

# A new small carder bee species from the eastern Canary Islands (Hymenoptera, Megachilidae, Anthidiini)

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## Abstract

Recent field surveys in the eastern Canary Islands (Spain), followed by contributions of new occurrence records through the citizen science platform iNaturalist.com and the social media photo repository Flickr.com have revealed the presence of an overlooked small carder bee species (genus *Pseudoanthidium* Friese (Megachilidae: Anthidiini)) on the islands of Lanzarote and Fuerteventura. Here, we combined morphology, DNA barcodes (mitochondrial cytochrome *c* oxidase subunit I, *COI*) and ecological data (distribution, altitudinal ranges and environmental niche classification) to describe this species as *Pseudoanthidium* (*Pseudoanthidium*) *jacobii* sp. nov. We provide an illustrated description along with diagnostic morphological characters to separate it from *P.* (*P.*) *canariense* (Mavromoustakis, 1954), the only other congeneric species known from the neighbouring islands of La Gomera, Tenerife and Gran Canaria and from which it is separated by a genetic distance of 2.7%. We also evaluated the extent of shared environmental niche space among the two *Pseudoanthidium* species, and our results show a significant difference in elevation range as well as a very small (less than 1%) overlap between the modelled climatic niche of *P. jacobii* and that of *P. canariense*. Given the extremely restricted geographic distribution and the fragile and isolated nature of the habitat and host plants of this new island endemic species, we assign it an IUCN conservation status of “EN” (endangered) and discuss avenues for future research on the ecology and conservation of wild bees in the Canary Islands and neighbouring regions.

## Keywords

Archipelago, biogeography, Canary Islands, COI mtDNA, genetic divergence, IUCN assessment, Red List, taxonomy

## Introduction

Within Macaronesia and its oceanic islands, the Canary Islands (CI) archipelago encompasses seven islands with contrasting climates, topography, and geological history. Among the many fascinating facets of the CI archipelago for the island biogeographer is the diversity of environmental conditions, as well as the ecological and geological gradients observed within and among the islands. The CI are a well-known hotspot of biological endemism ever since Von Humboldt's first visit in 1799, for both plants and animals (Kunkel 1976; Fernández-Palacios et al. 2004; Fernández-Palacios and Whittaker 2008; Bowler 2018); to some naturalists, including the entomologist WM Wheeler, author of a review on the ants of the CI in the early 20<sup>th</sup> century, the Canaries "bear much the same relation to the south Palearctic fauna that [...] the Galapagos bear to those of South and Central America" (Wheeler 1927). The CI have long been a popular destination for European entomologists, including lepidopterists who by the end of the 19<sup>th</sup> century had already listed all butterfly species inhabiting the archipelago (Wiemers 1995 and references therein). Likewise, coleopterists have investigated the fauna of the archipelago for decades, including in some relict communities of laurel forest (Laurisilva) and thermophilous vegetation on the island of Fuerteventura (Machado 1976).

By contrast, historical surveys across the CI by hymenopterists (except myrmecologists), have lagged behind for decades. Although there are early reports on wild bees tracing back to the early 20<sup>th</sup> century, it was not until 1993 that the first comprehensive and annotated catalogue of the 127 species and subspecies of wild bees (of which 38% are strict CI endemics) was published (Hohmann et al. 1993), at a time when most European regions and countries still lacked species checklists. The availability of this 1993 "baseline" represents a cornerstone piece of information, as well as one of the pillars of contemporary research, and it has stimulated more surveys in the CI and the collection of biological occurrence records by Canarian and continental European entomologists ever since (Tkalčú 1993, 2001a, 2001b; Kuhlmann 2000; Dupont and Skov 2004; Pesenko and Pauly 2005; Smit 2007; Pérez and Marcías-Hernández 2012; Suárez et al. 2017; Kratochwil and Schwabe 2018, 2020; Kratochwil 2020). This, along with the development of citizen science projects (iNaturalist.com 2023) and standardised field surveys by and with local institutions, has radically improved our knowledge on the biodiversity and biogeography of wild bees in the CI archipelago.

Despite these advances, it is clear that gaps in our knowledge on CI bees are persistent, as demonstrated by the new island records of native species (Jacobi and Suárez 2018), or recent reports on exotic species reaching the archipelago (Pérez and Hernández 2012; Ortiz et al. 2016; Strudwick and Jacobi 2018; Ruiz et al. 2020; Lugo et al.

2022). Even locally intensive surveys on the most species-rich islands are likely still incomplete and have missed a certain number of species, opening the door for new discoveries. Photographs posted on online platforms such as iNaturalist.com or observations.org, as well as on Flickr.com and other similar online repositories, have recently served as the first evidence of new species in other parts of the world (Jaiswara et al. 2022; Masson Rosa et al. 2022; Zhang et al. 2022). These online portals represent an important new source of biological records for bees and other organisms, and an effective tool to engage anyone willing to produce new observations, armed with a camera, a little luck and some time spent in the field.

Here, we report on the results of recent field surveys focusing on wild bees in the CI archipelago, followed by observations shared through the citizen science platform iNaturalist.com and the social media photo repository Flickr.com. By combining detailed morphological analysis, DNA barcodes (mitochondrial cytochrome *c* oxidase subunit I, *COI*) and ecological data (distribution, altitudinal ranges and environmental niche classification), we concluded that specimens of a solitary bee belonging to the genus *Pseudoanthidium* (Megachilidae, Anthidiini) collected and photographed *in situ* in Lanzarote and Fuerteventura on multiple occasions in recent years, represents a hitherto unknown species of small carder bee that we describe below.

## Materials and methods

### Specimen collection and preparation, collection of occurrence records

As part of an ongoing collaboration between the Université libre de Bruxelles (NVJ, LM, JMM) and the Departamento Biología Animal, Edafología y Geología of the University of La Laguna (CR) on apple tree pollinators, as well as the biogeography of the Canary Islands bees and the development of new taxonomic tools on the bees of Europe, field surveys have been conducted on the islands of Tenerife, Fuerteventura and Lanzarote in April 2021.

On 18.iv.2021, a male *Pseudoanthidium* was photographed by NVJ (Fig. 1A, B) and collected with a hand net at Haría (Lanzarote); a female was collected with a hand net at the same site on the same day by JMM. The following day, on 19.iv.2021, two male *Pseudoanthidium* specimens were collected at Teguise (Lanzarote). All specimens were first assumed to be new island records of *P. canariense*, until a closer examination of pinned specimens under the microscope challenged this view. The type specimens curated at the ULB Agroecology Lab entomological collection (Brussels, Belgium) will be transferred to the DZUL entomological collection curated by CR at the University of La Laguna (Tenerife) upon the publication of this manuscript.

On 12.ii.2023, a female *Pseudoanthidium* was photographed at Bco. Valle del Palomo (Lanzarote) by MPG, and two female specimens were collected by MPG at Haría (Lanzarote), one on 21.ii.2023 (Bco. Valle del Palomo), and another one on 16.iv.2023 (Bco. de Elvira Sánchez). These specimens were sent to CR to be pinned,

prepared for identification and deposited at the entomological collection curated by CR at the University of La Laguna (Tenerife). On 19.iv.2023, CR collected one female *Pseudoanthidium* species at Bco. de Elvira Sánchez (Haría, Lanzarote) now included in the DZUL entomological collection at the University of La Laguna (Tenerife). Publicly available occurrence data on wild bees across the Canary Islands reveal a significant disparity in sampling (GBIF 2023a): Tenerife (3,211 records), Gran Canaria (787), La Palma (560), Lanzarote (449), La Gomera, (383), Fuerteventura (263) and El Hierro (16). These figures are consistent with the historical patterns published by Hohmann et al. (1993). As a result, although additional collection efforts are needed across the entire island group, we can reasonably conclude that the range of the new *Pseudoanthidium* species does not include Gran Canaria and Tenerife.

On 12.iii.2023 and on 16.iii.2023, two female *Pseudoanthidium* specimens were photographed by BJ at Mácher (Lanzarote) (Fig. 1C, D).

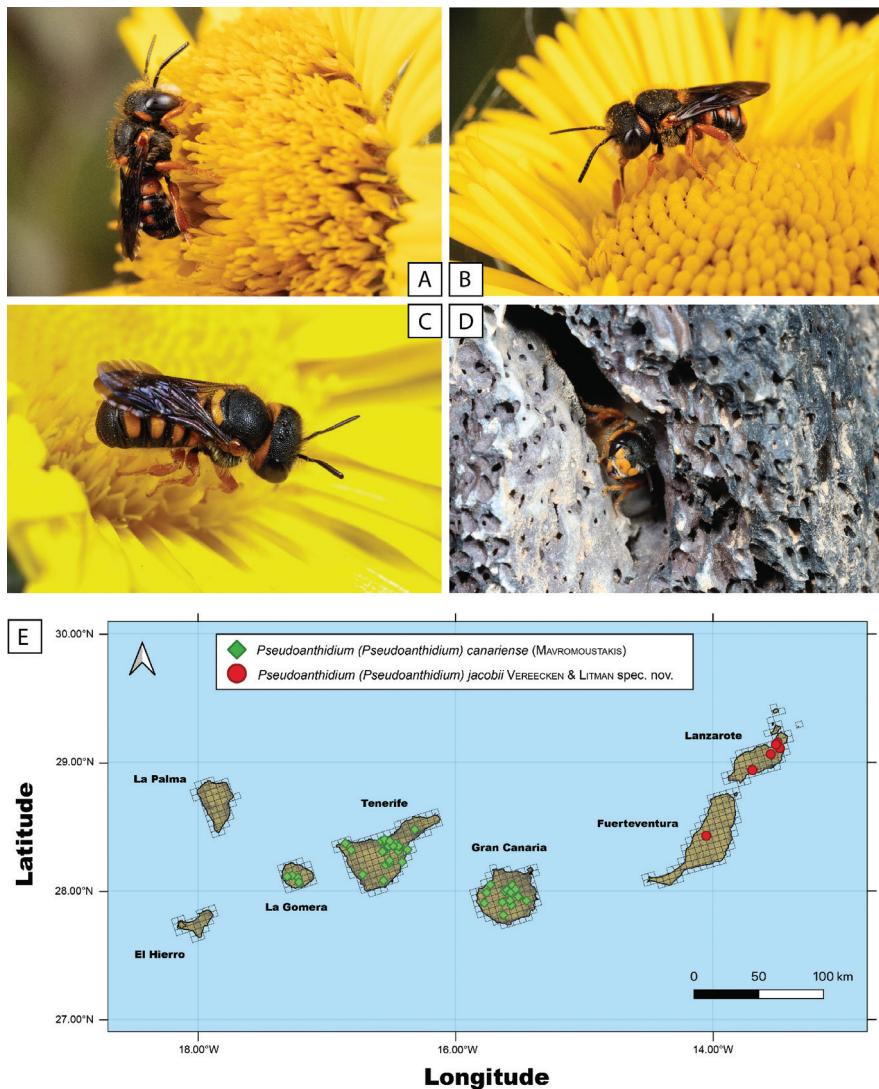
Finally, G. Peña Tejera notified CR of another observation made and published on Flickr.com on 7.iii.2020 at Betancuria (Fuerteventura) by photographer L. Mullins.

