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Developmental stages of the hooded beetle *Sericoderus lateralis* (Coleoptera: Corylophidae) with comments on the phylogenetic position and effects of miniaturization

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ABSTRACT

The first detailed morphological study of larvae, pupae and adults of a species of the hooded beetles (Coleoptera: Corylophidae) – *Sericoderus lateralis* – is presented. Histological sectioning, scanning and transmission electron microscopy, laser confocal microscopy and 3D-computer reconstruction were used. For the first time we report that according to the morphometric data of *S. lateralis*, at least some corylophid beetles have three larval stages. A phylogenetic position of Corylophidae within a cucujoid-cleroid clade is confirmed, and also the placement of Sericoderini within a corlyophid subgroup, which does not include Periptycinae and Foadiini. The larvae of *Sericoderus* are mainly characterized by plesiomorphic features compared to those of other corylophid tribes, notably Peltinodini and Rypobiini. Morphological and developmental consequences of miniaturization are discussed. Corylophid beetles display much less specific and far-reaching morphological consequences of miniaturization compared to Ptiliidae. We report the presence of unique modifications in the neural system not shared with any other insects, such as a distinctly asymmetric supraoesophageal ganglion in first instar larva, and a total displacement of the brain to the thorax in the adult stage. A highly unusual feature of the digestive tract is the sclerotised, V-shaped ventral wall of the pharynx. Developmental and size dependent changes in the relative volume of different organs are addressed. All organ systems change allometrically in the development of *S. lateralis*. Allometric trends in the volume of organs confirm that the factors limiting miniaturization are the size of the neural system, associated with the number and size of neurons (most critical for first instar larva), the mass of the skeleton, the egg size, and consequently the volume of the reproductive system (for free-living insects).

1. Introduction

A significant decrease of body size is a common trend in animal evolution and is known as miniaturization (Hanken and Wake, 1993). Miniaturization is believed to play a key role in the evolution of insects (Chetverikov, 1915). It is connected with distinct changes in general morphology (Rensch, 1948; Beutel and Haas, 1998; Grebennikov and Beutel, 2002; Beutel et al., 2005; Polilov, 2005, 2007, 2008; Grebennikov, 2008; Polilov and Beutel, 2009) and also allometric morphological changes (Polilov, 2007, 2008; Polilov and Beutel, 2009). In different groups of insects some general and many essentially different consequences of miniaturization were reported (Polilov, 2007, 2008; Grebennikov, 2008; Polilov and Beutel, 2009). Factors limiting the further decrease of body size can vary for various groups of insects (Polilov, 2007; Grebennikov, 2008). Up to now only two groups were studied in detail – Ptiliidae (Coleoptera) and Strepsiptera. However, for a better understanding of the miniaturization effects on insect morphology and for the assessment of factors limiting size reduction, the investigation of more groups of “micro-insects” is required.

Whereas Ptiliidae belong to a basal lineage of polyphagan beetles (Staphylinoidea), Corylophidae belong to the extremely species-rich advanced clade Cucujiformia, which also comprises the megadiverse phytophagous families Curculionidae, Chrysomelidae and Cerambycidae. Species of Corylophidae belong to the smallest Coleoptera and insects in general (total length 0.5–3 mm). Therefore the investigation of the external and internal morphology is apparently important for understanding effects of miniaturization in insects. Up to now, the available information on structural features of Corylophidae was extremely scarce. Not a single detailed

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morphological study of immature or adult representatives of the family has been published so far. External and few internal features of larvae and adults are covered in the Handbook of Zoology (Ślipiński et al., in press), but aside from this the morphology of adults was only treated in the context of systematic and taxonomic works (Matthews, 1899; Paulian, 1950; Bowestead, 1999; Ślipiński et al., 2009). Selected larval features are described for few genera (Bøving and Craighead, 1931; Paulian, 1950; Pakaluk, 1985; De Marzo, 2000). Internal structures were almost completely unknown. Therefore one of the goals of this work is a detailed documentation of the external and internal morphology of adults and larvae of *Sericoderus lateralis*. The systematic position of Corylophidae and *Sericoderus* is briefly discussed, based on the new morphological data. However, the main focus of the study is on miniaturization effects. It continues a series of the authors' studies devoted to this phenomenon in insects (Beutel and Haas, 1998; Grebennikov and Beutel, 2002; Beutel et al., 2005; Polilov, 2005, 2007, 2008; Polilov and Beutel, 2009).

2. Materials and methods

2.1. List of taxa examined

S. lateralis (Gyllenhal, 1827) (Coleoptera: Corylophidae), adults and different larval instars, collected in Jena, Germany (2008) by the first author.

For comparative purposes, specimens of adults and larvae of *Orthoperus atomus* (Gyllenhal, 1808) (Corylophidae), *Acrotrichis montandoni* (Allibert, 1844), *Ptilium myrmecophilum* (Allibert, 1844), *Mikado* sp. (Ptiliidae), and *Coccinella septempunctata* Linnaeus, 1758 (Coccinellidae) were studied. All of these specimens were collected in the Moscow area, Russia, except *Mikado* sp. that was collected in South Vietnam.

2.2. Histology

Adults and larvae of *S. lateralis* were fixed in formaldehyde–ethanol–acetic acid (FAE). They were embedded in Araldite (=epoxy resin), cut at 1 µm with a Microm microtome (HM 360), and stained with toluidine blue. The serial sections were photographed with a PixeLINK PL-A622C digital camera on a Zeiss Axioskop.

2.3. Three-dimensional reconstruction (3D)

Cross-section series were used for 3D reconstructions. The images were aligned with AutoAligner 6.4 software. Based on the obtained image stacks, structures of adults and larvae were reconstructed with Bitplane Imaris 5.7. All discrete structures were outlined manually and automatically transferred into surface objects by Imaris software. The data files were then transferred to Alias Maya 2008, in order to use the smoothing function, the specific display, and rendering options of this software. The volume of organs and the body (without legs, wings, antenna and palps) was calculated based on 3D models in the statistic module of Imaris.

2.4. Scanning electron microscopy (SEM)

After cleaning, the specimens were critical point dried (Hitachi HCP-1) and coated with gold (Hitachi IB-3). Pictures were taken with a Jeol JSM-6380.

2.5. Transmission electron microscopy (TEM)

Adults of *S. lateralis* were fixed in 2% glutaraldehyde solution in 0.1 M cacodylate buffer pH 7.2 and post-fixed with 1% osmium tetroxide in the same buffer. Specimens were embedded in Epon 812, cut at 35 nm with LKB ultramicrotomes, stained with lead citrate, and examined with a Jeol JEM-1011 transmission electron microscope.

2.6. Confocal laser scanning microscopy (CLSM)

For CLSM, specimens were mounted between two cover glasses in a drop of glycerine. Image stacks were created with a Zeiss LSM 510 using the auto fluorescence at 488 nm of argon laser.

2.7. Muscular nomenclature

The muscles are named following v. Kéler (1963) (head and abdomen) and Larsén (1966) (thorax). The numbers introduced for thoracic muscles by Beutel and Haas (2000) are used.

3. Results

In the following sections the external features and different organ systems of all life stages are described, including glands, central nervous system, digestive tract, excretory system, fat body and genital organs. All muscles of immature stages and adults are treated in Supplementary material, which also contains Figs. S17–S25.

3.1. Egg (Fig. 1A)

Egg ovate-oblong. Length 290–360 µm (mean value, $M = 332$, number of specimens, $n = 6$), width 140–180 µm ($M = 155$). Chorion smooth; process absent.

3.2. Larva

3.2.1. Differences between instars (Figs. 1 and 2)

The larval morphometry shows 3 non-overlapping clusters of measurements that suggest that *S. lateralis* has 3 larval stages (Fig. 2). The main differences in their morphology are described and discussed below.

3.2.2. First instar larva (Figs. 1B–C, 3–5, S16 and S17)

General appearance. Body length 540–660 µm ($M = 597$, $n = 5$). Body oval, slightly curved ventrally, not distinctly broadened. Integument white, weakly sclerotised, with characteristic star-shaped protuberant microrelief (Fig. 3A). Dorsal side with clavate bristle. Specialised setae absent from sides of body. Legs normally developed. Urogomphi absent. Abdomen with 10 visible segments.

Head capsule (Fig. 3B). Head prognathous, not distinctly broadened and transverse. Width 144–168 µm ($M = 155$, $n = 5$). All sutures absent. Two stemmata present on each side. Tentorium without anterior and dorsal arms. Posterior arms and tentorial bridge well developed, separated from each other.

Labrum. Separated from head capsule by thin fold.

Antenna (ant in Fig. 3B). Short, 2-segmented. Antennomere I very short, without sensilla. Antennomere II with large sensorium and several apical trichoid sensilla of different length.

Mandible (md in Fig. 3B). Slightly asymmetrical, without retinaculum and movable appendage. Apex with 3 teeth. Mola strongly prominent, with numerous small teeth on mesal surface.

Maxillae (Fig. 3B). Composed of fused cardo and stipes, movable mala with fringed apex, and 3-segmented palp.

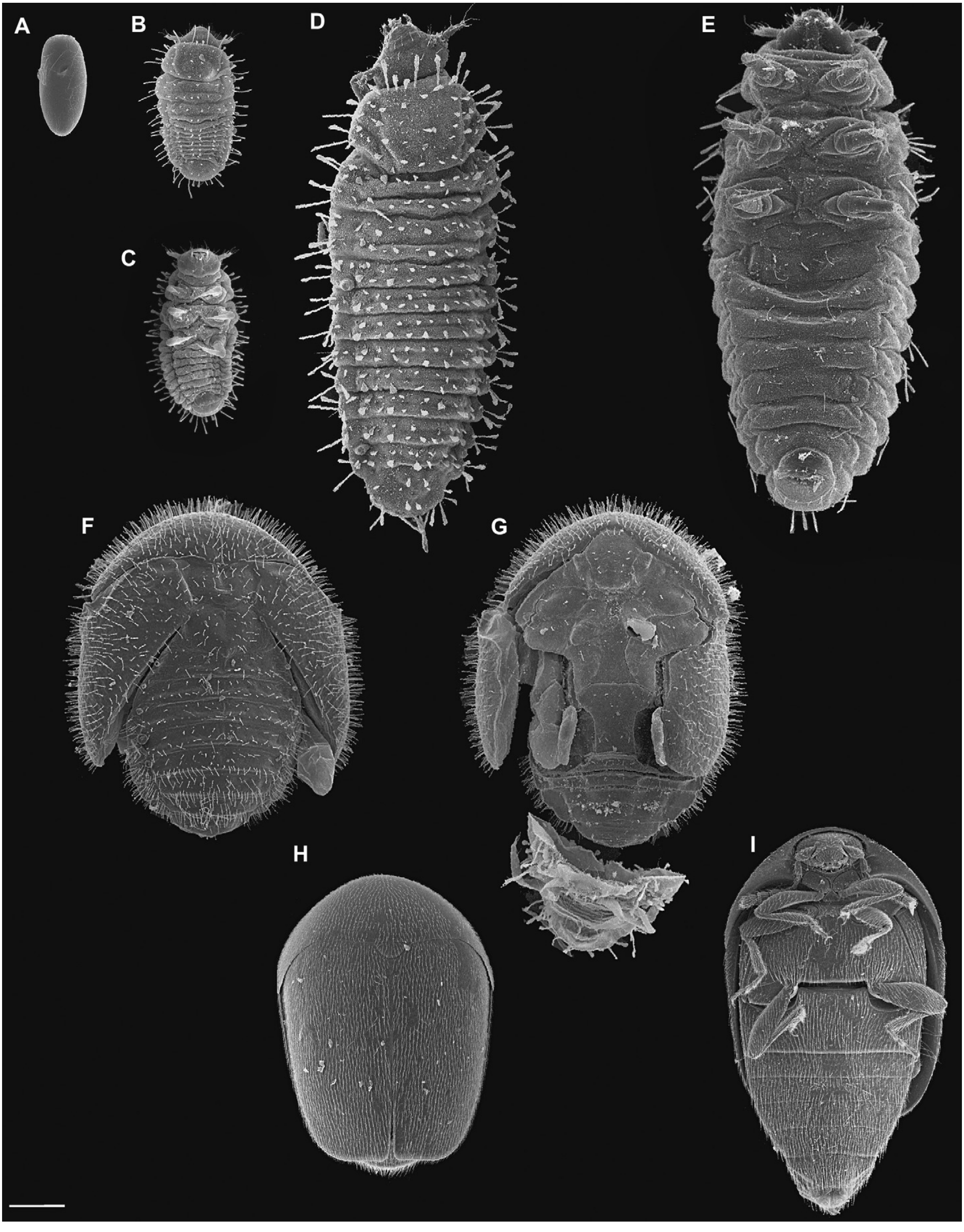

Fig. 1. *Sericoderus lateralis*, SEM images. (A) Egg; (B, C) first instar larva; (D, E) last instar larva; (F, G) pupa; (H, I) adult; (B, D, F, H) dorsal view; (C, E, G, I) ventral view Scale bar: 200 μm.

