A taxonomic review of Western Palaearctic and African wool carder bees of the genus Anthidium (Megachilidae: Anthidiini) with males armed with two acute spines on the apical visible tergum

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RESEARCH ARTICLE

A taxonomic review of Western Palaearctic and African wool carder bees of the genus *Anthidium* (Megachilidae: Anthidiini) with males armed with two acute spines on the apical visible tergum

Max Kasparek

Abstract

Globally, approximately 200 species of wool carder bees are classified under the genus *Anthidium* Fabricius, 1804, with nearly equal numbers of species distributed between the Eastern and Western Hemispheres. In most species, the male's apical tergum bears three processes, while only a few species exhibit just two. As the taxonomy of the latter is insufficiently known, the members of this group are redescribed herein based on rich new material, together with information on DNA sequences and distributional data. *Anthidium wuestneii* Mocsáry, 1887 is transferred here from *Anthidium* subgenus *Proanthidium* Friese, 1898 to the nominate subgenus (**subg. comb. n.**). *Anthidium villosulum* Smith, 1854 from western Africa is resurrected from synonymy with *A. tesselatum* Klug, 1832 and re-established as a distinct species (**stat. res.**). The *tesselatum* group of nominate *Anthidium* now comprises four species, found in the Western Palaearctic and Africa. The species from this group were compared with the Afrotropical *A. niveocinctum* Gerstaecker, 1858, whose male also possesses a two-spined apical tergum and for which the subgenus *Nivanthidium* Pasteels, 1969 had been established. The synonymy of *A. banzonis* Strand, 1912, from Cameroon, is here formalized with *A. niveocinctum* **(syn. n.)**, rendering this subgenus monotypic. Morphological and genetic analyses suggest that *A. niveocinctum* is not closely related to the *tesselatum* group, and that the observed similarities are likely the result of convergent evolution.

Keywords: convergent evolution, genetic barcoding, Hymenoptera, Oman, Nigeria.

Zusammenfassung

Weltweit sind etwa 200 Arten von Wollbienen der Gattung *Anthidium* Fabricius, 1804 bekannt, mit nahezu gleicher Artenzahl in der östlichen und westlichen Hemisphäre. Bei den meisten Arten weist das apikale Tergum des Männchens drei Vorsprünge auf, während nur wenige Arten lediglich zwei zeigen. Da die Taxonomie der letzteren Artengruppe nur unzureichend bekannt ist, werden die zugehörigen Arten hier anhand von neuem, umfangreichem Material sowie anhand von Informationen zu DNA-Sequenzen und Verbreitungsdaten neu beschrieben. *Anthidium wuestneii* Mocsáry, 1887 wird hier von *Anthidium* Subgenus *Proanthidium* Friese, 1898 in den Nominat-Subgenus transferriert (**subg. comb. n.**). Es wird gezeigt, dass es sich bei *Anthidium villosulum* Smith, 1854, aus Westafrika um eine valide Art und nicht um ein Synonym von *A. tesselatum* Klug, 1832 (**stat. res.**) handelt. Die *Anthidium tesselatum*-Gruppe umfasst nun vier Arten, die in der westlichen Paläarktis und in Afrika vorkommen. Darüber hinaus wurden die Arten dieser Gruppe mit der afrotropischen Art *A. niveocinctum* Gerstaecker, 1858, verglichen, dessen Männchen ebenfalls über ein zweistacheliges apikales Tergum verfügt und wofür das Subgenus *Nivanthidium* Pasteels, 1969 etabliert worden war. Die Synonymie von *A. banzonis* Strand, 1912, aus Kamerun, mit *A. niveocinctum* wird hier formalisiert (**syn. n.**), wodurch sich dieses Subgenus als monotypisch erweist. Die Ergebnisse der morphologischen und genetischen Analysen legen nahe, dass *A. niveocinctum* nicht eng mit der *tesselatum*-Gruppe verwandt ist und dass die beobachteten Ähnlichkeiten wahrscheinlich das Ergebnis konvergenter Evolution sind.

Introduction

Worldwide, around 200 species of wool carder bees are attributed to the genus *Anthidium* Fabricius, 1804 (Michener 2007; Kasparek 2022a), with an almost equal number of species in the Eastern and Western Hemispheres. While the *Anthidium* fauna of the Western Hemisphere has recently undergone a comprehensive revision, including the description of 21 new species (Gonzalez & Griswold 2013), our taxonomic knowledge of the species in the Eastern Hemisphere remains reliant on older works, such as those by Warncke (1980) for the Western Palaearctic or Pasteels (1984) for the Afrotropical Realm. More recent taxonomic studies have provided updates for specific areas, including the description of new species from China (Niu et al. 2020) and several new species from North Africa, the Middle East, and Central Asia (Kasparek & Schwarz 2020; Kasparek 2021, 2022b, 2024; Kasparek et al. 2022, 2024; Kasparek & Fateryga 2023). However, a comprehensive revision of Old World

taxa remains lacking. In most species belonging to the genus *Anthidium*, the male's apical tergum bears three processes, which can take the form of teeth, spines, or lobes. However, only two species exhibit five processes, the Neotropical *Anthidium vigintipunctatum* Friese, 1908 (Griswold & Michener 1988) and the Palaearctic *A. cingulatum* Latreille, 1809 (Kasparek 2022a), though the Neotropical *A. latum* Schrottky, 1902 and *A. meloi* Gonzalez & Griswold, 2013 have four strong teeth and a minute medial fifth tooth (Gonzalez & Griswold 2013). According to Griswold & Michener (1988), two species within *Anthidium* s. str. possess just two processes: *A. tesselatum* Klug, 1832, and *A. waltlii* Spinola, 1838. Despite the findings mainly by Schwarz & Gusenleitner (2003) and Fateryga et al. (2020), our taxonomic understanding of and identification tools for two-spined *Anthidium* species remain incomplete. In response, I have reviewed the current knowledge, provided illustrated redescriptions, including DNA barcodes, and examined the taxonomic relationship of these species with the Afrotropical *A. niveocinctum* Gerstäcker, 1858, which is regarded as the only representative of the monotypic subgenus *Anthidium* (*Nivanthidium*), and which also features a two-spined apical tergum in the male.

Material and methods

Morphology

T stands for tergum (T1, T2, T3, …), S for sternum (S1, S2, S3, …). The mandibular teeth are numbered from the apical-most, or "lowest", tooth (tooth 1) to the basal-most, or "upper" tooth. In the species treated here, S6 of the male consists of a basal plate (the primary flat structure of the sternum) and a process extending from it. This process is referred to here as "lateral projection". The other terminology follows Michener (2007).

Distribution

The label information from all examined specimens was captured and their localities georeferenced using Google EarthTM (http://earth.google.com). Some data could be downloaded from GBIF—the Global Biodiversity Information Facility (GBIF; available from https://www.gbif.org, downloaded in September 2024), and Discover Life (Ascher & Pickering 2024). Maps were prepared with SimpleMappr (Shorthouse 2010).

Photography

The photographs were taken with a Canon MP-E65/2.8 lens mounted on a Canon EOS 6D camera. A Canon Twin Lite MT24EX Macro Flash was used. The camera was moved between the shots with a Cognisys StackShot Rail and usually between 20 and 30 photographs were taken at different focal distances, to give a resulting image with a greater depth of field than any of the individual source images. Subsequently, the photographs were stacked using Helicon Focus (version 6.1.7). Post-processing of the images was made in Photoshop Elements 15 (Adobe Systems, USA).

Genetic analysis

DNA extraction, PCR amplification, and sequencing were conducted by the Canadian Centre for DNA Barcoding (CCDB), Guelph, using standardized high-throughput protocols (http://ccdb.ca/resources; Hebert et al. 2004). The results were submitted to the Barcode of Life Data System (BOLD), a cloud-based data storage and analysis platform developed by CCDB (https://boldsystems.org; Ratnasingham et al. 2024). BOLD assigns individuals to putative species, each identified by a unique Barcode Index Number (BIN). While BINs often correspond to recognized species, they do not necessarily align with species boundaries defined by traditional taxonomy (Ratnasingham & Hebert 2013).

For further analysis, DNA was aligned running Muscle Alignment on the MEGA11 software (Tamura et al. 2021). A Maximum Likelihood (ML) tree phylogenetic analysis was performed also using the MEGA software (Kumar et al. 2018), and bootstrap values were determined from 1,000 replicates using the Tamura 3-parameter (T92) model, which received the lowest BIC (Bayesian Information Criterion) scores and is therefore considered to best describe the substitution pattern. *Anthidium manicatum* (Linnaeus, 1785) was chosen as outgroup. Sequence numbers in BOLD are included in the material examined sections.

Abbreviations

AM	Albany Museum, Grahamstown (South Africa)
AUB	American University of Beirut (Lebanon)
BBSL	U.S. Department of Agriculture, Agricultural Research Service, Bee Biology and Systematics Laboratory, Logan, Utah (USA)
CMK	Collection Max Kasparek, Heidelberg (Germany)
GBIF	Global Biodiversity Information Facility (https://www.gbif.org)
MoA	Ministry of Agriculture (Mavromoustakis collection) (Cyprus)
MRSN	Museo Regionale di Scienze Naturali, Turin (Italy)
NBC	Naturalis Biodiversity Center, Leiden (The Netherlands)
NMW	Natural History Museum, Vienna (Austria)
OLL	Upper Austria Biodiversity Center (former Oberösterreichisches Landesmuseum, Biologiezentrum), Linz (Austria)
SEMC	Snow Entomological Collection, University of Kansas, Kansas (USA)
TUZ	Natural History Museum, University of Tartu (Estonia)
ZISP	Zoological Institute, Russian Academy of Sciences, St. Petersburg (Russia)
ZMB	Museum für Naturkunde, Humboldt-Universität, Berlin (Germany)

Taxonomy

Genus *Anthidium* Fabricius, 1804
Anthidium subg. *Anthidium* Fabricius, 1804 s. str.
Anthidium tesselatum species-group

The *Anthidium tesselatum* species group as understood here includes species which have, in both sexes, a longitudinal carina on the hind tibia and a crescent-shaped scutellum, male with brushes of white hairs on T1–T3 laterally, lateral hooks on T4–T6, and a bifid T7 with two strong

spines. A prominent row of strong setae is found along the pregradular line of T3–T5. All females have mandibles with 5–10 teeth and black hairs in the apical part of the scopa—a characteristic found only in a select few *Anthidium* species. The female does not have morphological traits which are unique to all members and unambiguously characterize this species group.

Anthidium (*A.*) *bischoffi* Mavromoustakis, 1954
(Figs. 1, 9–14)

Anthidium bischoffi Mavromoustakis, 1954a (Israel, male). "Type" (presumably holotype) and "allotype" in MoA according to MoA (1989).
Anthidium waltlii Spinola, 1838: 520 (Egypt) (sensu Warncke 1980: 201).
Anthidium bischoffi var. *hoggaricum* Mavromoustakis, 1954b (Algeria, female; type in OLL) (Warncke 1980).
not *Anthidium bischoffi dzhachrumicum* Popov, 1967 (Iran; 6 syntypes in ZISP) (sensu Warncke 1980; misspelled as "*dzhachramicum*").

Genetic Barcode Index Number (BIN): BOLD:AER0580.

Diagnosis

In colouration, most similar to *A. tesselatum*. The female can be distinguished from all congeners by its distinctive mandible pattern with 6 to 9 alternating large and small teeth (Fig. 13). The variation in tooth number is due to the inconsistent presence of small to minute teeth. The male is characterized by a broader base of T7, wider than the distance between the outer margins of the spines on T7 (nearly parallel in *A. tesselatum* and *A. wuestneii*). Additionally, S6 with a broadly rounded apex and semi-rectangular lateral projections (Fig. 11).

Taxonomy

Anthidium bischoffi Mavromoustakis, 1954 was regarded as a synonym of *A. waltlii* Spinola, 1838 by Warncke (1980). However, following Schwarz & Gusenleitner (2003), *A. waltlii* is treated here as a synonym of *A. tesselatum* Klug, 1832. Additionally, the subspecies *Anthidium bischoffi dzhachrumicum* Popov, 1967 has been transferred to *A. wuestneii* Mocsáry, 1887 (Fateryga et al. 2020).

Material examined

ALGERIA: 3♀♀, 1♂; Hoggar Tamannasset, 16 km NE Guelta (23.22°N 05.69°E), 890 m; 25.iii.1989; M. Schwarz leg. (CMK) (see also Aguib et al. 2010). – 2♀♀; Hoggar Tamannasset, 60 km E (22.80°N 05.84°E), 1500 m; 31.iii.1989; M. Schwarz leg. (CMK) (see also Aguib et al. 2010). – EGYPT: 1♂; Sinai: W of El-Tih (29.14°N 33.53°E), 70 m; 23.vi.1939; H. Priesner leg. (CMK). – 10♀♀, 6♂; Sinai: Wadi Digla (29.94°N 31.37°E), 210 m; various dates between 1931 and 1938 (June and July); H. Priesner leg. (CMK). – 1♂; Sinai: 5km SW Dahab, near road through wadi (28.46°N 34.44°E), 125 m; 23.iii.2011; S. Risch leg. (coll. S. Risch). – OMAN: 1♀; Dhofar prov.: Wadi Al Mughsayl (16.86°N 53.72°E), 120 m; 10.iv.2013, J. Halada leg. (CMK). – 2♀♀, 1♂; ABABX563-22; ABABX564-22; 5km N Aydam, R45 (17.03°N 53.34°E), 820 m; 06.x.2021, M. Halada leg. (CMK). – 1♀; 80 km S Salalah (16.84°N 53.31°E), 1000 m; 12.x.2021; M. Halada leg. (CMK).

