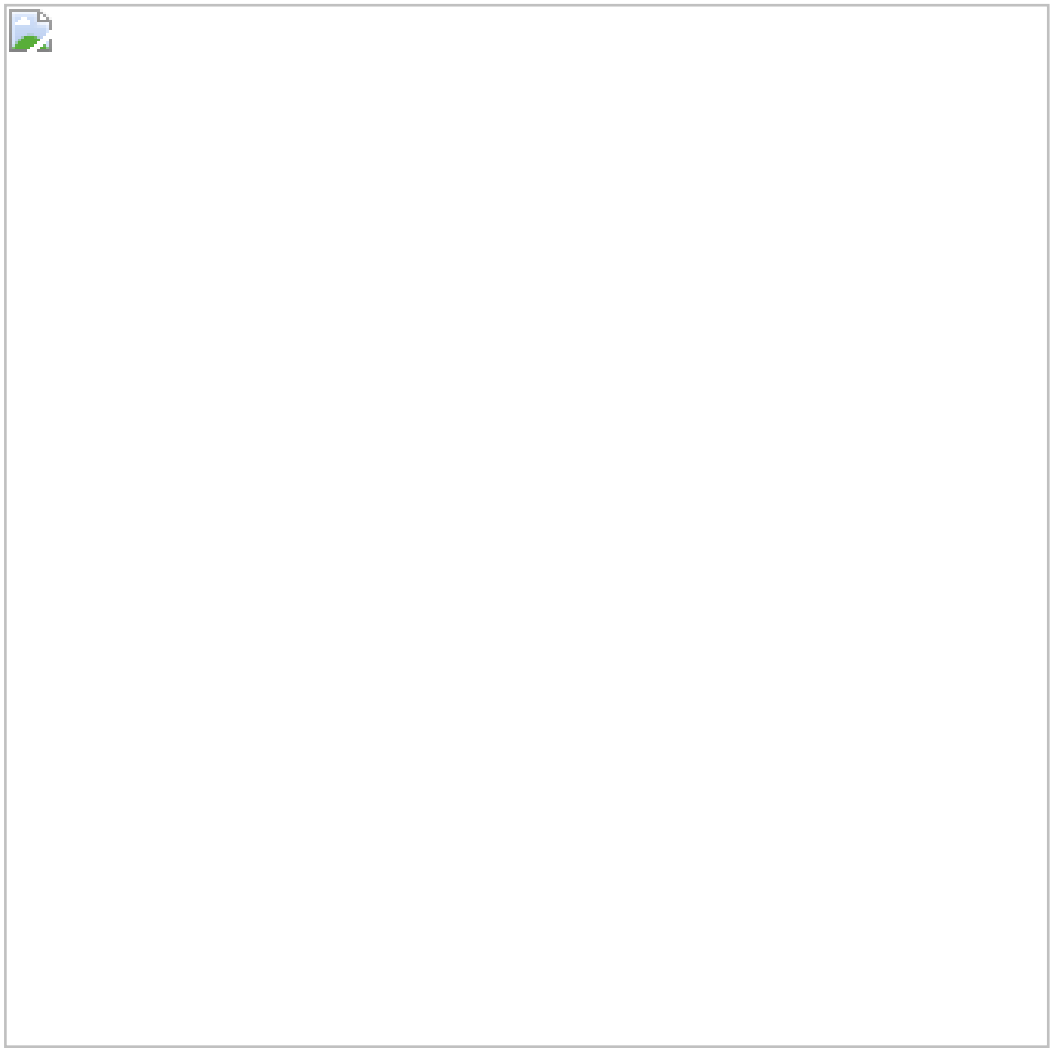

Taxonomic revision of the Afro-Arabian anthidiine bee Pseudoanthidium ochrognathum sensu lato (Apoidea: Anthidiini), based on morphological and genetic data

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RESEARCH ARTICLE

Taxonomic revision of the Afro-Arabian anthidiine bee *Pseudoanthidium ochrognathum* sensu lato (Apoidea: Anthidiini), based on morphological and genetic data

Max Kasparek[1], Martin Hauser[2] & Christian Schmid-Egger[3]

Abstract

The megachilid bee *Pseudoanthidium ochrognathum* (Alfken, 1933) is known from coastal and inland sand dunes of both North Africa and the Arabian Peninsula. While we found some differences in the colour pattern and punctation of the integument between these two populations, the DNA sequence of the mitochondrial cytochrome c oxidase I (*COI*) gene was found to be largely identical; the difference in the base sequence (Tamura 3-parameter) was less than 1% and therefore did not support species-level distinctiveness. After examining the holotypes of *Anthidium arenosum* Warncke, 1982, described from Iran, and *P. micronitens* Pasteels, 1981, described from Saudi Arabia, both taxa are proposed as junior synonyms (**syn. n.**) of *P. ochrognathum*. On the other hand, *Anthidium beaumonti* Benoist, 1950 (**stat. res.**), which was considered as a synonym of *P. ochrognathum*, is revealed to be different based on morphological and morphometric parameters, and its status as a valid species is resurrected. This taxon includes "*A. ochrognathum* var. *obscuratum* Benoist", which is considered herein to be a colour morph. Additionally, *P. rubellulum* Pasteels, 1969 (**stat. res.**) is treated as a valid, closely related species occurring in a limited range in southern Israel, and is therefore removed from synonymy with *P. ochrognathum*. The species-level differences in colouration and punctation between *P. rubellulum* and *P. ochrognathum* are confirmed by a genetic distance of 6.0–6.7% in the *COI* gene. It is suggested to refer to the three species *P. ochrognathum*, *P. beaumonti* and *P. rubellulum* as the *P. ochrognathum* species group.

Keywords: DNA barcoding; genetic distance; morphometry; synonyms; wool carder bees.

Zusammenfassung

Pseudoanthidium ochrognathum (Alfken, 1933) aus der Familie der Megachilidae ist von den Küsten- und Binnen-Sanddünen Nordafrikas und der Arabischen Halbinsel bekannt. Obwohl wir zwischen diesen beiden Populationen einige Unterschiede im Farbmuster und der Punktierung des Integuments gefunden haben, erwies sich die DNA-Sequenz des mitochondrialen *COI*-Gens (Cytochrom-c-Oxidase-I) als weitgehend identisch. Der Unterschied in der Basensequenz (Tamura 3-Parameter) betrug weniger als 1% und unterstützte daher keine Separierung auf Artniveau. Nach Untersuchung der Holotypen von der aus dem Iran beschriebenen *Anthidium arenosum* Warncke, 1982, und der aus Saudi-Arabien beschriebenen *P. micronitens* Pasteels, 1981, werden diese beiden Taxa als neue Synonyme (**syn. n.**) von *P. ochrognathum* vorgeschlagen. Andererseits zeigte sich, dass *Anthidium beaumonti* Benoist, 1950 (**stat. res.**), bisher als Synonym von *P. ochrognathum* betrachtet, sich in morphologischen und morphometrischen Merkmalen unterscheidet, so dass der Status als gültige Art wiederhergestellt wird. Dieses Taxon schließt *A. ochrognathum* var. *obscuratum* Benoist ein, das hier als Farbmorphe betrachtet wird. Darüber hinaus wird *P. rubellulum* Pasteels, 1969 (**stat. res.**), als gültige, eng verwandte Art betrachtet, die in einem begrenzten Gebiet im Süden Israels vorkommt, und damit aus der Synonymie mit *P. ochrognathum* entfernt wird. Die artübergreifenden Unterschiede in Färbung und Punktierung zwischen *P. rubellulum* und *P. ochrognathum* werden durch eine genetische Distanz von 6,0–6,7% im *COI*-Gen bestätigt. Es wird vorgeschlagen, die drei Arten *P. ochrognathum*, *P. beaumonti* und *P. rubellulum* als *P. ochrognathum*-Artengruppe zu bezeichnen.

