

Genus	Vol. 20(2): 225-242	Wrocław, 15 VII 2009
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Morphology of the developmental stages of *Pella* (=Zyras) *laticollis* (MÄRKELL, 1844) with remarks on its biology (Coleoptera: Staphylinidae)

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ABSTRACT. The egg, mature larva (L₂) and pupa of *Pella laticollis* (MÄRKELL, 1844) are described for the first time, with the illustrations of structural features provided. The differences and similarities between mature larvae of *Pella laticollis* and five other known larvae of species of Aleocharinae belonging to tribes: Athetini, Homalotini, Hoplandriini, Liparocephalini, Lomechusini and Oxypodini are presented. Some data on its distribution, environmental requirements and biology are also provided.

Key words: entomology, morphology, biology, Coleoptera, Staphylinidae, *Pella*, *Zyras*, egg, larva, pupa, adult, myrmecophilous beetle.

INTRODUCTION

The genus *Pella* STEPHENS, 1835 is represented by a few dozen species in the world, within them 41 species are described from Palearctic region, 16 species were recorded in Europe and 7 occur in Poland. These beetles belong to the subtribe Myrmedoniina of the tribe Lomechusini (family Staphylinidae, subfamily Aleocharinae), are distributed in the Holarctic region (BURAKOWSKI et al. 1981; MARUYAMA 2006).

As the myrmecophilous beetles, they are associated with ants of the genera: *Crematogaster* LUND, 1831; *Formica* LINNAEUS, 1758; *Lasius* FABRICIUS, 1804; *Liometopum* MAYR, 1861 and *Tapinoma* FOERESTER, 1850. *Pella* staphylinids are usually observed walking in the vicinity of the hosts' nests. Generally they feed on dead ants or garbage discarded around the nests but sometimes prey on living ant workers. The adults and larvae show defensive behavior and their tergal glands on abdomen produce defensive secretions. When encountering an ant, the insects discharge secretions from tergal glands,

flexing the abdomen at the same time (MARUYAMA 2006; PÄIVINEN et al. 2003).

The life cycles of the genus *Pella* are known for about ten species. The duration of the development of each immature stage is very short. At a temperature of 20°C (± 2) the whole life cycle from the egg to the adult stage lasted only 12 days, while 20-25 days in other species of *Aleocharinae*. Only two larval instars were noticed in all observed *Pella* species, whereas in other species of *Aleocharinae* there are generally three instars (HÖLLDOBLER et al. 1981; MARUYAMA 2006). The knowledge of the morphology of immature stages of the genus *Pella* is fragmentary. Recently, the detailed descriptions of adults morphology of all Palearctic *Pella* species, including *P. laticollis*, gave MARUYAMA (2006). The bodies of adult *Pella* are slender or somewhat robust, subparallel-sided with head almost circular; colour brown to black or reddish orange; length 3.4-7.0 mm (Fig. 43). With regard to immature stages, only TOPP (1978) provided the description of the structure of labrum and abdominal segment I of mature larva of *P. humeralis* (GRAV.).

The purpose of this study is to describe the morphology of so far unknown immature stages: egg, mature larval instar and pupa of *P. laticollis*. Some data on its distribution, ecology and biology are also given.

MATERIAL AND METHODS

All immature stages of *Pella laticollis*: eggs, two larval instars and pupa were obtained by rearing 4 specimens of adults identified by the first author. The insects were extracted from a nest of *Lasius fuliginosus* (LATREILLE, 1798) located in a beech trunk (*Fagus sylvatica*) in Wola Zarczycka (UTM: EA87, SE Poland), situated ca. 15 km west of Leżajsk on 16 April 2006. The adults of *P. laticollis* were kept in a plastic container (10 cm diameter \times 7 cm high), filled with humid soil. Imagines and larval instars were fed daily with ant larvae of various size. The rearing was conducted in a room temperature ($T = 20^\circ\text{C} \pm 2$) from 24 April to 3 July 2006. The reared immature stages were preserved in a 1:1 solution of glycerin and alcohol. For microscopic slides the punctured larvae were rinsed in distilled water, cleared in KOH and finally placed in glycerin. Habitus illustrations of egg, larva, pupa and adult were made on the basis of the photos. The drawings of morphological details were made using camera lucida. Chaetotaxy of *P. laticollis* was coded based on the principles used for description of *Atheta coraria* KRAATZ (Staphylinidae, Aleocharinae) by ASHE & WATROUS (1984).

The material examined: a) 15 eggs, 15 L₁, 14 L₂, 5 cocoons and 5 pupae were used for the study of morphology (all immature stages were reared from the eggs laid by collected adults); b) several specimens of eggs, larvae and pupae were used to study of life history.

RESULTS

DESCRIPTION OF THE DEVELOPMENTAL STAGES

Egg

Length: 1.03-1.14 mm (mean 1.09 mm), width: 0.72-0.81 mm (mean 0.76 mm); colour white; shape oval; surface smooth without visible microstructure (Fig. 1).

Larval stages

Body length (from anterior margin of labrum to the end of pygopod): L_1 – 2.02-4.00 mm (mean 3.13), L_2 – 4.30-4.80 mm (4.55 mm); head width (between stemmata): L_1 – 0.45-0.47 mm (0.46 mm), L_2 – 0.57-0.63 mm (0.60 mm).

Mature larva (L_2)

Body elongate, cylindrical, weakly sclerotized, head yellowish brown, antennae light brown, pro-, meso- and metanotum yellowish brown a little lighter than head, legs almost white, abdominal tergites gradually darkening from yellow of the first tergite to light brown of tergites VI-IX, pygopod and urogomphi yellowish brown, setae brown. Head distinctly narrower than thoracal segments, pro-, meso-, and metathorax of almost equal width, prothorax about 1.5 x longer than mesothorax, meso- and metathorax almost equal of length, abdomen slightly and gradually widened to segment V and then narrowed to the terminal segment of the body (Fig. 2). Head and abdominal sclerites with microstructure as in Figs 2A-C. All macro- and micro setae simple, the color of basal part (1/4-1/3 of length) of long setae lighter than apical (Fig. 2D).

Head (Figs 3-15): prognathous, slightly longer as wide, side margins distinctly rounded; dorsal ecdysial lines (Es) bifurcate below half of head length; each side of head with 1 round black ocellus (Oc) (Figs 3, 4). Chaetotaxy of dorsal part of head with: 16 epicranial, macro setae (codes: Em1, Em2, Ed2, El3, El1, El2, Ed1, Ed3), 8 posterior micro setae (codes: P1-4), 6 pores (codes: Ec1-3) and a pair of epicranial glands (Eg) located behind antennae (Fig. 3, 3A), 16 frontal setae (codes: Fm1, F11-3, Fd1-4) and a pair of frontal putative campaniform sensilla (code: Fc1). Lateral parts of head with: 4 temporal setae (T1, T2), 6 lateral setae (L1-3) and 6 lateral putative campaniform sensillae (Lc1-3) (Fig. 4). Ventral side (Fig. 5) with: 2 ventral setae (V1), 6 ventral lateral setae (V11-3) and 2 ventral campaniform sensillae (Vc1). Antenna (Figs 6, 7): 3-segmented, length ratio of segments I-III 1.4:2.3:1 respectively. Segment I almost 1.2 x as long as wide, with one pore dorso-apically; segment II 2.4 x as long as wide with 3 macro setae (1 ventrally, 1 dorso-apically and 1 laterally), one semispherical sensory appendage (Sa) and 3 solenidia (IIS1-3); segment III 2.2 times as long as wide, with 3 setae and 4 solenidia (IIS1-4) apically (Fig. 7).

