



Bee species newly recorded for the Moroccan fauna, including two new species of *Ammobatoides* and *Thyreus* (Hymenoptera: Anthophila)

Thomas J. Wood

To cite this article: Thomas J. Wood (2023): 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* (N.S.), DOI: [10.1080/00379271.2023.2215216](https://doi.org/10.1080/00379271.2023.2215216)

To link to this article: <https://doi.org/10.1080/00379271.2023.2215216>



Published online: 23 Jun 2023.



Submit your article to this journal [↗](#)



View related articles [↗](#)



View Crossmark data [↗](#)

Bee species newly recorded for the Moroccan fauna, including two new species of *Ammobatoides* and *Thyreus* (Hymenoptera: Anthophila)

Thomas J. Wood 

University of Mons, Research Institute for Biosciences, Laboratory of Zoology, Place du parc 20, 7000, Mons, Belgium

(Accepté le 15 mai 2023; publié en ligne le 23 juin 2023)

Summary. Morocco has a large and species-rich bee fauna, but due to its large size and diversity of habitats, it remains understudied. Expeditions during 2022 discovered 16 new species for the country, including several very rarely collected or poorly studied taxa. The female of *Thyreus mauretaniensis* (Strand, 1911) is described for the first time, and *Melitturga (Australomelitturga) rubricata* Morice, 1916 is rediscovered and confirmed as a valid species; a female specimen is designated as a neotype for this taxon. Additionally, two new species of brood parasitic bees were discovered: *Ammobatoides schwarzi* n. sp. is described from southern Morocco where it is probably the parasite of *Melitturga (Australomelitturga) albescens* Pérez, 1895, and *Thyreus rasmonti* n. sp. is described from south-western Morocco where it likely parasitises *Anthophora (Paramegilla)* species. *Lasioglossum (Evyllaesus) marginatum* (Brullé, 1832) is confirmed as present in Morocco in the Middle Atlas. Additional data are presented on the ecology and taxonomy of poorly known species. These findings further emphasise the understudied nature of both the Moroccan and broader North African bee fauna.

Résumé. Abeilles nouvellement signalées pour la faune marocaine, avec deux nouvelles espèces d'*Ammobatoides* et de *Thyreus* (Hymenoptera : Anthophila). Le Maroc présente une faune apicole importante et riche en espèces, mais reste très peu étudié en raison de sa grande superficie et de la diversité de ses habitats. Des expéditions menées en 2022 ont permis de découvrir 16 nouvelles espèces pour le pays, dont plusieurs taxons très rarement collectés ou peu étudiés. La femelle de *Thyreus mauretaniensis* (Strand, 1911) est décrite pour la première fois, *Melitturga (Australomelitturga) rubricata* Morice, 1916 est redécouverte et confirmée comme espèce valide ; un spécimen femelle est désigné comme un néotype de ce taxon. Deux nouvelles espèces d'abeilles parasites du couvain ont été découvertes : *Ammobatoides schwarzi* n. sp. est décrite du sud du Maroc où elle parasite probablement *Melitturga (Australomelitturga) albescens* Pérez, 1895, et *Thyreus rasmonti* n. sp. est décrite du sud-ouest du Maroc où elle parasite probablement des espèces du sous-genre *Anthophora (Paramegilla)*. Des données supplémentaires sont présentées sur l'écologie et la taxonomie d'espèces peu connues de ce pays. Ces résultats soulignent la nature peu étudiée de la faune apicole marocaine et plus largement de la faune d'abeilles nord-africaine.

<https://zoobank.org/References/883CD05E-9EAA-4CA5-8CB4-80183BD4DC83>

Keywords: North Africa; taxonomy; DNA barcoding; solitary bees; broodparasite

Morocco is a large country in north-western Africa bordering the Atlantic Ocean to the west, the Mediterranean Sea to the north, and the Sahara Desert to the south. These varied biogeographical influences have shaped a biodiverse flora and fauna, including a species-rich bee fauna that approaches 1000 species (Lhomme et al. 2020). During several expeditions in 2022 to collect material as part of ongoing studies to revise the Moroccan *Andrena* fauna, it was possible to collect in excess of 500 bee species from Morocco. Though the national fauna has been recently revised (Lhomme et al. 2020), some 16 of these bee species have not previously been recorded in

Morocco. Moreover, many are extremely rare and have not been studied, and so their ecologies are not clear. Some are known only from one sex or only from the type series. In addition, a new *Ammobatoides* Radoszkowski, 1867 species was discovered in dry rocky habitats in southern Morocco, and a new *Thyreus* Panzer, 1806 species was discovered in mountainous habitats in south-western Morocco. The opportunity is taken here to describe these new species, to report species newly recorded for Morocco, to describe the alternate sex for poorly known taxa, and also to detail the ecology or taxonomy of understudied species. None of the newly reported

Email: thomasjames.wood@umons.ac.be

© 2023 Société entomologique de France

species belong to the genus *Andrena*; *Andrena* species newly recorded for Morocco will be dealt with in an upcoming dedicated publication.

Methods

Bee species were collected in Morocco between March and July 2022. For descriptions, morphological terminology follows Michener (2007). The following abbreviations are used: A = antennal segments, S = metasomal sterna, and T = metasomal terga. Specimens were measured from the centre of the clypeus at the front of the head to the apical tip of the metasoma to the nearest 0.5 mm. Photographs were taken using an Olympus E-M1 Mark II with a 60 mm macro lens. Additional close-ups were taken with the addition of a Mitutoyo M Plan Apo 5X infinity corrected objective lens. Photographs were stacked using Helicon Focus B (HeliconSoft, Kharkiv, Ukraine) and plates were prepared in GNU Image Manipulation Program (GIMP) 2.10. Post-processing of some images was made in Photoshop Elements (Adobe Systems, San Jose, California, USA) in order to improve lighting to highlight specific characters.

DNA barcoding

For *Thyreus* and Dioxyine species, Moroccan and Spanish specimens were barcoded to investigate taxon relationships. For genetic barcoding, a single midleg was removed from pinned specimens and sent to the Canadian Center for DNA barcoding (CCDB) in Guelph, Canada, for DNA extraction and sequencing (Ivanova et al. 2006). Specimens were sequenced following standardised high-throughput protocols. The BeeCox1F1 primer was used (Bleidorn & Henze 2021) to target the COI-5 region. All sequences are published on the Barcode of Life Database (BOLD). Sequences were aligned using MAFFT (Kato & Standley 2013). Aligned sequences were analysed in Seaview (Gouy et al. 2010) using a maximum likelihood analysis which was run with 1000 bootstraps. Intra- and interspecific distances were calculated using MEGA-X (Kumar et al. 2018). The phylogenetic tree was supplemented with additional published sequences (e.g. Schmidt et al. 2015) that were downloaded from Genbank and the Barcode of Life Data System. The tree was also significantly enriched with sequences produced by the Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO, Portugal) as part of a collaboration to barcode the Portuguese bee fauna that will be published soon, and sequences will be available on BOLD. Sequences beginning with the code 'IBIHM' were generated by CIBIO. Sequences beginning with the code 'WPATW' were generated directly for this publication, and are released on the Barcode of Life Data System (<http://www.boldsystems.org>) as part of the dataset "DS-KLEPTMAR" (<http://dx.doi.org/10.5883/DS-KLEPTMAR>).

Abbreviations

AMC Andreas Müller personal collection, Wädenswil, Switzerland;
OÖLM Oberösterreiches Landesmuseum, Linz, Austria;
RMNH Naturalis Biodiversity Center, Leiden, the Netherlands;
SMFD Naturmuseum Senckenberg, Frankfurt am Main, Germany;
TJWC Thomas J. Wood personal collection, Mons, Belgium

Results

Ammobates (Ammobates) rufiventris Latreille, 1809

Material examined

Morocco. 1♀, Marrakech-Safi, Oukaimeden, 1 km E, steppe, 2500 m, 31.2091°N 7.8423°W, 11.VII.2022, leg. T.J. Wood (TJWC).

Remarks

Baldock et al. (2018) suggested *Tetralonia strigata* (Lepeletier, 1841) as a possible host. At the Oukaimeden site, two females and two males of *T. strigata* were also collected, supporting this tentative host association.

Distribution

Morocco, Algeria, Tunisia, Portugal, Spain, Italy (Kuhlmann et al. 2014).

Ammobatoides schwarzi n. sp.

Type material

Holotype. ♂, Morocco, Drâa-Tafilalet, Ouarzazate, P1507, 3 km SSE Irhels [also written as Ighels], 30.6993°N 7.0721°W, 12.IV.2022, leg. T.J. Wood (OÖLM).

Paratype. 1♀, Drâa-Tafilalet, Tazenakht, R108, 15 km E Tazenakht, 30.5333°N 7.0811°W, 17.IV.2022, leg. T.J. Wood (OÖLM).

Description

Female. *Body length:* 9 mm (Figure 1A).

Head: Dark, 1.3 times wider than long (Figure 1B). Clypeus domed, densely punctate over its basal 4/5ths, punctures confluent, margins slightly raised; apical 1/5th smooth and shining, impunctate. Labrum elongate, more or less rounded rectangular, slightly narrower apically than basally; approximately 2.5 times longer than basal breadth (Figure 1C). Surface of labrum with granular shagreen over majority of area, weakly shining, basal 1/6th strongly and densely punctate, punctures separated by <0.5 puncture diameters, with weak and sparse bristles; labrum basally above mandibles with strongly produced rounded projections, medially emarginate (Figure 1B, C). Gena narrower than width of compound eye; ocelloccipital distance 2.5 times diameter of lateral ocellus. Face predominantly white haired, forming hair patches on paraocular areas and clypeus; gena ventrally, frons, and vertex with sparse short black hairs. Antennae dark, A3 long, slightly shorter than A4 + 5, A4-12 all clearly longer than broad.

Mesosoma: Scutum and scutellum densely punctate, punctures separated by <0.5–0.5 puncture diameters, underlying surface smooth and shining (Figure 1E). Parapsidal lines long, extending 70% of length of scutum. Scutellum medially with longitudinal impression, thus produced into two rounded tubercles. Mesepisternum in dorsal half with dense patch of whitish pubescence, obscuring underlying surface. Mesepisternum in ventral half, scutum and scutellum and posterior face of propodeum with short black hairs. Legs dark, pubescence dark brown to black; outer surface of hind tibiae with sparse white pubescence. Tarsal claws with strong, apically truncate rectangular inner tooth. Wings weakly infusate over entire surface, pale hairs adjacent to veins Rr-m and 2m-cu and marginal and 1st cubital cells. 1st submarginal long, almost twice length of 2nd submarginal cell.

Metasoma: Terga dark, densely and uniformly punctate over entire surface, punctures separated by <0.5 puncture diameters, underlying surface shagreened, weakly shining (Figure 1G). T1–4 laterally with dense patches of white pubescence, obscuring underlying surface, widely separated on T1–3, on T4 separated by at least 3 times diameter of flagellum. T5 medially with weakly longitudinal raised ridge, with denser granular shagreen than surrounding punctures.

Male. *Body length*: 10 mm (Figure 2A).

Head: Dark, 1.3 times wider than long (Figure 2B). Clypeus structurally as in female. Labrum structurally as in female, with basal rounded projections more strongly produced (Figure 2B). Gena much narrower than width of compound eye, at most ½ as wide; ocellocipital distance large, exceeding 4 times diameter of lateral ocellus. Compound eyes large, bulbous, strongly converging apically, inner margin separated from lateral ocellus by 1 times its diameter. Face white haired, with dense patch of white hair on paraocular areas, supraclipeal area, and clypeus, obscuring underlying surface; gena ventrally with dark brown hairs, becoming white posteriorly and on vertex. Antennae dark basally, A3 apically and A4–12 ventrally obscure lightened orange. A13 expanded ventrally, dark, not strongly contrasting dark orange coloration of A12 (Figure 2E). A3 long, slightly shorter than A4+5, A4–12 quadrate, as long as broad.

Mesosoma: Scutum and scutellum structurally as in female. Entirety of mesosoma with short whitish pubescence, with at most occasional scattered dark hairs. Legs dark, pubescence dark brown to whitish on external face of legs. Tarsal claws with strong, apically truncate rectangular inner tooth. Wings weakly infusate, structurally as in female.

Metasoma: Terga dark, marginal areas apically narrowly lightened hyaline-brown; surface of terga densely and uniformly punctate over entire surface, punctures

separated by <0.5 puncture diameters, underlying surface shagreened, weakly shining (Figure 2C). T1–5 laterally with dense patches of white pubescence, obscuring underlying surface, widely separated on all terga. T7 produced into rectangularly rounded pygidial plate with raised margin, internal surface densely punctate, punctures separated by 0.5 puncture diameters. Sterna with loose whitish to light brownish hairs, not forming dense apical hair fringes. Genital capsule small, simple, gonostyli narrow with 1–2 hairs apically; each gonostylus narrower than penis valves which slightly broaden to reach maximal width subapically (Figure 2D).

Diagnosis – morphological

Ammobatoides are easily recognised parasitic bees within the subfamily Nomadinae due to the unique morphology of the males which have large bulbous eyes that converge dorsally, terminating from the lateral ocelli at most two times the diameter of a lateral ocellus (Figure 2B). Eight species are currently recognised from Morocco to northern China, including a disjunct species in South Africa (Michener 2007; Proshchalykin & Lelej 2014).

Two species are known from the West Mediterranean: *Ammobatoides scriptus* (Gerstäcker, 1869) (Morocco, Algeria, Portugal, Spain, France) and *Ammobatoides schachti* Schwarz, 1988 (Morocco and Tunisia). *Ammobatoides schachti* is known only from the male sex. *Ammobatoides schwarzi* can be separated from *A. scriptus* by the shape of A13 (Figure 2E), which is expanded ventrally, its ventral surface black, not strongly contrasting A4–12 which are ventrally and obscurely lightened dark orange (in *A. scriptus* with A13 apically and ventrally strongly expanded, ventral surface black, strongly contrasting A3–12 which are extensively lightened orange ventrally, Figure 2F) and by the genital capsule (Figure 2D) which has the gonostyli with only a few scattered hairs apically (in *A. scriptus* with the gonostyli covered with clear hair tufts; see Schwarz 1988, Figures 6 and 7).

