JHR 91: 375–428 (2022)
doi: 10.3897/jhr.91.82761
https://jhr.pensoft.net

RESEARCH ARTICLE

JOURNAL OF Hymenoptera RESEARCH
A peer-reviewed open-access journal
The International Society of Hymenopterists

Unexpected levels of cryptic diversity in European bees of the genus *Andrena* subgenus *Taeniandrena* (Hymenoptera, Andrenidae): implications for conservation

Christophe Praz[1,2], David Genoud[3], Killian Vaucher[1,2], Dimitri Bénon[1,2], Joseph Monks[4], Thomas J. Wood[5]

1 *University of Neuchâtel, Institute of Biology, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland* **2** *InfoFauna – Swiss Zoological Records Center, Avenue de Bellevaux 51, 2000 Neuchâtel, Switzerland* **3** *Avenue des Roses 2, 87240 Ambazac, France* **4** *Natural History Museum, Cromwell Road, London, UK* **5** *Laboratory of Zoology, University of Mons, Avenue du Champs de Mars 6, 7000 Mons, Belgium*

Corresponding author: Christophe Praz (christophe.praz@unine.ch)

Academic editor: Jack Neff | Received 25 February 2022 | Accepted 18 April 2022 | Published 30 June 2022

http://zoobank.org/3A5B9599-8502-4CB7-A83E-CAA998B678A9

Citation: 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

Abstract

Using a combination of DNA barcodes and morphology, we examine species boundaries in bees of the genus *Andrena* subgenus *Taeniandrena* in Europe. First, we solve the long controversy surrounding the status of *Andrena ovatula* (Kirby, 1802) and *A. albofasciata* Thomson, 1870, proposed to represent distinct species nearly 100 years ago, but mostly treated as conspecific in recent studies. Our results unambiguously support the presence of two taxa that are often found in sympatry: the first taxon, referred to as *A. ovatula*, is present in Northern Europe but also in Southern Europe along the Mediterranean coast; the second taxon is referred to as *A. afzeliella* (Kirby, 1802), **stat. rev.**, with *A. albofasciata* considered to be a junior synonym (**syn. nov.**), and is widely distributed in Europe. Second, we show that another widely distributed species has hitherto been overlooked in Europe: *A. ovata* Schenck, 1853, **stat. rev.** Third, we demonstrate that two taxa currently treated as subspecies should be given specific rank due to significant morphological and genetic differences: *A. croceiventris* Morawitz, 1871, **stat. rev.**, so far treated as a subspecies of *A. similis* Smith, 1849, and *A. vocifera* Warncke, 1975, **stat. nov.**, so far treated as a subspecies of *A. gelriae* van der Vecht, 1927. Both *A. croceiventris* and *A. vocifera* have particularly restricted ranges in Europe, being known only from central to southern Italy and Sicily, and continental France, respectively. Fourth, we describe a new species from Sardinia and Corsica, *A. antonellae* **sp. nov.** Lastly, the following new synonymies are proposed: *A. similis*, *A. ocreata cyprisina* Warncke, 1975 and *A. similis caraimica*

Osytshnjuk, 1994 are placed in synonymy with *A. russula* Lepeletier, 1841 (**syn. nov.**); *A. fuscata* (Kirby, 1802), *A. canescens* Schenck, 1853 and *A. pseudovatula* Alfken, 1926 are placed in synonymy with *A. afzeliella* (**syn. nov.**). Lectotypes are designated for *A. afzeliella*, *A. fuscata* (Kirby, 1802), *A. ovata* and *A. wilkella* (Kirby, 1802). Our results suggest a particularly fast diversification in this group of bees, leading to the presence of numerous species exhibiting particularly restricted geographic ranges. We discuss the implications for conservation of this astonishing cryptic diversity in European bees.

Keywords
Cryptic species, DNA barcoding, speciation, species delimitation

Introduction

Obtaining accurate taxonomic and distribution information on bees is crucial for the conservation and monitoring of native pollinators. However, new species are regularly uncovered even in regions with a long tradition in taxonomy such as northern and central Europe, following changes in taxonomy (e. g., Straka and Bogusch 2011; Pauly et al. 2019; Le Divelec 2020; Litman et al. 2021), the discovery of hitherto undetected taxa due to challenging identifications (e. g., Notton and Norman 2017; Falk et al. 2019), inventories in poorly sampled habitats (Johansson and Paukkunen 2017; Schmid-Egger et al. 2021), range expansions (Notton et al. 2016; Saure and Petrischak 2020), or the description of new species (e. g., Pauly et al. 2015; Praz et al. 2019). These recent updates in northern or central European countries, characterised by well-known faunas that are studied by numerous active bee specialists, give a worrisome hint at the huge taxonomic work necessary in southern European countries, which have rich but poorly investigated bee faunas. In agreement with this suspicion, is that numerous bee species have recently been described from Southern Europe (e.g., Müller 2012; Pauly et al. 2015; Wood and Cross 2017; Kasparek 2020; Wood et al. 2020, 2021; Litman et al. 2021; Wood 2021, 2022), and many more will undoubtedly be described in the near future.

The genus *Andrena* Fabricius, 1775 is exemplary in this context, as it is highly diverse and includes numerous species showing a restricted geographic range. In addition, morphological identifications are challenging, often relying entirely on subtle differences in the colour of the vestiture or in the sculpture. Accordingly, new species of *Andrena* are being uncovered at an accelerated pace (e.g., Pisanty et al. 2016; Praz et al. 2019; Sheffield 2020; Wood et al. 2020, 2021; Wood 2021, 2022). The subgenus *Taeniandrena* Hedicke, 1933 is no exception: Gusenleitner and Schwarz (2002) report ten species in Europe, a number that has grown to 14 following recent revisions (Wood et al. 2021; Wood 2022).

In the present study, we further examine species boundaries in the subgenus *Taeniandrena* using a combination of DNA barcodes and morphology. Our investigations lead to the recognition of three taxa hitherto considered to be subspecies or synonyms as valid species, to the description of a new species, and to a resolution of

a longstanding controversy in central European bee taxonomy: the status of *Andrena ovatula* (Kirby, 1802) and *A. albofasciata* Thomson, 1870, alternately considered as two valid species (e.g., Stöckhert 1930; Niemelä 1949; van der Smissen 2002, 2010; Herrmann 2007; Nilsson 2010; Le Divelec 2021) or as synonyms (e.g., Warncke 1967; Gusenleitner and Schwarz 2002; Amiet et al. 2010; Schmidt et al. 2015). We examine the status of these two taxa using DNA barcodes and morphology. Using specimens confidently identified using DNA barcodes, we present a new identification key for this challenging group of species. Our study raises the number of known species of *Taeniandrena* in Europe to 19, and three additional species are probably new and will be described elsewhere. Some of these taxa have exceptionally small geographic ranges, with one species strictly endemic to southern Italy and Sicily, one to continental France, and one to Sardinia and Corsica, in addition to previously documented species endemic to the Iberian Peninsula (Wood et al. 2021; Wood 2022). We briefly discuss the implications for conservation of such unexpected levels of cryptic diversity.

Material and methods

Lab protocols

We used mitochondrial genetic data (cytochrome oxidase I, hereafter COI; Hebert et al. 2004) for two different purposes: first, to complement morphology in species delimitation; second, to verify the identification of specimens in order to obtain accurate distribution data for the different taxa. All specimens included in genetic analyses are given in Suppl. material 1: Table S1, and all sequences and specimen information have been uploaded to the BOLD platform (www.boldsystems.org).

We aimed at obtaining at least one full-length mitochondrial barcode (658 base pairs, hereafter bp) for as many species as possible in Europe. We amplified two overlapping fragments of COI using the two primer pairs LepF/LepR (658 bp) and UAE3/LepR (409 bp) (see Hebert et al. 2004 and Praz et al. 2019 for primer sequences) in separate PCR tubes but with the same conditions [1' 94 °C // 5 × (1' 94 °C / 1' 30" 45 °C / 1' 15" 72 °C) // 35 × (1' 94 °C / 1' 30" 51 °C / 1' 15" 72 °C) // 5' 72 °C]. Whenever possible, we sequenced both fragments with the primers LepR (658 bp fragment) and UAE3 (409 bp fragment), respectively, yielding full length barcodes from two independent PCR reactions. This approach had the advantages of minimizing sequencing costs in case NUMTs or *Wolbachia* were amplified, and of allowing the processing of specimens with different DNA conditions simultaneously. *Wolbachia* or NUMT co-amplification was far more frequent with the primer pair LepF/LepR; sequencing with UAE3/LepR was overall more successful, especially for specimens older than 5–10 years.

For specimens older than 15 years, we used the specific primers COX-Taeniandr-F, COX-Taeniandr-R1 and COX-Taeniandr-R2 (see primer sequences in Wood et al. 2021) to produce a 180 bp (COX-Taeniandr-F and COX-Taeniandr-R1) or a 365-bp (COX-Taeniandr-F and COX-Taeniandr-R2) fragment nested within the UAE3/LepR

fragment of COI. Both PCR were conducted using the same PCR conditions [4' 94 °C // 35–45 × (45" 94 °C / 45" 56 °C / 45" 72 °C) // 7' 72 °C], and the longer amplicon obtained was sequenced with COX-Taeniandr-F. To minimize risk of contamination, specimens of similar age were processed together; for specimens older than 30 years, only the short fragment (180 bp) was amplified and the number of cycles was increased to 45.

Two barcodes from specimens collected in Israel were kindly provided by Gideon Pisanty. A selection of DNA barcodes available on BOLD, mostly from Schmidt et al. (2015) and Wood et al. (2021), were downloaded and included in phylogenetic analyses.

Phylogenetic analyses

Chromatograms were trimmed and assembled in Geneious 6.0.6 (Kearse et al. 2012) and exported consensus were aligned using MAFFT (Katoh and Standley 2013). The resulting matrices were examined and edited in Geneious. Not all specimens were included in phylogenetic analyses; when barcodes were merely generated for specimen identification, sequences were compared visually to reference sequences in Geneious. Genetic distances were computed using the Kimura 2-parameter (K2P) distance model in a test version of Paup 4.0 (Swofford 2002) kindly provided by D. Swofford.

For final phylogenetic analyses, we included a subset of all specimens, favouring long sequences and maximising both geographic representation and haplotype diversity within each species. Sequences originating near type localities were included whenever possible. Bayesian phylogenetic analyses were performed in BEAST ver. 1.10.4 (Suchard et al. 2018). The aligned matrix was divided into three partitions corresponding to the three codon positions. A HKY + G model was applied to each partition (more complex models resulted in poor estimation of some parameters); all parameters were unlinked across partitions; the clock model was set to "strict clock" and the tree prior was set to "speciation: Yule process". One sequence of *Andrena lathyri* Alfken, 1899 was included in the analysis, and a clade including all other terminals was constrained to be monophyletic to ensure proper rooting of the trees. The analysis was run for 10 million generations, sampling trees and parameters every 1000 generations. The software Tracer ver. 1.7.1 (Rambaut et al. 2018) was used to ensure that convergence was reached for every parameter (ESS values > 300). The first 1000 trees were discarded as burn-in and a majority-rule consensus tree was computed with the 9000 remaining trees.

Morphology

Morphological terminology follows Michener (2007). The abbreviations A, T and S are used for antennal segments, metasomal terga, and metasomal sterna respectively. For simplicity we use the term "terminal fringe" (German: Endfranse) for the prepygidial fimbria (apical fringe of hairs of T5) and pygidial fimbria (dense hairs on T6 of females, on each side of the pygidial plate).

Morphological identifications were performed alongside genetic analyses; specimens identified using DNA sequences were used as reference for morphological

examination, and initial genetic results were integrated to revise our morphological identifications. When not specified, the type material was examined by TJW. We do not provide a full list of synonyms for each species, but only list those discussed in the text or new synonyms based on our examination of the type material. The list of examined specimens (Suppl. material 2: Table S2) is not exhaustive; all Swiss records can be accessed freely on GBIF (Praz et al. 2022).

Material from the following institutions has been examined

CSEC Private collection of Christian Schmid-Egger, Berlin, Germany;
DGC Private collection of David Genoud, Ambazac, France;
KHC Private collection of Karl Hirt, Menziken, Switzerland;
MHC Private collection of Mike Herrmann, Konstanz, Germany;
MIB Collection of the ZooPlantLab of the University of Milano-Bicocca, Milano, Italy;
MNHN Muséum National d'Histoire Naturelle, Paris, France;
MSNL Museo cantonale di storia naturale, Lugano, Switzerland;
MWNH Museum Wiesbaden, Naturhistorische Sammlungen, Wiesbaden, Germany;
NHML Natural History Museum, London, UK;
NHRS Naturhistoriska riksmuseet, Stockholm, Sweden;
NMB Naturhistorisches Museum, Basel, Switzerland;
NMBE Naturhistorisches Museum der Burgergemeinde Bern, Switzerland;
OLML Oberösterreichisches Landesmuseum, Linz, Austria;
OUMNH University Museum of Natural History, Oxford, UK;
PRUN Research collection of Christophe Praz, University of Neuchatel, Switzerland;
RBINS Royal Belgian Institute of Natural Sciences, Brussels, Belgium;
RMNH Naturalis Biodiversity Center, Leiden, the Netherlands;
SIZK Scientific Collections of the Schmalhausen Institute of Zoology, Kiev, Ukraine;
SMFD Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany;
STC Private collection of Stefan Tischendorf, Darmstadt, Germany;
TJWC Private collection of Thomas J. Wood, Mons, Belgium;
ZMHB Museum für Naturkunde, Berlin, Germany;
ZML Zoological Museum, Lund, Sweden.

Results

DNA barcodes and genetic analyses

Of the 142 barcoded specimens, partial or full DNA barcodes were obtained for 121 (Suppl. material 1: Table S1). Sequencing of the short (180 bp) barcode was success-

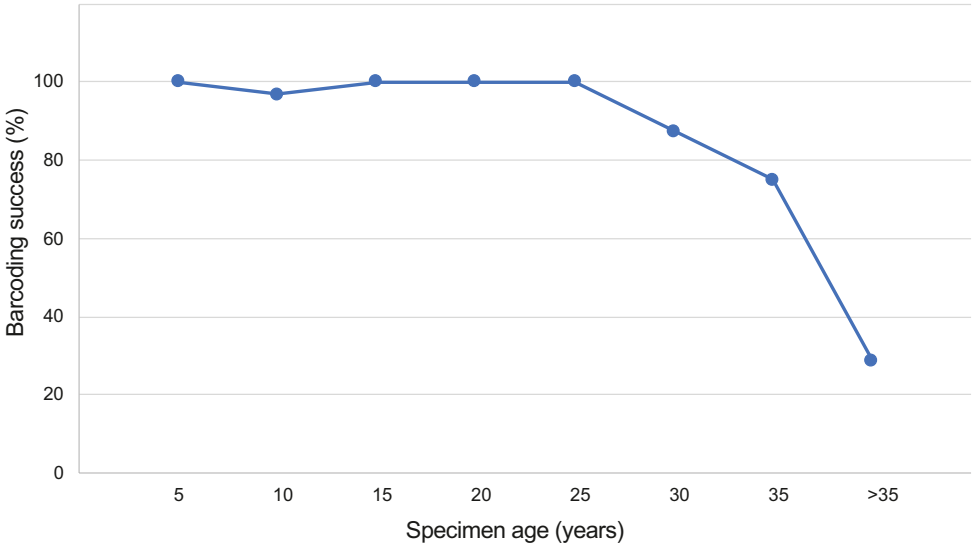


Figure 1. Relationship between barcoding success, as indicated by the proportion of specimens that yielded at least a diagnostic, 180-bp "mini-DNA barcode", and the age of the specimen.

ful in the majority of cases for all specimens < 30 years old; sequencing success then decreased to below 30% (Fig. 1), but high quality and diagnostic fragments were recovered for some specimens collected more than 70 years ago. The 180-bp fragment was diagnostic for all species investigated here.

Phylogenetic analyses (Fig. 2) highlight the following results. Two distinct species were recovered in what has so far been identified as *Andrena ovatula sensu lato*; these two species are referred to as *A. ovatula* and *A. afzeliella* (Kirby, 1802) (=*A. albofasciata*) (see below, systematic part: *A. afzeliella*). These two species formed two highly-supported clades (posterior probability, hereafter PP, of 1.0 in both cases) separated by distances comprised between 9.5 and 10.6%. All sequences of *A. ovatula* were identical (genetic distance of 0); the maximal genetic distance within *A. afzeliella* was 0.77%, between one specimen from UK (2084) and one specimen from the Netherlands (1660). Both the *ovatula* and the *afzeliella* clades included specimens collected in range sympatry in England, southern France, northern Germany and southern Italy. Specimens from northern Germany identified as "*A. albofasciata*" and *A. ovatula sensu stricto* by Jane van der Smissen were correctly placed in *A. afzeliella* and *A. ovatula*, respectively (Fig. 2, specimens with numbers 1664 and 1666). All specimens included in the DNA barcoding study of Schmidt et al. (2015) as *A. ovatula* were placed in *A. afzeliella*, suggesting that these authors did not sequence the true *A. ovatula*. Morphological examination of all sequenced specimens confirms the distinctiveness of these two species, especially based on the colour of the terminal fringe of the female (see below, taxonomic part).

Specimens of *Andrena similis* Smith, 1849 were included in a well-supported clade (PP 1.0), which comprised specimens from the Iberian Peninsula, Northern Europe, France, Italy, Cyprus, Morocco, as well as one specimen from Algeria (1533 in Fig. 2)

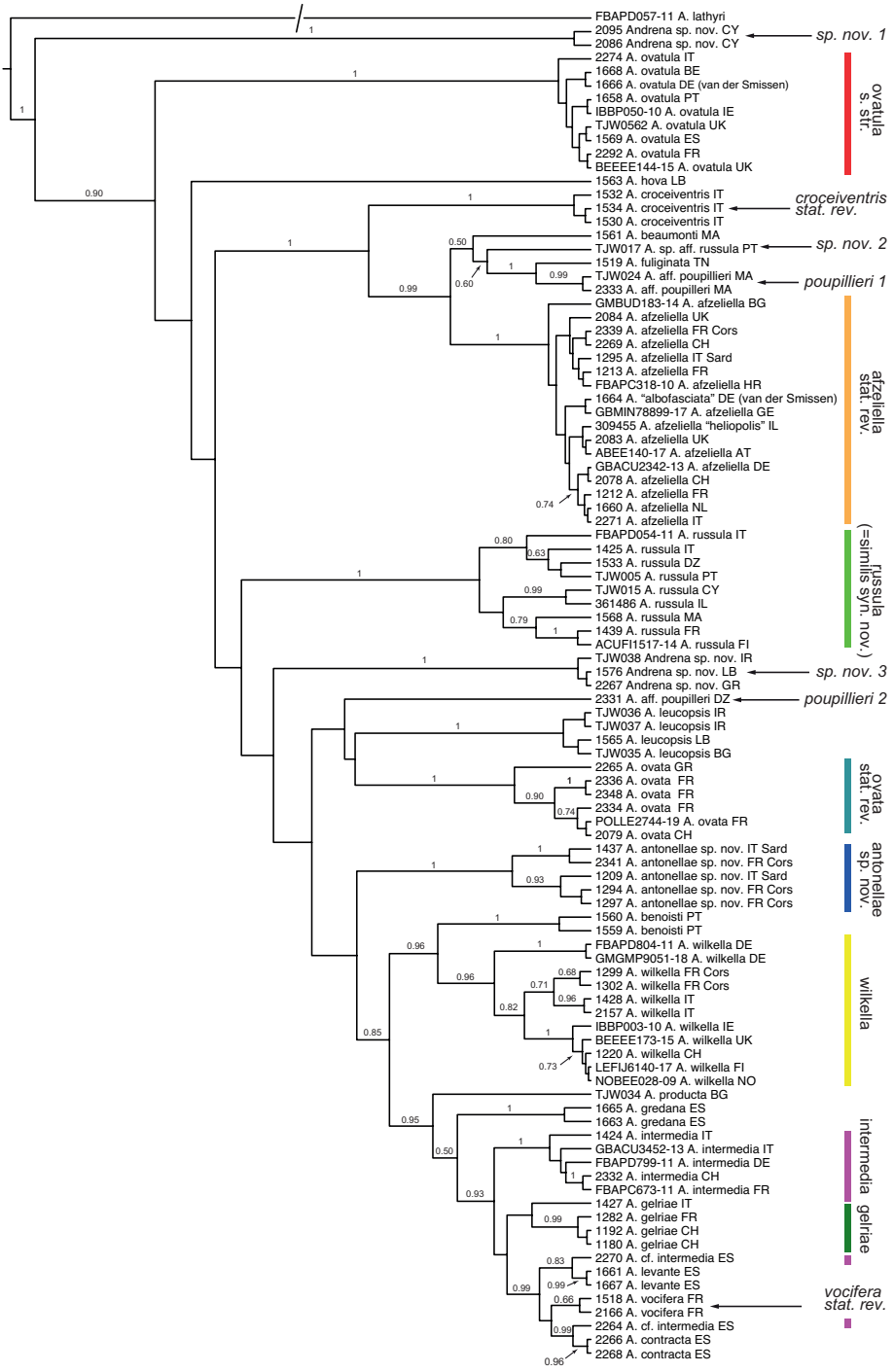


Figure 2. Maximum clade credibility tree found in Bayesian analyses of sequence data of the mitochondrial gene COI, showing the phylogenetic relationships among the different species of *Andrena* subgenus *Taeniandrena* investigated in the present study. Numbers above branches represent posterior probabilities (values < 0.5 are omitted). Taxa mentioned in the text are indicated by arrows or by vertical bars.

morphologically corresponding to the holotype of *A. russula* Lepeletier, 1841. Genetic distances within this clade were comprised between 0 and 2.26%; some structuring was observed within this clade, but without clear geographic association, and statistical support for most subclades was low. For this reason, *A. similis* is treated here as a synonym of *A. russula* (see below, taxonomic part). One specimen from Portugal (TJW0017) morphologically identified as *A. "similis"* (=*A. russula*) was genetically strongly divergent (genetic distances from *A. russula* 6.49–7.87%, average 7.36%). The identity of this specimen remains unclear, and this specimen is referred to here as "*Andrena* sp. aff. *russula*".

