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The genus *Andrena* Fabricius, 1775 (Hymenoptera, Andrenidae) in a Mediterranean biodiversity hotspot: community-wide relationships with plants and description of three new species

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Abstract

Evolutionary and ecological factors underlying the extensive, fast diversification of the species-rich bee genus *Andrena* (Andrenidae Latreille, 1802) are of general interest and require elucidation. Progress in evolutionary and ecological understanding of hyperdiverse *Andrena* assemblages, however, has been hindered in parts of the world where the genus reaches its highest species richness. The lack of well-established taxonomic resources has precluded studies on resource use and patterns of reciprocal relationships with plants which could potentially shed light on drivers of *Andrena* diversification. This paper presents an analysis of community-wide relationships between plants and *Andrena* bees in a western Mediterranean biodiversity hotspot (Cazorla mountain range, southeastern Spain). By combining information on pollinator composition of the regional community of entomophilous plants (292 species) with a state-of-the-art taxonomic treatment of the regional assemblage of *Andrena* (89 species), we assess here the distribution across the plant phylogeny of floral resources utilized by *Andrena*; the quantitative patterns of mutual dependence between species of plants and *Andrena*; and the completeness of our regional sampling of *Andrena* species. Three new species of *Andrena* from the study region, which were discovered in the course of the field study, are also described and illustrated: *A. officinalis* Wood, **sp. nov.**, *A. rostro* Wood, **sp. nov.**, and *A. cazorlae* Wood, **sp. nov.**

Keywords

Andrena, bee diversity, bee specialization, Sierra de Cazorla mountain range, Mediterranean habitats, phylogenetic signal, plant-bee relationships, species abundance distribution

Introduction

The mining bees (Andrenidae Latreille, 1802) are a major family with >3,000 described species, ~1740 of which belong to the predominantly Holarctic genus *Andrena* Fabricius, 1775, the second largest genus of bees (Michener 2007; Wood 2025). Several reasons have motivated in recent years a growing interest in the study of *Andrena* from evolutionary, taxonomic and ecological perspectives. As it is a monophyletic lineage of relatively recent origin, the evolutionary and ecological mechanisms which have contributed to its unusually fast diversification are of general interest and demand elucidation (Bossert et al. 2022; Pisanty et al. 2022; McLaughlin et al. 2023). *Andrena* species are found throughout the Holarctic region, obligately nest in the ground, predominantly make individual nests, and produce one to two generations per year depending on the species and local conditions; although many species are polylectic, many others are strictly oligolectic (Michener 2007; Wood 2023; Wood et al. 2023a). *Andrena* bees are important pollinators of many wild and cultivated plants in boreal and temperate habitats of Eurasia and North America, particularly of early-flowering plants which bloom in winter and early spring (Motten 1986; Herrera 1995; Kato 2000; Ostaff et al. 2015; Turley et al. 2022). This phenological pattern has prompted questions on, among other, the physiological features that enable or constrain species of *Andrena* to exploit thermally suboptimal environments, the possible role played by pollen resource partitioning in the diversification of the genus, or the expected negative impact of current climatic warming on their populations and the pollination service they deliver to plants (Robbirt et al. 2014; Wood and Roberts 2017, 2018; Hutchings et al. 2018; Bossert et al. 2022; Wood 2023; Herrera et al. 2023a).

Rather paradoxically, however, progress in evolutionary and ecological understanding of hyperdiverse *Andrena* assemblages has been hindered specifically in parts of the world where the genus reaches its highest species richness. In these geographical areas the lack of well-established taxonomic resources has precluded detailed studies on resource use by different *Andrena* species and the elucidation of their patterns of reciprocal relationships with plants, two aspects which could shed light on possible drivers of their diversification (Glaum et al. 2021). This is exemplified by the situation in the Mediterranean region, one *Andrena* diversity hotspot where the recent increase in attention has led to a profusion of new species and subgenera in the last few years (e.g., Pisanty et al. 2016; Wood et al. 2020a, 2020b, 2021, 2022; Praz et al. 2022; Wood and Ortiz-Sánchez 2022; Wood 2023; Wood et al. 2023b; Pisanty and Wood 2024; Annessi et al. 2025; and present study). Another factor contributing to the poor knowledge of the relationships between *Andrena* bees and their food plants in Mediterranean diversity hotspots has been the poor coverage of plant communities by ecologically-oriented studies of plant-pollinator relationships (Herrera 2020).

For example, the median number of plant species considered in one hundred "plant-pollinator networks" from the Iberian Peninsula included in Lanuza et al.'s (2025) exhaustive compilation was only 12 species, which falls short of a satisfactory coverage of local or regional Mediterranean plant diversity at the community level. These limitations have so far precluded biologically realistic assessments of the mutual relationships between *Andrena* and plants in those Mediterranean biodiversity hotspots where most diversity of *Andrena* is concentrated (but see Wood et al. 2022).

This paper presents a comprehensive analysis of community-wide relationships between plants and *Andrena* bees in a western Mediterranean biodiversity hotspot. By combining information on pollinator composition of the regional community of entomophilous plants (292 species) with state-of-the-art taxonomic treatment of the regional assemblage of *Andrena* (89 species, including three new ones described in this paper), we will describe for the first time the community-wide patterns of mutual relationships between species of *Andrena* and species of plants in a southern Iberian biodiversity hotspot (see Study area below). Particular emphasis will be placed on assessing (1) the distribution across the plant phylogeny of floral resources utilized by *Andrena*; (2) the quantitative patterns of mutual dependence between species of plants and *Andrena*; and (3) the completeness of our regional sampling of *Andrena* species. Results of these analyses will provide answers to the following specific questions: What plant taxa (species and families) are most visited by *Andrena*? Is there phylogenetic signal in *Andrena* – host relationships? What percentage of *Andrena* species are likely floral specialists? What is the estimated total diversity of *Andrena* in the region? One more general goal of this study is to highlight the importance of combining detailed ecological information (i.e., exhaustive natural history observations) and updated taxonomic knowledge for understanding patterns of flower resource use and the diversification of species-rich pollinator lineages (van der Niet 2020).

Materials and methods

Study area and bee fauna

Field data on flower visitation by *Andrena* and all *Andrena* specimens referred to in this paper were obtained between 1982–2025 in the Sierra de Cazorla mountain range, Jaén Province, southeastern Spain ("Cazorla range" hereafter). A map of sampling sites is shown in Herrera (2021), and photographs of the major habitat types sampled can be found in Appendix S1 to Herrera (2019). The Cazorla range is a large mountain system in the Betic ranges, characterized by well-preserved vegetation and outstanding plant and animal diversity (Médail and Diadema 2009; Gómez Mercado 2011; Molina-Venegas et al. 2015; Pugnaire et al. 2024). The regional bee fauna, with ~405 species recorded to date (C. M. Herrera *unpublished data*), roughly accounts for one third of the total Iberian species (Ortiz-Sánchez 2020) and is remarkably diverse in comparison with other western Mediterranean locations studied so far (Ortiz-Sánchez et al. 2023). About one quarter of total bee species recorded in the Cazorla range (24%) belong to the genus *Andrena*, a proportion which exceeds that found elsewhere in the Iberian Peninsula (Ortiz-Sánchez et al. 2023). The high species richness of *Andrena* in the Cazorla range partly reflects the coexistence of endemic Mediterranean taxa with others of more northern, western European distributions which reach there their southern distributional boundaries (Wood 2023; Ortiz-Sánchez et al. 2023). Recent studies on the ecology of bees in the Cazorla range in relation to the abiotic environment and the plants they pollinate include Herrera (1995, 2024) and Herrera et al. (2023a, 2023b).

Andrena-plant relationships

The significance of *Andrena* as pollinators of entomophilous plants was evaluated by means of standardized pollinator censuses conducted in the field during the period 1997–2024. Pollinator composition was assessed for 292 plant species in 187 genera and 54 families, which included virtually all insect-pollinated plants of the Cazorla range (see Herrera 2025 for the list of plant species). Plant identification and nomenclature followed Blanca et al. (2011) and Gómez Mercado (2011). The sampling unit for pollinator assessment was the "pollinator census", consisting of a 3-min watch of a flowering patch of the focal plant species. Bees visiting some flower in the focal patch during the timed census period were in most cases identified by photographic recording with a DSLR digital camera and 105 mm macro lens. Voucher specimens were regularly collected for identification or confirmation. A total of 38,506 pollinator censuses were conducted on 803 different dates spread over the study period (all plant species combined), in which 2,098 *Andrena* individuals from ~60 species were recorded. See Herrera (2019, 2020, 2021, 2024) for additional details on pollinator census methods and results of other analyses on this large pollinator data set.

Andrena specimens collected as vouchers during pollinator censuses over 1997–2024, in surveys of the bee fauna of the Cazorla range in the interval 1982–2024 (Ortiz-Sánchez et al. 2023), or in the course of research on *Andrena* thermal ecology (Herrera 1995, Herrera et al. 2023a; Herrera 2024), had associated data on the species of plant in whose flowers they were probing for nectar and/or gathering pollen when captured. All these data have been combined into a single dataset and used in this paper to elucidate the composition of food plants used by the species of *Andrena* recorded in the region. It was rarely possible to differentiate whether collected individuals were gathering pollen, feeding on nectar, or both, hence the associations between plant and *Andrena* species pairs considered here could not be subdivided according to the type of food resource gathered by the bees. The raw data on species-level pairwise associations between *Andrena* and plants used in this study are available in Herrera (2025), where lists of plant and *Andrena* species can also be found.

