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Three new species of the *Merodon ruficornis* group (Diptera: Syrphidae) discovered at the edge of its range

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Abstract

Further revision of material from the *Merodon ruficornis* group (Diptera: Syrphidae) revealed three new species, *M. acutus* Vujić et Radenković **sp. nov.** from Russia, *M. fulvitarsis* Vujić et Radenković **sp. nov.** from Iran, and *M. trispinus* Vujić et Radenković **sp. nov.** from Turkey. We provide an upgraded and illustrated identification key for the species of the group, as well as distribution maps for the new species. Moreover, we describe the female of *M. portschinskyi* Stackelberg, 1924. These new descriptions extend the range of the *M. ruficornis* group in almost all directions and bolster the very high level of endemism previously observed within this group. Of the 21 taxa (including the three new species described herein), 15 are narrow-range endemics.

Key words: COI gene, endemicity, hoverfly, identification key, morphology, taxonomy

Introduction

The genus *Merodon* Meigen, 1803 (tribe Merodontini) is one of the most species-rich hoverfly genera, distributed across the Palaearctic and Afrotropical Regions, comprising 195 described and a further 39 undescribed species (Vujić *et al.* 2021a, Vujić *et al.* 2021b). One species, i.e., *M. equestris* (Fabricius, 1794), has been introduced into the Nearctic Region and New Zealand (Speight 2020). Europe hosts 120 described species of the genus (Vujić *et al.* 2021) with the highest species diversity in the Mediterranean Basin (Vujić *et al.* 2012), which has been in linked to the high diversity of bulbous plant species that serve as larval host plants (Ricarte *et al.* 2008, 2017; Andrić *et al.* 2014; Preradović *et al.* 2018). Asia Minor and Eastern Europe (especially the Balkan Peninsula) are considered hotspots for the genus, harboring high endemism (Kaloveloni *et al.* 2015), as documented by several studies in the Eastern Mediterranean Basin (Vujić *et al.* 2015, 2020a, b, c; Ståhls *et al.* 2009, 2016; Radenković *et al.* 2011, 2020; Kaloveloni *et al.* 2015; Ačanski *et al.* 2016a, b; Likov *et al.* 2020).

The genus *Merodon* is divided into lineages, species groups, species subgroups and species complexes following the system proposed by Šašić *et al.* (2016) and based on various levels of morphological differentiation. A recent study summarized knowledge from taxonomic revisions and identified five monophyletic lineages namely *albifrons, aureus, avidus-nigritarsis, desuturinus* and *natans*, 24 species groups, two species subgroups and 10 unplaced taxa (Vujić *et al.* 2021a). The *albifrons* lineage comprises six species groups (*albifrons, constans, equestris, geniculatus, ruficornis* and *rufus*) and two unplaced taxa (Vujić *et al.* 2021a). The *Merodon ruficornis* species group has been characterized as a morphologically distinct group of species displaying several synapomorphic characters,

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especially with regard to the structure of the metalegs in males. Hitherto, a total of 18 species have been recognized in the species group of which 12 are limited-range endemics (Vujić *et al.* 2012). The group is predominantly distributed in the Eastern Mediterranean and especially the Anatolian Peninsula and the Caucasus Mountains show a high endemicity (Vujić *et al.* 2012).

Adults of the *M. ruficornis* species group feed on pollen and nectar, visiting the flowers of a broad range of plant species (Speight 2020). An examination of the gut contents of *Merodon loewi* van der Goot, 1964 in Serbia showed a preference for pollen of *Ornithogalum* spp. relative to other syrphids (Suturović 2008). The larval biology of *Merodon* species is poorly known, but all known species develop underground in the bulbs or corms of monocotyledonous species (Ricarte *et al.* 2008, 2017; Andrić *et al.* 2014; Preradović *et al.* 2018). Based on personal communication with a D. Doczkal, Speight (2020) highlighted that *M. armipes* Rondani, 1843 (*M. ruficornis* species group) appeared to be associated with the tassel hyacinth, *Leopoldiacomosa* (L.) Parl. (Asparagaceae) in southern Germany. Additionally, larvae of *M. loewi*, another member of this species group, under laboratory conditions, fed successfully in bulbs of Hyacinthaceae, namely *Scilla siberica* Haw. and *Leopoldia comosa* (L.) Parl. at the beginning of their development (Popov, 2009). Description of the immature stages of any species of the *M. ruficornis* species group remain unpublished.

Molecular taxonomic studies of hoverflies using both the 3' and 5' ends of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene have proven to be a powerful tool for species delimitation in various genera (Mengual *et al.* 2006; Marcos-García *et al.* 2011; Barkalov & Stĺhls 2015; Nedeljkoviă *et al.* 2015; Chroni *et al.* 2017; Nedeljković *et al.* 2020). Integration of molecular analyses with traditional taxonomy in the *Merodon* genus has allowed to describe high diversity and the presence of closely-related or cryptic species (Ståhls*et al.* 2009; Vujić *et al.* 2012, 2013b; Šašić *et al.* 2016; Mengual *et al.* 2018; Radenković *et al.* 2018; Vujić *et al.* 2020a; Zorić *et al.* 2020; Vujić et al. 2021a).

The aim of the present study was to: 1) review material of the *M. ruficornis* species group stored in several scientific institutions and private collections; 2) describe new species within this group and to present an updated identification key; 3) corroborate the new species' concepts within the *M. ruficornis* group by analysing the cytochrome c oxidase subunit I (COI); and 4) present a distribution map for the *M. ruficornis* species group.

Material and methods

Morphological analysis. A total of 32 specimens belonging to the *M. ruficornis* group from the Palaearctic Region were studied. The studied material is part of several museums, institutions and private collections: FSUNS—Faculty of Sciences, Department of Biology and Ecology, University of Novi Sad, Novi Sad, Serbia; IMTU—Insect Museum of Tabriz University, Tabriz, Iran; SJ coll. –Jeroen van Steenis personal collection, The Netherlands; SZMN—Siberian Zoological Museum of Systematic and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia; ZFMK—Zoologisches Forschungs museum Alexander Koenig, Bonn, Germany. All collecting information on specimens is stored in an electronic database of FSUNS.

Occurrence points (geographical coordinates) were entered into the Geographic Information System DIVA-GIS 5.2 software (Hijmans *et al.* 2012) to generate distribution maps.

Terminology follows Thompson (1999) for non-genitalic morphology, except "proepimeron" and "pleuron", which follows McAlpine (1981), and Marcos-García *et al.* (2007) for morphology of the male genitalia. Additionally, the term "fasciate maculae" follows Vujić *et al.* (2021).

Morphological characters were observed using a Nikon SMZ 745T stereomicroscope. Drawings were made with a FSA 25 PE drawing tube, while digital photographs were recorded with a Leica DFC 320 digital camera, both attached to a Leica MZ16 binocular microscope. Digital photographs were stacked using Combine Z software (Hadley 2006). Measurements were taken with an eyepiece graticule or micrometre. Photographs of the lectotype of *M. portschinskyi* were taken by PhD Nikolay Paramonov (Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia) with a Canon EOS 800D camera with an MP-E 65mm lens, after which the photos were stitched and processed using the Helicon Focus 6 software (Helicon Soft Ltd., www.heliconsoft.com). Body length was measured in lateral view in millimetres (mm) using an eyepiece micrometre from the lunula to the end of the abdomen. Wing length was measured from the tegula to the apex of the wing.

| الأستطمة بتملم متبارين وللمحليل الممالة | D | гацице | Longitude | Sex | Lab code | GenBank accession number of the COI |
|--|--|--------------|--------------|--------|----------|--|
| Manadam tuch and a strain Charles 1000 | | | | | | gene sequence |
| Merodon ireverticensis Silool, 1900 | Serbia, Dubašnica, Demižlok. 08.06.2011. Leg. A. Vujić | °N 44.016060 | °E 21.880220 | male | RU041 | ON562585 |
| <i>Merodon gallicus</i> Vujić et Radenković in Vujić <i>et al.</i> 2012 | France, Tende, Limitte Valaurette. 08.07.2013. Leg. T. Lebard | °N 44.068497 | °W 7.484583 | male | AU1820 | ON880572 |
| Merodon ruficornis Meigen, 1822 | France, Tende, Aval du parking de valmasque. 05.05.2016. Leg. T. Lebard | °N 44.111453 | °W 7.498858 | male | AU1821 | ON880573 |
| Merodon portschinskyi Stackelberg, 1924 | Georgia, Imereti, Sairme. 10.06.2019. Leg. M. Ximo | °N 41.993333 | °E 43.943333 | male | RU312 | ON880568 |
| Merodon portschinskyi Stackelberg, 1924 | Georgia, Samegrelo, ZemoSvaneti. 17.06.2019. Leg. M. Ximo | °N 43.000555 | °E 43.070000 | male | RU314 | ON880569 |
| Merodon portschinskyi Stackelberg, 1924 | Georgia, Imereti, Sairme. 10.06.2019. Leg. J. van Steenis | °N 41.860000 | °E 42.770000 | male | AU1830 | ON880570 |
| Merodon portschinskyi Stackelberg, 1924 | Georgia, Imereti, Sairme. 10.06.2019. Leg. J. van Steenis | °N 41.860000 | °E 42.770000 | male | AU1831 | ON880571 |
| <i>Merodon hoplitis</i> Hurkmans in Vujić <i>et al.</i> 2012 | Montenegro, Orjen, Vratlo. 11.04.2011. Leg. A. Vujić | °N 42.510451 | °E 18.559062 | female | RU185 | ON562623 |
| <i>Merodon trispinus</i> Vujić et Radenković sp. nov. | Turkey, Babadað. 05.07.2015. Leg. S. Radenković | °N 36.865139 | °E 29.34881 | male | RU191 | ON562604 |
| <i>Merodon trispinus</i> Vujić et Radenković sp. nov. | Turkey, Babadað. 05.07.2015. Leg. S. Radenković | °N 37.695179 | °E 28.99309 | male | RU192 | ON562605 |

