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Description of immature stages of *Laccobius kunashiricus*, with a key to genera of the Laccobiini based on larval characters (Coleoptera: Hydrophilidae)

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Abstract. Immature stages of *Laccobius* (*Laccobius*) *kunashiricus* Shatrovskiy, 1984 are described based on specimens reared from adults collected in the field. The egg-case, all larval instars and pupa are described in detail, including primary and secondary chaetotaxy of the larval head. The biology of the species was observed and is briefly discussed. We also summarize the knowledge of immature stages of *Laccobius* Erichson, 1837 and provide a key to identify larvae of the known Laccobiini genera.

Key words. Coleoptera, Hydrophilidae, Laccobiini, aquatic beetle, water scavenger beetle, egg-case, larva, pupa, morphology, behaviour, Japan, Palaearctic Region

Introduction

The aquatic hydrophilid genus *Laccobius* Erichson, 1837 of the tribe Laccobiini comprises more than 240 species worldwide. The genus represents one of the largest genera in the family Hydrophilidae (Short & Fikáček 2011). *Laccobius* species live in various aquatic habitats

such as standing and running waters as well as hygropetric habitats. In contrast to the species richness of the genus, its immature stages are poorly known. Larvae were described for 19 species only; most of the descriptions are moreover rather short and incomplete. Larval chaetotaxy was only briefly mentioned by Perkins (1972) and Fikáček et al. (2008) and has never been described in detail (Table 1).

The knowledge about the Japanese species is slightly better than in world-wide scale, but still limited. Hayashi (2008, 2009, 2011) provided photos and diagnoses of *L.* (*Microlaccobius*) *fragilis* Nakane, 1966, *L.* (*M.*) *oscillans* Sharp, 1884, and the presumable larva of *L.* (*Laccobius*) *inopinus* Gentili, 1980. Minoshima & Hayashi (2015) briefly commented on the biology of *L.* (*Laccobius*) *kunashiricus* Shatrovskiy, 1984 (Table 1).

In this study, we obtained immature stages of *L.* (*L.*) *kunashiricus* by rearing adults collected in the field. We herein describe egg-case, all larval instars, and pupa of the species, and provide also the first complete description of the larval chaetotaxy of the genus *Laccobius*.

Table 1. State of knowledge of the immature stages of *Laccobius* and source of information.

Species	Stages	References
L. (*Cyclolaccobius*) sp. (*tibialis*?)	L?	Bertrand (1936)
L. (*Dimorpholaccobius*) *atricolor* Orchymont, 1938	L?	Orchymont (1940)
L. (*D.*) *canariensis* Orchymont, 1940	L?	Valladares (1994)
L. (*D.*) *neapolitanus* Rottenberg, 1874	L3?	Pirisinu (1979)
L. (*D.*) *striatulus* (Fabricius, 1801)	L1	Fikáček (2006), Fikáček et al. (2008)
L. (*Hydroxenus*) *californicus* Orchymont, 1942	L1, L2	Perkins (1972)
L. (*H.*) *decipiens* Gentili, 1981	L3	Watts (2002)
L. (*H.*) *ellipticus* LeConte, 1855	E, L1	Cheary (1971)
	L1	Perkins (1972)
L. (*Laccobius*) *agilis* (Randall, 1838)	E, L1, L3, P	Richmond (1920)
	L?, P	Wilson (1923)
L. (*L.*) *borealis* Cheary, 1971	E, L2	Cheary (1971)
L. (*L.*) *bruesi* Cheary, 1971	L2	Cheary (1971)
L. (*L.*) *carri* Orchymont, 1942	E, L2	Cheary (1971)
	E, L1	Perkins (1972)
L. (*L.*) *inopinus* Gentili, 1980 (?)	L?	Hayashi (2009, 2011)
L. (*L.*) *kunashiricus* Shatrovskiy, 1984	E, L1, L2, L3, P	this study
L. (*L.*) *minutus* (Linnaeus, 1758)	E, L?, P	Bøving & Henriksen (1938)
L. (*L.*) *minutoides* Orchymont, 1942	E, L3, P	Archangelsky (1997)
L. (*L.*) *piceus* Fall, 1922	L1, L2	Perkins (1972)
L. (*Microlaccobius*) *fragilis* Nakane, 1966	L?, P	Hayashi (2008, 2009)
	L?	Hayashi (2011)
L. (*M.*) *oscillans* Sharp, 1884	L?	Hayashi (2008, 2009, 2011)
L. (subg?) *mineralis* Winterbourn, 1970	L?	Winterbourn (1970, 1973)
Laccobius sp.	L?	Orchymont (1913)

Material and methods

Rearing. Adults were kept in a plastic aquarium (15 cm in length, 19 cm in width, 6 cm in height) filled with 1–2 cm dechlorinated water and aquatic plants from the collecting site and commercially available (Fig. 1). Archangelsky (1997) suggested the use of fish food in flakes as a food source for adults. In line with that, we mainly used fish food, Hikari Tropical Algae Wafers (Kyorin Co., Ltd., Hyôgo, Japan), which contains plants and algae, as the food source for adults. This tablet-type fish food was preferred by adults of *Laccobius* (and also by *Enochrus* adults in other rearings). As it did not easily crumble into small pieces, the water did not become dirty soon after introducing the food. Egg cases, once found in the aquarium, were transferred on the tissue paper to small plastic cases (35 mm in diameter, 13 mm in height).

The hatched larvae were reared in the small case. *Laccobius* larvae do not require large amounts of water as other hydrophilids do; wet tissue paper was suitable for their rearing (Fig. 2B). Although they have cannibalistic behaviour, this was not a major problem as they were provided with plenty of food. Therefore, we reared them as a group. We used commercially available frozen chironomid larvae (Diptera) (Sanmi Co., Ltd., Aso Tropical Fish Co., Ltd., and Kyorin Co., Ltd., Japan) to feed them. An adequate amount of food was placed in the cases twice a day. For pupation, a small quantity of commercial soil (peat moss) was placed on the corner of the cases in which the larvae were reared (Figs 2C, D).

Morphological studies. Specimens were fixed in 80% ethanol or hot water in the laboratory. Larvae were preserved in screw-cap vials with 80% ethanol. Some larvae were mounted on HS-slides (Shirayama et al. 1993) (Kanto Rika Co., Ltd., Japan) with Euparal (Waldeck GmbH & Co. KG, Germany). The examined specimens are deposited in the authors' collections.

Our protocol generally follows that of Minoshima & Hayashi (2011) and Minoshima et al. (2012). Specimens were soaked in 10% KOH and stained with acid fuchsine when necessary. Observations were carried out using Olympus SZX12 and Leica MZ16 binocular microscopes, and Zeiss Axiophot and Olympus BX40 compound microscopes. Illustrations were prepared with the aid of a drawing tube attached to the BX40 and the MZ16. Line drawings were prepared using the software Paint Tool SAI (Systemax Inc., Japan) and Adobe Photoshop CC (Adobe Systems Inc., USA). Photographs were taken using digital cameras attached to microscopes or directly using digital cameras; the photos were subsequently adapted in Adobe Photoshop Lightroom and Photoshop CC in needed case. Composite images were created using the Image Stacking Software CombineZP (Hadley 2010).

Terminology. Morphological terminology follows Archangelsky (1997) and Minoshima et al. (2013); for the chaetotaxy of the larval head we refer to Fikáček et al. (2008) and Bytte-bier & Torres (2009). Following abbreviations are used: **AN –** antenna; **EC –** egg-case; **FR –** frontale; **gAN** – group of the apical antennal sensilla; **gAPP** – group of sensilla on inner appendage of maxilla; **gFR** – group of sensilla on frontale; **gLA** – group of the apical sensilla on labial palpus; **gMX** – group of the apical sensilla on maxilla; **L1, L2, L3** – first, second, and third instar; **L?** – larval instar uncertain; **LA** – labium; **MN** – mandible; **MX** – maxilla; **P** – pupa; **PA** – parietale; **SE** – sensorium.

Results and discussion

Genus *Laccobius* Erichson, 1837

Diagnosis of larva. Surface of head capsule smooth; frontal lines parallel, coronal line absent (Fig. 3A); nasale with median projection bearing a few teeth (Figs 4A, 9A); each epistomal lobe strongly projecting anteriorly, left lobe bearing a group of stout setae anteriorly, right lobe without setae (Figs 4A, 9A); mandibles strongly asymmetrical, apical inner tooth of left mandible with a group of ca. four to six seta-like projections (Figs 5C–D, 10C–D); submentum completely fused to head capsule (not even remnants of submental line are present); labium small, more or less reduced (Figs 5G–H, 10G–H); ligula reduced (Figs 5G–H, 10G–H); cervical sclerites present but narrow and indistinct (Fig. 7A); prosternal sclerite divided into two sclerites (Fig. 7B); mesonotum with three mesonotal sclerites on each side, posterior sclerites largest (Figs 2A, 7C); abdominal segments weakly lobate laterally (Fig. 2A); spiracular atrium developed, but small (Fig. 7D).

