

# Systematic position and composition of *Merodon nigratarsis* and *M. avidus* groups (Diptera, Syrphidae) with a description of four new hoverflies species

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## Abstract

The putative monophyly and systematic position of *Merodon nigratarsis* group was assessed based on morphological and molecular data of the mitochondrial COI and nuclear 28S rRNA genes. The previously reported concept of the group has been redefined, and *M. crassifemoris* Paramonov, 1925 is now excluded. The related *M. avidus* group is redefined here, including the *Merodon avidus* complex and *M. femoratus* Sack, 1913. Species delimitation of morphologically defined species of *M. nigratarsis* group was well supported by COI gene analysis, with the exception of *M. alagoezicus* Paramonov, 1925 and *M. lucasi* Hurkmans, 1993. Descriptions are given for three new species of the *M. nigratarsis* species group: *Merodon cohurnus* Vujić, Likov et Radenković sp. n., *Merodon longisetus* Vujić, Radenković et Likov sp. n. and *Merodon obstipus* Vujić, Radenković et Likov sp. n., and one new species from the *M. avidus* group: *Merodon rutatarsis* Likov, Vujić et Radenković sp. n. A lectotype is designated for *M. femoratus* Sack, 1913, and two new synonymies of this species were proposed: *M. biarcuatus* Curran, 1939 and *M. elegans* Hurkmans, 1993. Here we review 18 species from the *M. nigratarsis* group and six species from the *M. avidus* group and provide morphological diagnoses of the species groups. Additionally, diagnosis of 12 branches (groups or individual taxa) of *M. avidus-nigratarsis* lineage, an illustrated diagnostic key for the males, and distribution map are provided for the new species.

## Keywords

distribution – hoverfly – *Merodon cohurnus* sp. n. – *Merodon longisetus* sp. n. – *Merodon obstipus* sp. n. – *Merodon rutatarsis* sp. n. – mitochondrial COI – nuclear 28S rRNA

## Introduction

Representing a frontier between Europe, Asia and Africa, the Mediterranean region is one of the richest biodiversity zones on the planet. With the continuous discovery of new species in this area, the Mediterranean region is becoming a globally important species hotspot (Cuttelod et al., 2009). In particular, the high number of endemic plants in the Mediterranean region play a significant role in the life-cycle and survival of many insects, including

hoverflies (Diptera, Syrphidae) (Vujić et al., 2011).

The genus *Merodon* Meigen, 1803 (Syrphidae: Eristalinae: Merodontini) is restricted to the Palaearctic and Afrotropical regions (Ståhls et al., 2009; Šašić et al., 2016), except for *M. equestris* (Fabricius, 1794) which was introduced into the Nearctic and New Zealand (Speight, 2018). The highest species diversity is recorded for the Mediterranean area (Vujić et al., 2012), which is associated with a high diversity of bulb species in this region that

serve as larval host plants (Ricarte et al., 2008; Andrić et al., 2014; Preradović et al., 2018). Asia Minor and Eastern Europe (especially the Balkan Peninsula) is considered one of the centers of diversity and endemism of the genus (Kaloveloni et al., 2015), as documented by many studies of the *Merodon* fauna in the Eastern Mediterranean (Vujić et al., 2007, 2011, 2013, 2015; Ståhls et al., 2009, 2016; Radenković et al., 2011; Kaloveloni et al., 2015; Ačanski et al., 2016a). These recent studies describing many new taxa of the genus *Merodon* has resulted in the taxon being the most speciose the European hoverfly genus (Marcos-García et al., 2007; Vujić et al., 2007, 2012, 2013, 2015, 2018; Popov, 2010; Radenković et al., 2011; Ačanski et al., 2016a) comprises more than 160 species in the world (Ståhls et al., 2009; Vujić et al., 2013; Šašić et al., 2016; Speight, 2018).

The genus *Merodon* contains many complexes of cryptic and sibling species, which show minimal morphological differences. Consequently, recent studies have used an integrative taxonomic approach, combining methods such as geometric morphometry (Nedeljković et al., 2015; Ačanski et al., 2016a; Šašić et al., 2016), molecular characters of the mitochondrial (mtDNA) cytochrome c oxidase I (COI) gene (Milankov et al., 2008a, c; Francuski et al., 2011; Radenković et al., 2011; Milankov et al., 2013; Popović et al., 2015; Vujić et al., 2015; Radenković et al., 2018a) and environmental niche modelling (ENM) (Wiens & Graham, 2005; Raxworthy et al., 2007; Schluter, 2009; Ačanski et al., 2016b) to estimate divergences among closely related taxa.

Hurkmans (1993) gave the first and most comprehensive revision of the *Merodon* genus, dividing 61 species with tapering abdomen into eleven groups: *M. alagoezicus*, *M. alexeji*, *M. avidus*, *M. clavipes*, *M. crassifemoris*, *M. elegans*, *M. longicornis*, *M. nigratarsis*, *M. pruni*, *M. tarsatus* and *M. vandergooti*. Mengual et al. (2006) recognized four well supported groups based on molecular data among species

occurring in the Iberian Peninsula (*M. desuturinus*, *M. albifrons*, *M. nigratarsis* and *M. aureus* groups). Through introduction of the methods of integrative taxonomy, applying molecular (mtDNA COI gene, nuclear 28S rRNA gene) and phenotypic traits (geometric wing morphometry, surstylus shape and size and other morphological characters), many studies defined species groups of the genus *Merodon*, including species status and delimitation, e.g., within the *M. ruficornis* group (Radenković et al., 2002; Milankov et al., 2008a; Francuski et al., 2009; Vujić et al., 2012), *M. desuturinus* group (Milankov et al., 2008b; Vujić et al., 2018), *M. aureus* and *M. cinereus* groups (Milankov et al., 2008c; Francuski et al., 2011; Šašić et al., 2016; Veselić et al., 2017; Radenković et al., 2018a), *avidus* complex (Milankov et al., 2009; Ačanski et al., 2016a), *M. albifrons* group (Milankov et al., 2013), *M. nigratarsis* group (Vujić et al., 2013), *M. nanus* group (Vujić et al., 2015; Kočič Tubić et al., 2018) and for all *Merodon* taxa of Lesvos (Ståhls et al., 2009).

Vujić et al. (2018) summarising previously published data (Šašić et al., 2016; Radenković et al., 2018b), cited five monophyletic lineages inside the genus *Merodon*: *albifrons*, *aureus*, *avidus-nigratarsis*, *desuturinus*, and *natans*. All taxa considered here belong to the *avidus-nigratarsis* lineage.

The *M. nigratarsis* group *sensu* Hurkmans (1993) consisted of two species, *M. nigratarsis* Rondani, 1845 and *M. femoratoides* Paramonov, 1925. Radenković et al. (2011) re-defined the *M. nigratarsis* group with a description of one new species, *M. latifemoris* Radenković and Vujić, 2011. Vujić et al. (2013) conducted a large study of *Merodon* species from the Middle East and produced a revision of the *M. nigratarsis* group, presenting 15 species: *M. alagoezicus*, *M. angustus* Vujić and Radenković, 2013\*, *M. crassifemoris*, *M. femoratoides*, *M. hakkariensis* Vujić and Radenković, 2013\*, *M. latifemoris*, *M. lucasi*\*

*M. nigratarsis*, *M. nitidifrons* Hurkmans, 1993\*, *M. satdagensis* Hurkmans\*, 1993, *M. schachti* Hurkmans, 1993\*, *M. quadraticus* Vujić and Radenković, 2013\*, *M. taniniensis* Hurkmans, 1993\*, *M. testaceus* Sack, 1913 and *M. toscanus* Hurkmans, 1993 (species marked with \* only occur in Asia).

The *M. nigratarsis* group as defined by Radenković et al. (2011) comprises relatively large (11–17 mm) species with shared characteristics such as a black scutum with four white microtrichose vittae, a tapering black and orange colored abdomen with pairs of white microtrichose fasciae on terga 2–4, and a medium-wide and slightly curved metafemur. The taxonomy of the *Merodon avidus* complex taxa from Europe and Asia (closely related to the *M. nigratarsis* group) were recently revised (Popović et al., 2015; Ačanski et al., 2016a; Šašić et al., 2016) revealing four sibling species: *M. avidus* (Rossi, 1790), *M. ibericus* Vujić, 2015, *M. megavidus* Vujić & Radenković, 2016 and *M. moenium* Wiedemann in Meigen, 1822. Recently, Vujić et al. (2019) established 10 groups inside to the *avidus-nigratarsis* lineage (*M. aberrans*, *M. aurifer*, *M. avidus*, *M. clavipes*, *M. fulcratus*, *M. italicus*, *M. nigratarsis*, *M. pruni*, *M. serrulatus* and *M. tarsatus*), with addition of four individual species, also belonging to this lineage, *M. clunipes* Sack, 1913, *M. eumerusi* Vujić, Radenković & Likov, 2019, *M. murinus* Sack, 1913, and *M. ottomanus* Hurkmans, 1993, with similar distribution in the Middle East (Vujić et al., 2019).

Recent field work and revision of additional collections has discovered four new species from the Eastern Mediterranean and Middle East, which are described in the present paper. In addition, new molecular data based on new material have enabled revision of systematic positions and relations between taxa among *M. avidus* and *M. nigratarsis* species groups.

The aims of this paper are (i) to define the *M. avidus* group and to redefine the *M. nigratarsis* species group, (ii) to present the

systematic position and composition of *M. avidus* and *M. nigratarsis* species groups, (iii) to provide diagnosis for branches (groups or individual taxa) of *Merodon avidus-nigratarsis* lineage, (iv) to provide descriptions and diagnostic characters of four new species, and (v) to complete a key for males of *M. nigratarsis* and *M. avidus* groups.

## Material and methods

### Study sites

The occurrence points (geographical coordinates) were entered into the GenGIS (v2.5.1) (Parks et al., 2013) software to generate distribution map. Species richness map was created in DIVA-GIS (v 7.5) (Hijmans et al., 2012).

This paper includes new records from a few localities from SE Mediterranean: Greece (Chios island) and S-SW Turkey (Balıkesir, Burdur, Isparta, and Osmaniye provinces, Bozdağ and Rahat mountains, and around Köyceğiz lake) and Turkmenistan. Sampling localities of new species are shown on fig. 1.

### Morphological analysis

The studied material for newly described species are part of several museums which are specified in the form of the following abbreviations: AMNH (American Museum of Natural History, New York, USA); BMNH (Natural History Museum London, England); EMIT (Entomological Museum of Isparta, Turkey); FSUNS (Faculty of Sciences, University in Novi Sad, Serbia); NML (World Museum Liverpool, England); NBC (Natural Biodiversity Centre, Leiden, Netherlands); SZMN (Siberian Zoological Museum, Novosibirsk, Russia); ZMHB (Zoological Museum of Humboldt University of Berlin, Germany).

All information concerning specimens (locality, collector, etc.) are stored in the internal electronic database of the Faculty of Sciences, University of Novi Sad (FSUNS).

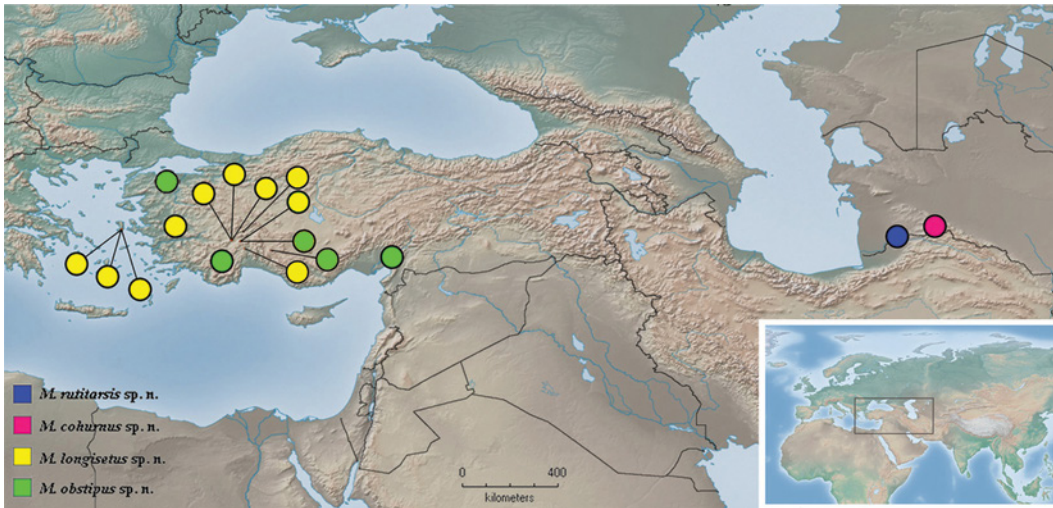


FIGURE 1 Geographic distribution of newly described species.

Terminology follows Thompson (1999) for non-genitalic morphology and Marcos-García et al. (2007) for morphology of the male genitalia. A description is provided for each new species, including figures of adult morphology. An identification key is also provided to enable the distinction of adult males. Because the new species described here are based partly on material from museum collections, ecological data and information on habitat preferences are sparse. Updated data on the biology of the genus *Merodon*, including species from the *M. nigratarsis* group, are presented in the database for European Syrphidae by Speight (2018).

The specimens were collected by sweep net. To study the male genitalia we follow methodology from Šimić (1987). 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. Photo of hypandrium of *Merodon avidus* (fig. 33C) was taken with a JEOL JSM 6460LV scanning electron microscope (SEM) operated at 20kV. Measurements were taken with an eyepiece graticule or micrometer. Morphological characters were observed using a Nikon SMZ 745T stereomicroscope. Identification of females

was difficult in some cases and dependent on subtle characters and sympatric occurrence with males.

### Molecular analysis

#### DNA extraction

Total genomic DNA was extracted using 1 to 3 legs from dry, pinned specimens following the procedure described by Chen et al. (2010). Genomic DNA vouchers were accordingly labelled and deposited at the Faculty of Sciences, Department of Biology and Ecology, University of Novi Sad (FSUNS) and Zoology unit, Finnish Museum of Natural History Luomus, Helsinki, Finland (MZH) (supplementary table S1).

#### PCR amplification and sequencing

The mtDNA COI 3' and 5' fragments were amplified using the following primers: forward primer C1-J-2183 (5'-CAACATTTATTTT-GATTTTTTGG-3') (alias JERRY) and reverse primer TL2-N-3014 (5'-TCCAATGCACTAATCT-GCCATATT-3') (alias PAT) (Simon et al., 1994); and forward primer LCO (5'-GCTCAACAAAT-CATAAAGATATTGG-3') and reverse primer HCO (5'-TAAACTTCAGGGTGACCAAAAAAT-CA-3') (Folmer et al., 1994), respectively. PCR

amplification of the D2-3 region of the nuclear 28S ribosomal RNA gene was performed using the following primer pair: forward 28S-F2 (5'-AGAGAGAGTTCAAGAGTACGTG-3') and reverse 28S-3DR (5'-TAGTTCACCATCTTT CGGGTC-3') (Belshaw et al., 2001). The reaction mix contained 1× reaction buffer (Thermo Scientific), 2.5 mM MgCl<sub>2</sub>, 0.1 mM of each nucleotide, 2 pmol of each primer, 1U Taq polymerase (Thermo Scientific), and approximately 50 ng template DNA in a total volume of 25 µl. Amplification was performed using the following conditions: initial denaturation at 95°C for 2 min; 30 cycles of 94°C for 30 s, 49°C (for 3' fragment COI) and 50°C (for 5' fragment COI and 28S rRNA) for 30 s; 72°C for 2 min; with the final extension at 72°C for 8 min. The PCR products were purified using ExoSAP (Thermo Scientific) following the manufacturer's recommendations. Sequencing was conducted using forward primer of each amplified region on an ABI3730xl Genetic Analyzer (Applied Biosystems, Foster City, CA, USA).

### Data analyses

In order to establish the systematic position and composition of the *M. nigratarsis* group, we included samples representing the *avidus-nigratarsis* lineage in addition to species belonging to the *albifrons+desuturinus*, *natans* and *aureus* lineages and two outgroups, *Platynochaetus maquarti* Loew, 1862 and *Eumerus grandis* Meigen, 1822. For the analyses of molecular data we created two datasets: 1) first dataset consisted of 35 ingroup species (and two outgroups) for which the combined two-genes data matrix (COI and 28S rRNA) was obtained and 2) second dataset of 105 specimens (and two outgroups) for COI gene sequences. For the names and GenBank accession numbers of examined species and outgroups, see supplementary table S1.

Alignment of obtained sequences was done using the ClustalW algorithm (Thompson et al., 1994) as implemented in BioEdit software

(Hall, 1999) with final adjustments conducted by eye. All sequences in both datasets were trimmed to equal lengths.

The final aligned and pruned first dataset including two-genes data matrix (COI+28S rRNA) comprised a total of 1862 nucleotide characters for in total 37 species (35 ingroup species of the studied genus *Merodon* lineages + two outgroups). Within the number of aligned sites for COI gene (concatenated 3' and 5' fragments of the gene) was 1273 nucleotides, while 589 nucleotides were included in analyses for the D2-3 region of the 28S rRNA gene.

The second dataset of the COI gene sequences, which included 84 specimens from the *Merodon avidus-nigratarsis* lineage, and specimens from *albifrons+desuturinus*, *aureus* and *natans* lineages and 2 outgroups, consisted of 107 sequences. A combined dataset of the 3' and 5' COI fragments contained 1371 nucleotides, among which the 5' fragment COI had a final length of 639 bp and the final length of the 3' fragment COI was 732 nucleotides. For construction of COI gene trees a combined dataset of the 3' and 5' fragment COI gene sequences was used and identical sequences were removed using DAMBE v.5 (Xia, 2013), so the final dataset for trees construction consisted of 94 haplotypes.

For both datasets trees were constructed using Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian analyses (BI). All obtained trees were rooted using *Platynochaetus macquarti* Loew, 1862.

Maximum Parsimony (MP) analysis was conducted using NONA (Goloboff, 1999), spawned with the aid of Winclada (Nixon, 2002). We used 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 (TBR) branch swapping. Nodal support was estimated using nonparametric bootstrapping with 1,000 replicates.

Maximum Likelihood (ML) trees were constructed using MEGA 7 (Kumar et al., 2015) under a general time-reversible (GTR) evolutionary model using a discrete Gamma distribution with five rate categories and by assuming that a certain fraction of sites are evolutionarily invariable, since this was shown to be the best evolutionary model for both generated datasets (as estimated in MEGA 7). Nodal support was estimated with 1000 non-parametric bootstrap replicates.

Bayesian analysis (BI) for second dataset (COI sequences) was carried out using the same evolutionary model as for ML tree, as priors in MrBayes ver.3.2 (Ronquist et al., 2012). In BI analysis the first dataset was divided into two partitions: COI gene and 28S rRNA gene sequences. We determined the best choice of the model for each partition using MEGA 7 (Kumar et al., 2015). The selected model, which is not implemented in MrBayes, was substituted by the closest over-parameterized model (Huelsenbeck & Rannala, 2004). The Tg2+G substitution model determined for the 28S partition was replaced by an HKY+G model. For the COI gene partition, a GTR+G+I model was selected. Two independent runs of four Markov chain Monte Carlo (MCMC) permutations were performed for 10,000,000 generations (the first dataset) and 20,000,000 generations (the second dataset) with sampling every 100 generations. For both datasets analyses were performed online using the CIPRES Science Gateway V 3.3. (Miller et al., 2010, <http://www.phylo.org/index.php/portal/v33>). The program Tracer 1.5 (Drummond & Rambaut, 2007; Rambaut et al., 2014) was used to check convergence and acceptable mixing. The first 25% of the sampled iterations/generations were discarded as burn-in, and 50% consensus trees were computed using FigTree v1.4.0 (Rambaut, 2014).

Additionally, with the aim to delineate species based on COI gene sequences, we used the Generalized Mixed Yule Coalescent

(GMYC) method (Pons et al., 2006; Monaghan et al., 2009; Fujisawa & Barraclough, 2013; Michonneau, 2015). The ultrametric trees required for this method were obtained using BEAST v1.8.0 (Drummond et al., 2012). GMYC analyses were performed as described in a tutorial by Michonneau (2016).

## Results

### *Phylogenetic analyses and systematic position of M. nigratarsis and M. avidus groups*

Aiming to resolve the systematic position of the *M. nigratarsis* group, the phylogenetic trees based on two-gene (COI and 28S rRNA) matrix were constructed (fig. 2, supplementary figs. S1 and S2). In obtained MP tree (fig. 2), the position of *Merodon avidus-nigratarsis* lineage is in agreement with the placement reported in Šašić et al. (2016) and Radenković et al. (2018b). *Merodon avidus-nigratarsis* lineage is here confirmed as one of four main lineages (bootstrap 89) in the genus *Merodon*, in addition to the *albifrons+desuturinus*, *aureus* and *natans* lineages. The ML tree with the highest log likelihood (-12147.4855) (supplementary fig. S1), as well as 50% majority-rule consensus tree resulting from MrBayes analysis (supplementary fig. S2) were consistent and in agreement with the MP tree supporting the four main lineages. The monophyly of the *avidus-nigratarsis* lineage was clearly supported by bootstrap values of 89 (MP, fig. 2) and 99 (ML, supplementary fig. S1), as well as by a posterior probability (PP) value of 100% (BI, supplementary fig. S2). Based on the morphological characters and supported by molecular data of available taxa, *M. avidus-nigratarsis* lineage is divided into 12 branches (groups or individual taxa): *M. aberrans*, *M. aurifer*, *M. avidus*, *M. clavipes*, *M. clunipes*, *M. crassifemoris*, *M. fulcratus*, *M. italicus*, *M. nigratarsis*, *M. ottomanus*, *M. pruni* and *M. serrulatus*.

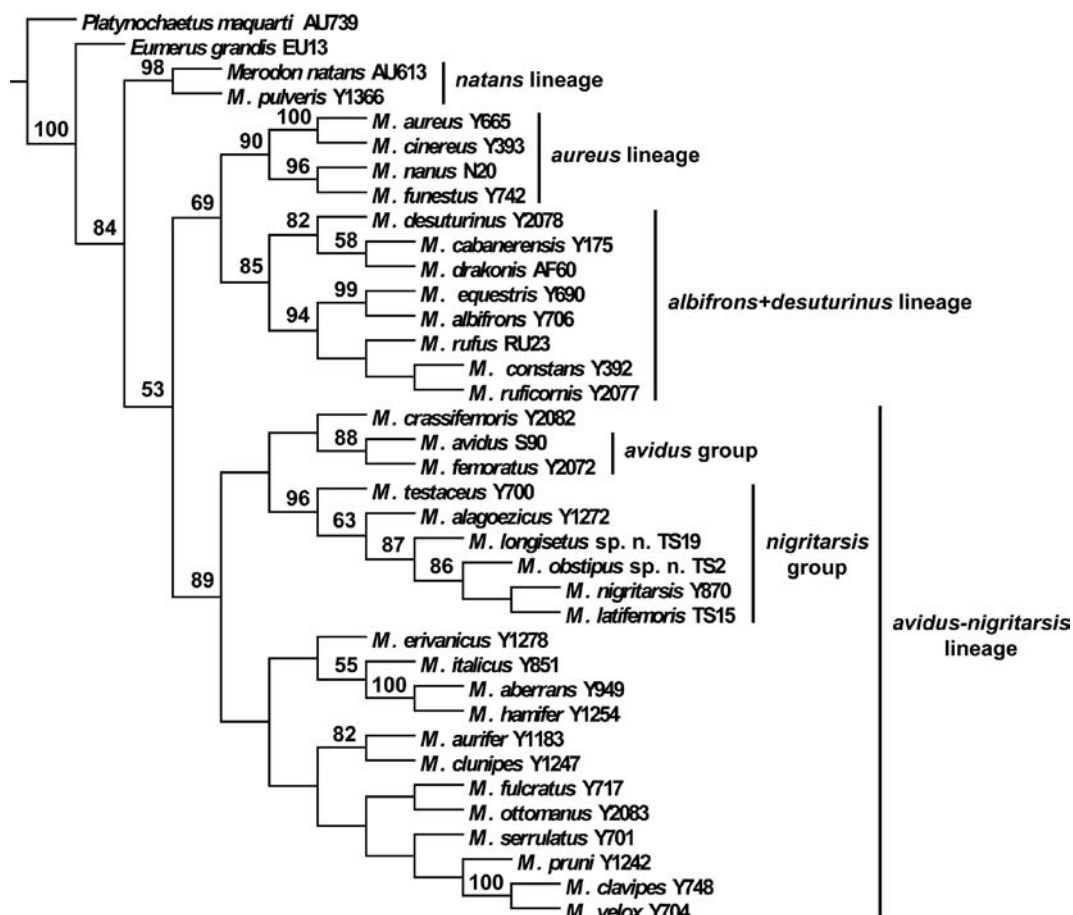


FIGURE 2 Strict consensus tree of two most parsimonious trees from the analysis of combined COI mitochondrial and 28S nuclear genes sequences. Length 2116 steps, Consistency Index (CI) 37, Retention Index (RI) 44. Bootstrap support values are depicted near nodes ( $\geq 50$ ). Numbers and letters after the species name referred to the DNA labcode IDs. Four lineages observed in genus *Merodon*, as well as two groups of *avidus-nigratarsis* lineage are marked on the tree.