| Species | Collecting locality | Latitude | Longitude | Sex | Lab code | GenBank accession number of the COI gene sequence |
|--|--|--------------|--------------|--------|----------|---|
| <i>Merodon trispinus</i> Vujić et Radenković sp. nov. | Turkey, Babadað. 05.07.2015. Leg. S. Radenković | °N 37.695179 | °E 28.99309 | male | RU193 | ON562606 |
| <i>Merodon trispinus</i> Vujić et Radenković sp. nov. | Turkey, Babadað. 05.07.2015. Leg. S. Radenković | °N 37.695179 | °E 28.99309 | male | RU194 | ON562607 |
| Merodon auripes Sack, 1913 | Greece, Drama. 12.05.2011. Leg. A. Vujić | °N 41.150440 | °E 24.152259 | male | RU058 | ON562588 |
| <i>Merodon acutus</i> Vujić et Radenković sp. nov. | Russia, Caucasus, Adygeya, Kamenomostskiy. 11.05.2015. Leg. E. Rattel | °N 44.326325 | °E 40.183335 | female | RU201 | ON562698 |
| <i>Merodon acutus</i> Vujić et Radenković sp. nov. | Russia, Caucasus, Adygeya, Kamenomostskiy. 11.05.2015. Leg. E. Rattel | °N 44.326325 | °E 40.183335 | female | RU202 | ON562699 |
| <i>Merodon papillus</i> Vujić, Radenković et Pérez-Bañón in Vujić et al. 2007 | Greece, Lesvos. 05.04.2010. Leg. A. Vujić | °N 39.233333 | °E 26.050000 | male | RU183 | ON562621 |
| <i>Merodon fulvitarsis</i> Vujić et Radenković sp. nov. | Iran, Osculu. Leg. S. Khaghaninia | °N 38.872483 | °E 46.8966 | male | RU189 | ON562626 |
| <i>Merodon fulvitarsis</i> Vujić et Radenković sp. nov. | Iran, Aynali forest. Leg. S. Khaghaninia | °N 38.895933 | °E 46.779417 | female | RU190 | ON562632 |
| Merodon armipes Rondani, 1843 | Serbia, Đerdap, Ciganskipotok. 06.04.2011. Leg. A. Vujić | °N 44.541040 | °E 22.020240 | male | RU103 | ON562657 |
| Merodon loewi van der Goot, 1964 | Greece, Mainalo, Kardaras. 05.04.2010. Leg. A. Vujić | °N 37.659728 | °E 22.259893 | female | RU150 | ON562689 |

Male genitalia were extracted from dry specimens and cleared by boiling them in water with diluted KOH pellets. This was followed by brief immersion in acetic acid to neutralize the KOH, immersion in ethanol to remove the acid, and storage in microvials containing glycerol which were added to the pin of the specimens.

Molecular analysis. Molecular analysis was performed on 20 individuals, and comprised each morphologically recognizable taxon of the M. ruficornis group. Total genomic DNA was extracted from meso- and metalegs using a SDS protocol (Chen et al. 2010). Two regions (the 3'-end and 5'-end) of the mitochondrial COI gene were sequenced. The 5'-end of the COI gene (DNA barcode region) was amplified using the LCO-1490/HCO-2198 (Folmer et al. 1994) primer pair, while the primers C1-J-2183(Jerry) and TL2-N-3014 (Pat) (Simon et al. 1994) were used for amplification of the 3'-end of the COI gene. Polymerase chain reactions (PCR) were performed in a 25µl reaction volumes containing: 1x Taq Buffer without MgCl, (ThermoScientific, Lithuania), 2mM MgCl,, 0.1mM of each nucleotide, 1.25U Taq polymerase (ThermoScientific, Lithuania), 5pmol of each primer, 50-100ng genomic DNA and ultrapure water. Amplification was carried out in an Eppendorf Personal Thermocycler using the following conditions for 5'-end COI: initial denaturation at 94°C for 3 min; 29 cycles of denaturation at 94°C for 30 s; annealing at 50°C for 45 s; extension at 72°C for 1 min; followed by a final extension at 72°C for 8 min. The PCR condition for 3'-end of COI gene were: initial denaturation at 95°C for 2 min; 29 cycles of denaturation at 94°C for 30 s; annealing at 49°C for 30 s; extension at 72°C for 2 min; followed by a final extension at 72°C for 8 min. Amplification products were enzymatically purified using Exonuclease I and Shrimp Alkaline Phosphatase enzymes (ThermoScientific, Lithuania) according to manufacturer's instructions. Sequencing was done using forward PCR primers by the Macrogen EZ-Seq service (Macrogen Europe, Amsterdam, the Netherlands) and all sequences were submitted to GenBank (for accession numbers see Table 1.

Chromatograms of all DNA sequences produced for this study were edited in BioEdit version 7.2.5. (Hall *et al.* 1999) and the COI gene fragments were aligned manually. Two sequence matrices were created, the first of which contained concatenated 3'-end and 5'-end COI gene sequences, and the second was comprised of 5'-end COI gene (barcode) sequences. Maximum parsimony (MP) and maximum likelihood (ML) trees were constructed using the concatenated COI sequence matrix. Maximum parsimony (MP) tree was performed in NONA (Goloboff 1999) spawned with the aid of Winclada ASADO (Nixon 2002), using the heuristic search algorithm with 1000 random addition replicates (mult*1000), holding 100 trees per round (hold/100), maxtrees set to 100 000 and applying tree-bisection-reconnection branch swapping. Nodal support for the tree was assessed in Winclada ASADO using non-parametric bootstrapping with 1000 replicates. The ML tree was constructed using RAxML 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). The nucleotide substitution model was estimated in MEGA X (Kumar *et al.* 2018) and selected using the Akaike Information Criterion (Akaike 1974). Nodal supports were estimated using rapid bootstrapping with 1000 rapid bootstrap replicates. The trees were rooted on *Merodon luteofasciatus* as Vujiã, Radenkoviã et Stíhls, 2018 *in* Vujić *et al.* (2018).

Uncorrected sequence distance values (p-distances) were calculated in MEGA X (Kumar *et al.* 2018) for both, individual barcode sequences and concatenated 3'-end and 5'-end COI gene sequences. Combined sequences of two COI fragments were analysed for the determination of the 'barcoding gap' between taxa of the *M. ruficornis* species group. Putative species limits were explored with the Automatic Barcode Gap Discovery (ABGD) software (Puillandre *et al.* 2012) using default settings (Pmin = 0.001, Pmax = 0.1, Steps = 10, X (relative gap width) = 1.5, Nb bins = 20).

Results

The Merodon ruficornis group

Morphological diagnosis. The *M. ruficornis* group represents a morphologically distinct group of species with several synapomorphic characters, especially in the structure of male metaleg. Metatrochanter, metafemur and metatibia usually with tubercle, calcar or lamina in the male (as in Fig. 1). Male genitalia usually with characteristic hook-like posterior surstyle lobe (as in Fig. 2A: pl), biramous anterior surstyle lobe (as in Fig. 2A: al) with moderately developed interior accessory lobe (as in Fig. 2A: il) and apical extension (as in Fig. 2A marked with arrow), cercus without prominences (as in Fig. 2A: c), and lateral sclerite of the aedeagus hammer-like with oval margins (as in

Fig. 9C: s). In females, tergum 4 usually with transversal depression (as in Fig. 3A: marked with arrow, 3B); terga dark, except tergum 2 with a pair of lateral red-orange maculae; terga 2–4 usually with a pair of white pollinose fasciate maculae; tergum 5 with two small lateral depressions (as in Fig. 3C: marked with arrow); vertex at the level of ocellar triangle shiny black (as in Fig. 3D) (Vujić *et al.* 2021a).



FIGURE 1. Part of metaleg of *Merodon* male. **A** *Merodon armipes* (ventral tubercle marked with arrow), **B** *M. acutus* **sp. nov.** (ventral tubercle marked with black arrow; lamella on metatibia marked with white arrow), **C** *M. nigripodus* (lamella on metatibia marked with arrow), **D** *M. ponticus* (lamella on metatibia marked with arrow), **E** *M. acutus* **sp. nov.** (inner, posteroventral spina on metatibia, marked with arrow). **a**—metatrochanter, **b**—metafemur, **c**—metatibia. Scale bar: **A**–**D** 1 mm, **E** 1.5 mm.

Morphological description of males and females of the *M. ruficornis* group. *Length.* We use the following three categories to describe the general body size of the species: Small species 7–10 mm; medium-sized species 10–12 mm; large species 12–14 mm. **MALE**. *Head* (as in Figs 4A–C). Antenna (as in Fig. 4A) brown-orange, baso-flagellomere 1.3 times as long as wide, 1.6 times longer than pedicel, concave dorsally, apex acute; arista basally pale and thickened, brown medially and dark brown apically, 1.5 times longer than basoflagellomere; covered with short, dense microscopic pile. Face and frons black, covered with long whitish-yellow pile and silver pollinosity.