The larva of *Laccobius* is most similar to that of *Oocyclus* Sharp, 1882, which has similar head morphology. On the basis of the description of the first instar larva of *Oocyclus* sp. by Archangelsky (1997), they are distinguishable by the following characters: sensillum SE1 is narrow and long in *Laccobius*, whereas short and stout in *Oocyclus*; dorsal cuticular spines on mentum are absent in *Laccobius*, whereas present in *Oocyclus*; frontal lines are parallel in *Laccobius*, whereas lyriform in *Oocyclus*; MX8 and MX9 slender setae in *Laccobius*, whereas stout setae bearing subapical tooth in *Oocyclus*; and mesonotal sclerites of *Laccobius* proportionally smaller than those of *Oocyclus*.

Laccobius (*Laccobius*) *kunashiricus* Shatrovskiy, 1984

(Figs 1–12)

Material examined. 4 EC, 13 L1, 5 L2, 4 L3, 3 P, **JAPAN: Niigata Pref.:** Jôganji, Nagaoka-shi, 27.v.2012 (adults collected in the field), Y. Iwata leg., Y. Minoshima rearing: R21.

Description of egg-case. Egg-case white in colour, constructed on substrate in water or at water's surface; spherical with narrow, long filiform mast of variable length, often extremely long (Fig. 1).

Description of larva. ***General morphology. Third instar.*** *Body* (Fig. 2A) rather thick with weak lateral projections, widest between abdominal segments 2–4. *Colour* pale brownish white with sclerotised areas darker, tubercles on abdomen dark brown.

Head. Head capsule (Figs 7A, 8–9) subquadrate; cervical sclerites small. Frontal line almost straight, parallel, almost invisible in third instar; coronal line absent; gular sulcus visible in basal part only. Surface of head capsule smooth. Six stemmata on each anterolateral corner of head capsule. Clypeolabrum (Fig. 9A) asymmetrical. Nasale with median projection bearing three teeth. Lateral lobes of epistome present; left lobe very strongly projecting anteriorly; right lobe strongly projecting anteriorly with membranous area laterally; both lobes projecting further than nasale, left lobe projecting further than right lobe. Left epistomal lobe bearing a group of stout, strongly bent ventrally, seta-like cuticular projections consisting of two rows (dorsal and ventral row) on inner margin, mesally to setae of gFR1. Ventral anterior margin

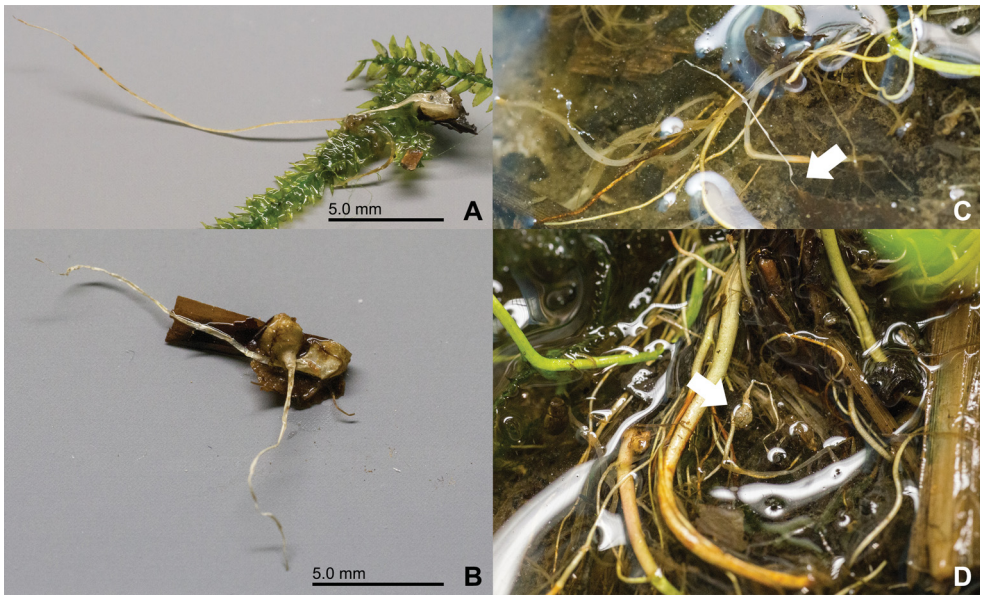

Fig. 1. Egg-case of *Laccobius kunashiricus* Shatrovskiy, 1984. Arrow indicates egg-case.

of head capsule slightly asymmetrical. Dorsal and ventral mandibular articulation of left side projecting anteriorly further than right one (Fig. 9).

Antenna (Figs 10A–B) 3-segmented, short, rather slender. Antennomere 1 straight, shorter than antennomere 2; antennomere 2 longest and slightly narrower than antennomere 1; antennomere 3 shortest and narrowest. *Mandibles* (Figs 10C–D) strongly asymmetrical; left mandible shorter than right one. Right mandible with two inner teeth closely aggregated on median part. Left mandible with one inner tooth; inner tooth bearing a small subbasal tooth anteriorly and a comb composed by five to six spine-like projections posteriorly. Subbasal part of inner face of mandible with several short cuticular spines and minute cuticular teeth. Longitudinal mandibular groove present dorsally on midline of left mandibular base to incisor area. *Maxilla* (Figs 10E–F) 6-segmented, longer than antenna. Cardo moderate in size, subtriangular. Stipes the longest and widest segment, longer than palpomeres 1–4 combined; inner face with cuticular spines dorsally along inner face. Maxillary palpus 4-segmented; palpomere 1 widest, longer than palpomere 2 and shorter than palpomeres 3 and 4, bearing about two minute cuticular spines on dorsal surface of intersegmental membrane between palpomeres 1 and 2; palpomere 2 the shortest, wider than palpomere 3; palpomere 3 about as long as and wider than palpomere 4; palpomere 4 narrowest; dorsal surface of palpomere 1 incompletely sclerotised; inner process sclerotised. *Labium* (Figs 10G–H) developed, but small. Submentum fused to head capsule, large, subpentagonal, wider than mentum; submental sulcus hardly visible. Mentum transverse, narrowly cylindrically sclerotised, slightly wider than prementum; dorsal surface bare. Prementum subquadrate, slightly transverse; anterior membranous area with a few short cuticular spines dorsally on lateral face. Ligula reduced

Fig. 2. *Laccobius kunashiricus* Shatrovskiy, 1984. A – third instar larva; B – feeding behaviour of larva; C–D – pupa in pupal chamber.

as small protuberance. Labial palpus long; palpomere 1 slightly wider than palpomere 2 and distinctly shorter than palpomere 2; intersegmental membrane between palpomeres 1 and 2 with a few short cuticular spines dorsally on median to inner part; palpomere 2 almost straight or slightly curved inwards in apical half.

Thorax. Thoracic membrane covered with fine cuticular pubescence. Prothorax wider than head capsule. Proscutum formed by one large plate subdivided by fine sagittal line, anterior part rather weakly sclerotised; whole sclerite bearing fine cuticular pubescence. Prosternal sclerite (Fig. 7B) divided into two closely aggregated plates thus can also be considered a subdivided single plate, bearing setae along anterior margin. Mesonotum with three sclerites on each side (Figs 2A, 7C); anterior two small, inner one larger than lateral one; posterior one large, subtriangular, bearing fine cuticular spines on lateral to posterior margin and setae of variable length. Two small tubercles present dorsally on each side; mesal one sclerotised, behind each posterior mesonotal sclerite; lateral one membranous, on laterodorsal surface,

