

## Description of the larva and puparium of the Oriental soldier fly *Prosopochrysa vitripennis* (Diptera: Stratiomyidae) and observations of its biology

Jana Nerudová<sup>1,2\*</sup>, Andrea Špalek Tóthová<sup>3</sup> & Damir Kovac<sup>4</sup>

**Abstract.** The larva and puparium of *Prosopochrysa vitripennis* from northern Thailand are described. This is the first in-depth description of immature stages for the entire tribe Prosopochrysini (Diptera: Stratiomyidae: Stratiomyinae), which includes 65 extant species worldwide. The larvae of *P. vitripennis* are aquatic and develop in puddles that form in or near streambeds during the dry season in northern Thailand. Mature larvae crawl ashore and use a secretion to attach themselves to the surfaces of fallen leaves protruding from the water. The larvae and puparia of *P. vitripennis* are illustrated by macro and SEM photographs and drawings, and their cuticle structures and basic diagnostic characters are documented. The morphological characters of *P. vitripennis* larvae are compared with those of the two other tribes of the subfamily Stratiomyinae, Stratiomyini, and Oxycerini. A key for the identification of the known larvae of the Oriental Stratiomyinae is given.

**Key words.** Stratiomyidae, *Prosopochrysa vitripennis*, immature, Oriental, Thailand, taxonomy, morphology

### INTRODUCTION

The family Stratiomyidae contains over 2,700 species worldwide (Pape & Thompson, 2017). Based on Woodley (2001, 2011), the aquatic subfamily Stratiomyinae is the largest with over 640 species, consisting of three tribes: Stratiomyini, Oxycerini and Prosopochrysini. However, there are no apomorphic characters to define the Stratiomyinae and the molecular data available to date (Brammer & von Dohlen, 2007) are insufficient to resolve their relationships. *Prosopochrysa vitripennis* (Doleschall, 1856) is a member of the tribe Prosopochrysini with 65 extant and 2 fossil species present in all biogeographical regions, with the greatest generic diversity in the Afrotropical Region (Woodley, 2001, 2011; Hauser et al., 2017; Lessard et al., 2019; Fachin et al., 2024). Most species in the tribe have a sinuate CuP vein and a recurved arcuate CuA vein (James, 1942, as Myxosargini; Woodley, 1985, 2011), but some genera lack this character (Fachin et al., 2024). The diversity of

characters, combined with the restricted and often isolated distribution of Prosopochrysini, may indicate that this is an older, more relict group (Fachin et al., 2024).

Five species are recognised in the genus *Prosopochrysa* de Meijere, 1907: *Prosopochrysa chusanensis* Ōuchi, 1938, *P. azurea* (Lindner, 1951), and *P. vitripennis* are Oriental, *P. sinensis* Lindner, 1940 (and *P. chusanensis*) have been recorded from Palearctic China and *P. lemanna* Lessard & Woodley, 2019 is Australian (James, 1975; Woodley, 2001; Lessard et al., 2019). *Prosopochrysa chusanensis*, *P. sinensis*, and *P. lemanna* can only be distinguished by some subtle colour differences and may be synonyms of *P. vitripennis* (M. Hauser, pers. comm.). The unusual presence of a pair of small scutellar spines in *P. azurea* (absent in all other species of the genus) suggests that this species may not be a member of *Prosopochrysa* (Lessard et al., 2019; Fachin et al., 2024) and will be eventually transferred to another genus (M. Hauser, pers. com.).

The other two Prosopochrysini genera occurring in the Oriental Region are *Nothomyia* Loew, 1869 (most species Neotropical, similar to *Prosopochrysa*) and *Rhaphiocerina* Lindner, 1936 (two species in China and Japan) (Woodley, 2001; Li et al., 2016). Both have a coronet of hydrofuge hairs on the anal segment. An Oriental *Nothomyia* species found by DK (pers. obs.) was aquatic while the Japanese *Rhaphiocerina hakiensis* (Matsumura, 1916) was found on the rocks of a stream feeding on lichen. At the time of collection and during rearing, it remained in a damp, non-submerged habitat.

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<sup>1</sup>Moravian Museum, Department of Entomology, Hviezdoslavova 29a, 627 00 Brno, Czech Republic; Email: jnerudova@mzm.cz (\*corresponding author)

<sup>2</sup>T. G. Masaryk Water Research Institute, Mojžírovo náměstí 16, 612 00 Brno, Czech Republic; Email: jana.nerudova@vuv.cz

<sup>3</sup>Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic; Email: tothova@sci.muni.cz

<sup>4</sup>Forschungsinstitut Senckenberg, Senckenberganlage 25, 60325 Frankfurt am Main, Germany; Email: damir.kovac@senckenberg.de

*Prosopochrysa* are mostly slender flies with antennae inserted at the apex of the prominence and a slender, elongate abdomen, widest about the width of the thorax, longer than wide. The colour is usually shiny metallic greenish blue, similar to some Hymenoptera (Borror et al., 1989; Woodley, 2001; Yang et al., 2014). The eyes are slightly separated in males, more so in females, the frons and face are slightly produced, with the antennae inserted at the apex of prominence. The antennae consist of six flagellomeres: the basal four flagellomeres are compressed anteroposteriorly to form a short ovoid complex and the apical two flagellomeres are slightly thickened at the base to form a long arista-like stylus. Frons and occiput are without pale markings. The scutellum is unarmed, only *P. azurea* has two small spines. The species of *Prosopochrysa* can be separated from Oxycerini by the wing, with  $R_4$  and  $M_3$  being absent,  $R_{2+3}$  arises from the radial sector just beyond the middle of the discal cell, terminating in the costa close to  $R_1$ ,  $M_4$  separated from the discal cell by a cross vein, alula rather broad, ovoid. Female cerci are short, one-segmented and ovoid (Lessard et al., 2019).

