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Redescription of immature stages of central European fireflies, Part 3: *Phosphaenus hemipterus* (Goeze, 1777) larva, and notes on its life cycle and behaviour, with a key to three central European lampyrid larvae (Coleoptera: Lampyridae)

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Abstract

The mature larva of the elusive firefly *Phosphaenus hemipterus* (Goeze, 1777) is thoroughly redescribed and illustrated with detailed images, including scanning electron microscope figures. The external sense organs and their significance is discussed, as well as the predatory behaviour and specific lifestyle of the larva. A key to the central European lampyrid larvae (viz. *P. hemipterus*, *Lamprohiza splendidula* (Linnaeus, 1767) and *Lampyrus noctiluca* (Linnaeus, 1758)) is provided as well as a comparative table of their morphological features.

Key words: Elateroidea, Lampyrinae, morphology, ecology, pheromone communication

Introduction

The genus *Phosphaenus* Laporte, 1833 (Lampyrinae) is represented by a single European species, widely distributed from England, Denmark, southern Sweden, Finland and Karelia through the central part of Europe to the Pyrenees, northern Italy, west Balkan Peninsula, Transylvania and Ukraine (Burakowski 2003; Geisthardt & Satô 2007). It seems to be the only European firefly that has been imported into another continent, since it is also present in Nova Scotia, Canada (Tyler 2002). The unintentional introduction was probably facilitated by its high tolerance of, or even preference for, human-altered environments. Published descriptions of this species are brief and the morphology, particularly the morphology of the larvae, is poorly known. Schematic illustrations in many published works are of variable quality, and detailed images and descriptions are missing (Reitter 1911; Korschefsky 1951; Kratochvíl 1957; Klausnitzer 1994; Burakowski 2003).

Phosphaenus hemipterus (Goeze, 1777) was considered a rare and poorly known species until recently. De Cock (2000) presumes that the reason for this is the fact that this firefly can be found mainly in areas with high levels of human disturbance. These include gardens, parks, parking lots and field edges, while much of the previous research has been conducted in areas mostly unaffected by humans. De Cock (2000) concludes that this species might not be as rare as previously thought, and furthermore, it can be found in areas which are not considered important from a conservation management point of view.

Interesting information may come from future studies of the poorly documented genus *Phosphaenopterus* Schaufuss, 1870 consisting of two species, one occurring in Romania and the other in Portugal and the French Pyrenees. Since the time of their descriptions, these species have not been reported again (De Cock 2009). Mikšić (1982) suggests they might be just macropterous forms of *Phosphaenus hemipterus*. Interestingly, these taxa occur on the outer borders of the distributional range of *Phosphaenus hemipterus* (De Cock 2009), but to be clear about their phylogenetic relationship, available type specimens will need to be examined or additional fresh material collected.

This paper represents the third and final part of a trilogy focusing on immature stages of firefly species occurring in central Europe. The larva together with male and female pupae of *Lampyrus noctiluca* (Linnaeus,

1758) were redescribed in the first part (Novák 2017), followed by a redescription of larva with male and female pupae of *Lamprohiza splendidula* (Linnaeus, 1767) in the second part (Novák 2018).

Material and methods

Specimens of *Phosphaenus hemipterus* were loaned from Petr Švácha, from the collection of the Institute of Entomology within the Biology Centre of the Academy of Sciences of the Czech Republic in České Budějovice. The specimens examined were found in forest litter in the Lednice area (48°47'58.8"N, 16°48'6.0"E), south Moravia, in April 1987, and stored in 80% alcohol. The area of Lednice is predominantly composed of quaternary sediments, with long temperate and dry summers and short mildly temperate dry winters. Average yearly rainfall is 1000 mm, average yearly temperature is 8.5 °C (Hučík *et al.* 2013).

Higher instar individuals were selected for subsequent analysis. Regarding the distinction of the individual instars, no work describing either morphological or biometric traits or chaetotaxy exists. To solve this problem, individuals approaching the maximum species length limit were selected.

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).

Phosphaenus hemipterus (Goeze, 1777)

Material examined. Lednice (Czech Republic), three higher-instar larvae out of eleven collected in April 1987.

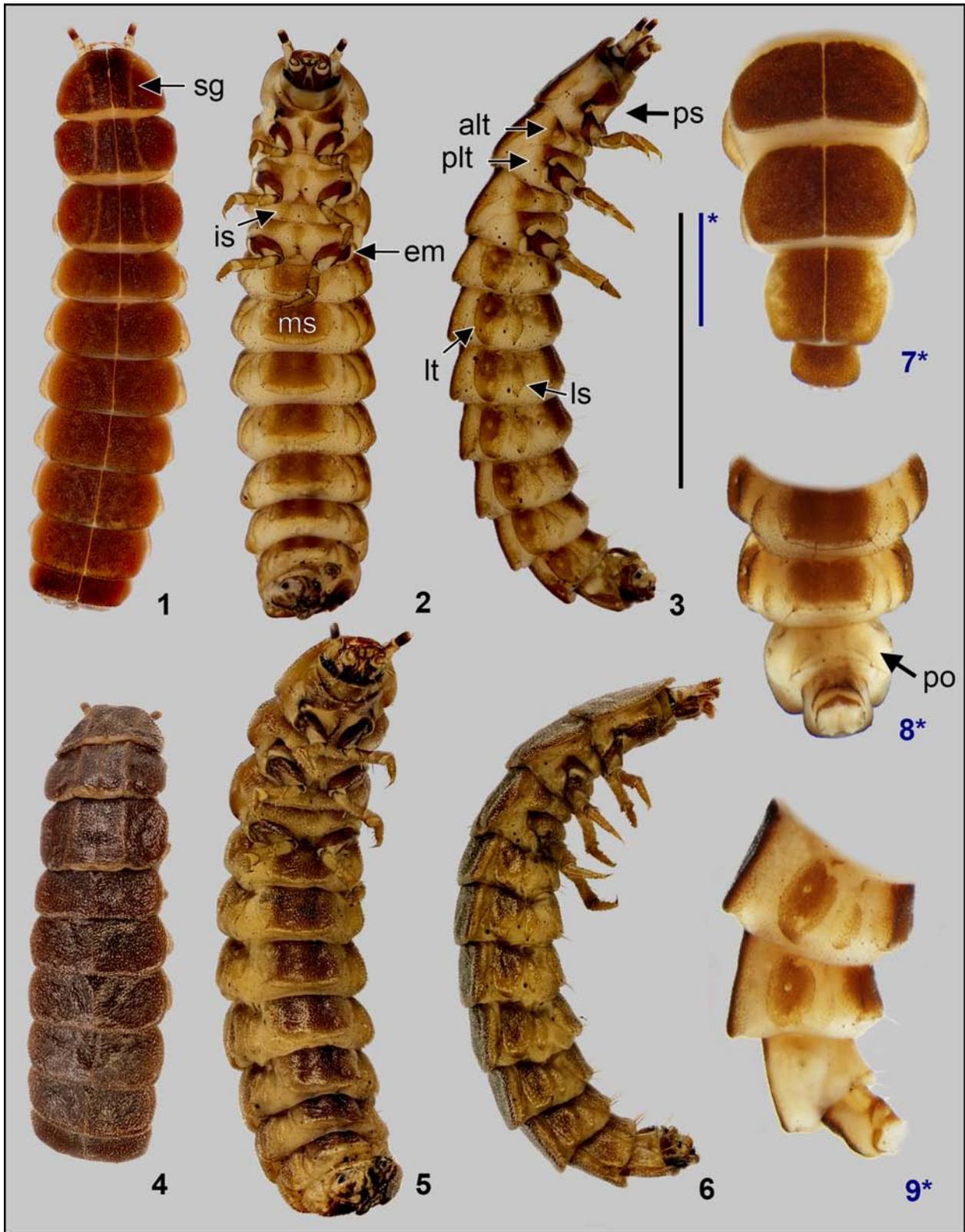
Diagnosis. Larvae oblong and slender; thoracic tergites subdivided with one parasagittal line of light pigmentation on each side subparallel to sagittal line; inner ventrolateral area of second antennomere with distinct longitudinal cleft; in addition to second antennomere, sensoria present also on third antennomere and distal segments of maxillary and labial palpi; mandible with short and blunt retinaculum; mandibular channel opening covered by a small hyaline appendage forming a subtriangular valve with fringing at the distal end; short fibrous setae growing from slightly sunken toroidal base covering antennae, legs and sclerites; photic organ consisting of a pair of white spots placed laterally on abdominal segment VIII.

