

First known larva of omicrine genus *Psalitrus* d'Orchymont (Coleoptera, Hydrophilidae)

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Abstract

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The larval morphology of the water scavenger beetle *Psalitrus yamatensis* Hoshina & Satō, 2005 is described based on a specimen collected from Fukuoka Prefecture, Kyushu, Japan. This is the first description of the larval morphology of the hydrophilid genus *Psalitrus* d'Orchymont, 1919, as well as the first description of larval chaetotaxy of the tribe Omicrini. Species-level identification of the larva was performed using DNA barcoding of a molecular marker: a 658 bp fragment of the mitochondrial cytochrome oxidase I. A description including chaetotaxy of head capsule and head appendages, diagnosis, and illustrations of the larva is provided. *Psalitrus* larvae can be distinguished from other known larvae of the tribe Omicrini by the morphology of the head and legs. The larva shares characters with other known larvae of Omicrini; potential plesiomorphies are shared with Cylominae and aquatic hydrophilids; some characters are also shared with larvae of Megasternini and Sphaeridiini.

Introduction

The tribe Omicrini, comprising 15 genera worldwide, is a group of small, terrestrial hydrophilid beetles belonging to the subfamily Sphaeridiinae (Hansen 1999; Short and Fikáček 2011). Members of the tribe inhabit various terrestrial habitats, such as decaying matter (Bameul 1992; Hoshina 2007) and bromeliads (Hansen and Richardson 1998; Albertoni and Fikáček 2014), or they are associated with termites (Schödl 1995). They are rarely collected relative to other groups of hydrophilid. The monophyly of Omicrini was not supported in the tree proposed by Short and Fikáček (2013); Fikáček et al. (2015) subsequently proposed an alternative hypothesis, in which Omicrini is monophyletic and an early-branching clade; however, the sister-group of Omicrini was still unstable in that study. Larvae of the tribe are only known from two species and one unidentified larva: *Peratogonus reversus*

Sharp, 1884 briefly illustrated by Hayashi (1986), *Omicrus ingens* Hansen & Richardson, 1998 described by Hansen and Richardson (1998), and an unidentified larva of *Noteropagus* Orchymont, 1919 or *Paromicrus* Scott, 1913 by Fikáček (in press).

Psalitrus d'Orchymont, 1919 is an omicrine genus containing 36 species from the Afrotropical, Oriental, Palearctic, and Australian regions (Short and Fikáček 2011, 2013). The known species of the genus are small, oval beetles which inhabit decaying matter, and most typically they are sifted from various types of leaf litter (Bameul 1992; Hoshina 2007). The phylogenetic position of the genus remains unclear; *Psalitrus* is in an early-branching clade of Sphaeridiinae together with *Aculomicrus* Smetana, 1990 and *Peratogonus* Sharp, 1884 in the tree proposed by Short and Fikáček (2013), but it was revealed as sister to *Tylomicrus* Schödl, 1995 + *Omicrogiton* Orchymont, 1919 by Fikáček et al. (2015). *Psalitrus* also stands

apart from the remaining omicrine genera because of its antennal morphology, as its antenna has eight antennomeres and a loosely segmented antennal club (in contrast to nine antennomeres and compact antennal club in all remaining Omicrini), further obscuring its phylogenetic placement. Larval morphology has played an essential role in systematic studies, and discovery of the *Psalitrus* larva is expected to provide useful information to enlighten omicrine systematics.

A tiny larva of a terrestrial hydrophilid resembling omicrine larvae was recently collected in Kitakyushu, Kyushu Island, Japan. The larva was collected together with two omicrine species: *Psalitrus yamatensis* Hoshina & Satō, 2005 and *Peratogonus reversus*. In this study, the larva is identified using a DNA barcoding method, described as the first known larva of the genus *Psalitrus*, and compared with other known larvae of the Sphaeridiinae and Cylominae.

Material and methods

Morphological study

A single larva extracted from leaf litter using Tullgren funnels was available for study (Table 1). The larva, unfortunately, completely dried up in a microtube after DNA extraction and thoracic and abdominal characters were strongly deformed. Moreover, most of thoracic and abdominal segments of the larva bear large amounts of dust, which did not wash off during DNA extraction (20 µl proteinase K and 180 µl Buffer ATL, approximately 48 h at 55 °C, mixed by vortexing several times). Detailed observation of the characters was therefore impossible. Under these circumstances thoracic and abdominal characters are only briefly described, and I mainly focus on characters of the head, which was not affected by the DNA extraction. The larva was mounted on HS-slides (Shirayama et al. 1993; Kanto Rika, Tokyo) with Euparal (Waldeck, Münster) for examination and preservation. It is deposited at the Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan (Y. Minoshima) (KMNH).

The specimen was examined using a Leica MZ16 (Leica Microsystems, Wetzlar) and an Olympus BX50 (Olympus, Tokyo). Illustrations were prepared with the aid of a drawing tube attached to the BX50; line drawings were prepared using the software Paint Tool SAI (Systemax Inc., Tokyo). Photographs were taken with digital cameras (Olympus OM-D E-M5 Mark II and E-M1 Mark II) attached to an Olympus SZX12 and the BX50. Composite images were created using focus stacking software Helicon Focus (Helicon Soft Ltd, Kharkov). Photographs were subsequently adapted in Adobe Photoshop Lightroom and Photoshop CC (Adobe Systems Inc., San Jose) as needed.

Morphological terminology follows Hansen and Richardson (1998) and Minoshima and Hayashi (2011) for general morphology; chaetotaxy follows Fikáček et al.

Table 1. List of specimens and GenBank Accession Number used in this study. AD: adult; L: larva.

Taxon	Stage	Extraction ID	Locality data / reference	Accession No.
<i>Psalitrus yamatensis</i>	L	YNME#16-9	JAPAN: Fukuoka Pref., Kitakyushu-shi, Yahatanishi-ku, Narumizu, Götōyama, 33°51.16'N, 130°46.51'E, 170 m; leaf litter; 11 Jun. 2016; YN Minoshima (Loc#2016-11)	LC484174
<i>Psalitrus yamatensis</i>	AD	YNME#85	Same as above (Loc#2016-11)	LC484175
<i>Psalitrus yamatensis</i>	AD	YNME#86	Same as above (Loc#2016-11)	LC484176
<i>Psalitrus yamatensis</i>	AD	YNME#16-4	JAPAN: Ōita Pref., Nakatsu-shi, Hon-yabakei-machi, Atoda, 33°28.57'N, 131°11.81'E, 120 m; leaf litter; 28 May 2016; YN Minoshima (Loc#2016-8)	LC484173
<i>Peratogonus reversus</i>	AD	YNME#16-2	Same as above (Loc#2016-8)	LC484172
<i>Armostus ohyamatsensis</i>	AD	YNME#90	Same locality as Loc#2016-11; see Minoshima (2018)	LC422744

(2008) and Byttebier and Torres (2009). Classification follows Short and Fikáček (2013) and Seidel et al. (2016). The following abbreviations are used: AN: antenna; 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; LA: labium; MN: mandible; MX: maxilla; PA: parietale; SE: sensorium.