Literature records

ALGERIA: 3♀♀, 1♂; Hoggar Tamannasset, 16 km NE Guelta (23.22°N 05.69°E), 890 m; 25.iii.1989; M. Schwarz leg. (CMK) (see also Aguib et al. 2010). – 2♀♀; Hoggar Tamannasset, 60 km E (22.80°N 05.84°E), 1500 m; 31.iii.1989; M. Schwarz leg. (CMK) (see also Aguib et al. 2010). – EGYPT: 1♂; Sinai: W of El-Tih (29.14°N 33.53°E), 70 m; 23.vi.1939; H. Priesner leg. (CMK). – 10♀♀, 6♂; Sinai: Wadi Digla (29.94°N 31.37°E), 210 m; various dates between 1931 and 1938 (June and July); H. Priesner leg. (CMK). – 1♂; Sinai: 5km SW Dahab, near road through wadi (28.46°N 34.44°E), 125 m; 23.iii.2011; S. Risch leg. (coll. S. Risch). – OMAN: 1♀; Dhofar prov.: Wadi Al Mughsayl (16.86°N 53.72°E), 120 m; 10.iv.2013, J. Halada leg. (CMK). – 2♀♀, 1♂; ABABX563-22; ABABX564-22; 5km N Aydam, R45 (17.03°N 53.34°E), 820 m; 06.x.2021, M. Halada leg. (CMK). – 1♀♀; 80 km S Salalah (16.84°N 53.31°E), 1000 m; 12.x.2021; M. Halada leg. (CMK).

Redescription

Female (morph with black ground colour). 8–9 mm. – Head: black with yellow lower paraocular area, clypeus, a small supraclypeal spot, and a medially interrupted preoccipital band; long yellow maculation along the lower outer orbit; clypeus convex, protruding, with evenly punctate, shiny surface; apical margin semi-transparent light brown, projecting outward; mandible shiny, with strongly carinate, semi-transparent outer ridge; yellow with dark brown teeth; six to nine, alternating large and small teeth (Fig. 13); antenna red-brown, underside of scape yellow or also red-brown. – Mesosoma: Scutum black with a short yellow band along the anterior margin; pronotal lobe yellow, carina absent; scutellum and axillae crescent-shaped in dorsal view, with median emargination; outer side yellow, inner side black; transition zone often reddish-brown. Outer faces of legs yellow, inner faces reddish-brown; basitarsi with felt-like pubescence; long black maculation around the carina on the hind tibia. – Metasoma: broad yellow bands on T1–T6, interrupted in the middle and constricted mediolaterally from the anterior (except sometimes the band on T1); scopa yellow with black apical hairs. [Note: in addition to the morph with black ground colour, there is a morph with red-brown ground colour. All other traits remain consistent.]

Male. 9–10 mm. – Head: black with yellow clypeus, lower paraocular area, lower supraclypeal area, and a longish spot behind the eye (sometimes with a narrow extension towards the middle); mandible yellow except for brown teeth; short yellow stripe along lower outer orbit sometimes present; clypeus convex with a straight, narrow, dark apical rim; head covered in long white pubescence, especially in the area below the anterior ocellus and gena; antenna dark brown above and red-brown

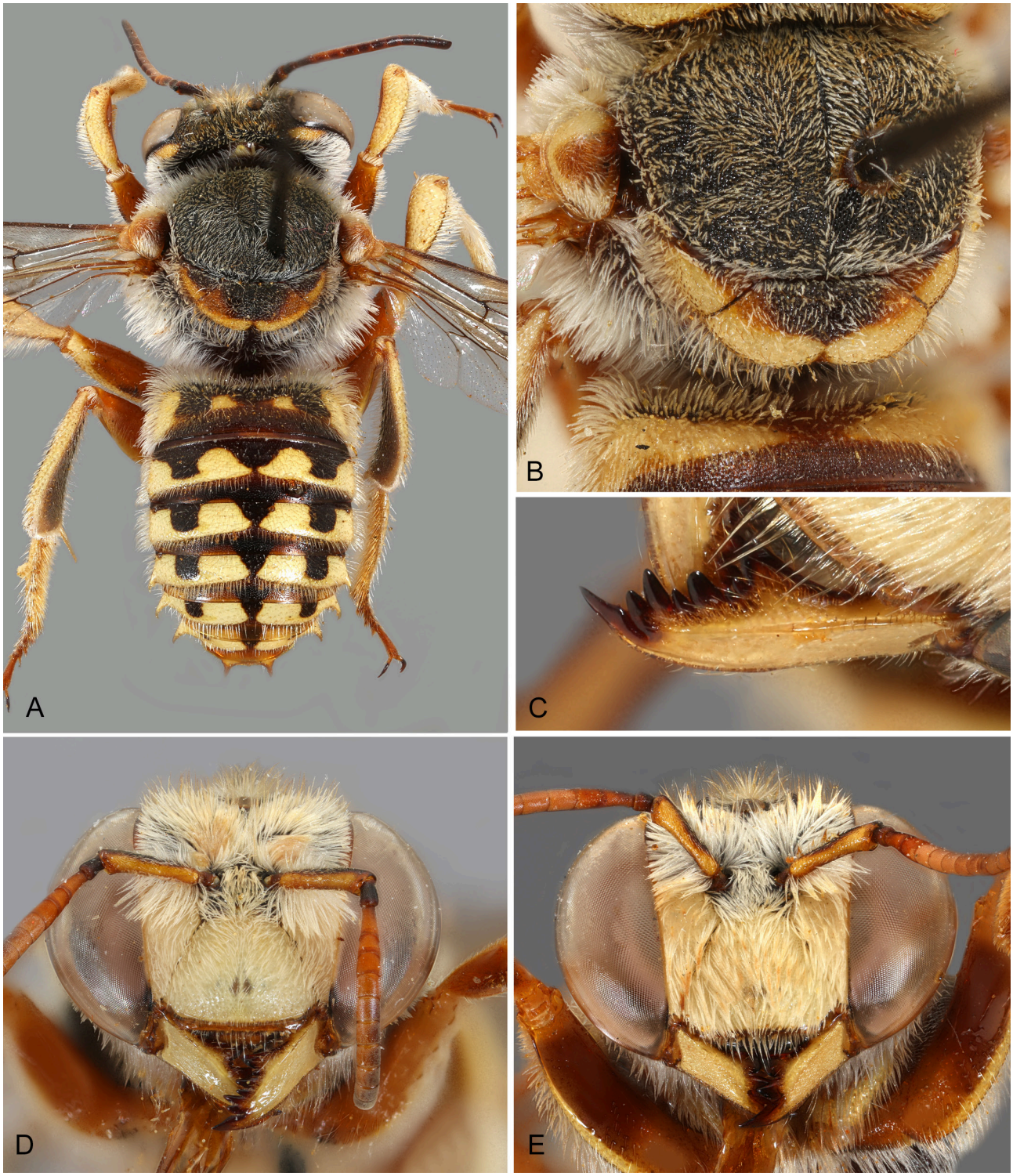

Fig. 1. *Anthidium bischoffi* Mavromoustakis, 1954. **A**. Female, dorsal habitus. **B**. Male, apical terga. **C**. Female, face. **D**. Male, face.

Fig. 2. *Anthidium tesselatum* Klug, 1932. **A**. Male, habitus dorsal. **B**. Scutum and scutellum, female. **C.** Mandible female. **D**. Face female. **E**. Face male.

Fig. 3. Holotype of *Anthidium lanitarse* var. *lloydi* Mavromoustakis, 1954 (NHMUK014026099; source: https://data.nhm.ac.uk), regarded as a synonym of *A. tesselatum* Klug, 1932 (red-brown colour morph).

underneath; underside of scape yellow. – Mesosoma: scutum black with short, mostly appressed white hairs; small yellow spot at the anterior margin; scutellum and axillae crescent-shaped in dorsal view, with a rounded posterior margin in profile; black anteriorly, yellow posteriorly, with a broad red-brown transition zone; pronotal lobe yellow, with carina (largely hidden by white hairs). Legs yellow with red-brown inner faces; hind tibia with long black macula around carina. – Metasoma: T1–T6 with broad yellow bands, interrupted in the middle and constricted mediolaterally from the anterior; T4–T6 with strong, acute, hooked spines laterally, increasing in size from T4 to T6; T7 bifid with slender spines; base of T7 broader than the outer distance between the spines; apex of S6 widely rounded; with rectangular lateral projections extending beyond the basal plate of the tergum (Fig. 11); apical median projection of S8 triangular (Fig. 12).

Biology

The species was found flying between March and July, in southern Oman also in October. The late records from Oman may represent a second generation in the post-monsoon season.

Distribution

Afro-Arabian faunal element with records from Algeria, Egypt, Israel, Jordan, and Oman (Fig. 16A).

Anthidium (*A.*) *tesselatum* Klug, 1832

(Figs. 2, 3, 8, 9–14)

Anthidium tesselatum Klug, 1832 ("Arabia felix", = SW Saudi Arabia according to the collectors' travel itinerary [e.g., Stresemann (1954)]; male).

Anthidium helvolum Klug, 1832 ("Arabia felix", = SW Saudi Arabia according to the collectors' travel itinerary; female [Klug described the male and the female under different names]) (Pasteels 1969).

Anthidium waltlii Spinola, 1838 (Egypt). Synonymy established by Schwarz & Gusenleitner (2003) following examination of the holotype in MRSN.

not *Anthidium waltlii* Spinola, 1838 sensu Warncke (1980) (see Schwarz & Gusenleitner 2003).

Anthidium signiferum Walker, 1871 (Sudan, male).

Anthidium tesselatum var. *aegyptiacum* Friese, 1897 (Egypt; male) (NMW).

Anthidium lanitarse Friese, 1917 (Algeria, female) (Pasteels 1984).

Anthidium lanitarse var. *lloydi* Mavromoustakis, 1936 (Nigeria). Type in NHMUK (examined; Fig. 3).

Anthidium tesselatum var. *zebra* Benoist, 1950 (Morocco, female).

Genetic Barcode Index Number (BIN): BOLD:AAO4833.

Diagnosis

Similar to *A. bischoffi*, with which it shares particularly the light colour pattern. The female of *A. tesselatum* has two yellow longitudinal stripes on the scutum next to

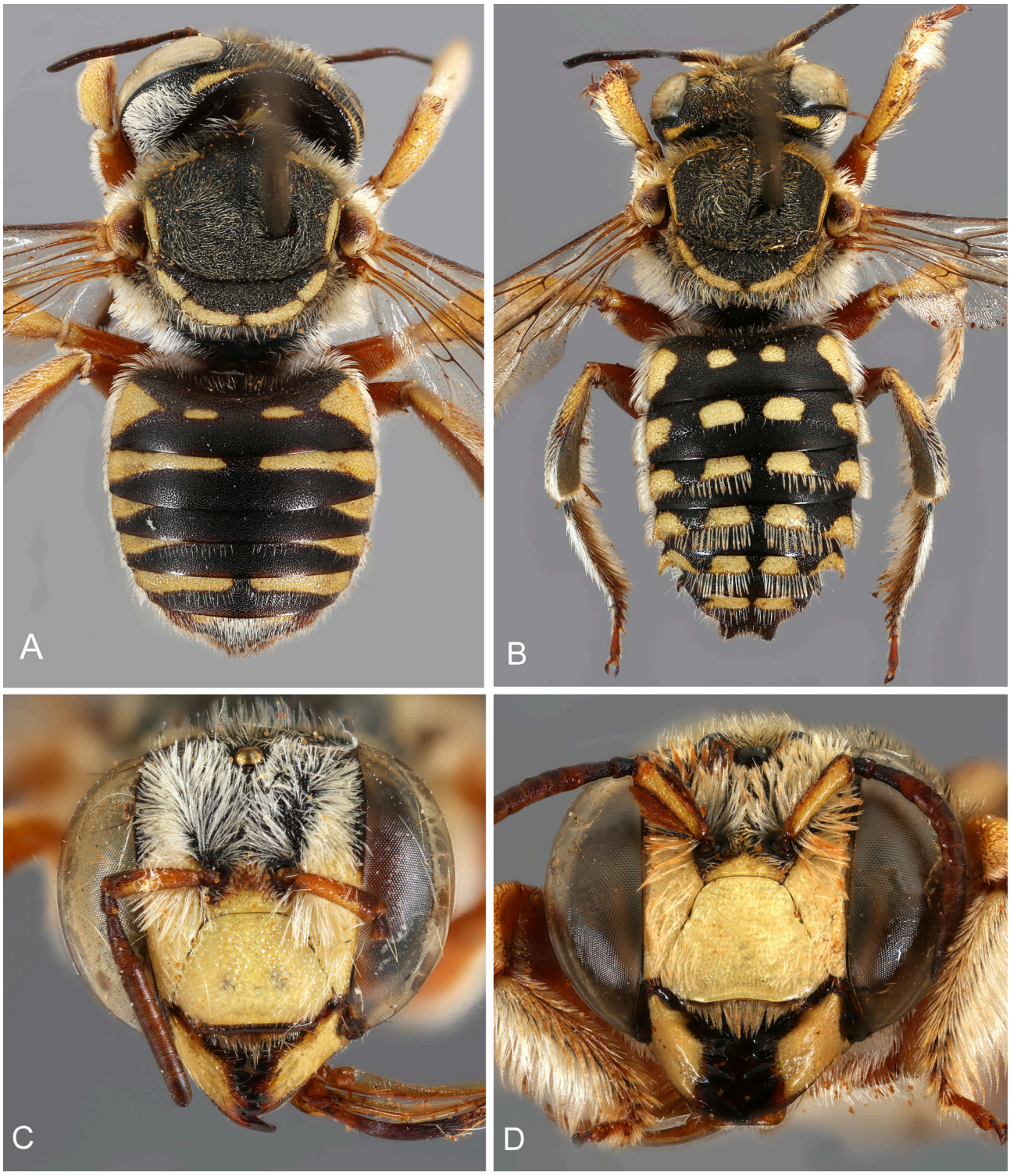

Fig. 4. *Anthidium villosulum* Smith, 1854; female (**A, C**) and male (**B, D**) from Nigeria.