Data analysis

Statistical analyses reported in this paper were carried out using the R environment (version 4.5.0; R Core Team 2025). The phylogenetic relationships among the plant species where pollinators were censused were obtained using the package V.PhyloMaker2 and the WP nomenclature standardization system (Jin and Qian 2022). Tests of phylogenetic signal (= the tendency for related species to resemble each other more than they resemble species drawn at random from the phylogenetic tree; Blomberg and Garland 2002) were conducted using Pagel's λ, which performs well to discriminate between random and Brownian motion patterns of trait distribution; is robust to variations in the number of species in the phylogeny and to incompletely resolved phylogenies or suboptimal branch-length information; and provides a reliable effect size measure (Münkemüller et al. 2012; Molina-Venegas and Rodríguez 2017). Computations were performed using the package phylosignal (Keck et al. 2016), and statistical significance of Pagel's λ was tested by randomization.

The species abundance distribution (SAD), or description of the abundance (number of individuals observed) of the different species encountered in a community, provides a basic descriptor of species sets (McGill et al. 2007). The SAD allows to estimate the true number of species of the sampled community, which in turn allows to assess both the completeness of the species sample and the expected number of species which occur in the community studied but have been not yet recorded ("dark diversity", *sensu* Pärtel et al. 2011). In the case of plant-bee relationships, species completeness of bee samples advises on robustness of the conclusions on the extent of reciprocal species-to-species dependence, while estimates of bees' dark diversity may provide guidance on the prospects of further species discovery from additional collecting effort. Estimates of the total number of *Andrena* species in the regional community sampled were obtained using the interpolation-extrapolation (Hsieh et al. 2016) and "singleton frequency" (Chao et al. 2017) methods. Computations were performed using the iNEXT package (Chao et al. 2014; Hsieh et al. 2025) and the online SuperDuplicates application (Chao et al. 2017; https://chao.shinyapps.io/SuperDuplicates/, accessed March 2025), respectively. For comparative purposes, similar analyses were conducted on the comprehensive, unpublished database of *Andrena* specimens from Spain maintained by one of the authors (TJW) that formed the basis for the Iberian revision of Wood (2023), which comprised 10,619 individuals from 238 species as of March 2025.

One specimen of each new species described here was sent for genetic analysis in the framework of the project Biodiversity Genomics Europe with the objective of generating a DNA barcode from the COI mitochondrial gene. Only a single specimen produced a viable barcode (see below). The sequence is available via this portal (https://portal.boldsystems.org/recordset/DS-BGEMS). Genetic distance from related species was calculated using MEGA-X.

Species description and illustration

Morphological terminology follows Michener (2007), with the exception of the antennal segments which are numbered A1–12(13), nervulus rather than vein cu-v in the forewing, and marginal areas rather than marginal "zones". Specimens were measured from the centre of the clypeus at the front of the head to the apical tip of the metasoma and rounded to the nearest 0.5 mm. Photographs were taken using an Olympus E-M1 Mark II with a 60mm macro lens. Additional close-ups were taken with the addition of a Mitutoyo M Plan Apo 10X infinity corrected objective lens in combination with an Olympus M.Zuiko 2× teleconverter lens, a 10mm Kenko DG extension tube, and a Meike MK-P-AF3B 10mm extension tube. Photographs were stacked using Helicon Focus B (HeliconSoft, Ukraine) and plates were prepared in GNU Image Manipulation Program (GIMP) 2.10. Post-processing of some images was made in Photoshop Elements (Adobe Systems, USA) to improve lighting to highlight specific characters.

Abbreviations

CMHC	Carlos M. Herrera Collection, Sevilla, Spain.
EBDC	Estación Biológica de Doñana, CSIC, Sevilla, Spain
MNCN	Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain.
RMNH	Naturalis Biodiversity Center, Leiden, the Netherlands

Results and discussion

Significance of *Andrena* for plants

Andrena were recorded visiting flowers of 166 different plant species in the study area, or 56.5% of the entomophilous flora surveyed by means of standardized pollinators censuses. The majority of these plants had their flowers visited by just 1–3 species of *Andrena* each (Fig. 1A; see Herrera 2025 for the raw data for individual plant species). There were, however, a few outstanding exceptions where the number of *Andrena* species visiting the flowers of individual plant species was higher. The most species-rich *Andrena* pollinator assemblages were found in a taxonomically disparate plant group comprising *Armeria filicaulis* (Boiss.) Boiss. (Plumbaginaceae, 8 *Andrena* species), *Ornithogalum umbellatum* L. (Asparagaceae, 7), *Rosa micrantha* Sm. (Rosaceae, 7), *Cistus albidus* L. (Cistaceae, 6), *Crataegus monogyna* Jacq. (Rosaceae, 6), *Prunus mahaleb* L. (Rosaceae, 6), *Ranunculus paludosus* Poir. (Ranunculaceae, 6) and *Sisymbrella aspera* (L.) Spach. (Brassicaceae, 6). All these plants share relatively large, radially-symmetric, bowl-shaped flowers with pollen and nectar readily accessible.

Species of *Andrena* accounted collectively for a modest proportion (10.8%) of the total number of bee individuals recorded in pollinator censuses (N = 19,387 bee individuals, all plant species combined). Per-minute visitation probability of flowering patches by all *Andrena* combined (VP hereafter), which provides a quantitative estimate of their abundance from the perspective of plants, was generally low or very low (Fig. 1B; see Herrera 2025 for the raw data for individual plant species). VP was <0.05 min^{-1} for the vast majority of plant species, meaning that the average interval between two successive flower patch visits by an *Andrena* bee (= 1/VP) was longer than 20 minutes for nearly all plants. A few, taxonomically unrelated plants stood out by their high *Andrena* visitation probabilities (>0.10 min^{-1}) and short intervals between successive patch visits. These included *Rosa canina* L. (Rosaceae, VP = 0.18), *Crepis vesicaria* L.

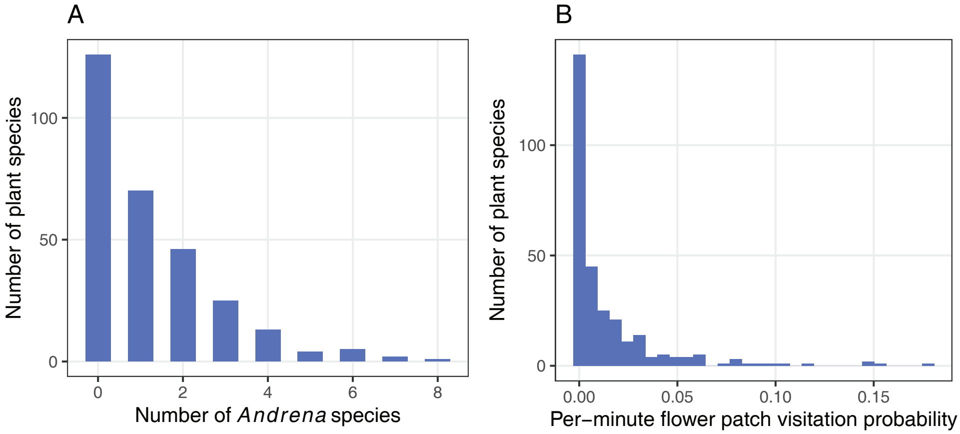

Figure 1. Frequency distributions of the number of *Andrena* species recorded visiting the flowers of individual plant species (**A**), and average flower patch visitation probability (**B**), in the set of $N = 292$ plant species surveyed for pollinator composition in the Cazorla range. Many plant species were not visited by *Andrena* (0-value bar in **A**), and most of those which did were by just 1–3 species and had very low visitation probabilities (<0.05 min^{-1}), which meant that average intervals between successive flower patch visits by some *Andrena* bee were >20 minutes.

(Asteraceae, 0.15), *Cistus salviifolius* L. (Cistaceae, 0.15), *Hormathophylla spinosa* (L.) P. Küpfer (Brassicaceae, 0.15), *Linum bienne* Mill. (Linaceae, 0.12), *Trifolium campestre* Schreb. (Fabaceae, 0.11) and *Narcissus hedraeanthus* (Webb & Heldr.) Colm. (Amaryllidaceae, 0.10).

Interspecific variation among plants in either number of associated *Andrena* species or combined probability of visitation to flower patches exhibited statistically significant phylogenetic signals (Pagel's $\lambda = 0.404$ and 0.179, $P = 0.0001$ and 0.0002, for number of species and visitation probability, respectively). Phylogenetic signal is apparent when the two estimates of *Andrena* significance for plants are mapped onto the plants' phylogenetic tree, showing that flower use by *Andrena* was very unevenly spread over the phylogenetic tree of the 292 plant species studied (Fig. 2). Certain particular plants clades had distinctly higher values for both *Andrena* species richness and visitation probability (e.g., Amaryllidaceae, Ranunculales, Malvales, Brassicaceae, Rosaceae, Asteroideae, Cichorioideae), while the reverse held true for other clades whose flowers remained unvisited or were visited quite infrequently by *Andrena* (e.g., Caryophyllaceae, Boraginaceae, Plantaginaceae, Carduoideae) (Fig. 2).

