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Research article

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Revisions to the faunas of Andrena of the Iberian Peninsula and Morocco with the descriptions of four new species (Hymenoptera: Andrenidae)

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Abstract. Iberia has one of the richest bee faunas in the world, and the genus *Andrena* is no exception with around 200 species known from the Peninsula. The fauna of Andrena was largely revised in the 1970s, but since then, it has received little attention. Molecular investigation of the taxonomically challenging subgenus *Taeniandrena* has revealed that the situation is more complicated than previously thought with several cryptic and overlooked species. From the species allied to Andrena (T.) gelriae van der Vecht, 1927, Andrena (T.) gredana Warncke, 1975 stat. nov. from Spain and Portugal is raised to species status, and *Andrena* (*T.*) *levante* Wood & Praz sp. nov. from southeastern Spain is newly described. Furthermore, Andrena (T.) benoisti Wood & Praz sp. nov. is described, having previously been referred to as Andrena (T.) wilkella beaumonti Benoist, 1961. Andrena (T.) beaumonti stat. rev. is itself distinct and restricted to the High Atlas Mountains of Morocco. Outside of the subgenus Taeniandrena, Andrena (Euandrena) fortipunctata Wood sp. nov. and Andrena (Charitandrena) hattorfiana nigricauda Wood subsp. nov. are described from Spain, and Andrena (Notandrena) juliana Wood sp. nov. is described from Spain and Portugal. The male of Andrena (Lepidandrena) baetica Wood, 2020 is also described. Andrena (Euandrena) impressa Warncke, 1967 stat. nov. is raised to species status, displaying a West Mediterranean distribution. Finally, a further two species of Andrena are newly recorded for Spain, Andrena laurivora Warncke, 1974 and Andrena confinis Stoeckhert, 1930. Altogether, these findings reinforce the fact that our understanding of the taxonomy and distribution of Andrena in southern Europe remains incomplete.

Keywords. Cryptic species, DNA-barcoding, Iberian endemic species, solitary bees, taxonomy.

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Introduction

The Iberian Peninsula is one of the most important places for wild bee diversity globally, with a known fauna of well over 1000 species including many endemics (Ortiz-Sánchez 2011, 2020; Wood *et al.* 2020). Its combination of Mediterranean climate, status as a glacial refugium, and wide variety of contrasting habitats (e.g., mountains, scrublands, steppes, and woodlands) supports many different floral communities, thereby offering a large number of distinct foraging niches for wild bee species. Despite a long history of study (e.g., Erichson 1835; Lepeletier 1841; Dours 1873; Pérez 1895; Friese 1897), new bee species continue to be described from Iberia, with the rate of publication actually increasing in recent years (Ortiz-Sánchez *et al.* 2001; Le Goff 2003; Patiny *et al.* 2005; Schwarz & Gusenleitner 2010; Müller 2012; Radchenko 2017; Wood & Cross 2017; Kuhlmann & Smit 2018; Le Goff & Gonçalves 2018; Smit 2018; Wood *et al.* 2020).

The fauna of the *Andrena* Fabricius, 1775 of Iberia was extensively revised by Klaus Warncke (1967, 1975a, 1976) who described 20 species currently accepted as valid from the Peninsula, including many endemics, as well as a large number of subspecies, some of which may well be valid species in their own right. However, since then, very little taxonomic attention has been paid to Iberian *Andrena* until recently (Dardón *et al.* 2014; Wood *et al.* 2020). Concurrently, molecular genetic techniques have increasingly been applied to identify and resolve outstanding problems in the taxonomy of *Andrena* (Manderey *et al.* 2008; Schmidt *et al.* 2015; Praz *et al.* 2019). The Iberian fauna of *Andrena*, with its rich diversity and numerous described subspecies, therefore represents an ideal study system to reveal potential cryptic species with contemporary molecular techniques given the diversity of forms found in this region.

The molecular aspect of this study focused on the monophyletic subgenus *A.* (*Taeniandrena*) Hedicke, 1933 (Pisanty *et al.* 2021), and specifically on taxa allied to *Andrena gelriae* van der Vecht, 1927. The subgenus itself can easily be recognised in most of Europe because of the broad flattened clypeus that is present in both sexes, and can only nominally be confused with the subgenus *Troandrena* Warncke, 1975 that is found on the Canary Islands and in the East Mediterranean (Gusenleitner & Schwarz 2002). The two eastern species of *Troandrena* have a clypeus that is in part clearly shiny (always predominantly dull in *Taeniandrena*), and the complex of species from the Canary Islands have an integument with clear metallic green tints (always non-metallic in *Taeniandrena*) and probably belong elsewhere (Pisanty *et al.* 2021).

Within Andrena (Taeniandrena), A. gelriae was described from the Netherlands. Following the broad taxonomic concept used by Warncke, it has a nominal distribution from Spain, through central and eastern Europe, north to Finland (Gusenleitner & Schwarz 2002). The concept of A. gelriae sensu Warncke included A. gelriae producta Warncke, 1973 which was described from eastern Austria, but this has been treated as a separate species by subsequent authors because of the lack of intermediate forms and distinct male genitalia (Schmid-Egger & Scheuchl 1997; Gusenleitner & Schwarz 2002). Whilst the situation in central Europe is generally clear, things are more challenging in southern Europe as Warncke described the subspecies A. gelriae gredana Warncke, 1975 from Portugal and Spain (Warncke 1975a), and A. gelriae vocifera Warncke, 1975 from southern France (Warncke 1975b). These subspecies have genitalia that markedly differ from the nominate form, but their statuses are unclear and they have not received detailed taxonomic investigation. Because of this lack of investigation, the current distinctions of where to draw the line between the species are somewhat arbitrary, with some publications treating A. gredana, but not A. vocifera, as a valid species (e.g., Nieto et al. 2014).

The present work resolves some of the issues surrounding Iberian *Taeniandrena*, describing two new species and elevating one species from Iberia and one from Morocco. A further two new Iberian species of *Andrena* are described, and a West Mediterranean subspecies of *Andrena* is elevated to species rank. The Spanish fauna of *Andrena* is also updated to the current level of taxonomic understanding following new discoveries, including a species previously thought to be endemic to Morocco. This work

is predominantly based on the examination of previously undetermined Spanish material of *Andrena*, largely from the Oberösterreichisches Landesmuseum (Austria), and the Naturalis Biodiversity Center, (Netherlands), comprising 2865 female and 1716 male specimens from 159 valid species, as well as investigations into the subgenera *Taeniandrena* and *Euandrena* Hedicke, 1933 more broadly at a West Palaearctic scale (Praz *et al.* 2019).

Material and methods

DNA barcoding was performed on Iberian Andrena (Taeniandrena) to examine the status of the species described here, and on taxa related to Andrena angustior (Kirby, 1802) and A. impressa Warncke, 1967 stat. nov. (subgenus Euandrena). The 658-bp 'barcoding' fragment of the mitochondrial gene cytochrome oxidase I was amplified and sequenced using the primer pair LepF/LepR (Hebert et al. 2004) using the PCR conditions given therein. The primer pair often fails for species of Andrena, possibly due to mismatch in the LepF binding site, resulting in frequent co-amplification and/or low-quality sequences of Wolbachia Hertig, 1936. For this reason, we designed the specific primers COX-Taeniandr-F (TTC TGA CTA YTA CCC CCA TCA A) and COX Taeniandr R2 (ATR GGR TCA AAG AAG GAT GA), which together amplify a 365 bp fragment in all species of *Taeniandrena* examined. Based on the initial comparison of sequences of Taeniandrena, this fragment contains sufficient nucleotide variation for separating all European species of *Taeniandrena*. For recently collected specimens (<5 years old), we first tried the combination LepF/LepR, and used the specific primers if the obtained sequences were not clean or if no amplification product was obtained. For older specimens, we used the specific primers mentioned above, and in case these primers did not work, we used the alternate reverse primer COX Taeniandr R1 (TGC TCC TAT RAT TGA TGA AAT ACC TG), which amplifies together with COX-Taeniandr-F a 181-bp fragment of CO1. PCR conditions for both specific primer pairs were the following: initial denaturing 94°C for 4 min.; 35–45 cycles of 45 min. at 94°C, 45 min. at 56°C, 45 min. at 72°C; final elongation 72°C for 7 min.

Lab protocols follow Praz *et al.* (2019); in brief, DNA was extracted from a single leg using DNA extraction kits (Nucleospin, Macherey-Nagel). The PCR products were visualized using agarose gel electrophoresis, purified enzymatically and sequenced with the PCR primers. Chromatograms were trimmed and assembled in Geneious ver. 2020.0.5 and exported consensus were aligned using MAFFT (Katoh & Standley 2013). The resulting matrices were examined and edited in Mesquite (Maddison & Maddison 2018) and converted to amino acid sequences to verify that no stop codon was present. Uncorrected p-distances were computed in a test version of Paup ver. 4.0 kindly provided by D. Swofford (Swofford 2002). Bayesian phylogenetic analyses were performed in BEAST ver. 1.10.4, applying one single partition to which a GTR + G model was applied; the clock model was set to 'uncorrelated relaxed clock' and the tree prior was set to 'speciation: Yule prior'. The analysis was run for 10 million generations, sampling trees and parameters every 1000 generations. The software Tracer ver. 1.7.1 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.

For the analysis of West Mediterranean *Taeniandrena*, a sequence from *Andrena lathyri* Alfken, 1899 was used to root the trees, as this species is morphologically divergent from other species of *Taeniandrena*. In the analysis of *Euandrena*, a sequence of *Andrena fulvago* (Christ, 1791) was used to root the tree, following Pisanty *et al.* (2021). In both cases, a monophyletic group was enforced for all other (ingroup) sequences. Sequences from related taxa were downloaded from BOLD (40 sequences, accession numbers visible in Figs 1–2), maximising the geographic coverage within widely distributed species. For the analysis of *Euandrena*, several North American members of subgenus *Ptilandrena* Robertson, 1902 were included, as these are the sister group to the Palaearctic *Euandrena* (Pisanty *et al.*

Table 1. Locality data (including co-ordinates) and BOLD accession numbers and GenSeq category (after Chakrabarty *et al.* 2013) for sequences produced in this study. 1 = holotype; 2 = paratype; 3 = topotype; 4 = vouchered specimens.

Voucher	Name	Sex	Country	Locality	GenSeq category	Latitude	Longitude	BOLD accession no.
TJW004	A. similis Smith, 1849	2	PT	Serra do Gerês (T. Wood)	4	41.7759	-7.9952	HYMAA233-21
TJW005	A. similis Smith, 1849	9	PT	Confurco, Várzea Cova (T. Wood)	4	41.4978	-8.0765	HYMAA234-21
TJW006	A. similis Smith, 1849	\$	PT	Castro Laboreiro (T. Wood)	4	42.0007	-8.1569	HYMAA235-21
TJW015	A. similis Smith, 1849	\$	CY	Limassol, Polemidia Park (A. Varnava)	4	34.7100	33.0083	HYMAA236-21
1568	A. similis Smith, 1849	\$	MA	Oukaimeden (K. Deneš)	4	31.2039	-7.8614	HYMAA237-21
1561	A. beaumonti Benoist, 1961	\$	MA	Oukaimeden (K. Deneš)	3	31.2039	-7.8614	HYMAA238-21
1559	A. benoisti sp. nov.	2	PT	Confurco, Várzea Cova (T. Wood)	1	41.4978	-8.0765	HYMAA239-21
1557	A. benoisti sp. nov.	8	PT	Serra do Gerês (T. Wood)	2	41.7759	-7.9952	HYMAA240-21
1560	A. benoisti sp. nov.	2	PT	Curalha (T. Wood)	2	41.7114	-7.5491	HYMAA241-21
1180	A. gelriae van der Vecht, 1927	2	CH	Schlieren, Kloster Fahr (C. Praz)	4	47.4078	8.4388	HYMAA242-21
1192	A. gelriae van der Vecht, 1927	8	CH	Schlieren, Kloster Fahr (C. Praz)	4	47.4078	8.4388	HYMAA243-21
1667	A. levante sp. nov.	8	ESP	E-Sierra Nevada, near Alboloduy (J. Halada)	2	37.0327	-2.6248	HYMAA244-21
1566	A. levante sp. nov.	8	ESP	Muela de Cortes reserv (J. Halada)	1	39.2186	-0.9572	HYMAA245-21
1567	A. levante sp. nov.	2	ESP	Sierra de Españula (J. Halada)	2	37.8654	-1.5363	HYMAA246-21
1661	A. levante sp. nov.	\$	ESP	Muela de Cortes reserv (J. Halada)	2	39.2186	-0.9572	HYMAA247-21
1663	A. gredana Warncke, 1975	2	ESP	Sierra de Gredos, La Plataforma (H./J.E. Wiering)	4	40.2740	-5.2335	HYMAA248-21
1665	A. gredana Warncke, 1975	8	ESP	Sierra de Gredos, La Plataforma (H./J.E. Wiering)	4	40.2740	-5.2335	HYMAA249-21
1569	A. ovatula (Kirby, 1802)	2	ESP	PR Cuenca Alta Manzanares (T. Wood)	4	40.7809	-4.0022	HYMAA250-21
1658	A. ovatula (Kirby, 1802)	2	PT	Cercal, Taimosas (T. Wood)	4	37.8166	-8.6835	HYMAA251-21
1668	A. ovatula (Kirby, 1802)	9	BE	Bossu-Bois (T. Wood)	4	50.4136	3.7717	HYMAA252-21
TJW019	A. ovatula (Kirby, 1802)	9	PT	Serra do Gerês (T. Wood)	4	41.7759	-7.9952	HYMAA253-21
TJW020	A. ovatula (Kirby, 1802)	9	PT	Serra do Gerês (T. Wood)	4	41.7759	-7.9952	HYMAA254-21
1551	A. angustior (Kirby, 1802)	9	PT	Pedraído, Fafe (T. Wood)	4	41.5054	-8.1274	HYMAA255-21
1552	A. impressa Warncke, 1967	\$	PT	Rossas, Touça (T. Wood)	4	41.5634	-8.1017	HYMAA256-21

2021). Details on locality information and BOLD accession numbers for all new specimens examined genetically are given in Table 1.

Morphological terminology follows Michener (2007). The abbreviations A, T and S are used for antennal segments, metasomal terga, and metasomal sterna respectively. Specimens were measured from the vertical plane of the front of the head to the tip of the metasoma. Images are presented without scale bars due to their small size and lack of precise submillimetric measuring equipment. Photographs were taken using an Olympus E-M1 Mark II with a 60 mm macro lens and were stacked using Zerene Stacker ver. 1.04 (Zerene Systems, USA) and plates were prepared in GNU Image Manipulation Program (GIMP) ver. 2.10. Post-processing of some images was made in Photoshop Elements (Adobe Systems, USA) in order to improve lighting to highlight specific characters.