*Merodon aberrans* group (*M. aberrans* Egger, 1860 and *M. hamifer* Sack, 1913) (fig. 3A-B) is characterized by: an elongated and narrow abdomen with dark terga; terga 2–4 with a pair of microtrichose fasciae; metafemur long and narrow; hypandrium with very long lingula (fig. 3B:1).

*Merodon aurifer* group contains taxa with very short body pilosity (fig. 3C), yellow baso-flagellomere, pale tibiae and tarsi. Beside *M. aurifer* Loew, 1862, group consists of at least one additional taxon, an undescribed species

from Turkey and Azerbaijan (Vujić et al., in prep.).

*Merodon avidus* group (*M. avidus* complex, *M. femoratus* and *Merodon rutitarsis* sp. n.) is characterized by elongated and tapering abdomen, at least tergum 2 with reddish-yellow lateral maculae (fig. 11A–C), and reddish-yellow tarsi (fig. 14A–D). Separation of the group is supported by bootstraps 88 and 98 (MP and ML, respectively) and PP = 100% (fig. 2, supplementary figs. S1 and S2).



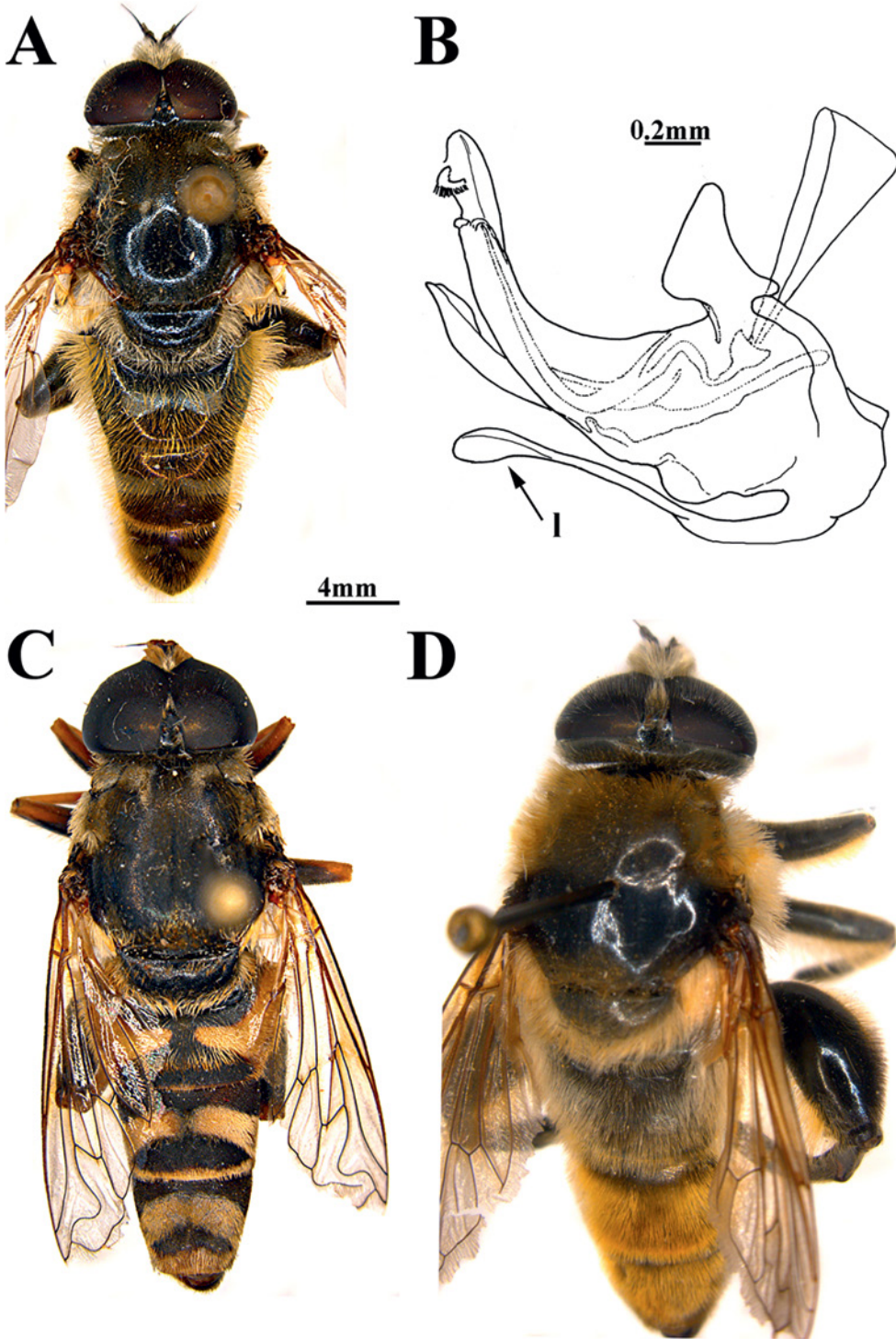


FIGURE 3 A) *Merodon aberrans*, male; body, B) *Merodon aberrans*, male; hypandrium, C) *Merodon aurifer*, male; body, D) *Merodon clavipes*, male; body. Scale: A), C–D) 4 mm, B) 0.2 mm. l–lingula.

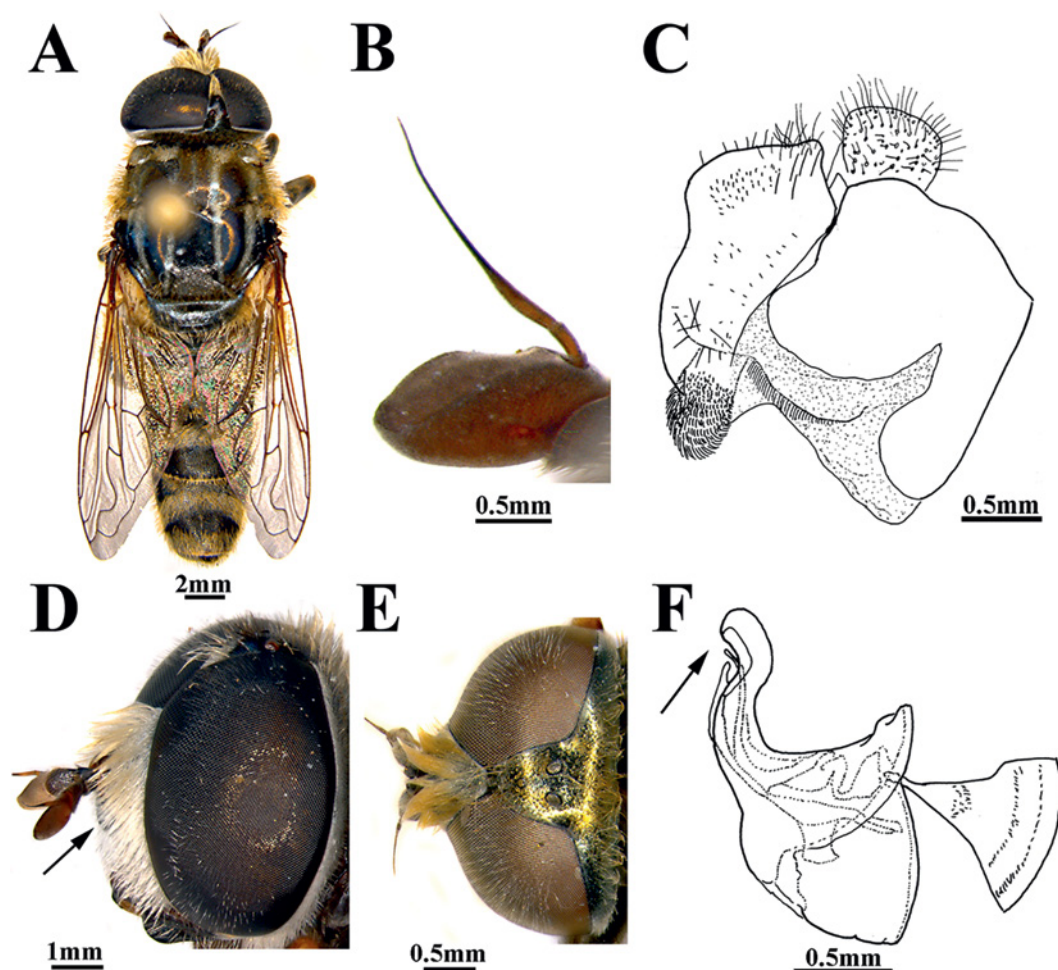


FIGURE 4 A) *Merodon clunipes*, male; body, B) *Merodon clunipes*, male; antennae, C) *Merodon clunipes*, male; epandrium, D) *Merodon crassifemoris*, male; head, E) *Merodon fulcratus*, male; head, F) *Merodon fulcratus*, male; hypandrium (lack of ctenidium marked with arrow). Scale: A) 2 mm, B–C), E–F) 0.5 mm, D) 1 mm.

*Merodon clavipes* group (*M. clavipes* (Fabricius, 1781) and *M. velox* Loew, 1869) includes large species (15–20 mm) with long body pilosity and broad metafemur covered with long pile (fig. 3D).

*Merodon clunipes* is a species with broad metatibiae and dark terga (fig. 4A), and has clear apomorphic diagnostic characters, including antennae shape (fig. 4B) and the characteristic shape of the surstyle lobe (fig. 4C).

*Merodon crassifemoris* is a taxon with tubercle on the face below the antenna (fig. 4D: marked with arrow), and a hook-like posterior

surstyle lobe (fig. 13A: pl) unique among all other taxa of the *avidus-nigritarsis* lineage.

*Merodon fulcratus* group is clearly separated from other groups from the lineage with distinctly dichoptic eyes (fig. 4E) and lack of ctenidium at hypandrium (fig. 4F: marked with arrow). Two species are known, *M. dichopticus* Stackelberg, 1968 and *M. fulcratus* (Becker, 1913).

*Merodon italicus* group includes species with elongate basoflagellomere (fig. 5D) and quadratic posterior surstyle lobe (fig. 6A–C: pl). Two species share these morphological

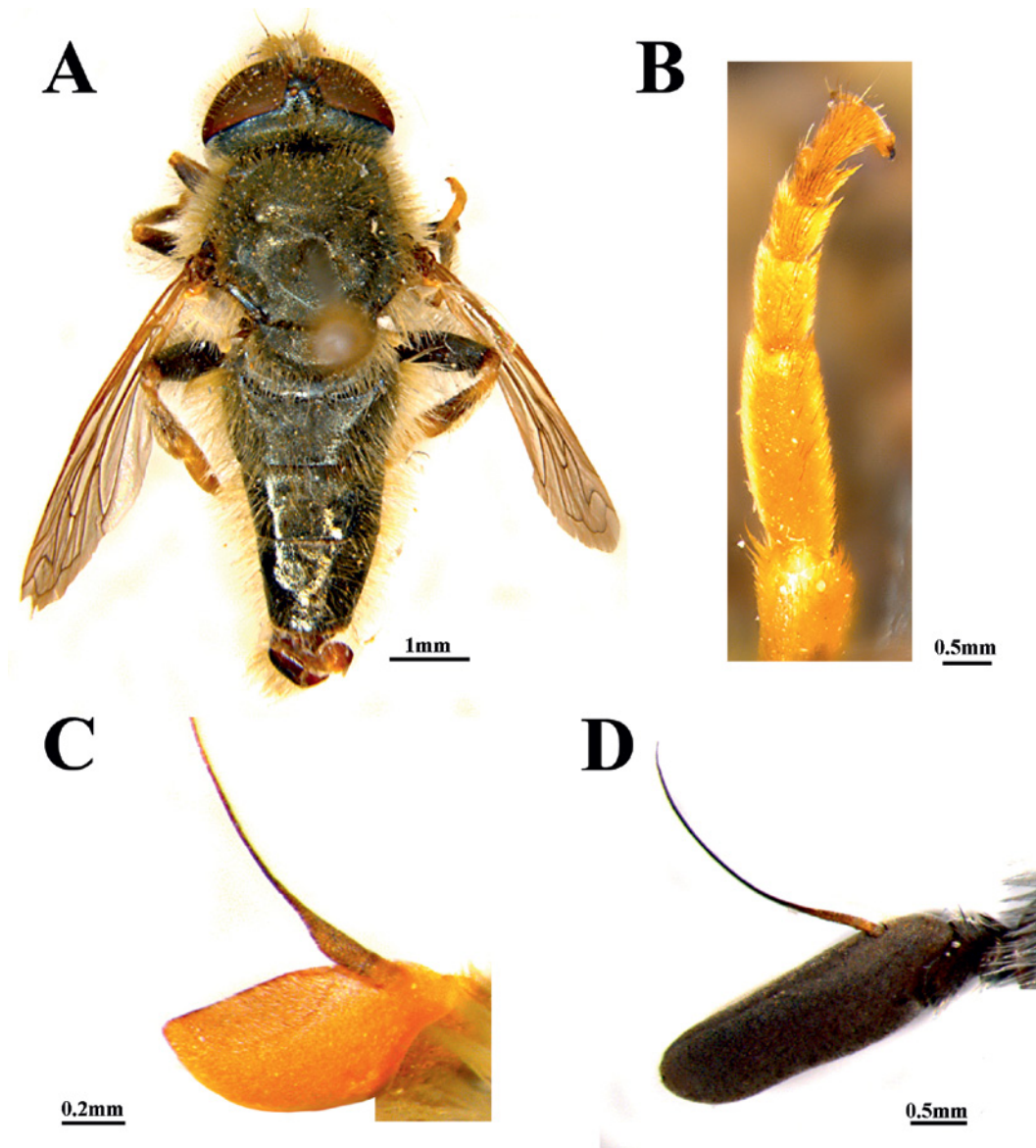


FIGURE 5 A) *Merodon ottomanus*, male; body, B) *Merodon ottomanus*, male; metabasotarsomere, C) *Merodon ottomanus*, male; basoflagellomere, (D) *Merodon italicus*, male; basoflagellomere. Scale: A) 1 mm, B) 0.5 mm, D) 0.5 mm, C) 0.2 mm.

features: *M. italicus* Rondani, 1845 and *M. erivanicus* Paramonov, 1925, but they are not resolved together in the tree (fig. 2).

*Merodon nigratarsis* group contains taxa with abdomen elongate, narrow and tapering (fig. 10A–B), tarsi dark brown/black dorsally and partly orange ventrally (fig. 14E–H). Male

genitalia: anterior surstyle lobe more or less rhomboid shape (as on fig. 13: al), except in *alagoezicus* subgroup where the anterior surstyle lobe is transformed into a narrow, elongate, strongly curved projection (as on fig. 12: al). Hypandrium with pair of apical thorns on ventral margin directed backwards (as on

fig. 24: th), but often with a pair of lateral projections near the base (as on fig. 30A, C: lp) and well-developed lingula (as on fig. 24A–D: l). Separation of the group is supported by bootstraps 96 and 99 (MP and ML, respectively) and PP = 100% (fig. 2, supplementary figs. S1 and S2). *Merodon nigratarsis* group includes 18 species (listed in Introduction with additional 3 here described species), from which 6 species belong to *alagoezicus* subgroup: *Merodon nitidifrons*, *M. alagoezicus*, *M. satdagensis*, *M. schachti*, *M. hakkariensis* and *M. lucasi*.

*Merodon ottomanus* is a species with dark abdomen (fig. 5A), reddish–yellow basoflagellomere (fig. 5C) and yellow tarsi of metaleg (at least basotarsomere) (fig. 5B).

*Merodon pruni* group is characterized by short body pilosity (scutum and abdomen) (fig. 7C) and short basoflagellomere, as long as broad (fig. 7A); metatrochanter with distinct thorn (fig. 7B: marked with arrow). Two species belong here: *M. pallidus* Macquart, 1842 and *M. pruni* Rossi, 1790.

*Merodon serrulatus* group includes taxa with characteristic basolateral protrusion on the posterior surstyle lobe at outer surface (fig. 8B: marked with arrow). This group includes five already known species: *M. bequaerti* Hurkmans, 1993, *M. hirsutus* Sack, 1913, *M. kawamurae* Matsumura, 1916, *M. sacki* Paramonov, 1936, and *M. serrulatus* Wiedemann in Meigen, 1822.

According to the results presented on the two-genes trees (fig. 2, supplementary figs. S1 and S2) *M. nigratarsis* group with previously identified species (in Vujić et al., 2013) is related to *M. avidus* group (*M. avidus* complex and *M. femoratus*). The supposed monophyletic position of *M. nigratarsis* group (Vujić et al., 2013) is confirmed and supported by high bootstrap values (MP 96, ML 99) and a posterior probability with a value of 100%; with the exception of *M. crassifemoris* species. This species was clearly separated from

members of the *M. nigratarsis* group. *Merodon avidus* group considered to be an independent line (MP bootstrap 88, ML bootstrap 98, PP = 100%), and includes taxa previously recognized as *M. avidus* complex, the taxon *M. femoratus* redefined here and the newly described species *M. rutatarsis* sp. n., which was not available for molecular analyses.

### **Species delimitation based on molecular data (COI gene)**

In order to reveal the composition of the *M. nigratarsis* group, we included 105 specimens representing *avidus-nigratarsis* (84 specimens), *albifrons+desuturinus*, *natans* and *aureus* lineages and applied analyses on COI gene sequences, which are proved to be highly informative for species delimitation. All obtained COI gene trees (ML, BI and MP) corroborate the four main lineages (putative subgenera) within the *Merodon* genus (MP bootstraps over 89, ML bootstraps over 98 and PP over 75% except for *aureus* lineage; fig. 15, supplementary figs. S3 and S4), as resolved in analyses of two-gene (COI and 28S rRNA) data matrix. Within the *M. avidus-nigratarsis* lineage, we observed clear differentiation of the *M. nigratarsis* group (MP bootstrap 98, ML bootstrap 100 and PP 97%; fig. 15, supplementary figs. S3 and S4) consisting of 9 species: *M. nigratarsis*, *M. obstipus* sp. n., *M. femoratooides*, *M. latifemoris*, *M. toscanus*, *M. longisetus* sp. n., *M. alagoezicus*, *M. lucasi* and *M. testaceus*. *Merodon crassifemoris*, previously known to belong to this group (Vujić et al., 2013) was not resolved into the *M. nigratarsis* group, but belongs to *avidus-nigratarsis* lineage. Additionally, two morphologically different species, *M. alagoezicus* and *M. lucasi*, were not separated in different clusters on COI gene trees. They are distributed into two clusters on all obtained trees, the first one consisted of 3 individuals of *M. alagoezicus* collected on Samos island in Greece (specimens with



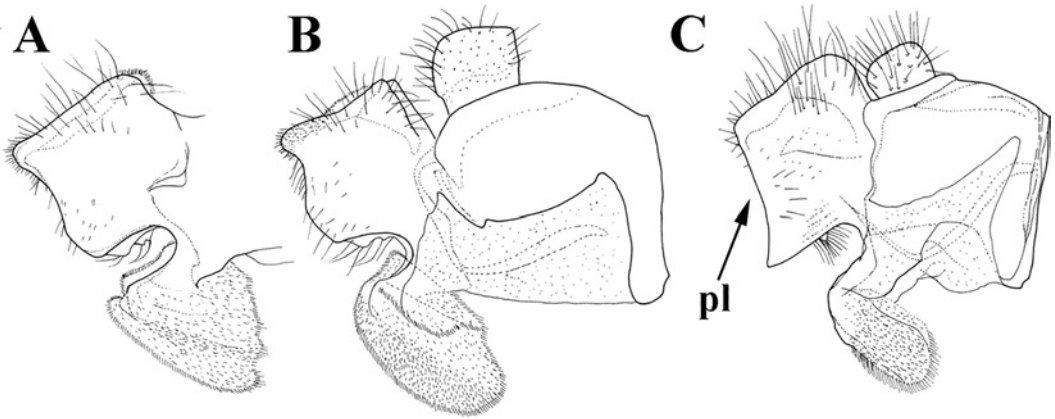


FIGURE 6 Male genitalia. Lateral view, A) *Merodon erivanicus*, surstyle lobe B) *Merodon erivanicus*, epandrium, C) *Merodon italicus*, epandrium. pl–posterior surstyle lobe.

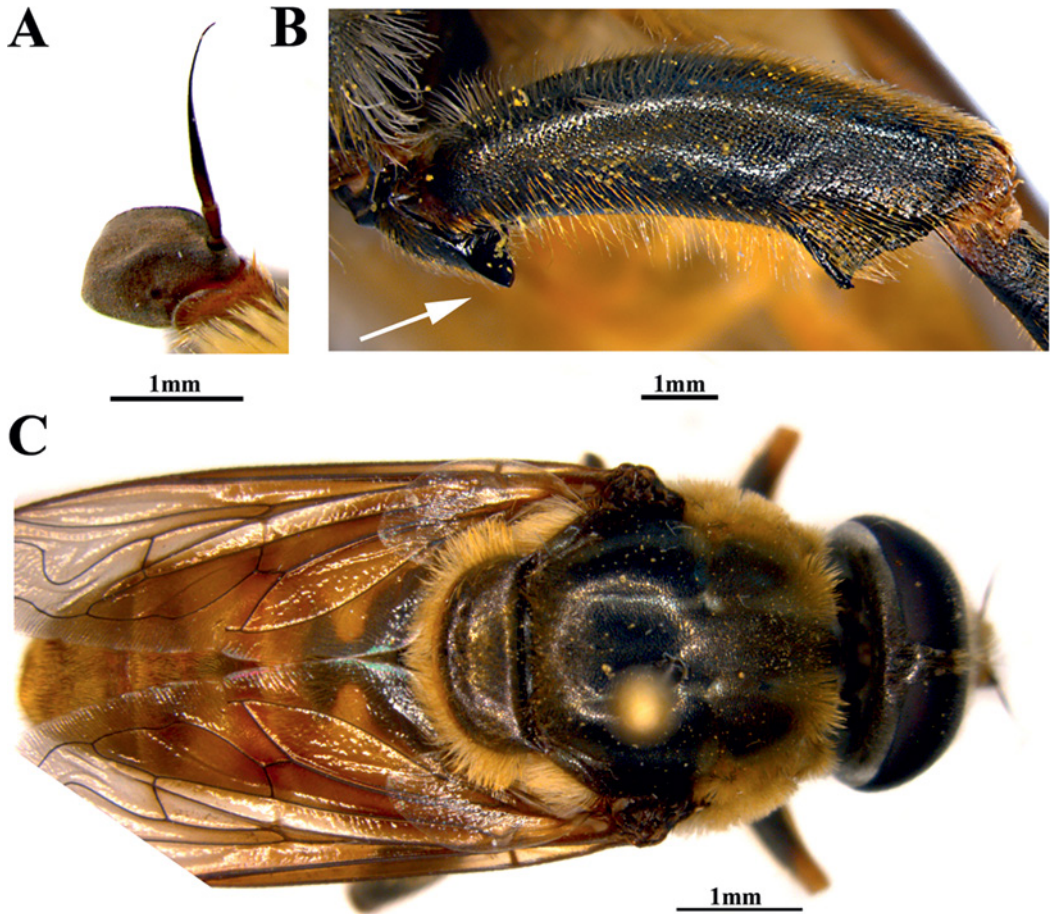


FIGURE 7 Male of *Merodon pruni*. A) basoflagellomere, B) metatrochanter and metafemur (distinct thorn on metatrochanter marked with arrow), C) body. Scale: 1 mm.

