



# First data about the preimaginal morphology of *Austroscaeva occidentalis* (Shannon, 1927) and re-description of larvae and pupae of *Dioprosopa clavata* (Fabricius, 1794) (Diptera: Syrphidae)

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## Abstract

Preimaginal morphology of *Austroscaeva occidentalis* (Shannon, 1927) is described for the first time, and the morphology of larvae and pupae of *Dioprosopa clavata* (Fabricius, 1794) is updated based on material obtained from captive rearing of wild females from Argentina and Venezuela, respectively. We describe the morphology of the third instar larva, head skeleton and puparium using optical microscopy, cryo-scanning and scanning electron microscope. The immature stages of both New World flower fly species are analysed and compared with the known preimaginal morphology of other taxa that belong to the evolutionary lineage of *Eupeodes-Scaeva*, where *Austroscaeva* Láska, Mazánek & Mengual, 2018, and *Dioprosopa* Hull, 1949, form a Neotropical radiation within, together with the genus *Notosyrphus* Vockeroth, 1969. Larvae of all members of this lineage have abdominal segments 5 and 6 with the tips of the locomotory prominences facing posteriorly, and the anal segment with a characteristic U-shaped grasping organ. Two other larval synapomorphies of this group of genera are the presence of metathoracic setae accompanying ventral sensilla, and the abdominal segments 1–7 with an extra lobe on each locomotory prominence. These two last characters cannot be assessed for *Macrosyrphus* Matsumura, 1917, and *Lapposyrphus* Dušek & Láska, 1967, based on published information on larval descriptions. Despite a similar colouration pattern of the fully grown larvae, larval morphology of *A. occidentalis* and *D. clavata* are quite distinct. The preimaginal morphology of *A. occidentalis* has a mixture of morphological characters from the taxa *Scaeva* Fabricius, 1805, *Semiscaeva* Kuznetzov, 1985, and *Dioprosopa*. The larvae of *D. clavata* show several unique diagnostic features, such as the presence of a slightly serrate outline due to the great development of the segmental spines and a pinnate ornamentation of the setae of its dorsal and dorsolateral sensilla. Regarding their biological cycle, the length of the preadult stages of *A. occidentalis* is almost 5 days longer than the length observed for *D. clavata*. In addition, new DNA barcodes are provided for *A. occidentalis*.

**Key words** biology, chaetotaxy, DNA barcoding, flower flies, head skeleton, hover flies, Neotropical Syrphinae.

## INTRODUCTION

True flies of the family Syrphidae (Insecta: Diptera) provide important ecosystem services. Commonly called hover or flower flies, adults are important pollinators (Szymank and Kearns 2009; Inouye *et al.* 2015) and can be used as bioindicators of environmental stress, woodland quality or landscape diversity (Haslett, 1988; Good & Speight, 1996; Sommaggio 1999), while larvae play an important role as decomposers (Lardé 1989; Rotheray *et al.* 2009; Martínez-Falcón *et al.* 2012) and biological control agents of pests (Schmidt *et al.* 2004; Bergh and Short 2008; Nelson *et al.* 2012; Eckberg *et al.* 2015).

The largest species radiation of Syrphidae is found in the Neotropical region, with more than 1800 species currently known and many more to be described (Thompson 1999; Thompson *et al.* 2010). The latest described Neotropical genus in the subfamily Syrphinae is *Austroscaeva* Láska,

Mazánek & Mengual, 2018, which comprises four species, that is, *Austroscaeva melanostoma* (Macquart, 1842), *Austroscaeva occidentalis* (Shannon, 1927), *Austroscaeva penai* (Marnet in Dušek and Láska 1985) and *Austroscaeva patagoniensis* (Kassebeer 1999) (see Mengual *et al.* 2018). This small group of Neotropical species has previously been included in *Scaeva* (Fabricius, 1805), although it has been recognised as a distinct group with some differences from *Scaeva* species such as having the face more produced forward and an almost straight vein  $R_{4+5}$  (Dušek and Láska 1985; Kassebeer 1999; Láska *et al.* 2006).

The genus *Austroscaeva* occurs in the Andean region of Colombia, Ecuador, Peru, Bolivia, Chile and Argentina (see Kassebeer 1999). Nothing is known about the life cycle and the morphology of the preimaginal stages of this genus. Regarding the natural history of the adult stage, some *Austroscaeva* species are floral visitors of the invasive *Taraxacum officinale* (L.) Weber ex F.H. Wigg. as well as native Asteraceae plants (Muñoz and Cavieres 2008, 2019), *Anemone multifida* Poir.

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(Ranunculaceae), and several Solanaceae, *Solanum* spp. (Johns and Keen 1986; Gavini *et al.* 2019). They are also members of the pollinator community of high alpine habitats in the Andes (Arroyo *et al.* 1982; Medan *et al.* 2002) and are floral visitors of several Rhamnaceae as *Ochetophila trinervis* (Gillies ex Hook.) Poepp. ex Endl. and *Kentrothamnus weddellianus* (Miers) (Miers) M.C. Johnst., *Erythranthe lutea* (L.) G.L. Nesom (Phrymaceae) and *Chaetanthera apiculata* F. Meigen and *C. lycopodioides* (Remy) Cabrera ex Cabrera (Asteraceae) (Medan and Devoto 2005; Torres-Díaz *et al.* 2007; Medan *et al.* 2013; Medel *et al.* 2018) in these areas. Muñoz and Arroyo (2004) reported that the presence of vertebrate predators significantly reduces the number of visits of *A. melanostoma* on flowers of the Andean shrub *Chuquiraga oppositifolia* D. Don, and Gavini *et al.* (2019) observed that the crab spider *Misumenops pallidus* (Keyserling, 1880) preys on adults of *A. occidentalis* with a sit-and-wait strategy on Ranunculaceae flowers.

*Austroscaeva* belongs to the predatory lineage of flower flies *Eupeodes-Scaeva*, a distinct 'natural group' sensu Dušek & Láška (1967; 1985), together with other genera of the subfamily Syrphinae. Within this evolutionary lineage, *Austroscaeva* is related to other Neotropical genera (i.e. *Dioprosopa* Hull, 1949 and *Notosyrphus* Vockeroth, 1969) based on molecular characters (Mengual *et al.* 2018). These three genera are resolved as a Neotropical radiation within the *Eupeodes-Scaeva* lineage, while the other members of the lineage (*Eupeodes* Osten Sacken, 1877, *Ischiodon* Sack, 1913, *Lapposyrphus* Dušek & Láška, 1967, *Scaeva* Fabricius, 1805, *Semiscaeva* Kuznetsov, 1985, *Simosyrphus* Bigot, 1882, and *Pseudodoros* Becker, 1903) are recovered in three other major groups (Mengual *et al.* 2018): *Eupeodes* (including the two subgenera *Macrosyrphus* and *Eupeodes*), *Lapposyrphus*, and the *Scaeva* clade (here defined to include *Semiscaeva*, *Scaeva*, *Ischiodon*, *Simosyrphus* and *Pseudodoros*). The close phylogenetic relationship of some of these taxa was previously reported based on the morphology of the immature stages (Láška *et al.* 2006).

The known larvae of this lineage have an autapomorphic set of locomotory structures at their rear end, the so-called U-shaped grasping organ (Rotheray 1987; Rotheray and Gilbert 1999). This U-shaped grasping organ consists of a well-developed grasping bar on the anal segment and two pairs of specially developed, large locomotory prominences on abdominal segments 6 and 7, each with up to four projecting lobes (Rotheray and Gilbert 2011). The mechanism of this organ is well explained by Rotheray and Gilbert (2011): 'Together, the grasping bar and these locomotory prominences are opposable, similar in function to the fingers and opposable thumb of the human hand, enabling cylindrical objects to be grasped and manipulated. The grasping organs grip the stem just like a hand, and the larva can let go with the rest of its body to cast and scan ahead. When moving up or down on a stem, the larva grips with either its mouthparts or the opposable grasping organs and moves up or down while curled around the stem'. These authors consider that 'The opposable grasping organs give these larvae a clear advantage when moving about on stems and petioles [...] these larvae rarely fall off and can search for prey more effectively and at

relatively faster speeds. Larvae without these organs do not curl round stems and can only move and scan one face at a time. Prey are able to escape simply by moving round to the other side of the stem'. There is no information on the biology, life cycle and morphology of the preimaginal stages of *Austroscaeva*, but according to its phylogenetic placement, the U-shaped grasping organ was hypothesised to be present in this genus (Mengual *et al.* 2018). In fact, within the Neotropical radiation in the *Eupeodes-Scaeva* lineage only the preimaginal morphology of the species *Dioprosopa clavata* (Fabricius, 1794) is relatively well known (Heiss 1938; De la Pava and Sepúlveda-Cano 2015).