Molecular study

Total genomic DNA was extracted from the whole body using a DNeasy Blood & Tissue Kit (Qiagen, Hilden) (Cruickshank et al. 2001). Vouchers and GenBank accession numbers are listed in Table 1; all vouchers are preserved at KMNH. I extracted and sequenced the presumed *Psalitrus* larva, three adults of *Psalitrus yamatensis*, and a single adult of *Peratogonus reversus* (both Omicrini). In addition, I used *Armostus ohyamatsensis* Hoshina & Satō, 2006 (Megasternini) (Gen Bank Accession #LC422744; Minoshima 2018) to compare the generic distance. A single fragment of 658 bp of mitochondrial cytochrome c oxidase I (COI) was sequenced using the primers LCO1490 and HCO2198 (Folmer et al. 1994). Protocols for the PCR were identical to those described in Minoshima et al. (2013). PCR products were purified using ExoSAP-IT (Affymetrix, Santa Clara). Each fragment was sequenced using the primers in both directions by MacroGen Japan Corporation (Kyoto). The sequenced data were assembled and edited manually in MEGA 7.0.26 (Kumar et al. 2016). I used pairwise *p*-distance analysis to associate the larva with adult individuals with the software.

Results

Identification

Pairwise *p*-distance analysis (Table 2) shows that the COI sequence of the presumed *Psalitrus* larva is identical to the sequenced adults of *Ps. yamatensis* collected at the same locality, as well as in Ōita Prefecture. Its pairwise *p*-distance from the adults of *Peratogonus* and *Armostus* is 15.7–17.9%. Hence, the larva is unambiguously identified as *Ps. yamatensis*. The head appendages of the examined larva lack secondary sensilla; on the basis of this, I infer that the larva likely represents the first instar, even though two additional setae are present close to PA8 on head capsule (Fig. 3A).

Description of larva

Psalitrus d'Orchymont, 1919

Diagnosis. Larva of *Psalitrus* can be distinguished from other known omicrine larvae (*Omicrus* Sharp, 1879, *Peratogonus*, and unidentified larva of *Noteropagus* or *Paromicrus*) by: (1) nasale with four distinct teeth; (2) asymmetrical median projection on nasale absent; (3) epistomal lobe absent; (4) mentum very deeply emarginate dorsally; and (5) legs four-segmented.

The *Psalitrus* larva is also similar to other terrestrial sphaeridiine larvae; however, it can be distinguished by the addition of following combination of characters: (1) coronal line absent; (2) PA6 and PA13 absent; (3) anten-

Table 2. Pairwise distances between individuals in analysis expressed as a percentage of nucleotide differences (*p*-distances).

	1	2	3	4	5
1. Larva (YNME16-9)					
2. <i>Psalitrus yamatensis</i> (YNME16-4)	0.0%				
3. <i>Psalitrus yamatensis</i> (YNME85)	0.0%	0.0%			
4. <i>Psalitrus yamatensis</i> (YNME86)	0.0%	0.0%	0.0%		
5. <i>Peratogonus reversus</i> (YNME16-2)	15.7%	15.5%	15.5%	15.5%	
6. <i>Armostus ohyamatensis</i> (LC422744)	17.9%	17.8%	17.8%	17.8%	18.4%

nomere 2 with a small basal additional pore dorsally; (4) antennal sensorium slender, long; (5) mandibles almost symmetrical, both mandibles with two teeth; (6) MN1 close to MN2; (7) MN2–4 forming a triangular group; (8) maxillae symmetrical; (9) maxilla with well-sclerotised inner appendage; (10) submentum without large lateral extension; (11) labium without hypopharyngeal lobe; (12) LA10 stout seta; (13) legs short, four-segmented; and (14) median lobe of spiracular atrium with median emargination posteriorly.

Psalitrus yamatensis Hoshina & Satô, 2005

Figs 1–4

Material examined. 1 presumably first instar larva; see Table 1.

Diagnosis of larva. See generic diagnosis.

Description of presumably first instar larva. General morphology. Length 1.2 mm in the specimen fixed

