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Redescription of immature stages of central European fireflies, Part 2: *Lamprohiza splendidula* (Linnaeus, 1767) larva, pupa and notes on its life cycle and behaviour (Coleoptera: Lampyridae)

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Abstract

The mature larva of the firefly *Lamprohiza splendidula* (Linnaeus, 1767) is thoroughly redescribed and illustrated with detailed images, including scanning electron microscope figures. External sense organs, structure of tergal plates and their significance are discussed, as well as photic manifestation of the larvae and pupae and prey hunting in larvae. Male and female pupae are briefly described, with notes on their developmental changes and behaviour, and the life cycle outlined.

Key words: Elateroidea, Lampyrinae, bioluminescence, morphology, ecology

Introduction

There are only eight described species in the genus *Lamprohiza* Motschulsky, 1853 (Lampyrinae) in Europe. Seven occur in the southwestern part of the continent and one across almost all of Europe (Burakowski 2003; Geisthardt & Satô 2007). Descriptions of the latter species, *Lamprohiza splendidula* (Linnaeus, 1767) are brief and the morphology, in particular the morphology of larvae, is poorly known. Schematic illustrations in many prior works are of variable quality, and none contain detailed images (Reitter 1911; Vogel 1913; Korschefsky 1951; Kratochvíl 1957; Medvedev & Ryvkin 1992; Klausnitzer 1994; Burakowski 2003), with exception of Geisthardt (1979), describing only larval thorax and Bugnion (1929) describing larva of related species *Lamprohiza delarouzei* Jacquelin du Val, 1859.

Lamprohiza splendidula (Linnaeus, 1767) is distributed in southeastern and central Europe, reaching the River Rhine to the west, the Caucasus Mountains to the east, the southern shore of Baltic Sea to the north, and central Italy and the Balkan Peninsula to the south (Burakowski 2003). It is the most common firefly in the Czech Republic (Hůrka 2005). The species inhabits moist and shaded open habitats of lowlands and uplands with deciduous forests, thickets, clearings, banks of rivers and streams, meadows and gardens (Schwalb 1961; Burakowski 2003; Hůrka 2005). It may occur syntopically with other firefly species (e.g. *Lampyris noctiluca* (Linnaeus, 1758), *Luciola* sp.; M. Novák, unpublished observation).

This paper represents the second part of a trilogy focusing on the immature stages of firefly species occurring in central Europe. The first part (Novák 2017) redescribes the larva together with male and female pupae of *Lampyris noctiluca* and the third final part (Novák 2018) will deal with *Phosphaenus hemipterus* (Goeze, 1777) and provide a dichotomous key to all three species and a comparative table of morphological features.

Material and methods

Larvae of *Lamprohiza splendidula* were collected from two localities in Prague, Czech Republic. Sixteen specimens were collected at the end of August 2013 from a hillside next to the Kunratický stream, behind the Thomayer Hospital (50°01'47.6"N, 14°27'47.8"E), commencing an hour after sunset. Subsequently, eleven

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additional specimens were collected in the same season the following year (2014) for rearing. The area is inside the deciduous Kunratický forest, where larvae are found mostly under bushes among decomposing moist leaves. The local rock consists mainly of slate, the climate is temperate, mildly arid characteristic for the Prague plain. The average yearly temperature is 8.8 °C; average annual rainfall is 476 mm (Dostálek 2009).

Three further specimens were collected at the beginning of September 2013 at Petřín hill, near a stairway under the statue of K. H. Mácha (50°04'54.4"N, 14°24'7.6"E). Petřín is a recently landscaped hill in the centre of Prague, an anthropoecosystem with a large amount of park greenery, although in higher parts, remains of the original thermophilic oak forest can still be found. Local rock consists of slates and siltstone, climate is continental with the majority of rainfall in the summer and autumn months. Average annual rainfall is 625 mm. Average yearly temperature is 7.6 °C, in summer the average is 18.5°C (Bratka *et al.* 2011). Specimens were found two hours after sunset, under bushes and low herbaceous vegetation.

From the eleven individuals collected in August 2014 only two survived and entered the stage of pupa in June 2015. One male and one female pupa were obtained.

Methods of identification and storing of the larvae and rearing of the pupae as well as methods of optical and electron microscope imaging are described in Novák (2017). Interpretation and terminology of larval and pupal descriptions follows Archangelsky & Fikáček (2004), LaBella & Lloyd (1991), description of thoracic and abdominal sclerites follows Ballantyne & Menayah (2002) and Lawrence & Ślipiński (2013).

Lamprohiza splendidula (Linnaeus, 1767)

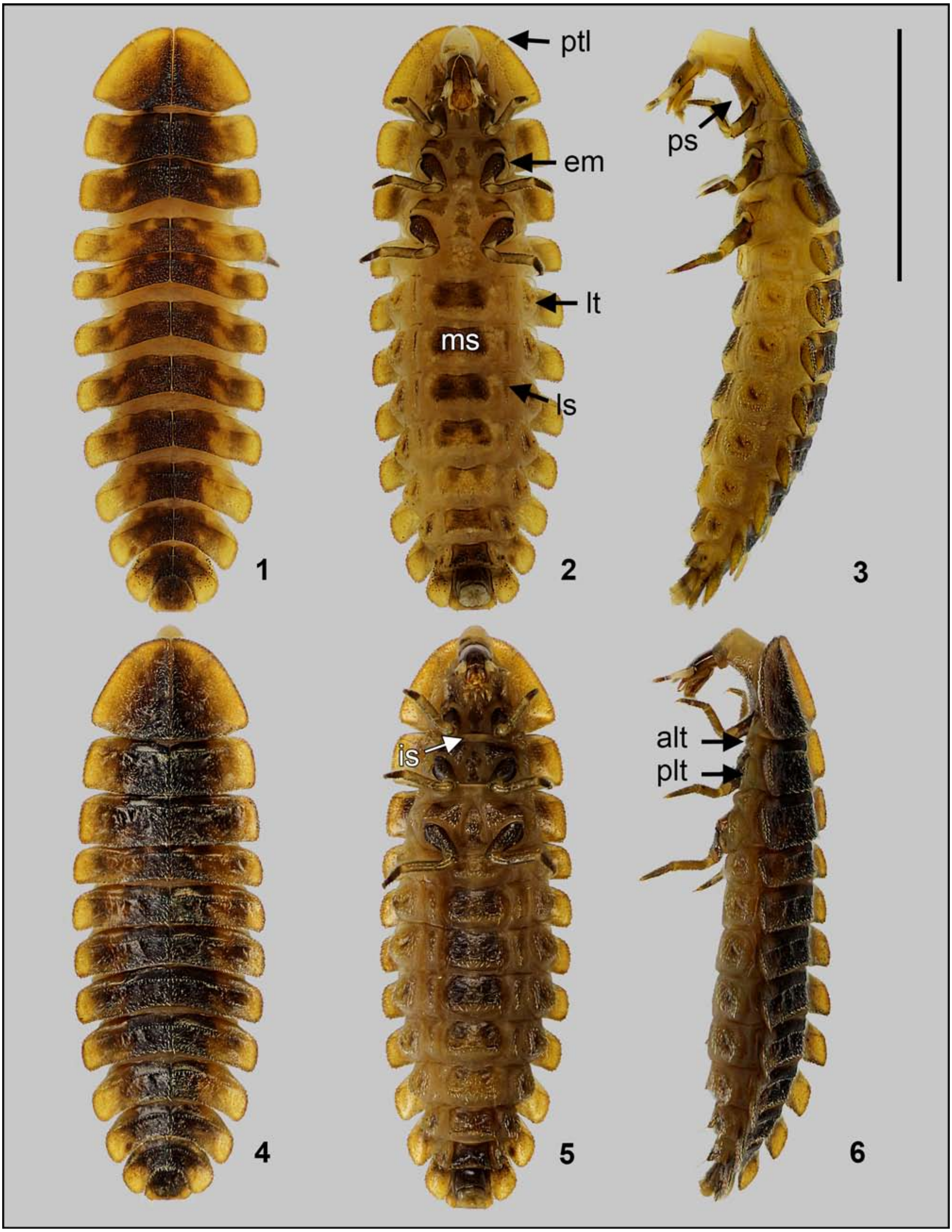
Material examined. Prague (Czech Republic), ten higher-instar larvae out of sixteen collected at the end of August 2013, one male and one female pupa were reared from eleven specimens collected at the end of August 2014.

