



Insights from the preimaginal morphology of the *constans* species-group, to reveal novel morphological patterns of the *Merodon albifrons*-evolutionary lineage (Diptera, Syrphidae)

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Abstract

Merodon triangulum Vujčić, Radenković & Hurkmans, 2020 is a European endemic hoverfly species belonging to *Merodon constans* species-group, inside *albifrons*-lineage. The distribution of this species is known to be mostly central Europe and Balkan peninsula and it has been categorized as Near Threatened in the European IUCN red list of hoverflies; this paper cites the species for the first time in Ukraine (western Ukraine, specifically). In the present study, the preimaginal stages of this species are described and figured using Scanning Electron Microscopy. The material used for the descriptions were larvae collected in Ukraine and Serbia feeding inside underground storage organs of the spring snowflake *Leucojum vernum* L., 1753. This morphological description constitutes the first one inside the *constans* species-group, and the sixth description of the *albifrons*-lineage, in which there is only one species-group left to have at least one species of the preimaginal stages described (i.e., *ruficornis* species-group). The descriptions were compared with the rest available of the genus, stating the diagnostic characters of the present species and the shared characters inside the lineage. The novel information provided on the trophic interaction between *M. triangulum* larvae and *Leucojum* bulbs is stated for the first time and further supports the association of the *constans* species-group with the underground storage organs of snowflakes and snowdrops (Galanthaceae) in their role as host plants.

Keywords Hoverflies · Host plant · *Merodon triangulum* · SEM · Immature stages

Introduction

Hoverflies and bees are the main players in natural plant pollination, moreover, hoverflies visit at least 72% of global food crops and over 70% of animal-pollinated wildflowers (Doyle et al. 2020; Toivonen et al. 2022). The genus *Merodon* Meigen, 1803 is of great importance in the study of the plant–pollinator relationship (Petanidou et al. 2013). It is also one of the richest hoverfly genera with 211 species known (more than 120 of them occurring in Europe), and the highest species diversity recorded in the Mediterranean Basin, a hotspot of species diversity and endemism (Vujčić et al. 2021, 2022). Phylogenetic analyses of the genus established 5 monophyletic evolutionary lineages and more than 20 species-groups, with *Merodon triangulum* Vujčić, Radenković & Hurkmans, 2020 belonging to the *albifrons*-lineage and the *constans* species-group (Vujčić et al. 2021). *Merodon triangulum* is considered a European endemic species, mainly distributed in central Europe and Balkan

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Peninsula, and categorized as Near Threatened species in the recently published IUCN European Red List (Janković and Radenković 2021).

The preimaginal biology and morphology of most *Merodon* species remain unknown, and only 14 species have the preimaginal stages described (Aracil et al. 2022b). However, the development of all known species occurs in underground storage organs of monocotyledonous plants of Liliales and Asparagales orders, and more specifically to families Liliaceae Juss., Amaryllidaceae J. St.-Hil. s. l., Asparagaceae Juss., and Iridaceae Juss. The relation of the genus with the host plant is not restricted only to larvae but also includes adult feeding and oviposition (Ricarte et al. 2017; Speight 2020), constituting a whole life cycle closely related with the plant, nevertheless, due to the lack of information, more studies are needed to determine the degree of specificity of the genus with these families.

Regarding the information available inside the *Merodon* genus, *albifrons*-lineage presents the highest number of preimaginal stages described, with 5 species described compared to the 3 available descriptions in *natans*-lineage and two described in each of the rest (*aureus*, *desuturinus* and *avidus-nigritarsis* lineages). Inside of *albifrons*-lineage, each of the species described belongs to a different species-group: *M. hurkmansi* Marcos-García, Vujić & Mengual 2007 to *albifrons* group, *M. equestris* (Fabricius 1794) to *equestris* group, *M. geniculatus* Strobl in Czerny & Strobl 1909 to *geniculatus* group, *M. rufus* Meigen, 1838 to *rufus* group and *M. luteihumerus* Marcos-García, Vujić & Mengual 2007 which is not placed in any group inside the lineage (Vujić et al. 2021). Recently, Langlois and Speight (2022) provided photos of the larva and puparium of *M. analis* Meigen, 1822 (*constants* species-group), but without description. Therefore, the present description of *M. triangulum* provides information on the first preimaginal stages described of the *constants* species-group (Aracil et al. 2022a), remaining only the *ruficornis* species-group to be described (data in prep) to complete the knowledge of the evolutionary lineage of *Merodon albifrons*.

