

## RESEARCH

# Comparative Morphology of the Larvae of the Rove Beetles of *Paederus*, *Lathrobium*, and *Tetartopeus*, With Notes on its Systematic Position (Coleoptera: Staphylinidae: Paederinae)

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**ABSTRACT.** The mature larvae of the rove beetles (Coleoptera: Staphylinidae) *Lathrobium lineatocolle* Scriba and *Tetartopeus quadratus* (Paykull) are described for the first time, and the larva of *Paederus littoralis* Gravenhorst is redescribed. Detailed illustrations of their structural features are provided. The description of *T. quadratus* is the first for that genus. Diagnostic larval, morphological characters for *Paederus*, *Lathrobium*, and *Tetartopeus* are proposed. Based on the earlier published and new data, morphological comparisons at the subtribal and genus levels within the subfamily Paederinae are given. The principal differences among subtribes and genera involve structures located on the head, but several relate to abdominal sclerites and urogomphi. Based on the current data, the previously proposed characters diagnostic for the subfamily Paederinae are verified. A status of *Paederidus* and *Tetartopeus* as genera as opposed to their subgeneric status within *Paederus* and *Lathrobium*, respectively, was confirmed.

**Key Words:** immature stage, description, character, Paederina, Latrobiina

Almost 600 species of the genus *Paederus* and 625 species of the genus *Lathrobium* are currently known worldwide. Thirty species of the genus *Tetartopeus* are presently recorded exclusively from the Palaearctic region. Among them, 10 species of *Paederus*, 24 of *Lathrobium*, and 6 of *Tetartopeus* occur in Central Europe (Assing 2012, Peng et al. 2012). Adults of those rove beetles have a medium-sized (5–15 mm), slender, and elongated body. The majority of the species, belonging to the genera mentioned herein, both larvae and adults, inhabit the ecotone zones of water-related habitats (e.g., peat bogs, lakes, ponds, former riverbeds, slow-flowing waters, floodplain meadows, and forests). Many of them are stenotopic species, associated with clear water-dependent natural microhabitats (Koch 1989). Thorough knowledge of their biology, also involving a morphological study of the immature stages, could be useful for designating potential indicators of the condition and quality of various types of seminatural wet habitats (Bohač 1999). However, larvae are hardly ever used in bioindicative studies, primarily because of difficulties associated with their capture and identification.

Surprisingly, little is known about the larval stages of Paederinae and particularly of the genera mentioned above. So far, the larval morphology of *Paederus* and *Lathrobium* has been described for 10, *Paederus alfieri* Koch, *Paederus basalis* Bernhauer, *Paederus caligatus* Erichson, *Paederus columbinus* Laporte, *Paederus fuscipes* Curtis, *Paederus hintzi* Bernhauer, *Paederus littoralis* Gravenhorst, *Paederus riparius* (L.), *Paederus sabaes* Erichson, and *Paederus tempestivus* Erichson, and 5, *Lathrobium brunnipes* (F.), *Lathrobium cavicola*, (H. Muller) *Lathrobium elongatum* (L.), *Lathrobium fulvipenne* (Gravenhorst), and *Lathrobium geminum* Kraatz, species, respectively. However, most of the existing descriptions are outdated, with poor and incomplete illustrations (e.g., Candeze 1861, Isaac 1934, Cerruti 1940, Gerini 1941, Paulian 1941, Bernhauer and Paulian 1942, Ahmed 1957, Ramirez 1966, Pototskaya 1967, Topp 1978). Hence, larval data have very limited application not only for morphological or phylogenetic analyses, very often for the determination of the species. With regard to larvae of other genera of Paederinae (*Domene*, *Eustilicus*, *Lobrathium*, *Medon*, *Paederidus*, and *Rugilus*), reasonable morphological descriptions were provided by

Kasule (1970), Watrous (1981), Frania (1985), Outerelo and Hernández (1992), Smoleński (1997), and Staniec et al. (2011).

*Paederus littoralis* Gravenhorst, 1802, *Lathrobium lineatocolle* Scriba, 1859, and *T. quadratus* (Paykull, 1789) are known from a major part of Europe, from some regions of Asia, and in the case of *P. littoralis*, also from North Africa (Algeria) (Smetana 2004). In Poland, *P. littoralis* and *T. quadratus* are common species, recorded from most regions of the country. *L. lineatocolle* is rare, known only from northwestern and southwestern parts of the country (Burakowski et al. 1979). *L. lineatocolle* and *T. quadratus* are eurytopic and stenotopic taxa, respectively. They are both hydrophilous and phytodetriticolous species, inhabiting the ecotone zones of various types of water-related habitats (e.g., peat bogs, banks of lakes and rivers, and wet meadows), where they occur in plant debris. *P. littoralis* is generally defined as a eurytopic, xerophilous species, observed in xerothermic sunny areas with dry and clayey soils. In Western Europe, also recognized as a hydrophilous and phytodetriticolous species.

Regarding the larval stages of the three aforementioned species, only Kasule (1970) provided first illustrations of the nasale, right maxilla, and labium of *P. littoralis*. The objective of this study is to provide the first larval description of *Tetartopeus*, based on the mature larva (L<sub>2</sub>) of *T. quadratus*; to describe, for the first time, the morphology of the larva (L<sub>2</sub>) of *L. lineatocolle*; to redescribe the mature larva (L<sub>2</sub>) of *P. littoralis*; and to conduct an intersubtribe and intergeneric morphological comparison.

## Materials and Methods

Larval stages of *P. littoralis*, *T. quadratus*, and *L. lineatocolle* were obtained by rearing 12, 6, and 12 specimens of adults, respectively. Adults of *P. littoralis* and *T. quadratus* were sifted on 23 April 2010 from wet moss at the foot of a xerothermic slope with calcareous soil, bordering on the Chodelka River valley, in Dobre near Kazimierz Dolny (51° 17'9" N, 21° 53'8" E; UTM: EB68; SE Poland). Imagines of *L. lineatocolle* were obtained on 18 May 2009 by sifting wet leaf litter at the foot of a loessic slope in a deep ravine overgrown with shaded deciduous forest, in Parchatka near Kazimierz Dolny (51° 21'54" N,

22° 0'11" E; UTM: EB69; SE Poland). Our research were carried on at the Department of Zoology, Faculty of Biology and Biotechnology, MCSU, Poland. Rearing of *P. littoralis*, *T. quadratus*, and *L. lineatocolle* was conducted from 17 May to 1 June 2010, from 15 May to 30 June 2010, and from 28 May to 2 June 2004, respectively, at room temperature ( $20 \pm 3^\circ\text{C}$ ). Adults and larvae were kept separately in plastic containers (18 cm by 18 cm by 7 cm in height), filled with humid soil. Larvae of various undetermined species of ants were supplied every day. The larval stages were killed by means of boiling water, and preserved in ethanol (75%). To prepare microscope slides, the punctured larvae were rinsed in distilled water, cleared in KOH, and finally placed in lactic acid. Habitus illustrations of the larval instar and some of its morphological structures were traced from photos taken by means of a digital camera mounted to an Olympus BX61 compound microscope or Olympus SZX16 compound microscope and corrected by means of graphic software CorelDRAW Graphics Suite X5 (Figs. 1–3, 1A–C, 2A–C, 3A–B, 8A, 9A, 10A, 11A, 12A, 20A, 21A, 23A, 24A, 25A–B, 26A, 27A–B, 28B, 29B, 30B, 31A, 33A, 35A, 37A, 40A, 42A, 44A, 46A, 49A–B, and 50A). Most larval, morphological structures were drawn based on light microscopy with the application of a camera lucida by the second author.

Terminology in a broad sense (including chaetotaxy, all cuticular structures, parts of the body etc.) were used as in our previous work (Staniec et al. 2011). In this previous study, we proposed a model description of the larval stage of Paederinae with a terminology based

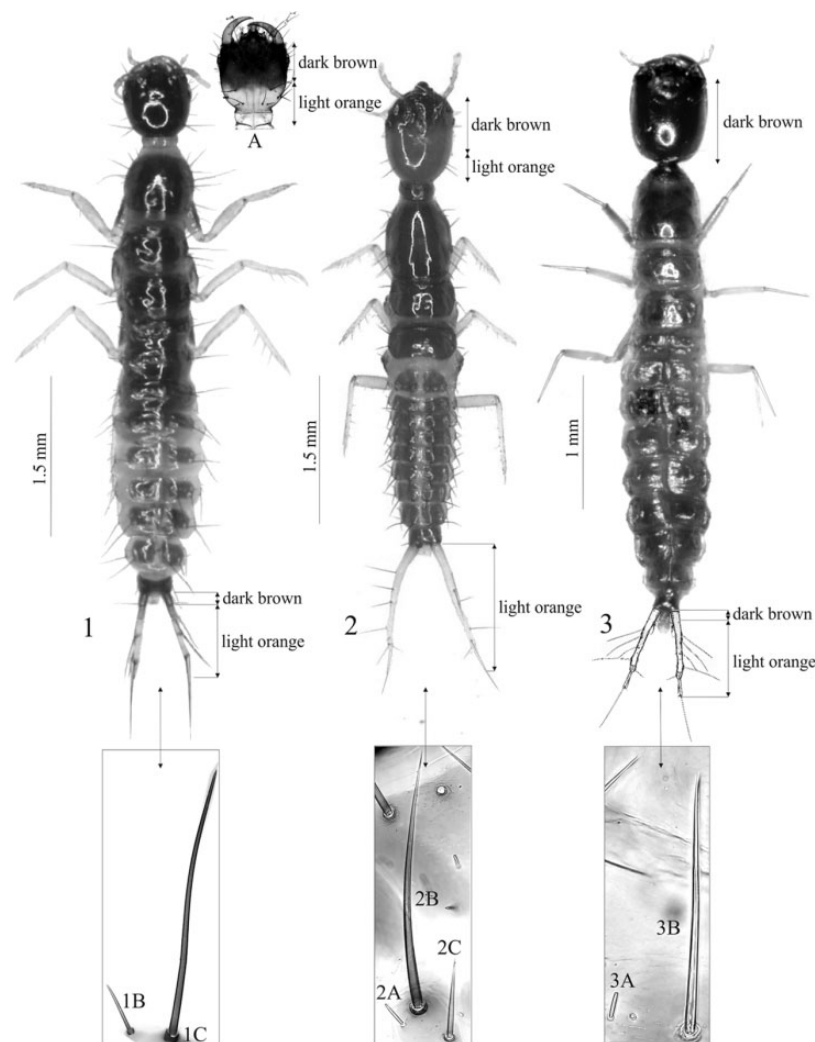
on the *Paederidus* larvae. It was a compilation of the terminology proposed by a few authors on the larval morphology of species belonging to different subfamilies (Ashe and Watrous 1984, Frania 1985, Schmidt 1994, Staniec and Pietrykowska-Tudruj 2009). All measurements are given in millimeters, with the averages provided in parentheses after the observed range. Measurements: body length—from anterior margin of nasale to the end of pygopod; head length—from anterior margin of nasale to neck; width of: head, prothorax, antennal segments, segments of maxillary, and labial palp and mala—maximum. In the description of the larva of *P. littoralis*, the urogomphi are omitted, because these parts of the body were damaged in all examined specimens.

Material examined: *P. littoralis*, 6 L<sub>2</sub>; *L. lineatocolle*, 9 L<sub>2</sub>; and *T. quadratus*, 2 L<sub>2</sub>. Voucher specimens are deposited in Department of Zoology Maria-Curie Skłodowska University. The identification of adults of studied species was carried out by the first author.