Andrena croceiventris Morawitz, 1871, treated so far as a subspecies of *A. russula* (Gusenleitner and Schwarz 2002), formed a separate clade from that taxon (distances to *A. russula* 6.65–8.79; average 7.81%) and is here treated as a distinct species (stat. rev.). One specimen of *A. russula* originating from Central Italy (1425 in Fig. 2, from Monte Vettore) confirms that both taxa have overlapping ranges. Likewise, specimens morphologically initially attributed to *A. russula* from Sardinia and Corsica formed a distinct clade (distances from *A. russula* 5.82–8.36%, average 7.04%). These specimens are sculpturally similar to both *A. croceiventris* and to the North African species *A. fuliginata* Pérez, 1895, from which they were separated by average distances of 4.69% and 5.73%, respectively. These specimens belong to a new species, *A. antonellae* sp. nov.

Our molecular analyses also highlight an additional hitherto overlooked species of *Taeniandrena*, *Andrena ovata* Schenck, 1853 (stat. rev.). Specimens of this taxon formed a well-supported clade including one specimen from Greece (2265), four specimens from France and one specimen from southern Switzerland. In addition, one full-length sequence from Spain, four short sequences from Italy (numbers 2371, 2376, 2375, 2377; Suppl. material 1: Table S1) and one short sequence from Germany (number 2373; Suppl. material 1: Table S1) were a 100% match with the sequence for the Swiss specimen (number 2079); these sequences are not included in Fig. 2. The maximal distance among these specimens was 1.88%. This new species appears to have some superficial similarities with the original description of the unclear north African taxon "*A. poupillieri* Dours, 1872", whose type is lost (see below, systematic part: *A. ovatula*). We included three specimens agreeing with the description of *A. poupillieri* from Morocco and Algeria; two of these three specimens formed a clade, the third was distantly related to that clade; these two units are referred to as "*A. poupillieri 1*" and "*A. poupillieri 2*", both distinct from *A. ovata*. In addition, our analyses suggest two additional undescribed species within *Taeniandrena*: *Andrena* (*Taeniandrena*) sp. nov. 1 from Cyprus, and *A. Taeniandrena* sp. nov. 3 from Greece, Iran and Lebanon. These taxa will be described in subsequent works.

One moderately well-supported clade (PP 0.95) included species associated with *Andrena gelriae* van der Vecht, 1927 and *A. intermedia* Thomson, 1870 (including *A. producta* Warncke, 1973, *A. gredana* Warncke, 1975, *A. levante* Wood & Praz, 2021 and *A. contracta* Wood, 2022). This clade is hereafter referred to as the *gelriae*-clade. Genetic distances within this clade were considerably lower than among the other species of *Taeniandrena*: on average 1.59% between *A. gelriae* and *A. intermedia* (excluding two divergent specimens of *A. intermedia* from Spain; see below), 3.54%

between *A. gelriae* and *A. gredana*, 1.98% between *A. gelriae* and *A. levante*, 2.35% between *A. gelriae* and *A. producta*. *Andrena vocifera* Warncke, 1975, so far treated as a subspecies of *A. gelriae*, was separated from the latter species by average distances of 1.21% and is treated here as a distinct species (stat. nov.). Within *A. gelriae*, one male specimen from southern Italy (1427) was sister to all other specimens of *A. gelriae*, but support for this relationship was low (PP less than 0.5); this specimen was separated from other specimens of *A. gelriae* by average distances of 1.12%. Lastly, specimens of *A. intermedia* did not form a monophyletic clade: central European specimens and one specimen from southern Italy formed a well-supported clade (PP 1.0, maximal genetic distances within this clade 1.12%); two male specimens from Spain morphologically highly similar to central European specimens of *A. intermedia* (referred to as *A. cf. intermedia* in Fig. 2) were not closely related to these central European specimens (average distances of 2.26%). They were also not closely related to one another (distance between these two specimens 0.74%): one specimen (2270) was closely related to *A. levante* (0.37%), the other to *A. contracta* (0.30%), despite the fact that the genital capsules of these three species are clearly divergent (Wood et al. 2021; Wood 2022).

All specimens initially identified as *A. gelriae* present in Swiss entomological collections were examined and most females were analysed genetically. The vast majority of occurrences (see map in Amiet et al. 2010) were based on misidentifications. Verified records of *A. gelriae* in Switzerland are restricted to: pre-1960 records from the Swiss Midland near Bern and Solothurn as well as from the Valais, and recent records in the Valais, near Geneva and near Zurich. All other records, including those from the Tessin or from the Alps, were based on erroneous identifications.

Systematic part

***Andrena afzeliella* (Kirby, 1802), stat. rev.**
Figs 3, 4, 9, 19, 29, 31, 33, 35, 45

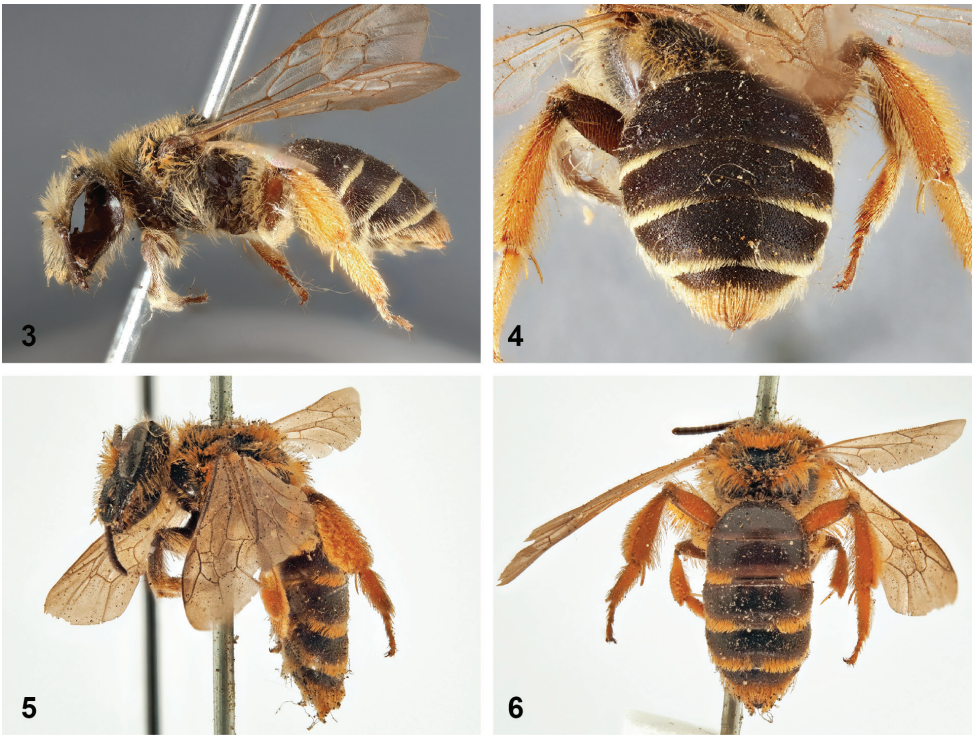
Melitta afzeliella Kirby, 1802: 169, ♀, "Barhamiae" [Barham, Suffolk, England]. Lectotype ♀ (NHML), by present designation (see below).
Melitta fuscata Kirby, 1802: 167, ♀, "Barhamiae" [Barham, Suffolk, England], Syn. nov. Lectotype ♀ (NHML), by present designation (see below).
Andrena canescens Schenck, 1853: 140, ♂, "Schierstein" [Schierstein, Wiesbaden, Germany], Syn. nov. Holotype ♂ (MWNH).
Andrena albofasciata Thomson, 1870: 154, ♀ ♂, "Sällsynt på Skånes sandmarker" [Rare on the sandy grounds of Scania; Sweden], Syn. nov. Lectotype ♀, by designation of Niemelä 1949: 117; see also Nilsson 2010: 78 (ZML).
Andrena afzeliella var. *heliopolis* Friese, 1914: 227, ♀ [Egypt]. Holotype ♀ (ZMHB)
Andrena pseudovatula Alfken, 1926: 107, ♂ [Egypt]. Syn. nov. Syntype ♂ (SMFD)

Material examined. Type material: ***Lectotype*** ♀ of *Melitta afzeliella* Kirby, 1802 (Figs 3, 4), by present designation, a female in moderately good condition (*Anthrenus*

damage visible on head and legs, antennae missing) (NHML). This female specimen is labelled as follows: 1. "6339" [handwritten on blue paper disc, NHML accession number 1863–39]; 2. "B" [handwritten]; 3. "Lectotype" [printed on white paper disc]; 4. "Lectotype ♀ *Andrena afzeliella* des. Wood and Monks, 2022" [printed]; 5. "NHMUK 012858874".

Lectotype ♀ of *Melitta fuscata* Kirby, 1802, by present designation, a female in good condition (NHML). This female specimen is labelled as follows: 1. "6339" [handwritten on blue paper disc, NHML accession number 1869-39]; 2. "Syntype" [printed on white paper disc]; 3. "B.M. Type/Hym/ 17a 2941" [handwritten]". 4. "Syntype ♀ *Melitta fuscata* Kirby det. D. Notton 1995"; 5. "Lectotype" [printed on white paper disc]; 6. Lectotype ♀ *Andrena fuscata* des. Wood and Monks, 2022" [handwritten]; 7. " NHMUK 014030702".

Holotype ♂ of *Andrena canescens* Schenck, 1853, a male in good condition (MWNH; examined by CP); see Andert (2010) for details. Since the original description does not specify the number of specimens, unlike in similar cases (e.g., *A. gibba*), and only mentions a single locality, it is assumed that the original description was based on this unique specimen, which is considered to be the holotype (by monotypy).



Figures 3–6. 3, 4 Lectotype female of *Andrena afzeliella* (Kirby, 1802) **3** profile **4** terga and terminal fringe. Copyright for these two images belongs to the trustees of the Natural History Museum, London **5, 6** lectotype female of *A. russula* Lepeletier, 1841 **5** profile **6** terga.

Holotype of *Andrena afzeliella* var. *heliopolis* Friese, 1914. Egypt: ♀, no locality information (ZMHB).

Syntype of *Andrena pseudovatula* Alfken, 1926. Egypt: ♂, no locality information, A. Andres leg. (SMFD).

Other material: Specimens from the UK, France (including Corsica), Switzerland, Italy (including Sardinia), the Netherlands, Germany, and Israel have been barcoded. Additional sequences are available on the BOLD website for specimens from Austria, Croatia and Georgia. Full details of examined material can be found in Suppl. material 2: Table S2.

Distribution. Widespread and abundant in Europe (Fig. 7) from the Iberian Peninsula, France including Corsica, UK, Germany, Switzerland, Italy including Sardinia and Sicily, Scandinavia, Eastern Europe, Turkey, Cyprus, Lebanon, Syria, Israel, Jordan, Egypt, and Iran (see notes on *Andrena afzeliella* var. *heliopolis* Friese, 1914 below, "geographic variation"). This species may reach Kazakhstan under the name *A. ovatula transcaspiensis* Osytshnjuk, 1994.

Pollen preferences. Analysis of 37 pollen loads from 19 localities suggests polylecty with a strong preference for Fabaceae, with 91.7% of pollen collected from this family. Rosaceae, Plantaginaceae, Boraginaceae, Cornaceae, Ranunculaceae, Brassicaceae, Dipsacaceae, and Asteraceae were detected in decreasing order of abundance (TJW, unpublished data). Use of Fabaceae pollen is more pronounced in the summer

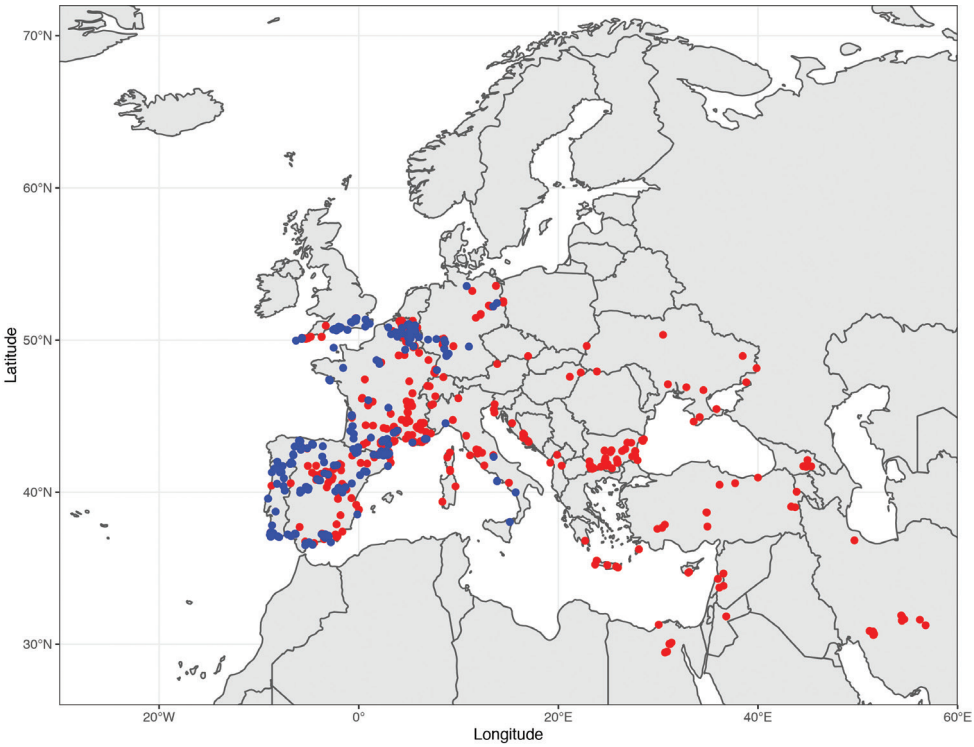


Figure 7. Distribution map of *Andrena ovatula* (blue dots) and *A. afzeliella* (red dots).

generation. Westrich (1989) listed "*A. ovatula*" as polylectic, with three botanical families utilised for pollen (Fabaceae, Asteraceae, Brassicaceae) – these observations probably relate to *A. afzeliella* which is more common in Central Europe.

Phenology. *Andrena afzeliella* is clearly bivoltine, with the peak of the first generation in May and early June, and that of the second generation in July and August (Fig. 8); where *A. afzeliella* and *A. ovatula* occur in sympatry, the first generation is found approximately one month after that of *A. ovatula* (Fig. 8), as already indicated by Stöckhert (1930; see Nilsson 2010).

Note. The status of this species, in particular its distinctiveness from *Andrena ovatula* has been a controversial topic, and consequently the identity of *A. afzeliella*, *A. albofasciata* and *A. ovatula* in the literature is confusing (Gusenleitner and Schwarz 2002: 565). Early work did not discriminate between these two taxa and the name *A. afzeliella* was used for both (e. g. Perkins 1888; Saunders 1896; Alfken 1905; Frey-Gessner 1899–1907; Schmiedeknecht 1907) until Perkins (1917, 1918) revised Kirby's type material for the British species of *Taeniandrena*, resurrected *A. ovatula* and placed *A. afzeliella* in synonymy with *A. ovatula*. The variability in the colour of the terminal fringe in the female was noted by several authors, for example by Schmiedeknecht (1907), who attributed it to inter-generational variation. Stöckhert (1930) was the

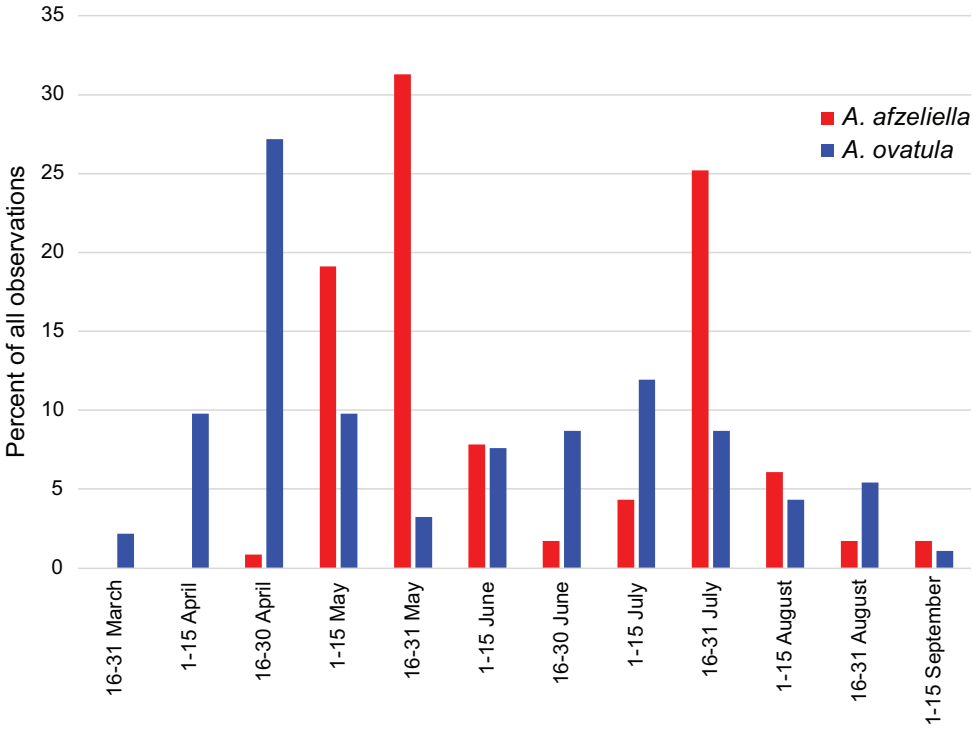


Figure 8. Phenology of *Andrena ovatula* (blue bars) and *A. afzeliella* (red bars) based on all examined specimens from Belgium, Netherlands and United Kingdom.

first to suggest the presence of two distinct, bivoltine species in Europe: he recognised a slightly larger species with comparatively dark vestiture, *A. ovatula sensu stricto*, and a smaller species with light vestiture, *A. albofasciata*. Niemelä (1949) presented an identification key to the northern European species of *Taeniandrena*, including *A. ovatula* and *A. albofasciata*. Both taxa were later synonymised by Warncke (1967: 206) but were mentioned in the identification key by Schmid-Egger and Scheuchl (1997), who listed the criteria of Niemelä (1949), stating however that they did not examine specimens of *A. albofasciata* from Germany.

