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Merodon chalybeus subgroup: an additional piece of the *M. aureus* group (Diptera, Syrphidae) puzzle

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In this study, we examined the morphology, genetics and distribution of the members of the *Merodon chalybeus* subgroup (*M. aureus* species group): *M. chalybeus* Wiedemann in Meigen, 1822, *M. minutus* Strobl, 1893 and *M. robustus* Veselić, Vujić & Radenković, 2017. Two of the species, *M. chalybeus* and *M. minutus*, are morphologically very similar and often misidentified in the literature. Here, by employing an integrative taxonomic approach we provide strong evidence for the separation of *M. chalybeus* and *M. minutus*. Our results show their clear allopatric distribution: *M. minutus* on the Balkan Peninsula, Sicily, Sardinia and Corsica, while *M. chalybeus* is a western Mediterranean species distributed on the Iberian Peninsula and northwest Africa. Data on the distribution of *M. robustus* were updated, with new records from Cyprus, Israel and Turkey, besides its type locality (Samos in Greece). We provide evidence for *M. chalybeus* and *M. minutus* representing a species complex, named the *M. chalybeus* complex, which together with *M. robustus* constitute the *M. chalybeus* subgroup.

Introduction

Merodon Meigen, 1803 is the largest hoverfly genus in Europe with more than 120 recognized species (Vujić *et al.* 2015). It is distributed in the Palaearctic and Afrotropical Regions and comprises 199 species (Vujić *et al.* 2021a, 2021c, 2021d). The number of species is still rising, and many new species have recently been described (Marcos-García *et al.* 2011, Radenković *et al.* 2011, 2018a, 2018b, 2020, Vujić *et al.* 2012,

2015, 2018, 2019, 2020a, 2020b, Ačanski *et al.* 2016, Šašić *et al.* 2016, Kočiš Tubić *et al.* 2018, Šašić Zorić *et al.* 2018, 2020, Likov *et al.* 2019, Djan *et al.* 2020). Adults of *Merodon* morphologically mimic bumblebees and bees (Hymenoptera: Apidae) and feed on pollen and nectar from early spring to late autumn (Speight 2020). *Merodon* larvae feed on underground storage organs of geophytes (Ricarte *et al.* 2008, Andrić *et al.* 2014, Preradović *et al.* 2018). The geophytes are especially diverse in the Mediterranean Region (Bazos

2005), where the highest diversity of *Merodon* species is recorded.

Merodon aureus species group (*sensu* Radenković *et al.* 2011) is distributed around the Mediterranean Basin and is known for its exceptionally high diversity and an especially large number of cryptic and endemic taxa (Šašić *et al.* 2016, Veselić *et al.* 2017, Radenković *et al.* 2018b, Šašić Zorić *et al.* 2018, 2020, Vujić *et al.* 2020b, 2021b). The group contains six subgroups of species (*M. aureus* subgroup; *M. bessarabicus* subgroup; *M. caerulescens* subgroup; *M. cinereus* subgroup; *M. dobrogensis* subgroup; *M. chalybeus* subgroup), and one unplaced species *M. unguicornis* Strobl, 1909 (Veselić *et al.* 2017, Šašić Zorić *et al.* 2018, Vujić *et al.* 2021b). The subgroups are defined according to species that have similar morphologies, but exhibiting small, consistent, interspecific differences. Each subgroup contains at least one complex of cryptic species although it can contain multiple species complexes and species outside complexes. Species complexes comprise morphologically inseparable species, which can only be resolved by employing an integrative taxonomy approach, which include the use of different data types such as molecular, geometric morphometric and ecological data (Šašić *et al.* 2016, Šašić Zorić *et al.* 2018, 2020, Radenković *et al.* 2018b, Vujić *et al.* 2020b).

The existence of the *chalybeus* complex was firstly mentioned by Šašić *et al.* (2016) and was later assigned to the homonymous subgroup (Šašić Zorić *et al.* 2018, 2020), while Vujić *et al.* (2021b), in their recent taxonomic revision of the genus, included three species within the *chalybeus* subgroup (*Merodon chalybeus* Wiedemann in Meigen, 1822, *Merodon minutus* Strobl, 1893 and previously unplaced species *Merodon robustus* Veselić, Vujić & Radenković, 2017).

Merodon chalybeus was described in 1822 based on a female specimen from Portugal (Meigen 1822). This species often appears in the literature under the name *Merodon spicatus* Becker, 1907, but was recently considered by Marcos-Garcia *et al.* (2007) to be a junior synonym of *M. chalybeus*. Mengual *et al.* (2006) analyzed, *inter alia*, the COI (cytochrome *c* oxidase subunit I) sequences of the two *M. chalybeus* specimens from Spain and confirmed the posi-

tion of this species within the *M. aureus* group. According to these authors, the distribution of *M. chalybeus* included Spain, southern France and the former Yugoslavia, while Marcos-Garcia *et al.* (2007) extended the distribution of this species to Portugal and northern Africa (Morocco). Later, several authors confirmed *M. chalybeus* in western Spain (Carles-Tolrà 2010, Kočiš Tubić *et al.* 2018) and Portugal (van Eck 2011, 2016), but also expanded its range to Greece (Ssymank 2012), Algeria (Haffaressasa *et al.* 2017) and Corsica (Speight 2020).

Merodon minutus was described by Strobl in 1893 from a female specimen from Dalmatia (Croatia) (Strobl 1893). This species occasionally appeared in publications as part of checklists or studies of specific areas. Speight and Sarthou (2008) updated the French list of hoverfly species replacing *M. minutus* with *M. chalybeus*. Petanidou *et al.* (2011) listed *M. minutus* from central Greece. Vujić *et al.* (2016) categorized *M. minutus* as a species distributed in the Balkans and eastern Mediterranean Islands, but not in the Anatolian Peninsula. *Merodon minutus* was cited from Muğla Province, western Turkey (Reemer & Smit 2007, Vujić *et al.* 2011, Saribiyik 2014), but this record needs to be confirmed. Vujić *et al.* (2016) also assigned *M. robustus* (as *M. aff. chalybeus*) as a taxon present on the Anatolian Peninsula and on the eastern Mediterranean Islands but absent from the Balkan Peninsula. According to Speight (2020), the distributional range of *M. minutus* includes Corsica, Mediterranean region of former Yugoslavia, Greece, Crete and Morocco; but it requires additional study due to the recent nomenclature changes and overlapping with *M. chalybeus* range.

The identification of *M. chalybeus* and *M. minutus* is further convoluted by the presence of morphologically similar *Merodon robustus*, recently placed within the *M. chalybeus* subgroup (Vujić *et al.* 2021b). According to Veselić *et al.* (2017), this recently described species is an endemic species from the Greek island Samos.

High morphological similarity between *M. chalybeus* and *M. minutus* and their potentially overlapping distributions make their taxonomic status questionable and stresses the need for further material to be examined using multiple data sources, such as traditional morphology,

molecular data, geometric morphometry and distributional data. Integrative taxonomic approach using data from different sources was proved to be useful in many recent studies on *Merodon* (e.g., Marcos-García et al. 2011, Ačanski et al. 2016, Šašić et al. 2016, Kočiš Tubić et al. 2018, Radenković et al. 2018a, 2018b, Šašić Zorić et al. 2018, 2020, Arok et al. 2019, Djan et al. 2020, Vujić et al. 2020a, 2020b). DNA barcoding of species based on analyses of the 5'-end of the COI gene has become standard practice in integrative taxonomy since its introduction by Hebert et al. (2003). In hoverflies, both 5'-end and 3'-end of the COI gene are of equal importance in species delimitation and can be used either separately or together (e.g., Vujić et al. 2013, Šašić et al. 2016, Nedeljković et al. 2018, 2020, Radenković et al. 2018a, 2018b, Grković et al. 2019, Djan et al. 2020). Integrative taxonomy-based studies of hoverflies often combine molecular data with wing and/or surstyle geometric morphometrics in resolving species boundaries. Both morphological structures have great discriminatory power and congruence with molecular data, as it has been shown in successful cryptic species delimitation among several hoverfly genera (*Chrysotoxum* Meigen, 1803, *Pipiza* Fallén, 1810, *Merodon* and *Eumerus* Meigen, 1822). Additionally, recent hoverfly studies that implemented geometric morphometrics analysis of wing and surstyle showed that the surstylus shape has greater discrimination power than the wing shape (Nedeljković et al. 2013, 2015, Ačanski et al. 2016, Šašić et al. 2016, Radenković et al. 2018b, Šašić Zorić et al. 2020).

To verify the species status of *M. chalybeus* and *M. minutus*, and to evaluate their position together with *M. robustus* within the *M. chalybeus* subgroup, we (1) re-examined diagnostic morphological character of these species, (2) used potential differences in the shape of wing and male genitalia to delimit these taxa by means of geometric morphometrics analyses, (3) determined the genetic variability between species using DNA barcoding, and (4) re-assessed the species distribution.

Material and methods

In total, 456 specimens belonging to the *M. cha-*

lybeus complex (265 of *M. chalybeus* and 191 of *M. minutus*) and 64 specimens of *M. robustus* were studied. Specimens originated from Albania, Algeria, Croatia, Cyprus, France, Greece, Israel, Italy, Libya, Morocco, Portugal, Spain, Tunisia and Turkey, and were collected between 1858 and 2018. They are deposited in: Natural History Museum, London, UK (BMNH); Benediktinerstift Admont, Admont, Austria (BSA); University of Alicante, Spain (CEUA); Entomological Museum of Isparta, Isparta, Turkey (EMIT); Faculty of Sciences, Department of Biology and Ecology, University of Novi Sad, Novi Sad, Serbia (FSUNS); Institut royal des Sciences naturelles de Belgique, Brussels, Belgium (IRSNB); The Melissotheque of the Aegean, University of the Aegean, Mytilene, Greece (MAegean); Museum für Naturkunde, Berlin, Germany (MfN); Musée National d'Histoire Naturelle, Paris, France (MNHN); Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland (MZH); Naturhistorisches Museum Wien, Vienna, Austria (NHMW); Naturalis Biodiversity Center, Leiden, the Netherlands (RMNH); Tel Aviv University, Tel Aviv, Israel (TAUI); World Museum Liverpool, Liverpool, UK (WML); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (ZFMK); Zoologisches Museum of the Humboldt University, Berlin, Germany (ZHMB); Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark (ZMUC); Bartak Miroslav Collection, Czech Republic (BM coll.); de Courcy Williams Michael collection, Greece (CWM coll.); Doczkal Dieter collection, Germany (DD coll.); Hauser Martin collection, USA (HM coll.); Palmer J. Chris collection, UK (PJC coll.); Ssymanck Axel collection, Germany (SA coll.); van Steenis Jeroen collection, the Netherlands (SJ coll.); Smit T. John collection, the Netherlands (STJ coll.); van Steenis Wouter collection, the Netherlands (SW coll.). In the material examined, specimens are ordered alphabetically by country and by increasing latitude (south to north) within the country.

The occurrence points (geographical coordinates) were entered into the Geographic Information System DIVA-GIS 5.2 software (Hijmans et al. 2005) to generate the distribution maps.

Morphological terminology of features other than genitalia follows Thompson (1999), and of male genitalia follows Marcos-García *et al.* (2007).

Preparation of male genitalia

To study the male genitalia, dry specimens were relaxed in humidity chamber, and the genitalia were extracted with an insect pin with a hooked tip. They were cleared by boiling them individually in tubes with water-diluted KOH pellets for 5 minutes. This was followed by brief immersion in acetic acid to neutralize KOH, and immersion in ethanol to neutralise acidity. Genitals were stored in microvials containing glycerol. Morphological characters were observed under a Nikon SMZ 745T stereomicroscope. A Leica MZ16 binocular microscope was used with a Leica DFC 320 digital camera for photographs. The photographs were stacked using the CombineZP software (<https://alan-hadley.software.informer.com/>). Measurements were taken with an eyepiece graticule or micrometer.

Molecular analyses

In total, 61 hoverfly specimens were used for molecular analyses. Genomic DNA was extracted from mid and hind legs of each hoverfly. The SDS (sodium-dodecyl-sulphate) DNA extraction was performed following Chen *et al.* (2010).

Polymerase chain reactions (PCR) were carried out in 25 µl reaction volumes as follows: 95 °C for 2 min; 29 cycles of 94 °C for 30 s each, 49 °C (for the 3'-end of the COI gene) or 50 °C (for the 5'-end of the COI gene) for 30 s; 72 °C for 2 min; with a final extension at 72 °C for 8 min. The reaction mixture contained 1× reaction buffer (Thermo Scientific, Vilnius, Lithuania), 2.5 mM MgCl₂, 0.1 mM of each nucleotide, 1.25 U Taq polymerase (Thermo Scientific, Vilnius, Lithuania), 5 pmol of each primer, and approximately 50 ng of template DNA. Amplifications were carried out in an Eppendorf Personal Thermocycler and in an Applied Biosystems Veriti 96 Well Thermal Cycler. Commercial

primers C1-J-2183 (also known as Jerry) and TL2-N-3014 (also known as Pat) were used for amplification and sequencing of 3'-end COI Simon *et al.* 1994), and LCO1490 and HCO2198 (Folmer *et al.* 1994) for amplification and sequencing of 5'-end COI. PCR products were purified using Exonuclease I and FastAP thermosensitive alkaline phosphatase (Thermo Scientific, Vilnius, Lithuania) according to the manufacturer's instructions. Sequencing was performed by the Sequencing Laboratory of the Finnish Institute for Molecular Medicine (Helsinki, Finland) and Macrogen Europe (Amsterdam, Netherlands).

Data processing

The COI gene sequences were edited for base-calling errors using BioEdit ver. 7.0.9.0. (Hall 1999) and aligned manually. The 3' and 5' COI gene sequences were concatenated and combined into a single sequence matrix. The GenBank accession numbers of all sequences are given in Appendix 1. The intraspecific and interspecific uncorrected pairwise p-distances were estimated using MEGA 7 (Kumar *et al.* 2016). Maximum parsimony (MP) analysis using the heuristic search algorithm was performed in NONA (Goloboff 1999) spawned with the aid of ASADO (<http://www.diversityoflife.org/win-clada>). The parameters were set as follows: maximum trees to keep (hold) = 100 000; number of replication (mult*) = 1000; starting trees per replication (hold/) = 100; search strategy with tree bisection-reconnection method of branch swapping, multiple TBR + TBR (mult*max*) option. The bootstrap support values for clades were calculated with 1000 replicates. The maximum likelihood (ML) tree was constructed using RAxML ver. 8.2.8 (Stamatakis 2014) using the CIPRES Science Gateway web portal (Miller *et al.* 2010) under the general time reversible (GTR) evolutionary model with a gamma distribution (GTRGAMMA) (Rodríguez *et al.* 1990). Nodal supports were estimated using rapid bootstrapping with 1000 replicates. The trees were rooted on *Platynochaetus macquarti* Loew, 1862. We also included the following outgroups: *Eumerus amoenus* Loew, 1848; *E. pulchellus*

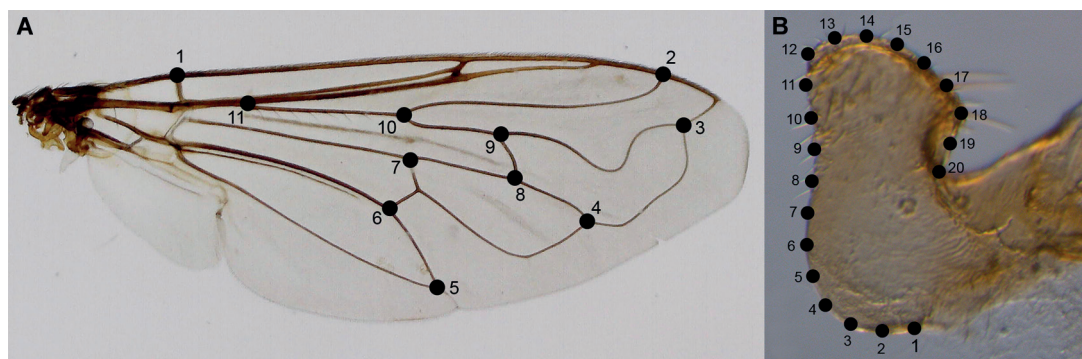


Fig. 1. Morphological traits used in geometric morphometric analysis of the *Merodon chalybeus* subgroup. — **A:** Right wing with locations of 11 landmarks. — **B:** Locations of 20 semi-landmarks on the right surstylus.

Loew, 1848; *E. pusillus* Loew, 1848; *Merodon luteofasciatus* Vujić, Radenković & Ståhls in Vujić *et al.* 2018; *M. desaturinus* Vujić, Šimić & Radenković, 1995; *M. equestris* (Fabricius, 1794); and *M. ruficornis* Meigen, 1822 (for GenBank accession numbers see Appendix 1). The number of haplotypes was estimated in DnaSP ver. 6.10.01 (Rozas *et al.* 2017) and the median-joining network of COI gene haplotypes was constructed using PopArt (Leigh & Bryant 2015).

Geometric morphometrics

The wing and the posterior surstyle lobe of male genitalia (hereinafter referred to as the surstylus) (Fig. 1) were used in geometric morphometric analysis. The right wing and surstylus of each specimen were dissected using microscissors (or scalpel for surstylus) under Nikon SMZ 745T Nikon stereomicroscope and mounted on a microscopic slide using Hoyer's medium (glycerol for surstylus). Both wings and surstyli were photographed using Leica DFC320 camera attached to a Leica MZ16 stereomicroscope, and labelled and archived with a unique code in the FSUNS database.