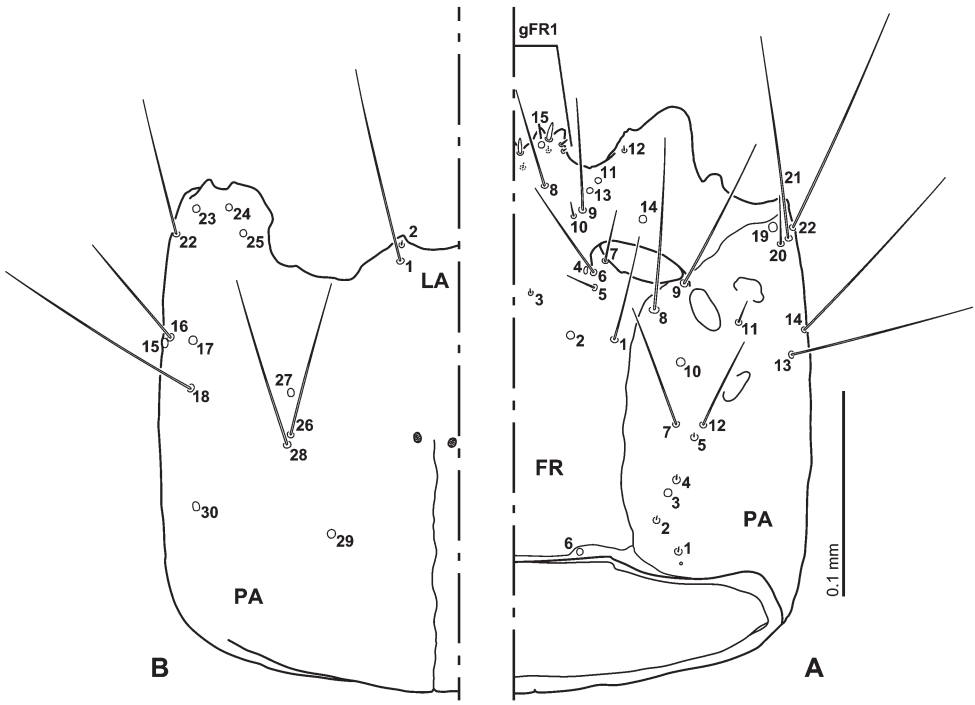

Fig. 3. First instar larva of *Laccobius kunashiricus* Shatrovskiy, 1984, head capsule, dorsal (A) and ventral (B) view.

behind mesonotal spiracle. Metanotum with one pair of subtriangular to oval metanotal sclerites. Three tubercles on each side; mesal one sclerotised, situated behind each sclerite; remaining two membranous, one posterolaterally to sclerite, one on laterodorsal face. Legs (Fig. 11B) moderate in length, slightly visible in dorsal view, 5-segmented; all three pairs similar in shape.

Abdomen (Fig. 2A) 10-segmented, tapering posteriad, covered with fine cuticular pubescence; segments 1 to 7 similar in shape and size. Segment 1 with one pair of small dorsal sclerites bearing one short seta, medially on anterior part; four partially sclerotised tubercles behind dorsal sclerites; two membranous tubercles situated on each lateral face, one laterally to sclerotised tubercles, one on posterior part. Segments 2 to 7 similar to segment 1, dorsal sclerites on segment 2–7 similar or slightly smaller than those on first segment. Spiracular atrium (Fig. 7D) small. Segment 8 with large oval dorsal plate covered with fine cuticular projections and setae of variable length; dorsal surface of posterior edge of segment 8 densely covered with fine pubescence; procercus incompletely sclerotised, with one long and two short setae. Segment 9 trilobed, partially sclerotised; each lateral lobe without distinct acrocercus; urogomphi short, one-segmented; prostyli absent.

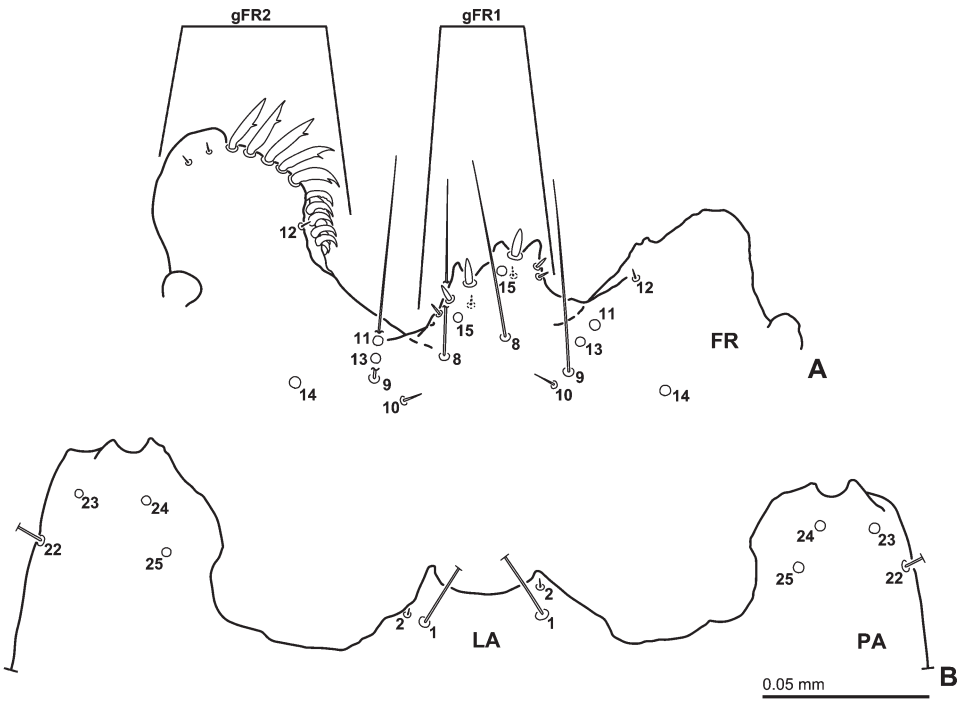

Fig. 4. First instar larva of *Laccobius kunashiricus* Shatrovskiy, 1984, anterior margin of head capsule, dorsal (A) and ventral (B) view (both views drawn from a slide with the head capsule mounted with dorsal side up).

***Second instar*.** Closely similar to third instar larva; sclerites on meso- and metathorax and abdominal segments more weakly sclerotised than in third instar.

Head. Frontal lines clearly visible; frontal line nearly straight, connecting lateral margin of antennal socket and posterior margin of head capsule; posterior end of frontal line unclear, possibly, frontal lines curved mesally at the base of head capsule.

Antenna and maxilla (Fig. 6) proportionally stouter than in third instar. *Thorax and abdomen*. Arrangements of cuticular projections and pubescence on thorax and abdomen similar to third instar but projections and pubescence finer than in third instar.

***First instar*.** Similar to second instar larva; sclerites on meso- and metathorax and abdominal segments more weakly sclerotised than in second instar.

Head. *Antenna* (Figs 5A–B) proportionally stouter than that of second and third instar larvae. *Mandible* (Figs 5C–D). Distal inner tooth of left mandible with four to five seta-like projections basally on posterior margin. *Maxilla* (Figs 5E–F). Intersegmental membrane between palpomeres 2 and 3 bearing a few small cuticular spines dorsally. *Labium* (Figs 5G–H) without small cuticular spines on anterior membranous area of prementum and intersegmental membrane between palpomeres 1 and 2.

