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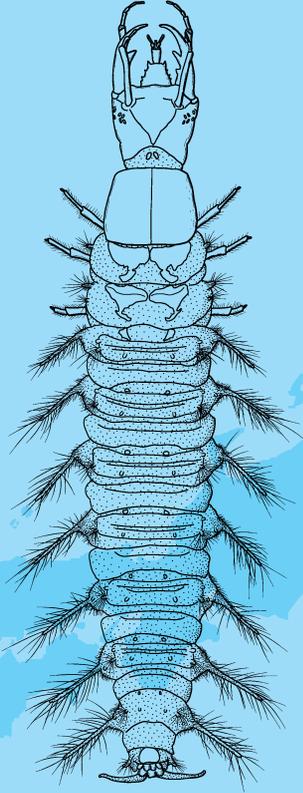




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Yûsuke Minoshima • Masakazu Hayashi

Hydrochara affinis



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Cover: Larva of *Hydrochara affinis* (Sharp, 1873) (Coleoptera: Hydrophilidae). Drawn by Yūsuke Minoshima.

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**Larval morphology of the Japanese species
of the tribes Acidocerini, Hydrobiusini and Hydrophilini
(Coleoptera: Hydrophilidae)**

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Abstract. Larval morphology of the Japanese representatives of the tribes Acidocerini, Hydrobiusini and Hydrophilini (Coleoptera, Hydrophilidae, Hydrophilinae) is described. Eleven species assigned to seven genera are studied: *Agraphydrus narusei* (Satô, 1960) (first and third instars), *Enochrus* (*Holcophilydrus*) *simulans* (Sharp, 1873) (all instars), *E. (H.) umbratus* Sharp, 1884 (third instar), *E. (Methydrus) japonicus* (Sharp, 1873) (all instars), *Helochares* (*Helochares*) *pallens* (MacLeay, 1825) (all instars), *H. (Hydrobaticus) anchoralis* Sharp, 1890 (first instar), *H. (Hydrobaticus) nipponicus* Hebauer, 1995 (all instars), *Hydrobius pauper* Sharp, 1884 (second and third instars), *Hydrochara affinis* (Sharp, 1873) (first and third instars), *Hydrophilus* (*Hydrophilus*) *acuminatus* Motschulsky, 1854 (all instars), and *Sternolophus* (*Sternolophus*) *rufipes* (Fabricius, 1792) (all instars). Three aspects of larval morphology were evaluated for each species studied: (1) general morphology; (2) chaetotaxy of the head capsule and its appendages; (3) morphological transformations between instars. Primary chaetotaxy is rather stable among taxa and instars examined, thus we were able to distinguish primary and secondary sensilla even in the majority of the second and third instar larvae studied. Secondary chaetotaxy shows slight intraspecific variation. Presence/absence of secondary sensilla may be useful at least for distinguishing the first larval instar from later instars, and often for distinguishing all three larval instars. The arrangement of primary and secondary sensilla shows differences among the tribes and genera studied, and between species in *Enochrus* Thomson, 1859 and *Helochares* Mulsant, 1844. The pattern of character transformations between larval instars is rather constant among taxa examined. Generic keys of aquatic Hydrophilidae, tribes Acidocerini and Hydrophilini from Japan, and key to Japanese species of *Enochrus* and *Helochares* with known larvae are provided.

Key words. Coleoptera, Hydrophilidae, Hydrophilinae, Acidocerini, Hydrobiusini, Hydrophilini, larva, morphology, chaetotaxy, morphological transformation, taxonomy, Japan

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1. Introduction

The water scavenger beetle tribes Acidocerini, Hydrobiusini and Hydrophilini (i.e., representatives of the former tribe Hydrophilini *sensu* HANSEN (1991)) represent together one of the largest groups of the family Hydrophilidae, containing about a quarter of the known species (HANSEN 1999, SHORT & HEBAUER 2006, SHORT & FIKÁČEK 2011). The representatives of these tribes occur in various aquatic habitats including artificial ones such as paddy fields and adjacent ponds. The larvae are predatory, while the adults are mainly herbivores or omnivores, thus they play different roles in freshwater ecosystems during their development. Several different phylogenetic hypotheses have been proposed for these groups in previous studies. HANSEN (1991) considered them to form together a monophyletic lineage (the tribe Hydrophilini *sensu* HANSEN (1991)) based mostly on adult morphology, and treated the Acidocerina, Hydrobiusina and Hydrophilina as subtribes. In contrast, ARCHANGELSKY (2004) performed a phylogenetic analysis based on morphology of both adults and immature stages, and suggested that the Hydrophilini *sensu* HANSEN (1991) is a polyphyletic group, whereas its subtribes are monophyletic. For this reason, the subtribes Acidocerina, Hydrobiusina and Hydrophilina were recently elevated to the tribal rank by SHORT & FIKÁČEK (2011).

The taxonomic and phylogenetic significances of immature stages of Coleoptera have been widely considered (e.g., EMDEN 1957, MEIER & LIM 2009). Immature stages of Hydrophilidae have been studied by several authors (e.g., SCHIÖDTE 1862, RICHMOND 1920, BØVING & HENRIKSEN 1938, BERTRAND 1972, ARCHANGELSKY 1997, FIKÁČEK et al. 2008). A nomenclatural system of the larval head chaetotaxy has recently been developed for the Hydrophilidae (FIKÁČEK et al. 2008, BYTTEBIER & TORRES 2009, TORRES et al. 2011). Larval chaetotaxy has been recognised as an informative source of characters in Coleoptera (e.g., SOLODOVNIKOV 2007) and is also expected to provide useful information for the taxonomic and phylogenetic studies of the Hydrophilidae (FIKÁČEK 2006, FIKÁČEK et al. 2008, BYTTEBIER & TORRES 2009, TORRES et al. 2011).

Identification of the immature stages as well as the recognition of instar stages are crucial problems in larval studies. Ways of identifying immature stages have recently been considerably improved by molecular-based methods (e.g., MILLER et al. 2005, LEVKANIČOVÁ & BOČÁK 2009, HAYASHI & SOTA 2010) which can associate the larvae and respective adults even without the time-consuming rearing or comparing multiple samples and the subsequent ‘association by an exclusion’. However, identification of larval stages is still problematic. Coleopteran larvae generally have three or more larval instars and show morphological transformations between them. The pattern of these transformations is often also taxonomically or phylogenetically significant, therefore, information about the character states in all larval instars is essential for an accurate evaluation of these characters (WHEELER 1990).

To date, the Japanese fauna of the Acidocerini, Hydrobiusini and Hydrophilini contain 30 species assigned to nine genera (HANSEN 1999, SHORT & HEBAUER 2006, SHORT & FIKÁČEK

Table 1. State of knowledge of the immature stages of the Japanese Acidocerini, Hydrobiusini and Hydrophilini genera.

Tribe	Genus	Larva	Pupa
Acidocerini	<i>Agraphydrus</i>	Known	Unknown
	<i>Megagraphydrus</i>	Unknown	Unknown
	<i>Chasmogenus</i>	Unknown	Unknown
	<i>Enochrus</i>	Known	Known
	<i>Helochares</i>	Known	Unknown
Hydrobiusini	<i>Hydrobius</i>	Unknown ¹	Unknown
Hydrophilini	<i>Hydrochara</i>	Known	Known
	<i>Hydrophilus</i>	Known ²	Known
	<i>Sternolophus</i>	Known	Known

¹ This list does not include a doubtful record of *Hydrobius fuscipes* (Linnaeus, 1758).

² WATTS (2002) described the larva of *Hydrophilus bilineatus bilineatus* (MacLeay, 1825) under the name *H. bilineatus*. The Japanese subspecies is *H. bilineatus cashmirensis* Redtenbacher, 1844. Thus, the description is not included in the list.

2011), which also includes a doubtful record of *Hydrobius fuscipes* (Linnaeus, 1758). The Japanese representatives of these tribes are intensively studied both taxonomically and faunistically, but the knowledge of their immature stages remains still very limited (e.g., HOSOI 1939a,b, 1947; MORIOKA 1955; HAYASHI 2008, 2009a) (Tables 1–2).

Morphological studies of the immature stages of the tribes Acidocerini, Hydrobiusini and Hydrophilini should provide a understanding of the biodiversity, phylogeny, ecology, and evolution of these groups. The aim of this study is to summarise the basic information on the morphology of larval stages of the Japanese representatives of these tribes, with emphasis on the primary chaetotaxy of the head and head appendages, and morphological transformations between the larval instars.

2. Materials and methods

Selected taxa and specimens. We studied the larvae of 11 species belonging to seven genera (Table 3). The examined material is deposited in the authors' collections (SEHU, HGF) unless specified. We referred to RICHMOND (1920), BØVING & HENRIKSEN (1938), BERTRAND (1972, 1977), and ARCHANGELSKY (1997) to confirm our identification of genera. Instars were identified by the relative size of the head capsule (usually by sorting the material in one sample into size categories), presence/absence of secondary sensilla, and/or by a key to larval instars provided by BYTTEBIER & TORRES (2009) for the genus *Enochrus*.

Specimens were mainly collected in Hokkaidô and Shimane Prefecture (Shimane-ken), Japan. Most of the specimens were collected in the field and associated with co-occurring

Table 2. State of knowledge of the immature stages of the Japanese species of Acidocerini, Hydrobiusini and Hydrophilini and source of information. **E** – egg case, eggs; **L1, L2, L3, L4** – larva of first, second, third, or fourth instar; **L?** – larval instar unknown; **P** – pupa.

Species	Stages	Reference
<i>Agraphydrus narusei</i> (Satô, 1960)	E, L?	HAYASHI (2009a): diagnosis
<i>Agraphydrus ishiharai</i> (Matsui, 1994)	L?	HAYASHI (2009a): briefly mentioned
<i>Enochrus (Holcophilydrus) simulans</i> (Sharp, 1873)	L?	SATÔ (1985): illustrated
	L?	SATÔ & YOSHITOMI (2005): illustrated (as <i>Enochrus (Lumetus) simulans</i>)
	L?	HAYASHI (2008): diagnosis
	L?	HAYASHI (2009a): diagnosis
<i>Enochrus (Holcophilydrus) umbratus</i> Sharp, 1884	E	WATANABE (1982): photo (as <i>Enochrus simulans umbratus</i>)
<i>Enochrus (Lumetus) bicolor</i> (Fabricius, 1792)	E, L?, P	SCHJØDTE (1862): description (as <i>Philydrus testaceus</i>)
	L?	BØVING & HENRIKSEN (1938): short description
<i>Enochrus (Methydrus) japonicus</i> (Sharp, 1873)	L?	HAYASHI (2009a): briefly mentioned
<i>Enochrus</i> sp. (<i>E. japonicus</i> ?)	L?	MORIOKA (1955): description (as <i>Enochrus</i> sp.)
	L?	TSUDA (1962): after MORIOKA (1955) (as <i>Enochrus</i> sp.)
<i>Helochares (Helochares) pallens</i> (MacLeay, 1825)	E	TAKAHASHI (1922): illustrated, biology (as <i>Helochares lewisius</i> Sharp, 1873)
	L?	HAYASHI (2008): diagnosis of the genus
	L?	HAYASHI (2009a): diagnosis
<i>Helochares (Hydrobaticus) nipponicus</i> Hebauer, 1995	E	HOSOI (1952): description (as <i>Helochares striatus</i> Sharp, 1873)
	L?	HAYASHI (2008): diagnosis of the genus
	L1, L2, L3	HAYASHI (2009a): diagnosis
<i>Hydrochara affinis</i> (Sharp, 1873)	E, L1	UWE (1922): illustrated, biological information
	L1, L2, L3, L4, P	HOSOI (1947): description, four instars reported
	L3?	MORIOKA (1955): description, as <i>Hydrophilus affinis</i>
	L3?	TSUDA (1962): illustrated (as <i>Hydrophilus affinis</i> , after MORIOKA (1955))
	L3	FUKUDA et al. (1959): diagnosis
	E	WATANABE (1982): photo
	E	YOSHIMURA (1992): photo, biology (as <i>Hydrophilus affinis</i>)
	L?	HAYASHI (2008): diagnosis
	L1, L2, L3	HAYASHI (2009a): diagnosis

Table 2 (continued).

Species	Stages	Reference
<i>Hydrophilus (Hydrophilus) acuminatus</i> Motschulsky, 1854	L1, L2, P	HOSOI (1939b): description, biology, as <i>Hydrous acuminatus</i>
	E, L1, L2, L3, P	HOSOI (1939a): description, biology (as <i>Hydrous acuminatus</i>)
	L3?	MORIOKA (1955): description (as <i>Hydrous acuminatus</i>)
	E, L1, P	YAJIMA & OGINO (1965): photo, biology
	L?	SHIRAKI (1969): illustrated (as <i>Hydrous</i> sp., after KAWAMURA (1932))
	L3?	TSUDA (1962): illustrated (as <i>Hydrous acuminatus</i> , after MORIOKA (1955))
	E, L?, P	WATANABE (1982): photo, biology
	L?	HAYASHI (1986): illustrated
	L?	SATÔ & YOSHITOMI (2005): illustrated
	L?	HAYASHI (2005): photo, briefly mentioned
	L1, L?	HAYASHI (2009a): diagnosis
<i>Hydrophilus</i> sp. (<i>Hydrophilus acuminatus</i> ?)	L?	KAWAMURA (1932): diagnosis
<i>Sternolophus (Sternolophus) rufipes</i> (Fabricius, 1792)	E	HOSOI (1952): description, biology
	L3	FUKUDA et al. (1959): diagnosis
	L?	YOSHIMURA (1959): description (as <i>Hydrocycclus</i> sp. B)
	E, L1, L2, L3, P	HUANG & PU (1984): diagnosis, biology
	L?	HAYASHI (2008): diagnosis
	L1, L2, L3	HAYASHI (2009a): diagnosis

adults and by the exclusion of the species/genera not occurring in the area. The hydrophilid fauna of our collecting sites and the surrounding area of Shimane-ken have been extensively studied (e.g., HAYASHI 2006a,b, 2007, 2008, 2009a,b,c, KAWANO et al. 2006, HAYASHI et al. 2008) and is very well known. Larvae that could not be identified with confidence were not used for this study. A portion of the larvae examined were reared from egg cases collected in the field or laid by the identified adults. The way of identification is specified under each species treated in this study (see also table 3).

Study techniques. Most larvae were fixed in 70–99.5% ethanol in the field or laboratory. Dissected specimens (see below) were mounted on microscope slides with Euparal (Chroma-Gesellschaft, Schmid & Co., Germany) or were preserved in screw-cap vial with 80% ethanol. Additional specimens were preserved in screw-cap vials with 70–99.5% ethanol.

Table 3. Selected taxa and instars examined in this paper. Identification: **A** – reared from adults or egg case collected with adult females (*Helochares*); **B** – reared from egg case collected in the field, and associated with adults; **C** – collected in the field and associated with adults; **L1, L2, L3** – larva of first, second, or third instars.

Species	L1	L2	L3
<i>Agraphydrus narusei</i> (Satô, 1960)	B	C	C
<i>Enochrus (Holcophilydrus) simulans</i> (Sharp, 1873)	B	C	C
<i>Enochrus (Holcophilydrus) umbratus</i> Sharp, 1884			C
<i>Enochrus (Methydrus) japonicus</i> (Sharp, 1873)	C	C	C
<i>Helochares (Helochares) pallens</i> (MacLeay, 1825)	A	C	C
<i>Helochares (Hydrobaticus) anchoralis</i> Sharp, 1890	A		
<i>Helochares (Hydrobaticus) nipponicus</i> Hebauer, 1995	A	C	C
<i>Hydrobius pauper</i> Sharp, 1884		C	C
<i>Hydrochara affinis</i> (Sharp, 1873)	B		C
<i>Hydrophilus (Hydrophilus) acuminatus</i> Motschulsky, 1854	B	C	C
<i>Sternolophus (Sternolophus) rufipes</i> (Fabricius, 1792)	C	C	C

At the beginning of the dissection, each larva was decapitated with tweezers; in large specimens, the body was also divided between abdominal segments 4 and 5. Specimens were then soaked with a 10% KOH solution for about one day at room temperature (the precise time and temperature was adjusted according to the body size). They were subsequently rinsed with 80% ethanol, stained in lactic acid containing acid fuchsine and warmed in the liquid for about 90–120 minutes at 40–60°C. Then, stained samples were rinsed in 80% ethanol and dehydrated in 99% ethanol. Dissected parts were mounted on standard or concavity microscope slide (Matsunami Glass Ind., Ltd., Japan or Toshinriko Co. Ltd, Japan) or HS-slide (Higgins-Shirayama slide; SHIRAYAMA et al. 1993) (Kanto Rika Co., Ltd., Japan) with glycerol or Euparal for examination. We examined large larvae, e.g., third instar larvae of *Hydrophilus*, in glycerol (body parts) and in 80% ethanol (body). If larvae were covered in dirt or soil, it was removed with a brush.

Observations and dissections were carried out using Olympus SZ40 and SZX12 stereoscopic microscopes, and Olympus BX40 and Zeiss Axiophot compound light microscopes. Illustrations were made with the aid of a drawing tube attached to Nikon SMZ-800 stereomicroscope and Olympus BX40 and BH2 compound light microscope. Line drawings were prepared using the software Paint Tool SAI (Systemax Inc., Japan) and Photoshop CS3 and CS5 (Adobe Systems Inc., USA). Photographs were taken with digital cameras attached to microscopes or directly by plain cameras. Composite images were created using the software Image J (National Institutes of Health, USA) with focus stacking plug-ins of Extended Depth of Field, Stackreg and Turboreg (Biomedical Imaging Group, Swiss Federal Institute of Technology Lausanne, Switzerland), or Image Stacking Software CombineZP (HADLEY 2010). The photographs were retouched with Adobe Photoshop CS5 in needed cases.

Format of species descriptions and illustrations. The larval descriptions are divided into two parts: ‘general morphology’ and ‘chaetotaxy of the head’. General morphology contains

all the morphological characters except for the head chaetotaxy and is based on the third instar larvae. The third instar, i.e., the last larval instar of the Hydrophilidae, is the most appropriate to observe the general morphology due to the larger size and stronger sclerotisation, allowing the observation of characters which are hardly recognisable in the first instar. If the third instar was not available, we chose the latest available instar for the description. General morphology of early instars is only shortly compared with that of the third instar in the descriptions. The description of the head chaetotaxy is based on the first instar (primary chaetotaxy) for two reasons: (1) the nomenclature system of the head chaetotaxy of Hydrophilidae was established for the first instar larvae; (2) the larval chaetotaxy of the second and third instars contains secondary sensilla which make the homologisation difficult or impossible, and therefore inappropriate for the chaetotaxic study. The primary chaetotaxy is shortly compared with the head chaetotaxy of later instars (secondary chaetotaxy) in the most cases. When the first instar larva was not available for the study, we chose the earliest instar for the chaetotaxy descriptions; primary sensilla (i.e., those present already in the first instar larva) may often be distinguished from the secondary ones (i.e., those appearing only in later instars) even in second and third instar larvae. In such cases, both primary and secondary chaetotaxy is described and the primary sensilla are numbered using the usual abbreviations introduced by FIKÁČEK et al. (2008) (see below). In the cases when secondary sensilla form a group with the primary sensilla and the homology cannot be defined for each sensillum separately, we marked the group with the number of the respective primary sensilla and a question mark (e.g., '6?' or '5–6?', see Figs. 11D–E, 15F–G).

Terminology. For the morphological terminology we largely followed RICHMOND (1920), SPANGLER (1991), and ARCHANGELSKY (1997) (see Figs. 3–5). For the primary chaetotaxy of the larval head we refer to FIKÁČEK et al. (2008), BYTTEBIER & TORRES (2009), and TORRES et al. (2011). Taxonomic nomenclature largely follows HANSEN (1991, 1999), with the exception of the understanding of the tribe Hydrophilini – we follow here the changes made by SHORT & FIKÁČEK (2011) who elevated the former subtribes Hydrophilina, Acidocerina and Hydrobiusina *sensu* HANSEN (1991) to the tribal rank.

Abbreviations. The following abbreviations are used throughout the paper:

Material examined. **MH** – Masakazu Hayashi (collector of the specimens); **L1, L2, L3** – first, second, and third instar; **L?** – unknown instar; **YM** – Yûsuke Minoshima (collector of the specimens).

Collection acronyms. **EUMJ** – Ehime University Museum, Matsuyama, Japan (M. Sakai, H. Yoshitomi); **HGF** – Hoshizaki Green Foundation, Shimane, Japan (M. Hayashi); **SEHU** – Systematic Entomology, Hokkaido University, Sapporo, Japan (M. Ôhara).

Chaetotaxy descriptions. **AN** – antenna; **FR** – frontale; **gAN** – group of antennal sensilla; **gAPP** – group of sensilla on inner appendage of maxilla; **gFR** – group of sensilla on frontale; **gLA** – group of sensilla on labium; **gMX** – group of sensilla on maxilla; **LA** – labium; **MN** – mandible; **MX** – maxilla; **PA** – parietale; **SE** – sensorium; **■** – additional sensillum (see FIKÁČEK et al. 2008); **◆** – secondary sensillum.

3. General morphology of Japanese Acidocerini, Hydrobiusini and Hydrophilini

Body. The body is slender to rather thick (Figs. 1–3), with nine pairs of spiracles: one pair is on mesothorax and eight pairs are on abdominal segments 1 to 8; the mesothoracic and the first seven pairs of abdominal spiracles are non-functional, biforous; the last pair is annular, large and functional, and is enclosed within the spiracular atrium.

Head (Figs. 4A–C). *Head capsule* is generally quadrate in shape; some genera of the tribe Hydrophilini have different shapes: subcircular in *Hydrophilus* (Fig. 58A), subtrapezoidal and widest anteriorly in *Hydrochara* and *Sternolophus* (Figs. 54A, 62A). Frontal lines are V-shaped or lyriform (e.g., Figs. 9A, 16A, 62A) in most representatives, but are U-shaped in *Hydrophilus* (Fig. 58A). The frontal lines are distinct in the first and second instars but indistinct in the third instar. Body chaetotaxy usually consists of pores and hair-like setae; in *Agraphydrus* and *Helochares*, several setae on the head capsule, as well as on the thoracic and abdominal segments are long and scale-like (Figs. 7, 12C–D, 38).

The clypeolabrum (nasale and epistome) is variably shaped in different genera (sometimes the shape differs interspecifically). The shape of clypeolabrum may range from symmetrical to asymmetrical. The nasale bears several teeth or is irregularly serrate on the anterior margin in most genera (e.g., Figs. 7C, 13C); less commonly, the anterior margin is straight and lacking teeth (e.g., in *Hydrophilus*; Fig. 56C). The nasale of *Agraphydrus*, *Helochares*, *Hydrobius*, and *Sternolophus* bear a few (usually five or six) distinct teeth (e.g., Figs. 7C, 29C, 60C). The nasale of *Enochrus* and later instars of *Hydrochara* is serrate on the anterior margin (e.g., Figs. 13C, 55A) and in *Enochrus* the serrate nasale may also bear one or two teeth (e.g., Figs. 13C, 15A, 17A). Chaetotaxy of the nasale generally consists of six stout setae (gFR1). The epistomal lobes vary in shape between genera and may be rounded (e.g., *Helochares* and *Sternolophus*, Fig. 38C, 60C) or sharply pointed (e.g., *Enochrus*, e.g., Fig. 24A) and each epistomal lobe bears a group of sensilla (gFR2) usually consisting of variably shaped setae and pore-like sensilla.