Wing morphometry

Wing and shape variation was studied in 125 specimens of the *M. chalybeus* complex: *M. chalybeus* (86), *M. minutus* (39), and 18 specimens

of the morphologically similar *M. robustus* (see Appendix 1). Two separate analyses were performed: first one to explore wing shape variation among the species, and the second to quantify phenotypic differences among geographically defined groups of specimens (herein treated as populations).

Eleven homologous landmarks, evenly distributed across the wing, were digitized using TpsDig ver. 2.31 (Rohlf 2017a) (Fig. 1A). Generalised least squares (GLS) Procrustes superimposition (PS) on the raw coordinates were performed using TpsRelw ver. 1.68 (Rohlf 2017b) to minimize non-shape variations in location, scale and orientation of wings, and to superimpose the wings in a common coordinate system (Rohlf & Slice 1990, Zelditch *et al.* 2004).

To explore variation in wing shape among the species and populations, discriminant function (DA) and canonical variate (CVA) analyses were employed. Additionally, a Gaussian naïve Bayes classifier was used to delimit species boundaries based on wing shape variation without a priori-defined groups. Phenetic relationships among the species were determined by UPGMA based on squared Mahalanobis distances, whereas population relationships were determined by neighbour-joining (NJ) analysis based on squared Mahalanobis distances. Superimposed outline drawings produced in MorphoJ ver. 2.0 (Klingenberg 2011) were used to visualize differences in wing shape between species pairs. All statistical analyses were performed in Statistica for Windows ver. 12 (www.statistica.com/en/).

Surstylus morphometry

Semi-landmark geometric morphometric shape analysis was carried out using surstyli from 43 male specimens of *M. chalybeus* (17), *M. minutus* (16) and *M. robustus* (10) (see Appendix 1). Due to the lack of homologous anatomical loci, 20 semi-landmarks were digitized (Fig. 1B) (from the membranous part of the epandrium to the end of the surstylus) using the option “resample curve by length” in tpsDig ver. 2.31 (Rolf 2017). CoordGen ver. 8 (Sheets 2012) with an integrated Semiland module was used for semi-landmark superimposition using a distance-minimizing protocol that minimized shape differences due to the arbitrary nature of semi-landmark positions along the curve (Bookstein 1997, Zelditch et al. 2004).

The dimensionality of the aligned semi-landmark variables was reduced using principal component analysis (PCA). To explore surstyle shape variation among the studied species, discriminant function (DA) and canonical variate (CVA) analyses were performed, using a subset of independent principal components (PCs) that describe the highest overall classification percentage calculated in stepwise discriminant analysis (Baylac & Frieß 2005). The phenetic relationships among species were determined by UPGMA based on squared Mahalanobis distances computed by the DA.

Correlations

We used Mantel’s test (Mantel 1967) with 9999 permutations to find pairwise correlations between morphometric (wing and surstyle), genetic (COI gene sequences) and geographic distances among the species. Morphometric distances were represented as a matrix of pairwise squared Mahalanobis distances, and genetic distances as a matrix of uncorrected pairwise p-distances. Geographic distances were calculated as the minimum distance between two species using QGIS (Quantum GIS Development Team, qgis.osgeo.org). Calculations were carried out using *ade4* R package (Dray & Dufour 2007).

Results

Molecular analysis

The matrix of 69 concatenated 5′-end COI and 3′-end COI sequences (including outgroups) was 1401 bp long. The sequences of the two COI ends did not overlap and the gap between them was 37 bp (not included in the sequence matrix). There were 388 variable sites, and 286 were parsimony informative. There were 38 COI gene haplotypes distributed in three haplotype groups corresponding to three species from the *M. chalybeus* subgroup (Fig. 2). The numbers of haplotypes in *M. chalybeus*, *M. minutus* and *M. robustus* were 19, 18 and 1, respectively (Fig. 2 and Appendix 1).

Maximum parsimony (MP) analysis produced two equally parsimonious trees whose lengths were 786 steps, and consistency and retention indexes 60 and 89, respectively. The strict consensus tree obtained using the MP approach had almost identical topology as the maximum likelihood (ML) tree (Figs. 3 and 4A). All species were resolved as reciprocally monophyletic and mostly well supported. *Merodon robustus* and *M. minutus* clades were supported with bootstrap value of 100 on both trees, while *Merodon chalybeus* clade had high bootstrap support (99) on the MP strict consensus tree, and lower (68) on the ML tree. The maximal intraspecific uncorrected pairwise p-distances were 1.71% and 1.57% for *M. chalybeus* and *M. minutus*, respectively. The minimal and average uncorrected pairwise p-distances between species pairs were 3.93% and 4.50% for *M. chalybeus* and *M. minutus*, 6.85% and 7.06% for *M. chalybeus* and *M. robustus*, and 7.92% and 8.41% for *M. minutus* and *M. robustus*.

Geometric morphometrics

Wing shape

Due to the presence of sexual dimorphism, analyses were performed separately on males and females. Discriminant function (DA) analysis showed that all pairs of species differed significantly in wing shape within males and females

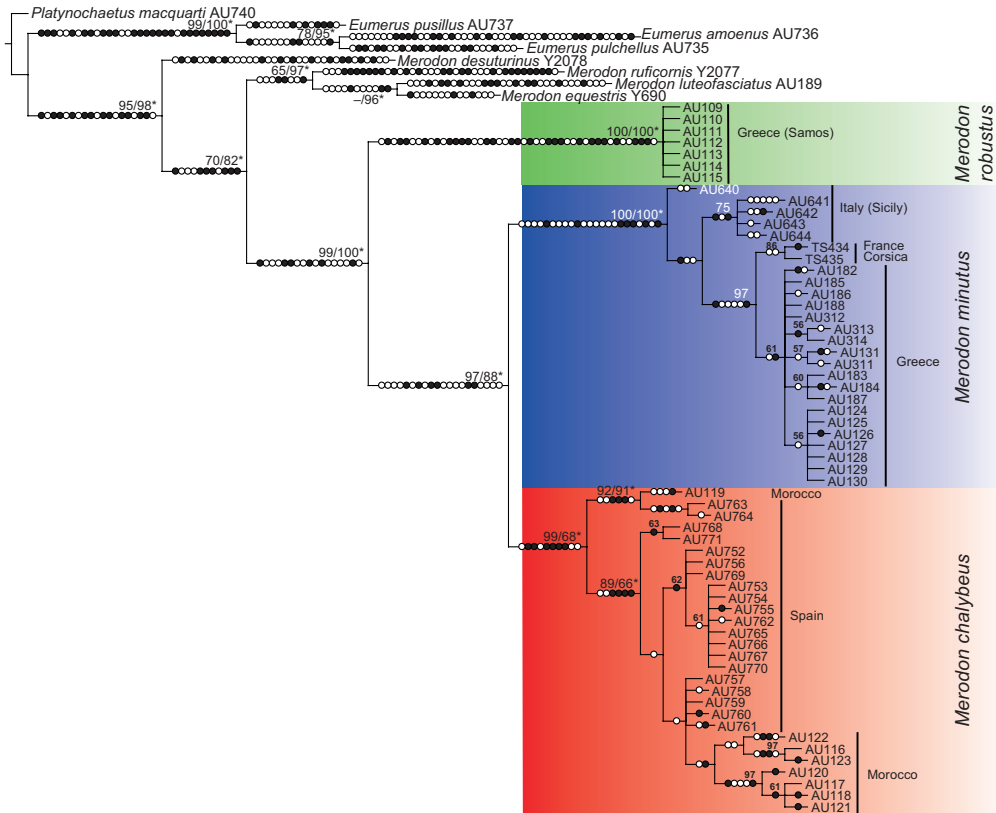


Fig. 3. Strict consensus tree of two equally parsimonious trees based on COI sequence analysis of *Merodon chalybeus* subgroup; black and white dots indicate unique and non-unique changes, respectively; bootstrap values ≥ 50 are given at the nodes; bootstrap values marked with asterisks (*) correspond to those from maximum likelihood trees.

256.7742, $p < 0.01$; CV2: Wilks' $\lambda = 0.2465$, $\chi^2 = 112.7389$, $p < 0.01$. Females: CV1: Wilks' $\lambda = 0.0675$, $\chi^2 = 103.7652$, $p < 0.01$; CV2: Wilks' $\lambda = 0.3320$, $\chi^2 = 42.4454$, $p < 0.01$).

In males, CV1 separated *M. minutus* from *M. chalybeus*, while CV2 *M. robustus* from *M. chalybeus* complex (Fig. 5A). In females, CV1 separated *M. minutus* from *M. robustus*, whereas CV2 *M. chalybeus* from *M. minutus* and *M. robustus* (Fig. 6A). Differences in wing shape between *M. minutus* and *M. chalybeus* were associated with prominent landmark displacements in the distal part of their wings (Figs. 5B and 6B), whereas between *M. chalybeus* and *M. robustus*, and *M. minutus* and *M. robustus* with evenly distributed landmark displacements across the wing (Figs. 5C and D, 6C and D).

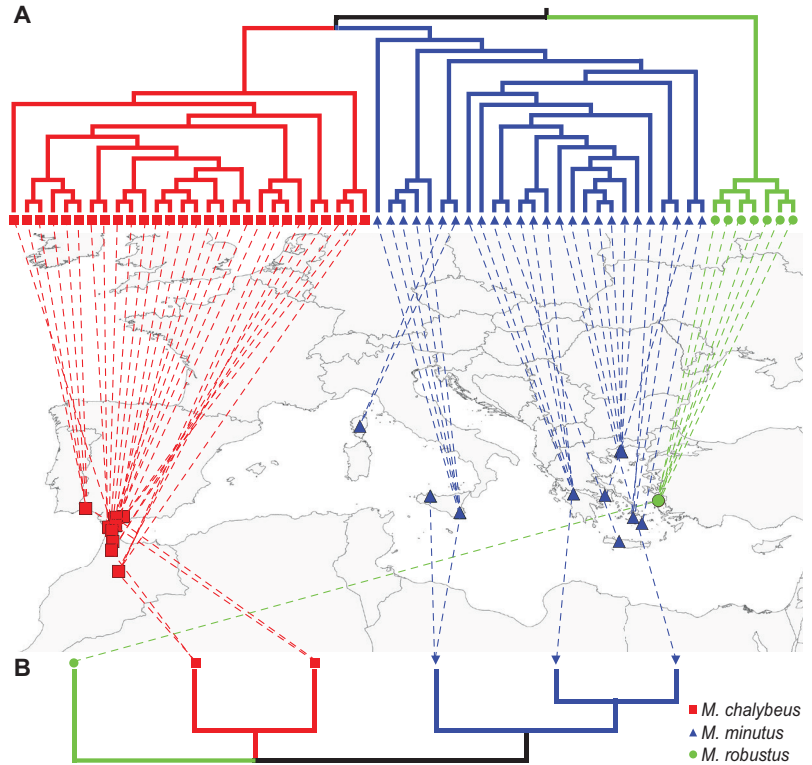
The UPGMA phenogram provided the same pattern for both sexes: *M. minutus* and *M. cha-*

lybeus were grouped according to species complex affiliation, whereas *M. robustus* had the most distinct wing shape (Figs. 5E and 6E).

Population-level analysis

Differences in wing shape among populations were evaluated using DA and CVA. Overall classification success was 91.18%. Out of 136 specimens, 12 were misclassified, 10 into other conspecific populations, and only 2 as other species (one specimen of *M. chalybeus* from Morocco as *M. minutus* from Sicily, Italy, and *vice versa*). All specimens of *M. robustus* from Samos, and *M. minutus* from Thassos were classified with 100% success. Also here, all conspecific populations were grouped together in the space defined by the first two canonical axes (Fig. 7A). CV1

Fig. 4. *Merodon chalybeus* subgroup plotted on the map of the Mediterranean basin. — **A:** Maximum likelihood tree of concatenated 3' and 5' COI sequences. — **B:** Neighbour-joining (NJ) phenogram constructed using squared Mahalanobis distances of wing shape.



(CV1: Wilks' $\lambda = 0.0164$, $\chi^2 = 505.3158$, $p < 0.01$) separated *M. minutus* from *M. chalybeus* and *M. robustus*, while CV2 (CV2: Wilks' $\lambda = 0.0750$, $\chi^2 = 318.6231$, $p < 0.01$) *M. robustus* from the *M. chalybeus* complex (Fig. 7A). CV3 represented variation in populations of *M. minutus*, separating Greek populations from the Italian (Sicily) ones (Fig. 7B). Neighbour-joining (NJ) geo-phenogram showed that all conspecific populations are clustered according to species (Fig. 4B). Within the *M. minutus* cluster, populations from Greece were closest to each other, while the population from Sicily (Italy) had the most distinct wing shape.

Surstylus shape

Surstylus shape of *Merodon chalybeus*, *M. minutus* and *M. robustus* was quantified and compared using semi-landmark geometric morphometrics. Stepwise discriminant analysis revealed that 25 out of 48 principal components (PCs) represented the highest overall classification per-

centage of the studied taxa. All species pairs showed significant differences in surstylus shape ($p < 0.01$) with 100% of correct classification into *a priori*-defined groups. CVA revealed two highly significant canonical axes: CV1 (CV1: Wilks' $\lambda = 0.0083$, $\chi^2 = 134.2526$, $p < 0.01$) separated *M. robustus* from *M. minutus* and *M. chalybeus* (Fig. 8A), whereas CV2 (CV2: Wilks' $\lambda = 0.1509$, $\chi^2 = 52.9439$, $p < 0.01$.) *M. minutus* from *M. chalybeus* (Fig. 8A). Phenetic relationships based on surstylus shape followed the pattern obtained for genetic and wing morphometry results (Fig. 8D). Surstylus shapes in *M. minutus* and *M. chalybeus* were the most similar, whereas in *M. robustus* it was the most distinct. Overall, differences in surstylus shape among the studied species were mostly due to differences in the posterior part of the posterior surstyle lobe (Fig. 8B and C).

Correlations

We found no correlations between morphometric

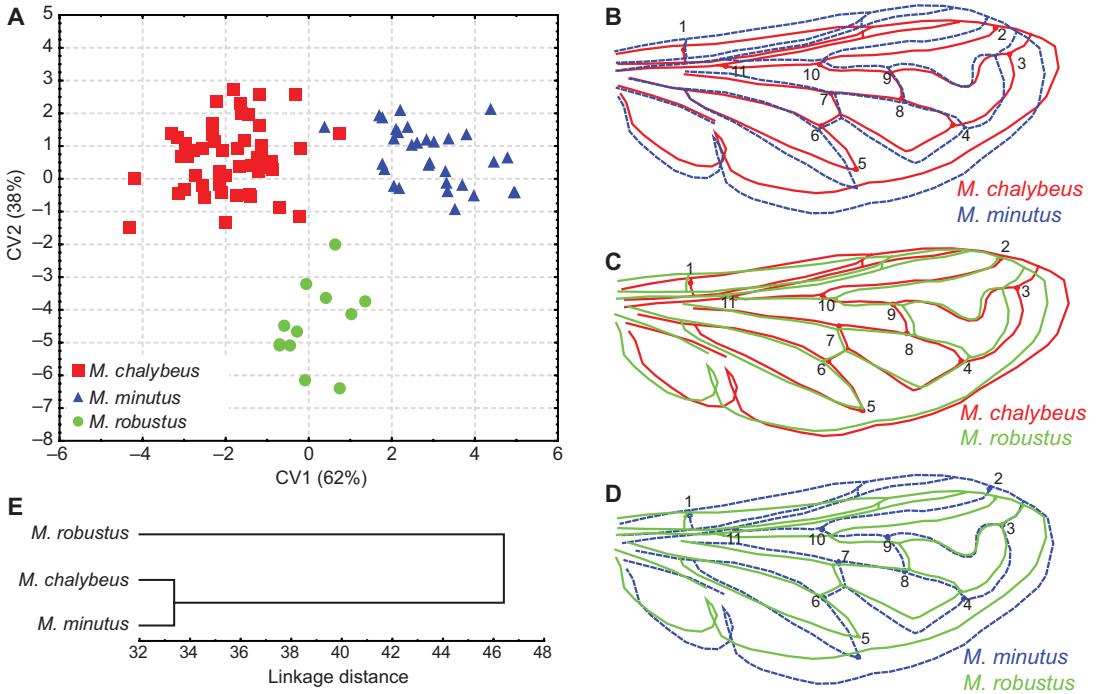


Fig. 5. Geometric morphometric analysis of the wing shape in males of *Merodon chalybeus*, *M. minutus* and *M. robustus*. — **A:** Position of male specimens in the space defined by CV1 and CV2 axes. — **B, C and D:** Drawings showing differences in wing shape for each species pair; differences between the species were exaggerated 3-fold to make them more discernible. — **E:** UPGMA phenogram constructed using squared Mahalanobis distances of wing shape.

(wing and surstyle), genetic (COI gene sequences) and geographic distances among the species.