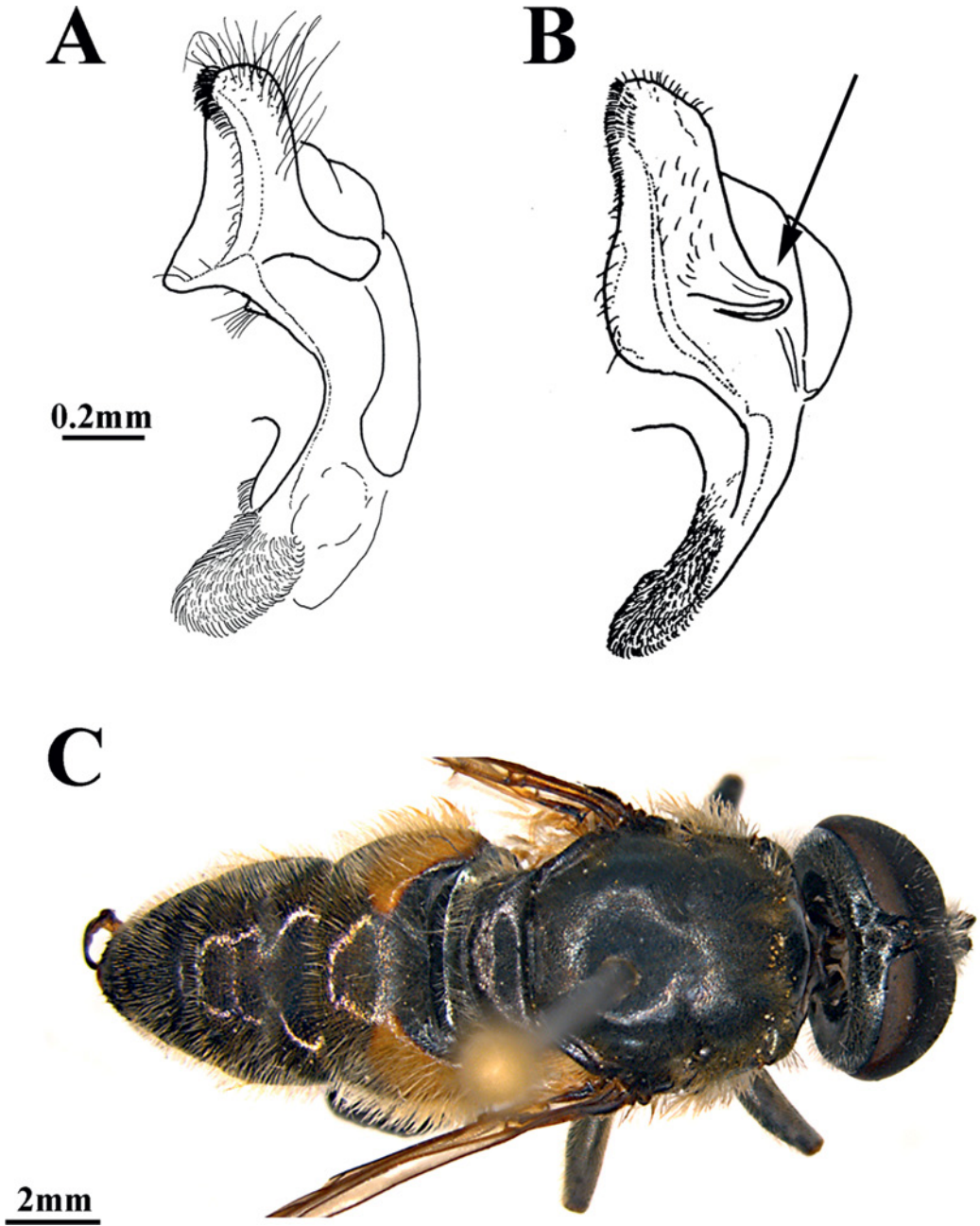


FIGURE 8 Male of *Merodon serrulatus*. A) and B) surstyle lobe (basolateral protrusion on the posterior surstyle lobe marked with arrow), C) body. Scale: A–B) 0.2 mm, C) 2 mm.

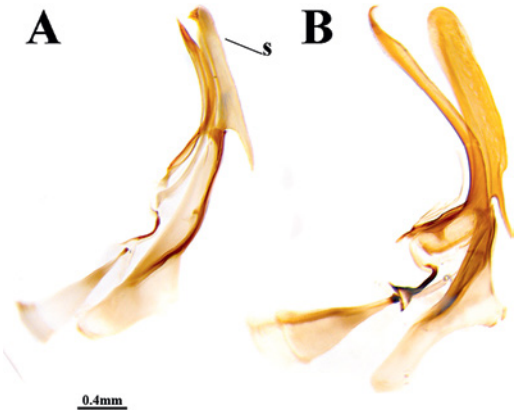


FIGURE 9 Male genitalia, aedeagus. Lateral view, A) *Merodon nigratarsis*, B) *M. avidus*. Scale 0.4 mm. s-lateral sclerite of aedeagus.

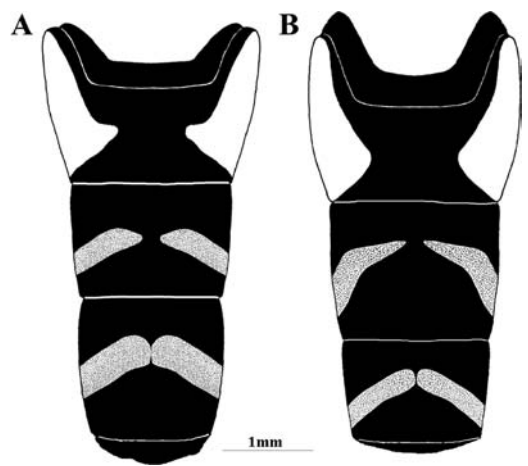


FIGURE 10 Abdomen of male. Dorsal view, A) *Merodon cohurnus* sp. n., B) *Merodon nigratarsis*. Scale: 1 mm.

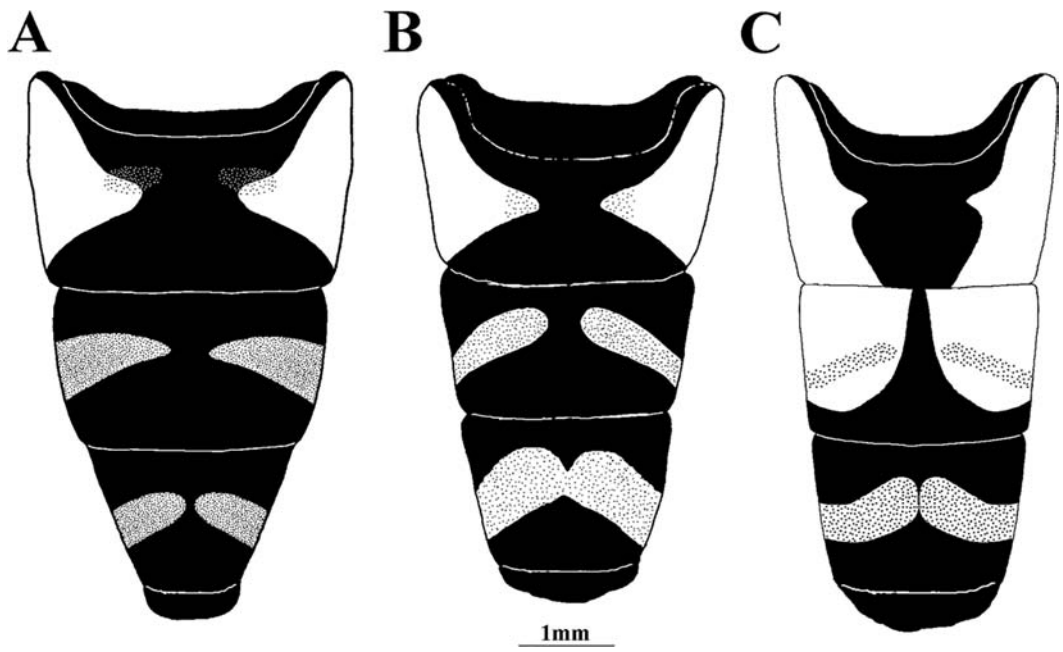


FIGURE 11 Abdomen of male. Dorsal view, A) *Merodon rutitarsis* sp. n., B) *Merodon quadraticus*, C) *Merodon toscanus*. Scale: 1 mm.

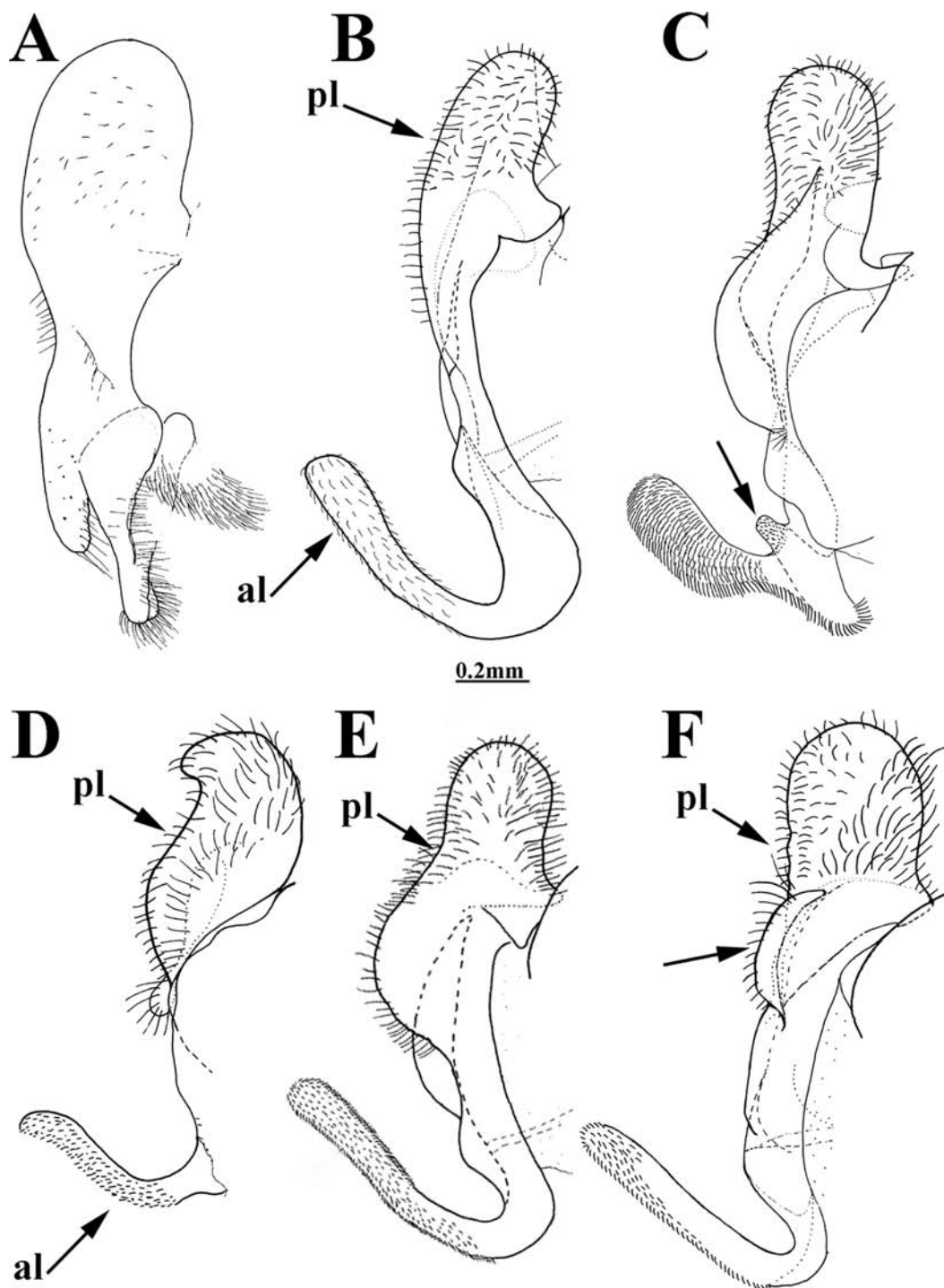


FIGURE 12 Male genitalia. Surstyle lobe. Ventral view, A) *Merodon nitidifrons*, B) *Merodon alagezicus*, C) *Merodon satdagensis* (basal extension marked with arrow), D) *Merodon schachti*, E) *Merodon hakkariensis*, F) *Merodon lucasi* (lamellar structure marked with arrow). Scale: 0.2 mm. al—anterior lobe of surstylus, pl—posterior lobe of surstylus.



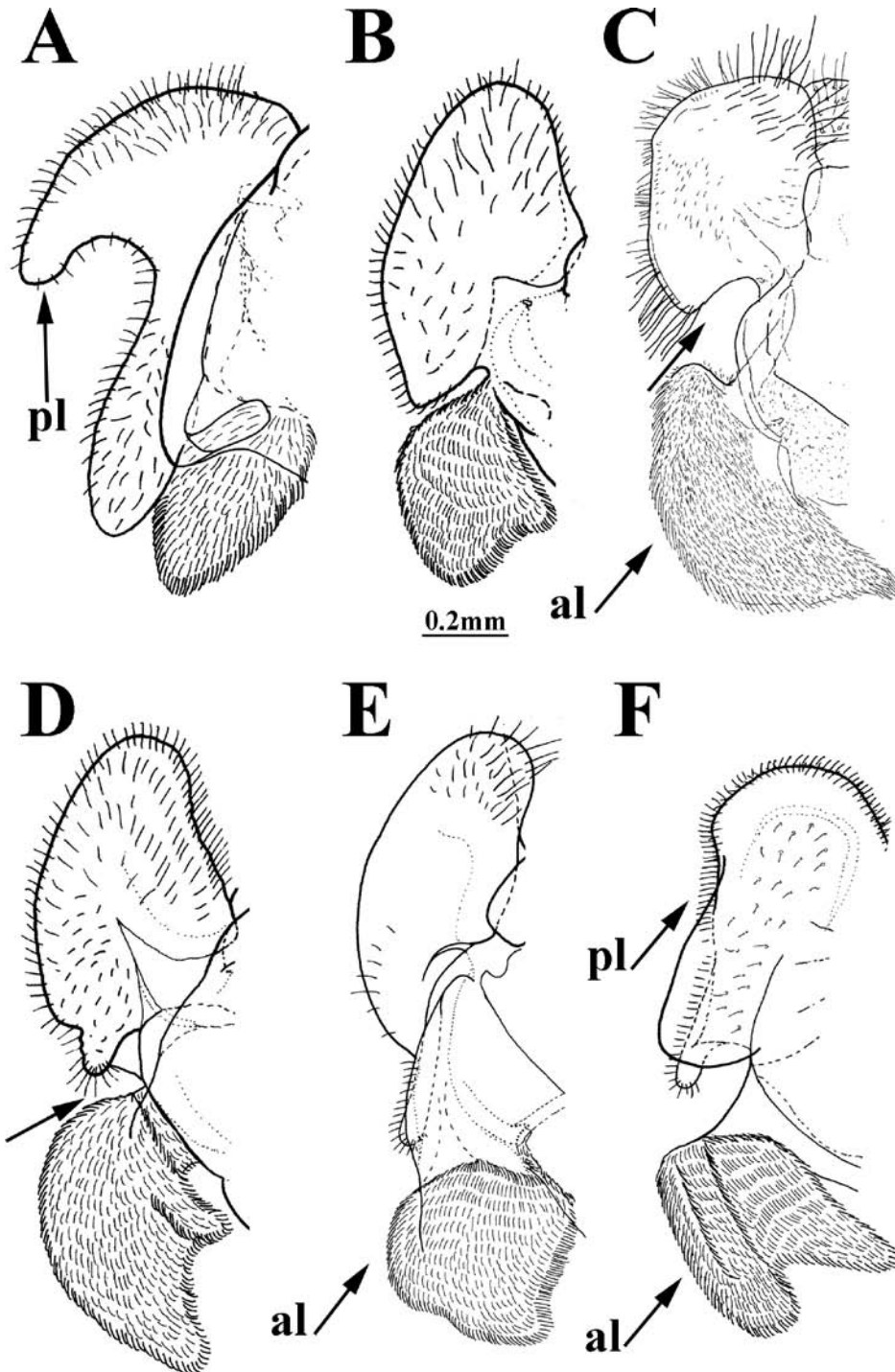


FIGURE 13 Male genitalia. Surstyle lobe. Ventral view, A) *Merodon crassifemoris*, B) *Merodon angustus*, C) *Merodon femoratus* (incision between anterior and posterior lobes of surstylus marked with arrow), D) *Merodon testaceus* (incision between anterior and posterior lobes of surstylus marked with arrow), E) *Merodon quadraticus*, F) *Merodon taniniensis*. Scale: 0.2 mm. al—anterior lobe of surstylus, pl—posterior lobe of surstylus.

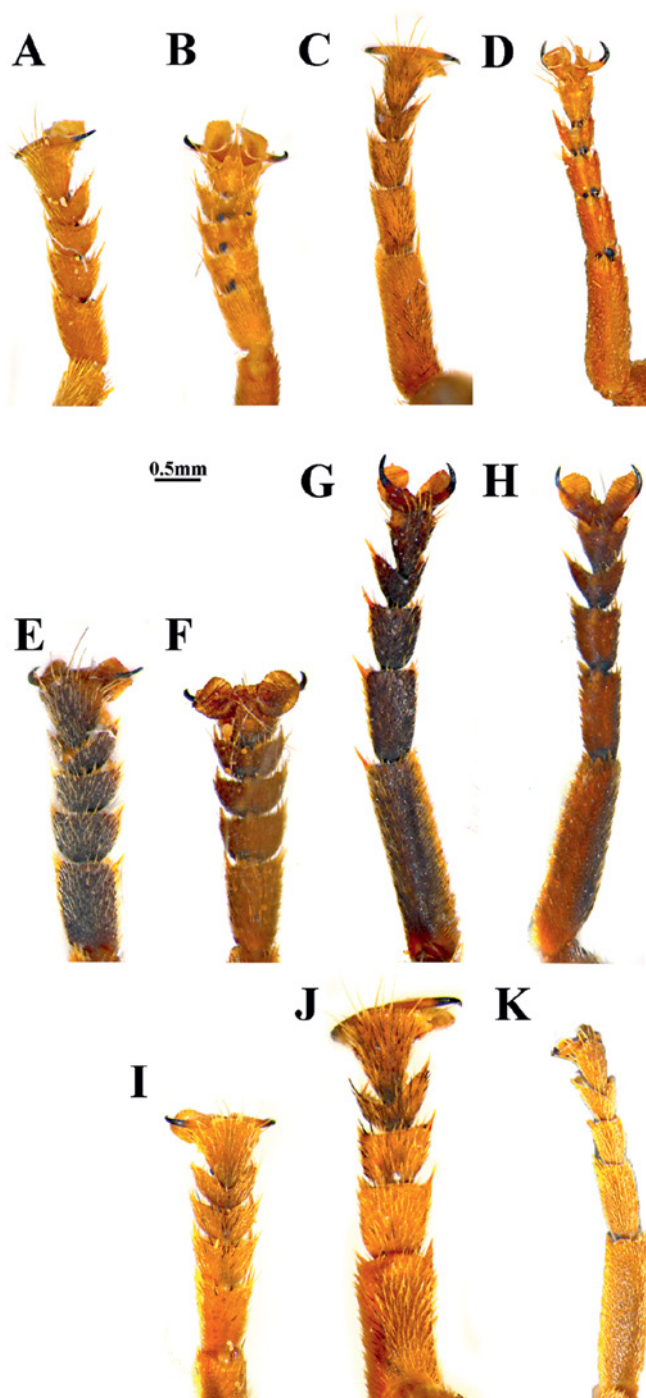


FIGURE 14 Tarsomeres of male. A) *Merodon avidus*, protarsus, dorsal view, B) *Merodon avidus*, protarsus, ventral view, C) *Merodon avidus*, metatarsus, dorsal view, D) *Merodon avidus*, metatarsus, ventral view, E) *Merodon nigratarsis*, protarsus, dorsal view, F) *Merodon nigratarsis*, protarsus, ventral view, G) *Merodon nigratarsis*, metatarsus, dorsal view, H) *Merodon nigratarsis*, metatarsus, ventral view, I) *Merodon femoratus*, protarsus, dorsal view, J) *Merodon femoratus*, metatarsus, dorsal view, K) *Merodon rutatarsis* sp. n., metatarsus, dorsal view. Scale: 0.5 mm.

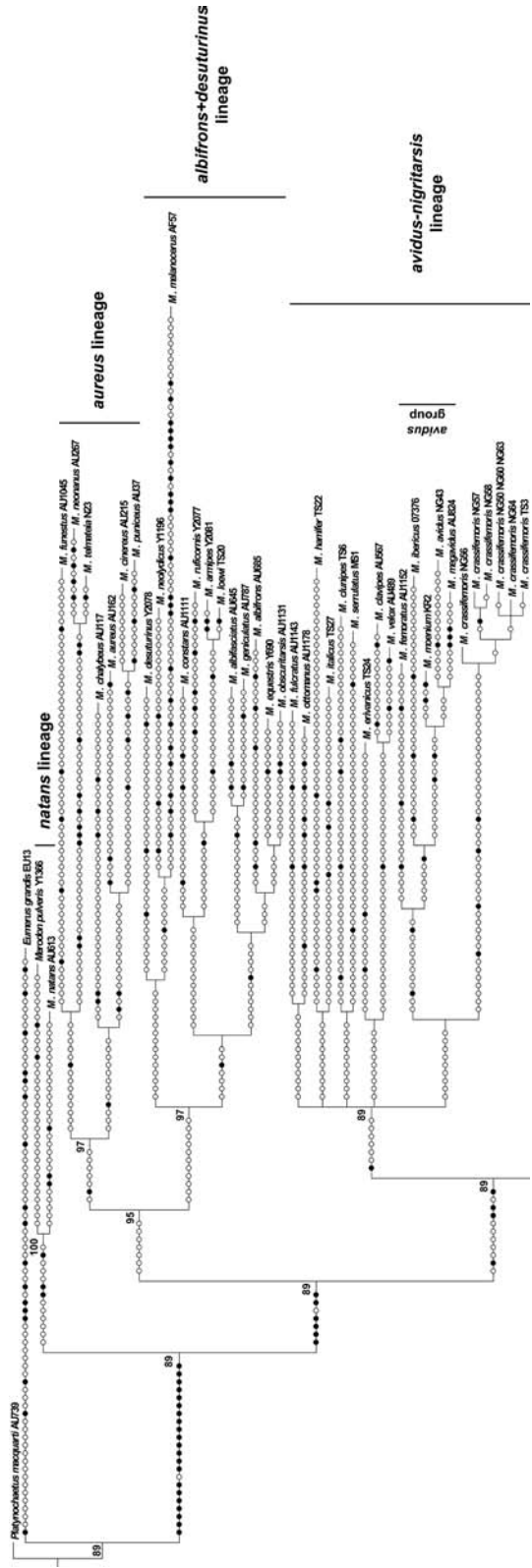


FIGURE 15A AND 15B Strict consensus tree based on 896 equally parsimonious trees from analysis of combined 3' and 5' fragments of the COI gene. Length 2169 steps, Consistency index (CI) 32, Retention index (RI) 71. Filled circles represent non-homoplasious changes and open circles are homoplasious changes. Bootstrap support values are depicted near nodes ( $\geq 50$ ). Numbers and letters after the species name referred to the DNA labcode IDs.