Antenna (Fig. 4D) is trimerous (consisting of three ‘antennomeres’) in most species, or tetramerous (consisting of four ‘antennomeres’) only in the second and third instars of *Hydrophilus* (Figs. 59A–B; also see Conclusions). The shape and relative lengths of the antennomeres and sensorium (SE1) differs between instars and the shape of the scape drastically changes between first and second instars especially in *Hydrochara* (Figs. 53A, 55B, 65B). In general, the antenna of the first instar is stouter and relatively shorter than that of third instar (Fig. 65A).

Mandibles (Fig. 4E) may have between one to three inner (retinacular) teeth. Mandibles can be roughly divided into three groups: (1) symmetrical (the number and shape of the inner teeth are almost identical in both left and right mandible; e.g., Figs. 49B–C); (2) slightly asymmetrical (both mandibles bear the same number of inner teeth, but the shape and size of the teeth differ between the left and the right mandible; e.g., Figs. 33C–D); (3) asymmetrical (the number of teeth differs between the left and the right mandible; e.g., Figs. 11B–C). The shape and the number of inner teeth of the mandibles are useful taxonomic characters especially for the identification of genera.

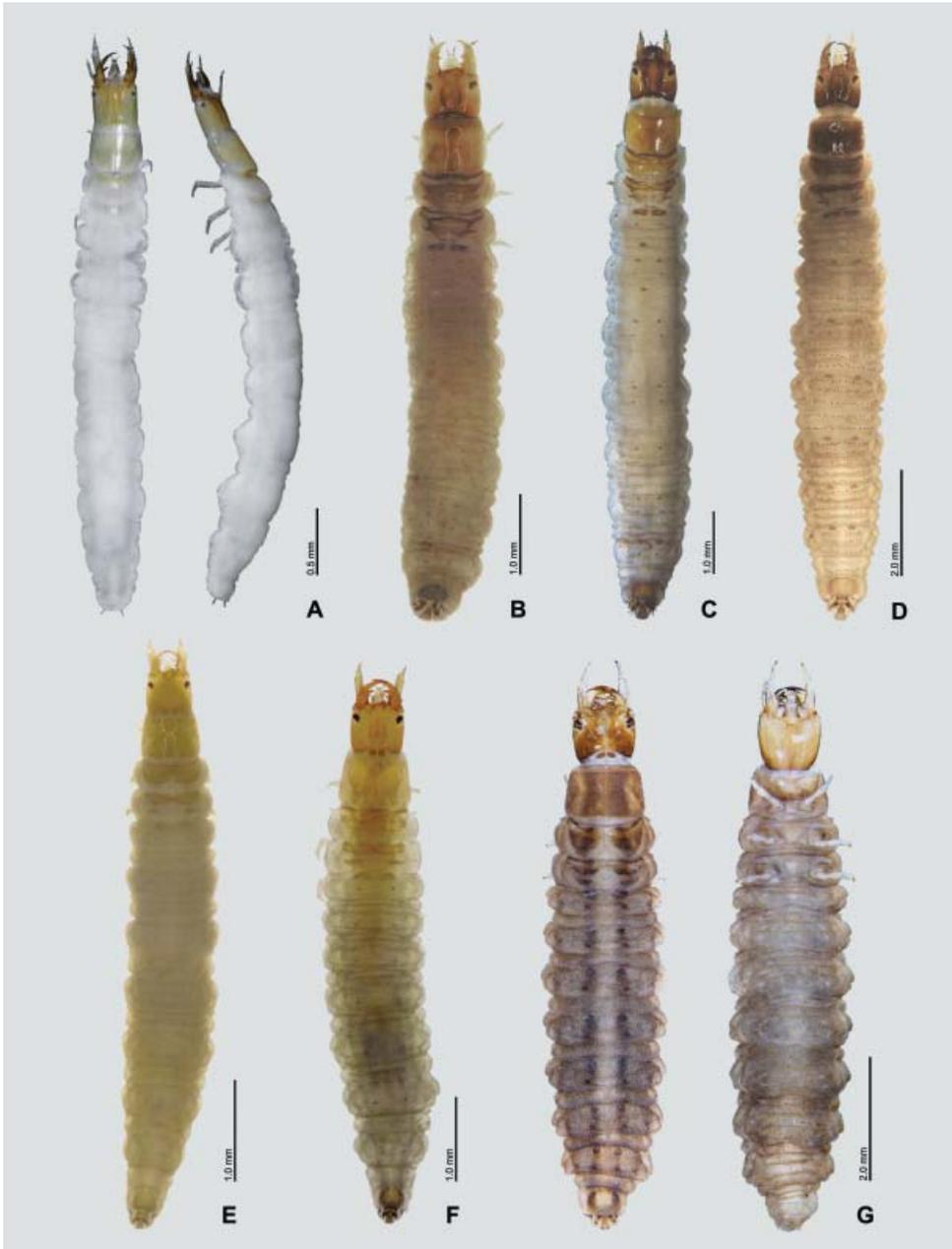


Fig. 1. Habitus of the third instar larvae of Acidocerini and Hydrobiusini. A – *Agropydrus narusei* (Satô, 1960), dorsal and lateral view; B – *Enochrus (Holcophilydrus) simulans* (Sharp, 1873), dorsal view; C – *E. (H.) umbratus* Sharp, 1884, dorsal view; D – *E. (Methydrus) japonicus* (Sharp, 1873), dorsal view; E – *Helochaes (Helochaes) pallens* (MacLeay, 1825), dorsal view; F – *H. (Hydrobaticus) nipponicus* Hebauer, 1995, dorsal view; G – *Hydrobius pauper* Sharp, 1884, dorsal and ventral view.



Fig. 2. Habitus of the larvae of Hydrophilini, dorsal view. A–B – *Hydrochara affinis* (Sharp, 1873): A – first instar; B – third instar. C – *Hydrophilus acuminatus* Motschulsky, 1854, third instar. D–E – *Sternolophus* (*Sternolophus*) *rufipes* (Fabricius, 1792): D – second instar; E – third instar.

Maxilla consists of 6 segments (Fig. 4F) and is composed of the cardo, stipes, and a 4-segmented palpus with a sclerotised inner process (inner appendage) on the first palpomere. The cardo is a small to moderately large, irregularly subtriangular sclerite. The stipes is cylindrical and bears five stout to rather stout primary setae on the inner face (MX7–11); a few species bear stout secondary setae on the inner face of the stipes in the second and third instars (e.g., Figs. 24E, 26E). A cuticular spine appears subdistally on the inner part of the sclerite of the stipes; only *Hydrobius* (as well as other representatives of the Hydrobiusini and Sperchopsini) bear the strong cuticular spine on the distal margin of the inner face of sclerite of stipes (Fig. 49D). The dorsal surface of palpomere 1 is completely sclerotised in most of the genera examined (Fig. 53D), but incompletely sclerotised e.g., in *Helochaeres*, *Agraphydrus* and *Hydrobius* (Fig. 49D). This character is quite difficult to observe in some cases because the border between the sclerite and the membrane is hardly recognisable, especially in weakly sclerotised larvae. The first palpomere bears a small sclerotised inner process on the inner face of the intersegmental membrane between palpomeres 1 and 2; a group of sensilla (gAPP) is situated in the apical membranous area of the process. The shapes of palpomeres 2–4 are variable; palpomere 2 is generally the shortest, palpomere 4 is the narrowest.

Labium (Figs. 4B, G): Submentum fused with the head capsule (Fig. 4B) but well defined by a suture. Mentum is generally subtrapezoidal; anterior corners of mentum project anteriorly in the tribe Hydrophilini (e.g., Figs. 55H, 61F); dorsal surface of the mentum bears tooth-like cuticular projections whose size ranges from large to small, and arrangement from

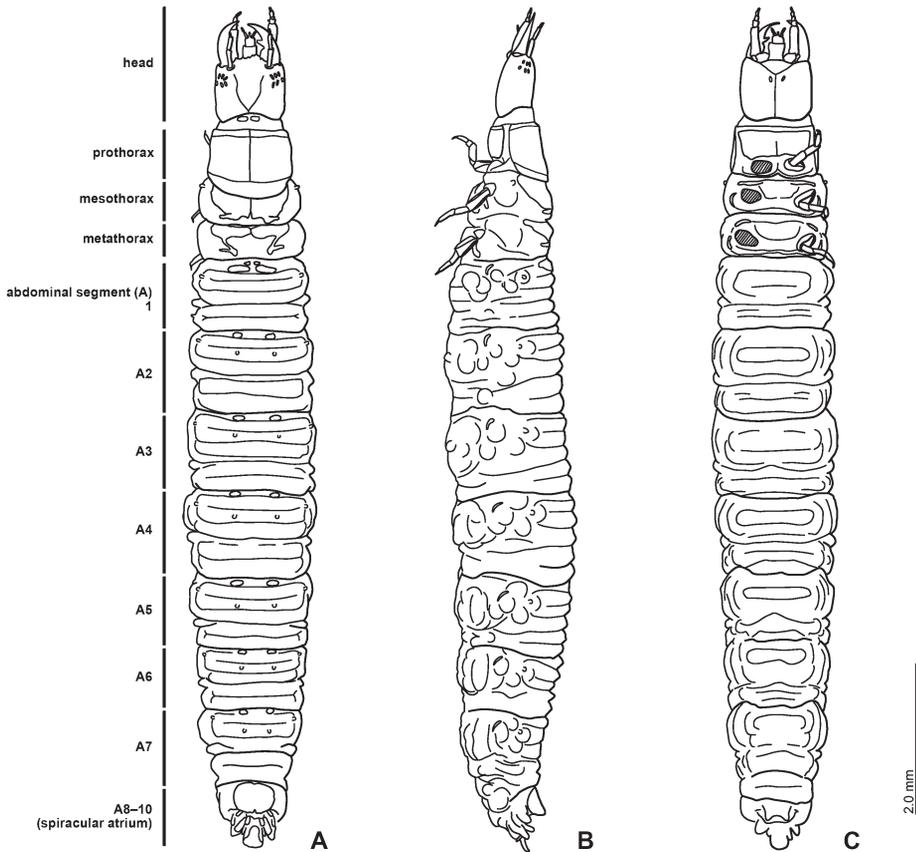


Fig. 3. Larva of *Enochrus japonicus* (Sharp, 1873) with basic morphological terms. A – dorsal view; B – lateral view; C – ventral view.

dense to sparse (e.g., Figs. 17G, 49F, 57F). Number of secondary setae on lateral portions of mentum may be of use for separation of the instars in *Enochrus* and *Helochares* species (see BYTTEBIER & TORRES (2009) for *Enochrus*, FERNÁNDEZ (2004) for *Helochares*). The prementum is slightly narrower than mentum in *Acidocerini* and *Hydrobiusini* (the mentum is less than twice as wide as the prementum; e.g., Figs. 17G–H), but much narrower than mentum in *Hydrophilini* (the mentum is at least twice as wide as the prementum; e.g., Fig. 55H). Ligula is well developed in all three tribes and is nearly completely or at least partially sclerotised. Labial palpus is 2-segmented; palpomere 1 is smaller than palpomere 2. Several species bear cuticular spines on intersegmental membrane between the prementum and the labial palpus, between palpomeres 1 and 2, and on the surface of palpomeres (e.g., *Helochares* and *Hydrobius*; Figs. 14F, 49F).

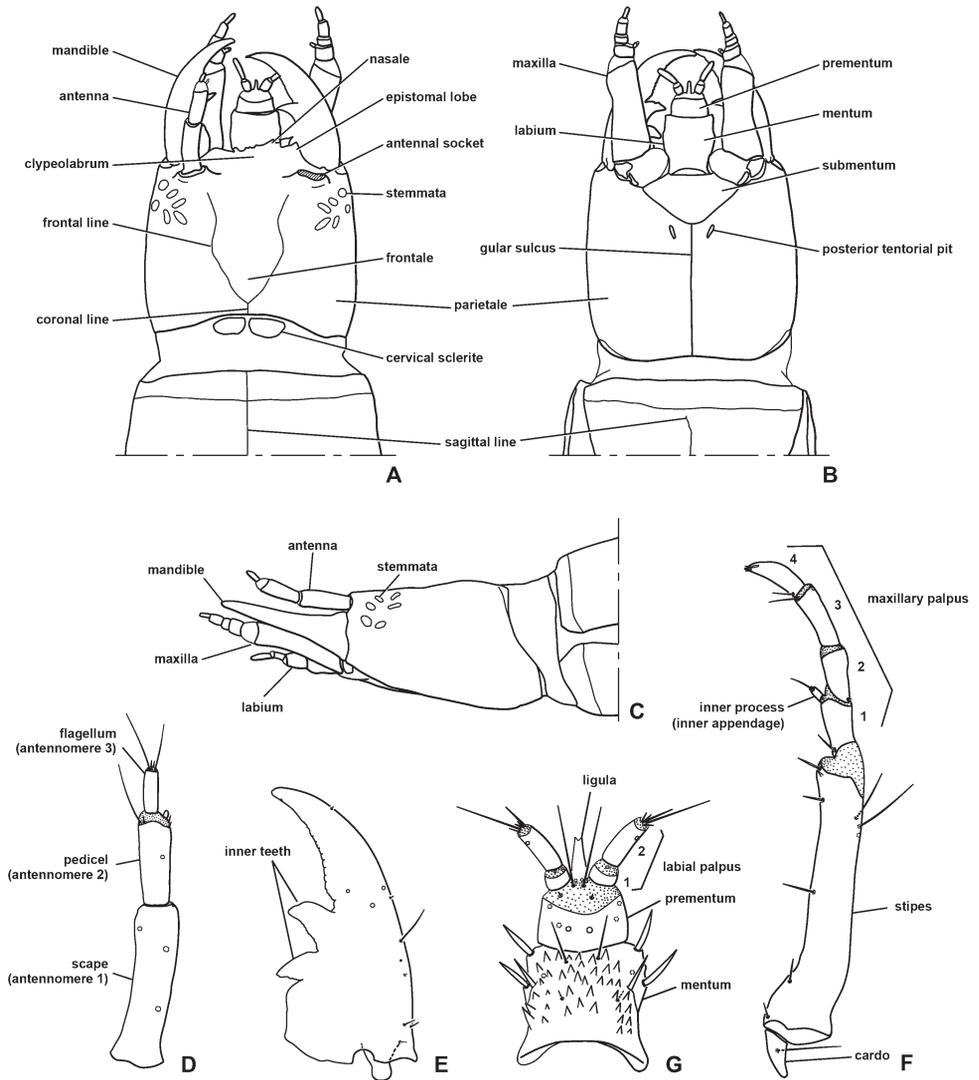


Fig. 4. General morphology of the head and mouthparts of the Acidocerini, Hydrobiusini and Hydrophilini. A–C – head and anterior part of thorax, schematic: A – dorsal view; B – ventral view; C – lateral view. D–G – head appendages, dorsal view: D – antenna; E – mandible; F – maxilla; G – labium (submentum omitted).

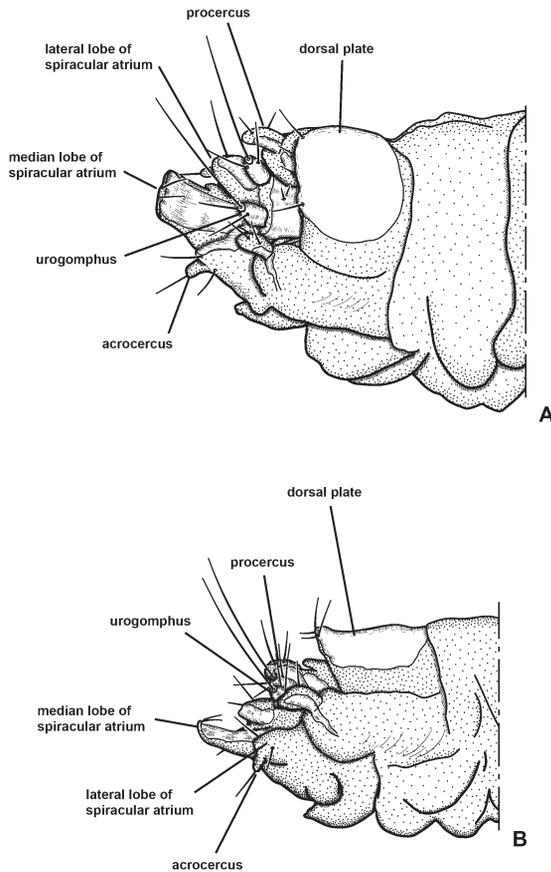


Fig. 5. Spiracular atrium of *Enochrus japonicus* (Sharp, 1873). A – dorsolateral view; B – lateral view.

Thorax. The morphology of thoracic segments is rather similar in most species examined. Colouration of thoracic segments is variable (Figs. 1–2). Proscutum is formed by a large plate subdivided by a fine sagittal line. Prosternum is developed as a large, subpentagonal to subtrapezoidal plate which is almost completely or incompletely subdivided by a fine sagittal line. Meso- and metathorax bear several dorsal sclerites, the largest sclerites on each side of the segment are irregularly-shaped, subtriangular or subtrapezoidal, remaining sclerites are very small (Figs. 6, 51).

Legs are 5-segmented and visible in dorsal view. Legs of the Hydrophilini are longer and bearing numerous long hair-like swimming setae (Figs. 64B–D); legs of Acidocerini and Hydrobiusini are short to moderately long and bearing short to long, sparsely arranged setae (Figs. 45, 50C).

Abdomen. Abdomen is 10-segmented, mostly membranous, tapering posteriad or almost parallel-sided (Fig. 3). Segments 8 to 10 form a spiracular atrium (Figs. 3, 5). Abdominal segments are rather similar in most examined species, especially in the species of the Acidocerini. In general, each abdominal segment bears one to three small dorsal sclerites and one small lateral sclerite on each side (Figs. 3, 6). Each abdominal segments of the Hydrophilini bears a pair of well defined setiferous lateral projections of variable length; the projections of *Hydrochara* are moderately to very long (Fig. 51A). Larvae of the genera *Agraphydrus*, *Chasmogenus* and *Enochrus* bear spinose prolegs on ventral surface of abdominal segments 3 to 7 (Figs. 12A–B, 28; ANDERSON 1976); the prolegs vary among species in the shape of the spines, being either narrow to stout or straight to curved.

Spiracular atrium (Fig. 5) consists of the following structures: dorsal plate, a pair of procerci and urogomphi, median lobe of spiracular atrium, lateral lobes of spiracular atrium, a pair of acrocerci and prostyli. Most species have a single dorsal plate on the abdominal segment 8 (e.g., Figs. 5, 9B); the dorsal plate of *Hydrophilus* is subdivided into two isolated sclerites (Fig. 58B). Shape of the posterior margin of dorsal sclerite is variable, e.g., almost rounded in *Enochrus* (e.g., Fig. 25B), quadrilobate in *Hydrochara* (Fig. 54B). Prostyli are reduced or absent in the most species, only *Hydrochara* and *Hydrophilus* have long, membranous prostyli (Figs. 54B, 58B). Abdominal segment 10 is reduced, situated on the ventral surface of the spiracular atrium.

4. Systematics

4.1. Tribe Acidocerini

Diagnosis. Dorsal surface of head capsule without densely arranged, strong tooth-like cuticular projections (Figs. 9A, 25A, 35A). Frontal lines V-shaped to lyriform, converging towards base of head capsule (Figs. 9A, 16A, 29A); coronal line present. Epistomal lobes not or moderately extended anteriorly, setation of lobes on both sides more or less similar (e.g., Figs. 10C, 24A, 29C). Shape of nasale variable (serrate or with at least two teeth; Figs. 7C, 13C, 29C, 40A), never with a single median tooth. Inner face of scape bare, without inner projection or seta. Sensorium (SE1) on intersegmental membrane between scape and pedicel (Figs. 11A, 24B, 30A, 40B). Stipes with one to several cuticular projections, never with densely arranged cuticular projections on most of inner face (Figs. 11D–E, 15F–G, 31E–F). Labium without well developed hypopharyngeal lobe; mentum less than twice as wide as prementum (Fig. 26G); anterior corners of mentum not projecting anteriad (Figs. 26G, 30F). Ligula well developed (e.g., Figs. 8F, 21F, 30F). Anterior margin of proscutum without fringe of long setae (e.g., Figs. 6, 51). Proscutum without lateral lobes. Legs moderately short to rather long, well developed, without fringes of long swimming hairs (Fig. 45). Abdominal segments without lateral projection and tracheal gills (Figs. 3, 6). Ventral surface with or without spinose prolegs. Median lobe of spiracular atrium simple, entire; prostyli reduced (Figs. 5, 9B, 25B, 32B).

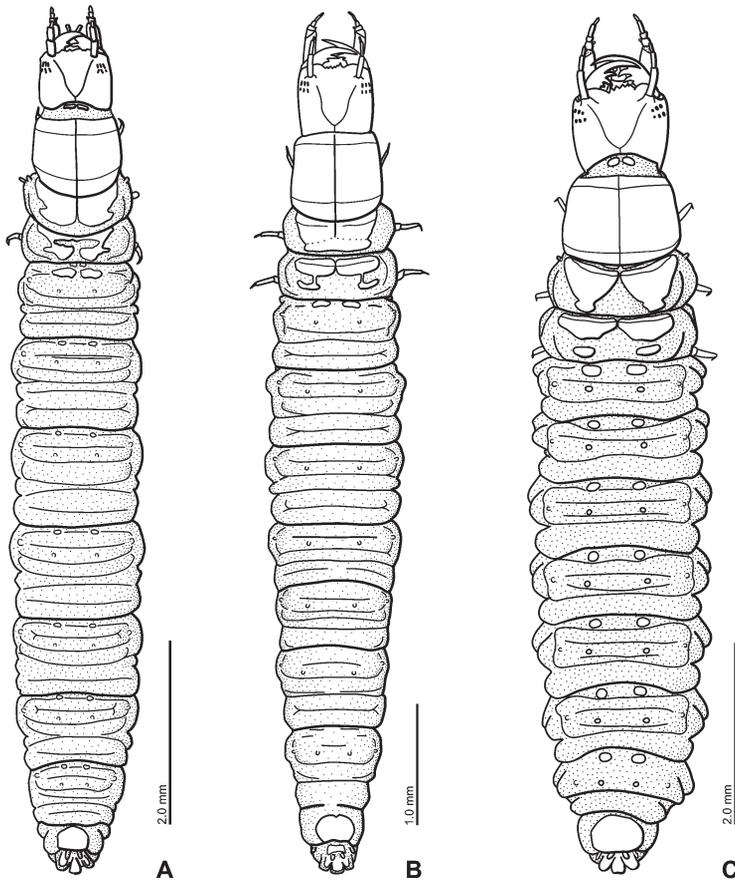


Fig. 6. Habitus of third instar larvae of the Acidocerini and Hydrobiusini, dorsal view. A – *Enochrus umbratus* Sharp, 1884; B – *Helochaeres nipponicus* Hebauer, 1995; C – *Hydrobius pauper* Sharp, 1884.

Key to the genera of the tribe Acidocerini from Japan (all instars)

Larvae of the Japanese species of *Chasmogenus* Sharp, 1882 are still unknown, therefore, we refer to ANDERSON (1976) for the genus; larvae of the genus *Megagraphydrus* Hansen, 1999 are also still unknown (see Table 1).