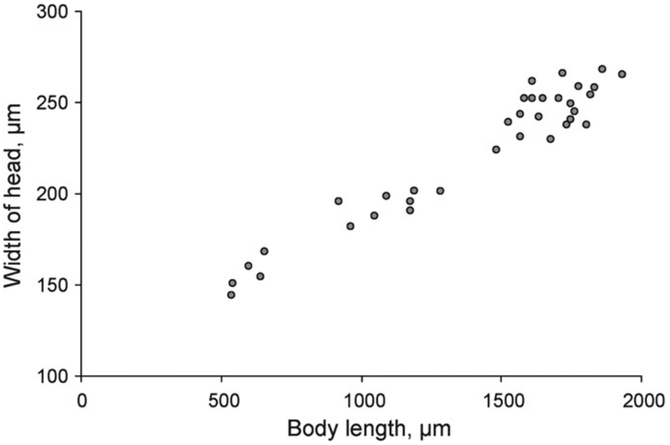

Fig. 2. Morphometry of larvae of *S. lateralis*.

Labium (Fig. 3B). Submentum fused with gula posteriorly and with the mentum anteriorly. Palp 2-segmented. Prementum internally subdivided by transverse furrow, with two strong setae.

Hypopharynx. Dorsal side with hypopharyngeal process. Hypopharyngeal sclerite well developed.

Pharynx (ph in Figs. 5 and S16B). V-shaped in cross-section. With strongly sclerotised ventral side.

Cerebrum and suboesophageal ganglion (cer and soeg in Fig. 4). Cerebrum almost completely shifted to pro- and mesothorax, strongly asymmetric. Suboesophageal ganglion located in prothorax, fused with prothoracic ganglion. Supraoesophageal and suboesophageal ganglion without connection anterior to tentorial bridge, forming secondary connective posterior to it.

Cephalic glands. Labial glands paired and tube-like. Distal orifice not clearly identified, probably located on anterior hypopharynx.

Prothorax. Distinctly longer than meso- and metathorax. Cuticle unpigmented, weakly sclerotised, except central part of notum. All sclerites indistinct. Discrete tergites, pleurites and sternites absent. Profurca very small. Legs well developed with long claw and

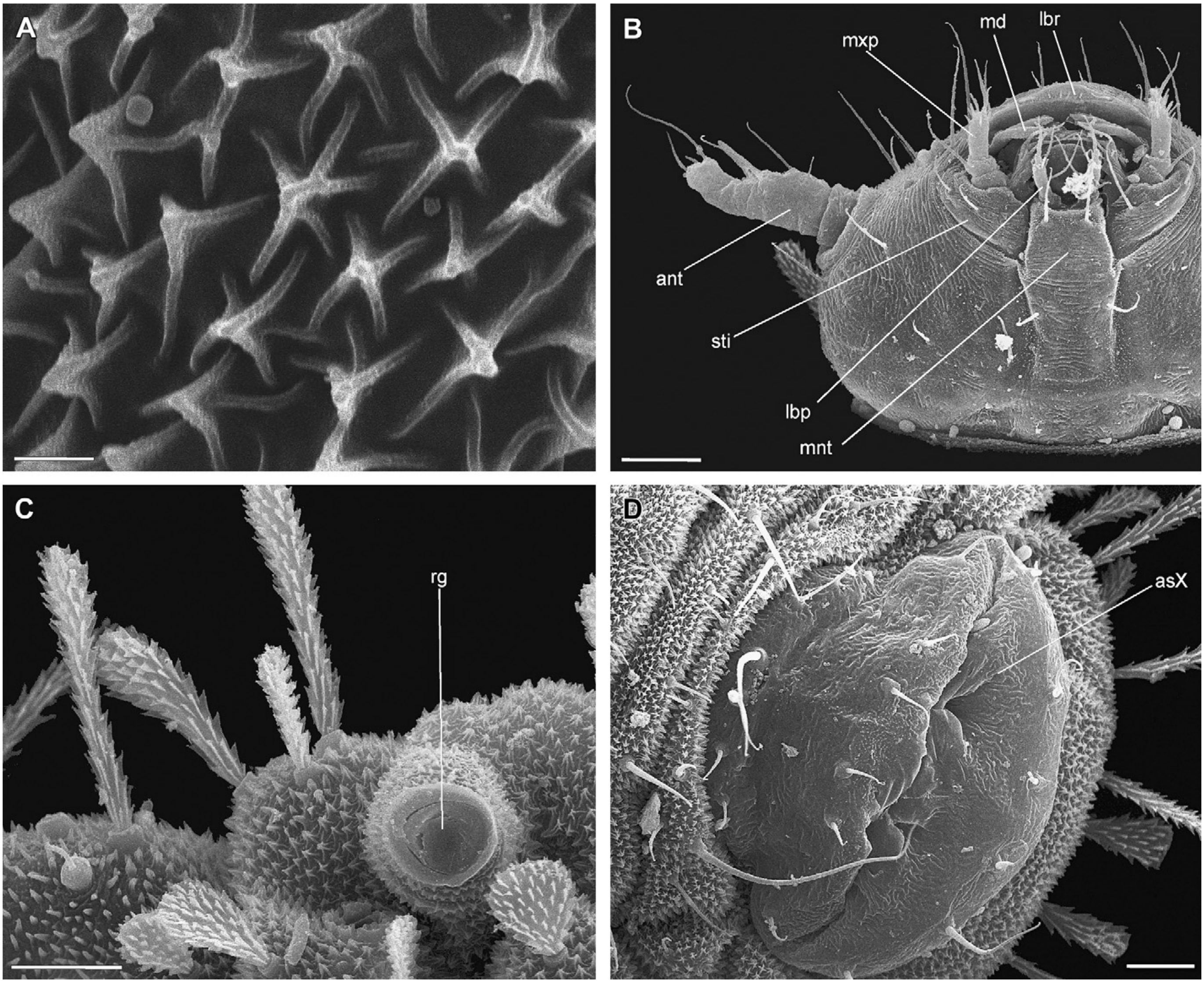

Fig. 3. First instar larva of *S. lateralis*, SEM images. (A) Cuticle of dorsal part of prothorax; (B) head, ventral view; (C) lateral part of abdominal segment I, dorsal view; (D) apex of abdomen, ventral view. Abbreviations: ant, antenna; asX, abdominal segment X; lbr, labrum; lbp, labial palp; md, mandible; mnt, mentum; mxp, maxillary palp; rg, repugnatorial gland; sti, stipes. Scale bar: A, 2 µm; B–D, 20 µm.

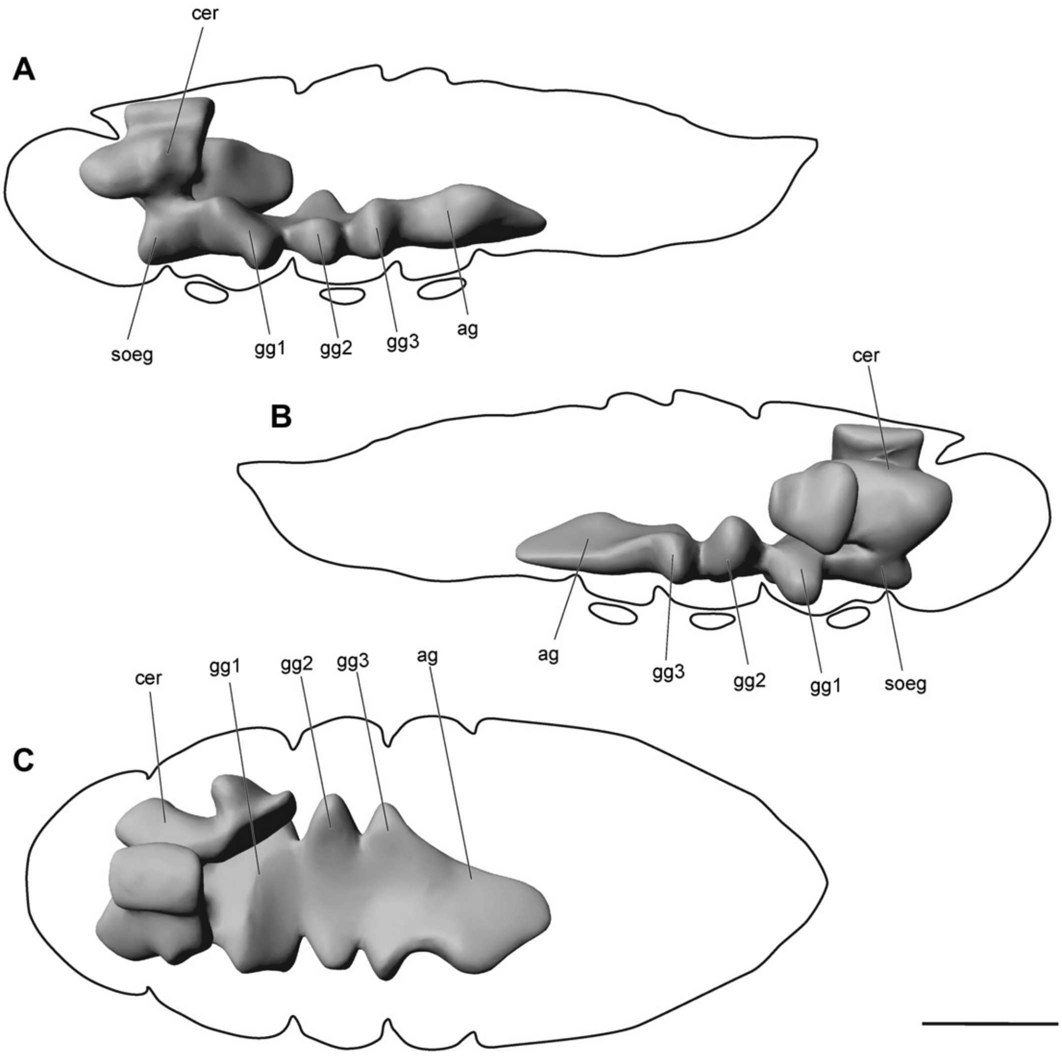

Fig. 4. Nervous system of first instar larva of *S. lateralis*, 3D reconstruction. (A, B) Lateral view; (C) dorsal view. Abbreviations: ag, abdominal ganglia; cer, cerebrum; gg1,2,3, pro-, meso- and metathoracic ganglia; soeg, suboesophageal ganglion. Scale bar: 100 μm.

elongated, trumpet-shaped empodium. Prothoracic ganglion not present as a discrete septate structure (see above).

Mesothorax. Distinctly shorter than prothorax. Without distinct tergites, pleurites and sternal sclerotizations. Legs and musculature similar to prothorax except for cervical muscles (see Supplementary material). Mesothoracic ganglion close to anterior part of pleural area.

Metathorax. Overall structure, legs and musculature very similar to mesothorax.

Abdominal segments I–VIII (Fig. 3C). Similar in shape, narrow, shorter than thoracic segments. Cuticle unpigmented, weakly sclerotised; sclerites indistinct. Segments I and VIII with paired repugnatorial glands (Fig. 3C). Segments I–VIII bear lateral groups of spherical sensilla. Abdominal ganglia: I–VIII fused with metathoracic ganglion.

Abdominal segments IX–X (Fig. 3D). Segment IX well developed, but without urogomphi; tergum IX slightly wider than VIII. Segment X circular, ventrally oriented, with protruding cuticular structure with unclear homology (referred to as pygopod in the following; Dybas, 1976: anal vesicle; Grebennikov and Beutel, 2002: pygopod). Anal hooks absent.

Postcephalic gut (Figs. 5 and S16C–H). Oesophagus short, approximately round in cross-section, with thin intima and ring muscle layer. Posterior part forms crop-like dilatation. Midgut straight and wide; wall formed by high cylindrical cells in anterior part and flat cells in posterior part. Hindgut long, forming a loop with large rectal ampulla; round in cross-section, with ring muscles. Rectum short, wider than hindgut, with much thicker wall.

