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Research Article

Black bees in the desert: Description of a new species of wool carder bee (Hymenoptera, Megachilidae, *Anthidium*) from the northern Sahara with colouration atypical for xeric environments

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Abstract

Bees inhabiting xeric environments often exhibit, like many other insects, brown, beige, and sandy colours, aligning with the hues of the desert landscape. In this study, we study two bee species belonging to the tribe Anthidiini that defy this general colour pattern. These species feature an almost entirely black integument, contrasting with the typical rich yellow or beige colour pattern found in most members of the genus *Anthidium* Fabricius, 1804. The new species, *A. nigrum* Kasparek, **sp. nov.**, was found in the deserts of the northern Sahara, where also another dark congener lives, the little-known *Anthidium pullatum* Morice, 1916, which is re-described here based on the rediscovery of the type material which has been thought lost. We hypothesise that this colouration phenomenon may be explained by an adaptation to the strong day-and-night temperature differences in the desert environment. The black colouration enables bees to harness solar energy early in the day, capitalizing on enhanced heat retention due to the lower reflectance of their integument. It is hypothesized that this allows bees to optimize their activity pattern during the brief period before temperatures rise to levels posing a high risk of overheating.

Key Words

Adaptation to extreme climates, colouration, desert dwellers, taxonomy, Thermal Melanism Hypothesis

Introduction

Bees, like many other insects inhabiting xeric environments, often exhibit light brown, beige, and sandy colours, blending with the hues of desert landscapes. This pale colouration serves a dual purpose: reflecting heat to prevent overheating and providing camouflage by matching the body colour with the pale soils and sparse vegetation typical of deserts, making them less visible to predators (Michener 2007). According to the Thermal Melanism Hypothesis (TMH), dark colouration may be considered unfavourable in hot environments as it could limit survival under extreme conditions (e.g., Kettlewell 1955; Watt 1968; Majerus 1998; Clusella-Trullas et al. 2008; Kuyucu et al. 2018). In fact, bees in xeric environments are predominantly pale, while species with dark body colouration are rare. Herein, we describe a previously unknown wool carder bees of the genus *Anthidium* Fabricius, 1804, from the northern Sahara, which defy this general colour pattern, and re-describe the poorly known *Anthidium pullatum* Morice, 1916, which shows similar characters.

Wool carder bees belonging to the genus *Anthidium* are distributed on all continents except Antarctica, and most are characterized by a more or less extensive pattern of yellow to cream-coloured (sometimes red) markings (Michener 2007). Typically, these bees exhibit yellow metasomal

bands, often interrupted medially, providing them with a wasp-like appearance. However, a few species lack these light markings on meso- and metasoma, also posing a challenge for immediate identification as belonging to this genus. A notable example is *Anthidium montanum* Morawitz, 1865, characterized by its dark colouration and rich pubescence. This species is unique among West Palaearctic *Anthidium* as it lacks yellow tergal bands in both sexes. In this species, light markings are limited to a very small pale-yellow spot behind the eye and, in the male, on the lower face (habitus photographs in Kasparek 2022). Similarly, the North African *A. pullatum* Morice, 1916, has in the female only a minute yellow dot behind the eye, while the male exhibits a richer yellow colouration pattern (Morice 1916; Pasteels 1981; Warncke 1980). Other dark species with a similar colour pattern include *Anthidium kashmirense* Mavromoustakis, 1937, and *A. pseudomontanum* Niu & Zhu, 2020 from Asia (Niu et al. 2020). Among the *Anthidium* species of the Nearctic realm, species with entirely black meso- und metasoma include *Anthidium rodriguezi* Cockerell, 1912 from Central America (Honduras, Guatemala, Mexico), and *Anthidium chamelense* Gonzalez & Griswold, 2013 from Mexico (Cockerell 1912; Gonzalez and Griswold 2013). The new species described here from the northern Sahara exhibits similar characteristics, being almost entirely black, which is atypical for members of *Anthidium*. In addition to describing this new species, we re-describe the little-known dark desert-dweller *A. pullatum*, whose types we rediscovered among unidentified material in the Natural History Museum London. We discuss the possible role of black body colour in surviving under extreme climatic conditions.

Methods

Photographs were taken with a Canon MPE65/2.8 lens mounted on a Canon EOS 6D camera. We used a Canon Twin Lite MT24EX Macro Flash. We moved the camera between the shots with a Cognisys StackShot Rail and took between 25 and 30 photographs at different focal levels to obtain images with a more extended depth of field than any of the individual source images. Subsequently, we processed the pictures with Helicon Focus (version 6.7.1) software to combine the pictures and to create one completely focused image from several partially focused images (image stacking). We then processed the resulting images with Adobe Photoshop Elements 15.

DNA extraction, PCR amplification and sequencing were conducted by the Canadian Centre for DNA Barcoding (CCDB), Guelph, using standardised high-throughput protocols (http://ccdb.ca/resources). The barcoding unit of the mitochondrial cytochrome c oxidase subunit I gene (COI) was sequenced, and the results were submitted to Barcode of Life Data System (BOLD), a cloud-based data storage and analysis platform developed by CCDB (https://www.barcodinglife.com).

The map was prepared with www.simplemappr.net (Shorthouse 2010).

Abbreviations

AMNH = American Museum of Natural History; **CMK** = collection Max Kasparek, Heidelberg, Germany; **NHMUK** = Natural History Museum London, UK; **RMNH** = Naturalis Biodiversity Centre, Leiden, the Netherlands; **TJW** = Thomas J. Wood collection, Leiden, the Netherlands.