The distinctiveness of *A. ovatula* and *A. albofasciata* was then advocated by J. van der Smissen, who wrote that she could unambiguously separate these two taxa in northern Germany based on Niemelä's key (van der Smissen 2002). She later presented a detailed key to Northern European *Taeniandrena*, including *A. ovatula* and *A. albofasciata* (van der Smissen 2010). Ongoing confusion after her work is possibly due to the fact that *A. albofasciata* appeared to be rarer than *A. ovatula* in the region studied by J. van der Smissen in northern Germany; *A. albofasciata* was categorised as "probably endangered" in the red list to the bees and wasps of Schleswig-Holsteins while *A. ovatula* was treated as "least concern" (van der Smissen 2001). The assumption that *A. albofasciata* was restricted while *A. ovatula* was widespread probably explains why the identity of these two taxa has remained unclear until now (but see Herrmann 2007). In a recent DNA barcoding study of the bees of Germany, Schmidt et al. (2015) presented barcodes for five specimens identified as *A. ovatula* and for one specimen identified as *A. albofasciata*; based on the shared barcodes of these six specimens, the authors suggested to treat these two species as synonyms. It appears however, that all specimens were in fact conspecific and belonged to *A. albofasciata* (see below).

Our initial DNA barcodes of Swiss and French *A. ovatula sensu lato* were similar to those obtained by Schmidt et al. (2015). Surprisingly, one sequence from Spain (see Wood et al. 2021) was 100% identical to a published sequence from Ireland (BOLD number IBBP050-10), originating from a specimen identified as *A. ovatula*, and widely divergent from all other specimens of *A. ovatula sensu lato* (Fig. 2). We then sequenced several additional specimens from numerous locations in Europe (Suppl. material 1: Table S1 and Fig. 2), including specimens identified as *A. ovatula sensu stricto* and *A. albofasciata* by J. van der Smissen from northern Germany. All female specimens with a dark terminal fringe (*A. ovatula sensu* Stöckhert, Niemelä and van der Smissen) formed a monophyletic clade including the sequence of *A. ovatula* from Ireland; this clade was widely separated from a clade containing all the female specimens with a light terminal fringe (*A. albofasciata*), as well as all the specimens sequenced by Schmidt et al. (2015). Although a clear morphological separation of these two species is sometimes challenging, e. g. in worn females and in some males, this clear segregation of the two colour forms among two widely separated clades is a strong indication that two distinct species exist in sympatry in Europe. In addition, other subtle differences can be found in the sculpture or the vestiture colour (see below), leaving no doubts that these two species are distinct. At the European scale, *A. albofasciata* is much more widespread and abundant than *A. ovatula*; in some parts of central Europe (see also Herrmann 2007), e.g., in Switzerland, only

A. albofasciata appears to be present (Fig. 7). Lastly, a clear phenological difference is visible, at least for the first generation, as already noted by Stöckhert (1930): *A. ovatula* is active from the end of March to the End of May, with a peak around April, while the first generation of *A. albofasciata* is found from the beginning of May until mid-June (Fig. 8; note that this figure is only based on records from Belgium, UK and the Netherlands to reduce variability caused by seasonal differences across a latitudinal gradient).

With respect to the names that can be applied to these two species, five names proposed by Kirby (1802) for the English fauna are currently placed as synonyms of *A. ovatula sensu lato* (Perkins 1918; Gusenleitner and Schwarz 2002); of these five names at least three have been used as valid names after 1899: *A. ovatula*, *A. afzeliella* and *A. fuscata* (Kirby, 1802). These names may apply to either taxon since both occur in England (Figs 2, 7). As far as we know, their type material has not been revised since Perkins (1918). No syntype of *A. picipes* (Kirby, 1802) and *A. barbata* (Kirby, 1802) are preserved in the Kirby collection and these names are considered here to be *nomina dubia*. Perkins (2017: 50) mentions that he has examined the type of *A. picipes* in the Drury collection (possibly in OUMNH).

Three males are preserved under *A. ovatula* in the Kirby collection (NHML). The original description of Kirby mentions a female ("*Descr: Acul.*" [the "aculeate sex" = the female]); however, as noted by Perkins (1918), this was likely a mistake and Kirby's description probably corresponds to a male (the flocculus is not mentioned, unlike in other descriptions of females). We are not confident in the identification of these three males: the tergal structure is suggestive of *A. ovatula sensu* Stöckhert (1930), but the antennal ratio is not clear; the genitalia are not exposed. To settle the identity of this species while minimising changes to current usage of *A. ovatula* and *A. albofasciata*, we propose to designate a neotype for *A. ovatula*, selecting a barcoded female from Surrey, UK (see below under *A. ovatula*). This neotype will ensure that the name *A. ovatula* continues to apply to the species referred to as *A. ovatula* by the few authors who have separated *A. ovatula* from *A. albofasciata* (Stöckhert 1930; Niemelä 1949; van der Smissen 2002, 2010).

Preserved syntypes of *A. afzeliella* in the Kirby collection include three females and one male, all of which probably belong to "*A. albofasciata*" (one female and the male are stylopised, rendering identifications challenging); the best-preserved female (Figs 3, 4) clearly corresponds to "*A. albofasciata*" based on the colour of the terminal fringe (Fig. 4) and the hairs flanking the basitibial plate. This female is designated as the lectotype of *A. afzeliella*. *Andrena albofasciata* is placed in synonymy with *A. afzeliella* (syn. nov.). A reversal of precedence (article 23.9 of the Code of Zoological Nomenclature) to maintain the prevailing usage of *A. albofasciata* is not justified since *A. afzeliella* has been used as a valid name after 1899 (e.g., Alfken 1905; Frey-Gessner 1899–1907; Schmiedeknecht 1907), therefore rejecting the first condition of article 23.9 of the code.

We tried to locate the type material of the *Taeniandrena* taxa described by A. Schenck, namely *A. albofimbriata* Schenck, 1853, *A. canescens*, *A. distincta* Schenck, 1861, *A. gibba* Schenck, 1853, *A. octostrigata* Schenck, 1853, *A. ovata* and *A. plantaris*

Schenck, 1853. In the Schenck collection (SMFD), several specimens are preserved under the names *wilkella*, *xanthura*, *afzeliella* and *convexiuscula*. These specimens belong to several species including *A. lathyri* (see Alfken 1899), *A. wilkella* and *A. afzeliella*, and possibly others. No specimen can be identified as syntype since no mention of the names of the taxa described by Schenck can be found, neither on labels on the specimens, nor anywhere in his collection. We conclude that either the types have been lost or destroyed, or, alternatively, Schenck himself removed these labels, possibly because he thought that his taxa were conspecific with previously described species. Support for the latter hypothesis comes from the fact that Schenck (1861: 255) places most of the taxa that he previously described in synonymy with "*A. convexiuscula*".

However, Schenck described numerous taxa based on material collected by C. Kirschbaum, and some of the type material for these taxa is preserved in the Kirschbaum collection (MWNH; Andert 2010). In addition to the male specimen of *A. canescens* mentioned above, two specimens of *A. gibba* are preserved and were examined. Both are stylopised, although one specimen mostly shows male characters and the other mostly female characters; these two specimens correspond to the original descriptions of the male and female of *A. gibba*, respectively. The identity of these two specimens cannot be established, although the first specimen probably belongs to either *A. afzeliella* or *A. ovatula*. *A. gibba* is thus treated as a *nomen dubium*. Similarly, *A. albofimbriata*, *A. distincta* and *A. octostrigata* are treated as *nomina dubia* given that their type material is presumably lost. *A. ovata* represents a distinct species (see below).

Several additional names are currently treated as synonyms of *A. ovatula sensu lato* (Gusenleitner and Schwarz 2002). The list of synonyms given here is incomplete. It is probable that most of these names will eventually be placed in synonymy with *A. afzeliella*.

Diagnosis. *Andrena afzeliella* and *A. ovatula* can be separated from the other central European species of *Taeniandrena* by a combination of characteristics, which are summarised in the identification key given below. The criteria allowing separation of *A. afzeliella* and *A. ovatula* are presented in Table 1. Males are often more difficult to separate than females and a confident identification is not possible in every case.

Geographic variation. *Andrena afzeliella* is widely distributed in the Western Palearctic. Two barcoded specimens from Corsica and from Sardinia, respectively, clustered with continental populations of *A. afzeliella* in our phylogenetic tree (Fig. 2); in these two specimens, as well as in other examined specimens from Corsica and Sardinia, the mesosomal and head vestiture is orange-red, the terminal fringe is dark brown-orange (as on Fig. 11), and the integument of the hind femora is partly orange (as in Fig. 21; see Table 2). We examined specimens from Israel, Lebanon, Syria, Jordan, Egypt, and Iran with the integument of the metasoma partly to extensively red, most typically on T1–2, but sometimes the red colouration extends to all terga. Where long sequences of specimens from the same site and day were available from Egypt, specimens vary from entirely black to red-marked forms. We therefore consider tergal colouration to be variable, and retain *A. afzeliella* var. *heliopolis*, caracterized by the red integumental colour, as a simple colour form of *A. afzeliella*.

Table 1. Comparison of *Andrena afzeliella* stat. rev. and *A. ovatula* (modified from van der Smissen 2010).

Females		
Characters (order of importance)	***Andrena afzeliella***	***Andrena ovatula***
Apical fringe of T5	Golden (Figs 4, 9) to whitish grey, rarely brown medially (Fig. 9), but never dark brown	Always dark brown to black medially, often lighter laterally (Fig. 10)
Pygidial fimbria	Mostly whitish laterally, light brown medially, sometimes entirely golden (Fig. 4), rarely brown (Fig. 9), but then with a reddish hue, not dark brown	Dark brown medially (sometimes a few light brown hairs laterally), without reddish hue (Fig. 10)
Apical fringe of hairs on femur, covering the base of basitibial plate	Orange to brown orange, never dark brown (Fig. 29)	Dark brown (Fig. 30)
Colour of scopal hairs	Entirely white or yellowish (Fig. 29)	White or yellowish, but nearly always with a few dark hairs dorsally near basitibial plate (Fig. 30)
Scutal vestiture	Long hairs yellowish white in fresh specimens; without short, dark hairs beneath long hairs (short hairs, if present, yellowish white).	Long hairs brownish yellow in fresh specimens; medially with dark, minute hairs beneath long hairs; this character is clearly visible in northern European populations, less so on the Iberian Peninsula.
Clypeal punctation and sculpture	On average comparatively fine and sparse (Fig. 31), sculpture matt, although there is considerable variation in this character and the condition overlaps with that observed in *A. ovatula.*	On average comparatively coarse, sculpture shiny (Fig. 32).
Size	On average slightly smaller, body length mostly 8–9 mm, although some specimens are up to 10 mm.	On average slightly larger, body length 9–10 mm
Males		
Character (order of importance)	***Andrena afzeliella***	***Andrena ovatula***
Antennal ratio	A3 = 0.9–1.0 × A4 (Fig. 35); A5–A12 only slightly longer than broad.	A3 = 0.8–0.9 × A4 (Fig. 36); A5–A12 visibly longer than broad.
Sculpture of disc of T3 and T4	Shiny, punctation coarse and comparatively sparse (Fig. 33)	Shagreened, punctation dense and shallow, punctures little visible (Fig. 34)
Gonostylus and valve	Gonostylus broader, external margin often straight; valve often slightly broader (Fig. 45)	Gonostylus more slender, external margin always concave, valve often more slender (Fig. 46)
Gonocoxae	Internal margins usually diverging apically (Fig. 45)	Internal margins usually parallel apically (Fig. 46)
Vestiture	Body vestiture often entirely greyish white even in fresh specimens (Fig. 33), although sometimes yellowish brown, especially in first generation	Body vestiture yellowish brown in fresh specimens (Fig. 34)
Width of tergal fringes	comparatively broad (Fig. 33)	comparatively narrow (Fig. 34)

Andrena antonellae Praz & Genoud, sp. nov.

http://zoobank.org/2F8E7138-5C8D-4142-9B68-603DDE55006B

Figs 11, 21, 37, 47, 56–61

Type material. ***Holotype*** ♀ (Figs 11, 21, 56–58), Italy • Sardinia, Buggerru, Cala Domestica; 39°22'36"N, 8°22'57"E [39.3767°N, 8.3825°E]; 17.iv.2017; leg. J. Litman, C. Praz; unique identifier: GBIFCH00117710 (PRUN) [DNA extraction number 1209].

Paratypes (Suppl. material 2: Table S2): 15 ♀ 5 ♂. France • ♀; Corse, Agriates («Désert des»); [42.6615°N, 9.1579°E]; 24.4.2011; leg. M. Aubert (DGC) [DNA extraction number 1210] • ♀; Corse, Bonifacio; 41.4034°N, 9.1204°E; 13.4.2017; leg. A. Cornuel; unique identifier: FER17ALCW2660 (MNHN) • ♀; Corse, Bonifacio; 41.3878°N, 9.1578°E; 6.4.2017; leg. A. Cornuel; unique identifier: FER17AL-

Table 2. Comparison of the females of *Andrena antonellae* sp. nov., and those of the populations of *A. afzeliella* and *A. wilkella* from Corsica and Sardinia. *Andrena wilkella* has so far only been reported from Corsica.

Characters (order of importance)	*Andrena afzeliella*	*Andrena antonellae* sp. nov.	*Andrena wilkella*
Apical fringe of T5 and pygidial fimbria	Brown-orange (bronze)	Brown-orange (bronze)	Greyish brown
Sculpture of T1	Fine but distinct on disc and on margin; underlying surface weakly shagreened, shiny	Mostly impunctate, sometimes with a few, scarcely visible punctures on disc and margin; underlying surface shagreened, weakly shiny (Fig. 21)	Fine but distinct on disc and margin, denser than in *A. afzeliella* but less so than in central European specimens of *A. wilkella*; underlying surface weakly shagreened, shiny
Sculpture of T2	Very densely punctate, punctures separated by less than 0.5 puncture diameters; underlying surface weakly shagreened, shiny; margin impunctate	Mostly impunctate, sometimes few barely visible punctures on disc (Fig. 21).	Moderately densely punctate, punctures separated by 1–2 puncture diameters (punctation less dense and less visible than in central European populations); underlying surface weakly shagreened, shiny; margin impunctate
Sculpture of T4	Very finely and very densely punctate, interspaces less than a puncture diameter, surface appearing shagreened	Very finely and very densely punctate, interspaces less than a puncture diameter, surface appearing shagreened (Fig. 11).	Finely and densely punctate, interspaces above one puncture diameter, surface appearing shiny
Colour of integument	Margin of T1–4 dark, sometimes slightly brownish apically. Femora 3 predominantly orange.	Margin of T1–4 predominantly yellowish brown, dark brown only basally (Fig. 21). Femora 3 predominantly orange (Fig. 21).	Margin of T1–4 entirely dark. Femora 3 dark.
Body size	8–9 mm	8–9 mm	10–11 mm

CW2589 (MNHN) • ♀; Corse, Bonifacio; 41.3878°N, 9.1578°E; 6.4.2017; leg. A. Cornuel; unique identifier: FER17ALCW2589 (MNHN) • ♀; Corse, Bonifacio; 41.4034°N, 9.1204°E; 13.4.2017; leg. A. Cornuel; unique identifier: FER17ALCW2660 (MNHN) • ♂; Corse, Bonifacio, Pertusato A; 41.3710°N, 9.1811°E; 11.4.2017; leg. A. Cornuel; unique identifier: FER17ALCW1806 (MNHN) [DNA extraction number 1301] • ♂; Corse, Bonifacio, Pertusato B; 41.3709°N, 9.1813°E; 11.4.2017; leg. A. Cornuel; unique identifier: FER17ALCW1811 (MNHN) • ♂; Corse, Bonifacio, Pertusato B; 41.3709°N, 9.1814°E; 11.4.2017; leg. A. Cornuel; unique identifier: FER17ALCW1811 (MNHN) • ♀; Corse, Bonifacio, Ville; 41.3865°N, 9.1550°E; 25.4.2017; leg. Perrard & Cornuel; unique identifier: C17 0600 (MNHN) • ♀; Corse, Bonifacio, Ville; 41.3865°N, 9.1550°E; 25.4.2017; leg. Perrard & Cornuel; unique identifier: C17 0600 (MNHN) • ♀; Corse, Ghisonacia, Pinia; [42.0305°N, 9.4796°E]; 17.5.2018; leg. D. Genoud (DGC) [DNA extraction number 1297] • ♂; Corse, La Trinité; 41.4035°N, 9.1203°E; 28.3.2017; leg. A. Perrard; unique identifier: C17 0197 (PRUN) [DNA extraction number 1294] • ♀; Corse, Pertusato; 41.3710°N, 9.1811°E; 24.4.2017; leg. A. Perrard; unique identifier: C17 0476 (MNHN) • ♀; Corse, Pertusato; 41.3710°N, 9.1811°E; 24.4.2017; leg. A. Perrard; unique identifier: C17 0476 (MNHN) • ♀; Corse, St-Julien; 41.3902°N, 9.1803°E; 27.3.2017; leg. A. Perrard; unique identifier: C17 0090 (PRUN) • ♀; Evisa, Col de Vergio; [42.2899°N, 8.8786°E]; 29.6.2019; leg. Bertrand Schatz (DGC) [DNA extraction number 2337] • ♀; Evisa, Col de Vergio; [42.2899°N, 8.8786°E]; 29.6.2019; leg. Bertrand Schatz (DGC) [DNA extraction number 2341] • ♀; Evisa,

Col de Vergio; [42.2899°N, 8.8786°E]; 29.6.2019; leg. Bertrand Schatz; unique identifier: GBIFCH00117729 (PRUN) [DNA extraction number 2340].

Italy • ♀; Sardinia, Buggerru, Cala Domestica; 39°22'36"N, 8°22'57"E [39.3767°N, 8.3825°E]; 17.iv.2017; leg. J. Litman; C. Praz (PRUN) • ♂; Sardinia, Monte Crescia; 39.295°N, 9.392°E; 7.5.2018; leg. D. Bénon; unique identifier: GBIFCH00117711 (PRUN) [DNA extraction number 1437].