The aim of this study is to present the first data about the preimaginal morphology (both larva and pupa) of this species, described using both optical and scanning electron microscopy (SEM).

Materials and methods

Collecting sites and sampling procedure

In Serbia and Ukraine, during a field investigation of the localities where stable populations of adult *Merodon* were previously recorded, seven *Merodon* larvae were found in the bulbs of the spring snowflake *Leucojum vernum* L.,

1753 (Amaryllidaceae). All larvae were collected feeding on the bulbs. Three larvae were kept frozen (− 20 °C) for several days and preserved in 70% ethanol, and four larvae were reared at an ambient temperature until adults emerged (after 55, 56 and 68 days in Serbia, and after 80 days in Ukraine). The studied material of puparia and larvae has been deposited in the collection of the Department of Biology and Ecology, Faculty of Sciences, University of Novi Sad, Serbia (FSUNS) and the Department of Environmental Sciences & Natural Resources of the University of Alicante, Spain (CEUA).

Morphological study

Terminology used for larval and pupal descriptions follows Rotheray (1991, 1993), head skeleton description was done following Courtney et al. (2000), Rotheray and Gilbert (2008) and Rotheray (2019) specifically regarding the concept of mouth-hook. The morphological analysis was performed following the methodology stated by Aracil et al. (2022b).

Puparia were cleaned before morphological analysis. To do so, they were immersed in water for several hours. Soil and debris were removed from the surface using pins and brushes, and puparia were placed in an ultrasonic cleaner for a few minutes until adherent material had fallen off the integument. The head skeleton was removed from the antero-ventral margin of the puparium using entomological pins, then soaked in 10% potassium hydroxide (KOH) and heated for 15 min to remove the remaining tissue. It was then soaked in acetic acid to neutralize the KOH, followed by 70% ethanol to eliminate the acid, for a few minutes each. The skeleton was then preserved and examined in glycerin.

Morphological studies on the puparium were conducted using a Hitachi SEM (Scanning Electron Microscope) S3000N (Hitachi Ltd, Tokyo, Japan) at 20 kV at variable-pressure (or low vacuum) mode. The examination of the general view of larva, puparium and head skeletons was conducted using a Nikon SMZ 745T (with Nikon Coolpix D7100 digital camera) (Nikon Corporation, Tokyo, Japan); dimensions were measured using an eyepiece micrometer attached to the stereomicroscope.

Material examined

UKRAINE, Starunya; 48.7083071 °N, 24.4664652 °E; 30.III.2020; V. Shparyk leg.; 1 (L3 instar) larva in the bulb of *Leucojum vernum*: reared, adult emerged 18.VI.2020 (♂); SIZK.2023.049; CEUA (puparium). SERBIA, Petrovaradinski rit; 45.229133°N, 19.898193°E; 29.IV.2020; A. Vujić, P. Radišić, M. Miličić, M. Janković, A. Šebić leg.; 6 (L3 instar) larvae in the bulbs of *Leucojum vernum*: 3 preserved and 3 reared, adults emerged 23.VI.2020 (♀), 24.VI.2020 (♀) and

06.VII.2020 (♀); FSUNS (imagoes, preserved larvae and one puparium); CEUA (2 puparia).

Results

Larvae overall characters

Length: 15.8 mm, greatest width: 6.4 mm, height: 4.8 mm ($n = 2$); sub-cylindrical in shape and sub-circular in cross section, flattened ventrally; anterior end truncated, and posterior end slightly tapered. Light to dark brown in color, getting darker after fixation (Fig. 1A). Mouth-hooks external, well developed and highly sclerotized (Fig. 1B). Rough integument with segmentation as transverse wrinkles, integumental vestiture well-developed, with short, pointy, directed backwards and sclerotized brown spicules being more pointed in dorsal surface and longer and densely aggregated in the anal segment (both in dorsal and ventral view); segmental sensilla conspicuous, consisting of wider basal papilla bearing long needle-like terminal setae projected backwards. Anal segment with one pair of lappets located ventrally, below posterior respiratory process (PRP) with fleshy projections (Fig. 1B).

