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ABSTRACT

The West Palaearctic wool carder bee *Anthidium dalmaticum* Mocsáry, 1884, is recognized in two subspecies: the nominate subspecies, widely distributed from the northern Adriatic Sea coasts to the Caspian Sea coastal areas, and *A. d.* ssp. *syriacum* Pérez, 1912, which has been regarded at times as distinct species and is found in the South Caucasus, the Levantine region and Iran. These two taxa are primarily distinguished by differences in colouration. In a genetic barcoding approach based on the sequence of the mitochondrial cytochrome c oxidase subunit 1 gene (COI), I was unable to differentiate between these two taxa. Additionally, a multivariate statistical analysis of nine body measurements did not reveal any significant morphometric differences between these two groups. However, a haplotype network analysis revealed that *A. dalmaticum* comprises three distinct evolutionary lineages. Of them, the Eurasian lineage covers most of the distribution range and includes members of both subspecies. The other two lineages are found in Iran and the Levant respectively, representing two independent evolutionary pathways. Notably, these two lineages exhibit significant genetic divergence, with each being more closely related to the Eurasian lineage than to each other. Based on these findings, it is concluded that the expansion of *A. dalmaticum* into the Iranian landmass and the Levant are two independent processes, which may have occurred in different phases of the climate oscillations between glaciations and warm cycles. The observed colour differences between the subspecies may be regarded as a convergent adaptation, possibly triggered by factors such as similar environmental conditions. Given that, on the one hand, the genetic lineages lack support from phenotypic traits and, on the other hand, the colour forms are not corroborated by genetic data, the available evidence is not yet regarded as sufficient to classify these forms as distinct taxonomic units. It is suggested to treat *A. dalmaticum* ssp. *syriacum* as a synonym of nominate *Anthidium dalmaticum*.

KEY WORDS
Wool carder bees,
mtDNA,
genetic barcoding,
species delimitation,
colour morphs,
subspecies,
Turkey,
Greece,
Levant,
new synonymy.

RÉSUMÉ

Résultats discordants obtenus à partir de la classification phénotypique et du barcoding génétique : une étude de cas de l'abeille anthidiine Anthidium dalmaticum *Mocsáry, 1884 (Megachilidae, Anthidiini).*
Deux sous-espèces sont reconnues chez l'abeille cardeuse de laine du Paléarctique occidental *Anthidium dalmaticum* Mocsáry, 1884 : la sous-espèce nominale, largement répandue depuis les côtes nord de la mer Adriatique jusqu'aux zones côtières de la mer Caspienne, et *A. d. syriacum* Pérez, 1912*,* qui a parfois également été considérée comme une espèce distincte et que l'on observe dans le sud du Caucase, dans la région du Levant et en Iran. Ces deux taxons se distinguent principalement par des différences de coloration. Dans une approche de barcoding génétique basée sur la séquence du gène de la sous-unité 1 (COI) du cytochrome c oxydase mitochondrial, nous n'avons pas pu différencier ces deux taxons. De plus, une analyse statistique multivariée de neuf mesures corporelles n'a révélé aucune différence morphométrique significative entre ces deux groupes. Cependant, une analyse du réseau d'haplotypes a révélé qu'*A. dalmaticum* comprend trois lignées évolutives distinctes. L'une de ces lignées est la lignée eurasienne qui couvre la majeure partie de l'aire de répartition et comprend des membres des deux sous-espèces. Les deux autres lignées se trouvent en Iran et au Levant, représentant deux voies évolutives indépendantes. La plupart des individus de ces lignées sont affectés à la sous-espèce *syriacum*. Notamment, ces deux lignées présentent une divergence génétique importante, chacune étant plus étroitement liée à la lignée eurasienne qu'entre elles. Sur la base de ces résultats, il est conclu que l'expansion d'*A. dalmaticum* dans le territoire iranien et dans le Levant sont deux processus indépendants qui ont pu survenir dans des phases différentes des oscillations climatiques entre les glaciations et les cycles chauds. Les différences de couleur observées entre les sous-espèces peuvent être considérées comme une adaptation convergente, éventuellement déclenchée par des facteurs tels que l'adaptation à des conditions environnementales similaires. Étant donné que, d'une part, les lignées génétiques ne sont pas étayées par des caractères phénotypiques et que, d'autre part, les formes colorées ne sont pas corroborées par des données génétiques, la classification de ces formes en tant qu'entités taxonomiques distinctes n'est pas supportée par des données suffisantes. Il est proposé de traiter *A. dalmaticum* ssp. *syriacum* comme un synonyme de l'*Anthidium dalmaticum*.

MOTS CLÉS
Abeilles cardères,
ADNmt,
barcoding génétique,
délimitation des espèces,
morphes de couleur,
sous-espèces,
Turquie,
Grèce,
Levant,
synonymie nouvelle.

INTRODUCTION

Most anthidiine bees (tribe Anthidiini Ashmead) have a striking yellow-and-black colour pattern, reminiscent of some wasps (Friese 1898). The shape of the yellow maculations and the extent of yellow exhibits significant variations across the geographic distribution in many species (Alfken 1936; Warncke 1980). However, little is known about the general principles by which the colouring pattern changes. While it is accepted that different environmental conditions are a main factor responsible for this variation, genetic and epigenetic factors also contribute to the phenotypic appearance (Fusco & Minelli 2010; Moczek 2015; Stevens 2016; Kasparek 2021; Putyatina *et al.* 2022; Kasparek *et al.* 2023a). In Anthidiini, it seems that different colour variants can result in reproductively isolated populations (Alfken 1936; Warncke 1980; Kasparek 2019, 2020) and thus represent at least in some species different levels of speciation. However, the taxonomic conclusions remain often ambiguous and inconsistent. Depending on the specific situation, the geographic colour variation has been described on the level of intraspecific variation, geographic clines, subspecies and closely related (sibling) species (Kasparek 2021, 2022; Kasparek *et al.* 2023a).

An interesting species that may contribute to the understanding of the principles of geographic variation in the anthidiine bees is *Anthidium dalmaticum* Mocsáry, 1884, which was described from the Croatian coast in 1884 (Mocsáry, 1884). Pérez (1912) described almost three decades later *Anthidium syriacum* Pérez, 1912 from Lebanon, but only Mavromoustakis (1939) recognized the similarity of these two taxa. He noted that these two species are distinct with respect to colouration, but that they are structurally not different. He concluded that *syriacum* is probably only a subspecies of *dalmaticum*. In the subsequent literature, *syriacum* was treated sometimes as a distinct species (e.g. Pasteels 1981; Boustani *et al.* 2021; Ascher & Pickering 2023), sometimes as a subspecies of *A. dalmaticum* (Mavromoustakis 1955; Warncke 1980, 1982; Fateryga *et al.* 2020), although no new arguments for one or the other treatment were raised.

I therefore examined the geographic variation of *Anthidium dalmaticum* in order to delineate the boundaries of the species, validate the described subspecies, and describe the haplotype variation and its relationship with phenotypic variation. This examination aimed to provide insights into distribution and evolutionary patterns of the species.