the middle, which are absent in *A. bischoffi*. The female is further distinguished from all other species treated here by its mandibular shape with normally 5 teeth (Fig. 13). It is the only species with five strong mandibular teeth (*A. villosum*: 6 teeth; *A. bischoffi* and *A. wuestneii*: > 7 teeth). In some rare cases, *A. tesselatum* has an additional minute tooth between teeth 4 and 5, which renders the mandible 6-toothed, as in *A. villosulum*. However, all teeth of *A. villosulum* are strong. Additionally, the apical rim of the clypeus of female *A. tesselatum* is bi-coloured, i.e., opaque yellow anteriorly and semi-transparent posteriorly, while it is entirely semi-transparent brownish in *A. bischoffi*.

The male of *A. tesselatum* is characterized by a lateral projection of S6 which does not protrude beyond the edge of the basal plate (in the other species treated here, it protrudes beyond the edge). Additionally, the lateral spine on T6 is shorter than that on T5, while in *A. bischoffi* the longest spine is on T6. The outer edge of T7 is almost straight, while it is broader at the base than at the projections in *A. bischoffi*.

Material examined

ALGERIA: 1♂; Amsel, 30 km S Tamanrasset (22.49°N 05.56°E), 1150 m; 01.iv.1989; M. Schwarz leg.; (CMK). – EGYPT: 1♂; Marsa Matruh, Wadi Natrun (30.48°N 30.17°E), 50 m; 10.vi.2007; E. & J. Hüttinger leg. (coll. L. Bertsch). – 1♂; Nil Valley, Wadi Katara, 10 km N Asswan (24.17°N 32.89°E); 23.iii.1988; M. Schwarz leg. (CMK). – 1♀; 2♂♂; ABABY066-23; ABABY067-23; Aswan, Tuosky Research Station (24.09°N 32.90°E), 100 m; 24.iv.2019; M. El Kelany leg. (c/o M. Shebl; CMK). – ISRAEL: 2♀♀; 6♂♂; 45 km N Eilat, sand dunes E Qetura (29.96°N; 35.10°E); 09.v.1998; M. Hauser leg. (CMK). – JORDAN: 1♀, 1♂; Wadi Rum (29.55°N 35.40°E), 1023 m; 04.-05.v.1996; Ma. Halada leg. (CMK). – 1♀; Wadi Rum Tuwayyil env. (c. 29.55°N 35.40°E); 16.iv.2000; M. Snizek leg. (CMK). – MOROCCO: 1♀; Tagounite, 50 km S Zagora (29.98°N -5.58°E), 610 m; 23.iv.1995; Ma. Halada leg. (CMK). – 1♀; ABABX434-22; 16 km NW Zagora, Tafdroust (30.47°N -5.92°E); 25.iv.2018; C. Schmid-Egger leg. (CSE). – OMAN: 1♀; ABABX211-21; Al Mudhaibi, Samad Ashan, Al quaibel (22.85°N 58.15°E); 18.ii.2019; Ali Al-Jahdhami leg. (CMK). – 2♀♀; 7 km S Mahda (24.35°N 55.98°E); 17.iii.2022; M. Halada leg. (CMK). – 1♀; Az Zahirah prov., Mahdan env. (24.37°N 56.00°E); 06.iv.2013; J. Halada leg. (CMK). – 2♀♀, 2♂♂; ABABX241-21; ABABX242-21; Ad-Dakhiliyach prov., 30 km SW Izky, W. Indam (22.77°N 58.00°E), 480 m; 27.iii.2015; J. Halada leg. (CMK). – 1♂; ABABX248-21; Ash Sharqiyah Jaalan Bani Bu Ali (21.28°N 59.40°E), 65 m; 15.iv.2013; J. Halada leg. (CMK). – 1♂; E of Sur (22.55°N 59.54°E), 50 m; 01.iii.2017; M. Snizek leg. (OLL). – 1♂; SW of Sur (22.52°N 59.46°E); 03.-05.iii.2017; M. Snizek leg. (OLL). – 1♀; NW of Bahla, E of Ibri (23.08°N 56.78°E), 450 m; 08.iii.2015; M. Snizek leg. (OLL). – 3♀♀; ABABX435-22; ABABX436-22; 17km SE Sur (22.43°N 59.58°E); 15.iii.2015; M. Snizek leg. (OLL). – 1♀; ABABX279-21; Dhofar, 13 km N Mirbat, Jb. Samhan (17.11°N 54.71°E); 04.ix.2019; C. Schmid-Egger leg. (CSE). – UNITED ARAB EMIRATES: 1♂; ABABX277-21; Wadi Bih, dam (25.80°N 56.07°E); 11.ii.2010; A. v. Harten leg. (CSE). – 3♂♂; Jebel Hafit (24.07°N 55.75°E); 11-19.iii.2009; C. Schmid-Egger leg. (CSE, CMK). – 1♀; Wadi Wurayah (25.40°N 46.28°E); 11-19.iii.2009; C. Schmid-Egger leg. (CMK). – 1♀; ABABQ168-24; Ain Al Waal, Al Ain, Jebel Hafeet (24.07°N 55.75°E); 30.iii.2024, H. Roberts leg. (CMK).

Literature records

ALGERIA: Tig'amaiin en tisita (Tamanraset region; locality not identified; according to the collector's travel itinerary, nr. Idlès (23.82°N 5.93°E)); 25.-30.iv.1914, Geyr von Schweppenburg leg.; type locality of *A. lantitarse* (Friese 1917). – CAUCASIA: Reported from Caucasia by Friese (1898), based on specimens in NMW. As the record is from far beyond the known distribution area, confirmation required. – EGYPT: W. Khoshbi (South Sinai) (c. 28.00°N 34.15°E); 16-18.iv.2016; A. Shahat leg. (Elshaier 2022). – Pyramids (Giza) (29°97°N 31.13°E); 5.vii.1952; Aly leg.; Elshaier (2022). – Barkash (Giza) (c. 30°00'N 31.17°E); 5.vi.1952; Aly leg. (Elshaier 2022). – Etaka (locality not identified); 19.vi.1953; Aly leg. (Elshaier 2022). – Wadi Hebran (Sinai) (c. 28.50°N 33.68°E); Mocsáry (1884). – Koubbeh and other localities near Cairo (30.04°N 31.23°E); Friese (1898). – Al-Ismailiyah (30.60°N 32.26°E); 18.iv.1978; F. D. Parker leg.; BBSL, Ascher & Pickering (2024). – Wadi Hagul, 30 km SW Suez (29.78°N 32.29°); 10.v.1993; BBSL, Ascher & Pickering (2024). – ERITREA: listed by Ascher & Pickering (2024) without details, possibly a misinterpretation of the record by Magretti (1884) for Ethiopia. – ETHIOPIA: Kor el Royan (c. 13.99°N 36.64°E); 1883; Magretti (1884). – IRAQ: At Tannumah ("Tanooma") (30.52°N 47.86°E); October; Harwood leg.; Morice (1921). – ISRAEL: Sappir (30.58°N 35.18°E); 09.v.2007; BBSL, Ascher & Pickering (2024). – LEBANON: Mentioned by Warncke (1980) without details. Not accepted for the country list of Lebanon by Boustani et al. (2021). – MALI: Recorded in Mali (center point: 17.57°N -3.99°E) according to Ascher & Pickering (2024), but no details available. – MOROCCO: Alnif (31.11°N -5.16°E), 877 m; type locality of *A. t. zebra*; Benoist (1950). – NIGERIA: Azare (11.67°N 10.20°E); 1924 (*A. lanitarse* var. *lloydi*); Mavromoustakis (1936). – Bauchi (10.30°N 09.84°E); Ascher & Pickering (2024). – SAUDI ARABIA: Type locality in "Arabia felix" [= SW Arabian Peninsula] (exact location unknown, perhaps near Al Qunfudhah (19.12°N 41.07°E); Klug (1832). – SENEGAL: Material in MZLU, not details available (GBIF). – SUDAN: Kassala (15.43°N 36°40'E); 1883; Magretti (1884). – Hor Tamanib (nr. Sawakin); 19.11°N 37.33°E; as *A. signiferum,* type locality; Walker (1871). – TUNISIA: Nefta (33.87°N 7.88°E); 04.v.1913; Schulthess (1924). – TURKEY: Record by Staněk (1968) attributed to *A. wuestneii*. – UNITED ARAB EMIRATES: Wadi Shawkah (25.10°N 56.05°E); 5-12.v.2007; Dathe (2009).

Genetic data

The DNA sequence of the barcoding unit of the *cyt b* gene was obtained from 11 specimens from across the distribution area, including Egypt, Morocco, Oman, and the United Arab Emirates (UAE). The topology allows to distinguish two groups: one with individuals from the Gulf States (UAE, Oman), the other with individuals from Egypt and Morocco, with a bootstrap value of 100 for the node which divides these groups in the ML tree. The genetic distance between these two groups is 1.25%. Because of this low genetic distance and the fact that no phenotypic traits are known to distinguish these two groups, they are regarded as lineages of the same species despite the high bootstrap value.

Fig. 5. *Anthidium villosulum* Smith, 1854; holotype male from The Gambia (NHMUK014026055; source: https://data.nhm.ac.uk).

Redescription

[Both sexes are represented by red-brown and black colour morphs.]

Female. 10–11 mm. – Head: black with yellow clypeus, lower paraocular area slightly extending to the upper paraocular area, lower supraclypeal area, mandible (except for teeth), and a broad preoccipital band; the preoccipital band extends to the upper third of the eye, has a characteristic shape around the eye, and is narrowly interrupted in the middle (Figs. 3, 14C, D); clypeus with a small impunctate area at its base, otherwise densely punctate; apical rim straight and smooth with a few crenulations, bi-coloured (opaque yellow anteriorly, semi-transparent light brown posteriorly); mandible shiny, with a strong, semi-transparent carina on the outer ridge; five strong teeth (Fig. 13), teeth 1 and 5 being the strongest, followed by teeth 2–3, then tooth 4; rarely, an additional minute tooth between teeth 4 and 5, which renders the mandible 6-toothed; head except vertex with dense white pubescence; antenna red-brown, changing to black towards the apical segments; underside of scape yellow. – Mesosoma: scutum black (rarely also some red-brown posteriorly) with broad anterolateral band and a yellow longitudinal stripe next to the midline; scutellum and axilla black (rarely red-brown) with a broad, yellow outer side; scutellum slightly emarginate medially; pronotal lobe yellow, carina absent; mesepisternum black (rarely red-brown); large yellow maculation in red-brown individuals, but barely visible under the dense white pubescence. Fore and mid-basitarsi with dense felt-like pubescence. – Metasoma: T1–T5 black or red-brown with broad yellow bands; T6 yellow, with a small emargination for the sting posteromedially; punctation of tergal discs irregular, with punctures of different sizes, distances, and shapes particularly in the apical terga; marginal zone densely and shallowly punctate; stronger setae on the premarginal line of T4 and T5.

Male. 10–13 mm. – Head: black with yellow on clypeus, lower paraocular area (extending slightly beyond antennal sockets), and lower supraclypeal area (yellow sometimes absent); mandible yellow (except black teeth); small yellow spot behind eye (sometimes elongate, nearly reaching the middle of vertex); apical clypeal rim smooth, narrow, brown or black; clypeus regularly punctate, with narrow impunctate preapical zone; face densely covered by long white hair, including clypeus, with “beard-like” brush of hairs on apical margin; antenna brown, anterior flagella red-brown, underside of scape yellow. – Mesosoma: Scutum black with yellow anterolateral yellow band sometimes absent or reduced to a few remnants; pronotal lobes small, yellow; scutellum/axillae crescent-shaped; scutellum with posteromedian emargination; colouration of scutellum and axilla ranging from black to red-brown and partly yellow. – Metasoma: Colouration highly variable; principally broad yellow bands on T1–T6, nearly reaching the middle. Mediolaterally, the bands are mostly constricted from the anterior or even interrupted, thus rendering the terga with four rows of yellow maculations. Individuals of the red-brown colour morph often have some black remnants in the space between the outer and the mediolateral yellow maculation. T4–T6 with curved lateral spines, T5 being the largest; the inner, posterior side of the spine of T6 with a transparent lamella; T7 with

Fig. 6. *Anthidium wuestneii* Mocsáry, 1887. **A**. Male, dorsal habitus. **B**. Female, dorsal habitus. **C**. Female, face. **D**. Male, face.