Malpighian tubules (mt in Fig. 5). Four Malpighian tubules present, forming several loops. With terminal connection to hindgut (cryptonephric).

Circulatory system and fat body. Tubular heart present in abdominal segments. Aorta passing through thorax. Anterior end not recognisable on microtome sections. Fat body lobes filling out considerable parts of body cavity. Fat body cells variously shaped, with large inclusions.

Tracheal system. Thoracic spiracles present between pro- and mesothorax. Abdominal spiracles present on segments I–VII. Longitudinal tracheal trunks developed in thoracic and abdominal segments.

3.2.3. Last instar larva (Figs. 1D–E, 6, 7, S18 and S19)

General appearance. Body length 1480–1950 μm ($M = 1700$, $n = 22$). Similar to first instar.

Head capsule (Fig. 6A, B). Width 220–270 μm ($M = 248$, $n = 22$). All structures of head capsule similar to first instar larva.

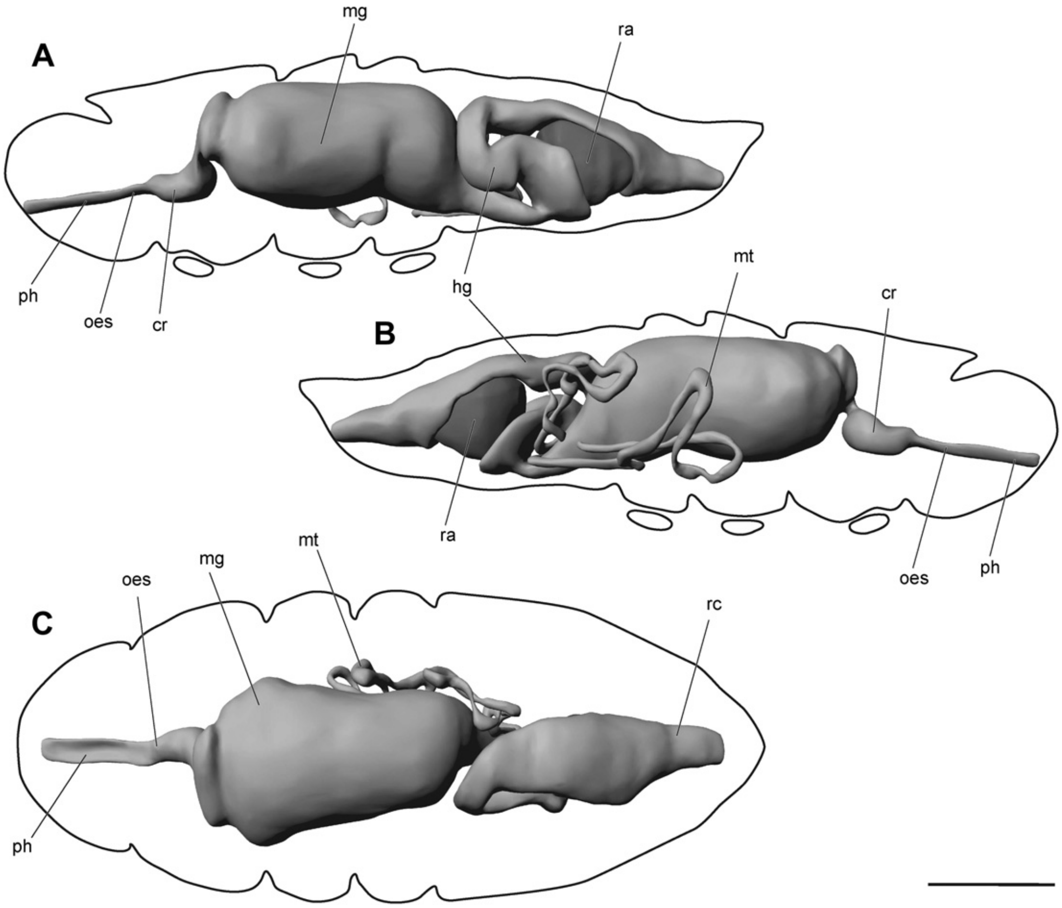

Fig. 5. Digestive system of first instar larva *S. lateralis*, 3D reconstruction. (A, B) Lateral view; (C) dorsal view. Abbreviations: cr, crop; hg, hind-gut; mg, mid-gut; mt, Malpighian tubules; oes, oesophagus; ph, pharynx; ra, rectal ampulla; rc, rectum. Scale bar: 100 μm.

Labrum (lbr in Fig. 6A, C). Similar to first instar.

Antenna (ant in Fig. 6A, B). Similar to first instar.

Mandible, *maxillae*, *labium*, *epipharynx*, *hypopharynx* and *pharynx* (Fig. 6A–D). Similar to first instar.

Cerebrum and suboesophageal ganglion (cer and soeg in Fig. 7D, E). Cerebrum completely shifted to prothorax. Tritocerebrum symmetrical. Suboesophageal ganglion located in prothorax and fused with prothoracic ganglion. Supraoesophageal and suboesophageal ganglion without connection anterior to tentorial bridge.

Cephalic glands (lbg in Fig. 7A), *Prothorax*. *Mesothorax and metathorox*, *Abdominal segments* (Fig. 6H, I), *Postcephalic gut* and *Malpighian tubules* (Fig. 7A, B), *Circulatory system and fat body*, *Tracheal system*. Similar to first instar.

3.3. Pupae (Figs. 1F, G and 8)

Pupa pupae are immobile and of the adecticous obtect type. Body oval, convex dorsally. Coloration white to slightly yellowish. Body length 1030–1280 μm ($M = 1130$, $n = 10$). Pronotum wider than long, widest at base. Antennae and mouthparts, and middle and fore legs firmly connected with body surface. Hind legs, wings and elytra closely attached to body. Elytral and hind wing sheaths inflected onto ventral side. Abdomen composed of seven distinct segments (Fig. 8).

3.4. Adult (Figs. 1H, I, 9–14 and S20–S23)

General appearance. Body oval, narrowed posteriorly, convex dorsally. Coloration yellowish to brown. Body length 950–1200 μm ($M = 1060$, $n = 10$). Pronotum wider than long, widest at base. Elytra narrowed posteriorly. Legs normally developed, with 4-segmented tarsi.

Head capsule. Head prognathous or slightly declined; appearing hypognathous in fixed specimens; when alive, disturbed beetles inflect their highly movable head under the dome-shaped pronotum. Width 195–220 μm ($M = 205$, $n = 10$). Cuticle smooth. Colour brown. All sutures absent. Clypeus and gula completely fused with rest of head capsule. Compound eyes large, rounded, protruding, consisting of 80–90 ommatidia each. Ocelli absent. Tentorium distinctly simplified. Dorsal and anterior arms and laminatentoria absent. Posterior arms elongate, thin and round in cross-section. Tentorial bridge well developed.

Labrum. Rounded anterolaterally. Movably attached to head capsule. Anterior and lateral margin without bristles and spines.

Antenna (ant in Fig. 9A). 10-segmented, with 3-segmented club. Antennomere X with terminal field of short digitiform sensilla.

Mandible (md in Fig. 9B, E). Distinctly retracted, slightly asymmetric, short and compact. Apical part with several teeth. Prostheca well developed, articulated semimembranous. Mola articulated.

Maxillae (Fig. 9D, F). Composed of cardo, stipes, lacinia and 3-segmented palp. Lacinia with apical tooth-like setae. Galea absent.

Labium (Fig. 9D). Submentum fused with gular area. Mentum small, triangular, movably connected with submentum. Prementum large, semimembranous. Ligula small with rounded anterolateral edges, semimembranous. Palp well developed, 2-segmented.

Epipharynx. Semimembranous, with well-developed median longitudinal epipharyngeal bulge.

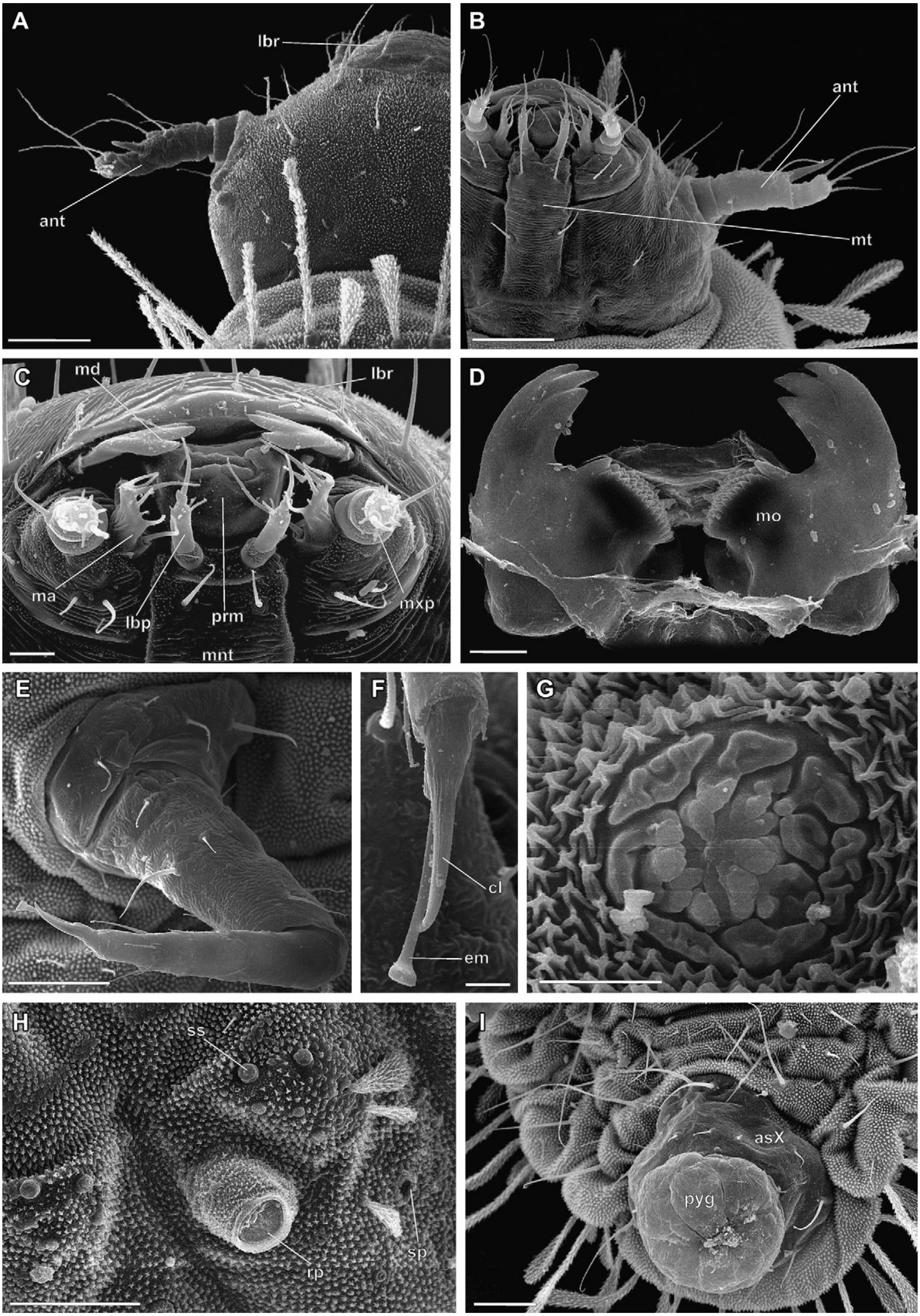

Fig. 6. Last instar larva of *S. lateralis*, SEM images. (A) Head dorsal view; (B, C) head ventral view; (D) mandible; (E, F) metothoracic leg; (G) spiracle of abdominal segment II; (H) lateral part abdominal segment I; (I) apex of abdomen. Abbreviations: ant, antenna; abdominal segment; cl, claw; em, empodium; lbp, labial palp; lbr, labrum; ma, mala; md, mandible; mnt, mentum; mo, mola; mt, mentum; mxp, maxillary palp; prm, prementum; pyg, pygopod; rg, repugnatorial gland; sp, spiracle; ss, spheric sensilla. Scale bar: A, B, E, H, I, 50 μm; C, D, F,G, 10 μm.