Oral margin shiny black, well protruded (as in Fig. 4A). Vertical triangle (as in Fig. 4B) isosceles, 2.5 times longer than eye contiguity, shiny black except in front of anterior ocellus white pollinose, covered with long whitish-yellow pile, except black pilose on ocellar triangle. Ocellar triangle (as in Fig. 4B) equilateral to slightly isosceles. Eye contiguity about 8–10 facets long (as in Fig. 4C). Eye pile as long as scape, pale. Occiput with whitish-yellow pile, along the eye margin dense, white pollinosity and posteriorly with metallic bluish-greenish lustre. Thorax. Mesonotum black with bronze lustre, covered with dense, erect, yellow pile, as long as basoflagellomere. Pleurae grey-green pollinose and the following parts with long yellow pilosity: anterior part of proepimeron, posterior part of anterior anepisternum, the larger part of posterior anepisternum except anterior end, anteroventral and posterodorsal part of katepisternum, anepimeron, metasternum; katatergum with dense, erect, short, light-brown pile. Wing hyaline, with dense, brown microtrichia. Calypter pale yellow. Halter with light brown pedicel and yellow capitulum (outer part dark). Femora dark brown to black, except usually paler apex; tibiae can be from completely dark to pale basally and apically; colour of tarsi variable. Metatrochanter (as in Fig. 1B: a) with calcar. Metafemur (as in Fig. 1B: b) thickened and curved, often with ventral tubercle (as in Fig. 1A: marked with arrow) in the basal 1/3 of its length. Metatibia (as in Fig. 1B: c) with apical lamina and/or spur(s). Abdomen (as in Figs 5A, C). Black with bronze reflections, slightly tapering, as long as mesonotum. Terga 2-4 black with more or less distinct pair of white pollinose fasciate maculae (absent in some species); tergum 2 with a pair of orange anterolateral maculae; pile on terga mainly erect and yellow, but terga 2-4 medially usually with some black pile. Sterna blackish-brown, covered with long, pale yellow pile. Genitalia. Posterior surstyle lobe rounded, pointed anteriorly (as in Fig. 2A: pl); margin of surstylus convex (as in Fig. 2A); anterior surstyle lobe with small interior accessory lobe (as in Fig. 2D): il); cercus oval or rectangular (as in Fig. 2A: c). Hypandrium with folded thecal ridge (as in Fig. 2C: marked with arrow). Lateral sclerite of aedeagus elongated and narrow, hammer-like in lateral view (as in Fig. 9C: s).

FEMALE. Similar to the male except for the normal sexual dimorphism and for the following characteristics: tergum 4 with transversal depression (as in Fig. 3A: marked with arrow, 3B); tergum 5 with two small, lateral depressions (as in Fig. 3C: marked with arrow); black pile on terga more conspicuous than in males: posterior margin of tergum 2, and terga 3–4 predominantly black pilose, except lateral sides and white pollinose fasciate maculae with pale pile.

New species of the M. ruficornis group

Merodon acutus Vujić et Radenković sp. nov.

ZooBank link: urn:lsid:zoobank.org:act:B6261D02-1B12-4EB7-A718-3CE714B3B67A GenBank accession number of the COI gene sequence: ON562698 (Figs 1B, 1E, 2A, 2C–D, 6A, 6C, 7A, 14A)

Type material. HOLOTYPE: RUSSIA, Kabardino-Balkaria, Chegemsky Canyon, Bulungu, 43.254402°N, 43.149387°E, 12.VII.1999, ♂, 058350, Leg. Barkalov A., SZMN. **PARATYPES:** RUSSIA, Caucasus, Republik Adygea, near Kamennomostsky, Belaya riverarea, 44.326325°N, 40.183335°E, 11.V.2015, 2♀, 09688, 09689, Leg. Rattel E., Gerzovskiy O., FSUNS.

Diagnosis. Legs black; male: calcar on metatrochanter long and distinct (Fig. 1B: a) similar to *M. armipes* (Fig. 1A), while small and pointed in morphologically related species *M. nigripodus* (Fig. 1C); metafemur with very small ventral protuberance (Fig. 1B: marked with black arrow), distinct in *M. armipes* (Fig. 1A: marked with arrow); metatibia with two apical processes: one medium-sized, anteroventral, apical lamella with straight ventral margin (Fig. 1B: marked with white arrow), and one twisted, distinct, inner, posteroventral spina (Fig. 1E: marked with arrow); anteroventral apical lamella with similar direction as in *M. ponticus*, but with blunt apex (Fig. 1D: marked with arrow), while in *M. nigripodus* the apical lamella is distinctly triangular, slightly undulate and directed towards metafemur (Fig. 1C: marked with arrow); male genitalia: anterior surstyle lobe biramous (Fig. 2A: al), with distinct and broad interior accessory lobe (Fig. 2D: il) and rectangular extension (Fig. 2A: marked with arrow), while in *M. nigripodus* the interior accessory lobe is shorter (Fig. 2E: il) and the extension is angular (Fig. 2B: marked with arrow). Female: similar to other Caucasian species *M. portschinskyi*, except angular metatrochanter with dense whitish pilosity (Figs 6A, 7A), rounded in *M. portschinskyi* (Figs 6B, 11B), and basoflagellomere longer than wide in *M. acutus* (Fig. 6C), while almost as long as wide in *M. portschinskyi* (Fig. 6D).



FIGURE 2. Male genitalia. A, C, D *Merodon acutus* sp. nov., B, E *M. nigripodus*. A epandrium, lateral view (extension marked with arrow), B surstylus, lateral view (extension marked with arrow), C hypandrium, lateral view (folded thecal ridge marked with arrow), D, E surstylus, ventral view. al—anterior surstyle lobe, c—cercus, il—interior accessory lobe, pl—posterior surstyle lobe, s—lateral sclerite of the aedeagus. Scale bar: 0.25 mm.



FIGURE 3. *Merodon* female. A *M. portschinskyi*, T4, lateral view, B *M. trispinus* sp. nov., T4, lateral view, tergum 5 dorsal. C *M. trispinus* sp. nov., T5, frontal view (depression marked with arrow), D *M. trispinus* sp. nov., frons, dorsal view. Scale bar: A, B 0.8 mm, C 1mm, D 0.6 mm.



FIGURE 4. Head of *Merodon trispinus* sp. nov.. A–C male, D–F female. A, D lateral view, B, E dorsal view, C, F frontal view. Scale bar: A, D 0.5 mm, B, C, E, F 0.75 mm.



FIGURE 5. Abdomen of *Merodon*, dorsal view. A, B *M. fulvitarsis* sp. nov., C, D *M. trispinus* sp. nov.. A, C male, B, D female. Scale bar: A, D 1 mm, B, C 0.9 mm.

Description. Length. Male: 9–10 mm; female: 9–10 mm. **MALE** (Figs 1B, 1E, 2, 7A). Small to medium sized, black species with pale pilose terga laterally and with some black pile medially; legs black, except for partially dark brown tarsi; metatrochanter with long and distinct process (Fig. 1B: a); metafemur with very small ventral protuberance (Fig. 1B: marked with black arrow), swollen, covered with short pile (Fig. 1B: b); metatibia narrow, with two apical processes: one medium-sized, anteroventral, apical lamella with straight ventral margin (Fig. 1B: marked

with white arrow), and one distinct, twisted, inner, posteroventral spina (Fig. 1E: marked with arrow). Genitalia: anterior surstyle lobe biramous (Fig. 2A: al), with distinct and broad interior accessory lobe (Fig. 2D: il) and rectangular extension (Fig. 2A: marked with arrow); posterior surstyle lobe hook-like (Fig. 2A: pl); cercus elongated (Fig. 2A: c); hypandrium sickle-shaped (Fig. 2C), with folded theca (Fig. 2C: marked with arrow).



FIGURE 6. A, B Metatrochanter of *Merodon* female. AMerodonacutus sp. nov., anterolateral view, B M. portschinskyi, lateral view; C, D basoflagellomera of Merodon female, lateral view. C M. acutus sp. nov., D M. portschinskyi. Scale bar: A, B 0.5 mm, C, D 0.25 mm.

FEMALE. (Figs 6A, 6C, 14A). Similar to the male except for the normal sexual dimorphism and for the following characteristics: metatrochanter angular (Fig. 7A); pollinose fasciate maculae on terga 2–4 narrow; terga pale pilose, except some black pile medially from posterior half of tergum 2 until anterior half of tergum 5; tergum 4 with clear transverse depression; tergum 5 with a pair of indistinct, lateral, longitudinal depression; vertex at the level of ocellar triangle, and frons with medial vitta of black pile.

Etymology. Participle "acutus" (masc.) meaning sharpened made sharp, sharp, having been sharpened, refers to the sharp inner posteroventral spina on metatibia. The name is to be treated as an adjective.

Distribution. *Merodon acutus* **sp. nov.** was recorded from the northern slopes of the Caucasus (390–1540 m above sea level) in Russia (Fig. 16).

Merodon fulvitarsis Vujić et Radenković sp. nov.

