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The immatures of lauxaniid flies (Diptera: Lauxaniidae) and their taxonomical implications

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Abstract

The immature stages of insects can provide valuable data both for taxonomy and phylogeny, but they are well known only for negligible proportion of the described species. Here we describe lauxaniid immatures for 17 species that were reared under laboratory conditions and subjected to morphological investigation. Following species were included in our study: *Cnemacantha muscaria*, *Homoneura biumbrata*, *Homoneura limnea*, *Minettia austriaca*, *Minettia fasciata, Minettia flaviventris*, *Minettia loewi*, *Minettia plumicornis*, *Peplomyza litura*, *Poecilolycia vittata*, *Pseudolyciella pallidiventris*, *Sapromyza apicalis*, *Sapromyza hyalinata*, *Sapromyza intonsa*, *Sapromyza sexpunctata*, *Sapromyzosoma quadripunctata*, *Sapromyzosoma quadricincta*. SEM images of the eggs are provided along with the illustrations of the cephaloskeleton and brief description of all three larval instars. The cephaloskeleton, as well as external morphology suggest that subgenus *Minettia* s. str. may not be monophyletic. Species *Sapromyza sexpunctata* and *Sapromyzosoma* spp., *Pseudolyciella pallidiventris* and *Poecilolycia. vittata* are probably closely related. *Sapromyza apicalis*, *S. hyalinata* and possibly also *S. intonsa* form a separate clade from the previous group. These results clearly support the long-standing suspicion, that genus *Sapromyza* is not monophyletic. *Sapromyza sexpunctata* should be considered a separate genus related to *Sapromyzosoma.*

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The spines on dorsal surface of labial lobe suggest relationships between *Peplomyza* and *Meiosimyza* species. Affinities of *Cnemacantha muscaria* remain uncertain. However, the extended Malpighian tubules suggest relationship to *Homoneura* or *Minettia.*

Key words: Diptera, Lauxaniidae, egg, larva, morphology, cephaloskeleton, SEM

Introduction

An accurate taxonomy is a precondition for testing hypotheses about past history events, reconstructing ancestral character states, estimating the timing of historical events etc. Molecular characters have many advantages and the number of studies using molecular characters for estimation of phylogeny is growing rapidly (Pagel 1999). The number of morphology based studies is growing as well. However, only minor publications use also immature morphology, praxis advocated by Hennig (Meier & Lim 2009). Recent papers, e.g. Beutel *et al.* (2010), demonstrate that morphological characters represent a vital source of data in insect systematics. Except for the imagines, the holometabolan insects offer an extra source of phylogenetic data: the immatures (Meier & Lim, 2009). The pupal stage allowed the larval and mature stages to evolve independently. This line of research in Diptera was started by Willi Hennig and his "Larvenformen der Dipteren" (Hennig, 1948, 1950, 1952). Several recent studies have shown, that the immatures of holometabolous insects bear considerable amount of information (reviewed by Meier & Lim 2009), e.g. in the phylogenetic study of the butterfly family Nymphalidae (Freitas & Brown 2004) the adults were shown to be the main source of conflict. The immatures, by the definition, cannot be subject to direct sexual selection, which can be the cause of rapid divergence among closely related species (e.g. Arnquist 1998, Kopp & True 2002, Puniamoorthy *et al.* 2010). Consequently, the immatures are more suitable to reveal deeper nodes in the phylogeny (Meier & Lim 2009).

Within the Cyclorrhapha, the larval stages are generally poorly known. The main obstacle is obtaining identified immature stages which usually require rearing. Such rearing efforts have been made for relatively few taxa either because of an interest by specialists (Berg & Knutson, 1978; Meier, 1996, Rotheray & Gilbert, 1999) or because the species were of medical importance or forensic importance. Not even the third instar of *Drosophila melanogaster* had been properly documented until recently (Wipfler *et al.* 2013). Within the fly families where the immatures are known, the information refers often only to the third instar (Teskey 1981). However, in several recent papers Szpila & Pape (2005, 2007, 2008) demonstrated that the first instar may dramatically differ from the later instars, as well as between species.

The family Lauxaniidae represents a species-rich family of acalyptrate flies (up to 2000 valid species, Gaimari in verb). The family is currently divided into three subfamilies (Lauxaniinae, Homoneurinae and Eurychoromyiinae, Gaimari & Silva 2010a). Eurychoromyiinae are restricted to the Neotropics (Gaimari & Silva 2010b), while the next two subfamilies are cosmopolitan. The European fauna is relatively well known, in spite of that new species are described quite commonly. For example Merz (2001, 2003, 2007a, 2007b) described six new European species within years 2001–2007, what demonstrates, how understudied this group of flies is. Systematics of the family is unsatisfactory as well. Subfamily Lauxaniinae is supposed not to be monophyletic, as well as some large genera, such as *Sapromyza* (Shewell 1987, Papp & Shatalkin 1998).

The lauxaniid flies are almost omnipresent in woodland and mesic habitats. Summary of their biology and immature morphology is given by Gaimari & Silva (2010a) and Papp & Shatalkin (1998), original papers were published by Meijere (1909), Hennig (1952), Miller & Foote (1975, 1976), Miller (1977a, 1977b, 1977c), Sasakawa & Ikeuchi (1982, 1983) and Semelbauer & Kozánek (2011, 2012, 2013). Generally, the larvae are phytosaprophagous and are easily reared in laboratory conditions on decaying deciduous tree leaves. The aim of this paper is to provide thorough descriptions of immatures for relatively broad scale of European lauxaniid genera.

Material and methods

Adult flies were obtained by sweeping the vegetation at several localities in western and northern Slovakia. The key of Shatalkin (2000) and its English translation (Schacht *et al.* 2004) were used for determination. Nomenclature follows Shatalkin (2000). Both males and females were kept in plastic jars filled with moss

(*Hypnum* sp.) to maintain suitable humidity. A mixture of honey and yeasts was used as an adult food source (Miller 1977b, 1977c). Eggs were laid on the moss singly by females. Eggs were transferred to glass dishes and kept at a temperature of 10±2°C. Rotting leaves of wild cherry (*Cerasus avium*) were added to glass dishes as a larval food source immediately after the first larvae appeared. Living larvae were washed in a stream of liquid water from a vaporizer except for the tiny first instars. Larvae were put in water and slowly heated until the temperature reached 45°C, consequently retaining an exposed pseudocephalon and a pair of extendable ambulatory lobes. Eggs and larval instars were stored in 80% ethanol. Preparation of larvae for SEM involved dehydration through 80, 90, and 99.5% ethanol series and soaking in hexamethyldisilazane (HMDS) (Brown 1993). For eggs, the ethanol series was replaced by soaking directly in 99.5% ethanol and then in HMDS. Larvae and eggs were coated with gold, gold-palladium mixture or platinum. SEM pictures were taken with a Quanta 3D 200i. Cephaloskeletons were photographed by Nikon Coolpix 990 digital camera mounted on a Nikon Eclipse E600 microscope under Nomarski contrast. Cephaloskeletons were extracted mechanically; for the first instar we used the whole anterior half of the body. Soaking in 4% KOH removed soft tissues. The line drawings were prepared directly from digital photographs in Adobe Photoshop, version 6.0.1 CE. Morphometrical data were taken in the program Micrometrics SE Premium—318-318004BF in combination with a Micrometrics camera mounted on a Zeiss binocular microscope Stemi 2000-C. Terminology follows Courtney *et al.* (2000) and Miller and Foote (1976).

One of the characters mentioned—the modification of the internal surface of the labial lobe—can be seldom spotted on the SEM images. This information was partly extracted from the photographs of the cephaloskeletons.

Results

General description of the lauxaniid immatures (external morphology)

Egg. Always white, oval to elongated, more or less carinated from the lateral view; usually with strong ridges and weak ribs. The ventral side more convex compared to the dorsal side. Micropylar pole with depression surrounded by more or less developed collar. Posterior pole shielded by tubercle.

Larva. Body cylindrical to moderately dorsoventrally flattened, tapering both on the anterior and posterior ends. The integument translucent. All instars amphipneustic, but in the first instar the anterior spiracles present as a small pore only. The body differentiated into pseudocephalon, three thoracic segments, seven abdominal segments and the anal division.

Pseudocephalon bilobed, bearing antenna, maxillary palpus, cirri, ventral organ and labial lobe. The antenna simple, dome shaped. The maxillary palpus consists of a cluster of several sensilla; sensilla arrangement stable across instars and species (four sensilla coeloconica, four sensilla basiconica and two accessory sensilla). The cirri differentiated into two types. The scraping cirri stand upright, form 5–7 transverse rows and occupy the anterior half of the facial mask. The peristomal cirri occupy posterior half of facial mask (closer to mouth opening) and bound to the surface of facial mask. The labial lobe with paired labial sensila.

Thoracic segments simple, cylindrical. The first thoracic segment with anteroventral collar; the collar covered with comb spines aligned in diagonal direction. The thoracic segments usually bear anteriorly comb spines both on dorsal and ventral side. Keilin's organ present.

Abdominal segments wrinkled intricately. Dorsally, the anterior creeping welt spinous, following welts smooth or hairy with four (probably sensoric) tubercules. The lateral parts of abdominal segments with three to four paired processes and lateral welt. Ventrally, abdominal segments with anterior spinous and posterior smooth creeping welt.

Anal division with one ventral creeping welt only; typically bears 4 pairs of processes: two lateral, one dorsal and one tiny ventral pair. Pair of extendable ambulatory lobes surrounds the anus. The posterior spiracles similar across all instars, placed on closely adjacent cylindrical sprouts. The spiracular plate of the posterior spiracle with three spiracular slits placed on ovoid elevations and with four peristigmatic tufts (first instar with two slits and three tufts).

First instar. The scraping cirri aligned in 4–5 transverse rows. The first row chitinized (amber-coloured), very compact and loosely attaching to the mouth-hooks; sometimes indicated with one more row posterior to the "first"

row. Remaining scraping cirri soft, slender and apically pointed. At the midline of facial mask two longitudinal rows of scraping cirri present. Lobe-like ventral organ lying on the first row of scraping cirri; typically equipped by two digitiform projections and a large central sensila. The peristomal cirri simple, filiform to triangular. The integument of body segments smooth except of anterodorsal parts of thoracic segments and creeping welts.

Second instar. The scraping cirri organized in six rows; tips with sclerotised back-curved papillae. Ventral organ cylindrical, located in the third row of scraping cirri. The peristomal cirri with soft marginal hairs. The body segments can be covered by spines and hairs in various pattern. The anterior spiracles simple, ovate, with tiny holes at periphery.

Third instar. The organisation of facial mask as in the second instar, but scraping cirri in seven rows. The spines and hairs usually more complex than in the second instar. The anterior spiracles usually fan-shaped, with several papillae.

General description of the cephaloskeleton

First instar. The cephaloskeleton delicate, distinct from the second and third instar in several aspects. The mouth hooks with two distinct parts; the distal part spatulate with row of several teeth, always sclerotised; the proximal part stalked, hyaline or sclerotised; the dental sclerites seldom developed. The intermediate sclerite and parastomal bars basally coalescing; the parastomal bars strong, the intermediate sclerite week. The ventral bridge arises approximately at the point of the coalescing of the intermediate sclerite and parastomal bars. The epistomal sclerite convex, semilunar, with lateral rounded windows; anteriorly differentiated labrum. The ligulate sclerites present as simple small plates. The subhypostomal sclerites joining to the intermediate sclerite. Rami absent. The dorsal cornua basally sclerotised, distal part hyaline. The ventral cornua broader than dorsal ones, with indicated dorsal apodeme and concave distal third. The cibarium with light-fracturing structure resembling a tree.

Second instar. The basic organisation of the cephaloskeleton the same, as in the third instar, but tips of the mouth hooks bear at least two teeth (with few exceptions) and cibarium only with 7 cibarial ridges.

Third instar. The base of the mouth hook flattened, contiguous to tip of intermediate sclerite; dorsally, near the base developed apodeme; the tips always simple; the dental sclerite present. The intermediate sclerite H-shaped from dorsal view; discrete, not coalescing to the posterior sclerite or parastomal bars; the apical parts often slightly bend down from lateral view. The epistomal sclerite as convex plate with paired lateral opening. The ligulate sclerites as vertical converging plates. The subhypostomal sclerites mostly bar-like. Rami slender, rod like, located medially to slender and rod-like parastomal bars. The parastomal bars arise from the basal sclerite just over the base of the intermediate sclerite. The dorsal bridge, dorsal and ventral cornua connected via vertical plates. The dorsal bridge semilunar to trapezoid. The dorsal cornua simple, ventral margin strongly sclerotised. The ventral cornua often broader then dorsal ones, with dorsal hyaline apodeme. The area between apodeme and vertical plates often with weakened sclerotization. The cibarium with 9 cibarial ridges.

Description of the immatures of individual species

Altogether seventeen species in eight genera were included in this study. Unfortunately, for a few species the descriptions are incomplete, mainly due to the failure to obtain all larval instars in sufficient number. In our opinion, the inclusion of even partial descriptions brings more benefits, than excluding a whole species.

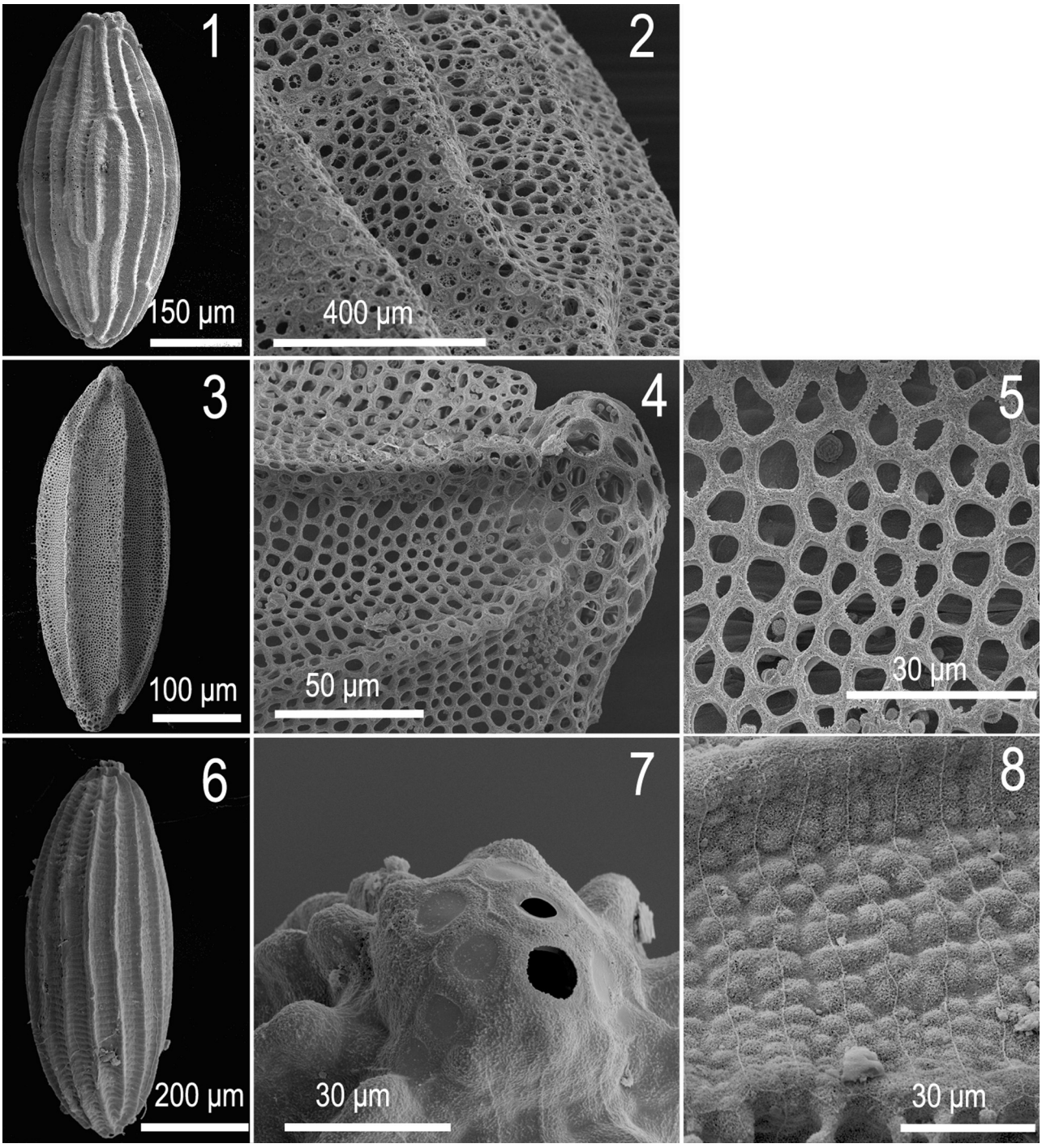
Cnemacantha muscaria (Fallén 1823)

The living larvae with marked crevices, white, dull due to hairy integument, the Malpighian tubules extended.

Egg (Figs 1, 2). Length 0.61–0.65 mm. Ridges well developed; ribs slightly indicated; Chorion smooth in close view but often perforated; posterior tubercle with well developed perforation.

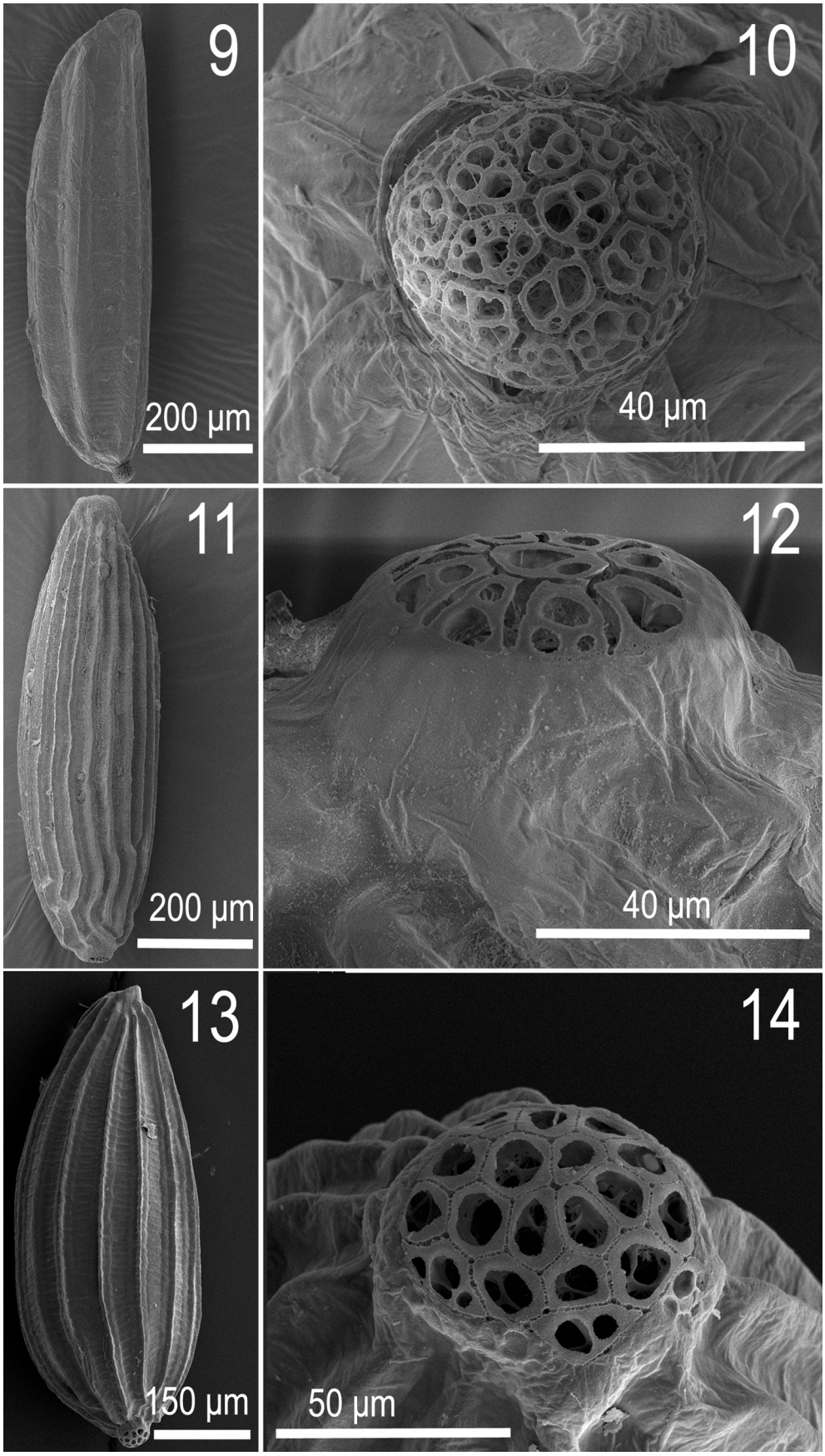
First instar (Figs 33, 34). Length 1.04–1.64 mm. Facial mask moderate, (25 scraping cirri per row); the second row of scraping cirri medially shortened. The peristomal cirri filamentous. The ventral organ lobe-like, with two digitiform processes.

Cephaloskeleton (Fig. 162). Length 0.36–0.27 mm. Mouth hooks with 4–5 apical teeth, the teeth more or les directed laterally; stalked part hyaline.

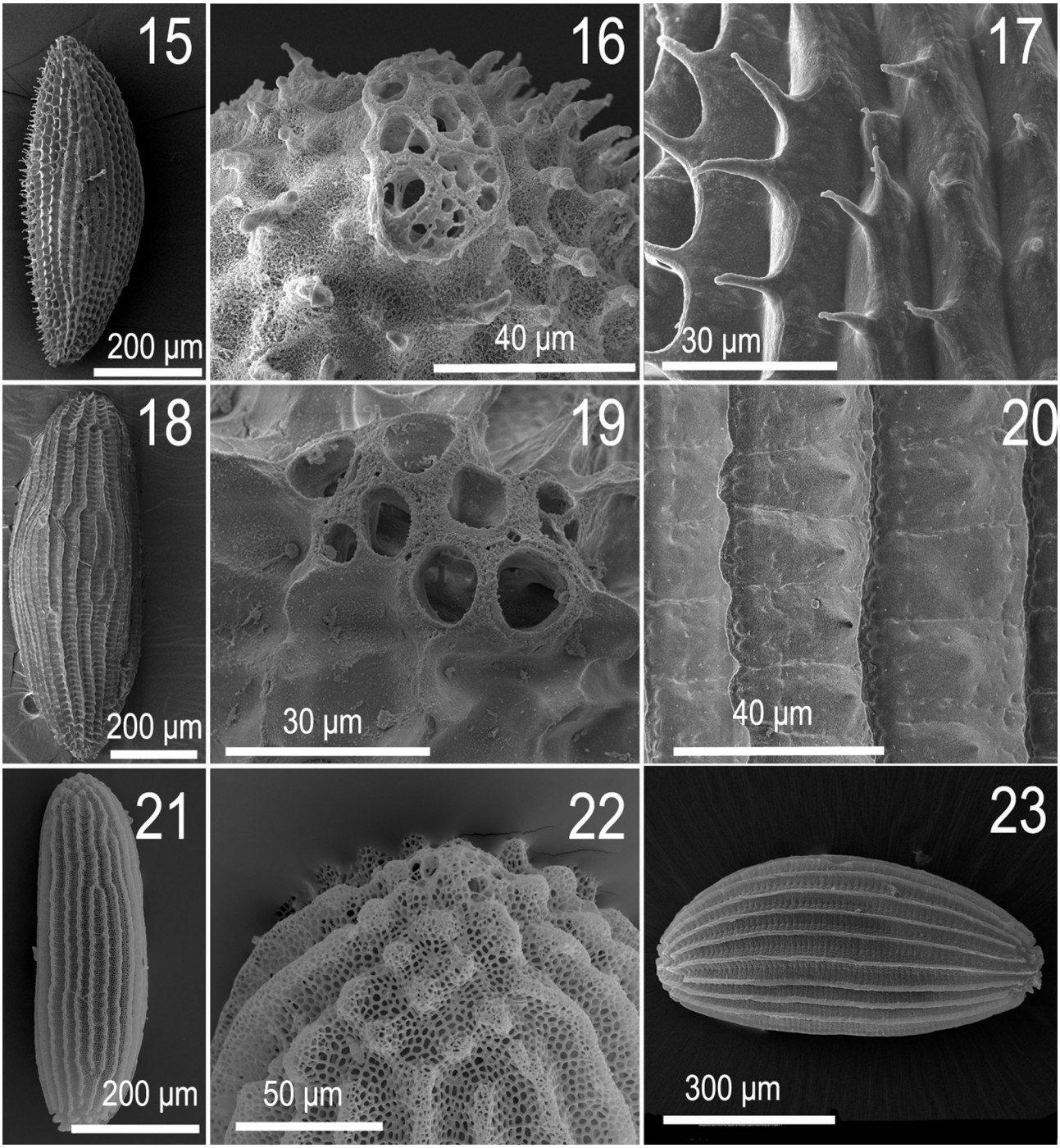


FIGURES 1–8. Eggs of *Cnemacantha muscaria*, *Homoneura biumbrata* and *H. limnea*. 1. *C. muscaria*, dorsal view. 2. Same, detail of egg chorion. 3. *H. biumbrata*, dorsal view. 4. Same, lateral view of posterior tubercle. 5. Same, detail of the egg chorion. 6. *H. limnea*, ventral view. 7. Same, detail of the posterior tubercle. 8. Same, detail of the egg chorion.

Second instar (Figs 35, 36). Length 1.57–2.23 mm. Facial mask narrow, up to 10 scraping cirri per row; the scraping cirri in first row very short. The peristomal cirri of two types. Thoracic segments with comb spines anterodorsally. Abdominal segments and anal division covered by stout spines. Anterior spiracles simple, oval.



FIGURES 9–14. Eggs of species of *Minettia*. 9. *M. austriaca*, lateral view. 10. Same, detail of the posterior tubercle. 11. *M. loewi*, dorsal view. 12. Same, detail of the posterior tubercle. 13. *M. plumicornis*, lateral view. 14. Same, detail of the posterior tubercle.

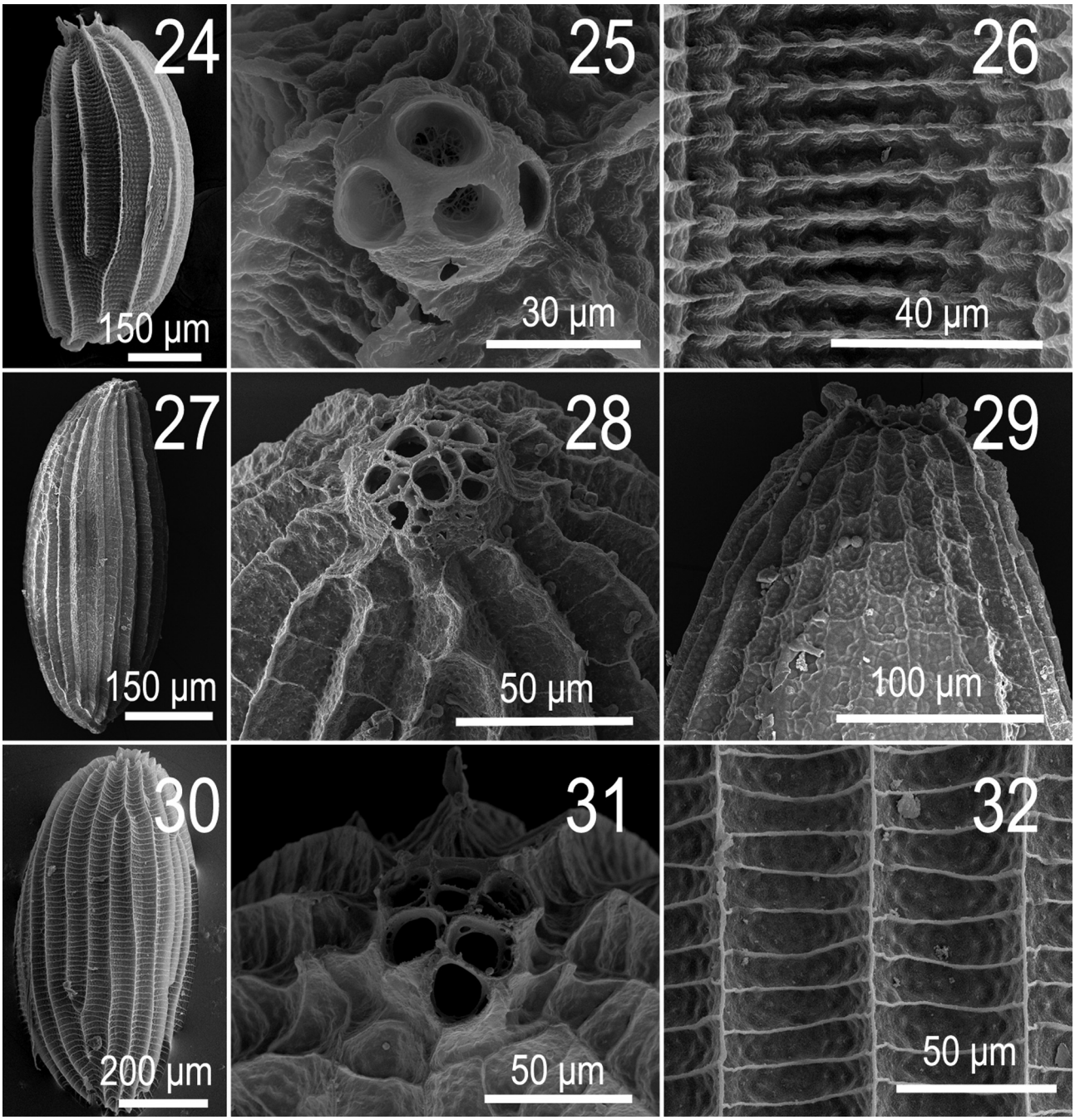


FIGURES 15–23. Eggs of *Poecilolycia vittata*, *Pseudolyciella pallidiventris*, *Sapromyza hyalinata* and *S. apicalis*. 15. *P. vittata*, lateral view. 16. Same, detail of the posterior tubercle. 17. Same, detail of the egg chorion. 18. *P. pallidiventris*, ventral view. 19. Same, detail of the posterior tubercle. 20. Same, detail of the egg chorion. 21. *S. hyalinata*, ventral view. 22. Same, detail of the posterior tubercle. 23. *S. apicalis,* ventral view.