### DNA extraction, polymerase chain reaction (PCR) and sequencing of COI sequences

DNA extractions were performed on single legs from one male and one female specimen of this new species using Nucleospin tissue DNA extraction kits (Macherey - Nagel). A 658 base pair fragment of the mitochondrial gene cytochrome c oxidase (CO1) was amplified using the primers Lep-F1 and Lep-R1 under the PCR conditions described in Hebert et al. (2004). PCR products were purified using a combination of exonuclease and FastAP thermostensitive alkaline phosphatase (Fermentas) and sequencing was performed using the same primers as those used for PCR reactions.

### Sequence alignment and phylogenetic analysis of COI

Sequences were edited using Geneious (Kearse et al. 2012) and aligned with eight other CO1 sequences representing the closely related species *Pseudoanthidium canariense* (Mavromoustakis, 1954), *P. scapulare* (Latreille, 1809), *P. nanum* (Mocsáry, 1880), *P. palestinianum* (Mavromoustakis, 1938), *P. tenellum* (Mocsáry, 1880), *P. cibratrum* (Morawitz, 1875) and *P. stigmaticorne* (Dours, 1873), as well as the more distantly related *P. reticulatum* (Mocsáry, 1884) as an outgroup (see Suppl. material 1 for taxon list). Alignments were performed using MAFFT v7.520 (Katoh and Standley 2013) and were verified visually using Mesquite v3.81 (Maddison and Maddison 2023). Data were divided into two partitions, with first and third codon positions in one partition and second codon positions in another. Model testing and maximum likelihood analyses were performed using the IQTree web server (Trifinopoulos et al. 2016). One thousand bootstrap replicates were performed on the partitioned dataset using the models TIM2+F+I (first and third codon positions) and HKY+F+G4 (second codon positions). Calculations of genetic distance were performed under a K2P model using Mesquite v3.81 (Maddison and Maddison 2023).



**Figure 1.** Ecology and distribution of *Pseudoanthidium jacobii* in the Canary Islands **A, B** male nectaring on an inflorescence of *Asteriscus intermedius* (Asteraceae) (Photos NJ Vereecken) **C** female collecting pollen on an inflorescence of *A. intermedius* (Photo B Jacobi) **D** female nesting in a pre-existing cavity located in a volcanic lava rock (Photo B Jacobi) **E** distribution map showing all occurrence records available to us and relevant to both *P. canariense* and *P. jacobii* in the Canary Islands.

### Specimen depositories

- ULB** Agroecology Lab, Brussels School of Bioengineering, Université libre de Bruxelles, Belgium
- DZUL** Departamento Biología Animal, Edafología y Geología of the University of La Laguna, Tenerife, Spain
- FLR** Private collection of F. La Roche, San Cristóbal de La Laguna, Tenerife, Spain

## Morphological diagnosis

The morphological terminology used in the description follows Michener (2007), Litman et al. (2021), Niu et al. (2021) as well as Kasperek and Ebmer (2023). All absolute measurements are made in millimetres (mm) and are used for body length. For all other structures, relative measurements are used. Abbreviations used in the description and diagnosis section below are as follows:

- BL** (body length): measured as the shortest absolute distance from the base of the antennal socket to the apex of the metasoma (see Niu et al. 2021);
- ITD** (inter-tegular distance): measured as the shortest absolute distance between the tegulae (scale-like structure covering the insertion point of the wings on the thorax) in dorsal view;
- OOD** (ocellar-occiput distance): assessed in dorsal view, under a stereomicroscope with continuous LED light, as a ratio between the distance separating the lateral ocelli and the posterior occiput (dorsal margin of the vertex) on one hand, and the ocellar diameter on the other hand;
- MPD** (median punctuation density): assessed as the ratio between the distance separating neighbouring points in the median region of the tergites and the puncture diameter;
- LPD** (lateral punctuation density): measured as the ratio between the distance separating neighbouring points in the lateral region of the tergites, particularly on T2 (second tergite) and T3 (third tergite), and the puncture diameter;
- SSPD** (scutum and scutellum punctuation density): measured under a stereomicroscope with continuous LED light as the distance between neighbouring points on the scutum (dorsal side of the thorax/mesonotum) and on the scutellum (dorso-apical plate of the thorax/mesonotum) on one hand, and the puncture diameter;
- TEG** (tegulae): colour of the scale-like structures covering the insertion point of the wings on the thorax/mesonotum;
- ProN** (pronotum): colour of the dorsal lobe of the first thorax/mesonotum segment;
- ProLo** (pronotal lobe): colour of the protonal lobe (also known as “humeral tubercles”) located just next to the tegulae, towards the anterior site of the thorax/mesonotum;
- TCP** (tergite colour patches): colour, size and delineation between the orange colour patches on the tergites and the surrounding black cuticle;
- FACE** (face): colour of the clypeus, mandibles, lower part of paraocular region;
- LEGS** (legs): colour of the coxae, femurs, tibiae on each pair of legs.

Photographs of the type material were taken using a Leica S8APO equipped with a Leica MC190 HD digital camera and a Leica LED3000 DI light dome. Series of shots were taken by manually adjusting the precision dial to cover the sharpness of the target body parts. The specialized hooked and waved hairs on the metasomal sterna

(S3-S4-S5) in males were photographed using a Canon 5DS R equipped with a Canon MP-E 65mm lens at 5× and (set at f/3.2 and ISO 100), mounted on a StackShot macro rail (distance/step = 0.01mm) and lit with two custom diffused, IR-operated Godox 860vii cobra flashes. All resulting photos were stacked with Helicon Focus (version 8.2.6.) using the software's "Depth Map mode (Method B)". Resulting stacked shots were slightly edited in Adobe Lightroom and cleaned in Adobe Photoshop 2023.

### Mapping of occurrence records

Shapefiles and map data derived from OpenStreetMap (copyrighted OpenStreetMap contributors and available from <https://www.openstreetmap.org>) were downloaded from GeoFabrik (<https://download.geofabrik.de>). Species distribution points were plotted using QGIS 3.22 -Białowieża (QGIS Development Team 2023). We have included a series of 35 "research-grade" occurrence records of *P. canariense* from GBIF.org (GBIF 2023b) and we have estimated the coordinates of another 15 conspecific specimens cited by Hohmann et al. (1993) based on the approximate center of the most specific locality given from the island of Gran Canaria. All new *Pseudoanthidium* records relevant to the islands of Lanzarote and Fuerteventura resulting from specimens collected in the field or macrophotographs exhibiting enough detail to allow for an identification at the species level were included on the map too.

Finally, we used the *elevatr* package (version 0.4.2.) (Hollister 2022) to compute the elevation associated with each occurrence record of both *Pseudoanthidium* species. Boxplots of all records were prepared with the "ggplot2" package (Wickham 2016). All records, including their latitude/longitude coordinates in decimal degrees (WGS84), their elevation, the date of each record and their source are compiled in Suppl. material 2. All analyses were performed with RStudio (RStudio Team 2020) for R (version 4.2.2; R Core Team 2022).

### Ecological niche characterisation

To evaluate the extent of shared environmental niche space among the two *Pseudoanthidium* species, we conducted an analysis of ecological niche characteristics. Significant niche differentiation is anticipated owing to the contrasting habitats between the eastern islands of Lanzarote and Fuerteventura and the western islands. The comparison is intended to illustrate the prevailing climatic conditions for the two species. For each occurrence record of the two species, we extracted environmental data from a 200m buffer. BIOCLIM data was obtained from CHELSA (Climatologies at High resolution for the Earth's Land Surface Areas) climate dataset at 30 arc seconds resolution (Karger et al. 2017). We selected 4 bioclim variables to cover precipitation and temperature range, and variation (mean annual temperature/precipitation, temperature/precipitation seasonality). Elevation data was obtained from the "elevatr" package as described above. The background niche space was calculated based on 2,000 randomly generated points within the Canary Islands. These data were then used to classify the ecological niche space

occupied by the two *Pseudoanthidium* species. Following Broennimann et al. (2012), we used a principal component analysis (PCA) that was calibrated based on the complete environmental space encompassing the Canary Islands, that applies smoothers to the species presences in environmental space for the purpose of selecting and weighting the environmental variables. We then computed niche overlap between the two species with Schoener's  $D$  statistic (Schoener 1968; Warren et al. 2008). Finally, we tested whether the niche overlap of the two species is less equivalent than random by means of a niche equivalence test with 1,000 repetitions (Broennimann et al. 2012). These analyses were conducted with RStudio (RStudio Team 2020) for R (version 4.2.2; R Core Team 2022) using the “ecospad” package (version 3.5.1; Broennimann et al. 2023).

### EOO,AOO and extinction risk assessment using IUCN criteria

We used the “red” package (version 1.5.0) (Cardoso 2017) and all occurrence records to compute the extent of occurrence (EOO) and area of occupancy (AOO) of *P. canariense* and the newly discovered *Pseudoanthidium* species described below. EOO encompasses the total geographic range of a species, while AOO focuses on the current occupied area of a species within its known habitat; both metrics are vital for assessing a species' conservation status and can influence its IUCN Red List categorization. We then used the *rCAT* package (version 0.1.6) (Moat 2020) to calculate the IUCN rating of each species based on their EOO in km<sup>2</sup>.