This places it very close to *A. schachti*. The two taxa differ slightly in size, the male of *A. schwarzi* measuring 10 mm, whereas the male of *A. schachti* averages 10–12.5 mm (Schwarz 1988), though this is not significant in and of itself due to potentially large intraspecific size variation known in parasitic bee species (e.g. Radchenko 1985). The difference is in the sternal morphology. *Ammobatoides schachti* has the hairs of S5 before the apical depression long and upstanding, medially forming a posteriorly directed brush. These hairs and the remaining sternal hairs are uniformly black. In *A. schwarzi*, S5 has loose hairs that do not form a posteriorly directed brush medially (Figure 2G). The sternal hairs are light brown to white. *Ammobatoides scriptus* is clearly different, with S5 medio-apically with a strong brush of black hairs

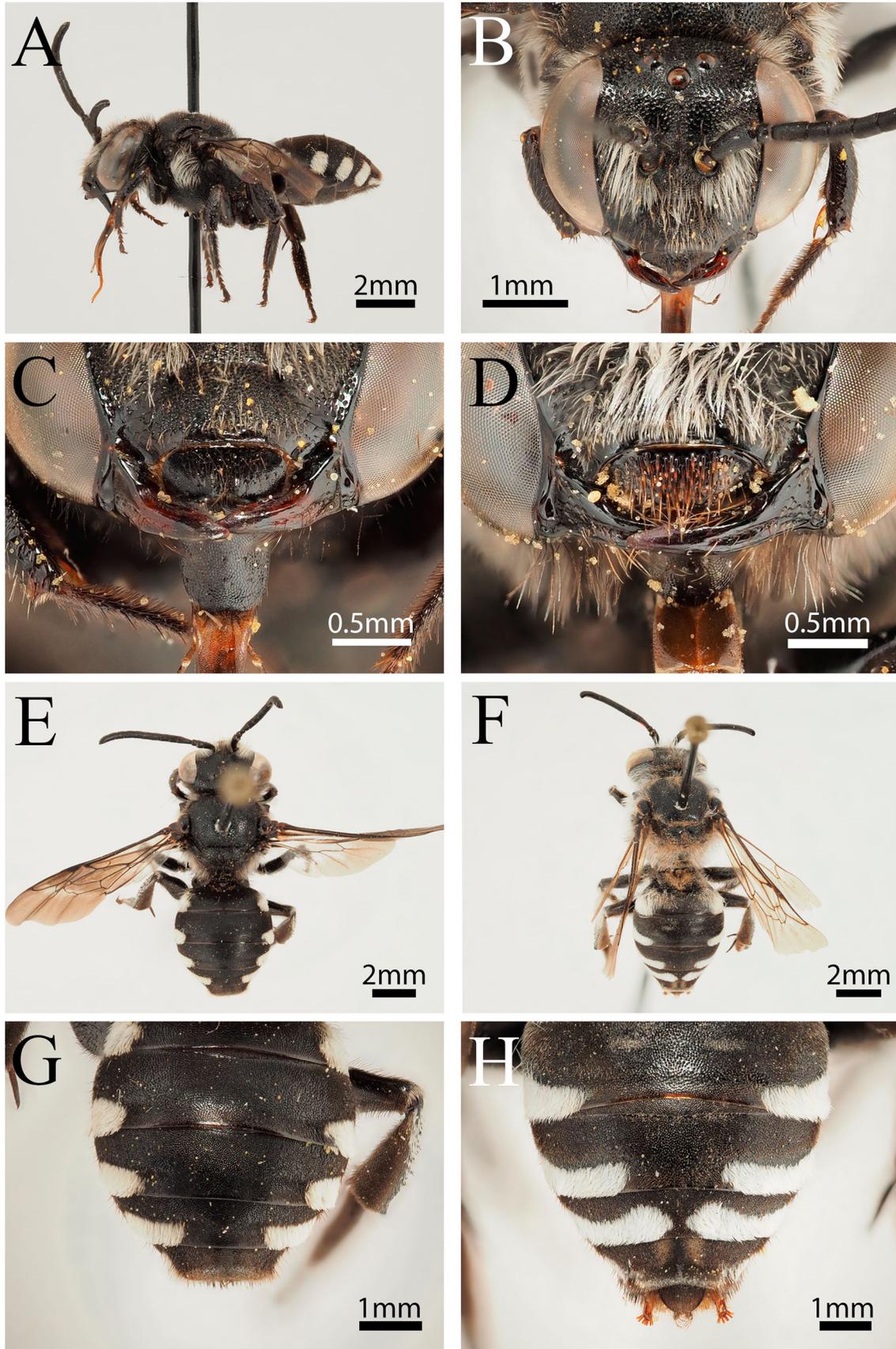


Figure 1. A–C, E, G, *Ammobatoides schwarzi* n. sp., female: A, profile; B, face, frontal view; C, labrum, ventral view; E, dorsum; G, terga, dorsal view. D, F, H, *Ammobatoides scriptus* (Gerstäcker, 1869), female: D, labrum, ventral view; F, dorsum; H, terga, dorsal view.

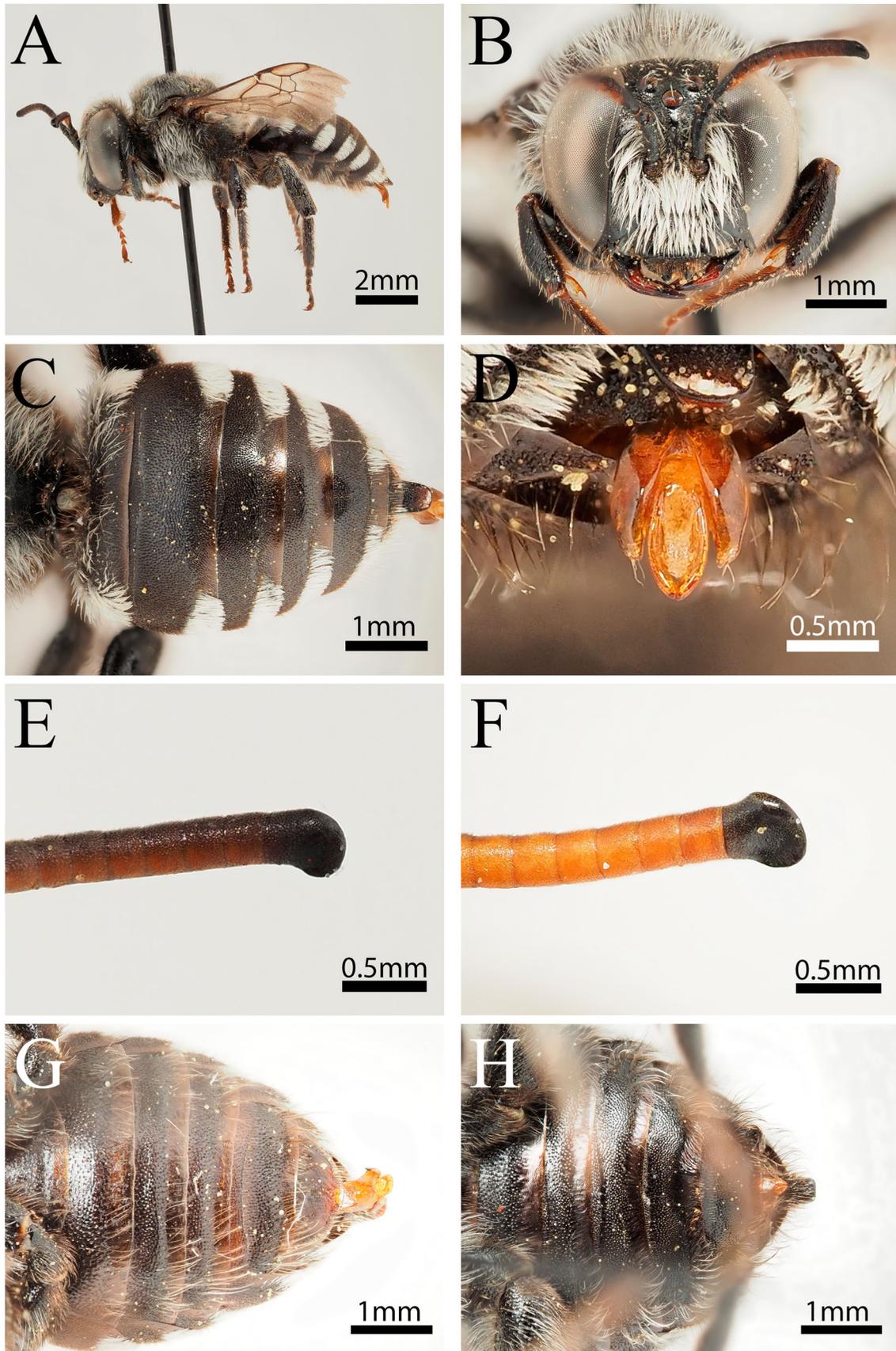


Figure 2. A–E, G, *Ammobatoides schwarzi* n. sp., male: A, profile; B, face, frontal view; C, terga, dorsal view; D, genital capsule, dorsal view; E, antenna, A6–13; G, sternum, ventral view. F, H, *Ammobatoides scriptus* (Gerstäcker, 1869), male: F, antenna, A6–13; H, sternum, ventral view.

(similar to but stronger than in *A. schachtii*), medio-laterally with two patches of around 30 strong black bristles (Figure 2H). There is also a slight difference in the structure of the genital capsule, with *A. schwarzi* having the gonostyli apically narrowing, with their apexes individually narrower than the width of the penis valves (Figure 2D). In *A. schachtii*, the gonostyli are apically truncate, their apexes as wide as the width of the penis valves (see Figure 5 in Schwarz 1988).

Female *A. schwarzi* can easily be separated from *A. scriptus* by its smaller size (9 mm vs 10–11 mm), but also structurally by the weak and fine hair-like bristles of the surface of the labrum basally (Figure 1C; in *A. scriptus* the labrum is covered basally with a dense fringe of thick and long bristles that obscure the underlying surface, Figure 1D), by the broadly separated apical hairbands, on T4 separated by 3 times the diameter of a flagellum (Figure 1G; in *A. scriptus* hairbands wider, on T4 separated by the width of a flagellum, Figure 1H), and by the darker dark brown to black hairs on the posterior face of the hind basitarsi (in *A. scriptus* with these hairs light brown).

Diagnosis – ecological

It is important to discuss the host of *A. schwarzi* for additional ecological justification of its species status. *Ammobatooides* species are known to attack *Melitturga* and *Melitturgula* species (Popov 1933), with *Ammobatooides abdominalis* (Eversmann, 1852) a well-known parasite of *Melitturga clavicornis* (Latreille, 1806) (e.g. Bischoff 1952; Amiet et al. 2007) and *Ammobatooides scriptus* (Gerstäcker, 1869) a parasite of *Melitturga caudata* Pérez, 1879 (Baldock et al. 2018). In the Ouarzazate–Tazenakht area where *A. schwarzi* was collected (*locus typicus*, Figure 3A), only one *Melitturga* species was present; *M. albescens* Pérez, 1895 (Figure 3C; see section below on *Melitturga rubricata* Morice, 1916 for examined material). Based on co-occurrence, size (*M. albescens* averages 9–11 mm), and lack of alternative *Melitturga* hosts, *M. albescens* is considered to be the host of *A. schwarzi*.

In contrast, *A. schachtii* was described from Mediterranean Tunisia (Kasserine, 10.V.1973) and Mediterranean Morocco (Tangier, in 1897). *Melitturga albescens* does not occur in the Mediterranean parts of northern Morocco, and was listed only from the provinces of Drâa-Tafilalet and Souss-Massa by Lhomme et al. (2020). This fits its ecology, as it flies in dry habitats where it is likely a specialist of Brassicaceae (Figure 3B, C; see below). In the Mediterranean parts of Morocco, two *Melitturga* species can be found, *Melitturga caudata* and *M. oraniensis* Lepeletier, 1841, which are larger and average 12–14 mm in length. *Melitturga caudata* is known to host *A. scriptus* (Baldock et al. 2018), which makes sense as *A. scriptus* is larger,

averaging 10–12 mm. Likewise, *A. schachtii* is large-bodied, averaging 10–12.5 mm (Schwarz 1988). The known distribution of *A. schachtii* (Morocco and Tunisia) closely matches the distribution of *M. oraniensis*, which is found in Morocco, Algeria, and Tunisia, with one unclear record listed from Egypt (Patiny 2012). It is therefore considered highly unlikely for *A. schwarzi* to be conspecific with *A. schachtii* since one occurs in humid Mediterranean habitats and likely attacks the larger *M. oraniensis* (Figure 3D, E), and the other occurs in rocky and arid habitats (Figure 3A, B) and likely attacks the smaller *M. albescens*.

Etymology

Dedicated to the Austrian entomologist Maximilian Schwarz who has for many decades worked intensively on and significantly advanced our knowledge of wild bees, with a particular concentration on parasitic bees.

Distribution

Southern Morocco (Drâa-Tafilalet).

Anthophora (Paramegilla) blanda Pérez, 1895

Material examined

Morocco. 6♂, Souss-Massa, R203, Ait Maalla, 500 m E, 730 m, 30.7602°N 8.4080°W, 11.III.2022, leg. T.J. Wood (TJWC); 1♂, R203, Souss-Massa, Tajgalt (nr Tafingoult), 900 m, 30.7914°N 8.3885°W, leg. T.J. Wood (TJWC).

Distribution

Morocco, Algeria, Egypt, Israel (Rasmont 2014).

Camptopoeum (Camptopoeum) handlirschi Friese, 1900

Syn. *Camptopoeum (Camptopoeum) verhoeffi* Noskiewicz, 1962.

Material examined

Algeria. 1♂, (no locality information), 5.V.1898, leg. A. Weis (SMFD) (possible syntype).

Morocco. 4♂, 3♀, Oriental, Guercif, P5427, 1 km N of Laksar, 34.0081°N 3.4420°W, 13.V.2022, leg. T.J. Wood (TJWC).

Tunisia. 1♀ paratype of *C. handlirschi verhoeffi*, Djerba, 14–20.IV.1955, leg. P.M.F. Verhoeff (RMNH).

Remarks

Friese (1900) described this species from Biskra in north-eastern Algeria. An additional species *C. verhoeffi* was

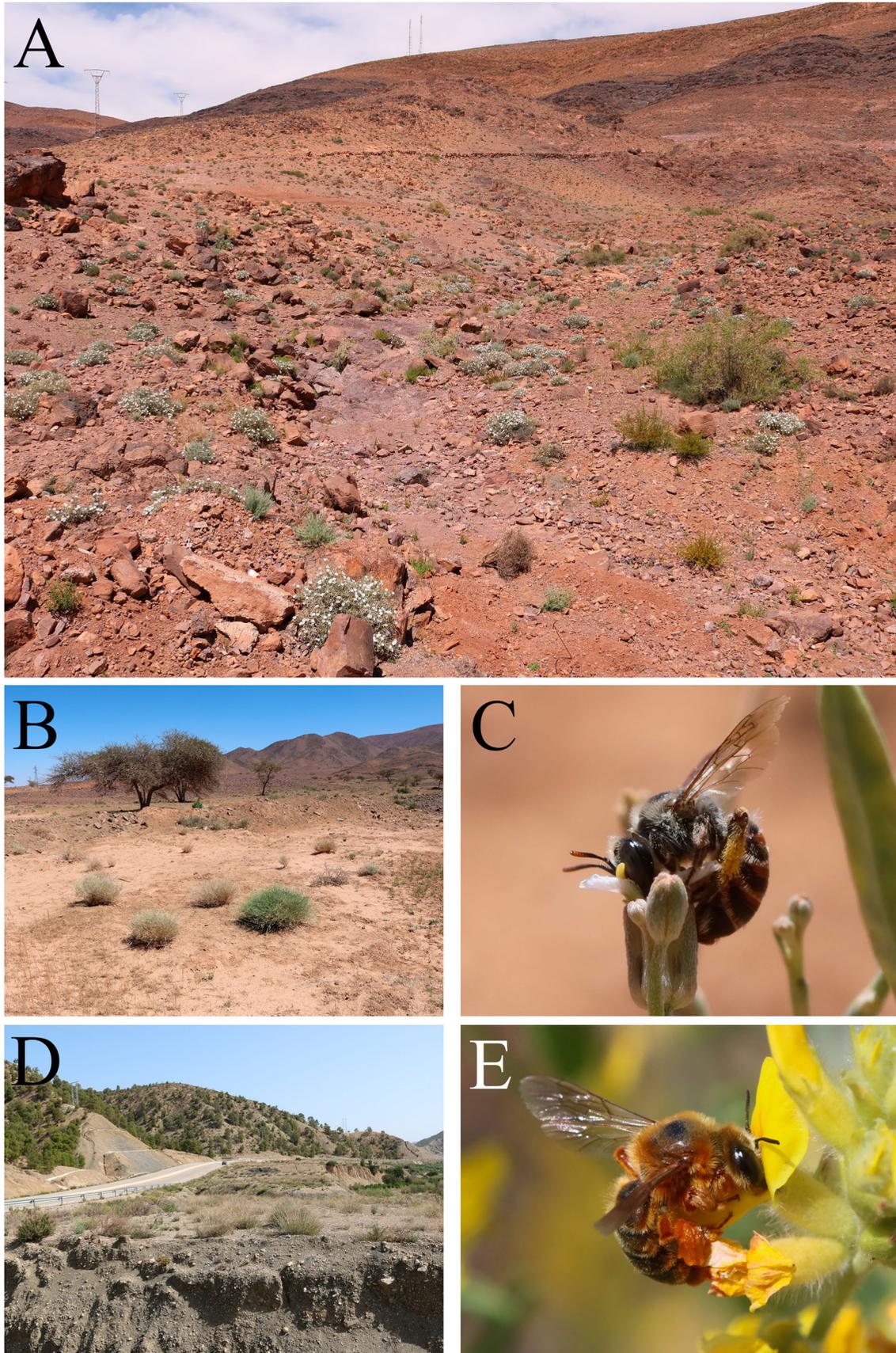


Figure 3. **A**, Drâa-Tafilalet, Ouarzazate, 3 km SSE Irhels [also written as Ighels], *locus typicus* of *Ammobatoides schwarzi* n. sp.; **B**, Drâa-Tafilalet, 5 km SW Agdz, habitat of *Melitturga (Australomelitturga) albescens* Pérez, 1895; **C**, *Melitturga albescens* female collecting pollen from Brassicaceae sp.; **D**, Fès-Meknès, Taza, 10 km S of Douar Ouled Taounza, habitat of *Melitturga (Petrusianna) oraniensis* Lepeletier, 1841; **E**, *Melitturga oraniensis* collecting pollen from Fabaceae sp.

later described from the island of Djerba in Tunisia, and was placed in combination with *C. handlirschi* as a subspecies by Warncke (1972). Until now, these were the only specimens known from this elusive species which is the smallest known *Camptopoeum* s. str. (5–6 mm in length), and the only *Camptopoeum* s. str. species known from North Africa.

