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## Redescription of immature stages of central European fireflies, Part 1: *Lampyris noctiluca* (Linnaeus, 1758) larva, pupa and notes on its biology (Coleoptera: Lampyridae: Lampyrinae)

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### Abstract

The mature larva of *Lampyris noctiluca* (Linnaeus, 1758) is redescribed and illustrated in detail, including scanning electron microscope images. Male and female pupae are briefly described, including notes on behaviour as well as light production of the immature stages. Observed structures, life cycle and behaviour of larvae and pupae are discussed.

**Key words:** *Lampyris noctiluca*, larva, pupa, morphology, ecology

### Introduction

The genus *Lampyris* Geoffroy, 1762 (Lampyrinae) consists of 60 described species, distributed predominantly in the Palaearctic Region, of which 29 occur in Europe and only one, *Lampyris noctiluca* (Linnaeus, 1758), in the Czech Republic (Burakowski 2003; Geisthardt & Satô 2007). Descriptions of this species are brief and the morphology, particularly that of larvae, is poorly known. Schematic illustrations of variable quality are given in many works, but detailed images and descriptions are missing (e.g. Reitter 1911; Vogel 1913; Korschefsky 1951; Kratochvíl 1957; Medvedev & Ryvkin 1992; Klausnitzer 1994; Burakowski 2003). There are nine synonyms assigned to *Lampyris noctiluca* (Geisthardt & Satô 2007).

This firefly mostly inhabits warmer humid areas with limestone substrate, bordered by deciduous forest (Schwalb 1961; Burakowski 2003). It can be found in lowlands as well as in mountains of high-altitudes, of up to 1800 m a.s.l. (Hůrka 2005). According to Schwalb (1961), the geographical and vertical distribution of this species show a rather high tolerance with regards to temperature and exposure. The species may occur syntopically with other firefly species (e.g. *Lamprohiza splendidula* (Linnaeus, 1767); M. Novák, pers. obs.).

This work is the first of a proposed trilogy focusing on the immature stages of firefly species occurring in central Europe and at the same time the only species occurring in the author's homeland, the Czech Republic. The outdated knowledge of their morphology needs to be revisited. The second part will redescribe the larva and pupae of *Lamprohiza splendidula* and, the final part the larva of the diurnal *Phosphaenus hemipterus* (Goeze, 1777), and will present a dichotomous key and comparison of features of all three species.

### Material and methods

Larvae of *Lampyris noctiluca* were collected in Ljubljana, Slovenia, in the first half of September 2013 and 2015. Overall six specimens were collected at the forest edge next to Koseze Pond (Koseški Bajer; 46°3'58.4"N, 14°28'10.7"E), on decomposing wood and on leaf litter, two and a half hours after sunset. The area of Koseze Pond is a landscape park, geologically mostly comprised of slates and limestones, with predominantly acidic soil. The area has many small streams and sources. The climate is continental with rainfall mostly in the summer and autumn months. Average annual rainfall is 1350 mm. Average yearly temperature is 9.7 °C, in summer the average is 19.6 °C (Anonymous 2012).

The collected specimens were identified using the key in Burakowski (2003). All collected larvae were identified as higher instars and selected for subsequent analysis. Regarding the distinction of the individual instars, no work describing either morphological or biometric traits nor chaetotaxy exists. Furthermore, the total number of instars is not yet reliably determined. To solve this problem, individuals approaching the maximum species length limit were selected. Additionally, Schwalb's figure for the average larval sizes in each year of the 3-year cycle was used for confirmation of higher instar status (Schwalb 1961: p. 51, fig. 34).

Three of the larvae were fixed and stored in 60% ethanol and kept at a low temperature for subsequent morphological investigation. The material is housed in the author's personal collection. The remaining three specimens were kept alive for observations on their behaviour and obtaining pupae and adults. The larvae were kept separately, in round plastic containers 10 cm diameter and 4 cm high, padded with thick layers of moist tissues to prevent desiccation. The containers were placed in a ventilated room with a natural light source to provide the appropriate temperature and light period for the season. Each container was also provisioned with a *Cepaea* sp. snail as a food source. Cleaning of the containers with antiseptic cleaner and replacement of tissues took place every week. Two female pupae and one male pupa were obtained. They were kept alive during the whole pupal and consequent imaginal stage for developmental period verification, sex determination, behavioural observations and the possibility of photographing their glow. Since adults of this species no longer feed, a simple replacement of wet tissues every week was sufficient to keep pupae and imagines alive. The adults were additionally moved into deeper containers to provide them with larger comfort.

**Optical imaging.** The fixed specimens were cleaned using a small fine hair brush and then placed in a Digital Ultrasonic Cleaner PS-06A. The detached heads were afterwards boiled in 10% KOH (potassium hydroxide) for clearer visibility of delicate parts. Habitus was photographed while the specimen was submerged in ethanol, heads were photographed while submerged in glycerol (due to better optical properties and higher stability owing to the greater density of the glycerol). Images were taken using a Canon macro photo lens MP-E 65 mm and EF-S 60 mm on a Canon 550D body, attached to a sliding frame, using EOS Utility program. Sets of pictures of each habitus taken were consequently stacked into a final image with a high depth of field in Zerene Stacker (64-bit) by Zerene Systems LLC.

Living pupae were placed in small glass bowls and their habitus was photographed using the same equipment and consequently stacked into final images. Pupae were photographed in a dark environment, since the light of the reflectors causes discomfort and agitates them to move.

For morphological studies, two specimens were dissected and their body parts examined separately using Olympus SZX7 stereo microscope. The images of isolated maxillae and mandibles submerged in ethanol were taken using an Olympus XC30 Digital Colour Camera attached to Olympus CX41 biological microscope and consequently stacked into a sharp final image in Zerene Stacker (64-bit) by Zerene Systems LLC.

**Electron imaging.** Larvae were examined in the Faculty of Science of Charles University in Prague. The specimens were first dehydrated by passing them through a series of increasing alcohol concentrations. The samples were transferred sequentially through 60%, 70%, 80%, 90% and 95% alcohol for ca. 0.5 h each. Dehydrated samples were then dried by the Critical Point Drying method. Dry samples were subsequently attached to an aluminium disk target and coated with gold in a Bal-Tec Sputter Coater SCD 050, to ensure conductivity. The electron imaging was performed using JSM-6380LV (JEOL) Scanning Electron Microscope (SEM) with a high resolution of 3.0 nm (30 kW).

Interpretation and terminology of larval and pupal descriptions follows Archangelsky (2004) and LaBella & Lloyd (1991).

Interpretation of sensory organs follows Shields (2008) as follows: *Sensilla trichodea* can vary greatly in length and are freely moveable on a basal membrane, can be solely mechanosensitive, dually mechano- and contact chemosensitive, olfactory, or thermosensitive; *sensilla chaetica* usually takes form of bristles or spines similar to the sensilla trichodea, is typically set in a socket and can be mechano- or contact chemosensitive; *sensilla coeloconica* is defined as a basiconic peg or cone set in a shallow pit, most often chemo-, thermo-, or hygrosensitive.

## Results

### *Lampyris noctiluca* (Linnaeus, 1758)

**Material examined.** Ljubljana (Slovenia), three higher instar larvae out of six collected in the first half of September 2013 and 2015, three pupae reared from remaining collected larvae.

**Diagnosis.** Larvae robust, dark brown or black; with light coloured spots on posterolateral margins on pronotum and every tergite except caudal segment; pronotum concave on posterior margin; maxillary palpomere II with inner-lateral sagittal slot; mandibles with retinaculum forming a sharp inner tooth; mandibular channel covered with thick blunt seta; microscopic granulate protuberances, densely occurring on sclerites and legs; photic organ represented by a pair of conspicuous whitish spots located on pleurites of abdominal segment VIII.

