A new bee species of the genus *Dasypoda* from North Africa uncovered by morphology and ultraconserved element phylogenomics (Hymenoptera: Melittidae)

Guillaume Ghisbain[A,*] , Denis Michez[A] , Michael G. Branstetter[B] , Vladimir G. Radchenko[C] , Piluca Álvarez Fidalgo[D] and Thomas J. Wood[A,E]

For full list of author affiliations and declarations see end of paper

* **Correspondence to:**]***Correspondence to:**

Guillaume Ghisbain Laboratory of Zoology, Research Institute for Biosciences, University of Mons, Place du Parc 20, BE-7000 Mons, Belgium Email: guillaume.ghisbain@umons.ac.be

Handling Editor: Andy Austin

Received: 11 September 2024 **Accepted:** 8 January 2026 **Published:** 13 February 2026

Cite this: Ghisbain G *et al.* (2026) A new bee species of the genus *Dasypoda* from North Africa uncovered by morphology and ultraconserved element phylogenomics (Hymenoptera: Melittidae). *Invertebrate Systematics* **40**, IS24073. doi:10.1071/IS24073

ABSTRACT Among the six bee families recorded from the African continent, Melittidae is a species-poor group that includes the pantaloon bees of the genus *Dasypoda* Latreille. Using an integrative approach combining morphological examination and phylogenomic analysis based on ultraconserved elements (UCEs), we describe and diagnose a new species, *D.* (*Heterodasypoda*) *rosaella* Ghisbain & Wood, **sp. nov.**, from Morocco and Tunisia. This species has been historically misidentified as the European species *D.* (*Heterodasypoda*) *albimana* Pérez, 1905. We designate a sequenced neotype for the closely related *D. albimana* from southern France, facilitating comparisons with *D.* (*Heterodasypoda*) *rosaella* **sp. nov.** and *D.* (*Heterodasypoda*) *michezi* Radchenko, 2017. To further clarify the taxonomy of the genus, we confirm that *D.* (*Heterodasypoda*) *bolivari* Quilis is a junior synonym of *D.* (*Heterodasypoda*) *albimana*, and retain *D.* (*Dasypoda*) *panzeri* Spinola, 1838 as a junior synonym of *D.* (*Dasypoda*) *hirtipes* (Fabricius, 1793), although issues with the lectotype designation obscure the *terra typica*, excluding this species from Egypt’ s fauna. We finally present an updated checklist and key of African *Dasypoda*, comprising 13 species, including 6 endemics. Our findings refine our understanding of African *Dasypoda* diversity and underscore the need for integrative taxonomic approaches in resolving cryptic species complexes.

ZooBank: urn:lsid:zoobank.org:pub:AF50AD0A-A8A5-485A-A988-A4C39C0124BB

Keywords: genetics, identification key, integrative taxonomy, melittid bees, Morocco, pantaloon bees, phylogenetics, Tunisia, ultraconserved elements, wild bees.

Introduction

With nearly 21,000 species described globally, wild bees (Hymenoptera: Anthophila) constitute a particularly diversified group of hymenopteran pollinators (Michener 2007). Beyond playing a key role in agricultural pollination of a large proportion of the world' s cultivated plants, bees facilitate the sexual reproduction of hundreds of thousands of flowering plants globally, making them essential for the functioning of ecosystems (Ollerton *et al.* 2011; Garibaldi *et al.* 2013). In recent years however, an increasing number of studies have detected sharp patterns of decline in bee diversity and abundance, most clearly all in the Northern Hemisphere (Nieto *et al.* 2014; LeBuhn and Vargas Luna 2021; Rasmont *et al.* 2021; Zattara and Aizen 2021; Ghisbain *et al.* 2024). Setting the stage for present or future implementation of bee conservation schemes has therefore become a priority for an increasing number of biologists (Winfree 2010; Drossart and Gérard 2020; Ghisbain *et al.* 2020*a*; Woodard *et al.* 2020; Michez *et al.* 2023; Reverté *et al.* 2023). In this context, clearly recognisable and properly diagnosed species constitute indispensable elements to implement local inventories for naturalists and scientists (Dubois 2003; Mace 2004; Vogel Ely *et al.* 2017; Boustani *et al.* 2021; Ghisbain *et al.* 2021*a*, 2023*a*, 2025; Bartomeus *et al.* 2022).

With fewer than 250 valid species known globally, Melittidae is the second most species-poor family of bees after the Australian endemic Stenotritidae (Michener 2007). Among melittid bees, the representatives of the genus *Dasypoda* Latreille are a group of relatively uncommon bees known as 'pantaloon bees' . This small genus includes ~40 species globally and is notable for the unique morphology of its females, which have unusually prominent pollen-collecting hairs (scopae) on their hind legs (Michez *et al.* 2004*a*; Radchenko *et al.* 2019). From the beginning of the millennium, *Dasypoda* bees have received increased attention from taxonomists, with numerous species being discovered and described (Baker 2002; Michez 2002, 2005; Michez *et al.* 2004*a*). This was further demonstrated in recent years with the discoveries of *D. morawitzi* Radchenko (Radchenko 2016), *D. michezi* Radchenko (Radchenko 2017), *D. schwarzi* Radchenko & Michez (Radchenko *et al.* 2022), *D. delectabilis* Ghisbain & Michez (Ghisbain *et al.* 2023*b*) and *D. radchenkoi* Ghisbain & Wood (Ghisbain *et al.* 2023*c*).

In this work, we mostly focus on the Iberian and African fauna of *Dasypoda*. We especially focus on the subgenus *Heterodasypoda* Michez, for which a phylogenomic analysis based on ultraconserved elements (UCEs) supports the presence of a *D. rosaella* sp. nov., a new species most likely endemic to North Africa. We facilitate its diagnosis by comparing it to the closely related and morphologically similar European taxa *D. michezi* Radchenko, 2017 and *D. albimana* Pérez, 1905, and by establishing a neotype for the latter species for which the original type cannot be found and is presumed to be lost. We further review the type material of *D.* (*Heterodasypoda*) *bolivari* Quilis, 1928, which was previously synonymised with *D. albimana* and review the type material of *D.* (*Dasypoda*) *panzeri* Spinola, 1838, which is of doubtful identity. Based on our overall findings, we provide an updated checklist of the *Dasypoda* species present in Africa and propose an updated identification key to all *Dasypoda* species recorded on this continent.

Material and methods

Phylogenomics of *Heterodasypoda* bees

Sample collection A total of 22 individuals belonging to the subgenus *Heterodasypoda* were used in the phylogenetic analyses for this study (Supplementary Table S1). The ingroup includes six species (*D. albimana* Pérez, *D. michezi* Radchenko, *D. morotei* Quilis, *D. pyrotrichia* Förster, *D. radchenkoi* Ghisbain & Wood, and *D. rosaella* sp. nov.), all of which are sequenced for the first time for ultraconserved elements (hereafter referred to UCEs).

In recent years, UCE sequencing has been used to resolve the phylogenetic relationships within an increasing number of bee groups (Bossert *et al.* 2019, 2022; Branstetter *et al.* 2021; Odanaka *et al.* 2022; Orr *et al.* 2022; Almeida *et al.* 2023; Freitas *et al.* 2023) and other groups of Hymenoptera (Branstetter *et al.* 2017*a*, 2017*b*; Blaimer *et al.* 2023), above all because both recently collected and historical specimens (potentially >100 years old) can be used as part of the analyses (Freitas *et al.* 2023). For the outgroup, and to root the tree, we selected one *Dasypoda* belonging to the closely related subgenus *Microdasypoda* (*D. iberica* Warncke). All data are newly presented here.

DNA sequence generation, matrix assembly and phylogenomic analysis

We employed the UCE approach to phylogenomics, combining target enrichment of UCEs with multiplexed, next-generation sequencing (Faircloth *et al.* 2012, 2015; Branstetter *et al.* 2017*a*). The UCE molecular work was performed following the methodology described in earlier research (Branstetter *et al.* 2021), which includes DNA extraction, library preparation, UCE enrichment, sample pooling, and sequencing on Illumina instruments. For UCE enrichment, we used the bee-ant version (Grab *et al.* 2019) of the Hymenoptera (ver. 2) UCE probe set (Branstetter *et al.* 2017*a*). Five samples were sequenced on Illumina HiSeq 2500 (PE125, ver. 4, performed at the University of Utah genomics core facility) and 18 samples were sequenced on HiSeq X (PE150, performed by Novogene Inc. in Sacramento, CA, USA).

The sequenced UCE data were demultiplexed by the sequencing centre or using *BBTools* (ver. 39.99, see https:// github.com/bbushnell/BBTools; Bushnell 2014). Data were later cleaned, assembled and aligned using the *Phyluce* software package (ver. 1.6 and 1.7, see https://github.com/ faircloth-lab/phyluce; Faircloth 2016) following the workflow of Branstetter *et al.* (2021). Within the *Phyluce* environment, *Illumiprocessor* (ver. 2.10, see https://github.com/ faircloth-lab/illumiprocessor) and *Trimmomatic* (ver. 0.39, see http://www.usadellab.org/cms/index.php?page=trimmomatic; Bolger *et al.* 2014) were used for quality trimming raw reads, *SPAdes* (ver. 3.14.1, see https://github.com/ablab/spades; Bankevich *et al.* 2012) for *de novo* assembly of reads into contigs, and *LASTZ* (ver. 1.02, see https://github.com/lastz/ lastz; Harris 2007) for identifying UCE contigs from all contigs, with the min-coverage and min-identity parameters set to 70 and 75 respectively. After extracting contigs, we aligned each UCE locus using *MAFFT* (ver. 7.130b, see https://mafft.cbrc. jp/alignment/software/; Katoh and Standley 2013) and we trimmed poorly aligned regions (internal and external) using the program *Gblocks* (ver. 0.91b, see http://phylogeny.lirmm. fr/phylo_cgi/one_task.cgi?task_type=gblocks; Talavera and Castresana 2007), run with the following reduced stringency parameters: b1:0.5, b2:0.5, b3:12, b4:7. Another *Phyluce* script was then used to filter the initial set of alignments so that each alignment was required to include data for 75% of taxa. Following this step, we concatenated the loci and conducted a quick tree search using the maximum likelihood-based program *IQ-TREE* (ver. 2.2, see https://github.com/iqtree/iqtree2; Minh *et al.* 2020).

The preliminary tree search revealed several long-branched samples, which is likely an artefact of poor sample quality and the challenge of aligning DNA fragments of different lengths. To remove the long branches, we performed additional taxonbased trimming using the program *Spruceup* (ver. 2022.2.4, see https://github.com/marekborowiec/spruceup; Borowiec 2019). For this analysis we used a rooted guide tree with no branch lengths, the Jukes–Cantor distance method, a lognormal distribution, a global cutoff of 0.93, and several manual cutoffs (Dasypoda_morotei_ BLX3284: 0.015, Dasypoda_rosaella_BLX3285: 0.015, Dasypoda_rosaella_BLX3286: 0.015, Dasypoda_rosaella_ BLX3259: 0.015). Following trimming, we split the concatenated matrix using *AMAS* (ver. 0.98, see http://github.com/ marekborowiec/AMAS/; Borowiec 2016) and then removed gap only columns from each alignment using a custom python script (https://github.com/marekborowiec/remove_ empty_columns). We then re-concatenated the matrix using *Phyluce* and performed another quick tree search using *IQ-TREE* to confirm that we had successfully shortened the long branches. We used two *Phyluce* scripts to calculate UCE statistics for each sample ('phyluce_assembly_get_fasta_lengths') (Supplementary Table S2) and for the final data matrix ('phyluce_align_get_align_summary data').

We used the Sliding-Window Site Characteristics based on entropy (SWSC-EN) approach (Tagliacollo and Lanfear 2018) to partition the UCE data for phylogenetic analysis. It uses a sliding window to partition UCE loci into right flank, core, and left flank regions (see Faircloth *et al.* 2012 for the rationale behind this process).

We implemented the approach using the program *CURE* (ver. 1.0.3, see https://github.com/ vhfsantos/CURE; Freitas *et al.* 2023), which parallelises the computation. The resulting data subsets were then merged using *ModelFinder* (see http://www.iqtree.org/ModelFinder/; Kalyaanamoorthy *et al.* 2017) in *IQ-TREE 2*. For this analysis, we used the 'rclusterf' algorithm, AICc model selection criterion, and the GTR + G model of sequence evolution. The resulting best-fit partitioning scheme included 631 data subsets and had a significantly better log likelihood than the unpartitioned analysis. After merging subsets we inferred phylogenetic relationships of *Heterodasypoda* species using *IQ-TREE* (ver. 2.2; Nguyen *et al.* 2015). For the analysis we performed full model testing for each partition (-m MFP) and we calculated clade support by conducting 1000 replicates of the ultrafast bootstrap (UFB) approximation (Minh *et al.* 2013; Hoang *et al.* 2018) and also 1000 replicates of the branch-based, SH-like approximate likelihood ratio test (SH-aLRT) (Guindon *et al.* 2010). For these support measures, values ≥95 and ≥80% respectively, indicate that a clade is supported. To reduce the risk of overestimating branch supports with UFB we used the -bnni option in *IQ-TREE*, which performs an extra hill-climbing nearest neighbour interchange search on each bootstrap alignment.

An alternative assessment of relationships and branch supports was obtained by a coalescent-based species tree analysis on the dataset using the summary program *ASTER* (see https://github.com/chaoszhang/A-pro; Zhang *et al.* 2025) and the weighted ASTRAL method (*wASTRAL*, ver. 1.15.2.3, see https://github.com/chaoszhang/ASTER/blob/master/tutorial/ wastral.md; Zhang *et al.* 2018; Zhang and Mirarab 2022). We estimated gene trees for the complete set of 1991 UCE loci using *IQ-TREE 2*, with the '-m MFP' option selected for model selection and AICc selected as the model selection criterion. We generated support values for each gene tree by performing 1000 UFB replicates. We combined the gene trees into a single file and created a mapping file, whereby each terminal was assigned to one of the seven species. We then conducted the *wASTRAL* analysis using the default local posterior probabilities for support.

COI barcode extraction

Although we focused on the analysis of UCE data for recovering phylogeny and testing species boundaries, the 658-bp cytochrome *c* oxidase I (*COI*) barcode region is a useful molecular marker for bee taxonomy and identification, given that a large reference library exists for bees and efforts have been made to systematically sequence this gene for several decades. Consequently, we attempted to extract the *COI* gene as by-catch from our UCE sequence data in order to provide a molecular voucher for our data set that will be useful for future species identification and monitoring efforts. This was done using a *Phyluce* script ('phyluce_assembly_match_contigs_to_barcodes') and a bait sequence for *Dasypoda hirtipes* (BCHYM1435-13), which was downloaded from the Barcode of Life Data System (BOLD) database (Ratnasingham and Hebert 2007). The script aligns the bait sequence to matching sequences in the assembly files and extracts the information for each species. After running the script, we combined the outputs and manually checked the results for completeness and quality. We checked and removed non-bee contaminants by querying all sequences over 80 bp in BOLD. We aligned the remaining sequences using *MAFFT*, checked for indels or stop codons and combined fragmented sequences that overlapped or appeared to be of good quality. As a final quality check, we inferred a phylogenetic tree using *IQ-TREE* and examined the tree for sensible placement.