Head skeleton

Mandibles, with black sclerotized hooks with a pair of small accessory teeth on their inner side. Mouth-hooks projecting downwards along each side of the mouth, fused to the

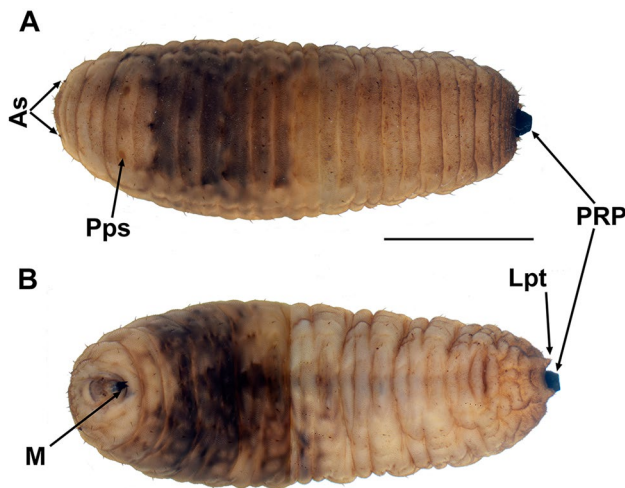


Fig. 1 Habitus images of a third instar larva of *Merodon triangulum* in dorsal (A) and ventral (B) view. Note that the posterior respiratory process is patently visible in both dorsal and ventral view. As pair of larval anterior spiracles, Lpt lappet, M mouth-hooks, Pps primordium of the left pupal spiracle, PRP posterior respiratory process. Scale bars: A, B 5 mm

black sclerotized external mandibular lobes (Figs. 2, 3A and B). Dorsal cornu narrowed and tapered slightly downwards towards the sharp apex, representing almost whole length of ventral cornu, giving a pear shape to the basal sclerite; dorsal bridge, vertical plate and intermediate sclerite apparently fused together and all highly sclerotized; ventral cornu elongate and narrow in profile view, with cibarium located at the base, bearing barely developed ridges, wider and more heavily sclerotized at the posterior end, forming grinding mill of pestle and mortar construction (Fig. 2).

Pseudocephalon and thorax

Dorsal lip smooth with no ornamentation. Lateral and ventral lips not very developed, with similar ornamentation as the rest of the integument, being more pointed than ventral surface ornamentation (Fig. 3B). Well-developed and sclerotized antenno-maxillary organs placed on top of a pair of fleshy rounded projections placed between dorsal lip and dorsal surface of the prothorax and a basal cushion covered with rounded and domed spicules posteriorly. Antenno-maxillary organs consist of two pairs of cylindrical to conical-shaped structures with sensilla on top, one big sensillum on top of antenna and some small ones on top of maxillary palpi (Fig. 3B and C). The dorsal surface of the prothorax with five longitudinal grooves, with conspicuous aggregated light-brown spicules. Ornamentation on the two central ridges of the prothorax elongated progressively, forming a rectangular patch of longer spicula between the third pair of sensilla of the prothorax and mesothorax (Fig. 3C). Pair of anterior larval spiracles almost twice as long as broad at the base, sclerotized, reddish-brown in color, cylindrical with a big scar at the base (Fig. 4B), facing outwards the larval

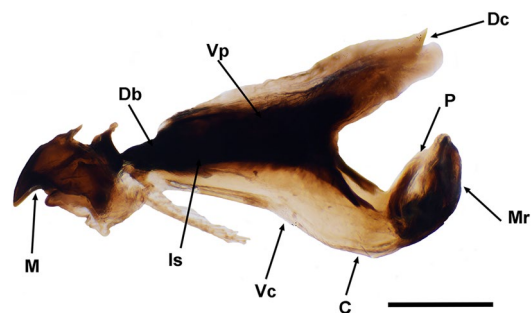


Fig. 2 Lateral view of the larval head skeleton removed from a puparium. Mouth-hooks fused centrally and heavily sclerotized. Dorsal cornua are joined together at the anterior part by the dorsal bridge and fused to ventral cornua by the vertical plate and intermediate sclerites. Ventral cornua with the cibarium at the base and with posterior part forming a grinding mill structure with two heavily sclerotized structures: the mortar and the mobile pestle. Db dorsal bridge, Dc dorsal cornu, C cibarium, Is intermediate sclerite, M mouth-hooks, Mr mortar, P pestle, Vc ventral cornu, Vp vertical plate. Scale bar: 300 μ m