Fig. 7. *Anthidium niveocinctum* Gerstaecker, 1858; female (**A, C**) and male (**B, D**) from Nigeria.

Fig. 8. *Anthidium* spp. **A, C.** *Anthidium wuestneii* Mocsáry, 1887. – **A**. Female, apical terga. **C**. Hind leg. **B, D.** *Anthidium tesselatum* Klug, 1932. **B**. Female, apical terga. **D**. Hind leg.

two long, slender spines and a U-shaped emargination in between; strong setae on the premarginal line of T2 and T6; basal plate of S6 semicircular, apex slightly flattened and undulate; lateral projections not reaching beyond the plate's lateral margins; apical median projection of S8 wider at apex than at base (Fig. 12).

Distribution

Afro-Arabian faunal element with records from Algeria, Egypt, Eritrea, Ethiopia, Israel, Iraq, Jordan, Morocco, Nigeria, Oman, Saudi Arabia (exact location unknown), Sudan, Tunisia, and the United Arab Emirates (Fig. 16B).

***Anthidium* (*A.*) *villosulum* Smith, 1854, stat. res.**

(Figs. 4, 5, 9–13)

Anthidium villosulum Smith, 1854 (The Gambia, male).
Anthidium tesselatum Klug, 1832 (sensu Pasteels 1984).

Genetic Barcode Index Number (BIN): not available.

Diagnosis

The female mandible features six teeth with teeth 2, 3, and 5 almost equal in strength, while tooth 4 is slightly smaller (Fig. 13). This dental configuration distinguishes it from the other species treated here. The male is structurally similar to *A. tesselatum*, but with notable differences: the apical spines are, on average, stronger and shorter, and the distance between the two spines is reduced (averaging 0.54 mm at the apex, compared to 0.80 mm in *A. tesselatum*; based on N=10 for each species). Furthermore, the lateral projections of the basal plate of S6 are more robust than those in *A. tesselatum*. In terms of colouration, *A. villosulum* is characterized by a dark brown to black ground colour, contrasting with the typical mix of black and red-brown found in *A. tesselatum*.

Material examined

THE GAMBIA: 1♂; [centre point: 13.44°N -15.1°E], 20 m; examined from photograph (Fig. 5) (Smith 1854). – NIGERIA: 9♀♀, 14♂♂; Jebba: Bacita environs (9.07°N 4.95°E); various dates in November and December 1973; G. F. Mees leg. (NBC).

Redescription

Female. 8–9 mm. – Head: black with yellow on clypeus, lower paraocular area, lower half of upper paraocular area, lower supraclypeal area, mandible (black teeth only), and a thin preoccipital band interrupted in the middle; clypeus slightly convex with a smooth, straight dark brown apical rim; mandible with six black teeth, teeth 1 and 6 strong-

est, teeth 2, 3, and 5 smaller and almost equally strong, tooth 4 smallest; punctation dense, finer around ocelli than on vertex; antenna red-brown, darker above than beneath; underside of scape yellowish. – Mesosoma: scutum black with yellow anterolateral band, often interrupted in the anterolateral corner; mesepisternum angulate, anterior side smooth and shiny; scutellum and axillae crescent-shaped; outer side yellow; scutum, scutellum, and axilla densely punctate, similar to vertex; pronotal lobe yellow. Femora light red-brown with yellow stripes, tibiae predominantly yellow with light red-brown mainly on inner sides; hind tibia with a strong longitudinal carina embedded in a dark red-brown mark; dense felt-like pubescence on fore and mid-basitarsi, less dense on hind basitarsus. – Metasoma: black with yellow maculation; depressed marginal zone longer than premarginal zone, densely punctate with narrow, shagreened interstices; distance of punctures on disc approximately 1–2 puncture diameters on T1, and approximately 0.5–1.0 puncture diameters on subsequent terga; T1 with triangular lateral and mediolateral yellow maculation; T2–T5 with lateral bands not reaching the middle; T6 with a lateral yellow spot; T1–T6 with brushes of white hairs laterally; T6 like a curly brace in dorsal view, with a small apical emargination for the sting; scopa dirty-white except for black hairs around the apex.

Male. 10–12 mm. – Head: black with yellow clypeus, lower paraocular area (extending slightly beyond antennal socket), lower supraclypeal area, mandible (black teeth excluded), and small spot or elongated maculation behind the eye; clypeus slightly convex with a smooth, impunctate, straight apical edge; mandible shagreened, with a strongly carinate, semi-transparent outer ridge; antenna dark brown above, reddish-brown beneath, underside of scape yellow. – Mesosoma: scutum black with anterolateral yellow band, often reduced or absent; scutellum, axillae, and pronotal lobe as in female. – Metasoma: T1–T5 black with two rows of semi-rectangular yellow maculations; strong brushes of white hair on T1–T3 laterally, less dense on subsequent terga; curved spines on T4–T6 laterally, median spine largest; spine on T4 and T5 black and yellow, on T6 black; T7 with two apical spines; dense ventral pubescence; hairs visible from above between the spines black, others silvery (Figs. 9B, 10B); basal plate of S6 slightly flattened apically, with strong lateral projections with black margins (Fig. 11); apical median projection of S8 slender, parallel-sided (Fig. 12).

Distribution

West Africa, with records from The Gambia and Nigeria (Fig. 16A).

Fig. 9. Apical terga of the five species of *Anthidium* treated in this study. **A**. *Anthidium bischoffi* Mavromoustakis, 1954. **B**. *Anthidium villosulum* Smith, 1854. **C**. *Anthidium niveocinctum* Gerstaecker, 1858. **D**. *Anthidium tesselatum* Klug, 1932. **E**. *Anthidium wuestneii* Mocsáry, 1887.

Fig. 10. Apical sterna of the five species of *Anthidium* treated in this study. **A**. *Anthidium bischoffi* Mavromoustakis, 1954. **B**. *Anthidium villosulum* Smith, 1854. **C**. *Anthidium niveocinctum* Gerstaecker, 1858. **D**. *Anthidium tesselatum* Klug, 1932. **E**. *Anthidium wuestneii* Mocsáry, 1887.

Anthidium (*A.*) *wuestneii* Mocsáry, 1887
(Figs. 6, 7, 9–13)

Anthidium wuestneii Mocsáry, 1887 ("Syria", not necessarily identical with today's Syria).
Anthidium wüstneii ssp. *hellenicum* Mavromoustakis, 1959 (Greece: Rhodes).
Anthidium bischoffi var. *dzhachrumicum* Popov, 1967 (Iran). Synonymy established by Fateryga et al. (2020).
Anthidium (*Proanthidium*) *wuestneii* Mocsáry, 1887 (Pasteels 1969).

Genetic Barcode Index Number (BIN): BOLD:ADE1479.

Diagnosis

The female is distinguished by its mandible with four strong teeth and mostly six smaller teeth in between. The male features—as in *A. bischoffi*—curved lateral spines on T4–T6, with T6 largest (T5 largest in *A. tesselatum* and *A. villosulum*). In *A. wuestneii*, the spines are conspicuously stronger than in *A. bischoffi*. S6 is semioval in *A. wuestneii*, while it is semi-circular in the other species treated here (Fig. 13).

Taxonomy

Here newly combined with the nominate subgenus from its previous placement in the subgenus *Proanthidium*, **subg. comb. n.** *Anthidium bischoffi* ssp. *dzhachrumicum* Popov, 1967 from Iran was assigned to *Anthidium waltlii* Spinola, 1838 by Warncke (1980), but was recognized as a synonym of *Anthidium wuestneii* Mocsáry, 1887 by Fateryga et al. (2020).

Material examined

ARMENIA: 2♀♀, 1♂; ABABY071-23; Meghri (38.91°N 46.27°E); 14.vi.2018; V. Soon leg. (TUZ). – 1♂; Yerevan: Memorial Park (40.18°N 44.49°E), 1060 m; 30.vi.2015; Léo Correia da Rocha Filho (unpubl. photograph). – AZERBAIJAN (NAKHCHIVAN AUTONOMOUS REPUBLIC): 1♀, 1♂; ABABX331-21; ABABX332-21; Julfa: Gazanchi (39.21°N; 45.68°E); 26-27.vii.2018; M. Proshchalykin, Kh. A. Aliyev, & M. M. Maharramov leg. (coll. A. Fateryga). – GREECE: 1♀; Chios: E Lithi (38.20°N 26.00°E), 100-250 m; 15.vi.2007; A. W. Ebmer leg. (CMK). – 1♀; Rhodes: Tsambika (36.23°N 28.14°E), 10 m; 26.v.-03.vi.1986; M. C. Day & M. G. Fitton leg. (NHMUK). – 1♂; Monemvasia (36.68°N 23.05°E), 20 m; 18.-26.v.1977; K. Guichard leg. (CMK). – IRAN: 2♀♀, 1♂; Kerman prov.: 30 km S Sirjan (29.13°N 55.74°E), 1730 m; 07.vi.2010; Mi. Halada leg. (CMK). – LEBANON: 2♂; Ba lshmayh (33.81°N 35.63°E); 03.vii.1975 (AUB, M. Boustani). – 2♂♂; Arz al Barouk (33.68°N 35.68°E); 18.vi.1975 (AUB, M. Boustani). – 2♀♀; Sawfar (33.80°N 35.70°E); 21.vi.1973 (AUB, M. Boustani). – 4♀♀; Darhouna (33.83°N 35.83°E); 16-17. vi.1975 (AUB, M. Boustani). – 1♀; Qornael (33.85°N 35.72°E); 07.vii.1975 (AUB, M. Boustani). – 1♀; Salima; (33.86°N 35.68°E); 21.vi.1973 (AUB, M. Boustani). – 1♀; Bekaa: AUB Farm (33.92°N 36.07°E); 02.vi.1962 (AUB, M. Boustani). – TURKEY: 1♀; Antalya: 28 km NW (37.12°N 30.52°E), 820 m; 03.vi.2001; G. Hölzler leg. (CMK). – 6♀♀, 9♂♂; Antalya: Konaklı (36.64°N 31.87°E); 27.vi.2024; M. Kasparek leg. (CMK). – 2♂♂; Denizli: Acıgöl Çardak env. (38.81°N 29.66°E); 07.vii.1993; K. Denes &

Jirousek leg. (CMK). – 1♀; Izmir: Dikili env. (39.07°N 26.88°E), 10 m; 19.vi.1998; J. Halada leg. (CMK). – 2♀♀; Mersin: Mut (36.63°N 33.43°E), 305 m; 10.-13.vi.1965; M. Schwarz leg. (CMK). – 1♀; ABABX060-20; Muğla env. (37.21°N 28.39°E), 665 m; 15.vii.2017; M. Kasparek & O. Özgül leg. (CMK). – 2♂♂; Muğla: Akyaka (Çitlik) (37.03°N 28.41°E), 80 m; 30.ix.2013; M. Kasparek leg. (CMK). – 4♂♂; Muğla: Akyaka env. (37.05°N 28.32°E), 40 m; 15.-24.ix.2013; M. Kasparek leg. (CMK). – 3♀♀, 5♂♂; Muğla: Akyaka, Yeşilova (37.05°N 28.42°E), 70 m; 29.viii., 01.ix.2012; M. Kasparek leg. (CMK). – 3♀♀, 1♂; Muğla: Akyaka, Akbük (37.03°N 28.10°E), 10 m; 08.x.2012; M. Kasparek leg. (CMK). – 3♀♀, 1♂; Muğla: Akyaka env. (37.05°N 28.32°E), 40 m; 15.-24.ix.2013; M. Kasparek leg. (CMK). – 2♀♀; Muğla: Akyaka env. (37.05°N 28.33°E), 6♂♂; ix.2012; V. Bartak leg. (CMK, OLL). – 3♀♀, 4♂♂; ABABX061-20; ABABX062-20; Nevşehir: Ihlara Vadisi S Selime (38.27°N 34.28°E), 1200 m; 27.-28.vii.2016; M. Kasparek & O. Özgül leg. (CMK). – 1♀; Pazarcık, Ganidağı (37.48°N 37.43°E), 1000 m; 11.vi.2008; M. Kafka leg. (CMK). – 1♂; Urfa: Halfeti env. (37.24°N 37.86°E), 400 m; 03.-05.v.1994; Mi. Halada leg. (CMK).

