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An in-depth description of head morphology and mouthparts in larvae of the black soldier fly *Hermetia illucens*

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ABSTRACT

The larvae of the black soldier fly (BSF) *Hermetia illucens* are increasingly being used for waste management purposes given their ability to grow on a wide range of organic decaying materials. Although significant efforts have been spent to improve the mass rearing of BSF larvae on specific substrates and their bioconversion capability, little is known about the biology of this insect, especially with regards to the digestive system.

In this study, we analyzed the morphology of the head and buccal apparatus of *H. illucens* larvae by using optical and scanning electron microscopy, evaluating the different mouthparts and their modifications during larval development.

Our analysis showed that the larval head of *H. illucens* presents similarities to those of campodeiform insect larvae, whereas the mandibular-maxillary complex represents a food intake solution typical of Stratiomyidae that enables BSF larvae to ingest semiliquid food. The mouthparts resemble a "tunnel boring machine", where the hypopharynx separates finer organic particles from coarser and inorganic ones.

1. Introduction

The larvae of the black soldier fly (BSF), *H. illucens* (L.) (Diptera, Stratiomyidae, Hermetiinae), are nowadays increasingly being used for waste management purposes because of their extraordinary ability to feed on a wide variety of organic materials (Wang and Shelomi, 2017; Lalander et al., 2019). In particular, these generalist detritivores can grow and develop on different substrates derived from the agri-food industry, such as fruit and vegetable waste (Jucker et al., 2017), by-products of the transformation chains (Saadoun et al., 2020), rice straw (Manurung et al., 2016), and brewers' spent grains (Chia et al., 2018). In this scenario, a related, interesting aspect is the possibility to bioconvert such low-quality biomasses into animal protein, which can be used to formulate feedstuffs (Wang and Shelomi, 2017). The European Commission Regulation No 2017/893 granted the use of processed animal proteins (PAPs) from BSF for aquaculture, as long as these are derived from larvae reared on substrates devoid of biological and chemical contaminants (European Commission, 2017). Accordingly, efforts have been spent to investigate the influence of different parameters, such as temperature (Gligorescu et al., 2018), humidity (Holmes et al., 2012), light (Heussler et al., 2018), and larval density (Barragan-Fonseca et al., 2018), on the life cycle of BSF. This research helped define the best rearing conditions to grow the larvae on selected, nonhazardous substrates that do not harbor material of ruminant or human origin and are thus authorized for feed production by the European legislative landscape (IPIFF, 2019). However, it is noteworthy that BSF larvae can also reduce other waste substrates such as poultry, dairy and swine manure (Li et al., 2011; Miranda et al., 2019), human feces (Banks et al., 2014), municipal organic solid waste, kitchen waste, fish offal, and

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slaughterhouse waste (St-Hilaire et al., 2007; Diener et al., 2011; Lalander et al., 2019). The use of such materials is not permitted in mass rearing of larvae for feed production, but this evidence renders insect-mediated bioconversion a promising waste treatment technology (Gold et al., 2018, 2020).

Although many studies have investigated the conversion process of waste substrates by BSF larvae, addressing aspects such as the feed conversion ratio and growth rate of the insects (Manurung et al., 2016; Chia et al., 2018), and have evaluated the nutritional composition of *H. illucens* meal and its use to formulate animal feed (Spranghers et al., 2017), little information about the biology of this insect is available, especially regarding the digestive system. Indeed, the digestive system of the larva plays a major role in the bioconversion process, since it is responsible for the digestion of the feeding substrate and nutrient absorption (Caccia et al., 2019); however, it has been completely neglected for a long time and the midgut of BSF was only recently characterized in depth (Bonelli et al., 2019; Bruno et al., 2019a). However, to better understand the extraordinary dietary plasticity of this dipteran and to fully exploit its bioconversion capabilities, knowledge of the larval midgut needs to be complemented by a detailed investigation of the larval mouthparts, which are involved in ingesting the feeding substrate. In fact, BSF larvae can process substrates of different texture, from hard to soft materials, from solid to liquid substrates, as well as with different moisture content, and this ability seems to be supported by a well-developed mandibular-maxillary complex (Kim et al., 2010).

An overview of the literature on the head anatomy of Stratiomyidae larvae confirmed that the preimaginal morphology of *H. illucens* is poorly known and studies of larval mouthparts are scarce so far (Kim et al., 2010; Oliveira et al., 2015; Purkayastha et al., 2017; Barros et al., 2019a). Moreover, recent descriptions, which are mainly based on scanning electron microscopy images that are not suitable for any type of morphofunctional interpretation (Oliveira et al., 2016), are incomplete and/or entomological terms are not well-defined (Kim et al., 2010; Purkayastha et al., 2017; Barros et al., 2019a). In older times the larvae of *H. illucens* were described by a limited number of authors (McFadden, 1967; Woodley, 1989), and some useful details are reported in Gobbi (2012). The intrapuparial development of this species was carefully described by Barros-Cordeiro et al. (2014). The work of Schremmer (1951a, b) on the genera *Hermione* and *Stratiomys*, the very comprehensive article of Vaillant and Delhom (1956), and the book of Courtney et al. (2000) provided a good foundation for current research and this literature was very helpful in assessing nomenclatorial doubts and possible homologies of the mouthparts. Finally, the timeless work of Snodgrass (1928) on the head appendages of insects has been a good reference.

Aim of the present study is to describe the head and mouthpart morphology of *H. illucens* larvae in an attempt to relate it to the better-known Stratiomyidae anatomies and to increase our knowledge of the morphofunctional aspects of this insect.