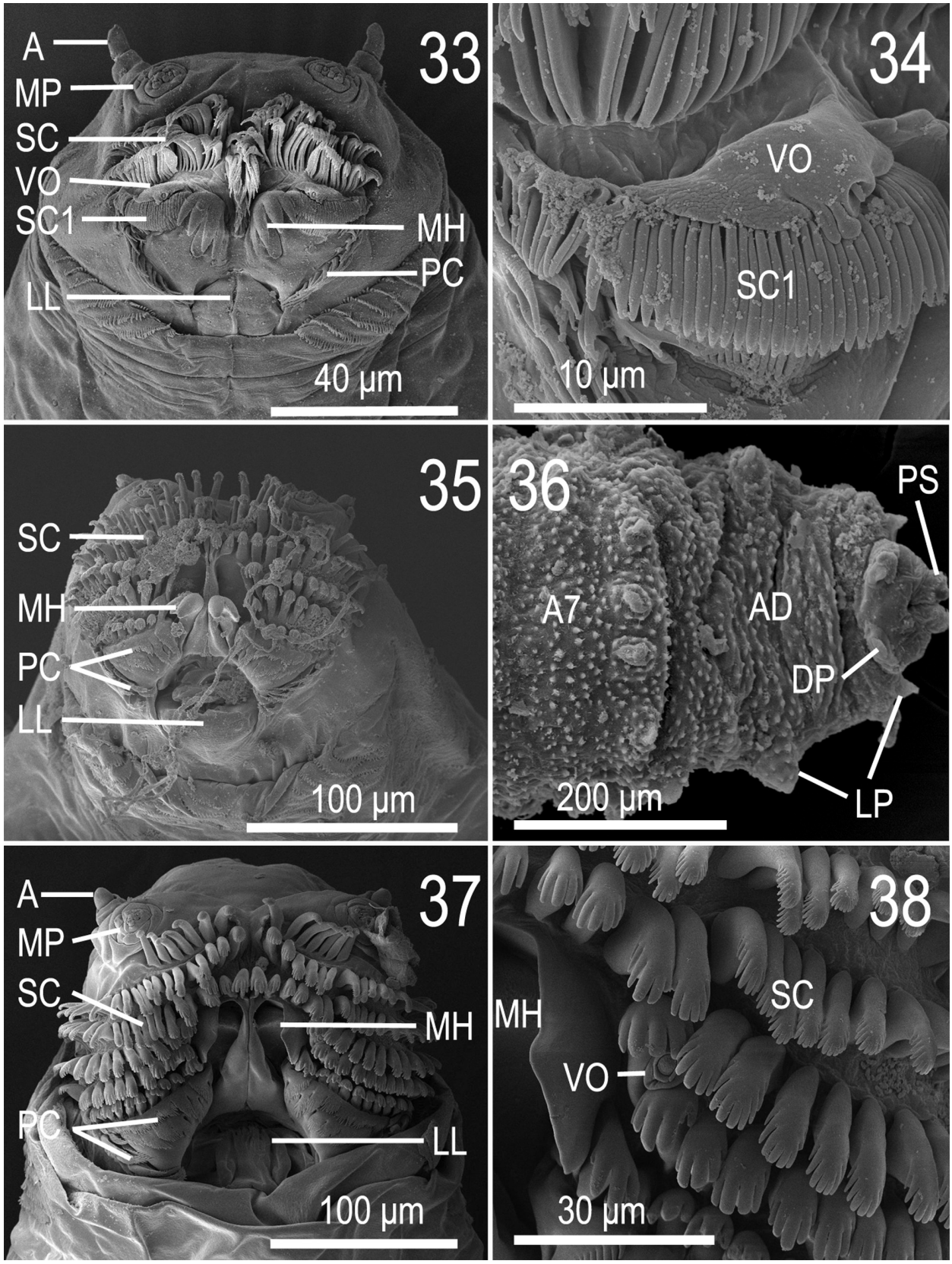
Cephaloskeleton (Fig. 177). Length 0.42–0.45 mm. Mouth hooks robust, strongly converging, ending in 3 robust teeth; dental sclerite massive. Intermediate sclerite strong. Epistomal sclerite semilunar from dorsal view, posterior hyaline plate with two corners at posterior margin. Subhypostomal sclerites stalked, subparallel, anterior tips opposite. Dorsal bridge trapezoid, as long as wide. Dorsal and ventral cornua roughly equal; posterior third of ventral cornua hyaline. Cibarium hyaline.

Third instar (Figs 37, 38). Length 2.23–3.15 mm. The facial mask as in second instar. First thoracic segment dorsally and laterally with comb spines; second and third ones with comb spines all around anterior border. Body segments evenly covered by stout spines. Anterior spiracles with 4 papillae.

Cephaloskeleton (Fig. 192). Length 0.68–0.78 mm. Mouth hooks strong, converging. Intermediates sclerite short, straight from lateral view, tips arched and converging; ventral bridge narrow and arched from ventral view. Epistomal sclerite shorter than broad, posterior hyaline plate with two corners. Subhypostomal sclerites stalked, converging. Dorsal bridge semilunar. Ventral cornua posteriad weakly sclerotised. Cibarium hyaline.



FIGURES 24–32. Eggs of *Sapromyza intonsa*, *S. sexpunctata* and *Sapromyzosoma quadricincta*. 24. *S. intonsa*, lateral view. 25. Same, detail of posterior tubercle. 26. Same, detail of the egg chorion. 27. *S. sexpunctata*, lateral view. 28. Same, detail of the posterior tubercle. 29. Same, detail of the apical end of the egg, ventral view. 30. *S. quadricincta*, dorsal view. 31. Same, detail of the posterior tubercle. 32. Same, detail of the egg chorion.



FIGURES 33–38. *Cnemacantha muscaria*, first (33, 34), second (35, 36) and third (37, 38) instars. 33. Cephalic segment. 34. Detail of the ventral organ. 35. Cephalic segment. 36. The anal division, dorsal view. 37. Cephalic segment. 38. Detail of the facial mask showing the ventral organ. A, antenna; AD, anal division; A7, seventh abdominal segment; DP, dorsal process; LL, labial lobe; LP, lateral process; MH, mouth hooks; MP, maxillary palpus; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; SC1, first row of scraping cirri; VO, ventral organ.

***Homoneura biumbrata* (Loew 1873)**

Living larvae only moderately dorsoventrally flattened, the distal parts of Malpighian tubules expanded.

Egg (Figs 3–5). Length 0.77–0.79 mm. Scaphoid from lateral view, dorsal side with 4–5 marked ridges, ventral side with ridges suppressed but more numerous. The chorion perforated. Posterior tubercle prominent and asymmetrical from lateral view.

First instar (Figs 39, 40). Length 1.60–1.83 mm. Medially to the mouth hooks flat rounded outgrowths present. The peristomal cirri rather stout. The ventral organ flatwith three digitiform outgrowths.

Cephaloskeleton (Fig. 163). Length 021–0.25 mm. The mouth hooks with three strong apical teeth; basal part sclerotised, the dental sclerites indistinguishable.

Second instar (Figs 41). Length 1.89–3.27 mm. Facial mask relatively narrow (12 scraping cirri per row). The peristomal cirri rather stout and few in numbers. The lateral of abdominal segments covered by bumps.

Cephaloskeleton (Fig. 178). Length 0.35–0.38 mm. Mouth hooks converging, 2 apical teeth. Intermediate sclerite strong, ventral bridge narrow. Epistomal sclerite shorter than broad, posterior hyaline plate with two symmetric lobes. Ligulate sclerites stalked, converging. Subhypostomal sclerites converging. Dorsal bridge semilunar. Dorsal cornua broader than ventral cornua from lateral view; distal third of ventral cornua hyaline. Cibarium hyaline.

Third instar (Figs 42–44). Length 3.57–4.05 mm. The facial mask relatively narrow (8–15 scraping cirri per row). The scraping cirri in anterior rows either bifid or trifid. The peristomal cirri stout and few in number. Labial lobe large and broad. The first thoracic segment with broad dorsal belt of comb spines. The second and third thoracic segment with narrow belt of comb spines and laterally with bumps. The anterior spiracles fan-shaped with 5 papillae. The processes of anal division poorly yet clearly developed. The posterior spiracles on stout short sprouts, the peristigmatic tufts small and simple.

Cephaloskeleton (Fig. 193). Length 0.59 mm (n=1). Mouth hooks converging. Intermediate sclerite robustly built, ventral bridge narrow. Epistomal sclerite narrow with posterior hyaline process. Ligulate sclerites as converging vertical plates. Subhypostomal sclerite as converging arms. Rami and parastomal bars rather thick. Dorsal bridge semilunar. Dorsal cornua broader than ventral ones. Distal third of ventral cornua hyaline. Cibarium hyaline.

***Homoneura limnea* (Becker 1895)**

Living larvae moderately dorsoventrally flattened, the distal parts of Malpighian tubules expanded.

Egg (Figs 6–8). Length 0.65–0.78 mm. Ridges prominent, not fusing, edge of the ridges can bear irregular denticles. The posterior pole with prominent tubercle. Chorion tuberculous, with fine rectangular net laid over, the transversal septa very dense.

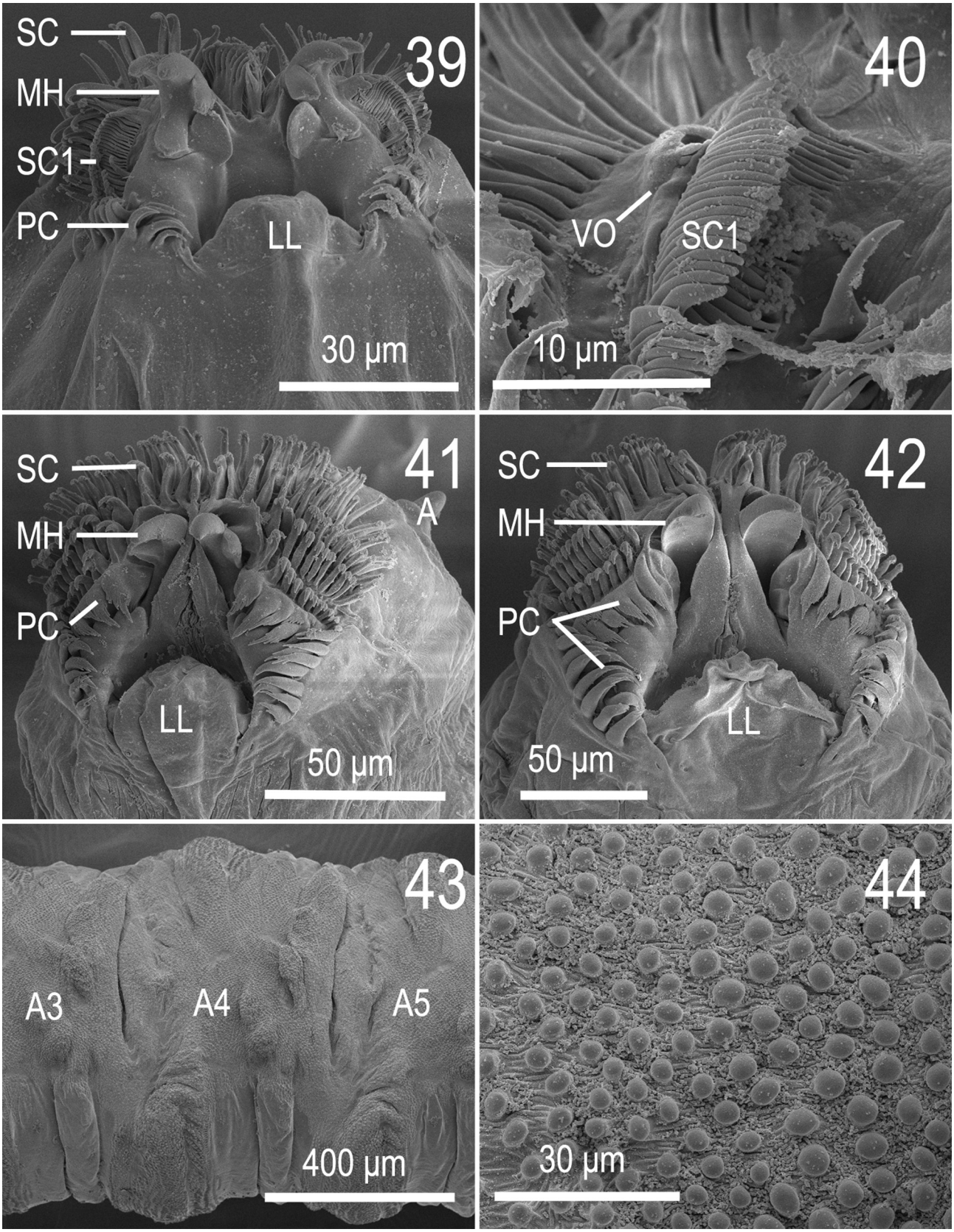
First instar (Figs 45–48). Length 0.95–1.15 mm. The ventral organ with two simple digitiform projections. The first thoracic segment with broad band of comb spines anterodorsally, second one completely smooth, third one with narrow band of comb spines both dorsally and ventrally. Dorsal creeping welts of the first abdominal segments with comb spines, towards the posterior end successively changing into simple spines. Processes of the anal division slightly indicated.

Cephaloskeleton (Fig. 164). Length 0.25–0.26 mm. Mouth hooks with 4–5 teeth, stalked part hyaline and widely separated. Labrum with three distinct corners from the dorsal view.

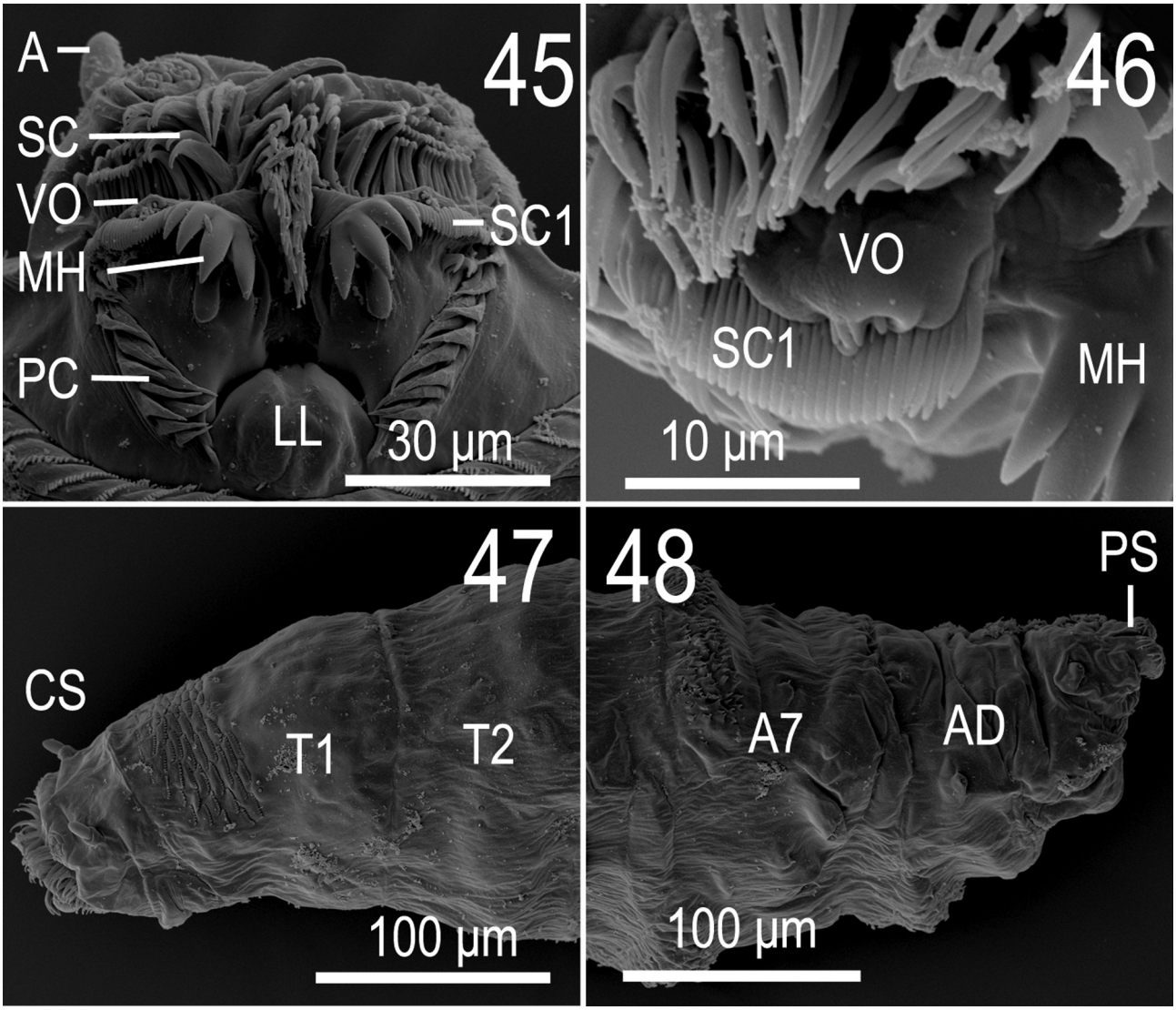
Second instar (Fig. 49). Length 1.25–3.26 mm. The characters of external morphology similar to previous species.

Cephaloskeleton (Fig. 179). Length 0.33–0.38 mm. The mouth hooks converging, with 2–3 apical teeth. Ventral bridge narrow. Epistomal sclerite shorter than broad, with posterior hyaline plate. Ligulate sclerites as vertical converging plates. Subhypostomal sclerite as arched bars with anterior swelling. Dorsal bridge longer than broad. Ventral cornua with posterior third hyaline.

Third instar (Figs 50–58). Length 3.05–6.12 mm. The facial mask very similar to previous species, as well as the pattern of spinulation on body segments. The anterior spiracles fan-shaped with 7 papillae.



FIGURES 39–44. *Homoneura biumbrata*, first (39, 40), second (41) and third (42–44) instars. 39. Cephalic segment. 40. Detail of the ventral organ, lateral view. 41. Cephalic segment, ventral view. 42. Cephalic segment, ventral view. 43. Abdominal segments, lateral view. 44. Detail of the integument of abdominal segment. A, antenna; A3–A5, third to fifth abdominal segments; LL, labial lobe; MH, mouth hooks, PC, peristomal cirri; SC, scraping cirri, SC1, first row of scraping cirri; VO, ventral organ.



FIGURES 45–48. *Homoneura limnea*, first instar. 45. Cephalic segment, ventral view. 46. Detail of ventral organ, anterior view. 47. Cephalic and first two thoracic segments, lateral view. 48. Anal division and last abdominal segment, lateral view. A, antenna; A3–A5, third to fifth abdominal segments; LL, labial lobe; MH, mouth hook, PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri, SC1, first row of scraping cirri; T1–T2, first to second thoracic segments; VO, ventral organ.

Cephaloskeleton (Fig. 194). Length 0.65–0.71 mm. The mouth hooks converging. The ventral bridge of intermediate sclerite narrow. The epistomal sclerite shorter than broad with posterior hyaline plate. Ligulate sclerites as converging vertical plates. Subhypostomal sclerite parallel with almost opposite tips. Dorsal bridge longer than broad, anteriorly rounded. The posterior third of ventral cornua hyaline, but the dorsal edge slightly sclerotised.

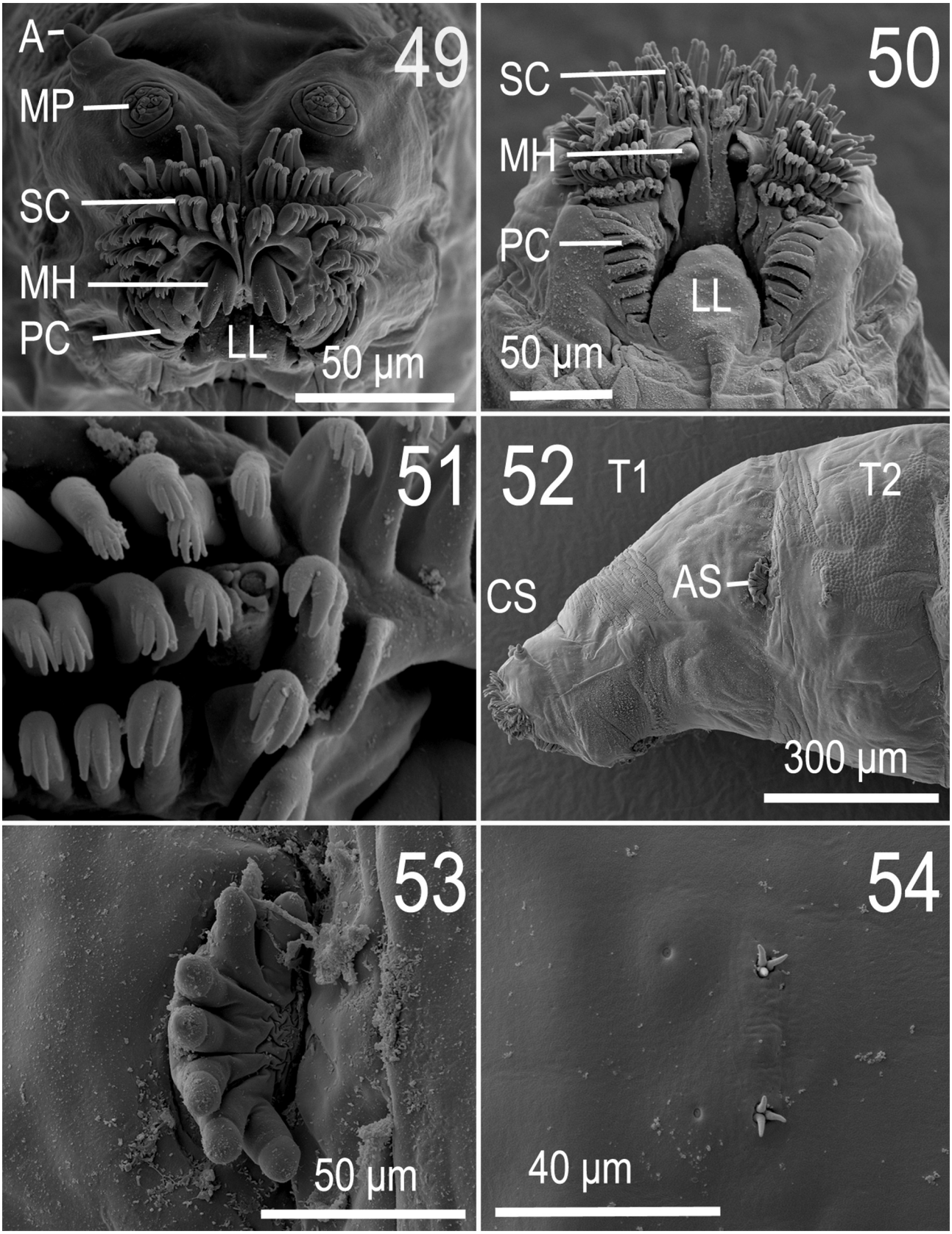
Minettia austriaca Hennig 1951

Living larvae cylindrical, the distal parts of Malpighian tubules expanded.

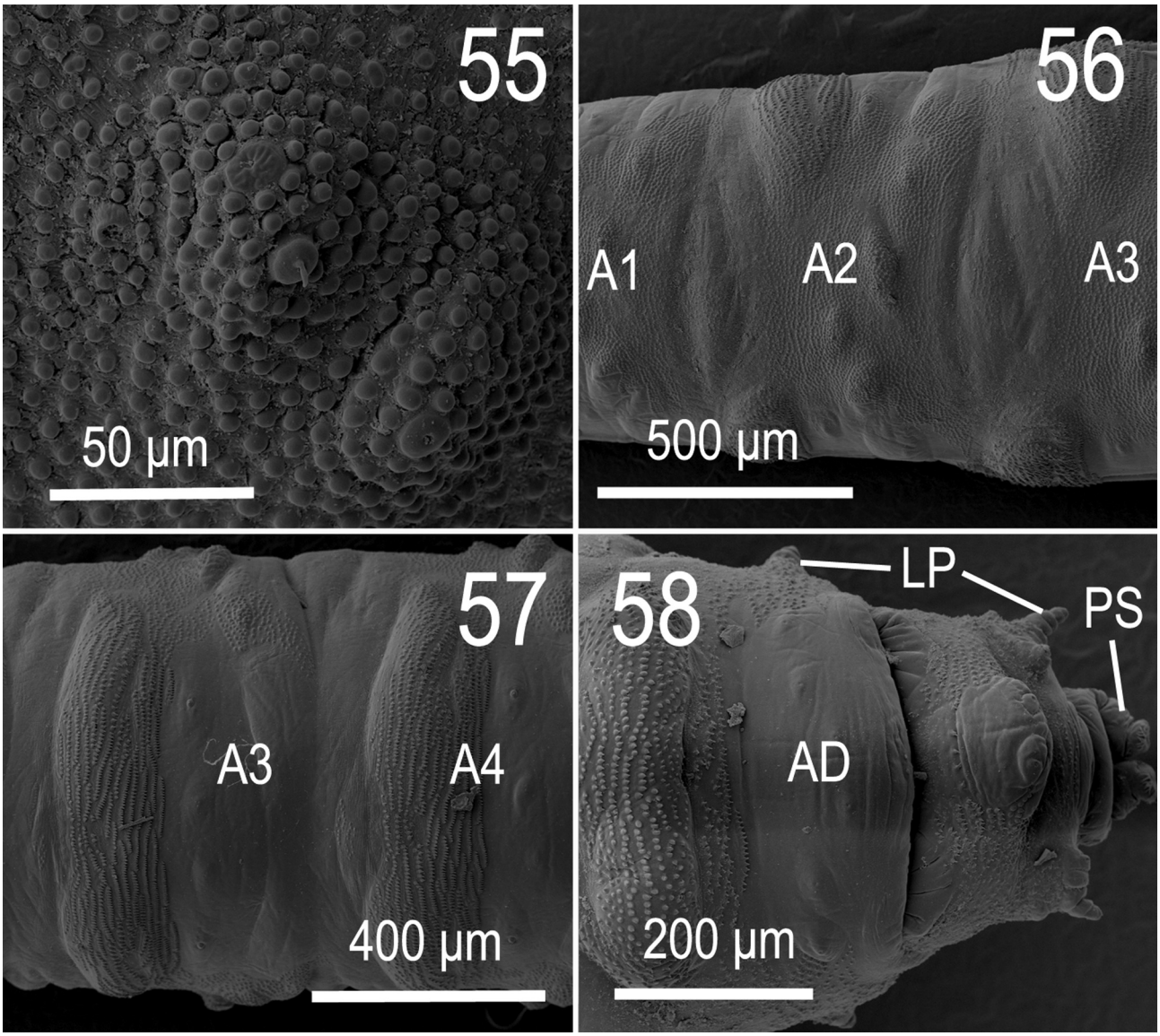
Egg (Figs 9, 10)**.** 0.81–0.93 mm. Narrow and scaphoid from lateral view, with 6 poorly developed ridges. Posterior tubercle globular and spongy.

First instar. Length 1.40–1.92 mm. Number of scraping cirri per row large (up to 30 in the first row). Row of scraping cirri developed posteriorly to the first one.

Cephaloskeleton (Fig. 165). Length 0.27–0.28 mm. Mouth hooks with 6–7 teeth, stalked part hyaline. Labrum with indicated apical tooth.



FIGURES 49–54. *Homoneura limnea*, second (49) and third (50–54) instars. 49. Cephalic segment, frontal view. 50. Cephalic segment, ventral view. 51. Detail of the ventral organ. 52. Cephalic and thoracic segments, lateral view. 53. Anterior spiracle, lateral view. 54. Keilin's organ on the first thoracic segment, ventral view. A, antenna; AS, anterior spiracles; CS, cephalic segment; LL, labial lobe; MH, mouth hooks; MP, maxillary palpus; PC, peristomal cirri; SC, scraping cirri; T2, second thoracic segment; VO, ventral organ.