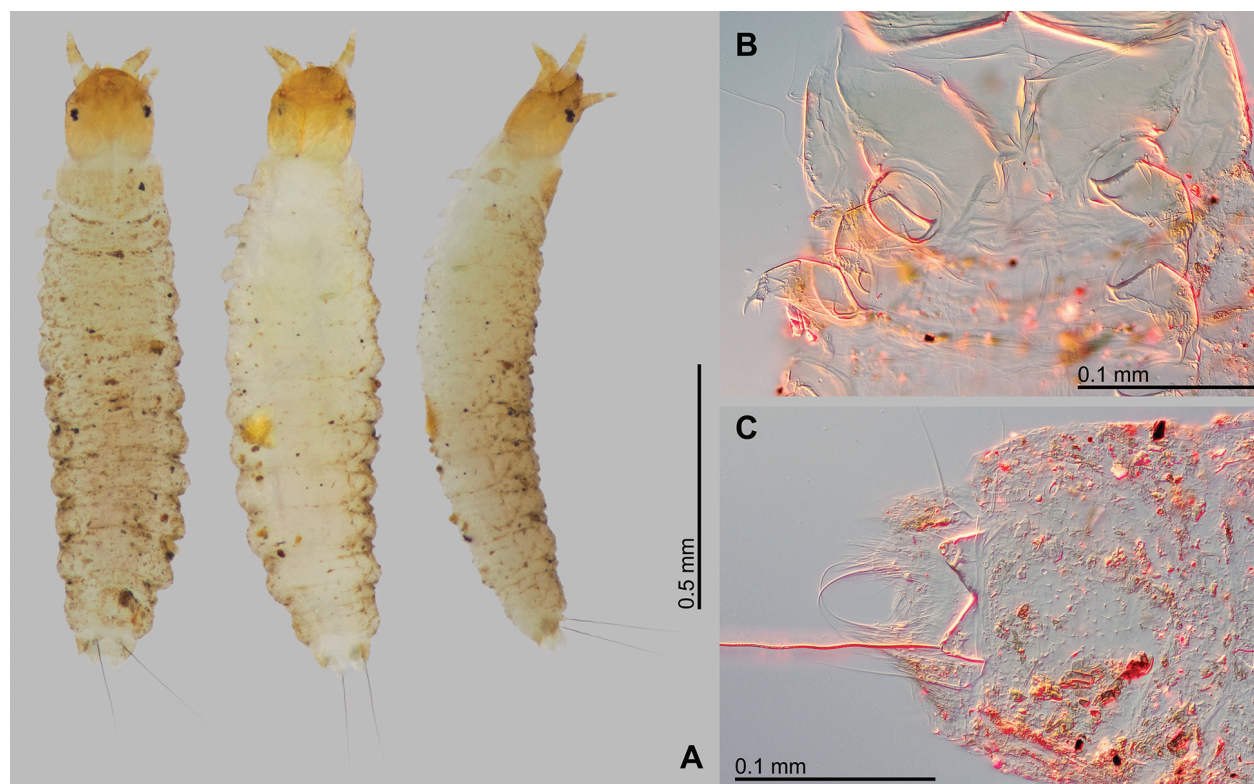


Figure 1. Larva of *Psalitrus yamatensis* Hoshina & Satô. **A.** Habitus, dorsal (left), ventral (middle), and lateral (right) view; **B.** Thorax, ventral view; **C.** Spiracular atrium, dorsal view.

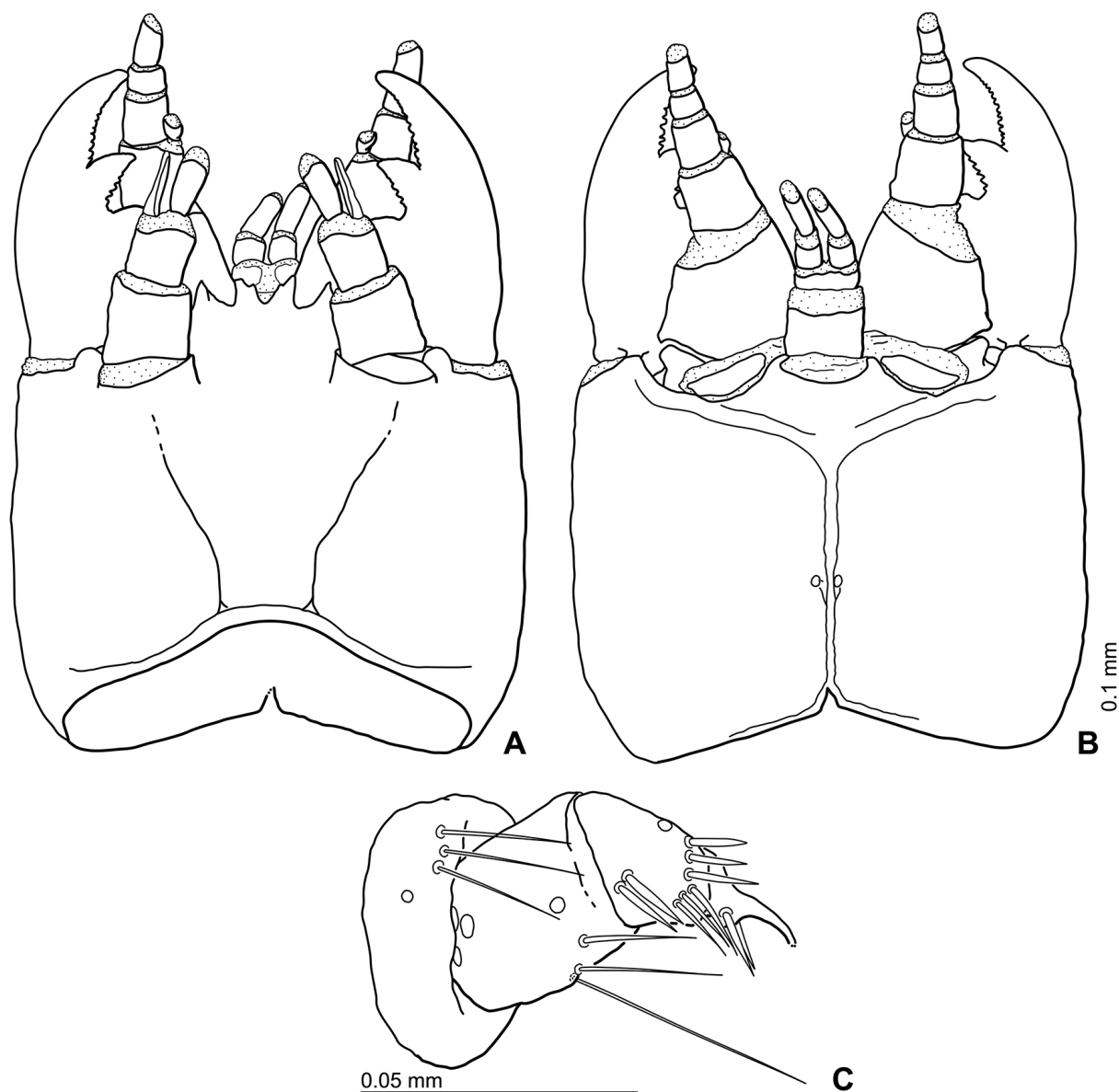


Figure 2. Larva of *Psalitrus yamatensis* Hoshina & Satô. **A, B.** Head, dorsal (A) and ventral (B) view; **C.** Foreleg, anterior view.

by ethanol; head width 0.2 mm. Body (Fig. 1A) maggot-like in shape, widest between abdominal segments 3–6. **Colour.** Head capsule and thoracic sclerites yellowish, membranous parts milky white.

Head. Head capsule subquadrate (Fig. 2A); cervical sclerites undetectable. Frontal lines U-shaped at base, then divergent laterally, ending behind outer margin of antennal socket; coronal line absent. Surface of head capsule smooth; stemmata present on each anterolateral portion of head capsule; number of stemmata unclear but two (groups of) stemmata detectable: posterior one oval; anterior one wider than posterior one. Posterior tentorial pits present, on midlength of and close to submental sulcus. Clypeolabrum symmetrical in shape (Fig. 3C) but asymmetrical in arrangements of setae (see description of chaetotaxy). Nasale distinctly projecting, with four

large teeth; all teeth almost similar in size and equidistant. Asymmetrical median projection absent. One pair of presumably egg-bursters present behind median two teeth of nasale. Epistomal lobe absent (Fig. 3C); lateral part of epistome almost straight.