The genus *Dioprosopa* comprises only two New World species. *Dioprosopa vockerothi* Kassebeer 2000 occurs in the Andes, with a distribution area extending from northern Chile to Ecuador. The second species, *D. clavata* (Fabricius, 1794), is very abundant and widely distributed from southern USA to Chile and Argentina (Kassebeer 2000). Even though *Dioprosopa* is a very characteristic genus, its taxonomic status has changed many times. This species is commonly listed as *Baccha clavata* (Fabricius, 1794) in most catalogues and publications of the first half of the 20th century (e.g. Fluke 1956; Wirth *et al.* 1965). Hull (1949a, 1949b) erected *Dioprosopa* as subgenus of *Baccha* Fabricius, 1805 for *Syrphus clavatus* Fabricius, 1794, but Thompson *et al.* (1976) synonymised *Dioprosopa* under *Pseudodoros* and the species became known as *Pseudodoros clavatus* for the last five decades. Kassebeer (2000) described a second species and advocated full generic status for *Dioprosopa*, leaving *Pseudodoros* with a single species, *Pseudodoros nigricollis* Becker, 1903, present exclusively in the Eastern Mediterranean and Afrotropics (van Eck and Makris 2016). Recently, based on molecular characters, Mengual *et al.* (2018) resolved both taxa as separate valid genera in a comprehensive phylogenetic study.

*Dioprosopa clavata* is widely distributed in the tropical and subtropical areas of the Nearctic and the Neotropical regions (Kassebeer 2000). Several authors have highlighted the importance of this species as a natural enemy of at least twenty species of aphids (see Campbell and Davidson 1924; Heiss 1938; Guagliumi 1962; Cermeli 1983; Rojo *et al.* 2003; Díaz *et al.* 2004), the grapevine phylloxera (Silva *et al.* 1968 cited in Freitas 1982) and some species of psyllids, mealybugs, whiteflies and spider mites (Thompson and Simmonds 1965; Michaud 2002). The biology and life cycle of *D. clavata* have been studied mainly in the laboratory under captive rearing (Belliere and Michaud 2001; Auad 2003; Torrealba and Arcaya 2014; Arcaya *et al.* 2018), but it is also known to be predatory on aphids tended by ants in nature (Bächtold and Del-Claro 2013). Regarding previous morphological studies of the preimaginal stages of *D. clavata*, the descriptions made so far are generally incomplete and superficial. The most pioneering work was done by Townsend (1897) who made, after emergence of a male, a brief description of the puparium, but without presenting any figure. Subsequently, Campbell and Davidson (1924) presented the first illustrations of its larva, including a very general description of both the larva and the puparium. The most complete description of its preimaginal morphology was given in the classic monograph of Elizabeth



Heiss in 1938. Later, Freitas (1982) described and illustrated the head skeleton of the third larval stage and more recently, De la Pava and Sepúlveda-Cano (2015) described briefly the three larval instars, focusing on the changes occurring in the cephalic morphology and the head skeleton.

The aims of the present work are to describe for the first time the preimaginal morphology of the genus *Austroscaeva* and to compare it with the preimaginal morphology of *D. clavata*. With these goals, we want to increase our knowledge of this Neotropical radiation and to provide new biological information that potentially improves our understanding of the evolution of morphological characters in the *Eupeodes-Scaeva* lineage. In addition, DNA barcodes (Hebert *et al.* 2003a, 2003b) of *A. occidentalis* were sequenced to facilitate molecular species identification.

## MATERIALS AND METHODS

### Captive rearing methodology

*Austroscaeva occidentalis* (Shannon, 1927)

Gravid wild females were collected on December 2018, feeding on *Rosa eglanteria* L. flowers, in Las Picas stream, El Manzano Histórico, Tunuyán, Mendoza, Argentina (33.696483°S 69.413469°W, 1800 m.a.s.l.). The females were isolated and introduced into plastic rearing cages with fresh pollen, sugar, honey, water and *Sonchus oleraceus* L. leaves and stems infested with the aphid *Uroleucon sonchi* (Linnaeus, 1767). Larvae were maintained at  $25 \pm 6^\circ\text{C}$ ,  $50 \pm 10\%$  RH with natural light in a lab in Mendoza, Argentina. The eggs obtained from the adult females were transferred to 140 mm diameter Petri dishes until first instar larvae hatched. Each larva was individually reared on Petri dishes feeding *ad libitum* with nymphs of the aphid *U. sonchi* until pupation. Larvae, puparia and emerged adults were preserved in ethyl alcohol 70%. The length of the conserved preimaginal stages was recorded.

*Dioprosopa clavata* (Fabricius, 1794)

Wild adults were collected on March 2010 hovering in experimental crops of the *Universidad Centroccidental Lisandro Alvarado* located in Tarabana, municipality of Palavecino (Lara State, Venezuela). In the laboratory, females were transferred into a rearing box ( $50 \times 38 \times 35$  cm) with a supply of pollen, sugar and a honey solution. The cowpea plant *Vigna unguiculata* (L.), infested with the aphid *Aphis craccivora* Koch, 1854, was also placed to stimulate the oviposition. After hatching, each larva was fed daily with aphids of various ages. Larvae, puparia and emerged adults were preserved in ethyl alcohol 70%. The length and width of the preimaginal stages were measured.

### Descriptions of preimaginal stages

Third instar larvae were selected for preservation after the hind gut was naturally emptied prior to pupation as normally occurs

in predatory syrphines (Rotheray 1993). Obtained larvae were extended and fixed by immersion in gentle boiling water following the methodology of Láska *et al.* (2006). To study the thorax morphology, the three segments were extended by lightly pressing the first abdominal segments. Afterwards, larvae were preserved in 70% alcohol solution. Dimensions were measured on preserved material using a binocular microscope (Leica MZ95) with an eyepiece micrometre. Larvae were studied using the cryo-scanning technique (cryo-SEM) at the Polytechnic University of Valencia (Spain). Larvae were fixed on a holder with a thin layer of O.C.T. compound (Tissue-Tek O.C.T. Compound, Sakura Finetek). The specimens were frozen for 2 min in liquid nitrogen and transferred into a cryo-SEM system (Quorum PP3010T). The samples were sublimated from  $-150^\circ\text{C}$  to  $-90^\circ\text{C}$  to remove ice crystals for 5 min. A thin layer of platinum was sputtered onto the specimens for 30 s. Once the samples were prepared for observation, they were transferred into the SEM (FESEM ZEISS Ultra-55). Secondary electron images were recorded at an accelerating voltage of 3 kV.

The puparia were cleaned by removing the debris adhered to the external integument placing the specimens in an ultrasonic cleaner for a few minutes. The cleaned specimens were mounted on stubs and examined with a scanning electron microscope (S3000N Hitachi) using an accelerating voltage of 15–20 kV.

The head skeleton was removed from the leading ventral edge of the interior of the puparium and placed in warm 10% potassium hydroxide (KOH) for 3–4 min. Then, the head skeleton was immediately washed in distilled water and preserved in pure glycerine prior to examination. The terminology used for descriptions of head skeleton follow Rotheray and Lyszkowski (2015) and Rotheray (2019).

Descriptions are based on preserved third instar larvae and puparia of *A. occidentalis* and *D. clavata*. Larval characters were checked against living specimens (or photographs), when possible. The specimens were stored in the Entomological Collection of the University of Alicante, CEUA at the Department of Environmental Sciences and Natural Resources. The terminology used for descriptions of larvae and puparia follows Rotheray (1993). The positions of the sensilla are numbered sequentially from the dorsal to the ventral surface for each segment (Rotheray 1991).

### DNA barcoding

The molecular sequence of the cytochrome *c* oxidase subunit I (COI) gene was obtained from three specimens of *A. occidentalis*. One leg from specimens in alcohol was used for DNA extraction. The extraction protocol follows Mengual *et al.* (2018), and the specimens were preserved and labelled as DNA voucher specimens for the purpose of morphological studies and deposited at the Zoological Research Museum Alexander Koenig (ZFMK, Bonn, Germany). DNA primers and PCR amplification protocols follow Roza-Lopez and Mengual (2015).