1. Mandibles only slightly asymmetrical, both mandibles similar in shape, bearing two inner teeth (Figs. 30B–C); ventral surface of abdomen without spinose prolegs. *Helochaeres* Mulsant, 1844
- Mandibles strongly asymmetrical, left mandible with one inner tooth, right mandible with two inner teeth (Figs. 24C–D); ventral surface of abdomen with spinose prolegs (Figs. 12A–B, 28). 2
2. Nasale serrate on anterior margin, with only one or two lateral teeth (Fig. 24A). *Enochrus* Thomson, 1859

- Nasale with more than two distinct teeth, without serrate anterior margin (Figs. 7C, 10C). 3
3. Nasale strongly asymmetrical (Figs. 7C, 10C). *Agraphydrus* Régimbart, 1903
- Nasale almost symmetrical (ANDERSON 1976: Fig. 9).
..... *Chasmogenus* Sharp, 1882

Genus *Agraphydrus* Régimbart, 1903

(Figs. 1A, 7–12, 44A, 45A)

Diagnosis. The genus *Agraphydrus* is similar to other genera of the Japanese Acidocerini, but is distinguished from them by the following characters: (1) head capsule with long scale-like setae (Figs. 7, 9A, 10, 12C); (2) nasale with distinct teeth, not serrate or smooth (Figs. 7C, 10C); (3) antennal sensorium (SE1) rather long (Figs. 8A, 11A); (4) mandibles asymmetrical, left mandible with one inner tooth, right mandible with two teeth (Figs. 8B–C, 11B–C); (5) abdominal segments with spinose prolegs (Figs. 12A–B).

***Agraphydrus narusei* (Satô, 1960)**

(Figs. 1A, 7–12, 44A, 45A)

Material examined. JAPAN: HONSHÛ: Shimane-ken: 14 L1, Inome, Inome-chô, Izumo-shi, 7.vi.2008 (egg cases collected in the field), 9.vi.2008 (date of fixation), MH; 2 L1, same locality, 22.vii.2008, MH; 2 L3, same locality, 29.vii.2008, MH; 1 L1, downstream of Inome-gawa river, Inome-chô, Izumo-shi, 7.vi.2008, MH.

General morphology. Third instar. *Body* slender, almost parallel-sided (Fig. 1A). *Colour.* Head and sclerotised parts light yellowish brown; membranous parts milky white (Fig. 1A).

Head (Fig. 9A). Head capsule subquadrate. Frontal lines V-shaped, fused at base of head capsule, coronal line short. Surface of head capsule smooth. Six stemmata closely aggregated on each anterolateral portion of head capsule. Clypeolabrum asymmetrical. Nasale with six teeth, three on right side more closely aggregated and projecting further than three on left. Epistomal lobes asymmetrical, not projecting further than nasale; each epistomal lobe emarginate medially, right lobe projecting further than left lobe.

Antenna (Fig. 11A) 3-segmented, slender. Scape slightly longer than pedicel. Flagellum the shortest, small.

Mandibles (Figs. 11B–C) asymmetrical; right mandible with two inner teeth, distal one large, slightly bifurcated at apex, weakly serrate on margins, basal one small; inner face of right mandibular apex weakly serrate. Left mandible with one large inner tooth, slightly bifurcated at apex, weakly serrate around margin; inner face of left mandibular apex serrate.

Maxilla (Figs. 11D–E) 6-segmented (including cardo), distinctly longer than antenna. Cardo small, irregularly shaped. Stipes the longest, longer than palpomeres 1–4 combined; a small spine-like cuticular projection on apical part of inner face of stipes. Maxillary palpus 4-segmented; palpomere 1 the widest, incompletely sclerotised on dorsal surface; palpomere 2 the shortest, slightly shorter than palpomere 4, wider than palpomeres 3 and 4; palpomere 3 longer and wider than palpomere 4, narrower than palpomere 2; inner process largely sclerotised.

Labium (Figs. 10B, 11F–G) well developed. Submentum (Fig. 10B) fused to head capsule, large, subpentagonal, wider than mentum. Mentum subquadrate, longer and wider than prementum, with dense and rather short cuticular spines on dorsal surface. Prementum subtrapezoidal. Ligula shorter than labial palpi, largely sclerotised. Labial palpi about as long as prementum.

Thorax. Prothorax wider than head capsule (Fig. 1A). Proscutum formed by a large plate subdivided by fine sagittal line, with scale-like setae, anterior and posterior margins weakly sclerotised. Prosternum subpentagonal, with incomplete, short, fine sagittal line in basal half (Fig. 44A). Mesonotum with incomplete sagittal line, with two dorsal sclerites on each side; anterior sclerite small, narrow, posterior sclerite large, each sclerite with long to short setae, some of setae scale-like (e.g., Fig. 12D). Metanotum with one large dorsal sclerite on each side, with very to moderately long setae, some of them scale-like in shape. Legs rather short, visible in dorsal view, 5-segmented, bearing short as well as moderately long setae, lacking swimming hairs (Fig. 45A); all three pairs similar in shape.

Abdomen. Abdomen 10-segmented, almost parallel-sided, covered with fine pubescence on membranous parts; segments 1 to 7 similar in shape and size (Fig. 1A). Abdomen mostly membranous, dorsal and lateral sclerites undetectable, dorsal sclerites slightly visible on first segment only; abdominal segments 1 to 7 with scale-like setae on each side, four very long setae situated on posterior half; segments 3 to 7 with spinose prolegs, spines of prolegs stout and curved (Fig. 12B).

Spiracular atrium (Fig. 9B): Segment 8 with oval dorsal plate bearing three setae on each side: two very long on lateral margin, one rather short on median part; one very long seta on each side of segment 8. Posterior edge of dorsal plate almost rounded, median part with two small projections bearing two short setae; procercus incompletely sclerotised, bearing two rather short setae and one long seta. Segment 9 trilobed, partially sclerotised; each lateral lobe with rather short, membranous acrocercus bearing one long seta apically; urogomphi short, one segmented, with one very long seta on apical membranous area; prostyli reduced.

First instar. Similar to third instar larva, more weakly sclerotised than in third instar.

Head (Fig. 7). Right epistomal lobe weakly emarginate medially; left epistomal lobe strongly projecting and sharply pointed apically.

Antenna short, stout (Fig. 8A); stouter than in third instar. Scape about as long as pedicel.

Mandibles (Figs. 8B–C): Distal inner tooth of right mandible serrate on margin; inner face of right mandibular apex serrate; inner tooth of left mandible serrate on margins.

Maxilla (Figs. 8D–E): Maxillary palpomere 2 the shortest, palpomere 3 as long as palpomere 4, palpomere 4 longer than palpomeres 1 and 2.

Labium (Figs. 8F–G): Prementum about as long as mentum.

Thorax. Mesonotal plate with one long, scale-like seta, and four very long and two moderately long trichoid setae on each sclerite; metanotal plate with one long, scale-like seta, and three very long and one or two long trichoid setae on each sclerite.

Primary chaetotaxy of head. *Frontale* altogether with 41 sensilla (Figs. 7A, C). Central part with three pairs of sensilla divergent posteriad; FR1 rather short seta close to frontal line; FR2 pore-like, situated anteromesally to FR1 at midlength between FR1 and FR3; FR3 short seta, situated even more anteriorly and slightly more mesally than FR2. Moderately

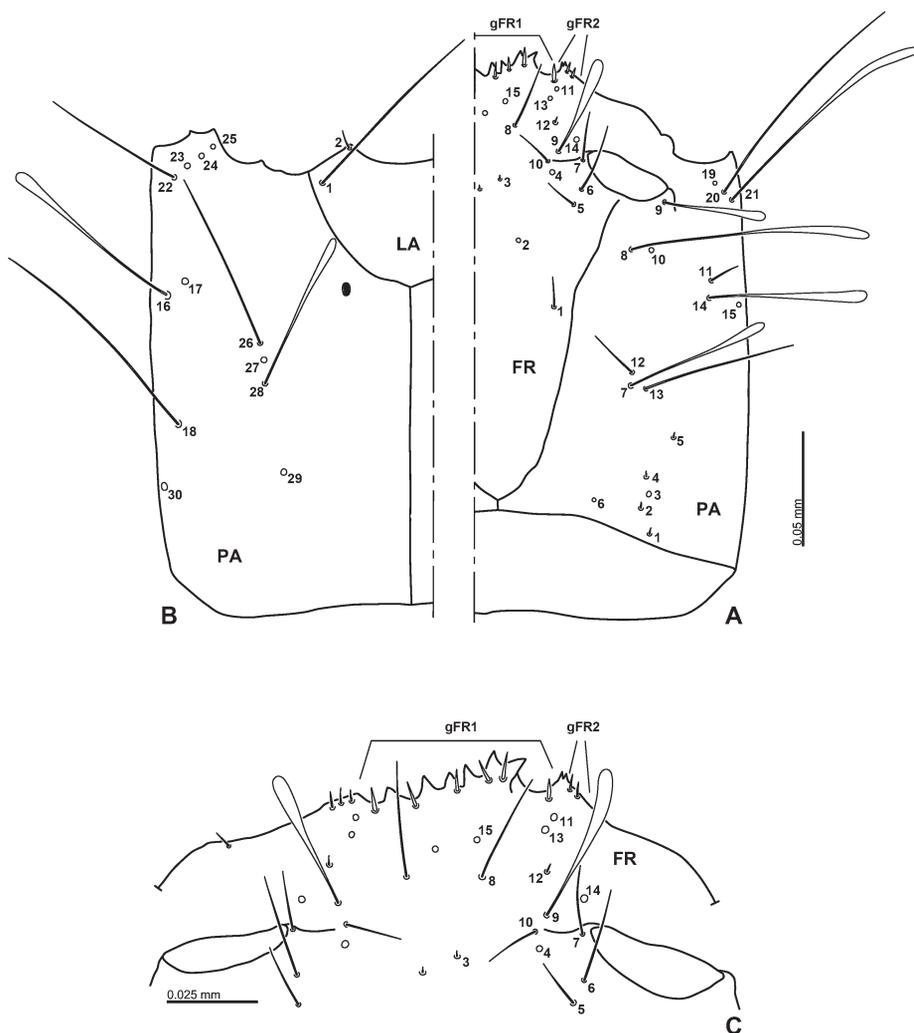


Fig. 7. Head capsule of *Agraphydrus narusei* (Satô, 1960), first instar. A – dorsal view; B – ventral view; C – detail of anterior margin of head capsule, dorsal view.

long setae (FR5–6) and pore-like sensillum FR4 situated slightly posteromesally to antennal socket; FR6 longer than FR5. Seta FR7 moderately long, close to inner margin of antennal socket; FR4, FR6 and FR7 forming a triangular group. Nasale with a group of six stout, short setae (gFR1), lateral-most seta on each side placed in grooves between nasale and epistomal lobes. Epistomal lobes altogether with five setae (gFR2); right lobe with two short setae; left lobe with three short setae, inner one slightly shorter than remaining ones. FR15 pore-like, situated posteriorly to median setae of nasale; seta FR8 long, situated posteriorly to FR15. Two setae (FR9 and FR12) and one pore-like sensillum (FR14) forming a triangular group

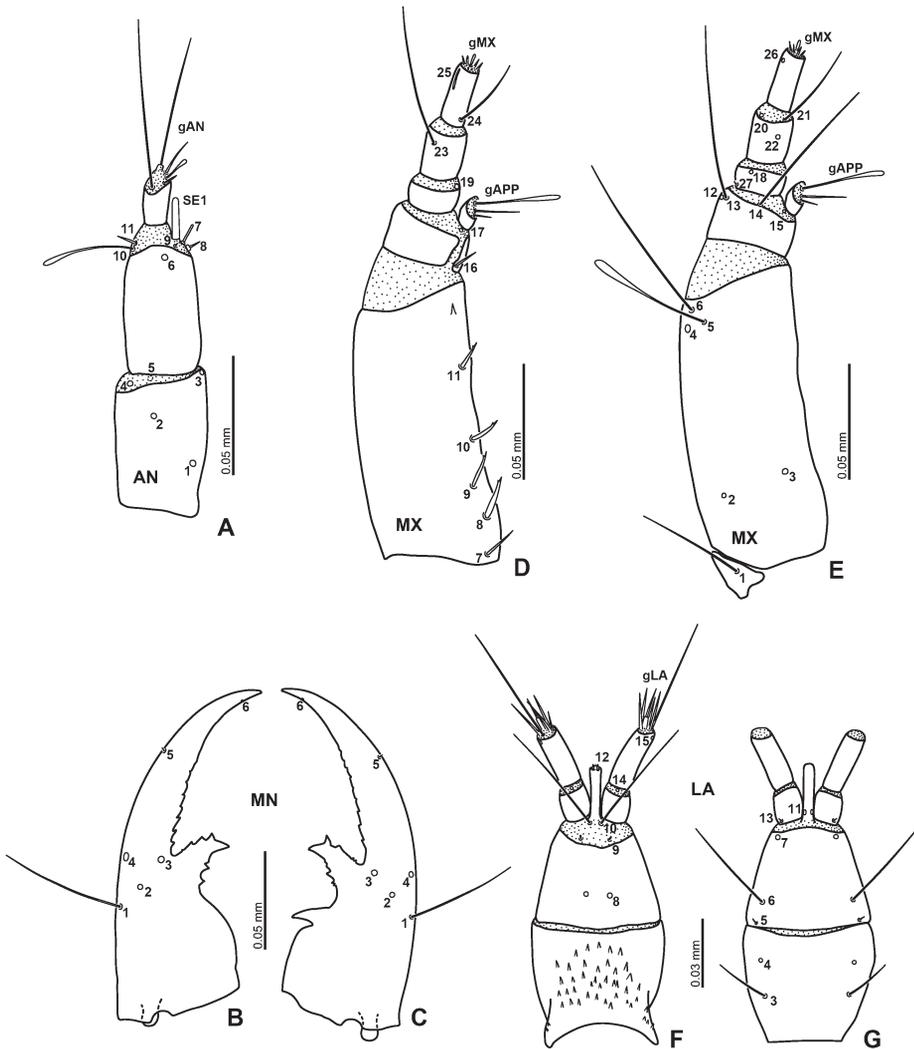


Fig. 8. Head appendages of *Agraphydrus narusei* (Satô, 1960), first instar. A – antenna, dorsal view; B–C – mandibles, dorsal view; D – maxilla, dorsal view; E – maxilla, ventral view; F – labium, dorsal view; G – labium, ventral view.

situated medioanteriorly to antennal socket; FR9 long, scale-like; FR12 short, stout. Seta FR10 rather long, placed slightly anteriorly to FR4; FR12 at midlength between FR9 and FR13. Inner part of epistomal lobes with two pore-like sensilla (FR11 and FR13); FR11 situated anteriorly to FR13.

Parietale with 30 sensilla each (Figs. 7A–B). Posterior portion of dorsal surface with a group of four sensilla (PA 1–4) in longitudinal row at midwidth; PA3 pore-like, between short

setae PA2 and PA4; seta PA1 short, situated posteriorly to PA 2–4. Seta PA5 short, situated anterolaterally to PA1–4. PA6 pore-like, located posteromesally, more distant from posterior margin of head than PA1. PA7, PA12 and PA13 forming a closely aggregated triangular group located at midlength between antennal socket and posterior margin of head. Seta PA7 very long, scale-like (e.g., Fig. 12C); seta PA12 rather long; seta PA13 very long. PA8 and PA10 situated posteriorly to antennal socket; PA8 more closely to frontal line than PA10; seta PA8 very long, scale-like; sensillum PA10 pore-like, situated close to PA8. Seta PA9 long, scale-like, situated close to outer margin of antennal socket. Two pore-like sensilla (PA15 and PA17) and three setae (PA11, PA14, and PA16) situated laterally in anterior third of parietale; PA11 short, PA14 and PA16 very long, scale-like; PA16 longer than PA14; PA11, PA14, and PA15 situated more dorsally than PA16 and PA17. Anterior corner of head capsule with four pore-like sensilla (PA19 and PA23–25) and three long to very long setae (PA20–22); PA19–21 dorsolateral, PA22–25 ventrolateral; PA19 situated anteromesally to PA21, PA20 very long, trichoid, between PA19 and PA21, PA21 very long, scale-like; PA22 long, trichoid, PA25 situated anteromesally to PA22–24, close to ventral mandibular acetabulum; PA24 at midlength between PA25 and PA23; PA23 at midlength between PA22. Seta PA18 very long, located laterally on posterior third of parietale. Two setae (PA26 and PA28) and pore-like sensillum PA27 situated at midlength of parietale on ventral surface; PA26 very long, trichoid; PA28 very long, scale-like; PA27 at midlength between PA 26 and PA28. Pore-like sensilla PA29 located ventrally on posterior fourth of parietale, behind PA28; pore-like sensilla PA30 located laterally on posterior third of parietale, behind PA18.

Antenna (Fig. 8A): Antennomere 1 with five pore-like sensilla (AN1–5); AN1 situated on basal 0.36 of dorsolateral face, AN2 on distal third of dorsal surface; AN3–5 on distal margin, AN3 lateral, AN4 on inner face, AN5 ventral. Antennomere 2 with one pore-like sensillum (AN6) situated dorsally close to distal margin of sclerite and five setae (AN7–11) on intersegmentary membrane between antennomeres 2 and 3; AN7 short, rounded apically, AN8 short, rather stout, AN9 minute; AN7–9 on outer face of antenna next to sensorium (SE1); setae AN10–11 on inner face of antenna; AN10 long, scale-like, AN11 short, stout, both setae close to each other. SE1 rather large, slightly shorter than antennomere 3. Antennomere 3 with five setae (gAN) on apical membranous area: two long and three short setae.

Mandible (Figs. 8B–C) with two setae (MN1 and MN5) and four pore-like sensilla (MN2–4 and MN6). MN1 long, on outer face of mandible. Sensilla MN2–4 pore-like, forming a triangular group at midlength of dorsal surface; MN2 at midlength between MN1 and MN3; MN4 on lateral face. Seta MN5 minute, situated at midlength of outer mandibular face between MN4 and MN6. MN6 situated subapically on inner face of mandible.

Maxilla (Figs. 8D–E): Cardo with one long ventral seta (MX1). Stipes with a row of five rather short, stout setae (MX7–11) situated dorsally along inner face; MX7–11 equidistant, MX11 more distant than MX7–11 from each other; MX8–11 with small subapical tooth. Stipes with two pore-like sensilla (MX2 and MX3) situated ventrally on about basal fourth; three sensilla (MX4–6) situated subapically on outer face; MX4 pore-like sensillum, MX5 long, scale-like seta, MX6 long, trichoid seta. Palpomere 1 with one moderately short spiniform seta (MX16) situated basally on dorsal inner face, and with pore-like sensillum (MX12) and two long setae (MX13–14) on ventral surface; MX13 on outer face of anterior corner; MX14

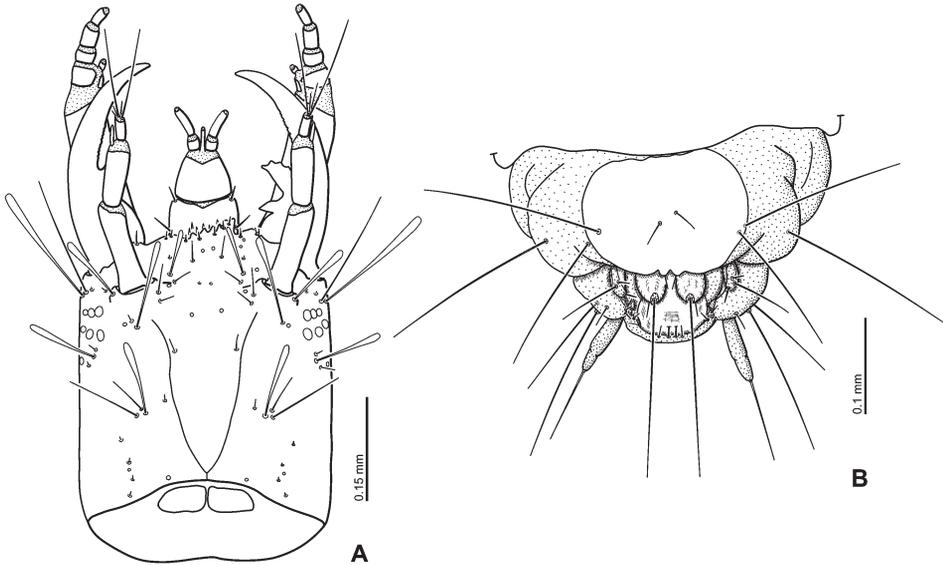


Fig. 9. *Agraphydrus narusei* (Satô, 1960), third instar. A – head, dorsal view; B – spiracular atrium, dorsal view.

between MX13 and MX15. Two pore-like sensilla (MX15 and MX17) on membrane behind inner appendage; MX17 dorsal, MX15 ventral. Inner appendage with one long, scale-like seta and two trichoid setae (gAPP). Palpomere 2 with two pore-like sensilla (MX18–19) and a minute seta (MX27); MX18 ventral, MX19 dorsal; MX27 on outer face of posterolateral corner. Palpomere 3 with one very long seta at midlength of dorsal surface, and with two pore-like sensilla (MX20 and MX22) and one long, trichoid seta (MX21) on ventral surface; MX22 at midlength of ventral surface, MX20 and MX21 close to distal margin of sclerite. Palpomere 4 with one long seta (MX24) on inner face of basal part, and with a digitiform sensillum (MX25) and a pore-like sensillum (MX26) situated subapically on outer face of sclerite; MX25 dorsal, MX26 ventral. Apical membranous area of palpomere 4 with several minute setae (gMX).