Antenna (Fig. 4A) three-segmented, short and stout; surface of antenna smooth. Antennomere 1 widest, distinctly wider than antennomere 2; antennomere 3 narrowest. Antennomeres 2 slightly shorter than antennomere 1; antennomere 3 slightly shorter than antennomere 2. Antennal sensorium present, as long as antennomere 3.

Mandibles (Fig. 4B) stout, distinctly widened in basal part, almost symmetrical; median part with two inner teeth; incisor area and basal margin of inner teeth weakly serrate.

Maxilla (Fig. 4C) six-segmented, stout, longer than antenna, asymmetrical. Cardo irregularly triangular.

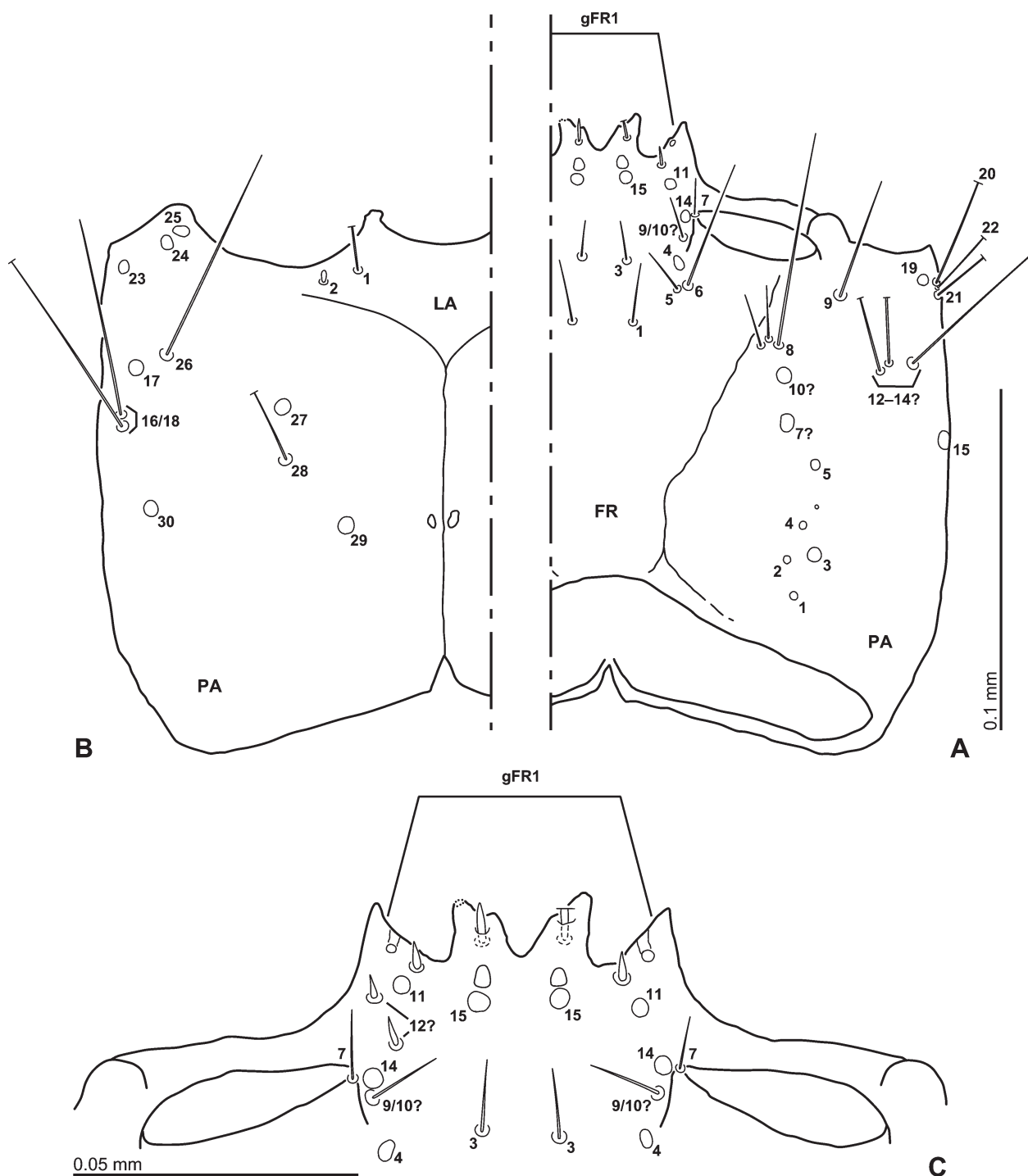


Figure 3. Larva of *Psalitrus yamatensis* Hoshina & Satô. **A, B.** Head capsule, dorsal (**A**) and ventral (**B**) view; **C.** Anterior part of head capsule, dorsal view.

Stipes widest and longest, shorter than palpomeres 1–4 combined; maximum length of stipes as long as maximum width. Maxillary palpus somewhat stout, four-segmented; palpomeres 1–3 wider than long, 4 longer than wide. Approximate ratios of length of palpomeres 1–4 as follows: 1:0.6:0.6:0.7. Palpomere 1 widest and longest, completely cylindrically sclerotised; inner process small, sclerotised. Palpomere 2 shorter and narrower than pal-

pomere 1, as long as palpomere 4. Palpomere 3 shortest, narrower than palpomere 2. Palpomere 4 narrowest.

Labium (Fig. 4D) developed. Submentum subpentagonal, transverse, fused with head capsule; submental sulcus present. Submentum without large lateral extension, i.e., not fused with associate sclerites of cardo. Mentum subquadrate from ventral view; sclerite of dorsal face very deeply emarginated medially, narrowly and very strongly