Diagnosis. Larvae flat, laterally explanate, brown and ochre towards the lateral edges of tergites with pairs of lighter pigmented spots on abdominal tergites I–VI; protergum with narrow emargination anteromedially; light-coloured spot posteriorly behind each stemma; antennal sensorium with distinct basal constriction; retinaculum absent; mandibular channel opening covered by long feather-like or rounded-trapezium hyaline appendage; pretarsal claw ventrally bearing two long setae; photic organ of variable pattern, usually consisting of paired larger spots ventrolaterally on abdominal segments II and VI, sometimes with additional smaller spots ventrolaterally on abdominal segments III–V.

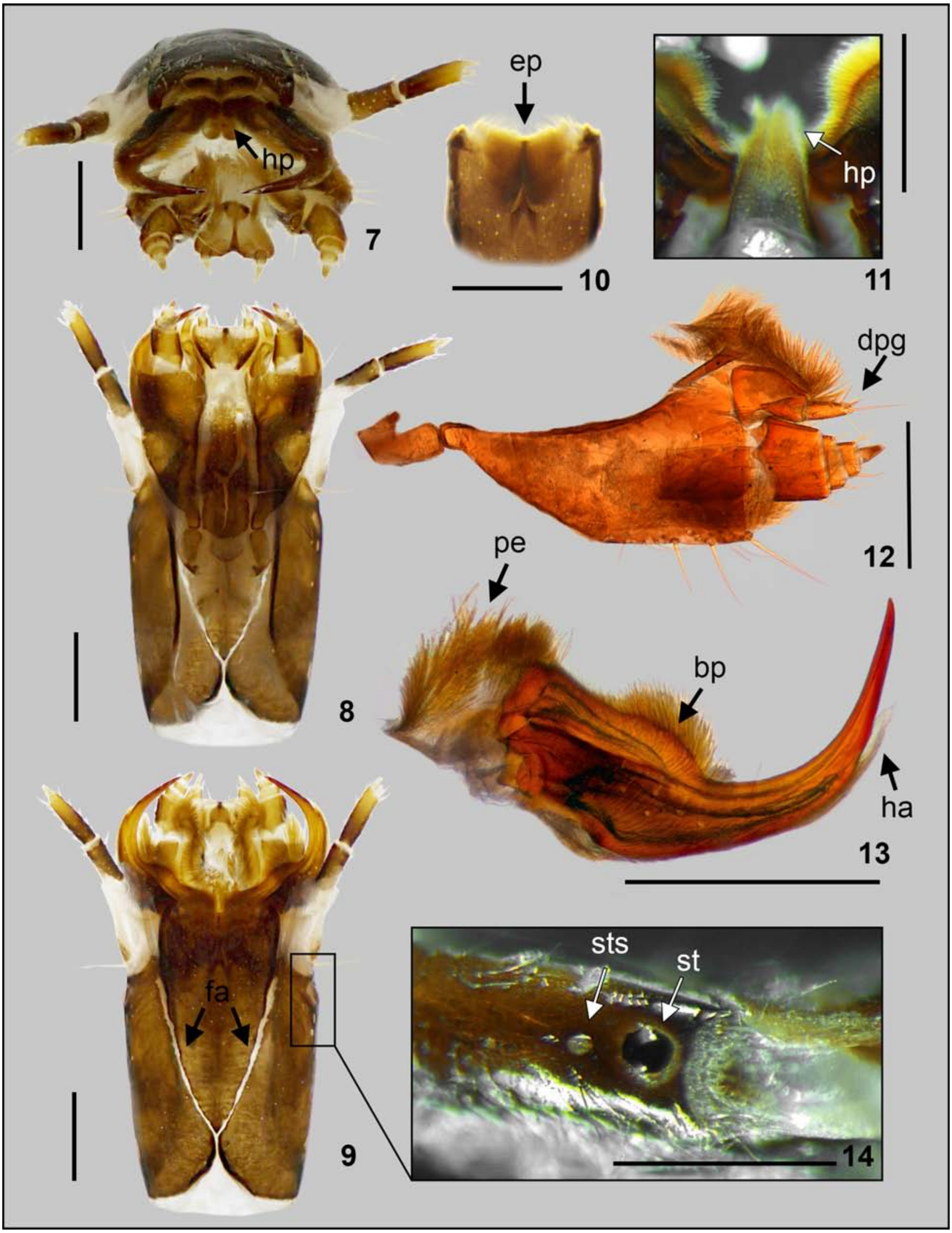
Description of mature larva (Figs 1–6). Elongate and onisciform; dorsoventrally flattened, tergites of thorax and abdomen finely setose on the edges (Figs 4, 15, 28), and strongly laterally explanate (Figs 1, 2, 4, 5). Body length ca. 11–12 mm (from the anterior margin of protergum to the apex of caudal segment); with 3 thoracic and 10 abdominal segments. Tergites from protergum to abdominal segment IX divided by sagittal line in dorsal view (Fig. 1). Colouration: dorsally brown and ochre towards the lateral edges of tergites; with pairs of lighter pigmented spots on abdominal tergites I–VI (Fig. 1), under which a variable number of localized photic organs may occur. Ventral region much lighter than dorsal, with ochre to light brown colouration, except central parts of sternal sclerites which are darker and more sclerotized. Spiracles on pleural plates are of dark brown colouration.

Types of general cuticular outgrowth observed. 1. Stout, long, erect setae (Figs 21, 22; les); 2. thin, short, erect setae (Figs 21, 22; tes); 3. flat setae, lying on/adjacent to the surface (Figs 15, 21, 29; fs).