Assessing the extinction risk of a species, including of hitherto overlooked, or newly described taxa, requires using a series of criteria listed by the International Union for the Conservation of Nature (IUCN) Red List (IUCN Standards and Petitions Committee 2022). These criteria are based on indicators of extinction risk and ultimately help assign a ranked threat category, such as critically endangered (CR), endangered (EN) and vulnerable (VU) (Mace et al. 2008; Nieto et al. 2014). In a nutshell, the five key components of an IUCN extinction risk assessment are: population reduction (Criterion A), restricted geographic range (Criterion B), small population size and decline (Criterion C), very small or restricted population size (abundance) (Criterion D) and a quantitative analysis of decline (Criterion E). For each criterion, threshold values are defined and associated with different threat categories; we performed the assessment for the new *Pseudoanthidium* species following practical guidelines (Rodríguez et al. 2015) and using as much direct (and to some extent, indirect) evidence as possible (Le Breton et al. 2019).

## Results

Our study reveals the presence of a hitherto overlooked species within the subgenus *Pseudoanthidium* (*Pseudoanthidium*) in the Canary Islands. A closer examination of the only earlier and unpublished record of a *Pseudoanthidium* from Lanzarote, a female specimen collected by F. La Roche in Lanzarote 1997, curated in the private collection

of F. La Roche (San Cristóbal de La Laguna, Spain) and identified by the late Czech entomologist B. Tkalčú as *P. stigmaticorne*, revealed that this specimen also belongs to the species we describe here below.

***Pseudoanthidium (Pseudoanthidium) jacobii* Vereecken & Litman, sp. nov.**

<https://zoobank.org/BD67A8C7-F34B-45AB-9E85-45813F167E33>

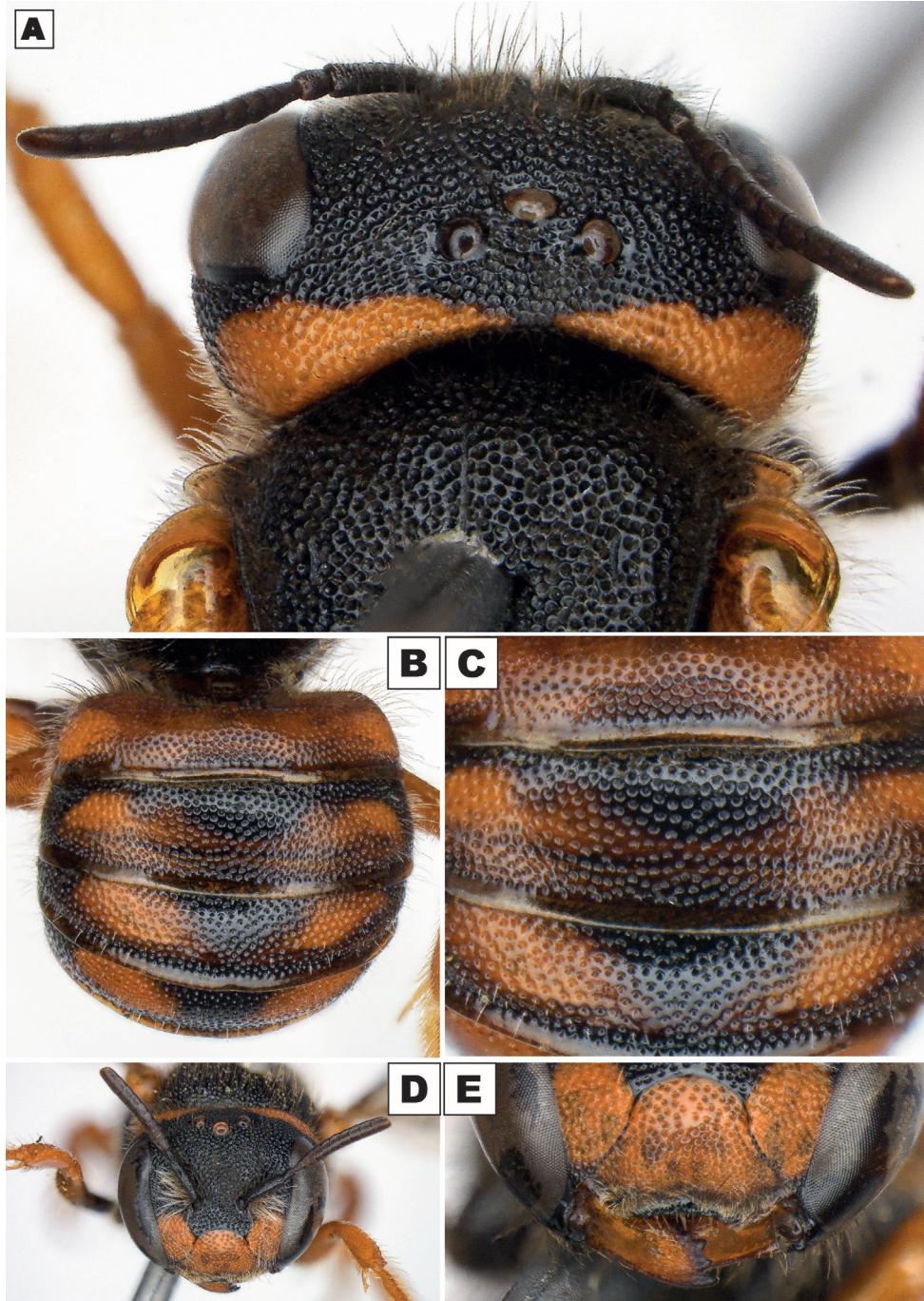
**Type material. Holotype.** SPAIN • 1♂; Lanzarote, Haría, 19 Apr. 2021; NJ Vereecken leg.; DZUL.

**Paratypes.** SPAIN • 1♀; Lanzarote, Haría, 18 Apr. 2021; J-M Molenberg leg.; ULB • SPAIN • 1♂; same collection data as for preceding, 19 Apr. 2021; J-M Molenberg leg.; ULB • 1♂; same collection data as for preceding, 18 Apr. 2021; J-M Molenberg leg.; DZUL.

**Other material.** SPAIN • 1♂; Lanzarote, Haría; 21 Feb. 2023; M Pérez-Gil leg.; DZUL • 1♀; Haría, 16 Apr. 2023; M Pérez-Gil leg.; DZUL • 1♀; Haría, 19 Apr. 2023; C Ruiz leg.; DZUL • 1♀; Lanzarote, Guatiza, 25 Mar. 1997, F La Roche leg.; FLR.

**Diagnosis.** Besides differences in their distribution pattern across the Canary Islands archipelago (Fig. 1), males and females of *P. canariense* and the newly described *P. jacobii* can be unambiguously identified based on a number of morphological criteria described below, including their relative size, as well as the density of the punctuation, the colour and the shininess of their cuticle as shown on Figs 2–4. Fig. 5 illustrates the structure of specialized hooked and waved hairs on the metasomal sterna (S3–S4–S5) in males, as well as their apicolateral combs on each lateral arm of S5.

**Female.** The female of *P. jacobii* may be distinguished from *P. canariense* by the following combination of characters: **BL** minimally only half size (4–7 mm in *P. jacobii*, 6–9 mm in *P. canariense*), **ITD** shorter (on average: 2.13 mm in *P. jacobii*, 2.91 mm in *P. canariense*), **OOD** shorter (~ 1 ocellar diameter in *P. jacobii*, ~ 1.5–2 ocellar diameters in *P. canariense*), **TPD** lower (spaces between points at least ~ 1–1.5 diameter of a single point in *P. jacobii*, < 0.5 diameter of a single point in *P. canariense*), **SSPD** slightly higher (~ 0.5 diameter of a single point in *P. jacobii*, < 0.5 diameter of a single point in *P. canariense*), **TEG** brighter (orange-yellow in *P. jacobii*, black in *P. canariense*), **ProN** brighter (orange-yellow in *P. jacobii*, black in *P. canariense*), **ProLo** mostly brighter (orange-yellow like the tegulae in *P. jacobii*, black in *P. canariense*, but more specimens of each species should be examined), **TCP** wider, brighter (wide and orange-yellow in *P. jacobii*, narrower and dark orange in *P. canariense*), and with a better defined maculation margin (gradual infiltration of the black colour into the orange yellow maculations of the integument in *P. jacobii*, well-defined colour boundary/contrast between darker orange maculations and black cuticle in *P. canariense*), **FACE** brighter (orange-yellow clypeus, mandibles, lower part of paraocellar region in *P. jacobii*, all black in *P. canariense*) and wider (face broader than long in *P. jacobii*, face longer than broad in *P. canariense*), **LEGS** brighter (all legs black only from the coxa to the very base of the femur black, the rest of the femur and other leg segments are orangish yellow in *P. jacobii*, all coxae, femurs but only posterior tibiae black in *P. canariense*).