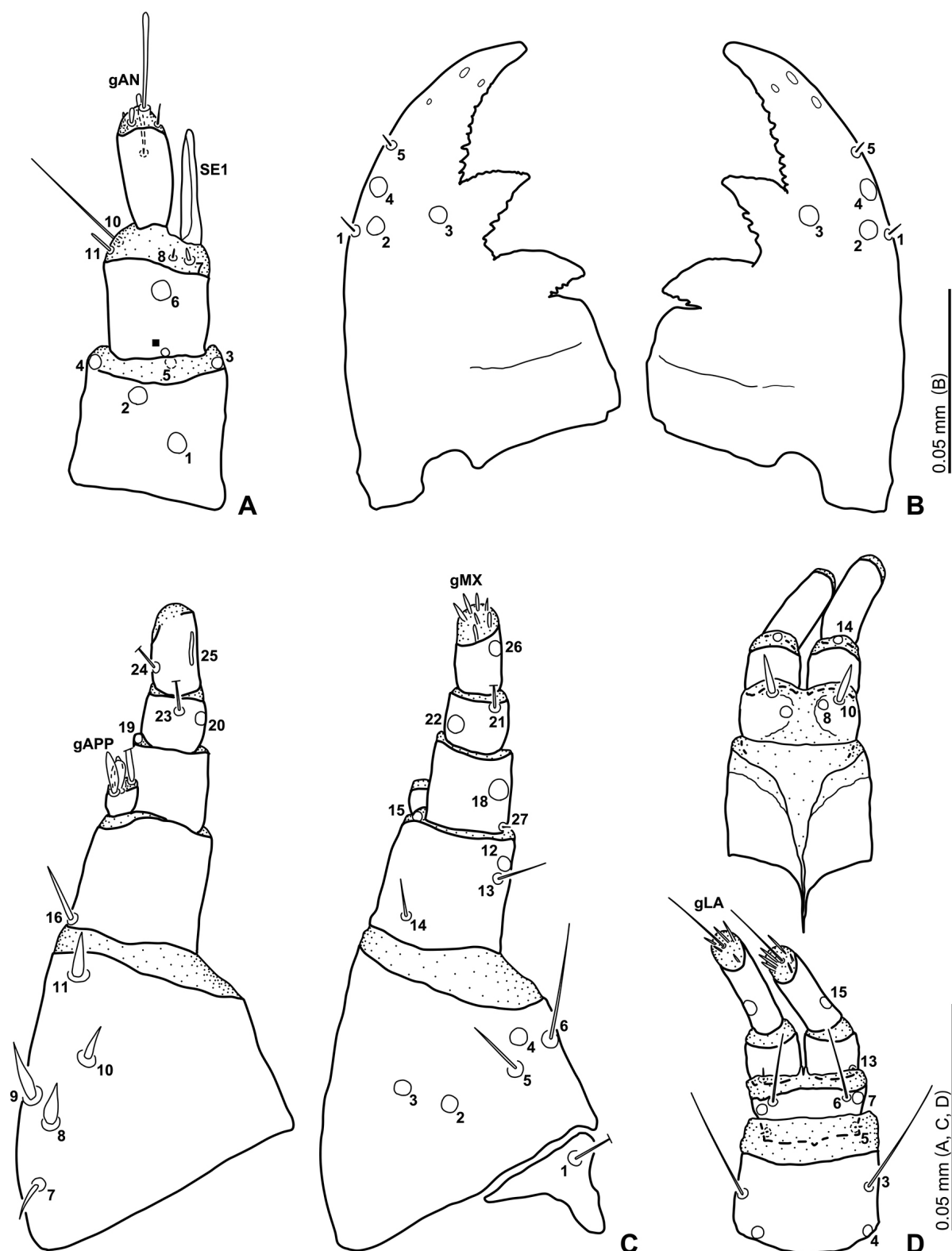


Figure 4. Larva of *Psalitrus yamatensis* Hoshina & Satô. **A.** Antenna, dorsal view; **B.** Mandibles, dorsal view; **C.** Maxilla, dorsal (left) and ventral (right) view; **D.** Labium (excluding prementum), dorsal (top) and ventral (bottom).

projected posteriorly at midwidth; border of sclerotised and membranous portions indistinct. Prementum subquadrate, transverse; median part of dorsal surface membranous. Ligula apparently absent or reduced to a minute membranous projection between palpomeres. Labial

palpus moderately long, palpomere 1 wide, palpomere 2 narrower and distinctly longer than palpomere 1.

Thorax. Thoracic segments bearing microtrichiae, which may catch and securely keep the dirt on its integument, except for ventral area between legs; this area bare

and not bearing dust as other parts. Prothorax slightly wider than head capsule (Fig. 1A). Proscutum formed by one large plate bearing several very long setae, subdivided by fine sagittal line, anterior and posterior margins weakly sclerotised. Prosternal sclerite transverse, not clearly detectable in the specimen. Mesothoracic spiracles forming small tubercle. Legs short, reduced to four segments, well sclerotised (Figs 1B, 2C). Trochanter and femur fused into a segment or trochanter reduced; coxa, tibiotarsus and claw (pretarsus) well defined.

Abdomen 10-segmented, widest in anterior half, then tapering posteriad (Fig. 1A). Membranous part densely bearing microtrichiae, covered with dirt. One pair of spiracles on lateral part of dorsal surface, weakly tuberculate. Spiracular atrium (Fig. 1C): segment 8 with oval dorsal sclerite bearing sparse microtrichiae and setae. Segment 9 trilobed, bearing long microtrichiae except for dorsal surface; median lobe of spiracular atrium with median emargination posteriorly. A pair of sclerotised urogomphi short, conical, bearing extremely long seta, fused basally, thus, outline of urogomphi looks to be V-shaped.

Primary chaetotaxy of head. Frontale (Fig. 3A, C). Rather long seta FR1 situated mesally at midlength of frontale. FR2 absent. FR3 short seta, anterior and slightly mesal to FR1. FR4–6 located behind inner margin of antennal socket; FR4 pore-like, slightly elongate, anterior to FR5 and FR6; rather long seta FR5 and long seta FR6 very closely situated, FR5 mesal to FR6. FR7 on inner margin of antennal socket. Two sensilla close to inner margin of antennal socket; pore-like sensillum FR14 mesal to antennal socket, rather short seta FR^{9/10} behind FR14. FR13 absent. Pore-like sensillum FR11 between FR14 and gFR1; left FR11 situated more anteriorly on than right one. Two short, stout setae (FR12 and additional seta) present between FR11 and FR14 (both marked as “12?” in Fig. 3C) on left; these absent on right. Pair of pore-like sensilla FR15 behind median two setae of gFR1. Six sensilla (gFR1) present on anterior margin of nasale; mesal four short, stout setae; character state of lateral ones unclear.