Labrum (Fig. 8): trapeziform, narrowed anteriorly, almost 1.7 x wider at the base than anterior margin; anterior margin almost straight, with 8 macro and 6 micro setae. Adoral surface of labrum (epipharynx) membranous, divided by transverse, narrow, sclerotized strip (Trs) into two areas: anterior (A) and posterior (P) (Fig. 9); almost whole surface, except for central and hind parts of posterior area, with numerous thick, tiny cuticular processes (microtrichia); with 14 pores (2 anteriorly, 8 centrally, 4 posteriorly).

Mandibles slender, about 2.3 x as long as wide at the base (Figs 10, 11): with 1 broad internal tooth and 1 more elongated apical tooth, edge below internal tooth regular or at most slightly rolling, 2 setae at the outer margin and 2 pores dorsally.

Maxilla (Fig 12, 13) consists of triangular cardo (Cdo), stipes (Stp) fused with mala (Ma), palpifer (Pf) and 3-segmented maxillary palp (Pm). Cardo with 1 setae ventrally; stipes with 3 setae and 1 pore; palpifer with 1 seta and 1 pore; mala (Fig. 13) with 3 setae (2 ventrally, one at the outer margin), 1 pore ventro-laterally and a few dozen

cuticular processes dorsally; adoral margin of mala with 1 micro seta and ctenidium of 27-31 blunt denticles. Maxillary palp (Pm) (Fig. 12): length ratio of segments I-III: 1.7:1:2.3 respectively; segment I with 2 pores ventro-apically, segment II with 2 setae (1 ventrally, 1 laterally) and 1 pore ventrally, segment III with 1 digitiform sensory appendage latero-basally.

Hypopharynx as in Fig. 14. Labium (Fig. 15) consists of ligula (Lg) fused with prementum (Pmnt), mentum (Mt), submentum (Smnt) and labial palps (Lp). Submentum trapeziform with 2 setae; mentum with 4 setae and 2 pores, prementum (Pmnt) with 4 setae (2 micro) and 2 pores, ligula wide distinctly sinuate in the central part. Labial palps (Pl) 2-segmented, length ratio of segment I and II 1:1.3, segment I 1.1 x as long as wide, segment II 2.4 x as long as wide with one pore and a few micro sensory appendages apically.

Thorax (Fig. 16). Pronotum with 52 setae (2x [A1-5, L1-7, Da1-3, Db1-2, Dc1-2, P1-5]) and 8 pores (2x C1-4); mesonotum and metanotum each with 40 (2x [A1-6, L1-7, Da2-3, Db1-2, Dc1-2, P1-5]) setae and 4 pores (2x C1-2). The lateral area between pro- and mesothorax with a pair of functional spiracles (Spf), and between meso- and metathorax with a pair of weakly visible, atrophied spiracles (Spa); 1 micro seta under each spiracle (Fig. 17, 17A). Ventral side of thorax (Fig. 20): prothorax with 22 setae (2x [Eu1-2, Ls1-2, Pr1-3, Prehy1-2, St1-2]), microstructure as in (Fig. 20A); meso- and metathorax each with 10 setae. Foreleg (Figs 18, 19): coxa (Cx) with 10 setae (Ad1-3, Al1-3, Pl1-3, V1) and 3 pores (C1-3), trochanter (Tr) with 7 setae (Av1-3, Al1, Pl1, Pv1, V1) and 6 campaniform sensilla (C1-6) probably, femur (Fm) with 8 setae (Ad1, Al1, Av1-2, D1, Pd1, Pv1-2), tibia (Tb) with 9 setae (Ad1-3, Av1-2, Pd1, Pl1-2, Pv1), tarsungulus (Ts) with 2 spine-shaped setae and 2 finger-shape processes (Fsp) (Fig. 19). Length ratio of femur, tibia and tarsungulus 2.3:2.2:1 respectively.

Abdomen (Figs 21-27). Chaetotaxy of tergites I-VIII (Fig. 21): each with 30 setae (2x [A3, A4, A6, Da3, Db2, Dc1-2, L2-4, P1-5]) and 6 pores (2xC1-3); sternite I (Figs 22, 23) with 16 setae (2x [D1-3, P1-4, Ps1]), sternites II-VIII (Figs 22, 23) with 20 setae (2x [D1-3, P1-6, Ps1]); tergites I-VIII each with a pair of spiracles laterally (Fig. 22A).

Segment IX: tergite and sternite fused in uniform ring with 28 setae and 2 pores (6 setae and 4 pores dorsally, 14 setae ventrally and 8 setae laterally). Urogomphi 2-segmented (Figs 24-27); basal segment fused with segment IX, with 1 macro seta laterally; segment II slender, narrowed apically, 2.7 as long as wide, 1.2 x as long as segment I, with 1 seta laterally in half of length, 1 macro seta apically and 2 pores basally (Fig. 27); length ratio of segment IX, urogomphus (without seta apically) and segment X (pygopod) 2.5:1:1.7 respectively.

Cocoon (Figs 28-30)

Before pupation the mature larva (L_2) constructs an oval, silken cocoon covered by substrate with silken window (Fig. 29); length: 3.0-4.5 mm.

Pupa (Figs 31-42)

Body length: 2.91-3.19 mm (mean 3.13 mm); maximal width (between hind knees): 1.61-1.82 mm (mean 1.7 mm); head width (between eyes): 0.74-0.78 mm (mean 0.76