**Description of mature larva** (Figs 1–8). Fusiform and robust; slightly flattened dorsoventrally. Body length 20–23 mm (from the anterior margin of pronotum to the apex of caudal segment); with 3 thoracic and 10 abdominal segments. Tergites from pronotum to abdominal segment IX extending laterally to cover the rest of the body and divided by sagittal line in dorsal view. Colouration: body dark brown or black, with distinct pinkish or yellowish spots on posterolateral margins on pronotum and every tergite except caudal segment. Spiracles on pleural plates of light colouration. Photic organ represented by a pair of whitish spots located on pleurites of abdominal segment VIII.

*Cuticular outgrowths*. 1. Stout, short, blunt, oblique setae (Figs 14, 20, 26; st); 2. dense granulate protuberances (Fig. 26; gp); 3. long stout setae (Figs 20, 23, 25; sch); 4. coeloconical receptors (Figs 14, 20, 21; sc).

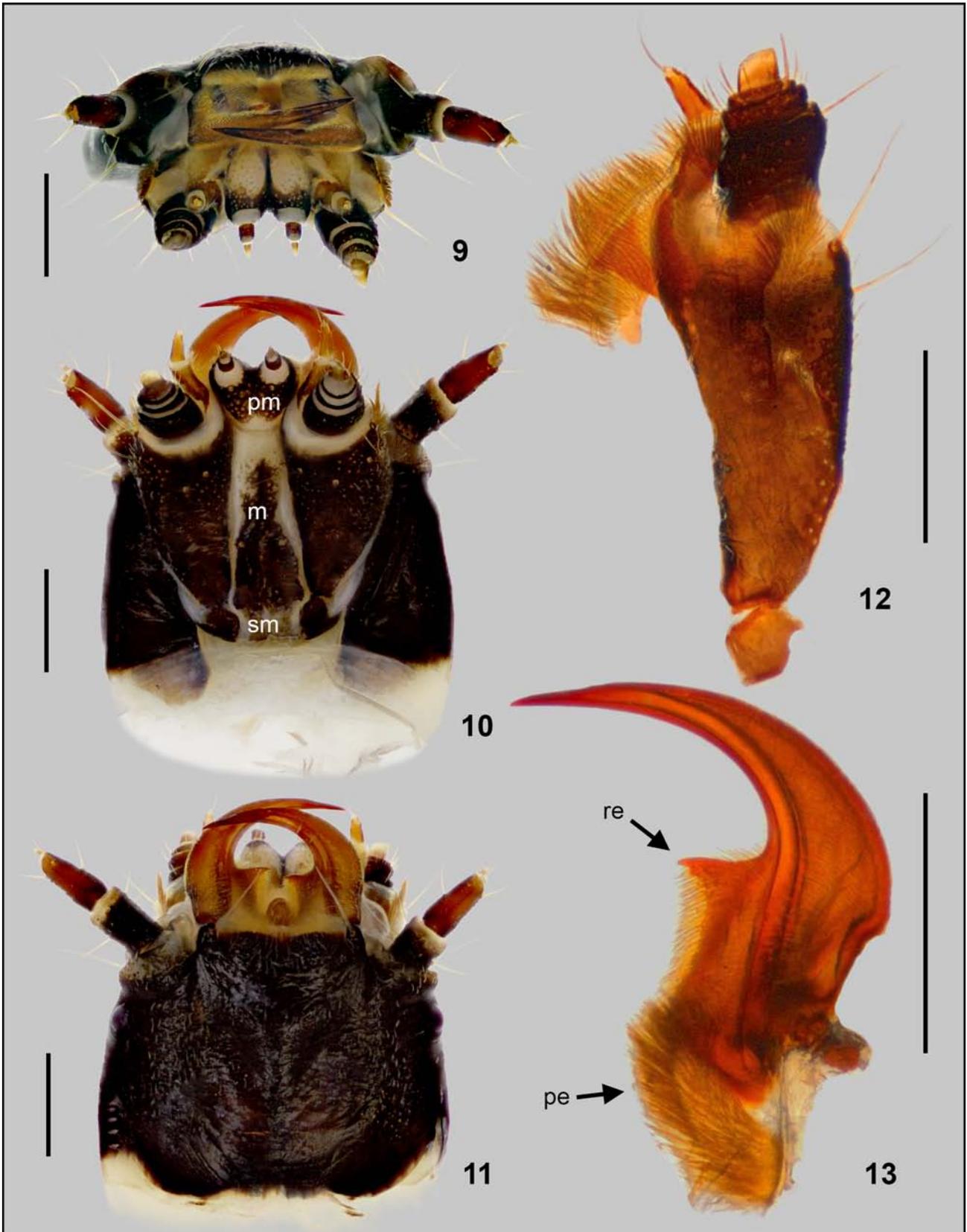
*Head capsule* (Figs 9–11, 14–16). Prognathous; retractable within prothorax, extensible neck membrane forming a two layered envelope around retracted head; of equal width and length; slightly widening posteriorly. Epicranial plate laterally about the same size as width of head capsule at its shortest width, with one stout seta anterolaterally close to the base of antenna. Head capsule dorsally covered with short blunt setae lying on surface and coeloconical receptors (Figs 14, 21; sc). Epicranial suture hardly distinguishable for its dark pigmentation, but present (Fig. 11). One stemma on each side of head. Labrum fused to clypeus forming a clypeolabrum, covering base of mandibles in dorsal view. Clypeolabrum slightly double-arched in anterior view, with one long seta on each lateral corner, reaching the apex of mandibles (Fig. 14). Epipharynx formed by two plates, and an anterior pair of brushes of long setae on each plate, which project centrally past anterior margin of head. Hypopharynx covered with long setation. Gula absent (Fig. 10).

*Antenna* (Figs 20–22). Trimerous, inserted on lateral distal margin of epicranial plate; partially retractable within membranous socket. Basal antennomere widest, fully sclerotized, bearing short setae lying on surface, coeloconical receptors and several long oblique setae near the apical region (Fig. 20). Several long stout setae placed radially on the anterior margin, with a distinct seta on inner lateral area of antennomere. Second antennomere slightly shorter than first, laterally flattened; bearing numerous short setae lying on surface irregularly scattered over the antennomere, together with several coeloconical receptors (Fig. 21; sc) and four stout setae—first three in the middle and on apex of inner margin of antennomere, fourth on apical region of outer lateral margin of antennomere. Sensorium of second antennomere (Figs 21, 22; as) oval, widest at the base, closely touching second antennomere, shorter than third antennomere with no visible surface pattern. Third antennomere (Figs 21, 22; aIII) shortest, bearing four short setae; one basal and three apical, together with a pair of short cuticular projections; ventrally apical thick and dorsal-apical thin.