Description of mature larva (Figs 1–6). Oblong and slender, cylindrical. Body length ca. 10–11 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 VIII divided by sagittal line in dorsal view (Fig. 1). Thoracic tergites then subdivided with one parasagittal line of light pigmentation on each side, subparallel to sagittal line (Fig. 1; sg). Colouration: dorsally dark reddish-brown, ventrally pink/ochre/light brown with darker plates on laterotergites and sternum. Spiracles on laterotergites of light colouration. Paired photic organs placed laterally on venter of abdominal segment VIII.

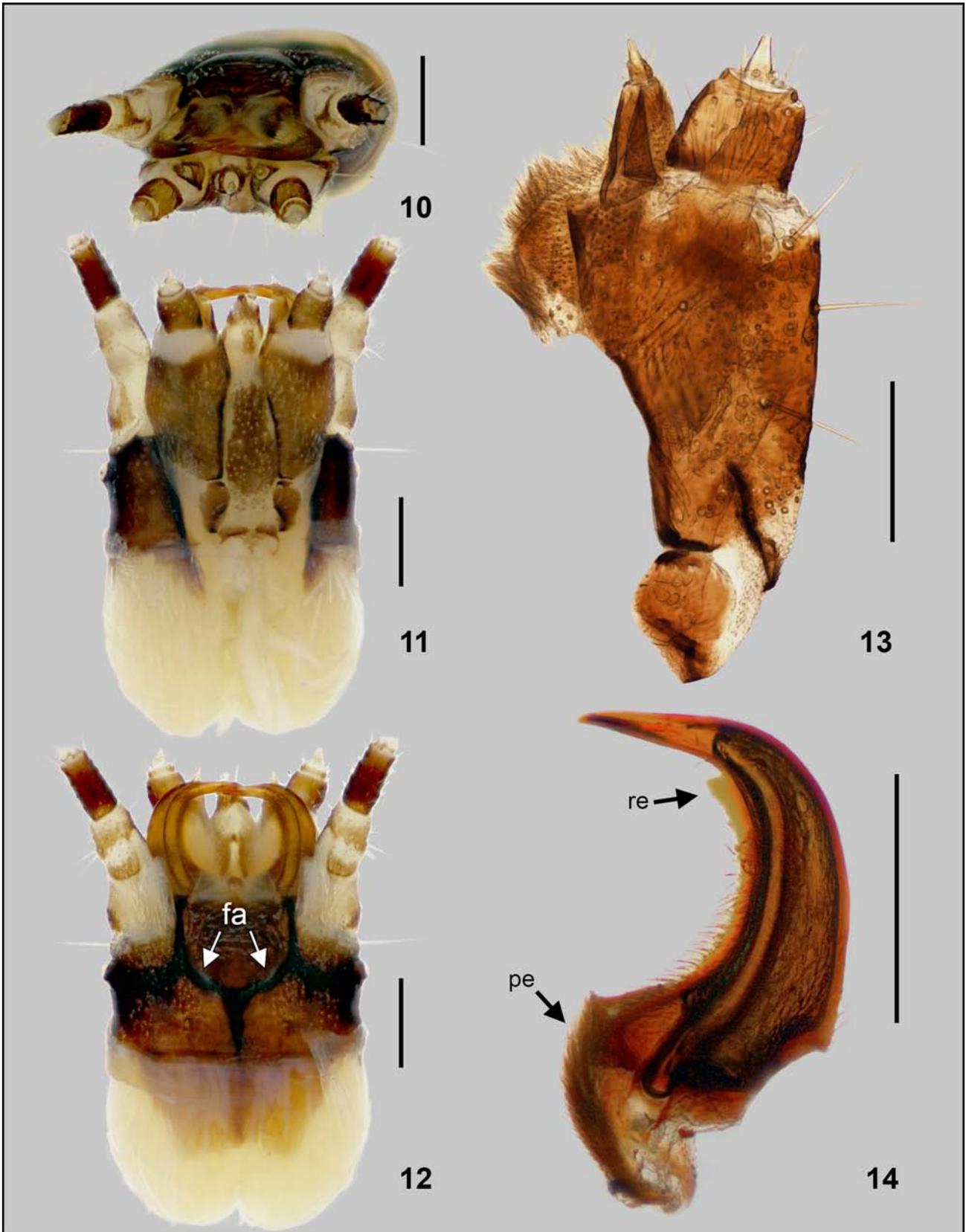
Types of general cuticular outgrowth observed. 1. Short, blunt, setae lying on surface (Figs 15, 29; bs); 2. stout, long setae (Figs 15, 27; ls); 3. flagellar setae growing from a slightly sunken toroidal socket (hereafter called toroidal setae; Figs 15, 20, 29; ts).

Head capsule (Figs 10–12, 15–17). Prognathous; retractable within prothorax, extensible neck membrane covered in extremely short spines and forming a two-layered envelope around retracted head; wider than long. Epicranial plate laterally about 1/3 of the width of the head capsule, slightly concave, with one stout seta anterolaterally, close to the base of antennae. Head capsule dorsally covered with short blunt setae lying on its surface (Fig. 15; bs). Epicranial suture dark, Y-shaped, frontal arms U-shaped (Fig. 12; fa). Gula not present (Fig. 11). One stemma on each side of the head. Labrum fused with clypeus forming clypeolabrum, covering base of mandibles in dorsal view. Clypeolabrum flat in anterior view, with two setae reaching one fourth of the length of mandibles, positioned on outer lateral sides (Fig. 15). Epipharynx formed by two plates, and an anterior brush of long setae, which project centrally past anterior margin of the head. Hypopharynx with short setation.

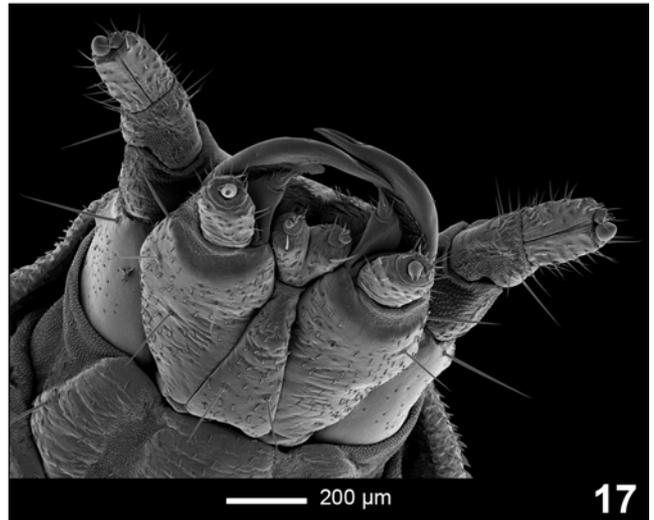
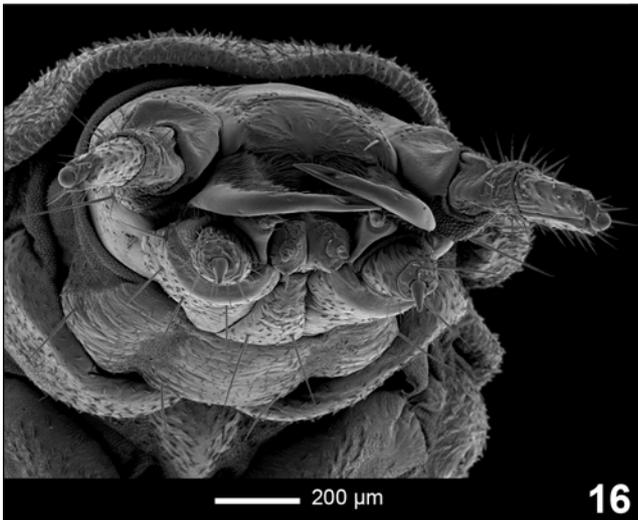
Antenna (Figs 24–26). Trimerous, inserted on lateral distal margin of epicranial plate; partially retractable within membranous socket. Basal antennomere widest, poorly sclerotized, slightly bulging on the dorsal side,