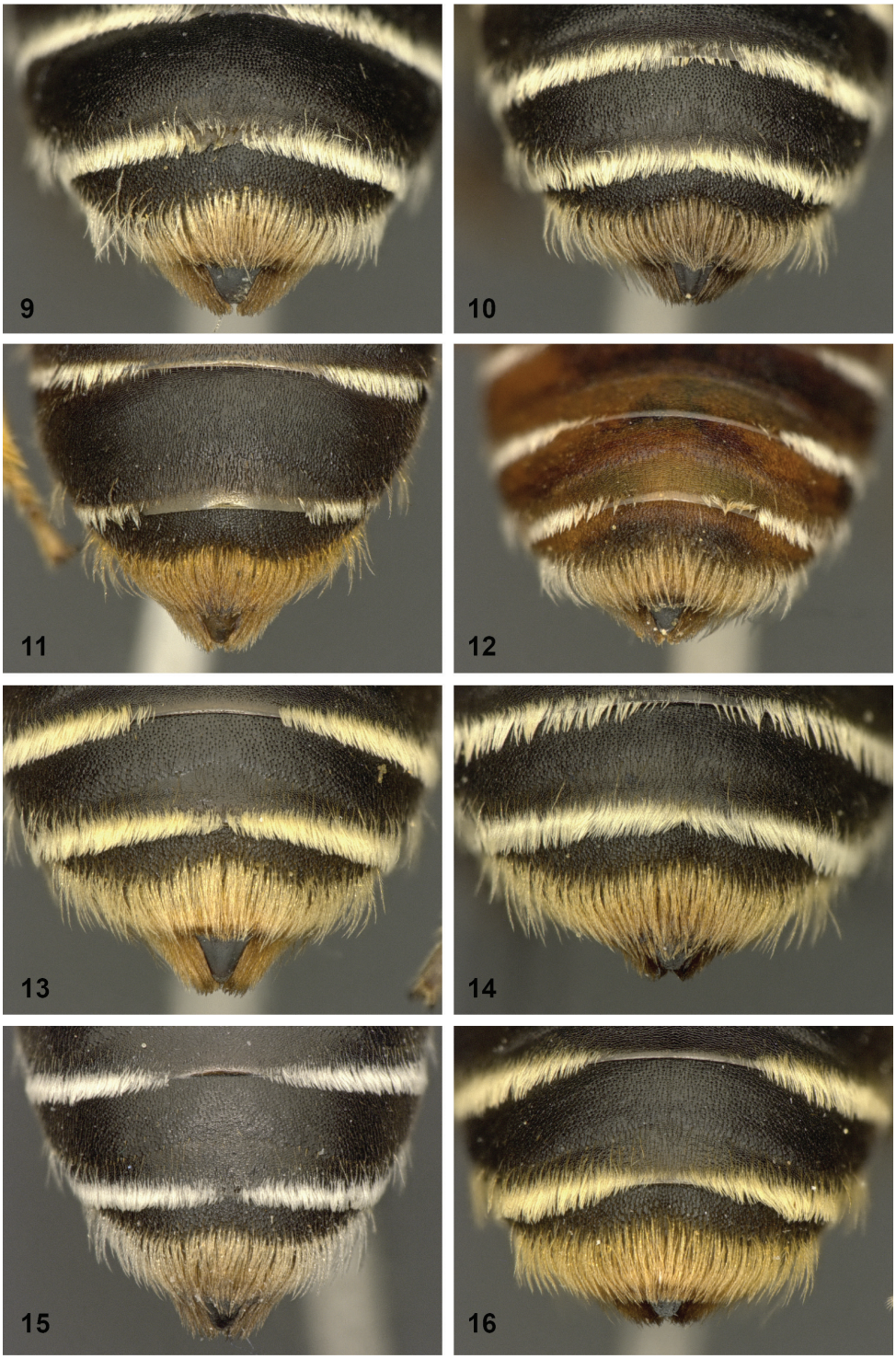
Distribution. So far known only from the Islands of Sardinia and Corsica. In Corsica, the species is known from several localities in the south near Bonifacio, one locality along the east coast, as well as one locality in the north of the Island. In Sardinia, the species is known from two localities in the south of the Island. *Andrena antonellae* sp. nov. is probably widely distributed on both islands.

Pollen preferences. Unknown; two females have been captured on an unidentified yellow Fabaceae shrub (CJP, unpublished data).

Phenology. Presumably univoltine with one generation from March until the end of June depending on elevation.

Diagnosis. Female. Females of *Andrena antonellae* sp. nov. are characterised by the small body length (8–9 mm), the brown-orange vestiture of the mesosoma and the head (Fig. 56; this colour pattern is shared with *A. afzeliella* on Sardinia and Corsica), the bronze, dark orange colour of the terminal fringe (Fig. 11), and the very shallow (nearly indiscernible) punctation of terga 1 and 2 (Fig. 21). An unusual feature is the partly orange colour of the hind femora (Fig. 21), a character shared by Corso-Sardinian populations of *A. afzeliella*.

Andrena antonellae sp. nov. is morphologically most similar to *A. russula* (=*A. similis*), *A. fuliginata* and *A. croceiventris*; according to current knowledge, these three taxa are absent from Sardinia and Corsica [the map for *Andrena russula* (=*A. similis*) presented in Gusenleitner and Schwarz (2002: 1175) includes a mention from Corsica; this mention probably refers to *A. antonellae* sp. nov.]. Compared to *A. russula*, which also has shallow punctation on T1–2, *A. antonellae* sp. nov. is smaller, the vestiture on the scutellum is less dense, both scutum and scutellum are usually less shiny (Fig. 57) (scutum entirely matt, scutellum weakly shiny, compared to scutum weakly and scutellum strongly shiny in *A. russula*), and the tergal hairbands are much shorter (compare Figs 21 and 26). *Andrena fuliginata* is sculpturally similar to *A. antonellae* sp. nov.; in the latter species, T1 and T2 are shinier (Fig. 21), the scutellum less densely punctate (Fig. 57) and the clypeus more shiny and more coarsely punctate (Fig. 58). In addition, *A. fuliginata* is characterised by the brown-orange vestiture on the scutum with short dark hairs intermixed with the longer brown-orange hairs, and the terminal fringe is dark brown; in *A. antonellae* sp. nov., the scutal vestiture is lighter, there are no or only very few short dark hairs intermixed with the longer hairs (Figs 56, 57), and the terminal fringe is brown-orange (Fig. 11). Lastly, *A. croceiventris* is sculpturally close to both *A. fuliginata* and *A. antonellae* sp. nov., although the terga are shinier in *A. croceiventris* (Fig. 22), the clypeus weakly punctate with the underlying surface strongly shagreened, unlike in *A. antonellae* sp. nov. *A. croceiventris* is characterised by the red integument colour of the terga (Figs 12, 22); the extent of the red colour is variable but at least some parts of the discs of T1–2 are usually red.



Figures 9–16. Terminal fringes of females of *Taeniandrena* **9** *Andrena afzeliella* **10** *A. ovatula* **11** *A. antonellae* sp. nov. **12** *A. croceiventris* **13** *A. gelriae* **14** *A. intermedia* **15** *A. ovata* **16** *A. russula*.

Figures 17, 18. Terminal fringes of females of *Taeniandrena* **17** *Andrena vocifera* **18** *A. wilkella*.

The Corso-Sardinian populations of *A. wilkella* (Kirby, 1802) and *A. afzeliella*, the only two other species of *Taeniandrena* known so far from Sardinia and Corsica, also have an orange vestiture on the mesosoma, as *A. antonellae* sp. nov. Since all three species are found in sympatry, the criteria allowing for the identification of the female are summarised in Table 2.

Male. The males of *Andrena antonellae* sp. nov. are sculpturally nearly identical to those of *A. croceiventris* and *A. fuliginata*. All three species have a comparatively elongate, oval-shaped genitalia with a narrow penis valve (Figs 47, 48), nearly exactly as in *A. wilkella* (Fig. 54). The latter species can be recognised by the comparatively short antennal segment 3 (Fig. 44), which is at most 0.7× as long as A4, and the markedly denser and coarser tergal punctation. In *A. croceiventris*, *A. fuliginata* and *A. antonellae* sp. nov. A3 is 0.8 times as long as A4 (Figs 37, 38), and the tergal discs are strongly shagreened and weakly punctate. In the lone male specimen of *A. croceiventris* examined, the integument of all tergal margins, of the pregradular area of T2–4, and of the lateral, declivous parts of T1–5 is orange, and the integument of the hind tibiae is dark. In *A. antonellae* sp. nov. and the lone male specimen of *A. fuliginata* examined, the integument of the terga is predominantly dark, the tergal margins are slightly lightened apically, and the hind tibiae are orange (partly brown basally and medially in *A. fuliginata*). No sculptural difference could be found between the male of *A. antonellae* sp. nov. and *A. fuliginata*, although only one specimen of *A. fuliginata* has been examined. Lastly, the males of these three species are similar to those of *A. russula* (= *A. similis*), but in the latter the broadened, parallel-sided base of the valve is longer, only tapering near the base of the valve opening (Fig. 52), and the antennal segment 3 is usually longer (Fig. 42).

Description. Female. Measurements. Body length 8–9 mm.

Head. Head 1.3 times as wide as long. Clypeus dark, flattened over most of its area, densely and uniformly punctate with exception of a narrow central impunctate line, punctures separated by 0.5 puncture diameters, underlying surface weakly shagreened, usually shiny, especially apically (Fig. 58). Face, gena, vertex, and scape with light brownish hairs, longest approximately three quarters of scape in length. Antennae

dark, A4–12 lightened to light brown below. Foveae broad, occupying almost all area between lateral ocellus and top of compound eye, filled with short, dark brown hairs.

Mesosoma. Scutum densely punctate, punctures separated by < 0.5 puncture diameters over majority of surface except becoming slightly sparser centrally and posteriorly, underlying surface strongly shagreened (Fig. 57). Scutellum with sparser punctures separated by up to 4 puncture diameters medially, shagreenation weaker, surface weakly shiny. Episternum and propodeum with dense raised reticulation, underlying surface dull, propodeal triangle weakly indicated by weak carina, little differentiated from general reticulation. Scutum and scutellum with erect, orange, shortly plumose hairs, episternum with longer light orange hairs. Front legs, mid coxa, trochanter and femur, hind coxa and trochanter dark brown, mid tibia dark basally and orange apically, mid tibia, tarsi and hind femur, tibia and tarsi orange (Figs 21, 56). Leg pubescence light brown basally, becoming orange apically, flocculus, femoral and tibial scopae light brown to golden. Wings hyaline to weakly infuscate, venation brown orange, stigma light brown.

Metasoma. Terga dark, strongly shagreened, weakly shiny (Fig. 21), margins yellowish brown apically, slightly lighter than tergal discs. T1 nearly impunctate, usually only very few punctures scarcely visible against shagreenation on disc, sometimes weakly punctate with very shallow punctures; vertical anterior area entirely impunctate; margin strongly shagreened, impunctate. T2–3 slightly more densely and visibly punctate, punctures little visible, separated by 0.5–1 puncture diameters (Fig. 21). T4 very densely punctate, punctures little visible, separated by less than 0.5 puncture diameters (Fig. 11). T1 without hairband, with a few short hairs laterally, hairs not forming dense hairbands. T2–4 with short, narrow lateral spots, hairband covering a third of tergal width on T2 and T4 and half tergal width on T3 (Fig. 21). Remaining tergal surface covered with very short, dark hairs visible when viewed obliquely or in profile. Disc of T4 near margin with a few longer, erect dark hairs. Apical fringe of T5 and hairs flanking pygidial plate bronze-orange (Fig. 11), pygidial plate rounded, flat, medially slightly raised, without raised margin.

Male. Measurements. Body length 8–9 mm.

Head. Head 1.3 times as wide as long (Fig. 60). Clypeus flattened and densely punctate, punctures separated by < 0.5 puncture diameter, underlying surface shiny. Gena, lower part of face, scape and vertex with greyish-white hairs becoming light brown on scape and vertex, longest equalling length of scape. Antennae dark. A3 0.8× as long as A4 (Fig. 37).

Mesosoma. Scutum, scutellum, episternum, and propodeum structurally as in female, punctation overall sparser. Scutum and scutellum with fine yellowish grey hairs that equal length of scape. Front legs dark, mid legs dark except tarsi, orange, hind legs dark, tibiae and tarsi orange (Fig. 59). Wings hyaline, venation dark orange, stigma dark orange with brown margin.

Metasoma. Terga dark, finely shagreened and weakly shiny, apical part of marginal areas lightened, semi-translucent brown (Fig. 61). Terga finely but clearly punctate, punctures separated by 2 puncture diameters. T2–5 laterally with weak apical hairbands of whitish hairs, hairbands interrupted on all terga (Fig. 61). Sterna apically

with loose, long fringe of yellowish hairs. S8 strap-like, slightly broadened apically, uniformly hairy. Genitalia elongated oval-shaped in dorsal view, gonocoxa with inner margins weakly diverging (Fig. 47). Penis valve comparatively narrow, basally parallel-sided before tapering apically. Gonostyli comparatively long, apical blades longer than wide, their external margin weakly concave (Fig. 47).

Variation. Female specimens from one high elevation locality in Corsica (Evisa, Col de Vergio 1477 m; one specimen is included in Fig. 2 with number 2341) have broader and more furnished tergal hair bands.

Etymology. This species is named in honour of Antonella Soro for her contributions to the field of conservation genetics of bees.

Note. *Andrena antonellae* sp. nov. is sculpturally highly similar to *A. croceiventris* and *A. fuliginata*, both in the female and male sexes. Based on current evidence, these three taxa do not occur in sympatry. The highly similar morphology in these three taxa conflicts with our DNA barcoding results, which suggest that the three taxa are only distantly related. This discrepancy between molecules and morphology is reminiscent of the strong genetic divergences between *A. afzeliella* and *A. ovatula*; these two cases are puzzling and are further discussed below. While *A. antonellae* sp. nov., *A. fuliginata* and *A. croceiventris* are morphologically close, there are still subtle differences among them; these differences include the colour of the terminal fringe, the colour of the integument, the presence or absence of short dark intermixed hairs on the scutum, the sculpture of T1 and T2, and the sculpture of the clypeus. In *Taeniandrena*, such differences, although subtle, generally correspond to between-species differences. For this reason and based on the strongly divergent DNA barcodes, we treat these three taxa as distinct.

Andrena croceiventris Morawitz, 1871, stat. rev.

Figs 12, 22, 38, 48

Andrena croceiventris Morawitz, 1871: 219, ♀, "Calabria" [Italy].

Andrena stefanii Pérez, 1895: 41, ♀ 'Sicile' [Italy]. Synonymy in Warncke 1967: 185 (with *A. russula* ssp. *croceiventris*). Lectotype ♀, by designation of Warncke 1967: 185 (MNHN).

Material examined. Type material: ***Lectotype*** ♀ of *Andrena stefanii* Pérez, 1895. Italy • Sicile [Sicily], no further information (MNHN).

Other material (Suppl. material 2: Table S2): Italy • ♀; Castiglione d'Orcia; [43.005°N, 11.616°E]; 37.5.2001; leg. K. Hirt; unique identifier: GBIFCH00131712 (KHC) [DNA extraction number 1534] • ♀; Montalcino; [43.056°N, 11.49°E]; 7.6.1998; leg. K. Hirt; unique identifier: GBIFCH00131713 (KHC) [DNA extraction number 1530] • ♀; Montalcino, Croce; [43.056°N, 11.49°E]; 25.6.2004; leg. K. Hirt; unique identifier: GBIFCH00117709 (PRUN) [DNA extraction number 1532] • ♂; Pesaro; 7.7.1962; leg. S. Erlandsson (OLML) • ♀; Sicily; 17.5.1954; leg. Dr. Enslin (OLML) • ♀; Sicily; Selinute [Selinunte]; 13.4.1965; leg. K. M. Guichard

(OLML) • ♀; Latium, Caprarola; [42.3287°N, 12.2406°E]; 22.5.1979; leg. R. Hensen; unique identifier: ZMA.INS.5104369 (RMNH).

Distribution. Only known from Italy between Tuscany and Calabria, as well as from Sicily.

Diagnosis. Female. The most distinctive feature of *Andrena croceiventris* is the partly reddish colour of the integument of the metasoma, especially T1–3 (Fig. 22) In some specimens however, the reddish colour is limited to small areas on T1–2. The hind femora are dark. Females of *A. croceiventris* are sculpturally very similar to *A. antonellae* sp. nov. and *A. fuliginata*, especially in the nearly impunctate T1 and T2. *Andrena russula* (=*A. similis*) has the scutum and especially the scutellum shinier, the vestiture longer, for example on the scutum and scutellum; the apical tergal hairbands are also longer (compare Figs 22 and 26). In *A. croceiventris*, the terminal fringe is yellowish orange, the vestiture on the mesosoma and head is orange-brown, and the white apical hairbands of hairs are narrow and restricted to the side of the terga. Differences with *A. antonellae* sp. nov. are given under that species.

Male. As mentioned above, the male of *A. croceiventris* is sculpturally nearly identical to those of *A. antonellae* sp. nov. and *A. fuliginata*. The lone specimen of *A. croceiventris* examined has part of the metasomal integument dark orange (tergal margins, pregradular areas and lateral, declivous parts), a unique feature in European species of *Taeniandrena*. Differences compared to *A. wilkella* and *A. russula* are mentioned under *A. antonellae* sp. nov. or in the identification key.

Note. This species has so far been treated as a subspecies of the widespread species *A. russula* (=*A. similis*; see below) (Warncke 1967: 212, 1986). *Andrena russula* is present in Central Italy (see below), so the ranges of both *A. russula* and *A. croceiventris* overlap. The morphological differences, combined with the striking genetic differences (Fig. 2) observed in spite of range overlap, lead us to recognize *A. croceiventris* as a distinct species.

Andrena gelriae van der Vecht, 1927

Figs 13, 23, 39, 49, 70

Andrena gelriae van der Vecht, 1927: 87, ♀ ♂, „Putten" [Holland]. Syntypes (RMNH).
Andrena gelriae karelica Niemelä, 1949: 114, ♀ ♂, [Finland].

Material examined (Suppl. material 2: Table S2). Belgium • ♂; [almost illegible] ?Gistoux; [50.6835°N, 4.6943°E]; 29.6.1931; leg. A. Crèvecoeur (RBINS) • ♂; Bossut-Gott [Bossut-Gottechain]; [50.7607°N, 4.6912°E]; 18.8.1927; leg. P. Maréchal (RBINS) • ♂; Chaudfont[aine]; [50.5851°N, 5.6397°E]; 4.7.1943; leg. P. Maréchal (RBINS).

France • ♂; Avignon; [43.908°N, 4.878°E]; 11.5.2012; leg. N.-J. Vereecken; unique identifier: scwe057 (DGC) • ♀; Rouffach; [47.959°N, 7.298°E]; 18.6.1992; leg. F. Amiet; unique identifier: GBIFCH00117688 (NMBE) [DNA extraction number 1223] • ♀; Rouffach; [47.959°N, 7.298°E]; 18.6.1992; leg. F. Amiet; unique

identifier: GBIFCH00117689 (NMBE) [DNA extraction number 1224] • ♀; Rouffach; [47.959°N, 7.298°E]; 18.6.1992; leg. F. Amiet; unique identifier: GBIFCH00117690 (NMBE) [DNA extraction number 1225] • ♂; Valensole; 43.871°N, 5.88°E; 4.6.2018; leg. C. Praz/M. Aubert; unique identifier: GBIFCH00117716 (PRUN) [DNA extraction number 1282] • ♀; Virieu le Grand Clairefontaine; [45.8526°N, 5.6441°E]; 21.6.2014; leg. D. Goy (DGC) [DNA extraction number 2350].

Italy • ♂; Italy, Basilicata, Monte Pollino; 39.904°N, 16.181°E; 4.7.2011; leg. Trunz, Litman, Praz; unique identifier: GBIFCH00117715 (PRUN) [DNA extraction number 1427].

Distribution. Northern and Central Europe, including Scandinavia, the Netherlands, Belgium, Germany, Switzerland, France as far south as Valensole and Avignon (Fig. 55); southern Italy. The distribution in Central and Eastern Europe (e.g. Bulgaria, Romania, Austria, Poland), requires further examination due to confusion with *Andrena producta*, which was described as a subspecies of *A. gelriae* (see discussion in Gusenleitner 1984).

Pollen preferences. Probably oligolectic on Fabaceae (Westrich 1989), although the difficulties in identifications prevent solid conclusions. In Switzerland the species was observed foraging on *Medicago* sp. and on *Trifolium pratense* (DB and CJP, unpublished data).

Phenology. Univoltine, in central Europe from early June until mid-July, slightly after *A. wilkella* (although this species has a long flight period; see below) and *A. intermedia*, as in northern Europe (Niemelä 1949).

Note. Warncke (1967, 1973, 1975a, 1975b; see also Gusenleitner and Schwarz 2002) considered *A. gelriae* to be composed of several subspecies distributed from Spain and Portugal (*A. gredana*; see Wood et al. 2021), southern France (*A. vocifera*), Central and Northern Europe (*A. gelriae sensu stricto*), Finland (*A. gelriae karelica* Niemelä, 1949) and Austria to south-eastern Europe and Turkey (*A. producta*). Gusenleitner (1984), Schwarz and Gusenleitner (1997) and Wood et al (2021) have respectively demonstrated that *A. producta* and *A. gredana* represent distinct species. *Andrena vocifera* is also raised here to a distinct species (see below). Following Niemelä (1949), we keep *A. gelriae karelica* in synonymy with *A. gelriae*, though the status of *A. gelriae karelica* requires investigation given the cryptic diversity present in this group.

This species is particularly challenging to identify in the female sex. Nearly all recent mentions from Switzerland (Amiet et al. 2010) were based on misidentified females.

Diagnosis. See Schmid-Egger and Scheuchl (1997), Amiet et al. (2010) and the identification key below.