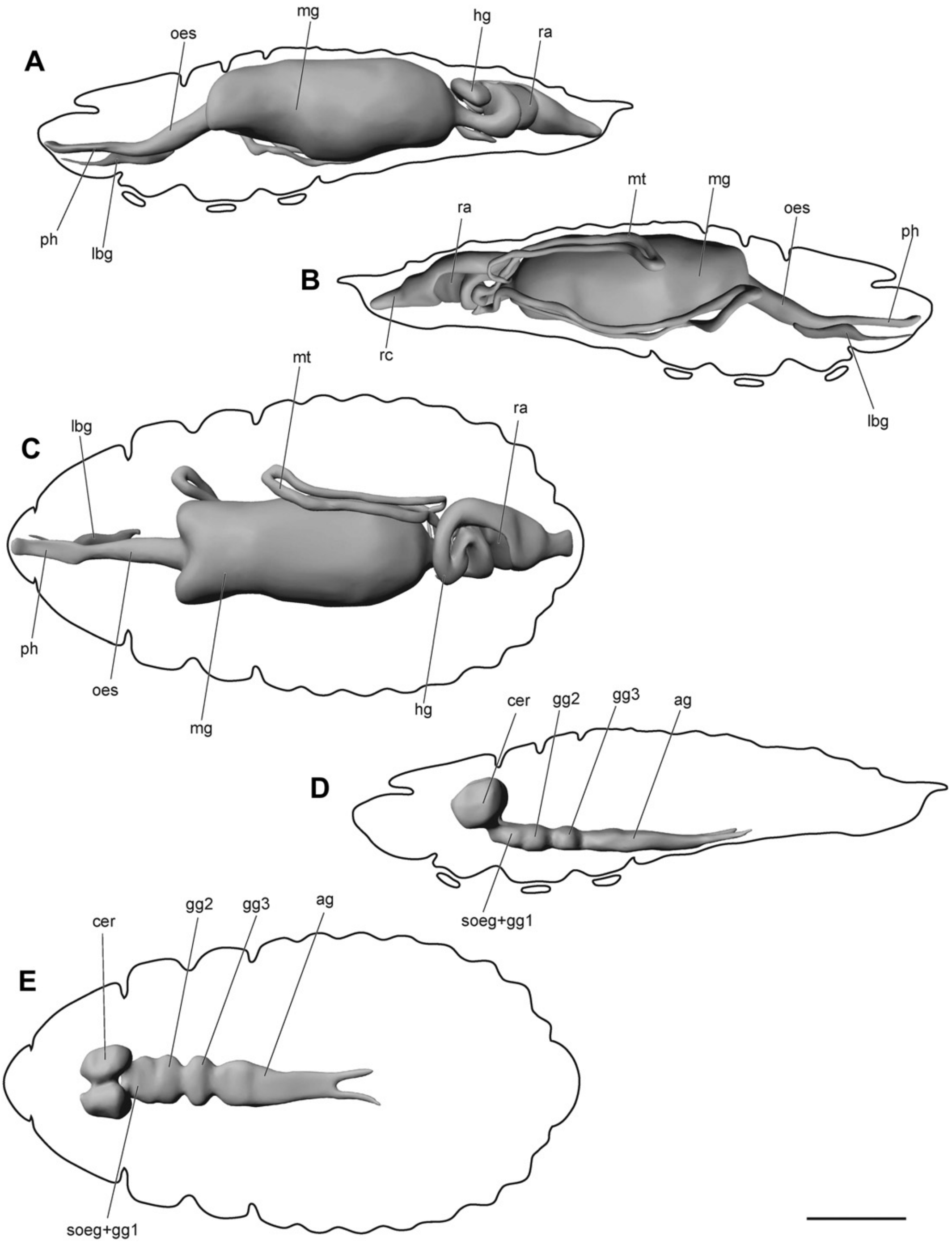

Fig. 7. Digestive tract (A-C) and nervous system (D, E) of last instar larva of *S. lateralis*, 3D reconstruction. (A, B, D) Lateral view; (C, E) dorsal view. Abbreviations: ag, abdominal ganglia; cer, cerebrum; gg1,2,3, pro-, meso- and metathoracic ganglia; hg, hind-gut; lbg, labial gland; mg, mid-gut; mt, malpighian tubules; oes, oesophagus; ph, pharynx; ra, rectal ampulla; rc, rectum; soeg, suboesophageal ganglion. Scale bar: 100 μm.

Hypopharynx. Not clearly separated from dorsal side of anterior labium.

Pharynx. Moderately wide and U-shaped in cross-section. Anterior part with strongly sclerotised ventral side.

Cerebrum and suboesophageal ganglion (cer and soeg in Figs. 12 and 13C–D). Cerebrum completely shifted to prothorax. Suboesophageal ganglion located in prothorax and fused with prothoracic ganglion. Supraoesophageal and suboesophageal ganglion without connection anterior to tentorial bridge. Neuron cell bodies 2–6 μm in diameter.

Cephalic glands. Not developed.

Prothorax. Cervical membrane connecting head and prothorax without sclerotised areas, cervical sclerites absent. Pronotum large, light brown, hood-like and covering head. Posterior pronotal angles strongly projecting posteriorly, embracing elytral humeri. Hypomeron well developed. Trochantinopleuron not visible externally; upper part forming apodemal plate. Prosternum very narrow. Notosternal suture absent. Procoxal cavities closed posteriorly. Procoxa large, slightly transverse. Trochanter small, obliquely attached to femur. Femur wide, slightly flattened. Tibia slender,

Fig. 8. Pupa of *S. lateralis*, SEM image, ventral view. Abbreviations: le1,2,3, pro-, meso- and metathoracic legs. Scale bar: 100 μm.

with several spines near apex. Tarsi with 3 distinct segments. Two simple claws inserted on apical palpomere 3. Unguitractor plate with transverse comb. Protothoracic ganglion fused with suboesophageal ganglion.

Mesothorax (Fig. 10). Dorsal side weakly sclerotised, except for mesoscutellar shield. Ventral side strongly sclerotised. Pleuron divided from ventrite. Anepisternum and epimeron fused. Mesosternal process very wide. Mesofurca well developed, with long anterior and lateral arms. Elytra truncate, not completely concealing abdomen. Epipleura wide anteriorly and narrow posteriorly, inflected. Two patches of microtrichia on inner surface of elytra interact with corresponding fields located on metanotum and abdominal segment I. Ganglia of meso- and metathorax and abdomen form large, compact complex within metathorax.

Metathorax (Figs 10 and 11). Metanotum divided into prescutum, scutum, scutellum and postnotum; weakly sclerotised and pigmented except for scutellum. Alacristae and area enclosed by them strongly elongated, narrowed posteriorly. Anepisternum separated from ventrite and epimeron. Discrimen absent; transverse suture present. Mesofurca well developed. Metacoxae transverse, large, straddling, without coxal plates. Metaventral postcoxal lines absent. Wings with narrow wing plate and fringe of hairs extending along entire margin. Folded twice transversely in resting position. Medial fleck (Kukalová-Peck and Lawrence, 1993) absent. Homology of wing venation unclear, three veins present, probably representing subcosta, radius anterior and media posterior (Bowestead, 1999: costal, subcostal and cubital).

Abdomen (Figs. 10D and 12). Eight apparent tergites present, I–V weakly sclerotised and unpigmented. Wing folding patches present on tergites IV–VI. Ventral side divided into six visible sclerotised sternites.

Postcephalic gut (Figs. 12 and 13A, B). Oesophagus short, approximately round in cross-section, difficult to distinguish from posterior pharynx; with thin intima and ring muscles. Proventriculus well developed, with thick cuticular intima and four transverse muscles (dorsally, ventrally and laterally). Midgut wide and short; wall much thicker anteriorly than posteriorly; epithelium formed by single layer of cylindrical cells in anterior part (15–25 similar cells visible in cross-sections) and flat cells in posterior part. Hindgut long, with rectal ampulla in loop; circular in cross-section, with ring muscles. Rectum short, noticeably wider than hindgut.

Malpighian tubules (mt in Fig. 13A, B). Four Malpighian tubules present, forming several loops and terminally connected with hindgut (cryptonephric).

Circulatory system and fat body (Fig. 12A, C). Very similar to condition in larvae.

Tracheal system. Spiracles placed in membranous area between pro- and mesothorax, and on lateral areas of tergites I–VII. Longitudinal tracheal tracts present in thorax and abdomen.

Reproductive system (Figs. 12 and 14). Male reproductive system composed of paired spiral-shaped testes, sperm duct, accessory glands, and copulatory apparatus consisting of penis and tegnum. Female reproductive system composed of paired ovaries (each with three telotrophic ovarioles), oviduct, receptaculum seminis (spermatheca), and accessory glands.

4. Discussion

The first two parts of the discussion are focussed on the effects of miniaturization on different organs systems and factors limiting size reduction. The systematic position of Corylophidae and *Sericoderus* is discussed in the third part.

4.1. *Effects of miniaturization on structural features of Corylophidae*

The identification of characteristics likely linked to miniaturization is based on comparisons with other groups, notably the non-related miniaturized Myxophaga and Ptiliidae, and related cucujiform lineages (e.g., Coccinellidae [cerylonid series, see above]), which are of medium size. Features occurring in the former groups, but not in the latter are likely effects of size reduction.

4.1.1. *Skeleton*

A suite of morphological simplifications is found in the skeleton of adults of *S. lateralis*. This includes fusions of pleural parts in the thorax, the absence of joints, simplifications of endoskeletal elements, and reductions in the number of tarsomeres and antennal segments. Similar changes do also occur in other groups of beetles affected by miniaturization, such as Myxophaga and Ptiliidae (Beutel et al., 1999; Polilov, 2005, 2008; Polilov and Beutel, 2009). Larvae, which are less strongly sclerotised and pigmented and possess a much less differentiated skeletal apparatus, display a distinctly lower degree of modification. The relative volume of the skeleton increases during the ontogeny (Fig. 15A), a pattern already observed in Ptiliidae (Polilov and Beutel, 2009).

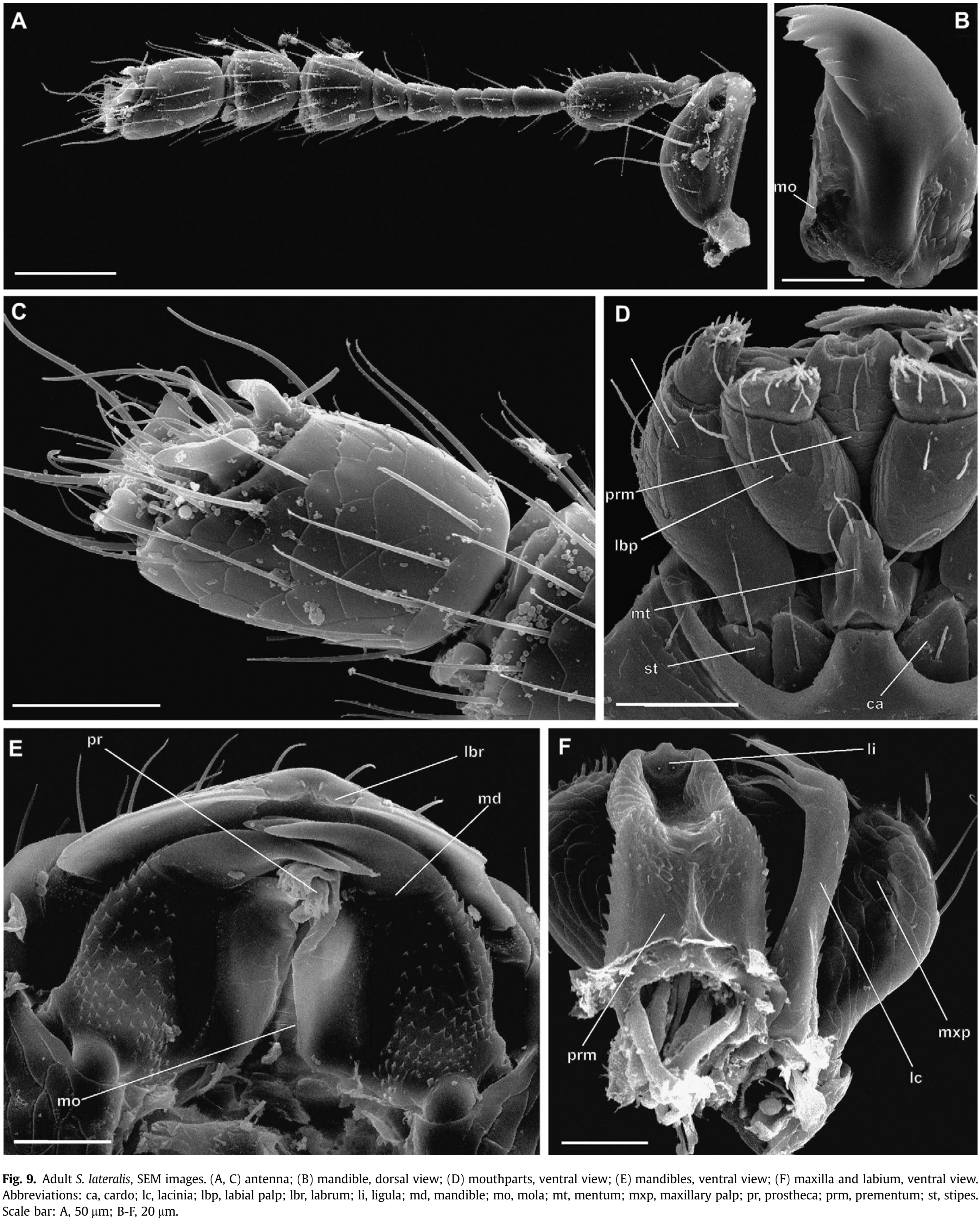

Fig. 9. Adult *S. lateralis*, SEM images. (A, C) antenna; (B) mandible, dorsal view; (D) mouthparts, ventral view; (E) mandibles, ventral view; (F) maxilla and labium, ventral view. Abbreviations: ca, cardo; lc, lacinia; lbp, labial palp; lbr, labrum; li, ligula; md, mandible; mo, mola; mt, mentum; mxp, maxillary palp; pr, prostheca; prm, prementum; st, stipes. Scale bar: A, 50 μm; B-F, 20 μm.