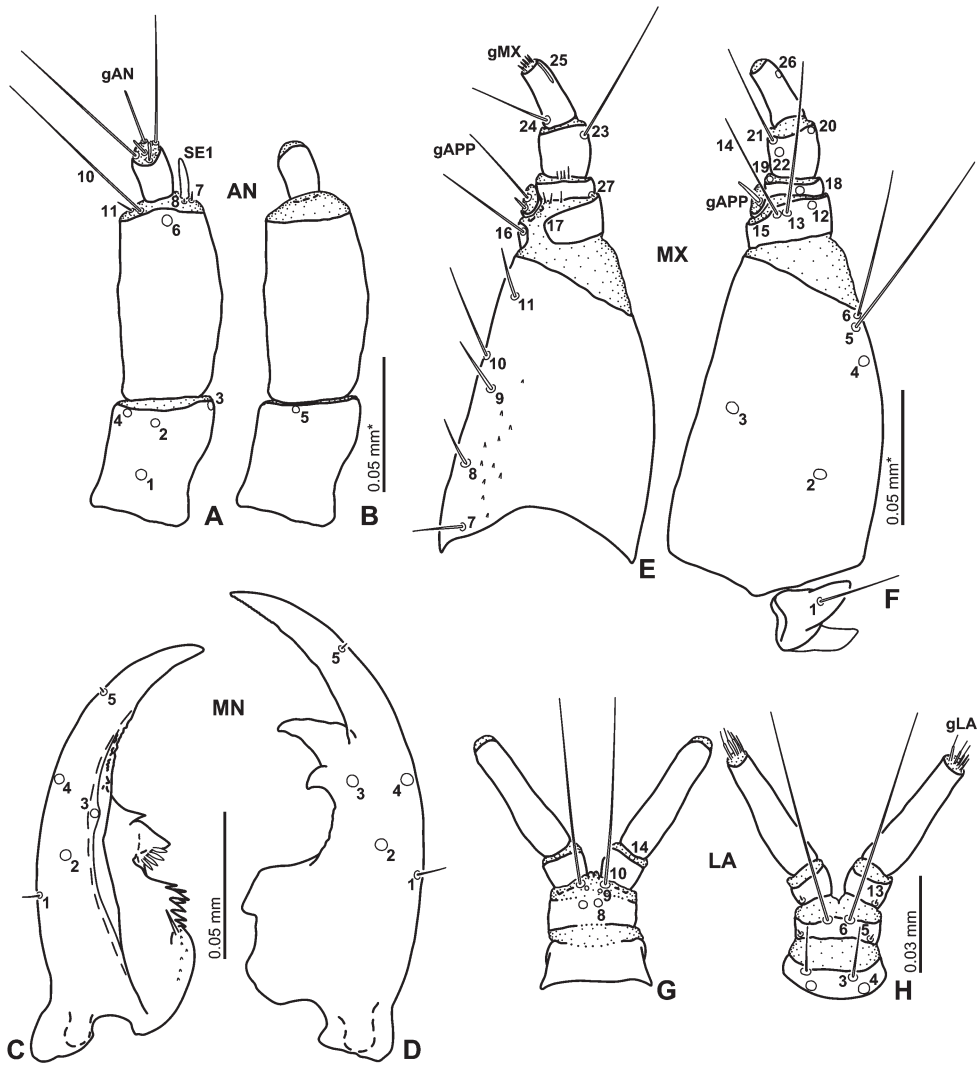

Fig. 5. First instar larva of *Laccobius kunashiricus* Shatrovskiy, 1984, head appendages. A–B – antenna, dorsal (A) and ventral (B) view; C–D – mandible, dorsal view; E–F – maxilla, dorsal (E) and ventral (F) view; G–H – labium, dorsal (G) and ventral (H) view. Asterisk (*) in the scale bar means same scale.

Thorax and abdomen. Arrangements of cuticular projections and pubescence on thorax and abdomen similar to third instar but projections and pubescence finer than in second instar.

Chaetotaxy of head. Primary chaetotaxy. *Frontale* (Figs 3A, 4A). Median part with three pairs of sensilla (FR1–3); long seta FR1 situated close to frontal line, minute seta FR3 on mesal part, pore-like sensillum FR2 between FR1 and FR3, posteriorly to line connecting FR1 and FR3. Three setae FR5–7 and pore-like sensillum FR4 situated behind antennal socket, close to each other; FR5 and FR7 rather short, FR6 long; FR7 on inner margin of antennal socket; FR4 and FR6 very close to each other, slightly posteromesally to FR7; FR4 mesally to FR6; FR5 situated posteriorly to FR6. Long seta FR8 situated on mesal part of clypeolabrum, posteriorly to nasale; pore-like sensillum FR15 on median part of nasale; pore-like sensillum FR14 anteriorly to antennal socket. Three setae (FR9–10 and FR12) and two pore-like sensilla (FR11 and FR13) situated mesally on epistome; FR9 long, FR10 short, FR12 very short. FR9–FR11 and FR13 forming a slightly irregular oblique row, FR10 situated posteriorly, FR11 anteriorly, FR9 and FR13 between FR10 and FR11, FR9 posteriorly to FR13; FR12 on inner margin of epistomal lobe, distance between FR12 and FR11 on left side longer than on right. Nasale with group of six short setae, and with (at least) two short ventral setae (gFR1); left one and right two narrow, remaining ones stout. Left epistomal lobe with group of setae (gFR2); lateral two short, remaining ones stout, with small apical tooth; within stout setae, lateral five are true setae but remaining ones could possibly not be true setae (i.e., seta-like cuticular spines); therefore left epistomal lobe may bear two short setae and five stout setae; gFR2 on right lobe absent.

Parietale (Figs 3, 4B). Dorsal surface with a group of five sensilla (PA1–5) forming an irregularly longitudinal row close to frontal line in posterior part of parietale; PA1–2 and 4–5 short setae, PA3 pore-like; a very small pore-like and sensilla-like structure situated posteriorly to PA1. PA6 pore-like, situated behind frontale, on posteromesal margin of head capsule. Long setae PA7 and PA12 situated laterally and close to midlength of frontal line, anteriorly and close to PA5; PA12 laterally to PA7. Very long setae PA8–9 situated behind antennal socket, PA9 on outer margin of antennal socket, PA8 posteromesally to PA9 and close to frontal line. Pore-like sensillum PA10 situated at midlength of line connecting PA8 and PA12. Four setae (PA13–14, PA16 and PA18) and two pore-like sensilla (PA15 and PA17) situated on about anterior third of lateral surface of parietale; PA13–14 and PA18 very long, PA16 long. PA13–17 forming irregular transverse row; PA13 dorsally to remaining ones, posteromesally to PA14; PA14–16 closely aggregated, PA14 dorsally to PA15–16, PA16 ventrally to PA14–15, PA15 between PA14 and PA16; PA 17–18 situated ventrally to PA13–16, PA17 mesally to PA16, and PA18 posteriorly to PA17. Short seta PA11 situated between PA9 and PA13. PA19–22 closely aggregated on anterior corner of head capsule, PA19 pore-like, PA20 rather short seta, PA21–22 very long setae; PA19–20 situated dorsally to PA21–22, PA19 anteriorly to PA20, and PA22 anteroventrally to PA22. Pore-like sensilla PA23–25 situated close to ventral mandibular articulation; PA23 laterally to PA24–25; PA25 posteromesally to PA25. Two very long setae (PA26 and PA28) and pore-like sensillum PA27 situated ventrally on median part of parietale; PA27 situated anteriorly to PA26 and PA28, PA26 between PA27 and PA28, very close to PA28. Two pore-like sensilla (PA29–30) on posterior third of ventral parietale; PA29 mesally to PA30, posteromesally to PA26–28; PA30 on lateral part.

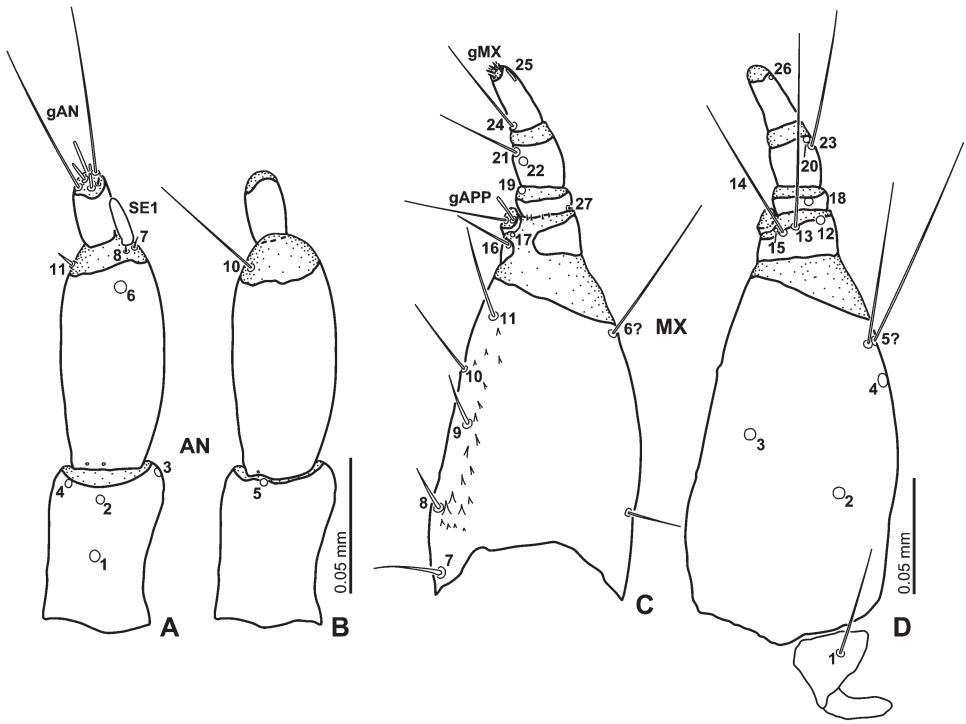

Fig. 6. Second instar larva of *Laccobius kunashiricus* Shatrovskiy, 1984, head appendages. A–B – antenna, dorsal (A) and ventral (B) view; C–D – maxilla, dorsal (C) and ventral (D) view.

Antenna (Figs 5A–B). Antennomere 1 with five pore-like sensilla (AN1–5); AN1 situated dorsally on about posterior third; AN2–5 on anterior margin of sclerite, AN2 dorsally on median part, AN3 on outer face, AN4 inner face, AN5 ventrally on median portion. Antennomere 2 with one pore-like sensillum (AN6) situated dorsally on apical portion of sclerite; minute setae AN7–8 and sensorium SE1 closely aggregated on outer face of intersegmental membrane between antennomeres 2 and 3, AN9 absent; SE1 slender, about as long as to slightly shorter than antennomere 3; setae AN10–11 situated on inner face of intersegmental membrane between antennomeres 2 and 3, AN10 very long, AN11 short, both setae close to each other. Antennomere 3 with apical sensilla (gAN) in apical membranous area; gAN with two rather long setae and a few short setae of variable shape.