In an area of extremely dry semi-desert south of Guercif (Figure 4A), small patches of *Frankenia* cf. *laevis* (Frankeniaceae) were observed growing close to the road (Figure 4B). This genus typically hosts an unusual bee fauna (e.g. Müller 2014), including specialists such as *Halopanurgus baldocki* (Wood & Cross, 2017). Inspecting the *Frankenia*, a number of very small black and yellow panurgine bees were present and collecting pollen (Figure 4C, D). This was highly unexpected, because all studied *Camptopoeum* s. str. species to date are specialists of Asteraceae, typically Cardueae. Morphologically, the small size of *C. handlirschi* and its long tongue typical of *Camptopoeum* s. str. give it an extremely similar appearance to *H. baldocki* that is a specialist of *Frankenia* and was originally described as a *Camptopoeum*. The phylogenetic affinities of *H. baldocki* were only recently clarified (Wood et al. 2022) with the finding that it represents a separate genus distinct from *Camptopoeum*, the ancestors of the two genera having diverged approximately 45 million years ago (Bossert et al. 2022). Examination of *C. handlirschi* confirms that it unambiguously belongs to the genus *Camptopoeum* based on its genital capsule.

Given the habitat in which it was found and the known specialised foraging shown by panurgine bees including those of the genus *Camptopoeum*, it is very difficult to imagine that *C. handlirschi* is anything other than a specialist of *Frankenia*. If true, this means that both *H. baldocki* and *C. handlirschi* have independently evolved to use this host plant which has presumably driven their convergent evolution of body size and tongue morphology. Specifically, the long tongue is necessary for small-bodied species in order to reach the *Frankenia* nectaries which are situated at the base of the flowers, even though the anthers protrude from the corolla and are easily accessible for pollen collection (Wood et al. 2022). Since other *Camptopoeum* s. str. possess a long tongue for accessing the nectaries of Cardueae species (typically *Centaurea*), and all members of genera immediately related to *H. baldocki* have short tongues, this suggests only host plant switching in *C. handlirschi* but host plant switching combined with morphological change in *H. baldocki*.

It is important to note that the status of the type material for *C. handlirschi* is unclear. In the SMFD collection, a male specimen is separated and labelled 'Type' (Figure 4E, F). Friese often put 'Type' labels on his specimens to indicate

that it was part of the type series, but it does not signify that it is the holotype. The specimen is identified as *C. handlirschi* by Friese, but the only label information is that it comes from 'Algeria', was collected on 5.V.1898, and comes from the collection of A. Weiss. In his description, Friese (1900) lists specimens from Biskra (♂, 25.V.1891 leg. Handlirsch; ♀, 20.V.1898 leg. Eaton). He also says that Morice brought additional males from Biskra from 4.V.1898. The SMFD specimen therefore does not match any of these precise details, since it comes from 5.V.1898. Perhaps Morice received the specimen from A. Weiss before passing it on to Friese. Clearly, Morice was part of this expedition, since he collected specimens from the same localities and passed them on to Friese, for example *Camptopoeum variegatum* (Morawitz, 1876) from Biskra 15.V.1898 (Friese 1901). Though the SMFD specimen is indeed *C. handlirschi*, it is not unequivocally a syntype. Friese (1901) indicates that the material collected by Handlirsch in 1891 is in the Vienna Museum; if it can be located, it would be better to designate a lectotype from this collection.

Distribution

Morocco, Algeria, Tunisia (Warncke 1972).

Chelostoma (Foveosmia) campanularum (Kirby, 1802)

Material examined

Morocco. 1♂, 1♀, Marrakech-Safi, Amroud, route to Sidi Chamarouch, 2300 m, 31.1058°N 7.9177°W, 10.VII.2022, leg. T.J. Wood (AMC).

Remarks

This subgenus is very rare in North Africa, with only this single species confidently recorded there. At the capture locality, *C. campanularum* was flying at flowers of *Campanula* (Campanulaceae) with *Hoplitis (Alcidamea) praestans* (Morawitz, 1894), both species being specialists on this genus. This High Atlas population of *C. campanularum* is likely relictual.

Distribution

Morocco, Algeria, Europe to Russia and Turkey (Kuhlmann et al. 2014), introduced in North America (Eickwort 1980).

Coelioxys (Boreocoelioxys) osmiae Alfken, 1928

Material examined

Morocco. 1♀, Fès-Meknès, Ifrane, P7231, 1 km E of Lac Hachlaf, 1700 m, 33.5440°N 4.9840°W, 24.V.2022, leg. T.J. Wood (TJWC).

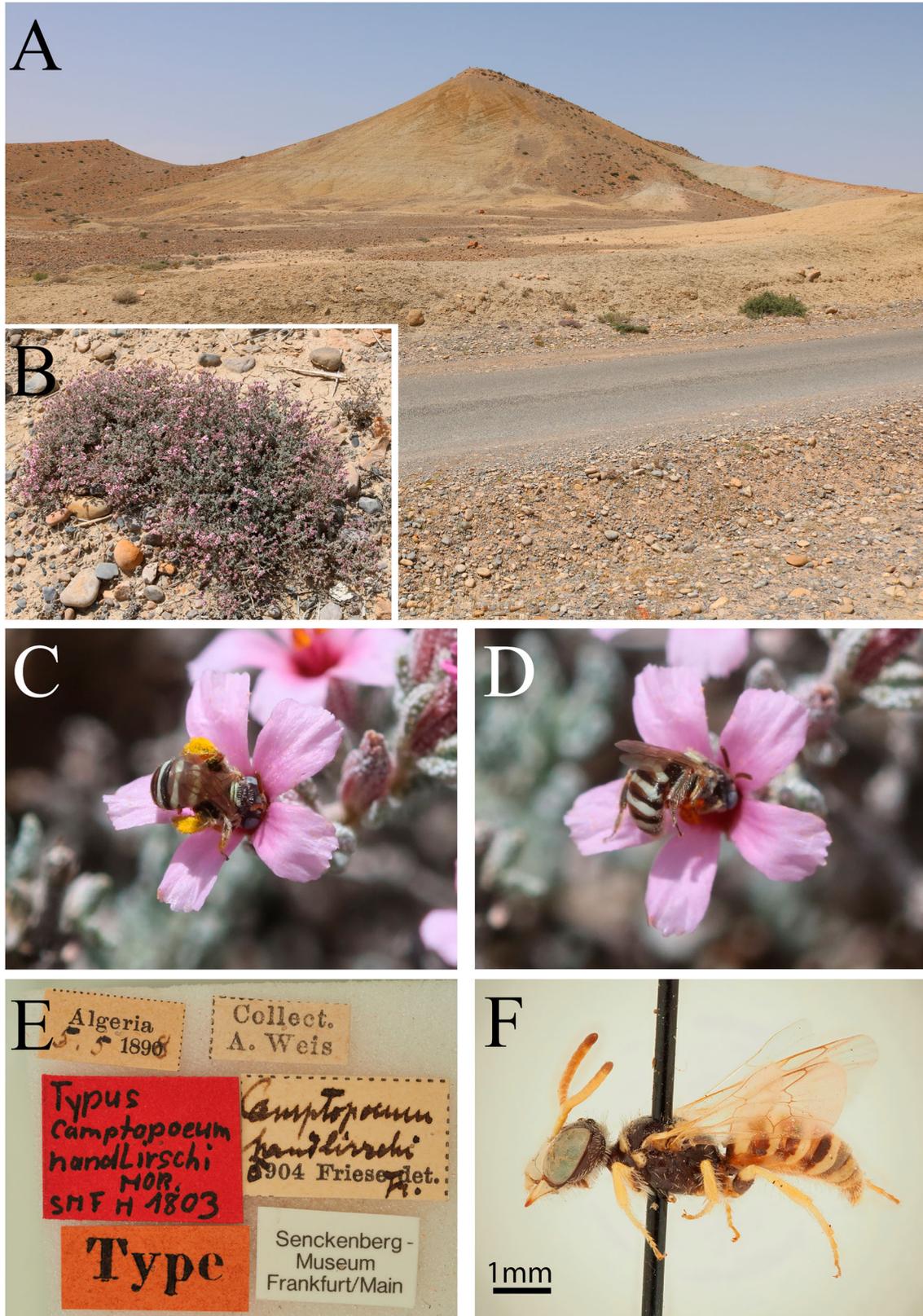


Figure 4. *Camptopoeum (Camptopoeum) handlirschi* Friese, 1900. **A**, Oriental, Guercif, 1 km N of Laksar, collecting location; **B**, *Frankenia* cf. *laevis* (Frankeniaceae) growing by road edge; **C**, female nectaring at *F. laevis* with pollen in scopae; **D**, female nectaring at *F. laevis* with scopae empty; **E**, label details of possible syntype; **F**, possible male syntype, profile.

Distribution

Morocco, Algeria, Tunisia, Portugal, Spain (Kuhlmann et al. 2014).

Dioxys chalicodus* Lucas, 1849*Material examined**

Morocco. 1♀, Oriental, Guercif, Debdou, 2 km S of Debdou, 1500 m, 33.9495°N 3.0524°W, leg. T.J. Wood (TJWC) [BOLD accession number: WPATW748-22].

Remarks

At an area of high steppe on the Massif de Debdou in north-eastern Morocco, a large exposed rocky area hosted many foraging *Megachile* (*Chalicodoma*) individuals from three species, namely *M. parietina* (Geoffroy, 1785), *M. rufitarsis* (Lepeletier, 1841), and *M. sicula* (Rossi, 1794). At this site, a small number of *D. chalicodus* could be seen flying low and rapidly across these rocky areas, scarcely stopping.

The name *D. chalicodus* in combination with its large body size suggests that *M.* (*Chalicodoma*) species are the host. Lucas (1849, p. 207) described *D. chalicodus* from an unpublished name of Lepeletier; he writes that “Je n’ai rencontré que quelques individus de cette espèce; je les ai pris dans les derniers jours de mars, aux environs d’Oran, en brisant leur nid fait avec une terre très-dure; je les ai surpris dans leurs loges” (he collected only a few specimens of this species at the end of March near to Oran [Algeria], breaking their nests made of very hard mud and surprising them within). These nests would of course not be made by *D. chalicodus* but by a *M.* (*Chalicodoma*) species. The precise host is unknown because I was not able to observe *D. chalicodus* locating or entering nests. None of the three *M.* (*Chalicodoma*) species present have a distributional range that corresponds precisely to that of *D. chalicodus*, being either much larger (*M. parietina*, *M. sicula*) or too small (*M. rufitarsis* has a restricted distribution across Morocco, Algeria, and Tunisia; Lhomme et al. 2020). In any case, this observation supports the hypothesis that *D. chalicodus* attacks *M.* (*Chalicodoma*) species. Its presence in north-eastern Morocco is expected, as *D. chalicodus* has been recorded from Oran in north-western Algeria, for example from the Fort of Santa Cruz (Alfken 1914).

It is important to note the generic affiliation of *D. chalicodus*. Within Dioxyine bees, the current classification (Michener 2007) utilises eight genera, each with a small number of species. In the West Palaearctic region, all eight genera of Dioxyini are found, with a total of 23 species present (Rasmont et al. 2017). Simple analysis of the COI gene produces a phylogeny

in which *Dioxys* Lepeletier & Serville, 1825 is polyphyletic (three lineages), with the genera *Allodioxys* Popov, 1947, *Aglaoapis* Cameron, 1901 and *Ensliniana* Alfken, 1938 nested within this broad *Dioxys* (Figure 5). Clearly, this analysis is based on a single gene, only four of the eight Dioxyine genera are included, and no strong conclusions should be drawn; more powerful genetic techniques are required. However, since Dioxyine classification is based largely on the presence or absence of spines and carinae on the mesosoma, it is entirely possible that they have been gained and/or lost multiple times during the evolution of this group, and it may be best to return to a broad *Dioxys* concept employing multiple subgenera. In any case, as *D. chalicodus* falls close to the type species of *Dioxys*, *D. cinctus* (Jurine, 1807), it will remain a *Dioxys* s. str. in any future revision.

Finally, the name is often spelt *chalicoda*, but following Rasmont et al. (2017), the gender of the genus *Dioxys* is masculine, and hence a masculine termination must be used, i.e. *D. chalicodus*, as seen in previous publications (e.g. Alfken 1914).

Distribution

Morocco, Algeria, Tunisia, Libya, Egypt, Gibraltar (?) (Warncke 1977).

Hoplitis (Anthocopa) peniculifera* Müller, 2012*Material examined**

Morocco. 2♂, Fès-Meknès, Boulemane, R503, SE of Ait Karmosse, 1750 m, 33.2440°N 4.6762°W, 22.V.2022, leg. T.J. Wood (AMC/TJWC); 1♀, Marrakech-Safi, Oukaimeden, 1 km SE, P2030, 2600 m, 31.1953°N 7.8536°W, 8.VII.2022, leg. T.J. Wood (AMC).

Remarks

This species was described from south-eastern Spain from the provinces of Granada, Jaén, and Murcia (Müller 2012). Several species of *Andrena* described from Spain and thought to be endemic there have recently been or will soon be documented (T. J. Wood, in prep.) occurring in the dry areas immediately to the east of the Middle Atlas of Morocco (e.g. *A.* (incertae sedis) *relata* Warncke, 1975; Wood et al. 2020). In this context, the presence of *H. peniculifera* in this region is less surprising.

Distribution

Morocco & Spain (Müller 2012).