FIGURES 55–58. *Homoneura limnea*, third instar. 55. Integument and lateral tubercles of the abdominal segments, lateral view. 56. Abdominal segments, lateral view. 57. Abdominal segments, dorsal view. 58. Anal division, ventral view. A1–A4, first to fourth abdominal segments; AD, anal division; LP, lateral processes; PS, posterior spiracles.

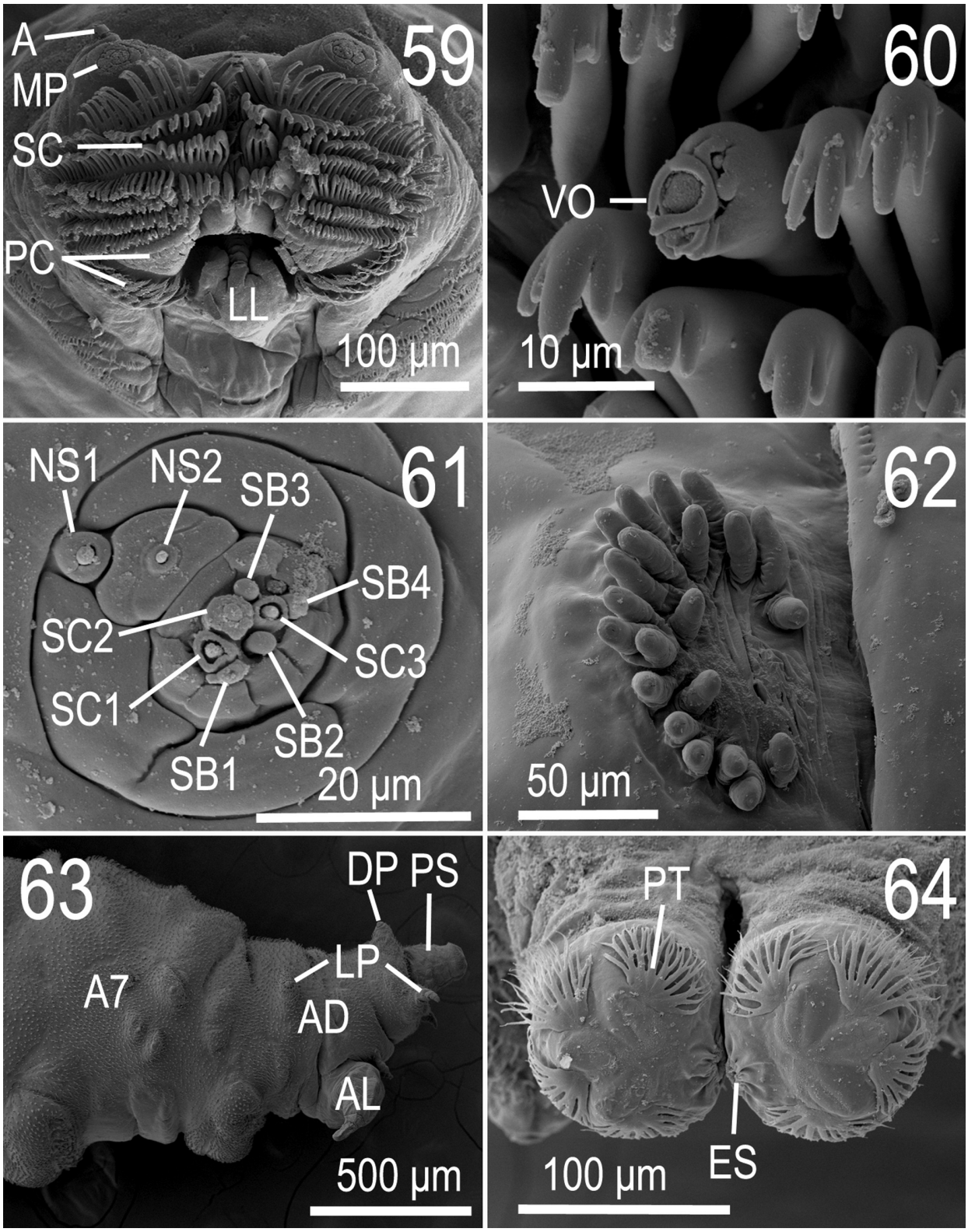
Second instar. Length 2.56–3.56 mm. Preparation for SEM was not successful.

Cephaloskeleton (Fig. 180). Length 0.60–0.61 mm. Mouth hooks subparallel, tips ending in two teeth; dental sclerite week. Ventral bridge descending posteriad. Epistomal sclerite broad, arched from dorsal view, hyaline plate present. Subhypostomal sclerites slightly diverging with converging tips. Dorsal bridge trapezoid. Basal portion of the ventral cornua and the vertical plates striolated, dorsal margin sclerotised, posterior end convex. Cibarium slightly pigmented.

Third instar (Figs 59–64). Length 3.38–5.75 mm. Dorsal surface of labial lobe with transversal lamellae in three rows.

Thoracic segments mostly smooth. Abdominal segments villous from lateral and partly from dorsal side. Anterior spiracles with number of papillae organized in horseshoe-like manner.

Cephaloskeleton (Fig. 195). Length 0.91–1.07 mm. Mouth hooks subparallel, dorsal apodeme converging, dental sclerite weak, simple. Intermediate sclerite with tips bend ventrally; ventral bridge simple, descending posteriad. Epistomal sclerite semilunar, as long as broad, posterior hyaline plate semilunar. Subhypostomal sclerites arched, diverging; ligulate sclerites as large converging vertical plates. Dorsal bridge semilunar to rectangular, dorsal cornua slender comparing to ventral cornua, medial part of ventral cornua finely striolated, auricle only indicated, posterior half of ventral cornua sclerotised and convex. Cibarium slightly pigmented.



FIGURES 59–64. *Minettia austriaca*, third instar. 59. Cephalic segment, frontal view. Note the transversal lamellae on the dorsal surface of labial lobe. 60. Detail of the ventral organ. 61. Detail of the maxillary palpus. 62. Anterior spiracle, lateral view. 63. Last abdominal segment and the anal division. 64. Posterior spiracles, postero-dorsal view. A, antenna; A7, seventh abdominal segment; AD, anal division; AL, ambulatory lobe; DP, dorsal process; ES, ecdysial scar; LL, labial lobe; LP, lateral process; MP, maxillary palpus; NS1, NS2, first and second accessory sensilla; PC, peristomal cirri; PS, posterior spiracles; PT, peristigmatic tufts; SB1-SB4, first to fourth sensilla basiconica; SC1-SC3, first to third sensilla coeloconica; SC, scraping cirri; VO, ventral organ.

Minettia fasciata (Fallén 1820)

Living larvae moderately dorsoventrally flattened, with marked belts and crevices, the distal parts of Malpighian tubules expanded.

Egg. Preparation for SEM was not successful.

First instar (Figs 65, 66)**.** Length 1.38–1.76 mm. Facial mask broad, the peristomal cirri thin and numerous. The ventral organ with two slender digitiform projections. The perstigmatic tufts of posterior spiracles long.

Cephaloskeleton (Fig. 166). Length 0.298 (n=1). Mouth hooks with 5 teeth, basal part hyaline. Epistomal sclerite longer than broad; labrum with two lateral and one apical corner. Ventral bridge arched from ventral view, with rounded cut-out on posterior margin.

Second instar (Figs 67–70)**.** Length 2.20–3.51 mm. Facial mask moderately broad (13–23 scraping cirri per row). The posterior row of peristomal cirri dense, shape variable (from filiform to robust). The anterior spiracle rounded. The first and second thoracic segments smooth except of comb spines; the rest body segments covered by stout spine-like hairs laterally, the posterior-most segments even dorsally.

Cephaloskeleton (Fig. 181). Length 0.58–0.61 mm. Essentially the same as in *M. austriaca*, subhypostomal sclerites parallel.

Third instar (Figs 71–76)**.** Length 2.82–6.30 mm. Internal side of labial lobe naked. The first thoracic segment smooth. Remaining body segments heavily spinous from dorsal and lateral sides; ventral side with smooth areas. Anterior spiracles fan-shaped, 11 papillae.

Cephaloskeleton (Fig. 196). Length 0.83–0.97 mm. Mouth hooks subparallel. Intermediate sclerite strong, ventral bridge simple and descending posteriad. Epistomal sclerite semilunar with extensive posterior hyaline plate. Subhypostomal sclerite stalked, converging; ligulate sclerites as concave converging plates. Dorsal bridge trapezoid. Dorsal cornua slender; ventral cornua broad from lateral view, medial part of ventral cornua and basal part of vertical plates finely striolated, posterior margin convex and sclerotised. Cibarium slightly pigmented.

Minettia flaviventris (Costa 1844)

Egg. Preparation for SEM was not successful.

First instar. Length 1.25–1.84 mm. The first row of scraping cirri poorly differentiated. Number of scraping cirri per row very small (8 in the first row). The thoracic segments with broad belts of comb spines anteriorly.

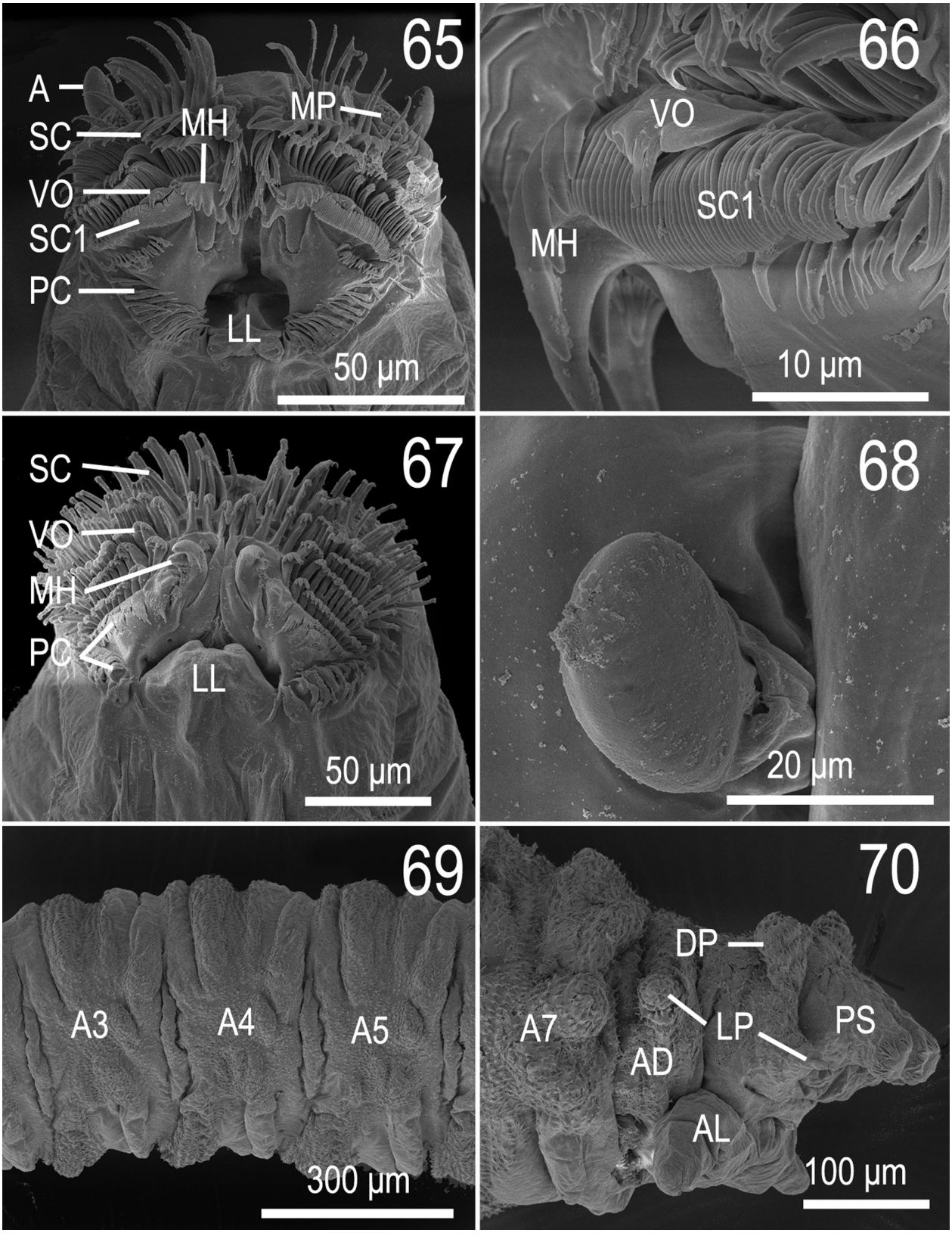
Cephaloskeleton (Fig. 167). Length 0.23–0.24 mm. The basal part of the mouth hooks coalescing into a single plate with two medial perforations, tips ending in two teeth. The parastomal bars very strong.

Second instar. Length 2.48–3.61 mm. Scraping cirri in six rows, 6–7 cirri per row, tips of cirri simple in first rows. The first thoracic segment with wide belt of comb spines dorsally.

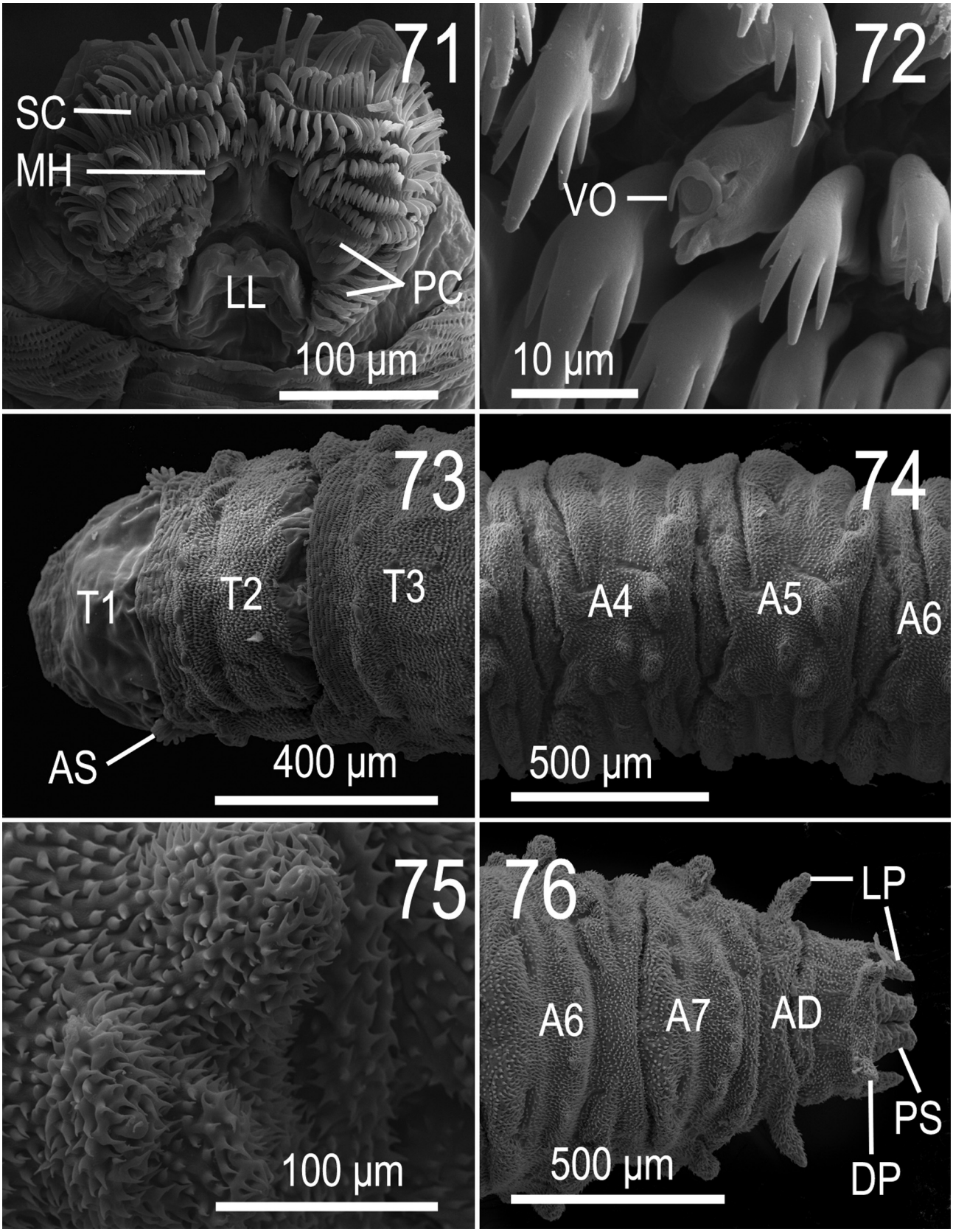
Cephaloskeleton (Fig. 182). Length 0.32–0.34 mm. Mouth hooks converging, two apical teeth; dental sclerite unusually large. Epistomal sclerite narrow and arched from dorsal view; posterior hyaline plate rectangular. Subhypostomal sclerites converging, tips converging. Ligulate sclerites arched from ventral view. Rami strong, straight. Parastomal bars strong, connected to the intermediate sclerite via thin sclerotised cuticle. Dorsal bridge trapezoid. Distal part of ventral cornua hyaline, dorsal margin concave. Cibarium hyaline.

Third instar. Length 3.1–5.95 mm. Preparation for SEM was not successful.

Cephaloskeleton (Fig. 197). Length 0.76 mm (n=1). Mouth hooks strongly converging, tips parallel. Intermediate sclerite strong; ventral bridge shallow from lateral view. Epistomal sclerite narrow and arched from dorsal view, posterior hyaline process with two slightly sclerotised corners. Ligulate and subhypostomal sclerites stalked, converging. Dorsal bridge trapezoid, as long as broad. Dorsal cornua as broad as ventral cornua from lateral view, distal third of ventral cornua only slightly sclerotised, concave. Cibarium pigmented, anterior edge with sclerotised band.



FIGURES 65–70. *Minettia fasciata*, first (65, 66) and second (67–70) instars. 65. Cephalic segment, ventral view. 66. Detail of the ventral organ, lateral view. 67. Cephalic segment, ventral view. 68. Anterior spiracle, lateral view. 69. Abdominal segments, lateral view. 70. Last abdominal segment and the anal division, lateral view. A, antenna; A3–A7, third to seventh abdominal segment; AD, anal division; AL, ambulatory lobe; DP, dorsal process; LL, labial lobe; LP, lateral process; MH, mouth hooks MP, maxillary palpus; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; SC1, first row of scraping cirri; VO, ventral organ.



FIGURES 71–76. *Minettia fasciata*, third instar. 71. Cephalic segment, ventral view. 72. Detail of the ventral organ. 73. Thoracic segments, dorsal view. 74. Abdominal segments, lateral view. 75. Lateral tubercules of the abdominal segments. 76. Last abdominal segments, and the anal division, dorsal view. A4–A7, fourth to seventh abdominal segments; AD, anal division; DP, dorsal process; LL, labial lobe; LP, lateral process; MH, mouth hooks; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; T1–T3, first to third thoracic segments; VO, ventral organ.

***Minettia loewi* (Schiner 1864)**

Living larvae cylindrical, the distal parts of Malpighian tubules expanded with typical ventral loop. Posterior pole with characteristic cylindrical tubercle.

Egg (Figs 11, 12). Length 0.60–1.73 mm. Slender, with numerous ridges, ribs not developed; Chorion smooth. Micropylar pole dorsoventrally flattened. Posterior pole with cylindrical.

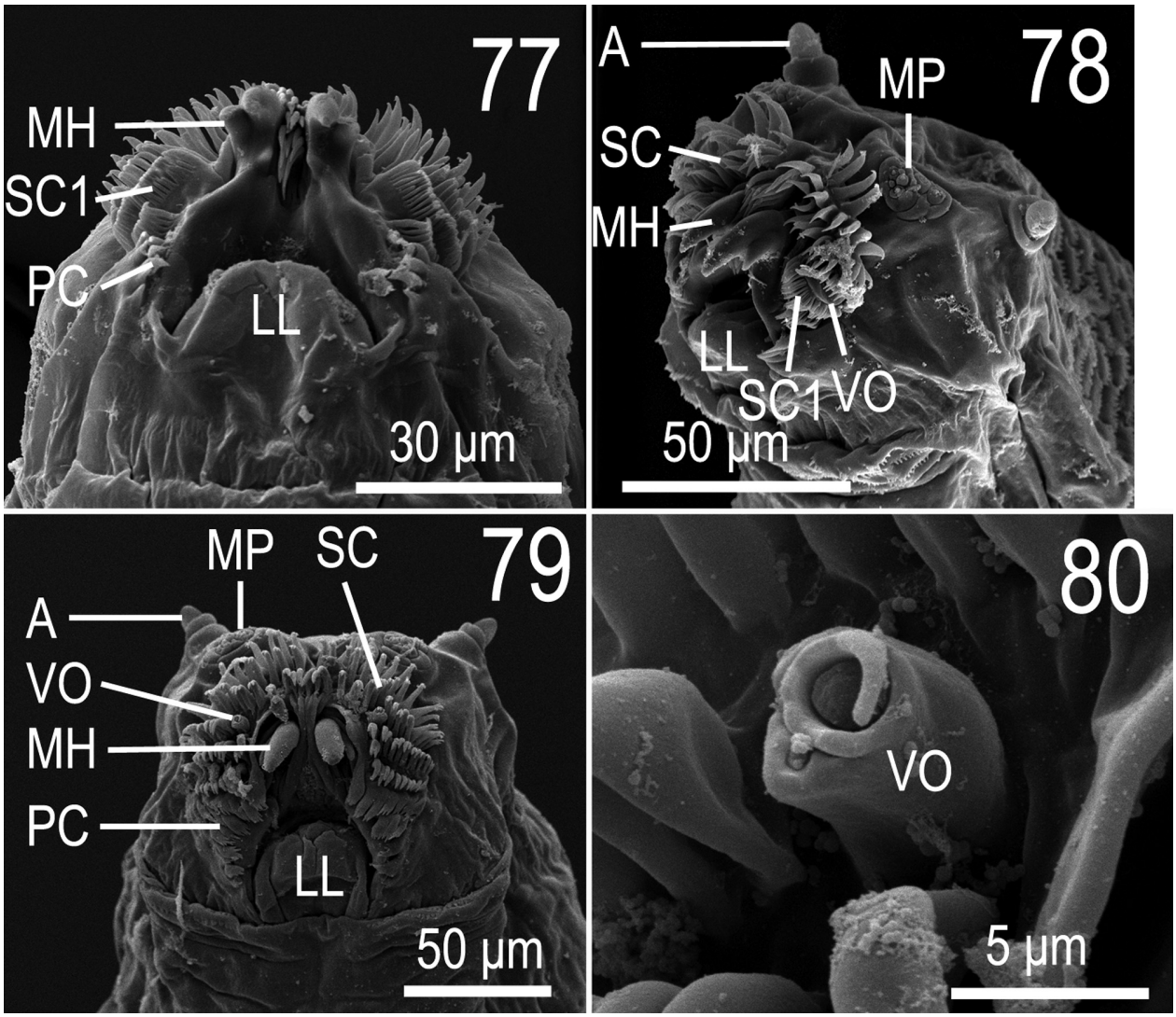
First instar. Length 1.34–2.17 mm. Cephalic segment: an additional small row of scraping cirri present posteriorly to the first row of the scraping cirri. Number of cirri per row large (up to 32). Peristomal cirri in few rows. Labial lobe with shallow apical incision, smooth on inner surface.

Cephaloskeleton (Fig. 168). Length 0.27–0.24 mm. Mouth hooks with 5–6 teeth, stalked part hyaline.

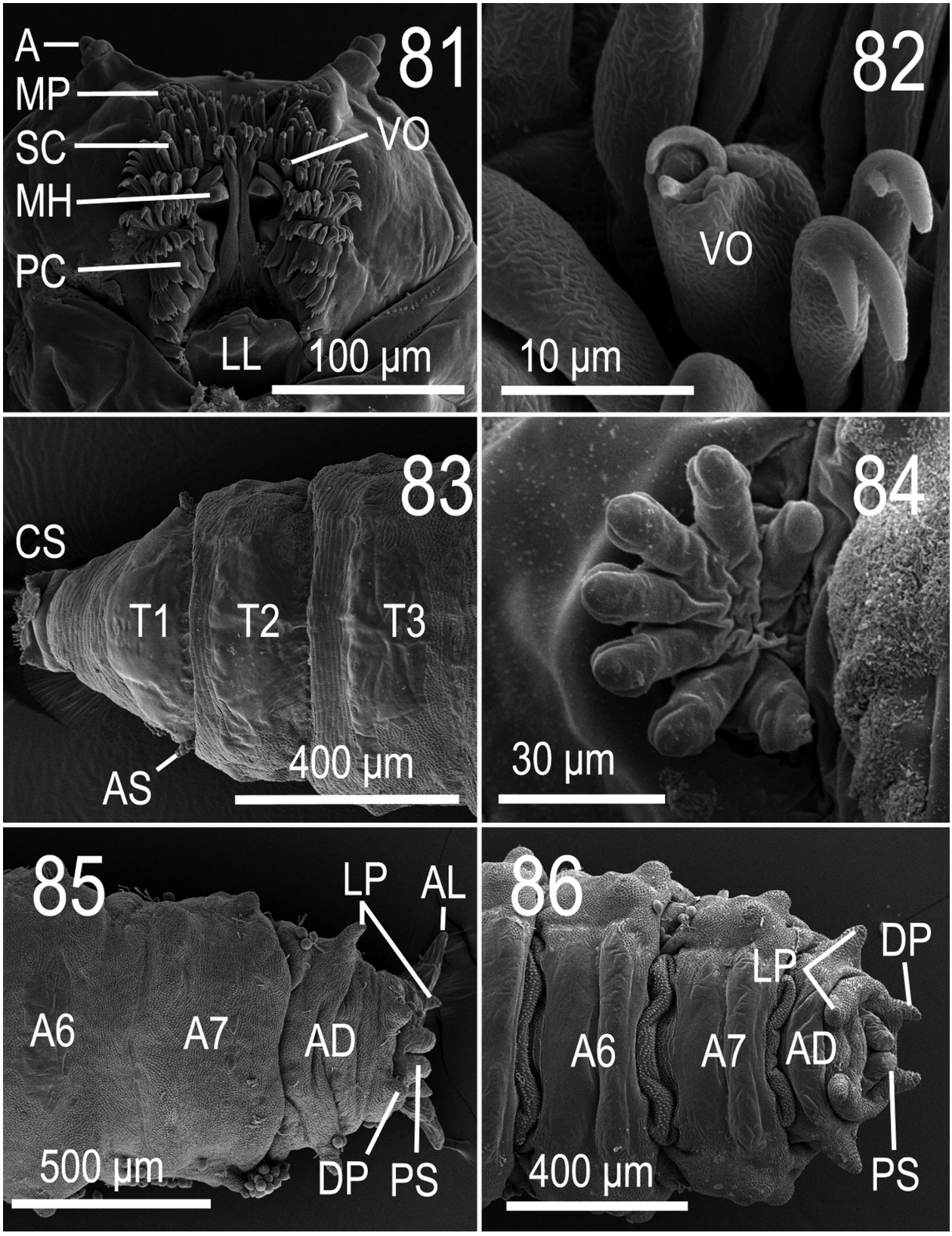
Second instar. Length 2.14–3.37 mm. Scraping cirri in 20 per row. The first thoracic segment with narrow belt of comb spines dorsally.

Cephaloskeleton (Fig. 183). Length 0.42 mm (n=1). Mouth hooks converging, two apical teeth. Epistomal sclerite shorter than broad, arched from dorsal view, posterior hyaline plate present. Subhypostomal sclerites parallel with opposite tips. Dorsal bridge trapezoid. Ventral cornua virtually straight and sclerotised along the dorsal margin. Cibarium hyaline.

Third instar was not acquired.



FIGURES 77–80. *Minettia plumicornis*, first (77, 78) and second (79, 80) instars. 77. Cephalic segment, ventral view. 78. Cephalic segment, dorso-lateral view. 79. Cephalic segment, ventral view. 80. Detail of the ventral organ. A, antenna; LL, labial lobe; MH, mouth hook; MP, maxillary palpus; PC, peristomal cirri; SC, scraping cirri; SC1, first row of scraping cirri; VO, ventral organ.



FIGURES 81–86. *Minettia plumicornis*, third instar. 81. Cephalic segment, ventral view. 82. Detail of the ventral organ. 83. Thoracic segments, dorsal view. 84. Anterior spiracle, lateral view. 85. Last abdominal segments and the anal division, dorsal view. 86. Last abdominal segments and the anal division, ventral view. A, antenna; A6–A7, sixth to seventh abdominal segments; AD, anal division; AL, ambulatory lobe; CS, cephalic segment; DP, dorsal process; LL, labial lobe; LP, lateral process; MH, mouth hook; MP, maxillary palpus; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; SC1, first row of scraping cirri; T1–T3, first to third thoracic segments; VO, ventral organ.

***Minettia plumicornis* Fallén 1820**

Living larvae moderately dorsoventrally flattened, distal parts of Malpighian tubules inflated, with typical ventral loop.

Egg (Figs 13, 14)**.** Length 0.61–0.78 mm. Robust, with number of ridges, ribs slightly indicated. Posterior tubercle prominent with marked perforations.