Mandibles (Figs 5C–D). Mandible with two setae (MN1 and MN5) and three pore-like sensilla (MN2–4); MN1 short, MN5 minute. Pore-like sensillum MX6 undetectable. MN1 situated on posterior third of lateral face of mandible. MN2–4 situated on median part of mandible; MN3 situated mesally to MN1–4, MN2 between MN1 and MN3; MN4 and MN5 situated on lateral face anteriorly to MN1; MN5 subapically, MN4 at midlength between MN1 and MN5 on left mandible, closer to MN1 on right.

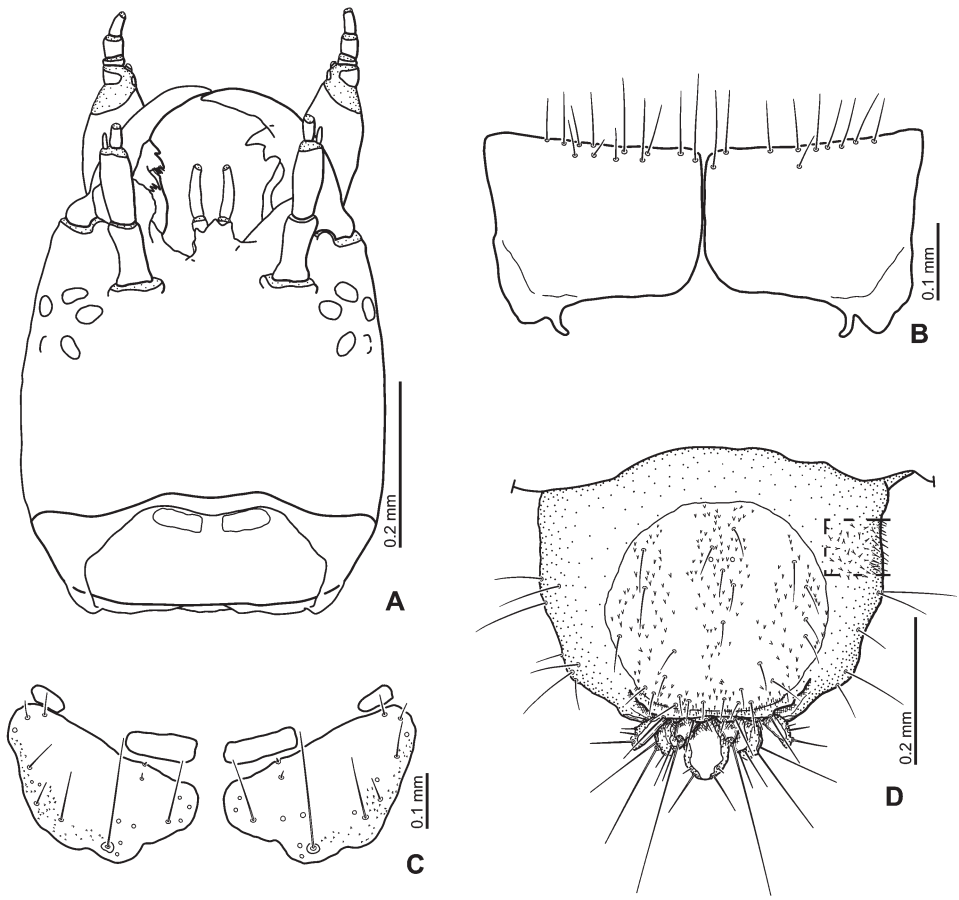

Fig. 7. Third instar larva of *Laccobius kunashiricus* Shatrovskiy, 1984. A – head, dorsal view; B – prosternal sclerite, ventral view; C – mesonotal sclerites, dorsal view; D – spiracular atrium, dorsal view.

Maxilla (Figs 5E–F). Cardo with one rather long ventral seta (MX1). Stipes with a slightly irregular row of five setae (MX7–11) situated dorsally along inner face; MX7–9 and MX11 somewhat stout, rather long, MX10 trichoid, long; MX7–9 and MX11 almost equidistant from each other; MX10 located between MX9 and MX11, close to MX9. Two very long setae (MX5–6) present apically on outer face of sclerite; MX5 longer than MX6; MX5 situated posteriorly and very close to MX6; pore-like sensillum MX4 posteriorly to MX5. Pore-like sensilla MX2–3 situated ventrally on median part of sclerite; MX2 on outer part, posterolaterally to MX3, MX3 on inner part. Dorsal surface of palpomere 1 with one long trichoid seta (MX16) situated on inner face. Ventral surface of sclerite with three sensilla (MX12–14) along distal margin of sclerite; MX12 pore-like on lateral part, MX13 very long seta between MX12 and MX14, MX14 long seta, very close to MX13. Pore-like sensilla

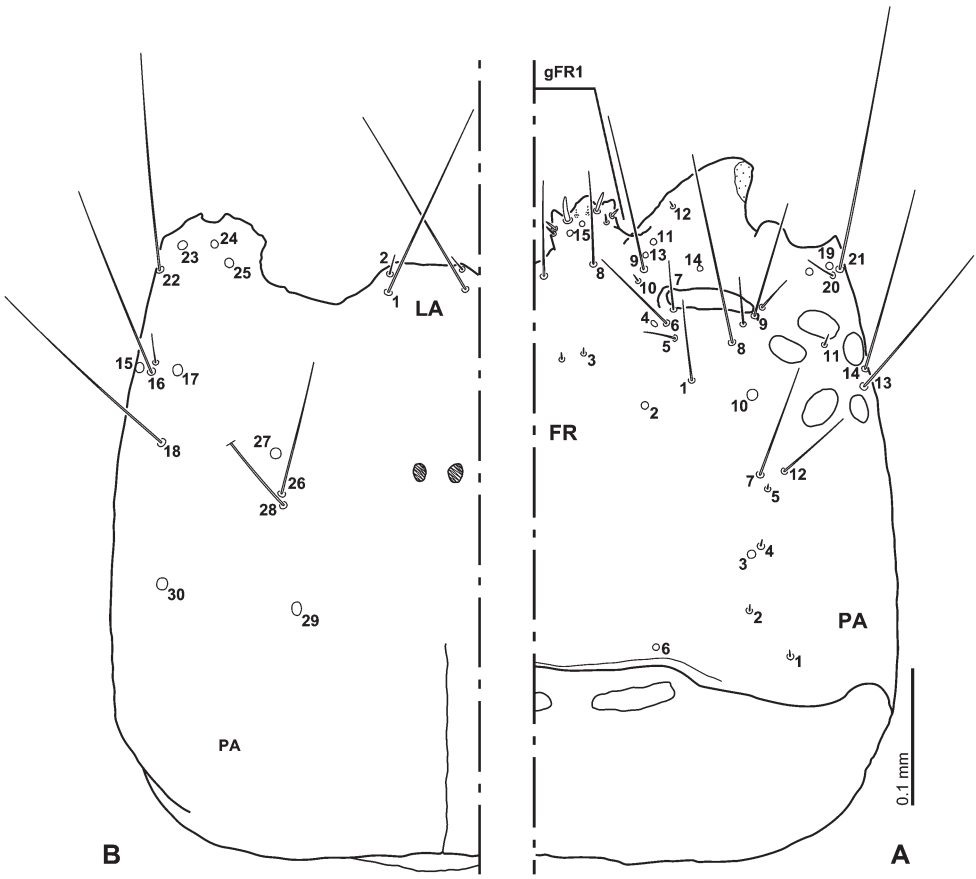

Fig. 8. Third instar larva of *Laccobius kunashiricus* Shatrovskiy, 1984, head capsule, dorsal (A) and ventral (B) view.

(MX15 and MX17) situated on membrane behind inner appendage; MX17 dorsally, MX15 ventrally. Inner appendage with one long seta and a few short setae (gAPP). Palpomere 2 with two pore-like sensilla (MX18 and MX19) and one minute seta (MX27); MX18 situated ventrally on median to lateral portion of sclerite; MX19 on inner face of intersegmental membrane between palpomeres 2 and 3; MX27 basal on outer face of sclerite. Palpomere 3 with two setae (MX21 and MX23) and two pore-like sensilla (MX20 and MX22); MX21 long, MX23 very long; MX20 situated on distal margin of outer surface of sclerite; MX23 posterodorsal and close to MX20; MX21–22 on inner face of sclerite, MX21 on distal margin, MX22 posteroventrally to MX21. Palpomere 4 with one long seta (MX24) situated basally on inner face, and with digitiform sensillum (MX25) and pore-like sensillum (MX26) apically on outer face of sclerite; MX25 dorsally, MX26 ventrally. Apical membranous area of palpomere 4 with several minute setae (gMX).