Fig. 3 Prothorax of a third instar larva. Frontal view of the prothorax (A) showing the position of the anterior spiracles, antenno-maxillary organs, and mouth-hooks. Ventral view (B) showing SEM images of the antenno-maxillary organs, the dorsal and lateral lips and the mouth-hooks. Dorsal view (C) showing SEM images of the five longitudinal grooves of the prothorax (numbered 1–5), the dorsal segmental sensilla and the base of antenno-maxillary organs. *Ao* antenno-maxillary organs, *As* anterior spiracles, *Bao* base of antenno-maxillary organs, *DI* dorsal lips, *LI* lateral lips, *M* mouth-hooks, *Sn* segmental sensillum. Scale bars: A, B 700 μ m; C 1 mm

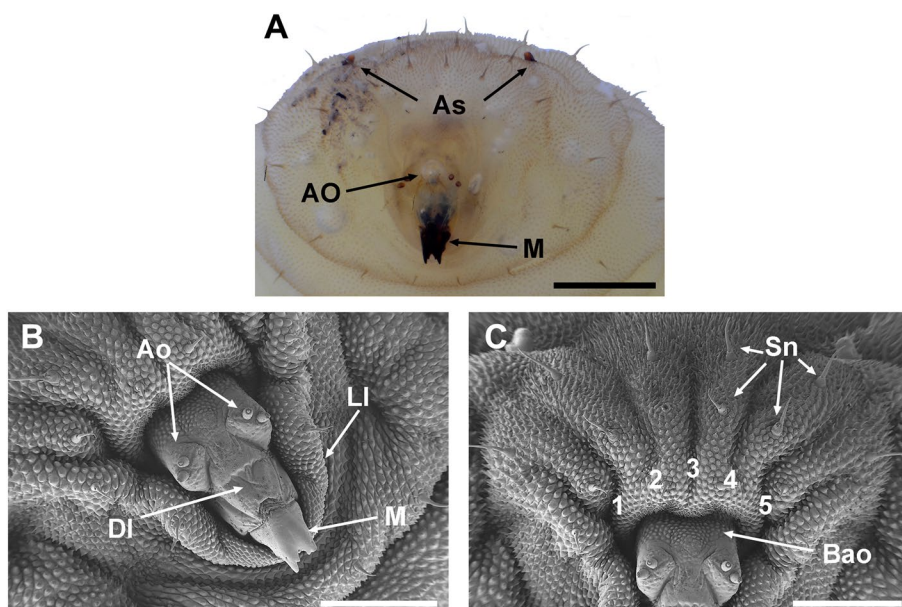
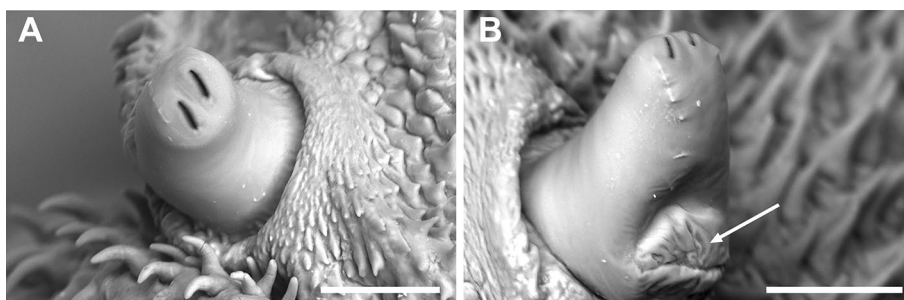


Fig. 4 SEM images of the larval anterior spiracle (photographed in the puparium). Zenithal view (A) showing two linear spiracular openings in a parallel position, and in lateral view (B) with a big scar at the base. Scale bars: A, B 100 μ m



body, with two linear spiracular openings, in a parallel position, at the apex (Fig. 4A). Mesothoracic prolegs absent.

Abdomen

Primordia of pupal spiracles present on the dorsal surface of the first abdominal segment, indicating the third larval stage (Fig. 1A). Absence of prolegs, raised elongated domes present in 1–7th abdominal segments as locomotory organs, lacking crochets. Circular patch of shorter, blunter, and densely aggregated spinules present at the external bases of the domes (Fig. 5). Dorsally, abdominal segments 1–6th bearing three folds each, segmental sensilla 1st and 2nd present in the second fold and segmental sensilla 3rd and 4th slightly posterior; on the abdominal segment 7th, three folds present, bearing first segmental sensilla on the second fold and 2nd and 3rd in third fold. Anal segment bearing three very thin folds, only one pair of lappets present, located ventrally below the PRP (Posterior Respiratory Process), bearing longer fleshy papilla totally covered with long spiculae (of the same ornamentation, but longer, looking more like setae) with sensillum