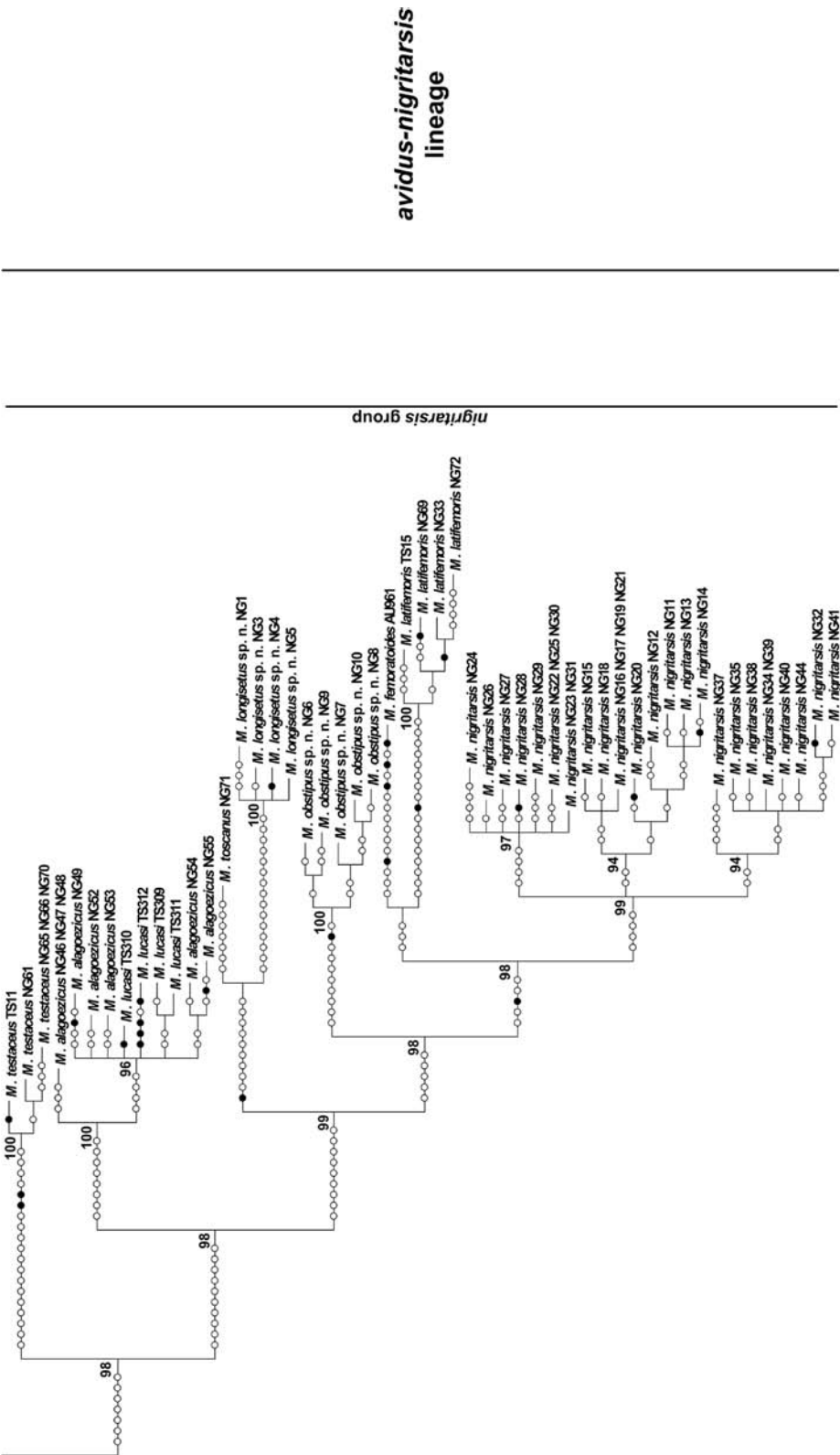


FIGURE 15A AND 15B (cont.)

codes NG46-48) and the second consisted of 5 individuals *M. alagozeicus* (specimens with codes NG49, NG52-55) and 4 individuals *M. lucasi* (specimens with codes TS309-312), all collected in Turkey. Furthermore, individuals that belong to *M. nigratarsis* species showed three genetic clusters on COI gene trees: one with samples collected in Spain (specimens with codes NG22-31), the second with samples collected in Turkey (specimens with codes NG32, NG34-35, NG37-41 and NG44) and the third with samples collected in Serbia and Montenegro (specimens with codes NG11-21).

Species delineation using GMYC was consistent across the different priors used: Yule, Constant Coalescent and Relaxed Clock, but using Relaxed Clock did not reach convergence even with an extension of the number of MCMCs, so this prior was excluded from further analyses. For both, Yule and Constant Coalescent priors, the number of maximum-likelihood clusters was 11 (supplementary fig. S5A), while the number of ML entities was 48 due to the fact that some species were represented only by one sequence. GMYC confidently delineates the following species: *M. latifemoris*, *M. obstipus* sp. n., *M. femoratooides*, *M. longisetus* sp. n., *M. toscanus*, *M. testaceus* and *M. crassifemoris* (outside of *M. nigratarsis* group), but not *M. alagozeicus*, *M. lucasi* and *M. nigratarsis* (supplementary fig. S5B). For these species, multiple candidate nodes with possible threshold positions were observed, indicating that we might be dealing with more than one species within these clusters. For species *M. alagozeicus* and *M. lucasi*, similar cluster differentiation was observed as on ML, BI and MP trees, where for cluster of *M. alagozeicus* individuals collected on Samos Island in Greece the observed threshold was 0.68, while for cluster of individuals of *M. alagozeicus* and *M. lucasi* collected in Turkey, multiple candidate nodes were detected indicating two species within this cluster. For

*M. nigratarsis* multiple candidate nodes were also detected indicating we might be dealing with 3 species/subspecies within this cluster, congruent with clustering observed in MP, ML and BI trees.

## Discussion

### *The position of M. nigratarsis and M. avidus groups into Merodon avidus-nigratarsis lineage*

Although many recent taxonomic papers which dealt with the genus *Merodon* have studied different groups of species (Vujić et al., 2012, 2013, 2015; Ačanski et al., 2016a; Šašić et al., 2016; Veselić et al., 2017; Kočiš Tubić et al., 2018; Radenković et al., 2018a), there is still an apparent need for a subgeneric classification and resolving the taxonomic status of some species and groups.

Recently Šašić et al. (2016) provided a system of four ranks of classification of the genus *Merodon* based on morphological differentiation and previous results of Mengual et al. (2006) that also included molecular data. The first level constitutes four monophyletic clades, including the *M. avidus* (*nigratarsis*) clade, while the second presents morphologically defined species groups within clades. Previously, Vujić et al. (2012) recognized two sister groups *albifrons* and *desuturinus* as one clade, resolved here as well. Later on, Radenković et al. (2018b) based on COI data, besides the three previously established lineages, *albifrons+desuturinus*, *aureus* (sensu lato) and *avidus-nigratarsis*, recognized one more lineage, named *natans*, that is in congruence with here produced trees using both mitochondrial COI and nuclear 28S rRNA genes. Here we examined the systematic position and composition of the groups within the *M. avidus-nigratarsis* lineage. Phylogenetic analyses based on the combined sequences of two genes (COI and 28S rRNA) resolved the

*M. nigratarsis* and *M. avidus* groups as branches within one common lineage.

Furthermore, both groups comprise the same lineage in COI gene trees, including larger number of individuals and longer COI gene sequence. Regarding the *M. nigratarsis* group, data from the present study agree broadly with those of Vujić et al. (2013). The concept of this group is here redefined, now consisting of the previously identified species (Vujić et al., 2013) and here described new species, with exclusion of *M. crassifemoris* species. The excluded taxon was clearly separated from the other members of the studied group based on MP, ML and BI trees generated from both molecular datasets, as well by lack of subapical thorns on ventral margin of hypandrium (apomorphic morphological character of the *M. nigratarsis* group) and unique hook-like shape of posterior surstyle lobe that additionally strengthened this exception. *Merodon avidus* group of species is defined here by molecular and morphological data (clearly different by yellow tarsi contrary to *M. nigratarsis* group characterized by dorsally dark tarsi). It includes besides, previously defined *M. avidus* complex (Popović et al., 2015; Ačanski et al., 2016a), the new species *Merodon rutitarsis* sp. n. and also *M. femoratus*. The present study establishes a clear distinction of 12 separate branches within the *Merodon avidus-nigratarsis* lineage based on phylogenetic analyses and supported by apomorphic morphological characters, namely 9 groups: *M. aberrans*, *M. aurifer*, *M. avidus*, *M. clavipes*, *M. fulcratus*, *M. italicus*, *M. nigratarsis*, *M. pruni* and *M. serrulatus*, and three species with separate position (*M. clunipes*, *M. crassifemoris*, and *M. ottomanus*). Besides the above mentioned groups, the *avidus-nigratarsis* lineage includes one additional group named *M. tarsatus* and two species *M. eumerusi* Vujić, Radenković & Likov, 2019 and *M. murinus* Sack, 1913, without obtained molecular data, distributed in the Middle East (Asia) (Vujić et al., 2019).

### *Species delimitation based on COI data*

The in depth analysis, focusing on species delimitation in the *M. nigratarsis* group, employed COI gene sequences, which is proved to be genetic marker with an adequate resolution for species delimitation in genus *Merodon* and other genera in Syrphidae family (Masseti et al., 2006; Mengual et al., 2006; Marcos-García et al., 2011; Vujić et al., 2012, 2013; Nedeljković et al., 2015; Popović et al., 2015; Šašić et al., 2016; Chroni et al., 2017). Moreover, analyses of the COI gene has proven to be a reliable tool for revealing cryptic taxa in the genus *Merodon* (Vujić et al., 2012; Šašić et al., 2016; Radenković et al., 2018a). Analyses based on COI gene sequences included multiple specimens per species within the *M. nigratarsis* group (except for *M. femoratooides* and *M. toscanus* where only one individual per species was available) and those of the longest and of the best quality 3' and 5' fragment COI gene sequences (in order to yield the maximum information for species delimitation; after processing total length of 1371 nucleotides).

MP, ML and BI analyses based on the COI gene sequences allowed us to clearly separate 7 species: *M. nigratarsis*, *M. obstipus* sp. n., *M. femoratooides*, *M. latifemoris*, *M. toscanus*, *M. longisetus* sp. n., and *M. testaceus*, while species *M. alagoezicus* and *M. lucasi* were not clearly separated, and shown to be clustered together (fig. 15, supplementary figs. S3 and S4). Applied cluster analyses allowed us to confirm the exclusion of *M. crassifemoris* from the *M. nigratarsis* group, and to conclude that this species belongs to the *avidus-nigratarsis* lineage as a separate genetic entity. Morphologically defined species *M. alagoezicus* and *M. lucasi* clustered together in all gene trees, and to try to resolve their position we further used Generalized Mixed Yule Coalescent method for additional identification of putative species within the *M. nigratarsis* group. The GMYC, as one of the most popular coalescent-based species delimitation methods, is designed for

single-locus data (Fujisawa & Barraclough, 2013) and has proven to be a powerful tool for evaluating species limits (Birky et al., 2011; Michonneau, 2015) and therefore should be added to integrative taxonomy studies. For our dataset, GMYC additionally confirmed the following species: *M. latifemoris*, *M. obstipus* sp. n., *M. femoratooides*, *M. longisetus* sp. n., *M. toscanus*, *M. testaceus* and *M. crassifemoris* (the latter outside of the *M. nigritarsis* group). For species *M. alagoezicus* and *M. lucasi* GMYC analyses showed that we may be dealing with more than one species, even though individuals belonging to these species were mixed in one cluster on constructed gene trees. Inspection of such constructed trees, together with GMYC results, revealed that three specimens morphologically defined as *M. alagoezicus* and all collected on Samos Island in Greece represent a one genetic cluster, while five *M. alagoezicus* specimens and four *M. lucasi* (all collected in Turkey) were clustered together in separate cluster, for which GMYC showed multiple candidate nodes indicating that more than one species belong to this cluster. The low COI divergence between these species in separate geographic region may be explained by retained polymorphism or mitochondrial introgression between the taxa, as was earlier shown to be case for the *Merodon* genus (Ståhls et al., 2009). On the other hand, genetic clustering of COI sequences of *M. alagoezicus* from Samos Island may be consequence of founder effect typical for isolated island populations which were formed by specimens migrating from the continental population. Subsequent genetic drift might led to fixation of one single observed haplotype (all three individuals share the same COI haplotype). In order to clearly understand *M. alagoezicus* and *M. lucasi* species boundaries in Turkey, additional research should be performed, namely distribution of the taxa, their interaction with plants, and inclusion of new genetic/genomic methods. In addition, GMYC

analyses revealed multiple candidate nodes within *M. nigritarsis* species, and three genetic clusters that contained specimens from the following countries and Peninsulas: 1) Spain (Iberian Peninsula); 2) Turkey (Anatolian Peninsula); and 3) Serbia and Montenegro (Balkan Peninsula). Observed genetic differentiation of the COI gene within *M. nigritarsis* may be a consequence of geographical distribution of analyzed individuals and it is possible that we might be dealing with three independent taxa, where speciation is result of geographical isolation and adaptation to different environmental conditions. Nevertheless, it is noteworthy to mention that there are studies where GMYC delivered a higher species number than it is observed by morphology (Esselstyn et al., 2012; Paz & Crawford, 2012; Sauer & Hausdorf, 2012; Talavera et al., 2013). It is shown that GMYC produces more splits when intra- and interspecific pairwise distances are low (Zhang et al., 2013) and this is usually a case in the recently differentiated species lacking a 'barcode gap' (Wiemers & Fiedler, 2007; Dupuis et al., 2012).

### *Diversity and new taxa*

The present study is an additional contribution that illustrates the great diversity of the *Merodon avidus-nigritarsis* lineage, and especially the *M. nigritarsis* and *M. avidus* groups. The species richness of the *M. nigritarsis* group (18 species) is one of the highest in comparison with other recognized species groups of the genus *Merodon*: the *M. ruficornis* group with 18 (Vujić et al., 2012), the *M. nanus* group with six (Kočiš Tubić et al., 2018), and the *M. constans* group with 14 members (Vujić et al., in prep.), with exception of the *M. aureus* group which contains an extremely high number of 39 detected species (Veselić et al., 2017). From an initial number of only two species (Hurkmans, 1993), through the 15 species later presented in Vujić et al. (2013), our present results increased the number of taxa

to 18, including three new species from the *M. nigratarsis* group. Additionally, in the present study we described one new species from the *M. avidus* group, *Merodon rutitarsis* sp. n., thus the recent number of this species group is six.

Among newly collected and revised material, based on morphological characteristics, especially male genitalia, four new species from the *M. nigratarsis* and *M. avidus* groups have been discovered and described. *Merodon obstipus* sp. n. is related to *M. femoratoides*, based on both morphological and molecular data. *Merodon longisetus* sp. n. is a sister species to *M. toscanus*, with morphological similarities, but quite distinct with respect to the shape of male genitalia. *Merodon cohurnus* sp. n. has male genitalia structures that are most similar to *M. longisetus* sp. n., while *M. rutitarsis* sp. n. shows some morphological similarities (yellow tarsi) with members of *M. avidus* complex. In contrast, it is hard to distinguish females, and their identification will be subject to future studies using a combined integrative approach.

### Distribution

According to Myers et al. (2000), the Mediterranean Basin was identified as a biodiversity hotspot, with a high concentration of endemic species. According to Speight (2018) *Merodon* is the largest genus of European hoverflies and has predominantly a Mediterranean distribution (Ståhls et al., 2016), with the Eastern Mediterranean as the main centre of diversification of this genus (Vujić et al., 2011). These areas connect different biogeographic regions between Asia, Africa and Europe, providing passages for species spread (Vujić et al., 2015). Iberian (Marcos-Garcia et al., 2007), Balkan (Kaloveloni et al., 2015) and Anatolian Peninsulas (Vujić et al., 2011), including the Greek islands (Vujić et al., 2007), have the largest number of *Merodon* species. The higher diversity in these areas could be a result of typical Mediterranean climatic conditions (Çelik et al., 2004), and an evolutionary result

of the high diversity of geophytes in the Mediterranean flora, as *Merodon* species larval development is closely related to bulbous plants (Kaloveloni et al., 2015) mainly of the families Liliaceae, Amaryllidaceae, and Hyacinthaceae (Ståhls et al., 2016; Preradović et al., 2018). The present study represents an additional contribution to the already reported high diversity of the *M. avidus* and *M. nigratarsis* groups in Mediterranean region.

*Merodon nigratarsis* species group comprises taxa with a mainly mountainous distribution, mostly on the Balkan, Anatolian, Apennine and Iberian Peninsulas, in central Europe as well as the Middle and Near East. The richest localities with the presence of more than 8 different species are mountains in the western and eastern parts of Anatolian Peninsula (fig. 16). Anatolia is a bridge between Asia and Europe, and was an important refugium during the Quaternary ice ages (Çiplak, 2003). The widest distribution within *M. nigratarsis* group is shown by the species *M. nigratarsis*, occurring throughout Central Europe, the European part of Mediterranean basin and areas surrounding the Black and Caspian Sea.

Members of *M. avidus* group are distributed all across Europe, mainly in the central and southern parts, and less in the Near and Middle East and in North Africa (Algeria and Libya). They are most abundant in the S–SW Mediterranean and in Morocco (fig. 17). *Merodon avidus* is the most widely distributed species in this group, mostly in Europe, and in areas surrounding the Black and Caspian Seas, with occurrence in Morocco and Libya as well.

Out of the 18 species that are members of the *M. nigratarsis* group, 12 are endemics, which illustrates the exceptionally high level of endemism within this species group (66%). Most of these species occur in mountainous regions of the Balkan and Anatolian Peninsulas, on larger islands in the Eastern Mediterranean and in Asia Minor and the Middle East.



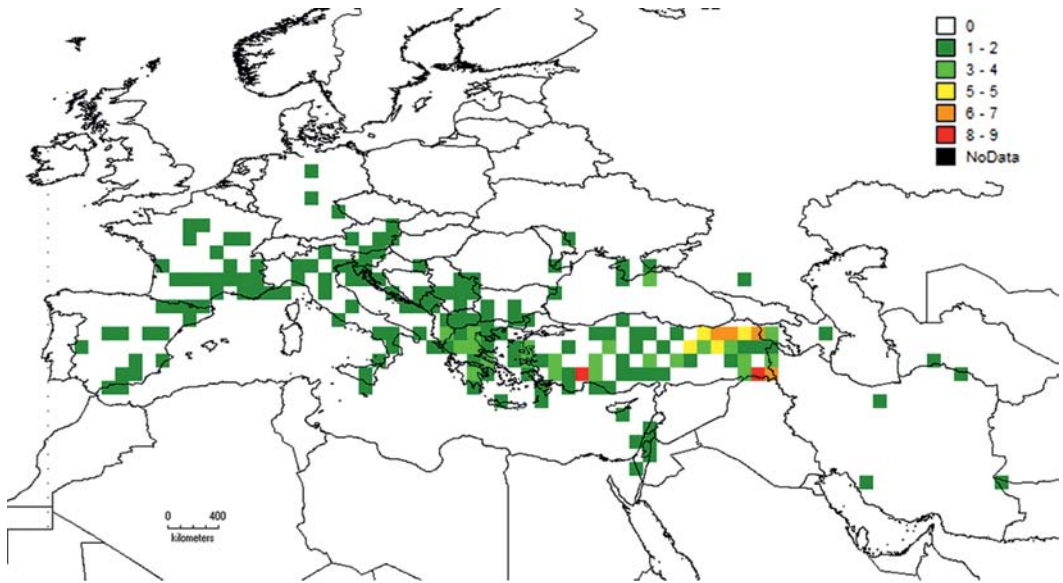


FIGURE 16 Species richness map of *Merodon nigritarsis* species group.

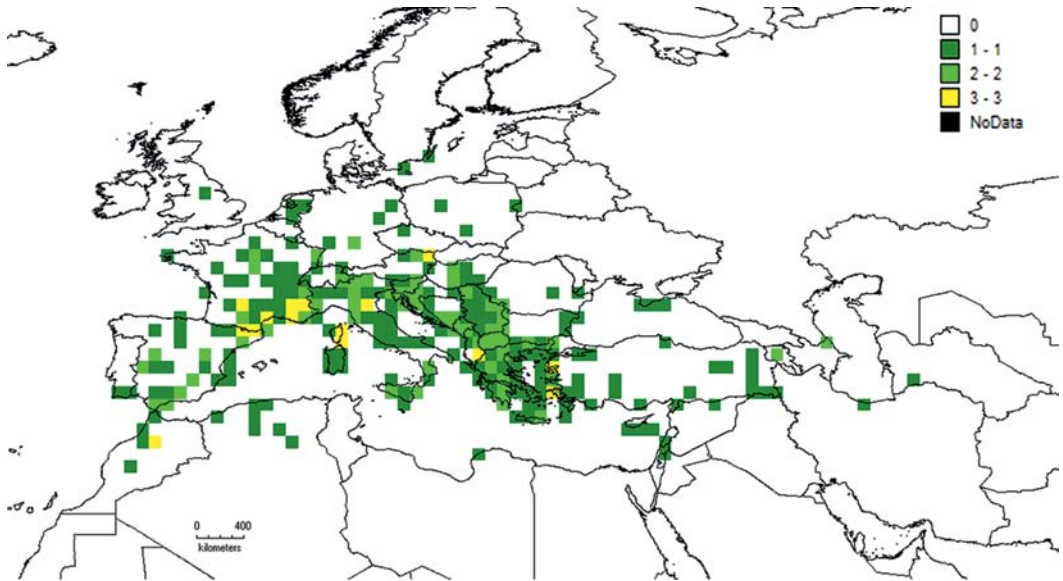


FIGURE 17 Species richness map of *Merodon avidus* species group.

Based on the limited distribution of the four new described species, these are considered to be endemic to the Anatolian Peninsula (*M. longisetus* sp. n. and *M. obstipus* sp. n.) and the Middle East (*M. rutitarsis* sp. n. and *M. cohurnus* sp. n.), respectively. *Merodon rutitarsis* sp. n. is a species found at the lowest elevation

(58 m), while other species from the *Merodon avidus-nigritarsis* lineage reach up to 3000 m.