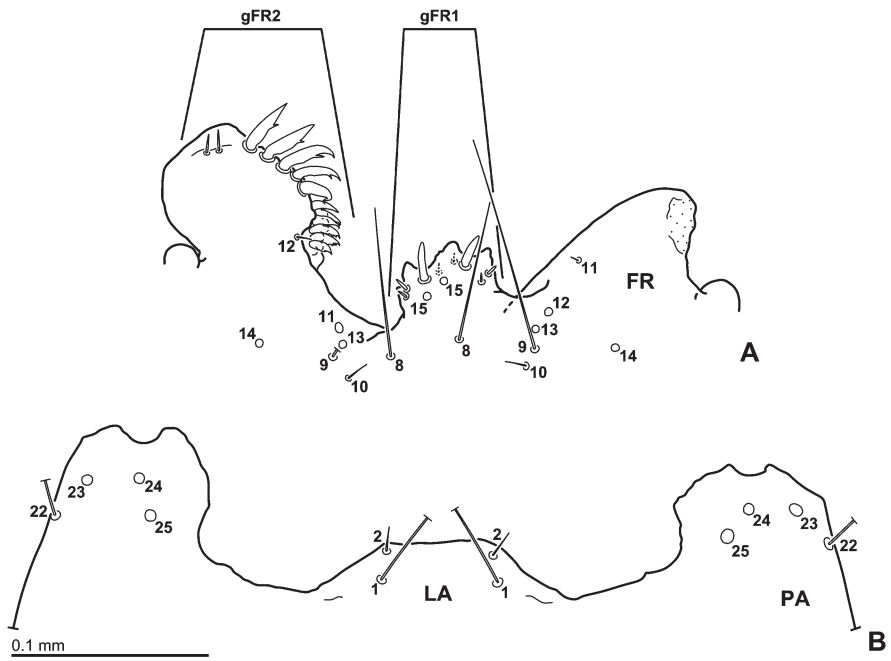

Fig. 9. Third instar larva of *Laccobius kunashiricus* Shatrovskiy, 1984, anterior margin of head capsule, dorsal (A) and ventral (B) (both drawn from dorsal).

Labium (Figs 4B, 5G–H). Submentum with two pairs of setae (LA1–2); LA1 very long, LA2 very short, both situated on anterolateral portion; LA1 very close and posteriorly to LA2. Ventral surface of mentum with one pair of rather long setae (LA3) and pore-like sensilla (LA4); LA4 situated behind LA3, LA3 close to distal margin, LA4 close to proximal margin. Prementum with three pairs of sensilla (LA8–9 and LA10) on dorsal surface and with two pairs of sensilla (LA5–6) on ventral surface. Pore-like sensillum LA8 situated medially, very long seta LA10 on anterior membranous area, anteriorly to LA8; LA9 close to LA8; LA11–12 absent. Minute seta LA5 situated ventrally at base of outer face; very long seta LA6 on median part, on borderline between sclerite and membrane of prementum. One minute seta (LA13) situated lateroventrally on basal margin of palpomere 1; pore-like sensillum LA14 on dorsal surface of intersegmental membrane between palpomeres 1 and 2. LA15 absent. Apical membranous area of palpomere 2 with several setae of variable length and shape (gLA).

Second instar. Primary sensilla on second instar similar to those of first instar, and secondary chaetotaxy on second instar similar to that of third instar. *Frontale* (e.g., Figs 8A, 9A). Median two setae of gFR1 proportionally longer and stouter than in first instar, rounded apically. Parietale with three secondary setae and one pore-like secondary sensillum (e.g., Fig. 8); two short setae close to lateral edge of antennal socket and PA9, one situate between PA8 and PA9, one on anterolaterally to PA9; one pore-like sensillum very close to PA20–21; one short seta close to PA16.

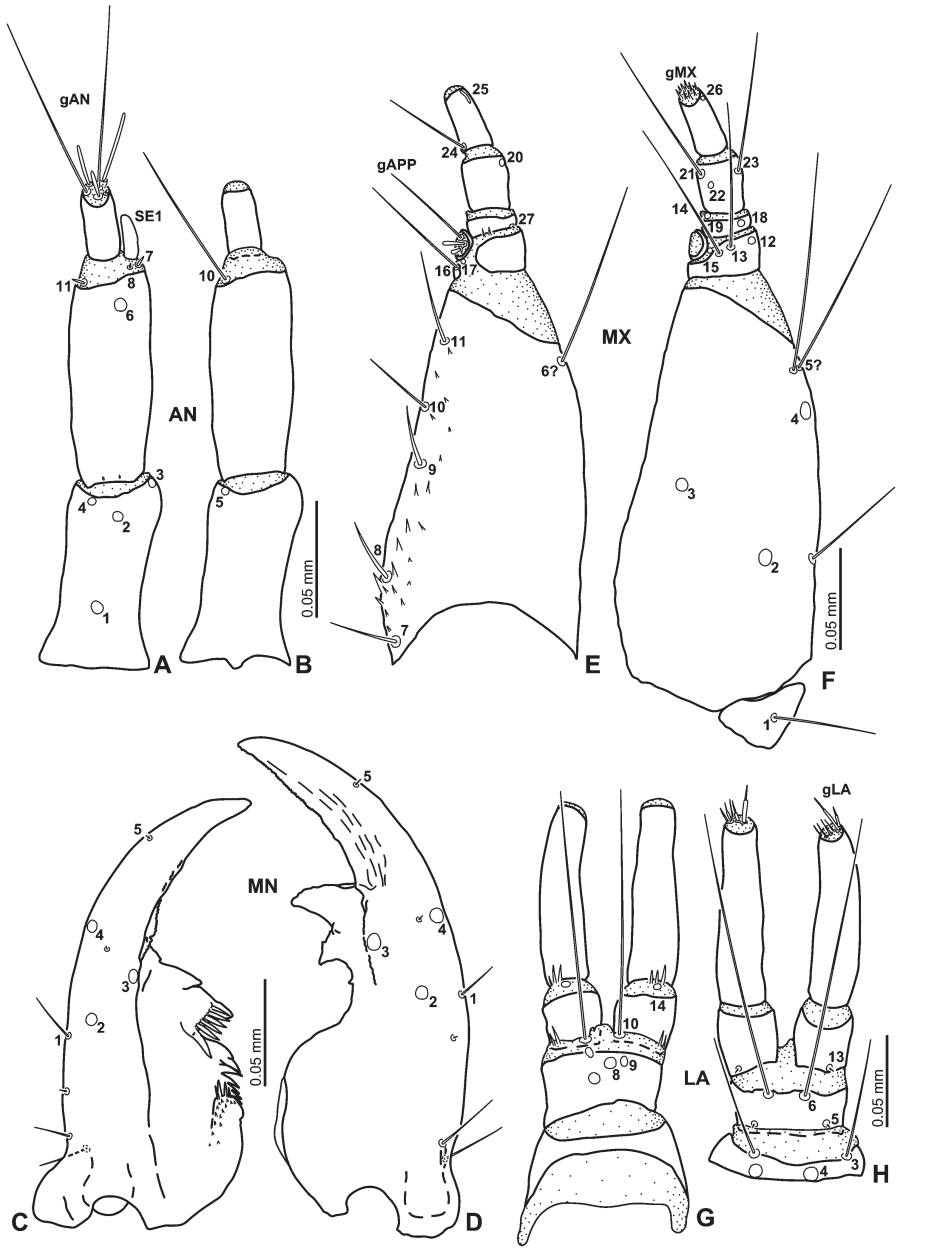

Fig. 10. Third instar larva of *Laccobius kunashiricus* Shatrovskiy, 1984, head appendages. A–B – antenna, dorsal (A) and ventral (B) view; C–D – mandible, dorsal view; E–F – maxilla, dorsal (E) and ventral (F) view; G–H – labium, dorsal (G) and ventral (H) view.