Anthidium pullatum Morice, 1916

Figs 1–3

Type material (examined). ***Lectotype***, by present designation. • ♀, ALGERIA: "Oued Nça, Mzab county, April 16.–30.1914 (E. H. & C. H.)", "British Museum 1024-292"; "101"; NHMUK. – ***Paralectotype*:** • 1 ♀, data as for lectotype. – Notes: "E. H." surely stands for Ernst Hartert, and "C. H." for Carl Hilgert, two ornithologists who jointly conducted zoological research in Algeria in 1914. Ernst Hartert was at that time curator of birds at W. Rothschild's Museum at Tring (Herts) and a large part of this zoological collection was later transferred to the NHMUK, which may explain the deposition of the bee material there. The type locality is Wadi N'sa ("Oued Nça"), Ghardaia Province of Algeria, in the M'zab ("Mzab") region. According to the travel itinerary (Hartert 1915), the collectors stayed at a rest house in Hassi er Rebib (32.65°N, 4.172°E) on the collection date. Pasteels (1981) reported that, despite extensive efforts, he was unable to locate the type material of *A. pullatum*. The specimens discussed here were not labelled as type material and had been stored for over a century in a drawer of unidentified material at the NHMUK. However, the labels on these two females unequivocally indicate that they are the types described by Morice (1913), which were previously believed to be lost.

Other material (examined). MOROCCO • 1 ♀; 10 km N Mhamid; 29.89°N, 5.72°E; 21.–22 Apr. 1995; Mi. Halada leg.; CMK. • 1 ♀; 20 km SE Quarzazate, 30.78°N, 6.72°W; 10 Apr. 1996; M. Schwarz leg.; CMK • 9 ♀, 1 ♂; 20 km W Boudnib, 32.05°N, 3.77°W; 09 Apr. 1995; Mi. Halada leg.; CMK • 1 ♀; 40 km W Quarzazate, 5 km S Amerzgane, 31.01°N, 7.17°W; 08 Apr. 1996; O. & M. Niehuis leg.; CMK • 1 ♂; 80 km S Er Rachidia, 20 km W Rissani, 31.27°N, 4.41°W; 04 Apr. 1996; O. & M. Niehuis leg.; CMK) • 1 ♂; Agdz, 30 km NW, 30.85°N, 6.63°W; 01 Apr. 1986; M. Schwarz leg.; CMK • 6 ♀, 2 ♂; Draa-Tafilalet: Quarzazate, P1507, 3 km SSE Irhels, 30.70°N, 7.07°W; 12 Apr. 2022; T. Wood leg.; TJW (including barcoded specimens tjw274 and tjw283) • 1 ♀, 2 ♂; Draa-Tafilalet: Tazenakht, P1507, 5 km NE Tazenakht, 30.62°N, 7.14°W; 17 Apr. 2022; T. Wood leg.; TJW • 3 ♀, 3 ♂; Foum Zguid, 50 km N, 30.49°N, 6.88°W; 30 Mar. 1986; M. Schwarz leg.; CMK • 1 ♂, Guelmim-Oued Noun: Ouaaroun, 28.91°N, 10.16°W; 23 Mar. 2023; A. Aglagane & O. Errguibi leg.; coll. Skaou Ayyoub, Marrakesh, Morocco • 1 ♀; Imi-n'Kem, 50 km E Agdz, 30.86°N, 5.96°W; 15 Apr. 1996; M. Schwarz leg.; CMK • 1 ♂; Guelmim-Oued Noun: Ouaaroun, 28.91°N,