Labium (Figs. 7B, 8F–G): Submentum (Fig. 7B) with two pairs of setae (LA1–2); LA1 very long in lateral corners, LA2 short on anterior lobes (Fig. 7B). Ventral surface of mentum with two pairs of sensilla (LA3 and LA4) on lateral part; LA3 rather long seta in posterior two-fifths; LA4 pore-like sensilla in anterior third. Dorsal surface of prementum with one pair of pore-like sensilla (LA8) at midwidth in posterior two-fifths of sclerite. Ventral surface of prementum with three pairs of sensilla close to lateral face; seta LA5 short, on posterolateral corner; LA6 long, situated anteriorly to LA5; LA7 pore-like, close to distal margin of sclerite. Membrane between prementum and palpi with one pair of long setae (LA10) on base of ligula, and one pair of minute setae (LA9) close to distal margin of sclerotised part of

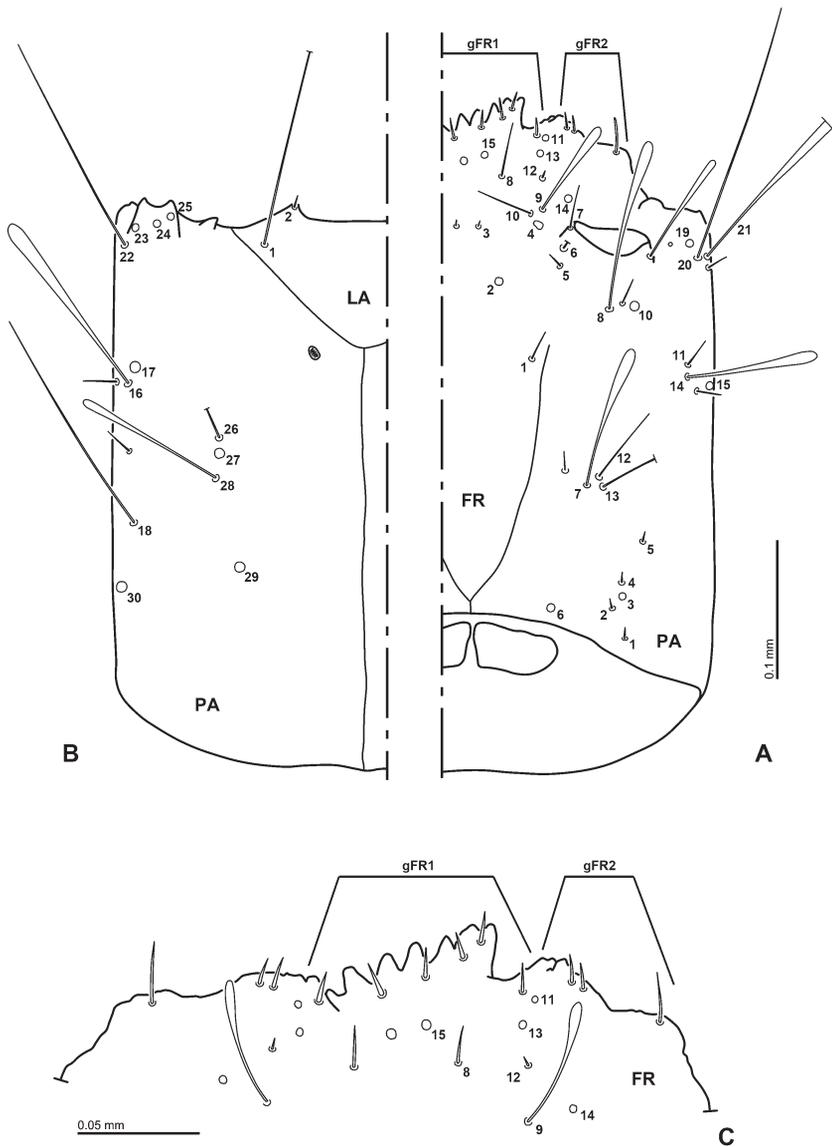


Fig. 10. Head capsule of *Agraphydrus narusei* (Satô, 1960), third instar. A – dorsal view; B – ventral view; C – detail of anterior margin of head capsule, dorsal view.

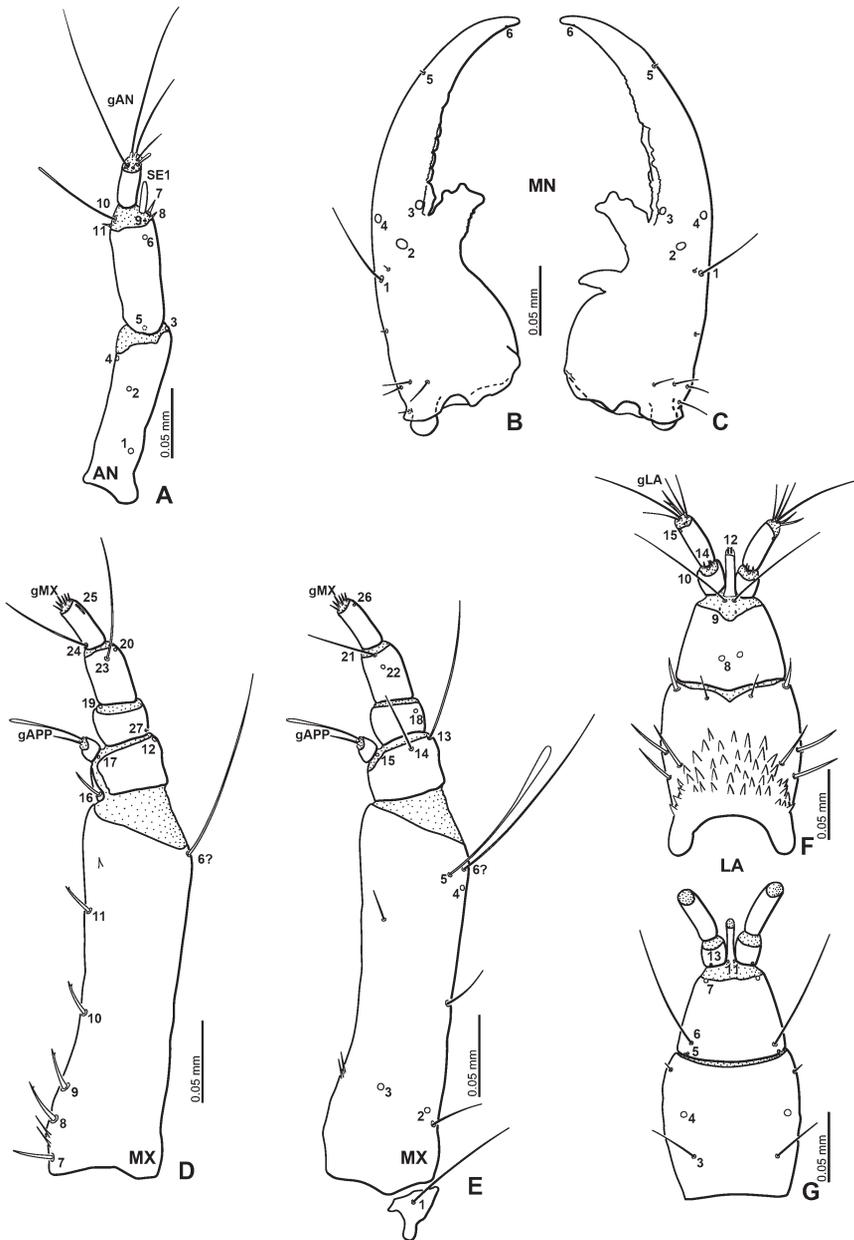


Fig. 11. Head appendages of *Agraphydrus narusei* (Satô, 1960), third instar. A – antenna, dorsal view; B–C – mandibles, dorsal view; D – maxilla, dorsal view; E – maxilla, ventral view; F – labium, dorsal view; G – labium, ventral view.

prementum. Ligula with one pair of small seta-like sensilla (LA12) on apical part, and with one pair of pore-like sensilla (LA11) in basal part of ventral surface. Palpomere 1 with one minute seta (LA13) in basal part of outer face; LA14 situated dorsally on intersegmentary membrane between palpomeres 1 and 2. Palpomere 2 with one pore-like sensillum (PA15) situated subapically on outer face. Apical membranous area of palpomere 2 with one long seta and five moderately long setae (gLA).

Secondary chaetotaxy of head. Third instar. Parietale (Figs. 10A–B): One rather short secondary seta close to frontal line, at midlength between PA6 and PA8 but mesally of line connecting PA6 and PA8. One rather long secondary seta situated close to PA8, anteriorly to line connecting PA8 and PA10. One rather long secondary seta and one pore-like secondary sensillum close to outer margin of antennal socket, seta close to PA9, pore-like sensillum close to PA19. One rather short secondary seta situated posteriorly to PA21; one rather long secondary seta situated at midlength between PA14 and PA15, but posteriorly to line connecting PA14 and PA15. One pore-like secondary sensillum close to PA16; one rather long secondary seta between PA16 and PA18, close to PA18.

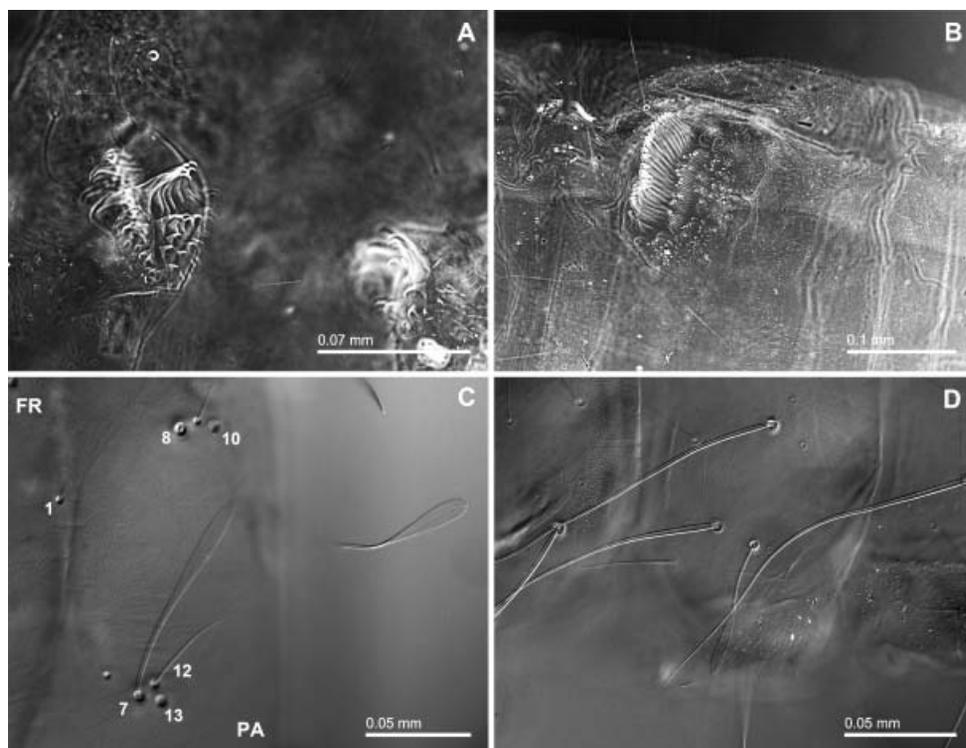


Fig. 12. *Agraphydrus narusei* (Satô, 1960). A–B – prolegs, ventral view: A – first instar; B – third instar. C–D – shape of setae, dorsal view: C – median part of parietale, third instar, dorsal view; D – thoracic segments, first instar, dorsal view. Seta on PA8 and PA13 missing. Photographs were taken with compound light microscope.

Mandible (Figs. 11B–C): Outer face of mandible with two short secondary setae, one close to MN1, one posterior to MN1; basal part of mandible with four rather short secondary setae on outer part.

Maxilla (Figs. 11D–E): Outer face of stipes with three trichoid secondary setae, one very long on distal part, one rather long in basal two-thirds. One rather short secondary seta on inner part of ventral surface, in distal fourth.

Labium: Dorsal surface of mentum (Fig. 11F) with four rather short, stout secondary setae on lateral portion, one on distal margin, three on median part; one pair of rather short secondary setae situated medially on distal margin of dorsal surface of mentum; one short secondary seta situated ventrally in anterior corner of ventral surface of mentum (Fig. 11G).

Habitat. Running water. Egg cases were found on the undersides of rocks. Larvae were found under rocks on the wet ground next to streams. It is possible that they live above the water level (HAYASHI 2009a).

Identification. Three species of *Agraphydrus* are known from Japan, one in the Ryūkyū Islands (SW Japan), two in Honshū, Shikoku and Kyūshū. Only one species of *Agraphydrus*, *A. narusei* was collected from the collecting sites together with the larvae used for the above description. This species usually co-occurs with representatives of the genera: *Hydrocassis* Fairmaire, 1878 (tribe Sperchopsini), *Crenitis* Bedel, 1881 (tribe Anacaenini) and *Laccobius* Erichson, 1837 (tribe Laccobiini) whose larvae are easily distinguishable from the *Agraphydrus* larvae (BØVING & HENRIKSEN 1938; MORIOKA 1955; BERTRAND 1972, 1977; ARCHANGELSKY 1997; ARCHANGELSKY & FIKÁČEK 2004).

Genus *Chasmogenus* Sharp, 1882

Note. Two species of the genus *Chasmogenus* are known from Japan, but immature stages of these Japanese species are unknown. However, judging from a description of *C. nitescens* (Fauvel, 1883) from Australia (ANDERSON 1976, as '*Helochares nitescens*'; described mainly according to third instar larvae), the third instar larvae of *Chasmogenus* should be distinguished from the larvae of remaining Japanese Acidocerini by the following characters: (1) frontal lines V-shaped; (2) clypeolabrum almost symmetrical (ANDERSON 1976: Fig. 9); (3) nasale with five equally large teeth, almost symmetrical (ANDERSON 1976: Fig. 9); (4) mandibles asymmetrical, left mandible with one tooth, right mandible with two teeth (ANDERSON 1976: Fig. 9); (5) abdominal segments with spinose prolegs.

Genus *Enochrus* Thomson, 1859

(Figs. 1B–D, 3, 5, 6A, 13–28, 44B, 45B, 65A, 66A–C, 67A)

Species examined. *Enochrus* (*Holcophilydrus*) *simulans* (Sharp, 1873) (L1–3), *Enochrus* (*Holcophilydrus*) *umbratus* Sharp, 1884 (L3), *Enochrus* (*Methydrus*) *japonicus* (Sharp, 1873) (L1–3).

Diagnosis. Larvae of the genus *Enochrus* are similar to other genera of the Japanese Acidocerini, but may be distinguished from them by the following characters: 1) head capsule without

long scale-like setae; 2) nasale serrate (Figs. 13C, 26A); 3) antennal sensorium (SE1) rather long (in first instar; Fig. 14A) to small (in third instar; Fig. 17B); 4) mandibles asymmetrical, left mandible with only one inner tooth or with one large and one small inner teeth (e.g., Figs. 17C–D); 5) abdominal segments with spinose prolegs (Fig. 28).

General morphology. *Body* slender, almost parallel-sided, widest between second and fourth abdominal segments (Fig. 6A).

Head. Head capsule subquadrate (Fig. 25A). Frontal lines nearly V-shaped (Fig. 13A) to weakly lyriform (Fig. 19A), fused at base of head capsule, coronal line short. Surface of head capsule smooth. Six stemmata on each anterolateral portion of head capsule. Clypeolabrum asymmetrical (Fig. 20C). Nasale serrate, sometimes with distinct tooth on both sides. Anterior margin of epistome asymmetrical, projecting anteriorly on inner portion, then straight to emarginate.

Antenna 3-segmented, short, stout (in first instar; Fig. 14A) to rather slender (in third instar; Fig. 17B) (Fig. 65A). Scape stout (first instar) to slender (third instar). Pedicel slightly shorter to longer than scape. Flagellum the shortest.

Mandibles asymmetrical (Figs. 17C–D, 26C–D); right mandible with two inner teeth of almost same size; left mandible with one large inner tooth.

Maxilla (Figs. 14D–E, 15F–G, 17E–F) 6-segmented (including cardo), distinctly longer than antenna. Cardo small, irregularly shaped. Stipes the longest, longer than palpomeres 1–4 combined; apical part of inner face with a small spine-like cuticular projection. Maxillary palpus 4-segmented; palpomere 1 the widest, completely sclerotised; inner process sclerotised.

Labium well developed (Figs. 13B, 14F–G, 15H–I, 17G–H). Submentum (e.g., Fig. 13B) fused to head capsule, large, subpentagonal, wider than mentum. Mentum subquadrate, wider and longer than prementum, with small cuticular spines on dorsal surface. Prementum subquadrate, with narrow, short cuticular spines on intersegmental membrane between prementum and labial palpomere 1, close to base of palpomere 1. Ligula small, distinctly shorter than labial palpi, largely sclerotised. Labial palpi 2-segmented, covered with short cuticular spines on intersegmental membrane and palpomere 2.

Thorax. Prothorax wider than head capsule (Fig. 6A). Proscutum formed by large plate subdivided by fine sagittal line, anterior and posterior margins weakly sclerotised. Presternum rectangular, incompletely divided by fine sagittal line (Fig. 44B). Mesonotum incompletely divided by fine sagittal line, with two dorsal sclerites on each side, anterior one small and narrow, posterior one large, with setae of variable length. Metanotum with one large dorsal sclerite on each side; anterior part larger than posterior part, each sclerite with setae of variable length. Legs short, visible in dorsal view, 5-segmented, bearing short to rather long stout setae, lacking swimming hairs (Figs. 45B–C); all three pairs similar in shape.

Abdomen. Abdomen (Fig. 6A) 10-segmented, almost parallel-sided, tapering towards posterior end. Segments 1 to 7 similar in size and shape, covered with fine pubescence on membranous parts; segments 8 to 10 forming spiracular atrium (Figs. 3, 5). Segment 1 with four dorsal sclerites on each side; two of them situated on anteromedian part of segment: anterior one small, posterior one larger than anterior one; remaining two sclerites very small,

sometimes undetectable, in posterior part of segment; each small sclerite bearing rather long seta; lateral sclerites of segment 1 very small (Fig. 3). Segments 3 to 7 with spinose prolegs; shape of spines variable, from stout and strongly curved (Figs. 28A–D) to slender and not strongly curved (Figs. 28E–G).

Spiracular atrium (Figs. 5, 16B): Segment 8 with large, oval dorsal plate; procercus incompletely sclerotised. Segment 9 trilobed, partially sclerotised; median lobe with one small, incompletely sclerotised projection on each side; each lateral lobe with short, membranous acrocercus; urogomphi short, one-segmented; prostyli reduced.

Primary chaetotaxy of head. *Frontale* altogether with 40–42 sensilla (Figs. 13A, C, 22A, C). Central part with three pairs of sensilla divergent posteriad; FR1 rather short seta close to frontal line; FR2 pore-like, situated anteromesally to FR1 at midlength between FR1 and FR3; FR3 short seta situated even more anteriorly and mesally than FR2, behind FR8. Setae FR5 and FR6 situated posteriorly to antennal socket; FR7 moderately long seta close to inner margin of antennal socket. FR4 pore-like, placed mesally to FR7. Nasale with a group of six stout, short setae (gFR1). Anterior margin of epistomal lobes with variable number of sensilla (gFR2). FR15 pore-like, behind nasale; seta FR8 long, situated posteriorly to FR15. Two setae (FR9 and FR10) situated medioanteriorly to antennal socket. FR11 and FR13–15 pore-like sensilla. FR11 and FR13, and short seta FR12 on inner part of epistome; location of the setae asymmetrical.

Parietale with 30 sensilla each (Figs. 13A–B, 22A–B). Dorsal surface with a group of five sensilla (PA1–5) situated posteriorly at midwidth of parietale, forming a longitudinal group; PA1–2 and PA4–5 short setae, PA3 pore-like; PA6 pore-like, located posteromesally close to joint of coronal and frontal lines, more distant from posterior margin of head than PA1. Very long seta PA7 and rather long seta PA12 on median part of dorsal surface of parietale; PA8 very long, situated posteriorly to antennal socket; pore-like sensillum PA10 at midlength between PA7 and PA8. Seta PA9 long, close to outer margin of antennal socket. Six sensilla (PA13–18) at midlength of lateral part; PA13, PA14, PA16 and PA18 setae, PA15 and PA17 pore-like sensilla; PA14–17 situated about anterior third; PA13 and PA18 on median part of parietale, PA13 situated more dorsally than PA18. Seta PA11 at about midlength between PA9 and PA13. Pore-like sensillum PA29 at about posterior fourth and midwidth of ventral surface of parietale; PA30 at about basal fourth of ventral surface of parietale, behind PA18. Anterior corner of epicranium with one pore-like sensillum (PA19) and three rather long setae (PA20–22); PA19 situated dorsally to remaining setae. Three pore-like sensilla (PA23–25) on anterior margin close to ventral mandibular acetabulum. Two long setae (PA26 and PA28) and one pore-like sensillum (PA27) situated ventrally at midlength of parietale; PA27 between PA26 and PA27.

Antenna (Figs. 14A, 23A): Antennomere 1 with five pore-like sensilla (AN1–5), AN1 at midlength; AN2 on distal part; AN3–5 on distal margin, AN3–4 dorsal, AN5 ventral. Antennomere 2 with one pore-like sensillum (AN6) situated dorsally on distal 0.26–0.28 of sclerite, three setae (AN7–9) on intersegmentary membrane between antennomeres 2 and 3, and on outer face of antenna next to sensorium (SE1); AN7 short, rounded apically, AN8 short, rather stout, AN9 minute; setae AN10 and AN11 situated apically or subapically on

inner face of antennomere 2; AN10 long, AN11 short, stout; both setae close to each other. SE1 rather large, slightly shorter than antennomere 3. Antennomere 3 with apical sensilla (gAN) in apical membranous area.

Mandible (Figs. 14B–C, 23B–C) with two setae (MN1 and MN5) and four pore-like sensilla (MN2–4 and MN6). MN1 rather long, on outer face of mandible. Sensilla MN2–4 pore-like, forming a triangular group in midlength on dorsal surface; MN2 located posteriorly to line connecting MN3 and MN4; MN4 on lateral surface. Minute seta MN5 and pore-like sensilla MN6 situated subapically on apical mandibular tooth, MN5 on outer face, MN6 on inner face.

Maxilla (Figs. 14D–E, 23D–E): Cardo with one long ventral seta (MX1). Stipes with a row of five rather short, stout setae (MX7–11) situated dorsally along inner face; MX7–11 equidistant, MX7 shorter than others. Ventral surface of stipes with three pore-like sensilla (MX2–4) and two long setae (MX5–6); MX2 and MX3 located ventrally, MX2 on about basal third, MX3 on posterolateral part; MX4–6 located subapically on outer face of sclerite; MX5 between MX4 and MX6; MX6 situated distally to MX4–5. Palpomere 1 with one moderately short spiniform seta (MX16) situated basally on dorsal inner face. Pore-like sensillum (MX12) and two long setae (MX13–14) situated ventrally on anterior margin of sclerite; MX13 on anterior part of outer face, between MX12 and MX14. Two pore-like sensilla (MX15 and MX17) on membrane behind inner appendage: MX17 dorsal, MX15 ventral. Inner appendage with one rather long seta and two rather short setae (gAPP). Palpomere 2 with two pore-like sensilla (MX18–19) and minute seta (MX27); MX18 on ventral surface of sclerite; MX19 on inner face of intersegmental membrane between palpomeres 2 and 3; MX27 at base of outer face. Palpomere 3 with two long setae (MX21 and MX23) and two pore-like sensilla (MX20 and MX22). Palpomere 4 with one long seta (MX24) on base of inner face, and with digitiform sensillum (MX25) and pore-like sensillum (MX26) situated subapically on outer face; MX25 dorsal, MX26 ventral. Apical membranous area of palpomere 4 with several minute setae (gMX).

Labium (Figs. 13B, 14F–G, 22B, 23F–G): Submentum (Figs. 13B, 22B) with two pairs of setae (LA1–2); LA1 very long on lateral corners, LA2 short on anterior lobes. Ventral surface of mentum with one pair of rather long setae (LA3) and one pair of pore-like sensilla (LA4) at midlength of lateral part of mentum; LA3 on distal 0.36; LA3 behind LA4. Dorsal surface of prementum with one pair of pore-like sensilla (LA8). Ventral surface of prementum with three pairs of sensilla (LA5–7) on lateral part; seta LA5 short, situated posterolaterally; LA6 very long, close to LA5; LA7 pore-like, close to distal margin of sclerite. Membrane between prementum and palpi with one pair of long setae (LA10) close to base of ligula, and one pair of minute setae (LA9) close to distal margin of premental sclerite. Ligula with one pair of small seta-like sensilla (LA12) on apical membranous area, and with one pair of pore-like sensilla (LA11) at base of ventral surface. Palpomere 1 with one pore-like sensillum (LA13) situated ventrally on outer part, close to basal margin of sclerite; LA14 situated dorsally on intersegmentary membrane between palpomeres 1 and 2. Palpomere 2 with one pore-like sensillum (PA15) situated subapically on outer part of dorsal surface of sclerite. Apical membranous area of palpomere 2 with several sensilla (gLA).