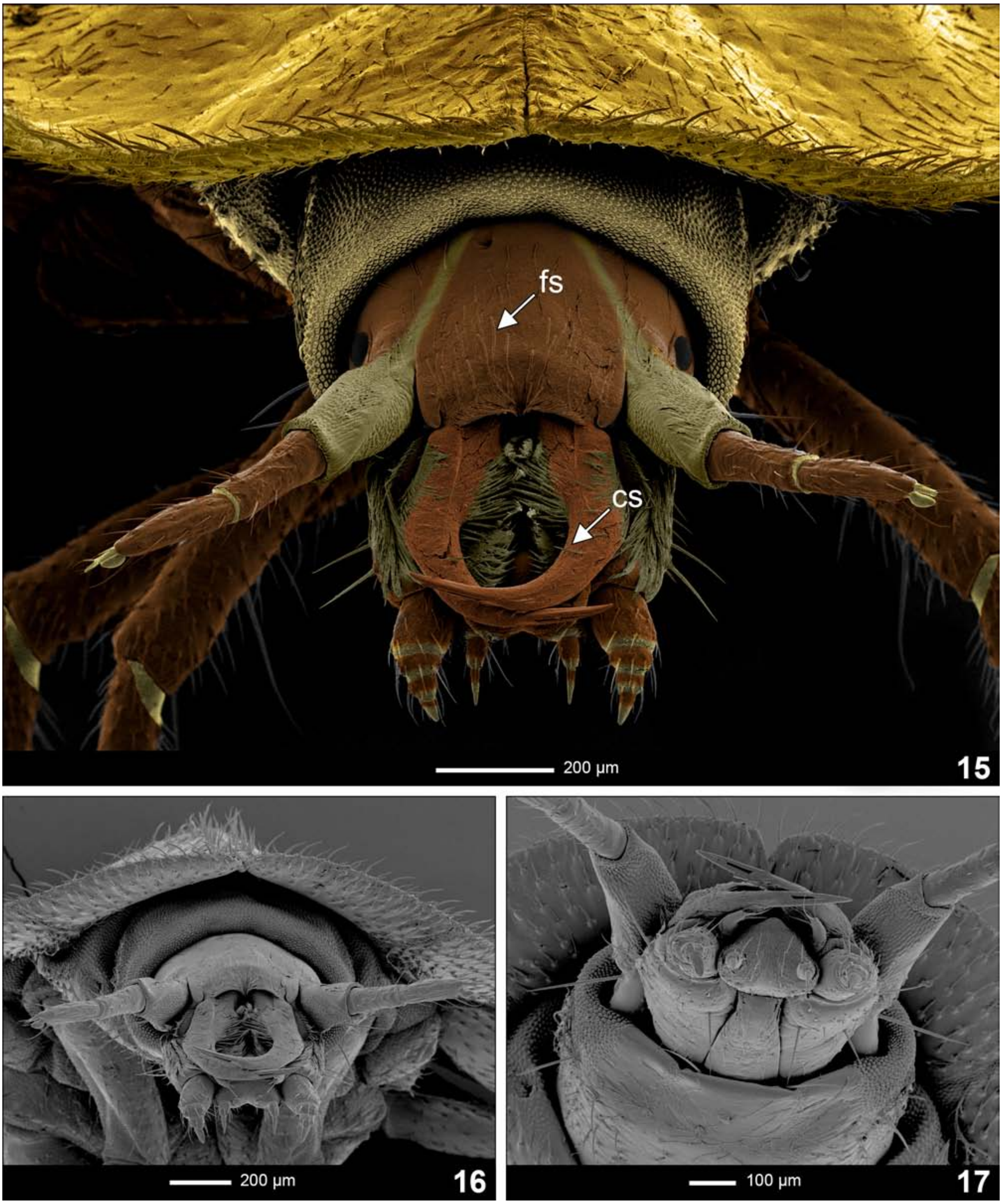
Head capsule (Figs 7–9, 15–17). Prognathous; retractable within prothorax, extensible neck membrane covered in extremely short spines and forming a two-layered envelope around retracted head; longer than wide, slightly tapering posteriorly. Epicranial plate laterally about 1.2 times longer than head capsule at its longest width, with one stout seta anterolateraly close to the base of antennae. Head capsule dorsally covered with long setae lying on surface (Fig. 15; fs). Epicranial suture of light colouration, Y-shaped, with a very short epicranial stem, frontal arms V-shaped (Fig. 9; fa). Gula not present (Fig. 8). One stemma on each side of the head, with a light-coloured spot placed posteriorly behind the stemma (Fig. 14; sts), possibly being a sensory organ. Labrum fused with clypeus forming clypeolabrum, covering the base of mandibles in dorsal view. Clypeolabrum double-arched in anterior view (Figs 15, 16), with no distinguishable setae on lateroapical margins. Epipharynx (Fig. 10; ep) formed by two plates and an anterior brush of long setae, which project centrally past anterior margin of the head. Hypopharynx (Figs 7, 11; hp) with long setation.



FIGURES 1–6. *Lamprohiza splendidula*. General habitus of mature larva photographed in alcohol in dorsal (1); ventral (2) and lateral (3) views. General habitus of mature larva photographed dry in dorsal (4); ventral (5) and lateral (6) views. Abbreviations: alt—anterior laterotergite; em—epimeron; is—intersternite; ls—laterosternite; lt—laterotergite; ms—median sternite; plt—posterior laterotergite; ps—prosternum; ptl—light-pigmented lines on protergum. Scale bar: 5 mm.



FIGURES 7–14. *Lamprohiza splendidula*. Detail of head in anterior (7); ventral (8) and dorsal (9, framed area enlarged in Fig. 14) views; detail of clypeolabrum in ventral view with epipharynx (10); detail of head with hypopharynx, after removal of maxillolabial complex, in ventral view (11); right maxilla in dorsal view (12); right mandible in dorsal view (13); detail of stemmal area (14). Abbreviations: bp—blunt protuberance on mandible; dsg—distal segment of galea; ep—epipharynx; fa—frontal arms; ha—hyaline appendage; hp—hypopharynx; pe—penicillus; st—stemma; sts—spot behind stemma. Scale bars: 0.25 mm.



FIGURES 15–17. *Lamprohiza splendidula*. SEM image of head in dorsal view (15, false colour); anterior (16) and ventral (17) views. Abbreviations: cs—distinct mandibular seta; fs—flat seta lying on surface.

Antenna (Figs 21–23). Trimerous, inserted on lateral distal margin of epicranial plate; partially retractable within membranous socket. Basal antennomere slightly wider than second antennomere, unsclerotized on posterolateral margin, bearing long flat setae lying on surface and erect setae lengthening towards the apical region. Second antennomere slightly narrower and longer than basal; bearing only erect setae equally spread across the antennomere, and with two longer setae on the outer apical region, next to sensorium. Sensorium of second antennomere (Figs 22, 23; as) oblong, potato-shaped, with distinct basal constriction as a connection with the second antennomere; with no visible surface pattern. Third antennomere (Fig. 22; a3) of similar size to sensorium of the second antennomere, bearing three setae on the apex, one seta on its body, and three cuticular projections (Fig. 23); first longer and thick (cp1), second longer and thin (cp2), third one placed on the body of antennomere forming a small bulge (cp3).