MATERIAL AND METHODS

Since *A. dalmaticum* is an uncommon species, it was necessary to gather materials from several private and public collections. Finally, it was possible to examine 147 specimens, including 80 females and 67 males from 18 private and public collections (Table 1). The collection data are given in Appendix 1.
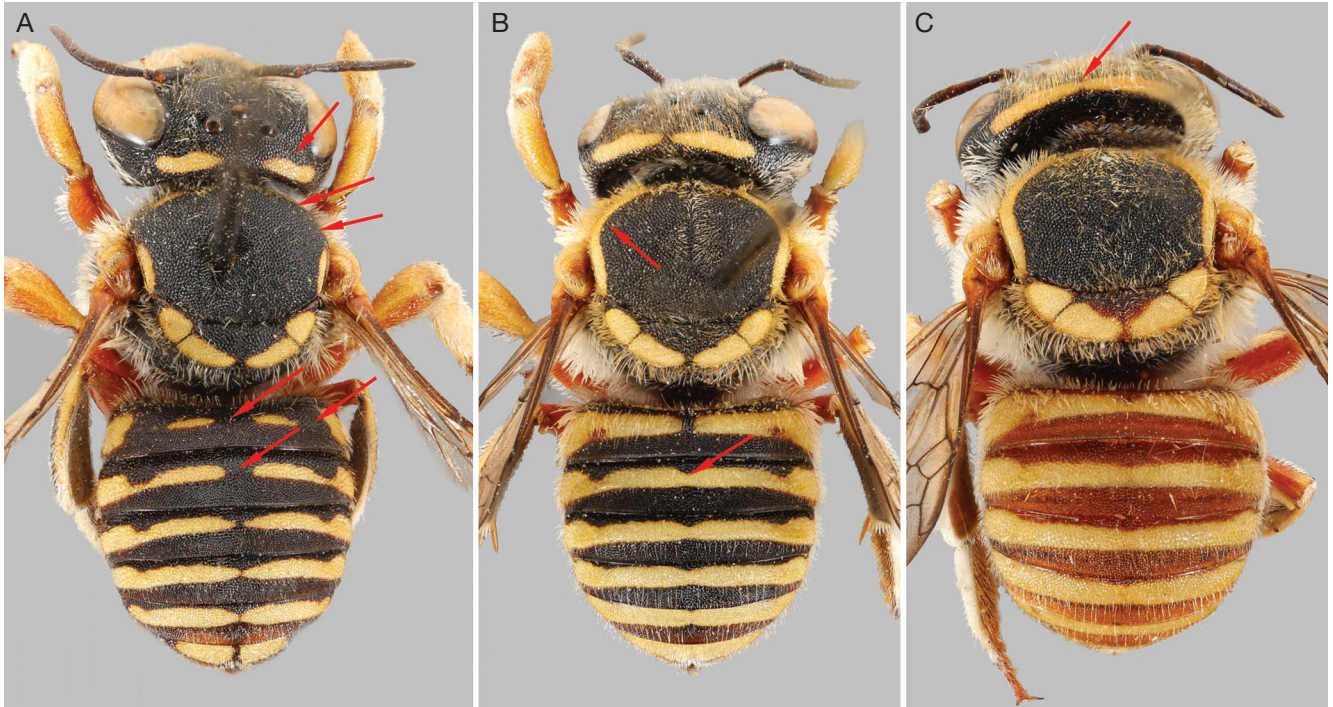
Fig. 1. — Three different females of *Anthidium dalmaticum* Mocsáry, 1884: **A**, the nominate subspecies (Bulgaria); **B**, a specimen assigned to *Anthidium dalmaticum syriacum* Pérez, 1912 with black background colour of the terga (Turkey); **C**, colour variant of *A. d. syriacum* with red-brown background colour of the terga (Turkey). The arrows point to some distinguishing features in the colour pattern.

While males of *A. dalmaticum s.l.* can easily be identified (identification keys in Warncke 1980; Kasparek & Schwarz 2020; Kasparek 2022), females are often difficult to distinguish from the females of *A. taeniatum* Latreille, 1809. The following characters were used: 1) the clypeus of *A. dalmaticum s.l.* is almost flat, while it is slightly convex at its lower third in *A. taeniatum*; 2) the tubercles on the apical margin of the clypeus are lower and more confluent in *A. taeniatum* than in *A. dalmaticum*; 3) the apical margin of the clypeus is shallowly emarginate in *A. taeniatum* in dorsal view, but almost straight in *A. dalmaticum*; 4) the disc of abdominal tergite 2 (T2) is bulging laterally and strongly elevated above the marginal depression in *A. dalmaticum*, but only weakly so in *A. taeniatum*; 5) in *A. dalmaticum*, the punctation of the disc of T2 is conspicuously larger and deeper laterally than on the lateral depression, whereas in *A. taeniatum*, the punctures on the disc are only slightly larger than on the depression. The combined application of these character states enabled the unambiguous identification of almost all female specimens.

For a morphometric analysis, the following nine parameters were used: clypeus length, clypeus width at base, lateral length of clypeus, clypeus surface area, eye-ocellus distance, ocellus-preoccipital distance, length of the marginal cell, width of the spine of the abdominal tergite 7 (T7), and width of the emargination of T7. The methodology is described in Kasparek (2019, 2020, 2021). Morphological terminology follows Michener (2007).

Table 1. — Repository of the material of *Anthidium dalmaticum s.l.* Mocsáry, 1884 examined for this study.

	Female	Male	Total
Collection Mira Boustani	1	–	1
Collection Andreas W. Ebmer	5	2	7
Collection Alexander Fateryga	1	1	2
Collection Markus Fuhrmann	1	1	2
Collection Martin Hauser	1	–	1
Collection Gerald Hölzler	1	3	4
Collection Max Kasparek	33	22	55
Collection Hanno Korten		1	1
Collection Wolf-Harald Liebig	2	1	3
Collection Gerd Reder	1	–	1
Collection Stefan Risch	2	–	2
Collection Heinz Wiesbauer	–	1	1
University of Mons (UMONS)	1	3	4
Natural History Museum London (NHMUK)	2	–	2
Naturkundemuseum Berlin (ZMB)	8	5	13
Oberösterreich. Landesmuseum Biologiezentrum Linz (OLL)	17	22	40
Senckenberg-Museum Frankfurt (SMF)	2	–	2
Zoological Museum Hamburg, University of Hamburg (ZMH)	2	5	7
Total	80	67	147

In the morphometric analysis, the length of the marginal cell was used as indicator of body size. It was found in other anthidiine bees that the length of the marginal cell is highly suitable for this purpose as on the one hand it is highly correlated with other morphometric parameters, and on the other hand, the measurement error is lower than in certain other parameters (Kasparek *et al.* 2023a).

Table 2. — Geographic origin of the material of *Anthidium dalmaticum s.l.* Mocsáry, 1884 examined in this study.

	Female	Male	Total
Algeria	1	–	1
Azerbaijan	2	1	3
Bulgaria	1	–	1
Croatia	11	10	21
Greece	15	13	28
Iran	8	5	13
Jordan	1	–	1
Lebanon	2	1	3
Palestine and Israel	8	7	15
Russia: Dagestan	1	2	3
Syria	1	2	3
Turkey	29	26	55
Unknown (Croatia?)	1	–	1
Total	80	67	147

A genetic analysis was conducted on 14 specimens of *A. dalmaticum*. DNA extraction, PCR amplification and sequencing were conducted by the Canadian Centre for DNA Barcoding (CCDB), Guelph, using standardised high-throughput protocols (http://ccdb.ca/resources). The 'barcoding' fragment of the mitochondrial cytochrome c oxidase subunit 1 gene (COI) was sequenced, with LepF1 as forward, LepR1 as reverse, and LepR1 as sequence primer (see BOLD sequence pages). The results were submitted to Barcode of Life Data System (BOLD), a cloud-based data storage and analysis platform developed by CCDB (www.barcodinglife.com). DNA alignments were made with the Clustal Alignment (Clustal W), run on MEGA11 software (Tamura *et al.* 2021). MEGA11 was also used for selecting an appropriate nucleotide substitution model. A model with the lowest Bayesian Information Criterion (BIC) score are considered to describe the substitution pattern the best (for a discussion of model selection, see e.g. Srivathsan & Meier 2012).