Merodon aureus group sensu Radenković et al. (2011) (Fig. 9)

DIAGNOSIS. *Merodon aureus* group differs from other *Merodon* groups by having mesocoxa posteriorly with long pile, anterior anepisternum with a pilosity ventral to postpronotum, anterior surstyle lobe undeveloped in male genitalia (Fig. 10C). These are small-sized (8–13 mm) species with a short, rounded abdomen (Fig. 11), males have a distinct calcar on the metatrochanter (indicated with arrow in Fig. 12), and a characteristic structure of the male genitalia: posterior surstyle lobe with parallel margins and rounded apex (Fig. 10A), narrow, elongated, sickle-shaped hypandrium (Fig. 10B), and aedeagus without lateral sclerite (Fig. 10E). The *Merodon aureus* group consists of six subgroups

each containing 1–4 complexes (11 in total) and one unplaced species (Vujić et al. 2021b) (Fig. 9).

Merodon chalybeus subgroup

DIAGNOSIS. This subgroup includes species with olive-brown or blue lustre and moderate punctate scutum and terga (Fig. 11). Mesonotum (in both sexes) and terga (in males) predominantly covered with gray to yellow-gray pilosity. Pile on scutellum in male shorter than metabasitarsus. Tibiae and tarsi predominantly black (Fig. 12). Terga uniformly dark. Terga in females without or with very small pollinose fasciae (Fig. 13I and J).

One complex (*Merodon chalybeus* complex, with two species *M. chalybeus* and *M. minutus*) and one species *M. robustus* belong to this subgroup.

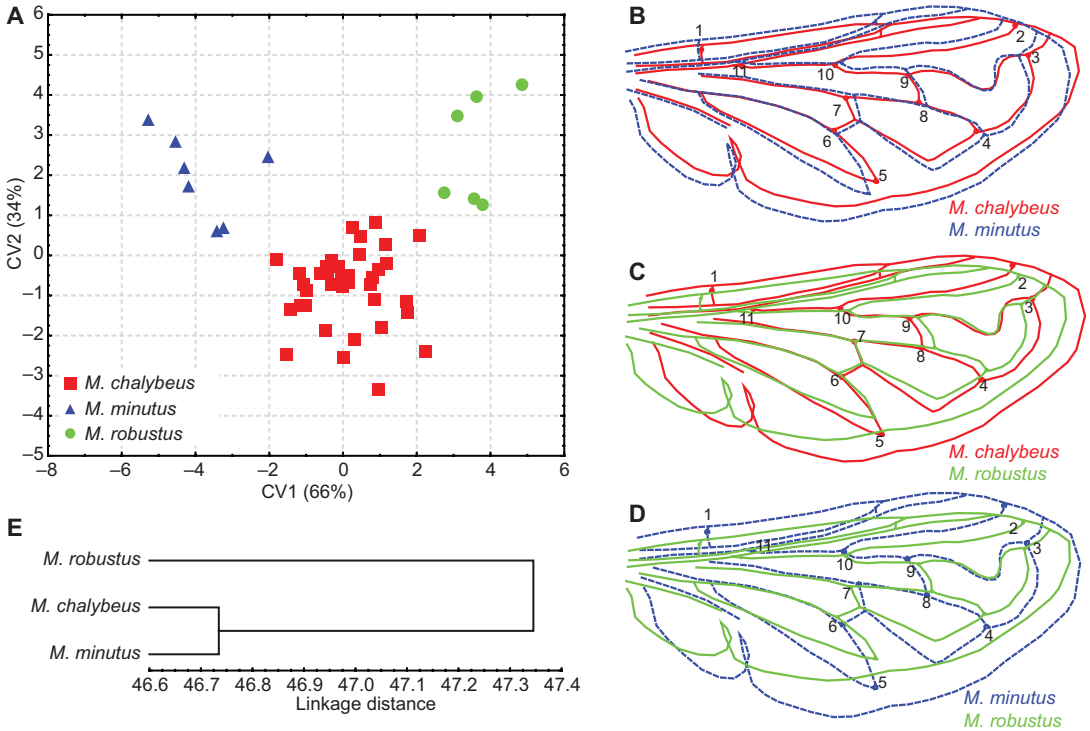


Fig. 6. Geometric morphometric analysis of the wing shape in females of *Merodon chalybeus*, *M. minutus* and *M. robustus*. — **A**: Position of female specimens in the space defined by CV1 and CV2 axes. — **B**, **C** and **D**: Drawings showing differences in average wing shape for each species pair. Differences between the species were exaggerated 3-fold to make them more discernible. — **E**: UPGMA phenogram constructed using squared Mahalanobis distances of wing shape.

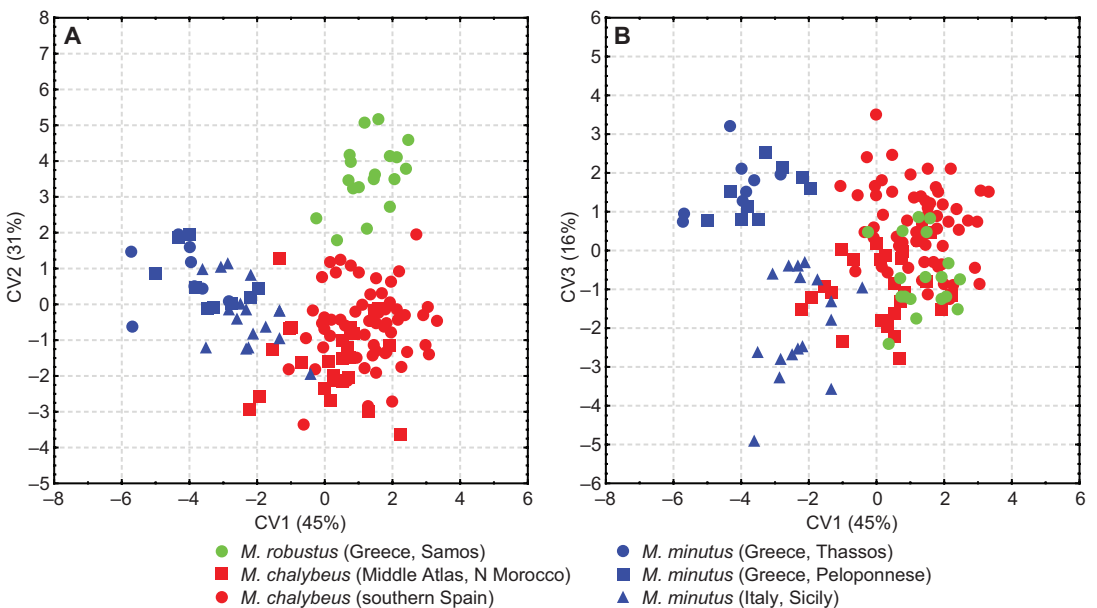


Fig. 7. Wing shape differences among populations of *Merodon chalybeus*, *M. minutus* and *M. robustus*. — **A**: CV1 and CV2 individual scores. — **B**: CV1 and CV3 individual scores.

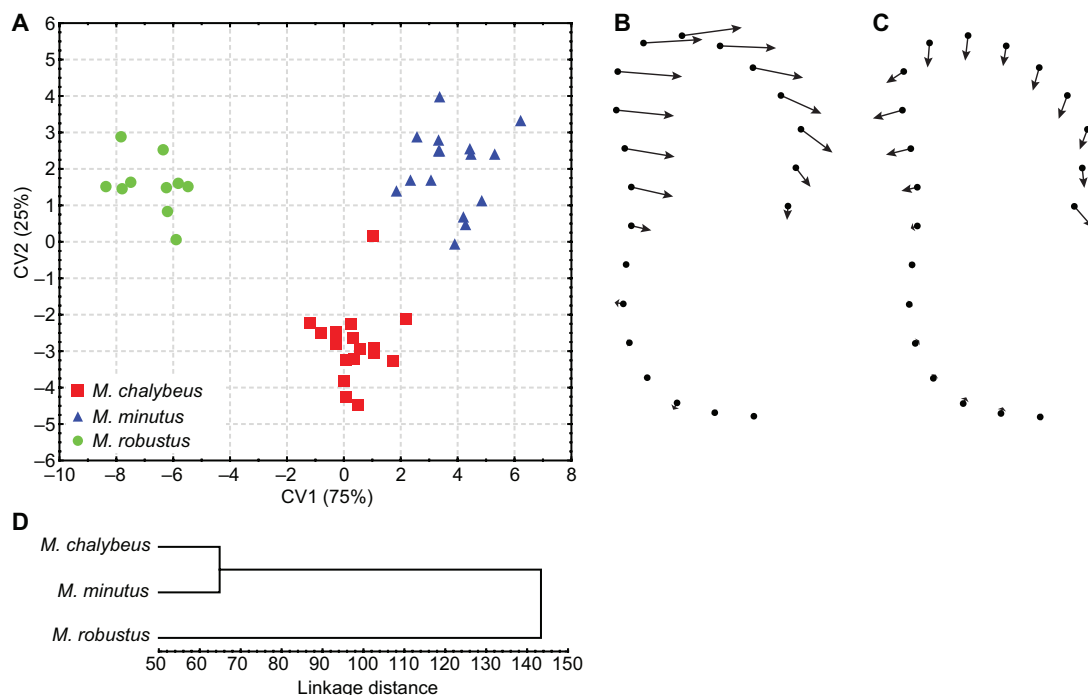


Fig. 8. Geometric morphometric analysis of the surstylus shape of *Merodon chalybeus*, *M. minutus* and *M. robustus*. — **A:** Position of specimens in the space defined by CV1 and CV2 axes. — **B:** Shape changes associated with CV1 axis. — **C:** Shape changes associated with CV2 axis. — **D:** UPGMA phenogram constructed using squared Mahalanobis distances of surstylus shape.

Merodon robustus Veselić, Vujić & Radenković, 2017

DIAGNOSIS. Stocky abdomen without any trace of pollinose fasciate maculae; terga dark olive-brown covered with short light-yellow pilosity (Fig. 14A and C); frons above antennae swollen and striated, with median tubercle above lunulae (Fig. 15); metatarsus of metaleg with small dorsal depression (Fig. 16B). This species is similar to the species from the *Merodon chalybeus* complex (*M. chalybeus* and *M. minutus*), but there are also differences: whitish to yellowish pile at wing basis in *M. robustus*, black one in *M. chalybeus* and *M. minutus*; pale pilosity on metafemur in *M. robustus*, many black pile in the apical half; *M. robustus* with shiny terga without any trace of pollinosity in *M. chalybeus* and *M. minutus*, pollinose fasciate maculae at least on tergum 2 in *M. robustus*, but not in *M. chalybeus* and *M. minutus*.

DISTRIBUTION. Samos (Greece), Cyprus, Israel, and Turkey (Fig. 17). Records from

Cyprus, Israel and Turkey are published here for the first time.

HABITAT AND BIOLOGY. Preferred environment: open areas in evergreen Mediterranean oak forest and maquis. Period of flight: spring (April–May). Developmental stages and host plant unknown.

MATERIAL EXAMINED. **Holotype:** Greece, Samos, Pyrgos, 37.712686°N, 26.79914°E, 15.IV.2011, 1♂, leg. Vujić A., F55, FSUNS. **Paratypes:** Greece, Samos, Pyrgos, 37.712686°N, 26.79914°E, 15.IV.2011, 19♂, 6♀, identifiers: F40, F41, F42, F43, F44, F45, F46, F47, F49, F50, F51, F52, F53, F54, F56, F57, F58, F59, F60, F61, F62, F64, F65, F66, leg. Vujić A., FSUNS; Samos, Pyrgos, 500 m a.s.l., 37.712686°N, 26.79914°E, 21–22.IV.1988, 3♂, 13♀, leg. Lucas J. A. W., RMNH; Samos, Platanos, 600 m a.s.l., 37.738333°N, 26.745277°E, 23.IV.1988, 5♂, 1♀, leg. Lucas J. A. W., 03527, 03528, RMNH; Samos, Spatharaioi-Pag-hondhas, 37.675049°N, 26.816749°E, 15.IV.2011, 1♂, leg. Vujić A., F28, FSUNS; Samos, Karvouni, 1100 m a.s.l., 37.72395°N, 26.81485°E, 26.V.1997, 1♀, leg. Duffels J. P., RMNH.

SPECIMENS EXAMINED. **Cyprus:** Akrotiri, 34.634592°N, 32.968659°E, IV.1936, 2♂, leg. Mavroumoustakis G. A., s.n., BMNH; Anarita, 34.734130°N, 32.537745°E, 3.IV.1999, 2♂,

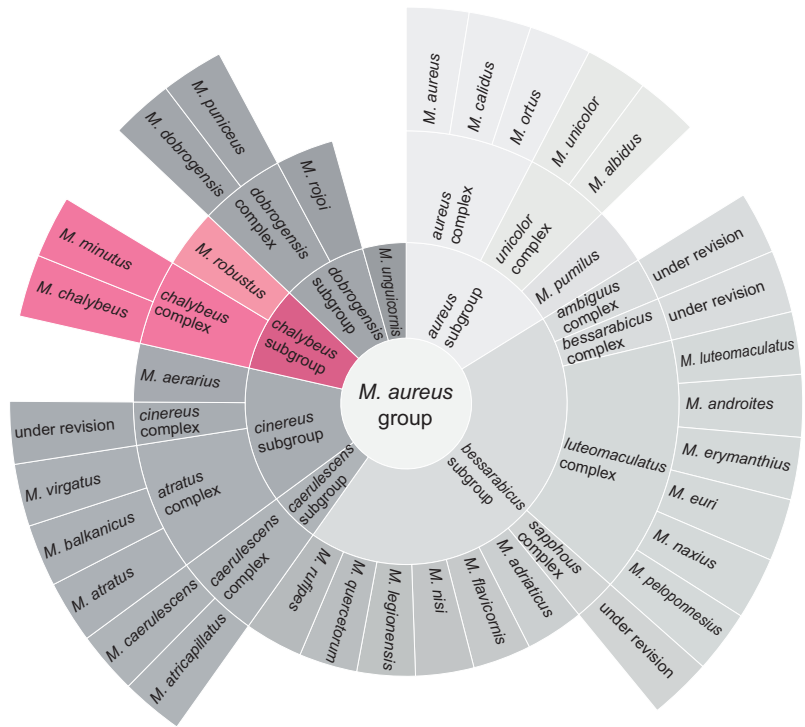


Fig. 9. Diversity of the *Merodon aureus* species group. Hierarchical levels of classification are illustrated as concentric circles declining outward (based on Vujić *et al.* 2021b).

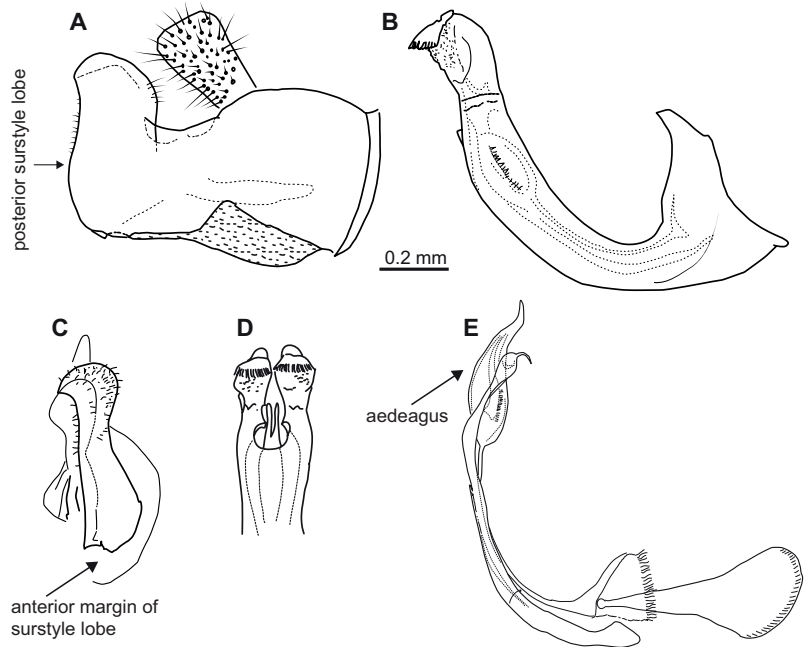


Fig. 10. *Merodon chalybeus*, male genitalia. — **A:** Epandrium, lateral view. — **B:** Hypandrium, lateral view. — **C:** Epandrium, anterior view. — **D:** Distal part of hypandrium, anterior view. — **E:** Aedeagus and associated structures.