The larvae of Stratiomyinae live in stagnant or running water or in semi-aquatic situations (Mathur, 1933; Oldroyd, 1969; Stubbs & Drake, 2001; Nerudová & Kovac, 2008; Khaghaninia & Kazerani, 2016). They are scavengers with highly specialised mouthparts that feed on decaying organic detritus, algae, and perhaps even small crustaceans (Rozkošný, 1982). As in other Stratiomyidae, the pupa remains enclosed in the last unmodified larval skin ('puparium'), a feature shared only with Xylomyidae in the lower Brachycera (Orthorrhapha) (Kovac & Rozkošný, 1997). Thus, most larval characters are retained in the puparium, but the integument is usually hardened and some puparia have elongated anterior spiracles (*Oxycera* Meigen, 1803) or rod-like pupal respiratory horns on the abdominal segments (*Oxycera*, Beridinae, Pachygastrinae, Sarginae, Clitellariinae) (Rozkošný, 1982).

Knowledge of the larvae of Stratiomyinae in the Oriental Region is very poor (Woodley, 2001; Nerudová-Horsáková et al., 2007; Wang et al., 2007; Yang et al., 2012, 2014). So far, only six larvae of Stratiomyini have been described, of which four species belong to the genus *Odontomyia* Meigen, 1803 and one species each to the genera *Oplodontha* Rondani, 1863 and *Stratiomys* Geoffroy, 1762. *Odontomyia cyanea* Brunetti, 1920 was described in detail by Mathur (1933) and SEM micrographs with diagnostic characters were presented by Nerudová-Horsáková et al. (2007). *Odontomyia luteiceps* de Meijere, 1911 (described as *O. latitibia*) and *O. pulcherrima* Brunetti, 1920 were described by Rozkošný & Kovac (1994, 2001). Diagnostic characters of the larvae of *Odontomyia ochropa* Thomson, 1869 were published in detail by Nerudová-Horsáková et al. (2007), who also proposed an identification key for the known Oriental larvae of the genus. The larvae of *Oplodontha rubrithorax* (Macquart, 1838) and *Stratiomys reducta* Nerudová, Kovac & Rozkošný, 2007, both found by Damir Kovac in northern Thailand, were described in detail in the papers of Nerudová et al. (2007, 2015).

In Prosopochrysinini, there are only two superficial larval descriptions worldwide. McFadden (1967: 35) described the puparium of the Nearctic *Myxosargus nigricornis* Greene, 1918 and provided figures, while Kawai & Ohishi (2015) described the Palearctic *Rhaphiocerina hakiensis* from Japan and provided a simple drawing of the larval habitus and photographs of the larva. The known larval habitats of the Oriental Stratiomyinae are diverse: *Odontomyia cyanea* was found in tree holes and rock pools (Mathur, 1933; Nerudová-Horsáková et al., 2007), *O. ochropa* in a duck pond (Nerudová-Horsáková et al., 2007), *O. luteiceps* in water-filled cavities in trees and bamboo (Rozkošný & Kovac, 1994; Nerudová-Horsáková et al., 2007), *O. pulcherrima* on the surface of permanently wet rocks, e.g., at waterfalls (Rozkošný & Kovac, 2001), *Oplodontha rubrithorax* at the edge of a hot spring (Nerudová et al., 2015), and *Stratiomys reducta* in spring pools (Nerudová & Kovac, 2008).

## MATERIAL AND METHODS

The examined larvae of *Prosopochrysa vitripennis* were collected individually by Damir Kovac in April and May 2014 in Mae Hong Son, near Ban Nam Rin and Soppong (Thailand, Mae Hong Son Province). Larvae were reared within 2–11 days after collection (9 males, 3 females). Larvae and puparia were preserved in 70% ethanol. External structures were examined using an Olympus SZ61 stereoscopic microscope and measurements were taken using an ocular micrometer. All drawings were made using a camera lucida and photographs were taken using a Leica MSV266, with stacked images being combined using Helicon Focus 7.0. Larvae and puparia were prepared for SEM as follows: after cleaning, larvae and puparia were preserved in 70% ethanol, dehydrated in a graded series of ethanol solutions and dried by the critical point technique with CO<sub>2</sub>. Dried specimens were mounted on stubs, coated with palladium gold, and examined under a Hitachi scanning electron microscope (CamScan CS24). Terminology, including chaetotaxy, follows the monograph by Rozkošný (1982) and a general review of the dipteran larval morphology by Courtney et al. (2000). The studied material is deposited in the Moravian Museum, Brno, Czech Republic and in the Senckenberg Museum, Frankfurt am Main, Germany.

## RESULTS

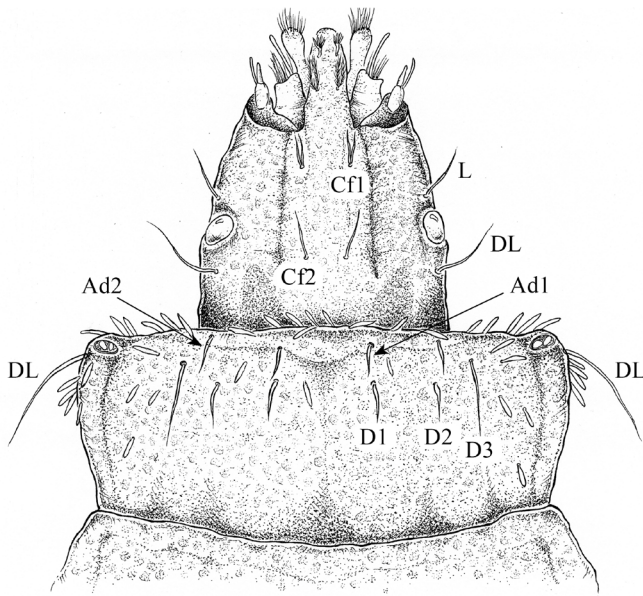
### *Prosopochrysa vitripennis* (Doleschall, 1856)