These results suggest that, at the plants' macroevolutionary scale, observed patterns in *Andrena* resource use could be explained by differences across plant families in flowering phenology and floral morphology, which is consistent with predictions advanced by Glaum et al. (2021). *Andrena* were mostly associated with plant lineages with early-blooming and/or easily accessible flowers (e.g., Amaryllidaceae, Brassicaceae, Cistaceae, Geraniaceae, Ranunculaceae, Rosaceae), while tended to be absent or underrepresented in lineages with comparatively late-blooming and restrictive floral morphology (e.g.,

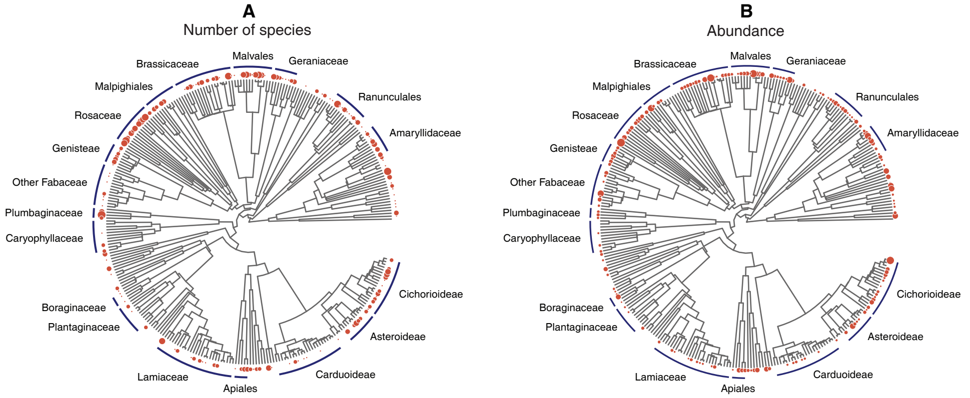

Figure 2. Phylogenetic relationships of the $N = 292$ plant species surveyed for pollinator composition in the Cazorla range, and associated variation across plant species in number of species (**A**) and abundance (**B**) of *Andrena* pollinators, all species combined. Within each graph, tips without symbols correspond to species which were not visited by *Andrena*, hence the distribution of gaps and clusters of symbols across the plants' phylogeny parsimoniously denotes the aggregation of *Andrena* on certain clades and their absence from others. In those species visited by *Andrena*, variable size of symbols denote variation in number of species (**A**) and their combined abundance (**B**). *Andrena* abundance in a given species' pollinator assemblage was estimated as the average probability of visitation of a flowering patch per 3-min watching period. As illustrations of the phylogenetic signal that underlies the data (see text), representative clades exhibiting either high or low values for *Andrena* diversity or abundance are highlighted.

Boraginaceae, Carduoideae, Lamiaceae, Plantaginaceae). These phylogenetic patterns confirm and expand previous accounts of resource use by western Mediterranean *Andrena* (Wood et al. 2022; Wood 2023; Herrera et al. 2023a), which have been related to intrinsic limitations set by their short mouthparts (though see *Andrena solenopalpa* Benoist, 1945 for a counter example; Wood 2023) and thermal biology features. These latter include a poor capacity for autonomous endothermy, weak thermoregulatory capability, low flight muscle temperature and power output, low tolerance to high ambient temperatures, low minimum temperatures for takeoff and flight, and low thoracic temperatures (Herrera 1995, 2024; Herrera et al. 2023a; and references therein).

Significance of plants for *Andrena*

The association between species of *Andrena* and their food plants in the Cazorla range was established using 1,948 reliably identified voucher specimens from 89 species which had data on the identity of plants whose flowers they were visiting at the time of collection. This large sample was associated with flowers of 129 different plant species from 81 genera in 33 families, which confirms the wide taxonomic range of flowers exploited collectively by *Andrena* as revealed by pollinator census data (Fig. 2).

The frequency distributions of the number of plant species, genera and families recorded for each *Andrena* species are shown in Fig. 3 separately for male and female

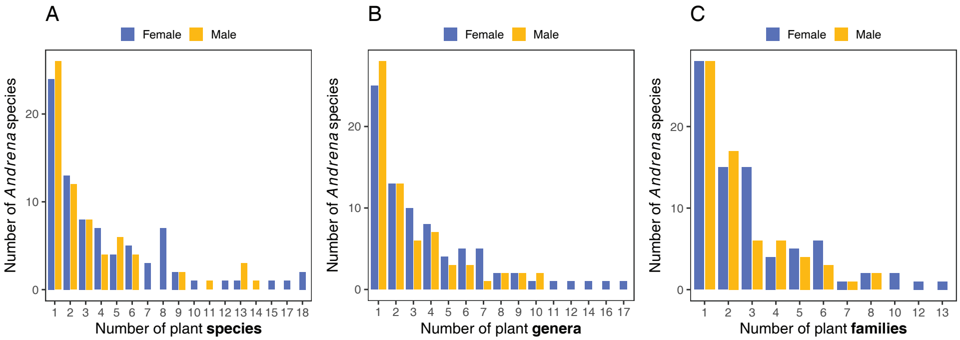

Figure 3. Frequency distributions of the number of plant species (**A**), genera (**B**), and families (**C**) associated with the 89 species of *Andrena* from the Cazorla range whose specimens had associated information on the plant they were feeding on at the time of collection (N = 1,948 specimens, all species combined). Distribution data for females and males are shown separately for comparison.

individuals. Irrespective of plant taxonomic level (species, genus or family), the vast majority of the 89 species of *Andrena* were each recorded visiting the flowers of one or a few plant taxa, with males and females exhibiting similar patterns (Fig. 3). A small set of species, however, stood apart by visiting the flowers of a remarkably diverse taxonomic array of plants: *A. nigroaenea* (Kirby, 1802) (26 plant species, 22 plant genera, 16 plant families), *A. flavipes* Panzer, 1799 (25, 19, 14), *A. bicolor* Fabricius, 1775 (21, 19, 16), *A. trimmerana* (Kirby, 1802) (21, 14, 9), *A. haemorrhoa* (Fabricius, 1781) (15, 11, 8), *A. labialis* (Kirby, 1802) (15, 12, 6), *A. tibialis* (Kirby, 1802) (15, 9, 8), *A. lavandulae* Pérez, 1902 (13, 11, 10), and *A. pilipes* Fabricius, 1781 (13, 10, 5) (data for the two sexes combined are for each species). This small set of species are likewise characterized by their broad pollen diets (Wood et al. 2023a). With the exception of *A. lavandulae*, the species with exceptionally broad food spectra in the Cazorla range all share wide geographical distributions which encompass most of western Europe (Gusenleitner and Schwarz 2002). The consistent similarity between male and female individuals in the shape of distributions of floral resource widths, regardless of the plant taxonomical level chosen (Fig. 3), supports the notion that the contrast between sexes in floral resource use customarily assumed in wild bee studies (i.e., nectar in males, nectar and pollen in females) might not hold universally in *Andrena* (Urban-Mead et al. 2022).

Dark diversity

The species abundance distribution for the collection of *Andrena* specimens (including the three new species described below) followed the usual "hollow curve" indicative of a few very abundant species and many rare species (McGill et al. 2007) (Fig. 4). Application of the interpolation-extrapolation and singleton frequency methods to these data led to similar projected estimates of 102 species for the community of *Andrena* studied, implying that about 12% of the species actually existing in the region remain undetected so far. This extent of dark diversity is noticeably larger than that

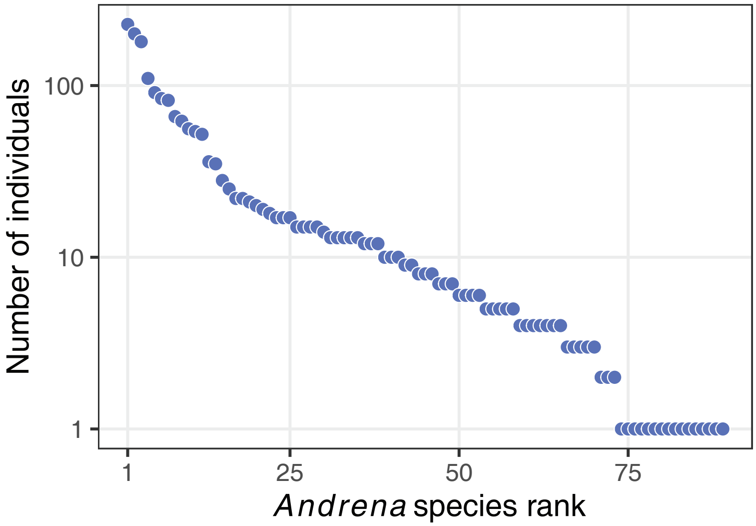

Figure 4. Rank-abundance plot depicting the species abundance distribution in the collection of *Andrena* specimens from the Cazorla range.

obtained by applying the same methods to the whole database of Spanish specimens, for which the observed and projected species numbers were 238 and 249, respectively, or only 4% dark diversity. This contrast emphasizes the difficulty, noted in the Introduction, of evaluating *Andrena* species richness in regional biodiversity hotspots even after long-term, extensive pollinator sampling, mainly because most diversity seems to be accounted for by a pleiade of rare species each visiting only a few plant species. Furthermore, as exemplified by the large number of new species described in recent years (see references in the Introduction), the *Andrena* dark diversity in Mediterranean biodiversity hotspots is likely to include some undescribed species which could vanish before being detected (Liu et al. 2022). This seems a biologically plausible scenario in the Cazorla range, given the weak thermoregulatory ability and low upper tolerable limit of body temperature of *Andrena*, and the fast increase in ambient temperature currently underway in the region (Herrera et al. 2023a).