## RESULTS

### TAXONOMY

#### *Austroscavea occidentalis* (Shannon, 1927)

(Figs. 1-7)

*Scaeva occidentalis* Shannon, 1927: 29

*Syrphus sexmaculatus* Macquart, 1850: 457. Preoccupied by Palisot de Beauvois, 1819.

*Syrphus chilensis* van der Goot, 1964: 214. New name for *Syrphus sexmaculatus* Macquart, 1850.

### DESCRIPTION

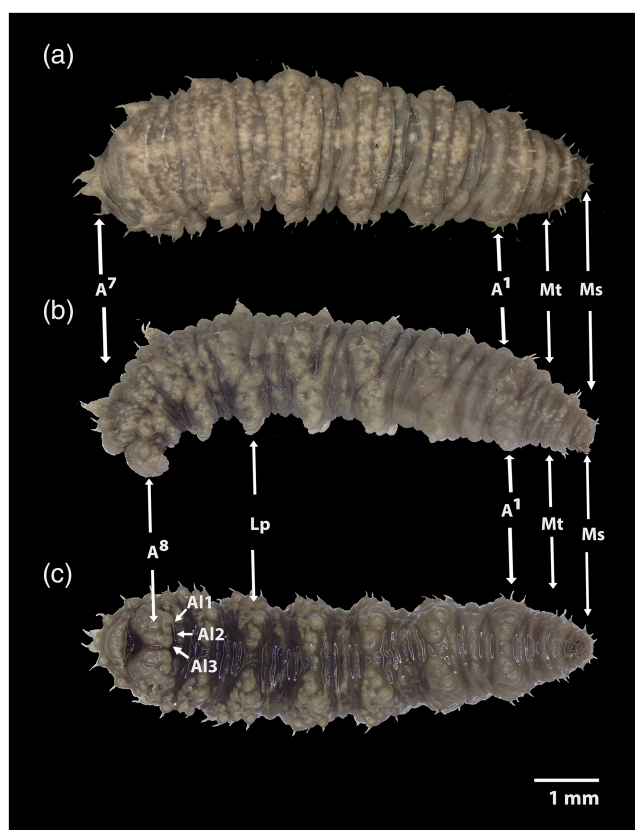
#### Larva

**Overall appearance.** Length  $9.27 \pm 0.80$  mm, maximum width  $2.0 \pm 0.11$  mm ( $n = 4$ ). Oval in cross-section with a little flattened ventral surface, tapering anteriorly and slightly truncate posteriorly (Fig. 1). Dorsal habitus wrinkled (Fig. 1a), last abdominal segments slightly serrate owing to fleshy projections with

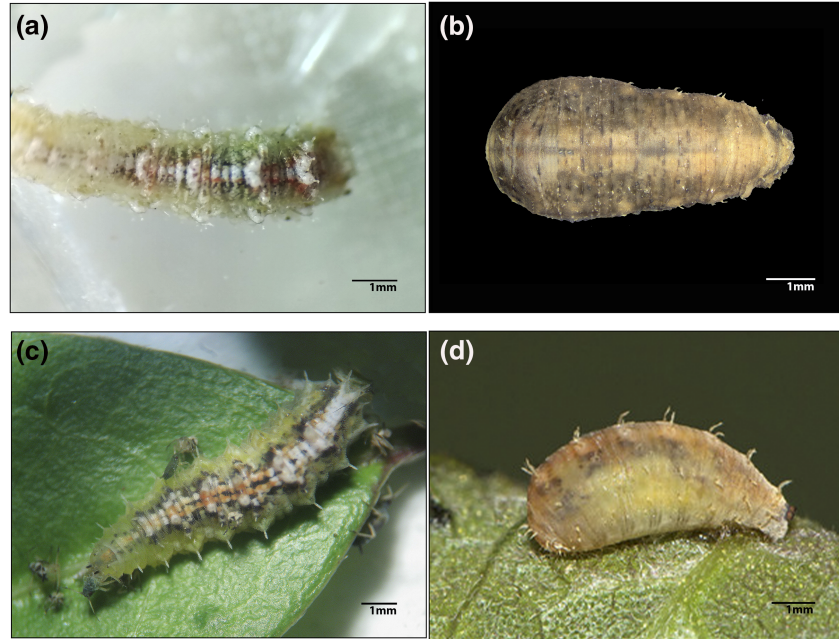
segmental spines (sensilla with setae) (Fig. 1a,b). Colour pattern yellowish light green translucent showing white central spots with a reddish-brown margin on the last five abdominal segments. The black gut content is visible between the white-reddish spots as an interrupted background. On the last abdominal segments, basal papilla of the dorsolateral segmental spines sometimes white in colour due to the accumulation of adipose tissue (Fig. 2a). Prothorax and mesothorax normally retracted into metathorax. Boundaries between segments obscured by secondary grooves and folds in integument (Fig. 1). Abdominal segments bearing five secondary folds. The pattern of segmental spines is very useful for orientation in primary segmentation, mainly the position of the segmental spines of each side of abdominal segments. Pairs one and two of segmental spines both located on second fold in metathorax and first abdominal segment; in other abdominal segments, pair two of segmental spines located just on the next fold (Fig. 1a,b). Integumental vestiture consisting in dome-shaped tubercles, of cuticle colour or brown pigmented, being smaller in groves and on ventral surface. Posterior respiratory process (prp) very short, and normally recessed in a fleshy depression.

**Head.** Very reduced as is usual in predatory syrphine larvae (Fig. 1). Antenno-maxillary organs well developed. Mouthparts adapted for piercing-feeding with distinctive features of predacious syrphid larvae (Rotheray and Lyszkowski 2015; Rotheray 2016) (see Fig. 3). Lateral margins of mouth with a pair of black triangular pointed sclerites that are basally attached to the integument. Labrum heavily sclerotised, elongated and tapered with the apex fused. Labial plate also sclerotised, elongated, narrow, tapered and projected forward free under the slightly longer labrum. The labial plate articulates with the labial sclerites which are embedded in the sides of the head skeleton with muscles inserting on a postero-ventral apodeme. The mandibles are bar-shaped, tapered posteriorly, lack muscles and are embedded into the lateral margins of the head skeleton. The labrum acts as the upper lip, whereas the labium acts as the lower lip with the two mandibles situated on the side. Basal sclerite with ventral cornu clearly longer than dorsal cornu (Fig. 3).

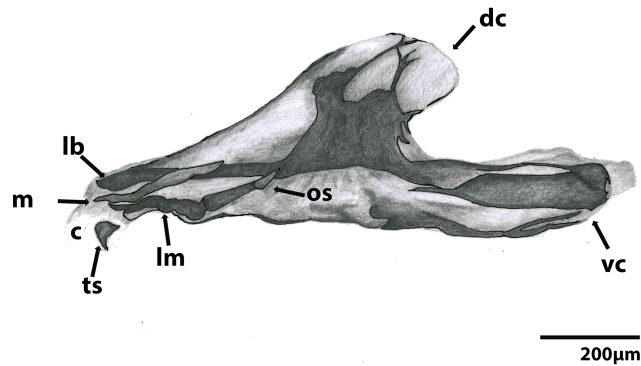
**Thorax.** Prothorax with 11 pairs of sensilla hardly visible by light stereomicroscopy (Fig. 4). Dorsal surface of prothorax with anterior respiratory process sclerotised and short, with three or four semi-circular openings on its anterior margin (Fig. 5a). Vestiture of prothorax above sensilla  $4^P$  reduced, giving the integument a clear shining appearance. Mesothorax with eight pairs of sensilla arranged in two main transverse rows: dorsal row with short segmental spines 1–3 and ventral row located slightly anteriorly bearing five pairs of sensilla, two pairs of dorsolateral segmental spines followed by three pairs of ventral papilliform sensilla (Figs 4 and 5b). Metathorax with nine pairs of sensilla arranged in two main transversal rows: dorsal row with four pairs of segmental spines and ventral row located slightly anteriorly with five pairs of segmental spines of unequal length; setae on sensilla  $7^{Mt}$  and  $9^{Mt}$  shorter than others (Figs 4 and 5b,c). One extra pair of sensory organs



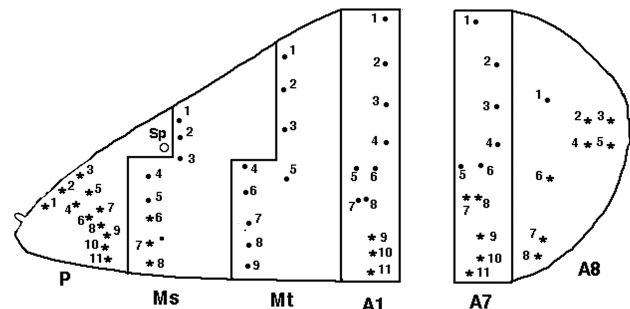
**Fig. 1.** Third instar larva of *Austroscavea occidentalis*. (a) Dorsal view. (b) lateral view. (c) ventral view. Ms, mesothorax; Mt, Metathorax;  $A^{1-8}$ , abdominal segments one to eight; Al, anal lobes (1–3); Lp, locomotory prominences.