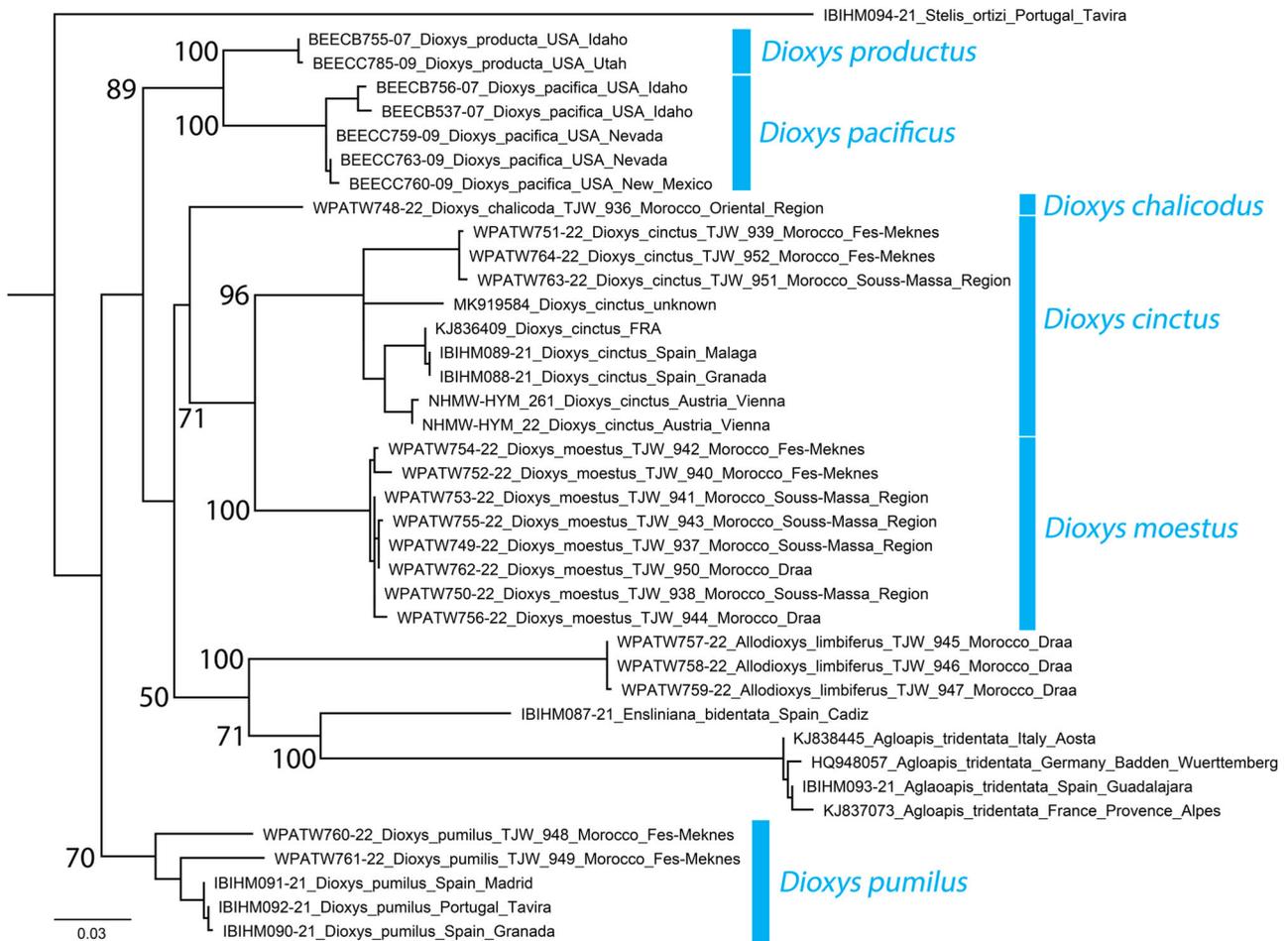


Figure 5. Phylogenetic tree (maximum likelihood) of bees from the tribe Dioxyini based on the mitochondrial COI gene. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted). Species currently recognised as belonging to the genus *Dioxy* Lepelletier and Serville, 1825 are highlighted with blue.

Lasioglossum (Evyllaesus) marginatum (Brullé, 1832)

Material examined

Morocco. 3♀, Fès-Meknès, Ahermoumou, P504, 8 km SE of Faj Azrar, 1450 m, 33.7224°N 4.2564°W, 15.V.2022, leg. T.J. Wood (TJWC); 4♀, Fès-Meknès, Taza, P5420, 7 km S Ademame, 1200 m, 33.9863°N 4.1691°W, 16.V.2022, leg. T.J. Wood (TJWC); 2♀, Fès-Meknès, Azrou forest, P7217, 1 km SW Maison de la cédraie, 1750 m, 33.4161°N 5.1898°W, 18.V.2022, leg. T.J. Wood (TJWC).

Remarks

Warncke (1982) reported this species from Morocco from Ifrane in the Middle Atlas. However, Ebmer (1995) questioned these data and considered them to be erroneous as no specimens could be found in Warncke's collection. The new specimens presented here, including some collected only a few kilometres from Ifrane, confirm the validity of Warncke's original data. In the Middle Atlas, the

species can be found at altitude in areas with *Quercus* woodland. The unusually restricted activity period of *L. marginatum* (females foraging only during the spring time, males emerging very late in the season) may have prevented prior detection.

Distribution

Morocco, Europe to southern Russia, Turkey, the Levant; elsewhere to the Himalayas (Kuhlmann et al. 2014; Pauly 2016a).

Lasioglossum (Hemihalictus) puncticolle (Morawitz, 1872)

Material examined

Morocco. 1♀, Fès-Meknès, Tiguelmamine, Col du Zad, 2100 m, 33.0614°N 5.0382°W, 21.V.2022, leg. T.J. Wood (TJWC).

Remarks

The Col du Zad hosts species with very restricted North African distributions; flying with *L. puncticolle* were *Andrena* (*Micrandrena*) *fabrella* Pérez, 1903 and *Rophites* (*Rophites*) *algirus* Pérez, 1895 (see Lhomme et al. 2020). In this context, its presence is less surprising as a species with a relictual distribution.

Distribution

Morocco, Algeria, Europe to the Ural Mountains and Iran (Kuhlmann et al. 2014; Pauly 2016a).

Megachile* (*Xanthosaurus*) *lagopoda* Linnaeus, 1761*Material examined**

Morocco. 1♂, Fès-Meknès, Boulemane, Ait Ammou, 1600 m, 33.3834°N 4.7311°W, 19.V.2022, leg. T.J. Wood (TJWC); 1♂, Marrakech-Safi, Aroumd, 1.5 km S, 2000m, 31.1127°N 7.9226°W, 10.VII.2022, leg. T.J. Wood (TJWC); 1♂, Marrakech-Safi, Oukaimeden, 1 km E, steppe, 2500 m, 31.2091°N 7.8423°W, 11.VII.2022, leg. T.J. Wood (TJWC); 1♂, 1♀, Marrakech-Safi, Imlil, 500 m N, 1800 m, 31.1490°N 7.9233°W, 14.VII.2022, leg. T.J. Wood (TJWC).

Distribution

Morocco, Algeria, Europe to Russia, Central Asia, China, the Korean Peninsula, and Japan (Kuhlmann et al. 2014; Ascher & Pickering 2021).

Megachile* (*Eutricharaea*) *rubrimana* Morawitz, 1893*Material examined**

Morocco. 4♀, Drâa-Tafilalet, Midelt, R503, 7 km NE of Ait Ben Yacoub, 1600 m, 33.0217°N 4.8197°W, 21.V.2022, leg. T.J. Wood (TJWC); 1♂, Fès-Meknès, Boulemane, R503, SE of Ait Karmosse, 1750 m, 33.2440°N 4.6762°W, 22.V.2022, leg. T.J. Wood (TJWC).

Remarks

These records mean that *M. rubrimana* shows a remarkable disjunct distribution of Morocco, eastern Turkey, and Central Asia. This distribution has been obscured by the erroneous suggestion that *M. rubrimana* was conspecific with *M. (Eutricharaea) flabellipes* Pérez, 1895, leading to the creation of scattered records from Southern and Eastern Europe and the Levant (e.g. Ascher & Pickering 2021; Boustani et al. 2021). Type examination shows that the two species are distinct (C. Praz *in*

litt.), and European and Levantine records refer to *M. flabellipes*.

In this context, given the true distribution of *M. rubrimana*, this distributional pattern is very similar to that of *Seladonia* (*Vestitohalictus*) *nasica* (Morawitz, 1876) which is found in Morocco and also Iran and Central Asia (Pauly 2016b; Lhomme et al. 2020). All female specimens were collecting pollen from *Peganum harmala* (Nitrariaceae) in elevated semi-desert habitats.

Distribution

Morocco, eastern Turkey, and Central Asia (C. Praz, *in litt.*)

Megachile* (*Eutricharaea*) *thevestensis* Ferton, 1909*Material examined**

Morocco. 2♂, Fès-Meknès, Boulemane, R503, SE of Ait Karmosse, 1750 m, 33.2440°N 4.6762°W, 22.V.2022, leg. T.J. Wood (TJWC); 1♀, Fès-Meknès, Boulemane, P5108, 10 km E Enjil, 1600 m, 33.1833°N 4.4551°W, 23.V.2022, leg. T.J. Wood (TJWC).

Distribution

Morocco, Algeria, Portugal, Spain (Kuhlmann et al. 2014).

Melitturga* (*Australmelitturga*) *rubricata* Morice, 1916*Material examined**

Morocco. Neotype (present designation): ♀, Oriental, Guercif, P5427, 500 m N of Al Koualit, 34.0925°N 3.4091°W, 13.V.2022, leg. T.J. Wood (OÖLM).

Remarks

Morice (1916) travelled through western Algeria, and described two new species including *M. rubricata* from Aïn Séfra (32.77°N 0.59°W), a species characterised by its extensively red-marked terga. The status of this species has remained obscure, because it was known only from the holotype female which seems to be lost. Patiny (2001) suggested that, given the unavailability of the type, the status of this taxon was dependent on which genus is truly belonged to, potentially becoming a junior synonym if it was associated with *Borgatomelissa brevipennis* (Walker, 1871) (Mauritania, Niger, Ethiopia, Djibouti, Yemen, Saudi Arabia, Oman) due to the red coloration of its terga.

South of Guercif in north-eastern Morocco, in an olive plantation surrounded by semi-desert, a female *Melitturga* with extensively red-marked terga was captured collecting

pollen from weedy Brassicaceae. Based on Morice's description, the specimen is a match for *M. rubricata*, including the longitudinal black oval marking covering the lateral spiracles on T2 (Figure 6F), the predominantly red-marked metasomal segments with a subtriangular mark ventrally on S3 (Figure 6G), the scattered pale pubescence, the white scopal hairs with fulvous hairs on the ventral side of the hind basitarsi (Figure 6A), and the terminal fringe which is dark brown medially on T5 and laterally white, and entirely dark brown on T6 (Figure 6H; the hairs flanking the pygidial plate). The collection site was approximately 300 km from Aïn Séfra, further supporting this association. On the basis of this excellent match, the specimen is here designated as a neotype and deposited in the OÖLM collection to validate the species and ensure comparative material for future workers.

The phylogenetic position of *M. rubricata* is important to define. Patiny (1999) described the subgenus *Australomelitturga* Patiny, 1999, initially only including sub-Saharan species, but later including *M. albescens* (e.g. Patiny 2001; Lhomme et al. 2020). Morphologically, *M. rubricata* is closest to *M. albescens*. Following the criteria of Patiny (1999), *M. rubricata* can be placed into the subgenus *Australomelitturga* due to the short galea that is shorter than the length of the head (Figure 6A), the red-marked T1–3 (Figure 6E), the tergal margins that are decolored and lightened hyaline-white (Figure 6F), and the process of the labrum that is not noticeably elongate. The surface of the galea is not smooth, but is instead finely shagreened and weakly shining (Figure 6C). However, this character does not seem to be consistent in defining the subgenus, as in *M. albescens* the surface of the galea is more strongly shagreened and dull. In fact, other than tergal coloration (*M. albescens* having red markings confined to the very edge of the tergal discs adjacent to the marginal areas, not extensively covering the discs; Figure 3C), the finer sculpture of the galea is a good character to separate *M. rubricata* from *M. albescens*. Both species are highly likely to be specialised on Brassicaceae, as *M. albescens* was exclusively observed collecting pollen from members of this family in dry parts of southern Morocco (Figure 3B, C). In contrast, the two other *Melitturga* species known from Morocco, *M. caudata* and *M. oraniensis*, are members of the subgenus *Petrusianna* Patiny, 1998 and are associated with Fabaceae and are likely specialists on this family (Baldock et al. 2018). All observations of these two species in Morocco were made on Fabaceae (Figure 3E). A provisional hypothesis can be made that members of the subgenus *Australomelitturga* have a shorter tongue because they are specialists of Brassicaceae, whereas members of the subgenus *Petrusianna* have a longer tongue (see Patiny 1999) because they are

specialists on Fabaceae. Further work is needed to quantify the pollen preferences of *Melitturga* and to see if these correspond to the existing subgeneric concepts which are currently known to be reciprocally monophyletic (Bossert et al. 2022).

Distribution

Morocco & Algeria (Morice 1916).

Other material examined (*Melitturga albescens* Pérez, 1895)

Morocco. 4♀, Drâa-Tafilalet, Ouarzazate, P1507, 3 km SSE Irhels [also written as Ighels], 30.6993°N 7.0721°W, 12.IV.2022, leg. T.J. Wood (TJWC) (Figure 3A); 5♂, 2♀, Drâa-Tafilalet, Agdz, R108, 5 km SW Agdz, 30.6692°N 6.5182°W, 14.IV.2022, leg. T.J. Wood (TJWC) (Figure 3B, C); 3♀, Drâa-Tafilalet, Tazenakht, R108, 10 km E Tazenakht, 1450 m, 30.5491°N 7.1454°W, 17-19.IV.2022, leg. T.J. Wood (TJWC).

Other material examined (*Melitturga caudata* Pérez, 1879)

Morocco. 3♂, Fès-Meknès, Taza, R505, 10 km S of Douar Ouled Taounza, c. 800 m, 34.5589°N 3.8671°W, 14.V.2022, leg. T.J. Wood (TJWC).

Other material examined (*Melitturga oraniensis* Lepeletier, 1841)

Morocco. 2♂, Souss-Massa, Tafraoute, Imskrn (5 km SE Tanalt), 29.7443°N 9.1148°W, 13–21.III.2022, leg. T.J. Wood (TJWC); 1♀, Souss-Massa, Tiznit, Tanalt, oasis between Ait Moussa and Anadia, 29.8651°N 9.2862°W, 22.III.2022, leg. T.J. Wood (TJWC); 1♂, 1♀, Fès-Meknès, Taza, R505, 10 km S of Douar Ouled Taounza, c. 800 m, 34.5589°N 3.8671°W, 14.V.2022, leg. T.J. Wood (TJWC) (Figure 3D, E).

Nomada judaica Schwarz & Smit, 2018

Material examined

Morocco. 1♂, Drâa-Tafilalet, Ouarzazate, P1505, 2 km S Amerzgane, 1300 m, 31.0248°N 7.2224°W, 13.IV.2022, leg. T.J. Wood (TJWC).

Distribution

Morocco, Algeria, Tunisia, Israel, Jordan, Turkey (Schwarz & Smit 2018).