mm). Pupa of exarata type, body stocky, semi-cylindrical, lightly sclerotized, with numerous setae growing from basal, cuticular protuberances (Figs 35, 36); color cream white, long setae brown, short setae almost colorless (Figs 31-33). Head: directed downwards with 26 setae: 6 very small on the top of labrum, 2 at the base of labrum, 4 between the basal part of antennae, 8 between eyes, 6 posteriorly (Figs 31, 32). Antennae curved, laying on the fore and middle knees, with numerous protuberances located around antennal segments III-XI, almost reaching hind margin of shortened elytra. Pronotum: widest in the posterior part, 1.6 x as wide (in the widest place) as long, posterior angles not marked, lateral margins distinctly rounded; with 38 setae - 8 centrally, 14 anteriorly, 8 laterally, 8 posteriorly (Fig. 33). Meso- and metanotum each with 8 setae. Metanotum about 1.4 longer than mesonotum. Hind margin of shortened elytra well visible. Wings reaching (or slightly protruding beyond) anterior margin of abdominal sternite II. Tibiae and tarsi (except fore tarsi) directed obliquely to the middle of the body. Hind tarsi reaching anterior margin of abdominal sternite V (Fig 31). Abdomen with 9 tergites and 8 visible sternites, sternite VIII invisible from ventral view (Figs 31-33). Abdomen gradually widened to segment IV, and then narrowed below this segment to the terminal parts of the body. Abdominal tergite I about 1.5 x as long as tergite II. Last tergite IX extended into two, relatively short abdominal processes. Chaetotaxy of abdominal tergites with short setae only (Fig. 33): I with 4, II with 8, III with 10, IV with 12, V with 10, VI-VIII each with 14 and IX with 16 setae; abdominal processes each with 2 setae and terminal dagger-shape prolongation (Fig. 42). Chaetotaxy of abdominal sternites with long and short setae (Figs 31-33, 40 41): II with 10 setae, III with 10-12 setae, IV and V each with 18 setae, VI with 18-20 setae, VII with 16 and VIII with 6 setae. Microstructure of abdominal sclerites as in Fig. 34. Spiracles situated on the dorsal side, between abdominal tergites and sternites (Fig. 33): 2 functional pairs (Spf) on abdominal segment I-II, the first pair larger than second (Figs 37, 38); 6 atrophied pairs (Spa) on abdominal segments III-VIII (Fig. 39). Terminal segments with well marked sexual dimorphism. Gonotheca in male single (Fig. 40), in female double (Fig. 41).

REMARKS ON THE DISTRIBUTION, ECOLOGY AND BIOLOGY

Pella laticollis (adult habitus and aedeagus as in Figs 43-45) is an European species distributed generally in the central and south part of Europe. In Poland it is rather rare and sporadically occurring species, known from several localities. However, locally it was observed to occur in large numbers. It is defined as a eurytopic, humicophilous and myrmecophilous species. It is associated exclusively with nests of *Lasius fuliginosus*. That species of ant inhabits moist and moulding tree trunks in forests, river valleys and other boggy areas (BURAKOWSKI et al. 1981; KOCH 1989; STANIEC & ZAGAJA 2088). *P. laticollis* occupies close vicinity or inside of the ants' nests.

In the south-eastern part of Poland *P. laticollis* may make up almost 25% of the total number of specimens of the Staphylinidae collected in *L. fuliginosus* nests (STANIEC & ZAGAJA 2008). The highest abundance of the adults was recorded in autumn (September). The examined species was observed together with the following rove-beetles: *Drussilla canaliculata* (FABR.), *Geostiba circeralis* (GRAV.), *Habrocerus capillicornis*

(GRAV.), *Haploglossa gentiles* (MÄRKEL), *Medon piceus* (KRAATZ), *Othius subuliformis* STEPH., *Oxypoda vittata* MÄRKEL, *Pella cognata* (MÄRKEL), *P. funesta* (GRAV.), *P. humeralis* (GRAV.), *P. lugens* (GRAV.), *Phylodreppa floralis* (PAYK.), *Quedius brevis* ER. and *Sepedophilus marshami* (STEPH.).

During the rearing, conducted from April 24th to July 3rd 2006, the copulation was observed on April 28th. Eggs were laid from April 30th. The period of highest intensity of oviposition was observed from May 8th to 15th. From the middle of May to the beginning of June the rate of oviposition was gradually decreasing. The larval stages were observed from the beginning of May to the end of conducted observations (July 3rd). On the basis of laboratory studies and measurements of the head width and body length two larval instars of *P. laticollis* were recognized. Shortly before pupation the larvae were becoming less and less active and made silken cocoon strengthen by soil lumps (Figs 28-30). The pupae were observed at the end of the first decade of May.

TAXONOMIC REMARKS

Diagnosis of larva. The combination of characters that distinguishes the mature larva (L₂) of *P. laticollis* from the some other known larvae of subfamily Aleocharinae (TOPP 1973; ASHE 1981, 1985; AHN 1997; THAYER et al. 2004) is as in Table 1.

Considering the above-mentioned morphological diagnosis, *P. laticollis* (Lomechusini tribe) larva is most similar to the larva of *Atheta coriaria* (Athetini tribe). Among 33 characters used in the study, 14 were identical or similar in both mentioned species. The most similarities are present in the chaetotaxy of dorsal side of thorax and abdominal segments. In the larvae of other compared species: *Meronera venustula* (ER.), *Liparocephalus cordicollis* LECONTE, *Hoplandria klimaszewskii* GÉNIER and *Bolitochara lunulata* PAYK., the similarities between them and *P. laticollis* range from 1 to 5 characters (Tab.).

The production of silken pupal cocoon similar to *P. laticollis* was observed in several tribes of Aleocharinae, including Lomechusini (ASHE 1981; THAYER et al. 2004). THAYER et al. (2004) suggest that this behavior may be a basal condition of the higher classification of Aleocharinae at least. With regard to the pupal stage, the present study of *P. laticollis* provided the first such detailed description of species of Aleocharinae. Previous, very schematic descriptions with poor illustrations without studying chaetotaxy and are useless in tribe-level comparative analyses.

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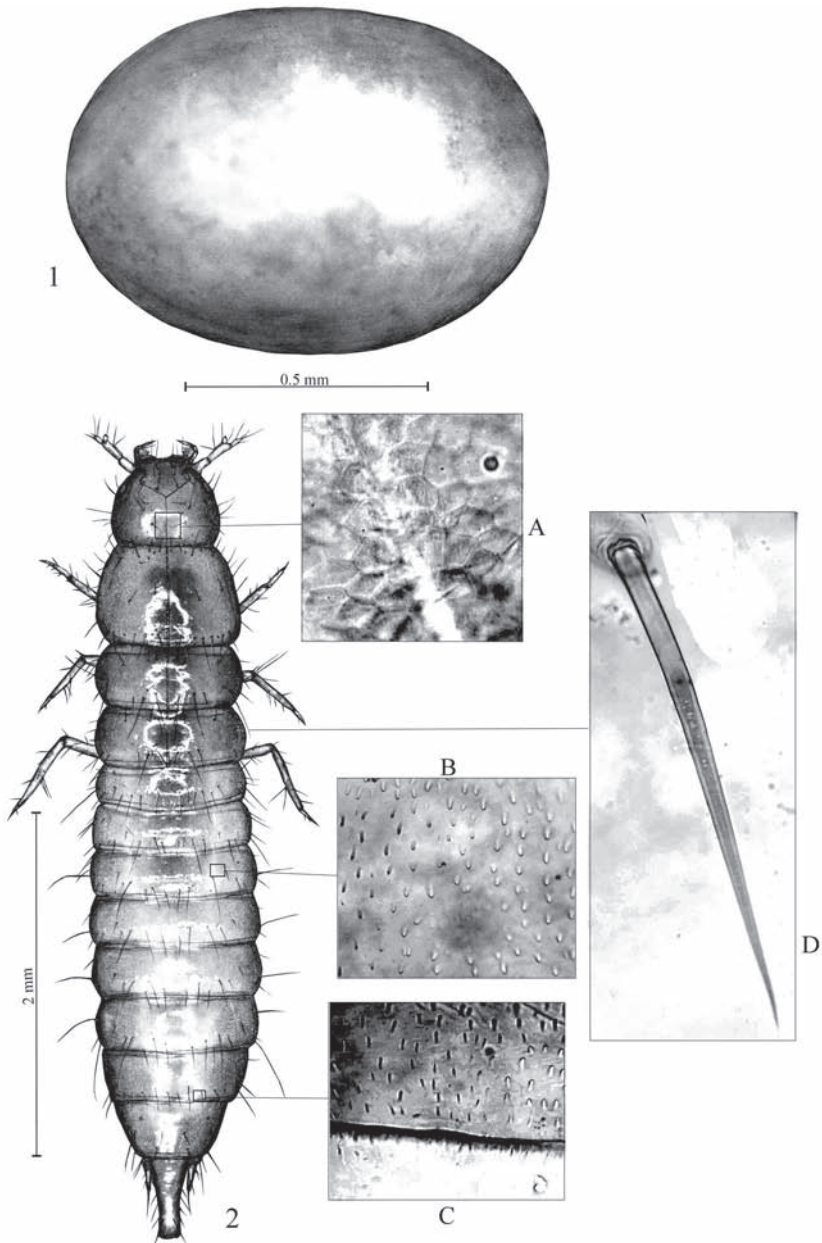
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Tab. Some diagnostic morphological characters of the known mature larvae of selected *Aleocharinae* species. (Alaw - as long as widw; Cx - coxa; D - dorsal part; Fe - femur; Nd - number of denticles (spines) on adoral margin of mala; Np - number of processes; Lg - ligula; Lr - length ratio; Ns - number of setae; Nso - number of solenidia; Ltwr - length to width ratio; Pl - labial palp; Pm - maxillary palp; Pmnt - prementum; Sa - sensory appendage of segment II; Sg - segment; Sp - seta apically; Tb - tibia; Trs - transverse strip sclerotized; Tr - trochanter; Ts - tarsungulus; Wr - width ratio; Ug - urogomphus; Wrba - width ratio of labrum at the base [between setae Lm2] to the anterior margin [between setae Lm1]; measurements in mm).