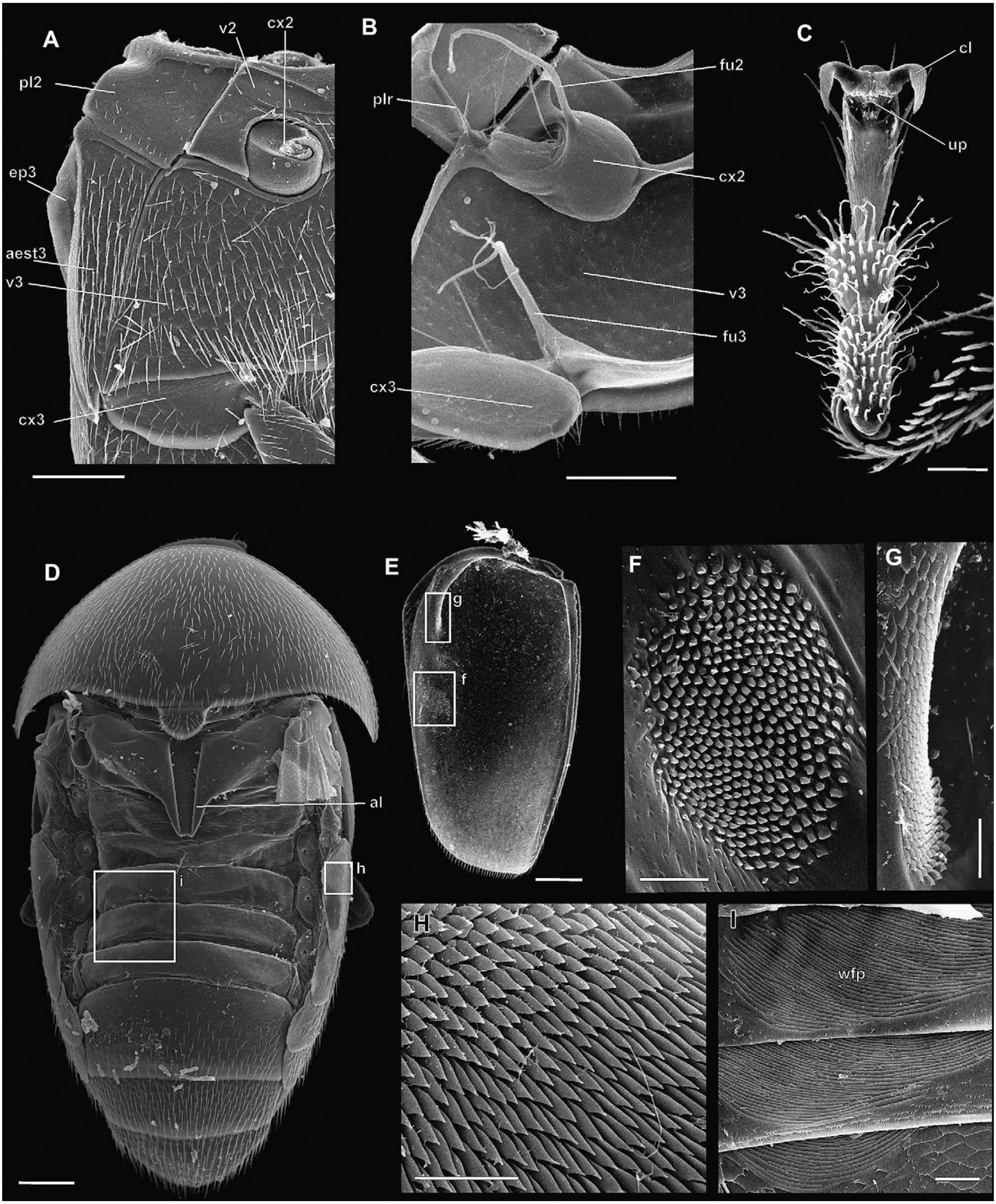

Fig. 10. Adult *S. lateralis*, SEM images. (A, B) meso- and metathorax; (C) tarsus; (D) body without elytra and wings; (E–G) elytra; (H) lateral part of tergites; (I) dorsolateral part of abdominal segment I; (A, C, E–G), ventral view; (B) dorsal view on inner surface; (D, H, I) dorsal view; (F,G) close view of (E), (I) close view of (D). Abbreviations: aest3, metaepisternum; al, alacristae; cl, claw; cx2,3, meso- and metacoxa; ep3, metepimeron; fu2,3, meso- and metafurca; pl2, mesopleurite; plr, pleural ridge; up, unguitractor plate; v2,3, meso- and metaventrite; wfp, wing folding patches. Scale bar: A, B, D, E, 100 μm; C, F–I, 20 μm.

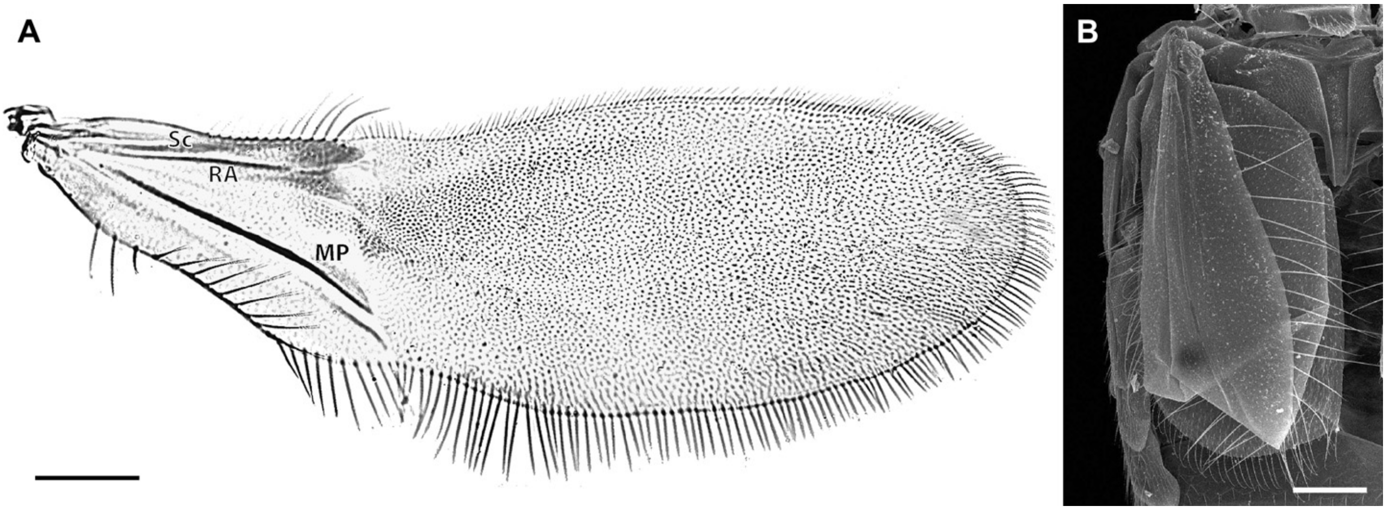

Fig. 11. Wing of *S. lateralis*. (A) unfolded; (B) folded. Abbreviations: (MP) Medius posterior; (RA) radius anterior; (Sc) subcosta. Scale bar: 20 µm.

4.1.2. *Muscles (see Supplementary material and Table 1)*

Nearly all muscles found in larger relatives are present in *Sericoderus* (Table 1). The same pattern was observed in Ptiliidae (Polilov and Beutel, 2009) and first instar larvae of Strepsiptera (Osswald et al., 2010). In larval *S. lateralis* 16 muscles were found of a total of 19 muscles reported from the head of all studied larger relatives (Cucujiformia) and in the adult head and thoracic segments 64 of 76 (Table 1). Only seven unique features of the muscle system do not occur in larger relatives (Cucujiformia, Table 1). During the larval development, the muscle volume shows an isometric growth (Fig. 15B). The relative muscle volume in adults is 1.5 times larger compared to the larval stages, which is likely due to the increased agility of adults and the presence of well-developed flight muscles (Fig. 15B). In Ptiliidae we observed similar changes,

