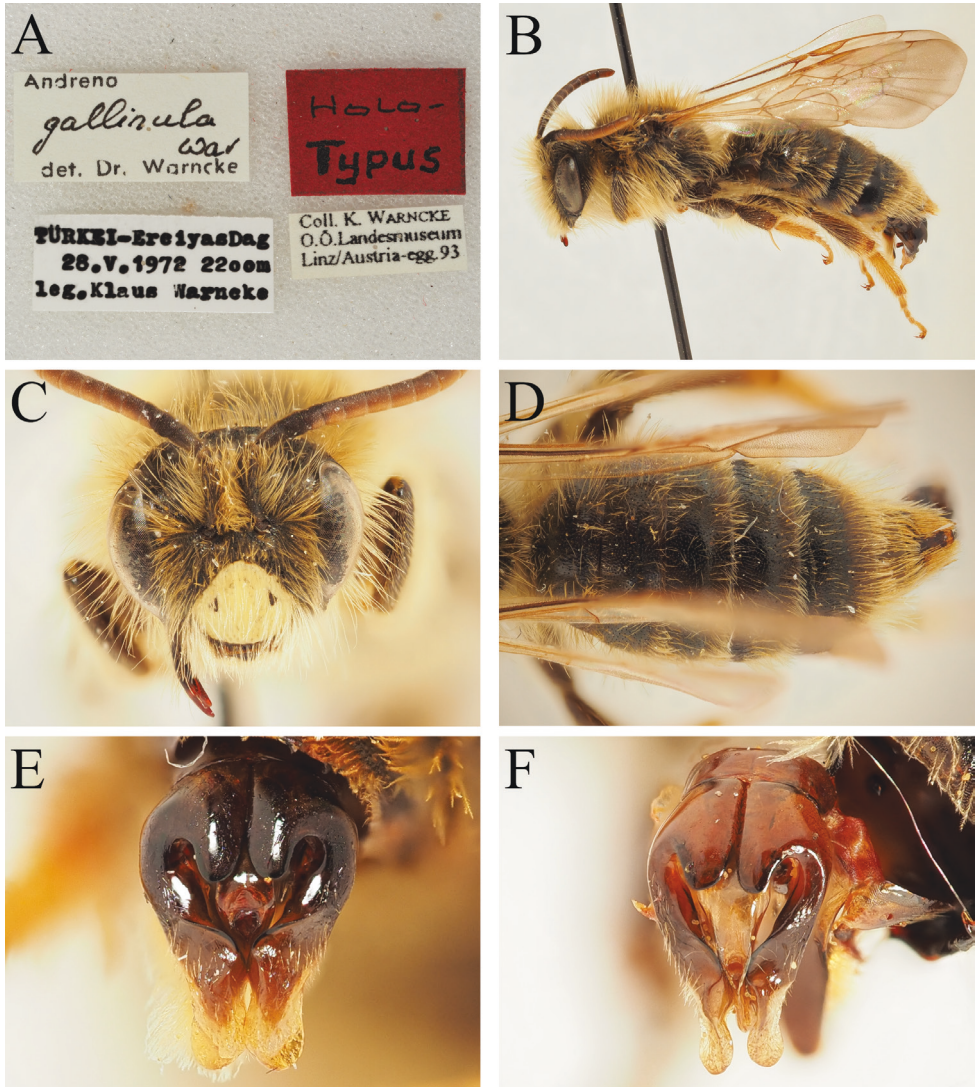
### Identification key for females of the *meridionalis*-group

- 1 Body with pubescence almost entirely dark, metasoma without pale apical hairbands that contrast the dark underlying integument. Found in Egypt and Libya.....*A. (N.) oblonga* Warncke
- Body with pubescence pale to light brown, always with pale metasomal hairbands that contrast the dark underlying integument. Distribution otherwise ..... **2**
- 2 Metasomal hairbands long and poorly-defined, laterally exceeding the length of the marginal areas and extending onto the base of the following tergum. Head with pubescence buffish to light brown. Terminal fringe brown. Found in Albania and continental Greece .....  
.....*A. (N.) meridionalis* Dalla Torre & Friese
- Metasomal hairbands comparatively shorter and well-defined, laterally not exceeding the length of the marginal areas, and only narrowly extending onto the base of the following tergum. Head with pubescence white to whitish. Terminal fringe pale golden. Distribution otherwise ..... **3**
- 3 Tergal discs with comparatively dense punctures, punctures on the discs of T2–4 separated by <0.5–1 puncture diameters. Found in the East Mediterranean, from Lesbos across Turkey to Cyprus and the Levant.....  
.....*A. (N.) clanga* Warncke
- Tergal discs slightly less densely punctate, with punctures on the discs of T2–4 separated by 0.5–1.5 puncture diameters. Found in the West Mediterranean, in Spain and Morocco .....*A. (N.) albipila* Warncke

### Subgenus *Orandrena* Warncke, 1968

**Genetics.** The situation for morphological identification in this subgenus is challenging. Warncke considered a widespread species that was originally described from Uzbekistan, *Andrena oralis* Morawitz, 1876 (see Astafurova et al. 2022: 148 for illustration of lectotype), as present across the Eurasian steppe to the Pannonian basin and also descending to Greece and Turkey (Gusenleitner and Schwarz 2002). He determined specimens from Delphi, presenting them in Warncke (1965a: 40). He then later described *Andrena gallinula* Warncke, 1975 from Turkey (Warncke 1975: 33), very briefly diagnosing it against *A. oralis*. The two species are extremely similar

morphologically, and Warncke did not give the key characters precisely. Specifically, the genital capsule of the male has the apical part of the gonostyli short and broad in *A. gallinula* (Fig. 43E) whereas this is comparatively long and narrow in *A. oralis* (Fig. 43F). In the female sex, I have only been able to find the ocellocipital distance to have discriminative power some of the time, approximately 1.5–2 times the diameter of a lateral ocellus in *A. oralis* (Figs 44B, D) and being equal to the diameter of a lateral ocellus in *A. gallinula* (Fig. 44F, H).



**Figure 43.** *Andrena (Orandrena) gallinula* Warncke, 1975 holotype male (OÖLM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Metasoma, dorsal view; **E.** Genital capsule, dorsal view; *Andrena (Orandrena) oralis* Morawitz, 1876 male. **F.** Genital capsule, dorsal view.



**Figure 44.** *Andrena (Orandrena) oralis* Morawitz, 1876 females. **A.** Label information; **B.** Vertex, dorsal view; **C.** Label information; **D.** Vertex, dorsal view. *Andrena (Orandrena) gallinula* Warncke, 1975 paratype females (OÖLM). **E.** Label information; **F.** Vertex, dorsal view; **G.** Label information; **H.** Vertex, dorsal view.

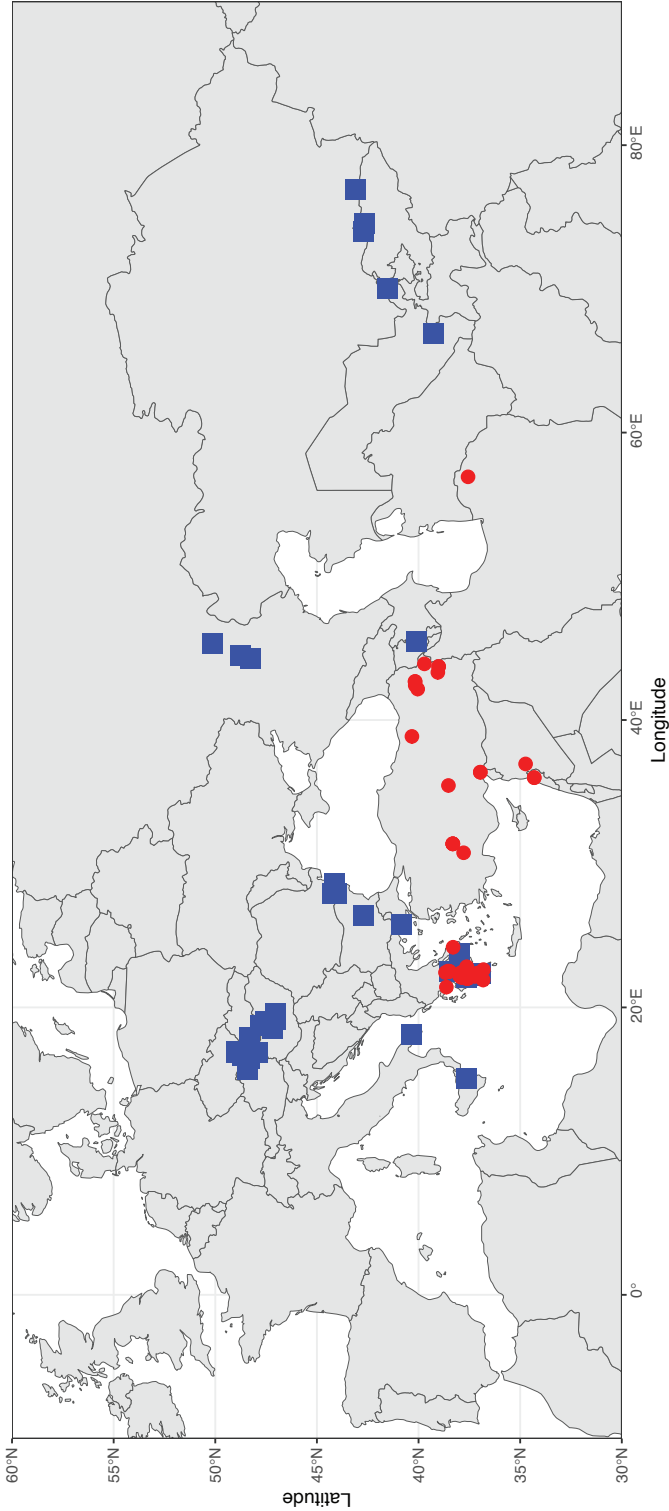
Examination of *Andrena* specimens from Greece has produced specimens showing both genital types (see Suppl. material 2 for full specimen details). In fact, *A. gallinula* is much more commonly encountered in Greece than *A. oralis*, with 55 and 11 examined specimens, respectively (Fig. 45). Most examined specimens were collected by H. Teunissen, and dissected males clearly show the short and broad apex of the gonostyli of *A. gallinula*. However, many ambiguous females can be found in these Greek collections which seem to show intermediate ocelloccipital distances and hence are difficult to place.

Generation of DNA barcodes does not offer clarity (Fig. 46). Five sequences are available, one from Austria (ABEE105-17) which must be *A. oralis*, and four from Greece. BGENL2355-24 is a dissected male from Karkalou in the Peloponnese showing a typical *A. oralis* genital capsule. The remaining three sequences are unfortunately difficult to determine female specimens, two of which (BGENL2352-24 and BGENL2353-24) were determined as *A. oralis* by K. Warncke and W. Grünwaldt, and one of which (BGENL2354-24) was determined as *A. gallinula* by myself. However, the topology of the tree does not clearly show two taxa (Fig. 46). The one possible *A. gallinula* female sequence is nested with *A. oralis* sequences, and the one male sequence of *A. oralis* is placed at the base of the other four sequences. The highest average genetic distance of 4.40% (range 4.06–5.41%) was actually seen between the Austrian sequence and all Greek sequences, with the highest individual difference of 5.41% between the Austrian sequence and the *A. oralis* male from Karkalou.

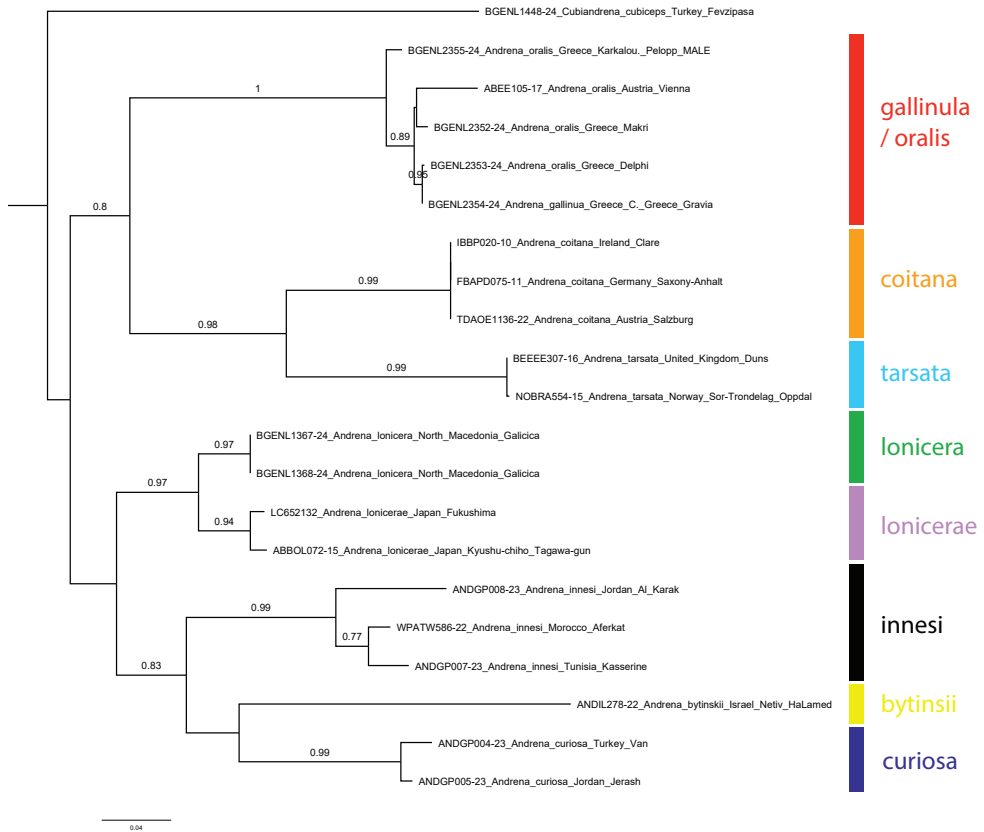
This pattern is challenging to understand given the clear presence of two genital forms in southern Greece. To illustrate this point, a male *A. oralis* was captured on 3 Apr. 2024 near the village of Georgitsi in the central Peloponnese (Fig. 47A, C), and a male *A. gallinula* was captured on 9 Apr. 2024 on Mount Parnassus (Fig. 47B, D). The genital capsules clearly and unambiguously differ. It is currently not possible to explain this incongruence between DNA barcodes and morphology. It may be that *A. oralis* and *A. gallinula* were historically separated, and have now come back into contact and are hybridising in southern Greece. It may be that incomplete lineage sorting has occurred. It may be that all the sequences presented here actually belong to *A. oralis*, and *A. gallinula* remains unsampled. In the absence of additional data which would allow for detailed investigation of these problems, a morphological species concept is followed which distinguishes the two species on the basis of the male genital capsule, and *A. gallinula* is considered to be present in southern Greece. The female ocelloccipital distance is tentatively given as an identification character, but it is clear that additional work is needed to full characterise *Orandrena* species in the East Mediterranean.

### **Subgenus *Poecilandrena* Hedicke, 1933**

**Genetics.** The subgenus *Poecilandrena* has its greatest species richness in the East Mediterranean (Pisanty et al. 2018), with only two species known from the Iberian Peninsula (Wood 2023b). DNA barcodes (Fig. 48) were recently produced for many East Mediterranean species for the first time (Pisanty et al. 2022b; present work),



**Figure 45.** Global distribution map of *Andrena (Orandrena) oralis* Morawitz, 1876 (blue squares) and *Andrena (Orandrena) gallinula* Warncke, 1975 (red circles). Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.



**Figure 46.** Phylogenetic tree (maximum likelihood) of *Andrena* subgenera *Orandrena* Warncke, 1968 and *Stenomelissa* Hirashima & LaBerge, 1965 based on the mitochondrial COI gene. *Cubiandrena cubiceps* (Friese, 1914) is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

allowing species concepts to be validated. For the species in the subgenus showing partially metallic integument, the relatively recently described Greek endemics *Andrena neovirida* Grünwaldt, 2005 and *Andrena standfussorum* Scheuchl, 2010 were strongly separated from the widespread *Andrena viridescens* Viereck, 1916 (Fig. 48). The results also further support the species status of *Andrena veronicae* Pisanty & Wood, 2022 as distinct from the more northerly *Andrena semirubra* Morawitz, 1875 (see Pisanty et al. 2022b for discussion), as sequences of *A. veronicae* from Israel were separated by an average genetic distance of 13.15% (range 12.92–13.37%) from *A. semirubra* sequences from Turkey and Armenia.

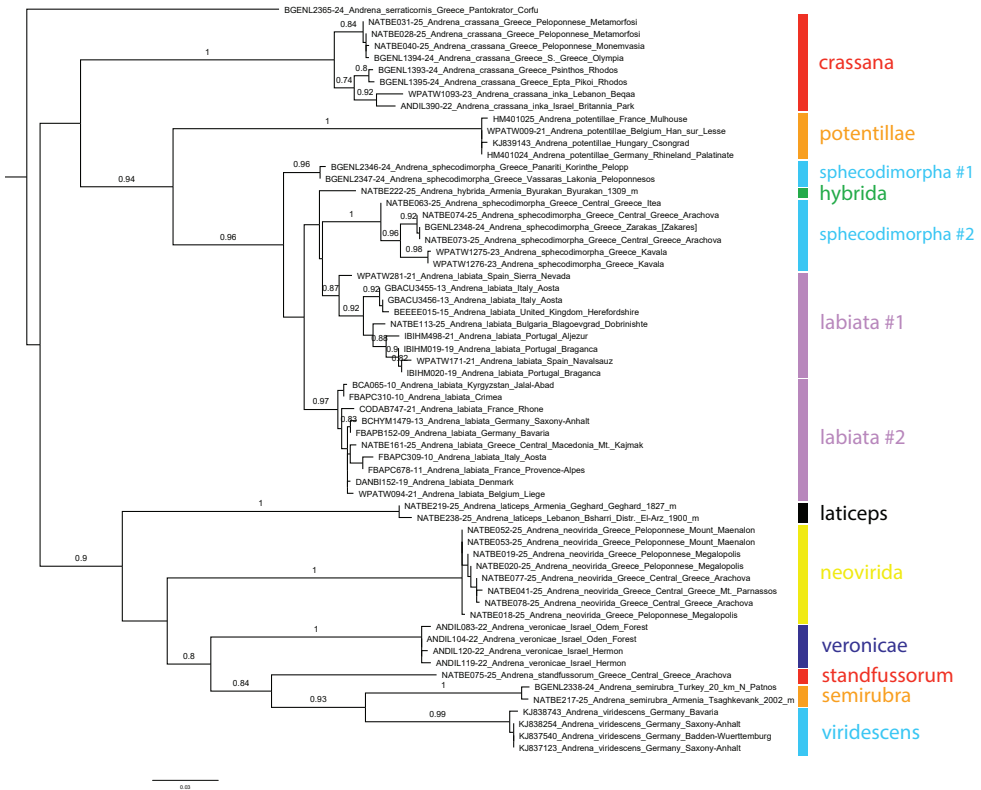
However, the results in the non-metallic clade of *Poecilandrena* were more complex. Although *Andrena crassana* Warncke, 1965 showed minimal differentiation of the “subspecies” *inka* Warncke, 1969, with sequences from the island of Rhodes intermediate between mainland Greek and Levantine sequences (implying



**Figure 47.** *Andrena (Orandrena) oralis* Morawitz, 1876 male. **A.** Label information; **C.** Genital capsule, dorsolateral view. *Andrena (Orandrena) gallinula* Warncke, 1975 male. **B.** Label information; **D.** Genital capsule, dorsolateral view.

separation by distance), three red-marked taxa showed a confusing picture. Specifically, these were *Andrena labiata* Fabricius, 1781, *Andrena sphecodimorpha* Hedicke, 1942, and *Andrena hybrida* Warncke, 1975. *Andrena labiata* is very widespread, occurring from Iberia to Central Asia, whereas *A. sphecodimorpha* is restricted to the Balkans and Crimean Peninsula. *Andrena hybrida* is possibly a species complex, with two described subspecies; ssp. *uralskia* Warncke, 1975 from western Kazakhstan, southern European Russia, Ukraine, and Crimea; ssp. *tauriensis* Warncke, 1975 from southern Turkey and newly reported from western Turkey and the island of Lesbos (Fig. 49; see species entry below); and *hybrida* s. str. from Turkey, Armenia\*, Iran, and Iraq (Gusenleitner and Schwarz 2002; Wood et al. 2024; see Suppl. material 2).

In the phylogenetic tree, these three main taxa were intermixed. Two clades of *A. labiata* were seen (Fig. 48), the first (*labiata* #1) with sequences from Portugal, Spain (including the Sierra Nevada), Italy, the United Kingdom, and Bulgaria, and the second (*labiata* #2) with sequences from France, Belgium, Denmark, Germany, Italy, Greece, Crimea, and Kyrgyzstan. The clades were separated by an average genetic distance of 4.53% (range 3.43–5.47%) and received bootstrap support of 87 and 97,



**Figure 48.** Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Poecilandrena* Hedicke, 1933 based on the mitochondrial COI gene. *Andrena (Truncandrena) serraticornis* Warncke, 1965 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

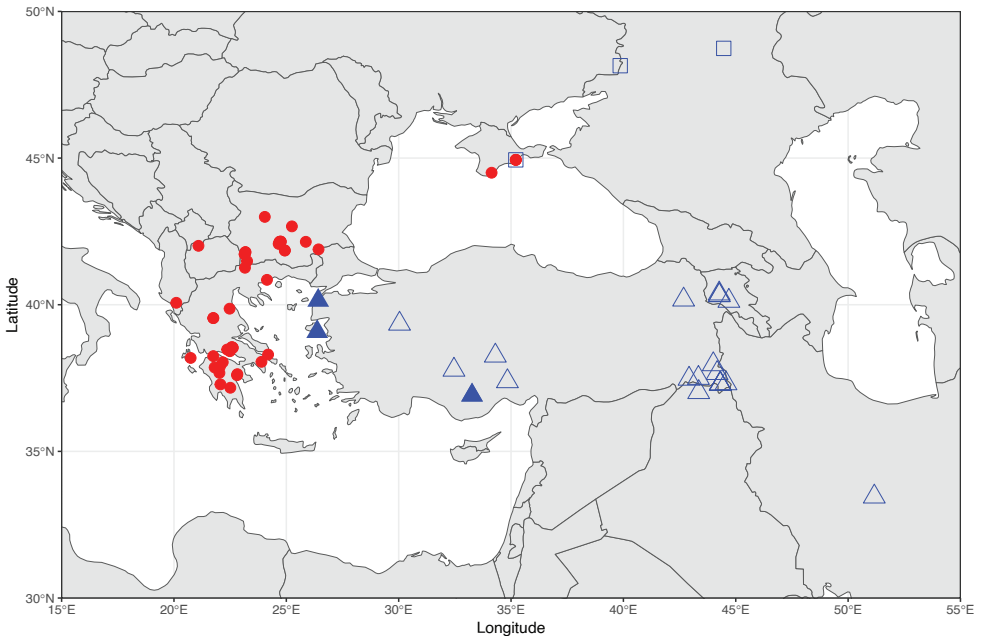
respectively. *labiata* #1 showed within-clade variation of 1.79% (range 0.15–2.69%) and *labiata* #2 showed within clade variation of 1.04% (range 0.17–2.07%).

The two clades of *A. labiata* did not form a monophyletic clade, as *labiata* #1 was closer to a clade of *A. sphecodimorpha* (*sphedodimorpha* #2) containing sequences from Greece (Central Greece and East Macedonia). A second clade (*sphedodimorpha* #1) contained sequences from the Peloponnese. *sphedodimorpha* #2 showed within clade variation of 1.56% (range 0.00–2.49%) and was separated from *sphedodimorpha* #1 by an average genetic distance of 6.72% (range 6.01–7.62%). Between these clades was the single available sequence of *A. hybrida*. However, it is important to stress that the topology of this part of the tree is very weakly supported; all of the key nodes have <75 bootstrap support, and the branches are very short. The tree is therefore fragile, and subject to structural changes if sequences are added or removed.

Regarding *A. labiata*, understanding this pattern is not possible with only evidence from DNA barcodes. It may be that this is a result of incomplete lineage sorting, but

it is also possible that speciation started to begin in geographic isolation, leading to the accumulation of differences in the COI gene. Populations may then have come back into contact, re-establishing gene flow, halting speciation, and leading to distinct mitochondrial lineages within a single biological species (e.g. Kearns et al. 2023 for an example in ravens). Based on the morphology of the male genital capsule, there is no reason at the present time to believe that these two mitochondrial lineages represent two different biological species in Europe, and the concept of *A. labiata* has been more-or-less stable for over 200 years (albeit with a few clarifications needed regarding the appropriate name for this species; Gusenleitner and Schwarz 2002). No taxonomic action is therefore taken here, pending the generation of additional barcodes and ideally nuclear DNA sequences.

The holotype of *A. sphecodimorpha* (from Sofia, 17 Apr. 1915, leg. A.K. Drenowski) is lost, as are all Hedicke types which were placed in his personal collection (Wood 2025a). It is currently considered premature to designate a neotype, both due to the two observed clades of *A. sphecodimorpha*, and also because genetic data from Bulgaria (the *terra typica*) are lacking. Based on the geographic distribution of the sequences presented here, *A. sphecodimorpha* should fall into *sphecodimorpha* #2, as this contains sequences from Eastern Macedonia in northern Greece which are closer to the *terra typica* (Fig. 49).



**Figure 49.** Distributions of *Andrena (Poecilandrena) sphecodimorpha* Hedicke, 1942 (red circles) and *Andrena (Poecilandrena) hybrida* Warncke, 1975 (blue shapes); subspecies *hybrida* s. str. (blue open triangles); subspecies *tauriensis* Warncke, 1975 (blue closed triangles); subspecies *uraliskia* Warncke, 1975 (blue open squares). Displayed distributions are not comprehensive. Specimen details in Suppl. material 2.

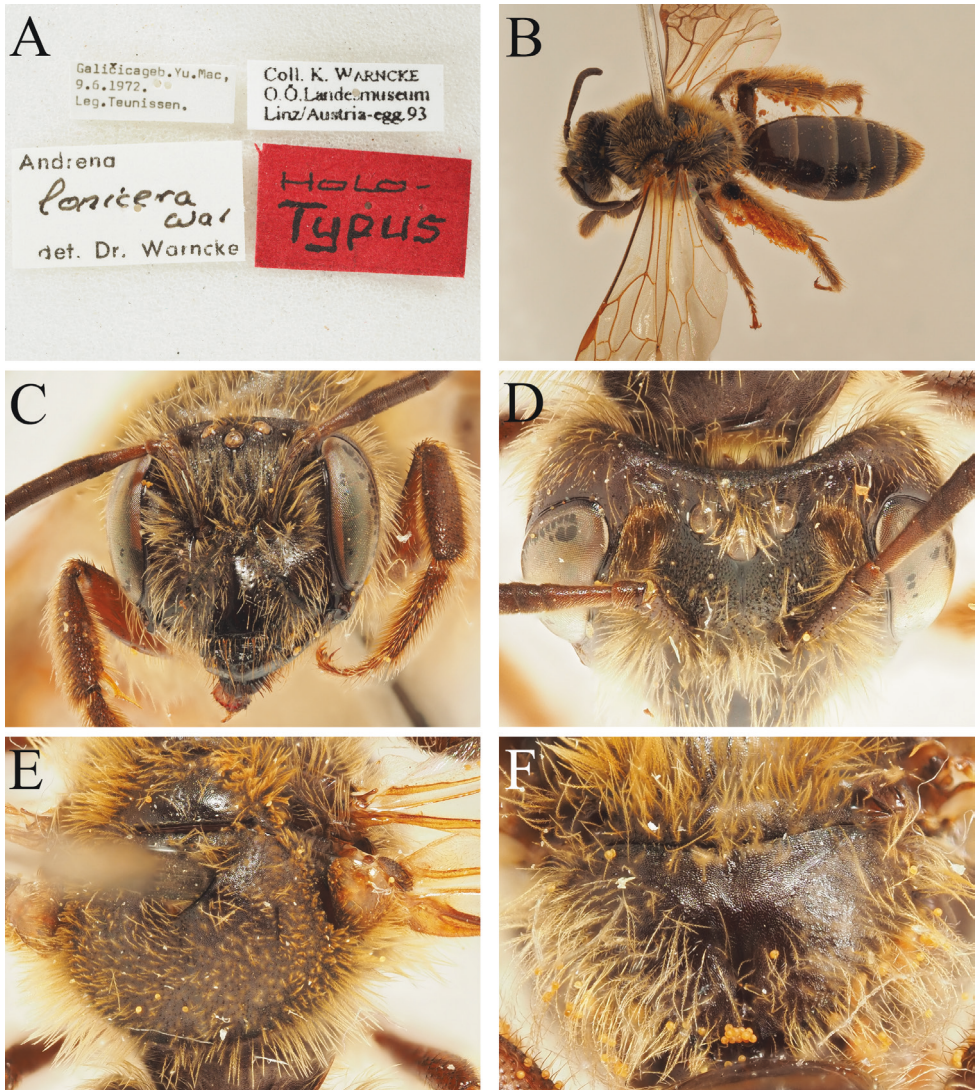
**Subgenus *Stenomelissa* Hirashima & LaBerge, 1965*****Andrena lonicera* Warncke, 1973 and *Andrena loniceræ* Tadauchi & Hirashima, 1988**

The subgenus *Stenomelissa* is traditionally considered to contain three species restricted to East Asia (the Russian Far East, China, the Korean Peninsula, and Japan) (Tadauchi and Hirashima 1988; Gusenleitner and Schwarz 2002; Xu and Tadauchi 2008). However, the species *Andrena lonicera* was originally described from North Macedonia in the subgenus *Hoplandrena* Pérez, 1890. It was listed as part of the subgenus *Stenomelissa* by Grace (2010: 71), placed there in the framework of the STEP project (Rasmont et al. 2013), and is currently listed there by Ascher and Pickering (2025). These treatments probably derive from study of the type series by Erwin Scheuchl who observed striking similarities between the male of *A. lonicera* and the East Palaearctic *Andrena* (*Stenomelissa*) *halictoides* Smith, 1869; this information was communicated to Fritz Gusenleitner and Andrew Grace (E. Scheuchl, pers. comm.).

*Andrena lonicera* was described based on six females and one male collected by Herman Teunissen from an altitude of 1800 m on the Galičica Planina mountain in south-western North Macedonia. Warncke (1973: 35) described this species as an addendum to his main article after receiving specimens from Teunissen, and indicated that the specimens were collected from *Lonicera* (Caprifoliaceae) in difficult conditions (unter Schwierigkeiten) at the edge of the tree line. The species was therefore named after this plant genus. Of the original seven specimens, two female paratypes have been located in the RMNH collection, but in the OÖLM collection only the female holotype (Fig. 50) and one female paratype could be found. As for *A. caprimulga*, unfortunately the single male paratype appears to be missing from the OÖLM collection, despite being indicated as present by Blank and Kraus (1994). As to the remaining two female paratypes, their location is unclear. No further specimens of *A. lonicera* have yet been encountered in field or museum collections.

Tadauchi and Hirashima (1988: 72) described *Andrena loniceræ* from eastern and southern Japan (type material Kyushu University, Fukuoka, Japan) where it is endemic (Xu and Tadauchi 2008). It predominantly visits *Lonicera gracilipes* Miq., on which it appears to be specialised (Shimizu et al. 2014). The name therefore also derives from the genus *Lonicera*. Although the names are very similar, they are both valid, as they differ by a single letter (ICZN Article 57.6), and *A. loniceræ* does not meet the exceptions to this rule laid out under Article 58.

It was possible to generate barcodes from the two female paratype specimens of *A. lonicera* in the RMNH collection (Fig. 48). In the barcode tree, *A. lonicera* clustered most closely to *A. loniceræ* (sequences from Genbank), the sequences separated by an average genetic distance of 5.68% (range 5.58–5.78%). Together, *A. lonicera* + *A. loniceræ* placed closer to sequences from the subgenera *Warnckandrena* Pisanty, 2024 and *Uncandrena* Pisanty, 2024 which are the most basal *Andrena* subgenera known (Pisanty et al. 2022a; Pisanty and Wood 2024). Whilst ultra-conserved element genetic data for members of the subgenus *Stenomelissa* are lacking, and



**Figure 50.** *Andrena (Stenomelissa) lonicera* Warncke, 1973 holotype female (OÖLM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Head, dorsal view; **E.** Scutum, dorsal view; **F.** Propodeum, posterior view.

ultimate confirmation or rejection of the phylogenetic placement of *Stenomelissa* must wait, the placement close to *Warnckandrena*+*Uncandrena* combined with the morphology of *A. lonicera* is highly suggestive. Importantly, *A. lonicera* has the propodeum nearly completely declivous, without defined horizontal and vertical parts. This is most strongly observed in the genus *Cubiandrena* Warncke, 1968, and then most strongly observed in the subgenera *Warnckandrena* and *Uncandrena* (Pisanty and Wood 2024).

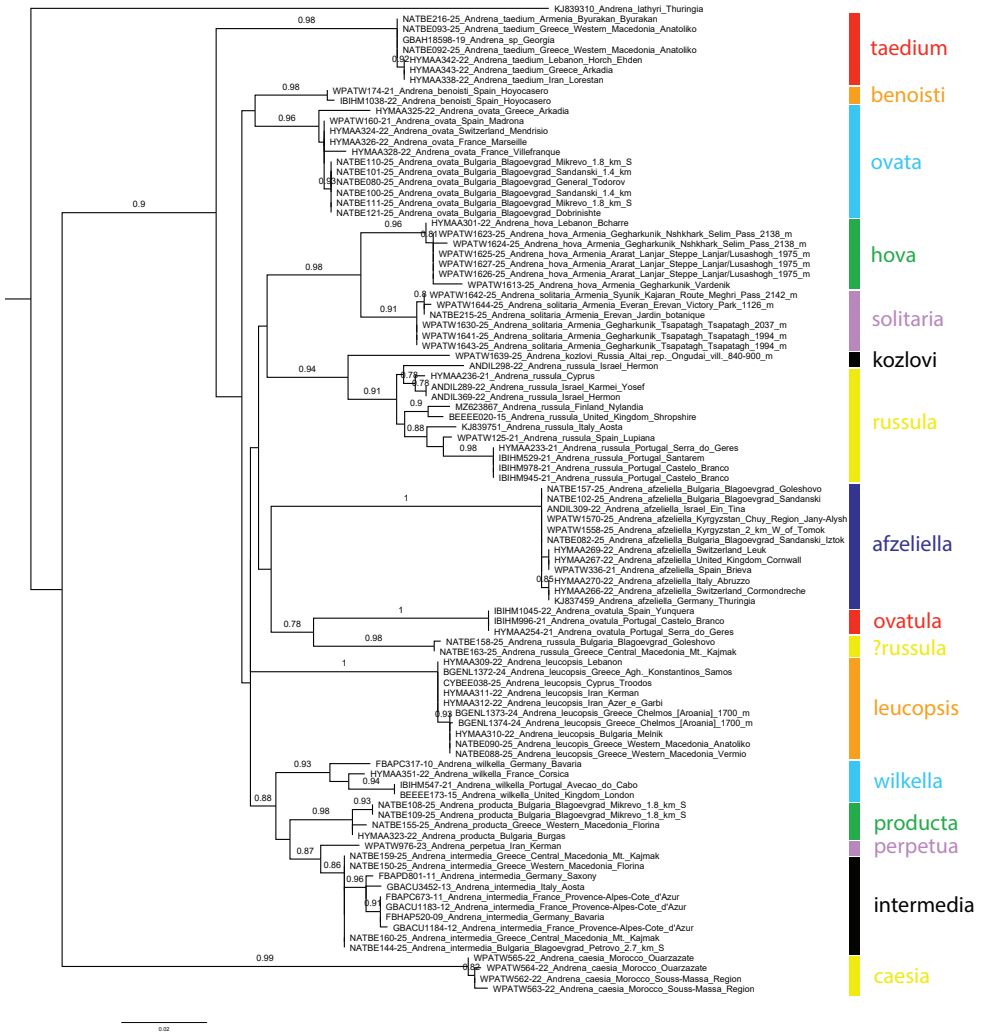
*Andrena lonicera* is therefore considered to be part of the subgenus *Stenomelissa*, and to represent an extremely isolated member. This is slightly reminiscent of the situation in subgenus *Warnckandrena*, with the most easterly member found in northern Iran, with a seemingly closely related but isolated species found on the Tibetan Plateau in central China (*Andrena remota* Wood, 2024; Pisanty and Wood 2024). The use of *Lonicera* by *A. lonicera* and *A. lonicerae* is also highly unusual for *Andrena* species, and this seemingly linked niche use requires further study if populations of *A. lonicera* can be located in the southern Balkans in the present day.

### Subgenus *Taeniandrena* Hedicke, 1933

This subgenus has received much taxonomic attention in the past few years (e.g. Wood et al. 2021; Praz et al. 2022; Wood 2022, 2023b, 2023c). New samples from the southern Balkans and the Caucasus (Fig. 51) do not greatly change our understanding relative to the situation presented in Praz et al. (2022), but they do further support those conclusions. The main findings are additional sequences of *Andrena afzeliella* (Kirby, 1802) (from Bulgaria), *Andrena hova* Warncke, 1975 (from Armenia), *Andrena intermedia* Thomson, 1870 (from Bulgaria and Greece), *Andrena leucopsis* Warncke, 1967 (from Greece), *Andrena ovata* Schenck, 1853 (from Bulgaria), *Andrena producta* Warncke, 1973 (from Bulgaria and Greece), *Andrena solitaria* Warncke, 1975 (from Armenia), and *Andrena taedium* Wood, 2023 (from Greece and Armenia). Both *A. leucopsis* and *A. taedium* (Fig. 52) are confirmed to be species distributed from the Balkan Peninsula to western Iran.

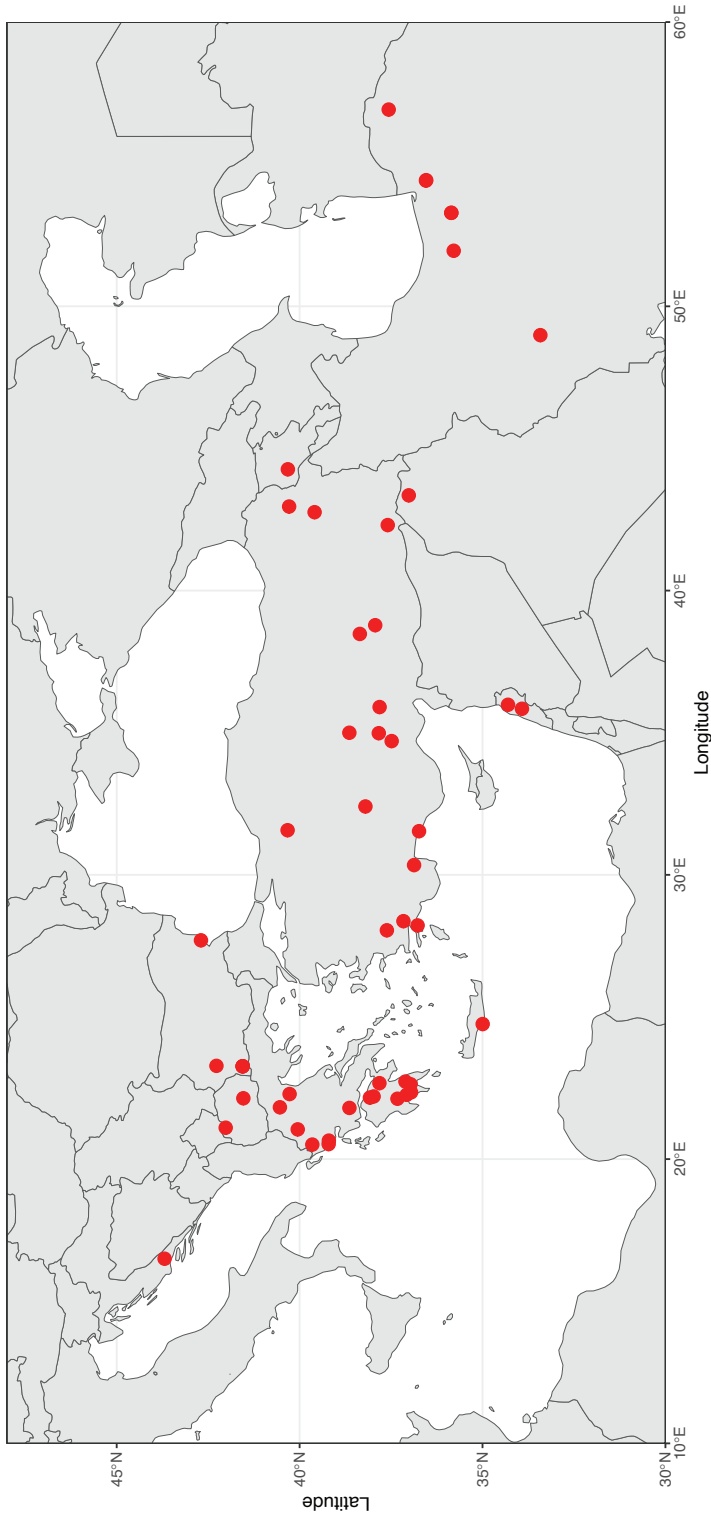
The greatest area of uncertainty surrounds *Andrena russula* Lepelletier, 1841 and *Andrena phoenicura* Warncke, 1975. *Andrena russula* is widely distributed across the West Palaearctic (Praz et al. 2022), with sequences available from Finland, Cyprus, and Israel in the east (Fig. 51). However, two sequences from northern Greece (NATBE158-25) and southern Bulgaria (NATBE163-25) were very widely separated from the main *A. russula* clade by an average genetic distance of 5.76% (range 4.97–6.53%). *Andrena russula* remains very difficult to understand, as away from the main central clade of sequences (the clade presented in Praz et al. 2022 and here; Fig. 51), multiple “cryptic” lineages can be seen in south-western Iberia, Morocco, and now the southern Balkans (Praz et al. 2022; Wood 2023b, 2023c; Wood et al. 2024a). The Greek+Bulgarian sequences do not match either of the West Mediterranean “cryptic” lineages.

No actions are taken here due to the number of names of incompletely understood *Taeniandrena* species that are available in Turkey. Warncke described *Andrena phoenicura* from Turkey, and this species was listed from Greece (Kuhlmann et al. 2014) and Bulgaria (Wood 2021), specifically from specimens from Sandanski and Slančev Brjag (Sunny Beach). Re-examination of some of these specimens published in 2021 show that they are actually *Andrena taedium*, a species described in 2023 (Wood 2023a). It has not been possible to locate all of the specimens deposited in the OÖLM (Kocourek collection) that were presented in Wood (2021), as the material (including all *Andrena* specimens determined by myself between 2019–2024) is in the



**Figure 51.** Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Taeniandrena* Hedicke, 1933 based on the mitochondrial COI gene. *Andrena (Taeniandrena) lathyri* Alfken, 1899 is used as an outgroup (see Praz et al. 2022). Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

process of being curated into the main collection. However, the specimens retained in my personal collection conform to *A. taedium*. Given the new records of *A. taedium*, including many from Greece, the revised global distribution is presented in Fig. 52). It was not possible to directly examine any specimens of *A. taedium* from Georgia, but on BOLD the sequence [GBAH18598-19](#) which was originally identified as *Andrena wilkella* (Kirby, 1802) is clearly nested with *A. taedium* (Fig. 51), and is considered to represent the first record of the species from this country.



**Figure 52.** Global distribution of *Andrena (Taenianandrena) taedium* Wood, 2023. Specimen details in Suppl. material 2.

The type material of *A. phoenicura* (OÖLM) has now been carefully studied (Fig. 53), and it is a taxon close to *A. russula*. Barcodes were generated from possible *A. russula* females from Armenia, but these matched males of *Andrena solitaria*, a species described only in the male sex which has a highly distinctive genital capsule (Warncke 1975). The holotype of *A. phoenicura* is a male, and so it can be confidently concluded that it is not conspecific with *A. solitaria*, but the characters allowing determination of the females of these two species are not clear. Currently, no barcodes



**Figure 53.** *Andrena (Taeniandrena) phoenicura* Warncke, 1975 holotype male (OÖLM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Base of metasoma, dorsal view; **E.** Metasoma, dorsal view; **F.** Genital capsule, dorsal view.

from the southern Balkans match sequences of *A. solitaria* (Fig. 51). It is considered unlikely that the two “*A. russula*” sequences from Greece and Bulgaria are actually *A. phoenicura*, as the specimen from Greece (NATBE158-25) is a male which has a genital capsule which is slimmer than in *A. phoenicura* and lacks the more strongly flattened and spatulate apices of the gonostyli. It has A3 slightly shorter than A4, whereas in some *A. russula* specimens A3 exceeds the length of A4, but this has already been noted to be a “variable” character (Praz et al. 2022) and is difficult to characterise even in European specimens. At the present time, *A. phoenicura* is considered unproven from the southern Balkans and must be treated as a *species inquirenda*.

### *Andrena (Taeniandrena) taedium* Wood, 2023

**Material examined.** ALBANIA • 1♀; Kukës, W of Perollaj; 26 May 2024; W. Vertommen leg.; WVC; ARMENIA • 1♀; Byurakan; 1309 m a.s.l.; 9 May 2023; V. Leclercq leg.; VLC; BULGARIA • 1♀; N Panitchishte vill.; 1237 m a.s.l.; 27 Jun. 2016; M. Naumova leg.; IBER • 2♂, 1♀; Sandanski; 1–30 Jun. 1969; M. Kocourek leg.; TJWC; CROATIA • 1♀; Split, Gornji Muc, malaise trap; 500 m a.s.l.; 14 May – 8 Jun. 2014; B. Kokan leg.; OÖLM; IRAQ • 1♀; Duhok gov., 5 km E of Ashewa, Mt. Gara; 1750–1950 m a.s.l.; 30 May – 12 Jun. 2024; D. Baiocchi leg.; MSVI; NORTH MACEDONIA • 1♂; Polog reg., Sirichino, quarry; 400 m a.s.l.; 12–17 Apr. 2021; V. Bureš leg.; JSPC • 2♀; Vardar reg., Papeliste, steppe; 130 m a.s.l.; 6–11 Apr. 2021; V. Bureš leg.; JSPC.

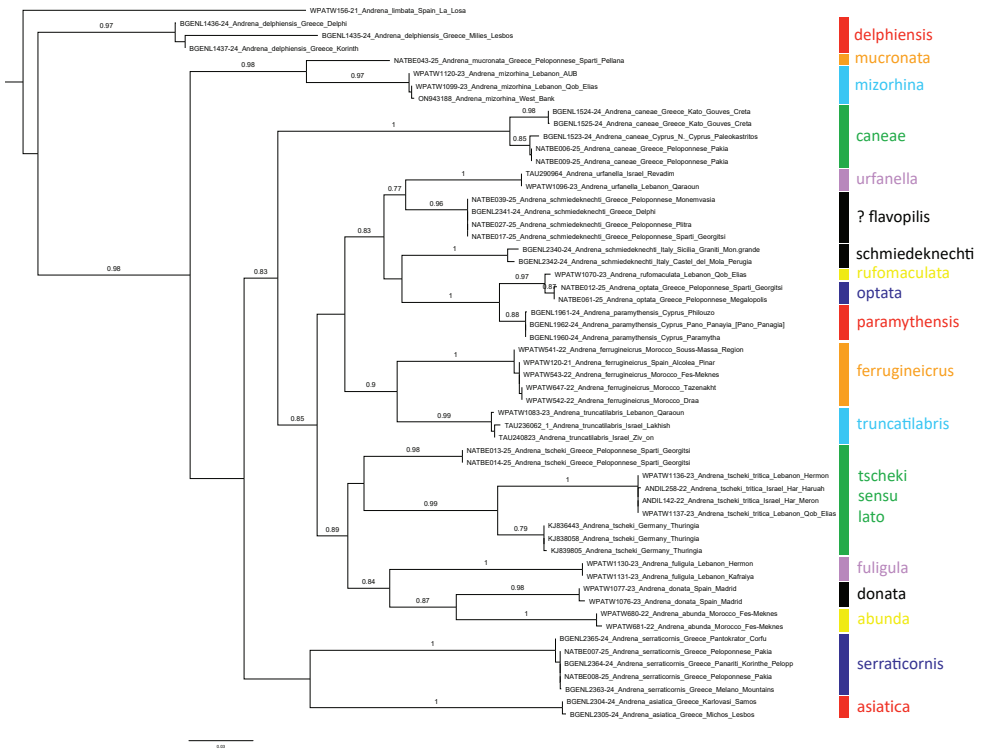
**Notes.** See Suppl. material 2 for full records, including from Greece.

**Global distribution.** Croatia\*, Albania\*, North Macedonia\*, Greece, Bulgaria\*, Turkey, Lebanon, Georgia\*, Armenia\*, Iraq\*, Iran (Wood 2023a) (Fig. 52).

### Subgenus *Truncandrena* Warncke, 1968

**Genetics.** The subgenus *Truncandrena* is taxonomically challenging, with many “sub-specific” names available due to Warncke’s broad species concepts and a high level of “variation” comprising different colour patterns (in both the integument and pubescence). This has led to the elevation of many of these subspecific concepts to full species status (e.g. Gusenleitner and Schwarz 2002; Pisanty et al. 2022b; Wood 2023b, 2024a). In this context, many new DNA barcodes were available for the East Mediterranean fauna. For many taxa, they offered good resolution; although females are challenging to separate morphologically, *Andrena canaeae* Strand, 1915 and *Andrena serraticornis* Warncke, 1965 were strongly separated genetically (Fig. 54).

Three major issues were detected in this subgenus. Firstly, *Andrena tscheki* Morawitz, 1872 *sensu lato* formed three distinct subclades, with sequences from 1) Greece, 2) Germany, and 3) Israel and Lebanon. Greek specimens were separated from German specimens by an average genetic distance of 9.63% (range 9.57–9.73%), and from Levantine sequences by an average of 11.21% (range 11.09–11.25%). German



**Figure 54.** Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Truncandrena* Warncke, 1968 based on the mitochondrial COI gene. *Andrena (Limbandrena) limbata* Eversmann, 1852 is used as an outgroup (see Praz et al. 2022). Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

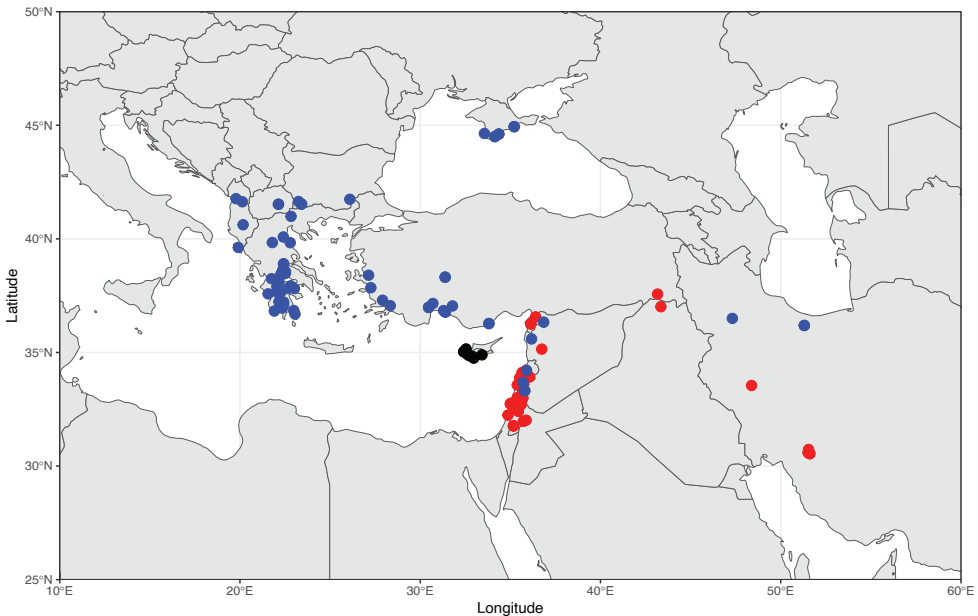
and Levantine sequences were separated by an average of 7.38% (range 7.29–7.45%). This issue is discussed below, along with morphological recognition of the taxa.

Secondly, *Andrena schmiedeknechti* Magretti, 1883 (described from Italy) formed two lineages, with sequences from Italy (Sicily) strongly separated from sequences from southern Greece by an average genetic distance of 6.28% (range 5.87–7.12%). Although smaller in absolute terms than the distances seen in *A. tscheki sensu lato*, this led to a topology where Italian *A. schmiedeknechti* were placed closer to members of the *rufomaculata*-group, and Greek *A. schmiedeknechti* were placed closer to *Andrena urfanella* Scheuchl & Hazir, 2012. The name *Andrena schmiedeknechti* ssp. *flavopilis* Warncke, 1965 is available for Greek populations, but additional study is required. The topology of the tree separating Italian and Greek sequences is unstable, with bootstrap support grouping Italian *A. schmiedeknechti* + *rufomaculata*-group of only 37. The addition of more sequences from this group (including *A. schmiedeknechti* ssp. *nigrorum* Warncke, 1967 from North Africa) could result in a monophyletic clade, as in *A. tscheki sensu lato*. There also do not appear to be structural differences between the genital capsules of *A. schmiedeknechti sensu lato* seen in Italy and Greece, and the

only difference is in the colouration of the hair (Warncke 1965a). As such, no action is taken here, and the broad species concept of Warncke is maintained.

The third issue surrounds the *rufomaculata*-group which contains the taxa *Andrena rufomaculata* Friese, 1921, *Andrena paramythensis* Mavromoustakis, 1957, and *Andrena optata* Warncke, 1975. Warncke (1974a, 1975) treated this as a broad taxon *A. rufomaculata*, with *A. rufomaculata* s. str. found in southern Turkey and the Levant (*locus typicus*: Turkey, Airan [an Armenian village, modern name not currently traceable] in the Taurus Mountains), *A. rufomaculata* ssp. *paramythensis* found in Cyprus (*locus typicus*: Cyprus, Paramytha), and *A. rufomaculata* ssp. *optata* found from central Anatolia across the Mediterranean coast to Greece, Albania, the Dalmatian coast, southern Hungary, and Crimea (*locus typicus*: Greece, Lamia). Although Warncke and Gusenleitner and Schwarz (2002) used this broad concept, subsequent authors (e.g. Hazir et al. 2014) have treated the three as distinct, though this has led to some confusion between *A. paramythensis* and *A. optata*, with the latter being reported as the former in some studies (e.g. Hazir et al. 2014; Pisanty et al. 2018).

Although Warncke considered these “subspecies” not to have overlapping ranges, *A. optata* and *A. rufomaculata* actually appear to have overlapping ranges in the Levant, with *A. optata* descending to Lebanon and northern Israel (Mount Hermon) (Pisanty et al. 2018, as *A. paramythensis* misidentification; Wood et al. 2020; Fig. 55). Whilst the morphological characters appear solid, available genetic sequences indicate that



**Figure 55.** Global distributions of members of the *Andrena* (*Truncandrena*) *rufomaculata*-group. *Andrena* (*T.*) *rufomaculata* Friese, 1921 (red circles); *A.* (*T.*) *paramythensis* Mavromoustakis, 1957 (black circles); *A.* (*T.*) *optata* Warncke, 1975 (blue circles). Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

the differences within this group are very small. Three sequences of *A. paramythensis* showed very low intraspecific variation of 0.04% (range 0.00–0.06%). These were separated from two sequences of *A. optata* (Greece: Peloponnese) plus one sequence of *A. rufomaculata* (Lebanon) by an average genetic distance of 3.61% (range 3.33–3.81%). The sequences of *A. optata* were separated from *A. rufomaculata* by only 0.84% (range 0.76–0.91%). In absolute terms, this is a small genetic difference. Inclusion of additional sequences from Cyprus and the Levant actually show more complexity, with no consistent topological differences and sequences of all three taxa intermixed (G. Pisanty, pers. comm.). However, the ecological affinities of the two taxa suggest genuine species-level differences. In the Levant, *A. optata* is found at high altitude on Mount Hermon and the Mount Lebanon chain between 1200–2200 m a.s.l. whereas *A. rufomaculata* is much more thermophilic and is found at low to moderate altitudes. Specimens morphologically conforming to *A. paramythensis* are found only on the island of Cyprus. Consequently, as a temporary solution, *A. optata* is retained here as a good species despite the only weak to non-existent genetic separation from *A. rufomaculata*. This remains an area for future investigation using more powerful genetic tools to quantify realised gene flow in this group.

Overall, the genetic results from within subgenus *Truncandrena* paint a challenging picture in which it is difficult to consistently translate high genetic distances into species-specific differences within existing morphological species concepts, and some existing morphological species concepts receive low to non-existent genetic support. Whilst the conclusions presented here are conservative, they maintain nomenclatural stability and allow morphological recognition of taxa which is beneficial for ecological study and monitoring of bee species pending further study.

### *Andrena (Truncandrena) tscheki* Morawitz, 1872

*Andrena nigrifrons* Smith, 1853: 106, ♀♂ [Greece, OUMNH, lectotype by present designation] nec. Eversmann, 1852 (Fig. 56)

*Andrena tscheki* Morawitz, 1872: 366, ♀ [Austria, ZISP, examined by photograph]

*Andrena tscheki* spp. *tritica* Warncke, 1965a: 36, ♀♂ [Greece, OÖLM, examined] (Fig. 57)

**Material examined.** GREECE • 1♂, 1♀; 446. Alb<sup>nia</sup>; OUMNH (female **lectotype** of *Andrena nigrifrons* Smith by present designation, male **paralectotype**).

**Notes.** Gusenleitner and Schwarz (2002: 783) gave the NHMUK as the repository for the type of *A. nigrifrons* Smith, but the species was stated as being described from the collection of William Wilson Saunders, which was acquired by the OUMNH in 1873 (Anon 1879). A female and male labelled as “446. ♀. Alb<sup>nia</sup>” and “446. ♂. Alb<sup>nia</sup>” were collected by Sir Sidney Smith Saunders, and are syntypes. Sidney S. Saunders (1809–1884) was cousin of W.W. Saunders, and was appointed as British Consul in “Albania” between 1835–1859.



**Figure 56.** *Andrena (Truncandrena) nigrifrons* Smith, 1853 nec. Eversmann female lectotype (OUMNH). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Metasoma, dorsal view.

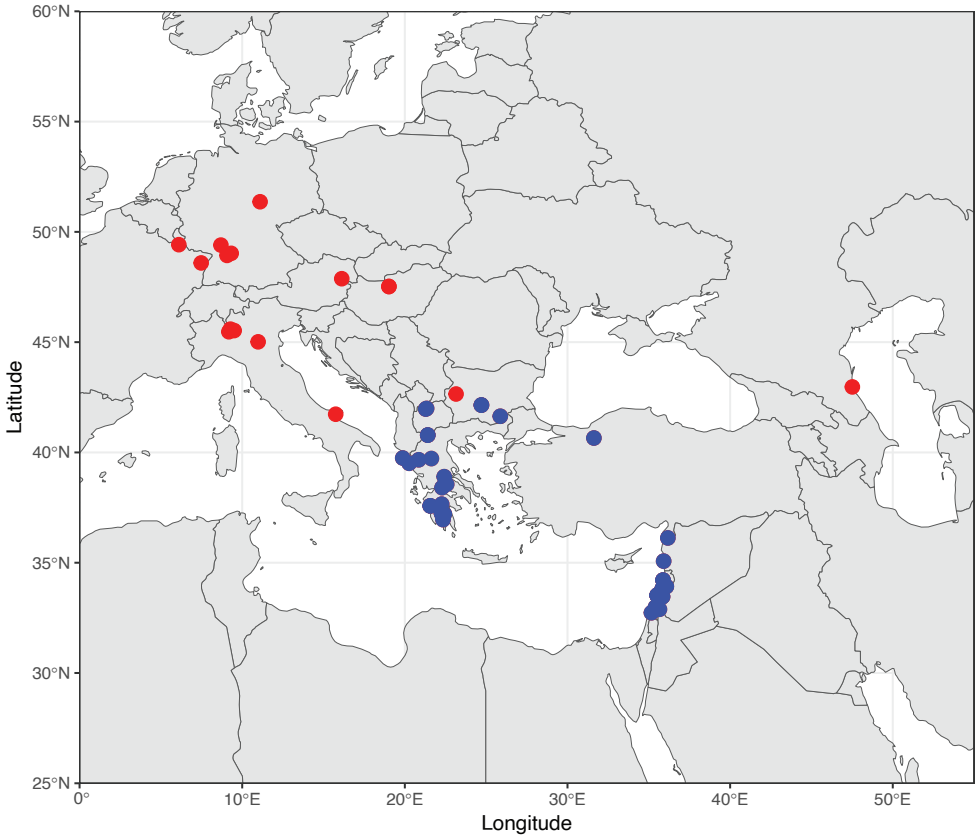
It is necessary to discuss what “Albania” actually constituted at this time. After the creation of the First Hellenic Republic in 1822, the Ottoman Empire retained control of what is now northern Greece, Albania, North Macedonia, and Bulgaria. Importantly, the Ottoman Empire retained control of the town of Preveza, which today is in modern Greece. Under the Ottomans, this town was the centre of the Sanjak of Preveza. This covered the period during which S.S. Saunders was appointed consul at “Prevesa” [=Preveza] (Wilson 2011), i.e. within Ottoman Albania. Greece did not formally acquire the territories including Preveza until the First Balkan War and the 1913 treaty of London. Consequently, most of the material collected by S.S. Saunders in “Albania” is likely to be from within the borders of modern Greece, and following Baker (1993) it is treated as such.

Baker (1993: 132) located this material and stated that he labelled the female as lectotype, but this is not a valid designation as Baker (1993) is an unpublished thesis and hence fails Articles 8 and 9 (ICZN 1999). Moreover, Baker did not label the specimens. The female is now finally designated as the lectotype. Whilst the name is not available due to homonymy, Smith’s types morphologically conform to what Warncke called *A. tscheiki* spp. *tritica*; the apical margin of T4 has a complete hairband, whereas in the nominate subspecies T4 is entirely dark-haired.



**Figure 57.** *Andrena* (*Truncandrena*) *tscheki* ssp. *tritica* Warncke, 1965 holotype female (OÖLM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Metasoma, dorsal view.

Based on the analysis of the COI fragment, three subclades were found within a broad *A. tscheki* which do not agree with the observed morphology (Fig. 54). Specimens from Greece were strongly separated from both German and Levantine sequences, despite morphologically being closer to Levantine specimens. Purely based on the morphology (Fig. 58), *A. tscheki* s. str. can be found across Central Europe to Vitosha mountain by Sofia in Bulgaria, with specimens from lower altitudes confirming to *A. tscheki* spp. *tritica* across the southern Balkans, across Turkey (see Warncke 1974a: 92 for additional localities), and to the Levant. Additionally, and there are two female specimens from southern Russia (Dagestan) in the ZSM which were determined as “aff *tscheki*” by Osytsnjuk (see Suppl. material 2) which do seem to meet the morphologically criteria for *A. tscheki* s. str. In short, there does not appear to be a clear way to split *A. tscheki*; if split, the Levantine taxon would have to be described, and structurally, there do not appear to be any differences in the genital capsule or integument across the range from eastern France to the Levant. As such, the broad *A. tscheki* species concept of Warncke is maintained in this work.



**Figure 58.** Global distribution of *Andrena (Truncandrena) tscheki* Morawitz, 1872 *sensu lato*; subspecies *tscheki* (red circles); subspecies *tritica* Warncke, 1965 (blue circles).

**Subgenus *Ulandrena* Warncke, 1968**

***Andrena (Ulandrena) concinna* Smith, 1853**

*Andrena concinna* Smith, 1853: 106, ♀ [Greece, OUMNH, lectotype by present designation] (Fig. 59)

**Material examined. GREECE** • 1♀; OUMNH (**lectotype** by present designation).

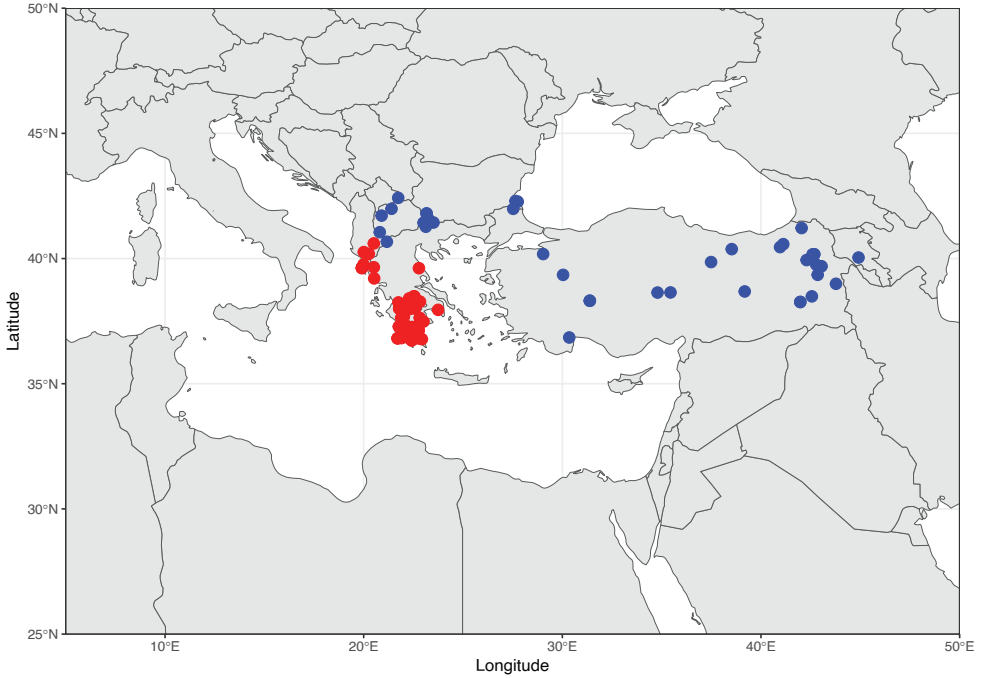
**Notes.** Wood (2024a) discussed the *concinna*-group, and commented that the type of *A. concinna* was not in the NHMUK, the stated type repository (Gusenleitner and Schwarz 2002: 198). As for *A. nigrifrons* Smith, the species was described from the collection of W.W. Saunders. A single female labelled as “A. 314” is from “Albania”, with the same caveat as applied above to *A. nigrifrons* Smith given the likely geographical



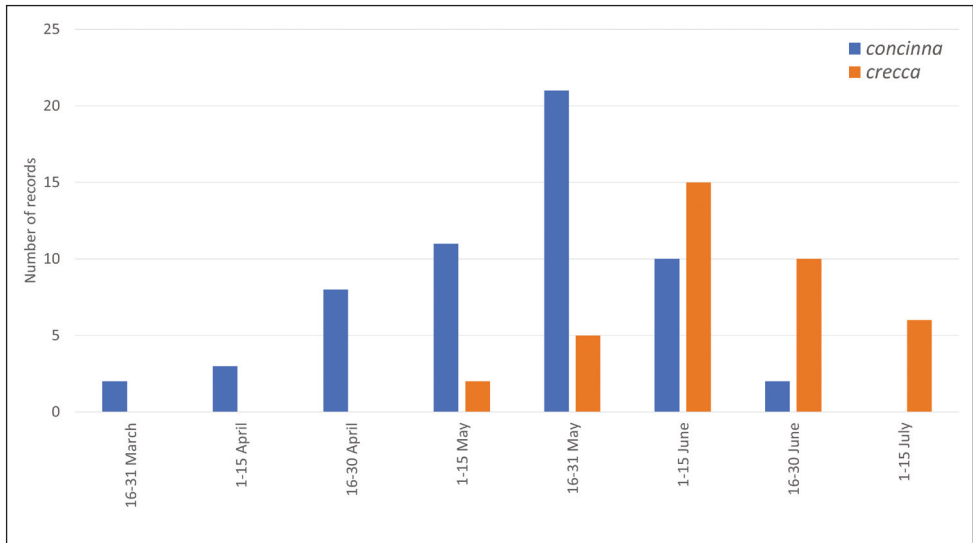
**Figure 59.** *Andrena (Ulandrena) concinna* Smith, 1853 lectotype female (OUMNH). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Metasoma, dorsal view.

place of capture. Baker (1993: 133) concluded that it was the holotype and stated that he labelled it as such, but no label was found. Following ICZN (1999) recommendation 73F, I do not assume that it is the holotype (as Smith's description does not indicate the number of specimens used to describe the species), and designate it instead as the lectotype. It conforms to the expected species, as *A. concinna* is the only member of this species complex that occurs in coastal parts of western Greece, though it geographically comes close to the more continental *A. crecca* Warncke, 1965 (Wood 2024a; Fig. 60).

In addition to the morphological differences illustrated by Wood (2024a), *A. concinna* shows an earlier phenology than *A. crecca*. *Andrena concinna* peaks between 16–31 May, with *A. crecca* peaking between 1–15 June (Fig. 61). Based on the median record, the respective dates are 19 May for *A. concinna* and 13 June for *A. crecca*. For this analysis, 89.0% of the specimens used (see Suppl. material 2) were collected after 1980, suggesting that any confounding effects of climate change would be minor. Thus, despite having very similar ecological niches (specialists of Asteroidae (Asteraceae), see section on the dietary niches of Balkan *Andrena*), they have slightly different climatic affinities and phenologies.



**Figure 60.** Global distributions of *Andrena (Ulandrena) concinna* Smith, 1853 (red circles) and *Andrena (Ulandrena) crecca* Warncke, 1965 (blue circles). Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.



**Figure 61.** Phenological plot of *Andrena (Ulandrena) concinna* Smith, 1853 and *Andrena (Ulandrena) crecca* Warncke, 1965 based on recorded flight date of examined pinned specimens.

***Andrena (Ulandrena) subglobosa* Dours, 1873, sp. resurrected.**

*Campylogaster (Andrena) subglobosus* Dours, 1873: 287, ♀♂ [Greece: Corfu, MSNG, lectotype by present designation] (Fig. 62)

*Andrena punctatissima* Kriechbaumer, 1873: 59, ♀ [Croatia, ZSM, examined] nec. Morawitz, 1866 (Fig. 63)

*Andrena kriegbaumeri* Schmiedeknecht, 1883: 569, nom. nov. *pro Andrena punctatissima* syn. nov.

**Material examined.** CROATIA • 1 ♀; Lesina [=Croatian island of Hvar]; Heller leg.; ZSM (**syntype** of *Andrena punctatissima* Kriechbaumer); GREECE • 1 ♂; Corfu; MSNG (**lectotype** of *Andrena subglobosa* by present designation). See Suppl. material 2 for additional examined material.

**Notes.** The name *Andrena kriegbaumeri* has been used for many years to refer to an *Ulandrena* species found in the East Mediterranean which can rapidly be recognised due to the strongly postfurcal nervulus of the forewing. *Andrena kriegbaumeri* was created as a replacement name, as *Andrena punctatissima* Kriechbaumer is a junior primary homonym of *Andrena punctatissima* Morawitz (1866: 14) (see Astafurova et al. 2021). The species was described from what is now the island of Hvar in southern Croatia, and a single female syntype was present in the ZSM labelled with a typical Kriechbaumer label (Fig. 63). The species was described from two females, but it is not considered necessary to designate a lectotype at the present time.

The name *Andrena subglobosa* was created as *Campylogaster subglobosus*, but as Dours (1873: 286) created *Campylogaster* as a subgenus of *Andrena*, the name can be used in combination with *Andrena* without Dours' name in parentheses. *Andrena subglobosa* was treated by Warncke (1967b: 311) as a junior synonym of *Andrena (Ulandrena) fulvitaris* Brullé, 1833 based only on the description. As for *A. gravis* Dours, the type material was considered lost, but a male specimen was located in the Gribodo collection (MSNG). It was labelled as “*Campylogaster subglobosus* Typus Dours”, and coming from Corfu (Fig. 62). The male description is scanty, but Dours indicates that the clypeus is yellow-marked. Overall, the description of the female is quite generic and does not allow recognition at a specific level, and so the synonymy by Warncke, whilst speculative, is understandable.

Nevertheless, this discovered specimen is not *A. fulvitaris*, since the forewing shows the strongly postfurcal nervulus (Fig. 62D), and the genital capsule is of the *A. polita* Smith, 1847 type (Fig. 62F; shared with multiple species including *A. kriegbaumeri*). The specimen was examined by W. Grünwaldt and labelled as *A. kriegbaumeri*, but he either did not recognise its significance, or specifically did not recognise it as syntypic. Warncke (1967b: 311) gave the Cyclades as the *locus typicus*, but as Dours (1873: 288) only indicates “*Iles de l'Archipel grec.*”, Warncke's interpretation is not immediately justified. In Dours' immediately preceding work, Dours (1872: 293) writes that specimens used for the description of Greek species come “*surtout dans les îles de l'Archipel grec: Syra, Tinos, Micanos, Corfou, etc.*”. Following the reasoning of Wood and Bossert (2025),



**Figure 62.** *Andrena (Ulandrena) subglobosa* Dours, 1873 lectotype male (MSNG). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Left forewing, dorsal view; **E.** Metasoma, dorsal view; **F.** Genital capsule, dorsal view.

it is clear that Dours considered Corfu to be part of the Greek Archipelago, and since the specimen comes from Corfu and from the collection of Gribodo who was known to exchange specimens with Dours, this specimen is considered to be syntypic (as for taxa dealt with by Wood and Bossert 2025) and is hereby designated as the lectotype.

The purpose of the ICZN (1999) code is to promote nomenclatural stability. However, stability is not a universal criterion which overrides all other considerations. Although both *A. subglobosa* and *A. punctatissima* Kriechbaumer were described in

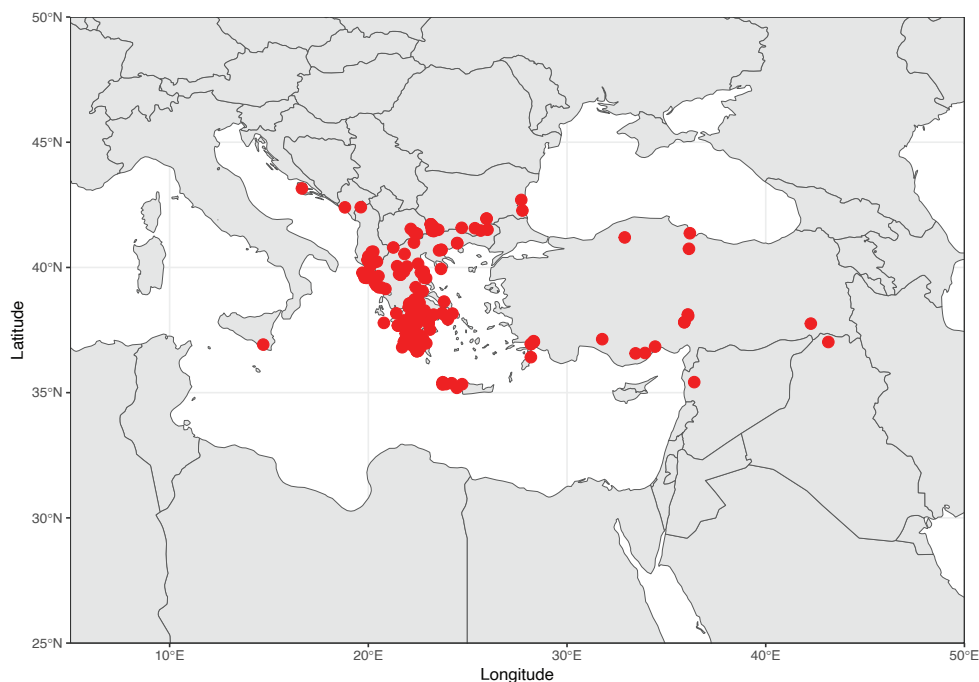


**Figure 63.** *Andrena (Ulandrena) punctatissima* Kriechbaumer, 1873 nec. Morawitz syntype female (ZSM). **A.** Label information; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Metasoma, dorsal view.

the same year, the replacement name *A. kriechbaumeri* is junior to *A. subglobosa* by 10 years. Under Article 23, it would be beneficial to apply for Reversal of Precedence (23.9) to maintain the use of *A. kriechbaumeri*. However, *A. kriechbaumeri* fails Condition 23.9.1.1 (the senior synonym or homonym has not been used as a valid name after 1899) because Paganetti-Hummler (1912: 380) and Cockerell (1922: 549) use *A. subglobosa* as a valid name. Additionally, it also fails Condition 23.9.1.2 (the junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years) because I could find only 15 validly published works between 1976–2025 which mention *A. kriechbaumeri* in the main body of their text.

Given the limited use of the name *A. kriechbaumeri* in the literature (in the past 50 years, as defined by the ICZN), the position is taken that referring this case to the ICZN Commission under Article 23.9.3 would be unlikely to be successful. *Andrena subglobosa* sp. resurrect. is therefore returned to species status, and *A. kriechbaumeri* syn. nov. is synonymised with it.

**Distribution.** Italy, Croatia, Bosnia & Herzegovina, Montenegro, Albania, North Macedonia, Bulgaria, Greece, Turkey, Syria, and Iraq (Fig. 64; Gusenleitner and Schwarz 2002; Wood et al. 2024b).

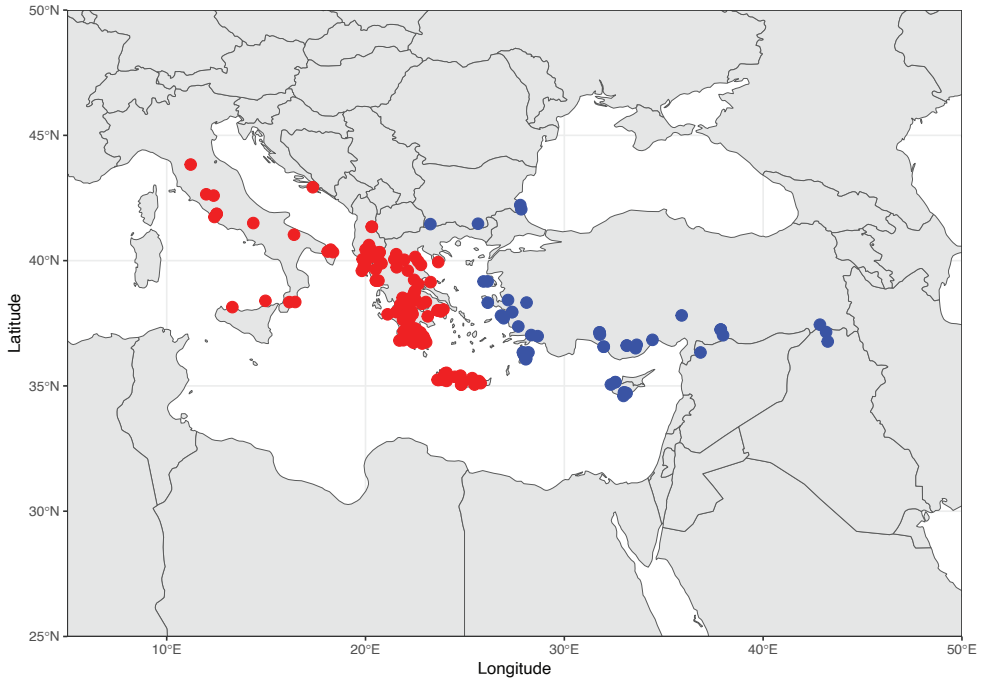


**Figure 64.** Global distribution of *Andrena (Ulandrena) subglobosa* Dours, 1873. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

***Andrena (Ulandrena) waschulzi* Strand, 1921 and *Andrena (Ulandrena) neocyprica* Mavromoustakis, 1956**

**Material examined (*Andrena neocyprica*).** **BULGARIA** • 3♀; Krumovgrad; 2 Jun. 1965; N. Atanassov leg.; NZMS • 1♂; Petrich env., steppes near Struma river; 100 m a.s.l.; 10 May 2018; D. Benda leg.; JSPC; **GREECE** • 1♂; Agh. Konstantinos (Samos); 3 May 1977; H. Teunissen leg.; RMNH • 1♀; Faliraki, Rhodes; 23 Apr. 1976; H. Teunissen leg.; RMNH • 2♂, 2♀; Karfas/Chios; 11–15 May 1985; W. Perraudin leg.; OÖLM • 1♀; Lesvos, Eressos; 12–16 May 1988; K.M. Guichard leg.; RMNH • 1♂; Parakila (Lesbos); 14–17 May 1980; H. Teunissen leg.; RMNH • 2♀; Rhodes, fields 1 km WSW of Archipoli; 210 m a.s.l.; 28 May 2025; TJWC • 1♂; Rhodes, Kamiros; 21 Apr. 1970; v. Oostroom leg.; RMNH • 1♀; Rhodes, Psinthos; 1 May 1976; H. Teunissen leg.; RMNH • 1♀; Rhodos, Mt. Profitis Ilias; 23 Apr. 1970; v. Oostroom leg.; RMNH • 1♀; Rodos, 5 km ZW v. Lindos; 29 Mar. 1970; A.C. & W.N. Ellis leg.; RMNH • 1♀; Rodos, Lindos; 6 Apr. 1970; A.C. & W.N. Ellis leg.; RMNH • 1♀; Samos, Kakkari [Kokkari], 1 km E; 7–19 Jun. 2019; J. Straka & A. Straková leg.; JSPC • 1♀; Samos, Pythagorio, Umg. Hotel Maritsa Bay; 18–31 May 2006; J. Tiefenthaler leg.; OÖLM.

**Notes.** *Andrena waschulzi* was described from Crete (previously known as *Andrena schulzi*, see Wood 2024a for discussion as to the correct spelling of his name), and *A. neocyprica* was described from Cyprus. Warncke (1967b: 230) described *Andrena schulzi* ssp. *alba* Warncke, 1967 from continental Greece, as the continental European



**Figure 65.** Global distributions of *Andrena (Ulandrena) waschulzi* Strand, 1921 (red circles) and *Andrena (Ulandrena) neocyprica* Mavromoustakis, 1956 (blue circles). Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

population shows slight differences from the Cretan population. Warncke (1974a: 89) indicated that *A. schulzi* was present on the island of Rhodes and probably the western coast of Turkey, and Hazir et al. (2012) reported *A. waschulzi* (as *A. schulzi*) from Çanakkale.

However, all examined material from the East Aegean Islands (Chios, Lesbos, Rhodes, and Samos) belongs to *A. neocyprica*, and *A. neocyprica* moves across western Turkey to southern Bulgaria, and it has not been possible to find any *A. waschulzi* from the eastern side of the Aegean sea (Fig. 65). Additional Bulgarian specimens were presented by Wood (2021). *Andrena waschulzi* is therefore considered to have its eastern range limit in continental Greece, and to display an allopatric distribution with *A. neocyprica*. See Suppl. material 2 for full details on all examined material.

## 2. Description of new species

### *Andrena (Cryptandrena) testudo* sp. nov.

<https://zoobank.org/AFA76162-019E-470C-AD34-EBD5228E3395>

Figs 66A–C, E, G, 67A–E

**Type material. Holotype. GREECE** • 1♀; Crete, Plateau Katharo [W of Katharon]; 35.1473°N, 25.5598°E; 1160 m a.s.l.; 1 Jun. 2023; R. Le Divelec leg.; RMNH, RMNH.INS.1716253; [BOLD accession number [ORB190-23](https://doi.org/10.31212/ORB190-23)].

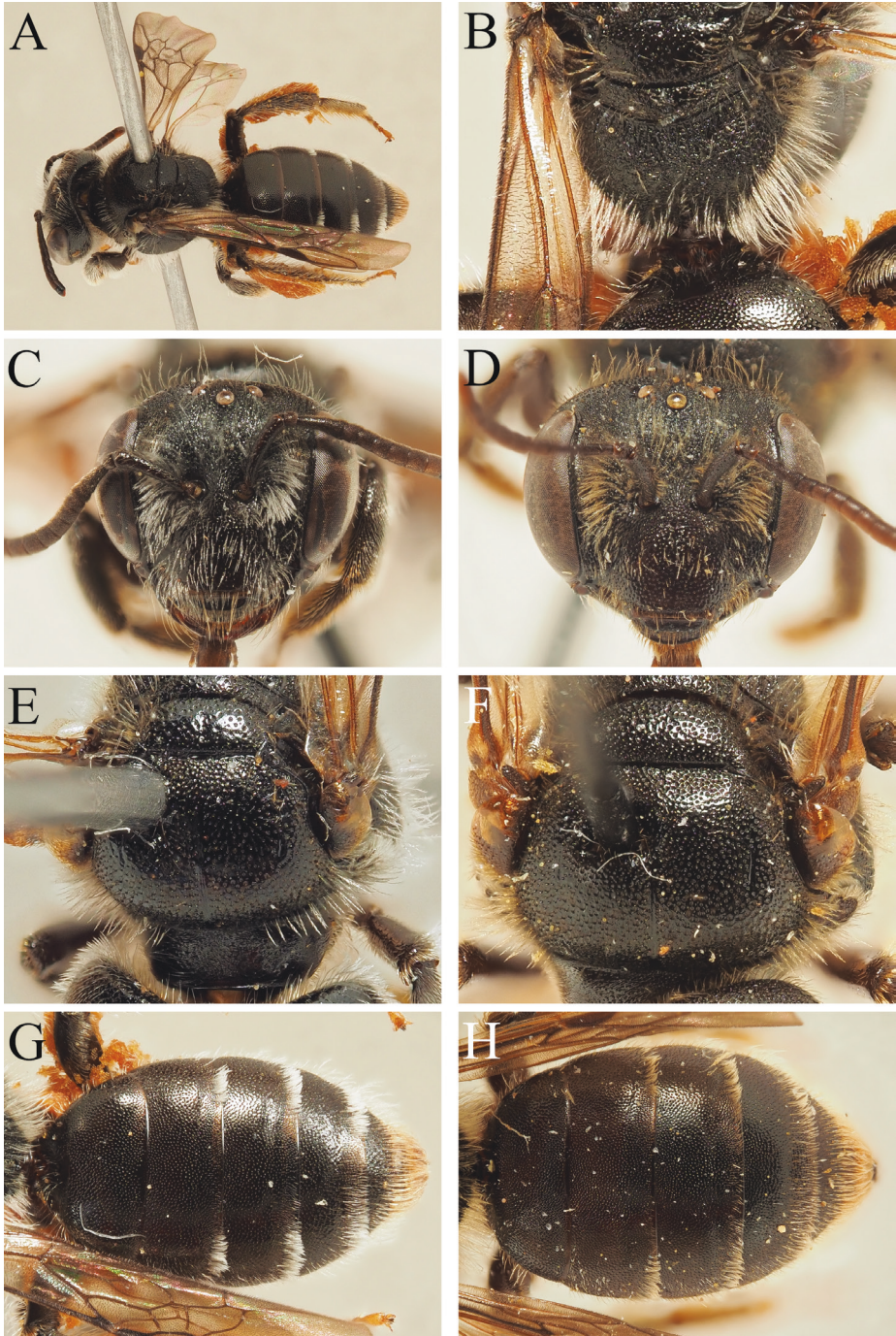
**Paratypes. GREECE** • 1♂; Crete, Plateau Katharo [W of Katharon]; 35.1473°N, 25.5598°E; 1160 m a.s.l.; 1 Jun. 2023; R. Le Divelec leg.; RMNH, RMNH.INS.1716254 • 1♀; Crete, Plateau Katharo [W of Katharon]; 35.1473°N, 25.5598°E; 1160 m a.s.l.; 1 Jun. 2023; R. Le Divelec leg.; TJWC • 2♂; Crete, Dept. Chania, Mescla [Meskla]; 3 May 1973; v. Ooststroom leg.; RMNH, RMNH.INS.1264915 • 1♂, 1♀; Crete, Lasithi, 15 km NW Males; 850 m a.s.l.; 14 May 2003; O. Sauša leg.; OÖLM • 1♂; Crete, SE, Kato Simi; 1000 m a.s.l.; 6 May 2003; O. Sauša leg.; OÖLM • 1♂; Kreta sept., Bali; 6–11 May 2003; B. & O. Tkalcù leg.; OÖLM • 1♀; Kreta, Chania, Lefka Ori, 5 km SW Omalos; 1200–1250 m a.s.l.; 4 Jun. 1993; H. & R. Rausch leg.; OÖLM • 1♂; Kreta, Rethimnon [Rethimno]; 19–30 Apr. 1998; H. Wolf leg.; OÖLM.

**Description. Female.** Body length: 6–6.5 mm (Fig. 66A). **Head:** Dark, 1.2 times wider than long (Fig. 66C). Clypeus domed, medially slightly flattened, surface polished and shining, densely punctate, punctures separated by 0.5–1 puncture diameters. Process of labrum rounded rectangular, 3 times broader than long, surface polished. Gena slightly exceeding width of compound eye; ocellocipital distance subequal to diameter of lateral ocellus. Foveae dorsally occupying slightly >1/2 space between compound eye and lateral ocellus, poorly defined, ventrally slightly narrowing, still exceeding diameter of scape; facial foveae filled with pure white hairs. Head covered with short whitish hairs, none equalling length of scape. Antennae dark, A5–12 ventrally lightened by presence of orange-brown scales; A3 equalling A4+5.

**Mesosoma:** Scutum and scutellum polished and shining, slightly irregularly punctate, puncture separated by 0.5–1.5 puncture diameters, scutum posteromedially with punctures separated by almost 2 puncture diameters (Fig. 66E). Pronotum rounded. Mesepisternum and dorsolateral parts of propodeum irregularly roughened with network of rugosity, surface weakly shining. Propodeal triangle laterally weakly indicated by presence of carina, internal surface covered with raised longitudinal ridges with short lateral carinae (Fig. 66B). Mesepisternum with finely plumose whitish hairs, becoming shorter and light brown on scutum and scutellum. Propodeal corbicula lacking anterior fringe, dorsal fringe composed of shortly plumose buffish hairs, internal surface with long buffish simple hairs. Legs dark, pubescence light brown, hind tarsal claws with inner subapical tooth. Posterior face of hind femur with row of posteriorly-projecting 6 short tooth-like pegs. Flocculus complete, composed of white plumose hairs; femoral and tibial scopae composed of white predominantly simple hairs, tibial scopae at most with some lateral hairs plumose. Wings hyaline, stigma and venation dark brown, nervulus interstitial.

**Metasoma:** Terga dark, apical rims narrowly lightened hyaline brown (Fig. 66G). Tergal discs polished and shining, densely punctate, punctures separated by 0.5–1 puncture diameters; punctures extending onto tergal margins. Tergal discs with very short and obscure scattered hairs, T2–4 laterally with dense white apical hairbands, interrupted medially, obscuring underlying surface. T5 and hairs flanking pygidial plate orange to orange-brown; pygidial plate rounded triangular, surface dull.

**Male.** Body length: 5–6 mm (Fig. 67A). **Head:** Dark, 1.4 times wider than long (Fig. 67B). Clypeus dark, structurally as in female. Process of labrum rounded trape-



**Figure 66.** *Andrena (Cryptandrena) testudo* sp. nov. female holotype (RMNH). **A.** Habitus, lateral view; **B.** Propodeum, dorsal view; **C.** Head, frontal view; **E.** Scutum, dorsal view; **G.** Metasoma, dorsal view. *Andrena (Cryptandrena) brumanensis* Friese, 1899 female. **D.** Head, frontal view; **F.** Scutum, dorsal view; **H.** Metasoma, dorsal view.

zoidal, 2 times wider than long. Gena equalling width of compound eye; ocelloccipital distance slightly shorter than diameter of lateral ocellus. Head covered with moderately long whitish hairs, none equalling length of scape. Antennae dark, A4–13 ventrally lightened by presence of brownish scales; A3 exceeding length of A4, slightly shorter than A4+5 (Fig. 67E).

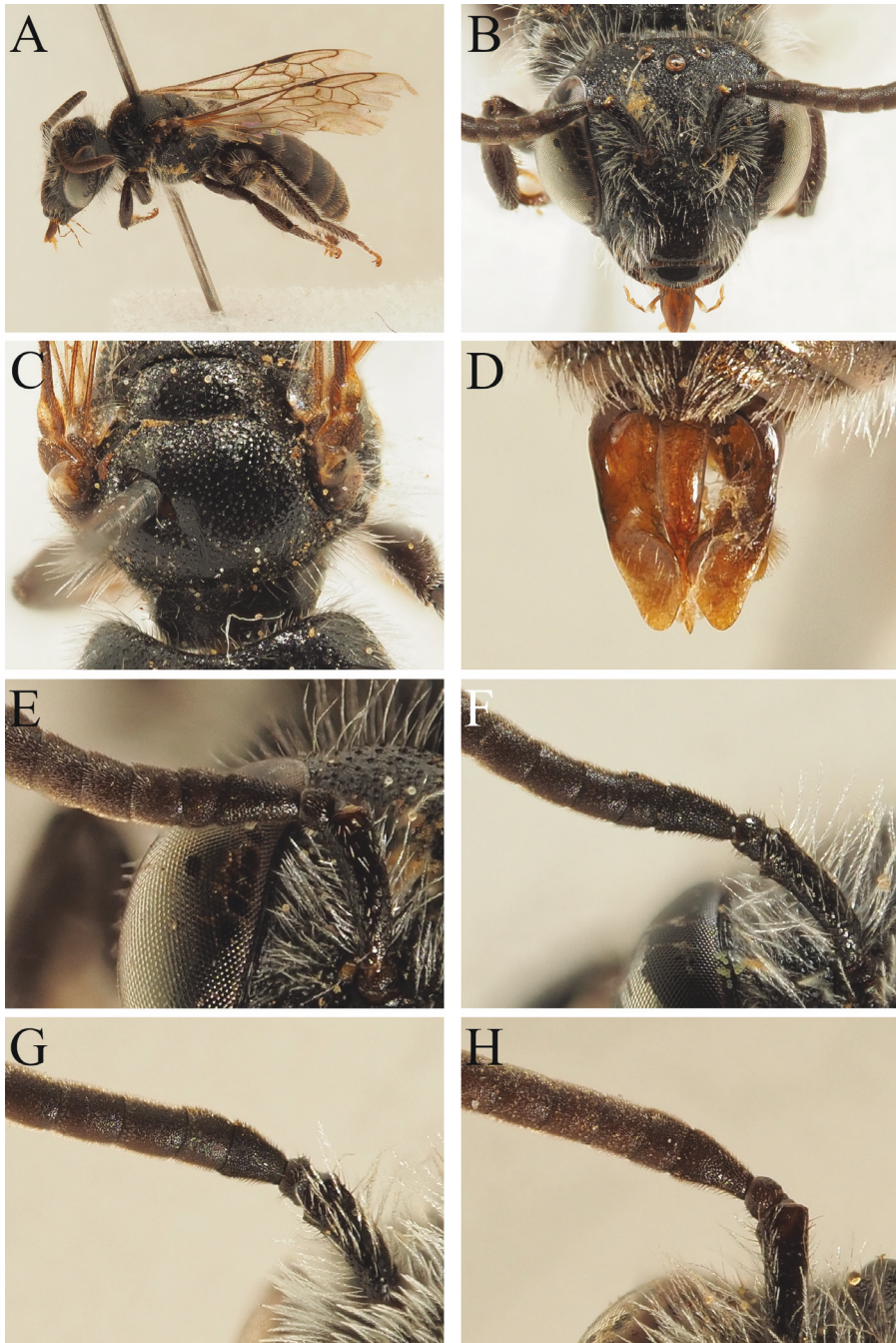
**Mesosoma:** Scutum and scutellum polished and shining, moderately densely punctate, punctures separated by 1–2 puncture diameters (Fig. 67C). Pronotum rounded. Mesepisternum and propodeum as in female. Mesosoma covered in long white hairs. Legs dark, apical tarsal segments lightened orange-brown, pubescence whitish to light brownish, hind tarsal claws with small subapical tooth. Wings hyaline, stigma and venation brown, nervulus interstitial.

**Metasoma:** Terga dark, apical margins lightened brown to hyaline brown. Tergal discs finely microreticulate, weakly shining, moderately punctate, punctures separated by 1–2 puncture diameters, extending onto marginal areas. Tergal discs covered with short whitish hairs, not forming distinct apical hairbands. S8 narrow, apex rounded, ventral surface covered with short fringe of light brown hairs. Genital capsule slightly elongate, more-or-less parallel sided, gonocoxal teeth very slightly produced into narrowly rounded points (Fig. 67D). Gonostyli broadly flattened-triangular apically, surface slightly concave, internal angle raised and rounded. Penis valves long, occupying 1/3 space between gonostyli, gradually tapering, acutely pointed apically.

**Diagnosis.** *Andrena testudo* can swiftly be recognised as a *Cryptandrena* due to the presence of a row of short tooth-like spines on the posterior face of the hind femur (females only) combined with the small body size (<7 mm), short and broad process of the labrum (around 3 times broader than long), simple scopal hairs (not plumose), and densely punctate metasomal terga (Fig. 66G; punctures separated by <1 puncture diameter), as well as by the typical male genital capsule which is relatively long and narrow, with the apices of the gonostyli flattened and weakly triangular with the inner angle upturned, and with long narrow penis valves (Fig. 67D).

After excluding *Andrena monacha* Warncke, 1965 and *Andrena aruana* Warncke, 1969 which lack spines on the posterior face of the female hind femur and belong in an undescribed subgenus (Pisanty et al. 2022a; S. Bossert, G. Pisanty, T.J. Wood, unpublished data), only three other species are found in this subgenus: *A. brumanensis*, *A. rotundata*, and *A. ventricosa*. The intriguing geographic distributions are discussed in the section on Subgenus *Cryptandrena* Pittioni, 1948 (Fig. 5). *Andrena testudo* can be separated from the most widespread member of the group *A. ventricosa* due to the male A3 which is much longer than A4, and almost as long as A4+5 (Fig. 67E; in *A. ventricosa* with the male A3 essentially equal to the length of A4, Fig. 67G) and the female scutum which is relatively sparsely punctate, with punctures separated by 0.5–1.5 puncture diameters (Fig. 66E; in *A. ventricosa* with the female scutal punctures separated by around 0.5 puncture diameters, therefore almost confluent).

The difference from *A. brumanensis* is subtle, but in side-by-side comparison, the differences can be clearly seen. In both sexes, the clypeus is distinctly longitudinally domed in its median half (Fig. 66C; in *A. brumanensis* with the clypeus almost



**Figure 67.** *Andrena* (*Cryptandrena*) *testudo* sp. nov. male paratype (RMNH). **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Scutum, dorsal view; **D.** Genital capsule, dorsal view; **E.** Basal antennal segments, frontal view. *Andrena* (*Cryptandrena*) *brumanensis* Friese, 1899 male. **F.** Basal antennal segments, frontal view. *Andrena* (*Cryptandrena*) *ventricosa* Dours, 1873 male. **G.** Basal antennal segments, frontal view. *Andrena* (*Cryptandrena*) *rotundata* Pérez, 1895 male. **H.** Basal antennal segments, frontal view.

flattened, Fig. 66D), the male clypeus is entirely dark (in *A. brumanensis* males with the clypeus showing a yellow median marking of variable size), the female scutum has relatively spaced punctures separated by 0.5–1.5 puncture diameters and approaching 2 puncture diameters posteromedially (Fig. 66E; in *A. brumanensis* with the scutum showing punctures separated by 0.5–1 puncture diameters at most, Fig. 66F), the male scutum has punctures separated by 1–2 puncture diameters and with the interspaces shining (Fig. 67C; male *A. brumanensis* have the scutum with punctures separated by <1 puncture diameters, scutum appearing relatively dull), and in the female with the tergal punctation separated by 0.5–1 puncture diameters, interspaces shining, metasoma therefore appearing relatively shiny (Fig. 66G; in *A. brumanensis* females with the metasomal punctation denser, separated by <0.5–0.5 puncture diameters, overall metasoma therefore appearing more dull, Fig. 66H). *Andrena brumanensis* is also a slightly but distinctly larger bee, with females around 8 mm in length and in side by side comparison appearing broader.

These same differences allow for separation from *A. rotundata*, which have the clypeus as flattened as in *A. brumanensis*, the male A3 is only slightly longer than A4 (Fig. 67H; not almost as long as A4+5 in *A. testudo*, Fig. 67E), and the female scutum with punctures separated by at most 1 puncture diameter.

**Etymology.** From the Latin *testudo* meaning tortoise in reference to the (relatively) domed clypeus, and also the dense integumental punctation typical of *Cryptandrena* species which poetically resembles a tight-knit defensive formation, like the *testudo* formation used by Roman soldiers in the capture of (amongst other cities) Heracleium in Macedon in Ancient Greece in 169 B.C. (described by Livy and Polybius). It is a noun in apposition.

**Distribution.** Greece (Crete) (Fig. 5).

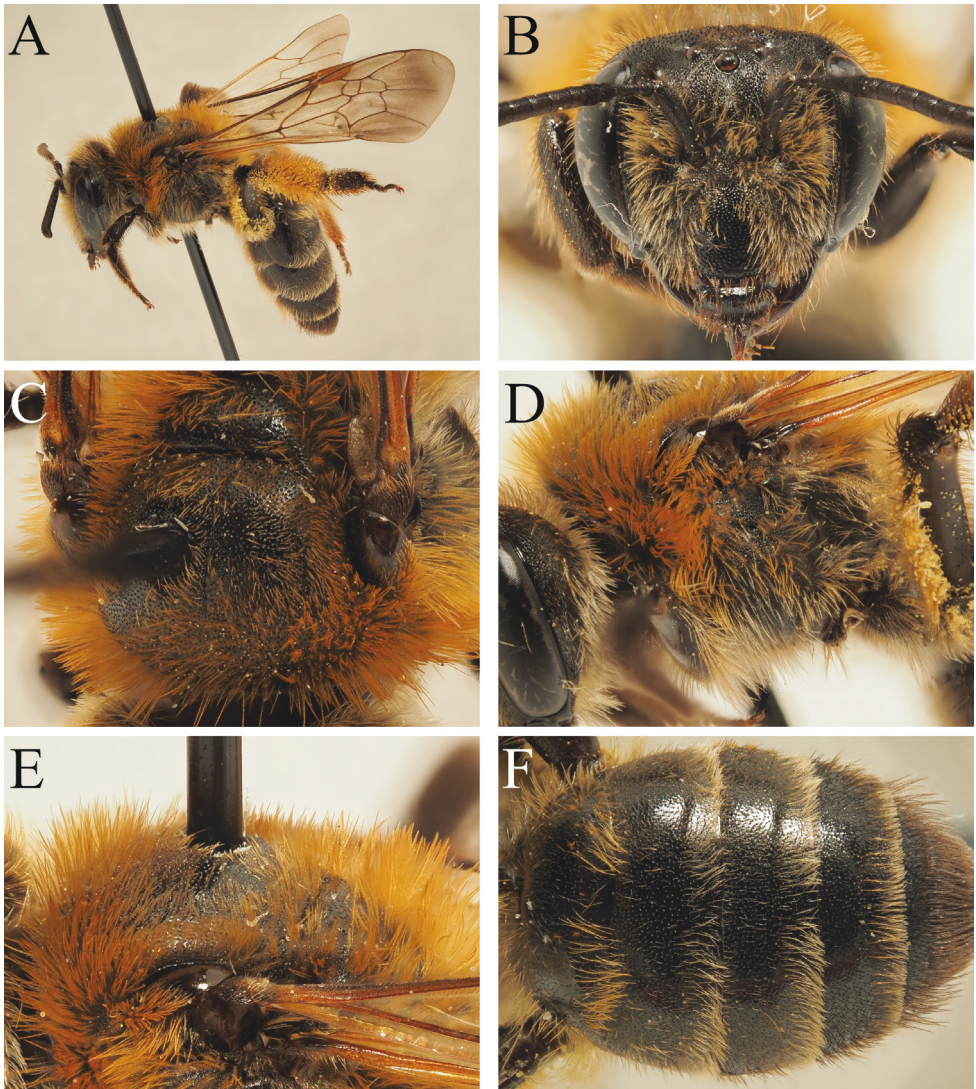
***Andrena (Euandrena) bulgarica* sp. nov.**

<https://zoobank.org/AF53F5A5-F0FA-4910-8090-29121617BC5A>

Fig. 68

**Type material. Holotype.** BULGARIA • 1♀; Blagoevgrad, General Todorov, 2 km E; 41.4563°N, 23.3106°E; 120 m a.s.l.; 19 May 2024; T.J. Wood leg.; RMNH, RMNH.INS.1152454 [BOLD accession number [NATBE081-25](#)].

**Paratypes.** BULGARIA • 1♀; Blagoevgrad, Sandanski, 3.5 km W, Struma river; 110 m a.s.l.; 23 May 2024; T.J. Wood leg.; RMNH, RMNH.INS.1152503 [BOLD accession number [NATBE112-25](#)] • 1♀; Petrich env., steppes near Struma river; 100 m a.s.l.; 10 May 2018; D. Benda leg.; NMPC [BOLD accession number [WPATW994-23](#)] • 3♀; Slančev Brjag [Sunny Beach]; 10 Jun. 1972; M. Kocourek leg.; OÖLM • 1♀; Slančev Brjag [Sunny Beach]; 1–30 Jun. 1972; M. Kocourek leg.; OÖLM; GREECE • 1♀; Western Macedonia, Filotas, 3 km N of Antigonos; 600–700 m a.s.l.; 11 Jun. 2024; T.J. Wood leg.; RMNH, RMNH.INS.1152611 [BOLD accession number [NATBE173-25](#)].



**Figure 68.** *Andrena (Euandrena) bulgarica* sp. nov. female holotype (RMNH). **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Scutum, dorsal view; **D.** Mesepisternum, lateral view; **E.** Mesosomal dorsum, lateral view; **D.** Metasoma, dorsal view.

**Description. Female.** Body length: 10–11 mm (Fig. 68A). **Head:** Dark, 1.2 times wider than long (Fig. 68B). Clypeus weakly domed, medially somewhat flattened, surface polished and shining; densely punctate, punctures separated by  $<0.5$ –1 puncture diameters, punctures denser laterally, becoming slightly sparser apically. Process of labrum weakly trapezoidal, 2.5 times wider than long, apical margin broadly and shallowly emarginate. Gena slightly exceeding width of compound eye; ocellocipital distance 1.5 times diameter of lateral ocellus. Foveae dorsally occupying  $1/3$  space between compound eye

and lateral ocellus, narrowing ventrally to just below lower margin of antennal insertions; facial foveae filled with dark brown hairs. Head covered with brown hairs, light brown on face and lower part of gena, becoming golden brown on vertex; occasional black hairs on upper frons laterally; no hairs equalling length of scape. Antennae dark, A5–12 ventrally slightly lightened by presence of greyish scales; A3 equalling A4+5.

**Mesosoma:** Scutum anteriorly and laterally shagreened, weakly shining, becoming polished and shining in posteromedial 1/2 (Fig. 68C); surface densely punctate, punctures separated by 0.5–1 puncture diameters over majority of surface, becoming slightly sparser medially. Scutellum dull posteriorly and laterally, medially broadly shining, irregularly punctate, punctures separated by 0.5–2 puncture diameters. Pronotum rounded. Mesepisternum and dorsolateral parts of propodeum finely microreticulate, covered with shallow irregular punctures, separated by 0.5–2 puncture diameters on mesepisternum, density increasing to 0.5–1 puncture diameters on propodeum; surface dull. Propodeal triangle laterally not delineated by carinae, internal surface impunctate, covered with fine granular shagreen, basomedially with network of fine wrinkles. Mesepisternum with brown hairs, pale whitish brown ventrally, becoming golden brown dorsally (Fig. 68D); hairs on scutum and scutellum shorter, densely plumose but not subsquamous, golden brown (Fig. 68E). Propodeal corbicula lacking anterior fringe, dorsal fringe composed of long golden brown plumose hairs, internal surface with long partially-plumose golden hairs. Legs dark, pubescence dark brown, hind tarsal claws with inner subapical tooth. Flocculus complete, composed of buff plumose hairs; femoral and tibial scopae composed of simple orange hairs. Wings hyaline, stigma and venation dark orange-brown, nervulus interstitial to weakly antefurcal.