First instar (Figs 77, 78)**.** Length 1.18–1.76 mm. Facial mask narrow (eight scraping cirri per row); peristomal cirri very few and robust, almost spine-like.

Cephaloskeleton (Fig. 169) robustly build. Length 0.23–0.27 mm. Mouth hooks with only two apical teeth, basal part sclerotised, dental sclerite absent. Parastomal bars strong. Subhypostomal sclerites converging.

Second instar (Figs 79, 80)**.** Length 1.78–2.79 mm. The facial mask narrow, 11–12 scraping cirri per row, scraping cirri in first rows with simple tips; peristomal cirri robust. Labial lobe with smooth internal surface. The thoracic segments with dense rows of comb spines anteriorly. The body segments beginning with the second thoracic laterally covered by small bumps, the last body segments covered by bumps even dorsally. The posterior spiracles robust with small and simple peristigmatic tufts.

Cephaloskeleton was not acquired. Mouth hooks with two apical teeth.

Third instar (Figs 81–86). Length 2.99–5.16 mm. The external features conform to that of the second instar.

Cephaloskeleton (Fig. 198) robustly build. Length 0.51–0.54 mm. The mouth hooks converging, as large as the intermediate sclerite. The epistomal sclerite as narrow transversal and arched strip; posterior hyaline process with two sclerotised corners. The subhypostomal sclerites converging. The intermediate sclerite and the parastomal bars interconnected via strip of cuticle. The dorsal cornua broad. The ventral cornua posteriorly hyaline.

***Peplomyza litura* (Meigen 1826)**

Living larvae cylindrical, glassy shining; with thin distal parts of the Malpighian tubules.

Egg. Length 0.64–0.72 mm. Apical pole attenuated, posterior pole with small tubercle with few perforations. Egg covered by distinct ridges and transversal septa. Cell delimited by ridges and septa with small central pit.

First instar. Length 1.12–1.59 mm. The ventral organ as flattened lobe with two digitiform projections.

Cephaloskeleton. Length 0.25–0.26 mm. Mouth hooks with 5 apical teeth, basal part hyaline. Labrum rounded.

Second instar (Figs 87, 88)**.** Length 1.25–3.78 mm. 18 scraping cirri in the first row, internal surface of labial lobe with strong hairs. Integument smooth except of the creeping welts.

Cephaloskeleton (Fig. 184). Length 0.42–0.45 mm. Mouth hooks converging, ending in three teeth. Ventral bridge arched in ventral view. The epistomal sclerite slightly shorter than broad. Subhypostomal sclerites slightly converging. Ventral cornua hyaline in posterior third, except of dorsal margin. Cibarium slightly pigmented.

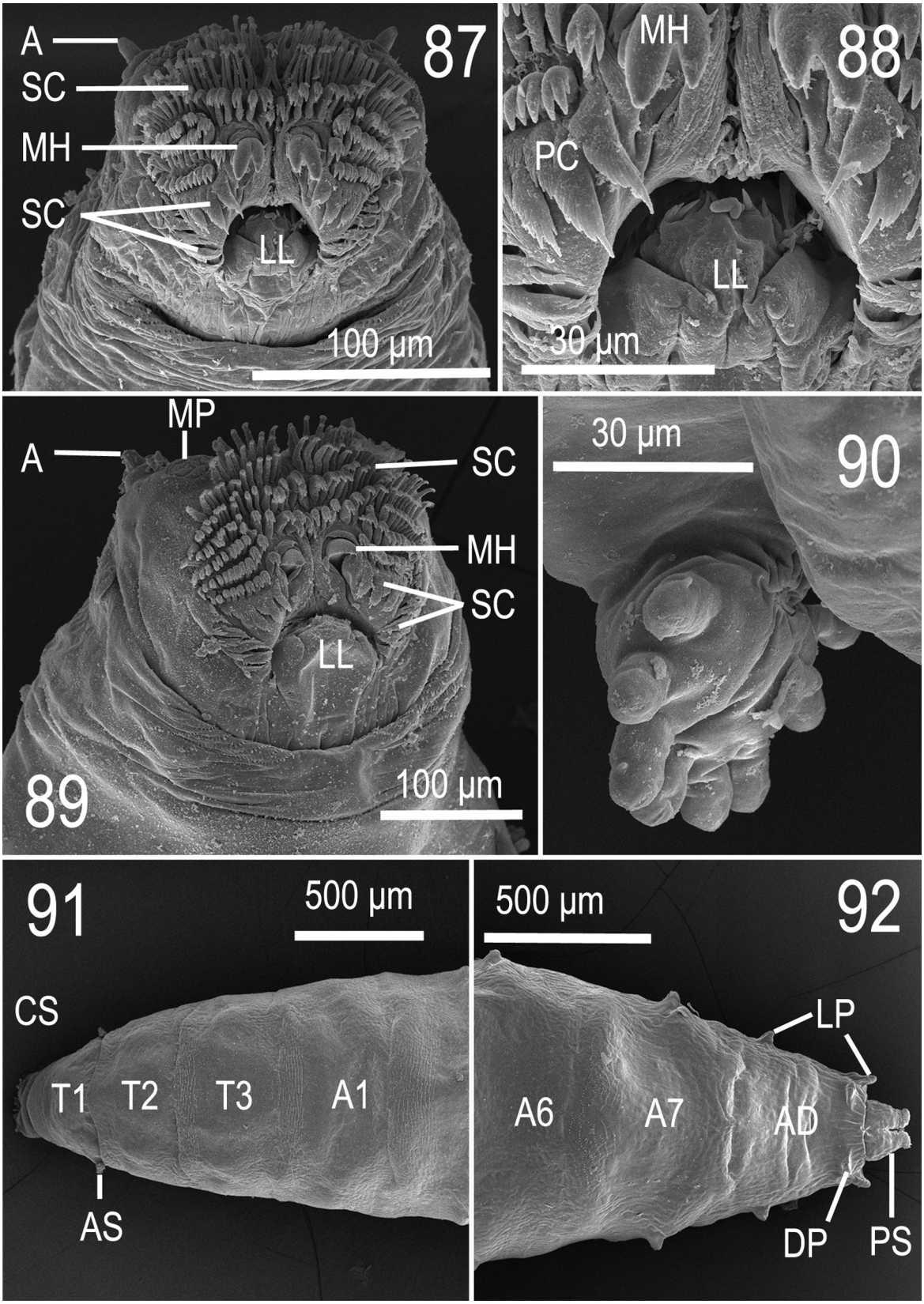
Third instar (Figs 89–92)**.** Length 3.68–5.18 mm. 17 scraping cirri in the third row. Body integument smooth except of the creeping welts. Anterior spiracles fan-shaped with 8 papillae.

Cephaloskeleton (Fig. 199). Length 0.62–0.64 mm. Mouth hooks slightly converging. The ventral bridge slightly arched in ventral view. Epistomal sclerite shorter than broad, posterior hyaline plate rectangular with sclerotised posterior margin and corners. Subhypostomal sclerites slightly converging, as well as ligulate sclerites. Dorsal bridge semilunar, longer than wide. Posterior third of ventral cornua hyaline, with sclerotised and concave dorsal margin. Cibarium slightly pigmented.

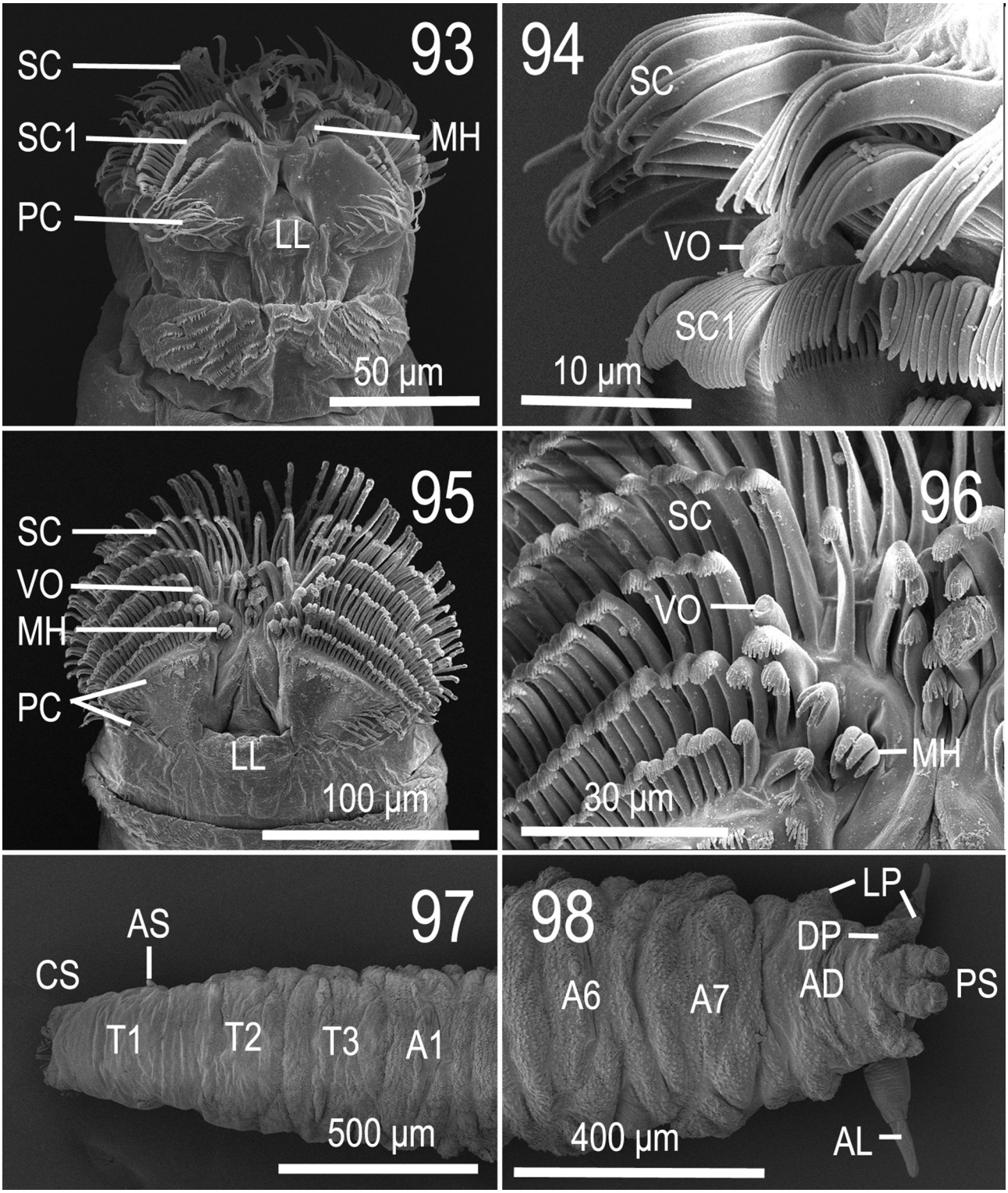
***Poecilolycia vittata* (Walker 1849)**

Living larvae translucent, dorsoventrally flattened and with marked welts and crevices. The Malpighian tubules moderately expanded and form a typical ventral loop; in the first instar filled with white matter, in the second and third instars the loop filled with light-orange matter, remaining parts of the tubules filled with white matter; more intensive colours are typical for the older larvae.

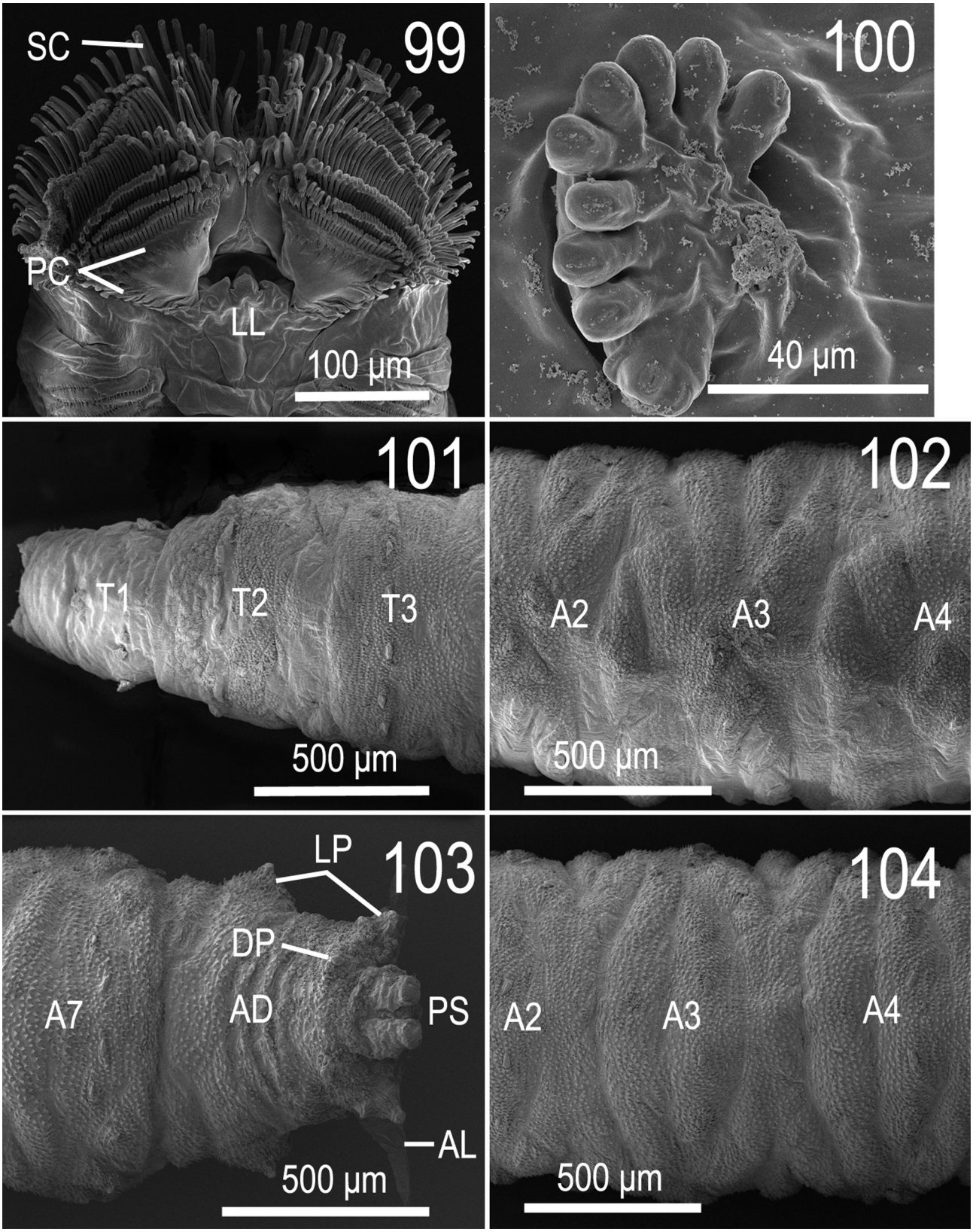
Egg (Figs 15–17). Length 0.65–0.69 mm. Chorion with dense and marked ridges. Dorsal side of egg with elongated spines on the ridges, ventral side without spines, but edge of the ridges undulated.



FIGURES 87–92. *Peplomyza litura*, second (87, 88) and third (89–92) instars. 87. Cephalic segment, ventral view. 88. Detail of the facial mask, note the small spines on dorsal surface of labial lobe. 89. Cephalic segments, latero-ventral view. 90. Anterior spiracles, postero-dorsal view. 91. Thoracic and abdominal segments, dorsal view. 92. Last abdominal segments and anal division. A, antenna; A1–A7, first to seventh abdominal segments; AD, anal division; DP, dorsal process; LL, labial lobe; LP, lateral process; MH, mouth hooks; MP, maxillary palpus; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; T1–T3, first to third thoracic segments.



FIGURES 93–98. *Poecilolycia vittata*, first (93, 94) and second (95–98) instars. 93. Cephalic segment, ventral view. 94. Detail of the ventral organ. 95. Cephalic segment, ventral view. 96. Detail of the facial mask. 97. Thoracic and abdominal segments, dorsal view. 98. Last abdominal segments and the anal division, dorsal view. A1–A7, first to seventh abdominal segments; AD, anal division; AL, ambulatory lobe; AS, anterior spiracles; CS, cephalic segment; DP, dorsal process; LL, labial lobe; LP, lateral process; MH, mouth hook; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; SC1, first row of scraping cirri; T1–T3, first to third thoracic segments; VO, ventral organ.



FIGURES 99–104. *Poecilolycia vittata*, third instar. 99. Cephalic segment, ventral view. 100. Anterior spiracle, lateral view. 101. Thoracic segments, lateral view. 102. Abdominal segments, lateral view. 103. Last abdominal segment and the anal division, dorsal view. 104. Abdominal segments, dorsal view. A2–A7, second to seventh abdominal segment; AD, anal division; AL, ambulatory lobe; DP, dorsal process; LL, labial lobe; LP, lateral process; MH, mouth hooks; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; T1–T3, first to third thoracic segments.

First instar (Figs 93, 94). Length 1.08–2.23 mm. Number of scraping cirri per row large (< 40), before the first row is one more row of small cirri. The peristomal cirri filamentous, arranged almost in horizontal row. The ventral organ essentially lobate, peculiar. The ambulatory lobes slender, appear two-segmented. The sprouts of posterior spiracles swelled; peristigmatic tufts long.

Cephaloskeleton (Fig. 170). Length 0.27–0.28 mm. Mouth hooks with 10–12 teeth, stalked part hyaline and slender. Intermediate sclerite and parastomal bars almost equal in diameter; ventral bridge broad and strongly arched in ventral view. The epistomal sclerite convex, longer than broad, with apical tooth. Subhypostomal sclerites opposite.

Second instar (Figs 95–98). Length 2.02–4.11 mm. Facial mask broad, up to 30 of scraping cirri per row. The peristomal cirri differentiated in two types: filamentous and flat triangular. The body segments covered by stout spines; the first thoracic segment smooth; the processes of anal division stout, ambulatory lobes slender, two-segmented.

Cephaloskeleton (Fig. 185). Length 0.46–0.49 mm. Mouth hooks week, basal third converging, otherwise parallel, 5 apical teeth. The epistomal sclerite rounded. The intermediate sclerite slender; ventral bridge broad and descending posteriad. Subhypostomal sclerites as horizontal perforated plates. Ligulate sclerites as vertical converging plates. Dorsal bridge narrow, equally broad along whole length. Dorsal cornua week, shorter than ventral ones. Posterior half of ventral cornua hyaline with sclerotised and convex dorsal margin. Basal part of dorsal and ventral cornua and vertical plates finely striolated. Cibarium slightly pigmented, inter-ridge distances large.

Third instar (Figs 99–104). Length 3.13–6.19 mm. The facial mask very similar to previous instar, up to 40 scraping cirri per row. Labial lobe very short, trilobite. The anterior spiracles fan-shaped, with 9 papillae, one apparently fused from several papillae. The first thoracic segment smooth, the second one sparsely covered by spines dorsally; rest body segments covered by stout spines. The anal division as in previous instar.

Cephaloskeleton (Fig. 200). Length 0.81–0.82 mm. Mouth hooks weak, straight and slightly converging. The epistomal sclerite rounded and convex. Remaining features largely as in the second instar, but the ventral cornua almost completely slightly sclerotised.

Pseudolyciella pallidiventris (Fallén 1820)

The living larvae soft and translucent, with marked welts and crevices. The third instar larvae large and dorsoventrally flattened; massive lobes arises from second and third thoracic and abdominal segments. Distal parts of Malpighian tubules thin, filled with white matter.

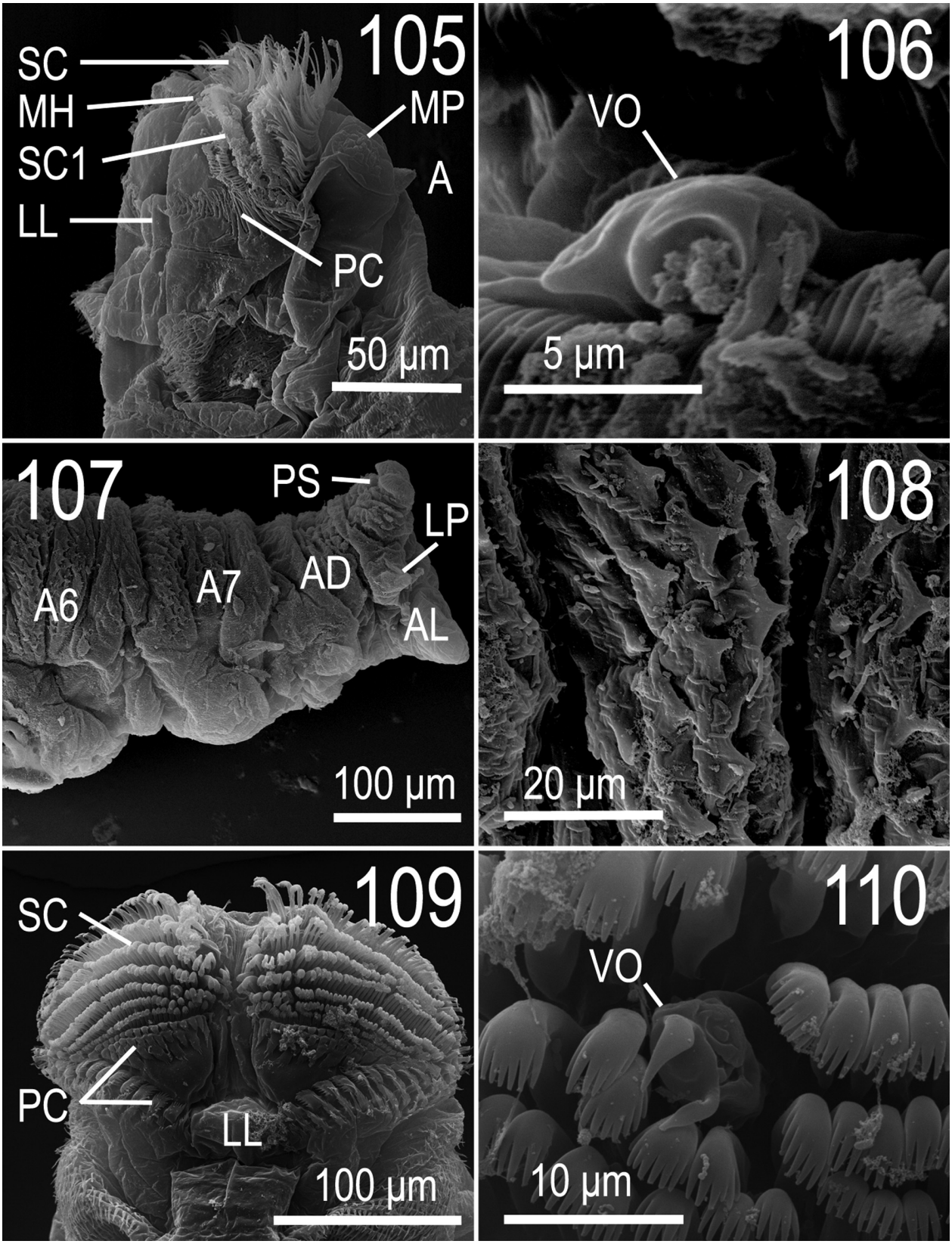
Egg (Figs 18–20). Length 0.78–0.81 mm. The shape of egg asymmetrical from lateral view, with the micropylar pole up-turned. The posterior tubercle small, with few openings. The chorion with numerous ridges; towards the egg's poles the ridges become exaggerated with zig-zag margin; the transversal ribs indicated; small pits between the ribs and ridges sometimes indicated.

First instar (Figs 105–108). Length 1.26–2.37 mm. The peristomal cirri very slender and long. The ventral organ with two digitiform processes, the lobe laterally to the processes reduced. The integument of body segments covered by fine wrinkles, ventral side smooth. The thoracic segments without spines. The abdominal segments with spinous creeping welts, but the spines on dorsal creeping welts flat and triangular, resembling folds of the skin rather than spines. Only one (lateral) pair of processes developed on the anal division. Sprouts of the posterior spiracles short, compact; the peristigmatic tufts elongated.

Cephaloskeleton (Fig. 171). Length 0.31–0.33 mm. The distal part of mouth hooks with 5–7 teeth; stalk parts hyaline, slender and closely adherent one to another. The epistomal sclerite elongated, two times as long as broad. The ventral cornua sclerotised along dorsal margin. Other features as in previous species.

Second instar (Figs 109, 110). Length 2.19–3.58 mm.

Cephaloskeleton (Fig. 186). Length 0.51–0.53 mm. Mouth hooks very slender, basal parts converging, otherwise parallel; tips simple. The epistomal sclerite longer than broad, rounded on anterior margin, convex. Subhypostomal sclerites peculiar, resembling eyeglasses in ventral view. Intermediate sclerite slender. Ventral bridge very broad, with two corners on posterior edge. Parastomal bars ascend apically. Dorsal bridge and dorsal cornua narrow in whole length. Ventral cornua broad, dorsal margin sclerotised and convex. Cibarium hyaline.



FIGURES 105–110. *Pseudolyciella pallidiventris*, first (105–108) and second (109, 110) instars. 105. Cephalic segment, lateral view. 106. Detail of the ventral organ. 107. Last abdominal segments and the anal division. 108. Detail of the integument of first instar larva. 109. Cephalic segment, ventral view. 110. Detail of the ventral organ. A, antenna; A6–A7, sixth to seventh abdominal segments; AD, anal division; AL, ambulatory lobe; LL, labial lobe; LP, lateral process; MH, mouth hook; MP, maxillary palpus; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; SC1, first row of scraping cirri; VO, ventral organ.

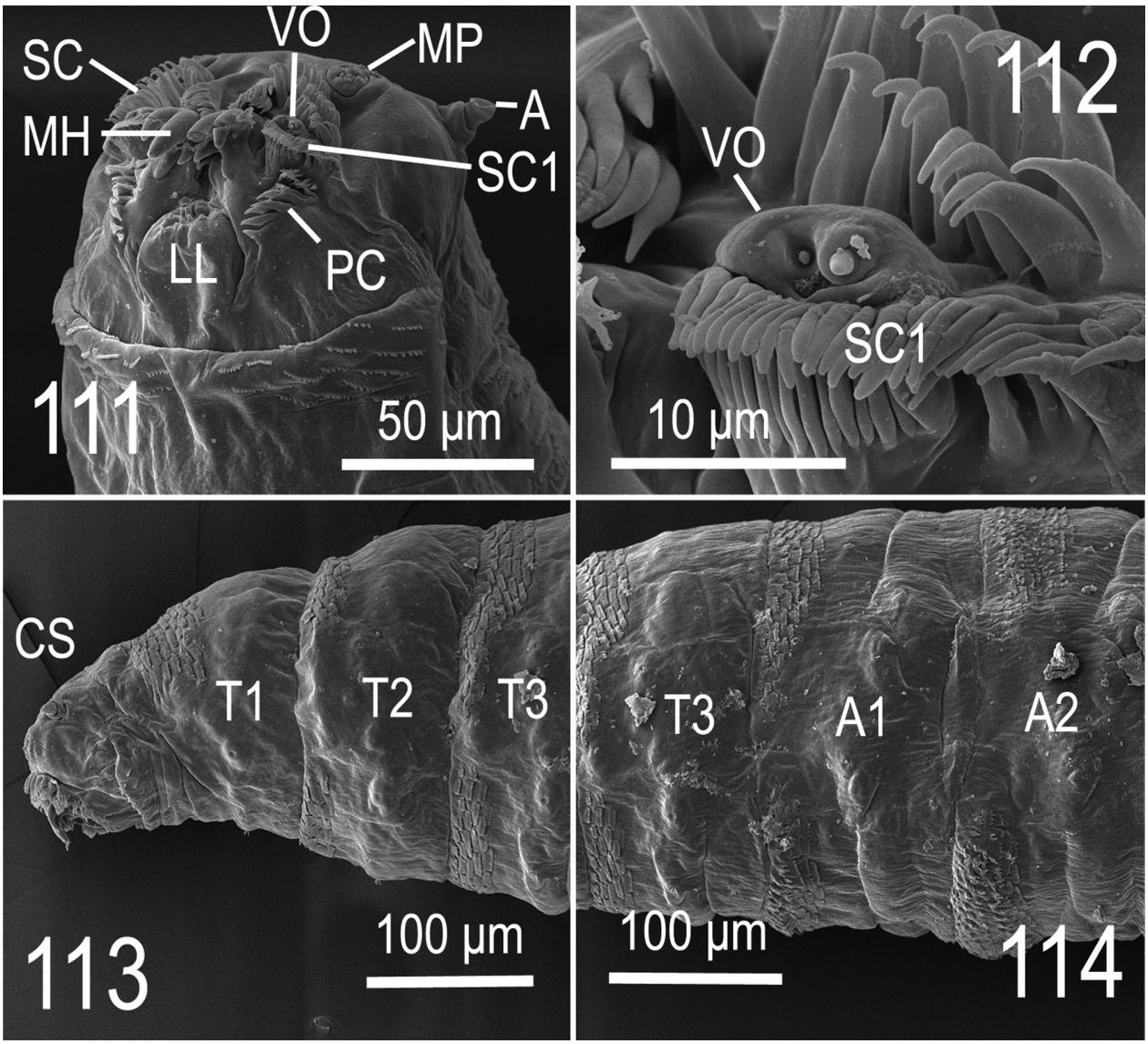
Third instar (pictures were of low quality and were not included in the present work). Length 3.35–5.37 mm. The facial mask extensive, broader than long (up to 45 scraping cirri per row). The peristomal cirri well developed, long. The ventral organ with long and slender two apical outgrowths. The thoracic segments ventrally smooth, but the ventral collar with unusually long spines. The laterals of body segments finely villous.