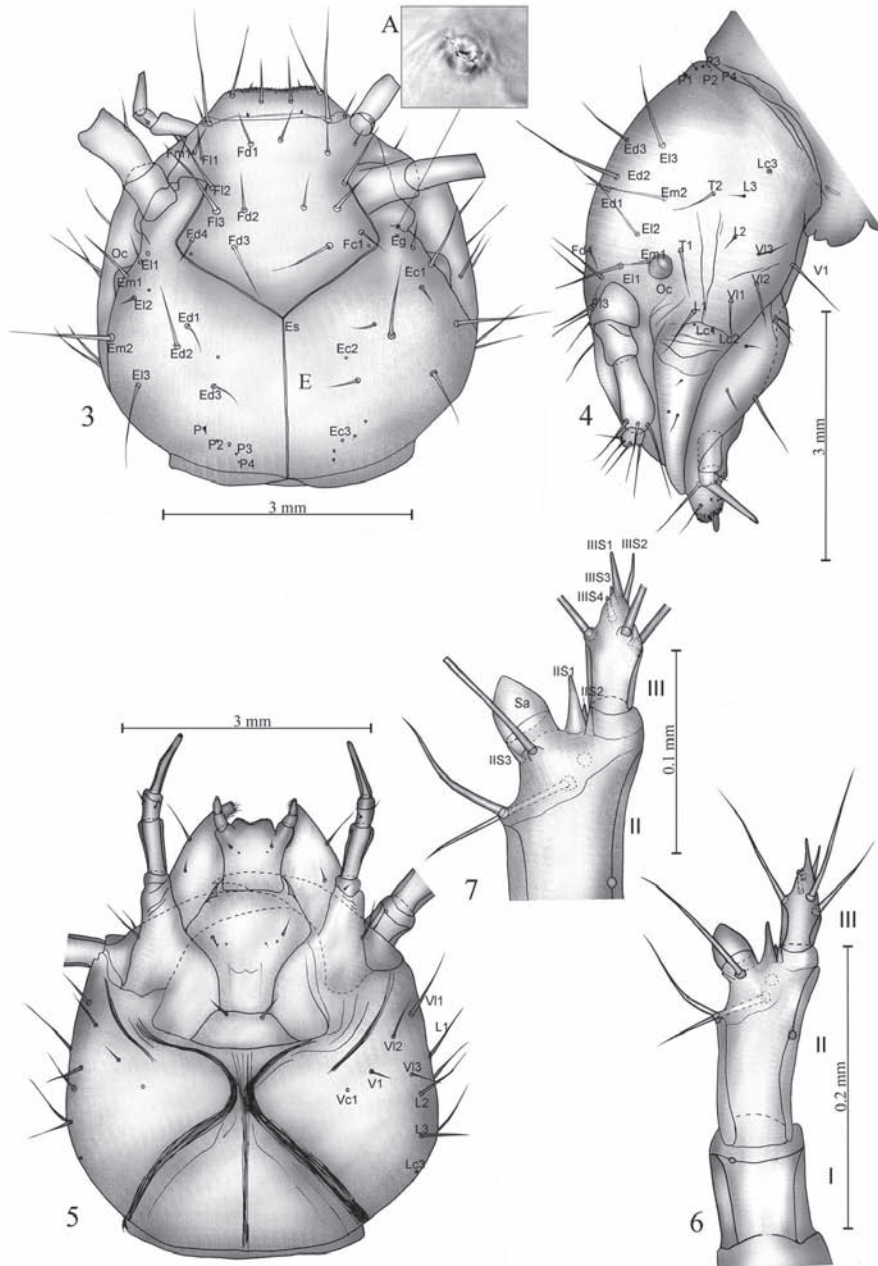
Characters	Tribe/Species					
	Lomechusini	Athetini	Oxyopidini	Liparocephalini	Hoplandriini	Homalotini
Body length	<i>Pella laticollis</i> 4.30-4.80	<i>Atheta coriaria</i> 2.90-3.50	<i>Meronea venustata</i> 2.20-2.70	<i>Liparocephalus cordicollis</i> 3.0-3.40	<i>Hoplandria klimaszewskii</i> 8	<i>Bolitochara lunulata</i> 3.70-4.70
Width	0.45-0.47	0.40	0.23-0.29	?	0.60	0.50
Epitranial setae	16 (lack Em3)	18	12 (lack Ed1, Em2, Em3)	22	16 (lack Em1)	?
Head						
Antenna						
Lr of Sg I-III	1.4:2.3:1	1:1.5:1	1.3:2:1.8	1.2:2.4:1	1.3:3:1	1.3:1.5:1
Ltwr of Sg I	1.2 x	0.7 x	0.4 x	1 x	1 x	1.3 x
Ltwr of Sg II	2.4 x	1.5 x	1.6 x	2.8 x	2.5 x	1.5 x
Ltwr of Sg III	2.2 x	1.5 x	2.2 x	3 x	1.7 x	2.7 x
Shape of Sa	semispherical	semispherical	inflated, sides parallel, bluntly pointed	club-shaped	extremely large, slender and tapered from base to apex	club-shaped
Labrum						
Seta Ld2	thin	stout	thin	stout	stout	stout
Anterior margin	straight	slightly rounded	central part slightly protruding	almost straight	distinctly rounded	distinctly rounded
Wrba	1.7:1	1.6:1	?	1.4:1	1.3:1	1.6:1
Epipharynx						
Trs	present	absent	absent	absent	?	?
Distribution of cuticular processes	whole surface, except for central part	1 group in central part generally	1 group in central part generally	2 groups separated by central surface	?	?
Mandible (right)						
Interior edge of apical tooth	slightly rolling	thinly serrated	thinly serrated	serrated	regular	regular