Andrena intermedia Thomson, 1870

Figs 14, 24, 40, 50

Andrena intermedia Thomson, 1870: 154, ♀ ♂, "Norrland" [Sweden]. Lectotype ♀, by designation of Niemelä 1949: 108; see also Nilsson 2010: 80 (ZML).

Material examined (Suppl. material 2: Table S2). Italy • ♀; Basilicata, Monte Pollino; 39.904°N, 16.181°E; 4.7.2011; leg. Trunz, Litman, Praz; unique identifier:

GBIFCH00117719 (PRUN) [DNA extraction number 1424]; 1♀ 2♂; Basilicata, Monte Pollino; 39.904°N, 16.181°E; 4.7.2011; leg. Trunz, Litman, Praz (PRUN) • 2♂; Abruzzo, Maiella, Blockhaus; 42.1442°N, 14.1119°E; 28.6.2011; leg. Trunz, Litman, Praz (PRUN).

Spain • ♂; Sierra Nevada, El Dornajo, 1700 m; 37.132335°N, -3.439249°E; 6.6.2021; leg. T.J. Wood; unique identifier: TJW0398 (TJWC) [DNA extraction number 2264] • ♂; Cuenca, Cueva de los Morceguillos; 40.181797°N, -2.01305°E; 21.6.2021; leg. T.J. Wood; unique identifier: TJW0460 (TJWC) [DNA extraction number 2270].

Distribution. Northern and Central Europe, restricted to mountainous areas in Southern Europe.

Pollen preferences. Probably oligolectic on Fabaceae (Westrich 1989).

Phenology. Univoltine, from early May until July depending on the elevation. According to Niemelä (1949), this species is active a little earlier than *Andrena gelriae*, which is in agreement with the occurrences from Switzerland, where the main flight period extends from early May until the end of July. In one locality in Southern Italy (Monte Pollino), males of *A. intermedia* and *A. gelriae* were observed on the same day in early July.

Note. *Andrena intermedia* did not form a monophyletic group in our phylogenetic tree (Fig. 2) due to the placement of two specimens from Spain; these two specimens (numbers 2264 and 2270 in Fig. 2) were more closely related to *A. contracta* and *A. levante*, respectively, than to central European populations of *A. intermedia*, although morphologically they can be identified as *A. intermedia* due to their genital capsule which has both the gonocoxa with inner margins that diverge apically, and a wide penis valve with a strongly broadened valve opening. However, there are slight differences in the overall construction of the genital capsule, as the inner margins of the gonocoxa diverge from their base, not from halfway between the base and the apex as in central European *A. intermedia* (Fig. 50, compare illustrations in Wood 2022). Both male and female material also have terga with stronger and denser punctures than those of central European specimens. This case is further discussed below.

Diagnosis. See Schmid-Egger and Scheuchl (1997), Amiet et al. (2010) and the identification key below.

Andrena ovata Schenck, 1853, stat. nov.

Figs 15, 25, 41, 51, 62–68

Andrena ovata Schenck, 1853: 133, ♀ ♂, "[Nassau, Germany]. Lectotype ♂ (MWNH) by present designation (see below).

Material examined. Type material: ***Lectotype*** ♂ of *Andrena ovata* Schenck, 1853, by present designation, a male in good condition (Fig. 65; MWNH). This male specimen is labelled as follows: 1. "Collection Kirschbaum" [printed]; 2. "♂" (printed); 3. "*Andrena ovata* Sch ♂" [handwritten]; 4. "*Andrena gibba* Schenck 1853 Typenmaterial

des. Andert 2008". 5. "Lectotype *Andrena ovata* des. C. Praz 2022". 6. "mwnh-sch-161" [unique identifier].

Other material (Suppl. material 2: Table S2): France • ♀; Fontvieille, barycentre commune; [43.7263°N, 4.707°E]; 25.4.1992; leg. Gérard Le Goff (DGC) • ♀; Dijon; [47.3017°N, 5.0366°E]; 14.6.2021; leg. Lise Ropars (DGC) • 2♀; Dijon; [47.3491°N, 5.0574°E]; 16.6.2021; leg. Lise Ropars (DGC and PRUN) • ♀; Lussan, le lac de Beth; [44.1819°N, 4.3739°E]; 24.5.2016; leg. D. Genoud; unique identifier: GBIFCH00117722 (PRUN) [DNA extraction number 2335] • 2♀; Lussan, Lac de Beth; [44.1819°N, 4.3739°E]; 24.5.2016; leg. D. Genoud (DGC) • ♀; Saint-Ay; 47.8541°N, 1.7515°E; 4.6.2018; leg. Romain Ledeux UNIV. Orléans (DGC) [BOLD accession number POLLE2744-19] • ♀; Villefranque, Quartier bas; [43.4647°N, -1.4758°E]; 11.5.2011; leg. D. Genoud (DGC) • ♀; Saint-Léger-la-Montagne, RN des Dauges - Nord-ouest; 46.0106°N, 1.4111°E; 4.6.1996; leg. Jean-Marie Sibert (Laurent Chabrol) • ♀; Bouches-du-Rhônes (13); Marseille, Parc des Bruyères; [43.275°N, 5.4395°E]; 17.5.2016; leg. L. Ropars (DGC) [DNA extraction number 2334] • ♂; Bugarach; [42.8783°N, 2.3294°E]; 29.4.2016; leg. D. Genoud; unique identifier: GBIFCH00117723 (PRUN) [DNA extraction number 2343] • ♂; Riols; [43.4858°N, 2.8124°E]; 1.5.2008; leg. D. Genoud (DGC) [DNA extraction number 2348] • ♂; Roquebrune sur Argens; [43.4754°N, 6.6151°E]; 23.4.2010; leg. D. Genoud (DGC) [DNA extraction number 2347] • ♂; Saint-Martin-de-Seignanx, Arrousset; [43.513°N, -1.3685°E]; 19.4.2007; leg. D. Genoud (DGC) [DNA extraction number 2345] • ♂; Sournia Chapelle Saint-Michel; 42.7241°N, 2.4278°E; 7.5.2013; leg. X. Lair (DGC) [DNA extraction number 2344] • ♀; Villefranque, Quartier Bas; [43.4647°N, -1.4758°E]; 11.5.2011; leg. D. Genoud (DGC) [DNA extraction number 2336] • ♂; B-du-Rhône, Eyguières Roquemartine; 29.4.1991; leg. C. Schmid-Egger (OLML) • 3♂; Vaucluse, Carpentras, Le Beaucet; [43.9809, 5.1212]; 30.4.1991; leg. C. Schmid-Egger (OLML) • 7♂; Vaucluse, 2 km E Roussillon FJ86; 1.5.1991; leg. C. Schmid-Egger (OLML).

Germany • ♀; Rheinland-Pfalz, Mechtersheim NSG Tongruben RLP MV5555 Standort 3; 28.5.1995; leg. Niehuis (CSE) [DNA extraction number 2373] • 2 ♀; Hessen-Höchst a.M. SO 46 Gutachten Industriepark Wiese, Lotus; 50.0907, 8.5494; 22.5.2020; leg. S. Tischendorf (STC and PRUN) • ♀; Hessen, Babenhausen Kiesgrube nördl. Bab, Düne 1; 7.6.1996; leg. S. Tischendorf (STC) • ♀; Hessen-Riedstadt MTB 6116 R3455-H5526 UTM MA52 sw Geinsheim Kiesbaggerei Kiebert; 24.5.2004; leg. S. Tischendorf (STC) • ♀; Hessen-Wattenheim; 49.689595, 8.40162; 1.6.2021; leg. S. Tischendorf (STC) • ♀; Hessen-Kelkheim/T MTB 5816 R3461-H5555 UTM MA65 Streuobstwiese; 14.6.2004; leg. S. Tischendorf (STC) • ♀; Hessen-Höchst a.M. SO 14 Gutachten Industriepark GS 24 trockene Wiese; 50.08654, 8.545; 22–31.5.2020 (STC) • ♀; Hessen, Babenhausen Kiesgrube nördl. Bab, Düne 1; 17.6.1996; leg. S. Tischendorf (PRUN) • ♀; Hessen-Darmstadt TK 6117-7522 Eberstadt, Prinzenberg; 28.5.1998 (STC) • ♂; Hessen-Bensheim TK 6317 3475/5505; 15.5.1994; leg. S. Tischendorf (STC) • ♂; Hessen-Höchst a.M. SO 14, trockene Wiese Gutachten Höchst AG GS 17; 8–17.5.2020; leg. S. Tischendorf (STC) • ♂; Hessen-Biebesheim FO19 Rheinufer Ufer

Gras Proj. Blaues Band; 49.768567, 8.45083; 30.5.2017; leg. S. Tischendorf (STC) • ♂; Rhl.-Pfalz Ingelheim Rheindamm 6; 24.5.1992; leg. M. Hauser (STC).

Greece • ♀; Arkadia, 2 km NW Kosmas; 37°06'24"N, 22°43'42"E [37.1067°N, 22.7283°E]; 2.vi.2014; leg. J. Litman & C. Praz; unique identifier: GBIFCH00117721 (PRUN) [DNA extraction number 2265].

Italy • 2♂ 2♀; Lombardia, Magenta; 45.43553, 8.831499; 10.05.2019; leg. P. Biella (MIB) [unique identifiers MIB:ZPL:08811; MIB:ZPL:08812; MIB:ZPL:08813; MIB:ZPL:08814] • ♀; Gargano, San Giovanni; 41.717778, 15.724722; 24.v.2011; leg. S. Gerber, I. Mercerat; unique identifier GBIFCH00132003 (PRUN) [DNA extraction number 2375] • ♀; Gargano, San Giovanni; 41.673056, 15.726111; 24.v.2011; leg. S. Gerber, I. Mercerat; unique identifier GBIFCH00132004 (PRUN) [DNA extraction number 2377] • ♀; Levanto; 31.v–5.vi.1999; leg. M. Herrmann (MHC) [DNA extraction number 2371] • ♂; Levanto; 31.v–5.vi.1999; leg. M. Herrmann (MHC) [DNA extraction number 2376].

Spain: ♂; Segovia, Madrona, 500 m NE, Arroyo del Hocino; 40.9006°N, -4.1559°E; 15.5.2021; leg. T.J. Wood (TJWC).

Switzerland • ♀ Mendrisio TI [Ticino], Meride, 603 m; 717163/83448 [Swiss coordinates; 45.8927°N, 8.9481°E]; 8.v.2020; leg. L. Giollo; unique identifier: GBIFCH00124927 (MSNL) [DNA extraction number 2079].

Distribution. Peloponnese (Greece), southern and northern Italy, southern Switzerland (Tessin), western Germany (Hessen and Rheinland-Pfalz), southern and central France, northeast to Dijon and northwest to Orléans, and Segovia Province, Spain (Fig. 55).

Pollen preferences. Unknown.

Phenology. Presumably univoltine with one generation from April until mid-June.

Diagnosis. Female. Females of *Andrena ovata* are characterised by the pale, grey vestiture on scutum and head (Figs 62, 63), the narrow, snow-white hairbands on the metasomal terga (Figs 15, 25), and the brownish-grey to dark brown terminal fringe (Fig. 15). The punctation is also very distinctive: the clypeal punctation is shallow, with indistinct punctures on the strongly shagreened clypeal disc (Fig. 64). On the scutum, the punctures are equally shallow and comparatively indistinct (Fig. 63); a similar condition is sometimes observed in *A. wilkella*, but not in *A. afzeliella* or *A. ovatula*. T1 and the base of T2 are nearly impunctate, with only a few indistinct punctures that are hardly visible in the strong shagreening (Fig. 25). No other species has such a combination of characters: the tergal sculpture is as in *A. russula*, and unlike any other species of *Taeniandrena*, but *A. ovata* can easily be separated from *A. russula* by the much paler vestiture, the narrow tergal hair bands and the darker terminal fringe. *Andrena afzeliella* and *A. ovatula* both have the tergal discs much more distinctly punctate and shinier (Figs 19, 20), much coarser clypeal and scutal punctation, and thicker tergal hair bands. *Andrena wilkella* has the terga distinctly punctate, especially T1 and T2, including the margin of T2 (Fig. 28); another useful difference between *A. wilkella* and *A. ovata* is the colour of the scutal hairs (yellowish brown in A. wilkella, grey-brown in A. ovata) and of the fringe of hairs on the propodeum (yellowish brown in *A. wilkella*

and whitish-grey in *A. ovata*). *Andrena gelriae* and *A. intermedia* have the terminal fringe orange (Figs 13, 14) and thicker tergal hairbands (Figs 23, 24). All these species have brown vestiture on the scutum, which differs from the grey vestiture of *A. ovata*.

Females of *Andrena ovata* are superficially highly similar to those of *A. poupillieri incana*, restricted to the Balearic Islands. Both species have light vestiture, snow white tergal hair bands and a comparatively dark terminal fringe. *Andrena poupillieri incana* has thicker tergal hair bands, slightly coarser punctation on the scutum and denser clypeal punctation; in addition, the scopa is partly dark dorsally near the basitibial plate, while it is entirely yellowish white in *A. ovata*.

Male. The males of *A. ovata* are most similar to those of *A. wilkella*, with which they share the short third antennal segment (A3 = 0.6–0.7× A4; Figs 41, 44) and the genitalic structure (Figs 51 and 54), namely a narrow valve and comparatively elongate gonostyli. A particularly distinctive feature of the male of *A. ovata* is the dense, snow white vestiture on the clypeus, forming a dense fringe of hairs through which the cuticula of the apical part of the clypeus is hardly visible (Figs 65, 66). Such a character is absent even in fresh males of *A. wilkella*. Overall, the vestiture is nearly entirely snow-white (greyish brown on the scutum), lighter than in *A. wilkella*, which has yellowish grey vestiture in fresh specimens. In *A. ovata*, the tergal discs are particularly matt with indistinct punctures (Figs 67, 68), a character that differentiates the males of *A. ovata* from those of *A. wilkella* (Fig. 69), *A. gelriae* (Fig. 70) and *A. vocifera* (Fig. 71), all three of which have a short A3. Compared to *A. wilkella*, the males of *A. ovata* have the declivous, anterior part of T1 nearly impunctate and the margins of T2–T4 with only very weak punctures (Figs 67, 68); the tergal punctures (e.g., on the disc of T2) are finer and less conspicuous. Compared to *A. gelriae*, the males of *A. ovata* have the hind tibia and metatarsus dark (at least metatarsus orange in *A. gelriae*). *Andrena poupillieri incana* has genitalia similar to *A. ovatula*, with a broader valve, and A3 subequal to A4.

Note. We initially treated this taxon as an undescribed species, until its presence in Hessen and Rheinland-Pfalz in Germany was brought to our attention. We thus examined the type material of the taxa described by Schenck and found one male syntype (Fig. 65) of this taxon bearing the label "*A. ovata*", in perfect agreement with Schenck's original description. Although it is unfortunate that this name is highly similar to *A. ovatula*, we are confident that this specimen is the only existing syntype of *A. ovata*.

Andrena ovata belongs to a group of species characterised in the female by nearly entirely greyish white vestiture and weakly punctate terga. This group includes *A. poupillieri incana*, known only from the Balearic Islands, as well as *A. poupillieri* from North Africa (see note regarding this taxon under *A. ovatula*). No genetic data was available from *A. poupillieri incana*. The status of this subspecies remains unclear, but the male is sculpturally different from that of *A. ovata*: the genitalia of *A. poupillieri incana* are similar to those of *A. ovatula*, and A3 is subequal to A4, unlike the condition in *A. ovata*.

Lastly, it is probable that the females of "*A. poupillieri*" mentioned by Michez et al. (2004) in the Pyrenees belong to *A. ovata*.

***Andrena ovatula* (Kirby, 1802)**
Figs 10, 20, 30, 32, 34, 36, 46

Melitta ovatula Kirby, 1802: 149, ♂ [indicated as female], "Barhamiae" [Barham, Suffolk, UK]. See note below for information on the type material.

Material examined. Type material: Only three males are preserved in the Kirby collection (NHML). These males are probably syntypes, even if the original description only mentions the female (see Perkins 1918 and note above, under *Andrena afzeliella*). Both *A. ovatula* sensu Stöckhert (1930) and *A. afzeliella* occur in the United Kingdom near the type locality of *A. ovatula* (Fig. 7). We are not confident in the identification of these three males (see above under *A. afzeliella*). For this reason, we submitted a request to the International Commission on Zoological Nomenclature (case 3878) to set aside the existing male syntypes, allowing for the designation of a neotype for *A. ovatula*. The female specimen proposed to be the neotype has been collected in Surrey, some 130 km southwest of the type locality of *A. ovatula*. It has been barcoded (specimen with number TJW0562 in Fig. 2) and agrees both morphologically and genetically with the species referred to as *A. ovatula* by the few authors who have separated *A. albofasciata* and *A. ovatula* (Stöckhert 1930; Niemelä 1949; van der Smissen 2002, 2010). We are not aware of other available names for this species (see note above with respect to the missing type material of *A. barbata* and *A. picipes*).

Other material: Barcoded material includes specimens from Belgium, France, Germany, Italy, Portugal, Spain, the United Kingdom; in addition, sequences from Ireland are available on BOLD. Examined material additionally includes specimens from Andorra; see full list of examined specimens in Suppl. material 2: Table S2.

Distribution. Widespread in north-western Europe (France, England, Belgium, the Netherlands, Germany; Fig. 7); presence in Scandinavia unclear: Niemelä (1949: 119) mentions that this species has not been reported from Finland, but that he has examined specimens from southern Sweden in the collection D. Gaunitz (possibly in NHRS). Records from the Iberian Peninsula have been presented by Wood et al. (2021). The eastern limit of its distribution needs to be further examined. We also examined specimens from the Atlas Mountains, Morocco, which are morphologically highly similar to European populations; the identity of these specimens should be confirmed using DNA barcodes (TJ Wood, in prep.). For this reason, no records are presented from north-western Africa until more extensive barcoding has been conducted.

Pollen preferences. Analysis of 30 pollen loads from 20 localities strongly suggest oligolecty on Fabaceae, with 99.6% of pollen collected from this family (TJW, unpublished data). This taxon is particularly associated with members of the tribe Genisteae in Atlantic-influenced environments across Western Europe, such as *Cytisus*, *Genista*, and *Ulex*. This association with Fabaceae shrubs may explain the particular distribution of *A. ovatula*, which appears to be more frequent in coastal areas than in the central parts of Europe.

Phenology. Bivoltine, first generation in Northern Europe from the end of March until the end of May, second generation from early June until early September, approximately a month earlier than *A. afzeliella* (Fig. 8; see under *A. afzeliella*).

Note. The identity of *Andrena poupillieri*, a species that has been treated as a subspecies of *A. ovatula*, remains unclear because the Dours collection, presumably including all syntypes of this taxon, has been destroyed. Warncke (1967: 176) treated *A. poupillieri* as a subspecies of *A. ovatula sensu lato* restricted to Northern Africa, southern Spain and Crete according to the map presented by Gusenleitner and Schwarz (2002: 1143). As far as we know, he did not designate a neotype for *A. poupillieri*. In 1975, he described *A. poupillieri incana* Warncke, 1975 from the Balearic Islands (Spain), suggesting that he then considered *A. poupillieri* as a valid species. The identity of *A. poupillieri* will remain unclear until a neotype is designated. We refrain from doing so until the diversity of the northern African species of *Taeniandrena* has been examined more carefully. Some specimens identified as *A. poupillieri* in the Benoist and Warncke collections have a dark terminal fringe, contradicting Dours' original description ["cinquième segment et anus garnis de poils cendré roux" (T5 and T6 furnished with ashen-reddish hairs)]; specimens with dark terminal fringe, including the type of *A. lecerfi* Benoist, 1961, are possibly conspecific with *A. ovatula sensu stricto*, however Dours' original concept of *A. poupillieri* may be a distinct species. We present barcodes for three specimens possibly corresponding to Dours' original description, one with light terminal fringe (TJW024) and two with dark terminal fringe (2331 and 2333). Two of these three specimens form a clade, the third was only distantly related; neither was closely related to *A. ovatula* or to *A. afzeliella*. Future barcoding efforts for the *Andrena* fauna of north-western Africa are needed before the identity of *A. poupillieri* is settled through the designation of a neotype. Once this is achieved, the status of *A. poupillieri incana* should be examined; this taxon may be conspecific with *A. poupillieri*, or may represent another narrowly distributed species of *Taeniandrena*.