Morphological examination and diagnosis

Some specimens used for the description of the new species were collected by G. Ghisbain and T. J. Wood as part of field trips in Morocco, whereas the other specimens were loaned from the institutions indicated below. Reference specimens of the other *Heterodasypoda* species are stored in the Laboratory of Zoology of the University of Mons (Belgium). The following abbreviations (following the nomenclature of Michener 2007) were used for morphological structures: A1, A2, etc., first, second antennomeres; S1, S2, etc., first, second metasomal sternum; T1, T2, etc., first, second metasomal tergum.

Abbreviations of institutions

MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN, Muséum national d' Histoire naturelle, Paris, France; MRSN, Museo Regionale di Scienze Naturali di Torino, Turin, Italy; OÖLM, Oberösterreichisches Landesmuseum, Linz, Austria; RMNH, Naturalis Biodiversity Center, Leiden, Netherlands; UMONS, University of Mons research collection, Mons, Belgium.

Species concept

The main species concept historically used for the description of most bee species worldwide (including nearly all *Dasypoda*) was strictly 'morphological' (in a broad sense), i.e. mainly based on diagnostic differences in colour patterns or in exoskeletal morphology (Michener 2007). Taking the especially well-studied bumble bees (*Bombus*) as an example, taxa that diverge solely by colour pattern of the integument or of body hair have more recently tended to be synonymised as a single species (Williams *et al.* 2019, 2020) or explicitly separated as subspecies (Brasero *et al.* 2021; Lhomme *et al.* 2021; Rasmont *et al.* 2021; see also Ghisbain and Michez 2022). The rationale behind grouping taxa with similar structural features is supported by the fact that hair colour is expected to be more rapidly evolving than the sculpture of the cuticle, which is thought to be more conserved intraspecifically (Williams *et al.* 2020; Rasmont *et al.* 2021; Wood *et al.* 2021; Wood 2023*a*). Genetic analyses tend to confirm this trend, except for fully cryptic or near-cryptic bee species (i.e. species not or barely separable based on phenotype) for which morphology appears to be highly conserved even in relatively distant lineages (Williams *et al.* 2012, 2023; Ghisbain *et al.* 2020*b*). In the present work, we conservatively follow a unified theoretical concept that considers species as 'evolutionarily independent lineages' (detailed in De Queiroz 2007). As a proxy for this concept, species are recognised within an integrative framework, by considering multiple lines of evidence if available, applicable or relevant. These lines of evidence can include biogeographical records, ecological divergence (e.g. in habitat use or plant–pollinator interactions), genetic divergence (e.g. phylogenetic distance or reciprocal monophyly), divergence in body hair colour and exoskeletal structure if visible. Although no universal threshold of any of these characters can bring consensus regarding what species are, we attempt to be transparent and consistent by evaluating divergences individually in these attributes and explicitly justifying species delineations.

Results

UCE phylogenomics We recovered a mean of 1998 UCE loci per sample, with a range of 39–2278 loci. The mean UCE contig length was 795 bp, with a range of 225–1615 bp. After trimming and filtering alignments, 1991 UCE alignments were retained for analysis. The concatenated matrix included 1,516,770 bp of sequence data, 37,898 informative sites, and 27.8% missing data (gaps or missing) (Supplementary Table S2).

Phylogenetic results were assessed as one source of evidence for testing species boundaries in *Heterodasypoda*. We focused on monophyly and clade support as critical pieces of information to test morphology-based species hypotheses. We also used the UCE matrix and the program *MEGA11* (ver. 11.0.13, see https://www.megasoftware.net; Stecher *et al.* 2020; Tamura *et al.* 2021) to calculate *p*-distances within and among species. This was done for descriptive purposes only and was not an explicit test of species boundaries. Phylogenomic analyses supported the existence of the already described five species within *Heterodasypoda*, and of an additional undescribed species from North Africa (Fig. 1). The latter taxon, described as *D. rosaella* sp. nov., is phylogenetically close to *D. albimana* and *D. michezi* as expected by morphological examination. Using UCE-based, *p*-distances, the average genetic differentiation between *D. rosaella* sp. nov. and *D. albimana* is 0.64%, and 0.54% between *D. rosaella* sp. nov. and *D. michezi*. The analyses also support the differentiation of the newly described *D. radchenkoi* Ghisbain & Wood from southern Spain from the closely related *D. morotei* Quilis (0.36% average divergence). The other species included in the tree (*D. pyrotrichia*) is sister to the clade including *D. morotei* Quilis and *D. radchenkoi* Ghisbain & Wood with maximum support. Sampling within *D. morotei*, *D. rosaella* sp. nov. and *D. michezi* revealed additional, internal clades, but in light of other evidence, we view these clades as representing internal genetic structure rather than evidence of species differences.

The *wASTRAL* species tree analysis recovered identical relationships among species compared to the concatenated analysis, with all clades receiving maximum support.

DNA barcodes

We recovered full or partial *COI* sequence data for 18 out of the 23 samples sequenced for UCEs. We recovered at least one sequence for each species, and for most species, we recovered one sequence that was >600 bp in length. The exception is *D. pyrotrichia*, for which we only recovered a 325-bp fragment. The sequences ranged in length from 100 to 658 bp. All barcodes have been deposited into GenBank (Supplementary Table S3).

Species delineation The undescribed North African taxon revealed in Fig. 1 shows reciprocal monophyly with its sister taxon, *Dasypoda michezi*, as well as consistent morphological differentiation in exoskeletal structure (Fig. 2–4). The taxon has, at the moment, only been collected in North Africa. It was previously identified as *D. albimana*, a taxon that comes as a separate monophyletic clade on Fig. 1, with a

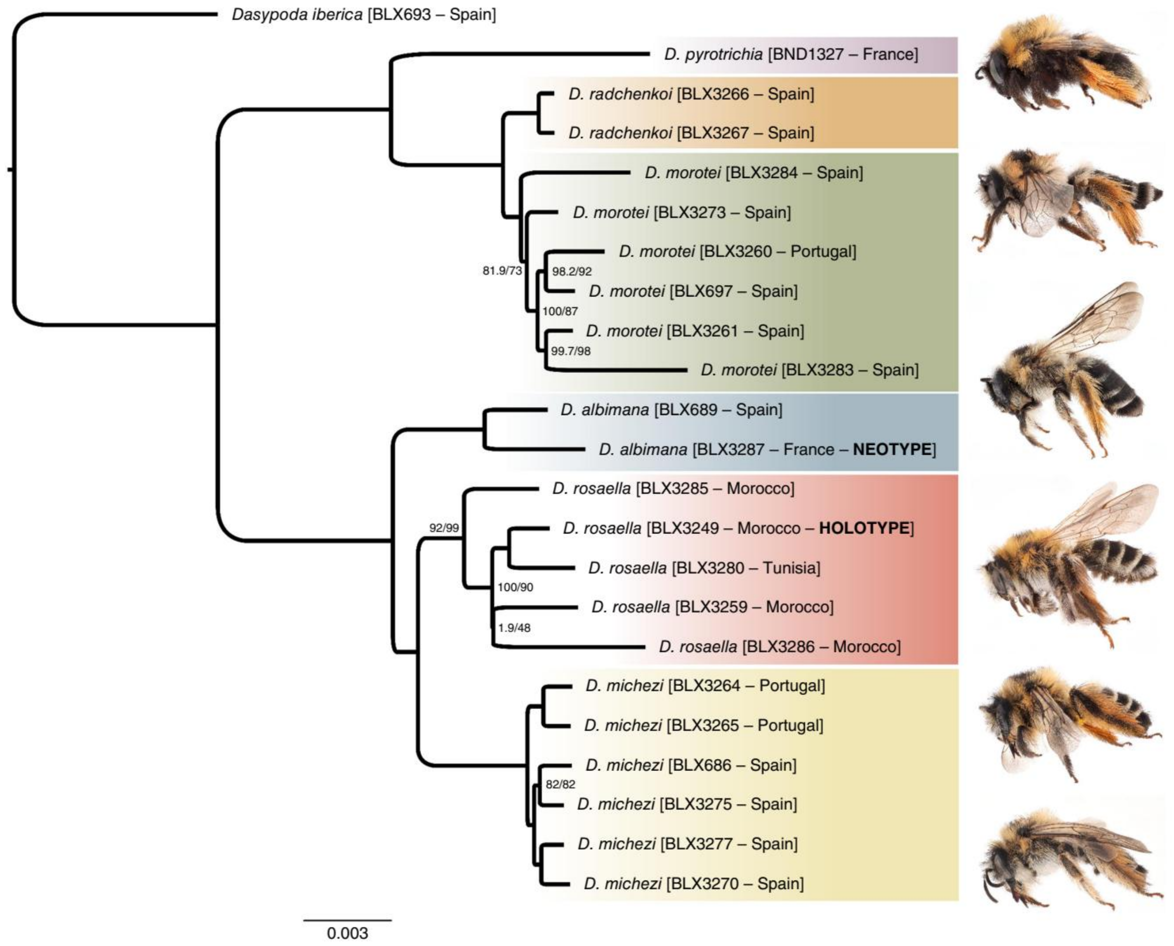

Fig. 1. Phylogenetic tree of the global fauna of the bees belonging to the subgenus *Heterodasypoda* Michez based on the analysis of 1991 ultraconserved elements (UCEs). The ingroup includes six species (*D. albimana* Pérez, *D. michezi* Radchenko, *D. morotei* Quilis, *D. pyrotrichia* Förster, *D. radchenkoi* Ghisbain & Wood, and *D. rosaella* **sp. nov.**), all of which are sequenced for the first time for UCEs. The scale bar indicates the number of substitutions per site. Support values on nodes are UFB/SH-aLRT/, with only values less than 100/100 shown. The species *Dasypoda* (*Microdasypoda*) *iberica* Warncke was chosen as the outgroup.

consistently divergent exoskeletal morphology. No taxon bearing the morphological features of *D. albimana* and *D. michezi* is currently known from the authors in North Africa, suggesting a geographical separation between the range of the new taxon and that of *D. albimana* and *D. michezi*. The overall genetic, biogeographical and morphological differentiation between this new taxon and its European relatives leads us to describe it as a new species for science, that we name *Dasypoda rosaella* Ghisbain & Wood, sp. nov.

Taxonomy

Genus *Dasypoda* Latreille, 1802

Type species: *Andrena hirtipes* Fabricius, 1793.

Comments The genus *Dasypoda* Latreille consists of ~40 species globally, including 20 in Europe (Ghisbain *et al.* 2025) and 13 in Africa (see below). Except for one Sub-Saharan species, the group is strictly Palaearctic, and mostly diversified in the West-Palaearctic region, especially around the Mediterranean Basin. The East-Palaearctic fauna is much less diversified (see Wu 1978, 2000), although the taxonomy of these Asian species requires revision (G. Ghisbain *et al*., unpubl. data). The genus *Dasypoda* was divided into four subgenera (*Dasypoda* Latreille s. str., *Heterodasypoda* Michez, *Megadasypoda* Michez and *Microdasypoda* Michez) by Michez *et al.* (2004*b*). Multiple undescribed species were discovered in the last decade (Radchenko 2016, 2017; Radchenko *et al.* 2022; Ghisbain *et al.* 2023*b*, 2023*c*). Here follows the description and diagnosis of a new species from North Africa.

Subgenus *Heterodasypoda* Michez, 2004

Type species: *Dasypoda pyrotrichia* Förster, 1855.

Dasypoda rosaella Ghisbain & Wood, sp. nov.

(Fig. 2–4.)

ZooBank: urn:lsid:zoobank.org:act:B55CED5C-EF74-42C2-955D-61306CE2109A

Diagnosis *Dasypoda rosaella* **sp. nov.** belongs to the subgenus *Heterodasypoda* Michez (following the subgeneric concept of Michez *et al.* 2004*b*) due to the combination of its diagnostic features. All representatives of the subgenus *Heterodasypoda* are characterised by a medium to large body size (contrast *Microdasypoda* that are the smallest representatives of the genus). The subgenus *Heterodasypoda* also significantly differs from all other *Dasypoda* subgenera by the structure of the male genitalia: the gonostylus is always trilobed, with one small inner lobe with a scaly surface, one small medial lobe and one larger outer lobe (contrast *Dasypoda* s. str. in the West-Palaearctic region in which the gonostylus is bilobed with a membranous structure between the two lobes; contrast *Megadasypoda* in which it is trilobed but without a scaly surface on the inner lobe; contrast *Microdasypoda* in which the gonostylus is either unilobed with one basal tooth, or bilobed without a membranous structure that connects these lobes).

The apomorphies of *Heterodasypoda* must be regarded with a distinct combination of other characters that may be individually shared with some other subgenera. First, the malar space of *Heterodasypoda* is always much shorter than the length of the pedicel (contrast most representatives of *Megadasypoda*). Their maxillary palpi and galea of all representatives are of a sub-equal length (contrast *Dasypoda* s. str. in which the palpi/galea ratio is in the range of 0.5–0.75 and *Megadasypoda* in which it is less than 0.25). The nervulus (*cu-v*) of *Heterodasypoda* is antefurcal (contrast most *Megadasypoda*). The division between the disc and the marginal area of T2 has a relatively straight marginal line (contrast *Megadasypoda* and some *Dasypoda* s. str. in which this division is curved). The apical lobes of S6 of *Heterodasypoda* have a dense pubescence (contrast *Dasypoda* s. str. and *Megadasypoda* that have a shorter and sparser pilosity). *Heterodasypoda* lack lateral hooks at the basal half of

S8 (contrast *Dasypoda* s. str. and some *Megadasypoda*). The pygidial plate of *Heterodasypoda* is always glabrous (contrast *Megadasypoda*).

Females and males of *D. rosaella* **sp. nov.** can be separated from those of all other *Heterodasypoda* species by a combination of morphological features. The punctation of the galea of *D. rosaella* **sp. nov.** is irregular (Fig. 4*e*) but predominantly sparse (most punctures separated by 1 puncture diameter or more), the surface between the points is weakly shagreened (more weakly shagreened in females, slightly more strongly shagreened in males) but essentially still shiny over its entire surface (contrast *D. michezi*, *D. morotei* and *D. radchenkoi* in which the galea is fully covered with small tubercles and hence dull, and contrast *D. pyrotrichia* in which the galea is covered with wave-like structures basally and hence partially dull).