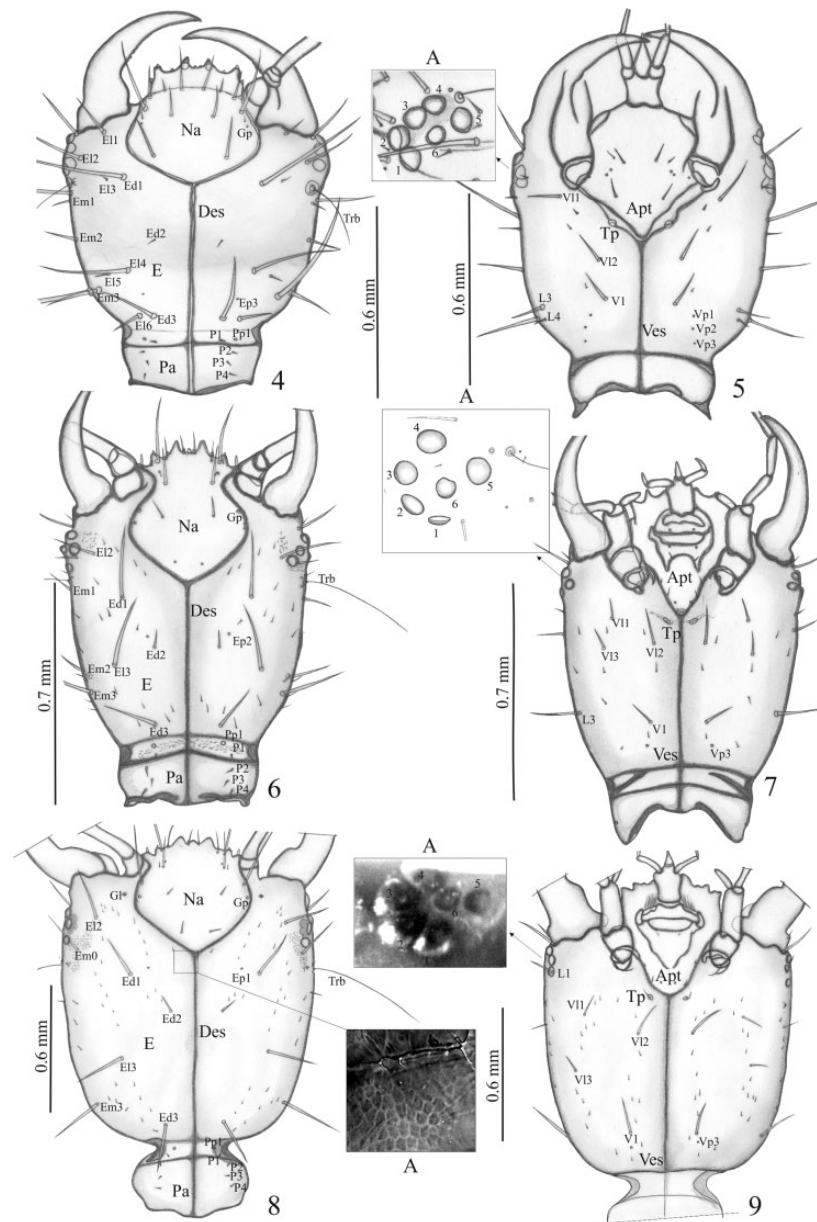
## Results

### Paederus.

**Generic Diagnosis of the Mature Larvae.** The diagnostic characters of the genus *Paederus* are determined based on morphological data of the following species: *P. alferii*, *P. columbinus*, *P. fuscipes*, *P. sabaeus*—limited data; *P. caligatus*—very limited data; *P. basalis*, *P. riparius*—extremely limited data and *P. littoralis*, presented in this article (Isaac 1934, Cerruti 1940, Paulian 1941, Ahmed 1957, Kurosa 1958, Ramirez 1966, Pototskaya 1967, Kasule 1970, Topp



**Figs. 1–3.** *P. littoralis* (1, 1A–C), *T. quadratus* (2, 2A–C), *L. lineatocolle* (3, 3A–B), mature larva. (1–3) General aspect. (1A) Head, dorsal aspect. (1B–C, 2B–C, 3B) Simple setae of abdominal tergite VI. (2A, 3A) Match-shaped setae of abdominal tergite VI.

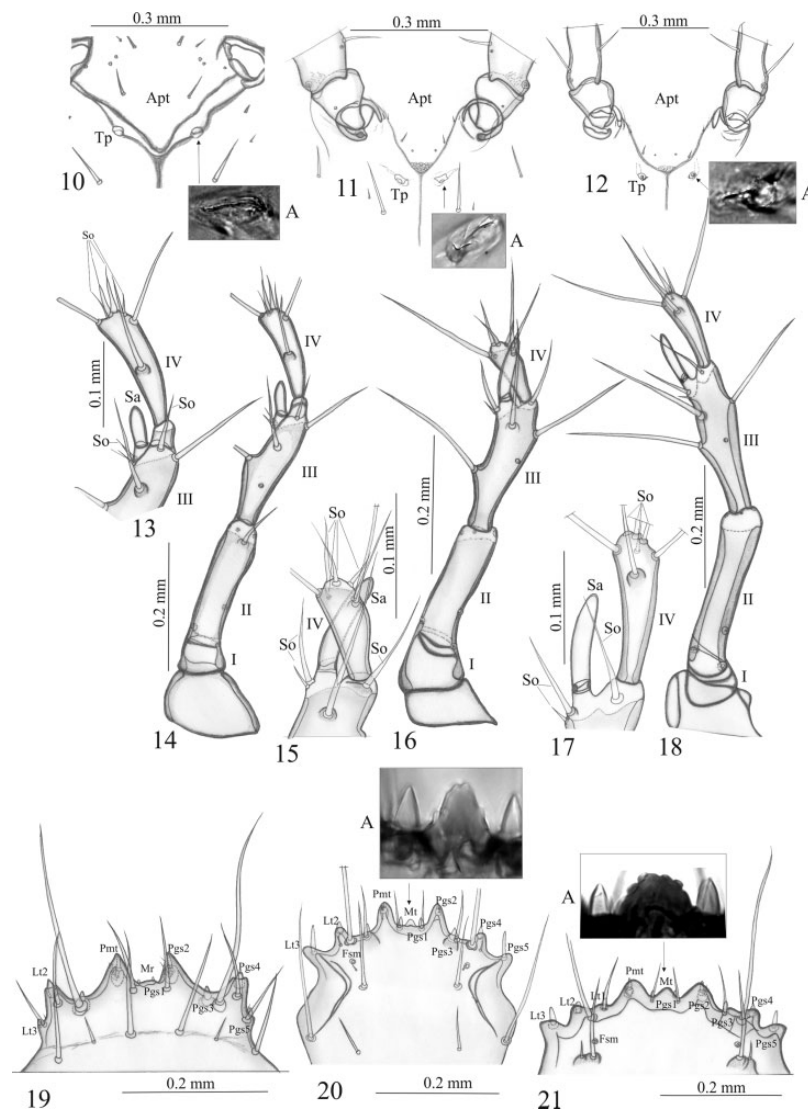


**Figs. 4–9.** *P. littoralis* (4, 5, 5A), *T. quadratus* (6, 7, 7A), *L. lineatocolle* (8, 8A, 9, 9A), mature larva, head. (4, 6, 8) Dorsal aspect. (8A) Microstructure. (5, 7, 9) Ventral aspect. (5A, 7A, 9A) Stemmata. Apt, apotome; Des, dorsal ecdysial suture; E, epicranial part; Ep, epicranial pore; Ed, epicranial dorsal seta; El, epicranial lateral seta; Em, epicranial marginal seta; Gl, gland; Gp, glandular pit; Na, nasale; L, lateral seta; P, posterior seta; Pa, posterior area; Pp, posterior pore; Trb, trichobothrium; Tp, tentorial pit; V, ventral seta; Ves, ventral ecdysial suture; Vl, ventral lateral seta; Vp, ventral pore.

1978). The combination of characters that allow to distinguish the mature larvae of *Paederus* from known larvae of all genera within the subfamily Paederinae include: 1) only simple setae, present; 2) stemmata (Stm) arranged in a cluster of two rows; 3) antennal segment II with a seta; 4) antennal sensory appendage straight; 5) antennal sensory appendage short (less than half as long as segment IV); 6) tooth on medial region of nasale, absent; 7) peg setae on anterior margin of nasale present; 8) epipharynx with a tuft of long cuticular processes medially; 9) mandible with one seta; 10) bunch of microtrichia on mandible, present; 11) inner margin of mandible with teeth; 12) stipes trapeziform; 13) mala tiny (less than half as narrow and half as long as segment I of maxillary palp); 14) seta on inner margin of maxillary palp at the base of segment II; 15) terminal segments of maxillary and Lp with ring of wrinkled cuticula; 16) sternum of prothorax smooth and

17) tergite and sternite (St) of abdominal segment VIII divided (Paulian 1941, Pototskaya 1967, Kasule 1970, Topp 1978).

**Description of the Mature ( $L_2$ ) Larvae of *P. littoralis*.** Body length: 4.95–5.11 mm (4.97 mm); head width: 0.82–0.86 mm (0.84 mm); head length: 0.73–0.94 mm (0.87 mm); and pronotum width: 0.88–1.03 mm (0.95 mm). Coloration, dorsal side: head two-colored as in Fig. 1A, antennae and mouth parts light orange, thoracic tergites, abdominal tergites I–IV and IX dark brown, V–VIII brown, X gray, legs pink, urogomphi two-colored as in Fig. 1; ventral side: presternum and posterior abdominal sternites (Sts) (VIII and IX) brown, mesosternum almost colorless, metasternum, and anterior abdominal Sts (I–VII) yellowish brown, setae black. Body elongate, pronotum distinctly wider than head, meso- and metanotum almost equal in length and width, legs relatively long and slender, abdomen slightly and gradually widened to segment V and then narrowed to

