

Revision of the *leachella* group of *Megachile* subgenus *Eutricharaea* in the Western Palaearctic (Hymenoptera, Apoidea, Megachilidae): A renewed plea for DNA barcoding type material

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Abstract

The leafcutting bees of the *leachella* group of *Megachile* Latreille subgenus *Eutricharaea* Thomson are revised for the Western Palaearctic region using a combination of morphology and phylogenetic analyses of three genes (COI, LW-Rhodopsin, CAD). Although only seven species are recognized, much effort was needed to link delimited taxonomic units to taxon names because of the difficulties in identifying type specimens. Numerous types were in a poor state of conservation, preventing straight-forward identification using morphology. This was in some cases aggravated by the fact that they often belonged to a sex that could not easily be identified; one type was a gynandromorph specimen whose identification is even more challenging. In several cases, the type locality was vague or unclear; in three cases, the type specimens originated from introduced populations for which the source of the introduction needed to be determined using DNA barcoding. In two cases, the type specimens consisted of several body parts not originating from a single individual but from two heterospecific specimens. We argue that this tedious nomenclatural work would have been greatly facilitated if a reference library of type specimens had been available. Our revision leads to the following taxonomic changes. *Megachile argentata* (Fabricius, 1793), described from northern Africa and with a convoluted taxonomic history, is demonstrated, based on morphometric analyses of its lectotype, to be conspecific with the species hitherto known as *M. pilidens* Alfken, 1924. After discussing and excluding several alternative options that would minimize nomenclatural changes, we place *M. pilidens* in synonymy with *M. argentata* (**syn. nov.**). Two new subspecies are described for morphologically slightly divergent insular populations, *M. leachella cretica* Praz, **ssp. nov.**

from Crete, and *M. leachella densipunctata* Praz, **ssp. nov.** from Cyprus. In addition, *M. albipila* Pérez, 1895 is treated as a subspecies of *M. leachella* Curtis, 1828 (**stat. nov.**). The following new synonymies are proposed: *M. compacta* Pérez, 1895 (not *M. compacta* Smith, 1879) and the replacement name *M. crassula* Pérez, 1896, *M. argyrea* Cockerell, 1931 and *Perezia maura* Ferton, 1914, are placed in synonymy with *M. argentata* (**syn. nov.**). *M. beaumonti* Benoist, 1951, is newly treated as a valid species (**stat. rev.**). *M. schmiedeknechti* Costa, 1884 is treated as a subspecies of *M. argentata* (**stat. nov.**), and *M. xanthopyga* Pérez, 1895 is placed in synonymy with *M. argentata schmiedeknechti* (**syn. nov.**). *M. bioculata* Pérez, 1902, *M. discriminata* Rebmann, 1968 and *M. ichnusae* Rebmann, 1968 are placed in synonymy with *M. leachella* (**syn. nov.**). *M. variscopa* Pérez, 1895, *M. timberlakei* Cockerell, 1920, *M. atratula* Rebmann, 1968, *M. striatella* Rebmann, 1968 and *M. sudai* Ikudome, 1999 are placed in synonymy with *M. pusilla* Pérez, 1894. Lectotypes are designated for *M. albipila*, *M. bioculata*, *M. compacta* Pérez, *M. pusilla*, *M. variscopa* and *M. xanthopyga*.

Keywords

DNA barcoding, morphometry, speciation, species delimitation, subspecies

Introduction

The subgenus *Eutricharaea* Thomson, 1872 of the genus *Megachile* Latreille, 1802 (Hymenoptera: Megachilidae) is taxonomically difficult: it includes numerous species with rather homogeneous morphology, leading to challenging identifications and intricate species boundaries. In addition, in the absence of proper examination of their type material, the status of several taxa remains unclear. The subgenus is native to the Eastern Hemisphere but has been introduced both accidentally (*Megachile apicalis* Spinola, 1808, *M. pusilla* Pérez, 1884, *M. concinna* Smith, 1879) and intentionally [*M. rotundata* (Fabricius, 1793)] into the Western Hemisphere. The latter species was introduced into North America and is reared commercially for the pollination of alfalfa (*Medicago* sp.) (Pitts-Singer and Cane 2011). In the Eastern Hemisphere, the subgenus is particularly diverse throughout the Palearctic and in Africa. It also occurs in Southeast Asia and in Australia, although some Australian species included in this subgenus probably belong somewhere else (e. g., the species of the *M. chrysopyga* group; see Trunz et al. 2016). Many small leafcutting *Megachile* in the Eastern Hemisphere belong to this species-rich subgenus.

In the Palearctic no comprehensive revision is available for this subgenus. Otto Rebmann described several species and presented identifications keys for some species groups (Rebmann 1967–1970), but he did so without a full revision of the type material. Species of *Eutricharaea* fall into several species groups segregated based on male genitalia, mainly the *rotundata* group [sometimes referred to as a distinct subgenus, *Neoeutricharaea* Rebmann, 1967; see Rebmann (1967a)] and the *leachella* group (Praz 2017), which include much of the diversity observed in the subgenus in the Palearctic. In males, both groups can easily be separated based on the structure of the gonostylus (Praz 2017: figs 54, 56) as well as several other morphological criteria (see Praz 2017). Females are more difficult to separate; those of the *rotundata* group are mostly

characterized by the presence of a rounded, glabrous, impunctate and matt area on each side of the disc of T2, sometimes also on T3. This area is referred to as a “fovea”, following Gonzalez et al. (2010). Species of the *leachella* group do not have a clearly delimited fovea on either T2 or T3, although the area of T2 where the fovea would be if present is very finely punctate and covered with short hairs, thus slightly different in its appearance from the rest of the tergal disc.

The *leachella* group includes two widely distributed species in the Palaearctic, *M. pilidens* Alfken, 1924 and *M. leachella* Curtis, 1828, which are the only species present in Central Europe (Amiet et al. 2004; Peeters et al. 2006; Scheuchl 2006). Both are easy to distinguish in the male sex, especially in the shape of S4, which has a small median tubercle covered by white hairs in *M. pilidens* and no tubercle but a patch of yellowish hairs in *M. leachella* (Amiet et al. 2004; Peeters et al. 2006; Scheuchl 2006). In addition, the *leachella* group includes the species allied to *M. concinna* (hereafter *concinna* complex), which are distributed from South Africa to Europe and Central Asia, and introduced into the Western Hemisphere (including South and North America) and probably into Japan, Hawaii and Australia (see note under *M. pusilla*). Species boundaries in the *concinna* complex are challenging and were examined by Soltani et al. (2017), who suggested the presence of four taxa in the Palaearctic, *M. anatolica* Rebmann, 1968, *M. leucostoma* Pérez, 1907, *M. pusilla* and *M. viridicollis* Morawitz, 1875. These taxa mostly represent geographic replacement “forms” with some evidence of phenetic intergradation along their contact zone. The arrangement of three forms around the Mediterranean Sea suggests a pattern of “speciation in a ring”, where the two ends of the ring, *M. anatolica* and *M. pusilla*, coexist and maintain phenotypic and genetic integrity in sympatry over the region comprised between Greece and Italy; along the ring, there is apparent phenetic intergradation between *M. anatolica* and *M. leucostoma*, with transitional populations in the Levant (Soltani et al. 2017: fig. 6), and then possible intergradation between *M. leucostoma* and *M. pusilla* in northern Africa. *Megachile concinna* and *M. venusta* Smith, 1853 are considered to be Afrotropical species that are absent from the western Palaearctic (Soltani et al. 2017); *Megachile concinna* is introduced into the Caribbean, incidentally its type locality. Additional species in the *leachella* group include *M. walkeri* Dalla Torre, 1896, mainly distributed on the Arabian Peninsula, the northern African and Middle Eastern species *M. inexpectata* Rebmann, 1968 (not to be confused with *M. inexpectata* Pasteels, 1973 described from tropical Africa), and a species restricted to Sardinia, Corsica and Malta, *M. schmiedeknechti* Costa, 1884. Numerous additional names, many of which were proposed by Rebmann (1968), remain with an unclear taxonomic status (see Gonzalez et al. 2010 and Praz et al. 2021 for a treatment of some of these names). One name that has remained unclear for decades is *Apis argentata* Fabricius, 1793 (hereafter *M. argentata*), described from “Barbaria”, the region in North Africa extending from Algeria to Libya. Much of the present work deals with settling the identity of this taxon, which has remained obscure for more than two centuries.

In the present study, we use a combination of genetic analyses and morphology to delimitate the species of the *leachella* group of the Western Palaearctic, and examine most type specimens to present a comprehensive revision of this challenging group of bees.

Methods

Molecular methods

The 658-bp fragment of the mitochondrial gene Cytochrome Oxidase I (DNA barcoding fragment; hereafter COI) was generated using the primers LepF and LepR or, if this primer pair did not yield amplicons or high-quality sequences, the alternate forward primer UAE3. Primer sequences and lab protocols are given in Trunz et al. (2016). All new DNA barcodes have been submitted to the Barcode of Life Data System (BOLD) platform (Ratnasingham and Hebert 2007) with process-ID numbers [PAMEG016-22](#) to [PAMEG058-22](#) (locality information is given in Suppl. material 1). In addition, we also sequenced the two nuclear genes CAD and LW-Rhodopsin (Soltani et al. 2017), given the known limitations of relying on a single mitochondrial genetic marker for species delimitation (Praz et al. 2019; Gueuning et al. 2020). We used the primers mentioned in Soltani et al. (2017) to amplify and sequences these two nuclear genes. Sequences of the nuclear genes have been submitted to Genbank with accession numbers [OQ095208–OQ095231](#). Chromatograms were edited using Geneious 6.0.6 (Kearse et al. 2012) and the resulting sequences were aligned with Mafft (Katoh and Standley 2013). Single gene phylogenetic trees were reconstructed using maximum likelihood inference with RAxML 8.2.10 (Stamatakis 2014) with 1000 bootstrap replicates, applying a GTR + G model to a unique partition. For the two nuclear genes, the introns were removed; heterozygous specimens were excluded (see Soltani et al. 2017). The two nuclear genes were then concatenated and analyzed with RAxML, implementing a GTR + G model with two partitions (one by gene). Soltani et al. (2017) suggested introgression and allele sharing between some populations of *M. leachella* and *M. anatolica* for the gene LW-Rhodopsin. Single gene analyses for this gene suggested gene flow from *M. leachella* to *M. anatolica*. We therefore excluded LW-Rhodopsin sequences for *M. anatolica*, as did Soltani et al. (2017), in concatenated analyses (but not in single gene analyses). Genetic distances (presented only for COI) were computed using the Kimura 2-parameter (K2P) distance model in a test version of Paup 4.0 (Swofford 2002) kindly provided by D. Swofford.

Criteria used for species delimitation

We used our genetic analyses as a complement to morphology for species delimitation. We also used DNA barcodes for the identification of female specimens, which are often challenging to identify in the *leachella* group. For species delimitation, particular attention was given to the structure of male genitalia. The morphology of male sterna, the colour of front tarsi and the shape of a tooth on the gena just behind the base of the mandible were also important characters. In females, sculptural differences were primarily used for species delimitation, in particular the punctuation of the terga (especially the disc of T4) and of the vertex, the length of the ocelloccipital distance and the shape of the apical clypeal margin. Vestiture colour was given low

priority for species delimitation given the known variation in this character, even if vestiture colour is useful for identification if geographic variation is considered. We recognize subspecies in a few cases for geographically well-separated, allopatric forms diverging from conspecific forms by either a single significant morphological feature, or by a small number of insignificant features, taking into account the molecular results. A significant morphological feature corresponds to morphological differences typically observed between species in the subgenus *Eutricharaea*; examples include significant and discriminating differences in tergal punctuation, the length of the ocell-occipital distance, or differences in the structure of the genital capsule. Insignificant features include weak differences in punctuation, differences in vestiture colour, or differences in integument colour. Taxa presenting a broad morphological cline (that is, intergradation of morphological features over a large geographic distance, typically over 100 km or so) were not separated as distinct subspecies. A rationale for recognizing subspecies is presented in each case. Overall, we favor a broad species concept, where geographically isolated forms are preferably treated as subspecies rather than split as distinct species.

Morphology

Morphology follows Michener (2007) and Praz (2017). The abbreviations T, S and OOD are used for metasomal terga, metasomal sterna and ocell-occipital distance, respectively. All pictures were taken using a Keyence VHX 1000 digital imaging system.

The females in the *leachella* group are notoriously difficult to identify, particularly in northwestern Africa, where four species occur, all of which exhibit snow white vestiture, unlike in southern Europe where vestiture colour can be used to separate at least *M. pilidens* from *M. leachella*, *M. anatolica* and *M. pusilla*. The lectotype of *M. argentata* (Figs 1–3) is a female specimen originating from northwestern Africa. To establish the identity of the lectotype of *M. argentata* with confidence, we first delimited operational taxonomic units based on morphology (mostly male characters) and molecular results; second, we associated 29 female specimens to these taxonomic units from northwestern Africa using DNA barcodes; these barcoded females served as reference specimens for morphological examination. This approach suggested that the punctuation of the vertex was a good discriminant character in northwestern Africa. We thus measured punctuation in confidently identified specimens (mostly DNA barcoded specimens, otherwise morphologically typical specimens from localities with males and females caught together; Suppl. material 1) and in the lectotype of *M. argentata* to allow for statistically robust comparisons. To do so, we measured the size of the punctures in a designated area of the vertex on pictures taken using a Keyence VHX 1000 digital imaging system with the stacking option turned off. The specimens were placed in a way that the left ocellus, the right margin of the compound eye and the occipital ridge behind the lateral ocellus were in sharp focus, with the preoccipital ridge more or less horizontal on the picture. Pictures were processed with the software ImageJ 1.48 (Abràmoff et al. 2004). A picture of a microscope stage micrometer taken with the

Keyence imaging system applying the same setting was used; using that picture, the scale was set with the “set scale” command in ImageJ.

Once the scale was set, we first rotated, if necessary, each picture so that the two lateral ocelli would form a horizontal line. We measured the ocelloccipital distance (OOD), defined as the shortest distance between the posterior margin of the left ocellus (including the black, shiny, circular margin of the ocellus) and the occipital ridge (Fig. 1). We then drew a horizontal line tangential to the posterior margin of the left ocellus, and a vertical line tangential to the right border of the left eye (Fig. 1). We placed a rectangle with dimensions $1.1 \times \text{OOD} \times 0.55 \times \text{OOD}$ so that its upper right corner was on the intersection of the two tangentials (Fig. 1). The area of each puncture within this rectangle was measured by drawing a circle or an ellipse on the puncture. A puncture along the margins of the rectangle was measured if more than half of its area was in the rectangle. For each puncture an estimate of the diameter was derived from its area (diameter equal to twice the square root of the area divided by pi), assuming that the puncture was a circle.

Material examined

Material from the following institutions has been examined. The type material has been examined by one of us (CP), and the distribution given for each species is based on material examined by CP.

| | |
|--------------|---|
| AMHN | American Museum of Natural History, New York, USA. |
| BMNH | Natural History Museum, London, UK. |
| CPCN | Collection of Christophe Praz, University of Neuchatel, Neuchatel, Switzerland. |
| CSE | Collection of Christian Schmid-Egger, Berlin, Germany. |
| ETHZ | Entomological Collection of ETH Zurich, Zurich, Switzerland. |
| MHNN | Muséum d’Histoire Naturelle de Neuchâtel, Neuchâtel, Switzerland. |
| MNHN | Muséum National d’Histoire Naturelle, Paris, France. |
| MZL | Musée cantonal de zoologie, Lausanne, Switzerland. |
| NHMD | Natural History Museum of Denmark, Copenhagen, Denmark. |
| NMB | Naturhistorisches Museum, Basel, Switzerland. |
| NMBE | Naturhistorisches Museum der Burgergemeinde Bern, Switzerland. |
| NMW | Naturhistorisches Museum, Vienna, Austria. |
| OLML | Oberösterreichisches Landesmuseum, Linz, Austria. |
| OUMNH | University Museum of Natural History, Oxford, UK. |
| PCYU | Collection of Laurence Packer, York University, Toronto, Canada. |
| SMFD | Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany. |
| SMNH | Steinhardt Museum of Natural History, Tel Aviv University, Israel. |
| USNM | Smithsonian institution, National Museum of National History, Washington, USA. |
| ZMHB | Museum für Naturkunde, Berlin, Germany. |

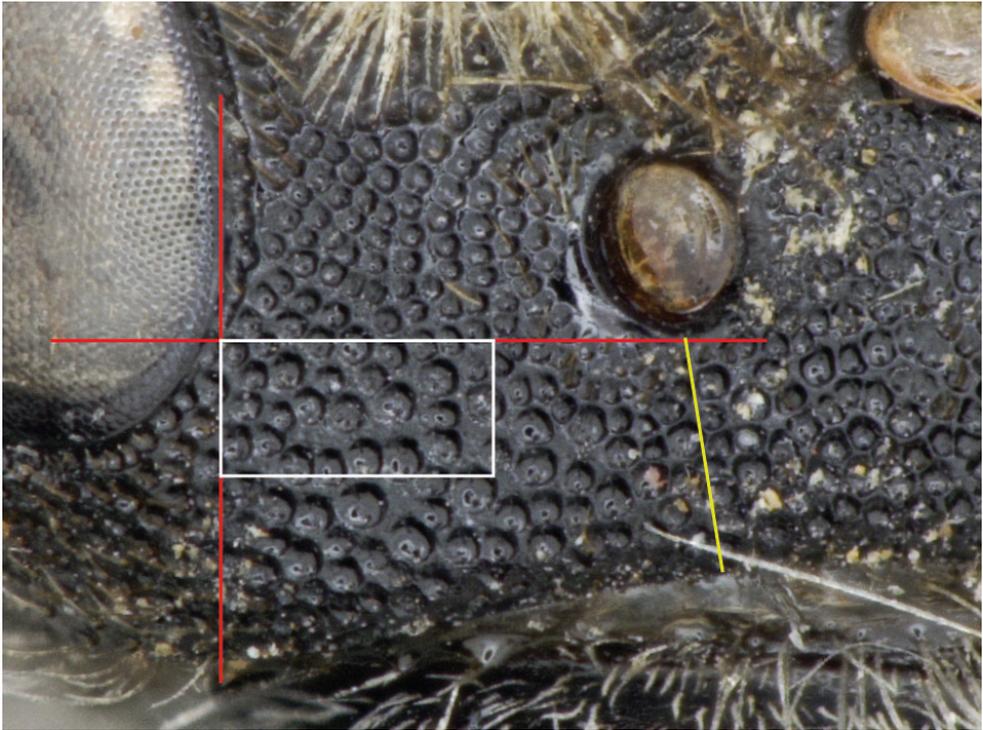


Figure 1. Vertex of the lectotype female of *Megachile argentata* (Fabricius, 1793), showing the ocellocapital distance OOD (yellow line), two tangentials placed behind the lateral ocellus and along the inner margin of the compound eye (red lines), and the white rectangle with dimensions $1.1 \times \text{OOD} \times 0.55 \times \text{OOD}$ within which the punctures were measured in our morphometric analyses.

Results

Lectotype of *Megachile argentata*

Identification of type specimens was performed after species delimitation had been done using combined molecular and morphological data (see below) but is presented first to settle the names of the different taxa before discussing their morphology and phylogenetic relationships.