Description of new species

***Andrena* (*Euandrena*) *officinalis* Wood, sp. nov.**

https://zoobank.org/9D5CDFCD-EF42-4962-ACB2-10F86B6E6121

Type material. ***Holotype:*** Spain • 1♂; Jaén, Sierra de Cazorla, La Sarga; 37.9225°N, -2.9205°W; 13 Mar. 2024; C.M. Herrera leg.; RMNH; RMNH.INS.1715578; BOLD accession number BGENL3104-25.

Paratypes: Spain • 1♂; Sierra de Cazorla, Cuesta del Bazar; 16 Apr. 1989; C.M. Herrera leg.; RMNH • 1♂; Sierra de Cazorla, Coto del Valle; 10 Mar. 2023; C.M. Herrera leg.; CMHC • 1♂; Sierra de Cazorla, Coto del Valle; 11 Mar. 2023; C.M. Herrera leg.; EBDC • 1♂; Sierra de Cazorla, La Sarga; 27 Mar. 2023; C.M. Herrera leg.; MNCN • 1♂; Sierra de Cazorla, La Sarga; 29 Apr. 2022; C.M. Herrera leg.; MNCN • 1♀; Sierra de Cazorla, La Sarga; 25 Apr. 2022; C.M. Herrera leg.; MNCN • 1♀; Sierra de Cazorla, La Sarga; 7 May 2022; C.M. Herrera leg.; EBDC • 2♀; Sierra de Cazorla, La Fresnedilla; 29 Apr. 1985; C.M. Herrera leg.; RMNH • 1♀; Sierra de Cazorla, Barranco del Guadalentín; 20 May 2005; C.M. Herrera leg.; CMHC.

Description. Female. Body length: 8–10 mm (Fig. 5A). ***Head:*** Dark, 1.15 times wider than long (Fig. 5B). Clypeus weakly domed, somewhat flattened medially, surface laterally shagreened and dull, more or less shining over majority of surface; surface densely but irregularly punctate, punctures separated by 0.5–1 puncture diameters, up to 2 puncture diameters medially with weak indication of obscure longitudinal impunctate midline. Process of labrum rounded trapezoidal, 2 times wider than long. Mouthparts moderately long, approaching ½ length of head; 6 mandibular palpi, 4 labial palpi. Mandibular palpi with segments of approximately equal length, segment 2 1.2 times length of other segments. Mandibles slightly elongate, weakly crossing apically, with inner subapical tooth. Gena slightly exceeding width of compound eye; ocelloccipital distance subequal to diameter of lateral ocellus. Foveae dorsally occupying ⅓ space between compound eye and lateral ocellus, ventrally narrowing further, narrower than diameter of flagellum; foveae filled with dark brown hairs. Face with golden-brown to whitish-grey hairs on supraclypeal area and around antennal insertions, hairs black elsewhere; gena and vertex with intermixed black and golden-brown to whitish-grey hairs. Antennae dark, A3 slightly exceeding A4+5.

Mesosoma: Scutum and scutellum densely and shallowly punctate, punctures separated by 0.5–1 puncture diameters over majority of surface, slightly sparser posteriormedially and visible against underlying surface sculpture of fine granular microreticulation, weakly shining (Fig. 5C). Pronotum rounded. Mesepisternum and dorsolateral parts of propodeum finely microreticulate, microreticulation overlain with network of fine reticulation; network forming small circular reticulation-free patches, surface dull. Propodeal triangle narrow, laterally delineated by slight carinae, internal surface with fine granular microreticulation. Mesepisternum with long finely plumose golden-brown hairs, not equalling length of scape, hairs continuing onto scutum, scutellum, and propodeum, without intermixed black hairs. Propodeal corbicula incomplete, composed of golden-brown plumose hairs, internal surface with long simple hairs. Legs dark, pubescence dark brown. Flocculus complete, composed of light brown plumose hairs; femoral and tibial scopae composed of golden-brown to orange simple hairs, tibial scopa with hairs dark brown dorsally at basitibial plate. Hind tarsal claws with inner tooth. Wings hyaline, stigma and venation dark orange, nervulus interstitial.

Metasoma: Tergal discs dark, marginal areas narrowly but distinctly lightened hyaline orange-brown on apical rims, colouration exceeding diameter of lateral ocellus but

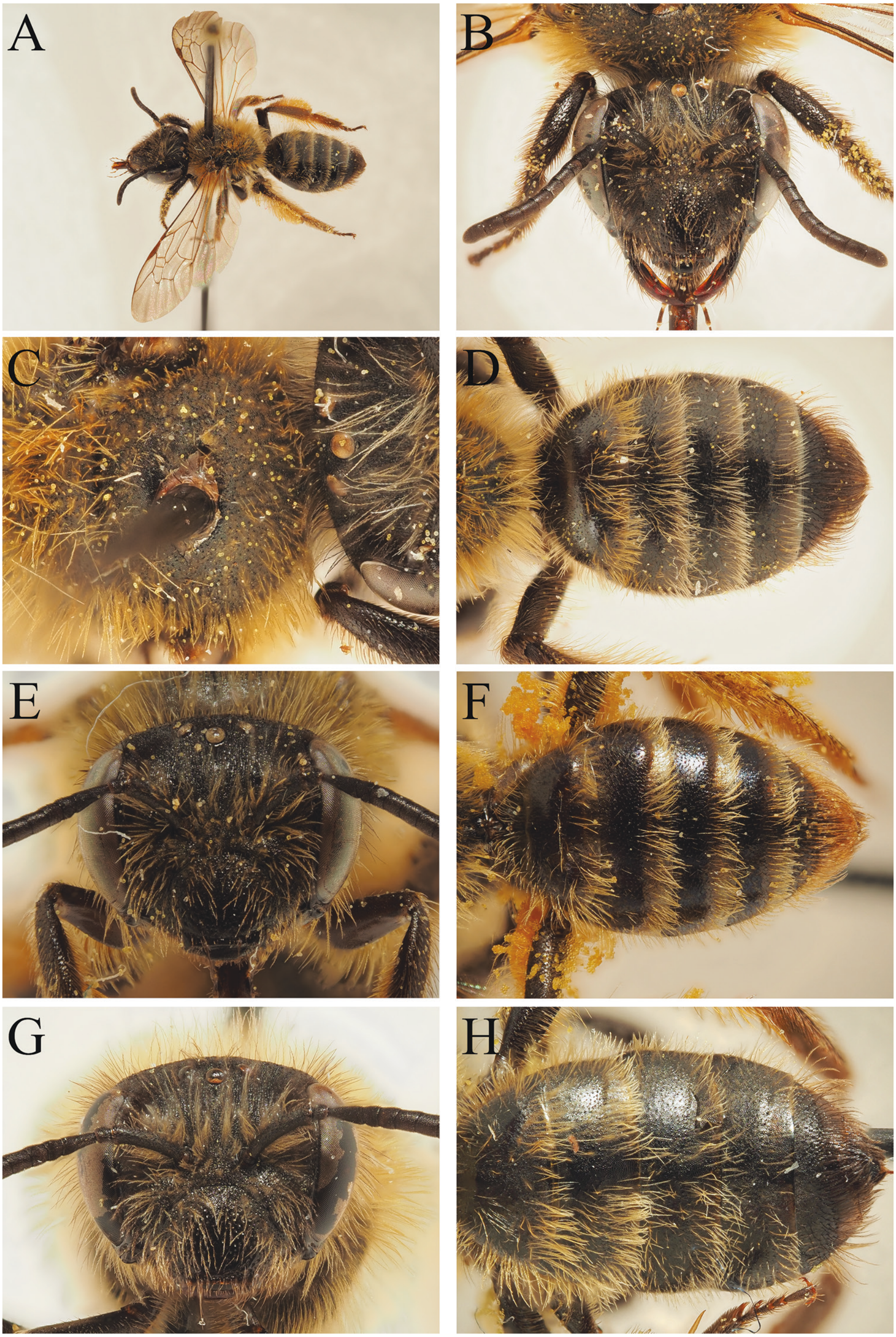

Figure 5. *Andrena* (*Euandrena*) *officinalis* Wood, sp. nov. female. **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Scutum, dorsal view; **D.** Terga, dorsal view; *Andrena* (*Euandrena*) *vulpecula* Kriechbaumer, 1873 female. **E.** Head, frontal view; **F.** Terga, dorsal view; *Andrena* (*Euandrena*) *rufula* Schmiedeknecht, 1884 female; **G.** Face, frontal view; **H.** Terga, dorsal view.

not occupying more than ½ of marginal areas (Fig. 5D). Marginal areas of T2–4 slightly but distinctly depressed, marginal area of T2 almost forming step-like junction with disc. Terga finely and weakly shagreened, discs of T2–4 almost polished and shining, moderately punctate, punctures separated by 1–2 puncture diameters. Discs of T1–2 with long upstanding hairs, remaining terga with shorter golden-brown hairs; margins of T2–4 with hairs forming shaggy, poorly-defined, and long apical hairbands extending onto disc of following tergum. Apical fringe of T5 and hairs flanking pygidial plate dark brown to black. Pygidial plate rounded triangular, surface obscurely punctate, dull.