FIGURES 1–9. *Phosphaenus hemipterus*. 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. Detail of distal abdominal segments VI to X in dorsal (7); ventral (8) and lateral (9) views. Abbreviations: alt—anterior laterotergite; em—epimeron; is—intersternite; ls—laterosternite; lt—laterotergite; ms—median sternite; plt—posterior laterotergite; po—photic organ; ps—prosternum; plt—light-pigmented lines on protergum; sg—parasagittal line. Scale bars: Figs 1-6, 5 mm; Figs 7-9, 1 mm.



FIGURES 10–14. *Phosphaenus hemipterus*. Detail of head in anterior (10); ventral (11) and dorsal (12) views; right maxilla in dorsal view (13); right mandible in dorsal view (14). Abbreviations: fa—frontal arms; pe—penicillus; re—retinaculum. Scale bars: 0.25 mm.



FIGURES 15–17. *Phosphaenus hemipterus*. SEM image of head in dorsal (15); anterior (16) and ventral (17) views. Abbreviations: bs—short, blunt, setae lying on surface; ls—stout, long setae; ts—toroidal setae.

densely covered by three types of setae; short blunt setae lying on surface and toroidal setae mainly posterolaterally, and several stout, almost perpendicular long setae around apical region (which are longest on this antennomere in comparison with the other antennomeres) easily observable under high magnification (Fig. 24). Second antennomere slightly longer, narrower and laterally flattened in comparison to basal antennomere; bearing only toroidal setae and blunt setae equally and abundantly spread across the antennomere. Inner ventrolateral area

of second antennomere with sensillum consisting of distinct longitudinal cleft; a sensory slot (Fig. 24; ses). Several sensilla coeloconica are present apically (Fig. 26; sc). Sensorium of second antennomere oval (Figs 24–26; as1), widest at the base, closely adhering to the second antennomere, slightly longer than the third antennomere, with very fine helical ridges from apex to bottom. Third antennomere (Fig. 24; a3) shortest, reaching about 1/2 of length of the sensorium of second antennomere and adjoining it, bearing a small sensorium, three short setae and three cuticular projections (Fig. 25); first longer and thick (cp1), second longer and thin (cp2) and third very short (cp3).

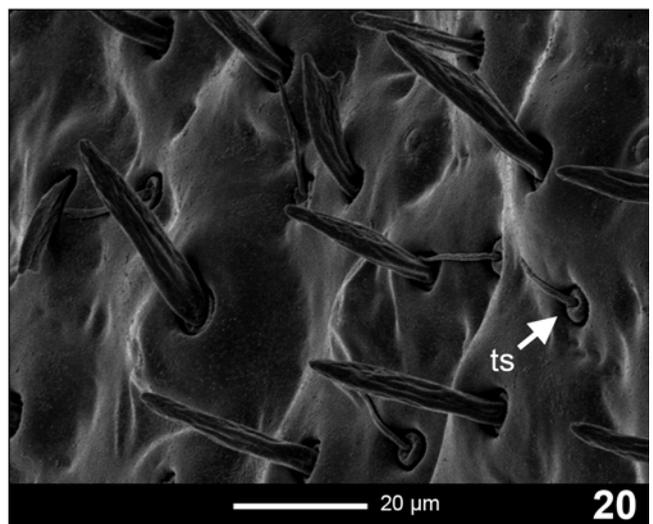
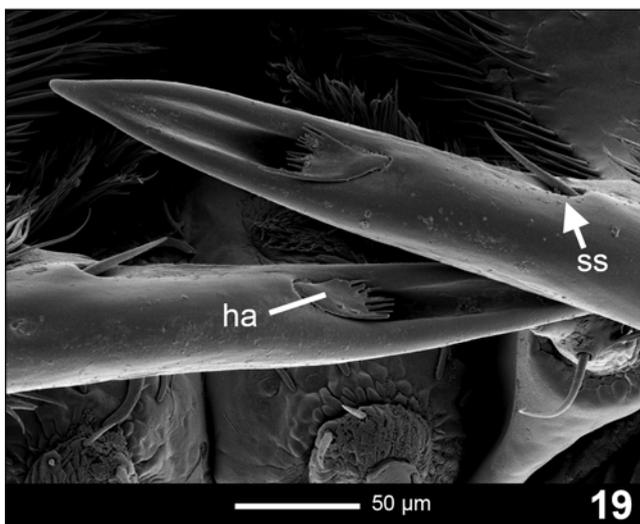
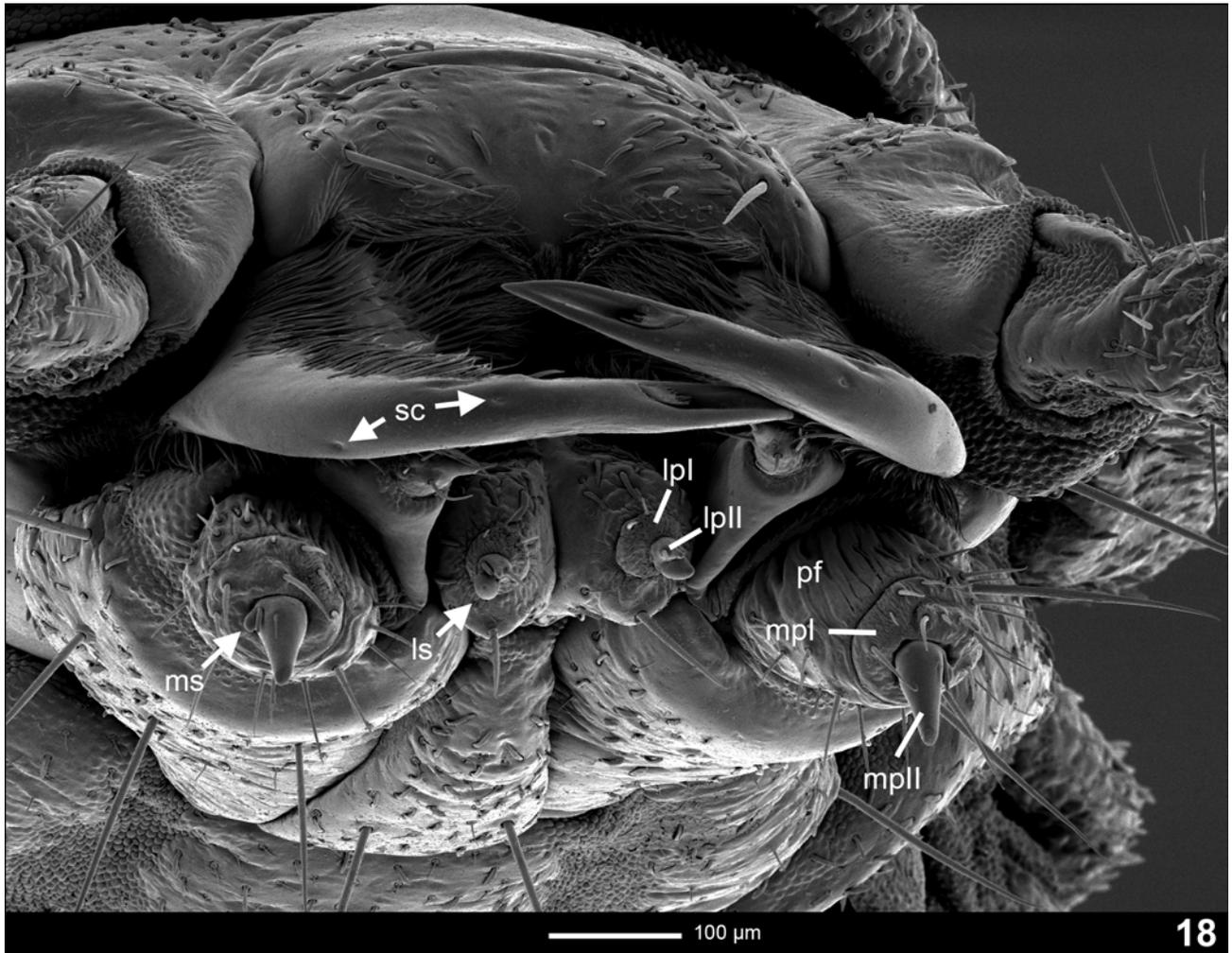
Maxilla (Fig. 13). Consisting of five parts, attached to labium forming a maxillo-labial complex. Cardo vertical, bulbous, with wider side adjacent to stipes. Stipes elongated, subtrapezoidal, ventrally covered with short blunt setae lying on its surface and four long and stout setae, three anteriorly and one medially. Galea bimerous, with basal part larger than distal, subtriangular in anterior view (with the tip of subtriangle aiming ventrally). Distal part conical, rotated medially with setae shorter than its body. Lacinia covered with brush of long setae on outer lateral margin. Maxillary palpifer large (Fig. 21; pf), subrectangular, slightly longer than wide. Maxillary palpus bimerous (Fig. 21; mp1, mp2), basal palpomere short and wide. Palpifer and basal palpomere covered with setae. Palpomere II (Fig. 22; mp2) bearing two setae, one thin and sharp placed dorsally and second slightly thicker and blunt, paired with sensorium near base on lateral surface (Fig. 22; ms).