In females, the centre of the scutum includes an area with dark hairs (contrast western *D. pyrotrichia* populations in which the whole scutum is covered with a ginger pubescence, and eastern *D. pyrotrichia* populations in which only a small number of black hairs can be found on the scutum medially). The female propodeal triangle of *D. rosaella* **sp. nov.** is covered with fine and regular scale-like granular shagreen (Fig. 3*h*) (contrast *D. radchenkoi* in which the propodeal triangle shows fine latitudinal ridges). The pubescence of the external face of the mesotibia and mesobasitarsus of females is comprised of brownish and relatively short hairs (Fig. 3*i*), in profile view these hairs not greatly extending beyond the posterior margin of the mesobasitarsus (contrast *D. albimana* for which the pubescence of this segment is generally entirely white, the hairs of the mesobasitarsus long, in profile view clearly extending beyond its posterior margin). The scopa of the metatibia of the female of *D. rosaella* **sp. nov.** is bicoloured orange and dark brown (Fig. 3*k*) (contrast with *D. radchenkoi* in which the scopa is uniformly orange). The pubescence of the central part of T5 is homogeneously black in *D. rosaella* **sp. nov.** (in *D. albimana* and most specimens of *D. michezi* the pubescence is most often brown centrally and white laterally, though dark or abraded individuals of *D. michezi* can be found for which the majority of hairs of T5 are dark).

In males, a striking character is the shape of the apical part of the external lobe of the gonostylus, which is twisted, angulous, spiky and covered with wave-like structures (Fig. 3*l*, 4*f*) (contrast *D. albimana* in which it is flatter, more rounded and with uniform scale-like shagreen (Fig. 4*b*), contrast all other

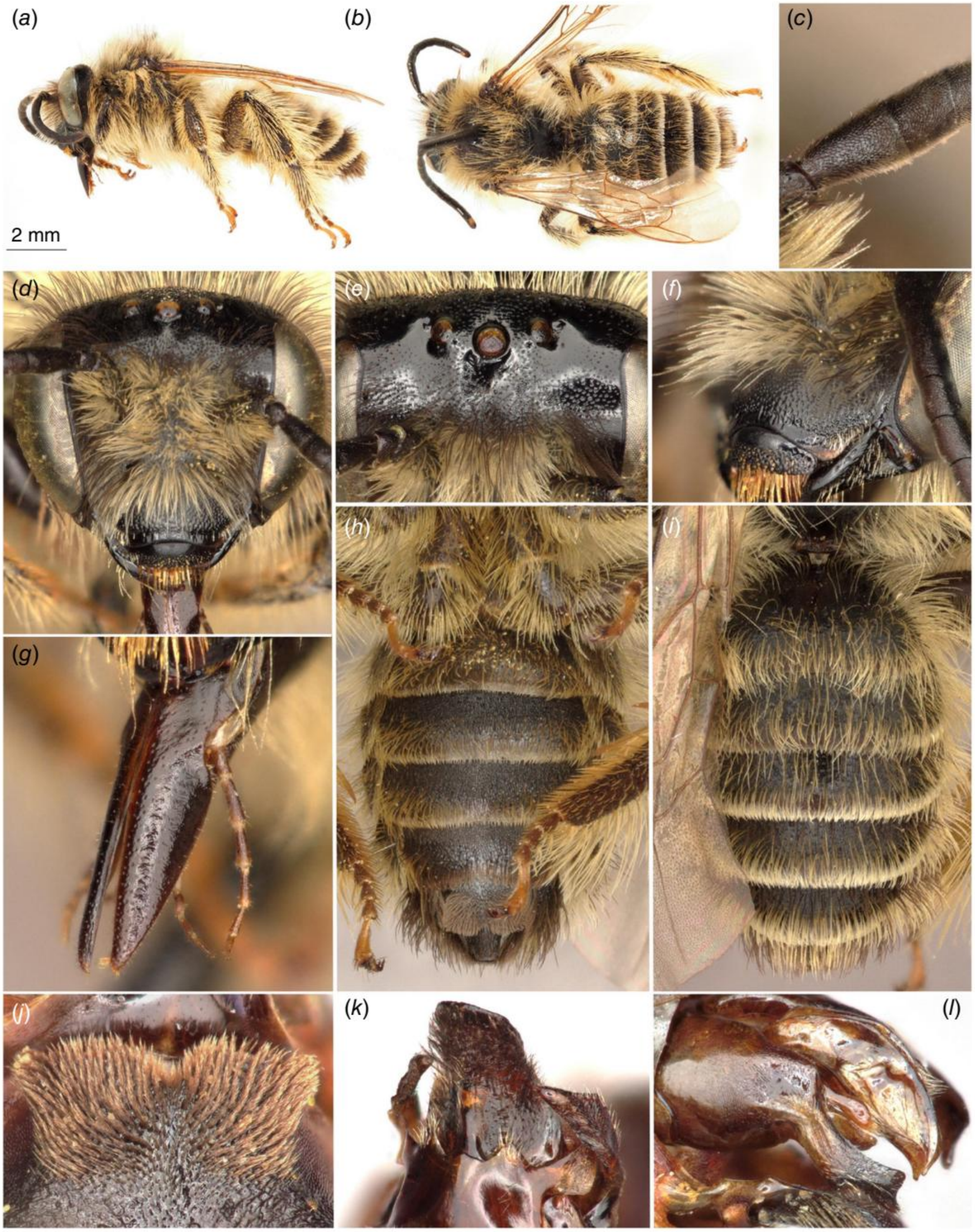

Fig. 2. Male of *Dasypoda rosaella* **sp. nov**. (*a*) Lateral view. (*b*) Dorsal view. (*c*) Antenna, with a focus on the relative sizes of antennomeres 3 and 4. (*d*) Head in frontal view. (*e*) Vertex and ocellar field. (*f*) Lower part of the head in oblique view, highlighting the malar space, clypeus structure and labrum. (*g*) Galea and maxillary palp in oblique view. (*h*) Metasoma in ventral view. (*i*) Metasoma in dorsal view. (*j*) Sternum 6 in ventral view. (*k*) Sterna 7 and 8 in ventral view (with external lobes of gonostylus visible around sternum 7). (*l*) Genitalia in

oblique lateral view.

Heterodasypoda in which the external lobe is much more lanceolate). The outer face of the external lobe of the gonostylus also only shows scattered hairs (contrast *D. michezi* for which the outer face of the external lobe of the gonostylus has a weak and anteriorly directed tuft of moderately long yellowish hairs, Fig. 4*d*). The genitalia of '*D. albimana*' illustrated in fig. 56 of Radchenko (2017) actually belong to a specimen of *D. rosaella* **sp. nov.** from North Africa. The typical external lobe of the gonostylus of the true *D. albimana* is illustrated here (Fig. 4*b*) and can be used for reference in future research.

Fig. 3. Female of *Dasypoda rosaella* **sp. nov**. (*a*) Lateral view. (*b*) Dorsal view. (*c*) Antenna, with a focus on the relative sizes of the first flagellomeres. (*d*) Head in frontal view. (*e*) Vertex and ocellar field. (*f*) Lower part of the head in oblique view, highlighting the malar space, clypeus structure and labrum. (*g*) Galea in oblique view. (*h*) Highlight on the cuticular sculpture of propodeum. (*i*) Femur, tibia and basitarsus of the mid-leg in lateral

view. (*j*) Last terga and pygidial plate in dorsal view. (*k*) Hind leg with scopa and metasoma in oblique ventral view. (*l*) Metasoma in dorsal view.

Sex pairing in *D. michezi* and *D. rosaella* **sp. nov.** is unequivocally supported by the UCE data. Although no genetic sequence is yet available for the female of *D. albimana*, pairing in this species remains unambiguous based on morphology. In all regions where males conform to the

diagnostic features shown in Fig. 4*a*, *b*, the corresponding females consistently exhibit the characteristic glossy, sparsely punctured galea illustrated in Fig. 4*a*. This pattern holds in southern France, from where our neotype originates, as well as in Catalonia, the locus typicus of *D. albimana*. In both of

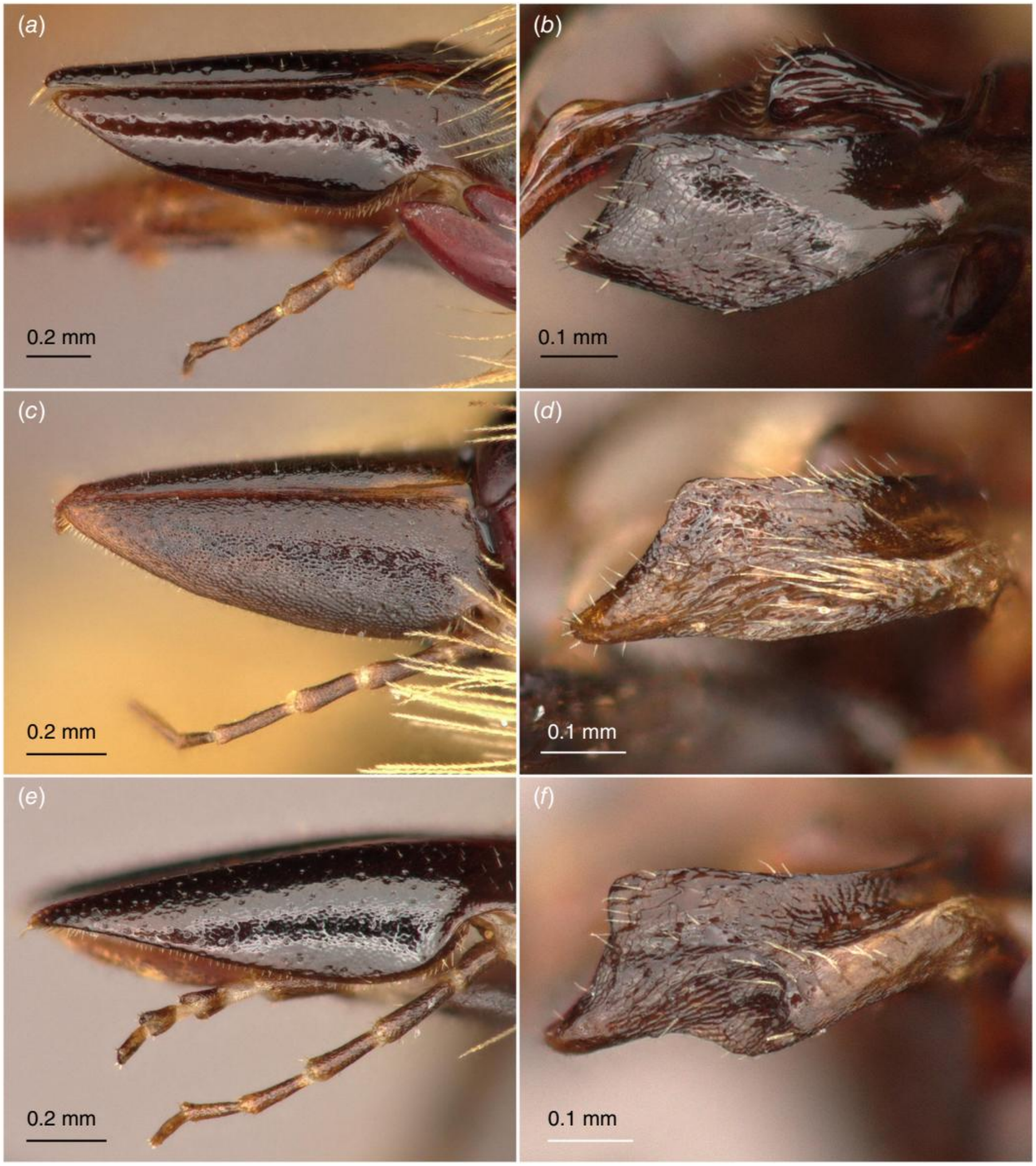

Fig. 4. Structure of the male galea and maxillary palp (*a*, *c*, *e*) and apex of the external lobe of the gonostylus (*b*, *d*, *f*) of *Dasypoda albimana* (*a*, *b*), *D. michezi* (*c*, *d*) and *D. rosaella* **sp. nov.** (*e*, *f*).

these places, only *D. albimana* exists to the best of our knowledge. To support future taxonomic work, identification of both sexes can also be assisted by sequencing the *COI* barcode fragment, which we provide on GenBank (Supplementary Table S3).

Note *Dasypoda delectabilis* Ghisbain & Michez was also recently described from south-eastern Iran as a member of the subgenus *Heterodasypoda*. The species was considered to be 'morphologically intriguing' by the authors due to a previously unknown combination of morphological features of both the subgenera *Heterodasypoda* and *Dasypoda* s. str. (Ghisbain *et al.* 2023*b*). Preliminary unpublished UCE data suggest additional complexity in the subgeneric placement of this species, which explains why no diagnosis with this species is provided here. A detailed diagnosis of *D. delectabilis* with other *Dasypoda* bees is provided as part of the original description (Ghisbain *et al.* 2023*b*).

Description of male (Fig. 2, 4*e*–*f*)

Head (Fig. 2*c*–*g*) Clypeus, supraclypeal and paraocular areas covered by long and erect white to pale yellow pilosity, with thin band of darker brown hairs along internal margin of compound eye (Fig. 2*d*). Clypeal surface typically obscured by dense pilosity in well preserved specimens, densely punctate, punctures separated by <1 puncture diameter (Fig. 2*f*). Vertex covered with sparse and erect brown pilosity (posteriorly intermixed with white or pale yellow hairs), vertex laterally, between lateral ocellus and the compound eye, clearly shiny, with more or less pronounced wave-like structures (depending on the specimen) between the punctures close to the compound eye (Fig. 2*e*). Gena behind compound eye shiny and densely punctate, covered with brown pilosity (becoming pale yellow laterally). Malar space short (Fig. 2*f*). Mandible shagreened basally and shiny apically, hairless and reddish. Base of mandible externally with pale yellow hairs. Galea more or less weakly sculptured but always clearly shiny (Fig. 2*g*, 4*e*). Scape ventrally covered with dense pale yellow pilosity. Pedicel and flagellum black. Flagellomeres largely cylindrical but slightly bent medially, slightly concave ventrally, densely covered with very short, pale yellow pilosity. A3 longer than A4 (Fig. 2*c*), shorter than A4 + 5.

Mesosoma (Fig. 2*a*, *b*)

Scutum and anterior part of scutellum clearly shiny between punctures. Posterior part of scutellum, metanotum and propodeum moderately shiny to mat and shagreened between punctures, covered with pale yellow erect pilosity. Scutum medially with occasional discrete brown hairs. Nervulus (*cu-v*) antefurcal. Wing very slightly infuscate. Femur, tibia and basitarsus with cuticle black but all tarsi dark orange. Colour of leg hairs pale yellow. Spurs of the meso- and metatibia pale yellow.