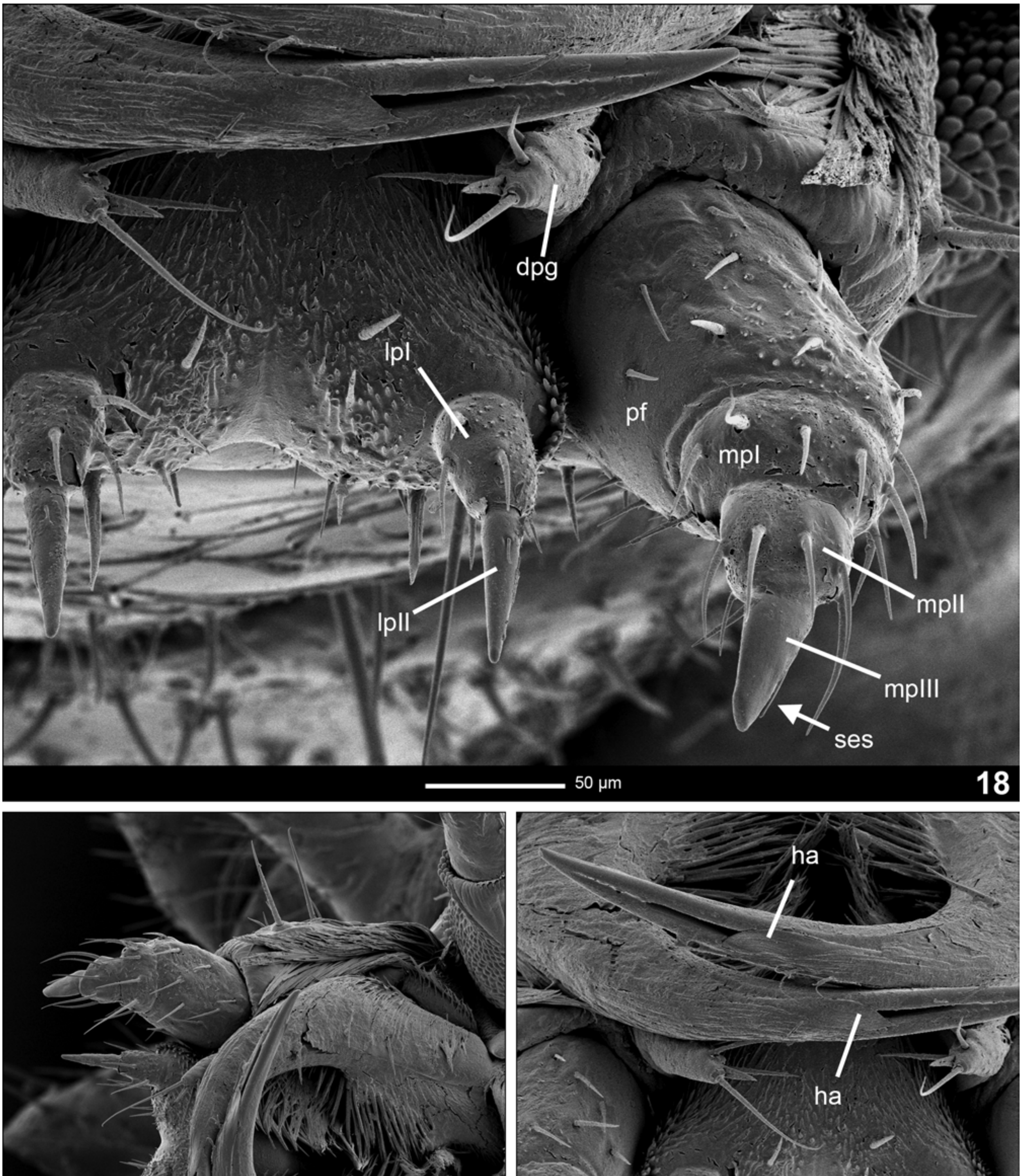
Maxilla (Fig. 12). Consisting of five parts, attached to lateral margins labium forming a maxillo-labial complex. Cardo vertical, subrectangular, about twice as long as wide. Stipes elongated, ventrally covered with erect setae, with three long stout setae placed radially on the ventral apical region. Outer dorsolateral area covered with long dense setation reaching the base of maxillary palpus (Fig. 19). Galea bimerous, with basal part larger than distal; distal part subcylindrical, pointing centrally, with short setae and one apical seta longer than body of the distal part and a blade-like flat cuticular projection on the apex (Figs 12, 18; dpg). Lacinia covered with brush of long setae on outer lateral margin (Fig. 12). Maxillary palpifer (Figs 18, 19; pf) large, subrectangular, of similar length and width. Maxillary palpus trimerous (Figs 18, 19; mp1, mp2, mp3), basal and second palpomeres short and wide. Palpifer and palpomeres I–II covered with setae; palpomere III subconical, narrow, sharp, bare, with outer lateral longitudinal depression, possibly a sensory slot, covered with thick blunt seta (Fig. 18; ses).

Labium (Figs 7, 8, 17, 18). Closely attached to maxilla, formed by a short and strongly sclerotized prementum, mentum and mostly membranous submentum (Fig. 8). Glossae absent. Prementum subtriangular, slightly heart-shaped in ventral view; covered with brush of short setae and bearing several pairs of longer setae along sagittal line of the apex, shortening towards ventral region and with one pair of longer, stout setae on central regions of ventral part. Labial palpus bimerous (Fig. 18; lp1, lp2); basal palpomere rectangular, longer than wide, bearing several setae; distal palpomere conical, longer and narrower than basal, bearing one short, thin seta lying on surface placed dorsally on basal part. Mentum elongated and subtriangular, unsclerotized on lateral margins, bearing numerous long setae lying on surface ventrally and a pair of long, erect setae posteromedially.

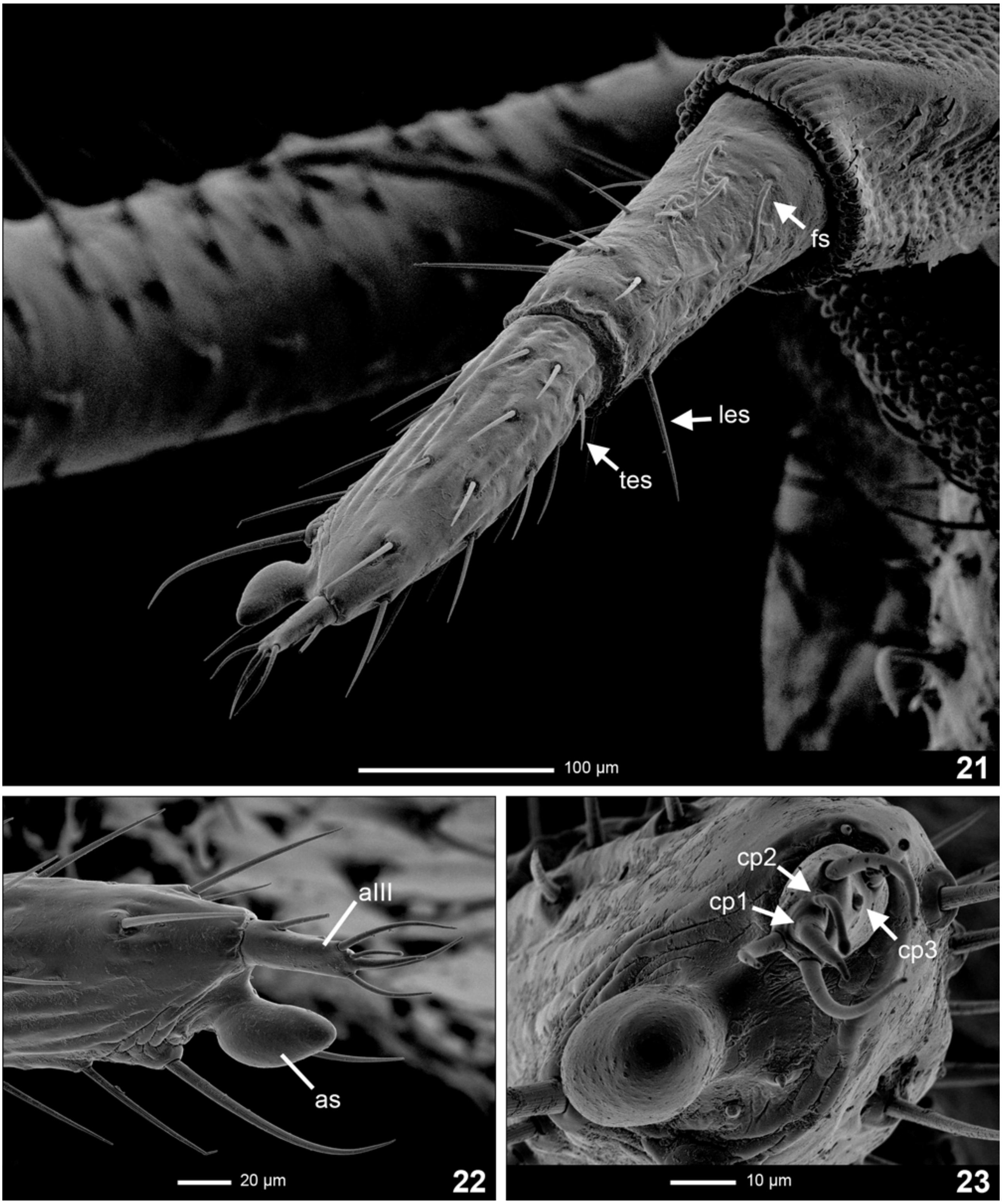
Mandible (Figs 7-9, 13, 15-17, 20). Symmetrical, falcate, with an internal channel opening subapically on outer edge (Fig. 20). Penicillus well developed (Fig. 13; pe). Retinaculum featureless, present only as a blunt protuberance on basal third of the mandible (Fig. 13, bp). Basal half on inner margin of mandible covered with a brush of stout setae, being longest on the retinaculous protuberance. Basal two-thirds of mandible ventrally with dense setation adjacent to the surface aimed centrally. Dorsal part of mandibles with several stout setae aiming centrally and a strong distinct seta aimed centrally (Fig. 15; cs), approximately in the central dorsal region of mandible. Lateral margin covered by brush of short setae lying on surface of basal two-thirds. Channel opening is partly covered by a feather-like or rounded-trapezium hyaline appendage with longer trapezoidal base situated ventrally (Figs 13, 20; ha).