Labium (Fig. 21, 23). Closely attached to maxilla, formed by a short prementum, mentum and mostly membranous submentum (Fig. 11). Glossae absent. Prementum narrow, heart-shaped in ventral view; bearing three types of setae: blunt short setae lying on surface, sensory setae and a pair of long and stout setae underneath the palpi. Labial palpus bimerous (Fig. 23; lp1, lp2); basal palpomere wide and short, bearing several setae dorsally; second palpomere short, bearing a large sensorium ventrally (Fig. 23; ls), one thin seta between the apex and the sensorium, and two stout setae laterally around the apex: one sharp on the inner side and one blunt on the outer side. Mentum elongated, subtriangular, unsclerotized on lateral margins, ventrally bearing numerous short, blunt, setae lying on surface, numerous toroidal setae and a pair of large, stout setae posteromedially.

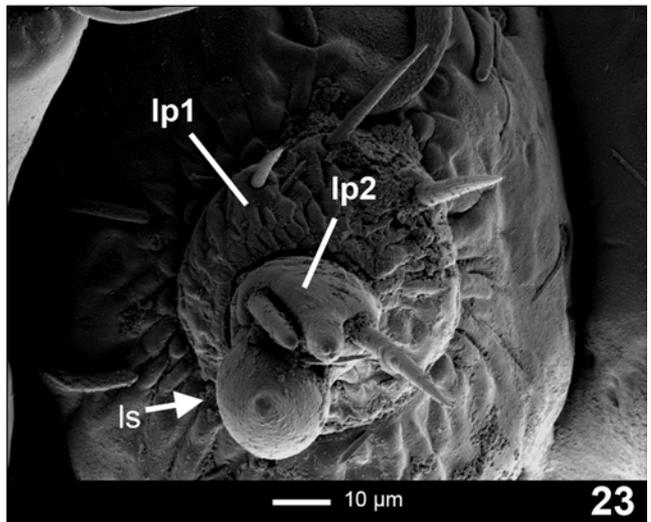
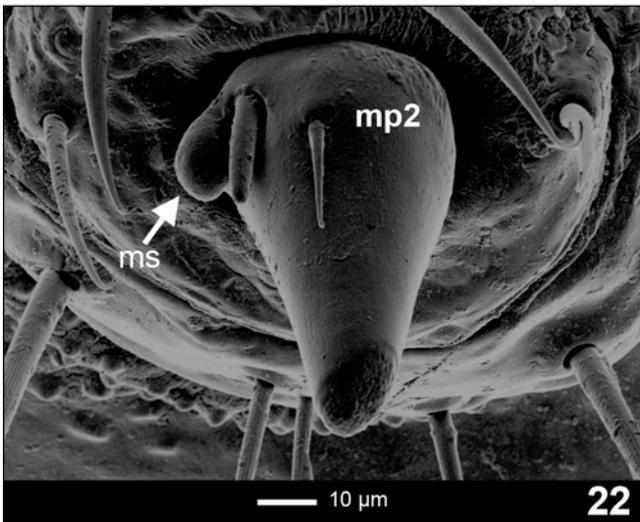
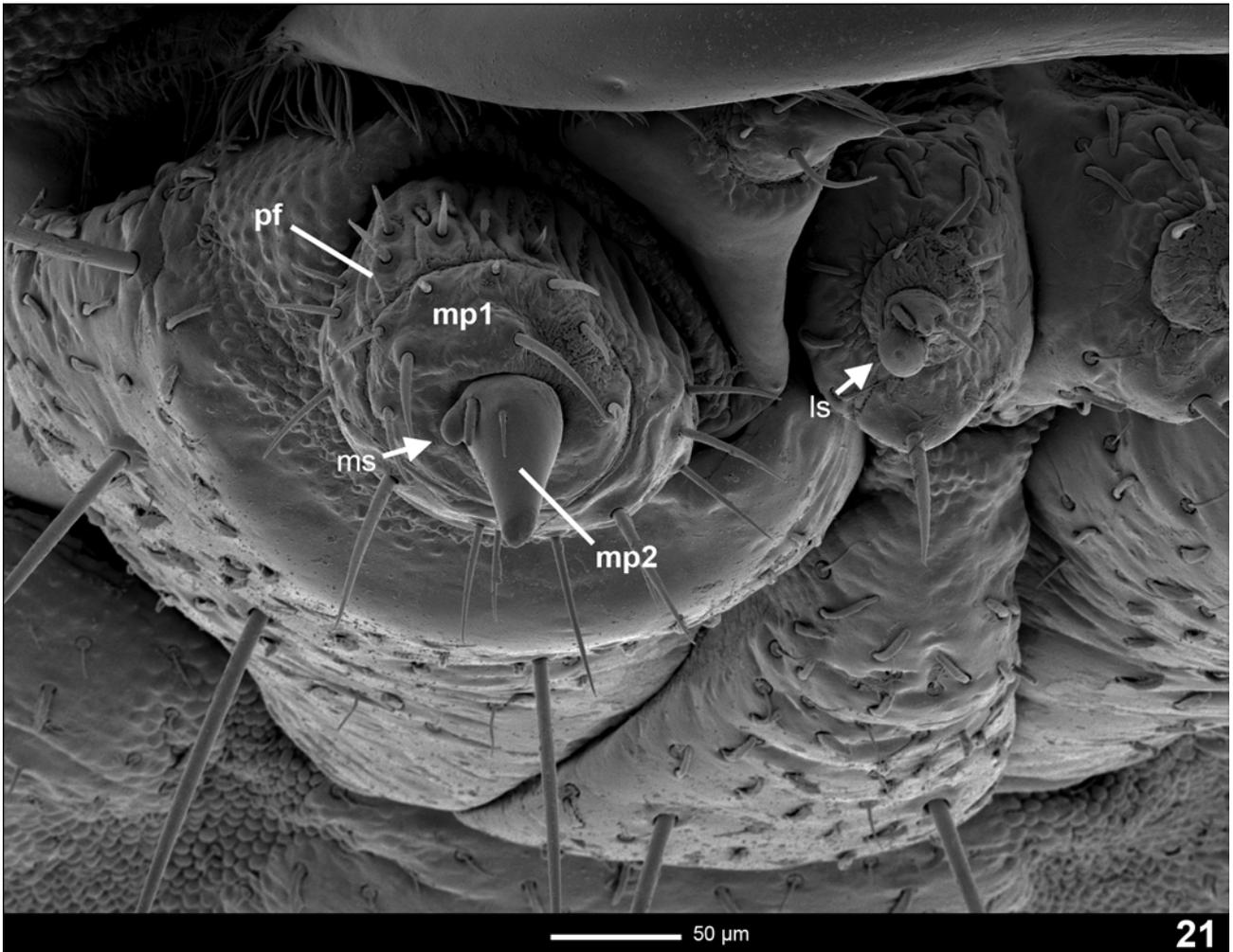
Mandible (Fig. 14). Symmetrical, falcate, with an internal channel opening subapically on outer edge (Fig. 19). Penicillus well developed (Fig. 14; pe). Retinaculum present, forming one thin and blunt hyaline process on apical third of mandible (Fig. 14; re). Inner margin of mandible from retinaculum to the base covered with stout setae, lengthening towards the base of mandible (Fig. 14). Ventrally, basal two-thirds of mandible covered with dense setation lying on surface, aimed medially. Dorsally, basal two thirds with sagittal line of dense, stout, setation lying on surface, of equal length, erect in its last third, aiming medially (Fig. 15). Lateral margin without setation. Sensory (hyaline) appendage on outer margin of mandible present before channel opening, forming a subtriangular valve with fringing at the distal end (Fig. 19; ha). A thin stout short seta present dorsally in retinaculum region on both mandibles (Fig. 19; ss). Several sensilla coeloconica present on the post-retinaculum apical part (Fig. 18; sc).