Megachile argentata was described from “Barbaria”, a region corresponding to the coastal area of northern Africa from Algeria to Libya. The specimens available to Fabricius were collected by R. L. Desfontaines, probably in modern Tunisia or eastern Algeria [“régences de Tunis et d’Alger” (Beylik of Tunis and Ottoman Algeria); Dureau de la Malle 1838]. Depending on the author, this name was used until 1968 for one of the species currently known as *M. leachella* or *M. pilidens*, or for both. In early works these two species were probably lumped under *M. argentata* (e. g. Schenck 1861; Morawitz 1875). In England or in Scandinavia, where *M. pilidens* does not occur, *M. argentata* has long been used as the valid name for *M. leachella* (e.g., Thomson 1872; Saunders 1896;

Perkins 1925); the type species of *Eutricharaea* (*M. argentata*), described in Thomson's second volume of "Hymenoptera scandinaviae", thus confidently refers to *M. leachella*.

Pérez (1879) was possibly the first author to be aware of the presence of two species closely related to *M. argentata*, which he referred to as *M. dorsalis* (= *M. leachella*; see Gogala 1998) and *M. argentata* (probably =*M. pilidens*). Unfortunately, he wrongly associated with the precisely diagnosed female of *M. dorsalis* a male of a species of the *rotundata* group with modified front tarsi; this male was redescribed later as *M. burdigalensis* Benoist, 1940. Due to this erroneous sex association, confusion has long persisted on the identity of *M. dorsalis* (e. g. van der Zanden 1996; Banaszak and Romasenko 1998), until Gogala (1998) examined the type material of *M. dorsalis* and of *M. burdigalensis*, confirmed that the lectotype female of *M. dorsalis* was conspecific with *M. leachella*, and described both sexes of *M. burdigalensis*. Friese (1899a) was also aware of the presence of two distinct species in this group, and in his key to the males he recognizes one species (*M. argentata*) with a yellow spot of hairs along the margin of S4 (cf. Fig. 53; probably *M. leachella*, contrary to Pérez's use of the name *M. argentata*) and one species with a small tubercle covered with white hairs (cf. Fig. 23; *M. pilidens*), which he refers to as *M. xanthopyga* Pérez, 1895, a species native, according to him, to Northern Africa, probably because *M. xanthopyga* was described with no locality information in Pérez's "Mellifères de Barbarie" [the bees of Barbaria]; *M. xanthopyga* was in fact described from Sardinia and has since then been placed in synonymy with *M. schmiedeknechti* (Benoist 1940).

Also aware of the presence of two distinct species in this group, Alfken (1924) treated *M. argentata* as the valid name for the species currently known as *M. leachella*; based on the male described by Pérez he considered *M. dorsalis* to be a species allied to *M. flabellipes* Pérez, 1895 in the *rotundata* group (thus likely *M. burdigalensis*); and he described *M. pilidens* for the second species. His differential diagnosis of both sexes of *M. argentata* and *M. pilidens* (Alfken 1924) clearly points to *M. leachella* and *M. pilidens* in their current usage. After this, *M. argentata* has mostly been used for *M. leachella* (e.g., Schmiedeknecht 1930; Erlandsson 1960) until 1967; Benoist (1940) however, used *M. argentata* for *M. pilidens* and "*argentata* var. *dorsalis*" for *M. leachella*.

Unfortunately, although Alfken clearly differentiated these two widespread European species, he did not examine the type specimen of *M. argentata*. Hurd (1967) examined four specimens preserved in the Fabricius collection in Copenhagen and designated a female specimen as the lectotype (Figs 1–3). He briefly describes this specimen and writes that it was not conspecific with the species known as *Megachile argentata* auct. (= *M. leachella*) in Europe, with no further details. Based on this description and presumably on additional notes sent by Hurd, but without examining the type, Rebmann (1967b) also stated that the type of *M. argentata* was not conspecific with the northern European taxon known as *M. argentata* auct. (= *M. leachella*), but that it was instead a member of the *rotundata* group. He thus resurrected the name *M. leachella* for the species so far referred to as *M. argentata* auct. and treated *M. argentata* as a *nomen dubium* in the *rotundata* group. This treatment was rejected by Warncke (1986), who argued "that the change of the name [of *M. argentata*] was fully unnecessary and that [Hurd's] lectotype designation was erroneous" since, according to him, the type material of



Figures 2, 3. Lectotype female of *Megachile argentata* **2** dorsal view **3** head in front view.

M. argentata should be deposited in the Defontaine collection in Paris, where it could not be located. He thus resurrected *M. argentata* as the valid name for *M. leachella*, a decision that was not followed (e.g., Westrich 1989; Gogala 1998; Banaszak and Romasenko 2001; Amiet et al. 2004; Scheuchl 2006). More recently, Schwarz and Gusenleitner (2011) examined the lectotype of *M. argentata* and published pictures and a redescription. They suggested that *M. argentata* was possibly conspecific with the species currently known as *M. pilidens* but refrained from formally placing *M. pilidens* in synonymy until more material from Northern Africa could be studied.

We have examined the lectotype female of *M. argentata* (Figs 1–3). This specimen perfectly agrees with the original description; we are also confident that it originates from northern Africa (see below). The lectotype undoubtedly belongs to the *leachella* group of species, based on the absence of a fovea laterally on T2, the presence of two spots of appressed, white hairs on the disc of T6 (Fig. 2), and the sculpture of the apical margin of the clypeus (Fig. 3). The latter two criteria exclude with certainty the taxon of the *concinna* complex present in northwestern Africa, *M. pusilla* (Soltani et al. 2017), which is smaller and characterized by reduced spots of appressed white hairs on the disc of T6 and the narrowly emarginate apical margin of the clypeus, with a comparatively wide impunctate premarginal area. The lectotype thus belongs to one of three species present in northwestern Africa, namely *M. pilidens*, *M. leachella* or *M. inexpectata*, which probably all occur in Algeria and Tunisia, the type locality of *M. argentata*.

The separation of the females of these three taxa can be difficult: unlike in central and northern Europe, the vestiture of both *M. leachella* and *M. pilidens* is snow-white in northern African populations, just as in *M. inexpectata*. Moreover, the differences in the punctuation of the disc of the terga, especially T4, between *M. leachella* and *M. pilidens* appear to be less pronounced in northwestern Africa than in Europe, where this characteristic mostly (but not always) allows for the separation of both species (Amiet et al. 2004). The examination of 29 northwestern African females of the *M. leachella* group (excluding *M. pusilla*) identified using DNA barcodes revealed several morphological features allowing for a separation of the northwestern African females of *M. leachella*,

Table 1. Comparison of the females of *Megachile inexpectata*, *M. leachella albipila* and *M. argentata* in northwestern Africa.

| Characters | <i>Megachile inexpectata</i> | <i>Megachile leachella albipila</i> | <i>Megachile argentata</i> |
|------------------------------------|--|---|---|
| Vestiture | | | |
| Vestiture of dorsal side of scutum | Entirely consisting of white hairs; short scale hairs present over entire disc of scutum (Fig. 28) | As in <i>M. inexpectata</i> | scutum covered with intermixed light and dark hairs; short scale-like hairs mostly present anteriorly and posteriorly; less abundant on central parts of disc of scutum |
| Lateral hairs on terga | Dark, erect hairs restricted to lateral parts of T6, sometimes T5 (Fig. 25) | As in <i>M. inexpectata</i> (Fig. 34) | Dark, erect hairs present laterally on T3-T6 (Fig. 15) |
| Light hairs on disc of T6 | Sometimes forming one large spot of hairs (Fig. 25) | Mostly forming two separated spots of hairs | always forming two well-separated spots of hairs (Fig. 15) |
| Sculpture | | | |
| Punctuation of vertex | Dense, punctures small (diameter on average 40 µm) (Fig. 27) | As in <i>M. inexpectata</i> , puncture diameters 35–40 µm, punctuation slightly less dense, often with shagreened interspaces (Fig. 41) | Punctures larger (on average 50 µm), punctuation less dense, interspaces up to one puncture diameter, surface of interspaces smooth (Figs 1, 20) |
| Punctuation of disc of T4 | Dense, interspaces mostly smaller than one puncture diameter (Fig. 26) | Mostly sparse, interspaces mostly larger than one puncture diameter (Fig. 34) | Dense, interspaces smaller than one puncture diameter (Fig. 19) |

M. pilidens and *M. inexpectata* (Table 1). A separation of *M. pilidens* is mostly possible, but the separation of the other two species is sometimes difficult. Based on these features (Table 1), the lectotype of *M. argentata* clearly agrees with *M. pilidens*. The punctuation is dense on the disc of T4 (Fig. 2); there are numerous erect, dark setae laterally on T4 and T5 (a condition not observed frequently in *M. inexpectata* and *M. leachella* in northwestern Africa). The vestiture is snow white in northwestern African populations of *M. pilidens*, and nowhere else, strongly suggesting that the lectotype indeed originates from “Barbaria”. Fabricius’s original description mentions that the head and the thorax have “ash-coloured” vestiture, which corresponds better to the northern African populations of *M. pilidens*, than to those of *M. leachella* (Table 1). The description also mentions that the top of the metasoma is black, the margin of the segments white; this possibly refers to the short, dark vestiture on the disc of the terga, which is more extensively developed in *M. pilidens* than in *M. leachella* in northwestern Africa.

This identification is confirmed by our measurements of the OOD and of the size of the punctures on the vertex (Figs 1, 4): OOD-values were significantly different across the three species (Fig. 4) (ANOVA, $F=12.03$, $df=2, 24$, $P<0.001$); Tukey’s post hoc test suggests that the OOD values were significantly larger in *M. pilidens* than in the other two species ($P<0.026$ in both cases), which did not significantly differ ($P=0.66$). The OOD value for the lectotype of *M. argentata* was 361 µm, in the range of the values measured for *M. pilidens*, but not for the other two species (Fig. 4). Lastly, the average diameters of the punctures on the vertex were significantly different across the three species (ANOVA, $F=71.76$, $df=2, 24$, $P<0.001$): Tukey’s post hoc test suggests that all three species have significantly different average puncture diameters (*M. leachella* versus *M. inexpectata*: $P=0.043$; other comparisons $P<0.001$). With an average puncture diameter of 50.8 µm, the lectotype of *M. argentata* was again in the range of values measured for *M. pilidens*, but not for the other two species. Combining

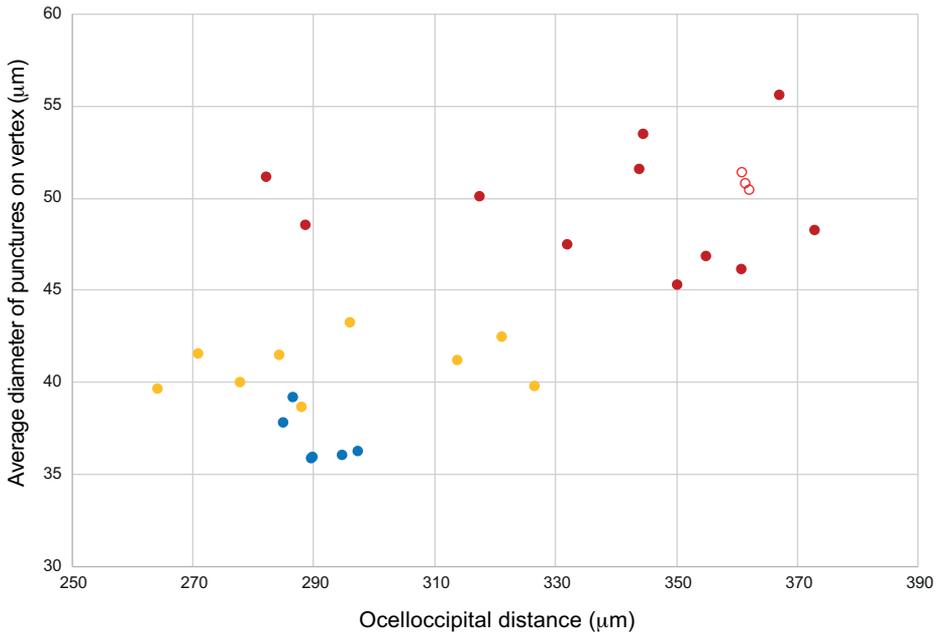


Figure 4. Results of the morphometric analyses of female specimens of *Megachile argentata* (red circles), *M. inexpectata* (yellow) and *M. leachella* (blue); three measurements of the lectotype of *M. argentata* are shown as open red circles; relationship between the ocelloccipital distance and the average diameter of the punctures included in the white rectangle of Fig. 1.

the OOD-values with the average diameter of the punctures on the vertex allowed for an unambiguous separation of *M. pilidens* and the other two species, which were more difficult to separate; three replicate measurements of the lectotype of *M. argentata* clearly clustered within *M. pilidens* (Fig. 4).

In summary, the identity of the lectotype designated by Hurd (1967) is clearly established as *M. pilidens*; it is likely that this specimen originates from northwestern Africa, since it has snow white vestiture; and Fabricius' original description, although vague, better corresponds to *M. pilidens* than to any other species of the *leachella* group. The synonymy of *M. pilidens* with *M. argentata* represents a nomenclatural change for a widely distributed species. We briefly discuss here alternative options regarding the treatment of this name.

The first option would be to follow Warncke's (1986) view that the lectotype was not part of the type series and more generally that the identity of *Megachile argentata* auct. should not have been changed, as has been done for other names by Linnaeus [e.g., *M. centuncularis* (Linnaeus, 1758), where a putative syntype was in fact *M. ligniseca* (Kirby, 1802)], or by Fabricius. A notorious example is *M. rotundata*: the lectotype, which was in agreement with the original description, was in fact a male of *M. centuncularis*. Roberts (1974) proposed to suppress this lectotype and to designate a neotype corresponding to *M. rotundata* auct. Although *M. rotundata* auct. is probably not native to Denmark (Erlandsson 1960; Holm 1982), the type locality

of *M. rotundata*, the proposal was accepted because of the economic importance of *M. rotundata* and the large number of scientific papers using this name (Roberts 1978). In the case of *M. argentata*, discarding the current lectotype does not appear appropriate, for the following reasons. First, we do not agree with Warncke (1986) that the lectotype designation was erroneous, for reasons explained above. Second, it would not be correct to state that the lectotype of *M. argentata* cannot be identified using morphology, as demonstrated above. Third, *M. argentata* has been used as a valid name until 1967 (although mostly for *M. leachella*, but also for *M. pilidens*), and in fact in many museums, specimens of *M. pilidens* and *M. leachella* are still mixed under *M. argentata*. Fourth, and most importantly, according to our species delimitation hypothesis (see below), another name has priority over *M. pilidens*: *M. schmiedeknechti*, a name currently in usage (e. g., Rebmann 1968; Rasmont et al. 1995; Nieto et al. 2014; Balzan et al. 2016; Cassar and Mifsud 2020). Therefore, neither a protection of *M. pilidens* nor of *M. schmiedeknechti* appear to make sense, since either approach would result in a major nomenclatural change. Furthermore, a reversal to the pre-1967 situation with *M. argentata* being the name of *M. leachella* would also constitute a major nomenclatural change since all current works use the latter name.

Two additional aspects need to be discussed. First, given that the lectotype of *M. argentata* originates from an undersampled geographic region (Algeria and Tunisia), could it belong to an additional, hitherto unknown taxon? We consider this possibility as very unlikely. In contrast to other groups of bees, such as osmiine (e.g., Müller 2012, 2022) or *Andrena* species (e.g., Wood 2021; Wood et al. 2021; Praz et al. 2022), most species of *Megachile* have broad distributions. We have examined hundreds of *Eutricharaea* from Morocco and Tunisia (admittedly fewer from Algeria); while northwestern Africa still hosts numerous unclear *Eutricharaea* taxa, these all belong to the more diverse *rotundata* group. The chance that an unknown species of the *leachella* group still exists in northwestern Africa is therefore considered to be small. The numerous barcoded specimens presented here also minimize the chance that additional cryptic diversity is found in this group in northwestern Africa.

Second, there are minimal morphological differences between northwestern African populations of “*M. pilidens*” (in the following paragraph “*argentata*”), and other western Palearctic populations of this taxon (“*pilidens*”): vestiture is snow white in “*argentata*” (Fig. 15), except the dark vestiture on the thorax; it is yellowish brown in “*pilidens*” (Fig. 16), including on the thorax; in addition, the fringe of hairs on the margin of T5 in the male is continuous in “*argentata*” while it is reduced in other populations (except in populations of the taxon currently named *M. schmiedeknechti*). On the Island of Pantelleria, located between Tunisia and Sicily, the white form (“*argentata*”) occurs, while on Sicily the regular-looking “*pilidens*” occur; in Malta, populations are morphologically divergent and have been attributed to *schmiedeknechti* (see below). Given these differences, could future studies suggest that “*argentata*” and “*pilidens*” represent two closely related, distinct, allopatric species? We argue that these two forms are conspecific, for the following reasons. First, we do not consider the minimal morphological differences between them as indicative of distinct species,

based on comparisons with other species of the *leachella* group. Variation in vestiture colour is for example larger in *M. leachella* than in *M. argentata/pilidens*. Second, our genetic data, including both mitochondrial and nuclear markers, also strongly suggest that “*argentata*” and “*pilidens*” belong to one unique evolutionary lineage; there were minimal differences between both, although these differences were considerably smaller than within-species differences in *M. leachella*. Third, a few specimens of “*pilidens*” examined from southern Spain have the vestiture lighter than in the rest of continental Europe, bridging the small morphological gap between “*pilidens*” and “*argentata*”.

Based on the evidence assembled here, we thus place *M. pilidens* in synonymy with *M. argentata* (syn. nov.).

Holotypes of *Megachile inexpectata* and *M. striatella*

Megachile inexpectata was described from a single male specimen collected in Mut, Turkey in 1965 by Maximilian Schwarz. The holotype is in poor condition, probably because it has been relaxed for the preparation of the genitalia. It is labeled as follows (here and throughout the paper, the order of labels starts with the label closest to the body): 1. [a cardboard piece to which the genitalia and a T7 are glued]; 2. “Türkei Mut 12.VI.1965 leg. M. Schwarz”. 3. [A yellow label with number 27, handwritten]. 4. “*inexpectata* n. sp. ♂ det. Dr Rebmann 1966”. 5. “Typus” [printed on red paper, with SMFH 1866, handwritten on the reverse side]. 6. Senckenberg-Museum Frankfurt/Main. 7. “*Megachile walkeri* ♂? D. B. Baker det. 1990”. The examination of the holotype reveals the following issue. The nearly entire metasoma, including T7, is still attached to the pinned specimen. The genitalia have been extracted and are glued on a piece of cardboard attached to the same pin (Fig. 31); an additional T7 is glued to the piece of cardboard alongside the genitalia. Body and genitalia do not appear to be conspecific: the gonostylus is like that of *M. walkeri*, as indicated in the original description of *M. inexpectata* (Rebmann 1968: fig. 11), thus with a short, blunt preapical process (Figs 30, 31). Only two Palearctic species of *Eutricharaea* species have such a gonostylus: *Megachile walkeri* and the species hitherto referred to as *M. inexpectata*. The pinned specimen, however, does not belong to either species, as there is a pointed tooth behind the mandibular base (cf. Fig. 12), which suggests that it belongs either to *M. leachella* or to a species of the *concinna* complex. Both *M. walkeri* and *M. inexpectata* have a blunt, truncate tooth behind the mandibular base, as in *M. pilidens*.