Thorax (Figs 1–6). Three-segmented, thoracic tergites divided by sagittal line in dorsal view. Protergum subtriangular, wider than long, rounded at posterolateral corners, with narrow emargination anteromedially; ventrally with two light-pigmented lines, leading diagonally from the margin towards anterolateral corners of prosternum (Fig. 2; ptl). Meso- and metatergum subrectangular with round corners, ca. 4 times wider than long. Venter of prothorax composed of subrectangular, longer than wide prosternum (Fig. 3; ps), subdivided into three well sclerotized areas; lateral ones extending above and to the sides of coxae fusing with episterna; medial area arrow-shaped (tip aiming anteriorly). Epimera forming thin sclerotized strands (Fig. 2; em). Lateral areas of meso- and metathorax poorly sclerotized, composed of two laterotergites (Fig. 3; alt, plt); anterior one bearing a well developed bilabiate spiracle in mesothorax. Anterior ventral area of meso- and metathorax formed by membranous intersternite (Fig. 5; is) margined by paired anterior laterotergites (Fig. 3; alt). Posterior ventral area subrectangular, wider than long, subdivided into three well sclerotized areas; lateral ones extending anteriorly and laterally to coxae, joining episterna; medial area hourglass-shaped. Epimera forming thin sclerotized strands.

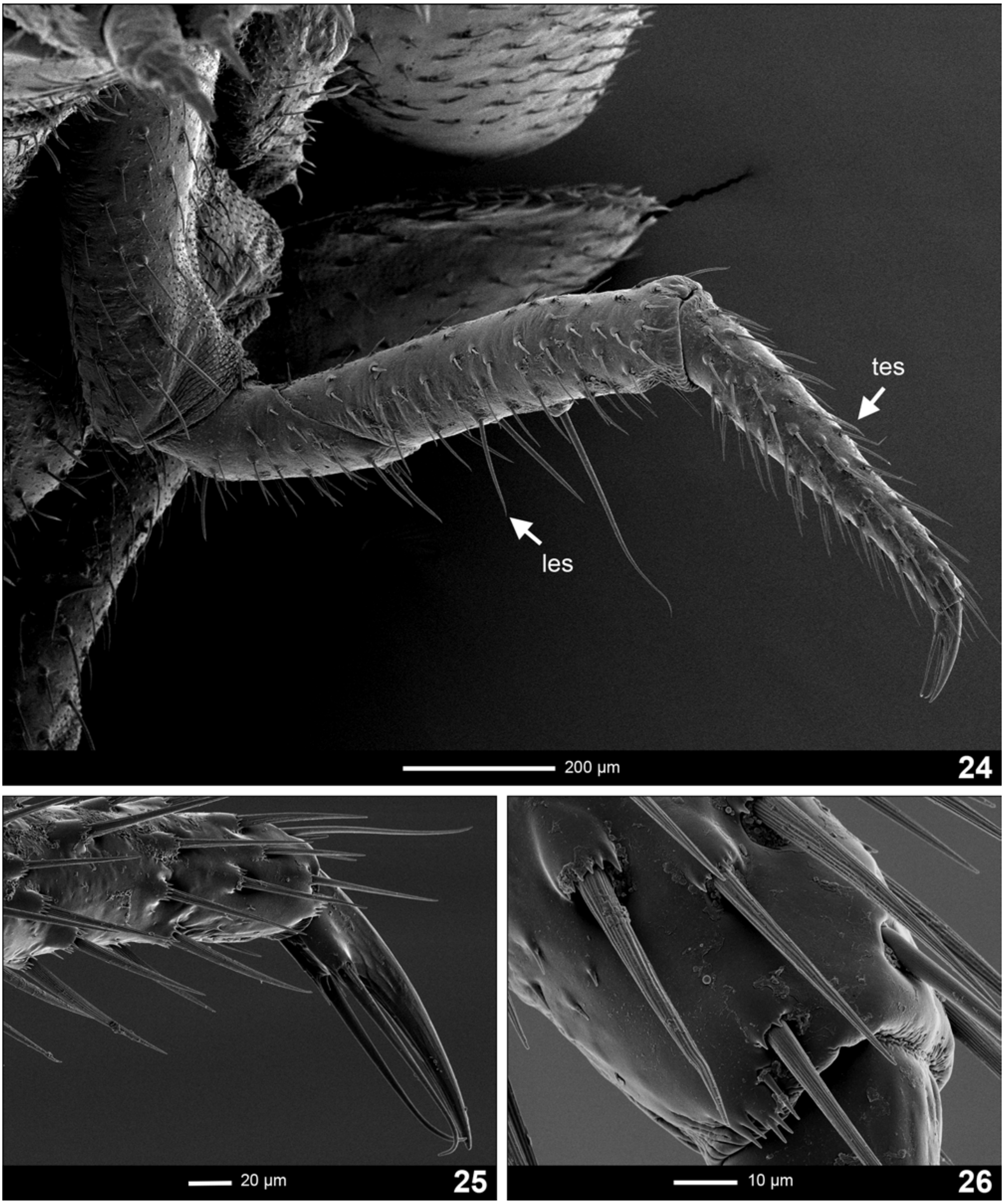
Legs (Figs 24–26). Pentamerous, all pairs similar in shape and size. Coxa large, stout, bearing stout setae. Coxal-trochanteral membrane reaching ca. 1/3 of coxal longitudinal length (Fig. 2). Trochanter smaller, elliptical in lateral view, shorter than femur, bearing shorter setae inclining to its surface and long stout setae, lengthening towards distal apex. Femur narrow and cylindrical in lateral view, bearing shorter setae inclining to its surface and long stout setae, lengthening ventrally, with one very long stout seta ventrally (Fig. 24). Tibiotarsus as long as femur, narrower, tapering towards distal end, bearing stout setae (Fig. 26). Pretarsus composed of a claw with fine ridges, ventrally bearing two long setae hooked apically towards each other, reaching the apex of the claw (Fig. 25).