Literature records

ARMENIA: Kotayk Prov.: Jrvezh (40.18°N 44.62°E); 18.ix.1959; V. A. Richter leg. [ZISP]; Fateryga et al. (2020). – AZERBAIJAN (Nakhchivan Autonomous Rep.): Ordubad (38.90°N 46.02°E), 830 m; Warncke (1980) (erroneously assigned to Armenia by Warncke). – Julfa, Milakh (39.25°N 45.72°E); 27.vii.2018; M. Proshchalykin, Kh. A. Aliyev, M. Maharramov leg. [coll. A. V. Fateryga]; Fateryga et al. (2020). – Julfa, Gazanchi (39.22°N 45.68°E), 26–27.vii.2018; M. Proshchalykin, Kh. A. Aliyev, M. Maharramov leg. [coll. A. V. Fateryga]; Fateryga et al. (2020). – Julfa, 5 km N of Dize (39.05°N 45.75°E); 20.vi.2019; M. Proshchalykin, Kh. A. Aliyev, M. Maharramov leg. [coll. A. V. Fateryga] (Fateryga et al., 2020). – CHINA: "Sedshouan [= ? Szetschwan]" (Warncke, 1980). Record not regarded as reliable. – GREECE: Chios: Armolia (38.27°N 26.04°E); Ascher & Pickering (2024). – Corfu (39.62°N 19.92°E); Grace (2010). – Lesbos: Mytilene (39.08°N 26.57°E); 16.viii.2016; J. Devalez leg. (in: Ascher & Pickering, 2024). – Rhodes: Empona (36.22°N 27.85°E); 18.-19.vi.1958; Mavromoustakis (1959). – Rhodes: Petaloudes (36.36°N 28.07°E), 110 m; Mavromoustakis (1959). – IRAN: Fars: 25 km SE of Jahrom ("Джахрум", = "Dzhakhrum") (28.33'N 53.72°E); 16.vii.1955; D. Steinberg leg. (*A. b. dzhachrumicum*; type locality) (ZISP); Fateryga et al. (2020); Popov (1967). – Yazd: Mehriz, Damgahan (31.52, 54.32°E), 1970 m; 27.vi.2012; 03.vii.2013; L. Dehghan leg.; Dehghan Dehnavi et al. (2014). – Mehriz, Madvar (31.52°N 54.20°E), 2422 m; 08.vii.2012; L. Dehghan leg.; Dehghan Dehnavi et al. (2014). – Taft: Dashtak (31.65°N 54.02°E), 2214 m; 26.vii.2013; L. Dehghan leg.; Dehghan Dehnavi et al. (2014). – Isfahan province, Chadegan, Sade Zayandehroud (32.44°N 50.43°E), 2067 m; 19.vii.2012; Khodarahmi Ghahnavieh & Monfared (2019), Zakikhani et al. (2021). – Elburs Mountains: Zanak, 11 km N Ab Ali (35.85°N 51.96°E), 2300 m; 11.vii.1964; Warncke (1982). – LEBANON: Bcharré (34.25°N 36.01°E), 1,400 m., 5.-11.viii.1928; R. Ebner leg. (NHW); Mavromoustakis (1955). – SYRIA: Type locality, exact location unknown (not necessary in today's boundaries of Syria); Mocsáry (1887). – TURKEY: Afyon: Sultandağı, Yeşilçiftlik (38.53°N 31.22°E), 998 m; 25.vii.2007; Güler (2011). – Antalya: Alanya (36.54°N 31.99°E); 22.vii.1966; M. Leclercq leg.; Staněk (1968), as *A. tesselatum*, but description allows identification as *A. wuestneii*. – Antalya: Side (36.77°N 31.39°E); 17.vi.1987; Özbek & van der Zanden (1993). – Bergama (39.12°N 27.17°E); 13.vii.2013; J. Devalez photographed (www.flickr.com/photos/habropoda/10352031243). – Denzli: Pamukkale (37.91°N 29.11°E), 1000 m; 26.vii.1985; Özbek & van der Zanden (1993). – Erzurum: Tortum (Meydanlar) (40.34°N 41.34°E); 4.vii.1991; Özbek & van der Zanden (1993). – Erzincan: Bayırbağ (Üzümlü) (39.69°N 39.72°E), 1380 m; 10.viii.1992; Özbek & van der Zanden (1993). – Isparta (37.96°N 30.50°E), 1180 m; 04.viii.2009; Güler et al. (2014). –

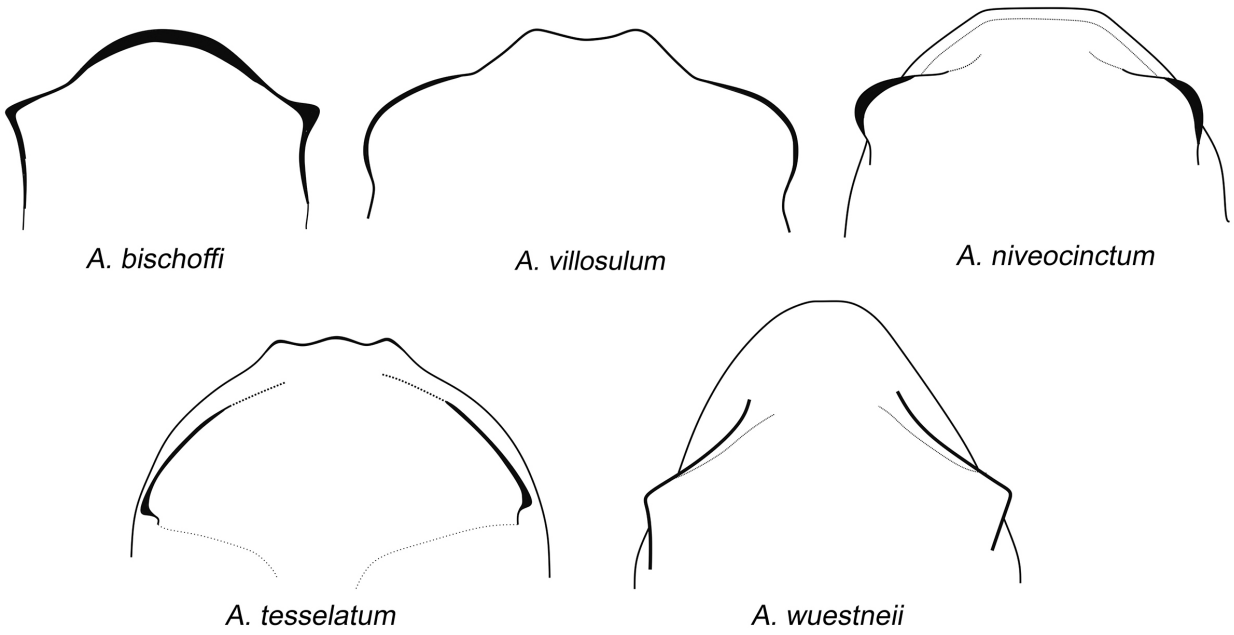

Fig. 11. Sternum 6 of the five species of *Anthidium* treated in this study.

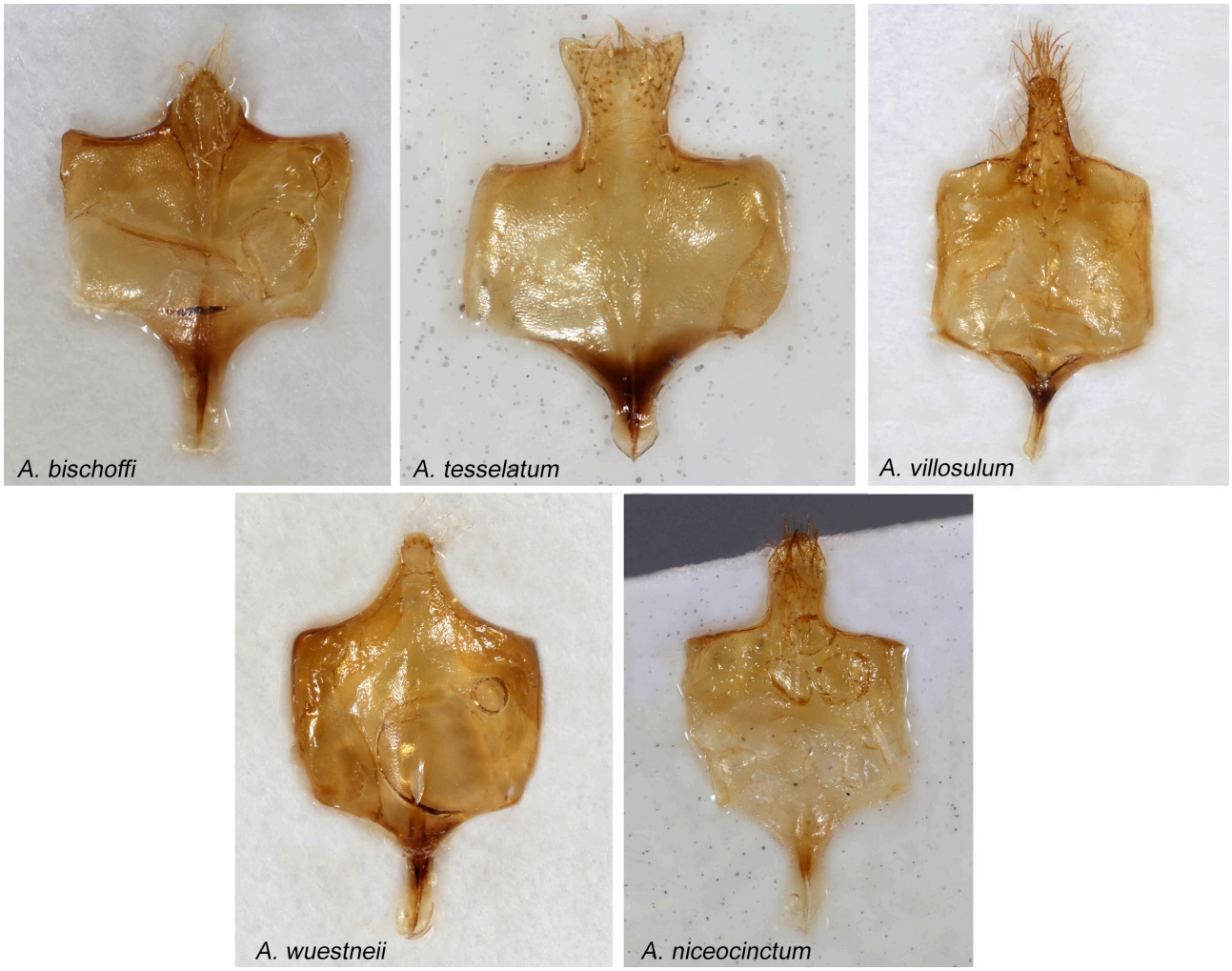

Fig. 12. Hidden sternum 8 (S8) of the five species of *Anthidium* treated in this study.

Konya: Karaman (37.18°N 33.22°E); 7.ix.2013; Ö. Kocak photographed (www.inaturalist.org/taxa/1472035). – Muğla: Köyceğiz (36.96°N 28.68°E); 12.vi.1987; Özbek & van der Zanden (1993).

Redescription

[There are black and red-brown colour morphs.]

Female. 10–11 mm. – Head: black with a yellow clypeus, lower paraocular area, lower supraclypeal area, mandible (black teeth excluded), and narrow preoccipital band between the eyes (interrupted in the middle); lower gena red-brown; clypeus evenly punctate, occasionally somewhat scattered around midline anteriorly; apical rim black, shallowly crenulate (semi-transparent ochreous in the red-brown morph); mandible with four large teeth and mostly six small to minute teeth in between. – Mesosoma: scutum black with dense, honeycomb-like punctation; yellow anterolateral band often interrupted in the corner; narrow, yellow longitudinal stripe next to the middle, often present only in remnants or absent; scutellum lamellate posterolaterally and emarginate medially; outer side of scutellum and axilla yellow, inner side black (or red-brown in the red-brown morph); pronotal lobe yellow, carinate; sides of mesosoma black (red-brown in the red-brown morph). Femora and inner side of tibiae light red-brown; hind tibia with a longitudinal carina, surrounded by black or red-brown maculation; fore and mid-basitarsus with short, felt-like pubescence. – Metasoma: terga black (or red-brown) with yellow bands, wedge-shaped, incised in the middle; band on T1 tapering towards the middle (not in the specimen belonging to the red-brown morph), interrupted in the middle; T6 yellow with some black maculation in the middle; scopa golden yellow, apical hairs black.

Male. 10–14 mm. Head: black with yellow clypeus, lower paraocular area, a small spot behind the eye, and mandible (except for black teeth); antenna dark brown to blackish. – Mesosoma: black; long white hairs laterally;

pronotal lobe carinate; scutellum sometimes with a yellow, narrow transverse stripe. Legs black with yellow maculation on tibiae; long hairs on tibiae and basitarsi laterally; basitarsi approximately as long as tibiae; very long distitarsus. – Metasoma: T1–T6 with yellow bands mostly interrupted in the middle; mediolaterally attenuated or interrupted, thus rendering the terga with four rows of yellow maculations; T3 with a small projection laterally; T4–T6 with strong, curved spines laterally, the apical one being the strongest; spines on T4–T5 mostly yellow, on T6 black and yellow; T7 bifid with two strong straight spines; punctation on terga much finer than on scutum; T3–T5 with a dense row of bristles emerging from premarginal line; T1 to T3 or T4 with strong brushes of white hairs laterally; S6 oval with strong lateral projections (Fig. 13); apical median projection of S8 tapering toward apex (longer than in *A. bischoffi*) (Fig. 12).

[Note. The examined material included an exceptionally large individual (14 mm) with reduced yellow maculation, clypeus partly black, and medio-lateral yellow spots only present on T2–T4 as small remnants; legs with some yellow only on mid-basitarsus. Notably, this individual was collected in the southern Peloponnese, which seems to be an isolated occurrence in Greece to the west of the mid-Aegean trench.]