To root the phylogenetic tree, I chose *Anthidium berbericum* Pasteels, 1981 and *A. taeniatum* Latreille, 1909 as outgroup. These two species belong to the same subgenus and are among the closest relatives of *A. dalmaticum*. For *A. berbericum*, three specimens were selected from Morocco, and for *A. taeniatum*, two specimens from Croatia and one specimen from Turkey (specimen data in Appendix 3).

Maximum likelihood (ML) phylogenetic analysis was performed using MEGA version 11.0.11 (Tamura *et al.* 2021). Bootstrap values were determined from 1000 replications using the Tamura 3-parameter model with uniform rates among sites and are presented here as percentages.

Network analysis was carried out with PopART (Population Analysis with Reticulate Trees) Version 1.7 (Bandelt *et al.* 1999). From the 14 COI sequences available, one had only 438 base pairs (bp) and was excluded from the analysis. The other sequences were trimmed after alignment to an equal length of 599 bp.

The distribution maps were prepared with www.simplemappr.net (Shorthouse 2010).

RESULTS

CHARACTERISATION OF THE SYRIACUM TAXON
A detailed comparison of the females and males of the *syriacum* form, which is considered either as a species or subspecies depending on the author, with nominate *A. dalmaticum* showed the following colour differences (characters in parentheses correspond to nominate *A. dalmaticum*) (see also Fig. 1):
– A broad yellow preoccipital band between the summits of the eyes, sometimes interrupted in the middle (a small elongate spot on each side);
– A yellow continuous L-shaped anterolateral band on the scutum (small yellow elongate maculae on scutum separated in two, laterally and anteriorly; in rare cases yellow maculae entirely absent);
– Scutellum and axilla with broad yellow bands along outer margins (yellow bands mostly limited in extent and narrower);
– T2 with broad yellow transverse band (narrow yellow band, constricted or interrupted mediolaterally and medially);
– T7 in the male yellow with narrow dark margins (broad black margins or almost entirely black).

I found intermediate forms that exhibit some of these characteristics but not all of them. These have mostly anterolateral bands on the scutum as in the *syriacum* form, but the preoccipital band is interrupted medially and the band on T2 in constricted as in nominate specimens. Out of the 148 specimens examined, 8 (5.4%) could not be unambiguously attributed to one of these two taxa.

Within the *syriacum* form, the black ground colour of the terga is sometimes replaced by red-brown (Fig. 1C). Six out of 25 males (= 24%) and five out of 39 females (= 13%) showed lighter colouration.

While nominate *dalmaticum* is widely distributed throughout the east-west direction range (Fig. 2), the *syriacum* form is primarily found in the Levantine and the Iranian regions (Fig. 2). The distribution includes the north the Hakkâri Mountains in eastern Turkey and the foothills of the Lesser Caucasus in the Nakhchivan Autonomous Republic of Azerbaijan (see Appendices 1; 2 for distribution data). The easternmost records are from southern Iran. A record from Afghanistan (Dunford *et al.* 2014; Ascher & Pickering 2023); requires confirmation. Both taxa are found at elevations ranging from sea level to over 2100 metres.

The border between these two subspecies is relatively distinct, with little overlap. Individuals with colour traits typical for *syriacum* have exceptionally been recorded as far west as Greece (Euboea) and the Turkish South Aegean region, as well as in a transition zone along the northern limit of its distribution in south-eastern Turkey, in Dagestan (Russia) and in the Gilan province of Iran.

GENETIC ANALYSIS
The Tamura 3-parameter model (T92 model) achieved in a comparison of 24 models the lowest BIC score (2958.7), while Kimura 2-parameter (K2P) resulted in a somewhat higher BIC of 3186.9. However, both models achieved identical results in the taxon ID tree.
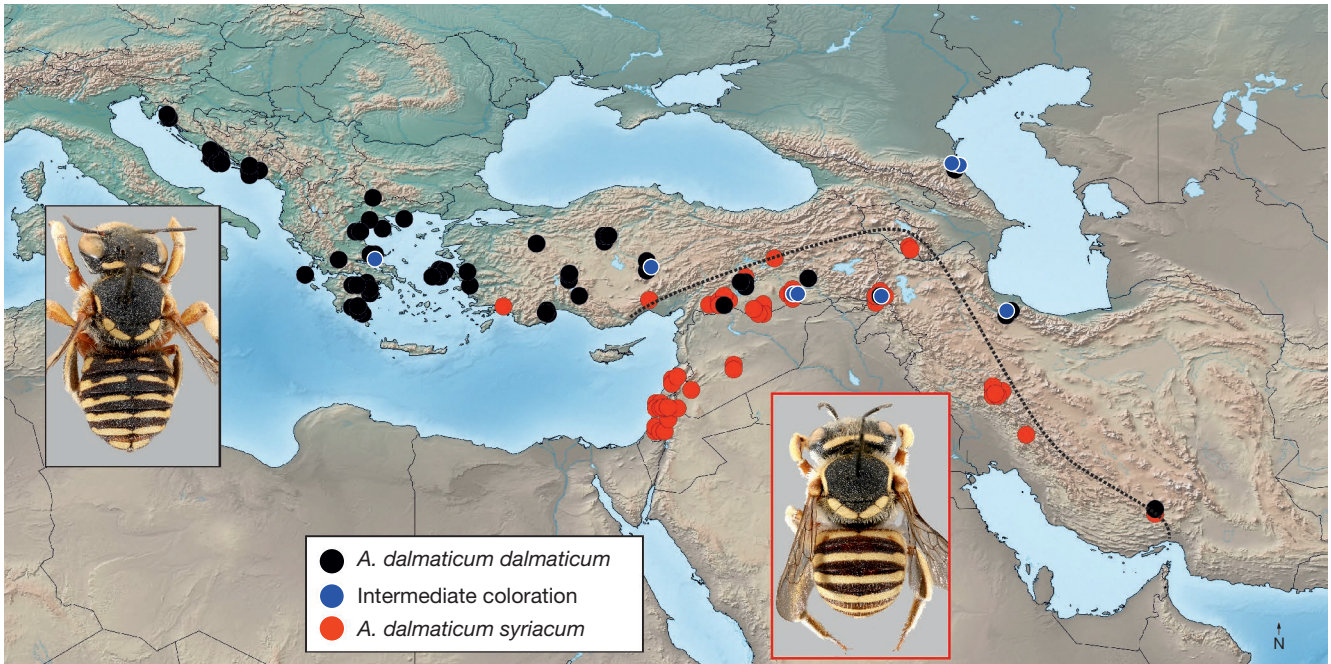
Fɪɢ. 2. — Distribution of *Anthidium dalmaticum* Mocsáry, 1884, based on literature data and unpublished collection material (Appendix 1; 2). **Black dots** show records of the nominate subspecies, **red dots** specimens which were assigned to *A. dalmaticum* ssp. *syriacum*, and **blue dots** to intermediate forms.

The analysis of the mitochondrial COI gene sequences of 14 specimens of *A. dalmaticum* under the T92 model revealed three clearly distinct lineages in the taxon ID tree (Table 3; Fig. 3): A Eurasian clade, a Levantine clade and an Iranian clade. The Levantine clade is sister to a clade containing both the Eurasian and Iranian clades, strongly supported by a Maximum Likelihood (ML) bootstrap value of 100%. The Iranian clade proved to be sister to the Eurasian clade. The node is well-supported by a bootstrap value of 90%. The genetic distance between the Eurasian clade and the Iranian clade (intergroup distance) is 2.50%, while the distance between the Eurasian clade and the Levantine clade is 3.33%. Notably, the distance between the Iranian and Levantine clades is the highest at 3.96% (Table 3).