Metasoma (Fig. 2*a*, *b*, *h*–*l*, 4*f*) Cuticle of tergal discs more or less shiny, covered with large punctures, interspaces shagreened. Distance between punctures equals 1–3 point diameters. Apical parts of terga with cuticle dark orange, very slightly translucent in some specimens. Tergal discs with hair yellow, with dense band of whitish hairs apically on marginal areas (Fig. 2*i*). T6–7 covered with brown hairs. S1–5 densely shagreened and punctured, covered with yellow to brownish pilosity (Fig. 2*h*). S6 apically with dense tufts of brown hairs that radiate from the centres of apical processes (Fig. 2*h*, *j*). S7 with two apical spots of yellow hair and with latero-apical processes shaped as in Fig. 2*k*. Apical part of S8 truncated, shaped as in Fig. 2*k*. Genitalia with gonostylus in three lobes, the external lobe being twisted, angulous, spiky and covered with wave-like structures (Fig. 2*l*, 4*f*). Penis valve large and curved.

Description of female (Fig. 3) Note: the following description is based on three specimens collected from three different localities in Morocco. Further observations of additional specimens might reveal currently unknown intraspecific colour variability in the species.

Head (Fig. 3*c–g*)

Clypeus covered with whitish pilosity, supraclypeal and paraocular areas covered with long and erect whitish pilosity intermixed with black hairs and yellowish hairs around antennae (Fig. 3*d*). Clypeus strongly punctured over its surface and shiny between punctures, punctures separated by <1 puncture diameter, becoming slightly sparser apically (Fig. 3*f*). Frons and vertex covered with sparse, erect, black pilosity, with some yellowish hairs posteriorly. Lateral parts of vertex, between lateral ocellus and compound eye weakly shagreened, broadly shining (Fig. 3*e*). Gena weakly sculptured, more or less shining with dense punctation, covered with black pilosity dorsally, becoming yellowish to whitish ventrally. Malar space short (Fig. 3*f*) and distinctively narrower than diameter of flagellum. Mandible strongly shagreened and shiny basally, matt apically, here its cuticle becoming slightly reddish. Basal part of mandible with long yellow hairs on external margin (Fig. 3*f*). Galea black, sparsely covered with large but irregular punctures, punctures separated by 0.5–1 puncture diameters, underlying surface finely shagreened and shiny across its entire surface (Fig. 3*g*, 4*e*). Scape ventrally covered with long yellowish pilosity, with occasional short black hairs dorsally. Flagellum cylindrical, with black cuticle (except for apical flagellar segments A5–12 with slightly reddish cuticle) and covered with very short whitish pilosity. A3 clearly longer than A4 (Fig. 3*c*), equalling A4 + 5.

Mesosoma (Fig. 3*a*, *b*, *h*) Scutum moderately shiny and strongly punctured, punctures separated by 1 puncture diameter, more strongly shagreened apically. Hairs on scutum black centrally and yellowish laterally (close to the tegulae), anteriorly, and posteriorly, so that darker pilosity appears as diffuse spot on mesosoma (Fig 3*a*, *b*). Scutellum shiny and densely punctured, metanotum less shiny, densely punctured and shagreened, propodeum with scale-like granular shagreen over majority of its area, weakly shining (Fig. 3*h*). Tegula dark brown and finely shagreened. Wing transparent, hyaline, with nervulus (*cu-v*) distinctively antefurcal. Profemur covered with a majority of yellowish hairs (some darker hairs intermixed apically), external face of protibia and probasitsarsus covered with dark grey pilosity, posterior face of protibia and apical part of posterior face of profemur covered with bright orange pilosity. Mesofemur with yellowish and whitish–greyish pilosity, external face of mesotibia basally with whitish–greyish hairs and apically with a tuft or adpressed whitish pilosity (Fig. 3*i*), internal face with brown–black pilosity. Mesobasitarsus with whitish–greyish to brownish pilosity on external face. Metafemur with yellow pilosity. Scopa on metatibia and metabasitarsus yellow anteriorly, brown externally and light brown posteriorly (Fig. 3*k*, bright orange hairs visible in image from internal side of segments). Leg cuticle black, stained with reddish colouration on all basitarsi, tarsi and on metatibia ventrally. Claws orange basally, dark brown apically, with strong internal tooth.

Metasoma (Fig. 3*a*, *b*, *j–l*)

T1 covered with semi-erect yellowish hairs, distance between points of cuticle equal to 1–2 puncture diameter, underlying surface finely shagreened, apical margin of T1 with short white adpressed pilosity laterally, glabrous medially (Fig. 3*l*). T2 with disc covered with semi-erect, shorter yellowish pilosity, underlying surface matt. T3 disc covered with short, semi-erect, dark brown pilosity, underlying surface mat. T4 disc covered with short, semi-erect, dark brown to black pilosity, underlying surface matt but with punctures more distinct than on T2–3. Apical margins of T2–4 with short white adpressed pilosity (Fig. 3*l*). T5 disc covered with semi-erect black hairs, followed by denser tuft of black hairs medially (Fig. 3*j*), with underlying cuticle much shinier with distinct punctures separated by 1 or <1 point diameter. Pygidial plate strongly depressed, without apical excision, surrounded by black pilosity (Fig. 3*j*). Hairs on S1 yellowish, dark brown on all other sterna (Fig. 3*k*), underlying surface strongly sculptured.

Materials examined

Specimens collected in Morocco –the following specimen is designated as the holotype: 1 ⍰: 1st label 'Morocco: Drâa-Taf., 21.iv.2022, Tazenakht, Anezal, 5 km NE Ait Igga, 30.7280, −7.4670, TJ Wood' , 2nd label (yellow) 'Genetic sample TJW_0900 Voucher specimen' , 3rd label '[manuscript] Dasypoda albimana [printed] Det. T. Wood 2022' , collection RMNH, 4th label (red): 'HOLOTYPE/*Dasypoda* (*Heterodasypoda*) *rosaella*/Ghisbain & Wood' .

The following specimen is designated as a male allotype: 1 ⍰: 1st label 'Marokko/Oukaimeden 2700 m/28.6.1987/leg. Max. Schwarz', 2nd label '*Dasypoda albimana*/Pérez 1905/Det. Michez 2008', 3rd label (red): 'ALLOTYPE/*Dasypoda* (*Heterodasypoda*) *rosaella*/Ghisbain & Wood', collection OÖOLM.

All the specimens cited hereafter are paratypes and are indicated as such with a red label 'PARATYPE/*Dasypoda* (*Heterodasypoda*) *rosaella*/ Ghisbain & Wood'. 1 ⍰: 'Morocco, Marrak-Safi, Oukaimaden, P2030, 31.2119N, 7.8497W, 2500 m, 08.VII.2022 –leg. G. Ghisbain', collection UMONS. 1 ⍰: 1st label 'Mischliffen bei Ifrane/MAROKKO 17.7.1975/leg. Gusenleitner 1900 m', 2nd label '[printed] Dasypoda/[manuscript] albimana/Per./Det. Dr. Warncke', collection OÖLM. 11 ⍰: 1st label 'Marokko/ Oukaimeden 2700 m/25.6.1987/leg. Max. Schwarz', 2nd label '*Dasypoda albimana*/Pérez 1905/Det. Michez 2008', collection OÖLM. 1 ⍰: 1st label 'Marokko/Oukaimeden 2700 m/26.6.1987/leg. Max. Schwarz', 2nd label '*Dasypoda albimana*/Pérez 1905/Det. Michez 2008', collection OÖLM. 7 ⍰: 1st label 'Marokko/Oukaimeden 2700 m/27.6.1987/leg. Max. Schwarz', 2nd label '*Dasypoda albimana*/Pérez 1905/Det. Michez 2008'. 10 ⍰: 1st label 'H. Atlas Oukaimeden/MAROKKO 2600–2800 m/leg. J. Gusenleitner 8.7.1975', 2nd label '[printed] Dasypoda/[manuscript] albimana/Per./Det. Dr. Warncke', collection OÖLM. 3 ⍰: 1st label 'Marocco/Haut-Atlas/ Oukaimeden', 2nd label '25.-26.1987/leg. W. Schacht', 3rd label 'Coll. K. WARNCKE/O.Ö.Landesmuseum/Linz/Austria-egg. 93', collection OÖLM. 3 ⍰: 1st label 'Marocco/Haut-Atlas/Oukaimeden', 2nd label '27.-28.1987/ leg. W. Schacht', 3rd label 'Coll. K. WARNCKE/O.Ö.Landesmuseum/Linz/ Austria-egg. 93', collection OÖLM. 1 ⍰: 1st label: 'Morocco/40km S Guercif/15-17.5.1995/Ma Halada lgt.', 2nd label '*Dasypoda albimana*/ Pérez 1905/Det. Michez 2008'. 1 ⍰: 1st label: ' Morocco/40km S Guercif/

15-17.5.1995/Ma Halada lgt.', 2nd label '*Dasypoda albimana*/Pérez 1905/ Det. Michez 2002'. 1 ⍰: 1st label 'MAROKKO/Oukaimeden H. Atlas/ 25.6.1988/leg. J. Schmidt', 2nd label '*Dasypoda albimana*/Pérez 1905/ Det. Michez 2008'. 1 ⍰: 1st label 'MAROCCO/Moyen Atlas/v. Oorsohot, Coene/& Kruseman c. s.', 2nd label 'MICHLIFFEN/2000 m/13-VII-1975', 3rd label '*Dasypoda albimana*/Pérez 1905/Det. Michez 2003', collection RMNH. 1 ⍰: 1st label 'Maroc. Marrakech/Oukaimeden. vallon principal/ 30.VI.2000 p.m./leg. S. Patiny', 2nd label '*Dasypoda albimana*/Pérez 1905/Dét. Michez 2008', collection UMONS.

Specimens collected in Tunisia –2 ⍰: 1st label 'TUNISIA/10km SW LE KEF/15.4.2001/leg. M. Halada', 2nd label '*Dasypoda albimana*/Pérez 1905/Det. Michez 200[?]', collection OÖLM. 1 ⍰: 1st label 'TUNISIA/ 10km SW LE KEF/15.4.2001/leg. M. Halada', 2nd label 'Dasypoda/albimana Quilis 1928/Det. D. Michez 2002', collection OÖLM.

All specimens are returned to their original institution with the exception of the holotype of *D. rosaella* **sp. nov.**, which is deposited in the RMNH collection.

Distribution

Morocco and Tunisia; unknown or absent from Algeria (Fig. 5*c*).

Remarks The flight period extends from April to July depending on altitude. The species was recently found by G. Ghisbain and T. J. Wood in the Anti-Atlas (Fig. 5*a*) and at Oukaïmeden in the High-Atlas (Fig. 5*b*). One of the females was observed visiting an unidentified yellow Asteraceae.

Etymology The species is dedicated to the Italian entomologist Paolo Rosa, a global authority on the taxonomy of Chrysididae (Hymenoptera: Chrysidoidea), and the nerve centre of the European Project ORBIT ('Developing resources for European bee inventory and taxonomy'), as well as a mentor and a friend.

Neotype designation for *Dasypoda albimana* Pérez, 1905

One male specimen from southern France was chosen as a neotype for the taxon *Dasypoda albimana* Pérez, 1905 (sample BLX3287 in Fig. 1). The choice to create a neotype is motivated by the fact that it has not been possible to locate the original type material of *D. albimana* used by Pérez (1905). Ornosa and Ortiz-Sánchez (1998) noted that the type might be lost after examining numerous collections, specifically (i) the collection of the Department of Entomology of the Universidad Complutense de Madrid (Madrid, Spain), (ii) the Department of Animal Biology and Ecology of the Universidad de Granada (Granada, Spain), (iii) the Estación Experimental de Zonas Áridas de Almería (Almería, Spain), (iv) the Museu de Ciènces Naturals de Barcelona (former Museu Zoològic de Barcelona) (Barcelona, Spain), (v) the Museo Nacional de Ciencias Naturales (Madrid, Spain) and (vi) the Museu da Ciência da Universidade de Coimbra (Coimbra, Portugal). The authors also note that they examined specimens from the MNHN that houses most of Pérez' s specimens. In addition, we also examined relevant specimens from the RMNH collection. Despite this in-depth search, type material of *D. albimana* could not be recovered. Searches by Michez *et al*. (2004*a*) in the MNHN, where the likelihood of finding the type is the highest, were also unsuccessful. We therefore consider the type material to be lost. Therefore, the designation of a neotype is justified and necessary in order to fix the name to the European population from which it was described, and to ensure nomenclatural clarity and stability of the taxon relative to *D. michezi* and *D. rosaella* **sp. nov.** Key identification characters to distinguish *D. albimana* from these two taxa can be found in the identification key below.