Key to the known species of the genus *Enochrus* from Japan (all instars)¹

1. Secondary sensilla between PA6 and PA7 absent (Fig. 13A); mandible with two setae (MN1 and MN5) (Figs. 14B–C); distal part of outer face of stipes with two setae (MX5 and MX6) (Figs. 14D–E); lateral face of mentum without stout setae (Figs. 14F–G). First instar. 3
 - Secondary sensilla between PA6 and PA7 present (Fig. 18); mandible with more than two setae (Figs. 17C–D); distal part of outer face of stipes with three setae (Figs. 17E–F); lateral face of mentum with stout setae (Figs. 17G–H). 2
2. Lateral face of mentum with two stout setae (Figs. 15H–I). Second instar. 4
 - Lateral face of mentum with more than three setae (usually four to five) (Figs. 17G–H). Third instar. 5
3. Prolegs with stout spines, the spines strongly curved to apex (Figs. 28A–D). *E. (Holcophilydrus) simulans* (Sharp, 1873)
 - Prolegs with slender spines, the spines not strongly curved to apex (Figs. 28E–G). *E. (Methydrus) japonicus* (Sharp, 1873)
4. Inner face of stipes with more than six stout setae (Figs. 24E–F); prolegs with slender spines (Fig. 28F). *E. (Methydrus) japonicus* (Sharp, 1873)
 - Inner face of stipes with five stout setae (Figs. 15F–G); prolegs with stout spines (Fig. 28B). *E. (Holcophilydrus) simulans* (Sharp, 1873)
5. Inner face of stipes with more than six stout setae (Figs. 26E–F); prolegs with slender spines (Fig. 28G). *E. (Methydrus) japonicus* (Sharp, 1873)
 - Inner face of stipes with five stout setae (Figs. 17E–F); prolegs with stout spines (Figs. 28C–D). *E. (Holcophilydrus) simulans* (Sharp, 1873) and *E. (H.) umbratus* Sharp, 1884

***Enochrus (Holcophilydrus) simulans* (Sharp, 1873)**

(Figs. 1B, 13–18, 28A–C, 66A, C, 67A)

Material examined. JAPAN: HONSHŪ: Shimane-ken: 1 L2, Hii-kawa river, Nishidai-bashi bridge, Hikawa-chō, 14.x.2007, MH; 1 L1, 1 L2, mouth of Kando-gawa river, Izumo-shi, 10.ix.2007, MH; 1 L3, Nakanosu, Nadabun-chō, Izumo-shi (fallow paddy field), 23.vii.2007, MH; 2 L3, Okinoshima, Sono-chō, Izumo-shi (artificial pond for conservation of the biotope), 11.v.2007, MH; 1 L3, same locality, 23.vii.2007 (fixed), MH leg. & reared; 1 L3, same locality, 13.ix.2007, MH; 2 L3, Okinoshima, Sono-chō, Izumo-shi (paddy field), 10.vi.2007, MH; 37 L1, 4 L2, same locality, 8.v.2008, MH; 1 L2, Shakunouchi-kōen, Kisuki-chō, Un-nan-shi, 23.ix.2007, MH.

General morphology. Third instar. Colour. Head and sclerotised parts light yellowish brown; membranous parts milky white (Fig. 1B).

Head (Figs. 16A, 17A). Frontal lines almost V-shaped. Nasale serrate and with one tooth on left side. Right epistomal lobe strongly projecting, projecting as far as nasale; left lobe weakly projecting than right lobe, not projecting further than nasale. Lateral portion of anterior margin of epistome emarginate.

¹ Based on all instars of *E. (H.) simulans* and *E. (M.) japonicus*, and third instar of *E. (H.) umbratus*. *Enochrus (Lumetus) bicolor* (Fabricius, 1792) was excluded from the key.

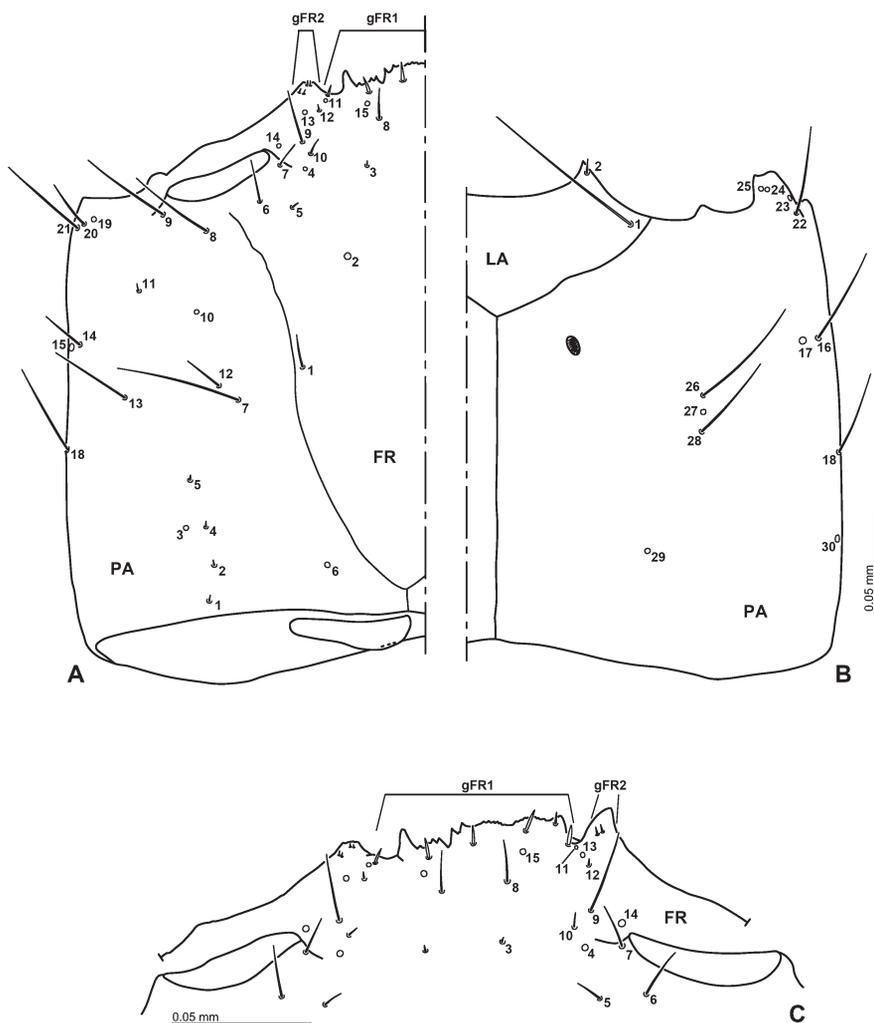


Fig. 13. Head capsule of *Enochrus (Holcophilydrus) similans* (Sharp, 1873), first instar. A – dorsal view; B – ventral view; C – detail of anterior margin of head capsule, dorsal view.

Antenna (Fig. 17B) short, rather slender. Scape about as long as pedicel. Pedicel with inner membranous area completely surrounded by sclerite on apical third.

Mandibles (Figs. 17C–D) asymmetrical; inner edges of distal tooth and anterior part serrate; right mandible with two large inner teeth, left mandible with one large inner tooth.

Maxilla (Figs. 17E–F): Maxillary palpomere 1 about as long as palpomere 4, palpomere 2 the shortest, palpomere 3 longer than palpomere 4; palpomere 2 moderately wider than palpomere 3.

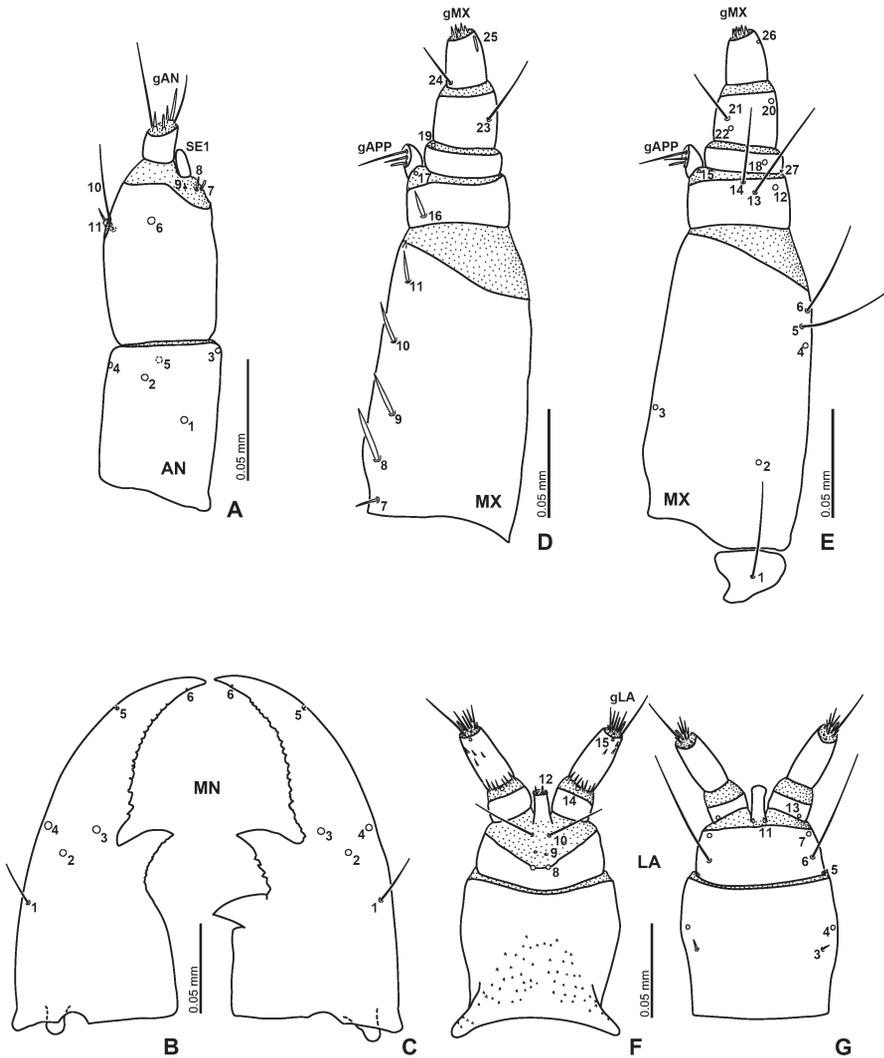


Fig. 14. Head appendages of *Enochrus (Holcophilydrus) simulans* (Sharp, 1873), first instar. A – antenna, dorsal view; B–C – mandibles, dorsal view; D – maxilla, dorsal view; E – maxilla, ventral view; F – labium, dorsal view; G – labium, ventral view.

Labium (Figs. 17G–H): Mentum with small cuticular spines on basal half of dorsal surface. Labial palpi longer than prementum, covered with narrow cuticular spines on intersegmental membrane between palpomeres 1 and 2, and on apical and outer parts of palpomere 2.

Abdomen. Abdominal segments 2 to 7 similar to segment 1 except anteromedian part with only one small sclerite, lateral sclerites narrow, very small; segments 3 to 7 with spinose prolegs, spines of prolegs stout, strongly curved apically (Fig. 28C).

Spiracular atrium (Fig. 16B): Segment 8 with large, oval dorsal plate, posterior edge of plate almost rounded, bearing four very weak projections, each projection with one moderately short stout seta; procercus incompletely sclerotised, with two rather long and one short setae.

Second instar. Similar to third instar larva, more weakly sclerotised than third instar larva.

Head. Frontal lines more distinct than those in third instar.

Antenna short, slightly more slender than in third instar (Fig. 15B).

Maxilla: Maxillary palpomere 3 slightly shorter than palpomere 4 (Figs. 15F–G).

First instar. Similar to second instar larva, more weakly sclerotised than second instar larva.

Head (Fig. 13). Right epistomal lobe projecting further than nasale; left epistomal lobe weakly projected.

Antenna short, stout (Fig. 14A). Scape shorter than pedicel.

Maxilla (Figs. 14D–E): Maxillary palpomere 3 about as long as palpomere 4.

Labium (Figs. 14F–G): Mentum subquadrate, slightly wider than prementum; small cuticular spines on dorsal surface smaller than those of second and third instars.

Primary chaetotaxy of head. *Frontale* altogether with 42 sensilla (Figs. 13A, C). Short seta FR5 and moderately long seta FR6 behind antennal socket. Second seta from right one of gFR1 shorter than other ones. Anterior margin of epistomal lobes with six setae altogether (gFR2); right lobe with two short setae; left lobe with four short setae, the setae shorter than those on right lobe. Two setae (FR9 and FR10) and one pore-like sensillum (FR14) situated medioanteriorly to antennal socket; FR9 long; FR10 short. Each epistomal lobe with three sensilla; location of setae asymmetrical; FR12 between FR11 and FR13 on left side; FR13 between FR12 and FR11, FR12 behind FR13 on right side.

Parietale (Figs. 13A–B): PA1–2 and PA4–5 forming a longitudinal row; PA3 located laterally of line connecting PA1 and PA5. PA10 situated laterally of line connecting PA7 and PA8. PA11 short seta. PA14 rather short seta; PA13, PA16 and PA18 rather long setae. PA23 more distant from PA24–25 than the latter from each other.

Antenna (Fig. 14A): AN2 on distal 0.18 of antennomere 1. Setae AN10–11 on inner membranous area surrounded by sclerite. Apical sensilla (gAN) with one long seta, two rather long setae, and a few short sensilla.

Maxilla (Figs. 14D–E): MX2 located ventrally on basal 0.31 of sclerite; MX3 on basal 0.38 of inner face. MX23 at midlength of outer face of sclerite; MX20 on lateral face of apical part; MX21–22 on inner part of sclerite; MX22 behind MX21.

Labium (Figs. 13B, 14F–G): LA8 situated dorsally at midwidth on posterior third of prementum, on borderline of sclerite and membranous area between prementum and palpi. Apical membranous area of palpomere 2 with one rather long setae and several short setae (gLA).

Secondary chaetotaxy of head. **Second instar.** *Frontale* (Figs. 18A–C): One rather short secondary seta located anteriorly to FR1.

Parietale (Figs. 18A–C): One very small secondary sensilla close to PA5, sometimes absent. One to three rather short secondary setae along frontal line, between PA6 and PA7 but mesally of line connecting PA6 and PA7. Two rather short secondary setae behind outer part of antennal socket; one between PA8 and PA9, close to PA8; another one situated more medially than PA8. One pore-like secondary sensillum and one rather short secondary seta

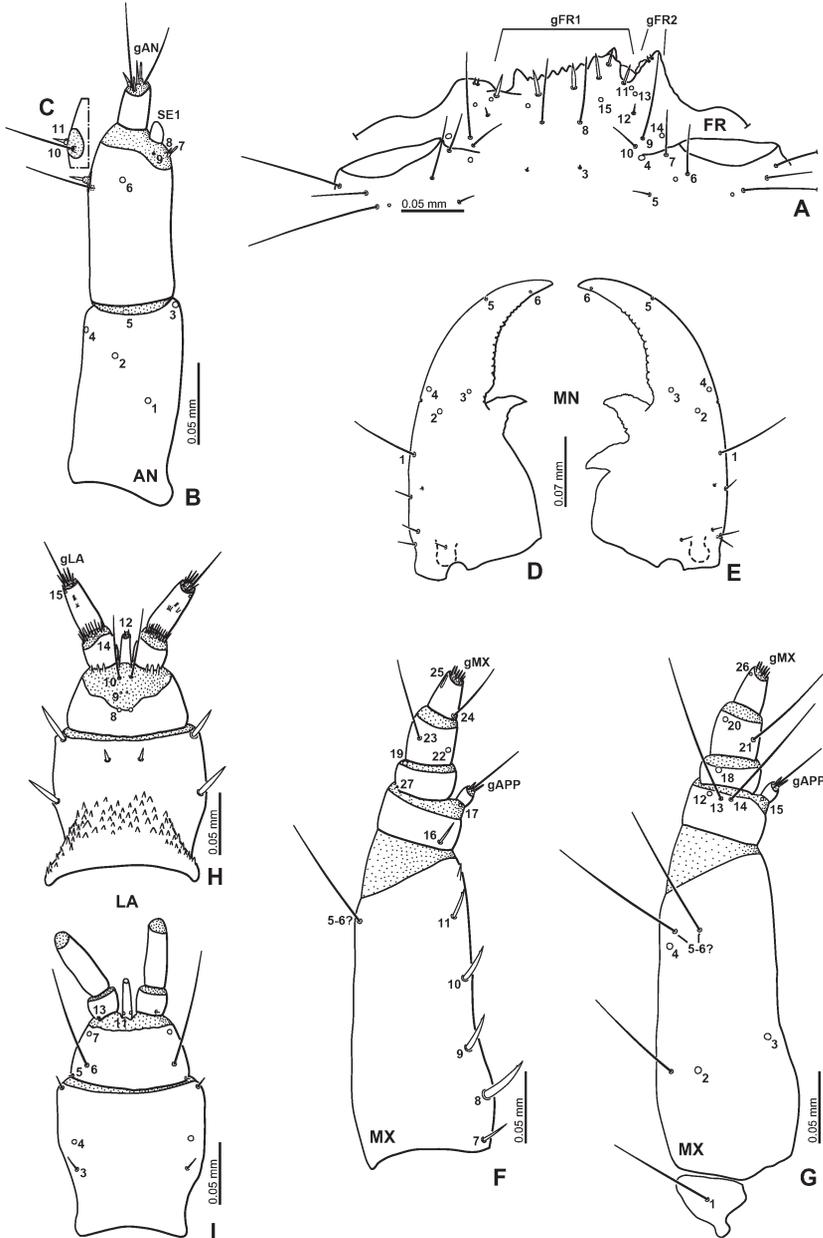


Fig. 15. *Enochrus (Holcophilydrus) simulans* (Sharp, 1873), second instar. A – clypeolabrum, dorsal view; B – antenna, dorsal view; C – antenna, detail of outer membranous area on pedicel, ventral view; D–E – mandibles, dorsal view; F – maxilla, dorsal view; G – maxilla, ventral view; H – labium, dorsal view; I – labium, ventral view.

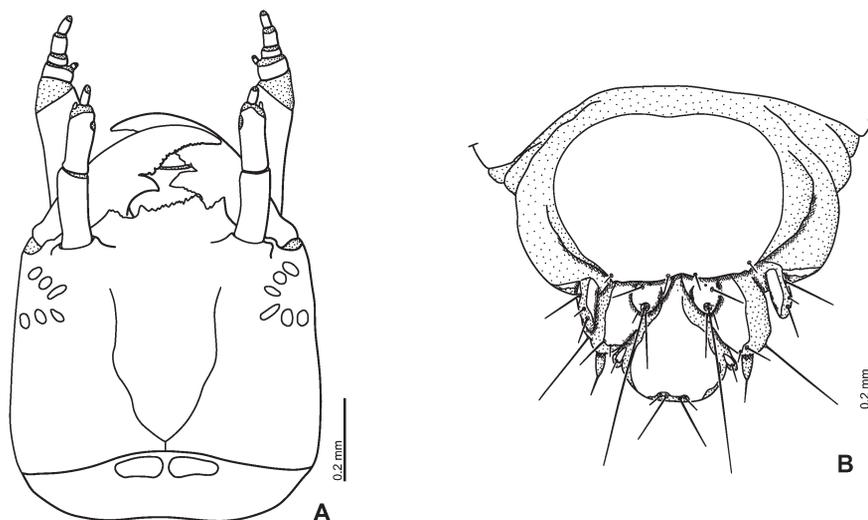


Fig. 16. *Enochrus (Holcophilydrus) simulans* (Sharp, 1873), third instar. A – head, dorsal view; B – spiracular atrium, dorsal view.

close to outer margin of antennal socket, seta situated more mesally than pore-like sensillum. One short secondary seta behind PA21; one short secondary seta behind PA15; one rather long secondary seta situated slightly mesally to PA13; two rather short secondary setae situated anteriorly to PA16–17; one rather long secondary seta located anteriorly to PA18; one rather long secondary seta situated ventrally between PA18 and PA28, close to PA18.

Antenna: Antennal sensorium (SE1) proportionally smaller than in first instar (Fig. 15B).

Mandible (Figs. 15D–E): Outer face of mandible with two small secondary setae; one on median part, close to MN4; one on basal fourth; four to five rather short secondary setae in basal part of mandible; one in basal fourth, others located more basally.

Maxilla (Figs. 15F–G): Outer face of stipes with two long secondary setae; one on apical part of sclerite, the other on basal third of sclerite.

Labium: Dorsal surface (Fig. 15H) with two rather short, stout secondary setae on lateral face; one pair of short, stout secondary setae situated anteromedially, close to distal margin; ventral surface (Fig. 15I) with one short secondary seta in each anterior corner.

Third instar. Similar to second instar larvae.

Parietale (Figs. 18D–F): Three to five rather short secondary setae between PA6 and PA7, on line connecting PA6 and PA7.

Antenna (Figs. 17B): Pedicel with one very small, indistinct secondary sensillum situated dorsally on basal margin of sclerite. Antennal sensorium (SE1) proportionally smaller than in second instar.

Labium: Dorsal surface of mentum (Fig. 17G) with four to five rather short, stout secondary setae laterally; one pair of short, stout secondary setae medioanteriorly.

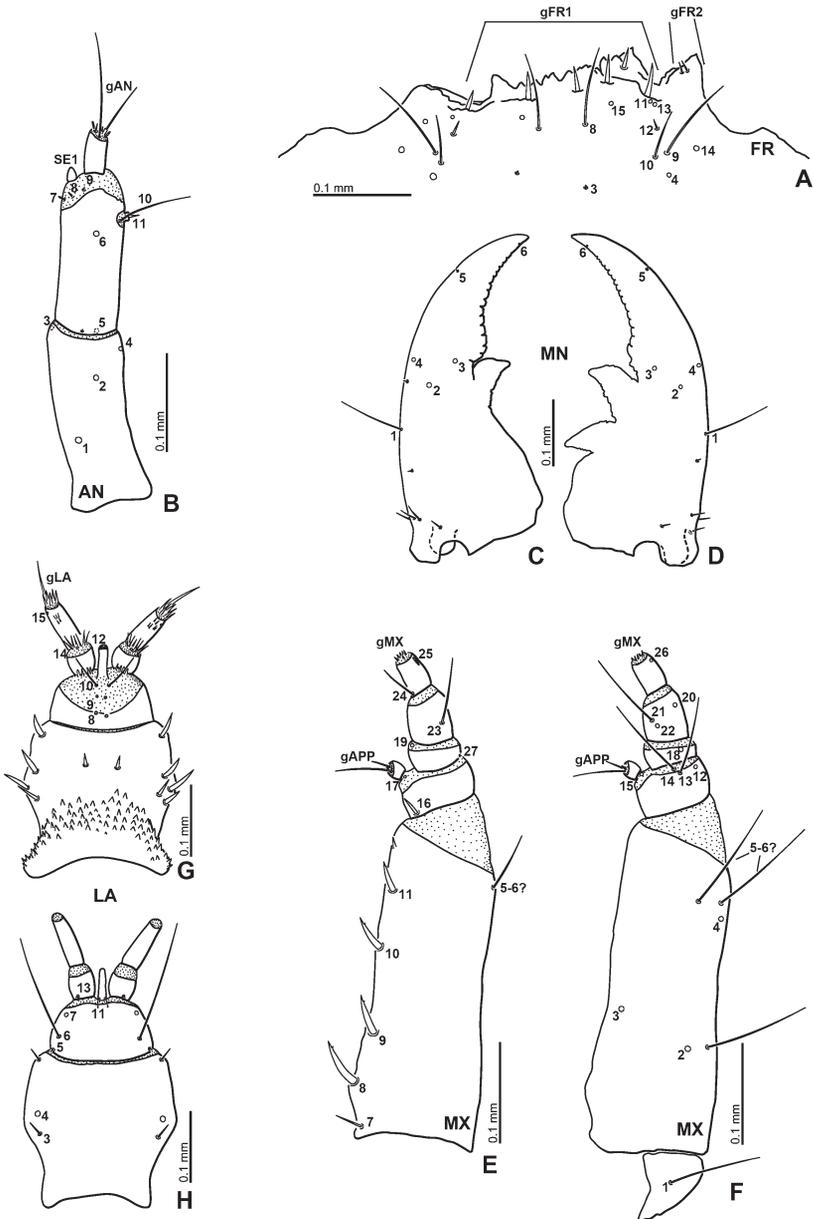


Fig. 17. *Enochrus (Holcophilydrus) simulans* (Sharp, 1873), third instar. A – clypeolabrum, dorsal view; B – antenna, dorsal view; C–D – mandibles, dorsal view; E – maxilla, dorsal view; F – maxilla, ventral view; G – labium, dorsal view; H – labium, ventral view.