ZooBank link: urn:lsid:zoobank.org:act:6A9E56E0-6162-476B-9465-AAC1D7902A4A GenBank accession number of the COI gene sequence: ON562626 (Figs 5A, 5B, 7B, 8A, 9A, 9C–D)

Type material. HOLOTYPE: IRAN, Osculu, 38.872483°N, 46.8966°E, ♂, 10286, Leg. Khaghaninia, IMTU. **PARATYPE:** IRAN, Anali forest, 38.895933°N, 46.779417°E, ♀, 10292, Leg. Khaghaninia, IMTU.

Diagnosis. Male terga with indistinct pollinose fasciate maculae (Fig. 5A); metatibia in male with plate-like

apical lamella (Fig. 8A: marked with white arrow), in female metatibia curved in apical third (Fig. 7B); metafemur without ventral calcar (Fig. 8A). Similar to *Merodon lamellatus* from which differs in medium sized process on metatrochanter in male (Fig. 8A): marked with black arrow), [very small in *M. lamellatus* (Fig. 8B: marked with black arrow)], metatibia with larger plate-like apical lamella (Fig. 8A: marked with white arrow) [smaller in *M. lamellatus* (Fig. 8B: marked with white arrow)], metatibia with larger plate-like apical lamella (Fig. 8A: marked with white arrow) [smaller in *M. lamellatus* (Fig. 8B: marked with white arrow)], and narrow metatibia (Fig. 8A) [broader in *M. lamellatus* (Fig. 8B)]; male genitalia: anterior surstyle lobe biramous (Fig. 9A: al), with narrow and elongated interior accessory lobe (Fig. 9D: il) and angular extension (Fig. 9A: marked with arrow), while in *M. lamellatus* the interior accessory lobe is less developed and smaller (Fig. 9E: il) and extension is broader (Fig. 9B: marked with arrow). Female can be distinguished from *M. lamellatus* by angular metatrochanter (Fig. 7B: marked with black arrow), while rounded in *M. lamellatus* (Fig. 7C: marked with black arrow), and two apical tarsomere in *M. fulvitarsis* black (7B: marked with white arrows), while in *M. lamellatus* two apical only slightly darker than basal two tarsomeres (7C: marked with white arrows).



FIGURE 7. Part of metaleg of *Merodon* female, lateral view. A *M. acutus* sp. nov., B *M. fulvitarsis* sp. nov. (metatrochanter marked with black arrow; two apical tarsomere marked with white arrows), C *M. lamellatus* (metatrochanter marked with black arrow; two apical tarsomere marked with white arrows), D *M. trispinus* sp. nov., E *M. ovaloides.* Scale bar: 0.5 mm.

Description. Length. Male: 9–10 mm; female: 9–10 mm. **MALE** (Figs 5A, 8A, 9). Small to medium sized species; terga with indistinct pollinose fasciate maculae (Fig. 5A), covered with pale pilosity laterally and black pile medially; metatrochanter with medium sized process (Fig. 8A: marked with black arrow); metafemur narrow, without ventral protuberance, covered with pile shorter than the width of metafemur (Fig. 8A); metatibia with one plate-like, apical lamella (Fig. 8A: marked with white arrow); basal three tarsomeres of all legs reddish-yellow, apical two black (Fig. 8A). Male genitalia: anterior surstyle lobe biramous (Fig. 9A: al), with narrow and elongated interior accessory lobe (Fig. 9D: il) and angular extension (Fig. 9A: marked with arrow); posterior surstyle lobe hook-like (Fig. 9A: pl); cercus rectangular (Fig. 9A: c); hypandrium sickle-shaped (Fig. 9C), with folded theca (Fig. 9C: marked with arrow).

FEMALE (Figs 5B, 7B). Similar to the male except for normal sexual dimorphism and for the following characteristics: metatrochanter angular (Fig. 7B: marked with black arrow); metatibia curved in the apical third (Fig. 7B); terga with distinct white-greyish pollinose fasciate maculae (Fig. 5B); terga with pale pilosity, except black pile medially from posterior half of tergum 2 until tergum 5; tergum 4 with weak transverse depression; tergum 5 with a pair of indistinct, lateral, longitudinal depressions; vertex at the level of ocellar triangle black pilose, frons with medial vitta of few black pile.

Etymology. The adjective "fulvus" (fulvi in genitive) means reddish-yellow, referring to the color of basal three tarsomeres on legs.

Distribution. *Merodon fulvitarsis* **sp. nov.** has been recorded in mountainous areas of northern Iran (1220–1540 m asl) (Fig. 16).



FIGURE 8. Metaleg of *Merodon* male, lateral view. A *M. fulvitarsis* sp. nov. (lamella on metatibia marked with white arrow; processes on metatrochanter marked with black arrow; anterodorsal end of metatibia marked with gray arrow), B *M. lamellatus* (lamella on metatibia marked with white arrow; process on metatrochanter marked with black arrow; anterodorsal end of metatibia marked with grey arrow), C *M. loewi* (lamella on metatibia marked with white arrow; anterodorsal end of metatibia marked with grey arrow). Scale bar: A 2 mm, B, C 0.8 mm.

Merodon trispinus Vujić et Radenković sp. nov.

ZooBank link: urn:lsid:zoobank.org:act:93F2A6E3-F105-4697-A0F4-28A19C507C6D GenBank accession number of the COI gene sequence: ON562606 (Figs 3B–D, 4, 5C–D, 7D, 15B, 15E, 10A, 10C–D)

Type material. HOLOTYPE: TURKEY, Bozdað Mountain, 38.332693°N, 28.109671°E, 07.VI.2014, ♂, 06927, Leg. Vujić A., Ačanski J., FSUNS. **PARATYPES:** TURKEY:38.332693°N, 28.109671°E,07.VI.2014, 4♂, ♀, 06928, 06929, 06930, 06937, 06938, Leg. Vujić A., Ačanski J., FSUNS; Bozdað Mountain, 38.411655°N, 28.081503°E, 02.V.2014, ♀, 06292, Leg. Vujić A., Ačanski J., FSUNS; Fethiye, Akdað, Cemalani, 36.600998°N, 29.515234°E, 04.VI.2014, 5♂, ♀, 06874, 06882, 06883, 06884, 06885, 06887, Leg. Vujić A., Ačanski J., FSUNS;



FIGURE 9. Male genitalia. A, C, D *Merodon fulvitarsis* sp. nov., B, E *M. lamellatus*. A epandrium, lateral view (extension marked with arrow), B surstylus, lateral view (extension marked with arrow), C hypandrium, lateral view (folded thecal ridge marked with arrow), D, E surstylus, ventral view.al—anterior surstyle lobe, c—cercus, il—interior accessory lobe, pl—posterior surstyle lobe, s—lateral sclerite of the aedeagus. Scale bar: 0.25 mm.



FIGURE 10. Male genitalia. A, C, D *Merodon trispinus* sp. nov., B, E *M. portschinskyi*. A epandrium, lateral view (extension marked with arrow), B surstylus, lateral view (extension marked with arrow), C hypandrium, lateral view (folded thecal ridge marked with arrow), D, E surstylus, ventral view.al—anterior surstyle lobe, c—cercus, il—interior accessory lobe, pl—posterior surstyle lobe. Scale bar: 0.25 mm.

Izmir, 38.271148°N, 27.175597°E, 06.VI.2014, ♂, 06922, Leg. Vujić A., Ačanski J., FSUNS; Babadað, near Denizli, 37.695179°N, 28.99309°E, 05.VII.2015, 3♂, 09726, 09727, 09728, Leg. Vujiă A., Radenkoviă S., Ačanski J., Veličkoviă S., Stĺhls G., Gökhan S., FSUNS; Boncuk Daðlari, near Ballik, 36.865139°N, 29.34881°E, 04.VII.2014, 2♂, ♀, 09723, 09724, 09725, Leg. Vujiă A., Radenkoviă S., Ačanski J., Veličkoviă S., Stĺhls G., Gökhan S., FSUNS.



FIGURE 11. Female of *Merodon*. A *M. acutus* sp. nov., abdomen, lateral view, B *M. portschinskyi*, abdomen, lateral view, C *M. portschinskyi*, head, dorsal view, D *M. planiceps*, head, dorsal view. Scale bar: A, B 0.35 mm, C, D 1 mm.

Diagnosis. Similar to *M. portschinskyi* and *M. turcicus*. Males differ by apical part of metatibia with strong, inner, posteroventral spina (Fig. 15E: marked with black arrow) [much smaller in *M. portschinskyi* and *M. turcicus* (Figs 15D and 15F: marked with black arrow)], distinct anteroventral spur projected backwards at undulate lamella (Fig. 15E: marked with white arrow) (toward the apex in *M. portschinskyi* and *M. turcicus* (Figs 15D and 15F: marked with white arrow), and small carina in between (Fig. 15E: c); process on metatrochanter small (Fig. 15B: marked with black arrow), while medium sized in *M. portschinskyi* and *M. turcicus* (Figs 15A and 15C: marked with black arrow); basal part of metafemur ventrally usually less curved (Fig. 15B: marked with white arrow), while strongly curved in *M. portschinskyi* (Fig. 15A: marked with white arrow). Male genitalia: anterior surstyle lobe biramous (Fig. 10A: al), with slightly developed interior accessory lobe (Fig. 10D: il) and rounded extension (Fig. 10A: marked with arrow), Female: legs mostly black, tarsi at least ventrally, femora apically, and tibiae apically and basally brownish; tergum 4 with distinct transverse depression (Fig. 3B), much less expressed in *M. portschinskyi* appears on Caucasus mountains, *M. turcicus* was recorded on North Anatolian Mountains, and *M. trispinus* **sp. nov.** has a range in mountains of South West Anatolia (Fig. 17).