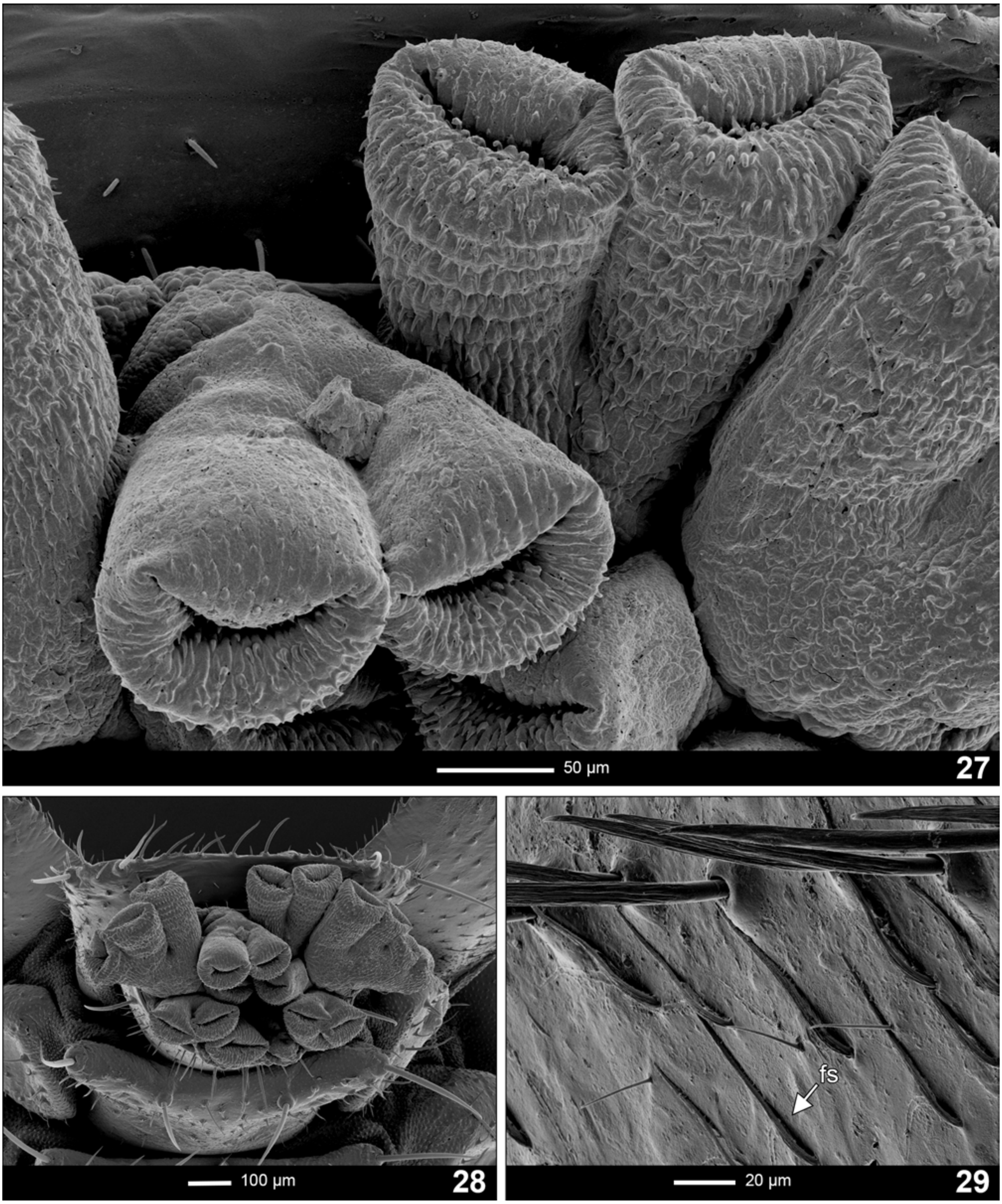
FIGURES 18–20. *Lamprohiza splendidula*. SEM image of maxillolabial complex in anterior (18) and dorsal (19) views; detail of mandibles (20). Abbreviations: dpg—distal part of galea; ha—hyaline appendage; lp1, lp2—labial palpus 1, 2; mp1–3—maxillary palpus 1–3; pf—maxillary palpifer; ses—sensory slot.



FIGURES 21–23. *Lamprohiza splendidula*. SEM image of antenna in general view (21); detail of sensorium and third antennomere (22); anterior view (23). Abbreviations: a3—third antennomere; as—antennal sensorium; cp1–3—cuticular projections 1–3; fs—flat seta lying on surface; les—long erect seta; tes—thin erect seta.



FIGURES 24–26. *Lamprohiza splendidula*. SEM image of left prothoracic leg in general view (24); pretarsus (25); detail of distal end of tibiotarsus (26). Abbreviations: les—long erect seta; tes—thin erect seta.



FIGURES 27–29. *Lamprohiza splendidula*. SEM image of pygopod in detailed (27) and general (28) views; detail of body surface of protergum (29). Abbreviation: fs—flat seta lying on surface.

FIGURES 30–37. *Lamprohiza splendidula*. General habitus of male pupa in ventral (30); dorsal (31); and lateral (32) views. Glowing male pupa in ventral (33) and lateral (34) views. General habitus of glowing female pupa in ventral (35); dorsal (36) and lateral (37) views. Abbreviations: mp—male photic organ. Scale bars: 5 mm.

Abdomen (Figs 1–6). Ten-segmented, tapering towards posterior end, segments I to VIII subdivided by fine sagittal line in dorsal view. Tergites of segments I to VII subrectangular, similar in shape and colouration, ca. 4 times wider than long; tergite of segment VIII subcrescentiform; tergite of segment IX subsemicircular; segment X forming a narrow, incompletely sclerotized dark ring, bearing the holdfast organ—pygopod (Figs 27, 28)—with several eversible processes. Segments I to VIII have single laterotergites (Fig. 2; lt) on each side with poorly sclerotized plates bearing bilabiate spiracles; the venter of segments I to VIII consists of median sternite (Fig. 2; ms), on segments I to V margined by paired narrow laterosternites (Fig. 2; ls). Median sternites of segments I to VIII subrectangular, wider than long, bearing a pair of long stout setae posterolaterally; median sternite and laterosternites of segment I membranous. Sternite of segment IX well sclerotized, rectangular and dark. Sternites of segment V and VI less sclerotized. Functioning photic organs do not follow a solid pattern; composed of paired or single spots placed ventrolaterally on abdominal segments II to VI in variable number; most common configuration consisting of larger, usually paired spots on abdominal segments II and VI; possible additional smaller spots, if present, paired or single, on abdominal segments III—V.

Notes on larval behaviour. During the collecting of larvae, specimens were, thanks to their glow, frequently spotted from several metres away. While searching between bushes, the collecting team caused noise and vibrations, which were probably perceived by the larvae. However, when collected from the ground and handled, larvae often substantially reduced their glow, thus sometimes making the actual collecting almost impossible without a flashlight.