Tab. (cont.) Some diagnostic morphological characters of the known mature larvae of selected *Aleocharinae* species. (Alaw - as long as widw; Cx - coxa; D - dorsal part; Fe - femur; Nd - number of denticles (spines) on adoral margin of mala; Np - number of processes; Lg - ligula; Lr - length ratio; Ns - number of setae; Nso - number of solenidia; Ltwr - length to width ratio; Pl - labial palp; Pm - maxillary palp; Pmnt - prementum; Sa - sensory appendage of segment II; Sg - segment; Sp - seta apically; Tb - tibia; Trs - transverse strip sclerotized; Tr - trochanter; Ts - tarsungulus; Wr - width ratio; Ug - urogomphus; Wrba - width ratio of labrum at the base [between setae Lm2] to the anterior margin [between setae Lm1]; measurements in mm).

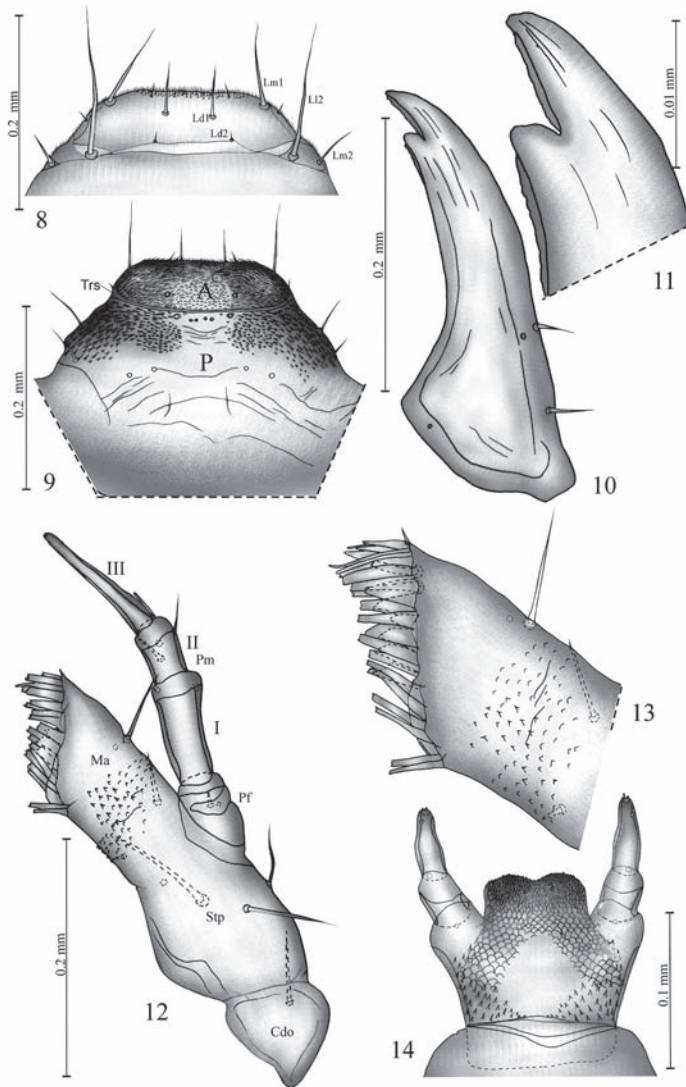
Maxilla						
Nd	27-31	12-18	at most 10	several	about 10 large and numerous small	about 10 slender, narrowed apically
Mala shape	equilateral	slightly widened anteriorly	distinctly widened anteriorly	slender, narrowed apically	distinctly widened anteriorly	
Lr Sg I-III of Pm	1.7:1:2.3	1.1:1:2.3	1.5:1:2.3	?	?	1.4:1:1.9
Labium						
Lg and Pmnt	fused	separated	separated	separated	fused	?
Shape of Lg	wide, short, sinuate anteriorly	elongated, finger shaped	wide, rounded anteriorly	narrow, elongated	elongated, finger shaped	?
Lr seg I-II of Pl	1:1.3	1:1.8	1:1.2	1:1.7	1:1	?
Thorax						
Ns of Cx, Tr, Fe, Tb, Ts	10, 7, 8, 9, 2	15, 8, 8, 9, 2?	9, 7, 8, 9, 2	?, ?, ?, ?, 2	7, 5, about 25, at least 60, 2	4?, 8, 7, 9, 2
Np of Tr	2	2?	0	2	0	0
Lr of Fe, Tb, Ts	2.3:2.2:1	2.4:2.2:1	1.8:2:1	?	?	/
Pronotum - Ns	52	52	34	about 90	64	?
Mesonotum - Ns	40	38	26	50	30	?
Abdomen						
Tergite I - Ns	30	30	22	?	26	?
Sternite I - Ns	16	16	?	?	?	?
Sternite II - Ns	20	20	?	?	?	?
Segm. IX - Ns, D	6	6	6?	about 20	About 90	?
Seg X - Ns, D	4	4	8	?	about 10	?
Urogomphus (Ug)						
Ltwr Seg II	2.7 x	4.5 x	3 x	about 2.5?	2 x	5 x
Lr of seg II to Sp	1:1.3	1:1.8	1:2.3	1:2.4?	1:4.3	1:2.0
References	Present study	Ashe, Watrous (1984)	Ashe (1985)	Ahn (1997)	Thayer, Ashe, Hanley (2004)	Topp (1973)