Description. Length. Male: 10–11 mm; female: 10 mm. MALE (Figs 4A–C, 5C, 15B, 15E, 10A, 10C–D). Medium-sized species with pale pilose terga; terga 2–4 with distinct pollinose fasciate maculae (Fig. 5C); metatrochanter with medium sized process (Fig. 15B: marked with black arrow); metafemur swollen, without ventral protuberance, ventrally covered with long pile (Fig. 15B); metatibia apically with strong, inner, posteroventral spina (Fig. 15E: marked with black arrow), with distinct anteroventral spur projected backwards at undulate lamella (Fig. 15E: marked with white arrow) and with small carina in between (Fig. 15E: c); tarsomeres of all legs dorsally pale brown to black, ventrally reddish. Male genitalia: anterior surstyle lobe biramous (Fig. 10A: al), with slightly developed interior accessory lobe (Fig. 10D: il) and rounded extension (Fig. 10A: marked with arrow); posterior surstyle lobe hook-like (Fig. 10A: pl); cercus oval (Fig. 10A: c); hypandrium sickle-shaped (Fig. 10C), with folded theca (Fig. 10C: marked with arrow).

FEMALE (Figs 3B–D, 4D–F, 5D, 7D). Similar to the male except for normal sexual dimorphism and for the following characteristics: metafemur covered with shorter pilosity (Fig. 7D); metatrochanter slightly angular (Fig. 7D); pollinose fasciate maculae on terga 2–4 well defined, white-greyish (Fig. 5D); terga pale pilose, except black pile medially from posterior half of tergum 2 until anterior half of tergum 5; tergum 4 with distinct transverse depression (Fig. 3B); tergum 5 with a pair of distinct lateral, longitudinal depression (Fig. 3C: marked with arrow); vertex at the level of ocellar triangle and frons medially black pilose (Fig. 3D).

Etymology. The noun "spinus" meaning thorn-bush refers to three extensions of the exoskeleton at apical part of metatibiae.

Distribution. Merodon trispinus sp. nov. occurs in west and southwest Turkey (Figs 16-17).



FIGURE 12. Female of Merodon ilgazenze, terga 4-5. Lateral depression marked with arrow. Scale bar: 1 mm.

Description of the female of Merodon portschinskyi Stackelberg, 1924

GenBank accession number for the COI gene sequence: ON880568 (Figs 3A, 6B, 6D, 13, 14, 15A, 15D, 10B, 10E, 11B–C)

Material examined. GEORGIA: Samegrelo-ZemoSvaneti, 42.910056°N, 43.007000°E, 18.VI.2019, ♂, 25117, Leg. Mengual X., ZFMK; Saimre, 41.86°N, 42.77°E, 10.VI.2019, 2♂, 24499, 24501, Leg. van Steenis J., SJ coll.; Abastumani, 41.82°N 42.84°E, 11.VI.2019, ♂, 24500, Leg. van Steenis J., SJ coll.; Imereti, road from Abastumani to Sairme, 41.864333N, 42.778433E, 10.VI.2019, 2♂, 25115, 25116, 11.VI.2019, ♀, 25118, Leg. Mengual X., Det. Mengual X, ZFMK.

Taxonomic notes. Stackelberg (1924) described the male of *Merodon portschinskyi*, based on two specimens collected by J. Portschinskyi deposited in the collection of the Zoological Institute of Russian Academy of Sciences—ZIN RAS (St. Petersburg). A male syntype from Georgia, Kakheti (toponym Lagodekhi) was designated as lectotype by Richter & Kuznetsov (2007). The female remained undescribed. Recently, Mengual *et al.* (2020) collected new material in Georgia and provided us with a female specimen of *M. portschinskyi*. We present here the first description of the female.

Description. Length. Female: 11 mm. **FEMALE** (Figs 3A, 6B, 6D, 14, 11B–C). Similar to the male except for the normal sexual dimorphism and for the following characteristics: metafemur less curved and narrower (Fig. 14A) than in male (Fig. 15A); metatrochanter rounded (Fig. 6B); pollinose fasciate maculae on terga 2–4 well defined, narrow, white-greyish (Fig. 14B); terga pale pilose, except adpressed black pile medially from posterior half of tergum 2 until posterior margin of tergum 5; tergum 4 with transverse depression (Fig. 3A: marked with arrow); tergum 5 with a pair of indistinct, lateral, longitudinal depressions; sternum 5 predominately black pilose (Fig. 11B); vertex at the level of ocellar triangle black pilose, and frons medially with a stripe of black pile; frons with narrow, lateral pollinose vittae along eye margins (Fig. 11C).



FIGURE 13. Lectotype of Merodon portschinskyi, male, lateral view. Scale bar: 0.5 mm.

Additions to the key for the species of *M. ruficornis* group in Vujić *et al.* (2012)

In addition to the previously published key (Vujić *et al.*, 2012), the one presented in the 'Supplementary Materials 1' of this paper includes males and females of the three new species, the previously unknown females of *Merodon portschinskyi* and *M. ilgazenze*, as well as a variation of *M. alexandri* with fasciate maculae on terga 2–4. The female of *M. nigripodus* is still unknown and so, not included in this key.



FIGURE 14. Merodon portschinskyi, female. A metaleg, lateral view, B abdomen, dorsal view. Scale bar: 1 mm.

Molecular data on the M. ruficornis group

In total, 20 specimens from the *Merodon ruficornis* species group were included in the molecular analysis. Amplification of both the 3'-end and 5'-end of the COI gene was successful for all individuals. The total length of the concatenated COI alignment was 1377 bp, among which the 5' fragment COI had a final length of 613 nucleotides. The total number of polymorphic sites within the ingroup sequences matrix was 166, of which 99 were parsimony informative.

Both MP and ML analyses of the combined 5' and 3' regions of the COI gene showed the same topology, revealing a clear distinction of the new species (*Merodon acutus* **sp. nov.**, *M. fulvitarsis* **sp.nov.** and *M. trispinus* **sp. nov.**) from the *M. ruficornis* group, corroborating their morphologically-defined boundaries (Fig. 16 and Fig. 17). MP analysis resulted in six equally parsimonious trees of 296 steps in length (Consistency Index = 76, Retention Index = 81). The parsimony strict consensus tree is shown in Fig. 16.

Molecular results of the concatenated 3' and 5' COI gene fragments showed p-distances from 0% to 5.45% among species from the *M. ruficornis* species group (Table S1). Whereby, the uncorrected pairwise distances that distinguish three new species within *M. ruficornis* group were in the range between 2.32–3.34% (for *M. trispinus* **sp. nov.**), 1.05–3.12% (for *M. acutus* **sp. nov.**) and 0.65–3.2% (for *M. fulvitarsis* **sp. nov.**), with the average values of 3.04%, 1.86% and 1.79%, respectively (Table 1 of 'Supplementary Materials 2'). Moreover, the same pattern of uncorrected genetic distances between species pairs within the *M. ruficornis* species group was revealed using dataset based on the DNA barcode sequences (5'-end of the COI gene) (Table 2 of 'Supplementary Materials 2'). The uncorrected pairwise distances of the combined 3' and 5' COI sequences were analysed for the determination of the 'barcoding gap' between taxa of the *M. ruficornis* species group. The ABGD analysis resulted in sequences partitioning into nine groups with prior distance values between 0.001–0046. Resolved groups correspond to *M.*

trebevicensis, M. auripes, M. armipes+M. loewi+M. papillus+M. fulvitarsis **sp. nov.**, M. hoplitis, M. trispinus **sp. nov.**, M. acutus **sp. nov.**, M. portschinskyi, M. gallicus, M. ruficornis.



FIGURE 15. Part of metaleg of *Merodon* male. **A**, **D** *M. portschinskyi*, **B**, **E** *M. trispinus* **sp. nov.**, **C**, **F** *M. turcicus*. **A–C** metaleg, lateral view (process on metatrochanter marked with black arrow; basal curve of metafemur marked with white arrow), **D–F** processes on apical part of metatibia (inner spina marked with arrow; ventral spur marked with white arrow).**c**—carina. Scale bar: **A–C** 1 mm, **D–F** 0.5 mm.

Discussion

Taxonomy. Numerous studies on *Merodon* have shown the potential of integrative taxonomy for identifying species within this genus, defining new species and identifying cryptic taxa (e.g., Mengual *et al.* 2006; Marcos-García *et al.* 2007, 2011; Ståhls *et al.* 2009; Radenković *et al.* 2011, 2018; Vujić et al. 2012, 2013, 2015, 2020a, 2020b, 2020c; Šašić *et al.* 2016; Kočiš Tubić *et al.* 2018; Popović *et al.* 2015; Likov *et al.* 2020). Species groups within *Merodon* are often composed of morphologically closely related taxa, with diagnostic characters being very subtle such as small differences in the structures of the male genitalia in the *M. nanus* (Vujić *et al.* 2012) and *M. nigritarsis* (Vujić *et al.* 2013a) groups, or the shape of the metalegs as in the *M. ruficornis* group (Vujić *et al.* 2012). Here, we described three new species within the *M. ruficornis* species group which show clear morphological differences in the male genitalia. In contrast, females of the *M. ruficornis* species group display a similar morphology and can only be distinguished through subtle differences related mostly to the metaleg. Indeed, up to now no diagnostic characters were found to distinguish between the females of some species. In the present study, we applied an integrative taxo-

nomic approach combining morphology, molecular, and distribution data in order to differentiate three new species in the *M. ruficornis* species group. Moreover, based on molecular data, we were able to identify a female specimen of *M. fulvitarsis* Vujić et Radenković **sp. nov.** from Iran.