*Chrijsoclora vitripennis* Doleschall, 1856: 408.  
*Microchrysa albitarsis* Brunetti, 1913

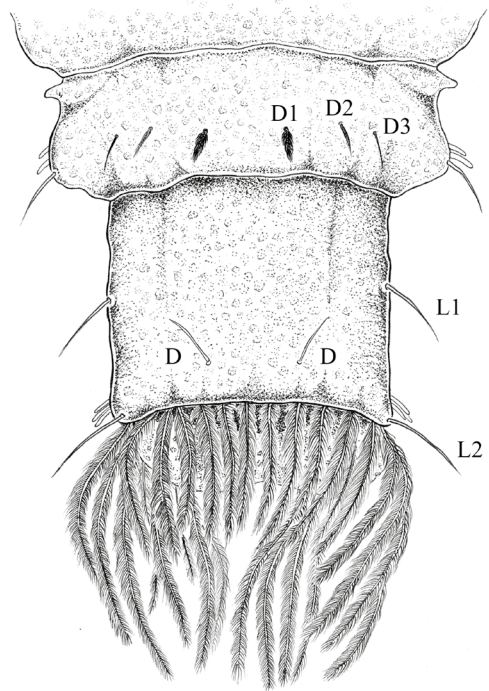
### Description of larva and puparium

**Mature larva (Figs. 1–17).** Shape and colour (Fig. 17). Elongate, slightly dorsoventrally flattened, abdominal segments slightly tapering and elongated towards caudal end. Head mostly yellowish-brown, only dorsomedial and ventral sclerites darkened brown. Lateral sclerites (genae, ocular

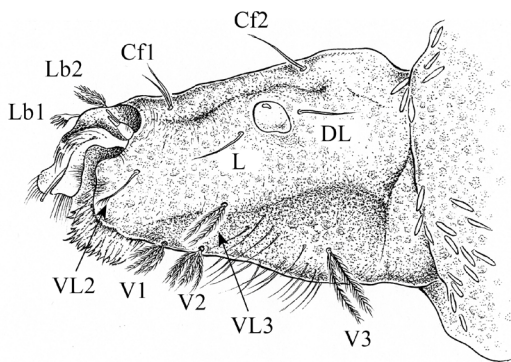
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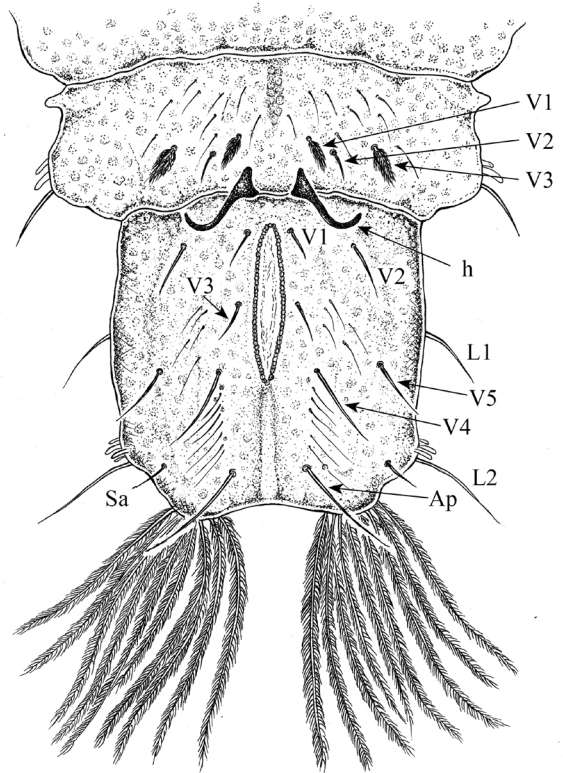
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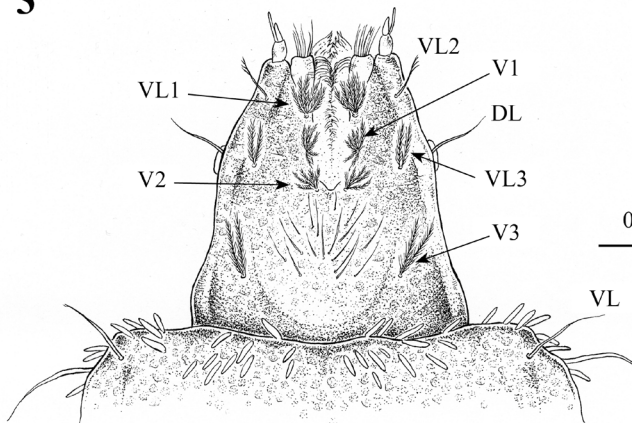
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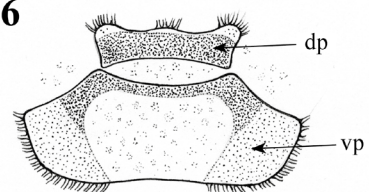


3



0.50 mm

6



Figs. 1–6. *Prosopochrysa vitripennis*. Mature larva: 1, head and thoracic segment 1, dorsal view; 2, head, lateral view; 3, head, ventral view; 4, last two abdominal segments, dorsal view; 5, last two abdominal segments, ventral view; 6, spiracular plate complex. h – hooks, dp – dorsal plate, vp – ventral plate, Ad1, Ad2, Ap, Cf1, Cf2, D, D1, D2, D3, DL, L, L1, L2, Lb1, Lb2, Sa, V1, V2, V3, V4, V5, VL, VL1, VL2, VL3 = constant setae (= setae that are always present, part of the ground plan of the larvae of Stratiomyidae).

plates) predominantly yellowish-brown. Oral opening and basal segment of antenna brown. Body segments yellowish brown in ground colour, with brown and yellow pattern. Thoracic segment 1 yellowish brown with six (= three pairs) yellow anteroposteriorly elongated patches forming distinct bands on each side of the darkened middle. All pairs of bands extend to posterior edge of segment; lateral yellow bands extend to lateral edges of segment. Small round or oval dark brown spots arranged in small groups either of 4-6 or irregularly over entire segment area. Thoracic segment 2 with yellow and brown patches and spots forming a distinct pattern. The same pattern is more or less distinct on all other segments except the last abdominal segment. The pattern on the last abdominal (anal) segment is limited to a brown central band and brownish longitudinal narrow stripes on each side. Venter of body segments yellowish-brown in ground colour. All thoracic and abdominal segments with small dark brown spots, sometimes arranged in circular or lateral symmetrical groups.