Diagnosis. See under *Andrena afzeliella* (Table 1), and identification key below

Andrena russula Lepeletier, 1841

Figs 5, 6, 16, 26, 42, 52

Andrena russula Lepeletier, 1841: 251, ♀, "Oran" [Algeria]. Holotype ♀ (MNHN).
Andrena similis Smith, 1849: lx, ♂, "Bristol" [UK], syn. nov. Syntype or holotype ♂ (OUMNH).
Andrena ocreata cyprisina Warncke, 1975c: 78, ♀,♂, "Limassol" [Cyprus], syn. nov. Holotype ♀ (OLML).
Andrena similis caraimica Osytshnjuk, 1994: 33, ♀,♂ [Crimea], syn. nov. Holotype (SIZK).

Material examined. Type material: ***Holotype*** of *A. russula* (MNHN, Figs 5, 6). ***Holotype*** of *A. o. cyprisina* ♀ Cyprus • Limassol (OLML).

Other material (Suppl. material 2: Table S2): Algeria • ♀; S. Kabylia, Ait Hassem; [36.583, 4.197]; 16–17.6.1971; leg. A. Hoffer, J. Hordk (OLML) [DNA extraction number 1533].

Crimea • 23♂ 28♀; Karadagh [Kara Dag], Vodianja balka; 44°56'22"N, 35°12'44"E; 21.4.2003; leg. Y. Budaschkin (OLML) • ♂ 13♀; Kap Kasantyp steppe [Kazantyp]; 45°27'47"N, 35°50'40"E; 1.5.2003; leg. Y. Budaschkin (OLML)

Iran • ♀; Lorestan province, Dorud Lanjaban env, 960 m; 33.419°N, 48.986°E; 10.5.2016; leg. M. Kafka (TJWC) [DNA extraction number TJW038].

Italy • ♀; Marche, M. Sibillini, M. Vettore; 42.8011°N, 13.2711°E; 30.6.2011; leg. Trunz, Litman, Praz; unique identifier: GBIFCH00117708 (PRUN) [DNA extraction number 1425] • ♀; Umbria, Castel Viscardo, 10 km NW Orvieto; 42.7574°N, 12.0023°E; 28.5.1991; leg. J. Gusenleitner (OLML) • ♀; Umbria, Panicale, S of L. Trasimeno; 43.0306°N, 12.0969°E; 9.5.2011; leg. D.W. Baldock (TJWC) • ♂; VA, Luino; 46.0007°N, 8.7463°E; 2.5.1983; leg. H. Teunissen (RMNH).

Libya • ♀; Tripolitaine, Djebel Ghariane; 4.1899; leg. Alluaud (OLML) • ♀; Tripolitania, Leptis Magna; 15.1.1955; leg. K. M. Guichard (OLML) • ♀; Tripolitania, Sidi Mesri; 3.1940; leg. G. M. Martelli (OLML) • ♂; Tripolitania, Tripoli; 4.2.1954; leg. K. M. Guichard (OLML) • 2♂; Tripolitania, Tripoli; 30.1.1955; leg. K. M. Guichard (OLML).

Tunisia • ♀; Tunis; 189? (OLML).

Distribution. Widely distributed throughout Europe, including the Iberian Peninsula, France, Central Italy, Bulgaria, Cyprus, Crimea, northern Africa from Morocco to Libya, Turkey, the Caucasus, the Levant (Israel, Syria, Lebanon, Jordan) and Iran.

Pollen preferences. Oligolectic on Fabaceae (Westrich 1989, as *A. similis*).

Phenology. Univoltine, in Switzerland from the end of April to early June at low elevations, slightly later at high elevations.

Note. This widespread species has so far mostly been referred to as *A. similis*. A first change to this view was advocated by Warncke (1967: 174), who stated that *A. russula* was the "form" with red-coloured vestiture of *A. similis* in Northern Africa, and that the European form of *A. similis* should thus be named *A. russula* ssp. *similis*. In 1970, he resurrected the name *Andrena ocreata* (Christ, 1791) for this taxon based on his interpretation of the vague original description of *Apis ocreata* (Warncke 1970). While he invokes article 23b of the 1958's edition of the International Code of Zoological Nomenclature to uphold numerous junior synonyms in the same article, he does not do so for *A. similis*, possibly because he considered *Hylaeus similis* Fabricius, 1793 to be a synonym of *Andrena barbilabris* (Kirby, 1802), making *Andrena similis* Smith a junior secondary homonym. The then prevailing version of the code did not allow for a reversal of precedence in the case of secondary homonymy, which possibly explains Warncke's decision to resurrect the name *ocreata* for this taxon. The reason why he does not mention *A. russula* in the 1970 article is unclear. He later designated a neotype for *Apis ocreata*, selecting a female of "*Andrena similis* Smith" collected in Erlangen,

Germany (Warncke 1986). His interpretation of *A. ocreata* has not been followed (e.g., Westrich 1989; Gusenleitner and Schwarz 2002), and the name *A. similis* has mostly been used until now for this taxon. We consider *Hylaeus similis* Fabricius and *Apis ocreata* Christ to be *nomina dubia*.

This species is widely distributed in the Western Palearctic; geographic variation in structural morphology is minimal, and variation that does exist such as in the strength of tergal punctation follows no clear pattern or gradient. In north-western Africa, in populations referred to as "*A. ocreata* ssp. *russula*" by Warncke (see Gusenleitner and Schwarz 2002: 1175), the vestiture of the females is bright red orange, as opposed to brown orange in Europe. This pattern of increased orange intensity in North African populations can clearly be seen in unrelated taxa such as *A. lepida* Schenck, 1861 and *A. numida* Lepeletier, 1841 (possibly conspecific with the European taxon *A. hypopolia* Schmiedeknecht, 1884; Wood, unpublished data). In addition, the integument of the hind legs of the females of north-western African populations of *A. russula*, in particular of the hind femora, is sometimes entirely orange, although not consistently so. Sculpturally, *Andrena "russula"* (or the north-western African populations) and *Andrena "similis"* (or the European populations) are morphologically very close and no character allows for an unambiguous separation; in males of "*A. russula*", the antennal segment 3 is slightly shorter than A4, while in "*A. similis*", A3 is as long as or longer than A4 (Fig. 42). The length of A3 and A4 is highly variable throughout the range of "*A. similis*" and we consider this criterion as variable within this taxon. We were able to obtain a short COI sequence from one specimen of *Andrena "russula"* from northern Algeria, likely corresponding to the type locality of *Andrena russula* (specimen 1533 in Fig. 2). This sequence clusters within a large clade that includes numerous specimens of *A. similis* from Europe, Morocco, Cyprus and Israel. We consequently place *A. similis* as a synonym of *A. russula* and consider one largely distributed taxon. As for *A. afzeliella* and *A. albofasciata*, a reversal of precedence (article 23.9 of the Code of Zoological Nomenclature) to maintain the prevailing usage of *A. similis* is not justified since *A. russula* has been used as a valid name after 1899 (e.g., Warncke 1967; Tengö and Bergström 1975; Gusenleitner and Schwarz 2002), therefore rejecting the first condition of article 23.9 of the code.

Diagnosis. See Schmid-Egger and Scheuchl (1997), Amiet et al. (2010) (both as *Andrena similis*) and the identification key below.

***Andrena vocifera* Warncke, 1975, stat. nov.**
Figs 17, 27, 43, 53, 71

Andrena gelriae vocifera Warncke, 1975a: 136, ♂ ♀, "Bordeaux[sic]/Drôme" [likely Bourdeaux, a municipality in the Drôme Departement, France]. Holotype ♂ (OLML).

Material examined. Type material: *Holotype* ♂ (OLML).

Other material (Suppl. material 2: Table S2): France • ♂; Daglan, la Bégonie; 44.7351°N, 1.1884°E; 15.6.2011; leg. Christophe Philippe (DGC) • ♀; Arjuzanx, Réserve Nationale Nord; 44.0512°N, -0.8297°E; 11.5.2012; leg. Michel Lague (DGC) • ♀; Sore, le Plata tente Malaise; 44.3407°N, -0.6146°E; 22.5.2008; leg. D. Genoud (DGC) • ♀; Sore, le Plata tente Malaise; 44.3407°N, -0.6146°E; 25.6.2008; leg. D. Genoud (DGC) • 2♂; Montayral, aérodrome; 44.4612°N, 1.0154°E; 14.6.2009; leg. D. Genoud (DGC) • ♂; Villeneuve-sur-Lot, Teyssonat; 44.3832°N, 0.7500°E; 28.6.2008; leg. Jean-Philippe Tamisier (DGC) • ♀; La Jonte [Gorge de la]; 44.1908°N, 3.2321°E; 28.5.2019; leg. D. Bénon; unique identifier: GBIFCH00117717 (PRUN) [DNA extraction number 2166] • ♂; La Jonte [Gorge de la]; 44.1908°N, 3.2321°E; 28.5.2019; leg. D. Bénon; unique identifier: GBIFCH00117718 (PRUN) [DNA extraction number 1518].

Distribution. So far only known from southern France between the Drôme and the Landes departments (Fig. 55).

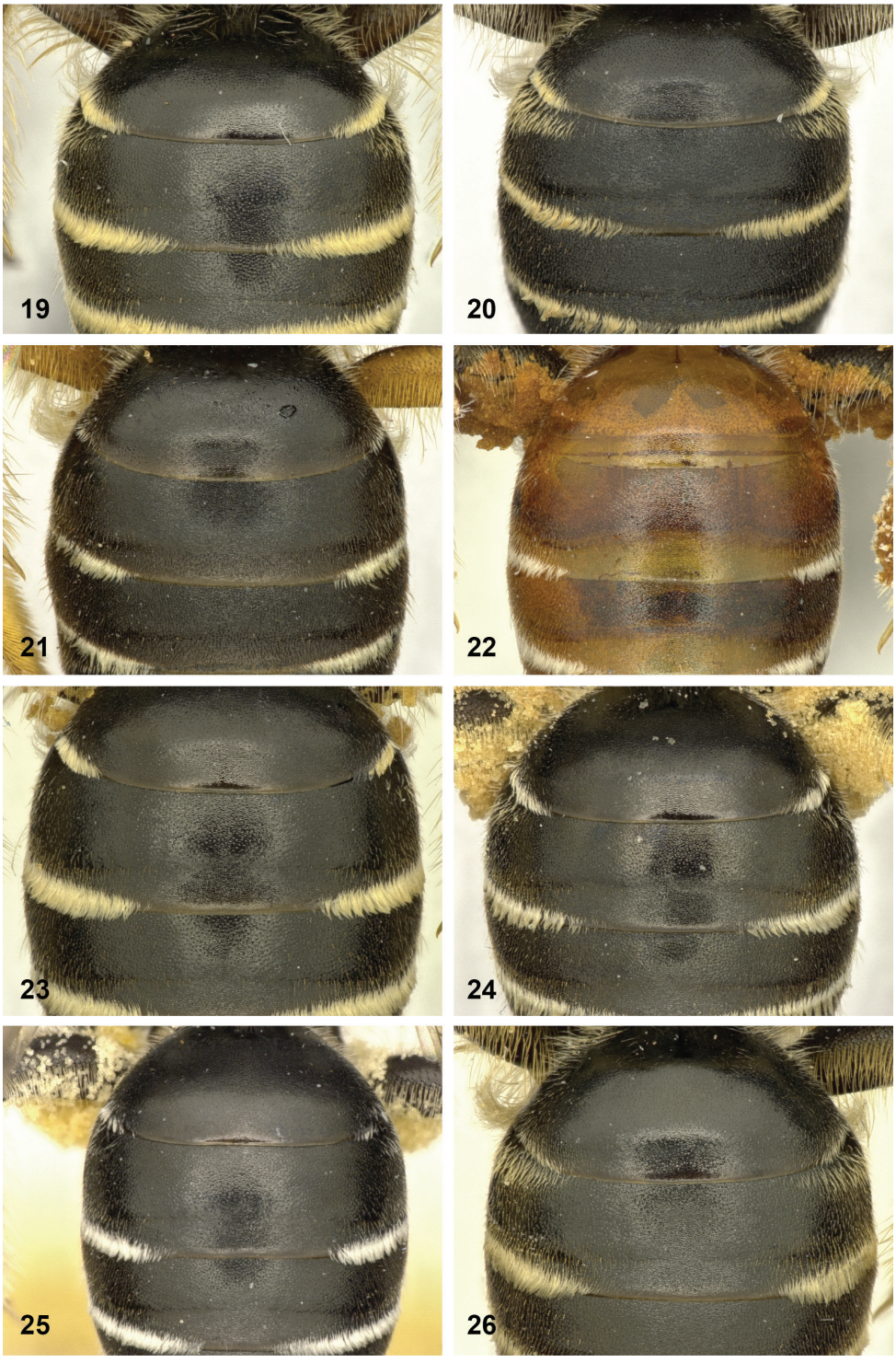
Pollen preferences. Unknown.

Phenology. Presumably univoltine with one generation from the end of May until the end of June.

Note. The map presented for *Andrena gelriae s. l.* in Gusenleitner and Schwarz (2002: 1050), reflecting Warncke's concept of this group of species, gives the impression that *A. gelriae sensu stricto* is absent from southern France. This statement is contradicted by our report of two typical males of *A. gelriae sensu stricto* in Southern France approximately 100 km south of some records of *A. vocifera* (Fig. 55). This range overlap, in addition to the strong morphological differences between *A. gelriae* and *A. vocifera*, as well as the distinct DNA barcodes of both taxa, makes it clear that *A. vocifera* represents a separate species. Warncke (1975a)'s indication that the female of *A. gelriae vocifera* does not show any difference compared to that of *A. gelriae* suggests that the female specimen that he examined was not conspecific with the male holotype.

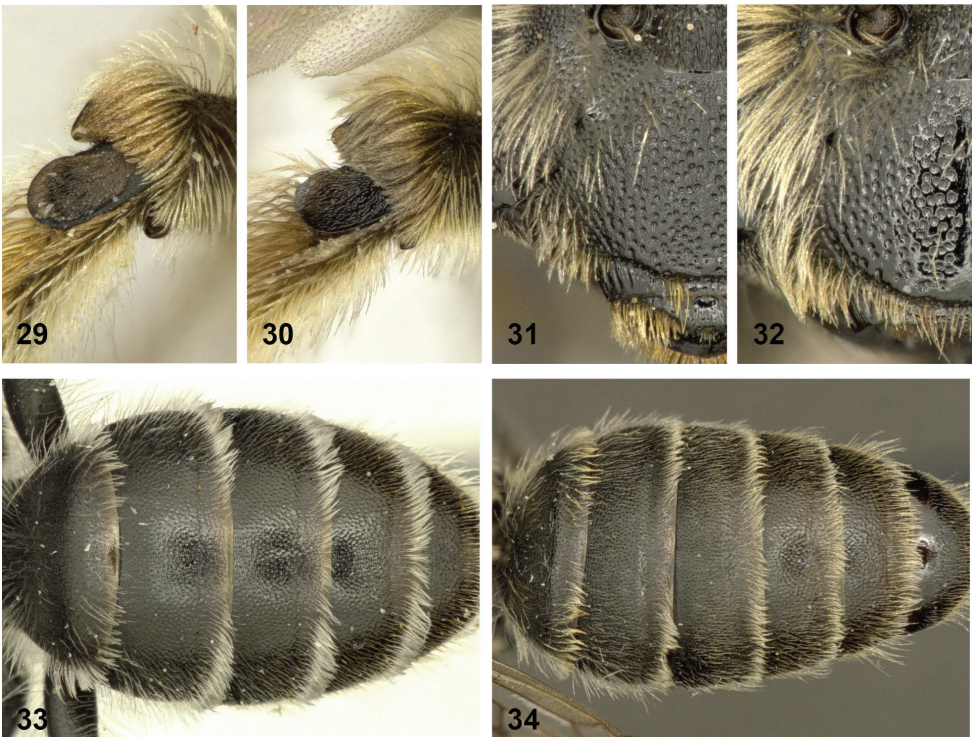
Diagnosis. Female. The female of *A. vocifera* is unique among all European *Taniandrena* for the dense and coarse punctation of the terga, and for the shiny, hardly shagreened underlying sculpture (Figs 17, 27). It is approximately 11 mm long, the vestiture is orange on the vertex, the upper parts of the face, the scutum and the scutellum, and yellowish white on the clypeus and the sides of the mesosoma. The flocculus is whitish, the scopa yellowish orange and the terminal fringe orange (Fig. 17), as in *A. gelriae*. There is a small, white hairband laterally on T1, and a dense white hairband on T2–T4, the hairband is interrupted medially on T2 and only slightly narrowed medially on T3 (Figs 17, 27). The integument is black, except parts of the tarsi of the mid legs, the hind tibiae and tarsi, which are orange.

Male. This species can be identified by the genital structure, with a comparatively broad valve (width = 1.5 × diameter of lateral ocellus) with long, parallel-sided base (Fig. 53); the internal margins of the gonocoxae are not diverging, and the gonostyli are more elongate than in *A. afzeliella*. The antennae are as in *A. gelriae*, with A3 distinctly shorter than A4 (Fig. 43). The tergal discs are shiny and coarsely punctate, their



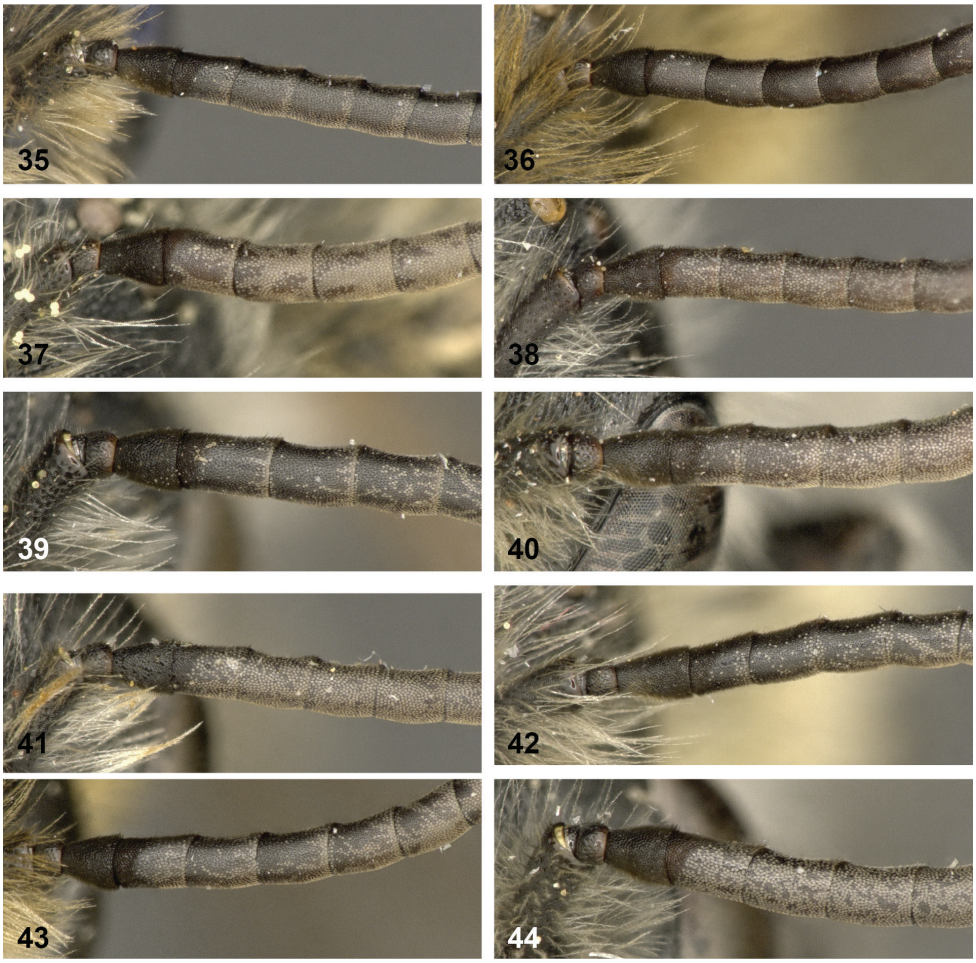
Figures 19–26. Metasomal terga 1–3 of females of *Taeniandrena* **19** *Andrena afzeliella* **20** *A. ovatula* **21** *A. antonellae* sp. nov. **22** *A. croceiventris* **23** *A. gelriae* **24** *A. intermedia* **25** *A. ovata* **26** *A. russula*.