Thorax (Figs 1–6). Protergum wider than long, subsemicircular, wider posteriorly. Meso- and metatergum suboval, wider than long, with rounded margins. Venter of prothorax composed of subquadrate prosternum (Fig. 2; ps), subdivided into three well sclerotized areas; lateral ones narrow and transverse, extending above and to the sides of coxae fusing with episterna; medial area subrhomboid. Epimera forming thin sclerotized strands (Fig. 2; em). Lateral areas of meso- and metathorax composed of two laterotergites; anterior one sclerotized (Fig. 2; alt), bearing a well-developed bilabiate spiracle in mesothorax; posterior one membranous (Fig. 2; plt). Anterior ventral area of meso- and metathorax formed by mostly membranous intersternite (Fig. 2; is) with two darker-pigmented sagittal bands centrally, margined by paired anterior laterotergites. Posterior ventral area subdivided into triangular, wider than long basisternum and smaller sternellum. Basisternum subdivided into three darker-pigmented areas; lateral ones extending anteriorly and laterally to coxae, joining episterna; medial subrhomboid. Sternellum membranous, with sclerotized triangular centre touching with medial subrhomboid area of basisternum with its tip.

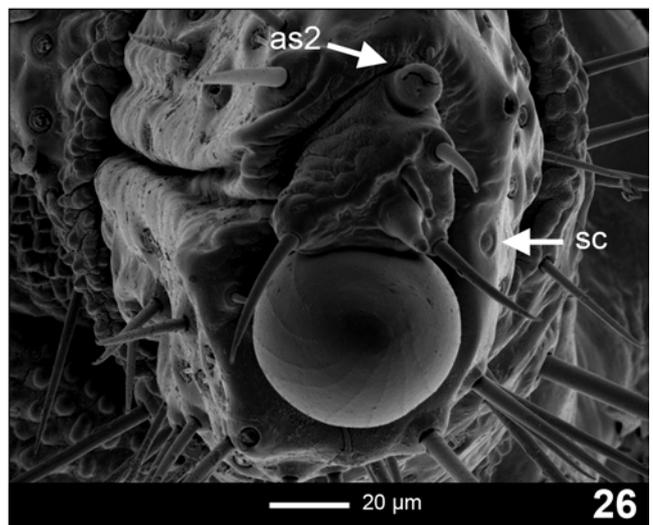
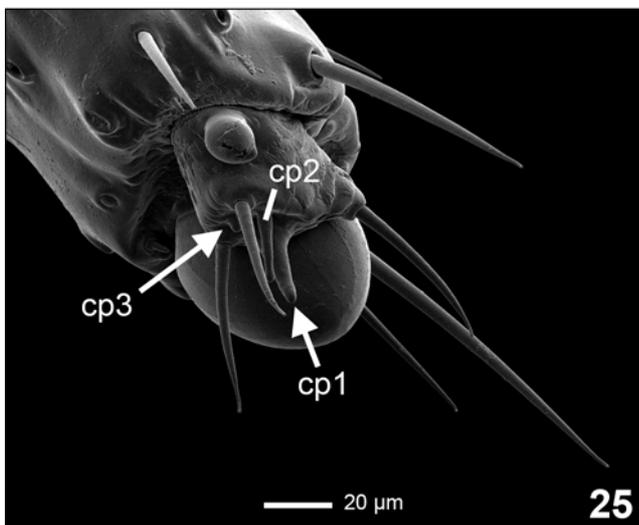
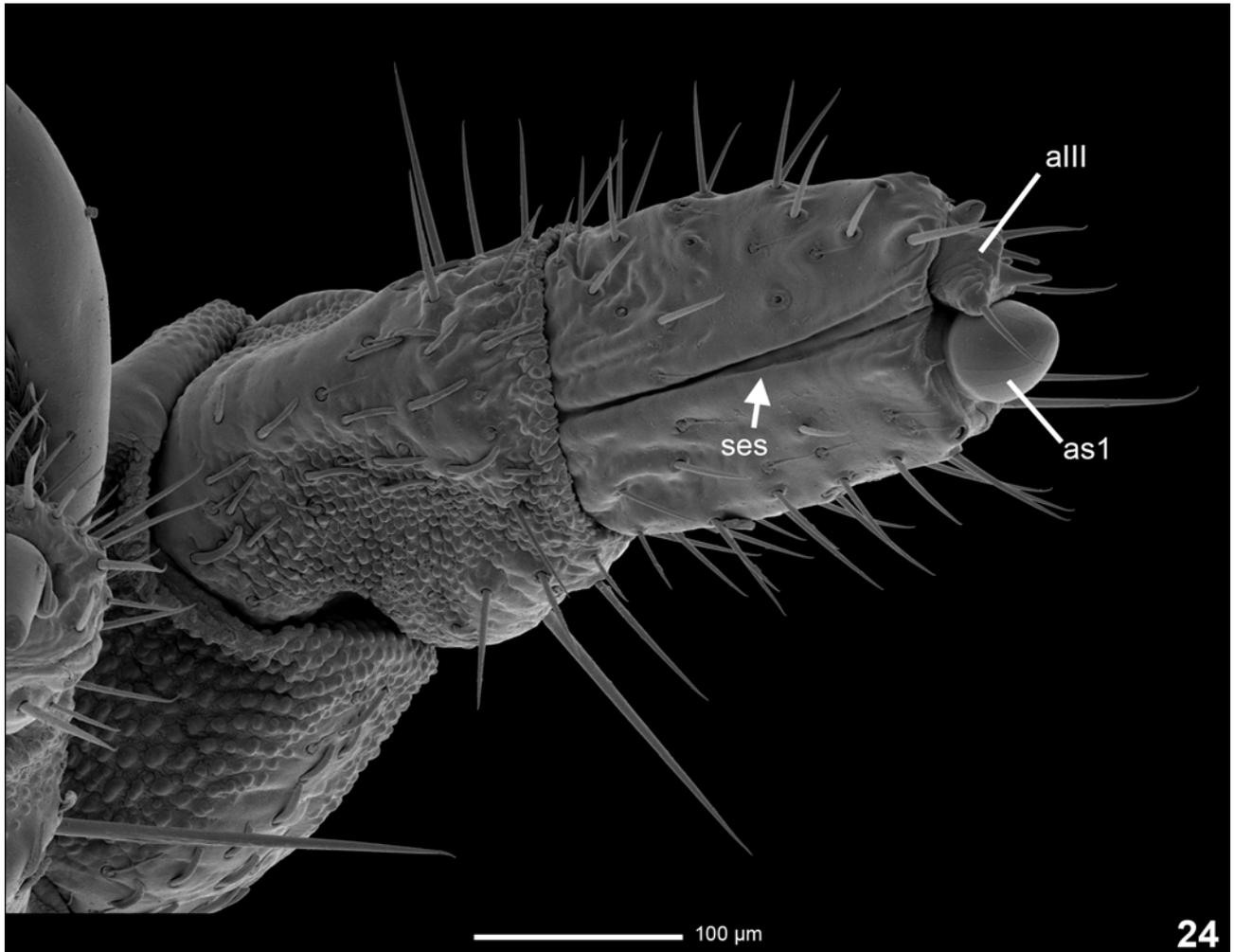
Legs (Figs 27–29). Pentamerous, all pairs similar in shape and size. Coxa large, stout, bearing short blunt setae lying on its surface, toroidal setae and stout long setae. Coxal-trochanteral membrane reaching more than 1/2 of coxal longitudinal length (Fig. 2). Trochanter smaller, subtriangular in lateral view, about the same size as femur, bearing short blunt setae lying on its surface, toroidal setae, and stout long setae, with long stout seta on distal venter, together with several shorter stout setae radially on distal end. Femur fusiform in lateral view, bearing short blunt setae lying on its surface, toroidal setae, and stout long setae, with one very long stout seta on the centre of ventral area (Fig. 27) and several shorter stout setae radially on distal end. Tibiotarsus as long as femur, narrower, tapering towards distal end, covered predominantly by stout sharp setae, lengthening dorsally. Pretarsus composed of a claw with fine ridges, ventrally bearing three short setae (Fig. 28).