2♀, leg. Palmer C. J., 04381, 04380, PJC coll.; Paphos, Anarita, 34.741666°N, 32.533333°E, 3.IV.1999, 1♂, leg. Palmer C. J., 03532, FSUNS; Stavrovouni Monastery, 34.885038°N, 33.435068°E, 26.IV.1982, 1♂, 1♀, leg. Stubbs A. E., 04356, 04356, BMNH. **Israel:** Golan, 5 km

S of Onaitra, 32.973796°N, 35.591672°E, 15.IV.1982, 1♂, leg. Kaplan F., 04939, TAU; Mount Hermon, 1400–1600 m a.s.l., 33.4°N, 35.85°E, 18.V.1976, 1♂, *s.coll.*, 03531, RMNH. **Turkey:** Muğla, University campus, 700 m a.s.l., 37.161667°N, 28.3725°E, V.2013, 2♀, leg. Dursun O.,

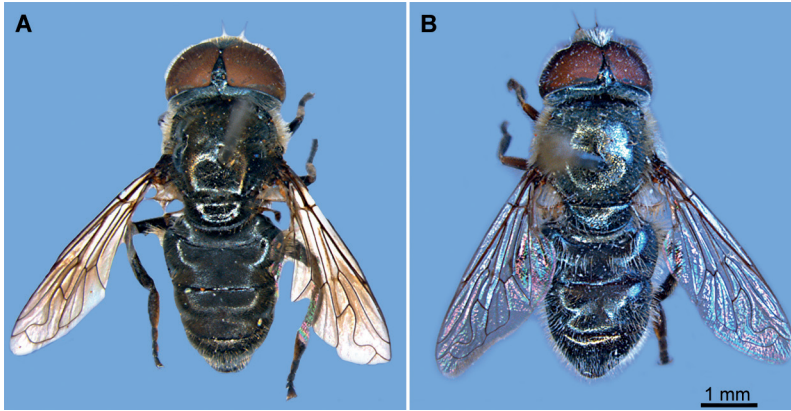


Fig. 11. Habitus, male, dorsal view. — **A:** *Merodon minutus*. — **B:** *M. chalybeus*.

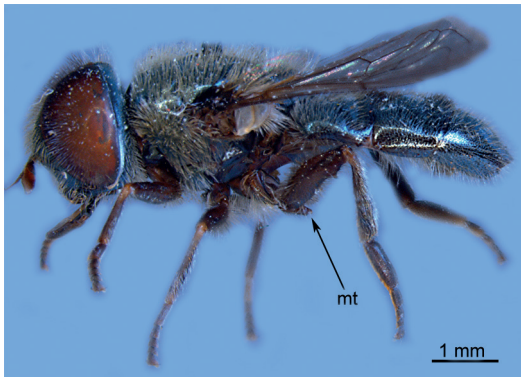


Fig. 12. *Merodon chalybeus*, habitus, lateral view. mt – calcar on metatrochanter.

10438, 10456, BM coll.; Muğla, University campus, 700 m a.s.l., 37.161667°N, 28.3725°E, IV.2014, 1♀, leg. Dursun O., 10457, BM coll.; Izmir, Samsun Dagi National Park, 37.666667°N, 27.25°E, 24–26.IV.1993, 1♀, leg. Michelsen V., 04332, ZMUC.

Merodon chalybeus complex

DIAGNOSIS. Small (6.6–8.0 mm) species; basoflagellomere reddish to brown; upper (and lower) part of eyes with dark pile; pilosity of the body not so dense as in other species in the *Merodon aureus* group, pile whitish-grey to yellowish-grey; mesonotum usually with black pile, at least near wing bases; mesonotum and terga with dark-olive to blue tegument; tergum 2 on posterior 1/3 and central parts of tergum 3 (except pale stripes on the middle) with black pile; terga 2 and 3 with small pollinose fasciate maculae;

legs dark, tibiae at both ends and tarsi in part can be paler; apical part of hind femora with black pile; male genitalia similar to other species of *M. aureus* group (Fig. 10).

This species complex comprises two species: *M. chalybeus* and *M. minutus*. They are similar to *Merodon robustus*, but there are also differences: black pile at wing basis in *M. chalybeus* and *M. minutus*, whitish to yellowish in *M. robustus*; many black piles in the apical half on metafemur in *M. chalybeus* and *M. minutus*, pale pilosity in *M. robustus*; pollinose fasciate maculae at least on tergum 2 in *M. chalybeus* and *M. minutus*, shiny terga without any trace of pollinosity in *M. robustus*.

DESCRIPTION. Male: Head (Fig. 18). Antenna (Fig. 13C and D) brown; basoflagellomere dark brown to reddish-brown, 1.3–1.5 times longer than pedicel, dorsal margin concave between the arista and the apex, apex rounded; arista dark brown, slightly longer than pedicel and basoflagellomere together. Face shiny black, covered with whitish pile. Frons black with indistinct scarce grayish pollinosity, covered with whitish pilosity. Vertical triangle isosceles, shiny black, predominantly covered with long black pile. Eye slightly separated with shiny stripe (as in Fig. 19B); eye contiguity variable from three to 20 facets long. Ocellar triangle variable, from isosceles to equilateral. Eye pile long, black in the upper half or less and lower corner, pale gray between. Occiput shiny, silver-green without pollinosity, and covered with grayish pile.

Thorax (Fig. 11): Mesonotum dark with olive-brown to blue lustre, moderate to rough

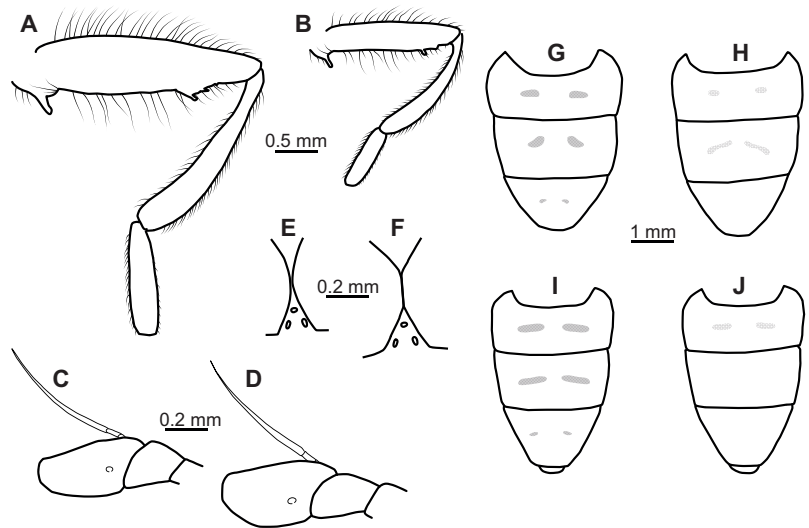


Fig. 13. *Merodon chalybeus*. — **A** and **B**: Male left metaleg, lateral view. — **C** and **D**: Male right antenna, inner view (basoflagellomere and pedicel). — **E** and **F**: Male eye contiguity, dorsal view. — **G** and **H**: Male terga 2–4, dorsal view. — **I** and **J**: Female terga 2–4, dorsal view.

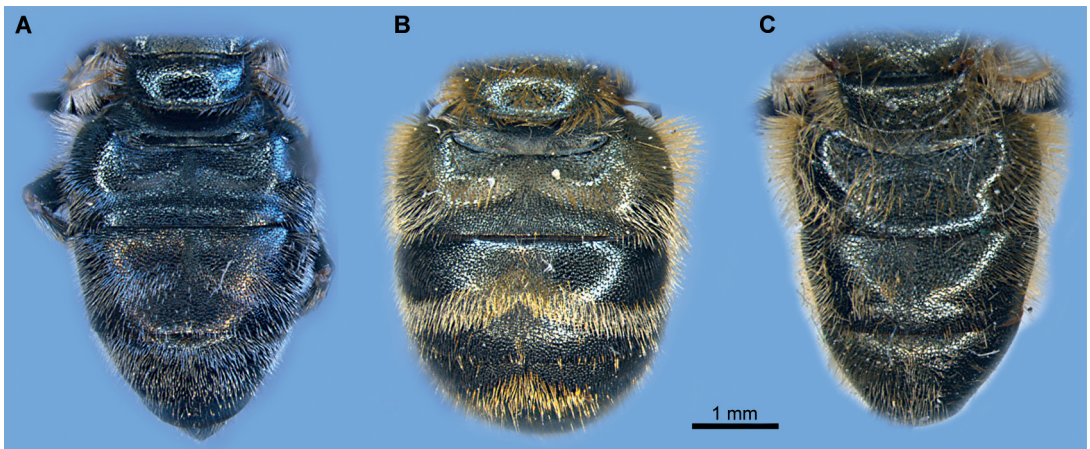


Fig. 14. Abdomen, dorsal view. — **A**: *Merodon robustus*, female. — **B**: *M. cinereus*, female. — **C**: *M. robustus*, male.

punctate, covered with dense, erect whitish yellow to gray-yellow pile; scutum usually without or with very weak vittae of dark brown microtrichia; covered predominantly with whitish gray to gray-yellow pilosity and few black pile near wing base. Posterior anepisternum, anepimeron and dorsal part of katepisternum with long whitish to yellow pile. Wing hyaline, with dark-brown veins. Calypteres whitish. Halteres with dark brown pedicel and capitulum. Femora black with dark brown apex; pile on pro- and mesofemur predominantly whitish; metafemur predominantly covered with whitish to yellow pile except short black ones in the

apical 1/4. Tibiae and tarsi black, except for the dark brown base of tibiae, covered with yellow pile with some intermixed black ones. Metatrochanter with inner calcar ending in two angular points (one corner more protruded).

Abdomen (Fig. 11): Dark brown to partly blue with green-olive lustre; oval, slightly longer than mesonotum. Terga covered with yellow to gray pile, except posterior half of terga 2 and 3 with short black pile medially; terga 2 (and 3) with pairs of white pollinose fasciate maculae. Sterna shiny black, covered with long whitish pile. Male genitalia similar to those in all other species of the *M. aureus* group (Fig. 10).



Fig. 15. *Merodon robustus*, frons of male, dorsal view. Red arrow indicates median tubercle on frons.

Female similar to male except for normal sexual dimorphism and the following features: frons shiny black; vertex mostly covered with black pile; metatrochanter without a calcar; abdomen shiny dark brown to partly bluish, with a pairs of white pollinose fasciate maculae on terga 2 (and 3–4); on tergum 2 these fasciate maculae are subparallel to the anterior margin of the tergum, whereas on terga 3–4 these fasciate maculae are narrow and oblique if they are present; pilosity on terga shorter and more scarce.

Body size ($n = 80$): body length = 5–8.5 mm, wing length = 2.5–5.8 mm.

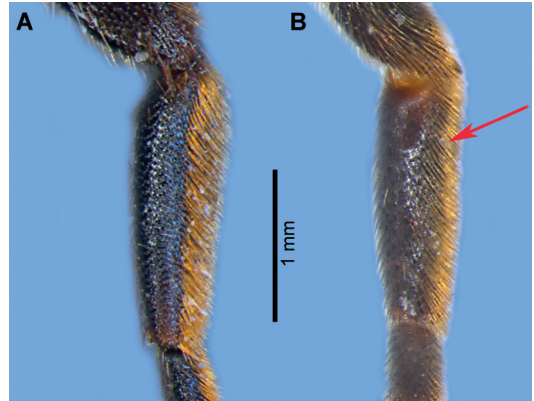


Fig. 16. Metatarsus of male metaleg. — A: *Merodon chalybeus*. — B: *M. robustus*. Red arrow indicates small dorsal depression at metatarsus of metaleg.

VARIABILITY. These species can be very variable in size (5–8.5 mm), length of eye contiguity line in males (Figs. 12A and B, 13E and F), pollinosity on mesonotum and terga: from pollinose areas present on all terga (Fig. 13G and I) to shiny terga, except small pollinose maculae on tergum 2 (Fig. 13H and J), length, color and density of body pile.

Merodon chalybeus Wiedemann in Meigen, 1822

Merodon chalybeus Wiedemann in Meigen, 1822: 365.

syn. *Merodon spicatus* Becker, 1907: 251 (synonymized by Marcos-Garcia *et al.* 2007: 546)

Merodon chalybeus was described from a single specimen in the Meigen collection accepted as the holotype in Marcos-Garcia *et al.*

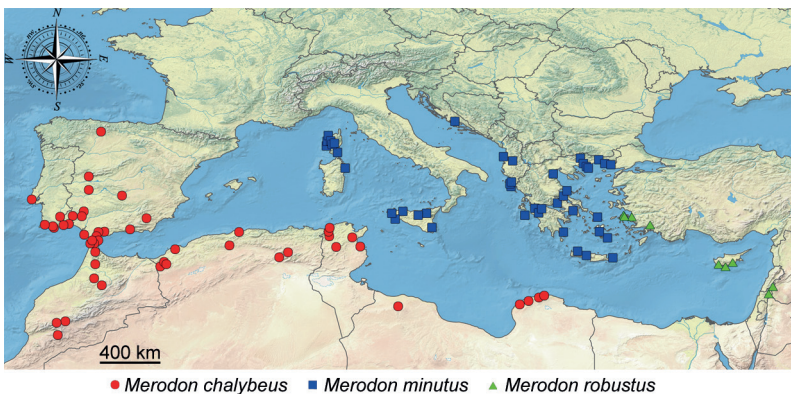


Fig. 17. Distribution of species of the *Merodon chalybeus* subgroup.

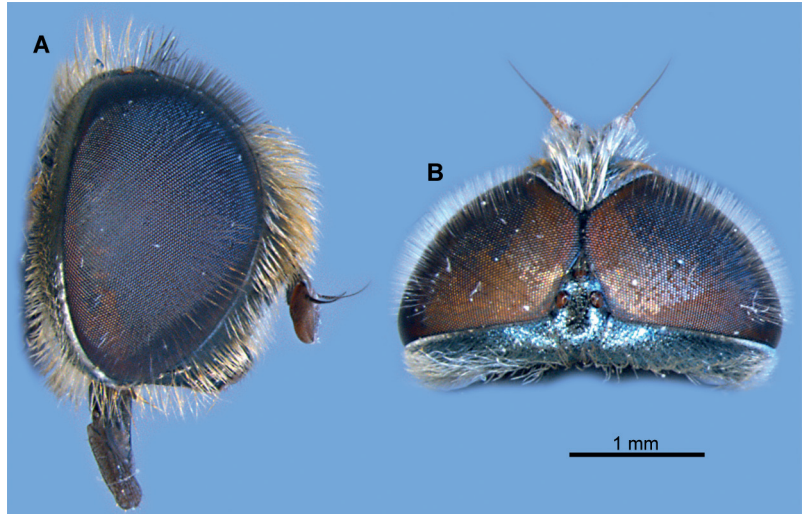


Fig. 18. *Merodon chalybeus*, male head. — **A:** Lateral view. — **B:** Dorsal view.

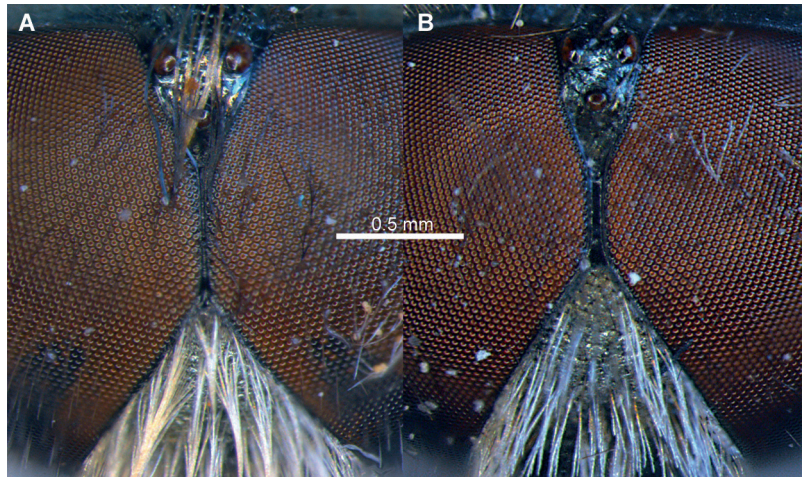


Fig. 19. Eye contiguity in males. — **A:** *Merodon chalybeus*. — **B:** *M. minutus*.

(2007): female “var. *chalybea* / Lusitania / Hoffmannsegg S. / Type” (Portugal) (MFNB). *Merodon spicatus* was described from an unspecified number of males and females. The lectotype and paralectotype were designated by Marcos-Garcia *et al.* (2007) based on syntype specimens: lectotype: male “*spicatus* det. Becker / Tunisia 17.4.98 / Coll. J. Villeneuve *Lampetia spicata* R.M.H.N. Belg.” (KBIN); paralectotype: female “Tunis” (Becker collection, MFNB).

DIAGNOSIS. Uniformly pollinose and strongly punctured scutum (c in Fig. 20A); at least lateral sides of tergum 2, but usually ocellar triangle, occiput, mesonotum and tergum 3 (and 4) with bluish lustre (Fig. 11B). In males, distance

between eyes as broad as eye margin (Fig. 19A), eye contiguity eight to 20 facets long, and pile on tergum 4 usually longer than basoflagellomere. In females, distance between posterior pair of ocelli usually as long or longer than the distance between ocelli and eye margin (Fig. 21A). Molecular data, distribution and morphometric characters of wing and male genitalia clearly separate *M. chalybeus* from *M. minutus*.

DISTRIBUTION. *Merodon chalybeus* is distributed on the Iberian Peninsula (Spain, Portugal) and North Africa (Fig. 17).