2. Materials and methods

2.1. Experimental animals

Insects used in this study derived from a colony established in 2015 at the University of Insubria (Varese, Italy). *H. illucens* larvae were reared as described in Pimentel et al. (2017) and Bruno et al. (2019b). Briefly, flies were kept at 27 ± 0.5 °C, under a 12:12-h light:dark photoperiod, 70 ± 5% relative humidity, with water supply and egg traps to promote oviposition. After hatching, larvae were grown on standard diet for Diptera (Hogsette, 1992), composed of 50% wheat bran, 30% corn meal, and 20% alfalfa meal mixed with water at a ratio of 1:1 (dry matter:water). They were maintained at 27 ± 0.5 °C, 70 ± 5% relative humidity, in the dark.

For this study, insects from first to sixth larval instar were examined. Some insects at sixth instar were in the postfeeding phase and the dissection showed that the pupariation process was already underway.

2.2. Sample collection and preparation

Three types of specimens were collected and prepared for morphological analyses:

1) for the analysis at stereomicroscope and optical microscope, larvae were collected from the rearing substrate, washed with water to remove the excess of diet, and then boiled (2 s at 100 °C) and conserved in 70% ethanol until use. Although the whole larva was processed, only the insect head was observed under the microscope;
2) for SEM analysis of the larvae, insects were fixed and processed after boiling (see point 1) as described in the section “Scanning electron microscopy (SEM)”. In this case, too, only the head was analyzed;
3) histological sections were obtained by embedding the larval heads in polyfreeze cryostat embedding medium and freezing them in liquid nitrogen. Samples were stored at −80 °C until use. Subsequently, transverse and sagittal sections (40-μm-thick) were obtained with a CM 1850 cryostat (Leica, Nussloch, Germany) and slides were stored at −20 °C until use. Sections on slides were fixed and processed for SEM as described in the section “Scanning electron microscopy (SEM)”.

2.3. Stereomicroscopy and optical microscopy

Larval heads were dissected and partly cleaned in 1% KOH (w/v) for 24-48 h to highlight finer chitinous structures, then observed with a Zeiss Stereomicroscope Stemi SV11 PlanApo (Zeiss, Oberkochen, Germany) equipped with an 8-MP videocamera (Optikam PRO8 Digital Camera, model C-P8, Optika, Bergamo, Italy). Images were acquired with the Optika Proview software. Further photographs were obtained with a Zeiss Axioskop (Zeiss), using differential interference contrast (Nomarski optic) and a Canon PowerShot G16 digital camera (Canon, Tokyo, Japan).

2.4. Scanning electron microscopy (SEM)

For SEM analyses, all the samples were fixed with 4% glutaraldehyde in 0.1 M Na-cacodylate buffer (pH 7.4) for 1 h at room temperature. After 5 washes in Na-cacodylate buffer, they were postfixed in a solution of 1% osmium tetroxide and 1.25% potassium ferrocyanide for 1 h in the dark. After 5 washes in Na-cacodylate buffer, samples were dehydrated in an increasing series of ethanol and washed twice (8 min each) with hexamethyldisilazane, promoting the drying of tissues. Dried specimens were mounted on stubs, gold-coated with a Sputter K250 coater, and then observed with a SEM-FEG XL-30 microscope (Philips, Amsterdam, The Netherlands).

3. Results

The general head anatomy and the mouthparts in *H. illucens* are conserved throughout the entire larval development. However, an increase in their size and numbers of fans and spiny rows can be observed. The following description mainly refers to last instar larvae unless otherwise specified.

3.1. Head morphology

The head is prognathe, conical in shape, with the transverse section more or less rounded, more flattened on its ventral side, dark reddish-brown in color and the membranous parts yellow (Fig. 1). Dorsally, the fronto-clypeal apotome extends from the labrum to the occipital margin, and frontal sutures run parallel (Fig. 1C). The parietale is characterized by two very pronounced genal lobes (Fig. 1C, D) that protect the mandibular-maxillary apparatus, with an antennal pad at the level of the clypeolabral suture. An "ocular bulge" is found at middle head length (Fig. 1C), some rounded corneae are normally present, and pigmented stemmata spots are just visible under the thick chitinous wall. The labrum is conical and very robust (Fig. 1A, C), with a short protuberance at its tip (Fig. 2F), where some sensilla are placed. Two dorsolateral furrows cover the entire length, with a pair of setae at the base and a second pair at the anterior end (Fig. 1A). The ventral head side is characterized by a large oral cavity that occupies the front third of the head and is laterally defined by the genal border and at the rear by the ventral plate (Fig. 1B, D). The border of the oral cavity bears a dense fringe of spines and two posterior semilunar membranous lobes (Fig. 1D) that reach the prementum. The largest part of the cavity lodges the mandible-maxillary apparatus, with a curved epipharynx in the middle and a membranous prementum at the rear, that is entirely covered by soft spines (Figs. 1B, D and 2B). At the center the ventral border of the hypopharynx can be clearly recognized. The ventral plate is actually composed of parts usually found on the head of campodeiform insect larvae: a triangular mentum and a gula (or postmentum according to other authors). No openings or ventral exhalant orifices are present, as instead documented for other Stratiomyidae larvae (Schremmer, 1951a; Vaillant and Delhom, 1956; Courtney et al., 2000).

3.2. Antennae

The antennae are biarticulate and very short in the aged instars (Fig. 1A, B), proportionally longer in the younger larvae (Fig. 2A). When the head is protruded into the feeding substrate, they are protected from damage by a large and robust antennal pad.