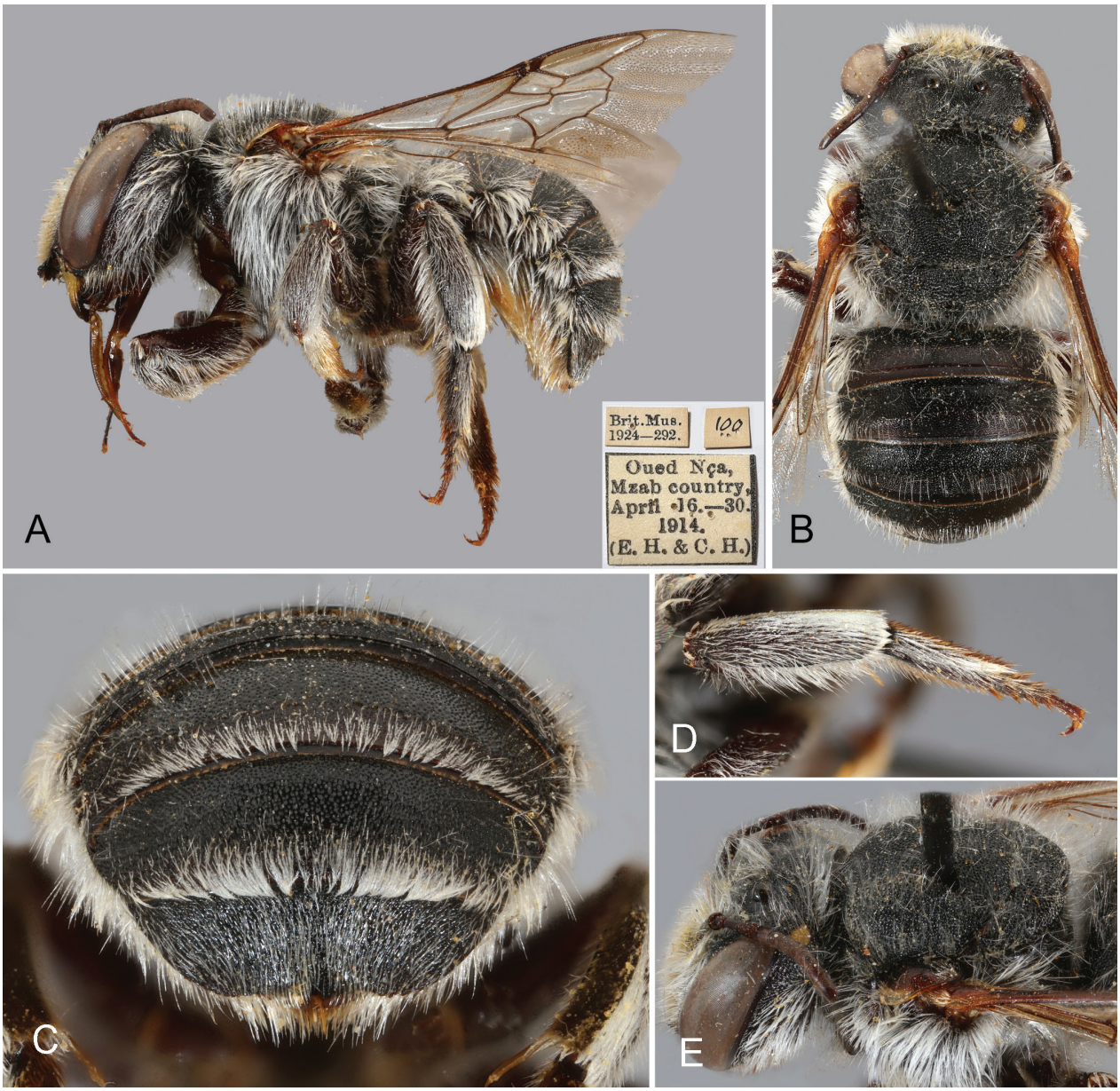

Figure 1. *Anthidium pullatum*, female, lectotype. **A.** Habitus, lateral; **B.** Habitus, dorsal; **C.** Apical terga; **D.** Hind tibia and tarsus; **E.** Head and mesosoma, dorsolateral.

10.16°W; 23.iii.2023; A. Aglagane. O. Errguibi leg.; coll. Ahlam Sentil, Mons, Belgium • 1 ♂; Quaouzagour: 30 km E Agdz, 30.68°N, 6.13°W; 14 Apr. 1996; J. Gusenleitner leg.; CMK • 1 ♀; Tagounite: 60 km S Zagora, 29.98°N, 5.58°W; 23.iv.1995; Mi. Halada leg.; CMK • 2 ♂; Tizi-n-Fedrhate: 60 km NE Quarzazate, 31.11°N, 6.66°W; 11.iv.1996; M. Schwarz leg.; CMK) • 2 ♀, 1 ♂; Zagora, 30.38°N, 5.85°W; 09 Mar. 992; H.-J. Flügel leg.; CMK.

Material (not examined). • 2 ♀, 1 ♂; 19 km SE Errachidia ("Ksar-es-Souk"), 31.93°N, 4.42°W; 20 Apr. 1968; J. G. Rozen & E. Suissa leg.; AMNH (Warncke 1980; Pasteels 1981) • 1 ♀, 2 ♂; Erfoud, 31.43°N, 4.23°W; 21 Mar. 1990; leg. Teunissen; RMNH (van der Zanden 1996) • 1 ♂; Uarz., Agdz, (30.70°N, 6.45°W; 8 Mar. 1988; Lefeber leg.; RMNH (van der Zanden 1996 • 1 ♀; 32 km SE Quarzazate, 30.84°N, 6.59°W; 17 Apr. 1968 (Warncke 1980).

Diagnosis. Robust *Anthidium* species; female entirely black except for a minute yellow spot behind the eye (Fig. 1B); depression of terga 4 and 5 with fringe of appressed white hairs (Fig. 1C); hind tibia with strong longitudinal carina; mandible yellow with brown margins (Fig. 2). The female is distinguished from other dark *Anthidium* species in the West Palaearctic by the presence of a longitudinal carina on hind tibia (absent in *A. montanum* and *A. nigrum* sp. nov.), a whitish-yellow scopa (dark brown hairs in *A. nigrum* sp. nov.), and yellow mandibles with black teeth (mandibles and teeth black in *A. montanum* and *A. nigrum* sp. nov.). The male is characterized by the shape of tergum 7, which has a strong median spine and elongated lateral lobes, combined with a strongly reduced yellow maculation of the terga, featuring a small lateral yellow spot on terga 3 and 4, and lateral and mediolateral spots on tergum 5 (Fig. 3A, C).

Figure 2. Face of *Anthidium pullatum*, female, lectotype.

Genetic barcode. The DNA sequences of the barcoding unit of the mitochondrial cytochrome c oxidase subunit 1 gene (COI) has been obtained from two specimens from Morocco (tjw274, tjw283) and was made publicly available on the BOLD platform (https://www.boldsystems.org) for species identification purposes. The DNA sequence was assigned a new Barcode Index Number (BIN), BOLD:AFC0815. BINs are unique identifiers assigned to clusters of DNA barcode sequences that represent distinct species or operational taxonomic units (OTUs).