Parietale (Fig. 3A, B). Dorsal surface with a group of five sensilla (PA1–5) forming irregular longitudinal row in posterior part; PA1–2 and 4–5 may be short setae, PA3 pore-like. Minute additional pore present between PA4 and PA5. PA6 absent. Probable PA7 situated anterolaterally to PA5; PA7 may be a seta which is missing in the specimen. Very long seta PA8 and pore-like sensillum (probable PA10) anterior to PA7; PA8 close to frontal line; PA10 between PA7 and PA8. Two rather short additional setae close and mesal to PA8. Group of three long to very long setae lateral to PA8 and PA10; homology of them unclear (probably PA12–14); PA11 likely absent. Pore-like sensilla PA15 situated laterally at anterior two-fifths. Long seta PA9 posterolateral to antennal socket. PA19–22 situated dorsolaterally on anterior corner of head capsule; PA19 pore-like, dorsal to PA20–22; PA20–22 assumed very long to long setae, very closely aggregated; PA20 anterior to PA21; PA22 ventral to PA20

and PA21. Pore-like sensilla PA23–25 lateroventral, close to ventral mandibular articulation; PA23 lateral to PA24; PA24 and PA25 closely situated; PA24 posterolateral to PA25. Pore-like sensilla PA17 situated lateroventrally on anterior fourth of head capsule. Two very long setae (PA16 and PA18) posterior to PA17, precise homology of respective sensilla unclear. Very long seta PA26 close and mesal to PA17. PA27 and PA28 situated on median part of parietale, slightly anterior to midlength of head capsule; PA27 pore-like, anterior to PA28, PA28 seta. PA29 pore-like, posteromesal to PA28. Pore-like sensillum PA30 laterally on midlength of ventral surface.

Head appendages. Antenna (Fig. 4A). Antennomere 1 with five pore-like sensilla (AN1–5). AN1 situated dorsally on midlength of dorsal surface of sclerite. AN2 anterolateral to AN1, close to borderline between sclerite and membrane. AN3 and AN4 apically on intersegmental membrane or borderline between sclerite and membrane; AN3 on inner face, AN4 lateral face. AN5 apically on ventral surface. Antennomere 2 with seven sensilla. AN6 dorsally on subapical part of sclerite. One small additional or secondary pore-like sensillum on basal margin of sclerite. Minute setae AN7 and AN8, long seta AN10, short seta AN11, and sensorium SE1 on intersegmental membrane between antennomeres 2 and 3. AN7 and AN8 dorsally on lateral part, behind SE1. AN9 absent. AN10 and AN11 on lateral face. SE1 situated on outer face, slender and long, as long as antennomere 3, partly sclerotised. Antennomere 3 with group of apical sensilla (gAN) in apical membranous area. One ventral seta of gAN situated posterior to remaining sensilla; although borderline between membrane and sclerite hardly visible and almost undetectable, the seta seems to be on the borderline based on examination of very fine line indicated borderline.

Mandibles (Fig. 4B). Five sensilla (MN1–5) on anterior one-third to two-fifths; MN1 and MN5 short setae, MN2–4 pore-like sensilla. MN1 on anterior to midlength of mandible. MN2 mesal to MN1. MN4 anterior to MN2, between MN2 and MN5. MN3 lateral to MN2 and MN4. MN5 anterior to MN4. MN6 undetectable; three sensilla-like structures present on subapical part of mandible.

Maxilla (Fig. 4C). Cardo with one ventral seta (MX1). Inner face of stipes with irregular longitudinal row of five rather short setae (MX7–11); MX7 at base, slenderer than others; MX8–11 stout. Pore-like sensilla MX2 and MX3 situated ventrally on median part, MX2 posterolateral to MX3. Pore-like sensilla MX4, rather long seta MX5, and long seta MX6 situated subapically and ventrally on lateral face. MX6 lateral to MX4, MX5 posterior to MX4. Rather long seta MX16 basally on inner face of palpomere 1. Pore-like sensillum MX12 and rather long seta MX13 situated subapically on lateral face; MX12 anterior to MX13. MX14 ventrally and subbasally on inner part of sclerite. Pore-like sensillum MX15 ventrally on membrane behind inner appendage; MX17 absent. Inner appendage with few short apical setae of variable length (gAPP). Palpomere 2 with pore-like sensillum MX18 and minute seta MX27 on sclerite. MX18 lateroventral-

ly at midlength; MX27 basally on lateral face. Pore-like sensillum PA19 on inner face of intersegmental membrane between palpomeres 2 and 3. Palpomere 3 with two pore-like sensilla (MX20 and MX22), and two setae (MX21 and MX23). MX23 and MX20 on subapical part of sclerite; MX23 dorsal, MX20 lateral. MX21 apically on lateroventral part. MX22 on posteroventral part of inner face. Palpomere 4 with three sensilla (MX24–26) on sclerite. MX24 seta on inner face; digitiform (MX25) and pore-like (MX26) sensilla on lateral face, MX25 dorsal, MX26 ventral. Apical membranous area of palpomere 4 with several minute setae (gMX).

Labium (Fig. 4D). Submentum with two pairs of setae (LA1 and LA2); LA1 trichoid, situated mesally to LA2; LA2 short, leaf-like, on lateral part. Mentum with one pair of very long setae (LA3) and pore-like sensilla (LA4) on lateroventral face; LA4 at base, LA3 anterior to LA4. Prementum with 5 pairs of sensilla (LA5–8, LA10). LA5–7 situated laterally on ventral face; minute seta LA5 at base; long seta LA6 and pore-like sensillum LA7 on apical part of sclerite; LA7 lateral to LA6. LA8 pore-like, dorsally on median part. Stout short seta LA10 anterolateral to LA8. LA9, LA11, and LA12 absent. Labial palpomere 1 with minute seta LA13 lateroventrally at base. Pore-like sensillum (LA14) dorsally on intersegmental membrane between palpomeres 1 and 2. Palpomere 2 with one pore-like sensillum (LA15) situated subbasally on outer face; several minute sensilla of variable shape and length (gLA) on apical membranous area.

Biology. Adults and the larva were collected from leaf litter (for the photograph of collecting locality, see Minoshima 2018: fig. 1H). They were collected together with adults and larvae of *Peratogonus reversus* (Omicrini), *Cercyon* sp., and *Armatus ohyamatensis* Hoshina & Satō, 2006 (both Megasternini).