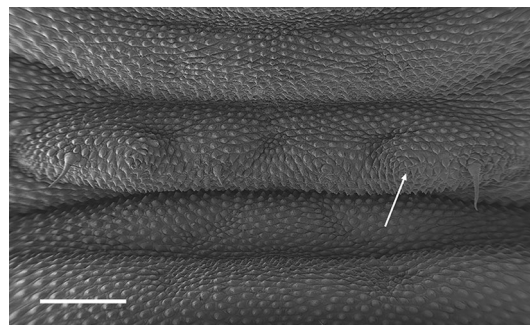
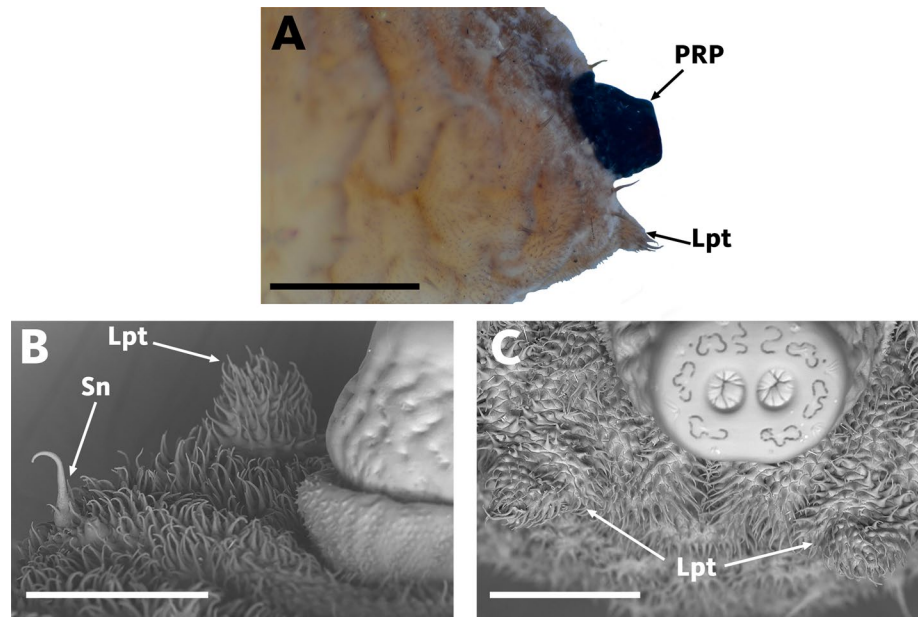


Fig. 5 SEM image of the right abdominal locomotory organ of a third instar larva looking as raised elongated domes, lacking crochets. Scale bar: 500 μ m

4th on top (Fig. 6A and C). Dorso-laterally, sensilla 2nd and 3rd are very close to each other but not on top of fleshy projections so they are not considered as lappets (Fig. 6B). Ventrally, the central lobe of the anal segment is wider anteriorly, becoming slightly narrower towards the posterior apex (parallel margins), sensilla 4–5 are between sensilla 6 and 7 (Fig. 1B).

Fig. 6 Anal segment of a third instar larva. Lateral view (A), of the posterior respiratory process and the ventral lappets. SEM images. B, C Detail, in dorsal view (B), of the ventral lappets totally covered with long spiculae and third left segmental sensillum. Zenithal view (C), showing the pair of lappets located ventrally below the posterior respiratory process. *Lpt* lappets, *PRP* posterior respiratory process, *Sn* segmental sensillum. Scale bars: A, 1.5 mm; B, C 500 μ m