A haplotype network analysis confirmed these three clades (Figs 4; 5). Members of the Eurasian clade are found from the northern Adriatic coast to the coastal hills of the Caspian Sea. The Levantine clade was found in Israel and Lebanon, and the Iranian clade in southwestern and southern Iran. The haplotype network confirms that the Iranian clade emerged from the Eurasian clade and there are no direct interconnections between the Iranian and the Levantine clades (Figs 4; 5).

The examination of 14 specimens with known COI sequences showed the following subspecies affiliation: In the Eurasian clade, three sequences were affiliated with the nominate subspecies, four sequences with *syriacum*, and two sequences with intermediate forms. In the Levantine clade, both sequences were attributed to *syriacum*, and in the Iranian clade, one sequences was attributed to the nominate subspecies and the two other to *syriacum*. Consequently, the COI sequence grouping does not align with the recognized subspecies.

TABLE 3. — Estimates of evolutionary divergence over sequence pairs between three clades of *Anthidium dalmaticum* Mocsáry, 1884. The number of base substitutions per site from averaging over all sequence pairs between groups are shown. Analyses were conducted using the Tamura 3-parameter model. This analysis involved 14 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd + Noncoding. All ambiguous positions were removed for each sequence pair (pairwise deletion option). The numbers below the diagonal show the distances, the numbers above the diagonal the standard errors. Evolutionary analysis was conducted in MEGA11.

	Eurasian clade	Levantine clade	Iranian clade
Eurasian clade	–	0.0073	0.0063
Levantine clade	0.0333	–	0.0080
Iranian clade	0.0250	0.0396	–

MORPHOMETRIC ANALYSIS

In contrast to my preliminary assumption, the marginal cell length of all males (N = 63), used as an indicator of overall body size, exhibited a negative correlation with geographic latitude (R = −0.313, p = 0.012).

Males of the *syriacum* form throughout their distribution range are the same size as males of the nominate subspecies. The average length of the marginal cell was 1.76 ± 0.148 mm in *A. d. dalmaticum* (N = 36) and 1.75 ± 0.172 mm in "*syriacum*" (N = 25), and this difference was not statistically significant (t-test, p = 0.834). The marginal cell length of intermediate individuals (N = 5) was with an average of 1.75 ± 0.080 mm in the same range.

To gain a more comprehensive understanding of potential morphometric differences between nominate *dalmaticum* and the *syriacum* form, I additionally conducted a Principal Component Analysis (PCA) on five body measurements (Fig. 6). The combined measurements of specimens belong-
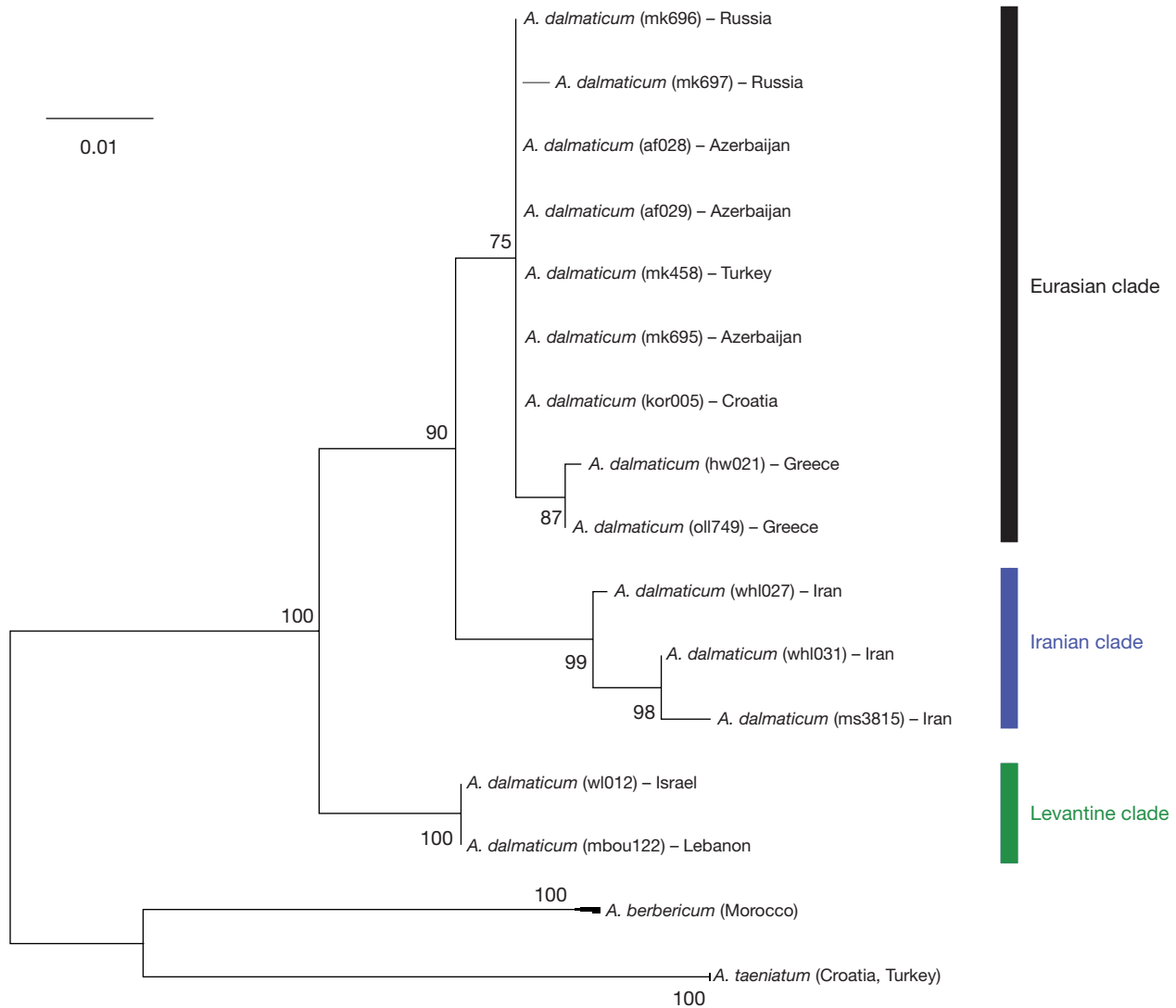
Fig. 3. — Phylogenetic tree of *Anthidium dalmaticum* Mocsáry, 1884 based on the DNA sequence of the barcoding unit of the mitochondrial cytochrome c oxidase I (COI) gene. Numbers shown at nodes are maximum likelihood bootstrap values based on 1,000 bootstrap replicates. *Anthidium berbericum* Pasteels, 1981 and *A. taeniatum* Latreille, 1909 were used as outgroups (Appendix 3). The scale shows the genetic distance.

ing to the "*syriacum*" form and specimens belonging to the intermediate form fell within the overall range of nominate *dalmaticum*. A similar outcome was obtained in a Discriminant Function Analysis (DFA), in which individuals are pre-defined to one of the groups (Fig. 6). The DFA produced only slightly better differentiated clusters for the three groups. The cluster of nominate *dalmaticum* was in the scatterplot the largest one, and this indicates a higher variability of the morphometric parameters in this group. This can obviously be explained by the large distribution of nominate *dalmaticum*, and herewith by a higher geographic variation within this group. Specimens of the "*syriacum*" form, which is more geographically restricted, has a much smaller cluster in the scatterplot than nominate *dalmaticum*; the *syriacum* cluster lies almost entirely within the borders of the nominate *dalmaticum* cluster, indicating that it cannot be considered as a morphometrically distinct group.