Discussion

The larva of *Psalitrus* shows us multiple differences from other known larvae of Omicrini (*Omicrus*, *Peratogonus*, and an unidentified larva of *Noteropagus/Paromicrus*; Hayashi 1986; Hansen and Richardson 1998; Fikáček in press). The nasale bears clearly separated teeth in *Psalitrus* and *Peratogonus* (e.g., Fig. 3C), whereas it has aggregated irregular teeth in *Omicrus* and *Noteropagus/Paromicrus*. The median projection of the nasale is absent in *Psalitrus* (Fig. 3C), whereas *Omicrus* has the projection (the projection seems to be also present in *Peratogonus*; Y.N. Minoshima pers. obs. 2018). The epistomal lobe is absent in *Psalitrus* (Fig. 3C), whereas it is present in *Omicrus*, *Peratogonus*, and *Noteropagus/Paromicrus*. The surface of the head capsule is smooth in *Psalitrus*, whereas it is granulated in *Noteropagus/Paromicrus*; however, the surface structure is often different between first and third instar larvae. Although shape and relative length of head appendages are different between instars, short antenna and very wide and short maxillary stipes

are possible apparent characters of *Psalitrus* (Fig. 4A, C). The morphology of the dorsal surface of the mentum (Fig. 4D) is unique within the known larvae of Hydrophilidae; the mentum is morphologically variable between genera but never deeply emarginate as in *Psalitrus* (e.g., Archangelsky 1997; Archangelsky et al. 2016a). The legs are reduced to four segments (Fig. 2C), whereas they are five-segmented in *Omicrus* and *Noteropagus/Paromicrus*.

The phylogenetic position of the members of Omicrini, which is an early-diverging clade within the subfamily Sphaeridiinae (Short and Fikáček 2013; Fikáček et al. 2015), is reminiscent of ancestral characters of omicrine larvae. Short and Fikáček (2013) supposed two plesiomorphic characters of the larvae: the presence of teeth on the nasale (Fig. 3C) and well-developed legs (Fig. 2C). Larval morphology of *Psalitrus* supports their hypothesis, as *Psalitrus* larva shares several symplesiomorphies with aquatic clades as discussed below (Table 3).

The *Psalitrus* larva have distinct teeth on the nasale (Fig. 3C). Within Sphaeridiinae, the larvae of Megasternini and Protosternini do not have distinct teeth on the nasale (Archangelsky 1997, 1999; Fikáček et al. 2015, 2018a); the larvae of Sphaeridiini bear a simple, low, median projection (Archangelsky 1997); the nasale of Coelostomatini is more or less variable, ranging from that with a simple median projection resembling that of *Sphaeridium* Fabricius, 1775 (e.g., *Dactylosternum cacti* (LeConte, 1855) in Archangelsky 1994) to closely aggregated teeth-like projections resembling that of *Omicrus* (e.g., *Phaenonotum exstriatum* (Say, 1835) in Archangelsky et al. 2016b). In comparison to Cylominae, which is a sister taxon of Sphaeridiinae, distinct teeth on the nasale are common in the known aquatic or semi-aquatic larvae of Cylominae (*Anticura* Spangler, 1979, *Cylomissus* Broun, 1903, *Cylorygmus* Orchymont, 1933, and *Rygmodes* White, 1846; Minoshima et al. 2015, 2018; Seidel et al. 2018), and only the terrestrial genera *An-dotypus* Spangler, 1979 and *Austrotypus* Fikáček, Minoshima & Newton, 2014 do not have distinct teeth on the nasale (Fikáček et al. 2014). It seems probable that the reduction of the toothed nasale corresponds to specialized prey preference and feeding behaviour in many terrestrial hydrophilid larvae. The reduction of teeth on the nasale is often associated with further modifications of mouthparts, i.e., asymmetry of nasale, mandibles and maxillae, and presence of an asymmetrical hypopharyngeal lobe (Archangelsky 1999; Fikáček et al. 2018a). The *Psalitrus* larva does not show such modifications, thereby resembling the larvae of the aquatic Cylominae and the majority of Acidocerinae (sister taxon of Cylominae + Sphaeridiinae) (e.g., Archangelsky 1997; Minoshima and Hayashi 2011). This outgroup comparison illustrates that the toothed nasale of larval Omicrini is a plesiomorphy as supposed by Short and Fikáček (2013), and a reduced nasale is an apomorphy that evolved independently in the Sphaeridiinae and the Cylominae.

Asymmetry of mandibles and maxillae are characteristics of megasternine and sphaeridiine larvae. Asymme-

Table 3. Morphological characters of Sphaeridiinae and Cylominae larvae.

	Sphaeridiinae					Cylominae
	Omicrini	Coelostomatini	Protosternini	Sphaeridiini	Megasternini	
Nasale	With teeth	With median projection to aggregated teeth-like projection	Without teeth	With a median projection	Without teeth	With/Without teeth
Asymmetrical median projection on nasale	Present/absent	Absent	Absent	Absent	Absent	Absent
Epistomal lobe	Present/absent	Present	Present	Absent	Absent	Present
Notch on left side of nasale	Absent	Absent	Absent	Present	Present	Absent
FR2	Absent	Present	Present	Present	Present	Present
FR7	Present	Present	Present	Absent	Absent	Present
PA6	Absent	Present	Present	Present	Present	Present
Mandibles	Symmetrical	Symmetrical/Asymmetrical	Symmetrical/Asymmetrical	Asymmetrical	Asymmetrical	Symmetrical/Asymmetrical
Stipes	Symmetrical	Symmetrical	Symmetrical/Asymmetrical	Asymmetrical	Asymmetrical	Symmetrical/Slightly asymmetrical
Chaetotaxy of inner face of stipes	MX7–11	gMX2	MX7–11	gMX2	gMX2	MX7–11/gMX2
MX17	Absent	Present	Present	Present	Absent	Present
Hypopharyngeal lobe	Absent	Present/Absent	Absent	Present	Present	Present/Absent
LA9	Absent	Present	Present	Absent	Absent	Present
LA10	Stout	Trichoid	Trichoid	Trichoid	Trichoid	Trichoid
LA11	Absent	Present/Absent	Present	Present	Absent	Present
LA12	Absent	Present/Absent	Present	Present	Present	Present
Legs	Reduced to 4 segments/5-segmented	5-segmented	5-segmented	Short rod-like, 5-segmented	Reduced, unsclerotized to 2-segmented	5-segmented
Basal additional pore on dorsal surface antennomere 2	Present	Absent	Absent	Absent	Present	Absent

try of mandibles has evolved multiple times in different clades within Hydrophilidae, including Coelostomatini and Protosternini; in contrast, asymmetry of maxillae is less common in Hydrophilidae (Archangelsky 2016; Fikáček et al. 2018a). Symmetry of mandibles and maxillae in Omicrini could be considered as plesiomorphies.