Cephaloskeleton (Fig. 201). Length 0.89 mm (n=1). Mouth hooks weak, slightly converging. Intermediate sclerite slender, ventral bridge broad with two corners on posterior edge. Epistomal sclerite rounded, as long as broad. Subhypostomal sclerites resemble eyeglasses. Parastomal bars slender, apical part ascends. Dorsal bridge and dorsal cornua narrow. Ventral cornua broad, dorsal margin sclerotised and convex. Cibarium hyaline.

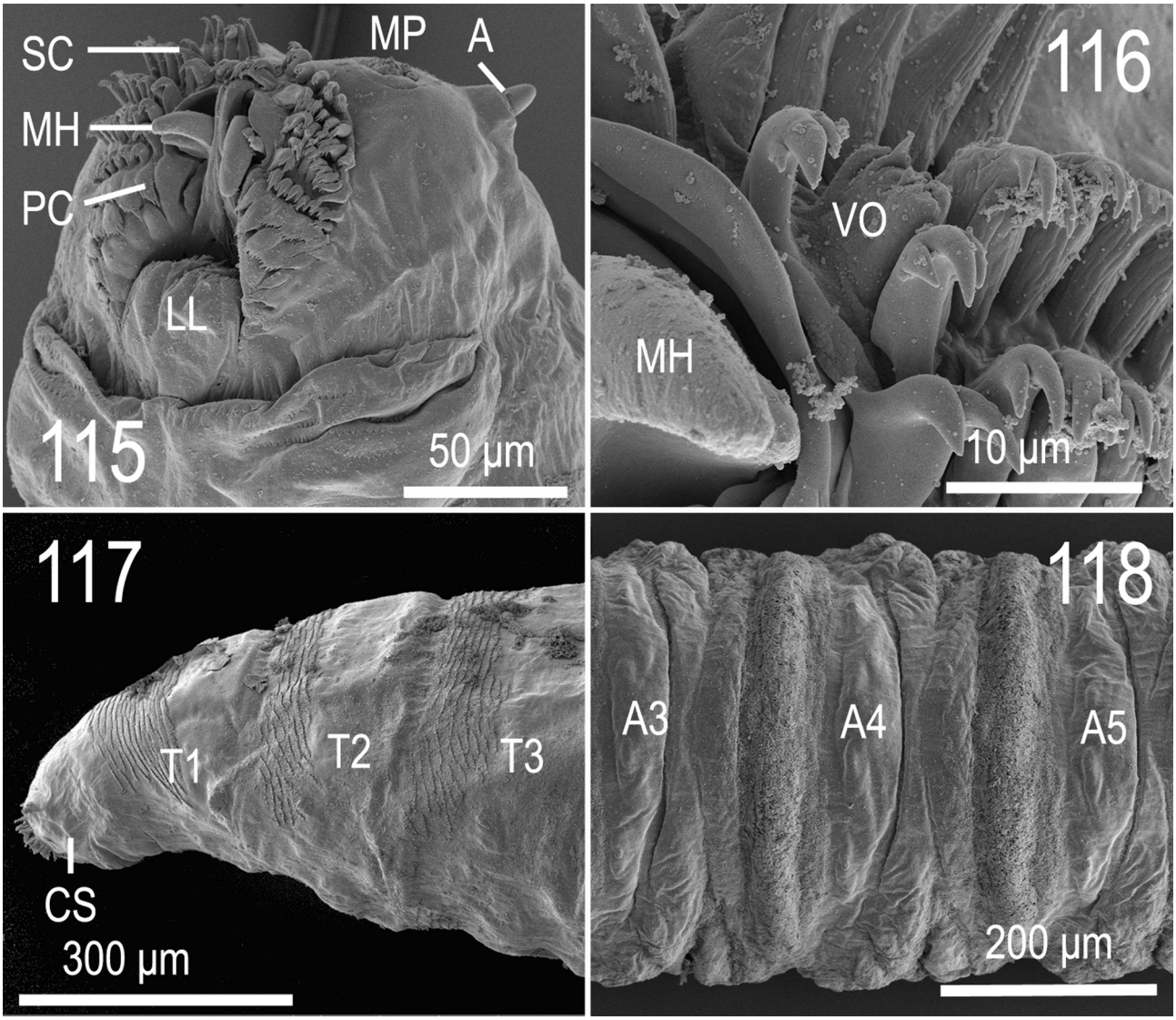
Sapromyza apicalis Loew 1847

Living larvae cylindrical and glassy shining. Malpighian tubules moderately inflated to thin, forming typical ventral loop, but it may not be fully developed in some specimens.

Egg robust (Fig. 23). Length 0.71–0.75 mm. Relatively high number (16–19) of well developed ridges, ribs not developed. Chorion tuberculous. Posterior pole flat with few (ca. 10) openings.



FIGURES 111–114. *Sapromyza apicalis*, first instar. 111. Cephalic segment, latero-ventral view. 112. Detail of the ventral organ. 113. Thoracic segments, lateral view. 114. Abdominal segments, lateral view. A, antenna; A1–A2, first and second abdominal segments; CS, cephalic segment; LL, labial lobe; MH, mouth hooks; MP, maxillary palpus; PC, peristomal cirri; SC, scraping cirri; SC1, first row of scraping cirri; T1–T3, first to third thoracic segments; VO, ventral organ.



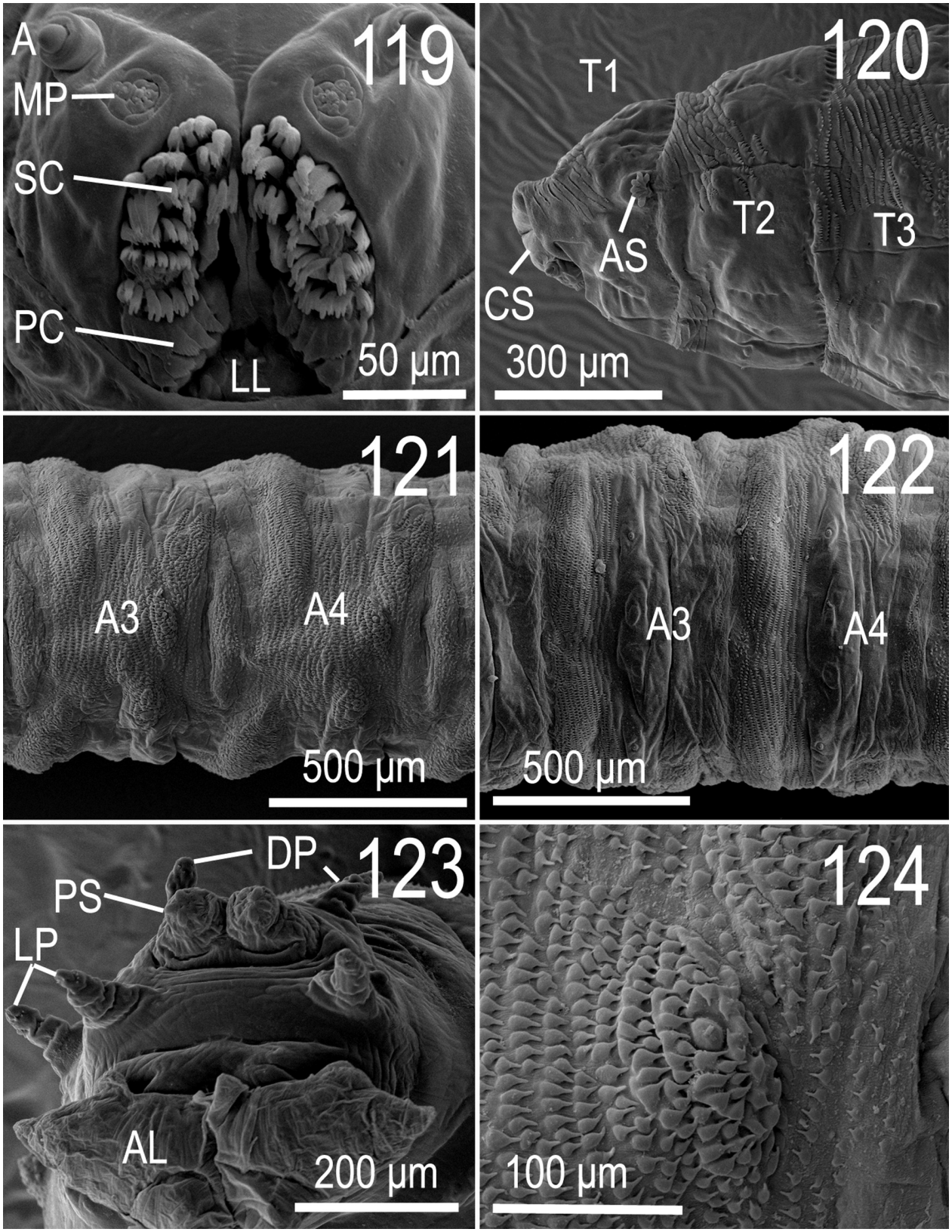
FIGURES 115–118. *Sapromyza apicalis*, second instar. 115. Cephalic segment, latero-ventral view. 116. Detail of the ventral organ. 117. Thoracic segments, lateral view. 118. Abdominal segments, dorsal view. A, antenna; A3–A5, third to fifth abdominal segments; CS, cephalic segment; LL, labial lobe; MH, mouth hook; MP, maxillary palpus; PC, peristomal cirri; SC, scraping cirri; VO, ventral organ.

First instar (Figs 111–114). Length 1.02–2.12 mm. The ventral organ robust, without slender digitiform outgrowths, a large partly immerged sensila developed instead. Only four rows of scraping cirri present. The thoracic segments with wide belts of anterior comb spines.

Cephaloskeleton (Fig. 172) strongly build. Length 0.23–0.25 mm. Mouth hooks strongly sclerotised, apically touching; three strong apical teeth; dental sclerite large and coalescing to basal part of the mouth hook. Labrum not recognisable. The epistomal sclerite anteriorly hyaline. The ventral bridge narrow and pronounced in lateral view. Parastomal bars very strong. Dorsal bridge semilunar from dorsal view.

Second instar (Figs 115–118). Length 2.15–3.84 mm. Facial mask narrow (5–8 scraping cirri per row), the scraping cirri with few (3–6) apical papillae. The peristomal cirri robust. The labial lobe massive, with inner hairs. The ventral organ robust and relatively short, as tall as wide. The thoracic segments with broad belts of comb spines. The body segments smooth except of creeping welts.

Cephaloskeleton (Fig. 187). Length 0.42–0.43 mm. Mouth hooks converging, two apical teeth. Intermediate sclerite with dorsal ridge beginning anteriorly to ventral bridge. Subhypostomal sclerites stalked, converging. Rami coarse. Epistomal sclerite narrow and arched in dorsal view. Ventral bridge simple, narrow and prominent in lateral view. Dorsal bridge trapezoid. Ventral cornua with straight dorsal margin and hyaline distal half.



FIGURES 119–124. *Sapromyza apicalis*, third instar. 119. Cephalic segment, lateral view. The mouth hooks are retracted and consequently not visible. 120. Thoracic segments, lateral view. 121. Abdominal segments, lateral view. 122. Abdominal segments, dorsal view. 123. Anal division, postero-lateral view. 124. Detail of the integument of the abdominal segments. A, antenna; A3–A4, third and fourth abdominal segments; AL, ambulatory lobe; CS, cephalic segment; DP, dorsal process; LL, labial lobe; LP, lateral process; MP, maxillary palpus; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; SC1, first row of scraping cirri; T1–T3, first to third thoracic segments.

Third instar (Figs 119–124). Length 3.75–6.14 mm. The facial mask narrow (6–11 scraping cirri per row), the scraping cirri with few equal-sized papillae. The peristomal cirri few and robust. The thoracic segments with broad belts of comb spines anteriorly. The laterals of body segments covered by sharp robust spines (indicated also on the second and third thoracic segments and dorsally on last body segments). The anal division with three pairs of processes. The anterior spiracles fan-shaped, with 6 papillae. The posterior spiracles short, stout, with small peristigmatic tufts.

Cephaloskeleton (Fig. 202) robustly built. Length 0.67–0.70 mm. The mouth hooks massive, as long as the intermediate sclerite, converging. The intermediate sclerite with dorsal ridge. The ventral bridge narrow and prominent in lateral view. The epistomal sclerite narrow and arched in dorsal view. The subhypostomal sclerites stalked, converging. Rami and parastomal bars coarse. The dorsal bridge longer than broad. The dorsal cornua as broad as ventral cornua; distal part of the ventral cornua hyaline, dorsal margin slightly concave. Cibarium hyaline.

Sapromyza hyalinata (Meigen 1826)

Living larvae cylindrical, the Malpighian tubules non-expanded.

Egg (Figs 21–22). Length 0.71–0.79 mm. Elongated, carinated, with numerous longitudinal ridges. The chorion very soft, resembling spider's web, mesh of regular size. Posterior tubercle inconspicuous, anterior pole with asymmetric funnel.

First instar. Length 0.95–1.97 mm. The two digitiform processes of ventral organ with slightly condensed. The second row of scraping cirri shortened medially. The thoracic segments missing comb spines, though the ventral collar of the first thoracic segment present.

Cephaloskeleton (Fig. 173). Length 0.19–0.22 mm. Mouth hooks with 6 teeth. The stalk part of mouth hook thin, distal part almost hyaline, basal part deeply pigmented; dental sclerites well developed.

Second instar. Preparation for SEM microscopy was not successful.

Cephaloskeleton (Fig. 188). Length 0.36–0.39 mm. Mouth hooks converging, broad in lateral view; two apical teeth. The bars of intermediate sclerite with inconspicuous dorsal ridge. Ventral bridge narrow. Epistomal sclerite shorter than broad, arched in dorsal view. Dorsal bridge trapezoid. Posterior third of the ventral cornua hyaline but with sclerotised dorsal margin. Cibarium hyaline.

Third instar (Figs 125–130). Length 2.92–5.05 mm. The third row of scraping cirri begins by the ventral organ. Number of scraping cirri in first three rows 10–12, number of papillae 3–5.

Labial lobe covered by flat folds of the integument with fine marginal hairs. The anterior spiracles fan-shaped, number of papillae varies (8–11). The first thoracic segment covered by comb spines on anterior half. Posterior half covered by extensive flat bumps equipped by hairs on posterior end. The second and third thoracic segments with similar pattern. The dorsal and ventral sides of abdominal segments more or less smooth except of creeping welts. The sides sparsely covered by spines. The anal division sparsely spinous. Processes well developed. Posterior spiracles corrugated.

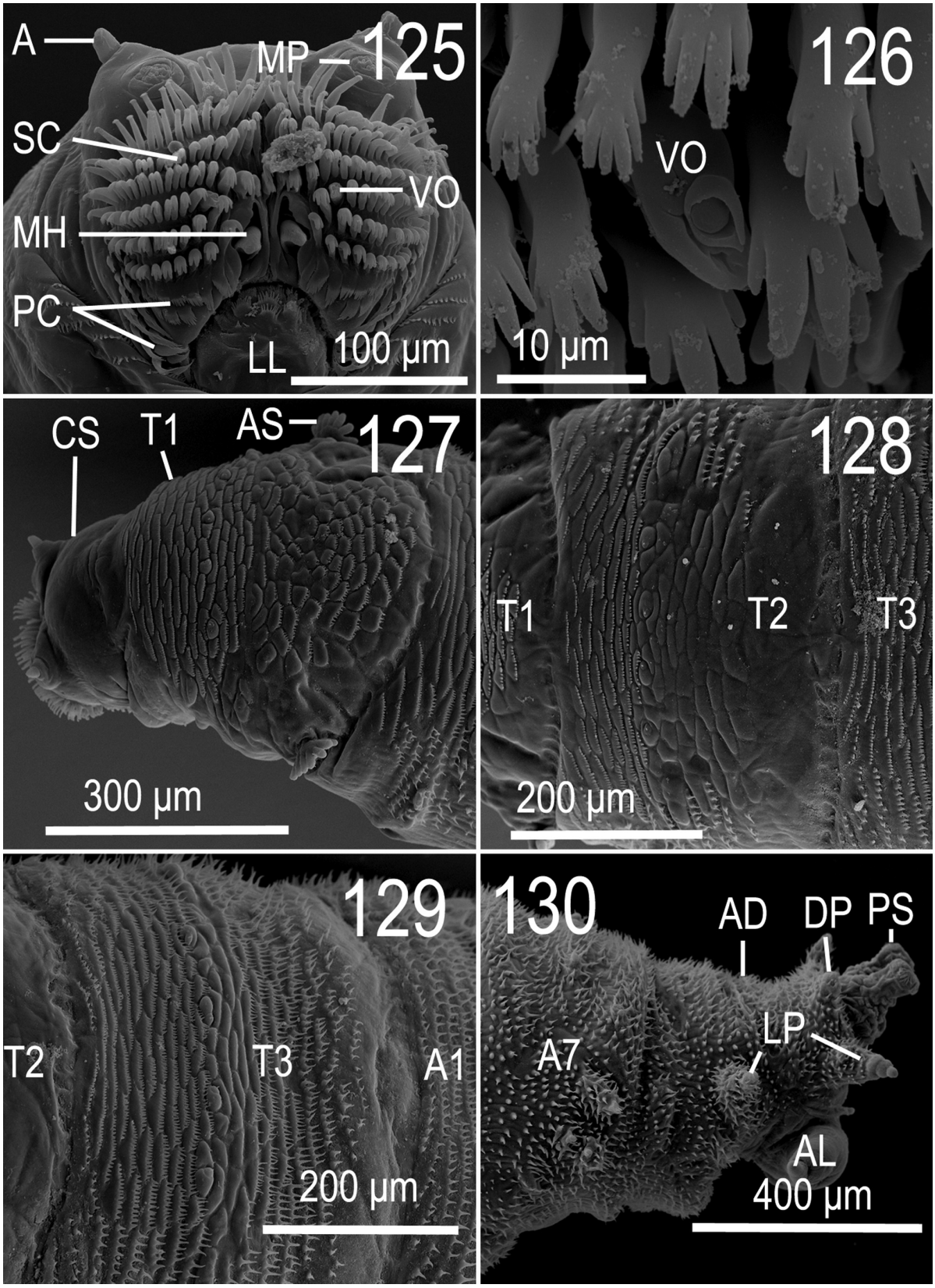
Cephaloskeleton robust (Fig. 203). Length 0.63–0.68 mm. Mouth hooks converging, as long as the intermediate sclerite. Intermediate sclerite with dorsal ridge. Ventral bridge narrow and prominent in lateral view. Epistomal sclerite narrow and arched in dorsal view. Subhypostomal sclerite stalked, converging. Dorsal bridge rounded or acute, as long as broad. Dorsal cornua broad. Distal third of ventral cornua hyaline, dorsal margin slightly sclerotised, straight. Cibarium hyaline.

Sapromyza intonsa Loew 1847

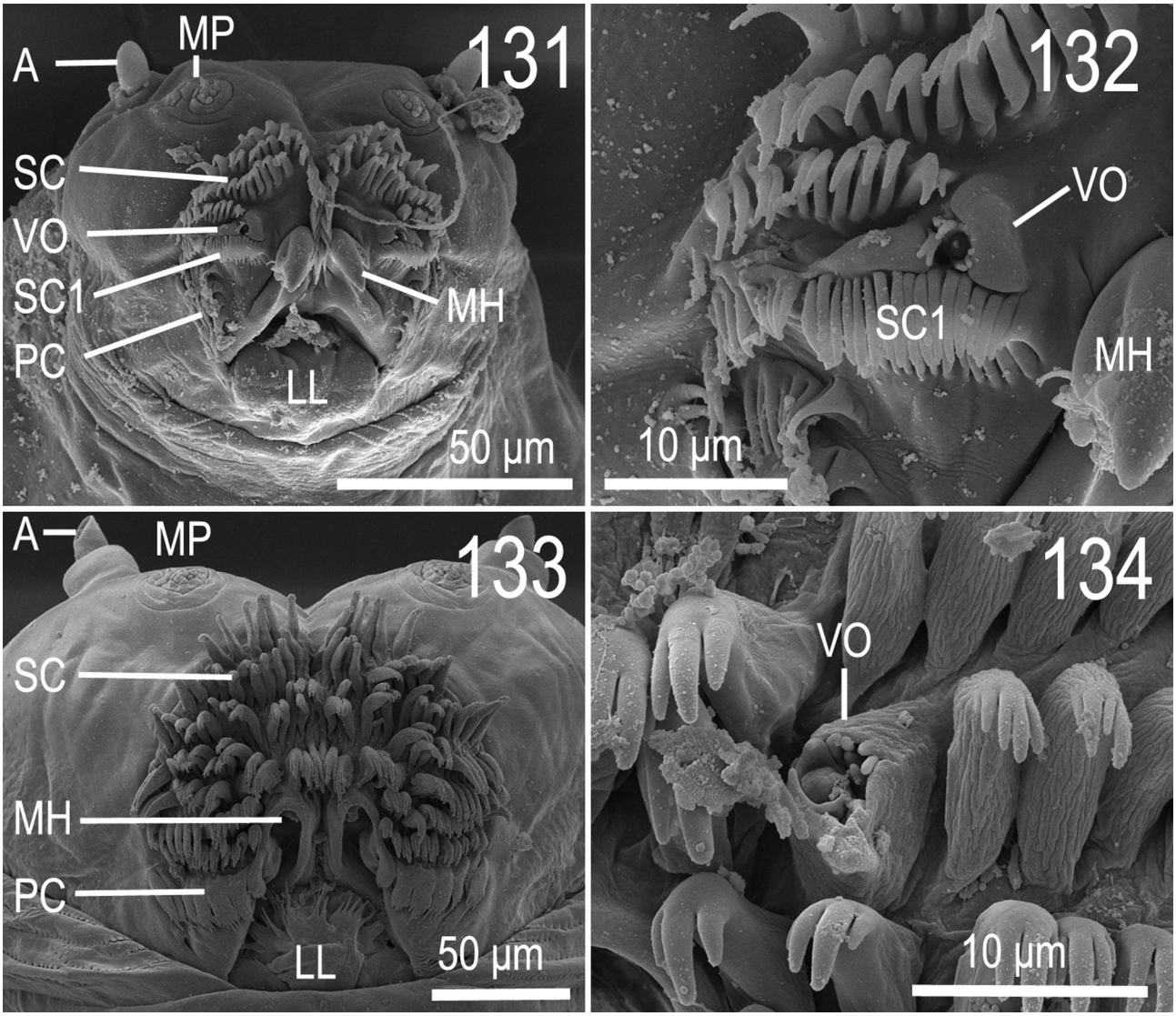
Living larvae cylindrical, glassy shining. Distal part of Malpighian tubules moderately and irregularly inflated.

Egg (Figs 24–26). Length 0.59–0.68 mm. Ridges sharp and few in numbers. Ribs dense. Apical pole with star-like collar.

First instar (Figs 131, 132). Length 1.59–2.24 mm. The ventral organ peculiar, retaining the lobe-like appearance, but the large central sensila nested deep within the lobe and surrounded by 6 slender digitiform outgrowths. The lobe of ventral organ expands apically, consequently the second row of scraping cirri is shortened and a relatively large free area left over the mouth hooks. Medial row of scraping cirri developed. Labial lobe with strong spiny hairs on internal surface.



FIGURES 125–130. *Sapromyza hyalinata*, third instar. 125. Cephalic segment, ventral view, note the processes on dorsal surface of labial lobe. 126. Detail of the ventral organ. 127. First thoracic segment, dorsal view. 128. Second thoracic segment, dorsal view. 129. Third thoracic segment, dorsal view. 130. Last abdominal segment and the anal division, lateral view. A, antenna; A1,A7, first and seventh abdominal segments; AD, anal division; AL, ambulatory lobe; DP, dorsal process; LL, labial lobe; LP, lateral process; MH, mouth hook; MP, maxillary palpus; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; T1–T3, first to third thoracic segments; VO, ventral organ.



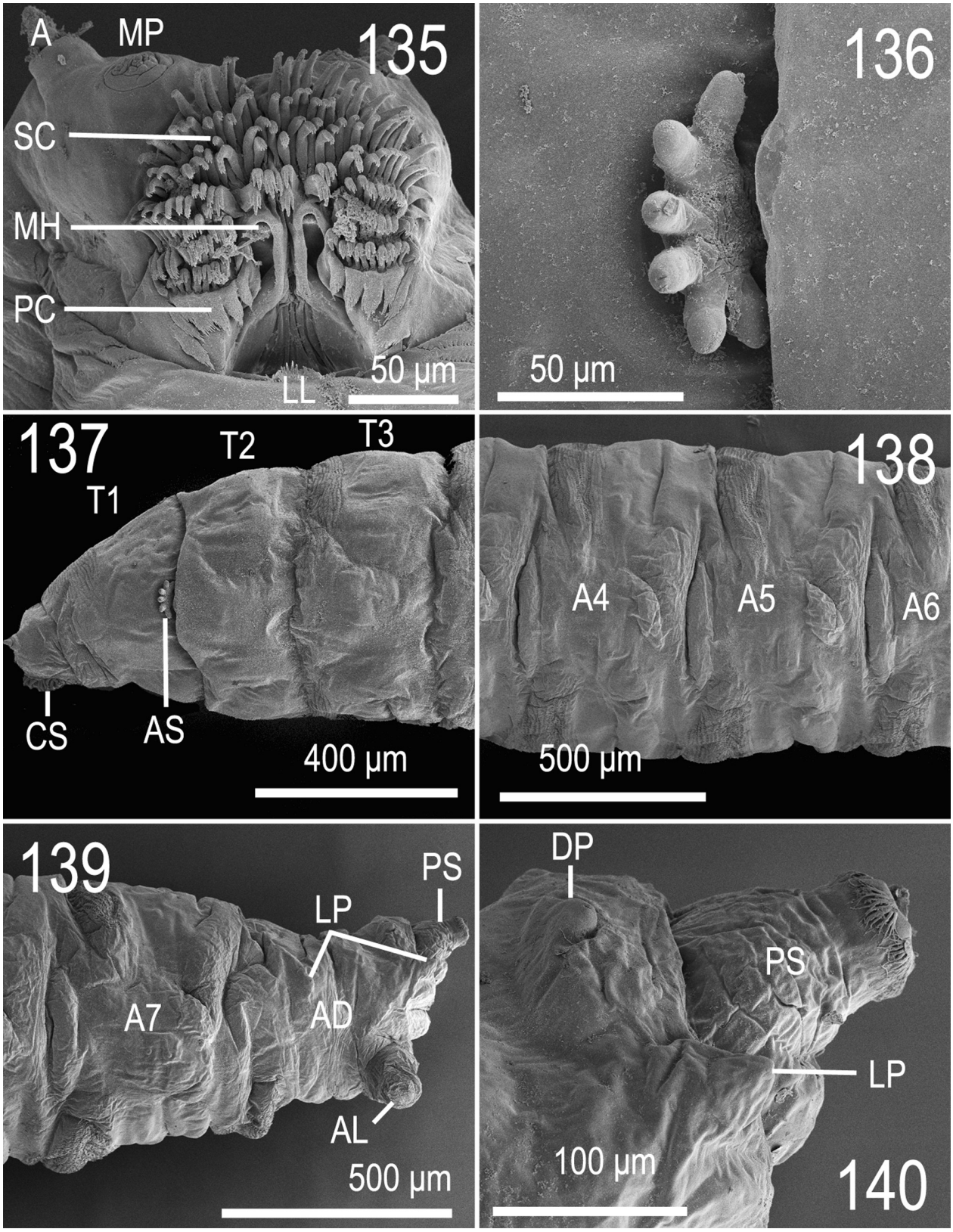
FIGURES 131–134. *Sapromyza intonsa*, first (131, 132) and second (133, 134) instars. 131. Cephalic segment, ventral view. 132. Detail of the ventral organ. 133. Cephalic segment, ventral view. 134. Detail of the ventral organ. A, antenna; LL, labial lobe; MH, mouth hook; MP, maxillary palpus; PC, peristomal cirri; SC, scraping cirri; VO, ventral organ.

Cephaloskeleton (Fig. 174). Length 0.17 mm (n=1). Mouth hooks strong, converging, compact; two teeth at apex; distal part more sclerotised comparing to the basal part. Parastomal bars strong, with longitudinal groove. Epistomal sclerite completely hyaline, almost unrecognisable. Subhypostomal sclerites converging. Ligulate sclerites small and rounded. Ventral bridge narrow. Dorsal bridge semilunar.

Second instar (Figs 133, 134). Length 2.42–3.58 mm. The labial lobe with inner hairs. 8–10 scraping cirri in the third row. Other features essentially as in the third instar.