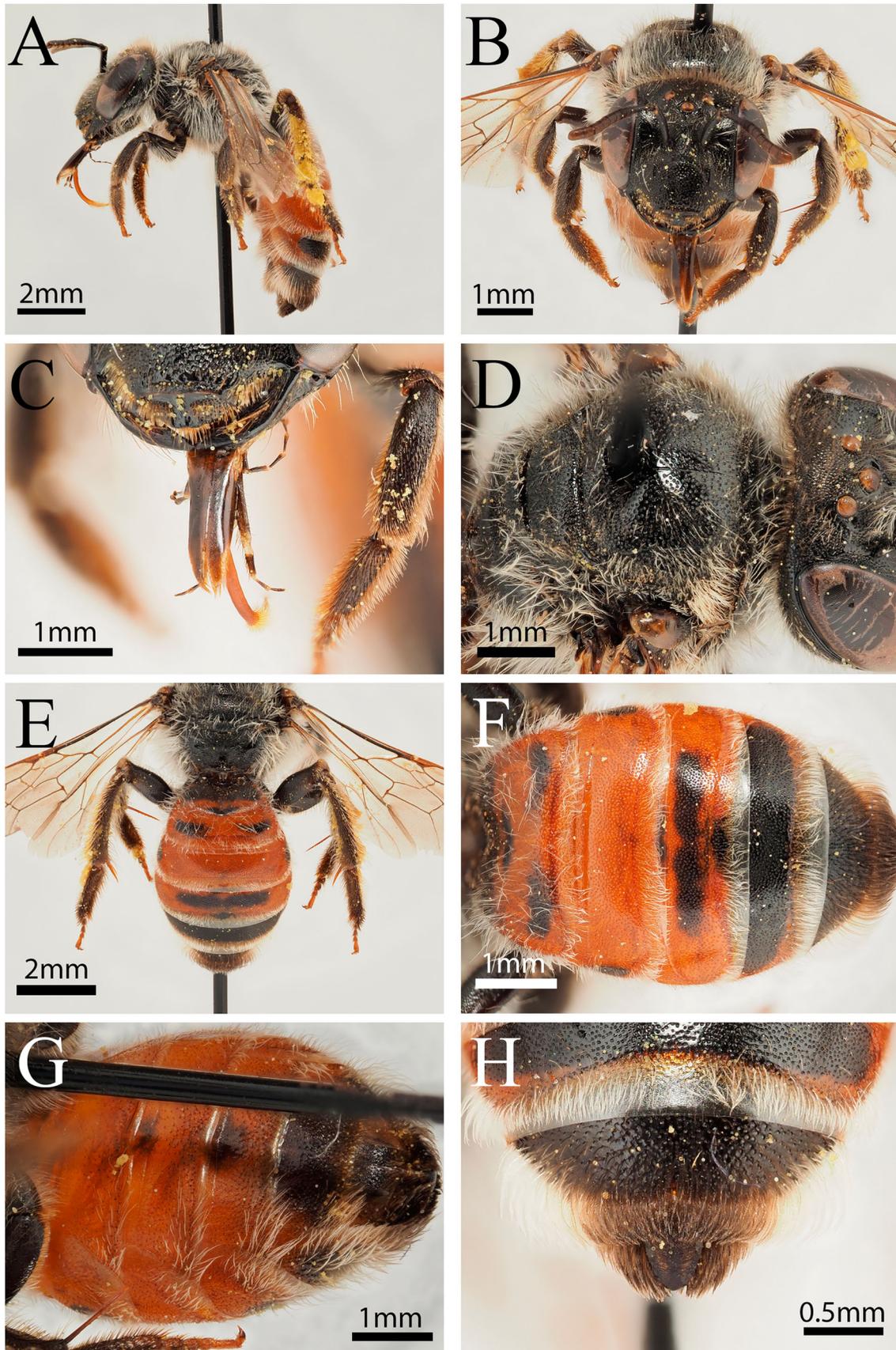


Figure 6. *Melitturga (Australomelitturga) rubricata* Morice, 1916, female. **A**, Profile; **B**, face, frontal view; **C**, tongue, frontal view; **D**, scutum, dorsolateral view; **E**, terga, dorsal view; **F**, terga detail, dorsal view; **G**, sterna, ventrolateral view; **H**, T4-5 and pygidial plate, dorsal view.

Sphecodes majalis* Pérez, 1903*Material examined**

Morocco. 1♂, 1♀, Béni Mellal-Khenifra, Khenifra, P7306, 10 km E of Aroggou, 1500 m, 32.9399°N 5.4582°W, 20.V.2022, leg. T.J. Wood (TJWC).

Remarks

Sphecodes majalis is the special parasite of *Lasioglossum (Lasioglossum) pallens* (Brullé, 1832) (Warncke 1992; Bogusch & Straka 2012) which is known from the Middle Atlas from the provinces of Béni Mellal-Khénifra and Fès-Meknès (Lhomme et al. 2020). *Sphecodes majalis* is rare in collections, in part due to its very short activity period during March to May, including the vernal appearance of males which is unusual in *Sphecodes*. It has clearly been overlooked in Morocco for these reasons.

Distribution

Morocco, Algeria, Europe to Russia, the Caucasus, Turkey, Jordan, and Iran (Warncke 1992; Bogusch & Straka 2012; Astafurova et al. 2019).

Sphecodes pinguiculus* Pérez, 1903*Material examined**

Morocco. 1♀, Drâa-Tafilet, Midelt, R503, 7 km NE of Ait Ben Yacoub, 1600 m, 33.0217°N 4.8197°W, 21.V.2022, leg. T.J. Wood (TJWC).

Distribution

Cape Verde, Morocco, Algeria, Tunisia, warm part of Europe to Russia, Turkey, the Levant, Arabian Peninsula, Central Asia, northern China, and Mongolia (Warncke 1992; Bogusch & Straka 2012; Kuhlmann et al. 2014; Astafurova et al. 2019).

Thyreus mauretaniensis* (Strand, 1911)*Material examined**

Morocco. 1♀, Souss-Massa, Tafraoute, Imskrn (5 km SE Tanalt), 29.7443°N 9.1148°W, 13.III.2022, leg. T.J. Wood (TJWC) [BOLD accession number: WPATW835-22]; 1♂, Souss-Massa, Tiznit, Inskat, Barrage Youssef Ben Tachfine, 29.8380°N 9.4968°W, 22.III.2022, leg. T.J. Wood (TJWC) [BOLD accession number: WPATW845-22]; 1♂, Souss-Massa, Tiznit, Tanalt, oasis between Ait

Moussa and Anadia, 29.8651°N 9.2862°W, 22.III.2022, leg. T.J. Wood (TJWC) [BOLD accession number: WPATW846-22]; 1♀, Fès-Meknès, Ifrane, P7231, 1 km E of Lac Hachlaf, 1700m, 33.5440°N 4.9840°W, 24.V.2022, leg. T.J. Wood (TJWC) [BOLD accession number: WPATW834-22].

Description of female

Body length: 9 mm (Figure 8A).

Head: Dark, 1.25 times wider than long (Figure 8B). Clypeus flattened over almost entire area, densely punctate with elongate punctures, punctures separated by <0.5–0.5 puncture diameters; underlying surface shining. Labrum rectangular, slightly longer than broad, with longitudinal weakly impressed midline, basally weakly produced into two tubercles laterally (Figure 8C). Gena slightly narrower than width of compound eye; ocelloccipital distance 2.5 times diameter of lateral ocellus. Hind margin of vertex with short and obscurely raised carina. Face between antennal insertions with raised longitudinal carina. Frons very densely punctate, punctures confluent, becoming sparser dorsally, separated by 0.5–2 punctures on vertex. Face predominantly white-haired, with scattered black hairs on clypeus and lower paracocular areas; gena ventrally and posteriorly with abundant black hairs, vertex with scattered black hairs, predominantly white haired. Antennae dark, measured along ventral surface A3 slightly exceeding A4, A4–12 more or less quadrangular, of an equivalent length, all slightly broader than long.

Mesosoma: Scutum and scutellum densely and regularly punctate, punctures separated by <0.5–0.5 puncture diameters, underlying surface shiny. Scutum in anterior half with raised white and black pubescence which does not obscure underlying surface, forming three white spots in broad triangle (Figure 8D). Scutum posteriorly with two patches of white hair laterally, at junction with axillae. Scutellum posteriorly strongly produced into two projecting points, scutellum clearly overhanging vertical face of propodeum, medially widely emarginate with medial notch; scutellum with posteriorly projecting tuft of white hair medially (Figure 8E). Mesepisternum in dorsal half with dense patch of white hairs that obscure underlying surface, in ventral half with sparser black hairs, underlying surface clearly visible. Legs dark, with abundant white pubescence on outer face of tibiae and tarsi (Figure 8F). Forewings weakly infuscate over majority of area, with exception of areas adjacent to veins Rr-m and 2m-cu and marginal and 1st cubital cells.

Metasoma: Terga dark, tergal discs punctate with hair-bearing punctures, punctures presenting short, posteriorly projecting black plumose hairs, punctures separated by

0.5–2 puncture diameters (Figure 8G). T1–4 laterally with L-shaped patch of white hairs, on T3 clearly interrupted laterally, thus appearing to be two hair patches. Pygidial plate narrowly triangular, apically rounded, medially with strongly raised longitudinal carina (Figure 8H).

Diagnosis

Comparison of barcoded *T. mauretaniensis* and *T. orbatus* females shows no apparent differences in typical areas of *Thyreus* morphological variation such as the pattern of pubescence, shape of the pygidial plate, antennal ratios, sculpture, and puncture density. The limited number of *T. mauretaniensis* females available show little black pubescence on the face, but this can be variable within *T. orbatus*, and so no conclusion is drawn to its utility as a diagnostic character. In fact, the *T. mauretaniensis* females were originally identified as *T. orbatus* before barcoding results were available. At the present time, female *T. mauretaniensis* and *T. orbatus* must be considered inseparable, which may explain why Lieftinck was unable to recognise the female sex in his comprehensive Palaearctic revision. The presence of true *T. orbatus* in Morocco must be confirmed with males or barcoded females.

Remarks

Strand (1911) described *T. mauretaniensis* from a single male specimen from an unclear locality in Algeria (Lieftinck 1968). Lieftinck examined this specimen and concluded that it was a good species, noting that it was still only known from the type despite his revisionary efforts. Collections in south-western Morocco captured two males corresponding to this description, and barcoding was able to associate two female specimens with these males (Figure 7). The four sequences were separated by an average of 1.11% (range 0.00–2.22%), with the greatest distance observed between the two male specimens. The closest genetic relative was *Thyreus orbatus* (Lepeletier, 1841) which was separated by an average of 6.84% (range 6.37–7.48%). Each clade showed strong bootstrap support, 96 for *T. orbatus* and 100 for *T. mauretaniensis*. Morphologically, *T. mauretaniensis* is extremely close to *T. orbatus*. In the key of Lieftinck (1968), male *T. mauretaniensis* falls away from *T. orbatus* because it has pale pubescence on the face below the antennal insertions, not black pubescence. This early separation means that the morphological similarities between these two species in the male sex are somewhat missed; both share the useful character that the apex of the inner margin of the hind tibia is produced into a clear, ventrally projecting tooth. As some individuals of *T. orbatus* can be found for which the dark facial pubescence is reduced or abraded, the only clear character to separate the two species is the genital capsule (see Lieftinck 1968, figures 11 and 16).

Examination of material in the Lieftinck collection (RMNH) could not locate male material of *T. orbatus* or *T. mauretaniensis* from North Africa. Only a small number of females could be found; since there are no clear morphological features that allow confident determination of female specimens, these specimens cannot be used to demonstrate the species' presence or absence. It is not clear if *T. orbatus* actually occurs in North Africa, which potentially poses a problem, since Lepeletier (1841) described the species based on material from France and Algeria. The type appears to be lost, since Lieftinck (1968) did not mention inspecting it, and Beaumont (1939) does not appear to have seen it either, instead writing that the species was sufficiently well described by Lepeletier and that there cannot be any doubt concerning its identification (Beaumont 1939, p. 169). There are two possibilities. Either *T. orbatus* is absent from North Africa, in which case a neotype should be designated based on material from Europe, or both *T. orbatus* and *T. mauretaniensis* are present in North Africa, in which case a neotype should be designated based on material from Europe or barcoded material from North Africa. Since the Paris collection has not been sufficiently interrogated for *Thyreus* type material, neither option is pursued at this time, but records purporting to be *T. orbatus* from North Africa should be treated with a degree of suspicion if they are based on female material.

Distribution

Morocco & Algeria (Lieftinck 1968).

Other material examined [*Thyreus orbatus* (Lepeletier, 1841)/*Thyreus mauretaniensis* agg.]

Algeria. 1♀, Mascara, 1902, leg. Dr. Cros (RMNH), misidentified as *Thyreus hirtus* (Beaumont, 1939) by Lieftinck and listed as such in Lieftinck (1968).

Morocco. 4♀, Sidi Ifni, 1948, leg. Morales (RMNH); 1♀, Rte Taroudant, Tizi n'Test, 6.II.1987, leg. H. Teunissen (RMNH).

Thyreus rasmonti n. sp.

Type material

Holotype. ♂, Morocco, Souss-Massa, Tafraoute, Imskrn (5 km SE Tanalt), 29.7443°N 9.1148°W, 13.III.2022, leg. T.J. Wood (RMNH) [BOLD accession number: WPATW836-22].

Paratypes. 4♂, Morocco, Souss-Massa, Tafraoute, Imskrn (5 km SE Tanalt), 13.III.2022, leg. T.J. Wood (RMNH/TJWC); 3♂, 2♀, Marrakech-Safi, Oukaimeden, 1 km SE, P2030, 2600 m, leg. T.J. Wood & G. Ghisbain (RMNH/

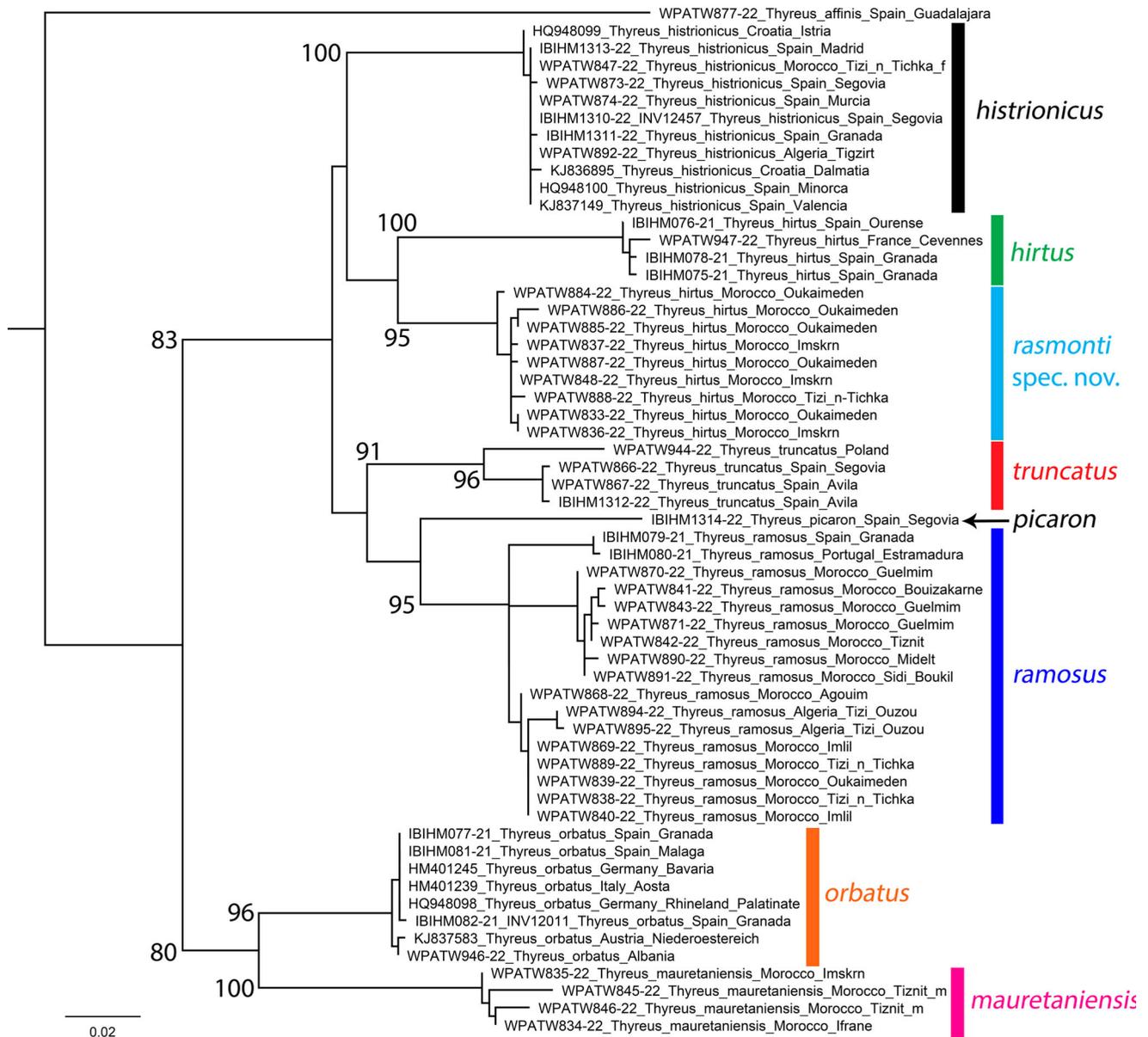


Figure 7. Phylogenetic tree (maximum likelihood) of bees from the genus *Thyreus* Panzer, 1806 based on the mitochondrial COI gene. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

TJWC); 1♀, Marrakech-Safi, Tizi n’Tichka, Source de Tichka, 2200 m, leg. G. Ghisbain (TJWC).