HABITAT AND BIOLOGY. Preferred environment: forest/open ground; open areas in evergreen oak maquis and more open, almost bare ground in

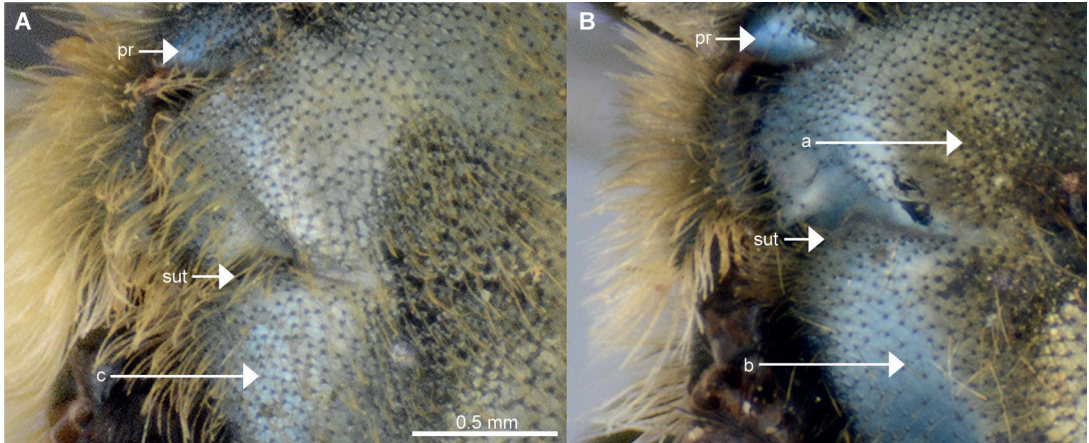


Fig. 20. Part of the scutum, dorsal view. — **A:** *Merodon chalybeus*. — **B:** *Merodon minutus*. a = pollinose medial part, b = less punctured lateral side, c = densely punctured lateral side, pr = postpronotum, sut = transverse suture.

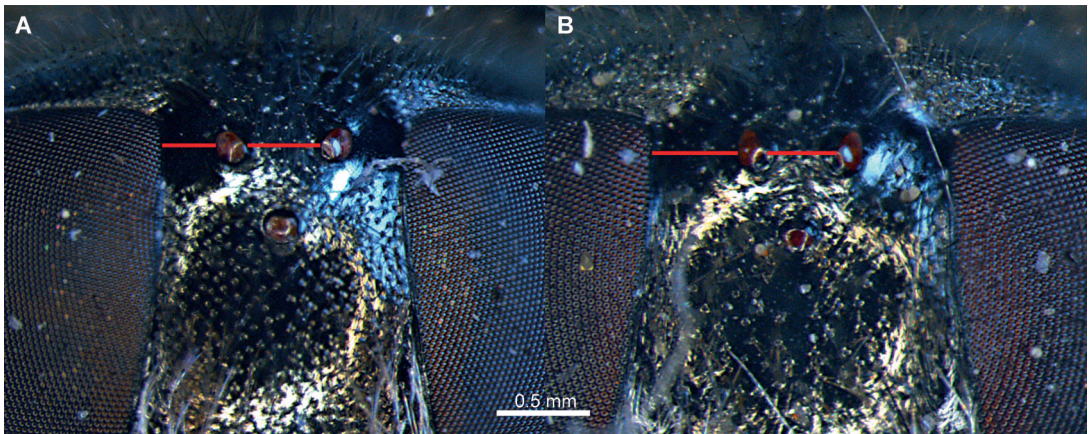


Fig. 21. Ocellar triangle. — **A:** *Merodon chalybeus*. — **B:** *M. minutus*. Red lines indicate distance between posterior pair of ocelli (right), and distance between ocelli and eye margin (left).

semi-arid conditions. Period of flight: April–September. Developmental stages and host plant unknown.

SPECIMENS EXAMINED. **Algeria:** W of Tlemcen, Khemis, Rhar el Khal, 34.6425°N, 1.5625°W, 10.VI.1981, 5♂, *s.coll.*, *s.n.*, RMNH; Tlemcen, Ain Fezza, Aven de Yebdar, 34.836111°N, 1.177222°W, 13.IV.1983, 1♂, *s.coll.*, *s.n.*, RMNH; Tlemcen, Mansourah, 34.865°N, 1.346666°W, 11.IV.1983, 5♂, 3♀, *s.coll.*, *s.n.*, RMNH; Batna, El Kantara, 35.221944°N, 5.7075°E, 14.IV.1981, 1♀, *s.coll.*, *s.n.*, RMNH; Batna, Lambese, 35.486388°N, 6.255277°E, VI.1891, 1♀, leg. Handl, *s.n.*, NHMW; Oran, La Senia, 35.651111°N, 0.634166°W, 21.IV.1910, 1♀, leg. Bequaert J., PM1257, MNHN; Boghari, 35.916742°N, 2.690984°E, 1911, 1♀, leg. Seurat G., PM1264, MNHN; Alger, Rouiba, 36.739166°N, 3.285277°E, V–VI.1911, 1♀, 03484, MNHN. **Libya:** Tripo-

litania, Garian Hills, 32.178668°N, 13.003568°E, 5–6.XI.1958, 2♂, leg. Guichard K. M., BMNH; Garian Hills, 32.18271°N, 13.00799°E, 5–16.II.1958, 2♂, leg. Guichard K. M., 05646, 05647, RMNH; Cyrenaica, 25.VII.1958, 1♀, leg. Guichard K. M., *s.n.*, BMNH; Cyrenaica, near Barce, 32.513202°N, 20.911552°E, 14.III.1958, 3♀, leg. Guichard K. M., *s.n.*, BMNH; Cyrenaica, Wadi Kuf., 32.70081°N, 21.569812°E, 1.IV.1954, 1♀, leg. Guichard K. M., *s.n.*, BMNH; Cyrenaica, Cyrene, 32.827624°N, 21.873387°E, 3.IV.1954, 1♀, leg. Guichard K. M., *s.n.*, BMNH. **Morocco:** Taddert, Marrakech–Ouarzazate, 30.408471°N, 7.791398°W, 26.III.1983, 1♀, *s.coll.*, 03874, PJC coll.; High Atlas, 15 km of N Taddert, 30.408471°N, 7.791398°W, 26.III.1983, 1♂, leg. Else G. R., *s.n.*, BMNH; 15 km of N Taddert, Marrakech–Ouarzazate road, 30.408471°N, 7.791398°W, 26.III.1983, 1♀, leg. Else G. R., *s.n.*, BMNH; High Atlas, Massif Toubkal, Oukaimeden, 2000 m a.s.l., 31.2°N, 7.86°W, 1.V.1987, 1♂, 03873, PJC coll.; High Atlas, Massif Toubkal, Oukaimeden,

- 31.2°N, 7.86°W, 3.VII.1974, 2♀, *s.coll.*, *s.n.*, RMNH; High Atlas, Massif Toubkal, Oukaïmeden, 2500 m a.s.l., 31.2°N, 7.86°W, 27–28.VI.1987, 1♂, 1♀, leg. Schacht W., 03483, 03482, RMNH; South, Tizi-Tichank, 2000 m a.s.l., 31.292088°N, 7.379143°W, 20.IV.1987, 1♂, 1♀, leg. Edwards M., *s.n.*, WML; Ifrane, cedar forest, 1500 m a.s.l., 33.31°N, 5.06°W, 1♀, leg. Vrabec V., BC697, BM coll.; Middle Atlas, Ifrane National Park 1, 33.496176°N, 5.166997°W, 1.V.2013, 21♂, 9♀, leg. Vujić A., Radenković S., Đ31, Đ32, Đ39, Đ40, Đ72, Đ73, Đ74, Đ75, Đ76, Đ77, Đ78, Đ79, Đ80, Đ81, Đ82, Đ83, Đ84, Đ85, Đ86, Đ87, Đ88, Đ89, Đ90, Đ91, Đ92, Đ93, Đ94, Đ95, Đ96, Đ97, FSUNS; Meknes, 550 m a.s.l., 33.911526°N, 5.556945°W, 10.VI.1918, 1♀, leg. Benoist R., PM1202, MNHN; near Ouzzane, 34.778238°N, 5.529655°W, 1♀, leg. Vujić A., Radenković S., *s.n.*, FSUNS; Tetouan-Tanger, 35.549827°N, 5.52842°W, 4.V.2013, 2♂, 1♀, leg. Vujić A., Radenković S., Veselić S., Đ51, Đ54, Đ55, FSUNS; Oukaïmeden, 25.VI.1998, 1♀, leg. Schmidt, *s.n.*, ZFMK.
- Portugal:** Algarve, Aeroporto de Faro, 37.017323°N, 7.971954°W, 24.III.1995, 1♂, *s.coll.*, *s.n.*, RMNH; Algarve, E of Quarteira, 37.066667°N, 8.1°W, 19.IV.1985, *s.coll.*, *s.n.*, 1♂, RMNH; Algarve, E of Quarteira, 37.066667°N, 8.1°W, 24.IV.1985, 2♂, 1♀, *s.coll.*, *s.n.*, RMNH; Algarve, Farol de Alfanzina 5 km S of Lagos, 37.190955°N, 8.552856°W, 20.III.1995, 1♀, *s.coll.*, *s.n.*, RMNH; Algarve, Castro Marim, 37.216667°N, 7.433333°W, 18.IV.1985, 2♀, *s.coll.*, *s.n.*, RMNH; Alentejo, Mertola river bed 4 km S of Vale de Évora, 37.633333°N, 7.666667°W, 30.IV.2004, 1♀, leg. Michelsen V., ZMUC00513411, ZMUC; Estoril, River Tagus, 38.719901°N, 9.394298°W, 21.III.1896, 1♂, leg. Thomas O., *s.n.*, RMNH. **Spain:** Tarifa, 36.023329°N, 5.585750°W, 28.IV.1981, 36♀, 1♂, leg. Stubbs A. E., *s.n.*, BMNH; Bolonia 2, 36.092518°N, 5.784151°W, 30.IV.2015, 1♀, leg. Vujić A., Obreht D., 09420, FSUNS; Bolonia 3, 36.107328°N, 5.733183°W, 3.V.2015, 4♂, 3♀, leg. Vujić A., Obreht D., 09431, 09434, 09440, 09441, 09442, 09443, 09444, FSUNS; Bolonia, near road, 110 m, 36.126156°N, 5.705076°W, 2.X.2016, 1♀, leg. Vujić A., Radenković S., 13303, FSUNS; Andalusia, Algeciras, 36.1275°N, 5.453889°W, 1–10.V.1925, 1♂, *s.coll.*, 03487, NHMW; Cadiz, Rio Palmones, Algeciras, 36.1275°N, 5.453889°W, 7.IV.1982, 3♂, *s.coll.*, *s.n.*, RMNH; Cádiz, Tarifa, Rio Jara, 36.056074°N, 5.630059°W, 8.IV.2002, 1♀, leg. van Steenis W., Bakker E.S., X70, SW coll.; Algeciras, beach near Santa Margarita, 36.210684°N, 5.326997°W, 2.V.2015, 2♂, 2♀, leg. Vujić A., Obreht D., 09394, 09395, 09393, 09396, FSUNS; Algeciras, Mirador, 36.221668°N, 5.35059°W, 1.V.2015, 1♂, 3♀, leg. Vujić A., Obreht D., 09387, 09388, 09390, 09391, FSUNS; Algeciras, 36.222377°N, 5.359717°W, 1.V.2015, 14♂, 3♀, leg. Vujić A., Obreht D., 09370, 09371, 09372, 09373, 09374, 09375, 09376, 09377, 09378, 09379, 09380, 09381, 09382, 09383, 09384, 09385, 09386, FSUNS; Jimene de la Frontera, 36.433911°N, 5.459107°W, 5.V.2015, 2♀, leg. Vujić A., Obreht D., 09457, 09459, FSUNS; Cortes de la Frontera, way to Grazalema, 36.593905°N, 5.312444°W, 6.V.2015, 1♀, leg. Vujić A., Obreht D., 09464, FSUNS; Andalusia, Puerto de Santa Maria, 36.6°N, 6.233333°W, 23.IX.1952, 1♀, leg. Bär, Blöte, de Jong, Osse, *s.n.*, RMNH; Grazalema, Ubrique, 36.618550°N, 5.432673°W, 7.VI.2018, 1♂, leg. Vujić A., 19861, FSUNS; Grazalema, 813 m a.s.l., 36.725421°N, 5.329296°W, 30.IX.2016, 3♂, 2♀, leg. Vujić A., Radenković S., Juslén A., 10848, 10849, 10850, 10851, 10852, FSUNS; 40 km W of Malaga, Yunquera, 800 m a.s.l., 36.733333°N, 4.916667°W, 29.IV.2003, 3♀, leg. Halada J., 03493, 03494, 03495, BM coll.; Grazalema, 36.758889°N, 5.358889°W, 750 m a.s.l., 30.IX.2016, leg. Stähls G., 5♂, GJ.1765, GJ.1818, GJ.1819, GJ.1820, GJ.1821, MZH; Grazalema, 36.750254°N, 5.345474°W, 8.VI.2018, 3♂, 2♀, leg. Vujić A., 19868, 19869, 19870, 19876, 19877, FSUNS; Grazalema, 810 m a.s.l., 36.76212°N, 5.358537°W, 30.IX–1.X.2016, 3♂, 3♀, leg. Vujić A., Radenković S., Stähls G., Juslén A., 10777, 10778, 10779, 10780, 10781, 10782, FSUNS; Grazalema, 36.76216°N, 5.358541°W, 7.V.2015, 3♂, 1♀, leg. Vujić A., 09481, 09474, 09475, 09479, FSUNS; Andalusia, 20 km NE of Ronda, 100 m a.s.l., 36.762744°N, 5.209596°W, 30.IV.2003, 1♂, leg. Halada J., 03491, BM coll.; Grazalema, 825 m a.s.l., 36.767081°N, 5.357503°W, 30.IX.2016, 2♂, leg. Vujić A., Radenković S., 10836, 10837, FSUNS; Grazalema, Puerto Alamillo, 36.767081°N, 5.357503°W, 8.V.2015, 1♂, leg. Vujić A., 09483, FSUNS; Granada, Barranco de Miranda 8 km SW of Orgiva, 300 m a.s.l., 36.902239°N, 3.423990°W, 23.IV.1966, 1♂, leg. Lineb. Martin Langem, ZMUC00513499, ZMUC; Cartaya-El Portil, 37.254453°N, 7.109302°W, 27.IV.2015, 11♂, 4♀, leg. Vujić A., Obreht D., 08914, 08915, 08916, 08917, 08918, 08919, 08920, 08921, 08922, 09321, 09322, 08923, 08924, 08925, 09320, FSUNS; Andalusia, Algeciras, Punta Tarifa, 37.583333°N, 2.416666°W, 2.V.2003, 1♂, 1♀, leg. Halada J., 03490, 03492, BM coll.; Provincia de Huelva, River Tamujoso, W Calanas, 37.65°N, 6.883333°W, 13.IV.1982, 1♀, *s.coll.*, *s.n.*, RMNH; Archidona, 229 m a.s.l., 37.703914°N, 6.299737°W, 4.X.2016, 1♂, 3♀, leg. Vujić A., Radenković A., 13333, 13334, 13335, 13336, FSUNS; Cala, 37.963893°N, 6.230937°W, 29.IV.2015, 1♀, leg. Vujić A., Obreht D., 09368, FSUNS; Ciudad Real, Sierra de Santa Maria, Viso del Marques, 660 m, 38.966666°N, 3.916666°W, 20–27.IV.1999, 5♀, leg. Irwin M. E., 00332, 03339, 03340, 03341, 03329, HM coll.; Cáceres, Embalse de Guadiloba, 39.48333°N, 6.28333°W, 16.IV.2002, 1♂, leg. van Steenis W., 00002081, CEUA; El Torno, 350 m a.s.l., 40.138090°N, 5.938554°W, 4.IV.1981, 2♂, leg. Marcos M. A., 03488, 03489, FSUNS; Léon, Valdoré near Rio Esla, 42.8667°N, 5.1667°W, 26.VI.1977, 2♂, leg. Pronk P. H., *s.n.*, RMNH. **Tunisia:** Bizerte La Corniche, 35.8425°N, 10.629166°E, 5.V.1984, 1♂, RMNH; Silyanah, 15 km SW of Makthar, 35.860555°N, 9.205833°E, 21.IV.1994, 1♀, *s.coll.*, *s.n.*, RMNH; 10 km E of Zaghouan, Droge Rivier, 36.4°N, 10.15°E, 8.IV.1988, 1♀, *s.coll.*, *s.n.*, RMNH; Jundubah, 40 km W of Jendouba, 36.501111°N, 8.779444°E, 17.V.1988, 2♂, 4♀, 03467, 03469, 03468, 03470, 03477, 03479, ZMUC; Jundubah, Ain Draham, 36.777222°N, 8.6925°E, 5–18.V.1988, 7♂, 2♀, *s.coll.*, 03471, 03472, 03473, 03474, 03476, 03478, 03480, 03475, ZMUC00513439, ZMUC; Jundubah, 25 km SE of Ain Draham, 36.777222°N, 8.6925°E, 10–16.V.1988, 1♂, 1♀, ZMUC00513506, 03481, ZMUC; Jundubah, Tabarka coast, 36.954444°N, 8.758055°E, 15.V.1993, 2♂, 4♀, leg. Hauser, M., *s.n.*, ZFMK; Tabarka coast, 36.954444°N, 8.758055°E, 11.V.1993, 1♂, leg. Geller-Grimm F., *s.n.*, ZFMK; Tabarka coast, 36.954444°N, 8.758055°E, 11.V.1993, 1♀, leg. Geller-Grimm F., 04543, EMIT; Jundubah, Tabarka coast, 36.954444°N, 8.758055°E,

12.V.1993, 1♂, *s.coll.*, *s.n.*, RMNH; Jundūbah, Tabarka coast, 36.954444°N, 8.758055°E, 11.V.1993, 1♂, 1♀, *s.coll.*, *s.n.*, RMNH.