DISCUSSION

Nominate *dalmaticum* and the "*syriacum*" form inhabit distinct distribution ranges. Minor morphometric differences can easily be explained by geographic variation rather than by differences between these two forms. The morphometric results thus do not support the concept of two distinct taxa. Additionally, the DNA sequence of the barcoding subunit of the COI gene is not linked to the two colour forms. Notwithstanding these results, it was found that *A. dalmaticum* is split into three distinct clades: a Eurasian clade, which covers most of the distribution area from the northern Adriatic coast to the coastal belt of the Caspian Sea, and two clades which are found in restricted ranges south of this area, in the Levant and in Iran. The Eurasian/Iranian clades are sister to the Levantine clades, and the Iranian clade diverged from the Eurasian clade (Figs 4; 5). No geographic and climatic
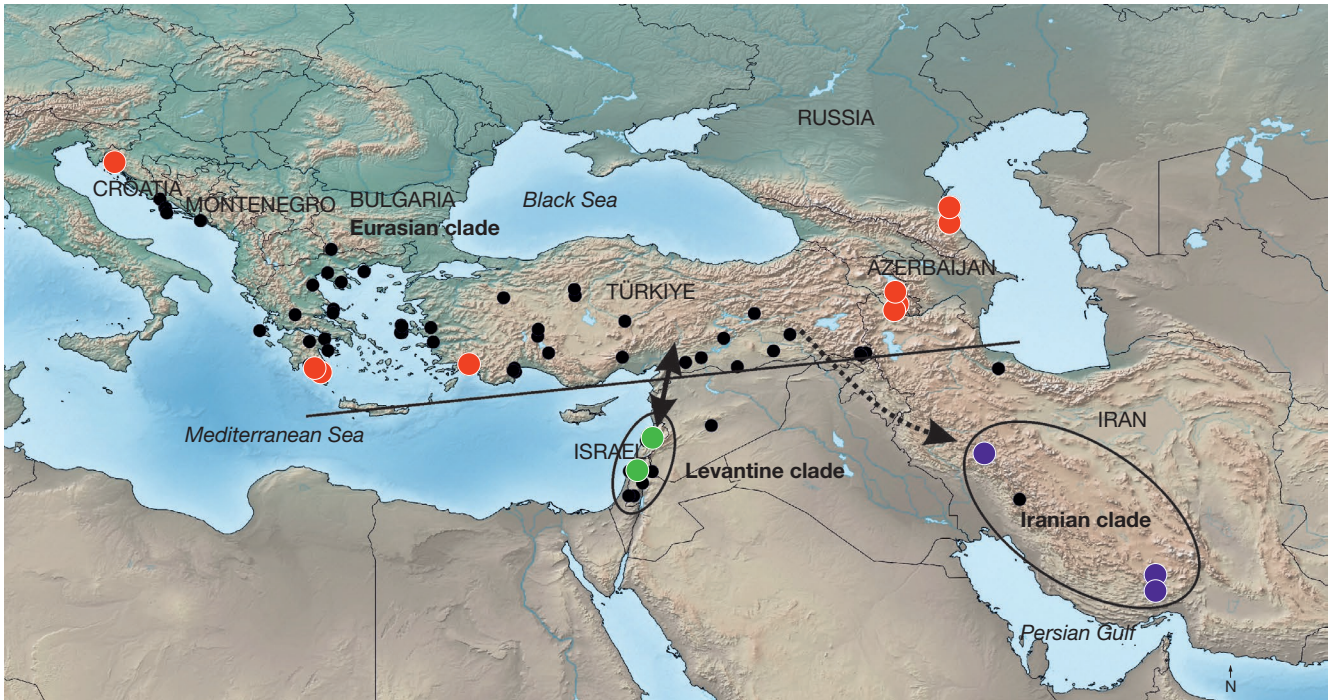
FIG. 4. — Geographic distribution of specimens associated with the three clades identified from COI sequences of *Anthidium dalmaticum* Mocsáry, 1884. **Red**, **green** and **blue dots** show the individuals whose COI sequences were analysed, black dots material examined, but not barcoded. The arrows show a hypothetical evolutionary trajectory based on a haplotype network analysis. The Iranian clade has split off from the Eurasian clade after the separation of the Eurasian from the Levantine clade.
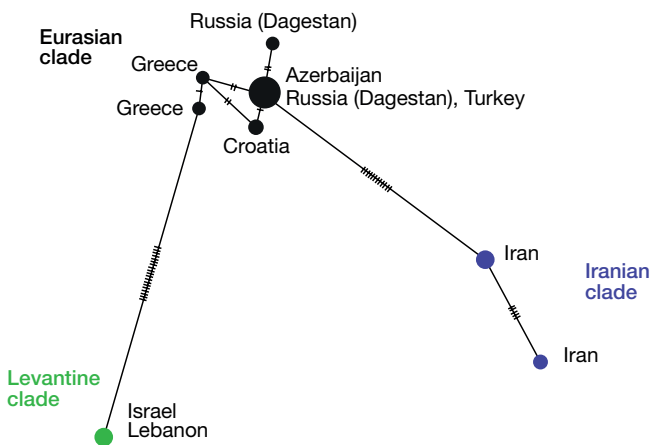

FIG. 5. — Haplotype network of *Anthidium dalmaticum s.l.* Mocsáry, 1884 in the eastern Mediterranean and the Middle East. The sizes of the circles correspond to the frequency of each haplotype over all populations and the length of the lines is proportional to the number of mutations. Haplotypes from Iran (Iranian clade) are shown in **blue**, haplotypes from Israel and Lebanon (Levantine clade) in **green**. All other countries in **black**.

barriers are known that could explain the emergence of these three clades. With a distribution including different climatic zones and altitudes ranging from sea level to over 2100 m, *Anthidium dalmaticum* appears to be a relatively adaptive species. It is unlikely that external reproductive barriers exist under the current environmental conditions that led to the emergence of these isolated clades. It is therefore likely that the three clades are the result of a historical phylogeographic

process, which may have occurred during the glacial period (see e.g., Taberlet *et al.* 2002). The COI sequence suggests that the colonisation of the Iranian landmass and the Levant are independent processes, which possibly occurred during different phases of the climate oscillations between glaciations and warm cycles.