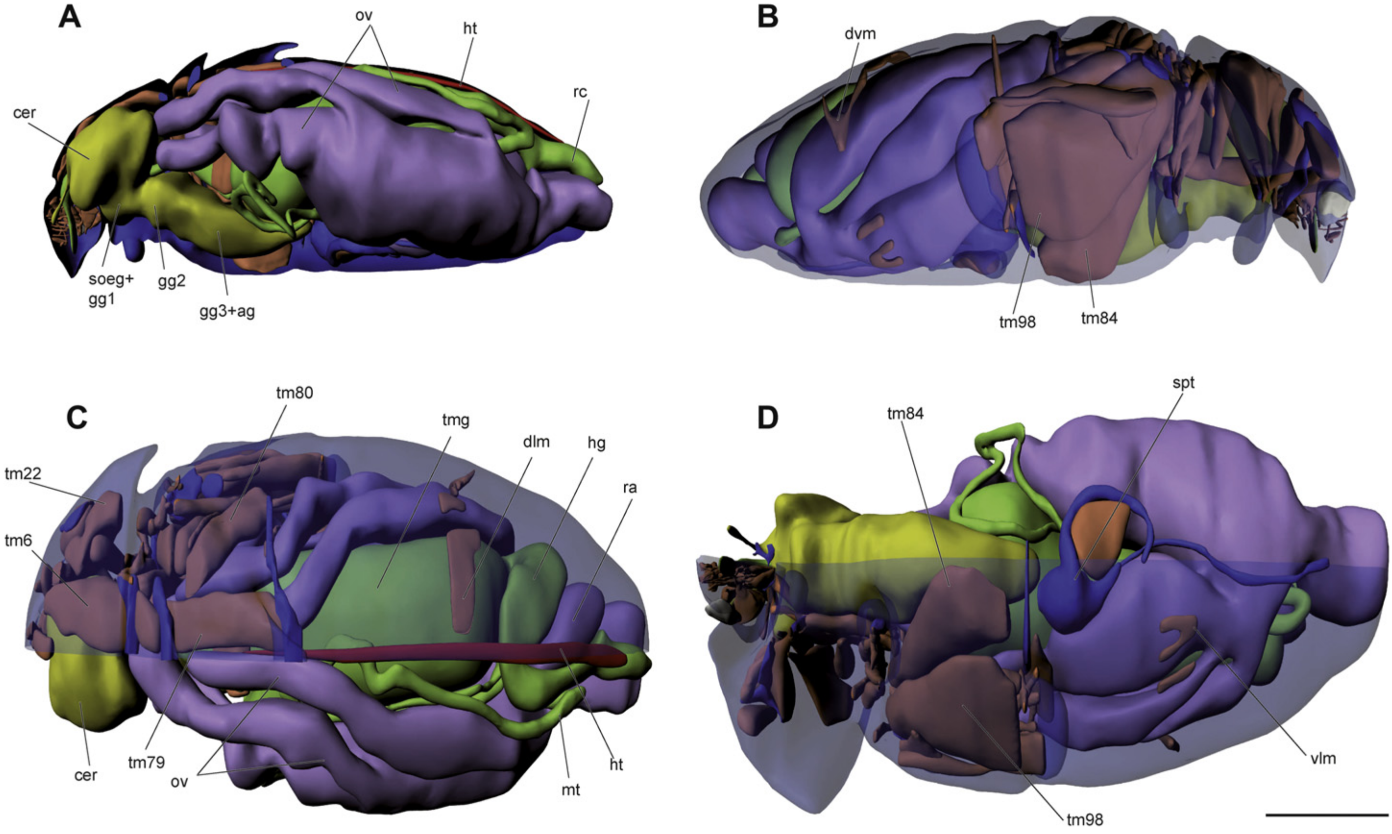

Fig. 12. Anatomy of adult *S. lateralis*, female, 3D reconstruction (skeleton, blue; musculature, brown; gut and malpighian tubules, green; nervous system, yellow; heart, red; reproductive system, gray and violet). (A, B) Lateral view; (C) dorsal view; (D) ventral view. Abbreviations: ag, abdominal ganglia, cer, cerebrum; gg1,2,3, pro-, meso- and metathoracic ganglion; hg, hind-gut; ht, heart; tm6, M. pronoti quartus; tm22, M. nototrochantinalis; *notocoxales*; tm79, M. metanoti primus; tm84, M. dorsoventralis primus; tm98, M. sternobasalaris; mt, malpighian tubules; ov, ovariole; ra, rectal ampulla; rc, rectum; soeg, suboesophageal ganglion; spt, spermatheca. Scale bar: 200 µm.

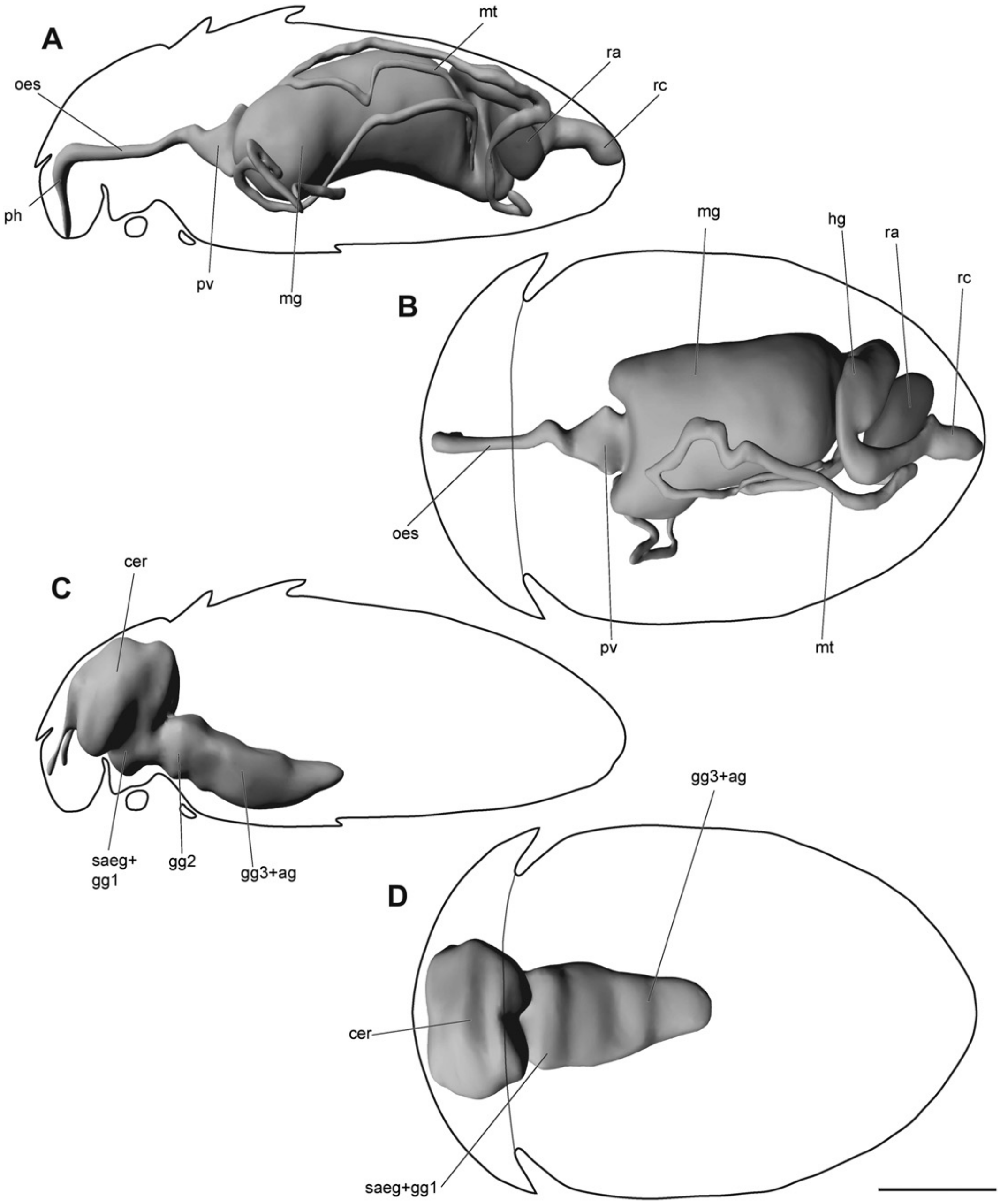

Fig. 13. Digestive tract (A, B) and nervous system (C, D) of adult *S. lateralis* 3D reconstruction. (A, C) Lateral view; (B, D) dorsal view. Abbreviations: ag, abdominal ganglia; cer, cerebrum; gg1,2,3, pro-, meso- and metathoracic ganglia; hg, hind-gut; mg, mid-gut; mt, malpighian tubules; oes, oesophagus; ph, pharynx; pv, proventriculus; ra, rectal ampulla; rc, rectum; saeg, suboesophageal ganglion. Scale bar: 200 μm.

but with a more distinct difference between the relative volumes of muscles in larvae and adults (Polilov and Beutel, 2009).

4.1.3. Digestive and excretory system

Corylophids do not show any changes in the morphology of the digestive system caused by miniaturization, with the possible exception of a distinctly sclerotised, V-shaped ventral wall of the pharynx (Figs. S16B and S18B). The postcephalic digestive tract is very similar structurally to that of related, distinctly larger coccinellid beetles (Landis, 1936; Pradhan, 1939; Ibrahim, 1948; Stathas et al., 2002). The relative volume of the metabolic system in *S. lateralis* is significantly larger than in similarly sized representatives of Ptiliidae and Staphylinidae (Polilov and Beutel, 2009). This is most likely due to their specific diet. They feed on fungal hyphae, which are not easy to digest and assimilate. The relative size of the digestive system is highest in last instar larvae (Fig. 15C), which is apparently due to the required extra-resources for energy accumulation in preparation for metamorphosis. The relative size of the excretory system increases during ontogeny (Fig. 15D). This indicates intensification of metabolism and growth of the metabolic rate.

4.1.4. Circulatory system

In the morphology of the circulatory system Corylophidae do not display distinct modifications associated with miniaturization. This is in sharp contrast to the condition found in Ptiliidae,

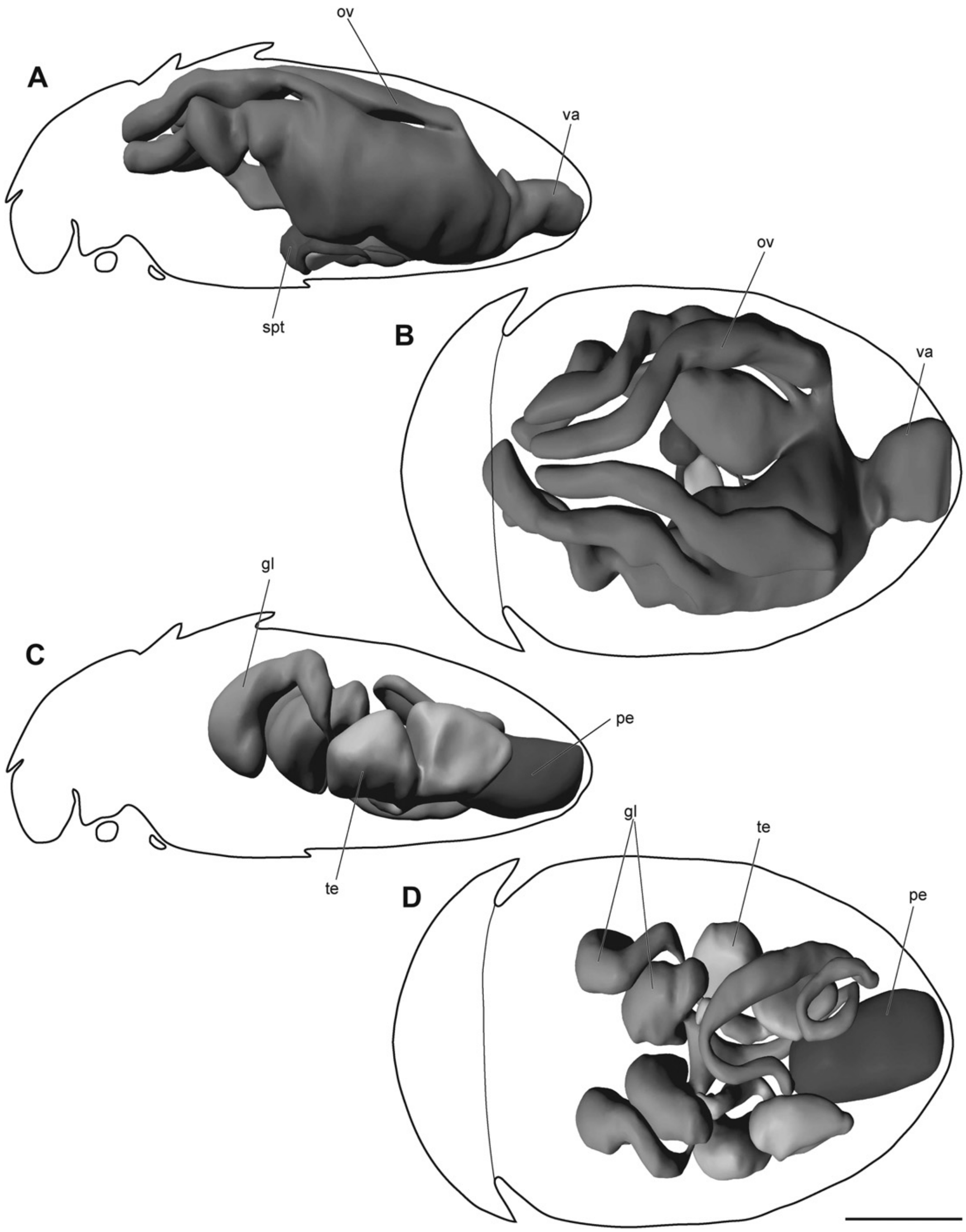

Fig. 14. Reproductive system of *S. lateralis*, 3D reconstruction (A, B) Female; (C, D) male; (A, C) Lateral view; (B, D) dorsal view. Abbreviations: gl, gland; ov, ovariole; pe, penis; spt, spermatheca; te, testis; va, vagina. Scale bar: 200 μm.

where the circulatory system is greatly simplified, without a heart and with the fat body occupying nearly the entire spare volume of the body cavity, thus almost completely displacing the hemolymph (Polilov, 2005, 2008; Polilov and Beutel, 2009).

4.1.5. Tracheal system

The tracheal system of corylophid beetles is much less simplified than that of Ptiliidae. Adults and larvae are equipped with longitudinal tracheal trunks and with the complete set of spiracles found in larger relatives. Due to the extremely small diameter of the tracheae it was not possible to calculate the exact volume of the tracheal system.