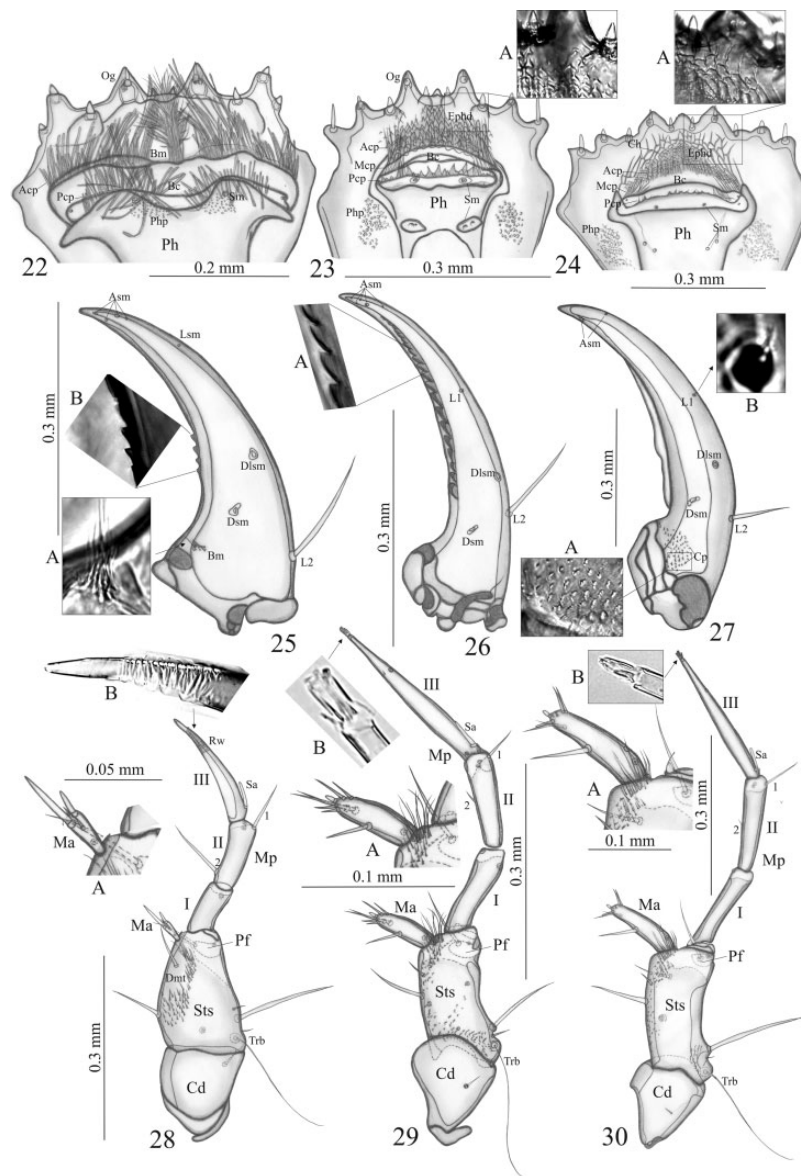


**Figs. 10–21.** *P. littoralis* (10, 10A, 13, 14, 19), *T. quadratus* (11, 11A, 15, 16, 20, 20A), *L. lineatocolle* (12, 12A, 17, 18, 21, 21A), mature larva. (10, 11, 12) Apotome. (10A, 11A, 12A) Tentorial pits. (14, 16, 18) Right antenna in dorsal aspect. (13, 15, 17) Apical part of right antenna in dorsal aspect. (19, 20, 21) Nasale with middle tooth (20A, 21A). I–IV, antennal segments; Apt, apotome; Fsm, frontal sensilla; Lt, lateral tooth; Mr, median region; Mt, median tooth; Pgs, peg seta; Pmt, paramedian tooth; Sa, sensory appendages; So, solenidia; Tp, tentorial pit.

the terminal segment of the body, urogomphi very long, sclerites with simple setae (Figs. 1, 1B, and 1C).

Head. Almost as long as wide, narrowing from the stemmata (Stm) posteriorly to the base; dorsal ecdysial suture (Des) bifurcate before half of head length (Fig. 4). Epicranial part (E) (Fig. 4): with 12 pairs of setae (coded: Ed1–3, E11–6, Em1–3), a pair of pores (Ep3) and a pair of hair-like trichobothria (Trb); posterior area (Pa) with four pairs of micro setae (P1–4) and a pair of pores (Pp1). Nasale (Na) (Figs. 4 and 19) with: nine pairs of simple setae and a pair of lateral glandular pits (Gp), anterior margin with six teeth (four large, distinctly pointed [Pmt, Lt2] and two vestigial [Lt3]) and five pairs of peg setae, equal in length (Pgs1–5); paramedian tooth (Pmt) about twice as long as lateral tooth (Lt2), each paramedian tooth with large olfactory organ ventrally (Og) (Fig. 22); medial region (Mr) almost flat. Each side of head with six, oval or circular Stm in clusters, each cluster consists of two rows of subequal Stm, Stm numbered one to four contacting one with another (Fig. 5A); ventral side of head with five pairs of long setae (coded: L3–4, V1, V11–2), five pairs of micro setae (not coded), and three pairs of ventral pores (Vp1–3) (Fig. 5). Apotome (Apt) completely formed (Figs. 5 and 10), clearly extending beyond tentorial pits (Tp) (Fig. 10A), with three

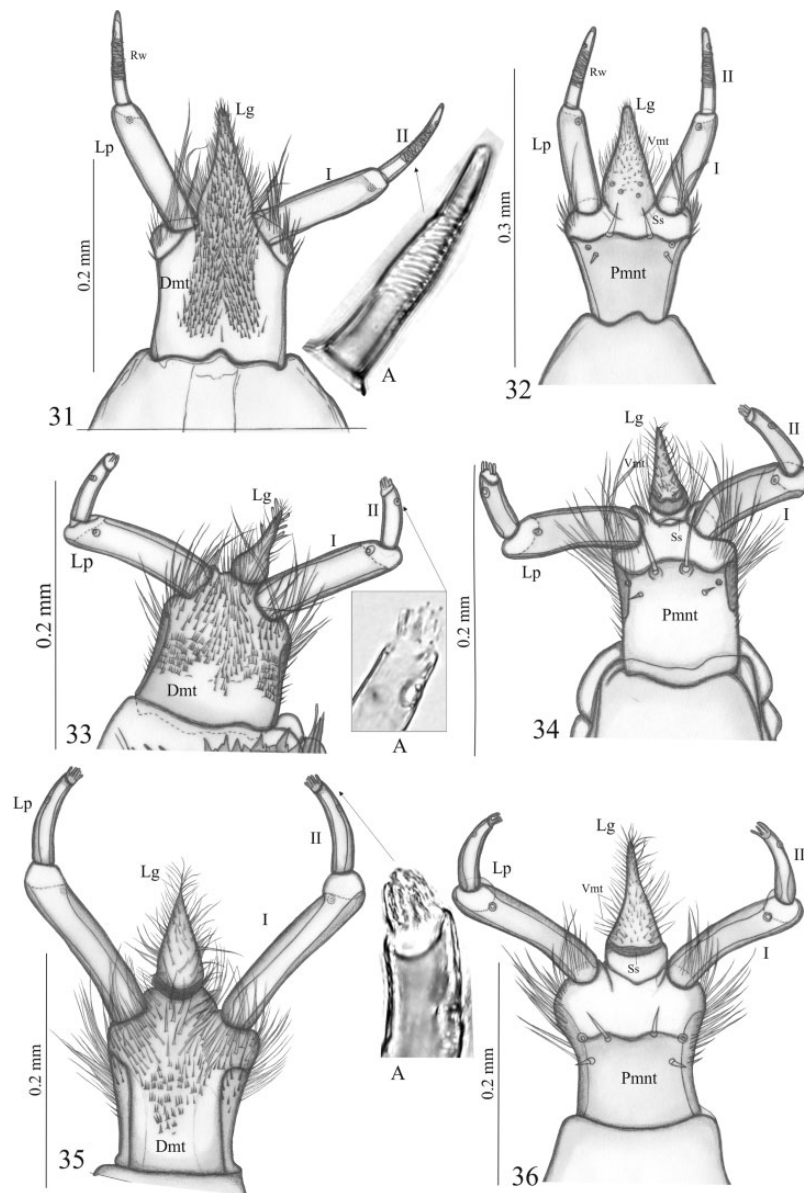
pairs of setae and three pairs of pores (Fig. 10). Antenna (Figs. 13 and 14): four-segmented, length ratio of segments I–IV: 1.0:4.1:4.4:3.0, respectively; segment I 1.6× as wide as long; segment II 3.3× as long as wide, with a dorsoapical seta and five pores (three ventroapical, one lateroventral, one ventrobasal); segment III 3.9× as long as wide, with three macro setae (lateral, lateroapical, dorsal), three solenidia (So) (one long, two short) and moderately elongated, straight finger-shaped sensory appendage (Sa), 2.9× as long as wide; segment IV club-shaped, gradually widened apically, 3.8× as long as wide, 2.9× as long as antennal sensory appendage, with three long setae and four apical solenidia (So), unequal in length (two long, two short). Epipharynx (Fig. 22) with two transverse rows of cuticular processes; the anterior (Acp) with about 120 long cuticular processes along anterior margin of buccal cavity (Bc), incomplete with a tuft of long cuticular processes medially; the posterior (Pcp) with about 100 short cuticular processes along posterior margin of Bc, incomplete medially; pharynx (Ph) with 85–95 pharyngeal pores (Php) in two anterior clusters and a pair of sensilla (Sm). Mandibles (Fig. 25): long and moderately broad; inner margin serrate along 1/10 of its length, serrate part consist of four teeth (Fig. 25B); with one long seta (L<sub>2</sub>) on the outer margin, a dorsobasal



**Figs. 22–30.** *P. littoralis* (22, 25, 25A–B, 28, 28A–B), *T. quadratus* (23, 23A, 26, 26A, 29, 29A–B), *L. lineatocolle* (24, 24A, 27, 27A–B, 30, 30A–B), mature larva. (22–24) Epipharynx with microstructure (23A, 24A). (25–27) Right mandible in dorsal aspect with bunch of microtrichia (25A), inner margin (25B, 26A), cuticular processes (27A) and micro setae (27B). (28–30) Right maxilla with apical part of maxillary palp (28B, 29B, 30B) in dorsal aspect. (28A, 29A, 30A) Detail of right mala in dorsal aspect. I–III, segments of maxillary palp; 1, 2, code of setae; Acp, anterior cuticular processes; Asm, apical sensillum; Bc, buccal cavity; Bm, bunch of microtrichia; Cd, cardo; Ch, channels; Cp, cuticular processes; Dism, dorsolateral sensillum; Dsm, dorsal sensillum; Ephd, epipharyngeal denticles; L1, L2, code of mandibular setae; Lsm, lateral sensillum; Ma, mala; Mcp, medial cuticular processes; Mp, maxillary palp; Og, olfactory organs; Pcp, posterior cuticular processes; Pf, palpifer; Ph, pharynx; Php, pharyngeal pore; Rw, ring of wrinkled cuticula; Sa, sensory appendage; Sm, sensillum; Sts, stipes; Trb, trichobothrium.

bunch of a few microtrichia (Bm) (Fig. 25A) and seven sensilla (large: dorsal [Dsm] and dorsolateral sensillum [Dism], small: lateral [Lsm] and apical [Asm]). Maxilla (Fig. 28): length ratio of cardo (Cd) and stipes (Sts) 1:1.3, respectively; cardo almost quadrangular as long as wide with a seta ventrally; stipes narrowed anteriorly, 1.4× as long as wide, with six setae (long: lateral, ventrolateral, anterodorsal, and anteroventral, two short, lateral), a ventrobasal trichobothrium (Trb), a dorsal longitudinal band of 55–60 microtrichia and a Vp; mala (Ma) tiny, finger-shaped (Fig. 28A), about 2.8× as long as wide, with three apical setae and a ventrobasal pore, the longest seta distinctly longer than mala, segment I of maxillary palp twice as long as mala. Palpifer (Pf) (Fig. 28) crescent-shaped with a long seta and a pore. Maxillary palp (Mp) (Fig. 28): three-segmented, length ratio of segments I–III: 1.0:1.5:2.4, respectively; segment I 1.9× as long as wide, with two

ventroapical pores; segment II 2.8× as long as wide with two setae (coded: 1 [lateroapical], 2 [laterobasal]) and two ventroapical pores; segment III slightly curved inside, gradually narrowed to apex, 5.8× as long wide, with sensory appendage (Sa) laterobasal and a ring of wrinkled cuticula (Rw) at two-thirds of segment length (Figs. 28 and 28B), width of Rw to length of segment III ratio: 1:4, segment III 4.4× as long as sensory appendage (Sa). Hypopharynx (Fig. 31): dorsal side of labium membranous and densely pubescent excluding posterior and lateral parts. Labium (Fig. 32): ventral side of prementum (Pmnt) sclerotized, trapeziform with four setae (two short, two long) and two pores anterior; ligula (Lg) conical, 2.1× as long as wide, about as long and 1.6× as wide as segment I of labial palp (Lp), with numerous ventral microtrichia (Vmt) and four pores, ligula and prementum partly separated by sclerotized strip (Ss). Lp two segmented (Figs. 31 and 32):