Distribution

Eastern Mediterranean and Middle Eastern species with records from Armenia, Azerbaijan (Nakhchivan Autonomous Republic), Greece, Iran, Lebanon, and Turkey (Fig. 17).

Anthidium subg. *Nivanthidium* Pasteels, 1984

This subgenus of *Anthidium* is distinguished by a strongly pronounced scutellum that is conspicuously emarginate medially, shiny, and sparsely punctate, with posterior edge terminating in a lamella (Michener & Griswold 1994). Both sexes exhibit a longitudinal carina on the hind tibia. The male is further characterized by a bifid T7. Notably, this subgenus is now represented by a single species.

Anthidium (*N.*) *niveocinctum* Gerstaecker, 1858

(Figs. 7, 9–13)

Anthidium niveocinctum Gerstaecker, 1858 (Mozambique, male; ZMB, examined from photograph). Full description in Peters (1862).

Anthidium banzonis Strand, 1912, **syn. n.** (Cameroon, male; ZMB). The type in ZMB was labelled as a synonym of *A. niveocinctum* by Pasteels in 1961, but this had not been published so far.

Genetic Barcode Index Number (BIN): BOLD:ADU3273.

Diagnosis

Robust species; marginal zone of T1 in both sexes impunctate except laterally. Scutellum in both sexes long, with a deep emargination posteromedially. Male T7 with strong, obtuse, semi-parallel spines and dark brown pubescence (Fig. 9C). Mandible of female with six teeth, the inner four almost equally strong (Fig. 13).

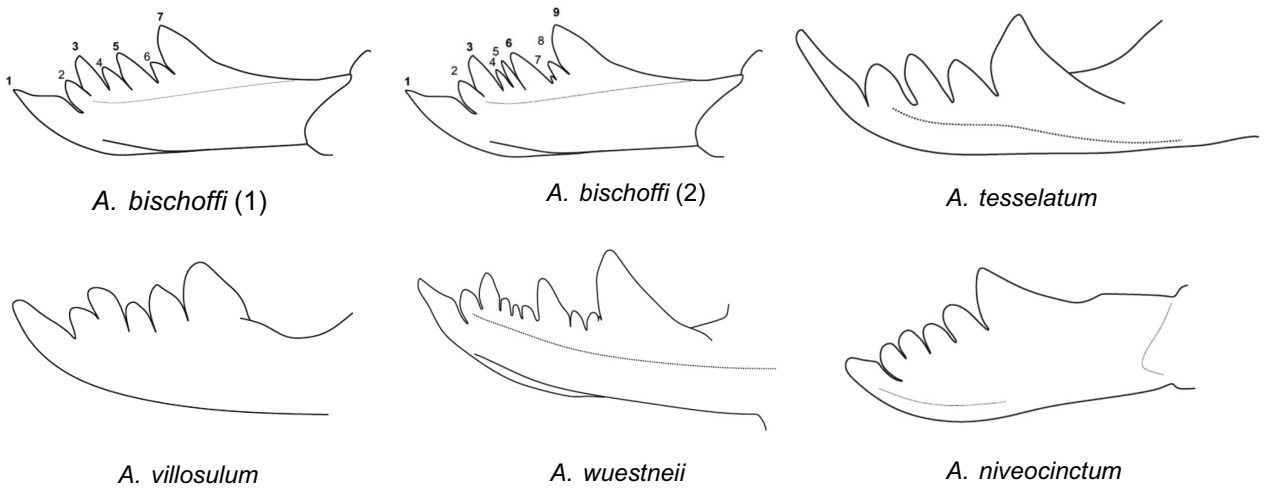

Fig. 13. Female mandibles of the four species of the *Anthidium tesselatum* species-group and *Anthidium niveocinctum* Gerstaecker, 1858. As the number of small teeth is variable in *Anthidium bischoffi* Mavromoustakis, 1954, two drawings are given: one from the lower and the other from the upper range.

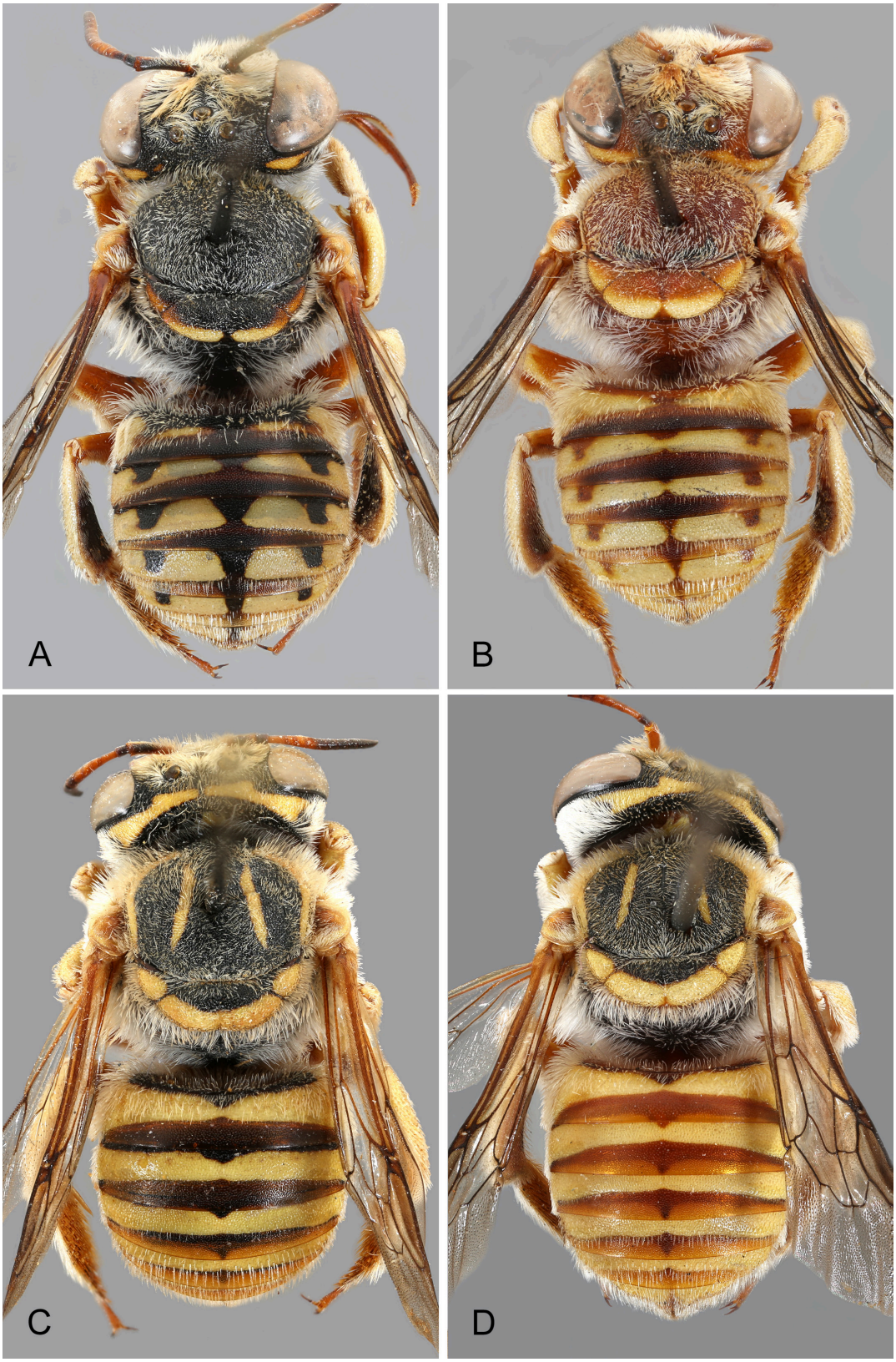

Fig. 14. Colour morphs in *Anthidium bischoffi* Mavromoustakis, 1954 (**A, B**) and *Anthidium tesselatum* Klug, 1932 (**C, D**). The females of *A. bischoffi* were collected together in Oman, those of *A. tesselatum* were collected in Jordan (C) and in the UAE (D).

Material examined

CAMEROON: 1♂; Kumbo ("Humbo") Banzo (Kumbo is the capital of the Banso settlement area) (6.22°N 10.67°E); 28.xii.1908; S. G. Riggenbach leg. (as *A. banzonis;* type locality); ZMB, photograph examined; Strand (1912, 1927). – KENYA: 1♀; Taita Hills (-3.37°N 38.32°E); 11.iii.2024; L. Floeck & C. Moser leg. (coll. P. Geisendörfer). – MOZAMBIQUE: Type locality Mozambique (exact locality unknown); W. C. H. Peters leg.; ZMB; photograph examined; Gerstäcker (1858), Peters (1862). – NIGERIA: 1♂; Jebba: Bacita environs (9.07°N 4.95°E); 14.xii.1973; G. F. Mees leg.; RMNH (NBC064). – 2♀♀, same locality, 24.xi.1973 and 14.xii.1973; RMNH (NBC062, NBC063).

Literature records

DEMOCRATIC REPUBLIC OF THE CONGO: Kasaï: Tshikapa (-6.40°N 20.80°E); iv.1939; Mevr. Bequaert leg.; RMCA; Tshibungu Nkulu (2023). – Lomami: Luputa (-11.00°N 26.73°E); 1935; Dr. Bouvier leg.; RMCA; Tshibungu Nkulu et al. (2023). – ETHIOPIA: Mentioned by Pasteels (1984), no details available. – Oromia (center point: 6.34°N 40.63°E); 13.ix.2024; Abuna Tafa leg. (NHMUK); NHMUK010838878, BOLD Database. – KENYA: Makindu (-2.41°N 37.97°E); 22.iii.2007; M. Otiendo leg. (BBSL; GBIF). – Samburu, Rift valley: Buffalo Springs (0.52°N 37.59°E); 15.-18.vii.1987; H. R. Feijen leg. (NBC; GBIF). – MALAWI: Liwonde (-15.06°N 35.23°E); 23.iv.1975; G. G. M. Schulten leg. (NBC; GBIF). – Salima, Grand Beach Hotel (-13.76°N 34.60°E); 15-16.iv.1973; H. R. Feijen leg. (NBC; GBIF). – Cape Maclear (-14.01°N 34.85°E); 04.iv.1970, 07.v.1971; G. G. M. Schulten leg. (NBC; GBIF). – Thuchila ("Tuchlia") (-15.91°N 35.35°E); 4.v.1971; G. G. M. Schulten leg. (NBC; GBIF). – Monkey Bay, Lake Malawi (-14.07°N 34.90°E); 23.iv.1967; Ch. Michener leg. (BBSL, SEMC; GBIF). – MOZAMBIQUE: "Porto Henrique" (-15.31°N 39.98°E (?)); 15.xii.1980 (NBC, see GBIF). – NAMIBIA: Oshivelo, 7.iv.1996 (-18.61°N 17.16°E) (Gess & Gess 2007, 2014; see also GBIF). – Ondong(u)a (Ondangwa) (-17.92°N 15.95°E); SAM (GBIF). – NIGERIA: Cross River State: Old Calabar (4.79°N 8.46°E); Friese (1909). – SOUTH AFRICA: Waterpoort, SE (-20.03°N 30.68°E), iv.1978, M. Botha leg. (SANC); Combey (2008). – Groothoek Mine (-24.50°N 30.68°E), 6.iv.1980, A. P. du Toit leg. (SANC); Combey (2008). – Limpopo: Langjan Nature Reserve (-23.86°N 29.23°E), 23-24.i.1982, C. D. Eardley leg. (SANC); Combey (2008), see also GBIF. – Ranium (-25°08°N 28°28°E), 3.iii.1989, P. Snyman leg. (SANC); Combey (2008). – Schuitdrift Road, 9 km SW Tshipise (-22°66°N 30°06°E), 4.iii.1990, C. D. Eardley leg. (SANC); Combey (2008; see also GBIF). – TANZANIA: Kigonsera ("Kigousera") W of Lake Malawi (-10.76°N 35.76°E); Friese (1904, 1909). – Tabora (-05.04°N 32.82°E); 30.v.1985; G. G. M. Schulten leg. (NBC; GBIF). – Mkomazi Game Reserve, Ibaya (-3.96°N 37.80°E); 8.v.1995, A. Russell leg. (SANC); Combey (2008). – Mwanza (-2.51°N 32.91°E); 18-19.i.1968; D. Gillissen & L. Blommers leg. (NBC; GBIF). – UGANDA: Hoima (1.42°N 31.34°E), C. C. Gowdey leg.; Mavromoustakis (1940). – ZAMBIA: Mbala ("Abercorn") (-8.85°N 31.36°E), 1615 m; v.1944; H. J. Bredo leg. (AM); Mavromoustakis (1945). – Mpulungu (-08.76°N 31.13°E); 02.v.1944, 16.v.1944; SAM (GBIF). – ZIMBABWE: Que Que (-18.76°N 29.73°E); 01.iv.1938; SAM (GBIF).