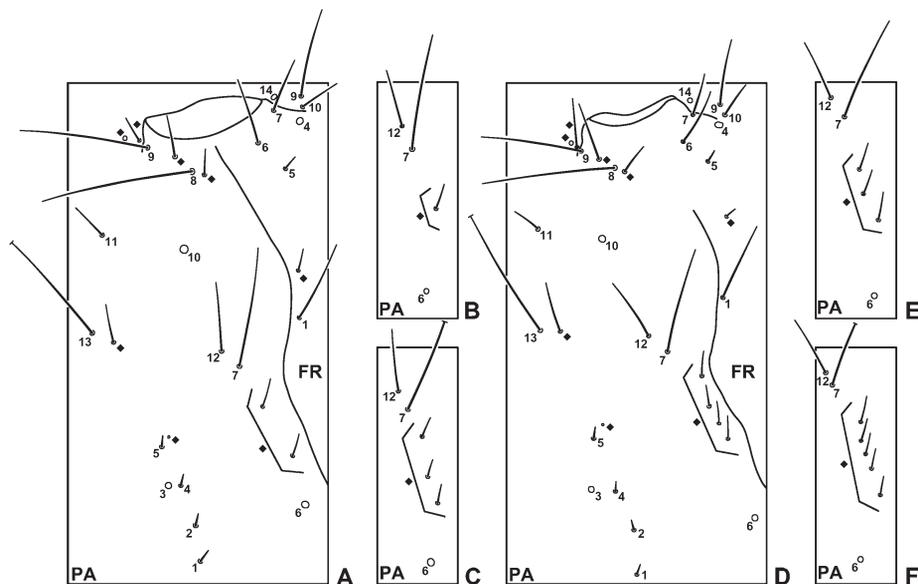


Fig. 18. *Enochrus (Holcophilydrus) simulans* (Sharp, 1873), chaetotaxy of head capsule, dorsal view. A–C – second instar larva. A – median part of head capsule; B–C – intraspecific variation of secondary sensilla between PA6 and PA7. D–F – third instar larva. D – median part of head capsule; E–F – intraspecific variation of secondary sensilla between PA6 and PA7. Secondary sensilla are marked by a black rhombus.

Habitat. Standing water. Larvae were found in water, they seem to prefer shallow and muddy areas (HAYASHI 2009a).

Identification. Only the adults of *E. simulans* occurred in the sampling sites, no other closely related species of *Enochrus* or other Acidocerini was found during the intensive survey by the second author. Therefore, we identified the *Enochrus* larvae collected at these sites as *E. simulans*.

Enochrus (Holcophilydrus) umbratus Sharp, 1884

(Figs. 1C, 6A, 19–21, 28D, 44B, 45B)

Material examined. JAPAN: HOKKAIDŌ: 2 L3, Shinoro, Sapporo-shi, 26.vi.2009, YM; 6 L3, Kamishinoro, Shinorochō, Sapporo-shi, N43°08.38', E141°22.27', 11.vii.2009, YM.

General morphology. Third instar. Colour. Head and sclerotised parts light yellowish brown; membranous parts milky to slightly greyish white (Fig. 1C).

Head (Figs. 19A, 20). Frontal lines slightly lyriform. Nasale serrate. Right epistomal lobe strongly projecting about as far as nasale; left lobe strongly projecting, not projecting further than nasale; lateral sides of anterior margin of epistome emarginate.

Antenna (Fig. 21A) short, slightly slender. Scape slightly longer than pedicel. Pedicel with inner membranous area completely surrounded by sclerite situated on apical 0.18 of inner face of sclerite.

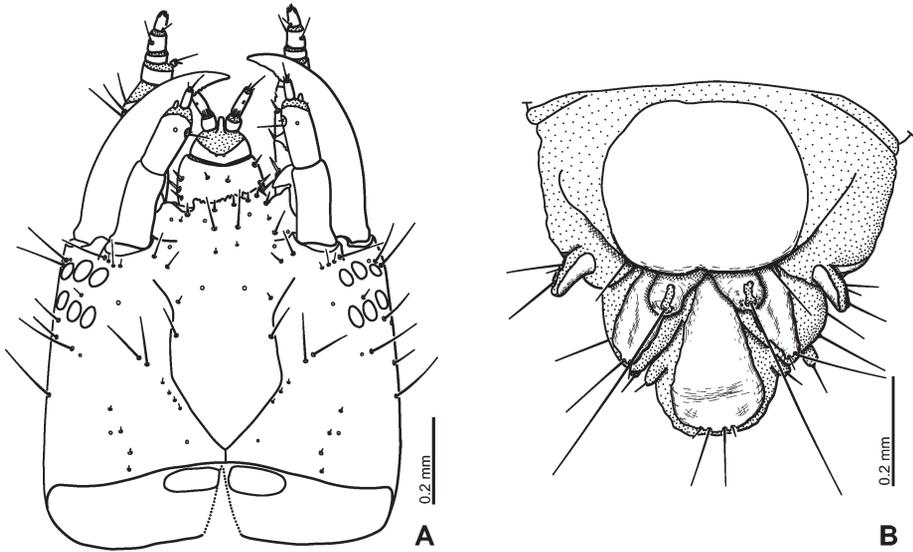


Fig. 19. *Enochrus (Holcophilydrus) umbratus* Sharp, 1884, third instar. A – head, dorsal view; B – spiracular atrium, dorsal view.

Mandibles (Figs. 21B–C) asymmetrical; left mandible with one moderately large inner tooth, the tooth slightly serrate; inner edge of mandibular apex serrate.

Maxilla (Figs. 21D–E): Maxillary palpomere 1 about as long as palpomere 4, palpomere 2 the shortest, palpomere 3 slightly shorter than palpomere 4.

Labium (Figs. 21F–G): Mentum subquadrate, with small cuticular spines on basal half of dorsal surface. Ligula about as long as labial palpomere 1. Labial palpi much shorter than mentum, covered with narrow cuticular spines on intersegmental membrane between palpomeres 1 and 2, and on dorsal surface of sclerite of palpomere 2.

Abdomen. Abdominal segments 2 to 7 similar to segment 1 but anteromedian part with only one small, oval dorsal sclerite on each side; lateral sclerites narrow, very small; segments 3 to 7 with spinose prolegs, spines of prolegs stout, strongly curved at apex (Fig. 28D).

Spiracular atrium (Fig. 19B): Segment 8 with large, oval dorsal plate; posterior edge of sclerite slightly emarginate medially; procercus incompletely sclerotised, with two long and one rather short setae.

Chaetotaxy of head. Third instar. *Frontale* altogether with 42 primary sensilla and two secondary sensilla (Figs. 20A, C). One short secondary seta at midlength between FR1 and FR5. Rather short setae (FR5 and FR6) behind antennal socket. Second seta of gFR1 of right side shorter than others. Anterior margin of epistomal lobes each with two setae and one pore-like sensillum (gFR2). Two setae (FR9 and FR10) and one pore-like sensillum (FR14) situated medioanteriorly to antennal socket; FR9 moderately long; FR10 rather short. Each epistomal lobe with three sensilla; location of sensilla asymmetrical; FR12 between FR11 and FR13 on right side; FR12 behind FR13 on left side.

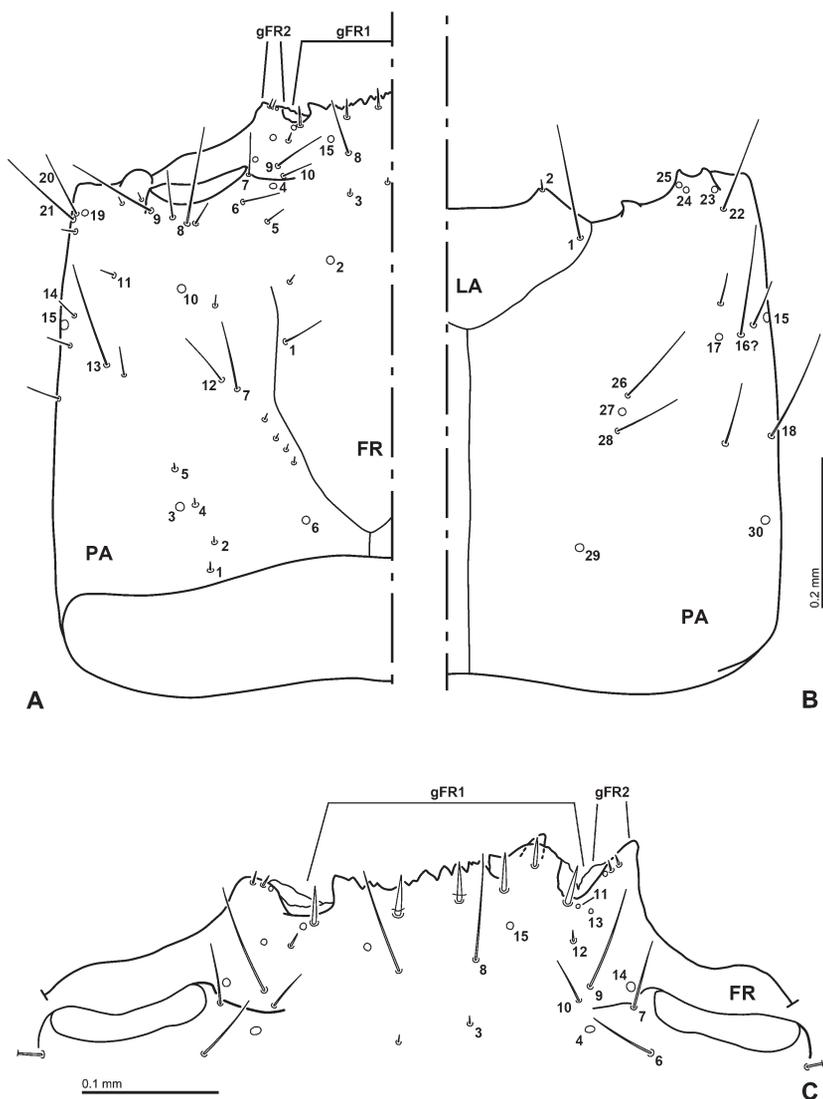


Fig. 20. Head capsule of *Enochrus (Holcophilydrus) umbratus* Sharp, 1884, third instar. A – dorsal view; B – ventral view; C – detail of anterior margin of head capsule, dorsal view.

Parietale with 30 sensilla and several secondary sensilla each (Figs. 20A–B). PA1–2 and PA4–5 forming longitudinal row; PA3 close to PA4, lying laterally of the latter. Three to four short secondary setae situated along frontal line, between PA6 and PA7 but medially of line connecting PA6 and PA7. PA10 situated laterally of line connecting PA7 and PA8. One moderately long secondary seta between PA8 and PA9; one rather short secondary seta situated slightly medially of PA8. One short secondary seta close to PA10, but sometimes absent. Two

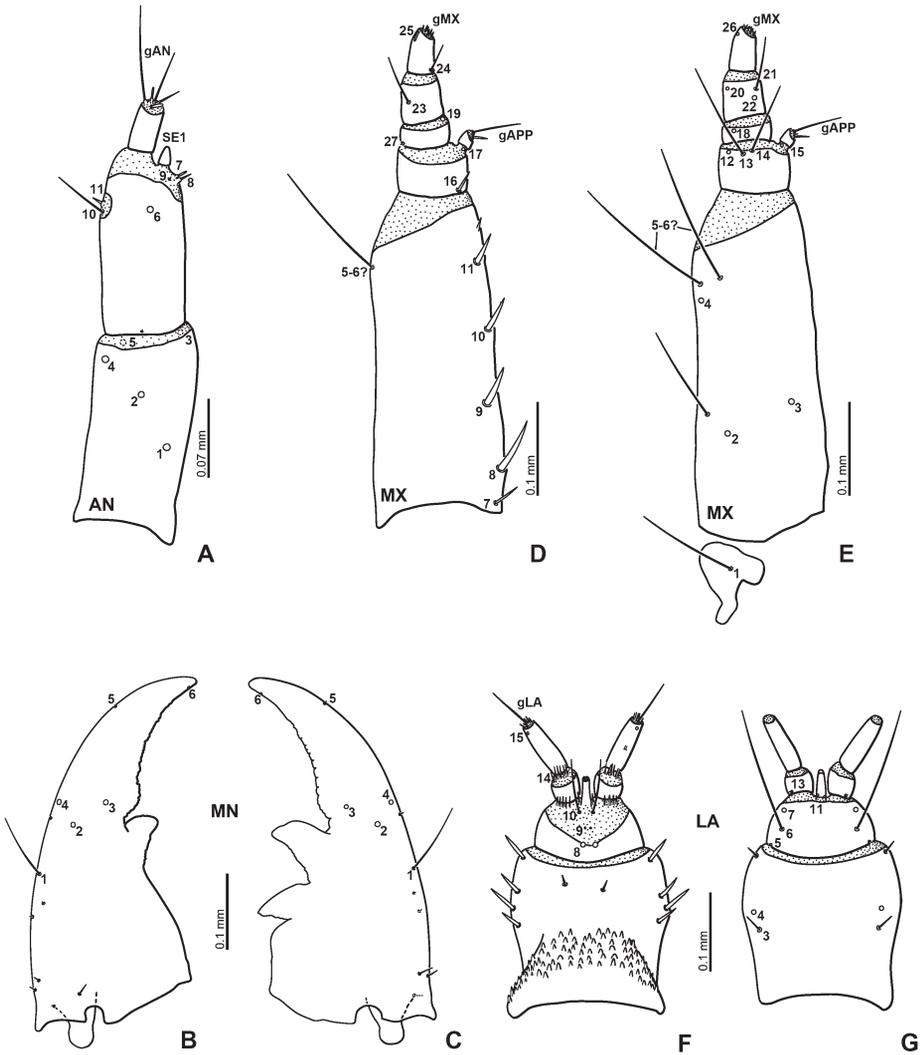


Fig. 21. *Enochrus (Holcophilydrus) umbratus* Sharp, 1884, third instar. A – antenna, dorsal view; B–C – mandibles, dorsal view; D – maxilla, dorsal view; E – maxilla, ventral view; F – labium, dorsal view; G – labium, ventral view.

rather short secondary setae close to outer margin of antennal socket. One short secondary seta slightly behind PA21; one short secondary seta slightly behind PA15; one rather short secondary seta slightly medioposteriorly to PA13; two rather short setae close to PA15–17, one between PA15 and PA16, the other anterior to PA17; one rather short secondary seta located anteriorly to PA18; one moderately long secondary seta between PA18 and PA28 close to PA18. PA14 rather short seta; PA13, PA16 and PA18 long setae. PA11 short seta. PA23 more distant from PA24–25 than the latter from each other, close to PA22.

Antenna (Fig. 21A): AN2 on distal fourth of antennomere 1. Antennomere 2 with one very small secondary sensillum on basal margin of dorsal surface of sclerite; setae AN10–11 on inner membranous area surrounded by sclerite; SE1 small. Apical sensilla (gAN) with one long trichoid seta, two rather long setae, and several short setae.

Mandible (Figs. 21B–C): Outer face of mandible with three small secondary setae; one on median part close to MN4; two on basal fourth; three to four rather short secondary setae on basal part of mandible.

Maxilla (Figs. 21D–E): Outer face of stipes with two long secondary setae; one on apical part of sclerite, one on basal third of sclerite. MX2 on basal third; MX3 on basal two-fifths. MX23 at midlength of outer face of sclerite; MX20 on subapical part of outer face; MX21–22 situated ventrally on inner part of sclerite; PA22 behind PA21.

Labium (Figs. 21F–G): Dorsal surface of mentum with four rather short, stout secondary setae on lateral face; one pair of short, stout secondary setae situated anteromedially close to distal margin; ventral surface with one short secondary seta on anterior corners. LA8 at midwidth and on posterior third of prementum, on borderline of sclerite and membranous area between prementum and palpi. Apical membranous area of palpomere 2 with one rather long seta and several short setae (gLA).

Habitat. Standing or very slowly flowing water. Larvae were found in water.

Identification. This species is distributed in eastern Japan, and co-occurs with *Enochrus* (*Methydrus*) *vilis* (Sharp, 1884) in the collecting site in Sapporo, Hokkaidô. The adults of *E. umbratus* are much larger than those of *E. vilis* and the same may be expected of their larvae. Hence, for this study we have used only the largest third instar larvae collected at the locality – they are all too large to belong to *E. vilis* and may therefore be clearly associated with *E. umbratus*.

Enochrus (*Methydrus*) *japonicus* (Sharp, 1873)

(Figs. 1D, 3, 5, 22–27, 28E–G, 65A, 66B)

Material examined. JAPAN: HOKKAIDÔ: 1 L1, 1 L2, 3 L3 (SEHU, EUMJ), Tôge-shita, Rumoi-shi, 18.vii.2007, H. Yoshitomi leg.; 4 L2, Tôge-shita, Rumoi, 7.–10.vii.2009, YM; 2 L1, 9 L2, 7 L3, 3.5km WSW of Okusawa-suigenchi, pond near upstream of Katsunai-gawa river, Otaru-shi, alt. 360 m, N43°08.51'E140°56.20', 2.vii.2009, YM & M. Ôhara leg.

General morphology. Third instar. Colour. Head and sclerotised parts dark brown to brown; membranous parts greyish white; abdominal segments with transverse rows of small blackish spots (Fig. 1D).

Head (Figs. 25A, 26A). Frontal lines slightly lyriform. Nasale serrate with one tooth on each side. Right epistomal lobe projecting further than nasale; left lobe weakly projecting, not reaching further than nasale; lateral sides of anterior margin of epistome emarginate.

Antenna (Fig. 26B) short, rather slender. Scape as long as pedicel. Pedicel with inner membranous area surrounded by sclerite on apical third.

Mandibles (Figs. 26C–D) asymmetrical; right mandible with two inner teeth, distal one slightly larger than basal one, inner faces of distal tooth and apex of right mandible serrate; left mandible with one large slightly serrate inner tooth; inner face of apex of left mandible serrate.

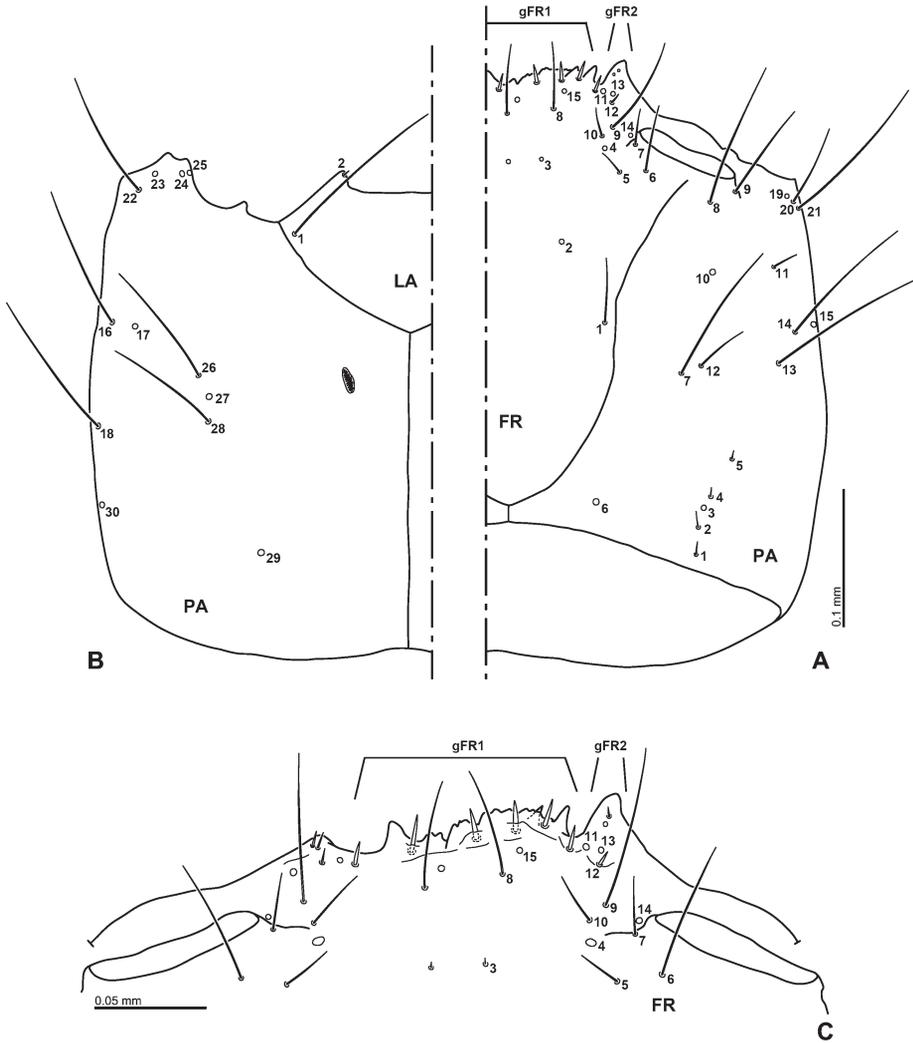


Fig. 22. Head capsule of *Enochrus (Methyrus) japonicus* (Sharp, 1873), first instar. A – dorsal view; B – ventral view; C – detail of anterior margin of head capsule, dorsal view.

Maxilla (Figs. 26E–F): Maxillary palpomere 1 about as long as palpomeres 3 and 4, palpomere 2 the shortest; palpomere 2 as wide as palpomere 3; palpomere 4 the narrowest.

Labium (Figs. 26G–H): Mentum subquadrate, with small cuticular spines dorsally. Ligula about as long as labial palpomere 1. Labial palpi shorter than mentum, covered with narrow cuticular spines on intersegmental membrane between palpomeres 1 and 2, and on dorsal surface of sclerite of palpomere 2.