Introduction

Pseudoanthidium ochrognathum (Alfken, 1933) is a small wool carder bee of the tribe Anthidiini, which was described from Egypt and is known from coastal and inland sand dunes of the Arabian Peninsula and North Africa (Alfken 1933). Two subsequently described taxa, *Anthidium beaumonti* Benoist, 1950 from Morocco and *Pseudoanthidium rubellulum* Pasteels, 1969 from Israel, were placed in synonymy with *P. ochrognathum* by Warncke (1980). This remained the prevailing opinion in the literature and only a few papers (Lhomme et al. 2020; Ascher & Pickering 2022; ITIS 2022) have treated *P. beaumonti* as a distinct species. Material we examined from Algeria, Chad, Egypt, Israel, Jordan, Mali, Morocco, Oman, and the United Arab Emirates (UAE) allowed us to

Fig. 1. Habitus of members of the *Pseudoanthidium ochrognathum* species group; females in upper row, males in lower row. **A, D**. *P. beaumonti* (Benoist, 1950) from Morocco. **B, E**. *P. ochrognathum* (Alfken, 1933) from Morocco; **C, F**. *P. ochrognathum* from UAE.

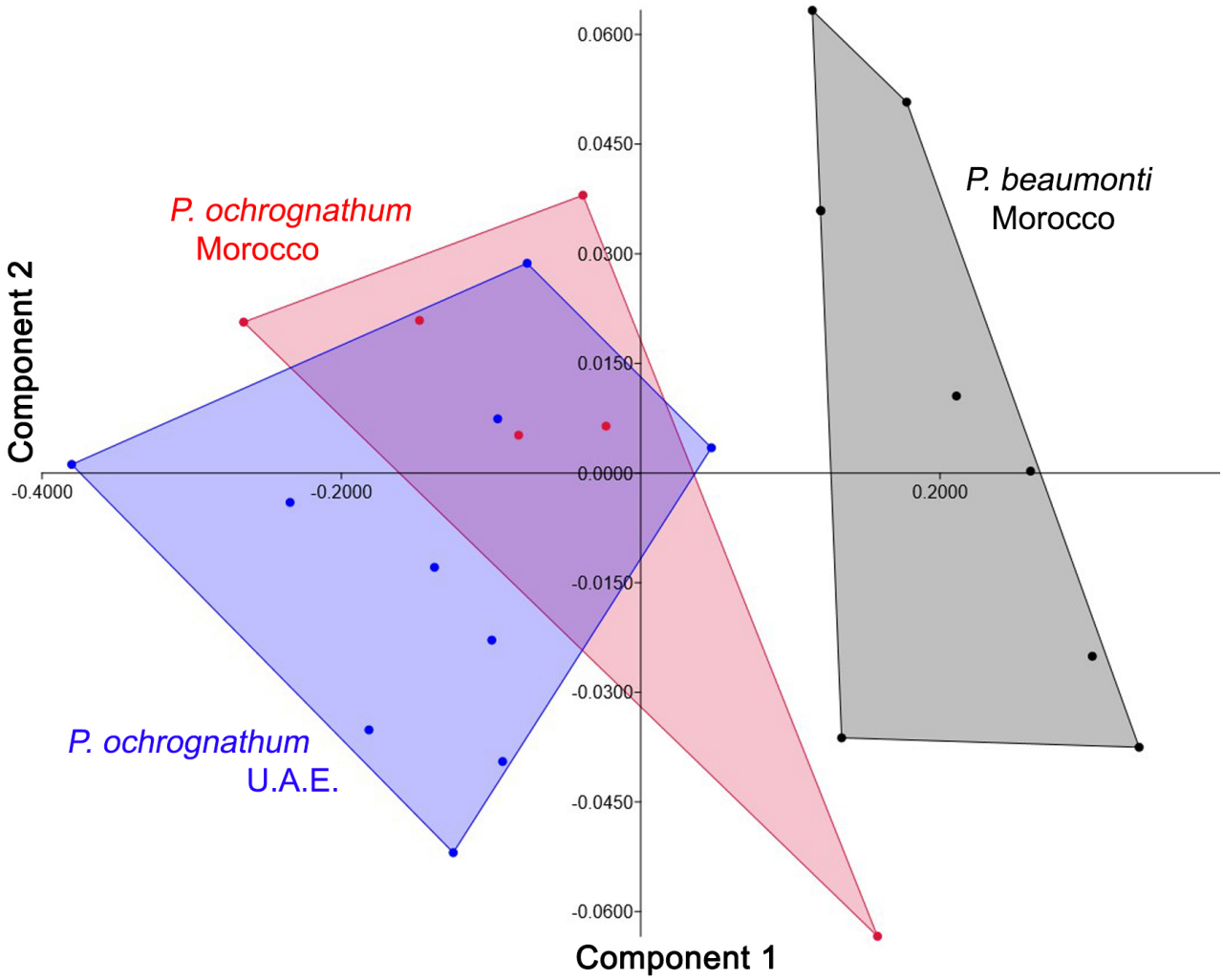

Fig. 2. Results of a Principal Component Analysis (PCA) of four morphometric parameters of females of the *Pseudoanthidium ochrognathum* species group. Different colours show the species/populations to which the material was assigned.

review the taxonomic relationships of these taxa. In addition to morphological and morphometric comparisons, our analysis includes a comparison of the DNA sequence of the mitochondrial cytochrome c oxidase I (*COI*) gene (DNA barcoding).

Material and methods

A total of 79 specimens of *Pseudoanthidium ochrognathum* sensu lato were examined. In addition to the material in the private collections of the authors, material was examined from the Muséum Cantonal des Sciences Naturelles, Lausanne (Switzerland), the Natural History Museum, London (UK), the Natural History Museum, University of Tartu, Tartu (Estonia), and the Oberösterreichisches Landesmuseum, Biologiezentrum, Linz (Austria). The reference number of the Anthidiini database of the first author is stated for all specimens in the list of materials.

For a morphometric comparison, eye-ocellus distance, ocellus-vertex distance, scutum width, and marginal cell length were used. A multivariate Linear Discriminant Function Analysis was performed to test differences between groups. The methodological approach was described by Kasparek (2020a, 2020b).

Photographs were taken with a Canon MPE65/2.8 lens mounted on a Canon EOS 6D camera equipped with a Canon Twin Lite MT24EX Macro Flash. The camera was moved between the shots with a Cognisys StackShot Rail and usually between 25 and 30 photographs were taken at different focal distances. Subsequently, the pictures were stacked with the Helicon Focus (version 8.2.0) software to create a completely in-focus image. The resulting images were further processed with Adobe Photoshop Elements 15.

For examination of the DNA sequences, a mid leg was removed from fresh specimens. 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). The mitochon-

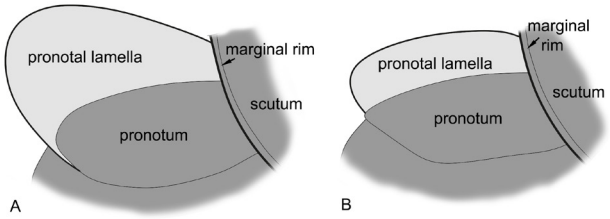

Fig. 3. Schematic view of the pronotal lobe in the *Pseudoanthidium ochrognathum* (**A**) and *P. scapulare* (**B**) species groups.

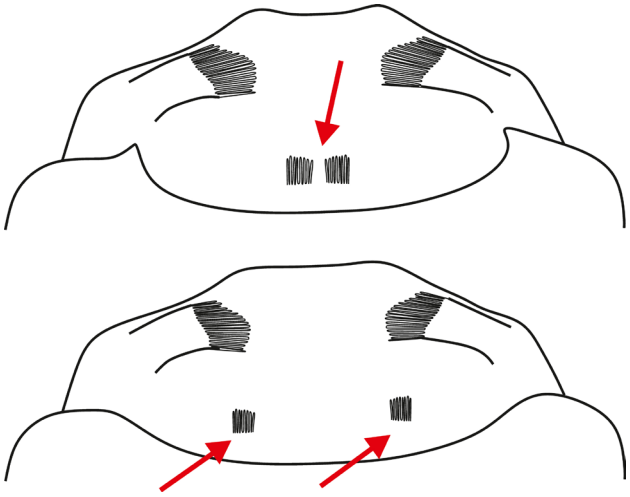

Fig. 4. Fifth sternum (S5) of *Pseudoanthidium beaumonti* (Benoist, 1950) from Morocco (above) and *P. ochrognathum* (Alfken, 1933) from the UAE (below); arrows show different positions of the combs on either side of the midline of S5.

drial cytochrome c oxidase subunit 1 gene (*COI*) was sequenced and the results were submitted to the Barcode of Life Data System (BOLD), a cloud-based data storage and analysis platform developed by CCDB (http://www.boldsystems.org). DNA sequences were retrieved from six specimens of *P. ochrognathum* s. l. (Table 1). DNA alignments were made with Clustal Alignment in the MEGAX software. The Maximum Likelihood (ML) phylogenetic analysis was performed using MEGA version 11.0.11 (Kumar et al. 2018). Bootstrap values were determined from 1,000 replications using the Tamura 3-parameter model with uniform rates among sites, and are presented here as percentages.