Many recent taxonomic publications have shown a large number of newly described taxa belonging to this genus and primarily in the Middle East and SE Mediterranean (Radenković et al., 2011; Vujić et al., 2011, 2013,

2015, 2018, 2019; Ricarte et al., 2012; Ačanski et al., 2016a; Šašić et al., 2016). These findings serve as proof that areas of the Balkan and Anatolian Peninsulas, as well as the surrounding Caucasus, represent one of the most important glacial refugia of the Palaearctic region during the last glaciations (Ačanski et al., 2016b). The significance of the eastern Mediterranean region as a hotspot for hoverflies is reaffirmed by the results presented in this paper.

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## Supplementary material

Supplementary material is available online at: <https://doi.org/10.6084/m9.figshare.9741323>

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## APPENDIX

## Taxonomy

*Merodon nigratarsis* group

**Diagnosis.** Relatively large (11–17 mm) species with white microtrichose vittae on black scutum and white microtrichose fasciae on orange-brown (in females orange-black) terga (as on figs. 21, 26, 10, 11); at least tergum 2 with a pair of reddish–orange maculae. Scutum covered with erect, yellow pile. Pile on metasternum erect, as long as those on metacoxa. Abdomen elongate, narrow and tapering, always longer than scutum and scutellum together (as on figs. 3A, C–D, 4A, 7C). Posterior part of mesocoxa without long pile. Tarsi dark brown/black dorsally and orange ventrally. Basoflagellomere about 1.5–2 times as long as wide (fig. 18). Legs without spinae or other protuberances (fig. 20A–D). Male genitalia: anterior surstyle lobe (as on figs. 13, 35: al) more or less of rhomboid shape, covered with dense short pile, except in the *alagoezicus* subgroup where the anterior surstyle lobe is transformed into a narrow, elongate, strongly curved projection (as on fig. 12: al); posterior surstyle lobe with oval apical part (as on figs. 12–13, 35: pl) usually longer than the anterior surstyle lobe; cercus rectangular, without prominences (as on figs. 23A, 27A: c). Hypandrium narrow, elongate and sickle-shaped (as on figs. 24A, C, 30A, C), with a pair of subapical thorns on ventral margin directed backwards (as on fig. 24: th), and often with a pair of lateral projections near the base (as on fig. 30A, C: lp) and well-developed lingula (as on fig. 24A–D: l); apical part of lateral sclerite of aedeagus tapering (fig. 9A: s).

*Merodon longisetus* Vujić, Radenković et Likov sp. n.

*Merodon* aff. *nigratarsis* in Vujić et al., 2016

**Type material.** Holotype. Male. Greece: Chios, Armolia valley, 38.2833N, 26.0333E, 23.ix.2009, leg. Vujić (FSUNS). Paratypes. Greece, one male, Chios, Armolia valley, 38.2833N, 26.05E, 20.v.2003, leg.

Taylor (NML) (det. C.J. Palmer as *Merodon toscanus*); one male, Chios, Armolia valley, 38.2833N, 26.0333E, 16.v.2003, leg. Taylor (NML) (det. C.J. Palmer as *Merodon toscanus*); one male, Chios, Armolia valley, 38.2863N, 26.0494E, 16.v.2003, leg. M.J. Taylor (NML). Turkey, three male, Isparta, eastern campus of Süleyman Demirel University, 37.8405N, 30.5380E, 13.ix.2014, leg. Vujić (FSUNS); two male, two female, Isparta, Keçiborlu, Gülköy, 1502 m a.s.l., 37.9066N, 30.1758E, 22.vi.2015, leg. Vujić, Hayat, Uzal, Gök (EMIT); two male, Isparta, Keçiborlu, between Kavak and Kaplanlı, 1500m a.s.l., 37.9269N, 30.1908E, 22.vi.2015, leg. Vujić, Hayat, Uzal, Gök (EMIT); two male, Isparta, between Keçiborlu and Yeniköy, 1740 m, 37.8764N, 30.2075E, 8.vii.2015, leg. Vujić, Hayat, Demirözer, Uzal, Gök (EMIT); three male, one female, Isparta, Gönen, Güneykent road, 1033 m, 37.95927N, 30.483611E, 01.ix.2015, leg. Hayat, Demirözer, Gök, Uzal (EMIT); two male, Isparta, Senirkent, Kabaca-Yalvaç road, 950 m, 38.19825N, 30.722444E, 01.ix.2015, leg. Hayat, Demirözer, Gök, Uzal (EMIT); three male, Bozdağ mountain, Sart to Bozdağ 1, 994 m a.s.l., 38.4030N, 28.0805E, 16.ix.2013, leg. Vujić (FSUNS).

**Diagnosis.** Large species (13–15 mm), with bronze lustre; black scutum with four whitish microtrichose vittae, and covered with erect, yellowish pile, except some black ones at the wing basis; tapering black abdomen with pairs of microtrichose fasciae on terga 3 and 4; at least tergum 2 with a pair of lateral orange maculae (fig. 21); metafemur moderately swollen and curved, with long yellow pile postero- and anteroventrally, pile about as half of width of metafemur (fig. 20A); tarsi dark brown dorsally and orange ventrally; male genitalia: anterior surstyle lobe rhomboid shape, and 2.5 times shorter than posterior surstyle lobe (fig. 23A: al). *Merodon longisetus* sp. n. belongs to the *M. nigratarsis* group and closely related to *M. toscanus*. They can be separate based on the structure of male genitalia: anterior surstyle lobe in *M. toscanus* is about long as wide (fig. 23C: al), while in *M. longisetus* sp. n. is about two times wider than long

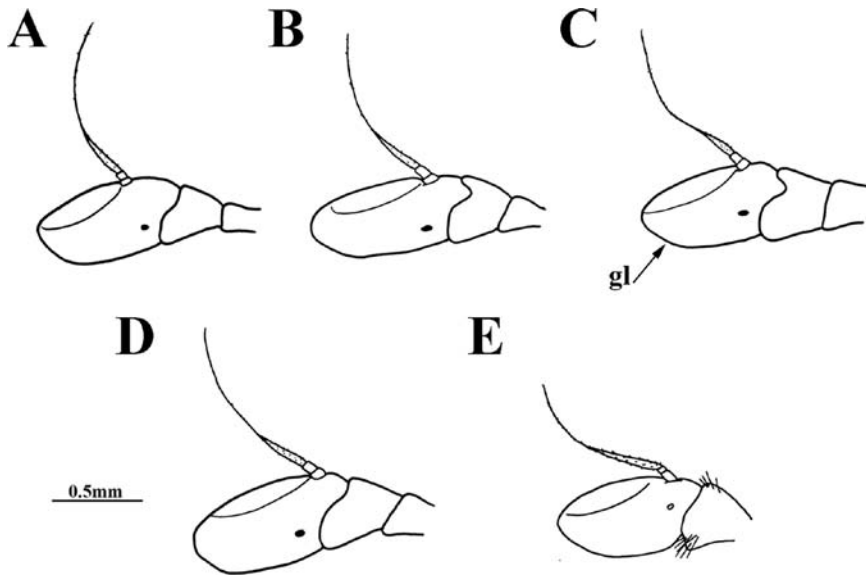


FIGURE 18 Antenna. Lateral view, A) *Merodon longisetus* sp. n., male, B) *Merodon longisetus* sp. n., female, C) *Merodon obstipus* sp. n., male, D) *Merodon obstipus* sp. n., female, E) *Merodon cohurnus* sp. n., male. Scale: 0.5 mm. gl—basoflagellomere.

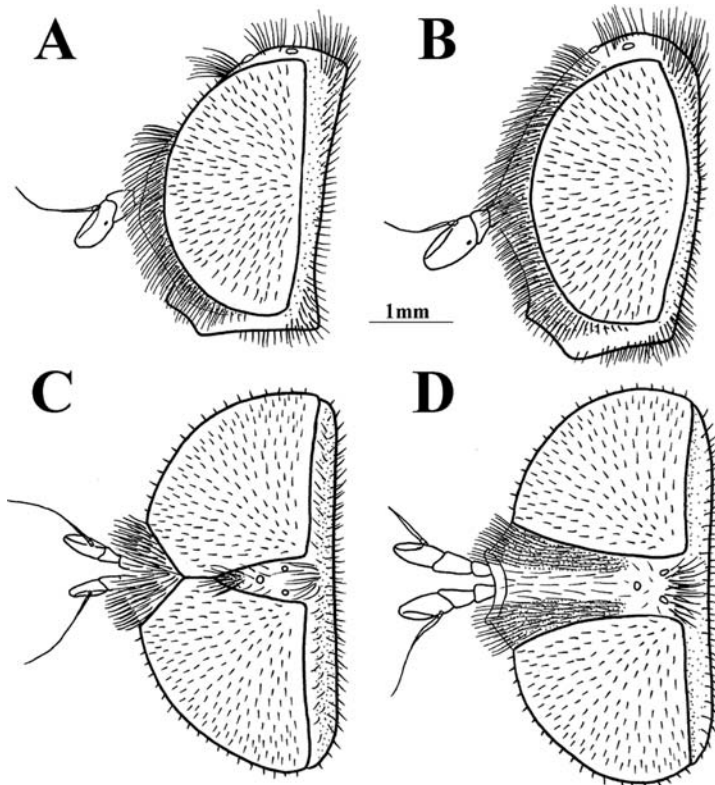


FIGURE 19 Head of *Merodon longisetus* sp. n. A) male, lateral view, B) female, lateral view, C) male, dorsal view; D) female, dorsal view. Scale: 1 mm.



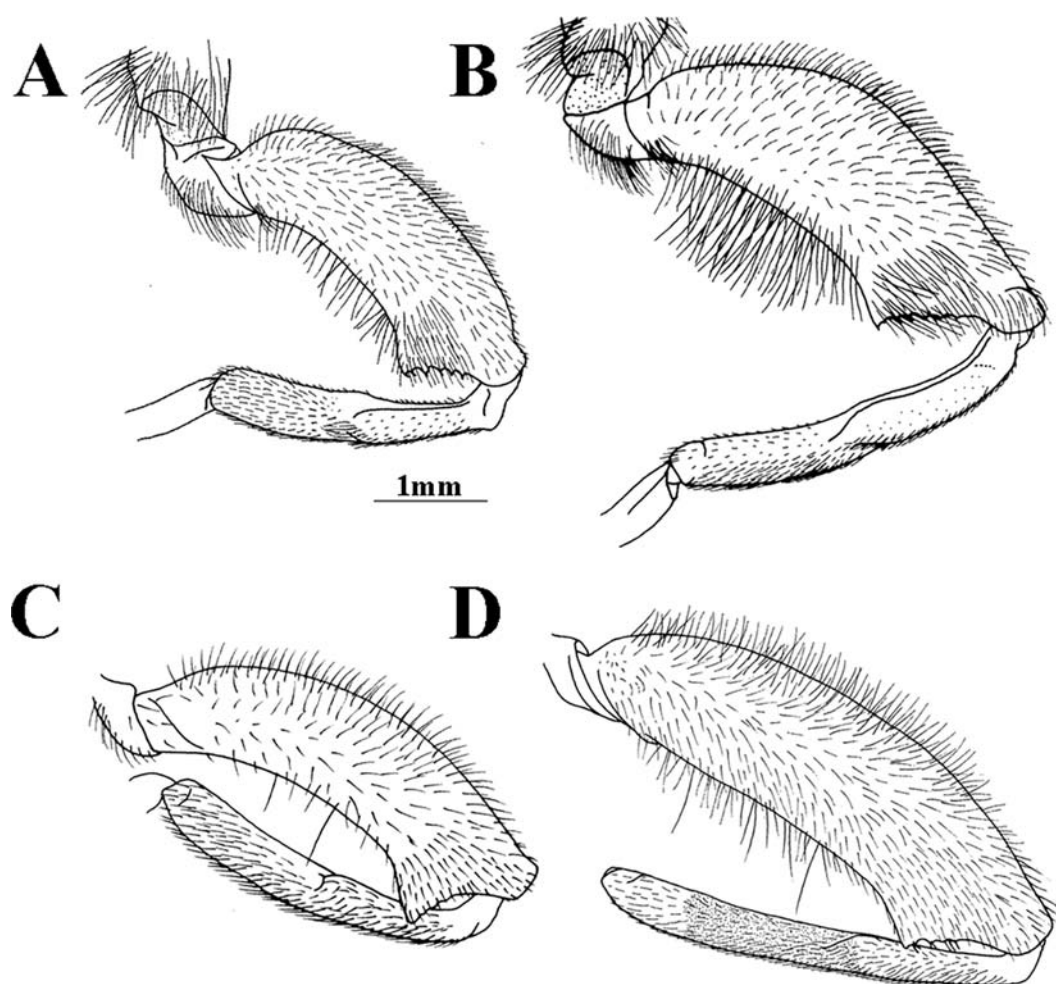


FIGURE 20 Metaleg of male (without metatarsi). Lateral view, A) *Merodon longisetus* sp. n., B) *Merodon obstipus* sp. n., C) *Merodon cohurnus* sp. n., D) *Merodon rutitarsis* sp. n. Scale: 1 mm.

(fig. 23A: al); posterior and anterior surstyle lobe separated by deeper incision in *M. longisetus* sp. n. (fig. 23A: i); hypandrium with longer lingula in *M. longisetus* sp. n., pointed upward (fig. 24A–B: l).

**Distribution.** *Merodon longisetus* sp. n. belongs to Eastern Mediterranean endemic species, with type locality on Aegean island Chios, and distributed in south-eastern part of Anatolian Peninsula, recorded on Bozdağ Mountain, on Isparta plateau and on high mountains around (fig. 1).

**Description. Male. Head** (figs 18A, 19A, C). Antennae reddish/dark brown; basoflagellomere

about 1.5 times as long as wide, and about 1.8 times as long as the pedicel, with acute apex; arista dark brown and thickened, covered with dense microtrichia; arista about 1.5 times as long as basoflagellomere (fig. 18A); face and frons black, covered with dense whitish pile, and silver microtrichia except for shiny ventral part of face shiny; vertical triangle isosceles, shining black, except in front of anterior ocellus with whitish microtrichia, pilosity long, pale yellow-whitish (in some cases mixed with few black pile on the ocellar triangle); ocellar triangle equilateral; eyes covered with dense pile;

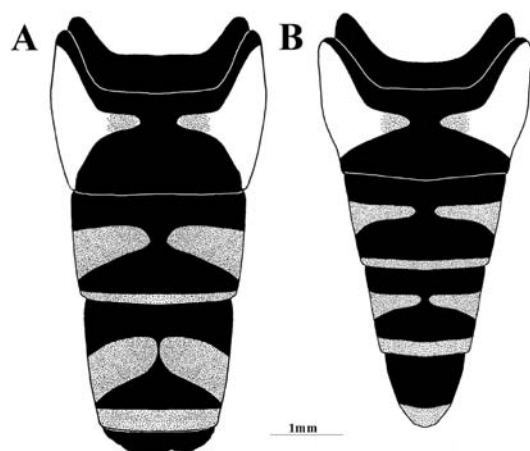


FIGURE 21 Abdomen of *Merodon longisetus* sp. n. Dorsal View, A) male, B) female. Scale: 1 Mm.

eye contiguity about 12 facets long; occiput with whitish–yellow pile, covered with a dense, white microtrichia; vertical triangle: eye contiguity: ocellar triangle = 2 : 1 : 0.8 (fig. 19C).

**Thorax** (fig. 20A). Scutum and scutellum black with bronze lustre, covered with dense, erect, yellow pile; sides of scutum at wing basis with patch of black pile; scutum with four microtrichose vittae, anteriorly connected and posteriorly reaching the scutellum and postalar callus; posterodorsal part of anterior anepisternum, posterior anepisternum (except anteroventral angle), anterior anepimeron, dorsomedial anepimeron, and posterodorsal and anteroventral parts of katepisternum with long, dense pale yellow pile and greyish microtrichia; wings covered with microtrichia (except basal parts of cells R, BM and CuP sparsely microtrichose); wing veins brown; calypteres pale yellow; halteres yellow, in some cases with dark brown knob; legs without spinae or other protuberances; legs mostly black, except pale yellow apex of pro- and mesofemora (but sometimes apex of metafemora also), basal half of pro- and mesotibiae, basal 1/3 of metatibiae, and all tarsi ventrally; pile on legs pale yellow; metafemur moderately broad and curved, about as 3 times longer than wide; long pile on postero- and anteroventral surface yellow and sparse, and about as

half of width of metafemur, but much longer than the pile on the dorsal surface (fig. 20A).

**Abdomen** (figs. 21A, 22A). Tapering, about 1.2 times longer than mesonotum; terga dark, except for a pair of yellow–orange, triangular, lateral maculae on tergum 2; terga 3 and 4 each with pairs of white microtrichose, wide, oblique fasciae (on tergum 2 a pair of smaller microtrichose spot, weaker or stronger developed); additionally terga 3 and 4 with microtrichose fasciae at posterior margins of terga (fig. 21A); pile on terga yellow; sterna light brown, translucent, covered with long whitish/yellow pile; sternum 4 with large posteromedial notch, reaching to the 2/3 of the length of sternum (fig. 22A: cf) and rectangular posterolateral corner (fig. 22A: p).

**Male genitalia** (figs 23A–B, 24A–B). Anterior surstyle lobe rhomboid shape, about 2 times wider than long, covered with dense, short pile (fig. 23A: al); posterior surstyle lobe oval (fig. 23A: pl); cercus rectangular (fig. 23A: c); hypandrium sickle-shaped, without lateral projections; lingula narrow and long (fig. 24A–B: l).

**Female** (figs. 18B, 19B, D, 21B). Similar to the male except for normal sexual dimorphism and for the following characteristics: basoflagellomere with rounded tip, about 2 times longer than wide (fig. 18B); frons with wide, microtrichose vittae along eye margins (fig. 19D); ocellar triangle covered with dense black pile; tergum 2 with yellow pile, terga 3 and 4 with mixed whitish/yellow and black pile; microtrichose fasciae on terga 3 and 4 narrower (fig. 21B); sterna 2 and 3 light brown, sternum 4 dark brown; sternum 4 with central longitudinal dent/suture.

**Etymology.** The name *longisetus* is derived from Latin words *longus* (adjective) and *setus* (meaning hair/pile), referring to long pile on the ventral surface of the metafemur.

**Remarks.** Two specimens previously determined by C.J. Palmer as *Merodon toscanus* from Chios island are included in paratypes. This species was reported under name *M. aff. nigratarsis* in biogeographic analysis of the genus in Eastern Mediterranean (Vujić et al., 2016).

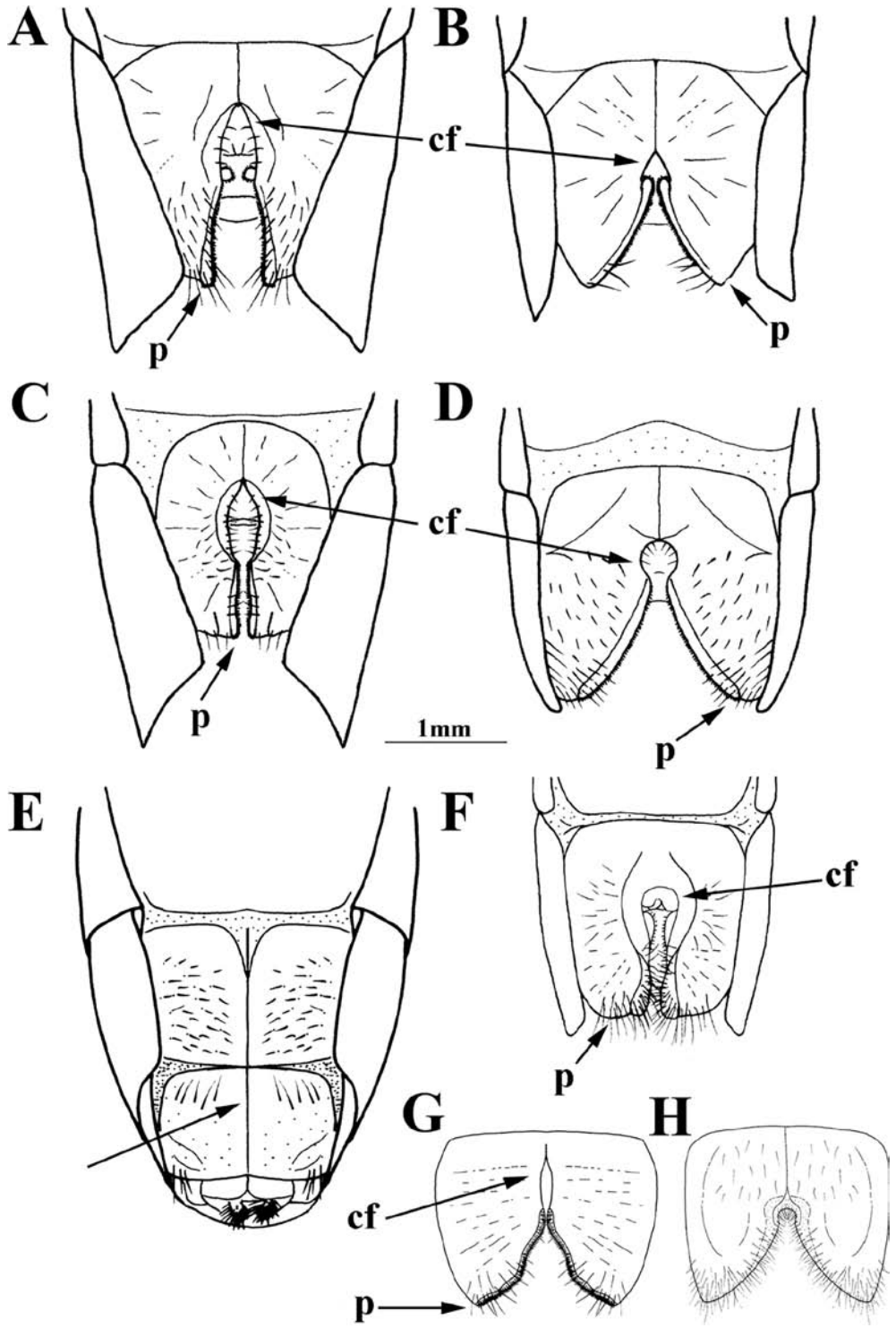


FIGURE 22 Sternum 4. Ventral view, A) *Merodon longisetus* sp. n., male, B) *Merodon nigritarsis*, male, C) *Merodon obstipus* sp. n., male, D) *Merodon femoratooides*, male, E) *Merodon obstipus* sp. n., female (central longitudinal suture marked with arrow), F) *Merodon cohurnus* sp. n., male, G) *Merodon rutitarsis* sp. n., male, H) *Merodon avidus*, male. Scale: 1 mm. cf—central notch, p—posterolateral corner.