Description female. Length: 10 mm. Intertegular distance: 6.65±0.36 mm (N=25); radial cell length: 3.66±0.19 mm (N=25). ***Head*.** Black with a small round, yellow spot behind the eye (Fig. 1B); lower paraocular area sometimes with subtle, light brown brightening; clypeus slightly protruding at the longitudinal midline; punctation dense, somewhat denser apically than on rest of surface; clypeal apical margin black, protruding, with contiguous and confluent tubercles (Fig. 2); clypeal surface with apically curved hairs (but hairs often worn with ends broken off); mandible yellow with five black teeth separated by acute notches; acetabular carina sharp, extending to the second tooth (counted from the apical tooth); antenna dark brown; long silvery hairs around the antennal socket and on gena, less dense also on vertex. ***Mesosoma*.** Black; omaulus angular; punctation dense, with punctures separated by narrow ridges; punctures on scutellum and axilla slightly larger than on scutum; scutellum and axillae crescent-shaped in dorsal view, rounded in profile; scutellum depressed medioapically; pronotal lobe with anterior lamella. ***Metasoma*.** Terga 1–6 with very fine punctation, much finer than on scutum and scutellum; punctation on discs irregular with punctures of different diameters and shapes; punctation on depressions finer and regular; very narrow impunctate apical margin; depression of terga 4 and 5 with appressed fringe of silvery hairs (fringe denser on tergum 5 than on tergum 4); tergum 6 semi-trapezoid, depressed laterally and with an apical emargination to accommodate the sting; terga 1–6 with white hairs laterally; metasomal scopa silvery. Among 25 females examined, three had a minute lateral yellow spot on tergum 3, and one female had such spots on terga 2–5. ***Legs*.** Chestnut-brown; tibiae covered with long white hairs; hind tibia with strong longitudinal carina; inner face of tarsi with short, brown setae. ***Wing*.** Slightly infuscated; veins brown; the second recurrent vein intersects with, or is only slightly distal to, the second submarginal crossvein.

Description male. Length: 11–15 mm. Intertegular distance: 7.43±0.71 mm (N=15); radial cell length: 4.50±0.48 mm (N=15). ***Head***. Black, with bright yellow clypeus and lower paraocular area (Fig. 3B); small yellow spot behind the eye; apical margin of clypeus straight, dark brown; mandible yellow with three strong, black teeth; face with long silver hairs, partly concealing the clypeal surface; antenna black. ***Mesosoma***. As in female. ***Metasoma***. Tergum 1 black, tergum 2 with small, tergum 3 with somewhat larger lateral yellow spot; terga 4 and 5 with larger lateral and mediolateral spots; tergum 6 with acute lateral spine, apical margin denticulate; yellow, except for a black midline and broad apical margin; tergum 7 with a strong median spine and an elongate lateral lobe (Fig. 3C); S6 with a rectangular median projection (3–4 times as broad as long) and small lateral spines. ***Legs***. Black with white pubescence; hind tibia with strong, hind basitarsus with weak longitudinal carina; basitarsi long and slender. ***Wing***. As female.

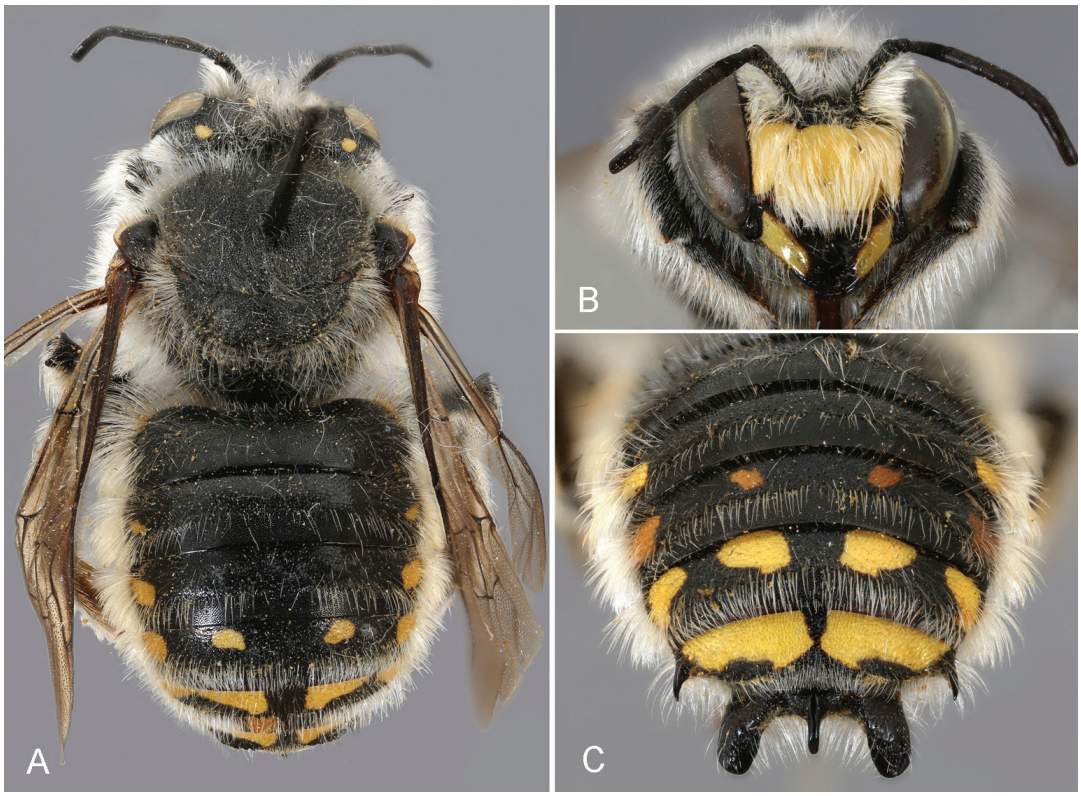

Figure 3. *Anthidium pullatum*, male. **A.** Habitus dorsal; **B.** Face; **C.** Apical terga.

Relationships. According to the structure of tergum 7 (elongated lateral lobes) and the venation of the wing, the Middle Eastern and Central Asian *Anthidium taschenbergi* Morawitz, 1894 may be closely related. The DOI barcoding sequence shows the closest similarity with *Anthidium cingulatum* Latreille, 1809.