Posterior respiratory process

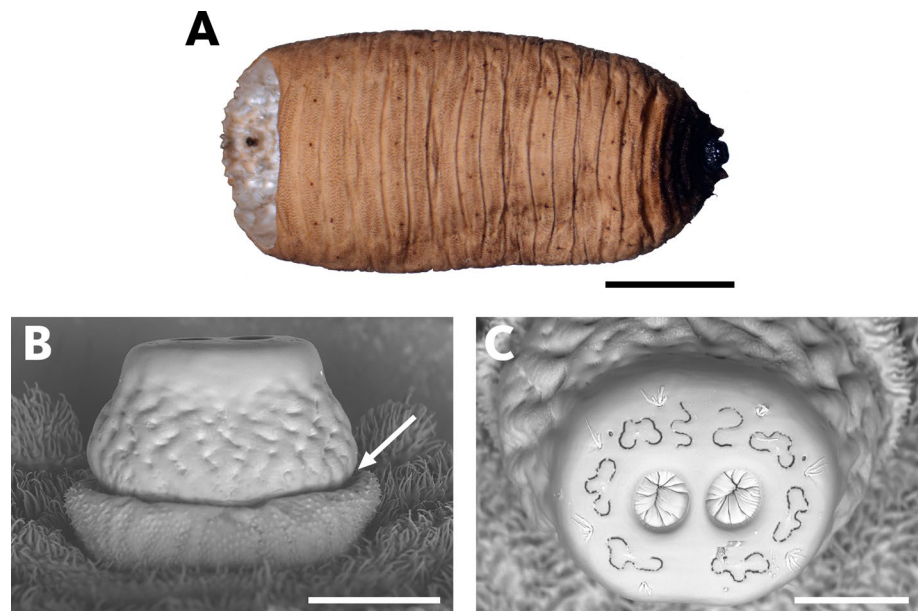
Black and shiny, clearly visible from dorsal view, in the shape of a truncated cone, slightly wider than long, with base slightly wider than apex, with an annular groove at the base; entirely coriaceous and conspicuously ornamented from base to central area, smooth surface at the very apex; lateral surface with undulate grooves and small dents above annular groove and granulated below annular groove (Fig. 7B); the outline of the spiracular plate sub-elliptical and mostly regular in polar view; four pairs of well-developed inter-spiracular setae emerging from the edge of the spiracular plate; spiracular plate with four pairs

of slightly convoluted irregularly-shaped spiracular openings around two central scars; spiracular scars in a pair of abrupt cavities, sunken depressions in the middle of the spiracular plate (Fig. 7C).

Chaetotaxy

Prothorax (Pr) with 10 pairs of sensilla (9th and 10th together, not separated). Mesothorax (Ms) and metathorax (Mt) with 8 pairs of sensilla. First to seventh abdominal segment with 9 pairs of sensilla. The anal segment with 7 pairs of sensilla.

Fig. 7 Empty puparium. Dorsal view (A). SEM images of the posterior respiratory process. B lateral view showing the shape of a truncated cone with an annular groove at the base. C zenithal view of the spiracular plate, with two central scars and 4 pairs of undulated slits. Scale bars: A 3 mm; B, C 500 μ m



Puparium overall description

Sub-circular in cross-section, slightly tapered posteriorly and flattened ventrally. Light brown in colour rough integument with larval segmentation persisting as transverse folds and wrinkles (Fig. 7A). The length including PRP is 13.35 ± 1.04 mm, the maximum width is 6.45 ± 0.59 mm and maximum height is 6.15 ± 0.73 mm ($N=4$). Pupal spiracles are projected from the upper part of the operculum, being separated by a distance about four times the length of one spiracle.

Pupal spiracles

Sclerotized, dark brown in color, stout, cylindrical in shape, slightly tapered towards the apex; length ≈ 0.6 mm, 2–3 times as long as broad; separated by distance of ≈ 4 times their length; with the exception of the lower part of ventral surface, the whole structure covered with irregularly-spaced, oval-shaped domed tubercles on top of multiple layers (3–7) each; spiracular surface reticulated, ventral surface not bearing tubercles smoother, granulated at the apex (Fig. 8A and B); 4–9 radially arranged sub-elliptical spiracular openings on each tubercle (Fig. 8C).