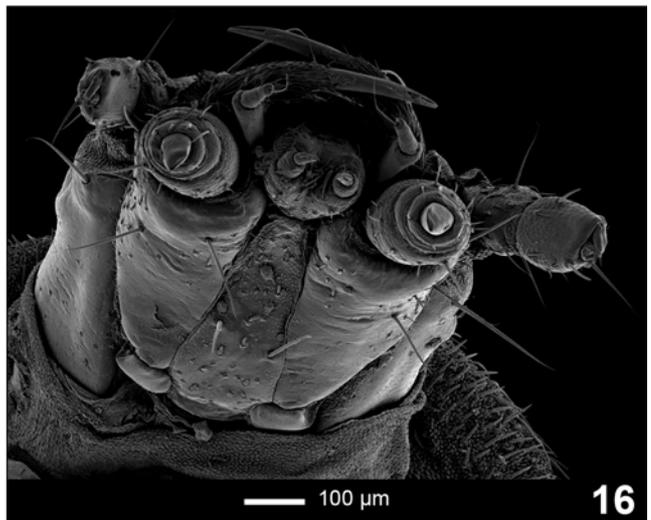
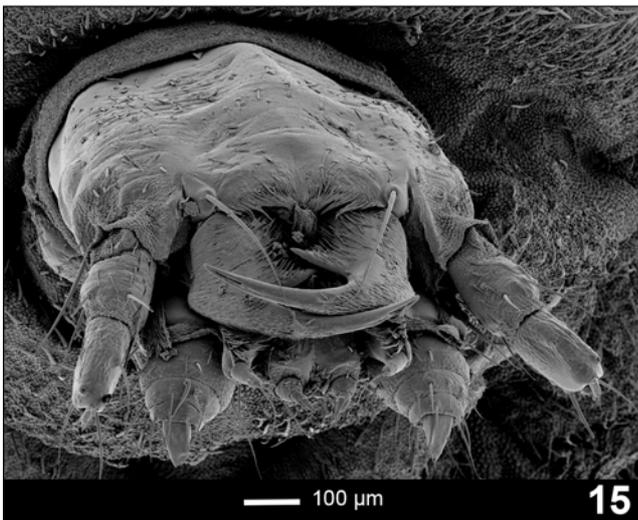
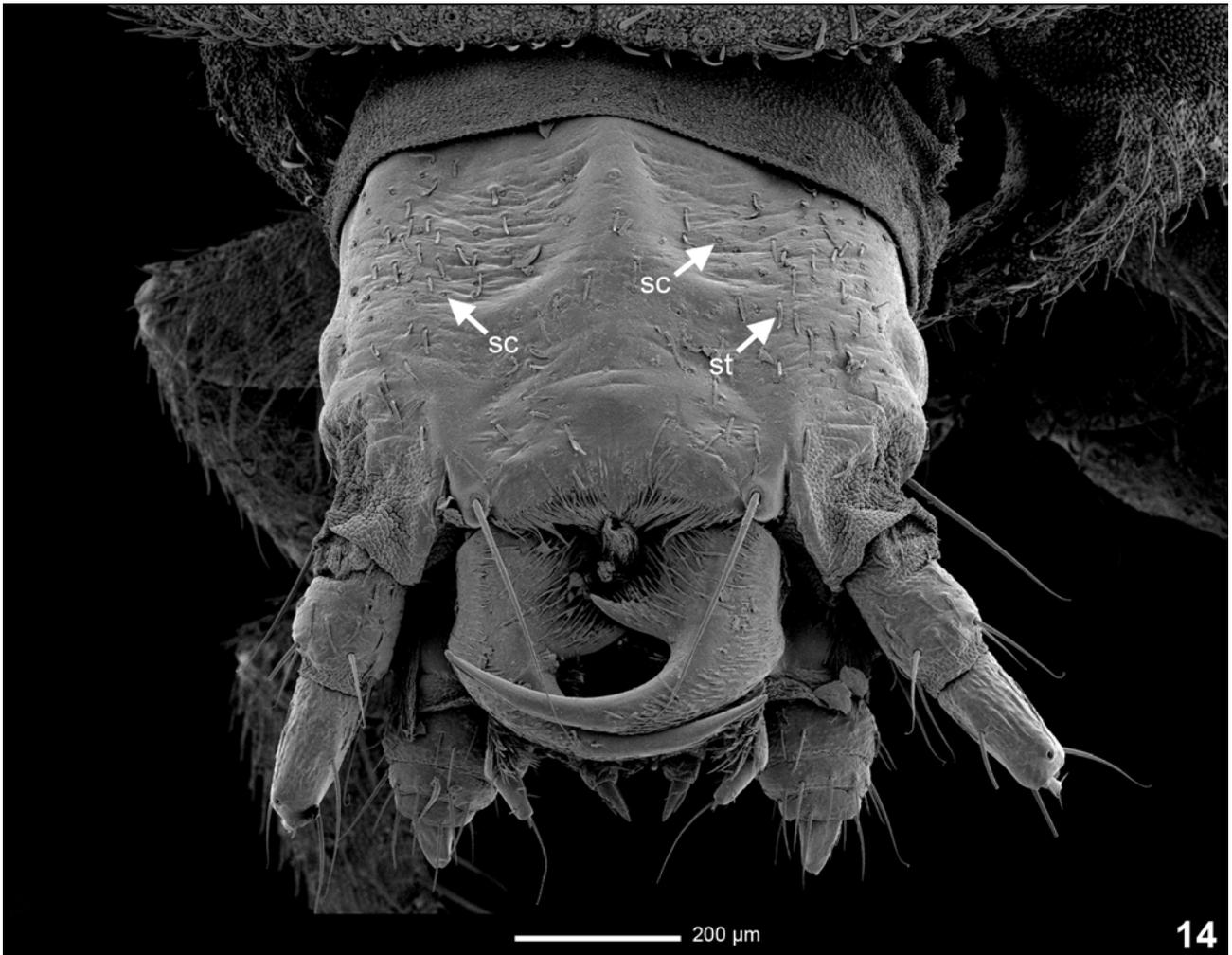
*Maxilla* (Fig. 12). Consisting of five parts, attached by membrane to labium forming a maxillo-labial complex (Fig. 17). Cardo transverse, sub-rectangular, slightly wider than long. Stipes elongated, ventrally relatively glabrous, setae mainly on distal half, with three long stout setae placed radially on ventral apical region; dorsolaterally covered with short setation lying on surface. Galea bimerous, basal part sub-cylindrical, slightly wider than distal, with long dorsal setation partially covering distal part; distal part sub-cylindrical, inclined centrally, with short setae and one apical seta longer than body of the distal part. Lacinia with a brush of long setae on outer lateral margin. Palpifer (Fig. 17; pf) large, rectangular, about the same length and width. Maxillary palpus trimerous (Figs 17, 18; mpI, mpII, mpIII), basal and second palpomere short and wide. Palpifer and palpomeres I–II covered with several setae mainly on outer dorsolateral margin; palpomere III (Fig. 18; mpIII) irregularly sub-conical, thick, blunt, with an inner longitudinal lateroapical sensory slot (Fig. 18; ses), small seta on outer lateral region and short outer lateral longitudinal sensory slot covered with thin seta lying on surface.