**Fig. 2.** Pre imaginal stages of both studied species. (a) Detail of the third instar larvae abdomen of *A. occidentalis*: dorsal view. (b) Pupa of *A. occidentalis*, dorsal view. (c) Third instar larvae of *D. clavata* dorsal view. (d) Pupa of *D. clavata* lateral view.

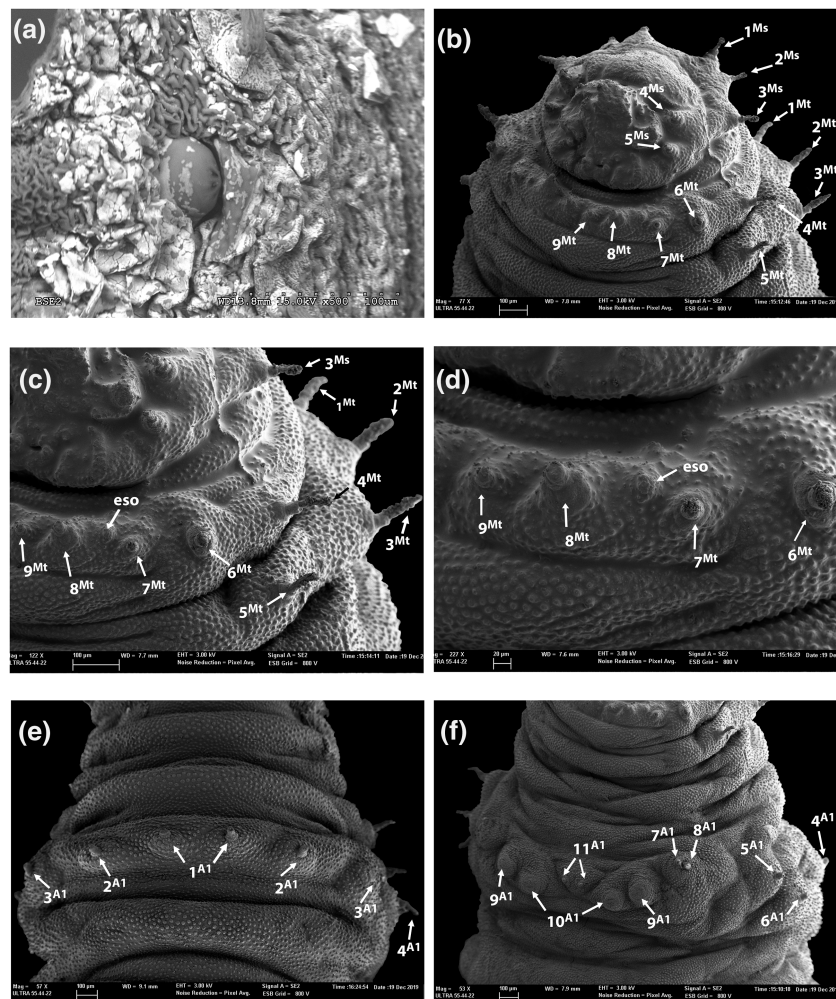


**Fig. 3.** Head skeleton of *A. occidentalis*, lateral view. lb, labrum; m, mandible; lm, labium; ts, triangular sclerite; os, labial sclerite; c, connecting tissue; dc, dorsal cornu; vc, ventral cornu.



**Fig. 4.** Map of the chaetotaxy of the third instar larva of *A. occidentalis* showing the positions of the groups of sensilla (based on Lásková *et al.* 2006). P, prothorax; Ms, mesothorax; Mt, metathorax; A<sup>1</sup>, A<sup>7</sup>, first and seventh abdominal segments; A<sup>8</sup>, eighth abdominal segment with posterior respiratory process (prp); Sp, anterior respiratory process. Symbols: \*segmental sensilla without setae, ●segmental spines, ■extra pair of sensory organs.





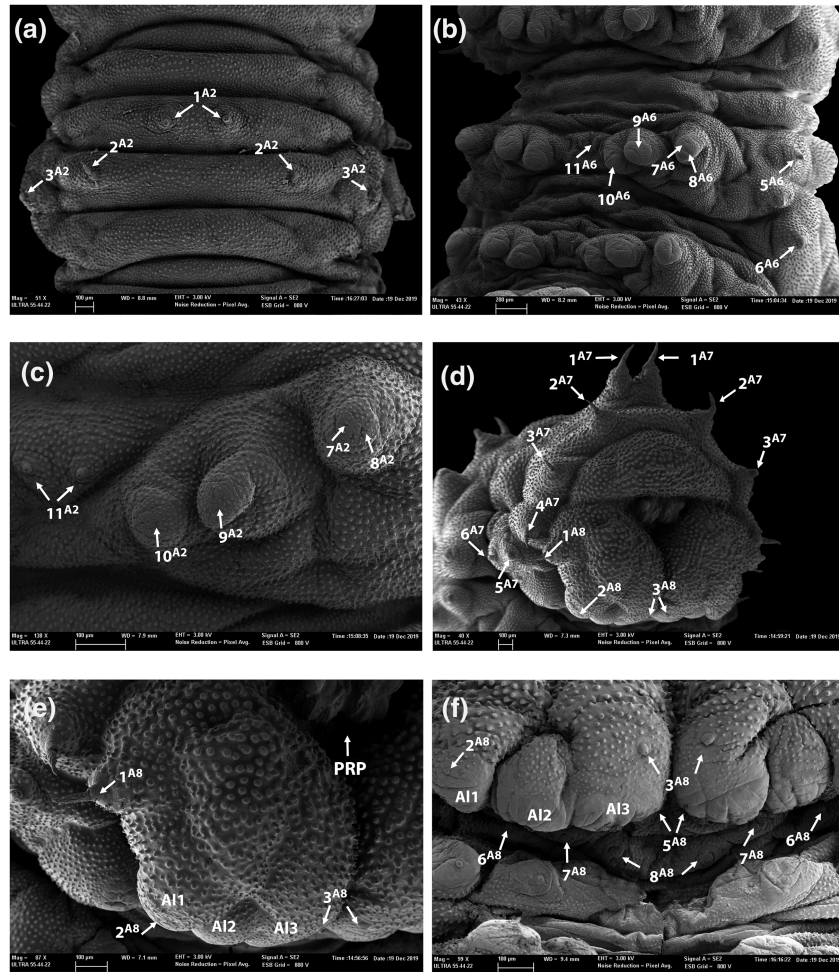
**Fig. 5.** Third instar larva of *A. occidentalis*. (a) Anterior respiratory process. (b) Mesothorax sensilla  $1^{Ms}$ – $5^{Ms}$  distribution. (c) Metathorax sensilla  $1^{Mt}$ – $9^{Mt}$  distribution. (d)  $1^{Mt}$ – $9^{Mt}$  sensilla and extra sensorial organ (eso) detail. (e) First abdominal segment dorsal view with  $1A^1$ – $4A^1$  sensilla distribution detail. (f) First abdominal segment latero-ventral view with  $4A^1$ – $11A^1$  sensilla distribution.

(eso) near sensilla  $7^{Ms}$  and  $7^{Mt}$  (hardly visible by light stereomicroscope) (Figs 4 and 5d).