Head (Figs. 1-3; 7-11) only slightly retracted into thoracic segment 1, longer than wide in dorsal view, head index (length: width) 1.3-1.4. Labrum slightly longer than anterolateral corners of head capsule. Eyes distinctly convex, in dorsolateral position, same colour as surrounding area. Two-segmented long antennae located at the anterolateral angles of the head capsule (a, in Figs. 10, 11). Basal segment of antenna about twice as long as wide; apical segment more than three times as long as wide, and conical. One long finger-like sensilla, longer than apical segment of antenna, and three short finger-like sensilla visible beside apical segment (se, in Fig. 11).

Mandibular-maxillary complex densely haired, with more or less distinct transverse rows of flat setae, finger-like maxillary palpus relatively long. Ventral opening of head capsule well-developed, covered with fine membrane.

Body segments. Larval body composed of three thoracic and eight abdominal segments. Thoracic segment 1 (prothorax) more than twice as wide as long. Thoracic segments 2 and 3 almost four times as wide as long. Abdominal segments gradually narrowing and elongating towards distal end: segments 1-3 almost three times as wide as long, segment 5 almost three times as wide as long, segment 7 almost 2.5 times as wide as long. Strong ventral hooks developed on posterior margin of abdominal segment 7 (h, in Figs. 5, 15). Anal segment short, almost as long as wide (index of mature larvae about 0.9). Oval anal slit located near base of anal segment occupying almost half of segment length (Figs. 5, 15). The sclerotised lips of the spiracular opening form spiracular plates. Dorsal spiracular plate narrow, ventral spiracular plate large and deeply emarginated in middle (dp, vp, in Figs. 6, 16). Pointed, conspicuous lateral projection present on anterior corners of thoracic segment 3 and all abdominal segments except last (anal) segment (Figs. 4, 5). Thoracic segments 2 and 3 adorned with rounded lateral projections near posterior margin of segment; projection on segment 2 larger than on segment 3. Narrow sternal patches present on abdominal segments 6 and 7.

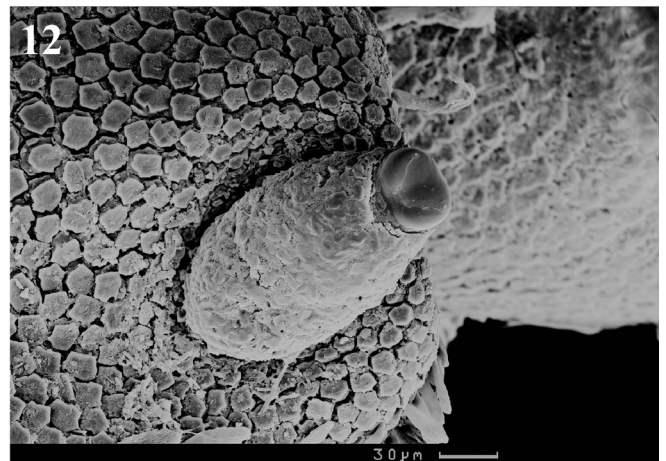
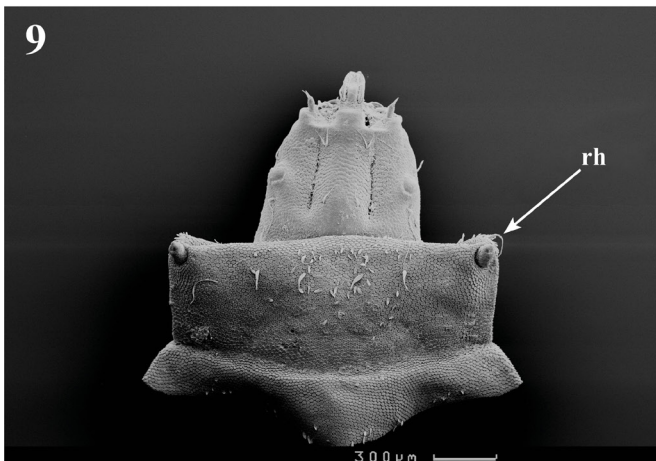
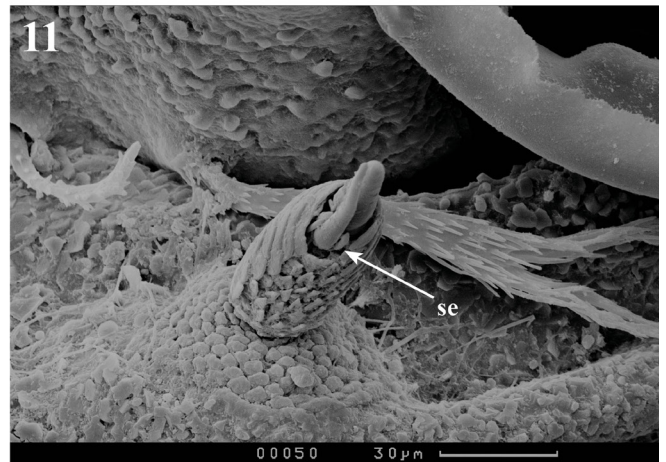
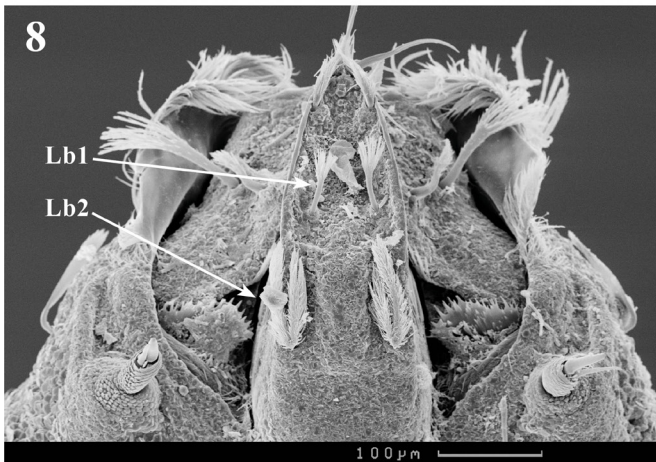
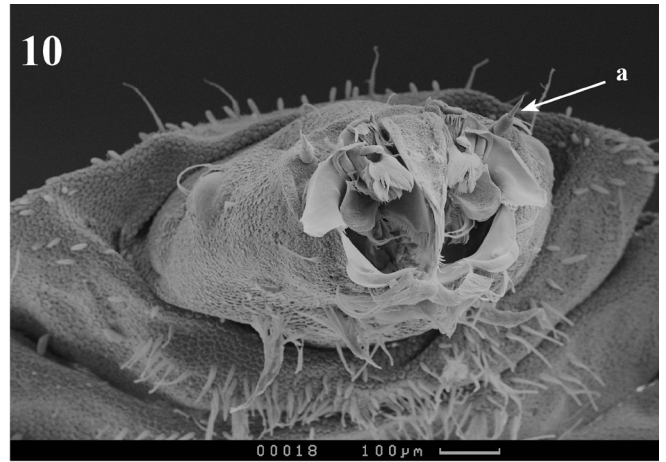
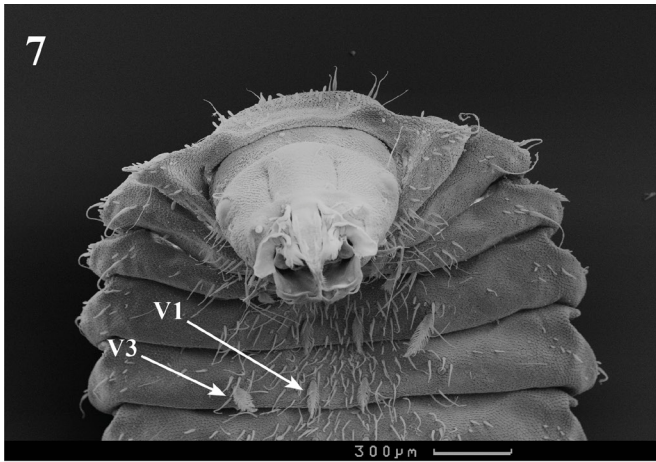
Respiratory system. Anterior spiracle, placed on conical tubes on each side of thoracic segment 1, small, oblique oval (Fig. 1). Usually small, inconspicuous, rudimentary and non-functional spiracles on abdominal segments 2-5, poorly visible. Transverse spiracular opening at distal end of anal segment surrounded by pinnate float hairs arising from dorsal and ventral spiracular plate (Figs. 5, 6, 15, 16).