4.1.6. Neural system

The morphology of the central nervous system is similar to that of other minute insects. Corylophidae (*Sericoderus* and *Orthoperus*) display a distinct oligomerization and concentration of the ganglia. The larval brain is totally displaced to the thoracic segments, as it is also the case in many other small larvae (Beutel and Haas, 1998; Beutel and Hörnschemeyer, 2002; Beutel et al., 2005; Polilov and Beutel, 2009). The first instar larva described here is characterized by a distinct asymmetry of the supraoesophageal ganglion (Fig. 4), a feature not yet described for any other insect, with the exception of first instar larvae of Ptiliidae, where this asymmetry is much less pronounced. In adults, the brain is totally displaced to the

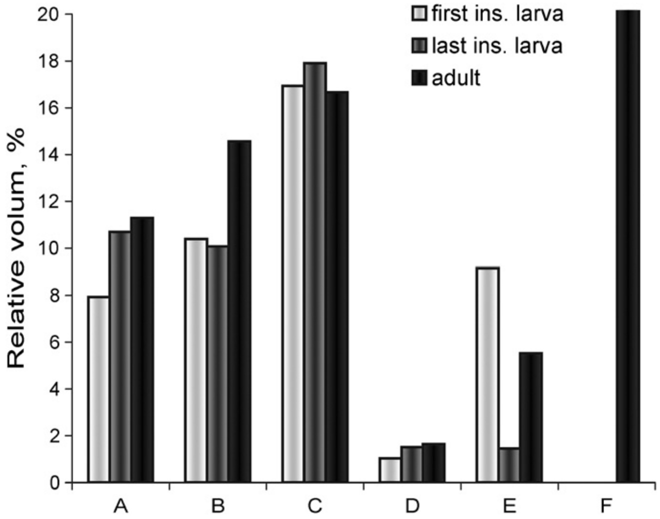

Fig. 15. Relative volume of organs of *S. lateralis* in ontogenesis. (A) Skeleton; (B) musculature; (C) digestive system; (D) excretory system; (E) nervous system; (F) reproductive system. Single measurements for all systems except for the reproductive organs (mean between male and female system).

prothorax, a modification previously unknown in adult insects. This peculiar modification is possibly related to an exceptionally small relative head size, which in turn is related to a specific defensive adaptation – when disturbed, corylophid beetles pull in their very flexible head under the dome-shaped pronotum. Decrease of neuron body size and increase of relative neuron nuclear size is a pattern described earlier in other minute insects (Polilov, 2007, 2008). The first instar larva shows the largest relative volume of the entire central nervous system during the ontogeny (Fig. 15E). The relative volume is significantly larger in adult beetles than in last instar larva. Similar changes were also observed in Ptiliidae (Polilov and Beutel, 2009).

4.1.7. *Reproductive system*

The reproductive system of Corylophidae is not recognisably affected by size reduction. Its morphology is similar to what is described for larger relatives such as for instance Coccinellidae (Ibrahim, 1948; Stathas et al., 2002). Since corylophid beetles retain two ovaries and two testes, the relative volume of the reproductive system in *S. lateralis* (Fig. 15F) is more than two times larger than in ptiliid beetles of the same size (Polilov, 2008). The relative egg size in Corylophidae increases compared to larger female beetles. The similarly shaped eggs measure 0.31 of the body length in *S. lateralis*, 0.16 in *C. septempunctata*, and 0.2 in *Rhyzobius lophanthae* (calculated from data in Stathas, 2001). The number of simultaneously laid eggs decreases to just two eggs in *S. lateralis*, whereas the average number of eggs in one clutch of *C. septempunctata* is 35 (Honek et al., 2008).

4.2. *Factors limiting miniaturization of insects*

New data on Corylophidae confirm previously proposed and discussed hypotheses on factors limiting insect miniaturization (Polilov, 2007, 2008; Polilov and Beutel, 2009).

Like in other very small insects, the neuron size in *S. lateralis* is distinctly smaller than in related larger beetles, and approaches the minimum size, which is determined by the minimum size of the neuron nucleus. Our results on ontogenetic changes in the relative volume of the neural system correspond well to the pattern of the increase of the relative neural volume with increasing miniaturization. This is especially distinct in first instar larvae.

Like in other free-living minute insects, when compared to larger relatives, *S. lateralis* shows an increase of relative egg size, whereas the number of eggs that can be produced simultaneously decreases. Even the relative volume of the reproductive system increases significantly.

The relative volume of the skeletal parts fits well with the pattern of its relative increase with body size reduction, which was described earlier for representatives of Staphylinoidea (Polilov and Beutel, 2009).

Thus three main factors limiting miniaturization in free-living insects are confirmed: the size of the neural system, limited by the required number and size of neurons (apparently crucial for first instar larva), the skeletal mass and egg size, and consequently, the size of the reproductive system. The latter limiting factor only applies only to free-living insects, not to parasitic forms.

4.3. *Phylogenetic implications*

Interestingly, the small or very small Corylophidae were placed with staphylinoids near the extremely miniaturized Ptiliidae, or alternatively in a broadly defined Silphidae in early classifications (see Matthews, 1887; Ślipiński et al., in press). They were considered as a subgroup of Coccinellidae by LeConte (1852) (see Ślipiński et al., in press). Sharp and Muir (1912) suggested "cucujoid" affinities based on characters of the male genitalia and Crowson (1955) included the family in his cerylonid cucujoid subseries (see also Ślipiński and Pakaluk, 1991). Corylophidae were not included in a recent morphology based investigation of the interrelationships of "basal Cucujoidea" (Leschen et al., 2005). The monophyly of the cerylonid series including Corylophidae (as sistergroup of the endomychid subfamily Anamorphinae) was confirmed in a recent study based on 18S and 28S rDNA (Robertson et al., 2008), with Corylophidae forming a clade with an endomychid subgroup, Discolomatidae, and paraphyletic Latridiidae. However, this placement of the family should be considered as preliminary, as the clades including Corylophidae and the above mentioned groups lack solid support (Bootstrap values below 50). The question of the placement of Corylophidae was not addressed in a recent morphology based study on the phylogenetic relationships within the group (Ślipiński et al., 2009).

A clade comprising paraphyletic Cucujoidea with a monophylum Cleroidea nested within them was suggested in studies on larval head structures (Beutel and Pollock, 2000; Beutel et al., 2000; Beutel and Ślipiński, 2001). However, internal studies of corylophid larvae were not taken into consideration and were largely unknown by that time. The present study confirms the presumptive cucujoid–cleroid apomorphy, the origin of a subcomponent of *musculus tentoriostipitalis* from the floor of the anterior digestive tract. The muscle is usually attached anterior to or below the position of the frontal ganglion (Beutel and Ślipiński, 2001), but is shifted posterior to it in larvae of *Sericoderus*. This unusual condition may be correlated with the sclerotised pharyngeal floor of the larvae, a potential autapomorphy of Corylophidae. A larval apomorphy shared by Cleroidea and the cucujoid families Coccinellidae, Endomychidae and Nitidulidae is also found in Corylophidae, the separation of the tentorial bridge from the posterior tentorial arms, which are shifted anteriorly. As it is probably generally the case in larvae of Cucujiformia, the anterior and dorsal tentorial arms are reduced in *Sericoderus*. A presumptive synapomorphy of Coccinellidae and Corylophidae (Ślipiński et al., 2009), the fused larval stipes and cardo, could be confirmed for *Sericoderus*.

Autapomorphies suggested for Corylophidae (Ślipiński et al., 2009, in press) are confirmed for *Sericoderus*. In contrast to other

Table 1
Muscles of *S. lateralis*, some Cucujiformia (partly based on Schneider, 1981; Beutel and Haas, 2000; Beutel and Ślipiński, 2001; Schunger et al., 2003). For number of muscles see Supplementary material.

Taxon	Head muscles of larva																				
	1	2	4	7	9	11	12	15	17	18	19	28	29	30	41	43	45	46	48	50	52
Sericoderus, first ins.	–	×	×	×	×	×	×	×	a	a	×	×	×	–	×	×	×	×	–	–	–
Sericoderus, last ins.	×	×	×	×	×	×	×	×	a	a	×	×	×	–	×	×	×	×	–	–	–
Sphindus	×	×	×	×	×	×	×	×	×	×	×	×	–	–	×	×	×	×	×	–	×
Ericmodes	×	×	×	–	×	×	×	×	×	×	×	×	×	–	×	×	×	×	×	–	×
Prostomis	×	×	×	–	–	×	×	–	×	×	×	×	–	–	×	×	×	×	×	–	×

	Thoracic muscles of larva																									
	1	2	3	4	5	6	7	8	9	10	11	12	15	19	20	Y1	Y2	Y3	Y4	Y5	Y6	Y7	Y8	Y9	Y10	Y11
Sericoderus, first ins.	×	×	×	×	a	a	b	–	b	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Sericoderus, last ins.	×	×	×	×	×	×	b	–	b	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×

	28	29	30	37	40	44/45	48	Y4	Y5	Y6	Y7	Y8	Y9	Y10	Y11	Y12	Y13	Y14	Y15
Sericoderus, first ins.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Sericoderus, last ins.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×

	Head muscles of adult																								
	1	2	3	4	7	9	11	12	15	17	18	19	29	30	41	42	43	45	46	48	51	52	67	68	69
Sericoderus	×	×	–	×	×	×	×	×	×	a	a	×	b	b	×	–	×	×	×	–	–	×	–	×	–
Mikado	×	×	–	×	×	–	×	×	×	×	×	×	×	×	×	×	×	×	×	–	–	×	–	×	–
Lytta	×	×	×	×	×	×	×	×	×	×	×	×	?	×	×	?	×	×	×	×	–	?	×	×	×

	Thoracic muscles of adult																												
	1	2	3	6	9	10	12	13	14	15	16	17	18	22	23	24	25	30	31	39	40	42	43	47	52	53	55	60	61
Sericoderus	×	×	–	×	×	×	×	–	–	×	×	×	×	×	×	×	–	×	×	×	×	×	–	×	–	×	×	×	×
Coccinella	×	×	–	×	×	×	×	–	×	×	×	×	×	–	×	×	–	×	×	×	×	×	–	×	×	×	×	×	×
Lytta	×	×	–	×	×	×	×	–	×	×	×	×	×	×	×	×	×	–	×	×	×	×	×	×	×	×	×	×	×
Meloe	×	×	–	×	×	×	×	–	×	×	×	×	×	×	×	×	×	–	×	×	×	×	×	×	–	×	–	×	×
Tenebrio	×	×	–	×	×	×	×	×	–	×	×	×	×	×	×	×	–	–	×	×	×	×	–	×	×	×	×	×	×
Cassida	×	×	–	×	×	×	×	–	–	×	×	×	×	×	×	×	–	×	×	×	×	×	–	×	×	×	×	×	×
Donacia	×	×	×	×	×	×	×	×	–	×	×	×	×	×	×	×	–	–	×	×	×	×	–	×	×	×	×	×	×

	65	66	67	70	71	72	79	80	82	84	85	86	90	93	94	95	96	97	98	00	01	02	03	04	05	07	08	09	13
Sericoderus	×	–	×	–	×	×	×	×	–	×	a	a	×	×	×	b	b	×	×	×	×	×	×	–	×	×	×	×	×
Coccinella	–	×	×	×	–	×	×	×	×	×	×	×	×	×	×	b	b	×	×	×	–	×	×	–	–	×	×	×	×
Lytta	×	×	×	×	–	×	×	×	×	×	×	×	×	×	×	b	b	×	×	×	×	×	×	×	×	×	×	×	×
Meloe	×	×	×	–	–	×	–	–	×	–	×	–	–	–	–	b	b	×	–	–	–	×	×	–	–	×	×	×	×
Tenebrio	×	–	×	×	–	×	×	×	×	×	×	×	×	×	×	b	b	–	×	×	×	×	×	×	–	×	×	×	×
Cassida	×	–	×	×	–	×	×	×	×	×	×	×	×	×	×	b	b	–	×	×	–	×	×	×	–	×	×	×	×
Donacia	×	–	×	×	–	×	×	×	×	×	×	×	×	×	×	b	b	–	×	×	–	×	×	–	×	×	×	×	×

×, Present; –, absent; a, b, parts of muscle.

cucujoid groups the maxilla of adults lacks a galea and only two stemmata are present in larvae. The complete shift of the adult brain to the prothorax and the asymmetric suboesophageal ganglion are further potential autapomorphies, but confirmation for other representatives of the groups is needed. A prominent hood-like pronotum covering the head from above was retrieved as an apomorphy of a large corylophid clade excluding Periptycinae and Foadiini (Ślipiński et al., 2009). This condition (apparently coded as 1.1. instead of 0.1 in the matrix in Ślipiński et al., 2009) is present in *Sericoderus*. The absence in *Orthoperus* is apparently due to reversal. Another presumptive apomorphy of the clade, a reduced anterior tentorial arm, was also confirmed for *S. lateralis*.