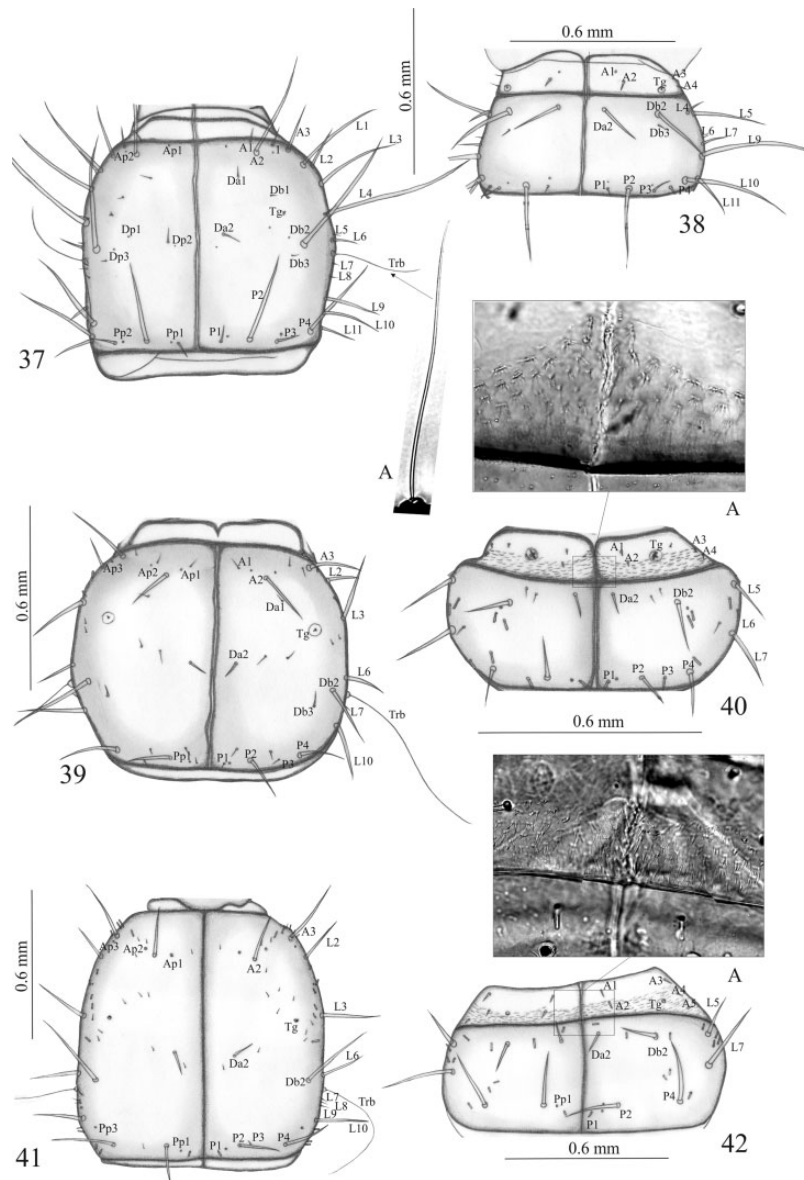
**Figs. 31–36.** *P. littoralis* (31, 31A, 32), *T. quadratus* (33, 33A, 34), *L. lineatocolle* (35, 35A, 36), mature larva. (31, 33, 35) Hypopharynx with apical part of Lp (31A, 33A, 35 A). (32, 34, 36) Labium in ventral aspect. I–II, segments of Lp; Dmt, dorsal microtrichia; Lg, ligula; Lp, labial palp; Pmnt, prementum; Rw, ring of wrinkled cuticula; Ss, sclerotized strip; Vmt, ventral microtrichia.

segment I 1.5× as long as segment II, 4× as long as wide, with a pore ventroanterior; segment II about 7× as long as wide, with a pore lateral and ring of wrinkled cuticula (Rw) at about half length of segment II, width of Rw to length of segment II ratio: 1:2.3–2.5 (Fig. 31A). Neck wide relatively, about 1.9× narrower than head (Fig. 4).

**Thorax.** Thoracic tergites with midlongitudinal ecdysial line. Pronotum (Fig. 37): slightly broader than mesonotum, with transverse carina anterior and posterior (Fig. 37), 1.1× as long as wide, moderately rounded on sides, widest at half its length, with 24 pairs of setae (coded: A1–3, Da1–2, Db1–3, L1–11, P1–4, 1 additional), a pair of trichobothria (Trb) and a pair of tergal glands (Tg) and a pair of pores (Ap1). Mesonotum (Fig. 38): almost 1.5 as wide as long, distinctly rounded on sides, widest at one-third of its length, with transverse carina anterior and 18 pairs of setae (coded: A1–4, Da2, Db2–3, L4–7, L9–11, P1–4). Prosternal region (Fig. 43): presternum (Pr) oval and wide, respectively, divided by medial longitudinal line; with five pairs of setae (one long, four short); sternum (Stp) moderately elongated, divided into two sternites (Sts), each sternite (St) longer than wide with six

short setae, St widely separated by membranous area, membranous area one-fourth of St width. Metanotum almost equal in width as mesonotum, with similar chaetotaxy. Fore leg (Fig. 44): coxa (Cx) moderately elongate about 2.8× as long as wide, with 28 setae (5 of them long), dorsal region with numerous spine-shaped cuticular processes (Cp) (Fig. 44A); trochanter (Tr) divided, with seven setae (five of them long) and a few pores; femur (Fe) elongated and moderately slender, 4.9× as long as wide, with 30 simple setae (12 of them long) and a pore; tibia (Tb) elongated and extremely slender, 11.3× as long as wide, with 21 setae (10 of them long) and two pores; tarsungulus (Ts) almost straight (Fig. 45), about 3.9× as long as wide, with two spine-shaped setae on base. Length ratio of coxa, trochanter, femur, tibia, and Ts: 4.8:1.5:5.1:5.2:1, respectively. The region between pro- and mesothorax with large, elliptical spiracles (Sp); 1 dorsal seta of Sp (Fig. 43).

**Abdomen.** Tergites and Sts of abdominal segments I–VIII divided by weakly sclerotized, longitudinal membranes (Figs. 1 and 52). Segment I: tergite with transverse carina anterior, 11 pairs of setae (coded: A2–4, Da2, Db2, L5–6, P1–4) and a pair of tergal glands (Tg)



**Figs. 37–42.** *P. littoralis* (37, 37A, 38), *T. quadratus* (39, 40, 40A), *L. lineatocolle* (41, 42, 42A), mature larva. (37, 39, 41) Pronotum with trichobotrium (37A). (38, 40, 42) Mesonotum with microstructure of carina (40A, 42A). A, anterior seta; Ap, anterior pore; Da, discal seta of row a; Db, discal seta of row b; Dp, dorsal pore; L, lateral seta; P, posterior seta; Pp, posterior pore; Tg, tergal gland; Trb, trichobotrium.

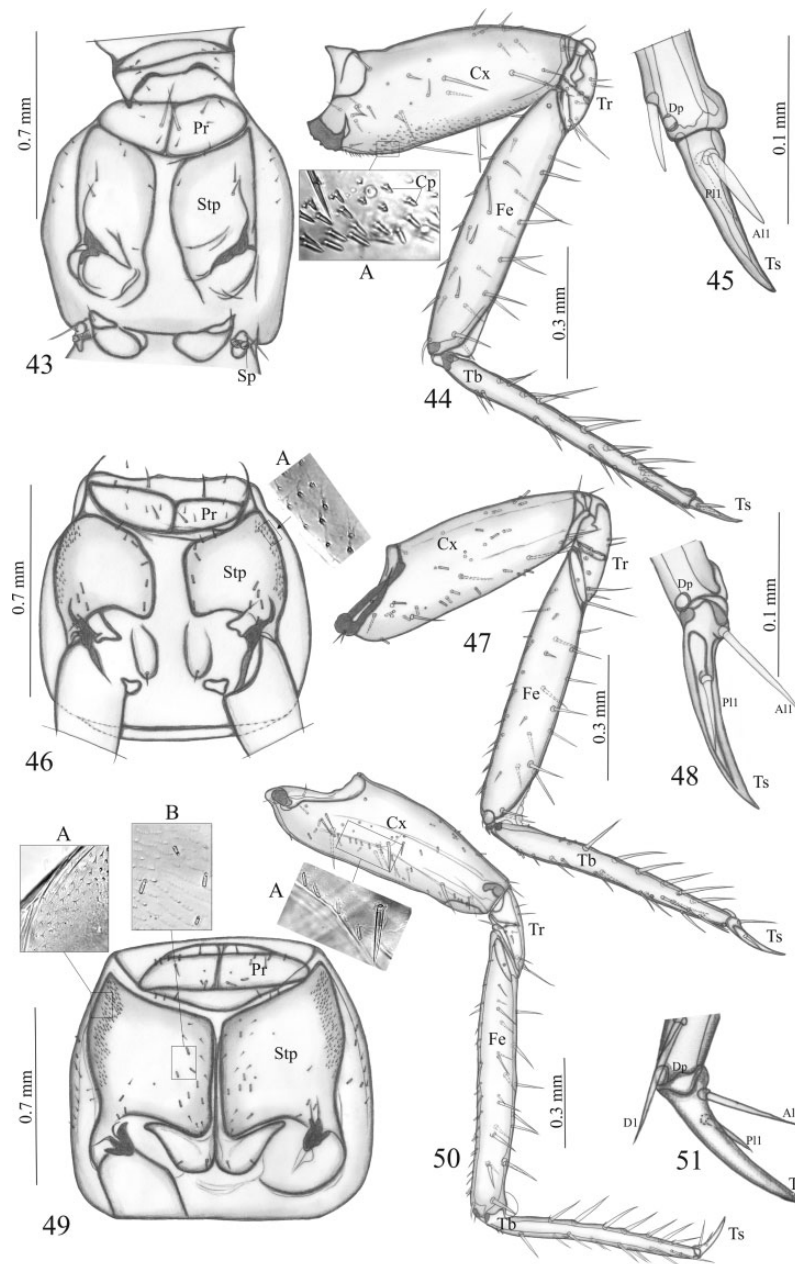
(Fig. 52); paratergite (Pt) and rudimentary parasternite (Ps) on each side, with four setae and one short seta, respectively (Fig. 53); rudimentary sternite with two pairs of short setae (Fig. 54). Segments II–VIII: tergite (Fig. 52) with 11 pairs of setae (coded: A2–4, Da2, Db2, L5–6, P1–4) and a pair of pores (Ap1); elongate paratergite (Pt) and parasternite (Ps), well developed on each side, with four setae each (Fig. 53); sternites II–VIII well developed, with nine pairs of setae (coded: A3, A4, Da2, Db2, L5, P1–4), a pair of pores (Pp2) on sternite II, two pairs of pores on sternites III–VIII. Abdominal segments I–VIII, each with a pair of circular Sp- located between tergites and paratergites (Fig. 53).