Discussion

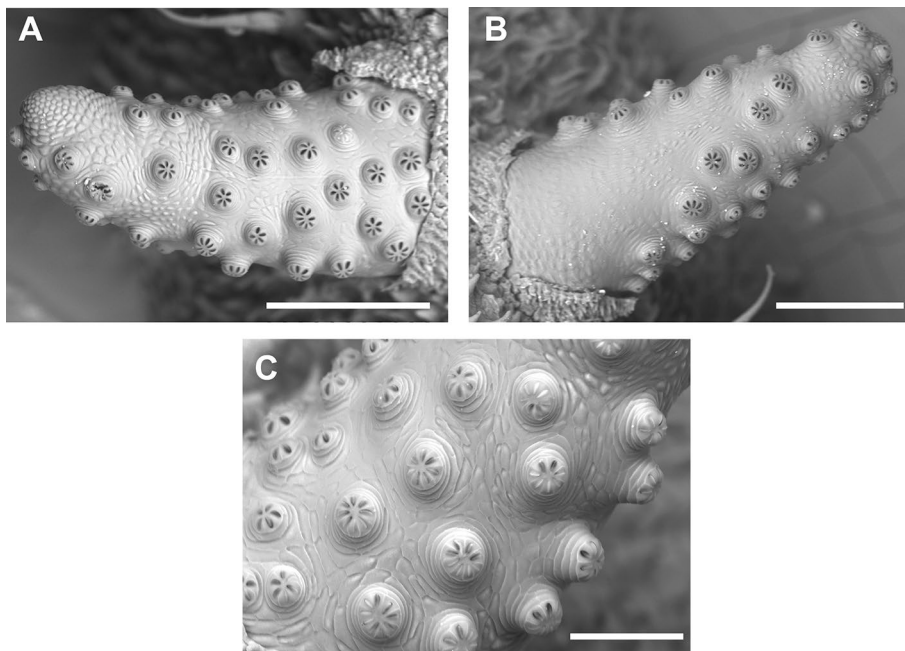
The overall preimaginal morphology of *Merodon triangulum* fits with the main diagnostic characters of the *Merodon* genus, for example the external and sclerotized mouth-hooks

or the shape of the locomotory organs (Ricarte et al. 2008). It also supports the new common characters for the genus stated by Aracil et al. (2022b), i.e., four spiracular openings in the PRP and the cylindrical pupal spiracles with a rounded protuberance on top.

As already mentioned before, this study increases our knowledge of the preimaginal stages of evolutionary *Merodon albifrons*-lineage adding information related to *constans* species-group. All the species that have been already described inside this evolutionary lineage, share a similar morphology, nevertheless some differences can be noticed to distinguish between them. The most different species of the lineage is *M. rufus*, which presents a PRP much wider than long, with the base wider than the apex, markedly narrowed on its apical third (see Fig. 3E and F in Preradović et al. 2018). Moreover, the pupal spiracles present a polygonal pattern in the whole surface, deeply marked (Fig. 2D in Preradović et al. 2018).

Moreover, *M. triangulum* has also significant differences compared with rest of the species of lineage. Then, comparing with *M. luteihumerus* it can be noticed that the surface of the PRP in the apical part is reticulated in this species (Fig. 8B in Ricarte et al. 2008), while in *M. triangulum* is totally smooth. The surface between the tubercles in the pupal spiracles also differs, being smooth in *M. luteihumerus* (Fig. 8 C and D in Ricarte et al. 2008) and reticulated in *M. triangulum*. On the other hand, *M. hurkmansi* (described as *M. constans* in Ricarte et al. 2008) larvae presents shorter spicules in dorsal area of the body (as long as basally broad) compared to *M. triangulum*, which present longer spicules more setae alike. Additionally, according to the description,

Fig. 8 SEM images of the pupal spiracles. Dorsal surface (A) completely covered with irregularly spaced, oval-shaped domed tubercles. Ventral surface (B) covered with domed tubercles except at the lower part. C detail of spiracular tubercles and the reticulated surface. Scale bars: A 250 μ m; B 200 μ m; C 100 μ m



M. hurkmansi has well-developed dorsal lappets on the anal segment, located on top of fleshy papillae (Ricarte et al. 2008); this structure is not present in *M. triangulum*. Furthermore, the differences between *M. equestris* and *M. triangulum* are in the transversal groove and surface of the PRP, the transversal groove in *M. equestris* is placed at the basal third of the structure (Dixon 1960), while in *M. triangulum* is more basal, being placed at 1/4 of it. Regarding the surface above this groove in the PRP, in *M. equestris* it presents deep longitudinal furrows up to the apex (Dixon 1960), but in *M. triangulum* the apex is completely smooth, and some undulated grooves and small dents are present in the central area above the groove. On the other hand, *M. geniculatus* is also mostly different from *M. triangulum* in the shape and size of the PRP, in *M. triangulum* PRP is about 0.8 mm long and presents a shape like a truncated cone, with the margins converging but *M. geniculatus* has a PRP half of the length of *M. triangulum* (around 0.4 mm according to Fig. 5D in Ricarte et al. 2017) and it presents a rectangular shape with parallel margins (Ricarte et al. 2017).