The holotype of *M. striatella* Rebmann, 1968, also in poor condition, is labeled as follows: 1. a cardboard with the genitalia glued; 2. “El Kantara [Algeria], 7. Juli 1904, Dr. Gulde”. 3. Typus [printed on red paper]; SMF H 1593 [written on reverse side of label]. 4. *Megachile concinna* D. B. Baker det. 1990. 5. Senckenberg Museum Frankfurt am Main. Examination of this specimen reveals that the body of the holotype is most probably *M. inexpectata*, as indicated by the lack of tooth behind the mandibular base and the conspicuous patch of yellow hairs medially on S4 (cf. Fig. 29); T7 is missing and not found alongside the genitalia. The latter, glued on a piece of paper, are like in the *concinna* complex (cf. Fig. 14, 66), with a simple gonostylus. Since all

members of the *concinna* complex have a distinct tooth behind the mandibular base, we conclude that the body of the holotype is not conspecific with the genitalia. Male paratypes clearly belong to the *concinna* complex, probably to *M. pusilla*, the only member of the *concinna* complex so far known in Algeria (Soltani et al. 2017).

Rebmann relaxed his specimens during 24 hours for the preparation of the hidden sterna (Rebmann 1968); during this process, the locality labels have to be removed. We hypothesize that the body of *M. inexpectata* and of *M. striatella* have been associated with the wrong genitalia during preparation. Following this hypothesis, the genitalia and T7 glued on a piece of cardboard beneath the holotype of *M. inexpectata* probably belong to the pinned body of the holotype of *M. striatella*; and the genitalia of the holotype of *M. striatella* probably belong to the pinned specimen of the holotype of *M. inexpectata*. This hypothesis is further substantiated by the following fact: we examined numerous bees collected by M. Schwarz during his 1965 trip to Turkey; all of them were pinned using entomological pins with a glass head (hereafter “new pin”), a type of pin little used, possibly not at all, at the beginning of the century, when the type series of *M. striatella* was collected in Algeria. All paratypes of *M. striatella* have another type of pin (“old pin”), where the head is made of a small piece of curled metal. The body of the holotype of “*M. striatella*”, although supposedly collected in 1904, is pinned with a pin of the new type, just like all the specimens collected by M. Schwarz in Turkey, while the body of the holotype of “*M. inexpectata*” is pinned with an old pin. The most probable hypothesis is therefore that the genitalia and body of both holotypes of *M. striatella* and *M. inexpectata* have been mixed during relaxation. All dissected specimens in the Rebmann collection have been examined, and no additional inconsistencies (in particular, a missing T7) have been found.

Assuming that our hypothesis is correct, we are left with the following two possibilities to resolve this confused taxonomic situation. The first possibility would be to submit a request to the International Commission on Zoological Nomenclature to discard current holotypes and to designate neotypes for both taxa. The second possibility is to invoke article 73.1.5 of the code, which states that “if a subsequent author finds that a holotype which consists of a set of components (e.g. disarticulated body parts) is not derived from an individual animal, the extraneous components may, by appropriate citation, be excluded from the holotype”. Following this last approach, we assume that the genitalia (but not the body) of the specimens originate from the correct location (Mut, Turkey for the genitalia of the holotype of *M. inexpectata* and Kantara, Algeria for the genitalia of the holotype of *M. striatella*), exclude the body of these two specimens from the holotype, and declare that only the genitalia serve as name-bearing types for these two taxa. Based on current knowledge of this group of bees in Turkey and Algeria, only *M. inexpectata* (see Norfolk and Dathe 2019; Boustani et al. 2021; Praz et al. 2021) has the genitalia of the “*walkeri*” type in Turkey; and only *M. pusilla* has a simple gonostylus in Algeria. We therefore place *M. striatella* in synonymy with *M. pusilla* (syn. nov). The cardboard with the genitalia (Fig. 31) and T7 of *M. inexpectata* has been placed onto a separate pin, together with all the labels (see above). An eighth label has been added, handwritten on red paper: “Holotypus *Megachile inexpectata*

Rebmann C. Praz 15.09.2021". The body of the specimen is kept next to this holotype, with the following two new labels. 1. "*Megachile* cf. *pusilla* det C. Praz 2021". 2. (handwritten on white paper) "Specimen originally associated with the holotype genitalia of *M. inexpectata* Rebmann. Of no type value. C. Praz 2021". In addition, one male specimen of *M. inexpectata* with the following label information: 1. "Jordan W, 30km W Tafila, 2.5.1996 leg. Marek Halada" and 2. "*Megachile inexpectata* Rebmann det. C. Praz 2021" is deposited next to the holotype (genitalia). Under *M. striatella*, the cardboard with the genitalia has been placed onto a separate pin with the label "Holotypus *Megachile striatella* Rebmann C. Praz 15.09.2021". The body of the specimen is kept next to this holotype, with the following labels: 1. "*Megachile* cf. *inexpectata* det C. Praz 2021". 2. (handwritten on white paper) "Specimen originally associated with the holotype genitalia of *M. striatella* Rebmann. Of no type value. C. Praz 2021".

Phylogenetic analyses

COI

The labelling of the taxa in the tree is done in anticipation of our final delimitation and taxonomic decisions. For clarity, specimens of *M. argentata* from outside of northwestern Africa are labeled as "*pilidens*", those from Sardinia and Malta as *M. schmiedeknechti*. The phylogenetic tree (Fig. 5) inferred using the mitochondrial gene COI recovered all species as monophyletic group, except for *M. viridicollis*, which formed a grade from which *M. anatolica* arose. Support was maximal (Bootstrap support of 100%) for all species except for *M. leachella* (67%) and *M. anatolica* (73%).

Within-species distances in the taxa of the *concinna* complex have been presented elsewhere (Soltani et al. 2017) and are not discussed here. Within-species distances were small (less than 0.2%) in *M. walkeri*. In *M. inexpectata*, there were two clades, one including specimens from Israel, and one with northwestern African specimens. Genetic distances within these clades were low (0–0.6%), and the average distance between these clades was 3.4% (minimum 2.9, maximum 4.0%).

By contrast, within-species genetic distances were considerable in *M. leachella*. First, two specimens from Crete (treated here as a new subspecies, *M. leachella cretica* ssp. nov.) were divergent and formed a well-supported clade that was sister to all other specimens of *M. leachella* (Fig. 5). Genetic distances between this clade and other specimens of *M. leachella* were on average 5.3% (minimum 4.4, maximum 6.1%). Within the rest of *M. leachella*, there was weak structuring, with one clade composed of specimens from Iran, Kyrgyzstan, Israel and Greece, and one clade of all specimens from northwestern Africa (delineated here as the subspecies *M. leachella albipila* Pérez, 1895), all specimens from the Sardinia, and two specimens from Cyprus (delineated here as the subspecies *M. leachella densipunctata* ssp. nov.); several specimens from different localities (Italy, Austria, the UK, Spain, etc) formed a grade outside of these two clades. The average genetic distance among all specimens of *leachella* (except for the specimens from Crete) was 0.9% (minimum 0, maximum 2.5%). The two individuals

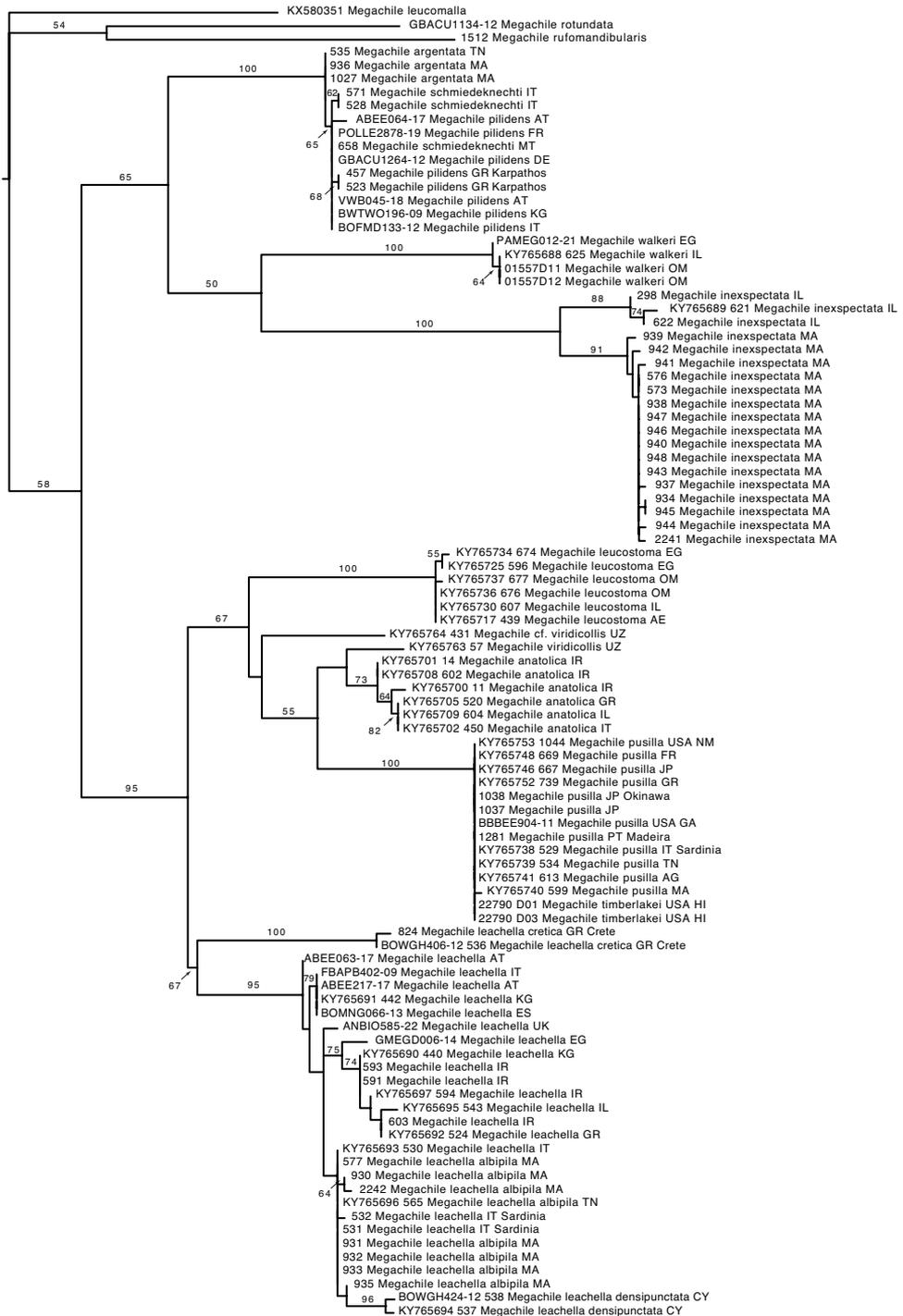


Figure 5. Best tree found in maximum likelihood analyses of sequence data of the mitochondrial gene COI showing the phylogenetic relationships among the Palearctic species of the *leachella* group of *Megachile* (*Eutricharaea*). Bootstrap support values are based on 1000 bootstrap replicates.

from Cyprus (belonging to the subspecies *M. leachella densipunctata* ssp. nov.) were separated from other specimens of *M. leachella* (excluding those from Crete) by an average distance of 1.3% (minimum 0.8, maximum 2.5%).

Within *M. argentata*, within-species genetic distances were small (max: 0.5%). Three specimens from northwestern Africa were weakly divergent from all other specimens (average genetic distances 0.2%; minimum 0.2, maximum 0.5%). Two specimens from Sardinia, attributed to the subspecies *M. argentata schmiedeknechti*, were only weakly separated from all other specimens (average genetic distances 0.2%; minimum 0.2, maximum 0.5%). One specimen from Malta, attributed to *M. argentata schmiedeknechti*, had identical sequence with several specimens from central Europe (Fig. 5).

Nuclear genes

Single genes phylogenies based on opsin and CAD (data not shown) were little resolved, but all species were recovered as monophyletic groups, except as follows: *Megachile pusilla* did not form a monophyletic group in analyses of opsin, and *M. leucostoma* in analyses of CAD; in analyses of opsin, some populations of *M. leachella* shared an allele with *M. anatolica* and *M. viridicollis* (see Soltani et al. 2017). In analyses of the concatenated, two-genes dataset (Fig. 6), all species formed monophyletic groups, except *M. leucostoma*, which formed an unresolved polytomy with one specimen of *M. viridicollis* and a clade containing all specimens of *M. anatolica*. Within *M. leachella*, two specimens from Cyprus (*M. leachella densipunctata* ssp. nov.) formed a clade that was sister to a clade containing all other specimens. There were two clades within the latter clade, one including specimens from Kyrgyzstan, Greece and Israel; and one including all other specimens. Unlike in COI-based phylogenies, the only sequenced specimen from Crete (*M. leachella cretica*) was not strongly divergent from *M. leachella sensu lato*. This specimen was more closely related to western European and western Mediterranean populations, than to the nearby southeastern European populations, in agreement with some morphological characters (see below).

Within *M. argentata*, the only sequenced specimen from northwestern Africa was sister to all other specimens; both specimens from Sardinia (*M. argentata schmiedeknechti*) were weakly divergent from two specimens from Greece and Switzerland.

Species delimitation

Megachile argentata

This species is sculpturally very uniform throughout its range. The colour of the vestiture is however variable geographically. As discussed above, the populations from northwestern Africa (Fig. 15) have lighter vestiture than the continental populations (Fig. 16); similarly light-coloured populations are also found on the Island of Pantelleria. We do not recognize different subspecies for continental (“*pilidens*”) and northwestern African (“*argentata*”) populations because the morphological differences are minor, and because southern Iberian specimens appear to be intermediate.

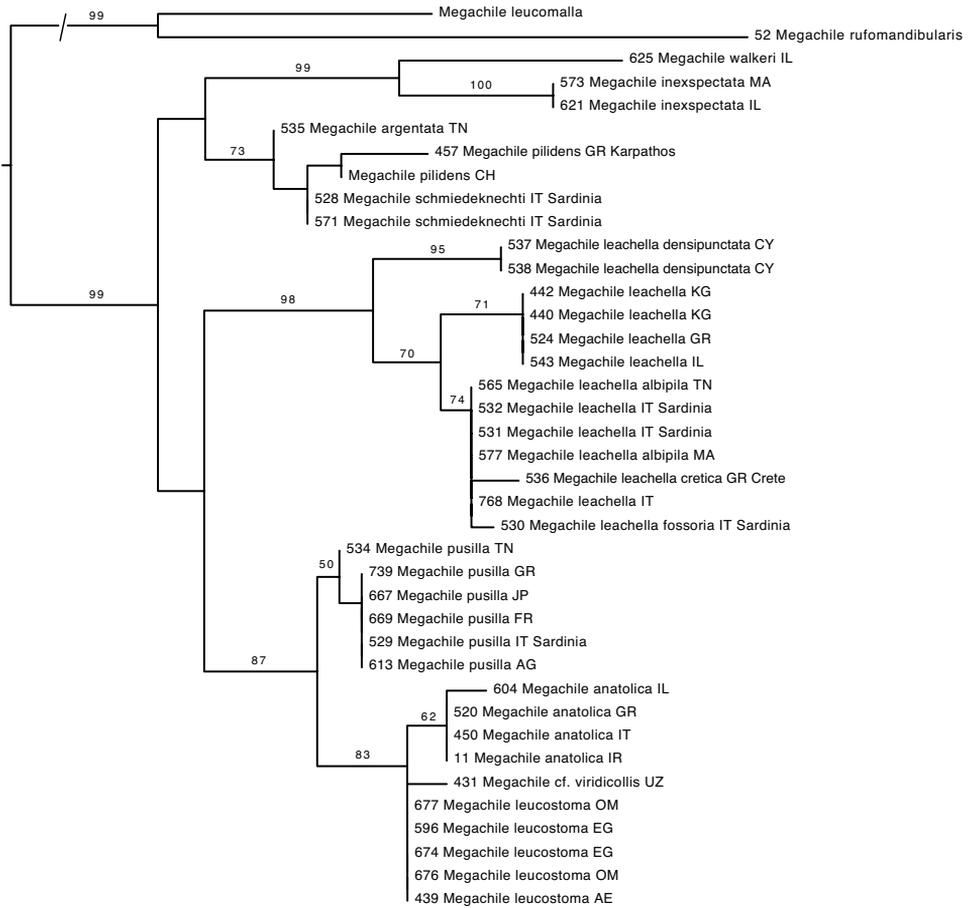


Figure 6. Best tree found in maximum likelihood analyses of sequence data of the two nuclear genes *lh* rhodopsin and *CAD* showing the phylogenetic relationships among the Palearctic species of the *leachella* group of *Megachile* (*Eutricharaea*). Bootstrap support values are based on 1000 bootstrap replicates. The oblique line along the branch joining the outgroup taxa and the ingroup indicates that this branch has been shortened for better graphic representation.

The vestiture is red-orange on the Islands of Malta (Fig. 17), and yellow-orange on Corsica and Sardinia (Fig. 18); this insular form has so far been referred to as *M. schmiedeknechti*, described from Sardinia. van der Zanden (1983: 138) stated that the form found in Malta was not conspecific with *M. schmiedeknechti* due to subtle differences in punctuation, and treated the Maltese form as *M. xanthopyga*, probably assuming that *M. xanthopyga* had been described from northern Africa (see above). Our genetic data does not support the recognition of *M. schmiedeknechti* as a distinct species. Rebmann (1968) indicated that *M. schmiedeknechti* and *M. pilidens* differed in the structure of S5 and S6; we have dissected and examined several males of both taxa and did not find any consistent difference, neither could we confirm the characters presented by Rebmann (1968). Moreover, Rebmann (1968) mentioned the presence

of *M. pilidens* on the Island of Sardinia; we have not been able to locate specimens to verify this hypothesis, which probably relies on misidentified specimens. Benoist (1940: 65) mentions that *M. schmiedeknechti* occurs in Southern France [Var: Callian]. A specimen from Callian, Var, leg. Berland 1924, is preserved in MNHN under *M. schmiedeknechti*; although it bears the identification label "*M. schmiedeknechti* det. van der Zanden", it is a female specimen of *M. melanopyga*. It is probable that Benoist's record of *M. schmiedeknechti* from Callian is based on this specimen. Mentions of *M. schmiedeknechti* (or from *M. xanthopyga*) from northern Africa (e.g., Friese 1899a; Benoist 1940) probably refer to the erroneously assumed type locality of *M. xanthopyga*.