Where available, pollen was removed from scopae of female *Andrena* in order to investigate their dietary preferences following the method of Wood & Roberts (2017). Dietary classification followed Müller & Kuhlmann (2008). Maps were made in R ver. 3.6.0 (R Core Team 2019) using the package ggplot2 (Wickham 2016).

Abbreviations

CPC = Christophe Praz Collection, Neuchâtel, Switzerland

ETHZ = Collection of Eidgenössische Technische Hochschule, Zürich, Switzerland

HCOE = Hope Entomological Collection, Oxford, United Kingdom

ICC = Ian Cross Collection, Briantspuddle, United Kingdom
MSC = Maximillian Schwarz Collection, Ansfelden, Austria

NMB = Naturhistorisches Museum Bern, Switzerland

NMLU = Natur-Museum Luzern, Switzerland

NMNL = Naturalis Biodiversity Center, Leiden, the Netherlands *
OÖLM = Oberösterreichisches Landesmuseum, Linz, Austria *
TJWC = Thomas James Wood Collection, Mons, Belgium

ULB = Université libre de Bruxelles, Belgium ZMHB = Museum für Naturkunde, Berlin, Germany

Results

Species descriptions

Class Insecta Linnaeus, 1758 Order Hymenoptera Linnaeus, 1758 Family Andrenidae Latreille, 1802

Genus Andrena Fabricius, 1775

Molecular analyses

In the phylogenetic relationships among species of *Taeniandrena* (Fig. 1), all species represented by more than one individual formed well-supported monophyletic groups, with the exception of *A. wilkella* (Kirby, 1802), for which support was low (posterior probability, hereafter PP, of 0.74). These analyses confirm the distinctiveness of *A. beaumonti* Benoist, 1961 stat. rev. and *A. wilkella*, which form two separate clades with *A. benoisti* Wood & Praz sp. nov. sister to *A. wilkella* and *A. beaumonti* sister to *A. benoisti+A. wilkella*. The distinctiveness of *A. gelriae* s. tr. and *A. gredana* stat. nov. is also supported; these taxa do not form a monophyletic group. The sampled specimens of *A. ovatula* (Kirby, 1802) were similar to specimens of *A. ovatula* s. str. from northern Europe, a taxon that we consider distinct from most populations of '*A. ovatula* auct.' from central and southern Europe (Praz & Wood, in prep.). Lastly, *A. levante* Wood & Praz sp. nov. was the sister species to *A. gelriae* s. str. (PP less than 0.5).

Average within-species, uncorrected genetic distances were low for *A. ovatula*, *A. gredana*, *A. levante* sp. nov. and *A. benoisti* sp. nov. (0.022%, 0.66%, 0.0% and 0.43%, respectively) and considerably higher for *A. wilkella* (1.18%) and *A. similis* Smith, 1849 (1.17%). Uncorrected genetic distances between *A. benoisti* sp. nov. and *A. wilkella* were on average 3.30% (range 2.86–3.86%), those between *A. benoisti* sp. nov. and *A. beaumonti* stat. rev. 7.31% (range 7.13–7.61); *Andrena beaumonti* was on average 6.89% divergent from *A. wilkella* (range 6.62–7.26%). Distances between *A. gredana* and *A. gelriae* were on average 3.02% (range 2.98–3.07), those between *A. levante* sp. nov. and *A. gelriae* 1.67% (range 1.51–1.75).

The analyses of the *Ptilandrena-Euandrena* (Fig. 2) clade strongly support the recognition of *A. impressa* stat. nov. as a distinct species and not as a subspecies of *A. angustior*; these taxa were not closely related in our trees (Fig. 2). The placement of *A. impressa* (sister to a clade composed of *A. fulvata* Stoeckhert, 1930, *A. angustior*, *A. allosa* Warncke, 1975 and *A. amieti* Praz, Müller & Genoud, 2019) was surprising given that *A. impressa* shares numerous morphological features with *A. fulvata* and *A. angustior*, in particular the broadened gena and long male mandible, this character being absent in

^{* =} representing the large majority of inspected specimens

A. allosa and A. amieti, displaying the 'typical' unbroadened gena found in Euandrena. Support for this arrangement was however very weak. Average genetic distances within A. angustior and A. fulvata were 0.20% and 0.38%; distances between these two taxa were on average 3.56% (range 3.10–4.15). The distances between the single specimen of A. impressa and these two taxa were considerably higher: on average 8.22% for distances with A. fulvata (range 8.08–8.40) and 8.61% with A. angustior (range 8.39–9.22). With the exception of the difference between A. gelriae and A. levante sp. nov., these between species genetic distances are well above the 2% divergence metric that typically indicates species-level differences (Schmidt et al. 2015).

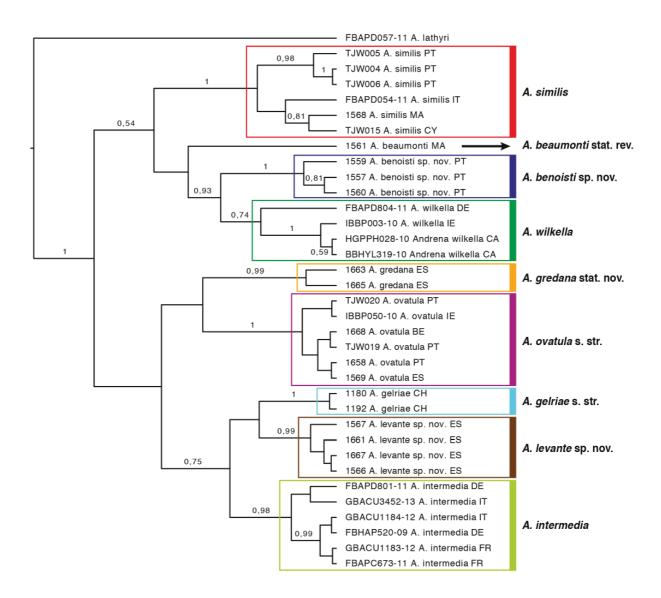


Fig. 1. Molecular phylogeny of the subgenus *Taeniandrena* Hedicke, 1933 with a focus on West Mediterranean species. Maximum clade credibility tree found in Bayesian analyses of sequence data of the mitochondrial gene COI; numbers above branches indicate posterior probabilities; values below 0.5 are omitted.

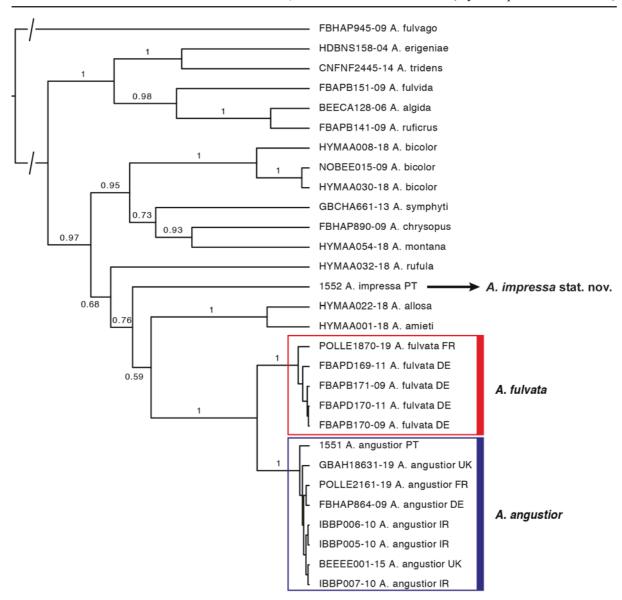


Fig. 2. Molecular phylogeny of the *Andrena angustior* (Kirby, 1802) group within the broader *Ptilandrena-Euandrena* group. Maximum clade credibility tree found in Bayesian analyses of sequence data of the mitochondrial gene COI; numbers above branches indicate posterior probabilities; values below 0.5 are omitted.

Andrena (Taeniandrena) gredana Warncke, 1975 stat. nov. Figs 3–8

Andrena gelriae gredana Warncke, 1975a: 310 (Spain, Sierra de Guadarrama, ♂).

Material examined

Holotype

SPAIN • ♂; Sierra de Guadarrama; Dusmet leg.; OÖLM.

Other material

Literature records (Warncke 1976)

PORTUGAL: Coimbra. SPAIN: Ávila, Puerto del Pico; Pontevedra, Tuy; León, Puerto de Leitariegos; Segovia, San Rafael; Segovia, Valsain; Cáceres, Banos; Madrid, Cercedilla; Madrid, El Escorial; Madrid, Ribas de Jarama.

Remarks

Identification of female material from species close to *A. gelriae* is highly challenging without access to confidently determined comparative material. In Iberia, female *A. gredana* can be recognised by the dense punctures of the base of T2 (smooth to weakly and sparsely punctate in *A. similis* Smith, 1853),

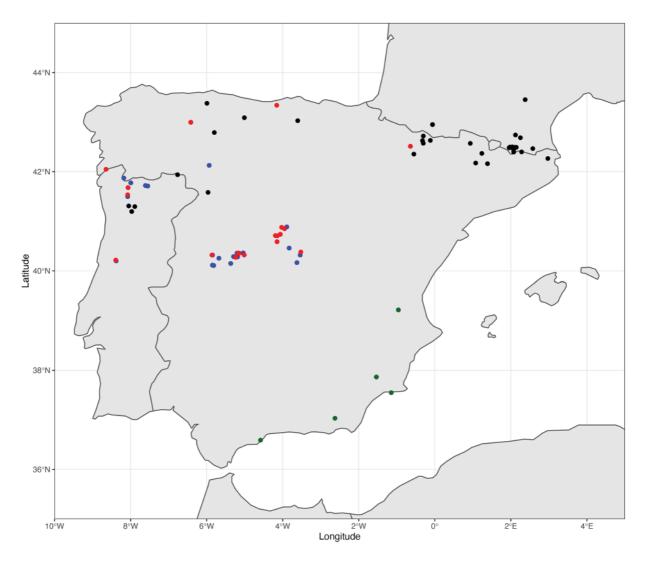
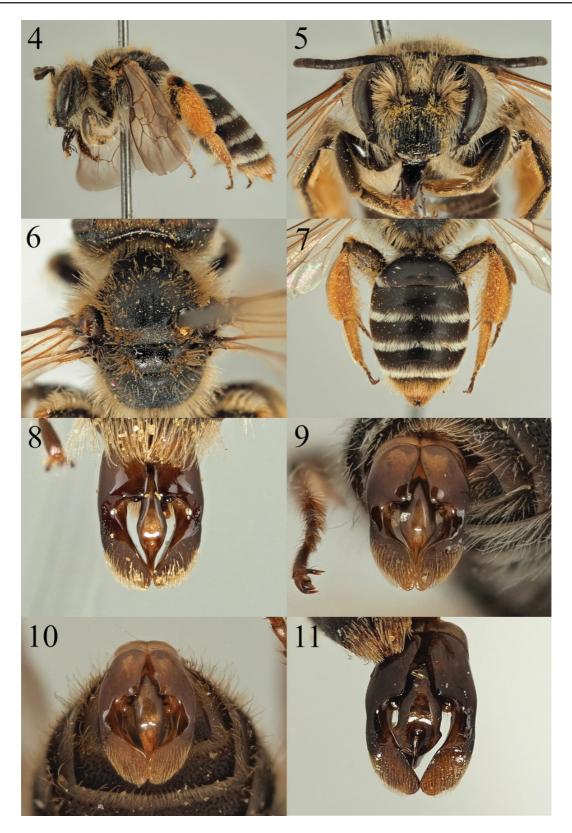


Fig. 3. Distribution of *Andrena* (*Taeniandrena*) *benoisti* Wood & Praz sp. nov. [blue dots], *A.* (*T.*) *wilkella* (Kirby, 1802) [black dots], *A.* (*T.*) *gredana* Warncke, 1975 stat. nov. [red dots], and *A.* (*T.*) *levante* Wood & Praz sp. nov. [green dots] in Iberia. Not to scale.



Figs 4–11. 4–8. *Andrena gredana* Warncke, 1975 stat. nov. (TJWC). **4.** Female profile. **5.** Female face. **6.** Female scutum. **7.** Female terga. **8.** Male genitalia. **9.** *Andrena gelriae* van der Vecht, 1927, male genitalia. **10.** *Andrena levante* Wood & Praz sp. nov., male genitalia. **11.** *Andrena intermedia* Thomson, 1870, male genitalia. Not to scale.

faint punctures on the disc of T1 (strongly punctate in *A. wilkella* (Kirby, 1802)), fore part of clypeus shiny (Fig. 5), contrasting the central and basal areas which are dull (uniformly dull in other species), the sculpturing of the scutum (Fig. 6), which is shagreened but centrally has a circular area where the shagreenation is comparatively weaker when viewed dorsolaterally (other species uniformly shagreened or with a clearly shiny central circular area), and the comparatively wide hair bands on the terga (Fig. 7) that are complete on T2+3+4 (either much thinner, or not complete on T2 and/or T3),

Males are significantly easier to identify, and can initially be recognised by the length ratios of the antennal segments, being part of the group where A3 is equal to A4 in length. In this group, the genitalia of *A. gredana* are highly distinctive, showing gonocoxa that diverge only slightly at their apexes, and with a penis valve that is clearly narrowed basally and widened to its maximum width centrally before tapering to its apex (Fig. 8). This character allows separation from all other Iberian *Taeniandrena*. In fact, molecular data shows that this taxon is not closely allied to *A. gelriae* (Fig. 1), and the divergent structure of the penis valve would support this conclusion when compared to the species allied to *A. gelriae* (Figs 9–11). Given these differences and its phylogenetic placement, *A. gredana* is formally raised to species status.

Distribution

Central and northern Spain and Portugal (Warncke 1976; Fig. 3). The distribution in Iberia is montane, and it may also occur in the French Pyrenees (see record from Huesca Province; Fig. 3), but no specimens have yet been reported from this region.

Andrena (Taeniandrena) levante Wood & Praz sp. nov. urn:lsid:zoobank.org:act:6B3F3AE1-AD7B-4A22-A351-04E8B4A6E911 Figs 3, 10, 12–19

Diagnosis

Females of *Andrena levante* Wood & Praz sp. nov. are close to those of *A. gelriae*, with hair bands that are not as dense, as wide, or as complete as in *A. gredana* stat. nov. (Figs 7, 15). The clearest difference can be seen on the scutum which is strongly and densely shagreened and dull (Fig. 14), with dense punctures that are almost contiguous (except posteriorly), giving the overall surface a duller appearance than in either *A. gelriae* or *A. gredana* (Fig. 6) that have sparser punctation. The pubescence of the scutum and scutellum is also denser, shorter, and thicker than either comparison species (Figs 4, 12).