#### Tetartopeus.

**Generic Diagnosis of the Mature Larvae.** The diagnostic characters of the genus *Tetartopeus* are determined based on morphological data of *T. quadratus* only. The combination of characters that allow to distinguish the mature larvae of *Tetartopeus* from other larvae within the subfamily Paederinae include: 1) Stm in a scattered clusters; 2) mandible with inner margin serrate along about 4/5 of its length; 3) parasternite on abdominal segment I absent; and 4) urogomphal segment I very elongate, slender and curved with distinct microstructure.

**Description of the Mature ( $L_2$ ) Larvae of *T. quadratus*.** Body length: 4.51–4.89 mm (4.70 mm); head width: 0.71–0.75 mm (0.73 mm); head length: 0.92–0.95 mm (0.93 mm); pronotum width: 0.70–0.71 mm (0.70 mm). Coloration: dorsal side: head two-colored as in Fig. 2, antennae, mouth parts, and thoracic tergites as in *P. littoralis*, abdominal tergites I–VIII yellow brown, segment IX brown, legs, segment X and urogomphi pink; ventral side and setae as in *P. littoralis*. Body elongate, pronotum almost as wide as head and as long as meso- and metanotum together; meso- and metanotum almost equal in width and length; legs and abdomen as in *P. littoralis*; sclerites with simple and match-shaped setae (Mss) (Figs. 2 and 2A–C).

**Head.** Narrowing from the Stm posteriad to the base; 1.2× as long as wide; Des bifurcate at half the head length (Fig. 6). Epicranial part (E) (Fig. 6): with eight pairs of long setae (coded: Ed1–3, El2–3, Em1–3), 30–32 micro setae, a pair of pores (Ep2) and a pair of hair-like trichobotria (Trb); posterior area (Pa) with four pairs of micro setae (P1–4) and a pair of pores (Pp1). Nasale (Na) (Figs. 6 and 20): with eight pairs of setae, a pair of frontal sensilla (Fsm) and a pair of Gp; anterior margin with seven teeth—six distinct and one small, paramedian teeth (Pmt)

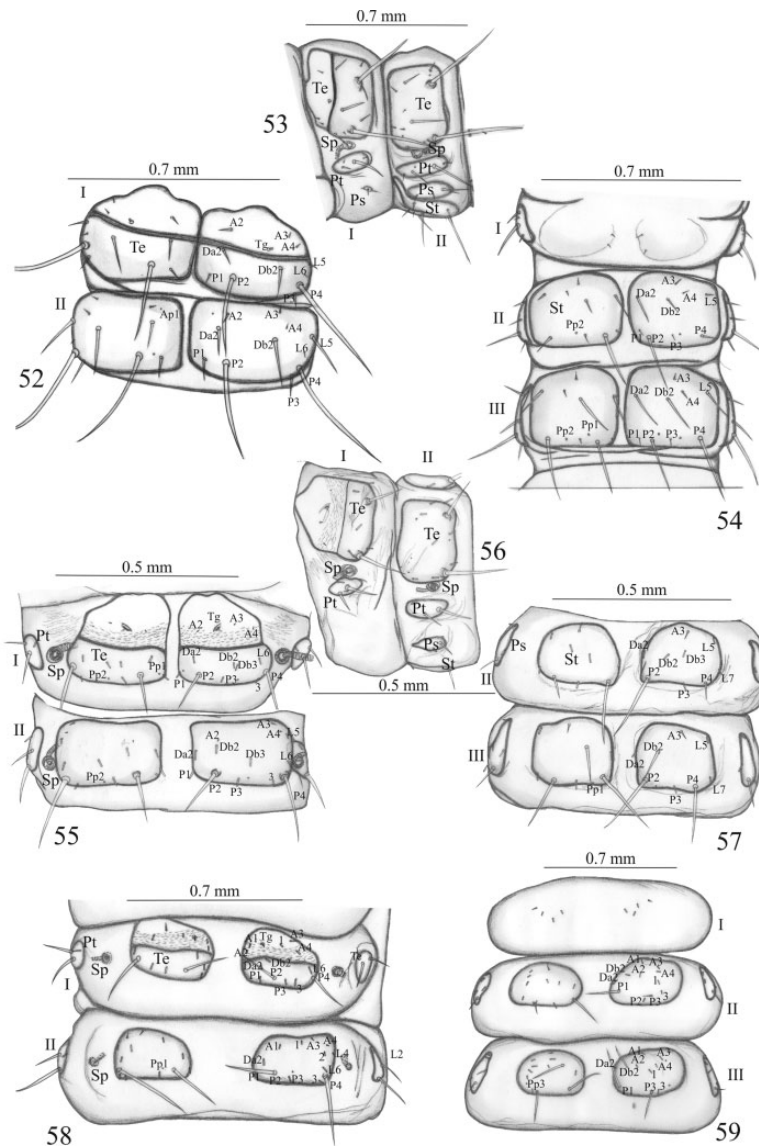


**Figs. 43–51.** *P. littoralis* (43, 44, 44A, 45), *T. quadratus* (46, 46A, 47, 48), *L. lineatocolle* (49, 49A–B, 50, 50A, 51), mature larva (43, 46, 49). Prothorax with microtricha (46A, 49A) and microstructure (49B) in ventral aspect. (44, 47, 50) Right fore leg with cuticular processes (44A) and setae (50A) in anterior aspect. (45, 48, 51) Details of fore tarsungulus. Al, anterolateral seta; Cp, cuticular processes; Cx, coxa; Dp, dorsal pore; Fe, femur; Pl, posterolateral seta; Pr, presternum; Sp, spiracle; Stp, sternum; Tb, tibia; Tr, trochanter; Ts, tarsungulus.

about  $3.6\times$  as long as median tooth (Mt) and more than twice as long as lateral teeth (Lt2), each paramedian tooth with large ventral olfactory organ (Og); five pairs of peg setae (Pgs1–5), setae Pgs5 more than twice as long as others (Figs. 20, 20A and 23). Each side of head with six oval or circular Stm in a scattered clusters (Fig. 7A). Ventral side of head with five pairs of long setae (coded: L3, V1, V11–3), 16–19 micro setae, and a pair of ventral pores (Vp3) (Fig. 7). Apotome (Apt) completely formed (Figs. 7 and 11, 11A), reaching tentorial pits (Tp) (Fig. 11A), with two pairs of micro setae, a pair of pores and a small area of reticulate microstructure between bifurcation of suture. Antenna (Figs. 15 and 16): four-segmented, length ratio of segments I–IV: 1.0:2.0:2.3:1.1, respectively; segment I  $1.1\times$  as wide as long; segment II  $3.1\times$  as long as wide, with six pores (three ventroapical, lateroventral, ventrobasal, and dorsobasal); segment III  $3.5\times$  as long as wide, with sensory

appendage (Sa), strongly elongated, finger-shaped and slightly curved inside,  $5.2\times$  as long as wide, three macro setae (lateral, lateroapical, dorsal), three apical solenidia (So) (two long, one short) and one dorso-lateral pore; segment IV club-shaped, strongly widened apically, about  $2.6\times$  as long as wide, almost as long as sensory appendage of segment III, with three long setae and four apical solenidia (So) (three long, one short). Epipharynx (Fig. 23) with three transverse rows of cuticular processes, the first (Acp) with about 50 elongated cuticular processes along anterior margin of buccal cavity (Bc), the second (Mcp) incomplete, with 9–12 lateral processes only, the third (Pcp) with about 20 cuticular processes of unequal length, along posterior margin of Bc; more than 100 anterior epipharyngeal denticles (Ephd) (Fig. 23A); sides of pharynx (Ph) with 120–140 pharyngeal pores (Php), arranged in two clusters; pharynx with two pairs of sensilla (Sm) (posterior large





**Figs. 52–59.** *P. littoralis* (52–54), *T. quadratus* (55–57), *L. lineatocolle* (58, 59), mature larva. (52, 55, 58) Abdominal segments in dorsal aspect. (53, 56) Abdominal segments in lateral aspect. (54, 57, 59) Abdominal segments in ventral aspect. A, anterior seta; Ap, anterior pore; Da, discal setae of row a; Db, discal seta of row b; L, lateral seta; P, posterior seta; Pp, posterior pore; Ps, parasternite; Pt, paratergite; Sp, spiracle; St, sternite; Tg, tergal gland; Te, tergite; 1, 2, 3, additional setae.

and anterior small). Mandibles (Figs. 26, 26A): long and slim; inner margin serrate along about 4/5 of its length, serrate part including about 20 teeth; with two setae (tiny [L1] and long [L2]), a large sensillum dorsally (Dsm), a large sensillum dorsolaterally (Dlsm) and four small sensilla near apex (Asm). Maxilla (Fig. 29): length ratio of cardo (Cd) and stipes (Sts) 1:1.4; cardo triangular, with a seta ventrally; stipes almost rectangular, twice as long as wide, with five setae (long: anteroventral, lateral, laterobasal and short: dorsolateral, laterobasal), ventrobasal Trb, bunch of about 20 anterodorsal long macrotrichia, many short dorso-basal microtrichia and a few lateral pores; mala (Ma) long and stocky, finger-shaped (Fig. 29A), about 2.7× as long as wide, 1.6× shorter than segment I of maxillary palp, with seven setae (five subapical, one ventral, one lateral), a ventrobasal pore and a tiny, apical sensory appendage. Palpifer (Pf) (Fig. 29) crescent-shaped with a long seta ventral, and a pore. Maxillary palp (Mp) (Fig. 29): three-segmented, length ratio of segments I–III: 1.0:1.0:2.0, respectively; segment I 4.1× as long as wide, with two pores lateroapically; segment II slightly widened to apex, 4.2× as long as wide, with two setae (code: 1 [long, latero-apical] and 2 [short, lateral, in the half of segment length]) and 2

ventroapical pores; segment III gradually narrowed to apex, about 8× as long as wide, with a sensory appendage (Sa) laterobasal, a micro seta, two pores (laterodorsal and dorsalobasal) and a few minute finger-shaped sensory appendages apically (Fig. 29B); segment III 5.9× as long as sensory appendage (Sa). Hypopharynx (Fig. 33): dorsal side of labium membranous and densely pubescent excluding posterior part; sides with microtrichia grouped in short, transverse rows. Labium (Fig. 34): ventral side of prementum (Pm) sclerotized, rectangular, with four setae (two short, two long) and two pores anterior; ligula (Lg) bulbiform, with numerous long, Vmt, 2.3× as long as wide, about twice as wide as segment I of Lp, length ratio of ligula and segment I of Lp: 1:1.6, respectively; ligula and prementum completely separated by Ss. Lp two-segmented (Figs. 33 and 34): segment I 1.9× as long as segment II and about 2.9× as long as wide, with a pore ventroanterior; segment II slightly curved mediad, 3× as long as wide, with a few finger-shaped minute sensory appendages apically (Fig. 33A). Neck relatively wide, about 1.8× narrower than maximum width of head (Figs. 6 and 7).