**Metasoma:** Terga dark, apical rims narrowly lightened hyaline brown (Fig. 68F). Tergal discs predominantly polished and shining, with obscure weak sculpturing most visible at base of discs. Tergal discs irregularly punctate, punctures separated by 0.5–2 puncture diameters, extending onto tergal margins, becoming slightly sparser and less distinct. Tergal discs with short hairs, pale on T1–3, black on T4–5, not obscuring underlying surface. Marginal area of T1 with loose light brown hairs, marginal areas of T2–4 with apical hairbands of pale hairs, complete in fresh specimens, obscuring underlying surface. T5 and hairs flanking pygidial plate dark brown; pygidial plate rounded triangular, surface dull and featureless.

**Male.** Unknown.

**Diagnosis.** *Andrena bulgarica* can be recognised as a *Euandrena* due to the moderate body size, facial foveae which dorsally occupy 1/3 of the space between the compound eye and a lateral ocellus and which further narrow ventrally (comma or drop-shaped), A3 = A4+5, and lack of any other distinctive characters (simple tibial scopae, simple propodeal triangle, posterior face of hind femur rounded, hind tibial spurs unmodified). Recognition is challenging, and requires experience within the group; use of the identification key is recommended to learn the major divisions within the subgenus in the southern Balkans.

Due to the pubescence which is brown to golden brown on the mesosomal dorsum (Fig. 68D) and the tibial scopae which are orange (Fig. 68A), it can be placed in

the group of species around *A. bicolor*. The clypeus is uniformly punctate and lacks a weak median longitudinal impunctate line medially and the pronotum is rounded, excluding *A. glidia*. The most similar species are consequently *A. aff limosa* and *A. bicolor*. *Andrena bulgarica* can be separated due to the facial pubescence which is almost entirely light brown with at most a few black hairs along the inner margins of the compound eyes (Fig. 68B; variable, either extensively black-haired in *A. bicolor* or partially black-haired in *A. aff limosa*, but in all cases with clear black hairs on the clypeus), clypeus densely punctate but with the underlying surface and hence interspaces strongly polished and shining (Fig. 68B; in *A. bicolor* and *A. aff limosa* with the clypeus densely punctate with interspaced shagreened and shagreened and weakly shining to dull), mesepisternum with pubescence light brown to golden brown, without black hairs (Fig. 68D; highly variable, but usually in *A. bicolor* with black hairs on the mesepisternum, in *A. aff limosa* usually with the mesepisternum with entirely brown hairs), and scutum widely polished and shining over most of its posterior half (Fig. 68C; in *A. aff limosa* with the scutum also extensively polished medially, in *A. bicolor* the condition is quite variable, sometimes with small shining area medially, sometimes almost entirely dull; this character is variable between Levantine populations which always have the scutum dull to European populations which are most extensively polished). A final character is body size, with *A. bulgarica* reasonably large for a *Euandrena* at 10–11 mm in length, whereas *A. bicolor* and *A. aff limosa* tend to average a little smaller at 8–10 mm on average. This character can only be appreciated with series assembled together, at which point it becomes easier to observe. Through this combination of characters, it is possible to diagnose *A. bulgarica*, but consultation of barcoded or reliably determined specimens is preferable until the concept has been appreciated.

**Notes.** All records to date come from low to moderate altitude sites (100–700 m a.s.l.); based on current evidence, *A. bulgarica* does not seem to be a species of mountains.

**Etymology.** Named after the country of Bulgaria, which currently lacks an eponymous species given the synonymy of *Andrena bulgariensis* Warncke, 1965 with *Andrena inconstans* Morawitz, 1877 (Wood 2023a). It is an adjective in the feminine singular nominative form.

**Distribution.** Bulgaria (Blagoevgrad, Burgas) and Greece (Western Macedonia).

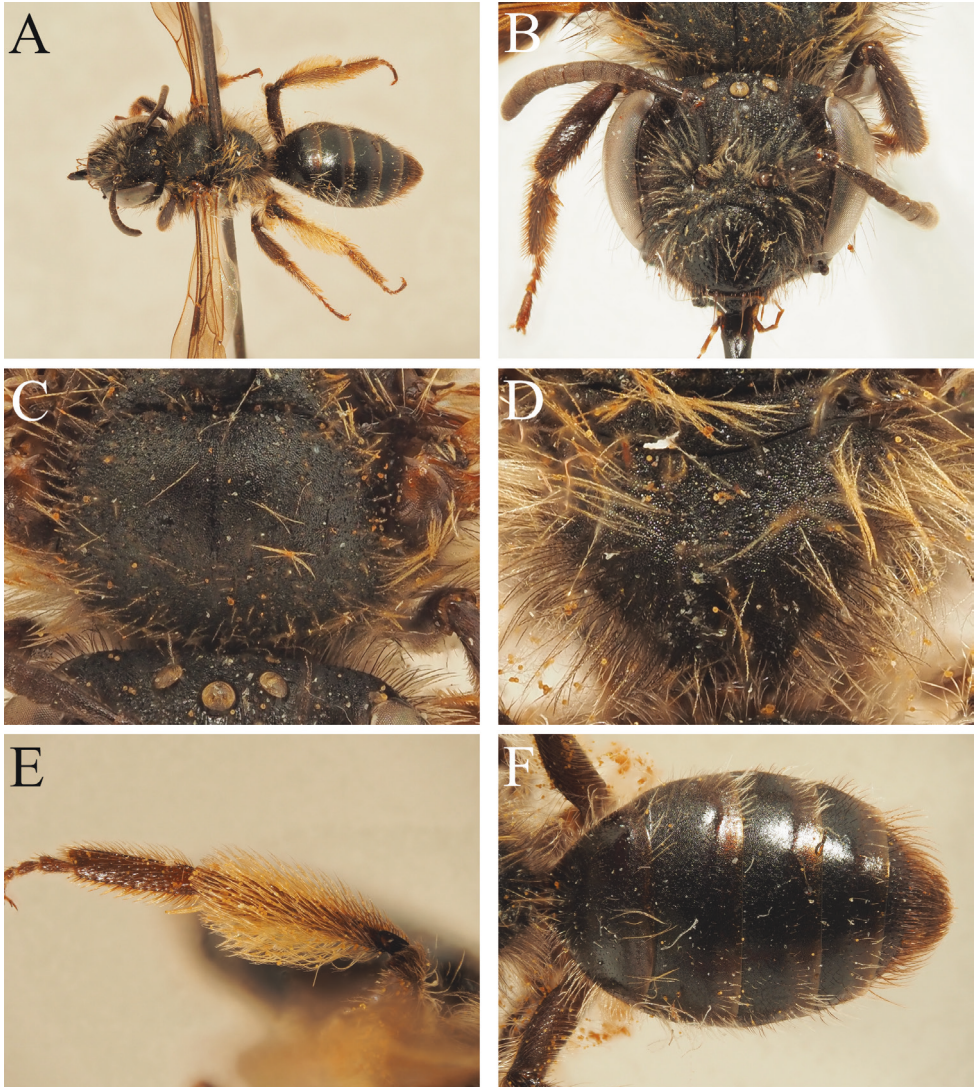
***Andrena (Euandrena) obscuricrus* sp. nov.**

<https://zoobank.org/E04DD384-7E15-4FF1-A12B-6C022E55F1CA>

Fig. 69

**Type material. Holotype.** GREECE • 1♀; Creta, Lassithi Ebene [Plateau]; 24 Apr. 1973; H. Teunissen leg.; RMNH, RMNH.INS.1716258.

**Paratypes.** GREECE • 3♀; Lasithi Vlake [Plateau]; 17 Apr. 1982; H. Teunissen leg.; RMNH, RMNH.INS.1716259 • 1♀; Creta, Omalos; 2 Jun. 1987; Kudrna leg.; ÖÖLM • 1♀; W. Kreta, Rhodhákion [Ano Rodakino] nahe S. Küste; 20 Mar. 1925;



**Figure 69.** *Andrena (Euandrena) obscuricus* sp. nov. female holotype (RMNH). **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Scutum, dorsal view; **D.** Propodeum, dorsal view; **E.** Hind leg, lateral view; **F.** Metasoma, dorsal view.

A. Schulz leg.; OÖLM • 1 ♀; Kreta, Mesa Potami; 28 Apr. 2004; R. & W. Zarre leg.; OÖLM • 1 ♀; Kreta, Spili; 4 Jun. 1980; M. Kraus leg.; OÖLM.

**Description. Female.** Body length: 8.5–10 mm (Fig. 69A). **Head:** Dark, 1.2 times wider than long (Fig. 69B). Clypeus weakly domed, surface covered with fine granular microreticulation, basally dull, becoming weakly shining apically; surface with large and distinctly separated punctures separated by 0.5–3 puncture diameters, typically by 1–2 puncture diameters. Process of labrum rounded trapezoidal, 2 times wider

than long, apical margin straight. Gena slightly exceeding width of compound eye; ocellocipital distance slightly exceeding diameter of lateral ocellus. Foveae dorsally occupying 1/3 space between compound eye and lateral ocellus, narrowing ventrally to just below lower margin of antennal insertions; facial foveae filled with brown hairs. Face with whitish hairs on clypeus and around antennal insertions, with black hairs along inner margins of compound eyes and frons. Gena ventrally with whitish hairs, becoming weakly golden on vertex; no hairs equalling length of scape. Antennae dark, A5–12 ventrally slightly lightened by presence of greyish scales; A3 slightly exceeding A4+5, shorter than A4+5+6.

**Mesosoma:** Scutum and scutellum finely microreticulate, dull, surface with irregular scattered shallow punctures separated by 0.5–3 puncture diameters (Fig. 69C). Pronotum rounded. Mesepisternum with fine granular microreticulation, dull. Dorsolateral parts of propodeum with fine granular microreticulation, microreticulation slightly raised, forming network of weak pseudopunctures, surface dull. Propodeal triangle narrow, weakly indicated, internal surface with dense fine granular microreticulation, with raised rugae in basal 1/3–1/2 (Fig. 69D). Mesepisternum with intermixed light brown and black hairs, scutum and scutellum with shorter light brown hairs intermixed with shorter dark hairs. Propodeal corbicula lacking anterior fringe, dorsal fringe composed of mixture of light brown and black plumose hairs, internal surface with weakly plumose light brown hairs. Legs dark, apical tarsal segments brownish, pubescence brown, hind tarsal claws with inner subapical tooth. Flocculus complete, composed of pale plumose hairs; femoral and tibial scopae composed of pale golden to orange hairs. Tibial scopae composed of mixture of simple and obscurely plumose hairs (Fig. 69E). Wings hyaline, stigma and venation dark orange-brown, nervulus interstitial.

**Metasoma:** Terga dark, marginal areas obscurely lightened brownish, apical rims narrowly lightened hyaline-whitish (Fig. 69F). Tergal discs with fine granular microreticulation, weakly shining; surface obscurely punctate, with small scattered very fine punctures, appearing broadly impunctate. Tergal discs with scattered short hairs, marginal areas of T2–4 with weak apical hairbands laterally, widely interrupted, not obscuring underlying surface. T5 and hairs flanking pygidial plate dark brown; pygidial plate rounded triangular, lateral margins impunctate, remaining surface densely punctate, punctures almost confluent; surface dull.

**Male.** Unknown.

**Diagnosis.** *Andrena obscuricrus* can be recognised as a *Euandrena* due to the moderate body size, facial foveae which dorsally occupy 1/3 of the space between the compound eye and a lateral ocellus and which further narrow ventrally (comma or drop-shaped), A3 slightly exceeding A4+5, and lack of any other distinctive characters (simple propodeal triangle, posterior face of hind femur rounded, hind tibial spurs unmodified). It should be noted that, unusually for a West Palaearctic *Euandrena*, the tibial scopae of *A. obscuricrus* is composed of partially plumose hairs (Fig. 69E). It is difficult to neatly categorise this as either simple or plumose.

Warncke (1965a: 50) listed *Andrena (Euandrena) ruficrus* Nylander, 1848 from “Westkreta” based on a specimen collected by Schulz on 20 Mar. 1925. It has been

possible to examine a specimen with this collecting information, which now forms part of the type series. The two are genuinely morphologically similar due to the largely impunctate terga, dull and shallowly punctate scutum, and predominantly pale facial vestiture with the exception of black hairs along the inner margins of the compound eyes. However, apart from the strong geographic separation (the nearest confirmed records of *A. ruficrus* come from around Croatia and Hungary, with two additional specimens from Mount Olympus in Greece; Gusenleitner and Schwarz 2002, see below), *A. obscuricrus* can be separated due to its clypeus which has large and distinctly separated punctures which are separated by 0.5–3 puncture diameters but typically by 1–2 puncture diameters (Fig. 69B; in *A. ruficrus* with the clypeus covered in small regular punctures separated by 0.5–1 puncture diameters), the dark legs (Fig. 69E; hind tibiae and tarsi lightened orange in *A. ruficrus*), and the partially plumose tibial scopae (tibial scopae with simple hairs in *A. ruficrus*).

*Andrena obscuricrus* is more likely to be confused with *A. glidia* which occurs on Crete (Fig. 15). However, *A. obscuricrus* can be rapidly recognised due to the rounded pronotum (*A. glidia* with the pronotum laterally displaying a subtle but distinct humeral angle), entirely dull scutum (Fig. 69C; *A. glidia* with the scutum extensively polished and shining, at least medially), sparsely punctate clypeus (*A. glidia* with the clypeus covered with dense punctures separated by 0.5–1 puncture diameters), pale facial vestiture with black hairs along the inner margins of the compound eyes (*A. glidia* with uniformly light brown facial vestiture), and tergal discs almost impunctate (Fig. 69F; tergal discs of *A. glidia* with weak but distinct punctures separated by around 1–2 puncture diameters, most visible laterally).

**Etymology.** Since *ruficrus* (*rufus* + *crus*) means red-legged in Latin, and the Cretan specimens have dark legs, they are named *obscuricrus* from *obscurus* + *crus*. It is a compound noun.

**Distribution.** Greece (Crete) (Warncke 1965a, as *A. ruficrus* misidentification).

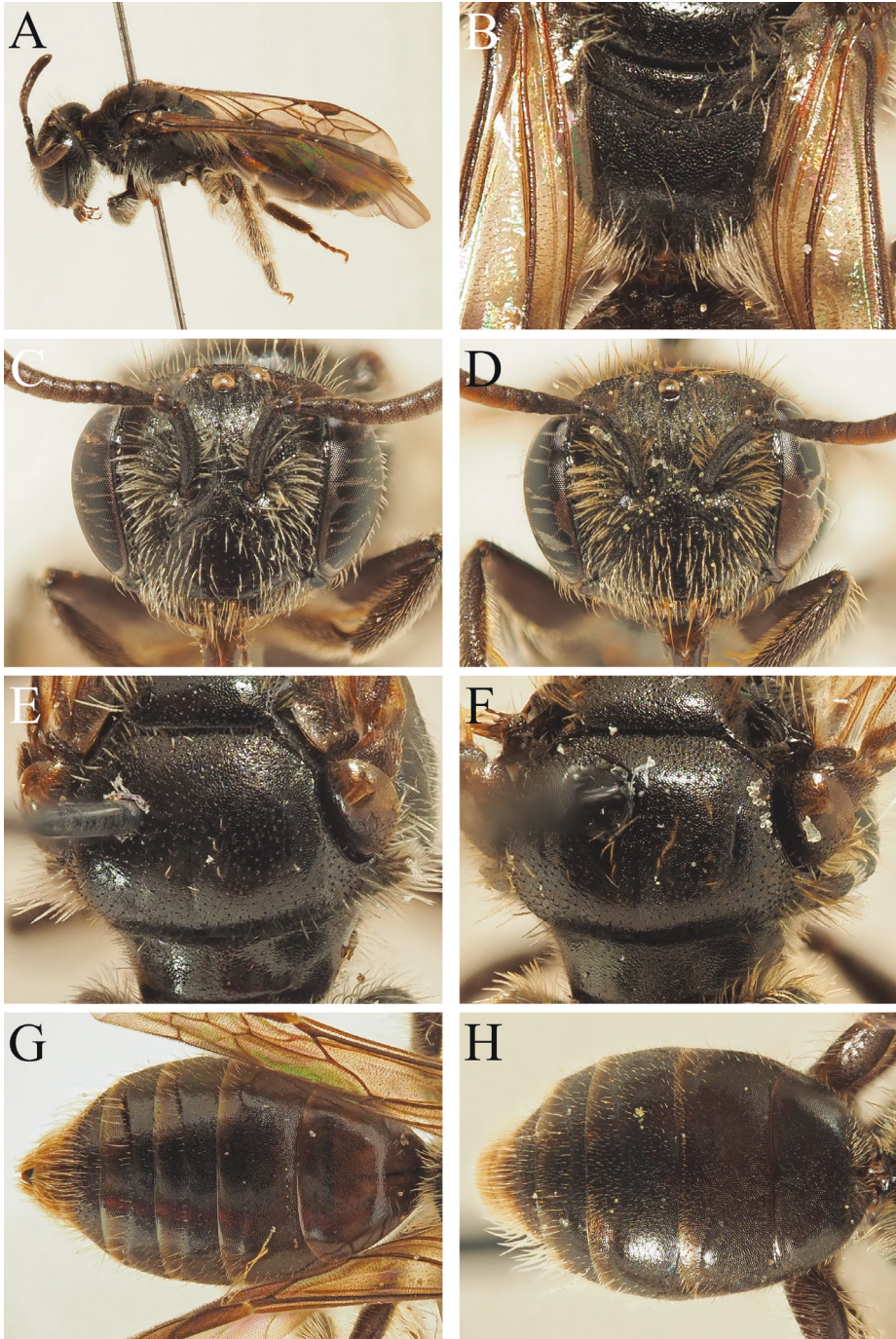
***Andrena (Graecandrena) cretica* sp. nov.**

<https://zoobank.org/0F9AD6E9-E976-408F-9755-6511F13FCB52>

Fig. 70A–C, E, F

**Type material. Holotype.** GREECE • 1♀; Crete, Plateau Katharo [W of Katharon]; 35.1473°N, 25.5598°E; 1160 m a.s.l.; 1 Jun. 2023; R. Le Divelec leg.; RMNH, RMNH.INS.1716255; [BOLD accession number [ORBIT180-23](#)].

**Paratypes.** GREECE • 1♀; Crete, Plateau Katharo [W of Katharon]; 1160 m a.s.l.; 1 Jun. 2023; R. Le Divelec leg.; RMNH, RMNH.INS.1716256 • 5♀; Crete, Foinikilas [E of Agios Ioannis]; 450 m a.s.l.; 6 Jun. 2023; R. Le Divelec leg.; RLDC • 1♀; Crete, Mousoures [W of Prases]; 500 m a.s.l.; 9 Jun. 2023; R. Le Divelec leg.; RLDC • 1♀; Crete, Dept. Chania, Mescla [Meskla]; 3 May 1973; v. Ooststroom leg.; RMNH, RMNH.INS.1264834 • 1♀; Kriti, Spilia – Drakona, 25 km W of Chania; 18 May 1982; J.P. Duffels leg.; RMNH; ZMA.INS.5103925.



**Figure 70.** *Andrena (Graecandrena) cretica* sp. nov. female holotype (RMNH). **A.** Habitus, lateral view; **B.** Propodeum, dorsal view; **C.** Head, frontal view; **E.** Scutum, dorsal view; **G.** Metasoma, dorsal view. *Andrena (Graecandrena) hyemala* Warncke, 1973 female. **D.** Head, frontal view; **F.** Scutum, dorsal view; **H.** Metasoma, dorsal view.

**Description. Female.** Body length: 5 mm (Fig. 70A). **Head:** Dark, 1.25 times wider than long (Fig. 70C). Clypeus weakly domed, finely shagreened and weakly shining, moderately punctate, punctures separated by 1–3 puncture diameters. Process of labrum small, narrowly trapezoidal, slightly wider than long. Gena slightly exceeding width of compound eye; ocellocipital distance slightly  $<1/2$  diameter of lateral ocellus. Foveae occupying  $1/3$  space between compound eye and lateral ocellus, equalling width of flagellum, moderately impressed, ventrally extending below lower level of antennal insertions; foveae filled with light brown hairs. Head covered with pale to light brown hairs, none equalling length of scape. Antennae dark, A5–12 ventrally lightened by presence of greyish scales; A3 equalling A4+5.

**Mesosoma:** Scutum and scutellum very weakly sculptured, almost polished and shining, weakly punctate, punctures separated by 1–3 puncture diameters (Fig. 70E). Pronotum rounded. Mesepisternum and dorsolateral parts of propodeum with fine granular microreticulation, dull to weakly shining. Propodeal triangle broad, laterally not differentiated from dorsolateral parts of propodeum, basally with greatly reduced rugae, present only immediately adjacent to the junction between the propodeum and metanotum, not exceeding the width of a flagellum in length (Fig. 70B). Mesepisternum with whitish densely plumose hairs, becoming shorter and sparser on scutum and scutellum. Propodeal corbicula lacking anterior fringe, dorsal fringe composed of long plumose whitish hairs, internal surface with long scattered simple pale hairs. Legs dark, apical tarsal segments lightened brownish, pubescence light brown. Flocculus incomplete, composed of long scarcely curving white plumose hairs, femoral and tibial scopae composed of white simple hairs. Inner tarsal claws with inner subapical tooth. Wings hyaline, stigma and venation brownish orange, nervulus interstitial.

**Metasoma:** Terga dark, apical rims narrowly lightened hyaline brown (Fig. 70G). Tergal discs with fine granular microsculpture, completely impunctate, weakly shining. Tergal discs with scattered short hairs, not forming apical hairbands. T5 and hairs flanking pygidial plate orange-brown; pygidial plate narrowly rounded triangular, surface dull.

**Male.** Unknown.

**Diagnosis.** *Andrena cretica* can be recognised as a *Graecandrena* due to the small body size, hind tarsal claws with a small inner subapical tooth, and propodeal triangle which is predominantly covered with granular shagreen with the exception of a narrow section at its base with very short rugae (Fig. 70B). Due to the short ocellocipital distance (less than the diameter of a lateral ocellus), it is closest to *A. hyemala* (mainland southern Balkans) and *A. repressa* (the island of Rhodes only). It can be separated from both comparison species (treated together) by the clypeus which is finely shagreened and weakly shining (Fig. 70C; in comparison species with the clypeus microreticulate and dull, Fig. 70D), propodeal triangle with basal rugae greatly reduced, present only immediately adjacent to the junction between the propodeum and metanotum, not exceeding the width of a flagellum in length (Fig. 70B; in comparison species with the propodeal triangle more extensively wrinkled basally, rugae extending to the midpoint of the propodeal triangle, exceeding the width of a flagellum in length), scutum very

weakly sculptured, almost polished and shining (Fig. 70E; in comparison species with the scutum shagreened, at most weakly shining, Fig. 70F), and frons with weak and superficial sculpturing, with only hints of longitudinal striations (Fig. 70G; in comparison species with the frons dull, showing raised longitudinal striations, Fig. 70H). *Andrena cretica* is also very slightly smaller at 5 mm in length compared to 6 mm in the comparison species, but a series of specimens is required to appreciate this difference. As demonstrated above, the biogeography of *A. cretica* suggests a non-overlapping distribution, with neither *A. hyemala* or *A. repressa* present on Crete.

**Etymology.** Named after the island of Crete. It is an adjective in the feminine singular nominative form.

**Distribution.** Greece (Crete) (Fig. 23).

***Andrena (Lepidandrena) haladai* sp. nov.**

<https://zoobank.org/1B7D0282-6F54-4214-A4AA-759DE5D3BE42>

Figs 71, 72A, B

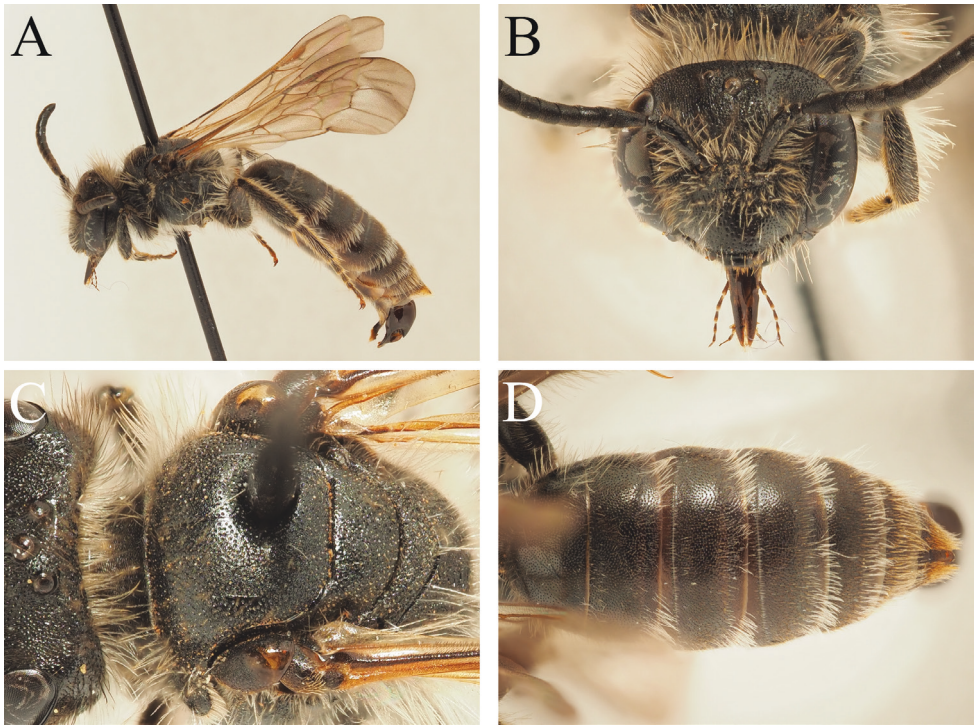
**Type material. Holotype.** GREECE • 1♂; Central Greece, Erateini, 3 km N of Panormos; 38.3998°N, 22.2553°E; 600 m a.s.l.; 10 Apr. 2024; T.J. Wood leg.; RMNH, RMNH.INS.1148903 [BOLD accession number [NATBE001-25](#)].

**Paratypes.** GREECE • 1♂; Central Greece, Erateini, 3 km N of Panormos; 600 m a.s.l.; 10 Apr. 2024; T.J. Wood leg.; RMNH, RMNH.INS.1148904 • 1♂; Peloponnes/Elis, Lambia-Geb, 5 km SW Lambia; 21 May 1992; H. Rausch leg.; OÖLM • 1♂; Peloponnes, 12 km NWW Sparti; 26 May 2005; M. Kadlecová leg.; OÖLM • 4♂; Peloponnes, 35 km NW Tripoli, Langadia SW [Lagkadia]; 3 May 2005; M. Kadlecová & J. Halada leg.; OÖLM.

**Description. Female.** Unknown.

**Male.** Body length: 8–9 mm (Fig. 71A). **Head:** Dark, 1.2 times wider than long (Fig. 71B). Clypeus weakly domed, basally and laterally shagreened and dull, medially becoming polished and shining; surface punctate, punctures separated by 0.5–2 puncture diameters. Process of labrum rounded trapezoidal, apical margin emarginate, slightly thickened and upturned. Surface of galea polished and shining over majority of surface, becoming shagreened only apically. Gena slightly exceeding width of compound eye; ocellocipital distance slightly exceeding diameter of lateral ocellus. Head covered with long whitish hairs, some black hairs laterally on paraocular areas; longest hairs not equalling length of scape. Antennae basally dark, A4–13 ventrally lightened by presence of greyish scales; A3 exceeding length of A4, shorter than A4+5.

**Mesosoma:** Scutum and scutellum densely but somewhat irregularly punctate, punctures separated by <0.5–1 puncture diameters, underlying surface shagreened, weakly shining (Fig. 71C). Pronotum rounded. Mesepisternum irregularly roughened with network of rugosity, forming weak pseudopunctures, surface weakly shining. Propodeum with posterior and lateral faces covered in dense network of rugosity, surface dull. Propodeal triangle laterally indicated by fine carinae, internal surface with raised areolate

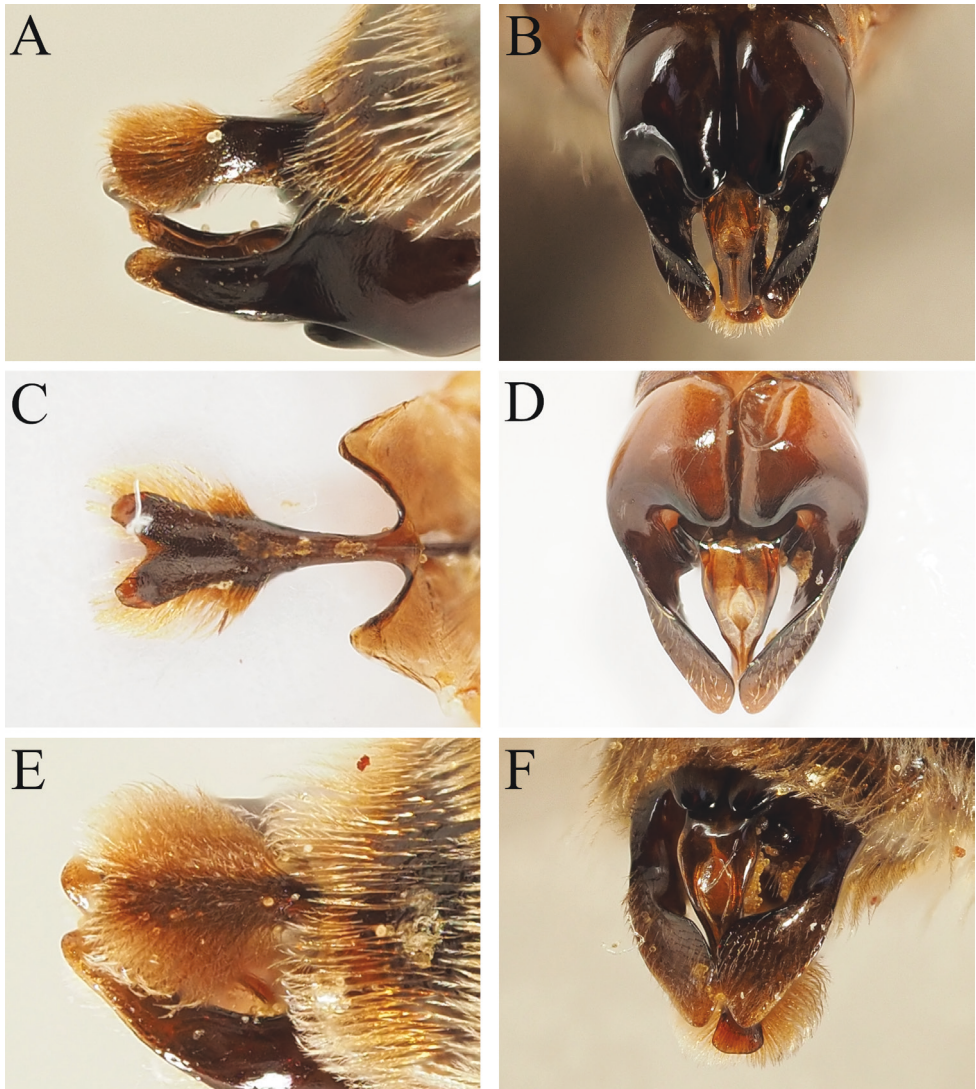


**Figure 71.** *Andrena (Lepidandrena) haladai* sp. nov. male holotype (RMNH). **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Scutum, dorsal view; **D.** Metasoma, dorsal view.

rugae, interspaces shining. Mesosoma covered with long whitish hairs, none equalling length of scape. Legs dark, pubescence light brown, hind tarsal claws with small subapical tooth. Wings hyaline, stigma and venation orange-brown, nervulus postfurcal.

**Metasoma:** Terga dark, apical rims narrowly lightened hyaline brown (Fig. 71D). Terga densely and uniformly punctate, punctures separated by 0.5–1 puncture diameters, punctures extending onto tergal margins; underlying surface polished and shining. Tergal discs with short scattered pale hairs, T2–5 laterally with long loose hair fringes of pale hairs, not obscuring underlying surface. S8 compact, robust, stem parallel-sided, disc rounded, ventral surface covered with dense fringe of light brown hairs (Fig. 72A). Genital capsule compact, gonocoxal teeth short but strongly produced, gonostyli short, narrow, spatulate and parallel-sided, only slightly exceeding apical breadth of penis valves (Fig. 72B). Penis valves narrow, medially occupying 1/2 space between gonostyli, slightly narrowing apically.

**Diagnosis.** *Andrena haladai* can be recognised as a *Lepidandrena* due to the densely and uniformly punctate terga (Fig. 71D), moderately long A3 (Fig. 71B), narrow and moderately indicated propodeal triangle, S8 with produced disc ventrally covered with dense hairs (Fig. 72A), and genital capsule compact with moderately produced gonocoxal teeth (Fig. 72B). These are not particularly strong characters in isolation,



**Figure 72.** *Andrena (Lepidandrena) haladai* sp. nov. male holotype (RMNH). **A.** Sternum 8, ventrolateral view; **B.** Genital capsule, dorsal view. *Andrena (Lepidandrena) paucisquama* Noskiewicz, 1924 male. **C.** Sternum 8, ventrolateral view; **D.** Genital capsule, dorsal view. *Andrena (Lepidandrena) pandellei* Pérez, 1895 male. **E.** Sternum 8, ventrolateral view; **F.** Genital capsule, dorsal view.

but they are typical for *Lepidandrena* males, and the placement of *A. haladai* is supported by its DNA barcode (Fig. 16).

*Andrena haladai* has the external faces of the galea polished and shining, separating it from species around *A. mocsaryi*. Determination can be made by the combination of S8 and the genital capsule. The disc of S8 is short and thumb-shaped and is not noticeably wider or narrower than the stem (Fig. 72A), whereas in *A. paucisquama*

the stem of S8 is very narrow before broadening into the disc which has its lateral margins concave and apical margin deeply emarginate (Fig. 72C). The structure of S8 is much more like *A. pandellei* (Fig. 72E) and *A. curvungula*, but in these two species the gonostyli are apically broadened, shaped like the apex of an ice hockey stick and even slightly broadening up to their apices (Fig. 72F). In contrast, *A. haladai* has the gonostyli apically narrow, only slightly broader than the breadth of the penis valves, definitely not broadening towards their apices (Fig. 72B). This genital capsule form is much more similar to that seen in *A. paucisquama* (Fig. 72D). In short, *A. haladai* displays a genital capsule similar to that of *A. paucisquama*, but a S8 similar to that of *A. pandellei*; this combination of characters allows immediate recognition.

The female of *A. haladai* is currently unknown. There is a distinct possibility that it is very similar to the female of *A. pandellei* or *A. paucisquama* and is currently being misidentified as that. DNA barcoding of *Lepidandrena* females from sites with *A. haladai* present is necessary to convincingly locate the unknown female and study its morphology.

**Remarks.** The males from Panormos were collected flying around a *Campanula* species (Campanulaceae). Given the known specialisation of *A. curvungula*, *A. pandellei*, and *A. paucisquama* on *Campanula* (Westrich 1989; Schmid-Egger and Scheuchl 1997), it seems highly likely that *A. haladai* is also narrowly oligolectic on this plant genus.

**Etymology.** Named after the Czech collector Jiří Halada who for many years has travelled the world collecting insects, many of which are deposited in the OÖLM collection and have served as the basis in whole or in part for (probably) hundreds of new species descriptions. His collections, along with those of other members of his family, have immeasurably increased our understanding of insect biodiversity. The name is in the genitive form.

**Distribution.** Greece (Peloponnese, Central Greece).

### *Andrena* (incertae sedis) *lasithi* sp. nov.

<https://zoobank.org/1CAA6BBE-0AA4-4A07-850E-5298AF46D981>

Figs 73, 74

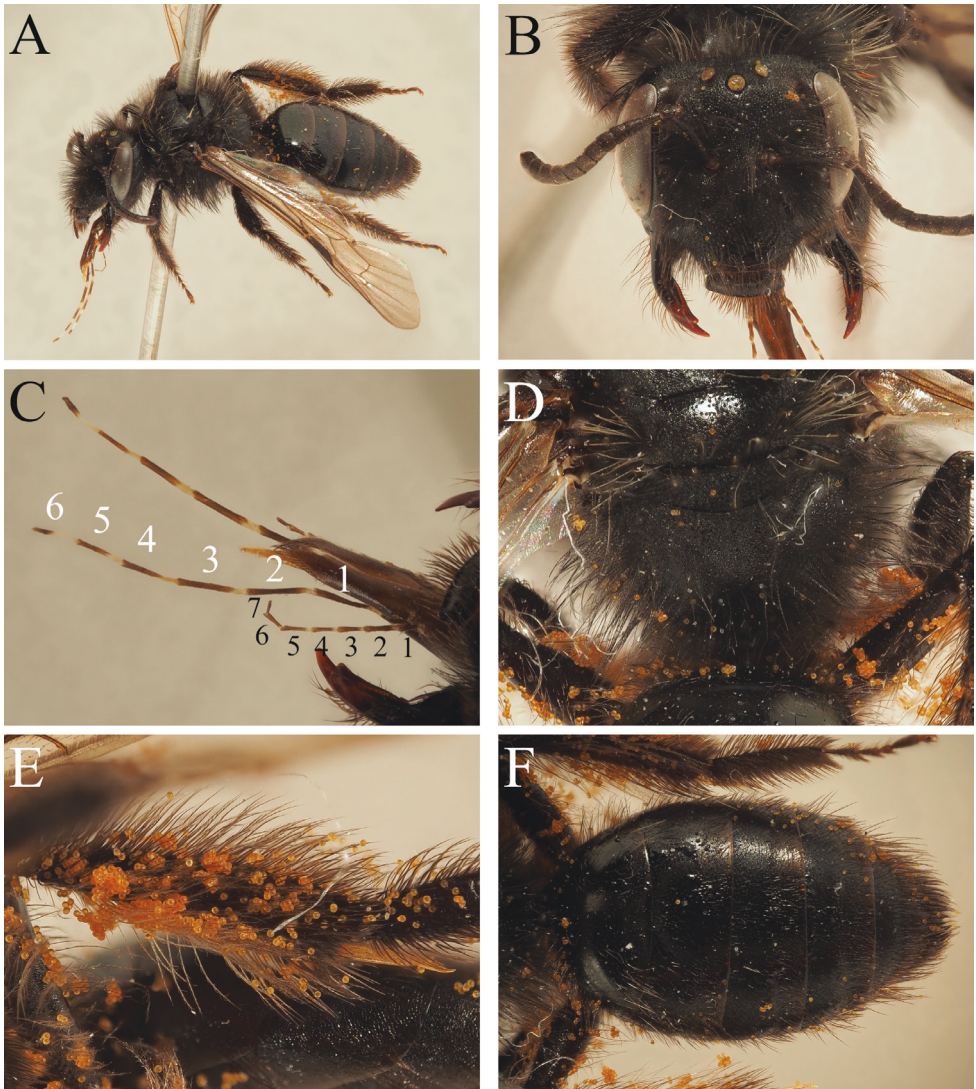
**Type material. Holotype.** GREECE • 1♂; Crete, Mesa Lasithi; 35.1830°N, 25.5120°E; 27 Nov. 1986; H. Teunissen leg.; RMNH, RMNH.INS.1716262.

**Paratypes.** GREECE • 2♂; Crete, Mesa Lasithi; 3 Oct. 1985; H. Teunissen leg.; RMNH • 10♂, 12♀; Crete, Mesa Lasithi; 1 Nov. 1985; H. Teunissen leg.; OÖLM/RMNH/SMNHTAU • 6♂, 3♀; Crete, Mesa Lasithi; 3 Nov. 1985; H. Teunissen leg.; RMNH • 1♂, 12♀; Crete, Mesa Lasithi; 4 Nov. 1985; H. Teunissen leg.; OÖLM/RMNH • 5♀; Crete, Mesa Lasithi; 11 Nov. 1985; H. Teunissen leg.; RMNH • 5♀; Crete, Mesa Lasithi; 12 Nov. 1985; H. Teunissen leg.; RMNH • 4♀; Crete, Mesa Lasithi; 14 Nov. 1985; H. Teunissen leg.; RMNH • 9♀; Crete, Mesa Lasithi; 15 Nov. 1985; H. Teunissen leg.; RMNH • 10♀; Crete, Mesa Lasithi; 17 Nov. 1985; H. Teunissen leg.; RMNH/TJWC • 2♂, 14♀; Crete, Mesa Lasithi; 19 Nov. 1985; H.

Teunissen leg.; RMNH • 8♀; Crete, Mesa Lasithi; 20 Nov. 1985; H. Teunissen leg.; RMNH • 1♀; Crete, Mesa Lasithi; 29 Nov. 1985; H. Teunissen leg.; RMNH • 1♂, 1♀; Crete, Mesa Lasithi; 19 Oct. 1986; H. Teunissen leg.; RMNH • 9♂, 13♀; Crete, Mesa Lasithi; 21 Oct. 1986; H. Teunissen leg.; OÖLM/RMNH/SMNHHTAU • 1♂; Crete, Mesa Lasithi; 26 Oct. 1986; H. Teunissen leg.; RMNH • 8♂, 10♀; Crete, Mesa Lasithi; 27 Oct. 1986; H. Teunissen leg.; OÖLM/RMNH/TJWC • 15♀; Crete, Mesa Lasithi; 28 Oct. 1986; H. Teunissen leg.; OÖLM/RMNH/SMNHHTAU • 1♂, 6♀; Crete, Mesa Lasithi; 29 Oct. 1986; H. Teunissen leg.; RMNH • 10♀; Crete, Mesa Lasithi; 30 Oct. 1986; H. Teunissen leg.; RMNH • 1♂, 1♀; Crete, Mesa Lasithi; 31 Oct. 1986; H. Teunissen leg.; RMNH • 1♀; Crete, Mesa Lasithi; 1 Nov. 1986; H. Teunissen leg.; RMNH • 23♀; Crete, Mesa Lasithi; 3 Nov. 1986; H. Teunissen leg.; RMNH/TJWC • 19♀; Crete, Mesa Lasithi; 4 Nov. 1986; H. Teunissen leg.; RMNH • 4♂; Crete, Plati – Lasithiplain; 11 Nov. 1985; H. Teunissen leg.; RMNH • 1♂; Crete, Plati – Lasithiplain; 12 Nov. 1985; H. Teunissen leg.; RMNH • 1♂; Kriti, Nom. Iraklion, Malia, 34 km OZO v. Iraklion; 29 Oct. 1972; A.C. & W.N. Ellis leg.; RMNH • 5♂; Lasithi, Lasithi; 850 m a.s.l.; 7 Nov. 1984; H. Teunissen leg.; RMNH.

**Description. Female.** Body length: 10–11 mm (Fig. 73A). **Head:** Dark, 1.1 times wider than long (Fig. 73B). Clypeus very weakly domed, more-or-less flattened over majority of surface, finely microreticulate in basal 1/2, weakly shining, becoming polished and shining in apical 1/2; surface punctate, punctures separated by 0.5–1 puncture diameter with exception of impunctate longitudinal midline. Process of labrum broadly trapezoidal, short, three times wider than long. Mouthparts long, at maximum extent exceeding length of head (Fig. 73A); surface of galea finely microreticulate, weakly shining. Mouthparts with seven maxillary palpi, six labial palpi (Fig. 73C). Gena slightly exceeding width of compound eye; ocelloccipital distance 1.5 times diameter of lateral ocellus. Foveae dorsally occupying 1/3 space between compound eye and lateral ocellus, of uniform width, equalling diameter of flagellum; facial foveae filled with dark brown hairs. Head covered with long black hairs, longest equalling length of scape, with few whitish hairs on posterior part of vertex. Antennae dark, A4–12 slightly lightened ventrally by presence of greyish-brown scales; A3 exceeding A4+5, slightly shorter than A4+5+6.

**Mesosoma:** Scutum with regular granular microreticulation, weakly shining, irregularly and shallowly punctate, punctures separated by 1–3 puncture diameters. Scutellum posteriorly with granular microreticulation, dull, anteriorly becoming polished and shining; more regularly punctate, punctures separated by 1–2 puncture diameters. Pronotum with humeral angle. Mesepisternum and dorsolateral parts of propodeum with regular dense microreticulation, weakly shining. Propodeal triangle laterally delineated with weak carinae, internal surface with weak rugae in basal 1/2 (Fig. 73D). Mesepisternum with long black hairs, exceeding scape in length, hairs becoming slightly shorter on scutum and scutellum, with occasional intermixed pale hairs. Propodeal corbicula lacking anterior fringe, dorsal fringe composed of loose long black plumose hairs, internal surface with simple brownish hairs. Legs dark, apical tarsal segments lightened brownish, pubescence dark brown to blackish. Flocculus complete,



**Figure 73.** *Andrena* (incertae sedis) *lasithi* sp. nov. female paratype (RMNH). **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Mouthparts, lateral view; seven maxillary palpi and six labial palpi segments indicated; **D.** Propodeum, dorsal view; **E.** Tibial scopa, lateral view; **F.** Metasoma, dorsal view.

composed of dark brown plumose hairs; femoral and tibial scopae composed of finely plumose hairs, femoral scopae and ventral part of tibial scopae whitish, dorsal part of tibial scopae dark brown (Fig. 73E). Hind tarsal claws with inner subapical tooth. Wings hyaline, stigma and venation dark brown, nervulus interstitial to postfurcal.

**Metasoma:** Terga dark, apical rims narrowly lightened hyaline brown. Disc of T1 polished and shining, disc of T2–4 finely shagreened, weakly shining. Disc of T1 with scattered punctures, punctures separated by 2–4 puncture diameters, discs of T2–4

with punctures separated by 2–3 punctures; punctures weakly extending onto tergal margins, here becoming obscure. Tergal discs with sparse obscure dark hairs, tergal margins with weak obscure dark hairs, not forming apical hairbands and not obscuring underlying surface. T5 and hairs flanking pygidial plate dark brown; pygidial plate rounded triangular, lateral margins slightly raised, internal surface extremely densely punctate, punctures confluent, surface dull.

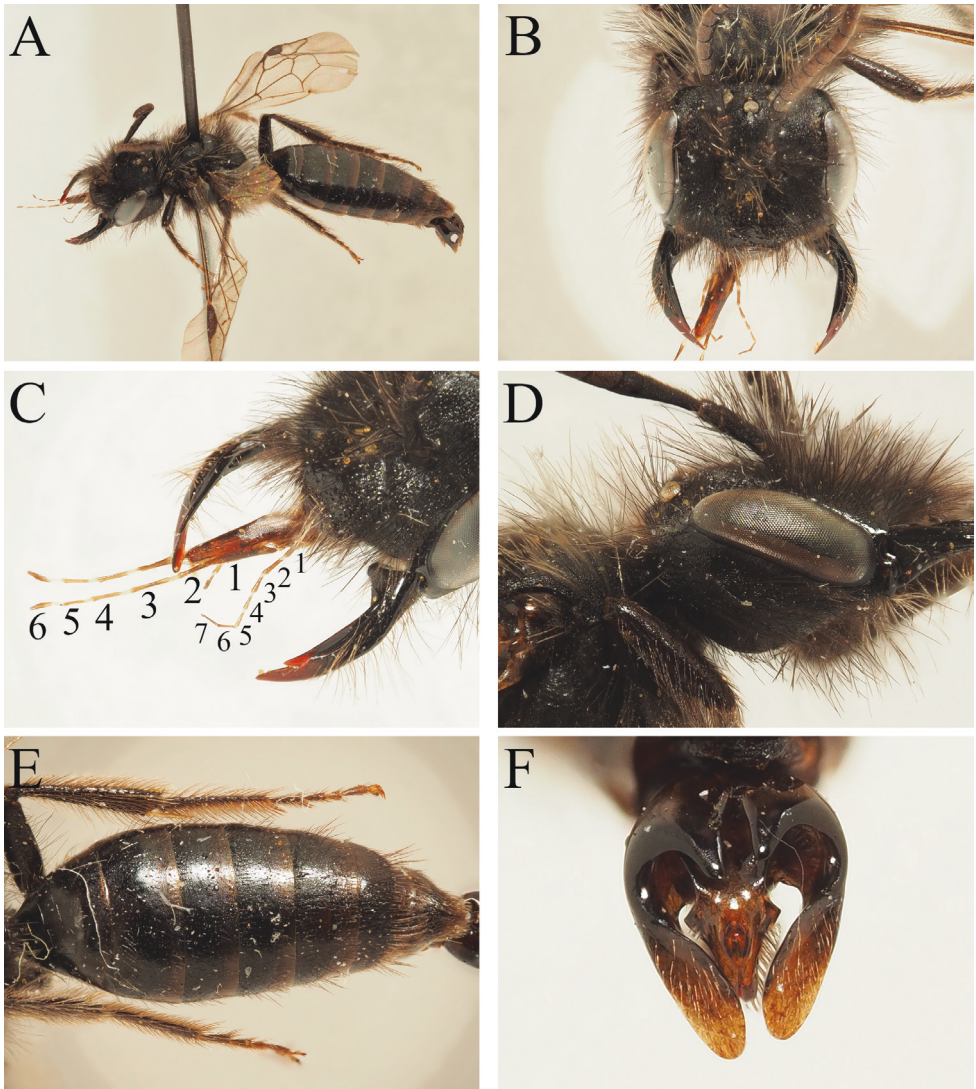
**Male.** Body length: 9–10 mm (Fig. 74A). **Head:** Dark, 1.3 times wider than long (Fig. 74B). Clypeus more-or-less flattened, with weak longitudinal depression along apical margin; surface finely microreticulate, weakly shining, surface punctate, punctures separated by 0.5–1 puncture diameters, with unclear longitudinal impunctate midline. Process of labrum undifferentiated from labrum. Mouthparts as in female (Fig. 74C). Gena strongly exceeding width of compound eye (Fig. 74D); ocellocipital distance 1.5 times diameter of lateral ocellus. Head covered with long dark hairs, longest equalling length of scape, becoming intermixed with white hairs on posterior part of vertex. Antennae dark, A5–13 lightened ventrally by presence of greyish-brown scales; A3 exceeding A4+5, slightly shorter than A4+5+6.

**Mesosoma:** Mesosoma structurally as in female. Mesosoma covered with long intermixed black and whitish hairs, longest hairs exceeding length of scape; pale hairs most abundant dorsally and ventrally, black hairs most abundant medially. Legs dark, apical tarsal segments lightened brown, pubescence light to dark brown; hind tarsal claw with inner subapical tooth. Wings hyaline, stigma dark brown, venation orange brown, nervulus interstitial to weakly postfurcal.

**Metasoma:** Metasoma structurally as in female (Fig. 74E). Tergal discs with scattered short dark hairs, not obscuring underlying surface. S8 columnar, ventral surface covered with thick fringe of dark brown hairs, apex with clear triangular emargination. Genital capsule elongate-rounded, gonocoxal teeth strongly produced into long rounded teeth, gonostyli strongly flattened and broadened apically, apices rounded (Fig. 74F). Penis valves occupying slightly less than 1/2 space between gonostyli, laterally produced into sharp projecting points.

**Diagnosis.** *Andrena lasithi* can quickly be recognised as a member of the undescribed subgenus best referred to as the *crocusella*-group (see Pisanty et al. 2022a) due to the elongate palpi (Fig. 73A), pronotum with a humeral angle (strongly produced in the male sex), barely indicated propodeal triangle (Fig. 73D), oviform metasoma (Figs 73E, 74E), long and narrow foveae that remain a consistent width along their length, and elongate mandibles in the male sex (Fig. 74B) which strongly cross apically (when closed), expanded gena which exceeds the width of the compound eye (Fig. 74D), and genital capsule with the penis valves laterally produced into sharp projecting points (Fig. 74F).

It can immediately be recognised due to the structure of the mouthparts; *Andrena lasithi* has seven maxillary palpi and six labial palpi (Figs 73C, 74C). Within the *crocusella*-group, *Andrena grossella* Grünwaldt, 1976 has nine maxillary palpi and nine labial palpi. All other members of the group (and essentially all other *Andrena* species) have just six maxillary palpi and four labial palpi. *Andrena lasithi* is also the only member of



**Figure 74.** *Andrena* (incertae sedis) *lasithi* sp. nov. male holotype (RMNH). **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Mouthparts, lateral view; seven maxillary palpi and six labial palpi segments indicated; **D.** Head, lateral view; **E.** Metasoma, dorsal view; **F.** Genital capsule, dorsal view.

the *crocusella*-group currently reported from Crete; it may be the undescribed species from Crete mentioned by Pisanty et al. (2016: 514), but that was diagnosed as having seven maxillary palpi and seven labial palpi, but *A. lasithi* has seven maxillary palpi and only six labial palpi. There may be a second species of the *crocusella*-group present on Crete, but I have examined no specimens meeting this description.

**Remarks.** Several specimens have large spherical yellow-orange pollen grains in their scopae (Fig. 73E). These are strongly suspected to be *Crocus* (Iridaceae) pollen –

dietary specialisation on this plant genus would fit the behaviour (including autumn/early winter emergence) observed in *A. grossella* (Grünwaldt 1976).

**Etymology.** Named after the Lasithi Plateau in eastern Crete where Teunissen collected the species in numbers. It is a noun in apposition.

**Distribution.** Greece (Crete).

### 3. Updated faunal list

As discussed in the methodology, given the fragmentary study of the Balkan fauna, it is preferable to list all species and present appropriate (but not comprehensive) literature supporting their historical presence in the four countries considered here. For ease of use and to future-proof the list against upcoming subgeneric reorganisation, species are listed alphabetically. Short notes are given where appropriate. An Excel file with the summarised checklist, together with the subgeneric classification, can be found in Suppl. material 1.

#### 1. *Andrena (Ulandrena) abbreviata* Dours, 1873

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Dours (1873); Warncke (1973); Standfuss et al. (2011, as *Andrena osychniukae* Osytsnjuk, 1977); Wood (2021); Wood (2024a).

**Notes.** The confused treatment of this taxon by Warncke (1965a, 1967b) was discussed by Wood (2024a). The confusion derives from the lost type material, which unlike *A. subglobosa* could not be retrieved in the Gribodo collection. Although the species was described from “*Iles de l’Archipel grec.*”, the precise island is not identifiable without locating any possible remaining syntypes. Wood (2024a: 28) designated a neotype from a Bulgarian specimen in order to fix the concept on the widespread continental *Ulandrena* species present across the southern Balkans, and not the taxon present on the island of Crete (which is *Andrena incustodita* Wood, 2024).

#### 2. *Andrena (Taeniandrena) aberrans* Eversmann, 1852

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Warncke (1988, as *Andrena ratisbonensis* Stöckhert, 1924); Standfuss et al. (2011); Wood (2021); Ascher and Pickering (2025).

**Material examined.** **BULGARIA** • 1♀; Blagoevgrad, Petrovo, 2.7 km S of Goleshovo; 950 m a.s.l.; 25 May 2024; T.J. Wood leg.; RMNH; **GREECE** • 4♀; Make-donien, Serres, Vron-dous-Gebirge; 1350 m a.s.l.; 19 May 2009; H. & R. Rausch leg.; OÖLM/TJWC • 3♂; NE, E of Kilkis, Isoma env. [Ipsoma Kampani]; 5 May 2014; M. Snížek leg.; OÖLM/TJWC.

**Notes.** This uncommon species has declined in Central Europe, and is only occasionally encountered in the southern Balkans. Records are presented here to

highlight this; the southern Balkans may be the best part of Europe in which to study this rare species.

### 3. *Andrena (Ulandrena) acerba* Warncke, 1967

**Countries present.** Greece (mainland, East Aegean Islands), North Macedonia\*.

**References.** Grace (2010); Rasmont et al. (2017).

**Material examined.** NORTH MACEDONIA • 1 ♀; Vardar reg., Papeliste, orchard; 140 m a.s.l.; 16–21 Apr. 2021; V. Bureš leg.; JSPC • 1 ♂; Vardar reg., Papeliste, steppe; 130 m a.s.l.; 11–16 Apr. 2021; V. Bureš leg.; JSPC.

**Notes.** Reported from East Macedonia, Thrace, and the East Aegean Islands including Lesbos and Samos. The records presented here extend the range to the west into North Macedonia.

### 4. *Andrena (Aciandrena) aciculata* Morawitz, 1886

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a, as *Andrena tenicula* Stöckhert, 1950); Warncke (1973); Wood (2021).

**Material examined.** ALBANIA • 5 ♀; Tepelenë; 27 May 2013; K. Deneš leg.; OÖLM.

### 5. *Andrena (Aenandrena) aeneiventris* Morawitz, 1872

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Paganetti-Hummler (1912); Nedialkov (1914); Warncke (1965a); Warncke (1967a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1 ♂; Cajupi Gjirokaster; 11 Jul. 2017; K. Janssen leg.; KJCB • 1 ♀; Krosmishtë [Krosnishtë mountain, N Zvarrisht]; 5 Jun. 2017; M. Jacobs leg.; KJCB • 1 ♂; N Arras; 3 Jun. 2013; K. Deneš leg.; OÖLM • 2 ♀; Rivierbedding Devolij Gorge [Drenije Gorge]; 10 Jun. 2018; K. Janssen leg.; KJCB • 1 ♀; slaapplek Novaj [3 km N Therapelë]; 13 Jun. 2018; K. Janssen leg.; KJCB.

### 6. *Andrena (Taeniandrena) afzeliella* (Kirby, 1802)

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Paganetti-Hummler (1912); Warncke (1973, as *Andrena ovatula* (Kirby, 1802)); Wood (2021, as *Andrena albofasciata* Thomson, 1870); Standfuss et al. (2011, as *Andrena ovatula*); Praz et al. (2022).

### 7. *Andrena (Melandrena) albopunctata* (Rossi, 1792)

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Nediaikov (1914, as *Andrena funebris* Panzer, 1798); Warncke (1965a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

### 8. *Andrena (Micrandrena) alfkenella* Perkins, 1914

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Strand (1915, as *Andrena caneibia* Strand, 1915); Warncke (1965a, as *Andrena caneibia*); Warncke (1969b); Warncke (1973); Wood (2021).

### 9. *Andrena (Micrandrena) alfkenelloides* Warncke, 1965

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a); Warncke (1973).

**Material examined.** ALBANIA • 1♀; Ksamil bij Butrinti; 25 May 2018; K. Janssen leg.; KJCB • 1♀; Tepelenë; 27 May 2013; K. Deneš leg.; OÖLM.

### 10. *Andrena (Micrandrena) alutacea* Stöckhert, 1942

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Schmid-Egger (2005); Wood (2021); Ascher and Pickering (2025).

**Material examined.** ALBANIA • 1♀; Çerem Leem; 14 Jul. 2021; M. Jacobs leg.; KJCB • 3♀; Devolij Gorge [Drenije Gorge]; 9 Jun. 2018; K. Janssen leg.; KJCB • 1♀; Malil Tomorrit [Mount Tomorr]; 31 May 2017; M. Jacobs leg.; KJCB • 1♀; schuin-helling Gjirokaster; 28 May 2018; K. Janssen leg.; KJCB.

### 11. *Andrena (Euandrena) amieti* Praz, Müller & Genoud, 2019

**Countries present.** Greece\*, North Macedonia\* (Fig. 8).

**Notes.** See discussion in subgenus *Euandrena* Hedicke, 1933 in the Results. Almost certainly present also in Albania.

### 12. *Andrena (Nobandrena) anatolica* Alfken, 1935

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1965a); Warncke (1967a); Warncke (1973); Wood (2021).

**13. *Andrena (Andrena) apicata* Smith, 1847**

**Countries present.** Bulgaria\*.

**Material examined.** BULGARIA • 1♂; W Yundola; 1630 m a.s.l.; 3 Apr. 2024; T. Trifonov leg.; IBER.

**Notes.** The first record of the species from the southern Balkans. Further study of the spring *Andrena* fauna on the high mountains of south-western Bulgaria (Rila, Pirin) is needed to fully capture the extent to which temperate species are present.

**14. *Andrena (Plastandrena) apiformis* Kriechbaumer, 1873**

**Countries present.** Greece, North Macedonia.

**References.** Warncke (1965a, as *Andrena grossa* Friese, 1887); Warncke (1973).

**Material examined.** GREECE • 1♂; Delphi; 22–23 Apr. 1980; H. Teunissen leg.; RMNH.

**Notes.** This species is extremely rare in collections; it has only been possible to examine a single specimen from the southern Balkans in the course of this study.

**15. *Andrena (Leucandrena) argentata* Smith, 1844**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Warncke (1966); Warncke (1973); Wood (2021).

**16. *Andrena (Nobandrena) asiatica* Friese, 1921**

**Countries present.** Greece, Bulgaria\*.

**References.** Schubert et al. (2001); Rasmont et al. (2017).

**Material examined.** BULGARIA • 1♀; Resovo [Rezovo]; 16 Jun. 1968; N. Atanassov leg.; NZMS • 1♀; S Sinitovo vill.; 322 m a.s.l.; T. Ljubomirov leg.; IBER; GREECE • 2♂; Karlovasi (Samos); 26 Apr. 1977; H. Teunissen leg.; RMNH • 1♂; Kokkari (Samos); 2 May 1977; H. Teunissen leg.; RMNH • 2♂; Michos (Lesbos); 16 May 1980; H. Teunissen leg.; RMNH • 1♀; Posedonia (Samos) [Posidonio]; 1 May 1975; H. Teunissen leg.; RMNH.

**Notes.** Previously reported from the East Aegean Islands of Lesbos, Samos and Kos, these new specimens meaningfully extend the range north-west into Bulgaria.

**17. *Andrena (Melandrena) assimilis* Radoszkowski, 1876**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Paganetti-Hummler (1912); Drenowski (1934, as “*Andrena gallica* (Pér.) Schmied. (= *assimilis*)”); Drenowski (1936, as *Andrena gallica* “Schrk.”); Warncke (1965a); Warncke (1966); Standfuss et al. (2011); Wood (2021); Ascher and Pickering (2025).

**Material examined. NORTH MACEDONIA** • 1♀; Pelagonia reg., Velushina, pasture; 690 m a.s.l.; 31 Mar. – 5 Apr. 2021; V. Bureš leg.; JSPC.

**Notes.** Original literature supporting the listing of *A. assimilis* from North Macedonia by Ascher and Pickering (2025) could not be found, but can be supported by a contemporary specimen.

### 18. *Andrena (Chlorandrena) astica* Warncke, 1967

**Countries present.** Bulgaria.

**References.** Wood (2021).

**Notes.** The presence of this species in Greece is unclear. It was listed as present by Schwenninger (2015: 268), but this was a mistake (H.R. Schwenninger, pers. comm.). Female specimens from Crete (RMNH) determined by Warncke and Teunissen as *A. astica* are misidentified, and are referable to *A. taraxaci* Giraud, 1861 following the criteria of Schwenninger (2015) (see species entry below). Currently, the only specimen of *A. astica* that it has been possible to examine for the southern Balkans is the one from Sunny Beach (Bulgaria) identified and presented by Wood (2021).

### 19. *Andrena (Nobandrena) athenensis* Warncke, 1965

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined. ALBANIA** • 1♂, 2♀; Tepelenë; 27 May 2013; K. Deneš leg.; OÖLM/TJWC.

### 20. *Andrena (Parandrenella) atrata* Friese, 1887

**Countries present.** Greece\*, Bulgaria, Albania\*.

**References.** Wood (2021).

**Material examined. ALBANIA** • 1♀; Quark Korça, Gem Korça, Drenova, Drenova NP; 1120–1320 m a.s.l.; 29–30 Jun. 2016; H. & R. Rausch leg.; OÖLM • 2♀; vervallen huisje Boboshticë; 7 Jun. 2018; K. Janssen leg.; KJCB • 1♀; Voskopojë; 8 Jun. 2018; K. Janssen leg.; KJCB • 2♂, 1♀; Kukës, W of Perollaj; 26 May 2024; W. Vertommen leg.; WVC; **GREECE** • 1♀; N, SE of Grevena; 500 m a.s.l.; 24 May 2016; L. Bica leg.; OÖLM • 2♀; Western Macedonia, Anatoliko, 6.3 km E, Church of the Holy Apostles; 1000 m a.s.l.; 15 Jun. 2024; T.J. Wood leg.; TJWC.

**Notes.** Present in seasonal continental parts of Albania and northern Greece, representing the southern extent of the European range (Gusenleitner and Schwarz 2002).

### 21. *Andrena (Melandrena) atrotegularis* Hedicke, 1923

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 2♀; Lopan [Lapanj] 3 rivieren; 14 Jun. 2018; K. Janssen leg.; KJCB.

### 22. *Andrena (Melandrena) barbareae* Panzer, 1805

**Countries present.** Greece, Bulgaria, Albania\*.

**References.** Nediaikov (1914, as *Andrena fumipennis* Schmiedeknecht, 1880); Atanassov (1962, 1964); Ebmer (2003); Wood (2021).

**Material examined.** ALBANIA • 1♀; Korab [Mount Korab]; 23–31 Jul. 1918; E. Stöckhert det.; NHMW; GREECE • 1♀; Central Macedonia, Mt. Kajmakčalan, ski centre environs; 2000 m a.s.l.; 12 Jun. 2024; T.J. Wood leg.; TJWC • 1♀; Korfu, Pantokrator (south side); 700–800 m a.s.l.; 9 Jun. 2006; R. & W. Zarre leg.; OÖLM • 1♀; Magnesia, Othris-Geb [Mount Othrys], NE Berg Mavrika; 1230 m a.s.l.; 24 May 2009; H. & R. Rausch leg.; OÖLM • 1♀; Siatista env.; 700 m a.s.l.; 14 May 2017; K. Deneš leg.; OÖLM • 1♀; Western Macedonia, Florina, 3 km N of Vigla; 1800–1900 m a.s.l.; 13 Jun. 2024; T.J. Wood leg.; TJWC.

**Notes.** Warncke (1965a: 32) considered *A. cineraria* to be present in the southern Balkans, but subsequent authors (e.g. Scheuchl and Willner 2016) have considered most Balkan records to refer to *A. danuvia* Stöckhert, 1950. In addition to *A. danuvia*, *A. barbareae* is considered to be present in mountainous areas; it was first reported from Greece from the Vermio mountains at an altitude of 1550 m a.s.l. by Ebmer (2003: 336). Additional records are presented here. The three species remain challenging to separate morphologically, and so care should be taken when using the identification key.

### 23. *Andrena (Leucandrena) barbilabris* (Kirby, 1802)

**Countries present.** Greece, Bulgaria\*.

**References.** Warncke (1965a, as ?*Andrena sericea* (Christ, 1791)).

**Material examined.** BULGARIA • 1♀; S Slanchevo vill.; 111 m a.s.l.; 5 May 2023; T. Ljubomirov leg.; IBER; TURKEY • 3♀; Ezine; 6 Apr. 2025; L. Efil leg.; IUZC.

**Notes.** It has not been possible to examine any specimens of this species from Greece, but some recently captured specimens from western Turkey were examined. The presence of *A. barbilabris* in northern Greece is therefore considered to be plausible.

#### 24. *Andrena (Micrandrena) biarmica* Warncke, 1975

**Countries present.** Greece (East Aegean Islands).

**References.** Gusenleitner and Schwarz (2002).

#### 25. *Andrena (Euandrena) bicolor* Fabricius, 1775

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Nedialkov (1914, as *Andrena gwynana* (Kirby, 1802)); Warncke (1966); Warncke (1973); Standfuss et al. (2011); Wood (2021).

#### 26. *Andrena (Melandrena) bicolorata* (Rossi, 1790)

**Countries present.** Greece.

**References.** Warncke (1965a).

**Material examined.** GREECE • 3♀; Central Greece, Antikyra, ruderal park by Church Agios Nikolaos; 8 Apr. 2024; T.J. Wood leg.; TJWC • 1♂; Crete, NW of A. Viannos, Thomadiano; 7 Apr. 2004; J. Batelka & H. Batelková leg.; OÖLM • 1♀; Gjumurdzina [Komotini]; 24 Apr. 1914; I. Buresch leg.; NZMS • 2♀; Kreta, Rethimnon [Rethimno]; 19 Apr. 1998; H. Wolf leg.; OÖLM • 2♀; Kriti, Zakros; 20 Apr. 1985; R. Leys leg.; RMNH • 4♀; Kriti, Lasithi, Zakros [Kato Zakros]; 20 Apr. 1985; R. Leys leg.; RMNH • 4♀; Kriti, Lasithi, Zakros [Kato Zakros]; 20 Apr. 1985; R. Leys leg.; RMNH • 1♀; Peloponnese, 10 km W Korinthos [Corinth]; 6 May 2005; J. Halada leg.; OÖLM • 2♀; Peloponnese, 15 km N Sparta; 600 m a.s.l.; 29 Apr. 2014; K. Deneš leg.; OÖLM • 1♀; Peloponnese, Megalopolis, Kiparissi, immediately to north; 450 m a.s.l.; 3 Apr. 2024; T.J. Wood leg.; TJWC • 2♀; Peloponnese, Sparti, Pellana, Irakleous road fields; 350 m a.s.l.; 5 Apr. 2024; T.J. Wood leg.; TJWC.

**Notes.** More commonly recorded in the West Mediterranean, a surprisingly large population of *A. bicolorata* exists in Greece, including Crete (Gusenleitner and Schwarz 2002).

#### 27. *Andrena (Ulandrena) biguttata* Friese, 1923

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Friese (1923); Warncke (1973); Wood (2021).

**Notes.** The identity and application of the name *A. biguttata* was clarified by Wood (2021).

#### 28. *Andrena (Plastandrena) bimaculata* (Kirby, 1802)

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Nedialkov (1914, as *Andrena morawitzi* Thomson, 1872); Warncke (1965a); Warncke (1966); Standfuss et al. (2011); Wood (2021); Ascher and Pickering (2025).

### 29. *Andrena (Aenandrena) bisulcata* Morawitz, 1877

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 2♀; Novaj [3 km N Therepelë]; 12 Jun. 2018; K. Janssen leg.; KJCB • 2♂, 2♀; Voskopojë; 8 Jun. 2018; K. Janssen leg.; KJCB.

### 30. *Andrena (Pallandrena) braunsiana* Friese, 1887

**Countries present.** Greece, Bulgaria.

**References.** Wood et al. (2023).

### 31. *Andrena (Cryptandrena) brumanensis* Friese, 1899

**Countries present.** Greece, Bulgaria, North Macedonia, Albania (Fig. 5).

**References.** Brullé (1833, as *Andrena clypeata* Brullé, 1833 nec. Illiger, 1806); Warncke (1965a, as *Andrena clypeata*); Warncke (1966, as *Andrena clypeata*); Warncke (1973, as *Andrena clypeata*); Standfuss et al. (2011); Wood (2021).

### 32. *Andrena (Hoplendrena) bucephala* Stephens, 1846

**Countries present.** Greece, Bulgaria.

**References.** Warncke (1967a); Ebmer (2009); Wood (2021).

**Material examined.** GREECE • 2♀; Megapolis [Megalopolis] (Peloponn. Arkadia); 11 Apr. 1988; H. Teunissen leg.; RMNH • 3♀; Mesa sin-Trikala [Mesi Sinikia Trikalon], Korinthe; 26 Apr. 1988; H. Teunissen leg.; RMNH • 2♂, 1♀; Peloponnese, 20 km S Megalopoli; 1 May 2005; J. Halada leg.; OÖLM • 1♂, 2♀; Peloponnese, 35 km NW Tripoli, Langadia SW [Lagkadia]; 3 May 2005; J. Halada leg.; OÖLM/TJWC • 1♂, 2♀; Peloponnese, 5 km E Kalvrita [Kalavryta]; 5 May 2005; J. Halada leg.; OÖLM • 2♂; Peloponnese, Profitis Ilias, N of Manganiari Spring; 1000–1100 m a.s.l.; 2 Apr. 2024; T.J. Wood leg.; TJWC • 2♂, 6♀; Peloponnese, Profitis Ilias, Toriza environs; 750 m a.s.l.; 2 Apr. 2024; T.J. Wood leg.; TJWC • 4♂; Peloponnese, Sparti, Georgitsi, immediately to north; 750 m a.s.l.; 3 Apr. 2024; T.J. Wood leg.; TJWC • 1♀; Rte Sparti-Tripolis, Pelop.; 12 Apr. 1988; H. Teunissen leg.; RMNH.

**Notes.** *Andrena bucephala* was first reported from Greece from the Taygetos mountains in the Peloponnese by Ebmer (2009: 61) who noted that it seemed completely

isolated from populations in Bulgaria. He also noted that *A. bucephala* preferred tree blossoms and was consequently difficult to record. These observations are fully supported by revision of material and new collections; all Greek specimens of *A. bucephala* examined to date come from the Peloponnese. At the right moment, it can be commonly encountered on mountains in the Peloponnese when *Acer* (Sapindaceae) trees are flowering. Its special parasite *Nomada hirtipes* Pérez, 1884 was present at the Manganiari Spring site (TJWC), and has been recorded from Greece in the past (Smit 2018).

### 33. *Andrena (Euandrena) bulgarica* sp. nov.

**Countries present.** Greece, Bulgaria.

**Notes.** ENDEMIC to the southern Balkans.

### 34. *Andrena (Truncandrena) canaeae* Strand, 1915

**Countries present.** Greece, North Macedonia\*.

**References.** Strand (1915); Warncke (1965a).

**Material examined** (illustrative). **GREECE** • 1♀; Canea [Chania] (Creta); 1 Mar. – 30 Jun. 1914; Paganetti leg.; DEI (**holotype**); **NORTH MACEDONIA** • 1♀; Vardar reg., Papeliste, orchard; 140 m a.s.l.; 26 Apr. – 1 May 2021; V. Bureš leg.; JSPC • 1♂; Vardar reg., Papeliste, steppe; 130 m a.s.l.; 26 Apr. – 1 May 2021; V. Bureš leg.; JSPC.

**Notes.** Originally described from Crete, the holotype is in the DEI collection.

### 35. *Andrena (?Avandrena) canohirta* (Friese, 1923)

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Friese (1923); Warncke (1965a, as *Andrena balcanica* Warncke, 1965); Warncke (1973); Standfuss et al. (2011); Wood (2021); Wood (2024a).

**Notes.** The phylogenetic placement of this species is unclear, as it belongs to the spineless *Avandrena* Warncke, 1968 (the species lacking posteriorly projecting spines on the hind face of the hind femorae). A new subgenus may be necessary following phylogenetic analysis.

### 36. *Andrena (Ulandrena) cantiaca* Warncke, 1975

**Countries present.** Greece.

**References.** Grace (2010).

**Material examined.** **GREECE** • 27♂, 2♀; Peloponnese, 12 km NWW Sparti; 26–27 May 2005; M. Kadlecová & J. Halada leg.; OÖLM/TJWC • 1♂; Peloponnese, Molaoi, Municipal Football Stadium (east side); 30 Mar. 2024; T.J. Wood leg.; TJWC.

**Notes.** Grace (2010: 59) stated that *A. cantiaca* could be found on the island of Lesbos, but the source of this record is not stated. Examination of male specimens from the Peloponnese have produced individuals with a genital morphology close to that of *A. cantiaca*. The situation remains complex, as medium-sized *Ulandrena* species including *A. abbreviata*, *A. biguttata*, *A. cantiaca*, and *A. combaella* Warncke, 1966 are more-or-less impossible to separate morphologically, and the males can only be separated by dissection of the genital capsule. Moreover, *A. cantiaca* presents a genital morphology that has the gonocoxal teeth produced into rounded truncate bumps, whereas they are short teeth in *A. biguttata* and long teeth in *A. abbreviata*. *Andrena cantiaca* is therefore cautiously accepted as present in Greece, with an emphasis on the need for clearer delineation of species boundaries in this subgenus.

**37. *Andrena (Micrandrena) cedricola* Wood, 2020**

**Countries present.** Greece\* (Fig. 32).

**Notes.** See Subgenus *Micrandrena* Ashmead, 1899 in the Results.

**38. *Andrena (Aciandrena) chelma* Warncke, 1975**

**Countries present.** Greece.

**References.** Warncke (1974a, 1975).

**Notes.** ENDEMIC to Greece and the southern Balkans.

**39. *Andrena (Euandrena) chrysopus* Pérez, 1903**

**Countries present.** Bulgaria, North Macedonia.

**References.** Warncke (1973); Wood (2021).

**40. *Andrena (Melandrena) chrysopyga* Schenck, 1853**

**Countries present.** Bulgaria.

**References.** Nedialkov (1914); Drenowski (1936); Scheuchl and Willner (2016); Wood (2021).

**Material examined.** BULGARIA • 1♀; Golo Bardo; 25 Jun. 1990; E. Vasileva leg.; T.J. Wood det.; NZMS.

**Notes.** It has only been possible to examine a single specimen of this species from the southern Balkans. For Greece, Warncke (1965a: 54) lists only Paganetti-Hummler (1912: 380), who did indeed list the name from Corfu. Warncke (1966: 389) later concluded that this was a misidentification. Given the large number of historical misidentifications of *A. chrysopyga*, which is largely a temperate to continental species, it

cannot currently be considered part of the Greek fauna. Nedialkov (1914) listed the species from Ihtiman, Stara Zagora, and Burgas which is consistent with the record from Golo Bardo.

#### 41. *Andrena (Notandrena) chrysoceles* (Kirby, 1802)

**Countries present.** Greece\*, Bulgaria.

**References.** Gusenleitner and Schwarz (2002); Wood (2021).

**Material examined.** BULGARIA • 1♀; Hrabrino; 15 Jun. 1997; A. Zaykov leg.; OÖLM • 1♂; Plovdiv; 1 May 1996; A. Zaykov leg.; OÖLM; GREECE • 1♂; Thslq, Kato Nevrokopi [4 km NE Volakas]; 750 m a.s.l.; 24 May 2023; R. Le Divelec leg.; RLDC.

**Notes.** This species does not seem to have been previously reported from Greece.

#### 42. *Andrena (Melandrena) cineraria* (Linnaeus, 1758)

**Countries present.** Bulgaria.

**References.** Scheuchl and Willner (2016); Wood (2021).

**Material examined.** BULGARIA • 1♀; S Momino vill.; 175 m a.s.l.; 27 Apr. 2018; T. Ljubomirov leg.; IBER.

**Notes.** Some authors like Warncke (1965a) have listed *A. cineraria* from Greece. See the comments under *A. barbareae* and *A. danuvia* Stöckert, 1950. Only a single specimen conforming morphologically to *A. cineraria* could be examined from Bulgaria. More study is required to clearly define the overall range limits of *A. cineraria*, *A. barbareae*, and *A. danuvia* in the West and Central Palaearctic.

#### 43. *Andrena (Chlorandrena) cinerea* Brullé, 1833

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Brullé (1833); Paganetti-Hummler (1912); Warncke (1965a); Warncke (1967a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1♂; Mount Tomorr; 12 Jun. 2018; K. Janssen leg.; KJCB • 1♂; N Arras; 3 Jun. 2013; K. Deneš leg.; OÖLM.

#### 44. *Andrena (Chlorandrena) cinereophila* Warncke, 1965

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1965a); Warncke (1967a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

#### 45. *Andrena (Notandrena) clanga* Warncke, 1965

**Countries present.** Greece (East Aegean Islands) (Fig. 42).

**References.** Grace (2010, as *Andrena stellaris* misidentification); Rasmont et al. (2017, as *Andrena stellaris* misidentification).

#### 46. *Andrena (Andrena) clarkella* (Kirby, 1802)

**Countries present.** Bulgaria.

**References.** Scheuchl and Willner (2016).

**Notes.** This species was supposed to be listed from Bulgaria by Wood (2021) as species no. 32, but was accidentally deleted during the production of the proof.

#### 47. *Andrena (Hoplandrena) clusia* Warncke, 1966

**Countries present.** Greece, North Macedonia.

**References.** Warncke (1973, as *Andrena clusia* ssp. *prilepensis* Warncke, 1973); Grace (2010).

**Material examined.** GREECE • 2♀; Central Macedonia, Mt. Kajmakčalan, ski centre environs; 2000 m a.s.l.; 12 Jun. 2024; T.J. Wood leg.; TJWC; NORTH MACEDONIA • 1♀; Yugoslav, Prilep; 1 Jun. 1968; K. Warncke leg.; OÖLM (holotype of *Andrena clusia* ssp. *prilepensis*).

**Notes.** It is unclear what underpins the listing of Grace (2010: 60) who wrote “Central Turkey and northern Continental Greece”. This is strange, as Warncke (1973) explicitly described *A. clusia* ssp. *prilepensis* from North Macedonia. Grace may have been looking at the distribution map presented in Gusenleitner and Schwarz (2002) which showed dots that are not confidently assignable to either North Macedonia or Greece. In any case, *A. clusia* can be confirmed from northern Greece based on specimens collected at high altitude on the border with North Macedonia.

#### 48. *Andrena (Chlorandrena) chypella* Strand, 1921

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Strand (1921); Warncke (1973, as *Andrena chypella* ssp. *hasitata* Warncke, 1973); Standfuss et al. (2011).

**Material examined.** ALBANIA • 1♂; berghellin Rehovë Ersekë; 6 Jun. 2018; K. Janssen leg.; KJCB • 1♀; Burrel-Lis [between Burrel and Lis]; 1000 m a.s.l.; 6 Jun. 2013; K. Deneš leg.; OÖLM • 2♂; Buz [Buzë]; 28 May 2017; M. Jacobs leg.; KJCB • 1♂, 1♀; Lopan [Lapanj] 3 rivieren; 14 Jun. 2018; K. Janssen leg.; KJCB • 1♂, 2♀; N Arras; 3 Jun. 2013; K. Deneš leg.; OÖLM • 1♂; NW Boge [Bogë]; 10 Jun. 2013; K.

Deneš leg.; OÖLM • 1♂; Permet env.; 500 m a.s.l.; 1 May – 30 Jun. 2013; K. Deneš leg.; OÖLM • 1♀; Radanj orchideenwai, Korçë; 3 Jun. 2018; K. Janssen leg.; KJCB • 1♂, 1♀; Rivierbedding Devolij Gorge [Drenije Gorge]; 10 Jun. 2018; K. Janssen leg.; KJCB • 1♂; rotshelling Topovë; 29 May 2018; K. Janssen leg.; KJCB • 1♀; SH75 draaihals slaapplek Korçë; 4 Jun. 2018; K. Janssen leg.; KJCB • 1♂; Sheper valle, Gjirokaster; 28 May 2018; K. Janssen leg.; KJCB • 2♀; Tepelenë; 27 May 2013; K. Deneš leg.; OÖLM • 1♂; Tepelenë, Bënçë; 23–24 May 2001; A. v. Niewenhuyzen leg.; RMNH • 5♂, 15♀; Tirana; 25 May 1992; G.G.M. Schulten leg.; RMNH • 1♀; Tropojë; 15 Jul. 2021; M. Jacobs leg.; KJCB • 1♀; Voskopojë; 8 Jun. 2018; K. Janssen leg.; KJCB.

**Notes.** Described from Crete. This species was supposed to be listed from Bulgaria by Wood (2021) as species no. 33, but was accidentally deleted during the production of the proof. Warncke (1973: 28) described *Andrena chypella* ssp. *hasitata* with a holotype from Prilep in North Macedonia. Based on new material, the species is common in Albania.

#### 49. *Andrena (Oreomelissa) coitana* (Kirby, 1802)

**Countries present.** Greece\*, Bulgaria\*.

**References.** Ascher and Pickering (2025).

**Material examined.** BULGARIA • 1♀; Pamporovo; 8 Aug. 1963; N. Atanassov leg.; NZMS • 1♀; Pirin, Kozia dolina [valley]; 2300 m a.s.l.; 10 Aug. 2005; J. Straka leg.; JSPC; GREECE • 2♂; Drama, Rhodope mountains, Mt. Sara; 18 Aug. 1989; L. Blank leg.; OÖLM/TJWC.

**Notes.** Listed for Greece from Crete by Ascher and Pickering (2025) from the American museum of Natural History database (AMNH\_BEES75413). This is clearly a misidentification, as *A. coitana* is Euro-Siberian species found in temperate habitats. However, examination of material from the mountains of Greece and Bulgaria has demonstrated that *A. coitana* is present in the southern Balkans, albeit marginally. It is considered newly reported for both countries.

#### 50. *Andrena (Brachyandrena) colletiformis* Morawitz, 1873

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Paganetti-Hummeler (1912); Strand (1915, as *Andrena nanana* Strand, 1915); Maidl (1922); Drenowski (1936, as *Andrena dissidens* Schmiedeknecht, 1884); Warncke (1965a); Warncke (1966); Warncke (1973); Standfuss et al. (2011).

**Notes.** This species was supposed to be listed from Bulgaria by Wood (2021) as species no. 34, but was accidentally deleted during the production of the proof.

**51. *Andrena (Ulandrena) combaella* Warncke, 1966**

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1973); Wood (2021).

**52. *Andrena (Simandrena) combinata* (Christ, 1791)**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Paganetti-Hummler (1912); Warncke (1965a); Warncke (1966); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Notes.** *Andrena combinata* here contains within it *Andrena mehelyi* Alfken, 1936 due to a lack of confidence in the consistent recognition of this taxon, and a lack of molecular evidence to support its status as a distinct species. Warncke (1966: 397) reported *A. combinata* ssp. *mehelyi* from Albania, before later not even recognising it at a subspecies level (see Gusenleitner and Schwarz 2002: 193, 1007).

**53. *Andrena (Ulandrena) concinna* Smith, 1853**

**Countries present.** Greece, Albania (Fig. 60).

**References.** Smith (1853); Warncke (1965a); Warncke (1966); Standfuss et al. (2011); Wood (2024a).

**Notes.** ENDEMIC to the southern Balkans.

**54. *Andrena (Simandrena) confinis* Stöckhert, 1930**

**Countries present.** Greece\*, Bulgaria.

**References.** Wood (2021).

**Material examined.** BULGARIA • 1♂; Lozenska Mt., SE German vill.; 1000 m a.s.l.; 1 Apr. 2016; I. Todorov leg.; NZMS; GREECE • 1♀; Central Macedonia, Mt. Kajmakčalan, ski centre environs; 2000 m a.s.l.; 12 Jun. 2024; T.J. Wood leg.; TJWC • 1♂; Peloponnese, Profitis Ilias, N of Manganiari Spring; 1000–1100 m a.s.l.; 2 Apr. 2024; T.J. Wood leg.; TJWC.

**Notes.** *Andrena confinis* and *A. congruens* Schmiedeknecht, 1884 are morphologically very close and taxonomically challenging. Warncke treated them as conspecific, but more recent workers have considered them as distinct (Schmid-Egger and Scheuchl 1997). In line with the morphological concepts of Schmid-Egger and Scheuchl, both *A. confinis* and *A. congruens* are considered to be present in the southern Balkans, but more molecular study of this putative species pair is required for increased certainty.

**55. *Andrena (Simandrena) congruens* Schmiedeknecht, 1884**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Maidl (1922); Warncke (1965a); Warncke (1966); Warncke (1973); Wood (2021).

**Material examined.** BULGARIA • 1♀; Witosha Geb. [Witosha mountain]; 14 Apr. 1963; D. Gogov leg.; NZMS; GREECE • 1♀; Olympos, Spilios Agapilos; 2100 m a.s.l.; 28 Jul. 1965; Blommers leg.; RMNH; NORTH MACEDONIA • 1♀; Galicia-Pl. [Galičica mountain], Maced.; 2 Jul. 1965; Kgm.; K. Warncke det.; ZMHB.

**Notes.** *Andrena congruens* in a strict sense does seem to be present in the southern Balkans, and is always recorded at high altitude mountain sites, such as Witosha, Olympus, and Galičica, as presented here.

**56. *Andrena (Cordandrena) cordialis* Morawitz, 1877**

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1965a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**57. *Andrena (Poecilandrena) crassana* Warncke, 1965**

**Countries present.** Greece, North Macedonia.

**References.** Warncke (1965a).

**58. *Andrena (Ulandrena) crecca* Warncke, 1965**

**Countries present.** Greece, Bulgaria, North Macedonia (Fig. 60).

**References.** Warncke (1973, as *Andrena resoluta* Warncke, 1973); Rasmont et al. (2017); Wood (2021, as *Andrena resoluta*); Wood (2024a).

**Notes.** Wood (2024a) extensively discussed this case, and synonymised *A. resoluta* (provisionally restricted to North Macedonia and Bulgaria) under *A. crecca*.

**59. *Andrena (Graecandrena) cretica* sp. nov.**

**Countries present.** Greece (Crete) (Fig. 23).

**Notes.** ENDEMIC to the southern Balkans.

**60. *Andrena (Melandrena) cretica* Strand, 1915**

**Countries present.** Greece (Crete) (Fig. 29).

**References.** Strand (1915, as *Andrena cretica* Strand, 1915); Warncke (1965a, as *Andrena vachali* ssp. *cretica*).

**Notes.** ENDEMIC to the southern Balkans.

**61. *Andrena (Warnckandrena) curiosa* (Morawitz, 1877)**

**Countries present.** Greece (East Aegean Islands).

**References.** Paulus and Gack (1990); Paulus (1997); Gusenleitner and Schwarz (2002); Pisanty and Wood (2024).

**Material examined.** GREECE • 1♂; Lesbos, River Potamia, 2.9 km W Skala Kallonis; 26 Mar. 2011; M. Hull leg.; WML.

**Notes.** The first record of *A. curiosa* in Europe was indirectly reported by Paulus and Gack (1990: 100) who demonstrated visitation of *A. curiosa* males to *Opyrys lesbis* Gözl & H.R. Reinhard on the island of Lesbos. Reference to this was repeated by Paulus (1997: 145). The specimens were identified by Klaus Warncke, and Warncke's dot maps indicate the presence of *A. curiosa* on Lesbos (Gusenleitner and Schwarz 2002) which is further confirmed through new specimen examination.

**62. *Andrena (Notandrena) curvana* Warncke, 1965**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a); Warncke (1973); Wood (2021).

**Material examined.** ALBANIA • 1♂, 1♀; slaapplek Novaj [3 km N Therepelë]; 13 Jun. 2018; K. Janssen leg.; KJCB.

**Notes.** Friese (1922: 211) described *Andrena cyanescens* var. *rufescens* (type ZMHB) from "Balkan", this being a junior primary homonym of *Andrena rufescens* Pérez, 1895, Warncke (1965a: 29) provided a replacement name. As the *locus typicus* was given so imprecisely, it is not possible to understand where exactly the type specimen was collected. It should be re-inspected in the ZMHB collection to see if additional information is available.

**63. *Andrena (Lepidandrena) curvungula* Thomson, 1870**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a); Warncke (1973); Wood (2021).

**Material examined.** ALBANIA • 1♀; Poliçan; 30 May 2017; M. Jacobs leg.; KJCB • 1♀; Rivierbedding Devolij Gorge [Drenije Gorge]; 10 Jun. 2018; K. Janssen leg.; KJCB • 1♂, 1♀; rotshelling Topovë; 29 May 2018; K. Janssen leg.; KJCB • 1♂, 2♀; warmwaterbr Petran; 31 May – 1 Jun. 2018; K. Janssen leg.; KJCB.

#### 64. *Andrena* (*incertae sedis*) *dacia* Wood, 2024

**Countries present.** Southern Romania, and most probably Bulgaria.

**References.** Wood (2024a).

**Notes.** Part of the *crocusella*-group (subgenus currently undescribed). Whilst strictly not recorded from Bulgaria, Wood (2024a: 130) recorded *A. dacia* from Vama Veche on Romania's Black Sea coast, a locality just 1 km north of the Bulgarian border. Consequently, the species is extremely likely to also be present in Bulgaria, and hence is included in the faunal total presented here, as well as the identification key. ENDEMIC to the southern Balkans.

#### 65. *Andrena* (*Melandrena*) *danuvia* Stöckhert, 1950

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Warncke (1966, as *Andrena cineraria* (Linnaeus, 1758)); Warncke (1973, as *Andrena cineraria*); Standfuss et al. (2011); Wood (2021).

#### 66. *Andrena* (*Holandrena*) *decipiens* Schenck, 1861

**Countries present.** Greece, Bulgaria, Albania\*.

**References.** Alfken (1904, as *Andrena fimbriata* var. *paganettii* Alfken, 1904); Dours (1872, as *Andrena fonscolombii*); Warncke (1965a); Standfuss et al. (2011); Wood (2021); Wood and Bossert (2025).

**Material examined.** ALBANIA • 1♀; Fier region, Lushnje env., pastures and steppes; 177 m a.s.l.; 29 Jun. 2018; D. Benda leg.; JSPC.

**Notes.** Wood and Bossert (2025) clarified the status of *Andrena fonscolombii* Dours, 1872 which was described from Corfu, and which is a junior synonym of *A. decipiens*. It shares this *locus typicus* with *Andrena fimbriata* var. *paganettii* which was also described from this island (Alfken 1904). See section on Subgenus *Holandrena* Pérez, 1890 in the Results for discussion of the status of *A. flavilabris* which is here considered as conspecific with *A. decipiens*.

#### 67. *Andrena* (*Truncandrena*) *delphiensis* Warncke, 1965

**Countries present.** Greece, North Macedonia\*.

**References.** Warncke (1965a).

**Material examined.** NORTH MACEDONIA • 1♀; Vardar reg., Papeliste, orchard; 140 m a.s.l.; 1–6 May 2021; V. Bureš leg.; JSPC.

**Notes.** Warncke (1965a: 35) described *A. delphiensis* as a subspecies of *A. minapalumboi* Gribodo, 1894. Gusenleitner and Schwarz (2002) elevated it to specific status, a position followed here. The species is present also in western Turkey (Hazir et al. 2012, 2014).

### 68. *Andrena (Cnemidandrena) denticulata* (Kirby, 1802)

**Countries present.** Bulgaria.

**References.** Wood (2021).

**Material examined.** BULGARIA • 1♀; Rhodopi, Erkiupria [Wondrous Bridges]; 29 Jul. 1965; N. Atanassov leg.; NZMS.

**Notes.** Rare in the southern Balkans, a female specimen from the Western Rhodopes was examined in addition to the single male presented by Wood (2021).

### 69. *Andrena (Truncandrena) derbentina* Morawitz, 1886

**Countries present.** Greece (East Aegean Islands).

**References.** Grace (2010).

**Material examined** (*Andrena* aff *derbentina*) GREECE • 1♂; Lesbos, Mytilene Castle; 13 Apr. 2022; J. Devalez leg.; TUZ, TUZ392648 (examined by photograph).

(*Andrena derbentina*) TURKMENISTAN • 2♂, 1♀; Gury Houdan, Kopet Dagh, nh. Shemli [Shamli]; 560–600 m a.s.l.; 20 Apr. 1995; W. Dolin leg.; A.Z. Osytshnjuk det.; ZSM.

**Notes.** Listed from Lesbos without precise specimen details, some discussion of this species is required. This group of species (the *doursana*-group) is challenging to work with and has been confused over time due to the morphologically homogenous females (see Pisanty et al. 2022b). Warncke (1967b: 180) placed *A. derbentina* in combination with *Andrena doursana* Dufour, 1853 before later describing *Andrena mizorbhina* Warncke, 1975 (as a subspecies of *A. doursana*) and noting that *A. derbentina* was distinct (Warncke 1975: 43 “♂: *Clypeus* [of *A. mizorbhina*] ohne Gelbfärbung, ganz dunkel. Vordem als ssp. *derbentina* Mor. bezeichnet: *A. derbentina* stellt aber eine eigene Art dar”).

Some clarification was made by Pisanty et al. (2022b), who elevated *A. mizorbhina* and restricted the distribution to Turkey (only the Antakya area), Lebanon, and Israel & West Bank (Wood et al. 2020; Pisanty et al. 2022b). This species can be separated from other members of the *doursana*-group in the male sex due to its entirely dark clypeus. However, examination of males from Lesbos show a bee presenting a genital capsule that is typical of the *doursana*-group of species, but with dark and almost non-metallic metasomal integument and an entirely dark clypeus. Whilst the clypeus is dark, it cannot be *A. mizorbhina* due to the dark metasomal integument, whereas *A. mizorbhina* has

conspicuously metallic blue metasomal integument. Furthermore, *A. mizorbina* is a Levantine species with Turkish records restricted to Antakya in Hatay province, a region with strong Levantine faunal influences. Given the lack of records of *A. mizorbina* from south-western and western Turkey, it will not be present on the East Aegean Islands.

Concerning *A. derbentina*, a female lectotype was designated by Astafurova et al. (2021) from Derbent (Russia: Dagestan), but the male is not illustrated. Morawitz (1886: 63) gave very scanty details as to the characters of the male, and did not describe the colour of the clypeus. Gusenleitner and Schwarz (2001: 117) were able to examine males from the ZISP type series, and highlighted that the apex of the clypeus was yellow-marked. They also mentioned additional non-type specimens determined by Grünwaldt showing this character. Males from the Kopet Dag in Turkmenistan that I could examine also showed a partially yellow-marked clypeus. Consequently, the material from Lesbos is of uncertain affiliation. It may be *A. derbentina* but simply lacking yellow colouration on the clypeus. It is definitely not *Andrena mucronata* Morawitz, 1871, the only other member of the *doursana*-group currently known from the southern Balkans, and so it here referred to as *A. aff. derbentina* and included in the identification key to facilitate its further study.

#### 70. *Andrena (Micrandrena) distinguenda* Schenck, 1871

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Nedialkov (1914); Warncke (1965a); Warncke (1973, as *Andrena obsoleta* Pérez, 1895 *sensu acutorum*); Standfuss et al. (2011); Wood (2021).

#### 71. *Andrena (Lepidandrena) dorsalis* Brullé, 1833

**Countries present.** Greece, Bulgaria.

**References.** Brullé (1833); Warncke (1965a); Standfuss et al. (2011); Wood (2021).

#### 72. *Andrena (Simandrena) dorsata* (Kirby, 1802)

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Paganetti-Hummler (1912); Warncke (1965a); Warncke (1966); Warncke (1973); Standfuss et al. (2011); Wood (2021).

#### 73. *Andrena (Melandrena) dubiosa* Kohl, 1905

**Countries present.** Greece.

**References.** Warncke (1965a).

**Material examined.** GREECE • 1♀; Asprovalta; 14 Jun. 2022; V. Major leg.; SFC • 6♂, 9♀; Eastern Macedonia and Thrace, Kavala, Apovathra, headland to E; 22–23 May 2023; C. Tourbez, R. Le Divelec & A. Dorchin leg.; ADC/RLDC/TJWC/UMONS • 1♀; Eleftera-Kloster bei Kawala [Eleftheres, Kavala]; 30 May 1918; D. Iltschew leg.; NZMS.

**Notes.** The location of the type specimen (from Turkey) is unclear; Gusenleitner and Schwarz (2002) list the NHMW, but it could not be found there during recent searches. However, the morphological concept in current use is clear, at least in the female sex. Known in the southern Balkans from a few historical specimens, the species was collected commonly during a recent expedition to Eastern Macedonia in 2023. Warncke (1965a: 70) lists “1♀ Süd-Morea (leg. Holtz)”. It is unclear if this is truly *A. dubiosa* since no other specimens from the southern Peloponnese have been located, but this is ultimately a minor quibble; the species is clearly established in the Greek part of Thrace.

#### 74. *Andrena (incertae sedis) ebmerella* Scheuchl, 2011

**Countries present.** Greece (Samos).

**References.** Scheuchl (2011).

**Notes.** This extremely rare species is not considered to be endemic to Greece as a specimen was reported from southern Turkey by Wood (2023a: 67). It remains unclear if the Turkish specimen is conspecific with Greek material, and targeted collection is required to clarify the species, as well as its phylogenetic placement which is completely unknown and currently unassignable.

#### 75. *Andrena (Lepidandrena) eburnea* Warncke, 1975

**Countries present.** Greece\* (East Aegean Islands).

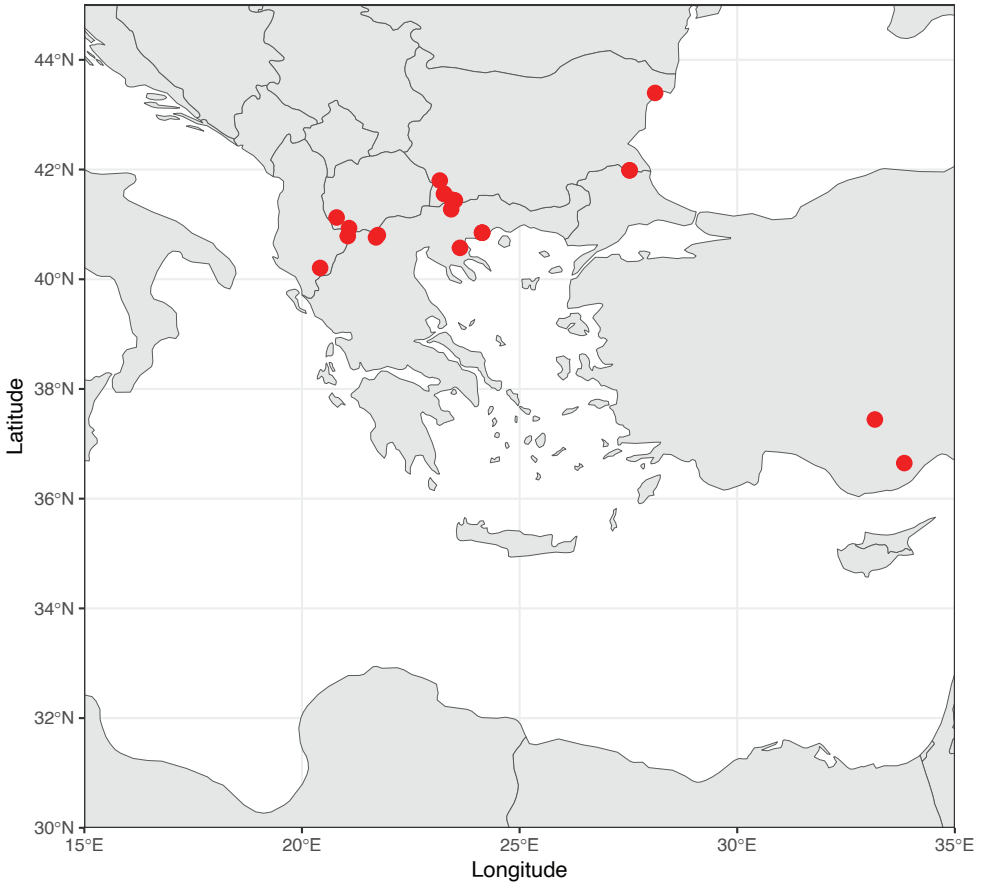
**Notes.** Originally described as a Turkish subspecies of *A. gamskrucki*, Dubitzky et al. (2010) elevated it to species status. Both sexes can be differentiated from *A. gamskrucki* s. str. following the characters in the identification key, and their distributions in the southern Balkans. Whilst *A. gamskrucki* s. str. is restricted to the mainland part of the southern Balkans, specimens of “*A. gamskrucki*” from Lesbos belong to *A. eburnea* (J. Devalez, pers. comm.), which is therefore newly reported for Greece and Europe.

#### 76. *Andrena (Ulandrena) elegans* Giraud, 1863

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1973); Wood (2021).

**Material examined.** ALBANIA • 1♂, 1♀; warmwaterbr Petran; 1 Jun. 2018; K. Janssen leg.; KJCB.



**Figure 75.** Distribution of *Andrena (Ulandrena) elegans* Giraud, 1863 in the southern Balkans. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

**Notes.** Warncke (1966: 389) argued that records from south-east Europe and western Asia were misidentifications of *A. concinna*. Warncke (1973) later changed his mind, and many records of *A. elegans* are available from northern parts of the southern Balkans (Fig. 75). The two species do not or only marginally seem to occur in sympatry due to their respective Mediterranean and continental climatic affinities, as is the case with *A. concinna* and *A. crecca* (Fig. 60).

#### 77. *Andrena (incertae sedis) elsei* Scheuchl & Gusenleitner, 2009

**Countries present.** Greece, North Macedonia.

**References.** Wood (2024a).

**Material examined.** GREECE • 2♀; Avgonima, Xios; 21 Mar. 1996; M.J. Taylor leg.; WML.

**Notes.** Part of the *crocusella*-group (subgenus currently undescribed). Newly reported from the East Aegean Islands (Chios). Female specimens of *A. elsei* present seemingly variable tibial scopae; from the type series and specimens from Chios, the tibial scopae are strongly plumose, but specimens from the Peloponnese and North Macedonia have the tibial scopae weakly and obscurely plumose. It is not clear if this is a specific difference, or just morphological variation. Consequently, for maximum utility the species is included in the female identification key twice, once with and once without plumose scopal hairs.

### 78. *Andrena (Micrandrena) enslinella* Stöckhert, 1924

**Countries present.** Greece, Bulgaria.

**References.** Wood (2021).

### 79. *Andrena (Campylogaster) erberi* Morawitz, 1871

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Morawitz (1871); Dours (1873, as *Andrena fulvocrustata* Dours, 1873); Nedialkov (1914, as *A. kozarowi*); Warncke (1965a); Warncke (1967b); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Notes.** Described from the island of Syra (=Syros) from Erber material (Morawitz 1871). Warncke (1967b: 233) described *Andrena erberi* ssp. *migrans* Warncke, 1967 from Crete.

### 80. *Andrena (Chlorandrena) exquisita* Warncke, 1975

**Countries present.** Greece\*, Bulgaria.

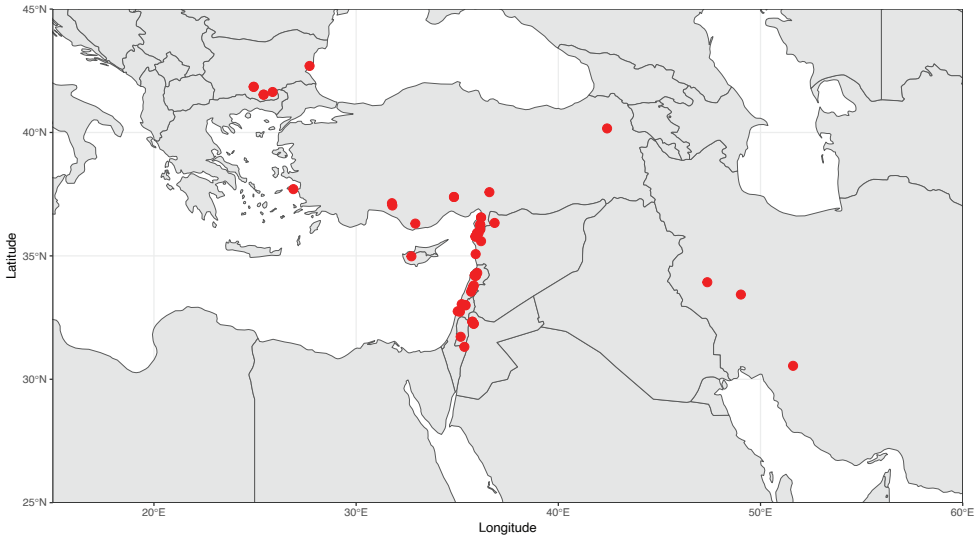
**References.** Warncke (1974a, 1975); Wood (2021).