Cephaloskeleton (Fig. 189). Length 0.39 mm (n=1). Mouth hooks very strong, broad in lateral view, converging, but apices parallel, two unequal teeth at apex. Intermediate sclerite robust, massive ventral bridge. Parastomal bars and the intermediate sclerite interconnected. Epistomal sclerite shorter than broad, arched from dorsal view. Subhypostomal sclerites converging, widened at anterior end; ligulate sclerites tiny. Dorsal bridge semilunar. Dorsal cornua broad in lateral view. Vertical plates narrower than dorsal cornua. Ventral cornua with posterior third hyaline, slightly convex. Cibarium hyaline.

Third instar (Figs 135–140). Length 3.41–5.16 mm. The facial mask narrow, (up to 12 scraping cirri per row), the scraping cirri in first row with reduced number of apical papillae (3). The stalks of scraping cirri appear to be only slightly laterally flattened and longitudinally corrugated (possibly artefact of preparation for SEM, but it indicates that they are rather rounded on cross-section in living larva). The peristomal cirri monomorphic, stout and



FIGURES 135–140. *Sapromyza intonsa*, third instar. 135. Cephalic segment, ventral view. 136. Anterior spiracle, lateral view. 137. Thoracic segments, lateral view. 138. Abdominal segments, lateral view. 139. Last abdominal segments and the anal division. 140. Detail of the posterior spiracles, lateral view. A, antenna; A4–A7, first to seventh abdominal segments; AD, anal division; AL, ambulatory lobe; CS, cephalic segment; DP, dorsal process; LL, labial lobe; LP, lateral process; MH, mouth hook; MP, maxillary palpus; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; T1–T3, first to third thoracic segments; VO, ventral organ.

few in number. The ventral organ stout with 6 additional digitiform processes. The labial lobe with long internal hairs. The anterior spiracles fan shaped with 6 papillae. The body segments essentially bare; the first thoracic segment with broad belt of comb spines dorsally; the second thoracic segment smooth; the third thoracic segment with narrow band of comb spines dorsally. The processes of anal division barely developed. The sprouts of posterior spiracles basally inflated; the peristigmatic tufts long.

Cephaloskeleton (Fig. 204). Length 0.54–0.58 mm. Mouth hooks strong, converging, apices subparallel. Intermediate sclerite shorter than mouth hooks. The parastomal bars and the intermediate sclerite fused via dorsal ridge; ventral bridge strong. Epistomal sclerite as a narrow transverse strip, arched in dorsal view; posterior hyaline plate rectangled. Subhypostomal sclerites converging, club-shaped. Ligulate sclerites tiny. Dorsal cornua slightly narrower comparing to the ventral cornua. Ventral cornua hyaline in the posterior third. Cibarium hyaline.

Sapromyza sexpunctata Meigen 1826

The mature larvae soft and dorsoventrally flattened with marked welts and crevices. The Malpighian tubules slightly and irregularly inflated.

Egg (Figs 27–29)**.** Length 0.69–0.75 mm. Ridges clearly developed and sharp, in the dorsal side ridges pronounced with indicated transversal septa. In the ventral side the ridges suppressed, near the apical pole with hexagonal structure, towards the posterior pole the ridges become more apparent.

First instar (Fig. 141). Length 0.58–0.97 mm. The scraping cirri elongated and numerous (>25 in a single row).

Cephaloskeleton (Fig. 175). Length 0.21 mm (n=1). The mouth hooks with 10 apical teeth; stalked part hyaline, slender.

Second instar (Figs 142–144). Length 2.16–3.58 mm. The scraping cirri elongated and 23–26 per row. The posterior rows of peristomal cirri very slender, almost filamentous. The first and second thoracic segment smooth, the third one sparsely spinous. The abdominal segments densely spinous. The ambulatory lobes slender.

Cephaloskeleton (Fig. 190). Length 0.45–0.49 mm. Very similar to *P. vittata*. Major difference represents only the shape of subhypostomal sclerites.

Third instar (Fig. 145). Length 3.11–4.04 mm. The scraping cirri up to 40 per row. The first and second thoracic segments smooth. The abdominal segments spinous.

Cephaloskeleton (Fig. 205). Length 0.77–0.81 mm. Mouth hooks slender, slightly converging; distal part relatively strong and hook-shaped. Intermediates sclerite slender. Epistomal sclerite trapezoid, anterior margin concave. Subhypostomal sclerites peculiar. Rami and parastomal bars very slender. Dorsal bridge approximately as long as broad. Dorsal cornua slender, almost as long as ventral ones. Ventral cornua very broad, mildly sclerotised. Cibarium slightly pigmented.

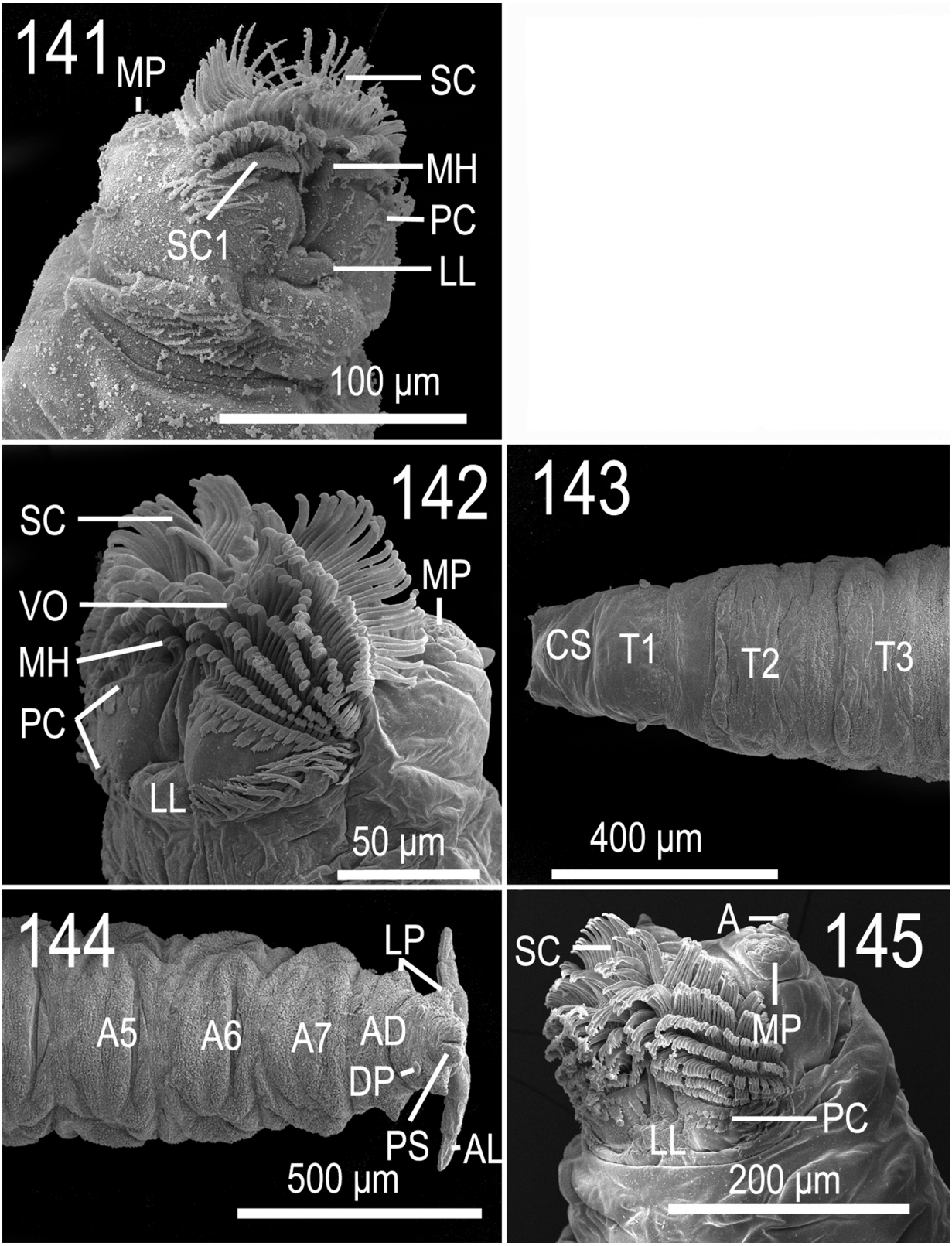
Sapromyzosoma quadricincta (Becker 1895)

The mature larvae relatively large, soft and dorsoventrally flattened, the welts and crevices well developed. The Malpighian tubules slightly and irregularly inflated.

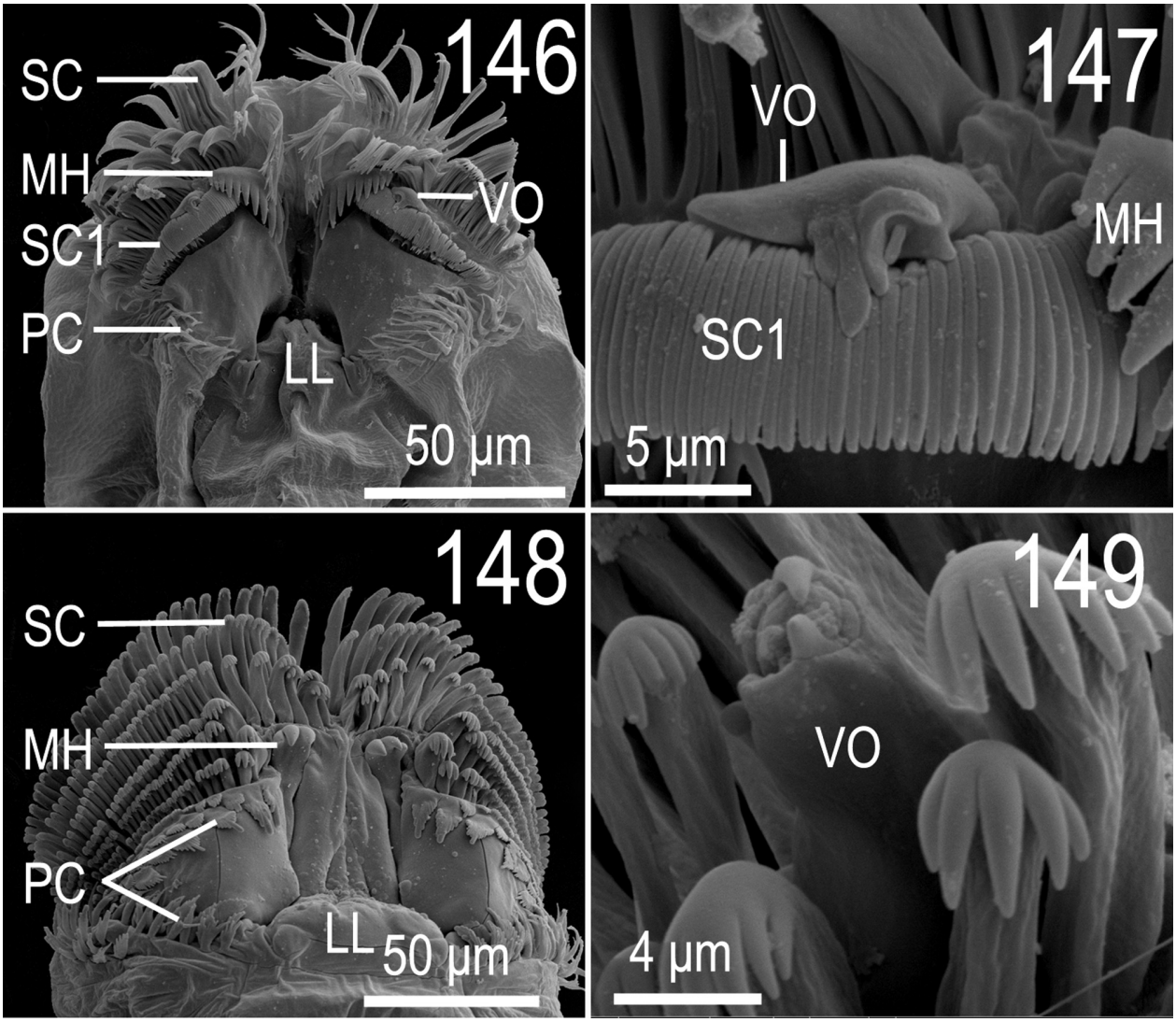
Egg (Figs 30–32)**.** Length 0.81–0.95 mm. Robust, dorsal and ventral side poorly differentiated; ridges well developed, seldom fusing; micropylar pole with star-like collar; posterior pole with tubercle with several aeropyles.

First instar (Figs 146, 147). Length 1.25–1.98 mm. The first row of scraping cirri very dense, long (number of cirri exceeds 60) and directed oblique to the longitudinal body axis; below the first row are visible several small and sparse cirri. The ventral organ with two digitiform process; the central sensilla with outer horn as long as the outer digitiform process.

Cephaloskeleton (Fig. 176). Length 0.27–0.32 mm. Mouth hooks broad, spatulate, with 10–12 teeth, basal part hyaline and slender. Epistomal sclerite longer than broad, with prominent beak-like outgrowth from apical part of labrum. Parastomal bars slender. Subhypostomal sclerites opposite. Posterior sclerite voluminous. Very similar to *P. vittata*.



FIGURES 141–145. *Sapromyza sexpunctata*, all instars. 141. Cephalic segment of the first instar, latero-ventral view. 142. Cephalic segment of the second instar, latero-ventral view. 143. Thoracic segments of the second instar, dorsal view. 144. Abdominal segments and the anal division of the second instar, dorsal view. 145. Cephalic segment of the third instar, latero-ventral view. A, antenna; A4–A7, fifths to seventh abdominal segments; AD, anal division; Al, ambulatory lobes; CS, cephalic segment; DP, dorsal process; LL, labial lobe; LP, lateral process; MH, mouth hook; MP, maxillary palpus; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; SC1, first row of scraping cirri; T1–T3, first to third thoracic segments; VO, ventral organ.



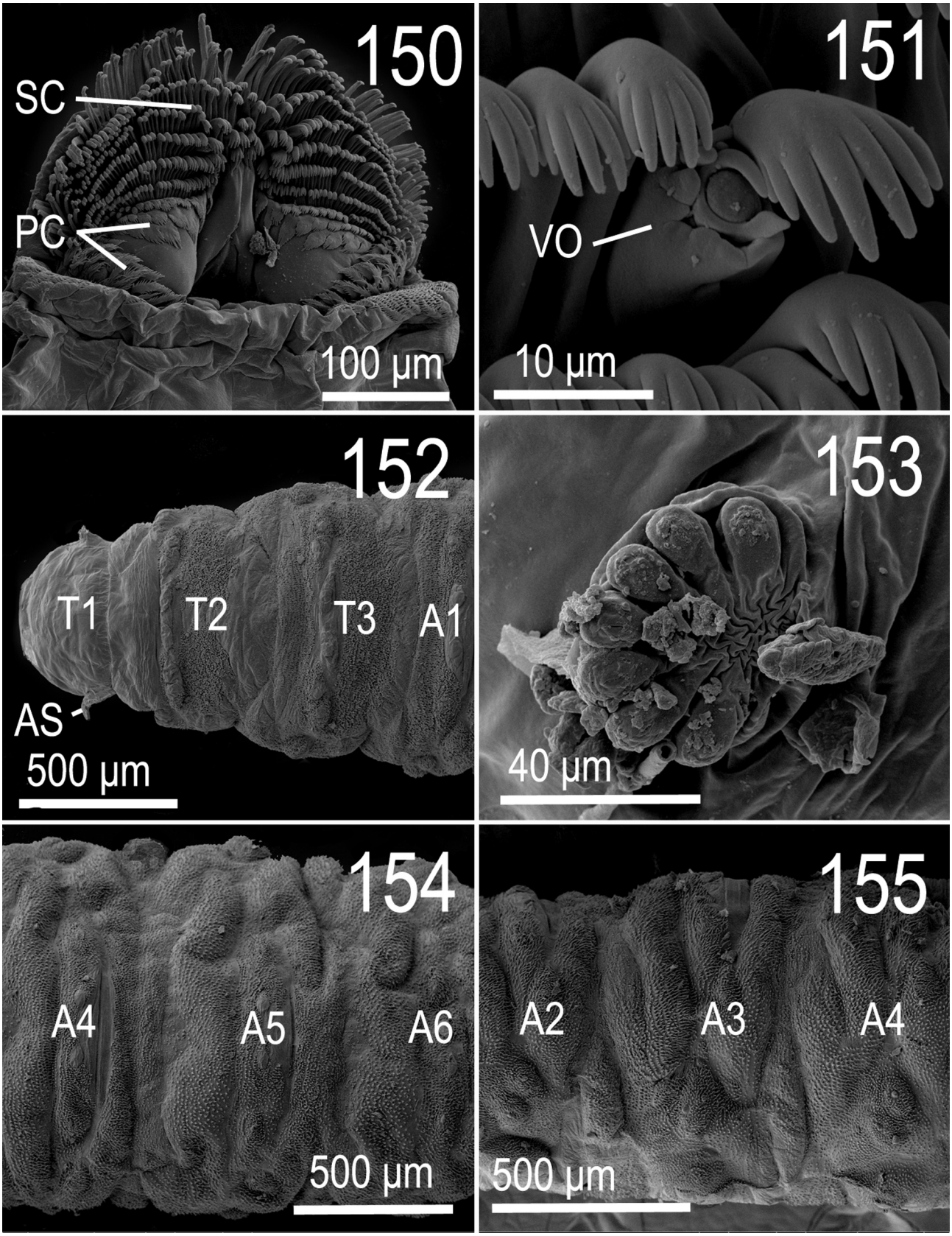
FIGURES 146–149. *Sapromyzosoma quadricincta*, first (146, 147) and second (148, 149) instars. 146. Cephalic segment, ventral view. 147. Detail of the ventral organ. 148. Cephalic segment, ventral view. 149. Detail of the ventral organ. A, antenna; LL, labial lobe; MH, mouth hook; MP, maxillary palpus; PC, peristomal cirri; SC, scraping cirri; SC1, first row of scraping cirri; VO, ventral organ.

Second instar (Figs 148, 149). Length 2.11–2.98 mm. The facial mask broad and flat, number of scraping cirri per row exceeds 30. The peristomal cirri triangular to filamentous, with long marginal hairs.

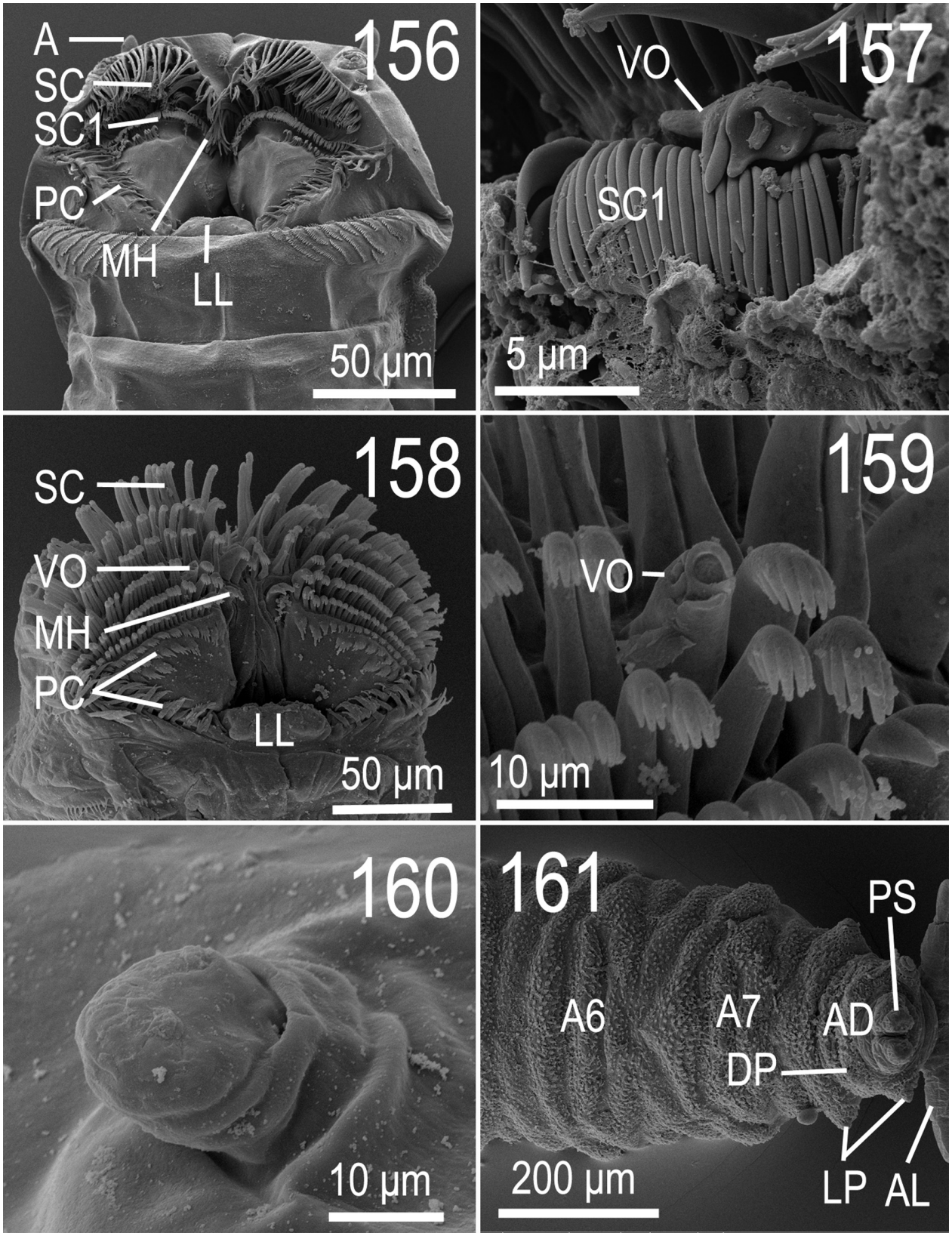
Cephaloskeleton (Fig. 191). Length 0.59–0.60 mm. Mouth hooks almost parallel, slender, with 4–5 apical teeth. Intermediate sclerite slender; ventral bridge very broad, descending posteriad. Epistomal sclerite rounded. Subhypostomal sclerites peculiar, resembling sunglasses. Parastomal bars and rami very slender. Dorsal bridge trapezoid. Dorsal cornua slender, shorter than ventral ones. Ventral cornua very broad, finely striolated at connection with the vertical plates, dorsal margin convex and sclerotised. Cibarium hyaline.

Third instar (Figs 150–155). Length 3.89–6.17 mm. The facial mask as in the second instar, but the number of scraping cirri per row reaches 40. The first thoracic segment smooth; the second thoracic segment with smooth anterior third and two large dorso-lateral areas covered by hairs; the third thoracic segment anteriorly with comb spines, posteriorly covered by hairs. The abdominal segments densely covered by spines and hairs, except of small area behind dorsal pair of medial tubercles; ventrally, the spines and hairs are more gentle and sparse. Anal division relatively small and strongly tapering; completely covered by spines; the posterior spiracles on short sprouts. Anterior spiracles with 7 papillae.

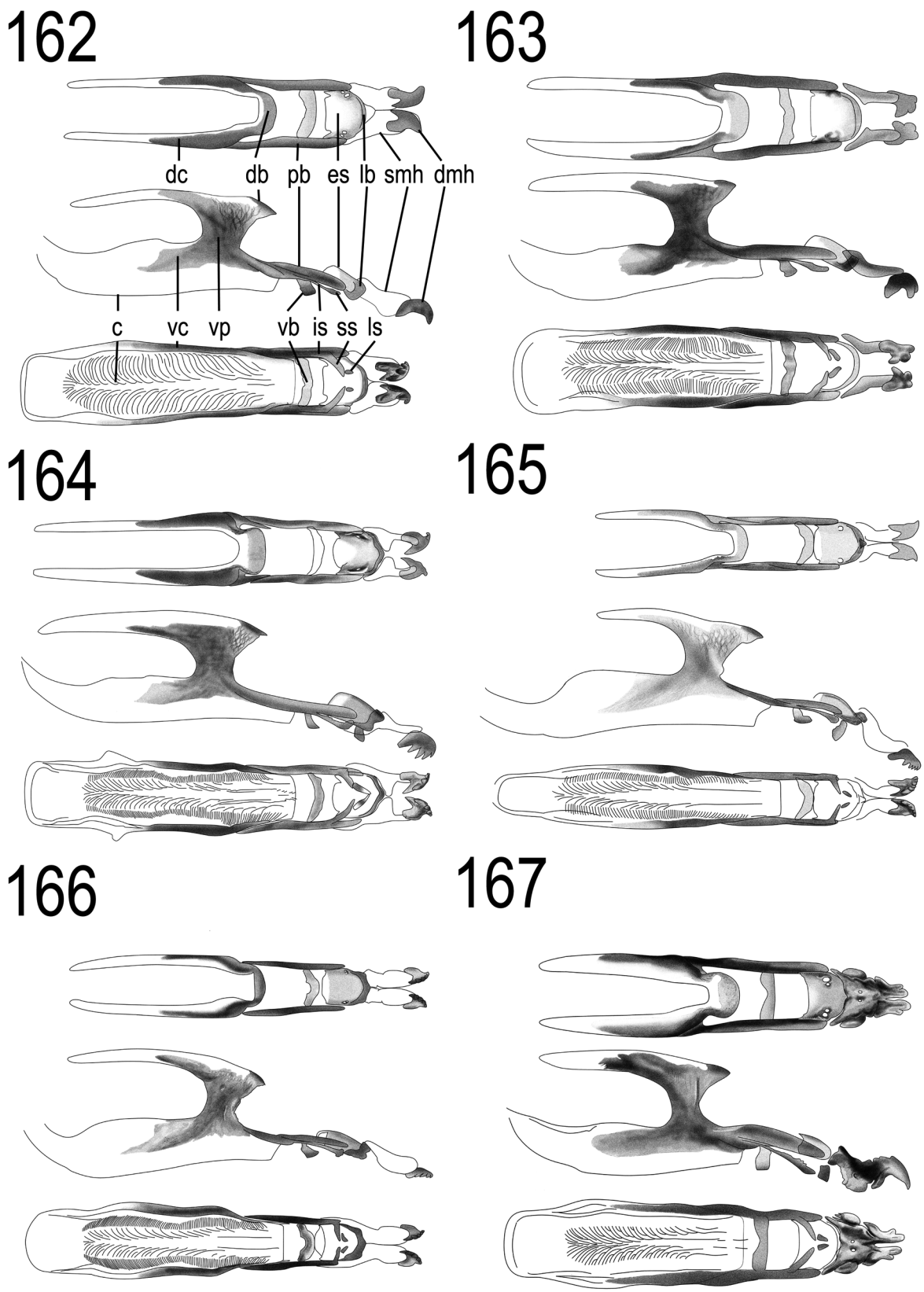
Cephaloskeleton (Fig. 206). Length 0.98–1.01 mm. Basic organization as in the second instar, but tips of mouth hooks simple.



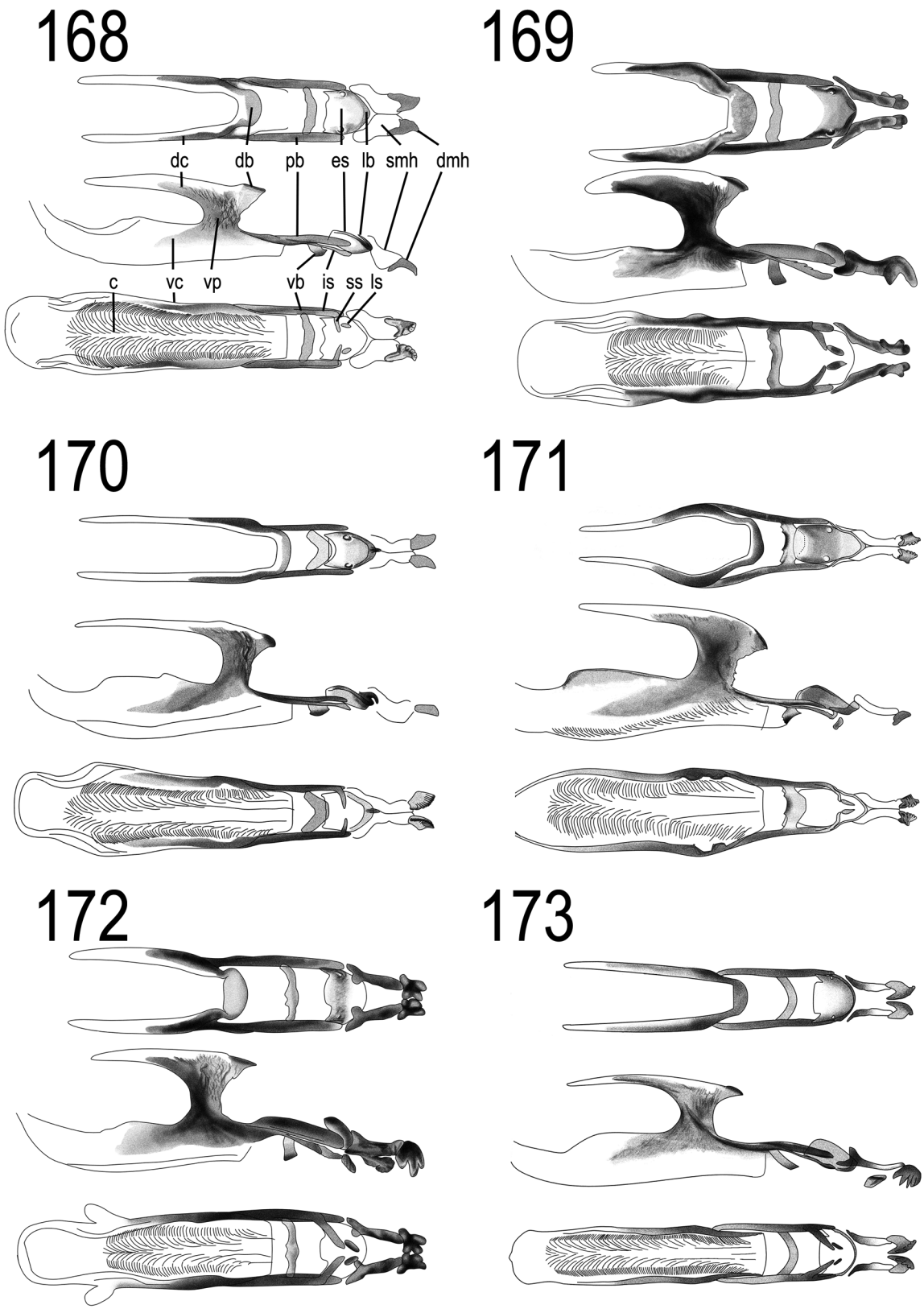
FIGURES 150–155. *Sapromyzosoma quadricincta*, third instar. 150. Cephalic segment, ventral view. The mouth hooks are retracted and consequently not visible. 151. Detail of the ventral organ. 152. Thoracic segments, dorsal view. 153. Anterior spiracle, lateral view. 154. Abdominal segments, dorsal view. 155. Abdominal segments, lateral view. A1–A6, first to sixth abdominal segments; AS, anterior spiracles; MH, mouth hooks; MP, maxillary palpus; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; T1–T3, first to third thoracic segments; VO, ventral organ.