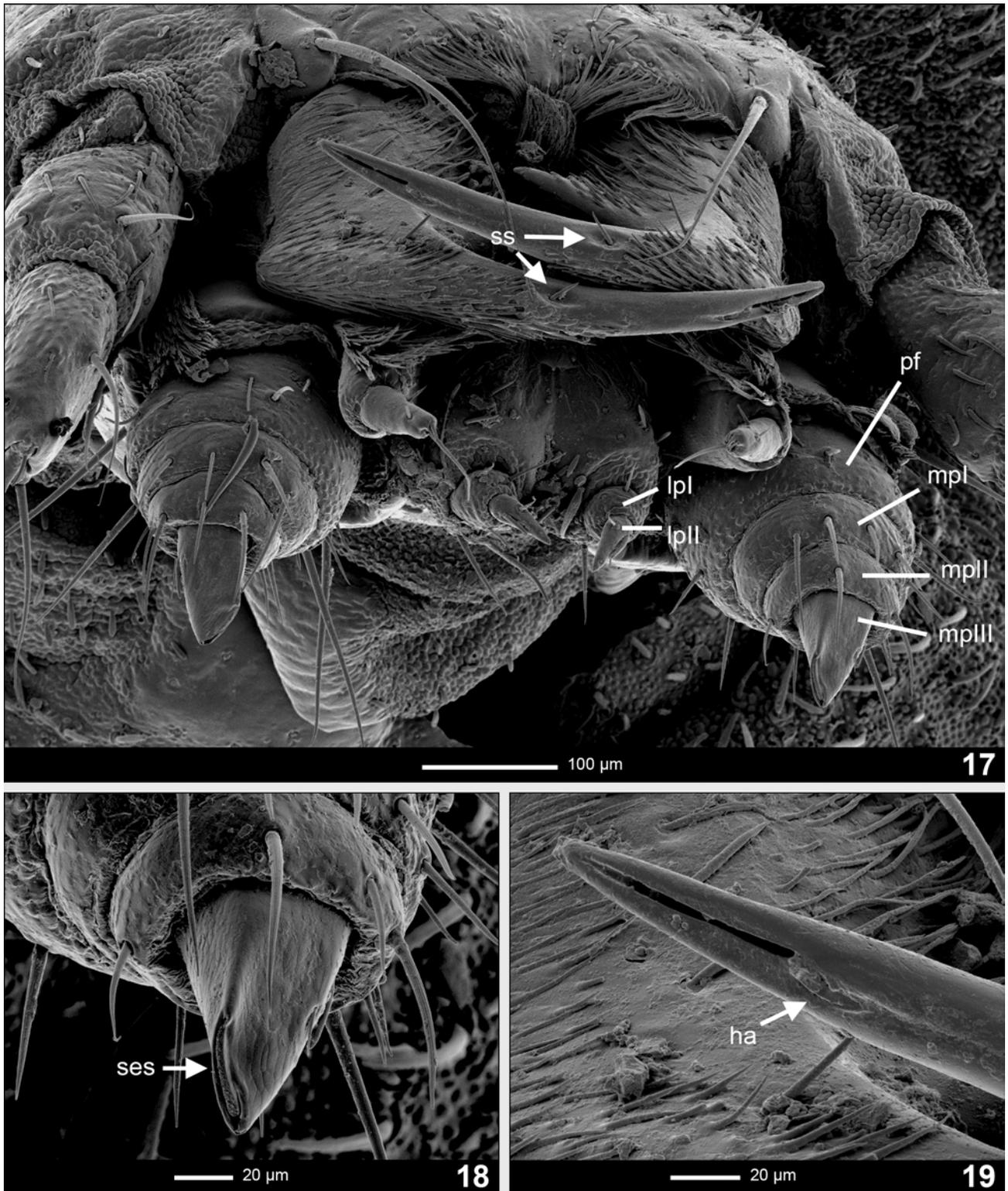
**FIGURES 1–8.** *Lampyris noctiluca*. General habitus of mature larva photographed in alcohol in dorsal (1) and ventral (2) views; abdominal segments VII to X in ventral view (3); lateral view (4). General habitus of mature larva photographed dry in dorsal (5) and ventral (6) views; abdominal segments VII to X in ventral view (7); lateral view (8). Scale bar: 5 mm.



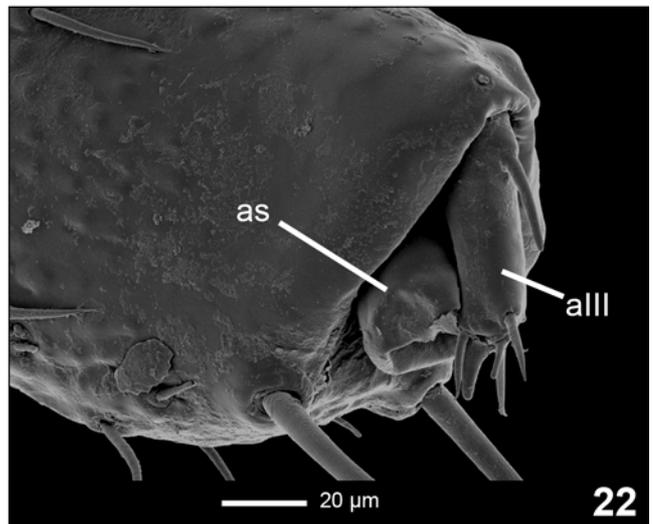
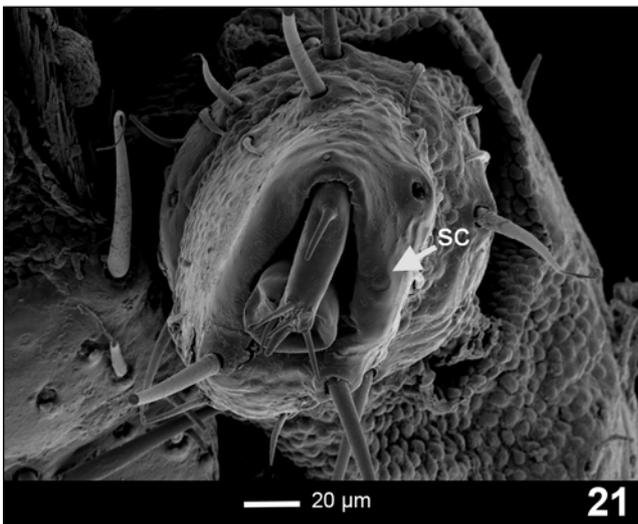
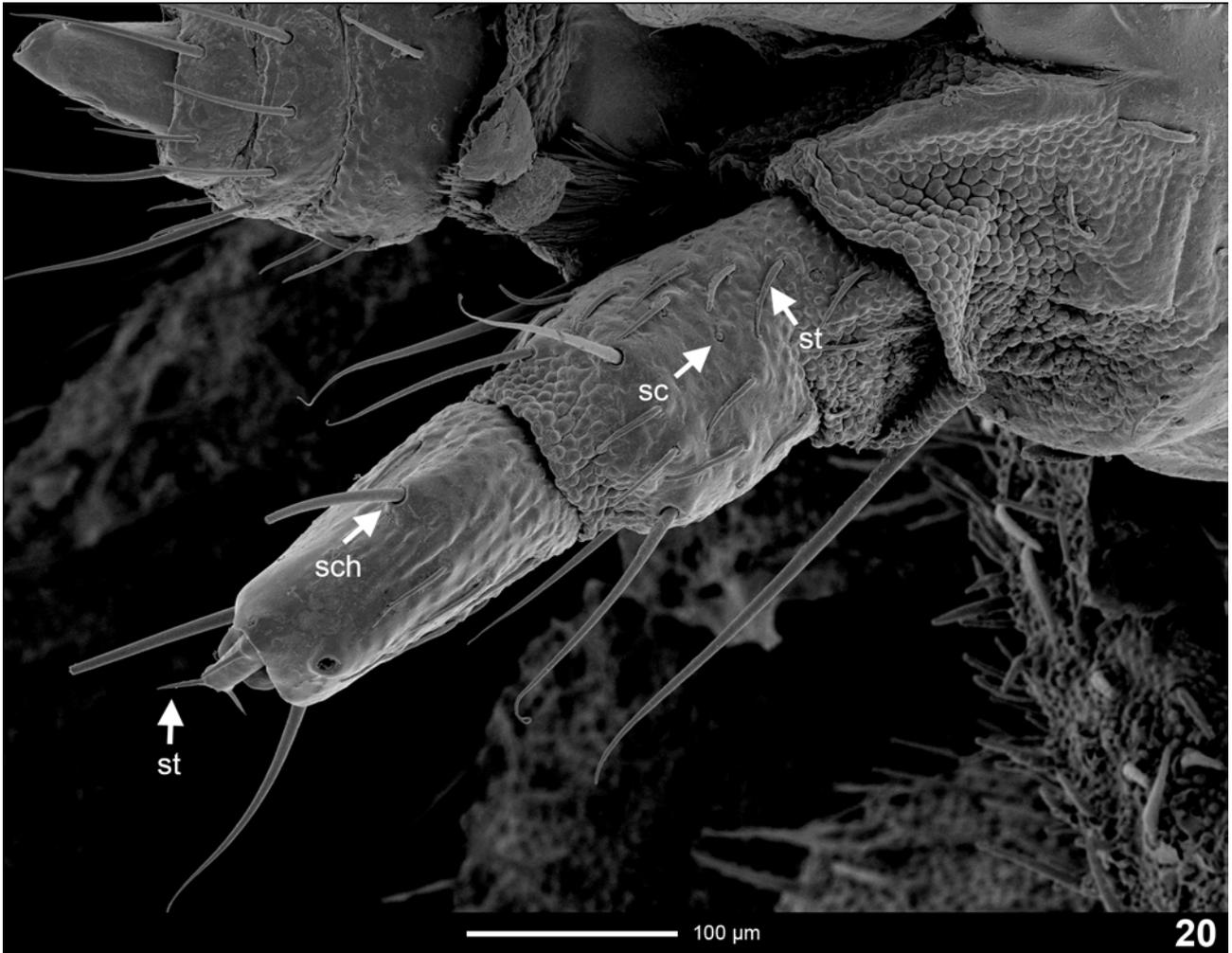
**FIGURES 9–13.** *Lampyris noctiluca*. Detail of head in anterior (9); ventral (10) and dorsal (11) views; right maxilla in dorsal view (12); right mandible in dorsal view (13). Abbreviations: pe—penicillus; re—retinaculum; p—prementum; m—mentum; sm—submentum. Scale bars: 0,5 mm.