FIGURE 16. Strict consensus tree based on 9 equally parsimonious trees from analysis of combined COI sequences. Length 318 steps, Consistency index (CI) 70, Retention index (RI) 42. Bootstrap values ≥ 60 are indicated near nodes. Filled circles represent non-homoplasious changes and open circles homoplasious changes.



FIGURE 17. Maximum Likelihood tree of the *Merodon ruficornis* species group based on combined 3' and 5' COI sequences. The bootstrap values are indicated near nodes.

Species delimitation based on COI data. The advent of relatively inexpensive and rapid DNA barcode sequencing has emerged as an important tool for identifying and differentiating morphologically similar species (Bickford et al. 2007). To date, just a limited set of useful genetic markers have been used in the integrative taxonomy of hoverflies (Šašić et al. 2016). Molecular evidence based on COI sequence divergence represents one of the most widely used molecular approaches for discriminating closely related hoverfly species. Despite the great utility of COI gene sequences in resolving taxonomic relationships within the genus Merodon, molecular identification of species in the M. ruficornis group remains challenging (Vujić et al. 2012; Andrić et al. 2017). Neither the 3' nor 5' COI fragments have proven sufficiently informative in this species group (Milankov et al. 2008; Ståhls et al. 2009). Studies in the Balkan Peninsula have revealed that M. loewi shares the same 3' COI haplotype as M. armipes, despite these two species show clear morphological differences (Milankov et al. 2008). Furthermore, using DNA barcoding, Ståhls et al. (2009) showed that all Merodon taxa of Lesvos can be unambiguously identified, except for two morphospecies of the M. ruficornis group, i.e. M. loewi and M. papillus. However, in the present study, we clearly distinguished M. loewi and M. papillus based on combined 3' and 5' COI fragments. Moreover, COI sequences enabled us to successfully delineate all three new species of the M. ruficornis group. Our analyses of the concatenated 3' and 5'-end of the COI gene revealed distance rates in range from 0% to 5.45% among species from the M. ruficornis group and quite similar values as well as the same pattern of uncorrected distances were obtained using only the DNA barcode region (0-5.22%). Whereby, the expected absence of the COI gene distance was observed between M. armipes and M. loewi (0%), while distance rates among all other species pairs were between 0.65–5.45% for both barcode and combined datasets. Some of these values are lower than the suggested 2% barcoding gap (Avise 2000), including the pairwise distances that distinguish M. acutus sp. nov. as well as M. fulvitarsis sp. nov. from certain species from the *M. ruficornis* group. However, they are still in the range of values (0.3-2.5%) recorded for cryptic and closely-related hoverfly species (Marcos-García et al. 2011; Vujić et al. 2013b; Nedeljković et al. 2015; Popović et al. 2015; Šašić et al. 2016; Radenković et al. 2018). In addition, beside the M. ruficornis group, there are evidences of the shared COI haplotypes between morphologically different insect species (Mengual et al. 2006; Marcos-García et al. 2011; Haarto & Stlhls 2014; Popoviă et al. 2015). On the other hand, there are cases in which morphologically well-defined species express an intraspecific divergence level that exceeds the interspecies level of divergence of the group (Cognato 2006). Thus, the standard percent of species distance should be elucidated separately for each species group in the light of other taxonomic data and cannot be generally defined. Given their expression of species-specific haplotypes, the COI gene proved to be useful in the identification of three new species of the M. ruficornis group. In this regard, COI sequences can be useful for determining the taxonomic identity of larval specimens of these newly described species during the various stages of their development (Ståhls et al. 2009). Apart from helping to identify hoverfly-plant associations, COI sequence divergence represents a powerful tool for linking the sexes, especially in the absence of distinguishable diagnostic characters among the females, representing a particularly significant challenge for the M. ruficornis species group. However, there is a need to develop and evaluate additional molecular markers for the identification of all species within this group and to get insight into their evolutionary relationships.

Distribution. The M. ruficornis species group exhibits a predominately Eastern Mediterranean distribution and a very high level of endemism (Vujić et al. 2021a). This species group is absent from the Western Mediterranean (Marcos-García et al. 2007). The Anatolian Peninsula and Caucasus Mountains are the two regions with the highest levels of endemism in the M. ruficornis species group (Vujić et al. 2021a). Of the 21 described taxa, 15 are limitedrange endemics occurring in particular mountain areas or only in a small part of the total range of the group (see Table 2). The description of three new species herein extends the known range of the *M. ruficornis* species group to the North, South and East. The distribution of M. acutus sp. nov. from the Russian Caucasus partially overlaps with records of *M. planiceps*, a species with a disjunct range. *Merodon acutus* **sp. nov.** was found at lower altitudes of the northern Caucasus, i.e. on the eastern distributional border of the M. ruficornis species group. M. fulvitarsis sp. nov. from mountainous areas of northern Iran and M. ponticus from northwestern Azerbaijan together define the south-eastern edge of the species group's distributional range. Likewise, M. trispinus sp. nov. represents a species at the edge of the group's distributional range, having been collected in Western and South-western Turkey (Figs 16–17). All three newly described species occur in biodiversity hotspots (https://www.conservation.org/priorities/ biodiversity-hotspots). Merodon acutus sp. nov., M. lamellatus, M. nigripodus, M. ponticus, M. portschinskyi, and M. turcicus are six endemic species of the M. ruficornis group in the Caucasus hotspot. This biodiversity hotspot encompasses a system of high mountains and closed basins harbouring a diverse range of habitats. In this hotspot, where Europe and Asia meet, natural barriers, corridors and refugia co-exist (Vujić *et al.* 2020a). *M. fulvitarsis* **sp. nov.** is the only endemic species of the *M. ruficornis* species group in the Irano-Anatolian hotspot, an area previously identified as providing ideal ecological conditions for high biodiversity and speciation (Darvish *et al.* 2014), and consequently presenting many endemic plant species (Manafzadeh *et al.* 2017). Some of these plant species, especially bulb-forming species and other geophytes, have been deemed to contribute to maintaining the high diversity of the *M. ruficornis* species group (Vujić *et al.* 2019). Three species of that group, i.e. *M. trispinus* **sp. nov.**, *M. hoplitis*, and *M. papillus*, occur in different parts of the Mediterranean Basin hotspot, the main diversification centre of the *Merodon* genus (Vujić *et al.*, 2011), with the diverse Mediterranean geophytic flora having also been attributed as promoting high hoverfly diversity (Likov *et al.* 2020) (Figs 16, 17).

| Species name | Endemism | Distribution |
|---|-------------|--|
| Merodon abruzzensis van der Goot, 1964 | endemic | Abruzzi Mountains in Italy |
| Merodon acutus Vujić et Radenković sp. nov. | endemic | Russian part of Caucasus |
| Merodon alexandri Popov, 2009 | endemic | Ukraine and Russian steppes |
| Merodo narmipes Rondani, 1843 | non endemic | from France and Germany in the west to |
| | | Caucasus in the east |
| Merodon auripes Sack, 1913 | non endemic | the Balkan and Apennine peninsulas, Central Europe and Ukraine |
| Merodon fulvitarsis Vujić et Radenković sp. nov. | endemic | Iran |
| Merodon gallicus Vujić et Radenković in Vujić et al. 2012 | endemic | France |
| Merodon hoplitis Hurkmans in Vujić et al. 2012 | endemic | Endemic to the Dinaric Mountains along |
| | | Adriatic coast on the Balkan Peninsula |
| <i>Merodon ilgazense</i> Vujić, Marcos- García, Sarýbýyýk et Ricarte, 2011 | endemic | Ilgaz Mountain in Turkey |
| Merodon lamellatus Vujić et Radenković in Vujić et al. 2012 | endemic | Turkish part of Caucasian region |
| Merodon loewi van der Goot, 1964 | non endemic | from Apennine Peninsula to Caucasus and Ukrainian steppes |
| Merodon nigripodus Vujić et Hayat in Vujić et al. 2012 | endemic | Turkey, part of Erzurum province that be- longs to Caucasian region |
| Merodon ovaloides Vujić et Radenković in Vujić et al. 2012 | endemic | Kastamonu province in Turkey |
| <i>Merodon papillus</i> Vujić, Radenković et Pérez-Bañón in Vujić <i>et al.</i> 2007 | endemic | Greece, Lesvos and western Turkey |
| Merodon planiceps Loew, 1862 | non endemic | disjunct range, recorded in Italy, Greece and Turkey |
| Merodon ponticus Vujić et Radenković in Vujić et al. 2012 | endemic | Caucasus Mountains, with range between Black and Caspian seas |
| Merodon portschinskyi Stackelberg, 1924 | endemic | North Caucasian Mountains |
| Merodon ruficornis Meigen, 1822 | non endemic | central parts of Europe, including France to the west and Apennine and Balkan peninsulas to the south, and Transdnieper in Ukraine |
| Merodon trebevicensis Strobl, 1900 | non endemic | from the Alps in the west, to Crimea and central Turkey in the east |
| Merodon trispinus Vujić et Radenković sp. nov. | endemic | south western Turkey |
| Merodon turcicus Vujić et Hayat in Vujić et al. 2012 | endemic | Turkey, south Caucasus |

TABLE 2. Distribution and endemism of species from the Merodon ruficornis group.