Figures 27, 28. Metasomal terga 1–3 of females of *Taeniandrena* **27** *Andrena vocifera* **28** *A. wilkella*.



Figures 29–34. 29, 30 apical fringe of hairs on femur, covering the base of basitibial plate in females **29** *Andrena afzeliella* **30** *A. ovatula* **31, 32** Female clypeus **31** *A. afzeliella* **32** *A. ovatula* **33, 34** male metasoma **33** *A. afzeliella* **34** *A. ovatula*.

basis and the tergal margin strongly impressed, so that the disc is convex (Fig. 71); in *A. gelriae*, the sculpture of the tergal discs is less shiny, more finely punctate, and the basis is not strongly impressed (Fig. 70). In *A. vocifera*, the entire vestiture is yellowish brown, the integument is dark except the tarsi of the hind legs.



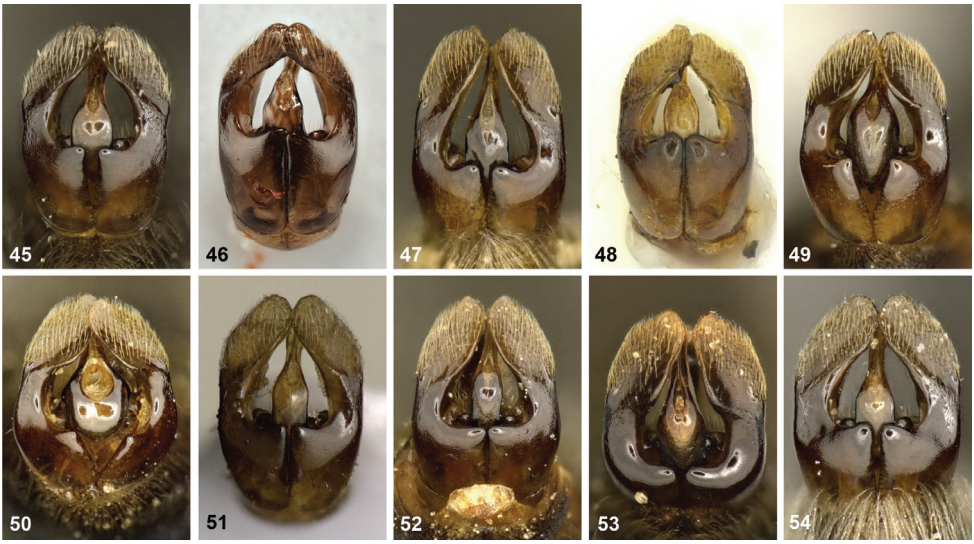
Figures 35–44. Male antennae **35** *Andrena afzeliella* **36** *A. ovatula* **37** *A. antonellae* sp. nov. **38** *A. croceiventris* **39** *A. gelriae* **40** *A. intermedia* **41** *A. ovata* **42** *A. russula* **43** *A. vocifera* **44** *A. wilkella*.

Andrena wilkella (Kirby, 1802)

Figs 18, 28, 44, 54, 69

Melitta wilkella Kirby, 1802: 145, ♀, "prope Londinium" [near London, England]. Lectotype ♀ (NHML), by present designation (see below).

Material examined. Type material: ***Lectotype*** ♀ of *Melitta wilkella* Kirby, 1802, by present designation, a female in good condition (NHML). This female specimen is labelled as follows: 1. "6339" [handwritten on blue paper disc, NHML accession number 1863–39]; 2. "Syntype" [printed on white paper disc]; 3. "B.M.Type/ Hym/ 17a 2921" [handwritten]; 4. "Syntype ♀ *Melitta wilkella* Kirby det. D. Notton 1995"; 5. "Lectotype" [printed on white paper disc]; 6. "Lectotype ♀ *Andrena wilkella* des. Wood and Monks, 2022" [handwritten]; 7. "NHMUK 014030682".



Figures 45–54. Male genitalia **45** *Andrena afzeliella* **46** *A. ovatula* **47** *A. antonellae* sp. nov. **48** *A. croceiventris* **49** *A. gelriae* **50** *A. intermedia* **51** *A. ovata* **52** *A. russula* **53** *A. vocifera* **54** *A. wilkella*.

Other material: numerous specimens, only some of which are listed in Suppl. material 2: Table S2.

Distribution. From northern Iberia (absent from Morocco, see Wood et al. 2021) across Europe (including Corsica and southern Italy; see Suppl. material 2: Table S2) to Turkey, the Caucasus, and Russia. Probably absent from Cyprus, though this requires confirmation.

Pollen preferences. Chambers (1968) indicated possible polylecty in *Andrena wilkella*, though quantitative reanalysis of his data still showed 92.4% of collected pollen came from Fabaceae (Wood and Roberts 2017). Other analyses clearly show that *A. wilkella* is oligolectic on Fabaceae (Westrich 1989; Wood and Roberts 2017), and since Chambers was not aware of the cryptic and weakly polylectic *A. afzeliella* in Britain, some of the '*A. wilkella*' samples he analysed may have been from this species.

Phenology. Considered to be univoltine (Westrich 1989; Amiet et al. 2010), although the flight period extends from the end of April until the end of August in England (Bees, Wasps & Ants recording society 2022) or in Switzerland, suggesting a possible partial second generation.

Note. In our genetic analysis, *A. wilkella* forms three clades separated by average distances comprised between 1.49 and 3.04% (Fig. 2). One clade included specimens from Germany, another clade specimens from Ireland, the United Kingdom, Finland, Norway and Switzerland, and the third clade specimens from Italy and from Corsica. The specimens from the first clade have not been examined; those from Italy and Corsica are morphologically similar to *A. wilkella*, but the tergal punctation is less distinct, breaking an otherwise good diagnostic trait of *A. wilkella*. The identification of such specimens is challenging and relies on the narrower tergal hairbands (see also Table 2 for the identification of the specimens from Corsica). Similar specimens with

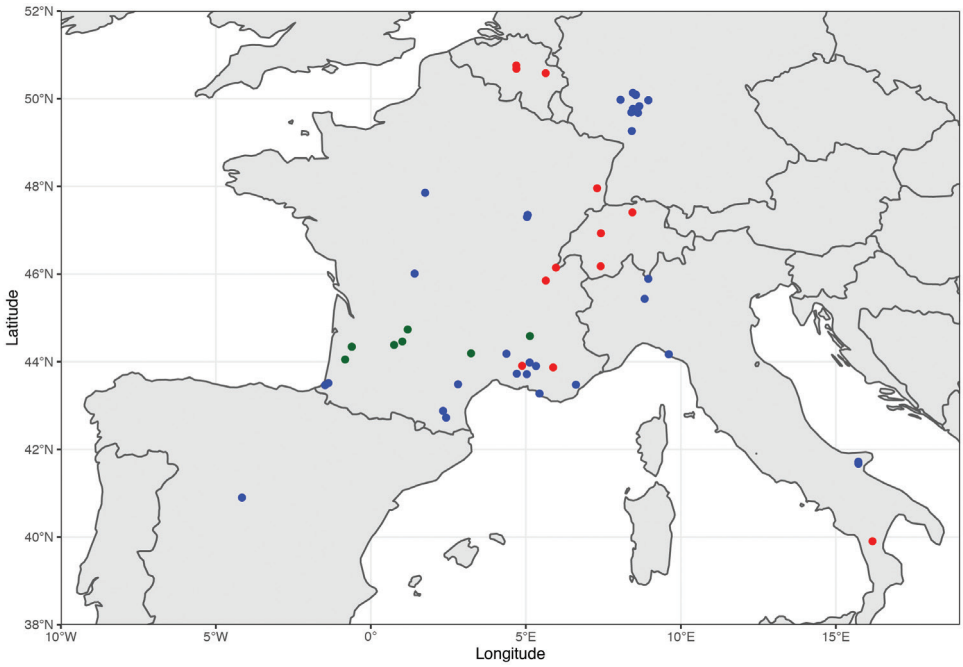


Figure 55. Distribution map of *Andrena gelriae* (red dots), *A. ovata* (blue dots) and *A. vocifera* (green dots).

weak tergal punctation are also known from Eastern Europe. Future research is needed to determine whether these slight genetic and morphological differences point to the presence of additional cryptic diversity in *A. wilkella*.

Diagnosis. See Schmid-Egger and Scheuchl (1997), Amiet et al. (2010) and the identification key below.

Identification key for the species of *Taeniandrena* in France (excluding Corsica), Germany, Switzerland and Italy (excluding Sardinia); *A. lathyri* is excluded.

Unique characters in bold, non-unique characters in regular font; characters given in order of importance.

Females

1 **Surface of tergal discs shiny with hardly any shagreenation (Fig. 27). Punctation of tergal discs comparatively strong and dense, punctures clearly visible (Fig. 27)**, including on marginal areas. Scutal vestiture comparatively short, brown-orange. Apical hairband of T3 continuous. Terminal fringe orange (Fig. 17). Body length approximately 11 mm ..... ***Andrena vocifera***

– Surface of tergal discs shagreened. Punctation of tergal discs weaker and less dense, tergal margins clearly punctate only in *A. wilkella* (Fig. 28). Scutal

vestiture, apical hairband of T3, colour of terminal fringe and body length variable **2**

2 **Terga comparatively strongly and densely punctate, punctures comparatively clearly visible in shagreenation (Fig. 28), in particular on declivous, anterior part of T1, where punctation is dense and clearly visible (interspaces = 1 puncture diameter), on the base of T2 (interspaces commonly less then 1 puncture diameter) and on apical margin of T2 (interspaces 2–3 puncture diameters basally, becoming small and dense apically)** (see note above under *A. wilkella* regarding variation in the punctation of Italian specimens). Apical tergal hairbands interrupted on T2–3, comparatively narrow, maximal length on T3 0.75 × length of tergal margin medially (Figs 18, 28). Terminal fringe mostly orange (Fig. 18). Body length 10–12 mm ..... ***Andrena wilkella***

– Terga less strongly and densely punctate, punctures less visible and often nearly imperceptible in shagreenation, especially on anterior, declivous part of T1 (interspaces commonly 2–3 puncture diameters) and on apical margin of T2. Width of apical tergal hairbands variable, usually larger (except in *A. ovata*). Colour of terminal fringe variable **3**

3 **Vestiture on scutum and scutellum bright orange, particularly dense, especially on lateral parts of scutellum.** Terga with shallow, nearly indiscernible punctures (Fig. 26). Integument of hind tibia and tarsi orange. Terminal fringe orange. Tergal fringes of hairs long, but interrupted medially on T4 (Fig. 16)..... ***Andrena russula***

– Vestiture on scutum yellowish brown, brown-orange or grey, less dense. Tergal punctation, colour of integument of hind tibia and tarsi, colour of terminal fringe and tergal fringes variable **4**

4 **Integument of T1–T4 partly red (Figs 12, 22)**, rarely brown, but then margin or parts of tergal discs reddish brown. T1 nearly impunctate (Fig. 22). Disc of T2 very sparsely (interspaces over 3 puncture diameters) and faintly punctate, punctures hardly discernible (Fig. 22). Apical hairbands of T2–T4 very narrow, white (Fig. 22). Scutellum weakly shagreened even centrally. Body length 8–9 mm. ..... ***Andrena croceiventris***

– Integument of T1–T4 dark brown. Punctation of terga variable, but if disc of T1 nearly impunctate and disc of T2 very sparsely punctate, then body size > 10 mm. Width of tergal fringes variable. Scutellum usually partly shiny. Body length variable **5**

5 **Terga strongly shagreened, punctures little visible, disc of T1 and margins of T2–T4 appearing impunctate (Fig. 25). Scutal punctures comparatively shallow, little visible (Fig. 63)**. Clypeus shagreened, punctation sparse and shallow (Fig. 64). Tergal fasciae narrow, snow white, interrupted on T3 (Figs 15, 25). Scutal vestiture predominantly greyish white in fresh specimens (Fig. 62). Terminal fringe brownish grey (Fig. 15). Body length 10–12 mm..... ***Andrena ovata***

– Terga more shiny and distinctly punctate. Scutal punctures deep and clearly visible. Sculpture of clypeus variable. Colour of tergal fasciae variable, often brownish in fresh specimens, wider, interrupted or not on T3. Scutal vestiture

usually darker in fresh specimens. Colour of terminal fringe variable. Body length variable **6**

6 Apical hairbands of T3 not interrupted medially in fresh specimens (Figs 19, 20). Terminal fringe dark brown, grey-white to yellowish white, generally not uniformly orange (Figs 9, 10). Slightly smaller, on average 8–10 mm **7**

– Apical hairbands of T3 interrupted medially even in fresh specimens (Figs 13, 14, 23, 24). Terminal fringe mostly uniformly orange (Figs 13, 14). Slightly larger, 9–12 mm **8**

7 Terminal fringe dark brown (Fig. 10). Hairs flanking basitibial plate of hind tibia dark brown (Fig. 30); dorsal part of tibial scopa usually with a few dark hairs (Fig. 30). Vestiture on vertex, scutum and scutellum grey-brown, scutum mostly with minute, dark hairs beneath longer vestiture. Apical tergal hairbands often yellowish. In direct comparison, clypeal punctation on average coarser, underlying sculpture shiny (Fig. 32). Slightly larger, body length 9–10 mm..... ***Andrena ovatula***

– Colour of terminal fringe variable (Figs 4, 9), but always lighter, from light grey-white to yellowish white or yellowish orange, rarely brown (Fig. 9), then always with orange hue. Hairs flanking basitibial plate of hind tibia golden or brown, then with orange hue (Fig. 29); tibial scopa without dark hairs dorsally. Vertex and scutal vestiture yellow-brown, apical tergal hairbands often white. Clypeal punctation on average shallower and sparser, underlying sculpture matt (Fig. 31). Slightly smaller, body length 8–10 mm..... ***Andrena afzeliella***

The following two species are particularly difficult to separate in the female sex.

8 Vestiture on scutum slightly longer, nearly twice as long as width of antennae; punctation on terga on average less dense and less visible (Fig. 24) .... ***Andrena intermedia***

– Vestiture on scutum shorter (as in *A. wilkella*). Punctation on terga on average denser, punctures more visible, approaching condition observed in *A. wilkella*, from which *A. gelriae* can be separated by the broader and more conspicuous apical tergal fringes (Fig. 23)..... ***Andrena gelriae***

Males

1 Tergal discs coarsely and sparsely punctate, **underlying surface nearly completely shiny with almost no shagreenation (Fig. 71). Terga impressed basally and apically, so that disc is convex (Fig. 71). Width of valve basally 1.5 × diameters of lateral ocellus (Fig. 53)**, intermediate between *A. gelriae* and *A. afzeliella*. Internal margins of gonocoxae parallel, not diverging (Fig. 53)..... ***Andrena vocifera***

– Tergal discs more finely punctate, underlying surface usually shagreened, especially when tergal punctation is coarse (e.g., in *A. wilkella* and *A. gelriae*;

Figs 69, 70). Terga not visibly impressed basally, disc evenly flattened. Width of valve and opening between internal margins of gonocoxae variable..... **2**

2 Valve basally broad, its maximal width approximately equal to 2 diameters of lateral ocellus (Figs 49, 50). Opening between internal margins of gonocoxae comparatively large, margins adjacent basally and abruptly divergent apically **3**

– Valve basally less broad, its width at most 1.5 × diameters of lateral ocellus (Figs 45–48, 51, 52, 54). Opening between internal margins of gonocoxae smaller, margin less strongly and abruptly divergent..... **4**

3 **Valve basally approximately as wide as maximal width of gonostylus (Fig. 50). Opening of valve very wide, wider than surface of median ocellus (Fig. 50)**. Antennal segment 3 0.8–1.0 × A4 (Fig. 40) ..... ***Andrena intermedia***

– Valve less wide than maximal width of gonostylus (Fig. 49). Opening of valve much smaller than surface of median ocellus (Fig. 49). A3 shorter, approximately 0.6 × A4 (Fig. 39)..... ***Andrena gelriae***

4 **Integument of terga partly orange brown, especially margins, pregradular area and lateral, declivous parts**. Tergal discs very faintly punctate, punctures little visible in shagreenation. Terga with comparatively narrow apical hairbands laterally, hairbands broadly interrupted on all terga. A3 0.7–0–8× as long as A4 (Fig. 38). Genitalia Fig. 48 ..... ***Andrena croceiventris***

– Integument of terga dark, at most with apical parts of margins light brown. Punctation of terga, apical hairbands and length of A3 variable **5**

5 **A3 short, approximately 0.6–0.7 × A4, the following segments approximately 1.7 times longer than wide (Figs 41, 44)**. T1 without apical hairband laterally, hairs erect, not hiding integument, sometimes forming a weak hairband, then hair band visibly less dense than those on the other terga (Figs 67–69). Apical hairbands on T2–T4 narrow, interrupted medially on T2 and T3 (Figs 67–69). Penis valve comparatively narrow basally, gonostylus comparatively long (Figs 51, 54)..... **6**

– A3 longer, 0.8–1.2 × A4, the following segments 1.5 times longer than wide (Figs 35, 36, 42). Hairbands usually present on T1 laterally, and either interrupted on T2–T3 but then broader, or continuous on T2–T3 (Figs. 33, 34). Shape of penis valve and gonostylus variable..... **7**

6 **Clypeus with dense, snow white vestiture, vestiture hiding underlying sculpture on apical parts of clypeus (Fig. 66)**. Entire body vestiture whitish grey (slightly darker only on scutum) (Fig. 65). Terga strongly shagreened, punctation fine, little visible (Figs 67, 68), anterior, declivous part and disc of T1 nearly impunctate. Margins of T2–T4 nearly impunctate or with only faint punctures (Figs 67, 68)..... ***Andrena ovata***

– Clypeus without particularly dense vestiture. Body vestiture yellowish grey in fresh specimens. Terga weakly shiny and distinctly punctate (Fig. 69), especially on anterior, declivous part and disc of T1. Margins of T2–T4 distinctly punctate (Fig. 69) ..... ***Andrena wilkella***

7 **Broad, parallel-sided basal part of penis valve long and narrow (Fig. 52)**. In central Europe (not always elsewhere), **A3 as long as or slightly longer than A4 (Fig. 42)**. Tergal punctures little visible in shagreenation. At least apical part of tibiae and tarsi of hind legs orange. Slightly larger, body length 10–12 mm..... ***Andrena russula***

– Parallel-sided part of penis valve shorter and broader (Figs 45, 46). A3 0.8.-1.0 × A4 (Figs 35, 36). Terga distinctly punctate (Figs 33, 34). Colour of integument of hind legs variable, tibiae usually dark. Body length 7–10 mm..... **8**

The following two species are difficult to separate in the male sex.