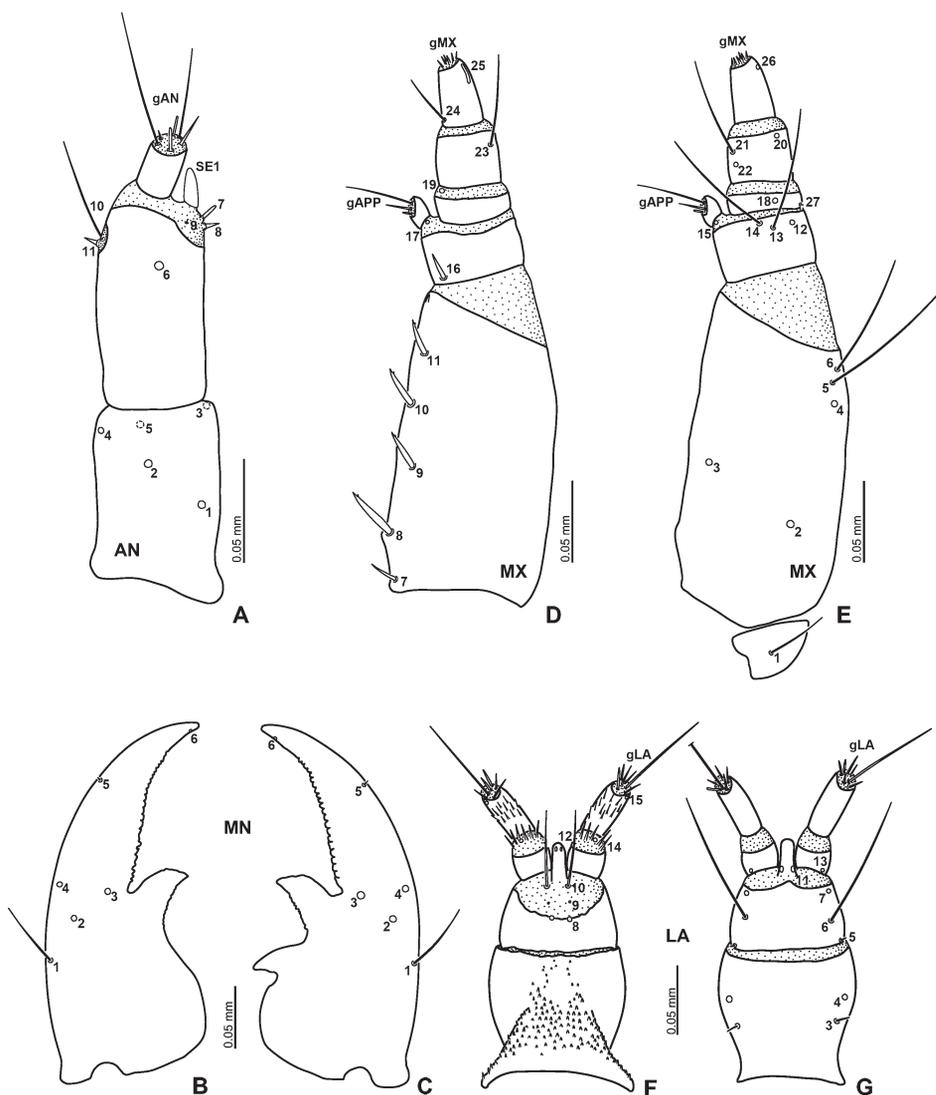


Fig. 23. Head appendages of *Enochrus (Methydrus) japonicus* (Sharp, 1873), first instar. A – antenna, dorsal view; B–C – mandibles, dorsal view; D – maxilla, dorsal view; E – maxilla, ventral view; F – labium, dorsal view; G – labium, ventral view.

Abdomen (Fig. 3). Abdominal segments with very small transverse setiferous projections on membranous parts. Segments 2 to 7 similar to segment 1 but anteromedian part with one small, oval dorsal sclerite on each side; lateral sclerites narrow, very small; segments 3 to 7 with spinose prolegs, spines of prolegs narrow, weakly curved towards apex (Fig. 28G).

Spiracular atrium (Figs. 5, 25B): Segment 8 with moderately large, oval dorsal plate; the plate with a small emargination on median part of posterior edge; procercus incompletely sclerotised, with two long and one rather short setae.

Second instar. Similar to third instar larva, more weakly sclerotised than third instar.

Head. Frontal lines more distinctly than those in third instar.

Antenna (Fig. 24B) proportionally short, slender. Scape slightly shorter than pedicel.

Maxilla (Figs. 24E–F): Maxillary palpomere 2 slightly wider than palpomere 3.

First instar. Similar to second instar larva, more weakly sclerotised than second instar. *Colour.* Head and sclerotised parts brown to light brown.

Head. *Antenna* (Fig. 23A) proportionally short, stouter than that of second instar.

Labium (Figs. 23F–G): Labial palpi slightly shorter than mentum.

Abdomen. *Spiracular atrium:* Segment 8 with moderately large, oval dorsal plate; the plate with a small emargination and two projections on median part of posterior edge, projections with one short seta; posterior edge of the plate with one pair of setae.

Primary chaetotaxy of head. *Frontale* altogether with 40 sensilla (Figs. 22A, C). Rather long setae (FR5–6) behind antennal socket. Anterior margin of epistomal lobes with four sensilla altogether (gFR2); right lobe with one short seta and one pore-like sensillum; left lobe with two short setae. Two setae (FR9 and FR10) and one pore-like sensillum (FR14) situated medioanteriorly to antennal socket; FR9 very long; FR10 short; FR10 at midlength between FR4 and FR9. Each epistomal lobe with three sensilla; location of setae asymmetrical: FR13 situated between FR11 and FR12, laterally of line connecting FR11 and FR12 on right side, FR12 between FR11 and FR13 on left side.

Parietale (Figs. 22A–B): PA1–5 forming longitudinal row; PA3 between PA2 and PA4. PA10 situated slightly laterally of line connecting PA7 and PA8. PA13, PA14, PA16 and PA18 long setae. PA11 rather short seta. PA23 more distant from PA24–25 than the latter from each other, lying close to PA22.

Antenna (Fig. 23A): AN2 on distal 0.28 of antennomere 1. Setae AN10–11 on inner membranous area surrounded by sclerite. Apical sensilla (gAN) with two long trichoid setae, others short.

Maxilla (Figs. 23D–E): MX8–11 with subapical tooth. MX2 located ventrally on basal 0.33 of sclerite; MX3 placed on basal 0.44 of inner face. MX23 in distal part of outer face of sclerite; MX20 placed laterally, close to distal margin of ventral surface of sclerite; MX21–22 situated on inner part of sclerite; MX21 situated apically; MX22 behind MX21.

Labium (Figs. 23F–G): LA8 situated dorsally at midwidth on borderline of sclerite and membranous area between prementum and palpi. Apical membranous area of palpomere 2 with one long setae and several short setae (gLA).

Secondary chaetotaxy of head. **Second instar.** *Parietale* (Figs. 27A–C): One very small sensilla close to PA5, sometimes absent. Three to five rather short secondary setae situated along frontal line, between PA6 and PA7, mesally of line connecting PA6 and PA7. Two rather short secondary setae situated posteriorly to outer part of antennal socket; one between PA8 and PA9; one situated more medially than PA8, at midlength between frontal line and PA8. One pore-like secondary sensillum and one rather short secondary seta close to outer

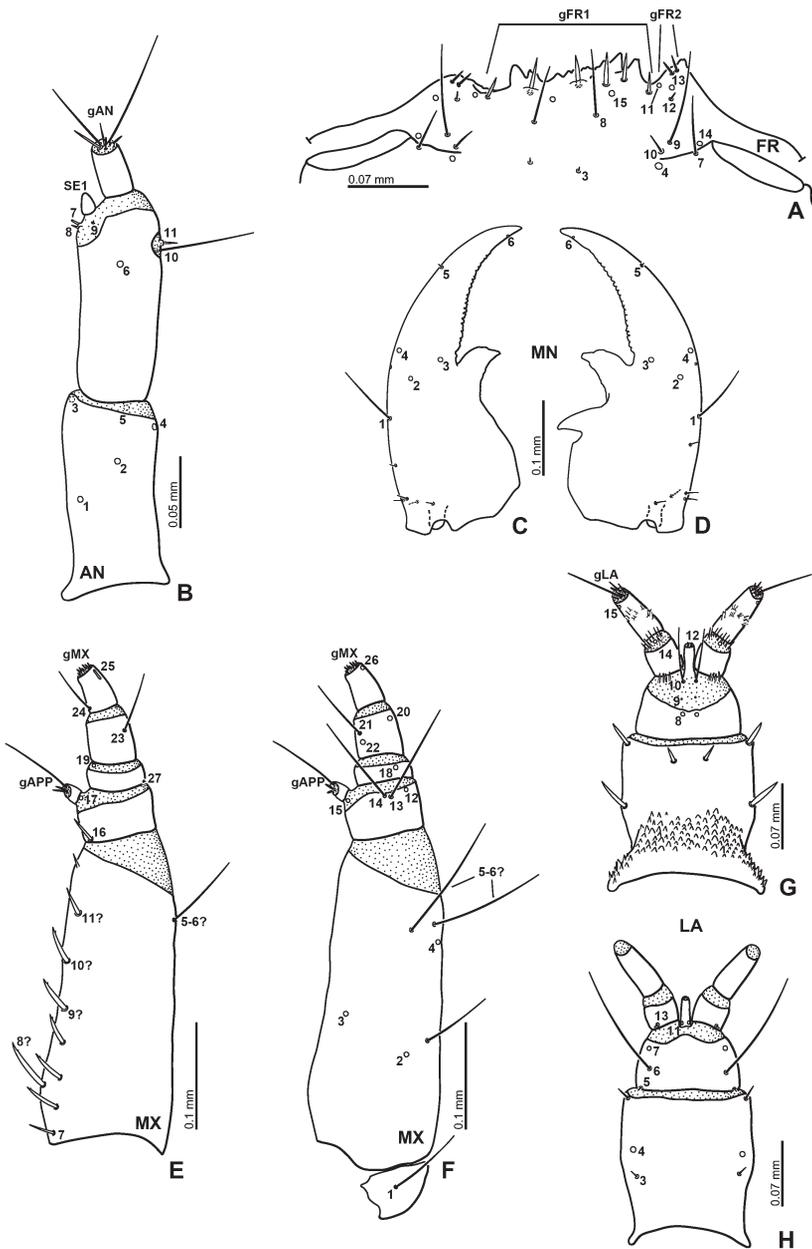


Fig. 24. *Enochrus (Methyrus) japonicus* (Sharp, 1873), second instar. A – clypeolabrum, dorsal view; B – antenna, dorsal view; C–D – mandibles, dorsal view; E – maxilla, dorsal view; F – maxilla, ventral view; G – labium, dorsal view; H – labium, ventral view.

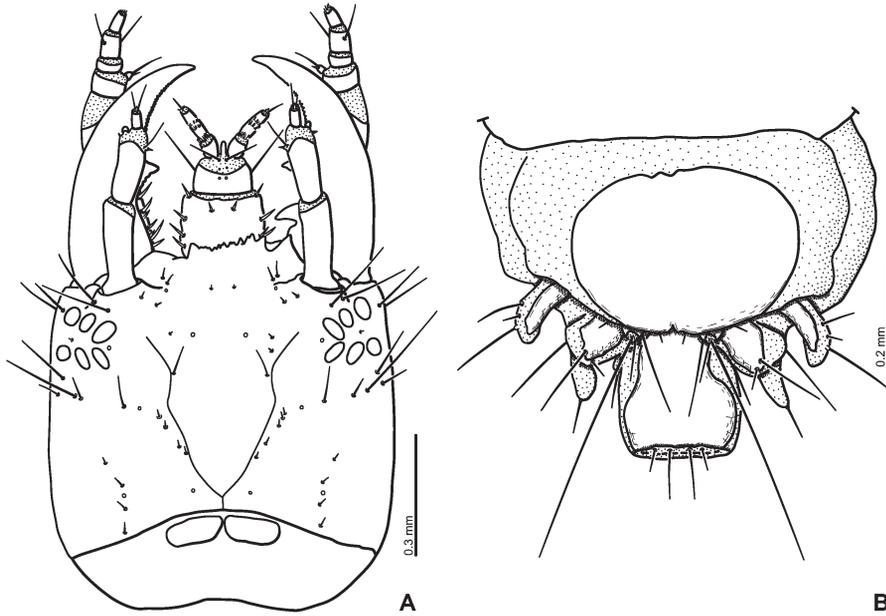


Fig. 25. *Enochrus (Methydrus) japonicus* (Sharp, 1873), third instar. A – head, dorsal view; B – spiracular atrium, dorsal view.

margin of antennal socket, seta situated more medially than pore-like sensillum. One short secondary seta located slightly more posteriorly to PA21, sometimes absent; two rather short secondary setae close to PA15, one ventral, the other dorsal; one rather short secondary seta lying slightly medioposteriorly to PA13; one rather long secondary seta situated anteriorly to PA18; two to three rather long secondary setae between PA17 and PA30.

Antenna (Fig. 24B): Antennal sensorium (SE1) proportionally smaller than in first instar.

Mandible (Figs. 24C–D): One pore-like secondary sensillum close to MN1; five short setae on basal part of mandible, behind MN1.

Maxilla (Figs. 24E–F): Outer face of stipes with two long secondary setae; one on apical part of sclerite, one on basal third of sclerite; inner face of stipes with four rather short, stout secondary setae, all secondary setae with small subapical tooth; setae on inner face of stipes undistinguishable from primary sensilla.

Labium (Figs. 24G–H): Dorsal surface of mentum with two rather short, stout secondary setae on lateral face; one pair of short, stout setae situated anteromedially, close to distal margin; ventral surface with one pair of short secondary setae on anterior corners.

Third instar. Similar to second instar larvae.

Antenna (Fig. 26B): Antennal sensorium (SE1) proportionally smaller than in second instar.

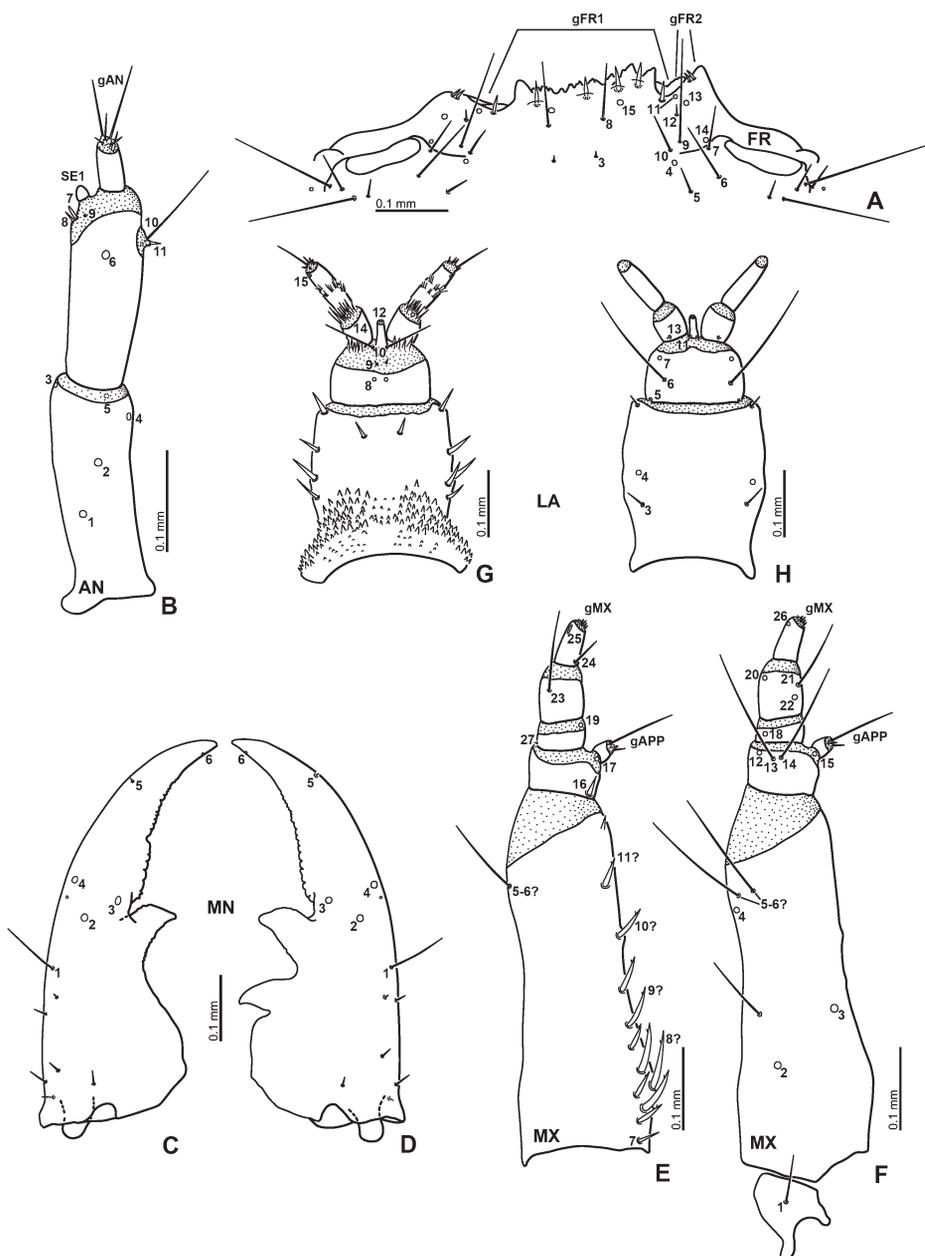


Fig. 26. *Enochrus (Methyrus) japonicus* (Sharp, 1873), third instar. A – clypeolabrum, dorsal view; B – antenna, dorsal view; C–D – mandibles, dorsal view; E – maxilla, dorsal view; F – maxilla, ventral view; G – labium, dorsal view; H – labium, ventral view.

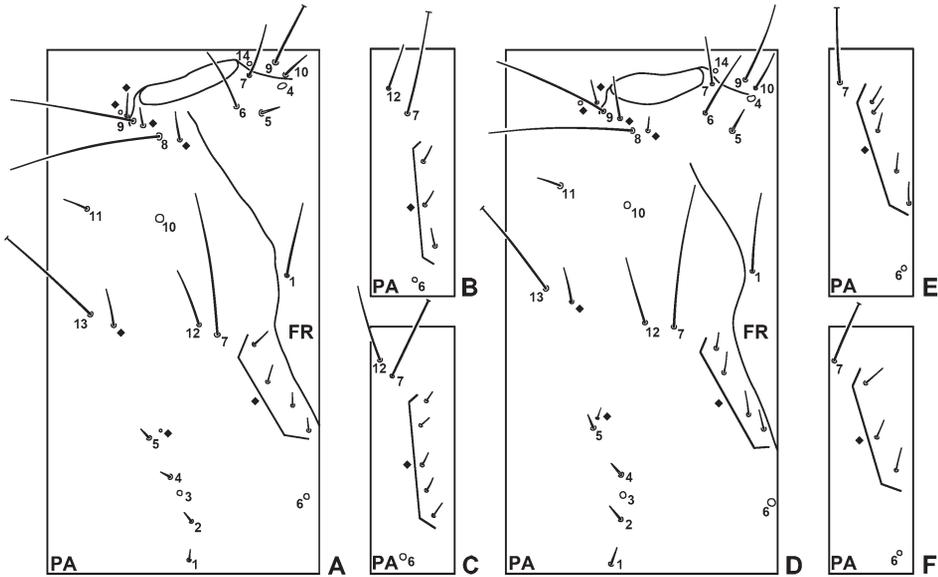


Fig. 27. *Enochrus (Methydrus) japonicus* (Sharp, 1873), chaetotaxy of head capsule, dorsal view. A–C – second instar larva: A – median part of head capsule; B–C – intraspecific variation of secondary sensilla between PA6 and PA7. D–F – third instar larva. D – median part of head capsule; E–F – intraspecific variation of secondary sensilla between PA6 and PA7. Secondary sensilla are marked by a black rhombus.

Mandible (Figs. 26C–D): Outer part of basal half of mandibles with six small to rather short setae situated behind MN1.

Maxilla (Figs. 26E–F): Inner face of stipes with seven rather short, stout secondary setae, all secondary setae with small subapical tooth.

Labium (Figs. 26G–H): Dorsal surface of mentum with four to five rather short, stout secondary setae situated laterally.

Habitat. Standing water. Larvae were found in very shallow water, on the muddy banks of a pond, or in very slowly flowing water. They usually hide below the fallen leaves or in the mud.

Identification. No other closely related species occurs in the collecting sites and the morphology of the above larva moreover corresponds with the morphology of the larvae of *E. simulans* and *E. umbratus*, which are most similar to *E. japonicus*. Hence, the larvae were identified as *E. japonicus*.

Remarks. MORIOKA (1955) described an unidentified *Enochrus* larva collected in the field as *Enochrus* sp. He pointed out that the larvae were collected together with adults of *E. japonicus*, and no other hydrophilid species occurred in the collecting site. The larvae probably belong to *E. japonicus*, but we are not able to confirm the species-level identification as the description does not include enough details for a reliable comparison.

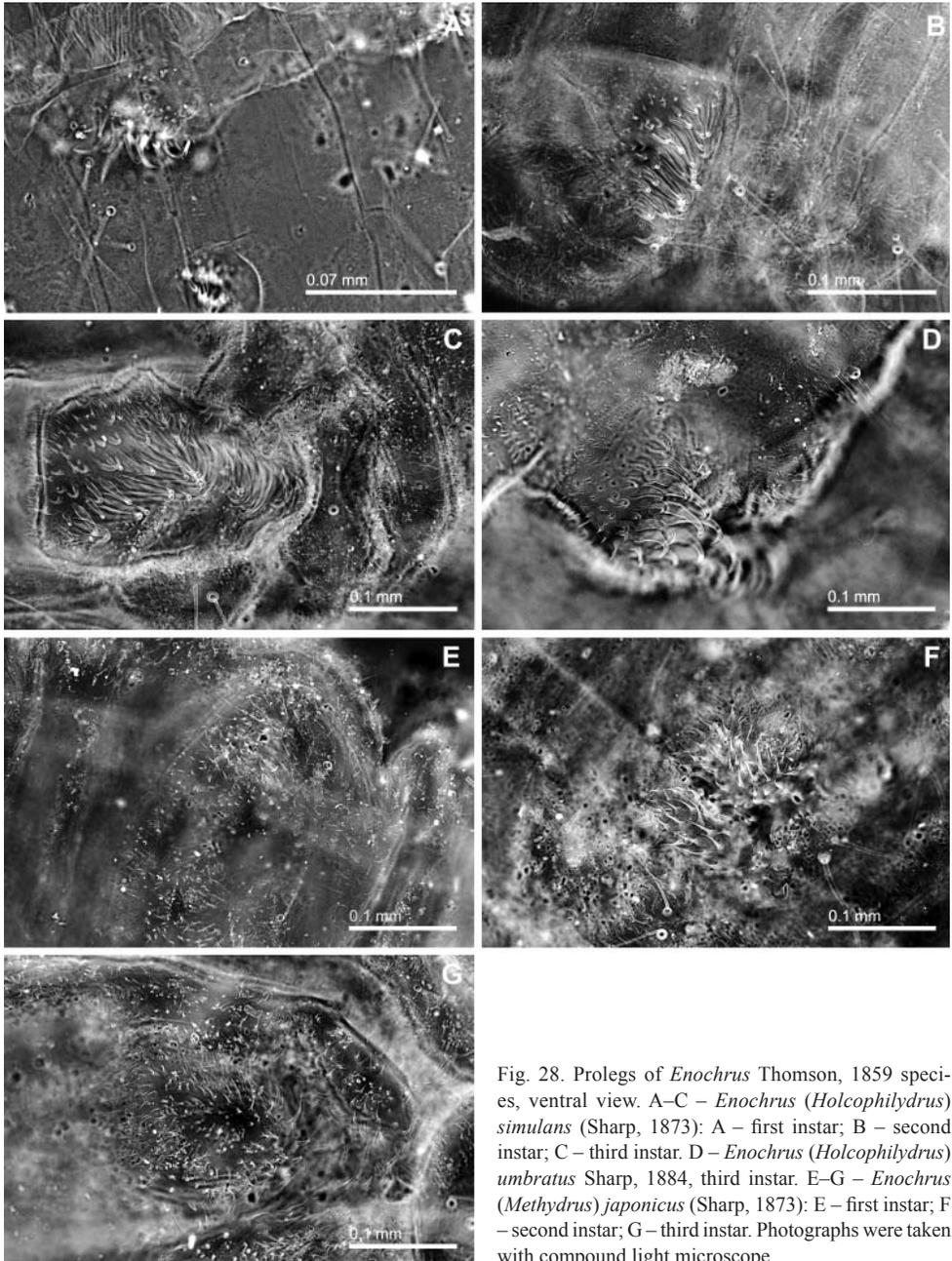


Fig. 28. Prolegs of *Enochrus* Thomson, 1859 species, ventral view. A–C – *Enochrus (Holcophilydrus) simulans* (Sharp, 1873): A – first instar; B – second instar; C – third instar. D – *Enochrus (Holcophilydrus) umbratus* Sharp, 1884, third instar. E–G – *Enochrus (Methydrus) japonicus* (Sharp, 1873): E – first instar; F – second instar; G – third instar. Photographs were taken with compound light microscope.