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Merodon minutus was described from a single specimen at BSA. In the Strobl collection there is one female specimen designated as holotype by Hurkmans ‘Dalmatien [Adriatic coastal region, Croatia] Erber / *Merodon minutus* m. det. Loew’.

DIAGNOSIS. Scutum less punctured, lateral sides of scutum with shiny and finely punctured stripes, without pollinosity (**b** in Fig. 20B) in contrast to pollinose and strongly punctured medial part (**a** in Fig. 20B); at most posterolateral corner of tergum 2 with bluish lustre in some specimens, usually all body dark brown to olive-brown (Fig. 11A). In males, distance between eyes two times greater than eye margin (Fig. 19B), eye contiguity 3–12 ommatidia long, and pile on tergum 4 usually shorter than basoflagellomere. In females, distance between posterior pair of ocelli usually shorter than the distance between ocelli and eye margin (Fig. 21B). Molecular data, distribution and morphometric characters of wing and male genitalia clearly separate *M. minutus* from *M. chalybeus*.

DISTRIBUTION. *Merodon minutus* is found on the Balkan Peninsula (Albania, Croatia, Greece), France (Corsica), and Italy (Sicily, Sardinia) (Fig. 17).

HABITAT AND BIOLOGY. Preferred environment: roadsides and meadows in Mediterranean forest, and semi-arid, open, natural grasslands in typical Mediterranean landscapes. Period of flight: spring (April–June) and autumn (September–October). Developmental stages and host plant unknown.

TAXONOMIC NOTE: Diagnostic features in *Merodon chalybeus* and *M. minutus* are applicable for most populations and specimens, but both taxa show great variability. As a result of this variability, most of the characters overlapped and some specimens from one taxa possess character

states of other taxa and *vice versa*. Only one character is stable and diagnostic, namely lateral sides of scutum, with shiny and finely punctured stripes, without pollinosity in *M. minutus*, but pollinose and rough punctured in *M. chalybeus* (Fig. 19). Also, molecular data and distribution clearly delineate these two species (Fig. 17).

SPECIMENS EXAMINED. **Albania:** Elbasan, 41.083333°N, 20.0°E, 21.VI.1918, 1♀, leg. Karny, *s.n.*, NHMW; Durazzo, 41.323055°N, 19.441388°E, V.1891, 1♂, *s.coll.*, 03514, NHMW. **Croatia:** Splitsko Dalmatinska county, Spalato, 43.513888°N, 16.455833°E, 1862, 1♀, leg. Mann C. H., *s.n.*, NHMW. **France:** Corsica, Golfe de la hiscia, 6.V.1978, 1♂, leg. Stubbs A. E., *s.n.*, BMNH; Corsica, Porto-Vecchio, 41.583333°N, 9.283333°E, 1.V.1963, 1♂, *s.coll.*, *s.n.*, RMNH; Corsica, Porto-Vecchio, 41.583333°N, 9.283333°E, 2.V.1963, 1♀, leg. Lambeck H. J. P., *s.n.*, RMNH; Corsica, Porto-Vecchio, 41.583333°N, 9.283333°E, 2.V.1965, 2♂, 3♀, *s.coll.*, *s.n.*, RMNH; Corsica, Porto-Vecchio, 41.583333°N, 9.283333°E, 2.V.1978, 1♂, *s.coll.*, *s.n.*, RMNH; Corsica, Ajaccio, 41.916232°N, 8.693388°E, 27.V.1951, 2♀, leg. Bayard A., PM0839, PM0841, MNHN; Corsica, 42.0°N, 9.0°E, IV.1988, 1♂, leg. Hauser M., 03510, FSUNS; Corsica, Calcatoggio, Orcino, 42.037777°N, 8.738888°E, 8–18.V.1968, 1♀, leg. van Ooststroom, *s.n.*, RMNH; Corsica, near Vizzavona, 1150 m a.s.l., 42.1126°N, 9.1142°E, 1.VI.2017, 1♂, 1♀, leg. Vujić A., Ačanski J., Likov L., 17760, 17761, FSUNS; Corsica, Piania, 42.240123°N, 8.649099°E, 5.VI.1951, 1♀, leg. Bayard A., PM0861, MNHN; Corsica, forest Valdu Niellu, forest house Poppaghja (Rairies), 1057 m a.s.l., 42.285371°N, 8.923955°E, 23.VI.1909, 1♀, leg. de Haut E. G., PM0844, MNHN; Corsica, Calvi, 42.567°N, 8.721°E, 17.V.1972, 1♀, *s.coll.*, *s.n.*, RMNH. **Greece:** Monophatsi, 35.11711°N, 26.110044°E, 25.V.1925, 1♀, leg. Schulz A. S. G., *s.n.*, ZHMB; Chania, 3 km before Armeni, 35.285762°N, 24.468983°E, 25.IV.2014, 1♂, leg. Vujić A., 06446, FSUNS; Karpathos, Menetes, 35.4793°N, 27.1427°E, 2.V.2012, 1♂, .leg. Vavitsas I., AB7, FSUNS; Chania, W coast of Falasarma, 35.512222°N, 24.015555°E, 7.V.1973, 1♂, *s.coll.*, *s.n.*, RMNH; Anafi, Zoodohos Pigi, 36.3581°N, 25.8303°E, 11.IV.2013, 2♀, leg. Petanidou T., Devalez J., 07002, 07006, MAegean; Anafi, Zoodohos Pigi, 36.3581°N, 25.8303°E, 11.IV.2013, 4♀, leg. Petanidou T., Devalez J., G2913, G2914, G2915, G2916, FSUNS; Anafi, Vagia, 36.363°N, 25.7348°E, 10.IV.2013, 1♂, leg. Petanidou T., Devalez J., G2835, FSUNS; Laconia, 5 km S of Monemvasia, 36.687587°N, 23.052738°E, 28.IV.1984, 1♀, leg. Christensen Georg, ZMUC00513369, ZMUC; Laconia, 5 km S of Monemvasia, 36.686831°N, 23.054912°E, 26.IV.1984, 1♀, leg. Christensen Georg, ZMUC00513413, ZMUC; Laconia, 5 km S of Monemvasia, 36.686831°N, 23.054912°E, 15.X.1983, 1♂, leg. Christensen Georg, ZMUC00513409, ZMUC; Laconia, 5 km S of Monemvasia, 36.686831°N, 23.054912°E, 11.X.1983, 1♂, leg. Christensen Georg, ZMUC00513412, ZMUC; Laconia, 5 km S of Monemvasia, 36.686831°N, 23.054912°E, 1.IV.1983, 1♂, 1♀, leg. Skule, ZMUC00513462, ZMUC00513419, ZMUC; Ios, Mersinia

Rema, 36.7013N, 25.3103E, 14.IV.2013, 1♂, 2♀, leg. Petanidou T., Devalez J., 07004, 07005, 07003, MAegean; Ios, Mersinia Rema, 36.7011°N, 25.309°E, 14–16.IV.2013, 3♀, leg. Petanidou T., Devalez J., G2832, G2833, G2834, MAegean; Tinos, Volax, 37.5894°N, 25.1777°E, 2.IV.2014, 1♂, leg. Petanidou T., 10128, FSUNS; Zakynthos, 1 km SW of Keri Macchie, 37.75°N, 20.75°E, 12.V.1996, 1♂, *s.coll.*, *s.n.*, RMNH; Andros, Korthi, 37.7672°N, 24.9633°E, 24–26.IV.2015, 1♂, leg. Adami I., 10127, FSUNS; Iliia, near Panopoulos, 37.842194°N, 21.662308°E, 22.V.2014, 1♂, leg. Vujić A., Ačanski J., 06529, FSUNS; Attiki, Daphni, near Athens, 38.010888°N, 23.635763°E, 7.X.2012, 1♀, leg. Vujić A., Radenković S., G2517, FSUNS; Attiki, Daphni, 38.008056°N, 23.641944°E, 30.IV.1992, 1♀, leg. Petanidou T., *s.n.*, RMNH; Achaia, near Erimanthos 1, 38.115177°N, 21.772531°E, 20.IV.2014, 11♂, leg. Vujić A., 06465, 06466, 06469, 06470, 06471, 06473, 06475, 06479, 06482, 06484, 06486, FSUNS; Achaia, Kalogria, 38.15879°N, 21.373375°E, 1.V.1979, 2♂, 6♀, leg. Stubbs A. E., *s.n.*, BMNH; Volotia, 4 km NW of Levadia, 38.461284°N, 22.760001°E, 6.V.1979, 1♂, 1♀, leg. Stubbs A. E., *s.n.*, BMNH; Evia, Sterea Ellada, Polilofo, 38.861632°N, 23.098446°E, 13.V.2012, 1♂, leg. van Steenis J., 24579, SJ coll.; Magnisias, Platania, 39.154834°N, 23.314782°E, 24.IX.2009, 1♀, leg. Standfuss K., 05006, MZH, <http://id.luomus.fi/GJ.2077>; Magnisias, Platania, 39.154834°N, 23.314782°E, 23.IV.2000, 2♂, 1♀, leg. Standfuss L., 03520, 03525, 03519, DD coll.; Magnisias, Platania, 39.154834°N, 23.314782°E, 17.IX.1999, 1♀, leg. Standfuss L., 03523, DD coll.; Magnisias, Platania, 39.154834°N, 23.314782°E, 15.IV.2006, 1♂, leg. Standfuss K., 05005 (GJ.2076), MZH; Magnisias, Platania, 39.154834°N, 23.314782°E, 5.V.2000, 2♂, 1♀, leg. Standfuss K., 03521, 03522, 03524, DD coll.; Magnisias, Argalasti, 325 m a.s.l., 39.23325°N, 23.254556°E, 23.IX.2008, 1♂, leg. de Courcy, 10363, CWM coll.; Ionian island, Strongyli, 39.505833°N, 19.905833°E, 30.IV.1978, 7♂, *s.coll.*, *s.n.*, RMNH; Ionian island, Strongyli, 39.505833°N, 19.905833°E, 4.V.1978, 10♂, *s.coll.*, *s.n.*, RMNH; Ionian island, Strongyli, 39.505833°N, 19.905833°E, 3.V.1978, 14♂, 3♀, RMNH; Ionian island, Strongyli, 39.505833°N, 19.905833°E, 1.V.1988, 6♂, 1♀, *s.coll.*, *s.n.*, RMNH; Corfu, Dassia 5 km SE of Korakiana, 39.6833°N, 19.8333°E, 30.V.1971, 1♀, *s.coll.*, *s.n.*, RMNH; Corfu, Pantokrator, 39.746944°N, 19.871111°E, 30.V.1981, 1♀, *s.coll.*, *s.n.*, RMNH; Corfu, Ag. Spiridon, 39.799999°N, 19.85°E, IV.1985, 1♂, White I. M., *s.n.*, BMNH; Mountain Olympos, Neokesaria, 40.272136°N, 22.427074°E, 19.V.1997, 1♂, leg. Šimić S., *s.n.*, FSUNS; Mountain Olympos, Neokesaria, 40.272136°N, 22.427074°E, 19.V.1997, 2♂, leg. Radenković S., 03513, FSUNS; Thasos, Potos, 40.612972°N, 24.619528°E, 4♂, 1♀, AL37, AL38, AL39, AL40, AL42, FSUNS; Thasos, Potos, 40.612972°N, 24.619528°E, 11–12.VI.2012, 2♂, 1♀, leg. de Courcy W., G2838, G2839, G2837, MAegean; Thasos, Potos, 40.612972°N, 24.619528°E, 12.VI.2012, 1♀, leg. de Courcy W., G2840, MAegean; Thasos, Skala Marion, 40.6475°N, 24.540056°E, 10.IV.2012, 2♂, *s.coll.*, AL34, AL36, FSUNS; Thasos, Skala Marion, 40.6475°N, 24.540056°E, 11–12.IV.2012, 1♂, leg. de Courcy W., G2836, MAegean; Evros, Delta, 2 m a.s.l., 40.835861°N, 26.003194°E, 2.V.2010, 1♂, leg. de Courcy W., *s.n.*, CWM coll.; Kavala, Eleftheroupoli,

50 m, 40.868055°N, 24.301944°E, 20.IV.2007, 1♀, leg. Ssymank A., *s.n.*, FSUNS; Kavala, Eleftheroupoli, 50 m a.s.l., 40.868055°N, 24.301944°E, 20.IV.2007, 1♀, leg. Ssymank A., 04248, SA coll.; Evros, Mesembria, 25 m a.s.l., 40.870639°N, 25.630667°E, 3.IV.2007, 1♂, leg. de Courcy, 10362, CWM coll.; Evros, Mesembria, 28 m a.s.l., 40.871166°N, 25.630860°E, 3.IV.2008, 1♂, 1♀, leg. de Courcy W., *s.n.*, CWM coll.; Evros, Papikio Mountain, 506 m a.s.l., 41.1545°N, 25.258861°E, 1.V.2007, 1♂, leg. de Courcy W., 10364, CWM coll.; 3 km NW of Poros, 27.IV.1996, 1♀, leg. Miksch, G., *s.n.*, ZFMK. **Italy:** Sicily, near Noto, 36.987167°N, 15.027086°E, 7.IV.2015, 4♂, leg. Vujić A., Radenković S., Nedeljković Z., Miličić M., Ačanski J., 09305, 09306, 09307, 09308, FSUNS; Sicily, Selinute, 37.583333°N, 12.816666°E, 13.IV.1965, 1♀, *s.coll.*, 03512, RMNH; Sicily, 37.75°N, 14.25°E, 1858, 1♀, leg. Mann C. H., *s.n.*, NHMW; Sicily, 37.75°N, 14.25°E, 1.VIII.1958, 1♀, *s.coll.*, *s.n.*, RMNH; Sicily, above Trapani, 37.833333°N, 12.666666°E, 16.IV.1965, 1♀, leg. Guichard K. M., *s.n.*, BMNH; Sicily, Cesaro, 1150 m a.s.l., 37.833333°N, 14.716666°E, 23.IV.1989, 1♂, leg. Mahler J., 00513425, ZMUC; Palermo, Lago di Piana degli Albanesi, 600–650 m a.s.l., 37.966667°N, 13.3°E, 1.V.2002, 3♂, 1♀, leg. Merlin T., 03501, 03486, 03498, 03506, DD coll.; Palermo, Lago di Piana degli Albanesi, 600–650 m a.s.l., 37.966667°N, 13.3°E, 1.V.2002, *s.coll.*, 3♂, 03496, 03497, 03507, DD coll.; Palermo, Piana degli Albanesi, Portella della Ginestra, 800–1000 m a.s.l., 38.000036°N, 13.283254°E, 1.V.2002, 8♂, 1♀, leg. Merlin T., 03502, 03500, 03485, 03499, 03503, 03504, 03508, 03509, 03505, DD coll.; Sardinia, Siniscola, Pineta, 40.57216°N, 9.770101°E, IV.1989, 1♀, leg. Hauser M., 03511, HM coll.; Siniscola, Pineta, IV.1989, 6♀, leg. Hauser, M., *s.n.*, ZFMK; 2♀, no data, 03516, 03518, NHMW; 2♂, no data, 03515, 03517, NHMW; Sardinia, province of Nuoro, Monte Limbara, 1045 m a.s.l., 40.852533°N, 9.151217°E, 25.V.2008, 2♂, leg. G. Stähls, GJ.2708, GJ.2071, MZH; Sardinia, Nuoro dist., Tempio, Vallicciola, 40.851817°N, 9.150667°E, 25.05.2008, 2♂, 2♀, leg. Laasonen E. M. & Laasonen L., GJ.2072, GJ.2072, GJ.2074, GJ.2075, MZH.

Key to subgroups, complexes and species in the *Merodon aureus* group (modified from Veselić *et al.* 2017)

1. Body pilosity very short (Fig. 22A), pile on dorsal surface of metafemur shorter than scape; pile on terga 2 and 3 shorter than basoflagellomere; distal half of metatibia, and metatarsi dorsally darkened
..... *Merodon nisi* (*Merodon bessarabicus* subgroup in part)
1. Body pilosity longer, pile on terga 2 and 3 as long as or longer than basoflagellomere 2
2. Tibiae and tarsi mostly pale, at least basal half of pro- and mesotibiae and tarsi ventrally (Fig. 22B) 3
2. Tibiae and tarsi predominantly black 4
3. Terga reddish (Fig. 22C)
..... *Merodon dobrogensis* subgroup
3. Terga dark, exceptionally with small orange maculae on lateral sides of terga 2 and 3 (Fig. 22D)
..... *Merodon bessarabicus* subgroup

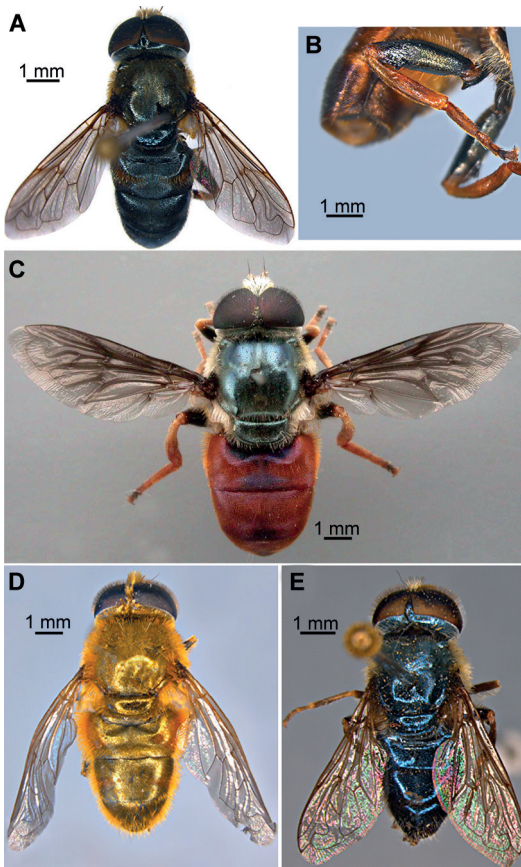


Fig. 22. — **A:** *Merodon nisi*, male habitus, dorsal view. — **B:** *M. dobrogensis*, male, metaleg. — **C:** *M. puniceus*, male habitus, dorsal view. — **D:** *M. luteomaculatus*, male habitus, dorsal view. — **E:** *M. atricapillatus*, male habitus, dorsal view.