Biology. Flight season March and April. The species was collected in Morocco flying at *Lotus* sp. (Fabaceae) and *Antirrhinum* cf. *ramosus* (Plantaginaceae) (M. Schwarz). The apically curved hairs on the clypeus of *A. pullatum* have been interpreted as an adaptation for pollen uptake from specific types of flowers (Gonzalez and Griswold 2013; Müller 1969). Kasparek et al. (2022) noted relatively high pollen loads on the clypeus of *A. pullatum* (Fig. 2), similar to *A. pectinatum*, where the clypeus also serves for pollen transportation.

Distribution. Saharo-Arabian faunal element. Known from deserts and semi-deserts to the south of the High Atlas range in Morocco and the Mzab region in the northern Sahara in Algeria (Fig. 6).

Anthidium nigrum Kasparek, sp. nov.

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Figs 4, 5

Material. ***Holotype.*** • MOROCCO: ♀, 10 km S Bouarfa, 32.41°N, 1.97°E, 20.v.1995, Ma. Halada leg. (CMK, ms2750).

Derivatio nominis. The epithet, an adjective, refers to the black colouration of the species.

Diagnosis (female). Entirely black integument except for spot behind eyes (Fig. 4A, B). Terga shiny, with dense white pubescence laterally. Lower margin of the clypeus strongly protruding in a lip-like ridge with approximately eight prominent tubercles (Fig. 5). Distinguished from *A. montanum* in many characters, including the pubescence (dense white pubescence on episternum and on terga 1–5 laterally in *A. nigrum*, long yellow-brown pubescence on meso and metasoma in *A. montanum*), a black scopa (golden-yellow in *A. montanum*), short and strong bristles on the outer face of the tibiae (long and thin hairs in *A. alpinum*), and high and prominent tubercles on the apical margin of the clypeus (low and somewhat confluent tubercles in *A. montanum*). The species is distinguished from *A. pullatum* by the hairless marginal zones of terga 4 and 5 (dense, appressed fringe of hairs in *A. pullatum*), punctation of the scutum (distance between the punctures up to two puncture diameters in *A. nigrum*, fine punctures nestled together in *A. pullatum*), absence of a longitudinal carinae on hind tibia and basitarsus (present in *A. pullatum*) and the colour of the mandible (chestnut-brown and black in *A. nigrum*, and yellow with dark brown teeth and margins in *A. pullatum*).

Description female. Length: 11 mm; intertegular distance: 7.7 mm; radial cell length: 4.6 mm. Black except for a very small light spot on vertex behind eye. ***Head.*** Clypeus almost flat, only slightly protruding; anterior margin almost as long as posterior margin (Fig. 5); anterior margin slightly curved concavely; angle between anterior and lateral margin almost rectangular; densely punctate, with punctures less dense and larger medially