Chaetotaxy. All characteristic setae of head present. Head capsule with conspicuously haired ventral surface (Figs. 2, 3), some major ventral setae barely visible between long dense hairs. Labral setae (Lb1) short and broadly pinnate, Lb2 two-branched with short hairs (Figs. 2, 8), clypeofrontal setae (Cf1) two-branched and slender, posterior clypeofrontal setae (Cf2) at level of posterior eye margin with one or two branches (Figs. 1, 2). Slender dorsolateral seta (DL) posterior to eye-prominence and long lateral seta (L) anterior to eye (Figs. 1, 2). Three pairs of setae present on ventral side of the head. Seta V1 close to ventral opening, bush-like but often almost invisible between marginal hairs of genal lobes, setae V2 bush-like with numerous pubescent branches, setae V3 with two or exceptionally three branches with long pubescence. Ventrolateral setae arranged in an elongated triangle: VL1 in middle of genal lobe bush-like, VL2 between lateral seta (L) and antenna pubescent in apical part, VL3 in front of V3, two exceptionally three branches with long pubescence (Figs. 2, 3).

Setae on body segments mostly poorly visible, weak and hyaline. Chaetotaxy of thoracic segment 1 is complete: 2 pairs of anterodorsal (Ad) and 3 pairs of dorsal (D) setae, setae Ad1 and Ad2, same shape as setae D1 and D2. Setae D3 very weak and long, poorly visible, shifted anteriorly to the transverse line of Ad setae (Fig. 1). One dorsolateral (DL) and one ventrolateral seta (VL) on each side, both of equal length, almost half as long as segment (Figs. 1, 3). Ventral side with long and slender outer ventral setae (V2) and simple, partly flattened and short-haired pubescence ventral setae (V1) inserted more medially and slightly anterad. Sparse, pale, short, finger-like hairs present on anterior dorsal margin of segment. Dense, short hairs well developed along anterior ventral margin of segment, occupying slightly more than medial third. Setae D1 and D2 on thoracic segments 2 and 3 in same position, dorsal setae D3 shifted posteriorly to the same transverse line as D1 and D2. Anterodorsal setae absent.

Configuration of dorsal setae on abdominal segments 1-7 very similar to thoracic segments 2 and 3; dorsal D1 and D2 setae pubescent, inserted on same transverse line on abdominal segments 1-3, D2 setae shifted slightly anteriorly on abdominal segments 4-7; D3 setae poorly visible (Fig. 4). Dorsolateral and ventrolateral setae mostly distinct, on each side of abdominal segments, but only fine and short. Ventral side with three pairs of setae, V1 and V3 setae distinctly flattened and pubescent, simple V2 shifted slightly posteriorly, closer to V1 than to V3 (Figs. 5, 13, 14).