**Material examined.** GREECE • 2♀; Samos, Pithagorion; 20 Apr. 1988; J.A.W. Lucas leg.; RMNH.

**Notes.** Given the substantial range increases reported for this species (e.g. Pisanty et al. 2018; Wood and Monfared 2022), it is beneficial to present an updated distribution map (Fig. 76), since the reported range has greatly increased since the state of knowledge published by Gusenleitner and Schwarz (2002). The species is also present in north-eastern Greece in Thrace (J. Devaléz, pers. comm., in the National Forest Park of Dadia – Lefkimi – Soufli, E. Scheuchl, pers. comm.).

### 81. *Andrena (Leimelissa) fallax* Eversmann, 1852.

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.



**Figure 76.** Global distribution of *Andrena (Chlorandrena) exquisita* Warncke, 1975. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

**References.** Warncke (1966, as *Andrena ispida* Warncke, 1965); Warncke (1973, as *Andrena ispida*); Wood (2021, as *Andrena ispida*).

## 82. *Andrena (Micrandrena) falsifica* Perkins, 1915

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Dárdon et al. (2014); Wood (2021); Ascher and Pickering (2025).

**Material examined.** **BULGARIA** • 2♀; Kjustendil, Bobosevo [Boboshevo, Бобошево]; 2 May 2012; M. Snížek leg.; OÖLM; **GREECE** • 1♀; Central Macedonia, Mt. Kajmakčalan, ski centre environs; 2000 m a.s.l.; 12 Jun. 2024; T.J. Wood leg.; TJWC • 1♀; Thslq, Kato Nevrokopi [1 km SSW Volakas]; 1200 m a.s.l.; 24 May 2023; R. Le Divelec leg.; RLDC • 1♀; Thslq, Kato Nevrokopi [4 km NE Volakas]; 750 m a.s.l.; 24 May 2023; R. Le Divelec leg.; RLDC.

**Notes.** Largely a species of temperate grasslands, *A. falsifica* is uncommonly recorded in mountainous areas of the southern Balkans. It was first recorded from Greece by Dárdon et al. (2014) from Kaimaktsalan [=Kajmakčalan]. During new searches of Mount Kajmakčalan, the species was observed collecting pollen from *Potentilla* (Rosaceae); *A. falsifica* is either specialised on this plant genus, or at least very strongly associated with it.

## 83. *Andrena (Hoplandrena) ferox* Smith, 1847

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Standfuss et al. (2011); Wood (2021); Ascher and Pickering (2025).

**Material examined.** GREECE • 1♀; Makedonien, Pieria, Pieria-Geb, W Vria; 450–470 m a.s.l.; 1–2 May 2005; H. & R. Rausch leg.; OÖLM.

**Notes.** Very infrequently recorded in the southern Balkans.

**84. *Andrena (Parandrenella) figurata* Morawitz, 1866**

**Countries present.** Bulgaria, North Macedonia.

**References.** Warncke (1973); Wood (2021).

**85. *Andrena (Holandrena) fimbriata* Brullé, 1833**

**Countries present.** Greece, Albania\*.

**References.** Brullé (1833); Paganetti-Hummeler (1912); Warncke (1965a, as *A. forsteri* Warncke, 1965; see clarification in Warncke 1967b: 205).

**Material examined.** ALBANIA • 1♀; Gjerbës; 2 Jun. 2017; M. Jacobs leg.; KJCB • 1♀; Gollomboç; 6 Jun. 2017; M. Jacobs leg.; KJCB • 1♀; landbouwgeb Barmash; 4 Jun. 2018; K. Janssen leg.; KJCB • 1♀; Radanj orchideenwai, Korçë; 3 Jun. 2018; K. Janssen leg.; KJCB • 1♀; sperwer Delvinë, Vlorë; 26 May 2018; K. Janssen leg.; KJCB.

**Notes.** ENDEMIC to the southern Balkans.

**86. *Andrena (Melandrena) flavipes* Panzer, 1799**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Paganetti-Hummeler (1912); Nedialkov (1914); Maidl (1922); Drenowski (1934); Atanasov (1962, 1964); Warncke (1965a); Warncke (1966); Warncke (1967a); Warncke (1969b); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**87. *Andrena (Nobandrena) flavobila* Warncke, 1965**

**Countries present.** Greece.

**References.** Warncke (1965a).

**88. *Andrena (Bryandrena) florea* Fabricius, 1793**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Nedialkov (1914); Warncke (1966); Wood (2021); Ascher and Pickering (2025).

**89. *Andrena (Micrandrena) floricola* Eversmann, 1852**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Paganetti-Hummeler (1912); Warncke (1965a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1♀; berghellin Rehovë Ersekë; 6 Jun. 2018; K. Janssen leg.; KJCB • 2♀; Quark Korça, Gem Korça, Drenova, Drenova NP; 1120–1320 m a.s.l.; 29–30 Jun. 2016; H. & R. Rausch leg.; OÖLM • 1♂, 1♀; vervallen huisje Boboshticë; 7 Jun. 2018; K. Janssen leg.; KJCB.

**90. *Andrena (Lepidandrena) florivaga* Eversmann, 1852**

**Countries present.** Greece, Bulgaria\*.

**References.** Warncke (1965a, as *Andrena molbusina* Blüthgen, 1914).

**Material examined.** BULGARIA • 1♂; S Sinitovo vill; 310 m a.s.l.; 24 Apr. 2023; T. Trifonov leg.; IBER • 1♀; S Touriya vill.; 470 m a.s.l.; 28 Apr. 2023; T. Ljubomirov leg.; IBER; GREECE • 1♂; Thslq, Kato Nevrokopi [1 km SSW Volakas]; 1200 m a.s.l.; 24 May 2023; R. Le Divelec leg.; RLDC.

**Notes.** Very uncommonly recorded in the southern Balkans.

**91. *Andrena (Holandrena) forsterella* Osytshnjuk, 1978**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\* (Fig. 24).

**References.** Schubert (1995, as *A. wilhelmi*); Schönitzer et al. (1995); Wood (2021).

**Notes.** Inclusive of *A. wilhelmi*; see discussion in section Subgenus *Holandrena* Pérez, 1890 in the Results.

**92. *Andrena (Andrena) fucata* Smith, 1847**

**Countries present.** Greece, North Macedonia, Albania\*.

**References.** Warncke (1966); Warncke (1973).

**Material examined.** ALBANIA • 1♀; NW Boge [Bogë]; 10 Jun. 2013; K. Deneš leg.; OÖLM • 1♂, 1♀; 3 km N of Valbonë; 28 May 2024; W. Vertommen leg.; WVC.

**93. *Andrena (Truncandrena) fuligula* Warncke, 1965**

**Countries present.** Greece (East Aegean Islands).

**References.** Rasmont et al. (2017).

**94. *Andrena (Andrena) fulva* (Müller, 1766)**

**Countries present.** Greece, Bulgaria.

**References.** Drenowski (1936); Grace (2010); Wood (2021).

**95. *Andrena (Chrysandrena) fulvago* (Christ, 1791)**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Warncke (1965a); Warncke (1966); Warncke (1967a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**96. *Andrena (Euandrena) fulvata* Stöckhert, 1930**

**Countries present.** Greece\*, Bulgaria.

**References.** Wood (2021); Wood et al. (2021).

**Material examined.** **BULGARIA** • 1♀; Blagoevgrad, Dobrinishte, 5.3 km NEE, Nestos River Bridge environs; 21 May 2024; T.J. Wood leg.; TJWC; **GREECE** • 1♀; Peloponnese, 38 km road Kalmata, Sparti; 25 Apr. 2005; J. Halada leg.; OÖLM • 1♀; Peloponnese, Mt. Taigetos [Taygetus], 30 km NWW Sparti; 29 Apr. 2005; J. Halada leg.; OÖLM • 1♀; Thslq, Kato Nevrokopi [1 km SSW Volakas]; 1200 m a.s.l.; 24 May 2023; R. Le Divelec leg.; RLDC • 1♀; Thslq, Kato Nevrokopi [3.8 km SE Volakas]; 1400 m a.s.l.; 24 May 2023; R. Le Divelec leg.; RLDC.

**Notes.** Uncommonly recorded in the southern Balkans, favouring cooler temperate habitats. See discussion in Subgenus *Euandrena* Hedicke, 1933 in the Results.

**97. *Andrena (Notandrena) fulvicornis* Schenck, 1861**

**Countries present.** Greece\*, Bulgaria, North Macedonia.

**References.** Wood (2021).

**Material examined.** **GREECE** • 1♀; Chalkidiki [Halkidiki], Kassandria, Paliouri; 18 May 2014; M. Snížek leg.; OÖLM • 4♀; Peloponnese, 30 km SEE Olympia, Loutra; 2 May 2005; M. Kadlecová leg.; OÖLM • 1♂; Rhodes, Tsambika, Malaise trap; 26 May – 3 June 1986; M.C. Day & M.G. Fitton leg.; NHMUK.

**Notes.** Seemingly not previously recorded from Greece in a narrow sense (i.e. not within Warncke's broad species concept of *Andrena nitidiuscula* Schenck, 1853).

**98. *Andrena (Ulandrena) fulvitaris* Brullé, 1833**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Brullé (1833); Warncke (1965a); Warncke (1967a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1♂; Burrel-Lis [between Burrel and Lis]; 1000 m a.s.l.; 6 Jun. 2013; K. Deneš leg.; OÖLM • 1♀; N Arras; 3 Jun. 2023; K. Deneš leg.; OÖLM • 2♀; Permet env.; 500 m a.s.l.; 1 May – 30 Jun. 2013; K. Deneš leg.; OÖLM/TJWC; ROMANIA • 1♂; Dobrogea [Dobruja], Canaraua Fetii; 22 May 1994; L. Székely leg.; OÖLM.

**Notes.** Newly recorded also for Romania\*.

### 99. *Andrena (Cnemidandrena) fuscipes* (Kirby, 1802)

**Countries present.** Bulgaria, Albania.

**References.** Nedialkov (1914, as *Andrena pubescens* (Kirby, 1802)); Atanassov (1962); Scheuchl and Willner (2016); Ascher and Pickering (2025).

**Notes.** It has not been possible to examine any specimens of *A. fuscipes* from the southern Balkans.

### 100. *Andrena (Melandrena) fuscocalcarata* Morawitz, 1877

**Countries present.** Greece, Bulgaria\*, Albania\*.

**References.** Grace (2010).

**Material examined.** ALBANIA • 1♂; Tepelenë, Bënçë; 23 May 2001; A. van Nieuwenhuyzen leg.; RMNH.

**Notes.** Grace (2010) mentioned the species from Lesbos; a specimen from this island labelled “Lesvos, 1.8 km NW Vatousa; 220 m a.s.l.; 29 Apr. 2004; E. Lam-born leg.” has been observed (E. Scheuchl pers. comm.). Additional specimens from Greece (“Samos, Kerkis-Süd, Pinus/Quercus ilex zone; 700–900 m a.s.l.; 17 May 2000; A.W. Ebmer leg.”) and Bulgaria (“5 km N Harmandli; 200 m a.s.l.; 14 Jun. 2008; M. + Z. Halada leg.; OÖLM”) have also been observed (E. Scheuchl, pers. comm.).

### 101. *Andrena (Melanapis) fuscosa* Erichson, 1835

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Nedialkov (1914, as *Andrena ephippium* Spinola, 1838); Warncke (1965a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1♂; Fier region, Lushnjë env.; 177 m a.s.l.; 29 Jun. 2018; D. Benda leg.; JSPC.

**Notes.** This common and widespread species does not previously appear to have been reported from Albania.

**102. *Andrena (Orandrena) gallinula* Warncke, 1975**

**Countries present.** Greece\* (Fig. 45).

**Notes.** See discussion in Subgenus *Orandrena* Warncke, 1968 in the Results. *Andrena gallinula* was actually listed for Greece by Petanidou (1991) in the technical species list for what would go on to be published as Petanidou and Ellis (1993). Specimens of *Andrena* are listed as being determined by J. Gusenleitner and H. Teunissen, but no precise records were presented, and the species has never been listed as part of the European bee fauna (Ghisbain et al. 2023, 2025); the present work is therefore considered to be the first substantiated report of its presence in Greece and Europe.

**103. *Andrena (Lepidandrena) gamskrucki* Warncke, 1965**

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1965a); Warncke (1973); Wood (2021).

**Notes.** ENDEMIC to the southern Balkans.

**104. *Andrena (incertae sedis) garrula* Warncke, 1965**

**Countries present.** Bulgaria.

**References.** Wood (2021).

**Notes.** Formerly placed in the subgenus *Orandrena*, it was found to be closely related to but distinct from this grouping (Pisanty et al. 2022a). It must therefore currently be placed as *incertae sedis* despite its close proximity.

**105. *Andrena (Euandrena) glabriventris* Alfken, 1935**

**Countries present.** Greece\*.

**Notes.** See Subgenus *Euandrena* Hedicke, 1933 in the Results.

**106. *Andrena (Chrysandrena) glandaria* Warncke, 1975**

**Countries present.** Greece (East Aegean Islands).

**Material examined.** GREECE • 1♂; Rhodos, Afandou, Prof. Illias to Elousa; 258 m a.s.l.; 24 May 2017; E. Ockermüller leg.; OÖLM • 2♂, 2♀; Rhodos, Kamiros, Salakas Villas; 215 m a.s.l.; 22 May 2017; E. Ockermüller leg.; OÖLM/TJWC.

**References.** Gusenleitner and Schwarz (2002).

**Notes.** Gusenleitner and Schwarz (2002) indicate the presence of *A. glandaria* on the island of Rhodes, and recently collected specimens are available. *Andrena glandaria*

remains challenging to consistently separate from *A. hesperia* Smith, 1853; a subgeneric revision is ongoing (G. Pisanty, TJW, in prep.).

### 107. *Andrena (Euandrena) glidia* Warncke, 1965

**Countries present.** Greece (Fig. 15).

**References.** Warncke (1965a); Standfuss et al. (2011).

### 108. *Andrena (Graecandrena) graecella* Warncke, 1965

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Pittioni and Stöckhert (1950, as *Andrena strymonia* Pittioni, 1950 ♀ nec. ♂); Warncke (1965a); Warncke (1973); Wood (2021).

**Material examined.** ROMANIA • 3♀; Filiasi [Filiași]; 13 May 1994; Mi. Halada & K. Deneš leg.; OÖLM.

**Notes.** ENDEMIC to the southern Balkans. Reported also as new for Romania\*.

### 109. *Andrena (Euandrena) granulosa* Pérez, 1903

**Countries present.** Greece\*, Bulgaria, North Macedonia.

**References.** Warncke (1973); Wood (2021).

**Material examined.** GREECE • 1♂; 35 km NE Kalambaka; 15 May 2005; J. Halada leg.; OÖLM • 2♂, 2♀; Attika, Agios Pedios W Nea Makri; 520 m a.s.l.; 4 May 1992; H. Rausch leg.; OÖLM • 1♀; Central Greece, Arachova, 3.3 km NW of Arachova; 1150 m a.s.l.; 9 Apr. 2024; T.J. Wood leg.; RMNH • 1♂; Chelmos [Aroania]; 1700 m a.s.l.; 19 May 1987; H. Teunissen leg.; RMNH • 1♂; Eastern Macedonia and Thrace, Drama, Volakas, 2.6 km S of Volakas; 1150 m a.s.l.; 24 May 2023; T.J. Wood leg.; TJWC • 1♂; Ep., Thesprotien, Souliou-Geb., NE Koukoulii; 1150–1200 m a.s.l.; 25 May 1993; H. & R. Rausch leg.; OÖLM • 1♂; Epirus, NW Neohori [Neochori], Thesprotien; 250 m a.s.l.; 3 May 1992; H. Rausch leg.; OÖLM • 4♂; Mount Mavrovuni, 35 km N Volos; 12 May 2005; J. Halada leg.; OÖLM/TJWC • 1♂; Olympos, Prionia valley; 17 May 1991; J. Batelka leg.; OÖLM • 1♂; Peloponnes/Messenien, Oros Tetrazio N Kefalovrisi [Kefalovrysi]; 17 May 1992; H. Rausch leg.; OÖLM • 1♂; Peloponnese, 12 km NWW Sparti; 26 May 2005; J. Halada leg.; OÖLM • 2♂; Peloponnese, 20 km S Megalopoli; 1 May 2005; J. Halada leg.; OÖLM • 1♂; Peloponnese, Mt. Taigetos [Taygetus], 30 km NWW Sparti; 29 Apr. 2005; J. Halada leg.; OÖLM.

**Notes.** Surprisingly frequently encountered in Greece, but seemingly not previously recorded. Some specimens may have been misidentified as *A. vulpecula* Kriechbaumer, 1873.

**110. *Andrena (Melandrena) gravida* Imhoff, 1832**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Nedialkov (1914, as *Andrena extricata* Smith, 1849); Warncke (1973); Standfuss et al. (2011).

**Material examined.** ALBANIA • 2♀; Malil Tomorrit [Mount Tomorr]; 31 May 2017; M. Jacobs leg.; KJCB • 1♀; N of Valbonë; 28 May 2024; W. Vertommen leg.; WVC.

**Notes.** This species was supposed to be listed from Bulgaria by Wood (2021) as species no. 73, but was accidentally deleted during the production of the proof. *Andrena gravida* can be commonly encountered in Bulgaria (IBER, JSPC, NZMS, OÖLM).

**111. *Andrena (Notandrena) griseobalteata* Dours, 1872**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Paganetti-Hummler (1912, as *Andrena erythrocnemis* Morawitz, 1871 *sensu auctorum*); Warncke (1966, as *Andrena erythrocnemis*); Warncke (1973, as *Andrena erythrocnemis*); Standfuss et al. (2011, as *Andrena erythrocnemis*); Wood (2021, as *Andrena erythrocnemis*)

**Notes.** The nomenclatural situation was clarified by Wood (2023b).

**112. *Andrena (incertae sedis) grossella* Grünwaldt, 1976**

**Countries present.** Greece.

**References.** Grünwaldt (1976); Standfuss et al. (2011).

**Notes.** Part of the *crocusella*-group (subgenus currently undescribed). **ENDEMIC** to Greece and the southern Balkans.

**113. *Andrena (Trachandrena) haemorrhoea* (Fabricius, 1781)**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Nedialkov (1914, as *Andrena albicans* (Müller, 1776) *sensu auctorum*); Warncke (1965a); Warncke (1966); Warncke (1969b); Ascher and Pickering (2025).

**Notes.** This species was supposed to be listed from Bulgaria by Wood (2021) as species no. 74, but was accidentally deleted during the production of the proof.

**114. *Andrena (Lepidandrena) haladai* sp. nov.**

**Countries present.** Greece.

**Notes.** **ENDEMIC** to the southern Balkans.

**115. *Andrena (Charitandrena) hattorfiana* (Fabricius, 1775)**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Brullé (1833, as *Andrena dimidiata* Brullé, 1833); Meunier (1897); Paganetti-Hummeler (1912); Nedialkov (1914); Atanassov (1964); Warncke (1965a); Warncke (1966); Warncke (1967a); Warncke (1973); Standfuss et al. (2011).

**Notes.** This species was supposed to be listed from Bulgaria by Wood (2021) as species no. 75, but was accidentally deleted during the production of the proof.

**116. *Andrena (Ulandrena) heinrichi* Grünwaldt, 2005**

**Countries present.** Greece (Samos).

**Notes.** This species is not endemic to Greece, but it has a remarkably tiny distributional range restricted to the island of Samos and a small part of western Turkey around Kuşadası.

**References.** Grünwaldt et al. (2005); Wood (2024a).

**117. *Andrena (Micrandrena) helenica* Warncke, 1965**

**Countries present.** Greece (Fig. 22).

**References.** Warncke (1965a); Standfuss et al. (2011).

**Notes.** ENDEMIC to Greece and the southern Balkans.

**118. *Andrena (Andrena) helvola* (Linnaeus, 1758)**

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Nedialkov (1914); Warncke (1988); Gusenleitner and Schwarz (2002); Wood (2021); Ascher and Pickering (2025).

**119. *Andrena (Chrysandrena) hesperia* Smith, 1853**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Warncke (1965a); Warncke (1973); Standfuss et al. (2011); Wood (2021); Ascher and Pickering (2025).

**120. *Andrena (Chlorandrena) humabilis* Warncke, 1965**

**Countries present.** Greece, Bulgaria, North Macedonia\*.

**References.** Warncke (1965a); Wood (2021).

**Material examined.** NORTH MACEDONIA • 1♂; Polog reg., Sirichino, meadow; 430 m a.s.l.; 2–7 Apr. 2021; V. Bureš leg.; JSPC • 1♀; Vardar reg., Papeliste, orchard; 140 m a.s.l.; 1–6 Apr. 2021; V. Bureš leg.; JSPC.

### 121. *Andrena (Chlorandrena) humilis* Imhoff, 1832

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Paganetti-Hummeler (1912); Nedialkov (1914); Warncke (1965a); Warncke (1966); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Notes.** *Andrena humilis* is treated here in a broad sense, containing the “subspecies” *A. humilis* ssp. *cucullata* Warncke, 1975 (described from Greece: Athens), *A. humilis* ssp. *hiaticula* Warncke, 1975 (described from Crete: Knossos), and *A. humilis* ssp. *indigena* Warncke, 1975 (described from Turkey: Şereflikoçhisar). At the present time, it is not possible to comment on the potential validity of these names as full species. *Andrena humilis* in the West Mediterranean shows both morphological and genetic variation based on barcodes (2023b: 254–255), but it does not seem possible to consistently delineate more than one taxon. The status of these eastern names must remain an open question for now.

### 122. *Andrena (Poecilandrena) hybrida* ssp. *tauriensis* Warncke, 1975

**Countries present.** Greece\* (Fig. 49).

**Material examined.** GREECE • 1♀; Aghiossos (Lesbos); 11 May 1980; H. Teunissen leg.; RMNH • 3♂, 1♀; Lesbos, Olympus Rd.; 907 m a.s.l.; 21 Apr. 1997; C. Clee leg.; WML; TURKEY • 1♂, 1♀; Çanakkale; 2024; L. Efil leg.; IUZC • 1♀; Mut, Sertavul [Sertavul Geçidi]; 1600 m a.s.l.; 2 Jun. 1967; J. Gusenleitner leg.; OÖLM (**holotype**) • 2♀; Mut, Sertavul [Sertavul Geçidi]; 1600 m a.s.l.; 31 May 1967; J. Gusenleitner leg.; OÖLM (**paratypes**).

**Notes.** Newly reported from Greece and the southern Balkans as a whole; the RMNH specimen was originally determined as *A. sphecodimorpha* by Teunissen. Additional specimens were found in the WML collection, supporting Teunissen’s capture and reducing the likelihood that it was a mislabelled specimen. *Andrena hybrida* ssp. *tauriensis* and *A. sphecodimorpha* can be separated using the characters in the identification key below. Additionally, new specimens from western Turkey were located, extending the Turkish range westwards from south-west Turkey (Warncke 1974a, 1975). This “subspecies” may well deserve species status, but further study is required given the small number of known specimens and the current complexity found in the non-metallic members of the subgenus *Poecilandrena*.

### 123. *Andrena (Graecandrena) hyemala* Warncke, 1973

**Countries present.** Greece, Bulgaria, North Macedonia, Albania (Fig. 23).

**References.** Warncke (1973); Dylewska (1987); Standfuss et al. (2011); Wood (2021); Ascher and Pickering (2025).

**Material examined.** ALBANIA • 1♂; Mali Dajti [Mali i Dajtit]; 28 May 1959; J. Moucha leg.; NMPC • 4♀; NW Boge [Bogë]; 10 Jun. 2013; K. Deneš leg.; OÖLM • 1♀; Radanj orchideenwai, Korçë; 3 Jun. 2018; K. Janssen leg.; KJCB.

**Notes.** *Andrena hyemala* was listed from Albania by Dylewska (1987: 549) without presenting specific records. It can be supported here by newly examined material.

#### 124. *Andrena (incertae sedis) hypopolia* Schmiedeknecht, 1884

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Warncke (1973, as *Andrena numida* Lepeletier, 1841); Wood (2021); Ascher and Pickering (2025).

**Notes.** Formerly placed in the strictly Nearctic subgenus *Thysandrena* Lanham, 1949 (Pisanty et al. 2022a), it is instead part of an undescribed subgenus best referred to as the *numida*-group.

#### 125. *Andrena (Aenandrena) hystrix* Schmiedeknecht, 1883

**Countries present.** Bulgaria\*.

**Material examined.** BULGARIA • 1♀; Blagoevgrad, Katuntsi, 2.6 km ESE of Katuntsi; 300 m a.s.l.; 25 May 2024; T.J. Wood leg.; RMNH, RMNH.INS.1152477; TURKEY • 1♀; 30 km N Kutahya [Kütahya]; 13 Jun. 2000; M. Halada leg.; OÖLM • 1♀; Burdur, 20 km SW Burdur; 940 m a.s.l.; 7 Jul. 2006; M. Halada leg.; OÖLM • 1♂; Denizli, 10 km NE Denizli; 270 m a.s.l.; 5 Jul. 2006; J. Halada leg.; OÖLM.

**Notes.** This species was unexpectedly encountered in south-western Bulgaria on warm grassland fragments surrounded by forest. Warncke (1975: 71) described *A. hystrix* ssp. *rufilata* Warncke, 1975 from central Turkey, and the closest Turkish specimens I could examine are found approximately 600–650 km to the east and east-south-east in the provinces of Kütahya, Burdur, and Denizli. In this context, *A. hystrix* is simply considered to have a marginal and, until recently, overlooked presence in the southern Balkans.

#### 126. *Andrena (Micrandrena) illyrica* Warncke, 1975

**Countries present.** Greece, North Macedonia\*.

**References.** Warncke (1974a, 1975).

**Material examined.** GREECE • 2♀; Thessaloniki, Thessaloniki; 19 Apr. 1991; T. Petanidou leg.; RMNH; NORTH MACEDONIA • 1♂; Vardar reg., Papeliste, steppe; 130 m a.s.l.; 1–4 Apr. 2021; V. Bureš leg.; JSPC • 1♀; Vardar reg., Papeliste, steppe; 130 m a.s.l.; 16–26 Apr. 2021; V. Bureš leg.; JSPC; UKRAINE • 1♀; Cherson [Kher-son]; 7 May 1943; W. Grünwaldt leg.; W. Grünwaldt det.; RMNH.

**Notes.** Warncke (1975: 49) described *A. illyrica* with a holotype from Romania, paratypes from Crimea, and a paratype from “Saloniki” (=Thessaloniki). Due to the rarity of specimens in collections, all examined non-type specimens are presented here. It is unclear why *A. illyrica* is so uncommonly encountered; given the confusing genetic results from barcode analysis, further study is merited. A male was collected in North Macedonia which shows the same broad ocelloccipital distance as the female, allowing recognition. It is not considered necessary to formally describe this specimen, and this character is integrated into the identification key below.

### 127. *Andrena (Graecandrena) impunctata* Pérez, 1895

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a, as *Andrena paula* Noskiewicz, 1939); Warncke (1969b); Wood (2021).

**Material examined.** ALBANIA • 3♀; Tepelenë; 27 May 2013; K. Deneš leg.; OÖLM.

### 128. *Andrena (incertae sedis) incisa* Eversmann, 1852

**Countries present.** ?North Macedonia.

**References.** Noskiewicz (1924); Kinel and Noskiewicz (1930).

**Notes.** *Andrena incisa* forms a species pair with *A. lateralis* Morawitz, 1876 that currently lacks a subgenus; it is placed very close to subgenus *Brachyandrena* Pittioni, 1948 and may potentially be included within it in the future (S. Bossert, G. Pisanty, T.J. Wood, *unpublished data*). The two cited works list *A. incisa* only from “Macedonia”. It has not been possible to examine any specimens of *A. incisa* from the southern Balkans, with the nearest confirmed records coming from western Turkey (Burdur). However, based on these works, it can cautiously be accepted as part of the fauna of the southern Balkans.

### 129. *Andrena (Micrandrena) incognita* Warncke, 1975

**Countries present.** North Macedonia\*.

**Material examined.** NORTH MACEDONIA • 1♂, 1♀; Vardar reg., Papeliste, steppe; 130 m a.s.l.; 1–6 Apr. 2021; V. Bureš leg.; JSPC.

**Notes.** Newly reported for both North Macedonia and for Europe.

### 130. *Andrena (Andrena) inconstans* Morawitz, 1877

**Countries present.** Greece\*, Bulgaria.

**References.** Warncke (1965a, as *Andrena bulgariensis*); Wood (2023a).

**Material examined.** GREECE • 1♀; Livadies [co-ordinates given, 15 km SW Lamia]; 1800 m a.s.l.; 9 Jun. 1987; H. Malicky leg.; OÖLM.

**131. *Andrena (Ulandrena) incustodita* Wood, 2024**

**Countries present.** Greece (Crete).

**References.** Warncke (1965a, as *Andrena abbreviata* Dours, 1873 *sensu auctorum*); Wood (2024a).

**Notes.** This case was extensively discussed by Wood (2024a); **ENDEMIC** to the southern Balkans and specifically to the island of Crete.

**132. *Andrena (Taeniandrena) intermedia* Thomson, 1870**

**Countries present.** Greece, Bulgaria, Albania\*.

**References.** Warncke (1973); Wood (2021).

**Material examined.** ALBANIA • 1♂; Malil Tomorrit [Mount Tomorr]; 12 Jun. 2018; K. Janseen leg.; KJCB • 1♀; Shkodër reg., Bogë env.; 1047 m a.s.l.; 25 Jun. 2018; D. Benda leg.; JSPC • 5♂; Tropojë; 15 Jul. 2021; M. Jacobs leg.; KJCB.

**133. *Andrena (Simandrena) kocourecki* Wood, 2021**

**Countries present.** Bulgaria.

**References.** Wood (2021).

**Notes.** **ENDEMIC** to Bulgaria and the southern Balkans.

**134. *Andrena (Holandrena) labialis* (Kirby, 1802)**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Paganetti-Hummeler (1912); Nedialkov (1914); Atanassov (1962, 1964); Warncke (1965a); Warncke (1966); Warncke (1969b); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**135. *Andrena (Poecilandrena) labiata* Fabricius, 1781**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Nedialkov (1914, as *Andrena cingulata* (Fabricius, 1775) *sensu auctorum*); Hedicke (1942); Warncke (1973); Ebmer (2009); Wood (2021).

**Material examined.** ALBANIA • 1 ♀; berghellin Rehovë Ersekë; 6 Jun. 2018; K. Janssen leg.; KJCB • 1 ♀; Burrel-Lis [between Burrel and Lis]; 1000 m a.s.l.; 6 Jun. 2013; K. Deneš leg.; OÖLM • 1 ♂; Malil Tomorrit [Mount Tomorr]; 31 May 2017; M. Jacobs leg.; KJCB • 3 ♀; Mount Tomorr; 20 Jul. 2017; K. Janssen leg.; KJCB • 1 ♂, 1 ♀; NW Boge [Bogë]; 10 Jun. 2013; K. Deneš leg.; OÖLM • 1 ♂; Tropojë; 15 Jul. 2021; M. Jacobs leg.; KJCB • 1 ♀; Voskopojë; 8 Jun. 2018; K. Janssen leg.; KJCB.

**136. *Andrena (Aciandrena) lamiana* Warncke, 1965**

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1965a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**137. *Andrena (Andrena) lapponica* Zetterstedt, 1838**

**Countries present.** Bulgaria, North Macedonia, Albania\*.

**References.** Wood (2021).

**Material examined.** ALBANIA • 2 ♀; Tropojë; 16 Jul. 2021; M. Jacobs leg.; KJCB.

**138. *Andrena (incertae sedis) larisana* Warncke, 1965**

**Countries present.** Greece.

**References.** Warncke (1965a).

**Notes.** The placement of *A. larisana* and the species around it (the *tunetana*-group, see Wood 2025a: 230) remains unclear. It is best currently treated as only a species group. This species is not endemic to the southern Balkans, as it can be found also in western Turkey (Hazir et al. 2014).

**139. *Andrena (incertae sedis) lasithi* sp. nov.**

**Countries present.** Greece (Crete).

**Notes.** Part of the *crocusella*-group (subgenus currently undescribed). **ENDEMIC** to the southern Balkans and specifically to the island of Crete.

**140. *Andrena (incertae sedis) lateralis* Morawitz, 1876**

**Countries present.** Greece, Bulgaria\*, North Macedonia, Albania\*.

**References.** Warncke (1965a); Warncke (1973).

**Material examined.** ALBANIA • 1♂; berghellin Rehovë Ersekë; 5 Jun. 2018; K. Janssen leg.; KJCB • 2♀; Gjerbës; 2 Jun. 2017; M. Jacobs leg.; KJCB • 1♀; landbouwgeb Barmash; 4 Jun. 2018; K. Janssen leg.; KJCB • 1♀; Rivierbedding Devolij Gorge [Drenije Gorge]; 10 Jun. 2018; K. Janssen leg.; KJCB • 2♂; Voskopojë; 8 Jun. 2018; K. Janssen leg.; KJCB; BULGARIA • 1♂; Witosha Geb. [Vitosha mountain], Marchaevo; 18 May 1939; N. Atanassov leg.; NZMS.

**Notes.** *Andrena lateralis* forms a species pair with *A. incisa* that currently lacks a subgenus; it is placed very close to subgenus *Brachyandrena* Pittioni, 1948 and may potentially be included within it in the future (S. Bossert, G. Pisanty, T.J. Wood, *unpublished data*). Friese (1923: 205) described the synonymous *Andrena sexmaculata* Friese, 1923 from Nikolatal (=Karanikolica) and Jostoff (=Josifovo) in North Macedonia.

#### 141. *Andrena (Taeniandrena) lathyri* Alfken, 1899

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1973); Standfuss et al. (2011); Wood (2021).

#### 142. *Andrena (Aciandrena) lediveleci* Wood, 2024

**Countries present.** Greece (Crete).

**References.** Wood (2024a).

**Notes.** ENDEMIC to the southern Balkans and specifically to the island of Crete. Placement of *Andrena sandanskia* Warncke, 1973, the sister species of *A. lediveleci*, has been uncertain, but it is likely best placed in the subgenus *Aciandrena* (S. Bossert, G. Pisanty, T.J. Wood, *unpublished data*). *Andrena lediveleci* is therefore also placed in this subgenus.

#### 143. *Andrena (Simandrena) lepida* Schenck, 1861

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Atanassov (1962, 1964, as *Andrena separanda* Schmiedeknecht, 1880); Warncke (1966); Warncke (1973); Wood (2021).

#### 144. *Andrena (Taeniandrena) leucopsis* Warncke, 1967

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1973); Standfuss et al. (2011); Wood (2021).

**145. *Andrena (Melandrena) limata* Smith, 1853**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Warncke (1965a); Standfuss et al. (2011); Wood (2021); Ascher and Pickering (2025).

**146. *Andrena (Limbandrena) limbata* Eversmann, 1852**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Nedialkov (1914); Atanassov (1962, 1964); Warncke (1965a); Warncke (1966); Warncke (1967a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**147. *Andrena (Euandrena) afflimosa* Warncke, 1969**

**Countries present.** Greece, Bulgaria\*, Albania\* (Fig. 15).

**References.** Rasmont et al. (2017, as *Andrena limosa*).

**Notes.** See section Subgenus *Euandrena* Hedicke, 1933 in the Results.

**148. *Andrena (Stenomelissa) lonicera* Warncke, 1973**

**Countries present.** North Macedonia.

**References.** Warncke (1973).

**Notes.** ENDEMIC to North Macedonia and the southern Balkans.

**149. *Andrena (Melandrena) magna* Warncke, 1965**

**Countries present.** Greece, Bulgaria\*.

**References.** Warncke (1965a).

**Material examined.** BULGARIA • 15♀; NE Bulgarevo vill.; 83 m a.s.l.; 4–5 May 2023; T. Ljubomirov leg.; IBER • 3♀; SW Balchik; 211 m a.s.l.; 5 May 2023; T. Ljubomirov leg.; IBER.

**150. *Andrena (Micrandrena) magunta* Warncke, 1965**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a); Warncke (1973); Wood (2021).

**Material examined.** ALBANIA • 1♂, 1♀; vervallen huisje Boboshticë; 7 Jun. 2018; K. Janssen leg.; KJCB • 1♂, 2♀; Voskopojë; 8 Jun. 2018; K. Janssen leg.; KJCB.

### 151. *Andrena (Margandrena) marginata* Fabricius, 1777

**Countries present.** Greece\*, Bulgaria, North Macedonia, Albania.

**References.** Nedialkov (1914, as *Andrena cetii* (Schrank, 1781)); Warncke (1966); Wood (2021); Ascher and Pickering (2025).

**Material examined.** GREECE • 1♂; Ilis, Olympia; 2–3 Oct. 1962; Ent. Exc. Zool. Mus. leg.; RMNH; NORTH MACEDONIA • 2♀; Ohrid lac, Sveti Naum; 8 Aug. 1972; R. Wahis leg.; K. Warncke det.; CEGX.

**Notes.** The listing of this species from North Macedonia by Ascher and Pickering (2025) can be independently confirmed through a Warncke-determined specimen. The specific record comes from the collection of Donald Baker (KSEM973096) housed at the Kansas Natural History Museum. *Andrena marginata* does not seem to have been previously recorded from Greece.

### 152. *Andrena (Notandrena) meridionalis* Dalla Torre & Friese, 1895

**Countries present.** Greece, Albania\* (Fig. 42).

**References.** Dours (1873); Warncke (1965a, as *Andrena langadensis*).

### 153. *Andrena (Chrysandrena) merula* Warncke, 1969

**Countries present.** Greece, Bulgaria, Albania\*.

**References.** Gusenleitner and Schwarz (2002); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1♀; rotshelling Topovë; 29 May 2018; K. Janssen leg.; KJCB • 1♀; schuinhelling Gjirokaster; 27 May 2018; K. Janssen leg.; KJCB.

**Notes.** *Andrena merula* was originally described from Israel, and given the complexity that exists within the subgenus *Chrysandrena* Hedicke, 1933 (G. Pisanty, pers. comm.; *unpublished data*), it may well be that the taxon present in the southern Balkans is not actually the true *A. merula*; a focused subgeneric revision is required.

### 154. *Andrena (Micrandrena) minutula* (Kirby, 1802)

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Paganetti-Hummler (1912, as *Andrena parvula* (Kirby, 1802)); Nedialkov (1914, as *A. minutula* and *A. parvula*); Warncke (1965a, as *Andrena minutula* and *Andrena dargia* Warncke, 1965); Warncke (1967a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1♂, 1♀; NE Arras; 2 Jul. 2012; K. Deneš leg.; OÖLM • 1♀; NW Boge [Bogë]; 10 Jun. 2013; K. Deneš leg.; OÖLM • 1♀; sperwer Delvinë, Vlorë; 26 May 2018; K. Janssen leg.; KJCB • 1♀; Valbona [Valbonë]; 8 Jul. 2012; K. Deneš leg.; OÖLM • 1♂; vervallen huisje Boboshticë; 7 Jun. 2018; K. Janssen leg.; KJCB • 2♀; Voskopojë; 8 Jun. 2018; K. Janssen leg.; KJCB.

**155. *Andrena (Micrandrena) minutuloides* Perkins, 1914**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Warncke (1966); Warncke (1973); Wood (2021).

**156. *Andrena (incertae sedis) mistrensis* Grünwaldt, 2005**

**Countries present.** Greece.

**References.** Grünwaldt (2005); Wood (2025a).

**Notes.** The phylogenetic placement of this species is completely unclear, and no genetic data are currently available.

**157. *Andrena (Andrena) mitis* Schiedeknecht, 1883**

**Countries present.** Greece, Bulgaria.

**References.** Warncke (1965a); Wood (2021).

**158. *Andrena (Lepidandrena) mocsaryi* Schiedeknecht, 1884**

**Countries present.** Greece, Bulgaria, Albania.

**References.** Nedialkov (1914); Warncke (1965a); Standfuss et al. (2011); Wood (2021); Ascher and Pickering (2025).

**159. *Andrena (incertae sedis) monacha* Warncke, 1965**

**Countries present.** Greece (East Aegean Islands).

**References.** Grace (2010).

**Material examined.** GREECE • 1♀; Aghiossos (Lesbos); 11–13 May 1980; H. Teunissen leg.; RMNH.

**Notes.** *Andrena monacha* is part of an undescribed subgenus that is best referred to as the *monachal*-group at the present time (containing also *Andrena aruana* Warncke, 1969). Listed from Lesbos by Grace (2010); this can be confirmed with specimens.

**160. *Andrena (Euandrena) montana* Warncke, 1973**

**Countries present.** Greece, North Macedonia, Albania.

**References.** Warncke (1973); Warncke (1988); Gusenleitner and Schwarz (2002); Ascher and Pickering (2025).

**Material examined.** GREECE • 3♀; Central Macedonia, Mt. Kajmakčalan, ski centre environs; 2000 m a.s.l.; 12 Jun. 2024; T.J. Wood leg.; TJWC.

**Notes.** Very uncommon in collections, but *A. montana* is present on high mountains in the southern Balkans. At Mount Kajmakčalan, it was observed collecting pollen from *Potentilla* (Rosaceae) in alpine grassland (Fig. 85E).

**161. *Andrena (Melandrena) morio* Brullé, 1833**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Brullé (1833); Paganetti-Hummler (1912); Hedicke (1942); Atanasov (1962, 1964); Warncke (1965a); Warncke (1966); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**162. *Andrena (Didonia) mucida* Kriechbaumer, 1873**

**Countries present.** Greece, Bulgaria, Albania\*.

**References.** Maidl (1922); Warncke (1965a); Wood (2021).

**Material examined.** ALBANIA • 2♀; Malësi e Madhe; 23 Jul. 2021; M. Jacobs leg.; KJCB • 2♂; Tepelenë; 27 May 2013; K. Deneš leg.; OÖLM.

**163. *Andrena (Truncandrena) mucronata* Morawitz, 1871**

**Countries present.** Greece, Albania\*.

**References.** Morawitz (1871); Paganetti-Hummler (1912, as “*Andrena doursiana* Duf.” [sic]); Gusenleitner and Schwarz (2002); Standfuss et al. (2011).

**Material examined.** ALBANIA • 4♀; Tepelenë, Bënçë; 21–24 May 2021; A. v. Niewenhuyzen leg.; RMNH/TJWC.

**Notes.** The record of Paganetti-Hummler (1912) from Corfu will be *A. mucronata*, as *Andrena doursana* Dufour, 1853 is not known from the North Mediterranean region. *Andrena mucronata* was also described from Corfu based on specimens collected by Erber, further supporting this conclusion.

**164. *Andrena (incertae sedis) muscaria* Warncke, 1965**

**Countries present.** Greece.

**References.** Warncke (1965a); Standfuss et al. (2011).

**Notes.** Part of the *crocusella*-group (subgenus currently undescribed). **ENDEMIC** to Greece and the southern Balkans.

**165. *Andrena (Micrandrena) nana* (Kirby, 1802)**

**Countries present.** Bulgaria, North Macedonia\*.

**References.** Banaszak and Dochkova (2014); Scheuchl and Willner (2016); Wood (2021).

**Material examined.** **BULGARIA** • 1 ♀; Slančev Brjag [Sunny Beach]; 27 Jul. 1968; M. Kocourek leg.; OÖLM; **NORTH MACEDONIA** • 1 ♂; Vardar reg., Papeliste, orchard; 140 m a.s.l.; 1–6 Apr. 2021; V. Bureš leg.; JSPC • 1 ♀; Vardar reg., Papeliste, steppe; 130 m a.s.l.; 1–6 Apr. 2021; V. Bureš leg.; JSPC.

**Notes.** Paganetti-Hummmler (1912) recorded *A. nana* from Corfu; it is probably a mis-identification, but it is very difficult to conclude on the record's validity without seeing the original specimen(s). Warncke (1965a: 67) expressed doubts about records from “Morea” in Brullé (1833), indicating that they were likely to belong to *A. magunta*. Based on a small number of examined specimens, *A. nana* does appear to have a marginal occurrence in the southern Balkans.

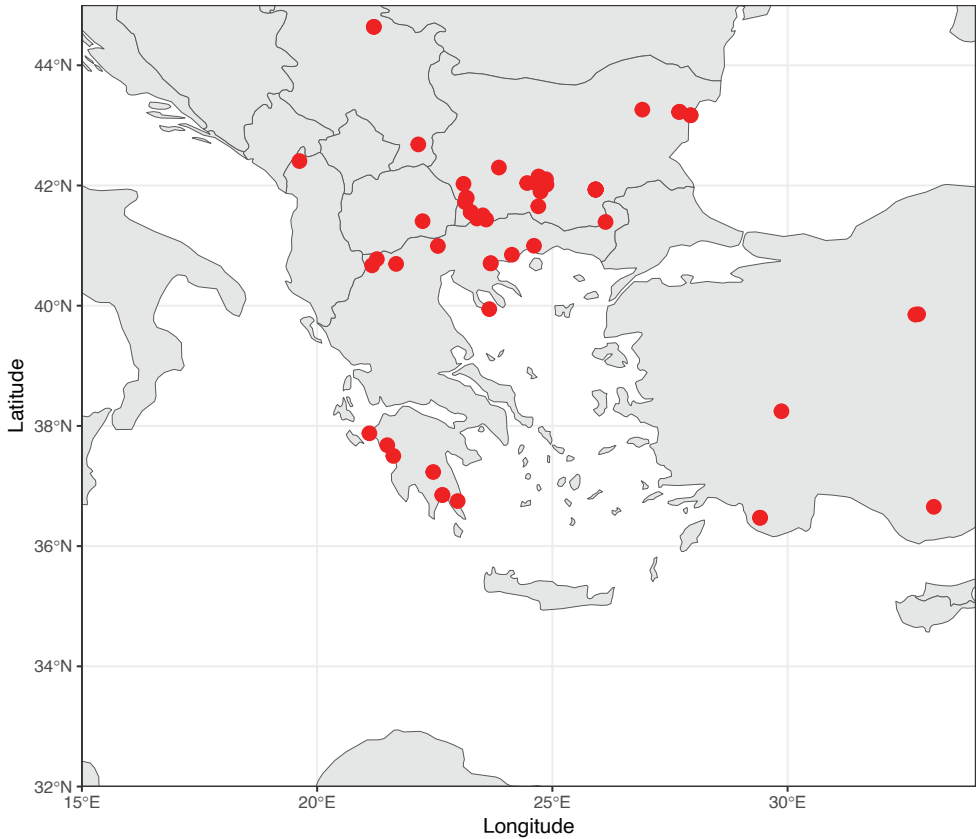
**166. *Andrena (Hamandrena) nasuta* Giraud, 1863**

**Countries present.** Greece\*, Bulgaria, North Macedonia, Albania.

**References.** Nediaikov (1914); Warncke (1973); Reverté et al. (2023).

**Material examined (illustrative).** **GREECE** • 1 ♀; Western Macedonia, Florina, immediately north of Vigla; 1500 m a.s.l.; 9 Jun. 2024; T.J. Wood leg.; TJWC • 4 ♂, 16 ♀; Peloponnese, Skala env; 27 Mar. 2016; M. Snížek leg.; OÖLM • 1 ♀; Chalkidiki [Halkidiki], Kassandria, Paliouri; 18 May 2014; M. Snížek leg.; OÖLM • 1 ♀; Prov. Florina, Amindeo [Amyntaio], 700 m a.s.l.; 9 May 1991; J. Tiefenthaler leg.; OÖLM. See Suppl. material 2 for full details on all examined material.

**Notes.** Surprisingly, it was not possible to find previous literature records for *A. nasuta* in Greece, although the species was commonly encountered in museum material all across the country (Fig. 77). Reverté et al. (2023) cited the species for Greece, but without giving precise specimen records; the current work is therefore considered to constitute the first published records from this country.



**Figure 77.** Distribution of *Andrena (Hamandrena) nasuta* Giraud, 1863 in the southern Balkans. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

**167. *Andrena (Ulandrena) neocypriaca* Mavromoustakis, 1956**

**Countries present.** Greece, Bulgaria (Fig. 65).

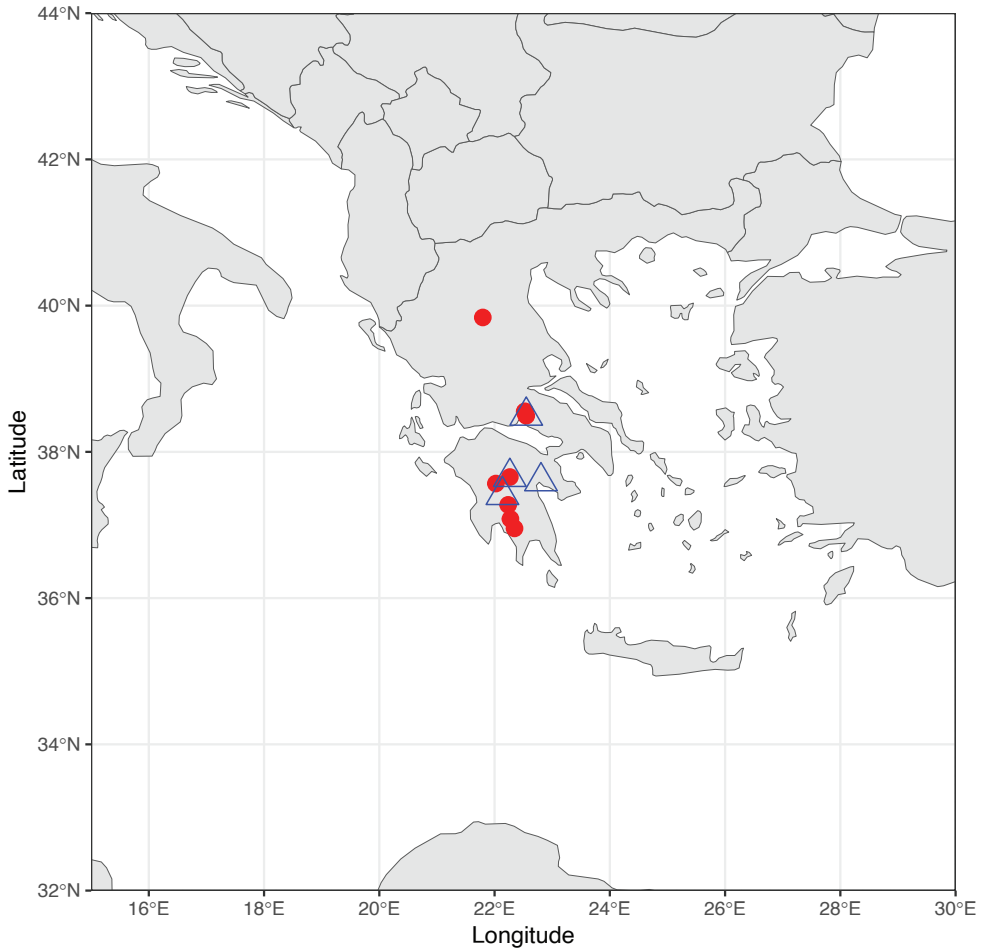
**References.** Warncke (1965a); Warncke (1966); Wood (2021).

**168. *Andrena (Poecilandrena) neovirida* Grünwaldt, 2005**

**Countries present.** Greece.

**References.** Grünwaldt (2005); Standfuss et al. (2011).

**Material examined.** GREECE • 1♀; 35 km NE Kalambaka; 15 May 2005; M. Kadlecová leg.; OÖLM • 4♀; Central Greece, Arachova, 3.3 km NW of Arachova; 1150 m a.s.l.; 9 Apr. 2024; T.J. Wood leg.; RMNH/TJWC • 1♀; Central Greece, Mt. Parnassos, 4.4 km NNW of Kalyvia Livadiou Arachovas; 1250 m a.s.l.; 9 Apr. 2024; T.J.



**Figure 78.** Distributions of *Andrena (Poecilandrena) neovirida* Grünwaldt, 2005 (red circles) and *Andrena (Poecilandrena) standfussorum* Scheuchl, 2010 (blue open triangles) in the southern Balkans. Displayed distributions are not comprehensive. Specimen details in Suppl. material 2.

Wood leg.; RMNH • 1 ♀; Fokis [Phocis], Parnassos, 7 km NW Arachova [Arachova]; 29 Apr. 1990; J.A.W. Lucas leg.; TJWC • 1 ♂; Melano [Menalon?] Mountains, Peloponnese; 1600 m a.s.l.; 16 May 1987; H. Teunissen leg.; RMNH • 7 ♀; Peloponnese, Megalopolis, Kiparissi, immediately to north; 450 m a.s.l.; 3 Apr. 2024; T.J. Wood leg.; RMNH/TJWC • 4 ♂; Peloponnese, Mount Maenalon, 4.5 km NW Kardaras; 1600 m a.s.l.; 4 Apr. 2024; T.J. Wood leg.; RMNH/TJWC • 1 ♂, 1 ♀; Peloponnese, Mt. Taigetos [Taygetus], 30 km NWW Sparti; 29 Apr. 2005; J. Halada leg.; TJWC • 1 ♀; Peloponnese/Taigetos, Sparta-Kalamata, 1100–1200 m a.s.l.; 15 May 1992; H. Rausch leg.; OÖLM.

**Notes.** ENDEMIC to Greece and the southern Balkans (Fig. 78). It was not possible to find the type of this species at the ZSM, the stated type depository.

**169. *Andrena (Cnemidandrena) nigriceps* (Kirby, 1802)**

**Countries present.** Greece, Bulgaria.

**References.** Warncke (1965a); Wood (2021).

**170. *Andrena (Melandrena) nigroaenea* (Kirby, 1802)**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Paganetti-Hummler (1912); Warncke (1966); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**171. *Andrena (Melandrena) nigroolivacea* Dours, 1873**

**Countries present.** Greece.

**References.** Paganetti-Hummler (1912); Warncke (1965a); Standfuss et al. (2011).

**172. *Andrena (Melandrena) nitida* (Müller, 1776)**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Maidl (1922); Warncke (1966); Warncke (1973); Wood (2021).

**173. *Andrena (Melandrena) nitidemula* Scheuchl & Hazir, 2012**

**Countries present.** Greece (East Aegean Islands).

**References.** Rasmont et al. (2017).

**Notes.** Recorded from Samos.

**174. *Andrena (Notandrena) nitidiuscula* Schenck, 1853**

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Nedialkov (1914, as *Andrena lucens* Imhoff, 1868); Warncke (1965a); Warncke (1973); Wood (2021).

**175. *Andrena (Micrandrena) niveata* Friese, 1887**

**Countries present.** Bulgaria.

**References.** Banaszak and Dochkova (2014); Scheuchl and Willner (2016).

**Notes.** It has not been possible to examine any specimens of this species from the southern Balkans. The distribution maps of Gusenleitner and Schwarz (2002) indicate a possible marginal presence in northern Bulgaria, and hence the species is retained in the fauna and the identification key.

**176. *Andrena (Nobandrena) nobilis* Morawitz, 1873**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Atanassov (1962); Warncke (1965a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1 ♀; rotshelling Topovë; 29 May 2018; K. Jansen leg.; KJCB.

**177. *Andrena (Simandrena) nucleola* Warncke, 1973**

**Countries present.** Greece, Bulgaria.

**References.** Warncke (1973); Wood (2021).

**178. *Andrena (Hoplandrena) nuptialis* Pérez, 1903**

**Countries present.** Bulgaria.

**References.** Wood (2021).

**179. *Andrena (Andrena) nycthemera* Imhoff, 1868**

**Countries present.** Bulgaria, North Macedonia\*.

**References.** Nedialkov (1914); Wood (2021).

**Material examined.** NORTH MACEDONIA • 1 ♀; Polog reg., Sirichino, quarry; 400 m a.s.l.; 2–7 Apr. 2021; V. Bureš leg.; JSPC.

**180. *Andrena (Euandrena) obscuricrus* sp. nov.**

**Countries present.** Greece (Crete).

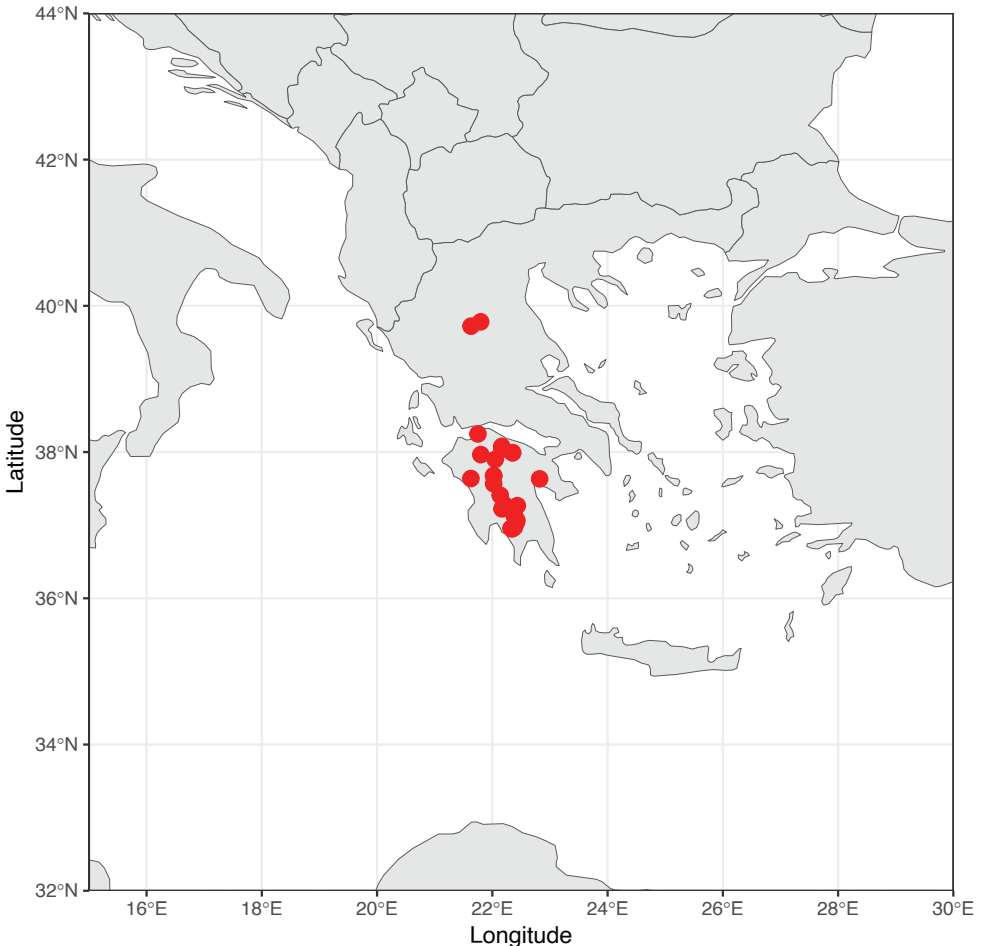
**Notes.** ENDEMIC to the southern Balkans and specifically to the island of Crete.

### 181. *Andrena (incertae sedis) olympica* Grünwaldt, 2005

**Countries present.** Greece.

**References.** Grünwaldt (2005).

**Notes.** ENDEMIC to Greece and the southern Balkans. It was not possible to find the holotype of this species at the ZSM, the stated type depository, although three female and four male paratypes were present. Overall 189 specimens (158 female, 31 male) could be examined (Fig. 79). The species was placed in subgenus *Poecilandrena* (Grünwaldt et al. 2005), but based on morphology and pollen specialisation (see below), this placement seems unlikely. It is best treated as *incertae sedis* at the present time; it may be best placed in a group with *Andrena seminuda* Friese, 1896 (*seminuda*-group) and a small number of related species (S. Bossert, G. Pisanty, T.J. Wood, unpublished data).



**Figure 79.** Global distribution of *Andrena (incertae sedis) olympica* Grünwaldt, 2005. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

**182. *Andrena (Truncandrena) optata* Warncke, 1975**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania (Fig. 55).

**References.** Warncke (1965a, as *Andrena rufomaculata* ssp. *paramythensis*); Warncke (1966, as *Andrena rufomaculata* ssp. *paramythensis*); Warncke (1973, as *Andrena rufomaculata* Friese, 1921); Warncke (1975, as *Andrena rufomaculata* ssp. *optata*); Standfuss et al. (2011); Wood (2021).

**Notes.** The consistent separation of this taxon from *A. rufomaculata* and *A. paramythensis* remains challenging; see discussion under Subgenus *Truncandrena* Warncke, 1968 in the Results.

**183. *Andrena (Orandrena) oralis* Morawitz, 1876**

**Countries present.** Greece, Bulgaria, North Macedonia (Fig. 45).

**References.** Warncke (1965a); Wood (2021); Ascher and Pickering (2025).

**184. *Andrena (Chlorandrena) orientana* Warncke, 1965**

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1965a); Schwenninger (2015); Wood (2021).

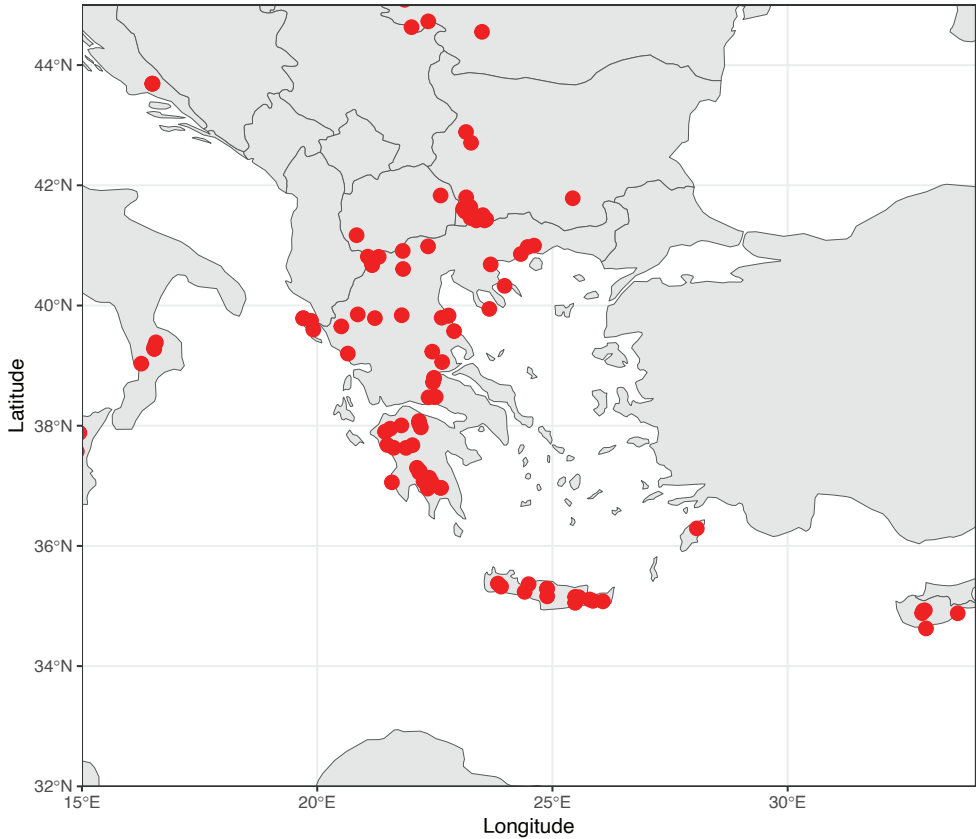
**185. *Andrena (Taeniandrena) ovata* Schenck, 1853**

**Countries present.** Greece, Bulgaria\*, North Macedonia\*, Albania\*.

**References.** Praz et al. (2022).

**Material examined (illustrative).** **ALBANIA** • 2♂, 1♀; Berat, E of Bogovë; 30 May 2024; W. Vertommen leg.; WVC; **BULGARIA** • 1♂; Belidiehan [Beledie Han, Беледие хан]; 16 Jun. 1967; N. Atanassov leg.; NZMS • 3♀; Kresnensko defile [Kresna Gorge]; 2 Jun. 1961; N. Atanasov leg.; NZMS • 1♂; Zapadan park; 16 May 1976; E. Vasileva leg.; NZMS; **GREECE** • 1♀; Rodos [Rhodos], 10 km N v. Malona [Malonas]; 11 Apr. 1970; A.C. & W.N. Ellis leg.; RMNH • 2♀; E-Kreta, Sitia-Gebirge, Tripti [Thripti]; 1000–1200 m a.s.l.; 28 Apr. 1980; W. Schedl leg.; OÖLM • 1♂; Corfu, Sidari; 1 Jun. 1981; H. & M. Koponen leg.; MZH • 2♂; Erimanthos Mts (Peloponn); 28 May 1987; H. Teunissen leg.; RMNH; **NORTH MACEDONIA** • 2♂, 2♀; Kosel, near Lake Ohrid; 10 Jun. 2014; D. Benda leg.; NMPC.

**Notes.** This species was only recently recognised as valid, with only some of its global range being clarified at that time (Praz et al. 2022). However, based on the additional revision of material, it can now confidently be said to be very common



**Figure 80.** Distribution of *Andrena (Taeniandrena) ovata* Schenck, 1853 in the southern Balkans. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

in the southern Balkans (Fig. 80), typically being identified incorrectly as *Andrena ovatula* (Kirby, 1802) (females) or *Andrena wilkella* (Kirby, 1802) (males). It was possible to examine 49 specimens from Bulgaria, 221 specimens from Greece, and four specimens from North Macedonia. Some illustrative museum specimens are presented above; see the Suppl. material 2 for full details. Unfortunately, most of my examined Turkish material was revised in 2020–2021 before the recognition of *A. ovata* as a distinct species in 2022, and needs to be re-visited; the shortage of records from western Turkey presented in Fig. 80 should not be considered evidence of absence.

### 186. *Andrena (Micrandrena) paganettina* Warncke, 1965

**Countries present.** Greece, North Macedonia.

**References.** Warncke (1965a); Warncke (1973).

**187. *Andrena (Pallandrena) pallidicincta* Brullé, 1833**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Brullé (1833); Paganetti-Hummeler (1912); Warncke (1965a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1 ♀; rotshelling Topovë; 29 May 2018; K. Janssen leg.; KJCB • 3 ♀; Tepelenë, Bënçë; 21–24 May 2001; A. v. Niewenhuyzen leg.; RMNH.

**188. *Andrena (Lepidandrena) pandellei* Pérez, 1895**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a); Warncke (1973); Wood (2021).

**Material examined.** ALBANIA • 1 ♂, 4 ♀; berghelling Rehovë Ersekë; 5–6 Jun. 2018; K. Janssen leg.; KJCB • 2 ♀; Malil Tomorrit [Mount Tomorr]; 12 Jun. 2018; K. Janssen leg.; KJCB • 1 ♀; Tirana; 25 May 1992; G.G.M. Schulten leg.; RMNH • 3 ♀; warmwaterbr Petran; 31 May – 1 Jun. 2018; K. Janssen leg.; KJCB.

**189. *Andrena (Chlorandrena) panurgimorpha* Mavromoustakis, 1957**

**Countries present.** Greece, Bulgaria, North Macedonia\*, Albania.

**References.** Warncke (1965a); Standfuss et al. (2011); Wood (2021); Wood and Monfared (2022).

**Material examined.** NORTH MACEDONIA • 1 ♀; Vardar reg., Papeliste, steppe; 130 m a.s.l.; 26 Apr. 2021; V. Bureš leg.; JSPC.

**190. *Andrena (Avandrena) panurgina* De Stefani, 1889**

**Countries present.** Greece\*.

**Material examined.** GREECE • 1 ♀; Corfu; [undated]; O. Schmiedeknecht leg.; E. Stöckert det.; ZSM.

**Notes.** This is the first confirmed record of this species from the East Mediterranean. The next nearest population can be found in southern mainland Italy and in Sicily (Gusenleitner and Schwarz 2002).

**191. *Andrena (Leucandrena) parviceps* Kriechbaumer, 1873**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a); Warncke (1973); Wood (2021).

**Material examined.** ALBANIA • 1 ♀; berghellin Rehovë Ersekë; 5 Jun. 2018; K. Janssen leg.; KJCB.

### 192. *Andrena (Lepidandrena) paucisquama* Noskiewicz, 1924

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1 ♀; berghellin Rehovë Ersekë; 6 Jun. 2018; K. Janssen leg.; KJCB • 1 ♀; Devolij Gorge [Drenije Gorge]; 9 Jun. 2018; K. Janssen leg.; KJCB • 1 ♀; dode bomen Çarçovë; 2 Jun. 2018; K. Janssen leg.; KJCB • 1 ♀; Krosmishtë [Krosnishtë mountain, N Zvarrisht]; 5 Jun. 2017; M. Jacobs leg.; KJCB • 3 ♀; Malil Tomorrit [Mount Tomorr]; 31 May 2017; M. Jacobs leg.; KJCB • 1 ♀; Malil Tomorrit [Mount Tomorr]; 12 Jun. 2018; K. Janssen leg.; KJCB • 1 ♀; NW Boge [Bogë]; 10 Jun. 2013; K. Deneš leg.; KJCB • 2 ♀; rotshelling Topovë; 29 May 2018; K. Janssen leg.; KJCB • 2 ♀; Tepelenë, Bëncë; 21–23 May 2001; A. van Nieuwenhuyzen leg.; RMNH.

### 193. *Andrena (Micrandrena) pelagica* Warncke, 1975

**Countries present.** Greece (Crete).

**References.** Warncke (1974a, 1975); Wood (2024a).

**Notes.** ENDEMIC to the southern Balkans and specifically to the island of Crete.

### 194. *Andrena (Euandrena) pelagonia* Wood, 2021

**Countries present.** North Macedonia.

**References.** Wood (2021).

**Notes.** ENDEMIC to North Macedonia and the southern Balkans. Highly likely to be present also in Greece and Bulgaria.

### 195. *Andrena (Margandrena) pellucens* Pérez, 1895

**Countries present.** Greece, Bulgaria\*.

**References.** Standfuss and Standfuss (2010); Standfuss et al. (2011).

**Material examined.** BULGARIA • 1 ♀; Bansko; 9 Sep. 1921; D. Ioakimov leg.; NZMS.

**Notes.** First recorded for the southern Balkans (Greece) by Standfuss and Standfuss (2010), *A. pellucens* was unexpectedly found in the NZMS collection. Modern surveys are required to understand if the species still persists in Bulgaria; it is clearly under-recorded in the southern Balkans.

**196. *Andrena (Graecandrena) pelopa* Warncke, 1975****Countries present.** Greece.**References.** Warncke (1974a, 1975).**Notes.** ENDEMIC to Greece and the southern Balkans.**197. *Andrena (Euandrena) pileata* Warncke, 1975****Countries present.** Greece, Bulgaria.**References.** Warncke (1974a, 1975); Gusenleitner and Schwarz (2002); Praz et al. (2019); Wood (2024a).**198. *Andrena (Plastandrena) pilipes* Fabricius, 1781****Countries present.** Greece, Bulgaria, North Macedonia, Albania.**References.** Smith (1853, as *Andrena spectabilis* Smith, 1853); Paganetti-Hummler (1912, as *A. carbonaria* (Linnaeus, 1767) *sensu acutorum*); Nedialkov (1914, as *A. carbonaria*); Drenowski (1934, as *A. carbonaria*); Atanassov (1962, as *A. carbonaria*); Warncke (1965a, as *A. carbonaria*); Warncke (1969b, as *A. carbonaria*); Warncke (1973, as *A. carbonaria*); Standfuss et al. (2011); Wood (2021).**199. *Andrena (Micrandrena) pirinia* Wood, 2021****Countries present.** Bulgaria.**References.** Wood (2021).**Material examined.** BULGARIA • 1 ♀; Rhodopes, Pamporovo env; 1600 m a.s.l.; 23 Jun. 2016; Barták & Kubik leg.; OÖLM.**Notes.** ENDEMIC to Bulgaria and the southern Balkans. Highly likely to be present in Greece in the western Rhodopes. Wood (2021: 32) recorded this specimen as *Andrena spreta* aggregate, before redetermining it in 2024 after the revisionary work on the *spreti*-group (Wood 2023b).**200. *Andrena (Ulandrena) polita* Smith, 1847****Countries present.** Greece, Bulgaria, North Macedonia, Albania.**References.** Nedialkov (1914); Warncke (1966); Warncke (1973); Wood (2021).

**201. *Andrena (Notandrena) pontica* Warncke, 1972**

**Countries present.** Albania\*.

**Material examined.** ALBANIA • 1♂; Voskopojë; 8 Jun. 2018; K. Janssen leg.; KJCB.

**202. *Andrena (Troandrena) praecocella* Cockerell, 1917**

**Countries present.** Greece (East Aegean Islands).

**References.** Warncke (1974a, 1975, as *Andrena saettana* Warncke, 1975); Wood (2024b, as *Andrena saettana*).

**Notes.** Whilst describing the species with a *locus typicus* in Cyprus, Warncke (1974a, 1975) included a paratype from Rhodes. Grace (2010: 80) indicates both Samos and Rhodes.

**203. *Andrena (Andrena) praecox* (Scopoli, 1763)**

**Countries present.** Bulgaria\*, North Macedonia\*.

**Material examined.** BULGARIA • 1♀; Lulun Geb. [Lyulin Mountain]; 21 Apr. 1964; D. Marinova leg.; NZMS • 1♀; Rhodopi Mts: SE Krusstava; 1209 m a.s.l.; 23 Apr. 2015; T. Ljubomirov leg.; IBER • 3♀; Witosha Geb. [Vitosha mountain]; 14 Apr. 1963; D. Gogov leg.; NZMS; NORTH MACEDONIA • 1♀; Popova Sapka [Popova Shapka]; 1820 m a.s.l.; 7 Jun. 2014; D. Benda leg.; NMPC.

**204. *Andrena (Nobandrena) probata* Warncke, 1973**

**Countries present.** Greece, North Macedonia, Albania\*.

**References.** Warncke (1973); Ebmer (2009).

**Material examined.** ALBANIA • 1♂, 1♀; boven Malil Tomorrit [Mount Tomorr]; 12 Jun. 2018; K. Janssen leg.; KJCB • 1♀; 3 km N of Valbonë; 28 May 2024; W. Ver-tommen leg.; WVC.

**205. *Andrena (Taeniandrena) producta* Warncke, 1973**

**Countries present.** Greece\*, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1973); Wood (2021).

**Material examined.** ALBANIA • 1♂; Rivierbedding Devolij Gorge [Drenije Gorge]; 10 Jun. 2018; K. Janssen leg.; KJCB • 1♂; rotshelling Topovë; 29 May 2018; K. Janssen leg.; KJCB; GREECE • 3♂; Central Macedonia, Stavros, 1 km W New

Vrasna; 22 May 2023; D. Michez leg.; UMONS • 1♀; Western Macedonia, Florina, immediately south of Akritas; 1000 m a.s.l.; 9 Jun. 2024; T.J. Wood leg.; RMNH, RMNH.INS.1152575.

**206. *Andrena (Simandrena) propinqua* Schenck, 1853**

**Countries present.** Bulgaria, Albania\*.

**References.** Wood (2021).

**Material examined.** ALBANIA • 1♀; Burrel-Lis [between Burrel and Lis]; 1000 m a.s.l.; 6 Jun. 2013; K. Deneš leg.; OÖLM • 6♂, 41♀; Tepelenë; 27 May 2013; K. Deneš leg.; OÖLM.

**207. *Andrena (Micrandrena) proxima* (Kirby, 1802)**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Paganetti-Hummler (1912); Nedialkov (1914); Drenowski (1936); Warncke (1965a); Warncke (1966); Warncke (1973); Schmid-Egger (2005); Wood (2021).

**208. *Andrena (Micrandrena) pusilla* Pérez, 1903**

**Countries present.** Greece, Bulgaria, Albania.

**References.** Warncke (1966); Banaszak and Dochkova (2014, as *Andrena spreta* ssp. *pusilla*).

**209. *Andrena (Melandrena) pyropygia* Kriechbaumer, 1873**

**Countries present.** Greece.

**References.** Warncke (1965a);

**210. *Andrena (Melandrena) quadrimaculata* Friese, 1921**

**Countries present.** Greece, Albania.

**References.** Warncke (1966); Wood and Bossert (2025).

**Notes.** First reported for Europe by Warncke (1966) from Uji Ftohte [=Uji i Ftohtë, literally cold water] south of Tepelenë in Albania. Wood and Bossert (2025) illustrated the holotype, reported the species new for Greece, and presented an additional Albanian specimen collected in 2013.

### 211. *Andrena (Micrandrena) querquedula* Warncke, 1975

**Countries present.** Greece (East Aegean Islands), Bulgaria\*.

**References.** Rasmont et al. (2017).

**Material examined.** BULGARIA • 1♀; SE Dobrich vill., [near Haskovo]; 120 m a.s.l.; 27 Apr. 2018; T. Ljubomirov leg.; IBER.

**Notes.** The species was first reported for Europe from the East Aegean Islands (Rasmont et al. 2017). It is unexpectedly newly reported from central Bulgaria.

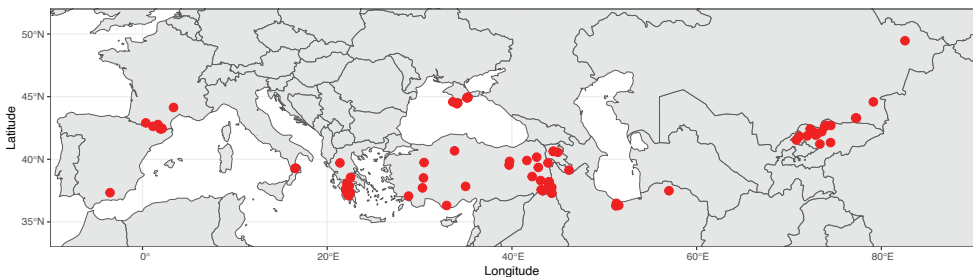
### 212. *Andrena (incertae sedis) ranuncolorum* Morawitz, 1877

**Countries present.** Greece.

**References.** Scheuchl and Willner (2016); Westrich (2016).

**Material examined (illustrative).** GREECE • 1♀; Kastania [Trikala]; 29 Apr. 1969; W. Grünwaldt leg.; W. Grünwaldt det.; CSE • 1♂, 2♀; Menalo Mts, Arkadia; 1600 m a.s.l.; 26 May 1986; H. Teunissen leg.; RMNH • 1♂; Trypi [Tripi]; 16 May 1973; W. Groß leg.; W. Grünwaldt det.; RMNH • 1♂; Central Greece, Mt. Parnassos, 4.4 km NNW of Kalyvia Livadiou Arachovas; 1250 m a.s.l.; 9 Apr. 2024; T.J. Wood leg.; TJWC; SPAIN • 1♀; Granada, Sierra Harana, Orduña; 1550 m a.s.l.; 5 Jun. 1982; R. Leys leg.; RMNH.

**Notes.** *Andrena ranuncolorum* has only recently been recorded from Greece, which is a surprise given the many available specimens encountered in museums. In total, it was possible to examine 41 specimens (16 females, 25 males) from Greece (see Suppl. material 2). In the context of its global distribution, the Greek population fits the pattern of isolated populations in southern Spain, the Pyrenees, the Alps, southern Italy, and Crimea before reaching the more extensive Asian populations (Fig. 81). The species is well known from Switzerland, but I have not been able to examine any specimens directly. The single record for southern Spain is remarkable, and is presented here as the species has never previously been reported away from the Pyrenees in the Iberian



**Figure 81.** Global distribution of *Andrena (incertae sedis) ranuncolorum* Morawitz, 1877. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

Peninsula (Gusenleitner and Schwarz 2002). It further illustrates the extent to which relictual populations of this species are present in the mountains of southern Europe (Mendicino et al. 2026). Formerly placed in the strictly Nearctic subgenus *Thysandrena* Lanham, 1949 (Pisanty et al. 2022a), it is instead part of an undescribed subgenus best referred to as the *numida*-group.

**213. *Andrena* (*Graecandrena*) *repressa* Warncke, 1975**

**Countries present.** Greece (East Aegean Islands) (Fig. 23).

**References.** Warncke (1974a, 1975, as *A. hyemala* ssp. *repressa*).

**214. *Andrena* (*Euandrena*) *robusta* Warncke, 1975**

**Countries present.** Greece (East Aegean Islands: Rhodes).

**References.** Warncke (1974a, 1975); Standfuss et al. (2011).

**Material examined.** GREECE • 1 ♀; Manolates (Samos); 25 Apr. 1977; H. Teunissen leg.; RMNH • 1 ♀; Milies, Lesbos; 21 May 1980; H. Teunissen leg.; RMNH • 1 ♀; Peloponnes, Araxos hist. Burgani; 8 May 1999; W-H. Liebig leg.; WHLC • 2 ♀; Peloponnes, Beach Gianiscari; 8 May 1999; W-H. Liebig leg.; WHLC/TJWC • 2 ♀; Peloponnes, Polani nl. Kalamata; 9 May 1999; W-H. Liebig leg.; WHLC • 1 ♀; Rhodes, Faliraki dunes; 24 Apr. 1970; v. Ooststroom leg.; RMNH • 1 ♀; Rhodos, Mte. Profeta Elia [Mount Profitis Ilias]; 10 May 1935; O. Wettstein leg.; K. Warncke det.; OÖLM (**holotype**) • 2 ♀; Rhodos, Rodini; 22 Apr. 1970; H. Teunissen leg.; Warncke det.; OÖLM (**paratypes**).

**Notes.** Currently **ENDEMIC** to Greece and the southern Balkans, but as it is known from Rhodes, it is almost certainly occurs also in western Turkey; species of *Andrena* (*Euandrena*) remain highly challenging to delineate in the East Mediterranean.

**215. *Andrena* (*Hoplandrena*) *rosae* Panzer, 1801**

**Countries present.** Bulgaria\*.

**Notes.** Warncke (1965a) listed *A. rosae* from eastern Crete, but this is considered to be unlikely and a probable misidentification. No individuals of *A. rosae* have been examined from the southern Balkans (in Eastern Europe, confirmed as present south to Serbia and Romania) or from western Turkey (see Wood 2023a for records from eastern Turkey). However, the species can be reported as new to Bulgaria and the southern Balkans as a whole based on the record: “1 ♀; sept.-or., Albena; 14 Jul. 1976; B. Tkalců leg.; E. Scheuchl personal collection” (E. Scheuchl, pers. comm.). It is not considered to be present in Greece.

**216. *Andrena (Truncandrena) rotundilabris* Morawitz, 1877**

**Countries present.** Greece.

**References.** Rasmont et al. (2017).

**Material examined.** GREECE • 7♀; Makri; 8 May 1971; W. Grünwaldt leg.; W. Grünwaldt det.; ZSM • 1♀; Makri; 8 May 1971; W. Grünwaldt leg.; W. Grünwaldt det.; RMNH.

**Notes.** The species was first reported for Europe from the East Aegean Islands (Rasmont et al. 2017). Additional specimens from Thrace are listed here.

**217. *Andrena (Euandrena) ruficrus* Nylander, 1848**

**Countries present.** Greece.

**References.** Warncke (1965a).

**Material examined.** GREECE • 2♀; Olympos, Prionia valley; 40.0838°N, 22.4068°E; 17–18 May 1991; J. Batelka leg.; OÖLM (Fig. 82).

**Notes.** Listed from western Crete from 20 Mar. 1925 (Warncke 1965a) and Albania from 17–26 Jun. 1918 (Warncke 1966). Specimens from Crete belong to *A. obscuricrus* (see above). Warncke (1973: 33) noted that his previous records from Albania actually belonged to what was then the newly described *A. montana*. However, two specimens from Olympus in Greece were examined that seem to match *A. ruficrus*, but had the scutum with weak shagreen medially (Fig. 82C), had longer hairs on the terga (Fig. 82F) and the clypeus appeared to be slightly shorter (Fig. 82B). Given the taxonomic challenges present in the subgenus, it is not considered prudent to describe this material as new without additional genetic evidence, or at least additional specimens; it can be considered as *Andrena* aff *ruficrus*. Warncke's distribution maps (Gusenleitner and Schwarz 2002) do not include any dots for the southern Balkans.

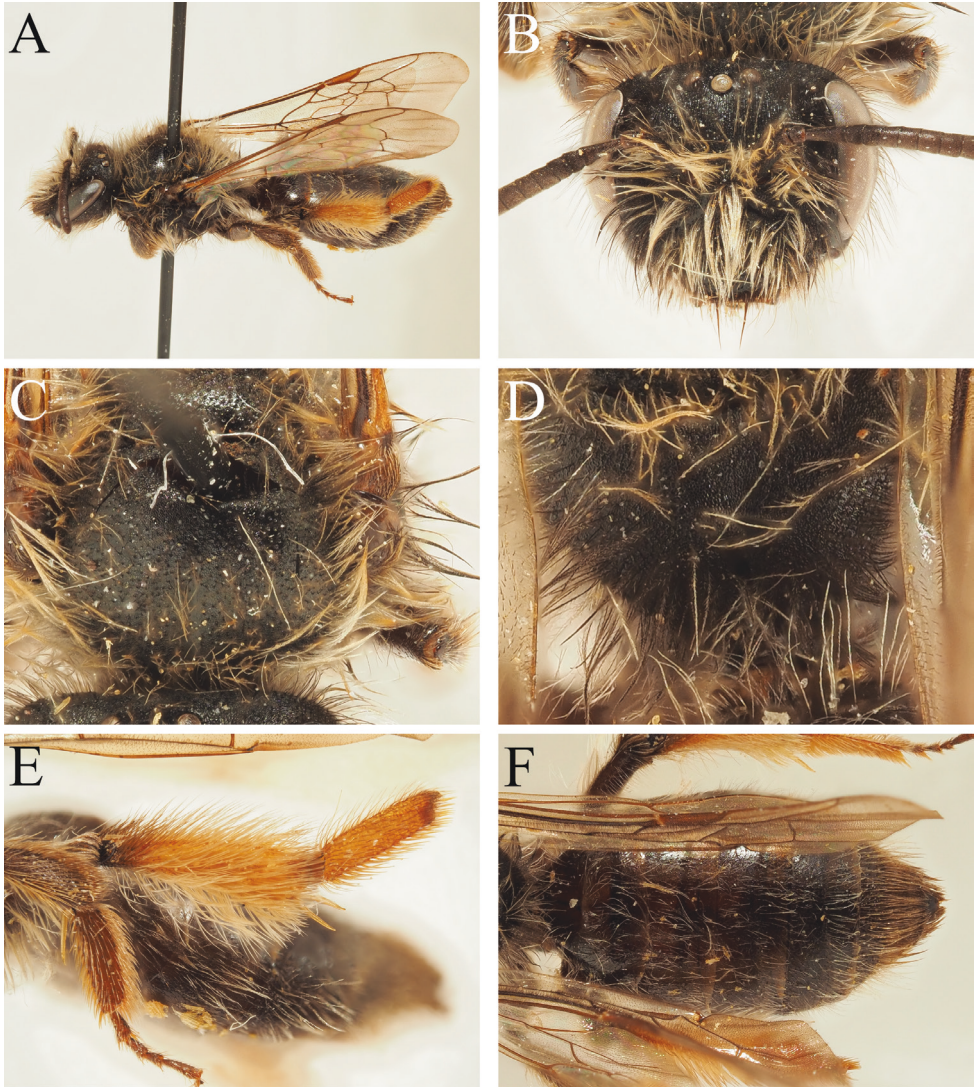
**218. *Andrena (Lepidandrena) rufizona* Imhoff, 1834**

**Countries present.** Greece\*, Bulgaria.

**References.** Wood (2023a).

**Material examined.** BULGARIA • 1♀; Rhodopi, Erkiupria [Wondrous Bridges]; 29 Jul. 1965; N. Atanassov leg.; NZMS.

**Notes.** Wood (2023b) reported *A. rufizona* as new for Bulgaria and Turkey. An additional Bulgarian specimen was located in the NZMS, further supporting its presence in the Rhodope mountains. The species can also be reported as new for Greece from the southern flank of the Rhodope mountains based on a specimen caught at: “Nomos Drama Falakro, Scheitel der Bergstraße [summit of the mountain road]; 1700–1750 m a.s.l.; 28 Jul. 1992; A.W. Ebmer leg.” (E. Scheuchl, pers. comm.).



**Figure 82.** *Andrena* (*Euandrena*) *aff. ruficrus* Nylander, 1848 from Mount Olympus in Greece. **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Scutum, dorsal view; **D.** Propodeum, dorsal view; **E.** Hind leg, lateral view; **F.** Metasoma, dorsal view.

**219. *Andrena* (*Euandrena*) *rufula* Schmiedeknecht, 1883**

**Countries present.** Greece, North Macedonia.

**References.** Paganetti-Hummeler (1912); Warncke (1965a); Standfuss et al. (2011); Ascher and Pickering (2025).

**Notes.** Often encountered flying with *A. bucephala* in *Acer*-dominated temperate woodlands in the central Peloponnese.

**220. *Andrena (Micrandrena) rugothorace* Warncke, 1965**

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1965a); Warncke (1973); Standfuss et al. (2011).

**Material examined. ROMANIA** • 1♂; Dobrogea [Dobruja], Canaraua Fetii; 22 May 1994; L. Székely leg.; OÖLM.

**Notes.** Newly reported for Romania\*.

**221. *Andrena (Micrandrena) rugulosa* Stöckhert, 1935**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a); Warncke (1973); Wood (2021).

**Material examined. ALBANIA** • 1♀; Quark Korça, Gem Korça, Drenova, Drenova NP; 1120–1320 m a.s.l.; 29–30 Jun. 2016; H. & R. Rausch leg.; OÖLM • 1♀; Radanj orchideenwai, Korçë; 3 Jun. 2018; K. Janssen leg.; KJCB.

**222. *Andrena (Taeniandrena) russula* Lepeletier, 1841**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Paganetti-Hummler (1912, as *Andrena rufohispida* Dours, 1872); Warncke (1965a, as *Andrena similis* Smith, 1849); Warncke (1966, as *Andrena russula* ssp. *similis*); Warncke (1967a, as *Andrena russula* ssp. *similis*); Warncke (1973, as *Andrena ochreatea* (Christ, 1791)); Standfuss et al. (2011, as *Andrena similis*); Wood (2021, as *Andrena similis*).

**223. *Andrena (Aciandrena) sandanskia* Warncke, 1973**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Warncke (1973); Wood (2021); Wood (2023a).

**Notes.** Placement of this species has been uncertain, but it is likely best placed in the subgenus *Aciandrena* (S. Bossert, G. Pisanty, T.J. Wood, unpublished data).

**224. *Andrena (Micrandrena) saxonica* Stöckhert, 1935**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1973); Gusenleitner and Schwarz (2002); Ebmer (2009); Wood (2021).

**Material examined. ALBANIA** • 1♀; berghellin Rehovë Ersekë; 6 Jun. 2018; K. Janssen leg.; KJCB • 10♀; NW Boge [Bogë]; 10 Jun. 2013; K. Deneš leg.; OÖLM.

**225. *Andrena (Opandrena) schencki* Morawitz, 1866**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Nedialkov (1914); Maidl (1922); Warncke (1965a); Warncke (1966); Warncke (1967a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**226. *Andrena (Notandrena) schlettereri* Friese, 1896**

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1965a); Wood (2021); Ockermüller et al. (2023).

**227. *Andrena (Truncandrena) schmiedeknechti* Magretti, 1883**

**Countries present.** Greece, North Macedonia.

**References.** Warncke (1965a); Warncke (1967a); Warncke (1973); Standfuss et al. (2011).

**Notes.** Warncke (1965a: 35) described the subspecies *A. schmiedeknechti* ssp. *flavopilis* Warncke, 1965 from Greece, but it is not considered necessary to recognise a subspecies here (see discussion in section on Subgenus *Truncandrena* Warncke, 1968 above).

**228. *Andrena (Scitandrena) scita* Eversmann, 1852**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Atanassov (1962); Warncke (1965a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1 ♀; Benjë-Novoselë; 4 Jul. 2021; M. Jacobs leg.; KJCB • 1 ♀; Buz [Buzë]; 16 Jul. 2017; K. Janssen leg.; KJCB • 1 ♀; Gjerbës; 2 Jun. 2017; M. Jacobs leg.; KJCB • 1 ♀; Gjirokaster env.; 200 m a.s.l.; 1 May – 30 Jun. 2013; K. Deneš leg.; OÖLM • 1 ♀; sperwer Delvinë, Vlorë; 26 May 2018; K. Janssen leg.; KJCB • 5 ♂, 2 ♀; Tepelenë; 27 May 2013; K. Deneš leg.; OÖLM/TJWC • 1 ♂, 1 ♀; warmwaterbr Petran; 31 May 2018; K. Janssen leg.; KJCB.

**229. *Andrena (Hoplandrena) scotica* Perkins, 1916**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Warncke (1966, as *Andrena carantonica* Pérez, 1903); Warncke (1973, as *Andrena sabulosa* (Scopoli, 1763)); Standfuss et al. (2011, as *Andrena carantonica*); Wood (2021).

**Material examined.** BULGARIA • 1♂; Kresna [Кресна]; 1–30 May 1967; M. Kocourek leg.; OÖLM • 1♂; Slančev Brjag [Sunny Beach]; 18–30 May 1989; J. Haladada leg.; OÖLM • 1♂; Sofia; 10 Jun. 1964; D. Marinova leg.; NZMS; GREECE • 2♂; Ep. Thesprotein, Paramithias-Geb., Ag. Kiriaki; 900–1000 m a.s.l.; 26 May 1993; H. & R. Rausch leg.; OÖLM.

**Notes.** Due to the complexity and confusion surrounding the correct name to apply to this widespread univoltine spring-flying taxon (Wood et al. 2022), only confirmed spring males (with bidentate mandibles) are presented here for reference.

### 230. *Andrena (incertae sedis) seminuda* Friese, 1896

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Warncke (1973); Gusenleitner and Schwarz (2002); Wood (2021); Ascher and Pickering (2025).

**Notes.** Best placed in a species group (*seminuda*-group) with a small number of related species (S. Bossert, G. Pisanty, T.J. Wood, unpublished data).

### 231. *Andrena (Leucandrena) sericata* Imhoff, 1868

**Countries present.** Greece, Bulgaria.

**References.** Warncke (1965a); Wood (2021).

### 232. *Andrena (Truncandrena) serraticornis* Warncke, 1965

**Countries present.** Greece, Albania\*.

**References.** Warncke (1965a).

**Material examined.** ALBANIA • 1♀; Terpan [Tërpan]; 29 May 2017; M. Jacobs leg.; KJCB.

### 233. *Andrena (Micrandrena) sillata* Warncke, 1975

**Countries present.** Greece (East Aegean Islands).

**References.** Warncke (1975); Wood (2024a).

### 234. *Andrena (Cnemidandrena) simillima* ssp. *sischkai* Warncke, 1988

**Countries present.** Greece, Bulgaria.

**References.** Drenowski (1936, as *Andrena simillima* Smith, 1851 s. str.); Warncke (1988); Wood (2021).

**Notes.** The taxa around *Andrena simillima* require molecular investigation, as they present considerable morphological variation (e.g. Wood 2025).

### 235. *Andrena (Micrandrena) simontornyella* Noskiewicz, 1939

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a, as *Andrena simontornyella* and *Andrena corpana* Warncke, 1965); Warncke (1967a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1♀; Voskopojë; 8 Jun. 2018; K. Janssen leg.; KJCB.

**Notes.** Warncke (1965a) described *A. corpana* from Greece, but there is currently no evidence to recognise Balkan populations as specifically distinct (Gusenleitner and Schwarz 2002).

### 236. *Andrena (Poecilandrena) sphaecodimorpha* Hedicke, 1942

**Countries present.** Greece, Bulgaria, North Macedonia\*, Albania\* (Fig. 49).

**References.** Hedicke (1942); Warncke (1965a); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1♀; Sheper vallei, Gjirokaster; 28 May 2018; K. Janssen leg.; KJCB; NORTH MACEDONIA • 1♀; Polog reg., Sirichino, meadow; 430 m a.s.l.; 2–7 May 2021; V. Bureš leg.; JSPC.

### 237. *Andrena (Micrandrena) spreta* Pérez, 1895

**Countries present.** Greece.

**Material examined.** GREECE • 1♀; Korfu-Nord, Umg. Roda; 6 Jun. 2016; J. Tiefenthaler leg.; OÖLM.

**Notes.** The concept of *Andrena spreta* has been greatly confused over time; it was clarified by Wood (2023b). Most records of “*Andrena spreta*” from the southern Balkans refer to *A. pusilla*. Only a single specimen of the true *A. spreta* could be found on the island of Corfu, which seems to often support species more typical of the West Mediterranean (e.g. *Andrena panurgina*).

### 238. *Andrena (Poecilandrena) standfussorum* Scheuchl, 2010

**Countries present.** Greece.

**References.** Scheuchl (2010); Standfuss et al. (2011).

**Material examined.** GREECE • 2♀; Central Greece, Arachova, 3.3 km NW of Arachova; 1150 m a.s.l.; 9 Apr. 2024; T.J. Wood leg.; RMNH/TJWC • 1♀; Megapolis, Arkadia, Peloponnese; 11 Apr. 1988; H. Teunissen leg.; RMNH • 1♀; Peloponnese,

Mount Maenalon, 4.5 km NW Kardaras; 1600 m a.s.l.; 4 Apr. 2024; T.J. Wood leg.; TJWC • 1♀; Peloponnese, N of Naflipto, NE of Limnos; 21 Mar. 2016; M. Snížek leg.; OÖLM.

**Notes.** ENDEMIC to Greece and the southern Balkans (Fig. 78). The records presented here expand the distribution away from the *locus typicus* (chalk grassland by Plataniá/Volos in east-central Greece).

### 239. *Andrena (Micrandrena) strohmella* Stöckhert, 1928

**Countries present.** North Macedonia\*.

**Material examined.** ITALY • 1♀; Molise, IS [Isernia], Paduli; 1100 m a.s.l.; 24 Apr. 2017; M. Fede leg.; MZUR; NORTH MACEDONIA • 1♀; NP Mavrovo, near Bibaj; 1247 m a.s.l.; 9 Jun. 2014; D. Benda leg.; NMPC.

**Notes.** *Andrena strohmella* is a typical spring species of temperate woodland in Central Europe, extending to northern Italy and Hungary. It was therefore a surprise to encounter a specimen from North Macedonia. However, an additional specimen from the Apennine mountains in south-central Italy was also unexpectedly encountered, suggesting an emerging pattern of *A. strohmella* populations in mountainous areas of southern Europe. Further surveys of Balkan mountains are needed to draw stronger conclusions.

### 240. *Andrena (Ulandrena) subglobosa* Dours, 1873

**Countries present.** Greece, Bulgaria, North Macedonia, Albania (Fig. 64).

**References.** Dours (1873); Paganetti-Hummler (1912); Warncke (1966, as *A. kriechbaumeri*); Warncke (1967a, as *A. kriechbaumeri*); Warncke (1973, as *A. kriechbaumeri*); Standfuss et al. (2011, as *A. kriechbaumeri*); Wood (2021, as *A. kriechbaumeri*).

### 241. *Andrena (Micrandrena) subopaca* Nylander, 1848

**Countries present.** Greece, Bulgaria, North Macedonia.

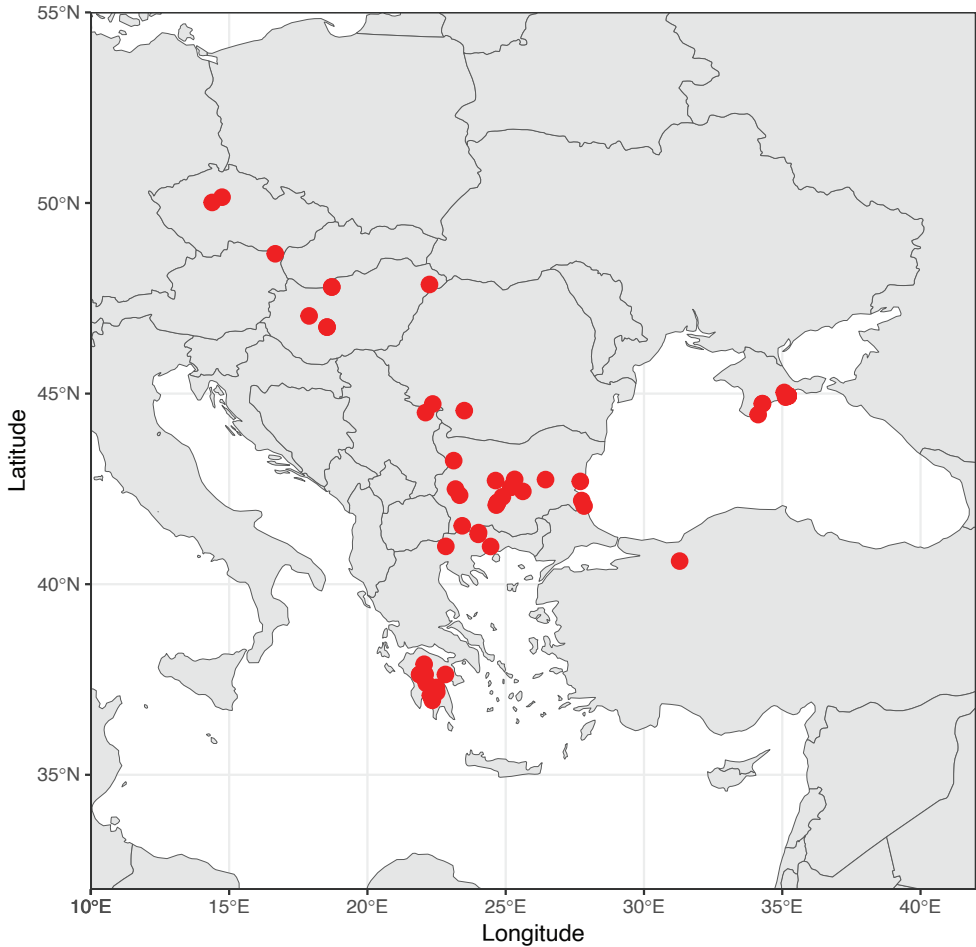
**References.** Drenowski (1934); Warncke (1965a); Warncke (1973); Wood (2021).

### 242. *Andrena (Simandrena) susterai* Alfken, 1914

**Countries present.** Greece, Bulgaria.

**References.** Gusenleitner and Schwarz (2002); Wood (2021).

**Notes.** The distribution maps of Gusenleitner and Schwarz (2002) indicate a single dot somewhere between Bulgaria and Greece. The presence of this species in Greece can be confirmed based on numerous examined specimens (Fig. 83; see Suppl. material 2).



**Figure 83.** Global distribution of *Andrena (Simandrena) susterai* Alfken, 1914. Displayed distribution is not comprehensive. Specimen details in Suppl. material 2.

The species is particularly common in Bulgaria and also the Peloponnese. It shows a surprisingly similar distribution to *A. nasuta* (Fig. 77), present in the north of Greece before seemingly disappearing and reappearing in the Peloponnese.

#### 243. *Andrena (Euandrena) symphyti* Schmiedeknecht, 1883

**Countries present.** Greece, Bulgaria, North Macedonia\*, Albania.

**References.** Warncke (1965a); Ebmer (2009); Standfuss et al. (2011); Wood (2021); Ascher and Pickering (2025).

**Material examined.** NORTH MACEDONIA • 1♂; Polog reg., Sirichino, quarry; 400 m a.s.l.; 22–27 Apr. 2021; V. Bureš leg.; JSPC.

**244. *Andrena (Taeniandrena) taedium* Wood, 2023**

**Countries present.** Greece, Bulgaria\*, North Macedonia\*, Albania\* (Fig. 52).

**References.** Wood (2021, as *Andrena phoenicura* misidentification); Wood (2023a).

**Notes.** See discussion in Subgenus *Taeniandrena* Hedicke, 1933 in the Results.

**245. *Andrena (Micrandrena) taprobana* Warncke, 1975**

**Countries present.** Greece.

**References.** Gusenleitner and Schwarz (2002).

**Material examined.** GREECE • 1 ♀; Corfu, Pelekas; 12 May 1978; M. Viitasaari leg.; MZH.

**Notes.** Warncke (1974a, 1975) described *A. taprobana* from Gürün and Erzurum in central Turkey. However, the distribution map of Gusenleitner and Schwarz (2002) indicates a single point in the Peloponnese. It has not been possible to locate a specimen from the Peloponnese, but a single female could be examined from Corfu, supporting the presence of this species in Greece.

**246. *Andrena (Chlorandrena) taraxaci* Giraud, 1861**

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Nedialkov (1914); Drenowski (1934); Warncke (1973); Standfuss et al. (2011); Schwenninger (2015); Wood (2021).

**Material examined.** GREECE • 1 ♀; Thripti (Ora Sitias) [East Crete]; 29 Apr. 1982; H. Teunissen leg.; RMNH (determined as *A. astica* by Teunissen) • 1 ♀; W. Creta, Anogia; 27 Apr. 1973; H. Teunissen leg.; RMNH (determined as *A. astica* by K. Warncke) • 2 ♀; Katharo Vlakte (Kreta); 22 Apr. 1982; H. Teunissen leg.; RMNH (determined as *A. astica* by Teunissen) • 1 ♀; Elounta (Kreta) [Schisma Eloundas]; 26 Apr. 1982; H. Teunissen leg.; RMNH (determined as *A. astica* by Teunissen).

**Notes.** As noted above, Warncke considered *A. astica* to be present on Crete (see distribution maps of Gusenleitner and Schwarz 2002). However, all examined material from Crete confirms to *A. taraxaci* under the criteria of Schwenninger (2015). It is not impossible that Cretan material represents another undescribed species in the *taraxaci*-group given the taxonomic complexity this lineage presents (Schwenninger 2015), and the presence of many endemic Cretan *Andrena* as presented here, but without a male or genetic evidence it is difficult to comment further. Additional study is required.

**247. *Andrena (Tarsandrena) tarsata* Nylander, 1848**

**Countries present.** Greece, Bulgaria.

**References.** Gusenleitner and Schwarz (2002); Grace (2010); Wood (2021).

**Material examined.** BULGARIA • 46♂, 56♀; Popina Luka [Попина Лъка]; 1800 m a.s.l.; 14 Jul. 1966; M. Kocourek leg.; NZMS/OÖLM/TJWC • 1♂; Tschaira, Rodopi [Чаирски езера]; 29 Jul. 1969; N. Atanassov leg.; NZMS; GREECE • 1♂; Drama, Rhodope mountains, Mt. Sara; 18 Aug. 1989; L. Blank leg.; OÖLM.

**Notes.** The distribution maps of Gusenleitner and Schwarz (2002) suggested the presence of *A. tarsata* in Greece, as subsequently indicated by Grace (2010). Examination of a few specimens demonstrates the presence of *A. tarsata* in the western Rhodopes; the Greek specimen was caught in sympatry with *A. coitana*, another summer-flying species of temperate grasslands.

#### 248. *Andrena (Cryptandrena) testudo* sp. nov.

**Countries present.** Greece (Crete) (Fig. 5).

**Notes.** ENDEMIC to the southern Balkans and specifically to the island of Crete.

#### 249. *Andrena (Simandrena) thomsonii* Ducke, 1898

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Warncke (1965a); Warncke (1966); Warncke (1973); Standfuss et al. (2011); Wood (2021).

#### 250. *Andrena (Melandrena) thoracica* (Kirby, 1802)

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Paganetti-Hummler (1912); Nedialkov (1914); Atanassov (1962, 1964); Warncke (1965a); Warncke (1966); Warncke (1973); Standfuss et al. (2011); Wood (2021).