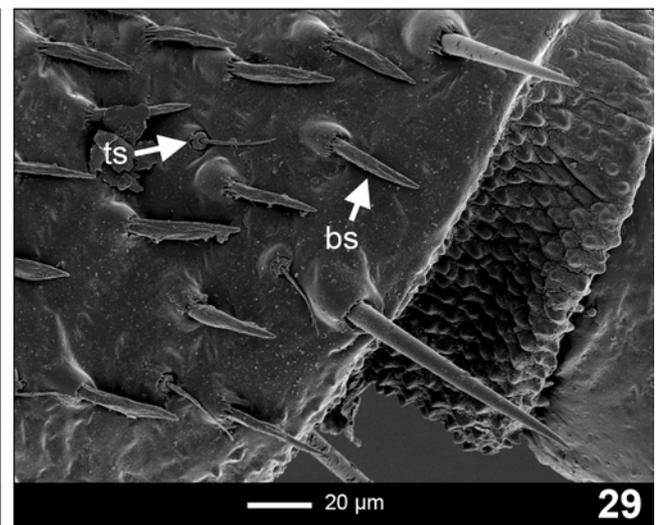
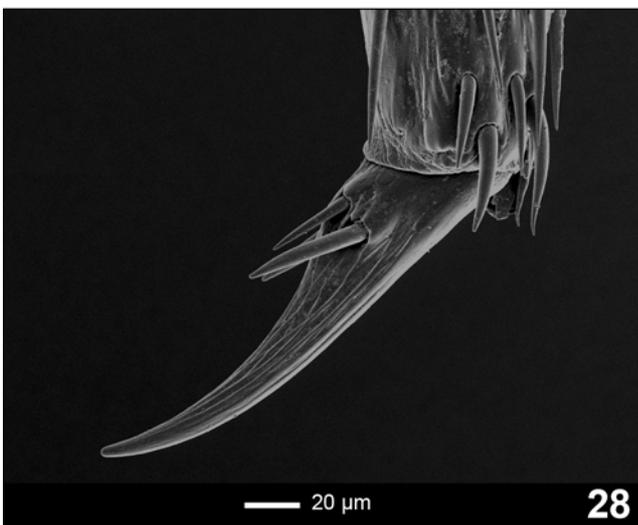
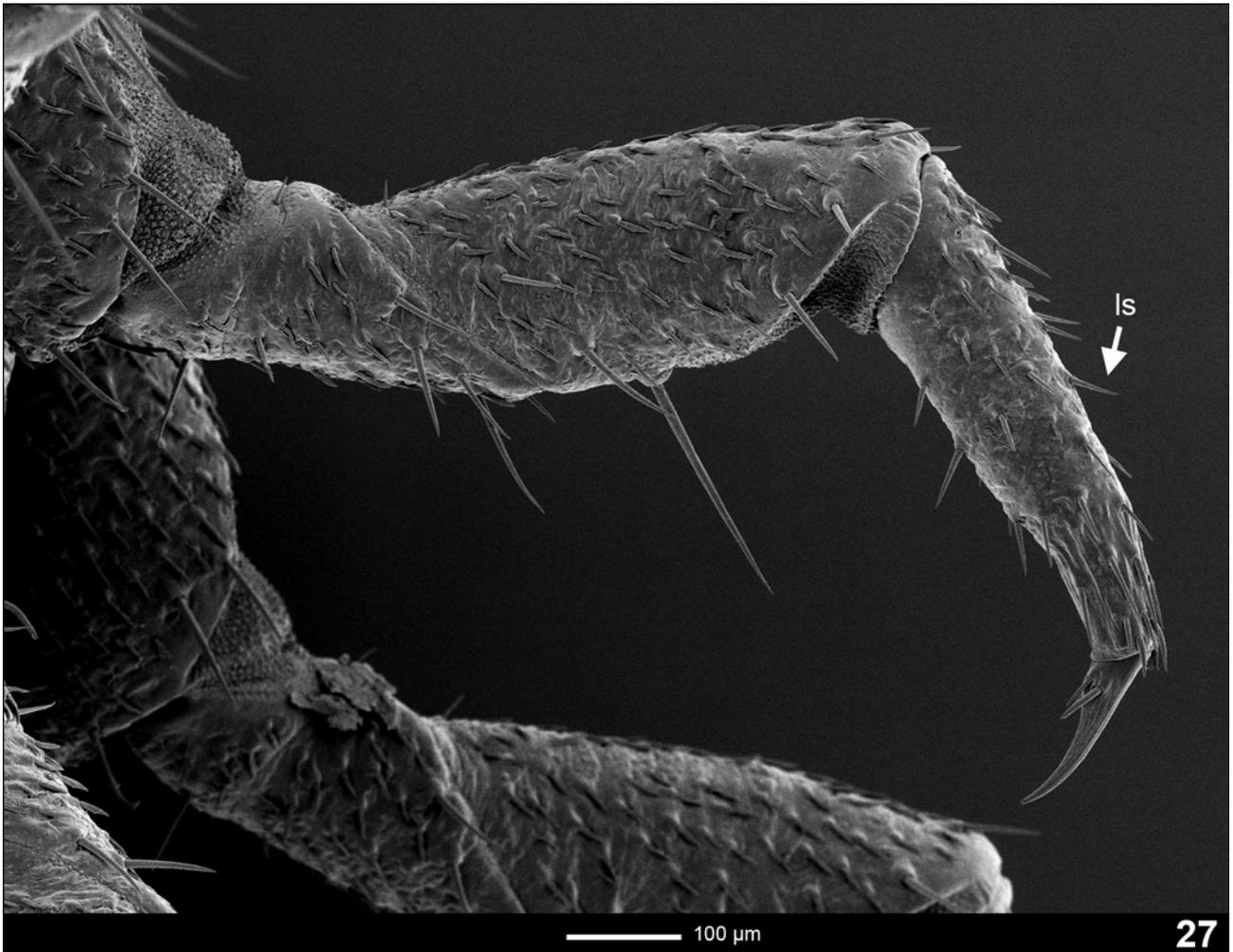
FIGURES 18–20. *Phosphaenus hemipterus*. SEM image of maxillolabial complex in anterior view (18); detail of mandibles (19); detail of body surface on protergum (20). Abbreviations: ha—hyaline appendage; lp1, lp2—labial palpus 1, 2; ls—labial sensorium; mp1, 2—maxillary palpus 1, 2; ms—maxillary sensorium; pf—maxillary palpifer; sc—sensillum coeloconicum; ss—solitary seta, ts—toroidal seta.