Similar distribution patterns have also been observed in other species of Anthidiini. *Anthidium melanopygum* Friese, 1917 is widely distributed from the south Balkans over to Central Asia, while its close relative, *Anthidium spiniventre* Friese, 1899 (both taxa were treated as conspecific in the past), has isolated distribution areas in the southern Levant and southern Iran (Kasparek & Fateryga 2023). Also, *Eoanthidium flavifrontale* Kasparek, 2021 and *E. crenulatum* Warncke, 1982, which are closely related, are found in disjunct distribution areas. *Eoanthidium flavifrontale* Kasparek, 2021 is found in the northern Levant (south-eastern Turkey), whereas *E. crenulatum* is found in southern Iran and around the Gulf of Oman (Kasparek & Griswold 2021). *Eoanthidium nasiculum nasiculum* Pasteels, 1969 occurs in Turkey, and the subspecies *E. nasiculum orientale* Kasparek, 2019 is found in Iran, while the closely related *E. nasicum* occurs in the Levant (Kasparek 2019). Within the sibling species *Eoanthidium pasteelsi* (Warncke, 1980) and *E. judaeense* (Mavromoustakis, 1945), *E. pasteelsi* is found in Turkey and the Caucasus, while *E. judaeense* occurs in the Levantine countries (Kasparek 2020). Similarly, *Eoanthidium clypeare* (Morawitz, 1874) is distributed from the northern Adriatic coast to the Caucasus, and the closely related *E. hoplostomum* (Mavromoustakis, 1945) is found
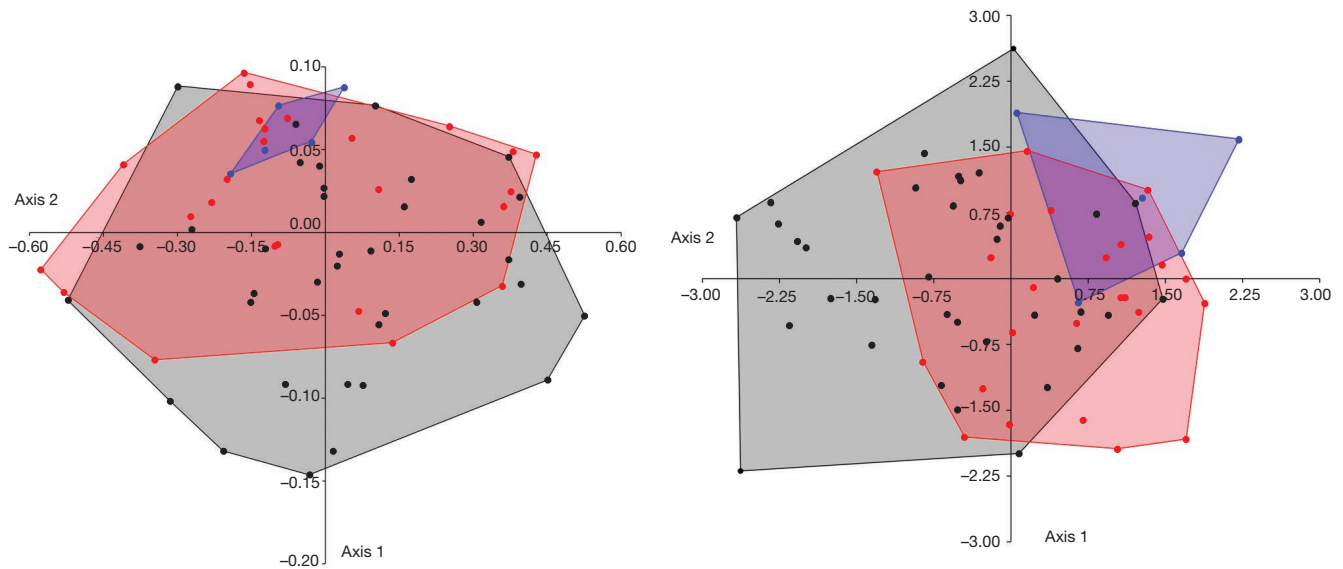
Fig. 6. — Scatter plots of the results of a principal component analysis (PCA) (**A**) and a discriminant function analysis (DFA) (**B**) of nine morphometric parameters of *Anthidium dalmaticum* Mocsáry, 1884. **Black dots** (and the **grey** area) show specimens attributed to *A. d. dalmaticum*, **red dots** (and **red** shadow) specimens attributed to "*syriacum*". **Blue** shows intermediate forms.

in the Levant (Kasparek 2020). The distribution of all these species pairs appears to follow a very similar phylogeographic pattern with three distinct population clusters in Anatolia, Iran and the Levant. Depending on the taxonomic units, these population clusters have reached different evolutionary levels, reaching from genetic lineages over subspecies to full species.

BOLD assigned different BINs to the three species clusters of *A. dalmaticum*: AEH0781 for the Eurasian clade, AEH0782 for the Iranian clade, and AEH0783 for the Levantine clade. The genetic distance between the Eurasian clade and the Levantine clade was found to be 3.3%, the distance between the Eurasian and the Iranian clade was 2.5%, and the distance between the Iranian and the Levantine clades was 3.96%. Genetic distance to the nearest neighbour is known to be low in bees, and generally lying below 3% (e.g., Gibbs 2018; Gueuning *et al.* 2020; Kasparek 2021; Litman *et al.* 2021; Kasparek & Fateryga 2023; Kasparek *et al.* 2023a, b). The three genetic clades of *A. dalmaticum* identified here could therefore be considered as distinct taxa, potentially constituting "cryptic species". However, in the absence of morphological, ecological behavioural, or other traits (e.g., distribution data indicating evidence for sympatric or allopatric occurrence) that would further support such a decision, I do not yet regard the available evidence as sufficient to classify either the colour forms or the genetic clusters as distinct taxonomic units. It is suggested to treat *A. dalmaticum* ssp. *syriacum* as a synonym of nominate *Anthidium dalmaticum*.

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APPENDICES

Appendix 1. — Distribution of *Anthidium dalmaticum* Mocsáry, 1884 (literature data).

BBSL   U.S. National Pollinating Insects Collection;
GBIF   Global Biodiversity Information Facility, available from https://www.gbif.org;
Melissotheque database   University of the Aegean.

Anthidium dalmaticum Mocsáry, 1884

Anthidium dalmaticum dalmaticum Mocsáry, 1884

DISTRIBUTION. — **Croatia**. Dalmatia (Mocsáry 1884); Split (45°2'N, 15°5'E), 7.VI.1948, V. Balthasar leg. (Snow Entomological Museum Collection, GBIF); Split [possibly identical with previous record] (Warncke 1980); Gravosa-Lapad, Ragusa [Gravosa today a district of Dubrovnik]. VI.1914 (Maidl 1922).
Greece (mainland). Central Macedonia: Litochoron (40°7'N, 22°30'E) (Warncke 1980). — Thessalia: Platania env. (*c*. 39°09'N, 23°16'E), V-VI.1999-2003 (Standfuss *et al.* 2003). — Central Greece (Attica region): Mt. Penteli (Nea Penteli) = Pendeli nr. Athens, VI.1957 (Mavromoustakis 1958). — Peloponnes: Loutraki (Warncke 1980).
Greece (islands). Argo-Saronic Islands, Ag. Marina-Portes (37.72°N, 23.52°E), 15.-17.VI.2013, S. Margaroni leg. (Melissotheque database). — Chios: Gridia (38.2155°N, 26.1016°E), 11.VI.2014, G. Nakas leg. (University of the Aegean, Melissotheque database). — Korfu (Warncke 1980). — Lesvos: 10.0 km S Mytilene (39.014°N; 26.59°E), 100 m, 28.V.2004 (BBSL, GBIF). — Lesvos: 1.3 km WSW Loutra (39.058°N; 26.535°E), 68 m, 16.VI.2004 (BBSL, GBIF). — Rhodes: Petaloudes, Kremasti, and Phileremos, VI.1958 (Mavromoustakis 1959, Warncke 1980). — Thasos Island: Astris (40°58'N, 24°65'E), 21.VI.2012, M. de Courcy leg. (Melissotheque database).
Iran. Tehran, listed without further details (Esmaili & Rastegar 1974; see also Samin *et al.* 2015). — Isfahan: Kashan (34°00'N, 51°20'E) (Samin *et al.* 2015).

Israel. Har Meron (33°00'N, 35°40'E), 1968, S. Frommer & D. Gerling leg. [as *A. dalmaticum*] (BBSL, GBIF).
Turkey. Afyon: Dinar (Özbek & van der Zanden 1993). — Ankara, 12. + 28.VI.1934 (Alfken 1935). — Aydın: Kuşadası (Staněk 1968 misidentified as *Anthidium variegatum* Fabr. var. *meridionale* Giraud, 1863; see Warncke1980). — Erzurum: Pehlivanli, Tortum (Özbek & van der Zanden 1993). — Erzurum: Kân-Ispir [Aslandede Kân Köyü] (Özbek 1979). — Tunceli: Gözeler, Ovacık (Özbek & van der Zanden 1993).