#### 251. *Andrena (Plastandrena) tibialis* (Kirby, 1802)

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1973); Standfuss et al. (2011); Wood (2021).

#### 252. *Andrena (Limbandrena) toelgiana* Friese, 1921

**Countries present.** Greece (East Aegean Islands).

**References.** Grace (2010).

**Notes.** See section in Subgenus *Limbandrena* Wood, 2023 in the Results.

**253. *Andrena (Micrandrena) tomora* Warncke, 1975**

**Countries present.** Greece, Albania.

**References.** Warncke (1966, as *Andrena djelfensis* Pérez, 1895); Warncke (1974a, 1975); Standfuss et al. (2011).

**254. *Andrena (Cordandrena) torda* Warncke, 1965**

**Countries present.** Greece (Crete, East Aegean Islands).

**References.** Gusenleitner and Schwarz (2002).

**Material examined. GREECE** • 1♂; Attaviros [Attavyros] (Rhodos); 24 Apr. 1976; H. Teunissen leg.; RMNH • 2♀; Chania, 2 km N of Kournas; 31 Mar. 1991; S.P.M. Roberts leg.; SPMRC • 1♀; Chania, 2 km S of Vrises; 27 Mar. 1991; S.P.M. Roberts leg.; SPMRC • 1♂; Chania, 6 km S of Vrises; 4 Apr. 1991; S.P.M. Roberts leg.; SPMRC • 3♂, 1♀; Chania, 7 km S of Vrises; 27 Mar. 1991; S.P.M. Roberts leg.; SPMRC • 1♂; Kriti, Nom. Iraklion, Ag. Varvara; 17 Mar. 1978; J.P. Duffels leg.; RMNH • 1♂; Rhodos; 26 Apr. 1976; K. Vegter leg.; K. Warncke det.; RMNH.

**Notes.** The distribution map of Gusenleitner and Schwarz (2002) indicates the presence of *A. torda* on the East Aegean Islands, but the species is also present on Crete.

**255. *Andrena (Simandrena) transitoria* Morawitz, 1871**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Morawitz (1871); Warncke (1973); Wood (2021).

**Material examined. ALBANIA** • 1♀; Fier region, Lushnje env., pastures and steppes; 177 m a.s.l.; 29 Jun. 2018; D. Benda leg.; JSPC.

**Notes.** Described from the island of Syra (=Syros) from Erber material (Morawitz 1871).

**256. *Andrena (Ulandrena) trikalensis* Warncke, 1965**

**Countries present.** Greece.

**References.** Warncke (1965a).

**Material examined. GREECE** • 1♂, 1♀; Trikala; 17–18 Apr. 1962; K. Warncke leg.; K. Warncke det.; OÖLM (male **holotype**, female **paratype**) • 1♂; Delphi; 11 Apr. 1963; K. Warncke leg.; K. Warncke det.; OÖLM (**paratype**) • 1♀; Peloponnes pen., Kastelli; 900 m a.s.l.; 22 Apr. 2014; R. Mucska leg.; OÖLM • 4♀; Peloponnes, 20 km S Megalopoli; 1 May 2005; M. Kadlecová leg.; OÖLM/TJWC • 2♂, 1♀; Peloponnes, NE of Molai, NE of Metamorfofi; 28 Mar. 2016; M. Snížek leg.; OÖLM/

TJWC • 1♀; Peloponnese, Zarakas, 1.3 km SWW; 550 m a.s.l.; 31 Mar. 2024; T.J. Wood leg.; TJWC • 1♀; Peloponnese, Zarakas, 4 km SW; 700 m a.s.l.; 31 Mar. 2024; T.J. Wood leg.; TJWC.

**Notes.** ENDEMIC to Greece and the southern Balkans. Much less frequently recorded than *A. waschulzi*, probably in part due to its slightly earlier flight period.

### 257. *Andrena (Hoplاندrena) trimmerana* (Kirby, 1802)

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1973); Gusenleitner and Schwarz (2002); Wood (2021).

### 258. *Andrena (Micrandrena) tringa* Warncke, 1973

**Countries present.** Greece\*, Bulgaria, North Macedonia.

**References.** Warncke (1973); Wood (2021).

**Material examined.** GREECE • 1♀; 18 km SE of Kozani; 3 Jul. 1975; M.J. & J.P. Duffels leg.; RMNH • 1♀; Western Macedonia, Anatoliko, 6.3 km E, Church of the Holy Apostles; 1000 m a.s.l.; 15 Jun. 2024; T.J. Wood leg.; RMNH.

**Notes.** Surprisingly not previously recorded from Greece; Grace (2010) highlighted the need to search for this species in northern Greece.

### 259. *Andrena (Truncandrena) truncatilabris* Morawitz, 1877

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\*.

**References.** Warncke (1965a); Warncke (1967a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 1♂, 2♀; Ksamil bij Butrinti; 25 May 2017; K. Janssen & M. Jacobs leg.; KJCB • 1♀; Rivierbedding Devolij Gorge [Drenije Gorge]; 11 Jun. 2018; K. Janssen leg.; KJCB • 1♂; sperwer Delvinë, Vlorë; 25 Jun. 2018; K. Janssen leg.; KJCB • 16♀; Tepelenë; 27 May 2013; K. Deneš leg.; OÖLM/TJWC.

### 260. *Andrena (Truncandrena) tscheki* ssp. *tritica* Warncke, 1967

**Countries present.** Greece, Bulgaria, North Macedonia, Albania (Fig. 58).

**References.** Smith (1853, as *Andrena nigrifrons* Smith); Paganetti-Hummler (1912, as *A. tscheki* Morawitz, 1872); Nediaikov (1914, as *A. nigrifrons* Smith); Warncke (1965a); Warncke (1966); Warncke (1967a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**261. *Andrena (Truncandrena) ulula* Warncke, 1969**

**Countries present.** Greece (East Aegean Islands).

**References.** Rasmont et al. (2017).

**Notes.** Rasmont et al. (2017) reported this species as: “Greece: newly recorded from the Greek mainland (confirmed by E. Scheuchl, pers. comm.)”. However, there was a misunderstanding, and *A. ulula* was newly recorded from the island of Chios only. The records were: “1♀; Chios, E Gridia; 10 m a.s.l.; 26 Apr. 2004; A.W. Ebmer leg.” and “1♂; Chios, SW Nénita; 26 Apr. 2004; 170 m a.s.l.; A.W. Ebmer leg.” (E. Scheuchl, pers. comm.).

**262. *Andrena (Notandrena) ungeri* Mavromoustakis, 1952**

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Warncke (1967a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**263. *Andrena (incertae sedis) urdula* Warncke, 1965**

**Countries present.** Greece.

**References.** Warncke (1965a).

**Notes.** The presence of this species in Greece is a mystery; it was described from a single specimen collected at Larisa on 20 Apr. 1962 by Warncke (OÖLM). It has never been recorded again, and almost all records of this species come from Spain and Morocco where the species can be collected in open habitats rich in Brassicaceae, often on light calcareous soils containing gypsum in the Madrid region of Spain (pers. obs.). Morphologically, western material is consistent with the Greek holotype. It must be considered part of the Greek fauna, but contemporary records would be welcome. The phylogenetic placement of this species remains unclear (S. Bossert, G. Pisanty, T.J. Wood, unpublished data).

**264. *Andrena (Melandrena) vaga* Panzer, 1799**

**Countries present.** Bulgaria, North Macedonia.

**References.** Wood (2021); Ascher and Pickering (2025).

**Material examined.** BULGARIA • 2♀; Pernik; 24 Apr. 1910; NZMS.

**Notes.** In addition to the specimens caught at the unusual flight date of July (Wood 2021), additional specimens caught at a more normal date in April were also found in museum material.

**265. *Andrena (Holandrena) variabilis* Smith, 1853**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Smith (1853); Nedialkov (1914, as *Andrena piceicornis* Dours, 1872); Warncke (1965a); Warncke (1966); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Notes.** The species was described from “Albania” by Smith (1853: 107), but the type specimen in the NHMUK (type no. 17a, 1300) has no locality label. It is unclear if this is another S.S. Saunders specimen, and if it was actually collected from Greece. This distinction is purely academic since the species is widespread across the southern Balkans and beyond, with a stable species concept (Schönitzer et al. 1995).

**266. *Andrena (Andrena) varians* (Kirby, 1802)**

**Countries present.** Bulgaria.

**References.** Nedialkov (1914); Wood (2021).

**Material examined.** BULGARIA • 1♀; Kresna [Кресна]; 1–31 May 1967; M. Kocourek leg.; OÖLM • 6♂; Slančev Brjag [Sunny Beach]; 1966; K. Poláček leg.; OÖLM/TJWC • 1♂, 3♀; Slančev Brjag [Sunny Beach]; 26 Jun. 1968; M. Kocourek leg.; OÖLM/TJWC • 1♀; Sofia; 1–31 May 1907; N. Nedelkova [Nedialkov] leg.; K. Warncke det.; NZMS • 4♀; Sofia; 5 May 1964; D. Marinova leg.; NZMS/TJWC • 3♀; Sofia; 25 May 1964; D. Marinova leg.; NZMS.

**Notes.** Frequently recorded in Bulgaria in the 1960s, no further material has been examined from more recent collections.

**267. *Andrena (Leucandrena) ventralis* Imhoff, 1832**

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Nedialkov (1914); Warncke (1965a); Wood (2021).

**Material examined.** BULGARIA • 1♀; Sofia; 25 May 1964; D. Marinova leg.; NZMS • 3♂; Arda valley, NE Madzharovo; 160 m a.s.l.; 12 Mar. 2001; H. Etarska leg.; IBER.

**Notes.** Uncommonly encountered.

**268. *Andrena (Cryptandrena) ventricosa* Dours, 1873**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania\* (Fig. 5).

**References.** Dours (1873); Maidl (1922); Warncke (1965a); Warncke (1967a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Notes.** The type material for this species is lost, but the species concept is quite clear and no neotype designation is necessary.

**269. *Andrena (Poecilandrena) viridescens* Viereck, 1916**

**Countries present.** Greece, Bulgaria, North Macedonia.

**References.** Paganetti-Hummeler (1912, as *Andrena cyanescens* Nylander, 1852); Warncke (1965a); Standfuss et al. (2011); Wood (2021); Ascher and Pickering (2025).

**270. *Andrena (Euandrena) vulpecula* Kriechbaumer, 1873**

**Countries present.** Greece, Bulgaria, Albania\*.

**References.** Drenowski (1936); Standfuss et al. (2011); Wood (2021).

**Material examined.** ALBANIA • 3♂, 1♀; 3 km N of Valbonë; 28 May 2024; W. Vertommen leg.; WVC.

**271. *Andrena (Ulandrena) waschulzi* Strand, 1921**

**Countries present.** Greece (Crete), North Macedonia, Albania (Fig. 65).

**References.** Strand (1921); Warncke (1965a, as *A. schulzi* Strand, 1921); Warncke (1966, as *A. schulzi*); Warncke (1967a, as *A. schulzi*); Warncke (1973, as *A. schulzi*); Standfuss et al. (2011, as *A. schulzi*).

**272. *Andrena (Ulandrena) westensis* Warncke, 1965**

**Countries present.** Greece, Albania\*.

**References.** Warncke (1965a); Standfuss et al. (2011).

**Material examined.** ALBANIA • 1♀; Tepelenë, Bënçë; 20 May 2021; A. v. Niewenhuyzen leg.; RMNH.

**273. *Andrena (Taeniandrena) wilkella* (Kirby, 1802)**

**Countries present.** Greece, Bulgaria, North Macedonia, Albania.

**References.** Maidl (1922); Atanassov (1964); Warncke (1965a); Warncke (1973); Standfuss et al. (2011); Wood (2021).

**Notes.** It is quite possible that many records of “*Andrena wilkella*” in the southern Balkans actually refer to *Andrena ovata* which has only recently been recognised as a valid species. Wood (2021) only reported males of *A. wilkella* from Bulgaria; males of *A. ovata* and *A. wilkella* in southern Europe have historically been confused under the latter name as they both present a long A4 (see Praz et al. 2022). Genetic samples confirming the presence of true *A. wilkella* from countries in the southern Balkans would be beneficial.

## Species excluded from the fauna of the southern Balkans

### *Andrena (Ulandrena) caspica* Morawitz, 1886 and *Andrena (Ulandrena) uncinata* Friese, 1899

**References.** Grace (2010).

**Notes.** Grace (2010: 59) lists *A. caspica* inclusive of *A. uncinata* from continental Greece and the south-eastern Aegean islands, without precise specimen details. This subset of *Ulandrena* species (the *polita*-group) are highly challenging, with fluid species concepts employed by Warncke, and a lack of morphological and molecular clarity. An attempt was made to clarify this group (Wood et al. 2020), but a comprehensive revision is ongoing (G. Pisanty & TJW, in prep.). At the present moment, there is no support for additional members of this complex in the southern Balkans beyond *A. polita* (broadly northern temperate parts of the southern Balkans) and *A. westensis* (broadly warmer and more Mediterranean parts of Albania and Greece).

### *Andrena (Micrandrena) dargia* Warncke, 1965

**References.** Warncke (1965a).

**Notes.** Synonymised with *A. minutula* by Pisanty et al. (2025).

### *Andrena (Micrandrena) djelfensis* Pérez, 1895

**References.** Warncke (1966); Gusenleitner and Schwarz (2002).

**Notes.** Warncke (1966: 403) recorded *A. djelfensis* from Albania and Greece. However, he later realised that eastern specimens belonged to a new species, *Andrena tomora* (Warncke 1974a: 98; Warncke 1975: 58). The species is named after Tomor in Albania (=Tomorr). The dot map of *A. djelfensis* presented by Gusenleitner and Schwarz (2002: 1023) still included points for Italy, Albania, Greece, and Turkey following Warncke's pre-1975 concept of *A. djelfensis* (see also Wood et al. 2023).

### *Andrena (Taeniandrena) gelriae* van der Vecht, 1927

**References.** Warncke (1973); Banaszak and Dochkova (2014); Scheuchl and Willner (2016); Wood (2021, no. 70).

**Notes.** Given the recognition of *A. producta* as a valid species (see Praz et al. 2022), true *A. gelriae* does not seem to be present from eastern Austria eastwards. All southern Balkan records of this taxon will refer to *A. producta*.

***Andrena (Ulandrena) leucorbina* Morawitz, 1876**

**References.** Warncke (1965a).

**Notes.** Warncke reported this Central Asian species from Greece, before later considering it to be better referred to as *A. abbreviata sensu lato*. See Wood (2024a) for discussion.

***Andrena (Brachyandrena) miegiella* Dours, 1873**

**References.** Grace (2010).

**Notes.** Listed from northern Lesbos without precise specimen details, but this must be a misidentification as *A. miegiella* is a West Mediterranean species with no confirmed records from the East Mediterranean (Pisanty et al. 2022b; unpublished data).

***Andrena (Micrandrena) nanaeformis* Noskiewicz, 1924**

**References.** Warncke (1966).

**Notes.** Listed from North Macedonia by Warncke (1966: 392) as a “+” within his distributional table, but no specimen details were ever presented. His dot maps later did not indicate the presence of this species in Hungary, Romania, Serbia, or Bulgaria (Gusenleitner and Schwarz 2002: 1114). This listing is therefore considered to be doubtful.

***Andrena (Micrandrena) oedicnema* Warncke, 1975**

**References.** Gusenleitner and Schwarz (2002); Rasmont et al. (2017).

**Notes.** See Subgenus *Micrandrena* Ashmead, 1899 in the Results.

***Andrena (Taeniandrena) phoenicura* Warncke, 1975**

**References.** Kuhlmann et al. (2014); Wood (2021, no. 125).

**Notes.** See discussion in Subgenus *Taeniandrena* Hedicke, 1933 in the Results.

***Andrena (Poecilandrena) potentillae* Panzer, 1809**

**References.** Paganetti-Hummler (1912); Nedialkov (1914, as *Andrena genevensis* Schmiedeknecht, 1884); Scheuchl and Willner (2016).

**Notes.** *Andrena potentillae* has been reported from Corfu and Bulgaria, but there are no contemporary records of this species from the southern Balkans, and I have not been able to locate any historical specimens in the museum collections examined thus far. I strongly suspect that these records refer to another *Poecilandrena* Hedicke, 1933 species,

probably *Andrena sphaecodimorpha* which was not yet described at the time of Paganetti-Hummler and Nedialkov. Wood (2021, no. 129) reported *A. potentillae* for Bulgaria based on the listing of Scheuchl and Willner, but it is best considered as absent from the fauna of the southern Balkans; its typical distribution is across Central Europe into European Russia (Gusenleitner and Schwarz 2002), not descending below the Pannonian basin.

***Andrena (Taeniandrena) ovatula* (Kirby, 1802)**

**References.** Warncke (1965a, 1966, 1973); Atanassov (1972); Standfuss et al. (2011); Banaszak and Dochkova (2014).

**Notes.** Records of *A. ovatula* from the southern Balkans refer either to *A. afzeliella* or *A. ovata*, or possibly even to other *Taeniandrena* species. The true *A. ovatula* is an Atlantic species that does not enter south-eastern Europe (Praz et al. 2022).

***Andrena (Taeniandrena) poupillieri* Dours, 1872**

**References.** Gusenleitner and Schwarz (2002), as *A. ovatula* ssp. *poupillieri*.

**Notes.** Gusenleitner and Schwarz (2002: 1143) indicated that *A. ovatula* ssp. *poupillieri* sensu Warncke is present on Crete. Following the work of Praz et al. (2022) and Wood (2023b, 2023c), *A. poupillieri* is considered to be a predominantly North African species with marginal occurrence in southern Iberia and on the Balearic islands. Records from Crete are considered to be misidentified specimens of the recently revalidated *A. ovata*.

***Andrena (Aciandrena) pulicaria* Warncke, 1975**

**References.** Warncke (1974a, 1975).

**Notes.** See section on *Andrena chelma* in Subgenus *Aciandrena* Warncke, 1968 in the Results.

***Andrena (Notandrena) stellaris* Warncke, 1965**

**References.** Grace (2010); Rasmont et al. (2017).

**Notes.** See section on Subgenus *Notandrena* Pérez, 1890 in the Results.

***Andrena (Micrandrena) semilaevis* Pérez, 1903**

**References.** Banaszak and Dochkova (2014); Scheuchl and Willner (2016); Wood (2021, no. 142).

**Notes.** The species concepts in the subgenus *Micrandrena* have changed substantially over recent years as molecular tools have been applied (e.g. Wood 2023b). Based on these revised concepts, there is no evidence for the presence of *A. semilaevis* in the southern Balkans and it is excluded from the fauna.

***Andrena (Melandrena) vachali* Pérez, 1895**

**References.** Warncke (1965a).

**Notes.** Now referable to *A. creticola* (see above).

***Andrena (Simandrena) vetula* Lepeletier, 1841**

**References.** Warncke (1965a).

**Notes.** Listed from Greece based on a single undated specimen labelled simply as “Graecia”, Warncke (1966: 389) concluded that the species must be mislabelled, since no credible records exist.

***Andrena (Micrandrena) virgata* Warncke, 1975**

**References.** Grace (2010).

**Notes.** Listed from Lesbos, without precise specimen details. It has only been possible to examine the type series of *A. virgata* from eastern Turkey (Horasan, Arastal; OÖLM). At the present time, this listing from Lesbos is implausible and cannot be considered further without precise specimen details and repository.

#### 4. Dietary niches of Balkan *Andrena* species

Results are presented here for some Balkan species for which no or very little previous dietary data have been published. As in Wood (2023b), it was not considered necessary to duplicate the work of Westrich (1989) in Central Europe. It was possible to examine 247 pollen loads from 39 species, almost entirely from Bulgaria and Greece. Findings are summarised in Table 1, with *Andrena* species grouped by subgenus to highlight their often conserved patterns of pollen collection.

This total of analysed pollen loads and studied species is smaller compared to previous work focused on the West Mediterranean (Wood 2023b, 2023c) due to less time available for fieldwork; many visits to Iberia and Morocco were possible between 2014–2022, with comparatively few visits to Bulgaria and Greece conducted only between 2023–2025. However, the overall pattern of specialisation seen in the southern Balkans is more straightforward, and few total pollen loads need to be collected in order to understand dietary specialisation in clades that are species-rich in the southern

**Table 1.** Host plant use and dietary classification for selected Balkan *Andrena* species. *n*, total number of pollen loads; *N*, number of pollen loads from different localities. Plant taxa: AMA, Amaryllidaceae; API, Apiaceae; ASP, Asparagaceae; AST, Asteraceae; BRA, Brassicaceae; CAM, Campanulaceae; CAR, Caryophyllaceae; CIS, Cistaceae; CON, Convolvulaceae; CRA, Crassulaceae; FAB, Fabaceae; HYP, Hypericaceae; LAM, Lamiaceae; PAP, Papaveraceae; PLA, Plantaginaceae; RAN, Ranunculaceae; RES, Resedaceae; ROS, Rosaceae. Countries: BG, Bulgaria; FRA, France; GR, Greece.

Species	<i>n</i>	<i>N</i>	Origin (and number of pollen loads)	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
<i>Aciandrena</i> Warncke							
<i>A. sandanskia</i> Warncke	3	2	BG (2); GR (1)	CRA 100.0	100.0	100.0	Narrowly oligolectic ( <i>Sedum</i> , Crassulaceae)
<i>Campylogaster</i> Dours							
<i>A. erberi</i> Morawitz	2	1	GR (2)	RES 100.0	100.0	100.0	Further study required
<i>Chlorandrena</i> Pérez							
<i>A. cinereophila</i> Warncke	4	2	GR (4)	AST (Cichorioideae) 100.0	100.0	100.0	Broadly oligolectic (Cichorioideae, Asteraceae)
<i>A. chypella</i> Strand	4	2	BG (3); GR (1)	AST (Cichorioideae) 100.0	100.0	100.0	Broadly oligolectic (Cichorioideae, Asteraceae)
<i>A. humabilis</i> Warncke	1	1	GR (1)	AST (Cichorioideae) 100.0	100.0	100.0	Broadly oligolectic (Cichorioideae, Asteraceae)
<i>A. panurgimorpha</i> Mavromoustakis	2	1	GR (2)	AST (Cichorioideae) 100.0	100.0	100.0	Broadly oligolectic (Cichorioideae, Asteraceae)
<i>Cryptandrena</i> Pittioni							
<i>A. brumanensis</i> Friese	7	3	BG (3); GR (4)	FAB 100.0	100.0	100.0	Possibly broadly oligolectic (Fabaceae)
<i>Euandrena</i> Hedicke							
<i>A. pileata</i> Warncke	7	3	BG (1); GR (6)	ASP ( <i>Scilla</i> , <i>Ornithogalum</i> ) 81.1, BRA 13.7, RAN 2.8, others 2.4	71.4	85.7	Polylectic, possibly with a strong preference (Asparagaceae)
<i>A. aff. limosa</i> Warncke	18	5	BG (13); GR (5)	CAM ( <i>Campanula</i> ) 78.0, CAR 7.9, ROS 5.5, LAM 3.0, AST 2.0, others 3.6	27.8	100.0	Polylectic with a strong preference ( <i>Campanula</i> , Campanulaceae)
<i>Holandrena</i> Pérez							
<i>A. fimbriata</i> Brullé	10	4	GR (10)	FAB 100.0	100.0	100.0	Broadly oligolectic (Fabaceae)
<i>Graecandrena</i> Warncke							
<i>A. helenica</i> Warncke	14	4	GR (14)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
<i>A. hyemala</i> Warncke	11	2	GR (11)	API 100.0	100.0	100.0	Broadly oligolectic (Apiaceae)

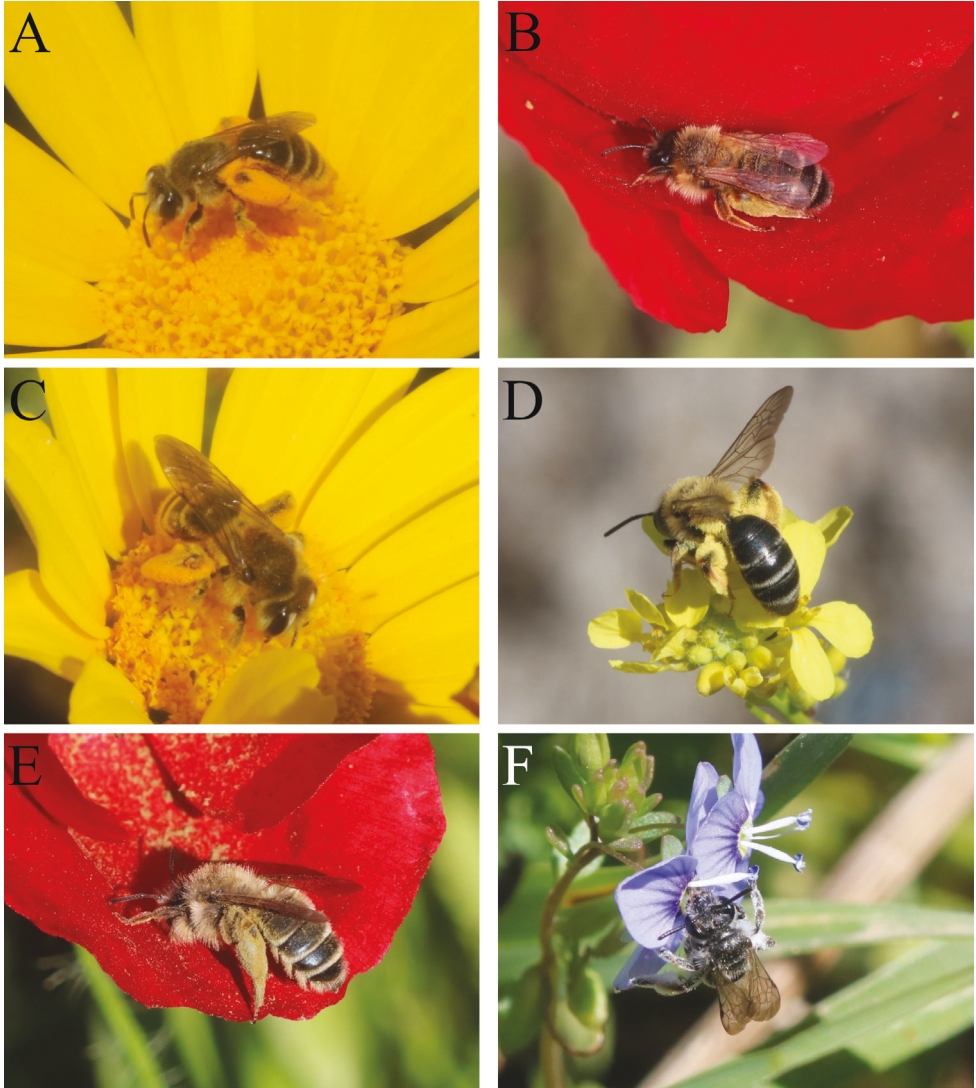
Species	<i>n</i>	<i>N</i>	Origin (and number) of pollen loads	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
<i>Leimelissa</i> Osytsnjuk							
<i>A. fallax</i> Eversmann	5	3	BG (4), GR (1)	FAB ( <i>Onobrychis</i> ) 100.0	100.0	100.0	Narrowly oligolectic ( <i>Onobrychis</i> , Fabaceae)
<i>Limbandrena</i> Wood							
<i>A. limbata</i> Eversmann	5	4	BG (2); GR (3)	ROS ( <i>Potentilla</i> ) 84.1, CAR 4.0, HYP 2.9, LAM 2.7, AST 2.6, API 2.6, CIS 1.1	40.0	100.0	Polylectic with a strong preference ( <i>Potentilla</i> , Rosaceae)
<i>Melandrena</i> Pérez							
<i>A. atrotegularis</i> Hedicke	8	1	GR (8)	HYP 52.3, ROS 21.3, RES 13.3, AMA 4.6, LAM 3.6, CIS 2.5, AST 2.1, CON 0.2	0.00	75.0	Broadly polylectic
<i>Micrandrena</i> Ashmead							
<i>A. magunta</i> Warncke	11	4	GR (11)	API 81.9, BRA 18.1	18.1	100.0	Polylectic with a strong preference (Apiaceae)
<i>A. rugothorace</i> Warncke	10	6	GR (10)	AST (Asteroideae) 100.0	100.0	100.0	Broadly oligolectic (Asteroideae, Asteraceae)
<i>Notandrena</i> Pérez							
<i>A. griseobalteata</i> Dours	5	2	FR (2); GR (3)	API 100.0	100.0	100.0	Broadly oligolectic (Apiaceae)
<i>A. ungeri</i> Mavromoustakis	3	1	GR (3)	API 100.0	100.0	100.0	Broadly oligolectic (Apiaceae)
<i>Taeniandrena</i> Hedicke							
<i>A. ovata</i> Schenck	20	11	BG (16); GR (4)	FAB 100.0	100.0	100.0	Broadly oligolectic (Fabaceae)
<i>Poecilandrena</i> Hedicke							
<i>A. crassana</i> Warncke	3	2	GR (3)	CAM ( <i>Legousia</i> ) 100.0	100.0	100.0	Narrowly oligolectic ( <i>Legousia</i> , Campanulaceae)
<i>A. neovirida</i> Grünwaldt	6	2	GR (6)	PLA ( <i>Veronica</i> ) 100.0	100.0	100.0	Narrowly oligolectic ( <i>Veronica</i> , Plantaginaceae)
<i>A. sphaecodimorpha</i> Hedicke	9	3	GR (9)	BRA 70.5, ASP 28.6, others 0.9	44.4	66.7	Probably broadly polylectic
<i>A. standfusorum</i> Scheuchl	1	1	GR (1)	PLA ( <i>Veronica</i> ) 100.0	100.0	100.0	Probably narrowly oligolectic ( <i>Veronica</i> , Plantaginaceae)
<i>Truncandrena</i> Warncke							
<i>A. canaeae</i> Strand	6	2	GR (6)	PAP ( <i>Papaver</i> ) 100.0	100.0	100.0	Narrowly oligolectic ( <i>Papaver</i> , Papaveraceae)
<i>A. delphiensis</i> Warncke	6	1	GR (6)	BRA 100.0	100.0	100.0	Probably broadly oligolectic (Brassicaceae)
<i>A. mucronata</i> Morawitz	18	4	GR (18)	PAP ( <i>Papaver</i> ) 100.0	100.0	100.0	Narrowly oligolectic ( <i>Papaver</i> , Papaveraceae)
<i>A. optata</i> Warncke	3	2	GR (3)	BRA 100.0	100.0	100.0	Probably broadly oligolectic (Brassicaceae)

Species	<i>n</i>	<i>N</i>	Origin (and number) of pollen loads	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
<i>A. schmiedeknechti</i> Magretti	2	1	GR (2)	BRA 100.0	100.0	100.0	Probably broadly oligolectic (Brassicaceae)
<i>A. serraticornis</i> Warncke	2	1	GR (2)	PAP ( <i>Papaver</i> ) 100.0	100.0	100.0	Narrowly oligolectic ( <i>Papaver</i> , Papaveraceae)
<i>Ulandrena</i> Warncke							
<i>A. abbreviata</i> Dours	7	1	GR (7)	AST (Asteroideae) 100.0	100.0	100.0	Broadly oligolectic (Asteroideae, Asteraceae)
<i>A. biguttata</i> Friese	7	2	BG (4); GR (3)	AST (Asteroideae) 100.0	100.0	100.0	Broadly oligolectic (Asteroideae, Asteraceae)
<i>A. concinna</i> Smith	1	1	GR (1)	AST (Asteroideae) 100.0	100.0	100.0	Broadly oligolectic (Asteroideae, Asteraceae)
<i>A. crecca</i> Warncke	1	1	GR (1)	AST (Asteroideae) 100.0	100.0	100.0	Broadly oligolectic (Asteroideae, Asteraceae)
<i>A. elegans</i> Giraud	3	2	BG (1); GR (2)	AST (Asteroideae) 100.0	100.0	100.0	Broadly oligolectic (Asteroideae, Asteraceae)
<i>A. fulvitaris</i> Brullé	8	4	GR (8)	AST (Asteroideae) 100.0	100.0	100.0	Broadly oligolectic (Asteroideae, Asteraceae)
<i>A. waschulzi</i> Strand	6	2	GR (6)	AST (Cichorioideae) 100.0	100.0	100.0	Broadly oligolectic (Cichorioideae, Asteraceae)
<i>A. westensis</i> Warncke	1	1	GR (1)	AST (Cichorioideae) 100.0	100.0	100.0	Broadly oligolectic (Cichorioideae, Asteraceae)
<i>incertae sedis</i>							
<i>A. olympica</i> Grünwaldt	7	1	GR (7)	CAR ( <i>Cerastium</i> ) 100.0	100.0	100.0	Narrowly oligolectic ( <i>Cerastium</i> , Caryophyllaceae)

Balkans, such as *Ulandrena*; all members of this clade seem to be specialists of Asteraceae, utilising either the subfamily Asteroideae or Cichorioideae. The pollen analysis is supported by direct observations (Figs 84A, 84C, 85B, C), and it is not considered necessary to exhaustively examine dozens of pollen loads.

Analysis of southern Balkan *Andrena* pollen loads highlights several trends to be discussed here. The first is the aforementioned pattern seen in the subgenus *Ulandrena*. Whilst across most of Central, Northern, and Western Europe (with only marginal occurrence in the Iberian Peninsula), workers only encounter a single representative of the subgenus, *A. polita*. This species flies in the summer, and is broadly oligolectic on Cichorioideae (Asteraceae) (Westrich 1989; Schmid-Egger and Scheuchl 1997). However, from Lower Austria (the edge of the Pannonian basin) and northern Italy to the Balkans, a large diversified clade of *Ulandrena* are encountered totalling 17 species within the geographic scope defined here. The majority of this species fly earlier in the spring, and utilise both Cichorioideae and Asteroideae (Asteraceae), specialising

on one or the other (Table 1). Some of the earlier flying species like *A. waschulzi* (and almost certainly its close relative *A. trikalensis*; *pers. obs.*) and *A. westensis* use Cichorioideae and all of the later flying species like *A. biguttata* (Fig. 85B) and *A. elegans* (Fig. 85C) use Asteroideae, many spring-flying species also use Asteroideae, such as *A. abbreviata* (Fig. 84A) and *A. concinna* (Fig. 84C). The species-richness of *Ulandrena*

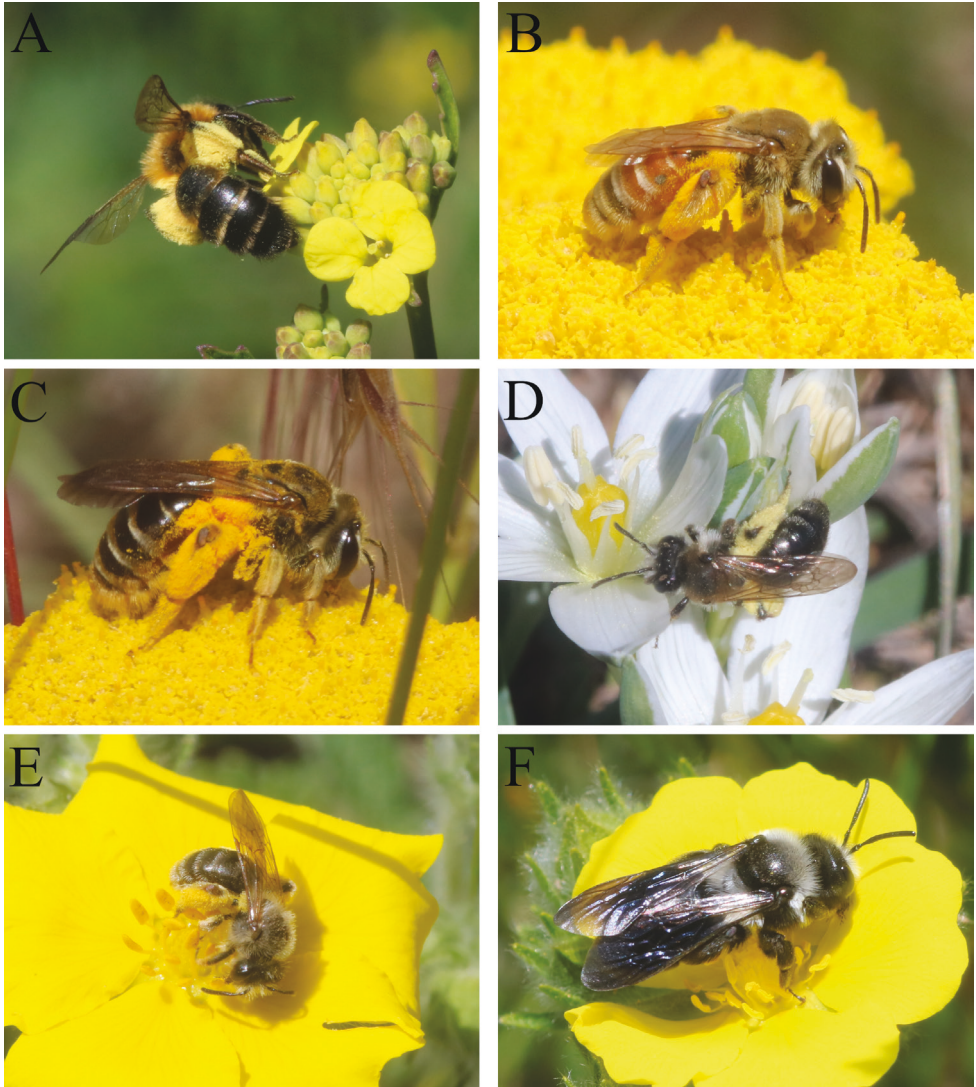


**Figure 84.** Female *Andrena* species collecting pollen. **A.** *Andrena (Ulandrena) abbreviata* Dours, 1873 on Asteroideae (Asteraceae); **B.** *Andrena (Truncandrena) canaeae* Strand, 1915 on *Papaver* (Papaveraceae); **C.** *Andrena (Ulandrena) concinna* Smith, 1853 on Asteroideae (Asteraceae); **D.** *Andrena (Truncandrena) delphiensis* Warncke, 1965 on Brassicaceae; **E.** *Andrena (Truncandrena) mucronata* Morawitz, 1871 on *Papaver* (Papaveraceae); **F.** *Andrena (Poecilandrena) neovirida* Grünwaldt, 2005 on *Veronica* (Plantaginaceae).

is one of the major faunal differences between the Iberian and Balkan peninsulas, whilst the similarly Asteraceae-specialised subgenus *Chlorandrena* is moderately diversified in both. Currently, all Balkan *Chlorandrena* appear specialised on Cichorioideae (Table 1), whereas Iberian *Chlorandrena* contain a number of Asteroideae specialists, underlining the importance of local trends and adaptations as well as the need to study individual species preferences.

When dealing with the subgenus *Truncandrena*, dietary specialisation on Brassicaceae is well-known (Westrich 1989; Wood 2023b, 2023c). It is therefore not a surprise to see this pattern in the southern Balkans (Table 1; Fig. 84D). *Andrena tscheki* ssp. *tritica* shows the same behaviour as the nominate subspecies, collecting pollen only from Brassicaceae (Fig. 85A). What was unexpected was the extensive use of *Papaver* (Papaveraceae) pollen by members of this subgenus, specifically *A. canea* (Fig. 84B), *A. mucronata* (Fig. 84E), and *A. serraticornis* (Table 1). During the morning typically before 10 am, at fields of *Papaver* are alive with bees and beetles visiting flowers and vigorously removing pollen, often almost “swimming” though the numerous anthers. Searching away from *Papaver* or inspecting these flowers after 10 am rarely if ever produced females of these three species. It must be concluded that they are specialised on *Papaver* pollen, and hence prioritise morning flight to utilise this resource before it is depleted; in the Balkans, *Papaver* flowers bloom only for a single day, with plants producing multiple flowers during the bloom period. This contradicts the statement by Standfuss et al. (2011: 296) that *A. mucronata* was a strong oligolege of *Geranium* and *Erodium* (Geraniaceae). This use of *Papaver* pollen is probably seen also in the unrelated *A. (Warnckandrena) curiosa* (Pisanty and Wood 2024).

The subgenus *Poecilandrena* contains species with metallic and non-metallic (usually black or red) integument. Like *Ulandrena*, this subgenus is particularly diversified in the East Mediterranean (Pisanty et al. 2018). The metallic members of the subgenus have been associated with *Veronica* (Plantaginaceae), whereas the non-metallic species are more typically polylectic (Westrich 1989; Scheuchl 2010; Standfuss et al. 2011; Wood and Roberts 2017; Pisanty et al. 2018, 2022b). This pollen analysis (Table 1) provided further support for narrow oligolecty on *Veronica* for *A. neovirida* (Fig. 84F) and *A. standfussorum*, and whilst *A. sphecodimorpha* is probably polylectic, *A. crassana* was found to be narrowly oligolectic on *Legousia* (Campanulaceae) based on pollen load analysis and direct observations. In the Peloponnese, on the island of Rhodes, and in Lebanon *A. crassana* can be observed flying low over *Legousia* flowers (pers. obs.); a single female was recorded on *Campanula* in Israel (G. Pisanty, pers. comm.). Whilst specialisation on Campanulaceae is well-known in the subgenus *Lepidandrena*, specifically on *Campanula* (Westrich 1989; Schmid-Egger and Scheuchl 1997), association with *Legousia* has not previously been reported. Placed into the subgenus *Poecilandrena* by its original authors (Grünwaldt et al. 2005), *A. olympica* was surprisingly found to be narrowly oligolectic on *Cerastium* (Caryophyllaceae). The shorter mouthparts can be clearly seen when comparing *Veronica*- and *Cerastium*-associated species. Further phylogenetic work is needed to understand where *A. olympica* belongs.



**Figure 85.** Female *Andrena* species collecting pollen. **A.** *Andrena* (*Truncandrena*) *tscheki* ssp. *tritica* Warncke, 1965 on Brassicaceae **B.** *Andrena* (*Ulandrena*) *biguttata* Friese, 1923 on Asteroideae (Asteraceae); **C.** *Andrena* (*Ulandrena*) *elegans* Giraud, 1863 on Asteroideae (Asteraceae); **D.** *Andrena* (*Euandrena*) *pileata* Warncke, 1975 on *Ornithogalum* (Asparagaceae); **E.** *Andrena* (*Euandrena*) *montana* Warncke, 1973 on *Potentilla* (Rosaceae); **F.** *Andrena* (*Melandrena*) *barbareae* Panzer, 1805 on *Potentilla* (Rosaceae).

For small black *Andrena*, the perspective from Northern Europe (therefore almost invariably concerning only the subgenus *Micrandrena*) is that most species have broad dietary niches. However, this changes as one proceeds southwards, and many are dietary specialists in the Mediterranean (Wood 2023b, 2023c). *Andrena* (*Micrandrena*) *rugothorace* was found to be broadly oligolectic on Asteroideae (Asteraceae), and the

two *Graecandrena* species *A. helenica* and *A. hyemala* were found to be broadly oligolectic on Brassicaceae and Apiaceae, respectively (Table 1). These three botanical families (Asteraceae, Apiaceae, and Brassicaceae) feature prominently in the diets of specialised small black *Andrena* from the subgenera *Aciandrena*, *Graecandrena*, and *Micrandrena* (Wood 2023b, 2023c). Whilst it is too soon to investigate in a more structured way as was done for the use of Fabaceae-Boraginaceae pollen by osmiine bees (Sedivy et al. 2013), there does seem to be a link between Apiaceae and Brassicaceae in the diets of small black *Andrena*. This is illustrated further by *A. magunta* which consistently collected Apiaceae pollen in every analysed load, but this was almost always mixed with at least some Brassicaceae pollen. This is reminiscent of the case of *Andrena (Graecandrena) verticalis* Pérez, 1895 and *Andrena (Micrandrena) nana* which were found to be mesolectic on Apiaceae and Brassicaceae and polylectic with a strong preference for Apiaceae, respectively (Wood 2023b). That *A. magunta* and *A. nana* show such a similar pollen diet is not surprising given their close morphological similarity and phylogenetic relatedness, but more broadly suggest that there is some kind of similarity between Apiaceae and Brassicaceae pollen that produces this emerging dietary syndrome; further study is required (Sedivy et al. 2013).

Compared to the swarm of *Andrena (Taeniandrena)* diversity in Iberia (Wood et al. 2021; Praz et al. 2022; Wood 2022; Wood 2023b), the *Taeniandrena* in the southern Balkans are more manageable taxonomically. Now that it has been recognised as a valid species, one of the most commonly encountered taxa is *A. ovata*; it can be commonly collected from *Vicia* in the spring, and was found to be broadly oligolectic on Fabaceae (Table 1), using also *Trifolium*-type pollen grains. The unrelated species *A. (Leimelissa) fallax*, the most westerly distributed member of this small subgenus, was found to also be specialised on Fabaceae, but was more narrowly oligolectic on *Onobrychis*. This restricted diet relative to species using Fabaceae more broadly is unusual in *Andrena*; to my knowledge, no other *Andrena* species has previously been reported as narrowly oligolectic on *Onobrychis*. No other quantitative data are available for other members of the subgenus *Leimelissa* Osytshnjuk, 1983.

Conversely, the narrowly distributed *A. (Holandrena) fimbriata* seems to be broadly oligolectic on Fabaceae, collecting abundantly from *Vicia* and *Trifolium*. This is interesting, as pollen preferences have been incompletely studied in the subgenus *Holandrena*; whilst in Central Europe, *A. (Holandrena) labialis* shows a very strong association with Fabaceae (Westrich 1989), this association is weaker on the edge of its range (Wood and Roberts 2017; unpublished data). The preferences of other species in this group support polylecty (Westrich 1989; Mandery et al. 2008, unpublished data). The taxonomic actions published here provide a level of taxonomic clarity in this troublesome subgenus, cementing the bivoltine species as definitively polylectic.

Concerning more troublesome subgenera, the subgenus *Euandrena* presents both taxonomic complexity and complex pollen diets. Following the recent improved taxonomic delineation of both *A. pileata* and *A. aff. limosa*, it can now be seen that they are both polylectic but potentially showing different preferences (Table 1). *Andrena pileata* was observed collecting pollen from *Ornithogalum* sp. (Asparagaceae; Mount Parnassos,

Greece; Fig. 85D), *Scilla* sp. (Asparagaceae; Mount Maenalon, Greece), and *Barbarea vulgaris* (Brassicaceae; above Popina Luka, Pirin Mountains, Bulgaria). Pollen analysis consequently suggested polylecty with a strong preference for Asparagaceae. As a species present at lower altitudes, *A. aff. limosa* was observed foraging extensively from *Campanula*; indeed, all examined pollen loads contained at least some *Campanula*, and polylectic with a strong preference for *Campanula* is consistent with the behaviour seen in some other *Euandrena* species, such as the second generations of *A. amieti* and *A. bicolor* (Praz et al. 2019). Whilst *A. aff. limosa* seems to be univoltine as opposed to these two bivoltine species, the attraction to *Campanula* is similarly expressed. Finally, *A. montana* was observed collecting pollen at high altitude (2000 m a.s.l.) from *Potentilla* (Rosaceae; Fig. 85E). This pollen host was only a tiny proportion of pollen used by *A. montana* in the Alps (Praz et al. 2019); given the scarcity of *A. montana* records in the Balkans, further study is required to identify if this is a regionally important pollen source for this polylectic species.

When taken collectively, it is now possible to make broad comparisons between the Iberian and Balkan peninsulas with relation to the local dietary adaptations presented by *Andrena*. In terms of pollen diets in *Andrena* that are present in the east but not the west, compared to Iberia, including our understanding based on the literature, the southern Balkans presents narrow floral specialists on *Anchusa* (Boraginaceae; *A. nasuta*), *Cerastium* (Caryophyllaceae; *A. olympica*), *Crocus* (Iridaceae; *A. grossella* and possibly *A. lasithi*), *Legousia* (Campanulaceae; *A. crassana*), *Muscari* (Asparagaceae; *A. muscaria*), *Onobrychis* (Fabaceae; *A. fallax*), *Papaver* (Papaveraceae: *A. canaeae*, *A. mucronata*, *A. serraticornis*, and probably *A. curiosa*), and probably *Lonicera* (Caprifoliaceae; *A. lonicera*).

In contrast, Iberia presents specialists of *Asphodelus* (Asphodelaceae; *Andrena sardoia* Lepeletier, 1841), *Lithodora* (Boraginaceae; *Andrena solenopalpa* Benoist, 1945), *Ranunculus* (Ranunculaceae; *Andrena ranunculi* Schmiedeknecht, 1883), *Plantago* (Plantaginaceae; *Andrena orbitalis* Morawitz, 1871), and *Reseda* (Resedaceae; *Andrena blanda* Pérez, 1895, *Andrena corax* Warncke, 1967, *Andrena laurivora* Warncke, 1974, *Andrena oviventris* Pérez, 1895, *Andrena relata* Warncke, 1967, and probably *Andrena murana* Warncke, 1967 and *Andrena rhypara* Pérez, 1895) (see illustrations in Wood 2023b). At a family level, the truly unique elements are hence specialisation on Asparagaceae, Caryophyllaceae, Iridaceae, and Papaveraceae in the east, and specialisation on Asphodelaceae, Plantaginaceae, Ranunculaceae, and Resedaceae in the west.

Both faunas therefore present richly different specialisations, with a slight bias towards plant species of dry habitats and sclerophytic scrublands in the west (*Asphodelus*, *Lithodora*, *Reseda*), and plant species of moderately humid fields, scrubland margins (*Anchusa*, *Cerastium*, *Legousia*, *Muscari*, *Onobrychis*, *Papaver*) and autumnal rains (*Crocus*) in the east. Both faunas are now characterised to a high degree, with just 21 species (7.7%) in the southern Balkans and 27 species (11.4%) in Iberia having unclear lecty statuses (Wood 2023b; unpublished data). Including these unknown species, overall, Iberia presents an estimated 55% (62% when excluding unclear species) oligolecty rate for *Andrena* species, compared to an estimated rate of 50% (54% when excluding unclear species) for the southern Balkans. This includes an estimated 17% of Iberian species broadly oligolectic on Brassicaceae, compared to an estimated 11%

of species broadly oligolectic on Brassicaceae in the southern Balkans; Brassicaceae specialisation appears to be more typical of the dry habitats of the West Mediterranean, increasing to an estimated 21% of the Moroccan *Andrena* fauna (unpublished data). Although more precise work is needed to further characterise these faunas, those of Iberia and the southern Balkans can be considered to have broadly equivalent rates of dietary specialisation with compositional tendencies as highlighted above.

### 5. Identification key to the *Andrena* of the southern Balkans

The female of *A. haladai* and the males of *A. bulgarica*, *A. cretica*, *A. dacica*, *A. elsei*, *A. nucleola*, *A. obscuricrus*, *A. pelagonia*, *A. pirinia*, *A. robusta*, *A. taprobana*, *A. toelgiana*, and *A. urdula* are unknown. Additional illustrations, images, and characters can be consulted in the following works which are not exhaustive, and not all the taxonomic concepts contained therein are followed here: Warncke (1965a, 1965b, 1973, 1975); Grünwaldt (1976); Schönitzer et al. (1995); Schmid-Egger and Scheuchl (1997); Gusenleitner and Schwarz (2002); Grünwaldt et al. (2005); Osytsnjuk et al. (2005, 2008); Schmid-Egger (2005); Scheuchl (2010, 2011); Schwenninger (2013, 2015); Praz et al. (2019, 2022); Wood (2021, 2023b, 2023d, 2024a); Pisanty et al. (2025).

Specifically, because this current work aims to be a companion piece to Wood (2023b), the key intentionally follows a very similar structure; that work and its included images can therefore be consulted at comparative points in the keys; minimal efforts are made here to reproduce images already presented in that work. Finally, the key presented here naturally does not account for the morphological variation expressed in stylised *Andrena* specimens. Identification should not be attempted for these specimens until one becomes deeply familiar with the fauna.

The female and male keys are separated for convenience and ease of numbering. For the female key, the following shortcuts can be used. The shortcuts must be worked through sequentially; they cannot be skipped, and they correspond to the major couplets within the full key itself. Note that additional information and detail is found in the main text of the key.

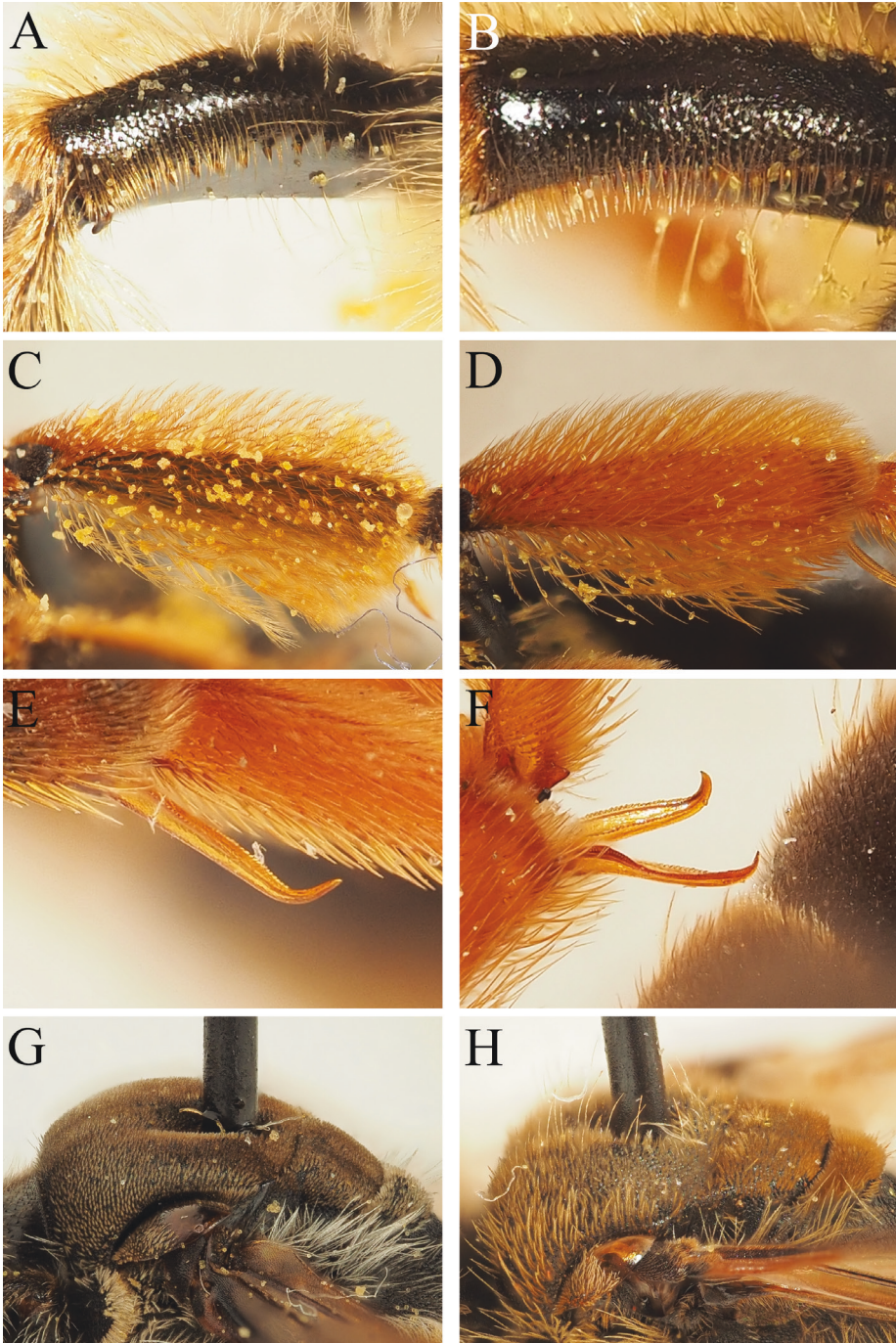
- A       Posterior face of hind femur with latitudinal row of spines or teeth (see caveats in main couplet entry)..... **go to 2**
- B       Hind tibial spur clearly broadened, either at its base or submedially.....  
..... **go to 30**
- C       Terga with marginal areas of T2–4 very broad, occupying 3/4–all of the visible ...segment, marginal areas overlain by long hairs emerging from the tergal base ..... **go to 56**
- D       Hairs of the tibial scopae clearly plumose (see caveats in main couplet entry) ..... **go to 58**
- E       Propodeal triangle clearly defined by strongly raised carinae, internal surface rugose-areolate..... **go to 71**
- F       Scutum and scutellum covered with short squamous hairs ..... **go to 73**

- G Propodeal scopa complete (dorsal and anterior fringe present) AND with inner surface hairless (subgenus *Simandrena* Pérez) ..... **go to 84**
- H Fovea strongly constricted medially, dorsally strongly diverging from the inner margin of the compound eye (*bicolorata*-group)..... **go to 92**
- I At least some tergal discs extensively red-marked ..... **go to 94**
- J Head, mesosoma, or tergal discs with metallic reflections..... **go to 103**
- K Surface of galearia covered with abundant laterally-projecting bristles ..... **go to 111**
- L Disc of T1 laterobasally with a pair of distinct flattened carinae ..... **go to 113**
- M Small black species, body length under 8 mm, or if up to 10 mm then with lateral faces of the propodeum with clear pattern of raised star-shaped wrinkles (all members of the subgenera *Aciandrena* Warncke, *Graecandrena* Warncke, *Micrandrena* Ashmead)..... **go to 115**
- N Clypeus flattened over majority of its surface. Species strongly associated with Fabaceae (subgenus *Taeniandrena* Hedicke) ..... **go to 163**
- O Fovea dorsally narrow, occupying at most 1/3 of the space between lateral ocellus and compound eye, ventrally narrowing strongly. Propodeal triangle “T-shaped”, very narrow apically (subgenus *Euandrena* Hedicke)..... **go to 173**
- P Clypeus punctate, interspaces forming weakly raised longitudinal wrinkles (*flavipes*-group) ..... **go to 191**
- Q Dorsolateral surface of the propodeum reticulate, with large and shallow punctures, clearly contrasting the shagreened and shiny propodeal triangle, this lacking lateral carinae and becoming shinier on the declivity (subgenus *Hoplendrena* Pérez, *partim*) ..... **go to 195**
- R Mesepisternum deeply and distinctly punctate, punctures separated by <1 puncture diameters, with weakly shiny interspaces ..... **go to 202**
- S Pronotum laterally keeled or angulate (with a humeral angle), keel or angle runs up dorsally to an angled corner ..... **go to 204**
- T Large species (over 12 mm in length). Typically with abundant black, brown, and/or..white pubescence. Clypeus strongly domed. Ocelloccipital distance long, at least 2 ....times the diameter of a lateral ocellus (subgenus *Melandrena* Pérez, *partim*)..... **go to 241**
- U Tergal discs finely microreticulate, with very widely scattered punctures or impunctate; tergal discs with surface largely hairless. Marginal areas of T2–4 slightly but distinctly depressed. Propodeum with dorsal part slightly elongate, propodeal triangle slightly elevated, distinctly and densely covered with fine granular microreticulation. Head slightly to distinctly elongate (subgenus *Nobandrena* Warncke) ..... **go to 253**
- V Head clearly longer than broad. Terga smooth and shiny, T2–T4 with dense apical hairbands composed of snow-white hairs, bands continuous on T3 and T4, obscuring the underlying surface. Hind tibiae orange. Associated with *Asparagus* (Asparagaceae)..... **go to 257**

- W Propodeum covered with long abundant pubescence, no meaningful difference between hairs of the dorsal fringe of the propodeal corbícula and those on the dorsal surface of the propodeum (subgenus *Truncandrena* Warncke, *partim*)..... **go to 258**
- X Remaining species..... **go to 270**

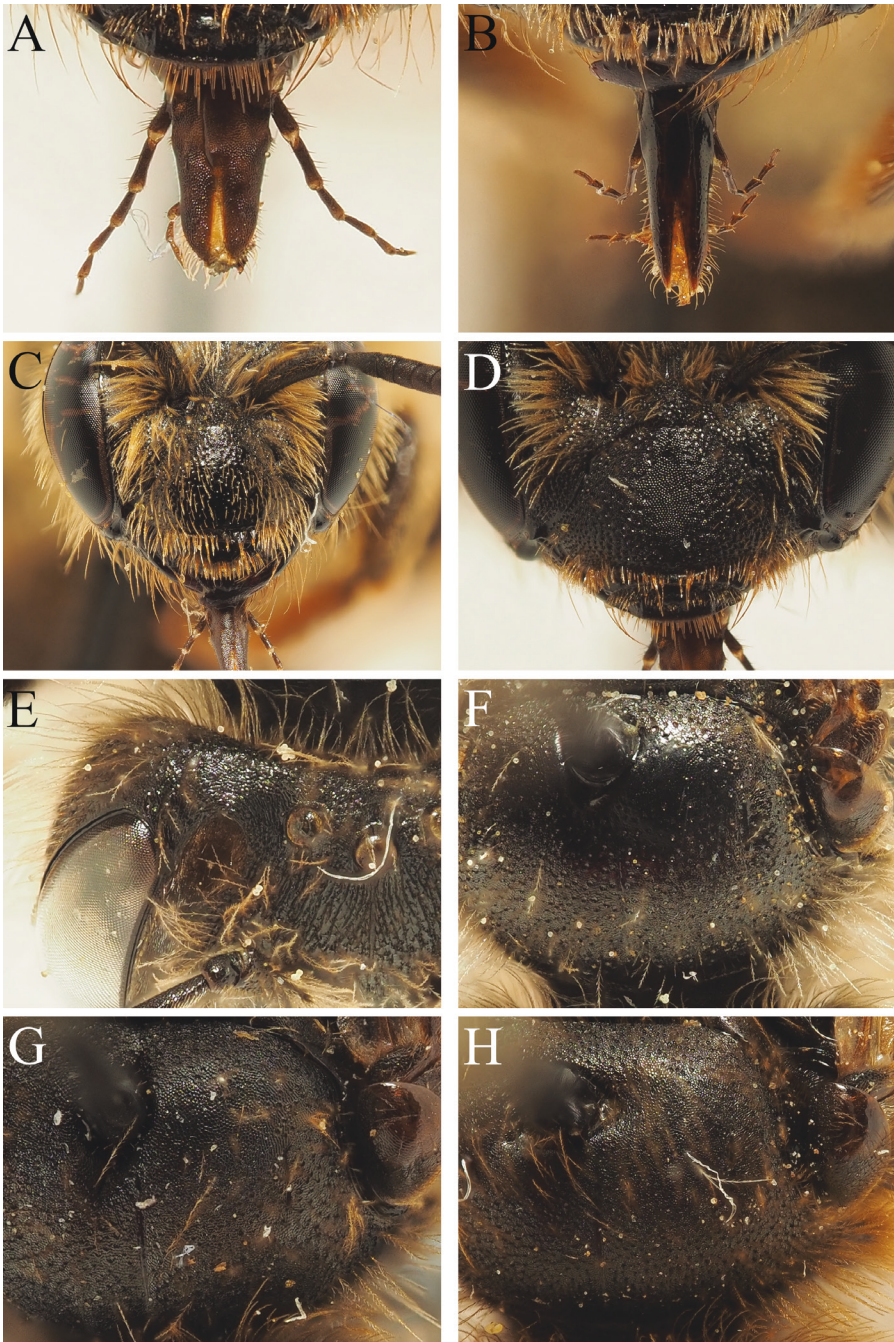
**Females**

- 1 Posterior face of hind femur with latitudinal row of spines or teeth (Fig. 86A, B). Note, if there is also a developed latitudinal carina, then the spines can be difficult to see (subgenus *Lepidandrena* Hedicke); these species have abundantly and densely punctate terga with the punctures separated by <1 puncture diameter, and predominantly with squamous hairs on the scutum and scutellum)..... **2**
- Posterior face of hind femur without latitudinal row of spines or teeth. A latitudinal carina may be present (e.g. *Andrena flavipes*) ..... **29**
- 2 Hind tibiae on their outer faces with the hairs of the tibial scopa composed of finely and densely plumose hairs (Fig. 86C, D)..... **3**
- Tibial scopa composed of simple hairs ..... **23**
- 3 Mid leg with the tibial spur distinctive, apically bent almost 90° (Fig. 86E). Hind tibial spurs both apically hooked (Fig. 86F). Clypeus strongly flattened medially, almost concave ..... **4**
- Legs with all tibial spurs straight. Clypeus not so flattened..... **5**
- 4 Terminal fringe composed of coppery-brown hairs. Apical margins of T2–4 with obscure to weakly developed hairbands. Found in continental Greece and Bulgaria ..... ***A. gamskrucki* Warncke**
- Terminal fringe composed of golden-orange hairs. Apical margins of T2–4 with narrow but strongly developed hairbands, complete on T3–4. Found on the East Aegean Islands (Lesbos)..... ***A. eburnea* Warncke**
- 5 Posterior face of hind femur with latitudinal carina with sparse and fine bristles. Most species with the scutum and scutellum dorsally with short, squamous hairs, hairs shorter than the diameter of a lateral ocellus (Figs 17G, 86G), sometimes with longer hairs or mixture of shorter and longer hairs (Fig. 86H). Metasomal terga strongly, densely, and uniformly punctate (remaining members of the subgenus *Lepidandrena* Hedicke)..... **6**
- Posterior face of hind femur with rounded or with obscure carina, with distinct row of robust teeth or spines. All species with the scutum and scutellum displaying longer hairs, clearly exceeding the diameter of a lateral ocellus, hairs never squamous. Most species with the metasoma displaying irregular punctures, often with “crater punctures” with their rims distinctly raised (subgenus *Chlorandrena* Pérez) ..... **13**



**Figure 86.** *Andrena (Chlorandrena) clypella* Strand, 1921 female. **A.** Hind femur, dorsal view; **C.** Hind tibial scopae, lateral view. *Andrena (Lepidandrena) mocsaryi* Schmiedeknecht, 1884 female. **B.** Hind femur, dorsal view; **D.** Hind tibial scopae, lateral view; **H.** Metasomal dorsum, lateral view. *Andrena (Lepidandrena) gamskrucki* Warncke, 1965 female. **E.** Mid tibial spur, lateral view; **F.** Hind tibial spurs, posterior view. *Andrena (Lepidandrena) pandellei* Pérez, 1895 female. **G.** Metasomal dorsum, lateral view.

- 6 Scutum and scutellum dorsally with uniformly short, squamous hairs, hairs shorter than the diameter of a lateral ocellus (Figs 17G, 86G)..... 7
- Scutum and scutellum dorsally displaying longer hairs, clearly exceeding the diameter of a lateral ocellus; some specimens showing a mixture of shorter and longer hairs, never uniformly short and squamous (Fig. 86H).....12
- 7 Metasoma with red markings on T2–3. Scutum and scutellum with squamous hairs dark brown to black. In the southern Balkans, restricted to the Rhodope mountains in Bulgaria ..... ***A. rufizona* Imhoff**
- Metasomal terga with the discs uniformly dark. Scutum and scutellum with squamous hairs greyish to brown (Fig. 86G). More widespread across the southern Balkans..... 8
- 8 Galea with the outer surface with strong microsculpture, uniformly dull (Fig. 87A). Not associated with *Campanula* (Campanulaceae) ..... 9
- Galea with the outer surface weakly sculptured, smooth and shiny (Fig. 87B). Associated with *Campanula*..... 10
- 9 Clypeus with a broad longitudinal impunctate midline around the width of 4 puncture diameters (Fig. 87D). Process of labrum very small, slightly wider than long. Apical margins of T2–4 with dense and complete white hairbands in fresh specimens. Associated with *Ornithogalum* (Asparagaceae)....  
..... ***A. mocsaryi* Schmiedeknecht (partim)**
- Clypeus irregularly punctate, punctures separated by 0.5–2 puncture diameters, without a longitudinal impunctate midline. Polylectic, not associated with a specific plant group ..... ***A. dorsalis* Brullé**
- 10 Tarsal segment 5 of the hind leg elongate and strongly bent. Larger, 13–14 mm..... ***A. curvungula* Thomson**
- Tarsal segment 5 of the hind leg shorter, at most as long as the 2 preceding segments taken together, only weakly bent. Somewhat smaller, not larger than 12 mm..... 11
- 11 Squamous hairs very thick; viewed dorsally, in fresh specimens the underlying scutal punctures are obscured. Midline of the scutum is only slightly impressed. Process of labrum markedly elongate with a clear apical emargination in the fore margin. Larger, 10–12 mm ..... ***A. pandellei* Pérez**
- Squamous hairs moderately thick; viewed dorsally, the underlying scutal punctures clearly visible through the hairs. Midline of the scutum clearly impressed. Process of labrum regularly trapezoidal, not elongate, fore margin almost straight. Smaller, 8–10 mm..... ***A. paucisquama* Noskiewicz**
- 12 Clypeus polished and shining in its apical 1/2, with a narrow poorly defined longitudinal midline around the width of 2 puncture diameters (Fig. 87C). Process of labrum normally sized, trapezoidal, 2 times wider than long. Polylectic, not associated with a specific plant group ..... ***A. florivaga* Eversmann**
- Clypeus uniformly dull, with a broad longitudinal impunctate midline around the width of 4 puncture diameters (Fig. 87D). Process of labrum very small, slightly wider than long. Associated with *Ornithogalum* (Asparagaceae) ..... ***A. mocsaryi* Schmiedeknecht (partim)**



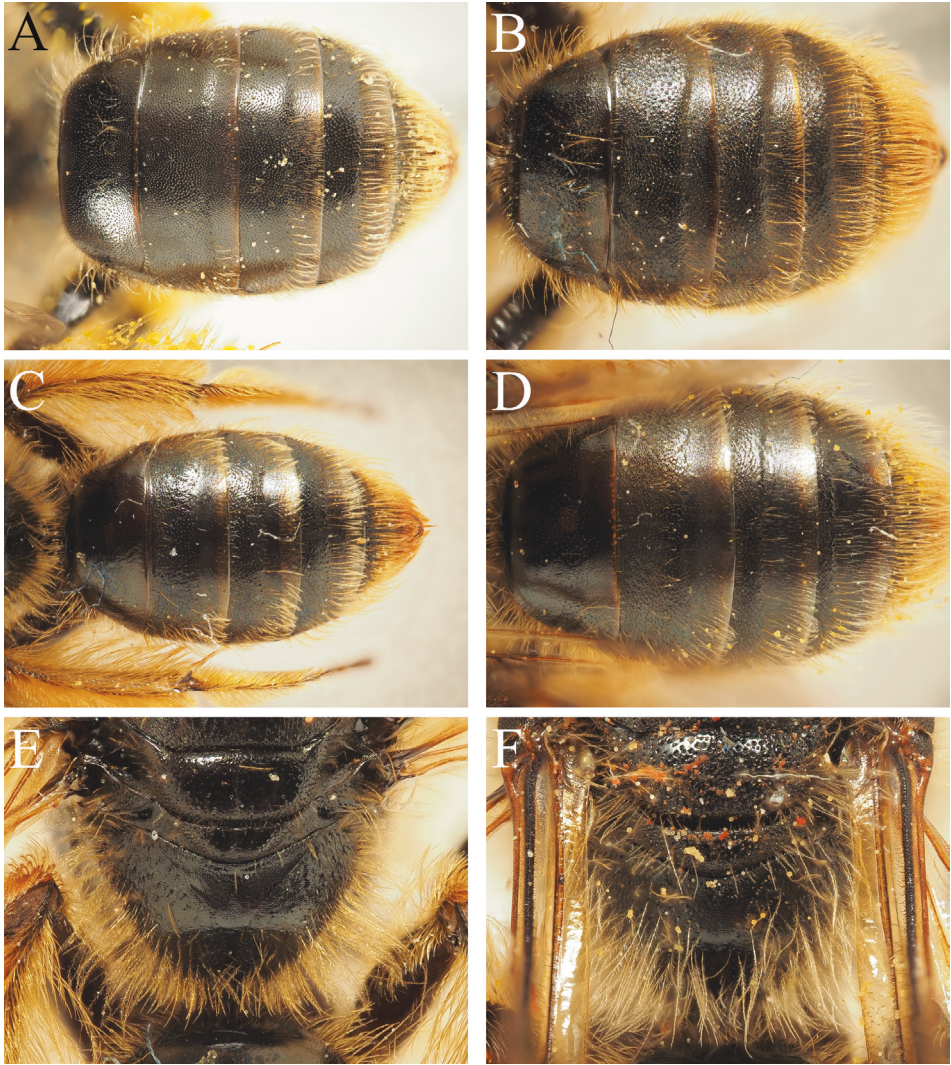
**Figure 87.** *Andrena* (*Lepidandrena*) *mocsaryi* Schmiedeknecht, 1884 female. **A.** Mouthparts, frontal view; **D.** Clypeus, frontal view. *Andrena* (*Lepidandrena*) *pandellei* Pérez, 1895 female. **B.** Mouthparts, frontal view. *Andrena* (*Lepidandrena*) *florivaga* Eversmann, 1852 female. **C.** Clypeus, frontal view. *Andrena* (*Chlorandrena*) *orientana* Warncke, 1965 female. **E.** Vertex and facial foveae, dorsal view; **F.** Scutum, dorsal view. *Andrena* (*Chlorandrena*) *astica* Warncke, 1967 female. **G.** Scutum, dorsal view. *Andrena* (*Chlorandrena*) *taraxaci* Giraud, 1861 female. **H.** Scutum, dorsal view.

- 13 Facial fovea with the outer margin adjacent to the inner margin of the compound eye dorsally diverging from it and curving inwards towards the lateral ocellus. Terga with variable but usually clear metallic green-blue reflections ..... ***A. nigroolivacea* Dours**
- Facial foveae with the margin adjacent to the compound eye remaining close, not obviously diverging from it dorsally (Fig. 87E). Terga dark, always non-metallic ..... **14**
- 14 Foveae strongly constricted ventrally, here narrower than the width of a flagellum (*taraxaci*-group) ..... **15**
- Foveae not strongly constricted ventrally, more-or-less as wide as dorsally, not narrower than the width of a flagellum (*humilis*-group) ..... **17**
- 15 Facial foveae bright, filled with yellow hairs (Fig. 87E). Face with almost uniformly bright hairs, at most with an occasional dark brown hair here or there. Scutum posteromedially polished and sparsely punctate, contrasting anterior and lateral parts of scutum which are dull (Fig. 87F) .....  
..... ***A. orientana* Warncke**
- Facial foveae dark, filled with dark brown to black hairs. Face with brown to dark brown hairs. Scutum uniformly sculptured and dull, never shining posteromedially (Fig. 87E, F)..... **16**
- 16 Scutum with punctation very shallow, disappearing into the sculpture; this is most visible posteromedially (Fig. 87G). Scutellum dull. Rare in the southern Balkans, confirmed only from south-eastern Bulgaria..... ***A. astica* Warncke**
- Scutum clearly punctate, this visible across the disc including posteromedially. Scutellum more weakly sculptured than the scutum, shagreened and weakly shining (Fig. 87H). Common and widespread in the southern Balkans..... ***A. taraxaci* Giraud**
- 17 Metasoma with T2–4 densely and uniformly punctate, punctures extending onto marginal areas, separated by 0.5–1 puncture diameters, those on T1 slightly more sparsely punctate. Terga finely sculptured, shining to weakly shining, no distinction in sculpture between discs and marginal areas (Fig. 88A) ..... ***A. chypella* Strand**
- Metasomal terga variably punctate, but marginal areas noticeably more obscurely punctate than discs, in many cases impunctate or at least with punctures difficult to distinguish against the underlying sculpture. Terga variably sculptured, always with a noticeable difference between the discs and marginal areas (Fig. 88B–D) ..... **18**
- 18 Propodeum strongly to weakly polished, dorsolateral parts with strong to weak crater punctures (Fig. 88E–F). Entirety of T1 (disc and marginal area) polished and shining. Discs of T2–4 strongly punctate and contrasting impunctate marginal areas (Fig. 88C, D) ..... **19**
- Propodeum microreticulate and dull, obscurely punctate, never with crater punctures. T1 variably sculptured, but never with the marginal area polished and shining (e.g. Fig. 88B). Discs of T2–4 variably punctate, often poorly differentiated from the punctation of the marginal areas..... **20**

- 19 Scutellum polished and shining, medially with punctures irregular and sparse, separated by 1–4 puncture diameters (Fig. 88E). Marginal areas of T3–4 occupying <50% of the visible surface (Fig. 88C). Dorsolateral parts of propodeum with poorly-defined crater punctures. Smaller, 8–9 mm. Currently known from southern Bulgaria, north-eastern Greece (Thrace), and the East Aegean Islands (Fig. 76) ..... ***A. exquisita* Warncke**
- Scutellum shagreened, only weakly shining due to dense punctures separated by <0.5–0.5 puncture diameters medially (Fig. 88F). Marginal areas of T3–4 occupying >50% of the visible surface, almost 75% on T4 (Fig. 88D). Dorsolateral parts of propodeum with strong, large, and well-defined crater punctures. Larger, 10–11 mm. More widespread across the southern Balkans ..... ***A. humabilis* Warncke**
- 20 Scutum posteromedially with a more-or-less circular area with sculpture becoming weak, weakly to strongly polished and shining. Clypeus variably sculptured but usually becoming weakly sculptured and somewhat shining in its apical 1/2, with very subtle metallic green-purple hints ..... ***A. panurgimorpha* Mavromoustakis**
- Scutum uniformly sculptured, without a shining area posteromedially. Clypeus usually uniformly dull, never with subtle metallic hints ..... **21**
- 21 T2 between the punctures weakly shagreened, comparatively shiny (Fig. 88B). Larger species, over 10 mm in length ..... ***A. humilis* Imhoff**
- T2 between the punctures strongly shagreened and dull. Smaller species, under 10 mm in length ..... **22**

The following two species are challenging to separate because the characters are mostly relative, and have a level of variation; association with concurrently active males should be made.

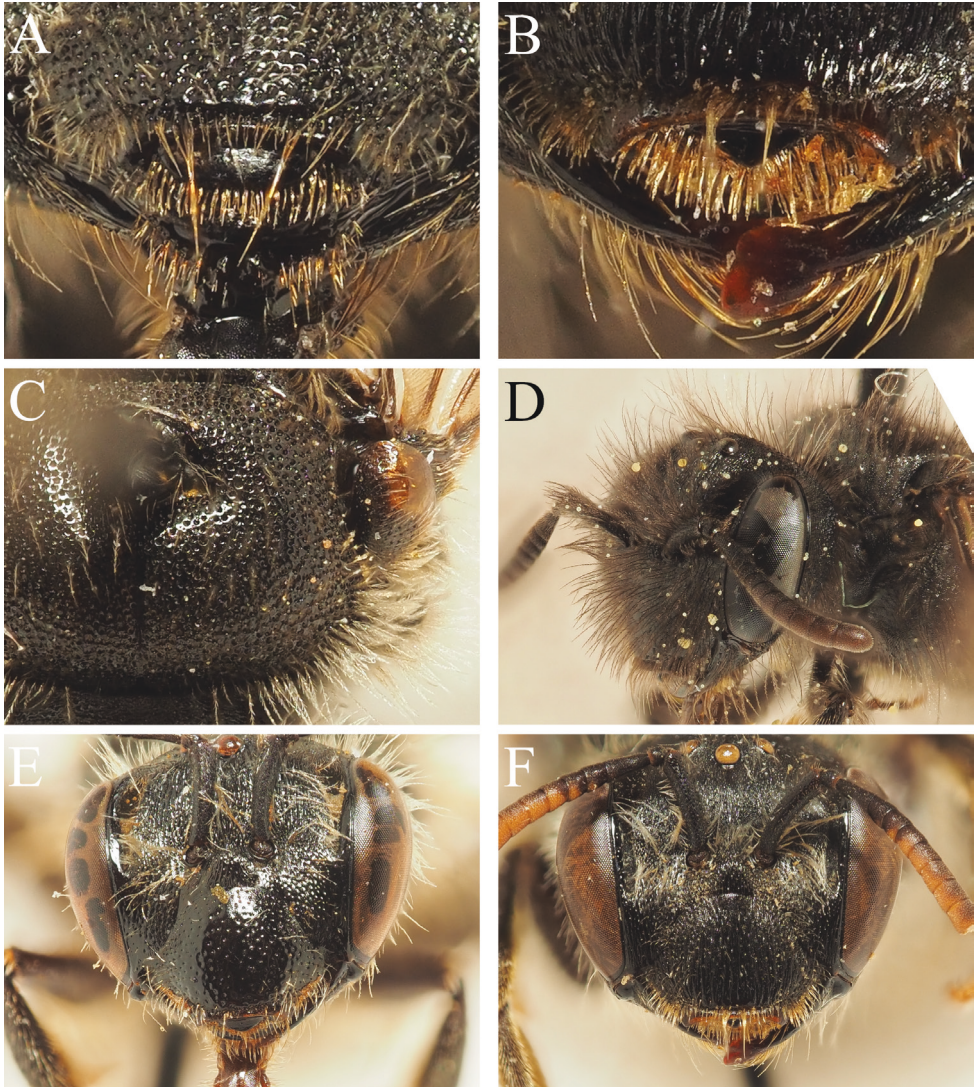
- 22 Nervulus typically interstitial to weakly postfurcal. Disc of T1 relatively more strongly sculptured, rarely smooth and shining, more densely punctate, punctures separated by 1–2 puncture diameters ..... ***A. cinerea* Brullé**
- Nervulus typically antefurcal. Disc of T1 smooth and shining, sparsely punctate, punctures separated by 1–3 puncture diameters ..... ***A. cinereophila* Warncke**
- 23 Process of labrum rectangular, 3–4 times broader than long (Fig. 89A). Metasoma with integument densely and uniformly punctate on both the discs and marginal areas. Small species, always <9 mm in length (subgenus *Cryptandrena* Pittioni) ..... **24**
- Process of labrum narrower, narrow and pointed (e.g. Fig. 89B) or rounded, but at most only slightly broader than long. Metasomal integument variable. Usually exceeding 8 mm in length ..... **26**



**Figure 88.** *Andrena (Chlorandrena) chypella* Strand, 1921 female. **A.** Metasoma, dorsal view. *Andrena (Chlorandrena) humilis* Imhoff, 1832 female. **B.** Metasoma, dorsal view. *Andrena (Chlorandrena) exquisita* Warncke, 1975 female. **C.** Metasoma, dorsal view; **E.** Propodeum and scutellum, dorsal view. *Andrena (Chlorandrena) humabilis* Warncke, 1965 female. **D.** Metasoma, dorsal view. **F.** Propodeum and scutellum, dorsal view.

All members of the subgenus *Cryptandrena* are challenging to determine; consultation of confidently determined or barcoded specimens is advised.

- 24 Scutum very densely punctate, punctures confluent to separated by 0.5 puncture diameters (Fig. 89C) ..... ***A. ventricosa* Dours**
- Scutum comparatively less densely punctate, punctures separated by 0.5–1.5 puncture diameters ..... **25**



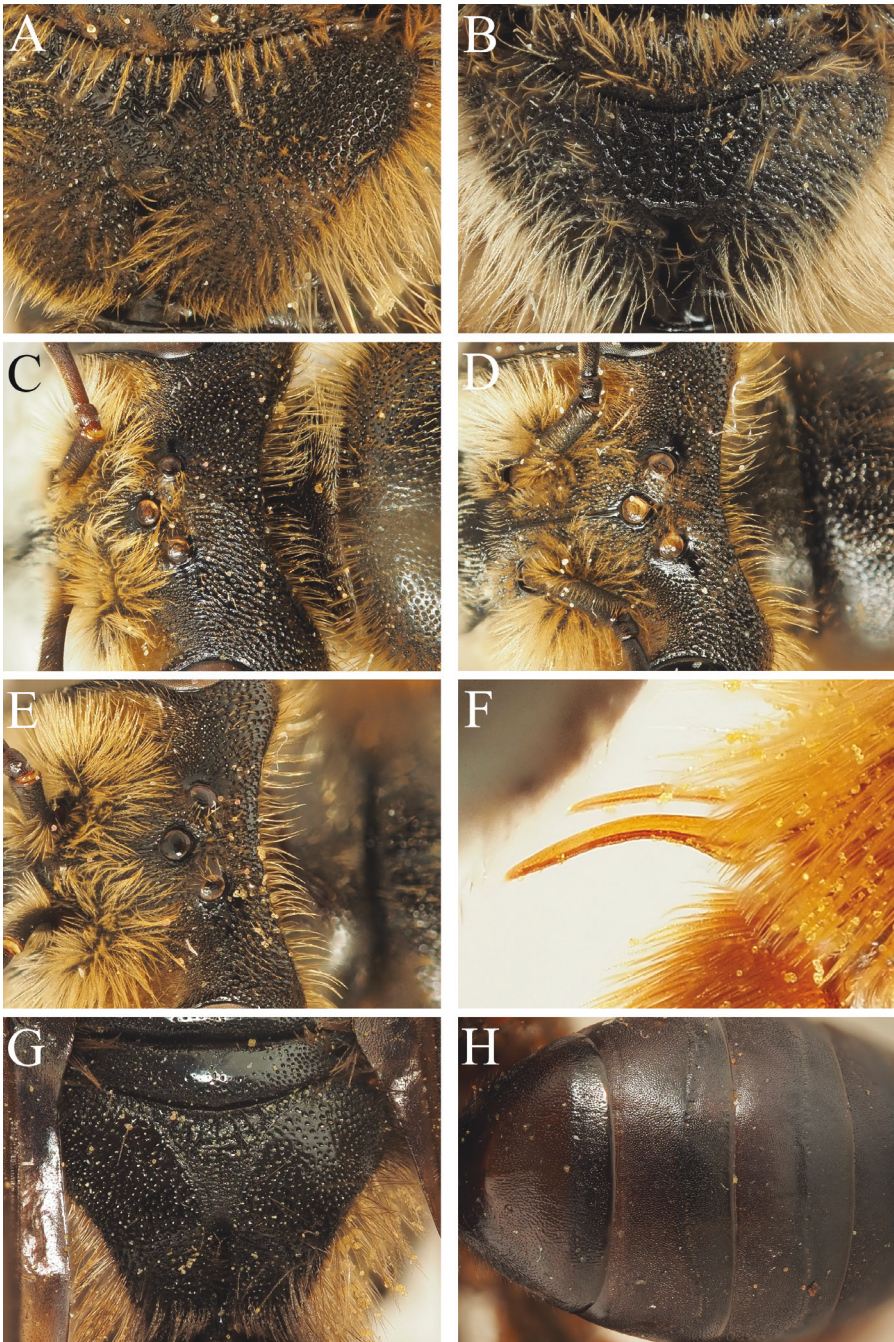
**Figure 89.** *Andrena (Cryptandrena) ventricosa* Dours, 1873 female. **A.** Process of labrum, ventral view; **C.** Scutum, dorsal view. *Andrena (Orandrena) oralis* Morawitz, 1876 female. **B.** Process of labrum, ventral view; **F.** Head, frontal view. *Andrena (Avandrena) panurgina* De Stefani, 1889 female. **D.** Head, lateral view. *Andrena (incertae sedis) garrula* Warncke, 1965 female. **E.** Head, frontal view.

- 25      Clypeus more-or-less flattened over its surface. Scutum with punctures separated by 0.5–1 puncture diameters at most (Fig. 66F). Metasomal punctation dense, separated by <0.5–0.5 puncture diameters (Fig. 66H). Widespread across the southern Balkans but not on the island of Crete (Fig. 5).  
 ..... *A. brumanensis* Friese
- Clypeus is distinctly longitudinally domed in its median 1/2. Scutum with relatively spaced punctures separated by 0.5–1.5 puncture diameters and

- approaching 2 puncture diameters posteromedially (Fig. 66E). Metasomal punctation less dense, separated by 0.5–1 puncture diameters with the interspaces shining, metasoma therefore appearing relatively shiny (Fig. 66G). Found on the island of Crete (Fig. 5) ..... ***A. testudo* sp. nov.**
- 26 Tergal discs and margins impunctate. Head and metasoma with abundant black pubescence (Fig. 89D). In the southern Balkans, found only on the island of Corfu. Associated with *Erodium* (Geraniaceae) ..... ***A. panurgina* De Stefani**
- At least tergal discs punctate, often with tergal margins also punctate. Head and mesosoma with pale to brownish pubescence, never with abundant black hairs. More widespread across the southern Balkans. Associated with Brassicaceae ..... **27**
- 27 Clypeus polished and shining medially, without any longitudinal striations (Fig. 89E). Process of labrum evenly rounded, not pointed and triangular. Tergal discs punctate, marginal areas impunctate..... ***A. garrula* Warncke**
- Clypeus with longitudinal striations, surface dull (Fig. 89F). Process of labrum triangular, narrow and acutely pointed (Fig. 89B). Tergal discs and margins uniformly punctate..... **28**

The following two species may not be separable in the female sex; association with concurrently active males should be made pending further study.

- 28 Ocelloccipital distance relatively long, 1.5–2 times the diameter of a lateral ocellus (Fig. 44B, D). Slightly larger bee, 10–11 mm ..... ***A. oralis* Morawitz**
- Ocelloccipital distance relatively short, equalling the diameter of a lateral ocellus (Fig. 44F, H). Slightly smaller bee, 8–9 mm ..... ***A. gallinula* Warncke**
- 29 (1). Hind tibial spur clearly broadened, either at its base or submedially (Fig. 90F) ..... **30**
- Hind tibial spur parallel-sided, not broadened basally or submedially ..... **56**
- 30 Propodeum dorsolaterally with dense punctures, punctures separated by <1 puncture diameter. Propodeum rounded in lateral view, without clearly separated horizontal and vertical parts (Fig. 90A; subgenus *Holandrena* Pérez) ..... **31**
- Propodeum dorsolaterally either with raised reticulation or rugosity (e.g. Fig. 90B), without dense punctures, or without punctures at all. Propodeum with separated horizontal and vertical parts..... **35**
- 31 Vertex strongly elongate, ocelloccipital distance equalling or exceeding 3 times the diameter of a lateral ocellus (Fig. 90C) ..... ***A. variabilis* Smith**
- Vertex shorter, never exceeding 2 times the diameter of a lateral ocellus (Fig. 90D, E) ..... **32**



**Figure 90.** *Andrena (Holandrena) labialis* (Kirby, 1802) female. **A.** Propodeum, dorsal view; **D.** Vertex, dorsal view. *Andrena (Plastandrena) bimaculata* (Kirby, 1802) female. **B.** Propodeum, dorsal view; **F.** Inner hind tibial spur, dorsal view. *Andrena (Holandrena) variabilis* Smith, 1853 female. **C.** Vertex, dorsal view. *Andrena (Holandrena) decipiens* Schenck, 1853 female. **E.** Vertex, dorsal view. *Andrena (Scitandrena) scita* Eversmann, 1852 female. **G.** Propodeum, dorsal view. *Andrena (Melanapis) fuscosa* Erichson, 1835 female. **H.** Metasoma, dorsal view.

- 32 Disc of T1 shagreened to finely microreticulate, predominantly dull. Disc of T1 densely punctate, majority of punctures separated by <0.5–0.5 puncture diameters. Clypeus with granular microreticulation, dull, sparsely punctate, punctures separated by 1–3 puncture diameters..... ***A. fimbriata* Brullé**
- Disc of T1 polished and shining. Disc of T1 slightly less densely punctate, most punctures separated by at least 0.5–1 puncture diameters. Clypeus variably sculptured, often shining between interspaces, always more densely punctate, punctures separated by at most 1–1.5 puncture diameters, often denser ..... **33**
- 33 Ocelloccipital distance equalling 2 times the diameter of a lateral ocellus. Clypeus strongly flattened and extremely densely punctate, punctures confluent (separated by <0.5 puncture diameters). Bivoltine, specimens from the summer generation can show short sub-squamous hairs around the margins of the scutum and scutellum, integument of clypeus, mesosoma, and metasoma often variably red-marked..... ***A. forsterella* Osytshnjuk**
- Ocelloccipital distance shorter, 1–1.5 times the diameter of a lateral ocellus (Fig. 90D, E, note the stacking of photographs exaggerates this distance, under a microscope these ratios are correct). Clypeus weakly to obscurely flattened, less densely punctate, punctures separated by 0.5–1.5 puncture diameters. Univoltine or bivoltine, but summer active specimens without sub-squamous hairs or red-marked integument..... **34**
- 34 Disc of T1 densely punctate, punctures typically separated by 1 puncture diameter. Scutellum dull between punctures. Ocelloccipital distance 1.5 times the diameter of a lateral ocellus (Fig. 90D). Tergal hair bands interrupted medially. Univoltine, flying in the late spring and early summer (May–July) ..... ***A. labialis* (Kirby)**
- Disc of T1 more sparsely punctate, punctures separated by greater than 1 puncture diameter, typically by 2 puncture diameters. Scutellum shiny between punctures. Ocelloccipital distance equalling or slightly exceeding the diameter of a lateral ocellus (1–1.5 times the diameter of a lateral ocellus) (Fig. 90E). Tergal hair bands complete (beware abraded specimens). Bivoltine, flying in the spring (April–May) and summer (July–August)..... ***A. decipiens* Schenck** (inclusive of *flavilabris* Schenck)
- 35 Hind tibial spur broadened at its base (Fig. 90F). Propodeal triangle clearly defined laterally by strongly raised carinae, internal surface with dense network of strongly raised honeycomb-like rugosity (Fig. 90B)..... **36**
- Hind tibial spur broadened submedially. Propodeal triangle simply defined laterally by weak and obscurely raised carinae, internal surface without a dense network of strongly raised honeycomb-like rugosity ..... **41**
- 36 Mesepisternum and dorsolateral parts of propodeum polished and shining, deeply punctate (Fig. 90G). Terga usually extensively red-marked..... ***A. scita* Eversmann**
- Mesepisternum and propodeum sculptured and dull, never shining and with clear visible punctures. Terga variably coloured ..... **37**

- 37 Pronotum with humeral angle. Terga finely and extremely densely punctate, punctures almost confluent (Fig. 90H).....***A. fuscosa* Erichson**  
 – Pronotum rounded, never with a raised humeral angle. Terga more coarsely punctate, always with shining interspaces of at least 0.5 puncture diameters between punctures (subgenus *Plastandrena* Hedicke) ..... **38**

All members of the subgenus *Plastandrena* are very challenging to separate in the female sex due to high levels of variation in punctation density, integument colour, and pubescence colour; modern species concepts remain incompletely established and refined. Care must be taken, and association with concurrently active males should be made where possible. Not all specimens can be confidently determined.

- 38 Tibial scopae composed of predominantly white hairs, with a variable extent of black hairs along the dorsal margin close to the basitibial plate OR with the tibial scopae entirely black (e.g. on the island of Karpathos). Mesosoma with predominantly black pubescence, sometimes entirely black, sometimes with greyish hairs dorsally (this may be referable to *Andrena nigrospina* Thomson, 1872 which is not yet positively demonstrated from the southern Balkans). Mesosoma either entirely black-haired, or with narrow white apical hairbands (f. *spectabilis* Smith, 1853) .....***A. pilipes* Fabricius**  
 – Tibial scopae variable, unicolourous or bicoloured but neither predominantly composed of white hairs NOR entirely black. Pubescence of mesosoma variable shades of brown, but never black. Mesosoma never with abundant black pubescence or narrow apical white hairbands ..... **39**
- 39 Tibial scopae bicoloured, dorsally brown, ventrally greyish-white. Scutum uniformly and very densely punctate. Metasoma with the marginal areas lightened reddish-hyaline yellow. Tergal discs covered with long shaggy yellowish hairs, forming weak loose apical hairbands. Hind tibiae dark. Very rare, currently recorded only in the spring (April) .....***A. apiformis* Kriechbaumer**  
 – Without this precise combination of characters; tibial scopae unicolourous, usually orangish. Scutal punctation variable, often with punctures sparse posteromedially, separated by 2–3 puncture diameters. Metasoma variable, from entirely black to partially red-marked, marginal areas entirely dark to lightened hyaline red-yellow. Tergal discs typically without long shaggy hairs, hairs shorter, sometimes forming pale apical hairbands. Hind tibiae sometimes orange. More frequently recorded, flying in the spring and summer ..... **40**
- 40 Depression of T1 sparsely punctate, punctures separated by more than 2 puncture diameters. Scutum posteromedially with maximum interspace distance around 2 puncture diameters. Nominally univoltine, flying only in the spring ..... ***A. tibialis* (Kirby)**  
 – Depression of T1 densely punctate, punctures separated by 0.5–1 puncture diameters. Scutum posteromedially with maximum interspace distance exceeding 3 puncture diameters. Nominally bivoltine, flying in the spring and the summer ..... ***A. bimaculata* (Kirby)**

- 41 Tibial scopa ventrally composed of long plumose hairs. Posterior face of the hind femora with clear latitudinal carina. Associated with scabious species (Dipsacoideae; Caprifoliaceae) ..... ***A. hattorfiana* (Fabricius)**
- Tibial scopa entirely composed of simple hairs, at most with the occasional plumose hair, never abundantly plumose ventrally. Posterior face of the hind femorae typically rounded, without a latitudinal carina, though with a weak carina in *A. fulvitaris*; this species has a distinct impression on the disc of T1 (Fig. 91A), see the next couplet. Associated with Asteraceae (Figs 84A, C, 85B, C; subgenus *Ulandrena* Warncke) ..... **42**

Members of the subgenus *Ulandrena* species present many identification challenges in the female sex; association with concurrently active males, biogeographical context, and comparison with confidently determined or barcoded specimens is strongly recommended.

- 42 Disc of T1 with weak and obscure punctures, medially with a slight longitudinal ridge with the areas laterally adjacent to said ridge slightly but distinctly depressed (Fig. 91A). Moderately large body size of 12–13 mm .  
..... ***A. fulvitaris* Brullé**
- Disc of T1 variably punctate, in many cases abundantly, deeply, and densely punctate, but never with a longitudinal ridge with the lateral areas depressed (e.g. Fig. 91B–D, G, H). Body size variable, but typically either larger (exceeding 14 mm in length) or smaller (under 10 mm in length) ..... **43**
- 43 Large species, at least 14 mm in length (*concinna*-group) ..... **44**
- Smaller species, usually not exceeding 10 mm in length, but sometimes up to 13 mm in length (*A. westensis*) ..... **47**
- 44 Hind tarsal claws unidentate, without an inner subapical tooth. Scutellum polished and shining, finely punctate with punctures separated by an average of 1 puncture diameter; interspaces therefore bright and clearly visible  
..... ***A. elegans* Giraud**
- Hind tarsal claws with an inner subapical tooth. Scutellum finely microreticulate, very densely punctate with punctures separated by an average of 0.5 puncture diameters; surface therefore dull without clearly visible interspaces..... **45**

It has not been possible to examine female specimens of *A. heinrichi*, but the other two possible species are not yet known from this island, and hence it is diagnosed based on its geographic distribution.

- 45 Present on the island of Samos..... ***A. heinrichi* Grünwaldt**
- Present elsewhere in the southern Balkans..... **45**
- 46 Tergal margins with weak apical hairbands, those on T1–2 not obscuring the underlying surface, becoming stronger on T3–4 (Fig. 59D). Ocellocapital distance around 3 times the diameter of a lateral ocellus. Present

in Albania and Mediterranean continental Greece (Fig. 60), flying slightly earlier in the season (Fig. 61) ..... ***A. concinna* Smith**

– Tergal margins with strong apical hairbands of uniform strength across T1–4, obscuring the underlying surface. Ocelloccipital distance around 4–5 times the diameter of a lateral ocellus. Present in continental Greece, Lesbos, North Macedonia, and Bulgaria (Fig. 60), flying slightly later in the season (Fig. 62)..... ***A. crecca* Warncke**

47 Small species, 6–8 mm in length, scutum with slight greenish metallic hints (Fig. 91E, F; *waschulzi*-group) ..... **48**

– Larger species, 8–13 mm in length, scutum never with greenish metallic hints ..... **50**

48 Scutum with comparatively weak punctation, the punctation relatively difficult to distinguish against the fine granular microreticulation of the scutum (Fig. 91E). Punctures separated by 1 puncture diameter, interspaces dull to at most, weakly shining. Clypeus shallowly and obscurely punctate, punctures partially disappearing into the underlying sculpture. Continental Greece only..... ***A. trikalensis* Warncke**

– Scutum with strong, clearly-defined punctation that is easily visible against the sculpture of the scutum (Fig. 91F). Punctures separated by <0.5 puncture diameters. Clypeus distinctly punctate, punctures clearly visible against the underlying sculpture. Distribution variable ..... **49**

49 Scutum with punctures separated by 0.5 puncture diameters, interspaces weakly shining, scutum therefore appearing to be weakly shining (Fig. 91F). Albania, continental Greece, and Crete (Fig. 65).....

..... ***A. waschulzi* Strand**

– Scutum with punctures separated by <0.5 puncture diameters, essentially confluent, scutum therefore appearing dull. Southern Bulgaria and the East Aegean Islands (Fig. 65)..... ***A. neocypriaca* Mavromoustakis**

50 Forewing with the nervulus strongly postfurcal (c.f. Fig. 60D).....

..... ***A. subglobosa* Dours**

– Forewing with the nervulus interstitial..... **51**

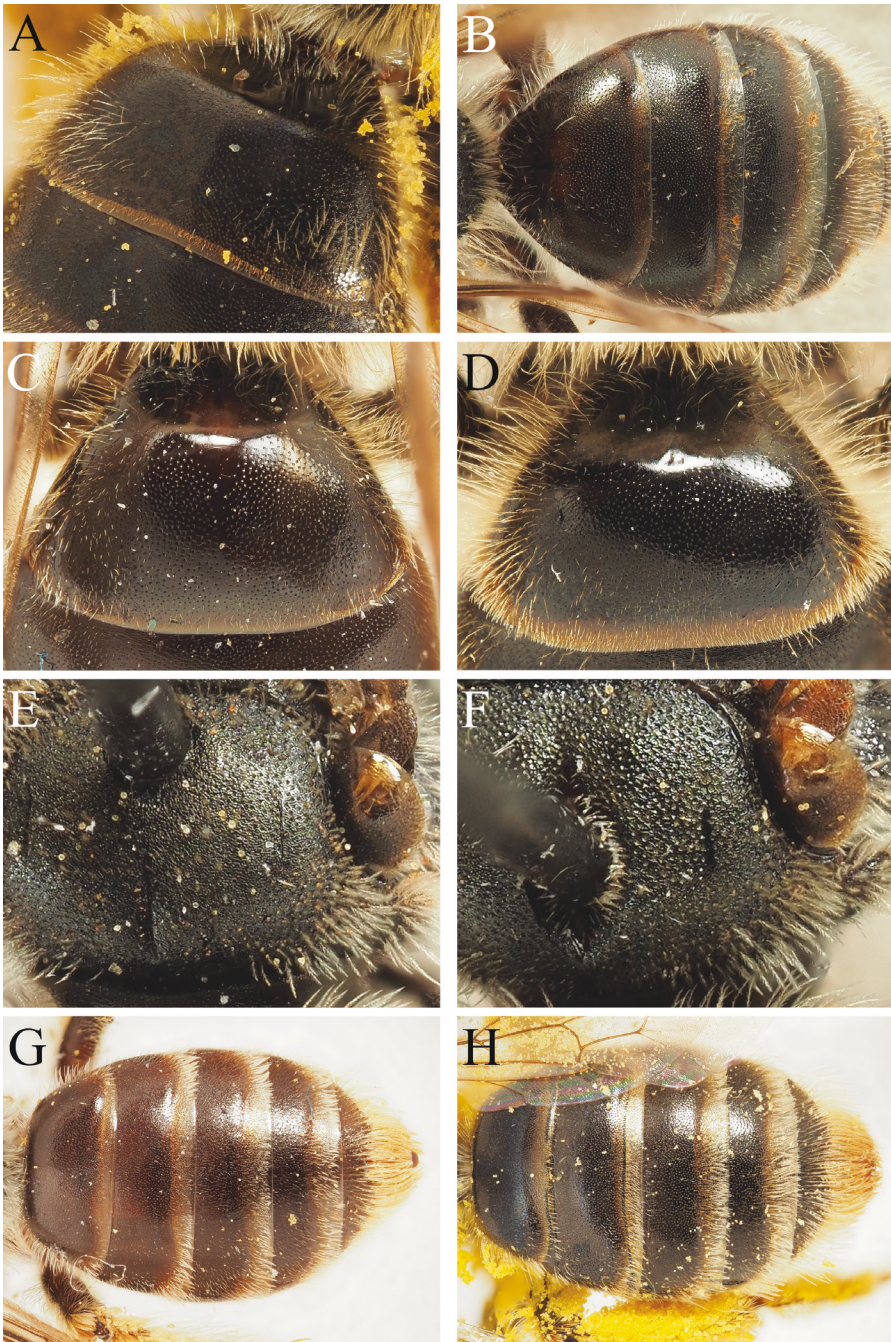
51 Larger species, 12–13 mm in length (*polita*-group) ..... **52**

– Smaller species, 8–10 mm in length (*abbreviata*-group) ..... **53**

52 Disc of T1 with a distinct impunctate longitudinal line beginning medially and descending onto the declivity (Fig. 91C). Scutum finely, densely, and distinctly punctate, punctures separated by 0.5 puncture diameters, interspaces weakly shining. Widespread across the southern Balkans, though avoiding strongly Mediterranean habitats. Flying later in the season (predominantly June–July)..... ***A. polita* Smith**

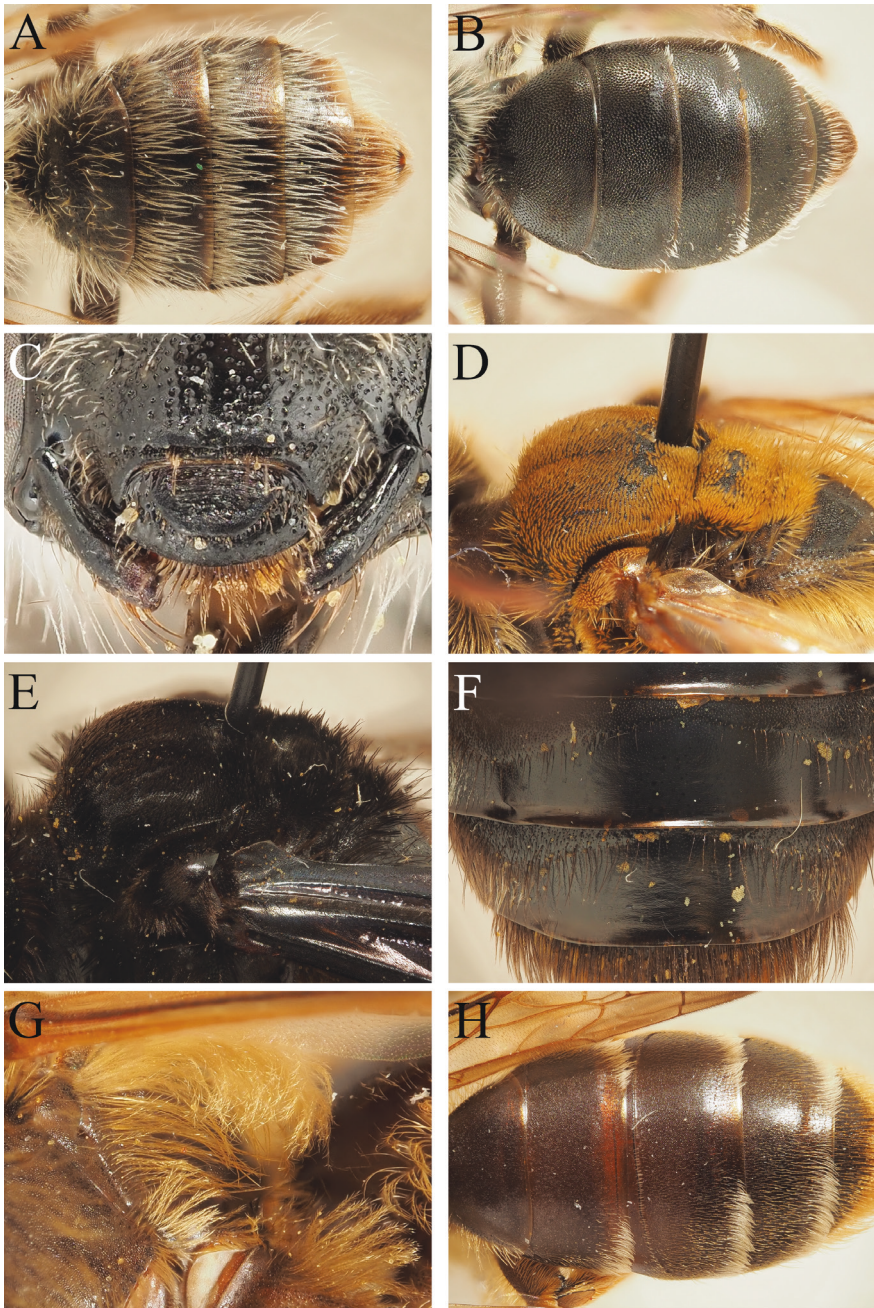
– Disc of T1 with uniform punctures, without a distinct impunctate longitudinal line (Fig. 91D). Scutum indistinctly punctate, punctures separated by 0.5–1 puncture diameters, interspaces dull. Found in Albania and Greece only. Flying earlier in the season (predominantly April–May) .....