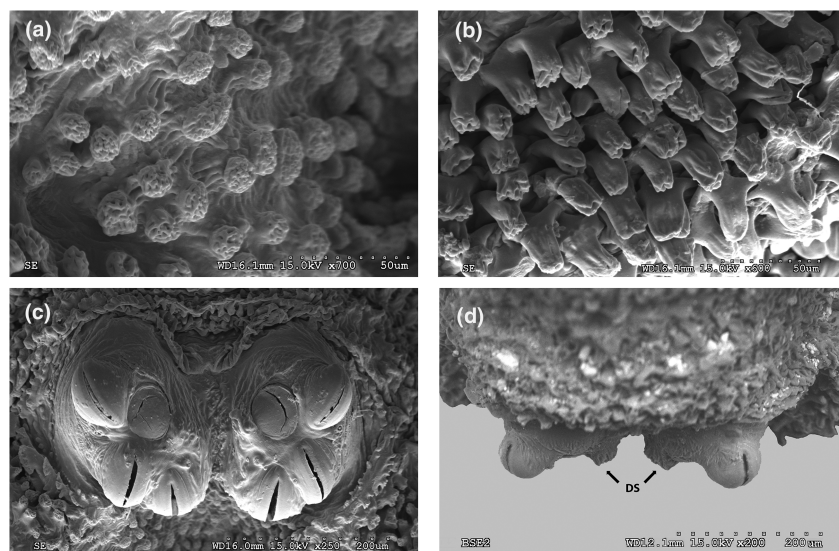
**Abdomen.** Abdominal segments with 11 pairs of sensilla. First abdominal segment with eight pairs of segmental spines ( $1A^1$ – $8A^1$ ) dorsolaterally (Figs 4 and 5e) and three pairs of papilliform sensilla ventrally ( $9A^1$ – $11A^1$ ) (Fig. 5f). Dorsal pairs of segmental spines  $1A^1$ – $4A^1$  located on the same fold (Figs 1, 4 and 5e). Second to seventh abdominal segments with six pairs of segmental spines dorsolaterally and five papilliform sensilla ventrally (Fig. 4). Second to seventh abdominal segments with the segmental spines  $1A^{2-7}$  on second fold and segmental spines  $2A^{2-7}$  on third fold together with the segmental spines  $3A^{2-7}$  and  $4A^{2-7}$  (Fig. 6a). Locomotory prominences well developed; seven pairs present on abdominal segments 1–7 (Figs 1b,c and 6b,c). On the seventh abdominal segment, pair of segmental spines  $1A^7$  separated from base of prp by two folds, the posterior distinctly more developed (almost two times or more) and with microtrichia slightly enlarged in medial area (Fig. 6d). Tip of anal segment with three pairs of lobes in ventral view (Figs 1c

and 6d); posterior surface of lobes covered with densely aggregated spicules, tip of lobes without vestiture (Figs 6e,f). On the anal segment, eight pairs of sensilla (Fig. 4), only first pair with setae (Figs 6d–f). Integumental vestiture of the depression below prp reduced in small nodules that have a honeycomb appearance due to the networks of ridges with pits composing the distal end (Fig. 7a). Dorsal area of the anal lobes covered by rectangular microtrichia with two or three grooves at the distal part and rounded end (Fig. 7b).

**Posterior respiratory process.** Very short, almost sessile, (length  $89.20 \pm 1.8 \mu\text{m}$ ), pale to dark brown in colour, lustrous. Spiracular plates divided by a V-shape median groove almost as deep as the length of prp (Fig. 7c). Dorsal spur presents but not well defined (Fig. 7d); slits II and III almost parallel, slit III inserted nearly 1/2 of length of slit II; carinae I and III extending down the sides of prp; carinae I and II distinctly more developed than carina III (Fig. 7c). Periorificial setae mounted inside of circular nodules; periorificial setae between slits I and II closed but border of their nodules separated.



**Fig. 6.** Abdominal chaetotaxy and locomotory prominences detail of *A. occidentalis* third instar larva. (a) second abdominal segment dorsal view,  $1^{A2}$ – $3^{A2}$  sensilla distribution. (b) Sixth abdominal segment ventral view,  $5^{A6}$ – $11^{A6}$  sensilla distribution. (c) Detail view of second abdominal segment locomotory prominences. (d) Seventh and eighth abdominal segment, dorsolateral view, distribution of  $1^{A7}$ – $5^{A7}$  and  $1^{A8}$ – $2^{A8}$  sensilla. (e) Anal lobes (Al) 1–3 detail. (f) Eighth segment, ventral view distribution of  $2^{A8}$ – $8^{A8}$  sensilla.



**Fig. 7.** Anal lobes and prp of *A. occidentalis*. (a) Detail of the integumental vestiture of the depression below posterior respiratory process (prp), (b) detail of the rectangular shape microtrichia that covers the anal lobes, (c) prp frontal view, (d) prp dorsal view with detail of dorsal spurs (DS).



### Puparium

**Overall appearance.** Length  $5.86 \pm 0.05$  mm, maximum width  $2.62 \pm 0.02$  mm. Cask-like, sub-cylindrical in cross-section with the last abdominal segments narrowed almost half of the first ones (Fig. 1b). Anterior extreme dome-shaped, slightly tapering posteriorly and flattened ventrally. Anal segment reduced and facing down. Sclerotised prp almost without changes, black in colour and not easily visible in dorsal view. Colour dull bright light brown, sometimes with dark segmental patterns caused by pigmented cuticle, variable at intraspecific level. Integumental vestiture and segmental spines persisting. Segmental spines slightly light than cuticle colour, about the same length as in larvae, but dried rests of fleshy projections bearing segmental spines usually inconspicuous.

### *Dioprosopa clavata* (Fabricius, 1794)

(Figs. 2, 8-10)

*Syrphus clavatus* Fabricius, 1794: 298.

*Baccha fusciventris* Wiedemann, 1830: 95.

*Paragus? scutellaris* Walker, 1836: 342.

*Baccha varia* Walker, 1849: 548.

*Baccha babista* Walker, 1849: 549.

*Baccha facialis* Thomson, 1869: 504.

*Syrphus albomaculatus* Smith, 1877: 84. Preoccupied by Macquart, 1842.

*Conops quadrimaculata* Ashmead, 1880: 69.

*Baccha minor* Stahl, 1882: 206.

*Baccha clavata* Stahl, 1882: 206. Misspelling of *clavatus* Fabricius, 1794.

*Spazigaster bacchoides* Bigot, 1884: 326.

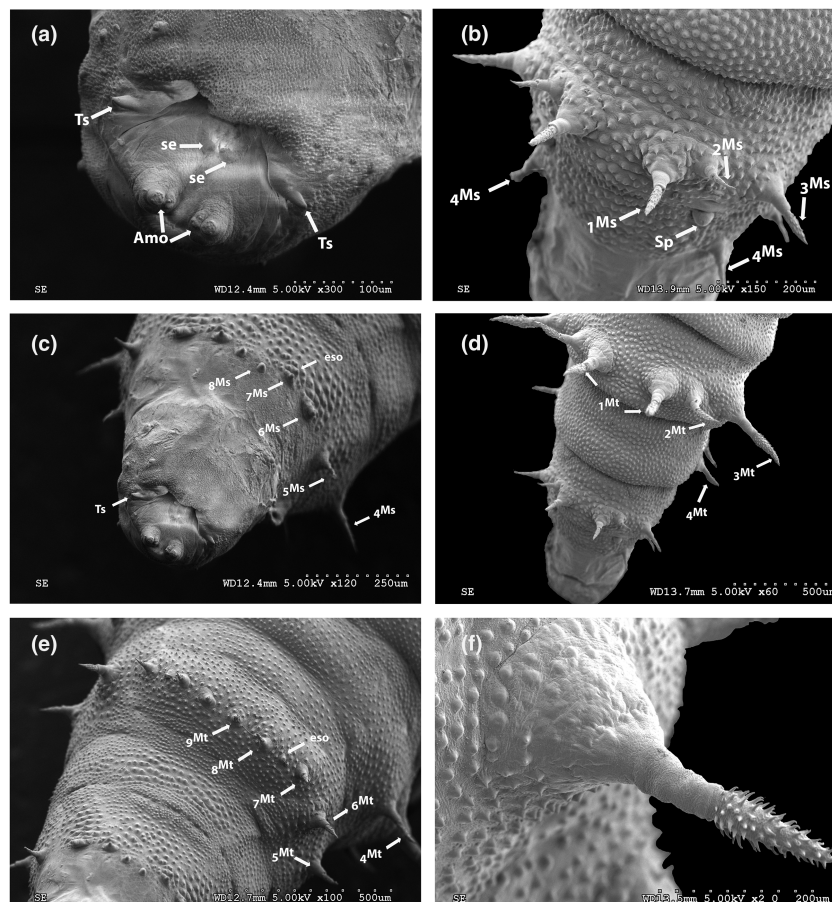
*Paragus scutellatus* Williston, 1886: 323 [*Mixogaster?*]. Misspelling of *scutellaris* Walker, 1836.

*Syrphus smithi* van der Goot, 1964: 215. New name for *Syrphus albomaculatus* Smith, 1877.