Redescription

Female. 11–12 mm. –Head: black with yellow maculation. Yellow areas include lower paraocular area, clypeus (except small black spot at the base and black apical margin), a small spot in the lower upper supraclypeal area, the mandible (black teeth excluded), and a spot in the preoccipital area; apical margin of clypeus straight, black, and shiny; mandible with six teeth, with teeth 2–5 almost equally strong; white pubescence on face below anterior ocellus and on gena; punctation of vertex dense, with narrow, shiny ridges between the punctures (at most one fourth of a puncture diameter); punctures smaller close to ocelli and larger behind the eye. – Mesosoma: scutum convex; remnants of a lateral yellow stripe rarely present; also, yellow longitudinal stripe close to the midline; punctation shallow, with punctures 0.5–1.0 puncture diameters apart anteriorly and 1–3 puncture diameters posteriorly; scutellum and axilla large, nearly flat, shiny; thin, slightly upward-curved posteriorly; scattered punctation with small, shallow punctures up to 3–4 puncture diameters apart; deep median incision on scutellum mediposteriorly; sides of mesosoma with long white pubescence. Femora brown; tibiae brown with yellow maculation on upper side and red-brown on underside; fore and midbasitarsi with dense felt-like pubescence; hind tibia with longitudinal carina. – Metasoma: extent of yellow maculation variable; T1 typically with lateral yellow maculation; T2–T4 with lateral yellow bands not reaching the middle and an oval constriction mediolaterally from the anterior (sometimes only a lateral yellow spot present); T6 with a mediolateral yellow spot and a lateral extension; narrow incision for the sting apically; T1 medially with very fine, scattered punctation, denser laterally; T2–T4 finely punctate, interstices on average one puncture diameter; T6 with large, dense punctures; T1–T6 laterally with dense brushes of white hairs; scopa pale yellow, apically black.

Male. 14 mm. – Head: black; yellow are clypeus, lower paraocular area, lower half of supraclypeal area, mandible except for teeth, and two spots on vertex behind the eye; clypeus slightly convex, anterior margin slightly arcuate, apical margin semi-transparently brown, almost straight; impunctate along anterior margin, otherwise with regular punctation; mandible strong, almost impunctate and shiny; one strong apical and two strong inner teeth; shortest distance between clypeus and antennal socket approximately one antennal width; punctation of vertex dense, with narrow, smooth interstices; inner orbit of eye semiparallel; antenna dark brown; scape yellow beneath. – Mesosoma: scutum black with an anterolateral yellow band; yellow, longitudinal crescent-shaped stripe next to the middle of the scutum; punctation of scutum fine and dense anteriorly (interstices on average half a puncture diameter), becoming more scattered towards the posterior (interstices up to 1–2 puncture diameters); mesosoma with dense white pubescence laterally; pronotal lobe low, yellow, with anterior carina, largely hidden under pubescence; scutellum large, widely rounded posterolat-

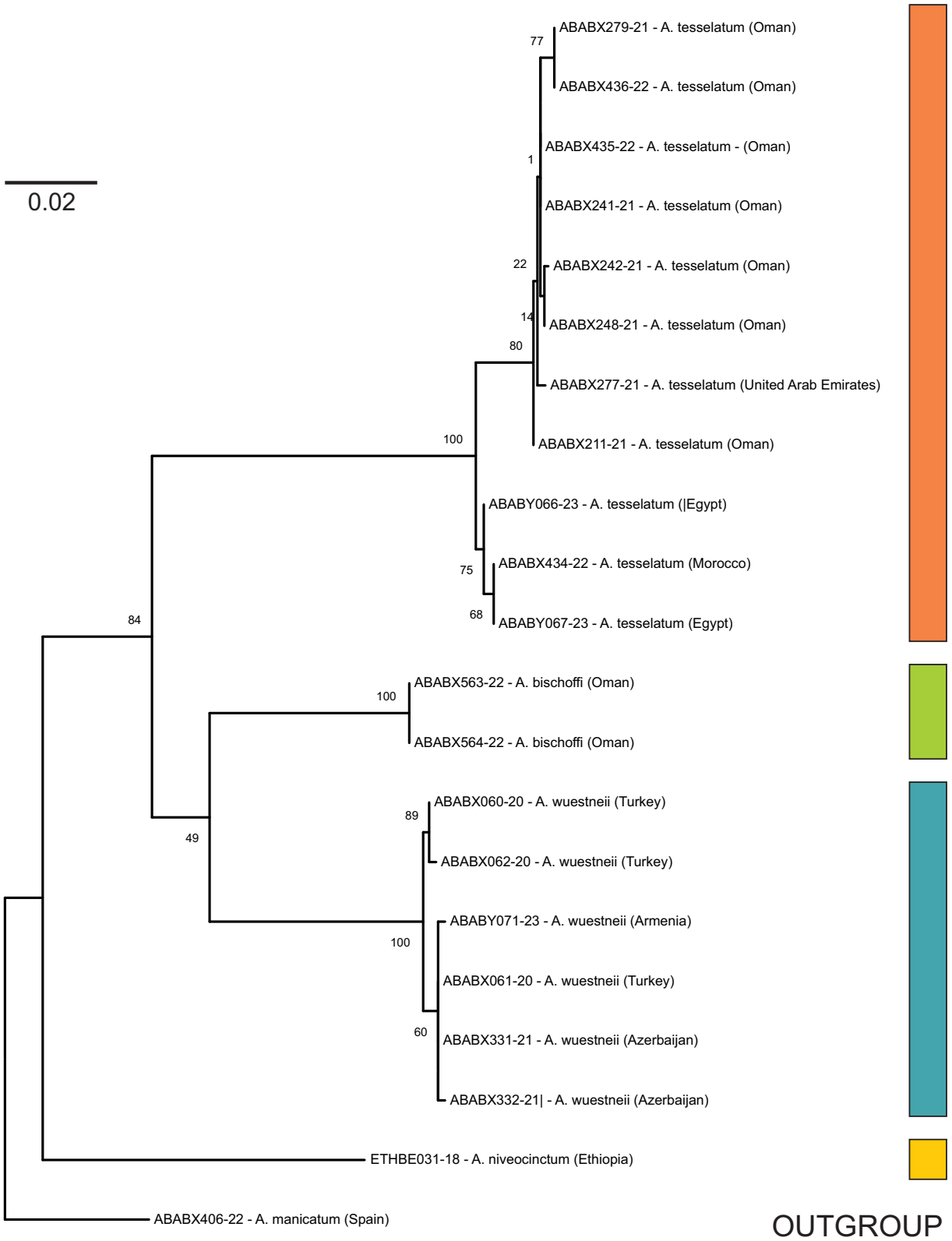

Fig. 15. Species Identification Tree (ML tree) for three species of the *Anthidium tesselatum* species-group and *Anthidium niveocinctum* Gerstaecker, 1858, based on the DNA sequence of the mitochondrial gene *cyt b* (barcoding unit). Numbers close to the nodes represent bootstrap values.

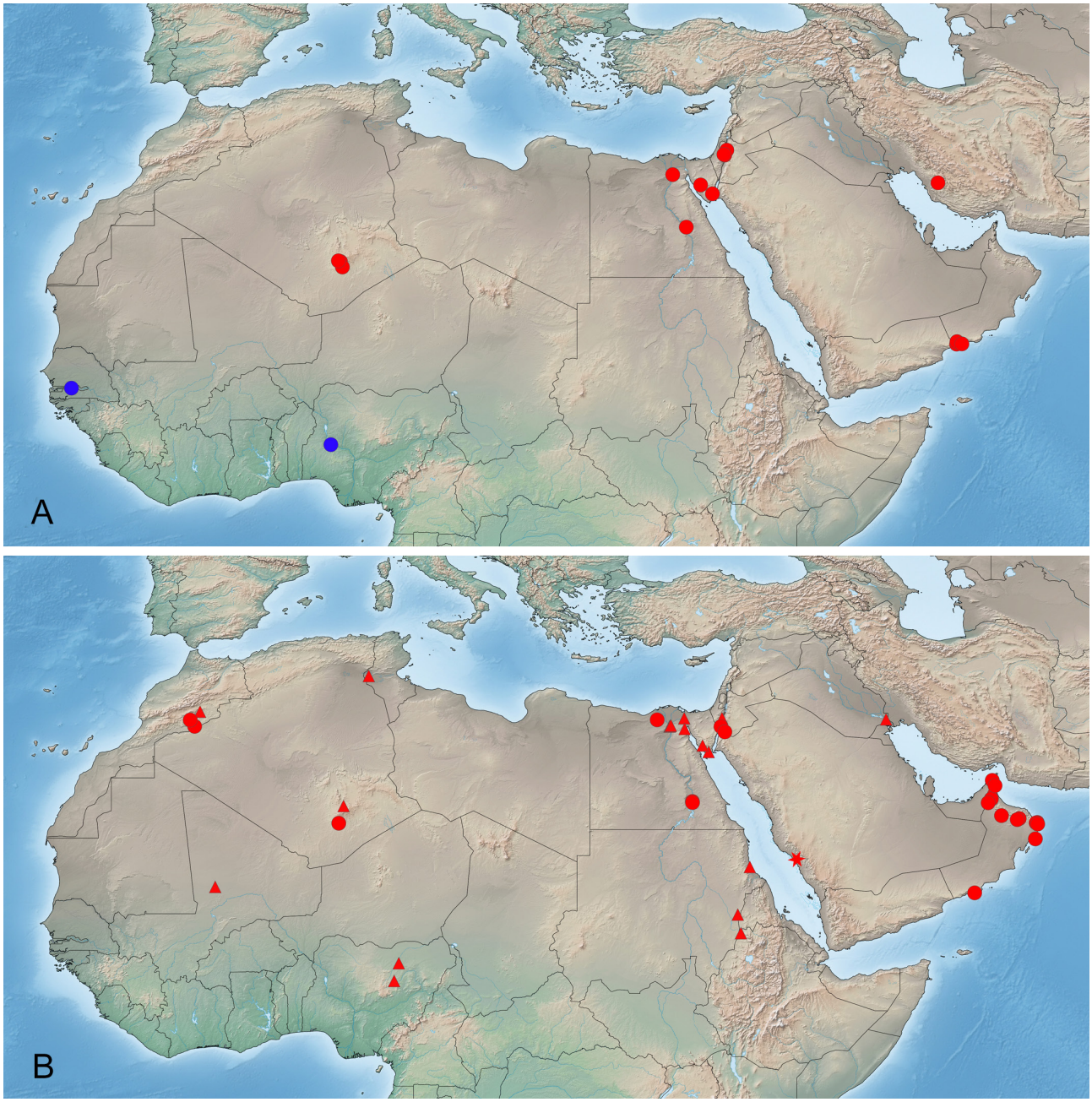

Fig. 16. Distribution of *Anthidium bischoffi* Mavromoustakis, 1954 (**A**, red dots), *Anthidium villosulum* Smith, 1854 (**A**, blue dots), and *A. tesselatum* Klug, 1932 (**B**, dots refer to material examined, triangles to literature data). The star indicates the approximate location of the type locality of *A. tesselatum*, as its exact position remains unknown.

erally and with a deep posteromedian emargination; apical margin lamellate; scutellum and axilla with narrow, yellow posterior band; fine punctation with small, shallow punctures 2–4 puncture diameters apart; interstices shallowly shagreened, shiny. Femora red-brown with yellow maculations; tibiae red-brown beneath, brown with yellow maculation on upper side; fore and hind tibiae semi-parallel-sided, mid-tibia club-shaped; hind tibia with a longitudinal carina; mid spur brown, hind spurs black; mid basitarsus slender, longer than tibia, hind basitarsus approximately as long as tibia. – Metasoma: dark red-brown with yellow maculations; terga shiny; T1 with lateral yellow maculation, T2–T6 with yellow lateral and submedian lateral maculations (linked by a yellow pos-

terior stripe); T7 black; T4 with a small lateral projection; T5 with a yellow lateral spine with black apex; T6 with a strong, curved black and yellow lateral spine; T7 with strong, obtuse, semi-parallel spines and dark brown pubescence; depression of T1 impunctate except laterally; depressions of T2–T6 with very fine, shallow punctation, punctures mostly 1–2 puncture diameters apart; punctation of discs somewhat coarser than on depressions; surface of T7 with longitudinal ridges; apical median projection of S8 broad and parallel-sided (Fig. 12).

Genetic data

The sole DNA sequence obtained from this species showed an average genetic distance (Tamura 3-parameter) of 11.8% from *Anthidium bischoffi*, 14.1% from *A. wuestneii*, and 17.5% from *A. tesselatum* (cf. also Fig. 15).

Biology

Gess & Gess (2007, 2014) reported the species as visiting Asteraceae.

Distribution

Widely distributed across Sub-Saharan Africa, approximately between 9°N and -25°N, with records from Cameroon, the Democratic Republic of the Congo, Ethiopia, Kenya, Malawi, Mozambique, Namibia, Nigeria, South Africa, Tanzania, Uganda, Zambia, and Zimbabwe (Fig. 18).

Discussion and conclusions

Colour morphs

In *A. bischoffi*, *A. tesselatum*, and *A. wuestneii*, the ground colour is either red-brown or black (see Fig. 14). Occasionally, there are red-brown individuals with some black, and also black individuals with some red-brown, but no fully intermediate individuals were found. Red-brown colouration was principally confined to the scutellum/axilla and the terga, and in those specimens the yellow tergal bands were also broader than in individuals with black ground colour. In *A. wuestneii*, I noted only one red-brown individual among 62 black individuals, while red-brown specimens were more abundant in the other two species. It is suggested that this is a case of colour dimorphism. In *A. bischoffi*, a specimen with a red-brown ground colour was collected together with a specimen with black ground colour , confirming the co-occurrence of these two forms. Additionally, the DNA sequence of the *COI* gene also supports their status as conspecific. The colour morphs were found in both sexes.