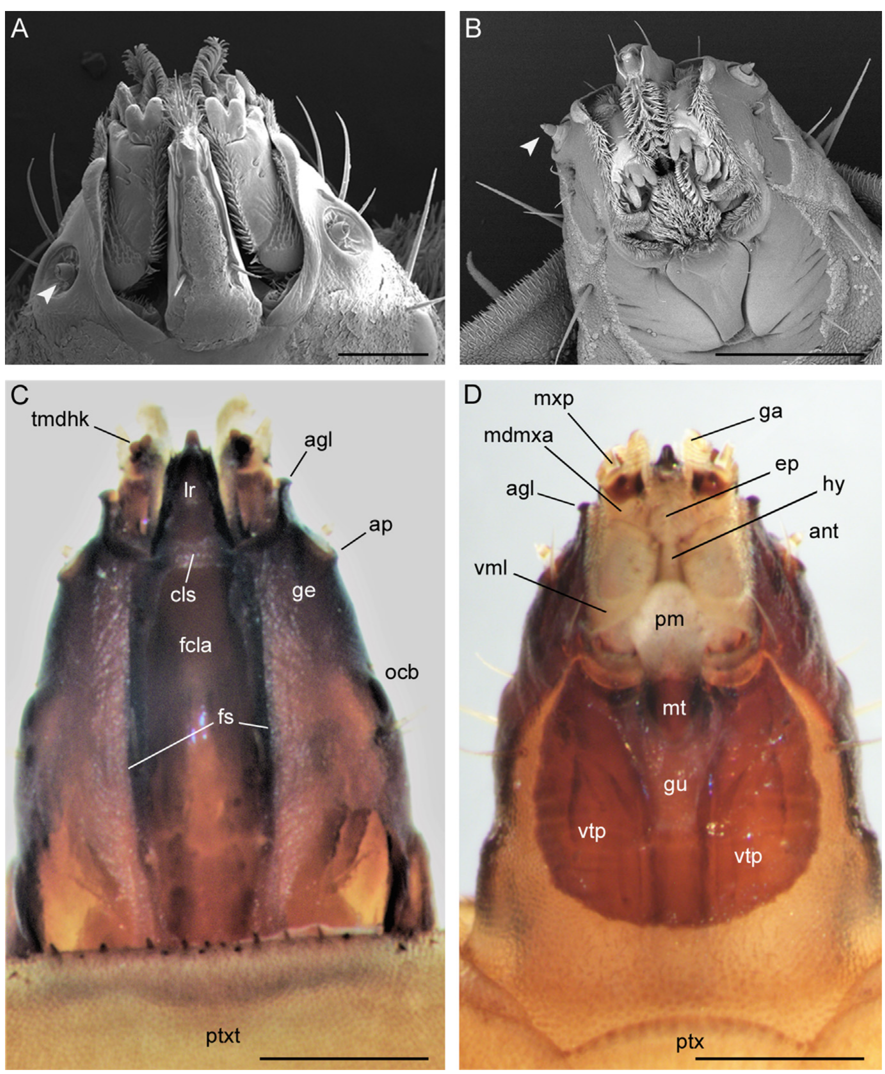

Fig. 1. SEM and stereomicroscope vision of *H. illucens* head in last instar larvae. A: dorsal vision of mouthparts. B: ventral aspect of mouthparts. C: head and prothorax edge, dorsal. D: head and prothorax edge, ventral. Abbreviations: agl – anterior genal lobe, ant – antenna, ap – antennal pad, cls – clypeolabral suture, ep – epipharynx, fcla – frontoclypeal apotome, fs – frontal suture, ga – galea, ge – gena, gu – gula, hy – hypopharynx, lr – labrum, mdmxa – mandibular-maxillary apparatus, mt – mentum, mxp – maxillary palpus, ocb – ocular bulge, pm – prementum, ptx – prothorax, ptxt – prothorax tergum, tmdhk – three-toothed mandibular hook, vml – ventral membranous lobe, vtp – ventral plate of the head. Arrowhead: antenna. Scale bars: 200 μm (A), 500 μm (B-D).