Different attempts have been made to find a distinctive character of preimaginal stages to taxonomically distinguish each *Merodon* lineage, PRP appears to be the most feasible character for this purpose, clear differences have been observed for *avidus-nigritarsis* and for *aureus*-lineage (Aracil et al. 2022b). However, up to now, the characteristics of *albifrons*, *desutrinus* and *natans* lineages cannot be clearly separated. The present description does not contribute with any enlightening different character, neither in the PRP, nor in any other structure. Nevertheless, giving the lack of published data on *Merodon* preimaginal stages, these findings represent a valuable piece of the puzzle in the quest of revealing characters of taxonomical importance, but more descriptions are needed to perform a deep comparative analysis and to find the proper diagnostic traits.

Before this paper, *M. triangulum* was only known from northeastern Italy, northern Austria, eastern Hungary, Slovenia, Croatia, Serbia, Montenegro, North Macedonia (Vujić et al. 2020a; Janković and Radenković 2021) but after our records, the species is also present in western Ukraine. Also, its larval biology remained unknown, but recently a close relation with *Leucojum vernum* bulbs, was detected (Aracil et al. 2022a). In fact, spring snowflakes have also been reported as alternative host plant for other species of the *constans*-group such as *M. analis*/*M. constans* (Langlois 2022; Langlois and Speight 2022). Interestingly, snowflakes (*Leucojum* L.) are phylogenetically very close to snowdrops (*Galanthus* L.), which have previously been recorded in connection with larval habits of the *constans*-group (Hurkmans & de Goffau 1995; Popov 2013; Popov and Mishustin 2019). This would confirm the close relationship of the group of species with the underground storage organs of snowflakes and snowdrops (Amaryllidaceae: Galantheae) as host plants.

Plant population of *L. vernum* in Petrovaradinski rit (Serbia), where *M. triangulum* larvae were found, is extremely high. But despite of almost two hectares covered with densely distributed spring snowflakes, larvae were only found on the edge of this area, near to forest edge, where the plant population density is much smaller. That may be related to habits of *M. triangulum* adults which prefer less exposed habitats near to the forest. This preference has also been reported for *M. analis/constans* ("trou de lumière" or small spaces of up to 10 m²) near areas with presence of snowflake bulbs and preimaginal stages of this species, whose morphological description is being currently studied (Langlois and Speight 2022).

In addition, bulbs of other Amaryllidaceae were recorded as larval food for other species groups of the *albifrons*-lineage. Namely, *Narcissus* L. is known to be the host for larvae of *M. geniculatus*, *M. equestris*, *M. eques* (Fabricius, 1805), and *M. neofasciatus* Ståhls & Vujić in Vujić et al. 2018, while latter species and *M. luteofasciatus* Vujić, Radenković & Ståhls in Vujić et al. 2018 are related to taxon referred to as "*Amaryllis*", most likely *Sternbergia* Waldst. & Kit. (Pehlivan and Akbulut 1991; Ricarte et al. 2017; Vujić et al. 2018; Speight 2020). Finally, it should be noted that the genus *Merodon* and the polyphagous species *Merodon equestris* has also been generically related with imported bulbs of *Leucojum* sp. or gardens (Fryer 1914 in Hodson 1932; Doucette et al. 1942; Rotheray 1993). However, although it is possible that related species-groups of *Merodon* may use the same trophic resources as larval hosts plants (Vujić et al. 2020b), this relationship needs to be confirmed with accurate taxonomic identifications as they may correspond to other species (Doucette et al. 1942; Smit and Langeveld 2018). In this regard, it has been reported that *Merodon analis/constans* larva was unable to survive on the common snowdrop (*Galanthus nivalis* L.) bulbs replanted in gardens in France which could be related to some requirement of its life cycle (Speight and Langlois 2020) or to a high trophic specificity of the *constans* species-group (data in prep). As the host plants of less than one tenth of all *Merodon* species described so far, no definite conclusions could be drawn in this context and further studies are needed to clarify the exact nature of interactions between plants and this relevant and diverse group of hoverflies.

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Author contributions Conceptualization: RM, VS; Methodology: AAR, AAn, CP-B; Formal analysis and investigation: GP, SRo; Writing – original draft preparation: AAR, AAn; Writing – review and editing: All authors; Funding acquisition: SRA, CP-B; Resources and supervision: AV, CP-B and SRo.

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Declarations

Conflict of interest The authors have no competing interest to declare that are relevant to the content of this article.

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