Genetic distance was calculated as the number of base substitutions per site from estimation of the net average between groups of sequences. Analyses were conducted using the Tamura 3-parameter model (T92 model) (Tamura 1992; Tamura et al. 2021). All ambiguous positions were removed for each sequence pair (pairwise deletion option). Evolutionary analyses were conducted in MEGA X version 11.0.11 (Kumar et al. 2018).

The map was prepared with the SimpleMappr software (Shorthouse 2010).

Abbreviations

CMK	Coll. Max Kasparek, Heidelberg, Germany;
CSE	Coll. Christian Schmid-Egger, Berlin, Germany;
CWHL	Coll. Wolf-Harald Liebig, Bad Muskau, Germany;
MWNH	Museum Wiesbaden, Naturhistorische Sammlung (coll. Martin Hauser);
MZLS	Muséum Cantonal des Sciences Naturelles, Lausanne (Switzerland);
NHMUK	Natural History Museum London (United Kingdom);
OLL	Oberösterreichisches Landesmuseum, Biologiezentrum, Linz (Austria);
SEMC	Snow Entomological Museum Collection, University of Kansas Biodiversity Institute, Lawrence, Kansas, USA;
TUZ	Natural History Museum, University of Tartu, Tartu (Estonia).

Taxonomy

Subgeneric classification versus species groups

The taxon *ochrognathum* was described by Alfken (1933) in the genus *Anthidium* Fabricius, 1804. Pasteels (1969a) erected the monotypic subgenus *Carinellum* to accommodate this taxon, which he found to be different from all other members of the genus. He stated that this subgenus is very close to *Paraanthidiellum* Michener, 1948 (which today is considered synonymous with the nominate subgenus of *Pseudoanthidium* Friese, 1898) and differs from it by a few features: (a) the pronotal lobe is surmounted by a very broad lamella that is raised anteriorly and laterally (Fig. 3); (b) the omaulus has a distinct carina in its upper half (i.e., it does not extend to the lower surface of the thorax); (c) the mandible of the female has five teeth, of which the upper one strongly predominates. Later, Pasteels (1969b) added *P. rubellulum* to this subgenus. Michener & Griswold (1994) thought that the few apomorphic characters relative to other *Pseudoanthidium* do not warrant giving *Carinellum* status as a separate subgenus. Consequently, they assigned the species of *Carinellum* to the nominate subgenus of *Pseudoanthidium* and regarded *Carinellum* as synonymous.

The type species of *Pseudoanthidium* s. str., *P. alpinum* (Morawitz, 1874), is insufficiently known (Kasparek 2022; Kasparek & Ebmer 2023). The habitus of the taxa examined here is similar to that of the *Pseudoanthidium scapulare* species group, which consists of ten species (Litman et al. 2021). However, they are clearly distinguishable by the lamellate omaulus (angulate in the *P. scapulare* species group) and the high anterolateral pronotal lamella that is almost as high as the pronotal lobe is wide (lower and confined to the anterior side in the *P. scapulare* group) (Fig. 3). The dentation of the mandibles, however, was found not to be suitable for distinguishing these two groups.

Table 1. Material of *Pseudoanthidium ochrognathum* s. l. from which DNA sequences of the mitochondrial *COI* gene were retrieved for genetic barcoding. BIN is the Barcode Index Number System of BOLD Systems.

Species	Collection	Country	Sex	BIN
P. ochrognathum	CSE: seg100	UAE	♀	BOLD:AEK7168
P. ochrognathum	OLL: oll800	UAE	♀	BOLD:AEK7168
P. ochrognathum	OLL: oll798	UAE	♂	BOLD:AEK7168
P. ochrognathum	WHL: whl005	Jordan	♂	BOLD:AEK7168
P. ochrognathum	OLL: oll823	Morocco	♀	BOLD:AEK7168
P. rubellulum	OLL: oll825	Israel	♀	BOLD:AEO7128

It is suggested to refer to *P. ochrognathum* and its close relatives described below as members of the *P. ochrognathum* species group, thus distinguishing them from the *P. scapulare* species group. As the infrageneric classification of *Pseudoanthidium* is not enough understood and awaits further clarification and revision (Kasparek & Ebmer 2023), we prefer to use species groups instead of introducing formal new taxa.

Pseudoanthidium beaumonti (Benoist, 1950), stat. res.

(Figs. 1A, D, 3A, 4, 5A, 6C)

Anthidium beaumonti Benoist, 1950: 189. Morocco (Agadir), ♀, ♂ (MZLS; examined).

Anthidium beaumonti var. *obscuratum* Benoist, 1950: 189. Morocco (Agadir), ♂ (MZLS; examined). Homonym (ITIS 2022).

Anthidium ochrognathum ssp. *beaumonti* Benoist, 1950: Warncke (1980).

Pseudoanthidium (Pseudoanthidium) beaumonti (Benoist, 1950): Lhomme et al. (2020).

Material examined

ALGERIA: 1♂, Biskra, 04.IV.1897, E. Saunders leg. (NHMUK). – CHAD: 1♂, Tibesti [Mountains], Zonar, 21.III.1953, K. M. Guichard leg. (NHMUK) [Pasteels (1969a: 80) apparently referred to this record without giving further details]. – EGYPT: 1♀, 1♂, Gebel Asfar [El-Gebel El-Asfar], IV.1937, A. Mochl leg. (NHMUK). – ISRAEL: 1♂, 8km NNE Ashqelon, Nizzanim (31°45'N, 34°37'E), 13.V.1996, leg. M. Hauser (MWNH: mh091). – 1♀, 3♂♂, Palmachim [c. 12km S of Tel Aviv], 30.V.1075, Guichard leg. (NHMUK). – MOROCCO: 1♀, Essaouira (31°29'30"'N 9°45'01"'W), 18 m a.s.l., 28.IV.2015, V. Soon leg. (TUZ: tuz030, TUZ 036630). – 1♂, Essaouira, 09.V.1995, Mi. Halada leg. (CMK: ms4312). – 3♀♀, 5♂♂, 10km E Essaouria (31°30'N 09°44'W), 22.III.1997, M. Hauser leg. (CMK, MWNH: mh083-90). – 3♀♀, Tamri, 23.V.1985 and 12.IV.1987, K. M. Guichard leg. (NHMUK). – 2♀♀, 2♂♂, Agadir, 24.IV.1947, 25.IV.1947, 13.VI.1947, J. de Beaumont leg. [holotype and paratypes of *Anthidium beaumonti* and *A. beaumonti* var. *obscuratum*; lectotype and paralectotypes designated by G. van der Zanden 1988 (MZLS), see Benoist (1950)]. – 10♀♀, 3♂♂, Agadir and Agadir coast, 09.III., 20.III., and 15.VI.1974, 12–16.V.1975, 11.III.1985, G. R. Else & K. M. Guichard leg. (NHMUK). – 1♀, Tamri, 70km N Agadir, 08.V.1995, M. Halada leg. (CMK: ms4308). – 1♀, Massa, 50km S Agadir, 17.IV.1979, K. Warncke leg. (CMK: ms4638). – 1♂, 40km S Agadir, S Rabat, 30.V.1995, C. Schmid-Egger leg. (CSE: seg203). – 2♀♀, 1♂, Sidi Rbat, 60km S Agadir (beach), 31.V.1995, M. Hauser leg. (MWNH: mh080-82). – 1♀, 6km S Sidi Ifni-Goulimine [Guelmim] Road, 29.III–01.IV.1974, G. E. Else leg. (NHMUK).

Diagnosis

Within the *P. ochrognathum* species group, *P. beaumonti* is characterized by a dense, regular and deep punctation of the scutum and scutellum and a completely black T1 (often also T2), without yellow-orange markings. The vertex has no or only small remnants of yellowish markings. In the male, the distance between the median combs on S5 is about twice the width of a comb.