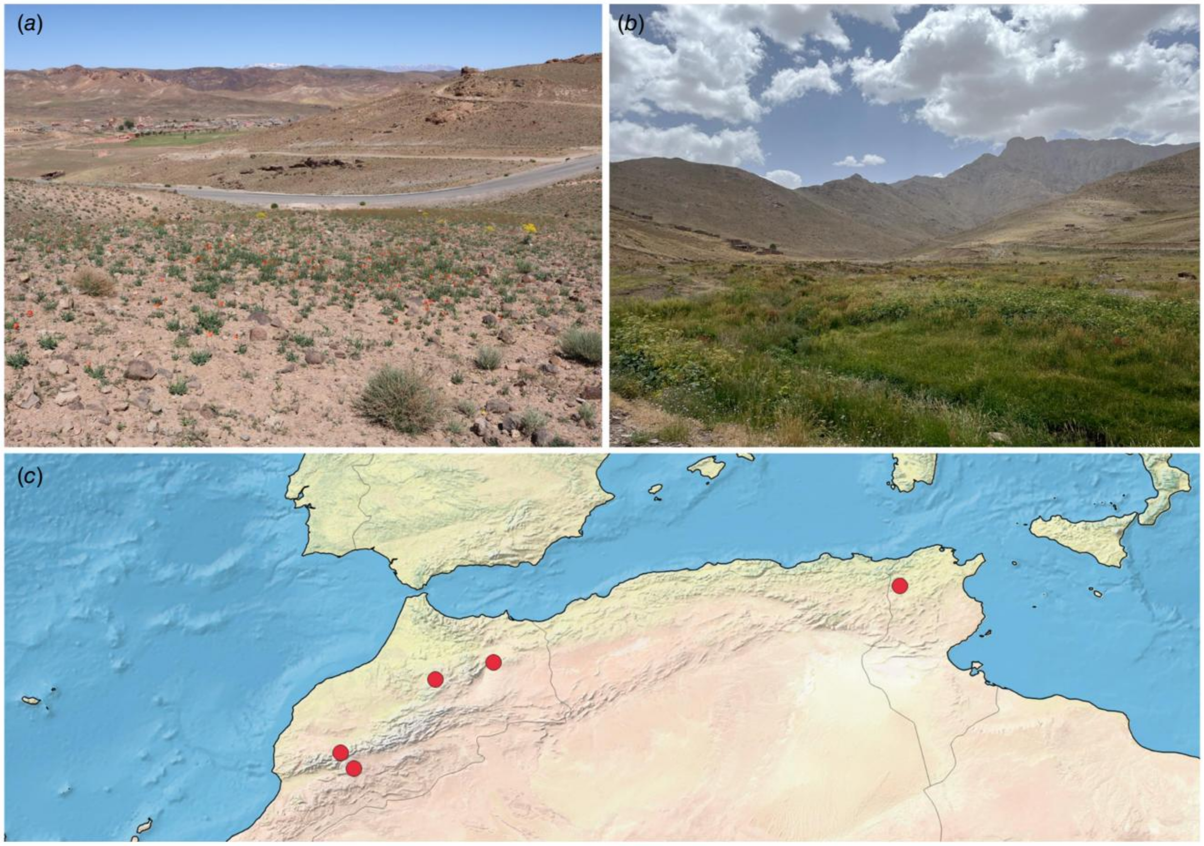

Fig. 5. Sites in which fresh specimens of *Dasypoda rosaella* **sp. nov**. have been recently collected by G. Ghisbain and T. J. Wood in Morocco, and known distribution of the species. (*a*) Drâa-Taf (Tazenakht, Anezal, 5 km NE Ait Igga) in the Anti-Atlas (*locus typicus*, in which specimen BLX3249 from Fig. 1 was collected). (*b*) Oukaïmeden, in the High-Atlas, where many paratypes collected in the 20th Century also come from. (*c*) Known distribution of *D. rosaella* **sp. nov**. in North Africa.

Although the original description of *D. albimana* was made based on a female specimen (caught around Barcelona, Spain), we chose a male neotype as this sex can be more reliably distinguished from other *Heterodasypoda* species, including *D. rosaella* **sp. nov.** (Fig. 4). This pattern is actually consistent in other *Heterodasypoda*, for which females generally differ mostly by colour characters, whereas males vary also by a combination of morphological features (Michez *et al*. 2004*a*; Radchenko 2017; Ghisbain *et al*. 2021*b*; but see Ghisbain *et al.* 2023*c* as a counterexample). Furthermore, the most wellknown character that allows the identification of the female of *D. albimana*, i.e. the colour the pubescence of the mesotibia, can be hard to appreciate as some darker hairs can sometimes be present on this segment ventrally or dorsally. Therefore, we chose to select a male with both the genitalia and tongue structure properly dissected and visible as a neotype for *D. albimana*. The neotype specimen comes from southern France, as suitable specimens from north-eastern Spain of an age that could be used for genetic sequencing were not available.

The following labels are associated with the neotype of *Dasypoda albimana* Pérez, 1905: 1st label 'B. du Rhône/ Eygalieres/[manuscript] Carriere [*sic*]/R. Fonfria/[manuscript] 11.V.93', 2nd label 'Biologiezentrum Linz,/Austria (LI)/ex. Coll. Borek Tkalců/Eingang Nov. 2013', 3nd label 'determined by Tkalcu/[*sic*] probably as Dasypoda albimana [*sic*] Pér./labeled 2004', 4th label 'Phylogenomics L_011/ BLX3287', 5th label: 'Phototype/*D. albimana* m1', 6th label 'NEOTYPE/*Dasypoda* (*Heterodasypoda*) *albimana* Pérez, 1905/Design. Ghisbain & Wood 2023'. The specimen is deposited in the OÖLM. The galea and external lobe of the gonostylus depicted in Fig. 4*a*, *b* belong to this specimen.

In addition, we confirm the synonymy of *Dasypoda bolivari* Quilis, described from 'Vaciamadrid' (Spain) with *D. albimana* Pérez, after careful examination of the type material of *D. bolivari* at the MNCN by one of us (P. Álvarez Fidalgo). Although this synonymy had already been established by Warncke (1973), an updated revision was required to ensure that *D. bolivari* was not a senior synonym of *D. michezi*, whose distribution is now thought to extend more widely in the Iberian Peninsula than previously suggested in Radchenko (2017) and Ghisbain *et al.* (2021*b*) (G. Ghisbain, unpubl. data).

Distribution

To our current knowledge, *D. albimana* appears to be distributed in southern France, the northern half of Spain and in a likely isolated population in the Sierra Nevada (sample BLX689 sequenced as *D. albimana* in Fig. 1 is a male collected there and its morphological criteria match those of the designated neotype), although the exact boundaries of its geographical range remain unclear. A proper revision of museum material previously identified as *D. albimana* is required to delineate the distribution of the species, with regard to that of the closely related *D. michezi*. At the moment, both *D. albimana* and *D. michezi* are listed as 'Data Deficient' in the updated Red List of European bees (Michez *et al*. 2026) precisely because of this lack of clarity regarding their respective distributions.

Examination of African *Dasypoda* type material in the Spinola collection (Turin, Italy)

It was recently possible to visit the Spinola collection (MRSN), which was closed and hence inaccessible during the period in which the monographic *Dasypoda* revision of Michez *et al*. (2004*a*) was written. Spinola (1838) described two species of *Dasypoda*, one of which is currently considered valid. The first taxon is *D.* (*Dasypoda*) *albipila* Spinola, 1838, which was described from Egypt, and Baker (2002) designated a male lectotype.

The second taxon is *D.* (*Dasypoda*) *panzeri* Spinola, 1838. This taxon has been the subject of confusion from the very beginning, as Spinola (1838, p. 508) referred to it as '*Andrena succincta* Panz.', stating that he believed that it was actually a taxon close to but distinct from *D. hirtipes*. As summarised by Baker (2002), the name *D. panzeri* was not described in the typical manner used by Spinola in other parts of the same publication. Baker (2002, p. 91) used the term 'replacement name', but we disagree with the use of this term, since Panzer (1793) did not create a new nomenclatural act, referring to the taxon as '*Andrena succincta* Fabricius' (ultimately referring back to *Apis succincta* Linnaeus, 1758, which is now *Colletes succinctus*), and therefore it was not a preoccupied name that would require replacement. *Dasypoda panzeri* can simply be considered to be a species newly described by Spinola, who considered it to be the same taxon as illustrated by Panzer (1793).

Spinola wrote that '*La* Dasypoda panzeri*, qui ne paraît pas rare en Egypte, se trouve aussi en Grèce, en Sicile et en Italie* [*Dasypoda panzeri*, that does not seem rare in Egypt, is also present in Greece, Sicily and Italy]' (p. 508). In examining material preserved in the Spinola collection (see also Casolari and Casolari 1980), Baker identified a male and female from Egypt and two males from Sicily as part of the original syntypic series used by Spinola.

Both specimens from Egypt come from D. Waltl (see Casolari and Casolari 1980), as was the case for many of the bee taxa described in Spinola (1838), such as *D. albipila*. Spinola (1838) described the species from both the male and female sex, and Baker selected a male specimen as the lectotype, which has been labelled by someone other than Spinola (see Baker 2002, p. 91) as coming from Egypt. Baker then identified this lectotype as *D. altercator* (Harris, 1780) (functionally = *D. hirtipes* (Fabricius, 1793)), with the Egyptian female syntype identified as *D. sinuata* Pérez, 1895. Two additional syntype males nominally from Sicily were labelled as paralectotypes (Baker 2002, p. 92).

Morphologically, the male lectotype does not appear to be *D. sinuata*, as it lacks the projections at the apex of the metatibia that characterise this species in the male sex (Michez *et al*. 2004*a*). However, *D. hirtipes* does not occur in North Africa outside of Morocco and has never been recorded from Egypt or the Levant (Michez *et al*. 2004*a*, the dots in Algeria and Tunisia from Michez 2012 and Radchenko *et al.* 2020 are considered to be erroneous). In this context, we are sceptical that the lectotype specimen selected by Baker is actually from Egypt. Spinola’ s specimens were never labelled directly, and instead stand over large labels indicating their name and origin. Since Spinola’ s type series of *D. panzeri* contains, or at least originally contained, individuals from Greece, Italy, and Egypt, it is not impossible that they became mixed during transfer to their more modern boxes and Baker unintentionally selected one of the European specimens. The lectotype is accompanied by a handwritten label indicating that this specimen comes from Egypt, but this label was not written by Spinola and has been added more recently. Since Baker’ s lectotype designation is valid (because the specimens are genuine syntypes), and as Spinola’ s syntypic series is polytypic and as we have no ability to determine which specimen comes from which country, *D. panzeri* is best retained as a synonym of *D. hirtipes* but with a *terra typica* that is unclear.

Table 1. Dasypoda species recorded from Africa.

Species	Records in Africa	Source
Subgenus Dasypoda Latreille, 1802 s. str.		
Dasypoda albipila Spinola, 1838	Algeria, Egypt	Spinola (1838), Dalla Torre (1896)
Dasypoda dusmeti Quilis, 1928	Morocco, Tunisia	Warncke (1973), Michez et al. (2004 a), Michez (2012),Lhomme et al. (2020)
Dasypoda hirtipes (Fabricius, 1793)	Morocco	Warncke (1973), Michez et al. (2004 a), Michez (2012), Radchenko (2016), Lhomme et al. (2020), Radchenko et al. (2020). The records cited by Michez (2012) and Radchenko et al. (2020) correspond to different misidentified Dasypoda s. str. species.
Dasypoda maura Pérez, 1895* Note: some female specimens of D. maura observed from Morocco present brown hairs intermixed with their overall orange scopa, contrasting with all other Dasypoda s. str. that are thought to present unicolourous scopae (Michez et al. 2004 a , 2004 b ; Radchenko 2016).	Morocco, Algeria	Pérez (1895), Alfken (1931), Maidl (1933), Warncke (1973), Michez et al. (2004a), Louadi et al. (2007), Patiny and Michez (2007), Michez (2012), Lhomme et al. (2020)
Dasypoda oraniensis Pérez, 1895*	Morocco, Algeria	Pérez (1895), Michez et al. (2004 a), Patiny and Michez (2007), Michez (2012), Lhomme et al. (2020)
Dasypoda riftensis Michez & Pauly, 2012*	Ethiopia + Tanzania	Michez and Pauly (2012), A. Pauly (pers. comm.)

Species	Records in Africa	Source
Dasypoda sinuata Pérez, 1895	Canary Islands, Morocco, Algeria,Tunisia, Libya, Egypt	Cockerell (1931), Warncke, 1973, Michez et al. (2004 a), Michez (2012), Shebl et al. (2015), Lhomme et al. (2020)
Subgenus Heterodasypoda Michez, 2004		
Dasypoda rosaella Ghisbain & Wood, sp. nov.*	Morocco, Tunisia	Michez (2003, as Dasypoda albimana auctorum), Radchenko (2017, idem), present study.
Subgenus Megadasypoda Michez, 2004		
Dasypoda visnaga (Rossi, 1790)**	Morocco, Algeria, Tunisia	Warncke (1973), Michez et al. (2004 a), Michez (2012),Lhomme et al. (2020)
Subgenus Microdasypoda Michez, 2004		
Dasypoda brevicornis Pérez, 1895*	Algeria, Tunisia	Pérez (1895), Michez et al. (2004 a), Patiny and Michez (2007), Radchenko et al. (2022)
Dasypoda cingulata Erichson, 1835	Morocco, Algeria	Warncke (1973), Michez et al. (2004 a), Michez (2012),Radchenko et al. (2022)
Dasypoda crassicornis Friese, 1896	Morocco	Warncke (1973), Michez et al. (2004 a), Michez (2012),Radchenko et al. (2022)
Dasypoda schwarzi Radchenko & Michez, 2022*	Morocco, Tunisia	Radchenko et al. (2022)

Species marked with an asterisk (*) are endemic to the continent, with *D. riftensis* being the only pantaloon bee known from Sub-Saharan Africa. Double asterisks (**) indicate that the subgeneric classification of *D. visnaga* requires more in-depth revision.

A request could be submitted to the International Commission for the Zoological Nomenclature to reject Baker’s male lectotype and replace it with the female lectotype (which must come from Egypt since *D. sinuata* does not occur in Sicily or Greece), but since this would then give *D. panzeri* priority over *D. sinuata*, this would lead to nomenclatural instability and is not our favoured approach. Reference to *D. panzeri* having priority over *D. sinuata* in Ghisbain *et al.* (2023a, p. 72) resulted from a misinterpretation of the lectotype of *D. panzeri*, which was thought to be conspecific with the female syntype. Under our current interpretation that maintains the greatest nomenclatural stability, we consider the

terra typica of *D. panzeri* to be unclear, and therefore do not consider *D. hirtipes* to be part of the Egyptian fauna (Table 1).

Updated key to the Dasypoda species of Africa

Females Note 1: the female of *D.* (*Microdasypoda*) *schwarzi* is unknown. Its morphology is expected to be close to those of the consubgeneric species *D.* (*Microdasypoda*) *brevicornis*

and *D.* (*Microdasypoda*) *crassicornis*. Note 2: illustrations of the morphological characters discussed here below are available in Michez *et al.* (2004*a*, 2004*b*). Further specieslevel character pictures are available in the works of Michez and Pauly (2012, for *D. riftensis*) and Radchenko *et al.* (2022, for the North African *Microdasypoda*).

- **1** Protibia with cuticle yellowish. Tergal discs medially hairless and shiny..................*Dasypoda* (*? Megadasypoda*) *visnaga* (**Rossi**) Protibia with cuticle dark. Tergal discs medially at least partially hairy, with the cuticle sculptured..**2**

- **2** Ratio between the length of the maxillary palpus and the galea between 0.5 and 0.75. Cuticle of the galea never shiny between the punctures. Hairs on the marginal parts of S2–S4 forming complete wide bands of dense, semi-erect, and long plumose hairs, which are corkscrew-shaped apically. Scopa typically unicolourous, rarely bicoloured. Scopal hairs conspicuously plumose...............................Subgenus *Dasypoda* **Latreille s. str, 3**
  - Ratio between the maxillary palpus and the galea close to 1 (Fig. 4*a*). Cuticle of the galea either shiny or dull between the punctures (Fig. 4*a*, *c*). Hairs on the marginal parts of the S2–S4 and of the scopa not plumose. Scopa always bicoloured (Fig 3*a*, *k*)..**.9**
- **3** Metatibia (beneath scopa) with a completely orange cuticle. Species from Sub-Saharan Africa ....*Dasypoda* (*Dasypoda*) *riftensis* **Michez & Pauly**

Metatibia with a black cuticle (at most slightly reddish locally on the apical part of the segment). Species from North Africa........**4**

- **4** Scutum entirely covered with ginger hairs..*Dasypoda* (*Dasypoda*) *maura* **Pérez** Hairs on scutum bicoloured, with darker hairs in the centre of the segment **5**

- **5** Clypeus with white hairs, and face with black hairs (at most intermixed with few white–yellow hairs but the overall appearance is black). Even in fresh specimens, apical margin of T4 with the hair band interrupted in the centre...