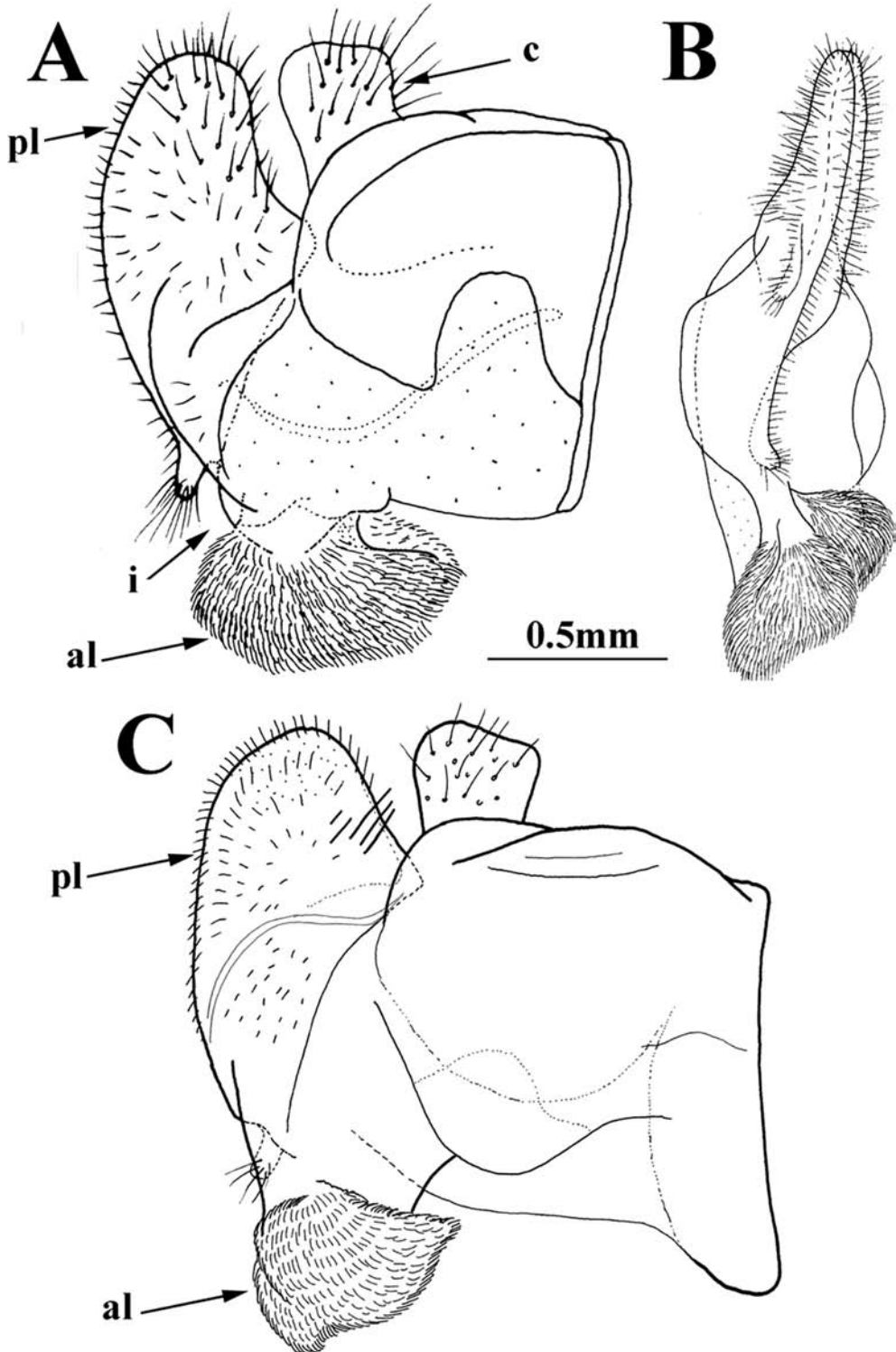


FIGURE 23 Male genitalia. Epandrium. A) *Merodon longisetus* sp. n., lateral view, B) *Merodon longisetus* sp. n., ventral view of surstyle lobe, C) *Merodon toscanus*, lateral view. Scale: 0.5 mm. al—anterior surstyle lobe, c—circus, i—incision, pl—posterior surstyle lobe.

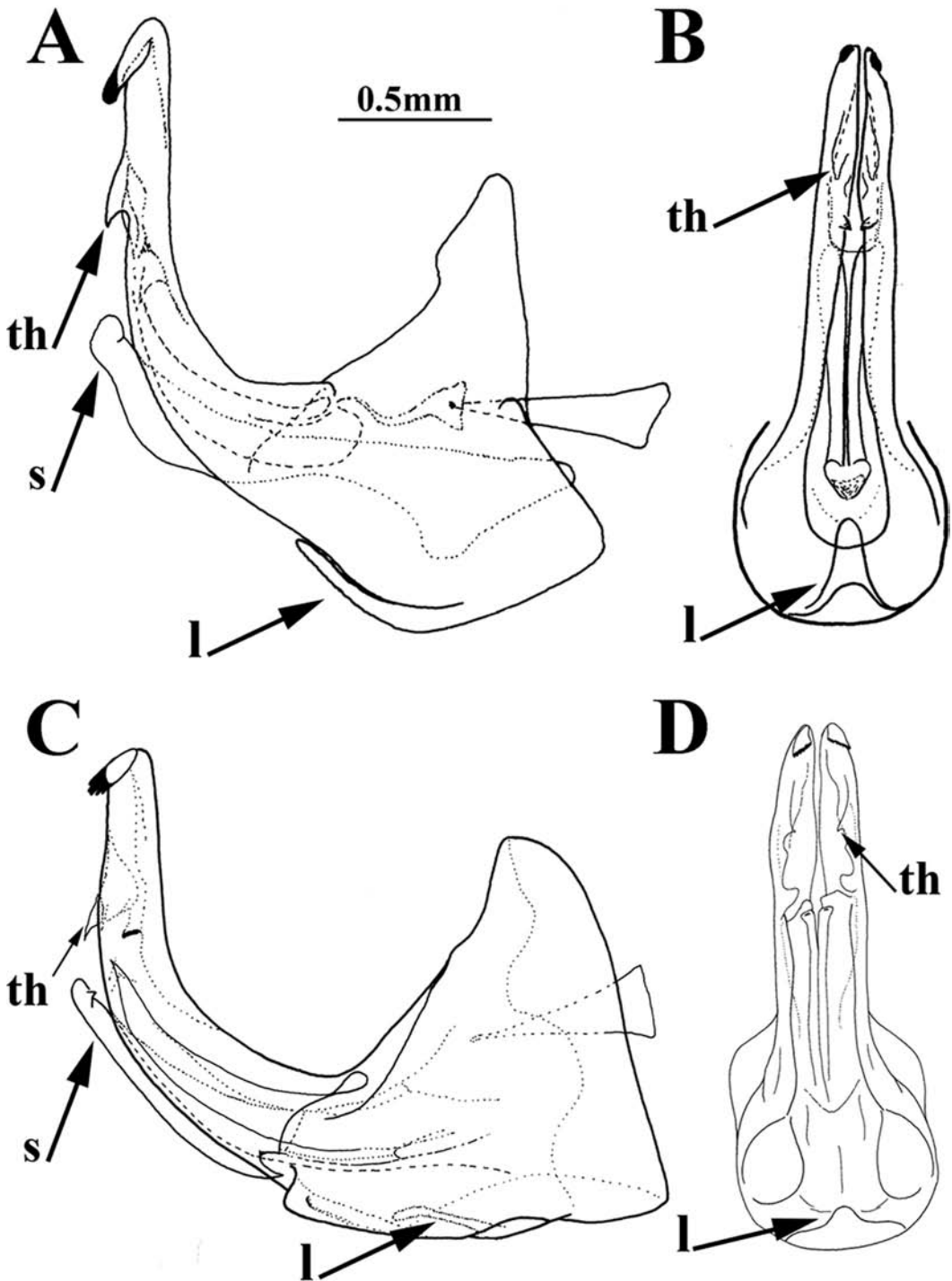


FIGURE 24 Male genitalia. Hypandrium. A) *Merodon longisetus* sp. n., lateral view, B) *Merodon longisetus* sp. n., ventral view, C) *Merodon toscanus*, lateral view, D) *Merodon toscanus*, ventral view. Scale: 0.5 mm. l—lingual, s—lateral sclerite of aedeagus, th—subapical thorn on ventral margin.

*Merodon obstipus* Vujić, Radenković et Likov sp. n.

**Type material.** Holotype. Male. Turkey: Burdur, Rahat mountain, near Osman kalfalar, 2100 m a.s.l., 37.1303N, 29.8372E, 3.vii.2015, leg. Vujić (FSUNS). Paratypes. Turkey, one male, Balıkesir, Gönen, 230 m a.s.l., 40.1336N, 27.5891E, 08.vi.2006, leg. Demirözer (EMIT); one male, Isparta, Sütçüler, 1250 m, 37.664747N, 30.983819E, 10.vi.2014, leg. Hayat, Demirözer, Gök, Uzal (EMIT); one male, Isparta, eastern campus of Süleyman Demirel University, 1017 m a.s.l., 37.8431N, 30.5419E, 14.v.2015, leg. Uzal, Gök (EMIT); 7 male, three female, Isparta, eastern campus of Süleyman Demirel University, 1017 m a.s.l., 37.8430N, 30.5419E, 22.v.2015, leg. Uzal, Gök (EMIT); one female, Isparta, eastern campus of Süleyman Demirel University, 1017 m a.s.l., 37.8377N, 30.5380E, 02.vi.2016, leg. Uzal (EMIT); one male, Isparta, eastern campus of Süleyman Demirel University, 1017 m a.s.l., 37.8377N, 30.5380E, 03.vi.2016, leg. Hayat (EMIT); one male, Isparta, Davraz mountain, 1700 m a.s.l., 37.7825N, 30.7591E, 20.vi.2016, leg. Hayat, Vujić, Demirözer, Uzal, Ačanski (EMIT); one male, Osmaniye, 670 m a.s.l., 37.25N, 36.25E, 19.vi.1960, leg. Guichard, Harvey (BMNH) (det. Hurmansk as *Merodon femoratoides*).

**Diagnosis.** Large sized species (14–15 mm) with bronze lustre; black scutum with four microtrichose vittae; abdomen black and elongated, terga 3 and 4 with a pairs of whitish microtrichose fasciae; at least tergum 2 with a pair of reddish/orange lateral maculae (fig. 26A); at least metatarsi dark brown dorsally; metafemur moderately swollen and curved, with very long pile antero- and posteroventrally, pile slightly longer than half of width of metafemur (fig. 20B); male genitalia: anterior surstyle lobe long and curved downwards, tapering, with pointed apex (fig. 27A: al). *Merodon obstipus* sp. n. belongs to the *M. nigratarsis* group, resembling to *alagoezicus* species subgroup by male genitalia (fig. 12B–F) (anterior surstyle lobe narrow and elongated) but without ventrolateral lamella in apical part of metatibia, apomorphic character in *alagoezicus* subgroup (as on fig. 36B: la); male genitalia of *M. obstipus* sp. n. easily can be separated from *alagoezicus* subgroup based on

direction of elongated anterior surstyle lobe: in *M. obstipus* sp. n. curved downwards with pointed apex directed towards base of epandrium (fig. 27A: al), while in *alagoezicus* subgroup curved upwards (as on fig. 12: al). Other morphological characters of *M. obstipus* sp. n. are very similar to *M. femoratoides*, but they can be distinguished by shapes of male genitalia (figs. 35C, 27A) and sternum 4 (in *M. obstipus* sp. n. with larger circular central notch (fig. 22C: cf) than in *M. femoratoides* (Fig. 22D: cf), and the posterolateral corners are rectangular in *M. obstipus* sp. n. (fig. 22C: p), while they are rounded in *M. femoratoides* (fig. 22C–D: cf, p)).

**Distribution.** *Merodon obstipus* sp. n. is distributed in coastal areas of the Anatolian Peninsula, mainly recorded at altitudes up to 1000 m, at Balıkesir, Burdur, Isparta and Osmaniye provinces (fig. 1). This taxon is an additional Anatolian endemic.

**Description.** **Male.** **Head** (figs. 18C, 25A, C). Antennae dark brown/reddish, with acute apex; basoflagellomere 1.2 times longer than wide, and 1.8 times longer than pedicel; arista 1.5 times longer than basoflagellomere, covered with dense microtrichia, light brown at base, but dark and thickened at tip (fig. 18C); face and frons black, densely covered with microtrichia and with pale yellow-whitish, long pile; ventral part of face shiny; vertical triangle isosceles, shining black except in front of anterior ocellus covered with whitish microtrichia, pilosity long whitish (except for some black pile on the ocellar triangle); ocellar triangle equilateral; eye pile long and dense; eye contiguity about 11 facets long; occiput with whitish-yellow pile, along the eye margins with dense white microtrichia; vertical triangle: eye contiguity: ocellar triangle = 2 : 1 : 1 (fig. 25A, C).

**Thorax** (fig. 20B). Scutum and scutellum black with bronze lustre, covered with relatively long, dense, pale yellow pile; side of scutum at wing basis with patch of black pile; scutum with four microtrichose vittae, anteriorly connected and posteriorly reaching the scutellum and postalar callus; posterodorsal part of anterior anepisternum, posterior anepisternum (except anteroventral angle), anterior anepimeron, dorsomedial anepimeron,

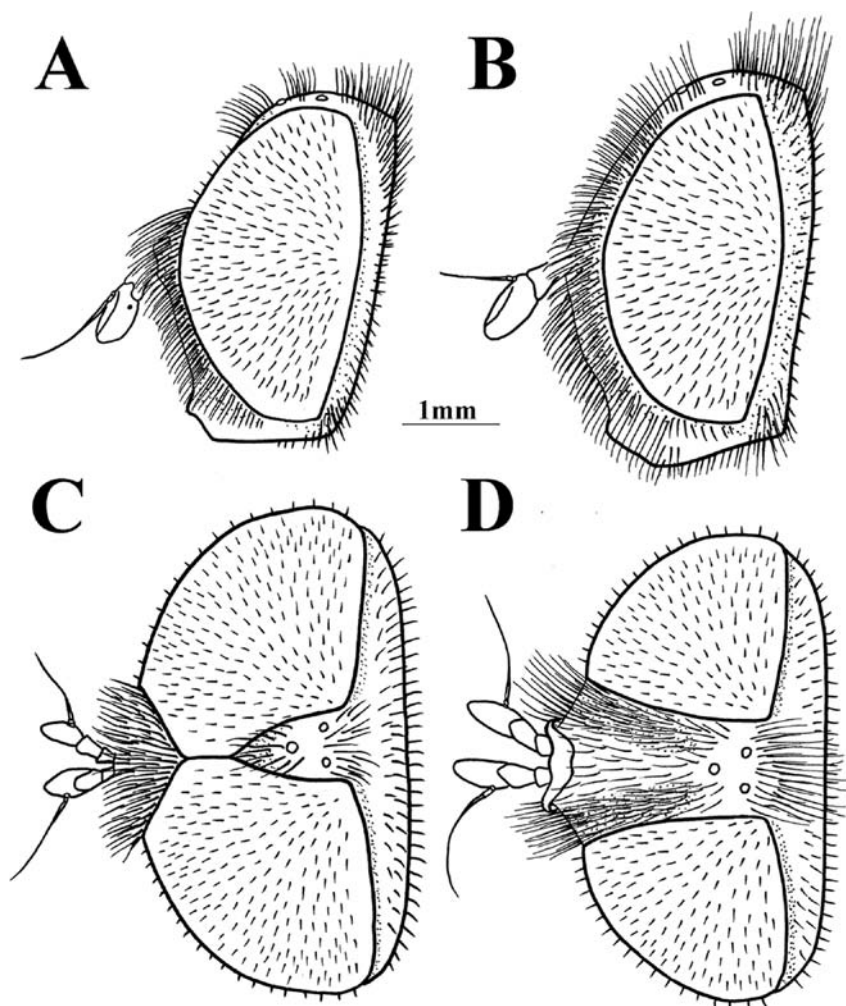


FIGURE 25 Head of *Merodon obstipus* sp. n. A) male, lateral view, B) female, lateral view; C) male, dorsal view, D) female, dorsal view. Scale: 1 mm.

and posterodorsal and anteroventral parts of kat-episternum with long, dense yellow pile and greyish microtrichia; wings covered with microtrichia (except basal parts of cells CuP, R and BM sparsely microtrichose); wing veins brown; calypteres pale yellow; halteres often with brown pedicel and yellow capitulum; legs predominantly black, except pale yellow apex of pro- and mesofemora, basal half of pro- and mesotibiae, basal  $\frac{1}{3}$  of metatibia, and at least metatarsi ventrally; pile on legs yellow; posterior part of mesocoxa without long pile; metafemur moderately swollen and curved, about

3 times longer than wide; long pile on postero- and anteroventral surface yellow and sparse, slightly longer than half of width of metafemur and much longer than those on dorsal surface (fig. 20B).

*Abdomen* (figs. 22C, 26A). Black with bronze lustre, 1.2 times longer than mesonotum; terga black except for a pair of yellow/orange lateral maculae on tergum 2; terga 3 and 4 usually with a pairs of whitish microtrichose fasciae (on tergum 2 exceptionally present); additionally posterior margin of tergum 4 narrowly microtrichose (fig. 26A); pile on terga yellow; **sterna translucent, covered**

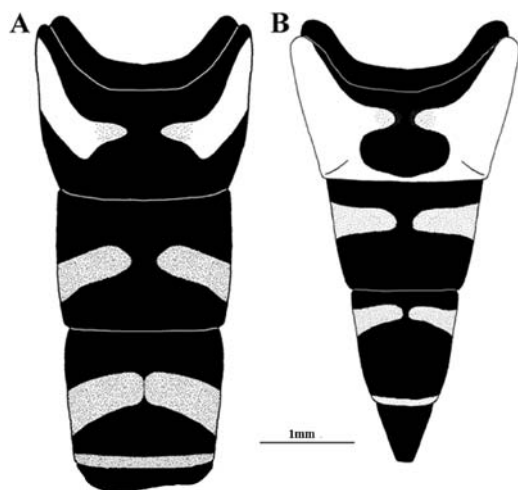


FIGURE 26 Abdomen of *Merodon obstipus* sp. n. Dorsal view, A) male, B) female. Scale: 1 mm.

circular central notch and rectangular posterolateral corner (fig. 22C: cf, p).

**Male genitalia** (fig. 27A–D). Posterior surstyle lobe with parallel margins (fig. 27A: pl); anterior surstyle lobe elongated, sickle-shaped, tapering with pointed apex directed towards base of epandrium (fig. 27A: al); cercus rectangular, without prominences (fig. 27A: c); hypandrium elongated, sickle-shaped, with a small lateral projections near the base (fig. 27C: lp); lingula short (fig. 27C–D: l).

**Female** (figs. 18D, 22E, 25B, D, 26B). Similar to the male except for normal sexual dimorphism and for the following characteristic: frons with wide, white microtrichose vittae along eye margins (fig. 25D); basoflagellomere about 2 times longer than wide, with rounded apex (fig. 18D); tergum 2 with yellow pile, terga 3–5 with mixed yellow and black pile (fig. 26B); microtrichose fasciae on terga 3 and 4 narrower; sterna dark, except lighter brown sternum 2; sterna 4 and 5 with central longitudinal dent/suture (fig. 22E: marked with arrow).

**Etymology.** The name *obstipus* is derived from a Latin adjective for crooked, bent sideways or at an angle, referring to the shape of the anterior surstyle lobe.

**Remarks.** One specimen determined by Hurkmans (1987) as *Merodon femoratoides* from locality Osmaniye area is included in paratypes.

***Merodon cohurnus*** Vujić, Likov et Radenković sp. n.

**Type material.** Holotype. Male. Turkmenistan: Kopet mountain range, canyon Aj-Dere river, 38.4088N, 56.7202E, 21.vi.1977 (SZMN). Paratypes. Turkmenistan, two male, Kopet mountain range, canyon Aj-Dere river, 38.4088N, 56.7202E, 21.vi.1977 (SZMN).

**Diagnosis.** Medium sized species (12–14 mm) with bronze lustre; black scutum usually with barely visible four microtrichose vittae; abdomen black with a pairs of yellow–orange maculae on terga 2–4 (fig. 10A); metafemur moderately broad and slightly curved, with some long, pale yellow pile only antero- and posteroventrally (fig. 20C). *M. cohurnus* sp. n. belongs to the *M. nigratarsis* group, and is closely related to species *M. longisetus* sp. n. and *M. nigratarsis*, from which can be distinguished by the different shape of anterior surstyle lobe (in *M. cohurnus* sp. n. high boot shaped (fig. 29A: al), while in *M. longisetus* sp. n. oval (fig. 23A: al) and in *M. nigratarsis* tapering and pointed (fig. 35A: al)), and by different shape of sternum 4 (fig. 22A–B, F).

**Distribution.** *Merodon cohurnus* sp. n. is known only from Turkmenistan, found on the Kopet Dag mountain range (fig. 1).

**Description. Male. Head** (figs. 18E, 28A–B). Antennae brown-red with acute apex; basoflagellomere about 1.3 times longer than wide, and about 1.5 times longer than pedicel; arista light brown in basal 1/3, and thickened and dark brown at apical 2/3, covered with microtrichia; arista is about 1.5 times longer than basoflagellomere (fig. 18E); face and frons black, with pale yellow–whitish pile, and dense silver microtrichia; ventral part of face shiny; vertical triangle isosceles, shining black, except in front of anterior ocellus covered with microtrichia, pilosity long, pale yellow–whitish (except some black pile on ocellar triangle); ocellar triangle isosceles; eyes covered with dense pile; eye contiguity about 12 facets long; occiput with pale yellow pile, covered with a dense silver microtrichia; vertical triangle: eye contiguity: ocellar triangle = 3 : 1.5 : 1 (fig. 28A–B).



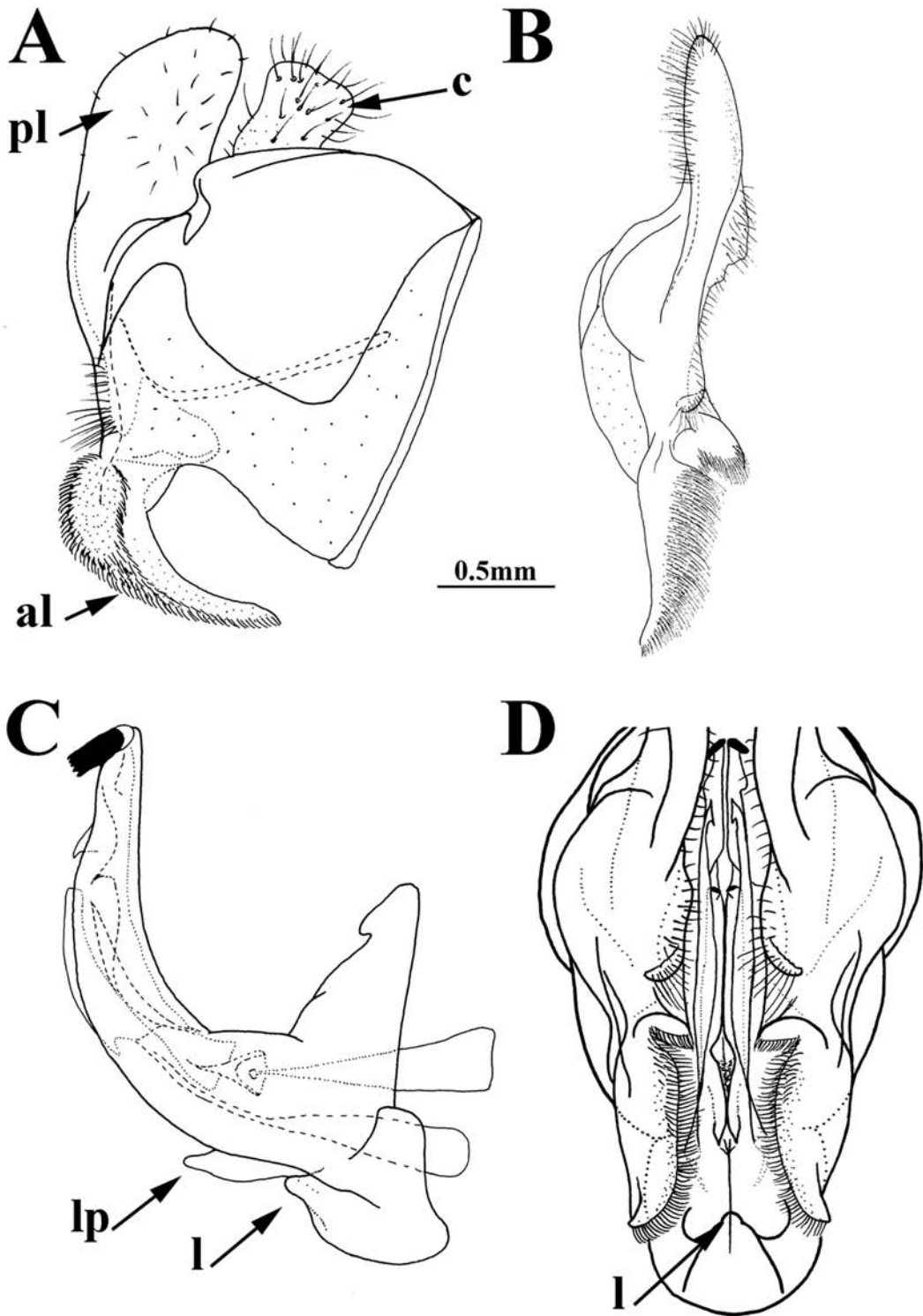


FIGURE 27 Male genitalia of *Merodon obstipus* sp. n. A) epandrium, lateral view, B) surstyle lobe, ventral view, C) hypandrium, lateral view, D) anterior end of male genitalia, ventral view. Scale: 0.5 mm. al—anterior lobe of surstylus, c—circus, l—lingual, pl—posterior lobe of surstylus.