On dorsal side of anal segment (= abdominal segment 8) one pair of relatively short setae on distal third and two pairs



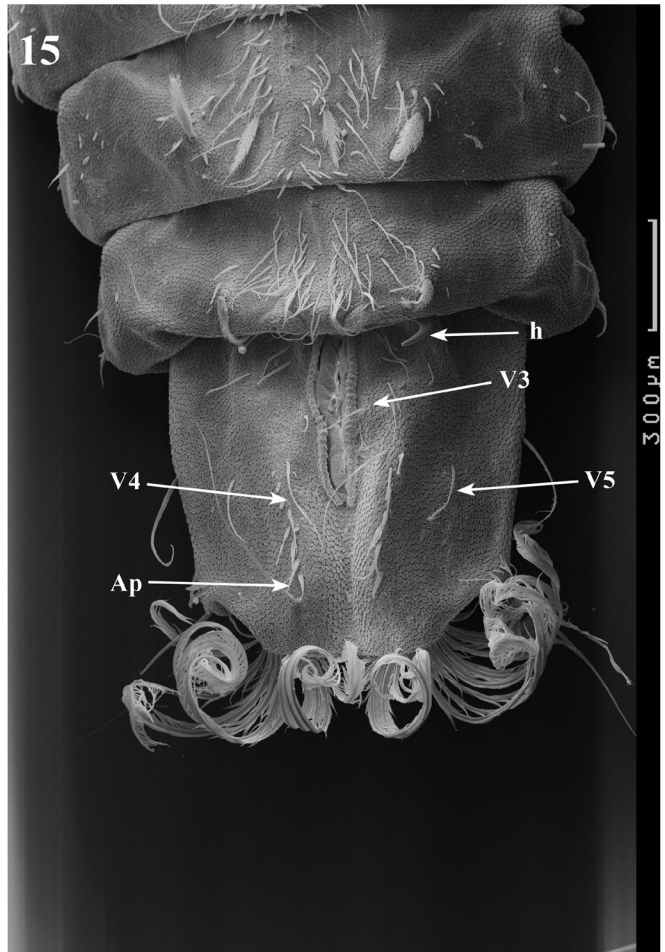
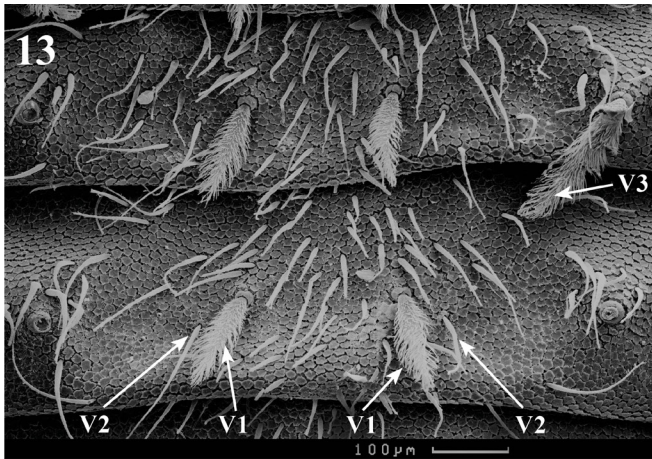
Figs. 7–12. *Prosopochrysa vitripennis*. Mature larva and puparium: 7, head and body segments 1-6, ventral view; 8, head and thoracic segment 1, dorsal view; 9, head and thoracic segment 1 (puparium), dorsal view; 10, head, frontal view; 11, antenna; 12, respiratory horn on the right side of the thoracic segment 1 (puparium), dorsal view. a – antenna, rh – respiratory horn, se – sensilla, Lb1, Lb2, V1, V3 = constant setae.

of lateral setae: L1 above middle of segment relatively long; L2 at each posterolateral corner distinct, longer than half of segment length (Figs. 4, 5). Ventral side with 5 pairs of simple and slender ventral setae being more or less distinct between thick and long hairs (V1 at sides of anal slit, V2 more lateral, V3 at sides of anal slit, approximately in the middle of its length, V4 at level of distal end of anal slit between anal slit and lateral margin of segment and V5 at same level but more medial). Pair of very long apical setae

(Ap) distinct on ventral side just above apical coronet. Subapical setae (Sa) present (Figs. 5, 15).

Measurements. Length: 8.3–10.1 mm; maximum width: 2.0–2.3 mm. Seven larvae examined.

**Puparium.** The puparium has the same characteristics as the mature larva, with the same length and maximum width. Respiratory horns are present on prothorax (rh, in Figs. 9, 12).



Figs. 13–16. *Prosopochrysa vitripennis*. Mature larva: 13, abdominal segments 3-5, ventral view; 14, abdominal segments 6 and 7, ventral view; 15, abdominal segments 6-8, ventral view; 16, spiracular plate complex. h – hooks, dp – dorsal plate, sp – sternal patch, vp – ventral plate, Ap, V1, V2, V3, V4, V5 = constant setae.

**Habitat and biology.** The larvae of *Prosopochrysa vitripennis* were found in northern Thailand during the dry season in April and May. They lived in puddles in dry streambeds or on the banks of streams and rivers that had been cut off from the main stream by the falling water levels (Figs. 18, 19). The puddles were filled with fallen leaves from trees and bamboo. The larvae crawled in the water between the leaves, presumably scraping food particles from the leaf surface. They used a coronet of hydrofuge hairs on the last

abdominal segment to breathe at the surface of the water (Fig. 17). Mature larvae crawled ashore and attached themselves with their posterior ends to the lower, hidden surfaces of fallen leaves protruding from the water. A secretion produced in the anal region was used for fixation. After hardening, the secretion became white and later yellow. The larvae shared their habitat with larvae of the water beetle family Scirtidae, which also use a secretion to attach themselves to leaves before pupation (Kovac & Klausnitzer, 2020).