Differential diagnosis

Compared to the other species of the *P. ochrognathum* species group, *P. beaumonti* is a somewhat larger, relatively robust species. In the female, the marginal cell (as an indicator of body size) is for example on average 1.23 mm long (n=9), whereas it is 1.04 mm (n=16) in *P. ochrognathum*. However, there is overlap in morphometric measurements. In a Principal Component Analysis with four body measurements (ocello-ocular distance, distance between lateral ocelli and vertex, scutum width, length of marginal cell), the females of *P. beaumonti* formed a cluster distinct from those of *P. ochrognathum* (Fig. 2). Also a Discriminant Function Analysis carried out on the same dataset produced almost identical results, i.e., a clear separation of the cluster containing *A. beaumonti* from the cluster containing *A. ochrognathum*. The two species are thus well separated by morphometric traits.

The female of *P. beaumonti* is further distinguished from *P. ochrognathum* by the dense, regular, and deep punctation of the scutum and scutellum (scattered and shallow, mostly irregular punctation with larger impunctate areas in between in *A. ochrognathum*), the absence of yellow lateral maculation on T1 (and mostly also T2) and a denser and deeper punctation on the terga (distance between punctures on the disc of T3 up to half a punc-

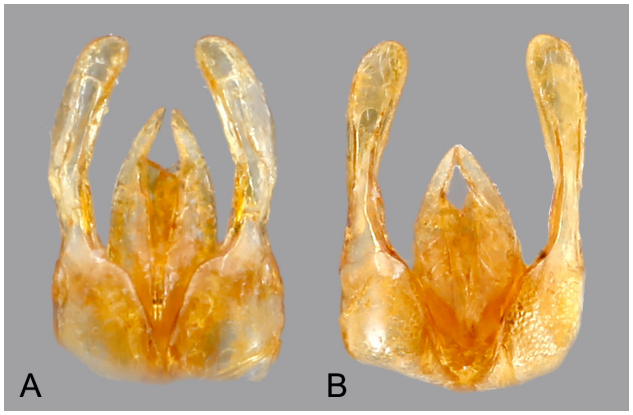

Fig. 5. Male genitalia of *Pseudoanthidium beaumonti* (Benoist, 1950) from Morocco (**A**) and *P. ochrognathum* (Alfken, 1933) from the UAE (**B**).

ture diameter in *P. beaumonti*; up to two puncture diameters in *A. ochrognathum*) (Fig. 6). It is distinguished from *P. rubellulum* by the dark depressions of the terga (diffuse red-brown bands in *P. rubellulum*) (Figs. 1, 9).

The male of *P. beaumonti* is distinguished from *P. ochrognathum* by the absence of a lateral yellow spot on T1 (rarely very small yellow spot present; yellow spot or band present in *P. ochrognathum*) and deeper, larger, and more regular punctures on the scutum, scutellum, and terga. The median patches of combs on S5 (additional to the combs on the lateral arms) are close to each other and are separated by less than the width of a patch (several patches wide in *P. ochrognathum*) (Fig. 4).

Description

Female. 5–6 mm long. *Head:* Large (as in other *Pseudoanthidium).* Clypeus black, bell-shaped. Punctation somewhat finer apically than at base. Apical margin emarginate, mostly entirely hidden under a moustache-like pubescence (similar to the members of the *P. scapulare* species group). Mandible broad with smooth surface, red-brown with five black teeth; the uppermost tooth is the strongest one, followed by a small tooth and three nearly equally large teeth. White pubescence around the antennal sockets. Small triangular red-brown maculation on the pre-occipital ridge behind the eye, sometimes reduced to a narrow line. – *Mesosoma* entirely black with scattered inconspicuous white hairs on scutum and dense white pubescence on mesepisternum. Scutum convex; scutum and scutellum with dense punctation with finely shagreened interspaces between punctures; distance between punctures less than half a puncture diameter. Scutellum overhanging metanotum; apical margin thin and laterally lamellate; pronotal lobe with high anterolateral lamella. – *Legs* dark brown, inner faces and tarsi light brown. Hair on basitarsi approximately as long as the width of the basitarsi. – *Metasoma*: T1 black; T2 black, rarely with small lateral yellow spot; T3–T4 with large lateral spot; T5 black, rarely with remnant of yellow spot; T6 black. Punctation of T1–T4 dense and deep, like on scutum. Punctation on discs and depressions identical; broad impunctate apical zone, slightly curled upward. Punctures on T5 and T6 sometimes confluent. T6 with median lamellate flange.

Male. 6 mm long. *Head* black, rarely with a narrow red-brown stripe along the preoccipital ridge behind the eye; face covered by long white hair obscuring most of the clypeus; clypeus apically retracted inwardly; mandible broad and short with three strong acute teeth; mandible yellow, teeth dark brown, transition zone reddish brown; punctation of head dense and regular; scape black, flagellomeres light brown. – *Mesosoma*: Punctation of scutum shallow, punctures small; punctation less dense than on vertex, punctures up to 1–2 puncture diameters apart; pronotal lobe as in female; tegulum reddish brown. – *Legs*: Femora dark brown with lighter apex; tibiae and tarsi brown to light orange-brown, but a male from Israel with entirely orange-brown tibiae and tarsi. – *Metasoma*: T1 black, T2–T4 with mediolateral yellow spot, T5–T6 black, T7 light yellowish. Terga with broad impunctate reddish brown apical margins. S1 with long hairs at apical margin; S2 covered with dense, felt-like pubescence with unbranched hairs; S3 with apically hooked and waved hairs; S4 hidden under S5; S5 with lateral arm and a broad comb at its apex. Additionally, a comb on each side of the middle of S5, with the distance between these two combs less than a comb's width (Fig. 4). – *Genitalia*: The shape of the male genitalia (Fig. 5) is in accordance with the general shape of the genitalia of the genus *Pseudoanthidium*. The gonostyli are unnotched at the apex. The penis valves are some distance apart, but touch at the tip. Not different from *P. ochrognathum* (Fig. 5).

Genetic analysis

No fresh material was available for the extraction of DNA.

Taxonomic note

In addition to *Anthidium beaumonti*, Benoist (1950) described "var. *obscuratum*" with an entirely black clypeus. Warncke (1980) regarded *obscuratum* as synonymous with *beaumonti* (which in turn he considered as a subspecies of *ochrognathum*). Nevertheless, ITIS (2022) presented *obscuratum* as a subspecies of *Pseudoanthidium beaumonti*, but noted that as per ICZN Article 45.6.4, *Anthidium* [*Pseudoanthidium*] *beaumonti obscuratum* Benoist, 1950 should be regarded as a junior primary homonym of *Anthidium* [*Pseudoanthidium*] *obscuratum* Morawitz, 1875. Examination of the holotype of *obscuratum* showed that its punctation is completely consistent with that of *A. beaumonti*

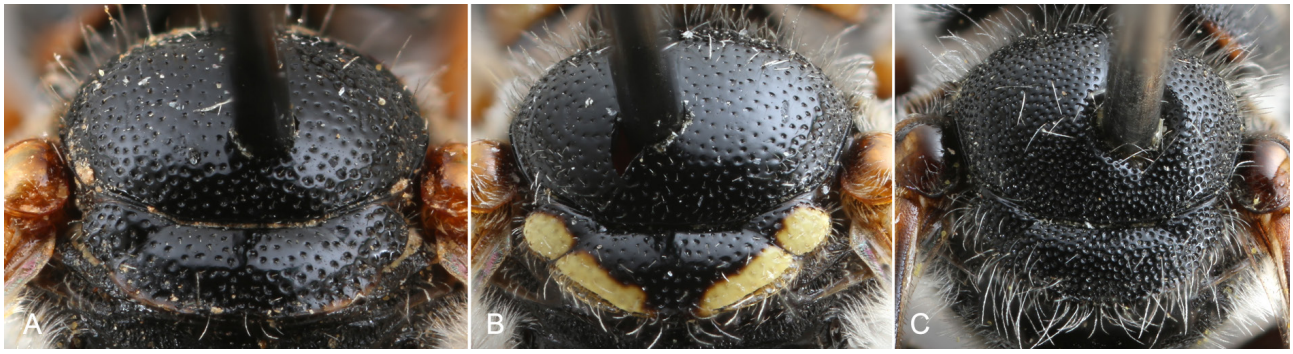

Fig. 6. Dorsal mesosoma (scutum, scutellum, and axillae) of *Pseudoanthidium ochrognathum* (Alfken, 1933) from Morocco (**A**) and the UAE (**B**), and *P. beaumonti* (Benoist, 1950) from Morocco (**C**). *Pseudoanthidium ochrognathum* (A, B) has shallower, more scattered punctures than *P. beaumonti* (C).

s. str., and that there are no colour or structural features to indicate that this specimen would belong to a different taxon. The colour pattern of the clypeus of *P. beaumonti* is variable and in Morocco, 8 out of 11 males examined have black clypei, and only three have yellow clypei (Fig. 7).