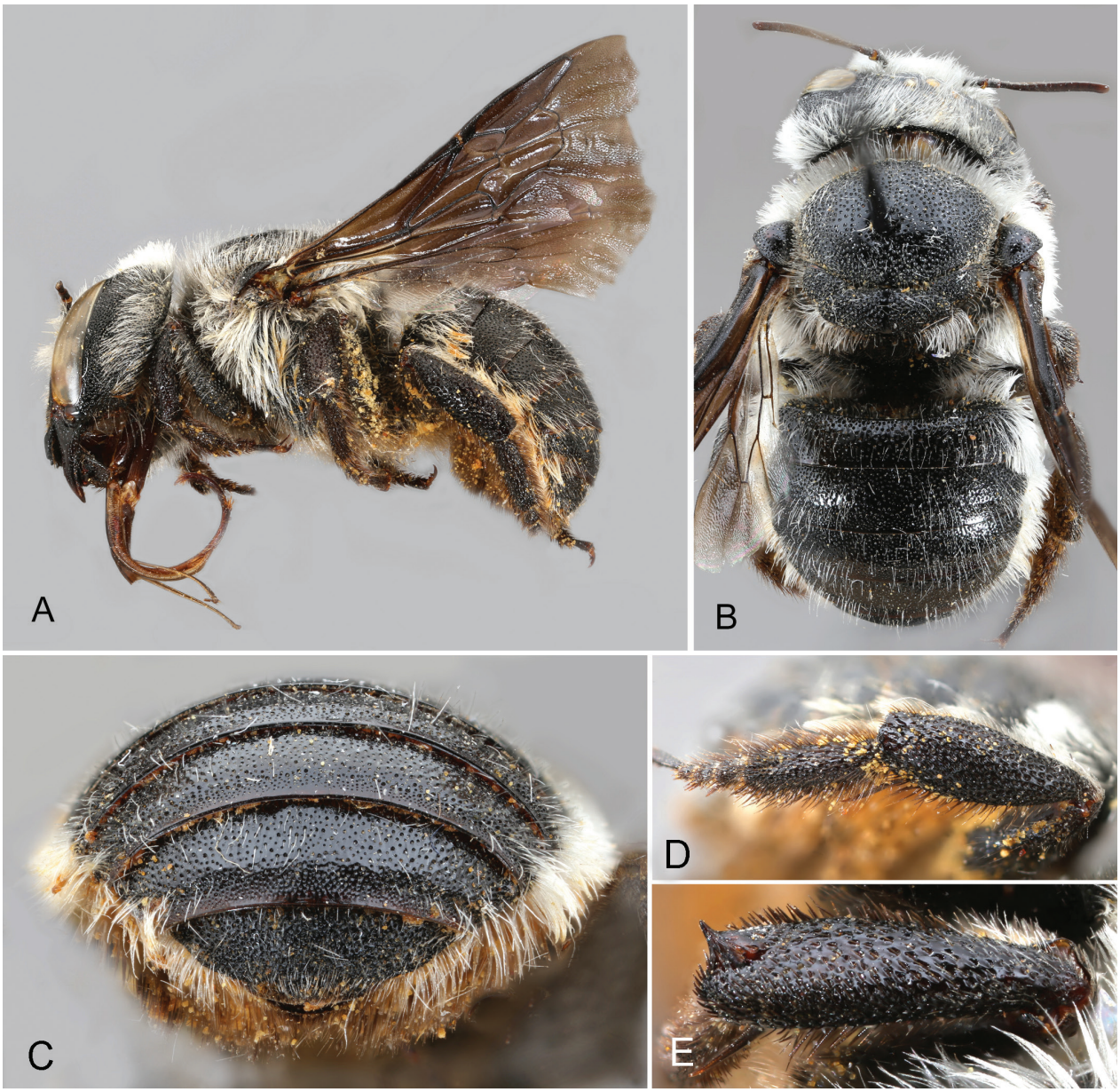

Figure 4. *Anthidium nigrum* sp. nov., female, holotype. **A.** Habitus, lateral; **B.** Habitus, dorsal; **C.** Apical terga; **D.** Tibia and tarsus of mid leg; **E.** Hind tibia.

than laterally; punctation towards apical margin very fine; clypeal apex fully exposed and protruding in a lip-like transverse ridge, with eight strong tubercles; clypeus without conspicuous pubescence; mandible chestnut-brown with six almost equally-sized black, sharp teeth, separated by acute notches; mandibular acetabulum (upper articulation) and mandibular condyle (lower articulation) large, brown, and shining; head black with fine punctation and shining interstices; lower supraclypeal area and around ocelli impunctate, shining; long, white pubescence around antennal sockets; white, somewhat shorter pubescence on vertex and gena; upper side of antenna dark brown, underside light brown. ***Mesosoma***. Scutum densely punctate laterally, scattered punctate medially; interstices shining; punctures in the centre of the scutum separated by up to 3–4 times of their own diameter (Fig. 4B); pronotal lobe strongly lamellate; tegula dark brown to black, centrally with scattered and laterally with dense punctation; scutellum/axillae crescent-shaped, bulging upwards; in profile, rounded medially and angulate posterolaterally; median emargination of scutellum absent; slightly overhanging the propodeum; scutellum and axilla densely punctate except for impunctate, shining median part; basal zone of propodeum densely punctate, otherwise smooth and shining; mesepisternum covered by long, dense white hair. ***Metasoma***. Width of terga tapering towards the apex (tergum 2 about 1.3 times as wide as tergum 2); punctures on tergal discs mostly separated by 1–2 (medially up to 3–4) their diameters; punctation on depressions finer and denser; impunctate, dark brown apical margin; disc about 3–4 times as wide as depression; tergum 4 and 6 laterally bulging;

Figure 5. Face of *Anthidium nigrum* sp. nov., female, holotype. Note the shape, punctation and hairlessness of the clypeus.

tergum 6 medially with narrow, lamellate flange, with small median apical emargination to accommodate sting; punctation of tergum 6 irregular and rugulose, with confluent punctures (Fig. 4C); ventral scopa with strong dark brown hairs; terga 1–5 with scattered, thin, white hairs, but long white hair laterally. ***Legs*.** Tibiae dark brown with coarse punctation and dark brown bristles on outer, and longer, thinner and lighter hairs on inner faces (Fig. 4D, E). ***Wing*.** Forewing strongly, brownly infuscated; hind wing slightly brown-tinted towards apex.

Relationships. The species superficially resembles *A. montanum*, as the females of both species share several characteristics, including colouration, a protruding, crenulate apical margin of the clypeus, the absence of a carina on hind tibia and basitarsus, and fine, shallow punctation on the terga with often confluent punctures. However, a definitive classification remains premature due to the lack of information on male characteristics.

Biology. The only specimen known was collected in May. It was collected south of Bouarfa in the Moroccan hamada (Arabic: ḥammāda), the arid landscape consisting of hard rocky plateaus, where most of the sand has been removed by deflation.

Distribution. Only known from the Oriental (= Oujda) Region, an administrative unit in northeastern Morocco (Fig. 6).

Remarks. The species is not a typical member of *Anthidium* not only for its unusual colouration, but also in other characteristics including the shape of the metasoma, which in dorsal view strongly tapers towards the apex, more than in most other *Anthidium* species. Also, the small flange on T6 is not typical for the genus.

Identification Key

The identification key for the species of *Anthidium* s. l. by Warncke (1980) is the only key that includes the species occurring in northern Africa, but it is outdated in many respects. The key to the European and West Turkish species of Anthidiini (Kasparek 2022) can be used with the following extensions to accommodate the two species treated here.