Male. Body length: 9–10 mm (Fig. 6A). ***Head:*** Dark, 1.1 times wider than long (Fig. 6B). Clypeus domed to slightly flattened medially, densely punctate, punctures predominantly separated by 0.5 puncture diameters, slightly sparser medially with hints of impunctate longitudinal midline; underling surface shagreened basally to weakly shining medially and apically. Process of labrum trapezoidal, slightly broader than long, surface polished and shining. Galea with outer surface finely shagreened, weakly shining (Fig. 6C). Mouthparts moderately long, approaching ½ length of head. Maxillary palps with 6 segments, labial palps with 4 segments; segments of labial palpi slightly elongate. Mandibular palpi with segments of approximately equal length, segment 2 1.2 times length of other segments. Mandibles elongate, strongly crossing apically, with strong inner subapical tooth. Gena broad, almost twice width of compound eye, posterior margin rounded; ocelloccipital distance 1.5 times diameter of lateral ocellus (Fig. 6D). Head with mixture of light and dark hairs, face medially with greyish hairs on supraclypeal area, paraocular areas, scape, and around antennal insertions, hairs becoming black on clypeus and inner margins of compound eyes; gena and vertex with intermixed light brown and black hairs, longest hairs exceeding length of scape. Antennae basally dark, A4–13 ventrally uniformly lightened by presence of grey scales; A3 exceeding A4, shorter than A4+5, A4 only slightly longer than broad, A5–13 rectangular, clearly longer than broad.

Mesosoma: Scutum and scutellum microreticulate, dull, obscurely punctate with punctures disappearing into the underlying sculpture. Pronotum with strong humeral angle. Mesepisternum and dorsolateral parts of propodeum finely microreticulate, overlain with network of fine reticulation forming pattern of areolate hair-bearing pseudo-crater punctures, surface dull. Propodeal triangle narrow, poorly defined, lacking areolate pseudopunctures but otherwise almost indistinguishable from dorsolateral parts of propodeum. Mesosoma covered with very long golden-brown hairs, hairs intermixed with black on mesepisternum. Legs dark, apical tarsal segments lightened orange-brown, pubescence light brown to brownish. Hind tarsal claws with inner tooth. Wings hyaline, stigma dark brown, venation orange-brown, nervulus interstitial.

Metasoma: Tergal discs dark, apical margins obscurely lightened brownish (Fig. 6E). Tergal discs shagreened to finely microreticulate, weakly shining, sculpture reduced on tergal margins, slightly more brightly shining; surface with fine punctures separated by 1–2 puncture diameters, somewhat disappearing into underlying sculpture. Terga covered in loose light brown hairs, not obscuring underlying surface, T2–4 laterally with very weak apical hair fringes, broadly interrupted medially. T6–7 with

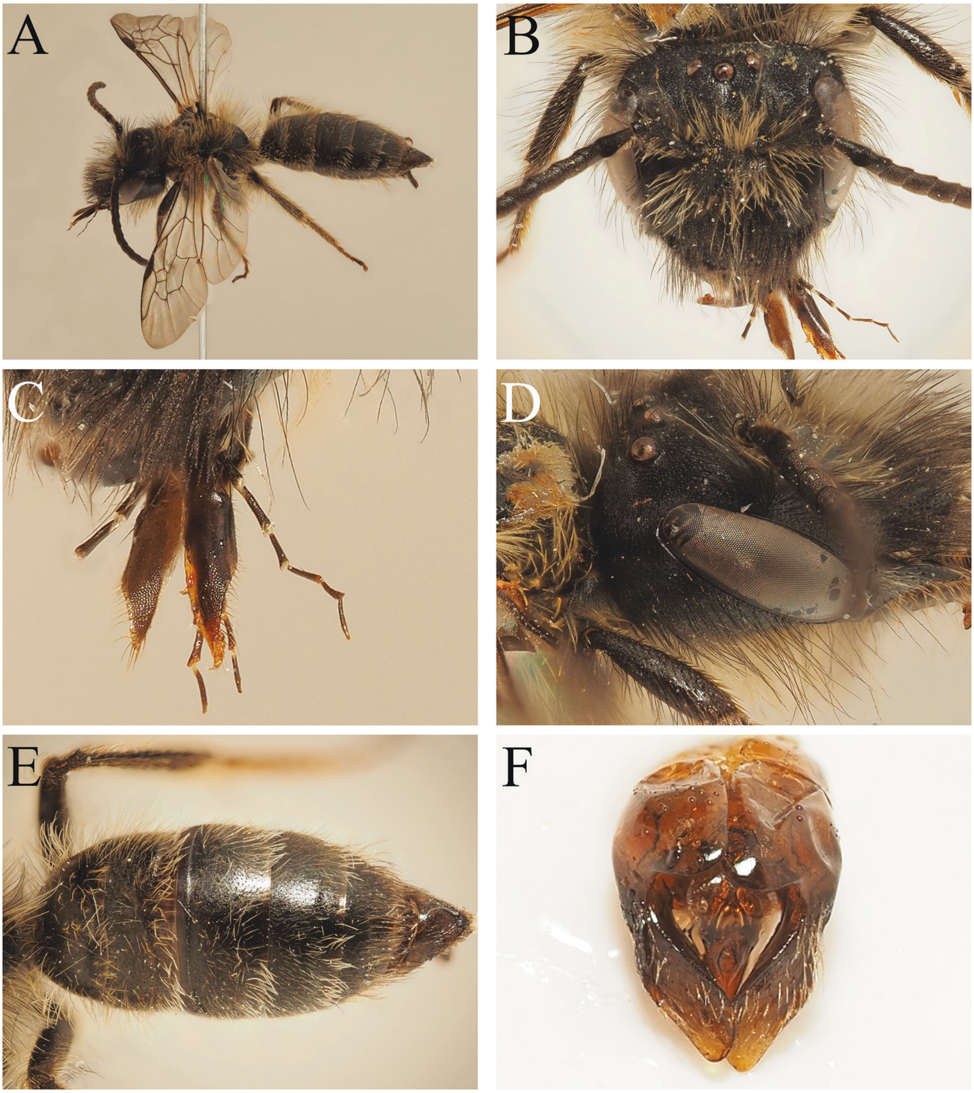

Figure 6. *Andrena* (*Euandrena*) *officinalis* Wood, sp. nov. male. **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Galea and palpi, frontal view; **D.** Gena, lateral view; **E.** Terga, dorsal view; **F.** Genitalia, dorsal view.

dark brown hairs. S8 columnar, apically truncate, ventral surface covered with fan of dark brown hairs. Genital capsule with gonocoxae produced into broad rounded apical teeth, gonostyli basally slightly constricted before strongly broadening, forming rectangular spatulate blades (Fig. 6F). Penis vales basally broadened with lateral hyaline extensions, occupying majority of the space between the penis valves.

Diagnosis. For females, the character of facial foveae dorsally narrow, occupying at most ⅓ of space between lateral ocellus and compound eye, and then strongly narrowing strongly ventrally in combination with the lack of other distinctive characters allows placement into Group L (subgenus *Euandrena* Hedicke, 1933) in the key of Wood (2023). The head is relatively rounded (only 1.1 times wider than long), but the mouthparts do not even approach twice the length of the head (at most ½ the length of the head), excluding *A. solenopalpa* Benoist, 1945, and the clypeus has only a narrow and poorly-defined impunctate longitudinal midline, not a broad and raised shining impunctate longitudinal midline as in *A. symphyti* Schmiedeknecht, 1883. The clypeal mid-line is also not impressed and the pronotum lacks a clear humeral angle, excluding the *angustior*-group (couplet 155), and the terga are finely punctate (excluding *A. fortipunctata* Wood, 2021).

This brings the species to couplet 157 of the female key at which point a diagnosis against all remaining *Euandrena* species is necessary. It is not part of the *bicolor*-group (couplets 160+161) as the facial pubescence is a mixture of black and golden-brown hairs and the mesepisternum is entirely covered with brown hairs), it is neither *A. granulosa* Pérez, 1902 or *A. vulpecula* Kriechbaumer, 1873 because the tergal margins only have their apical rim narrowly lightened hyaline-yellow to whitish (Fig. 5D) and the clypeus medially weakly shagreened and more or less shining with clearly visible punctures (Fig. 5B; tergal margins broadly lightened with this lightened area clearly exceeding the diameter of an ocellus and clypeus largely shagreened with punctures disappearing into the underlying sculpture in *A. granulosa* and *A. vulpecula*, Fig. 5E–F), and it is not *A. rufula* Schmiedeknecht, 1884 because the head is 1.15 times longer than wide and the surface of the clypeus is medially weakly shagreened and more or less shining (Fig. 5B; in *A. rufula* with the head 1.25 times wider than long and with the surface of the clypeus more strongly shagreened, shining only along its apical margin, Fig. 5G), and the tergal margins have a distinct hyaline rim (Fig. 5D; in *A. rufula* with the tergal margins showing at most an obscure brownish rim, Fig. 5H). *Andrena rufula* is also known in Iberia only from the Pyrenees, and hence the Sierra de Cazorla is widely separated geographically.