Other material examined (Thyreus hirtus)

France. 2♂, Basses-Alpes, Digne, 26.VI.1936, det. & leg. J. de Beaumont (RMNH); 1♀, Var, Montauroux, Bagnols e. F. [Bagnols-en-Forêt], 26.VI.1960, leg. J. v. d. Vecht, det. M.A. Lieftinck (RMNH); 1♂, Cévennes, Cabrespine, 26.VI.2014, leg. K. Janssen (TJWC); 1♀, Var, Saint-Aygulf, 24.VII.1957, leg. P.M.F. Verhoeff, det. M.A. Lieftinck (RMNH).

Portugal. 1♂, Manteigas, Serra Estrella, 28.VI.1929, leg. Kriecheldorf, det. M.A. Lieftinck (RMNH); 3♀, Trás-os-Montes, Hills East of Moimenta, 2.VII.2016, leg. T.J. Wood (TJWC).

Spain. 1♀, Granada, Sierra Nevada, Central Hidroeléctrica del Poqueira environs, 2.VII.2021, leg. T.J. Wood (TJWC); 1♂, Granada, Sierra Nevada, Tivenque, Refugio de Rosales environs, 30.VI.2021, leg. T.J. Wood (TJWC); 2♂, 1♀, Ourense, Pena Trevinca, Penouta, Mina da Penouta, 15.VII.2020, leg. T.J. Wood (TJWC); 6♂, Parada de Rubiales, Salamanca, 24.VI.1961, leg. Weibes &

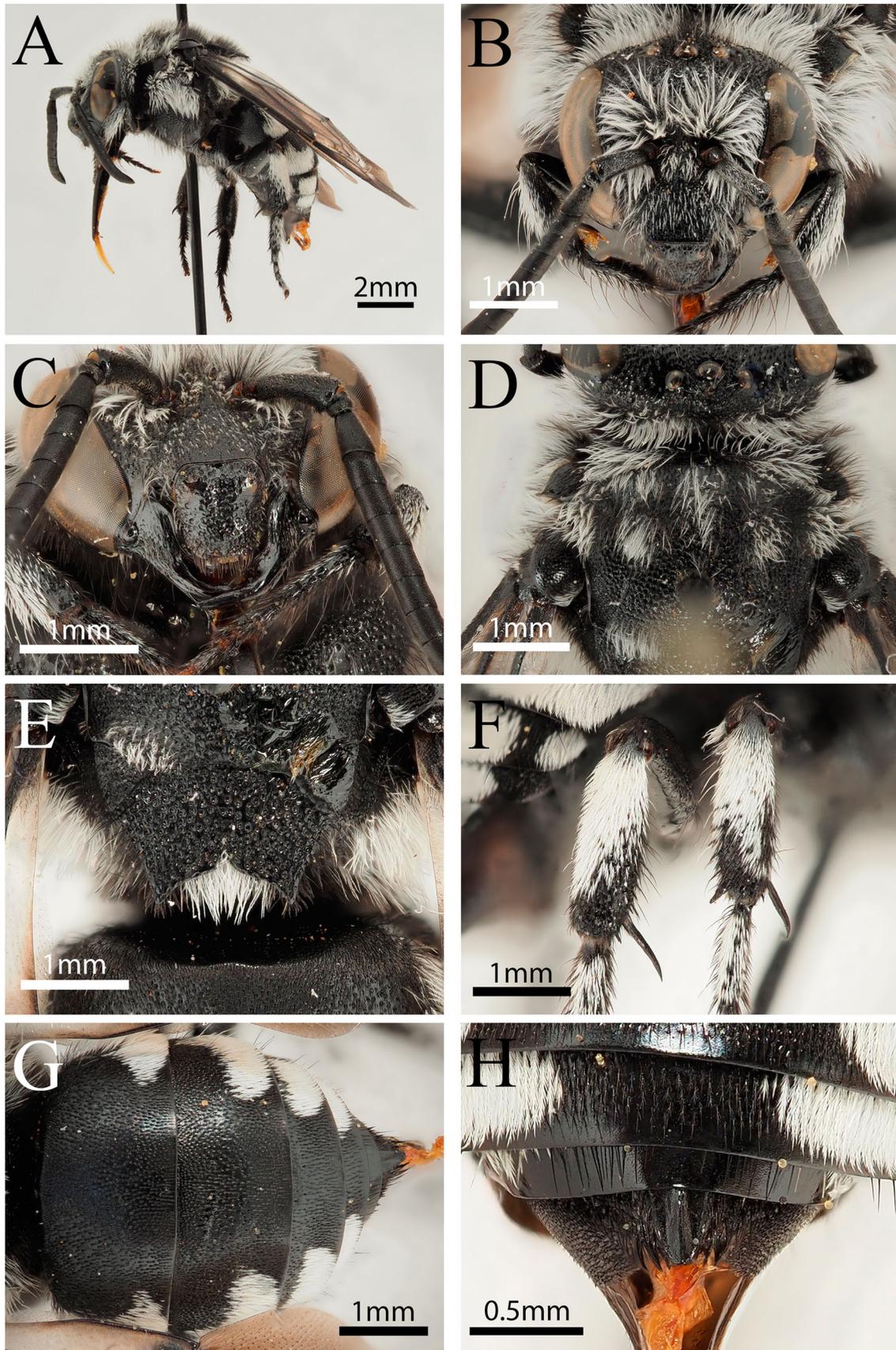


Figure 8. *Thyreus mauretaniensis* (Strand, 1911), female. **A**, Profile; **B**, face, frontal view; **C**, labrum, ventral view; **D**, scutum, dorsal view; **E**, scutellum, dorsal view; **F**, mid and hind tibiae, lateral view; **G**, terga, dorsal view; **H**, T4–5 and pygidial plate, dorsal view.

C. v. Heijningen, det. M.A. Liefstinck (RMNH); 1♂, Mecina Bombarón (Granada), 19.VI.1953, leg. J. Suárez, det. M.A. Liefstinck (RMNH); 2♀, Pontevedra, Villajuan [Vilaxoan], 14.VII.1963, leg. J.A.G. Delfos, det. M.A. Liefstinck (RMNH); 1♀, N.E. Spain, Cadaqués, 18.VI.1965, leg. J. v. d. Vecht, det. M.A. Liefstinck (RMNH); 1♀, Soria, 16.VI.1964, leg. W. Linsenmaier, det. M.A. Liefstinck (RMNH); 1♂, 1♀, Cádiz, Puerto Real, 30.VI.1969, leg. P.M.F. Verhoeff, det. M.A. Liefstinck (RMNH).

Switzerland. 1♀ paratype (Figure 9A–D), Wallis, Stalden, 25.VI.1902, leg. Steck, det. J. de Beaumont (RMNH); 2♀, Euseigne, 20.VI.1949; 4.VII.1951, leg. W. Linsenmaier, det. M.A. Liefstinck (RMNH).

Other material examined (?*Thyreus hirtus*)

Algeria. 1♂, Yakouren, Kabylie foret, 26.VI.1954, leg. G.L. v. Eyndhoven, det. *T. hirtus* by M.A. Liefstinck (RMNH).

Greece. 1♂, Crete, Sitia, 19.V.1963, leg. M. Schwarz, det. *T. hirtus* by M.A. Liefstinck (RMNH).

Genetics

Specimens of *T. hirtus* from France and Spain showed low intraspecific variation of 0.28% (range 0.00–0.55%). Specimens originally identified as *T. hirtus* from southern Morocco also showed low intraspecific variation of 0.57% (range 0.00–1.11%), but this group was strongly separated from European *T. hirtus* by an average genetic distance of 5.81% (range 4.98–5.49%). As a result, these two groups formed distinct clades with bootstrap support of 100 for *T. hirtus* and 95 for the Moroccan lineage. This strong genetic support supports a species-level difference between the European and Moroccan populations, and the latter is described as *Thyreus rasmonti* n. sp.

Description

Female. Body length: 9–12 mm (Figure 10A).

Head: Dark, 1.4 times wider than long (Figure 10B). Clypeus flattened over almost entire area, densely punctate, punctures separated by <0.5–0.5 puncture diameters; underlying surface shining. Labrum rectangular, slightly longer than broad, with longitudinal strongly impressed midline terminating subapically, surface here produced



Figure 9. *Thyreus hirtus* (Beaumont, 1939), female paratype. **A**, Label details; **B**, profile (scale bar = 2 mm); **C**, face, lateral view; **D**, terga, dorsal view.

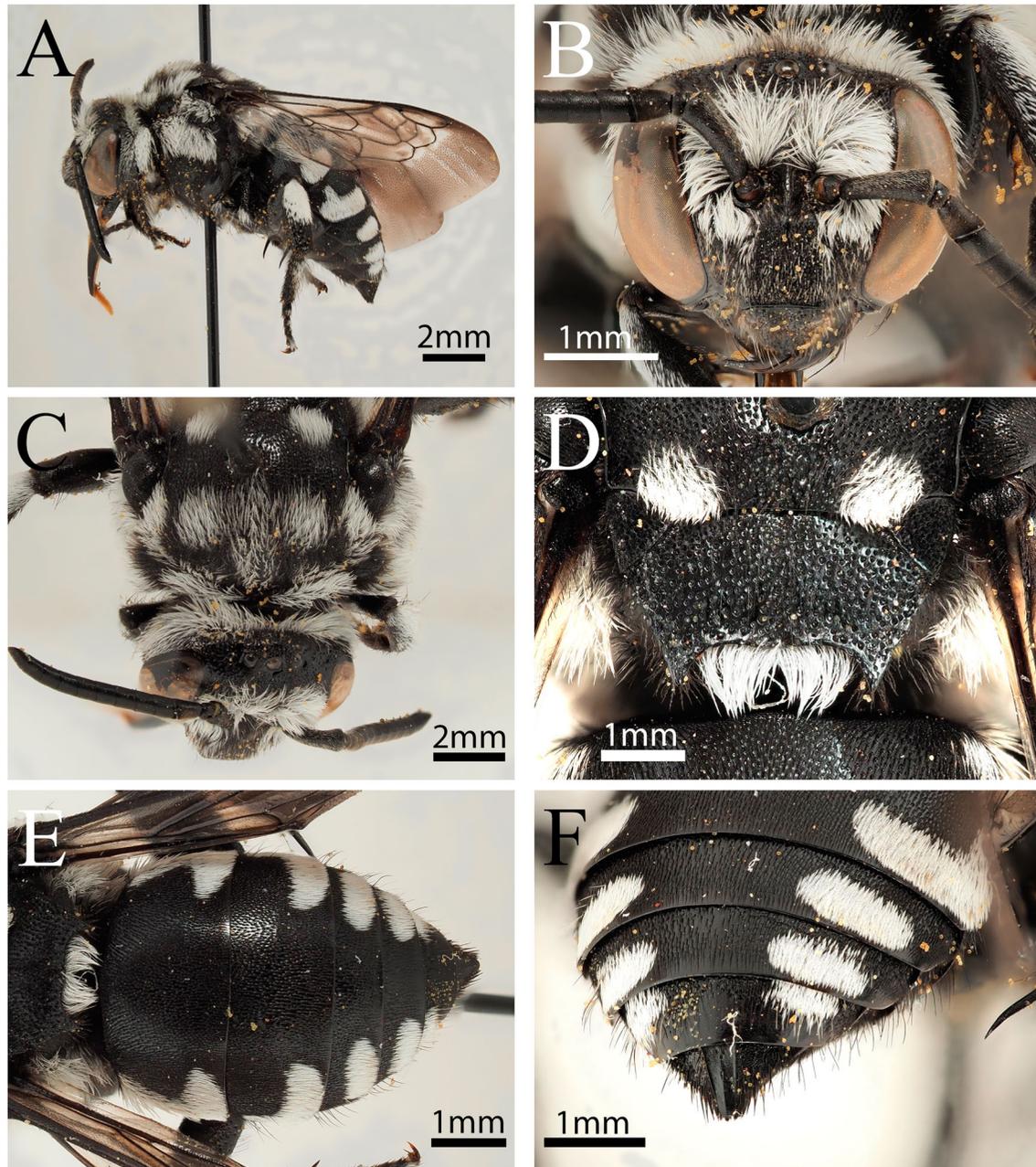


Figure 10. *Thyreus rasmonti* n. sp., female. **A**, Profile; **B**, face, frontal view; **C**, scutum, dorsal view; **D**, scutellum, dorsal view; **E**, terga, dorsal view; **F**, apical tergal segments and pygidial plate, posterior view.

into small triangular tooth; labrum basally weakly produced into two tubercles laterally. Gena slightly narrower than width of compound eye; ocelloccipital distance 2 times diameter of lateral ocellus. Hind margin of vertex with slightly raised carina-like rim. Face between antennal insertions with raised longitudinal carina. Frons densely punctate, punctures separated by 0.5 puncture diameters, becoming sparser dorsally, separated by 0.5–2 puncture diameters on vertex. Face with pubescence variable, frons and upper paraocular areas always white-haired, lower paraocular areas either extensively white-haired

with scattered dark brown hairs to more extensively dark-haired with scattered white hairs, not entirely dark-haired. Gena ventrally with black hairs, becoming white-haired posteriorly and dorsally, vertex medially with sparse black hairs. Antennae dark, Antennae dark, measured along ventral surface A3 equalling A4, A4–12 more or less quadrangular, slightly broader than long.

Mesosoma: Scutum and scutellum densely and regularly punctate, punctures typically separated by <0.5–0.5 puncture diameters, up to one puncture diameter on scutellum, underlying surface shiny. Scutum in anterior half with

raised white and black pubescence that does not obscure underlying surface, white pubescence forming poorly defined partial '+' sign medially (Figure 10C). Scutum posteriorly with white pubescence forming two distinct dense patches at base of axillae (Figure 10D). Scutellum broad, posteriorly weakly produced into two projecting points, medially widely but weakly emarginate with weak or absent medial notch; scutellum medially with large posteriorly projecting white hair tuft. Mesepisternum in dorsal half with dense patch of white hairs that obscure underlying surface, in ventral half with sparser black hairs, underlying surface clearly visible. Legs dark, with abundant white pubescence on outer face of tibiae and tarsi. Forewings weakly infusate over majority of their area, with exception of areas adjacent to veins Rr-m and 2m-cu and marginal and 1st cubital cells.

Metasoma: Terga dark, tergal discs punctate with hair-bearing punctures, punctures presenting short, posteriorly projecting black plumose hairs, punctures separated by 0.5–2 puncture diameters (Figure 10E). T1–2 laterally with L-shaped patch of white hairs, T3–5 with rectangular patches of white hairs, on T3 complete, not interrupted laterally but not reaching lateral margin of tergum (Figure 10F). Pygidial plate elongate, lateral margins raised, subparallel, weakly converging apically; pygidial plate medially with strongly raised longitudinal carina (Figure 10F).

Male. *Body length*: 8–13 mm (Figure 11A).

Head: Dark, 1.3 times wider than long (Figure 11B). Head structurally as in female, with following differences: labrum with medial longitudinal impression shallow. Antennal segments with rhinaria on posterior faces; A3 with single large oval rhinarium, A4–13 with pairs of rhinaria (Figure 11C), shallow and poorly defined, progressively becoming weaker, scarcely visible on A13 (Figure 12A).

Mesosoma: Mesosoma as in female, with following differences: scutum in anterior half with loose white pubescence, not forming poorly defined patches, with scattered intermixed dark hairs (Figure 11D). Scutum in posterior half with white pubescence forming two moderately dense patches at base of axillae (Figure 11E).