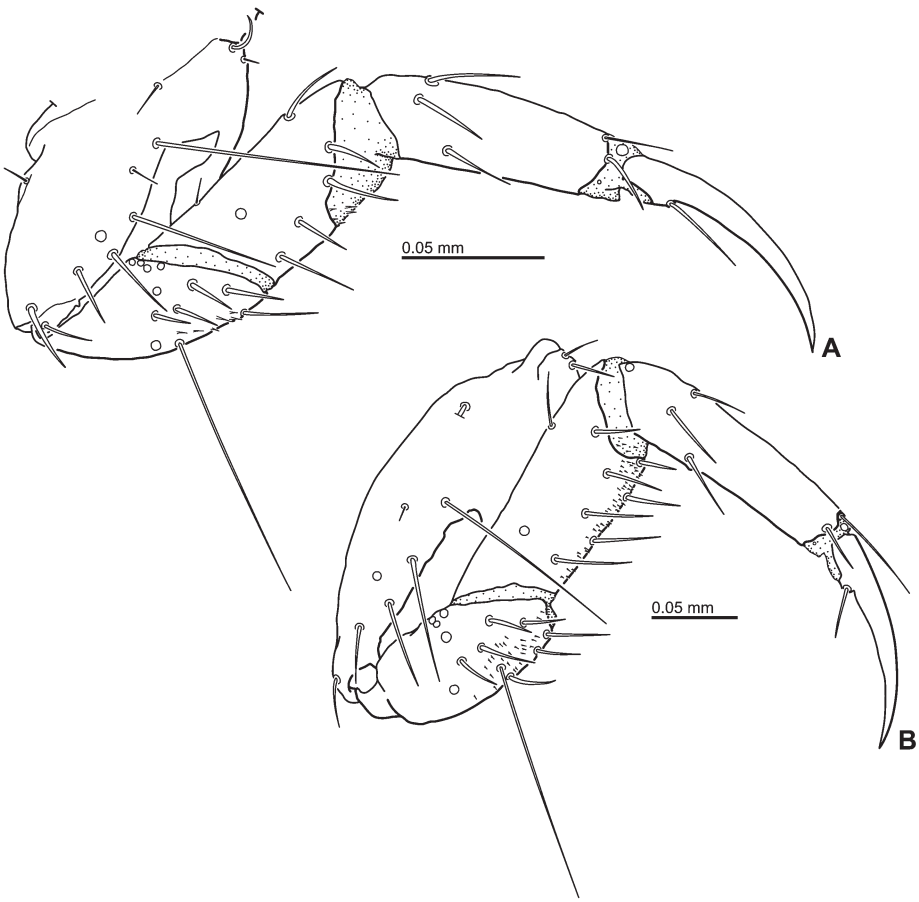

Fig. 11. Mesothoracic leg of *Laccobius kunashiricus* Shatrovskiy, 1984. First (A) and third (B) instar larva, anterior view.

Antenna (Figs 6A–B). Three minute sensilla-like structures present at base of antennomere 2, two dorsal and one ventral; the presence or absence of these is variable. SE1 stout, slightly shorter than antennomere 3. *Mandible* (e.g., Figs 10C–D) with four secondary sensilla on each mandible; one minute sensillum situated dorsally on lateral part, close to MN4; one minute to short seta posteriorly to MN1; two rather short setae on lateral face of mandibular base. *Maxilla* (Figs 6C–D). Stipes with two secondary setae; one rather short seta situated on about posterior third of outer face of sclerite, one long seta close to MX5–6.

***Third instar*.** Similar to second instar. Antennal sensorium SE1 stout, about two-third as long as antennomere 3 (Figs 10A–B).

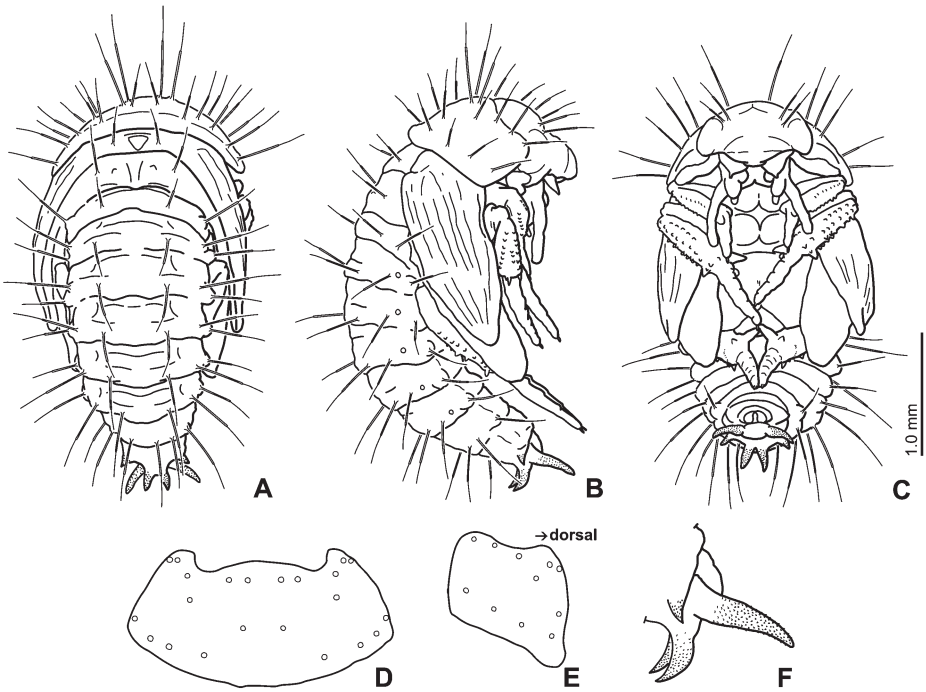

Fig. 12. Pupa of *Laccobius kunashiricus* Shatrovskiy, 1984. A–C – whole pupa, dorsal (A), lateral (B), and ventral (C) view; D–E – detail of position of styli on pronotum (styli removed), dorsal (D) and lateral (E) view; F – detail of abdominal apex, lateral view.

Description of pupa. *Body* (Figs 2C–D, 12) moderately broad. Head, thorax and abdomen with styli. *Colour*. Whitish when alive (Figs 2C–D); eyes yellowish white to reddish brown.

Head. Deflexed ventrally, covered by pronotum in dorsal view. Frontoclypeal sulcus partly visible. Antennae completely covered by head and pronotum in dorsal view; mouthparts visible in ventral view; maxillary palpi long. Styli on head: Two pairs of rather short supraorbital styli close to inner margin of each eye.

Thorax. Pro-, meso- and metathoracic legs visible in ventral view; metathoracic legs partially covered by wingpads, only tibiae to tarsi visible; meso- and metathoracic legs strongly bent ventrally. Apex of tarsi ending with one minute projection. One pair of small projections mesal to metanotal styli. Styli on thorax: Pronotum with 11 pairs of rather short styli (Figs 12D, E). Five pairs of styli on anterior margin of pronotum, three pairs situated laterally, two pairs mesally; mesal two pairs slightly longer than others. Two pairs of styli on median part, one posterior to anterior three pairs, one on mesal part. Four pairs of styli on posterior margin. Meso- and metanotum with one pair of styli on median part.

Abdomen. Abdomen with nine segments, attenuate towards apex. Posterior corner of segment 8 with triangular projection (Figs 12B, F). Segment 9 with well-developed,

non-articulated urogomphi; surface of urogomphi finely denticulated (Fig. 12F). Styli on abdomen: Abdominal styli rather short, almost equal in size and shape excluding segment 8. Abdominal segment 1 with two pairs of rather short styli, one on median part, one lateral. Segments 2 to 7 with a transverse row of three pairs of styli; one mesal, two on lateral face close to spiracle. Segment 8 with one pair of styli without apical hair on posterior margin, hook-shaped, finely denticulate (Fig. 12F).

Biology. Both adults and larvae of *L. kunashiricus* live in standing water. Two larvae likely belonging to this species were found at the edge of a pond in Hokkaido Prefecture (Y. N. Minoshima, personal observation). Larvae are sluggish, and do not swallow atmospheric air into the alimentary canal (see Minoshima and Hayashi (2015) for a more general discussion about this behaviour). We placed a living larva into water and confirmed that it sank in the water as it was not buoyed by air bubbles in the alimentary canal. Wilson (1923) mentioned that the larva of *L.* (*Laccobius*) *agilis* (Randall, 1838) sometimes hangs from the water surface supported by its spiracular atrium.