Contrasting the current view, we propose to treat *M. schmiedeknechti* as a subspecies of *M. argentata*, for the following reasons. First, only vestiture colour appears to separate it from continental (including northwestern African) populations, and no sculptural difference, except that tergal punctation in both sexes is finer and denser in *M. schmiedeknechti*, especially in the female; as discussed above, vestiture colour is variable in the *leachella* group and in bees in general. Second, DNA barcodes are shared or very similar between continental and insular forms (Fig. 5), unlike in other taxa restricted to Corsica and Sardinia, such as *Bombus (terrestris) xanthopus* (Kriechbaumer, 1870) (see note under table 4 in Williams et al. 2012; Williams 2021) or *Andrena antonellae* Praz & Genoud, 2022 (Praz et al. 2022). Third, in contrast to Sardinia and Corsica, the Island of Malta was connected to the Italian mainland at the end of the last glaciation (Furlani et al. 2013), suggesting that Maltese populations of *M. schmiedeknechti* may not have been isolated from continental ones for more than one glaciation cycle. Lastly, a form of *M. argentata* with partly orange scopa is known from the Island of Karpathos (Greece), indicating that the orange vestiture is not unique to *M. schmiedeknechti*. The following hypothesis can be formulated to explain the presence of this colour form of *M. argentata* on the Islands of Corsica, Sardinia and Malta. This colour morph may have been more widely distributed during or just after the end of the last Glaciation, explaining why it is currently found on distantly located Islands. After the end of the last glaciation, this orange form may have been replaced by the regular looking form currently present everywhere in Europe, possibly from an eastern refugium, except on these three Islands. This scenario could also explain why a slightly orange-coloured form is present on the Island of Karpathos, located over 1000 km from Malta. An alternative hypothesis is that the populations of *M. argentata schmiedeknechti* in Malta has independently converged to the orange colour observed on Sardinia and Corsica. Yet another possibility is that *M. argentata* colonized Malta or either Corsica or Sardinia from continental populations long ago; divergence and isolation may have resulted in the appearance of the orange vestiture condition, and then one event of long-distance dispersal could have enabled exchanges between Malta and either Corsica or Sardinia. Since *M. argentata* only rarely nests in dead wood, we consider this hypothesis as unlikely; a long-distance dispersal event between either Corsica or Sardinia and Malta, appears far less likely than dispersal between southern Italy and Malta.

We recognize *M. schmiedeknechti* as a valid subspecies of *M. argentata* and propose the following new combination: *Megachile argentata schmiedeknechti*, stat. nov. This subspecies is morphologically well characterized, geographically well-delimited and no intermediate form is known to exist (except for the populations found

on the Island of Karpathos, which are not located near the contact zone between *M. argentata schmiedeknechti* and the continental form). The main argument for treating this insular form as a subspecies and not simply as a geographic form is the abrupt contact zone with no transitional populations between Malta and the Italian mainland. Such an abrupt transition may be indicative of some reproduction interference between both forms, and suggests that the recognition of *schmiedeknechti* as a distinct conservation unit is meaningful. We do not recognize a distinct subspecies for the populations of Karpathos because the phenotypic differentiation of these populations with respect to those found in mainland Greece is weak. Our treatment of the Maltese populations as belonging to that subspecies has to be considered as tentative. Future work including more in-depth genetic analyses should further examine the relationships between mainland European, insular and northern African populations of *M. argentata*.

Megachile inexpectata

This taxon forms two putatively allopatric populations, one from the Sinai Peninsula to southern Turkey (eastern populations), the other in northwestern Africa (western populations). The mitochondrial genetic divergences between these two populations were considerable (3.4% in COI analyses; Fig. 5), but morphological differentiation or nuclear genetic differences (Fig. 6) were weak. The only character that separates these two populations is the white vestiture on the disc of T6: in eastern populations, this vestiture consistently forms a single spot (Fig. 25), while in western populations, two spots are often (but not always) separated by a thin line of black hairs, as in *M. leachella* (cf. Figs 32, 33, 36). We consider these genetic and morphological differences to be weak and do not recognize distinct subspecies within *M. inexpectata*.

Megachile leachella

Unlike *M. argentata*, *M. leachella* exhibits considerable morphological variation over its wide range, including variation in vestiture colour, in sculpture and in the structure of the genital capsule. There was also considerably more genetic structuring in *M. leachella* than in *M. argentata* (Figs 5, 6). Both taxa have comparable ranges, although the distribution of *M. leachella* expands further north than that of *M. argentata*. One explanation for this elevated variation within *M. leachella* is the association of this species with sandy habitats, which are not continuously distributed in central and southern Europe. Because some of the morphological variation in *M. leachella* corresponds to geographically isolated forms, we propose the recognition of several subspecies. Some of these forms exhibit pronounced morphological or genetic differences and could well be treated as distinct species. Since none of these delineated forms co-exists in sympatry with the regular-looking *M. leachella*, and since there is a continuum from weakly to strongly differentiated forms, we prefer a broad species-concept and the recognition of one widely distributed species with the most conspicuous forms split as subspecies.

In continental Europe and in the UK, phenotypic variation is essentially restricted to vestiture colour in the female sex (Schwarz and Gusenleitner 2012). In the UK, *M.*

leachella has a bright yellowish vestiture (Fig. 32), a condition not observed in continental Europe, where a grade is observed from snow-white vestiture in southern Europe (cf. Fig. 33) to gradually darker, grey-brown vestiture in central and northern Europe. The punctuation of the vertex appears to follow a similar pattern: in southern Europe, the punctuation is fine and dense (e.g., cf. Figs 41, 43); it becomes coarser towards the north and in the UK (Fig. 40). Since this pattern in vestiture colour and punctuation does not allow for the delineation of clearly delimited taxa, we do not recognize subspecies in continental Europe.

The populations from northwestern Africa (from Tunisia to Morocco) exhibit a striking difference in the structure of the genital capsule: the gonostylus has a short preapical process (Fig. 55), much shorter than anywhere else (Figs 54, 56). For this reason, the northwestern African populations are treated as a distinct subspecies, *Megachile leachella albipila* stat. nov. We do not recognize this taxon as a distinct species, for the following reasons. First, there is variation in this genital character, as the length of the preapical process of the gonostylus in northwestern African populations and in other populations of *M. leachella* is variable (e.g., Figs 54, 56), although the process is never as long in northwestern African as elsewhere. Second, *M. leachella leachella* appears to be replaced by *M. leachella albipila* in northwestern Africa; if both taxa were demonstrated to maintain distinctiveness in sympatry, they should be recognized as distinct taxa, but such evidence is currently lacking. Third, splitting *M. leachella albipila* as a distinct species would render *M. leachella* paraphyletic according to our genetic analyses (Figs 5, 6); while paraphyletic species are theoretically possible, we favor the delineation of monophyletic species. Fourth, our genetic analyses including both mitochondrial and nuclear genes suggest little differentiation between *M. leachella albipila* and central European *M. leachella*; the other subspecies of *M. leachella* are genetically more divergent from nominal populations of *M. leachella* (Figs 5, 6). As a final note, the following hypothesis for the divergent genital structure of *M. leachella albipila* can be formulated: it is possible that the northwestern African population of *M. leachella* are the outcome of past introgression with *M. pusilla*, given that the genital structure of *M. leachella albipila* (Fig. 55) is intermediate between that of *M. leachella leachella* (Figs 54, 56) and *M. pusilla* (Fig. 66). Our genetic data, however, indicates no signature of possible introgression between *M. leachella* and *M. pusilla*.

On the Islands of Crete, a distinct form is found, which is morphologically slightly divergent but genetically strongly divergent from all other populations of *M. leachella* (genetic distances in COI on average 5.3%). Morphological differences include the presence of numerous dark hairs laterally on the terga, smaller spots of white hairs on the disc of T6 (Fig. 35), the dark vestiture on the scutum, and some differences in the punctuation (Figs 38, 42) (see below, taxonomic part). The punctuation of the vertex is coarse (Fig. 42) as in northern European populations (Fig. 40), but unlike in southeastern Europe (cf. Figs 41, 43). The phylogeny based on nuclear genes also suggests a closer relationship with the central European populations than with the southeastern European ones. We propose to delineate the Crete populations as a new subspecies, *M. leachella cretica* ssp. nov. This taxon could be recognized as a distinct species based on COI-phylogenies and genetic distances. Nuclear genetic data however suggested a close relationship with other populations of *M. leachella sensu lato*, as does morphology. For this reason, this taxon is recognized as a subspecies and not as a distinct species.

On the Island of Cyprus, the populations of *M. leachella* are morphologically strongly divergent from those on continental Europe. The punctation of the terga in the female sex is fine and dense (Figs 36, 39), as in *M. argentata* (Figs 15–19) or *M. inexpectata* (Figs 25, 26) but strongly different from most other populations of *M. leachella* (Figs 32–34, 37), except for *M. leachella cretica* ssp. nov. (Figs 35, 38), which is intermediate between regular *M. leachella* and *M. leachella densipunctata* ssp. nov. Some specimens from the Levant also have comparatively dense tergal punctation and are intermediate between *M. leachella* and *M. leachella densipunctata* ssp. nov. In addition, the base of the terga is strongly impressed in *M. leachella densipunctata* (Figs 36, 39, 47), a condition not observed in other populations of *M. leachella*. The mitochondrial genetic analyses suggested only small divergences (on average 1.32%; Fig. 5) from continental populations of *M. leachella*. By contrast, the nuclear genetic data (Fig. 6) suggested considerable divergences from other populations of *M. leachella*, in agreement with the pronounced morphological differences. Thus as in *M. leachella cretica* ssp. nov., genetic results based on the mitochondrial gene were less in agreement with morphology than those based on nuclear genes; possibly the mitochondrial genome is more prone to repeated selective sweeps (e.g., Jiggins 2003; Bazin et al. 2006) or introgression events (Nicholls et al. 2012; Klopstein et al. 2016), compared to nuclear markers (Gueuning et al. 2020). We delineate the Cypriote populations as a new subspecies, *M. leachella densipunctata* ssp. nov. This taxon could be recognized as a distinct species based on a pure morphological concept. The absence of differences in male genitalia and hidden sterna, the high variability in punctation characters in *M. leachella sensu lato*, the comparatively low levels of genetic differentiation, and the fact that this subspecies is geographically well-isolated and does not co-occur with the other subspecies of *M. leachella* lead us to treat this taxon as a subspecies.

Lastly, the populations from Sardinia and to some extent Corsica exhibit weak morphological differentiation compared to continental European populations. In particular, in males the front tarsi are yellowish white (Fig. 50) and the last antennal segment slightly enlarged in Sardinian populations; in addition, the ventral surface of the second tarsal segment has a distinct dark maculation, approaching the condition observed in numerous species of *Megachile* with modified and enlarged front tarsi; elsewhere, the front tarsi are predominantly dark brown (there is considerable variation in this character; Figs 48, 49, 51, 52) and no distinct dark maculation is observed under the second segment; and the last antennal segment is usually not larger than the next to last. Females from Sardinian populations have the vestiture snow white (Fig. 33), as in southern European populations, but there are numerous dark hairs laterally on T4–T6; such dark hairs are mostly missing in southern European populations (but present for example in Crete; Fig. 35). Corsican populations appear to be intermediate between Sardinian and southern European populations: the male front tarsi are intermediate between the condition observed in Sardinia and that in European populations; no dark maculation is visible under the second tarsal segment. The female often has dark lateral hairs on T4–T6, as in Sardinian populations. The distinctiveness of the male from Sardinian populations has been noted before: Rebmann (1968) described *M. ichnusae* Rebmann, 1968 from two males collected in Sardinia (the female described as *M. ichnusae* belongs to *M. fertoni* Pérez,

1896, a member of the *rotundata* group of species). *Megachile argentata* var. *fossoria* Ferton, 1909 has been described from Corsican populations. Given that the morphological differences between the Sardinian populations and other populations are insignificant (although constant), given the intermediate nature of the Corsican populations, and given the weak genetic differentiation between Sardinian and other populations, we do not recognize a distinct subspecies for the Corso-Sardinian populations of *M. leachella*. Consequently, we place *M. ichnusae* in synonymy with *M. leachella* (syn. nov).

Lastly, we have examined several females of *M. leachella* from Lesbos, in which the ocellocipital distance was particularly long, approaching the condition observed in *M. anatolica* (cf. Fig. 9). In these specimens the clypeus apical margin was also atypical for *M. leachella*. Whether these specimens are aberrant specimens of *M. leachella*, or indicate a somehow introgressed population of *M. leachella* with *M. anatolica*, is not clear and requires additional research.

Systematic part

Western Palaearctic species

Megachile anatolica Rebmann, 1968

Figs 7–14

Megachile anatolica Rebmann, 1968: 37, ♂ nec ♀, “Mut [Turkey, approx. 36.64°N, 33.44°E]”. Holotype ♂ (SMFD).

Material examined. Type material. *Holotype* ♂ (SMFD) of *M. anatolica* (Fig. 11); one paratype ♀ (SMFD) examined is probably a female of *M. inexpectata*.

Other material. 104 specimens from the following countries: Croatia, Cyprus, Greece, Iran, Israel, Italy, Jordan, Lebanon, Turkey (Suppl. material 1).

Distribution. From Italy eastwards through the Levant including Lebanon, Turkey, Israel northwest of the Dead Sea, Iran; distribution in Central Asia remains to be established due to unclear relationship with *M. viridicollis*.

Geographic variation. The species varies in the colour of the vestiture as well as in body size and in the length of the OOD. In Italy, Greece, Cyprus and western Turkey, the scopa is white (black on S6) and the OOD is large (Fig. 9). In the Levant the species presumably intergrades with *M. leucostoma*; populations in northern Israel and northern Jordan have the scopa nearly entirely orange, as observed in eastern populations of *M. leucostoma* (see Praz et al. 2021). Moreover, the length of the OOD shows clinal variation from northern Israel (condition as in typical *M. anatolica*) to Southern Israel (condition as in typical *M. leucostoma*); specimens from Central Israel are intermediate (Soltani et al. 2017: Fig. 6). In Iran, the scopa is white (black on S6), but specimens are smaller and the OOD short, as in *M. leachella* or *M. pusilla*. While in some Iranian populations the clypeus margin is denticulate, as in typical *M. anatolica* (Fig. 10), in other populations (e.g., in the region of Teheran), the clypeus is as in *M. pusilla*



Figures 7–14. *Megachile anatolica* **7** female metasoma **8** female metasomal tergum **9** female vertex **10** apex of female clypeus **11** dorsal view of head of holotype male **12** front view of male head with distinct tooth behind mandibular base **13** male metasomal sterna 3–5 **14** male genitalia.

(cf. Fig. 64), making these populations superficially identical to *M. pusilla*, albeit genetically closer to *M. anatolica*. Whether the variation observed in Iran is the result of introgression with *M. leucostoma*, which has not been reported in Iran but is present on the Arabian Peninsula, e.g., in the United Arab Emirates, remains to be established.

Note. The relationship between *M. anatolica* and the Central Asian species *M. viridicollis* is not clear; these two taxa may eventually be treated as conspecific, in which case *M. anatolica* would be placed in synonymy with *M. viridicollis*; see under *M. viridicollis*.

Megachile argentata (Fabricius, 1793)

Figs 1–3, 15–24

Megachile argentata argentata (Fabricius, 1793)

Apis argentata Fabricius, 1793: 336 [sex not indicated], “in Barbaria” [Algeria or Tunisia]. Lectotype ♀ (NHMD), by designation of Hurd (1967).

Megachile compacta Pérez, 1895: 24, ♀, [Algeria]. Preoccupied, not *Megachile compacta* Smith, 1879. Lectotype ♀ (MNHN), by present designation (see below).

New Synonymy.

Megachile crassula Pérez, 1896: 1. *Nomen novum* for *M. compacta* Pérez. New synonymy.

Perezia maura Ferton, 1914: 233, ♀ [gynandromorph specimen], “Cimetière de Djidjelli” [Jijel, Algeria]. Holotype intersex (MNHN). Preoccupied, not *Megachile maura* Cresson, 1865. Synonymy with *M. centuncularis* in Pasteels (1969: 248).

Synonymy with *M. leachella* in van der Zanden (1988: 56). New synonymy.

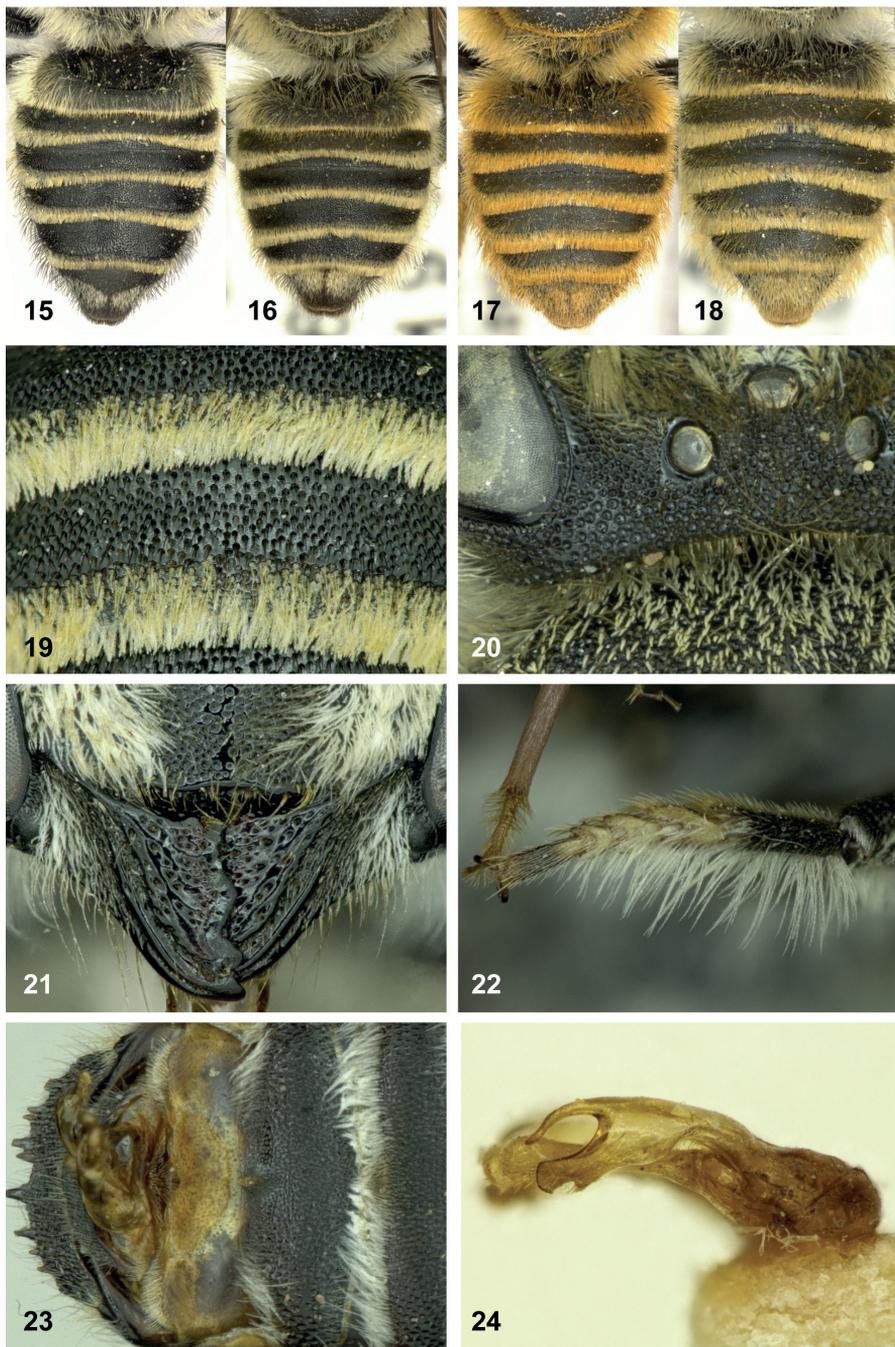
Megachile pilidens Alfken, 1924: 88, ♀ ♂, “Triest [Trieste, Italy]”. Lectotype ♀ (ZMHB), by designation of Tkalcû 1967: 100. New synonymy.

Megachile argyrea Cockerell, 1931: 275, ♀ ♂, “Asni [Morocco]”. Holotype ♀ (USNM), paratypes ♀ ♂ (BMNH). New synonymy. Synonymy with *M. pilidens* in Hedicke, 1933: 42.