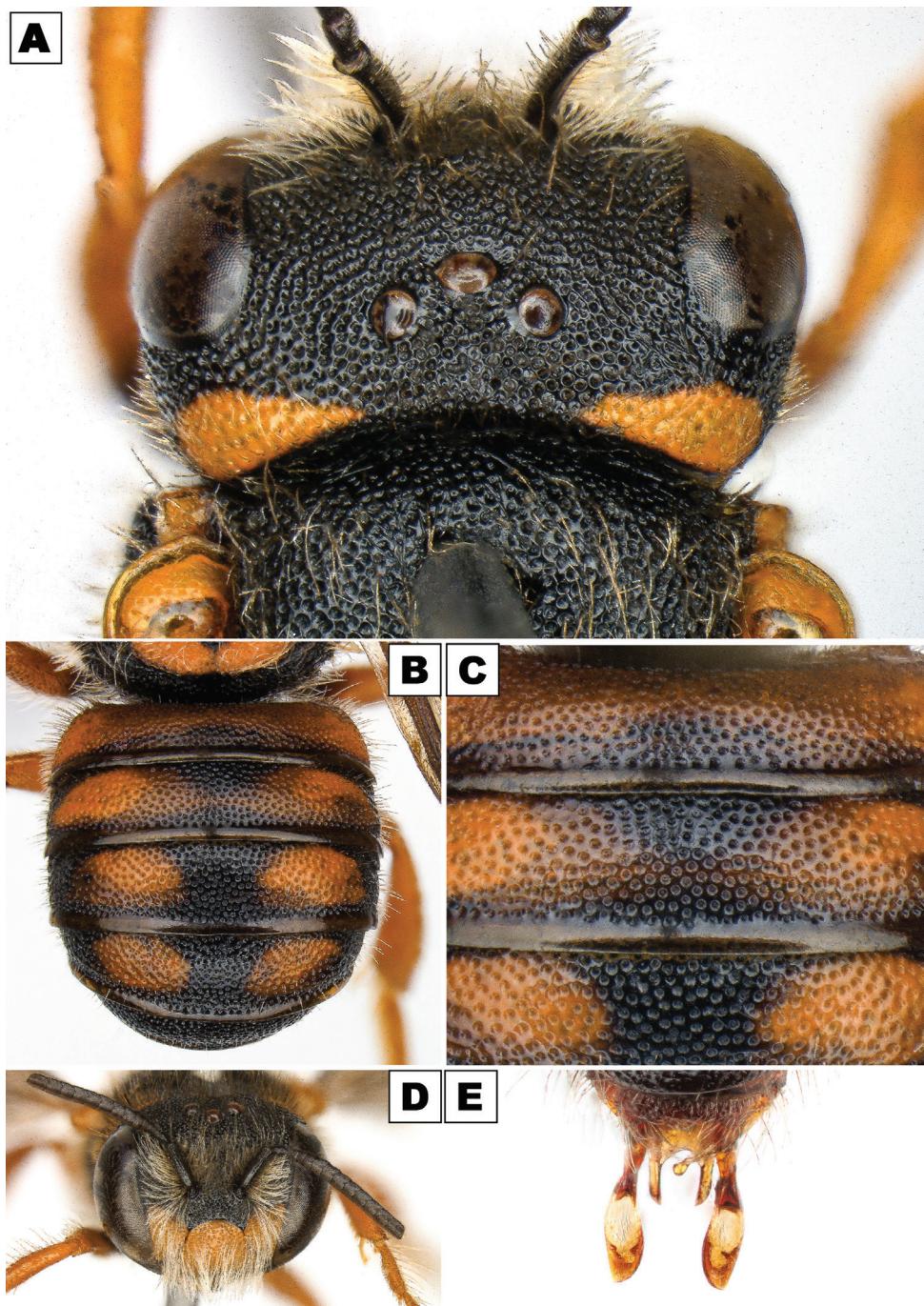


**Figure 2.** Illustration of some key morphological traits that characterise females of *Pseudoanthidium jacobii* **A** head capsule and first half of the mesonotum in dorsal view **B** abdomen in dorsal view **C** tergites 1-2 (from top to bottom) in dorsal view **D** face in frontal view **E** mandibles and clypeus in frontal view. Photos NJ Vereecken; see description of each sex and the diagnosis in the text for more details.

**Male.** The male of *P. jacobii* may be distinguished from *P. canariense* by the following combination of characters: **BL** minimally only half size (4–6 mm in *P. jacobii*, 6–8 mm in *P. canariense*), **ITD** shorter (on average: 2.22 mm in *P. jacobii*, 2.95 mm in *P. canariense*), **OOD** shorter (~ 1 ocellar diameter in *P. jacobii*, ~ 1.5–2 ocellar diameters in *P. canariense*), **TPD** lower (spaces between points at least ~ 1–1.5 diameter of a single point in *P. jacobii*, < 0.5 diameter of a single point in *P. canariense*), **SSPD** slightly higher (~ 0.5 diameter of a single point in *P. jacobii*, < 0.5 diameter of a single point in *P. canariense*), **TEG** brighter (orange-yellow in *P. jacobii*, black in *P. canariense*), **ProN** brighter (orange-yellow in *P. jacobii*, black in *P. canariense*), **ProLo** mostly brighter (orange-yellow like the tegulae in *P. jacobii*, black in *P. canariense*, but more specimens of each species should be examined), **TCP** wider, brighter (wide and orange-yellow in *P. jacobii*, narrower and dark orange in *P. canariense*), and with a better defined maculation margin (gradual infiltration of the black colour into the orange yellow maculations of the integument in *P. jacobii*, well-defined colour boundary/contrast between darker orange maculations and black cuticle in *P. canariense*), **FACE** brighter (orange-yellow clypeus, mandibles, lower part of paraocular region in *P. jacobii*, all black in *P. canariense*) and wider (face broader than long in *P. jacobii*, face longer than broad in *P. canariense*), **LEGS** brighter (all legs black only from the coxa to the very base of the femur black, the rest of the femur and other leg segments are orangish yellow in *P. jacobii*, all coxae, femurs but only posterior tibiae black in *P. canariense*). Brushes of thickened, wavy hairs on S3, as well as the lateral dark brown comb of S5, identical in both species.

**Description. Female.** **Head:** Mandible orange-yellow, except for teeth and apex of anterior margin, which are reddish-brown. Pilosity on clypeus and tufts at base of antenna white; on anterior margin of clypeus off-white, and on vertex blond. Clypeus dark yellow with black anterior margin. Punctures of clypeus dense and small anteriorly and laterally, with interspaces not larger than diameter of one-half puncture. Punctures become sparser and larger medially and posteriorly, where the maximum distance between punctures reaches two puncture diameters or more in the posterior-medial zone. Interspaces between punctures on clypeus shiny, most notably so where punctures are least dense. Paraocular area dark yellow and densely punctate, with interspaces not over the diameter of one-half puncture. Antenna with scape and pedicel black; flagellar segments dark brown. Flagellar segments shorter than wide, except for the first and the last, which are longer than wide. Frons with punctuation nearly honeycomb areolate, punctuation becoming slightly less dense toward the vertex, with shiny interspaces. Vertex with dark yellow triangle behind each eye, meeting or nearly meeting at midline of vertex. Vertex densely punctate, with interspaces not over 0.5 puncture diameter wide. Punctuation on vertex mostly homogenous, with punctures just posterior to median ocellus slightly larger. Gena densely, evenly punctate, with spaces between points less than 0.25 puncture diameter wide.

**Mesosoma:** Scutum black. Punctuation dense, with spaces between punctures shiny, not more than one-quarter puncture diameter wide. Tegula dark yellow anteriorly, translucent yellow posteriorly. Pronotal lobe dark yellow apically, black basally.

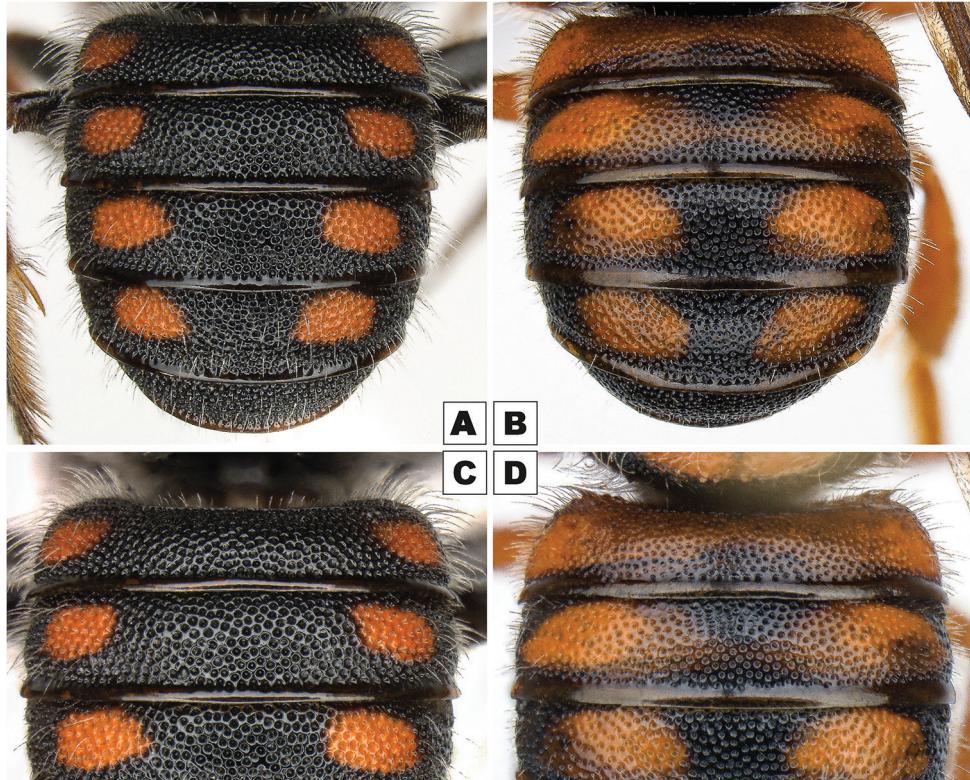


**Figure 3.** Illustration of some key morphological traits that characterise males of *Pseudoanthidium jacobii*. **A** head capsule and first half of the mesonotum in dorsal view **B** abdomen in dorsal view **C** tergites 1-2-3 (from top to bottom) in dorsal view **D** face in frontal view **E** gonostyli in dorsal view. Photos NJ Vereecken; see description of each sex and the diagnosis in the text for more details.

Scutellum black with dark yellow band medially on posterior margin. Punctures on black part of scutellum slightly larger and less dense than on scutum, with spaces between punctures on the median part of the scutellum shiny and up to one half a puncture diameter wide; punctuation on yellow part of scutellum even less dense, with spaces between punctures over one puncture diameter wide. Mesepisternum densely punctate, punctures becoming smaller and less dense around episternal groove; spaces between punctures shiny. Propodeum laterally and anteriorly finely, densely punctate; medially shiny and without punctuation. On all legs, coxa, trochanter and base of femur black; the rest of the femur, tibia and tarsal segments orange-yellow. Wings infuscate.

**Metasoma:** T1 anteriorly brownish-yellow, posteriorly reddish-brown. A dark yellow spot present laterally, slightly masked by the colour of the anterior margin of the tergite. Lateral spots vaguely joined medially on the tergite by a faint yellow band connecting the posterior margin of each spot. Punctuation relatively dense, even laterally, with spaces between punctures not greater than the diameter of half a puncture. T1 with unpunctured, shiny, translucent brown posterior margin measuring about two punctures wide. T2 anteriorly black with diffuse dark yellow lateral spots; posteriorly, T2 brownish-yellow. Lateral spots on T2 placed slightly medially to those on T1. Punctuation on T2 dense but less so than on T1, with spaces between punctures laterally up to nearly one puncture diameter. Diameter of punctures of T2 greater than those of T1. T2 with unpunctured, shiny, translucent brown posterior margin measuring about two punctures wide. T3 like T2 in colour, with punctuation slightly less dense. Punctuation of T4 similar to that of T3; T4 mostly black with yellow spots laterally and with shiny, translucent brown posterior margin; anterior edge of this margin with a single row of punctures medially. T5 black, densely punctate, with spaces between punctures shiny and measuring less than 0.25 puncture diameter. T6 black, densely punctate, spaces between punctures less shiny than those of T5 and measuring less than 0.25 puncture diameter, overall texture T6 somewhat rough.