FIGURES 21–23. *Phosphaenus hemipterus*. SEM image of detail of maxillolabial complex in anterior view (21); detail of maxillary palpus 2 (22); detail of labial palpus (23). Abbreviations: lp1, 2—labial palpus 1, 2; ls—labial sensorium; mp1, 2—maxillary palpus 1, 2; ms—maxillary sensorium; pf—maxillary palpifer.



FIGURES 24–26. *Phosphaenus hemipterus*. SEM image of antenna in general view (24); detail of sensorium and third antennomere (25); anterior view (26). Abbreviations: a3—third antennomere; as1, 2—antennal sensorium 1, 2; cp1–3—cuticular projections 1–3; ses—sensory slot; sc—sensillum coeloconicum.



FIGURES 27–29. *Phosphaenus hemipterus*. SEM image of left prothoracic leg in general view (27); pretarsus (28); detail of distal end of femur (29). Abbreviations: bs—short, blunt, setae lying on surface; ls—stout, long setae; ts—toroidal setae.

Abdomen (Figs 1–9). Ten-segmented, slightly tapering towards posterior end, segments I to VIII subdivided by fine sagittal line in dorsal view (Fig. 1). Tergites of segments I to VII subrectangular, similar in shape and colouration, wider than long; tergite of segment VIII suboval; segment IX subrectangular, wider than long; segment X forming a narrow sclerotized dark ring, bearing the holdfast organ—pygopod—with several eversible processes. Segments I to VIII have single laterotergites (Fig. 3; lt) on each side with sclerotized plates bearing

bilabiate spiracles; the venter of segments I to VII consists of median sternite, margined by paired narrow weakly sclerotized laterosternites (Fig. 3; ls). Sternites of segments I to VIII subrectangular, well sclerotized (except segment VIII) wider than long, with a pair of long stout setae on posterolateral margins. Venter and laterotergites of segment VIII membranous, bearing laterally a pair of white spots representing a functioning photic organ (Fig. 8; po). Sternite of segment IX sclerotized posteriorly, forming a thin ring supporting segment X.

Notes on life cycle and behaviour. The life cycle of *Phosphaenus hemipterus* lasts two or three years. Eggs are white, spherical, with a diameter of ca. 0.6 mm (De Cock 2000). According to De Cock, late-instar female larvae tend to be larger and fatter than males and are easily recognised in the field (De Cock 2003). Pupation takes place in April–May, the pupal stage lasts ca. 2 weeks. Mature individuals are collected occasionally and rarely from July to August (Burakowski 2003).

Unlike most of the firefly species, whose larvae feed on snails and slugs, larvae of *Phosphaenus hemipterus* are obligate earthworm (*Lumbricus* spp., Lumbricidae) predators (Majka & MacIvor 2009). Majka & MacIvor (2009) observed the larvae while feeding, using tarsal claws of the legs to anchor themselves to the body of the earthworm and their extended antennae moving over the surface of the earthworm's body. The process of injecting a toxin into its prey in order to kill it, as observed in other species of fireflies (Schwalb 1961), has not yet been observed for this species. However, the presence of a mandibular channel suggests that a toxin is also used by this species.

Like *Lampyris noctiluca*, *Phosphaenus hemipterus* larvae also glow spontaneously by emitting bioluminescent pulses while active at night (De Cock 2003).

Both adult sexes are flightless. Neotenic females stay in litter or lower parts of plants, are active mainly at dusk (De Cock 2000; Burakowski 2003) and are very rarely found (Burakowski 2003). In contrast, the males have vestigial elytra, are diurnal, and can often be found on herbaceous plants and shrubs (Burakowski 2003). The larvae are predominantly nocturnal. Both adult sexes are feebly bioluminescent, although they appear only to glow in response to disturbance (Majka & MacIvor 2009).

Discussion

External sensory organs. The abundance and positioning of sensilla chaetica and sensilla trichodea in *Phosphaenus hemipterus* corresponds with the findings in both *Lampyris noctiluca* and *Lamprohiza splendidula* (Novák 2017, 2018). Sensilla coeloconica (Figs 18, 26; sc), on the other hand, were observed both on antennae and apical parts of mandibles, while in *Lampyris noctiluca* they were observed on antennae and epicranial plate and in *Lamprohiza splendidula* not observed at all. This sensillum is defined by Shields (2008) as a basiconic peg or cone set in a shallow pit, most often chemo-, thermo-, or hygrosensitive. The presence of this type of sensilla on the mandibles of *Phosphaenus hemipterus* might be connected either with a different type of prey, or pheromone communication in adults, as will be discussed below.

A unique type of sensilla was observed on antennae, legs, and sclerotized parts of dorsum and venter. This is a fibrous, weak seta set in a shallow toroidal socket (Fig. 20; ts). There is uncertainty, whether this process is just a modification of sensillum chaeticum or is the sensillum coeloconicum. Arguments for sensillum chaeticum are the wide occurrence on the body of the larva and mechanoreceptive function, together with a fact that the observed sensillum is fibrous, instead of peg- or cone-shaped. Arguments for sensillum coeloconicum are the shallow socket, and the fact that the sensilla occurs with numerous modifications, together with unique prey type and ecology of *Phosphaenus hemipterus*, which may result in a need for different sensory organs.

Phosphaenus hemipterus adults, unlike most lampyrids, prefer pheromone communication to visual communication. In larvae of this species, a striking amount of *sensoria* were observed compared to other sympatric firefly species. While *Lampyris noctiluca* and *Lamprohiza splendidula*, sympatric species of fireflies with *Phosphaenus*, have single sensoria on second antennomeres only, *Phosphaenus hemipterus* bears sensoria on the distal palpomere of the maxillary palpus (Figs 21, 22; ms), the labial palpus (Figs 21, 23; ls) and the third antennomere (Fig 26; as2), in addition to the previously mentioned second antennomere (Fig. 24; as1). Additionally, the second antennomere bears a sensory slot throughout its whole length (Fig. 24; ses). A possible explanation for this phenomenon is broad pheromone utilization within this species. Whereas the larvae do not participate in sexual communication, the sensoria may simply be undeveloped functional organs of adults. Another

explanation may be the unique diet of this species, and possible use in prey tracking, in connection with the aforementioned higher number of sensilla coeloconica.