In the past, these colour morphs have given rise to taxonomic confusion. Friese (1897, 1898), for example, described the red-brown specimens of *A. tesselatum* as a taxonomic entity (*A. tesselatum* var. *aegyptiacum*) distinct from the nominate specimens, and Mavromoustakis (1936) described a red-brown individual of *A. tesselatum* from Nigeria as a distinct taxon (*A. lanitarse* var. *lloydi*). Finally, *A. bischoffi dzhachrumicum* turned out to be a red-brown form of *A. wuestneii* (Fateryga et al. 2020).

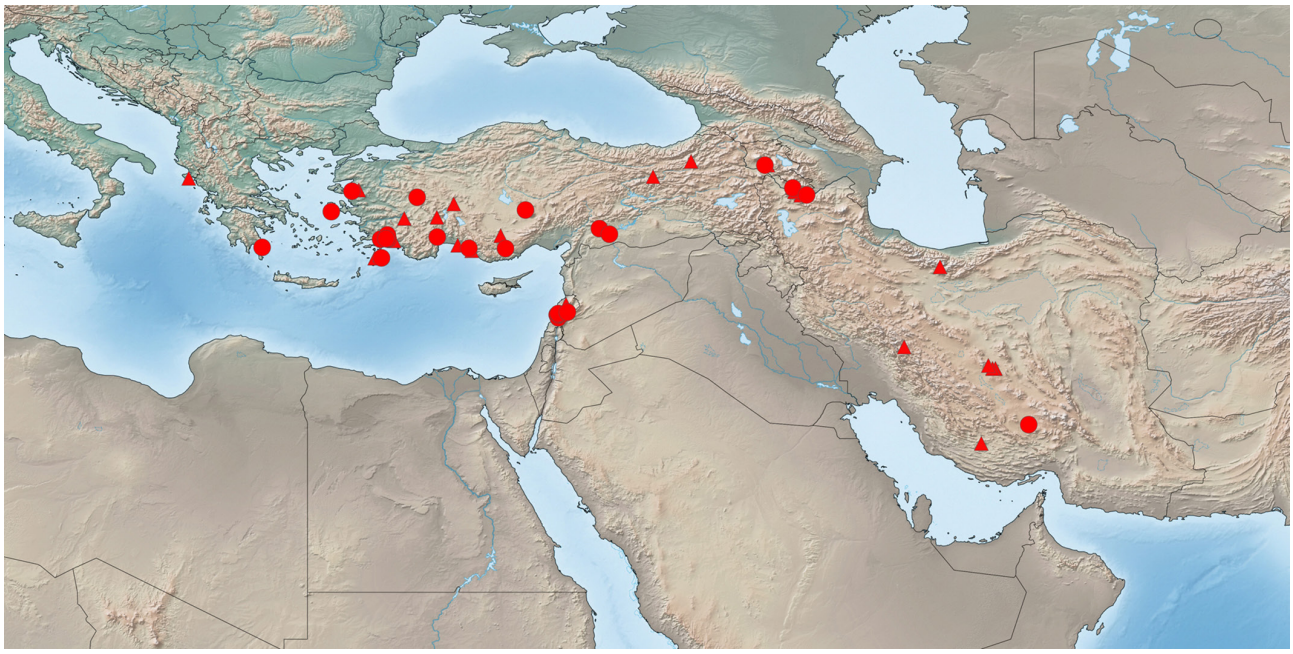

Fig. 17. Distribution of *Anthidium wuestneii* Mocsáry, 1887. Red dots refer to material examined, triangles to literature data.

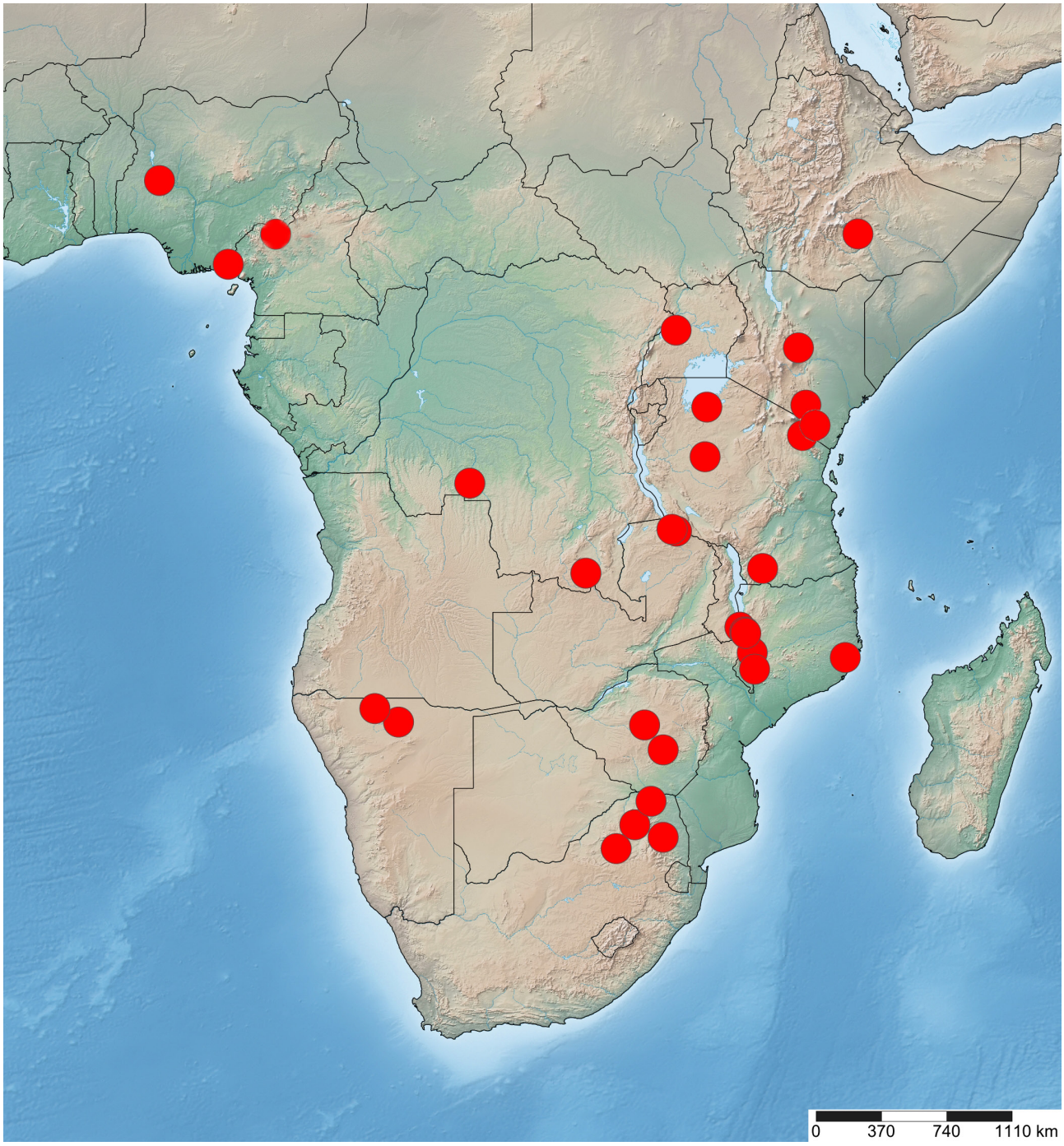

Fig. 18. Distribution of *Anthidium niveocinctum* Gerstaecker, 1858.

Similar colour morphs were not observed in *A. villosulum* and *A. niveocinctum*, but they are known for other species of *Anthidium*, specifically for *A. dalmaticum* Mocsáry, 1884, *A. undulatum* Dours, 1873, and a still undescribed species close to *A. undulatum*. In these species, specimens with red-brown ground colour and those with black ground colour could not be distinguished based on morphometry or DNA sequences of the *cty b* gene (Kasparek 2024; Kasparek & Boustani, in press).

Subgeneric affiliation

Friese (1898) defined within the genus *Anthidium* the *tesselatum* species-group, to which he assigned species in which the male has a two-toothed or two-lobed T7. In addition to *tesselatum* Klug, he attributed the following species to this group: *A. excisum* Mocsáry, *A. eximium* Giraud, *A. incertum* Morawitz, *A. trochantericum* Morawitz, and *A. unicum* Morawitz. In modern taxonomy, this group brings together species belonging to *Pseudoanthidium*, *Anthidium* (*Turkanthidium*), and *Anthidium* (*Proanthidium*) (Michener 2007; Kasparek 2022a). Mavromoustakis (1955) did not follow Friese's broad approach but confined the term "*tesselatum* group" to *A. bischoffi*, *A. tesselatum*, and *A. wuestneii*. Pasteels (1969), in his definition, included only *A. tesselatum* and *A. bischoffi* in the *tesselatum* group, while he placed *A. wuestneii* in the subgenus *Anthidium* (*Proanthidium*). This concept has been adopted in many publications including Ascher & Pickering (2024; and previous versions), but was questioned by Kasparek (2022a).

The four species of *Anthidium* treated here—*A. bischoffi*, *A. tesselatum*, *A. villosulum*, and *A. wuestneii*—share many morphological characters that support combining them to be grouped as the *A. tesselatum* species-group. Compared to Pasteels (1969), *A. villosulum* has been added to this group as it was removed from synonymy, and *P. wuestneii* was added as the number of teeth was the only trait linking it to the subgenus *Proanthidium*, while it shares a majority of characters with the species in the *tesselatum* group. The close phylogenetic relationship is confirmed by the results of the DNA analysis of the *cyt b* gene (Fig. 15). However, the status of *A. niveocinctum* has not been addressed in the discussion on the *tesselatum* species-group, despite this species exhibiting similar characters and sharing, in particular, the distinct bifid apical tergum in the male—a trait not found in other species of the genus *Anthidium*. The large, deeply emarginate scutellum and the largely shiny, sparsely punctate sculpture of the meso- and metasoma are also absent in the other species classified within the *tesselatum* group. Additionally, *A. niveocinctum* is distinguished from the other species treated here by a long, antler-like projection of the penis valve (Pasteels 1984, fig. 7a, b), much longer than in the other species treated here, and not unlike the projections found in *A. melanopygum*, *A. spiniventre*, and *A. trispinosum* (Kasparek & Fateryga 2023; Kasparek, unpublished). Finally, the results of the DNA sequence analysis of the *cyt b* gene show that *A. niveocinctum* is not closely related to the *tesselatum* group, at least not with the three members for which DNA sequences were available. Overall, it appears justified not to affiliate *A. niveocinctum* with the *tesselatum* group. The bifid apical tergum of the male appears to be a character that has arisen through convergent evolution.

Identification key

Females

1 Scutellum large with deep median emargination (Fig. 7); disc of T1 (except laterally) smooth and shiny, with only a few punctures ..... ***A. niveocinctum***
– Scutellum crescent-shaped with shallow posteromedian emargination (Figs. 1–6); disc of T1 with dense, shallow punctation **2**
2 Mandible with 5–6 teeth **3**
– Mandible with more than 6 teeth **4**
3 Mandible with 5 strong teeth (tooth 1 and 5 the largest, teeth 2–4 smaller and nearly equal-sized); rarely an additional minute tooth between teeth 4 and 5; broad, yellow, uninterrupted tergal bands; apical clypeal rim anteriorly opaque yellow, posteriorly semi-transparent .... ***A. tesselatum***
– Mandible with 6 strong teeth, tooth 4 the smallest; terga with narrow yellow bands, often interrupted or only remnants present; apical clypeal rim uniformly opaque dark brown or black ..... ***A. villosulum***
4 Mandible with 7–9 teeth, tooth scheme as in Fig. 13 ..... ***A. bischoffi***
– Mandible with 10–11 teeth, tooth scheme as in Fig. 13..... ***A. wuestneii***

Males

1 Scutellum large with deep median emargination (Fig. 7); disc of T1 (except laterally) smooth and shiny, with only a few punctures ..... ***A. niveocinctum***
– Scutellum crescent-shaped with shallow posteromedian emargination (Figs. 1–6); disc of T1 with dense, shallow punctation **2**
2 Emargination between lateral spines of T7 shallow (depth of emargination less than half its width; Fig. 9B)..... ***A. villosulum***
– Emargination between lateral spines of T7 deep (depth of emargination more than half its width; Fig. 9A, D, E)..... **3**
3 Lateral spines of T5 longer than spine of T6; median apical projection of S8 widening towards the apex (Fig. 12)..... ***A. tesselatum***
– Lateral spine of T5 shorter than spine of T6; median apical projection of S8 parallel-sided or triangular (Fig. 12)..... **4**
4 Lateral spines of T4–T6 robust (Fig. 9D); apex of basal plate of S6 half oval (Fig. 11) ..... ***A. wuestneii***
– Lateral spines of T4–T6 slender (Fig. 9A); apex of basal plate of S6 widely rounded (Fig. 11) ..... ***A. bischoffi***

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