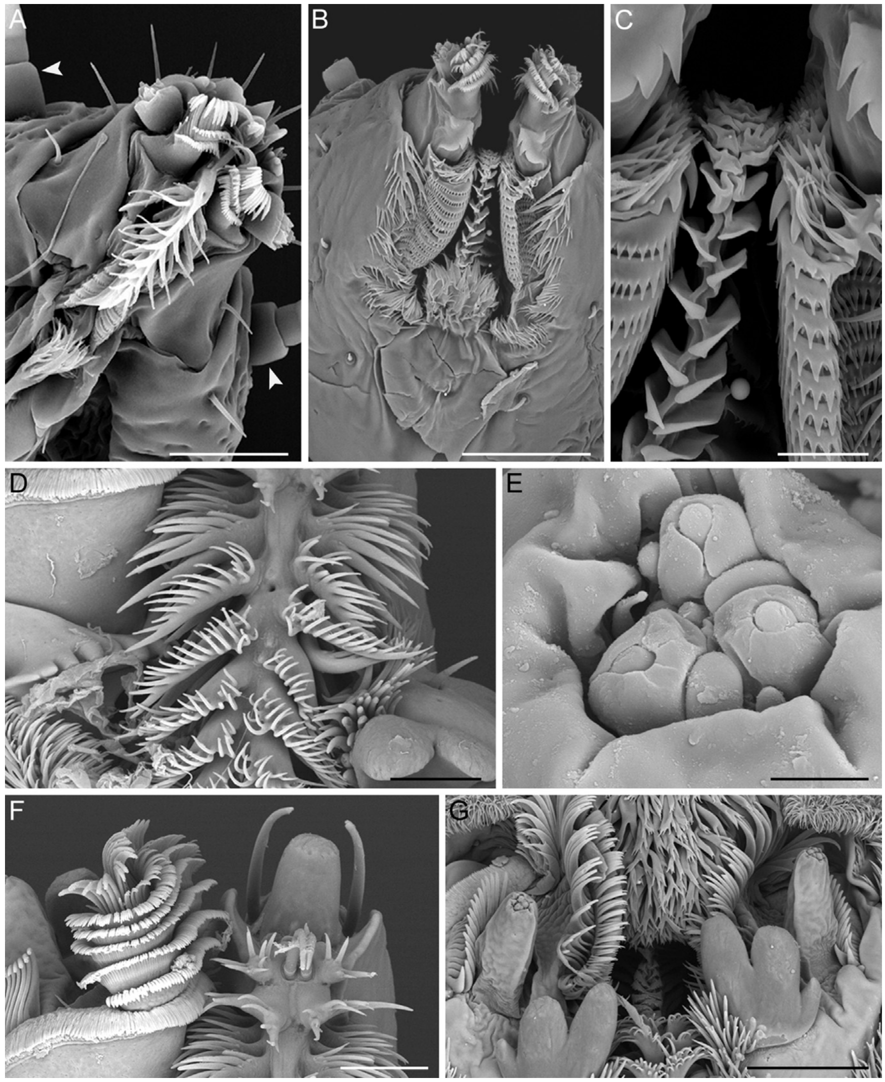

Fig. 2. SEM details of *H. illucens* mouthparts. A: first instar larva, ventral head side, with epipharynx, galea with three spiny fans, the proportionally longer antenna and maxillary palpi. B: second instar larva, mouthparts. The galea shows now four spiny fans, the grinding maxillar rasp shows already about 15 spiny rows, the lacinia bears one rounded and two sharp teeth. C: details of the maxillary rasp, of lacinia and of the median hypopharynx of second instar larva (strongly dehydrated). D: sixth instar larva, detail of the epipharynx with spiny rows and the sensorial hole. E: sixth instar larva, apex of the maxillary palpus with sensilla. F: sixth instar larva, galea with seven spiny fans, the labrum apex and the basal spiny protuberances of the epipharynx. G: sixth instar larva, with the three-toothed mandibular hooks, showing the relationships between mouthparts when the mandibular-maxillary apparatus is strongly adducted. Arrowhead: antenna. Scale bars: 20 μm (A), 50 μm (B, D, F), 10 μm (C), 5 μm (E), 100 μm (G).

3.3. Labrum

The labrum is a strong keel-shaped structure that protects the mandibular-maxillary apparatus and opens the way into the substrate. It is fused at its base with the genae and connected to the fronto-clypeal apotome through the clypeo-labral suture (Fig. 3C). On its ventral side a prevailingly membranous structure, the epipharynx, is grafted, rich in downwards-directed spines and with a sensory hole on its front border (Fig. 2A, D). The epipharynx shows two chitinous arched reinforcements (Fig. 4C) and covers the anterior border of hypopharynx with no contact.

3.4. Mandibular-maxillary apparatus

The mandibular-maxillary apparatus represents the fusion of the mandible and the maxilla and mainly moves in a vertical plane. At rest, the mandibular part of the structure is easy to identify from above, where it is seen as a double sclerite that bears a three-toothed hook at its front edge (Figs. 1 and 3A). When the apparatus is adducted, the whole appendage turns downwards and the hooks likely act as excavating organs. The lower part of the apparatus is composed of a large, swollen membranous cylinder ("molar area" that derives from the maxillary stipes and is covered by a "rasp" (Fig. 2B, C)), that grinds the food into smaller particles. On the inner lower side, the stipes ends in a six-toothed lacinia, which is moved by the long thin apodeme of the maxillary adductor and complements the rasp. The distal end of the stipes bears a galea equipped with seven fans of spines in the older stages, but with only three in the first instar (Figs. 2C, F and 3A). The maxillary palp is placed on the outer side of the galea. Its single article is equipped by several sensilla (Fig. 2E, G). The palp is protected by a lateral sclerite and a row of spines. The apparatus