Metasoma: Metasoma structurally as in female (Figure 12F) with following differences: T7 apically truncate, apical margin wavy (Figures 11F and 12C), dorsal surface finely shagreened, deeply punctate, punctures separated by 0.5–1 puncture diameter, interspaces shining. S7 apically projecting, deeply rounded-emarginate medially (Figure 11G). S8 produced apically into two columnar projections, apically truncate; between projections with 2–3 stiff projecting hairs (Figure 11H). Genital capsule complex, gonocoxae with broad semi-circular emargination housing base of penis valves, inner margin forming 90° angle apically before descending to gonostyli (Figure 12E). Gonostyli

rectangular in lateral view, dorsal half covered in long dark brown hairs, hairs clearly exceeding length of gonostyli (Figure 12G); gonostyli with fleshy inner margin covered in curled, bristle-like brown hairs, not filling entire space between gonostyli. Penis valves compact, abruptly descending between gonostyli, apically produced into sharp points (Figure 12G).

Diagnosis

Thyreus rasmonti can easily be recognised as a *Thyreus* within the Melectini due to the flattened scutellum that extends posteriorly over the metanotum (Figure 10D) and lack of arolia. Within the *Thyreus*, it is closest to *T. hirtus* due to the form of the genital capsule with strong and thick gonostyli showing elongate hairs on their dorsal surface, these hairs clearly exceeding the gonostyli apically (Figure 12E–H), the apically truncate T7 with a slightly wavy margin (Figure 12C, D), the relatively broad and generally weakly emarginate scutellum (posterior angles not produced into sharp points), and terga with strong and clear lateral white hairbands (Figure 9D, Figure 10E, Figure 11F), laterally unbroken on T3 (Figure 10F). Diagnosis is difficult, since the species is almost entirely cryptic with *T. hirtus*.

In the male sex, separation can best be made by the antennal rhinaria (Figure 11C). In *T. rasmonti*, the rhinaria are relatively weakly impressed, on T13 they are almost absent, extremely shallow and indistinct (Figure 12A). In *T. hirtus*, the rhinaria are comparatively strongly impressed, on A13 they are visible, forming a small circular shape (Figure 12B). The face of *T. rasmonti* is often almost entirely white-haired, with at most scattered and intermixed black hairs, but some individuals have more extensive black pubescence. Lieftinck writes that the “clypeal pubescence [of *T. hirtus* is] invariably black, not white”. This character can be clearly seen in the original type material (Figure 9C). However, it is not always consistent, as a barcoded female from the Sierra Nevada in southern Spain has almost no black hairs on the face, leading to its incorrect determination as *Thyreus histrionicus* (Illiger, 1806) before genetic data were available, and one male of *T. rasmonti* from Imskr has extensive black facial pubescence. Facial pubescence is therefore considered to be a weak diagnostic character. Finally, the surface sculpture of male *T. rasmonti* is also slightly weaker than in *T. hirtus*, with finer shagreen. This is most clearly seen on T7 which is shining between the punctures (Figure 12C) whereas in *T. hirtus* the disc of T7 is strongly shagreened and dull between the punctures (Figure 12D).

In the female sex, separation is not possible. Facial pubescence is too variable to be used as a character. Female diagnosis is always more challenging in *Thyreus*, as evidenced by the cryptic *T. orbatus*/*T. mauretaniensis* and the lack of confident recognition of the female of

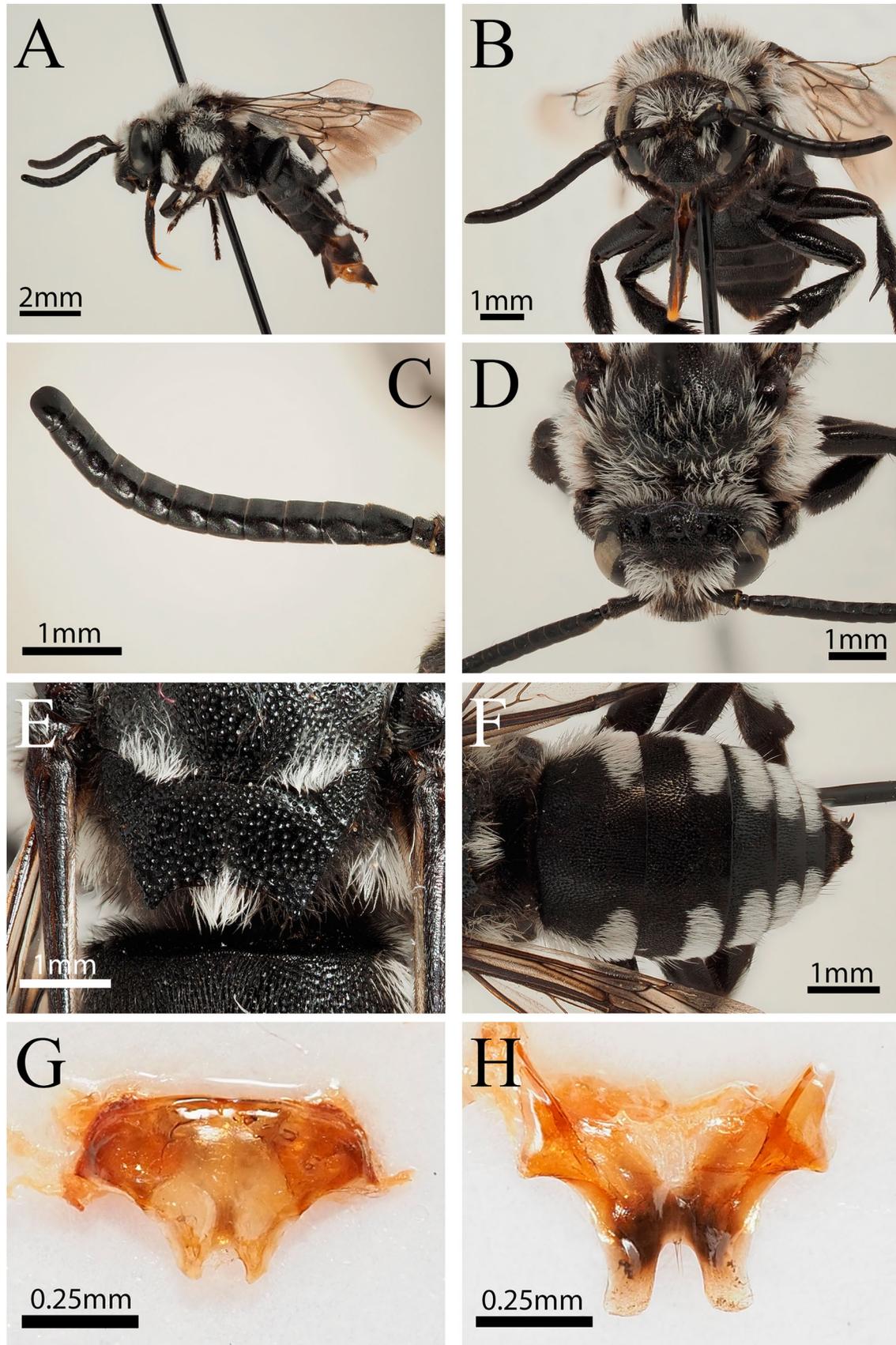


Figure 11. *Thyreus rasmonti* n. sp., male. A, Profile; B, face, frontal view; C, antenna, posterior view; D, scutum, dorsal view; E, scutellum, dorsal view; F, terga, dorsal view; G, S7, ventral view; H, S8, ventral view.

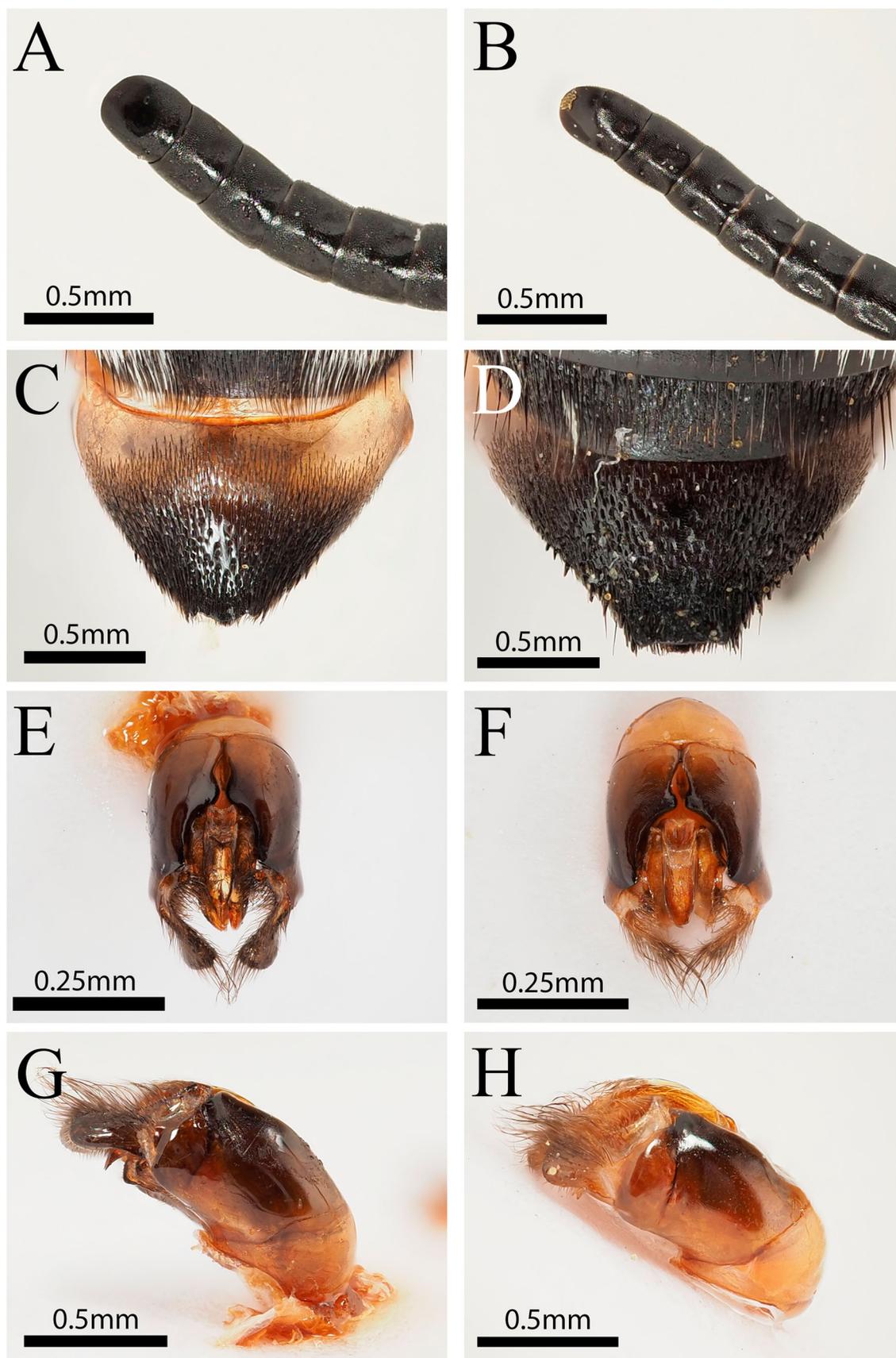


Figure 12. A, C, E, G, *Thyreus rasmonti* n. sp., male: A, antennal segment 13, dorsal view; C, T7, dorsal view; E, genital capsule, dorsal view; G, genital capsule, lateral view. B, D, F, H, *Thyreus hirtus* (Beaumont, 1939), male. B, antennal segment 13, dorsal view; D, T7, dorsal view; F, genital capsule, dorsal view; H, genital capsule, lateral view.

T. picaron Lieftinck, 1968 more than 50 years after its original description.

Finally, for clarity, *T. rasmonti* cannot be confused with *T. hohmanni* Schwarz, 1993 which was described from the Canary Islands (Gran Canaria; Schwarz 1993) because this species has the male genital capsule resembling *Thyreus ramosus* (Lepeletier, 1841), T7 is apically deeply and evenly rounded-emarginate, and the structures of S7–8 are completely different (see Figures in Schwarz 1993).

Remarks

Lieftinck (1968, p. 92) reported *T. hirtus* from the “whole Mediterranean area and West Asia”, but he presented specimen records predominantly from south-western Europe, with two additional specimens from Algeria, one from southern Russia, one from Greece, and one from Turkey. Examination of the specimen from Greece (Crete) shows that it has a face that is predominantly white-haired, which could be variation or could represent an unrecognised species. One of the specimens from Algeria is in fact a misidentified *T. mauretaniensis/orbatus* female (see above). The remaining male from northern Algeria does appear to be *T. hirtus* based on the diagnostic characters identified here, but maximum confidence requires genetic sequences from Algerian specimens. No *T. hirtus* specimens from Morocco were reported by Lieftinck, and none could be newly found in the RMNH collection. As for *T. orbatus*, the presence of true *T. hirtus* in Morocco must be confirmed with male or barcoded specimens.

Thyreus hirtus is suspected to attack *Anthophora* (*Paramegilla*) *femorata* (Olivier, 1789) (Baldock et al. 2018). It may also attack other *Paramegilla* species, as *A. femorata* is not present in Switzerland. In Switzerland, *T. hirtus* is restricted to the Valais canton in southern Switzerland, along with *A. (Paramegilla) balneorum* Lepeletier, 1841 (Amiet et al. 2007) which could serve as a host there. Both *A. femorata* and *A. balneorum* are specialists on *Echium* (Boraginaceae; Amiet et al. 2007; Baldock et al. 2018; TJW, unpublished data). Given the genetic and morphological similarity, it would be expected that *T. rasmonti* also attacks *Paramegilla* species.

In the Anti-Atlas, only one species of *Paramegilla* was recorded – *Anthophora blanda* Pérez, 1895. This species is morphologically very close to *A. femorata*. Specimens were not collected in direct sympatry with *T. rasmonti* specimens, but there is a good correspondence in size. At the Tizi n’Tichka and Oukaimeden sites in the High Atlas, anthophorine diversity was low. However, two members of the subgenus *Paramegilla* were common – *Anthophora podagra* Lepeletier, 1841 and *A. quadricolor* (Erichson, 1840). *Amegilla quadrifasciata* (de Villers, 1789) and *Amegilla albigena talaris*

(Pérez, 1895) (currently considered just a subspecies but highly likely to be a valid species; TJW, unpublished data) were also present, but these are not considered to be the host(s) because *A. quadrifasciata* is common and widespread and is attacked by *T. histrionicus* and *A. albigena talaris* is too small, and is additionally attacked by *T. ramosus*; both *T. histrionicus* and *T. ramosus* were common at the same collecting localities (see also Figure 7). The High Atlas *T. rasmonti* specimens from July are noticeably larger than those from the Anti-Atlas in March, but genetically are intermixed and show no morphological differentiation. The larger size corresponds well to the larger body size of *Anthophora podagra* and *A. quadricolor*. Whilst this must be considered only a hypothesis, I suspect that *T. rasmonti* attacks a range of *Paramegilla* species like its sister species *T. hirtus*. Additional study will be needed to confirm this hypothesis, but the patterns observed here are considered to be highly suggestive.

Etymology

Dedicated to the Belgian entomologist Pierre Rasmont who has also worked on bees intensively and productively for many decades, with a focus on *Bombus* and more recently Anthophorine and Melectine bees.

Distribution

Southern Morocco (Anti-Atlas and High Atlas).

Discussion

As discussed by Lhomme et al. (2020), Morocco has a large and species-rich bee fauna due to its remarkable biogeographical context. However, it is understudied due to its lack of resident bee experts and historical under-sampling when compared to neighbouring Algeria. These findings emphasise these points, with a wide variety of species from 14 different genera reported as new for the Moroccan fauna, with 14 of these species already previously recorded from Algeria. Importantly, these records also highlight the under-sampled nature of the Middle Atlas (Wood et al. 2020) and the elevated high steppe and semi-desert habitats to its immediate east and south-east (predominantly in the province of Fès-Meknès), with 11 of the 16 newly recorded species for Morocco coming in whole or in part from this region.