As for other similar species of *Taeniandrena*, male identification is much easier. Males can be recognised as part of the group with A3 equal to or slightly shorter than A4 (A3 1–1.03 times as long as A4). The genitalia are distinctive, with the gonocoxa diverging from close to their base (without their inner margins parallel for at least 50% of their length), the penis valve uniformly wide (not constricted medially), and with the blades of the gonostyli comparatively short, apically as wide as long (Fig. 10). *Andrena levante* sp. nov. differs from *A. gelriae vocifera* in numerous morphological features; this taxon will be characterised elsewhere (Praz & Wood, in prep.).

Etymology

The term 'El Levante' is the Spanish name for the eastern part of the Iberian Peninsula that constitutes the majority of the known range of this species (Almería, Granada, Málaga, Murcia, Valencia).

Material examined

Holotype

SPAIN • &; 80 km SW of Valencia, Muela de Cortes reserve; [39.219° N, 0.957° W]; 14 May 2003; J. Halada leg.; BOLD accession number: HYMAA245-21; OÖLM (illustrated Figs 10, 16–19).

Paratypes

Description

Female

Measurements. Body length 11–12 mm (Fig. 12).

HEAD. 1.3 times as wide as long (Fig. 13). Clypeus dark, flattened over most of its area, densely and uniformly punctate with exception of raised central impunctate line, punctures separated by < 0.5 puncture diameters, underlying surface shagreened, weakly shining, particularly apically. Face, gena, vertex, and scape with light brownish hair, longest not exceeding half 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 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 shagreened, weakly shining (Fig. 14). Scutellum with sparser punctures separated by 1 puncture diameter, shagreenation weaker, generally shining. 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 short, orange-brown, semi-squamiform hairs, episternum with longer light brownish to white hairs, becoming orange-brown on propodeum. Legs dark, hind tibiae and tarsi of mid and hind legs orange, general pubescence light brown basally, becoming orange apically, flocculus, femoral and tibial scopae light brown to golden. Wings hyaline, venation dark orange, stigma orange, nervulus interstitial.

Metasoma. Terga dark, finely shagreened and weakly shining, apical part of marginal areas lightened semi-translucent brown (Fig. 15). T1 very finely and subtly punctured, punctures on disc scarcely visible against shagreenation, those on margin more visible, separated by 1 puncture diameter. T2–4 more densely and visibly punctate, punctures separated by 0.5 puncture diameters. Terga with whitish hairbands, on T1 represented by two very widely separated spots (separated by almost entire width of tergal margin), T2 widely interrupted, T3+4 complete. Remaining tergal surface covered with short, fine brown to ferruginous hairs visible when viewed obliquely or in profile. Terminal fringe of T5 and hairs flanking pygidial plate golden, pygidial plate rounded, flat, without raised margin.

Male

Measurements. Body length 10–11 mm (Fig. 16).

HEAD. 1.3 times as wide as long (Fig. 17). Clypeus flattened and densely punctate, punctures separated by < 0.5 puncture diameter, sculpturing as in female. Gena and lower part of face with white hairs,



Figs 12–19. *Andrena levante* Wood & Praz sp. nov. (TJWC). 12. Female profile. 13. Female face. 14. Female scutum. 15. Female terga. 16. Male profile. 17. Male face. 18. Male scutum. 19. Male terga.

becoming light brown on scape and vertex, longest equalling length of scape. Antennae dark, A4–13 extensively lightened to dark brown below. A3 as long as A4.

Mesosoma. Scutum, scutellum, episternum, and propodeum structurally as in female (Fig. 18). Scutum and scutellum with fine light brown to golden hairs that equal length of scape, becoming light brown to whitish on propodeum and episternum. Legs dark, apical tarsal segments lightened dark red, pubescence whitish to light brownish. Wings hyaline, venation dark orange, nervulus slightly postfurcal.

Metasoma. Terga dark, finely shagreened and weakly shining, apical part of marginal areas lightened semi-translucent brown (Fig. 19). Terga finely but clearly punctate, puncture separated by 0.5–1 puncture diameter. T2–5 with hairbands, on T2 medially interrupted, complete on T3–5. S8 strap-like, slightly broadened apically, uniformly hairy. Genitalia elongated oval-shaped in dorsal view, gonocoxa with inner margins clearly diverging, not parallel, forming 90° angles apically (Fig. 10). Penis valve moderately broad, basally parallel sided before tapering apically. Gonostyli comparatively short, apical blades as wide as long.

Distribution

Areas broadly near the coast in southeastern Spain, from Málaga to Valencia (Fig. 3). All sites are mountainous (Sierra de Mijas, Sierra Nevada, Sierra de Españula, Muela de Cortes, Sierra de la Muela, Cabo Tiñoso y Roldán).

Andrena (Taeniandrena) beaumonti Benoist, 1961 stat. rev. Figs 21, 23, 25, 27, 29, 31, 33, 35

Andrena Beaumonti Benoist, 1961: 91 (Morocco, between Asni and Arroud, 18 Jun. 1947, ♀).

Material examined

MOROCCO • 1 \circlearrowleft ; Tizi-n-Test, S; 1900 m a.s.l.; 29 Jun. 1987; M. Schwarz leg.; OÖLM • 1 \circlearrowleft ; same collection data as for preceding; TJWC • 1 \circlearrowleft , 1 \circlearrowleft ; Oukaimeden; 2700 m a.s.l.; 8 May 2015; K. Deneš leg.; OÖLM (illustrated Figs 21, 23, 25, 27, 29, 31, 33, 35).

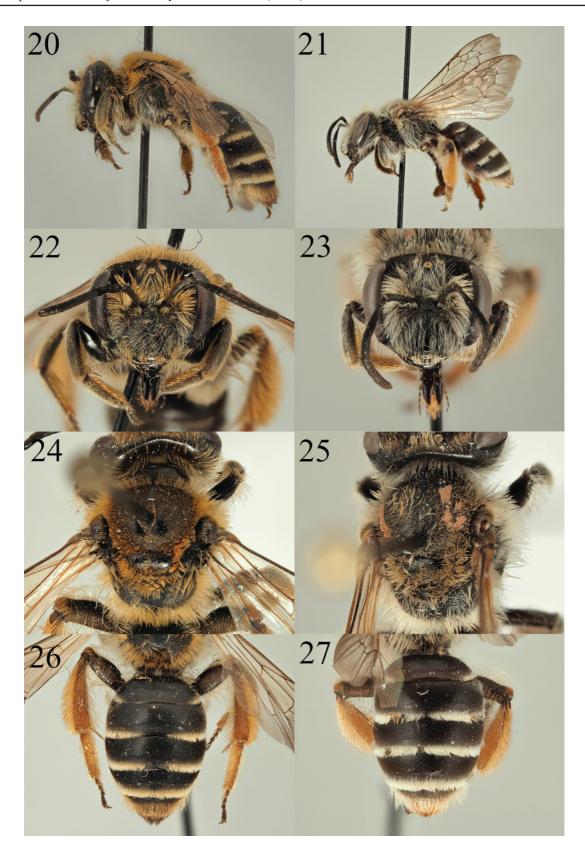
Description

Male

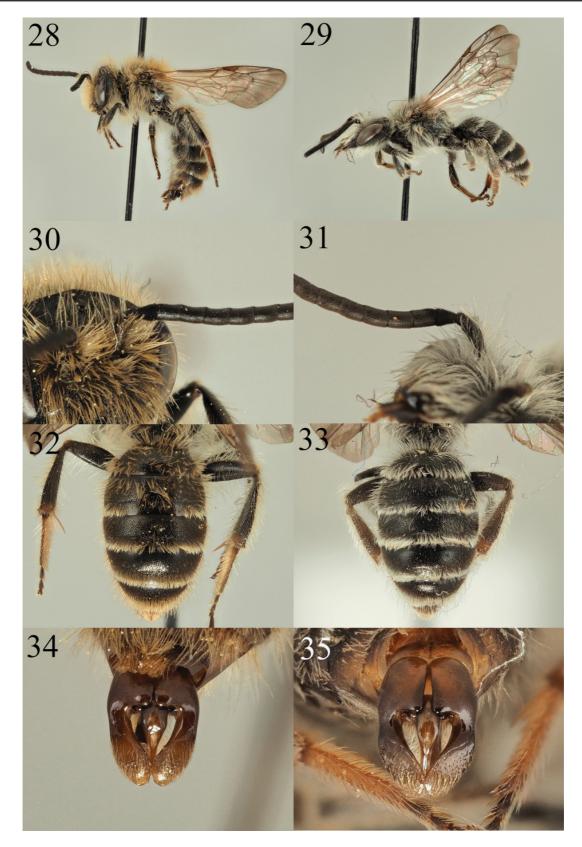
MEASUREMENTS. Body length 11 mm (Fig. 29).

HEAD. Dark, slightly as wide as long. Clypeus flattened, densely punctate, punctures separated by 0.5 puncture diameters, underlying surface shiny, without microsculpture. Gena, face, vertex, and scape covered with long whitish hairs that equal or exceed scape in length. Antennae dark, A4–13 slightly lightened grey below, A3 1.15 times as long as A4 (Fig. 31).

Mesosoma. Scutum shagreened and dull over majority of disc, becoming weaker centrally and posteriorly, here weakly shining, surface densely but shallowly punctured, punctures apically separated by 0.5 puncture diameters, centrally becoming sparser, here separated by 1–2 puncture diameters. Scutellum more uniformly shiny and densely punctate, punctures separated by 1 puncture diameter. Episternum and propodeum weakly reticulate, underlying surface weakly shining, propodeal triangle basally comparatively more strongly reticulate, this dispersing apically. All parts of mesosoma with long brownish (scutum and scutellum) to whitish (episternum and propodeum) hairs that exceed length of scape. Legs dark, apex of hind tibiae and entirety of hind basitarsi orange, pubescence whitish. Wings hyaline, venation orange, nervulus interstitial.



Figs 20–27. 20, 22, 24, 26. *Andrena benoisti* Wood & Praz sp. nov. (TJWC). 20. Female profile. 22. Female face. 24. Female scutum. 26. Female terga. — 21, 23, 25, 27. *Andrena beaumonti* stat. rev. (TJWC). 21. Female profile. 23. Female face. 25. Female scutum. 27. Female terga. Not to scale.



Figs 28–35. 28, 30, 32, 34. Andrena benoisti Wood & Praz sp. nov. (TJWC). 28. Male profile. 30. Male antennae. 32. Male terga. 34. Male genitalia. — 29, 31, 33, 35. Andrena beaumonti stat. rev. (TJWC). 29. Male profile. 31. Male antennae. 33. Male terga. 35. Male genitalia. Not to scale.

Metasoma. Terga dark, apical margins impressed, strongly impressed on T3–5, covered in short, thick, and complete white hair bands (Fig. 33). Terga densely punctate, punctures separated by 0.5–1 puncture diameters, underlying surface shagreened and dull basally, becoming weaker apically, T4–5 weakly shining. S8 columnar, parallel sided, apically slightly notched. Genitalia simple, gonocoxa with internal margins diverging apically, laterally with weak shagreenation, apical corners rounded (Fig. 35). Penis valve relatively narrow, apically tapering, gonostyli with broad bases, apical blades clearly longer than wide.

Remarks

In his original description, Benoist (1961) drew a comparison between A. beaumonti stat. rev. and Andrena flavipes Panzer, 1799, presumably because of the dense hair bands that help characterise this species. Warncke (1967) noted that this association was clearly incorrect at a subgeneric level, associating the bee with members of the subgenus Taeniandrena instead. On the basis of its large and dense puncturing, its golden hairs flanking the pygidial plate, and the orange metatarsi of the second pair of legs, Warncke (1967) associated this taxon with Andrena wilkella, but as a subspecies because of the unbroken hair bands on T3+4. He then went on to report A. wilkella beaumonti from Iberia (Warncke 1976; see also Ortiz-Sánchez 2011, 2020), giving it a distribution of Morocco, Spain, and Portugal (see also Lhomme et al. 2020). However, genetic barcoding shows that A. beaumonti is distinct, and Moroccan material is also morphologically different from Warncke's concept of A. wilkella beaumonti in Iberia, most obviously by lacking a shiny spot on the scutum that is well differentiated from the surrounding shagreenation. It can also be separated by the finer hairs on the scutum, the generally paler pubescence, and by the thicker and more complete hair bands on terga 2–4 (Figs 20–27), meaning that A. wilkella beaumonti sensu Warncke in Iberia is actually undescribed (see below). The previously undescribed male of A. beaumonti can also be distinguished using the same characters (colour of pubescence, nature of tergal hair bands) and also by the length of A4 which is 1.15 times as long as A3, whereas in A. benoisti Wood & Praz sp. nov. (see below) it is 1.3 times longer (Figs 30–31). There are also slight differences in the genitalia, with a comparatively narrower penis valve and more clearly separated gonocoxa (Figs 34–35) in A. beaumonti.

Distribution

Morocco, from the High Atlas Mountains in the area south of Marrakesh. The village of Asni is found at a moderate elevation of 1200 m. It is not clear exactly where Arroud is because of changes in spelling practices, but it probably refers to the village Around some 25 km SSE of Asni. Contemporary sampling locations of *A. beaumonti* stat. rev. are relatively close to Asni itself. Tizi-n-Test is some 60 km SW of Asni, and Oukaimeden is even closer, just 10 km to the SE. The site of Oukaimeden is at a much higher elevation of 3200 m, and the cluster of records in this region suggests that *A. beaumonti* is restricted to high-elevation sites flying in May and June.

Andrena (Taeniandrena) benoisti Wood & Praz sp. nov. urn:lsid:zoobank.org:act:7B5423C4-E358-4C5D-8C92-6A6074033347 Figs 3, 20, 22, 24, 26, 28, 30, 32, 34

Diagnosis

Andrena benoisti Wood & Praz sp. nov. can be recognised within the subgenus *Taeniandrena* by the combination of dense punctures on the base of T2, strong punctures on the disc of T1 (very similar to A. wilkella), thick hairbands that are only narrowly interrupted on T2 and complete on T3+4 (Fig. 26, thin and widely interrupted on T2+3 in A. wilkella), and the sculpturing of the scutum, which is shagreened except for the centre where it has a circular shining area that strongly contrasts with the remaining surface which is dull (Fig. 24).