  - ....*Dasypoda* (*Dasypoda*) *dusmeti* **Quilis** Clypeus with yellowish hairs, and face never entirely black in appearance (e.g. yellowish, or yellowish with black hairs intermixed). In fresh specimens, apical margin of T4 with the hair band continuous in the centre **6**

- **6** Apical fringe of T5 whitish or brown..**7** Apical fringe of T5 black..**.8**

- **7** Larger species (>11 mm). T2–3 with the bands interrupted. Internal face of the mesofemur with the hairs twice as short as the width of the femur......*Dasypoda* (*Dasypoda*) *sinuata* **Pérez** Smaller species (<11 mm). In fresh specimens, T2–3 with the bands continuous. Internal face of the mesofemur with the hairs at least as long as the width of the femur..

- ....*Dasypoda* (*Dasypoda*) *albipila* **Spinola 8** Scutum shagreened between the punctures, dull to weakly shining..........................*Dasypoda* (*Dasypoda*) *hirtipes* (**Fabricius**) Scutum smooth and shiny between punctures.................................

- ....*Dasypoda* (*Dasypoda*) *oraniensis* **Pérez 9** Medio-apical part of the clypeus entirely punctate, punctures separated by <0.5 puncture diameters (Fig 3*f*)..

  - *Dasypoda* (*Heterodasypoda*) *rosaella* **Ghisbain & Wood, sp. nov.** Medio-apical part of the clypeus with a clearly distinct circular area that is shiny and unpunctured...

- ....Subgenus *Microdasypoda* **Michez, 10 10** Hair of the face ginger intermixed with brown hairs...................... ....*Dasypoda* (*Microdasypoda*) *cingulata* **Erichson** Hair on the face including black and white................................**11**

- **11** Hairs on the face white medially and black laterally. Smooth area of the clypeus narrower than (or at most equal to) half of the length of the apical width of the segment...

  - ....*Dasypoda* (*Microdasypoda*) *crassicornis* **Friese** Hairs on the face intermixed black and white. Smooth area of the clypeus clearly broader than half the length of the apical width of the segment.......*Dasypoda* (*Microdasypoda*) *brevicornis* **Pérez**

Males

- **1** Protibia and A3 with cuticle yellowish……………………………………………………………*Dasypoda* (**?** *Megadasypoda*) *visnaga* (**Rossi**) Protibia and A3 with cuticle dark……………………………………………**2**
- **2** Ratio between the length of the maxillary palpus and the galea between 0.5 and 0.75. Apex of S6 with the cuticle distinctively visible through the pilosity. Baso-lateral part of S8 with two small teeth directed backwards. Gonostylus with two lobes linked with a membranous structure Subgenus……*Dasypoda* **Latreille s. str., 3**
    - Ratio between the length of the maxillary palpus and the galea between close to one (Fig. 2*g*). Apex of S6 with the cuticle hidden behind a dense pilosity (Fig. 2*j*). Baso-lateral part of S8 without two small teeth directed backwards. Lobes of the gonostylus not linked with a membranous structure (Fig. 2*k*)………………………**9**
- **3** Metatibia with a completely orange cuticle. Species from Sub-Saharan Africa…………………………………………………………………………
.
    - …………………***Dasypoda*** (*Dasypoda*) *riftensis* **Michez & Pauly** Metatibia with a black cuticle (at most slightly reddish locally on the apical part of the segment). Species from North Africa……**4**
- **4** Apical part of S6 laterally protruding. External lobe of the gonostylus truncated……………*Dasypoda* (*Dasypoda*) *dusmeti* **Quilis** Apical part of S6 laterally flat or nearly flat. External lobe of the gonostylus pointed …………………………………………………………**5**
- **5** Apical section of the inner side of the metatibia distinctively extended by a blade-like structure …………………………………………
- ……………………………………*Dasypoda* (*Dasypoda*) *sinuata* **Pérez** Apical section of the inner side of the metatibia not extended by a blade-like structure……………………………………………………………**6**
- **6** Pilosity of the internal lobe of the gonostylus dense and dark brown……………………………*Dasypoda* (*Dasypoda*) *maura* **Pérez** Pilosity of the internal lobe of the gonostylus sparse and yellow……**7**
- **7** S6 clearly concave apically. A3–4 of subequal length………………….
- ………………………………*Dasypoda* (*Dasypoda*) *oraniensis* **Pérez** S6 flat apically. A3 longer than A4 …………………………………………**8**
- **8** Tegula brown. Tergite discs with a ginger or black pilosity……………………………………*Dasypoda* (*Dasypoda*) *hirtipes* (**Fabricius**)
    - Tegula yellow. Tergite discs with a white pilosity………………………
- ………………………………*Dasypoda* (*Dasypoda*) *albipila* **Spinola 9** S7 apically with two large lateral membranous structures (Fig. 2*k*). Gonostylus with three distinct lobes (Fig. 2*i*), with a scaly surface
    - on the internal lobe…………………………………………………………. ……*Dasypoda* (*Heterodasypoda*) *rosaella* **Ghisbain & Wood, sp. nov.**
- S7 apically without lateral membranous structures. Gonostylus either made of one lobe with a small tooth at the base, or with two lobes……………………Subgenus *Microdasypoda* **Michez, 10**
- **10** Glossa 5 times as long as wide. S6 with apical pilosity directed laterally………*Dasypoda* (*Microdasypoda*) *cingulata* **Erichson** Glossa 2.5–3.5 as times as long as wide. S6 with apical pilosity directed radially …………………………………………………………**11**
- **11** Face with a pure patch of white hairs surrounded by a pure black pilosity. Gonostylus made of one lobe with a small tooth at the base……………*Dasypoda* (*Microdasypoda*) *crassicornis* **Friese** Face with black and white hairs intermixed or completely white. Gonostylus made of two lobes……………………………………………**12**

12 Face with a yellowish pilosity intermixed with black hairs, especially on the paraocular areas. Gonostylus with a dense pubescence on the inner side. External lobe of the gonostylus rounded apically…………*Dasypoda* (*Microdasypoda*) *brevicornis* **Pérez** Face with a white pilosity, except for the vertex and adjacent areas that are intermixed with black hairs. Gonostylus with a sparse pubescence on the inner side. External lobe of gonostylus truncated apically……………………………………………………………………

…*Dasypoda* (*Microdasypoda*) *schwarzi* **Radchenko & Michez**

Discussion

We provide the description of *Dasypoda rosaella* Ghisbain & Wood, sp. nov., a new species of pantaloon bee recorded from Morocco and Tunisia that was previously confused with the European endemic species *D. albimana*. We based our decision to recognise the new taxon on both a UCEbased phylogenomic analysis and a combination of diagnostic morphological characters in both males and females. The allopatric distribution of this new species with its close relatives (*D. albimana* and *D. michezi*) reinforces this hypothesis. Consequently, we now record 13 species of *Dasypoda* on the African continent, with only one of these found in Sub-Saharan Africa (*D. riftensis* Michez & Pauly). Out of the remaining 12 North African species, 6 are endemic to Africa whereas the 6 others also occur in Europe as defined by Rasmont *et al.* (2017). Only one species (*D. hirtipes*) is found in Europe, Africa and Asia.

Taxonomy and ecology

The combination of morphological characters displayed by both females and males of *Dasypoda rosaella* sp. nov. matches all the synapomorphies of the subgenus *Heterodasypoda* proposed by Michez *et al.* (2004*b*). Most specimens examined here were previously identified as *D.* (*Heterodasypoda*) *albimana* and recorded as such in Michez (2003) and subsequent publications. Although the females can generally be differentiated by size (*D. albimana* typically being smaller), we believe that this character should be used with caution. Indeed, solitary bees can vary in size at the intraspecific level only based on the quantity and quality of food they received at their larval stage (e.g. Grula *et al.* 2021), and it is therefore possible that some specimens of *D. rosaella* sp. nov. appear smaller than the average representative of the species. The best characters for differentiating females remain the structure of the tongue, the colour of the hairs on the mesotibia and the colour of the hair tuft on T5. Separating the males of both species is also relatively straightforward based on both the sculpture of the galea and the apex of the external lobe of the gonostylus. The UCE-based phylogenomic analysis confirms the close evolutionary relationship between the European *D. albimana* and *D. michezi* with the African *D. rosaella* sp. nov., as expected morphologically. It further suggests that *D. michezi* is the sister species of *D. rosaella* sp. nov., which is plausible biogeographically, as the overall centre of distribution of *D. michezi* is closer to North Africa than that of *D. albimana.* The UCE-based phylogeny acted as an especially powerful tool for confirming the accuracy of the morphological characters shown in Fig. 4 and therefore stabilising the morphological species concept of the three closely related species. Although all males examined from North Africa display genitalia identical to those of the male individuals sequenced as *D. rosaella* sp. nov., we cannot fully exclude a possible presence of *D. albimana* in Africa, but we consider it unlikely given its restricted distribution in southern France, the northern half of Spain and the Spanish Sierra Nevada. Other representatives of *Dasypoda* (e.g. *D. cingulata, D. crassicornis, D. dusmeti*, *D. hirtipes* and *D. visnaga*) are present both in the Iberian Peninsula and North Africa, showing that both regions share part of their fauna. Further research conducted in North Africa should help elucidate this matter (e.g. Wood 2023*a*, 2023*b*).

As for many melittid bees, *Dasypoda* rely on environments with a relatively specific flora. The subgenus *Heterodasypoda* is predominantly associated with Cistaceae, a trait that is shared with some species belonging to its sister subgenus *Microdasypoda* (Michez *et al.* 2004*b*; Radchenko *et al.* 2022). More work is needed to refine our understanding of the habitats and foraged plants of *D. rosaella* sp. nov. across its distribution in the Maghreb. Other observations of the species would be useful to help delineate more in detail the phenology relative to the altitude specimens are observed at. Based on the identified material, we can estimate that the flight period of *D. rosaella* sp. nov. is from (at least) April to July. Observations in Morocco indicate that *D. rosaella* sp. nov. is not found in Cistaceae-rich habitats, indeed, at the *locus typicus* in the Anti-Atlas, the habitat was predominantly elevated dry steppe between low-intensity agricultural fields (Fig. 5*a*). Flowering Cistaceae were not present, strongly suggesting that *D. rosaella* sp. nov. does not use this botanical family as a major pollen source. Equally, at Oukaïmeden, no flowering Cistaceae could be found, further supporting this hypothesis (Fig. 5*b*). Alternatively, *D. rosaella* sp. nov. could have a generalist diet like *D. albimana*. One of our females was indeed observed visiting a yellow, unidentified Asteraceae, although we could not assess whether this visit was for collecting pollen or solely nectar, particularly since the bee was collected at what we suspect is the very end of its flight period (mid-July).

Northern Africa as a bee-rich subcontinent

The known distribution of *D. rosaella* sp. nov. in Morocco and Tunisia strikingly recalls that of the newly described species *D. schwarzi* (Radchenko *et al.* 2022) and some other non-melittid bees (Patiny and Michez 2007; Wood 2023*c*) and suggests that the species should also be found in Algeria. The new *Dasypoda* described in this work is one of the six *Dasypoda* species endemic to the African continent and the only endemic *Heterodasypoda.*

The Maghreb displays a large variety of environments, from a Mediterranean climate in the north to highly xeric deserts southwards, and from Atlantic climates westwards to subalpine and alpine climates in its interior mountain ranges, these predominantly found in Morocco. Despite the fascinating richness of this subcontinent, North African countries remain relatively poorly investigated in comparison to Southern Europe, and certainly to Northern Europe (Michez *et al.* 2019). Although Morocco is slightly better surveyed than its neighbours (Lhomme *et al.* 2020), new bee species are continuously described or reported as newly recorded from this country (Ortiz-Sánchez and Patiny 2019; Müller 2020; Wood *et al.* 2020; Wood 2023*b*, 2023*c*). This implies that a great deal of survey work is required to fully understand the real diversity of this region and suggests that many species new to science are waiting to be described.

Supplementary material

Supplementary material is available online.