The other major under-sampled area of Morocco is that of the Drâa valley, predominantly in the province of Drâa-Tafilalet. It was in this region that *Ammobatoides schwarzi* n. sp. was discovered in dry rocky habitats. This part of Morocco contains many range-restricted and endemic

bee species, and when the fauna has received recent taxonomic attention, a large number of new species have been described (Wood et al. 2020; Müller 2022), many of which are likely to be endemic to this area. An upcoming revision of Moroccan *Andrena* (Wood, *in review*) will further support this trend. The Souss-Massa and Marrakech-Safi regions that contain the Anti-Atlas and High Atlas ranges in which *Thyreus rasmonti* n. sp. was discovered are slightly better sampled, but still produced isolated or overlooked populations of species such as *Ammobates rufiventris*, *Chelostoma campanularum*, and *Thyreus mauretaniensis*. Taken together, it is important to consider why the Souss-Massa, Drâa-Tafilalet, and Marrakech-Safi regions contain such a high number of endemic bee species, numbers that clearly make it one of the hot spots for endemism in the Mediterranean basin. Though nominally connected by land to the rest of North Africa, this region is ecologically isolated by multiple barriers. To the south and the east, the rocky desert becomes sandier, and upon reaching the province of Guelmim-Oued Noun and the provinces of Béchar and Tindouf in western Algeria, the landscape is increasingly featureless. This sandy desert does not retain water and humidity in valleys and ravines as effectively as rocky desert and consequently supports a lower diversity and abundance of flowering plants, and hence a lower diversity of bee species. To the north, the Atlas Mountains are both a barrier to northward expansion, and also provide high altitude mountainous habitats that cannot be found elsewhere in North Africa. They therefore isolate species that cannot cross them, and also isolate species that cannot disperse to ecologically similar high-altitude habitats which are not present until southern Spain or the Hoggar Mountains in southern Algeria. The impact of the Atlas Mountains in structuring vertebrate species is well known (e.g. Brown et al. 2002; Fritz et al. 2006), and whilst genetic study of the Moroccan bee fauna is in its infancy, comparative studies are likely to confirm a similar trend in bees based on the observed pattern of endemism seen in south-western Morocco.

Finally, none of the new species presented here come from the species-rich genera *Andrena*, *Eucera* and *Tetralonia*, or *Hylaeus* that are all undergoing taxonomic revisions. With these upcoming revisions, our knowledge of the Moroccan fauna will continue to undergo major changes. Increased sampling and the development of domestic Moroccan expertise will only contribute positively to an improved understanding in this extraordinarily species-rich region.

Acknowledgements

I am supported by an F.R.S.-FNRS fellowship (Chargé de recherches). My thanks go to the taxonomists who were instrumental in making or confirming identifications for the taxa presented here: Andreas Müller (Wädenswil, Switzerland), Christophe Praz (Neuchâtel, Switzerland), Jakub Straka

(Prague, Czech Republic) and Pierre Rasmont (Mons, Belgium). I thank Vladimir Radchenko and an anonymous reviewer for helpful comments that improved the manuscript. I also thank Frederique Bakker (RMNH) for access to the Lieftinck collection, and Esther Ockermüller and Martin Schwarz (OÖLM) for access to the Linz collection.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by Fonds De La Recherche Scientifique - FNRS [individual fellowship Chargé de recherches].

ORCID

Thomas J. Wood  <http://orcid.org/0000-0001-5653-224X>

References

- Alfken JD. 1914. Beitrag zur Kenntnis der Bienenfauna von Algerien. Mémoires de la Société entomologique de Belgique. 22:185–237.
- Amiet F, Herrmann M, Müller A, Neumeyer R. 2007. Apidae 5. *Ammobates*, *Ammobatoides*, *Anthophora*, *Biastes*, *Ceratina*, *Dasygoda*, *Epeoloides*, *Epeolus*, *Eucera*, *Macropis*, *Melecta*, *Melitta*, *Nomada*, *Pasites*, *Tetralonia*, *Thyreus*, *Xylocopa*. Fauna Helvetica 20, info fauna CSCF & SEG, Neuchâtel, 356 pp.
- Ascher JS, Pickering J. 2021. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Available from: https://www.discoverlife.org/mp/20q?guide=Apoidea_species (accessed 7 October 2022).
- Astafurova YA, Proshchalykin MY, Schwarz M. 2019. The distribution of the genus *Sphecodes* Latreille (Hymenoptera, Halictidae) of the Arabian Peninsula and surrounding countries with description of hitherto unknown female of *S. atlanticus* Warncke, 1992 and male of *S. dathei* Schwarz, 2010. Zookeys. 872:13–40. doi:10.3897/zookeys.872.35361.
- Baldock D, Wood TJ, Cross I, Smit J. 2018. The bees of Portugal (Hymenoptera: Apoidea: Anthophila). Entomofauna. Supplement 22:1–164.
- Beaumont J. de. 1939. Les *Crocisa* de la faune française. Annales de la Société entomologique de France. 58:161–171.
- Bischoff H. 1952. Über das Vorkommen der Schmarotzerbiene *Ammobatoides abdominalis* (Eversm.) in Deutschland und Bemerkungen zu ihrem Wirt: *Melitturga clavicornis* Latr. Nachrichten des Naturwissenschaftlichen Museums der Stadt Aschaffenburg. 35:55–68.
- Bleidorn C, Henze K. 2021. A new primer pair for barcoding of bees (Hymenoptera: Anthophila) without amplifying the orthologous *coxA* gene of *Wolbachia* bacteria. BMC Research Notes. 14:427. doi:10.1186/s13104-021-05845-9.
- Bogusch P, Straka J. 2012. Review and identification of the cuckoo bees of central Europe (Hymenoptera: Halictidae: *Sphecodes*). Zootaxa. 3311:1–41. doi:10.11646/zootaxa.3311.1.1.

- Bossert S, Wood TJ, Patiny S, Michez D, Almeida EAB, Minckley RL, Packer L, Neff JL, Copeland RS, Straka J, et al. 2022. Phylogeny, biogeography and diversification of the mining bee family Andrenidae. *Systematic Entomology*. 47:283–302. doi:10.1111/syen.12530.
- Boustani M, Rasmont P, Dathe HH, Ghisbain G, Kasperek M, Michez D, Müller A, Pauly A, Risch S, Straka J, et al. 2021. The bees of Lebanon (Hymenoptera: Apoidea: Anthophila). *Zootaxa*. 4976:1–146. doi:10.11646/zootaxa.4976.1.1.
- Brown RP, Suárez NM, Pestano J. 2002. The Atlas mountains as a biogeographical divide in North–West Africa: evidence from mtDNA evolution in the Agamid lizard *Agama impalearis*. *Molecular Phylogenetics and Evolution*. 24:324–332. doi:10.1016/S1055-7903(02)00218-X.
- Ebmer AW. 1995. Asiatische Halictidae, 3. Die Artengruppe der *Lasioglossum* carinate-*Evyllaes* (Insecta: Hymenoptera: Apoidea: Halictidae: Halictinae). *Linzer biologische Beiträge*. 27:525–652.
- Eickwort GC. 1980. Two European species of *Chelostoma* established in New York State (Hymenoptera: Megachilidae). *Psyche*. 87:315–323. doi:10.1155/1980/24124
- Friese H. 1900. Neue palaearktische Bienenart. *Entomologische Nachrichten*. 6:85–87.
- Friese H. 1901. Die Bienen Europa's (Apidae europaeae). VI. Innsbruck, Austria, 284pp.
- Fritz U, Barata M, Busack SD, Fritsch G, Castilho R. 2006. Impact of mountain chains, sea straits and peripheral populations on genetic and taxonomic structure of a freshwater turtle, *Mauremys leprosa* (Reptilia, Testudines, Geoemydidae). *Zoologica Scripta*. 35:97–108. doi:10.1111/j.1463-6409.2005.00218.x.
- Gouy M, Guindon S, Gascuel O. 2010. Seaview version 4: A multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molecular Biology and Evolution*. 27:221–224. doi:10.1093/molbev/msp259.
- Ivanova NV, Dewaard JR, Hebert PDN. 2006. An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Notes*. 6:998–1002. doi:10.1111/j.1471-8286.2006.01428.x.
- Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution*. 30:772–780. doi:10.1093/molbev/mst010.
- Kuhlmann M, et al. (co-authors as listed in “Contributors”). 2014. Checklist of the Western Palaearctic Bees (Hymenoptera: Apoidea: Anthophila). Available from: <http://westpalbees.myspecies.info> (accessed 7 October 2022).
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K. 2018. MEGA x: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution*. 35:1547–1549. doi:10.1093/molbev/msy096.
- Lepeletier de Saint-Fargeau ALM. 1841. Histoire naturelle des Insectes – Hyménoptères. Volume 2. Roret, Paris.
- Lhomme P, Michez D, Christmann S, Scheuchl E, El Abdouni I, Hamroud L, Ihsane O, Sentil A, Smaili MC, Schwarz M, et al. 2020. The wild bees (Hymenoptera: Apoidea) of Morocco. *Zootaxa*. 4892:1–159. doi:10.11646/zootaxa.4892.1.1.
- Lieftinck MA. 1968. A review of Old World species of *Thyreus* Panzer (= *Crocisa* Jurine) (Hym, Apoidea, Anthophoridae). Part 4. Palearctic species. *Zoologische Verhandlungen*. 98:1–139.
- Lucas H. 1849. Exploration scientifique de l'Algérie, Zoologie. Hyménoptères. Exploration scientifique de l'Algérie, 3, 141–344. Imprimerie royale, Paris, France.
- Michener CD. 2007. The Bees of the World, 2nd Edition. Baltimore: Johns Hopkins University Press. 972.
- Morice FD. 1916. List of some Hymenoptera from Algeria and the M'Zab country. *Novitates Zoologicae*. 23:241–246.
- Müller A. 2012. New European bee species of the tribe Osmiini (Hymenoptera: Apoidea: Megachilidae). *Zootaxa*. 3355:29–50. doi:10.11646/zootaxa.3355.1.2.
- Müller A. 2014. Palaearctic *Hoplitis* bees of the subgenus *Stenosmia* (Megachilidae, Osmiini): biology, taxonomy and key to species. *Zootaxa*. 3765:301–316. doi:10.11646/zootaxa.3765.4.1.
- Müller A. 2022. New Moroccan bee species of the tribe Osmiini (Hymenoptera: Apoidea: Megachilidae). *Zootaxa*. 5188:233–263. doi:10.11646/zootaxa.5188.3.2.
- Patiny S. 1999. Systématique générique et subgénérique des *Melitturga* Latreille-*Melitturgula* Friese-*Flavomelitturgula* Warncke (Hymenoptera, Andrenidae, Panurginae). *Bulletin de la Société entomologique de France*. 104:241–256. doi:10.3406/bsef.1999.16576.
- Patiny S. 2001. Monographie des Panurginae de l'ancien monde (Hymenoptera: Apoidea, Andrenidae) [dissertation]. Gembloux (Belgium): Faculté universitaire des Sciences agronomiques de Gembloux.
- Patiny S. 2012. Atlas of the European Bees: genus *Melitturga*. STEP Project, Atlas Hymenoptera, Mons, Belgium. <http://www.zoologie.umh.ac.be/hymenoptera/page.aspx?ID=234>.
- Pauly A. 2016a. Le genre *Lasioglossum*, sous-genre *Evyllaes* Robertson, 1902, de la Région Paléarctique. Atlas Hymenoptera, Mons, Belgium. <http://www.atlashymenoptera.net/page.aspx?id=95>.
- Pauly A. 2016b. Genus *Vestitohalictus* Blüthgen, 1961. Atlas Hymenoptera, Mons, Belgium. <http://www.atlashymenoptera.net/page.aspx?id=97>.
- Popov VV. 1933. Notes on the parasitic bees allied to the genus *Biastes* Panz. *Trudy Instituta Zoologii. Akademii Nauk SSSR*. 2:51–75.
- Proshchalykin MY, Lelej AS. 2014. Review of the genus *Ammobatoides* Radoszkowski, 1867 (Hymenoptera: Apidae, Nomadinae) from Russia and neighbouring countries. *Zootaxa*. 3852:445–460. doi:10.11646/zootaxa.3852.4.3.
- Radchenko VG. 1985. On the nesting of *Paranthidiellum lituratum* and parasitism in its nest by *Stelis punctulatissima*. *Vestnik Zoologii*. 3:77–79. [in Russian].
- Rasmont P. 2014. Atlas of the European Bees: genus *Anthophora*. 1st Edition. STEP Project, Atlas Hymenoptera, Mons, Gembloux. <http://www.atlashymenoptera.net/page.aspx?ID=260>.
- Rasmont P, Devalez J, Pauly A, Michez D, Radchenko V. 2017. Addition to the checklist of IUCN European wild bees (Hymenoptera: Apoidea). *Annales de la Société entomologique de France*. 53:17–32. doi:10.1080/00379271.2017.1307696.
- Schmidt S, Schmid-Egger C, Morinire J, Haszprunar G, Hebert PDN. 2015. DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees (Hymenoptera, Apoidea *partim*). *Molecular Ecology Resources*. 15:985–1000. doi:10.1111/1755-0998.12363.
- Schwarz M. 1988. Zur Kenntnis parasitärer Apiden aus Nord-Afrika (Hymenoptera, Apoidea). *Entomofauna*. 9:225–232.
- Schwarz M. 1993. Eine neue *Thyreus*-Art von der Kanarischen Inseln: *Thyreus hohmani* n.sp. (Insecta: Hymenoptera:

- Apoidea: Anthophoridae). Veröffentlichungen aus dem Übersee-Museum Bremen. 12:869–873.
- Schwarz M, Smit J. 2018. Neue paläarktische Wespenbienen der Gattung *Nomada* Scopoli, 1770 (Hymenoptera, Apidae). Entomofauna. 39:881–908.
- Strand E. 1911. Neue Afrikanische Arten der Bienengattungen *Melecta*, *Crocisa* und *Megachile*. 1:78–79.
- Warncke K. 1972. Westpaläarktische Bienen der Unterfamilie Panurginae (Hym., Apidae). Polskie Pismo Entomologiczne. 52:53–108.
- Warncke K. 1977. Beitrag zur Systematik der westpaläarktischen Bienengattung *Dioxys* Lep. & Serv. (Hymenoptera, Apoidea). Reichenbachia. 16:265–282.
- Warncke K. 1982. Beitrag zur Bienenfauna des Iran 14. - Die Gattung *Halictus* Latr., mit Bemerkungen über bekannte und neue *Halictus*-Arten in der Westpaläarktis und Zentralasien. Bollettino del Museo civico di Storia Naturale di Venezia. 32:67–166.
- Warncke K. 1992. Die Westpaläarktischen Arten der Bienengattung *Sphecodes* Latr. (Hymenoptera, Apidae, Halictinae). Bericht der Naturforschenden Gesellschaft Augsburg. 52:9–64.
- Wood TJ, Cross I. 2017. *Camptopoeum* (*Camptopoeum*) *baldocki* spec. nov., a new panurgine bee species from Portugal and a description of the male of *Flavipanurgus fuzetus* Patiny (Andrenidae: Panurginae). *Zootaxa*. 4254:285–293. doi:10.11646/zootaxa.4254.2.9.
- Wood TJ, Michez D, Cejas D, Lhomme P, Rasmont P. 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, Patiny S, Bossert S. 2022. An unexpected new genus of panurgine bees (Hymenoptera, Andrenidae) from Europe discovered after phylogenomic analysis. *Journal of Hymenoptera Research*. 89:183–210. doi:10.3897/jhr.89.72083.