FIGURE 18. Distribution map of *Merodon acutus* sp. nov., *M. fulvitarsis* sp. nov., *M. trispinus* sp. nov. and *Merodon ruficornis* species group.



FIGURE 19. Distribution map of *M. portschinskyi*, *M. trispinus* sp. nov. and *M. turcicus*.

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APPENDIX 1. Key to species of *M. ruficornis* species group

Males

| mules | |
|------------|--|
| 1. | Two wart-like prominences present in the middle of the posterior margin of sternum 4. Metatrochanter with small obtuse pro- cess; metafemur with distinct ventral protuberance; apex of metatibia with lamellar outer anteroventral spur and curved inner |
| | posteroventral spur (Fig. A1 A-B) Merodon papillus Vujić, Radenković et Pérez-Bañon |
| - | Sternum 4 without these prominences |
| 2. | Metafemur with long protuberance ventrally, as long as or longer than the process on metatrochanter (Fig. A7) |
| - | Metafemur without or with shorter protuberance ventrally (Fig. A6 C: pf) |
| 3. | Metafemur strongly thickened and swollen (Fig. A7 B). Cercus with characteristic shape; posterior surstyle lobe rectangular |
| | (Fig. A8 C: pl) |
| - 4. | Metafemur with extremely long ventral protuberance (more than one half of its width) (Fig. A9 A); metatibia with two apical |
| 4. | spurs, one outer anteroventral pointed vertically and another inner posteroventral directed horizontally |
| | <i>Merodon ilgazense</i> Vujić, Marcos-Garcia, Sarýbýyýk et Ricarte |
| _ | Protuberance on metafemur shorter (less than one half of its width) |
| 5. | Protuberance on metafemur distinctly longer than process on metatrochanter; inner posteroventral apical spur on metatibia long |
| 0. | and pointed (Fig. A7 C). Thorns on anterior surstyle lobe and inner side of posterior surstyle lobe strong (Fig. A8 A–B: al, pl) |
| _ | Protuberance on metafemur shorter or the same length as process on metatrochanter; inner posteroventral apical spur on metati- |
| | bia shorter (Fig. A7 A). Thorns on anterior surstyle lobe and inner side of posterior surstyle lobe shorter and less distinct (Fig. A8 D–E) |
| 6. | Metafemur with distinct protuberance ventrally (as on Fig. A3 A–B) |
| - | Metafemur without protuberance ventrally |
| 7. | Metatrochanter with very long calcar (0.7 width of metafemur) (Fig. 1A, B); metatibia with two distinct apical prolongations (as in Fig. 1A). |
| _ | Metatrochanter with shorter calcar (as in Fig. 1D); metatibia with one distinct apical prolongation (as in Fig. 1D) |
| 8. | Metatibia with twisted distinct, inner, posteroventral spina (Fig. 1E: marked with arrow); metafemur with indistinct ventral |
| | tubercle (Fig. 1B: marked with arrow) |
| - | Metatibia with narrow, pointed, inner, posteroventral spina (Fig. 1A); metafemur with distinct ventral tubercle (Fig. 1A: marked |
| | with arrow) |
| 9. | Anterior spur at the apex of metatibia directed backwards (as on Fig. A3 A) |
| - | Anterior spur at the apex of metatibia pointed forwards or upwards (as on Fig. A6 E) |
| 10. | Spur at the apex of metatibia triangular, thorn-like (Fig. A3 A). Thorns on anterior surstyle lobe and inner side of posterior surstyle lobe short, almost indistinct (Fig. A4 A: al, pl) |
| | Spur at the apex of metatibia rounded (Fig. A3 B). Thorns on anterior surstyle lobe and inner side of posterior surstyle lobe |
| - | distinct (Fig. A4 C–D) |
| 11. | Lamella behind the apical spur of metatibia with undulated fold (Fig. A6 D: lm) |
| - | Lamella behind the apical spur of metatibia with straight ventral margin (Fig. A6 E). Posterior surstyle lobe rounded; thorn on |
| | anterior surstyle lobe indistinct (Fig. A5 B–C: al, pl) |
| 12. | Tibiae at both ends and basal three tarsomeres pale |
| - | Legs predominantly dark. Basal metafemur strongly curved (as on Fig. A12 A) |
| 13. | Process on metatrochanter shorter and more pointed (Fig. A12 A–B). Posterior surstyle lobe rounded (Fig. A11 C: pl) |
| _ | Process on metatrochanter longer and broader (Fig. A13 A–B). Posterior surstyle lobe hook-like (Fig. A14: pl) |
| | |
| 14. | Legs dark |
| - | At least basal two (three) tarsomeres pale |
| 15. | Spur at the apex of metatibia small, triangular, lamella indistinct; process on metatrochanter small and pointed; ventral margin |
| | of metafemur without long and dense pile (Fig. A6 B); margin of anterior surstyle lobe with very strong dorsal extension (Fig. |
| | A11 B) |
| - 16 M- | Spur at the apex of metatibia larger, lamella present (as on Fig. A10 A) |
| 10. Me | tatibia with distinct inner posteroventral spina (Fig. 15E; marked with black arrow) |
| | |
| - 17. | Posterior surstyle lobe rounded and with indistinct inner thorn (Fig. A11 C: pl). Process on metatrochanter small and pointed; |
| 1/. | anteroventral spur at the apex of metatibia with innerly curved apical extension (Fig. A12 A–C); metafemur can be with trace |
| | of ventral protuberance |
| - | Posterior surstyle lobe with more or less flat dorsal margin |
| - 18. | Anteroventral apical spur of metatibia extended more than anterodorsal end of metatibia (Fig. A10 A); posterior side of apex of |
| | metatibia without small spur |
| - | Anteroventral apical spur of metatibia not extended more than anterodorsal end of metatibia (Fig. A15 A–D), posterior side of |
| | apex of metatibia usually with small spur (as on Fig. A15 D–E) |
| 19. | Process on metatrochanter wide and strong; pile on ventral side of metafemur two times shorter than its width (Fig. A10 A–B); |

| | cercus oval (Fig. A11 A: c) |
|-----|---|
| - | Process on metatrochanter narrower; pile on ventral side of metafemur long and dense, at least two thirds of its width (Fig. A13 |
| | A); cercus rectangular (Fig. A14) Merodon planiceps Loew |
| 20. | Long pile on trochanters predominantly black; metafemur anteriorly covered with mostly black pile; terga 3 and 4 with pol- |
| | linose fasciae clearly visible from lateral view; apical spur at posterior side of metatibia bigger (Fig. A15 D-E) |
| | |
| - | Long pile on trochanters predominantely pale; metafemur anteriorly covered with mostly pale pile; terga 3 and 4 without pol- |
| | linose fasciae (some specimens have traces of pollen on terga, but there are invisible from lateral view); apical spur at posterior |
| | side of metatibia small, in some specimens almost indistinct Merodon turcicus Vujić et Hayat |
| 21. | Metatibia with anteroventral apical plate-like lamella (Fig. 8A, B: marked with white arrow), not extended more than the an- |
| | terodorsal end of metatibia (Fig. 8A, B: marked with gray arrow) 22 |
| - | Metatibia with anteroventral apical prolongation (Fig. 8C: marked with white arrow) extended more than the anterodorsal end |
| | of metatibia (as in Fig. 8C: marked with gray arrow) 23 |
| 22. | Metatrochanter with very small calcar (Fig. 8B: marked with black arrow) |
| - | Metatrochanter with medium sized calcar (Fig. 8A: marked with black arrow) |
| | <i>Merodon fulvitarsis</i> Vujić et Radenković sp. nov. |
| 23. | Lamella behind apical spur of metatibiae with straight ventral margin (Fig. A6 A); posterior surstyle lobe rectangular (Fig. A5 |
| | A) |
| - | Lamella behind apical spur of metatibiae with rounded ventral margin (Fig. A10 A); posterior surstyle lobe hook-like (Fig. A11 |
| | A) |