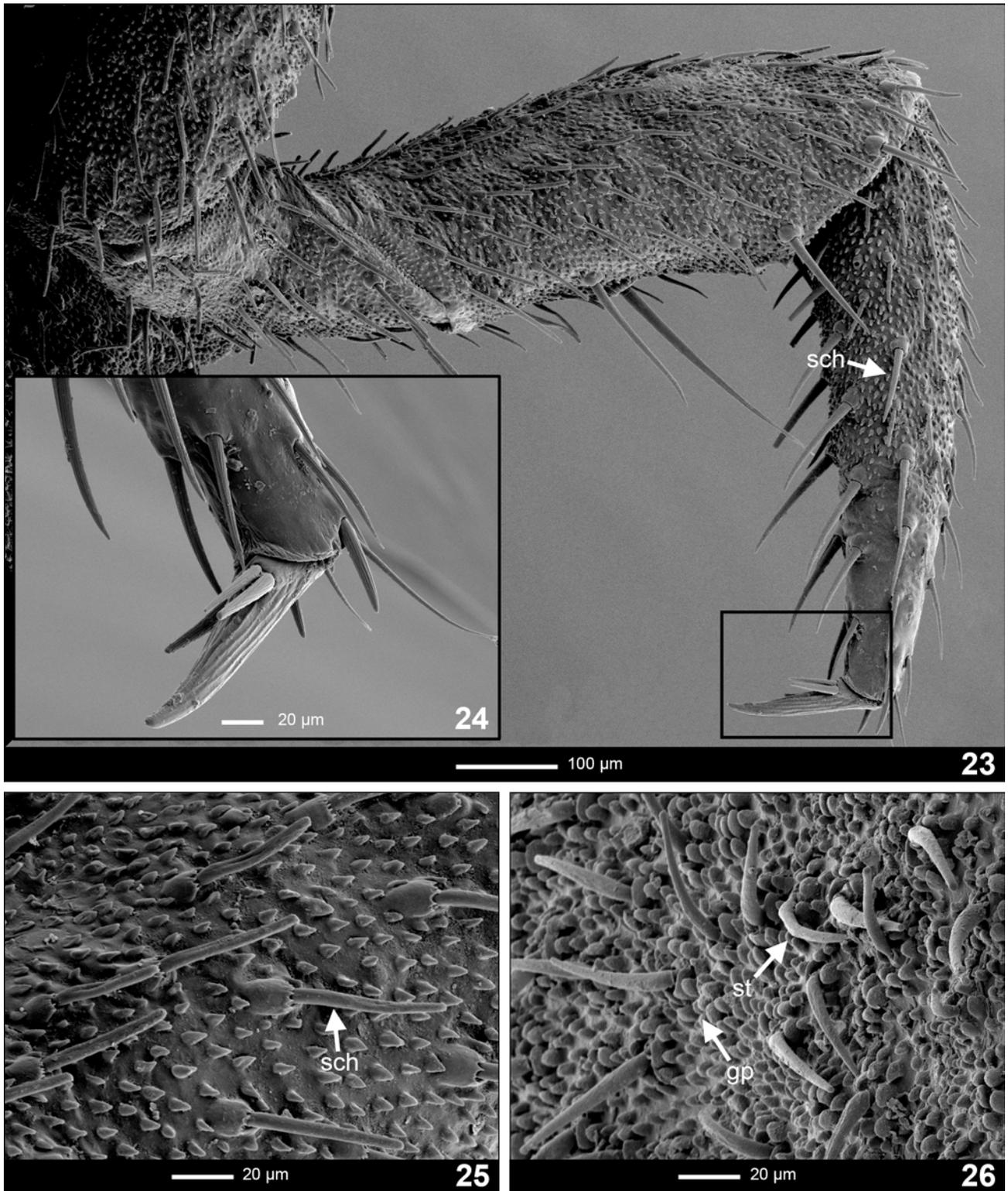
**FIGURES 14–16.** *Lampyris noctiluca*. SEM image of head in dorsal (14); anterior (15) and ventral (16) views. Abbreviations: sc—sensillum coeloconicum; st—sensillum trichodeum; sch—sensillum chaeticum.