Females

43	Outer face of hind tibia rounded (longitudinal carina on outer face absent)	**44**
–	Outer face of hind tibia with longitudinal carina	**67**
44	Mandible with 4–6 teeth (Fig. 5)	**45**
–	Mandible with >8 (usually 9–14) teeth	**65**
45	Lower margin of clypeus lip-like enlarged and fully exposed, obliquely protruding (Fig. 5)	**46a**
–	Lower margin of clypeus not lip-like enlarged, not obliquely protruding	**49**

46a	Metasoma black or black with small yellow spots (Fig. 4A, B)	**46b**
–	Metasoma with extensive yellow colouration	**47**
46b	Body with rich reddish-brown pubescence; tarsi with fine reddish-brown hairs; entire scutum with fine, dense punctation, punctures separated by narrow ridges; apical clypeal margin with contiguous and confluent tubercles; scopa yellowish-brown	***Anthidium montanum***
–	Body with white pubescence (particularly strong on terga laterally and on mesepisternum) (Fig. 4A); tarsi with dense, strong dark brown hairs (Fig. 4D, E); scutum medially with scattered punctures, distance between punctures on average twice as wide as puncture diameter; apical clypeal margin with tubercles clearly separated from each other (Fig. 5); scopa dark brown	***Anthidium nigrum* sp. nov.**
67	Mandible with >8 teeth	***Anthidium wuestneii***
–	Mandible with 5–6 (rarely 7) teeth (Fig. 2)	**67a**
67a	Body black except for small yellow on vertex behind eye (Fig. 1B, E) and rarely few minute yellow dots on terga	***Anthidium pullatum***
–	Body with extensive yellow markings	**68**

Male of *Anthidium pullatum*

84	Tergum 7 with small, median tooth	**85**
–	Tergum 7 with strong median spine, almost as long as lateral lobes (Fig. 3C)	**86a**
86a	Outer margin of lateral lobe of tergum 7 almost straight (Fig. 3C); second recurrent vein intersects with, or is only slightly distal to, the second submarginal crossvein	***A. pullatum***
–	Outer margin of tergum 7 partly concave (bilobed), convexly angulate or undulated; second recurrent vein distal to the second submarginal crossvein	**87**

Discussion

The females of the two species treated here exhibit numerous differences in various traits. These differences include the presence or absence of hairs on the clypeus, the presence or absence of a longitudinal carina on the hind tibia, and the presence of strong bristles as opposed to thin, long hairs on the legs, among others. Given these significant morphological differences, the authors believe that these species are not closely related, but rather that the absence of yellow colouration on meso- and metasoma has evolved independently during their evolutionary history. Notably, *Anthidium nigrum* sp. nov. shares more characteristics with *A. montanum* and may be closely related to it.

For the bee tribe Anthidiini, a general tendency has been reported for more southerly populations to be more yellow in colour than populations further north (Warncke 1980; Kasparek 2022). In *Rhodanthidium caturigense* (Giraud, 1863) and *Eoanthidium insulare* (Morawitz, 1874), the only two anthidiine species in which this phenomenon has been studied in detail, a direct correlation was found between the colouration on the integument and the geographic latitude, and this correlation followed a clinal character with the extent of black on the body surface increasing towards the north (Kasparek 2021; Kasparek et al. 2024). This result has been linked to the Thermal Melanism Hypothesis (TMH), which states that the darker colouration observed towards the north may be related to the ambient temperature (Kettlewell 1955; Watt 1968; Clusella-Trullas et al. 2008;). Darker coloured melanic individuals heat up faster and to higher temperatures than lighter-coloured individuals due to lower skin reflectance (e.g., Goulsen 1994; Kuyucu et al. 2018).

This observation does not conform with the phenomenon that the females of the two species treated here were found in the Saharan desert where temperatures rise to very high levels. For example, the highest monthly mean maximum day-time temperatures in July, the hottest month of the year, are 39.8 °C in Ghardaia, Algeria, and 37.8 °C in Quarzazate, Morocco. During the flight period of *A. pullatum*, these temperatures are 21.7 °C and 22.2 °C in March, and 26.0 °C and 25.2 °C in April (https://www.dwd.de). The occurrence of anthidiine species with a black integument in the hot climate of the Saharan desert is therefore unexpected, and neither in line with the general biological characters of this bee tribe nor with the provisions of the TMH.

The minimum thoracic temperature necessary for flight in bees varies from species to species but generally falls within the range of 20–30 °C (Danforth et al. 2019). The upper critical temperature that may trigger overheating and can kill a bee is approximately 45–50 °C (Willner and Stone 1997, 2004). Because bees generate significant heat when active, the maximum ambient temperature at which they can maintain activity may be somewhat below their upper critical body temperature. There is no indica-