..... ***A. westensis* Warncke**



**Figure 91.** *Andrena (Ulandrena) fulvitaris* Brullé, 1833 female. **A.** Tergum 1, dorsal view. *Andrena (Ulandrena) waschulzi* Strand, 1921 female. **B.** Metasoma, dorsal view; **F.** Scutum, dorsal view. *Andrena (Ulandrena) polita* Smith, 1847 female. **C.** Tergum 1, dorsal view. *Andrena (Ulandrena) westensis* Warncke, 1965 female. **D.** Tergum 1, dorsal view. *Andrena (Ulandrena) trikalensis* Warncke, 1965 female. **E.** Scutum, dorsal view. *Andrena (Ulandrena) incustodita* Wood, 2024 female. **G.** Metasoma, dorsal view. *Andrena (Ulandrena) abbreviata* Dours, 1873 female. **H.** Metasoma, dorsal view.

- 53 Terga with very weak punctation, tergal discs with fine shagreen, only weakly shining, punctures almost disappearing into the underlying shagreen (Fig. 91G). Crete only ..... ***A. incustodita* Wood**
- Terga with strong and distinct punctures, underlying surface polished and brightly shining (e.g. Fig. 91H). Widespread across the southern Balkans, but not on the island of Crete ..... **54**
- 54 Disc of T1 with punctures distinctly separated by an average of 1 puncture diameter. Clypeus relatively elongate, ventrally extending beyond line drawn between lower margins of compound eyes, surface clearly visible and not obscured by dense decumbent hairs ..... ***A. acerba* Warncke**
- Disc of T1 with punctures denser, separated by an average of 0.5 puncture diameters (Fig. 91H). Clypeus relatively short, not extending ventrally beyond line drawn between lower margins of compound eyes, surface obscured by presence of abundant white decumbent hairs ..... **55**
- 55 Metasoma with entirety or majority of discs of T1–3 marked with red (e.g. Fig. 85B). Found in continental parts of the southern Balkans between 40.5°N and 43.5°N (Macedonia *sensu lato*) ..... ***A. biguttata* Friese**
- Metasoma with tergal discs dark (Fig. 91H). Distribution variable. Females do not appear to be separable at the present time .....  
..... ***A. abbreviata* Dours, *A. cantiaca* Warncke, *A. combaella* Warncke**
- 56 (29). Terga with marginal areas of T2–4 very broad, on T2 occupying 3/4 of the visible surface and on T3–4 occupying the entire visible surface (Fig. 92A). Base of T2–4 with long hairs that overlay the marginal areas, most hairs extending the length of the segment. Propodeal corbicula with dorsal fringe composed of long, strongly plumose and almost curly hairs. Tibial scopae composed of a mixture of simple and plumose hairs, thus appearing ambiguously plumose. Moderately sized, 10–11 mm in length .....  
..... ***A. seminuda* Friese**
- Terga without such broad marginal areas overlain by long hairs; if marginal areas on T3–4 appearing very broad, then large bodied (exceeding 15 mm in length) and covered with abundant black and white pubescence ..... **57**
- 57 (56). Hind tibiae on their outer faces with the hairs of the tibial scopae clearly plumose, with a majority of strongly branched hairs across the entire width of the scopae ..... **58**
- Hind tibiae on their outer faces with the hairs of the tibial scopae entirely simple, or with at most a mixture of simple and scattered and weakly branched hairs. Many specimens presenting “non-plumose” hairs and hence following this couplet will show a few plumose hairs here and there, particularly laterally, but these are not sufficient to follow the alternative character state ..... **70**
- 58 Tibial scopae with dorsal and ventral fringes unusual, ventral hairs strongly elongate and strongly plumose (almost twice the medial width of the hind tibia) and dorsal hairs noticeably shorter and less conspicuously plumose



**Figure 92.** *Andrena* (incertae sedis) *seminuda* Friese, 1896 female. **A.** Metasoma, dorsal view. *Andrena* (*Poecilandrena*) *crassana* Warncke, 1965 female. **B.** Metasoma, dorsal view. *Andrena* (*Diodonia*) *mucida* Kriechbaumer, 1873 female. **C.** Process of the labrum, ventral view. *Andrena* (*Truncandrena*) *asiatica* Friese, 1921 female. **E.** Scutum and scutellum, lateral view; **F.** Metasomal terga 3–4, dorsal view. *Andrena* (*Melandrena*) *dubiosa* Kohl, 1905 female. **D.** Scutum and scutellum, lateral view; **G.** Propodeal corbicula (with both dorsal and anterior fringes), anterolateral view; **H.** Metasoma, dorsal view.

- (less than the medial width of the hind tibia). Process of the labrum broadly trapezoidal but with deep and distinct “V” shaped emargination medially. Hind wing lacking a jugal lobe (subgenus *Pallandrena* Warncke).....**59**
- Tibial scopae with dorsal and ventral fringes not noticeably different in length. Process of the labrum variably shaped. Hind wing with jugal lobe present..... **60**
- 59 Scutum densely but very shallowly and obscurely punctate, punctures extremely difficult to see against the strong granular microreticulation of the scutum. Tergal margins conspicuously and broadly lightened orange-yellow hyaline. Tergal discs often red-marked. Slightly larger, 10–11 mm..... *A. braunsiana* Friese
- Scutum densely and finely punctate, punctures separated by <0.5–0.5 puncture diameters, clearly visible against the scutal microsculpture. Tergal margins subtly lightened whitish-hyaline. Tergal discs always dark. Slightly smaller, 8–9 mm..... *A. pallidicincta* Brullé
- 60 Terga with discs extensively red-marked (some dark individual of *A. marginata* Fabricius with red markings restricted to the base of the tergal margins)..... **61**
- Terga dark, at most with depressions lightened, never with red markings at the base of the tergal depressions..... **62**
- 61 Clypeus with fore margin slightly upturned. Foveae short, ventrally reaching only to the level of the antennal insertions. Tibial scopae uniformly yellowish. Visiting many flower species..... *A. pellucens* Pérez
- Clypeus with fore margin straight, not upturned. Foveae long, ventrally extending beyond the level of the antennal insertions. Tibial scopae bicoloured, black-brown dorsally, brownish-white ventrally. Associated with scabious species (Dipsacoideae = Caprifoliaceae)..... *A. marginata* Fabricius
- 62 Small bee around 6 mm in length, with all pubescence white. Metasoma with dense uniform punctation, punctures separated by <0.5–0.5 puncture diameters (Fig. 92B). Propodeal triangle well-defined laterally with strong carinae. Associated with *Legousia* (Campanulaceae)..... *A. crassana* Warncke
- Larger species, typically exceeding 9 mm in length, often with brownish to golden-yellow pubescence. Metasoma with punctation never so uniformly dense, with at least some areas with punctures separated by >1 puncture diameter. Propodeal triangle poorly defined laterally with weak carinae, or without any carinae at all. Associated with other botanical families..... **63**
- 63 Pronotum with a humeral angle. Head and mesepisternum with abundant black pubescence (Fig. 73A). Facial foveae uniformly narrow, occupying at most 1/5 of the space between the compound eye and a lateral ocellus. Associated with *Crocus* (Iridaceae)..... **64**
- Pronotum rounded. Head and mesepisternum with greyish, brownish, or orangish hairs, never with abundant black pubescence. Facial foveae variable, either occupying 1/2 the space between the compound eye and a

- lateral ocellus, or occupying around 1/3 of their space and strongly narrowing ventrally. Associated with other botanical families ..... **66**
- 64 Mouthparts with 6 maxillary and 4 labial palpi. Scutum and scutellum typically with abundant greyish pubescence. Active in the spring (March–May) ..... ***A. elsei* Scheuchl & Gusenleitner (*partim*)**
- Mouthparts with 7 or more maxillary palpi and 6 or more labial palpi (e.g. Fig. 73C). Scutum typically with abundant black pubescence, with only a few greyish hairs. Active in the autumn (October–early December) ..... **65**
- 65 Mouthparts with 9 maxillary and 9 labial palpi. Found in southern continental Greece, the Cyclades, and East Aegean Islands (Chios) (J. Devalez, pers. comm.) ..... ***A. grossella* Grünwaldt**
- Mouthparts with 7 maxillary and 6 labial palpi (Fig. 73C). Restricted to the island of Crete ..... ***A. lasithi* sp. nov.**
- 66 Process of the labrum large, as long as broad, surface covered with latitudinal wrinkles (Fig. 92C). Fovea moderately broad, dorsally occupying 1/2 the space between the compound eye and a lateral ocellus, not narrowed ventrally. Flying in the summer (June–August), associated with scabious species (Dipsacoideae = Caprifoliaceae) ..... ***A. mucida* Kriechbaumer (*partim*, 2<sup>nd</sup> generation)**
- Process of labrum rounded trapezoidal, typically broader than long, ventral surface not covered with latitudinal wrinkles. Fovea relatively narrow, dorsally occupying 1/3 of the space between the compound eye and the lateral ocellus, clearly narrowing ventrally to 1/2 its dorsal width. On average flying a little earlier in the year (March–July), associated with Cichorioideae (Asteraceae) (subgenus *Chrysandrena* Hedicke) ..... **67**
- 67 Clypeus, scutellum, and scutum predominantly polished and shining. On average, flying later in the spring into summer (late May–July), mostly avoiding strongly Mediterranean habitats ..... ***A. fulvago* (Christ)**
- Clypeus, scutellum, and majority to entirety of scutum strongly shagreened and matt, at most with a few small areas polished and shining. On average, flying earlier in the spring (March–June) ..... **68**

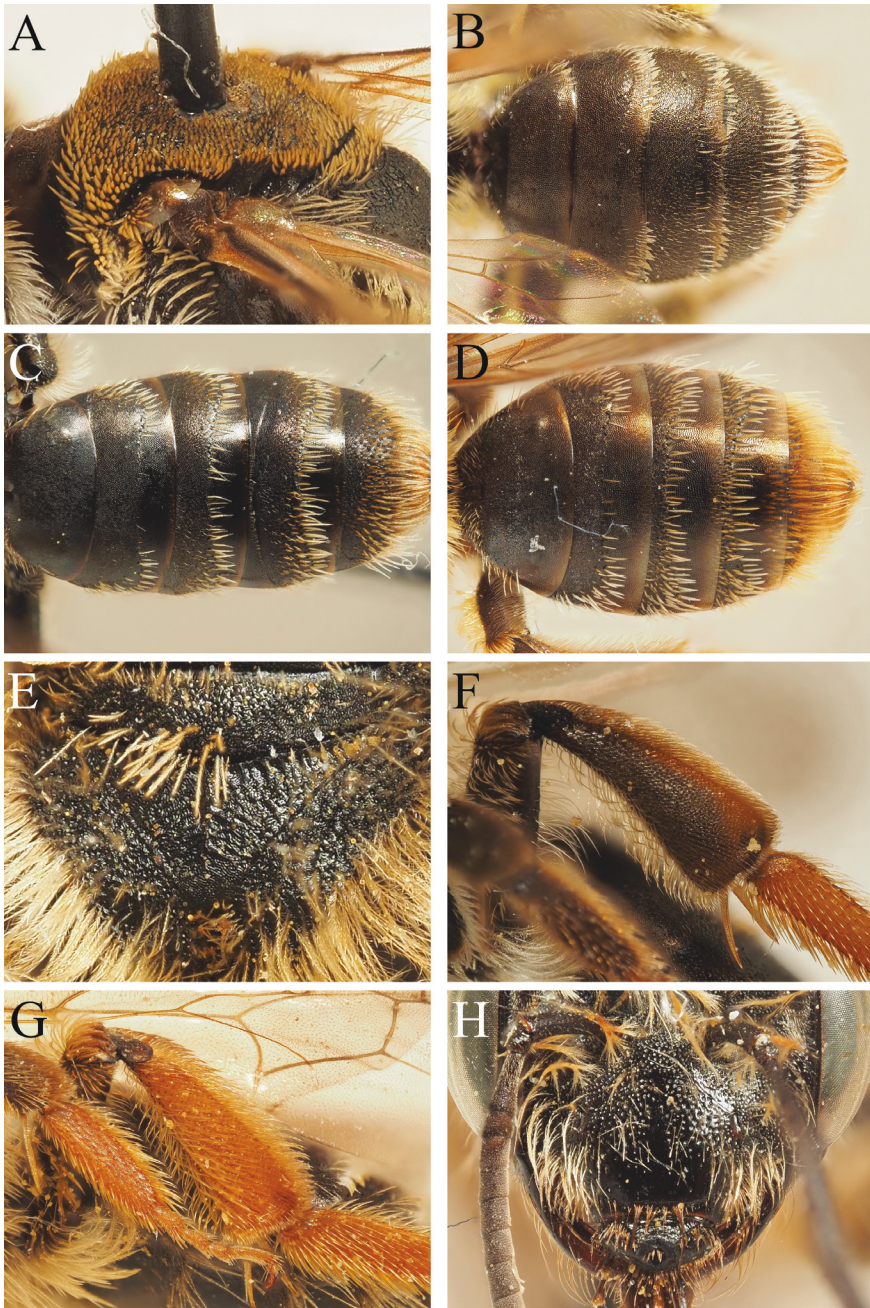
This group of species requires revision in the East Mediterranean (G. Pisanty, pers. comm.), and hence this part of the key should be considered only provisional.

- 68 Hind tibiae dark, tibial scopae composed of light yellow-brown hairs ..... ***A. merula* Warncke**
- Hind tibiae orange, tibial scopae composed of bright orange-yellow hairs .... **69**
- 69 Scutum posteromedially with a small but distinct area with reduced sculpture, this polished and shining. Found only on the island of Rhodes ..... ***A. glandaria* Warncke**
- Scutum entirely and uniformly densely microreticulate and dull. Widespread across the southern Balkans, including the East Aegean Islands ..... ***A. hesperia* Smith**

- 70(57) Propodeal triangle clearly defined by strongly raised carinae, internal surface rugose-areolate (c.f. Fig. 90B). Mesepisternum and dorsolateral parts of the propodeum with dense network of raised rugosity, never with abundant visible punctures, punctures separated by 0.5–1 puncture diameters .  
..... 71
- Propodeal triangle not strongly defined by lateral carinae with its internal surface rugose-areolate. Mesepisternum and dorsolateral parts of the propodeum with or without dense network of raised rugosity, sometimes with abundant visible punctures, punctures separated by 0.5–1 puncture diameters ..... 72
- 71 Foveae clearly medially constricted. Terga without hair bands, T2 laterally without a pair of small foveae. Hind tibiae usually orange (subgenus *Trachandrena* Robertson) ..... **A. haemorrhoea (Fabricius)**
- Foveae lacking medial constriction. Terga in fresh specimens with apical white hair bands, T2 laterally with a pair of small foveae. Hind tibiae always dark (subgenus *Brachyandrena* Pittioni) ..... **A. colletiformis Morawitz**
- 72(70) Scutum and scutellum covered with short squamous hairs, not exceeding the diameter of a lateral ocellus in length (Figs 3C, 19B, E, 92D, E, 93A)  
..... 73
- Scutum and scutellum without such squamous hairs, what hairs are present clearly exceeding the diameter of a lateral ocellus in length ..... 83
- 73 Large dark species, 16–18 mm in length with pubescence of the head and mesosoma predominantly dark brown to black, including the squamous scutal hairs which are entirely and uniformly deep black (Fig. 92E) .....  
..... 74
- Typically not exceeding 15 mm in length, never with such dark pubescence, squamous scutal hairs never black..... 75
- 74 Marginal areas of the terga broad, occupying 1/2 the visible surface of the disc on T2, increasing to almost the entire visible surface of the disc on T4 (Fig. 92F). Pronotum with a weak but distinct humeral angle. Terga finely and densely punctate, punctures on the disc of T2 separated by 0.5 puncture diameters. Confidently known only from Eastern Macedonia and Thrace in north-eastern Greece ..... **A. dubiosa Kohl**
- Marginal areas of the terga normal, not so broad, occupying at most 1/3 of the visible surface of each disc. Pronotum rounded. Terga slightly more coarsely and sparsely punctate, punctures on the disc of T2 separated by 0.5–1 puncture diameters. Widespread across the southern Balkans .....  
..... **A. atrotegularis Hedicke**
- 75 Viewed laterally, propodeal corbiculae complete (possessing both a dorsal and anterior fringe, Fig. 92G) AND internal surface hairless or nearly hairless ..... 76
- Propodeal corbiculae incomplete (possessing only a dorsal fringe) and internal surface with hairs ..... 77

- 76 Lateral faces of the propodeum (internal surface of the propodeal corbicula) hairless. Facial foveae occupying essentially the entire space between the compound eye and a lateral ocellus. T2–4 in fresh specimens with complete apical hairbands. Tergal discs very finely and densely punctate, punctures almost confluent, surface dull. Metasoma often red marked basally. Widespread in the southern Balkans..... ***A. transitoria* Morawitz**
- Lateral faces of the propodeum with at least some hairs laterally. Facial foveae occupying around 3/4 of the space between the compound eye and a lateral ocellus, separated from a lateral ocellus by a distance equal to its diameter. Terga with interrupted apical hairbands (Fig. 92H). Tergal discs with fine granular microreticulation, more-or-less impunctate. Metasoma never red marked. Restricted to eastern Bulgaria and the East Aegean Islands..... ***A. asiatica* Friese**
- 77 Mesepisternum clearly and densely punctate, punctures separated by 0.5–1 puncture diameters (c.f. Fig. 101D) ..... **78**
- Mesepisternum microreticulate and dull, obscurely punctate or entirely impunctate ..... **79**
- 78 Tergal margins distinctly and deeply depressed and filled with short subsquamous hairs, these forming complete transverse bands (Fig. 3D). Squamous hairs of the scutum and scutellum yellow-brown. Tibial scopae composed of yellow-orange hairs ..... ***A. erberi* Morawitz**
- Tergal margins not noticeably depressed, laterally with dense white hair patches which do not form complete transverse bands. Squamous hairs of the scutum and scutellum bicoloured, anteriorly and posteriorly white, medially with a broad black band. Tibial scopae composed of white hairs. .... ***A. lateralis* Morawitz**
- 79 Large bees, exceeding 12 mm in length. Tergal discs and margins densely and uniformly punctate, punctures separated by <0.5–0.5 puncture diameters (subgenus *Limbandrena* Wood)..... **80**
- Smaller bees, <10 mm in length. Tergal discs at least on T1–2 impunctate, discs of T3–4 in some species with punctures separated by at least 1 puncture diameter (Fig. 93B–D, subgenus *Aenandrena* Warncke)..... **81**
- 80 Ocellocipital distance long, around 3 times the diameter of a lateral ocellus. Clypeus usually dark, occasionally partially yellow-marked. Terga almost entirely dark. Widespread across the southern Balkans.... ***A. limbata* Eversmann**
- Ocellocipital distance shorter, around 1–1.5 times the diameter of a lateral ocellus (Fig. 19D). Clypeus almost entirely yellow-marked (Fig. 19C). Terga extensively red-marked (Fig. 19F). Restricted to the East Aegean Islands..... ***A. toelgiana* Friese**
- 81 Clypeus crossed by numerous transverse ridges separated by a puncture diameter. Metasoma with dull metallic green-bronze colouration (Fig. 93B). Body size around 7 mm ..... ***A. aeneiventris* Morawitz**
- Clypeus without any transverse ridges, punctures and puncture interspaces clearly visible. Metasoma dark, sometimes marked with red (not

- yet observed in the southern Balkans) but never metallic green-bronze (Fig. 93C, D). Body size 8–9 mm..... **82**
- 82 Tergal margins comparatively narrow, on T2–4 occupying 1/3–1/2 the visible surface (Fig. 93C). Basitarsi dark. Widespread across the southern Balkans..... ***A. bisulcata* Morawitz**
- Tergal margins comparatively broad, on T2–4 occupying 1/2–3/5 of the visible surface, on T4 occupying 4/5 of the visible surface (Fig. 93D). Basitarsi lightened orange. Currently known from only a single record from south-western Bulgaria..... ***A. hystrix* Schmiedeknecht**
- 83(72) Viewed laterally, propodeal corbicula with internal surface (lateral faces of the propodeum) hairless AND propodeal corbiculae complete (possessing both a dorsal and anterior fringe, c.f. Fig. 92G) (subgenus *Simandrena* Pérez)..... **84**
- Propodeal corbiculae either incomplete (possessing only a dorsal fringe) AND/OR internal surface with hairs ..... **92**
- 84 Propodeal triangle distinctive, triangular and clearly delineated laterally with carinae and with the internal surface showing a raised longitudinal ridge medially (Fig. 93E) ..... ***A. susterai* Alfken**
- Propodeal triangle without this unique shape, internal surface usually evenly sculptured ..... **85**
- 85 Tibial scopae with short hairs, dorsally these hairs only moderately exceeding the width of a lateral ocellus (Fig. 93F). Metasoma with punctures on tergal discs dense medially, becoming sparse laterally ..... **86**
- Tibial scopae with long hairs, clearly greatly exceeding the width of a lateral ocellus (e.g. Fig. 93G). Metasoma with consistently dense punctures, not becoming sparser laterally ..... **87**
- 86 Scutum medially strongly shagreened and dull. In fresh specimens, tergal hair bands short, not noticeably surpassing the apex of the tergal margins. Hind tibiae and basitarsi usually orange, but can be entirely dark ..... ***A. dorsata* (Kirby)**
- Scutum medially polished and shiny or extensively but weakly shagreened with a silky shine. In fresh specimens, tergal hair bands long, clearly surpassing the apex of the tergal margins. Hind tibiae and basitarsi usually dark, occasionally lightened orange-brown..... ***A. propinqua* Schenck**
- 87 Mid basitarsi and hind tibiae and basitarsi lightened clear orange (Fig. 93G). Clypeus with weak but distinct pattern of longitudinal sculpturing and wrinkles, leading to “rivulets” that converge on the anterior margin of the clypeus (found also in *A. lepida*). Scutum with sparse and irregular punctures separated by 1–4 puncture diameters, interspaces with weak almost greasy shine..... ***A. nucleola* Warncke**
- Combination of characters different; legs dark, clypeus (with exception of *A. lepida*) without longitudinal striations or wrinkles, scutum with punctation different..... **88**



**Figure 93.** *Andrena* (*Aenandrena*) *aeneiventris* Morawitz, 1872 female. **A.** Scutum and scutellum, lateral view; **B.** Metasoma, dorsal view. *Andrena* (*Aenandrena*) *bisulcata* Morawitz, 1877 female. **C.** Metasoma, dorsal view. *Andrena* (*Aenandrena*) *hystrix* Schmiedeknecht, 1883 female. **D.** Metasoma, dorsal view. *Andrena* (*Simandrena*) *susterai* Alfken, 1914 female. **E.** Propodeum, dorsal view. *Andrena* (*Simandrena*) *dorsta* (Kirby, 1802) female. **F.** Hind tibia, lateral view. *Andrena* (*Simandrena*) *nucleola* Warncke, 1973 female. **G.** Hind tibia, lateral view. *Andrena* (*Troandrena*) *praecocella* Cockerell, 1917 female. **H.** Clypeus, frontal view.

- 88 Disc of T1 strongly and densely punctate, punctures separated by <1 puncture diameter. Widespread across the southern Balkans at low to moderate altitudes ..... **89**
- Disc of T1 finely and sparsely punctate, punctures separated by >1 puncture diameter. Mostly restricted to mountainous areas in the southern Balkans ..... **90**

The following three species are best diagnosed together across multiple characters. Additional information and images can be found in Wood (2021).

- 89 Clypeus with deep irregular punctures, these separated by 0–1 puncture diameters, punctures forming a pattern of lateral furrows, clearly recessed, remaining surface very finely wrinkled, weakly shining. Scutum polished and shining over entire surface. Scutum densely and uniformly punctate, punctures separated by 0–0.5 puncture diameters. Currently known only from the Struma valley in south-western Bulgaria ..... ***A. kocoureki* Wood**
- Clypeus wrinkled by regular pattern of slightly raised lateral ridges, moderately punctate, punctures separated by 0.5–1 puncture diameters, remaining surface very finely wrinkled, weakly shining. Scutum microreticulate, weakly shining. Scutum densely and uniformly punctate, punctures separated by 0.5–1 puncture diameters. Widespread across the southern Balkans ..... ***A. combinata* (Christ)**
- Clypeus without lateral ridges, very finely wrinkled, wrinkles instead running more longitudinally, more densely punctured, punctures separated by 0–0.5 puncture diameters, remaining surface shagreened, dull to weakly shining apically. Scutum polished over majority of surface, shiny, laterally microreticulate, weakly shining. Scutum laterally regularly punctate, punctures separated by 1 puncture diameter, becoming weaker centrally, separated by 2–3 puncture diameters. Widespread across the southern Balkans ..... ***A. lepida* Schenck**
- 90 Head and mesosoma white-haired. Clypeus smooth and shiny between punctures ..... ***A. thomsonii* Ducke**
- Head and mesosoma with rich chestnut-brown hair. Clypeus shagreened and dull between punctures ..... **91**

The following two species are challenging to separate, and remain incompletely resolved across their European ranges. Additional detail can be seen in Schmid-Egger and Scheuchl (1997).

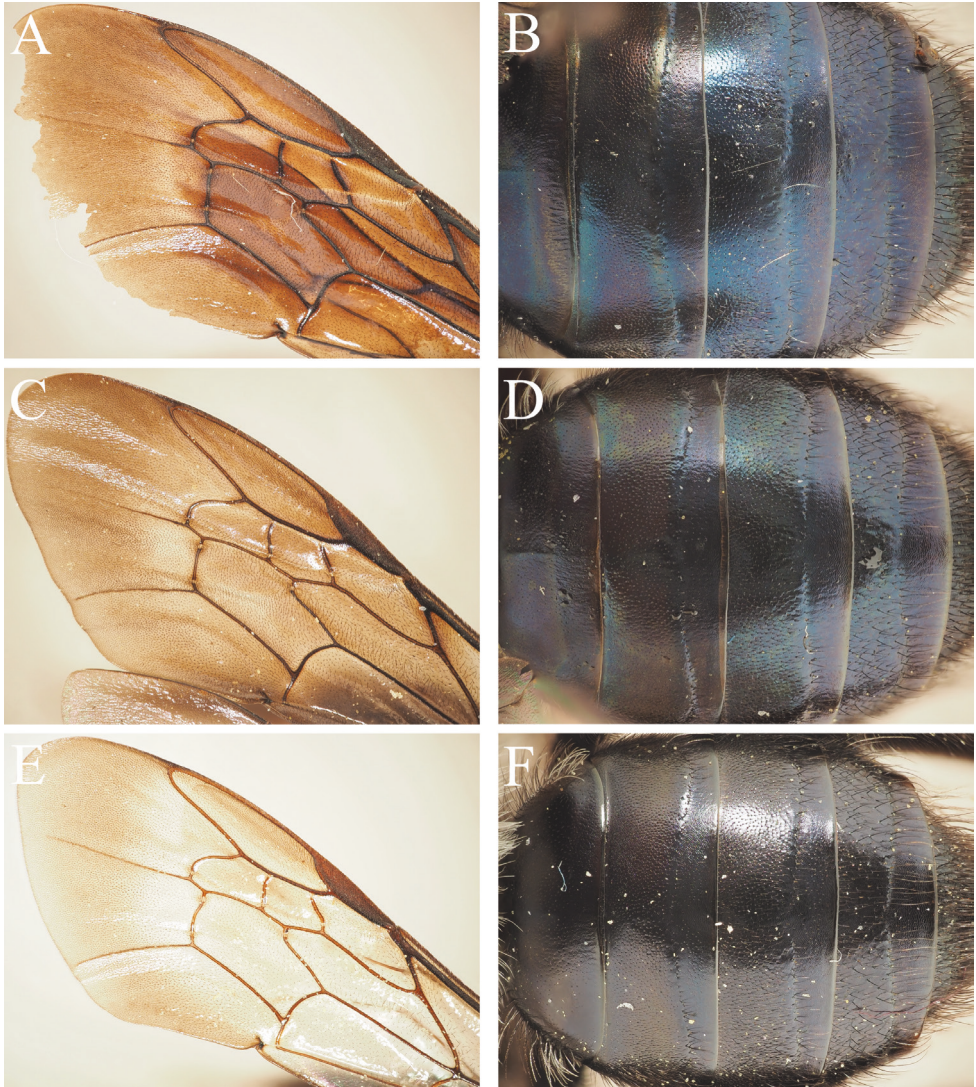
- 91 T2–4 with discs finely, densely, and strongly punctate. Terminal fringe dark brown ..... ***A. congruens* Schmiedeknecht**
- T2–4 with discs sparsely and obscurely punctate. Terminal fringe reddish-brown ..... ***A. confinis* Stöckhert**

- 92(83) Fovea strongly constricted medially, dorsally strongly diverging from the inner margin of the compound eye. Tibial scopae unicolourous black. Mesosoma entirely covered with light grey hairs (*bicolorata*-group) ..... *A. bicolorata* (Rossi)
- Fovea not constricted medially, not strongly diverging from the inner margin of the compound eye ..... 93
- 93(92) At least some tergal discs extensively red-marked ..... 94
- Never with tergal discs extensively red-marked..... 102
- 94 Small bees, never exceeding 9 mm in length AND fovea narrow, at most occupying 1/3 of space between the compound eye and the lateral ocellus ..... 95
- Larger bees, greater than 11 mm in length AND/OR fovea broader, occupying at least 1/2 the space between the compound eye and the lateral ocellus..... 97
- 95 Tibial scopa bicoloured, dorsally composed of brown hairs, ventrally composed of whitish hairs. Scutum with punctures separated by 0.5–1 puncture diameters, interspaces very weakly shagreened and more-or-less shining. Apical margin of T4 with weak apical whitish hairbands, terminal fringe whitish-brown ..... *A. labiata* Fabricius
- Tibial scopa entirely composed of black hairs. Scutum slightly more densely punctate, punctures separated by <0.5–1 puncture diameters, interspaces microreticulate and dull. Apical margin of T4 without a hairband, terminal fringe dark brown ..... 96
- 96 Head and mesosoma with the pubescence entirely black. Clypeus microreticulate and dull in its basal 1/2, becoming partially shiny only in its apical 1/2. Widespread across the southern Balkans (Fig. 49) but typically only on a few islands such as Limnos and Cephalonia (J. Devalez, pers. comm.) ...  
..... *A. sphecodimorpha* Hedicke
- Head and mesosoma with a mixture of white and brown pubescence, face and mesepisternum with particularly bright hairs. Clypeus more extensively shining over most of its surface, including the basal 1/2. Currently known only from the island of Lesbos (Fig. 49) .....  
..... *A. hybrida* ssp. *tauriensis* Warncke
- 97 Propodeal triangle clearly delineated laterally by fine carinae, internal surface with fine network of raised rugae. Clypeus densely and uniformly punctate, without a longitudinal impunctate midline. Lower paraocular areas sometimes with small yellow spots on the integument .....  
..... *A. schencki* Morawitz
- Propodeal triangle poorly defined, lacking lateral carinae, internal surface more-or-less smooth, without network of rugae. Clypeus densely or sparsely punctate, but either with a clear longitudinal impunctate midline or with a raised impunctate longitudinal ridge ..... 98

- 98 Clypeus medially flattened and polished, densely punctate in its basal 3/4 with punctures separated by <0.5–1 puncture diameters with exception of median longitudinal impunctate midline (Fig. 93H). Process of the labrum narrowly trapezoidal, apical margin truncate, thickened, and partially upturned; medially with clear “U” shaped emargination. Terga strongly but irregularly punctate, punctures separated by 0.5–2.0 puncture diameters. Restricted to the East Aegean Islands (Samos, Rhodes).....***A. praecocella* Cockerell**
- Clypeus not flattened medially, sculpture and puncture density variable. Process of the labrum otherwise. Terga variably punctate. Distribution widespread..... **99**
- 99 Terga strongly and densely punctate, punctures separated by 1 puncture diameter. Compound eyes with inner margins diverging ventrally. Excluding impunctate midline, clypeus comparatively sparsely punctate, punctures separated by 1–2 puncture diameters. Associated with *Bryonia* (Cucurbitaceae) .....***A. florea* Fabricius**
- Terga shallowly and obscurely punctate, punctures separated by 2–3 puncture diameters. Compound eyes with internal margins more-or-less parallel. Excluding impunctate midline or longitudinal ridge, clypeus comparatively densely punctate, punctures separated by 0.5–1 puncture diameters. Not frequently associated with *Bryonia* ..... **100**
- 100 Hind tibiae orange. Tibial scopae unicolourous orange. Clypeus medially with a clear raised longitudinal impunctate area, this area smooth and shining, strongly contrasting the remaining parts of the clypeus which are densely punctate (Fig. 101C). Univoltine, spring only .....  
.....***A. ferox* Smith (*partim*, light form)**
- Hind tibiae dark. Tibial scopae bicoloured, dorsally dark, ventrally whitish-golden. Clypeus with a longitudinal but flat impunctate midline. Bivoltine, spring and summer ..... **101**

Beware of abraded specimens when dealing with these two species.

- 101 T1–2 with long hair, equalling the length of the hair on the mesosoma. Widespread throughout the southern Balkans.....  
.....***A. trimmerana* (Kirby) (*partim*, light form)**
- T1–2 with shorter hair, never equalling the length of the mesosomal hair. With a very marginal occurrence in the southern Balkans, currently known only from the Black Sea coast of Bulgaria.....  
.....***A. rosae* Panzer (*partim*, light form)**
- 102(93) Head, mesosoma, or tergal discs with metallic reflections (Figs 94B, D, F, 95A, B, E, G; note, *A. nigroaenea* (Kirby) can have bronzy reflections on the terga; if the tibial scopae is composed of orange-red hairs or the tibial scopae is mainly dark with only the ventral hairs orange, go to 241) ..... **103**
- Body without metallic reflections..... **111**



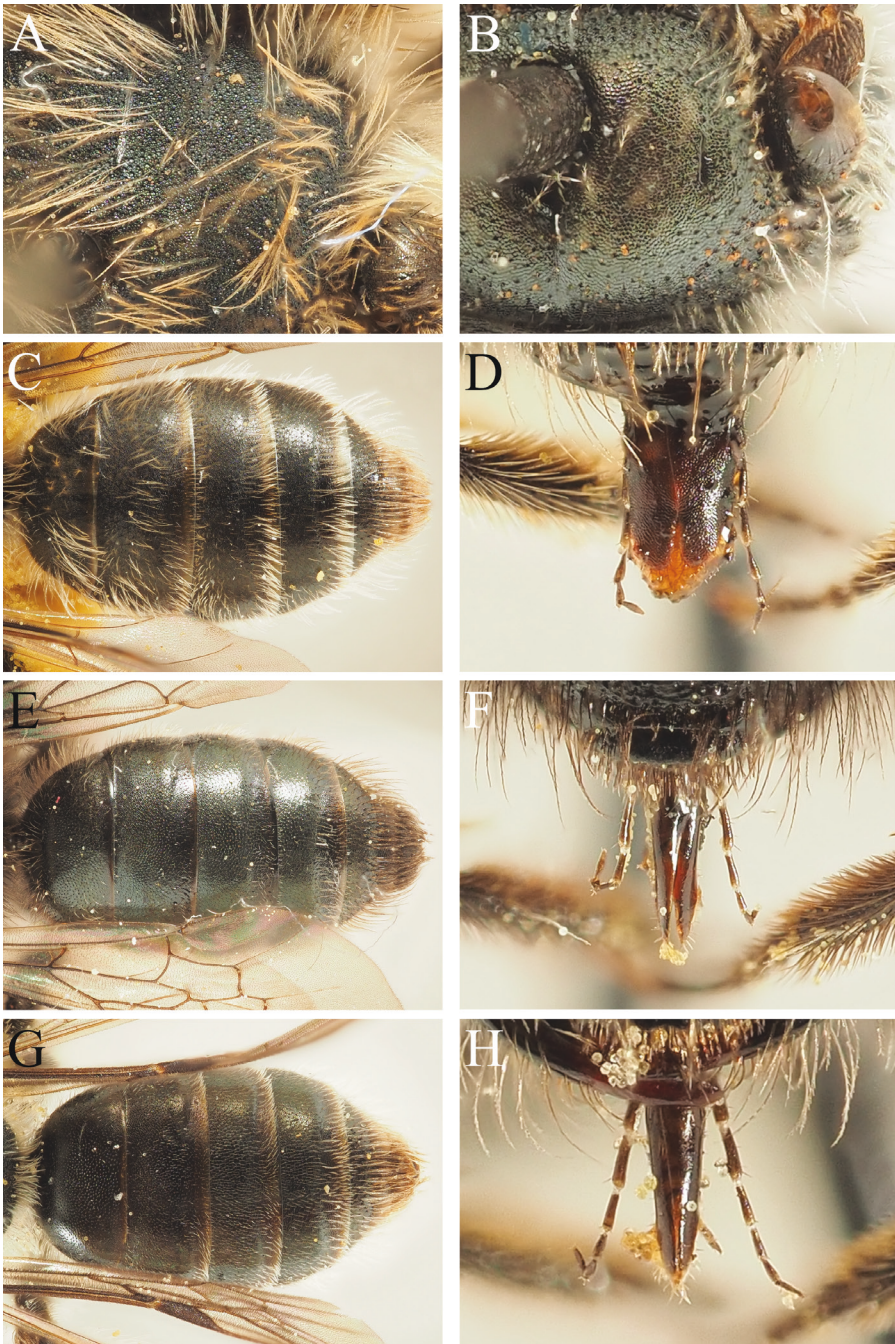
**Figure 94.** *Andrena (Melandrena) barbareae* Panzer, 1805 female. **A.** Forewing, dorsal view; **B.** Metasoma, dorsal view. *Andrena (Melandrena) danuvia* Stöckert, 1950 female. **C.** Forewing, dorsal view; **D.** Metasoma, dorsal view. *Andrena (Melandrena) cineraria* (Linnaeus, 1758) female. **E.** Forewing, dorsal view; **F.** Metasoma, dorsal view.

- 103 Mesosoma with strongly contrasting pattern of black and white hairs; mesosoma anteriorly and posteriorly with white hairs, medially with a band of black hairs (*cineraria*-group) ..... 104
- Mesosoma without strongly contrasting pattern of black and white hairs.. ..... 106

The members of the *cineraria*-group are challenging to separate consistently, and the morphological and molecular species boundaries are not full established.

- 104 Wings predominantly infusate, infuscation covering from the apex of the wing to the marginal vein (Figs 85F, 94A). Metasoma a rich deep blue with purple hints (Fig. 94B). Sterna with black hairs. Bivoltine, flying in the spring and the summer, found in mountainous areas ..... ***A. barbareae* Panzer**
- Wings hyaline or only weakly infusate (Fig. 94C, E). Metasoma variably coloured, from rich blue to dark indigo-blue (Fig. 94D, F). Sterna with black or white hairs. Univoltine, flying in the spring (April–May), typically found at lower altitudes ..... **105**
- 105 Metasoma deep blue with purple hints (Fig. 94D). Wing obscurely infusate (Fig. 94C). Common and widespread, found in warm Mediterranean habitats ..... ***A. danuvia* Stöckert**
- Metasoma dark indigo-blue, with metallic highlights minimal (Fig. 94F). Wing completely hyaline (Fig. 94E). Rare in the southern Balkans, probably found only in the north in areas with cooler temperate habitats ..... ***A. cineraria* (Linnaeus)**
- 106 Pronotum with a weakly carinate humeral angle. Terga finely microreticulate and obscurely punctate, superficially impunctate. Integument with metallic reflections restricted to the scutum. Around 8 mm in length. Associated with Brassicaceae ..... ***A. schlettereri* Friese**
- Pronotum rounded. Tergal variably punctate, from almost impunctate to showing abundant fine and dense punctures. Integument with metallic reflections not restricted to the scutum. Size variable. Associated with a different botanical family ..... **107**
- 107 Larger bee, 10–11 mm in length. Scutum with very dense shallow punctures, punctures essentially confluent (Fig. 95A). Propodeum covered with long abundant pubescence, no meaningful difference between hairs of the dorsal fringe of the propodeal corbicula and those on the dorsal surface of the propodeum. Associated with *Papaver* (Fig. 84E; Papaveraceae) ..... ***A. mucronata* Morawitz**
- Smaller bees, 6–8 mm in length. Scutum with slightly sparser punctures, interspaces always visible, separated by at least 0.5 puncture diameters, often by >1 puncture diameter (Fig. 95B). Propodeum with comparatively few hairs, these differentiated with propodeal corbicula distinctly differentiated. Associated with *Cerastium* (Caryophyllaceae) and *Veronica* (Plantaginaceae) ..... **108**
- 108 Mouthparts relatively short, 2 times longer than broad, surface of galea covered with granular microreticulation, dull (Fig. 95D). Terga with very fine and scattered hair-bearing punctures, punctures separated by 2–3 puncture diameters, terga broadly appearing impunctate (Fig. 95C). Associated with

- Cerastium* and restricted to continental Greece (Fig. 79) .....  
 ..... ***A. olympica* Grünwaldt**
- Mouthparts relatively long, 3–4 times longer than broad, surface of galea finely shagreened, shining (Fig. 95F, H). Terga finely and densely punctate, punctures distinct, separated by 0.5–1 puncture diameters (Fig. 95E, G). Associated with *Veronica* (Fig. 84F), distribution variable..... **109**
- 109 Pubescence of the body and the tibial scopae entirely black. Terga with apical margins dark, not lightened hyaline (Fig. 95F). Terminal fringe dark brown to black. Slightly larger, 8 mm in length ..... ***A. standfussorum* Scheuchl**
- Pubescence of the body and tibial scopae light, never black. Terga with apical margins moderately but distinctly lightened hyaline (Fig. 95G). Terminal fringe light brown. Slightly smaller, 6–7 mm in length..... **110**
- 110 Scutum covered with consistent granular microreticulation, uniformly dull (Fig. 95B). Disc of T1 densely and uniformly punctate, punctures separated by 0.5–1 puncture diameters, density not noticeably different to the puncture density on the disc of T2 (Fig. 95G). Restricted to continental Greece (Fig. 78) ..... ***A. neovirida* Grünwaldt**
- Scutum irregularly sculptured, with microreticulation of variable density, partially shining medially. Disc of T2 comparatively slightly more sparsely punctate, punctures separated by 1–1.5 puncture diameters, visibly less densely punctate than the puncture diameters on the disc of T2. Widespread across the southern Balkans but more frequently encountered in the north ..... ***A. viridescens* Viereck**
- 111(102) Surface of galea covered with abundant bristles which project away in a perpendicular fashion (Fig. 96A). Large dark bees around 13–14 mm in length, majority of pubescence (including tibial scopae) composed of black hairs. Associated with *Anchusa* (Boraginaceae) ..... ***A. nasuta* Giraud**
- Surface of galea without such bristles. Pubescence and body size variable ..  
 ..... **112**
- 112(111) Disc of T1 laterobasally (i.e. the “shoulders” of the disc) with a pair of distinct flattened carinae (Fig. 96B). Facial foveae narrow, dorsally occupying around 1/5–1/4 of the space between the compound eye and lateral ocellus. Small bees around 7 mm in length (subgenus *Parandrenella* Popov) ..... **113**
- Disc of T1 without such flattened carinae. If with weak angulations (*Andrena strobmella* Stöckhert), then with facial foveae clearly much broader dorsally. Size variable..... **114**
- 113 Tergal margins not noticeably broadened or depressed, occupying <1/2 the visible surface (Fig. 96C). Hind tibiae dark. Clypeus uniformly shagreened and dull ..... ***A. atrata* Friese**
- Tergal margins of T2–4 broad, occupying >1/2 the visible surface, very strongly depressed, forming a distinct hump with the discs of T2–4, bases of T2–3 distinctly depressed and trench-like (Fig. 96D). Hind tibiae orange. Clypeus dull basally, polished and shining in apical 1/3 ..... ***A. figurata* Morawitz**



**Figure 95.** *Andrena* (*Truncandrena*) *mucronata* Morawitz, 1871 female. **A.** Scutum, dorsal view. *Andrena* (*Poecilandrena*) *neovirida* Grünwaldt, 2005 female. **B.** Scutum, dorsal view. *Andrena* (*incertae sedis*) *olympica* Grünwaldt, 2005 female. **C.** Metasoma, dorsal view; **D.** Mouthparts, frontal view. *Andrena* (*Poecilandrena*) *standfussorum* Scheuchl, 2010 female. **E.** Metasoma, dorsal view; **F.** Mouthparts, frontal view. *Andrena* (*Poecilandrena*) *viridescens* Viereck, 1916 female. **G.** Metasoma, dorsal view; **H.** Mouthparts, frontal view.



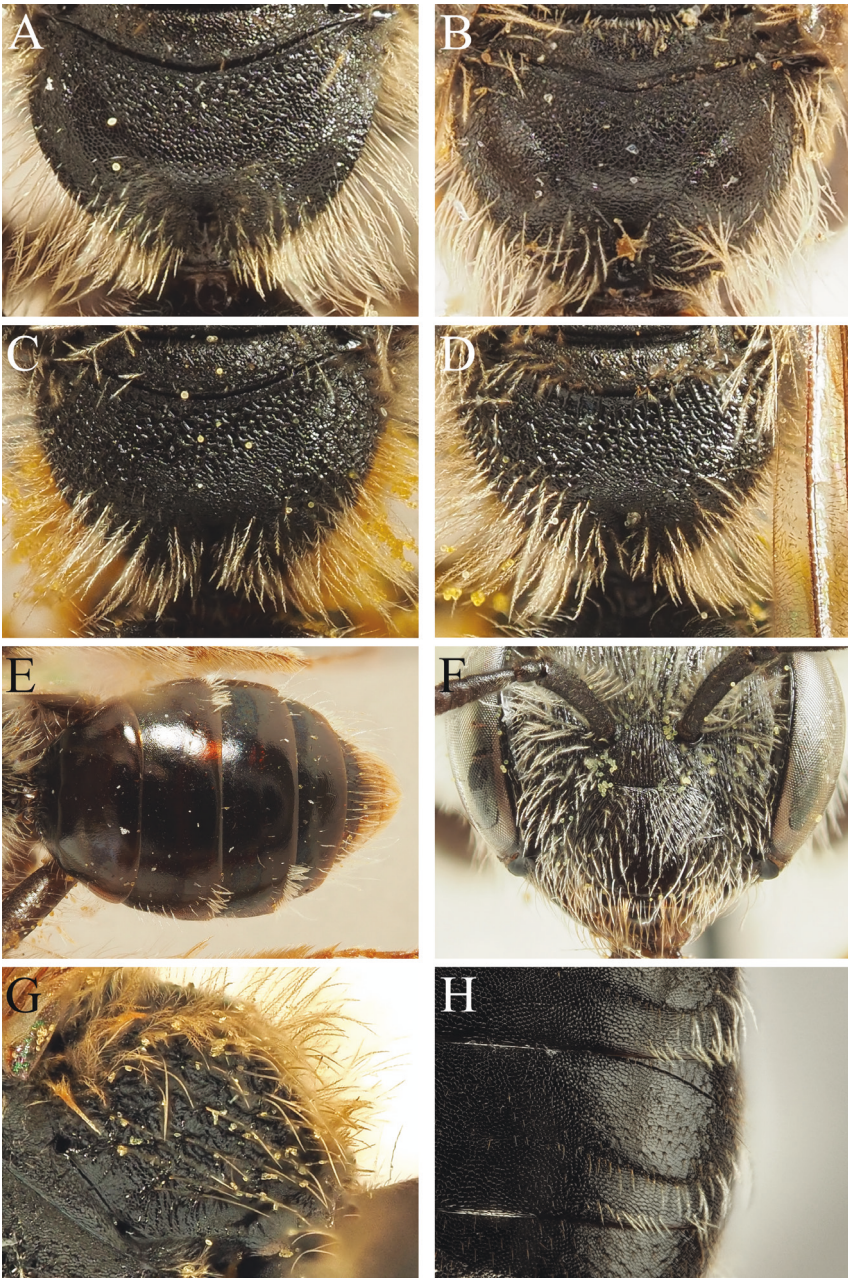
**Figure 96.** *Andrena* (*Hamandrena*) *nasuta* Giraud, 1863 female. **A.** Mouthparts, lateral view. *Andrena* (*Parandrenella*) *atrata* Friese, 1887 female. **B.** Tergum 1, dorsal view; **C.** Metasoma, dorsal view. *Andrena* (*Parandrenella*) *figurata* Morawitz, 1866 female. **D.** Metasoma, dorsal view.

- 114(112) Small black species without a keel laterally on the pronotum, body length under 8 mm, or if up to 10 mm then with lateral faces of the propodeum with clear pattern of raised star-shaped wrinkles (Fig. 97G; all members of the subgenera *Aciandrena* Warncke, *Graecandrena* Warncke, *Micrandrena* Ashmead, plus two additional small subgenera and one *incertae sedis* species) ..... **115**
- Species larger than 9 mm in length or with pronounced keel on the pronotum laterally..... **162**

Small black *Andrena* are challenging to identify due to the large number of species in the southern Balkans, and the subtle sculptural characters. Consultation of confidently determined reference material is advised.

- 115 Head short and broad, 1.4 times wider than long. Clypeus medially with a pronounced median bulge. Facial foveae broad, occupying 3/4 of the space between the compound eye and a lateral ocellus. A3 < A4+5. Propodeal corbicula perfect, with an anterior and dorsal fringe. Trochanteral flocculus

- composed of long strongly plumose hairs. Very rare, currently known only from the East Aegean Islands (Samos).....
- .....***A. ebmerella* Scheuchl**
- Without this combination of characters..... **116**
- 116 Propodeal triangle shagreened, not defined laterally by raised carinae, with internal surface lacking network of raised rugosity, at most with very short rugae at the base of the propodeal triangle (Fig. 97A, B). Never with tergal discs entirely polished and shining..... **117**
- Propodeal triangle either strongly defined by raised carinae, or with internal surface with network of raised rugosity covering at least the basal 1/2 and in most cases clearly covering the majority of the surface (Figs 97C, D, 98G, 99E, F). Tergal discs sometimes entirely polished and shining... .. **129**
- 117 Supraclypeal areas with longitudinal striations, these striations present also on the paraocular areas and extending to the lateral margins of the clypeus AND clypeus weakly but distinctly flattened, medially with a longitudinal impression.....***A. impunctata* Pérez**
- Supraclypeal area and paraocular areas without longitudinal striations OR clypeus without a longitudinal impression. If in doubt (e.g. *A. tomora*), then clypeus clearly domed..... **118**
- 118 Propodeal triangle short, basal 1/2 with distinct carinae or fine rugae radiating from the junction with the metanotum (Fig. 97A; *Graecandrena sensu stricto*)..... **119**
- Propodeal triangle with sculpture uniform, typically with fine granular microreticulation, at most with very short and obscure rugae basally at the junction with the metanotum, never occupying 1/2 the length of the propodeal triangle (Fig. 97B)..... **123**
- 119 Ocelloccipital distance 1.5 times the diameter of a lateral ocellus. Found in continental parts of northern Greece, North Macedonia, and Bulgaria.....
- .....***A. graecella* Warncke**
- Ocelloccipital distance clearly less than the diameter of a lateral ocellus, typically around 0.5 times this diameter..... **120**
- 120 Clypeus finely shagreened and weakly shining over its entire surface (Fig. 70C). Propodeal triangle with basal rugae reduced, present only immediately adjacent to the junction between the propodeum and metanotum. Scutum very weakly sculptured, almost polished and shining (Fig. 70E). Found only on the island of Crete (Fig. 23).....
- .....***A. cretica* sp. nov.**
- Clypeus entirely or predominantly microreticulate and dull, at most shining along its anterior margin (Fig. 70D). Propodeal triangle with basal rugae not reduced, the longest occupying 1/2 the length of the propodeal triangle. Scutum shagreened and at most weakly shining (Fig. 70F). Found elsewhere in the southern Balkans..... **121**



**Figure 97.** *Andrena* (*Graecandrena*) *hyemala* Warncke, 1973 female. **A.** Propodeum, dorsal view. *Andrena* (*Aciandrena*) *sandanskia* Warncke, 1973 female. **B.** Propodeum, dorsal view. *Andrena* (*Micrandrena*) *minutula* (Kirby, 1802) female. **C.** Propodeum, dorsal view. *Andrena* (*Micrandrena*) *rugothorace* Warncke, 1965 female. **D.** Propodeum, dorsal view. *Andrena* (*Micrandrena*) *querquedula* Warncke, 1975 female. **E.** Metasoma, dorsal view. *Andrena* (*Micrandrena*) *distinguenda* Schenck, 1874 female. **F.** Clypeus and supraclypeal area, frontal view. *Andrena* (*Micrandrena*) *proxima* (Kirby, 1802) female. **G.** Propodeum, lateral view. *Andrena* (*Micrandrena*) *minutuloides* Perkins, 1914 female. **H.** Tergum 3, lateral part, dorsal view with gradulus visible.

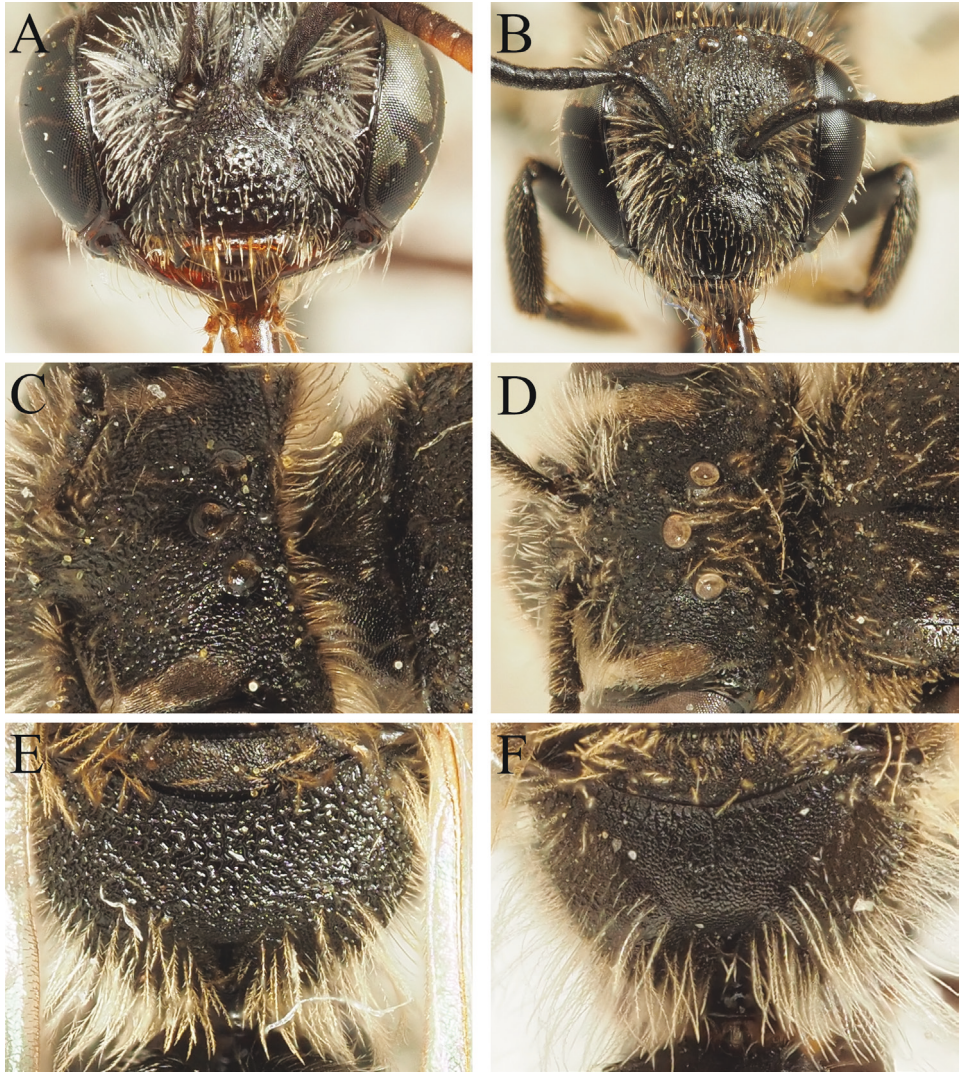


**Figure 98.** *Andrena (Micrandrena) pusilla* Pérez, 1903 female. **A.** Metasoma, dorsal view. *Andrena (Micrandrena) minutula* (Kirby, 1802) female. **B.** Metasoma, dorsal view. *Andrena (Micrandrena) cedricola* Wood, 2020 female. **C.** Metasoma, dorsal view. *Andrena (Micrandrena) magunta* Warncke, 1965 female. **D.** Metasoma, dorsal view. *Andrena (Micrandrena) alfskenelloides* Warncke, 1965 female. **E.** Metasoma, dorsal view. *Andrena (Micrandrena) falsifica* Perkins, 1915 female. **F.** Metasomal terga 1–2, dorsal view. *Andrena (Micrandrena) rugothorace* Warncke, 1965 female. **G.** Propodeum, dorsal view. *Andrena (Micrandrena) biarmica* Warncke, 1975 female. **H.** Clypeus, frontal view.

The following three species are very challenging to separate morphologically; geographical context and association with concurrently active males should be taken into account.

- 121 Clypeus along its anterior margin with a polished and shining strip occupying 1/5–1/4 of the surface, remaining parts microreticulate and dull. Found only in the Peloponnese, typically in mountainous areas ..... *A. pelopa* Warncke
- Clypeus entirely or almost entirely microreticulate and dull. Found in the Peloponnese or not ..... 122
- 122 Scutum with punctation comparatively dense, punctation around parapsidal lines separated on average by 0.5–1 puncture diameters (Fig. 70F). Process of the labrum trapezoidal, 1.5 times wider than long. Widespread across the southern Balkans (Fig. 23) ..... *A. byemala* Warncke
- Scutum with punctation comparatively sparse, punctation around parapsidal lines on average separated by 1–1.5 puncture diameters. Process of the labrum narrower, more quadrate, only slightly broader than long. Found only on the island of Rhodes (Fig. 23) ..... *A. repressa* Warncke
- 123 Facial foveae very narrow, slightly but distinctly narrower than the breadth of a flagellum, uniformly wide, not narrowing ventrally. Clypeus polished and shining in its apical 1/3, microreticulate and dull in its basal 2/3, overall with irregularly punctation separated by 0.5–3 puncture diameters. Nervulus strongly antefurcal. Known only from continental Greece (Fig. 22) ..... *A. helenica* Warncke
- Facial foveae broader, dorsal width equal to or clearly broader than the breadth of a flagellum; in some species, conspicuously narrowed ventrally. Clypeus variably sculptured, often with punctures much denser. Nervulus variable, interstitial to interfurcal. Distribution variable ..... 124
- 124 Supraclypeal area clearly and densely punctate, punctures separated by <0.5–1 puncture diameters, never with longitudinal striations. Lower paraocular areas strongly and densely punctate ..... 125
- Supraclypeal area at most obscurely punctate with shallow punctures separated by 1–2 puncture diameters or with longitudinal striations. Lower paraocular areas obscurely and sparsely punctate ..... 128
- 125 Hind tarsal claws unidentate, without an inner subapical tooth. Frons impunctate. Facial foveae medially constricted, distinctly narrower ventrally than dorsally. Associated with Brassicaceae ..... 126
- Hind tibial claws bidentate, with a small inner subapical tooth. Frons punctate. Facial foveae equally broad dorsally and ventrally. Associated with *Sedum* (Crassulaceae) ..... 127

It is not clear if the following two species can actually be separated in the female sex using morphological characters; both are widespread in the southern Balkans, and association with concurrently active dissected males must be made. The morphological character presented here is taken from Gusenleitner and Schwarz (2002: 56).



**Figure 99.** *Andrena (Micrandrena) tringa* Warncke, 1973 female. **A.** Clypeus, frontal view. *Andrena (Micrandrena) rugulosa* Stöckert, 1935 female. **B.** Head, frontal view; **C.** Vertex, dorsal view. *Andrena (Micrandrena) illyrica* Warncke, 1975 female. **D.** Vertex, dorsal view. *Andrena (Micrandrena) subopaca* Nylander, 1848 female. **E.** Propodeum, dorsal view. *Andrena (Micrandrena) incognita* Warncke, 1975 female. **F.** Propodeum, dorsal view.

- 126      Facial foveae comparatively broader ventrally, separated from the inner margin of the compound eye by a distance narrower than their ventral breadth. On average, encountered more in the northern parts of the southern Balkans. Bivoltine, predominantly recorded between April–July .....  
 .....*A. aciculata* Morawitz
- Facial foveae comparatively narrow ventrally, separated from the inner margin of the compound eye by a distance broader than their ventral breadth.

On average, encountered more in the southern parts of the southern Balkans. Univoltine, predominantly recorded between April – early June.....  
..... **A. lamiana Warncke**

The images in Wood (2024a) can be consulted to facilitate identification for the following two species.

127 Clypeus comparatively strongly punctate, clearly visible against the underlying sculpture. Frons densely and clearly punctate, punctures separated by 1 puncture diameter, contrasting the dull underlying surface. Scutum with uniform granular shagreen, dull to weakly shining, punctures separated by 0.5–1 puncture diameters. Terga with sparse lateral hair fringes. Widespread across the southern Balkans ..... **A. sandanskia Warncke**

– Clypeus comparatively weakly punctate, punctures disappearing into the underlying sculpture. Frons shagreened and weakly shining, comparatively more sparsely punctate with punctures separated by 1–2 puncture diameters, not strongly contrasting the underlying sculpture. Scutum finely shagreened and broadly shining, punctures separated by 1–2 puncture diameters. Terga with dense apical hair fringes laterally on T2–4. Found only on the island of Crete..... **A. lediveleci Wood**

128 Supraclypeal area with longitudinal striations. Scutum distinctly punctate, punctures separated by 0.5–1 puncture diameters, clearly visible against shagreened and weakly shining underlying surface. Nervulus interstitial to weakly antefurcal. Larger, 6–7 mm in length. Widespread across the southern Balkans ..... **A. tomora Warncke**

– Supraclypeal area without longitudinal striations. Scutum with dense granular microreticulation, dull, punctures disappearing into the underlying sculpture. Nervulus strongly antefurcal. Smaller, around 5 mm in length. Found only in mountains in southern continental Greece..... **A. chelma Warncke**

129 Entirety of terga strongly polished and shining, with essentially no difference in sculpture between the disc and marginal areas (Fig. 97E). Propodeal triangle poorly defined, with wrinkly basal rugae extending over approximately 1/2 the surface, reducing in strength posteriorly. Scutum with strong granular shagreen, dull and almost impunctate..... **A. querquedula Warncke**

– Tergal discs never entirely polished and shining, combination of characters different ..... **130**

130 Hind tibiae and basitarsi orange, tibial scopa composed of extremely short hairs. Restricted to mountainous areas in north-eastern Greece and southern Bulgaria (Rhodope and Pirin mountains). Associated with *Potentilla* (Rosaceae), flying in July–August..... **A. tarsata Nylander**

– Hind legs dark, tibial scopa with hairs normal, not extremely short .... **131**

- 131 Foveae long, dorsally extent reaching a line parallel to the hind margin of the lateral ocelli, foveae deeply impressed. Propodeal triangle not laterally delineated by carinae, internal surface weakly elevated, with irregular raised rugae that do not cover the entire area. Terga laterally with loose, white interrupted hair bands. Restricted to mountainous areas in north-eastern Greece and southern Bulgaria (Rhodope and Pirin mountains). Flying in July–August ..... ***A. coitana* (Kirby)**
- Foveae shorter, not reaching level of the lateral ocelli dorsally, only weakly impressed. Propodeal triangle clearly delineated laterally by carinae, internal surface evenly and regularly covered by fine network of raised rugae. Terga with lateral hair bands or not. Distribution and flight period variable ..... **132**
- 132 Clypeus and supraclypeal area covered with abundant longitudinal striations (Fig. 97F). Facial foveae strongly narrowed in their ventral 1/2, linear, much narrower than the width of a flagellum ..... ***A. distinguenda* Schenck**
- Clypeus and supraclypeal area without longitudinal striations. Facial foveae typically not noticeably narrowed in their ventral 1/2. If narrowed (*nana*-group), then without facial striations and with tergal discs noticeably polished and shining..... **133**
- 133 Large species, around 10 mm in length. Clypeus densely covered with latitudinal wrinkles. Lateral faces of the propodeum covered with pattern of raised star-shaped wrinkles (Fig. 97G; *proxima*-group) ..... **134**
- Most species smaller. Clypeus without latitudinal wrinkles and propodeum without pattern of raised star-shaped wrinkles (*Micrandrena* Ashmead *sensu stricto*) ..... **135**
- 134 Scutum dorsally with short black hairs intermixed between longer whitish hairs (view in profile). Discs and marginal areas of T2–3 evenly wrinkled and shagreened, dull and without glossy reflections. In fresh specimens, T4 with a complete apical hairband. Pubescence of metasoma whitish in fresh specimens. Typically flying later, mostly from June–August ..... ***A. alutacea* Stöckhert**
- Scutum dorsally with uniformly pale hairs, without intermixed black hairs, or at most with a few small scattered black hairs. Discs and marginal areas of T2–3 finely shagreened and shining, often with oily reflections. Apical margin of T4 always with the hairband interrupted, even in fresh specimens. Pubescence of metasoma yellowish in fresh specimens. Typically flying earlier, mostly from April–June ..... ***A. proxima* (Kirby)**
- 135 T3–4 with the marginal areas strongly depressed relative to the discs; this is most clearly seen on T4 (Fig. 98A)..... **136**
- T3–4 with the marginal areas only superficially depressed (Fig. 98B).. **139**
- 136 T2–3 laterally without a gradulus. Currently only known from the Pirin and western Rhodope mountains in southern Bulgaria, probably present also in northern Greece and North Macedonia ..... ***A. pirinia* Wood**
- T2–3 laterally with a gradulus (Fig. 97H); sometimes difficult to see basolaterally on T2. Distribution variable, typically not found in high mountains..... **137**

- 137 T2–4 with shaggy white “double” hairbands, with hairs emerging from the junction of the tergal disc and marginal area AND on the marginal rim itself. In fresh specimens, apical hairbands long, clearly extending onto the base of the following terga and obscuring the underlying surface. Discs of T2–4 finely microreticulate and weakly shining, with punctures visible against this sculpture. Facial foveae not noticeably constricted medially. Uncertainly recorded from the southern Balkans .....  
 ..... *A. niveata* Friese
- T2–4 with double hairbands, but these narrow and not shaggy (Fig. 98A). In fresh specimens, these hairbands barely extending onto the discs of the following terga. Discs of T2–4 with uniform microreticulation, dull to obscurely shining, punctures disappearing into underlying sculpture. Facial foveae slightly constricted medially. Widespread in the southern Balkans (*spretta*-group)..... **138**

The following two species are very challenging to separate; consultation of confidently determined reference material is necessary.

- 138 Scutum comparatively sparsely punctate, punctures separated on average by 1–1.5 puncture diameters. Surface of scutum finely shagreened and weakly shining. Widespread in the southern Balkans .....  
 ..... *A. pusilla* Pérez
- Scutum comparatively densely punctate, punctures separated on average by 0.5–1 puncture diameters, sometimes by less. Surface of scutum variably sculptured but usually very weakly shagreened to polished and shining, therefore on average more brightly shining despite denser punctuation. Very rare in the southern Balkans, known only from the island of Corfu .....  
 ..... *A. spreta* Pérez
- 139 Process of labrum very narrow, small and triangular, only slightly longer than broad. Marginal areas of T2–4 broadly polished and shining, occupying around 1/2 the visible tergal surface, contrasting the impunctate and finely microreticulate tergal discs (Fig. 98C). Apical margins of T2–4 with distinct lateral hair fringes, these messy and loosely mixing into whitish hairs at base of discs of T3–4. Known only from mountainous parts of Greece (Fig. 32) ..... *A. cedricola* Wood
- Combination of characters otherwise; process of labrum not small and triangular OR marginal areas of T2–4 dull or punctate OR tergal discs clearly punctate OR apical margins of T2–4 without distinct lateral hair fringes (e.g. Fig. 98D–F). Distribution variable..... **140**
- 140 Facial foveae uniformly narrow, narrower than the width of a flagellum, neither narrowing ventrally or broadening dorsally. Disc of T1 microreticulate and dull, strongly and densely punctate, punctures separated by 0.5–1 puncture diameters. Discs of T2–3 polished and shining, densely punctate with punctures clearly defined and separated by 0.5–1 puncture diameters.

- Marginal areas of T2–3 slightly depressed, microreticulate and dull. Very rare, known only from Corfu.....*A. taprobana* Warncke
- Combination of characters different; facial foveae broader or of variable width along their extent OR disc of T1 polished and shining OR discs and margins of T2–3 otherwise sculptured. Distribution variable..... 141
- 141 Disc of T1 polished and shining (Fig. 98D, E)..... 142
- Disc of T1 sculptured, strongly to weakly microreticulate, never polished and shining (e.g. Fig. 98B, F)..... 146
- 142 Facial foveae strongly narrowed in their ventral 1/2; dorsally subequal to the width of a flagellum, ventrally clearly narrower ..... 143
- Facial foveae not noticeably narrowed in their ventral 1/2, essentially as broad dorsally as ventrally ..... 144
- 143 Ocelloccipital distance long, exceeding 2 times the diameter of a lateral ocellus. Scutum densely but irregularly punctate, large punctures separated by 0.5–1.5 puncture diameters with minute “double punctures” scattered between them (punctures with a much smaller diameter, hence the scutum as a whole appears to have two distinct types of punctures and is doubly punctate). Metasoma with punctation strong and coarse (Fig. 98D). Widespread across the southern Balkans..... *A. magunta* Warncke
- Ocelloccipital distance relatively short, only slightly exceeding the diameter of a lateral ocellus. Scutum densely and uniformly punctate, punctures separated by <0.5–0.5 puncture diameters, without double punctation. Metasoma with punctation strong but fine. Uncommonly and unclearly recorded from North Macedonia and Bulgaria.....*A. nana* (Kirby)
- 144 Disc of T1 polished and shining, but discs of T2–4 microreticulate and dull (Fig. 98E). Discs of T2–4 finely punctate, but punctures challenging to see against underlying sculpture.....*A. alfenelloides* Warncke
- Discs of T1–4 polished and shining AND strongly and densely punctate, punctures clearly visible against the little underlying sculpture present..... 145
- 145 Clypeus polished and shining between punctures, at most with weak shagreen laterally. Posterior margin of the gena behind the ocelli angulate, almost carinae, forming a 90° angle.....*A. enslinella* Stöckhert
- Clypeus microreticulate and dull to at most weakly shining apically, never polished and shining over the majority of its surface. Posterior margin of the gena behind the ocelli evenly rounded .....*A. floricola* Eversmann
- 146 Marginal area of T1 wide, strongly thickened (in profile view almost appearing humped) and impunctate, contrasting the disc of T1 which is distinctly punctate medially (Fig. 98F). Restricted to mountainous areas northern parts of the southern Balkans, associated with *Potentilla* (Rosaceae) ..... *A. falsifica* Perkins
- Marginal area of T1 normal, not widened or thickened ..... 147

- 147 Clypeus with weakly to strongly produced latitudinal wrinkles or carinae, surface either impunctate or with wrinkles present between punctures (Fig. 98H). Wrinkles can be continuous or interrupted..... **148**
- Clypeus without such wrinkles ..... **152**
- 148 Propodeal triangle poorly defined, lacking or with very obscure lateral carinae (Fig. 98G). Internal surface of propodeal triangle with rugae reaching only halfway, not continuing to the junction with the vertical face, the surface here rounded and relatively smooth. Associated with Asteroideae (Asteraceae) (*rugothorace*-group)..... **149**
- Propodeal triangle well-defined, with clear and continuous lateral carinae present. Internal surface of propodeal triangle evenly and consistently covered with rugae, these continuing to the junction with the vertical face, the surface here distinctly wrinkled ..... **150**

The images in Wood (2024a) can be consulted to facilitate identification for the following two species.

- 149 Scutum consistently microreticulate and only weakly shining, punctures sometimes with slightly raised margins (crater punctures). Propodeal triangle medially with a fine network of basal rugae, comparatively closely spaced, appearing dull. Widespread in the southern Balkans, but not the island of Crete ..... *A. rugothorace* **Warncke**
- Scutum finely shagreened, more brightly shining, punctures without slightly raised margins, the scutum thus appearing smoother and less coarse. Propodeal triangle medially with strongly produced basal rugae, these irregular and comparatively widely spaced, comparatively brightly shining. Found only on the island of Crete..... *A. pelagica* **Warncke**
- 150 Tergal discs, specifically discs of T1–2, extremely densely punctate, punctures separated by 0.5 puncture diameters. Clypeus with latitudinal wrinkles strongly produced. Scutum with punctures separated by 1–2 puncture diameters. Rare, known only from the East Aegean Islands ..... *A. biarmica* **Warncke**
- Tergal discs finely microreticulate, obscurely punctate with the punctures disappearing into the underlying sculpture. Clypeus without latitudinal wrinkles strongly produced. Scutum with punctures separated by 0.5–1 puncture diameters. Distribution variable ..... **151**
- 151 Process of the labrum small, narrow, triangular, and acutely pointed. Body size very small, around 5 mm in length ..... *A. paganettina* **Warncke**
- Process of the labrum trapezoidal, twice as wide as long, apical margin more-or-less straight. Body size larger, around 7–8 mm in length ..... *A. simontornyella* **Noskiewicz**

- 152 Clypeus very sparsely punctate, punctures separated by around 2–5 puncture diameters, mostly by around 3 puncture diameters ..... **153**
- Clypeus more densely punctate, never with punctures separated by 3 puncture diameters on average, more typically by 1 puncture diameter..... **154**
- 153 Scutum very densely punctate, most punctures separated by <0.5–0.5 puncture diameters, separated by up to 1 puncture diameter at most postero-medially. Clypeus broadly flattened across almost its entire surface. Scutum strongly microreticulate, dull. Widespread across the southern Balkans, but seemingly not on the East Aegean Islands ..... ***A. saxonica* Stöckhert**
- Scutum slightly less densely punctate, punctures separated by 0.5–1 puncture diameters. Surface of scutum finely microreticulate, interspaces weakly shining. Clypeus slightly domed, only weakly flattened medially. Rare, known only from the East Aegean Islands (Rhodes) ..... ***A. sillata* Warncke**
- 154 Clypeus polished and shining over at least 2/3 of its surface (Fig. 99A). Body size small, 5–6 mm in length. Scutum finely microreticulate and weakly shining, finely punctate with punctures separated by 0.5–1.5 puncture diameters. Terga with fine granular microreticulation, weakly shining and essentially impunctate. Tergal margins with their apical rims narrowly lightened hyaline-brown, margins of T3–5 laterally with distinct apical whitish hair fringes. Found in northern parts of the southern Balkans..... ***A. tringa* Warncke**
- Clypeus either uniformly sculptured and weakly shining to dull, or if with the apical 1/3–1/2 shining, then body size 7–8 mm. Scutum often microreticulate, dull, and very densely punctate with the punctures almost confluent, not finely microreticulate and weakly shining. Tergal sculpture variable, apical margins with their rims typically not lightened hyaline-brown. Body size variable. Distribution variable ..... **155**
- 155 Clypeus in its apical 1/3 to 1/2 more-or-less shining, contrasting the basal 1/2–2/3 that are microreticulate and weakly shining to almost dull (Fig. 99B). Scutum and scutellum strongly microreticulate and dull. Scutum densely punctate, medially with punctures almost confluent (*rugulosa*-group)... **156**
- Clypeus uniformly sculptured and usually dull, without the apical portion shining. Scutum and scutellum variably sculptured but never so densely punctate. If there are hints of the apical margin of the clypeus shining, then scutum with punctures separated by around 2 puncture diameters..... **157**
- 156 Ocelloccipital distance subequal to or equalling the diameter of a lateral ocellus (Fig. 99C). Common and widespread ..... ***A. rugulosa* Stöckhert**
- Ocelloccipital distance exceeding 2 times the diameter of a lateral ocellus, almost 3 times this diameter (Fig. 99D). Very seldom encountered in the southern Balkans..... ***A. illyrica* Warncke**
- 157 Dorsolateral parts of T1 with slightly raised corners, visibly projecting and disrupting rounded profile when viewed from above. Clypeus slightly flattened centrally, with clear impunctate midline between large and well defined clypeal punctures. Discs of T2–3 impunctate medially, laterally with

- large punctures with raised margins (crater punctures). North Macedonia ..... ***A. strohmella* Stöckhert**
- Dorsolateral parts of T1 without such raised projections, in dorsal view evenly rounded. Clypeus not noticeably flattened, without an unambiguously defined impunctate midline, though in some species a weak impunctate midline may be formed. Terga either impunctate, or if punctate, then discs of T2–3 without a strong contrast between the medial and lateral punctures ..... **158**
- 158 Disc of T1 punctate, and disc of T2 more strongly, clearly, and extensively punctate; punctures not extending onto the marginal areas ..... ***A. alfenella* Perkins**
- Disc of T1 finely to strongly microreticulate, at most obscurely punctate with punctures disappearing into the underlying surface sculpture. Disc of T2 with at most a few punctures laterally, the majority of the medial surface essentially impunctate ..... **159**
- 159 Scutum finely, sparsely, and somewhat irregularly punctate, punctures separated by 1–3 puncture diameters. Underlying surface uniformly dull with punctures sometimes almost disappearing into the underlying sculpture ..... **160**
- Scutum more densely punctate, punctures separated by up to 2 puncture diameters, more typically by around 1 puncture diameter. Underlying surface dull to polished and shining; punctures always clearly visible against the underlying sculpture ..... **161**
- 160 Propodeal triangle well defined, laterally with strong carinae which merge with the internal rugae that uniformly cover the internal surface (Fig. 99E). Hind tarsi dark. Process of the labrum broadly trapezoidal, apical margin straight. Uncommon in cool temperate parts of the southern Balkans ..... ***A. subopaca* Nylander**
- Propodeal triangle poorly defined, laterally lacking a clear raised carinae, the internal rugae therefore disconnected from said lateral margins (Fig. 99F). Hind tarsi slightly orange. Process of the labrum more-or-less triangular, twice as broad as long, apical margin narrow. Very rare, currently recorded only from North Macedonia ..... ***A. incognita* Warncke**
- 161 Scutum and scutellum strongly and densely punctate, punctures separated by 0.5–1 puncture diameters, underlying surface dull (1<sup>st</sup> generation) to weakly shining (2<sup>nd</sup> generation). In fresh specimens (beware abrasion) tergal margins with strong lateral hair fringes. Foveae of uniform width throughout ..... ***A. minutula* (Kirby)**
- Scutum and scutellum strongly but slightly randomly punctate, punctures separated by 1–2 puncture diameters, underlying surface weakly shining (1<sup>st</sup> generation) to strongly shining (2<sup>nd</sup> generation). Tergal margins with extremely weak lateral hair fringes with a few hairs touching (1<sup>st</sup> generation) or all hairs separated (2<sup>nd</sup> generation). Foveae slightly narrowed ventrally ..... ***A. minutuloides* Perkins**

- 162(114) Clypeus flattened over majority of its surface. Species strongly associated with Fabaceae (subgenus *Taeniandrena* Hedicke) ..... **163**  
 – Clypeus not noticeably flattened. Species not usually associated with Fabaceae ..... **172**

Females of this subgenus are highly challenging and in some cases impossible to identify. Whilst many taxonomic issues in the subgenus have been resolved in recent years, and the Balkan fauna is not as complex as the Iberian fauna, there may still be unresolved diversity. Do not expect to identify this group without consulting confidently determined reference material, and ideally barcoded specimens. Many images were provided by Praz et al. (2022).

- 163 Glossa long, greatly exceeding the length of the galea; in lateral view, glossa bent medially with a distinct 90° angle, extending as far beyond the bend as before the bend (c.f. Fig. 117B, see also Müller and Westrich 2023). Clypeus medially slightly concave, strongly shagreened with shallow and obscure punctures. Pygidial plate apically emarginate.....  
 ..... ***A. lathyri* Alfken**  
 – Glossa normal, not or only slightly exceeding the length of the galea; in lateral view, without a 90° bend. Clypeus without a medial impression, surface often strongly and distinctly punctured. Pygidial plate apically rounded ..... **164**  
 164 Terga comparatively strongly and densely punctate; declivity of T1 with a distinct patch of strong and dense punctures, punctures separated by 1 puncture diameter. Disc of T2 with punctures distinct, separated by 0.5–1 puncture diameter. Tergal hairbands interrupted on T2–3, complete only on T4. Uncommonly encountered in the southern Balkans, probably restricted to mountainous areas..... ***A. wilkella* (Kirby)**  
 – Terga not so strongly punctate; declivity of T1 never with such a distinct patch of dense punctures. Disc of T2 with punctures variable, either absent or obscure and difficult to see. Tergal hairbands variable, but often complete on T3 as well as T4. Distribution variable ..... **165**  
 165 Terminal fringe dark chocolate brown-black. Hairs flanking the basitibial plate and those at the base of the dorsal surface of the tibial scopae dark chocolate-brown. Scutum and scutellum with predominantly white pubescence, medially with intermixed dark brown hairs. Remaining pubescence of head, mesepisternum, and tergal hairbands white..... ***A. leucopsis* Warncke**  
 – Terminal fringe and hairs flanking the basitibial plate various shades of orange to golden-brown, but never dark chocolate-brown. Scutum and scutellum with hairs light brown to rich orange-brown, but not a contrasting mixture of white-brown. Remaining pubescence of head, mesepisternum, and tergal hairbands brownish to orange-brown ..... **166**  
 166 Large species, 14–15 mm in length. Ocelloccipital distance long, 2 times the diameter of a lateral ocellus. Tergal discs almost impunctate, particularly

- on T1–2, remaining terga with fine and obscure punctures which do barely contrast the integumental sculpture. Associated with shrubby Fabaceae in open grasslands (such as *Chamaecytisus*).....***A. aberrans* Eversmann**
- Smaller species, not exceeding 12 mm in length. Ocelloccipital distance variable, from 1.5–2 times the diameter of a lateral ocellus. Tergal discs variably punctate, but usually with at least a few punctures visible on the disc of T2. Ecology variable ..... **167**
- 167 Pubescence of scutum and scutellum bright orange, particularly dense, especially on lateral parts of scutellum. Terga with shallow obscure punctures. Mid and hind tarsi and hind tibia orange. Tergal hair band composed of relatively long and thick hairs.....***A. russula* Lepelletier**
- Combination of characters different; pubescence of scutum and scutellum brownish to greyish. Terga with punctuation variable, often with abundant and visible punctures. Colouration of legs variable. Tergal hairbands narrower ..... **168**

The following five species are particularly challenging to separate; association with dissected males should be made, where possible.

- 168 Slightly larger, 10–12 mm in length. Terminal fringe rich golden-orange (*gelriae*-group)..... **169**
- Slightly smaller, 8–10 mm in length. Terminal fringe variable, from greyish-brown, whitish-orange, or brownish-orange, but typically not rich golden-orange (*ovatula*-group) ..... **170**
- 169 Metasoma more strongly punctate; in direct comparison, disc of T2 more densely punctate, punctures separated on average by 0.5 puncture diameters, tergal discs therefore comparatively more dull. Found in warm grasslands to moderate altitude in northern parts of the southern Balkans.....

..... ***A. producta* Warncke**
- Metasoma less strongly punctate; disc of T2 more sparsely punctate, punctures separated on average by 1 puncture diameter, tergal discs therefore comparatively more shiny. In the southern Balkans, typically found in mountainous areas, with this trend becoming more pronounced the further south one travels; in Greece, known from above 1500 m..... ***A. intermedia* Thomson**
- 170 Clypeus with very shallow punctures, some of these almost disappearing into the underlying sculpture; at its most extreme giving the clypeus the appearance of being dull and relatively featureless. Terga relatively finely and obscurely punctate, disc of T2 with abundant punctures but these partially disappearing into the microreticulate and relatively dull surface sculpture. Scutum uniformly microreticulate and dull .....***A. ovata* Schenck**
- Clypeus with deep and distinct punctures, these clearly visible against the surface. Terga finely but distinctly punctate, disc of T2 with abundant punctures which do not disappear into the relatively more finely microreticulate surface which can be weakly shining. Scutum variably sculptured ..... **171**

- 171 Scutum laterally microreticulate and dull, becoming finely shagreened and broadly shining over the majority of the central part of the disc. Tergal punctation slightly denser, punctures separated by <math>0.5-0.5</math> puncture diameters; terga thus appearing comparatively dull. In fresh specimens, head and mesosoma with golden-brown pubescence. Univoltine, late May to early July.....**A. taedium Wood**
- Scutum predominantly microreticulate and dull, at most with a very small weakly shining area medially. Tergal punctation slightly sparser, punctures separated by 0.5–1 puncture diameters; terga thus appearing comparatively weakly shining. In fresh specimens, head and mesosoma with paler light brown to whitish pubescence. Bivoltine, May to August .....**A. afzeliella (Kirby)**
- 172(162) Fovea dorsally narrow, occupying at most 1/3 of the space between lateral ocellus and compound eye, ventrally narrowing strongly. (Fig. 100A). Propodeal triangle “T-shaped”, very narrow apically, with lateral margins concave (subgenus *Euandrena* Hedicke). One species has the facial foveae ambiguous, and so is keyed under both character states ..... **173**
- Foveae either dorsally broader, or not strongly narrowing. Propodeal triangle variable in shape, often broader apically, overall more triangular, or with the lateral margins straight ..... **190**

Members of the subgenus *Euandrena* are highly challenging to identify morphologically, and it is likely that the characters presented here do not capture the full range of variation seen in the southern Balkans. Caution and discretion must be exercised; the key and images of Praz et al. (2019) should also be consulted.

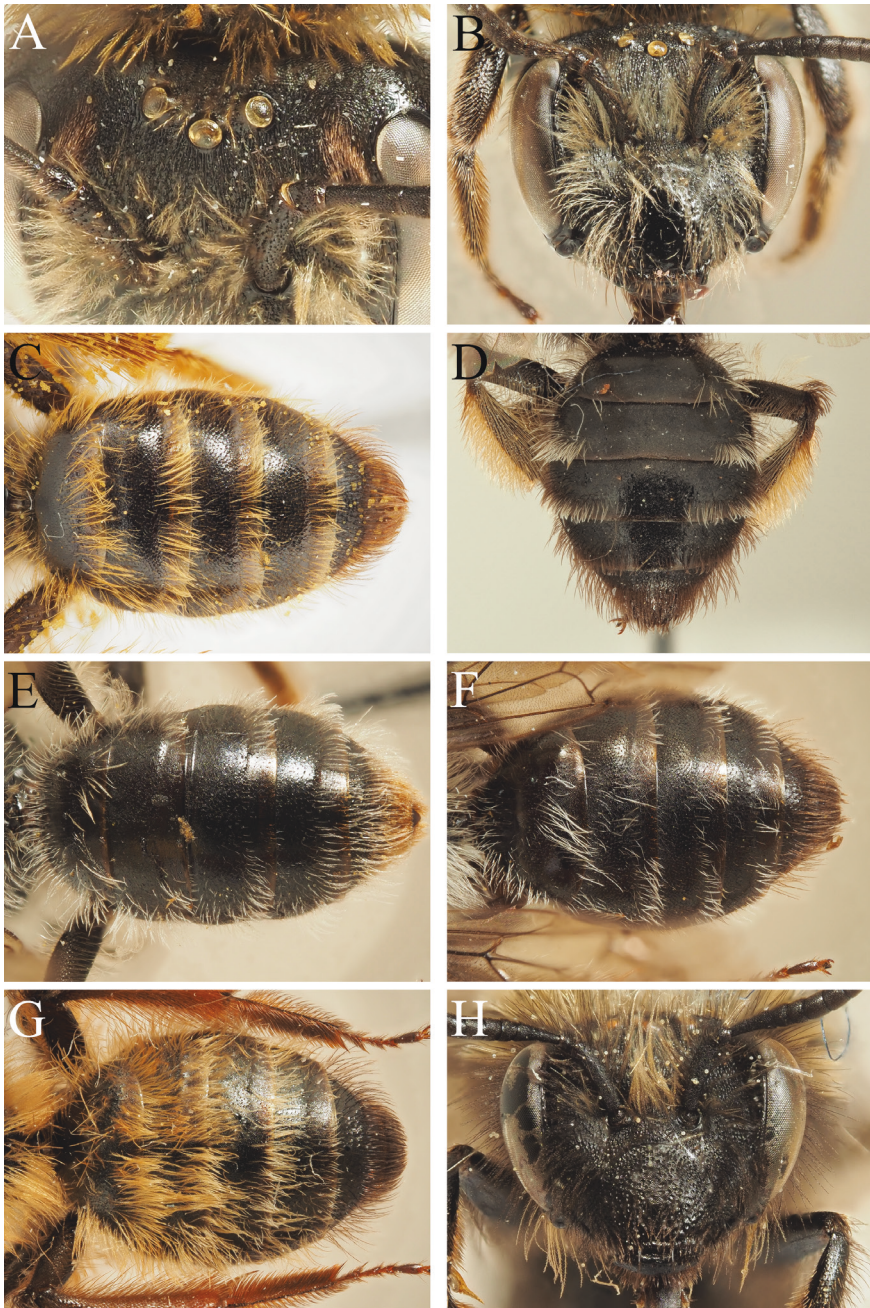
- 173 Clypeus strongly domed, densely and coarsely punctate with a raised longitudinal and impunctate shiny midline (Fig. 100B). Associated with *Symphytum* (Boraginaceae) .....**A. symphyti Schmiedeknecht**
- Clypeus domed or flattened, densely or weakly punctate, but never with a raised longitudinal impunctate shiny midline ..... **174**
- 174 Head longer than broad. Terga smooth and shiny, T2–T4 with dense apical hairbands composed of snow-white hairs, bands continuous on T3 and T4, obscuring the underlying surface. Hind tibiae orange. Associated with *Asparagus* (Asparagaceae) .....**A. chrysopus Pérez (partim)**
- Head round or broader than long. Tergal sculpture variable, without such snow-white dense apical hair bands. Hind tibiae variable. Not associated with *Asparagus* ..... **175**
- 175 Hind tibiae and basitarsi lightened orange (Fig. 82E). Terga finely shagreened, more-or-less impunctate. Face with pubescence light brown to buff medially, with black hairs along the inner margins of the compound eyes (Fig. 82B). Very rare in the southern Balkans, restricted to

- high altitude sites, associated with *Salix* (Salicaceae).....  
 ..... ***A. aff ruficrus* Nylander**  
 – Hind tibiae and basitarsi dark, like the integument of the other legs. Terga  
 variably sculptured, facial pubescence variable, distribution and ecology  
 variable ..... **176**  
 176 Apical margins of T1–4 extensively lightened yellow-hyaline, this lightened  
 area clearly exceeding the diameter of a lateral ocellus (Fig. 100C). Associ-  
 ated with Cistaceae ..... **177**  
 – Apical margins of T1–4 not extensively lightened yellow-hyaline, at most  
 narrowly so, this lightened area not exceeding the diameter of a lateral ocel-  
 lus (c.f. Figs 12D, 68F, 69F, 100D–G). Not specifically associated with  
 Cistaceae..... **178**

These two species are very difficult to separate in the female sex. Association with males should be made where possible.

- 177 Tergal margins comparatively more strongly depressed. Tergal discs on aver-  
 age more coarsely and densely punctate, punctures on the disc of T2  
 separated by 1.5–2 puncture diameters .....***A. granulosa* Pérez**  
 – Tergal margins comparatively more weakly depressed. Tergal discs on aver-  
 age less strongly and densely punctate, punctures on the disc of T2 sepa-  
 rated by 3–4 puncture diameters.....***A. vulpecula* Kriechbaumer**  
 178 Pronotum with a distinct humeral angle (Fig. 14D). Mesepisternum enti-  
 rely pale-haired, never with any black hairs. Clypeus medially with an  
 impressed longitudinal midline of variable strength ..... **179**  
 – Pronotum rounded. Often with scattered to abundant black hairs on the  
 mesepisternum. Clypeus either without an impressed longitudinal midline,  
 or IF with such a midline, then with abundant black hairs on the mesepis-  
 ternum..... **180**  
 179 Facial pubescence predominantly pale, with black hairs only on the frons.  
 Scutum medially at least partly polished and shining. T2–4 with complete  
 apical hairbands of dense yellowish hairs that obscure the underlying sur-  
 face. With a Mediterranean distribution in Albania and Greece, not found  
 in temperate habitats. Seemingly bivoltine, flying mostly in the spring  
 (March–May) and autumn (October) (Fig. 15).....***A. glidia* Warncke**  
 – Facial pubescence predominantly light, with a few black hairs along the in-  
 ner margins of the compound eyes AND on the frons. Scutum uniformly  
 microreticulate and dull. T2–4 with loose golden-brown hair fringes that  
 are interrupted medially and which do not obscure the underlying surface.  
 Found in temperate habitats, usually in mountains in the northern parts  
 Greece and Bulgaria .....***A. fulvata* Stöckhert**  
 180 Clypeus with a distinctly impressed longitudinal midline. Facial pubescence  
 predominantly black, with light brown hairs on the frons. Mesepisternum

- with abundant black pubescence. Margins of T2–3 with long white hair fringes laterally, strongly contrasting the dark brown hairs of T4–5 (Fig. 100D). Currently known only from the border of North Macedonia and Greece (Mount Kožuf).....***A. pelagonia* Wood**
- Combination of characters otherwise..... **181**
- 181 Found on the island of Crete. Clypeus with large and distinctly separated punctures which are separated by 0.5–3 puncture diameters but typically by 1–2 puncture diameters. Terga largely impunctate (Fig. 69F). Scutum shallowly punctate, punctures partially disappearing into the surface sculpture. Facial pubescence pale, with black hairs running along the inner margins of the compound eyes. Tibial scopae partially plumose .....  
..... ***A. obscuricrus* sp. nov.**
- Found on the island of Crete or elsewhere. Combination of any characters different; clypeus more densely punctate; terga with visible punctures; scutum more clearly punctate; facial pubescence different; tibial scopae always composed of simple hairs..... **182**
- 182 Terminal fringe yellow-white. Facial pubescence predominantly grey-white, with a few dark brown hairs along the inner margin of the compound eyes and on the frons. Mesepisternum with long greyish-white hairs, without any black hairs present. Tergal discs with fine and scattered punctures, punctures separated by 1–4 puncture diameters; tergal pubescence entirely whitish (Fig. 100E). Found at high elevation sites in mountainous parts of the southern Balkans, with confirmed records from 2000 m in altitude ....  
..... ***A. montana* Warncke**
- Combination of any characters different; terminal fringe dark brown to brown; facial pubescence rich orange brown to black with intermediate states; mesepisternum with brown to black pubescence; terga sometimes more clearly punctate; tergal pubescence different. Found at a variety of altitudes from low to high..... **183**
- 183 Mesepisternum with almost entirely whitish hairs, with at most the occasional black hair. Face with grey-white pubescence with only a few black hairs on the frons. Clypeus protruding, densely punctate except medially where punctures are separated by 1–2 puncture diameters. Tergal discs with short black hairs, apically with complete whitish hairbands on T2–4 (Fig. 100F). Tibial scopae greyish-white. Scutum smooth and shiny over the majority of its surface. Continental Greece and the East Aegean Islands.....***A. robusta* Warncke**
- Combination of any characters different; mesepisternum with either predominantly light brown hairs, black hairs, or mixture of black and pale hairs, and/or facial pubescence rich orange brown to black with intermediate states; terga without clear apical hairbands, or hairbands brownish; tibial scopae light brown to orange. Scutum variably sculptured. Distribution variable..... **184**



**Figure 100.** *Andrena* (*Euandrena*) *symphyti* Schmiedeknecht, 1883 female. **A.** Head, dorsal view; **B.** Head, frontal view. *Andrena* (*Euandrena*) *granulosa* Pérez, 1903 female. **C.** Metasoma, dorsal view. *Andrena* (*Euandrena*) *pelagonia* Wood, 2021 female. **D.** Metasoma, dorsal view. *Andrena* (*Euandrena*) *montana* Warncke, 1973 female. **E.** Metasoma, dorsal view. *Andrena* (*Euandrena*) *robusta* Warncke, 1975 female. **F.** Metasoma, dorsal view. *Andrena* (*Euandrena*) *rufula* Schmiedeknecht, 1883 female. **G.** Metasoma, dorsal view. *Andrena* (*Euandrena*) *pileata* Warncke, 1975 female. **H.** Head, frontal view.

- 184 Mesepisternum with predominantly light brown to orange-brown hairs, with at most a few black hairs ventrally (Fig. 68D) ..... **185**
- Mesepisternum with pubescence variable, from abundantly black-haired (e.g. Fig. 13C), showing a mixture of black and pale hairs, to predominantly pale-haired with a few intermixed black hairs; never predominantly covered with light brown hairs ..... **187**
- 185 Scutum uniformly microreticulate and dull, shallowly and obscurely punctate. Clypeus with punctures separated by around 1 puncture diameter, in its basal 1/2 with a distinct longitudinal impunctate line. Discs of T1–4 covered with long erect foxy-red hairs (in fresh specimens), not forming distinct and clearly defined apical hairbands (Fig. 100G). Typically more associated with flowering trees (e.g. *Acer*; Sapindaceae) ..... ***A. rufula* Schmiedeknecht**
- Scutum polished and shining over at least part of its surface, densely punctate with punctures easy to see against the underlying surface (e.g. Fig. 68C). Clypeus densely and uniformly punctate, punctures separated by <0.5–1 puncture diameters, without any indication of an impunctate longitudinal midline. At least T2–3 with weak but distinct apical hairbands of pale yellow-brown hairs (Figs 12D, 68F). Typically more associated with herbaceous plants (e.g. Brassicaceae, *Campanula*) ..... **186**
- 186 Facial pubescence almost entirely light brown with at most a few black hairs along the inner margins of the compound eyes (Fig. 68B). Clypeus densely punctate but with the underlying surface and hence interspaces strongly polished and shining..... ***A. bulgarica* sp. nov.**
- Facial pubescence intermixed black and light brown, typically (but not always, c.f. Fig. 12C) with abundant black hairs on the clypeus. Clypeus densely punctate with interspaces shagreened and weakly shining to dull.. ..... ***A. aff limosa* Warncke**
- 187 Terga irregularly and relatively sparsely punctate, punctures separated by 1–3 puncture diameters and with polished and shining interspaces (Fig. 13D). Currently only known from northern Greece (Western Macedonia) ..... ***A. glabriventris* Alfken**
- Terga more uniformly punctate, punctures typically not exceeding the diameter of a puncture on average and without large polished shining interspaces. Distribution variable ..... **188**

It is not currently clear if the following three species can be consistently separated morphologically in the southern Balkans due to variation in pubescence and sculpture. Additional genetic characterisation and testing of morphological characters is required; the characters presented here should be used under advisory.

- 188 Clypeus densely punctate with indications of an impunctate longitudinal midline equivalent to roughly 2 puncture diameters (Fig. 100H). In some specimens, a clear impunctate longitudinal midline is absent, but the apical

- part of the clypeus has impunctate areas equalling 3–4 puncture diameters. Scutum uniformly and finely microreticulate, dull and shallowly punctate ..... ***A. pileata* Warncke**
- Clypeus more-or-less uniformly punctate, without indication of an impunctate longitudinal midline; apical part of the clypeus with impunctate interspaces equalling at most 2 puncture diameters. Scutum variably sculptured, from dull to smooth and shiny ..... **189**
- 189 Mesonotum with brown pubescence intermixed with abundant and slightly shorter dark brown to black hairs, these exceeding 1/2 the length of the brown hairs. Mesepisternum typically with predominantly pale greyish hairs, with black hairs intermixed. Face always with abundant pale hairs medially around the antennal insertions. Scutum always at least partially shining medially, often predominantly smooth and shining. Restricted to mountainous areas ..... ***A. amieti* Praz, Müller & Genoud**
- Mesonotum without intermixed dark hairs, or intermixed dark hairs are less than 1/2 as long as the brown hairs. Mesepisternum with pubescence variable, from light to almost entirely dark. Facial pubescence variable, from entirely dark to with abundant pale hairs medially. Scutum variably sculptured, from entirely dull to broadly shining. Found in a wide variety of habitats, including mountains..... ***A. bicolor* Fabricius**
- 190(172) Clypeus punctate, interspaces forming weakly raised longitudinal wrinkles AND terga densely and uniformly punctate, punctures separated by around 1 puncture diameter or less (*flavipes*-group) ..... **191**
- Clypeus without longitudinal wrinkles and tergal punctation variable; in the case of *A. hypopolia* which has weak longitudinal wrinkles, then terga only obscurely punctate, never densely and uniformly punctate ..... **194**
- 191 Posterior face of the hind femur rounded ..... **192**
- Posterior face of the hind femur with a latitudinal carina ..... **193**
- 192 Tibial scopae black. Facial pubescence dark brown to black, at most with occasional pale hairs. Terga with dark brown to obscure pale brown apical hairbands, these not obscuring the underlying surface. Restricted to the island of Crete (Fig. 29) ..... ***A. cretica* Strand**
- Tibial scopae orange. Facial pubescence whitish with black hairs along the inner margins of the compound eyes. Terga with broad pale and shaggy apical hairbands, in fresh specimens obscuring the underlying surface. Found in cooler parts of the southern Balkans (including hills and mountains in the Peloponnese), and not present on the island of Crete ..... ***A. gravida* Imhoff**

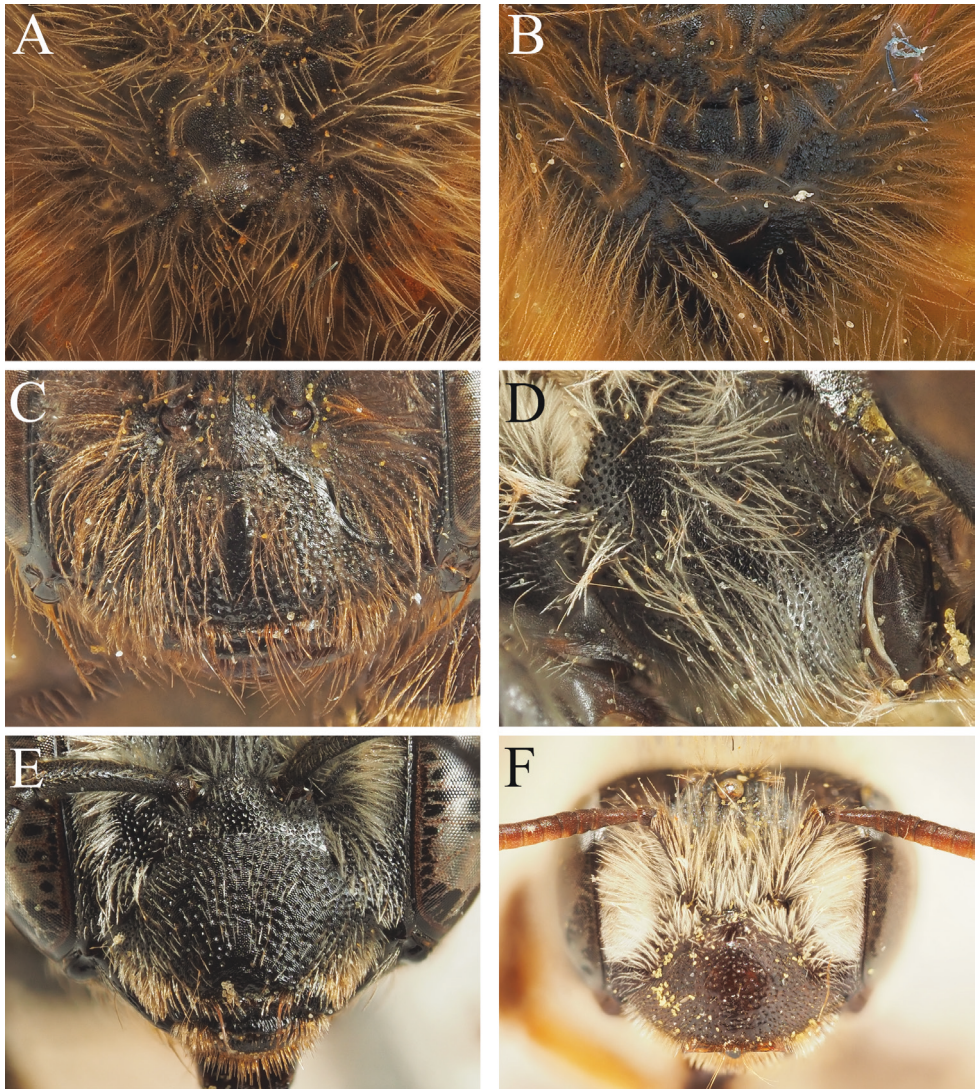
Comparative images of the terminal fringe of *flavipes*-group species were provided by Wood (2023d: 43).