This places it extremely close to the newly described *Andrena rostro* (see below). Whilst the males are clearly distinct, females exhibit the same relatively rounded face (only 1.1–1.15 times wider than long) and pubescence pattern. Care must be taken to separate the two species, and comparative material is essential; *Andrena officinalis* can be recognised due to the tergal margins which are slightly but distinctly impressed, almost forming a step-like junction on T2 (in *A. rostro* with the tergal margins weakly depressed, not forming such a junction on T2), scutum medially with punctures shallow but distinctly produced against the underlying granular microreticulation, with the scutum itself weakly shining (in *A. rostro* with the scutal punctures medially shallow and poorly defined, disappearing into the dull granular microreticulation), discs of T2–4 with very weak microsculpture, almost polished and shining (in *A. rostro* with the discs of T2–4 with faint microsculpture, enough that they are not polished and shining), marginal areas of T2–4 laterally with long messy apical hair fringes of hairs which clearly extend over the marginal areas and onto the disc of the following tergum (Fig. 5D; in *A. rostro* with T2–4 laterally with much shorter and tighter, only barely extending onto the disc of the following tergum, Fig. 7D), and the hyaline rims of the terga slightly exceed the diameter of an ocellus in breadth (Fig. 5D; in *A. rostro* with the hyaline-lightened marginal rim of the terga subequal to the diameter of an ocellus in breadth, Fig. 7D). These characters are very subtle, and so association with concurrently active males should be made.

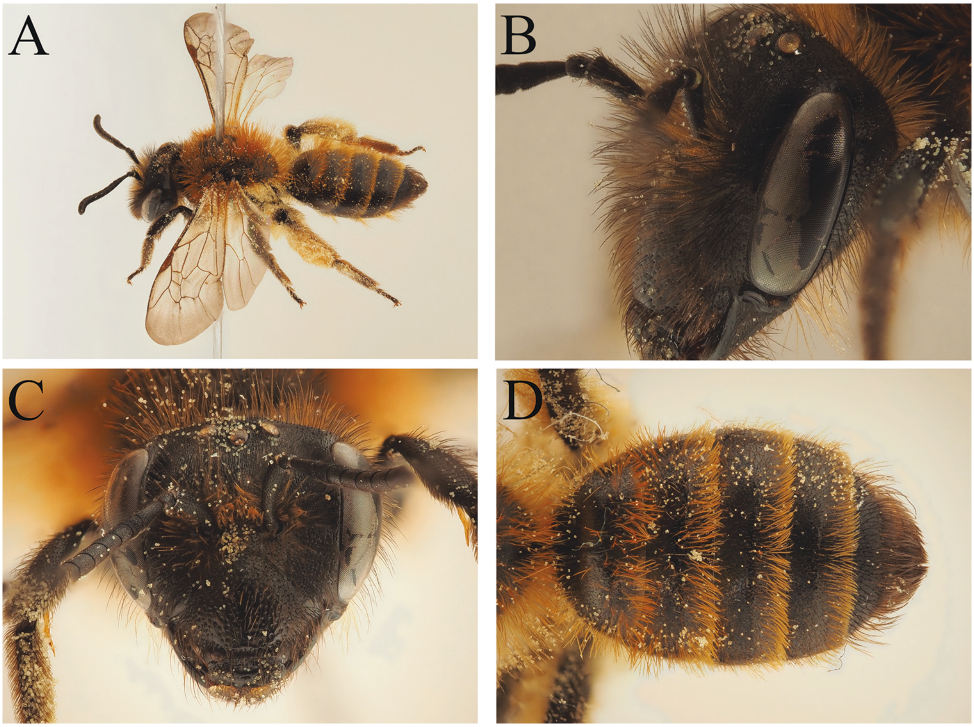

Figure 7. *Andrena* (*Euandrena*) *rostro* Wood, sp. nov. female. **A.** Habitus, lateral view; **B.** Head, lateral view; **C.** Head, frontal view; **D.** Terga, dorsal view.

In the male sex, due to the mandibles elongate, sickle-like, and strongly crossing apically, strong pronotal angle, and gena broadened, exceeding the diameter of the compound eye (Fig. 6D), this species keys to Group K in the male key of Wood (2023). Within this group, the elongate A3 (exceeding the length of A4), bidentate mandible, intermixed light and dark facial pubescence, moderate body size of 9 mm, and genital capsule without strongly projecting gonocoxal teeth (Fig. 6F) places it at couplet 158 (i.e. not continuing to subgenus *Andrena* s. str.) and next to *A. lavandulae* Pérez, 1895.

The two species are superficially close, but can be separated principally by the clypeus, the tergal margins, and the genital capsule. *Andrena officinalis* has the clypeus in frontal view elongate, ventrally extending far belong a line drawn between the lower margins of the compound eyes, the overall shape of the head therefore elongate, 1.15 times wider than long (in *A. lavandulae* with the clypeus apically truncate, only slightly extending belong a line drawn between the lower margins of the compound eyes, the overall shape of the head therefore broader, 1.25 times wider than long), the tergal margins are mostly dark with the apical rim obscurely lightened hyaline-white (in *A. lavandulae* with the tergal margins with their apical rim narrowly but conspicuously lightened hyaline-brown), and the genital capsule has the gonocoxal teeth broadly rounded and produced, the gonostyli are basally slightly constricted before strongly broadening to form flattened more-or-less rectangular spatulate apexes, and the penis valves are basally broadened with lateral hyaline extensions, occupying the majority of the space between the penis valves (in *A. lavandulae* with the gonocoxae apically truncate and not forming teeth, the gonostyli narrow and not apically expanded or spatulate, and the penis valves narrow and more-or-less parallel sided).

Genetically, a 658 bp sequence from the COI gene was generated. This was separated from *A. lavandulae* sequences by an average of 10.03% (range 9.88–10.33%), and from *A. angustior* by 4.22% (range 3.95–4.45%). The closest sequence was an *A. angustior* from the Sistema Central (Sierra de Alto Rey, Guadalajara province; IBIHM1039-22; Wood et al. 2024). Although *A. officinalis* does not key immediately adjacent to *A. angustior* and can easily be separated due to the lack of the distinctively depressed margin of T2 in both sexes, the barcode result suggests that *A. officinalis* is an isolated lineage separated from populations of *A. angustior* which are restricted in Iberia to regions with a temperate climate.

Biology. *Andrena officinalis* is strongly associated with *Rosmarinus officinalis* L. (Lamiaceae). All males have been collected from *R. officinalis* ($N = 6$), as well as most females ($N = 4$). One additional female has been collected from *Aquilegia vulgaris* (Ranunculaceae). Based on current knowledge, no *Andrena* species globally is known to be specialised for pollen collection on the family Lamiaceae; in an analysis of global bee pollen diets, *Andrena* (*Oreomelissa*) *coitana* (Kirby, 1802) was found to collect the most pollen from Lamiaceae of any *Andrena* species – a paltry 5.2% (Wood et al. 2023a). In this context, *A. officinalis* is a potential candidate to investigate for Lamiaceae pollen use within *Andrena*.

Etymology. Taken from the plant this species was captured foraging on, *Rosmarinus officinalis*; this specific name is an adjective in the masculine/feminine nominative form (two-termination adjective) indicating that a species is of interest for its pharmacological properties. This is obviously not the case for this bee, but it is worthwhile to highlight its association with this member of the Lamiaceae family, since this is unusual in the genus *Andrena*.

Distribution. Spain (Sierra de Cazorla).

***Andrena* (*Euandrena*) *rostro* Wood, sp. nov.**

https://zoobank.org/C67F33C5-9050-4BA2-82A0-DA7B927D7CA4

Type material. ***Holotype:*** Spain • 1♀; Jaén, Sierra de Cazorla, Vadillo-Castril; 37.9257°N, -2.9275°W; 22 Mar. 2024; C.M. Herrera leg.; RMNH; RMNH.INS.1715580.

Paratype: Spain • 1♂; Jaén, Sierra de Cazorla, Vadillo-Castril; 37.9257°N, -2.9275°W; 22 Mar. 2024; C.M. Herrera leg.; RMNH; RMNH.INS.1715579 • 1♂; Jaén, Sierra de Cazorla, Vadillo-Castril; 24 Mar. 2024; C.M. Herrera leg.; CMHC • 1♀; Jaén, Sierra de Cazorla, Roblehondo; 13 Apr. 1987; C.M. Herrera leg.; EBDC • 1♀; Jaén, Sierra de Cazorla, Vadillo-Castril; 22 Mar. 2024; C.M. Herrera leg.; MNCN.

Description. Female. Body length: 9–10 mm (Fig. 7A). ***Head:*** Dark, 1.15 times wider than long (Fig. 7C). Clypeus weakly domed, somewhat flattened medially, surface laterally shagreened and dull, shagreen weakening medially, more or less shining over majority of surface; surface densely but irregularly punctate, punctures separated by 0.5–1 puncture diameters, up to 2 puncture diameters medially with weak indication of obscure longitudinal impunctate midline. Process of labrum rounded trapezoidal, 2 times wider than long. Mouthparts moderately long, approaching ½ length of head; 6 mandibular palpi, 4 labial palpi. Mandibular palpi with segments of approximately equal length, segment 2 1.2 times length of other segments. Mandibles slightly elongate, weakly crossing apically, with inner subapical tooth. Gena slightly exceeding width of compound eye; ocelloccipital distance subequal to diameter of lateral ocellus. Foveae dorsally occupying ⅓ space between compound eye and lateral ocellus, ventrally narrowing further, narrower than diameter of flagellum; foveae filled with black hairs. Face with golden-brown hairs on supraclypeal area and around antennal insertions, hairs black elsewhere; gena and vertex with intermixed golden-brown and black hairs (Fig. 7B). Antennae dark, A3 slightly exceeding A4+5.