Thorax. Thoracal tergites with midlongitudinal ecdysial line (Figs. 39 and 40), about equal in width. Pronotum almost as long as

meso- and metanotum together, with transverse anterior and posterior carina (Fig. 39), 1.1× as long as wide, moderately rounded on sides, widest on the trichobothria (Trb) level, with 25–26 pairs of setae (coded—long and intermediate-size: A1–3, Da1–2, Db2–3, L2–3, L6–7, L10, P1–4; not coded short: 9–10), a pair of trichobothria (Trb), a pair of tergal glands (Tg) and four pairs of pores (Ap1–3, Pp1). Mesonotum (Fig. 40): almost twice as wide as long, distinctly rounded on sides, widest at one-third of its length, with transverse carina anterior and 21 pairs of setae (coded—long and intermediate-size: A1–4, Da2, Db2, L5–L7, P1–4; not coded short: 8) among them seven pairs of short Mss, and a pair of tergal glands (Tg); carina in the posterior part with scaly microstructure (Fig. 40A). Prosternal region (Fig. 46): presternum (Pr) elongated, divided by medial longitudinal line, with five pairs of setae (one long, four short); sternum of prothorax (Stp) transverse, divided into two sclerites, each sclerite as long as wide with 11 short setae (nine match-shaped, two simple) and a band of microtrichia at the outer margin (Fig. 46A), sclerites widely separated by membranous area (1/3 of sternite width). Fore leg (Fig. 47): coxa (Cx) elongate, about 3.4× as long as wide, with 31 setae (4 long, 20 short, match-shaped, 7 short, simple); trochanter (Tr) divided, with 5 setae and a few pores; femur (Fe) elongated, 5.6× as long as wide, with 33 setae (4 short and match-shaped, 29 simple) and a pore; tibia (Tb) elongated and slender, 8.7× as long as wide, with 23 setae (4 match-shaped, 19 simple) and 2 pores; Ts moderately curved (Fig. 48), about 4.8× as long wide, with two spine-shaped setae (longer at basal part and shorter in about 1/3 of Ts length). Length ratio of coxa, trochanter, femur, tibia, and Ts: 4:1.5:4.3:3.7:1, respectively.

**Abdomen.** Tergites and sternites of abdominal segments I–VIII divided by longitudinal membranes (Figs. 2 and 55). Segment I: tergite with transverse carina anterior and 12 pairs of setae: seven short match-shaped and five simple (coded: A2–4, Da2, Db2–3, L6, P1–4, 3–additional), a pair of tergal glands (Tg) and two pairs of pores (Pp1, Pp2) (Fig. 55); paratergite (Pt) well developed on each side with three setae (one short, match-shaped and two long, simple), parasternites and sternite absent (Fig. 56). Segments II–VIII: tergite (Fig. 55) with 13 pairs of setae (coded: A2–4, Da2, Db2, Db3, L5–6, P1–4, 3–additional) included six pairs of Mss and a pair of pores (Pp2); paratergite (Pt) elliptical and parasternite (Ps) elongated on each side, with four and three setae, respectively; sternite well developed, with nine pairs of setae on sternite II (coded: A3, Da2, Db2–3, L5, L7, P2–4), eight pairs of setae on sternites III–VIII (coded: A3, Db2, Da2, L5, L7, P2–4) and a pair of pores (Pp1) (Fig. 57). Abdominal segments I–VIII, each with a pair of circular spiracles (Sp) located between tergites and paratergites (Fig. 56). Segment IX (Figs. 60, 63, and 65): without paratergite and parasternite (Fig. 65), tergite with 12 pairs of setae (seven short match-shaped and five simple) and three pairs of pores dorsally (Figs. 60 and 65), sternite with seven pairs of setae (three short, match-shaped and four simple) and a pair of pores (Fig. 63). Urogomphus (Ug): two-segmented, very elongate; segment I slender and distinctly curved mediad, rather strongly sclerotized, whole surface with clearly visible microstructure, about 11.8× as long as wide, with 14 simple setae—seven long (coded: D1, L2, Ld2–3, M1, V2–3) and seven short (not coded); segment II very slender, about 8.5× as long as wide, distinctly narrower than segment I, with a long simple, apical and a short, subapical setae (Fig. 60); length ratio of segments I, II and apical seta of Ug: 4.9:1:1.7, respectively; Ug 6.3–6.6× as long (without apical seta) as pygopod. Segment X (pygopod): about as long and more than half as wide as segment IX, with 12–13 pairs of setae (simple: six long, three to four short and match-shaped: three short) and four pairs of pores (Figs. 60, 63, and 65).

#### **Lathrobium.**

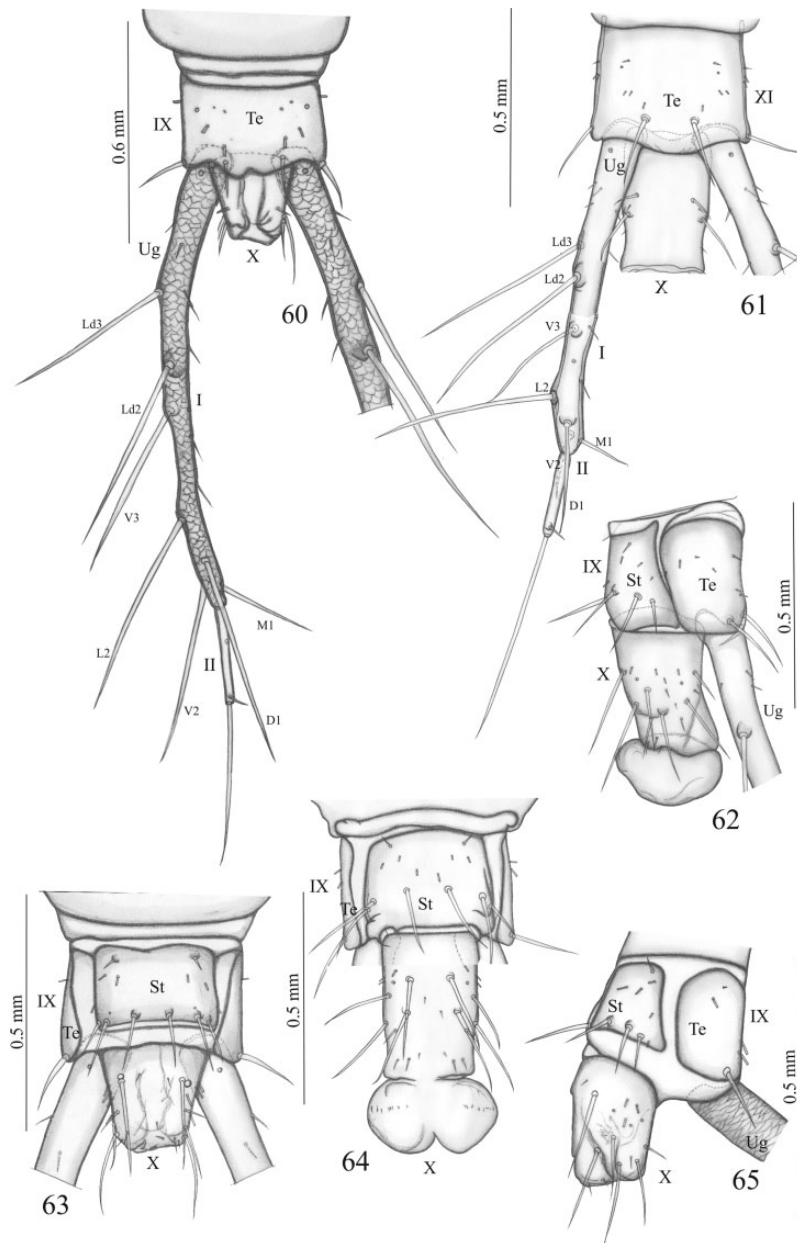
**Generic Diagnosis of the Mature Larvae.** The diagnostic characters of the genus *Lathrobium* are defined based on morphological data extracted from the following respective descriptions: *L. brunripes*, *L. elongatum*—limited data; *L. fulvipenne*, *L. geminum*—very limited data (Paulian 1941, Pototskaya 1967, Kasule 1970, Topp 1978) and *L. lineatocolle*, presented in this article. The combination of characters that allow to distinguish the

mature larvae of *Lathrobium* from the known larvae of closely related genera are the following: 1) head rounded on sides; 2) head more than twice as wide as neck; 3) antennal sensory appendage slightly curved mediad; 4) antennal sensory appendage more than 1.5× shorter than segment IV; 5) medial tooth on nasale conical; 6) anterior region of epipharynx with numerous denticles; and 7) segment II of Lp curved mediad.

**Description of the Mature (L<sub>2</sub>) Larvae of *L. lineatocolle*.** Body length: 4.12–5.17 mm (4.20 mm); head width: 0.78–0.89 mm (0.84 mm); head length: 0.90–1.17 mm (0.98 mm); pronotum width: 0.80–0.88 mm (0.85 mm).

Coloration, dorsal side: head dark brown, antennae, mouth part and pronotum as in *P. littoralis*, meso- and metanotum light brown, legs yellow, abdominal tergites I–VIII brown, IX black, X light brown, urogomphi two-colored as in Fig. 3; ventral side and setae as in *P. littoralis*. Body elongate, head oval, almost as wide as prothorax, prothorax almost as wide as long and 1.7× as long as mesothorax; meso- and metathorax almost equal in length and width; legs and abdomen as in *P. littoralis*, sclerites with simple and Mss (Figs. 3 and 3A–B).

**Head.** About 1.2× as long as wide, moderately rounded on sides, slightly widening from the Stm to the trichobothria (Trb), and then narrowing to the base; Des bifurcate at about 1/3 of head length (Fig. 8). Epicranial area (E) (Fig. 8): with seven pairs of long setae (coded: Ed1–3, El2, El3, Em3, Em0), 65–70 micro setae, a pair of pores (Ep1), a pair of hair-like trichobothria (Trb) and a pair of glands (Gl), microstructure as on Fig. 8A; posterior area (Pa) with four pairs of minute setae (P1–4), and a pair of pores (Ep1) (Fig. 8). Nasale (Na) (Figs. 8 and 21): labrum completely fused with frons; with nine pairs of setae, a pair of frontal sensilla (Fsm) and a pair of Gp; anterior margin with nine relatively low and wide teeth—seven well-visible triangular (Mt, 2Pmt, 2Lt2–3) and two very low, barely visible (Lt1), five pairs of peg setae (Pgs1–5), Ps5 distinctly longer than others, median tooth (Mt) almost as long as lateral teeth (Lt2 and Lt3), paramedian teeth (Pmt) about 1.7× as long as median tooth, each paramedian tooth with large ventral olfactory organ (Og) (Figs. 21 and 24). Each side of head with six oval or circular Stm in a cluster (Fig. 9A). Ventral side of head with five pairs of long setae (coded: L1, V1, and V11–3), more than 50–55 micro setae, and a pair of ventral pores (Vp3) (Fig. 9). Apotome (Apt) completely formed (Figs. 9 and 12, 12A), reaching tentorial pits (Tp), with two pairs of micro setae, a pair of pores and a small area of reticulate microstructure between bifurcation of suture. Antenna (Figs. 17 and 18): four-segmented, length ratio of segments I–IV 1.0:4.7:4.1:2.3, respectively; segment I 1.4× as wide as long; segment II 4.1× as long as wide, with six pores (three ventroapical, two ventrobasal, and one dorsolateral); segment III 3.6× as long as wide, with elongated, slightly curved mediad, finger-shaped sensory appendage (Sa), sensory appendage 5.3× as long as wide, three macro setae (two lateral, one laterodorsal), three solenidia apical (So) (two long, one short), a dorsal pore; segment IV club-shaped, strongly widened apical, about 3.3× as long as wide, 1.5× as long as sensory appendage of segment III, with three long setae and four solenidia (So) apical (three long, one short). Epipharynx (Fig. 24) with three transverse rows of cuticular processes: the first (Acp) complete, with about 25 elongated, cuticular processes along anterior margin of Bc; the second (Mcp) incomplete, with about 20 cuticular processes lateral only; the third (Pcp) incomplete, with about 20 rather short, cuticular processes lateral and medial along posterior margin of Bc; about 180 of Ephd and a branching system of channels (Ch) anteriorly (Fig. 24A); sides of pharynx (Ph) with about 200 pharyngeal pores (Php), arranged in two clusters; pharynx with three pairs of sensilla (Sm) (two pairs posterior and a pair anterior). Mandibles (Fig. 27): long and moderately slim; inner margin not serrate, with a wide and low tooth at about half length; with two setae (macro–L2, micro–L1) on outer margin, and four sensilla (one large dorsal [Dsm], one large dorsolateral [Dlsm], and two small near apex [Asm]) and about 60 cuticular processes (Cp) dorsobasal (Figs. 27A and B). Maxilla (Fig. 30): length ratio of cardo (Cd) and stipes (Sts) 1:1.6; cardo almost triangular, with a seta ventrally; stipes almost