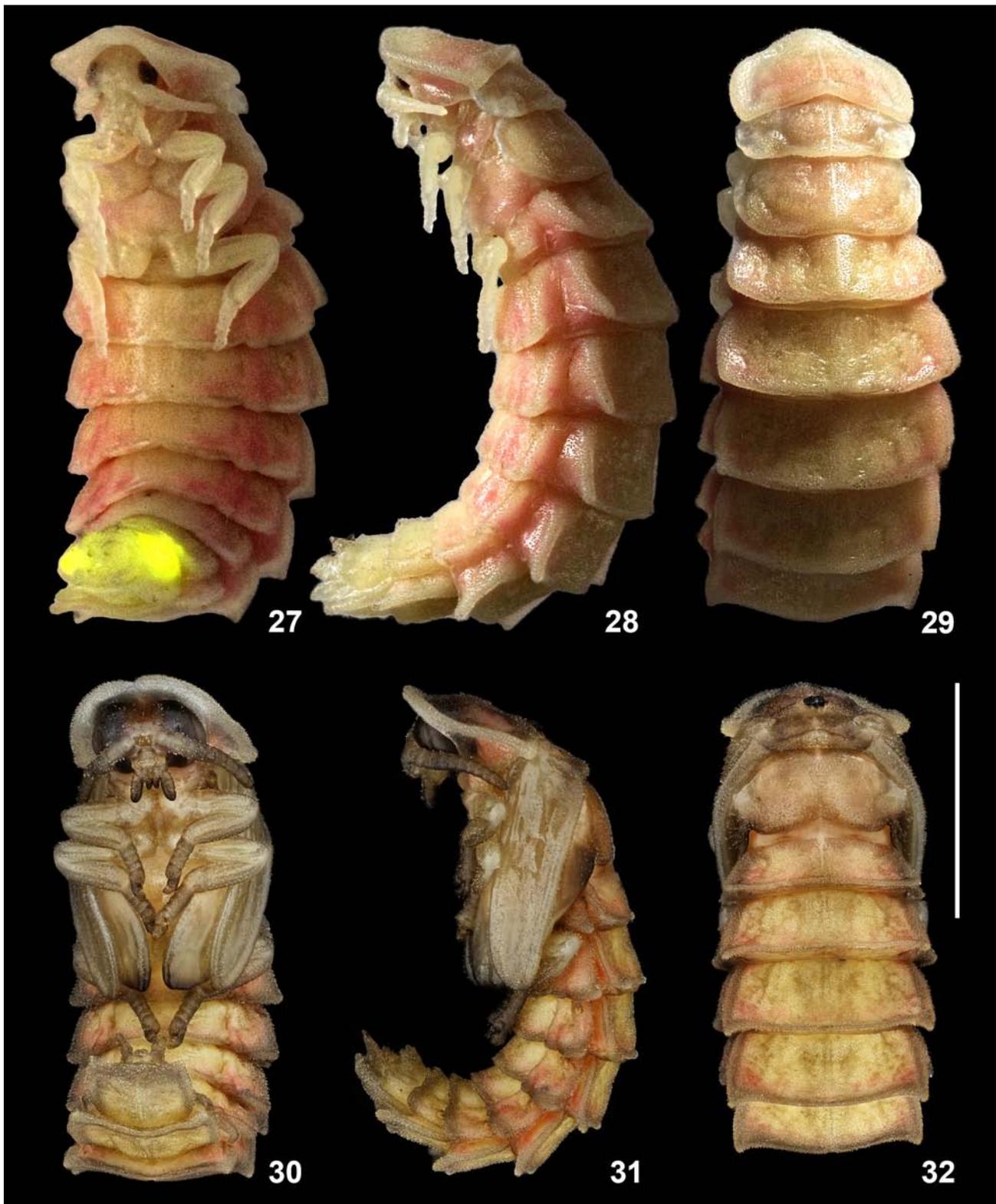
**FIGURES 17–19.** *Lampyris noctiluca*. SEM image of maxillo-labial complex in anterior view (17); maxillary palpus (18); channel opening on the left mandible (19). Abbreviations: ha—hyaline appendage; lp1, lp2—labial palpus 1, 2; mpl–III—maxillary palpus I–III; pf—maxillary palpifer; ses—sensory slot; ss—solitary seta.



**FIGURES 20–22.** *Lampyris noctiluca*. SEM image of antenna in general view (20); anterior view (21); detail of sensorium and third antennomere (22). Abbreviations: aIII—third antennomere; as—antennal sensorium; sc—sensillum coeloconicum; st—sensillum trichodeum; sch—sensillum chaeticum.



**FIGURES 23–26.** *Lampyris noctiluca*. SEM image of leg in general view (23, framed area enlarged in Fig. 24); pretarsus (24). Detail of body surface on legs (25) and pronotum (26). Abbreviations: st—sensillum trichodeum; sch—sensillum chaeticum; gp—granulose protuberances.



**FIGURES 27–32.** *Lampyris noctiluca*. Glowing female pupa in ventral view (27). Female pupa in lateral (28) and dorsal (29) views. Male pupa in ventral (30), lateral (31) and dorsal (32) views. Scale bar: 5 mm.

*Labium* (Fig. 17). Closely attached to maxilla, formed by a short and strongly sclerotized prementum, mentum and weakly sclerotized submentum (Fig. 10; pm, m, sm). Glossae absent. Prementum heart-shaped in ventral view; covered with very short setation; bearing several longer blunt setae, and a pair of long stout setae, placed centrally on ventral region. Labial palpus bimerous (Fig. 17; lp1, lp2); basal palpomere wider than long, bearing several

setae; distal palpomere conical, longer and narrower than basal, bearing a short thin erect seta on basal half dorsally, a longer, stout and blunt seta covering a sagittal slot positioned on outer margin and sensillum coeloconicum on outer ventrolateral side of apex. Mentum elongated, sub-triangular, unsclerotized on lateral margins, ventrally bearing numerous short setae lying on surface and a pair of long, erect setae centrally.

**Mandible** (Figs 13, 19). Symmetrical, falcate, with an internal channel opening subapically on outer edge (Fig. 19). Penicillus well developed (Fig. 13; pe). Retinaculum present, forming one sharp inner tooth on basal half of mandible (Fig. 13; re). Inner margin of mandible from retinaculum to the base covered with stout setae (Fig. 13). Basal two-thirds of mandible ventrally with dense setation lying on surface and aimed centrally. Dorsally, mandible covered with several strong setae lying on surface, aiming medially on proximal two-thirds of each mandible. Lateral margin covered by brush of short setae lying on surface of basal two-thirds (Fig. 17). Sensory (hyaline) appendage on outer margin of mandible before channel opening consists of a blunt thick seta (Fig. 19; ha). A distinct short, stout seta set in a shallow depression present dorsally at anterior end of lateral setation (Fig. 17; ss).

**Thorax** (Figs 1, 2, 4–6, 8). Three-segmented, thoracic tergites divided by sagittal line (Figs 1, 5). Pronotum of equal length and width, sub-trapezoidal, wider posteriorly, rounded at posterolateral corners, strongly concave on posterior margin. Meso- and metanotum sub-rectangular, wider than long, mesonotum longer than metanotum. Lateral areas of meso- and metathorax formed by episternum and epimeron; episternum of mesothorax bearing an annular spiracle. Prosternum rounded, wider than long, robust, well sclerotized, subdivided into three plates; lateral ones extending above and to the sides of coxae; medial plate sub-pentagonal. Meso- and metasternum subdivided by transverse fold into poorly sclerotized basisternum and well sclerotized sternellum; sternellum subdivided into three plates, lateral ones extending above and to the sides coxae, representing large episterna and smaller epimera, medial plate less sclerotized on margins, heart-shaped with wider margin posteriorly.

**Legs** (Figs 23, 24). Pentamerous, all pairs similar in shape and size. Coxa large, stout, covered by short sharp setae. Coxal-trochantal membrane (Figs 2, 6) reaching less than 1/2 of coxal length. Trochanter small, sub-triangular in lateral view, shorter than femur, covered by short sharp setae. Femur slightly fusiform, widening towards apex in lateral view, covered by short sharp setae, with several large setae ventrally. Tibiotarsus as long as femur, narrower, tapering towards distal end, bearing stout short sharp setae dorsally and strong sharp erect setae ventrally. Pretarsus (Fig. 24) composed of a claw with distinct ridges, ventrally bearing three short stout setae with fine ridges. Cuticle of leg (Fig. 25) densely covered with grainy protuberances except for apical half of tibiotarsus (Fig. 23).

**Abdomen** (Figs 1–8). Ten-segmented, tapering towards posterior end, segments I to VIII subdivided by fine sagittal line in dorsal view. Tergites of segments I to VIII sub-trapezoidal, similar in shape and colouration, wider than long; tergite of segment IX sub-rectangular; segment X forming a narrow, incompletely sclerotized dark ring, bearing the holdfast organ—pygopod (Fig. 3)—with several eversible processes. Ventriles of segments I to VIII sub-rectangular, slightly wider than long, well sclerotized, with a pair of long stout setae on posterolateral margins; ventrite of segment IX sub-trapezoidal. Pleural areas well sclerotized, pleural suture of segments I to V subdivide lateral areas into large sub-rectangular upper pleurite, bearing an annular spiracle, and narrow lower pleurite anteriorly covered; pleural segments VI to VIII with only upper pleurite bearing an annular spiracle. Segment VIII bearing photic organs ventrally on pleurites, appearing as two whitish spots (Fig. 3).