Distribution

Widely distributed in northern Africa from Morocco and Algeria across Chad to Egypt and in Israel.

***Pseudoanthidium ochrognathum* (Alfken, 1933)**

(Figs. 1B, C, E, F, 3A, 4, 5B, 6A, B, 7)

Anthidium ochrognathum Alfken, 1933 [“1932”]: 104. Egypt (Giza, Abu Rawash): ♂, ♀ (Collection of the Ministry of Agriculture in Gizeh).

Pseudoanthidium (*Paraanthidiellum*) *micronitens* Pasteels, 1981: 255, **syn. n.** Saudi Arabia (Hofuf): ♂ (NHMUK; examined).

Anthidium arenosum Warncke, 1982: 173, **syn. n**. IRAN (Irānshahr, Espakeh): ♀ (OLL; examined).

Material examined

IRAN: 1♀ (holotype of *Anthidium arenosum*). Sistan and Baluchestan Province: Irānshahr, NW Espakeh (“Rig Ispakeh”), 02.IV.1954, W. Richter & F. Schäuffele leg. (OLL: oll1113). – ISRAEL: 1♂, Hazeva [Chazewa], 27.III–03.IV.1988, K. M. Guichard leg. (NHMUK). – JORDAN: 1♂, Madaba: Wadi al Battan, near bridge (31.644N, 35.782E), 698 m, 19.III.2016, leg. J. Gebert (whl005). – MOROCCO: 1♀, 10km N Mhamid (29°55’N 05°43’W), 21–22.IV.1995, Ma. Halada leg. (CMK: ms4309). – 1♀, 20km N Foum-Zguid (30°15’N 06°50’W), 29–30.IV.1995, M. Halada leg. (CMK: ms4310). – 1♀, 30km SW of Foum Zguid, rd. no. 12 (29°54’N 07°03’W), 21.IV.2017, L. Cerny leg. (OLL: oll824). – 1♀, Foum Zguid env. (30°04’N 06°53’W), 21.IV.2017, M. Snizek leg. (OLL: oll823). – 1♂, 5km N Zagora (30°23’N 05°51’W), 24–25.IV.1995, M. Halada leg. (CMK: ms4311). – 2♀♀, Draa Valley, 30km SE Zagora (30°11’N 05°34’W), 28.V.1995, C. Schmid-Egger leg. (CSE: seg201-202). – SAUDI ARABIA: 1♂ (holotype of *P. micronitens*), Hofuf, 21.III–06.IV.1980, K. Guichard leg. (NHMUK, B.M. Type Hym 17a 31215). – UNITED ARAB EMIRATES: 3♀♀, Sharjah Breeding Centre (25°16.87’N, 55°41.44’E), 12.III.2008, leg. M. Hauser (CSE: seg095-097). Sharjah Desert Park (25.28°N 55.70°E), 25.V.2008, A. v. Harten leg. (CSE: seg078). – 2♀♀, Desert (25°08.16’N, 55°54.45’E), 15.III.2008, M. Hauser leg. (CSE: seg098-099) see also Dathe (2009). – 1♀, Mahafiz (25.20N, 55.73E), 11–19.III.2009, C. Schmid-Egger leg. (CSE: seg100). – 2♀♀, Abu Dhabi pr.: New Shwaib (24°44’N, 55°47’E), 08.III.2017, leg. M. Halada (OLL: oll795, 797). – 2♀♀, 4♂♂, Sarjan pr.: W of Dhaid (25°17’N, 55°51’E), 02.III.2017, leg. M. Halada (OLL: oll796, 798-802). – 1♂, Suweihan, 12.IV.1988, I. L. Hamer leg. (NHMUK). – 1♂, Abu Dhabi, 13.IV.1988, I. L. Hamer leg. (NHMUK).

Material from literature and internet sources

CHAD: 1 ex., Tibesti: Wadi Wour, 7.III.1953, K. M. Guichard leg. (SEMC) (https://www.gbif.org) [Probably a misidentification of *P. beaumonti* (see under that species)]. – EGYPT: 1♀ (holotype of *Anthidium ochrognathum*), Giza: Abu Rawash [= Abu Roash, Abu Rowasch], 7.viii.1926, R. Mabrouk leg. (Ministry of Agriculture, Egypt) [Alfken (1933); see also Salem & El Azab (2017) and Elshaier (2022)]. 1♂ (paratype of *Anthidium ochrognathum*), Assiout: Wadi Assiouti, 25.IV.1926, Kassim leg. (Plant Protection Research Institute, Giza, Egypt) (Alfken 1933, see also Salem & El Azab 2017 and Elshaier 2022). 1♂, Giza: Mansouria, 16.V.1934, leg. R. Mabrouk (Elshaier 2022). – PALESTINE: West Bank (Ascher & Pickering 2022). – SUDAN: Khor Arbaat Delta [Port Sudan, Red Sea coast], 1♂, 4.V.1926, leg. H. B. Johnston (Mavromoustakis 1945) [the (very brief) description does not unambiguously point to *P. ochrognathum*]. – UNITED ARAB EMIRATES: 3♀♀, Sharjah Desert Park, 12.III.2008, leg. M. Hauser. 3♀♀, 19.III.2008, leg. M. Hauser (Dathe 2009). 3♂♂, 2♀♀, Sweihan Road, 12.IV.1988, leg. I. L. Hamer (SEMC via https://www.gbif.org). Abu Dhabi, 12.IV.1988, leg. I. L. Hamer (SEMC via https://www.gbif.org).

Diagnosis

Pseudoanthidium ochrognathum is distinguished from the other taxa in this species group by large yellow markings on T1 and a shallow and scattered punctation on the scutum, scutellum, and terga. In the male, the combs at the base of S5 are separated from each other by several comb widths.

Fig. 7. Face colour pattern variation in male *Pseudoanthidium ochrognathum* (Alfken, 1933); A, B: UAE; C: Morocco; D: Jordan. **A**. Clypeus and parts of lower paraocular area yellow. **B**. Clypeus yellow, lower paraocular area black. **C**. Clypeus black with yellow median stripe. **D**. Face entirely black.

Differential diagnosis

See under *P. beaumonti* and *P. rubellulum*.

Description

Female. 5 mm long. *Head* black with yellow to orange triangular maculation on the preoccipital ridge behind the eye; punctation of clypeus scattered at base (with some impunctate areas at base of clypeus and in the supraclypeal area) and dense towards posterior margin; apical margin of clypeus shallowly emarginate, mostly covered by dense white pubescence; mandible yellow to red-brown with five dark brown teeth (upper tooth the strongest one, followed by a minute tooth and three large acute teeth); scapus, pedicel, and first flagellomere dark brown or black, other flagellomeres ochreous. – *Mesosoma:* Scutum convexly protruding; scutum, scutellum, and axillae polished and shining, with shallow punctures separated by half their diameter up to 2–3 times their diameter (scat-