Anthidium syriacum Perez, 1912

Anthidium dalmaticum syriacum Perez, 1912

DISTRIBUTION. — **Afghanistan**. Listed by Ascher & Pickering (2023) without detail; cited by Dunford *et al.* (2014).
Azerbaijan. Nakhchivan AR: Shakhbuz, Gizil Gishlag (39°28'N, 45°35'E), 19.VI.2019 (Fateryga *et al.* 2020).
Iran. Khuzestan: Basuft [locality not identified], Escalera leg. (Warncke 1982). — Kashan, Isfahan prov., 34°00'N, 51°20'E, VIII.2012 [listed as *A. dalmaticum*] (Samin *et al.* 2015).
Israel. Israel mentioned without further details (Warncke 1980). — Adulam Nature Reserve, 15 km S Ber Shemesh (31.64°N, 34.90°E), 5.-13.V.2005 (GBIF).
Israel/Palestine. Jerusalem (Mavromoustakis 1939).
Lebanon. Mount Lebanon: Broummana (Brumana, type locality of *syriacum*) (Pérez 1912). — Mount Lebanon: Ein ei Arar near Baabdate (Mavromoustakis 1955). — Mount Lebanon: Nahr el Kalb (Nahr el Kelb) (Mavromoustakis 1955). — Bekaa: Passage Akoura-Hadath (Boustani *et al.* 2021; see also under material examined).
Syria. Listed by Ascher & Pickering (2023).
Turkey. SE Turkey: Amanus Mountains (Warncke 1980). — Mersin: Mut (Warncke 1980). — Urfa: Halfeti (Warncke 1980). — Niğde/Mersin: between Ulukışla (Niğde) and Çiftehan (Mersin) (Warncke 1980).

Appendix 2. — Collection data of all specimens examined for this study.

ABBREVIATIONS
Private collections
coll. AF   collection of A. Fateryga, Feodosiya;
coll. AWE   collection of A. W. Ebmer, Puchenau;
coll. GH   collection of G. Hölzler, Vienna;
coll. GR   collection of G. Reder, Flörsheim-Dalsheim;
coll. HK   collection of H. Korten, Würzburg;
coll. HW   collection of H. Wiesbauer, Vienna;
coll. MB   collection of M. Boustani; Mons;
coll. MF   collection of M. Fuhrmann, Kreuztal;
coll. MH   collection Martin Hauser, Sacramento;
coll. MK   collection of Max Kasparek, Heidelberg;
coll. SR   collection of S. Risch, Leverkusen;
coll. WHL   collection of W. H. Liebig, Bad Muskau.

Institutions
NHMUK   Natural History Museum, London;
OLL   Biodiversitätszentrum Linz (Oberösterreichisches Landesmuseum);

SMF   Senckenberg Museum Frankfurt;
UMONS   University of Mons;
ZMB   Zoological Museum Berlin (Museum für Naturkunde);
ZMH   Zoological Museum Hamburg.

MATERIAL EXAMINED. — **Azerbaijan** • 1♀, 1♂; Nakhchivan AR: Shakhbuz, Gizil Gishlag; 39.47°N, 39.47°E; 19.VI.2019; M. Proshchalykin, Aliyev, Maharramov; coll. AF. — 1♀; Nakhichivan AR, Shakhbuz, Kulus; 39.35°N, 39.35°E; 26.VI.2020; M. Maharramov; coll. MK. — **Bulgaria** • 1♀; Lebnice [Lebnica = Lebnitsa in Sandanski]; 41.51°N, 41.51°E; 07.VII.1988; Brokes; coll. MK. — **Croatia** • 1♀; Dalmatien, Gravosa [= Gruz]; 42.65°N, 42.65°E; 18.VI.1914; OLL • 1♂; Dalmatien, Gravosa Lapad; 42.65°N, 42.65°E; VII.1914; Maidl; OLL • 3♀, 3♂; Dalmatien, J. Hvar Jelsa; 43.15°N, 43.15°E; 21.-24.VI.1939; F. Stöcklein; OLL • 1♀; Hvar Island; 43.15°N, 43.15°E; 24.VI.1953; H. H. F. Hamann; coll. MK • 1♀; Pag Island, 1 km SE Jakisnica; 44.83°N, 44.83°E; 29.VI.2003; leg. G. Hölzler; coll. GH • 1♀; Lapad [Stadtteil von Dubrovnik]; 42.65°N, 42.65°E; 20.VI.1914; OLL • 1♂; Primorje-Gorski Kotar, Krk, Stara Baska; 44.98°N, 44.98°E; 9.VII.2022;