**Male. Head:** Mandible orange-yellow, except for teeth and apex of anterior margin, which are reddish-brown. Pilosity on clypeus and tufts at base of antenna white; on anterior margin of clypeus off-white, and on vertex dark blond to brown. Clypeus rugose-punctate, orange-yellow with black anterior margin. Paraocular area orange-yellow and rugose-punctate, with interspaces not over the diameter of half a puncture. Antenna with scape and pedicel black; flagellar segments dark brown. Flagellar segments shorter than wide, except for the first and the last, which are longer than wide. Frons with punctuation nearly honeycomb areolate, punctuation becoming slightly less dense toward the vertex, with shiny interspaces. Vertex with orange-yellow triangle behind each eye, widely interrupted towards the midline of the vertex by a black punctured space. Vertex densely punctate, with interspaces not over 0.5 puncture diameter wide. Punctuation on vertex mostly homogenous, with interspaces between punctures increasing towards the eye margin and the latero-posterior part of the vertex. Gena densely, evenly punctate, with spaces between points less than 0.25 puncture diameter wide.



**Figure 4.** Illustration of some structural diagnostic morphological traits that help discriminate between *Pseudoanthidium canariense* (Mavromoustakis) (**A, C**) and *P. jacobii* (**B, D**). Photos NJ Vereecken; see description of each sex and the diagnosis in the text for more details.

**Mesosoma:** Scutum black. Punctuation dense, with spaces between punctures shiny, not more than one-quarter puncture diameter wide. Tegula orange-yellow anteriorly, translucent orange brown posteriorly. Pronotal lobe orange-yellow apically, black basally. Scutellum black with orange-yellow band medially on posterior margin. Punctures on black part of scutellum slightly larger and less dense than on scutum, with spaces between punctures on the median part of the scutellum shiny and up to one half a puncture diameter wide; punctuation on yellow part of scutellum even less dense, with spaces between punctures over one puncture diameter wide. Mesepisternum densely punctate, punctures becoming smaller and less dense around episternal groove; spaces between punctures shiny. Propodeum laterally and anteriorly finely, densely punctate; medially shiny and without punctuation. On all legs, coxa, trochanter and base of femur black; the rest of the femur, tibia and tarsal segments orange-yellow. Wings infuscate.

**Metasoma:** T1 brownish-orange on its anterior half, with an orange-yellow spot present laterally, slightly masked by the colour of the anterior margin of T1. Lateral spots joined medially on the tergite by a brownish-orange band connecting each spot.



**Figure 5.** Both *Pseudoanthidium jacobii* and *P. canariense* share the same overall structure of specialized hooked and waved hairs on their metasomal sterna (S3-S4-S5) in males, as well as their dark brown to black apicolateral combs on each lateral arm of S5. The present photo illustrates the structure in a male *P. jacobii* where S3 also exhibits a short, dense, velvety pubescence anteriorly, posteriorly with pre-marginal brush of hairs, hooked at the tips, as well as an underlying comb of thickened, wavy hairs (Photo NJ Vereecken).

Punctuation relatively dense, even laterally, with spaces between punctures not greater than the diameter of half a puncture. T1 with unpunctured, shiny, translucent brown posterior margin measuring about two punctures wide. T2 anteriorly black with diffuse orange-yellow lateral spots; posteriorly, T2 brownish. Lateral spots on T2 placed slightly medially to those on T1. Punctuation on T2 dense but less so than on T1, with spaces between punctures laterally up to nearly one puncture diameter. Diameter of punctures of T2 greater than those of T1. T2 with unpunctured, shiny, translucent brown posterior margin measuring about two punctures wide. Lateral spots on T3 placed slightly medially to those on T2. T3 similar to T2 in colour, with punctuation slightly less dense. Punctuation of T4 similar to that of T3; T4 mostly black with less diffuse orange-yellow spots laterally and with shiny, translucent brown posterior margin; anterior edge of this margin with a single row of punctures medially. T5 black, densely punctate, with spaces between punctures shiny and measuring less than 0.25 puncture diameter. T6 black, densely punctate, spaces between punctures less shiny than those of T5 and measuring less than 0.25 puncture diameter, overall texture T6 somewhat rough. T7 black, densely punctate, with rounded notch on posterior margin. Genitalia with semi-translucent, apically rounded (i.e., unnotched) and flattened

gonostyli; penis valves flattened and rounded. S3 with short, dense, velvety pubescence anteriorly, posteriorly with premarginal brush of hairs, hooked at the tips, as well as an underlying comb of thickened, wavy hairs. S5 laterally with dark brown comb.

**Etymology.** *Pseudoanthidium* (*Pseudoanthidium*) *jacobii* is dedicated to Mr. Bernhard Jacobi (Oberhausen, Germany), naturalist extraordinaire and talented macro-photographer who has a genuine and boundless passion for wild bees, particularly for species found in Europe and Australia. Bernhard's interest for the Canary Islands has grown steadily and uninterrupted ever since the publication of Hohmann et al.'s (1993) landmark volume on the bees, wasps and ants of the archipelago. He has since then investigated the entomofauna of all of the Canary Islands *in situ*, reporting and illustrating the occurrence and distribution of the European Beewolf, *Philanthus triangulum* (Fabricius, 1775) on the archipelago (Jacobi et al. 2013), as well as new records on the distribution and phenology of *Colletes perezi* Morice, 1904 on Fuerteventura (Jacobi and Suárez 2018) and the first record of the American species *Megachile* (*Chelostomoides*) *otomita* Cresson, 1878 established on Tenerife (Strudwick and Jacobi 2018). Bernhard and his wife have been regular visitors to Lanzarote for over three decades, particularly during the winter months, and he was the third person (after authors NJV on 18.iv.2021 and MPG 12.ii.2023) to photograph a live specimen of *P. jacobii* in Lanzarote on 12.iii.2023 (Fig. 1D). Bernhard has also recently contributed new occurrence records of the widespread small carder bee *P. nanum* near his home in the German state of North Rhine-Westphalia (Jacobi et al. 2021).

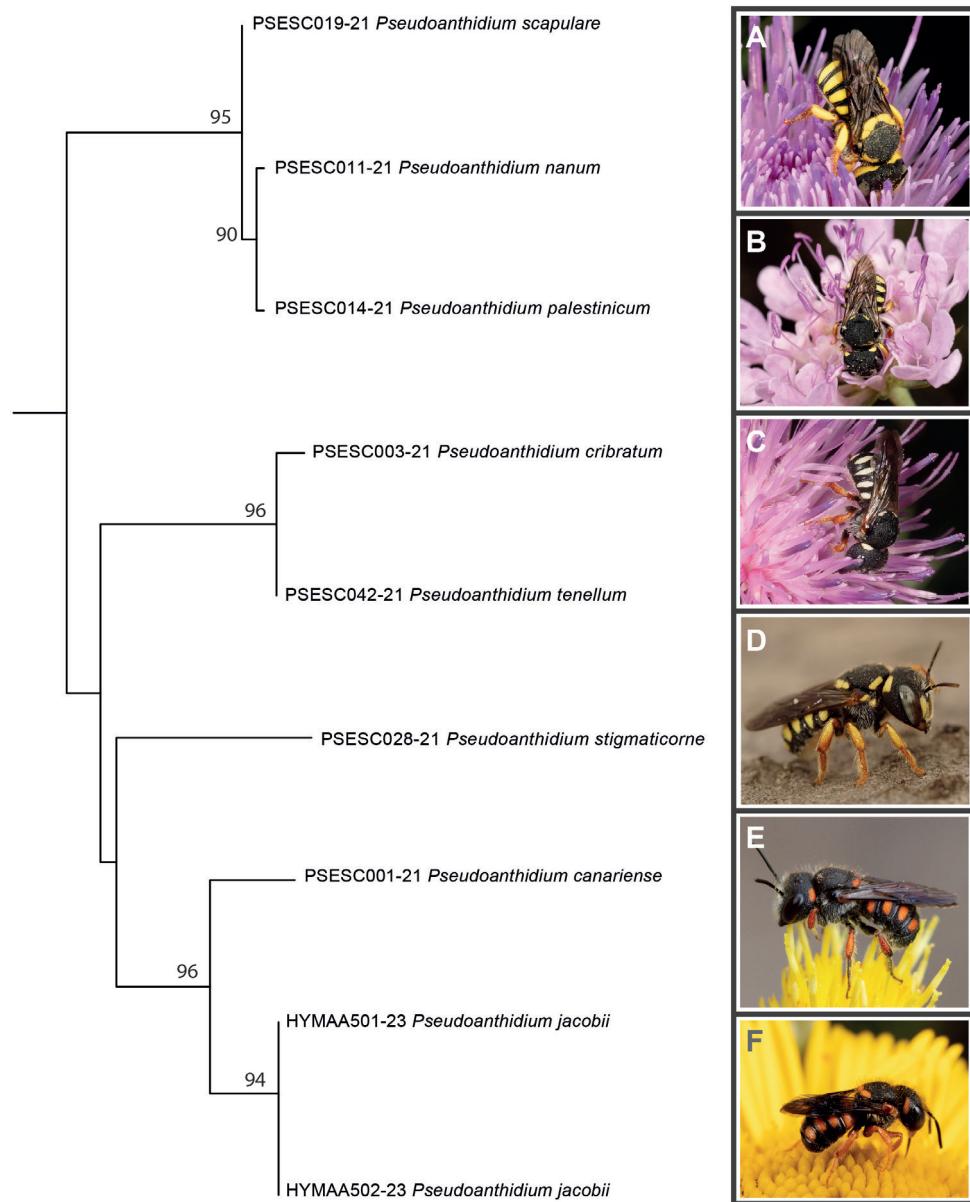
### Genetic differentiation between *P. jacobii* and other *Pseudoanthidium* species

The results of CO1 analyses demonstrate that *P. jacobii* is strongly supported as the sister species to *P. canariense* (ML bootstrap value = 96%) (Fig. 6). The two species are separated by a K2P-corrected genetic distance of 2.7%. Furthermore, *P. jacobii* exhibits an average K2P-corrected genetic distance of 5.9% from the clade consisting of *P. nanum* - *P. scapulare* - *P. palestinicum*; of 5.1% from *P. stigmaticorne*; and of 5.3% from the clade consisting of *P. tenellum* - *P. cibratrum*.