References

- Alfken J (1931) Beitrag zur Kenntnis einiger Bienen von Spanien und Nord-Afrika (Hym.) *Stettiner Entomologische Zeitung* **92**, 52–57. [In German]
- Almeida EAB, Bossert S, Danforth BN, *et al.* (2023) The evolutionary history of bees in time and space. *Current Biology* **33**(16), 3409–3422.e6. doi:10.1016/j.cub.2023.07.005
- Baker DB (2002) A provisional annotated list of the nominal taxa assigned to the genus *Dasypoda* Latreille, 1802, with the description of an additional species (Hymenoptera, Apoidea, Melittidae). *Deutsche Entomologische Zeitschrift* **49**(1), 89–103. doi:10.1002/mmnd. 20020490107
- Bankevich A, Nurk S, Antipov D, *et al.* (2012) *SPAdes*: a new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology* **19**(5), 455–477. doi:10.1089/cmb.2012.0021
- Bartomeus I, Lanuza JB, Wood TJ, *et al.* (2022) Base de datos de abejas ibéricas. *Ecosistemas* **31**(3), 2380–2380. [In Spanish] doi:10.7818/ ECOS.2380
- Blaimer BB, Santos BF, Cruaud A, *et al.* (2023) Key innovations and the diversification of Hymenoptera. *Nature Communications* **14**(1), 1212. doi:10.1038/s41467-023-36868-4
- Bolger AM, Lohse M, Usadel B (2014) *Trimmomatic*: a flexible trimmer for Illumina sequence data. *Bioinformatics* **30**(15), 2114–2120. doi:10.1093/bioinformatics/btu170
- Borowiec ML (2016) *AMAS*: a fast tool for alignment manipulation and computing of summary statistics. *PeerJ* **4**, e1660. doi:10.7717/ peerj.1660
- Borowiec M (2019) *Spruceup*: fast and flexible identification, visualization, and removal of outliers from large multiple sequence alignments. *Journal of Open Source Software* **4**(42), 1635. doi:10.21105/joss.01635
- Bossert S, Murray EA, Almeida EAB, *et al.* (2019) Combining transcriptomes and ultraconserved elements to illuminate the phylogeny of Apidae. *Molecular Phylogenetics and Evolution* **130**, 121–131. doi:10.1016/j.ympev.2018.10.012

- Bossert S, Wood TJ, Patiny S, *et al.* (2022) Phylogeny, biogeography and diversification of the mining bee family Andrenidae. *Systematic Entomology* **47**(2), 283–302. doi:10.1111/syen.12530
- Boustani M, Rasmont P, Dathe HH, *et al.* (2021) The bees of Lebanon (Hymenoptera: Apoidea: Anthophila). *Zootaxa* **4976**(1), 1–146. doi:10.11646/zootaxa.4976.1.1
- Branstetter M (2026) A new bee species of the genus *Dasypoda* from North Africa uncovered by morphology and ultraconserved element phylogenomics (Hymenoptera: Melittidae). *Zenodo* **2026**, version v1. [Dataset, published 26 January 2026] doi:10.5281/zenodo. 18379217
- Branstetter MG, Longino JT, Ward PS, *et al.* (2017*a*) Enriching the ant tree of life: enhanced UCE bait set for genome-scale phylogenetics of ants and other Hymenoptera. *Methods in Ecology and Evolution* **8**(6), 768–776. doi:10.1111/2041-210X.12742
- Branstetter MG, Danforth BN, Pitts JP, *et al.* (2017*b*) Phylogenomic insights into the evolution of stinging wasps and the origins of ants and bees. *Current Biology* **27**(7), 1019–1025. doi:10.1016/j.cub. 2017.03.027
- Branstetter MG, Müller A, Griswold TL, *et al.* (2021) Ultraconserved element phylogenomics and biogeography of the agriculturally important mason bee subgenus *Osmia* (*Osmia*). *Systematic Entomology* **46**(2), 453–472. doi:10.1111/syen.12470
- Brasero N, Ghisbain G, Lecocq T, *et al.* (2021) Resolving the species status of overlooked West-Palaearctic bumblebees. *Zoologica Scripta* **50**(5), 616–632. doi:10.1111/zsc.12486
- Bushnell B (2014) *BBMap*: a fast, accurate, splice-aware aligner. LBNL Report number LBNL-7065E. (Lawrence Berkeley National Laboratory) Available at https://escholarship.org/uc/item/1h3515gn
- Casolari C, Casolari M (1980) ‘Collezione imenotterologica di Massimiliano Spinola.’ (Museo Regionale di Scienze Naturali: Torino, Italy) [In Italian]
- Cockerell T (1931) XXXIV.—Descriptions and records of bees.—CXXVII. *Annals and Magazine of Natural History* **7**, 344–351. doi:10.1080/ 00222933108673321
- Dalla Torre CG (1896) ‘Catalogus hymenopterorum hucusque descriptorum systematicus et synonymicus. Vol. X. Apidae (Anthophila).’ (Engelmann: Lipsiae [Leipzig]) [In Latin]
- De Queiroz K (2007) Species concepts and species delimitation. *Systematic Biology* **56**(6), 879–886. doi:10.1080/10635150701701083
- Drossart M, Gérard M (2020) Beyond the decline of wild bees: optimizing conservation measures and bringing together the actors. *Insects* **11**(9), 649. doi:10.3390/insects11090649
- Dubois A (2003) The relationships between taxonomy and conservation biology in the century of extinctions. *Comptes Rendus Biologies* **326**, 9–21. doi:10.1016/S1631-0691(03)00022-2
- Faircloth BC (2016) *PHYLUCE* is a software package for the analysis of conserved genomic loci. *Bioinformatics* **32**(5), 786–788. doi:10.1093/ bioinformatics/btv646
- Faircloth BC, McCormack JE, Crawford NG, *et al.* (2012) Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. *Systematic Biology* **61**(5), 717–726. doi:10.1093/ sysbio/sys004
- Faircloth BC, Branstetter MG, White ND, *et al.* (2015) Target enrichment of ultraconserved elements from arthropods provides a genomic perspective on relationships among Hymenoptera. *Molecular Ecology Resources* **15**(3), 489–501. doi:10.1111/1755-0998.12328
- Freitas FV, Branstetter MG, Franceschini-Santos VH, *et al.* (2023) UCE phylogenomics, biogeography, and classification of long-horned bees (Hymenoptera: Apidae: Eucerini), with insights on using specimens with extremely degraded DNA. *Insect Systematics and Diversity* **7**(4), 3. doi:10.1093/isd/ixad012
- Garibaldi LA, Steffan-Dewenter I, Winfree R, *et al.* (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* **339**(6127), 1608–1611. doi:10.1126/science.1230200

- Ghisbain G, Michez D (2022) Book review: The bumblebees of the Himalaya –an identification guide, by Paul H. Williams. *Journal of Hymenoptera Research* **93**, 215–221. doi:10.3897/jhr.93.90874
- Ghisbain G, Michez D, Marshall L, *et al.* (2020*a*) Wildlife conservation strategies should incorporate both taxon identity and geographical context –further evidence with bumblebees. *Diversity and Distributions* **26**(12), 1741–1751. doi:10.1111/ddi.13155
- Ghisbain G, Lozier JD, Rahman SR, *et al.* (2020*b*) Substantial genetic divergence and lack of recent gene flow support cryptic speciation in a colour polymorphic bumble bee (*Bombus bifarius*) species complex. *Systematic Entomolog* **45**(3), 635–652. doi:10.1111/syen.12419
- Ghisbain G, Martinet B, Wood TJ, *et al.* (2021*a*) A worthy conservation target? Revising the status of the rarest bumblebee of Europe. *Insect Conservation and Diversity* **14**(5), 661–674. doi:10.1111/icad.12500
- Ghisbain G, Radchenko VG, Cejas D, *et al.* (2021*b*) Assessment and conservation status of an endemic bee in a diversity hotspot (Hymenoptera, Melittidae, *Dasypoda*). *Journal of Hymenoptera Research* **81**, 127–142. doi:10.3897/jhr.81.60811
- Ghisbain G, Rosa P, Bogusch P, *et al.* (2023*a*) The new annotated checklist of the wild bees of Europe (Hymenoptera: Anthophila). *Zootaxa* **5327**(1), 1–147. doi:10.11646/zootaxa.5327.1.1
- Ghisbain G, Flaminio S, Radchenko VG, *et al.* (2023*b*) *Dasypoda delectabilis* sp. nov., a morphologically intriguing pantaloon bee species from south-eastern Iran (Hymenoptera: Melittidae). *Zoology in the Middle East* **69**, 262–269. doi:10.1080/09397140.2023.2233762
- Ghisbain G, Michez D, Rosa P, *et al.* (2023*c*) Unexpected discovery of a near cryptic *Dasypoda* species in southern Spain (Hymenoptera: Melittidae). *Osmia* **11**, 27–38. doi:10.47446/OSMIA11.6
- Ghisbain G, Thiery W, Massonnet F, *et al.* (2024) Projected decline in European bumblebee populations in the Twenty-First Century. *Nature* **628**(8007), 337–341. doi:10.1038/s41586-023-06471-0
- Ghisbain G, Rosa P, Bogusch P, Brau T, Carion F, Manincor ND, Devalez J, Dorchin A, Flaminio S, Greil H, Hölzler G, Hopfenmüller S, Kasparek M, Kuhlmann M, Le Divelec R, Litman J, Maugendre A, Michez D, Müller A, Ortiz-Sánchez FJ, Praz C, Radchenko VG, Rasmont P, Risch S, Roberts SPM, Santerre R, Schmid-Egger C, Sentil A, Straka J, Williams PH, Wood TJ, Reverté S (2025) The new annotated checklist of the wild bees of Europe (Hymenoptera: Anthophila)—version 2025. *Zootaxa* **5736**, 1–126. doi:10.11646/ zootaxa.5736.1.1
- Grab H, Branstetter MG, Amon N, *et al.* (2019) Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. *Science* **363**(6424), 282–284. doi:10.1126/science.aat6016
- Grula CC, Rinehart JP, Greenlee KJ, *et al.* (2021) Body size allometry impacts flight-related morphology and metabolic rates in the solitary bee *Megachile rotundata*. *Journal of Insect Physiology* **133**, 104275. doi:10.1016/j.jinsphys.2021.104275
- Guindon S, Dufayard J-F, Lefort V, *et al.* (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of *PhyML* 3.0. *Systematic Biology* **59**(3), 307–321. doi:10.1093/sysbio/syq010
- Harris R (2007) Improved pairwise alignment of genomic DNA. PhD thesis, Pennsylvania State University, University Park, PA, USA. Available at https://www.proquest.com/openview/bc77cca0fb9390b44b9ef572fb574322/1?pq-origsite=gscholar&cbl=18750
- Hoang DT, Chernomor O, von Haeseler A, *et al.* (2018) *UFBoot2*: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* **35**(2), 518–522. doi:10.1093/molbev/msx281
- Kalyaanamoorthy S, Minh BQ, Wong TKF, *et al.* (2017) *ModelFinder*: fast model selection for accurate phylogenetic estimates. *Nature Methods* **14**(6), 587–589. doi:10.1038/nmeth.4285
- Katoh K, Standley DM (2013) *MAFFT* multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**(4), 772–780. doi:10.1093/molbev/mst010

- LeBuhn G, Vargas Luna J (2021) Pollinator decline: what do we know about the drivers of solitary bee declines? *Current Opinion in Insect Science* **46**, 106–111. doi:10.1016/j.cois.2021.05.004
- Lhomme P, Michez D, Christmann S, *et al.* (2020) The wild bees (Hymenoptera: Apoidea) of Morocco. *Zootaxa* **4892**(1), 1–159. doi:10.11646/zootaxa.4892.1.1
- Lhomme P, Williams SD, Ghisbain G, *et al.* (2021) Diversification pattern of the widespread Holarctic cuckoo bumble bee, *Bombus flavidus* (Hymenoptera: Apidae): the East Side story. *Insect Systematics and Diversity* **5**(2), 5. doi:10.1093/isd/ixab007
- Louadi K, Maghni N, Benachour K, *et al.* (2007) Présence de *Dasypoda maura* Perez, 1895, en Algérie. *Bulletin de la Société entomologique de France* **112**(2), 252. [In French] doi:10.3406/bsef.2007.16429
- Mace GM (2004) The role of taxonomy in species conservation. *Philosophical Transactions of the Royal Society of London –B. Biological Sciences* **359**(1444), 711–719. doi:10.1098/rstb.2003.1454
- Maidl F (1933) Verzeichnis der von Univ.Professor Dr. Franz Werner und Prof. Dr. Richard Ebner 1930 in Marokko gesam melten Sphegiden (Hym.) und Scoliiden (Hym.). Mit Beschreibung einer neuen Art und einem Vergencies der übrigen in Marokko gesammelten Hymenopteren. *Konowia* **12**, 121–128. [In German]
- Michener C (2007) ‘The bees of the world’, 2nd edn. (The Johns Hopkins University Press: Baltimore, MD, USA)
- Michez D (2002) *Dasypoda patinyi* sp. nov. (Hymenoptera, Apoidea, Melittidae), espèce nouvelle récoltée en Syrie. *Linzer Biologische Beiträge* **34**(1), 737–742. [In French]
- Michez D (2003) *Dasypoda albimana* Pérez, 1905 (Hymenoptera, Apoidea, Melittidae), espèce nouvelle pour la France et le Maroc. *Bulletin de la Société entomologique de France* **108**(1), 61–64. [In French] doi:10.3406/bsef.2003.16921
- Michez D (2005) *Dasypoda* (*Megadasypoda*) *intermedia* spec. nov. (Hymenoptera: Apoidea: Melittidae), a new species from Iran. *Zoologische Mededelingen* **79-2**(6), 123–127.
- Michez D (2012) Atlas of the European Bees: genus *Dasypoda*. (Mons, Gembloux STEP Project, Atlas Hymenoptera) Available at http:// www.atlashymenoptera.net/page.aspx?id=195
- Michez D, Pauly A (2012) A new species of the Palaearctic genus *Dasypoda* Latreille 1802 (Hymenoptera: Dasypodaidae) from the Great Rift Valley in Ethiopia. *Zootaxa* **3181**(1), 63. doi:10.11646/zootaxa.3181.1.5
- Michez D, Terzo M, Rasmont P (2004*a*) Révision des espèces ouestpaléarctiques du genre *Dasypoda* Latreille 1802 (Hymenoptera, Apoidea, Melittidae). *Linzer Biologische Beiträge* **36**, 847–900. [In French]
- Michez D, Terzo M, Rasmont P (2004*b*) Phylogénie, biogéographie et choix floraux des abeilles oligolectiques du genre *Dasypoda* Latreille 1802 (Hymenoptera: Apoidea: Melittidae). *Annales de La Société Entomologique de France (N.S.)* **40**(3–4), 421–435. [In French] doi:10.1080/00379271.2004.10697431
- Michez D, Rasmont P, Terzo M, *et al.* (2019) ‘Bees of Europe. Hymenoptera of Europe.’ (NAP Editions: Verrières-le-Buisson, France)
- Michez D, Radchenko VG, Macadam C, Wilkins V, Raser J, Axel Hochkirch A (2023) ‘Teasel-plant specialised bees in Europe –Conservation action plan 2023–2030.’ (Publications Office of the European Union: Luxembourg) doi:10.2779/191765
- Michez D, Boustani M, Sentil A, Benrezkallah J, de Manincor N, Wood TJ, Álvarez Fidalgo P, Aubert M, Bellotto V, Biella P, Bogusch P, Bosch J, Brau T, Browne K,Carion F, Castro L, Cederberg B, Clay J, Debont T, Bila Dubaić J, Dall’ Olio R, Dellicour S, Devalez J, Devorsine R, Dufrêne E, De la Rúa P, De Tandt B, Evrard D, Flaminio S, Fiordaliso W, Fontana P, Gadoum S, Galbany Casals M, Gaspar H, Gekière A, Gérard M, Geslin B, Kasparek M, Kierat J, Kohl PL, Kuhlmann M, Kryger P, Leclercq N, Le Divelec R, Lemaire S, Lescot S, Lhomme P, Litman J, Marshall L, McCormack GP, Moro A, Mudri Stojnić S, Ockermueller E, Oleksa A, Ortiz-Sánchez FJ, Patiny S, Paukkunen J, Perrard A, Petanidou T, Pinto MA, Potts SG, Praz C, Put SCL, Radchenko VG, Rasmont P, Requier F, Reverté S, Risch S, Rogenstein S, Rosa P, Ruiz C, Rutschmann B, Santerre R, Smit

J, Straka J, Thulier J, Tourbez C, Trottet A, Vereecken NJ, Williams PH, Winter E, Zimmermann D, Ghisbain G (2026) 'Measuring the pulse of European biodiversity using the Red List. European Red List of Bees.' (European Commission: Brussels, Belgium)