Material examined. Type material. Lectotype ♀ of *M. argentata* (NHMD) (Figs 1–3; see above, identity of type specimens).

Lectotype ♀ of *M. crassula* (MNHN), by present designation, a female in good condition labeled as follows: 1. “Algeria” [printed]; 2. *crassula* JP [handwritten, presumably by Pérez]; 3. “Museum Paris Coll. J. Pérez” [printed on blue paper]; 4. “Holotype *M. crassula* des. Baker 1991” [printed and handwritten on red paper]; 5. “Lectotype *M. crassula* des. C. Praz 2022”. Although the original description does not mention the number of specimens, we prefer to designate this specimen as the lectotype.

Holotype [gynandromorph] of *Perezia maura* (MNHN), labeled as follows: 1. “Djidjelli 17-8/13 p. 315” [handwritten by Ferton]; 2. “*Perezia maura* ♀ Fert” [handwritten by Ferton]; 3. Holotype [printed, red]; 4. Muséum Paris Ch. Ferton 1902 [printed, blue paper]; 5. *Megachile pilidens* Alfken [symbol for gynandromorph] det. G.v.d. Zanden 1986 ; 6. “*Perezia maura* Ferton = gynandromorph de



Figures 15–24. *Megachile argentata* **15** female metasoma of northwestern African populations, *M. argentata argentata* **16** female metasoma of European, Levant, Turkey and Central Asian populations, *M. argentata argentata* **17** female metasoma of Malta populations, *M. argentata schmiedeknechti* **18** female metasoma of Corsican and Sardinian populations, *M. argentata schmiedeknechti* **19** female metasomal tergum 4 **20** female vertex **21** apex of female clypeus **22** male front tarsi **23** male metasomal sterna 3–5 **24** male genitalia.

Megachile centuncularis J. Pasteels det., 1969⁹; 7. *Megachile argentata* intersex det C. Praz 2022. It is unclear why van der Zanden (1988) placed this taxon in synonymy with *M. leachella* since the label on the specimen suggests he correctly identified the holotype as *M. pilidens*.

Lectotype ♀ of *M. pilidens* (ZMHB). A female without metasoma, but clearly identified as *M. argentata* (see Tkalců 1967).

Paratypes ♀ and ♂ of *M. argyrea* (BMNH), all in good condition and clearly corresponding to *M. argentata*. We did not examine the holotype ♀ of *M. argyrea*, but pictures are available at <https://collections.nmnh.si.edu/search/ento/>; based on these pictures, the holotype agrees with *M. argentata* in the dark vestiture of the lateral parts of T5 (absent in *M. leachella albipila* and *M. inexpectata*). Punctuation of the vertex is not visible but the dense punctuation of the terga appears to exclude *M. leachella albipila*. This character and the identity of examined male and female paratypes (BMNH) collected in the same site confirm synonymy with *M. argentata*.

Note. *Megachile beaumonti* Benoist, 1951, is currently treated as a synonym of *M. crassula* (van der Zanden 1990: 53). We have examined the holotype ♀ of this taxon (MZL); *Megachile beaumonti* is not conspecific with *M. argentata*, but is a valid species of the *rotundata* group (stat. rev.).

Other material. 216 specimens from the following countries: Croatia, France, Germany, Greece, Iran, Italy, Kyrgyzstan, Lebanon, Morocco, Northern Macedonia, Portugal, Russia, Serbia, Spain, Switzerland, Tunisia, Turkey, Ukraine (Suppl. material 1).

Distribution. Widespread and abundant in southern Europe; in expansion in central and northern Europe, e.g., in northern Switzerland (C. Praz et al., in prep.), the Netherlands (Peeters et al. 2006) and Germany (LUBW 2007; Schweitzer and Theunert 2019). Present in the Levant (Turkey, Lebanon), but so far its presence has not been confirmed in Israel and Egypt (Praz et al. 2021). We have examined specimens from Rhodos, Lesvos, Samos, Karpathos, Patmos, Chios, but neither from Cyprus [the record of *M. pilidens* by Varnava et al. (2020) is probably an identification error and likely refers to *M. leachella densipunctata* ssp. nov.] nor from Crete. Further east, the species is present in Iran, Armenia and Kyrgyzstan.

Geographic variation. Geographic variation has been discussed above in detail. The northwestern African populations, as well as populations from the Island of Pantelleria, have overall snow-white vestiture in the female sex (Fig. 15) and dark vestiture on the mesonotum and vertex, and in the male sex a continuous fringe of hairs on the margin of T6. On the Island of Karpathos, the female scopa is orange on S5 and S6, approaching the condition observed in *M. argentata schmiedeknechti*.

Megachile argentata schmiedeknechti Costa, 1884

Megachile Schmiedeknechti Costa, 1884: 169, ♀ ♂, [Italy, Sardinia].

Megachile xanthopyga Pérez, 1895: 25, ♀ ♂, "Sassari [Italy, Sardinia]". Lectotype ♀ (MNHN), by present designation (see below). Paralectotypes ♀ (MNHN), by present designation.

Type material. *Lectotype* ♀ (MNHN) of *M. xanthopyga*, a female in good condition labeled as follows: 1. “MNHN Paris EY33616” [printed, with QR-code]; 2. [blue circular disc]; 3. “Sassari” [handwritten, presumably by Pérez]; 4. “Museum Paris Coll. Pérez 1915” [printed]; 5. “Lectotype *Megachile xanthopyga* des. Baker 1991” [printed and handwritten on red paper]; 6. “*Megachile schmiedeknechti* det. van der Zanden 1995” [printed]. This lectotype designation has not been published and is accepted here. Two additional females from Sassari, each with a label “paralectotype *M. xanthopyga* des. Baker 1991” are designated as paralectotypes. The type locality of *M. xanthopyga* is not given in the original description. In his handwritten catalogue (available at <https://science.mnhn.fr/catalogue/ey-bib-perez1>), Pérez indicates under *M. xanthopyga* “Bonifacio, Sassari, ♀ mai-août, ♂ mai-juillet”.

Note. We did not examine type specimens of *M. schmiedeknechti* and do not know whether syntypes exist. The identity of the species is clear from the original description. The date of the original description of *M. schmiedeknechti* is unclear; its first, very brief description in Latin was published in the “Rendiconto dell’Accademia delle Scienze fisiche e matematiche, fascicolo 12, anno XXIII, dicembre 1884”; it is unclear if this volume was printed in 1884. A longer description, including a description in Italian, was published in 1885 (Costa 1885a) in a separate book (“Tipografia della Reale Accademia delle Scienze Fis. e Mat., Napoli”). A third description, only in Latin, in the “Bulletino della Società Entomologica Italiana” (Costa 1885b).

Other material. 18 specimens from France (Corsica), Italy (Sardinia) and Malta (Suppl. material 1).

Distribution. Restricted to Malta, Corsica, and Sardinia.

Geographic variation. The Maltese populations have the vestiture bright red orange (Fig. 17), while the Corso-Sardinian populations yellowish orange (Fig. 18).

Note. As noted above, it is possible that the superficially similar appearance of the Maltese and Corso-Sardinian populations is the result of independent convergent evolution. Our genetic analyses did not suggest a close relationship between these populations (although no nuclear sequence data was available for the Maltese populations). Awaiting additional genetic results, we continue to refer the Maltese populations as *M. argentata schmiedeknechti*.

Megachile inexpectata Rebmann, 1968

Figs 25–31

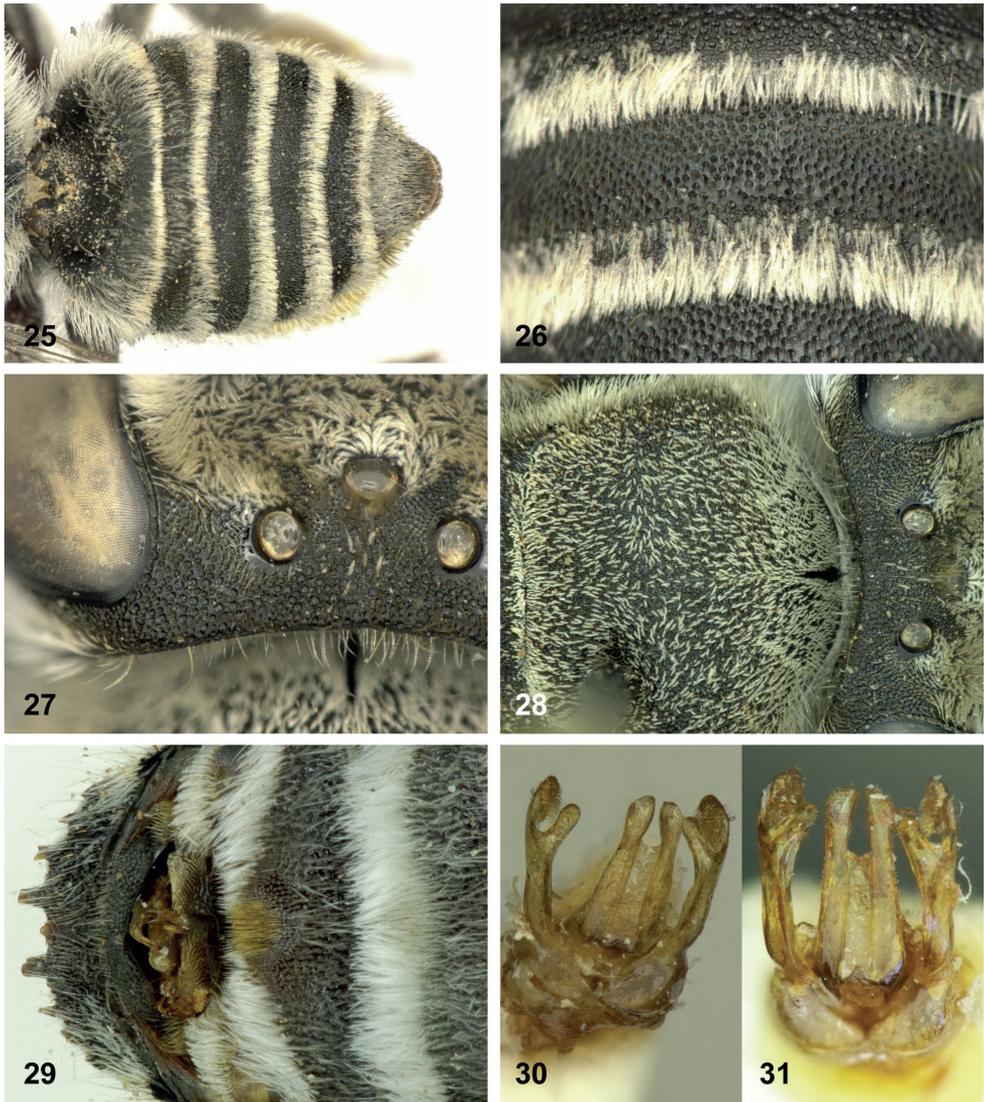
Megachile inexpectata Rebmann, 1968: 43, ♂, “Mut [Turkey, approx. 36.64°N, 33.44°E]”. Holotype ♂ (restricted to genitalia) (SMFD).

Material examined. Type material. *Holotype* ♂ of *M. inexpectata* (SMFD) (Fig. 31; see above).

Other material. 63 specimens from the following countries: Cyprus, Greece (Rhodes), Israel, Jordan, Lebanon, Morocco, Turkey (Suppl. material 1).

Distribution. Morocco, Egypt (Sinai), Israel, Lebanon, Cyprus, Rhodes, Turkey.

Geographic variation. See above, species delimitation.



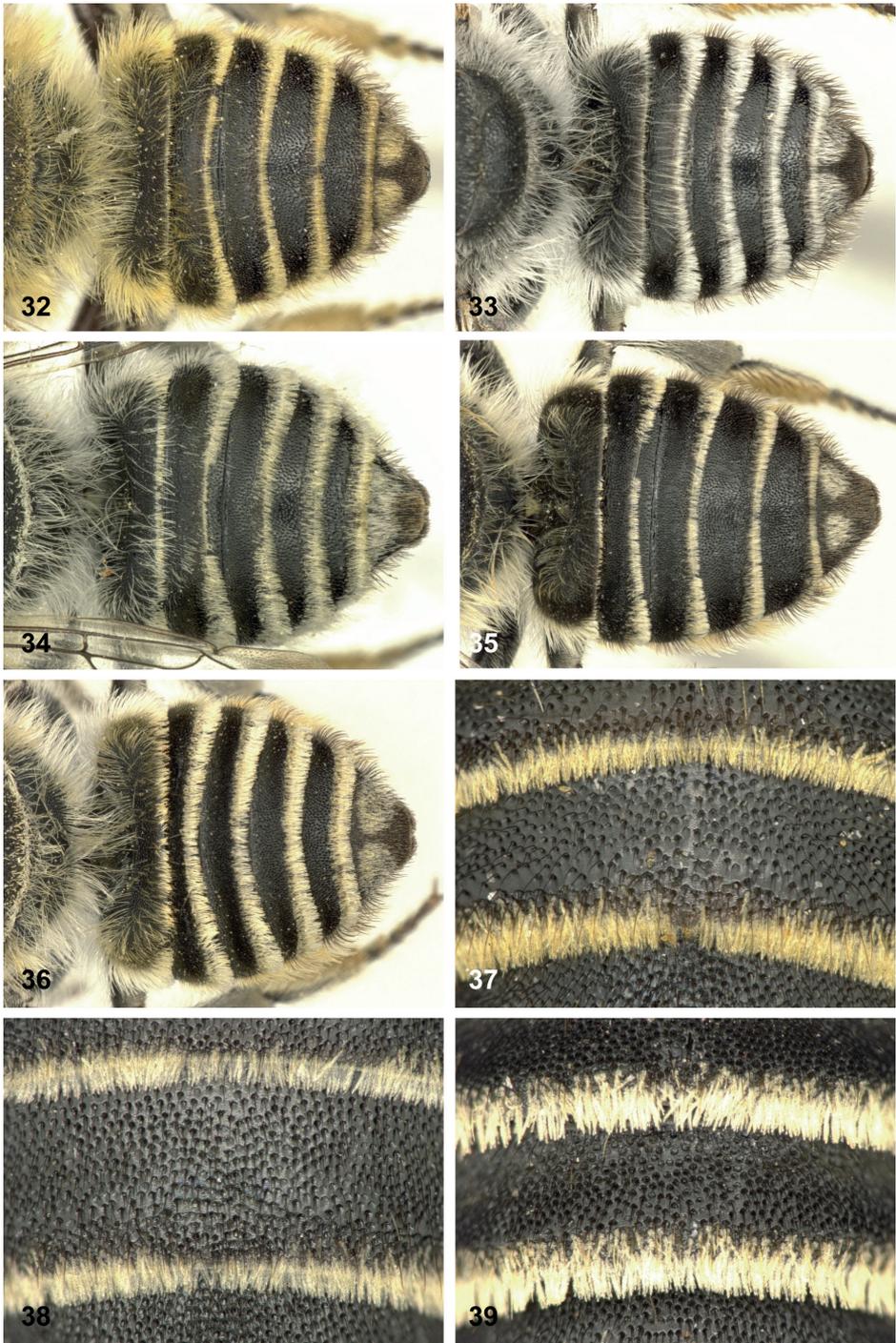
Figures 25–31. *Megachile inexpectata* **25** female metasoma **26** female metasomal tergum 4 **27** female vertex **28** female scutum **29** male metasomal sterna 3 and 4 **30** male genitalia **31** male genitalia, holotype of *M. inexpectata*.

***Megachile leachella* Curtis, 1828**

Figs 32–56

***Megachile leachella albipila* Pérez, 1895, stat. nov.**

Megachile albipila Pérez, 1895: 23, ♀ ♂, “Alger [Algeria]”. Lectotype ♂ (MNHN); paralectotype ♀ (MNHN), by present designation.



Figures 32–39. *Megachile leachella* **32–36** female metasoma **32** UK, *M. leachella leachella* **33** Corsica and Sardinia, *M. leachella leachella* **34** northwestern Africa, *M. leachella albipila* **35** Crete, *M. leachella cretica* ssp. nov. **36** Cyprus, *M. leachella densipunctata* ssp. nov. **37–39** female metasomal tergum 4 **37** UK, *M. leachella leachella* **38** Crete, *M. leachella cretica* ssp. nov. **39** Cyprus, *M. leachella densipunctata* ssp. nov.

Material examined. Type material. Lectotype ♂ (MNHN) of *M. albipila*, a male in good condition, the tip of the abdomen and the extracted genitalia are placed in a transparent vial preserved under the specimen. This lectotype is labeled as follows: 1. [red, circular disc]; 2. “Alger” [handwritten, handwriting of Pérez]; 3. “Museum Paris, Coll. J. Pérez 1915 [printed on blue paper]. 4. “Paralectotype *M. albipila* Pérez 1896 D. B. Baker des. 1991” [printed and handwritten on blue paper]. 5. “Lectotype *Megachile albipila* des. C. Praz 2022” [printed and handwritten on red paper]. Paralectotype ♀ (MNHN), also from Alger, labelled as follows: 1. [a green circular disc]; 2. “Alger [handwritten, handwriting of Pérez]; 3. “hôte de [host of] *Coelioxys afro*” [handwritten]. 4. “Museum Paris, Coll. J. Pérez [printed on blue paper]. 5. Lectotype *Megachile albipila* Pérez 1896 D. B. Baker des. 1991” [printed and handwritten on red paper]. 6. “Paralectotype *Megachile albipila* des. C. Praz 2022” [printed and handwritten on red paper]. D. Baker’s lectotype designation has not been published and is not accepted here; the male specimen, designated here as the lectotype, corresponds to the taxon delineated here as a subspecies of *M. leachella*; in particular, the short preapical process of the gonostylus is clearly visible. The female specimen, however, may belong to either *M. inexpectata* or to *M. leachella albipila*. Based on the punctuation of the tergal discs, it rather belongs to *M. inexpectata*, although this identification is tentative given the difficulties in separating females of these two species. For this reason, the male specimen is designated as the lectotype.

Other material. 44 specimens from Algeria, Morocco and Tunisia (Suppl. material 1).

Distribution. Morocco, Algeria and Tunisia. All males examined from these three countries had the preapical process of the gonostylus short (Fig. 55), the feature that characterizes this subspecies. We conclude that the nominal subspecies *leachella* s. str. is absent from northwestern Africa.

Megachile leachella cretica Praz, new subspecies

<https://zoobank.org/60AB1119-111D-4AEB-A51F-CBE81F8ECF11>

Type material. Holotype ♀ (Fig. 44), GREECE • Kreta [Crete], Ackerbrachen N Kournas See; 30m a.s.l.; 35°20.239'N, 24°16.766'E; 4.vi.2012; V. Mauss leg.; (CPCN).