The males can be recognised by the ratio of the antennal segments where A3 is clearly shorter than A4 in length (Fig. 30), the terga are strongly and densely punctate, the tergal margins are depressed with a thin, shiny, puncture-free apical zone, and T2–4 have thick hairbands, medially interrupted on T2, complete on T3+4 (Fig. 32). They are therefore closest to *A. wilkella*, but the thicker and more complete hair bands in combination with its larger body size (10–11 mm against 8–9 mm) allows for differentiation. Genetically, *A. benoisti* sp. nov. is placed as the sister of *A. wilkella*, a position that is corroborated by their morphological similarity.

Etymology

Named after Raymond Benoist, the French botanist and entomologist who described *Andrena beaumonti* stat. rev. from Morocco, this name being incorrectly applied at the subspecific level to the taxon we describe here.

Material examined

Holotype

PORTUGAL • ♀; Minho, Confurco, Várzea Cova; 41.4978° N, 8.0765° W; 14 May 2019; Wood leg.; BOLD accession number: HYMAA239-21; OÖLM (illustrated Figs 20, 22, 24, 26).

Paratypes

PORTUGAL • 1 ♂, 1 ♀; Minho, Ruivães, N103; 12 May 2019; Wood leg.; OÖLM • 1 ♂; Minho, 1.5 km E of Lindoso; 13 May 2019; Wood leg.; TJWC • 1 ♂; Minho, Serra do Gerês, 5 km W of Paradela; 12 May 2019; Wood leg.; OÖLM (illustrated Figs 28, 30, 32, 34) • 1 ♀; Trás-os-Montes, Curalha, A24 and N103 intersection; 16 May 2019; Wood leg.; TJWC • 1 ♀; Trás-os-Montes, Chaves, Estr. Braga, Rio Tâmega; 16 May 2019; Wood leg.; TJWC.

SPAIN • 1 &; Cáceres, W of Garganta la Olla; 1000 m a.s.l.; 9 May 1999; H. and J.E. Wiering leg.; NMNL • 4 & &; Cáceres, Piornal; 1050 m a.s.l.; 13 May 1999; H. and J.E. Wiering leg.; NMNL • 1 &; Cáceres, Madrigal de la Vera; 500 m a.s.l.; 9 May 1999; H. and J.E. Wiering leg.; NMNL • 3 & &; Ávila, Sierra de Gredos, La Plataforma; 1700 m a.s.l.; 19 May 1995; H. and J.E. Wiering leg.; NMNL • 1 &; Ávila, Navarredonda de la Sierra en Pico de Almanzor; 1400–1600 m a.s.l.; 5 Jun. 1976; P. Oosterbroek leg.; NMNL • 1 &; Ávila, Sierra de Gredos Puerto del Pico; 2 Jul. 1988; M. Schwarz leg. • 2 & &; Ávila, 2 km E of Hoyos Del Espino; 22 May 1995; H. and J.E. Wiering leg.; NMNL • 1 & &; Ávila, Hoyos del Espino; 1400 m a.s.l.; 18–22 May 1995; H. and J.E. Wiering leg.; NMNL • 1 & &; Gredos, Hoyos de Collado; 6 Jun. 1983; H. Teunissen leg.; NMNL • 1 &; Ávila, 6 km E of Parador del Gredos; 1 Jun. 1976; P. Oosterbroek leg.; NMNL.

Other material (unspecified, listed as Andrena wilkella beaumonti by Warncke 1976)

PORTUGAL • Coimbra, Pinhal de Marrocos; Ponte da Portella.

SPAIN • Parador Nacional de Gredos; Zamora, Alcubilla de Nogales; Cáceres, Banos do Montemayor; Cáceres Tornavacas; Madrid, Cercedilla; Madrid, Ciempozuelos; Madrid, El Chaparral; Madrid, El Escorial; Madrid, El Paular; Madrid, Sierra de Guadarrama; Madrid, Vaciamadrid.

Description

Female

Measurements. Body length 11–12 mm (Fig. 20).

HEAD. 1.3 times as wide as long (Fig. 22). Clypeus flattened, densely but shallowly and weakly punctured, punctures separated by 0.5 puncture diameters, faint impunctate line visible centrally, underlying surface shagreened, dull, slightly shining apically. Lower face and gena with whitish hairs, becoming light

brown to golden on scape, upper face, and vertex, hairs not exceeding length of scape. Antennae dark, A5–12 slightly lightened grey below. Foveae broad, occupying almost all area between lateral ocellus and top of compound eye, filled with short brown hairs.

Mesosoma. Scutum densely punctured over most of surface, underlying surface dull, punctures separated by 1 puncture diameter except becoming sparser centrally and posteriorly forming circular shape, here punctures separated by 2 puncture diameters, underling surface weakly shagreened, shining, contrasting remaining surface (Fig. 24). Scutellum shiny, densely punctate centrally, separated by 0.5 puncture diameters, punctures sparser laterally. Episternum with slightly raised reticulation, underlying surface dull, reticulation reaches lateral faces of propodeum but weakly, disappearing before propodeal triangle, this marked by change in surface sculpturing, internal surface with fine, sparse, and slightly raised reticulation. Scutum and scutellum with short, orange-brown, semi-squamiform hairs, episternum with longer light brownish to white hairs, becoming orange-brown on propodeum. Legs dark, hind basitarsi fully and hind tibiae partially orange, general pubescence light brown. Flocculus and femoral scopa whitish, tibial scopa golden. Wings hyaline, venation and stigma golden, nervulus postfurcal.

METASOMA. Terga dark, apical part of marginal areas lightened semi-translucent brown (Fig. 26). T1 with clear punctures on disc, separated by 0.5 puncture diameters, extending to tergal margin, becoming sparser, separated by 1–1.5 puncture diameters. T2–4 densely and uniformly punctate, punctures separated by 0.5–1 puncture diameters. T1 with very widely separated hair patches on margin, T2–4 with thick hair bands, on T2 interrupted, on T3+4 complete. Terminal fringe of T5 and hairs flanking pygidial plate golden, pygidial plate rounded with slightly raised longitudinal area centrally.

Male

Measurements. Body length 10–11 mm (Fig. 28).

HEAD. 1.3 times as wide as long. Clypeus flattened, densely punctate, punctures separated by 0.5 puncture diameters with exception of clear longitudinal impunctate line, underlying surface shiny. Gena, face, vertex, and scape with long whitish to light brownish hairs, equalling or exceeding scape in length. Antennae dark, A3 1.3 times as long as A4 (Fig. 30).

MESOSOMA. Scutum, scutellum, episternum, and propodeum structurally as in female, though propodeal reticulation a little more extensive. All parts of mesosoma with long light brown to golden hairs, equalling or exceeding scape in length. Legs dark, Hind tibiae entirely and hind tarsi apically coloured dark orange, pubescence whitish to light brown. Wings hyaline, venation dark orange, nervulus postfurcal.

Metasoma. Terga dark, apical margins slightly depressed, apical part of marginal areas lightened semitranslucent brown (Fig. 32). T1–5 with discs increasing densely punctate, on T1 punctures separated by 1 puncture diameter, almost contiguous on T5, underlying surface shagreened, weakly shining. Tergal discs with loose light to dark brown hairs, T2–4 with thick hair bands, on T2 widely interrupted, on T3+4 complete. S8 broadened apically, densely and uniformly hairy. Genitalia simple, gonocoxa with inner margins parallel, only slightly deviating apically, apical corners rounded (Fig. 34). Penis valve moderately broad, parallel sided basally before strongly tapering apically, gonostyli with broad bases, apical blades clearly longer than wide.

Distribution

From the Sistema Central around Madrid westwards through the Sierra de Gredos into central Portugal, and north into northern Portugal, Galicia, and Zamora (Fig. 3). Both *A. benoisti* sp. nov. and *A. gredana* stat. nov. show a remarkably similar distribution and occurring at many of the same localities (see also Warncke 1976), particularly in the Sistema Central from which true *A. wilkella* seems to be absent.

Andrena (Euandrena) fortipunctata Wood sp. nov. urn:lsid:zoobank.org:act:A2AD083A-AB1A-4B85-AE9D-F58DA0B653A7 Figs 36–39, 42–45

Diagnosis

In the female sex, *A. fortipunctata* Wood sp. nov. can be placed in the subgenus *Euandrena* because of the narrow, comma shaped fovea, antennal A3 longer than A4+5, metasomal integument brown haired, propodeal triangle weakly wrinkled, hind femur without thorn-like projections, and dorsolateral angle of propodeum without elevated transverse carina (Praz *et al.* 2019). The female resembles *A. bicolor* Fabricius, 1775 in general colour pattern, but differs by the combination of a coarsely and densely punctate clypeus (punctures separated by 0.5 puncture diameters, interspaces barely visible, in *A. bicolor* punctures separated by 0.5–1 puncture diameters, interspaces visible), strongly punctured tergal discs, and strongly depressed tergal margins (compare Figs 38–41).

Males are harder to place through specific subgeneric characters, in common with other *Euandrena* males as the subgenus is largely defined by female characters (Praz *et al.* 2019). However, *A. fortipunctata* sp. nov. males are instantly recognisable in the Iberian fauna by the wide and extremely strongly depressed tergal margins (Figs 43, 45) that are strikingly more pronounced that in either *A. granulosa* Pérez, 1902 or *A. vulpecula* Kriechbaumer, 1873 (Figs 47, 49), the other two European species of *A. (Euandrena*) known for their distinctive depressed tergal margins. These three species also share similar facial pubescence which is centrally yellow and laterally dark (Figs 46, 48), whereas other Iberian species of *Euandrena* have male facial pubescence that is either predominantly grey (*A. symphyti* Schmiedeknecht, 1883), brown (*A. rufula* Schmiedeknecht, 1883), dark (*A. bicolor*), or a mixture of grey and black (*A. allosa* Warncke, 1975).

Etymology

The name 'forti' ('strong') + 'punctata' ('punctured') was chosen because of the pronounced punctures visible in both sexes that help separate this taxon from other Iberian Euandrena.

Material examined

Holotype

SPAIN • &; Oveido-León, Puerto de Pajares; 1350–1700 m a.s.l.; [42.994° N, 5.763° W]; 11 Jul. 1972; V.S. May d. Groot and J.A.W. Lucas leg.; NMNL (illustrated Figs 36–39).

Paratype

SPAIN • 1 ♀; Ávila, Sierra de Gredos, 12 km SSW of Hoyos del Espino; 1950–2100 m a.s.l.; 4 Jul. 1972; V.S. May d. Groot and J.A.W. Lucas leg.; NMNL (illustrated Figs 42–45).

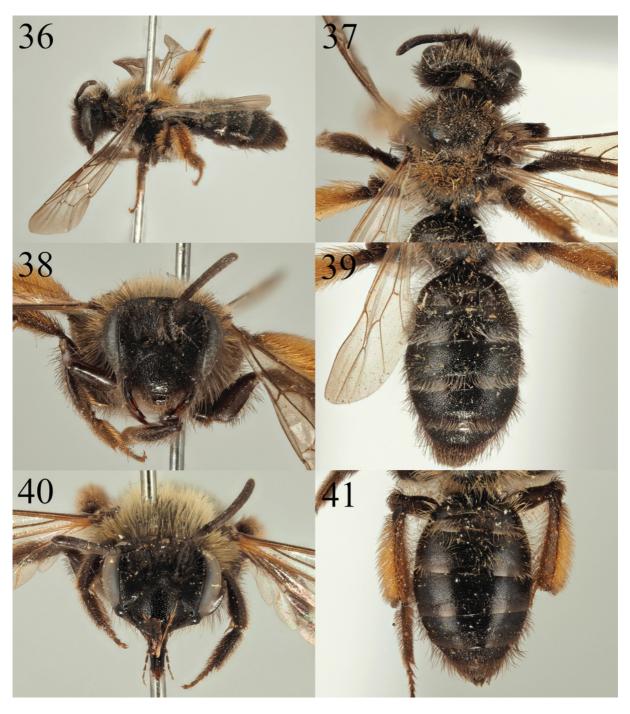
Description

Female

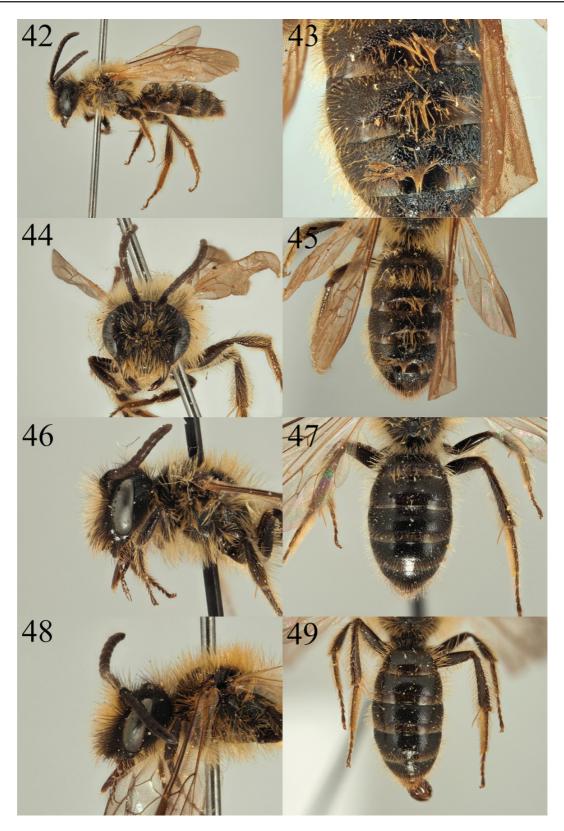
Measurements. Body length 10 mm (Fig. 36).

HEAD. 1.2 times as wide as long (Fig. 38). Clypeus weakly arched, very densely punctate, punctures separated by <0.5 puncture diameters to almost contiguous, underlying surface shiny. Gena, face, and scape with black hairs, face between antennal insertions with few grey hairs, vertex with intermixed black and golden hairs, hairs at most equalling length of scape. Antennae dark, A4–12 lightened grey below. Fovea narrow, occupying $\frac{1}{3}$ of area between lateral occllus and compound eye, comma shaped, filled with black hairs.