Description of female pupa (Figs 35–37). Type pupa adectica exarata libera. Curved, ventrally concave. Length 11–12 mm. Colouration: light yellow, with translucent protergum and abdominal tergites. Surface covered in short setae.

Head capsule. Completely covered by protergum in dorsal view. Eyes small, on sides of the head. Antennae short, extending laterally towards mid-femur of the prothoracic legs. Mouthparts visible in ventral view.

Thorax. Protergum similar in shape to larva, with long setae on the anterior edge. Meso- and metatergum smaller, subrectangular, bearing vestigial wing pads. All pairs of legs free, visible in ventral view. Spiracles present on pleural areas of mesothorax.

Abdomen. Abdominal segments subrectangular, wider than long. Tergites on segments I–IX covered with long setae on the edges, on segments I–VIII strongly laterally overlapping the body. Tergal plates on segments I–VII bearing pairs of depressions in cuticle, placed laterally around the sagittal line. Spiracles present on abdominal pleural areas of segments I–VIII. Segments II–VI bearing functioning larval photic organs with additional female photic organs on segments VII and VIII (Figs 35–37).

Description of male pupa (Figs 30–32). Type pupa adectica exarata libera. Curved, ventrally concave. Length 10–11 mm. Colouration: light beige on head, thorax and elytra, light yellow on abdomen, with distinctively black eyes and membranous wings (Fig. 30) and translucent protergum and abdominal tergites. Surface covered in fine short setae.

Head capsule. Completely covered by protergum in dorsal view. Eyes distinctly large, on sides of the head. Antennae short, extending laterally towards the distal end of femur of the prothoracic legs. Mouthparts visible in ventral view.

Thorax. Protergum similar in shape to larva, with long setae on the anterior edge. Meso- and metatergum smaller, subrectangular, bearing black wing pads covered externally with shorter elytra; wing pads reaching distal end of second abdominal segment when pupa is relaxed. Pro- and mesothoracic legs free, visible in ventral view; metathoracic legs almost completely covered by wing pads except for distal segments of tarsi, which extend past second ventrite. Spiracles present on pleural areas of mesothorax.

Abdomen. Abdominal segments subrectangular, wider than long. Tergites on segments I–IX covered with long setae on the edges, on segments I–VIII strongly laterally explanate, on segments I–VII bearing pairs of depressions in cuticle, placed laterally around the sagittal line. Spiracles present on abdominal pleural areas of segments I–VIII. Segment II–VI bearing functioning larval photic organs with additional male photic organs on ventrites of segments VI and VII (Figs 33, 34).

Notes on prepupae. The prepupal period begins when larva becomes inactive, lying curled up in a semicircle either on its side or back. Nevertheless, it still responds to any disturbance by activating its light organ and contracting its abdomen, a behaviour typical for pupae. Stage of prepupa in observed specimens lasted 3 days in female and 7 days in male.

Notes on ontogenetic changes in pupae. In the male, the pupa is generally indistinguishable from the female pupa (Figs 35–37) during the first three days. Moreover, as in the female, it glows from the same places as the larva. On the fourth day the wings begin forming and darkening in colour, signalling the beginning of the period when male and female pupae can be distinguished. On the fifth day the glow intensity of the larval lights is weaker than in the previous days. On the sixth day the male light organ activates and begins to glow (Fig. 34; mp). During this time larval lights still function and their glow intensity is back to normal. By this time the membranous wings, protruding under incipient elytra, are completely black (Fig. 30). The thorax starts to sclerotize, slowly darkening in colour. At the same time, the pupal eyes are turning into large male eyes, but their development is not yet complete, since they resemble a half-inflated balloon at this stage (Fig. 30). On the seventh day the male emerges. Its larval lights still operate and their glow is visible through the still incompletely sclerotized cuticle (this was also observed by Schwalb 1961). On the eighth day the cuticle of the adult male finally hardens and the larval lights are no longer visible.

The female pupa does not go through such obvious changes as the male does. It appears more or less similar throughout the whole pupal period (Figs 35–37), with the exception of slowly darkening small eyes and overall shift of the body colour towards a darker shade of yellow. The reason for this is neoteny as well as the paler pigmentation of the female. As in the male, the female emerges on the seventh day.

Notes on behaviour observed in pupae. The pupa is inactive, either lying on its side or back, responding only to disturbance. A response consisting of a ca. 10-second glow with quick intensification and gradual fading can be induced by handling the animal or even by vibrations. In the male pupa with the male photic organ already developed (Figs 33, 34), the response is similar, with exception of the newly developed lantern, which can still glow feebly at least three times longer than the larval lights. When under a strong light source, the pupa reacts in the same manner as pupa of *Lampyris noctiluca*, as described in Novák (2017).

Discussion

External sensory organs. Similar to *Lampyris noctiluca,* sensilla chaetica, and sensilla trichodea were observed on the same parts of the body. These types of sensilla, together with speculations of their possible functions, were already described in Novák (2017).

Lamprohiza splendidula possesses a unique feature, not found in other central European species and to my knowledge never observed in any other firefly larvae, with exception of sister species *Lamprohiza delarouzei* (figures in Bugnion (1929) suggest similar feature). It is a membranous spot placed posteriorly behind each stemma of the larva (Fig. 14; sts). The function of this organ seems sensory, nevertheless the exact purpose is unknown. It is possible that this organ is light-sensitive and helps the larva determine favourable light conditions within its environment. Among non-beetles, certain species of Blattodea possess vestigial ocelli degenerated to a pair of transparent areas in the cuticle called *fenestra* (Gillot 2005). Within beetles, vestigial paired dorsal ocelli occur in adults in some taxa of Staphylinoidea and in Derodontidae, so their presence is not excluded within Coleoptera and Polyphaga (Leschen & Beutel 2004). Nevertheless, in both previous cases, the vestigial ocelli are placed on the head dorsally, while in the firefly larva, they are positioned laterally behind stemmata. Another assumption may come from the fact that *Lamprohiza splendidula* is believed to react to disturbance in its surroundings by light emission (De Cock 2003). During my *in vivo* observations of larvae of this species, I have never observed a larva "turning-on" its light due to direct disturbance; in contrast, the light emitted by larvae was always observed from several metres away. This could mean that larvae of this species have a well-developed ability to detect vibration, perhaps by some kind of primitive tympanal organ represented by the membranous spot placed behind their eyes. However, the same sensory service could be provided by a standard sensilla without need of any specialized membrane. In conclusion, until a tissue analysis and further experiments are conducted, the precise function of this structure will remain unknown.

Walking in tergite armour. The larvae of *Lamprohiza splendidula* have conspicuous laterally extended tergal plates on both the thorax and abdomen (Figs 1, 2, 4, 5). This body shape is by no means an exception within the larvae of the Lampyridae (e.g. *Pyrogaster* Motschulsky, 1853, *Cratomorphus* Motschulsky, 1853, *Photuris*, etc.) nor within the order Coleoptera (e.g. Lycidae, Silphidae). However, the exact advantage of this morphological architecture is unknown. While collecting larvae in nature, I have often found the individuals pressed against moist dead foliage, with their head and legs hidden under tightly constricted tergal plates directly touching the substrate.

In this way, the vulnerable appendages and delicate parts of the body are protected against potential predators, while the pigmentation of the larva matches perfectly with the colour of dead leaves. However, this camouflage is probably just an added value to the protective function, since in other taxa, larvae of similar shape are often brightly coloured.