**Larval behaviour.** Larvae of *Lampyris noctiluca* were observed to “ride” the snails, which means mounting the shell and assuming a favourable position to inject the head of the snail or its upper tentacles with lethal toxin. The larva then remains on the shell until the snail shows no signs of life. Feeding can take up to two days. The larva avoids feeding on digestive organs and can sometimes remove these organs from the shell before resuming feeding on the rest of the body. After feeding, the larva remains passive for certain time and after ca. one day excretes a dark brown fluid from the back of its abdomen.

While collecting larvae in nature, a several seconds lasting glow was often observed, followed by a long period of darkness. In captivity, the larvae demonstrated this behaviour when disturbed. When undisturbed, the larvae occasionally showed photic behaviour of definite pulses of light lasting ca. 2 seconds, separated from the next one by a longer interval of darkness lasting ca. 4 seconds. The other photic manifestation consisted of continuous glow of weaker intensity, which could take several minutes.

**Description of female pupa** (Figs 27–29). Type of pupa: *adectica exarata libera*. Curved, ventrally concave. Length 20 and 23 mm. Colouration: yellowish white on tergites and parts that will become sclerotized in adult stage, pink especially in pleural region. Surface covered by short setae.

*Head capsule.* Completely covered by pronotum in dorsal view. Eyes small. Antennae short, extending laterally, without reaching posterolateral corners of pronotum. Mouthparts visible in ventral view.

*Thorax.* Pronotum similar in shape to that of larva, with more acute posterolateral corners and less elongated. Meso- and metanotum smaller, sub-rectangular; mesonotum significantly shorter than metanotum, bearing very short elytra which become vestigial in adult individual. All pairs of legs free, visible in ventral view, proportionally shorter to the overall body size than those of males. Spiracles present on pleural areas of mesothorax.

*Abdomen.* Abdominal segments sub-rectangular, wider than long. Ventrites on segments II–IV bearing a double sagittal line of depression in cuticle. Spiracles present on abdominal pleural areas of segments I–VIII. Segment VIII bearing functional larval photic organs (Fig. 27).

**Description of male pupa** (Figs 30–32). Type of pupa: *adectica exarata libera*. Curved, ventrally concave. Length 17 mm. Colouration on young pupae: ochred yellow on tergites and parts that will become sclerotized in adult stage, pink especially in pleural region in young pupae. Colouration on older pupae: beige to brown with a tint of olive or army green on pronotum, head, elytra and legs; inner surface of dorsal and abdominal tergites ochred yellow. Surface covered by short setae.

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

*Thorax.* Pronotum semicircular and proportionally longer than that of female when compared to overall body size (length of pronotum to body length ratio is 0.23 while in female the ratio is 0.15). Small narrow mesonotum and large wide metanotum sub-rectangular, bearing beige wing pads with dark brown apices, covered by beige elytra of about the same length; 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 sub-rectangular, wider than long. Spiracles present on abdominal pleural areas of segments I–VIII. Segment VIII bearing functioning larval photic organs.

**Pupal behaviour.** Both male and female pupae are commonly idle, either lying on their side or back, responding only to disturbance. A luminescent response can be induced by handling the animal or even by vibrations. It consist of one short glow, lasting several seconds, with a peak intensity lasting ca. 1 second and then quickly fading away. When under a strong light source, the pupa starts to move its abdomen, twiddling from side to side or doing “crunches”. This behaviour suggests an effort to move into darker area, i.e. positive thigmotaxis. The same behaviour can be observed in prepupae.

**Development period and ontogenetic morphological changes in pupae.** From the reared larvae, future male entered the stage of prepupa 1 day prior to pupation and future females 3–6 days prior to pupation. The pupal period lasted 8 days for male and 7–10 days for females.

The mesonotum of a female is laterally blunt in the first few days of pupal development, but later the lateral margins begin to sharpen to form vestigial elytra. On the other hand, in male pupae, the elytra and wings are already semi developed since the first day of the pupal stage. Therefore, the sex of future adult can be determined in any time of the pupal period.

## Discussion

**External sensory organs.** Close observation of larval anatomy revealed different types of *sensilla* and sensory organs. Since the exact determination of type and function of observed sensory organs would merit a separate work, the following paragraphs will be dedicated to only a brief description and speculations on possible functions, with regards to the ecological aspects.

*Sensilla trichodea* were mostly found on sclerotized parts of dorsum and venter (Fig. 26; st), head capsule (Fig. 14; st) and antennae (Fig 20; st). It seems plausible, that specifically on the third antennomere, some of these sensilla are in fact *flagella*. In addition, setae on ventrites have an auxiliary function during moulting (Tyler 2002).

Probably the most abundant sensilla observed on this species were the *sensilla chaetica*. Being found on the antennae (Fig. 20; sch) and legs (Figs 23, 25; sch), the chemosensitivity function could be possible for sensilla situated on the antennae, the mechanoreceptive function on legs.

*Sensilla coeloconica* was observed on the epicranial plate and antennae (Figs 14, 20, 21; sc), where chemo-, thermo-, or hygrosensitive function seems plausible. Additionally, this sensillum seems to have a different form on the apex of antennomere II (Fig. 21; sc) than the rest of the body (Figs 14, 20; sc).

**Granulose protuberances.** Sclerotized areas of the legs, dorsum and venter are densely littered with microscopic granulose protuberances (Figs 25, 26). This unique characteristic of the cuticle could be the reason why the body of *Lampyris noctiluca* gives the impression of being “velvet” like. Whether the function of these protuberances is sensory, insulatory or other is nevertheless unknown.

**Ontogeny.** Different authors present different data on the length of the developmental cycle of this species. According to Tyler (2002) the cycle takes 2 years with 2 overwinterings, while Schwalb (1961) states 3 years and 3 overwinterings. The possible difference in their conclusions may lie in the different geographical regions in which these authors conducted their observations. While Tyler’s observations are of species in the United Kingdom with a more humid and warmer climate, Schwalb’s are from Germany with a more continental climate. Additionally, the number of instars also vary according to different authors from 5 (Hůrka & Čepická 1978) to 4–6 (Schwalb 1961). Depending on the sex, it can also be 5 for males with possibly more for females (Tyler 2002), and the variability is believed to be dependent on environmental conditions and food availability. Both Schwalb (1961) and Tyler (2002) present similar developmental lengths for the pupal stage, which is not influenced by the environment, but by the internal settings of the organism. It is therefore possible, that both authors are correct about the cycle length in terms of the regional climate and that *Lampyris noctiluca* can prolong its life by an additional year and one overwintering, if the conditions are not favourable.

Larvae which are ready to pupate seem to switch into diurnal activity, and can often be seen striding along in broad daylight (Tyler 2002). The adult female rarely moves far before she dies, so Tyler (2002) presumes, that it may be that this final larval stage is the one in which glow-worms are able to spread out in search of new habitats. Larvae preparing to pupate the same year often gather together in small groups, and it is fairly common to find six or more side by side under one log (Tyler 2002). The result of the aggregating of pupating larvae may well be the reason why clusters of 2–6 glowing females can sometimes be found within a few centimetres of each other (Tyler 2002). This behaviour could be explained as a means of being more conspicuous for the males and thus having a higher chance of successful mating. Another possibility is finding the “perfect” spot in terms of environmental conditions for the larvae to successfully pupate, for the females to successfully lay eggs and for newly hatched larvae to survive. However, such a phenomenon might prevent the spreading of the population further in the biotope. In any case, this behaviour must provide more evolutionary advantages than disadvantages. The manner in which the larvae gather together is unknown, but may potentially support the intraspecific communication hypothesis (see below) if light manifestations are involved.