Mesosoma. Scutum and scutellum densely punctured, punctures separated by 0.5–1 puncture diameters, underlying surface shagreened, weakly shining (Fig. 37). Episternum and propodeum microreticulate, dull, propodeum with large irregular shallow punctures, separated by 0.5–1 puncture diameters, these not extending onto propodeal triangle, therefore defining it. Scutum and scutellum with golden-brown hairs, episternum centrally with black hairs, anteroventrally with white hairs, propodeum with mixture of whitish and brownish hairs, some black hairs intermixed. Legs dark, slightly lightened to dark red



Figs 36–41. 36–39. *Andrena fortipunctata* Wood sp. nov. (NMNL). **36.** Female profile. **37.** Female scutum. **38.** Female face. **39.** Female terga. — **40–41.** *Andrena bicolor* Fabricius, 1775 (TJWC). **40.** Female face. **41.** Female terga. Not to scale.



Figs 42–49. 42–45. *Andrena fortipunctata* Wood sp. nov. (NMNL). **42.** Male profile. **43.** Male terga detail. **44.** Male face. **45.** Male terga. — **46–47.** *Andrena vulpecula* Kriechbaumer, 1873 (TJWC). **46.** Male face, profile. **47.** Male terga. — **48–49.** *Andrena granulosa* Pérez, 1902 (TJWC). **48.** Male face, profile. **49.** Male terga. Not to scale.

apically, pubescence golden brownish. Flocculus a mixture of blackish and whitish hairs, femoral and tibial scopa golden. Wings hyaline, venation and stigma dark orange, nervulus interstitial.

Metasoma. Terga dark, margins strongly depressed and lightened semi-translucent brown (Fig. 39). Terga densely and uniformly punctate, punctures separated by 0.5–1 puncture diameters, punctures not extending onto depressed tergal margins, excluding margins underlying tergal surface shagreened, weakly shining. T2–4 with hair fringes arising from junction between disc and margin, fringes of sparse white hairs overlying marginal areas, not obscuring underlying surface. Terminal fringe of T5 and hairs flanking pygidial plate dark brown, pygidial plate with centrally raised longitudinal area and raised apical rim, weakly punctate, dull.

Male

Measurements. Body length 10 mm (Fig. 42).

HEAD. 1.2 times as wide as long (Fig. 44). Clypeus weakly arched, densely punctate, punctures separated by 0.5 puncture diameters. Gena, vertex, scape, clypeus, and face centrally with yellow hairs, lower paraocular areas to frons with black hairs. Antennae dark, A4–13 lightened brown below, A3 0.9 times as long as A4+5.

Mesosoma. Structurally as in female, entire surface with long light brown to golden hairs, exceeding scape in length. Legs dark, tarsi lightened, dark red apically, pubescence golden. Wings hyaline, venation and stigma orange, nervulus prefurcal.

METASOMA. Terga dark, apical margins wide and very strongly depressed, semi-translucent brown, impunctate and shiny (Fig. 43). Tergal discs arched, strongly contrasting depressed marginal areas, strongly and densely punctate, punctures separated by 1 puncture diameter, surface covered with loose golden hairs (Fig. 45).

Remarks

The subgenus *Euandrena* is taxonomically challenging, and it is likely that we are just scratching the surface of hidden species diversity in southern European mountain chains (Praz *et al.* 2019). The *Andrena* of the Iberian alpine areas have received little recent attention, and within this context, the presence of an undetected alpine *Euandrena* in the high mountains of Spain is less surprising, but emphasises how much more there is to learn about European diversity of *Andrena* even in a comparatively well-studied region.

Distribution

The Sierra de Gredos in the Sistema Central to the Cantabrian mountains in northwestern Spain in the province of Asturias.

Andrena (Charitandrena) hattorfiana nigricauda Wood subsp. nov. urn:lsid:zoobank.org:act:73F5116B-23D0-4071-BA9F-6B54A54405CC Figs 50, 52, 54, 56, 58, 60, 62, 64

Diagnosis

Andrena hattorfiana (Fabricius, 1775) can be very easily recognised as it is the only known member of the *Charitandrena* Hedicke, 1933 in the West Palaearctic. Females have a unique combination of a conspicuously carinate hind femur, a hind tibial spur that is convexly broadened towards the middle, and an elongate glossa. Males are harder to recognise through a combination of unique characters, but their

large body size, yellow clypeus, lack of a pronotal carina, and long glossa in combination with specific characters such as genital structure are sufficient to facilitate identification.

Andrena hattorfiana nigricauda Wood subsp. nov. differs from the nominate form (Figs 51, 53, 55) because it has an almost completely darkened integument and pilosity. True Andrena hattorfiana normally shows extensive variation in the colour of its abdominal integument, with individuals from the same location varying from extensively red marked to completely black. Its variability has resulted in a relative large number of synonyms for an Andrena (Gusenleitner & Schwarz 2002). However, what is consistent is that the hairs of T5 and those flanking the pygidial plate are uniformly golden-orange (Fig. 55). In the Spanish material presented here, these hairs are completely black (Fig. 54). In the male, there are no clear structural differences, but as in the female the pubescence is much darker across the whole body (Figs 58–63).

Etymology

The name 'nigri' ('black') + 'cauda' ('tail') was chosen to reflect the black hairs at the apex of the metasoma in the female sex, a clear point of difference from the nominate form.

Material examined

Holotype

SPAIN • ♀; Alicante, Puerto de Confrides; 1000 m a.s.l.; [38.686° N, 0.271° W]; 15 Jun. 1978; H. Teunissen leg.; NMNL (illustrated Figs 50, 52, 54, 56).

Paratypes

SPAIN • 2 $\lozenge\lozenge, 5 \circlearrowleft$; Alicante, Puerto de Confrides; 1000 m a.s.l.; 15 Jun. 1978; H. Teunissen leg.; NMNL (illustrated Figs 58, 60, 62, 64) • 1 \circlearrowleft ; same collection data as for preceding; OÖLM • 1 \circlearrowleft ; same collection data as for preceding; TJWC.

Other material (*Andrena hattorfiana*)

SPAIN • 1 &, 1 &; Madrid, Collado Mediano; 17 May 1995; H. and J.E. Wiering leg.; NMNL (illustrated Figs 59, 61, 63, 65) • 1 &; Pirineos Orient, 20 km NE of Ripoll; 1650 m a.s.l.; 31 Jul. 2011; J. Halada leg.; OÖLM (illustrated Figs 51, 53, 55, 57) • 1 &; Huesca, Mte Perdido; 1300 m a.s.l.; 1 Aug. 1977; P.M.F. Verhoeff leg.; NMNL • 1 &; Viella; 1100–1800 m a.s.l.; 27 Jul. 1963; H. Hamann leg.; OÖLM • 1 &; Cantabria, Picos de Europa, Camaleno; 600 m a.s.l.; 5 May 2014; D.W. Baldock leg.; TJWC • 1 &; Santander, Arredondo, Bustablado; 11 Jul. 1984; R. Leys leg.; NMNL.

Description

Female

Measurements. Body length 16–17 mm (Fig. 50).

HEAD. Black, 1.2 times as wide as long (Fig. 52). Clypeus domed, slightly flattened centrally and apically, underlying surface shagreened and dull basally and laterally, becoming weaker apically, weakly shining. Entire surface densely punctured with exception of faint impunctate central line, punctures separated by 0.5–1 puncture diameters. Process of labrum triangular, twice as broad as long, deeply emarginate apically. Gena, vertex, face, and scape with moderately long dark brown to black hairs, longest equalling length of scape. Antennae dark, A3 long, exceeding length of A4+5+6, A5–12 lightened orange below. Fovea of a uniform width, occupying half of area between lateral ocelli and top of compound eye. Vertex wide, as wide as three ocellar diameters.

Mesosoma. Scutum and scutellum finely shagreened, weakly shining, densely and evenly punctured, punctures separated by 1 puncture diameter. Episternum and propodeum evenly and finely rugose, propodeal triangle clearly marked by a lateral carina, internal surface with more strongly produced



Figs 50–57. 50, 52, 54, 56. *Andrena hattorfiana nigricauda* Wood subsp. nov. (NMNL). **50.** Female profile. **52.** Female face. **54.** Female terga. **56.** Female scopa, ventral view. — **51, 53, 55, 57.** *Andrena hattorfiana* (Fabricius, 1775) (TJWC). **51.** Female profile. **53.** Female face. **55.** Female terga. **57.** Female scopa, ventral view. Not to scale.

rugosity, broadly similar. Scutum and scutellum with short, episternum and propodeum with longer dark brown hair, at its longest not exceeding length of scape. Legs dark, apical tarsal segments lightened red-brown, pubescence dark brown to dark red. All scopal hairs dark brown, those of femoral and tibial scopa ventrally finely plumose, otherwise simple. Wings weakly infuscate, venation dark brown, nervulus interstitial.

METASOMA. Terga dark brown, only apical margins slightly lightened brown (Fig. 54). Tergal surface very weakly shagreened, generally shining, centrally punctured, punctures separated by 1–2 puncture diameters, punctures becoming sparse laterally, here separated by 3–4 puncture diameters. Hairs of T5 and those flanking pygidial plate dark brown to black, pygidial plate rounded, smooth, very weakly convex, impunctate.

Male

MEASUREMENTS. Body length 15 mm (Fig. 58).

HEAD. Black, 1.2 times as wide as long (Fig. 60). Characters as in female, but clypeus yellow with exception of two dark spots laterally, A3 slightly subequal to A4+5+6, and A4–13 lightened orange below.

Mesosoma. As in female.

METASOMA. As in female (Fig. 62). S7 deeply emarginate apically, S8 columnar, apical half hairy with two broad lateral tufts centrally and one tuft apically, apex truncate. Genitalia with pronounced but truncate gonocoxal teeth, penis valve broadly triangular, tapering apically, gonostyli long and narrow with slightly flattened apexes with short, white, sparse hairs (Fig. 64).

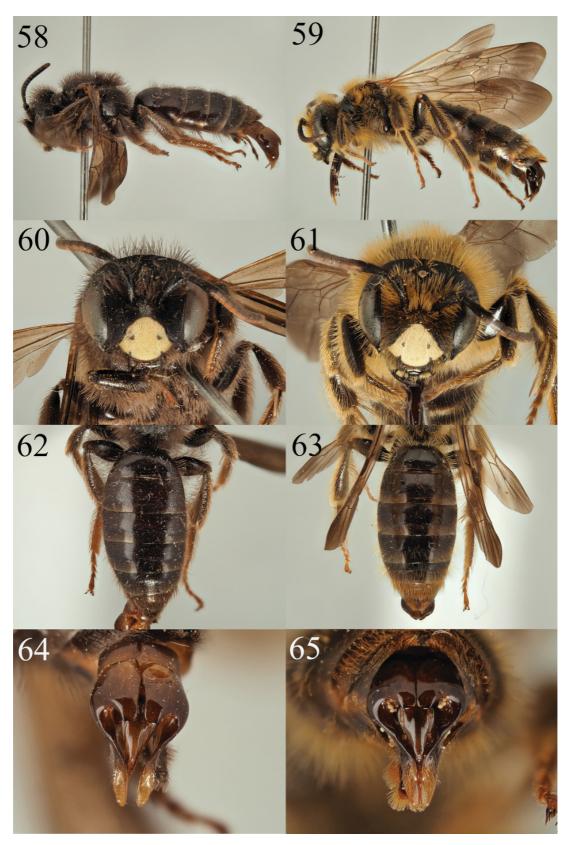
Remarks

The presence of *A. hattorfiana nigricauda* Wood subsp. nov. in the mountains of Alicante represents, at the very least, an isolated population showing a unique colour pattern. Other records of *A. hattorfiana* in Spain come from the Sistema Central around and to the west of Madrid, the Picos de Europa, and the Pyrenees (Gusenleitner & Schwarz 2002). The location in Alicante is therefore around 400 km from the nearest known populations of *A. hattorfiana* that conform to the typical hair colour pattern. However, separating this population as specifically distinct is premature without molecular investigation, and overall differences are slight outside of colouration; the male genitalia of the two colour forms are essentially indistinguishable. *Andrena hattorfiana nigricauda* subsp. nov. could simply be a melanic form, and molecular analysis could show whether it is nested within *A. hattorfiana* when considered across its whole range. Indeed, material of *A. hattorfiana* from the most southerly parts of the Balkan Peninsula has hairs flanking the pygidial plate that are dark brown, but otherwise this material shows typical red terga (treated as *A. h. dimidiata* Brullé, 1832 by Warncke, see Gusenleitner & Schwarz 2002).

Pollen removed from the scopae of four females of *A. hattorfiana nigricauda* subsp. nov. (Fig. 56) consisted of *Knautia*-type pollen (formerly Dipsacaceae Juss., now Caprifoliaceae Juss.). *Andrena hattorfiana* is a very well-studied specialist of this family (Fig. 57; Westrich 1989; Larsson & Franzén 2007), suggesting that the dietary niche itself is unchanged.

Distribution

Andrena hattorfiana is distributed from central and northern Spain across Europe to Greece, Turkey, and the Caucasus (Gusenleitner & Schwarz 2002).



Figs 58–65. 58, 60, 62, 64. Andrena hattorfiana nigricauda Wood subsp. nov. (NMNL). 58. Male profile. 60. Male face. 62. Male terga. 64. Male genitalia. — 59, 61, 63, 65. Andrena hattorfiana (Fabricius, 1775) (TJWC). 59. Male profile. 61. Male face. 63. Male terga. 65. Male genitalia. Not to scale.

Andrena (Lepidandrena) baetica Wood, 2020 Figs 66–69

Material examined

PORTUGAL • 1 ♂; Algarve, Tareja; [37.173° N, 7.879° W]; 13 Apr. 1991; J. v. Corstanje leg.; NMNL (illustrated Figs 66–69).

Description

Male

MEASUREMENTS. Body length 9 mm (Fig. 66).

HEAD. Black, 1.1 times as wide as long (Fig. 67). Clypeus black, slightly domed and slightly flattened centrally, densely punctured laterally with punctures separated by 0.5 puncture diameters, becoming sparser centrally, separated by 1 puncture diameter, narrow central impunctate line present. Gena, clypeus, and inter-antennal area with white hairs, vertex with a mixture of white, brown, and black hairs, and frons and inner margin with black hairs, all hairs variable in length, longest exceeding length of scape. Antennae uniformly dark, A3 slightly shorter than A4+5.

Mesosoma. Scutum shagreened, very weakly shining, densely punctured, punctures separated by 0.5–1 puncture diameter, slightly sparser centrally. Scutellum comparatively less shagreened, weakly shining,



Figs 66–69. *Andrena baetica* Wood, 2020 (NMNL). **66.** Male profile. **67.** Male face. **68.** Male terga. **69.** Male genitalia. Not to scale.

very densely punctured, punctures separated by <0.5 puncture diameters. Episternum and propodeum reticulate, dull. Propodeal triangle large, clearly marked with raised carina, internal surface with weak longitudinal rugae. All parts of mesosoma with long white hairs which exceed length of scape. Legs dark, apical tarsal segments lightened orange, including hind basitarsi. Wings hyaline, venation orange, nervulus interstitial.