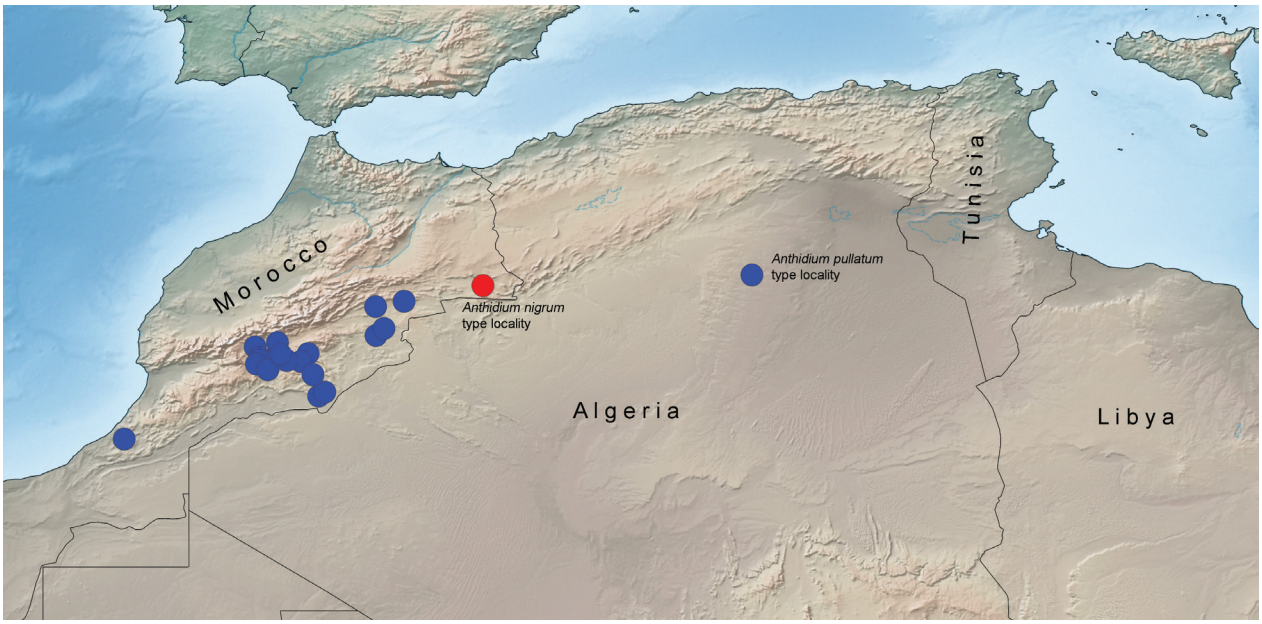

Figure 6. Distribution of *Anthidium pullatum* (blue dots) and *Anthidium nigrum* sp. nov. (red dot).

tion of major differences between temperate and desert species (Willner and Stone 1997).

It is therefore unlikely that the black body colouration of *A. nigrum* and *A. pullatum* is somehow an adaptation to the extremely high temperatures during the day in desert environments. Instead, it could be an adaptation to the low temperatures at night and in the early morning. Desert temperatures often drop dramatically at night, sometimes nearing 0 °C. Furthermore, it is well-known that the daytime temperature typically rises faster in the desert compared to temperate regions. The dry and sandy soil of deserts heats up rapidly during the day and retains heat, while the dry and clear air allows more solar energy to reach the Earth's surface and to be converted into heat. Consequently, poikilotherm animals in deserts often have only a small window in the morning for activity (Cloudsley-Thompson 1991). To overcome this challenge, bees with a black integument may become active early in the morning with basking, aiming to reach the minimum temperature required for foraging. This strategy would allow them to extend the short period before temperatures become too hot, forcing them to hide in the shade. The rapid transition from low night temperatures to the heat of the day might limit the time available for bees to engage in foraging and other activities. The black integument may help bees overcome this challenge by facilitating faster warming up in the morning. By basking in sunny spots to warm up their thoracic flight muscles, these bees can begin foraging and pollen collection earlier in the day. This potentially provides them with comparative advantage over light-coloured bee species in environments with limited resources.

We therefore hypothesise that *A. nigrum* and *A. pullatum* likely become active early in the day but may curtail or decrease their activities as temperatures rise during the morning. Consequently, they may need to cease their activities earlier than bee species with a light integument. Light-coloured anthidiine bees may not be able to commence their activities so early in the morning but may have an advantage in sustaining their activities towards peak temperatures.

Various temporal foraging patterns have been reported in bees. While some species have, for example, been found to exclusively forage early in the day, others exhibit a bimodal activity pattern, foraging both early in the day and in the late afternoon with a pronounced break in between (Danforth et al. 2019). For instance, Gottlieb et al. (2005) observed a clear bimodal daily activity pattern in the carpenter bee *Proxylocopa olivieri* Lepeletier, 1841 near Jerusalem, with foraging occurring mainly before sunrise and after sunset. The authors discussed a possible relationship with higher nectar availability in the morning and the evening, reduced competition with other bees, and the species' ability to fly at low light levels. Considering that *P. olivieri* is also predominantly dark-coloured, its capacity to absorb heat under low radiation conditions should also be considered. While the interactions between flowering plants and insect pollinators have been extensively studied, the temporal aspects of these interactions have received less attention (Bloch et al. 2017). Additionally, the role of the colouration of the bee's integument in its activity pattern remains largely unexplored. The adaptation of bees to the opening and closing of flowers in the diurnal cycle (van Doorn and van Meeteren 2003) may also be a factor worth considering.

The strategy of coping with ambient temperatures may differ in the few black or predominantly black Palaearctic *Anthidium* species. For instance, *A. montanum* is a species mostly inhabiting subalpine and alpine regions between 1500 and 2400 m (Ebmer 2003; Amiet et al. 2004; Kasparek 2022). The cooler climate in these high altitudes may account for the dark body surface

observed in this species. Also the Asian *A. kashmirense* and *A. pseudomontanum* with almost entirely black integument are found in high altitudes. *Anthidium kashmirense* was described from Gulmarg in Jammu and Kashmir (India) at 2650 m altitude (Mavromoustakis 1937) and was subsequently found in Burang County in Xizang (Tibet, China) at altitudes up to 5400 m (Niu et al. 2020). *Anthidium pseudomontanum* was found in Xinjiang Uygur Autonomous Region (China) at altitudes between 4400 and 4600 m (Niu et al. 2020). While the dark colouration of these high mountain species allows them to survive in high altitudes with a cool, harsh climate, the dark colouration of the females of the two desert species described here may enable them to overcome the challenges of the stark day-and-night temperature differences. We suspect that they utilize the early morning sun for heating up the body, before temperatures reach a lethal level. In both cases, the dark body colouration is considered a strategy for adapting to extreme climate conditions.

Despite increasing entomological research in Morocco in recent years (Lhomme et al. 2020), *A. nigrum* has been found only once, in 1995. In Algeria, *A. pullatum* has been recorded only once, about a hundred years ago. However, studies on wild bees in Algeria are scarce (e.g., Aguib et al. 2010). Additionally, the colouration of these two species may have contributed to their long-lasting undescribed status, as they cannot be readily identified as members of the *Anthidium* genus at first glance.

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