- 193 Terminal fringe composed of predominantly dark brown hairs, occasionally with reddish to yellowish hairs intermixed, but never entirely composed

- of pale hairs. Face with mixture of light and dark hairs, but predominantly dark-haired. Extremely common and widespread, the most frequently encountered *Andrena* species in the southern Balkans; without clear habitat associations ..... ***A. flavipes* Panzer**
- Terminal fringe composed entirely of golden hairs, without a single dark hair present. Face with predominantly pale hairs. Larger, 12–14 mm. Very rare in the southern Balkans, currently recorded only from Bulgaria; associated with steppe grasslands..... ***A. chrysopyga* Schenck**
- 194(190) Dorsolateral surface of the propodeum reticulate, with large and shallow punctures (can be small in *A. nuptialis*), clearly contrasting the shagreened and shiny propodeal triangle (Fig. 101A, B), this lacking lateral carinae and becoming shinier on the declivity (often entirely shagreened in *A. nuptialis*). Pronotum lacking lateral keel. Clypeus typically weakly to moderately domed, densely punctate (punctures separated by 1 puncture diameter, with more-or-less pronounced impunctate midline (subgenus *Hoplandrena* Pérez, *partim*)..... **195**
- Without this combination of characters, pronotum keeled or not ..... **201**
- 195 Hind tarsi golden-orange, hind tibiae golden-orange or dark ..... **196**
- Both hind tibiae and tarsi dark..... **197**
- 196 Hind tibiae golden-orange. Clypeus medially with a clear raised longitudinal impunctate area, this area smooth and shining, strongly contrasting the remaining parts of the clypeus which are densely punctate (Fig. 101C).....  
..... ***A. ferox* Smith (*partim*, dark form)**
- Hind tibiae dark. Clypeus with faint impunctate longitudinal line medially, but this is not raised and not shiny, therefore not strongly contrasting the remaining parts of the clypeus which are regularly punctate .....  
..... ***A. bucephala* Stephens**
- 197 A3 clearly exceeding the length of A4+5 ..... **198**
- A3 not clearly exceeding the length of A4+5, usually as long as or slightly shorter than A4+5..... **199**
- 198 Body covered in dark black hairs. Scutum uniformly shagreened, dull. Found at high altitude in mountainous areas of North Macedonia and northern Greece..... ***A. clusia* Warncke**
- Body covered in light brown hairs, at most with some dark brown hairs on the face. Scutum shagreened, but medially with a small circular area with reduced shagreen, this area therefore weakly shining. In the southern Balkans, known only from the Pirin mountain range ..... ***A. nuptialis* Pérez**
- 199 Metasomal terga with short hairs, most clearly seen in profile on T2–3 with hairs not exceeding width of a flagellum. With a very marginal occurrence in the southern Balkans, currently known only from the Black Sea coast of Bulgaria ..... ***A. rosae* Panzer (*partim*, dark form)**
- Metasomal terga with extensive and abundant long hairs, most clearly seen in profile on T2–3 with hairs clearly exceeding width of a flagellum. Widespread throughout the southern Balkans ..... **200**

The following two taxa cannot be confidently separated in the female sex in all cases (see Wood et al. 2022). Indicative characters are given here, but association with concurrently active males and consideration of habitat type and phenology should be made.

- 200 Tibial scopae in fresh specimens composed of dark hairs dorsally and golden hairs ventrally, but this can be ambiguous and fade to silver in older specimens or pinned material. Facial hair light to dark; typically darker in spring-flying individuals and lighter in summer-flying individuals. Bivoltine, usually flying March–May and July–August.....*A. trimmerana* (*partim*, **dark form**)
- Tibial scopae in fresh specimens composed of dark hairs dorsally and silvery hairs ventrally. Face usually with light brown pubescence. Usually univoltine, flying April–mid June, with sporadic emergence in August and September (not yet observed in the southern Balkans).....*A. scotica* **Perkins**
- 201(194) Mesepisternum deeply and distinctly punctate, punctures separated by <1 puncture diameters, with weakly shiny interspaces (Fig. 101D). Pronotum with a distinct or faint humeral angle..... **202**
- Mesepisternum finely to obscurely punctate or completely impunctate, never with deep and distinct punctures. Pronotum variable ..... **203**
- 202 Mesepisternum deeply and distinctly punctate, but dorsolateral parts of the propodeum covered with fine and dense network of rugosity. Clypeus covered with dense hairs in fresh specimens which obscure the underlying surface; below the pubescence, clypeus densely punctate, punctures essentially confluent, without a longitudinal impunctate midline. Ocelloccipital distance exceeding 3 times the diameter of a lateral ocellus. Propodeal triangle finely delineated laterally by raised carinae. Uncertainly recorded from the southern Balkans. Associated with Apiaceae.....*A. incisa* **Eversmann**
- Mesepisternum AND dorsolateral parts of the propodeum deeply and distinctly punctate. Clypeus almost hairless, irregularly punctate with punctures separated by <0.5–2 puncture diameters, with broad impunctate longitudinal midline (Fig. 101E). Ocelloccipital distance 1.5 times the diameter of a lateral ocellus. Propodeal triangle laterally undefined, without raised carinae. Frequent across the southern Balkans. Associated with *Onobrychis* (Fabaceae).....*A. fallax* **Eversmann**
- 203(201) Pronotum laterally keeled or angulate (with a humeral angle), keel or angle runs up dorsally to an angled corner ..... **204**
- Pronotum laterally rounded, without a keel or humeral angle ..... **240**
- 204 Process of the labrum extremely small and triangular, broader than long. Ocelloccipital distance very short, approximately 1/4 of the diameter of a lateral ocellus. Facial foveae very broad, occupying essentially the entire space between the compound eye and a lateral ocellus (Fig. 101F). Tarsi and hind tibiae orange. Found only in Greece, including the East Aegean Islands ..... *A. larisana* **Warncke**
- Without this combination of characters ..... **205**



**Figure 101.** *Andrena (Hoplandrena) nuptialis* Pérez, 1903 female. **A.** Propodeum, dorsal view. *Andrena (Hoplandrena) scotica* Perkins, 1916 female. **B.** Propodeum, dorsal view. *Andrena (Hoplandrena) ferox* Smith, 1847 female. **C.** Clypeus, frontal view. *Andrena (Leimelissa) fallax* Eversmann, 1852 female. **D.** Mesosoma, lateral view detail; **E.** Clypeus, frontal view. *Andrena (incertae sedis) larisana* Warncke, 1965 female. **F.** Head, frontal view.

205      Body with abundant light and dark pubescence; head predominantly white-haired, mesosoma dorsally with light hairs anteriorly and posteriorly separated by a transverse band of black hairs, and metasoma with conspicuous white hair patches laterally on T1–4. Tibial scopae bicoloured, dark dorsally and white ventrally. Large species, 15–16 mm in length ..... *A. fuscocalcarata* Morawitz  
 –      Without this combination of characters ..... 206

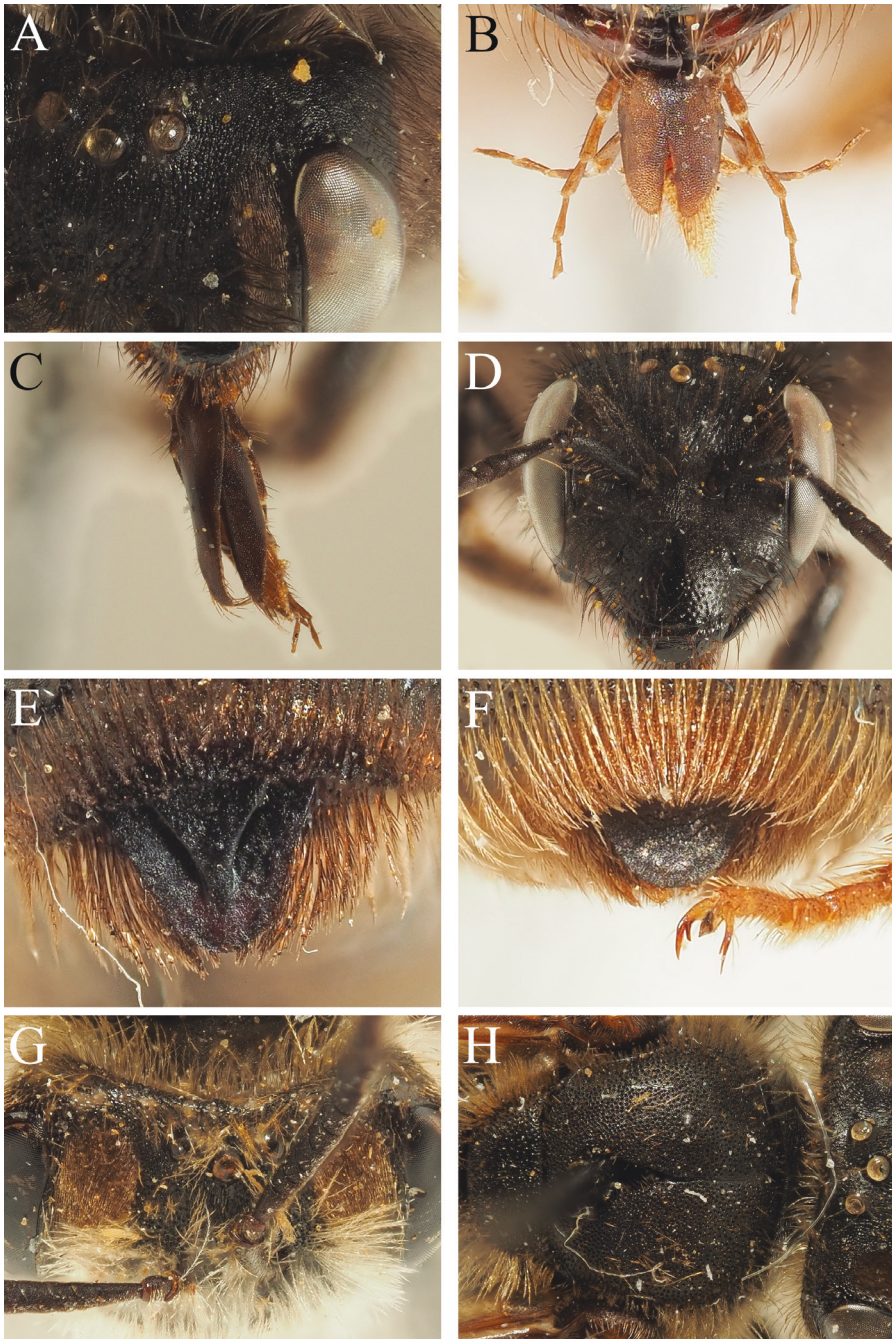
- 206 Scutum and scutellum strongly sculptured with dense granular microreticulation, dull, shallowly and obscurely punctate. Propodeum short, propodeal triangle with uniform granular microreticulation reminiscent of subgenus *Nobandrena* Warncke. Facial foveae broad, occupying the majority of the space between the compound eye and lateral ocellus, separated from the lateral ocellus by a distance subequal to its diameter (see images in Wood 2025a: 216). Process of the labrum trapezoidal. Found only in Greece .....  
 ..... ***A. mistrensis* Grünwaldt**
- Without this combination of characters ..... **207**
- 207 Face extensively black-haired, contrasting the almost entirely pale to light brown hair of the mesosoma. Clypeus elongate, clearly extending below the level of a line drawn between the lower margins of the compound eyes; surface of the clypeus predominantly polished and shining. Propodeum with surface entirely declivous, without differentiated horizontal and vertical parts (see Pisanty and Wood 2024: 456). Associated with *Papaver* (Papaveraceae). Restricted to the East Aegean Islands (Lesbos) ..... ***A. curiosa* (Morawitz)**
- Without this combination of characters ..... **208**
- 208 Facial foveae relatively narrow, occupying 1/5–1/3 of the space between the compound eye and a lateral ocellus (Fig. 102A). Propodeal triangle narrow and barely indicated, laterally without carinae, sculpturally almost identical to the dorsolateral parts of the propodeum (c.f. Fig. 73D). Head and mesepisternum with abundant black pubescence. Scutum shallowly, obscurely, and sparsely punctate, with punctures on the median part of the disc separated by 1–4 puncture diameters. Metasoma ovoid (c.f. Fig. 73F), very sparsely and finely punctate, punctures typically separated by >3 puncture diameters (*crocusella*-group, *partim*) ..... **209**
- Without this combination of characters ..... **211**
- 209 Surface of the galea covered with strong and coarse granular microreticulation, dull (Fig. 102B). Clypeus with dense granular microreticulation, covered with dense large punctures, laterally separated by 0.5–1 puncture diameters, medially with a broad impunctate longitudinal midline, as much as 7–8 puncture diameters wide. Smaller, 8–9 mm in length. Currently known only from southern Romania, including from very close to the Bulgarian border on the Black Sea ..... ***A. dacica* Wood**
- Surface of the galea finely shagreened and shining to moderately shagreened and weakly shining, but never strongly microreticulate and dull (Fig. 102C). Clypeus structurally otherwise, either less densely punctate or with the longitudinal impunctate midline narrower, not exceeding 3 puncture diameters in width. Larger, 10–11 mm in length. Currently known from Greece and North Macedonia ..... **210**
- 210 Facial foveae narrow, occupying 1/4 of the space between the compound eye and a lateral ocellus. Clypeus densely punctate, punctures typically separated by 0.5–1 puncture diameters, with a narrow impunctate median longitudinal line not exceeding 3 puncture diameters at its widest. Head

- wider than long; associated with *Crocus* (Iridaceae) .....  
 ..... ***A. elsei* Scheuchl & Gusenleitner (partim)**
- Facial foveae broader, occupying 1/5–1/3 of the space between the compound eye and a lateral ocellus (Fig. 102A). Clypeus relatively sparsely punctate, punctures typically separated by 1–2 puncture diameters, with broad impunctate median longitudinal line equalling 6–7 puncture diameters at its widest (Fig. 102D). Head rounded, as long as wide; associated with *Muscari* (Asparagaceae) ..... ***A. muscaria* Warncke**
- 211 Pygidial plate flat to weakly convex, outer margin usually somewhat elevated, without clearly raised area medially (Fig. 102F; subgenus *Notandrena* Pérez, partim) ..... **212**
- Pygidial plate with distinctly limited raised area medially (Fig. 102E; beware old specimens where the elevated area may have been abraded) ..... **220**
- 212 Facial foveae very broad, occupying 3/4 of the space between the compound eye and a lateral ocellus, separated from a lateral ocellus by a distance slightly greater than its diameter (Fig. 102G). Tarsi lightened orange. Rare in the southern Balkans, currently known only from Albania ..... ***A. pontica* Warncke**
- Facial foveae narrower, not exceeding 1/2 the space between the compound eye and a lateral ocellus. Tarsi light or dark ..... **213**
- 213 Scutum extremely densely punctate, with the majority of punctures separated by <0.5–0.5 puncture diameters, therefore appearing to be almost confluent (Fig. 102H) ..... **214**
- Scutum with punctures less dense, with some interspaces reaching at least 1–1.5 puncture diameters ..... **215**
- 214 Larger, 10–11 mm. Disc of T1 with puncture density relatively uniform, laterally with punctures separated by 1–2 puncture diameters. Scutellum medially with punctures separated by 1–2 puncture diameters. Tarsi and hind tibiae lightened orange ..... ***A. griseobalteata* Dours**
- Smaller, 7–8 mm. Disc of T1 with punctures becoming sparser laterally, here separated by 3–5 puncture diameters. Scutellum medially with punctures separated by 3–4 puncture diameters. Legs dark ..... ***A. ungeri* Mavromoustakis**
- 215 Hind tibia and all tarsi completely orange. Scutum between the punctures strongly microreticulate and dull, punctures therefore obscure. Uncommonly encountered in the southern Balkans, found in mountainous areas in the north ..... ***A. chrysoceles* (Kirby)**
- Hind tibia black, tarsi may be black or orange. Scutum typically less strongly microreticulate, often partially shining, punctures distinctly visible ..... **216**
- 216 T2–4 with thick white hairbands which obscure the underlying surface (Fig. 33F). Scutum and scutellum densely but somewhat irregularly punctate (Fig. 33D), punctures separated by 0.5–1.5 puncture diameters, surface polished and shining (*meridionalis*-group) ..... **217**
- T2–4 with comparatively weak apical hairbands that do not meaningfully obscure the underlying surface. Scutellum less densely punctate than the

- scutum, punctures separated by 1–5 puncture diameters, surface variably sculptured but not smooth and shining (*nitidiuscula*-group) ..... **218**
- 217 Tergal discs with comparatively sparse punctures, punctures on the discs of T2–4 separated by 1 puncture diameter on average. Metasomal hairbands long and poorly-defined, laterally exceeding the length of the marginal areas and extending onto the base of the following tergum (Figs 33F, 34D). Head with pubescence buffish to light brown (Figs 33C, 34C). Terminal fringe brown. Larger, 10–11 mm. Found in Albania and continental Greece (Fig. 42)..... ***A. meridionalis* Dalla Torre & Friese**
- Tergal discs with comparatively dense punctures, punctures on the discs of T2–4 separated by <0.5–1 puncture diameters. Metasomal hairbands comparatively shorter and well-defined, laterally not exceeding the length of the marginal areas, and only narrowly extending onto the base of the following tergum (Fig. 38F). Head with pubescence white to whitish (Fig. 38C). Terminal fringe pale golden. Smaller, 8–9 mm. Currently known only from Lesbos (Fig. 42) ..... ***A. clanga* Warncke**

The following three species are challenging to separate; Schwenninger (2013) should also be consulted.

- 218 Disc of T2 with extremely dense punctures, punctures separated by <0.5–0.5 puncture diameters ..... ***A. curvana* Warncke**
- Disc of T2 with comparatively slightly sparser punctures, punctures separated by 0.5–1 puncture diameters..... **219**
- 219 Central line in the front 1/2 the scutum strongly impressed. Hind basitarsi and tibiae dark. Univoltine (July–August)..... ***A. nitidiuscula* Schenck**
- Central line in the front 1/2 the scutum only weakly and superficially impressed. Hind basitarsi dark to often entirely lightened orange. hind tibiae sometimes lightened partially orange. Bivoltine, active in the spring and the summer..... ***A. fulvicornis* Schenck**
- 220 Flying exclusively in the summer (July–September). Hind tibiae triangular, clearly much broader apically than basally, with short scopal hairs not greatly exceeding the diameter of a lateral ocellus. Terga with strong and broad apical tergal hair bands (subgenus *Cnemidandrena* Hedicke). ..... **221**
- Flying predominantly in the spring, some species extending into July. Hind tibiae normal, not greatly broader apically than basally, with long scopal hairs, clearly greatly exceeding the diameter of a lateral ocellus. Terga with or without clear apical hair bands ..... **224**
- 221 Outer surface of the galea smooth and shiny. Associated with *Calluna vulgaris* (Ericaceae). Very rare and marginally present in the southern Balkans, probably restricted to high mountains with acidic soils..... ***A. fuscipes* (Kirby)**
- Outer surface of the galea shagreened and dull..... **222**



**Figure 102.** *Andrena* (incertae sedis) *muscaria* Warncke, 1965 female. **A.** Head, lateral part, dorsal view; **C.** Galea, frontal view; **D.** Head, frontal view. *Andrena* (incertae sedis) *dacia* Wood, 2024 female. **B.** Galea, frontal view. *Andrena* (*Leucandrena*) *barbilabris* (Kirby, 1802) female. **E.** Pygidial plate, dorsal view. *Andrena* (*Notandrena*) *griseobalteata* Dours, 1872 female. **F.** Pygidial plate, dorsal view; **H.** Scutum, dorsal view. *Andrena* (*Notandrena*) *pontica* Warncke, 1972 female. **G.** Head, dorsal view.

- 222 Mesosoma anteriorly and posteriorly with pale hairs, medially with abundant black hairs..... ***A. denticulata* (Kirby)**
- Mesosoma with pale to brown hairs, hairs essentially unicolourous, with at most occasional intermixed black hairs ..... **223**
- 223 Clypeus between the punctures shagreened and dull. Facial hair uniformly black. Mesosoma dorsally with bright reddish-brown hairs, mesepisternum with predominantly black hairs. Tibial scopae composed of black hairs..... ***A. nigriceps* (Kirby)**
- Clypeus between the punctures polished and shining. Facial hair predominantly light yellow-brown. Mesosoma with light yellow-brown hairs both dorsally and laterally on the mesepisternum. Tibial scopae composed of dark brown hairs.....***A. simillima* ssp. *sischkai* Warncke**
- 224 Process of the labrum either elongate (as long as or slightly longer than broad) or pointed triangular, never medially emarginate (subgenus *Leucandrena* Hedicke) ..... **225**
- Process of the labrum trapezoidal, always broader than long, usually medially emarginate, at least weakly (subgenus *Andrena* s. str.) ..... **229**

Comparative images of the process of the labrum were provided by Wood (2023b: 412).

- 225 Scutum and scutellum shagreened, dull. Process of labrum as long as broad, evenly rounded apically.....***A. barbilabris* (Kirby)**
- At least some part of the scutum or scutellum shiny. Process of labrum either pointed triangular or apically truncate, not evenly rounded apically ..... **226**
- 226 Process of labrum pointed triangular..... ***A. sericata* Imhoff**
- Process of labrum apically truncate, not pointed ..... **227**
- 227 Terga clearly finely and densely punctured, punctures separated by 1–2 puncture diameters, visible against weakly shagreened integument..... ***A. argentata* Smith**
- Terga with punctures sparse and difficult to see, separated by 3–5 puncture diameters ..... **228**
- 228 Process of labrum comparatively large, apex more rounded. Fovea, viewed dorsally, with dark brown hairs. Terminal fringe dark brown. Larger, 10–11 mm..... ***A. parviceps* Kriechbaumer**
- Process of labrum comparatively small, more clearly truncate. Fovea, viewed dorsally, with light brown hairs. Terminal fringe golden. Smaller, 7–9 mm.....***A. ventralis* Imhoff**
- 229 Terga densely covered with long hairs, in fresh specimens these obscuring the underlying surface. Face entirely black-haired ..... **230**
- Terga less thickly haired, sometimes with hair tufts on T1–2, but these not obscuring the underlying surface. Pubescence of face variable ..... **233**

- 230 Hind tibiae and basitarsi orange. Terga extensively black-haired, at least on T3–4 and often on all terga ..... **231**
- Hind tibiae and basitarsi dark. Tergal pubescence never predominantly black, either reddish-orange or grey ..... **232**
- 231 All terga covered with black hairs, at most with a few golden brown hairs at the base of T1. Mesosoma dorsally with rich chestnut brown hairs .....  
..... ***A. clarkella* (Kirby)**
- Terga with T1–2 covered with bright yellow-orange hairs, strongly contrasting T3–4 which are covered with black hairs. Dorsal surface of mesosoma covered with the same bright yellow-orange hairs..... ***A. inconstans* Morawitz**
- 232 Process of labrum trapezoidal. T1–5 with extensive reddish-orange pubescence. Mesepisternum with abundant black pubescence, strongly contrasting the reddish-orange pubescence of the dorsal part of the mesosoma .....  
..... ***A. fulva* (Müller)**
- Process of labrum triangular. T1–3 or sometimes T1–5 grey-haired. Mesepisternum predominantly grey-haired, not strongly contrasting the pubescence of the dorsal part of the mesosoma ..... ***A. nycthemera* Imhoff**
- 233 Face with entirely pale hairs, at most with a few scattered dark hairs along the inner margin of the compound eye ..... **234**
- Face with extensive black hairs, particularly around the antennal insertions and along the inner margin of the compound eye ..... **237**
- 234 Tibial scopa dorsally with abundant dark hairs, ventrally with white hairs .....  
..... ***A. varians* (Kirby) (*partim*, light form)**
- Tibial scopa with uniformly light hairs, whitish or golden. If some dark hairs are present on the dorsal side of the tibial scopae, then terga without dense hair tufts on T1–2 ..... **235**
- 235 Terga sparsely haired, with at most weak hair tufts on T1–2. Terga finely shagreened and thus weakly shining. Flying later in the year (June–August), associated with shrubs, particularly *Rubus* (Rosaceae)..... ***A. fucata* Smith**
- Terga typically with long hairs, in fresh specimens with clear and dense hair tufts on T1–2. Abraded or older specimens may lack such hair tufts, in which case use the following characters: Terga strongly shagreened, dull. Flying earlier in the year (March–May), associated with flowering trees ..... **236**
- 236 Basitarsus of hind tibia parallel sided, not converging apically.....  
..... ***A. helvola* (Linnaeus)**
- Basitarsus of hind tibia broader basally, narrower apically, therefore converging apically ..... ***A. mitis* Schmiedeknecht**
- 237 Face entirely black-haired, without any pale hairs. Terga basally (T1–2) with orange-brown hairs, apically (T3–4) with extensive and strongly contrasting black hairs. Species not typically associated with *Salix* (Salicaceae) ..... **238**
- Face with at least some pale hairs, particularly around the antennal insertions. Terga without extensive areas with black hairs, generally with mixture of predominantly yellowish to brownish hairs on T1–4. Species associated with *Salix* (Salicaceae) ..... **239**

- 238 Terga with orange-brown hairs on T1–2 denser and more extensive. Clypeus apically with small and narrow shiny impunctate longitudinal area. Associated with flowering trees, typically *Prunus* (Rosaceae) ..... ***A. varians* (Kirby) (*partim*, dark form)**
- Terga with orange-brown hairs on T1–2 sparse. Clypeus apically with shiny impunctate area larger, longer and broader. Associated with *Vaccinium* (Ericaceae), and restricted to mountainous areas in the southern Balkans.. ..... ***A. lapponica* Zetterstedt**
- 239 Smaller, 10–11 mm. Clypeus predominantly shagreened and dull, with only the surface of the narrow longitudinal impunctate midline weakly shiny. Terminal fringe dark brown.....***A. praecox* (Scopoli)**
- Larger, 11–14 mm. Clypeus comparatively shinier, only laterally shagreened and dull, apicomediaally broadly shiny adjacent to the comparatively broader longitudinal impunctate midline. Terminal fringe black .....***A. apicata* Smith**
- 240(203) Large species (over 12 mm in length). Typically with abundant black, brown, and/or white pubescence. Clypeus strongly domed. Ocelloccipital distance long, at least 2 times the diameter of a lateral ocellus. Facial foveae very broad, occupying almost the entire space between the compound eye and lateral ocellus (subgenus *Melandrena* Pérez, *partim*)..... **241**
- Without this combination of characters ..... **252**
- 241 Tergal discs T1–3(4) with upstanding mixture of short pale whitish to light brown hairs extending over both disc and marginal areas. Tibial scopae orange-red. Terga sometimes with greasy-bronzy metallic reflections..... ***A. nigroaenea* (Kirby)**
- Tergal discs never with this sort of pubescence, sometimes with white to brownish pubescence in basolateral corners of tergal discs, never extending onto marginal areas. Tibial scopae entirely black or a combination of black and white, never orange-red. Terga dark, without metallic reflections.....**242**
- 242 Mesosoma with entirely black (Fig. 30B) or mixture of black and white hairs, never with only brown or grey hairs..... **243**
- Mesosoma with entirely grey or entirely brown hairs..... **246**
- 243 Terminal fringe entirely composed of orange hairs, never with abundant black or dark brown hairs (Fig. 30D).....***A. pyropygia* Kriechbaumer**
- Terminal fringe composed of black to dark brown hairs ..... **244**
- 244 Tergal discs finely and densely punctate, punctures on discs of T2–3 separated by an average of 1 puncture diameter. T2–4 laterally with distinct white patches of pubescence..... ***A. albopunctata* (Rossi)**
- Tergal discs sparsely punctate, punctures separated by 2–3 puncture diameters. Terga with or without lateral white hair patches. If tergal punctures appear dense, then never with more than obscure greyish hairs laterally, not forming distinct hair patches..... **245**

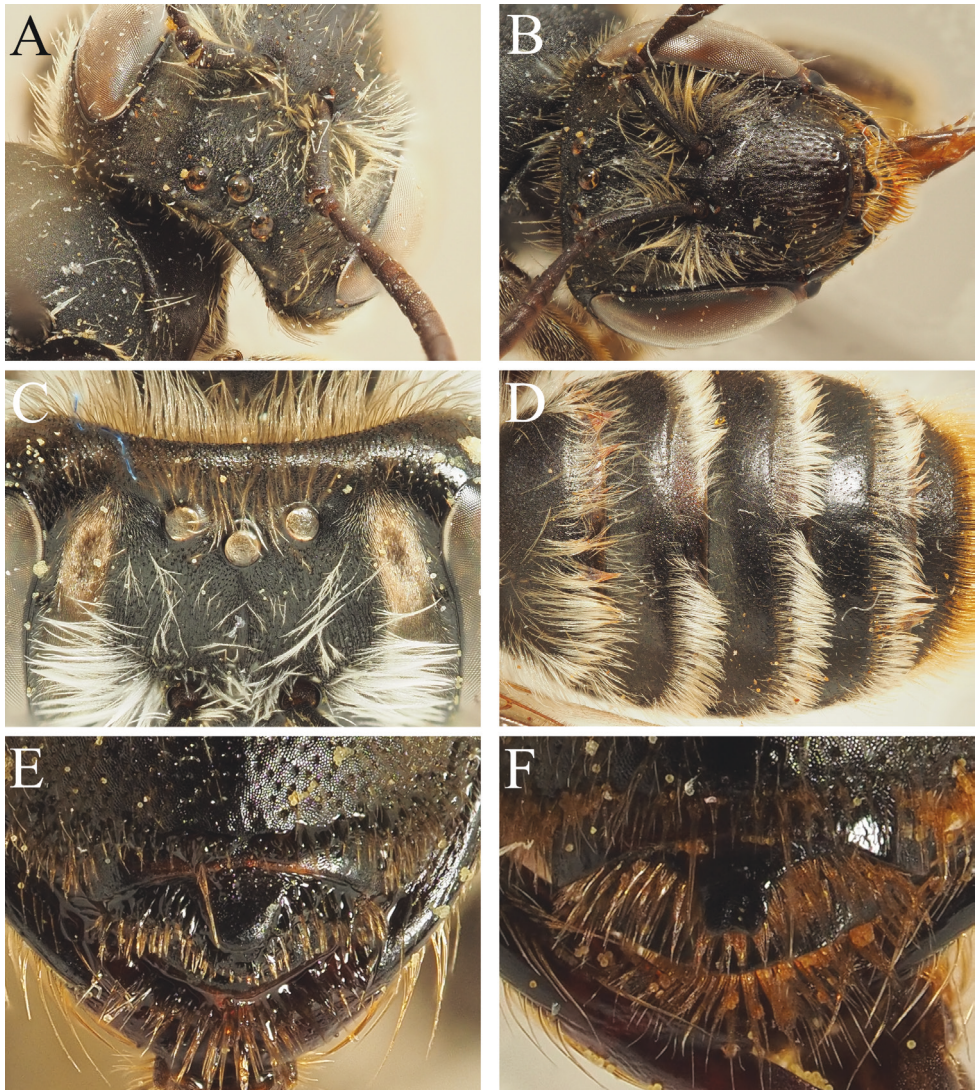
There may be taxonomic complexity inside *A. morio* Brullé (Wood 2023b); morphological and genetic variation remains high, and additional detailed study is required.

- 245 Metasoma laterally at most with obscure greyish hairs, not forming distinct hair patches. Mesosoma often with white hairs anteriorly or posteriorly, but can also be entirely black-haired. Tibial scopae composed of black hairs. Widespread in the southern Balkans ..... ***A. morio* Brullé**
- T2–4 laterally with distinct white patches of pubescence. Mesosoma always entirely black-haired. Tibial scopae composed of light whitish-brown hairs. Uncommon, seemingly favouring coastal habitats in Greece and eastern Bulgaria (near the Black Sea).....***A. magna* Warncke**
- 246 Mesosoma entirely grey-haired, without black hairs. Area between disc and marginal area of T1 with several longitudinal impressions. Typically flying in the spring (March–April) in temperate areas and associated with *Salix* (Salicaceae) .....***A. vaga* Panzer**
- Mesosoma never entirely grey-haired, hairs light to dark brown. Flight period variable, but often active during the summer ..... **247**
- 247 T2–4 apically with distinct lateral hair patches present, patches composed of light brown hairs and distinctly present on the marginal areas. Tibial scopae composed of light brown hairs.....***A. quadrimaculata* Friese**
- Terga without apical hair patches or bands, hairs when present found at the base of the tergal discs, most prominently at the base of T2. Tibial scopae variable, composed of light, dark, or intermixed light and dark hairs .....**248**
- 248 Disc of T1 shagreened and barely punctate, punctures scattered and obscure against the underlying sculpture.....***A. assimilis* Radoszkowski**
- Disc of T1 polished and shiny, strongly punctate, punctures clearly visible against the underlying sculpture (*nitida*-group)..... **249**
- 249 Tibial scopae composed of light rusty-yellow hairs. Disc of T1 with comparatively large and coarse punctures, these 1.5 times larger than those in the comparison species. Scutum medially polished and shining. Found only on the East Aegean Islands .....***A. nitidemula* Scheuchl & Hazir**
- Tibial scopae composed of entirely or partially dark hairs, never composed of entirely light rusty-yellow hairs. Disc of T1 with comparatively fine punctures. Scutum medially microreticulate and dull..... **250**

The following three species are challenging to separate morphologically, and further study of the species boundaries in the *nitida*-group is necessary.

- 250 Tibial scopae bicoloured, black dorsally and white ventrally. Mesosoma dorsally with bright orange-brown pubescence, laterally with pale pubescence, never with black hairs on the mesepisternum. Face typically with contrasting pubescence, predominantly pale with black hairs along the inner margins of the compound eyes. Univoltine, flying April–June. Found in northern temperate parts of the southern Balkans, southern range extent unclear.....***A. nitida* (Müller)**
- Tibial scopae entirely black. Mesosoma dorsally usually with the pubescence darker, laterally with pubescence never pale, usually with abundant

- black hairs, at most with pubescence of the mesepisternum brown. Facial pubescence usually uniformly dark, dark brown to black. Bivoltine, flying from March–August. Widespread ..... **251**
- 251 Disc of T1 with punctures comparatively sparse, separated by 2 puncture diameters ..... ***A. thoracica* (Kirby)**
- Disc of T1 with punctures dense, punctures separated by up to 1 puncture diameter, often separated by less ..... ***A. limata* Smith**
- 252(240) Tergal discs finely microreticulate, with very widely scattered punctures or appearing impunctate; tergal discs with surface largely hairless. Marginal areas of T2–4 slightly but distinctly depressed (e.g. Fig. 103D). Propodeum with dorsal part slightly elongate (longer than broad), propodeal triangle slightly elevated, distinctly and densely covered with fine granular microreticulation. Head slightly to distinctly elongate (subgenus *Nobandrena* Warncke) ..... **253**
- Combination of characters otherwise ..... **257**
- 253 Small species, not exceeding 10 mm in length. Facial foveae broad, occupying majority of space between compound eye and lateral ocellus, separated from lateral ocellus by a distance subequal to its diameter (Fig. 103A). Clypeus microreticulate and dull over 80% of its length, polished and shining along its apical margin, clypeal punctures slightly longitudinally elongate due to presence of obscure longitudinal grooves or faint striations (Fig. 103B) ..... ***A. anatolica* Alfken**
- Larger, at least 13 mm in length. Facial foveae narrower, separated from the lateral ocellus by a distance exceeding its diameter (Fig. 103C). Clypeus evenly microreticulate across its entire surface, punctures not appearing elongate. .... **254**
- 254 Disc of T1 with long shaggy whitish-buff hairs. T2–4 with long shaggy apical hairbands which substantially extend onto the disc of the subsequent tergum, complete on T3–4 (Fig. 103D). Mesosoma dorsally with long and dense golden-brown hairs, laterally with long whitish hairs ..... ***A. flavobila* Warncke**
- Disc of T1 with at most short hairs laterally. T2–4 with short narrow apical hairbands which comparatively only extend weakly onto the disc of the subsequent tergum, interrupted on T3–4. Mesosoma dorsally and laterally with sparse greyish-white hairs ..... **255**
- 255 Clypeus irregularly punctate, punctures laterally separated by 0.5–1 puncture diameters, medially separated by up to 6 puncture diameters. Ocellocipital distance equalling the diameter of a lateral ocellus. Found in mountainous areas at elevations typically exceeding 1000 m ..... ***A. probata* Warncke**
- Clypeus finely and mostly regularly punctate, punctures separated by 0.5–1.5 puncture diameters, with hints of an impunctate longitudinal line medially. Ocellocipital distance 1.5–2 times the diameter of a lateral ocellus. Widespread across the southern Balkans typically at low to moderate altitudes ..... **256**



**Figure 103.** *Andrena (Nobandrena) anatolica* Alfken, 1935 female. **A.** Head, dorsal view; **B.** Head, frontal view. *Andrena (Nobandrena) nobilis* Morawitz, 1873 female. **C.** Head, dorsal view; **E.** Process of the labrum, frontal view. *Andrena (Nobandrena) flavobila* Warncke, 1965 female. **D.** Metasoma, dorsal view. *Andrena (Nobandrena) athenensis* Warncke, 1965 female. **F.** Process of the labrum, frontal view.

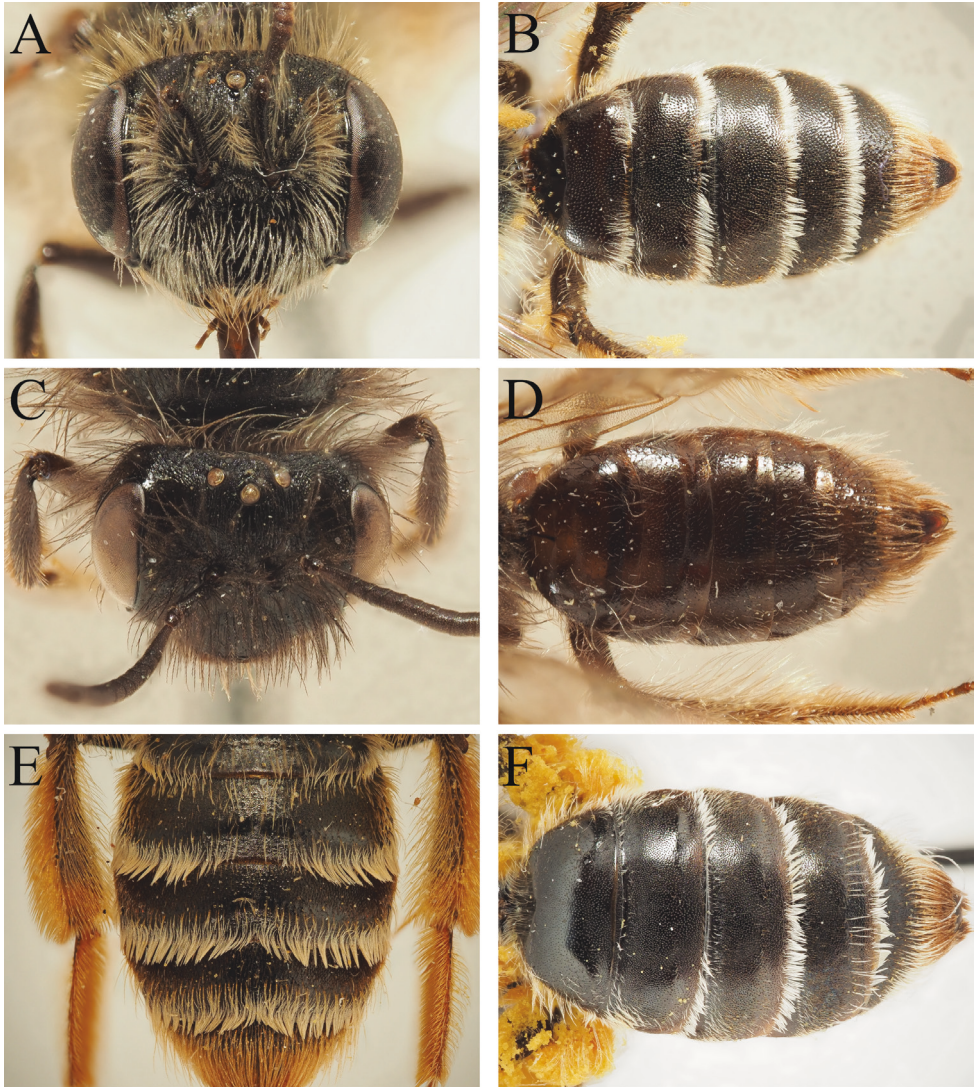
- 256 Process of the labrum evenly rounded triangular (Fig. 103E). Facial foveae relatively narrow, only slightly exceeding the width of a flagellum ..... *A. nobilis* Morawitz
- Process of the labrum distinctly not triangular, apically truncate (sometimes very shallowly emarginate) and parallel-sided before broadening basally (Fig. 103F). Facial foveae relatively broad, clearly exceeding the width of a flagellum ..... *A. athenensis* Warncke

- 257(252) Head clearly longer than broad. Terga smooth and shiny, T2–T4 with dense apical hairbands composed of snow-white hairs, bands continuous on T3 and T4, obscuring the underlying surface. Hind tibiae orange. Associated with *Asparagus* (Asparagaceae).....***A. chrysopus* Pérez (*partim*)**
- Combination of characters otherwise ..... **258**
- 258(257) Propodeum covered with long abundant pubescence, no meaningful difference between hairs of the dorsal fringe of the propodeal corbícula and those on the dorsal surface of the propodeum. Process of the labrum usually trapezoidal, broader than long, with or without an emarginate front margin. If unclear, then dorsolateral surfaces of the propodeum clearly and coarsely punctate. Terminal fringe from light brown to dark brown or almost black (subgenus *Truncandrena* Warncke, *partim*)..... **259**
- Remaining species..... **270**
- 259 Face entirely black-haired (Figs 56C, 57C). Hind tibiae and tarsi strongly to obscurely lightened orange (Fig. 56B)..... **260**
- Face not entirely black haired, either with entirely light pubescence or with black hairs restricted to the inner margins of the compound eyes. Hind tibiae and tarsi variably coloured, dark or lightened orange..... **261**
- 260 Metasoma with complete apical hairbands on T2–4 (Figs 56D, 57D). Hind tibiae and tarsi strongly lightened orange. Seemingly found in most parts of the southern Balkans (Fig. 58).....***A. tscheki* ssp. *tritica* Warncke**
- Metasoma with complete apical hairbands only on T2–3. Hind tibiae and tarsi usually strongly but sometimes obscurely lightened orange. Seemingly found in cooler, temperate parts of the southern Balkans (Fig. 58).....  
.....***A. tscheki* Morawitz s. str.**
- 261 Face with abundant black hairs laterally along the inner margins of the compound eyes. Associated with *Papaver* (Papaveraceae)..... **262**
- Face with predominantly pale pubescence, at most with some dark brown hairs laterally on the frons..... **263**
- 262 Process of the labrum comparatively narrower, only slightly broader than long. Terga with poorly defined apical hairbands, these loose and shaggy, partially blending into the long light brown hairs on the tergal discs. Disc of T2 with fine hair-bearing punctures relatively dense, typically separated by 1–2 puncture diameters.....***A. canaeae* Warncke**
- Process of the labrum weakly trapezoidal, as or slightly more than twice as broad as long. Terga with comparatively well-defined apical hairbands, these covering the marginal areas and not blending into the dark hairs on the tergal discs. Disc of T2 with fine hair-bearing punctures more scattered, typically separated by 3–4 puncture diameters..... ***A. serraticornis* Warncke**
- 263 Head and mesosoma with distinctly whitish to greyish pubescence. Tibial scopae composed of white hairs. Hind legs always dark..... **264**
- Head and mesosoma with distinctly brown pubescence, varying from pale light brown to rich orange brown, present at least on the dorsal surface of the mesosoma. Tibial scopae composed of dark brown, buff, light

- 264
266
 brownish, or orange hairs. Hind legs variably coloured, including sometimes lightened orange. Associated with Brassicaceae .....
- 264
265
 Terminal fringe whitish to buffish-white. Tergal segments with loose apical hairbands, those on T3–4 clearly exceeding the marginal areas and extending onto the base of the following tergum. Process of the labrum trapezoidal, slightly longer than wide, apically truncate. Currently known only from Lesbos ..... ***A. aff derbentina* Morawitz**
- 265
 Terminal fringe dark brown. Tergal segments with narrow apical hairbands, barely exceeding the length of the marginal areas. Process of the labrum otherwise, either apically rounded or clearly broader than long .....
- 265
265
 Process of the labrum evenly rounded, only slightly broader than long. Clypeus relatively sparsely haired, punctures obscure basally but becoming strongly and densely punctate in apical 1/2, punctures here separated by 0.5–1 puncture diameters, remaining clearly visible. Slightly larger, around 13 mm in length. Currently known from north-eastern Greece (Thrace) and the East Aegean Islands ..... ***A. rotundilabris* Morawitz**
- 266
 Process of the labrum rectangular, 3 times wider than long. Clypeus densely pubescent, surface with dense network of latitudinal wrinkles interspersed with punctures, punctures disappearing into this sculpture, obscure. Slightly smaller, around 10–11 mm in length, restricted to the East Aegean Islands (Chios) ..... ***A. ulula* Warncke**
- 266
267
 Head short, in frontal view clearly wider than long. Smaller, up to 10 mm in length but typically not exceeding 9 mm. Rare in the southern Balkans, restricted to the East Aegean Islands ..... ***A. fuligula* Warncke**
- 267
 Head long, in frontal view either round (as or almost as long as wide) or appearing longer than wide. Slightly larger, 11–13 mm in length. Generally widespread across the southern Balkans .....
- 267
268
 Head and mesosoma with rich orange-brown pubescence. Apices of mid tibiae, entirety of hind tibiae and all tarsi lightened orange. Tibial scopae composed of loose orange hairs. Metasoma with strong and clearly defined apical hairbands on T2–4 (Fig. 84D) ..... ***A. delphiensis* Warncke**
- 268
 Head and mesosoma with light brownish pubescence, becoming whitish on the mesepisternum. Hind tibiae and tarsi sometimes obscurely lightened orange, otherwise dark. Hind tibiae composed of tightly bound light to dark brown hairs. Metasoma with apical hairbands weakly to moderately defined, never so strongly contrasting .....
- 268
269
 Head elongate, 1.1 times longer than broad, apex of the clypeus clearly projecting far beyond a line drawn between the lower margins of the compound eyes. Tibial scopae composed of dark brown hairs .....
- 269
 ..... ***A. optata* Warncke**
- 269
 Head less strongly elongate, at most as long as broad, apex of the clypeus only slightly projecting beyond a line drawn between the lower margins of the compound eyes. Tibial scopae composed of light brown hairs .....

- 269 Apex of the clypeus with distinct rivulets or longitudinal wrinkles, giving it an irregular appearance. Terga with short hairs on the disc and at the junction between the marginal area and the disc, terga not appearing shaggily haired ..... ***A. truncatilabris* Morawitz**
- Apex of the clypeus with at most obscure sculpturing, consistent with the sculpture of the remaining parts of the clypeus. Terga with long hairs on the disc and at the junction between the marginal area and the disc, giving the metasoma the appearance of being shaggily haired .....  
..... ***A. schmiedeknechti* Magretti**
- 270(258) Propodeum with surface almost entirely declivous, without differentiated horizontal and vertical parts (Fig. 50F). Clypeus weakly domed, finely shagreened and weakly shining, with a broad impunctate longitudinal midline (Fig. 50C). Facial foveae noticeably depressed in their upper part (Fig. 50D). T1 polished and shining, discs of T2–4 finely shagreened. Marginal areas of T1–4 slightly depressed, lightened hyaline yellow-brown. A3 slightly exceeding A4+5 (Fig. 50C). Known only from the Galičica Planina mountain in south-western North Macedonia at an altitude of around 1800 m. Associated with *Lonicera* (Caprifoliaceae) ..... ***A. lonicera* Warncke**
- Without this combination of characters; propodeum never so declivous, facial foveae not typically depressed, antennal ratio variable, distribution otherwise ..... **271**
- 271 Process of the labrum large, as long as broad, apically rounded, ventral surface covered with latitudinal wrinkles (Fig. 92C). Fovea narrow, occupying slightly less than 1/2 the space between the compound eye and the lateral ocellus. Associated with *Muscari* (Asparagaceae) .....  
..... ***A. mucida* Kriechbaumer (*partim*, 1<sup>st</sup> generation)**
- Without this combination of characters; never with the process of the labrum this large and latitudinally wrinkled..... **272**
- 272 Head short and broad, 1.4 times wider than long (Fig. 104A). Clypeus broadly flattened medially, irregularly punctate with punctures separated by <0.5–2 puncture diameters, with variably and sometimes weakly indicated impunctate longitudinal midline. Process of the labrum rounded rectangular, 3 times wider than long. Propodeum with horizontal part very short, propodeal triangle very narrow and weakly differentiated from adjacent dorsolateral parts of the propodeum. Terga strongly and densely punctate, most punctures separated by <1 puncture diameter (Fig. 104B). Restricted to the East Aegean Islands (Lesbos) ..... ***A. monacha* Warncke**
- Without this combination of characters ..... **273**
- 273 Head, mesepisternum, and propodeum with abundant black pubescence. Head short and broad, 1.4 times wider than long. Facial foveae relatively short and broad, occupying 1/2 the space between the compound eye and lateral ocellus and barely reaching the upper margin of the antennal insertions; foveae filled with black hairs (Fig. 104C). Propodeal triangle relatively

- coarsely delineated, internal surface slightly depressed and covered in more strongly raised internal rugae. Terga sparsely and inconspicuously punctate, punctures separated by 2–4 puncture diameters (Fig. 104D) ..... *A. canohirta* (Friese)
- Without this combination of characters ..... 274
- 274 Terga sparsely and obscurely punctate, punctures blending into the underlying microsculpture, surface shagreened and at most weakly shining (Fig. 104E). Marginal areas of T1–4 with long pale brownish hairs, these forming largely complete hairbands which extend from the marginal areas onto the base of the following tergum; hairbands appearing uneven. Mid and hind basitarsi often lightened orange. Restricted to mountainous areas in continental Greece above 900 m in altitude (Fig. 81)..... *A. ranuncolorum* Morawitz
- Terga strongly and distinctly punctate, punctures separated by up to 2 puncture diameters but often by <1 puncture diameter, at least on the tergal discs medially; interspaces strongly to weakly shining (e.g. Fig. 104F). Terga with narrow apical hairbands composed of white hairs, less strongly extending onto the base of the following tergum and appearing more uniform in length. Mid and hind basitarsi always dark. Distribution variable, typically lowland species ..... 275
- 275 Scutum variably punctate, laterally with punctures separated by 1 puncture diameter, becoming sparser medially where punctures are separated by 1–3 puncture diameters. Surface of the scutum shagreened and dull laterally, shagreen weakening medially and on the scutellum, here shiny. Terga with extremely fine and dense punctures, punctures almost confluent (Fig. 104F). Very rare, known only from a single specimen from central Greece (Larisa) ..... *A. urdula* Warncke
- Scutum densely and uniformly punctate, punctures separated by at most 1.5 puncture diameters. Sculpture of scutum and scutellum variable, but uniform within individual species, not weakening medially. Terga variably punctate, but typically either not so finely or densely punctate. More widespread and frequently encountered..... 276
- 276 Propodeal triangle lacking raised carinae laterally, with internal surface covered with fine network of raised reticulation. Terga comparatively sparsely punctate, punctures on the tergal discs separated on average by 1–1.5 puncture diameters. In fresh specimens, with rich to light brown pubescence on the mesosomal dorsum, becoming pale ventrally..... *A. hypopolia* Schmiedeknecht
- Propodeal triangle laterally clearly defined by fine narrow raised carinae, internal surface covered with a dense network of raised rugae. Tergal punctures very dense, separated by <0.5–1 puncture diameters, punctures densest medially. In fresh specimens with mesosomal pubescence always pale (subgenus *Cordandrena* Warncke) ..... 277



**Figure 104.** *Andrena* (incertae sedis) *monacha* Warncke, 1965 female. **A.** Head, frontal view; **B.** Metasoma, dorsal view. *Andrena* (?*Avandrena*) *canohirta* (Fries, 1923) female. **C.** Head, dorso-frontal view; **D.** Metasoma, dorsal view. *Andrena* (incertae sedis) *ranunculorum* Morawitz, 1877 female. **E.** Metasoma, dorsal view. *Andrena* (incertae sedis) *urdula* Warncke, 1965 female. **F.** Metasoma, dorsal view.

The two following species are very difficult to separate in the female sex without contextual information. Association with the distinctive males should be made, and also consideration of the non-overlapping distributional ranges.

277      Widespread in the southern Balkans, but with a northern bias; rare in continental Greece and not found on the islands based on currently available

information. Scutum densely punctate, punctures separated by 0.5–1 puncture diameters over the majority of its surface, surface microreticulate and dull. Clypeus between punctures and wrinkles microreticulate and predominantly dull ..... ***A. cordialis* Morawitz**

- Found on Crete and the East Aegean Islands (Rhodes). Scutum slightly less densely punctate, punctures separated by 0.5–1.5 puncture diameters, underlying surface finely shagreened and comparatively more strongly shining. Clypeus between punctures and wrinkles shagreened and weakly but distinctly shining ..... ***A. torda* Warncke**

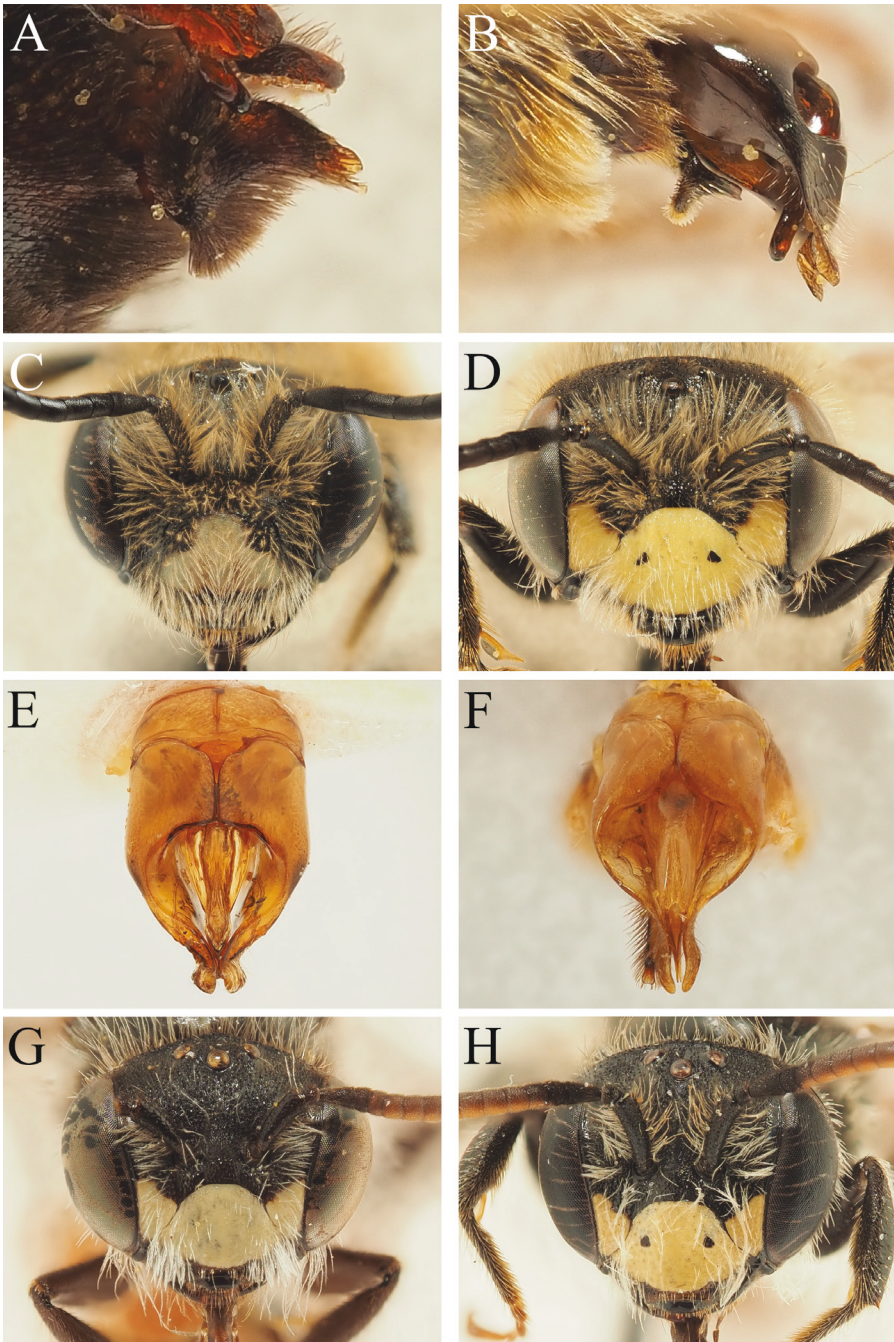
## Males

For the male key, the following shortcuts can be used:

- A Clypeus at least partly yellow-marked; the marking may be reduced to a small area medially or apically ..... **go to 2**
- B Mesepisternum conspicuously and densely punctate (punctures separated by 0.5 puncture diameters) AND ocelloccipital distance at least 3 times the diameter of a lateral ocellus (*incisa*-group) ..... **go to 91**
- C Propodeal triangle clearly defined by strongly raised carinae, internal surface rugose-areolate ..... **go to 93**
- D Genital capsule distinctive, with more-or-less 90° emargination in the outer parts of the gonostyli. The most common *Andrena* species in the southern Balkans ..... **go to *Andrena flavipes* Panzer**
- E Process of the labrum thickened and expanded, anteriorly projecting beyond the fore margin of the clypeus. Pronotum with strong humeral angle. Active in the summer (mid-June to September) (subgenus *Cnemidandrena* Hedicke and remaining *Margandrena* Warncke) ..... **go to 101**
- F Fore margin of clypeus upturned AND gena conspicuously broadened, wider than the width of the compound eye AND pronotum with a conspicuous humeral angle (remaining *Notandrena* Pérez) ..... **go to 106**
- G Small species, body length of 5–7 mm (exceptionally 8 mm), terga always dark (*Aenandrena* Warncke *partim*, *Avandrena* Warncke, *Cryptandrena* Warncke *partim*, *Graecandrena* Warncke, and almost all *Micrandrena* Ashmead) ..... **go to 110**
- H Clypeus flattened over majority of its surface (subgenus *Taeniandrena* Hedicke, subgenus *Troandrena* Warncke) ..... **go to 157**
- I At least some tergal discs red-marked ..... **go to 167**
- J Tergal discs with distinct metallic blue reflections ..... **go to 172**
- K Mandibles elongate, sickle-like, strongly crossing apically. Pronotum with strong humeral angle. Gena often expanded, broader than the width of a compound eye ..... **go to 176**

- L Ventral surface of A4–13 distinctly covered in a layer of shining scales, distinctly contrasting the surface of A3 which is dull (*Chrysandrena* Hedicke, *Cordandrena* Warncke, *numida*-group)..... **go to 203**
- M Measured along its ventral margin, A3 twice as long as A4..... **go to 211**
- N Measured along its ventral margin, A3 shorter than or as long as A4. If in doubt, then ocellocipital distance long, at least 2 times the diameter of a lateral ocellus ..... **go to 234**
- O Remaining species; measured along its ventral margin, A3 slightly longer than A4. Ocellocipital distance not exceeding the diameter of a lateral ocellus..... **go to 254**
- 1 Clypeus at least partly white, creamy-white, or yellow-marked; the marking may be reduced to a small area medially or apically (e.g. Figs 2D, 43C, 105C, D, 105G, H, 109A, 111D–F, 112A)..... **2**
- Clypeus always entirely dark, without any pale markings anywhere on its surface ..... **90**
- 2(1) Tergal margins with a strong latitudinal trench-like depressions, these depressions filled with short yellowish squamous hairs (c.f. Fig. 3D). Scutum with short squamous to sub-squamous yellowish hairs. Mesepisternum and dorsolateral parts of propodeum densely and deeply punctate, punctures separated by <0.5 puncture diameters. Ocellocipital distance long, exceeding 3 times the diameter of a lateral ocellus..... **A. erberi Morawitz**
- Without this combination of characters; tergal margins always flat, at most slightly depressed relative to the tergal discs ..... **3**
- 3 Mid leg with the tibial spur distinctive, apically bent almost 90° (c.f. Fig. 86E). Hind tibial spurs both apically hooked (c.f. Fig. 86F). Lower paraocular areas dark. Found on the East Aegean Islands (Lesbos) ..... **A. eburnea Warncke**
- Without this combination of characters; mid and hind tibial spurs never distinctly hooked apically. Paraocular areas with light markings or dark.. **4**
- 4 Propodeum almost entirely declivous, without clearly differentiated horizontal and vertical parts, or the division between these two areas ambiguous. Propodeum with dorsolateral parts adjacent to the propodeal triangle densely and deeply punctate, punctures separated by <0.5–2 puncture diameters (e.g. Fig. 90A). Inner hind tibial spur slightly broadened submedially (subgenera *Scitandrena* Warncke and *Holandrena* Pérez) or not (subgenus *Leimelissa* Osytshnjuk) ..... **5**
- Propodeum with either clearly differentiated horizontal and vertical parts, or if without such areas, then the dorsolateral parts of the propodeum without dense and deep punctures. Hind tibial spur variable ..... **11**
- 5 Propodeum and mesepisternum almost entirely polished and shining, punctures separated by 0.5–2 puncture diameters, interspaces brightly shining. Clypeus yellow-marked, lower paraocular areas variable from entirely dark

- to with small pale markings close to the mandibular bases. Inner hind tibial spur parallel-sided ..... ***A. fallax* Eversmann**
- Propodeum and mesepisternum more densely punctate, punctures separated by <0.5 to 0.5–1 puncture diameter, interspaces dull to obscurely shining (Fig. 90A). Pale facial markings variable. Inner hind tibial spur slightly broadened submedially (subgenera *Scitandrena* Warncke and *Holandrena* Pérez) .... **6**
- 6 Disc of T2 usually entirely red-marked, sometimes with red markings restricted to the lateral parts of the segment; red markings often present also on T1 and T3. Head relatively narrow, appearing rounded. S8 large, rectangular with weak lateral projections, and with an upstanding plate covered with abundant dark hairs (Fig. 105A). Small rounded yellow markings present on the lower paraocular area, not reaching to the upper margin of the clypeus ..... ***A. scita* Eversmann**
- Disc of T2 usually entirely dark, but can be red- to reddish-brown-marked (*A. forsterella*). Head broad, clearly wider than long. S8 small, with pale hairs, often but not always with a lamellate ventral projection of variable length (Figs 27B, 105B). Pale facial markings variable in extent, typically either absent from the lower paraocular areas OR present, large, and dorsally extending to more-or-less the upper margin of the clypeus (Fig. 105C, D; subgenus *Holandrena* Pérez) ..... **7**
- 7 Vertex wide, ocelloccipital distance at least as wide as 3 times the diameter of a lateral ocellus (c.f. Fig. 90C) ..... ***A. variabilis* Smith**
- Vertex variable in width, but not exceeding twice the diameter of a lateral ocellus (c.f. Fig. 90D) ..... **8**
- 8 Clypeus with the pale marking almost whitish, reduced in size, often not reaching the lateral and apical margins and forming an inverted “T” shape (Fig. 105C). Surface of the clypeus very shallowly and obscurely punctate, punctures disappearing into the underlying dull microsculpture, difficult to see against the median yellow colouration. Fore margin of the clypeus not upturned ..... ***A. fimbriata* Brullé**
- Clypeus with the pale marking more yellow-white, typically covering the entirety of the clypeus (with the exception of 2 small black marks lateromedially), often extending also onto the lower paraocular areas; never forming an inverted “T” shape. Surface of the clypeus finely shagreened and weakly shining, slightly more clearly punctate, with punctures typically visible against the microsculpture. Fore margin of the clypeus weakly to strongly upturned ..... **9**
- 9 S5 apically with extremely dense and pronounced thick fringe of yellowish hairs extending latitudinally across the width of the segment (Fig. 105B). Terga with apical hair bands broadly interrupted. Clypeus and lower paraocular areas always yellow-marked (Fig. 105D). Flying in the late spring and early summer (May–June) ..... ***A. labialis* (Kirby)**
- S5 apically without such a dense hairband, with scattered and sparse hairs. Terga with apical hairbands complete in fresh specimens; hairbands are most strongly produced in summer-flying individuals, and weakest in



**Figure 105.** *Andrena (Melanapis) fuscosa* Erichson, 1835 male. **A.** Sternum 8, ventrolateral view. *Andrena (Holandrena) labialis* (Kirby, 1802) male. **B.** Sternum 8, lateral view; **D.** Head, frontal view. *Andrena (Holandrena) fimbriata* Brullé, 1833 male. **C.** Head, frontal view. *Andrena (Poecilandrena) labiata* Fabricius, 1781 male. **E.** Genital capsule, dorsal view. *Andrena (Poecilandrena) sphaecodimorpha* Hedicke, 1942 male. **F.** Genital capsule, dorsal view; **G.** Head, frontal view. *Andrena (Poecilandrena) hybrida* Warncke, 1975 male. **H.** Head, frontal view.

- spring-flying individuals. Clypeus yellow-marked, lower paraocular areas yellow-marked or dark. Flying either in the spring (April–May) or the summer (July–August), but less commonly in June ..... **10**
- 10 Ocellocipital distance equalling 2 times the diameter of a lateral ocellus. Gena strongly broadened, almost twice the width of the compound eye, surface with a fingerprint-like network of striations, the underlying surface strongly shining. Bivoltine, integument often red- to reddish-marked in the summer generation ..... ***A. forsterella* Osytshnjuk**
- Ocellocipital distance shorter, at most 1.5 times the diameter of a lateral ocellus. Gena less strongly broadened, 1.5 times the width of the compound eye, surface with less strongly pronounced network of striations, weakly shining. Bivoltine, summer generation not typically showing lightened integument ..... ***A. decipiens* Schenck** (inclusive of *A. flavilabris* Schenck)

Some members of the subgenus *Truncandrena* Warncke can display an ambiguous state for the following character; they are consequently keyable following either choice.

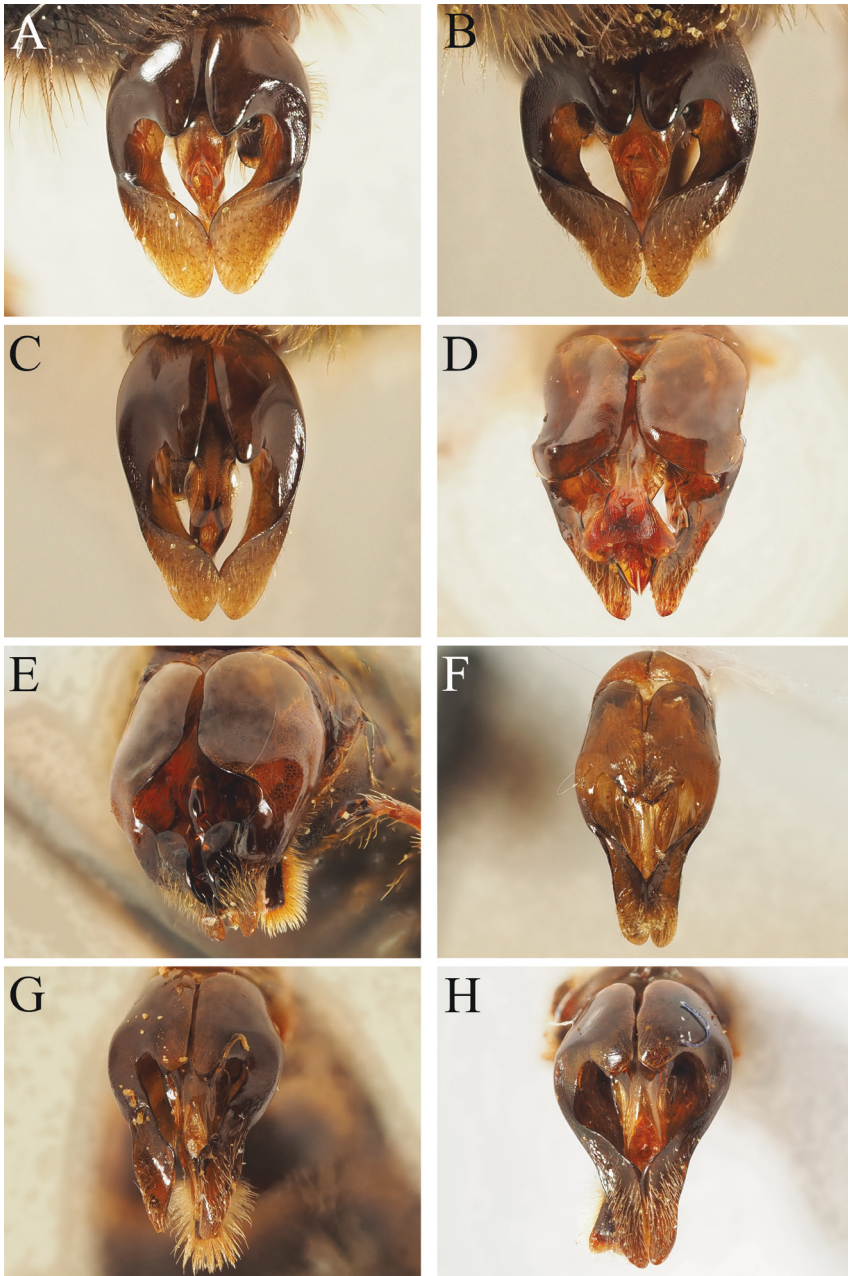
- 11 Clypeus and lower paraocular areas with yellow markings; paraocular markings may be reduced to small spots (Fig. 105G, H) ..... **12**
- Yellow facial markings restricted to the clypeus (sometimes reduced to just a small marking at the apex of the clypeus), paraocular areas entirely dark (Figs 2D, 43C, 109A, 111D–F, 112A) ..... **42**
- 12 Discs of T2–3 entirely and conspicuously red-marked ..... **13**
- Discs of T2–3 dark, at most with the apical margins lightened ..... **16**
- 13 Large species, 11–13 mm. Mandibles long, sickle-like, crossing in their apical 1/3. Head short, clearly broader than long. Genital capsule with gonostyli broad, more-or-less as broad as the gonocoxae ..... ***A. schencki* Morawitz**
- Smaller species, never exceeding 9 mm. Mandibles normal, not strongly crossing apically. Head more-or-less round. Genital capsule with gonostyli apically narrowed, conspicuously narrower than the gonocoxae (Fig. 105E, F) ..... **14**
- 14 Genital capsule with the gonostyli narrowing towards their apex before abruptly diverging, in dorsal view thus appearing to be strongly constricted subapically (Fig. 105E) ..... ***A. labiata* Fabricius**
- Genital capsule with the gonostyli parallel to one another, straight and lacking any kind of subapical constriction (Fig. 105F) ..... **15**

Further study is needed to identify better identification characters for these two species; however, geographic distribution can be used to aid identification with confidence.

- 15 Pale facial markings distinctly creamy-white (Fig. 105G). Widespread across the southern Balkans, but not found on the East Aegean Islands (Fig. 49) ..... ***A. sphecodimorpha* Hedicke**
- Pale facial markings distinctly yellow (Fig. 105H). Rare, restricted to the island of Lesbos (Fig. 49) ..... ***A. hybrida* ssp. *tauriensis* Warncke**

It has not been possible to locate and study the single known male of *A. lonicera*, and hence the species is keyed here due to a lack of knowledge as to certain character states.

- 16 Propodeum with surface almost entirely declivous, without differentiated horizontal and vertical parts. Pronotum with a strongly produced humeral angle. Known only from the Galičica Planina mountain in south-western North Macedonia at an altitude of around 1800 m. Associated with *Lonicera* (Caprifoliaceae)..... ***A. lonicera* Warncke**
- Propodeum with differentiated dorsal and horizontal parts. Pronotum variable. Distribution and ecology otherwise ..... **17**
- 17 Pronotum laterally keeled or angulate (with a humeral angle), keel or angle runs up dorsally to an angled corner. Tarsi lightened orange. Fore margin of clypeus upturned ..... **18**
- Pronotum laterally rounded, without a keel or humeral angle. Tarsi variably coloured. Fore margin of clypeus not upturned..... **19**
- 18 Scutum with very dense and even punctation across the entire surface of the disc, punctures separated by less than the diameter of a puncture, in some cases nearly touching (c.f. Fig. 102H). S3–5 with weak apical fringes of pale hairs, these not obscuring the underlying surface. Widespread in the southern Balkans..... ***A. griseobalteata* Dours**
- Scutum with irregular punctation, punctures separated by 0.5–3 puncture diameters. S3–5 with dense apical fringes of yellowish hairs, these obscuring the underlying surface. Rare in the southern Balkans, restricted to northern and mountainous areas..... ***A. chrysoceles* (Kirby)**
- 19 Mesepisternum and propodeum covered with fine granular microreticulation, shallowly punctate AND propodeal triangle with fine reticulation or granular shagreen, not or very weakly laterally delineated by raised carinae..... **20**
- Mesepisternum and propodeum with weakly to strongly raised reticulation AND/OR propodeal triangle laterally delineated by raised carinae with the internal surface covered with carinae, rugosity, or raised coarse reticulation..... **27**
- 20 Paraocular areas with very small yellow markings. Scutum usually coarsely shagreened, punctures usually not evident or coarser and indistinct. Metasoma with abundant upstanding hairs (subgenus *Truncandrena* Warncke *partim*)..... **21**
- Paraocular areas with large conspicuous markings. Scutum finely shagreened, finely, shallowly and sparsely punctate. Metasoma largely hairless, without abundant upstanding hairs (subgenus *Nobandrena* Warncke) ... **23**
- 21 Head relatively elongate, rounded, as long as wide. Lower paraocular areas with 2 distinct yellow spots only slightly smaller than the size of A4. Genital capsule as in Fig. 106A..... ***A. optata* Warncke**
- Head shorter, clearly wider than long. Lower paraocular areas with two tiny pale markings, much smaller than the size of A4. Genital capsules as in Fig. 106B, C..... **22**



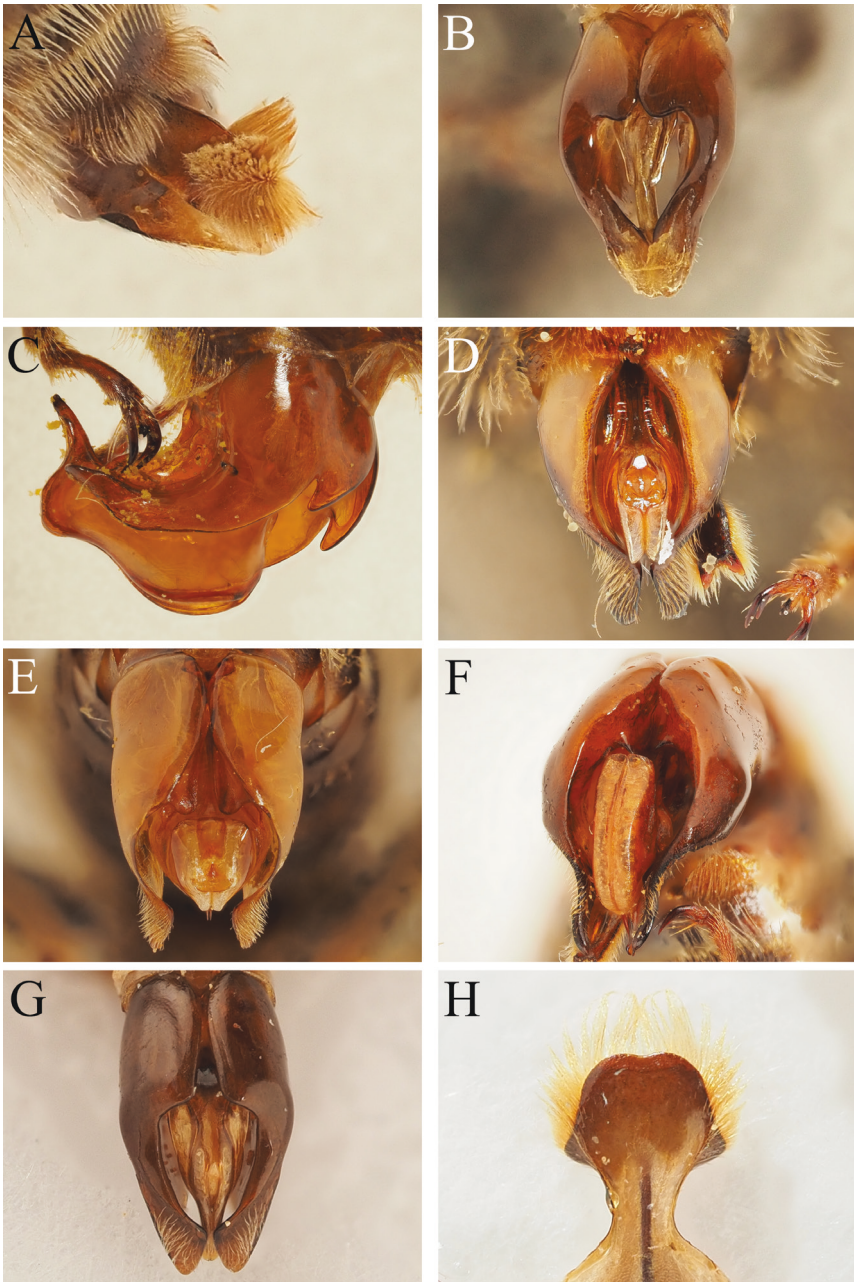
**Figure 106.** *Andrena (Truncandrena) optata* Warncke, 1975 male. **A.** Genital capsule, dorsal view. *Andrena (Truncandrena) schmiedeknechti* Magretti, 1883 male. **B.** Genital capsule, dorsal view. *Andrena (Truncandrena) truncatilabris* Morawitz, 1877 male. **C.** Genital capsule, dorsal view. *Andrena (Nobandrena) flavobila* Warncke, 1965 male. **D.** Genital capsule, dorsal view. *Andrena (Nobandrena) probata* Warncke, 1973 male. **E.** Genital capsule, dorsolateral view. *Andrena (Nobandrena) anatolica* Alfken, 1935 male. **F.** Genital capsule, dorsal view. *Andrena (Nobandrena) athenensis* Warncke, 1965 male. **G.** Genital capsule, dorsal view. *Andrena (Nobandrena) nobilis* Morawitz, 1873 male. **H.** Genital capsule, dorsal view.

- 22 Genital capsule compact, only slightly longer than wide, with the outer margin of the gonostyli slightly concave (Fig. 106B).....  
.....*A. schmiedeknechti* Magretti (*partim*)
- Genital capsule elongate, more-or-less twice as long as wide, with the outer margin of the gonostyli straight (Fig. 106C) .....  
.....*A. truncatilabris* Morawitz (*partim*)
- 23 Genital capsule large, inflated, gonocoxae truncate and forming rounded 90° angles, without distinct teeth (Fig. 106D, E) ..... 24
- Genital capsule normal, not large and inflated, gonocoxae forming distinct rounded apically-projecting teeth (Fig. 106F–H) ..... 25
- 24 Penis valves medially broadened, laterally produced into 2 distinct lobes, lobes overlaying the inner margins of the gonostyli (Fig. 106D). In dorso-lateral view, basal part of gonostyli with a distinct almost 90° kink. Gonostyli in their apical 1/2 flattened and spatulate, gently narrowing. Found in low-altitude habitats .....*A. flavobila* Warncke
- Penis valves medially narrowed, longitudinally compressed, apical part overlain by apical lobes of the gonostyli (Fig. 106E). In dorsolateral view, basal part of gonostyli thickened, without an inner kink. Gonostyli in their apical 1/2 bulbous and produced into 2 narrow finger-like projections. Found in mountainous areas at elevations typically exceeding 1000 m.....  
.....*A. probata* Warncke
- 25 Small species, 8–9 mm in length. Genital capsule with the gonostyli elongate, apically flattened and spatulate with their inner margins rounded without forming a clear angle (Fig. 106F). Gonostyli very narrow at their midpoint, with a small polished depression.....*A. anatolica* Alfken
- Larger species, 13–14 mm in length. Genital capsule with the gonostyli apically flattened and spatulate but with the inner margin forming a distinct 120° angle (Fig. 106G, H). Gonostyli variable, either broader medially or without a clear polished depression ..... 26
- 26 Clypeus with fine granular shagreen, weakly shining. Pale markings yellow. Gonostyli with a large distinct depression over most of their surface, clearly visible medially (Fig. 106G).....*A. athenensis* Warncke
- Clypeus with very weak shagreen, almost polished and shining. Pale markings light yellow. Gonostyli without a clear depression on their surface, medially with a smooth transition (Fig. 106H).....  
.....*A. nobilis* Morawitz
- 27 S8 basally strongly longitudinally compressed, forming a longitudinal carina, apex of S8 covered in 2 distinct dense hair tufts, one directly ventrally and one dorsally (Fig. 107A). A3 slightly exceeding A4 but much shorter than A4+5. Small species, 8 mm in length .....*A. atrata* Friese
- S8 without longitudinal compression, basal longitudinal carina, or double apical hair tufts. A3 equalling or exceeding A4+5. Size variable, but often greatly exceeding 8 mm in length..... 28

- 28 Terga very densely punctate, punctures separated by 0.5–1 puncture diameters. S8 long, approximately 4 times its basal width, medially weakly but distinctly constricted, thus resembling an hourglass. Lower paraocular areas with pale markings very small, almost disappearing. Genital capsule elongate with the penis valves only slightly broadened basally (Fig. 107B). Small species, 5–7 mm in length ..... **A. crassana Warncke**
- Terga usually less densely punctate, with interspaces of >1 puncture diameter. S8 variable. Lower paraocular areas often much more extensively pale-marked. Genital capsule variable, but usually with the penis valves conspicuously inflated or bulbous ..... **29**
- 29 Clypeus and pale facial markings with distinctive shape. Tergal discs sparsely punctate, punctures usually separated by 2–3(4) puncture diameters, marginal areas impunctate and shining. Restricted to mountainous areas in north-eastern Greece and southern Bulgaria (Rhodope and Pirin mountains). Flying in July–August. Widely polylectic and visiting a variety of botanical families ..... **A. coitana (Kirby)**
- Clypeus and pale facial markings otherwise. Tergal discs more densely punctate, punctures usually separated by 1–2 puncture diameters, punctures extending at least in part onto the marginal areas. Widespread and abundant across the southern Balkans. Flying in the spring and summer. Always associated with Asteraceae (subfamilies Asteroideae and Cichorioideae) (subgenus *Ulandrena* Warncke *partim*) ..... **30**

Extraction of the genital capsule is mandatory for the identification of male *Ulandrena* species; identification is made almost completed based on the morphological features displayed there.

- 30 Large species, exceeding 14 mm in length ..... **31**
- Smaller, never exceeding 12 mm in length, usually less than 10 mm in length ..... **34**
- 31 Gonocoxae viewed laterally with a distinct incision, thus the gonocoxae appear to have a sharp tooth towards their base (Fig. 107C) ..... **A. elegans Giraud**
- Gonocoxae viewed laterally with their outer margin completely smooth, without any kind of incision (Fig. 107D–F) ..... **32**
- 32 Genital capsule viewed dorsally with the gonocoxae presenting a smooth internal margin, without any sign of a longitudinal ridge or carina (Fig. 107D) ..... **A. concinna Smith**
- Genital capsule viewed dorsally with the gonocoxae presenting a strong longitudinal ridge along their inner margins, the apex of this ridge forming a rounded 60–80° angle (Fig. 107E, F) ..... **33**



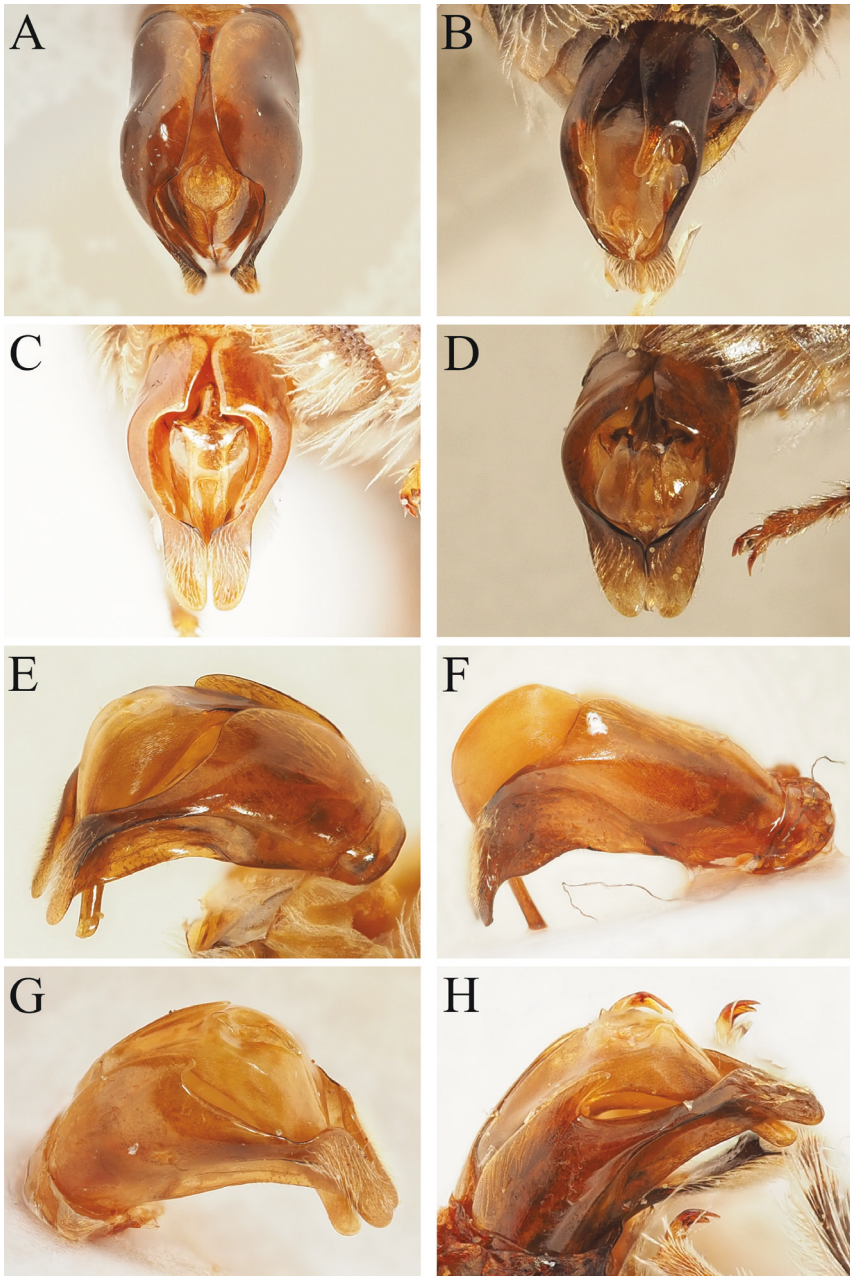
**Figure 107.** *Andrena* (*Parandrenella*) *atrata* Friese, 1887 male. **A.** Sternum 8, ventrolateral view. *Andrena* (*Poecilandrena*) *crasana* Warncke, 1965 male. **B.** Genital capsule, dorsal view. *Andrena* (*Ulandrena*) *elegans* Giraud, 1863 male. **C.** Genital capsule, lateral view. *Andrena* (*Ulandrena*) *concinna* Smith, 1853 male. **D.** Genital capsule, dorsal view. *Andrena* (*Ulandrena*) *heinrichi* Grünwaldt, 2005 male. **E.** Genital capsule, dorsal view. *Andrena* (*Ulandrena*) *crecca* Warncke, 1965 male. **F.** Genital capsule, dorsal view. *Andrena* (*Ulandrena*) *acerba* Warncke, 1967 male. **G.** Genital capsule, dorsal view. *Andrena* (*Ulandrena*) *fulvitaris* Brullé, 1833 male. **H.** Sternum 8, dorsal view.

- 33 Penis valves bulbous, grossly expanded and filling almost the entire space between the gonostyli (Fig. 107E). Restricted to the East Aegean island of Samos only ..... ***A. heinrichi* Grünwaldt**
- Penis valves not greatly expanded laterally, not occupying almost the entire space between the gonostyli (Fig. 107F). Found in continental Greece, Lesbos, North Macedonia, and Bulgaria..... ***A. crecca* Warncke**
- 34 Genital capsule in dorsal view rhomboidal, with the outer margins of the gonostyli essentially straight (Fig. 107G). Gonocoxae produced into a weak rounded 120° angle. Penis valves weakly inflated, central portion weakly but distinctly constricted subapically above lateral hyaline parts..... ***A. acerba* Warncke**
- Genital capsule otherwise; outer margins of gonostyli concave, gonocoxae produced into projecting teeth or angles of a different degree, or penis valves otherwise structured..... **35**
- 35 Process of S8 large, slightly broader than long and basolaterally produced into 2 small but distinct teeth, the ventral surface covered with long orange hairs that extend far beyond its apex (Fig. 107H). Penis valves strongly inflated, almost circular in dorsal view; gonocoxae with outer margins not produced into anteriorly projecting teeth or angulations (Fig. 108A)..... ***A. fulvitaris* Brullé**
- Process of S8 small, slightly longer than broad and broadening apically, not basolaterally produced into small teeth; ventral surface covered with short orange to silvery hairs which do not substantially extend beyond the apex. Genital capsule variable (Fig. 108B–H), often with gonocoxal teeth or angulations of various lengths..... **36**
- 36 Small bees, 7–8 mm in length. Pale facial markings often reduced, not covering the entirety of the clypeus or only a small part of the lower paraocular areas (*waschulzi*-group) ..... **37**
- Medium sized bees, 9–12 mm in length. Pale facial markings usually strongly produced, extending up as high as the lower margins of the antennal insertions (*abbreviata*-group)..... **39**
- 37 Genital capsule with the gonocoxae produced into long, narrow, finger-like and slightly curving teeth (Fig. 108B). Continental Greece only ..... ***A. trikalensis* Warncke**
- Genital capsule with the gonocoxae apically rounded or truncate, never produced into projecting pointed teeth (Fig. 108C, D). Distribution variable..... **38**
- 38 Genital capsule with the gonocoxae produced into roughly 90° angles, their apices slightly diverging (Fig. 108C). Basal antennal segments distinctly bowed along their ventral margins, hence appearing knobby in frontal view. Tergal discs densely and deeply punctate, punctures separated by 0.5 puncture diameters. Southern Bulgaria and the East Aegean Islands (Fig. 65)..... ***A. neocyprica* Mavromoustakis**
- Genital capsule with the inner margins of the gonocoxae also diverging apically but produced into 120° angles (Fig. 108D). Basal antennal segments

- with their dorsal and ventral margins parallel, not appearing knobby. Tergal discs densely but shallowly punctate, punctures separated by 0.5–1 puncture diameters. Albania, continental Greece, and Crete (Fig. 65).....  
 ..... *A. waschulzi* Strand
- 39 In lateral view, gonocoxae with their outer margins completely rounded, not forming projecting teeth or angulations (Fig. 106E) .....  
 ..... *A. cantiaca* Warncke
- In lateral view, gonocoxae with their outer margins showing a distinct angulation (Fig. 108F) or tooth (Fig. 108G, H) thus not appearing completely rounded..... 40
- 40 In lateral view, gonocoxae with their outer margins showing an angulation, this angulation being roughly 90° and somewhat rounded (Fig. 108F). Penis valves swollen, but in frontal view, not quite filling the entire space between the gonostyli; in lateral view, not obviously flattened, apex rounded .....  
 ..... *A. combaella* Warncke
- In lateral view, gonocoxae with their outer margins produced into a short or long tooth, this tooth pointed (Fig. 108G, H). Penis valves swollen and filling the entire space between the gonostyli; in lateral view, weakly flattened ..... 41

The following two species are almost identical in the male sex.

- 41 Gonocoxal teeth very short (Fig. 108G). Found in continental parts of the southern Balkans between 40.5°N and 43.5°N (*Macedonia sensu lato*).....  
 ..... *A. biguttata* Friese
- Gonocoxal teeth noticeably longer (Fig. 108H). More widespread across the southern Balkans..... *A. abbreviata* Dours
- 42 Discs of T2–3 clearly and extensively red-marked ..... 43
- Tergal discs dark, at most with the apical margins lightened..... 44
- 43 Pronotum with strong humeral angle. Fore margin of the clypeus laterally produced into 2 small but distinctly projecting points. Smaller, 7–9 mm.....  
 ..... *A. marginata* Fabricius
- Pronotum rounded. Fore margin of the clypeus normal, without lateral projections. Larger, 14–16 mm .....  
 ..... *A. hattorfiana* (Fabricius) (*partim, light form*)
- 44 Head, mesosoma, and/or metasoma with metallic green or blue reflections. This can be subtly present on the scutum of *A. schlettereri* and so it is keyed out under both choices ..... 45
- Body lacking metallic reflections ..... 50
- 45 Clypeus apically produced into a long pointed spine (Fig. 109A). Integument with metallic-blue reflections ..... *A. mucronata* Morawitz
- Clypeus without such a projection on the clypeus. With metallic green, bronze, or purplish reflections (at least on the scutum), but not blue .... 46



**Figure 108.** *Andrena (Ulandrena) fulvitaris* Brullé, 1833 male. **A.** Genital capsule, dorsal view. *Andrena (Ulandrena) trikalensis* Warncke, 1965 male. **B.** Genital capsule, dorsal view. *Andrena (Ulandrena) neocypriaca* Mavromoustakis, 1956 male. **C.** Genital capsule, dorsal view. *Andrena (Ulandrena) waschulzi* Strand, 1921 male. **D.** Genital capsule, dorsal view. *Andrena (Ulandrena) cantiaca* Warncke, 1975 male. **E.** Genital capsule, lateral view. *Andrena (Ulandrena) combaella* Warncke, 1966 male. **F.** Genital capsule, lateral view. *Andrena (Ulandrena) biguttata* Friese, 1923 male. **G.** Genital capsule, lateral view. *Andrena (Ulandrena) abbreviata* Dours, 1873 male. **H.** Genital capsule, lateral view.

- 46 Pronotum with a strong humeral angle. Gena strongly expanded, clearly broader than the width of the compound eye, dorsolaterally produced into an almost winged carina (Fig. 109B).....***A. schlettereri* Friese (*partim*)**
- Pronotum rounded. Gena not expanded, not exceeding the width of the compound eye and not dorsolaterally produced into any form of carina..... 47
- 47 Tergal discs with very scattered fine hair-bearing punctures, these obscure and separated by 3–4 puncture diameters. Mouthparts relatively short, 2 times longer than broad, surface of galea covered with granular microreticulation, dull (c.f. Fig. 95D). Associated with *Cerastium* (Caryophyllaceae) .....***A. olympica* Grünwaldt**
- Tergal discs finely but clearly and regularly punctate, punctures separated by 1–2 puncture diameters. Mouthparts relatively long, 3–4 times longer than broad, surface of galea finely shagreened, shining (c.f. Fig. 95F, H). Associated with *Veronica* (Plantaginaceae) ..... **48**

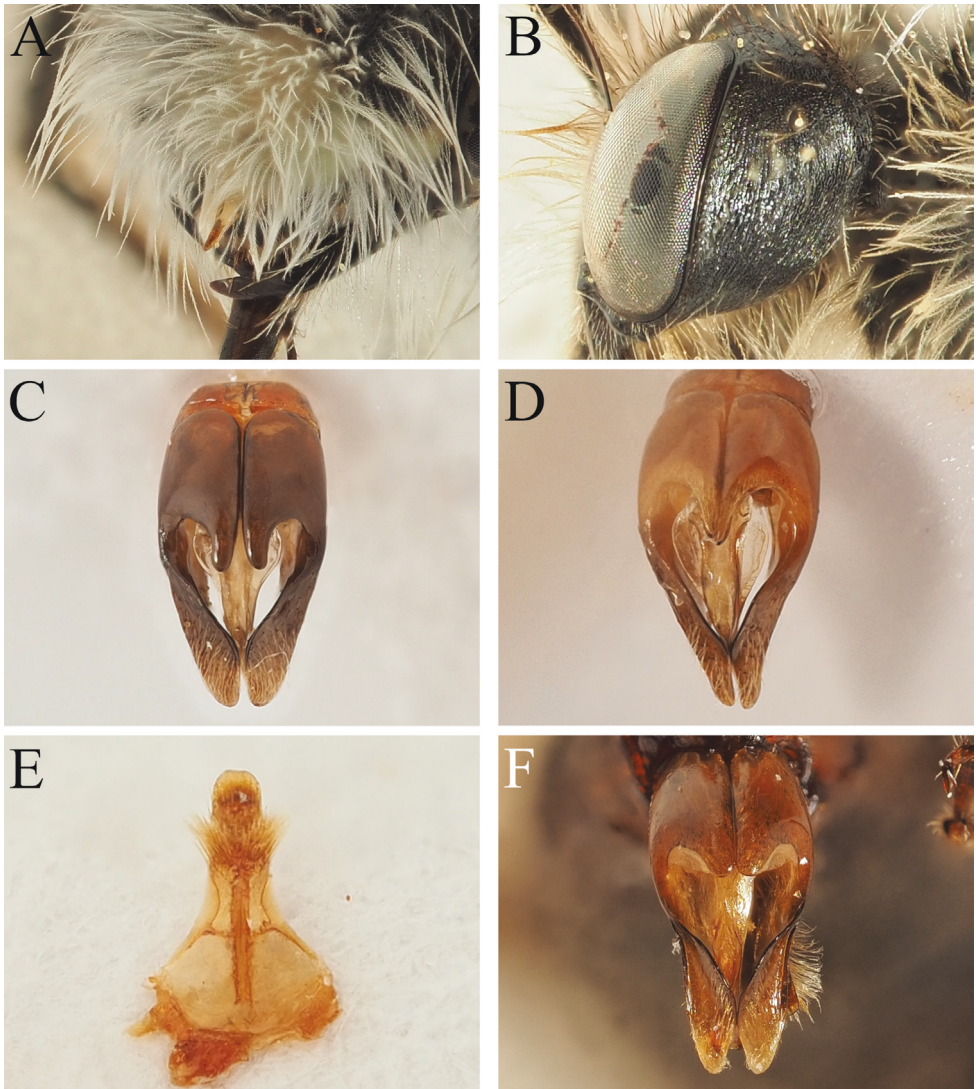
The following three species are challenging to separate in the male sex without access to confidently determined reference material.

- 48 Scutum densely punctate, punctures separated by 0.5–1 puncture diameters laterally, up to 2 puncture diameters medially .....  
.....***A. standfussorum* Scheuchl**
- Scutum sparsely punctate, punctures separated by around 2 puncture diameters laterally, up to 4 puncture diameters medially ..... **49**
- 49 Scutum densely microreticulate and uniformly dull. Gonostyli with their apical blades broad, clearly broadest medially before narrowing apically, at their widest clearly exceeding the width of the median (non-hyaline) part of the penis valves (Fig. 109C). Ocelloccipital distance slightly less than the diameter of a lateral ocellus. Restricted to continental Greece .....  
.....***A. neovirida* Grünwaldt**
- Scutum more finely microreticulate, weakly shining medially. Gonostyli with their apical blades narrow, not noticeably broadened medially, not noticeably broader than the width of the median (non-hyaline) part of the penis valves (Fig. 109D). Ocelloccipital distance slightly greater than the diameter of a lateral ocellus More widespread across the southern Balkans ..... ***A. viridescens* Viereck**
- 50 Fore margin of clypeus upturned (strongly or weakly) AND gena conspicuously broadened, wider than the width of the compound eye (Figs 35D, 39D, 109B) AND pronotum with a conspicuous humeral angle (*Notandrena* Pérez *partim*) ..... **51**
- Without this combination of characters ..... **54**
- 51 Tergal discs finely and obscurely punctate, punctures separated by 2–4 puncture diameters, underlying surface microreticulate and dull. Scutum with obscure metallic green-bronze reflections, surface with dense granular

- microreticulation, dull. Scutum shallowly, obscurely, and irregularly punctate, punctures separated by 0.5–4 puncture diameters ..... *A. schlettereri* Friese (*partim*)
- Tergal discs finely but clearly punctate, punctures dense or sparse but with shining interspaces. Scutum without metallic reflections, finely shagreened and weakly shining. Scutum clearly punctate, punctures separated by 0.5–2 puncture diameters ..... 52
- 52 Tergal discs densely punctate, punctures separated by 0.5–1 puncture diameters. Ventral surface of S8 with a pair of hair tufts basally that are directly anterolaterally, apical part of S8 essentially devoid of hairs (Fig. 109E).. ..... *A. ungeri* Mavromoustakis
- Tergal discs with scattered punctures, punctures separated by 2–4 puncture diameters. Ventral surface of S8 entirely and uniformly covered with hairs (*meridionalis*-group) ..... 53

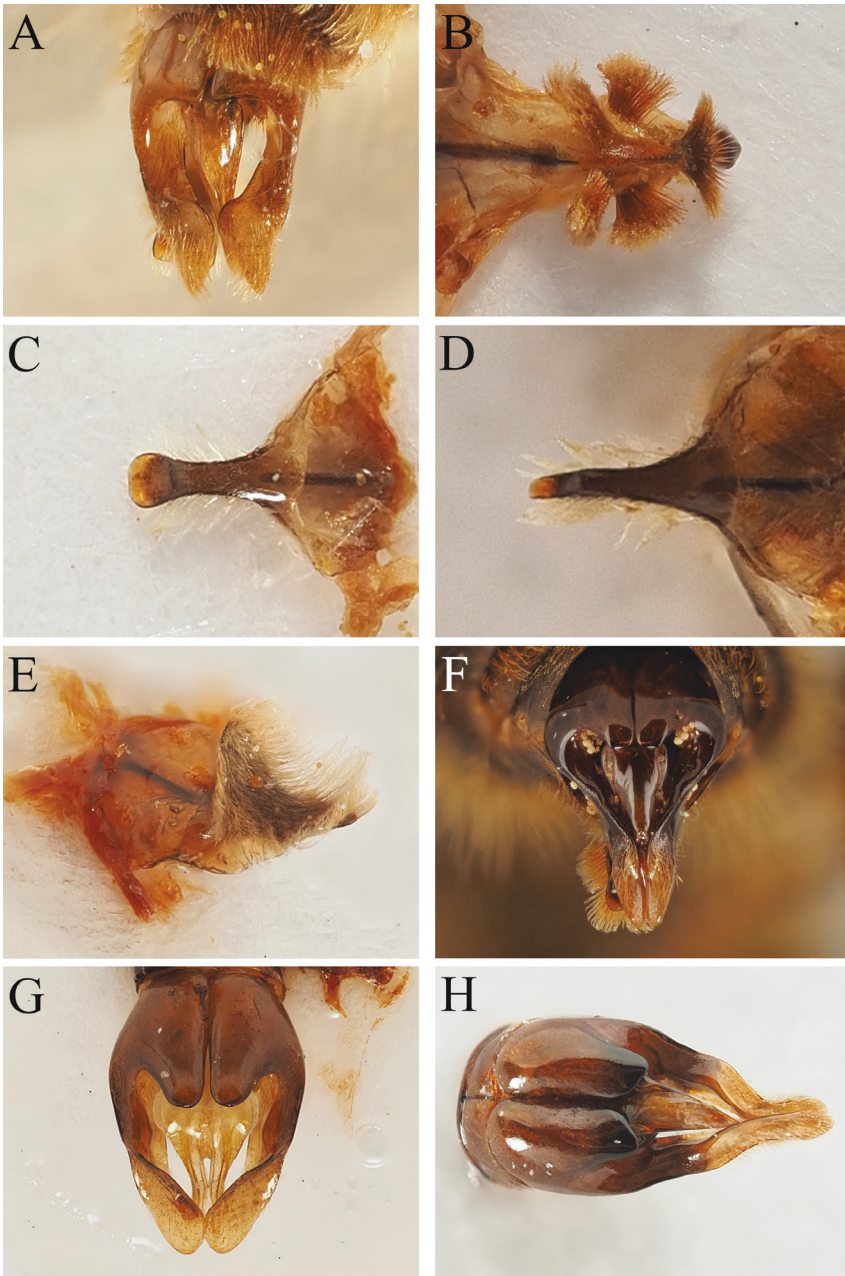
The following two species are insufficiently characterised in the male sex. Their geographic provenance along with concurrently active females should be used to aid identification.

- 53 Larger, 8–9 mm. Found in Albania and continental Greece (Fig. 42) ..... *A. meridionalis* Dalla Torre & Friese
- Smaller, 7–8 mm. Currently known only from Lesbos (Fig. 42) ..... *A. clanga* Warncke
- 54 Tergal margins broad, on T2 occupying 50% of the disc, on T3 occupying around 60% of the disc, and on T4 occupying around 70–80% of the disc. Genital capsule elongate, with strongly produced gonocoxal teeth, gonostyli with the blades showing strongly raised internal margins, and penis valves slightly constricted submedially with rounded lateral hyaline extensions (Fig. 109F) ..... *A. seminuda* Friese
- Tergal margins narrower, genital capsule otherwise ..... 55
- 55 Head short and broad, clypeus very broad with straight anterior margin, narrow lateral extensions, and bar-shaped median section; this median section only partially yellow-marked. Anterior margin of clypeus with long fringe of yellowish hairs, hairs exceeding the greatest vertical length of the clypeus itself. Mandibles relatively long and slightly but distinctly crossing apically. Gena relatively broad, slightly exceeding the width of the compound eye, posterior margin rounded. Pronotum without a humeral angle. Terga densely and regularly punctate, punctures separated by 0.5–1 puncture diameters. Tergal margins with narrow complete fringes of yellowish hairs on T2–4. Genital capsule with gonostyli apically produced into distinct flattened triangular blades (Fig. 110A; resembling members of the subgenus *Cryptandrena* Warncke). Restricted to the East Aegean Islands (Lesbos) ..... *A. monacha* Warncke
- Combination of characters otherwise; distribution variable ..... 56



**Figure 109.** *Andrena* (*Truncandrena*) *mucronata* Morawitz, 1871 male. **A.** Clypeus, fronto-lateral view. *Andrena* (*Notandrena*) *schlettereri* Friese, 1896 male. **B.** Head, lateral view. *Andrena* (*Poecilandrena*) *neovirida* Grünwaldt, 2005 male. **C.** Genital capsule, dorsal view. *Andrena* (*Poecilandrena*) *viridescens* Viereck, 1916 male. **D.** Genital capsule, dorsal view. *Andrena* (*Notandrena*) *ungeri* Mavromoustakis, 1952 male. **E.** Sternum 8, ventral view. *Andrena* (*incertae sedis*) *seminuda* Friese, 1896 male. **F.** Genital capsule, dorsal view.