Metasoma. Terga dark, apical margins lightened dark red, very densely and uniformly punctate, punctures separated by 0.5 puncture diameters, underlying surface weakly shagreened, shining (Fig. 68). T1–4 with loose apical hair bands, those on T1–3 interrupted, on T4 complete. S8 short, projecting area as wide as long, apical margin notched. Genitalia long, gonocoxa inflated, therefore forming a channel along their internal margins, apical teeth broadly rounded (Fig. 69). Penis valve triangular, narrowing apically to a rounded point. Gonostyli narrow and elongate, dorsal face flattened and bearing sparse, short hairs.

Remarks

Andrena baetica is morphologically close to A. mocsaryi Schmiedeknecht, 1883, but differs in the shorter, squamous hairs on the scutum (Wood et al. 2020). The discovery of this male material further confirms the proximity of A. baetica to A. mocsaryi through genital structure (Fig. 69, see illustrations in Schmid-Egger & Scheuchl 1997), but also confirms its specific status as it possesses an entirely black clypeus, whereas A. mocsaryi has a yellow clypeus, and the apex of S8 is truncate to slightly emarginate, whereas in A. mocsaryi it is slightly pointed (Schmid-Egger & Scheuchl 1997).

Distribution

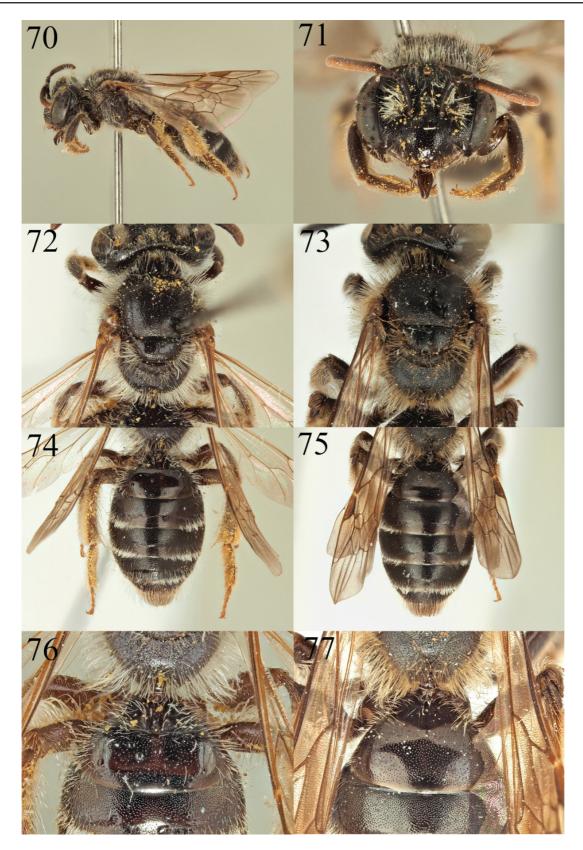
Southern Spain (Cadiz, Los Alcornocales; Cazorla, Sierra Pozo) and southern Portugal (Alentejo; Algarve) (Wood et al. 2020).

Andrena (Notandrena) juliana Wood sp. nov. urn:lsid:zoobank.org:act:D61A664D-0821-4470-8807-6CC3C7B93E9F Figs 70–72, 74, 76, 78–83

Diagnosis

This taxon can be placed in the subgenus *Notandrena* in the female sex because of its broad head (clearly broader than wide), the weakly rugose (not shagreened) propodeal triangle, the clearly punctured metasoma, and by the dorsolateral angle of the pronotum with a weak transverse ridge. In the male sex, recognition is easy because of the greatly enlarged and carinate gena in combination with the broadened apex of the gonostyli.

Eight species of the subgenus *Notandrena* are known from Iberia (Wood *et al.* 2020). Female *Andrena juliana* Wood sp. nov. can be recognised in the group of *A. nitidiuscula* Schenck, 1853 because of its small size (7–8 mm, excluding *A. erythrocnemis* Morawitz, 1870, *A. langadensis* Warncke, 1965, and *A. urdula* Warncke, 1965 which average 11–12 mm in length) and dark hind tibiae (orange in *A. chrysosceles* (Kirby, 1802)). Within this group, it lacks the distinctive shortened dorsal scopal hairs of *A. pallitarsis* Pérez, 1903, the gena and vertex are normal (vertex clearly less than the diameter of a lateral ocelli, clearly greater than this distance in *A. foeniculae* Wood, 2020), and there is no deeply impressed line on the front half of the scutum (clearly impressed in *A. nitidiuscula*). In an Iberian context, it is therefore closest to *A. fulvicornis* Schenck, 1853 (alternative character state in parentheses), but differs in the sparser punctures on T1, separated by 2–3 puncture diameters (separated by one puncture diameter, Fig. 77), by the shinier scutellum (scutellum shagreened and clearly dull, Fig. 73), and by the hind tibiae which are dark (orange). Outside of Iberia, *A. juliana* Wood sp. nov. is also close to *A. curvana* Warncke, 1965 which is distributed from southern Germany southwards and eastwards to Romania, Bulgaria,



Figs 70–77. 70–72, 74, 76. *Andrena juliana* Wood sp. nov. (NMNL). **70.** Female profile. **71.** Female face. **72.** Female scutum. **74.** Female terga. **76.** Female terga detail. — **73, 75, 77.** *Andrena fulvicornis* Schenck, 1853 (TJWC). **73.** Female scutum. **75.** Female terga. **77.** Female terga detail. Not to scale.

Greece, and the European part of Turkey (Gusenleitner & Schwarz 2002; Schwenninger 2013). It can be separated by the sculpturing of the clypeus which is shiny centrally (centrally shagreened) and by the sculpturing of the scutellum which is shiny (strongly shagreened and dull).

Males can be quickly recognised by their yellow clypeus in combination with their small size (7 mm), a character that is also found in *A. chrysosceles* and *A. pallitarsis* (*A. erythrocnemis*, *A. langadensis*, and *A. urdula* with the clypeus yellow marked, but larger, averaging 10 mm). In both these species, the yellow markings cover the entire clypeus and extend onto the lower paraocular areas, whereas in *A. juliana* sp. nov. this marking is restricted to the centre of the clypeus. The gena is noticeably more carinate, and as in the female the scutum is also noticeably shinier. The genitalia conform to the typical shape found in members of the *nitidiuscula* group (Fig. 83; see illustrations in Schmid-Egger & Scheuchl 1997; Schwenninger 2013). As for other members of this group, the gonocoxa are weakly shagreened in a similar fashion to that found in the *Zonandrena* Hedicke, 1933. However, the outer margin of the gonostyli is almost straight, whereas there is a clearer obtuse angle here in *A. chrysosceles*, *A. pallitarsis*, and *A. fulvicornis* (see illustrations in Schmid-Egger & Scheuchl 1997; Schwenninger 2013). As in the female sex, the male is also similar to the eastern *A. curvana*. However, apart from the yellow clypeus (black in *A. curvana*), the genitalia are different, with less pronounced gonocoxal teeth, and lacking the pronounced impressed channel in the basal section of the gonostyli (see illustration of this character in Schwenninger 2013).

Etymology

The name is taken from the locus typicus, San Julián.

Material examined

Holotype

SPAIN • \bigcirc ; Málaga, San Julián 8 km SW of Málaga; [36.666° N, 4.476° W]; 25 May 1962; Jeekel & Wiering leg.; NMNL (illustrated Figs 70–72, 74, 76).

Paratype

PORTUGAL • 1 &; Algarve, Gambello [Gambelas]; 5 Mar. 1986; H. Teunissen leg.; NMNL (illustrated Figs 78–83).

Description

Female

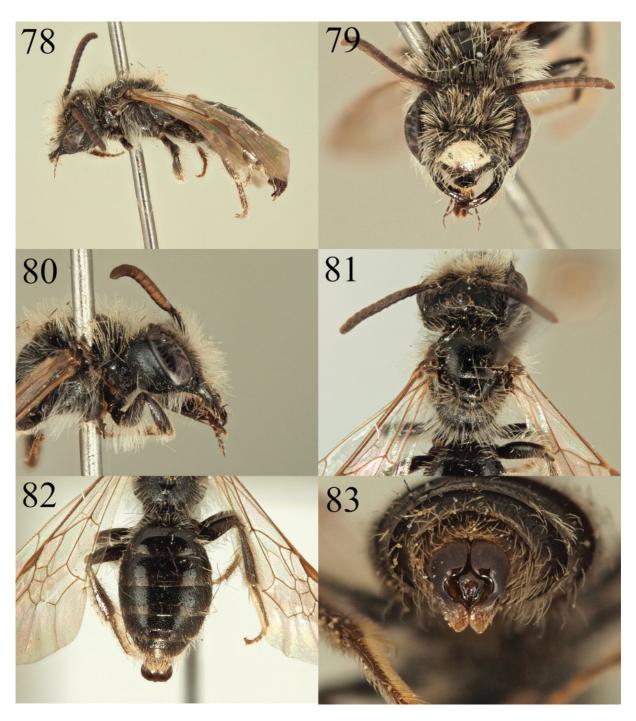
MEASUREMENTS. Body length 8.5 mm (Fig. 70).

HEAD. Dark, broad, 1.4 times as wide as long (Fig. 71). Clypeus domed, laterally and dorsally shagreened and densely punctate, punctures separated by 0.5 puncture diameters, centrally shiny and less densely punctate, punctures separated by 0.5–1.5 puncture diameters, weakly-marked impunctate line present. Process of labrum small, rectangular, front margin very weakly emarginate. Gena as wide as compound eye, gena, vertex, and face with whitish hairs, these not exceeding length of scape. Antennae dark, A5–12 lightened orange below, A3 equalling A4+5, both A4 and A5 clearly broader than long. Facial fovea neither wide nor narrow, occupying half space between lateral ocellus and compound eye. Ocelloccipital distance short, less than half diameter of lateral ocellus.

Mesosoma. Scutum weakly shagreened, gently shining, densely but shallowly punctured, punctures separated by 0.5–1 puncture diameter centrally (Fig. 72). Scutum in fore half with barely impressed mid line. Scutellum more clearly shiny, punctures dense only at margin and forming a central longitudinal line, otherwise sparse and separated by 3–4 puncture diameters. Episternum and propodeum finely reticulate, dull, propodeal triangle barely indicated by very fine carina, internal structure essentially

unchanged. Scutum and scutellum with short whitish pubescence through which longer hairs protrude, these approaching length of scape. Episternum and propodeum with longer whitish hairs, longest equalling length of scape. Legs dark, apical tarsal segments and apex of basitarsi coloured orange, this extending slightly onto apex of hind tibiae. Wings hyaline, venation orange, nervulus interstitial.

Metasoma. Terga dark, apical margins lightened yellow-brown, underlying surface weakly shagreened, shining (Fig. 74). T1 sparsely and finely punctate on disc, punctures separated by 2–4 puncture diameters



Figs 78–83. *Andrena juliana* Wood sp. nov. (NMNL). **78**. Male profile. **79**. Male face. **80**. Male gena. **81**. Male scutum. **82**. Male terga. **83**. Male genitalia. Not to scale.

(Fig. 76), strongly contrasting with following terga, T2–4 densely punctate on discs, punctures separated by 0.5–1 puncture diameter. Marginal areas of T1–4 less densely punctate, punctures separated by 1–2 puncture diameters. T2–4 with fringes of white hair, interrupted on T2–3, complete on T4. T5 and hairs flanking pygidial plate light brown, pygidial plate smooth, apically rounded, weakly shining.

Male

MEASUREMENTS. Body length 7 mm (Fig. 78).

HEAD. Dark, broad, 1.3 times as wide as long (Fig. 79). Clypeus yellow over majority of disc, all marginal areas black with two lateral triangular black marks. Underlying surface weakly shagreened, shining, centrally sparsely punctate, punctures separated by 2 puncture diameters, marginal areas densely punctate, punctures separated by 0.5–1 puncture diameter. Apical part of clypeus extended and upturned, process of labrum trapezoidal, apical margin upturned forming rounded ridge, apex emarginate. Gena exceeding width of compound eye, weakly carinate (Fig. 80). Gena, vertex, face, and scape with long brownish-white hairs, not exceeding length of scape. Antennae dark, A4–13 lightened orange below, A3 exceeding A4 but shorter than A4+5.

MESOSOMA. Scutum and scutellum laterally shagreened and dull, centrally shining, sparsely punctate, punctures separated by 2–3 puncture diameters (Fig. 81). Episternum, propodeum, and vestiture as in female. Legs dark, apical tarsal segments lightened orange. Wings as in female.

Metasoma. Terga dark, apical margins lightened brown, underlying surface very weakly shagreened, shining (Fig. 82). T1 almost impunctate, T2–4 with sparse and inconspicuous punctures, separated by 1–2 puncture diameters. S8 short, apically slightly broadened and rounded, basally with short and thick golden bristles that project laterally. Genitalia simple, gonocoxa with faint shagreenation, apical corners rounded, diverging (Fig. 83). Penis valve triangular, strongly narrowed apically. Gonostyli with straight external margin, weakly pointed apically, with slightly raised internal margin.

Remarks

Using the key to Iberian *Notandrena* of Wood *et al.* (2020), females of *A. juliana* Wood sp. nov. key to couplet seven which separates *A. fulvicornis* and *A. nitidiuscula*. It can be separated from *A. nitidiuscula* by the absence of an impressed longitudinal line on the front half of the scutum, and from *A. fulvicornis* by the less dense punctures of T1 and the shinier scutellum. No male key was produced because the male of *A. foeniculae* is unknown, but males of *A. juliana* sp. nov. should be identifiable by the combination of their genital structure and yellow clypeus. Additionally, *A. foeniculae* flies in August and September, and so based on the limited number of specimens collected to date, both taxa are unlikely to fly together at the same time. The similar species *A. curvana* and *A. fulvicornis* are bivoltine and fly in both the spring and the summer. Since *A. juliana* sp. nov. is known only from spring material, further study is needed to clarify its full period of activity.

Distribution

Southern Spain (Málaga) and southern Portugal (Algarve). Both localities are very close to the coast, adjacent to estuaries, specifically those of the Guadalhorce (San Julián) and Ribeira de São Lourenço (Gambelas). This habitat type should be searched during the spring, as it may contain habitat elements or flowering plants that are important for the ecology of *A. juliana* Wood sp. nov.