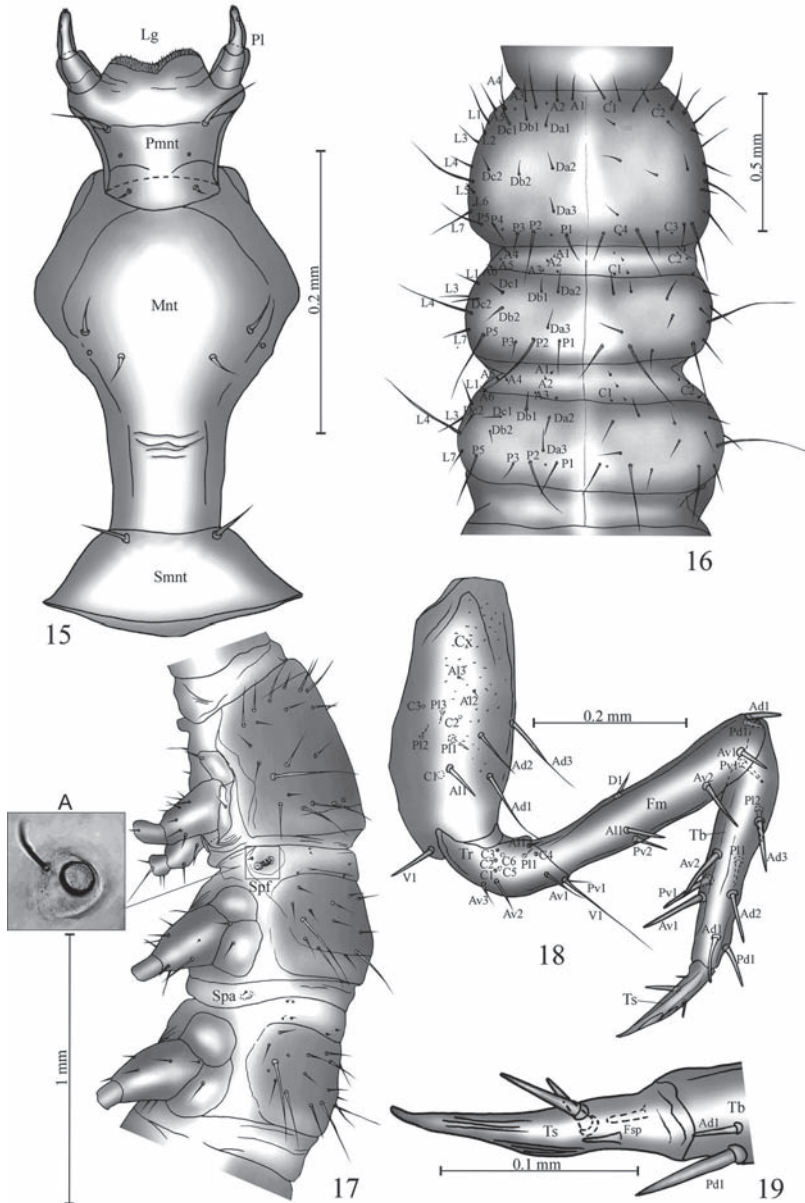
1, 2. *Pella laticollis*. 1, egg; 2, mature larva (habitus); 2A-C, microstructure of head (A) and abdominal tergites (B, C); 2D, long seta



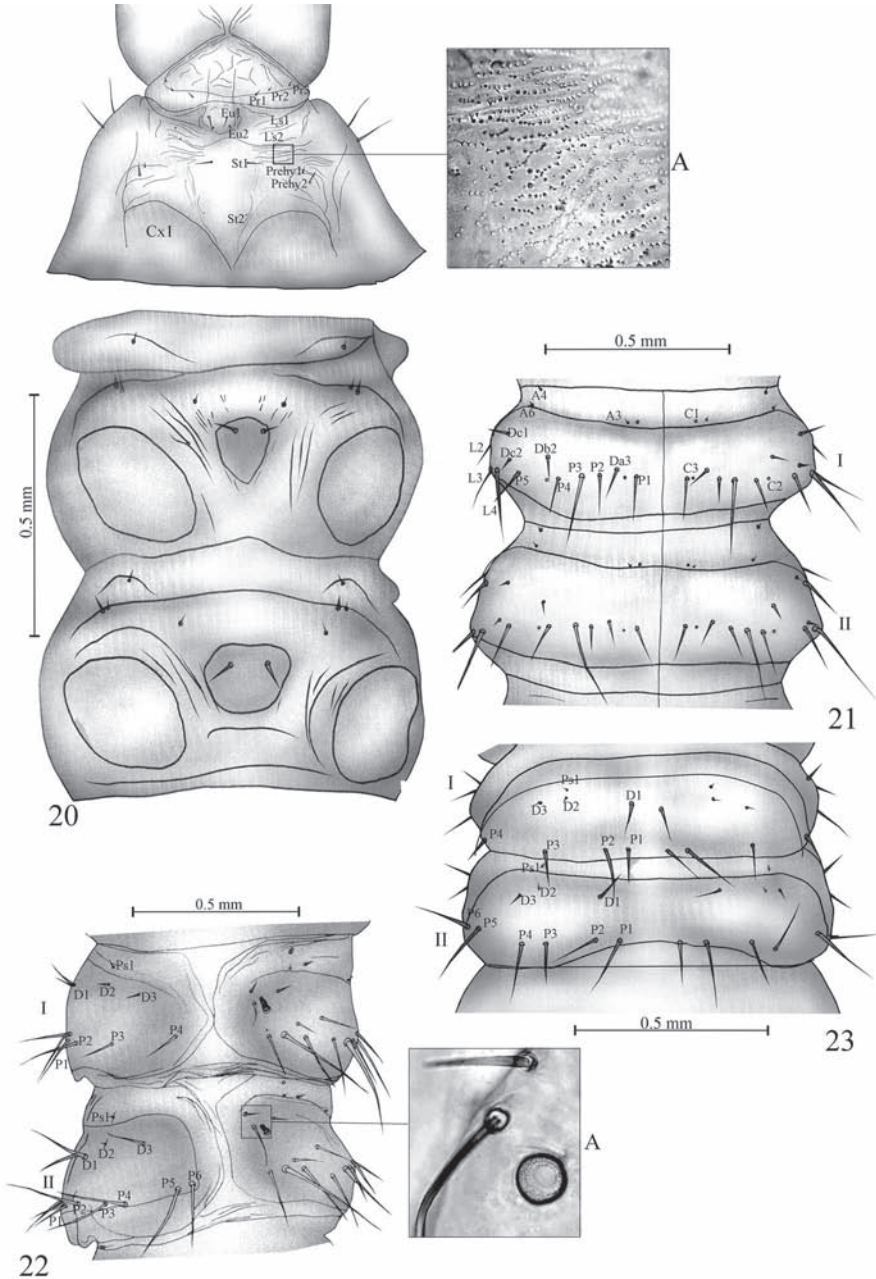
3-7. *P. laticollis*, mature larva, head. 3, dorsal view with epicranial gland (3A); 4, lateral view; 5, ventral view; 6, right antenna in dorsal aspect; 7, apical part of right antenna in dorsal aspect. Abbreviations: setae: Fd, frontal dorsal; Fl, frontal lateral; Fm, frontal marginal; Ed, epicranial dorsal; El, epicranial lateral; Em, epicranial marginal; P, posterior; L, lateral; T, temporal; V, ventral; V1, ventral lateral; campaniform sensilla: Fc, frontal; Ec, epicranial; Lc, lateral; Vc, ventral; Es, epicranial suture; Eg, epicranial gland; Oc, ocellus; I-III, antennal segments; IIS, solenidia of segment II; IIIS, solenidia of segment III; Sa, sensory appendage)