The larva enters the stage of prepupa 8–20 days prior to pupation according to Schwalb (1961), but from my observations this period can be shorter (1–6 days). During this time the larva lies curled up in a semicircle either on its side or back. The pupation lasts ca. 8–12 days for a female and 11–15 days for a male (Schwalb 1961; Tyler 2002), which concurs with my observations for females only. The discrepancy in the pupation period may nevertheless be caused by a small sample size.

**Hunting for prey.** *Lampyris noctiluca* larvae are reported to follow 2-day-old slime-trails forward, tracking the snails, and can detect polarization in dry, if not stale, trails (Lloyd 2008). The snail *Cepaea nemoralis* (Linnaeus, 1758) (Helicidae) is one of the preferred prey of this species and is known to occur in three colour variations; brown, yellow and banded yellow, with significant larval preference for non-banded types (O’Donald 1968). The reason for this preference remains unknown to this day (De Cock 2009). Larvae pierce the anterior part of the snail with their mandibles and inject them with a dark secretion, possibly a neurotoxin, which kills their victim (Schwalb 1961; Klots & Klots 1963; Hůrka & Čepická 1978). They are also known to “ride” the snails, i.e. mounting the shell and assuming a favourable position to attack the head of the snail or its upper tentacles. In either case this is the best way to get the poison as close as possible to the centre of the snail’s nervous system (Schwalb 1961; Tyler 2002). Contrary to a widespread belief (Klots & Klots 1963; Hůrka & Čepická 1978), the toxin itself does not appear to predigest the prey, but the larva rather seems to chop out pieces of flesh with its mandibles while using digestive intestinal secretion, as was observed by Schwalb (1961).

Specific experiments still need to be performed to understand the details of feeding in these animals, so the next lines represent conjecture only. Special, solitary sensilla were observed on the mandibles positioned apically before the opening of the inner channel (Fig. 17; ss). It may be possible, that the function of this sensilla is

mechanoreceptive. While the larva attempts a successful bite into its prey's body, the seta triggers the discharge of deadly liquid. Furthermore, a hyaline appendage, which gives the impression of a "shutter", composed of a blunt thick seta can be found at the base of the mandibular channel opening (Fig. 19; ha). This hyaline appendage nevertheless takes different form in each of the abovementioned species. The flow of the deadly liquid, theoretically triggered by the mechanoreceptive sensilla, may be controlled by this "shutter" or by the gland producing the fluid. On the other hand, this structure may just prevent the channel opening getting blocked by small particles. Similar sensilla and hyaline appendages were observed on larvae of *Lamprohiza splendidula* and *Phosphaenus hemipterus* (M. Novák, pers. obs.), as well as in *Lucidota atra* (Olivier, 1790) (Lampyrinae) (Branham & Archangelsky 2000). Still, in each of the abovementioned species, the sensilla and especially the hyaline appendage take different form. Additionally, one of the structures can be missing in other lampyrid species. In *Pyraetomena nigripennis* Solier (Lampyrinae), the hyaline appendage is missing but a strong seta is present anteriorly to the base of retinaculum (Archangelsky 2010) and in *Pyraetomena borealis* (Randall, 1838) (Lampyrinae) (Archangelsky & Branham 1998), the solitary seta is missing, but a large protruding hyaline appendage is present at the mandibular channel opening. It is possible that in the latter species, the structure also possesses triggering function, especially considering its protruding position.

**Photic behaviour.** According to Tyler (2002), the larva of *Lampyris noctiluca* can produce light in three different ways. One, when disturbed, it will sometimes switch on its lights for a few seconds and then turn them off again. This seems to be a defensive mechanism to scare off potential predators. Two, some larvae have been known to glow continuously for hours, without any apparent provocation. These are, according to Tyler (2002), often fully grown larvae ready to pupate. Therefore, this glow, which is very similar to that of an adult female, might be just part of the preparation for adulthood, at a time when the larva's body is undergoing internal changes. A third type of photic display described by Tyler (2002) is sometimes produced during movement. It consists of definite pulses of light lasting ca. 2 seconds, separated from the next one by a longer interval of darkness lasting ca. 4 seconds, although Dreisig (1974) reports glows lasting 7.3 seconds on average and the interval of darkness of 20.2 seconds on average. The intensity of each pulse gradually builds up, followed by a period of steady brightness and then a final period, during which the light fades and goes out altogether (Schwalb 1961; Tyler 2002). All three types of photic display were also observed in the described specimens.

The true cause of the last type of photic manifestation remains a mystery. Tyler (2002) proposes five possible causes; 1) the glow has no purpose and is just a by-product of the light organs' development; 2) the larva uses the light while tracking the prey; 3) the larva uses the light to attract the prey; 4) interspecific communication and 5) aposematic defence connected with unpalatability, which seems to be the only hypothesis supported by evidence (Sivinski 1981; Underwood *et al.* 1997; De Cock & Matthysen 2003; De Cock 2009; Moosman *et al.* 2009). Since Tyler (2002) adequately explains the pros and cons for each of the five points, I would like to address intraspecific communication only. Viviani (2001) supposedly witnessed possible intraspecific communication in an unidentified *Bicellonychia* sp., where larvae reacted to flashes emitted by adults, hypothesising the cause of this behaviour could be informing the adults of an occupied food niche. This nonetheless cannot be the case with *Lampyris noctiluca*, where the egg-bearing females are flightless, thus communication of larvae with adult males would be pointless. The way larvae flash differs from that of the females. If this was indeed a signal for the males to distinguish between the larvae and females, a simple darkness of the larvae seems like a more effective solution. Furthermore, larvae do not usually glow during the adult mating season (Schwalb 1961) and evidence suggests that luminescence in Lampyridae seems to have arisen first in larvae and then subsequently in the adults who use it for sexual communication (Branham & Wenzel 2003). Yet, the flash display may serve to communicate between larvae, for example for effective division of a food niche. On the other hand, larvae do not have developed eyes like adults, only simple ocelli, so this assumption seems doubtful. In conclusion, the utilisation of larval light in intraspecific communication with adults or even with other larvae seems unlikely.

Interestingly, low level luminescence was recently observed by Tisi *et al.* (2014) in the pairs of lightly-pigmented posterolateral spots on each tergite and even in the inactive light organ. Nevertheless, according to the authors, this luminescence is so weak, that it is most probably unrelated to aposematic signalization.

**Pupa and prepupa.** According to Schwalb (1961), the larva enters the stage of prepupa 8–20 days prior to pupation. From my observations, it was noticed that this period can be even shorter (1–6 days). The range presented by Schwalb seems to be quite wide. Besides different rearing conditions, a possible explanation may be a different period of prepupal stage depending on the sexes. But even in the pupal stage the difference between sexes is not that distinctive (8–12 days for a female and 11–15 days for a male; Schwalb 1961; Tyler 2002). Moreover,

the male pupa raised for the purpose of this article turned into an imago after 8 days only (M. Novák, pers. obs.). It may be that individuals staying in prepupa for 20 days might have fed more recently than individuals staying in prepupa for 8 days, i.e. needing a longer time to process the ingested food and expel the undigested waste. The prepupa is the stage of preparation of the larval body for entering the pupal stage, therefore the time needed for processing and elimination of food intake might influence the length of the prepupal stage.

Tyler (2002) describes the colour of pupa as pale yellow, turning olive green after several hours, but this only applies for the older male pupae (Figs 30–32), where the olive colour is especially distinct in dimmer light conditions. The female pupa (Figs 27–29) stays yellowish white with pink regions throughout the whole pupal period. Adult males are overall much darker compared to their female counterparts, but there is one more distinction between male and female pupae, which probably plays an important role in the colour difference. The pupal skin in the male seems to darken and harden as the pupa gets older. After the adults emerge, the exuvia left by a female pupa is extremely delicate and without any colouration. The exuvia of a male, on the other hand, is brown and still retains its original shape.

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