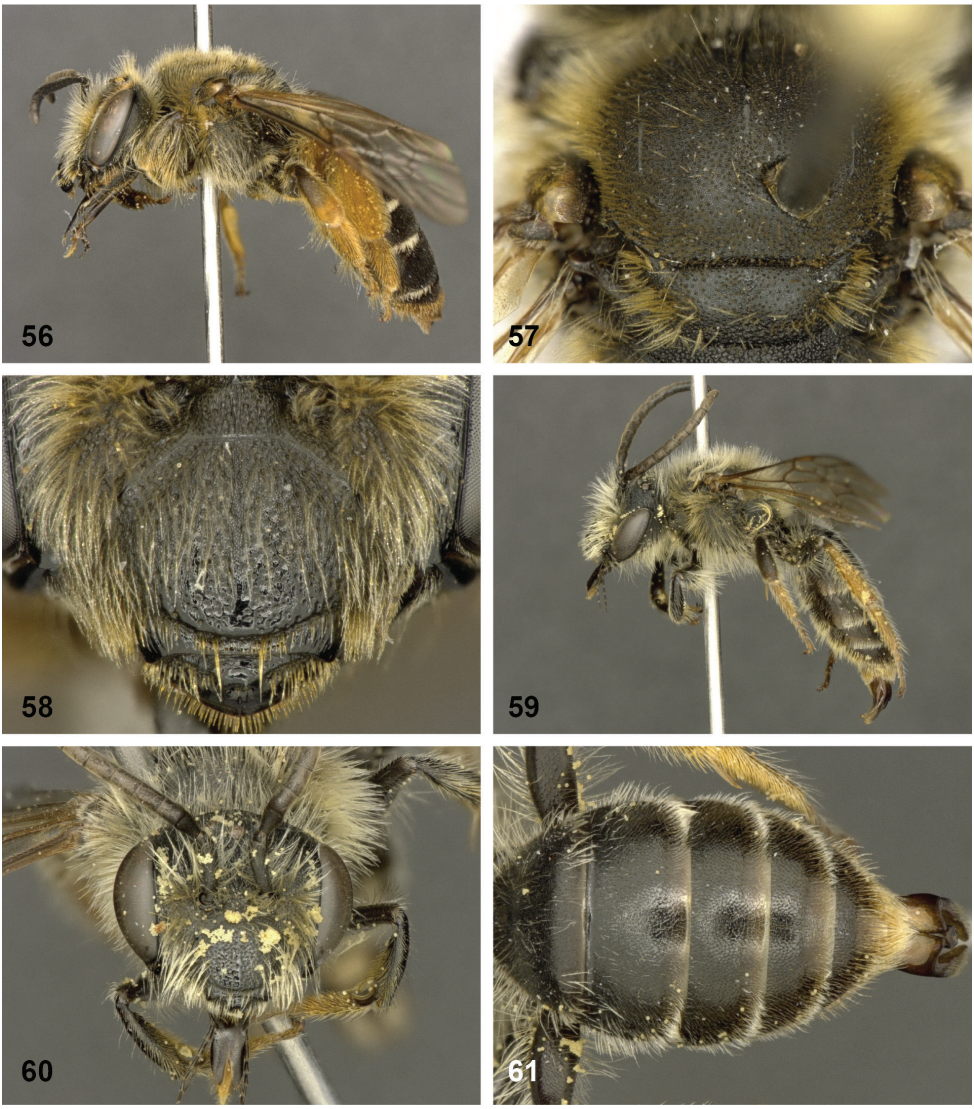
8 Terga more densely punctate, surface matt (Fig. 34). A3 slightly shorter than A4, approaching the condition observed in *A. wilkella* (Fig. 36). Genitalia comparatively more slender, gonostylus narrower, external margin weakly concave (Fig. 46). Internal margins of gonocoxae usually parallel apically (Fig. 46). Penis valve on average slightly narrower (Fig. 46). Body vestiture yellowish-brown in fresh specimens. Apical tergal fasciae narrower (Fig. 34)..... ***Andrena ovatula***

– Terga less densely punctate, surface weakly shiny (Fig. 33). A3 subequal to A4 (Fig. 35). Genitalia comparatively less elongate, gonostylus broad with external margin usually straight (Fig. 45). Internal margins of gonocoxae slightly divergent apically (Fig. 45). Penis valve slightly broader (Fig. 45). Body vestiture on average lighter even in fresh specimens. Apical tergal fasciae wider (Fig. 33)..... ***Andrena afzeliella***

Discussion

Solving the long controversy on the status of *Andrena ovatula* and *A. afzeliella*

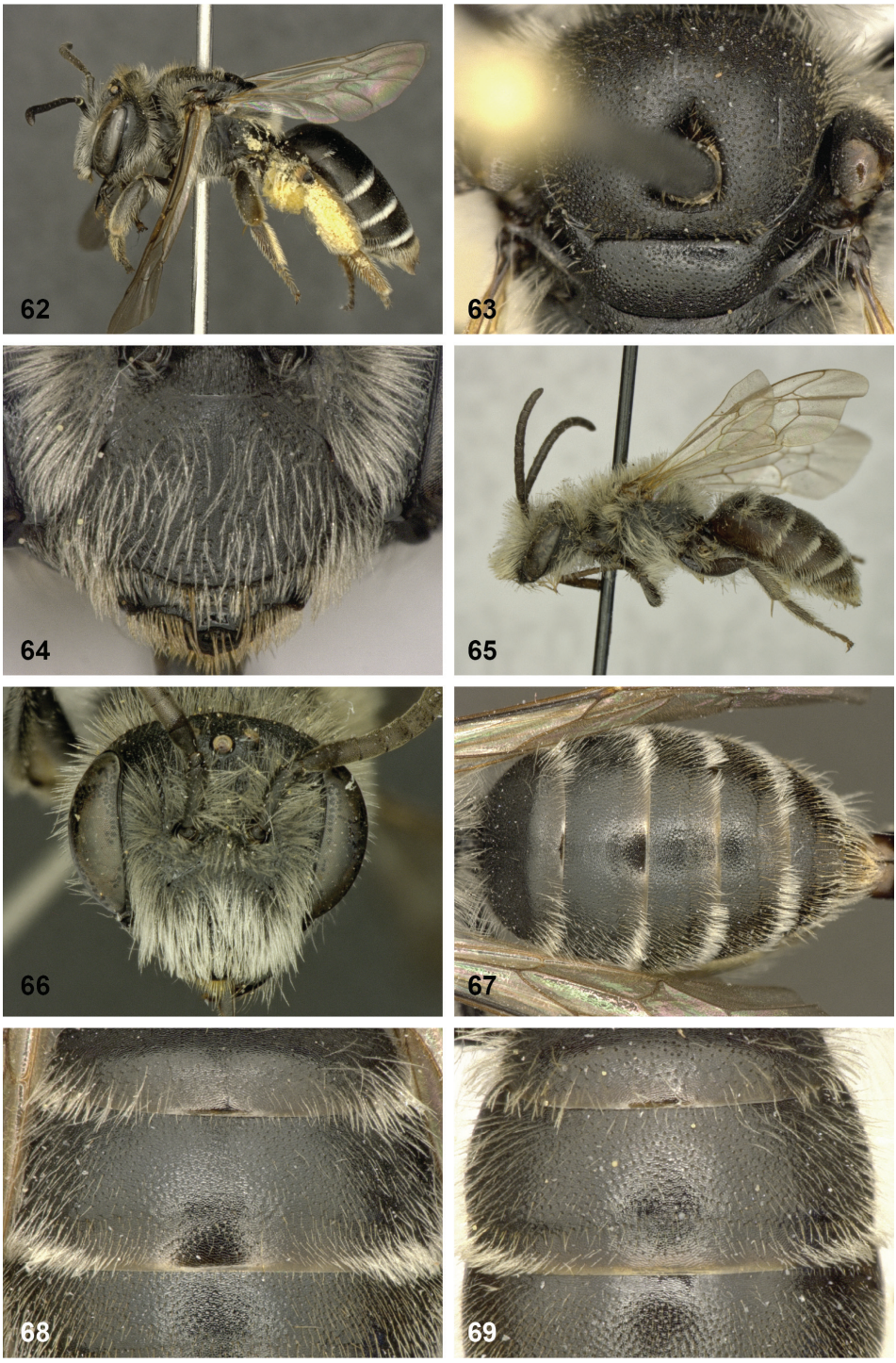
Our results lead to new hypotheses on species delimitation in the subgenus *Taeniandrena*. In particular, the long controversy on the status of *Andrena albofasciata* (referred to here as *A. afzeliella*) and *A. ovatula*, appears definitively solved: in spite of sympatry in northern Europe as well as on the Iberian Peninsula and along the Mediterranean coast (Fig. 7), divergent DNA barcodes were consistently associated with two distinct morphological types. Although the morphological differences are slight, they are consistent and allow for the separation of at least the females throughout the ranges of these taxa. Both taxa are not only genetically and morphologically distinct, they also present consistent differences in their ecology. While both are bivoltine, *A. ovatula* is active nearly a month earlier than *A. afzeliella* (Fig. 8). Future work should compare host-plant associations and habitat preferences of these two taxa; the restricted distribution of *A. ovatula* may point to specific ecological requirements of this species. By contrast, *A. afzeliella* is abundant and ubiquitous in Central and Southern Europe, but appears to be more restricted in northern Europe (van der Smissen 2001, 2002), though revision is required following the taxonomic clarification established here.



Figures 56–61. *Andrena antonellae* sp. nov. **56** female profile **57** female scutum and scutellum **58** female clypeus **59** male profile **60** male face **61** male metasoma.

When subspecies become endemic, narrowly distributed species

Two taxa hitherto treated as subspecies are raised to valid species, *Andrena croceiventris*, so far treated as a subspecies of *A. russula* (=*A. similis*), and *A. vocifera*, hitherto treated as a subspecies of *A. gelriae*. Both species pairs show distinct, but slightly overlapping geographic ranges: we document the presence of *A. gelriae sensu stricto* in southern France, and of *A. russula* in mountainous areas of central Italy, suggesting that these



Figures 62–69. 62–68 *Andrena ovata* **62** female profile **63** female scutum and scutellum **64** female clypeus **65** male holotype of *A. ovata*, profile **66** male face **67** male metasoma **68** male metasomal terga 1–3 **69** *A. wilkella*, male metasomal terga 1–3.

Figures 70–71. Male metasoma **70** *Andrena gelriae* **71** *A. vocifera*.

species pairs maintain morphological and genetic integrity in spite of range sympatry. This result is of more than academic importance, for the following reasons. First, both *A. croceiventris* and *A. vocifera* have a very narrow geographic range, with the former restricted to continental Italy and Sicily, and the latter to a small area in southern France between the Pyrenees and the Alps. A narrow geographic range is the basis for Criterion B in red list assessments, the most widely used criterion for insects. Second, both species appear to be particularly rare: we are aware of only nine specimens of *A. vocifera* collected in France in the last 40 years, despite intensive faunistic inventories; and the last known record of *A. croceiventris* in Italy was made in 2004. Both species are rather conspicuous, likely forage on "classical" bee host plants (Fabaceae), and are thus unlikely to be overlooked in surveys, raising questions on their conservation status. The very low number of records from these two taxa further stresses the poor knowledge of the southern European bee fauna and call for additional faunistic inventories in this important hotspot of bee diversity.

Cryptic diversity in southern European *Taeniandrena*

Our results highlight the presence of two newly recognized species in Europe. *Andrena ovata* appears to be widely distributed in Europe as demonstrated by the isolated records in Greece, Italy, Switzerland, Germany, France and Spain. This species has likely been overlooked due to challenging morphological identifications in *Taeniandrena*. DNA barcoding was pivotal in the detection of this species and in the association of sexes, as specimens were previously typically misidentified as *A. ovatula sensu lato* (females) or as *A. wilkella* (males).

The second species described here, *Andrena antonellae* sp. nov., shows a small geographic range restricted to the islands of Corsica and Sardinia. While several endemic insect species are known from these two islands, including the emblematic Corsican Swallowtail *Papilio hospiton* Gené, 1839, only few endemic bee species are so far known, including *Andrena corssubalpina* Theunert, 2007 and *Nomada legoffi* Dufrêne, 2021. Species delimitation in *A. antonellae* sp. nov., *A. croceiventris* and *A. fuliginata* was highly challenging, these three taxa being sculpturally nearly identical but forming

distant clades in the phylogenetic tree, with genetic distances among these taxa comprised between 4.69–5.73% (Fig. 2). The distant phylogenetic placement of these three taxa is difficult to explain. Technical artefacts (pseudogenes or NUMTs, or contamination) can be excluded given that several independent, high quality sequences were generated for each species using different primer pairs. Recent mitochondrial introgression can also be excluded given that none of these taxa presents barcode-sharing with any other known taxon. This situation is reminiscent of the lack of close phylogenetic relationship between other superficially similar species of *Taeniandrena*.

Discordance between morphology and DNA barcodes

More generally, two opposing trends can be highlighted in European *Taeniandrena* when comparing morphological results with those based on DNA barcodes: on the one hand, groups of morphologically highly similar taxa were found to be genetically only distantly related, as in the case of *Andrena croceiventris*, *A. fuliginata* and *A. antonellae* sp. nov.; against our expectations, *A. ovatula* and *A. afzeliella* were not closely related (genetic distances 9.5–10.6%); an unclear taxon on the Iberian Peninsula, *Andrena aff. russula* (TJW017), is morphologically nearly identical to *A. russula*, but only distantly related to that species (6.49–7.87%); and superficially similar specimens corresponding to the description of *A. poupillieri* were only distantly related in the tree (Fig. 2).

A second, contrasting pattern is observed in the *gelriae*-clade: in this clade, genetic differences were low, comprised between 1.12 and 3.54%, and even as low as 0.30 and 0.37% between *A. contracta*, *A. levante* and the Spanish specimens of *A. intermedia*. These comparatively low genetic distances strongly contrast with the marked morphological differences in male genitalia, which allow for a clear separation of these taxa (Figs 49, 50, 53; see also Wood et al. 2021; Wood 2022). In addition, *A. intermedia*, although delimitated based on male genitalia, was not recovered as a monophyletic group: two isolated populations from Spain were more closely related to other Spanish species (*A. levante* and *A. contracta*), than to central and northern European populations of *A. intermedia*.

A first hypothesis to account for these two contrasting patterns is that morphological similarity does not necessarily imply phylogenetic relatedness, especially given the morphological homogeneity in the subgenus. A second hypothesis is that the diversification rate is particularly high in the *gelriae*-clade, given the high number of species and the low genetic divergences among morphologically clearly delimitated species. In agreement with this fast diversification, some species pairs or triplets in the *gelriae*-clade exhibit narrow geographic range and parapatric or near parapatric distribution, as observed in *A. gelriae* and *A. producta* in Central Europe, and *A. levante*, *A. vocifera* and *A. gelriae* in western Europe. A more extreme example of parapatry can be found around the Sierra Nevada in southern Spain. *Andrena levante* is present in dry valleys at lower altitudes up to ~1200 metres, *A. intermedia* is found in subalpine habitats between 1200–2000 metres, and *A. contracta* is found in the alpine zone above 2000 metres (Wood 2022; Wood, unpublished data). Such parapatric distribution may point to recent

speciation and to only partially interrupted gene flow, leading to lack of true sympatry among the species (Lucek et al. 2020), or more generally to "geographic replacement species" (Descimon and Mallet 2009; Mallet 2013). Partially interrupted gene flow may also lead to introgression among closely related species, and congruently we hypothesize that recent mitochondrial introgression accounts for the paraphyly observed in *A. intermedia*. Under this scenario, isolated populations of this taxon in mountain ranges in Spain may have undergone mitochondrial introgression with the closely related species *A. levante* and *A. contracta*. Such mitochondrial introgression must have happened some time ago, given the current lack of barcode sharing among these three taxa. Interestingly, these Spanish specimens of *A. intermedia* present an intermediate morphology between central and northern European *A. intermedia* and other species of the *gelriae* clade which are present on the Iberian Peninsula, most clearly in the slightly divergent construction of their genital capsules. Whether this intermediate morphology is simply the result of random distribution of morphological characters, or of some pattern of introgression among closely related species, would be interesting to test. The pattern highlighted is coherent with fast diversification, recent divergences and not completely interrupted gene flow, possibly even with hybrid speciation (Mallet 2007; Schumer et al. 2014; Nieto Feliner et al. 2017; Hinojosa et al. 2022). Future work using genomic-scale markers is needed to reconstruct the phylogenetic relationships within European *Taeniandrena*, and to examine the pattern of fast speciation in this group of bees.

Conclusions

The use of DNA barcodes was pivotal in highlighting cryptic diversity in this group of bees, but also in obtaining crucial data on the distribution of several restricted bee species. Using short, but diagnostic barcodes (180 bp) we were able to generate genetic data for important records for which no recent material was available, and for confirming the morphological separation of *Andrena ovatula* and *A. afzeliella* performed more than 20 years ago in the absence of genetic data (van der Smissen 2002). In addition, we were able to obtain barcode data for a topotypical specimen of *A. russula* collected in 1971 in Algeria, a critical step for species delimitation and taxonomic decisions in the *A. russula-A. similis* clade. Lastly, our short barcodes allowed for the verification of numerous records of the endangered species *A. gelriae* in Switzerland, revealing that approximately 90% of these records (see map presented in Amiet et al. 2010) were based on misidentifications. Together with the uncovering of at least three hitherto overlooked European endemic species, *A. vocifera*, *A. croceiventris* and *A. antonellae* sp. nov., our results demonstrate the importance of accurate species delimitation hypotheses and curated databases for conservation. Our approach of first obtaining DNA barcodes from fresh specimens to complement morphology for species delimitation, and then of sequencing short, diagnostic barcodes to identify ambiguous museum specimens to obtain accurate distribution data, appears particularly promising and should be used extensively to improve taxonomic understanding of bees in the southern European biodiversity hot spot.

Acknowledgements

This study is dedicated to Jane van der Smissen, whose long commitment in the careful study of a local bee fauna has presciently led to the recognition of two closely related species long before genetic data could be used. Felix Amiet kindly donated specimens identified by Jane van der Smissen for genetic analysis. Gideon Pisanty and Sophie Cardinal made two barcodes of *A. afzeliella* available for this study. We thank Mike Herrmann, Paolo Rosa, Christian Schmid-Egger and Jessica Litman for discussions on earlier versions of this manuscript. Matthieu Aubert, Paolo Biella, Ian Cross, Eric Dufrêne, Lorenzo Giollo, Mike Herrmann, Kobe Janssen, Alireza Monfared, F. Javier Ortiz-Sánchez, Marino Quaranta, Lise Ropars, Bertrand Schatz, Christian Schmid-Egger, Maximillian Schwarz, Stefan Tischendorf, Peter Vanormelingen, and many others (see Suppl. material 2: Table S2) kindly made material available for study. Some Corsican specimens were contributed by Adrien Perrard and Alexandre Cornuel-Willermoz, who were supported by Labex BCDiv (MNHN). The genetic analyses were supported by the project "Référentiel génétique des abeilles de Suisse", BAFU-417.111-04.1-2469/2/1; we thank Danielle Hofmann (Swiss federal office for the Environment) for her support, and the team of info fauna, Neuchatel, in particular François Claude, for logistic assistance. Molecular work and databasing of French specimens were performed within the "inventaire du patrimoine naturel (inpn.mnhn.fr)" project with funding from UMS PatriNat (special thanks to Pascal Dupont) to DG. TJW is supported by an F.R.S.-FNRS fellowship "Chargé de recherches". We also thank Esther Ockermüller (OLML), Jennifer Steppler (SMFD), Stefanie Krause (ZMHB), and Agnièle Touret-Alby (MNHN) for their help accessing their respective collections. Fritz Geller-Grimm (MWNH) and Stefan Tischendorf generously hosted CP and arranged visits in Wiesbaden and Frankfurt.

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Supplementary material 1

Table S1. Specimens used in genetic analyses. The unique identifiers are identical to the Sample-ID on BOLD

Authors: Christophe Praz, David Genoud, Killian Vaucher, Dimitri Bénon, Joseph Monks, Thomas J. Wood

Data type: excel file

Explanation note: Table S1. Specimens used in genetic analyses. The unique identifiers are identical to the Sample-ID on BOLD. The primers used in PCR and the size of the fragment sequenced are indicated (primer names are abbreviated; see text). GenSeq category after Chakrabarty et al. 2013, Zookeys 346: 29–41 (1 = holotype; 2 = paratype; 3 = topotype; 4 = vouchered specimens).

Link: https://doi.org/10.3897/jhr.91.82761.suppl1

Supplementary material 2

Table S2. List of all examined specimens.

Authors: Christophe Praz, David Genoud, Killian Vaucher, Dimitri Bénon, Joseph Monks, Thomas J. Wood

Data type: excel file

Explanation note: Table S2. List of all examined specimens. Swiss occurrences are freely available on GBIF (Praz et al. 2022) and are not given here, with the exception of type material and specimens used in genetic analyses.

Link: https://doi.org/10.3897/jhr.91.82761.suppl2