Paratypes (Suppl. material 1): 16♀ 6♂. Greece • ♀; Anatoli [Crete]; 11.vi.2005; Le Goff leg.; G. Le Goff Coll. • ♀; Crete Armeni (N. Rethimnis); 27.vii.2007; Le Goff leg.; Unique identifier: GBIFCH00265014; CPCN • ♀; Crete, Paleochora Camping; 0m a.s.l.; 20.x.2011; A. Müller leg.; Unique identifier: GBIFCH00264819; CPCN • ♀; Crete, Paleochora Camping; 0m a.s.l.; 13.x.2011; A. Müller leg.; Unique identifier: GBIFCH00265010; CPCN • ♀; Crete, Paleochora Camping; 0m a.s.l.; 20.x.2011; A. Müller leg.; Unique identifier: GBIFCH00265011; DNA extraction number 536; BOLD: 14514-C03; CPCN • ♀; Crete, Paleochora Camping; 0m a.s.l.; 13.x.2011; A. Müller leg.; Unique identifier: GBIFCH00265012; CPCN • ♀; Crete, Paleochora Camping; 0m a.s.l.; 20.x.2011; A. Müller leg.; A. Müller Coll. • ♀; Crete, Paleochora Camping; 0m a.s.l.; 13.x.2011; A. Müller leg.; A. Müller Coll. • ♀; Crete, Sougia, Tamarix; 0m a.s.l.; 14.x.2011; A. Müller leg.; Unique identifier: GBIFCH00264820; CPCN • ♀; Kreta Spili; 6.x.1993; F. Amiet leg.; Unique identifier: GBIFCH00265047; CPCN • ♀, 2♂; Kreta [Crete], Agia



Figures 40–45. *Megachile leachella* **40–43** female vertex **40** UK, *M. leachella leachella* **41** northwestern Africa, *M. leachella albipila* **42** Crete, *M. leachella cretica* ssp. nov. **43** Cyprus, *M. leachella densipunctata* ssp. nov. **44** holotype female of *M. leachella cretica* ssp. nov. **45** holotype female of *M. leachella densipunctata* ssp. nov.

Galini; 5.x.1993; F. Amiet leg.; F. Amiet Coll. (NMBE) • ♂; Kreta [Crete], Berghang W von Amoudhari; 35°11.926'N, 24°04.396'E; 800–1100 m a.s.l.; 8.vi.2012; V. Mauss leg.; Unique identifier: GBIFCH00265018; CPCN • ♂; Kreta [Crete], S Stomio Phrygeana an Küste; 35°19.35'N, 23°33.04'E; 10 m a.s.l.; 10.vi.2002; A.W. Ebmer leg.; Unique identifier: GBIFCH00265016; CPCN • ♀; Kreta [Crete], S. Kallikratis Kulturland, obere Olea-Zone; 35°14.34'N, 24°15.38'E; 700 m a.s.l.; 6.vi.2002; A.W. Ebmer leg.; Unique identifier: GBIFCH00265013; CPCN • 2♀, ♂; Kreta [Crete], Spili; 6.x.1993; F. Amiet leg.; F. Amiet

Coll. (NMBE) • ♀; Kreta [Crete], Vai 10m Phoenix th-Zone, an Thymus; 35°15.08'N, 26°15.39'E; 25.iv.2001; A.W. Ebmer leg.; Unique identifier: GBIFCH00265015; CPCN • ♂; Kreta [Crete], W Levka Ori N Vigia, Felssteppe; 35°21.50'N, 23°49.13'E; 750–800 m a.s.l.; 7.vi.2002; A.W. Ebmer leg.; Unique identifier: GBIFCH00265017; CPCN • ♀; Kreta [Crete], Umg. Von Loutro; 35°11.926'N, 24°04.396'E; 10 m a.s.l.; 7.vi.2012; V. Mauss leg.; V. Mauss Coll. • 2 ♂; Graecia Kriti; Iraklio Rodià; 12.vi.1996; leg. Scaramozzino; Max. Schwarz Coll. (OLML) • ♂; Graecia Kriti; Iraklio Matala; 15–17.vi.1996; leg. Scaramozzino; Max. Schwarz Coll. (OLML) • ♀; Kreta; Matala, Korno-Beach, Sand; 21.10.1996; leg. Stefan Tischendorf; S. Tischendorf Collection.

Distribution. Restricted to the Island of Crete, Greece.

Description. Female: highly similar to southern populations of the nominal subspecies, differs as follows: apical tergal fringes snow white (Figs 35, 44), as in most southern European populations of the nominal subspecies; spots of white hairs of disc of T6 reduced to two well-separated spots (Fig. 35), a condition otherwise not frequently observed in *M. leachella*. Terga 2–6 laterally with numerous erect dark hairs; such dark hairs are present in the UK, in Central Europe and on Sardinia and Corsica, but not elsewhere (e.g., in Greece, Turkey), where dark hairs are restricted to T5-6. Vertex and scutum covered with black hairs intermixed with light hairs. Vertex punctation particularly coarse and sparse (Fig. 42), similar to or even coarser than in the UK (Fig. 40) or central European populations, but unlike in southern Europe, where the vertex punctation is comparatively small and dense (cf. Figs 41, 43). Punctuation on disc of T4 comparatively dense (Fig. 38), on average denser than in other populations (Fig. 37), except in *M. leachella densipunctata* ssp. nov. from Cyprus (Fig. 39). There is however considerable variation in this character in *M. leachella sensu lato* and the condition observed in Crete is within the observed range of variation in the species. *Megachile leachella cretica* ssp. nov. shows a combination of characters present in southern European (in particular the snow white vestiture) and central or northern European populations (dark hairs laterally on the terga, coarse punctation on the vertex).

Male: nearly identical to the nominal subspecies (Fig. 46); the front tarsal segments 2–4 are more consistently orange, approaching the condition observed in *M. leachella densipunctata* ssp. nov. (cf. Fig. 52) (usually at least partly dark brown in other populations of *M. leachella*; Figs 48, 49, 51); the preapical process of the gonostylus (Fig. 56) appears to be slightly shorter on average than in the nominal subspecies (Fig. 54), but only few males were available for study.

Etymology. The subspecies epithet refers to the geographic distribution of this taxon, which is probably restricted to the Island of Crete.

Megachile leachella densipunctata Praz, new subspecies

<https://zoobank.org/5F018807-57B4-4129-8C37-D4D76A9CA9B6>

Type material. Holotype ♀ (Fig. 45), CYPRUS • 8 km N Pafos, Mavrokolympus Res.; 34.85°N, 32.40°E; 20.vi.2013; Schmid-Egger leg.; (CPCN).

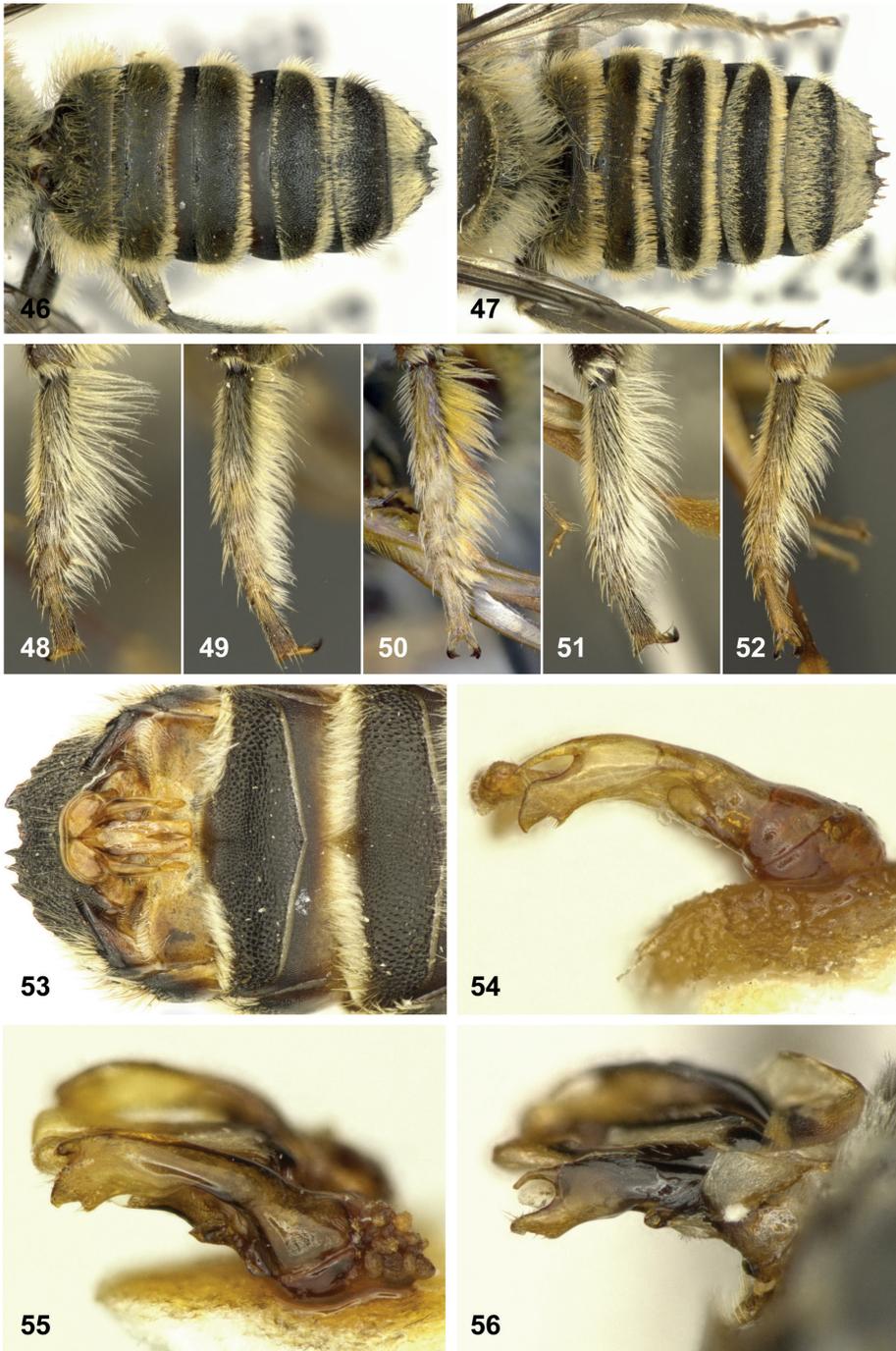
Paratypes (Suppl. material 1): 27♀ 19 ♂, Cyprus • ♂; 15 km SE Pafos, Kouk-
lia; 34.72°N, 32.55°E; 20.vi.2013; Schmid-Egger leg.; Unique identifier: GBIF-
CH00265023; CPCN • ♂; 15 km SE Pafos, Kouk-
lia; 34.72°N, 32.55°E; 20.vi.2013; Schmid-Egger leg.; Unique identifier: GBIFCH00265025; CPCN • ♂; 15 km SE
Pafos, Kouk-
lia; 34.72°N, 32.55°E; 20.vi.2013; Schmid-Egger leg.; Unique identi-
fier: GBIFCH00265026; CPCN • ♂; 15 km SE Pafos, Kouk-
lia; 34.72°N, 32.55°E; 20.vi.2013; Schmid-Egger leg.; A. Müller Coll. • 2♀ 2♂; 15 km SE Pafos, Kouk-
lia; 34.72°N, 32.55°E; 20.vi.2013; C. Schmid-Egger leg.; C. Schmid-Egger Coll. •
♀; 1 km SE Pano Panagia, Quercus infectoria-Zone; 34.54(.32)°N, 32.37(.34)°E;
800 m a.s.l.; 6.vi.2013; A. W. Ebmer leg.; A. W. Ebmer Coll. • ♀; 20 km NNW
Pafos, Lara Beach; 34.94°N, 32.31°E; 20.vi.2013; Schmid-Egger leg.; Unique iden-
tifier: GBIFCH00265019; CPCN • ♀; 20 km NNW Pafos, Lara Beach; 34.94°N,
32.31°E; 20.vi.2013; Schmid-Egger leg.; Unique identifier: GBIFCH00265020;
CPCN • ♀; 20 km NNW Pafos, Lara Beach; 34.94°N, 32.31°E; 20.vi.2013; Schmid-
Egger leg.; Unique identifier: GBIFCH00265021; CPCN • ♀; 20 km NNW Pafos,
Lara Beach; 34.94°N, 32.31°E; 20.vi.2013; Schmid-Egger leg.; Unique identifier:
GBIFCH00265022; CPCN • ♀; 20 km NNW Pafos, Lara Beach; 34.94°N, 32.31°E;
20.vi.2013; Schmid-Egger leg.; A. Müller Coll. • ♀; 20 km NNW Pafos, Lara Beach;
34.94°N, 32.31°E; 20.vi.2013; Schmid-Egger leg.; OLML • ♂; 20 km NNW Pa-
fos, Lara Beach; 34.94°N, 32.31°E; 20.vi.2013; Schmid-Egger leg.; Unique identifier:
GBIFCH00265027; CPCN • ♂; 20 km NNW Pafos, Lara Beach; 34.94°N, 32.31°E;
20.vi.2013; Schmid-Egger leg.; OLML • 6♀ 2♂; 20 km NNW Pafos, Lara Beach;
34.94°N, 32.31°E; 20.vi.2013; C. Schmid-Egger leg.; C. Schmid-Egger Coll. • ♀; 6
km W Polis, botanical Garden; 35.03°N, 32.37°E; 20.vi.2013; C. Schmid-Egger leg.;
C. Schmid-Egger Coll. • ♂; 8 km N Pafos, Mavrokolympos Res.; 34.85°N, 32.40°E;
20.vi.2013; Schmid-Egger leg.; Unique identifier: GBIFCH00265028; CPCN
• 2♀ 1♂; 8 km N Pafos, Mavrokolympos Res.; 34.85°N, 32.40°E; 20.vi.2013; C.
Schmid-Egger leg.; C. Schmid-Egger Coll. • ♂; ca 5 km N Lemithou Pinus-Zone;
34°58.08'N, 32°48.27'E; 1170 m a.s.l.; 15.vi.2013; A.W. Ebmer leg.; Unique identi-
fier: GBIFCH00265035; CPCN • 2♀; ca 5 km N Lemithou Pinus-Zone; 34°58.08'N,
32°48.27'E; 1170 m a.s.l.; 15.vi.2013; A. W. Ebmer leg.; A. W. Ebmer Coll. • ♀; ca
5 km N Lemithou Pinus-Zone; 34°58.08'N, 32°48.27'E; 1170 m a.s.l.; 15.vi.2013;
A.W. Ebmer leg.; Unique identifier: GBIFCH00265030; CPCN • 3♂; Moni Troodot-
issa Umg. P. brutia/Qu. alnifolia/Arbustus andrachne-Zone; 1350 m a.s.l.; 16.vi.2013;
A. W. Ebmer leg.; A. W. Ebmer Coll. • ♀; NE Nata, Ufer des Xerós/Obstgarten;
34°47.17'N, 32°35.38'E; 130 m a.s.l.; 7.vi.2013; A.W. Ebmer leg.; Unique identifier:
GBIFCH00265033; CPCN • 2♀; S Kakopetria, E Platania, P. Brutia/Qu. alnifolia/A.
andrachne; 34°56.54'N, 32°55.59'E; 1200 m a.s.l.; 12.vi.2013; A. W. Ebmer leg.; A.
W. Ebmer Coll. • ♀; S Kakopetria, E Platania, P. Brutia/Qu. alnifolia/A.andrachne;
34°56.54'N, 32°55.59'E; 130 m a.s.l.; 12.vi.2013; A.W. Ebmer leg.; Unique identifier:
GBIFCH00265031; CPCN • ♀; Strasse Prodromos>Troodos, an *Lotus corniculatus*;
34°56.55'N, 32°51.01'E; 1550 m a.s.l.; 16.vi.2013; A.W. Ebmer leg.; Unique iden-
tifier: GBIFCH00265032; CPCN • ♂; Troodos Mt. Olympos; 34.93°N, 32.86°E;

1900 m a.s.l.; 20.vi.2013; C. Schmid-Egger leg.; C. Schmid-Egger Coll. • ♂; W Polis, ca. 3 km W Neo Chorio, Ag. Minas ruderal/Feuchstelle; 35°01(.23)'N, 32°20(.36)'E; 240 m a.s.l.; 5.vi.2013; A.W. Ebmer leg.; Unique identifier: GBIFCH00265034; CPCN • ♀; 2011; Sedivy & Müller leg.; Unique identifier: GBIFCH00265024; DNA extraction number 538; BOLD 14514D09; CPCN • ♂; 2011; Sedivy & Müller leg.; Unique identifier: GBIFCH00265036; DNA extraction number 537; CPCN • ♀; Limassol Cherkes Chiftlik; Site 1 36SVD9916334336; 1.ix.2017; A. Varnava leg.; Unique identifier: AV-17-01331; A. Varnava Collection • ♀; Limassol Cherkes Chiftlik; Site 1 36SVD9916334336; 15.vii.2016; A. Varnava leg.; Unique identifier: AV-16-00324; CPCN • ♂; Limassol Cherkes Chiftlik; Site 3 36SVD99003334989; 21.ix.2017; A. Varnava leg.; Unique identifier: AV-17-01382; A. Varnava Collection • ♂ SBA Akrotiri, Site 1 36SVD9735128734; 1.ix.2017; A. Varnava leg.; Unique identifier: AV-17-01296; A. Varnava Collection • ♂ SBA Akrotiri, Site 1 36SVD9735128734; 1.ix.2017; A. Varnava leg.; Unique identifier: AV-17-01299; CPCN • ♂; Limassol Cherkes Chiftlik; Site 1 36SVD9916334336; 1.ix.2017; A. Varnava leg.; Unique identifier: AV-17-01335; A. Varnava Collection • ♂; Limassol Cherkes Chiftlik; Site 1 36SVD9916334336; 1.ix.2017; A. Varnava leg.; Unique identifier: AV-17-01330; CPCN • ♀; [Cyprus] Unique identifier: AV-16-01878; A. Varnava Collection • ♀; [Cyprus] Unique identifier: AV-16-02182; A. Varnava Collection • ♀; Chlorana (pan trap); 34.793°N, 32.408°E; 18.10.2021; leg. V. Soon; Natural History Museum of the University of Tartu • ♀; Akrotiri; 34.6346°N, 32.9198°E; 16.10.2021; leg. V. Soon; Natural History Museum of the University of Tartu.

Distribution. Restricted to Cyprus.

Description. Female: similar to southern populations of the nominal subspecies, differs as follows: apical tergal fringes yellowish white (Figs 36, 45), not snow white as in most southern European populations (e.g., Greece, Turkey) of the nominal subspecies; spots of white hairs of disc of T6 large (Fig. 36), unlike in *M. leachella cretica* ssp. nov., but as in southern European populations; Terga 3-6 laterally with dark hairs (Fig. 36), approaching the condition observed in *M. leachella cretica* ssp. nov. Fig. 35) but unlike in southern European populations of the nominal subspecies. Vertex punctation small and dense (Fig. 43), as in southern European populations, but unlike in *M. leachella cretica* ssp. nov. The most striking feature characterizing *M. leachella densipunctata* ssp. nov. is the particularly dense punctation of the terga, especially the disc of T4 (Fig. 39); moreover, the terga are conspicuously impressed basally (Figs 36, 39). Such dense punctation and impressed basis are otherwise not observed in *M. leachella sensu lato*; specimens from Israel also have comparatively dense tergal punctation, approaching the condition observed in *M. leachella densipunctata* ssp. nov.