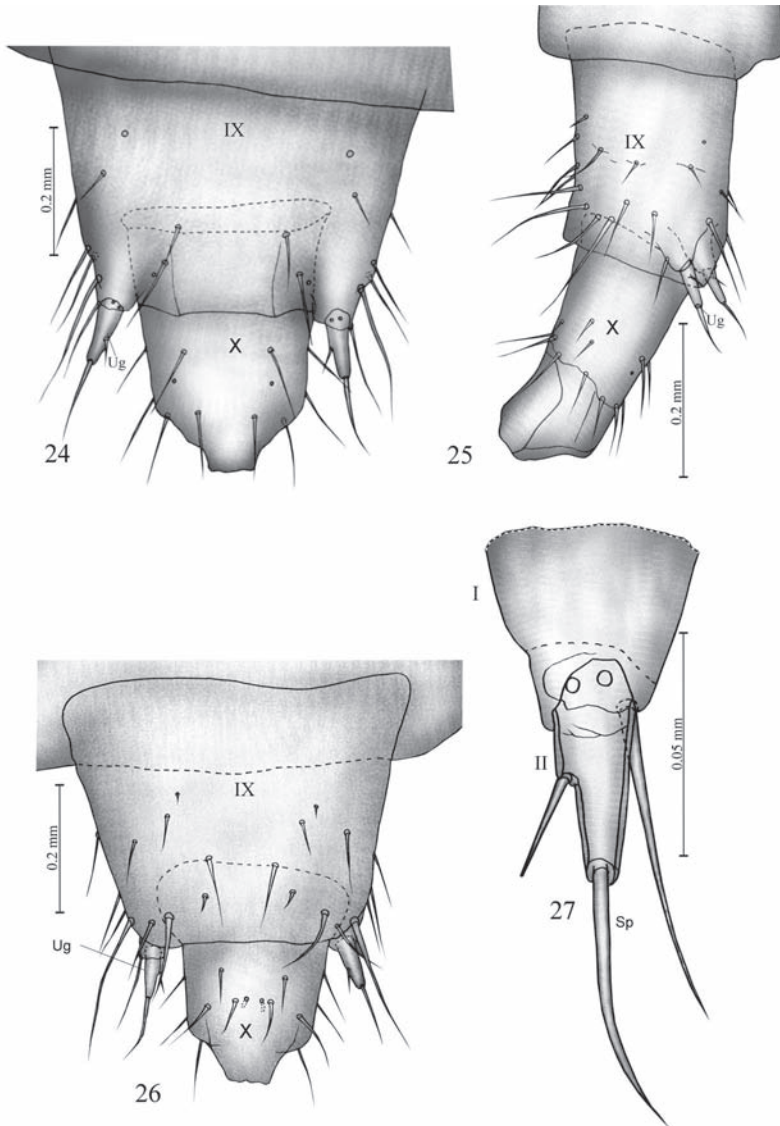
8-14. *P. laticollis*, mature larva. 8, labrum, dorsal view; 9, epipharynx; 10, 11, right mandible with detail of apical part (11), dorsal view; 12, 13, right maxilla with detail of mala (13), dorsal view; 14, hypopharynx. Abbreviations: Cdo, cardo; Stp, stipes; Ma, mala; Pf, palpifer; Pm, maxillary palp; Ld, labral dorsal setae; Lm, labral marginal setae; LI, labral lateral setae



15-19. *P. laticollis*, mature larva. 15, labium, ventral view; 16, thorax, dorsal view; 17, 17A, thorax with functional spiracle (Spf), lateral view; 18, 19, fore leg with detail of apical part (19), anterior view. Abbreviations: Lg, ligula; Pl, labial palp; Pmnt, prementum; Mnt, mentum; Smnt, submentum; Cx, coxa; Tr, trochanter; Fe, femur; Tb, tibia; Ts, tarsungulus; C, campaniform sensilla; Fsp, finger-shape processes; Spf, functional spiracle; Spa, atrophied spiracle; setae: A, anterior; D, discal, rows a-d; L, lateral; P, posterior; Ad, anterodorsal; Al, anterolateral; Av, anteroventral; Pd, posterodorsal; Pl, posterolateral; Pv, posteroventral

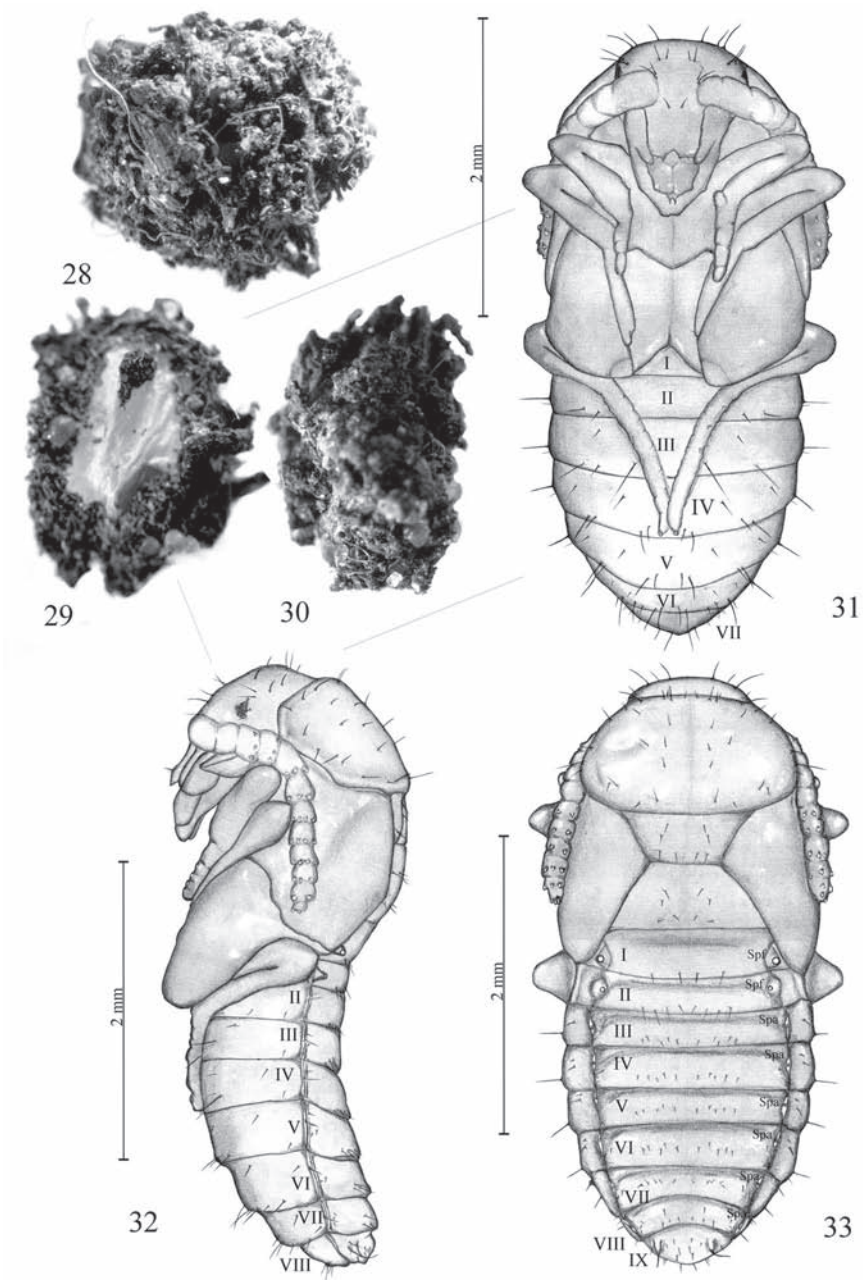


20-23. *P. laticollis*, mature larva. 20, 20A, thorax with microstructure of prothorax (20A), ventral view; 21, abdominal tergites I and II; 22, 22A, abdominal segments I and II with spiracle region (22A), lateral view; 23, abdominal sternites I and II. Abbreviations: C, campaniform sensilla; CxI, anterior coxa; Eu, eusternum; Ls, laterosternum; Prehyl, posthypopleuron; Pr, presternum; St, sternellum; setae: A, anterior; D, discal, rows a-d; L, lateral; P, posterior; Ps, presternal