Andrena (Euandrena) impressa Warncke, 1967 stat. nov. Figs 84–87, 89, 91, 93, 95, 97, 99

Andrena angustior impressa Warncke, 1967: 234 (Morocco, Tangier, 3).

Material examined (Andrena impressa)

Holotype

MOROCCO • ♂; Tangier; OÖLM (illustrated Fig. 86).

Paratypes

PORTUGAL • 1 ♂, 1 ♀; Cardigos; OÖLM • 1 ♀; Matto do Fundão; OÖLM (illustrated Fig. 85).

SPAIN • 1 &; Barcelona; O. Schmiedeknecht leg.; OÖLM • 1 &; Canet de Mar; 17 May 1963; Vergés leg.; OÖLM.

Other material

ALGERIA • 1 &; El Kseur, F. t. d'Akfadou; 22 May 1981; OÖLM.

MOROCCO • 1 ♀; Tangier; OÖLM • 1 ♀; Azil. Taddert; 1750 m a.s.l.; 10 Mar. 1988; V. Lefeber leg.; NMNL • 1♀; Issaguen, 150 km SE of Tanger; 1550 m a.s.l.; 12 May 2015; Mucska leg.; OÖLM.

PORTUGAL • 1 \updownarrow ; Bensafrim; 5 Mar. 2015; I. Cross leg.; ICC • 1 \updownarrow ; Rossas, Touça, N205 x M614; 14 May 2019; Wood leg.; TJWC (illustrated Figs 87, 89, 91) • 1 \updownarrow ; Vilarinha; 16 Apr. 2017; I. Cross leg.; ICC.

SPAIN • 1 &; Almeria, Enix; 300 m a.s.l.; 10 May 1978; Diller leg.; OÖLM • 1 &; Almeria: Bayarcal; 24 Jun. 1988; M. Schwarz leg.; MSC • 1 &; Ávila, Guisando; 750 m a.s.l.; 27 May 1995; H. and J.E. Wiering leg.; TJWC • 1 &; Cáceres; 4 Apr. 1921; J.M. Dusmet y Alonso leg.; OÖLM • 1 &; Cáceres, Rivera de Gata, W of Villasbuenas; 16 Jun. 1984; W. Schacht leg.; OÖLM • 1 &; Canet de Mar; 12 Apr. 1965; Vergés leg.; OÖLM • 1 &; Granada, Ventas del Molinello; 20 Jun. 1987; M. Schwarz leg.; TJWC • 1 &; Granada, Sierra de Almijara, Pico Lopera; 25 Mar. 2009; I. Cross leg.; ICC • 1 &; Málaga, Alcuzcuz, nr San Pedro de Alcantara; 18 Apr. 1983; NMNL • 4 & &; Málaga, Marbella; 14 May 1959; J. v. d. Vecht leg.; NMNL • 1 &; Málaga, Sierra Bermeja; 15 May 1959; J. v. d. Vecht leg.; NMNL • 1 &; Málaga, Sierra Bermeja; 15 May 1959; J. v. d. Vecht leg.; NMNL • 1 &; Mallorca, Soller; 1957; N. Briedé leg.; NMNL • 1 &; Mallorca, Tramuntana, Galilea; 22 May 2012; D.W. Baldock leg.; TJWC • 1 &; Murcia, Sierra de Españula; 11 May 2003; J. Halada leg.; TJWC • 1 &; Nof Figueres; 2 May 2003; M. Snižek leg.; OÖLM • 1 &; Ronda env.; 26 Feb. 2015; P. Kylies leg.; TJWC (illustrated Figs 93, 95, 97, 99) • 1 &; Ronda; 800 m a.s.l.; 23 Mar. 1986; C. v. Achterberg leg.; NMNL • 1 &; Sierra Filabres Albanchez; 23 Apr. 2003; J. Halada leg.; OÖLM.

Material examined (Andrena angustior)

BELGIUM • 1 \circlearrowleft , 1 \circlearrowleft ; Mons; 29Apr.–12 May 2019; W. Fiordaliso leg. • 1 \circlearrowleft ; Tromp, Stropersbos; 6 May 2020; Wood leg.; TJWC.

GERMANY • 1 $\ \$; Osterwald; 25 May 1926; J.D. Alfken leg.; ZMHB • 1 $\ \$; Sababurg; 30 May 1936; J.D. Alfken leg.; ZMHB.

PORTUGAL • 2 ♂♂, 2 ♀♀; Branca; 11 Mar.–2 Apr. 2019; H. Gaspar leg. • 1 ♀; Confurco, Várzea Cova; 14 May 2019; Wood leg.; TJWC • 1 ♀; 1 km south of Paradela, M308–4; 12 May 2019; Wood leg.; TJWC • 1 ♀; Pedraído, Fafe; 14 May 2019; Wood leg.; TJWC (illustrated Figs 88, 90, 92) • 1 ♀; Serra do Gerês, 5 km W of Paradela; 12 May 2019; Wood leg.; TJWC.

Material examined (Andrena fulvata)

AUSTRIA • 1 ♀; Fürberg, Wolfgangsee; 16 Apr. 1946; ZMHB.

BELGIUM • 1 ♂; Estinnes-Au-Mont, Les Trieux; 24 Mar. 2019; J. Dewaele leg.

BOSNIA AND HERZEGOVINA • 1 \circlearrowleft , 4 \circlearrowleft \circlearrowleft ; Gradiska, Turjak; 7–9 Apr. 2019; Mitrovic and Golubovic leg.; ULB.

BULGARIA • 1 &; Šípka mont [Shipka]; 12 May 1994; K. Deneš leg.; OÖLM.

CROATIA • 1 ♂; Zagreb; 22 Apr. 1897; ZMHB.

FRANCE • 3 \circlearrowleft \circlearrowleft 1 \circlearrowleft ; Belval-Bois-des-Dames, Domaine de Belval; 22 Mar.–21 Apr. 2019; C. Amy leg. • 1 \circlearrowleft ; Desvres; 15 May 2018; R. Vandeweghe leg. • 1 \circlearrowleft ; Eclusier-Vaux, Marais de Vaux; 5 Mar.–1 Apr. 2019; D. Adam leg. • 11 \circlearrowleft \circlearrowleft ; Elincourt-Sainte-Marguerite; 18 May–7 Jun. 2018; B. Piallat and C. Bocaux leg. • 1 \circlearrowleft ; Fresnoy-la-Rivière, Les petits Monts; 6 Apr. 2018; D. Top leg. • 1 \circlearrowleft ; Raismes, forêt de Saint-Amand; 13 Jun. 2005; J.-L. Vago leg. • 1 \hookrightarrow ; Xouaxange; 20 May 2019; C. Brelot and C. Filet leg. • 1 \circlearrowleft ; Ruy; 17 Mar. 2020; C. Triquet leg.

GERMANY • 3 \circlearrowleft \circlearrowleft \circlearrowleft \circlearrowleft \circlearrowleft \circlearrowleft \circlearrowleft ; Kaiserstuhl, Achkarren; 29 Mar.–20 Apr. 1937; S.G. Bischoff leg.; ZMHB • 1 \circlearrowleft ; Kaiserstuhl, Büchsenberg; 1 Apr. 1937; S.G. Bischoff leg.; ZMHB • 2 \circlearrowleft \circlearrowleft \circlearrowleft , 1 \circlearrowleft ; Kaiserstuhl, Liliental; 19–24 Apr. 1937; S.G. Bischoff leg.; ZMHB • 1 \circlearrowleft ; Kaiserstuhl, Vogtsburg; 20–21 May 1933; S.G. Bischoff leg.; ZMHB • 5 \circlearrowleft \circlearrowleft ; Kehl am Rh. [Rhine]; 1–5 Apr. 1937; L. Battes leg.; ZMHB.

ITALY • 1 ♂, 1 ♀; Bologna, Parco di Villa Ghigi; 9–16 Apr. 2017; G. Ghisbain leg.; TJWC • 1 ♂, 1 ♀; Lazio, Acquapendente; 26 May 1991; J. Gusenleitner leg.; TJWC.

SLOVENIA • 1 ♀; Styr, Podčetrtek; 28 Apr. 1932; Jaeger leg.; ZMHB • 1 ♀; Orechek [Orehek]; 28 May 2005; Egger leg.; OÖLM.

Material not directly examined (Andrena fulvata)

AUSTRIA • 1 ♀; Oberösterreich, Kremsmünster; 6 May 1972; J. Gusenleitner leg.; Zobodat • 1 ♀; Oberösterreich, Losenstein a.d. Enns; 25 Mar. 1979; K. Kremslehner leg.; Zobodat • 1 ♂; Oberösterreich, Magdalenaberg SE of Pettenbach; 16 May 1979; J. Gusenleitner leg.; Zobodat.

NETHERLANDS • 1 ♂; Limburg, Eys - Bronnen en Bronbos; 14 Apr. 2018; I. Raemakers leg.; Waarneming.nl • 1 ♀; Limburg, Savelsbos; 2 Apr. 2017; I. Raemakers leg.; Waarneming.nl.

ROMANIA • Băile Herculane • Bocsa Montana • Mehadia • Timisoara, all B. Tomozii pers. comm.

Remarks

Though placed in the subgenus Ptilandrena by Warncke (1967), the use of this subgenus should be restricted to the Nearctic (Pisanty et al. 2021). Therefore, A. impressa stat. nov. and related species are found within the Euandrena (see also Praz et al. 2019). Andrena angustior was originally described from England, and can rapidly be identified in the female sex by the combination of a central, longitudinal impression on the clypeus with the wide, depressed and shiny margins of the terga. In the male, in addition to the tergal sculpturing, the gena is enlarged and the mandibles are elongated in a manner similar to Andrena subgenus Andrena but without the presence of basal mandibular teeth. Andrena fulvata Stoeckhert, 1930 was later described from southern Germany. The two species are similar, but A. fulvata lacks the shiny depressed tergal margins, these are instead only weakly depressed, shagreened, and matt. Warncke considered A. fulvata to be a subspecies of A. angustior, and described A. a. impressa from Morocco, Portugal, and Spain, arguing that the variation across this geographic gradient merited a broad species concept (Warncke 1967). This form can easily be separated from A. angustior s. str. in the female sex by the structure of the terga which are weakly depressed, shagreened, only weakly shining, and also by the colouration of the hairs flanking the pygidial plate which are black (compare Figs 91-92), and the bee has an overall darker appearance (compare Figs 87–90). Males can be separated by the same differences in tergal structure (Figs 97–98) and overall darker pubescence, particularly on the head (Figs 93-96). The most obvious difference can be seen in the antennal ratios. In A. impressa, A4 is only slightly shorter than A3 (Fig. 99), whereas in A. angustior A4 is less than half the length of A3 (Fig. 100).

Subsequent authors have not followed Warncke's viewpoint, treating *A. angustior* and *A. fulvata* as good species (see Gusenleitner & Schwarz 2002; Nieto *et al.* 2014). These two taxa show different climatic affinities. For example, in Germany, *A. angustior* is present in the north, reaching as far south as Rhineland-Palatinate but not extending into Baden-Württemberg (Westrich 1989). To the east, the more northwestern *A. angustior* is completely replaced by the more continental *A. fulvata*. However, to date, the status of *A. a. impressa* has not been assessed, with the default position of Warncke being that *A. angustior* s. str. was absent from Iberia (Gusenleitner & Schwarz 2002; Ortiz-Sánchez 2011). Specimens collected from northern Portugal showed that both *A. angustior* and *A. a. impressa* were present in sympatry, with the two specimens barcoded here collected just 6 km apart. Molecular data strongly supports the species status of *Andrena impressa* stat. nov., as the Portuguese *A. angustior*

sequence closely matched sequences from northern European populations, and the phylogeny suggests that *A. impressa* is more strongly differentiated than *A. angustior* and *A. fulvata* are from each other (Fig. 2). Though the molecular phylogeny suggests that *A. impressa* is more distantly related to *A. angustior+A. fulvata* than *A. allosa+A. amieti*, support for this placement is weak, and based on the morphology of the male head we consider *A. angustior+A. fulvata+A. impressa* to form a trio of related but distinct species.

The diet of *A. angustior* in Britain was documented by Wood & Roberts (2017). Five additional analysed pollen loads from northwestern Iberia contained Caryophyllaceae Juss. (48.8%, *Arenaria* L.), Ericaceae Juss. (15.8%, *Erica* L.), Asparagaceae Juss. (10.5%, *Scilla* L.), Crassulaceae J.St.Hil. (8.4%, *Sedum* L.), Cistaceae Juss. (6.3%, *Cistus* L.), Brassicaceae Burnett (5.7%, *Raphanus*-type), Rosaceae Juss. (3.2%, *Potentilla* L.), and Ranunculaceae Juss. (1.3%, *Ranunculus* L.). The western distribution, the latespring flight period at the end of April into May, and these dietary preferences support the position that

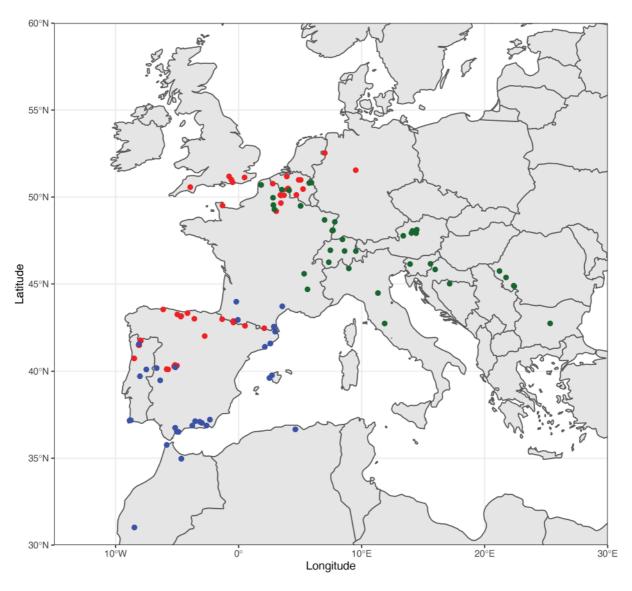
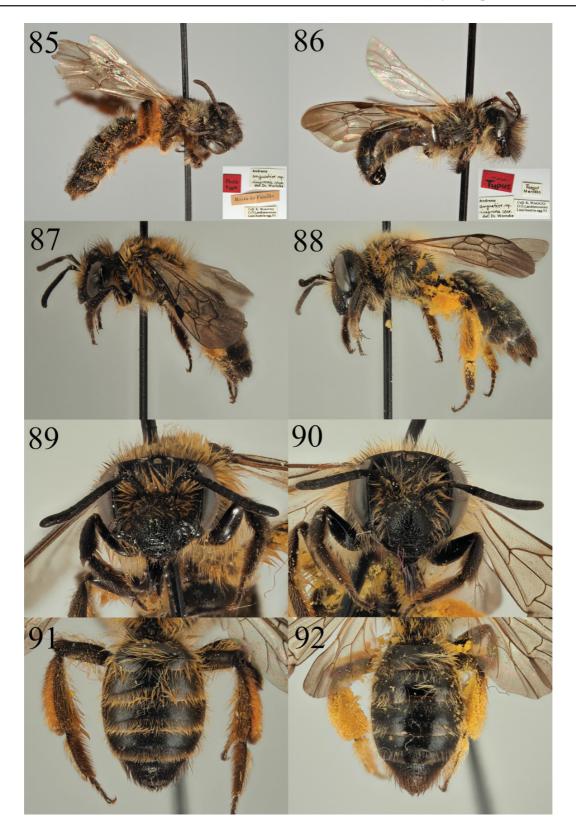


Fig. 84. Records of *Andrena* (*Ptilandrena*) angustior (Kirby, 1802) [red dots], *A.* (*P.*) fulvata Stoeckhert, 1930 [green dots] and *A.* (*P.*) impressa Warncke, 1967 stat. nov. [blue dots] showing Atlantic, Continental and West Mediterranean distributions, respectively. Records presented here are not exhaustive.