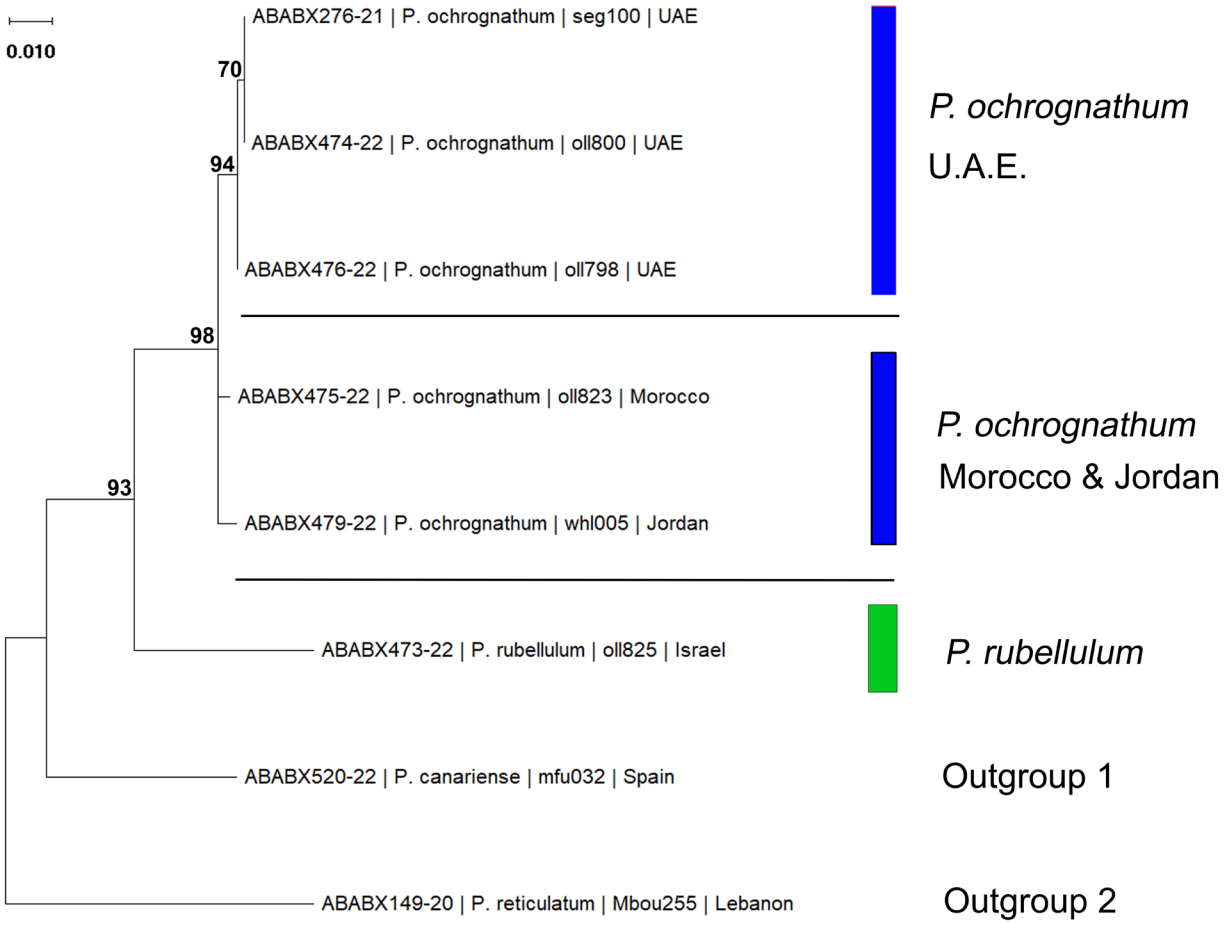

Fig. 8. Phylogenetic tree of some members of the *Pseudoanthidium ochrognathum* species group, based on the mitochondrial cytochrome c oxidase I (*COI*) gene. Numbers shown at the nodes are Maximum Likelihood bootstrap values. *Pseudoanthidium canariense* (Mavromoustakis, 1954) and *P. reticulatum* (Mocsáry, 1884) were used as outgroups.

tered punctation especially on scutellum); scutellum with lamellate margin. In the material examined, scutum and axillae with V-shaped yellow band in eastern populations, but entirely black in western populations. – *Legs:* Femora dark brown with lighter apex; tibiae and tarsi brown to light orange-brown. – *Metasoma:* Terga black or dark brown with light maculation; impunctate apical margins transparent brownish. T1 with pale yellow lateral spot, T2–T4 with large mediolateral bands almost reaching the middle; T5 black, sometimes with pale yellow spot, T6 with apical flange; black, apically often light brown.

Male. 5 mm long. Head black, with a yellow spot on the preoccipital ridge behind the eye(mostly absent in western populations). Clypeus and mandible similar to *P. beaumonti.* Face covered by dense white pubescence. Colour pattern of face highly variable (see below). – *Mesosoma*: Scutum convex and shining with small, shallow punctures separated by half their diameter. Yellow V-shaped marking on scutum/axillae (not always present). – *Legs*: As in the female. Specimens from the UAE with yellow instead of orange-brown. – *Metasoma*: Similar to female. T1 with pale yellow lateral spot, T2–T4 with pale yellow mediolateral stripes; T5–T6 mostly black (but reddish yellow in a specimen from Saudi Arabia), T7 pale yellow or reddish yellow with a shallow median apical emargination. S2 with dense felt-like unbranched hairs, S3 with apically hooked and waved hairs; S4 glabrous, apical margin straight; S5 with a small black comb at the base and a broad comb at the apex of the lateral arm (Fig. 4). The combs at the base are separated from each other by several comb widths. – *Genitalia*: As in Fig. 5. No difference was noted compared to *P. beaumonti*.

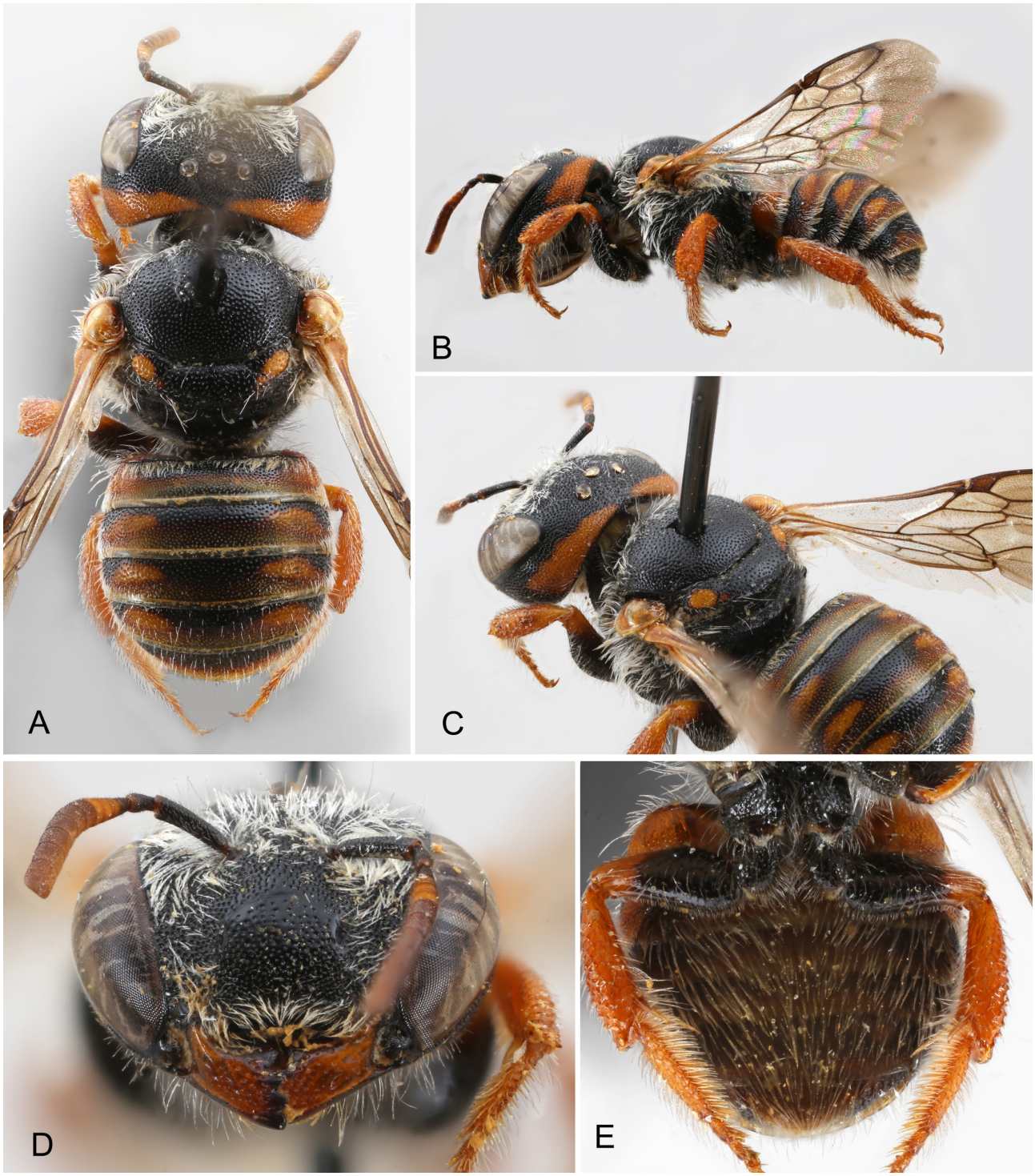

Fig. 9. *Pseudoanthidium rubellulum* Pasteels, 1969. Female from Israel. **A–C**. Habitus in dorsal, lateral, and oblique views. **D**. Face. **E**. Metasomal scopa.