**Figs. 60–65.** *T. quadratus* (60, 63, 65), *L. lineatocolle* (61, 62, 64), mature larva, abdominal segment IX, X and urogomphi. (60, 61) Dorsal aspect. (62, 65) Lateral aspect. (63, 64) Ventral aspect. D, dorsal seta; L, lateral seta; Ld, laterodorsal seta; M, medial seta; St, sternite; Te, tergite; Ug, urogomphus; V, ventral seta; I, II, urogomphal segments; IX–X, abdominal segments.

rectangular, almost  $2.2\times$  as long as wide, with six setae (long: laterobasal, lateral, ventral, ventroanterior and short: laterobasal, laterodorsal), a long Trb ventrobasal, two pores (ventral and ventroanterior), a bunch of about 15 long anterodorsal macrotrichia, a few tiny cuticular processes near the Trb and along the inner margin; mala (Ma) relatively long and stocky, finger-shaped (Fig. 30A), about  $3.5\times$  as long as wide, with six setae (five subapical, one longest lateral in the half of length), two pores dorsolateral in posterior part and two tiny sensory appendages apically; segment I of maxillary palp  $1.3\times$  as long as mala. Palpifer (Pf) (Fig. 30) crescent-shaped with a long seta and a pore ventrally. Maxillary palp (Mp) (Fig. 30): three-segmented, length ratio of segments I–III: 1.0:1.0:1.6, respectively; segment I  $4.2\times$  as long as wide, with two pores lateroapically; segment II slightly widened to apex  $4.1\times$  as long as wide with two setae (code: one [long, lateroapical], two [short, lateromedial]) and two ventroapical pores; segment III gradually narrowed to apex, about  $8.6\times$  as long as wide, with laterobasal sensory appendage (Sa), laterodorsal pore and a few minute,

finger-shaped sensory appendages apically (Fig. 30B), segment III  $6.1\times$  as long as sensory appendage (Sa). Hypopharynx (Fig. 35): dorsal side of labium membranous with the exception of sclerotized sides and pubescent excluding posterior and lateral parts; medial region with short microtrichia grouped in short, transverse rows (with two to three microtrichia each row); anterior part with long microtrichia, separated from each other. Labium (Fig. 36): ventral side of prementum (Pmnt) sclerotized with the exception of anterior, widened part, sclerotized region with four setae (two short, lateral and two long, anteromedial) and two pores anterior; ligula (Lg) bulbiform,  $2.4\times$  as long as wide, about twice as wide as segment I of Lp; length ratio of ligula and segment I of Lp: 1:1.4, respectively, with numerous long Vmt, ligula and prementum completely separated by Ss. Lp two-segmented (Fig. 36); segment I  $1.8\times$  as long as segment II and about  $3.9\times$  as long as wide, with a pore ventroanterior; segment II  $4\times$  as long as wide, with a few micro finger-shaped sensory appendages apically (Fig. 35A). Neck relatively narrow, about  $3.6\times$  narrower than head (Figs. 8 and 9).

Thorax. Thoracic tergites with midlongitudinal ecdysial line (Figs. 41 and 42), about equal in width. Pronotum almost as long as meso- and metanotum together, with narrow transverse carina anterior and posterior (Fig. 41): almost as long as wide, moderately rounded on sides, widest on the trichobotria (Trb) level, with 39–43 pairs of setae (coded: A2–3, Da2, Db2, L2–3, L6–10, P1–4; not coded: 25–29 short), a pair of trichobotria (Trb) and a pair of tergal glands (Tg) and 5 pairs of pores (Ap1–3, Pp1, Pp3). Mesonotum (Fig. 42): almost twice as wide as long, distinctly rounded on sides, widest at half of its length, with transverse carina anterior and 23 (12 pairs of coded + 11 pairs) pairs of setae (coded: A1–5, Da2, Db2, L5, L7, P1–2, P4; not coded: 11 short, match-shaped), a pair of pores (Pp1) and a pair of tergal glands (Tg); carina with microstructure, posterior (Fig. 42A). Prosternal region (Fig. 49): presternum (Pr) elongated and narrow, respectively, divided by medial longitudinal line; with eight pairs of short setae (three simple, five pairs rod-shaped); sternum (Stp) strongly developed, divided into two sternites by narrow, membranous area of 1/10 of sternite width; each sternite almost as long as wide with 18–20 short setae (9–10 match-shaped and 9–10 simple), 1–2 pores and band of microtrichia at the outer margin (Figs. 49A, B). Leg (Figs. 50 and 50A): coxa (Cx) elongated 2.8× as long wide, with about 50 setae (4 long, simple, 10 short, simple, and 34–36 short, match-shaped); trochanter (Tr) divided, with nine setae (three long, six short) and a few pores; femur (Fe) strongly elongated and slender, 7.4× as long as wide, with 47 setae (8 short, rod-shaped, 15 long, simple, 24 short, simple) and one pore; tibia (Tb) elongated and slender, 10.9× as long as wide, with 26 setae (20 long, simple, 5 short, simple, 1 short, match-shaped) and one pore; Ts curved moderately (Fig. 51), 3.5× as long wide, with two spine-shaped setae (A11—longer at basal part, P11—shorter in about 1/4 of Ts length). Length ratio of coxa, trochanter, femur, tibia, and Ts: 5.6:1.7:6.4:5.0:1, respectively.

Abdomen. Tergites and sternites of abdominal segments I–VIII divided by weakly sclerotized, longitudinal membranes (Figs. 3 and 58). Segment I: tergite with transverse carina and 13 pairs of setae, including 11 pairs of short Mss (coded: A1–4, Da2, Db2, L6, P1–P4 and 1, 3—additional) and 2 pairs of simple, long setae (P2, P4), a pair of tergal glands (Tg) (Fig. 58), microstructure as in Fig. 42A; well-developed paratergite (Pt) on each side with three simple setae (one short, two long), sternite vestigial with 4 pairs of micro setae (Fig. 59). Segments II–VIII: tergite (Fig. 58) with 13 pairs of setae, including seven match-shaped (coded: A1, A3–4, Da2, L4, L6, P1–4, and 1–3—additional) and a pair of pores (Pp1); sternite II (St) with 11 pairs of setae (coded: A1–A4, Da2, Db2, P1–3, and 1, 3—additional), 10 pairs of setae on sternites III–VIII (coded: A1–4, Da2, Db2, P1, P3, and 1, 3—additional) and a pair of pores Pp3 (Fig. 59). Abdominal segments I–VIII, each with a pair of circular spiracles (Sp) located between tergites and paratergites (Fig. 58). Segment IX (Figs. 61, 62, and 64): tergite with 20 setae (four long, simple and 16 short, match-shaped) and a pair of pores dorsally (Figs. 61 and 62), sternite with 14 setae (six long, simple, posterior; two short, simple, anterior, six match-shaped, medial) (Fig. 64). Ug: two-segmented, elongate, relatively long; segment I moderately slender and almost straight, about 8.5× as long as wide, with 14 setae—seven long (coded: D1, L2, Ld2–3, M1, and V2–3) and seven short (not coded); segment II moderately slender, about 6.7× as long as wide, distinctly narrower than segment I, with a long, apical and a short, subapical setae (Fig. 61); length ratio of segments I, II, and apical seta of Ug: 3.9:1:2.5, respectively; Ug 3.1–3.5× as long (without apical seta) as pygopod. Segment X (pygopod): about as long and more than half as wide as segment IX, with 19–20 pairs of setae (simple: seven long, eight to nine short and match-shaped: four short) and two pairs of pores (Figs. 61, 62, and 64).

**Comparison.** Based on the larvae ( $L_2$ ) of three species described in this article, and two species of *Paederidus* (Staniec et al. 2011), the inter- and intrasubtribal morphological comparison of the subtribes Paederina (*P*) and Lathrobiina (*L*) is presented in Table 1. The differences between the mentioned subtribes include: 1) Mss: absent—*P*, present—*L*; 2)

length of apotome: extending beyond tentorial pits—*P*, reaching tentorial pits—*L*; 3) position of tentorial pits: at half length of head—*P*, before half length of head—*L*; 4) seta on antennal segment I: present—*P*, absent—*L*; 5) shape of antennal sensory appendage: erect—*P*, curved—*L*; 6) median tooth on nasale: absent—*P*, present—*L*; 7) anterior row of cuticular processes on epipharynx: incomplete—*P*, complete—*L*; 8) tuft of cuticular processes in anterior row on epipharynx: present—*P*, absent—*L*; 9) Ephds: absent—*P*, present—*L*; 10) microtrichia on mandible: present—*P*, absent—*L*; 11) stipes shape: trapeziform—*P*, rectangular—*L*; 12) ring of wrinkled cuticula on terminal segment of maxillary and Lp: present—*P*, absent—*L*; 13) location of seta on inner margin of segment II of maxillary palp: basally—*P*, at half length—*L*; 14) apical sensilla on terminal segment of maxillary and Lp: rudimentary—*P*, elongated—*L*; 15) ligula shape: conical—*P*, bulbiform—*L*; 16) shape of segment II of Lp: erect—*P*, curved—*L*; 17) microtrichia on sternum: absent—*P*, present—*L*; and 18) cuticular processes on coxa: present—*P*, absent—*L*.

Regarding the intergeneric variation within Paederina, the morphological comparison between the recently described larvae of *Paederidus* (*Paederidus ruficollis* and *Paederidus rubrothoracicus*) (*Pd*) (Staniec et al. 2011) and the herein described larva of *P. littoralis* (*Pe*), the following differences: 1) body length: 5.17–8.47—*Pd*, 4.95–5.11—*Pe*; 2) Stm in cluster: scattered—*Pd*, in rows—*Pe*; 3) antennal sensory appendage shorter than segment IV: 2 x—*Pd*, 3x—*Pe*; 4) number of peg setae on nasale: 8—*Pd*, 10—*Pe*; 5) tuft cuticular processes on epipharynx: short—*Pd*, long—*Pe*; 6) number of teeth on mandible: 12—*Pd*, 4—*Pe*; 7) presternum: uniform—*Pd*, divided—*Pe*; 8) segments II and III of maxillary palp: stout—*Pd*, slender—*Pe*; and 9) tergite and sternite of abdominal segment VIII: uniform—*Pd*, divided—*Pe*.

Within the subtribe Lathrobiina, the principal differences between the larvae of *Tetartopeus* (*T. quadratus*) (*Tq*) and *Lathrobium* (*L. lineatocolle*) (*Ll*) are the following: 1) neck: wide—*Tq*, narrow—*Ll*; 2) length of antennal sensory appendage to segment IV: equal—*Tq*, 1.5 shorter—*Ll*; 3) nasale with teeth: 7—*Tq*, 9—*Ll*; 4) channels of epipharynx: absent—*Tq*, present—*Ll*; 5) inner margin of mandible: serrate—*Tq*, nonserrate—*Ll*; 6) cuticular processes on mandible: absent—*Tq*, present—*Ll*; 7) micro setae on head: numerous—*Tq* (about 50), very numerous—*Ll* (about 100); 8) micro setae on pronotum: absent—*Tq*, present—*Ll*; and 9) median tooth of nasale: narrow—*Tq*, broad—*Ll*.