Hunting for prey. *Phosphaenus hemipterus* is an obligate earthworm predator. Compared to other sympatric fireflies, preferring snails as their diet, this species is unique in its large number of sensoria and lack of dorsoventrally flattened body (Figs 3, 6). The possible intraspecific pheromone function has been mentioned above, as well as possible interspecific chemoreceptive function for tracking of prey. The round cross-section of the body may be an adaptation to earthworm hunting, enabling easier capture of prey that is retreating into a ground tunnel. The significance of body shape is supported by the fact that Nearctic species of *Photinus* Laporte, 1833, which are also reported to prey on earthworms (Lloyd 2008), have a very similar general body-shape. Moreover, certain diurnal fireflies are also known to hunt earthworms, such as *Lucidina* Gorham, 1883 and *Stenocladus* Deyrolle & Fairmaire, 1878 (De Cock 2009). In both cases, the cross-section of the larva is oval, but no surveys regarding the presence of special sensilla have been performed to my knowledge. Additionally, no detailed *in vivo* study of *Phosphaenus hemipterus* predation has been undertaken and therefore the presumed advantages of their morphology remain merely assumptions.

As well as in *Lampyrus noctiluca* and *Lamprohiza splendidula*, a special, solitary sensillum was observed on the mandibles positioned apically before the opening of the inner channel together with a hyaline appendage resembling a “shutter” found at the base of the mandibular channel opening (Fig. 19; ha; Novák 2017, 2018). As in the previously mentioned species, both structures also possess a unique shape in *Phosphaenus hemipterus*. The “shutter”, formed by a subtriangular valve with fringing at the distal end, gives the impression of preventing the channel opening from being blocked by rough particles, rather than serving as a seal.

The overall shape of the mandibles (Figs 14, 15) is yet another feature that distinguishes *Phosphaenus hemipterus* from its snail-hunting counterparts. While in snail feeders the mandibles are sickle shaped, in *Phosphaenus* they are more hooked. This shape may enable the larva to bite and remain attached to its prey. Since earthworms do not overproduce mucus as a defence, the larva could hypothetically hold on its prey and wait for the full dosage of toxin to get into its body—a variation on snail-riding observed in other taxa. The larva’s use of tarsal claws (Fig. 28) to attach itself to the body of the prey as discussed by Majka & MacIvor (2009) supports this hypothesis.

A key to three species of central European lampyrid larvae

The key presented in this work consists of two parts. The first part is a dichotomous key assembled from the most distinct morphological features, enabling quick orientation and determination of the genus and species. The second part is represented by a comparative table that goes into greater detail, addressing interspecific differences in specific body parts (Table 1).

- | | | |
|---|---|-------------------------------|
| 1 | Tergal margins on thorax and abdomen laterally explanate (“trilobite” larva) | <i>Lamprohiza splendidula</i> |
| - | Tergal margins on thorax and abdomen scarcely project | 2 |
| 2 | Thoracic and abdominal tergites dark brown or black, with pairs of light-pigmented spots on posterolateral margins of every segment of thorax and abdomen except IX and X | <i>Lampyrus noctiluca</i> |
| - | Tergites of thorax and abdomen fully dark brown or black; tergites of thorax subdivided by fine light-pigmented parasagittal lines on each side of sagittal line. | <i>Phosphaenus hemipterus</i> |

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TABLE 1. Comparison of larvae of central European Lampyridae.

Character/Species	<i>Lampyris noctiluca</i>	<i>Lamprohiza splendidula</i>	<i>Phosphaenus hemipterus</i>
Body shape			
Habitus	fusiform and robust; tergal margins scarcely project	elongate and fusiform; tergal margins laterally explanate	oblong and slender; tergal margins scarcely project
Cross-section	slightly dorsoventrally flattened	dorsoventrally flattened	Oval
Head capsule			
Epicranial suture colour	dark-coloured or indistinguishable	light-coloured	dark-coloured
Frontal arms shape	U-shaped	V-shaped	U-shaped
Clypeolabrum lateroapically	with 2 distinguishable long setae	no distinguishable setae; light-coloured spot posteriorly, behind each stemma	with 2 distinguishable long setae
Longitudinal length of epicranial plate laterally	larger or same length as 1/2 of width of head capsule	larger than width of head capsule	shorter than 1/2 of width of head capsule
Hypopharynx setation	long	long	short
Antenna			
Second antennomere	no distinct longitudinal cleft	no distinct longitudinal cleft	inner ventrolateral area with distinct longitudinal cleft
Sensorium	smooth surface, closely adhering to antennomere	smooth surface, distinct basal constriction	fine helical ridges from apex to bottom, closely adhering to antennomere
Maxilla			
Maxillary palpus	trimerous	trimerous	bimerous
Terminal maxillary palpomere	irregularly subconical, thick and blunt, with inner-lateral sagittal slot	subconical, narrow and sharp	subconical, with outer-lateral sensorium
Labium			
Terminal palpomere of labial palpus	bearing stout blunt seta covering outer-lateral sagittal slot	bearing short thin setae only	bearing sensorium ventrally
Mandible			
Retinaculum	present, forming distinguishable sharp inner tooth	absent	present, short and blunt
Mandibular channel opening	covered by blunt thick seta	covered by a distinguishable long feather-like or rounded-trapezium hyaline appendage	covered by a small hyaline appendage forming a subtriangular valve with fringing at the distal end
Thorax			
Thoracic tergites	divided by sagittal line into two parts; with distinct pinkish or yellowish spots on posterolateral margins	divided by sagittal line into two parts	divided by sagittal line into two parts, which are then subdivided with another clear line subparallel to sagittal line
Protergum	subtrapezoidal, strongly concave on posterior margin	triangular, convex posteriorly on each half divided by sagittal line, with narrow emargination anteriorly	semicircular, more or less straight posteriorly
Meso- and metatergum	ca. 2 times wider than long	ca. 4 times wider than long	ca. 2 times wider than long

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TABLE 1. (Continued)

Character/Species	<i>Lampyris noctiluca</i>	<i>Lamprohiza splendidula</i>	<i>Phosphaenus hemipterus</i>
Legs			
Pretarsus	claw ventrally bearing 3 short setae	claw ventrally bearing 2 long setae	claw ventrally bearing 3 short setae
Coxa	coxal-trochanteral membrane reaching less than 1/2 of coxal longitudinal length	coxal-trochanteral membrane reaching less than 1/2 of coxal longitudinal length	coxal-trochanteral membrane reaching more than 1/2 of coxal longitudinal length
Abdomen			
Abdominal tergites I–VI	ca. 2 or 3 times wider than long	ca. 4 times wider than long	ca. 2 or 3 times wider than long
Sternum of segment I	sclerotized	not sclerotized	sclerotized
Laterosternites	present on segments I to VII	present on segments I to V	present on segments I to VII
Spiracle colouration	light	dark	light
Specific cuticular processes	granulose protuberances, densely occurring on sclerites and legs	no granulose protuberances nor setae growing from toroidal base	short fibrous setae growing from slightly sunken toroidal base
Photic organ shape and position	conspicuous pair of white spots ventrally on abdominal segment VIII	barely distinguishable paired or single spots ventrolaterally on abdominal segments II and VI, with possible additional spots ventrolaterally on abdominal segments III–V	dull and barely distinguishable pair of spots, ventrally on abdominal segment VIII

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