The larvae of *Sericoderus* represent an intermediate type within Corylophidae. An apomorphic feature compared to the ancestral condition implied in Ślipiński et al. (2009) is the presence of paired glandular openings on abdominal segments I and VIII (shared with Peltinodini and Rypobiini) (Ślipiński et al., in press). We assume that this condition has evolved independently, as a close relationship between these tribes and *Sericoderus* would be in conflict with Ślipiński et al. (2009) and other characters. The rather elongate and nearly parallel larval body, the exposed head, which is not shortened and transverse, the free labrum, the exposed mandible with a well developed mola (Fig. 6D), and the protracted ventral mouthparts are apparently plesiomorphic features preserved in *Sericoderus* and other groups. A broadened disc-like body with fringes of specialised setae and a unidentate mandible are shared derived feature of Peltinodini and Rypobiini. Apomorphic conditions which have apparently evolved independently in these two tribes and in Perypticinae are an anterior pronotal margin at least partly covering the head, a fused labrum, and a vestigial or completely reduced mandibular mola. An apomorphic feature shared by Perypticinae and Rypobiini is the nearly endognathous mandible (Ślipiński et al., in press). The former group is placed as sister taxon of the remaining Corylophidae and the latter is deeply nested within Corylophinae (Ślipiński et al., 2009). Consequently, we consider this shared derived feature as a result of parallel evolution.

The clade Sericoderini, including *Sericoderus* and *Aposericoderus*, was supported by two synapomorphies in Ślipiński et al. (2009). The strongly projecting posterior angle of the pronotum is a conspicuous feature shared by the adults of both genera. The other presumptive apomorphy could not be fully confirmed by our observations. The mentum of *S. lateralis* is small, but rather triangular than transverse, and not fused to the prementum (Fig. 9D).

5. Conclusions

The evaluation of the morphological data shows that the effects of miniaturization are less far-reaching in the life stages of Corylophidae than in those of the distinctly smaller Ptiliidae. Nevertheless, different organ systems are affected by size reduction. Some of the modifications are commonly found in very small insects, whereas others are unique or highly unusual. Main factors limiting miniaturization in free-living insects are confirmed: the size of the neural system (crucial for first instar larva), the skeletal mass, the egg size, and the size of the reproductive system. Larval features suggest a phylogenetic position of Corylophidae within a cucujoid–cleroid clade, and a placement of Sericoderini within a corlyophid subgroup not including Periptycinae and Foadiini is confirmed. The larvae of *Sericoderus* are mainly characterized by plesiomorphic features compared to those of other corylophid tribes, notably Peltinodini and Rypobiini.

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Appendix A. Supplementary material

Supplementary material associated with this article can be found in the online version, at doi:10.1016/j.asd.2009.08.005.

References

Beutel, R.G., Haas, A., 1998. Larval head morphology of *Hydroscapha natans* LeConte 1874 (Coleoptera, Myxophaga, Hydroscaphidae) with special reference to miniaturization. Zoomorphology 18, 103–116.

Beutel, R.G., Haas, F., 2000. Phylogenetic relationships of the suborders of Coleoptera (Insecta). Cladistics 16, 103–141.

Beutel, R.G., Hörnschemeyer, T., 2002. Larval morphology and phylogenetic position of *Micromalthus debilis* LeConte (Coleoptera: Micromalthidae). Systematic Entomology 27, 169–190.

Beutel, R.G., Maddison, D.R., Haas, A., 1999. Phylogenetic analysis of Myxophaga (Coleoptera) using larval characters. Systematic Entomology 24, 1–23.

Beutel, R.G., Pohl, H., Hünefeld, F., 2005. Strepsipteran brains and effects of miniaturization (Insecta). Arthropod Structure and Development 34, 301–313.

Beutel, R.G., Pollock, D.A., 2000. Larval head morphology of *Phycosecis litoralis* (Pascoe) (Coleoptera, Phycosecidae) with phylogenetic implications. Invertebrate Taxonomy 14, 825–835.

Beutel, R.G., Ślipiński, S.A., 2001. Comparative study of head structures of larvae of Sphindidae and Protocucujidae (Coleoptera: Cucujoidea). European Journal of Entomology 98, 219–232.

Beutel, R.G., Weide, D., Bernhard, D., 2000. Characters of the larval head of *Mycetina cruciata* (Schaller) (Coleoptera; Endomychidae) and their phylogenetic implications. Annales Zoologici 50 (1), 7–14.

Boving, A.G., Craighead, F.C., 1931. An illustrated synopsis of the principal larvae forms of the Coleoptera. Entomologica Americana 11, 1–351.

Bowestead, S., 1999. A revision of the Corylophidae (Coleoptera) of the west Palaearctic region. In: Instrumenta Biodiversitatis, vol. 3. Muséum d'histoire Naturelle, Geneva, 203 pp.

Chetverikov, S.S., 1915. Main factor of insect evolution. Izvestiya Moskovskogo entomologicheskogo Obschestva 1, 14–24 (in Russian).

Crowson, R.A., 1955. The Natural Classification of the Families of Coleoptera. Nathaniel Lloyd and Co., London.

De Marzo, L., 2000. Larve di coleotteri in detriti vegetali di orgine agricola: lineamenti morfologici e presenza stagionale (Polyphaga: 20 famiglie). Entomologica, Bari 34, 65–131.

Dybas, H.S., 1976. The larval characters of featherwing and limulodid beetles and their family relationships in the Staphylinoidea (Coleoptera: Ptiliidae and Limulodidae). Fieldiana: Zoology 70 (3), 29–78.

Grebennikov, V.V., 2008. How small you can go: factors limiting body miniaturization in winged insects with a review of the pantropical genus *Discheramocephalus* and description of six new species of the smallest beetles (Pterygota: Coleoptera: Ptiliidae). European Journal of Entomology 105, 313–328.

Grebennikov, V.V., Beutel, R.G., 2002. Morphology of the minute larva of *Ptinella tenella*, with special reference to effects of miniaturisation and the systematic position of Ptiliidae (Coleoptera: Staphylinoidea). Arthropod Structure and Development 31, 157–172.

Hanken, J., Wake, D.B., 1993. Miniaturization of body size: organismal consequences and evolutionary constraints. Annual Review of Ecology and Systematics 24, 501–519.

Honek, A., Dixon, A.F.G., Martinkova, Z., 2008. Body size, reproductive allocation, and maximum reproductive rate of two species of aphidophagous Coccinellidae exploiting the same resource. Entomologia Experimentalis et Applicata 127, 1–9.

Ibrahim, M.M., 1948. The morphology and anatomy of *Coccinella undecimpunctata aegyptiaca* Reiche. (Coleoptera–Cocinellidae). Bulletin de la Société Fouad 1er d'Entomologie 32, 305–316.

Kéler, S.V., 1963. Entomologisches Wörterbuch. Akademieverlag, Berlin, p. 744.

Kukalová-Peck, J., Lawrence, J.F., 1993. Evolution of the hind wing in Coleoptera. The Canadian Entomologist 125, 181–258.

Landis, D.J., 1936. Alimentary canal and malpighian tubules of *Ceratomegilla fuscilabris* Muls. (Coleoptera, Coccinellidae). Annals of the Entomological Society of America 29, 15–27.

Larsén, O., 1966. On the morphology and function of locomotor organs of the Gyrinidae and other Coleoptera. Opuscula Entomologica (Supplementum) 30, 1–241.

LeConte, J.L., 1852. Remarks on the Coccinellidae of the United States. Proceedings of the Academy of Natural Sciences of Philadelphia 6, 129–145.

Leschen, R.A.B., Lawrence, J.F., Ślipiński, S.A., 2005. Classification of basal Cucujoidea (Coleoptera: Polyphaga): cladistic analysis, keys and review of new families. Invertebrate Systematics 19 (1), 17–73.

Matthews, A., 1887. New genera and species of Corylophidae in the collection of the British Museum. Annals and Magazine of Natural History 6 (20), 105–116.

Matthews, A., 1899. Monograph of the Coleopterous Families Corylophidae and Sphaeriidae. In: Mason, P.B. (Ed.). Janson & Son, London, p. 220.

Osswald, J., Pohl, H., Beutel, R.G., 2010. Extremely Miniaturised And Highly Complex: The Thoracic Morphology Of The First Instar Larva Of Mengenilla Chobauti (Insecta, Strepsiptera). Arthorpod Structure & Development 39, this issue.

Pakaluk, J., 1985. New genus and species of Corylophidae (Coleoptera) from Florida, with description of its larva. Annals of the Entomological Society of America 78, 406–409.

Paulian, R., 1950. Les Corylophidae d'Afrique. Memoires de l'Institut français d'Afrique Noire 12, 1–126.

Polilov, A.A., 2005. Anatomy of the feather-winged beetles *Acrotrichis montandoni* and *Ptilium myrmecophilum* (Coleoptera, Ptiliidae). Entomological Review 85, 467–475.

Polilov, A.A., 2007. Miniaturization-related structural features of Mymaridae. In: Studies on Hymenopterous Insects. KMK, Moscow, pp. 50–64 (in Russian).

Polilov, A.A., 2008. Anatomy of the smallest of the Coleoptera, feather-winged beetles from tribe Nanosellini (Coleoptera, Ptiliidae) and limits to insect miniaturization. Entomological Review 88, 26–33.

Polilov, A.A., Beutel, R.G., 2009. Miniaturization effects in larvae and adults of *Mikado* sp. (Coleoptera: Ptiliidae), one of the smallest free-living insects. Arthropod Structure and Development 38, 247–270.

Pradhan, S., 1939. The alimentary canal and pro-epithelial regeneration in *Coccinella septempunctata* L., with comparison of carnivorous and herbivorous Coccinellids. Quarterly Journal of Microscopical Science 81, 451–478.

Rensch, B., 1948. Histological changes correlated with evolutionary changes of body size. Evolution 2, 218–230.

Robertson, J.A., Whiting, M.F., McHugh, J.V., 2008. Searching for natural lineages within the cerylonid series (Coleoptera: Cucujoidea). Molecular Phylogenetics and Evolution 46, 193–205.

Schneider, W., 1981. Zur Kopfmorphologie der Imago des Ölkäfers *Lytta vesicatora* (Coleoptera: Meloidea). Entomologia Generalis 7, 69–87.

Schunger, I., Beutel, R.G., Britz, R., 2003. Morphology of immature stages of *Prostomis mandibularis* (Coleoptera: Tenebrionoidea: Prostomidae). European Journal of Entomology 100, 357–370.

Sharp, D., Muir, F., 1912. The comparative anatomy of the male genitalia tube in Coleoptera. Transactions of the Entomological Society of London, Part III, 477–642.

Ślipiński, S.A., Pakaluk, J., 1991. Problems in the classification of the Cerylonid series of Cucujoidea (Coleoptera). In: Zunino, M., Belles, X., Blas, M. (Eds.), Advances in Coleopterology. European Association of Coleopterology. Silvestrelli and Cappelletto, Torino, pp. 79–88.

Ślipiński, A., Tomaszewska, W., Lawrence, J.F., 2009. Phylogeny and classification of Corylophidae (Coleoptera: Cucujoidea) with descriptions of new genera and larvae. Systematic Entomology 34, 409–433.

Ślipiński, A., Lawrence, J.F., Cline, A.R. 10.34. Corylophidae LeConte, 1852. In: Leschen, R.A.B., Beutel, R.G., Lawrence, J.F. (Eds.), Handbook of Zoology, Part 39, Coleoptera, Beetles. Morphology and Systematics, vol. 2. Walter de Gruyter, Berlin, in press.

Stathas, G.J., 2001. Studies on morphology and biology of immature stages of the predator *Rhyzobius lophanthae* Blaisdell (Col.: Coccinellidae). Anzeiger für Schädlingskunde 74, 113–116.

Stathas, G.J., Eliopoulos, P.A., Kontodimas, D.C., Siamos, D.T., 2002. Adult morphology and life cycle under constant temperatures of the predator *Rhyzobius lophanthae* Blaisdell (Col., Coccinellidae). Anzeiger für Schädlingskunde 75, 105–109.