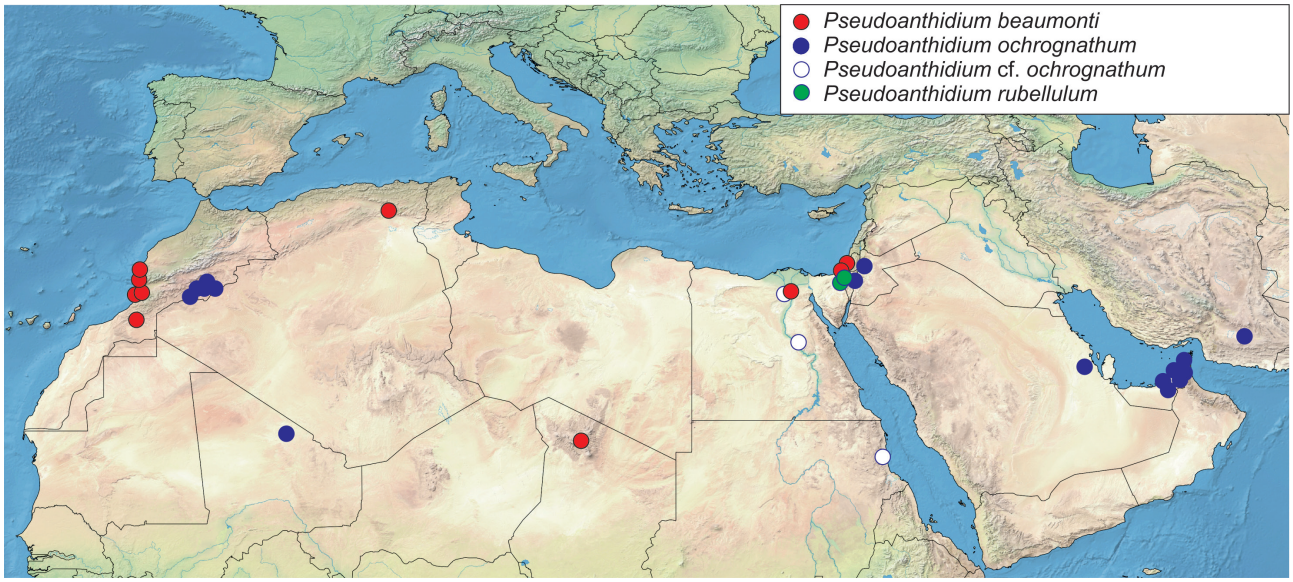

Fig. 10. Distribution of members of the *Pseudoanthidium ochrognathum* species group. *Pseudoanthidium* cf. *ochrognathum* refers to literature data (no material examined).

Variation

Specimens from the Arabian Peninsula and Iran are more yellow than those from northern Africa. In the female, all specimens from the UAE and Iran (N=11) have an orange or yellow spot behind the eye and a yellow V-shaped marking on the scutellum/axillae. All specimens from Morocco (N=6) have a light spot behind the eye, while none has yellow markings on the scutum and axillae. Three males from the UAE have a light spot behind the eye and a yellow V-shaped marking on the scutum/axillae, while one specimen does not have these yellow markings. A specimen from Jordan has no such markings either. A male from Morocco has light head markings, but no yellow markings on the scutum/axillae.

The face pattern of the male is also highly variable. The yellow pattern extends over the clypeus and the lower paraocular area in some specimens (Fig. 7A), but the face is entirely black in other specimens (Fig. 7D). Intermediate forms were found which had a varying extent of yellow on the clypeus (Fig. 7B, C).

Regarding punctation, there is a tendency for both females and males from the UAE to have a more scattered punctation on the scutum, scutellum, and axillae than specimens from the western part of the distribution area. However, there is individual variation and it was not possible to quantify this character and to establish diagnostic characteristics.

Genetic analysis

Regarding the DNA sequence of the *COI* gene, two specimens from Jordan and Morocco emerged in a well-supported clade (ML bootstrap value = 98%), sister to *P. ochrognathum* from the UAE (Fig. 8). However, the mean genetic distance between these two groups is only 1.14% (Table 2). As the samples of *P. ochrognathum* include material from distant places such as the UAE, Jordan, and Morocco, geographic genetic distance is considered very low.

Taxonomic note

Warncke (1982) described *Anthidum arenosum* (which is recognized here as a synonym to *P. ochrognathum*) as very similar to *P. ochrognathum*. He noticed that the punctation of the scutum of *A. arenosum* is finer and more scattered than in *P. ochrognathum*. In an examination of the holotype, this was not confirmed. However, Warncke (1982) did not recognize the difference between *P. ochrognathum* and *P. beaumonti*, so he possibly compared *arenosum* with *beaumonti*, which has a denser punctation. The holotype of *P. micronitens* Pasteels, 1981 is in poor condition and this may be the reason that Pasteels (1981) did not realize that it actually belongs to *P. ochrognathum* and is affiliated with his previously established genus *Carinellum* (Pasteels 1969a).

Flower preferences

Müller (1996), who analysed pollen packages of anthidiine bees in museum material, noted that *P. ochrognathum* is polylectic and that it collects pollen on five different plant families, the most important being Brassicaceae, Boraginaceae, and Leguminosae. No information is available on where Müller (1996) obtained his material from and whether it agrees with the taxonomic classification applied here. Gess & Roosenschoon (2016) reported from the UAE

that *P. ochrognathum* was most commonly observed visiting flowers of the Boraginaceae *Heliotropium kotschyi* Gürke and *Moltkiopsis ciliata* (Forssk.) I. M. Johnst., suggesting a preference for this family; however, one specimen was taken from *Aerva javanica* (Burm. f.) Juss. ex Schult. from the Amaranthaceae family, growing in close proximity to *M. ciliata*.

Distribution

Widely distributed in the Middle East and northern Africa. The species occurs from southern Iran (Sistan and Baluchistan) and the Arabian Peninsula (UAE) across Jordan and Israel to Morocco (Fig. 10).

Pseudoanthidium rubellulum **Pasteels, 1969, stat. res.**

(Fig. 9)

Pseudoanthidium (*Carinellum*) *rubellulum* Pasteels, 1969b: 426. Israel (holotype ♀ in coll. Bytinski-Salz, Tel Aviv, Israel; paratype ♀ in the Royal Belgian Institute of Natural Sciences, Brussels, Belgium).

Anthidium ochrognathum Alfken, 1933 (partim): Warncke (1980).

Pseudoanthidium ochrognathum (Alfken, 1933) (partim): Michener (2007), Ascher & Pickering (1922), and other sources.

Material examined

ISRAEL: 1 ♀, 10 km N Nizzana [Nitzana] (30.944N, 34.401E), 10.V.2019, M. Halada leg. (CMK: mk901).

Material not examined

2♀♀ (holotype and paratype), ISRAEL: Urim, 17.IV.1956 (leg. Bytinski-Salz) [holotype in coll. Bytinski-Salz, Tel Aviv, Israel; paratype in Institut Royal des Sciences Naturelles de Belgique, Brussels (Pasteels 1969b)].

Diagnosis

Only female known. Within the *P. ochrognathum* species group, *P. rubellulum* is characterized by the orange maculation on the scutellum and terga and the diffuse reddish brown colouration of the tergal depressions.

Differential diagnosis

The maculation on the scutellum and terga is yellow or pale yellow in *P. ochrognathum* and *P. beaumonti*, while it is orange in *P. rubellulum*. The tergal depressions are uniformly black in *P. ochrognathum* and *P. beaumonti*, while they are diffuse red-brown in *P. rubellulum*. *Pseudoanthidium rubellulum* is further distinct from *P. ochrognathum* by its fine, regular punctation of the scutum and scutellum (more scattered punctation in *P. ochrognathum*).