## DESCRIPTION

### Larva

**Overall appearance.** Length  $9.08 \pm 0.22$  mm, maximum width  $2.18 \pm 0.04$  mm ( $n = 10$ ), sub-cylindrical in cross-section with a flattened ventral surface, tapering anteriorly and slightly truncate posteriorly. Prothorax and mesothorax normally retracted into



**Fig. 8.** Morphology details of the third instar larva thoracic segments of *D. clavata*. (a) Prothorax detail. Ts, triangular sclerite; se, setae; Amo., Antenno-maxillary organ. (b) Anterior view of mesothorax. Distribution of 1<sup>Ms</sup>–4<sup>Ms</sup> sensilla, sp: anterior respiratory process. (c) Mesothorax ventro-lateral view, distribution of mesothorax 4<sup>Ms</sup>–8<sup>Ms</sup> sensilla. (d) Metathorax sensilla (1<sup>Mt</sup>–3<sup>Mt</sup>) dorsal view. (e) Distribution of metathoracic 5<sup>Mt</sup>–9<sup>Mt</sup> sensilla ventral view. (f) Thoracic spine detail.



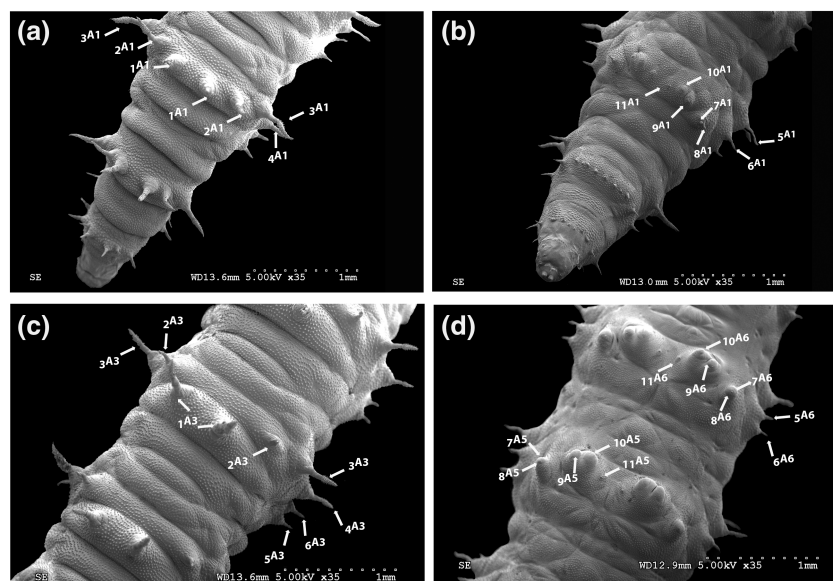
metathorax. Dorsal habitus wrinkled, dorsal outline clearly serrated due to the development of the fleshy projections and setae of the sensilla. Colour pattern light green, showing two faint longitudinal stripes orange in colour along the dorsal surface, almost parallel on thoracic segments that diverge towards the last abdominal segments (Fig. 2c). Integumental vestiture consisting in dome-shaped tubercles of cuticle colour.

**Head.** Very reduced as is usual in predatory syrphine larvae (Figs 2c and 8a). Mouthparts adapted for piercing-feeding with distinctive features of predacious syrphid larvae (Rotheray and Lyszkowski 2015; Rotheray 2016). The general structure of the head skeleton is very similar to that described in the papers of Freitas (1982) and De la Pava and Sepúlveda-Cano (2015). However, the terminology used by these authors differs among them and with that used in this work following Rotheray (2019). The equivalence to the terminology is: labrum (paraclipeal fragma in Freitas (1982); mandibles in De la Pava and Sepúlveda-Cano (2015)); labium (is also labium in de la Pava and Sepúlveda-Cano (2015) but maxillae of Freitas (1982)); mandibles (are also mandibles in Freitas (1982) but lateral bar in de la Pava and Sepúlveda-Cano (2015)). Lateral margins of mouth with a pair of black triangular pointed sclerites (Fig. 8a,c). Antenno-maxillary organs well developed presenting on the superior tip numerous sensilla mainly chemo- and mechano-receptors as in other predatory species (Fig. 8a) but not visible in our available samples of *A. occidentalis* (Fig. 5b). One pair of sensilla located above mouth and below antenno-maxillary organs (Fig. 8a).

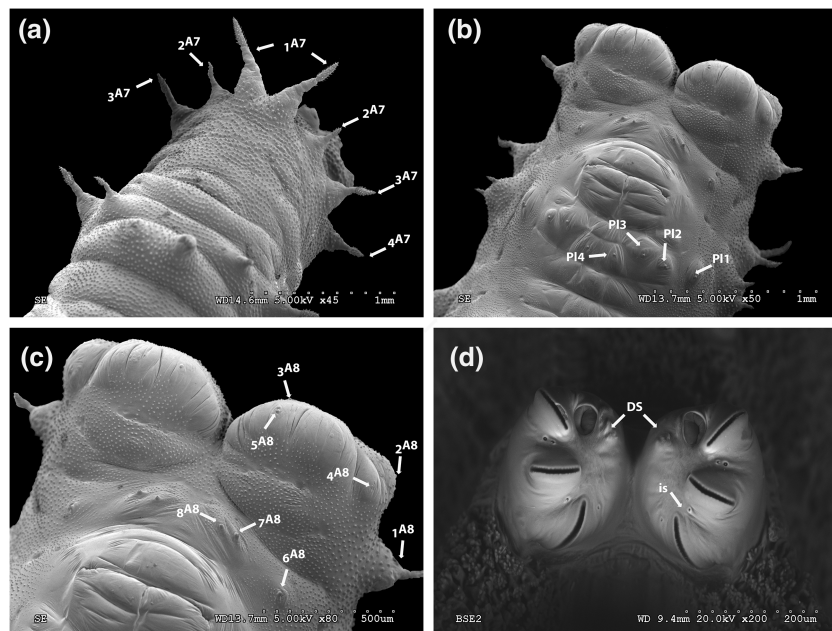
**Thorax.** Prothorax with 11 pairs of sensilla without terminal setae, hardly visible by optical stereomicroscopy. Anterior fold of prothorax with a ring (extending <10% of dorsal surface

and <60% of ventral surface) of small, backwardly directed spicules and densely aggregated (Fig. 8a). Vestiture of dorsal surface of prothorax above sensilla 4<sup>P</sup> reduced, giving the integument a clear shining appearance (Fig. 8b,d). Dorsal surface of prothorax with anterior respiratory process sclerotised and short (Fig. 8b). Vestiture of dorsal surface behind sensilla 4<sup>P</sup> of prothorax and ventral surface behind ventral sensilla of mesothorax covered with conical papillae, densely aggregated, giving the integument a soft grainy appearance (Fig. 8b–e). These conical papillae are smaller in grooves and on ventral surface (Fig. 8c,e). Mesothorax with eight pairs of sensilla arranged in two main transverse rows: dorsolateral row with segmental spines 1–3 (Fig. 8b) and ventral row located slightly anteriorly bearing two pairs of segmental spines followed by three pairs of ventral papilliform sensilla (Fig. 8c). Metathorax with nine pairs of sensilla arranged in two main transversal rows: dorsolateral row with four pairs of segmental spines (Fig. 8d) and ventral row located slightly anteriorly with five pairs of slightly shorter segmental spines (Fig. 8e). One extra pair of small sensory organs (eso) near sensilla 7<sup>Ms</sup> and 7<sup>Mt</sup> hardly visible with optical stereomicroscope (Fig. 8c,e).

**Abdomen.** Abdominal segments bearing five secondary folds (Fig. 9c). Each segment with 11 pairs of sensilla: six pairs of dorsolateral segmental spines and five ventral pairs of sensilla (Fig. 9a–d). First abdominal segment with dorsolateral pairs of segmental spines 1<sup>A1</sup>–4<sup>A1</sup> with setae, located on the same fold (Fig. 9a); lateral segmental spines 5<sup>A1</sup>, 6<sup>A1</sup> and 8<sup>A1</sup> also with setae (smaller on segmental spine 8<sup>A1</sup>) and lateral segmental spine 7<sup>A1</sup> papilliform without setae; ventral sensilla 9<sup>A1</sup>–11<sup>A1</sup> papilliform and very reduced (Fig. 9b). Second to sixth abdominal segments with the segmental spines 1<sup>A2–6</sup> on second fold and segmental spines 2<sup>A2–6</sup> on third fold together with the



**Fig. 9.** Larval abdominal morphology of *D. clavata* (I). (a) First abdominal segment dorsal view, 1<sup>A1</sup>–4<sup>A1</sup> sensilla distribution, (b) first abdominal segment ventral view, 5<sup>A1</sup>–11<sup>A1</sup> sensilla distribution, (c) third abdominal segment dorsolateral view, 1<sup>A3</sup>–6<sup>A3</sup> sensilla distribution, (d) fifth and sixth abdominal segments, proleg detail with 5–11 sensilla distribution.