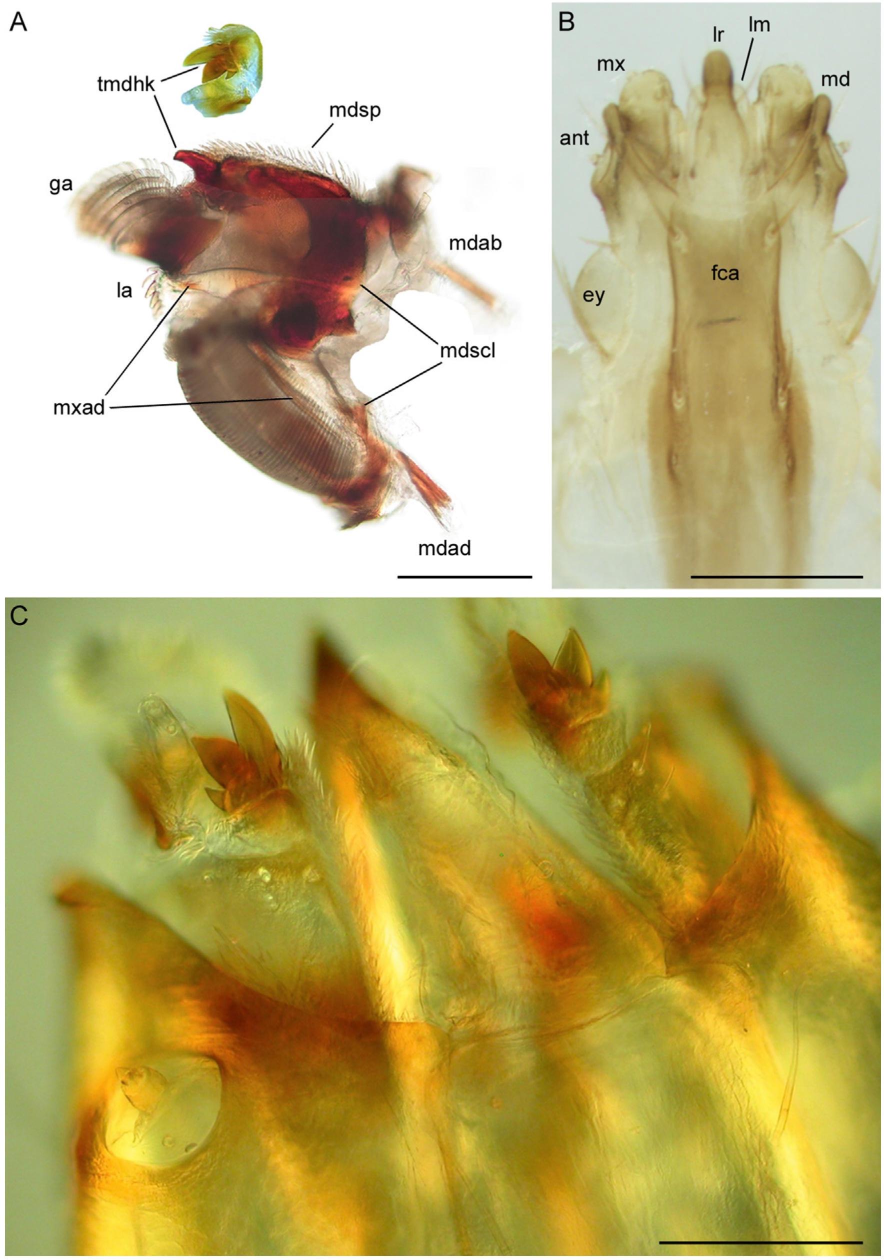

Fig. 3. Details of the mandibular-maxillary apparatus and puparial head of *H. illucens*. A: mandibular-maxillary apparatus, inner side of the right mouthpart (Axioskop). B: puparial chitinous coat extracted from the sixth instar larva, showing all the characteristics of the puparial head. C: head of the sixth instar larva, dorsal overview, KOH treatment (Axioskop, Nomarski optic). Abbreviations: ant – antenna, ey – puparial eye bulge, fca – fronto-clypeal apotome, ga – galea, la – the six-toothed lacinia, lm – labium, lr – labrum, md – mandible, mdab – apodeme of the abductor muscle of the mandibulo-maxillary complex, mdad – apodeme of the adductor muscle of the md-mx-complex, mdscl – mandibular sclerites of the md-mx-complex, mdsp – mandibular spiny row, mx – maxilla, mxad – apodeme of the maxillary adductor, connected to the lacinia, tmdhk – profile of three-toothed mandibular hook, also in dorsal view as in the Figure below. Scale bars: 200 μm (A, C), 500 μm (B).

articulates dorsally on the end of the anterior tentorial arm (abductor muscle involved), ventrally on the parietale as is common in prognate campodeiform larvae.

3.5. Labium

The labium forms the ventral part of the oral cavity and maintains a part of the typical structures found in larvae with a well-developed head, but the labial palpi are completely missing. A short triangular mentum articulates with a soft and spiny prementum (palatum, according to McFadden, 1967). The prementum is sustained by an internal pharyngo-labial sclerite that forms part of the mouth floor and reaches the mentum and the gula ventrally (Figs. 4B and 5).

3.6. Hypopharynx

The most hidden structure of the head is the hypopharynx, a sort of partially membranous lobe, sustained by a sclerified suspensorium that articulates with the pharyngo-labial sclerite and prolongs the mouth floor anteriorly. The same structure is called labium by Vaillant and Delhom (1956) and other authors (e.g.,