Table 1. The main morphological differences between the larvae and puparia of the tribes Prosopochrysinini, Stratiomyini, and Oxycerini of the Stratiomyinae. In Prosopochrysinini, only the larva and puparium of the species described here are known. Data on Stratiomyini and Oxycerini are taken from Rozkošný, 1982, 1983.

Characters	Prosopochrysinini	Stratiomyini	Oxycerini
Antenna	at the tip of lateral sclerite	at the tip of lateral sclerite	dorsolateral to the lateral sclerite
Ventral opening on head	present	present	present or absent
Lateral projections on abdomen	present	present or absent	absent
Ventral hooks	on abdominal segment 7	on abdominal segments 6, 7 or absent	on abdominal segments 6, 7 or absent
Sternal patch	segment 6 and 7	segment 6 and 7 or absent	segment 6 and 7 or absent
Length of anal segment	about square	longer than broad	about square
Coronet of hydrofuge hairs	present	present	present or absent
Spiracular plates complex	present	absent	present or absent
Head L setae	in front of eye	below eye	below eye
Abdominal D setae	in transverse row D2 shifted slightly anteriorly on segments 4-7	D2 shifted anteriorly	in transverse row
Abdominal V setae	almost in transverse row V2 shifted slightly posteriorly	semicircular position	transverse row
Puparial respiratory horns	on prothorax	absent	on prothorax and abdominal segments 2-5 or 2-4
Puparial attachment by secretion	present	absent	absent

## DISCUSSION

The larvae of *Prosopochrysa vitripennis* (tribe Prosopochrysinini) are aquatic as expected from the members of the subfamily Stratiomyinae. A coronet of pinnate hydrofuge hairs surrounds the posterior spiracular plates, and a pair of strong ventral hooks are present on the posterior margin of segment 7. Both characters are also found in the other two subtribes of Stratiomyinae, Stratiomyini, and Oxycerini (Table 1). The hydrofuge hairs are an important feature of aquatic larvae, anchoring them to the water surface and allowing them to breathe through the anal spiracles. Ventral hooks are common in the Stratiomyinae, but depending on the species they are located on different abdominal segments and sometimes they are missing, e.g., in *Stratiomys* or in some species of *Odontomyia*. According to Schremmer (1952) the strong ventral hooks are associated with running water. Species with ventral hooks, e.g., *Oxycera*, often live on wet rocks, in moss near waterfalls or in similar hygropetric habitats. They use their hooks to avoid being swept away by the current when the water level rises due to heavy rainfall (Schremmer, 1952). This also seems to be the case for *Prosopochrysa vitripennis*. Although they live in stagnant water, their habitat in dry stream beds or along rivers is threatened by rains that occur at the end of, or sometimes even during, the dry season in which they develop.

Other features associated with aquatic life are the presence of a ventral opening on the head, which is connected to the drainage channels of the filtering apparatus of the cibarium (Rozkošný, 1982), and the shape of the anal segment. In terrestrial species, the abdominal segments are usually much wider than long, and the posterior margin of the last (anal) abdominal segment is rounded. In aquatic species, the anal segment is approximately square, or longer than wide, with the lateral margins being parallel or slowly tapering, and the posterior margin more or less straight. In *Oxycera* the sclerotised lips of the spiracular opening form complex “spiracular plates” (Rozkošný, 1982). The long body form of some aquatic larvae living in larger bodies of water, e.g., *Stratiomys*, allows them to feed deeper in the water while still being able to breathe at the water surface. In *Prosopochrysa*, the ventral opening associated with filter feeding is well developed and the anal segment is approximately square, the sclerotised lips of the spiracular opening form spiracular plates similar to *Oxycera* larvae. A long abdominal segment would not be advantageous, as *P. vitripennis* larvae live in small leaf-filled water bodies where they can feed close to the surface.

The two-segmented antennae of the Stratiomyidae larvae have a long basal segment and a small apical segment and appear to be longer in aquatic forms (Rozkošný, 1982).



Fig. 17. A larva of *Prosopochrysa vitripennis* scraping food from the surface of a submerged leaf.

*Prosopochrysa vitripennis* has a finger-like sensillum that is longer than the apical segment and some adjacent smaller sensilla. The long finger-like sensilla are also found in Stratiomyini (Rozkošný, 1982; Rozkošný & Kovac, 2001) and Oxycerini (Rozkošný, 1983) and some terrestrial forms. However, there is a difference in the position of the antennae. In Prosopochrysinini and Stratiomyini the antennae are located anteriorly, at the tip of the lateral sclerites, whereas in Oxycerini and in terrestrial groups they are placed dorsolateral to the lateral sclerites (Rozkošný, 1982). Another feature common to *Prosopochrysa* and Stratiomyini is the lateral projections found on the anterior corners of the thoracic and abdominal segments. For example, in the Stratiomyini, they occur in *Stratiomys longicornis* Scopoli, 1763 (see Rozkošný, 1982, p. 332). The larval setae are smooth, branched, or pubescent, and their position varies among the different species of the Stratiomyinae. In general, the basic pattern remains the same in all three tribes, but there are also some differences. In *P. vitripennis* the seta L is located in front of the eye, forming a straight line with setae DL and VL2 (Fig. 2), whereas in the Stratiomyini, the seta L is shifted below the eye. There are also some differences in the arrangement of the thoracic and abdominal setae between the three tribes. In Oxycerini the abdominal dorsal D-setae and also the ventral V-setae are arranged in a single transverse row, whereas in Stratiomyini the abdominal dorsal D2-setae are shifted anteriorly and the V-setae are arranged in a semicircular position. In *Prosopochrysa* the D-setae of abdominal segments 1–3 are arranged on a transverse line (Fig. 4), while on abdominal segments 4–7 the D2-setae are shifted slightly anteriorly. The three pairs of V-setae are arranged almost in a transverse row, V2 setae are shifted posteriorly (Figs. 5, 13, 14).