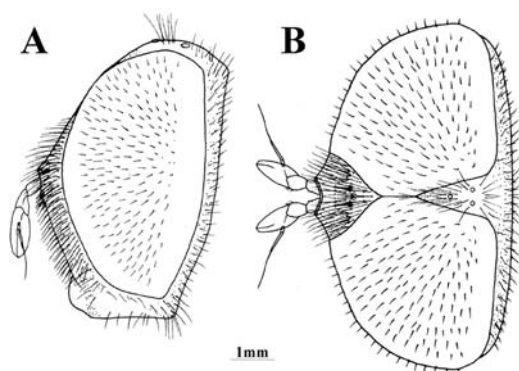


FIGURE 28 Head of male *Merodon cohurnus* sp. n. A) lateral view, B) dorsal view. Scale: 1 mm.

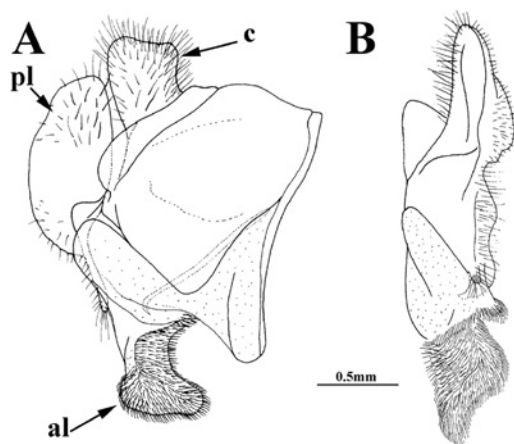


FIGURE 29 Male genitalia of *Merodon cohurnus* sp. n. A) epandrium, lateral view, B) surstyle lobe, ventral view. Scale: 0.5 mm. al—anterior lobe of surstylus, c—cercus, pl—posterior lobe of surstylus.

**Thorax** (fig. 20C). Scutum and scutellum black with bronze lustre, covered with pale, yellow pile, at wing bases a tuft of black pile; scutum with four microtrichose vittae, anteriorly connected; posterodorsal part of anterior anepisternum, posterior anepisternum (except anteroventral angle), anterior anepimeron, dorsomedial anepimeron, and posterodorsal and anteroventral parts of kat-episternum covered with long, pale yellow pile and silverish microtrichia; wings covered with microtrichia (except cells R and BM sparsely microtrichose); wing veins brown; calypteres pale

yellow-whitish; halteres light brown; legs mostly black, except pale yellow apex of pro- and meso-femora, basal half of pro- and mesotibiae, basal 1/4 of metatibia, and at least metatarsi ventrally; pile on legs pale yellow; metafemur moderately curved, about 3.5 times longer than wide; metafemur with some long yellow pile antero- and posteroventrally, much longer than pile on dorsal surface (fig. 20C).

**Abdomen** (figs. 22F, 10A). Dark, tapering, about 1.3 times longer than mesonotum; terga 2–4 with a pairs of lateral yellow maculae, on terga 3 and 4 maculae covered with microtrichia; yellow-orange maculae on tergum 2 triangular; microtrichose fasciae on tergum 4 connected medially (fig. 10A); pile on terga pale yellow; sterna translucent and yellow; sternum 4 with U-shaped posteromedial notch, reaching to the  $\frac{2}{3}$  of the length of sternum, and rounded posterolateral corner (fig. 22F: cf, p).

**Male genitalia** (figs. 29A–B, 30A–B). Anterior surstyle lobe high boot-shaped (fig. 29A: al); posterior surstyle lobe rhomboid-shape, about 2 times longer than wide (fig. 29A: pl); cercus rectangular (fig. 29A: c); hypandrium narrow, elongated, and sickle-shaped; lingula short (fig. 30A, B: l); lateral projections near the base with rectangular apex in lateral view, and characteristic shape (fig. 30A: lp).

**Female.** Unknown.

**Etymology.** The name *cohurnus* origin from the Latin noun *cohurnus* meaning high boot, refers to the shape of anterior surstyle lobe.

### *Merodon avidus* group

**Diagnosis.** Similar to *M. nigratarsis* group, but differs by red-yellow tarsi in *M. avidus* group (fig. 14A–D), while dark brown in *M. nigratarsis* group (fig. 14E–H) (apical tasomeres can be partly brown dorsally in *M. femoratus* (fig. 14I–J)), lack of subapical thorns on ventral margin of hypandrium (fig. 33A, B) (projections just behind the ctenidium can be present) (fig. 33C: marked with arrow) and shape of lateral sclerit of aedeagus (fig. 9B: s).

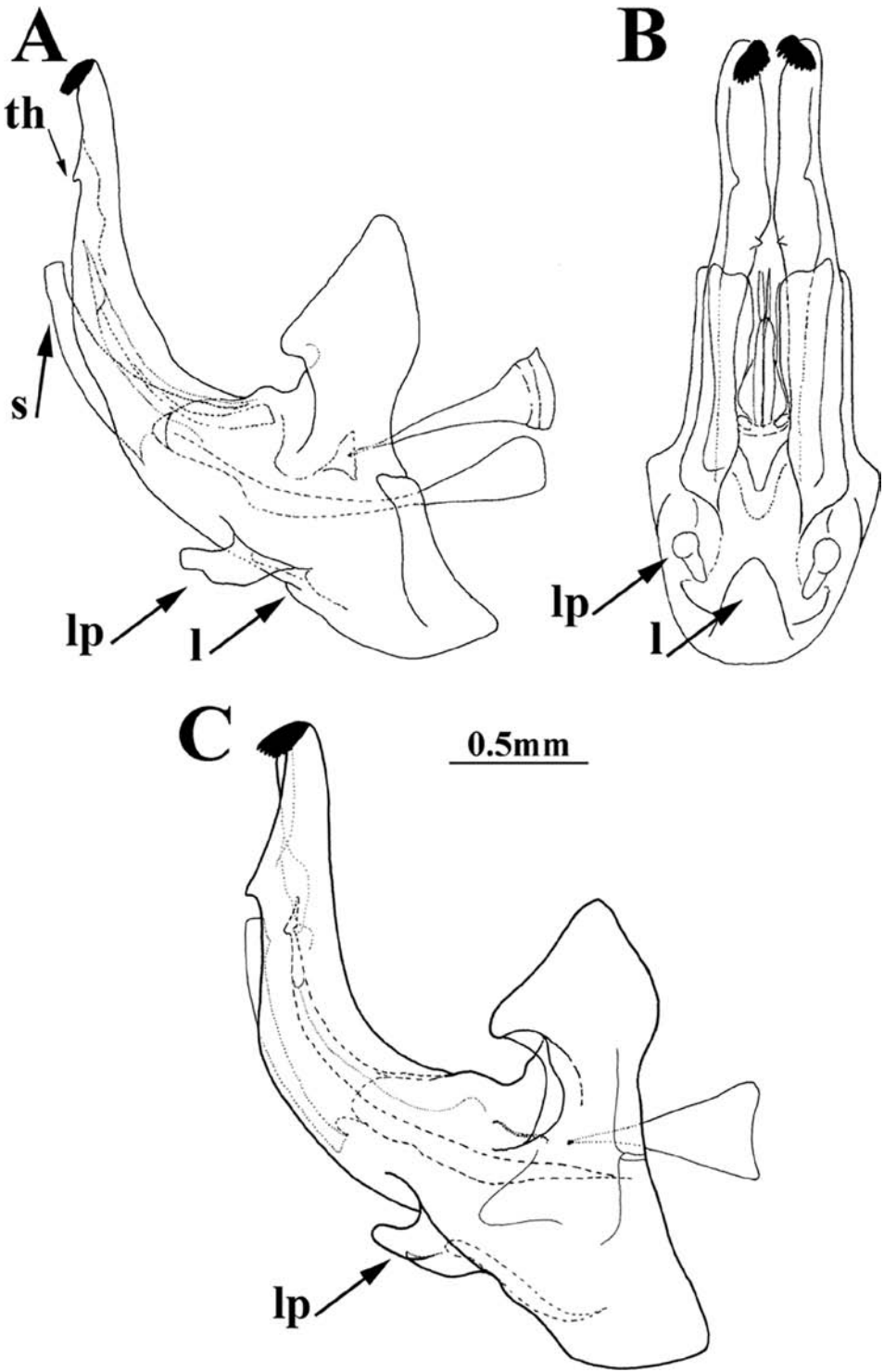


FIGURE 30 Hypandrium. A) *Merodon cohurnus* sp. n., lateral view, B) *Merodon cohurnus* sp. n., ventral view, C) *Merodon quadraticus*, lateral view. Scale: 0.5 mm. l–lingual, lp–lateral projection, s–lateral sclerite of aedeagus, th–subapical thorn on ventral margin.

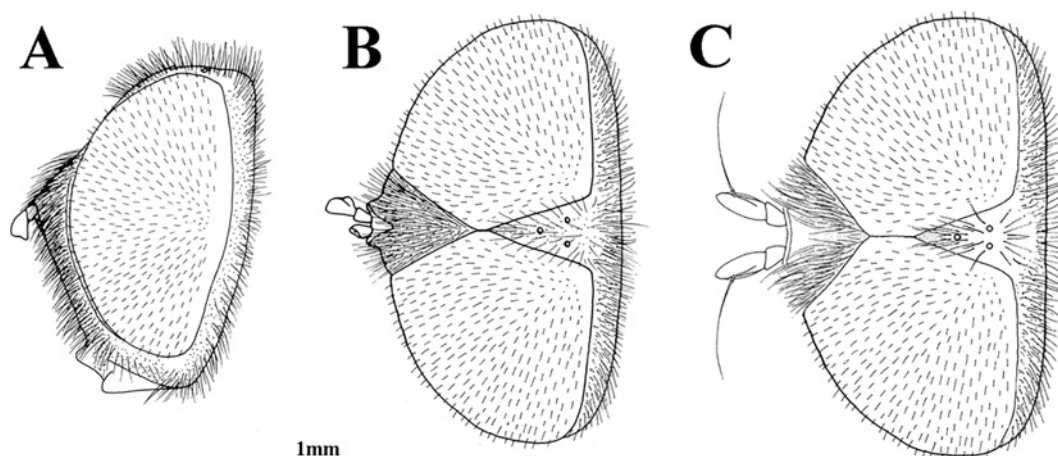


FIGURE 31 Head of male. A) *Merodon rutitarsis* sp.n., lateral view, B) *Merodon rutitarsis* sp. n., dorsal view, C) *Merodon avidus*, dorsal view. Scale: 1 mm.

*Merodon rutitarsis* Likov, Vujić et Radenković sp. n.

**Type material.** Holotype. Male. Turkmenistan: Chandyr river valley, tributary of Sumbara river, 38.0175N, 55.2955E, 26.iv.1933, leg. Ušinskii (SZMN).

**Diagnosis.** Medium sized species (12 mm); body black (except a pair of lateral orange maculae on tergum 2 (fig. 11A)), covered with long, pale yellow, erect, dense pile; metafemur elongated, with few longer pile on anteroventral surface (fig. 20D); all tarsi yellow; basotarsomere on metaleg narrow, about 4 times longer than wide (fig. 14K); face and frons black; pilosity of the head predominantly pale yellow (except some black pile on ocellar triangle); eye contiguity very short (about 4 facets) (fig. 31B); anterior surstyle lobe simple and short, oval (fig. 32A: al); posterior surstyle lobe with hump in apical half, and short, black setulae at the inner side (fig. 32A–B: pl). *Merodon rutitarsis* sp. n. is similar to *M. avidus* primarily based on yellow tarsi (fig. 14A–D, K), from which can be distinguished by the following characters: in *M. avidus* eye contiguity is much longer (about 14 facets long) (fig. 31C), by different shapes of sternum 4 (fig. 22G–H), and by shape of male genitalia: in *M. avidus* anterior surstyle lobe about 1.5 times longer than wide (fig. 32C: al), while in *M. rutitarsis* sp. n. is about as long as wide (fig. 32A: al); posterior surstyle lobe in *M. avidus* simple (fig. 32C: pl),

while in *M. rutitarsis* sp. n. is with a hump (fig. 32A: marked with arrow).

**Distribution.** *Merodon rutitarsis* sp. n. was recorded at only one locality in Turkmenistan, in the Chandyr river valley (fig. 1).

**Description. Male. Head** (fig. 31A–B). Antennae of the holotype are damaged, basoflagellomere with arista missing. Scape and pedicel light brown, scape covered with several long, while pedicel with many short pale yellow pile; face and frons black, covered with pale yellow pile and silver microtrichia (except ventral parts of face); vertical triangle isosceles, shining black, except in front of anterior ocellus covered with whitish microtrichia, pilosity long, pale yellow; ocellar triangle equilateral; eyes covered with dense, pale yellow pile; eyes contiguity short, about 4 facets; occiput covered with silver microtrichia and with long, pale yellow pile; vertical triangle: eye contiguity: ocellar triangle = 2,5 : 0,5 : 1 (fig. 31A–B).

**Thorax** (figs. 20D, 14K). Scutum and scutellum black; anterior half of scutum with bluish lust and scarce silver microtrichia; scutum and scutellum covered with pale, yellow, long and dense, erected pile; posterodorsal part of anterior anepisternum, posterior anepisternum (except anteroventral angle), anterior anepimeron, dorsomedial anepimeron, and posterodorsal and anteroventral parts of katapisternum covered with long, dense, pale

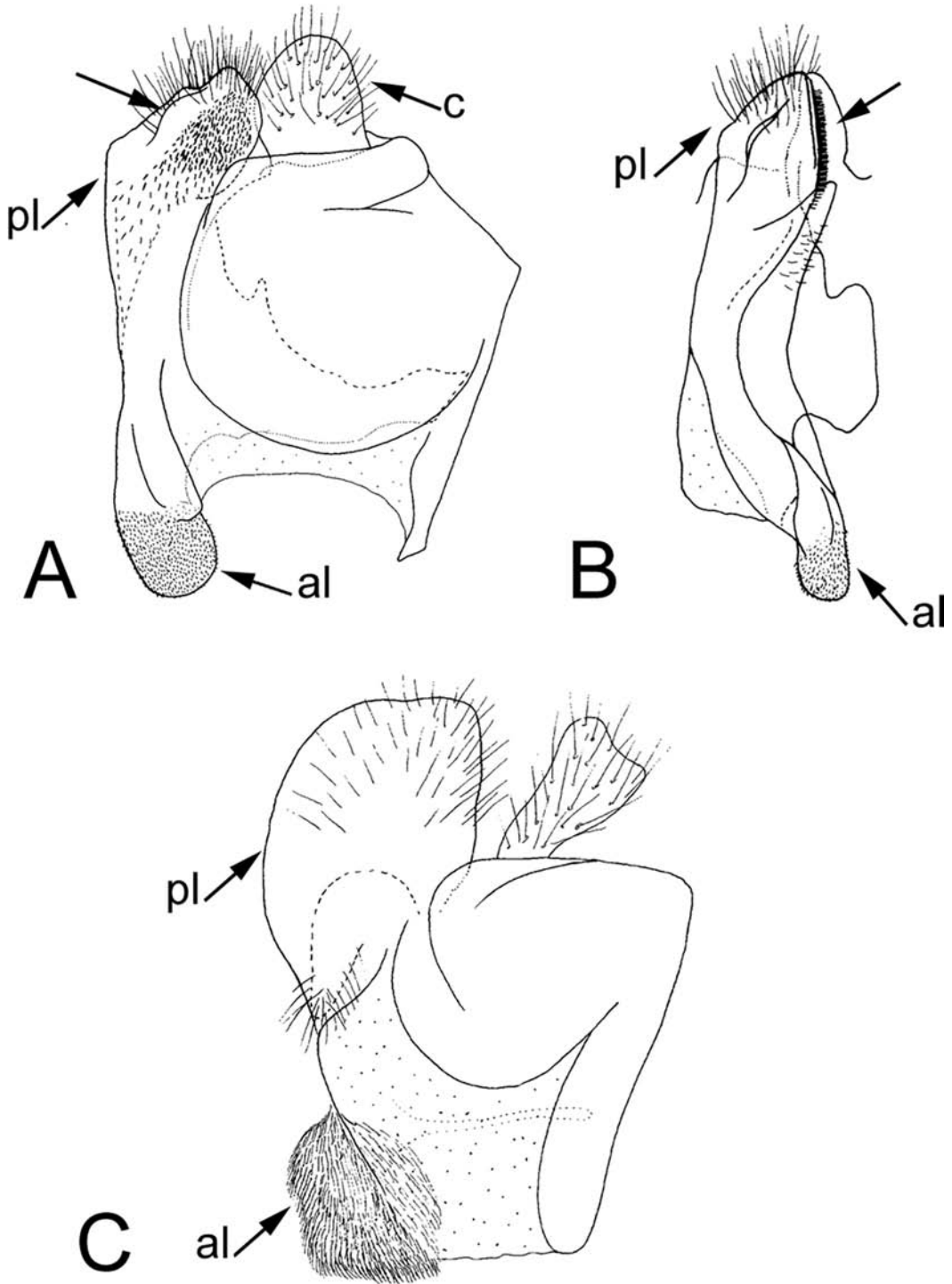


FIGURE 32 Male genitalia. A) *Merodon rutitarsis* sp. n., epandrium, lateral view (hump marked with arrow), B) *Merodon rutitarsis* sp. n., surstyle lobe, ventral view (black setulae marked with arrow), C) *Merodon avidus*, epandrium, lateral view. Scale: 0.5 mm. al—anterior lobe of surstylus, c—circus, pl—posterior lobe of surstylus.

yellow pile; wings covered with microtrichia (except basal parts of cell R with reduced microtrichia); wing veins light brown; halteres and calypteres sandy yellow/brown; all femora black (except yellow knees), all tibiae yellow, with broad black ring closer to apical end of tibiae, and all tarsi yellow (fig. 14K); pile on all legs yellow; metafemur elongated, narrow and only slightly curved, about 3.5 times longer than wide; some pile on anteroventral surface of metafemur as long as half of width of metafemur (fig. 20D).

**Abdomen** (figs. 22G, 11A). Slightly longer than mesonotum; all terga black, except a pair of yellow triangular maculae on tergum 2; inner ends of orange maculae slightly covered with microtrichia; terga 3 and 4 with a pairs of microtrichose fasciae, separated medially (fig. 11A); abdomen covered with dense, long, pale yellow pile, except for black pile on the posterior half of terga 3 and 4 near to the posterior margin; sterna translucent, light brown, covered with long, erect, pale yellow pile; sternum 4 with narrow but deep central notch, and angular posterolateral corners (fig. 22G: cf, p).

**Male genitalia** (figs. 32A–B, 33). Anterior surstyle lobe simple and short, oval, with a rounded margin, about as long as wide (fig. 32A: al); posterior surstyle lobe with hump in apical part (fig. 32A: marked with arrow), at inner side covered with short, black setulae (fig. 32B: marked with arrow); cercus triangular to rectangular (fig. 32A: c); hypandrium sickle-shaped, with enlarged and broad apex (fig. 33).

**Female.** Unknown.

**Etymology.** Name *rutitarsis* refers to the color of the tarsi, derived from the Latin adjective *rutilus*, meaning reddish-yellow.

## Identity of *Merodon elegans* Hurkmans

*Merodon elegans* was described by Hurkmans (1993) based on the large number of specimens collected in the Western Mediterranean. A recent study of all known *Merodon* types resulted with discovery of two names related to the same taxon. Vujić et al. (2011) cited this species

for Turkey under one of these names, *M. biarcuatus* Curran, 1939 based on the holotype found in AMNH. Syntype of *M. femoratus* Sack, 1913 found in ZMHB, resolved question about the oldest name that should be used for this species.

## *Merodon femoratus* Sack, 1913

syn. n. *biarcuatus* Curran, 1939

syn. n. *elegans* Hurkmans, 1993

**Types.** *Merodon femoratus* Sack, 1913: 446. **Type-locality.** Corsica, Greece, Asia Minor. Described based on unspecified number of males and females. One syntype was found in ZMHB: France, Corsica “Mann” “855”, a male designated here as lectotype.

*Merodon biarcuatus* Curran, 1939: 6. **Type-locality.** Morocco. **Holotype** (studied). ♀ forest of Namora, near Rabat, Morocco (AMNH), with clear apomorphic character, broad metafemur, ventrally covered with long whitish pile as in *M. femoratus*.

*Merodon elegans* Hurkmans, 1993. **Holotype** (studied). ♂ Italy, Sicilia, “V. S. v. d. Goot! Erna rif. Filiciusa 1400–1500m 22–28.vii.1961 / *Lampetia spinipes* det. V. S. v.d. Goot 1963 I Type A” (NMNL), conspecific with *M. femoratus*.

**Diagnosis.** Medium sized species (11–13 mm) similar to *M. avidus* complex, from which can be distinguished by broad metafemur (narrower in other members from *M. avidus* complex (fig. 37A–B)), ventrally covered with long whitish pile (fig. 37D), and by deep incision between anterior and posterior surstyle lobe in male genitalia (fig. 13C: marked with arrow) (absent in *M. avidus* complex fig. 32C).

**Distribution.** Northern Africa (Algeria, Morocco, Tunisia), south and southwest Europe (Croatia, France, Portugal, Spain, Italy).