Females

| 1. | Tergum 4 with transversal depression (Fig. A2 B–C: td) |
|-----|---|
| - | Tergum 4 without transversal depression (Fig. A2 A), tarsi dark, at least dorsally |
| _ | |
| 2. | Tergum without pollinose fasciae |
| - | Tergum 2–4 with clear pollinose fasciae |
| 3. | Sternum 4 with strong thorn-like protuberance (Fig. A2 C: pp) Merodon armipes Rondani |
| - | Sternum 4 without protuberance |
| 4. | Metafemur with protuberance ventrally |
| - | Metafemur without protuberance |
| 5. | Pile on metafemur short, adpressed, especially in apical third (Fig. A9 C). Mediotergite entirely dusted. Distribution: Adriatic |
| | mountains |
| - | Pile on metafemur longer (Fig. A9 B). Mediotergite postero-medially shiny. Some other range |
| 6. | Basal three tarsomeres of all legs pale |
| - | Tarsi darkened at least dorsally |
| 7. | Apex of metatibia rounded (Fig. A3 C) |
| - | Apex of metatibia angled (Fig. A12 D) |
| 8. | Tergum 5 with a pair of deep lateral depression (Fig. 15) Merodon ilgazense Vujić, Marcos-Garcia, Sarýbýyýk et Ricarte |
| - | Tergum 5 with a pair of weaker depression |
| 9. | Distribution: Italy, Abruzzi Mountains |
| - | Distribution: rest of Europe |
| 10. | Metatarsus of metaleg without or with only few black bristles |
| - | Metatarsus of metaleg with black bristles. Distribution: western of Alps to Caucasus area Merodon trebevicensis Strobl |
| 11. | Distribution: Turkey and Azerbaijan Warden Merodon ponticus Vujić et Radenković |
| - | Distribution: France |
| 12. | Distribution: western of Alps to Caucasus area. Metatarsus of metaleg with black bristles Merodon trebevicensis Strobl |
| - | Distribution: France. Metatarsus of metaleg without or with only few black bristles Merodon gallicus Vujić & Radenković |
| 13. | Three basal tarsomeres pale, at least of metaleg14 |
| - | Tarsi darkened at least dorsally |
| 14. | Apex of metatibia rounded (as on Fig. A3 C) 15 |
| - | Apex of metatibiae angled (as on Fig. A12 D) |
| 15. | Distribution: Europe |
| - | Distribution: Turkey |
| 16. | Distribution: Italy, Abruzzi Mountains Merodon abruzzensis Van der Goot |
| - | Distribution: rest of Europe Merodon ruficornis Meigen |
| 17. | Pile on ventral surface of metafemur long (the longest ones at least two thirds width of metafemur) |
| - | The longest pile on ventral surface of metafemur shorter, usually one half width of metafemur (Fig. A10 C) 19 |
| 18. | Distribution: Turkey and Azerbaijan Werodon ponticus Vujić et Radenković |
| - | Distribution: Europe |
| 19. | Metatrochanter angled (as in Fig. 7B) 20 |
| - | Metatrochanter rounded (Fig. 7C) Merodon lamellatus Vujić et Radenković |
| | (females of <i>M. alexandri</i> with faciate maculae on terga 2-4 also keyed here; distinction between females of these two species |
| | is based on distribution) |

| 20. | Metatibia curved in apical third (Fig. 7B) |
|-----|---|
| - | Metatibia not curved in apical third (Fig. 7F) |
| 21. | Apex of metatibia rounded (as on Fig. A3 C) |
| - | Apex of metatibia angled (as on Fig. A12 D) |
| 22. | Distribution: Italy, Abruzzi Mountains |
| - | Distribution: rest of Europe Merodon ruficornis Meigen |
| 23. | The longest pile on ventral surface of metafemur short, usually one half of width of metafemur (Figs. 7D, 7F) 24 |
| - | Pile on ventral surface of metafemur long (the longest ones at least ² / ₃ of width of metafemur) (Fig. 7E) |
| 24. | Tergum 4 with distinct transverse depression (Fig. 3B) Merodon trispinus Vujić et Radenković sp. nov. |
| - | Tergum 4 with less distinct transverse depression (as in Fig. 3A: marked with arrow) |
| 25. | Apex of metatibia with distinct lamella (Fig. A12 E–F: lm) |
| - | Apex of metatibia with smaller lamella (Fig. A13 C) |
| 26. | Tergum 5 and sternum 5 predominately pale pilose (a few black pile may be present) (Fig. 11A) |
| - | Tergum 5 and sternum 5 with numerous black pile medially (Fig. 11B) |
| 27. | Apical third of metafemur dorsally with shorter and adpressed pilosity (Fig. 7A) |
| | |
| - | Apical third of metafemur dorsally with longer and less adpressed pilosity (Fig. 7E) |
| | |
| 28. | Frons with narrow lateral pollinose vittae along eye margins (Fig. 11C); distribution: Caucasus, Georgia |
| - | Frons with broader pollinose vittae along eye margins (Fig. 11D); distribution: Italy, Greece (Rhodes) and Turkey |
| | |



FIGURE A1. Male of Merodon papillus. A left metaleg, lateral view, B left metatibia, ventral view. Scale bar: 1 mm.



FIGURE A2. Abdomen (segments 3–5) of female. A *Merodon papillus*, B *M. trebevicensis*, C *M. armipes*. pp—posterior process on sternum 4, td—transversal depression on tergum 4. Scale bar: 1 mm.



FIGURE A3. Left metaleg, lateral view. A Merodon ruficornis, B, C M. abruzzensis. A, B male, C female. Scale bar: 1 mm.



FIGURE A4. Male genitalia. A, B *Merodon ruficornis*, C, D *M. abruzzensis*. A epandrium, lateral view, B, D left surstyle, anterior view, C left surstyle, lateral view. **al**—anterior surstyle lobe, **pl**—posterior surstyle lobe. Scale bar: 0.4 mm.



FIGURE A5. Male genitalia. A *Merodon alexandri*, B, C *M. ponticus*. A, B epandrium, lateral view, C left surstyle, anterior view. Scale bar: 0.4 mm.



FIGURE A6. Left metaleg of male, lateral view. A *Merodon alexandri*, B *M. nigripodus*, C *Merodon armipes*, D *M. auripes*, E *M. ponticus*. Im—lamella of metatibia, pf—protuberance of metafemur. Scale bar: 1 mm.



FIGURE A7. Left metaleg of male, lateral view. A Merodon trebevicensis, B M. hoplites, C M. gallicus. Scale bar: 1 mm.



FIGURE A8. Male genitalia. A, B Merodon gallicus, C M. hoplitis, D, E M. trebevicensis. A, C epandrium, lateral view, B, E left surstyle, anterior view, D left surstyle, lateral view. al—anterior surstyle lobe, pl—posterior surstyle lobe. Scale bar: 0.4 mm.



FIGURE A9. Left metaleg, lateral view. A Merodon ilgazense, B M. trebevicensis, C M. hoplitis. A male, B, C female. Scale bar: 1 mm.



FIGURE A10. Left metaleg of Merodon loewi, lateral view. A, B male, C female. Scale bar: 1 mm.



FIGURE A11. Male genitalia. A *Merodon loewi*, **B** *M. nigripodus*, **C** *M. ovaloides*. **A**, **C** epandrium, lateral view, **B** left surstyle, lateral view. **c**—cercus; **pl**—posterior surstyle lobe. Scale bar: 0.4 mm.



FIGURE A12. Left metaleg. A–D *Merodon ovaloides*, E, F *M. turcicus*. A, B male, lateral view, C male metatibia, anterior view, D, E female, lateral view, F female, apex of metatibia. Im—lamella of metatibia. Scale bar: A–E 1 mm, F 0.4 mm.



FIGURE A13. Left metaleg of Merodon planiceps, lateral view. A, B male, C female. Scale bar: 1 mm.



FIGURE A14. Male genitalia of Merodon planiceps, epandrium, lateral view. pl-posterior surstyle lobe. Scale bar: 0.4 mm.



FIGURE A15. Left metaleg of male. A–C *Merodon turcicus*, D, E *Merodon portschinskyi*. A–D lateral view, E apex of metatibia. Scale bar: A–D 1 mm, E 0.5 mm.

APPENDIX TABLE 1. Uncorrected pairwise (p) distances between sequences of the combined 3' and 5' mitochondrial COI gene fragments.

| | 1 | 2 | 3 | 4 | 4 | 5 | 6 | 7 8 | 3 9 | 1(|) 11 | |
|-----------------------|-------|----|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| 1. M. trebevicensis | | | | | | | | | | | | |
| 2. M. auripes | 0.025 | 54 | | | | | | | | | | |
| 3. M. armipes | 0.027 | 5 | 0.0182 | | | | | | | | | |
| 4. M. loewi | 0.027 | 5 | 0.0182 | 0.0000 | | | | | | | | |
| 5. M. hoplitis | 0.022 | 25 | 0.0276 | 0.0298 | 0.0298 | | | | | | | |
| 6. M. papillus | 0.023 | 9 | 0.0160 | 0.0080 | 0.0080 | 0.0290 | | | | | | |
| 7. M. trispinus | | | | | | | | | | | | |
| sp. nov. | 0.028 | 86 | 0.0309 | 0.0334 | 0.0334 | 0.0232 | 0.0327 | | | | | |
| 8. M. fulvitarsis | | | | | | | | | | | | |
| sp. nov. | 0.026 | 51 | 0.0167 | 0.0073 | 0.0073 | 0.0298 | 0.0065 | 0.0320 | | | | |
| 9. M. acutus sp. nov. | 0.025 | 8 | 0.0163 | 0.0127 | 0.0127 | 0.0265 | 0.0105 | 0.0312 | 0.0127 | | | |
| 10. M. portschinskyi | 0.032 | 20 | 0.0327 | 0.0363 | 0.0363 | 0.0356 | 0.0341 | 0.0374 | 0.0334 | 0.0345 | | |
| 11. M. gallicus | 0.050 |)1 | 0.0530 | 0.0545 | 0.0545 | 0.0472 | 0.0523 | 0.0476 | 0.0537 | 0.0497 | 0.0516 | |
| 12. M. ruficornis | 0.037 | 8 | 0.0392 | 0.0414 | 0.0414 | 0.0378 | 0.0392 | 0.0418 | 0.0385 | 0.0410 | 0.0370 | 0.0494 |