Some puparial characters also differ between the three tribes compared. *Oxycera* has puparial respiratory horns on the prothorax and the abdomen, as do the larvae of several terrestrial stratiomyid families. *Prosopochrysa* has puparial respiratory horns only on the prothorax and the Stratiomyini lack them (Table 1). The puparia of *Prosopochrysa*, *Nothomyia* (DK, unpub. obs.) and *Rhaphiocerina hakiensis* (Kawai & Ohishi, 2015) are attached to the ground by a



Fig. 18. Puddle beside a river in the dry season in northern Thailand, habitat of *Prosopochrysa vitripennis*.



Fig. 19. Puddle in a dry streambed inhabited by *Prosopochrysa vitripennis*.

secretion, whereas no puparial attachment was recorded in Stratiomyini and Oxycerini.

The coronet of hydrofuge hairs, the shape and length of the anal segment, the ventral hooks, and possibly other structures such as the pupal respiratory horns, are likely to be strongly influenced by the larval habitat and may be less suitable for reconstructing the larval phylogeny because such structures may have evolved several times independently. The influence of the aquatic habitat on the larval morphology is illustrated by the probably secondary loss of the ventral opening on the head, the abdominal hydrofuge hairs, the ventral hooks, and the spiracular plates in the terrestrial *Oxycera leonina* (Panzer, 1798) (Rozkošný, 1983).

A comparison of the remaining morphological characters (Table 1) suggests that the Prosopochrysinini are more closely related to the Stratiomyini than to the Oxycerini, because, like the Stratiomyini, their antennae are placed at the tips of the lateral sclerites, the abdominal D2-setae are (at least partially) shifted anteriorly and there are lateral projections on the anterior corners of the thoracic and abdominal segments. However, the Prosopochrysinini larvae differ from the Stratiomyini (as mentioned above) as follows: a) seta L in front of the eye in *Prosopochrysa* (below the eye in



Stratiomyiini), b) in *Prosopochrysa* the abdominal D-setae 1–3 are arranged on a transverse line, whereas on abdominal segments 4–7 the D2-setae are shifted slightly anteriorly, c) the two pairs of V-setae are arranged in a single transverse row, whereas in Stratiomyiini the dorsal abdominal D2-setae are shifted anteriorly and the V-setae are arranged in a semicircular position, and d) *Prosopochrysa* has a developed spiracular plate complex, which is absent in Stratiomyiini. The Oxycerini differ from the other two Stratiomyinae tribes in that their antennae are placed dorsolaterally to the tip of the lateral sclerite, the abdominal D and V setae are arranged in a transverse row, and the puparial respiratory horns are present on the abdominal segments. All these characters are also found in the larvae of several terrestrial families. Rozkošný (1983) excluded the Oxycerini from Stratiomyinae and placed them in Clitellariinae on the basis of some adult and larval characters (absence of crossvein m-cu, larval antennae placed dorsolaterally to the tip), while Woodley (2001) treated them as Stratiomyinae on the basis of their aquatic lifestyle. However, he did not find any apomorphic character that would define Stratiomyinae as a subfamily.

Recent molecular studies on adults (Brammer & von Dohlen, 2007) suggest that the Stratiomyinae are closely related to the Raphiocerini. The morphology of the only known Raphiocerini larva, the Neotropical *Raphiocera armata* (Wiedemann, 1830), supports this hypothesis, as it has a coronet of long pinnate hairs like the aquatic larvae of the Stratiomyinae (and Nemotelinae) (Pujol-Luz et al., 2004). Although the larva was found on a decaying tree trunk and was reared to adulthood in a terrestrial environment, it may have been aquatic at least temporarily. The study of larvae shows that they can provide important character systems for intra/intergeneric analyses which can be combined with adult characters, biology, and molecular studies in order to contribute to the resolution of the unresolved and ambiguous parts of stratiomyid phylogeny.

#### Identification key for known larvae of the Oriental Stratiomyinae

1. Last abdominal (anal) segment elongate, about 3.5–4 times as long as wide .....2
  - Last abdominal segment shorter, less than 3 times as long as wide .....3
2. Posterior margins of abdominal segments without ventral hooks.....
  - ..... *Stratiomys reducta* Nerudová, Kovac & Rozkošný, 2007
  - Posterior margins of abdominal segments 2, 6 and 7 with paired ventral hooks ..... *Odontomyia luteiceps* de Meijere, 1911
3. Dorsal body roof-shaped, lateral margins of body segments with tufts of long setae about as long as the corresponding segments ..... *Odontomyia pulcherrima* Brunetti, 1920
  - Dorsal body slightly convex, lateral margins of body segments without long setae .....4
4. Ventral hooks or spines in transverse rows on margins of abdominal segments 1-7, seta V3 on ventral head smooth with 2 branches.....*Odontomyia ochropa* Thomson, 1869
  - Ventral hooks paired, not arranged in rows, seta V3 on ventral head pubescent, fan-like or with 2-3 branches .....5
5. Paired ventral hooks on posterior margins of segments 2 and 7, anal segment about twice as long as wide.....
  - .....*Odontomyia cyanea* Brunetti, 1920
  - Paired ventral hooks on posterior margin of segment 7 only, anal segment less than twice as long as wide.....6
6. Seta V2 on ventral head relatively long, simple and smooth, no conspicuous lateral processes on anterior corners of thoracic segment 3 and abdominal segments 1-7, anal segment conical, rounded at apex, about 1.5 times as long as wide.....
  - .....*Oplodontha rubrithorax* (Macquart, 1838)
  - Seta V2 on ventral head bush-like, with many pubescent branches (Figs. 2, 3), conspicuous lateral processes on anterior corners of thoracic segment 3 and abdominal segments 1-7 (Figs. 4, 5), anal segment almost quadrate, slightly shorter than wide, spiracular plates present.....
    - .....*Prosopochrysa vitripennis* (Dobleschall, 1856)

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