## Identification keys of males of *M. nigratarsis* and *M. avidus* groups and *Merodon crassifemoris*

Following a key to the males of the *M. nigratarsis* group (Vujić et al., 2013) we present an updated identification key for all known members of the *M. nigratarsis* and *M. avidus* groups. **Identification**

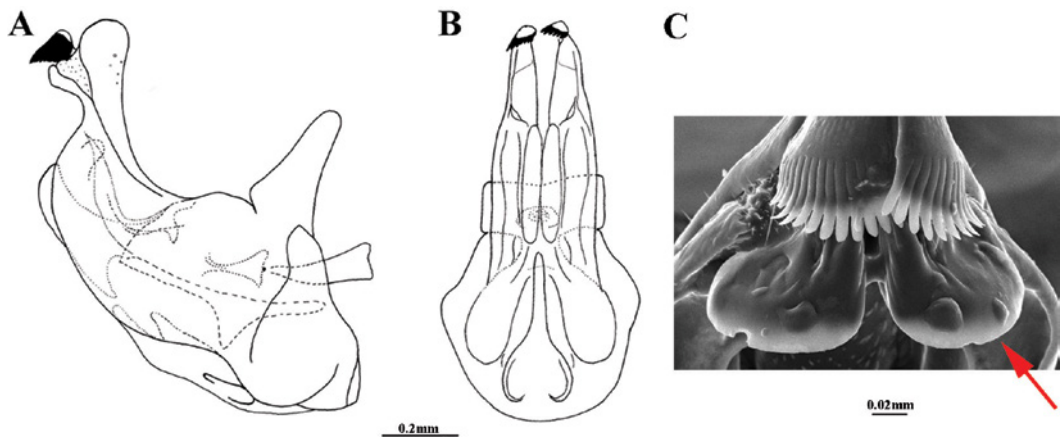


FIGURE 33 Male genitalia. A) *Merodon rutitarsis* sp. n., hypandrium, lateral view, B) *Merodon rutitarsis* sp. n., hypandrium, ventral view, C) *Merodon avidus*, apical part of hypandrium (projections behind the ctenidium marked with arrow) (SEM), ventral view. Scale: A–B) 0.2 mm, C) 0.002 mm.

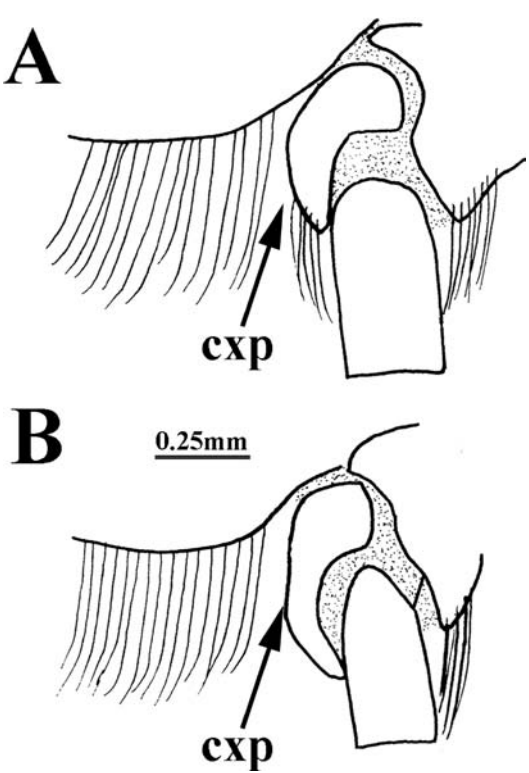


FIGURE 34 Part of mesothorax. Lateral view, A) *Merodon albifrons*, B) *Merodon nigratarsis*. Scale: 0.25 mm. cpx—posterior part of mid coxa (Marcos-García et al., 2007).

of females is very difficult and will be the subject of future studies, using a combined integrative approach.

- 1. Posterior part of mesocoxa without long pile (*Merodon avidus-nigratarsis* lineage) (fig. 34B: cpx) ..... 2
  - Posterior part of mesocoxa with long pile (fig. 34A: cpx).....
  - other *Merodon* lineages (not treated here)
- 2. Species with white microtrichose vittae on black scutum and white microtrichose fasciae on dark terga; at least tergum 2 with a pair of reddish-orange maculae laterally; abdomen elongated, narrow and tapering, always longer than scutum and scutellum together; legs without spinae or other protuberances; male genitalia: anterior surstyle lobe more or less rhomboid shape, except in the *alagoezicus* subgroup where it is transformed into a narrow, elongated, strongly curved projection (*M. nigratarsis* and *M. avidus* groups + *M. crassifemoris*) ..... 3
  - Species with different combination of characters ..... other species groups belonging to *Merodon avidus-nigratarsis* lineage (not treated here)

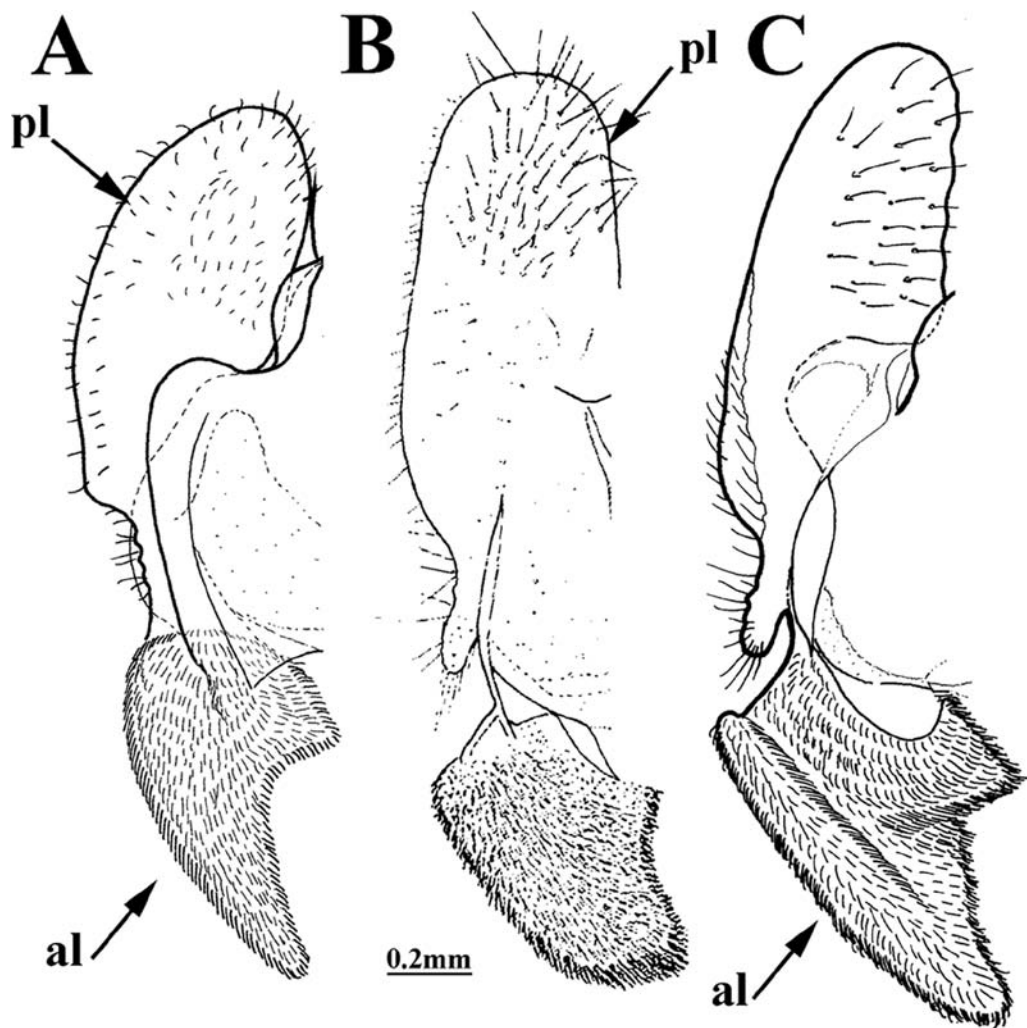


FIGURE 35 Male genitalia. Surstyle lobe, lateral view, A) *Merodon nigratarsis*, B) *Merodon latifemoris*, C) *Merodon femoratooides*. Scale: 0.2 mm. al–anterior lobe of surstylus, pl–posterior lobe of surstylus.

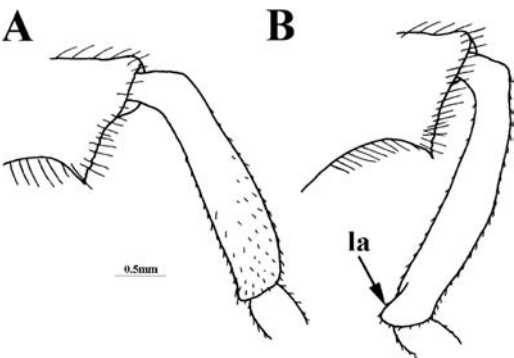


FIGURE 36 Metatibia of male. Lateral view, A) *Merodon lucasi*, B) *Merodon alagozicus*. Scale: 0.5 mm. la–lamella.

3.
- Tarsi dark brown/black dorsally and orange/brown ventrally (*M. nigratarsis* group) (fig. 14E–H) .....9
- Tarsi yellow dorsally and ventrally (*M. avidus* group) (fig. 14A–D) .....4
4.
- Posterior surstyle lobe with hump in apical half (ffig. 32A: marked with arrow); anterior surstyle lobe short and rounded, oval (fig. 32A: al).....*M. rutatarsis* sp. n.
- Posterior surstyle lobe simple; anterior surstyle lobe longer, rhomboid shape (fig. 32C: al) .....5



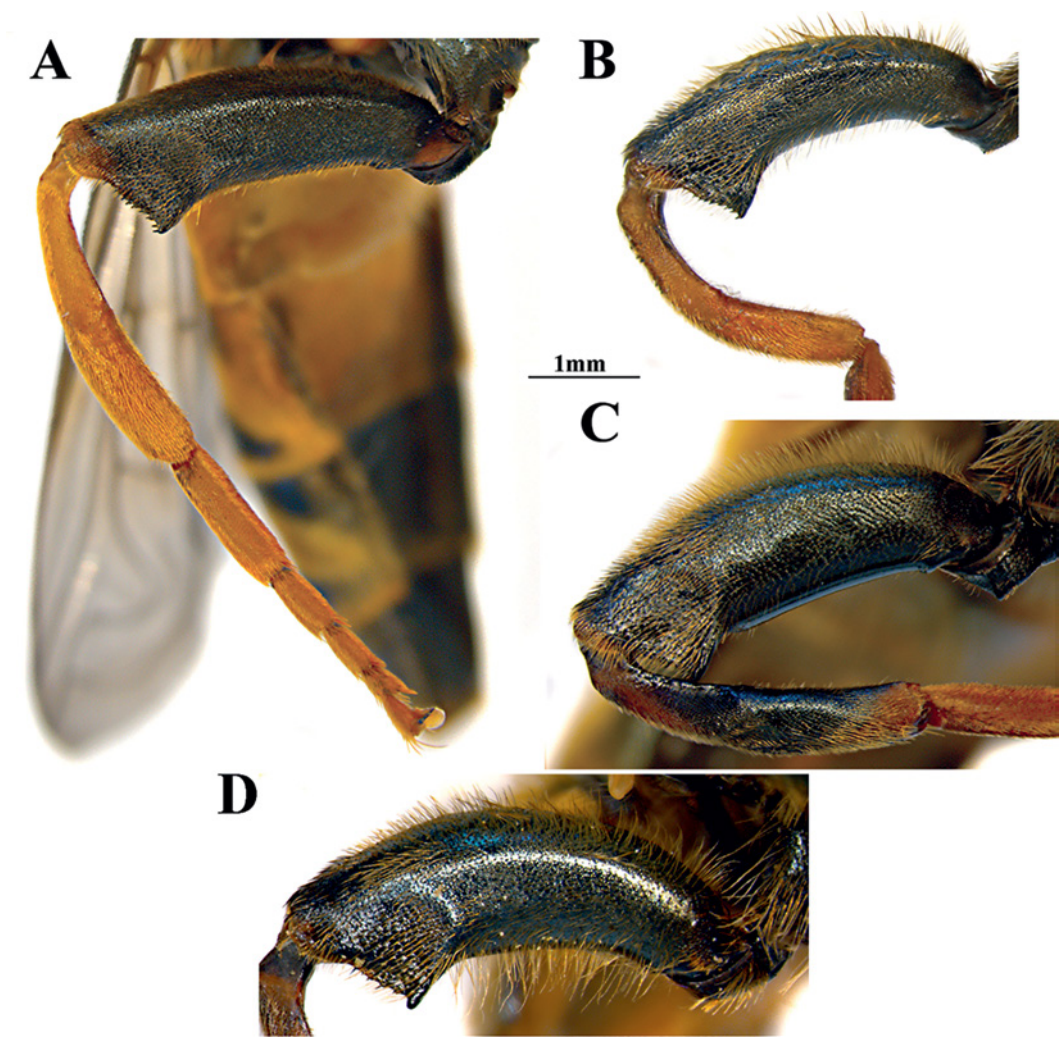


FIGURE 37 Metaleg of male. Lateral view, A) *Merodon megavidus*, metaleg, B) *Merodon avidus*, metafemur and metatibia, C) *Merodon moenium*, metafemur and metatibia, D) *Merodon femoratus*, metafemur. Scale: 1 mm.

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|---|--|
| <p>5.    Metafemur broad, ventrally covered with long whitish pile (Fig. 37D); surstyle with deep incision between anterior and posterior lobes (fig. 13C: marked with arrow) .....<i>M. femoratus</i></p> <p>     – Metafemur less broad, without long ventral pilosity (fig. 37A–C); surstyle without deep incision (fig. 32C).....6</p> <p>6.    Body pile golden; metafemur with very short pile (fig. 37A) ..... <i>M. megavidus</i></p> <p>     – Body pile yellow to pale/grayish; metafemur with longer pile (fig. 37B–C) ..... 7</p> | <p>7.    Distribution: western Mediterranean; clearly defined with genetic data (see Popović et al., 2015) ..... <i>M. ibericus</i></p> <p>     – Distribution: Europe, except Iberian Peninsula ..... 8</p> <p>8.    Tergum 2 with a pair of whitish, microtrichose spots; terga 3 and 4 with broad microtrichose fasciae (fig. 38A); tibiae usually pale (fig. 37B); body pile slightly shorter, especially on the tergum 4 (fig. 39A); tergum 3 with a pair of orange, lateral, triangular maculae, anterior part of tergum 3 is also</p> |
|---|--|

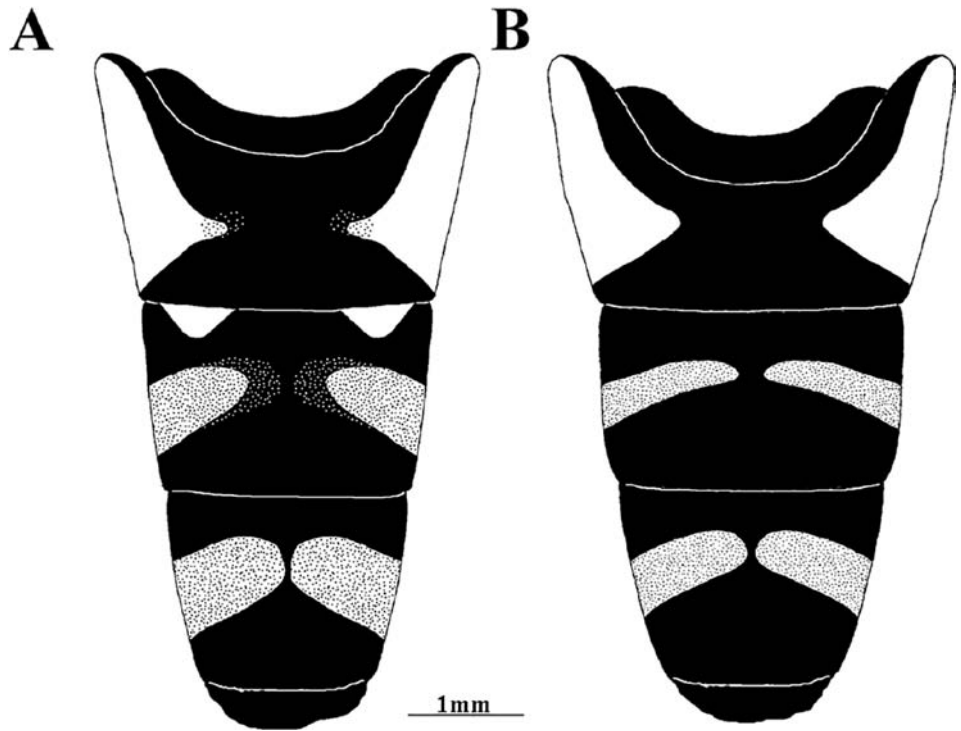


FIGURE 38 Abdomen of male. Dorsal view, A) *Merodon avidus*, B) *Merodon moenium*. Scale: 1 mm.

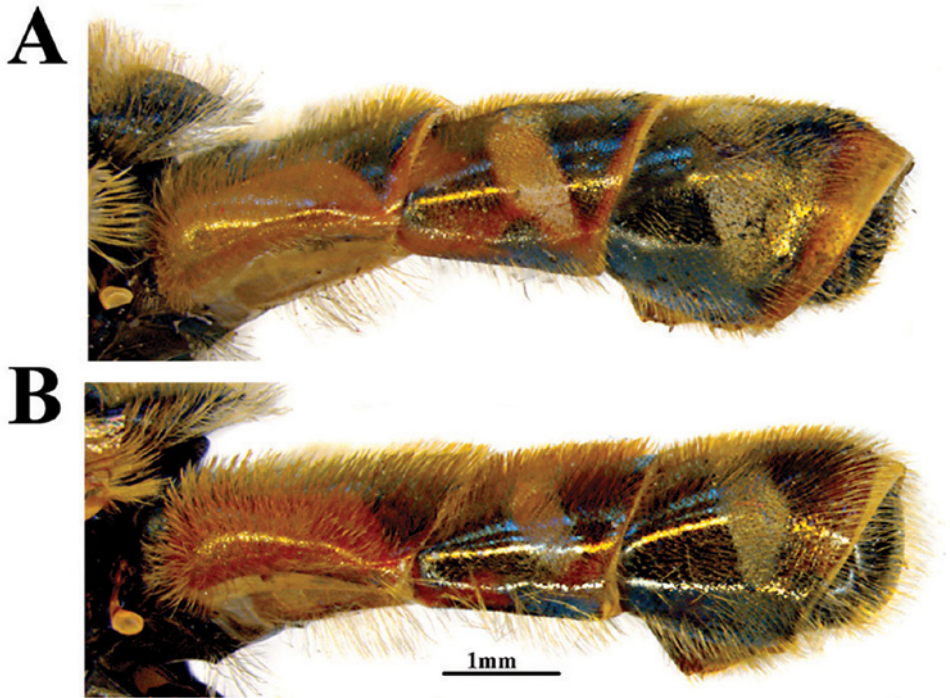


FIGURE 39 Abdomen of male. Lateral view, A) *Merodon avidus*, B) *Merodon moenium*. Scale: 1 mm.

- predominantly orange-red, except medially, where it is narrowly black (in darker specimens at least, small orange areas are present antero-sublaterally) ..... *M. avidus*
- Tergum 2 shiny, without microtrichia; terga 3 and 4 with narrow microtrichose fasciae (fig. 38B); tibiae always partly dark (fig. 37C); body pile longer (fig. 39B); tergum 3 black (in some specimens orange-red anterolaterally, but with a black posterior margin) ..... *M. moenium*
9. Metafemur narrow (about 4.5 times longer than wide); anterior surstyle lobe with strong interior accessory lobe (fig. 12A) ..... *M. nitidifrons*
- Metafemur broad (as on fig. 20A–B); anterior surstyle lobe without or with small interior accessory lobe ..... 10
10. Anterior surstyle lobe transformed to narrow, long, curved, pointed extension (fig. 12B–F) ..... 11
- Anterior surstyle lobe rhomboid or triangular shape ..... 16
11. Anterior surstyle lobe, sickle-shaped, curved downwards, with pointed apex directed towards base of epandrium (fig. 27A: al) ..... *M. obstipus* sp. n.
- Anterior surstyle lobe curved upwards (as on fig. 12B: al) ..... 12
12. Apical part of metatibia with clear ventrolateral lamella (fig. 36B: la) ..... 13
- Apical part of metatibia without clear ventrolateral lamella (fig. 36A) ..... 15
13. Posterior surstyle lobe two times as long as wide, straight (fig. 12B: pl); anterior surstyle lobe long, narrow, with rounded curve (fig. 12B: al); ..... *M. alagoezicus*
- Posterior surstyle lobe S-shaped; anterior surstyle lobe with angular curve (fig. 12C–D) ..... 14
14. Anterior surstyle lobe with additional basal extension (fig. 12C: marked with arrow) ..... *M. satdagensis*
- Anterior surstyle lobe without additional basal extension (fig. 12D) ..... *M. schachtli*
15. Abdomen covered with pale pile; tergum 2 without white microtrichose maculae; posterior surstyle lobe broader basally and narrower in apical part (fig. 12E: pl) ..... *M. hakkariensis*
- Abdomen with short black pile on posteromedial part of tergum 3 and medial parts of tergum 4; tergum 2 usually with a pair of white microtrichose spots; posterior surstyle lobe the same width along the entire length and with lamellar structure (fig. 12F: marked with arrow) ..... *M. lucasi*
16. Face with a bulge below antennae (fig. 4D: marked with arrow); posterior surstyle lobe hook-like (fig. 13A: pl); metafemur very broad ..... *M. crassifemoris*
- Face without bulge ..... 17
17. Pile on metafemur very short on ventral surface; surstylus on fig. 13B ..... *M. angustus*
- Pile on metafemur longer on ventral surface; surstylus of different shape ..... 18
18. Metafemur and metatibia extremely curved; male genitalia: posterior and anterior surstyle lobe separated by deep incision (fig. 13D: marked with arrow) ..... *M. testaceus*
- Metafemur and metatibia less curved; male genitalia: posterior and anterior surstyle lobe not deeply divided ..... 19
19. Metafemur broad and covered with long anteroventral and posteroventral pile, as long as half of width of metafemur (as on fig. 20A) ..... 20
- Metafemur narrower and covered with shorter pile, usually on posteroventral surface much shorter or absent ..... 24
20. Anterior surstyle lobe 2.5 times shorter than posterior surstyle lobe (as on fig. 23A: al) ..... 21
- Anterior surstyle lobe less than 2 times shorter than posterior surstyle lobe (as on fig. 35C: al) ..... 22
21. Lateral orange maculae on tergum 2 large, cover 2/3 of the posterior margin (fig. 11C);

- anterior surstyle lobe is about as long as wide (fig. 23C: al); lingula shorter (fig. 24C, D: l); distribution: Apennine Peninsula .....  
 ..... *M. toscanus*
- Lateral orange maculae on tergum 2 smaller, reaching the posterior margin only at outer corners of tergum (fig. 21A); anterior surstyle lobe is about 2 times wider than long (fig. 23A: al); lingula longer and pointed upward (fig. 24A, B: l); distribution: Anatolian Peninsula and Greece ..... *M. longisetus* sp. n.
22. Anterior surstyle lobe elongated, triangular; posterior surstyle lobe elongated and narrow (fig. 35C: al) .....  
 ..... *M. femoratoides*
- Anterior surstyle lobe shorter, not triangular; posterior surstyle lobe shorter ..... 23
23. Anterior surstyle lobe square-shaped (Fig. 13E: al); lateral projections on hypandrium gradually tapering to the tip (fig. 30C: lp) .....  
 ..... *M. quadraticus*
- Anterior surstyle lobe high boot-shaped (fig. 29A: al); lateral projections on hypandrium narrow only in apical 1/4 (fig. 30A: lp) ..... *M. cohurnus* sp.n.
24. Posterior surstyle lobe broad, anterior surstyle lobe very short (fig. 13F: al, pl) .....  
 ..... *M. taniniensis*
- Posterior surstyle lobe narrower, anterior surstyle lobe longer ..... 25
25. Posterior surstyle lobe shorter, 1.5 times as long as wide (fig. 35A: pl) .....  
 ..... *M. nigratarsis*
- Posterior surstyle lobe longer, 2.5 times as long as wide (fig. 35B: pl) .....  
 ..... *M. latifemoris*