Description

Female. Length: 5.5 mm. *Head*: Black with orange preoccipital band, tapering towards the middle (interrupted in the middle in the specimen examined, not interrupted in the type material) and extending to the upper third/middle of the gena. Clypeus with scattered punctation at the base and dense punctation apically. Apical margin of clypeus shallowly emarginate, covered by dense pubescence. Mandible red-brown with five black teeth (uppermost tooth strong, second uppermost tooth very small, other teeth equally strong). – *Legs*: Apices of tibiae, tarsi, and femora orange. – *Mesosoma*: Scutum black with shallow, dense punctation; punctation of scutellum and axilla similar; axilla with large orange spot; scutellum with small orange spot laterally. Pronotal lobe with high antero-lateral lamella. – *Metasoma*: T1–T5 with a diffuse red-brown band, broadening at their sides, where they include an orange spot. T6 black with an apical flange. Scopa off-white.

Male. Not known.

Genetic analysis

The genetic distance between *P. rubellulum* and *P. ochrognathum* ranges between 6.0 and 6.7% (average: 6.4%). At the same time, the within-group genetic distance of *P. ochrognathum* is 0.79% (Table 2), which is much smaller than the intergroup distance (see above). The analyzed specimen emerged in a well-supported clade (ML bootstrap value = 93%) sister to the *P. ochrognathum* lineage (Fig. 8).

Table 2. Pairwise genetic distance between six specimens of the *Pseudoanthidium ochrognathum* species group according to the Kimura 2-parameter model. Distance values > 5% are shown in **bold**. P.o. = *Pseudoanthidium ochrognathum*; P.r. = *P. rubellulum*. ISR = Israel, JOR = Jordan, MAR = Morocco, UAE = United Arab Emirates.

	P.o. seg100 UAE	**P.o. oll800 UAE**	**P.o. oll798 UAE**	**P.o. whl005 JOR**	**P.o. oll823 MAR**	**P.r. oll825 ISR**
P.o. seg100: UAE	–					
P.o. oll800: UAE	0.000	–				
P.o. oll798: UAE	0.002	0.002	–			
P.o. whl005: JOR	0.009	0.011	0.009	–		
P.o. oll823: MAR	0.011	0.009	0.008	0.008	–	
P.r. oll825: ISR	**0.066**	**0.070**	**0.067**	**0.067**	**0.065**	–

Taxonomic note

The material examined was not sufficient for a statistical morphometric analysis. In accordance with PASTEELS (1969b), the species was found to be very different from *P. ochrognathum* both in colouration and punctation, and no overlap was observed. PASTEELS (1969b) described it on the basis of two females from Israel and discussed the possibility that the taxon may be regarded as a subspecies of *P. ochrognathum*. However, he argued that these two taxa are sympatric, with no intermediates, and that they differ not only by their colour but also by the punctation of the thorax. WARNCKE (1980) argued that, had he examined more material, PASTEELS (1969b) would have recognized that the punctation of the mesonotum as well as the reddish yellow colouration of the body are subject to great variation. WARNCKE (1980) did not disclose what material he examined himself, but as he did not differentiate between *P. ochrognathum* and *P. beaumonti*, he necessarily may have gotten the impression of a greater variation than actually exists.

Biology

PASTEELS (1969b) noted that the holotype and the paratype, two females, are pinned with their nests, whose cells are made of plant fibres.

Identification keys

A modern identification key which includes the northern African and the Middle Eastern Anthidiini is not available, and despite requiring an update the key of WARNCKE (1980) is therefore still widely used. For species of the *P. ochrognathum* species group, WARNCKE's key to females leads to couplet 24, where additional couplets (24a/24b) should be inserted. For males, his key leads to couplet 25, where an additional couplet (25a) should be inserted.

Key to females

24 Omaulus lamellate almost to lower end; inner edge of malar area rounded **24a**
– Omaulus lamellate in the upper and rounded in the lower half; inner edge of malar area carinate, i.e., strong lateral preoccipital carina extending nearly to the posterior mandibular articulation **25**

24a Depressions of T1–T4 with indistinct, diffuse red-brown band; T3–T4 with orange maculations (Fig. 9A–C)..... ..... ***P. rubellulum***
– Depressions of T1–T4 black or dark brown; T3–T4 with yellow maculations (Fig. 1A–C) **24b**

24b T1 with yellow lateral spot (Fig. 1B, C); scutum and scutellum polished, with shallow, mostly irregularly scattered punctation (interstices up to a few puncture diameters) (Fig. 6A, B); tegula light brown ..... ***P. ochrognathum***
– T1 black (Fig. 1A); scutum and scutellum with deep, regular punctation (interstices always less than a puncture diameter) (Fig. 6C); tegula dark brown..... ***P. beaumonti***

Key to males

[The male of *A. rubellulum* is not known.]

25 Omaulus lamellate to lower end; S3 with long, undulate hairs; S5 with long lateral projection with a black comb at its apex (Fig. 4); lower preoccipital ridge rounded **25a**
– Omaulus lamellate in its upper and rounded in its lower half; hairs on S3 normal; black combs on S5 absent; lower gena with preoccipital lamella, upper gena rounded **26**

25a T1 with yellow band or lateral yellow spot (Fig. 1E, F); scutum and scutellum with shallow, often scattered punctation (Fig. 6A, B); combs at the base of S5 separated by several comb widths (Fig. 4) ..... ***P. ochrognathum***
– T1 black (small yellow spot sometimes present laterally) (Fig. 1D); scutum and scutellum with dense, regular punctation (Fig. 6C); combs at the base of S5 separated by less than one comb width (Fig. 4) ..... ***P. beaumonti***

Discussion

We have shown that *Pseudoanthidium beaumonti* and *P. rubellulum* are distinct species and have removed them from synonymy with *P. ochrognathum*. It is proposed to treat these three species as members of a *P. ochrognathum* species group. All three species live in sand dunes of the Arabian Peninsula and northern Africa, with overlapping distributions.

The punctation of the integument plays an important role in distinguishing the species of the *P. ochrognathum* group. The punctures on the scutum, scutellum, axillae, and metasomal terga are very shallow and the margins are not always clearly visible, especially in *P. ochrognathum*. Note, however, that different kinds of illumination and angles of incidence of light sometimes show different patterns of punctation that are, in fact, not present. Standard procedures for the quantitative description of punctation are not available.

The faces of the males of both *P. beaumonti* and *P. ochrognathum* show a high variability with respect to the extent of yellow. The clypeus may be entirely black, black with yellow maculation, or the yellow maculation may extend across the lower paraocular area. Specimens with different colour types can be found sympatrically, and this variation does not seem to be related to geographic location. Such intraspecific variations in the face pattern are rare in Anthidiini. Among West Palaearctic species, similar variations are known only in the female of *Afranthidium carduele* (Morawitz, 1876) (see KASPAREK 2022: 64).

The taxonomic status of *P. ochrognathum* confronts the observer with a dilemma: The eastern population around the Persian/Arabian Gulf can be distinguished from the western and northern populations (Jordan and Israel across Egypt to Morocco) by colour pattern and often also by the punctation of the integument. Eastern populations are usually richer in yellow than western/

northern populations. Additionally, eastern populations have a shinier scutum, scutellum, and axillae with shallow punctation and punctures often several puncture diameters apart, while the punctation is much denser in western populations, resulting in a less shiny integument. Some populations in between the east and west (e.g., Saudi Arabia) are insufficiently known. It was considered whether the eastern and western populations could be recognized as distinct species. However, the genetic distance between these populations as derived from the DNA sequence of the *COI* gene is very low. The genetic distance within the eastern population varies between 0.0 and 0.2%, and the distance between the eastern and the western populations between 0.9 and 1.1%. Sequence divergence thresholds such as 2% or 3% have been suggested for grouping specimens into provisional species (e.g., Hebert et al. 2004 for birds; Gibbs 2018 for bees of the Halictidae family). On the other hand, Kasparek et al. (2023) found an average genetic distance between two Mediterranean species of *Anthidiellum* of only 2.4%, whereas the within-species genetic distance between distant populations of *Rhodanthidium caturigense* (Giraud, 1863) was found to vary between 1.4% and 2.7% (Kasparek 2021). In the genus *Pseudoanthidium*, Litman et al. (2021) found very low levels of genetic divergence at the *COI* locus (< 1%) between some species of the *P. scapulare* species group. These figures show that there are no absolute thresholds for genetic distance in anthidiine bees that can be used as indicators of species-level distinctness. While the low genetic distance between eastern and western/northern populations of *P. ochrognathum* indicate that these populations belong to the same species, a final assessment is not yet possible due to our limited knowledge on the barcoding gap in anthidiine bees.

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