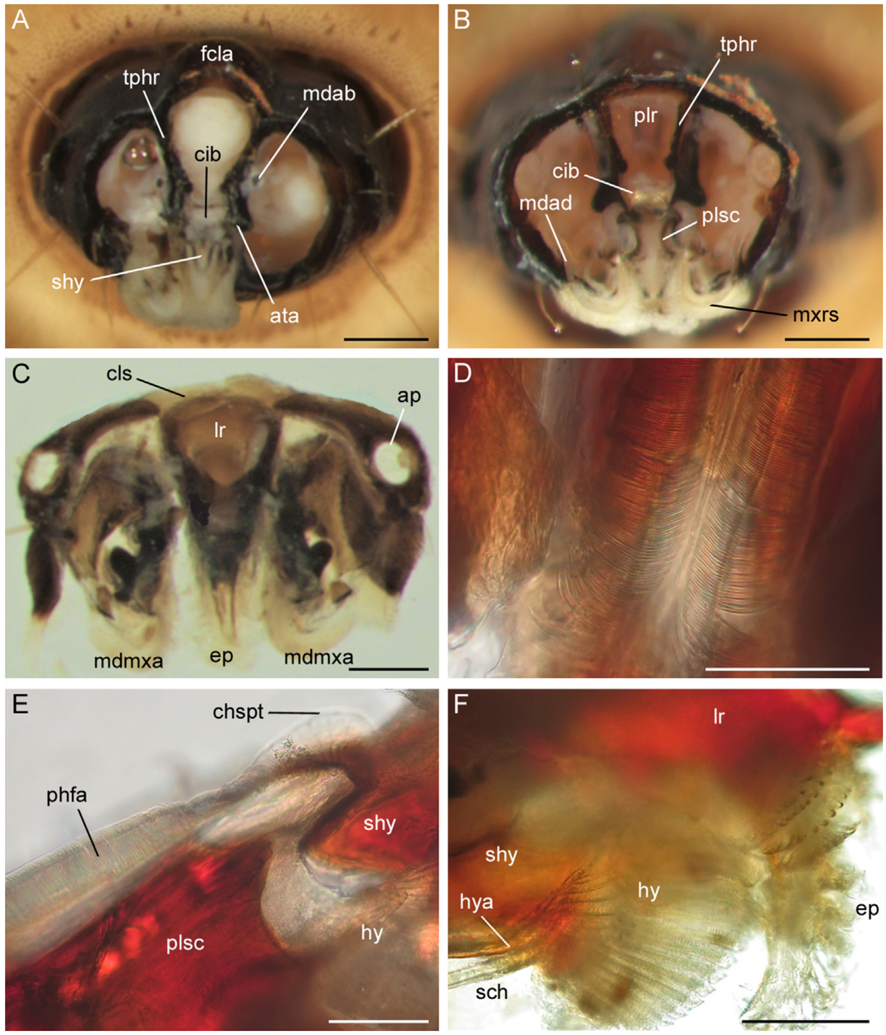

Fig. 4. Optic and stereomicroscope details of *H. illucens* head structures in last instar larvae. A: oblique transversal section of the head including the hypopharynx sclerites. Antennal pads and left mandibulo-maxillary apparatus cut out or removed. B: vertical section of the head behind the antennal pads, at the level of the fronto-clypeal suture. C: anterior part of the head cut of Figure B, after moderate KOH treatment, showing the epipharynx and the vertical lodgement of the mandibulo-maxillary apparatus. D: detail of the filtering apparatus of the pharynx (Axioskop). E: pharynx and hypopharynx at the cibarium opening, relationships between the pharynx filtering apparatus and the hypopharynx suspensorium (Axioskop). E: hypopharynx and epipharynx with salivary channel evidenced (Axioskop). Abbreviations: ap – antennal pad, ata – anterior tentorium arm, chspt – chitinous sept of the cibarium opening, cib – cibarium, cls – clypeolabral suture; ep – epipharynx, fcla – frontoclypeal apotome, hy – hypopharynx, hya – hypopharynx apodeme, lr – labrum, mdab – apodeme of the abductor muscle of the mandibulo-maxillary complex, mdad – apodeme of the adductor muscle of the md-mx-complex, mdmxa – mandibular-maxillary apparatus, mxrs – maxillary rasp section, phfa – pharyngeal filtering apparatus, plr – pupae labrum, plsc – pharyngo-labial sclerite, sch – salivary channel, shy – suspensorium of hypopharynx, tphr – tentorial phragma. Scale bars: 200 μm (A-C, F), 100 μm (D, E).

Cook, 1949), who believe that a hypopharynx is lacking in larval Diptera. In our opinion, this structure corresponds to the hypopharynx as described by Snodgrass (1928) and Courtney et al. (2000). The position of the salivary channel, which opens here, corroborates this interpretation. The hypopharynx is a small, vertical lobe that probably filters food particles collected by the maxillary stipes and separates the smaller and lighter particles from coarser and heavier ones (Figs. 1D, 2B, C, 4F and 5). A chitinous sept (Fig. 4E) that surrounds the suspensorium articulation probably helps in the same manner and deviates the heavier particles to the bottom of the oral cavity where they are expelled by prementum movements.

3.7. Inner anatomy of the head

The head of *H. illucens* is extremely robust and its internal chitinous armature, the tentorium, also reflects a heavy-duty adaptation (Figs. 4A–C and 6). The dorsal tentorial arms (tentorial phragma, according to Schremmer, 1951a) are thick and fused with the fronto-clypeal apotome along the frontal suture (Figs. 4A, B and 6). The anterior arms are prolonged up to the level of hypopharynx articulation, and give support to the upper (abductory) articulation of the mandibular-maxillary complex. The ventral arms of tentorium ("Strebepfeiler" according to Schremmer, 1951a) are small and fused with the gular ridges at the mentum level. The posterior arms are very long, as in Stratiomyinae, and partly fused with the pharyngeal sclerites. At the end of these arms is the "grinding mill", an organ that is thought to reduce the ingested food particles to very small grains. Along the pharynx a distinct filtering apparatus is observed (Figs. 4D and 6). It is composed of two longitudinal ridges of very thin chitinous lamellae (Figs. 4D and 5F). The pharyngeal filter does not correspond to any draining channel for the expulsion of surplus water, as observed in Stratiomyinae (Vaillant and Delhom, 1956; Courtney et al., 2000). A large metacephalic plate connects to the dorsal occipital edge of the head capsule and gives support to the head-retracting muscles (Fig. 6).