4. Terga 2 and 3 with red-orange lateral maculae *Merodon unguicornis*
4. Terga uniformly dark 5
5. Mesonotum only with pale pile *Merodon aureus* subgroup
5. Mesonotum, at least near wing base, with black pile .. 6
6. Strong blue body lustre (Fig. 22E) *Merodon caerulescens* complex
6. Predominantly dark brown or greenish body lustre 7
7. Body pile shorter; pile on scutellum in male shorter than metabasitarsus; terga in female without pollinose fasciate maculae, or with small ones on terga 2 and 3 (Figs. 13I and J, 14A) (*Merodon chalybeus* subgroup) 8
7. Body pile longer; pile on scutellum in male as long as or longer than metabasitarsus; terga 2 and 3 in female with a pair of clear pollinose fasciate maculae (Fig. 14B) *Merodon cinereus* subgroup
8. Terga without pollinosity, shiny dark olive-brown to black (Fig. 14A and C); frons above antennae swollen and striated, with median tubercle above lunule (indicated with

an arrow in Fig. 15); metatarsus of metaleg with small dorsal depression (indicated with an arrow in Fig. 16B) ..

- *Merodon robustus*
8. Terga with at least a trace of pollinose fasciate maculae; frons without median tubercle above lunule; metatarsus of metaleg without dorsal depression (Fig. 16A); *Merodon chalybeus* complex 9
9. Scutum less punctured; shiny lateral sides (as stripes) without pollinosity (b in Fig. 20B), in contrast to pollinose and strongly punctured medial part (a in Fig. 20B) .
..... *Merodon minutus*
9. Scutum strongly punctured and uniformly pollinose (Fig. 20A) *Merodon chalybeus*

Discussion

The *M. aureus* group was the object of many taxonomical studies during the last decade. Integration of morphology, genetics and morphometry has resulted in description of 18 new species since 2007 (Vujić *et al.* 2007, Radenković *et al.* 2011, 2018b, Šašić *et al.* 2016, Veselić *et al.* 2017, Šašić Zorić *et al.* 2018, 2020, Vujić *et al.* 2020b), and re-evaluation of two species (Šašić *et al.* 2016, Veselić *et al.* 2017). Thanks to integrative taxonomic approach, hierarchical levels of classification of this group into subgroups and complexes could be done (Fig. 9) (Šašić *et al.* 2016, Vujić *et al.* 2020b, 2021b). In this paper, we resolved the identities of the *M. chalybeus* subgroup members using an integrative taxonomic approach. We identified the *M. chalybeus* species complex which together with *M. robustus* constitutes the *M. chalybeus* subgroup within the *M. aureus* species group.

Both *M. chalybeus* and *M. minutus* show a great morphological variability within their geographical range. We found only one stable character, that is the lateral sides of scutum (*see* Fig. 20) to separate the two species. As a results of high morphological similarity between *M. chalybeus* and *M. minutus*, these two species have often been misidentified in the literature (*M. minutus* from former Yugoslavia as *M. chalybeus* in Mengual *et al.* 2006, Marcos-Garcia *et al.* 2007; *M. minutus* from France, Corsica as *M. chalybeus* in Speight & Sarthou 2008; *M. minutus* from Greece as *M. chalybeus* in Ssymank 2012). Speight (2020) stated that their distributional range is uncertain and overlapping, but our results showed a clear allopatric

distribution of two species. *Merodon minutus* is distributed in the Balkan Peninsula, Sicily, Sardinia and Corsica, while *M. chalybeus* is a western Mediterranean species distributed on the Iberian Peninsula and in northern Africa. Here, we confirmed a broader distribution of *M. robustus*: besides Samos (Greece) this species can be found in Cyprus, Israel and Turkey.

In a few earlier publications, *M. robustus* was recognised as an independent species within the *M. aureus* group (Šašić et al. 2016, Šašić Zorić et al. 2020, Veselić et al. 2017). In this study, we confirmed the recently published classification of *M. robustus* (see Vujić et al. 2021b) together with *M. chalybeus* complex to constitute the *M. chalybeus* subgroup.

Although morphologically almost identical, *M. chalybeus* and *M. minutus* differ in COI gene sequences. The average uncorrected pairwise p-distance (4.50%) between these two cryptic species is unusually high if compared with the distances between cryptic species of other complexes previously resolved within the *M. aureus* species group where it is mostly 0.3%–2.5% (Šašić et al. 2016, Šašić Zorić et al. 2018, 2020, Radenković et al. 2018b, Vujić et al. 2020b). The variability in COI haplotypes is also high in both species, which probably results from their wide distribution, and haplotype diversification seems to be an adaptive response to the diverse environment. We detected only one COI haplotype in *M. robustus*, which is endemic to the Eastern Mediterranean. This species is clearly different from the *M. chalybeus* complex based on the COI gene and morphological differences.

Here, we confirmed identifications made using wing shape by molecular findings which supports the results of some earlier taxonomic studies of cryptic hoverfly species (Nedeljković et al. 2013, 2015, Ačanski et al. 2016, Šašić et al. 2016, Radenković et al. 2018, Šašić Zorić et al. 2020, Djan et al. 2020, Vujić et al. 2020a, 2021b).

Posterior surstyle lobe has great taxonomic importance considering that shape of hoverfly male genitalia is stable, and for the majority of species most important diagnostic character. Thus far, geometric morphometric analysis of surstyle shape along with morphology and molecular findings, was confirmed a useful identification tool in three hoverfly genera: *Chrysotoxum* (Nedeljković

et al. 2013, 2015), *Merodon* (Ačanski et al. 2016, Šašić et al. 2016, Radenković et al. 2018, Šašić Zorić et al. 2020), and *Paragus* Latreille, 1804 (Tot 2021). It is important to emphasize that here, as in all analysed hoverfly genera, the majority of differences in surstylus shape were observed in the posterior part of the posterior surstyle lobe (or related structures). Hence, surstyle shape differences can be related to reproductive isolation if we consider surstyle function in gripping a female during copulation (Rotheray & Gilbert 2011).

Phenetic relationships constructed based on wing and surstylus shape were congruent with the COI gene tree topology, as well as with the external morphological similarity among species. Both wing and surstyle shape clearly separated *Merodon chalybeus* and *M. minutus* into a *M. chalybeus* complex.

Taking into account the distribution of the analysed species, it is important to stress that no significant correlations of wing, surstyle and genetic differences with geographical proximity among *M. chalybeus*, *M. minutus* and *M. robustus* were found.

Given the difficulties to readily distinguish the morphologically similar species *M. chalybeus* and *M. minutus*, as well as the presence of the morphologically similar species *M. robustus*, integrative taxonomy approach based on internal adult morphology, genetics, geometric morphometrics and distribution provided strong evidence for species separation. The COI-gene analysis results along with wing and surstyle shape results confirmed the *a priori* identification based on morphological identification alone.

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Appendix 1. List of *Merodon chalybeus* subgroup specimens used in geometric morphometric and genetic analyses.

Taxon	Specimen ID	Collection	Surstylus ID	Wing ID	Population	DNA ID	GenBank acc. no.			COI haplotype	Sex	Locality
							5' COI	3' COI				
<i>M. robustus</i>	F28	FSUNS	-	-	-	AU109	OL799168	OL799168	Hap38	♂	Greece, Samos, Spatharaioi-Pagmondhas	
<i>M. robustus</i>	F40	FSUNS	-	WM2239	GR, Samos	AU110	OL799169	OL799169	Hap38	♀	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F46	FSUNS	-	WM2240	GR, Samos	AU111	OL799170	OL799170	Hap38	♂	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F47	FSUNS	-	WM2241	GR, Samos	-	-	-	-	♀	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F49	FSUNS	F49	WM2242	GR, Samos	AU112	OL799171	OL799171	Hap38	♂	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F50	FSUNS	F50	WM2243	GR, Samos	AU113	OL799172	OL799172	Hap38	♂	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F51	FSUNS	F51	WM2244	GR, Samos	-	-	-	-	♂	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F52	FSUNS	F52	WM2245	GR, Samos	-	-	-	-	♂	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F53	FSUNS	-	WM2246	GR, Samos	-	-	-	-	♂	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F54	FSUNS	F54	WM2247	GR, Samos	-	-	-	-	♂	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F56	FSUNS	F56	WM2248	GR, Samos	-	-	-	-	♂	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F57	FSUNS	-	WM2249	GR, Samos	-	-	-	-	♀	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F58	FSUNS	-	WM2250	GR, Samos	-	-	-	-	♂	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F60	FSUNS	F60	WM2252	GR, Samos	AU114	OL799173	OL799173	Hap38	♂	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F61	FSUNS	F61	WM2253	GR, Samos	-	-	-	-	♂	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F62	FSUNS	F62	WM2256	GR, Samos	AU115	OL799174	OL799174	Hap38	♂	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F64	FSUNS	-	WM2254	GR, Samos	-	-	-	-	♀	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F65	FSUNS	-	WM2255	GR, Samos	-	-	-	-	♀	Greece, Samos, Pyrgos	
<i>M. robustus</i>	F66	FSUNS	-	WM2257	GR, Samos	-	-	-	-	♀	Greece, Samos, Pyrgos	
<i>M. robustus</i>	03528	RMNH	03528	-	-	-	-	-	-	♂	Greece, Samos, Platanos	
<i>M. minutus</i>	AL34	FSUNS	AL34	WM2304	GR, Thassos	AU126	OL799175	OL799175	Hap12	♂	Greece, Thassos, Skala Marion	
<i>M. minutus</i>	AL36	FSUNS	AL36	WM2305	GR, Thassos	AU125	OL799176	OL799176	Hap9	♂	Greece, Thassos, Skala Marion	
<i>M. minutus</i>	AL37	FSUNS	AL37	WM2300	GR, Thassos	AU124	OL799177	OL799177	Hap9	♂	Greece, Thassos, Potos	
<i>M. minutus</i>	AL38	FSUNS	-	WM2303	GR, Thassos	AU128	OL799178	OL799178	Hap9	♂	Greece, Thassos, Potos	
<i>M. minutus</i>	AL39	FSUNS	-	WM2301	GR, Thassos	AU129	OL799179	OL799179	Hap9	♂	Greece, Thassos, Potos	
<i>M. minutus</i>	AL40	FSUNS	AL40	WM2299	GR, Thassos	AU127	OL799180	OL799180	Hap9	♂	Greece, Thassos, Potos	
<i>M. minutus</i>	AL42	FSUNS	-	WM2302	GR, Thassos	AU130	OL799181	OL799181	Hap9	♀	Greece, Thassos, Potos	
<i>M. minutus</i>	G2517	MZegean	-	WM2316	-	AU131	OL799182	OL799182	Hap13	♀	Greece, Attiki, Monastery Daphni, near Atine	
<i>M. minutus</i>	G2840	DD coll.	-	ME063	GR, Thassos	-	-	-	-	♀	Greece, Thassos, Potos	
<i>M. minutus</i>	03485	DD coll.	-	WM2318	IT, Sicily	-	-	-	-	♂	Italy, Palermo, Piana degli Albanesi, Portella della Ginestra	
<i>M. minutus</i>	03486	DD coll.	-	WM2317	IT, Sicily	-	-	-	-	♂	Italy, Palermo, Lago di Piana degli Albanesi	
<i>M. minutus</i>	03497	DD coll.	03497	WM2320	IT, Sicily	-	-	-	-	♂	Italy, Palermo, Lago di Piana degli Albanesi	
<i>M. minutus</i>	03499	DD coll.	-	WM2319	IT, Sicily	-	-	-	-	♂	Italy, Palermo, Piana degli Albanesi, Portella della Ginestra	
<i>M. minutus</i>	03500	DD coll.	03500	WM2322	IT, Sicily	-	-	-	-	♂	Italy, Palermo, Piana degli Albanesi, Portella della Ginestra	
<i>M. minutus</i>	03501	DD coll.	03501	WM2323	IT, Sicily	-	-	-	-	♂	Italy, Palermo, Lago di Piana degli Albanesi	

continued

Appendix 1. Continued.

Taxon	Specimen ID	Collection	Surstylus ID	Wing ID	Population	DNA ID	GenBank acc. no.			COI haplotype	Sex	Locality
							5' COI	3' COI				
<i>M. minutus</i>	03502	DD coll.	03502	WM2324	IT, Sicily	-	-	-	-	♂	Italy, Palermo, Piana degli Albanesi, Portella della Ginestra	
<i>M. minutus</i>	03504	DD coll.	-	WM2326	IT, Sicily	-	-	-	-	♂	Italy, Palermo, Piana degli Albanesi, Portella della Ginestra	
<i>M. minutus</i>	03505	DD coll.	-	WM2327	IT, Sicily	-	-	-	-	♀	Italy, Palermo, Piana degli Albanesi, Portella della Ginestra	
<i>M. minutus</i>	03506	DD coll.	-	WM2328	IT, Sicily	-	-	-	-	♀	Italy, Palermo, Lago di Piana degli Albanesi	
<i>M. minutus</i>	03508	DD coll.	-	WM2330	IT, Sicily	-	-	-	-	♂	Italy, Palermo, Piana degli Albanesi, Portella della Ginestra	
<i>M. minutus</i>	03509	DD coll.	-	WM2331	IT, Sicily	-	-	-	-	♂	Italy, Palermo, Piana degli Albanesi, Portella della Ginestra	
<i>M. minutus</i>	07006	MAegean	-	-	-	AU311	OL799183	OL799183	Hap19	♀	Greece, Anafi	
<i>M. minutus</i>	07005	MAegean	-	-	-	AU312	OL799184	OL799184	Hap17	♀	Greece, Los	
<i>M. minutus</i>	07004	MAegean	-	-	-	AU313	OL799185	OL799185	Hap20	♀	Greece, Los	
<i>M. minutus</i>	07003	MAegean	-	-	-	AU314	OL799186	OL799186	Hap21	♂	Greece, Los	
<i>M. minutus</i>	09305	FSUNS	-	WM2621	IT, Sicily	AU640	OL799187	OL799187	Hap22	♂	Italy, Sicily, near Noto	
<i>M. minutus</i>	09306	FSUNS	-	WM2624	IT, Sicily	AU641	OL799188	OL799188	Hap23	♂	Italy, Sicily, near Noto	
<i>M. minutus</i>	09307	FSUNS	-	WM2622	IT, Sicily	AU642	OL799189	OL799189	Hap24	♂	Italy, Sicily, near Noto	
<i>M. minutus</i>	09308	FSUNS	-	WM2623	IT, Sicily	AU643	OL799190	OL799190	Hap25	♂	Italy, Sicily, near Noto	
<i>M. minutus</i>	09309	FSUNS	-	WM2625	IT, Sicily	AU644	OL799191	OL799191	Hap26	♂	Italy, Sicily, near Noto	
<i>M. minutus</i>	06446	FSUNS	-	-	-	AU182	OL799192	OL799192	Hap14	♂	Greece, Chania, 3 km pre Armeni	
<i>M. minutus</i>	06465	FSUNS	-	WM2311	GR, Peloponnese	AU184	OL799193	OL799193	Hap16	♂	Greece, Achaia, near Erimanthos 1	
<i>M. minutus</i>	06466	FSUNS	-	WM2312	GR, Peloponnese	AU185	OL799194	OL799194	Hap17	♂	Greece, Achaia, near Erimanthos 1	
<i>M. minutus</i>	06469	FSUNS	-	WM2313	GR, Peloponnese	AU186	OL799195	OL799195	Hap18	♂	Greece, Achaia, near Erimanthos 1	
<i>M. minutus</i>	06470	FSUNS	-	WM2306	GR, Peloponnese	-	-	-	-	♂	Greece, Achaia, near Erimanthos 1	
<i>M. minutus</i>	06471	FSUNS	-	-	-	AU187	OL799196	OL799196	Hap15	♂	Greece, Achaia, near Erimanthos 1	
<i>M. minutus</i>	06473	FSUNS	06473	WM2307	GR, Peloponnese	-	-	-	-	♂	Greece, Achaia, near Erimanthos 1	
<i>M. minutus</i>	06479	FSUNS	06479	ME064L	GR, Peloponnese	-	-	-	-	♂	Greece, Achaia, near Erimanthos 1	
<i>M. minutus</i>	06482	FSUNS	-	WM2310	GR, Peloponnese	AU183	OL799197	OL799197	Hap15	♂	Greece, Achaia, near Erimanthos 1	
<i>M. minutus</i>	06484	FSUNS	-	WM2314	GR, Peloponnese	AU188	OL799198	OL799198	Hap17	♂	Greece, Achaia, near Erimanthos 1	
<i>M. minutus</i>	06486	FSUNS	06486	WM2309	GR, Peloponnese	-	-	-	-	♂	Greece, Achaia, near Erimanthos 1	
<i>M. minutus</i>	03511	HM coll.	-	03511	-	-	-	-	-	♀	Italy, Sardinia, Siniscola, Pineta	
<i>M. minutus</i>	03507	DD coll.	03507	-	-	-	-	-	-	♂	Italy, Palermo, Lago di Piana degli Albanesi	
<i>M. minutus</i>	06446	FSUNS	06446	WM2315	-	-	-	-	-	♂	Greece, Chania, 3 km before Armeni	
<i>M. minutus</i>	06475	FSUNS	06475	-	-	-	-	-	-	♂	Greece, Achaia, near Erimanthos 1	
<i>M. minutus</i>	07003	MAegean	07003	-	-	-	-	-	-	♂	Greece, Ios, Mersinia Rema	
<i>M. minutus</i>	17760	FSUNS	-	17760	-	TS434	OL799224	OL799224	Hap10	♂	France, Corsica, near Vizzavona	
<i>M. minutus</i>	17761	FSUNS	-	17761	-	TS435	OL799225	OL799225	Hap11	♀	France, Corsica, near Vizzavona	

continued

Appendix 1. Continued.