- 56 Mandibles elongate, sickle-like, strongly crossing in their apical 1/3 AND pronotum with strong humeral angle AND gena broadened, clearly broader than the width of the compound eye, usually produced into a 90° angulation postero-ventrally ..... 57
- Without this combination of characters; mandibles either shorter, pronotum laterally rounded, and/or gena not exceeding width of compound eye ..... 59



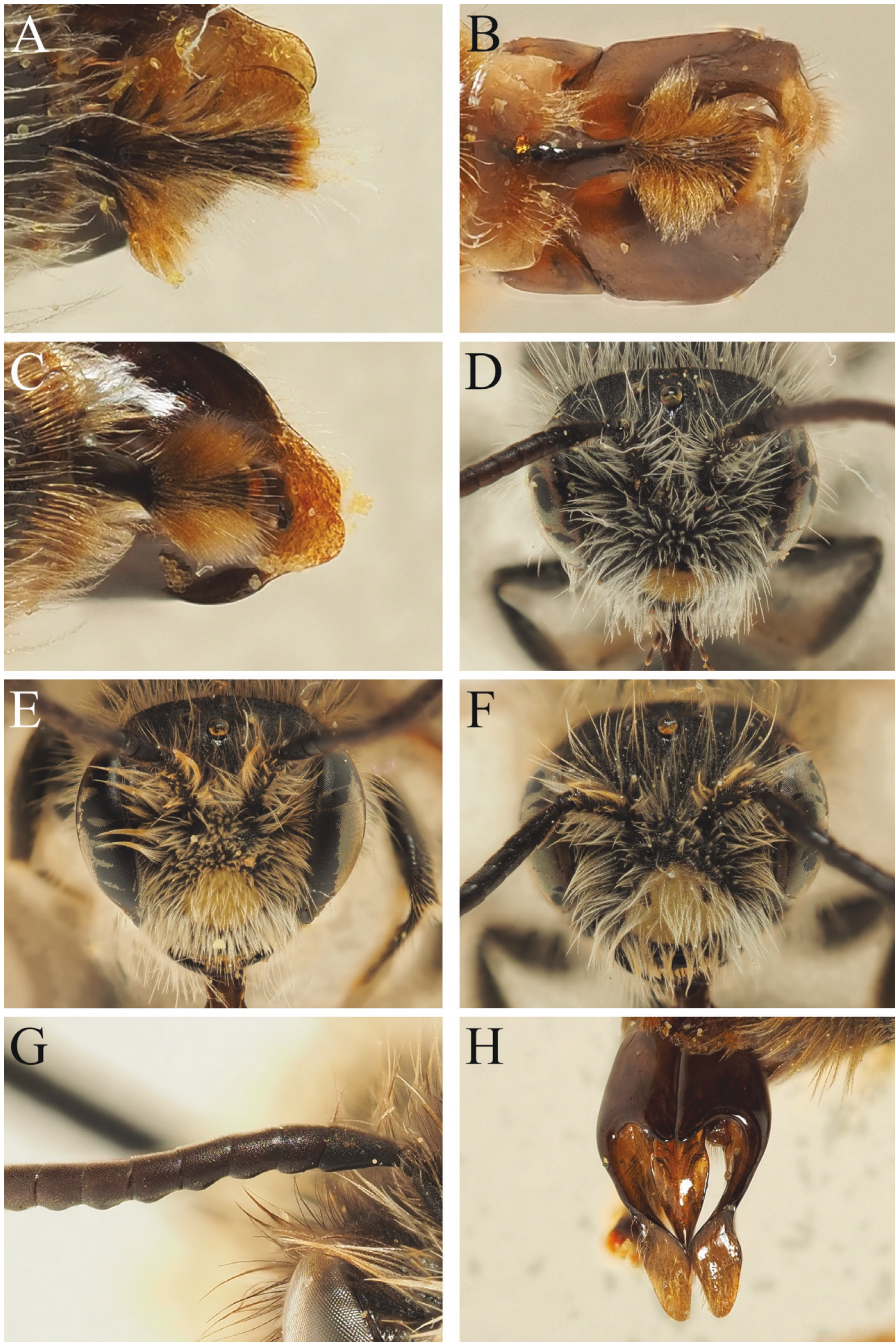
**Figure 110.** *Andrena* (incertae sedis) *monacha* Warncke, 1965 male. **A.** Genital capsule, dorsal view. *Andrena* (*Parandrenella*) *figurata* Morawitz, 1866 male. **B.** Sternum 8, ventral view. *Andrena* (*Aciandrena*) *aciculata* Morawitz, 1886 male. **C.** Sternum 8, dorsal view. *Andrena* (*Aciandrena*) *lamiana* Warncke, 1965 male. **D.** Sternum 8, dorsal view. *Andrena* (*Lepidandrena*) *dorsalis* Brullé, 1833 male. **E.** Sternum 8, ventrolateral view. *Andrena* (*Charitandrena*) *hattorfiana* (Fabricius, 1775) male. **F.** Genital capsule, dorsal view. *Andrena* (*Limbandrena*) *limbata* Eversmann, 1852 male. **G.** Genital capsule, dorsal view. *Andrena* (*Lepidandrena*) *mocsaryi* Schmiedeknecht, 1884 male. **H.** Genital capsule, dorsal view.

- 57 Ocelloccipital distance short, <0.5 times the diameter of a lateral ocellus. Genital capsule with gonocoxal teeth apically strongly diverging, apices pointed (see Wood 2023b: 425 fig. 76D for the capsule of the extremely similar *Andrena tunetana* Schmiedeknecht, 1900). Found in warm Mediterranean habitats in Greece, including the East Aegean Islands ..... *A. larisana* Warncke
- Ocelloccipital distance long, 1–2 times the diameter of a lateral ocellus. Genital capsule with gonocoxal teeth not strongly diverging, apices truncate. Found in temperate areas in the northern parts of the southern Balkans ..... **58**
- 58 Typically larger, 9–10 mm. Sterna uniformly dark. Genital capsule more elongate, gonocoxal teeth with apices comparatively narrow, gonostyli not noticeably constricted medially ..... *A. sericata* Imhoff
- Typically smaller, 7–9 mm. Sterna with marginal areas sometimes lightened reddish. Genital capsule more compact, gonocoxal teeth with apices comparatively broad, gonostyli strongly constricted medially ..... *A. ventralis* Imhoff
- 59 S8 strongly ornamented with multiple anteriorly, laterally, and ventrally-projecting short hair tufts (Fig. 110B). Tergal margins of T2–4 distinctly depressed, forming a weak hump where they meet the tergal discs. All tarsi and hind tibiae orange ..... *A. figurata* Morawitz
- Combination of characters otherwise ..... **60**
- 60 Small species, length not exceeding 8 mm ..... **61**
- Larger species, exceeding 10 mm in length ..... **66**
- 61 Hind basitarsi entirely lightened orange. Frons with contrasting black and white pubescence, black on the frons and gena posteriorly, intermixing with white around the antennal insertions, becoming white on the clypeus and on the gena ventrally. Restricted to mountainous areas in north-eastern Greece and southern Bulgaria (Rhodope and Pirin mountains). Associated with *Potentilla* (Rosaceae), flying in July–August ..... *A. tarsata* Nylander
- Combination of characters otherwise; ecologically different, typically flying in the spring and early summer (March–June) ..... **62**
- 62 Propodeal triangle laterally defined by raised carinae, internal surface with a network of raised rugae. All tergal discs uniformly punctate, punctures separated by 0.5 puncture diameters. Genital capsule elongate (c.f. Fig. 67D), with weakly pronounced gonocoxal teeth, gonostyli apically produced into triangular wedges (subgenus *Cryptandrena* Warncke *partim*) ..... **63**
- Propodeal triangle with smooth granular microreticulation, without raised rugosity (Fig. 2C). Tergal discs obscurely punctate. Associated with Brassicaceae (subgenus *Aciandrena* Warncke *partim*) ..... **64**
- 63 Antennae with A3 more-or-less equal to A4 in length (Fig. 67G) ..... *A. ventricosa* Dours (*partim*, light form)
- Antennae with A3 clearly exceeding A4 in length, almost as long as A4+5 (Fig. 67F) ..... *A. brumanensis* Friese (*partim*, light form)

- 64 Genital capsule elongate, clearly longer than broad (Fig. 2D). Found only in mountains in southern continental Greece.....***A. chelma* Warncke**
- Genital capsule short, rounded to slightly broader than long. Widespread across the southern Balkans, not restricted to mountains ..... **65**
- 65 Apex of S8 truncate (Fig. 110C). Pale marking of clypeus often reduced in size and not fully covering the surface. On average, encountered more in the northern parts of the southern Balkans. Bivoltine, predominantly recorded between April–July .....***A. aciculata* Morawitz**
- Apex of S8 narrowly pointed (Fig. 110D). Pale marking of clypeus typically covering the entire surface (with the exception of 2 small black marks). On average, encountered more in the southern parts of the southern Balkans. Univoltine, predominantly recorded between April – early June.....
- ..... ***A. lamiana* Warncke**
- 66 Propodeum unusual, entirely declivous and not differentiated into horizontal and vertical parts. Head appearing elongate, as long as broad. Genital capsule with strongly produced gonocoxal teeth, gonostyli with their apices flattened and broadly triangular, penis valves narrow and occupying at most only around 1/4 of the space between the gonostyli (see Pisanty and Wood 2024: 458). Restricted to the East Aegean Islands (Lesbos).....
- ..... ***A. curiosa* (Morawitz)**
- Combination of characters or geographic distribution otherwise..... **67**
- 67 Genital capsule compact (Fig. 62F), with projecting gonocoxal teeth that do not apically diverge and humped gonostyli which are slightly flattened at their apices (*polita*-group *partim*) ..... **68**
- Genital capsule otherwise..... **69**
- 68 Forewing with nervulus very strongly postfurcal, separated from the basal vein by at least 2 vein widths (Fig. 62D). Slightly smaller, 9–10 mm .....
- ..... ***A. subglobosa* Dours**
- Forewing with nervulus interstitial. Slightly larger, 10–11 mm .....
- ..... ***A. westensis* Warncke**
- 69 S8 viewed laterally conspicuously divided into a horizontal and vertical part (Fig. 110E; *florivaga*-group) ..... **70**
- S8 uniformly flat, without a vertical part ..... **71**
- 70 Terga with fine, obscure, and scattered punctures. Sterna with orange-yellow apical hair fringes. Head with uniformly pale hairs....***A. florivaga* Eversmann**
- Terga with dense strong punctures, punctures separated by 0.5–1 puncture diameters. Sterna with whitish to buffish apical hair fringes. Head with pale hairs medially, with abundant black hairs along the inner margins of the compound eyes and extending onto the frons ..... ***A. dorsalis* Brullé**
- 71 Large species, 14–16 mm. Genital capsule distinctive, elongate with projecting and apically truncate gonocoxal teeth (Fig. 110F).....
- ..... ***A. hattorfiana* (Fabricius) (*partim*, dark form)**
- Smaller, sometimes reaching 14 mm, but usually 7–12 mm. Genital capsule different; if elongate, then gonocoxal teeth pointed, not truncate..... **72**

- 72 Ocellocipital distance 3 times the diameter of a lateral ocellus. Terga very finely shagreened, more-or-less smooth and shiny. Tergal discs regularly and deeply punctate, punctures separated by 1–2 puncture diameters, punctures becoming smaller and continuing onto tergal margins. Hind basitarsus lightened orange. Genital capsule as in Fig. 110G ..... ***A. limbata* Eversmann**
- Ocellocipital distance <2 times the diameter of a lateral ocellus. Combination of characters otherwise..... **73**
- 73 Genital capsule elongate, with the gonostyli produced into very long finger-like or filiform projections (Fig. 110H). Gonocoxae with their apices broadly rounded. Associated with *Ornithogalum* (Asparagaceae) ..... ***A. mocsaryi* Schmiedeknecht**
- Genital capsule otherwise..... **74**
- 74 S8 large, roughly triangular with a truncate apex to elongate, ventral surface covered with abundant orange hairs. Genital capsule of a typical form, with strongly produced gonocoxal teeth and the gonostyli with a distinct latitudinal impression medially, giving them an almost wavy appearance (Figs 43E, F, 47C, D). Clypeus with subtle longitudinal wrinkles (*oralis*-group) ..... **75**
- Combination of characters otherwise..... **76**
- 75 Gonostyli with their apices relatively narrow, blade approximately 4–5 times longer than wide (Figs 43F, 47C)..... ***A. oralis* Morawitz**
- Gonostyli with their apices relatively broad, blade approximately 3 times longer than wide (Figs 43E, 47D)..... ***A. gallinula* Warncke**
- 76 Genital capsule with the gonocoxae almost completely truncate, their inner margins slightly diverging apically and with a more-or-less 90° angle which threatens to become an acute point. Penis valves medially forming a distinct longitudinal ridge, laterally almost with weak hyaline extensions. Gonostyli with the inner margin strongly raised, apices flattened and spatulate..... ***A. garrula* Warncke**
- Combination of characters otherwise..... **77**
- 77 Terga abundantly punctate, terga with at least T1 showing clear crater punctures (with the marginal rims conspicuously elevated hence resembling craters) (subgenus *Chlorandrena* Pérez *partim*)..... **78**
- Terga more obscurely punctate, covered with hair-bearing punctures but these fine and never with their apical rims raised (subgenus *Truncandrena* Warncke *partim*) ..... **82**
- 78 S8 shaped like an inverse “T”, basally with 2 small but pronounced lateral projections (Fig. 111A), apex of sternum usually emarginate. Ventral surface of S8 with 2 dense laterally projecting tufts of hairs, apically with long white hairs that project beyond the truncate apex of the sternum. Clypeus with pale marking reduced to a small patch long the apical margin, occupying <30% of the surface, sometimes reduced to a tiny speck ..... ***A. panurgimorpha* Mavromoustakis**
- S8 forming a single quadrate to rectangular shape without lateral projections (Fig. 111B, C), apex of sternum rarely emarginate. Ventral surface of

- S8 with a single patch of yellow-brown hairs that does not form distinct lateral projections or apically extend beyond the apex of the sternum. Clypeus with pale facial marking variable in size..... **79**
- 79 S8 elongate, more than 3 times longer than wide (Fig. 111B). Surface of S8 with a fan of long laterally projecting hairs over more-or-less its entire length, not forming a distinct basal tuft. Disc of T2 with dense, deep, and distinct punctures, punctures separated by 0.5–1 puncture diameters. Currently known from southern Bulgaria and the East Aegean Islands (Fig. 76)..... ***A. exquisita* Warncke**
- S8 more-or-less quadrate, around 1.5 times longer than wide (Fig. 111C). Surface of S8 with hairs largely present basally, forming a dense tuft with the apical part of the sternum in comparison with reduced hairs. Disc of T2 with sparser shallower punctures, punctures separated by 1–2 puncture diameters. More widespread across the southern Balkans ..... **80**
- 80 Nervulus typically antefurcal. Clypeus with pale marking reduced to a small patch long the apical margin, occupying <30% of the surface (Fig. 111D). Smaller, 7–8 mm ..... ***A. cinereophila* Warncke**
- Nervulus typically interstitial. Clypeus usually with pale marking large, covering the majority (>50%) of the surface. Slightly larger, 9–11 mm..... **81**
- 81 Tergal discs with fine shagreen, almost polished and shining. Punctuation fine, on T1 with only a few punctures with hints of displaying raised rims (more-or-less without crater punctures). Pale clypeal marking typically not reaching the fore margin of the clypeus and forming a vague circular shape, without 2 small black marks internally (Fig. 111E). Flying slightly later, from late April to late June..... ***A. clypella* Strand**
- Tergal discs densely microreticulate, dull to at most weakly shining in places. Punctuation stronger and somewhat coarse, on T1 with many punctures with obviously raised rims (crater punctures). Pale clypeal marking usually reaching the fore margin of the clypeus and forming a vague semi-circular shape, usually with 2 small black marks internally (Fig. 111F). Flying slightly earlier, from April to early June..... ***A. humilis* Imhoff**
- 82 Facial pubescence medially pale, with black hairs along the inner margins of the compound eyes ..... **83**
- Facial pubescence uniformly pale ..... **85**
- 83 Viewed frontally, apices of A3–8(9) ventrally expanded, hence giving the impression that the flagella have a wavy or serrate ventral margin (Fig. 111G)..... ***A. serraticornis* Warncke**
- Viewed frontally, antennal flagella with dorsal and ventral surfaces parallel ..... **84**
- 84 Hind basitarsi lightened orange. Area immediately anterior to median ocellus with longitudinal striations, dull..... ***A. tscheki* Morawitz sensu lato**
- Hind basitarsi dark. Area immediately anterior to median ocellus with reduced surface sculpture, weakly shining with a distinct narrow polished impression ..... ***A. canaeae* Strand**



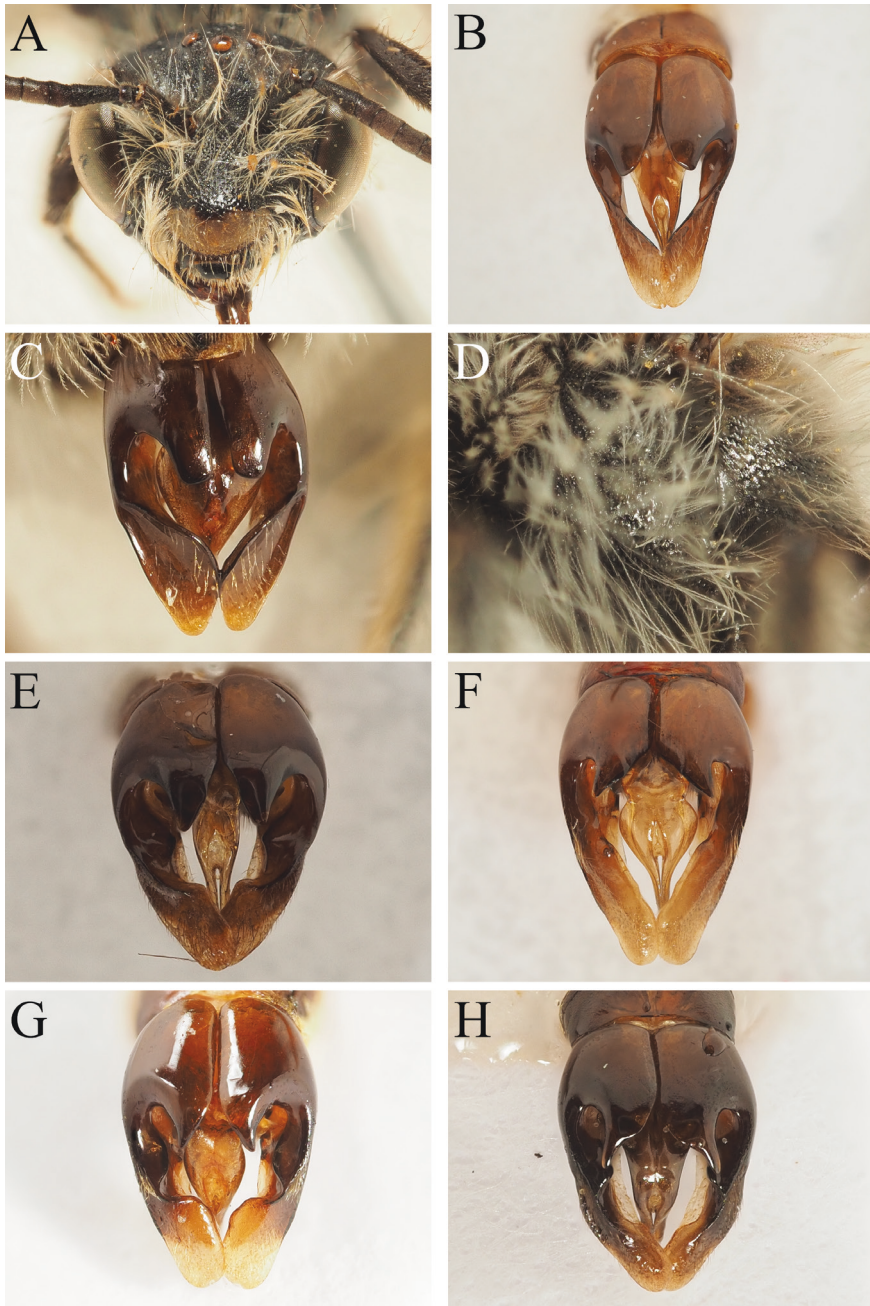
**Figure III.** *Andrena* (*Chlorandrena*) *panurgimorpha* Mavromoustakis, 1957 male. **A.** Sternum 8, ventral view. *Andrena* (*Chlorandrena*) *exquisita* Warncke, 1975 male. **B.** Sternum 8, ventral view. *Andrena* (*Chlorandrena*) *clypella* Strand, 1921 male. **C.** Sternum 8, ventral view; **E.** Head, frontal view. *Andrena* (*Chlorandrena*) *cinereophila* Warncke, 1965 male. **D.** Head, frontal view. *Andrena* (*Chlorandrena*) *humilis* Imhoff, 1832 male. **F.** Head, frontal view. *Andrena* (*Truncandrena*) *serraticornis* Warncke, 1965 male. **G.** Antennal flagellum, frontal view. *Andrena* (*Truncandrena*) *delphiensis* Warncke, 1965 male. **H.** Genital capsule, dorsal view.

- 85 Genital capsule with the gonostyli distinctly constricted medially, forming a more-or-less 120° angle on their outer margins (Fig. 111H)..... **86**
- Genital capsule with the outer margins of the gonostyli more-or-less straight or rounded but certainly not strongly constricted medially..... **87**
- 86 All tarsi and apices of hind tibiae lightened orange. Genital capsule with the penis valves broadly flattened, with at most hints of a raised ridge medially. Clypeus finely shagreened and at most weakly shining between punctures. S3–5 with long, loose, and erect golden-brown hair fringes that do not obscure the underlying surface. Found in North Macedonia, continental Greece, and the East Aegean Islands.....  
..... ***A. delphiensis* Warncke**
- All legs uniformly dark. Genital capsule with the penis valves strongly produced into a raised ridge medially. Clypeus polished and shining between the punctures, at least in its apical 1/2. S3–5 with long, dense, and decumbent whitish-brown hair fringes which obscure the underlying surface. Restricted to eastern Bulgaria and the East Aegean Islands.....  
..... ***A. asiatica* Friese**
- 87 Clypeus with the pale marking present only in its apical 1/2 (Fig. 112A). Antennae lightened orange ventrally. Genital capsule with long strongly projecting gonocoxal teeth and moderately broadened penis valves (Fig. 112B)..... ***A. rotundilabris* Warncke**
- Clypeus with the pale marking covering the entire surface (with the exception of 2 small black marks). Antennae dark to at most dark brown ventrally. Genital capsule otherwise..... **88**
- 88 Genital capsule with large rounded gonocoxal teeth that only weakly diverge apically (Fig. 112C). Penis valves bulbous and occupying the majority of the space between the gonostyli..... ***A. ulula* Warncke**
- Genital capsule with small rounded teeth which diverge apically. Penis valves not noticeably bulbous, occupying less than 1/2 the space between the gonostyli..... **89**
- 89 Genital capsule compact, only slightly longer than wide, with the outer margin of the gonostyli slightly concave (Fig. 106B).....  
..... ***A. schmiedeknechti* Magretti (*partim*)**
- Genital capsule elongate, more-or-less twice as long as wide, with the outer margin of the gonostyli straight (Fig. 106C).....  
..... ***A. truncatilabris* Morawitz (*partim*)**
- 90(1) Mesepisternum conspicuously and densely punctate (Fig. 112D; punctures separated by 0.5 puncture diameters) AND ocellocipital distance at least 3 times the diameter of a lateral ocellus (*incisa*-group)..... **91**
- Mesepisternum either impunctate and/or ocellocipital distance of less than 3 times the diameter of a lateral ocellus..... **92**
- 91 Face and mesosoma with light brown pubescence. T2–4 laterally without patches of white pubescence, at most with obscure whitish hair bands.

- Terminal fringe light brown. Doubtfully recorded from the southern Balkans ..... ***A. incisa* Eversmann**
- Face and mesosoma with a mixture of black and white pubescence. T2–4 laterally with widely separated patches of dense white pubescence on their apical margins that obscure the underlying surface. Terminal fringe black. Uncommon, but recorded from multiple localities across the southern Balkans ..... ***A. lateralis* Morawitz**
- 92(90) Propodeal triangle clearly defined by strongly raised carinae, internal surface strongly and coarsely rugose-areolate (c.f. Fig. 90B) ..... **93**
- Propodeal triangle different, not strongly defined by lateral carinae, and/or with its internal surface smooth, reticulate, or finely rugose-areolate ..... **99**
- 93 Small species, 6–7 mm in length. Clypeus, scutum, and terga extremely densely and deeply punctate with small punctures, punctures almost confluent. Each side of T2 laterally with a small but deep and clearly defined elongate fovea ..... ***A. colletiformis* Morawitz**
- Larger species, at least 8 mm in length, usually >10 mm. Body never so densely punctate, punctures always a little separated, never confluent. T2 with fovea obscure to absent ..... **94**
- 94 Pronotum laterally with strong humeral angle with well-developed carina. Fore margin of clypeus weakly upturned ..... ***A. fuscosa* Erichson**
- Pronotum laterally rounded. Fore margin of clypeus normal, not upturned ..... **95**
- 95 Hind basitarsi and majority of hind tibiae lightened orange. Body with integument uniformly dark. Pubescence bright, face and mesepisternum with light brown hairs, scutum and T6 with bright orange hairs. A3 clearly shorter than A4 ..... ***A. haemorrhoea* (Fabricius)**
- Without this combination of characters; either hind legs dark, metasomal integument partially lightened orange or hyaline, and/or with A3 equaling A4. Inner hind tibial spur slightly but distinctly broadened at its base (subgenus *Plastandrena* Hedicke) ..... **96**

Members of this subgenus are taxonomically challenging to delineate and recognise; there remains a lack of consensus as to how many species exist in the Palaearctic region. A conservative position is taken here, but this may be subject to change depending on future molecular revisions.

- 96 Mesosoma with grey and black pubescence, always with at least some black hairs laterally on the mesepisternum. Genital capsule with the penis valves relatively narrow (Fig. 112E). Bivoltine, flying in the spring and summer . ..... ***A. pilipes* Fabricius**
- Mesosoma with brown pubescence dorsally and laterally, at most with occasional black hairs. Genital capsule otherwise. Flight period variable .... **97**



**Figure 112.** *Andrena (Truncandrena) rotundilabris* Morawitz, 1877 male. **A.** Head, frontal view; **B.** Genital capsule, dorsal view. *Andrena (Truncandrena) ulula* Warncke, 1969 male. **C.** Genital capsule, dorsal view. *Andrena (incertae sedis) lateralis* Morawitz, 1876 male. **D.** Mesosoma, lateral view. *Andrena (Plastandrena) pilipes* Fabricius, 1781 male. **E.** Genital capsule, dorsal view. *Andrena (Plastandrena) apiformis* Kriechbaumer, 1873 male. **F.** Genital capsule, dorsal view. *Andrena (Plastandrena) tibialis* (Kirby, 1802) male. **G.** Genital capsule, dorsal view. *Andrena (Plastandrena) bimaculata* (Kirby, 1802) male. **H.** Genital capsule, dorsal view.

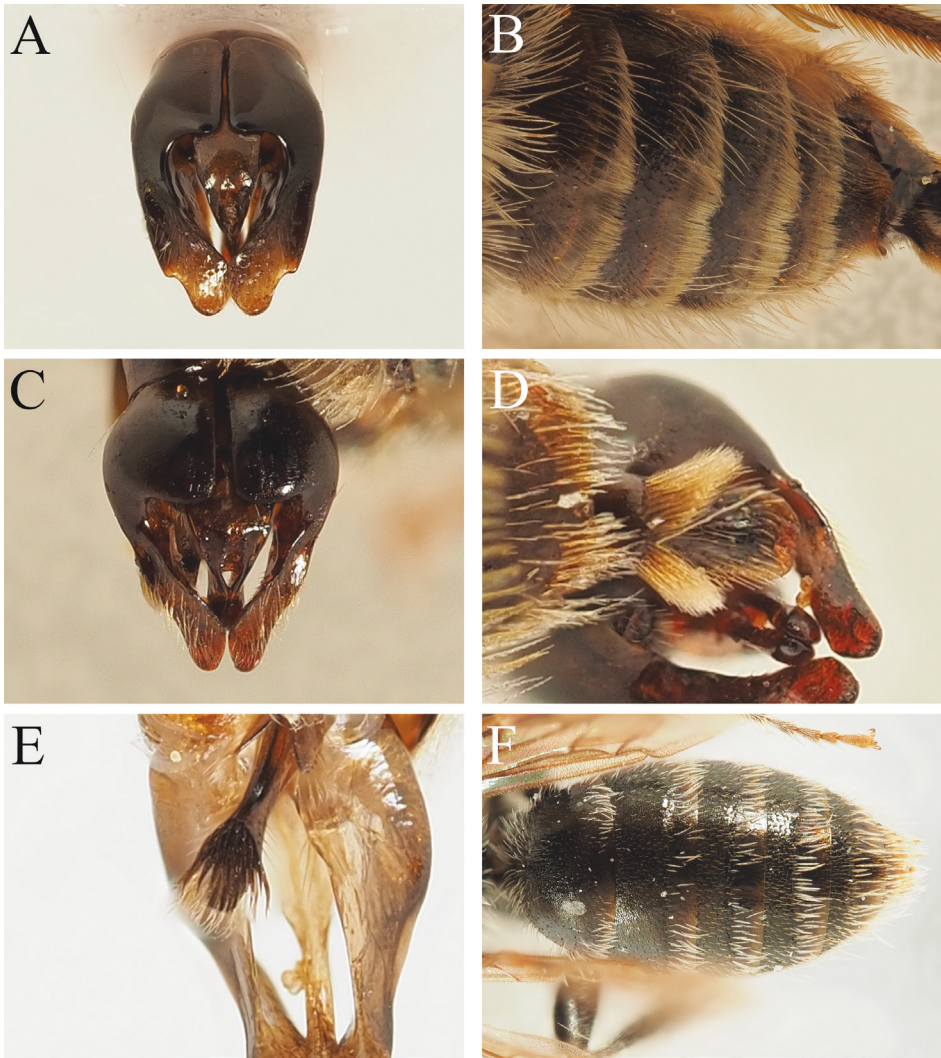
- 97 Tergal margins extensively lightened hyaline, reddish colouration extending at least partially onto T1–2. Genital capsule with the penis valves broadened, occupying the majority of the space between the gonostyli (Fig. 112F). Gonostyli in their apical part with their inner margins straight, without a distinct U-shaped emargination basally. Rare in the southern Balkans ..... ***A. apiformis* Kriechbaumer**
- Terga more typically dark, without reddish colouration. Penis valves variable in width, but apical part of the gonostyli always with a distinct U-shaped emargination basally (Fig. 112G, H) ..... **98**
- 98 Genital capsule with penis valves basally broad, apical part of the gonostyli relatively thickened (Fig. 112G). Nominally univoltine. Very rarely encountered in the southern Balkans ..... ***A. tibialis* (Kirby)**
- Genital capsule with penis valves basally narrow, apical part of the gonostyli normal, not relatively thickened (Fig. 112H). Bivoltine, flying in the spring and the summer. More commonly encountered in the southern Balkans ..  
..... ***A. bimaculata* (Kirby)**
- 99(92) Genital capsule distinctive, with more-or-less 90° emargination in the outer parts of the gonostyli (Fig. 113A). The most common *Andrena* species in the southern Balkans..... ***A. flavipes* Panzer**
- Genital capsule otherwise..... **100**
- 100 Process of the labrum thickened and expanded, anteriorly projecting beyond the fore margin of the clypeus. Pronotum with strong humeral angle. Active in the summer (mid-June to September) (subgenus *Cnemidandrena* Hedicke and remaining *Margandrena* Warncke) ..... **101**
- Without this combination of characters ..... **105**
- 101 T2–3 extensively red-marked. Clypeus with apical corners produced into distinct anteriorly projecting knobs. Typically found in low-lying warm Mediterranean or sub-Mediterranean habitats.....  
..... ***A. pellucens* Pérez**
- Terga dark, without red markings. Clypeus without apically projecting knobs anterolaterally. Found in cooler temperate habitats, usually in mountainous areas ..... **102**
- 102 Outer surface of the galea smooth and shiny. Associated with Ericaceae, and hence extremely marginal in the southern Balkans .....  
..... ***A. fuscipes* (Kirby)**
- Outer surface of the galea shagreened and dull..... **103**
- 103 Gena posteriorly produced into a strong winged carina. Scutum with abundant black hairs..... ***A. denticulata* (Kirby)**
- Gena posteriorly rounded. Scutum at most with occasional black hairs, usually entirely brown-haired..... **104**

The following two species are challenging to separate in the male sex. Association with concurrently active females should be made, if possible.

- 104 A3 at most as long as A4. Sterna with weak apical hairbands that do not obscure the underlying surface.....***A. nigriceps* (Kirby)**
- A3 slightly but distinctly longer than A4. Sterna with dense apical hairbands which obscure the underlying surface, these hairbands most visible on S2–5 (Fig. 113B).....***A. simillima* ssp. *sischkai* Warncke**
- 105(100) Fore margin of clypeus upturned AND gena conspicuously broadened, wider than the width of the compound eye AND pronotum with a conspicuous humeral angle (remaining *Notandrena* Pérez)..... **106**
- Without this exact combination of characters..... **109**
- 106 Genital capsule with the gonostyli narrow along their entire length, not broadening subapically (Fig. 113C). Gonostyli apically finger-like, slightly curving so that their outer margins are weakly but distinctly concave. S8 ventrally with 2 distinct apicolaterally projecting tufts of hairs, the ventral apex of the sternum bare (Fig. 113D).....***A. pontica* Warncke**
- Genital capsule with the gonostyli gently but distinctly broadening apically, broadest apically to subapically. Gonostyli flattened, outer margins not or only obscurely concave. S8 ventrally evenly covered with fine hairs..... **107**

The following three species are highly challenging to separate; care should be taken, and the detailed treatment and illustrations of Schwenninger (2013) consulted.

- 107 Disc of T2 basally finely and densely punctate, punctures separated by around 0.5 puncture diameters. Scutum shagreened and dull. Genital capsule with the gonostyli basally showing a strongly pronounced impression.....***A. curvana* Warncke**
- Disc of T2 basally with slightly more scattered punctation, punctures usually separated by around 1 puncture diameter or more. Scutum weakly shining to finely shagreened. Genital capsule with the gonostyli basally showing a weak or obscure impression..... **108**
- 108 Terga with marginal areas of T2–4 puncture-free. A3 shorter than A4+5, never twice as long as A4. Basitarsi usually dark, sometimes apically lightened orange. Typically in cooler parts of the southern Balkans; univoltine, flying on July–August.....***A. nitidiuscula* Schenck**
- Terga with punctures of discs of T2–4 extending onto marginal areas. A3 almost as long as A4+5, typically twice as long as A4. Basitarsi usually entirely lightened orange. Widespread across the southern Balkans; bivoltine, flying in April–May and July–August..... ***A. fulvicornis* Schenck**
- 109(105) Small species, body length of 5–7 mm (exceptionally 8 mm), terga always dark (*Aenandrena* Warncke *partim*, *Avandrena* Warncke, *Cryptandrena* Warncke *partim*, *Graecandrena* Warncke, and almost all *Micrandrena* Ashmead)..... **110**
- Larger species, at least 8 mm in length. Terga lightened red in some species, either on the discs or the margins. Hind tarsi or basitarsi lightened orange in some species..... **156**



**Figure 113.** *Andrena (Melandrena) flavipes* Panzer, 1799 male. **A.** Genital capsule, dorsal view. *Andrena (Cnemidandrena) simillima ssp. sischkai* Warncke, 1980 male. **B.** Mestasomal sterna, ventral view. *Andrena (Notandrena) pontica* Warncke, 1972 male. **C.** Genital capsule, dorsal view; **D.** Sternum 8, ventral view. *Andrena (Avandrena) panurgina* De Stefani, 1889 male. **E.** Sternum 8, ventral view. *Andrena (Aenandrena) bisulcata* Morawitz, 1877 male. **F.** Metasoma, dorsal view.

- 110 Mandibles elongate and crossing apically, basally strongly produced into a strong more-or-less 90° angle, this angle separated from the base of the mandible by a distance subequal to the basal breadth of the mandible (see fig. 1g, h in Scheuchl 2011). Very rare, currently known only from the East Aegean Islands (Samos) ..... *A. ebmerella* Scheuchl
- Mandibles variable in length, typically not or only weakly crossing apically, but never with a pronounced 90° angle at their base. Distribution variable ..... **111**

- 111 All tergal discs uniformly punctate, punctures separated by 0.5 puncture diameters, underlying surface weakly shiny. Genital capsule elongate (Fig. 67D), with weakly pronounced gonocoxal teeth, gonostyli apically produced into triangular wedges (subgenus *Cryptandrena* Warncke *partim*) ..... **112**
- Tergal discs more sparsely punctate or, if densely punctate, then genital capsule otherwise ..... **114**
- 112 Antennae with A3 more-or-less equal to A4 in length (Fig. 67G).....  
..... ***A. ventricosa* Dours (*partim*, dark form)**
- Antennae with A3 clearly exceeding A4 in length, almost as long as A4+5 (Fig. 67E, F) ..... **113**

Note, I have not personally encountered male specimens of *A. brumanensis* with a dark clypeus, but given the occurrence of dark specimens of *A. ventricosa*, this option is added here just in case.

- 113 Clypeus almost flattened. Scutum with punctures separated by <1 puncture diameter, interspaces relatively dull. Widespread across the southern Balkans but not on the island of Crete (Fig. 5).....  
..... ***A. brumanensis* Friese (*partim*, dark form)**
- Clypeus distinctly longitudinally domed (Fig. 67B). Scutum with punctures separated by 1–2 puncture diameters, interspaces shining (Fig. 67C). Found on the island of Crete (Fig. 5) ..... ***A. testudo* sp. nov.**
- 114 Terga with dull but distinct bronze lustre AND A3 short, equalling 1/2 the length of A4..... ***A. aeneiventris* Morawitz**
- Terga dark and non-metallic and/or A3 longer..... **115**
- 115 Head and mesepisternum with long and abundant black pubescence, hairs often exceeding the length of the scape, those on the mesepisternum may be intermixed with white hairs. A3 long, clearly exceeding A4 and only very slightly shorter than A4+5. Seemingly associated with *Erodium* (Geraniaceae) ..... **116**
- Head and mesepisternum without long and abundant black pubescence, usually with entirely pale and relatively short pubescence. A3 shorter, usually not exceeding the length of A4. Not associated with *Erodium*..... **117**
- 116 Ventral surface of S8 at its apex with a posteriorly-directed U-shaped fan of stiff black hairs (Fig. 113E). Ocelloccipital distance equalling to slightly exceeding the diameter of a lateral ocellus. Propodeal triangle poorly defined, lacking lateral carinae or internal rugae. In the southern Balkans, found only on the island of Corfu..... ***A. panurgina* De Stefani**
- Ventral surface of S8 with 2 laterally-directed tufts of dense brown hair positioned subapically. Ocelloccipital distance longer, around 3.5 times the diameter of a lateral ocellus. Propodeal triangle more strongly defined, laterally delineated by fine carinae and the internal surface with weakly raised fine rugae in its basal 1/2. Uncommon, but more widely distributed across the southern Balkans..... ***A. canohirta* (Friese)**

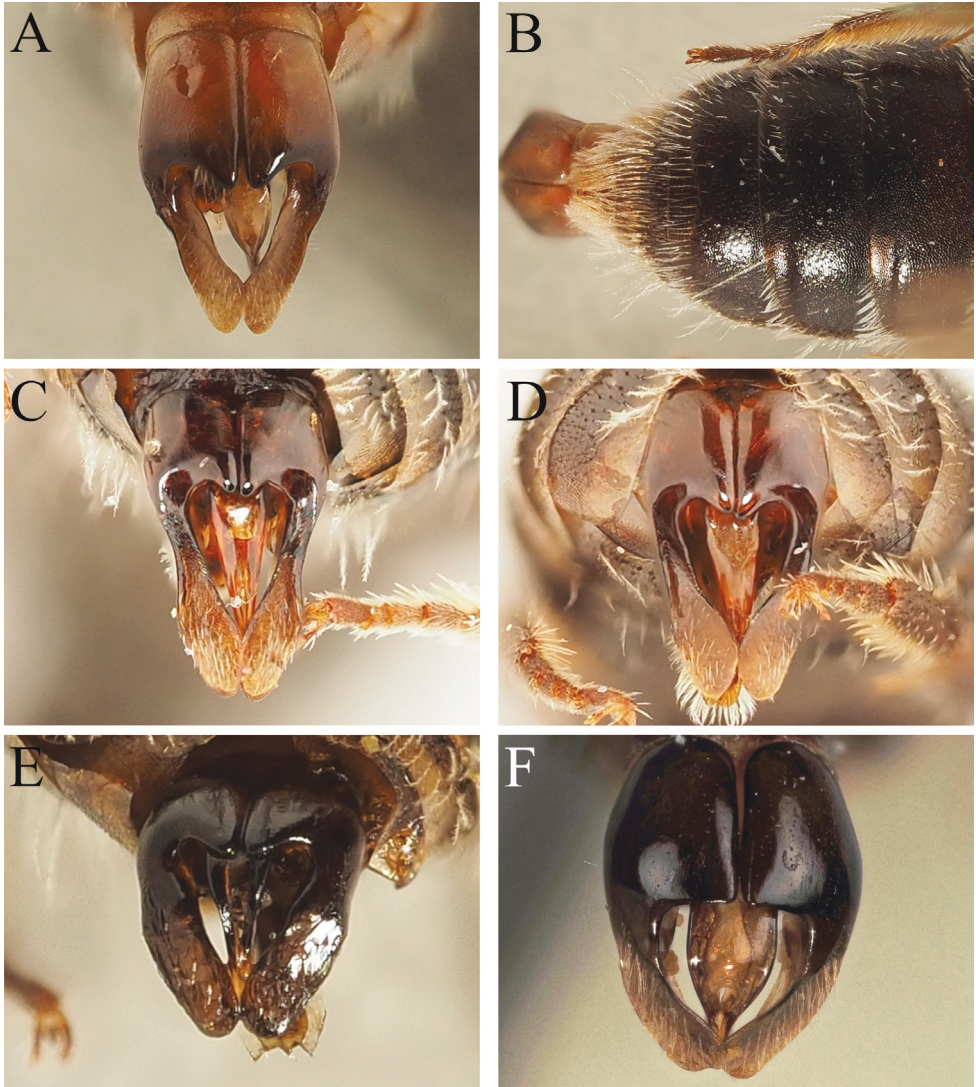
- 117 Marginal areas of T2–4 moderately wide (occupying 20–40% of the visible segment) and slightly but distinctly depressed, polished and shining and overlain by long densely plumose whitish hairs, in fresh specimens these almost obscuring the underlying surface (Fig. 113F). Ocelloccipital distance 1.5 times the diameter of a lateral ocellus. A3 exceeding the length of A4 which is distinctly sub-square (wider than long).....***A. bisulcata* Morawitz**
- Without this combination of characters..... **118**

As this character state can be ambiguous for some *Micrandrena* Ashmead species, they are keyed through both paths.

- 118 Propodeal triangle shagreened, not defined laterally by raised carinae, with internal surface lacking network of raised rugosity, at most with very short rugae at the base of the propodeal triangle (c.f. Fig. 97A, B). Tergal discs shagreened to microreticulate, more-or-less impunctate or with punctures obscure..... **119**
- Propodeal triangle either strongly defined by raised carinae or with internal surface with network of raised rugosity covering at least the basal 1/2 (c.f. Figs 97C, D, 98G, 99E, F). Tergal discs variably sculptured, often clearly punctate (subgenus *Micrandrena* Ashmead *partim*) ..... **128**
- 119 Genital capsule with the gonostyli flattened and parallel-sided AND with acutely pointed gonocoxal teeth (Fig. 114A). Tergal margins narrow, on T3–4 occupying <20% of the segment, distinctly depressed (Fig. 114B)...  
.....***A. tomora* Warncke (*partim*)**
- Genital capsule and tergal margins otherwise..... **120**
- 120 Genital capsule elongate (3 times longer than wide) with distinct anteriorly projecting pointed gonocoxal teeth (Fig. 114C, D) AND propodeal triangle completely without rugae, surface presenting fine granular shagreen. Associated with *Sedum* (Crassulaceae) (*sandanskia*-group) ..... **121**
- Genital capsule unusual, gonocoxae with their inner margins forming a 90°–120° angle, without or with the weakest indication of gonocoxal teeth (e.g. Figs 21E, F, 114E, F); if in doubt, genital capsule rounded, more-or-less as long as wide, never conspicuously elongate. Gonostyli often flattened with square truncate apices. Propodeal triangle basally with short but distinct rugae. Not typically associated with *Sedum*, more typically collected on Brassicaceae or Apiaceae (subgenus *Graecandrena* Warncke) ..... **122**
- 121 Scutum and scutellum with granular microreticulation, dull and relatively regularly punctate with punctures separated by 0.5–2 puncture diameters. Outer margin of the gonostyli slightly concave (Fig. 114C). Slightly larger (5–5.5 mm in length). Widespread across the southern Balkans.....  
.....***A. sandanskia* Warncke**
- Scutum and scutellum finely shagreened, weakly shining and irregularly punctate with punctures separated by 1–3 puncture diameters. Terga with the lateral margins of T2–4 with weak apical hair fringes. Outer margin of

- the gonostyli straight (Fig. 114D). Slightly smaller (4–4.5 mm in length). Found only on the island of Crete.....***A. lediveleci* Wood**
- 122 Nervulus strongly antefurcal, separated from the basal vein by at least 5 vein widths. Genital capsule with inner margins of the gonocoxae weakly produced into short rounded teeth (Fig. 114E). Known only from continental Greece (Fig. 22) .....***A. helenica* Warncke**
- Nervulus interstitial to at most weakly antefurcal. Genital capsule with the inner margins of the gonocoxae forming a 90°–120° angle. Distribution variable ..... **123**
- 123 Genital capsule with the inner margins of the gonocoxae forming a 90° angle (Fig. 114F). Penis valves broad, occupying the majority of the space between the gonostyli. Found only in the Peloponnese, typically in mountainous areas ..... ***A. pelopa* Warncke**
- Genital capsule with the inner margins of the gonocoxae forming an approximately 120° angle (e.g. Fig. 21E, F). Penis valves variable, often occupying under 1/2 the space between the gonostyli. Distribution variable, usually found at lower altitudes..... **124**
- 124 Clypeus broadly flattened in its basal 1/2. Supraclypeal area with distinct longitudinal striations. Genital capsule with the gonostyli forming broad and quadrately-truncate apices.....***A. impunctata* Pérez**
- Clypeus evenly domed. Supraclypeal area without striations. Genital capsule with the gonostyli narrowing apically, apices not quadrately-truncate (Fig. 21E, F) ..... **125**
- 125 Ocellocipital distance 1.5 times the diameter of a lateral ocellus. Found in continental parts of northern Greece, North Macedonia, and Bulgaria .....  
.....***A. graecella* Warncke**
- Ocellocipital distance clearly less than the diameter of a lateral ocellus, typically around 0.5 times this diameter..... **126**
- 126 Found on the island of Crete (male unknown, but will most likely be restricted to this island based on the study of females, Fig. 23) .....  
.....***A. cretica* sp. nov.**
- Not found on the island of Crete ..... **127**
- 127 Penis valves occupying the majority of the space between the gonostyli (Fig. 21E). Widespread across the southern Balkans (Fig. 23) .....  
..... ***A. hyemala* Warncke**
- Penis valves occupying less than 1/2 the space between the gonostyli (Fig. 21F). Found only on the island of Rhodes (Fig. 23) ..... ***A. repressa* Warncke**
- 128 Terga with the marginal areas broad and poorly defined, occupying around 1/2 the visible segment; these marginal areas are polished, shining, and finely and sparsely punctate with punctures separated by 2–3 puncture diameters. Genital capsule slightly elongate, gonocoxae weakly produced into rounded teeth, gonostyli long and parallel-sided, with their outer margins

- almost completely straight. Known only from mountainous parts of Greece (Fig. 32)..... *A. cedricola* Wood
- Combination of characters otherwise ..... 129
- 129 Genital capsule with the gonostyli flattened and parallel-sided AND with acutely pointed gonocoxal teeth (Fig. 114A). Tergal margins narrow, on T3–4 occupying <20% of the segment, distinctly depressed (Fig. 114B)...  
..... *A. tomora* Warncke (*partim*)
- Combination of characters otherwise ..... 130
- 130 Head with abundant pubescence, in fresh specimens with long hairs emerging from the clypeus which extent ventrally far beyond the apical margin of the clypeus. Genital capsule with very strongly produced rounded gonocoxal teeth, when viewed dorsally these covering the entirety of the base of the broadened penis valves (Fig. 115A). Gonostyli produced into rounded rectangular apices with their internal margins strongly raised and forming a roughly 100° angle ..... *A. querquedula* Warncke
- Combination of characters otherwise ..... 131
- 131 Genital capsule elongate, 3 times longer than wide with strongly produced narrow gonocoxal teeth. Penis valves relatively narrow, slightly broadened medially but overall occupying around 1/2 the space between the gonostyli (Fig. 115B). Propodeal triangle evenly covered with raised rugae, but poorly defined laterally and lacking raised carinae. North Macedonia .....  
..... *A. incognita* Warncke
- Combination of characters otherwise ..... 132
- 132 Genital capsule with penis valves clearly and strongly broadened basally, clearly bulbous in appearance and occupying almost all of the space between the gonostyli (e.g Fig. 115C) ..... 133
- Genital capsule with penis valves not strongly broadened basally ..... 135
- 133 Marginal area of T1 wide, strongly thickened, impunctate. Scutum with scattered punctures, punctures separated by 1–3 puncture diameters. Genital capsule with gonocoxal teeth weakly produced (Fig. 115C). Restricted to mountainous areas northern parts of the southern Balkans, associated with *Potentilla* (Rosaceae)..... *A. falsifica* Perkins
- Marginal area of T1 not strongly thickened, flat or slightly depressed. Genital capsule with gonocoxal teeth truncate or weakly produced..... 134
- 134 Clypeus flattened, with slight longitudinal impression medially. Inner margin of the gonostyli upturned, diverging dorsally from outer margin, forming a slight but visible ‘kink’. Associated with *Ornithogalum* (Asparagaceae). Widespread across the southern Balkans, but seemingly not on the East Aegean Islands..... *A. saxonica* Stöckhert
- Clypeus less strongly flattened. Inner margin of the gonostyli parallel with the outer margin, without a visible ‘kink’. Associated with flowering trees and shrubs. North Macedonia ..... *A. strohmella* Stöckhert

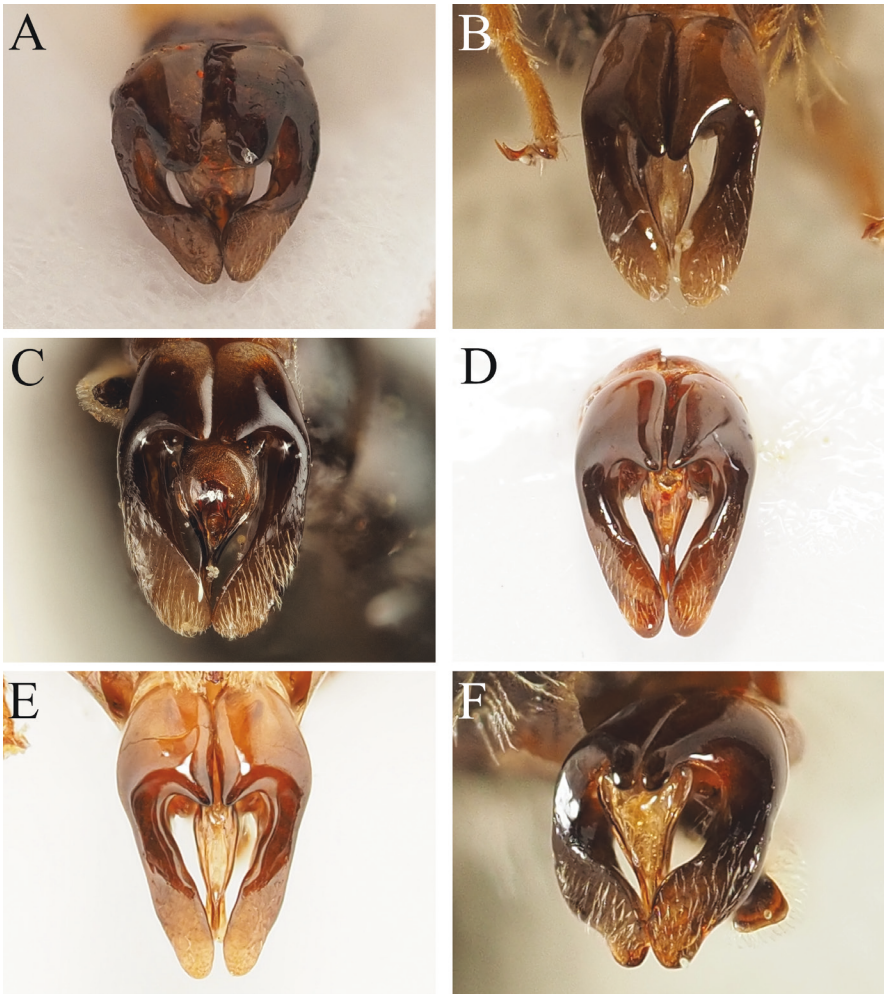


**Figure 114.** *Andrena (Micrandrena) tomora* Warncke, 1975 male. **A.** Genital capsule, dorsal view; **B.** Metasomal terga 2–4, dorsal view. *Andrena (Aciandrena) sandanskia* Warncke, 1973 male. **C.** Genital capsule, dorsal view. *Andrena (Aciandrena) lediveleci* Wood, 2024 male. **D.** Genital capsule, dorsal view. *Andrena (Graecandrena) helenica* Warncke, 1965 male. **E.** Genital capsule, dorsal view. *Andrena (Graecandrena) pelopa* Warncke, 1975 male. **F.** Genital capsule, dorsal view.

135

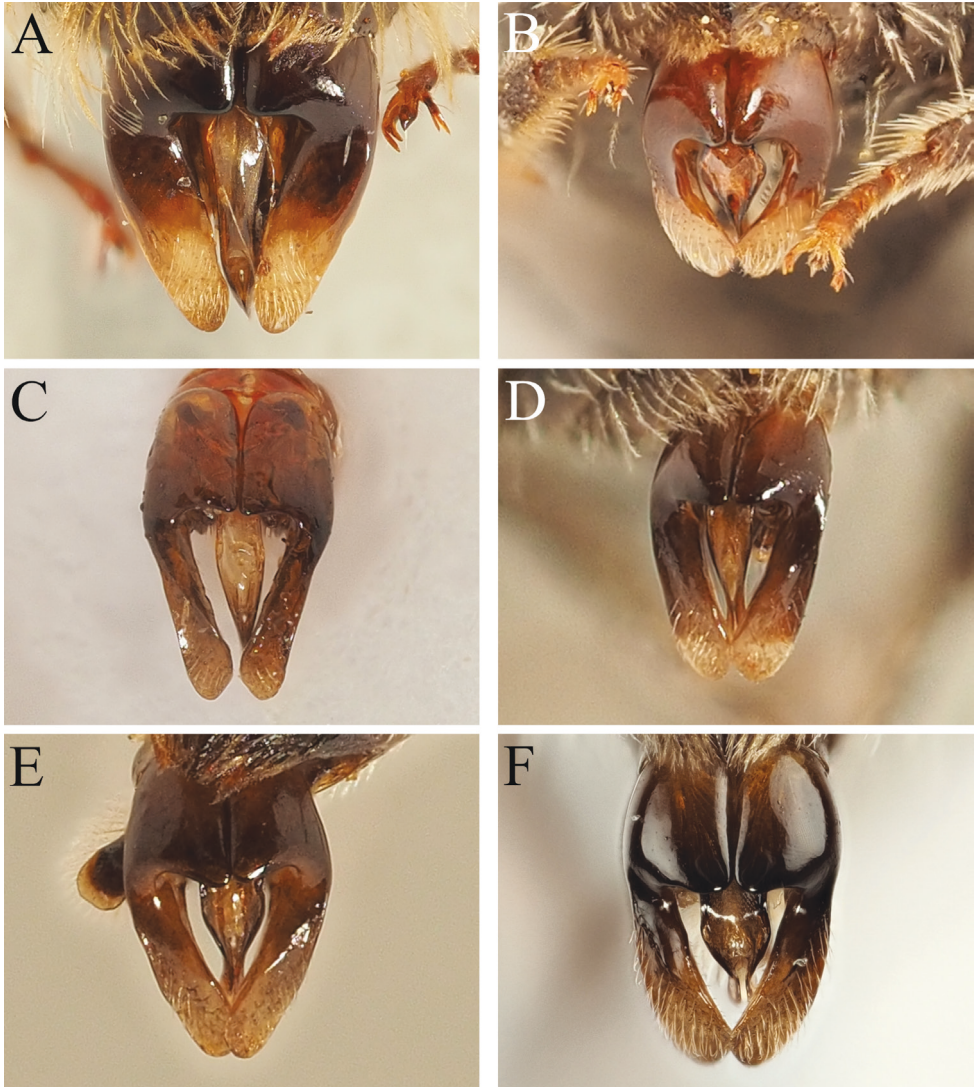
Propodeal triangle poorly defined, lacking or with very obscure lateral carinae. Internal surface of the propodeal triangle with rugae reaching only 1/2 way, not continuing to the junction with the vertical face, the surface here rounded and relatively smooth. Genital capsule elongate, with the outer margins of the gonostyli straight, and with the gonocoxae produced

- into moderately strong teeth (Fig. 115D, E). Associated with Asteroideae (Asteraceae) (*rugothorace*-group)..... **136**
- Propodeal triangle well-defined, with clearly produced lateral carinae. Internal surface of the propodeal triangle evenly covered by rugae. Not specifically associated with Asteraceae ..... **137**
- 136 Genital capsule with the inner and outer margins of the gonostyli more-or-less parallel, the outer margin evenly rounded from the gonocoxae to its apex (Fig. 115D). Gonostyli shorter, giving the overall capsule a more compact appearance in direct comparison. Widespread in the southern Balkans, but not the island of Crete ..... ***A. rugothorace* Warncke**
- Genital capsule with the gonostyli basally slightly constricted, with the inner and outer margins not parallel, the outer margin with a slight emargination, and the inner margin with a slightly produced bump (Fig. 115E). Gonostyli with their apices tapered and elongate, giving the overall capsule a more feeble and pointed appearance. Found only on the island of Crete ..... ***A. pelagica* Warncke**
- 137 Genital capsule with outer margins of the gonostyli concave (Fig. 115F). Clypeus strongly shagreened and dull ..... ***A. simontornyella* Noskiewicz**
- Genital capsule with outer margins of the gonostyli essentially parallel with the inner margins. Clypeus variable ..... **138**
- 138 Clypeus flattened, basally with obscure but distinct longitudinal striations, these covering the basal 1/4 of the clypeus and are channelled laterally along its margins..... ***A. distinguenda* Schenck**
- Clypeus typically domed, but always without longitudinal striations basally ..... **139**
- 139 Genital capsule elongate with penis valves converging apically to form a tapering point. Propodeum with propodeal triangle broad, laterally poorly defined with lateral carinae becoming shorter and weaker posteriorly. Uncertainly recorded from the southern Balkans..... ***A. niveata* Friese**
- Genital capsule and propodeal triangle otherwise..... **140**
- 140 Tergal discs, at least on T1, smooth and shiny, at most with very fine shagreen..... **141**
- Tergal discs including T1 shagreened or microreticulate, not strongly shiny, mostly dull and matt..... **146**
- 141 Forewing with first submarginal cross vein separated from the stigma by 3 times its own width..... **142**
- Forewing with first submarginal cross vein separated from the stigma by more-or-less its own width..... **145**
- 142 Genital capsule with the inner margins of the gonocoxae forming a 90° angle, the gonostyli consistently broad for their entire length, and the penis valves narrow and apically produced into a sharp point (Fig. 116A). A3 at least 1.6 times longer than A4..... ***A. enslinella* Stöckhert**
- Genital capsule otherwise. A3 at most 1.4 times longer than A4 ..... **143**



**Figure 115.** *Andrena (Micrandrena) querquedula* Warncke, 1975 male. **A.** Genital capsule, dorsal view. *Andrena (Micrandrena) incognita* Warncke, 1975 male. **B.** Genital capsule, dorsal view. *Andrena (Micrandrena) falsifica* Nylander, 1848 male. **C.** Genital capsule, dorsal view. *Andrena (Micrandrena) rugothorace* Warncke, 1965 male. **D.** Genital capsule, dorsal view. *Andrena (Micrandrena) pelagica* Warncke, 1975 male. **E.** Genital capsule, dorsal view. *Andrena (Micrandrena) simontornyella* Noskiewicz, 1939 male. **F.** Genital capsule, dorsal view.

- 143 Clypeus with distinct individual punctures, often with the interspaces shining. Stigma bright, yellowish to reddish. Discs of T2–3 densely but finely punctate, punctures separated by 0.5–1 puncture diameters. Sternal discs finely shagreened and shiny.....**A. floricola** Eversmann
- Clypeus microreticulate and covered with weakly raised rugosity, at most obscurely punctate due to this irregular roughness, overall clypeal surface appearing dull. Stigma dark brown. Discs of T2–3 very densely and coarsely punctate, punctures confluent. Sterna microreticulate and weakly shining to dull (*nana*-group) ..... **144**



**Figure 116.** *Andrena (Micrandrena) enslinella* Stöckhert, 1924 male. **A.** Genital capsule, dorsal view. *Andrena (Micrandrena) sillata* Warncke, 1975 male. **B.** Genital capsule, dorsal view. *Andrena (Micrandrena) biarmica* Warncke, 1975 male. **C.** Genital capsule, dorsal view. *Andrena (Micrandrena) paganettina* Warncke, 1965 male. **D.** Genital capsule, dorsal view. *Andrena (Micrandrena) minutula* (Kirby, 1802) male. **E.** Genital capsule, dorsal view. *Andrena (Micrandrena) minutuloides* Perkins, 1914 male. **F.** Genital capsule, dorsal view.

- 144 Scutum densely punctate, punctures separated by <0.5 puncture diameters, interspaces dull to at most weakly shining. Widespread across the southern Balkans ..... ***A. magunta* Warncke**
- Scutum slightly less densely punctate, punctures separated by 0.5–1 puncture diameters, interspaces polished and shining. Uncommonly and unclear recorded from North Macedonia and Bulgaria ..... ***A. nana* (Kirby)**

The following two species are challenging to separate without access to confidently determined reference material.

- 145 Spring generation (black to dark facial hair) with clypeus densely punctate, often with transverse striations basally, clypeus generally dull. Summer generation (pale facial hair) with clypeus densely punctate, punctures almost confluent, interspaces dull.....***A. alfkennelloides* Warncke**
- Spring generation (black facial hair) with clypeus comparatively more sparsely punctate, therefore more strongly shining, never with transverse striations. Summer generation (pale facial hair) with clypeus comparatively more sparsely punctate, punctures separated by up to 1 puncture diameter, interspaces polished and shining .....***A. alfkenella* Perkins**
- 146 Genital capsule with the gonocoxae produced into small but distinct apically projecting rounded teeth (Fig. 116B). Penis valves moderately broad, rhomboidal and distinctly constricted submedially at junction with gonocoxal teeth before broadening medially; at their widest, occupying slightly more than 1/2 the space between the gonostyli. Rare, known only from Rhodes.....***A. sillata* Warncke**
- Genital capsule otherwise..... **147**
- 147 Clypeus polished over the majority of its surface, at least in the apical 2/3, puncture interspaces distinctly shining. Body size small, 4–5 mm in length. Found in northern parts of the southern Balkans .....***A. tringa* Warncke**
- Clypeus microreticulate and dull. If with its apical margin shining (*rugulosa*-group), then considerably larger than 5 mm (around 7–8 mm) ..... **148**
- 148 Tergal discs with very strong granular microreticulation, most strongly produced on T1–2. Clypeus with weak but distinctly raised latitudinal striations. Scutum with strong and rough reticulation, dull and obscurely punctate. Genital capsule slightly elongate, relatively featureless (Fig. 116C). Rare, known only from the East Aegean Islands.....***A. biarmica* Warncke**
- Without this combination of characters; clypeus never with raised latitudinal striations ..... **149**
- 149 Terga with the marginal areas of T2–4 strongly depressed relative to the disc ..... **150**
- Terga with the marginal areas of T2–4 not or only weakly depressed relative to the disc ..... **153**
- 150 Measured ventrally, A3 distinctly longer than A4, almost as long as A4+5. Process of the labrum narrow, slightly longer than broad. Scutum with rough microreticulation, some punctures with raised margins, thus approaching a crater puncture-like state. Terga with the marginal areas of T2–4 comparatively less strongly depressed (*rugulosa*-group) ..... **151**
- Measured ventrally, A3 only very slightly longer than A4, clearly shorter than A4+5. Process of the labrum more-or-less rectangular, twice as broad as long. Scutum with fine microreticulation, punctures fine and without

- raised rims. Terga with the marginal areas of T2–4 comparatively more strongly depressed (*spretta*-group)..... **152**

151 Ocelloccipital distance subequal to or equalling the diameter of a lateral ocellus (c.f. Fig. 99C). Common and widespread... ***A. rugulosa* Stöckert**

– Ocelloccipital distance exceeding 2 times the diameter of a lateral ocellus, approaching 3 times this diameter (c.f. Fig. 99D). Very seldom encountered in the southern Balkans..... ***A. illyrica* Warncke**

It is not actually clear if males of the following two species can be consistently separated morphologically. A suggested character is given, but it may not actually work. Based on the distribution of female specimens, the geographic framework should be consulted to aid identification.

- 152 Scutum comparatively sparsely punctate, punctures separated on average by 1–1.5 puncture diameters. Surface of scutum finely shagreened and weakly shining. Widespread in the southern Balkans ..... ***A. pusilla* Pérez**

– Scutum comparatively densely punctate, punctures separated on average by 0.5–1 puncture diameters, sometimes by less. Surface of scutum variably sculptured but usually very weakly shagreened to polished and shining, therefore on average more brightly shining despite denser punctation. Very rare in the southern Balkans, known only from the island of Corfu ..... ***A. spreta* Pérez**

153 Very small species, 4–5 mm in length. Apical tarsal segments and sometimes basitarsi lightened orange. Genital capsule with the gonostyli apically truncate AND penis valves relatively narrow (Fig. 116D) ..... ***A. paganettina* Warncke**

– Slightly larger, 5–7 mm in length. Tarsi variable. Genital capsule otherwise; if with apices of the gonostyli truncate THEN with the penis valves slightly broadened basally (Fig. 116E, F)..... **154**

154 Scutum with fine and sparse punctation, punctures separated by 2–4 puncture diameters, underlying surface matt. All specimens always with pale facial pubescence. Uncommon in cool temperate parts of the southern Balkans ..... ***A. subopaca* Nylander**

– Scutum with clear punctation, punctures variably spaced, but at least some separated by 1 puncture diameter. Spring-flying individuals with dark facial pubescence, summer-flying individuals with pale facial pubescence. More widespread across the southern Balkans, though typically not in hot Mediterranean habitats ..... **155**

155 Scutum densely punctate, punctures typically separated by 1 puncture diameter. Scutum and scutellum shagreened and dull (spring generation, dark facial hair) to weakly shiny (summer generation, pale facial hair). Genital capsule as in Fig. 116E..... ***A. minutula* (Kirby)**

– Scutum more sparsely and irregularly punctate, punctures separated by 1–3 puncture diameters. Scutum and scutellum finely shagreened and weakly

- shiny (spring generation, dark facial hair) to polished and shiny (summer generation, pale facial hair). Genital capsule as in Fig. 116F.....  
 .....*A. minutuloides* Perkins  
 156(109) Clypeus flattened over majority of its surface (subgenus *Taeniandrena* Hedicke, subgenus *Troandrena* Warncke)..... 157  
 – Clypeus not flattened..... 166

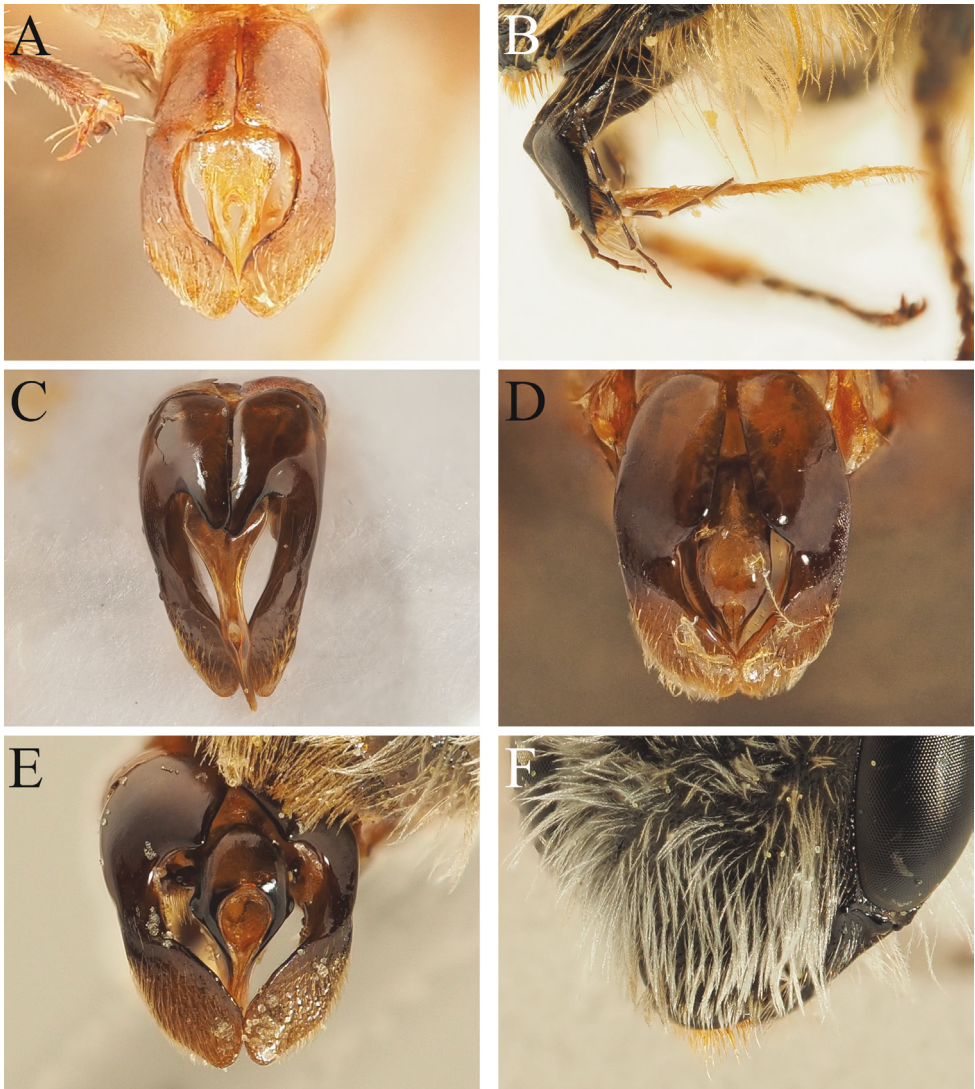
Extraction of the genital capsule is necessary for species-level identifications within this group of species.

- 157 Terga extensively or partly red-marked. Genital capsule with the inner margins of the gonocoxae forming a more-or-less 120° angle, without gonocoxal teeth (Fig. 117A). Clypeus with shining interspaces. Restricted to the East Aegean Islands (Samos, Rhodes).....*A. praecocella* Cockerell  
 – Terga uniformly dark, never red-marked. Genital capsule otherwise, with the inner margins of the gonostyli either produced into apically projecting teeth (Fig. 117C), remaining close together and forming a 90° angle (Fig. 118A–C), or widely diverging apically but still forming at most a 90–100° angle (Fig. 117E). In one species (*Andrena producta*) with the inner margins of the gonocoxae forming a more-or-less 120° angle (Fig. 117D), but this species has the gonostyli with strongly raised inner margins in addition to its continental distribution. Clypeus variable, often uniformly dull. Distribution variable (subgenus *Taeniandrena* Hedicke)..... 158  
 158 Mouthparts highly distinctive; glossa exceeding the length of the galea by at least twice the length of the galea itself, strongly bent medially and forming a 90° angle (Fig. 117B; see also Müller and Westrich 2023) .....  
 ..... *A. lathyri* Alfken  
 – Mouthparts otherwise, never with the glossa so strongly exceeding the length of the galea..... 159  
 159 Genital capsule with strongly produced gonocoxal teeth (Fig. 117A). Penis valves basally broad and flared before narrowing apically and produced into an acute point. Associated with shrubby Fabaceae in open grasslands (such as *Chamaecytisus*) .....*A. aberrans* Eversmann  
 – Genital capsule otherwise, never with such strongly produced gonocoxal teeth ..... 160  
 160 Genital capsule with the penis valves moderately broadened, and the inner margins of the gonocoxae strongly diverging and forming a more-or-less 120° angle apically (Fig. 117D). Found in warm grasslands to moderate altitude in northern parts of the southern Balkans.....  
 ..... *A. producta* Warncke  
 – Genital capsule otherwise, either with the penis valves narrower or the shape of the gonocoxae different ..... 161

- 161 Penis valves very strongly broadened, occupying the majority of the space between the gonostyli, with the median valve expanded and almost as wide as the diameter of a lateral ocellus (Fig. 117E). A4 slightly but distinctly longer than A3. In the southern Balkans, typically found in mountainous areas, with this trend becoming more pronounced the further south one travels; in Greece, known from above 1500 m .....  
 ..... ***A. intermedia* Thomson**
- Genital capsule otherwise, never with such strongly broadened penis valves. A4 variable..... **162**
- 162 A4 long, 1.4–1.6 times longer than A3 and hence clearly and noticeably longer than it..... **163**
- A4 not noticeably elongate, 0.8–1.2 times longer than A3, essentially the same length..... **164**
- 163 Clypeus in fresh specimens with a dense fringe of snow-white hairs, these ventrally projecting and obscuring the surface of the clypeus (Fig. 117F). Body with whitish pubescence. Terga finely but densely microreticulate, at most obscurely punctate; declivous part of T1 nearly impunctate. Common and widespread throughout the southern Balkans (Fig. 80).....  
 ..... ***A. ovata* Schenck**
- Clypeus without noticeably dense pubescence, never with a dense apical fringe. Body with yellowish pubescence, but beware of faded specimens. Terga distinctly punctate, particularly on the declivous part of T1. Uncommonly encountered in the southern Balkans (historical identifications usually belong to *A. ovata*), probably restricted to mountainous areas.....  
 ..... ***A. wilkella* (Kirby)**

As noted in the main text for subgenus *Taeniandrena* Hedicke, there is taxonomic complexity associated with *A. russula*. Material in this group should be treated with caution, pending a more detailed genetic assessment.

- 164 Genital capsule slightly elongate, penis valves very gently tapering and almost parallel-sided. A3 often slightly longer than A4, but this seem subject to variation and should be treated with caution. Terga with punctures generally obscure and difficult to see against the underlying sculpture. Tarsi orange, hind tibiae predominantly to partly orange. Terga typically without clear and complete apical hairbands ..... ***A. russula* Lepelletier**
- Genital capsule shorter and more rounded, penis valves often slightly broadened basally and then contracted medially, hence not gently tapering (Fig. 118A–C). A3 usually shorter than or as long as A4. Terga typically with dense and visible punctuation that contrasts the underlying sculpture. Leg colouration variable. Terga of fresh specimens with complete apical hairbands on T2–4 ..... **165**



**Figure 117.** *Andrena (Troandrena) praecocella* Cockerell, 1917 male. **A.** Genital capsule, dorsal view. *Andrena (Taeniandrena) lathyri* Alfken, 1899 male. **B.** Mouthparts, lateral view. *Andrena (Taeniandrena) aberrans* Eversmann, 1852 male. **C.** Genital capsule, dorsal view. *Andrena (Taeniandrena) producta* Warncke, 1973 male. **D.** Genital capsule, dorsal view. *Andrena (Taeniandrena) intermedia* Thomson, 1870 male. **E.** Genital capsule, dorsal view. *Andrena (Taeniandrena) ovata* Schenck, 1853 male. **F.** Clypeus, lateral view.

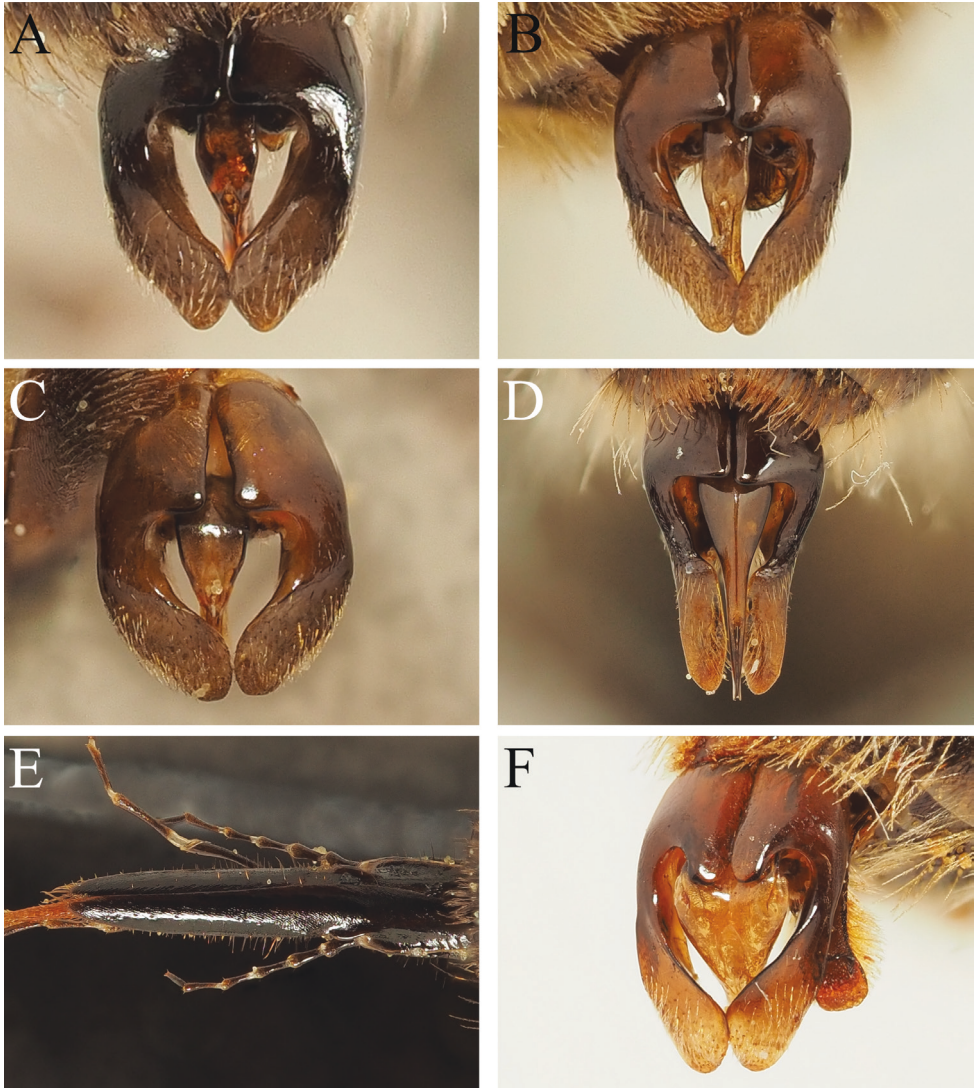
The following three species have very similar males and are best diagnosed concurrently.

165 Genital capsule with the penis valves not noticeably broadened basally and the apices of the gonostyli both truncate and produced into a slight anteriorly projecting point (Fig. 118A). Pubescence in fresh specimens white.

- Voltinism unclear, recorded from April to July at various altitudes .....  
 ..... *A. leucopsis* Warncke
- Genital capsule with the penis valves not noticeably broadened basally and the outer margins of the gonostyli slightly but distinctly concave (Fig. 118B). Pubescence in fresh specimens orange-brown. Univoltine, late May to early July..... *A. taedium* Wood
- Genital capsule with the penis valves slightly but distinctly broadened basally before being contracted medially and the outer margins of the gonostyli are slightly convex, hence the capsule appears rounded (Fig. 118C). Pubescence in fresh specimens orange-brown. Bivoltine, May to August...  
 ..... *A. afzeliella* (Kirby)
- 166(156) At least some tergal discs red-marked ..... 167
- Tergal discs never with red markings..... 171
- 167 A3 much shorter than A4, at most 1/3 the length ..... 168
- A3 clearly longer than A4 ..... 169
- 168 S8 apically truncate, lacking apical emargination. Mandibles always bidentate ..... *A. rosae* Panzer (*partim*, light form)
- S8 with clear apical emargination. Mandibles unidentate (1<sup>st</sup> generation) or bidentate (2<sup>nd</sup> generation) ..... *A. trimmerana* (Kirby) (*partim*, light form)
- 169 Head broad, inner margin of compound eyes diverging ventrally. Pronotum with strong humeral angle. Clypeus smooth and shiny with scattered punctures. Genital capsule unique, elongate, gonocoxae truncate with inner margin rounded, penis valves basally broad, strongly narrowing medially to become elongate and acutely pointed apically (Fig. 118D). Associated with *Bryonia* (Cucurbitaceae)..... *A. florea* Fabricius
- Without this combination of characters ..... 170
- 170 Clypeus shagreened and matt. Mesonotum and disc of T1 strongly and densely punctate. Hind basitarsi lightened orange. In the southern Balkans, restricted to the Rhodope mountains in Bulgaria, associated with *Campanula* (Campanulaceae)..... *A. rufizona* Imhoff
- Clypeus smooth and shiny. Mesonotum and disc of T1 weakly punctate with scattered punctures. Hind basitarsi dark. More widespread across the southern Balkans..... *A. parviceps* Kriechbaumer (*partim*, light form)
- 171(166) Tergal discs with distinct metallic blue reflections (c.f. Fig. 94B, D, F) ..... 172
- Tergal discs dark, without metallic reflections, or at most with greasy greenish or bronzy reflections laterally (see couplet 228), never with blue metallic reflections ..... 175
- 172 Tergal discs with abundant ‘crater punctures’ with raised rims. Pubescence of mesosoma and face light brown, never with abundant black and white hairs..... *A. nigroolivacea* Dours
- Tergal discs with simple punctures, without noticeably raised rims. Pubescence of mesosoma with abundant black and white hairs, on the mesosoma forming a striped pattern; white anteriorly and posteriorly, medially with a uniform black strip (*cineraria*-group) ..... 173

The members of the *cineraria*-group are challenging to separate consistently, and the morphological and molecular species boundaries are not fully established.

- 173 A3 0.6 times as long as A4. Facial hair shorter than the width of a compound eye. Antennal scape with intermixed black and white hairs. Bivoltine, flying in the spring and the summer, found in mountainous areas .....  
 ..... ***A. barbareae* Panzer**
- A3 as long or almost as long as A4. Facial hair exceeding the width of a compound eye. Antennal scape with uniformly white hairs. Univoltine (mostly April–May) ..... **174**
- 174 Smaller, 11–12 mm in length. Metasoma slender and elongate, with a faint bluish or purplish to blackish tinge. Rare in the southern Balkans, probably found only in the north in areas with cooler temperate habitats .....  
 ..... ***A. cineraria* (Linnaeus)**
- Larger, 13–14 mm in length. Metasoma broader, with a strong and bright metallic blue colour, never with purplish-black colouration. Common and widespread, found in warm Mediterranean to sub-Mediterranean habitats .....  
 ..... ***A. danuvia* Stöckhert**
- 175(171) Mandibles elongate, sickle-like, strongly crossing apically. Pronotum with strong humeral angle. Gena often expanded, broader than the width of a compound eye ..... **176**
- Without this combination of characters; mandibles normal, not elongate and strongly crossing apically. Pronotum usually without a strong humeral angle. Gena usually normal, equalling or shorter than the width of a compound eye ..... **202**
- 176 In frontal view, glossa equalling the length of the head. Surface of the glossa with fine but distinct laterally projecting bristles (Fig. 118E, compare the strength of the bristles in the female sex, Fig. 96A). Malar space slightly elongate, around 50% as long as the basal width of the mandible. Mesosoma with predominantly greyish pubescence, with intermixed black hairs on the mesepisternum and propodeum. Associated with *Anchusa* (Boraginaceae) ..... ***A. nasuta* Giraud**
- Without this combination of characters ..... **177**
- 177 Genital capsule with the penis valves laterally produced into sharp projecting points (Fig. 74F). Mouthparts with palpi distinctly elongated (Fig. 74C). Metasoma oviform (Fig. 74E). Associated with *Crocus* (Iridaceae) and *Muscari* (Asparagaceae) (*crocusella*-group) ..... **178**
- Combination of characters otherwise. Not associated with these plants ..... **180**
- 178 Mouthparts with 6 maxillary palpi and 4 labial palpi. Flying in the spring (March–April) and associated with *Muscari* ..... ***A. muscaria* Warncke**
- Mouthparts with at least 7 maxillary palpi and 6 labial palpi. Flying in the autumn (October–early December) and associated with *Crocus* ..... **179**



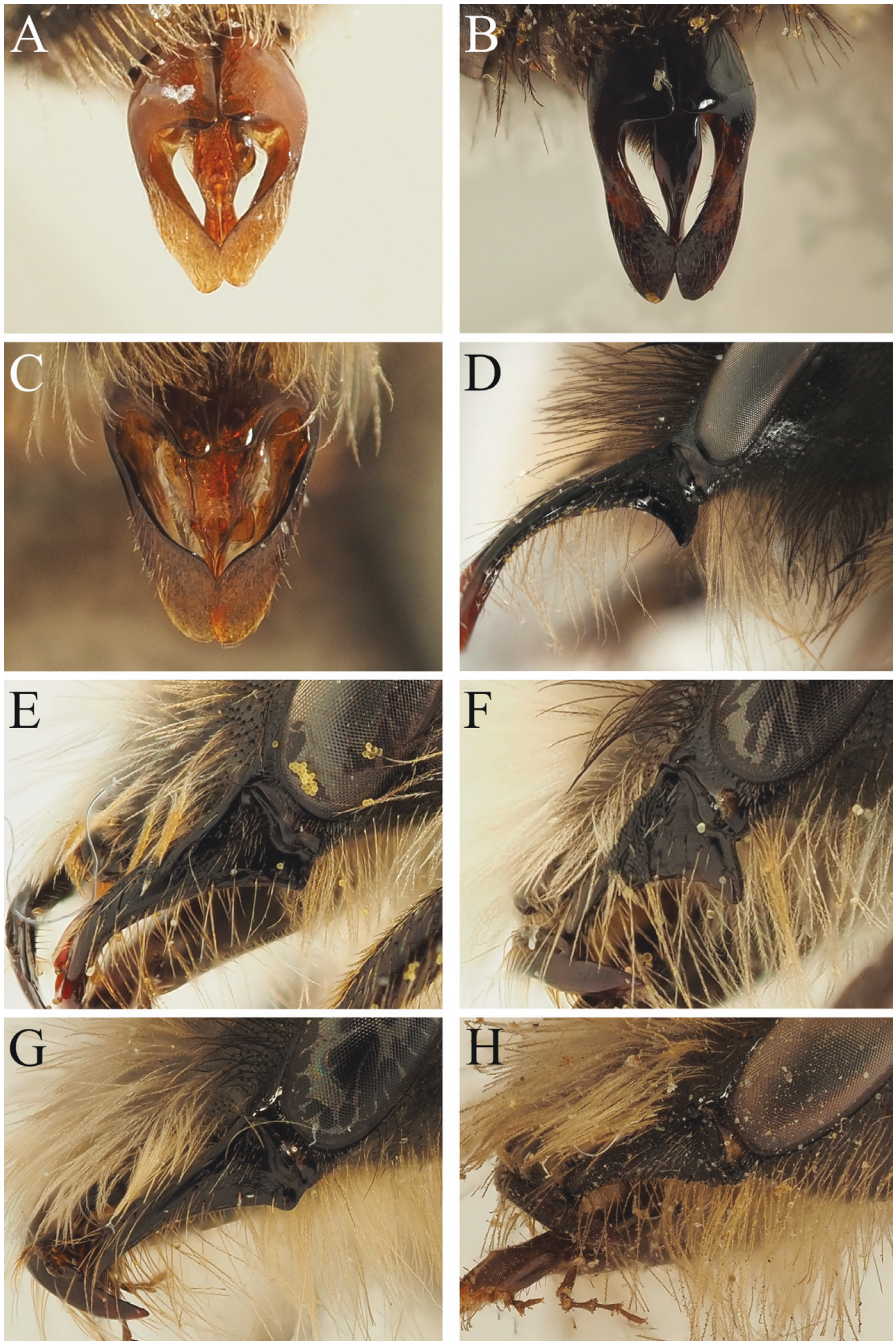
**Figure 118.** *Andrena* (*Taeniandrena*) *leucopsis* Warncke, 1967 male. **A.** Genital capsule, dorsal view. *Andrena* (*Taeniandrena*) *taedium* Wood, 2023 male. **B.** Genital capsule, dorsal view. *Andrena* (*Taeniandrena*) *afzeliella* (Kirby, 1802) male. **C.** Genital capsule, dorsal view. *Andrena* (*Bryandrena*) *florea* Fabricius, 1793 male. **D.** Genital capsule, dorsal view. *Andrena* (*Hamandrena*) *nasuta* Giraud, 1863 male. **E.** Mouthparts, lateral view. *Andrena* (*incertae sedis*) *mistrensis* Grünwaldt, 2005 male. **F.** Genital capsule, dorsal view.

- 179 Mouthparts with 9 maxillary and 9 labial palpi. Restricted to southern continental Greece ..... ***A. grossella* Grünwaldt**
- Mouthparts with 7 maxillary and 6 labial palpi (Fig. 74C). Restricted to the island of Crete..... ***A. lasithi* sp. nov.**

- 180 Genital capsule distinctive, gonostyli long and filiform, penis valves grossly expanded, occupying almost the entire space between the gonostyli. S8 elongate and strongly emarginate medially, forming a ‘Y’ shape ..... *A. bucephala* Stephens
- Genital capsule and S8 otherwise ..... 181
- 181 A3 extremely short, at most 1/3 the length of A4 and S8 with clear apical emargination ..... 182
- A3 longer, never this short, S8 variable. If in doubt, then terga with well-defined and narrow light brown apical hair bands ..... 185
- 182 S8 apically truncate, lacking apical emargination. Mandibles always bidentate ..... *A. rosae* Panzer (*partim*, dark form)
- S8 with clear apical emargination. Mandibles either unidentate or bidentate ..... 183
- 183 Mandible unidentate, lacking an inner subapical tooth. Gena usually with a long spine. Flying only in the spring (March–May, depending on elevation) .... *A. trimmerana* (Kirby) (*partim*, dark form, spring generation)
- Mandible bidentate, with an inner subapical tooth. Gena usually without a spine, sometimes with a very short spine. Flying in the spring or the summer ..... 184
- 184 Facial pubescence long. Usually univoltine, flying April–mid June, with sporadic emergence in August and September (not yet observed in the southern Balkans) ..... *A. scotica* Perkins
- Facial pubescence short. Bivoltine, usually flying March–May and July–August ..... *A. trimmerana* (Kirby) (*partim*, dark form, summer generation)
- 185 Mandible unidentate, without inner subapical tooth. Sometimes there may be a hint of a weakly formed or ancient subapical tooth; this state should be treated as unidentate. Head often grossly enlarged (macrocephalic) 186
- Mandible clearly bidentate, with a strong inner subapical tooth. Head not normally grossly enlarged ..... 187
- 186 A3 slightly shorter than A4. Clypeus in apical 1/3 bulging, surface smooth and shiny with scattered punctures, punctures separated by 1–4 puncture diameters. Hind tibiae and tarsi usually lightened orange. Univoltine, typically flying April–May in areas of deciduous woodland (usually with *Quercus*; Fagaceae) ..... *A. ferox* Smith
- A3 clearly longer than A4. Clypeus even, without bulging apical part, underlying surface evenly shagreened and regularly punctate. Hind tibiae and tarsi dark. Bivoltine, flying April–May and again July–August ... *A. nuptialis* Pérez
- 187 A3 shorter than A4. Genital capsule with penis valves very broadly expanded at their base before tapering apically, gonocoxae produced into long rounded teeth (Fig. 118F). A4–13 ventrally covered with a layer of very fine and distinctly shining scales, distinctly contrasting the surface of A3 which is dull. Found only in Greece ..... *A. mistrensis* Grünwaldt
- Combination of characters otherwise; A3 at least as long as A4, usually longer, genital capsule otherwise, distribution variable ..... 188

- 188 Mesosoma covered with a mixture of greyish and black pubescence. Large species, greater than 13 mm in length. Mandible never with a basal tooth ..... **189**
- Combination of characters otherwise; mesosoma without a mixture of grey and black pubescence, typically smaller, not exceeding 12 mm in length, mandible basally often with a basal tooth or angulation ..... **190**
- 189 Very large species, 16–20 mm in length. Scutum anteriorly and posteriorly with greyish hairs that are distinctly separated with a medial broad band of black hairs. Ocelloccipital distance enormous, between 4–6 times the diameter of a lateral ocellus. Viewed dorsally, vertex weakly shagreened medially, becoming polished and shining laterally above the compound eyes. Confidently known only from Eastern Macedonia and Thrace in north-eastern Greece ..... ***A. dubiosa* Kohl**
- Smaller, around 13–14 mm in length. Scutum variable, but often with greyish hairs with occasional black hairs intermixed, sometimes with a distinct transverse band of black hairs. Ocelloccipital distance large, 3 times the diameter of a lateral ocellus. Viewed dorsally, vertex uniformly microreticulate across its entire surface. With an unclear distribution in the southern Balkans, nominally known from the East Aegean Islands (Lesbos) and Albania ..... ***A. fuscocalcarata* Morawitz**
- 190 Genital capsule with the penis valves showing very small lateral hyaline extensions basally, gonostyli apically flattened and spatulate with parallel sides (Fig. 119A). Marginal area of T2 occupying 40% of the segment, slightly depressed and with fine granular shagreen, slightly shinier than the disc. Clypeus medially with a subtle longitudinal impression situated medially (challenging to see). Found in temperate habitats, usually in mountains in the northern parts Greece and Bulgaria ..... ***A. fulvata* Stöckhert**
- Without this combination of characters ..... **191**
- 191 Head, mesosoma, and propodeum laterally with abundant black hairs. Mandible straight at its base, without a ventrally projecting tooth. Genital capsule with the penis valves narrow, not basally broadened and without lateral hyaline extensions (Fig. 119B). Wings weakly but distinctly infusate. Found at high altitude in mountainous areas of North Macedonia and northern Greece ..... ***A. clusia* Warncke**
- Without this combination of characters; pubescence variable, mandible often with a pronounced tooth at its base, genital capsule usually expanded and with hyaline extensions basally (e.g. Fig. 119C), wings hyaline, distribution variable (subgenus *Andrena* s. str.) ..... **192**

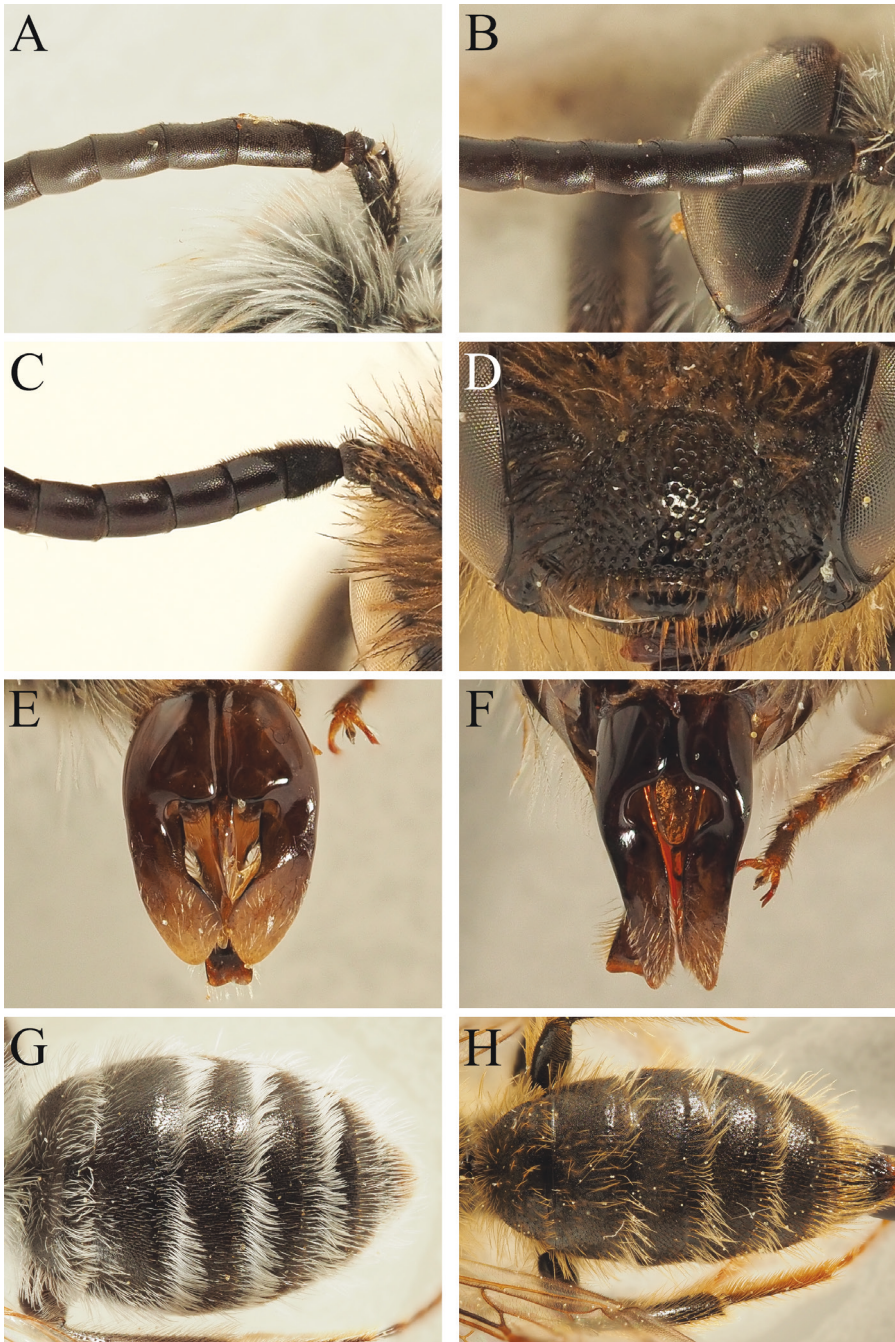
Members of this subgenus have a global distribution across cooler parts of the Northern Hemisphere, and hence show a bias towards northern parts of the southern Balkans which have a temperate climate, or very high mountains.



**Figure 119.** *Andrena (Euandrena) fulvata* Stöckert, 1930 male. **A.** Genital capsule, dorsal view. *Andrena (Hoplاندrena) clusia* Warncke, 1966 male. **B.** Genital capsule, dorsal view. *Andrena (Andrena) mitis* Schmiedeknecht, 1883 male. **C.** Genital capsule, dorsal view; **F.** Mandible, lateral view. *Andrena (Andrena) apicata* Smith, 1847 male. **D.** Mandible, lateral view. *Andrena (Andrena) fucata* Smith, 1847 male. **E.** Mandible, lateral view. *Andrena (Andrena) helvola* (Linnaeus, 1758) male. **G.** Mandible, lateral view. *Andrena (Andrena) varians* (Kirby, 1802) male. **H.** Mandible, lateral view.

- 192 Mandible at its base with a clearly pronounced tooth (Fig. 119D–F) ..... **193**
- Mandible at its base with either an angulation or straight (Fig. 119G, H).  
..... **199**
- 193 A3 1.8 times longer than A4. Hind tarsi lightened orange .....  
..... *A. fulva* (Müller)
- A3 at most 1.3 times longer than A4, usually more-or-less equal in length.  
Hind tarsi dark to reddish ..... **194**
- 194 Propodeum with majority of hairs black, at most with scattered pale hairs  
..... **195**
- Propodeum with majority of hairs pale, at most with scattered dark hairs .  
..... **196**
- 195 S8 apically emarginate. Slightly smaller, 9–11 mm .... *A. praecox* (Scopoli)
- S8 apically truncate. Slightly larger, 10–12 mm ..... *A. apicata* Smith
- 196 Head with a mixture of black and foxy-red hairs, black hairs largely  
concentrated around the lower paraocular areas, frons, and vertex.  
Mesosoma with largely foxy-red hairs with scattered intermixed black  
hairs. Tarsi and hind tibiae dark reddish. A poorly known species of high  
mountains in Bulgaria (Rhodopes, Pirin, Vitosha) and Greece .....  
..... *A. inconstans* Morawitz
- Without this combination of characters; head usually with abundant pale  
whitish hairs with at most scattered black hairs. Mesosoma usually with  
buffish brown hairs dorsally and pale whitish hairs laterally on the mesepi-  
sternum. Hind tarsi variable ..... **197**
- 197 Basal mandibular tooth short (Fig. 119E). Apical margins of S2–4 with  
long loose hairs that do not form clear fringes, hairs longer than the length  
of the hind basitarsis. Flying later in the year (June–August), associated  
with shrubs, particularly *Rubus* (Rosaceae) ..... *A. fucata* Smith
- Basal mandibular tooth long (e.g. Fig. 119F). Apical margins of S2–4 with  
dense fringes composed of short hairs, these hairs not exceeding the length  
of the hind basitarsis. Flying earlier in the year (March–June) ..... **198**
- 198 Hind tarsi dark. Genital capsule more compact, gonocoxal teeth strongly  
produced. Flying May–June, associated with *Vaccinium* (Ericaceae), and  
restricted to mountainous areas in the southern Balkans, usually at or above  
the tree line ..... *A. lapponica* Zetterstedt
- Hind tarsi reddish. Genital capsule more elongate, gonocoxal teeth com-  
paratively weak (Fig. 119C). Flying March–May, associated with *Salix*  
(Salicaceae) and whilst found in mountainous areas, not typically above the  
tree line ..... *A. mitis* Schmiedeknecht
- 199 Mandible without any kind of angulation at its base. Species flying in the  
early spring (March–April) and associated with *Salix* ..... **200**
- Mandible at its base with an angulation (Fig. 119G, H). Species flying in  
the mid to late spring (April–May) and associated with trees and shrubs but  
not specifically *Salix* ..... **201**

- 200 Large species, exceeding 13 mm in length. Mesosoma predominantly grey haired, with some black hairs on the propodeum ..... ***A. nycthemera* Imhoff**
- Smaller, usually 9–12 mm in length. Mesosoma with bright reddish brown hairs, with some black hairs on the mesepisternum ..... ***A. clarkella* (Kirby)**
- 201 Mandible at its base with the angulation forming a 90° angle (Fig. 119G). In fresh specimens, clypeus with golden hairs..... ***A. helvola* (Linnaeus)**
- Mandible at its base with angulation rounded, forming an obtuse angle (Fig. 119H, c. 120 °). In fresh specimens, clypeus with white hairs.....  
..... ***A. varians* (Kirby)**
- 202(175) Ventral surface of A4–13 covered in a layer of very fine and distinctly shining scales, distinctly contrasting the surface of A3 which is dull (Fig. 120A–C; *Chrysandrena* Hedicke, *Cordandrena* Warncke, *numida*-group) ..... **203**
- Ventral surface of A4–13 not differentiated from A3, without fine shining scales..... **210**
- 203 A3 very short, at most 1/4 of the length of A4 (Fig. 120A) ..... **204**
- A3 longer, at least 1/3 the length of A4 (Fig. 120B, C) ..... **205**
- 204 Genital capsule with the penis valves extremely narrow and parallel-sided, occupying a small fraction of the space between the gonostyli which are flattened but apically rounded (Fig. 120E). Widespread in the southern Balkans, but with a northern bias; rare in continental Greece and not found on the islands..... ***A. cordialis***
- Genital capsule with the penis valves elongate triangular, occupying all of the space between the gonostyli which are broadened, flattened, and strongly elongate-tapering (Fig. 120F). Found on Crete and the East Aegean Islands (Rhodes) ..... ***A. torda* Warncke**
- 205 Larger, 10–11 mm. Tergal discs shagreened to coarsely microreticulate, at most weakly shiny, with fine regular punctures or coarse ‘crater punctures’. Tergal margins at most with their apical rims narrowly lightened hyaline brown (Fig. 120G, H; *numida*-group) ..... **206**
- Smaller, 7–8 mm. Tergal discs finely shagreened, more-or-less smooth and shiny, with deep and distinct punctures, punctures on disc of T1 separated by 1–2 puncture diameters, on discs of T2–4 separated by 0.5–1 puncture diameter. Tergal margins often broadly lightened yellow-orange hyaline (subgenus *Chrysandrena* Hedicke)..... **207**
- 206 Terga shagreened, weakly shiny, with fine and dense punctation (Fig. 120G). Tergal margins comparatively weakly depressed, with narrow tight apical white hair bands. Hind basitarsi dark. Found in the southern Balkans but with a strong northern bias; very rare in continental Greece, and typically a lowland species ..... ***A. hypopolia* Schmiedeknecht**
- Terga strongly microreticulate, with coarse ‘crater punctures’ (Fig. 120H). Tergal margins comparatively strongly depressed, with long loose white apical hair bands that exceed the length of the marginal areas. Hind basitarsi often lightened orange. Restricted to mountainous areas in continental Greece above 900 m in altitude (Fig. 81)..... ***A. ranuncolorum* Morawitz**



**Figure 120.** *Andrena* (*Cordandrena*) *cordialis* Morawitz, 1877 male. **A.** Antennal flagellum, frontal view; **E.** Genital capsule, dorsal view. *Andrena* (*incertae sedis*) *hypopolia* Schmiedeknecht, 184 male. **B.** Antennal flagellum, frontal view; **G.** Metasoma, dorsal view. *Andrena* (*Chrysandrena*) *fulvago* (Christ, 1791) male. **C.** Antennal flagellum, frontal view; **D.** Clypeus, frontal view. *Andrena* (*Cordandrena*) *torda* Warncke, 1965 male. **F.** Genital capsule, frontal view. *Andrena* (*incertae sedis*) *ranunculorum* Morawitz, 1877 male. **H.** Metasoma, dorsal view.

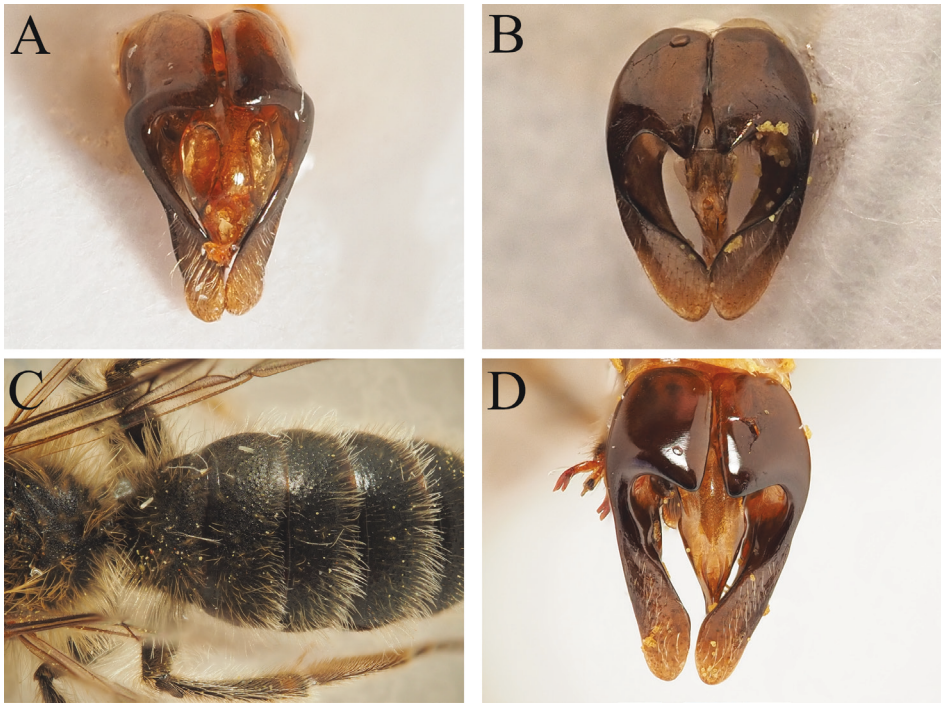
- 207 Clypeus polished and shining between punctures medially (Fig. 120D). A3 more-or-less equal to A4 in length (Fig. 120C) ..... ***A. fulvago* (Christ)**
- Clypeus uniformly microreticulate and dull. A3 clearly shorter than A4 ...  
..... **208**

This group of species requires revision in the East Mediterranean (G. Pisanty, pers. comm.), and hence this part of the key should be considered only provisional.