Mesosoma: Scutum and scutellum densely and shallowly punctate, punctures separated by 0.5–1 puncture diameters over majority of surface, slightly sparser posterior-medially, disappearing into underlying finely microreticulate surface sculpture, dull to obscurely shining medially. Pronotum rounded. Mesepisternum and dorsolateral parts of propodeum finely microreticulate, overlain with network of fine reticulation forming pattern of areolate hair-bearing pseudo-crater punctures, surface dull. Propodeal triangle narrow, laterally delineated by slight carinae, internal surface with fine granular microreticulation, contrasting pseudopunctures of remaining parts of propodeum. Mesepisternum with long finely plumose golden-brown hairs, not equalling length of scape, hairs continuing onto scutum, scutellum, and propodeum, without intermixed black hairs. Propodeal corbicula incomplete, composed of golden-brown plumose hairs, internal surface with long simple hairs. Legs dark, pubescence dark brown. Flocculus complete, composed of light brown plumose hairs; femoral and tibial scopae composed of golden-brown to orange simple hairs, tibial scopa with hairs dark brown dorsally at basitibial plate. Hind tarsal claws with inner tooth. Wings hyaline, stigma and venation dark orange, nervulus interstitial.

Metasoma: Tergal discs dark, marginal areas narrowly but distinctly lightened hyaline orange-brown on apical rims, subequal to diameter of lateral ocellus, with colouration not occupying more than ¼ of marginal areas (Fig. 7D). Terga finely and weakly shagreened, more-or-less shining, moderately punctate, punctures separated by 1–2 puncture diameters. Tergal discs with short golden-brown hairs, hairs becoming longer and denser on marginal areas, forming complete apical hairbands, T1–2 with long upstanding hairs. Apical fringe of T5 and hairs flanking pygidial plate dark brown to black. Pygidial plate rounded triangular, surface obscurely punctate, dull.

Male. Body length: 8–8.5 mm (Fig. 8A). ***Head:*** 1.15 times wider than long. Clypeus weakly flattened over majority of surface, densely and regularly punctate, punctures separated by 0.5–1 puncture diameter, interspaces polished and shining (Fig. 8B). Process of labrum rounded rectangular, 2 times wider than long, surface polished, anterior margin emarginate in ventral view. Mouthparts short, approaching ⅓ length of head; 6 mandibular palpi, 4 labial palpi. Mandibular palpi with segments of approximately equal length, segment 2 1.2 times length of other segments. Mandibles slightly elongate, weakly crossing apically, with inner subapical tooth. Gena equalling

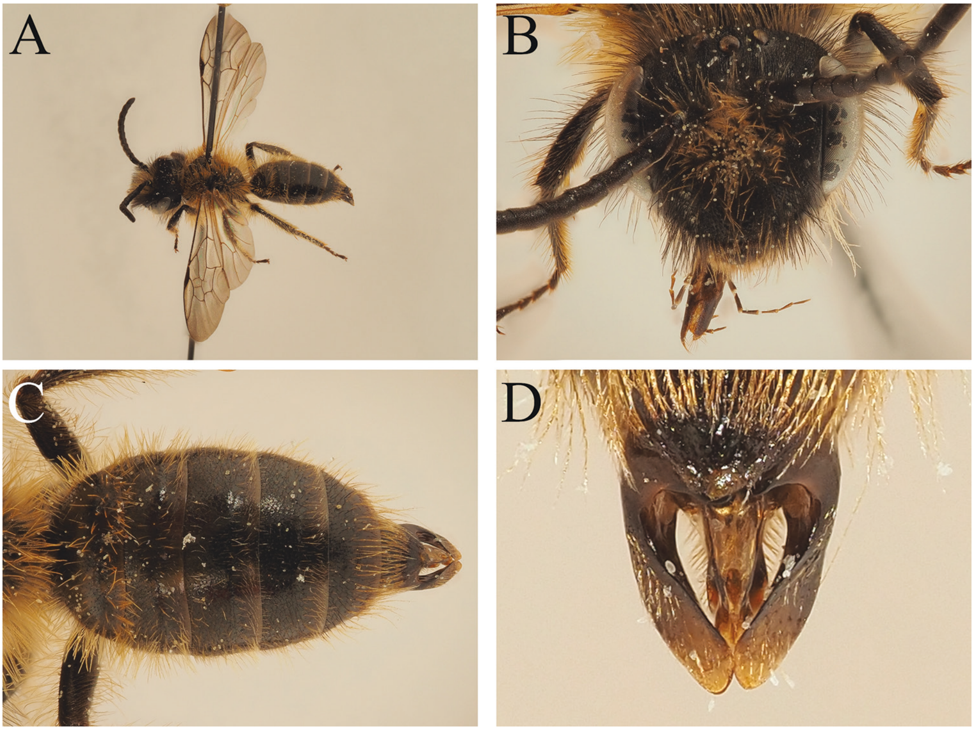

Figure 8. *Andrena* (*Euandrena*) *rostro* Wood, sp. nov. male. **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Terga, dorsal view; **D.** Genital capsule, dorsal view.

width of compound eye; ocelloccipital distance equalling diameter of lateral ocellus. Face with golden-brown hairs on supraclypeal area and around antennal insertions, hairs black elsewhere; gena and vertex with intermixed golden-brown and black hairs. Antennae basally dark, A4–13 ventrally lightened by presence of greyish scales, A3 exceeding A4, shorter than A4+5.

Mesosoma: Scutum and scutellum shallowly and irregularly punctate, punctures separated by 0.5–2 puncture diameters, surface finely microreticulate, dull. Pronotum rounded. Mesepisternum and dorsolateral parts of propodeum finely microreticulate, overlain with network of fine reticulation forming pattern of areolate hair-bearing pseudo-crater punctures, surface dull. Propodeal triangle narrow, internal surface covered with network of raised rugae, thus contrasting dorsolateral parts of propodeum. Mesosoma covered with long finely plumose golden-brown hairs, longest hairs on mesepisternum exceeding length of scape. Legs dark, pubescence light brown. Hind tarsal claws with inner tooth. Wings hyaline, stigma and venation dark brown, nervulus interstitial.

Metasoma: Tergal discs dark, marginal areas with apical rims narrowly lightened hyaline-brown (Fig. 8C). Terga finely and weakly shagreened, more-or-less shining, moderately punctate, punctures separated by 1–2 puncture diameters. Tergal discs with long loose light brown hairs, not obscuring underlying surface, T2–4 laterally with obscure pale hair fringes. T6–7 with brown hairs. S8 columnar, apically truncate, ventral surface covered with fan of brown hairs. Genital capsule with gonocoxae very slightly produced into rounded teeth, gonostyli gently broadening apically, spatulate (Fig. 8D). Penis valves narrow, occupying ½ space between gonostyli, constricted subapically before slightly broadening apically.

Diagnosis. For females, the character of facial foveae dorsally narrow, occupying at most ⅓ of space between lateral ocellus and compound eye, and then strongly narrowing strongly ventrally in combination with the lack of other distinctive characters allows placement into Group L (subgenus *Euandrena*) in the key of Wood (2023). *Andrena rostro* is extremely similar to *A. officinalis* in the female sex, and females are separated in the diagnosis for that species.

For males, recognition at a subgeneric level is always more challenging due to the derived phylogenetic placement of this subgenus which lacks distinctive characters and is defined on female characters. In Wood (2023), it keys to the final Group N (i.e. species lacking distinctive characters) with A3 exceeding A4 in length. Here at couplet 216, due to the elongate head which is only 1.15 times wider than long, it would come close to *A.* (*Euandrena*) *ramosa* Wood, 2022 but can be separated by the penis valves constricted subapically before slightly broadening (Fig. 8D; uniformly narrowing towards their apex in *A. ramosa*), gonocoxae slightly produced apically into short rounded teeth (gonocoxae apically truncate, forming 90° angle in *A. ramosa*), clypeus uniformly densely punctate over its entire surface, punctures separated by 0.5–1 puncture diameters, with interspaces shining (in *A. ramosa* with the clypeus basally dull and polished and shining in its apical ½, more irregularly punctate with punctures separated by 0.5–2 puncture diameters), and mesepisternum laterally with weakly plumose hairs (with strongly plumose hairs in *A. ramosa*). In terms of the shape of the genital capsule, it comes closest to *A. rufula* due to the apexes of the gonostyli which form somewhat acute points, but *A. rufula* has the apexes of the gonostyli sharply produced into triangular points, and the gonocoxae are produced into broad flattened truncate teeth (see illustrations in Praz et al. 2019). As for females, the relatively rounded head is the primary character for recognition. Confusion with *A. officinalis* is not possible due to the strongly broadened gena and more complex genital capsule of the former.

Biology. *Andrena rostro* has been collected from a variety of plants; males were collected from *Viburnum tinus* L. (*N* = 2), and females were collected from *Viburnum tinus* (*N* = 1), *Prunus avium* L. (*N* = 1), and *Rosmarinus officinalis* (*N* = 1).

Etymology. From the Latin *rostrum* and hence derived Spanish *rostro* meaning a bird's beak or animal's snout, in reference to the elongate head and clypeus of this species. It is a noun in apposition.

Distribution. Spain (Sierra de Cazorla).

***Andrena* (*Notandrena*) *cazorlae* Wood, sp. nov.**

https://zoobank.org/59B0A318-C996-451D-A025-D254E05BA538

Type material. ***Holotype:*** Spain • 1♀; Jaén, Sierra de Cazorla, La Cabrilla; 37.9314°N, -2.7806°W; 31 May 2022; A. Núñez leg.; RMNH; RMNH.INS.1715577.