Taxon	Specimen ID	Collection	Surstylus ID	Wing ID	Population	DNA ID	GenBank acc. no.			COI haplotype	Sex	Locality
							5' COI	3' COI	COI			
<i>M. chalybeus</i>	Đ31	FSUNS	–	WM2284	MA, N Morocco	AU117	MN514099	MN514099	Hap2	♀	Morocco, Middle Atlas, Ifrane National Park 2	
<i>M. chalybeus</i>	Đ32	FSUNS	Đ32	–	–	AU118	OL799199	OL799199	Hap3	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ39	FSUNS	–	WM2285	MA, N Morocco	AU119	OL799200	OL799200	Hap4	♀	Morocco, Middle Atlas, Ifrane National Park 3	
<i>M. chalybeus</i>	Đ40	FSUNS	–	WM2286	MA, N Morocco	AU120	OL799201	OL799201	Hap5	♀	Morocco, Middle Atlas, Ifrane National Park 3	
<i>M. chalybeus</i>	Đ45	FSUNS	–	WM2290	MA, N Morocco	AU121	OL799202	OL799202	Hap6	♀	Morocco, near Ouzzane	
<i>M. chalybeus</i>	Đ51	FSUNS	Đ51	WM2288	MA, N Morocco	AU122	OL799203	OL799203	Hap7	♂	Morocco, Tetouan, Tanger	
<i>M. chalybeus</i>	Đ54	FSUNS	–	WM2287	MA, N Morocco	AU123	OL799204	OL799204	Hap8	♂	Morocco, Tetouan, Tanger	
<i>M. chalybeus</i>	Đ72	FSUNS	Đ72	WM2266	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ73	FSUNS	Đ73	WM2267	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ74	FSUNS	Đ74	WM2268	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ75	FSUNS	Đ75	WM2269	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ76	FSUNS	Đ76	WM2270	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ77	FSUNS	–	WM2279	MA, N Morocco	–	–	–	–	♀	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ78	FSUNS	–	WM2271	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ79	FSUNS	–	WM2272	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ80	FSUNS	–	WM2280	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ81	FSUNS	Đ81	WM2276	MA, N Morocco	–	–	–	–	♀	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ82	FSUNS	–	WM2281	MA, N Morocco	–	–	–	–	♀	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ83	FSUNS	–	WM2282	MA, N Morocco	–	–	–	–	♀	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ85	FSUNS	Đ85	WM2265	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ86	FSUNS	Đ86	WM2273	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ87	FSUNS	Đ87	–	–	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ88	FSUNS	Đ88	–	–	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ89	FSUNS	Đ89	–	–	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ90	FSUNS	Đ90	–	–	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ92	FSUNS	Đ92	WM2275	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ93	FSUNS	–	WM2274	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ94	FSUNS	–	WM2283	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ95	FSUNS	–	WM2278	MA, N Morocco	–	–	–	–	♀	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ96	FSUNS	Đ96	–	–	AU116	OL799205	OL799205	Hap1	♀	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	Đ97	FSUNS	Đ97	WM2277	MA, N Morocco	–	–	–	–	♂	Morocco, Middle Atlas, Ifrane National Park 1	
<i>M. chalybeus</i>	03490	BM coil.	–	WM2291	SP, S Spain	–	–	–	–	♂	Spain, Andalusia, Algeciras, Punta Tarifa	
<i>M. chalybeus</i>	03492	BM coil.	–	WM2292	SP, S Spain	–	–	–	–	♀	Spain, Andalusia, Algeciras, Punta Tarifa	
<i>M. chalybeus</i>	03493	BM coil.	–	WM2293	SP, S Spain	–	–	–	–	♀	Spain, 40 km W of Malaga, Yunquera	
<i>M. chalybeus</i>	03494	BM coil.	–	WM2294	SP, S Spain	–	–	–	–	♀	Spain, 40 km W of Malaga, Yunquera	
<i>M. chalybeus</i>	08914	FSUNS	–	–	–	AU757	OL799206	OL799206	Hap30	♂	Spain, Cartaya-EI Portil	
<i>M. chalybeus</i>	08915	FSUNS	–	ME052	SP, S Spain	AU758	OL799207	OL799207	Hap31	♂	Spain, Cartaya-EI Portil	
<i>M. chalybeus</i>	08916	FSUNS	–	ME053	SP, S Spain	AU759	OL799208	OL799208	Hap30	♂	Spain, Cartaya-EI Portil	

continued

Appendix 1. Continued.

Taxon	Specimen ID	Collection	Surstylus ID	Wing ID	Population	DNA ID	GenBank acc. no.			COI haplotype	Sex	Locality
							5' COI	3' COI				
<i>M. chalybeus</i>	08917	FSUNS	—	ME054	SP, S Spain	AU760	MN623532	MN623532	Hap32	♂	Spain, Cartaya-EI Portil	
<i>M. chalybeus</i>	08918	FSUNS	—	ME046	SP, S Spain	—	—	—	—	♂	Spain, Cartaya-EI Portil	
<i>M. chalybeus</i>	08919	FSUNS	—	ME045	SP, S Spain	—	—	—	—	♂	Spain, Cartaya-EI Portil	
<i>M. chalybeus</i>	08920	FSUNS	—	ME055L	SP, S Spain	AU761	OL799209	OL799209	Hap33	♂	Spain, Cartaya-EI Portil	
<i>M. chalybeus</i>	08921	FSUNS	—	ME047	SP, S Spain	—	—	—	—	♂	Spain, Cartaya-EI Portil	
<i>M. chalybeus</i>	08923	FSUNS	—	ME049L	SP, S Spain	—	—	—	—	♀	Spain, Cartaya-EI Portil	
<i>M. chalybeus</i>	08924	FSUNS	—	ME056	SP, S Spain	—	—	—	—	♀	Spain, Cartaya-EI Portil	
<i>M. chalybeus</i>	08925	FSUNS	—	ME057	SP, S Spain	—	—	—	—	♀	Spain, Cartaya-EI Portil	
<i>M. chalybeus</i>	09320	FSUNS	—	ME058L	SP, S Spain	—	—	—	—	♀	Spain, Cartaya-EI Portil	
<i>M. chalybeus</i>	09321	FSUNS	—	ME050L	SP, S Spain	—	—	—	—	♀	Spain, Cartaya-EI Portil	
<i>M. chalybeus</i>	09322	FSUNS	—	ME051	SP, S Spain	—	—	—	—	♂	Spain, Cartaya-EI Portil	
<i>M. chalybeus</i>	09370	FSUNS	—	ME017	SP, S Spain	AU752	MH133976	MH133976	Hap27	♀	Spain, Algeciras 1	
<i>M. chalybeus</i>	09371	FSUNS	—	ME018	SP, S Spain	AU753	OL799210	OL799210	Hap28	♀	Spain, Algeciras 1	
<i>M. chalybeus</i>	09373	FSUNS	—	ME006	SP, S Spain	AU754	OL799211	OL799211	Hap28	♀	Spain, Algeciras 1	
<i>M. chalybeus</i>	09374	FSUNS	—	ME012	SP, S Spain	AU755	OL799212	OL799212	Hap29	♂	Spain, Algeciras 1	
<i>M. chalybeus</i>	09376	FSUNS	—	ME013	SP, S Spain	AU756	OL799213	OL799213	Hap27	♂	Spain, Algeciras 1	
<i>M. chalybeus</i>	09377	FSUNS	—	ME005	SP, S Spain	—	—	—	—	♂	Spain, Algeciras 1	
<i>M. chalybeus</i>	09379	FSUNS	—	ME008	SP, S Spain	—	—	—	—	♂	Spain, Algeciras 1	
<i>M. chalybeus</i>	09381	FSUNS	—	ME009	SP, S Spain	—	—	—	—	♂	Spain, Algeciras 1	
<i>M. chalybeus</i>	09382	FSUNS	—	ME010	SP, S Spain	—	—	—	—	♂	Spain, Algeciras 1	
<i>M. chalybeus</i>	09383	FSUNS	—	ME011L	SP, S Spain	—	—	—	—	♂	Spain, Algeciras 1	
<i>M. chalybeus</i>	09384	FSUNS	—	ME003	SP, S Spain	—	—	—	—	♂	Spain, Algeciras 1	
<i>M. chalybeus</i>	09385	FSUNS	—	ME004	SP, S Spain	—	—	—	—	♂	Spain, Algeciras 1	
<i>M. chalybeus</i>	09388	FSUNS	—	ME019L	SP, S Spain	—	—	—	—	♀	Spain, Algeciras 2, scenic viewpoint Mirador	
<i>M. chalybeus</i>	09390	FSUNS	—	ME016	SP, S Spain	—	—	—	—	♀	Spain, Algeciras 2, scenic viewpoint Mirador	
<i>M. chalybeus</i>	09391	FSUNS	—	ME007	SP, S Spain	—	—	—	—	♀	Spain, Algeciras 2, scenic viewpoint Mirador	
<i>M. chalybeus</i>	09394	FSUNS	—	ME001	SP, S Spain	—	—	—	—	♂	Spain, Algeciras 3, beach near Santa Margarita	
<i>M. chalybeus</i>	09395	FSUNS	—	ME002L	SP, S Spain	—	—	—	—	♂	Spain, Algeciras 3, beach near Santa Margarita	
<i>M. chalybeus</i>	09396	FSUNS	—	ME014L	SP, S Spain	—	—	—	—	♀	Spain, Algeciras 3, beach near Santa Margarita	
<i>M. chalybeus</i>	09420	FSUNS	—	ME023	SP, S Spain	—	—	—	—	♀	Spain, Bolonia 2	
<i>M. chalybeus</i>	09431	FSUNS	—	ME020	SP, S Spain	AU767	OL799214	OL799214	Hap28	♀	Spain, Bolonia 3	
<i>M. chalybeus</i>	09434	FSUNS	—	ME060	SP, S Spain	—	—	—	—	♂	Spain, Bolonia 3	
<i>M. chalybeus</i>	09440	FSUNS	—	ME061L	SP, S Spain	AU769	OL799215	OL799215	Hap27	♂	Spain, Bolonia 3	
<i>M. chalybeus</i>	09441	FSUNS	—	ME021	SP, S Spain	AU770	OL799216	OL799216	Hap28	♀	Spain, Bolonia 3	
<i>M. chalybeus</i>	09442	FSUNS	—	ME032L	SP, S Spain	AU771	OL799217	OL799217	Hap37	♂	Spain, Bolonia 3	

continued

Appendix 1. Continued.

Taxon	Specimen ID	Collection	Surstylus ID	Wing ID	Population	DNA ID	GenBank acc. no.			COI haplotype	Sex	Locality
							5' COI	3' COI				
<i>M. chalybeus</i>	09443	FSUNS	-	ME022	SP, S Spain	-	-	-	-	♀	Spain, Bolonia 3	
<i>M. chalybeus</i>	09444	FSUNS	-	ME031L	SP, S Spain	-	-	-	-	♂	Spain, Bolonia 3	
<i>M. chalybeus</i>	09474	FSUNS	-	-	-	AU762	OL799218	OL799218	Hap34	♂	Spain, Grazalema 1	
<i>M. chalybeus</i>	09475	FSUNS	-	ME038L	SP, S Spain	AU763	OL799219	OL799219	Hap35	♂	Spain, Grazalema 1	
<i>M. chalybeus</i>	09479	FSUNS	-	ME026	SP, S Spain	AU764	OL799220	OL799220	Hap36	♀	Spain, Grazalema 1	
<i>M. chalybeus</i>	09457	FSUNS	-	-	-	AU765	OL799221	OL799221	Hap28	♀	Spain, Jimene de la Frontera	
<i>M. chalybeus</i>	09459	FSUNS	-	-	-	AU766	OL799222	OL799222	Hap28	♀	Spain, Jimene de la Frontera	
<i>M. chalybeus</i>	09464	FSUNS	-	-	-	AU768	OL799223	OL799223	Hap37	♂	Spain, Cortes de la Frontera, road to Grazalema	
<i>M. chalybeus</i>	09481	FSUNS	-	ME034	SP, S Spain	-	-	-	-	♂	Spain, Grazalema 1	
<i>M. chalybeus</i>	10777	FSUNS	-	ME039	SP, S Spain	-	-	-	-	♂	Spain, Grazalema 1	
<i>M. chalybeus</i>	10779	FSUNS	-	ME040	SP, S Spain	-	-	-	-	♂	Spain, Grazalema 1	
<i>M. chalybeus</i>	10780	FSUNS	-	ME027	SP, S Spain	-	-	-	-	♀	Spain, Grazalema 1	
<i>M. chalybeus</i>	10782	FSUNS	-	ME028	SP, S Spain	-	-	-	-	♀	Spain, Grazalema 1	
<i>M. chalybeus</i>	10837	FSUNS	-	ME042	SP, S Spain	-	-	-	-	♂	Spain, Grazalema 2	
<i>M. chalybeus</i>	10848	FSUNS	-	ME043	SP, S Spain	-	-	-	-	♂	Spain, Grazalema	
<i>M. chalybeus</i>	10849	FSUNS	-	ME044	SP, S Spain	-	-	-	-	♂	Spain, Grazalema	
<i>M. chalybeus</i>	10851	FSUNS	-	ME024	SP, S Spain	-	-	-	-	♀	Spain, Grazalema	
<i>M. chalybeus</i>	10852	FSUNS	-	ME030	SP, S Spain	-	-	-	-	♀	Spain, Grazalema	
<i>M. chalybeus</i>	13303	FSUNS	-	ME029	SP, S Spain	-	-	-	-	♀	Spain, Bolonia near road	
<i>M. chalybeus</i>	19861	FSUNS	-	ME036	SP, S Spain	-	-	-	-	♂	Spain, Grazalema, Ubrique	
<i>M. chalybeus</i>	19868	FSUNS	-	ME025	SP, S Spain	-	-	-	-	♀	Spain, Grazalema, Grazalema	
<i>M. chalybeus</i>	19869	FSUNS	-	ME035	SP, S Spain	-	-	-	-	♀	Spain, Grazalema, Grazalema	
<i>M. chalybeus</i>	03339	HM coll.	-	WM2296	-	-	-	-	-	♀	Spain, Ciudad Real, Sierra de Santa Maria, Viso del Marques	
<i>M. chalybeus</i>	03341	HM coll.	-	WM2297	-	-	-	-	-	♀	Spain, Ciudad Real, Sierra de Santa Maria, Viso del Marques	
<i>M. equestris</i>	GJ.2774	MZH	-	-	-	Y690	EU431486	EU431486	-	♂	Finland, Askola	
<i>M. luteofasciatus</i>	06432	FSUNS	-	-	-	AU189	KU365486	KU365486	-	♂	Greece, Crete, Rethymon, Orne-Agia Galini	
<i>M. ruficornis</i>	GJ.3537	MZH	-	-	-	Y2077	MH496011	MH496011	-	♂	Montenegro, Durmitor, Susica lake	
<i>M. desuturinus</i>	GJ.3545	MZH	-	-	-	Y2078	LT882606	LT882606	-	♀	Spain, Serbia, Kopaonik, Jasle-Čukara	
<i>E. pulchellus</i>	09289	FSUNS	-	-	-	AU735	MN562427	MN562427	-	♂	Italy, Sicily, near Belpasso	
<i>E. amoenus</i>	09296	FSUNS	-	-	-	AU736	KU365485	KU365485	-	♂	Italy, Sicily, via Messina-Catania	
<i>E. pusillus</i>	09299	FSUNS	-	-	-	AU737	MN562428	MN562428	-	♂	Malta, Roud Triq Panoramika	
<i>P. macquarti</i>	09212	FSUNS	-	-	-	AU740	MN562429	MN562429	-	♂	Italy, Sicily, near Sortino	