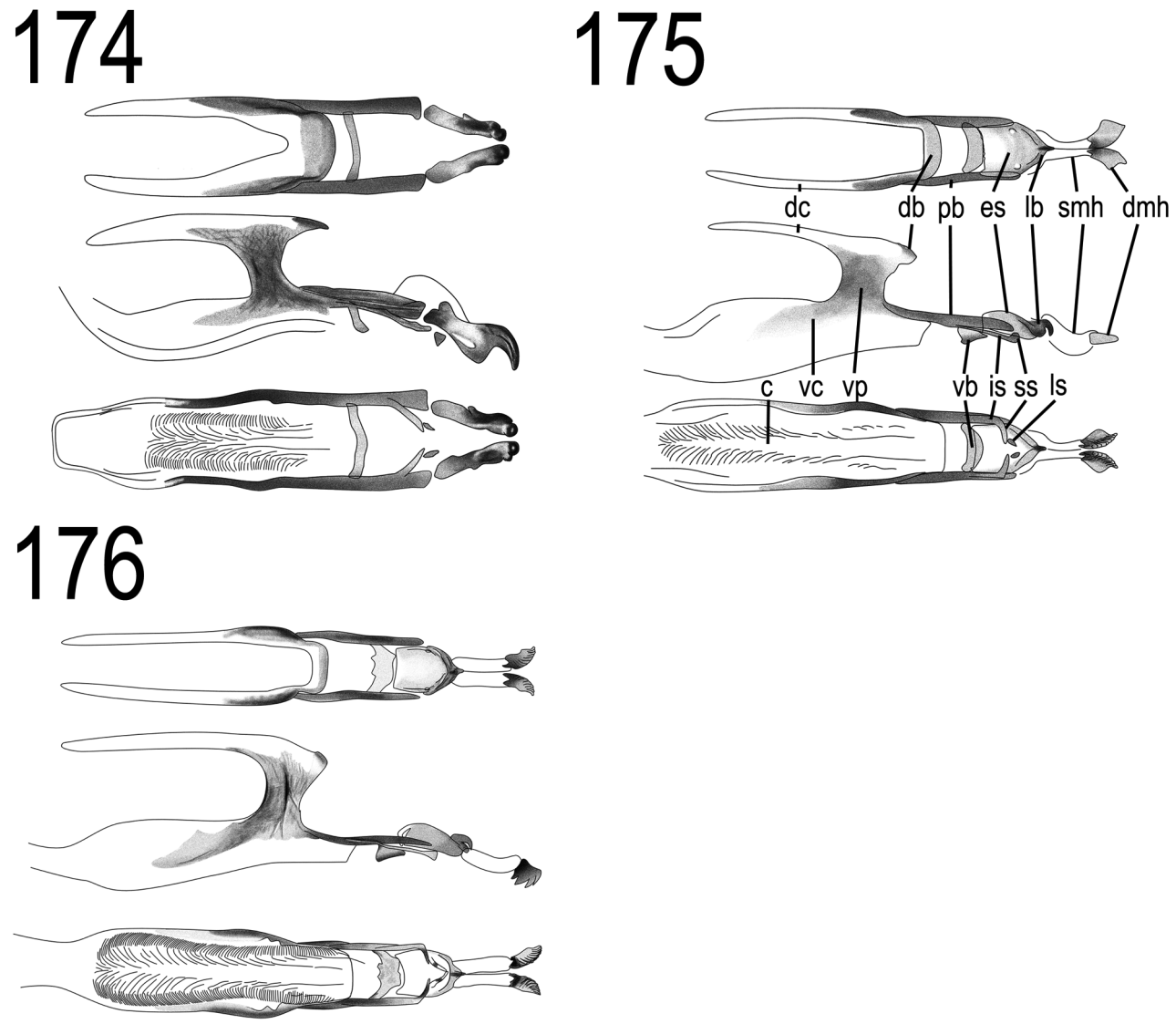
FIGURES 156–161. *Sapromyzosoma quadripunctata*, first (156, 157) and second (158–161) instar. 156. Cephalic segment, ventral view. 157. Detail of the ventral organ. 158. Cephalic segment, ventral view. 159. Detail of the central organ. 160. Anterior spiracle, lateral view. 161. Last abdominal segments and the anal division, dorsal view. A, antenna; A6–A7, sixth to seventh abdominal segments; AD, anal division; AL, ambulatory lobe; DP, dorsal process; LL, labial lobe; LP, lateral process; MH, mouth hook; MP, maxillary palpus; PC, peristomal cirri; PS, posterior spiracles; SC, scraping cirri; SC1, first row of scraping cirri; VO, ventral organ.



FIGURES 162–167. Cephaloskeletons of first larval instar, dorsal (top), lateral (middle) and ventral (bottom) view. 162. *Cnemacantha muscaria*. 163. *Homoneura biumbrata*. 164. *H. limnea*. 165. *Minettia austriaca*. 166. *M. fasciata*. 167. *M. flaviventris*. c, cibarium; db, dorsal bridge; dc, dorsal cornua; dmh, distal part of mouth hook; es, epistomal sclerite; is, intermediate sclerite; lb, labrum; ls, ligulate sclerite; smh, stalked part of mouth hook; pb, parastomal bar; ss, subhypostomal sclerite; vb, ventral bridge; vc, ventral cornua; vp, vertical plate.



FIGURES 168–173. Cephaloskeletons of first larval instar, dorsal (top), lateral (middle) and ventral (bottom) view. 168. *Minettia loewi*. 169. *M. plumicornis*. 170. *Poecilolycia vittata*. 171. *Pseudolyciella pallidiventris*. 172. *Sapromyza apicalis*. 173. *S. hyalinata*. c, cibarium; db, dorsal bridge; dc, dorsal cornua; dmh, distal part of mouth hook; es, epistomal sclerite; is, intermediate sclerite; lb, labrum; ls, ligulate sclerite; smh, stalked part of mouth hook; pb, parastomal bar; ss, subhypostomal sclerite; vb, ventral bridge; vc, ventral cornua; vp, vertical plate.



FIGURES 174–176. Cephaloskeletons of first larval instar, dorsal (top), lateral (middle) and ventral (bottom) view. 174. *Sapromyza intonsa*. 175. *S. sexpunctata*. 176. *Sapromyzosoma quadricincta*. c, cibarium; db, dorsal bridge; dc, dorsal cornua; dmh, distal part of mouth hook; es, epistomal sclerite; is, intermediate sclerite; lb, labrum; ls, ligulate sclerite; smh, stalked part of mouth hook; pb, parastomal bar; ss, subhypostomal sclerite; vb, ventral bridge; vc, ventral cornua; vp, vertical plate.

***Sapromyzosoma quadripunctata* (Linnaeus 1758)**

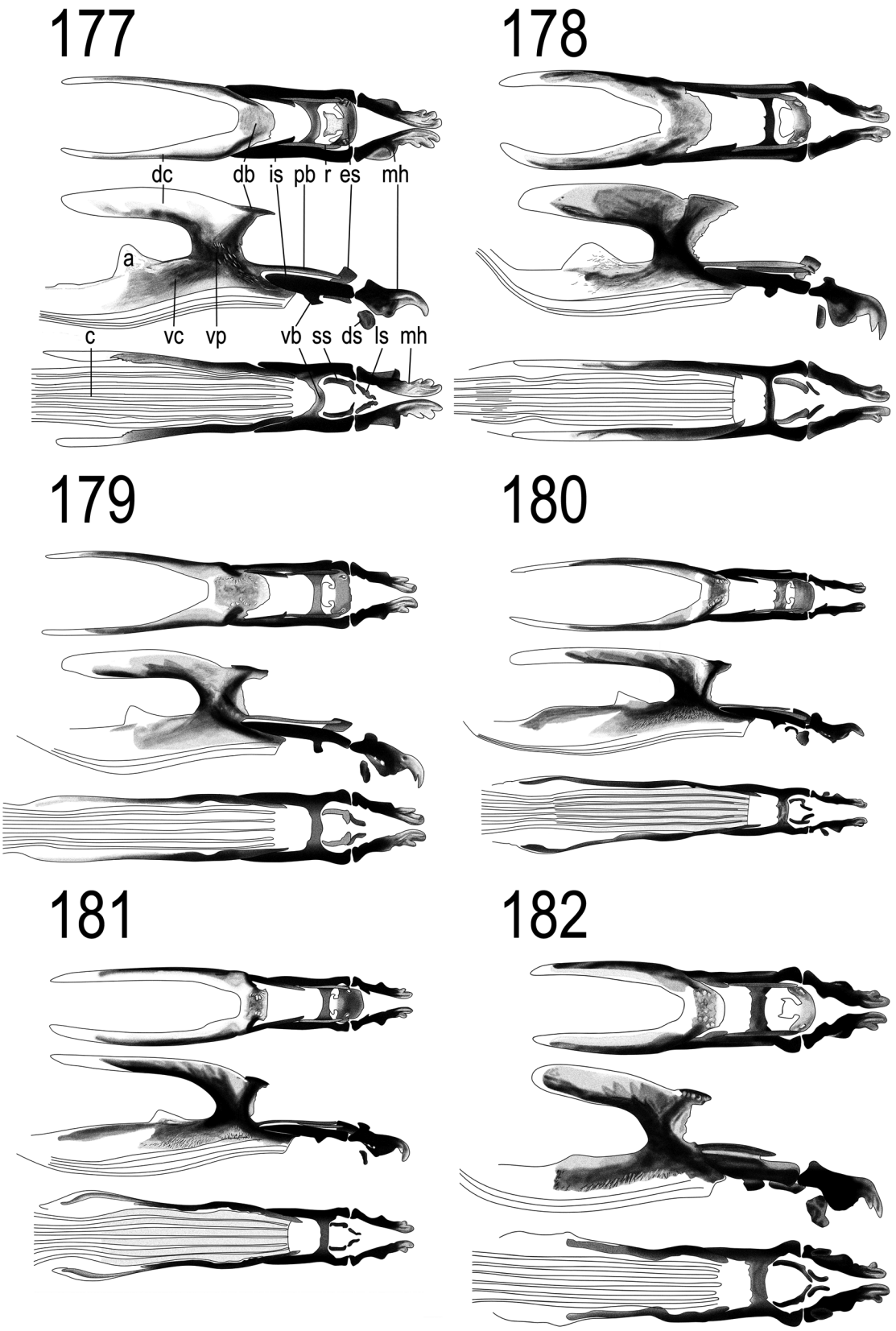
The mature larvae relatively large, soft and dorsoventrally flattened, welts and crevices well developed. The Malpighian tubules slightly and irregularly inflated.

Egg. Length 0.67–0.19 mm. The ridges and ribs well developed, sharp-edged, ribs creating small regular rectangles. Posterior pole with conspicuous tubercle with few openings. Small eggs with ribs only indicated, ridges simple, seldom fusing, the surface tuberculous.

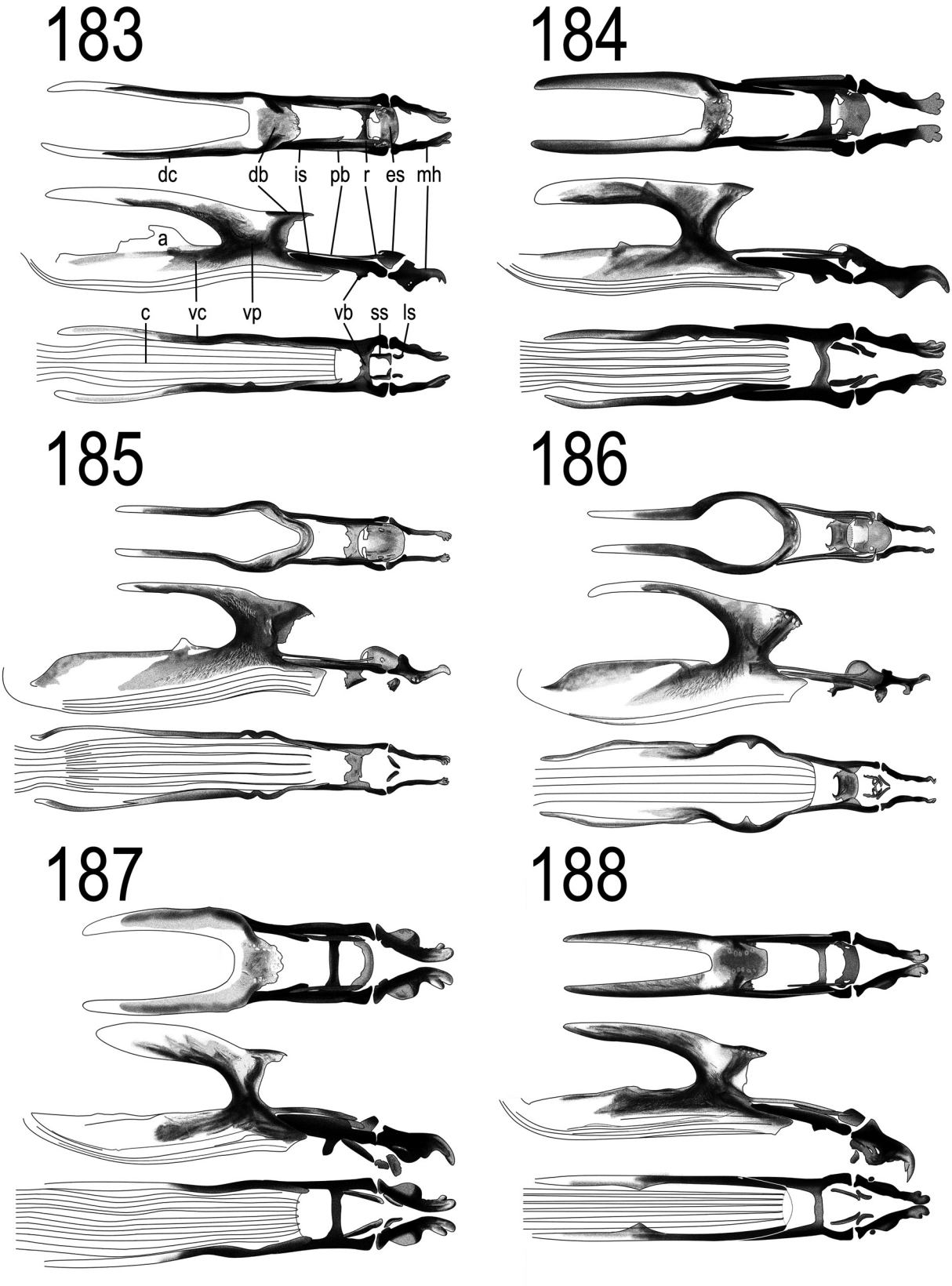
First instar (Figs 156, 157). Length 1.21–1.45 mm. The facial mask broad, number of scraping cirri per row large (up to 60). The peristomal cirri filiform, aligned in a diagonal row. The labial lobe small (shorter than long). The ventral organ with small basal lobe and two digitiform processes.

Cephaloskeleton. Length 0.25–0.26 mm, very similar to the previous species.

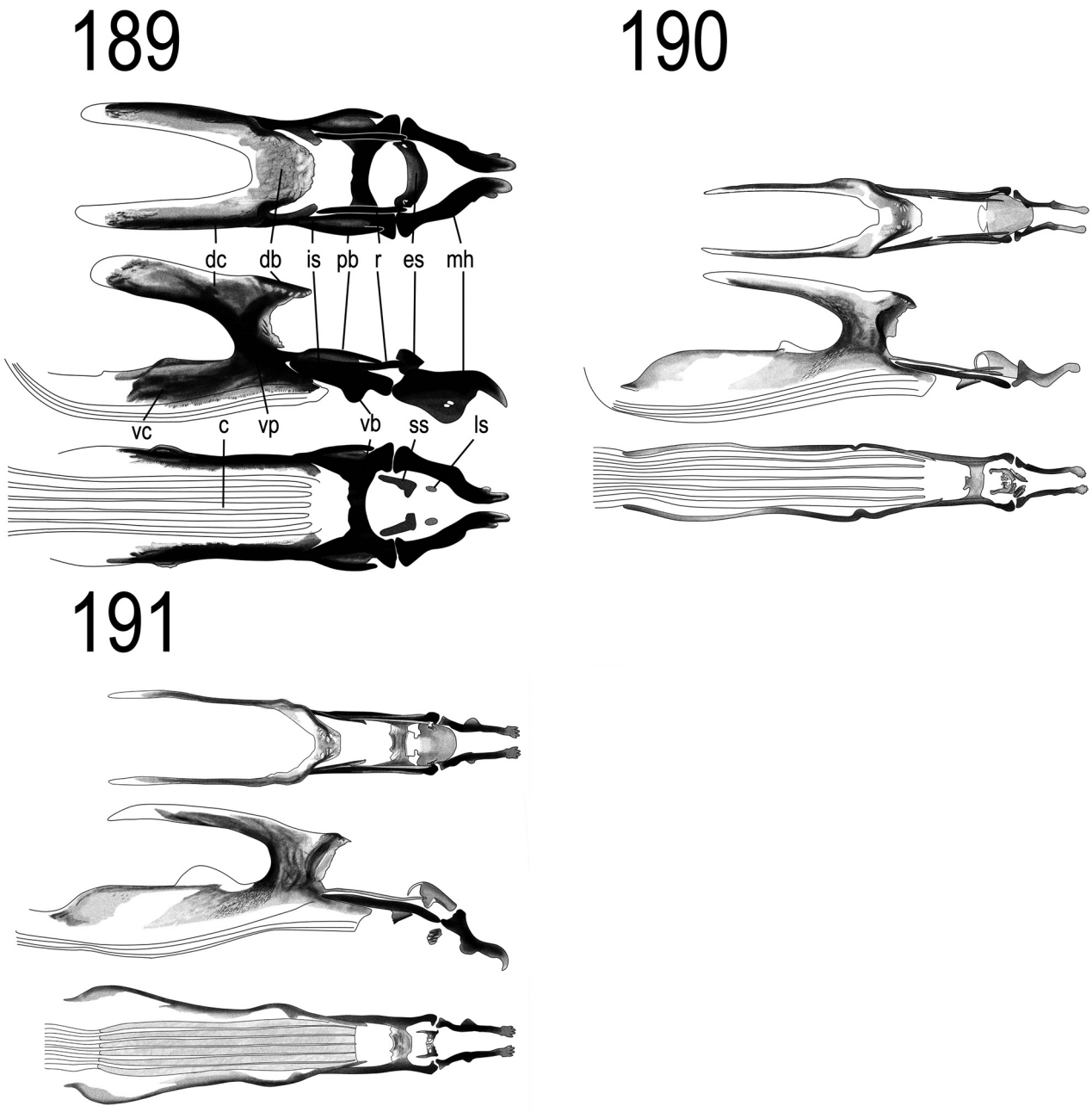
Second instar (Figs 158–161). Length 2.12–2.85 mm. Facial mask broad, with numerous cirri. First thoracic segment smooth; second one with narrow string of comb spines anterodorsally; third one with broad band of comb spines and hairs. Abdominal segments and anal division dorsally covered by robust spines, laterally by hairs and ventrally by spines on creeping welts.



FIGURES 177–182. Cephaloskeletons of second larval instar, dorsal (top), lateral (middle) and ventral (bottom) view. 177. *Cnemacantha muscaria*. 178. *Homoneura biumbrata*. 179. *H. limnea*. 180. *Minettia austriaca*. 181. *M. fasciata*. 182. *M. flaviventris*. a, apodeme of ventral cornu c, cibarium; db, dorsal bridge; dc, dorsal cornua; ds, dental sclerite; es, epistomal sclerite; is, intermediate sclerite; lb, labrum; ls, ligulate sclerite; mh, mouth hook; pb, parastomal bar; r, rami; ss, subhypostomal sclerite; vb, ventral bridge; vc, ventral cornua; vp, vertical plate.



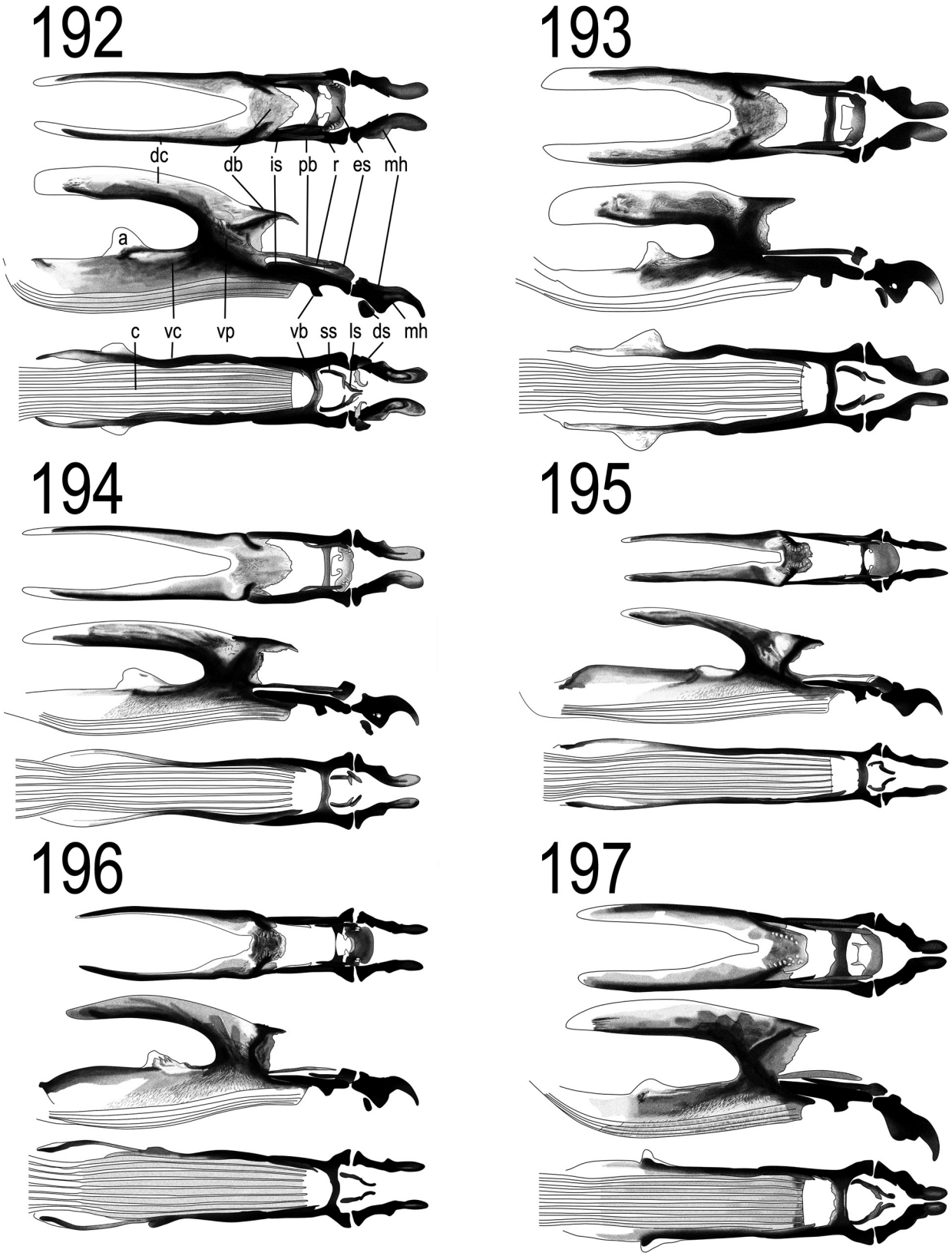
FIGURES 183–188. Cephaloskeletons of second larval instar, dorsal (top), lateral (middle) and ventral (bottom) view. 183. *Minettia loewi*. 184. *P. litura*. 185. *Poecilolycia vittata*. 186. *Pseudolyciella pallidiventris*. 187. *Sapromyza apicalis*. 188. *S. hyalinata*. a, apodeme of ventral cornu; c, cibarium; db, dorsal bridge; dc, dorsal cornua; es, epistomal sclerite; is, intermediate sclerite; lb, labrum; ls, ligulate sclerite; mh, mouth hook; pb, parastomal bar; r, rami; ss, subhypostomal sclerite; vb, ventral bridge; vc, ventral cornua; vp, vertical plate.



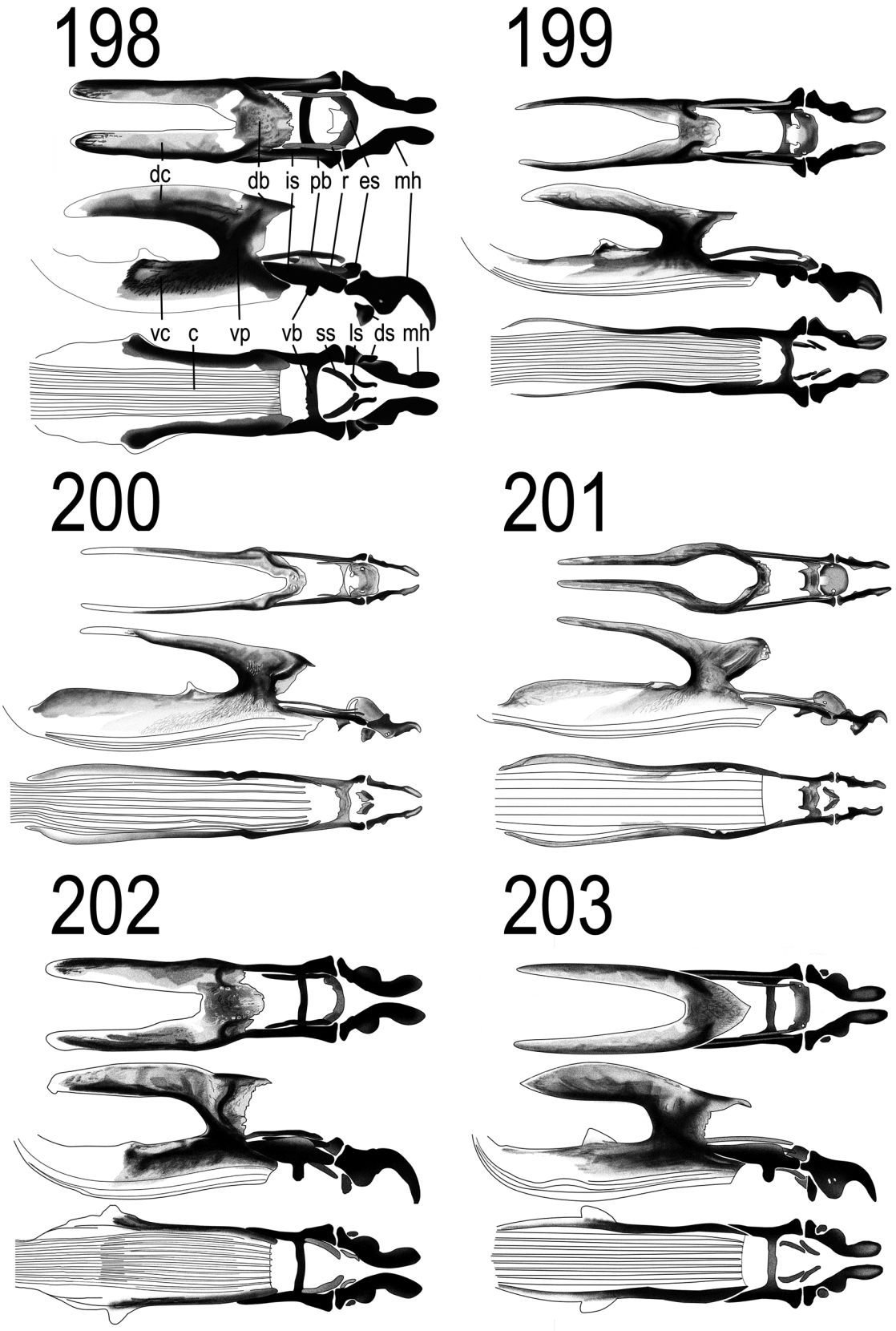
FIGURES 189–191. Cephaloskeletons of second larval instar, dorsal (top), lateral (middle) and ventral (bottom) view. 189. *Sapromyza intonsa*. 190. *S. sexpunctata*. 191. *Sapromyzosoma quadricincta*. a, apodeme of ventral cornu; c, cibarium; db, dorsal bridge; dc, dorsal cornua; es, epistomal sclerite; is, intermediate sclerite; lb, labrum; ls, ligulate sclerite; mh, mouth hook; pb, parastomal bar; r, rami; ss, subhypostomal sclerite; vb, ventral bridge; vc, ventral cornua; vp, vertical plate.