Description. Female. Body length: 9 mm (Fig. 9A). ***Head:*** Dark, 1.4 times wider than long (Fig. 9B). Clypeus weakly domed, fore margin upturned, surface microreticulate, weakly shining apically; surface with obscure punctures, punctures separated by <0.5–1 puncture diameters. Process of labrum trapezoidal, 2 times wider than long, anterior margin narrowly but distinctly emarginate. Gena slightly exceeding width of compound eye; ocelloccipital distance equalling diameter of lateral ocellus. Foveae dorsally occupying slightly >½ space between compound eye and lateral ocellus (Fig. 9C), slightly narrowing ventrally at level of antennal insertions; foveae filled with dark brown hairs, becoming lighter ventrally. Face and gena covered with short white hairs, becoming longer and light brown on vertex. Antennae dark, A5–12 slightly ventrally lightened by presence of greyish-orange scales; A3 equalling A4+5, A4 sub-square, slightly wider than long.

Mesosoma: Scutum densely punctate, punctures typically separated by 0.5–1 puncture diameters, surface finely microreticulate, dull (Fig. 9D). Scutellum more sparsely punctate, punctures separated by 0.5–4 puncture diameters over majority of disc; surface finely shagreened, weakly shining. Pronotum with weak humeral angle. Mesepisternum and dorsolateral parts of propodeum microreticulate overlain by network of dense and fine raised rugosity, surface dull. Propodeal triangle broad, laterally delineated by fine carinae, internal surface with fine network of raised rugae covering majority of surface. Mesepisternum with white finely plumose hairs, hairs becoming golden-brown on scutum. Propodeal corbicula incomplete, composed of whitish plumose hairs, internal surface with long simple hairs. Legs dark basally, tarsi and hind tibiae partially lightened orange, pubescence whitish. Flocculus complete, composed of white plumose hairs; femoral and tibial scopae composed of pale simple hairs, tibial scopa with dorsal and ventral fringes long, dorsal fringe not noticeably shorter than ventral fringe (Fig. 9E). Hind tarsal claws with small inner tooth. Wings hyaline, stigma and venation dark brown, nervulus interstitial.

Metasoma: Tergal discs dark, apical margins with rims narrowly lightened hyaline-brown (Fig. 9F). T1 with disc moderately punctate, punctures separated by 1–3 puncture diameters; discs of T2–4 densely punctate, punctures separated by 0.5–1 puncture diameter, punctures becoming sparser on marginal areas. Tergal surface finely shagreened, weakly to strongly shining depending on puncture density. Tergal discs with obscure short white hairs, not obscuring underlying surface, marginal areas of T2–4 with narrow apical hairbands composed of white hairs, broadly interrupted on T2, nearly complete but abraded on T3, and complete on T4. Apical fringe of T5 and hairs flanking pygidial plate golden-brown, becoming white laterally. Pygidial plate rounded triangular, medially very subtly depressed and shallowly and obscurely punctate.

Male. Unknown.

Diagnosis. *Andrena cazorlae* can be recognised as part of the subgenus *Notandrena* Pérez, 1890 due to the short and broad head (1.4 times wider than long), pronotum with a humeral angle (weak and challenging to see), the non-metallic integument, and lack of any other distinctive characters takes it to couplet 177 in the female key of Wood (2023). It can be separated from all Iberian *Notandrena* due to the combination of dense scutal punctures (separated by 0.5–1 puncture diameters, but not contiguous;

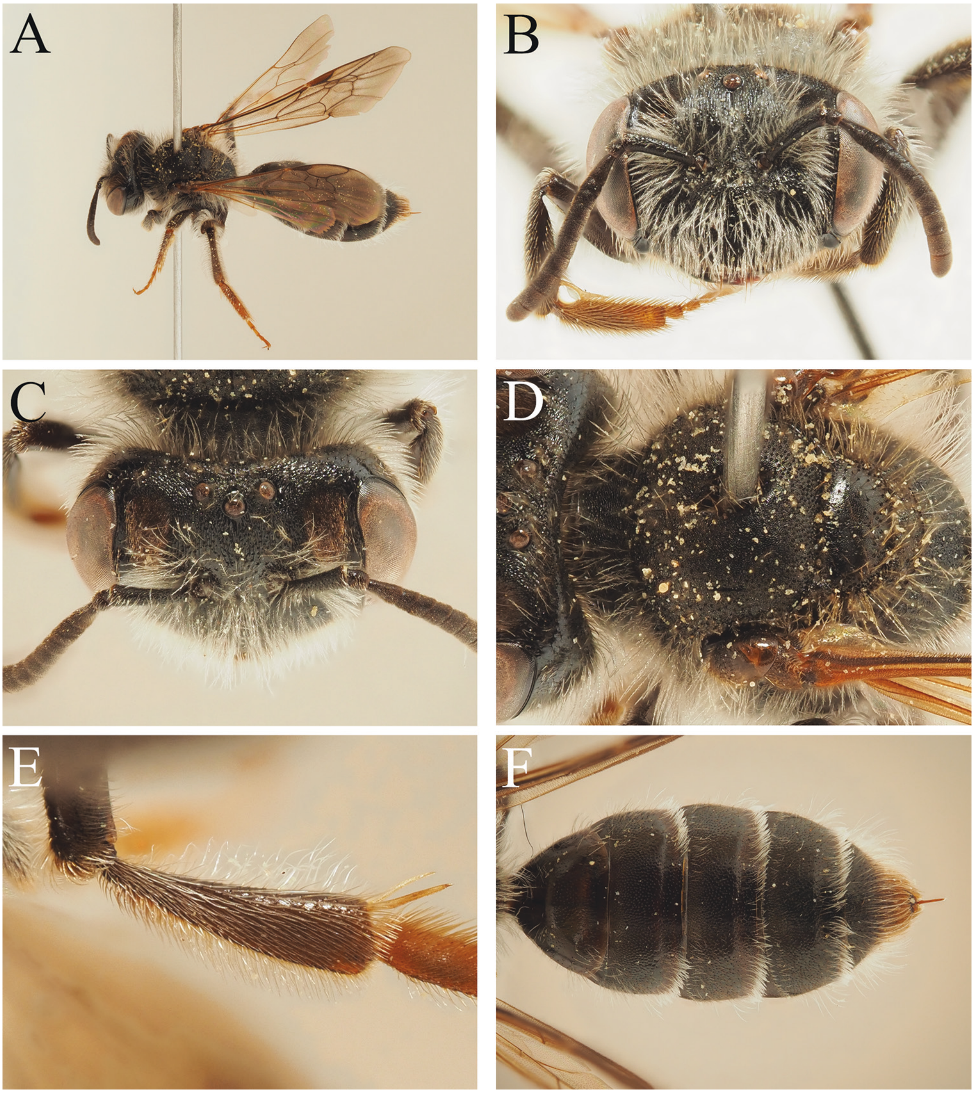

Figure 9. *Andrena* (*Notandrena*) *cazorlae* Wood, sp. nov. female. **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Facial foveae, dorsal view; **D.** Scutum, dorsolateral view; **E.** Tibial scopa, lateral view; **F.** Terga, dorsal view.

contiguous in *A. griseobalteata* Dours, 1872), facial foveae broad and occupying slightly >½ the space between the compound eye and lateral ocellus (narrower in all comparison species), body length of 9 mm (10–11 mm in *A. langadensis albipila* Warncke, 1967), and hind tibia with the dorsal scopal hairs clearly exceeding the diameter of a lateral ocellus in length, not meaningfully shorter than the ventral hairs (these hairs around 1–1.5 times the diameter of an ocellus in *A. pallitarsis* Pérez, 1903).

Finally, due to the broad facial foveae it is similar to *A. pontica* Warncke, 1972 (southern Germany to eastern Turkey), but apart from the distinct geographical range, this species has the facial foveae broader (occupying ¾ of the space between the compound eye and lateral ocellus) and the scutellar punctures more uniformly dense, separated by 0.5 puncture diameters.

Etymology. Taken from the name of the mountain range the Sierra de Cazorla in the genitive singular form, hence "the *Andrena* of Cazorla".

Conclusions

Long-term, extensive sampling of *Andrena* bees in the Cazorla biodiversity hotspot has documented their high species diversity, elucidated major features of relationships with plants, and contributed to assess the magnitude of the genus' dark diversity. Thorough investigation of pollinators at the plant community level made also possible the discovery of the three new species described here. The vast majority of *Andrena* species in the study area were rare or infrequent, with each of which associated with only a few plant taxa. This finding and the encompassing distribution of *Andrena* over the plant phylogeny are consistent with the interpretation that the remarkable diversification of *Andrena* might have been facilitated by broad food niche and interspecific resource partitioning at the local and regional levels. Particularly revealing at this regard was the observation that the few *Andrena* species which were each associated with many plant taxa tended to exhibit broad continental distributions and pollen food niche. Our high estimate of *Andrena* dark diversity in the Cazorla range prompts the warning that even thorough spatial and temporal sampling of plant-bee biodiversity hotspots may fail to provide truly comprehensive pictures of hyperdiverse bee assemblages when these are mostly made up of rare species. Further research in other regions with similarly high plant and bee diversities are needed to ascertain the generality of this conclusion.

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