The majority of the larvae of the species studied have the diagnostic characters of the subfamily Paederinae as proposed by Kasule (1970): head, stipes, and pronotum with trichobotria; head constricted to form a neck; antenna four-segmented with sensory appendages placed on inner face; six Stm in a cluster; maxillary and Lp three- and two-segmented, respectively; mala finger-shaped and articulated; ligula tapering anteriorly, unsclerotized and densely setose; ventral ecdysial line Y-shaped; legs slender and long, Ts with two setae; spiracles placed in a membranous area between pleurites and tergites; urogomphi two-segmented. In view of our recent (Staniec et al. 2011) and present study, however, two diagnostic characters require updating: 1) tergites and sternites of abdominal segment VIII: previously—divided; currently—divided in *Paederus*, *Lathrobium*, and *Tetartopeus*, uniform in *Paederidus* and 2) body with setae: previously—only simple; currently—only simple in *Paederus* and *Paederidus*, simple and match-shaped in *Lathrobium* and *Tetartopeus*.

Regarding the subtribal level, a number of distinct and consistent differences between subtribes Paederina and Lathrobiina are observed (see Table 1). The characters unique for the subtribe Paederina are the following: long apotome (extending beyond tentorial pits); tentorial pit located at half of head length, epipharynx with incomplete anterior row of cuticular processes, tuft of cuticular processes on epipharynx, present; sternum with microtrichia. The characters unique for Lathrobiina include: presence of median tooth on nasale, presence of denticles on epipharynx, terminal segment of Lp, curved (Isaac 1934, Cerruti 1940, Gerini 1941, Paulian 1941, Kurosa 1958, Ramirez 1966, Pototskaya 1967, Kasule 1970, Topp 1978, Frania 1985, Smoleński 1997, D.S., unpublished data).

**Table 1. Comparative characters of the larvae of *Paederus*, *Tetartopeus*, and *Lathrobium*, studied herein and the previously described larvae of *Paederidus***

Character	Subtribe/genus/species			
	Paederina		Lathrobiina	
	<i>Paederidus</i> <i>Paederi. ruficollis</i> , <i>Paederi. rubrothoracicus</i>	<i>Paederus</i> <i>P. littoralis</i>	<i>Tetartopeus</i> <i>T. quadratus</i>	<i>Lathrobium</i> <i>L. lineatocolle</i>
Body length	5.17–8.47	4.95–5.11	4.51–4.89	4.12–5.17
Mss	Absent	Absent	Present	Present
Head				
Wr: head to neck	1.7	1.9	1.8	3.6
Nls+Nms: epicranial part	24+0	24+0, Fig. 4	18+30–32, Fig. 6	14+65–70, Fig. 8
Nls+Nms: ventral side	8+0	10+10, Fig. 5	10+16–19, Fig. 7	10+50–55, Fig. 9
Ves: anterior branches, development	Partial	Entire	Entire	Entire
Stm in cluster	Scattered	In two rows, Fig. 5A	Scattered, Fig. 7A	Semiscattered, Fig. 9A
Apt: length	Long	Long, Fig. 10	Short, Fig. 11	Short, Fig. 12
Tp: position on head	At half length	At half length, Fig. 5	Anterior, Fig. 7	Anterior, Fig. 9
Antenna				
Sg II: seta	Present	Present, Fig. 14	Absent, Fig. 16	Absent, Fig. 18
Lwr: Sg II, IV	2.9×, 3.3×	3.3×, 3.8×	3.1×, 2.6×	4.1×, 3.3×
Sa: shape	Erect	Erect, Fig. 13	Curved, Fig. 15	Curved, Fig. 17
Lr: Sa and Sg IV	1:2.1	1:2.9	1:1	1:1.5
Nasale				
Nt.Am	4	6, Fig. 19	7, Fig. 20	9, Fig. 21
Npgs	8	10, Fig. 19	10, Fig. 20	10, Fig. 21
Mt	Absent	Absent, Fig. 19	Present, Fig. 20	Present, Fig. 21
Epipharynx				
Row of Acp	Incomplete	Incomplete, Fig. 22	Complete, Fig. 23	Complete, Fig. 24
Tuft of Cp	Present	Present	absent	Absent
Ar: channels	Absent	Absent, Fig. 22	Absent, Fig. 23A	Present, Fig. 24A
Ephd	Absent	Absent, Fig. 22	Present, Fig. 23A	Present, Fig. 24A
Mandible				
Seta: L1	Absent	absent	?	Present
Nt	12	4, Fig. 25	20, Fig. 26	0, Fig. 27
Mtr	Present	Present	Absent	Absent
Cp	Absent	Absent, Fig. 25	Absent, Fig. 26	Present, Fig. 27
Maxilla				
Stipes: shape	Trapeziform	Trapeziform, Fig. 28	Rectangular, Fig. 29	Rectangular, Fig. 30
Maxillary palp				
Lr: mala and Sg I	1:2.2	1:2.0	1:1.6	1:1.3
Wr: mala and Sg I	1:3.2	1:3	1:1.5	1:1
Lwr: Sg I–III	1.6×, 2×, 4.1×	1.9×, 2.8×, 5.8×	4.1×, 4.2×, 8×	4.2×, 4.1×, 8.6×
Lr of Sg I–III	1.0:1.6:2.4	1.0:1.5:2.4	1.0:1.0:2.0	1.0:1.0:1.6
Sg III: Rw	Present	Present, Fig. 28B	Absent, Fig. 29	Absent, Fig. 30
Sg II: seta 2: length/location	Long/basally	Long/basally, Fig. 28	Short/at half length of Sg	Short/at half length of Sg
Sg III: Tsm	Rudimentary	Rudimentary, Fig. 28B	Elongated, Fig. 29B	Elongated, Fig. 30 B
Labium				
Lg: shape	Conical	Conical, Figs. 31 and 32	Bulbiform, Figs. 33 and 34	Bulbiform Figs. 35 and 36
Lp				
Sg II: Rw	Present	Present, Fig. 31A	Absent, Fig. 33	Absent, Fig. 35
Sg II: Tsn	Rudimentary	Rudimentary, Fig. 31A	Elongated, Fig. 33A	Elongated, Fig. 35A
Sg II: shape	Erect	Erect, Fig. 31A	curved	Curved, Fig. 36
Thorax				
Mss	Absent	Absent	Present	Present
Ns: Pronotum	46	48	48–52	78–86
Ns: Mesonotum	32	34	42	44
Ns: Stp	6	6	11	20
Presternum	Uniform	Divided, Fig. 43	Divided, Fig. 46	Divided, Fig. 49
Sternum: Mtr	Absent	Absent, Fig. 43	Present, Fig. 46A	Present, Fig. 49A
Leg				
Cx: Mss	Absent	Absent, Fig. 44	Present, Fig. 47	Present, Fig. 50A
Cx: Cp	Present	Present	Absent	Absent
Abdomen				
Mss	Absent	Absent	Present	Present
Ns: Te I	24	22	24	26
Ns: Pa II–VIII	5	4	4	4
Ns: Te II	22	22	26	26
Sg I: Ps	Present	Present	Absent	?
Ns: St II	18	18	18	22
Ns: St III	20	18	16	20
Sg VIII: Te, St	Uniform	Divided	Divided	Divided
Urogomphi				
Sg I: Nrs	10	?	14	14
Lr: I, II, Sp	2.4–3.5:1.0:1.4	?	4.9:1.0:1.7	3.9:1.0:2.5
Sg I: Lwr	7:1	?	11.8:1	8.5:1
References	Staniec et al. (2011)	Present study		

Acp, cuticular processes along anterior margin of buccal cavity; Am, anterior margin; Apt, apotome; Ar, anterior region; Cp, cuticular processes; Cx, coxa; Ephd, epipharyngeal denticles; Lg, ligula; Lr, length ratio; Lwr, length to width ratio; Mss, match-shaped setae; Mt, median tooth; Mtr, microtrichia; Nls, number of long and intermedium length setae; Nms, number of micro setae; Npgs, number of peg setae; Nt, number of teeth; Ps, parasternite; Pt, paratergite; Rw, ring of wrinkled cuticula; Sa, sensory appendage; Sg, segment; St, sternite; Stm, stemmata; Stp, sternum of prothorax; Te, tergite; Tp, tenotorial pits; Tsm, terminal sensilla; Ves, ventral ecdysial suture; Wr, width ratio;?, no data; measurements in millimeter.

The characters common to Paederina and Cryptobiina (*Ochtheophilum*), are the following: seta on antennal segment I—present; antennal sensory appendage—erect; stipes—trapeziform; ring of wrinkled cuticula on terminal segment of maxillary and Lp present; sensilla on terminal segment of maxillary and Lp rudimental; ligula conical. This morphological similarity suggests a closer phylogenetic relationship between these two subtribes in comparison to the others (Pototskaya 1967, Kasule 1970, Topp 1978, D.S., unpublished data).

Within both subtribes, Paederina and Latrobiina, larvae differ in several distinct characters at the generic level. Most of them concern morphological structures on the head, while several refer to abdominal sclerites and urogomphi. Within the subtribe Paederina, this study confirms the majority of the recently proposed morphological differences between larvae of *Paederidus* and *Paederus* (Staniec et al. 2011). In view of new data, however, the following two previously proposed characters become invalid for the genus *Paederus*: parasternites on abdominal segment I absent; (updated—in *P. littoralis* present) and simple seta on lateral tooth of nasale, absent; (updated—in *P. littoralis* present). Previous studies did not consider the substantial differences in the structure of the tergites and sternites on abdominal segment VIII. Both sclerites are uniform in *Paederidus*, while divided in *Paederus*. Further detailed analyses of the morphology of the larvae of *Paederidus* and *Paederus* may reveal other important diagnostic characters of both genera, and confirm the validity of the already proposed ones.

Within the subtribe Lathrobiina, the comparative analysis of the larval morphology at the generic level is conducted for the first time. Morphological differences between *Tetartopeus* and *Lathrobium*, discussed in detail in the previous chapter, are crucial in the context of valid systematic positions of both taxa. Previously, *Tetartopeus* was considered a subgenus of the genus *Lathrobium* by many workers (e.g., Lohse 1964), but some of them suggested it was more appropriate to recognize *Tetartopeus* as a separate genus (Watrous 1981). Clear characters seen for larvae of these taxa seem to support their genus status. Because of the lack of earlier morphological descriptions of larvae of *Tetartopeus*, the suggestions are only based on current data concerning one species, namely *T. quadratus*, so further detailed morphological studies within that genus are required.

Based on the current knowledge of larvae of *Lathrobium*, the only distinguishing character of the larva of *L. lineatocolle* described above seems to be the smooth inner margin of the mandible (other *Lathrobium* have a serrate margin). The current, very poor state of knowledge on the larvae of *Lathrobium*, however, does not permit the unequivocal determination whether the character is actually specific to the species discussed (Paulian 1941, Pototskaya 1967, Kasule 1970, Topp 1978). Similarly, differences of *Paederus* larvae cannot be currently determined at the species level due to lack of complete illustrated descriptions of larvae of other species. That requires further detailed morphological studies, both at the species and higher taxonomical level. This long-term work is currently conducted by the authors.

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