### Ecology, distribution and ecological niche differentiation

#### Habitat and host plant associations

In Lanzarote, the vegetation at the localities of Haría and Bco. de Elvira Sánchez where males and females of *P. jacobii* were recorded was composed of a chamaephytic substitutional flowering plant community established on old agricultural land with deep soils, generally on eroded slopes and on stony slopes, ravines, ledges physiognomically characterised by the presence of *Asteriscus intermedius* (DC.) Pit. & Proust (Asteraceae) and *Lavandula pinnata* L. (Lamiaceae) among others (see also Rámon Arévalo et al. 2016). By contrast, the localities of Teguise and Macher are peri-urban



**Figure 6.** Maximum likelihood-based tree based on analysis of a 658 base pair fragment of COI sequenced from selected *Pseudoanthidium* species in the *P. scapulare* complex. Maximum likelihood bootstrap support values, based on 1,000 replicates, are shown over nodes; only nodes with support values >90% are shown. Terminals are labelled with species names, as well as the BOLD sample IDs corresponding to each specimen. Outgroup removed from figure for convenience. Individuals shown in photographs were not those sequenced for analysis **A** *P. scapulare* (Photo NJ Vereecken) **B** *P. nanum* (Photo NJ Vereecken) **C** *P. tenellum* (Photo B Jacobi) **D** *P. stigmaticorne* (Photo H Wallays) **E** *P. canariense* (Photo G Peña); and **F** *P. jacobii* (Photo NJ Vereecken).

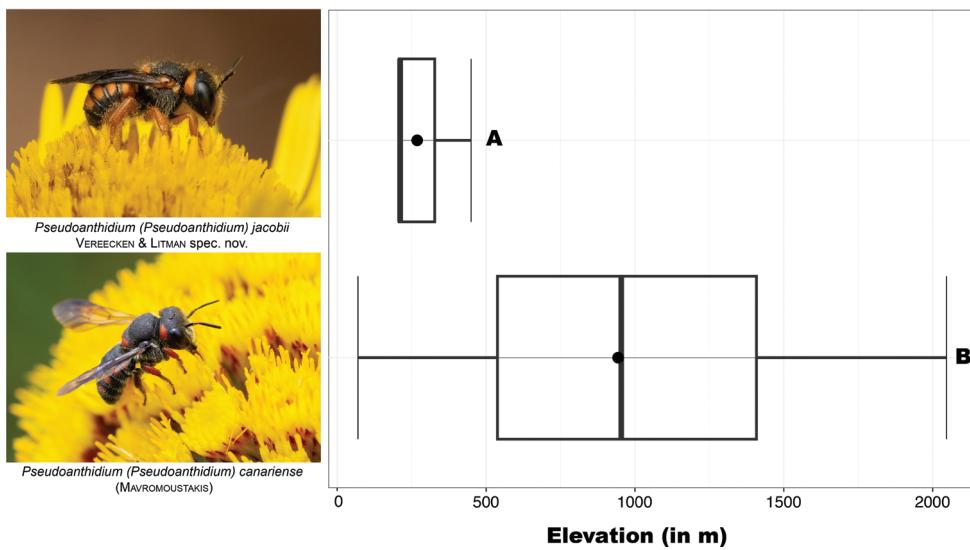
or rural anthropic areas with sparse natural vegetation, and the locality of Valle del Palomo is composed of xeric shrubland with a physiognomy of dendroid spurge shrubland, dominated by *Euphorbia regis-jubae* J. Gay (Euphorbiaceae). This is secondary vegetation typically found on abandoned arable or pastureland, roadsides and watercourse-beds (Reyes-Betancourt et al. 2001). In Fuerteventura, the locality of Betancuria where a female of *P. jacobii* was photographed is characterised by a flowering plant community consisting of dwarf chamaephytes exposed to strong winds and heavily grazed, where *Helianthemum canariense* (Jacq.) Pers. (Asteraceae) and *Spergularia fimbriata* Boiss. & Reut. (Caryophyllaceae) are dominant (del Arco Aguilar et al. 2018). Females of *P. (P.) jacobii* were observed collecting pollen on *A. intermedius* (DC.) Pit. & Proust (endemic to Fuerteventura and Lanzarote) (Fig. 1), *Pulicaria canariensis* subsp. *lanata* (Font Quer & Svent.) Bramwell & G. Kunkel (endemic to Lanzarote), and *Glebionis coronaria* (L.) Cass. ex Spach (syn. *Chrysanthemum coronarium* L., native and of Mediterranean origin) (Asteraceae). Males were also observed nectaring and patrolling for females on and around the same flowering plant species.

### Nesting behaviour

A single observation by co-author BJ in Lanzarote on 16.iii.2023 of a female nesting in a pre-existing cavity formed in a lava rock (Fig. 1D). All *Pseudoanthidium* species are reported to nest in pre-existing cavities or in pithy plant stems (see Litman et al. 2021 and references therein; Bogusch et al. 2022).

### Ecological niche differentiation

The environmental niche space occupied by *P. canariense* encompasses a large part of the total environmental niche space available in the Canary Islands, covering wide elevation (from 70 m to 2,046 m with a mean of 952 m), mean annual temperature (8.3 °C to 20.9 °C,  $\mu=15.2$  °C), and mean annual rainfall (135 kg m<sup>-2</sup> to 534 kg m<sup>-2</sup>,  $\mu=354.7$  mm) gradients with greater temperature (1.9 °C to 2.2 °C,  $\mu=2.1$  °C) and lower precipitation seasonality (73 kg m<sup>-2</sup>, 90 kg m<sup>-2</sup>,  $\mu=81.2$  kg m<sup>-2</sup>) gradients and occupying a variety of land cover types (Fig. 7). The environmental niche space of *PB* is almost entirely separate from the niche space occupied by *P. canariense* and is driven by low elevation (204 m to 460 m,  $\mu=268$  m) (Fig. 7), warmer (17.6 °C to 19.5 °C,  $\mu=18.7$  °C), and drier (101 kg m<sup>-2</sup> to 170 kg m<sup>-2</sup>,  $\mu=138.9$  kg m<sup>-2</sup>) areas with less variation in temperature (1.9 °C to 2.0 °C,  $\mu=2.0$  °C) and more varied rainfall (92 kg m<sup>-2</sup>, 100 kg m<sup>-2</sup>,  $\mu=96.9$  kg m<sup>-2</sup>) (Fig. 7). This comparison, as hypothesised, strongly represents the climatic and elevational differences between the islands where the species occur. The overlap between the two species represents the limits of the niche for *P. canariense*. As shown on Fig. 8, overall niche overlap between the two species is less than 1% and we can accept the alternative hypothesis that the two niches are less equivalent than random ( $p=<0.001$ ).

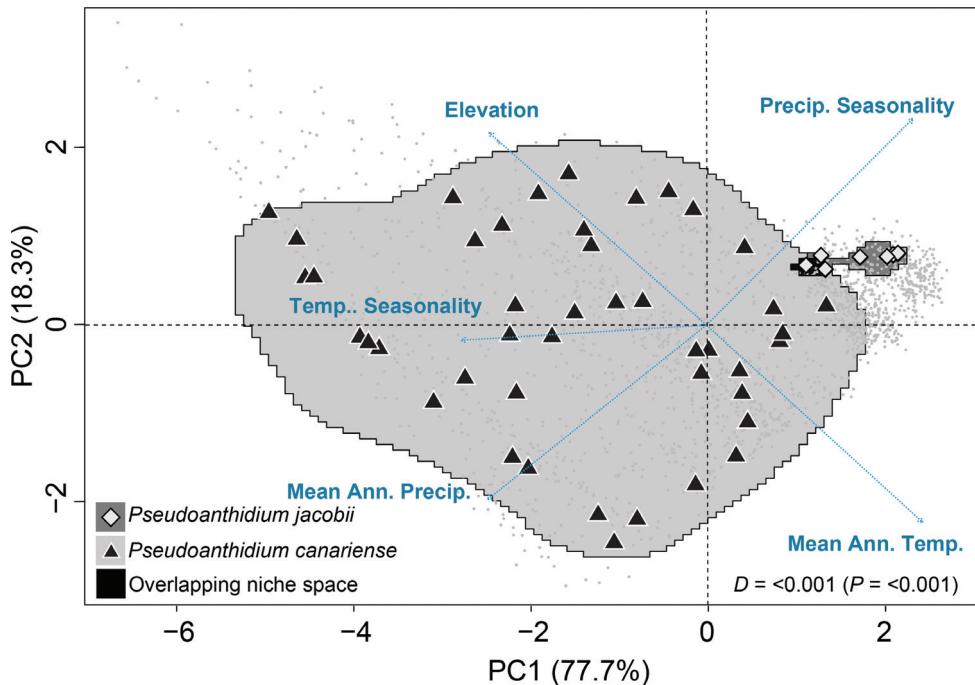


**Figure 7.** Distribution of elevation records relevant to **A** *Pseudoanthidium jacobii* and **B** *P. canariense* in the Canary Islands. Different letters right to the boxplots indicate highly significant differences in the elevation range and mean elevation of occurrence (black dot in boxplots) of both species (Kruskal-Wallis test:  $\chi^2 = 12.425$ , df = 1, *p*-value < 0.0005). Photo of *P. jacobii* M Pérez-Gil and of *P. canariense* G Peña.

## Distribution and threats

Due to a lack of historical baseline data, we could not evaluate *P. jacobii* using IUCN Criterion A (population reduction). However, with an EOO of 326 km<sup>2</sup> and an AOO of 28 km<sup>2</sup>, *P. jacobii* fulfils both Criteria B1 and B2 (restricted geographic range; EOO < 5,000 km<sup>2</sup> and AOO < 500 km<sup>2</sup>, respectively) (IUCN 2023).