Figs 85–92. 85–87, 89, 91. Andrena impressa Warncke, 1967 stat. nov. 85. Female profile (paratype, OÖLM). 86. Male profile (holotype, OÖLM). 87. Female profile (TJWC). 89. Female face (TJWC). 91. Female terga (TJWC). — 88, 90, 92. Andrena angustior (Kirby, 1802) (TJWC). 88. Female profile. 90. Female face. 92. Female terga. Not to scale.



Figs 93–100. 93, 95, 97, 99. *Andrena impressa* Warncke, 1967 stat. nov. (TJWC). **93**. Male profile. **95**. Male gena. **97**. Male terga. **99**. Male antennae. — **94, 96, 98, 100**. *Andrena angustior* (Kirby, 1802) (TJWC). **94**. Male profile. **96**. Male gena. **98**. Male terga. **100**. Male antennae. Not to scale.

A. angustior is a species of Atlantic woodland edges, utilising spring flowering herbs and shrubs but interestingly not the trees themselves. Fewer data are available for *Andrena impressa*; the two analysed pollen loads contained Cistaceae (50.3%, *Cistus*), Scrophulariaceae Juss. (42.9%, *Scrophularia* L.), and Asteraceae Bercht. & J.Presl (6.9%, *Anthemis*-type). Given its distribution, a diet more focused on Mediterranean herbs and shrubs is expected, but more study is required.

Distribution

The distribution map of Warncke (see Gusenleitner & Schwarz 2002) is broadly correct in the northern distribution of *A. angustior*, the continental distribution of *A. fulvata*, and the West Mediterranean distribution of *A. impressa* (France, Spain, Portugal, Algeria, Morocco), but incorrect in the omission of true *A. angustior* from cooler parts of Iberia (Fig. 84). This distribution indicates that *A. angustior* is not simply a northern species but rather one with an Atlantic affinity. Though we did not examine material from this region as part of this study, *A. angustior* is likely to be present in cooler parts of western France, joining the two distributions together. Warncke's map also does not capture the sympatric presence of *A. angustior* and *A. fulvata* populations in northern Europe as this is a more recent and ongoing phenomenon, with *A. fulvata* a recent colonist of Belgium for example (compare Patiny & Terzo 2010; Drossart *et al.* 2019). The lack of recognition of true *A. angustior* from the mountains of Iberia is strange, as Warncke (1967) made reference to males from the Pyrenees with shiny tergal margins, but he seemed to consider these intermediate between *A. angustior* and *A. impressa* stat. nov.

Species newly recorded for Spain

Andrena (incertae sedis) **laurivora** Warncke, 1974 Figs 101–108

Material examined

Holotype

MOROCCO • 1 ♂; Marraquesh; Mar. 1907; Escalera leg.; OÖLM (illustrated Fig. 86).

Paratype

MOROCCO • 1 ♀; Marraquesh; Mar. 1907; Escalera leg.; OÖLM.

Other material

SPAIN • 1 \circlearrowleft , 1 \circlearrowleft ; Sevilla, Los Pinares de Aznalcazar; 13 Mar. 2012; I. Cross leg.; ICC (illustrated Figs 105, 107) • 2 \circlearrowleft ; Huelva, Hinojos; 15 Mar. 2012; I. Cross leg.; *Reseda phyteuma*; ICC • 1 \circlearrowleft ; same collection data as for preceding; TJWC (illustrated Figs 101, 103).

Remarks

Material from southwestern Spain closely resembles Moroccan specimens, but are generally less hirsute, particularly in the single male Spanish specimen, although this may be simply due to the condition of the individual specimen (Figs 101–108). Structurally, there are no clear differences, and so they are considered to be conspecific. The pronouncedly Atlantic distribution of Morocco and southwestern Iberia is not unprecedented in bees, as the extremely rare *Lasioglossum musculoides* Ebmer, 1974 has a global distribution of the Souss Valley in southwestern Morocco and southwestern Portugal (Pauly 2015). Coastal areas of Huelva and Sevilla continue to produce records of range-restricted species



Figs 101–108. *Andrena laurivora* Warncke, 1974 (TJWC). 101, 103, 105, 107. Spanish material. 101. Female terga. 103. Female face. 105. Male terga. 107. Male face. 102, 104, 106, 108. Moroccan material. 102. Female terga. 104. Female face. 106. Male terga. 108. Male face. Not to scale.

Table 2. Plant host use and dietary categories for selected Iberian species of *Andrena* Fabricius, 1775 formerly placed in the subgenus *Poliandrena* Warncke, 1968. Abbreviations: N = number of analysed pollen loads; n = number of unique sampling localities. Plant taxa: AST = Asteraceae; BRA = Brassicaceae; CIS = Cistaceae; FAB = Fabaceae; RES = Resedaceae.

Species	N	n	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
Andrena blanda Pérez, 1895	18	7	RES 100.0	100.0	100.0	Narrowly oligolectic (Reseda)
Andrena corax Warncke, 1967	8	3	RES 99.6, AST 0.4	87.5	100.0	Narrowly oligolectic (Reseda)
Andrena farinosa Pérez, 1895	3	2	FAB (Ononis-type) 100.0	100.0	100.0	Possibly broadly oligolectic (Fabaceae)
Andrena laurivora Warncke, 1974	3	1	RES 100.0	100.0	100.0	Possibly narrowly oligolectic (Reseda)
Andrena oviventris Pérez, 1895	23	8	RES 98.1, CIS 1.7, BRA 0.2	82.6	100.0	Narrowly oligolectic (Reseda)
Andrena relata Warncke, 1967	1	1	RES 100.0	100.0	100.0	Possibly narrowly oligolectic (Reseda)

thought to be endemic elsewhere, such as *Flavipanurgus fuzetus* Patiny, 1999 which was discovered there in 2018 (Cross & Wood 2018).

Pollen loads taken from three specimens at a single Moroccan locality contained pure *Reseda*-type (Resedaceae Martinov) pollen (Table 2), so the floral observation data from Spain is consistent with this picture. Comparisons with other species are complicated because the former subgenus *Poliandrena* Warncke, 1968 in which it was placed (Warncke 1974) has been found to be strongly polyphyletic, and *Poliandrena* in a strict sense is now a synonym of the subgenus *Ulandrena* Warncke, 1968 (Pisanty *et al.* 2021). Excluding *A. polita* Smith, 1847 (now subgenus *Ulandrena*) and *A. florea* Fabricius, 1793 (the placement of this species necessitates the erection of a new subgenus) which clearly belong elsewhere (Pisanty *et al.* 2021), other members of the old concept of *Poliandrena* that can be found in Spain for which pollen data are available are predominantly associated with *Reseda* L., with the exception of *A. farinosa* Pérez, 1895 which is likely a specialist of Fabaceae (Table 2). These taxa fall into at least two clades (Pisanty *et al.* 2021), and so work is needed to establish their true subgeneric affinities in addition to their dietary choices.

Distribution

Previously thought to be endemic to Morocco, now also including Spain (Warncke 1974; Lhomme *et al.* 2020).

Andrena (Simandrena) confinis Stoeckhert, 1930

Material examined

SPAIN • 1 ♀, *Andrena confinis*; Cantabria, Picos de Europa, Camaleno; 600 m a.s.l.; 5 May 2014; E. Scheuchl det.; D.W. Baldock leg.; TJWC • 1 ♀, *Andrena congruens*; Pirineos Orient, 20 km NE of Ripoll; 1650 m a.s.l.; 31 Jul. 2011; J. Halada leg.; TJWC • 1 ♀, *Andrena congruens*; Pyrenees, Cavalers (exact location unclear); 11 Jul. 2002; H. Kohout leg.; OÖLM.

Remarks

This species pair is in need of molecular revision across Europe because of historical synonymy with *A. congruens* Schmiedeknecht, 1884 (e.g., Warncke 1967). Both species are present in central Europe (Schmid-Egger & Scheuchl 1997; Le Divelec 2020), and material examined from northern Europe (Belgium, northern France, United Kingdom) conforms to *A. confinis*, suggesting that it is the more northerly of the two. Currently, only *A. congruens* is listed for Spain (Ortiz-Sánchez 2011), but both

taxa are present in mountainous parts of northern Spain, though given the limited material available it is difficult to come to firm conclusions concerning their true distributions.

Distribution

The distribution of *A. confinis* is unclear because of continued confusion and synonymy with *Andrena congruens* Schmiedeknecht, 1884. At this moment, it is not possible to give an accurate picture of its true distribution, but both species are present in central Europe, with *A. congruens* having more southern and *A. confinis* more northern tendencies (Schmid-Egger & Scheuchl 1997).

Discussion

In total, this investigation into the fauna of Andrena of Iberia has identified three good taxa deserving a taxonomic elevation to species status, and four previously overlooked or cryptic species. Combined with the discovery of A. laurivora, previously thought to be endemic to Morocco, these findings comprise a total of seven species newly recorded for both the Spanish and broader European fauna, three for the Portuguese fauna, and the replacement of A. wilkella with the endemic A. beaumonti stat. rev. in Morocco.

In common with other recent investigations into the *Andrena* of central and southern Europe (Praz et al. 2019; Wood et al. 2020), targeted taxonomic attention has revealed a considerable complexity that was not sufficiently resolved by previous authors. This can partly be explained by philosophical differences. The leading West Palaearctic taxonomist of *Andrena* Klaus Warncke described much of the diversity he encountered at the subspecific level, in the case of this present study the taxa *A. gredana* stat. nov. and *A. impressa* stat. nov., or nested other good taxa within a broad species concept in the case of *A. beaumonti* stat. rev. As our power to distinguish between distinct lineages with molecular genetics has increased, our understanding of how *Andrena* should be classified at the species level has also changed, as what could be considered to simply be 'variable' lineages can be identified as distinct. As a result, the subspecific classifications of Warncke that are so prevalent in his work on the *Andrena* of the Mediterranean basin will continue to be revised (Praz et al. 2019), likely resulting in a substantial increase in species richness for the genus.

In addition to these philosophical changes, the Iberian Peninsula itself genuinely harbours an overlooked diversity. The major Iberian revision of Andrena by Warncke (1975a; 1976) was naturally limited by the material available for study, a large part of which came from the collection of Dusmet y Alonso who collected predominantly around Madrid. As such, much of the diversity of Andrena present in the eastern part of the Sistema Central and the region of La Mancha south of Madrid was described in those publications, but there was relatively little material available to study from mountains in Andalucía or in the northwestern part of the Peninsula. The absence of material from northwestern Iberia can be illustrated in the panurgine genus Flavipanurgus Warncke, 1972. The southern Iberian species F. ibericus (Warncke, 1972) was described well before its northwestern Iberian sister species F. kastiliensis (Warncke, 1987) after more material for study became available (Warncke 1972, 1987; elevated to species status by Cross & Wood 2018). A more recent study has revealed yet more hidden diversity of Andrena in this region (Wood et al. 2020), and these northwestern mountains, from the western part of the Sistema Central to northern Portugal and the Cantabrian, Léon, and Galician mountains host an endemic andrenid fauna of A. benoisti Wood & Praz sp. nov., A. fortipunctata Wood sp. nov., A. omnilaevis Wood, 2020, F. kastiliensis, and the majority of the population of A. gredana stat. nov., as well as serving as a transition zone where typically Atlantic or central European species such as A. angustior and A. wilkella can be found close to their Iberian or Mediterranean counterparts.

The second major area not well covered by Warncke's revisions were mountains in southern Iberia, and more broadly Andalucía itself as Dusmet collected relatively little from this region and Warncke did

not personally visit these areas either, and many of the endemic species they support have only been recently described (e.g., Müller 2012). As such, it should be less of a surprise that they host an endemic diversity of *Andrena* such as *A. levante* Wood & Praz sp. nov. What is more surprising is the presence of newly described taxa in southern Iberia that are close to taxa more typically found in central and eastern Europe, but which are separated by substantial distributional gaps. Wood *et al.* (2020) described *A. baetica* which is very close to the eastern *A. mocsaryi* Schmiedeknecht, 1883, and Kuhlmann & Smit (2018) described *Colletes jansmiti* Kuhlmann, 2018 which is very close to *Colletes punctatus* Mocsáry, 1877, the nearest records of both comparison species being found in eastern Austria. *Andrena juliana* sp. nov. can broadly be added to this collection because of its similarity to *A. curvana*, another typically eastern species. With limited material available for morphological or molecular study, all these taxa require further investigation to better understand their specific biogeographical situations and whether these are driven by consistent underlying trends.

Finally, studies of the subgenus A. (Taeniandrena) are far from complete, even in Iberia. We did not investigate the problems surrounding the A. ovatula (Kirby, 1802) complex that potentially contains up to three species in Iberia, and an unclear number across the entire Mediterranean basin. What is clear is, that there is a great deal of cryptic diversity present in southern European Andrena which is remarkable given that the European bee fauna is the best studied bee fauna globally. Given the discoveries made here, it illustrates the quantity of work needed to identify and delineate bee species in less well-studied parts of the world.

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Editorial note

As the authors are unable to add scale bars to their figures for technical reasons, the editors of *EJT* have decided to accept this paper without such indications. However, this is exceptional and cannot be seen as a precedent.

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