Male: nearly identical to the nominal subspecies, differs as follows: light vestiture of terga particularly developed, forming two conspicuous bands of hairs, one basally and one apically (Fig. 47); in particular the disc of T5 is nearly entirely covered with light hairs, unlike in most other populations of *M. leachella sensu lato*; specimens from Israel have similar tergal vestiture. Terga basally strongly impressed, so that disc is concave basally and strongly convex apically (Fig. 47); in all other populations of



Figures 46–56. *Megachile leachella* **46, 47** male metasoma **46** Switzerland, *M. leachella leachella* **47** Cyprus, *M. leachella densipunctata* ssp. nov. **48–52** male front tarsi **48** UK, *M. leachella leachella* **49** Switzerland, *M. leachella leachella* **50** Corsica and Sardinia, *M. leachella leachella* **51** Crete, *M. leachella cretica* ssp. nov. **52** Cyprus, *M. leachella densipunctata* ssp. nov. **53** male sterna 4–6 **54–56** male genitalia **54** UK, *M. leachella leachella* **55** northwestern Africa, *M. leachella albipila* **56** Crete, *M. leachella cretica* ssp. nov.

M. leachella, disc nearly flat. Front tarsal segments 2–4 consistently orange (Fig. 52) (usually at least partly dark brown in other populations of *M. leachella*; Figs 48, 49, 51). Genitalia as in the nominal subspecies.

Etymology. The subspecies epithet refers to the particularly dense punctation of the terga of the female.

Megachile leachella leachella Curtis, 1928

Megachile leachella Curtis, 1928: [explanation to Plate 218], [sex not indicated], “[England]”.

Megachile dorsalis Pérez 1879: 223, ♀ nec ♂, “Bordeaux; environs de l’étang de Ca-zaux; Arcachon; Royan [France]”. Lectotype ♀, by designation of van der Zanden (1996: 886) (MNHN).

Megachile bioculata Pérez, 1902: 119, ♀ [erroneously indicated as ♂], “Catalogne [Spain: Catalonia]”. Lectotype ♀, by present designation (see below) (MNHN).

Megachile argentata var. *fossoria* Ferton, 1909: 550, [sex not indicated], “Propriano [France, Corsica]”. Lectotype ♀, by designation of Schwarz & Gusenleitner (2011: 258) (MNHN); paralectotypes ♀ ♂ (MNHN).

Megachile ichnusae Rebmann, 1968: 31, ♂ nec ♀, “Sardinien, Siniscola” [Italy, Sardinia, approx. 40.58 N, 9.70 E]. Holotype ♂, (SMFD). New synonymy.

Megachile discriminata Rebmann, 1968: 34, ♂, “Turkestan, 189., Golodnaja Step. [Uzbekistan]”. Holotype ♂ (ZMHB); paratype ♂ (SMFD). New synonymy.

Megachile leachella maadiensis van der Zanden, 1986: 67, ♂, “[no locality given: Egypt]”. Details on type material or type locality not given.

Material examined. Type material. *Lectotype* ♀ (MNHN) of *M. dorsalis* (see also Gogala 1998; Schwarz and Gusenleitner 2011).

Lectotype ♀ (MNHN) of *M. bioculata*, a female specimen labeled as follows: 1. [red, circular disc]; 2. “Barcelone” [handwritten, handwriting of Pérez]; 3. “*bioculata* JP” [handwritten, handwriting probably of Pérez]; 4. “Muséum Paris Coll. J. Pérez 1915” [printed]; 5. Lectotype *Megachile bioculata* Pérez des. C. Praz 2022” [printed and handwritten on red paper]. 6. MNHN Pérez EY2292 [catalogue of type MNHN]. 7. *Megachile leachella* det. C. Praz 2022 [printed and handwritten].

Lectotype ♀ (MNHN) of *M. argentata* var. *fossoria* (see also Schwarz and Gusenleitner 2011).

Holotype ♂ (SMFD) of *M. ichnusae* (SMFD). The female paratype is a female of *M. fertoni*.

Holotype ♂ (ZMHB) and paratype ♂ (SMFD) of *M. discriminata*.

Other material. 174 specimens from the following countries: Croatia, Egypt, UK, France, Greece, Iran, Israel, Italy, Kyrgyzstan, Montenegro, North Macedonia, Portugal, Spain, Switzerland, Syria, Turkey, Uzbekistan (Suppl. material 1).

Distribution. Widely distributed in Europe from Portugal, Spain, France, north to the UK, Scandinavia, northern, central, southern and eastern Europe, Levant (Turkey, Leba-

non, Egypt, Israel), Iran, central Asia. We have examined specimens of the nominal subspecies from Chios, Lesbos, Rhodos and Santorini, but from no other Aegean Islands (see above for the populations of Crete and Cyprus). Highly similar (>98% similarity) DNA barcodes from unidentified specimens from the Beijing Region (Genbank accession number [KC560312](#); Chesters et al. 2013) strongly suggests the presence of this species in China.

Geographic variation. See above (species delimitation).

***Megachile leucostoma* Pérez, 1907**

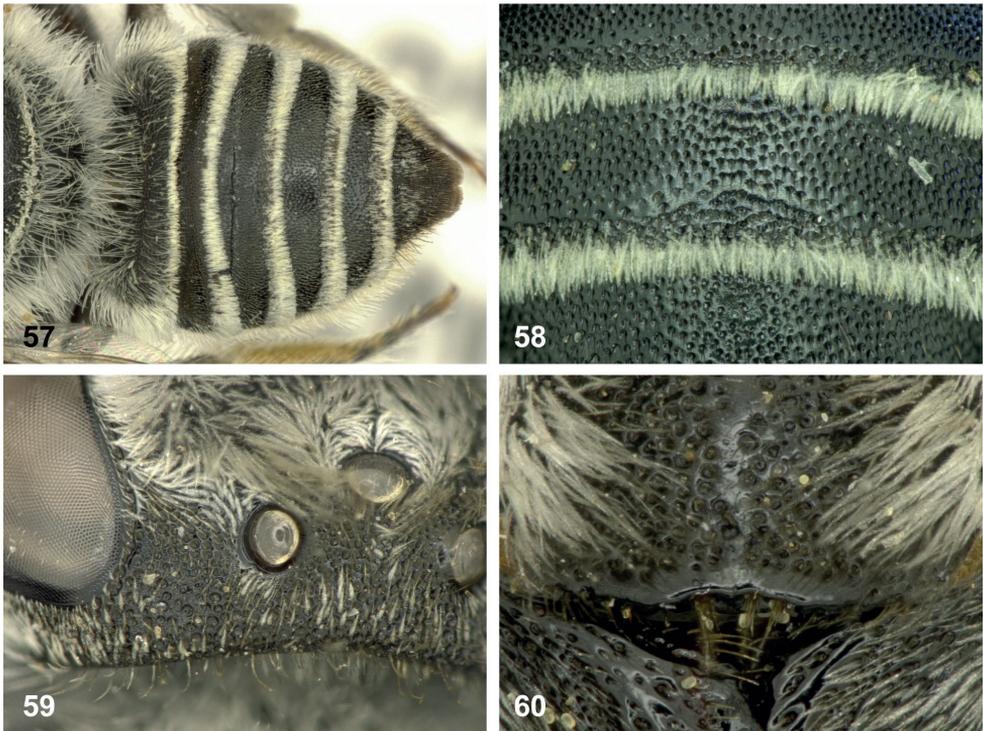
Figs 57–60

Megachile leucostoma Pérez, 1907: 489, ♂, “Dibba [Oman]”. Holotype ♂ (MNHN).

Megachile submucida Alfken, 1926: 126, ♀, ♂ partim, “Kingi [Maryut, sw von Alexandria; Egypt]”. Lectotype ♀, by designation of van der Zanden (1986: 66) (SMFD).
Synonymy in Praz et al. (2021).

Megachile microxantha Cockerell, 1937: 205, ♂, “Aden [Yemen]”. Holotype ♂ (BMNH).
Synonymy in Praz et al. (2021).

Megachile privigna Rebmann, 1968: 40, ♂, “Fayed [Egypt]”. Holotype ♂ (SMFD).
Synonymy in Praz et al. (2021).



Figures 57–60. *Megachile leucostoma* **57** female metasoma **58** female metasomal tergum 4 **59** female vertex **60** apex of female clypeus.

Examined material and distribution. See Praz et al. (2021).

Geographic variation. In Israel, Jordan and Oman, the scopa is nearly entirely orange (see above under *M. anatolica*); in the UAE, the scopa is mostly white, orange on S6. In Egypt, the scopa is usually dark on S6, white on S2–S5, but often slightly orange on S5. Whether the white scopa, as observed in Egypt, is the result of introgression with *M. pusilla*, remains unknown. It is also possible that the orange scopa is the result of introgression with the taxon referred to as *M. venusta* from Africa, which nearly always has orange scopa. Given its wide distribution in Egypt and in the Arabian Peninsula, *M. leucostoma* may in fact be present in the Afrotropical region, and could be conspecific with an African taxon, for example *M. modestissima* Dalla Torre, 1896 (a replacement name for *M. modesta* Smith, 1879, presumably described from the Karthoum area; see below). *Megachile modestissima* is currently placed in synonymy with *M. venusta*.

Megachile pusilla Pérez, 1884

Figs 61–66

Megachile pusilla Pérez, 1884: 263, ♀ ♂, “Portugal”. Lectotype ♀, by present designation (MNHN); paralectotypes ♀ (MNHN), by present designation.

Megachile variscopa Pérez, 1895: 24, ♀, “Bône” [Annaba, Algeria]. Lectotype ♀, by present designation. New synonymy.

Megachile timberlakei Cockerell, 1920: 119, ♂ ♀, “Kaimulai [sic], Oahu” [Kaimuki, Honolulu, Hawaii, USA; introduced]. Holotype ♂ (USNM). New synonymy.

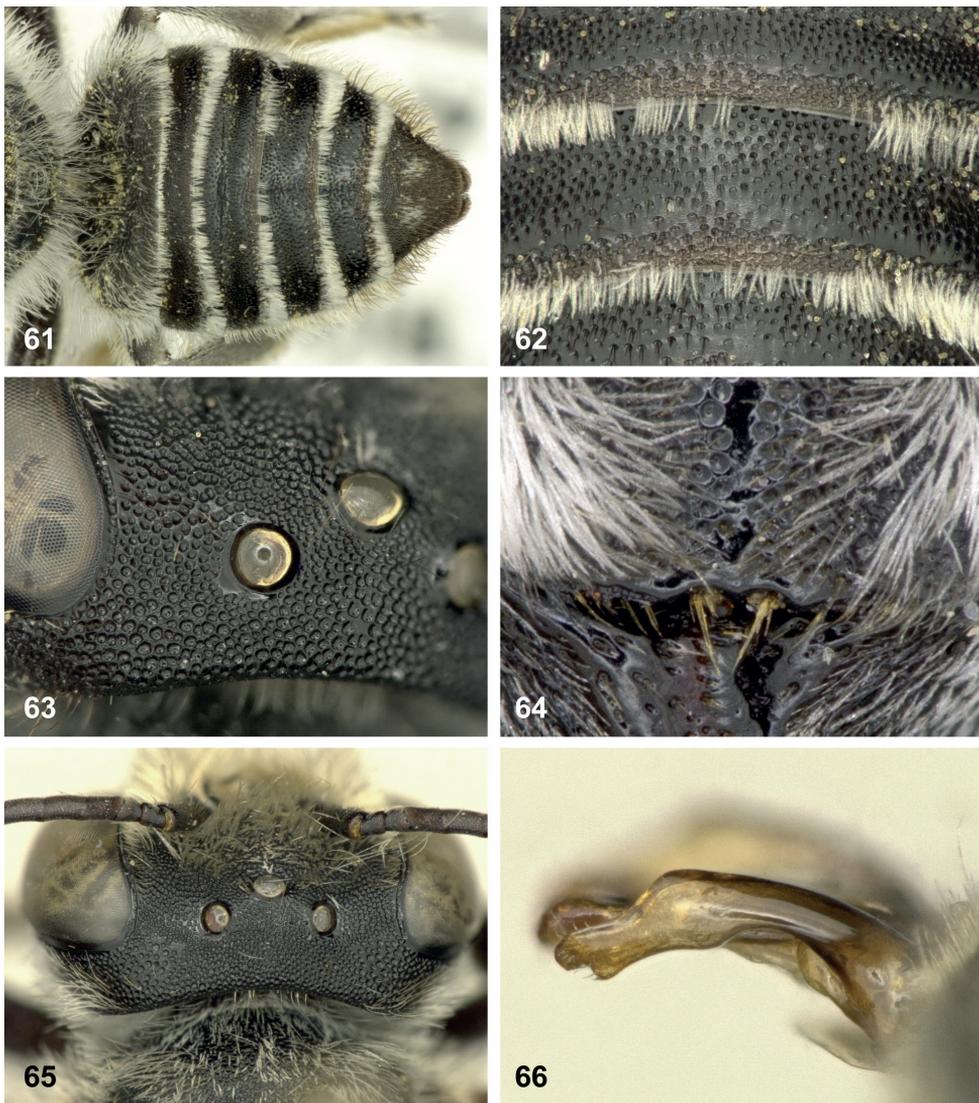
Megachile atratula Rebmann, 1968: 38, ♂ ♀, “Rapallo” [Italy]. Holotype ♂ (SMFD?), paratypes ♂ ♀ (SMFD). New synonymy.

Megachile striatella Rebmann, 1968: 41, ♂ ♀, “El Kantara” [Algeria]. Holotype ♂ (restricted to genitalia) (SMFD), paratypes ♂ ♀ (SMFD). New synonymy.

Megachile sudai Ikudome, 1999: 3, ♀, [Okinawa, Japan; introduced]. New synonymy.

Material examined. Type material. Lectotype ♀ (MNHN) of *M. pusilla*, a well-preserved female, by present designation. The specimen is labeled as follows: 1. “Portug [handwritten, handwriting of Pérez; = Portugal]. 2. “Muséum Paris Coll. J. Pérez 1915” [printed]. 3. Lectotypus *Megachile pusilla* ♀ Pérez design. Malisheva 1989 [printed and handwritten on red paper]; 4. Museum Paris EY0000002295. Two additional females labelled as follows are designated as paralectotypes. 1. “Portug” [handwritten, handwriting of Pérez; = Portugal]; 2. “Muséum Paris Coll. J. Pérez 1915” [printed]. 3. Paralectotypus *Megachile pusilla* ♀ Pérez des. C. Praz 2022 [printed and handwritten on red paper]; 4. Museum Paris EY0000002296; and 1. “Portugal” [printed]; 2. “Muséum Paris Coll. J. Pérez 1915” [printed]. 3. Paralectotypus *Megachile pusilla* ♀ Pérez des. C. Praz 2022 [printed and handwritten on red paper]; 4. Museum Paris EY0000002297.

Lectotype ♀ (MNHN) of *M. variscopa*, a well-preserved female labeled as follows: 1. “Bône” [handwritten, possibly by Pérez]; 2. “Muséum Paris Coll. J. Pérez 1915”



Figures 61–66. *Megachile pusilla* **61** female metasoma **62** female metasomal tergum 4 **63** female vertex **64** apex of female clypeus **65** dorsal view of male head **66** male genitalia.

[printed on blue paper]; 3. “Lectotype *M. variscopa* Pérez des. van der Zanden 1989” [printed and handwritten on red paper]. 4. “*Megachile albobirta* det. van der Zanden 1994”; 5. “*Megachile pusilla* det. C. Praz 2022” [printed and handwritten]. *Megachile albobirta* (Brullé, 1839) was considered to be conspecific with *M. concinna* by Tkalcu (1993), explaining van der Zanden’s identification as *M. albobirta* (see Praz 2017). One additional female from Bône is designated as a paralectotype. It is labeled as follows. 1. “Bône” [handwritten, possibly by Pérez]; 2. “Muséum Paris Coll. J. Pérez 1915” [printed on blue paper]; 3. “Paralectotype *M. variscopa* Pérez des. C. Praz 2022”

[printed and handwritten on red paper]; 4. “*Megachile pusilla* det. C. Praz 2022” [printed and handwritten].

Paratypes ♂ ♀ (SMFD) of *M. atratula*. The holotype, indicated to be in Rebmann’s collection (SMFD) could not be located.

Holotype ♂ (SMFD) of *M. striatella* (see above). **Paratypes** ♀ ♂ of *M. striatella* (SMFD).

Notes: we did not examine the holotype of *M. timberlakei*, but pictures are available on the online catalogue of USNM (<https://collections.nmnh.si.edu>; catalogue entry number 536683). The simple gonostylus, typical of the *concinna* complex is visible. In addition, two DNA barcodes for specimens collected in Hawaii and identified as *M. timberlakei* are 100% identical with *M. pusilla*.

We did not examine the type material of *M. sudai*, but examined and sequenced specimens from Okinawa kindly sent by H. Nagase; these specimens perfectly agree with *M. pusilla*; see Nagase (2016).

Other material. 54 specimens from the following countries: Argentina (introduced), France, Greece, Greece (Crete), Italy, Japan (introduced) Malta, Morocco, Spain, Tunisia, USA (introduced) (Suppl. material 1). *Megachile timberlakei* was mentioned from the Galapagos Islands (Rasmussen et al. 2012); identity of these specimens should be checked using DNA barcodes given the challenging identifications in this group; they likely belong either to *M. pusilla* or to *M. concinna*.

Distribution. See Soltani et al. 2017: fig. 3. Northwestern Africa (Tunisia, Algeria, Morocco), southern Europe (Portugal, Spain, France including Corsica, Italy including Sicily and Sardinia, Slovenia, Greece including Crete). Presumed introduced in Madeira (Kratochwil et al. 2018). Introduced in southern America, northern America, Japan, Hawaii, and probably Australia (see note below).

Geographic variation. Specimens from Algeria and Tunisia have the scopa often partly orange on S5; whether this condition results from introgression with *M. leucostoma* remains to be established.

Note. A published barcode generated from a specimen collected near Perth, Western Australia (BOLD accession number [MSAPB1368-19](#)) is 100% identical to sequences of *M. pusilla*, suggesting that *M. pusilla* has also been introduced into Australia. This specimen is identified as *M. obtusa* Smith, 1853. We examined a picture of the holotype of *M. obtusa* (OUMNH); this species has modified front tarsi and does not belong to the same species group as *M. pusilla*.

Megachile walkeri Dalla Torre, 1896

Megachile fulvescens Walker, 1871: 47, ♀ ♂, “Harkeko; Wādy Gennèh; Wādy Ferran; Mount Sinai [Arkiko, Eritrea; ?; Wadi Feiran, Sinai, Egypt; Sinai, Egypt]”. Preoccupied, not *M. fulvescens* Smith, 1853.

Megachile walkeri Dalla Torre, 1896: 452. Replacement name for *M. fulvescens* Walker, 1871.

Megachile argentata var. *moricei* Friese, 1899b: 334, ♀ ♂, “Elephantinen; Philae; Ober-Aegypten-Assuan [Egypt, Elephantine and Philae Island; Aswan].

Megachile blanda Rebmann, 1968: 44, ♂, “Luxor [Egypt]”. Holotype ♂, SMFD. Preoccupied, not *M. blanda* Mitchell 1930. Synonymy in Praz et al. (2021: 307).

Examined material and distribution. See Praz et al. (2021).

Additional, extralimital species

Megachile concinna Smith, 1879

Megachile concinna Smith, 1879: 79, ♀, “St. Domingo [Dominican Republic; introduced]”. Syntype (or holotype) ♀ (BMNH).

Megachile multidens Fox, 1891: 345, ♀ ♂, “Kingston [Jamaica; introduced]”.