- Minh BQ, Nguyen MAT, von Haeseler A (2013) Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution* **30**(5), 1188–1195. doi:10.1093/molbev/mst024
- Minh BQ, Schmidt HA, Chernomor O, *et al.* (2020) *IQ-TREE 2*: new models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* **37**(5), 1530–1534. doi:10.1093/molbev/msaa015
- Müller A (2020) Palaearctic *Osmia* bees of the subgenera *Hemiosmia*, *Tergosmia* and *Erythrosmia* (Megachilidae, Osmiini): biology, taxonomy and key to species. *Zootaxa* **4778**(2), 201–236. doi:10.11646/zootaxa.4778.2.1
- Nguyen L-T, Schmidt HA, von Haeseler A, *et al.* (2015) *IQ-TREE*: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* **32**(1), 268–274. doi:10.1093/ molbev/msu300
- Nieto A, De Meulemeester T, Manuel, *et al.* (2014) 'European red list of bees' . (Publications Office of the European Union) Available at https://data.europa.eu/doi/10.2779/51181
- Odanaka KA, Branstetter MG, Tobin KB, *et al.* (2022) Phylogenomics and historical biogeography of the cleptoparasitic bee genus *Nomada* (Hymenoptera: Apidae) using ultraconserved elements. *Molecular Phylogenetics and Evolution* **170**, 107453. doi:10.1016/j.ympev. 2022.107453
- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* **120**(3), 321–326. doi:10.1111/j.1600-0706. 2010.18644.x
- Ornosa C, Ortiz-Sánchez FJ (1998) Nuevos datos sobre la hembra de *Dasypoda albimana* Pérez, 1905, y *Dasypoda dusmeti niveocincta* Noskiewicz, 1959 syn. nov. (Hymenoptera, Apoidea, Melittidae). *Zoologica Baetica* **9**, 131–138. [In Spanish]
- Orr MC, Branstetter MG, Straka J, *et al.* (2022) Phylogenomic interrogation revives an overlooked hypothesis for the early evolution of the bee family Apidae (Hymenoptera: Apoidea), with a focus on the subfamily Anthophorinae. *Insect Systematics and Diversity* **6**(4), 7. doi:10.1093/isd/ixac022
- Ortiz-Sánchez FJ, Patiny S (2019) A new species of *Borgatomelissa* Patiny 2000 from eastern Morocco: *Borgatomelissa flavimaura* n. sp. (Hymenoptera, Andrenidae). *Annales de La Société Entomologique de France (N.S.)* **55**(5), 454–457. doi:10.1080/00379271.2019.1652115
- Patiny S, Michez D (2007) Biogeography of bees (Hymenoptera, Apoidea) in Sahara and the Arabian deserts. *Insect Systematics & Evolution* **38**, 19–34. doi:10.1163/187631207788784012
- Panzer GWF (1793) 'Favnae insectorvm Germanicae initia, oder, Deutschlands Insecten. Erster Iahrgang. I–XII. Heft.' (Felsecker: Nürnberg) [In German]
- Pérez J (1895) 'Espèces nouvelles de Mellifères de Barbarie (diagnose préliminaire).' (Gounouilhou: Bordeaux, France) [In French]
- Pérez J (1905) Espèces nouvelles d'Hyménoptères de Catalogne. *Butlletí de la Institució Catalana d'Història Natural* **5**(6), 81–88. [In French]
- Radchenko VG (2016) A new widespread European bee species of the genus *Dasypoda* Latreille (Hymenoptera, Apoidea). *Zootaxa* **4184**(3), 491. doi:10.11646/zootaxa.4184.3.4
- Radchenko VG (2017) A new bee species of the genus *Dasypoda* Latreille (Hymenoptera, Apoidea) from Portugal with comparative remarks on the subgenus *Heterodasypoda* Michez. *Zootaxa* **4350**(1), 164–176. doi:10.11646/zootaxa.4350.1.10

- Radchenko VG, Ghisbain G, Michez D (2019) Redescription of three rare species of *Dasypoda* bees with first description of *D. iberica* and *D. tibialis* females (Hymenoptera, Apoidea, Melittidae). *Zootaxa* **4700**(3), 326–344. doi:10.11646/zootaxa.4700.3.2
- Radchenko VG, Tomozii B, Ghisbain G, *et al.* (2020) New data on the morphology and distribution of the cryptic species *Dasypoda morawitzi* Radchenko 2016 (Hymenoptera: Melittidae) with corrections to the diagnosis of *Dasypoda* s. str. *Annales de La Société Entomologique de France* **56**(6), 455–470. doi:10.1080/00379271. 2020.1841570
- Radchenko V, Ghisbain G, Michez D (2022) A new bee species of the genus *Dasypoda* Latreille (Hymenoptera, Apoidea) from Northwest Africa with comparative remarks on the subgenus *Microdasypoda* Michez. *Zootaxa* **5188**, 74–86. doi:10.11646/zootaxa.5188.1.4
- Rasmont P, Devalez J, Pauly A, *et al.* (2017) Addition to the checklist of IUCN European wild bees (Hymenoptera: Apoidea). *Annales de La Société Entomologique de France* **53**(1), 17–32. doi:10.1080/00379271.2017. 1307696
- Rasmont P, Ghisbain G, Terzo M (2021) 'Bumblebees of Europe and neighbouring regions. Hymenoptera of Europe.' (NAP Editions: Verrieres-le-Buisson, France)
- Ratnasingham S, Hebert PD (2007) BOLD: the barcode of life data system. *Molecular Ecology Notes* **7**(3), 355–364. doi:10.1111/j.1471-8286. 2007.01678.x
- Reverté S, Miličić M, Ačanski J, *et al.* (2023) National records of 3000 European bee and hoverfly species: a contribution to pollinator conservation. *Insect Conservation and Diversity* **16**(6), 758–775. doi:10.1111/icad.12680
- Shebl MA, Patiny S, Michez D (2015) Supplementary note on the solitary bee fauna from the Suez Canal region of Egypt (Hymenoptera: Apoidea). *Journal of Melittology* (47), 1–5. doi:10.17161/jom.v0i47.4835
- Spinola M (1838) Compte rendu des Hyménoptères recueillis par M. Fischer pendant son voyage en Égypte, et communiqués par M. le Docteur Waltl à Maximilien Spinola. *Annales de la Société entomologique de France* **7**(4), 437–546. [In French]
- Stecher G, Tamura K, Kumar S (2020) Molecular Evolutionary Genetics Analysis (*MEGA*) for macOS. *Molecular Biology and Evolution* **37**(4), 1237–1239. doi:10.1093/molbev/msz312
- Talavera G, Castresana J (2007) Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology* **56**(4), 564–577. doi:10.1080/10635150701472164
- Tagliacollo VA, Lanfear R (2018) Estimating improved partitioning schemes for ultraconserved elements. *Molecular Biology and Evolution* **35**(7), 1798–1811. doi:10.1093/molbev/msy069
- Tamura K, Stecher G, Kumar S (2021) *MEGA11*: Molecular Evolutionary Genetics Analysis version 11. *Molecular Biology and Evolution* **38**(7), 3022–3027. doi:10.1093/molbev/msab120
- Vogel Ely C, Bordignon SAL, Trevisan R, Boldrini II (2017) Implications of poor taxonomy in conservation. *Journal for Nature Conservation* **36**, 10–13. doi:10.1016/j.jnc.2017.01.003
- Warncke K (1973) Die westpaläarktische Arten der Bienen Familie Melittidae (Hymenoptera). *Polskie Pismo Entomologiczne* **43**, 97–126. [In German]
- Williams PH, Brown MJF, Carolan JC, *et al.* (2012) Unveiling cryptic species of the bumblebee subgenus *Bombus* s. str. worldwide with *COI* barcodes (Hymenoptera: Apidae). *Systematics and Biodiversity* **10**(1), 21–56. doi:10.1080/14772000.2012.664574
- Williams PH, Berezin MV, Cannings SG, *et al.* (2019) The arctic and alpine bumblebees of the subgenus *Alpinobombus* revised from integrative assessment of species' gene coalescents and morphology (Hymenoptera, Apidae, *Bombus*). *Zootaxa* **4625**(1), 1–68. doi:10.11646/zootaxa.4625.1.1

- Williams PH, Altanchimeg D, Byvaltsev A, *et al.* (2020) Widespread polytypic species or complexes of local species? Revising bumblebees of the subgenus *Melanobombus* world-wide (Hymenoptera, Apidae, *Bombus*). *European Journal of Taxonomy* **719**(1), 1–120. doi:10.5852/ ejt.2020.719.1107
- Williams PH, An J, Dorji P, *et al.* (2023) Bumblebees with big teeth: revising the subgenus *Alpigenobombus* with the good, the bad and the ugly of numts (Hymenoptera: Apidae). *European Journal of Taxonomy* **892**, 1–65. doi:10.5852/ejt.2023.892.2283
- Winfree R (2010) The conservation and restoration of wild bees. *Annals of the New York Academy of Sciences* **1195**(1), 169–197. doi:10.1111/j. 1749-6632.2010.05449.x
- Wood TJ (2023*a*) The genus *Andrena* Fabricius, 1775 in the Iberian Peninsula (Hymenoptera, Andrenidae). *Journal of Hymenoptera Research* **96**, 241–484. doi:10.3897/jhr.96.101873
- Wood TJ (2023*b*) Bee species newly recorded for the Moroccan fauna, including two new species of *Ammobatoides* and *Thyreus* (Hymenoptera: Anthophila). *Annales de la Société entomologique de France* **59**(3), 177–203. doi:10.1080/00379271.2023.2215216
- Wood TJ (2023*c*) Revisions to the *Andrena* fauna of north-western Africa with a focus on Morocco (Hymenoptera: Andrenidae). *European Journal of Taxonomy* **916**, 1–85. doi:10.5852/ejt.2023.916.2381
- Wood TJ, Michez D, Cejas D, *et al.* (2020) An update and revision of the *Andrena* fauna of Morocco (Hymenoptera, Apoidea, Andrenidae) with the description of eleven new North African species. *ZooKeys* **974**, 31–92. doi:10.3897/zookeys.974.54794
- Wood TJ, Ghisbain G, Michez D, *et al.* (2021) Revisions to the faunas of *Andrena* of the Iberian Peninsula and Morocco with the descriptions of four new species (Hymenoptera: Andrenidae). *European Journal of Taxonomy* **758**, 147–193. doi:10.5852/ejt.2021.758.1431
- Woodard SH, Federman S, James RR, *et al.* (2020) Towards a US national program for monitoring native bees. *Biological Conservation* **252**, 108821. doi:10.1016/j.biocon.2020.108821
- Wu YR (1978) 中国准蜂科的研究及新种记述 (膜翅目: 蜜蜂总科) [A study of Chinese Melittidae with description of new species (Hymenoptera: Apoidea)]. 昆虫学报 *[Acta Entomologica Sinica]* **21**, 419–428. [In Chinese]
- Wu YR (2000) '中国动物志·昆虫纲 第二十卷 膜翅目 油蜂科 蜜蜂科 [Fauna Sinica. Insecta, Vol. 20: Hymenoptera: Melittidae, Apidae].' (Science Press: Beijing, PR China) [In Chinese with English summary]
- Zattara EE, Aizen MA (2021) Worldwide occurrence records suggest a global decline in bee species richness. *One Earth* **4**(1), 114–123. doi:10.1016/j.oneear.2020.12.005
- Zhang C, Mirarab S (2022) Weighting by gene tree uncertainty improves accuracy of quartet-based species trees. *Molecular Biology and Evolution* **39**(12), msac215. doi:10.1093/molbev/msac215
- Zhang C, Rabiee M, Sayyari E, *et al.* (2018) *ASTRAL-III*: polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinformatics* **19**(6), 153. doi:10.1186/s12859-018-2129-y
- Zhang C, Nielsen R, Mirarab S (2025) *ASTER*: a package for large-scale phylogenomic reconstructions. *Molecular Biology and Evolution* **42**(8), msaf172. doi:10.1093/molbev/msaf172

Data availability. All UCE sequence data have been deposited in NCBI under BioProject number PRJNA1149058. Extracted DNA barcodes have been deposited in GenBank. See Supplementary Table S3 for Accession numbers. Assembly contig files, DNA alignments and tree files have been deposited in *Zenodo* (Branstetter 2026).

Conflicts of interest. The authors declare that they have no conflicts of interest.

Declaration of funding. The research leading to this publication received funds from the Fonds de la Recherche Scientifique –FNRS (Brussels, Belgium) and 'The support of the priority research areas development of Ukraine' , KPKVK 6541230. T. J. Wood was funded by a F.R.S.-FNRS grant 'Chargé de recherches' . G. Ghisbain, V. G. Radchenko and D. Michez are partly funded by the European project ORBIT ('Developing resources for European bee inventory and taxonomy') contract number 09.029901/2021/848268/SER/ENV.D.2 (European Commission, DG Environment). Michael G. Branstetter is supported by the US Department of Agriculture (project number

2080-30500-001-000D) and the US National Science Foundation (DEB number 2127744). P. Álvarez Fidalgo is supported by the project TED2021-130795B-I00 (MCIU/ACI/UE –projects oriented towards the Ecological and Digital Transition) and by a work contract as technical staff funded by the Ministerio de Ciencia e Innovación of Spain (reference number PTA2020-018923-I).

Acknowledgements. We warmly thank Esther Ockermüller and Martin Schwarz (OÖLM) and Frederique Bakker (RMNH) for giving us access to their collections. We thank Mercedes París, curator of the collection of MNCN, for giving us access to the type of *Dasypoda bolivari*. We thank Antoine Gekière for his help in improving Fig. 1. We thank Erin Krichilsky and Kerrigan Tobin for assistance with molecular work. USDA is an equal opportunity provider and employer.

- **Author affiliations** A Laboratory of Zoology, Research Institute for Biosciences, University of Mons, Place du Parc 20, BE-7000 Mons, Belgium. Email: denis.michez@umons.ac.be; thomasjames.wood@umons.ac.be
- B US Department of Agriculture, Agricultural Research Service, Pollinating Insects Research Unit, Utah State University, Logan, UT 84322, USA. Email: michael.branstetter@usda.gov
- C Institute for Evolutionary Ecology of the National Academy of Sciences of Ukraine, acad. Lebedev, 37, UA-03143 Kyiv, Ukraine. Email: rvg@nas.gov.ua
- D Museo Nacional de Ciencias Naturales (MNCN-CSIC), Colección de Entomología, c./José Gutiérrez Abascal 2, E-28006 Madrid, Spain. Email: pilucaaf@gmail.com
- E Naturalis Biodiversity Center, Darwinweg 2, NL-2333 CR Leiden, Netherlands. Email: thomas.wood@naturalis.nl