Our current knowledge suggests that *P. jacobii* is known only from Mediterranean type shrubland vegetation localities on the islands of Lanzarote and Fuerteventura (Fig. 1). The key host plants exclusively visited by *P. jacobii* females for the collection of pollen include the herbaceous single-island endemic *Pulicaria canariensis* subsp. *lanata* (Font Quer & Svent.) Bramwell & G. Kunkel (endemic to Lanzarote), the archipelago endemic *Asteriscus intermedius* (DC.) Pit. & Proust (endemic to Fuerteventura and Lanzarote) and the native non-endemic *Glebionis coronaria* (L.) Cass. ex Spach, all belonging to the family Asteraceae. According to a recent study by Hanz et al. (2023), climate change will severely restrict the climatically suitable area of Canarian herbaceous plant species, particularly archipelago endemics and single-island endemic species, and particularly on the islands of Lanzarote and Fuerteventura, which are expected to experience less annual precipitation in the future. This phenomenon along with the negative impacts of invasive flowering plant species in the archipelago (del Arco Aguilar et al. 2018; but see Fernandez-Palacios et al. 2022), is very likely going to affect the availability of floral resources used by *P. jacobii* females, with cascading impacts on their population size and distribution.



**Figure 8.** Ecological niche overlap between *Pseudoanthidium jacobii* and *P. canariense* in the Canary Islands represented by a principal component analysis (PCA). Light grey diamonds represent occurrence records of *P. jacobii*, and the small underlying dark grey area represents its niche space. Black triangles represent occurrence records of *P. canariense* and the light grey underlying area represents its niche space. The small black area represents shared niche space between the two species. Small grey dots are background environmental samples from the Canary Islands. Schoener's  $D$  statistics and the  $p$ -value from the niche equivalence test are also shown. See methods and results sections for more details.

According to the IUCN, populations are considered “severely fragmented” if most individuals are found in small and relatively isolated subpopulations, where the probability of recolonization is reduced, should these subpopulations go extinct (IUCN 2023). Under this strict definition, populations of *P. jacobii*, restricted to extremely isolated pockets on Lanzarote and Fuerteventura, may be considered severely fragmented, thus fulfilling both criteria B1a and B2a. Furthermore, the continuous development of touristic infrastructures on both islands, the increase of pollution brought about by new roads facilitating transport and tourism across the islands (Martín-Cejas and Ramírez Sánchez 2010), the increase in car ownership and usage (Martín-Cejas 2015), and other pervasive forms of anthropogenic disturbance such as irresponsible off-roading practices (with associated pollution, damages on plant and animal life, and increased soil erosion rates), sand extraction, wind farms, and increased goat grazing (Nogales et al. 2006; Banos-González et al. 2016; Cubas et al. 2019) are all likely to have a severely negative impact on the extent and/or the quality of Mediterranean-type

shrubland vegetation favoured by *P. jacobii* and its key host plants. This, in turn, might lead to a continuous reduction of EOO, AOO, the number of subpopulations and the number of mature individuals stemming from a reduction in foraging resources. Following this scenario, *P. jacobii* also fulfils criteria B1ab(i,ii,iii,iv,v) and B2ab(i,ii,iii,iv,v).

Our field experience further suggests that *P. jacobii* is characterised by very small population sizes: this can be argued based on the fact (i) that we failed to collect more than two specimens at each sampled locality when the number of specimens should have been at its peak, (ii) that *P. jacobii* has been completely overlooked up to the present day, and (iii) that females and males are relatively conspicuous in colour, sharing their pollen host plant species with other Canarian bee species active at the same time of the year, namely in early Spring. Hence, *P. jacobii* also fulfils Criterion C2a(i) based on a conservative estimation of the total number of mature individuals < 2,500 across its distribution, as well as an estimated, projected, or inferred decline for reasons detailed above and < 250 mature specimens per subpopulation (IUCN 2023).

Because of a lack of population size estimation or comprehensive evaluation of the number of extant populations and their trends, we were unable to classify *P. jacobii* under Criteria D and E (IUCN 2023).

Last, we obtained convergent results through the parallel calculation of the IUCN rating based on EOO Area (in km<sup>2</sup>) with the “EOORating” function in the *rCAT* package, which suggests that *P. jacobii* should be classified as “EN” (endangered).

Given the above results, *P. jacobii* thus qualifies for “EN” (endangered) conservation status under IUCN Criteria B1ab(i,ii,iii,iv,v), B2ab(i,ii,iii,iv,v) and Criterion C2a(i); this status is also supported by the results of the “EOORating” analysis mentioned above. We thus propose an IUCN conservation status of “EN” (endangered) for this species.

## Discussion

### A new species of *Pseudoanthidium* from the Canary Islands

Twenty-two years after the last description of two new Megachilidae bee species in the CI archipelago, *Osmia palmae* Tkalçü (Tkalçü 2001a) and the cuckoo *Dioxys lanzarotensis* Tkalçü (Tkalçü 2001b), we provide evidence for the presence of a hitherto overlooked species of *Pseudoanthidium* on the islands of Fuerteventura and Lanzarote, the archipelago’s “Eastern Islands”. We describe this new species as *Pseudoanthidium (Pseudoanthidium) jacobii* Vereecken & Litman spec. nov., and we illustrate its close evolutionary relatedness to the Canarian endemic *P. canariense*. We have highlighted key diagnostic morphological traits to discriminate between the two Canarian *Pseudoanthidium* for each sex (Figs 1–5) and a degree of genetic divergence of 2.7%, lower than, yet still in keeping with, the genetic distances observed between other major clades in the *P. scapulare* complex (Litman et al. 2021). Last, our results illustrate that these two small carder bee species are allopatric in their contemporary distribution (Fig. 1),

they exhibit a significant differentiation in elevation range (Fig. 6), as well as a very low overlap (1%) in their respective ecological niches (Figs 7, 8), due in large part to the different climate of the islands on which they occur. Collectively, and in light of the criteria generally used to delineate species in this genus (Litman et al. 2021; Niu et al. 2021), our observations therefore suggest that *P. jacobii* deserves its own species status.

Most females in the subgenus *Pseudoanthidium* (*Pseudoanthidium*), and particularly in the *P. scapulare* species complex, appear to have a strong preference for host plants in the family Asteraceae (Litman et al. 2021; Niu et al. 2021; Kasparek and Ebmer 2023). A strong preference of *P. jacobii* for host plants in the family Asteraceae might therefore reflect a phylogenetic conservatism of pollen diet, a phenomenon already described in several other groups of wild bees in Europe (Müller and Kuhlmann 2008; Sedivy et al. 2008; Dötterl and Vereecken 2010; Wood et al. 2021; Dorchin et al. 2022).

### Canarian *Pseudoanthidium* species and other members of the *P. scapulare* complex

The *Pseudoanthidium scapulare* complex of species is distributed throughout the Palaearctic region. Certain members of the complex represent closely related species pairs that are sympatric throughout a part of their distributions, including *P. nanum* - *P. scapulare* and *P. tenellum* - *P. cibratum*. Both of these pairs are morphologically distinct but exhibit relatively low levels of genetic differentiation in analyses of CO1 (0.35% and 0.59%, respectively) (Litman et al. 2021). In recent analyses, however, neither *P. nanum* - *P. scapulare* nor *P. tenellum* - *P. cibratum* showed evidence of barcode-sharing and in both cases, historical mitochondrial introgression was deemed the most likely explanation for the low levels of genetic differentiation observed in these species pairs (Litman et al. 2021). This argument was further supported by a UCE analysis of *P. nanum* and *P. scapulare* that provided strong evidence of two genetically distinct lineages (Litman et al. 2021). In comparison, *P. canariense* and *P. jacobii* show consistent morphological differences but a K2P-corrected genetic distance of 2.7% at the CO1 locus, somewhat higher than the distances separating *P. nanum* - *P. scapulare* and *P. tenellum* - *P. cibratum*. *Pseudoanthidium canariense* and *P. jacobii* may thus represent species whose genetic divergence was facilitated by the reproductive barrier imposed by their distributions on different islands. Further analyses of genomic-level data are needed to better understand the evolutionary history of these taxa.

Our morphological analysis and that of Litman et al. (2021) illustrate that both *P. canariense* and *P. jacobii* have gonostyli that are approximately parallel-sided and exhibit a rounded (i.e., unnotched) apex. This is in marked contrast to other species in the *P. scapulare* complex (except *P. tropicum* (Warncke, 1982) known only from Iran so far, see Litman et al. (2021)), which have an obvious U-shaped notch at the apex of their gonostyli. Interestingly, the absence of a notch is also a feature shared with non-*scapulare* complex *Pseudoanthidium* species (see Niu et al. 2021; Kasparek and Ebmer 2023), which calls into question the ancestral or derived nature of the gonostylus notch in small carder bees.

Given the lack of resolution in our analyses of CO1, namely regarding the phylogenetic relationships among different clades within the complex, we can only propose hypotheses to explain the presence of a rounded gonostylus in *P. jacobii* and *P. canariense*. If the clade represented by these two species is the sister group to all other members of the *P. scapulare* complex, then one possible explanation is that the common ancestor of *P. jacobii* and *P. canariense* colonised the Canary Islands prior to the origin of other members of the *P. scapulare* complex (Litman et al. 2021), i.e., the presence of the rounded gonostylus may represent the plesiomorphic state for the complex. If this clade, however, turns out to be nested within the complex, another possible explanation is that the gonostylus in the common ancestor of *P. jacobii* and *P. canariense* may have undergone a reversion to an ancestral state. If speciation may be driven, at least partially, by morphological barriers to reproduction (Oneal and Knowles 2013; Huang et al. 2020), perhaps the marked differences in the shape of the gonostylus in other, closely related members of the *P. scapulare* complex (i.e., *P. nanum* and *P. scapulare*) may have been significant drivers of speciation, especially in sympatric populations. On the Canary Islands, where the diversity of closely related species is considerably lower than on the mainland, selective pressure on the shape of the gonostylus may be less intense, thus facilitating a reversion to an ancestral state. A future phylogenomic approach to an analysis of this genus using more samples of each species from across their distribution should shed light on the evolution of this and other traits in the genus *Pseudoanthidium* and contribute to improving our knowledge on the diversification and historical biogeography of small carder bees.