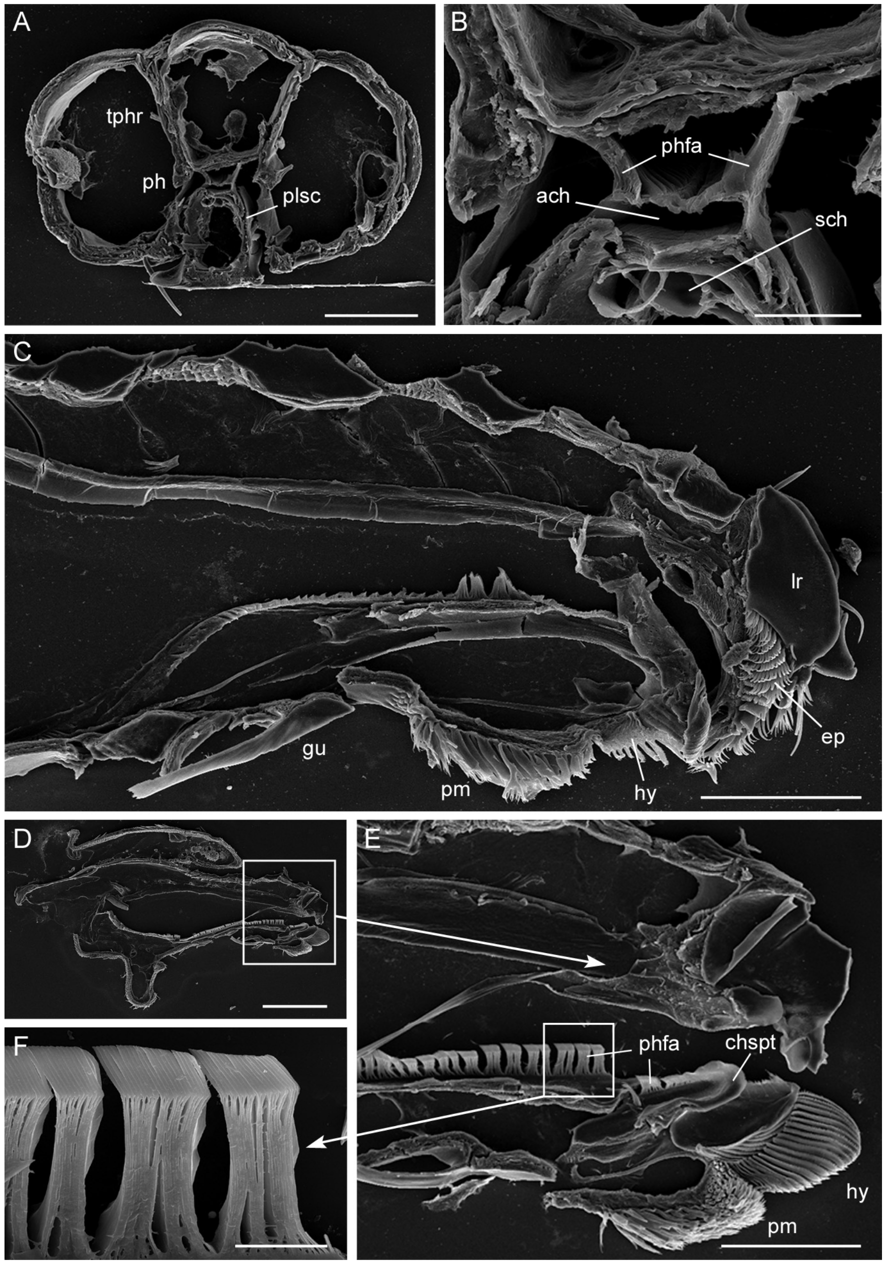

Fig. 5. SEM micrographs showing the inner structures of *H. illucens* head in last instar larvae. A: transverse section of the head at the level of the ventral tentorium arm. B: enlargement of the pharynx of Figure A, with filtering apparatus and salivary channel. C: sagittal section of the head showing the epipharynx and part of hypopharynx and prementum. D: sagittal section of the head with hypopharynx, prementum and the chitinous sept of the mouth opening that continues inside joining the pharyngeal filtering apparatus. E: details of the same mouthparts. F: detail of the lamellae of the filtering apparatus. Abbreviations: ach – alimentary channel, chspt – chitinous sept of the mouth opening, ep – epipharynx, gu – gula, hy – hypopharynx, lr – labrum, ph – pharynx, phfa – pharyngeal filtering apparatus, plsc – pharyngolabial sclerite, pm – prementum, sch – salivary channel, tphr – tentorial phragma. Scale bars: 200 µm (A, C, E, F), 50 µm (B), 500 µm (D).

3.8. Other inner structures of the head in postfeeding larva

After KOH treatment, the head of the postfeeding larva already shows the puparium chitinous envelope, which is easy to extract from the last larval "skin". It already shows the form of the puparial head (Fig. 3B) and represents a curious, oversimplified head structure in which the mandible rudiments are found in their original position, separated from the maxillae. The eyes already show the form of a compound insect eye and the labium is almost as long as the maxillae (Fig. 3B).

4. Discussion

The larvae of the black soldier fly are well known for their ability to grow on animal and human carcasses and have thus been largely used in forensic entomology (Pujol-Luz et al., 2008; Barros et al., 2019b). However, the increasing production of organic waste worldwide, with consequent problems regarding their disposal (Laufenberg et al., 2003), has focused attention on this insect species as a potential solution to that problem. Moreover, BSF larvae fed on waste material can be used to produce feed for fish, poultry,