Cephaloskeleton. Length 0.49–0.51 mm. Very similar to previous species. Potential differences include the shape of subhypostomal sclerites.

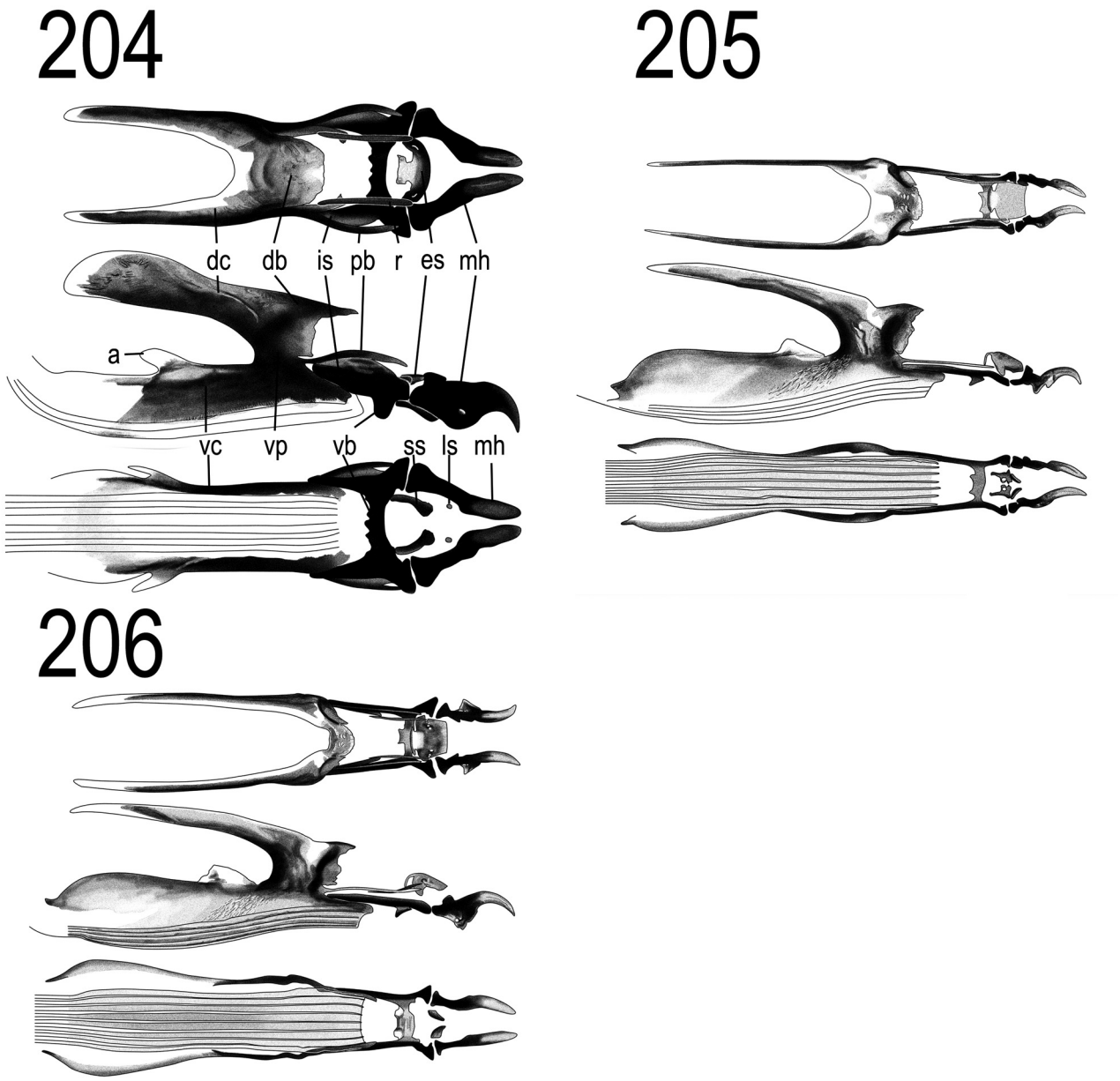
Third instar was not obtained.



FIGURES 192–197. Cephaloskeletons of third larval instar, dorsal (top), lateral (middle) and ventral (bottom) view. 192. *Cnemacantha muscaria*. 193. *Homoneura biumbrata*. 194. *H. limnea*. 195. *Minettia austriaca*. 196. *M. fasciata*. 197. *M. flaviventris*. a, apodeme of ventral cornu; c, cibarium; db, dorsal bridge; dc, dorsal cornua; es, epistomal sclerite; is, intermediate sclerite; lb, labrum; ls, ligulate sclerite; mh, mouth hook; pb, parastomal bar; r, rami; ss, subhypostomal sclerite; vb, ventral bridge; vc, ventral cornua; vp, vertical plate.



FIGURES 198–203. Cephaloskeletons of third larval instar, dorsal (top), lateral (middle) and ventral (bottom) view. 198. *Minettia plumicornis*. 199. *P. litura*. 200. *Poecilolycia vittata*. 201. *Pseudolyciella pallidiventris*. 202. *Sapromyza apicalis*. 203. *S. hyalinata*. a, apodeme of ventral cornu; c, cibarium; db, dorsal bridge; dc, dorsal cornua; es, epistomal sclerite; is, intermediate sclerite; lb, labrum; ls, ligulate sclerite; mh, mouth hook; pb, parastomal bar; r, rami; ss, subhypostomal sclerite; vb, ventral bridge; vc, ventral cornua; vp, vertical plate.



FIGURES 204–206. Cephaloskeletons of third larval instar, dorsal (top), lateral (middle) and ventral (bottom) view. 204. *Sapromyza intonsa*. 205. *S. sexpunctata*. 206. *Sapromyzosoma quadricincta*. a, apodeme of ventral cornu; apoc, cibarium; db, dorsal bridge; dc, dorsal cornua; es, epistomal sclerite; is, intermediate sclerite; lb, labrum; ls, ligulate sclerite; mh, mouth hook; pb, parastomal bar; r, rami; ss, subhypostomal sclerite; vb, ventral bridge; vc, ventral cornua; vp, vertical plate.

Discussion

Our results together with our previous works (Semelbauer & Kozánek 2011, 2012, 2013) and one Holarctic species described in Miller & Foote (1976) cover altogether 31 species from 13 genera of the 19 of total of the known European lauxaniid fauna. Currently, following European taxa have described immatures: *Cnemacantha muscaria* (monotypic species), *Aulogastromyia* (1 species), *Homoneura* (2 species), *Calliopum* (4 species), *Lauxania* (2 species), *Meiosimyza* (4 species), *Minettia* (7 species), *Peplomyza* (1 species), *Poecilolycia* (1 species), *Pseudolyciella* (1 species), *Sapromyza* (4 species), *Sapromyzosoma* (2 species) and *Tricholauxania* (1 species). From European representatives, only 6 genera are missing: *Eusapromyza*, *Neoparoecus*, *Pachycerina*, *Prosopomyia*, *Trigonometopus* and *Sciasminettia* Shewell, 1971 (Calres-Tolrá 2006).

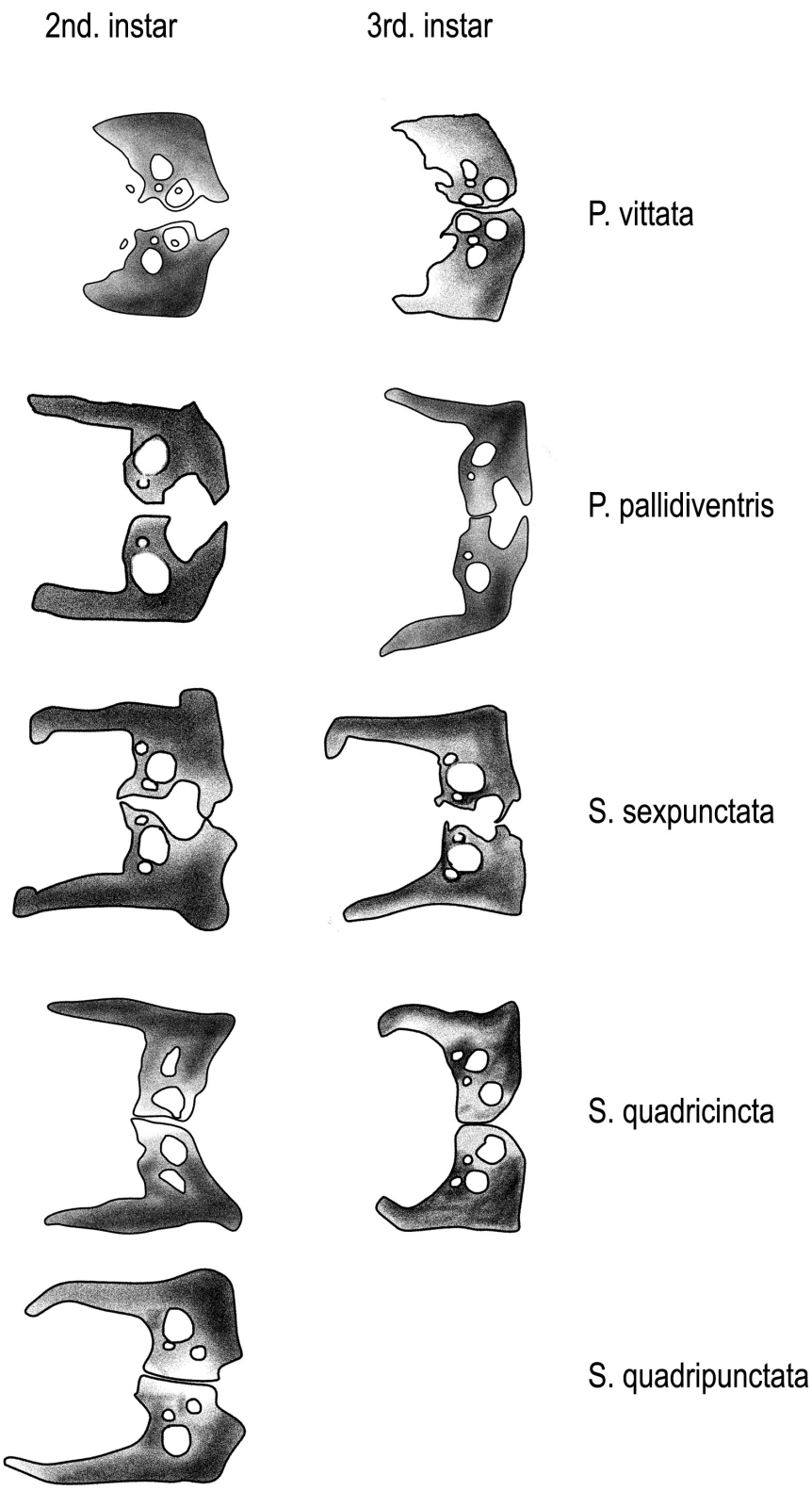


FIGURE 207. Ligulate sclerites of second and third instar of species *Poecilolycia vittata*, *Pseudolyciella pallidiventris*; *Sapromyza sexpunctata*, *Sapromyzosoma quadricincta* and *S. quadripunctata*, dorsal, resp. ventral views.

The egg. The eggs of lauxaniids are in good agreement with descriptions of Miller & Foote (1976). Generally, the egg shell (=chorion) evolves rather fast in other Cyclorrhapha (Kambyselis 1974, Meier & Hilger 1999). This also applies to Lauxaniidae. Even within single genus it is often complicated to find unique characters, which could characterise that group. Exception is the genus *Minettia*, which can be characterised through elongated shape, globular and almost ornamental posterior tubercle and suppressed ribs.

The external morphology of larvae. The basic organisation of larval morphology of lauxaniid immatures is very conservative as revealed by the species that have so far been studied. Among the stable features of lauxaniid larvae are included the elongated scraping cirri, enlarged ventral organ, abdominal ambulatory lobes and common organization of welts and crevices (Semelbauer & Kozánek 2011, 2012, 2013).

The first instar posses a unique lobe-like form of maxillary organ, the tips of scraping cirri are simple and the first row of scraping cirri is dense and chitinised. The mouth hooks are divided in two parts, the distal part is equipped with 2–10 teeth. The parastomal bars are enlarged and basally fusing to the intermediate sclerite. The cibarial ridges are missing.

The two parts of mouth hooks are in compliance with possible plesiomorphic state within larvae of Cyclorrhapha (Courtney *et al.* 2000)

The second and third instars are fairly uniform. Unique features held in common include the elongated cylindrical form of the maxillary organ and the scraping cirri with apical chitinised papillae. The second instar is characterised by simple form of the anterior spiracles (without papillae), the mouth hooks bear 2–5 apical teeth and there are only 7 cibarial ridges. The third instar is typical in having the anterior spiracles with papillae, the simple tips of the mouth hooks and 9 cibarial ridges.

At first sight, the larvae can be divided in two groups: larvae of the first group have a strongly inflated distal part of the Malpighian tubules filled with white matter. The white matter is used to cover the puparium during pupariation (Miller & Foote1976) and was observed also in *Minettia longipennis* (Semelbauer & Kozánek 2011), *M. austriaca*, *M. plumicornis*, *Homoneura limnea*, *H. notata*, *H. dilecta* and *H. biumbrata* (unpublished results). Larvae of the second group have no or only moderately inflated distal parts of the Malpighian tubules. In this case, the puparium remains bare, as in *Calliopum*, *Lauxania* (Semelbauer & Kozánek 2012), *Meiosimyza*, *Tricholauxania* and *Aulogastromyia* (Semelbauer & Kozánek 2013) and was observed also for *Sapromyza apicalis*, *S. hyalinata*, *Peplomyza litura* and *P. intermedia* (unpublished results). These results contrast with findings of Miller & Foote (1976), where all nine species belonged to the first type. The inflated Malpighian tubules are thus not a feature characterising lauxaniids as a whole.

While the basic organisation of larval body is stable, the vestiture of integument considerably varies from almost completely smooth to very complex pattern of spines, hairs or bumps, similarly as in Sepsidae (Meier 1996). The inner surface of labial lobe can be variously modified and falls within three main types: simple thorny hairs (*Peplomyza*, *Meiosimyza*, *Tricholauxania* and *Aulogastromyia*, Semelbauer & Kozánek 2013), hairs similar to short peristomal cirri (*Calliopum*, *Lauxania*, *Sapromyza intonsa*, *S. apicalis and S. hyalinata*) and essentially bare labial lobe with two longitudinal grooves (*Minettia* spp., *Cnemacantha muscaria*, *Homoneura* spp., *Pseudolyciella pallidiventris*, *Poecilolycia vittata*, *Sapromyza sexpunctata*, *Sapromyzosoma* spp.). In the first instar the labial lobe is always bare except of *S. intonsa.*

The form of the **anterior spiracles** is fan-shaped in most species though the exact number of papillae may differ. Species of subgenera *Frendelia* (*Minettia longipennis* and *M. austriaca*) have the anterior spiracles submerged; only the papillae remain in contact with air. The organization of papillae is specific both for *M. austriaca* (horseshoe) and *M. longipennis* (oval) (Semelbauer & Kozánek 2011).

The peristigmatic tufts of **posterior spiracles** are used to maintain contact to the atmospheric air in very moist or liquid media (Kirk-Spriggs *et al.* 2002). For example in the aquatic *Tetanocera* larvae (Sciomyzidae) the peristigmatic tufts in this case retain a bubble of air upon sinking (Chapman *et al.* 2006). The long tufts of most lauxaniids indicate life in humid conditions. Only *Minettia plumicornis* and *Sapromyza apicalis* have markedly shortened peristigmatic tufts, indicating relatively dry larval habitat.

The cephaloskeleton. Certain features of the cephaloskeleton are strongly correlated, e.g. sclerotised basal part of the mouth hooks and reduced number of the apical teeth in the first instar implies heavily sclerotised cephaloskeleton in the later instars. In the first instar this type of cephaloskeleton is typical in strong parastomal bars and broad, semilunar dorsal bridge. In the second and third instars, this type of cephaloskeleton has always

strong and converging mouth hooks and converging subhypostomal sclerites, strong intermediate sclerite, the epistomal sclerite is formed as a narrow transversal strip, the dorsal cornua tend to be broad, the posterior third of ventral cornua is hyaline and the dorsal apodeme of ventral cornua tends to move backwards. These features occur in genera *Calliopum* and *Lauxania* (Semelbauer & Kozánek 2012) and are most markedly developed in species *Homoneura biumbrata*, *Minettia flaviventris*, *M. plumicornis*, *S. apicalis*, and *S. intonsa*. From North American species, *Camptoprosopella confusa* Shewell 1939 and *Melanomyza gracilipes* Loew 1851 clearly exhibits these features (Miller & Foote 1976). The features as outlined here are somewhat exaggerated e.g. in Calliphoridae (Szpila 2010). As far as the cephaloskeleton is essentially food ingesting apparatus, we can suppose that the modifications reflect the food preferences or specialization of larvae.

To interpret the outlined cephaloskeleton characteristics, we can employ functional considerations based on the muscles attaching to the cephaloskeleton. Mouth hook depressor and mouth hook elevator span between the mouth hooks and the anterior part of ventral cornua (Schoofs *et al.* 2009, Hanslik *et al.* 2010, Wipfler *et al.* 2013). The strongly converging mouth hooks concentrate the power of right and left mouth hook depressor (Hanslik *et al.* 2010) to relatively small area, so we can hypothesize that these species actively rasp over vegetable matter. The cibarial dilator muscles span between the roof of cibarium and ventral side of dorsal cornua (Schoofs *et al.* 2009). The broad dorsal cornua indicate strong cibarial dilator muscles and an efficient sucking pump, which implies that the food is relatively viscose. The posterior part of ventral cornua is internally connected via transverse band of muscles, contraction of which closes the lumen of the cibarium. As the ventral cornua approaches, the roof of cibarium is forced to the floor (Dowding 1967). The unsclerotized—and hence flexible—posterior part of the ventral cornua thus probably facilitates the firm closure of cibarial lumen. We can suppose that the broad dorsal cornua and hyaline posterior third of ventral ones represent a complementary complex of characters: the strong, negative pressure developed by the cibarial dilator muscles must be outweighed by comparably firm closure of the cibarial lumen to prevent the reflux of the gut contents. On the other hand, it is not clear how some other features, like the shape of epistomal sclerite or concave dorsal margin of ventral cornua, are related to their function. Similar conclusions on a broader taxonomical scale were drawn by Rotheray & Gilbert (2008).

The opposite end of the spectrum is presented by following features: the hyaline basal part of the mouth hooks with higher number of apical teeth in the first instar, the parallel mouth hooks and slender intermediate sclerite in the second and third instars. The associated features include the broad epistomal sclerite, parallel subhypostomal sclerites, the dorsal cornua tend to be narrow, the posterior third of ventral cornua is sclerotised and the dorsal apodeme of ventral cornua tends to move forward. These features are typically developed in *Minettia fasciata*, *M. austriaca*, *Poecilolycia vittata*, *Pseudolyciella pallidiventris*, *Sapromyza sexpunctata*, *Sapromyzosoma* spp., partly also in *Peplomyza litura* and *Homoneura limnea*. We may suppose that these species "graze" on bacterial films coating the surface of fallen leaves (Rotheray & Gilbert 2008).

The form of cephaloskeleton is correlated also with the modification of the facial mask. The "strong" type of cephaloskeleton is accompanied by relatively narrow facial mask (small number of scraping cirri per row) with reduced number of apical papillae on the scraping cirri (1–3 in extreme case) and simplified peristomal cirri arranged more or less in longitudinal manner. The "soft" cephaloskeleton is accompanied by the large number of scraping cirri per row (up to 40), larger number of papillae on scraping cirri, peristomal cirri arranged in transverse manner and with fine and long marginal "hairs".

All instars of the genera with the strongly sclerotized type of cephaloskeleton have similar modifications across species and genera. Interestingly, in the first instar the modifications can be rather diverse. For example, *Sapromyza apicalis* has dental sclerites coalescing to the basal parts of mouth hooks, *S. intonsa* has each mouth hook coalescing into a single sclerite—like in later instars, and *Minettia flaviventris* has both mouth hooks coalescing into a single plate. Such organization suggests that they are likely apomorphic and we suppose that they are independently evolved from a "soft" cephaloskeleton.

Taxonomical implications. Generally, the morphology of cephaloskeleton within genera appears to be conservative and all the relationships discussed below are based on characters which are probably somewhat linked to food utilization. This may increase the chance for homoplasy. For example, *Minettia* is the genus with the largest interspecific variability in structure of the cephaloskeleton. It covers both the "soft" (*M. loewi*, *M. longipennis*, *M. austriaca*) and "strong" (*M. plumicornis*, *M. flaviventris*) type of cephaloskeleton. *Minettia plumicornis* and *Sapromyza apicalis* have habitually very similar form of the cephaloskeleton and they can be recognised only according to small details, such as presence/absence of ridge on intermediate sclerite. Most features shared

between the three species, as discussed earlier, are probably reflecting food specialization and can be considered as convergence. The interpretation of the lauxaniid relationships based on larval morphology thus must be very cautious.

The five studied species of ***Minettia*** represent all three subgenera recognised by Shatalkin (2000): *Plesiominettia* (*M. loewi*), *Frendelia* (*M. austriaca*) and *Minettia* s. str. (*M. fasciata*, *M. flaviventris*, *M. plumicornis*) (Shatalkin 2000). The publication of Miller & Foote (1976) includes species *M.* (*Frendelia*) *lyraformis* Shewell 1938 and *M.* (*Minettia*) *lupulina* (Fabricius 1787) and the publication of Semelbauer & Kozánek (2011) includes *Minettia* (*Frendelia*) *longipennis*. Furthermore, the three species of *Frendelia* are ascribed to the *longipennis* group (*M. longipennis*) or *obscura* group (*M. austriaca*, *M. lyraformis*) (Shatalkin 2000) while M. *plumicornis* represents the *biseriata* group. Genus *Minettia* is thus comparatively well represented.

The comparison of *Minettia* species shows that species of *Frendelia*, *M. loewi* and *M. fasciata* share the "soft" cephaloskeleton, while *M. plumicornis*, *M. flaviventris* and *M. lupulina* share the "strong" type (Miller & Foote 1976, Semelbauer & Kozánek 2011). Further, both *M. loewi* and *M. plumicornis* have developed small bumps in laterals of body. Whether they are developed also in *M. flaviventris* and *M. lupulina* remains to be confirmed. If we assume that the "strong" cephaloskeleton is apomorphic, than *M. plumicornis*, *M. flaviventris* and *M. lupulina* are closely related species. In *Minettia flaviventris* and *M. lupulina* this is easy to believe, as they are very similar in colour. Possible relative is *M. loewi* (supported by bumps on body laterals), which has retained the supposed ancestral "soft" cephaloskeleton.

Support for the monophyly of subgenus *Frendelia* comes from several characters both in the egg stage (elongated shape of the egg with stable and few number of ridges, globular posterior tubercle) and larval stage (almost identical shape of the cephaloskeleton in all instars, the submerged anterior spiracles—unique character among all studied lauxaniids, fine sparse hairs of the integument).

Genus ***Sapromyza*** is currently divided in several subgenera of which two are represented in our paper: *Sapromyza* s. str. (*S. apicalis*, *S. sexpunctata*, *S. intonsa*) and *Schumannimyia* (*S. hyalinata*). Shatalkin (2000) treated *Sapromyzosoma* as subgenera of *Sapromyza*. In our paper we agree with Merz (2013), who considers *Sapromyzosoma* as separate genus. From species of *Sapromyza* s. str., *S. intonsa* is regarded as a member of *S. intonsa* group erected by Papp (1981), distributed in the Mediterranean region and reaching the highest diversity in the Near East (Yarom 1990, Merz 2007a). *S. apicalis* is treated as a member of the *S. obsoleta* Fallén 1820 species group. *S. obsoleta* is the type species of *Sapromyza*. Thought this remains to be confirmed through phylogenetic analysis (Merz 2007b), *S. apicalis* is actually the closest known relative of *S. obsoleta* with described larva. Thus, *S. apicalis* is the best choice when comparing with other *Sapromyza* or *Sapromyza* related species.

S. hyalinata, ***S. intonsa*** and ***S. apicalis*** have rather similar ("strong") cephaloskeletons in the second and third instar. Unique character is the dorsal ridge of the intermediate sclerite (in *S. intonsa* coalescing to the parastomal bar). In the first instar they share e.g. retained only lateral part of second row of scraping cirri. In latter instars, they share e.g. broad belts of comb spines on the thoracic segments and cirri-like (hairy) processes on the dorsal surface of labial lobe. These characters suggest, that these species are relatively closely related, though they bear a number of species-specific features (e.g. the form of ventral organ in the first instar). We are well aware that these characters may be group specific, but their group-specific nature can not be revealed due to sparse sampling of species.

Probably the best defined group as suggested by the immature morphology includes species ***Sapromyza sexpunctata***, ***Sapromyzosoma quadripunctata***, ***S. quadricincta***, and rather surprisingly ***Poeciloycia vittata*** and ***Pseudolyciella pallidiventris***. The cephaloskeletons of these species are surprisingly similar, rather soft, with a voluminous basal sclerite. In the first instar, all species share the very slender, hyaline and adherent basal part of the mouth hooks, the apical part of mouth hooks without "heel" and (except of *Pseudolyciella*) beak-like outgrowth at the apex of labrum. In the second instar the mouth hooks bear five small apical teeth. The ligulate sclerites of the second and third instars are horizontal perforated plates (not vertical, as usual). The morphology of larva of *Poecilolycia browni* (Curran 1933) (Miller & Foote 1976) fits to our findings. The external morphology is also unique: the body is soft and dorsoventrally flattened, the scraping cirri are very numerous (ca. 40 per row), the facial mask is very large and the labial lobe is very small.

The rectangular epistomal sclerite and rounded dorsal margin of ventral cornua suggests close relationships between *Sapromyzosoma* spp. + *S. sexpunctata*, while the rounded epistomal sclerite and protruding narrow dorsal bridge supports relationships between *P. pallidiventris* and *P. vittata*. The close relationships of *S. sexpunctata* and

Sapromyzosoma spp. is supported also by the adult character: black dots on the abdominal tergites. Given that *S. sexpunctata* and *Sapromyzosoma* spp. appear more closely related to *Pseudolyciella* and *Poecilolycia* than to any other species or genera, they should be no longer included in *Sapromyza*. This could be possibly applied also to close relatives of *S. sexpuntctata*: *S. opaca* Becker 1895 and *S. zetterstedti* Hendel 1908.

The higher level relationships of lauxaniids remain poorly understood. The inflated Malpighian tubules (+ the calcareous deposit over the puparium) suggest a link between *Minettia*, *Homoneura* and possibly *Cnemacantha muscaria*. This is partly supported by the bumps on laterals of body segments in *M. plumicornis*, *M. loewi* and *Homoneura* spp. Another clade may be composed of *Meiosimyza* + *Tricholauxania* + *Aulogastromyia* and *Peplomyza*. These genera share a smooth body integument, simple spines on the inner surface of labial lobe and egg chorion characters (small pits between the ridges are developed in *T. praeusta*, *M. decempunctata*, *M. affinis* and *M. laeta*). A close relationship between *S. hyalinata, S. intonsa*, *S. apicalis* and *Calliopum* + *Lauxania* (Semelbauer & Kozánek 2012) is suggested by several larval features, e.g. the presence of dental sclerites in the first instar (except *S. intonsa*), the cirri-like hairs of labial lobe and the bare puparium (not known in *S. intonsa*) with darkened apical part (only in *S. hyalinata*, *Lauxania* and *Calliopum*, unpublished results). However, the immatures of many additional species will have to be studied before these characters can be fully evaluated. In particular, the larvae of suitable outgroups have to be studied in order to determine character polarities.

Conclusions

Our results support the non-monophyly of *Sapromyza*, what has been suspected for a long time (Shewell 1987, Papp & Shatalkin 1998). It is likely that genus *Sapromyza* should be sampled much more intensely than was feasible in our study. We conclude that immatures are a very promising source of data in lauxaniid taxonomy and systematics. We believe that future research of larval morphology in combination with cladistic analysis and molecular characters may establish a firm base for the higher-level classification of lauxaniid flies.

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