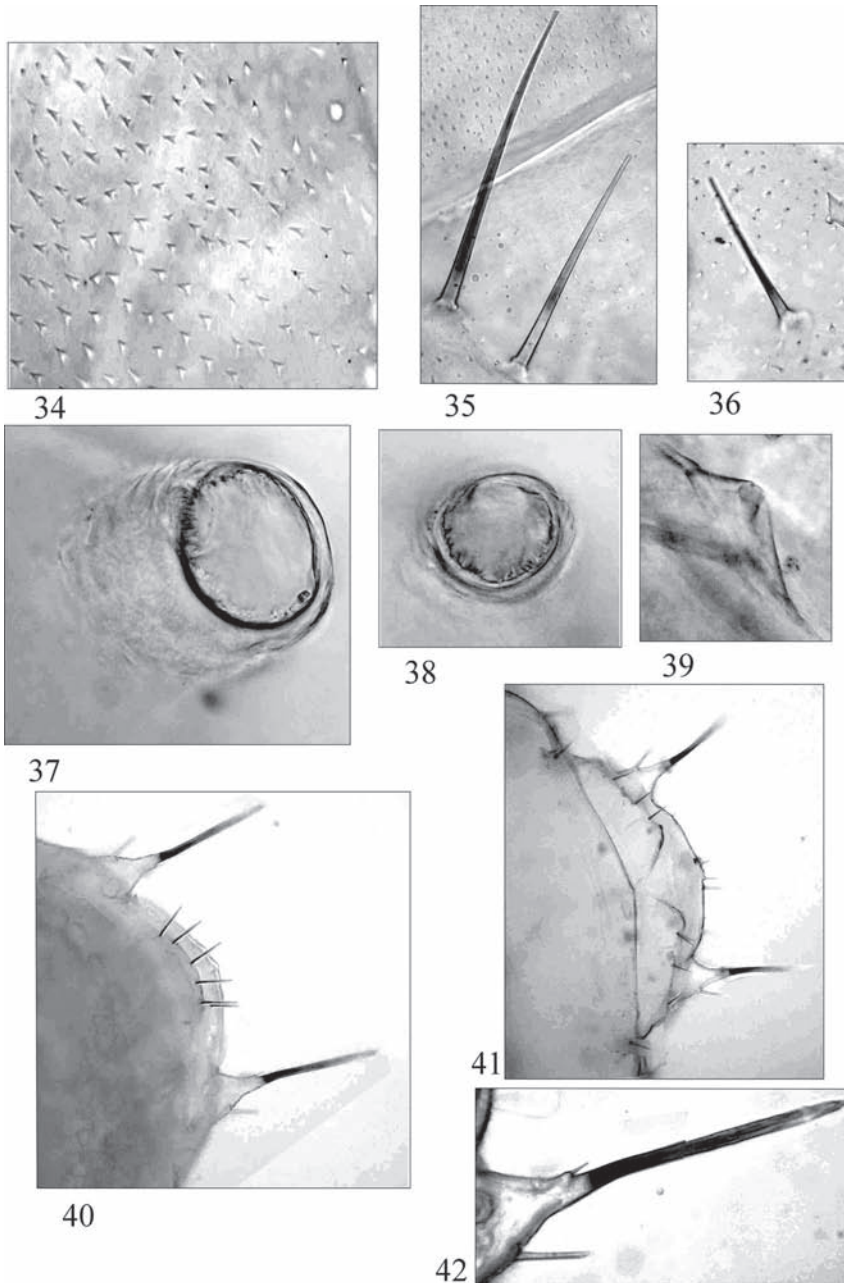


24-27. *P. laticollis*, mature larva. 24, abdominal segment IX and X, dorsal view; 25, abdominal segment IX and X, lateral view; 26, abdominal segment IX and X, ventral view; 27, right urogomphus, dorsal view.

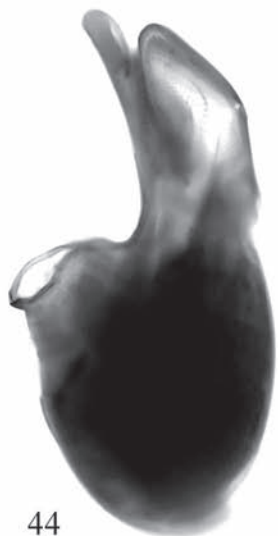
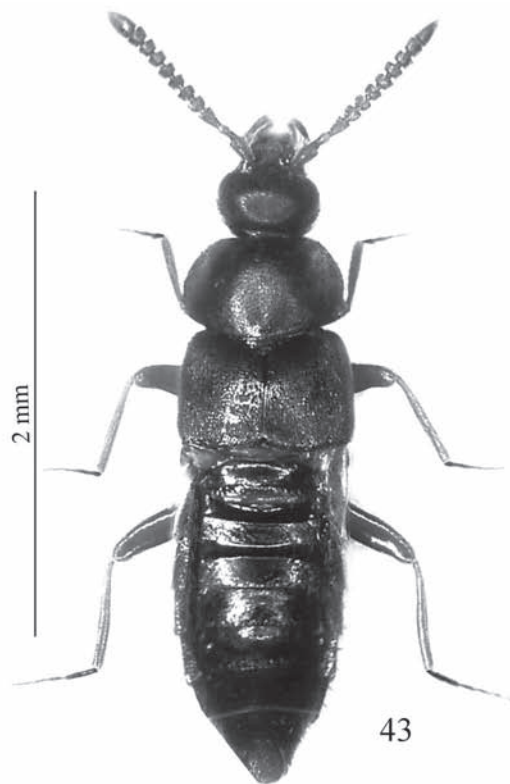
Abbreviations: I, II, segments of urogomphus; Ug, urogomphus



28-33. *P. laticollis*. 28-30, cocoon; 31-33, pupa, ventral view (31), lateral view (32), dorsal view (33). Abbreviations: I, II, III, abdominal tergites or sternites; Spf, functional spiracle, Spa, atrophied spiracle



34-42. *P. laticollis*, pupa. 34, microstructure of abdomen; 35, long setae; 36, short seta; 37, functional spiracle of first pair; 38, functional spiracle of second pair; 39, atrophied spiracle of sixth pair; 40, terminal segment of male, ventral view; 41, terminal segment of female, ventral view; 42, abdominal processes with terminal prolongation



43-45. *P. laticollis*, adult. 43, habitus; 44, aedeagus, lateral view; 45, aedeagus, ventral view