Mandibles, pygopod and hunting for prey. Larvae of *Lamprohiza splendidula* generally feed on soft, slimy invertebrates, predominantly snails, but they can also feed on fresh animal cadavers that offer access through wounds to soft body parts (Schwalb 1961; Lloyd 2008). The style of hunting is almost the same, as in *Lampyris noctiluca* (Novák 2017) and, in the larvae of both species, a hyaline appendage resembling a "shutter" on the base of mandibular channel opening (Fig. 20; ha) was observed. These structures, however, take different forms, as the "shutter" resembles a feather-like structure in *Lamprohiza splendidula*. Compared to the blunt thick seta found in *Lampyris noctiluca*, the form of this hyaline appendage suggests a function more concerned with protection of the mandibular channel from clogging, rather than a trigger for a toxin as speculated in Novák (2017).

The holdfast organ—pygopod (Figs. 27, 28)—helps the larva with locomotion, but also serves during hunting, being used for fastening the snail-attacking larva to the snail's shell as has been observed in *Lampyris noctiluca* (Tyler 2002; M. Novák, unpublished observation), thus giving it a safe position and room for biting manoeuvres. In addition, the pygopod is used also for body cleaning (among other uses) after feeding (Tyler 2002; M. Novák, unpublished observation), especially of the head appendages with dense setation.

Life cycle and pupal development. As well as in sympatric *Lampyris noctiluca*, the information about the developmental cycle of *Lamprohiza splendidula* differs among authors including my observations, perhaps because of certain level of flexibility in adjusting the life cycle to specific environmental conditions. According to Schwalb (1961) the biology of the two species differs only slightly. The development of *Lamprohiza splendidula* takes 2 years according to Hůrka (2005) or possibly 3 years, during which the larva overwinters 3 times according to Schwalb (1961). The number of instars varies between 4 and 6 (Schwalb 1961; Hůrka 2005). The larva enters the stage of prepupa ca. 8–20 days prior to pupation according to Schwalb (1961), however this period may be as short as 3 days (M. Novák, unpublished observation). The wide range of duration of the prepupal stage stated by Schwalb (1961) raises the same questions as in *Lampyris noctiluca*. These are already discussed in Novák (2017) and will not be addressed again here. Pupation in natural conditions occurs in the spring after hibernation; under fallen leaves, pieces of wood or stones, in dug out hemispherical chambers with the opening at the top (Schwalb 1961; Burakowski 2003) or possibly in a cell of small pieces of dead leaf litter (R. De Cock, pers. com.). The pupal stage period lasts 7 days on average in both sexes according to Schwalb (1961), which accurately corresponds with my observations. In the sympatric *Lampyris noctiluca*, pupation lasts ca. 8–12 days for a female and 11–15 days for a male (Schwalb 1961; Tyler 2002; Novák 2017). The longer period of the male pupal development could be explained by the larger amount of changes taking place in a male's body compared to the neotenous female. This raises the question of why the time of pupation in *Lamprohiza splendidula* is also not longer for males. It is possible that the production of eggs in the developing female (Schwalb 1961) prolongs the pupation period. On the other hand, the same egg production happens in *Lampyris noctiluca* (Schwalb 1961) and yet the periods differ. The reason for the same pupal period may in fact be the small size of *Lamprohiza splendidula*, especially in comparison with the much larger *Lampyris noctiluca*. The gap between sexes in the rebuilding times might be reduced in the former thanks to its relatively small body volume in relationship to the changes taking place.

An intriguing phenomenon was observed in the male pupa (Figs 30–32) on the fifth day of development, prior to the activation of the adult lantern. The glow intensity of the larval lights had weakened and the next day when the adult lantern activated (Fig. 34; mp), the intensity of the larval lights went back to normal. It is possible that the final phase of activation of the male lantern is accompanied by the transfer of compounds essential for light production (i.e. luciferin, luciferase) into the newly developed organ, thus temporarily weakening the light production in the larval lanterns. To exclude the possibility that such a phenomenon was not a coincidental exception, more male pupae will have to be observed, since only a single specimen was observed for this study.

Depending on the conditions of the local climate the mature forms appear starting May–July and can be seen until September (Burakowski 2003; Hůrka 2005). The glowing adult females can sometimes be found in clusters, which make them quite distinctive (M. Novák, unpublished observation). According to Tyler (2002), the same phenomenon occurs in females of the sympatric *Lampyris noctiluca* and is probably the result of larval pre-pupation "ganging up", as he calls it. It is thus possible that similar behaviour may be found in the larvae of this particular species.

Photic behaviour. The interpretation of emission of light due to disturbance or manipulation is complicated, according to my *in vivo* observations. The larvae of *Lamprohiza splendidula* appear reluctant to glow without external provocation. They emit a weak continuous glow when handled or even approached. They react both to vibrations and to loud noises (which, as a side effect, easily facilitates collecting them in the field). However, the light intensity may weaken or completely stop in certain cases, usually as a result of overstimulation (Schwalb 1961; M. Novák, unpublished observation). This type of behaviour seems similar to that described by Viviani (2001) in the Neotropical genera *Pyrogaster*, *Photuris* Dejean, 1833, and *Aspisoma* Laporte, 1833; the larvae respond to vibrations by glowing, but do not respond to mechanical manipulation. According to Viviani (2001), this behaviour is probably a collective defence against predators, which lies in distraction and confusion of the "enemy". In conclusion, what may seem like a collective defence of larvae of *Lamprohiza splendidula* may either be just a by-product of larval tolerance to a certain amount of stimuli or indeed a tool of collective defensive behaviour. This begs the question: why do the larvae—when in danger—only reduce their glow, and not stop it abruptly? This may be explained by an inability of the larval stage to alter its glow swiftly, as a result of the differing physiology of their photic organ compared to that of the adults (Timmins *et al.* 2001).

According to De Cock (2003), the spectrum of light emitted by the larvae of *Lamprohiza splendidula* and its sympatric counterparts *Lampyris noctiluca* and *Phosphaenus hemipterus*, unlike that of adults, is very similar, conserving the green emission. This agrees with the lack of an intraspecific function (mating) and increased importance of an interspecific function such as defence, as stated by Viviani (2001). On top of that, lampyrids are reported to be unpalatable prey in general (Underwood *et al.* 1997; De Cock & Matthysen 2003; Moosman *et al.* 2009). With regards to the abovementioned species, the tests of unpalatability have only been performed on *Lampyris noctiluca*. There is a possibility that Batesian or Müllerian mimicry could have evolved within and between these taxonomic groups. Schwalb (1961) states that adults of *Lamprohiza splendidula* are often found in spider webs, sucked dry. I have often witnessed males of this species stress-glowing from spider webs myself, but the question is whether they are indeed consumed by the spider. The glowing of individuals in webs (often for hours) suggests that they had not been approached and killed by the spider. On the other hand, males are often flying (and consequently found in the webs) in such large numbers that the spider may not be capable of attending to all its captures. If they are consumed, the spider is either immune to the defensive compounds of the firefly or the firefly does not possess them. In both cases, the Batesian or Müllerian mimicry has no effect. If they are avoided by the spider, it is possible that Schwalb (1961) had mistaken dried-up individuals caught in the web on previous days with the remains of other spider prey, and Batesian or Müllerian mimicry could still be operating. Which type of mimicry, if any, is used in these fireflies will still have to be determined by further experiments. Larvae and adults must be tested individually, since the existence of defensive compounds in the adults may not guarantee the existence of the same compounds in juvenile stages and vice versa.

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