Key to the known genera of the tribe Laccobiini

The tribe Laccobiini contains 11 genera (Short & Fikáček 2013), of which the larval morphology has been described in detail and based on reliably identified specimens for five genera (*Laccobius*, *Oocyclus*, *Paracymus* Thomson, 1867, *Tormus* Sharp, 1884, and *Tritonus* Mulsant, 1844) (e.g., Bøving & Henriksen 1938; Archangelsky 1997; Archangelsky & Fikáček 2004; Fikáček et al. 2013, 2017). The larva of *Pelthydrus* Orchymont, 1919 was mentioned by Bertrand (1936, 1974): it was first described as 'Hydrophilidae genus 1' and only later assigned to *Pelthydrus*. Since the description of the larva is very incomplete and the identification seems doubtful (Minoshima & Hayashi 2011), we are not including this larva into the key below. Larvae are not known for *Afrotormus* Hansen, 1999, *Arabhydrus* Hebauer, 1997, *Hydrophilomima* Hansen & Schödl, 1997, *Ophthalmocyclus* Komarek, 2003 and *Scoliopsis* Orchymont, 1919. Based on the phylogenetic position of these genera (Short & Fikáček 2013, Toussaint et al. 2016), we suppose that the larva of *Ophthalmocyclus* may be similar to that of *Oocyclus*, and the larva of *Scoliopsis* to that of *Tritonus*. Genera *Pelthydrus*, *Arabhydrus* and *Hydrophilomima* form a large separate clade within the Laccobiini whose larval morphology remains totally unknown. The larvae of Oriental species of *Oocyclus* are unknown and may not necessarily correspond with larvae of Neotropical *Oocyclus*, since Oriental *Oocyclus* seem phylogenetically closer to *Pelthydrus* + *Arabhydrus* + *Hydrophilomima*.

1 Both mandibles similar in shape and with same number of inner teeth (e.g., Figs 11C, D in Fikáček et al. 2013). 2
– Mandibles distinctly asymmetrical, with different number of inner teeth on each mandible; left mandible with fine combs on the base of the basal inner tooth (Figs 5C, D, 10C, D). 4

2 Frontal lines V-shaped, convergent posteriorly (Fig. 3A in Fikáček et al. 2017); coronal line present; sensorium SE1 small (Figs 5B, 6A in Fikáček et al. 2017); endemic to Madagascar and Seychelles. ..... ***Tritonus*** Mulsant, 1844
– Frontal lines parallel or oblique, not convergent posteriorly (Fig. 2 in Archangelsky 1999, Fig. 14A in Fikáček et al. 2013); coronal line absent; sensorium SE1 long, as long as antennomere 3 (e.g., Fig. 5 in Archangelsky 1999 and Figs 11A, 13A, 15A in Fikáček et al. 2013). 3
3 Frontal lines lyriform, almost parallel (Fig 34C in Archangelsky 1997, Fig. 2 in Archangelsky 1999); maxilla and mentum bearing sparsely arranged short cuticular spines (Figs 35D, E in Archangelsky 1997, Figs 6, 8 in Archangelsky 1999); labium not bearing

Table 2. Morphological characters of the larvae of Laccobiini.

	Laccobius	***Oocyclus***	***Paracymus***	***Tormus***	***Tritonus***
Nasale	3 weakly developed teeth	3 weakly developed teeth	3–4 teeth	3 teeth (left one more separated)	4 teeth (left one more separated)
Epistomal lobes	asymmetrical, prominent	asymmetrical, prominent	symmetrical	symmetrical	symmetrical
Setae on epistomal lobes	left one with series of setae, right one bare	left one with series of setae, right one bare	1–2 setae each	with 4 setae each	with 6 sensilla (4–5 setae) each
Frontal lines	straight	lyriform (slightly "constricted" at midlength)	straight, slightly lyriform	straight, converging posteriad	straight, converging posteriad
Coronal line	absent	absent	absent	absent	present
Submental sulcus	absent	weakly marked	present	present	present
PA27–29	setae next to each other	setae next to each other	pore between setae	pore between setae	pore between setae
Antennal sensorium (SE1)	long and thin	short and stout	long and thin	long and thin	minute
Mandibles	asymmetrical	asymmetrical	symmetrical	symmetrical	symmetrical
Retinacular teeth of mandibles	left with comb-like structures, right one with 2 teeth	left with comb-like structures, right one with 2 teeth	2 teeth	3 teeth	3 teeth
Dorsal surface of mentum	without cuticular teeth (whole mentum reduced)	with cuticular teeth	with cuticular teeth	with cuticular teeth	with cuticular teeth, bare centrally
Prementum	bare	bare	with short cuticular projections or bare	with long pubescence	with short cuticular projections
Ligula	absent	absent	present	absent	present
Mesonotal sclerites	large, widely separated mesally	large, contiguous mesally	large, contiguous mesally	narrow, contiguous mesally	large, contiguous mesally

densely arranged long hair-like projections (Fig. 35D in Archangelsky 1997, Fig. 8 in Archangelsky 1999); ligula present (Fig. 35D in Archangelsky 1997, Fig. 8 in Archangelsky 1999). ..... ***Paracymus*** Thomson, 1867

– Frontal lines almost straight, oblique (Figs 10A, 14A in Fikáček et al. 2013); maxilla and labium bearing densely arranged hair-like cuticular projections (e.g., Figs 11E, G, 15E, G in Fikáček et al. 2013); labiumligula absent (Figs 11G, 13G, 15G in Fikáček et al. 2013); endemic to New Zealand. ..... ***Tormus*** Sharp, 1884

4 Frontal lines parallel, almost straight (Fig. 3A); larger mesonotal sclerites rather small, separate medially (Figs 2, 7C). ..... ***Laccobius*** Erichson, 1837

– Frontal lines lyriform (Fig. 47B in Archangelsky 1997); larger mesonotal sclerites large, attached medially, finely divided by sagittal line. ..... ***Oocyclus*** Sharp, 1882

Discussion

Outside Laccobiini, the larval head of *Laccobius* and *Oocyclus* resembles that of *Berosus* Leach, 1817 and *Hemiosus* Sharp, 1882 (Berosini) in the shape and chaetotaxy of the nasale and left epistomal lobe, shape of mandibles and largely reduced labium with reduced ligula (see Minoshima & Hayashi 2015 for details). *Hybogralius* Orchymont, 1942 (Hydrobiusini) also has similar morphology of the anterior margin of the head capsule and mandibles (Watts 2002). These modifications are considered as adaptations for the benthic life styles in *Berosus* and *Hemiosus* (Archangelsky 2008). The same seems to be the case of *Laccobius* and *Oocyclus*. Our observations also reveal that *Laccobius* larvae do not usually have air bubbles in the alimentary canal as in *Berosus* larvae. Unlike *Berosus* larvae, *Laccobius* larvae lack abdominal tracheal gills and have a well-developed stigmatic atrium (and they hence correspond to the 'usual' metapneustic hydrophilid larval type, however see the discussion in Fikáček et al. 2017). *Laccobius* larvae can hence be considered as partially adapted for a benthic lifestyle, both morphologically and ecologically.

When the primary head chaetotaxy of *L.* (*Laccobius*) *kunashiricus* is compared to that of *L.* (*Dimorpholaccobius*) *striatulus* (Fabricius, 1801) (described in an unpublished thesis by Fikáček 2006 and partly mentioned by Fikáček et al. 2008), both species are very similar. A few differences may be observed in the chaetotaxy of the parietale, in which the positions of PA7–13 are slightly different. According to Fikáček et al. (2008), LA11 is present in *L. striatulus*, but they seem to be absent in *L. kunashiricus*. The sensilla are on reduced ligula and we cannot rule out presence of the sensilla in *L. kunashiricus*. In addition, Fikáček et al. (2008) considered that PA26 is a pore and PA27 and PA28 are long setae, whereas we consider PA27 is a pore and PA26 and PA28 are long setae on the basis of their character states. Perkins (1972) described the chaetotaxy of some head appendages (antenna, mandibles, and maxilla), the anterior part of the head capsule, and the legs based on four North American *Laccobius* species (Table 1). Judging from the description and figures in the paper, head chaetotaxy of *L. kunashiricus* is similar to these species. Due to the reduction and modification of the mentum of *Laccobius* larvae, the sensilla in this body part are difficult to see and to compare. Many sensilla seem to be reduced (absent), which is a common trend in hydrophilid species with a modified labium (e.g., Fikáček et al. 2008; Minoshima & Hayashi 2012, 2015; Rodriguez et al. 2015).

Within the tribe Laccobiini, larvae of the genus *Oocyclus* have a similar head morphology to that of *Laccobius* (Archangelsky 1997), whereas other genera with known larvae (*Paracymus*, *Tormus* and *Tritonus*: Archangelsky 1997, 1999; Fikáček et al. 2013, 2017) have unmodified head morphology with almost symmetrical mandibles and clypeolabrum, and a well-developed labium (Table 2). The modified head morphology may be a synapomorphy of the *Laccobius*-group of genera within Laccobiini; however, this needs to be confirmed by discovery of the larvae of the remaining genera of that clade (i.e. *Pelthydrus, Arabhydrus* and *Hydrophilomima*).

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