Material examined. Type material. *Syntype* (or holotype) ♀ of *M. concinna* (BMNH). The original description does not indicate the number of specimens, it is therefore not clear whether this specimen is the holotype (by monotypy) or a syntype. This female specimen agrees with the original description; it is slightly larger than other members of the *concinna* complex, as indicated by F. Smith, who gave its length as 4 lines (=approx. 8.4 mm), while the length given for *M. venusta* is 3 ¼ lines (7.8 mm); also as indicated in the original description, there are two spots of white hairs on the disc of T6, unlike in *M. venusta*.

Note: It is likely that *M. derelictula* Cockerell, 1937, described from Barbados, is also a synonym of *M. concinna*.

Other material. 13 specimens from the following countries: Benin, Cape Verde, Dominican Republic (introduced), French Guyana (introduced), Kenya, Republic of Trinidad and Tobago (introduced) (Suppl. material 1).

Note. This species is difficult to separate from other members of the *concinna* complex. The genetic analyses of Soltani et al. (2017) suggested that *M. concinna* and *M. venusta* are distinct and both widely distributed in Africa, although only few specimens have been analyzed; these authors also reported specimens of both species in sympatry in one site in Kenya (Suppl. material 1). For these reasons, these two species are treated as distinct. Compared to most other members of the *concinna* complex, *M. concinna* is on average slightly larger. The female has the scopa white (dark on S6), contrary to *M. venusta* which mostly has the scopa orange; the punctuation on the terga appears to be slightly denser in *M. concinna* compared to other members of the complex; and the disc of T6 has two distinct spots of hairs, unlike in *M. venusta* (Soltani et al. 2017: table S3). Based on the few specimens examined, the male of *M. concinna* can not be separated from the other species of the *concinna* complex. The identity of this species is based on DNA barcoded specimens from the Dominican Republic (the type locality of *M. concinna*), assuming that only one species of the *concinna* complex is present there.

***Megachile venusta* Smith, 1853**

Megachile venusta Smith, 1853: 159, ♀, “Port Natal; Cape of Good Hope [Durban; Cape of Good Hope; South Africa]”. Syntype ♀ (BMNH).

Megachile modesta Smith, 1879: 63, ♀, “White Nile. Collected by Consul Petherick [following Baker 2002: 22, the type locality is likely Khartoum, where John Petherick was the British Vice-Consul]”. Syntype ♀ (BMNH). Preoccupied, not *M. modesta* Smith, 1862.

Megachile modestissima Dalla Torre, 1896: 439. Replacement name for *M. modesta* Smith, 1879.

Material examined. Type material. *Syntype* ♀ of *M. venusta* (BMNH).

Syntype ♀ of *M. modesta* Smith, 1879 (BMNH).

Other material. 11 specimens from the following countries: Central African Republic, Kenya, Senegal, South Africa (Suppl. material 1).

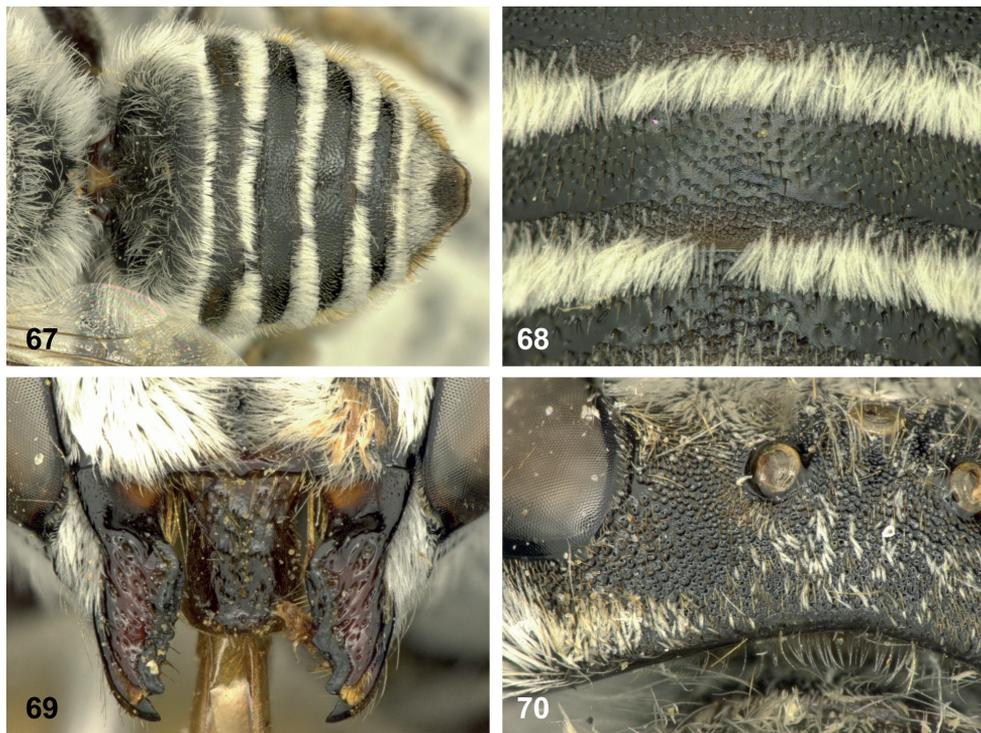
Note. The identity of this species is unclear and requires additional work; for this reason, the list of synonyms given above is incomplete. In the phylogenetic analyses of Soltani et al. (2017), two main clades were recovered, referred to as *M. venusta* clade 1 and *M. venusta* clade 2. Both contained specimens agreeing with members of the *concinna* complex; females of both clades are mostly characterized by the partly orange scopa (one barcoded female from Senegal had white scopa, black on S6, as in *M. concinna*). It is unclear whether these two clades are conspecific. Clade 2 was restricted to South Africa, while clade 1 contained specimens from Kenya, South Africa, the Central African Republic and Senegal. The name *M. modestissima* may apply to clade 1, *M. venusta* to clade 2, if these two clades are demonstrated to represent two distinct species. Additional work is needed to properly delineate species, to obtain data on their distribution, and to properly identify the relevant type material.

***Megachile viridicollis* Morawitz, 1875**

Figs 67–70

Megachile viridicollis Morawitz, 1875: 117, ♂, “поймать только раз в степи Кизиль кумь 15 мая у восточной окраины горы Каракъ [Caught only once in the steppe of Kyzyl Kum, the 15. May, at the eastern edge of the mountain Karak; Kyzyl Kum does not refer to the Kyzyl Kum Desert, but probably to the locality ҚЫЗЫЛҚҰМ, approx. 41.911N 67.988E, Kazakhstan]”.

Material examined. Type material. We were not able to examine the type material of *M. viridicollis*. The placement of this species into the *concinna* complex is based on the original description, which mentions that the species is highly similar to “*M. argentata*” (either *M. pilidens* or *M. leachella*), but markedly larger, and with a conspicuous tooth at the base of the mandible. We interpret this tooth as the tooth present just behind the



Figures 67–70. *Megachile viridicollis* **67** female metasoma **68** female metasomal tergum 4 **69** apex of female clypeus **70** female vertex.

base of the mandible (as in Fig. 12). We also examined one male specimen identified as *M. viridicollis* from “Baigakum bei Djulek Turkest. [Kazakhstan: Baygekum, Zholek; approx. 44.314 N 66.475 E]”, identified by L. Wollmann (who possibly had access to material identified as *M. viridicollis* by Morawitz) and perfectly agreeing with the original description of *M. viridicollis*. Baygekum is located approximately 200 km NE of the type locality of *M. viridicollis*.

Other material. Eight specimens from Kazakhstan and Uzbekistan (Suppl. material 1).

Description. The following description is based on one male specimen from Baygekum and several female specimens from Gazli, Uzbekistan, presumed to be conspecific.

Male: Member of the *concinna* complex, as determined by the presence of the tooth behind the mandibular base and the apically simple genitalia. OOD as in European populations of *M. anatolica* (as in Fig. 11), thus nearly as long as interocellar distance. Vestiture particularly long and dense, in particular tergal fasciae thicker and longer. Larger than all other species of the *concinna*-complex (body length 10 mm).

Female: similar to *M. anatolica*, differs from that species in the following characteristics: larger (body length 11 mm). Vertex laterally covered with short, brownish hairs, so that integument is not visible under vestiture unless the hairs are removed (Fig. 70); punctation dense and fine (Fig. 70). Clypeus apically without teeth, broadly emarginated (as in *M. pilidens*) but with a conspicuous, rounded, thickened margin,

medially with a small tooth (Fig. 69). Metasoma with snow white vestiture forming particularly dense tergal fasciae and entirely covering the base of T6. Punctuation of disc of T4 sparse (Fig. 68), similar to European populations of *M. anatolica* (Fig. 8).

Distribution. So far known only from few specimens from Kazakhstan and Uzbekistan.

Geographic variation and note. The identity of this taxon remains unclear, as very little material has been studied. Soltani et al. (2017) presented sequence data for two populations, one based on several male specimens from the region of Khiva, Uzbekistan (41.33N, 60.35E and 41.36N, 60.35E), and one based on several female specimens from Gazli, Uzbekistan (40.383N, 63.100E); these two populations were genetically strongly divergent (4.1 %). The male specimens from the Khiva region are markedly smaller than the male examined from Baygekum (see above), while the females from Gazli are particularly large for the *concinna* complex. It is possible that the populations from Khiva represent transitional populations to *M. anatolica*. Additional research including more material from Central Asia is needed to better delineate this species. *Megachile viridicollis* and *M. anatolica* are genetically closely related, and both may be treated as conspecific, in which case the name *M. viridicollis* would have priority. The striking differences in female morphology lead us to treat both taxa as distinct species.

Identification key for the species of the *leachella* group in the Western Palaearctic. Extralimital species (*M. concinna*, *M. venusta* and *M. viridicollis*) are excluded

Males

- 1 S4 medially with a small tubercle covered with yellowish to greyish hairs (Fig. 23). Front tarsal segments 2–4 whitish-brown (Fig. 22). Gena without tooth behind mandibular base. Gonostylus bifid, with a long and slender preapical process (Fig. 24) (Palaearctic, from Morocco to Central Asia) *Megachile argentata* (Fabricius)
- S4 medially without tubercle, with a small (Figs 13, 53) or large patch of yellowish hairs (Fig. 29). Front tarsal segments mostly dark brown (Figs 48, 49, 51, 52) (except in Sardinian populations of *M. leachella*; Fig. 50). Gena with or without tooth behind mandibular base. Gonostylus with or without preapical process 2
- 2 S4 medially with particularly dense patch of yellowish hairs (Fig. 29). Gena without tooth or only with short, truncate tooth behind mandibular base. Gonostylus bifid with a short, broad and strongly curved preapical process, process only 1.5 times as long as wide (Figs 30, 31). 3
- S4 with a small spot of yellowish hairs medially (Fig. 13). Gena with tooth behind mandibular base (Fig. 12) (best visible in front view, especially if mandibles are closed). Gonostylus either apically bifid, with short or long preapical process, but process of different shape (Figs 54–56), or simple (Figs 14, 66)..... 4

- 3 Integument of T1-T2 predominantly orange (Arabian Peninsula, Egypt including Sinai Peninsula, Israel, Iran)***M. walkeri* Dalla Torre**
- Integument of T1-T2 predominantly dark brown (Northern Africa, Israel, Sinai Peninsula, Lebanon, Turkey, Cyprus, Rhodos).....***M. inexpectata* Rebmann**
- 4 Gonostylus apically bifid, with short or long preapical process (Figs 54–56). Often slightly larger, body length 8–9mm ***Megachile leachella* Curtis**
- Gonostylus apically simple (Figs 14, 66). Often slightly smaller, body length 7mm (except *M. anatolica*, which can be distinguished by the longer ocellocipital distance) (*M. concinna* complex) **5**

The separation of the following species is difficult in the male sex

- 5 Vertex mostly longer, ocellocipital distance subequal to interocellar distance (Fig. 11) (the ocellocipital distance becomes gradually shorter towards the East, and in Iran, the condition is identical with the following species). Body size approximately 8–9 mm. (Italy, southeastern Europe, Turkey, Northern Israel, Syria, Lebanon, Iran) ***M. anatolica* Rebmann**
- Vertex shorter, ocellocipital distance shorter than interocellar distance (Fig. 65). Body size approximately 7–8 mm. (Southern Europe, Northern Africa, presumed absent from Northern Israel, Turkey, Lebanon)..... **6**
- 6 Southern Europe, northwestern Africa (identity of populations located between Egypt and Tunisia unclear)***M. pusilla* Pérez**
- Arabian Peninsula, southern Israel, Egypt ***M. leucostoma* Pérez**

Females

- 1 Integument of T1 and T2 predominantly brown-orange (Praz et al. 2021: fig. 8). Ventral surface of trochanters and femora 2 and 3 covered with short, modified, capitate hairs (Praz et al. 2021: cf. fig. 3).....***M. walkeri* (Dalla Torre)**
- Integument of T1 and T2 dark brown. Ventral surface of trochanters and femora 2 and 3 without short, modified hairs **2**
- 2 Vertex mostly longer, ocellocipital distance approximately equal to 1.5–1.8 x diameter of lateral ocellus (Fig. 9; this character gets gradually less pronounced towards the east; in Iran the condition is as in the following species). Body size approximately 8–9 mm. Apical clypeal margin with 5 comparatively large blunt teeth (Fig. 10). Disc of T6 with two small, separated spots of appressed white hairs (Fig. 7). (Southeastern Europe, Turkey, Northern Israel, Syria, Lebanon, Iran) ***M. anatolica* Rebmann**
- Vertex shorter, ocellocipital distance approximately subequal to diameter of lateral ocellus (e.g. Fig. 20). Apical clypeal margin straight without rounded teeth, or with fewer teeth, or with 5 less conspicuous teeth (Figs 21, 60, 64). Disc of T6 with vestiture variable, but if body size above 8 mm, then disc of

- T6 usually with large spots of appressed white hairs (Figs 15–18, 25, 32, 33, 34, 36)..... **3**
- 3 Apical clypeal margin with emargination narrow, often with only three little-visible, rounded teeth (Figs 60, 64). Disc of T6 either without appressed white hairs, or with two small, well-separated spots (Figs 57, 61). (*M. concinna complex*, in part)..... **4**
- Apical clypeal margin with emargination broad, either straight with little visible rounded teeth, or with five very small teeth (Fig. 21). Disc of T6 with extensive appressed, white vestiture (Figs 15–18, 25, 32–36)..... **5**
- 4 Scopa usually white, black on S6, sometimes with isolated orange hairs on S5. Southern Europe, northwestern Africa (identity of populations comprised between Egypt and Tunisia unclear)..... ***M. pusilla* Pérez**
- Scopa often extensively orange, sometimes entirely orange, although also white (dark on S6) in Egypt. Arabian Peninsula, southern Israel, Egypt..... ***M. leucostoma* Pérez**
- 5 Disc of T4 with comparatively sparse punctation (there is much variation in this character; a separation from *M. argentata* is not always straightforward, especially in regions where the vestiture colour of *M. leachella* is not snow white and does not offer additional discriminating characters with *M. argentata*), interspaces on average as large or larger than puncture diameters (Fig. 37) (except in Crete and Cyprus, ssp. *cretica* ssp. nov., Fig. 38, and *densipunctata* ssp. nov. Fig. 39). Vestiture brown in Northern Europe (Fig. 32), becoming progressively lighter towards southern Europe and northern Africa, where it is snow-white (Fig. 34). In northwestern Africa, see additional characters in Table 1..... ***M. leachella* Curtis**
- Disc of T4 more densely punctured (Figs 19, 26), interspaces on average smaller than puncture diameters. Vestiture brown or snow white..... **6**
- 6 Vestiture snow white (Fig. 25). Disc of T6 with extended area covered with white, appressed hairs, white hairs often not forming two separated spots (Fig. 25). Mesonotum densely covered by scale-like white hairs (Fig. 28). Terga 4 and 5 laterally mostly without erect dark hairs. Punctuation of vertex comparatively fine and dense, puncture diameters on average less than 45 µm (Fig. 27). Ocelloccipital distance often shorter than 300 µm..... ***M. inexpectata* Rebmann**
- Vestiture grey-brown (Fig. 16), yellow-orange in Corsica and Sardinia (Fig. 18), red-orange in Malta (Fig. 17), snow white in northwestern Africa (Fig. 15). Disc of T6 with two of white hairs clearly separated by dark hairs (Figs 15–18). Mesonotum usually with scale-like hairs restricted to anterior and posterior parts. Terga 4 and 5 laterally mostly with numerous erect dark hairs. Punctuation of vertex more coarse, punctures on average above 45 µm diameter (Fig. 20). Ocelloccipital distance mostly longer than 300 µm..... ***M. argentata* (Fabricius)**

Discussion

This taxonomic revision of a small group of widely distributed leafcutting bee taxa exemplifies one of the problems associated with taxonomic revisions: the identification of type material. This task was complicated by: i. poorly preserved types, where the morphological characters were difficult to examine (e.g., many holotypes of species described by O. Rebmann); ii. type specimens belonging to a sex that was not easily identified (e.g., *M. argentata*), or consisting of a gynandromorph individual (*Perezia maura*); iii. type specimens consisting of several body parts not originating from a single individual (*M. inexpectata*, *M. striatella*); iv. type specimens originating from introduced populations, where the source of the introduced population was initially unknown (*M. timberlakei* and *M. sudai*; *M. concinna*); and v. type specimens whose type locality is unclear (e.g., *M. modesta* Smith, 1879: type locality “White Nile”, a nearly 4000-km river segment that flows from Uganda to Sudan). DNA barcoding was pivotal for solving most of these issues, especially for confidently establishing the identity of introduced populations of *M. pusilla* and *M. concinna*. However, what should have been a simple taxonomic revision of seven rather well-characterized species turned into a tedious study. This case exemplifies a major paradox in taxonomy, as our study would have been completed at least twice as quickly if no previous taxonomic work had been conducted at all, enabling us to simply describe the species as new.

One approach would have strongly accelerated the process: the assembly of a DNA barcode reference library for the most problematic type specimens. We could have focused on the scientifically interesting part of a taxonomic revision – species delimitation – and the fastidious nomenclatural translation of species delimitation into names would have been more straightforward. Laboratory protocols are available to obtain full DNA barcodes from 19th century specimens (Strutzenberg et al. 2012; Prosser et al. 2015; Hausmann et al. 2016); this approach has not been tested for Hymenoptera although NGS sequencing of old museum specimens using a single leg has been conducted (Blaimer et al. 2016). We nevertheless argue against the systematic barcoding of all types, since our finding would certainly not apply to all bee genera or bee faunas. In some specific cases, however, we feel that the barcoding of type material would dramatically speed up taxonomic revisions: revising the Afrotropical fauna of *Megachile*, for example, would take decades at the current pace given the numerous unclear names (see note above under *M. venusta*) and the scarcity of recent material. Many species are probably widely distributed and geographically variable, as shown here for *M. venusta*. The type material of species described by T. D. A. Cockerell and J. J. Pasteels, representing a significant proportion of the Afrotropical *Megachile* fauna, are likely to yield usable DNA. Given the unprecedented rate of biodiversity decline and the implications of taxonomic impediments for bee conservation (Praz et al. 2022), we argue that any methodological innovation that speeds up taxonomic revisions is worth consideration. DNA-barcoded type material represents a thus-far little used application of DNA barcoding to speed up taxonomy and to alleviate one of the inevitable impediments of taxonomy – the problem of unclear names and type specimens.

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Supplementary material I

List of examined specimens, with BOLD and genbank accession numbers

Authors: Christophe J. Praz, Dimitri Bénon

Data type: Occurrences

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