leg. H. Korten; coll. HK • 1♀; Ragusa [= Dobrovnik]; 42.65°N, 42.65°E; V.1924; Lindner; ZMB • 3♂; Ragusa [= Dubrovnik]; 42.65°N, 42.65°E; vi.1926; ZMB • 1♂; same location; VI.1923; F. Wagner; ZMB • 1♀; Spalato [= Split]; 43.50°N, 43.50°E; [very old label without date (19. century?)]; S. Stein; ZMB • 2♀, 1♂; Velaluka Kurzola [Vela Luka]; 42.95°N, 42.95°E; 01-15.VI.1938; Dr Jaeger; OLL • 1♀; „Dalm.“; Vor 1896; ZMB. — **Greece** • 1♀; "Griechenland Stein. S." [?]; altes Etikett (19. Jh.?); ZMB • 1♂; Cephallonia N Paliki Peninsula, N of Atheras env.; 38.30°N, 38.30°E; 2.VII.2006; P. Bulirsch; coll. MK • 1♂; Chalkidiki, W of Nikiti; 40.22°N, 40.22°E; 12.-14.VI.2013; M. Snizek; OLL • 1♀; Chios, Ag. Ioannis NW Ag. Georg. Sykousis; 38.22°N, 38.22°E; 15.VI.2007; leg. A. W. Ebmer; coll. AWE • 1♀; Chios, N Fytá; 38.52°N, 38.52°E; 13.VI.2007; leg. A. W. Ebmer; coll. AWE • 1♀; Chios, Passhöhe E Vessa; 38.30°N, 38.30°E; 12.VI.2007; leg. A. W. Ebmer; coll. AWE • 1♀, 1♂; Chios, SW Pityos; 38.47°N, 38.47°E; 18.VI.2007; leg. A. W. Ebmer; coll. AWE • 1♀, 1♂; Chios, W Pyrgi to Kato Fanou; 38.22 °N, 38.22°E; 12.VI.2007; leg. A. W. Ebmer; coll. AWE • 1♀; Euböa: 2 rkm E Elliniká (Steinbruch); 39.00°N, 39.00°E; 18.VI.1994; A. Koch; coll. MH • 1♀; Hortiatis ES of Thessaloniki; 40.59°N, 40.59°E; 8.VII.2019; M. Halada; OLL • 1♀, 1♂; Litochoron; 40.10°N, 40.10°E; 17.VIII.1978; K. Warncke; OLL • 1♀; Loutraki, Golf von Korinth; 37.97°N, 37.97°E; 29.V.1963; M. Schwarz; coll. MK • 1♂; M.Veluchi, Evrytania; 38.93°N, 38.93°E; Holtz; coll. MK • 1♀; Morea merid. Kambos, Taygetos [Ort Kambos nicht identifiziert]; 36.95°N, 36.95°E; vi.1901; Holtz; ZMB • 2♂; Peloponnes: 2 km W of Stavropodi; 37.52°N, 37.52°E; 27.V.2016; M. Halada; OLL • 1♀, 1 ♂; Peloponnes: 40 km N Tripoli Scotini; 37.87°N, 37.87°E; 03.VII.1996; Ma. Halada; coll. MK • 1♂; Peloponnes: Mani Kap Tenaron; 36.67°N, 36.67°E; 10.V.2019; leg. H. Wiesbauer; coll. HW • 2♂; Peloponnese: Glossa, 15 km SW Skala; 36.80°N, 36.80°E; 2.VI.2016; M. Halada; OLL • 1♀, 1♂; Platania / Volos; 39.15°N, 39.15°E; 8.VI.2001; L. Standfuss; coll. MF • 1♀; Thasos Tripiti, 3 km W Limenaria; 40.63°N, 40.63°E; 15.-22.V.2014; leg. G. Reder; coll. GR. — **Iran** • 3♂; Gilan prov.: 15 km SE Tutkabon; 36.80°N, 36.80°E; 9.VI.2014; J. Halada; coll. MK • 1♀, 1♂; Hormozgan Hajiabad 4 km NW; 28.33°N, 28.33°E; 5.V.2019; leg. W. H. Liebig; coll. WHL • 6♀, 1♂; Lorestan prov.: 10 km SW Dorud; 33.45°N, 33.45°E; 27.V.2014; J. Halada; coll. MK • 1♀; SW Persia, Bazuft; 31.63°N, 31.63°E; 1900-61; Escalera; OLL. — **Israel** • 2♀; Eshtaol, Kesalon Valley; 31.77°N, 31.77°E; 23.V.1975; K. M. Guichard; NHMUK • 1♀; Israel North District: Bet Rimon N Kafr Kana FS; 32.77°N, 32.77°E; 06.V.2019; T. Kwast; coll. WHL • 2♀, 2♂; Mt. Carmel Nahal Nesher; 32.75°N, 32.75°E; 14.VI.2000; M. Török; ZMH • 3♂; Mt. Carmel Wadi Denya; 32.73°N, 32.73°E; 23.V.2000; M. Török; ZMH • 2♀; Upper Galilee Bet Rimon 1.8 km SE; 32.77°N, 32.77°E; 28.V.2011; leg. S. Risch; coll. SR. — **Israel/Palestine** • 1♂; Jerusalem; 31.77°N, 31.77°E; 26.V.1942; OLL. — **Jordan** • 1♀; Jordan valley: Mubalath [location not identified]; 32.28°N, 32.28°E; 27.IV.1996; Ma. Halada; coll. MK. — **Lebanon** • 1♀, 1♂; Nahr el Kelb; 33.95°N, 33.95°E; 12.V.1953; OLL • 1♀; Passage Akoura-Hadath; 34.05°N, 34.05°E; 7.VII.2019; G. Ghisbain; coll. MB. — **Palestine** • 1♀; Kirj. Anacorton [?]; VI.1946; H. Bytinski-Salz; OLL • 1♂; Jerusalem; 31.77°N, 31.77°E; 28.VI.1952; G. Mavromustakis; coll. MK. — **Russia: Dagestan** • 1♀, 2♂; Vicinity of Talgi; 42.88°N, 42.88°E; 13.VI.2021; A. Fateryga; coll. MK. — **Syria** • 1♀, 1♂; Homs: Palmyra env.; 34.55°N, 34.55°E; 6.VI.2000; K. Denes sen.; coll. MK. — **Turkey** • 1♀; 10 km W Gaziantep; 37.05°N, 37.05°E; 20.VI.1997; Ma. Halada; coll. MK • 1♀; 15 km S Ankara Beynam; 39.68°N, 39.68°E; 22.VII.1987; Kl. Reinhold; coll. MK • 3♀, 4♂; 20 km N Mardin; 37.50°N, 37.50°E; 21.VI.1997; Ma. Halada; coll. MK • 1♂; 30 km W Baykan; 38.15°N, 38.15°E; 30.VI.2000; M. Halada; coll. MK • 2♀; Ankara; 39.93°N, 39.93°E; 28.VI.1934; A. Seitz; SMF • 1♂; Antalya: 35 km SW Antalya, 5 km SW Beldibi; 36.67°N, 36.67°E; 6.VI.2001; leg. coll. GH • 2♀; "Asia Minor"; 1890; ZMB • 1♂; Aydin: Kuşadası; 37.85°N, 37.85°E; 10.VII.1965; OLL • 1♂; 10 km SW Antalya; 36.82°N, 36.82°E; 05.VI.2001; leg. G. Hölzler; coll. GH • 1♂; 30 km SW Antalya, 6 km vor Ovacık; 36.72°N, 36.72°E; 5.VI.2001; leg. G. Hölzler; coll. GH • 1♀; Gülek; 37.25°N, 37.25°E; H. Schulz; ZMB • 2♀; Hakkari, Varegöz/Sat Dağı [Sat Dağı =Ikiyaka Dağı]; 37.33°N, 37.33°E; 29.VI.1985; W. Schacht; OLL • 2♀; Hakkari: Beyetüşsebap 19 km S; 37.42°N, 37.42°E; 26.VI.1985; M. Schwarz; coll. MK • 1♀, 1♂; Hakkari: Oramar 10 km NE [Oramar = Daglica]; 37.42°N, 37.42°E; 29.VI.1985; M. Schwarz; coll. MK • 1♀, 2♂; Hakkari: Yüksekova 16 km SE; 37.42°N, 37.42°E; 28.VI.1985; M. Schwarz; coll. MK • 4♀, 3♂; Birecik: Halfeti; 37.23°N, 37.86°E; 28./31.V.1978; Ma. Halada; coll. MK • 1♀; Izmir; 38.42°N, 38.42°E; 12.VI.1964; H. H. F. Hamann; coll. MK • 2♀; Konya: 30 km S of Akşehir; 38.08°N, 38.08°E; 24.VI.1998; J. Halada; coll. MK • 1♂; Konya: Akşehir; 38.35°N, 38.35°E; 2.VIII.1991; K. Warncke; OLL • 1♂; Konya: Seydişehir; 37.42°N, 37.42°E; 4.VIII.1991; M. Halada; OLL • 1♂; Kütahya, 20 km NEE Kütahya; 39.60°N, 39.60°E; 13.VII.2006; J. Halada; OLL • 1♀, 3♂; Malatya, Gördük Dağları, N-Nemrut Dağı; 38.00°N, 38.00°E; 12.VII.1995; Y. Barbier & P. Rasmont; UMONS • 1♀; Muğla prov.: Köyceğiz (Toparlar, Şelale); 36.98°N, 36.98°E; 24.V.2019; M. Kasparek & O. Özgül; coll. MK • 1♀; NE Carmardi, Niğde; 38.98°N, 38.98°E; 10.VIII.1991; K. Warncke; OLL • 1♀, 5♂; Urfa, 40 km W Ceylanpınar; 36.87°N, 36.87°E; 17.V.1989; K. Warncke; OLL • 3♀; Zelve (Nevşehir); 38.67°N, 38.67°E; 12.VII.1997; Ma. Halada; coll. MK.

APPENDIX 3. — Specimen data of material used as outgroup in the genetic analysis. Abbreviations: **coll. HK**, collection of H. Korten, Würzburg; **coll. MK**, collection of Max Kasparek, Heidelberg; **coll. PG**, coll. P. Geisendörfer.

Anthidium berbericum. — **Morocco** • ABABY084-23; Tiznit, 2.75 km SW Ifrane Atlas Saghir; 7.IV.2017; R. Prosi leg.; coll. MK, rpr036 • ABABY085-23; Chtouka-Ait Baha, 20 km N Tafraout, 0.6 km NW Tizourgane; 15.IV.2017; R. Prosi leg; coll. MK: rpr037 • ABABY086-23; Azilal, Irherm; 6.V.2015; V. Soon leg. coll.: tuz009.

Anthidium taeniatum. — **Turkey** • ABABX139-20; Muğla, Kozağaç; 14.VII.2017; M. Kasparek leg.; coll. MK: mk510. — **Croatia** • ABABY088-23; Krk, Stara Baska; 9.VII.2022; leg. coll. PG; pge004 • ABABY089-23; Krk, Primorje-Gorski Kotar, Stara Baska; 9.VII.2022; leg. coll. HK; kor007.