**Fig. 10.** Larval abdominal morphology of *D. clavata* (II). (a) Seventh abdominal segment dorsolateral view,  $1^{A7}$ – $4^{A7}$  sensilla distribution. (b) seventh abdominal segment prolegs with the four locomotory prominences (Lp). (c) Eighth abdominal segment, ventral view  $4^{A8}$ – $8^{A8}$  sensilla distribution. (d) prp frontal view (is, inter-spiracle setae; DS, dorsal spur).

segmental spines  $3^{A2-6}$  and  $4^{A2-6}$  (Fig. 9c). Ventral sensilla  $7^{A2-6}$ – $11^{A2-6}$  papilliform and very reduced (Fig. 9d). On the seventh abdominal segment, pair of segmental spines  $1^{A7}$ – $4^{A7}$  located on the same fold being  $1^{A7}$  pair clearly developed and separated from base of prp by one-fold, notably reduced (Fig. 10a). Seven pairs of locomotory prominences (segments 1–7), on segments 2–6, with three lobes well developed, backward faced on segments 5 and 6. On segment 7, locomotory prominences less developed, with four lobes (Fig. 10b). Anal segment with eight pairs of papilliform sensilla poorly visible on dorsal view. On ventral view with three pairs of lobes constituting the U-shaped grasping organ (Fig. 10c).

**Posterior respiratory process.** Short, dark brown in colour, lustrous. Spiracular plates divided by a V-shape median groove almost as deep as the length of prp (Fig. 10d). Spiral plates slightly inclined towards the contact area between them. Dorsal spurs scarcely marked, vestigial; ecdysial scars dorsally displaced. Slits straight situated over oval well developed carinae (twice longer than width). Slits I, II and III almost equidistant inserted. Inter-spiracular setae very reduced inserted over conical protuberances hardly visible by optical stereomicroscope.

### Puparium

**Overall appearance.** Length including prp:  $5.44 \pm 0.14$  mm, maximum width  $2.39 \pm 0.06$  mm. Pear shape-like, sub-cylindrical in cross-section (Fig. 1d). Anterior extreme oval, slightly tapering posteriorly and flattened ventrally. Larval segmentation persistent as transverse folds. Anal segment notoriously narrowed on the prp basis. Green on colour with

**Table 1** Mean duration (days) and variation range of *A. occidentalis* and *D. clavata* reared under controlled conditions

Stage	<i>A. occidentalis</i>		<i>D. clavata</i>	
	Mean $\pm$ SE (days)	Range	Mean $\pm$ SE (days)	Range
Egg	$2.0 \pm 0.0$		$2.0 \pm 0.0$	
Larva	$8.8 \pm 0.17$	8–9	$6.0 \pm 0.12$	5–8
Pupa	$7.8 \pm 0.17$	7–8	$5.61 \pm 0.08$	5–7
Preadult stage	$18.7 \pm 0.21$	19–18	$13.61 \pm 0.12$	12–17

SE, standard error.

one dorsal light-orange spot and two black spots at the sides. Brown when mature. Sclerotised prp almost without changes, scarcely prominent.

### DNA barcoding

A total of three adult specimens of *A. occidentalis* were successfully sequenced and the 5r-COI sequences were submitted to GenBank (accession numbers MT216274, MT216275 and MT216276). The obtained DNA barcodes have an uncorrected pairwise distance of 0–0.008 among these Argentinean specimens and a p-distance of 0.0–0.009 with other specimens of *A. occidentalis* in BOLD (www.boldsystems.org). The Barcode Index Number (BIN) (Ratnasingham and Hebert 2013) for this species is BOLD:ADW2796. Specimens of *Notosyrphus goldbachii* (Fluke, 1950) with COI sequences in BOLD have a very similar DNA barcode (97.13–98.01%), as well as a specimen of *Austroscaeva melanostoma* (97.29–97.91%).

## Life cycle and preimaginal developmental time

The duration of the preadult stages of *A. occidentalis* and *D. clavata* are compared in Table 1. Under the rearing conditions, the total preimaginal developmental time (from egg to adult emergence) of *A. occidentalis* was 5 days longer than the time observed for *D. clavata*. In both species, the eggs hatched 2 days after oviposition. However, a difference of almost 3 days on mean value of the larval stage length and almost 2 days on the pupal mean length was observed (Table 1). The preimaginal time range (number or days) has more variation for *D. clavata*. We need to point out that although *U. sonchi* was used as prey for *A. occidentalis* in cage rearing, this aphid is originally a Palearctic species widely distributed in South America (de Carvalho *et al.* 1998). No larva of *A. occidentalis* was found among wild colonies of *U. sonchi* in the sampled area. It is important to mention that the values obtained for the lifecycle of *A. occidentalis* should be considered preliminary and may vary with further study due the low number of evaluated individuals.

## DISCUSSION

As expected, based on their phylogenetic placement, larvae of *A. occidentalis* and *D. clavata* share many morphological characters with other members of the *Eupeodes-Scaeva* clade (Mengual *et al.* 2018). The close relationship between genera of this lineage has been reported several times based on preimaginal morphological characters (Rotheray 1987; Rotheray and Gilbert 1999; Láska *et al.* 2006), molecular characters (Mengual *et al.* 2008; Mengual 2015) or a combination of both (Mengual *et al.* 2015). Known larvae of the members of the *Eupeodes-Scaeva* lineage (i.e. *Eupeodes*, *Austroscaeva*, *Dioprosopa*, *Scaeva*, *Semiscaeva*, *Ischiodon* and *Simosyrphus*) share the following morphological characters: (1) the presence of setae accompanying ventral sensilla on the metathorax (Figs 5b–d and 8e); (2) the tips of the locomotory prominences face backwards on abdominal segments 5 and 6 (Figs 6b, 9d); and (3) an extra lobe appears as part of each locomotory prominence on abdominal segments 1–7 and the U-shaped grasping organ is present on the anal segment (Figs 1c,d, 10b,c). These last two structures are used by the larvae for moving about on stems (Rotheray and Gilbert 1999, 2011). Unfortunately, larvae of *Eupeodes* (*Macrosyrphus*) and *Lapposyrphus* were not available for this study. Based on the existing illustrations and descriptions of *E. (M.) confrater* (Wiedemann, 1830) (see Ninomyia, 1957; Ohara, 1985; Kumar *et al.*, 1989) and *L. lapponicus* (Zetterstedt, 1838) (see Goeldlin de Tiefenau, 1974), we can say that at least the last two morphological characters (both related with the U-shaped grasping organ) are present in these taxa. Larvae of the genera *Notosyrphus* and *Pseudodoros* remain undescribed, but we hypothesise that they also share the above-mentioned characters.

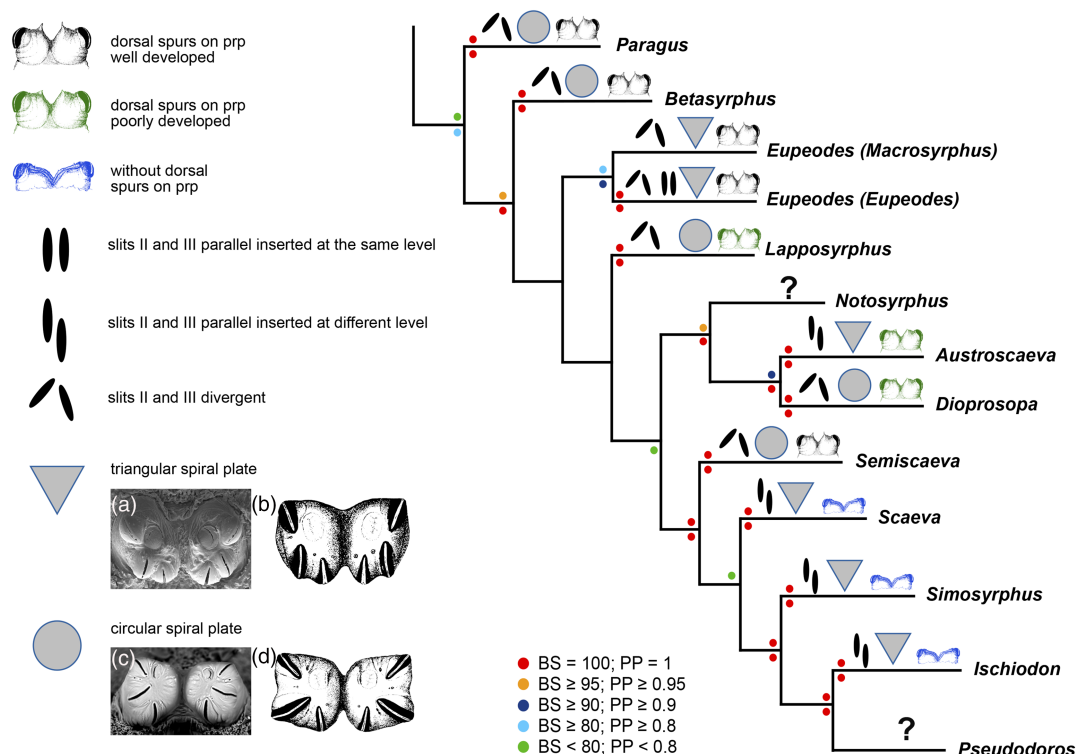
Members of the *Eupeodes-Scaeva* lineage can be arranged into two groups according to the shape of the spiracular plate outline (see Fig. 11). The first taxon group, comprising *Austroscaeva*, *Scaeva*, *Simosyrphus*, *Ischiodon*, *Eupeodes* and *Macrosyrphus*,