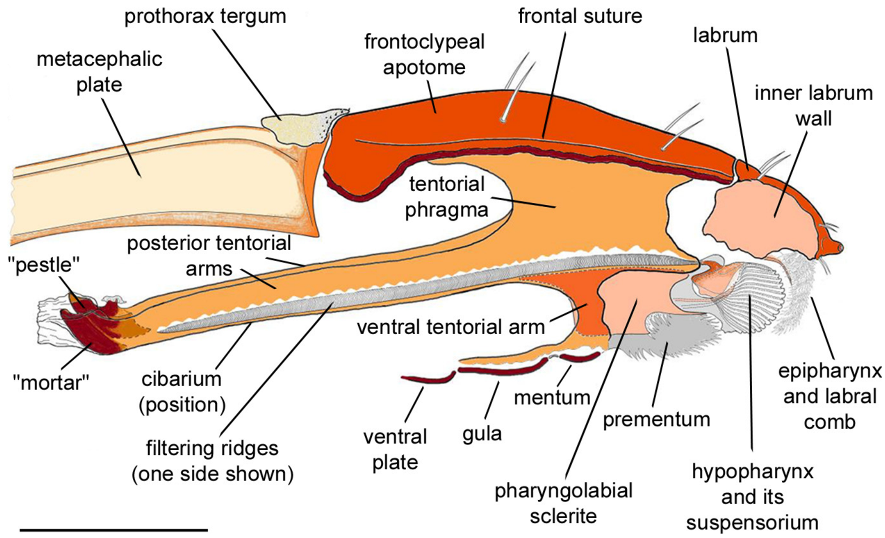

Fig. 6. Schematic representation of *H. illucens* head. Sagittal section of the head of last instar larvae is represented. Lateral head walls and mandibular-maxillary apparatus have been removed. Scale bar: 500 μm.

and livestock. Thus insect-mediated bioconversion of waste biomasses represents a sustainable application both from an environmental and economical point of view and could promote a circular economy (Lohri et al., 2017; Cappellozza et al., 2019). The extraordinary capability of BSF larvae to grow and develop on very different organic substrates is supported by a complex alimentary canal (Bonelli et al., 2019) as well as by functional mouthparts that are necessary for food processing and ingestion, as suggested by previous studies (Kim et al., 2010; Barros et al., 2019a). To gain insight into the latter aspect, we decided to combine optical and SEM analysis to obtain a general view of the buccal apparatus during larval development and also to analyze the mouthparts.

As in other Orthorraphous Dipterans, *H. illucens* conserves several elements of the primitive prognate caput of campodeiform insect larvae. This is particularly evident in the ventral plate, in the position of the mentum and the prementum, and in the shape of the maxillary part of the mandibulo-maxillary complex, which shows a distinct, soft cardo and a robust stipes. In addition, the position of the hypopharynx corresponds to the topography of the general head anatomy of insects (Snodgrass, 1928) and, thus, we do not think it belongs to the labium (as in Vaillant and Delhom, 1956 or Cook, 1949). Moreover, the dissection of postfeeding sixth instar larvae revealed that the morphology of the future pupal head represents a sort of compromise between the larval head and the adult one, clearly given by the shape of the compound eyes. In this sort of rudimental head, the mandibles and the maxillae return to two separate, nonfunctional remnants that attest to the primitive presence of these original mouthparts before they are reorganized into the mandibular-maxillary complex. According to Barros-Cordeiro et al. (2014), the development continues inside the puparium with the three stages of the cryptocephalic pupa, the pharate adult, and the imago.

We also provide a detailed description of the functional morphology of the mouth apparatus of *H. illucens*. The head walls are extremely robust and the conical shape makes it easy to penetrate the food substrate thanks to the pressure exerted by the entire larval body. The mouthparts resemble a sort of tunnel boring machine, like that used in modern times, but instead of a "whole section" disc grinder, the mouthparts move on a vertical plane, that of the mandibular-maxillary apparatus. According to the morphological evidence presented herein, we hypothesize that these two appendages rotate from a horizontal rest position onwards and downwards until the mandibular hooks touch and trespass the ventral membranous lobes, describing an angle of about 100/110°. In this way the hooks grasp more or less coarse particles of the semiliquid food and the finer rasp of the stipes grinds them into smaller parts, with the help of the lacinial teeth. The food is probably driven towards the mouth, and the hypopharynx and the chitinous septum above separate the finer particles from the coarse and inorganic particles, the last ones being expelled ventrally, probably also by contractions of the hypopharynx and the prementum. The "good" particles enter the pharynx and reach the "grinding mill", where they undergo the last mechanical treatment. The advancement into the food substrate is likely supported by the sensorial equipment of the epipharyngeal (labral) comb of sensorial appendages, which surround the hypopharynx anteriorly. The lack of exhalant orifices on the ventral part of the head, as found in *Stratiomys* or *Hermione* (Schremmer, 1951a, 1951b) is in agreement with the ingestion of semiliquid food in a terrestrial environment. In fact, the mouthpart morphology is very similar to that of other terrestrial Stratiomyidae, as described by several authors (Bischoff, 1924; Cook, 1949; Schremmer, 1951a, 1951b; McFadden, 1967; Rozkošny, 1982). The examined species have been described as detritivores or scavengers; McFadden (1967) speaks of a "micropantophagous" diet, while Rozkošny and Kovac (1998) found a similar mandibular-maxillary complex in the "sweeping apparatus" of the bamboo sprout-inhabiting larvae of *Ptecticus*, a Sargine Stratiomyid. Moreover, the mouthparts of the saproxylic *Pegadomyia pruinosa*, a Pachygastrine Stratiomyid (Bučánková et al., 2009), are also similar to that of *H. illucens*, a fact that corroborates the hypothesis of a multifunctional apparatus that easily adapts to ingesting semiliquid food derived from any possible decaying organic matter. The exact function of the epipharynx and the hypopharynx are still somewhat unclear and *in vivo* video recordings could perhaps give more insights into the exact role of all the mouthparts as a whole.

Author contributions

G.T. and P.B. designed the experiments; D.B., T.B., M.R., M.C., and A.G. performed the experiments; D.B., P.B., and G.T. wrote the manuscript; all authors reviewed the manuscript.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

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