Legs of *Psalitrus* larva are well sclerotised but short and reduced to four segments (Figs 1B, 2C) by the fusion of the trochanter and the femur or reduction of the trochanter. The reduction of the trochanter was observed by Hansen and Richardson (1998) in *Omicrus*, in which it is still present but rather narrowly ring-like. In contrast, the possible *Noteropagus* or *Paromicrus* larva has a moderately sized trochanter (Fikáček in press). The reduction of larval legs is an evolutionary trend of terrestrial Sphaeridiinae, especially in the Megasternini + Sphaeridiini clade, in which the segments of legs are more or less reduced, appearing as a minute tubercle (*Oosternum* and some *Cercyon*) to minute two segments (some *Cercyon* and *Armatus*) or five-segmented but short, rod-like (*Sphaeridium*) (Archangelsky 1997, 1999, 2018; Minoshima 2018). The presence of legs in Omicrini is a plesiomorphy as supposed by Short and Fikáček (2013) based on the fact that terrestrial and aquatic cylomine larvae and acidocerine larvae have well-developed legs (e.g., Archangelsky 1997; Minoshima and Hayashi 2011; Fikáček et al. 2014; Minoshima et al. 2018).

This is the first detailed description of the larval chaetotaxy of Omicrini. Even though only one larva is available in this study and intraspecific variation is therefore still unclear, the chaetotaxy of *Psalitrus* larva shows apparent differences from the other larvae of Sphaeridiinae. Homology of some setae are still unclear, further investigations of omicrine larvae are essential to solve the homology of the sensilla.

Absence of FR2 (Fig. 3A) is unique within Sphaeridiinae; outside Sphaeridiinae, *Paracymus subcupreus* (Say, 1825) (Hydrophilinae, Laccobiini) exceptionally does not have the sensillum (Fikáček et al. 2008). On the clypeolabrum, two unique character states are observed: absence of the seta FR8 and pore FR13. Homology of the rather short seta behind FR14 is unclear; it is likely FR9 or FR10 than FR8 based on the position of the seta. Absence of gFR2 is shared with the larvae of Megasternini and Sphaeridiini; in contrast gFR2 is present in Coelostomatini and Protosternini (Archangelsky 2016). This is a possible convergence associated with the reduction of the epistomal lobe.

On the parietale (Fig. 3A, B), absence of PA6 is unique within Hydrophilidae. Homology of PA7 and PA10 is unclear because of a possibly broken seta; anterior and posterior sensilla may be PA10 and PA7 based on their position, respectively. Closely aggregated setae PA12–14 are similar to other megasternine larvae, whereas the

position of PA18 resembles some aquatic clades rather than Megasternini (e.g., Fikáček 2006; Minoshima and Hayashi 2011; Minoshima et al. 2017). Anterolateral position of PA26 seems to be similar to sphaeridiine larvae; however, this character is relatively variable within the subfamily (e.g., Archangelsky 2016, 2018; Fikáček et al. 2018a). A small basal additional pore on the dorsal surface of antennomere 2 is present in *Psalitrus* (Fig. 4A); Archangelsky (2016, 2018) considered this is an essential character for Megasternini. The character has been likely overlooked until Archangelsky (2016, 2018) pointed it out, and, therefore, it has not been described in detail in the majority of Hydrophilidae. Although the sensilla or sensilla-like structures on the basal part of antennomere 2 may be observed in the wider spectrum of Hydrophilidae taxa (e.g., Minoshima and Hayashi 2011, 2015; Minoshima et al. 2015, 2017), a distinct large pore is surely notable in Megasternini and *Psalitrus* only.

Arrangements of mandibular sensilla MN1–3 (forming a transverse row) and MN2–4 (forming a triangular group) (Fig. 4B) of *Psalitrus* and *Noteropagus/Paromicrus* (Fikáček in press) are expected to be potential synapomorphies of Omicrini; however, these characters are often rather variable within the tribe and subfamily and therefore they should be carefully evaluated. Arrangements of MN1–4 resembles the myrmecophilous genus *Sphaerocetum* Fikáček, 2010 (Protosternini) and Coelostomatini (Clarkson et al. 2014; Fikáček et al. 2015; Archangelsky et al. 2016b); MN1 is situated more posteriorly than in other genera of Sphaeridiinae (e.g., Archangelsky 2018). Outside Sphaeridiinae, somewhat similar character states are present, e.g., in *Andotypus* and *Austrotypus* of Cylominae (Fikáček et al. 2014), and *Berosus* and *Regimbartia* of Berosini (Minoshima and Hayashi 2015; Rodríguez et al. 2018).

The inner face of stipes of maxilla bears five setae (MX7–11) (Fig. 4C); the character is shared with Protosternini and the majority of hydrophilids outside Sphaeridiinae, whereas Coelostomatini, Sphaeridiini, and Megasternini bear more than five setae (gMX2) (Fikáček et al. 2008, 2015, 2018a). The character is likely plesiomorphic because bearing gMX2 is a rather rare character outside Sphaeridiinae. The group of setae gMX2 is present in some Cylominae, and *Hydramara* of Hydrobiusini (Spangler 1979; Fikáček et al. 2014; Minoshima et al. 2015). The number of the setae rarely increases during larval development; five in the first instar larva but more than five in later instars in *Enochrus japonicus* (Sharp, 1873) (Minoshima and Hayashi 2011). Absence of MX17 is only shared with Megasternini, except for *Amphiops* Erichson, 1843 of Amphiopini, which does not bear MX17 and MX15 (Minoshima and Hayashi 2012).

The arrangement of LA1 and LA2 is unique, as LA1 is posterolateral to LA2 in other known hydrophilid larvae. The character state of LA10 (stout setae; Fig. 4D) is notable, as this sensillum is present as trichoid seta in the majority of Hydrophilidae with the exception of Megasternini and Sphaeridiini, in which LA10 is absent

(Fikáček et al. 2008). This character is shared with *Omicrus* (Hansen and Richardson 1998), and this is a possible synapomorphy of Omicrini. LA9, LA11, and LA12 are absent because of the reduction of labial structures. The reduction of labial sensilla is an evolutionary trend in several Hydrophilidae, which have modified labrum. Absence of LA9 is shared with Megasternini and Sphaeridiini, and absence of LA11 is shared with Megasternini, Sphaeridiini, and *Dactylosternum* (Coelostomatini); absence of LA12 is shared with *Dactylosternum* and *Laccobius* Erichson, 1837 (Laccobiini) (Archangelsky et al. 2016b; Minoshima et al. 2017; Archangelsky 2018; Fikáček et al. 2018b).

Psalitrus larva have characters shared with other known larvae of Omicrini, including potential synapomorphies of the tribe, the presumable plesiomorphies shared with aquatic hydrophilids and Cylominae, and the supposed derived characters, which are shared with Megasternini + Sphaeridiini, for an adaptation to terrestrial habitats.

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