has a slightly triangular spiracular plate outline, that is, the anterior part of the spiracular plate is broader than the posterior part, and the outer end of the slit I is more distant from middle line than the outer end of slit II (Figs 7c and 11a). The second group, including *Semiscaeva*, *Lapposyrphus* and *Dioprosopa*, has an almost circular spiracular plate outline, in other words, the anterior part of the spiracular plate is as wide as the posterior part, and the outer end of slit I is equally distant to the middle line as slit II (Figs 10d and 11b). Based on the arrangement of the slits on the spiracular plate as used by Láska *et al.* (2006), two other taxon groups can be recognised in the *Eupeodes-Scaeva* lineage: the first group (*Scaeva*, *Simosyrphus*, *Ischiodon* and *Austroscaeva*) has the slits II and III parallel or almost parallel, with the insertion of slit III beneath the level of the insertion of slit II (Figs 7c and 12a); while the second group (*Semiscaeva*, *Lapposyrphus*, *Macrosyrphus* and *Dioprosopa*) has slits II and III clearly divergent (Figs 10d and 12b), typically present in many other Syrphini. There is, however, a gradation of this character in the *Eupeodes* species with known larval morphology, from species with slits II and III almost parallel but with the insertion of slit III almost at the same level of the insertion of slit II (e.g. *E. corollae* (Fabricius, 1794)) to species with slits II and III clearly divergent like *E. latifasciatus* (Macquart, 1829). We do consider these parallel slits II and III in the genus *Eupeodes* as different from the parallel slits found in the previous taxa (*Scaeva*, *Simosyrphus*, *Ischiodon* and *Austroscaeva*), probably a product of reorganisation from divergent slits. Finally, the members of the *Eupeodes-Scaeva* can also be divided into three groups based on the presence or absence of dorsal spurs on the prp: (1) taxa without dorsal spurs on the prp (i.e. *Scaeva*, *Simosyrphus* and *Ischiodon*); (2) taxa with dorsal spurs on the prp well developed (*Semiscaeva*, *Eupeodes* and *Macrosyrphus*); and (3) genera with dorsal spurs on the prp poorly developed (*Austroscaeva*, *Lapposyrphus* and *Dioprosopa*). Note that in the case of *Dioprosopa*, the dorsal spurs are very rudimentary (see Fig. 10d).

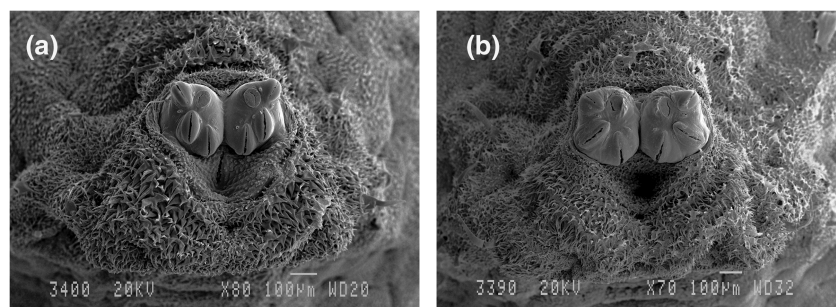
Based on molecular data, Mengual *et al.* (2018) resolved the two subgenera of *Scaeva* as monophyletic groups with high support, but not necessarily as sister groups (Fig. 11). Both *Scaeva* subgenera were recovered as sister taxa of the clade (*Simosyrphus* + (*Pseudodoros* + *Ischiodon*)). Current knowledge of the preimaginal morphology of this *Scaeva* clade supports the results from the molecular analysis, with a group of taxa (*Scaeva*, *Simosyrphus* and *Ischiodon*) having slits II and III parallel, a slightly triangular outline of the spiracular plate, and without dorsal spurs on the prp, and a second group (*Semiscaeva*) with a circa 90° angle between slits II and III, almost circular outline of the spiracular plate, and with dorsal spurs. The larva of *P. nigricollis* remains unknown, but according to the available evidence, we hypothesise that preimaginal stages of *P. nigricollis* likely have the slits II and III parallel, a slightly triangular outline of the spiracular plate, and no dorsal spurs on the prp.

*Austroscaeva* and *Dioprosopa* differ in their prp morphology and show a mixture of morphological characters found in other clades of the *Eupeodes-Scaeva* lineage (Fig. 11). In fact, the shape of the prp of *Dioprosopa*, with the spiracular plates clearly more separated in their ventral part than in the dorsal part, is





**Fig. 11.** Scheme (not a phylogram) of the phylogenetic relationships of the *Eupeodes-Scaeva* lineage indicating the commented larval characters for each taxon (modified from Mengual *et al.* 2018). Bootstrap support values (BS; indicated above) and Bayesian posterior probabilities (PP; indicated below) are depicted at the nodes (only >50 or >0.5, respectively). (a–d): posterodorsal view of the prp. (a) *Austroscaeva occidentalis*; (b) *Scaeva (Scaeva) pyrastris* (Linnaeus, 1758); (c) *Dioprosopa clavata*; (d) *Scaeva (Semiscaeva) selenitica* (Meigen, 1822). Parts (b) and (c) were adapted from Láška *et al.* (2006).



**Fig. 12.** Morphology of posterior respiratory process of subgenera of *Scaeva*. (a) *Scaeva (Scaeva) albomaculata* prp frontal view, (b) *Scaeva (Semiscaeva) selenitica* prp frontal view.

considerably different from the prp shape of the rest of the *Eupeodes-Scaeva* lineage. Nevertheless, live larvae of *A. occidentalis* and *D. clavata* share a similar colouration pattern (Fig. 1a,c). Larvae of *D. clavata* are morphologically distinct compared with the other members of the *Eupeodes-Scaeva* lineage and can be easily distinguished from all other taxa in this lineage by the following diagnostic characters: outline slightly serrate due to the great development of the segmental spines, both the fleshy projection of its base and the terminal setae (Figs 1c and 10a); the pinnate ornamentation of the setae of its dorsal and dorsolateral sensilla (Fig. 8f); first abdominal segment with the ventro-lateral segmental spine  $7^{A1}$  without seta (Fig. 9b); first pair of segmental spines on abdominal segment 7

very developed (mainly for the great development of the fleshy projection of its base) and almost alienated with pairs of sensilla 2–4 (in both subgenera of *Scaeva* and genus *Austroscaeva* this first pair of segmental spines is located posteriorly) (Fig. 10a); and first pair of segmental spines on abdominal segment 7 separated from the posterior respiratory process just by one thin fold (two folds in *Scaeva* subgenera and *Austroscaeva*).

Unfortunately, the preimaginal stages of *Notosyrphus* remain undescribed. The diverse preimaginal morphology of the Neotropical taxa (*Dioprosopa* and *Austroscaeva*) reported in this study makes it difficult to infer general trends in the larval morphology of *Notosyrphus*, except the likely presence of the U-shaped grasping organ. More field work and laboratory

rearing are needed to investigate the preimaginal diagnostic characteristics of the Neotropical clade of the *Eupeodes-Scaeva* lineage and to corroborate the hypothesised larval characters of *Pseudodoros*.

## CONFLICT OF INTEREST

The authors declare no potential conflicts of interest.

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