## Diversity and endemism in Lanzarote and Fuerteventura

Ever since Antiquity, historians, traders and (bio)geographers have acknowledged the peculiar nature of Lanzarote and Fuerteventura, these “Eastern Islands” of the Canary archipelago. Although they form two islands today, they are, geologically speaking, the oldest emerging part of the archipelago that used to be merged during the Pleistocene glacial cycles, forming the paleo-island of Mahan (Rijssdijk et al. 2014). These two islands were also historically referred to as the “Islas Purpurarias” (Garcia-Talavera 2016). The origin of this name supposedly traces back to the peak trade period of *Roccella canariensis* Darb. (Roccellaceae), a lichen species endemic to the Canary Islands and locally known as *orchilla*. This lichen grew on the cliffs of Lanzarote and Fuerteventura at the seashore and was unique as a natural source of the red-purple pigment orcein, a highly sought-after resource in the textile industry up until the end of the 19<sup>th</sup> century.

By describing *P. jacobii* as an endemic species from the Purpurarias, we provide further evidence for the peculiar environmental conditions met on the islands of Lanzarote and Fuerteventura within the Canary Islands archipelago, and how original life forms have evolved solely on these two islands. Single-island endemics are reported in the eastern CI, such as *Tetralonia lanzarotensis* Tkalçù, 1993 (Apidae) and *Dioxys (Dioxys) lanzarotensis* Tkalçù, 2001 (Megachilidae) from Lanzarote, or *Megachile (Eutricharaea) hohmanni* Tkalçù, 1993 (Megachilidae) and *Dufourea fortunata* Ebmer, 1993 (Halictidae), both recorded exclusively from Fuerteventura within the CI archipelago (Hohmann et al. 1993).

Examples of other wild bee species sharing a distribution restricted to these two islands include *Anthophora purpuraria* Westrich, 1993 (Apidae) (whose specific epithet derives directly from the “Purpurarias”), as well as other Anthophorini species like *A. (Heliophila) lanzarotensis* (Tkalçú, 1993), *A. (Heliophila) liefitincki* (Tkalçú, 1993), *A. (Pyganthophora) porphyrea* Westrich, 1993 (all endemic to Lanzarote and Fuerteventura) and some of their associated cuckoos such as *Melecta (Melecta) caroli* Liefitinck, 1958, and *M. (Melecta) prophanta* Liefitinck, 1980 (on Lanzarote only) (Hohmann et al. 1993). Other cuckoos of these narrow endemic and other more ubiquitous Anthophorini species might include *Thyreus histrionicus* (Illiger, 1806) and *T. ramosus* (Lepeletier, 1841) that have a Circum-Mediterranean distribution (Michez et al. 2019; Leclercq et al. 2022). Likewise, the family Megachilidae has a few endemic representatives, such as *Hoplitis (Tkalcua) zandeni* (Teunissen & van Achterberg, 1992) that nests in empty snail shells (Müller and Mauss 2016), *Megachile (Chalicodoma) fuerteventurae* (Tkalçú, 1993) and *M. (Eutricharaea) binominata* Smith, 1853 (Hohmann et al. 1993). The Andrenidae fauna of the Canary Islands also includes narrow endemics to Lanzarote and Fuerteventura, such as *Andrena (Chlorandrena) damara* Warncke, 1968 or *A. (Aciandrena) hillana* Warncke, 1968 (Hohmann et al. 1993).

It is important to note that some species originally described from a single island (such as *A. (H.) lanzarotensis* or *M. (C.) fuerteventurae*, as their specific epithet suggests) turned out to be discovered on both islands after a few decades of field surveys. These recent records contribute to the emergence of distribution patterns among closely related, endemic species in different groups of wild bees, with some restricted to the eastern islands and others present only in the central (and western) islands. For example, the three *Megachile (Chalicodoma)* species recorded in the archipelago exhibit such a distribution pattern similar to the *Pseudoanthidium* species discussed here, with *M. (C.) canescens* (Brullé, 1840) restricted to the central and western islands, whereas *M. (C.) sicula* (Rossi, 1794) and *M. (C.) fuerteventurae* are found only on the eastern islands (Lanzarote and Fuerteventura) (Hohmann et al. 1993). Likewise, *Megachile (Eutricharaea) canariensis* Pérez, 1902 is restricted to the central and western islands, whereas *M. (E.) binominata* is endemic to Lanzarote and Fuerteventura.

Interestingly, no species in the families Colletidae or Melittidae is endemic to Lanzarote and Fuerteventura: these families encompass CI endemic species distributed across the eastern, central and western islands, but none are restricted to eastern islands. Those that are found on these islands have a much wider distribution encompassing Morocco and sometimes extending to the Levant and even the Arabian Peninsula (e.g., for *Melitta schmiedeknechti* Friese, 1898 (Melittidae); see Shebl et al. (2016)).

At their nearest point, Lanzarote and Fuerteventura are located just under 100 km (60 miles) off the coasts of Morocco (García Talavera 1999; Florencio et al. 2021). This relative proximity is therefore likely to have favoured faunal exchanges across families of bees between the Canary Islands archipelago and the African continent. For example, *Andrena (Distandrena) mariana* s.str. Warncke, 1968 (Andrenidae) was described from the island of Fuerteventura in the Canary Islands, and its description was associated with a remark that the species could potentially be found in Morocco as well (Warncke 1968). A similar distribution bridging the Canary Islands archipelago and

the south-western coasts of Morocco has already been found in *Lasioglossum (Evylaeus) phoenicurum* (Warncke, 1975) (Pauly 2016), in *Nomiooides (Nomiooides) fortunatus* Blüthgen, 1937 (Pauly 2017) (both Halictidae), as well as in *Haetosmia circumventa* (Peters, 1974) (Müller 2022), and these findings could probably be echoed in different genera of the diverse family Apidae among others (A. Dorchin, pers. comm. July 2023; P. Rasmont, pers. comm. July 2023). More surveys along the coasts of south-western Morocco are needed to determine if other species considered as endemic to the Canary Islands, including *P. jacobii*, show similar patterns “bridging” the distribution gap with the African continent.

### Threats to a new bee species and the Canary Islands bee fauna

Are newly discovered species at a higher risk of extinction than those first described long ago? According to Liu et al. (2022), the trend is positive and significant across major vertebrate groups (amphibians, birds, fish, mammals, and reptiles), and it is driven by several factors, including their often-smaller population numbers and restricted distribution range making them vulnerable to habitat loss and fragmentation. Whether this applies to less intensively investigated groups of organisms like insects, and wild bees in particular, has not been adequately tested so far. Yet, these results suggest that extinction risk assessments that are based on overall threat status of all species combined may seriously underestimate the true number of species threatened with extinction (McKinney 1999).

Here, we classified the new species *P. jacobii* as Endangered (EN) according to IUCN Criteria B1ab(i,ii,iii,iv,v), B2ab(i,ii,iii,iv,v) and Criterion C2a(i), as well as based on the parallel calculation of the IUCN rating based on EOO Area (in km<sup>2</sup>). In other words, and practically speaking, this means that *P. jacobii* is threatened with extinction and might experience continuous decline unless conservation efforts are made. The results of our extinction risk assessment are also motivated by the fact that *P. jacobii*, similarly to other threatened wild bee species, typically occurs within a few small patches rather than a spatially continuous area of uniform presence. This patchy distribution implies that *P. jacobii* is exposed to comparatively higher extinction risks, because there is a greater chance that one or several of the identified threats will act in concert and will affect all or most of the distribution within a certain time frame. How imminent the identified risks are has remained elusive for a long time, but in recent years the Canary Islands and the “Purpurarias” in particular have seen droughts and heatwaves, just like large parts of the drought-stricken mainland. These changing weather patterns are the direct outcome of climate change operating in real time, and in the worst-case scenario they have even combined with environmental hazards like the 2021 Cumbre Vieja volcano eruption on the island of La Palma, followed in 2023 by massive wildfires breaking out and threatening all terrestrial forms of life on several of the Western Canary Islands. Such wildfires are less likely on Fuerteventura and Lanzarote due to their scarce vegetation and lack of forested areas (Carillo et al. 2022).

The Canary Islands archipelago, like many other insular ecosystems renowned for their breath-taking natural beauty, faces major challenges in achieving a delicate

balance between promoting recreational activities and preserving its fragile biodiversity as the effects of climate change become increasingly pronounced. Our study illustrates that our understanding of biodiversity in the archipelago is far from complete, and that international scientific collaborations with local experts and citizen science projects can help gain significant insights into species distribution and ecological interactions. This paper also confirms the vivid interest of the international scientific community towards the Canary Islands bee fauna and its conservation (see also Monasterio León et al. 2023), and highlights that more targeted field surveys and increased sampling efforts, primarily in the eastern and less sampled western islands, but also slightly before or after the typical “bee season” of January-April, and in high altitude ecosystems found on Gran Canaria and Tenerife still have the potential to reveal other unique taxa and contribute to refine our understanding of the spatial taxonomic, functional and phylogenetic patterns of diversity and endemism of the CI wild bees.

## Author contribution statement

**NJV:** Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Software; Validation; Visualization; Writing - original draft; Writing - review & editing. **CR:** Data curation; Project administration; Resources; Supervision; Validation; Writing - review & editing. **CJP:** Formal analysis; Funding acquisition; Investigation; Resources; Software; Visualization; Writing - review & editing. **MPG:** Data curation; Investigation; Visualization; Writing - review & editing. **BJ:** Data curation; Investigation; Writing - review & editing. **JMM:** Data curation; Investigation; Project administration; Resources. **LM:** Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Resources; Software; Visualization; Writing - review & editing. **FLR:** Data curation; Writing - review & editing. **JRL:** Conceptualization; Data curation; Investigation; Methodology; Resources; Supervision; Validation; Writing - review & editing.

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## Supplementary material 1

### Information on *Pseudoanthidium* specimens used for the barcoding

Author: Jessica R. Litman

Data type: csv

Explanation note: List of specimens and associated metadata used for the Maximum likelihood-based tree based on analysis of a 658 base pair fragment of COI sequenced from selected *Pseudoanthidium* species in the *P. scapulare* complex.

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Link: <https://doi.org/10.3897/jhr.96.111550.suppl1>

## Supplementary material 2

### Distribution data of each *Pseudoanthidium* species in the Canary Islands

Author: Nicolas J. Vereecken

Data type: csv

Explanation note: Distribution data including all occurrence records available to us and relevant to both *P. (P.) canariense* and *P. (P.) jacobii* Vereecken & Litman spec. nov. in the Canary Islands.

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