- 208 All legs uniformly dark. Pubescence of face (medially) and mesosoma greyish even in fresh specimens. Tergal margins narrowly and obscurely lightened whitish-hyaline ..... ***A. merula* Warncke**
- Tarsi and apices of hind tibiae lightened orange. Pubescence of face (medially) and mesosoma orange-brown in fresh specimens (beware faded individuals). Tergal margins broadly lightened orange-yellow hyaline ..... **209**
- 209 Scutum posteromedially with a small but distinct area with reduced sculpture, this area polished and shining. Found only on the island of Rhodes..  
..... ***A. glandaria* Warncke**
- Scutum entirely and uniformly densely microreticulate and dull. Widespread across the southern Balkans, including the East Aegean Islands .....  
..... ***A. hesperia* Smith**
- 210(202) Measured along its ventral margin, A3 twice as long as A4 or longer ..... **211**
- Measured along ventral margin, A3 longer or shorter than A4, clearly less than twice as long ..... **233**
- 211 S8 unique, columnar part elongate and broadening apically, apical portion deeply emarginate and hence resembling a fish tail (Fig. 72C). Genital capsule with the gonostyli narrow and more-or-less parallel sided (Fig. 72D) .  
..... ***A. paucisquama* Noskiewicz**
- S8 and genital capsule otherwise ..... **212**
- 212 Mid leg with the tibial spur distinctive, apically bent almost 90° (c.f. Fig. 86E). Outer hind tibial spur apically hooked, inner hind tibial spur not to only weakly hooked (c.f. Fig. 86F). Face entirely black-haired, clypeus weakly flattened medially and predominantly polished and shining .....  
..... ***A. gamskrucki* Warncke**
- Tibial spurs straight, never hooked. Other characters variable ..... **213**
- 213 Genital capsule with the gonocoxae produced into long, narrow, and apically diverging finger-like extensions. Gonostyli flattened and with their outer margins distinctly concave. A3 very long, just over 2 times the length of A4. Face with strongly contrasting pubescence, medially with light brown to whitish pubescence, inner margins of compound eyes with abundant black pubescence. Currently known only from Lesbos .....  
..... ***A. aff derbentina* Morawitz**
- Combination of characters otherwise ..... **214**

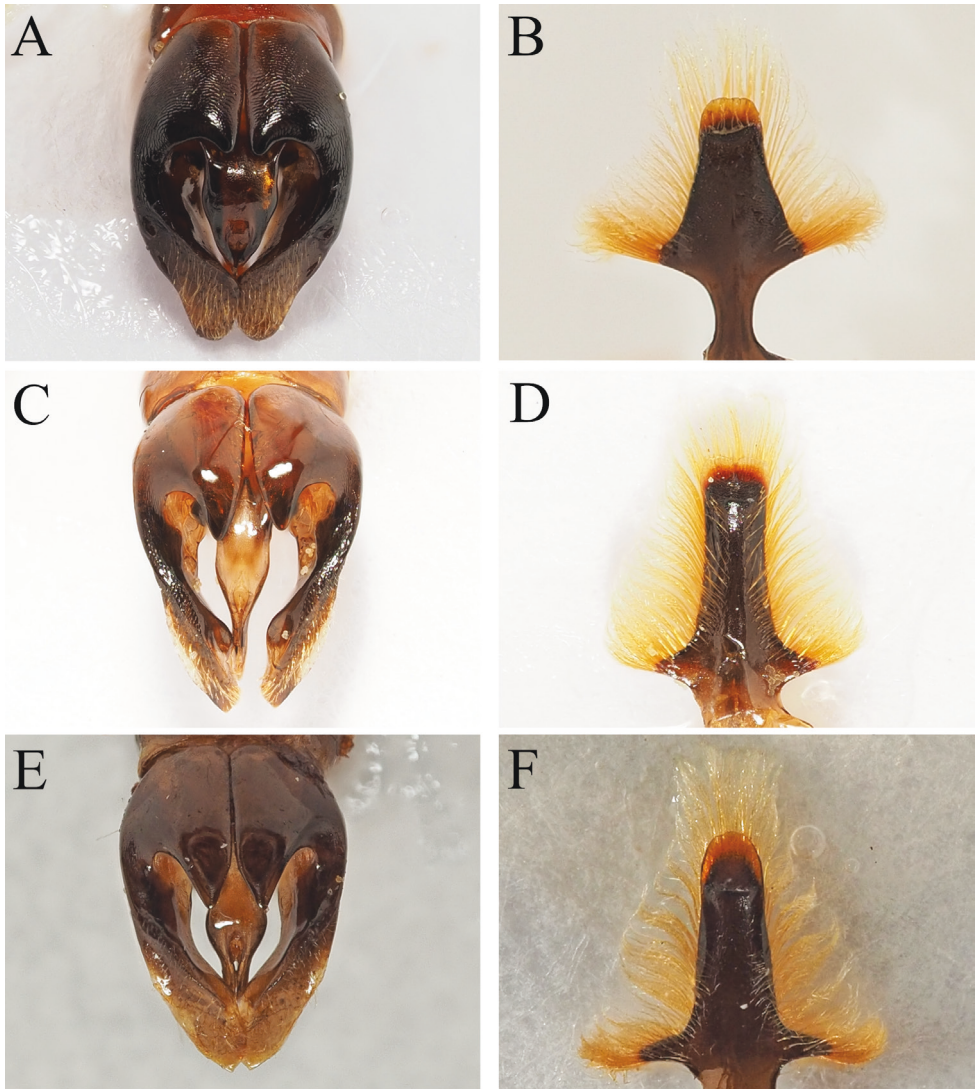
- 214 Tergal margins distinctly depressed, medially occupying 40% of the visible segment. Tergal discs densely punctate, punctures separated by 0.5–1 puncture diameters; tergal margins impunctate, lightened hyaline brown, sculpturally strongly contrasting tergal discs. Margins of T2–4 basally with long whitish plumose hairs that arise from the junctions with the discs and overly the marginal areas without obscuring the underlying surface. Currently known from only a single record from south-western Bulgaria.....  
..... ***A. hystrix* Schmiedeknecht**
- Without this combination of characters; distribution variable..... **215**
- 215 Gonostyli with outer margin concave (c.f. Fig. 113C), penis valves with weak lateral hyaline extensions (c.f. Fig. 119A). Size moderate, 8–9 mm in length..... **216**
- Genital capsule otherwise. Size variable..... **217**
- 216 Terga shiny and densely punctate, punctures separated by 1–2 puncture diameters. Mid and hind tarsi and usually also hind tibia ferruginous. Associated with *Asparagus* (Asparagaceae)..... ***A. chrysopus* Pérez**
- Terga microreticulate and dull, punctation obscure and partially disappearing into the underlying sculpture. Legs dark. Associated with *Symphytum* (Boraginaceae)..... ***A. symphyti* Schmiedeknecht**
- 217 Genital capsule broadest submedially before gently tapering apically, outer margins of the gonostyli concave; gonocoxae truncate to weakly produced into slightly projecting teeth (Fig. 121A). Jugal lobe of the hind wing conspicuously narrowed at its base (subgenus *Pallandrena* Warncke)..... **218**
- Genital capsule otherwise. Jugal lobe of the hind wing normal, not conspicuously narrowed..... **219**
- 218 Genital capsule with the penis valves very broad, occupying almost all of the space between the gonostyli (Fig. 121A). Clypeus densely microreticulate and uniformly dull. Tergal margins subtly lightened whitish-hyaline. Slightly smaller, 8–9 mm..... ***A. pallidicincta* Brullé**
- Genital capsule with the penis valves broad but clearly separated from the inner margins of the gonostyli. Clypeus dorsally and laterally shagreened and dull, medially polished and shining. Tergal margins conspicuously and broadly lightened orange-yellow hyaline. Slightly larger, 10–11 mm.....  
..... ***A. braunsiana* Friese**
- 219 Terga with fine hair-bearing punctures, these punctures with slightly elevated margins, separated by 1–3 puncture diameters (Fig. 121B). Marginal areas slightly depressed, without hair-bearing punctures, thus contrasting the tergal discs. Mesosoma with very long pale buffish to whitish hairs, the longest hairs on the mesepisternum equalling the length of the scape, pedicel and A3 combined. Head with predominantly pale pubescence with a few dark hairs along the inner margins of the compound eyes and laterally on the lower paraocular areas. Genital capsule compact, gonostyli with

- their inner margins strongly raised, penis valves with very small rounded lateral hyaline extensions (Fig. 121C). Rare in the southern Balkans, restricted to the East Aegean Islands ..... *A. fuligula* Warncke
- Without this combination of characters ..... 220
- 220 Face predominantly white-haired, with a few black hairs along inner margin of compound eyes. Mesosoma entirely covered with long white hairs, without any visible black hairs. Genital capsule elongate, relatively featureless (Fig. 121D). Tergal discs densely and finely punctate, punctures separated by 0.5 puncture diameters, covered with short and uniformly pale pubescence. Tergal margins slightly but distinctly depressed, with small, fine, and obscure punctures, the margins thus strongly contrasting the discs; underlying surface finely shagreened and weakly shiny .....
- ..... *A. bicolorata* Magretti
- Without this combination of characters ..... 221
- 221 Robust species, 14–15 mm in length. Ocellocipital distance long, equaling or exceeding 3 times the diameter of a lateral ocellus. Terga laterally with weakly to strongly produced white hair tufts ..... 222
- On average typically smaller, not exceeding 13–14 mm in length. Ocellocipital distance shorter, usually more-or-less equalling the diameter of a lateral ocellus. Terga either with or without complete apical hairbands, but not with distinct lateral hair tufts ..... 223
- 222 Face, mesepisternum, and lateral faces of propodeum with black pubescence, becoming greyish on vertex, majority of scutum, scutellum, and propodeal dorsum. T6 with hairs dark brown to black. Margins of T2–4 laterally with strongly produced distinct thick patches of white hairs. Uncommon, seemingly favouring coastal habitats in Greece and eastern Bulgaria (near the Black Sea) ..... *A. magna* Warncke
- Head and mesosoma with almost entirely black hairs, at most with the occasional grey hair. T6 with hairs orange. Margins of T2–3 laterally with hints of patches of whitish hairs. Rare in Greece but found in general rather than exclusively coastal habitats ..... *A. pyropygia* Kriechbaumer
- 223 Face with pale hairs medially and black hairs along the inner margin of the compound eyes. Genital capsule with surface of the gonocoxae with distinctive latitudinal granular shagreen, this extending onto the basal parts of the gonostyli (Fig. 122A). Terga shagreened, with large scattered punctures on tergal discs, these almost becoming crater-like on T1, but without clearly raised rims (*flavipes*-group, *partim*) ..... 224
- Without this combination of characters ..... 226
- 224 Genital capsule with outer margins of the gonostyli weakly emarginate (Fig. 122A). Reasonably frequent across the southern Balkans, found in cooler temperate locations (including hills and mountains in the Peloponnese) but not the island of Crete ..... *A. gravida* Imhoff
- Genital capsule with the outer margins of the gonostyli straight. Either restricted to Crete or very rare ..... 225



**Figure 121.** *Andrena* (*Pallandrena*) *pallidicincta* Brullé, 1833 male. **A.** Genital capsule, dorsal view. *Andrena* (*Truncandrena*) *fuligula* Warncke, 1965 male. **B.** Genital capsule, dorsal view; **C.** Metasoma, dorsal view. *Andrena* (*Melandrena*) *bicolorata* (Rossi, 1790) male. **D.** Genital capsule, dorsal view.

- 225 Large species, 12–13 mm in length. T5–6 with uniformly orange-golden hairs. Very rare in the southern Balkans, currently recorded only from Bulgaria; associated with steppe grasslands ..... ***A. chrysopyga* Schenck**
- Smaller species, 9–10 mm in length. T5–6 with brownish hairs, never with uniformly orange-golden hairs. Restricted to the island of Crete (Fig. 29), but commonly encountered there ..... ***A. cretica* Strand**
- 226 Terga densely and regularly punctate, punctures separated by up to 1 puncture diameter, underlying surface weakly shagreened to smooth and shiny. T2–4 with distinct white apical hair bands, often abraded and interrupted medially. Associated with *Campanula* (remaining *Lepidandrena* Hedicke) ..... **227**
- Terga shagreened, with large ‘crater punctures’ with raised rims. Tergal margins without apical hair bands. Associated with Cichorioideae (Asteraceae) (remaining *Chlorandrena* Pérez) ..... **229**
- 227 Genital capsule with the gonostyli apically small, spatulate and parallel-sided (Fig. 72B). Process of S8 very short with short hairs that do not spread laterally (Fig. 70A) ..... ***A. baladai* sp. nov.**
- Genital capsule with the gonostyli apically broad, broadening apically and hence not parallel-sided (Fig. 72F). Process of S8 variable, but sometimes with long laterally projecting hairs (Fig. 72E) ..... **228**



**Figure 122.** *Andrena (Melandrena) gravida* Imhoff, 1832 male. **A.** Genital capsule, dorsal view. *Andrena (Chlorandrena) astica* Warncke, 1967 male. **B.** Sternum 8, dorsal view. *Andrena (Chlorandrena) taraxaci* Giraud, 1861 male. **C.** Genital capsule, dorsal view; **D.** Sternum 8, dorsal view. *Andrena (Chlorandrena) orientana* Warncke, 1965 male. **E.** Genital capsule, dorsal view; **F.** Sternum 8, dorsal view.

- 228 S8 with short hairs that do not noticeably project laterally. Tarsal segment 5 of the hind leg elongate and bent. Slightly larger, 11–14 mm..... *A. curvungula* Thomson
- S8 with long, laterally projecting hairs (Fig. 72E). Tarsal segment 5 of the hind leg not noticeably bent. Slightly smaller, 9–10 mm..... *A. pandellei* Pérez

- 229 Process of S8 large, with triangular-shaped lateral projections covered with projecting hair tufts (Fig. 122B, D, F; *taraxaci*-group) ..... **230**
- Process of S8 large or small, but more-or-less parallel-sided, without triangular lateral projections or hair tufts (c.f. Fig. 111C; *humilis*-group, *partim*) ..... **232**
- 230 Process of S8 rhomboidal, lateral margins converging apically, overall twice as long as the maximum basal width (excluding the narrow basal stem) (Fig. 122B). Rare in the southern Balkans, confirmed only from south-eastern Bulgaria.....***A. astica* Warncke**
- Process of S8 more-or-less rectangular, outer margins more-or-less parallel-sided, overall 3–4 times longer than wide (excluding the broad basal stem) (Fig. 122D, F) ..... **231**
- 231 Lateral teeth of S8 less elongate and less acute, forming a roughly 50° angle, disc of process roughly 4 times longer than wide (Fig. 122D). Apices of gonostyli irregularly flattened and somewhat wavy, relatively narrow (Fig. 122C).....***A. taraxaci* Giraud**
- Lateral teeth of S8 acute and elongate, disc of process roughly 3 times longer than wide (Fig. 122F). Apices of gonostyli relatively broad and evenly flattened (Fig. 122E).....***A. orientana* Warncke**
- 232 Marginal areas of T3–4 occupying around 40–50% of the visible surface of the segment. Marginal areas polished, shining with fine shagreen forming latitudinal wrinkles, and more-or-less impunctate, contrasting the tergal discs which are dark and finely punctate. Genital capsule with the gonocoxal teeth very narrow and acutely pointed, only slightly diverging apically. Larger, 10–11 mm in length.....***A. humabilis* Warncke**
- Marginal areas of T3–4 occupying around 25–30% of the visible surface of the segment. Marginal areas microreticulate and dull, not strongly contrasting the tergal discs which have obscure punctation. Genital capsule with the gonocoxal teeth generally but not sharply pointed, clearly diverging apically. Smaller, 8–9 mm in length ..... ***A. cinerea* Brullé**
- 233(210) Measured along its ventral margin, A3 shorter than or only as long as A4. If in doubt, then ocelloccipital distance long, at least 2 times the diameter of a lateral ocellus..... **234**
- Remaining species; measured along its ventral margin, A3 slightly longer than A4. Ocelloccipital distance not exceeding the diameter of a lateral ocellus..... **254**
- 234 Larger species, 12–14 mm in length, usually with abundant black, white, or brown pubescence, usually with entirely dark black facial hair. Ocelloccipital distance >2 times the diameter of a lateral ocellus. Terga always without apical hair bands, sometimes with lateral hair patches (remaining *Melandrena* Pérez, *partim*)..... **235**
- Smaller species, 9–10 mm in length, usually with subdued pubescence, facial hairs often pale, though dark in *A. lepida* and *A. propinqua*. Ocelloccipital distance often shorter, <2 times the diameter of a lateral ocellus. Terga with or without hair bands (subgenus *Simandrena* Pérez) ..... **245**

*Andrena (Melandrena)* males are poorly characterised in some sexes, and confident identification is challenging or even currently impossible. The following characters should be treated with caution, as it is not clear how robust they are.

- 235 Mesosoma entirely grey-haired, with at most a few obscure black hairs here and there. Area between disc and marginal area of T1 with several small and shallow but distinct longitudinal impressions ..... *A. vaga* **Panzer**
- Mesosoma with mixture of white, grey, black, and/or brown pubescence, but never entirely grey-haired. T1 without longitudinal impressions ..... **236**
- 236 Mesosoma entirely or predominantly covered with brown hairs ..... **237**
- Mesosoma covered with white, grey, or black pubescence (or a combination of these colours), but without brown hairs ..... **242**
- 237 Terga shagreened, obscurely punctate, with punctures disappearing into the underlying sculpture ..... *A. assimilis* **Radoszkowski**
- Terga at most weakly shagreened, sometimes smooth and shiny, at least weakly shiny. Discs of T2–5 clearly and usually densely punctate, punctures typically separated by 1 puncture diameter ..... **238**
- 238 Face with white to whitish pubescence medially, with contrasting black hairs along the inner margins of the compound eyes. Mesepisternum with long white or rusty yellow pubescence, mesosoma dorsally with bright light brown pubescence. Univoltine, flying April–June..... **239**
- Without this pattern of pubescence; face either with extensive dark pubescence AND/OR mesepisternum with dark pubescence or mesosoma dorsally with dark chestnut brown pubescence. Flight period variable, but often bivoltine, hence flying also in July–August ..... **240**

The genital capsule illustrations in Scheuchl and Hazir (2012) should be consulted. Association with concurrently active females should also be made, where possible.

- 239 Genital capsule with penis valves displaying a lamellar dorsolateral extension on each side near the base. Found only on the East Aegean Island ..... *A. nitidemula* **Scheuchl & Hazir**
- Genital capsule with the penis valves lacking basal lamellar dorsolateral extensions. Found in northern temperate parts of the southern Balkans, southern range extent unclear ..... *A. nitida* (**Müller**)
- 240 Marginal areas of terga with narrow section of apical rims lightened hyaline-brown, tergal discs with weak bronzy reflections. Face with mixture of dark brown and black hairs ..... *A. nigroaenea* (**Kirby**)
- Marginal areas of terga with apical rims dark, not lightened, tergal discs dark, without weak bronzy reflections. Face with uniformly black hairs..... **241**

These two species are very difficult to separate in the male sex, and positive determination is not possible in many cases.

- 241 Disc of T1 with dense punctures, punctures separated by up to 2 puncture diameters ..... *A. limata* **Smith**
- Disc of T1 with more scattered punctures, punctures usually separated by over 3 puncture diameters..... *A. thoracica* (**Fabricius**)
- 242 Margins of T2–4 laterally with strongly produced distinct thick patches of white hairs. Mesosoma usually anteriorly and posteriorly with abundant white hairs bisected by black hairs medially, but dark forms with pale pubescence reduced to small patches are be seen in hotter areas .....  
..... *A. albopunctata* (**Rossi**)
- Terga without thick lateral patches of white hairs, at most with slight hints of thin patches or narrow hairbands formed by sparse dark brown, light brown, or pale hairs hairs. Pubescence of mesosoma variable..... **243**
- 243 Head and mesosoma entirely covered in whitish hairs, without any black hairs along the inner margins of the compound eyes. Metasoma with entirely pale pubescence, forming weak hints of lateral hair fringes on the apical margins of the terga. Wings hyaline. Typically a little smaller, 11–12 mm in length..... *A. quadrimaculata* **Friese**
- Head and mesosoma with a mixture of black and white or whitish pubescence, always with at least some black hairs along the inner margins of the compound eyes, or on the mesepisternum, or on the scutum, or entirely black-haired. Metasoma with abundant dark brown to black pubescence. Wings sometimes infuscate and dark. Typically a little larger, 12–14 mm in length ..... **244**

Despite long female series in collections, I have not been able to inspect any confidently determined or barcoded males of *A. atrotegularis*, and so the characters presented here may not be robust. The subgenus *Melandrena* would benefit from robust genetic interrogation of current species concepts.

- 244 Body with a mixture of light and dark pubescence. Wings sometimes infuscate, sometimes hyaline..... *A. morio* **Brullé**
- Body entirely dark-haired. Wings always infuscate and dark .....  
..... *A. atrotegularis* **Hedicke**

*Andrena* (*Simandrena*) males are challenging to identify due to the subtle morphological differences, and so access to confidently determined reference material is recommended.

- 245 A3 extremely short, at most 0.5 times the length of A4. Facial hair entirely (Mediterranean) or almost entirely (continental) black, with at most some paler hairs around the antennal insertions..... *A. lepida* **Schenck**
- A3 longer, at least 0.8 times as long as A4, often as long as A4. Facial hair variable, typically lighter and if dark, then not usually entirely and uniformly black..... **246**

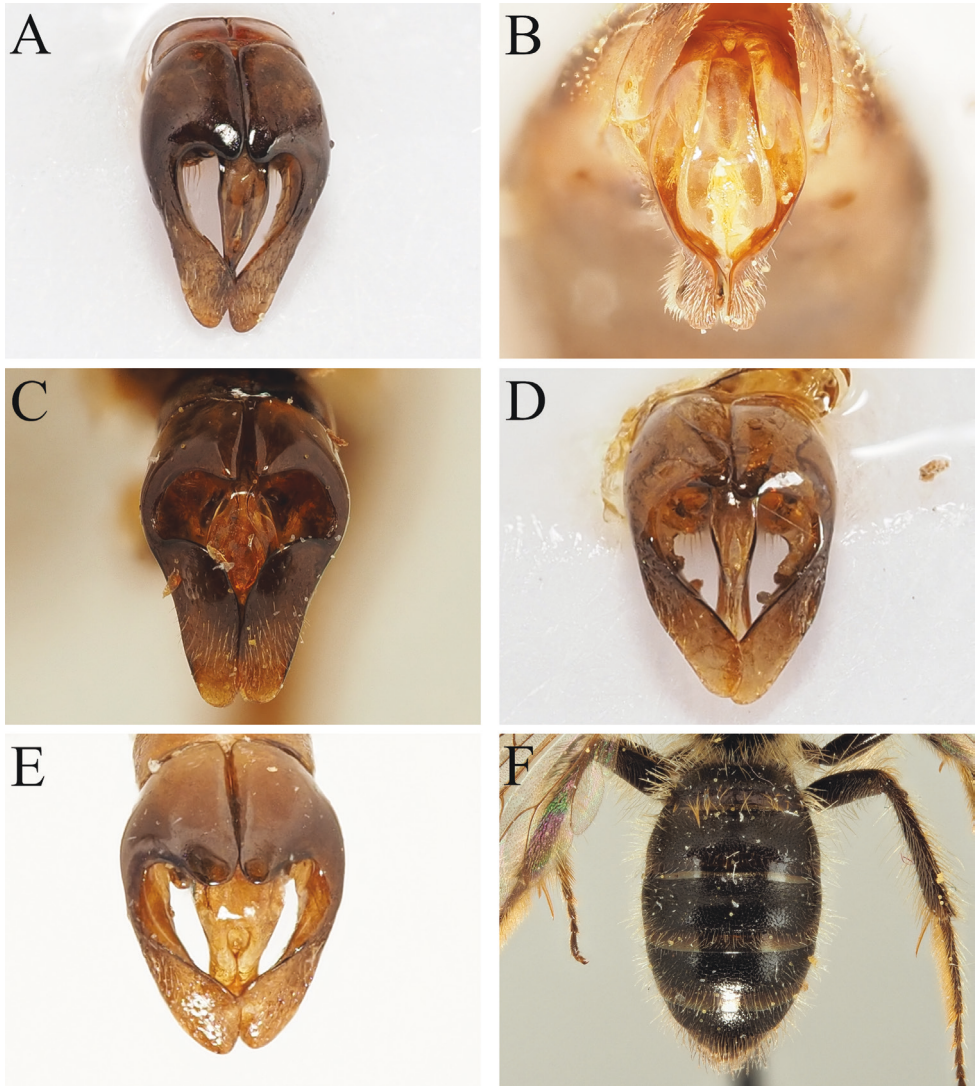
- 246 Propodeal triangle distinctive, triangular and clearly delineated laterally with carinae and with the internal surface showing a raised longitudinal ridge medially (c.f. Fig. 93E).....***A. susterai* Alfken**  
 – Propodeal triangle without this unique shape, internal surface usually evenly sculptured ..... **247**
- 247 Genital capsule distinctive, elongate, basally narrowed (Fig. 123A). Tergal discs with punctation uneven, medially dense and becoming sparser laterally, this contrast in punctation being most clearly visible on T2 ..... **248**  
 – Genital capsule otherwise. Tergal discs with uniform punctation ..... **249**

The characters presented for this species pair refer to typical individuals; some intermediate specimens can be found, and these specimens are often impossible to confidently assign to either species.

- 248 Face with predominantly dark hairs, with some light hairs intermixed around the antennal insertions. Scutum polished, shiny ..... ***A. propinqua* Schenck**  
 – Face with entirely light hairs. Scutum shagreened and dull. Hind tarsi lightened orange ..... ***A. dorsata* (Kirby)**
- 249 Terga uniformly polished and shining, densely and uniformly punctate, punctures separated by 0.5 puncture diameters on average..... **250**  
 – Terga either shagreened to microreticulate OR with punctation sparse, punctures clearly separated by >1 puncture diameter ..... **251**
- 250 Scutum polished and shiny over the entire disc. Facial hair predominantly light brown, some individuals with some darker hairs centrally on the clypeus and along the inner margin of the compound eye. Currently known only from the Struma valley in south-western Bulgaria..... ***A. kocourecki* Wood**  
 – Scutum uniformly microreticulate, dull. Facial hair light brown, at most with some scattered dark hairs at the base of the antennal insertions. Widespread across the southern Balkans..... ***A. combinata* (Christ)**
- 251 Mesepisternum and propodeum with abundant black-brown hairs; remaining pubescence whitish. Scutum comparatively less strongly shagreened, weakly shiny ..... ***A. thomsonii* Ducke**  
 – Mesepisternum, dorsum of mesosoma, and propodeum with bright yellowish pubescence, at most with occasional scattered black hairs. Scutum comparatively more strongly shagreened, dull ..... **252**
- 252 Metasoma microreticulate and dull, with obscure punctation. Clypeus microreticulate and dull with obscure punctation .... ***A. transitoria* Morawitz**  
 – Metasoma shagreened to polished and shining, with fine scattered punctures. Clypeus variable, from shagreened and weakly shining to polished and shining, but not microreticulate and dull with obscure punctation..... **253**

The following two species are challenging to separate and they remain incompletely resolved across their European ranges. Additional detail can be seen in Schmid-Egger and Scheuchl (1997).

- 253 Clypeus between the punctures smooth and shiny. Tergal discs without shagreen, smooth and shiny, clearly visible at the base of T2 .....  
 ..... *A. congruens* Schmiedeknecht
- Clypeus between the punctures shagreened, at most weakly shiny. Tergal discs shagreened, weakly shiny, most clearly visible on the base of T2 .....  
 ..... *A. confinis* Stöckert



**Figure 123.** *Andrena* (*Simandrena*) *propinqua* Schenck, 1853 male. **A.** Genital capsule, dorsal view. *Andrena* (*Ulandrena*) *incustodita* Wood, 2024 male. **B.** Genital capsule, dorsal view. *Andrena* (*Ulandrena*) *polita* Smith, 1847 male. **C.** Genital capsule, dorsal view. *Andrena* (*Euandrena*) *bicolor* Fabricius, 1775 male. **D.** Genital capsule, dorsal view. *Andrena* (*Leucandrena*) *parviceps* Kriechbaumer, 1873 male. **E.** Genital capsule, dorsal view. *Andrena* (*Euandrena*) *granulosa* Pérez, 1903 male. **F.** Metasoma, dorsal view.

- 254(233) Genital capsule with the penis valves swollen, occupying the entirety of the space between the gonostyli and gonocoxae produced into distinct short and anteriorly projecting teeth (Fig. 123B). Crete only ..... *A. incustodita* Wood  
 – Genital capsule otherwise..... 255
- 255 Genital capsule compact (Fig. 123C), with projecting gonocoxal teeth that do not apically diverge and humped gonostyli which are slightly flattened at their apices (*polita*-group *partim*) ..... *A. polita* Smith  
 – Genital capsule otherwise..... 256
- 256 Clypeus domed, covered with dense network of coarse and strongly raised transverse wrinkles. Dorsolateral surface of propodeum with dense network of raised rugosity that is almost indistinguishable from the propodeal triangle, this network extending onto the lateral faces of the propodeum (*proxima*-group)..... 257  
 – Without this combination of characters..... 258
- 257 Scutum entirely covered with dense microreticulation, wrinkles, punctures, and without shining interspaces between punctures. Discs of T1–4 largely impunctate with only scattered micropunctures, marginal areas almost impunctate. Terga with apical hairbands of T2–4 broadly interrupted. Pubescence of metasoma yellowish in fresh specimens. Typically flying earlier, mostly from April–June ..... *A. proxima* (Kirby)  
 – Scutum with shining interspaces between punctures. Discs of T1–4 distinctly punctate. Terga with apical hairbands of T3–4 broadly complete. Pubescence of metasoma whitish in fresh specimens. Typically flying later, mostly from June–August ..... *A. alutacea* Stöckhert
- 258 Penis valves narrow, more-or-less parallel-sided along their length (e.g. Fig. 9F; 123D; subgenera *Didonia* Gribodo and remaining *Euandrena* Hedicke)..... 259  
 – Penis valves basally broadened, clearly wider basally than medially or apically (Fig. 123E; remaining *Leucandrena* Hedicke)..... 269
- 259 Head relatively elongate. Process of the labrum large, slightly wider than long. Clypeus domed, with large irregular punctures, punctures separated by 0.5–2 puncture diameters, with unclear impunctate longitudinal midline. In fresh specimens, terga with clear unbroken apical hair fringes. Bivoltine, March–April and again in June–July..... *A. mucida* Kriechbaumer  
 – Head less elongate. Process of the labrum smaller, more clearly wider than long. Clypeus more weakly domed, shiny to shagreened. Terga without apical hair fringes (subgenus *Euandrena* Hedicke, *partim*) ..... 260

Members of this subgenus are very challenging to identify; several species lack a confidently known male, and hence the characters presented here may not be robust. Some specimens will be genuinely ambiguous and unassignable to any species with confidence. The key of Praz et al. (2019) should also be consulted.

- 260 Pronotum with a distinct humeral angle. Gena broadened, clearly exceeding the width of the compound eye. Clypeus slightly elevated and weakly flattened medially, strongly polished and shining. Facial hair predominantly black with pale hairs around the antennal insertions; specimens from Crete can have entirely black facial hair. With a Mediterranean distribution in Albania and Greece, not found in temperate habitats. Seemingly bivoltine, flying mostly in the spring (March–May) and autumn (October) (Fig. 15).....***A. glidia* Warncke**
- Without this combination of characters ..... **261**
- 261 Apical margins of T1–5 widely lightened hyaline-yellow (Fig. 123F). Terga impressed basally and apically, thus tergal discs appear humped. Species associated with Cistaceae ..... **262**
- Tergal margins at most with apical margins narrowly lightened yellowish. Tergal discs comparatively flat. Species not strongly associated with Cistaceae..... **263**
- 262 Base of terga and tergal margins comparatively strongly impressed, margins clearly separated from disc by a visible ‘step’. Tergal discs coarsely and densely punctate, punctures separated by 2 puncture diameters .....***A. granulosa* Pérez**
- Base of terga and tergal margins comparatively weakly impressed, margins not clearly separated from discs by a visible ‘step’, almost level with discs medially. Tergal discs less densely punctate, punctures separated by 3–4 puncture diameters .....***A. vulpecula* Kriechbaumer**
- 263 Gonostyli apically truncate, outer margin forming an acute point. A3 only slightly longer than A4. Pubescence entirely light brown with exception of occasional dark hairs laterally on the face .....***A. rufula* Schmiedeknecht**
- Gonostyli with outer margin rounded, never forming an acute point. A3 visibly longer than A4 ..... **264**
- 264 Hind tibia usually more-or-less lightened orange apically, hind basitarsus sometimes ferruginous. Face with pubescence predominantly white with at most a few dark hairs laterally on the paraocular areas. Mesosoma almost entirely covered with white hairs. Clypeus densely and finely punctate, interspaces narrow and dull. Very rare in the southern Balkans, restricted to high altitude sites, associated with *Salix* (Salicaceae).....***A. aff ruficrus* Nylander**
- Without this combination of characters ..... **265**
- 265 Facial hairs predominantly pale, with dark hairs restricted to a narrow strip along the inner margins of the compound eyes. Propodeum and mesepisternum with entirely pale hairs. Process of the labrum longer than wide. Found at high elevation sites in mountainous parts of the southern Balkans, with confirmed records from 2000 m in altitude..... ***A. montana* Warncke**
- Facial hairs variable, but always with abundant black hairs that cover more than a narrow strip along the inner margins of the compound eyes; in some cases, the face with entirely dark pubescence. Propodeum and mesepisternum with variable pubescence, but always with at least a few black hairs

- intermixed. Process of the labrum wider than long. Found across a variety of altitudes..... **266**
- 266 Face with predominantly or entirely black pubescence. Light hairs on dorsal parts of mesosoma, terga, and sterna light brown to yellowish white in fresh specimens (but fading to white). Found in a wide variety of habitats, including mountains..... **267**
- Face with a mixture of black and white hairs, with white hairs predominantly found medially on the clypeus and around the antennal insertions (Fig. 9B). Light hairs on dorsal parts of mesosoma, terga, and sterna white even in fresh specimens (Fig. 9D). Restricted to mountainous areas of the southern Balkans..... **268**

The following two species are very challenging to separate in the male sex. Given the relatively small number of available barcoded *A. aff limosa* males it is not clear how robust the characters are, and the degree of overlap in character states. Association with concurrently active females should be made, where possible, and determinations should therefore have a level of uncertainty attached pending further study.

- 267 Face with a mixture of black and pale hairs, with numerous pale hairs concentrated around the antennal insertions. Mesepisternum typically with brownish hairs with a few intermixed black hairs. Terga with thin, fine, and short hairs or broadly similar lengths and colouration, disc of T4 viewed laterally with short intermixed black and white hairs.....  
..... ***A. aff limosa* Warncke**
- Face with almost entirely black pubescence. Mesepisternum typically with abundant black pubescence. Terga with longer hairs, long and light golden-brown on T1–3, disc of T4 viewed laterally with abundant and almost uniform black hairs, thus metasomal hairs more strongly contrasting.....  
..... ***A. bicolor* Fabricius**
- 268 Clypeus densely punctate, punctures separated by <0.5–0.5 puncture diameters, interspaces microreticulate and dull. Tergal discs uniformly finely microreticulate and weakly shining (Fig. 9E). Marginal areas with fine granular shagreen, very slightly more shining than the tergal discs but not clearly contrasting them. Scutum densely shagreened and dull (Fig. 9C). Probably univoltine, flying only in the spring ..... ***A. pileata* Warncke**
- Clypeus equally densely punctate but interspaces polished and shining. Tergal discs variably sculptured, from very finely shagreened almost polished and shining to finely microreticulate and weakly shining. In both cases, marginal areas with very fine shagreen, almost polished, and hence contrasting the sculpture of the discs. Scutum finely shagreened and shining. Bivoltine, flying in the spring and the summer.....  
..... ***A. amieti* Praz, Müller & Genoud**

- 269 Terga very weakly shagreened, more-or-less smooth and shiny. Tergal discs with extremely scattered punctures, punctures separated by 3–4 puncture diameters or more ..... *A. parviceps* Kriechbaumer (*partim*, dark form)
- Terga either more strongly microreticulate (at least on discs of T2–3) or clearly and densely punctate, punctures separated by 1–2 puncture diameters ..... **270**
- 270 Tergal discs finely microreticulate, with obscure and scattered punctures, punctures separated by 2–4 puncture diameters. Tergal margins with narrow widely interrupted hair fringes situated apically.....
- ..... *A. barbilabris* (Kirby)
- Tergal discs at most finely shagreened, more-or-less smooth and shiny, clearly and regularly punctate, punctures separated by 2 puncture diameters. T2–4 apically with broad uninterrupted apical white hair bands, these exceeding the length of the tergal margins and obscuring the underlying surface ..... *A. argentata* Smith

**Discussion**

Although having a broader historical base of study than the *Andrena* fauna of Iberia (Wood 2023b), there were nonetheless major taxonomic and faunal changes of a similar magnitude that were necessary to produce this revisionary work on the fauna of the southern Balkans. From the first meaningful attempt to make a species list for part of this region, the 136 species recorded for Greece (Warncke 1965a) have now become faunal totals of 243 species (Greece, 89.0% of regional total), 186 species (Bulgaria, 68.1% of regional total), 153 species (North Macedonia, 56.0% of regional total), and 116 species (Albania, 42.5% of regional total). Overall, including newly described species and excluding from consideration species here removed from the regional faunas, 58 species are newly reported from Albania (100.0% faunal richness increase), 27 are newly reported from Greece (12.5% faunal increase), 15 are newly reported from North Macedonia (10.9% faunal increase), and 17 new from Bulgaria (10.0% faunal increase). Whilst the result for Albania is not surprising given the shortage of historical and modern study of this fauna, the surprisingly consistent result (as a percentage) for Bulgaria, Greece, and North Macedonia points to a general incompleteness in revision of museum material and study of the Balkan fauna, even for Greece. It is clear that the fauna of Albania remains greatly understudied, as there is no reason to believe that it is meaningfully smaller than that of neighbouring North Macedonia.

When it comes to overall faunal richness, it is appropriate to compare the Iberian Peninsula with the southern Balkans. Wood (2023b) produced a total of 228 *Andrena* species for peninsula Spain (excluding the Canary Islands), but with subsequent revisions (Wood 2024a; Herrera et al. 2025), the mainland Spanish total now sits at 236, with Iberia as a whole at 237 (see Gaspar et al. 2025). It is clear that the *Andrena* faunas of Greece and Spain are extremely similar in size, although mainland Spain is 3.7

times larger than Greece, resulting in very different species density values (Table 2). Spain has a total of 0.48 species per 1,000 km<sup>2</sup>, compared to 1.84 for Greece and 1.68 for Bulgaria. The species density decreases further to 0.40 when considering the Iberian Peninsula as a whole (peninsula Portugal plus Spain). When considering Albania, North Macedonia, Bulgaria, and Greece collectively (area of 297,412 km<sup>2</sup>;  $n$  species = 273), a density value of 0.91 is obtained, further supporting a genuinely higher species density in this region than in Iberia. This is reflected in different country size categories, which show a bias towards the Levant, the East Mediterranean, and Pannonian Europe, in that order (Table 2). Comparison outside of the West Palaearctic is challenging due to issues of scale and the much larger average size of non-Mediterranean countries (e.g. China, Russia, the United States of America). However, taking individual US states within the 100,000–300,000 km<sup>2</sup> class (data from Ascher and Pickering 2025), the state with the highest species density Utah (area 219,887 km<sup>2</sup>) achieves only a value of 0.65. The most species-rich state California (area 423,970 km<sup>2</sup>) achieves a species density value of 0.62, placing it between Italy and Turkey (Table 2). This suggests that the southern Balkans has a genuinely high species density of *Andrena* regardless of the comparative scale chosen, though a more sophisticated future analysis would be welcome.

However, where Iberia is superior to the southern Balkans is in the rate of *Andrena* endemism. Based on revisions (Wood 2023b, 2023c; Wood 2024a; Herrera et al. 2025), Iberia has 37/237 endemic species for an endemism rate of 15.7%, compared to 28/273 for the southern Balkans which is an endemism rate of 10.3%. Morocco sits inbetween with an endemism rate of 12.2% (25/205; Wood 2023c, 2025a; unpublished data). Somewhat overlooked by this discussion is the Italian Peninsula, with

**Table 2.** *Andrena* faunal richness and species density within political units; density is expressed as number of *Andrena* species per 1,000 km<sup>2</sup>. Data sources are published (e.g. Pisanty et al. 2018, 2022b; Wood 2023a, 2023b, 2023c, 2024a, 2025) and unpublished works of Wood combined with critical revision of published country lists and the country lists of Ascher and Pickering (2025). Countries in the southern Balkans are highlighted in bold. The total for Spain is that of peninsula Spain only (not including the Canary Islands).

Country area <50,000 km <sup>2</sup>					Country area 50,000–100,000 km <sup>2</sup>				
Rank	Country	Area (km <sup>2</sup> )	Species	Density	Rank	Country	Area (km <sup>2</sup> )	Species	Density
1	Lebanon	10,452	154	14.73	1	Croatia	56,594	144	2.54
2	Cyprus	9,251	77	8.32	2	Austria	83,879	151	1.80
3	Israel & West Bank	27,800	220	7.91	3	Czechia	78,867	133	1.69
4	Slovenia	20,273	122	6.02	4	Georgia	69,700	116	1.66
5	<b>North Macedonia</b>	25,713	153	5.91	5	Hungary	93,025	154	1.66
Country area 100,000–300,000 km <sup>2</sup>					Country area >300,000 km <sup>2</sup>				
Rank	Country	Area (km <sup>2</sup> )	Species	Density	Rank	Country	Area (km <sup>2</sup> )	Species	Density
1	<b>Greece</b>	131,957	243	1.84	1	Italy	301,340	218	0.72
2	<b>Bulgaria</b>	110,994	186	1.68	2	Turkey	783,562	392	0.50
3	Tunisia	163,610	154	0.94	3	Spain (pen.)	493,514	236	0.48
4	Syria	185,180	158	0.85	4	Morocco	446,550	205	0.46
5	Tajikistan	141,400	108	0.76	5	France	543,940	180	0.33

a rich fauna of 218 species but only three endemic species (six if both Corsica and Sardinia are included; Wood et al. 2023), giving an endemism rate of 1.4 or 2.8% depending on the specific definition used. Whilst the species density is high at 0.72 species/1000 km<sup>2</sup> (Table 2), it is clear that the Italic Peninsula is not a major centre of endemic *Andrena* diversity when compared to the Iberian and Balkan Peninsulas.

Concerning the major advances in our understanding of *Andrena* species in the southern Balkans presented and summarised here, beyond the simple revision of unidentified specimens sitting in museum collections, advances in knowledge can be broadly grouped into four categories; 1) characterisation of the “northern” fauna, 2) characterisation of the East Aegean Island fauna, 3) fine-grained discovery and study of uncommon endemics, and 4) study of the Cretan fauna. When considering the fauna of the southern Balkans, much attention has naturally fallen on the Mediterranean parts, but a major source of new species for the region and individual countries within the region has been species of temperate habitats that show largely Central European distributions and which have been found in mountainous areas of the southern Balkans. These mountains support many *Andrena* species that are often associated obligately or strongly with woody plants such as *Acer* (Sapindaceae), *Salix* (Salicaceae), or *Vaccinium* (Ericaceae) or herbaceous plants of cool grasslands. These include *A. apicata*, *A. bucephala*, *A. chrysoseles*, *A. coitana*, *A. falsifica*, *A. fulvata*, *A. lapponica*, *A. marginata*, and *A. tarsata*. These species are uncommon in collections due to their marginal occurrence in this region, but are also likely to be under-recorded as most collectors, especially visitors from outside of the region, preferentially visit Mediterranean and sub-Mediterranean habitats.

Study of the East Aegean fauna was partially conducted by Warncke (1974a, 1975) and more recently by Erwin Scheuchl working with the University of the Aegean on Lesbos (the Melissotheque of the Aegean collection). Some specific species names were published for checklists and future reference (Rasmont et al. 2017; Reverté et al. 2023), but no comprehensive revision of this collection has yet been made (J. Devalez, pers. comm.). Nonetheless, the East Aegean islands contribute greatly to the diversity of the southern Balkans since they host species with largely Anatolian distributions, along with Greek and Bulgarian parts of Thrace. Similar focused study has also produced new endemic or very rare species (Scheuchl 2010, 2011; Standfuss and Standfuss 2010; Standfuss et al. 2011). Whilst previously, much time may have passed between specimen collection and description (e.g. Schuberth 1995; Grünwaldt et al. 2005), this “lag” has decreased in recent years, allowing a more rapid characterisation and documentation of *Andrena* diversity, a necessary state of affairs in this massive genus.

It is more straightforward to discuss and highlight the incredible faunal endemism of Cretan *Andrena*, with eight species (*A. cretica*, *A. creticola*, *A. incustodita*, *A. lasithi*, *A. lediveleci*, *A. obscuricrus*, *A. pelagica*, *A. testudo*), all of which have only recently been treated as endemic following the baseline of Warncke (1967b). In functional terms, this means that the island has gone from one poorly understood and not actually endemic species (*Andrena caneibia* Strand, 1915, see Wood 2024a) to eight genuinely endemic species since July 2024 (the publication of Wood 2024a) to now, or a little

under two years. This partially reflects the narrowing of species concepts relative to the broad concepts used by Warncke with many “subspecies” of varying distinctiveness, but also reflects modern collecting and revision of material. For several species, it has not been possible to find historical specimens in collections, with the oldest available specimens for *A. cretica* (1973), *A. lasithi* (1972), *A. lediveleci* (1973), *A. pelagica* (1963), and *A. testudo* (1973) coming in the second half of the 20<sup>th</sup> century. Indeed, three of these species were caught seemingly for the first time by van Ooststroom and Teunissen during their 1973 trips to the island. Crete alone represents eight of the 28 *Andrena* species endemic to the southern Balkans and is consequently a major contributor to the endemic diversity of the region.

Based on a subset of the overall Greek data used in this work, 1,919 *Andrena* specimens from Crete could be examined, representing 53 species, giving an endemism rate of 15.1%, comparing reasonably with studies on ants (Formicidae), sawflies (Symphyta *sensu lato*), crickets and grasshoppers (Orthoptera), and beetle groups (Coleoptera) which report an endemism rate varying between 9–25% (Liston et al. 2015; Assing 2019; Salata et al. 2020; Kotitsa et al. 2025; Pavlou et al. 2025), and higher than the 6.1% reported for Lepidoptera (Heumer et al. 2025). Comparisons with other bee groups are challenging due to the need for modern revisions of the Cretan fauna in light of the major changes reported for the *Andrena* based on just a few years of concentrated study. A discussion of the precise mechanisms driving this level of endemism in *Andrena* is beyond the scope of this work, but the island is well-known to have been progressively separated and isolated beginning with the Mid-Aegean Trench formation around 12–9 million years ago followed by the end of the Messinian salinity crisis around 5.3–6.0 million years ago, and Crete was not reconnected to mainland Greece even during the last glacial maximum due to the depth of the Cretan sea (Pavlou et al. 2025).

As a corollary, there seems to be an emerging syndrome in small black *Andrena* on the island of Crete in that, relative to their closest mainland relatives, the integument of these bees becomes less strongly sculptured, the punctures become slightly more dispersed, and hence the integument appears more strongly polished and shining. This can be seen in the four unrelated lineages *A. (Graecandrena) cretica*, *A. (Aciandrena) lediveleci*, *A. (Micrandrena) pelagica*, and *A. (Cryptandrena) testudo*. Some Cretan *Andrena* species of variable size also show a dark clypeus in the male sex compared to their nearest relatives which show pale maculations, e.g. *A. (Ulandrena) incustodita* versus *A. abbreviata* and *A. testudo* versus *A. brumanensis*. This is presumably due to the local environmental conditions on Crete, but as to what these are, only speculation is possible at this time. A parallel can be drawn with the shinier integument seen in second generation (summer) individuals of bivoltine *Andrena* (*Micrandrena*), a phenomenon that is presumably associated with higher temperatures and more intense solar radiation.

Finally, it is important to talk about biogeography, and what patterns of *Andrena* distribution and speciation suggest about this genus. As well as the syndrome

of endemic Cretan specimens, two major and one minor pattern can be seen in distributions of certain southern Balkan *Andrena* species. This can be largely summarised as Greek taxa (major), Anatolian taxa (major), and Levantine taxa (minor). Species pairs such as *A. waschulzi* (Greek)/*A. neocyprica* (Anatolian) or *A. meridionalis* (Greek)/*A. clanga* (Anatolian/Levantine) show a strong division across the Aegean sea and the Thessaloniki-Kavala corridor (Figs 42, 65). The exact position of this tension zone changes taxon by taxon, for example in *A. concinna* (Greek)/*A. crecca* (Anatolian), with *A. crecca* essentially becoming Macedonia+Anatolia since the tension point is much further to the west (Fig. 60). This pattern can be somewhat modified to become Greek+Anatolian/Levantine, as in the case of *A. hyemala* (Greek+Anatolian)/*A. repressa* (Levantine) where the island of Rhodes acts as a “turning point” for the faunistic change (Fig. 23).

As mentioned in the section on species concepts, these faunal transition tension zones may well reflect the impacts of different glacial refugia, with differentiated taxa only now coming back into contact. Study of gene flow in *Andrena* is in its infancy; almost all genetic work aimed at characterising species status has used mitochondrial markers, with all their known issues (e.g. Kearns et al. 2023; Wüster 2025). What is known for certain is that *Andrena* have an exceptionally high speciation rate when set in context against all other lineages of bees (Bossert et al. 2022). In addition to this rapid speciation rate, the size of the genus with now just over 1,750 species (Pisanty et al. 2025; Herrera et al. 2025; Wood 2025a) makes them both as speciose as and considerably younger in evolutionary time than cichlid fishes, a textbook example of rapid vertebrate speciation (Friedman et al. 2013). Whilst the emerging pattern seems to be that *Andrena* species seem to break gene flow between populations relatively quickly when geographically isolated, with extreme examples existing in even on the same mountain in near sympatry or possibly even parapatry (Wood 2022), detailed study of gene flow is lacking for anything more than a handful of species (McLaughlin et al. 2022). When placed into the context of more formalised study of the evolution of reproductive isolation, it is clear that there are many unanswered questions in the *Andrena* model system relative to better studied Lepidoptera models (e.g. Kulmuni et al. 2020).

In conclusion, the southern Balkans represent an important area for *Andrena* diversity globally. Whilst it does not host quite as many basal lineages as Turkey and the Levant, nor achieve the extreme levels of *Andrena* species density seen in the Levant, the massively species-rich *Andrena* fauna of Turkey, or the degree of *Andrena* endemism seen in the Iberian Peninsula or Morocco, it remains an essential region for any student of the genus and is one of the two pillars of *Andrena* diversity in Europe, the other being the Iberian Peninsula. It is perhaps no surprise that it was the Greek *Andrena* fauna that was first studied by Klaus Warncke, the most prolific *Andrena* taxonomist of the 20<sup>th</sup> century, with study of this fauna opening the door to his later revision of the *Andrena* of Turkey. It is hoped that the present synthetic work may inspire works of equal magnitude in the future.

## Acknowledgements

I thank my colleagues Gideon Pisanty (Steinhardt Museum of Natural History, Tel-Aviv University, Israel) and Christophe Praz (University of Neuchâtel, Neuchâtel, Switzerland) for essential conversations on *Andrena* taxonomy, and company during collecting trips to Greece in April and June 2024, respectively. I also thank Silas Bossert (Washington State University, Pullman, USA) for collaboration on *Andrena* phylogenomics. I thank Paolo Rosa (UMONS) for discussion of the ICZN code, insect taxonomy in general, and help during a trip to the MSNG. I thank the reviewers Jelle Devalez, Gideon Pisanty, Erwin Scheuchl, and Hans R. Schwenninger for their detailed comments, communication of overlooked literature, and novel specimen information which substantially improved the manuscript, as well as the editor Jack Neff for his attention to detail. My thanks go to all curators or researchers who hosted me at their institutions, specifically (and in no particular order) Toshko Ljubomirov (IBER), Andrew Liston (DEI), Joseph Monks (NHMUK), Dominique Zimmermann (NHMW), Esther Ockermüller and Martin Schwarz (OÖLM), Fatih Dikmen (IUZC), James Hogan (OUMNH), Frederique Bakker (RMNH), Roberto Poggi and Marina Tavano (MSNG), Leanna Dixon and Tony Hunter (WML), Daniel Benda (NMPC), Stefanie Krause (ZMHB), and Olga Schmidt (ZSM). I particularly thank Toshko Ljubomirov for correspondence surrounding obscure literature on Bulgarian *Andrena*, and for help facilitating visits to Bulgaria. I also thank Teodor Trifonov (IBER) for help conducting fieldwork in Bulgaria and company during fieldwork, as well as Andreas Müller, Romain Le Divelec, Achik Dorchin, Rémi Santerre, Stuart Roberts, Simone Flaminio, Kobe Janssen, Wolf-Harald Liebig, Win Vertommen, Leander Bertsch, Marco Selis, Vincent Leclercq, Christian Schmid-Egger, Villu Soon, Curro Molina (EBDC), Maurizio Mei (MZUR), Juho Paukkunen (MZH), and Jakub Straka for generously sharing *Andrena* specimens with me. I also thank Mira Boustani for organising essential fieldwork in Lebanon in April 2023, and Doug Yanega (University of California, Riverside) for highlighting the issues surrounding the name *Leucandrena*. Specimens from Greece collected in 2023, 2024, and 2025 were authorised under permits A.Π.ΥΠΙΕΝ/ΔΔΔ/27675/905, A.Π.ΥΠΙΕΝ/ΔΔΔ/108820/3519, A.Π.ΥΠΙΕΝ/ΔΔΔ/49007/1635, and A.Π.ΥΠΙΕΝ/ΔΔΔ/14666/454 from the Ministry of Environment and Energy. Travel to the OUMNH and MSNG was supported by the Stichting Fonds Pontium. Major support for the overall work was provided by the project EPIC—Developing courses for European wild bee identification, EC DG ENV project Contract No.: 090201/2024/927644/SER/ENV.D2.

## References

- Alfken JD (1904) Über die von Brülle aufgestellten griechischen *Andrena*-Arten (Hym.). Zeitschrift für systematische Hymenopterologie und Dipterologie 4: 289–295.
- Alfken JD (1935) Beitrag zur Kenntnis der Bienenfauna von Kleinasien. Entomologische Rundschau 52: 110–162.

- Álvarez Fidalgo P, Álvarez Fidalgo M, Noval Fonseca N, Pascual Hergueta JI, Aguado Martín LO (2021) Description of the hitherto unknown male of *Andrena (Leucandrena) dinizi* Warncke, 1975 (Apoidea: Andrenidae) with the first record from the Iberian Peninsula of its potential broodparasite *Nomada leucophthalma* (Kirby, 1802) (Apoidea: Apidae). *Boletín de la Sociedad Entomológica Aragonesa (S.E.A.)* 69: 124–136.
- Anon (1879) William Wilson Saunders. *Nature* 20: 536–537. <https://doi.org/10.1038/020536a0>
- Ascher JS, Pickering J (2025) Discover Life bee species guide and world checklist (Hymenoptera: Apidae: Anthophila). [Available from:] [https://www.discoverlife.org/mp/20q?guide=Apoidea\\_species&flags=HAS](https://www.discoverlife.org/mp/20q?guide=Apoidea_species&flags=HAS) [Accessed on: 16 Apr. 2025]
- Assing V (2019) Monograph of the Staphylinidae of Crete (Greece). Part I. Diversity and endemism (Insecta: Coleoptera). *Contributions to Entomology* 69(2): 197–239. <https://doi.org/10.21248/contrib.entomol.69.2.197-239>
- Astafurova YuV, Proshchalykin MYu, Sidorov DA, Osytshnjuk AZ (2021) The type specimens of bees (Hymenoptera, Apoidea) deposited in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg. Contribution IV. Family Andrenidae, genus *Andrena* Fabricius, 1775, species described by F. Morawitz. *Zootaxa* 5037: 1–78. <https://doi.org/10.11646/zootaxa.5037.1.1>
- Astafurova YuV, Proshchalykin MYu, Sidorov DA (2022) The bees of the genus *Andrena* Fabricius, 1775 (Hymenoptera, Andrenidae) described by Ferdinand Morawitz from the collection of Aleksey Fedtschenko. *ZooKeys* 1120: 105–176. <https://doi.org/10.3897/zookeys.1120.90206>
- Atanassov N (1962) Untersuchungen über die Systematik und die Ökologie der Hymenopterenarten aus dem Gebiet von Petrič (Südwestbulgarien). *Bulletin de l'Institut de Zoologie et Musée* 12: 109–172. [In Bulgarian]
- Atanassov N (1964) Hymenopteraarten aus der thrakischen Tiefebene (Sudbulgarien). In: Paspalev G, Markov G, Pechev G (Eds) *Die fauna Thrakiens*. Band I. Verlag der Bulgarischen Akademie der Wissenschaften, Sofia, 145–206. [In Bulgarian]
- Atanassov N (1972) Arten Hymenoptera von West-Balkan-Gebirge: I. Teil. *Bulletin de l'Institut de Zoologie et Musée, Academie Bulgare des Sciences* 35: 179–228.
- Atanassov N, Vasileva E (1990) New Apian species (Hymenoptera, Apoidea) for the Bulgarian fauna. *Historia naturalis bulgarica* 2: 12–18. [In Bulgarian]
- Baker DB (1993) The Type Material of the Nominal Species of Exotic Bees described by Frederick Smith (Hymenoptera, Apoidea). DPhil thesis, Oxford University, St. John's College, 312 pp.
- Banaszak J, Dochkova B (2014) Bees (Hymenoptera, Apoidea, Apiformes) in the Agricultural Landscape of Bulgaria: Species Diversity. *Journal of Apicultural Science* 58: 29–49. <https://doi.org/10.2478/jas-2014-0003>
- Blank SM, Kraus M (1994) The nominal taxa described by K. Warncke and their types (Insecta, Hymenoptera, Apoidea). *Linzer biologische Beiträge* 26(2): 665–761.
- Bleidorn C, Henze K (2021) A new primer pair for barcoding of bees (Hymenoptera: Anthophila) without amplifying the orthologous *coxA* gene of *Wolbachia* bacteria. *BMC Research Notes* 14: 427. <https://doi.org/10.1186/s13104-021-05845-9>

- Bossert S, Wood TJ, Patiny S, Michez D, Almeida EAB, Minckley RL, Packer L, Neff JL, Copeland RS, Straka J, Pauly A, Griswold T, Brady SG, Danforth BN, Murray EA (2022) Phylogeny, biogeography and diversification of the mining bee family Andrenidae. *Systematic Entomology* 47: 283–302. <https://doi.org/10.1111/syen.12530>
- Brullé A (1833) Insectes. In: Expedition scientifique de Moree. *Zoologie*, Paris, Levrault 3(2): 1–29, 64–395.
- Christ JL (1791) *Naturgeschichte, Klassifikation und Nomenclatur der Insekten vom Bienen, Wespen und Ameisengeschlecht*. Frankfurt, Main, Herrmann, 1–535. <https://doi.org/10.5962/bhl.title.87724>
- Cockerell TDA (1922) LVI.—Descriptions and Records of Bees.—XCVI. The *Annals and Magazine of Natural History*, Series 9, 10: 544–550. <https://doi.org/10.1080/00222932208632802>
- Dalla Torre KW, Friese H (1895) Synonymischer Katalog der europäischen Sammelbienen. *Entomologische Nachrichten* 21: 21–26, 37–50, 53–62, 69–80.
- Dárdon MJ, Torres F, Ornos C (2014) The subgenus *Andrena* (*Micrandrena*) (Hymenoptera: Andrenidae) in the Iberian Peninsula. *Zootaxa* 3872(5): 467–497. <https://doi.org/10.11646/zootaxa.3872.5.3>
- Dours JA (1872) Hyménoptères nouveaux du bassin Méditerranéen. *Revue et magasin de zoologie pure et appliquée* 23: 293–311, 349–359, 396–399, 419–434.
- Dours JA (1873) Hyménoptères du bassin méditerranéen *Andrena* (suite). *Biareolina, Eucera*. *Revue et magasin de zoologie pure et appliquée* 1: 274–325.
- Drenowski A (1934) Beitrag zur Insektenfauna von Bulgarien und Mazedonien. *Mitteilungen der Bulgarischen Entomologischen Gesellschaft in Sofia* 8: 174–182. [In Bulgarian]
- Drenowski A (1936) Beitrag zur Insektenfauna Bulgariens u. Mazedoniens. II. *Mitteilungen der Bulgarischen Entomologischen Gesellschaft in Sofia* 9: 237–256. [In Bulgarian]
- Dubitzky A (2006) New palearctic species of the bee genus *Andrena* (Insecta: Hymenoptera: Andrenidae). *Zootaxa* 1284: 1–27. <https://doi.org/10.11646/zootaxa.1284.1.1>
- Dubitzky A, Plant J, Schönitzer K (2010) Phylogeny of the bee genus *Andrena* Fabricius based on morphology (Hymenoptera: Andrenidae). *Mitteilungen der Münchner Entomologischen Gesellschaft* 100: 137–202.
- Dylewska M (1987) Die Gattung *Andrena* Fabricius (Andrenidae, Apoidea) in Nord- und Mitteleuropa. *Acta Zoologica Cracoviensia* 30(12): 359–708.
- Ebmer AW (1999) Die westpaläarktischen Arten der Gattung *Dufourea* Lepeletier, 1841 (Insecta: Hymenoptera: Apoidea: Halictidae: Rophitinae) Vierter Nachtrag. *Linzer biologische Beiträge* 31(1): 183–228.
- Ebmer AW (2003) Hymenopterologische Notizen aus Österreich —16 (Insecta: Hymenoptera: Apoidea). *Linzer biologische Beiträge* 35(1): 313–403.
- Ebmer AW (2009) Bienenkundliche Forschungen am Peloponnes 1974–2008 Vortrag zur 75. Entomologentagung der Entomologischen Arbeitsgemeinschaft am Oberösterreichischen Landesmuseum in Linz am 9. November 2008. *Linzer biologische Beiträge* 41(1): 49–67.
- Eversmann E (1852) *Fauna hymenopterologica volgo-uralensis* (Continuatio). *Bulletin de la Société impériale des naturalistes de Moscou* 25(3): 3–137.
- Fahringer J, Friese H (1921) Eine Hymenopteren-Ausbeute aus dem Amanusgebirge. (Kleinasien und Nord-Syrien, südl. Armenien.). *Archiv für Naturgeschichte* 87A(3): 150–176.

- Friedman M, Keck BP, Dornburg A, Eytan RI, Martin CH, Hulsey CD, Wainwright PC, Near TJ (2013) Molecular and fossil evidence place the origin of cichlid fishes long after Gondwanan rifting. *Proceedings of the Royal Society B* 280: 20131733. <https://doi.org/10.1098/rspb.2013.1733>
- Friese H (1899) Neue palaearktische Sammelbienen. *Entomologische Nachrichten Berlin* 25: 321–346. <https://doi.org/10.5281/zenodo.16124719>
- Friese H (1922) Neue Formen der Bienengattung *Andrena* (Hym.). *Konowia* 1: 209–217.
- Friese H (1923) Eine Kriegsausbeute an Apiden (Bienen) aus Makedonien. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere* 46: 175–216.
- Gaspar H, Flaminio S, Soares A, Rufino C, Loureiro J, Castro S, Wood TJ (2025) New data from the historical bee collection (Hymenoptera, Anthophila) of the Science Museum of the University of Coimbra and additional faunistic updates for Portugal. *Journal of Hymenoptera Research* 98: 165–194. <https://doi.org/10.3897/jhr.98.142965>
- Gautam RK, Uniyal VP, Wood TJ (2024) A critical revision of the *Andrena* Fabricius, 1775 of India, with the description of two new species (Hymenoptera: Andrenidae) from Uttarakhand. *European Journal of Taxonomy* 948: 1–59. <https://doi.org/10.5852/ejt.2024.948.2637>
- Ghisbain G, Rosa P, Bogusch P, Flaminio S, Le Divelec R, Dorchin A, Kasperek M, Kuhlmann M, Litman J, Mignot M, Müller A, Praz C, Radchenko VG, Rasmont P, Risch S, Roberts SPM, Smit J, Wood TJ, Michez D, Reverté S (2023) The new annotated checklist of the wild bees of Europe (Hymenoptera, Anthophila). *Zootaxa* 5327(1): 1–147. <https://doi.org/10.11646/zootaxa.5327.1.1>
- Ghisbain G, Rosa P, Bogusch P, Brau T, Carion F, de Manincor N, Devalez J, Dorchin A, Flaminio S, Greil H, Hölzler G, Hopfenmüller S, Kasperek M, Kuhlmann M, Le Divelec R, Litman J, Maugendre A, Michez D, Müller A, Ortiz-Sánchez FJ, Praz C, Radchenko VG, Rasmont P, Risch S, Roberts SPM, Santerre R, Schmid-Egger C, Sentil A, Straka J, Williams PH, Wood TJ, Reverté S (2025) The new annotated checklist of the wild bees of Europe (Hymenoptera: Anthophila)—version 2025. *Zootaxa* 5736: 1–126. <https://doi.org/10.11646/zootaxa.5736.1.1>
- Gömöry D, Zhelev P, Brus R (2020) The Balkans: a genetic hotspot but not a universal colonization source for trees. *Plant Systematics and Evolution* 306: 5. <https://doi.org/10.1007/s00606-020-01647-x>
- Gouy M, Guindon S, Gascuel O (2010) SeaView version 4: A multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molecular Biology and Evolution* 27: 221–224. <https://doi.org/10.1093/molbev/msp259>
- Grace A (2010) *Introductory biogeography to bees of the Eastern Mediterranean and Near East*. Bexhill Museum Association, Bexhill, 283 pp.
- Grünwaldt W (1976) *Andrena grossella* n. sp., eine Insekten-Art mit 9gliedrigen Maxillar- und Labialpalpen (Hymenoptera, Apoidea). *Nachrichtenblatt der Bayerischen Entomologen* 25(4): 65–70.
- Grünwaldt W, Osytschnjuk AZ, Scheuchl E (2005) Neue *Andrena*-Arten aus der Paläarktis (Hymenoptera: Apidae: Andreninae). *Entomofauna* 26: 349–368.
- Gusenleitner F (1998) Neue westpaläarktische *Andrena*-Arten (Hymenoptera: Apidae: Andreninae). *Entomofauna* 19(6): 109–144.
- Gusenleitner F, Schwarz M (2001) Zur Morphologie verschiedener von F. Morawitz beschriebener *Andrena*-Arten (Hymenoptera: Apidae: Andreninae). *Entomofauna* 22(7): 93–196.

- Gusenleitner F, Schwarz M (2002) Weltweite Checkliste der Bienengattung *Andrena* mit Bemerkungen und Ergänzungen zu paläarktischen Arten (Hymenoptera, Apidae, Andreninae, *Andrena*). Entomofauna, Supplement 10: 1–1280.
- Gusenleitner F, Schwarz M, Ascher J, Scheuchl E (2005) Korrekturen und Nachträge zu Gusenleitner & Schwarz (2002): “Weltweite Checkliste der Bienengattung *Andrena* mit Bemerkungen und Ergänzungen zu paläarktischen Arten (Hymenoptera, Apidae, Andreninae, *Andrena*)”. Entomofauna 26(26): 437–472.
- Haeckel E (1872) Die Kalkschwämme. Eine Monographie in zwei Bänden Text und einem Atlas mit 60 Tafeln Abbildungen. G. Reimer: Berlin, (1: 1–484) 2: 1–418 (3: pls 1–60). <https://doi.org/10.5962/bhl.title.11323>
- Hazir C, Keskin N, Scheuchl E (2012) First record of four species of *Andrena* sand bees in Turkey (Hymenoptera: Apoidea: Andrenidae). Zoology in the Middle East 56: 141–143. <https://doi.org/10.1080/09397140.2012.10648951>
- Hazir C, Keskin N, Scheuchl E (2014) Faunistic, geographical and biological contributions to the bee genus *Andrena* (Hymenoptera, Andrenidae, Andreninae) from Turkey. Journal of Hymenoptera Research 38: 59–133. <https://doi.org/10.3897/jhr.38.7288>
- Hedicke H (1933) Beiträge zur Systematik der Gattung *Andrena* F. (Hym. Apid.). Mitteilungen aus dem zoologischen Museum in Berlin 19: 199–220.
- Hedicke H (1942) Über paläarktische Apiden. (Hym.) III. Mitteilungen der Deutschen Entomologischen Gesellschaft 11: 63–65.
- Herrera CM, Alonso C, Valverde J, Núñez A, Wood TJ (2025) The genus *Andrena* Fabricius, 1775 (Hymenoptera, Andrenidae) in a Mediterranean biodiversity hotspot: community-wide relationships with plants and description of three new species. Journal of Hymenoptera Research 98: 1039–1066. <https://doi.org/10.3897/jhr.98.165915>
- Heumer P, Berggren K, Aarvik L, Rennwald E, Hausmann A, Segerer A, Staffoni G, Aspaas AM, Trichas A, Hebert PDN (2025) Extensive DNA barcoding of Lepidoptera of Crete (Greece) reveals significant taxonomic and faunistic gaps and supports the First Comprehensive Checklist of the Island’s Fauna. Insects 16(5): 438. <https://doi.org/10.3390/insects16050438>
- ICZN [International Commission on Zoological Nomenclature] (1964) International Code of Zoological Nomenclature. Second Edition. The International Trust for Zoological Nomenclature, London, xx + 176 pp.
- ICZN [International Commission on Zoological Nomenclature] (1985) International Code of Zoological Nomenclature. Third Edition. The International Trust for Zoological Nomenclature, London, xx + 338 pp.
- ICZN [International Commission on Zoological Nomenclature] (1999) International Code of Zoological Nomenclature. 4<sup>th</sup> Edition. The International Trust for Zoological Nomenclature, London, xxix + 306 pp. <https://doi.org/10.5962/bhl.title.50608>
- Ivanova NV, Dewaard JR, Hebert PDN (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. Molecular Ecology Notes 6: 998–1002. <https://doi.org/10.1111/j.1471-8286.2006.01428.x>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30: 772–780. <https://doi.org/10.1093/molbev/mst010>

- Kearns AM, Restani M, Szabo I, Schröder-Nielsen A, Kim JA, Richardson HM, Marzluff JM, Fleischer RC, Johnsen A, Omland KE (2023) Genomic evidence of speciation reversal in ravens. *Nature Communications* 9: 906. <https://doi.org/10.1038/s41467-018-03294-w>
- Kinel J, Noskiewicz J (1930) Einige Bemerkungen über die zoogeographischen Verhältnisse von Podolien und Volhynien des polnischen Anteils. *Polskie Pismo Entomologiczne* 9(3–4): 272–288.
- Kotitsa N, Chobanov D, Trichas A, Mylonas M (2025) New and noteworthy records of Orthoptera (Insecta) from Crete (Greece) and its satellite islets. *Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa"* 68(1): 143–217. <https://doi.org/10.3897/travaux.68.e151701>
- Kriechbaumer J (1873) Hymenopterologische Beiträge. III. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 23: 49–68.
- Kuhlmann M, Ascher JS, Dathe HH, Ebmer AW, Hartmann P, Michez D, Müller A, Patiny S, Pauly A, Praz C, Rasmont P, Risch S, Scheuchl E, Schwarz M, Terzo M, Williams PH, Amiet F, Baldock D, Berg Ø, Bogusch P, Calabuig I, Cederberg B, Gogala A, Gusenleitner F, Josan Z, Madsen HB, Nilsson A, Ødegaard F, Ortiz-Sanchez J, Paukkunen J, Pawlikowski T, Quaranta M, Roberts SPM, Sáropataki M, Schwenninger HR, Smit J, Söderman G, Tomozei B (2014) Checklist of the Western Palaearctic Bees (Hymenoptera: Apoidea: Anthophila). <http://westpalbees.myspecies.info> [accessed 19 Sept 2024]
- Kulmuni J, Butlin RK, Lucek K, Savolainen V, Westram AM (2020) Towards the completion of speciation: the evolution of reproductive isolation beyond the first barriers. *Philosophical Transactions of the Royal Society B* 375: 20190528. <https://doi.org/10.1098/rstb.2019.0528>
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35: 1547–1549. <https://doi.org/10.1093/molbev/msy096>
- LaBerge WE (1987) A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part XII. Subgenera *Leucandrena*, *Ptilandrena*, *Scoliandrena* and *Melandrena*. *Transactions of the American Entomological Society* 112(3): 191–248.
- Liston AD, Jacobs H-J, Prous M (2015) The Sawflies of Crete (Hymenoptera, Symphyta). *Deutsche Entomologische Zeitschrift* 62(1): 65–79. <https://doi.org/10.3897/dez.62.4737>
- Maidl F (1922) Beiträge zur Hymenopterenfauna Dalmatiens, Montenegros und Albanien. 1. Teil: Aculeata et Chrysididae. *Annalen des Naturhistorischen Museums in Wien* 35: 36–106.
- Mandery K, Kosuch J, Schuberth J (2008) Untersuchungsergebnisse zum Artstatus von *Andrena decipiens* Schenck, 1861, *Andrena flavilabris* Schenck, 1874, und ihrem gemeinsamen Brutparasiten *Nomada stigma* Fabricius, 1804 (Hymenoptera: Apidae). *Nachrichtenblatt der Bayerischen Entomologen* 57: 30–41.
- McLaughlin G, Gueuning M, Genoud D, Frey JE, Praz C (2022) Why are there so many species of mining bees (Hymenoptera, Andrenidae)? The possible roles of phenology and *Wolbachia* incompatibility in maintaining species boundaries in the *Andrena proxima*-complex. *Systematic Entomology* 48(1): 127–141. <https://doi.org/10.1111/syen.12566>
- Mendicino F, Carlomagno F, Praz C, Wood TJ, Dorchin A, Flaminio S, Aubert M, Le Divelec R, Bonelli D, Di Biase E, Fumo F, Pezzi M, Luzzi G, Siclari A, Pellegrino G, Bonacci T (2026) New records of wild bees from Calabria and Basilicata highlight the hidden diversity of Anthophila in Italy. *Diversity* 18: 74. <https://doi.org/10.3390/d18020074>

- Meunier F (1897) Quelques mots sur les faunes hyménoptérologiques et diptérologiques de la Bulgarie septentrionale. *Annales de la Société des Sciences de Bruxelles* 22: 348–350.
- Michener CD (2007) *The Bees of the World*. 2<sup>nd</sup> Edn. Johns Hopkins University Press, Baltimore, 972 pp.
- Michez D, Boustani M, Sentil A, Benrezkallah J, de Manincor N, Wood TJ, Álvarez Fidalgo P, Aubert M, Bellotto V, Biella P, Bogusch P, Bosch J, Brau T, Browne K, Carion F, Castro L, Cederberg B, Clay J, Debont T, Bila Dubaić J, Dall'Olio R, Dellicour S, Devalez J, Devorsine R, Dufrière E, De la Rúa P, De Tandt B, Evrard D, Flaminio S, Fiordaliso W, Fontana P, Gadoum S, Galbany Casals M, Gaspar H, Gekièrè A, Gérard M, Geslin B, Kasperek M, Kierat J, Kohl PL, Kuhlmann M, Kryger P, Leclercq N, Le Divelec R, Lemaire S, Lescot S, Lhomme P, Litman J, Marshall L, McCormack GP, Moro A, Mudri Stojnić S, Ockermueller E, Oleksa A, Ortiz-Sánchez FJ, Patiny S, Paukkunen J, Perrard A, Petanidou T, Pinto MA, Potts SG, Praz C, Put SCL, Radchenko VG, Rasmont P, Requier F, Reverté S, Risch S, Rogenstein S, Rosa P, Ruiz C, Rutschmann B, Santerre R, Smit J, Straka J, Thulier J, Tourbez C, Trotter A, Vereecken NJ, Williams PH, Winter E, Zimmermann D, Ghisbain G (2026) Measuring the pulse of European biodiversity using the Red List. *European Red List of Bees*. European Commission, Brussels, Belgium, xii + 162 pp. <https://data.europa.eu/doi/10.2779/521877>
- Morawitz F (1866) Bemerkungen über einige von Prof. Eversmann beschriebene Andrenidae, nebst Zusätzen. *Horae Societatis Entomologicae Rossicae* 4: 3–28.
- Morawitz F (1871) Neue suedeuropäische Bienen. *Horae Societatis Entomologicae Rossicae* 8(3): 201–231.
- Morawitz F (1886) Neue transcaucasische Apidae. *Horae Societatis Entomologicae Rossicae* 20(1/2): 57–81.
- Müller A, Kuhlmann M (2008) Pollen hosts of western palaeartic bees of the genus *Colletes* (Hymenoptera: Colletidae): the Asteraceae paradox. *Biological Journal of the Linnean Society* 95: 719–733. <https://doi.org/10.1111/j.1095-8312.2008.01113.x>
- Müller A, Westrich P (2023) Morphological specialisation for primary nectar robbing in a pollen specialist mining bee (Hymenoptera, Andrenidae). *Journal of Hymenoptera Research* 95: 215–230. <https://doi.org/10.3897/jhr.95.98260>
- Nedialkov N (1914) Septième contribution à la faune entomologique de la Bulgarie. *Revue de l'Académie Bulgare des Sciences. Partie Seconde. Classe des Sciences Naturelles et Mathématique* 9: 181–210. [In Bulgarian]
- Noskiewicz J (1924) Nowe dla fauny Polski i rzadkie błonkówki. *Polskie Pismo Entomologiczne* 2(4): 176–186.
- Ockermüller E, Wood TJ, Scheuchl E (2023) Erstnachweis von *Andrena schlettereri* Friese, 1896 in Österreich (Hymenoptera, Apidae). *Linzer biologische Beiträge* 54(2): 601–607.
- Ortiz-Sánchez FJ (2011) Lista actualizada de las especies de abejas de España (Hymenoptera: Apoidea: Apiformes). *Boletín de la Sociedad Entomológica Aragonesa* 49: 265–281.
- Ortiz-Sánchez FJ (2020) Checklist of Fauna Ibérica. Serie Anthophila (Insecta: Hymenoptera: Apoidea) en la península ibérica e islas Baleares (edición 2020). In: Ramos MA, Sánchez Ruiz M (Eds) *Documentos Fauna Ibérica*, 14. Museo Nacional de Ciencias Naturales, CSIC, Madrid.

- Osytsnjuk AZ (1978) Identification of insects of the European part of the USSR. Volume III. Hymenoptera first part. Apoidea Andrenidae (ed. K.B. Gorodkov). Akademia Nauk SSSR, Leningrad 119: 315–369. [In Russian]
- Osytsnjuk AZ, Romasenko L, Banaszak J, Cierzniaik T (2005) Andreninae of the Central and Eastern Palaearctic. Part 1. Polish Entomological Monographs II. Polish Entomological Society, Poznań, Poland, 235 pp.
- Osytsnjuk AZ, Romasenko L, Banaszak J, Motyka E (2008) Andreninae of the Central and Eastern Palaearctic. Part 2. Polish Entomological Monographs V. Polish Entomological Society, Poznań, 233 pp.
- Paganetti-Hummler G (1912) Beitrag zur Apidenfauna zu Corfu. Zeitschrift für wissenschaftliche Insektenbiologie 8: 380–381.
- Paulus HF (1997) Signale in der Bestäuberanlockung: Weibchenimitation als Bestäubungsprinzip bei der mediterranen Orchideengattung *Ophrys*. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 134: 133–176.
- Paulus HF, Gack C (1990) Untersuchungen zur Pseudokopulation und Bestäuberspezifität in der Gattung *Ophrys* im östlichen Mittelmeergebiet (Orchidaceae, Hymenoptera, Apoidea). Jahresberichte des Naturwissenschaftlichen Vereins Wuppertal 43: 80–118.
- Pavlou C, Bolanakis G, Kardaki L, Trichas A (2025) Forty years of ground-beetle sampling in Crete. A major contribution to the Carabidae (Coleoptera, Adephaga) fauna of Crete (Greece). Contributions to Entomology 75(2): 269–288. <https://doi.org/10.3897/contrib.entomol.75.e158430>
- Petanidou T (1991) Pollinating fauna of a phrygic ecosystem: species list. Verslagen en Technische Gegevens 59: 1–11.
- Petanidou T, Ellis WN (1993) Pollinating fauna of a Phrygic Ecosystem: Composition and diversity. Biodiversity Letters 1(1): 9–22. <https://doi.org/10.2307/2999643>
- Pisanty G, Scheuchl E, Dorchin N (2016) Eight new species of *Andrena* Fabricius (Hymenoptera: Apoidea: Andrenidae) from Israel—a Mediterranean hotspot for wild bees. Zootaxa 4189(3): 485–515. <https://doi.org/10.11646/zootaxa.4189.3.3>
- Pisanty G, Scheuchl E, Dorchin N (2018) Taxonomic review of the subgenus *Andrena* (*Poecilandrena*) (Hymenoptera: Andrenidae) in Israel and the Levant. Zootaxa 4374(2): 151–188. <https://doi.org/10.11646/zootaxa.4374.2.1>
- Pisanty G, Richter R, Martin T, Dettman J, Cardinal S (2022a) Molecular phylogeny, historical biogeography and revised classification of andrenine bees (Hymenoptera: Andrenidae). Molecular Phylogenetics and Evolution 170: 107151. <https://doi.org/10.1016/j.ympev.2021.107151>
- Pisanty G, Scheuchl E, Martin T, Cardinal S, Wood TJ (2022b) Twenty-five new species of mining bees (Hymenoptera: Andrenidae: *Andrena*) from Israel and the Levant. Zootaxa 5185: 1–109. <https://doi.org/10.11646/zootaxa.5185.1.1>
- Pisanty G, Santerre R, Martin T, Cardinal S, Wood TJ (2025) Integrated taxonomic revision of the mining bee subgenus *Andrena* (*Micrandrena*) (Hymenoptera: Andrenidae) in the Levant and Cyprus. Arthropod Systematics & Phylogeny 83: 573–655. <https://doi.org/10.3897/asp.83.e166986>

- Pisanty G, Wood TJ (2024) The early-diverging subgenera of the bee genus *Andrena* (Hymenoptera: Andrenidae) in the Old World. *Zootaxa* 5474(5): 451–488. <https://doi.org/10.11646/zootaxa.5474.5.1>
- Pittioni B, Stöckhert E (1950) Über einige neue und verkannte *Andrena*-Arten (Hymenoptera, Andrenidae). Beiträge zur Kenntnis paläarktischer Apiden III. *Annalen des Naturhistorischen Museums in Wien* 57: 284–295.
- Postolache D, Popescu F, Paule L, Ballian D, Zhelev P, Fărcaș S, Paule J, Badea O (2017) Unique postglacial evolution of the hornbeam (*Carpinus betulus* L.) in the Carpathians and the Balkan Peninsula revealed by chloroplast DNA. *Science of the Total Environment* 599–600: 1493–1502. <https://doi.org/10.1016/j.scitotenv.2017.05.062>
- Poulakakis N, Kapli P, Lymberakis P, Trichas A, Vardinoyiannis K, Sfenthourakis S, Mylonas M (2015) A review of phylogeographic analyses of animal taxa from the Aegean and surrounding regions. *Journal of Zoological Systematics and Evolutionary Research* 53(1): 18–32. <https://doi.org/10.1111/jzs.12071>
- Praz C, Müller A, Genoud D (2019) Hidden diversity in European bees: *Andrena amieti* sp. n., a new Alpine bee species related to *Andrena bicolor* (Fabricius, 1775) (Hymenoptera, Apoidea, Andrenidae). *Alpine Entomology* 3: 11–38. <https://doi.org/10.3897/alpento.3.29675>
- Praz C, Genoud D, Vaucher K, Bénon D, Monks J, Wood TJ (2022) Unexpected levels of cryptic diversity in European bees of the genus *Andrena* subgenus *Taeniandrena* (Hymenoptera, Andrenidae): implications for conservation. *Journal of Hymenoptera Research* 91: 375–428. <https://doi.org/10.3897/jhr.91.82761>
- de Queiroz K (2007) Species concepts and species delimitation. *Systematic Biology* 56: 879–886. <https://doi.org/10.1080/10635150701701083>
- R Core Team (2024) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Rambaut A (2018) Figtree ver 1.4.4. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh. <http://tree.bio.ed.ac.uk/software/figtree>
- Rasmont P, Roberts SPM, Michez D, Schweiger O, Franzen M, De Meulemeester T, Tomozei B, Radchenko V (2013) Atlas of the European Bees: genus *Andrena*. 1<sup>st</sup> Edition. STEP Project, Atlas Hymenoptera, Mons, Gembloux. <http://www.zoologie.umh.ac.be/hymenoptera/page.aspx?ID=243>
- Rasmont P, Devalez J, Pauly A, Michez D, Radchenko VG (2017) Addition to the checklist of IUCN European wild bees (Hymenoptera: Apoidea), *Annales de la Société entomologique de France* (N.S.) 53(1): 17–32. <http://dx.doi.org/10.1080/00379271.2017.1307696>
- Rasmont P, Ghisbain G, Terzo M (2021) Bumblebees of Europe and neighbouring regions. NAP Editions, Verrières-le-Buisson, France, 631 pp.
- Rasmussen C, Ascher JS (2008) Heinrich Friese (1860–1948): Names proposed and notes on a pioneer melittologist (Hymenoptera, Anthophila). *Zootaxa* 1833: 1–118. <https://doi.org/10.11646/zootaxa.1833.1.1>
- Reverté S, Miličić M, Ačanski J, Andrić A, Aracil A, Aubert M, Balzan MV, Bartomeus I, Bogusch P, Bosch J, Budrys E, Cantú-Salazar L, Castro S, Cornalba M, Demeter I, Devalez J, Dorchin A, Dufrêne E, Đorđević A, Físlar L, Fitzpatrick Ú, Flaminio S, Földesi R, Gaspar H, Genoud D, Geslin B, Ghisbain G, Gilbert F, Gogala A, Grković A, Heimburg

- H, Herrera-Mesías F, Jacobs M, Janković Milosavljević M, Janssen K, Jensen J-K, Ješovnik A, Józán Z, Karlis G, Kaspárek M, Kovács-Hostyánszki A, Kuhlmann M, Le Divelec R, Leclercq N, Likov L, Litman J, Ljubomirov T, Madsen HB, Marshall L, Mazánek L, Milić D, Mignot M, Mudri-Stojnić S, Müller A, Nedeljković Z, Nikolić P, Ødegaard F, Patiny S, Paukkunen J, Pennards G, Pérez-Bañón C, Perrard A, Petanidou T, Pettersson LB, Popov G, Popov S, Praz C, Prokhorov A, Quaranta M, Radchenko VG, Radenković S, Rasmont P, Rasmussen C, Reemer M, Ricarte A, Risch S, Roberts SPM, Rojo S, Ropars L, Rosa P, Ruiz C, Sentil A, Shparyk V, Smit J, Sommaggio D, Soon V, Ssymank A, Ståhls G, Stavrinides M, Straka J, Tarlap P, Terzo M, Tomozii B, Tor T, van der Ent L-J, van Steenis J, van Steenis W, Varnava AI, Vereecken NJ, Veselić S, Vesnić A, Weigand A, Wisniewski B, Wood TJ, Zimmermann D, Michez D, Vujić A (2023) National records of 3000 European bee and hoverfly species: A contribution to pollinator conservation *Insect Conservation and Diversity* 16(6): 758–775. <https://doi.org/10.1111/icad.12680>
- Salata S, Borowiec L, Trichas A (2020) Review of ants (Hymenoptera: Formicidae) of Crete, with keys to species determination and zoogeographical remarks. *Monographs of the Upper Silesian Museum* 12: 5–296. <https://doi.org/10.5281/zenodo.3738000>
- Schenck A (1861) Die nassauischen Bienen. Revision und Ergänzung der früheren Bearbeitungen. *Jahrbuch des Vereins für Naturkunde Nassau* 14(1859): 1–414.
- Schenck A (1874) Aus der Bienenfauna Nassaus. *Berliner entomologische Zeitung* 18: 161–173: 337–347. <https://doi.org/10.1002/mmnd.18740180317>
- Scheuchl E (2010) Beitrag zur Kenntnis westpaläarktischer Bienen der Gattung *Andrena* (Hymenoptera: Apidae: Andreninae). *Linzer biologische Beiträge* 42(2): 1445–1455.
- Scheuchl E (2011) *Andrena ebmerella*, eine neue Sandbienen-Art von Samos (Hymenoptera: Apidae: Andreninae). *Linzer biologische Beiträge* 43(2): 1587–1593. <https://doi.org/10.5281/zenodo.5327088>
- Scheuchl E, Gusenleitner F (2009) *Andrena (Margandrena) elsei* nov. sp., eine neue türkische Sandbienenart (Hymenoptera, Apidae, Andreninae). *Linzer biologische Beiträge* 41(1): 947–962.
- Scheuchl E, Hazir C (2012) Description of three new *Andrena* species (Hymenoptera: Apoidea: Andrenidae) from Turkey. *Florida Entomologist* 95(4): 831–838. <https://doi.org/10.1653/024.095.0403>
- Scheuchl E, Willner W (2016) *Taschenlexikon der Wildbienen Mitteleuropas*. Quelle & Meyer Verlag GmbH & Co., Wiebelsheim, 917 pp.
- Schlick-Steiner BC, Steiner FM, Seifert B, Stauffer C, Christian E, Crozier RH (2010) Integrative taxonomy: a multisource approach to exploring biodiversity. *Annual Review of Entomology* 55: 421–438. <https://doi.org/10.1146/annurev-ento-112408-085432>
- Schmid-Egger C (2005) *Proxiandrena* subgen. nov. und Revision der west- und zentralpaläarktischen Arten der *Andrena proxima*-Gruppe (Hymenoptera, Apidae). *Revue Suisse de Zoologie* 112: 1029–1044. <https://doi.org/10.5962/bhl.part.80335>
- Schmid-Egger C, Scheuchl E (1997) *Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs und Berücksichtigung der Arten der Schweiz*. Band III Andrenidae. Velden, Eigenverlag, 180 pp.
- Schmidt S, Schmid-Egger C, Morinière J, Haszprunar G, Hebert PN (2015) DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees

- (Hymenoptera, Apoidea partim). *Molecular Ecology Resources* 15: 985–1000. <https://doi.org/10.1111/1755-0998.12363>
- Schmiedeknecht O (1882–1884) *Apidae Europaeae* (Die Bienen Europas) per genera, species et varietates dispositae atque descriptae. Tomus I. *Nomada*, *Bombus*, *Psithyrus* et *Andrena*. Gumperda & Berlin, 866 pp. [pages 1–413 published 1882; 414–678 published 1883; 679–866 published 1884] <https://doi.org/10.5962/bhl.title.14097>
- Schönitzer K, Grünwaldt W, Gusenleitner F, Osytsnjuk AZ, Schuberth J (1995) Klärung von *Andrena forsterella*, mit Hinweisen zu den anderen Arten der *Andrena labialis*-Gruppe (Hymenoptera: Apoidea: Andrenidae). *Linzer biologische Beiträge* 27: 823–850.
- Schuberth J (1995) Eine als neu erkannte Sandbienenart aus Südosteuropa: *Andrena wilhelmi* n. sp. (Hymenoptera, Apoidea, Andrenidae). *Linzer biologische Beiträge* 27(2): 807–821.
- Schuberth J, Grünwaldt W, Schönitzer K (2001) Klärung und Neubeschreibung der Sandbiene *Andrena asiatica* Friese, 1921. *Beiträge zur Entomologie* 51: 65–71. <https://doi.org/10.21248/contrib.entomol.51.1.65-71>
- Schulz WA (1906) Strandgut. In: *Spolia Hymenopterologica*. Paderborn (A. Pape), 76–269. <https://doi.org/10.5962/bhl.title.59757>
- Schwenninger HR (2013) Festlegung von Typen für *Andrena nitidiuscula* Schenck 1853 und *Andrena fulvicornis* Schenck 1861 sowie Erstnachweis von *Andrena curvana* Warncke 1965 für Deutschland (Hymenoptera, Andrenidae, *Andrena*, Subgenus *Notandrena*). *Linzer biologische Beiträge* 45: 1945–1962.
- Schwenninger HR (2015) Revision of the Western Palaearctic species of the *Andrena taraxaci*-group with description of four new species (Hymenoptera: Andrenidae). *Stuttgarter Beiträge zur Naturkunde A, Neue Serie* 8: 251–270.
- Sedivy C, Dorn S, Widmer A, Müller A (2013) Host range evolution in a selected group of osmine bees (Hymenoptera: Megachilidae): the Boraginaceae-Fabaceae paradox. *Biological Journal of the Linnean Society* 108: 35–54. <https://doi.org/10.1111/j.1095-8312.2012.02013.x>
- Shimizu A, Dohzono I, Nakaji M, Roff DA, Miller DG, Osato S, Yajima T, Niitsu S, Utsugi N, Sugawara T, Yoshimura J (2014) Fine-tuned Bee-Flower Coevolutionary State Hidden within Multiple Pollination Interactions. *Scientific Reports* 4: 3988. <https://doi.org/10.1038/srep03988>
- Smith F (1853) *Catalogue of Hymenopterous insects in the collection of the British Museum. Andrenidae and Apidae*. London, 197 pp. <https://doi.org/10.5962/bhl.title.8766>
- Smit J (2018) Identification key to the European species of the bee genus *Nomada* Scopoli, 1770 (Hymenoptera: Apidae), including 23 new species. *Entomofauna, Monograph* 3: 1–253.
- Standfuss K, Standfuss L (2010) *Andrena pellucens* Pérez, 1895 und *Nomada argentata* Herrich-Schäffer, 1839 in Griechenland (Hymenoptera, Andrenidae et Apidae). *Bembix* 30: 35–40.
- Standfuss K, Scheuchl E, Standfuss L (2011) Zur aktuellen Bienenfauna der Ölbaumzone in Südost-Thessalien / Griechenland (Hymenoptera: Apoidea: Apiformes). 4. Andrenidae. *Entomofauna* 32(19): 285–300.
- Strand E (1915) *Apidae von Creta*. *Archiv für Naturgeschichte* 81A: 145–168.
- Strand E (1921) Apidologisches, insbesondere über paläarktische *Andrena*-Arten, auf Grund von Material des Deutschen Entomologischen Museums. *Archiv für Naturgeschichte* 87A: 266–304.

- Tadauchi O, Hirashima Y (1988) Synopsis of *Andrena* (*Stenomelissa*) with a new species from Japan (Hymenoptera, Andrenidae). Journal of the Faculty of Agriculture, Kyushu University 33: 67–76. <https://doi.org/10.5109/23918>
- Ursenbacher S, Schweiger S, Tomović L, Crnobrnja-Isailović J, Fumagalli L, Mayer W (2008) Molecular phylogeography of the nose-horned viper (*Vipera ammodytes*, Linnaeus (1758)): Evidence for high genetic diversity and multiple refugia in the Balkan peninsula. Molecular Phylogenetics and Evolution 46(3): 1116–1128. <https://doi.org/10.1016/j.ympev.2007.11.002>
- Warncke K (1965a) Beitrag zur Kenntnis der Bienengattung *Andrena* Fabricius in Griechenland. Beiträge zur Entomologie 15(1–2): 27–76.
- Warncke K (1965b) Beitrag zur Kenntnis der Bienengattung *Andrena* F. in der Türkei (Hymenoptera, Apoidea). Mitteilungen der Münchner Entomologischen Gesellschaft 55: 244–273.
- Warncke K (1966) Ergebnisse der Albanien-Expedition 1961 des Deutschen Entomologischen Institutes. 50. Beitrag. Hymenoptera: Apidae II (Genus *Andrena* Fabricius). Beiträge zur Entomologie 16(3–4): 389–405. <https://doi.org/10.21248/contrib.entomol.16.3-4.389-405>
- Warncke K (1967a) Faunistische Bemerkungen über westpaläarktische Bienen der Gattung *Andrena* F. (Hymenoptera Apoidea). Bulletin des Recherches Agronomiques de Gembloux N.S. 2: 569–581.
- Warncke K (1967b) Beitrag zur Klärung paläarktischer *Andrena*-Arten. Eos 43: 171–318.
- Warncke K (1968) Die Untergattungen der westpaläarktischen Bienengattung *Andrena* F. Memórias e Estudos Muséu Zoológico da Universidade de Coimbra 307: 1–110.
- Warncke K (1969a) A contribution to the knowledge of the genus *Andrena* (Apoidea) in Israel. Israel Journal of Entomology 4: 377–408.
- Warncke K (1969b) Bienen der Gattung *Andrena* F. aus der Türkei und dem Balkan (Hymenoptera, Apoidea, Andrenidae). Bulletin des Recherches Agronomiques de Gembloux N.S. 4: 302–305.
- Warncke K (1973) Beitrag zur Bienenfauna Mazedoniens (Colletidae, Andrenidae und Melittidae/Apoidea). Mitteilungen aus dem zoologischen Museum in Berlin 49: 13–36.
- Warncke K (1974a) Die Sandbienen der Türkei (Hymenoptera, Apoidea, *Andrena*), Teil A. Mitteilungen der Münchner Entomologischen Gesellschaft 64: 81–116.
- Warncke K (1974b) Beitrag zur Kenntnis und Verbreitung der Sandbienen in Nordafrika (Hymenoptera, Apoidea, *Andrena*). Mitteilungen aus dem zoologischen Museum in Berlin 50: 3–54.
- Warncke K (1975) Die Sandbienen der Türkei (Hymenoptera, Apoidea, *Andrena*), Teil B. Mitteilungen der Münchner Entomologischen Gesellschaft 65: 29–102.
- Warncke K (1988) Isolierte Bienenorkommen auf dem Olymp in Griechenland (Hymenoptera, Apidae). Linzer biologische Beiträge 20: 83–117.
- Westrich P (1989) Die wildbienen Baden-Württembergs. Eugen Ulmer, Stuttgart, Germany, 972 pp.
- Westrich P (2010) Untersuchungen zum Blütenbesuch von Bienen (Hymenoptera, Apidae) an *Ornithogalum* s. l. (Milchstern, Hyacinthaceae). Eucera 1: 1–17.
- Westrich P (2016) Zum Pollensammelverhalten der auf Kreuzblütler spezialisierten Bienenarten *Andrena ranunculorum* und *Andrena probata* (Hymenoptera, Apidae). Eucera 10: 3–14.

- Williams PH, Altanchimeg D, Byvaltsev A, de Jonghe R, Jaffar S, Japoshvili G, Kahono S, Liang H, Mei M, Monfared A, Nidup T, Raina R, Ren Z, Thanosong C, Zhao Y, Orr M (2020) Widespread polytypic species or complexes of local species? Revising bumblebees of the subgenus *Melanobombus* world-wide (Hymenoptera, Apidae, Bombus). *European Journal of Taxonomy* 719: 1–120. <https://doi.org/10.5852/ejt.2020.719.1107>
- Williams PH, Sagot P, Martínez-López O, Ayala-Barajas R, Mérida-Rivas JA, Vandame R (2024) A new wave of Mesoamerican bumblebees? Revising the *weisi*-complex to reject numts and pseudospecies (Apidae: *Bombus*). *Zootaxa* 5514(3): 301–318. <https://doi.org/10.11646/zootaxa.5514.4.1>
- Wilson D (2011) List of British Consular Officials in the Ottoman Empire and its former territories, from the sixteenth century to about 1860. Online publication, 67 pp. [https://www.levantineheritage.com/pdf/List\\_of\\_British\\_Consular\\_Officials\\_Turkey\(1581-1860\)-D\\_Wilson.pdf](https://www.levantineheritage.com/pdf/List_of_British_Consular_Officials_Turkey(1581-1860)-D_Wilson.pdf) [accessed 24 Jul. 2025]
- Wood TJ (2021) Revision of the *Andrena* (Hymenoptera: Andrenidae) fauna of Bulgaria and North Macedonia with description of three new species. *Belgian Journal of Entomology* 117: 1–39.
- Wood TJ (2022) Two new overlooked bee species from Spain (Hymenoptera: Anthophila: Andrenidae, Apidae). *Osmia* 10: 1–12. <https://doi.org/10.47446/OSMIA10.1>
- Wood TJ (2023a) New Old World *Andrena* species, with a focus on Turkey (Hymenoptera: Andrenidae). *Zootaxa* 5266: 1–72. <https://doi.org/10.11646/zootaxa.5266.1.1>
- Wood TJ (2023b) The genus *Andrena* Fabricius, 1775 in the Iberian Peninsula (Hymenoptera, Andrenidae). *Journal of Hymenoptera Research* 96: 241–484. <https://doi.org/10.3897/jhr.96.101873>
- Wood TJ (2023c) Revisions to the *Andrena* fauna of north-western Africa with a focus on Morocco (Hymenoptera: Andrenidae). *European Journal of Taxonomy* 916: 1–85. <https://doi.org/10.5852/ejt.2023.916.2381>
- Wood TJ (2023d) The genus *Andrena* in Belgium: revisions, clarifications, and a key for their identification (Hymenoptera: Andrenidae). *Belgian Journal of Entomology* 135: 1–63. <https://doi.org/10.5281/zenodo.12638936>
- Wood TJ (2024a) Further revisions to the Palaearctic *Andrena* fauna (Hymenoptera: Andrenidae). *Zootaxa* 5483: 1–150. <https://doi.org/10.11646/zootaxa.5483.1.1>
- Wood TJ (2024b) New Asian *Andrena* species, with notes on the subgenus *Cnemidandrena* (Hymenoptera: Andrenidae). *Zootaxa* 5404(1): 167–188. <https://doi.org/10.11646/zootaxa.5404.1.11>
- Wood TJ (2025a) Additions, corrections, and other changes to the hyper-diverse bee genus *Andrena* Fabricius, 1775 (Hymenoptera: Andrenidae). *Animal Taxonomy and Ecology* 71(2): 143–316. <https://doi.org/10.1556/1777.2025.00082>
- Wood TJ (2025b) On the status of *Nomiapis valga* (Gerstäcker) and its distribution (Hymenoptera, Halictidae, Nomiinae), with an identification key for European *Nomiapis*. *Deutsche Entomologische Zeitschrift* 72(1): 85–100. <https://doi.org/10.3897/dez.72.153052>
- Wood TJ, Roberts SPM (2017) An assessment of historical and contemporary diet breadth in polylectic *Andrena* bee species. *Biological Conservation* 215: 72–80. <https://doi.org/10.1016/j.biocon.2017.09.009>

- Wood TJ, Roberts SPM (2018) Constrained patterns of pollen use in Nearctic *Andrena* (Hymenoptera: Andrenidae) compared with their Palaearctic counterparts. *Biological Journal of the Linnean Society* 124: 732–746. <https://doi.org/10.1093/biolinnean/bly080>
- Wood TJ, Monfared A (2022) A revision of the *Andrena* (Hymenoptera: Andrenidae) fauna of Iran, with the description of 16 new species. *European Journal of Taxonomy* 843: 1–136. <https://doi.org/10.5852/ejt.2022.843.1947>
- Wood TJ, Bossert S (2025) Primary bee types in the Genoa museum; a partial treatise with taxonomic and nomenclatural implications (Hymenoptera: Anthophila). *Annali del Museo Civico di Storia Naturale “Giacomo Doria”* 118: 267–379.
- Wood TJ, Boustani M, Rasmont P (2020) A revision of the *Andrena* (Hymenoptera: Andrenidae) of Lebanon with the description of six new species. *Annales de la Société entomologique de France (N.S.)* 56: 279–312. <https://doi.org/10.1080/00379271.2020.1794960>
- Wood TJ, Ghisbain G, Michez D, Praz CJ (2021) Revisions to the faunas of *Andrena* of the Iberian Peninsula and Morocco with the descriptions of four new species (Hymenoptera: Andrenidae). *European Journal of Taxonomy* 758: 147–193. <https://doi.org/10.5852/ejt.2021.758.1431>
- Wood TJ, Hogan J, Edwards M, Paxton RJ, Praz C, Seidel M, Schmid-Egger C (2022) *Andrena scotica* Perkins is the valid name for the widespread European taxon previously referred to as *Andrena carantonica* Pérez (Hymenoptera: Andrenidae). *British Journal of Entomology and Natural History* 35: 393–408.
- Wood TJ, Praz C, Selis M, Flaminio M, Mei M, Cornalba M, Rosa P, Le Divelec R, Michez D (2023) Revisions to the *Andrena* fauna of Italy, with the description of a new species (Hymenoptera: Andrenidae). *Fragmenta entomologica* 55(2): 271–310. <https://doi.org/10.13133/2284-4880/1542>
- Wood TJ, Gaspar H, Le Divelec R, Penado A, Silva TL, Mata VA, Veríssimo J, Michez D, Castro S, Loureiro J, Beja P, Ferreira S (2024a) The InBIO Barcoding Initiative Database: DNA barcodes of Iberian Bees. *Biodiversity Data Journal* 12: e117172. <https://doi.org/10.3897/bdj.12.e117172>
- Wood TJ, Ismael HR, Baiocchi D, Hamad MI, Bapir TT, Selis M (2024b) A first revision of the *Andrena* of Iraq (Hymenoptera, Andrenidae), with the description of two new species from Iraqi Kurdistan and additional records from surrounding countries. *Zookeys* 1205: 267–298. <https://doi.org/10.3897/zookeys.1205.120033>
- Wüster W (2025) Shedding the mitochondrial blinkers: A long-overdue challenge for species delimitation in herpetology. *Vertebrate Zoology* 75: 259–275. <https://doi.org/10.3897/vz.75.e161536s>
- Xu H-l, Tadauchi O (1997) Subgeneric positions and redescription of East Asian *Andrena* preserved in Two U. S. Natural History Museums (Hymenoptera, Andrenidae). *Esakia* 37: 177–185. <https://doi.org/10.5109/2619>
- Xu H-l, Tadauchi O (2008) The subgenera *Margandrena*, *Leimelissa*, *Stenomelissa* and *Zonandrena* of the genus *Andrena* of Eastern Asia (Hymenoptera, Andrenidae). *Journal of the Faculty of Agriculture, Kyushu University* 53(1): 63–66. <https://doi.org/10.5109/10072>
- Xu H-l, Tadauchi O (2009) A revision of the subgenus *Leucandrena* of the genus *Andrena* of eastern Asia (Hymenoptera: Apoidea: Andrenidae). *Zootaxa* 2145: 36–46. <https://doi.org/10.11646/zootaxa.2145.1.2>

## Supplementary material 1

### Checklist of the *Andrena* of the southern Balkans

Authors: Thomas J. Wood

Data type: xlsx

Explanation note: Southern Balkans *Andrena* species checklist, with national totals for Greece, Bulgaria, North Macedonia, and Albania, details on *loci typici* for species described from the southern Balkans, and dietary niche classifications.

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.99.179503.suppl1>

## Supplementary material 2

### Additional examined *Andrena* specimens

Authors: Thomas J. Wood

Data type: xlsx

Explanation note: Detailed specimen records for *Andrena* specimens examined during the course of this project which are not fully presented in the text, or which were used to create the presented distribution maps.

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.99.179503.suppl2>