Genus *Helochares* Mulsant, 1844

(Figs. 1E–F, 6B, 29–43, 44C, 45D, 65C)

Species examined. *Helochares (Helochares) pallens* (MacLeay, 1825) (L1–3), *Helochares (Hydrobaticus) anchoralis* Sharp, 1890 (L1), *Helochares (Hydrobaticus) nipponicus* Hebauer, 1995 (L1–3).

Diagnosis. The larvae of this genus are similar to those of other genera of the Japanese Aciderini, but are distinguished from them by the following characters: (1) head capsule with scale-like setae (Fig. 36); (2) nasale with distinct teeth, not serrate or smooth (Figs. 36C, 42A); (3) each epistomal lobe with one or two stout, short scale-like setae and two short setae (e.g., Fig. 36C); (4) antennal sensorium (SE1) rather long (Figs. 39A, 40B, 42B); (5) abdominal segments without spinose prolegs.

General morphology. *Body* slender, almost parallel-sided, tapering posteriad, widest between second and fourth abdominal segments (Figs. 1E–F, 6B).

Head (e.g., Fig. 32A, 35A). Head capsule subquadrate. Frontal lines lyriform, fused at base of head capsule, coronal line short. Surface of head capsule smooth. Six stemmata on each anterolateral portion of head capsule. Clypeolabrum (e.g., Figs. 29C, 33A) asymmetrical. Nasale asymmetrical, with six teeth, four on right projecting further than two on left. Epistomal lobes rounded, slightly to strongly asymmetrical.

Antenna 3-segmented, short, stout in first instar (e.g., Fig. 30A) to rather slender in third instar (e.g., Fig. 33B). Flagellum the shortest.

Mandibles (e.g., Figs. 33C–D) almost symmetrical, with two inner teeth, distal tooth larger than basal one; inner face of mandible serrate on basal part. Basal tooth of left mandible comparatively smaller than that of right mandible.

Maxilla (e.g., Figs. 33E–F) 6-segmented (including cardo), distinctly longer than antenna. Cardo small, irregularly shaped. Stipes the longest, longer than palpomeres 1–4 combined; subapical part of inner surface with spine-like cuticular projection; basal part of inner face bearing several cuticular projections. Maxillary palpus 4-segmented; palpomere 1 incompletely sclerotised on dorsal surface; inner process sclerotised.

Labium (e.g., Figs. 29B, 33G–H) well developed. Submentum fused to head capsule, large, subpentagonal, wider than mentum. Mentum subtrapezoidal in dorsal view, wider than prementum, bearing cuticular spines on dorsal surface. Prementum subquadrate, wider than long. Ligula largely sclerotised, distinctly shorter than labial palpi, longer than labial palpomere 1, with weakly bifid membranous apex. Labial palpi covered with narrow cuticular spines on intersegmental membrane between palpomeres 1 and 2.

Thorax. Prothorax slightly wider than head capsule (Figs. 1E–F, 6B). Proscutum formed by large plate subdivided by fine sagittal line, anterior and posterior margins weakly sclerotised; several very long to rather long setae situated on each side, some of them scale-like. Prosternum subpentagonal, incompletely subdivided by fine sagittal line (Fig. 44C). Mesonotum subdivided by fine sagittal line, with two dorsal sclerites on each side, anterior one small and narrow, posterior one large, each with very long to rather long setae. Metanotum with one large dorsal sclerite on each side, median part of sclerites sometimes indistinct (looking then as two dorsal sclerites on each side), anterior part larger than posterior part, each sclerite with very long to rather long setae. Legs (Fig. 45D) rather short, visible in dorsal view,

5-segmented, bearing several short to long, stout setae, lacking swimming hairs; all three pairs similar in shape.

Abdomen. Abdomen 10-segmented, tapering posteriad, covered with fine pubescence on membranous parts; segments 1 to 7 similar in size and shape, each with dorsal sclerites and small, narrow lateral sclerites; segments 8 to 10 forming spiracular atrium.

Spiracular atrium (Figs. 32B, 35B, 41B): Segment 8 with large, oval dorsal plate; posterior edge of plate projecting medially; procercus incompletely sclerotised, with one stout and two rather long setae. Segment 9 trilobed, partially sclerotised; median lobe with one small, incompletely sclerotised projection on each side; each lateral lobe with short, membranous acrocercus; urogomphi short, one-segmented; prostyli reduced.

Primary chaetotaxy of head. *Frontale* altogether with 44–46 sensilla (Figs. 29A, C, 36A, C). Central part with three pairs of sensilla divergent posteriad (FR1–3); FR1 rather long seta close to frontal line; FR2 pore-like; FR3 short seta situated more anteriorly than FR2. Three setae (FR5–7) situated posteriorly to antennal socket, FR6 between FR5 and FR7, FR7 close to inner margin of antennal socket. FR4 pore-like, slightly digitiform, situated posteromesally to antennal socket. Nasale with a group of six stout, short setae and a few sensilla (gFR1). Epistomal lobes with three to four short setae each (gFR2). Pore-like sensillum FR15 placed posteriorly to median portion of nasale; long seta FR8 behind FR15. Two setae (FR9–10) and one pore-like sensillum (FR14) situated medioanteriorly to antennal socket; one long seta (FR9) and one rather short seta (FR10) situated mesally to antennal socket. Two pore-like sensilla (FR11 and FR13) and one short seta (FR12) on inner part of epistomal lobe; FR11 close to each lateral seta of gFR1.

Parietale with 30 sensilla each (Figs. 29A–B, 36A–B). Dorsal surface with a group of five sensilla (PA1–5) situated posteriorly at midwidth, forming irregular to slightly irregular longitudinal row; PA1–2 and PA4–5 short setae, PA3 pore-like sensillum. PA6 pore-like, located posteromesally close to joint of coronal and frontal lines, about same distance from posterior margin of head as PA1. PA7 and PA12 on median part of dorsal surface of parietale, between PA5 and PA10; PA12 situated slightly anteromesally to PA7; seta PA8 very long, situated posteriorly to antennal socket, close to frontal line; pore-like sensillum PA10 situated between PA7 and PA8, but laterally of line connecting PA7 and PA8. Seta PA9 long, scale-like, close to outer margin of antennal socket. Very long setae PA13 and PA14 located laterally of PA7 and PA12, at midlength of laterodorsal part; PA14 between PA11 and PA13. PA11 rather short seta at about midlength between PA14 and PA20. anterior corner of epicranium with one pore-like sensillum (PA19) and three long trichoid setae (PA20–22); PA19 situated dorsally to PA20–22; PA20 rather to moderately long, PA21 very long, PA22 long; PA20 between PA19 and PA21; PA 22 situated ventrally to remaining sensilla. Two pore-like sensilla (PA15 and PA17) and one narrow scale-like seta (PA16) situated on about anterior third of lateral surface of parietale; PA15 situated more dorsally than PA16; PA17 situated more mesally than PA16; one very long seta (PA18) at midlength of lateral surface of parietale. Ventral surface with three pore-like sensilla (PA23–25) on anterior margin close to ventral mandibular acetabulum; PA23 situated close to PA22, more distant from PA24–25 than the latter from each other. Two very long setae (PA26 and PA28) and one pore-like sensillum (PA27) located at

midlength of parietale, slightly laterally of midwidth of parietale. PA27 between PA26 and PA28. Two pore-like sensilla (PA29–30) located ventrally in posterior part of parietale; PA29 behind PA28; PA30 situated posteriorly to PA18.

Antenna (Fig. 30A, 37A): Antennomere 1 with five pore-like sensilla (AN1–5); AN1 at midlength, AN2 on distal third, AN3–5 on distal margin, AN4 dorsal, AN3 and AN5 ventral. Antennomere 2 with one pore-like sensillum (AN6) situated dorsally on subapical part of sclerite, and five setae (AN7–11) situated subapically on intersegmental membrane between antennomeres 2 and 3. SE1 rather long, slender, about as long as antennomere 3. Antennomere 3 with apical sensilla (gAN) on apical membranous area; gAN with two long trichoid setae and a few short setae.

Mandible (Figs. 30B–C, 37B–C) with six sensilla; MN1 seta, MN2–4 and MN6 pore-like, MN5 seta or pore-like. MN1 rather long, on outer face of mandible. Sensilla MN2–4 forming a triangular group in median area of dorsal surface. MN5 situated subapically on outer face of mandible. MN6 situated subapically on inner face of mandible.

Maxilla (Figs. 30D–E, 37D–E): Cardo with one very long, trichoid ventral seta (MX1). Stipes with a row of five rather short, stout setae (MX7–11) situated dorsally along inner face; MX7–11 almost equidistant, each with subapical tooth, distance between MX8 and MX9 slightly shorter than distance between MX10 and MX11. Ventral surface of stipes with three pore-like sensilla (MX2–4) and two setae (MX5–6); MX2 on basal fourth of sclerite; MX3 on basal two-fifths of sclerite; MX4–6 on outer face of apical part of sclerite; MX5 very long scale-like seta; MX6 very long trichoid seta situated more distally than MX4–5. Palpomere 1 with four sensilla on sclerite (MX12–14 and MX16); one moderately short spiniform seta (MX16) situated basally on dorsal inner face; MX12–13 on lateral surface, MX14 on ventral surface; MX12 pore-like sensilla, MX13–14 long setae. Two pore-like sensilla (MX15 and MX17) on membrane behind inner appendage; MX17 dorsal, MX15 ventral. Inner appendage with one rather long scale-like seta and a few rather short to very short setae (gAPP). Palpomere 2 with two pore-like sensilla (MX18–19) and one minute seta (MX27); MX18 situated ventrally on outer portion of sclerite, MX19 on inner face of intersegmental membrane between palpomeres 2 and 3; MX27 at base of outer face. Palpomere 3 with two long setae (MX21 and MX23) and two pore-like sensilla (MX20 and MX22). Palpomere 4 with one long seta (MX24) on basal portion of inner face, and with a digitiform sensillum (MX25) and a pore-like sensillum (MX26) on subapical portion of outer face, MX25 dorsal, MX26 ventral. Apical membranous area of palpomere 4 with several minute setae (gMX).

Labium (Figs. 30F–G, 37F–G): Submentum with two pairs of setae (LA1–2); LA1 long in lateral corners, LA2 short on anterior lobes. Ventral surface of mentum with one pair of rather short setae (LA3) and one pair of pore-like sensilla (LA4) situated anterolaterally; LA4 located close to distal margin of sclerite, anteriorly to LA3. Dorsal surface of prementum with one pair of pore-like sensilla (LA8) on median part of sclerite. Ventral surface of prementum with three pairs of sensilla (LA5–7) on lateral portion; seta LA5 short on basal margin of sclerite; LA6 very long, located between LA5 and LA7, slightly mesally of line connecting LA5 and LA7; LA7 pore-like, on borderline of sclerite and membranous area between prementum and palpi. Membranous area between prementum and palpi with one pair of long setae (LA10) and small pore-like sensilla (LA9); LA10 close to base of ligula, LA9 on median portion of membranous

area. Ligula with two pairs of pore-like sensilla (LA11 and LA12); LA12 situated dorsally on apical membranous area, LA11 situated ventrally at base of ligula. Palpomere 1 with one minute seta (LA13) ventrally; LA13 close to basal margin of sclerite; LA14 on dorsal side of intersegmentary membrane between palpomeres 1 and 2. Palpomere 2 with one pore-like sensillum (LA15) situated subapically on lateral face of sclerite. Apical membranous area of palpomere 2 with one long seta and several rather long to short setae (gLA).

Key to the known species of the genus *Helochaeres* from Japan (all instars)²

1. Secondary sensilla between PA6 and PA7 absent (Fig. 29A); mandible with two setae (MN1 and MN5) (Figs. 30B–C); distal part of outer face of stipes with two setae (MX5 and MX6) (Figs. 30D–E); lateral face of mentum without stout setae (Figs. 30F–G). First instar. 2
 - Secondary sensilla between PA6 and PA7 present (Figs. 34, 43); mandible with more than two setae (Figs. 33C–D); distal part of outer face of stipes with three setae (Figs. 33E–F); lateral face of mentum with stout setae (Figs. 33G–H). Second and third instars. 4
2. Epistomal lobe with one short scale-like seta and two short, trichoid to spiniform setae (Fig. 29C). *H. (Helochaeres) pallens* (MacLeay, 1825)
 - Epistomal lobe with two short scale-like setae and two short, trichoid to spiniform setae (Fig. 36C). 3
3. Seta PA7 trichoid (Fig. 36A). *H. (Hydrobaticus) anchoralis* Sharp, 1890
 - Seta PA7 scale-like (Fig. 38A). *H. (Hydrobaticus) nipponicus* Hebauer, 1995
4. Epistomal lobe with one short scale-like seta and two short, trichoid to spiniform setae (Fig. 33A). *H. (Helochaeres) pallens* (MacLeay, 1825)
 - Epistomal lobe with two short scale-like setae and two short, trichoid to spiniform setae (Fig. 42A). *H. (Hydrobaticus) nipponicus* Hebauer, 1995

Helochaeres (Helochaeres) pallens (MacLeay, 1825)

(Figs. 1E, 29–34)

Material examined. JAPAN: HONSHŪ: Shimane-ken: 1 L2, 4 L3, Okinoshima, Sono-chō, Izumo-shi (artificial pond made for conservation purpose), 25.viii.2007, MH; 38 L1, same locality, 13.v.2008 (egg cases carried by adults collected in the field, 15.v.2008 fixed), MH.

General morphology. Third instar. Colour. Head and sclerotised parts light yellowish brown; membranous parts milky white (Fig. 1E).

Head. Nasale projecting further than epistomal lobes (Fig. 33A). Epistomal lobes rounded, somewhat asymmetrical; right lobe projecting further than left lobe.

Antenna (Fig. 33B) short, somewhat slender. Scape slightly shorter than pedicel.

Mandibles (Figs. 33C–D): Inner teeth of left mandible with a small subapical tooth; inner face of mandible serrate basally.

² Based on all instars of *H. (Helochaeres) pallens* and *H. (Hydrobaticus) nipponicus*, and the first instar of *H. (Hydrobaticus) anchoralis*.

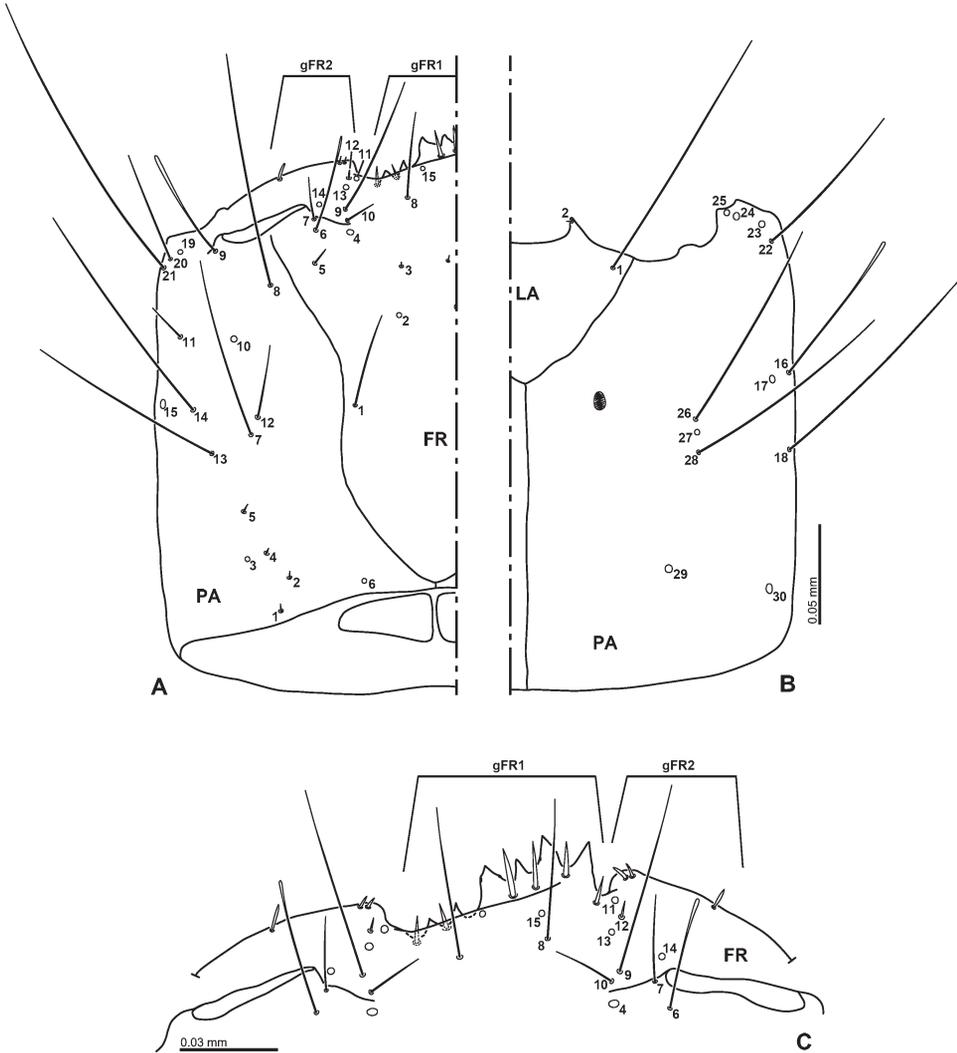


Fig. 29. Head capsule of *Helochares (Helochares) pallens* (MacLeay, 1825), first instar. A – dorsal view; B – ventral view; C – detail of anterior margin of head capsule, dorsal view.

Maxilla (Figs. 33E–F): Maxillary palpomere 1 about as long as palpomeres 3 and 4 each, palpomere 2 the shortest; palpomere 1 the widest.

Labium (Figs. 33G–H): Mentum bearing small, strong cuticular spines dorsally. Labial palpi about as long as mentum; palpomere 1 much shorter than palpomere 2.

Abdomen. Segment 1 with four dorsal sclerites on each side; two small sclerites on antero-medial part, posterior one larger than anterior one; remaining two sclerites very small,

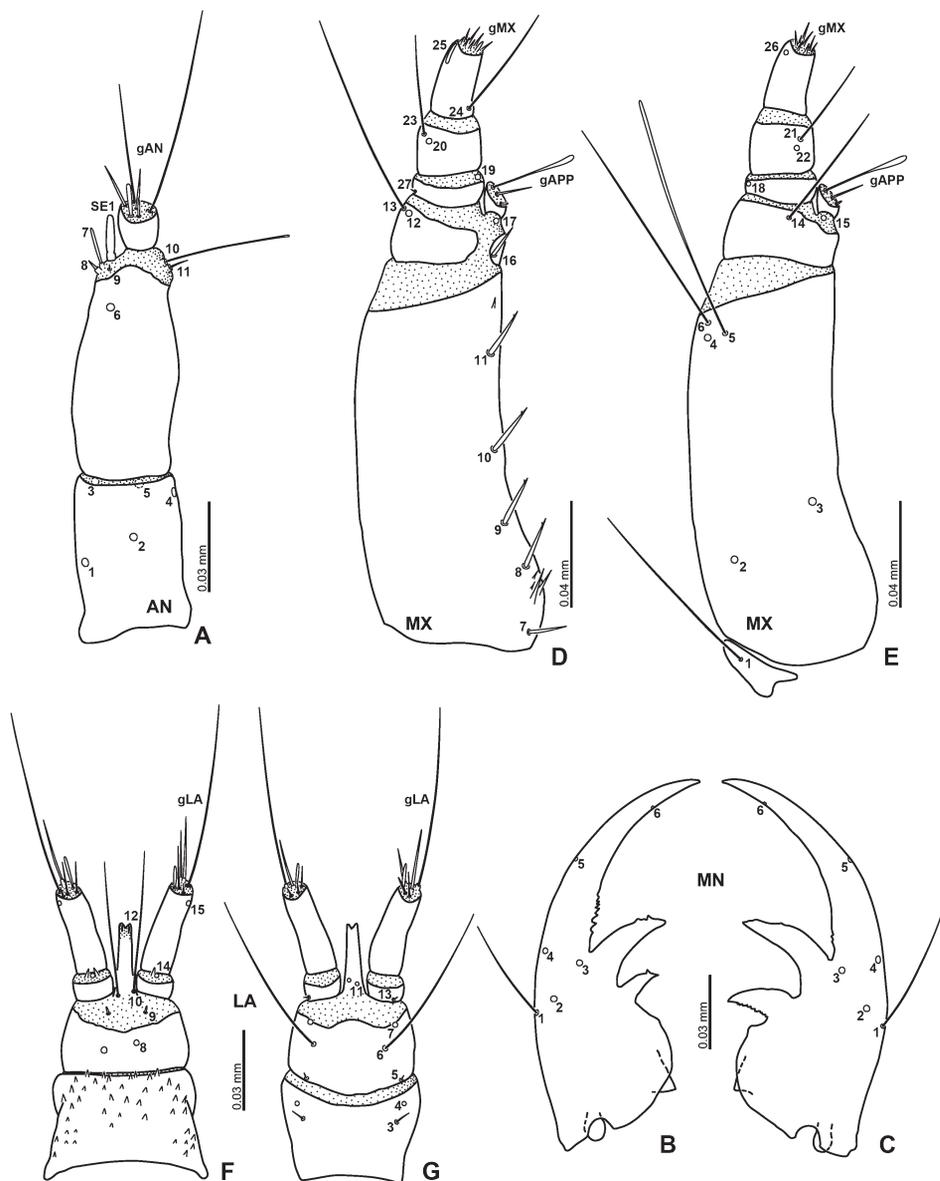


Fig. 30. Head appendages of *Helochares (Helochares) pallens* (MacLeay, 1825), first instar. A – antenna, dorsal view; B–C – mandibles, dorsal view; D – maxilla, dorsal view; E – maxilla, ventral view; F – labium, dorsal view; G – labium, ventral view.

situated behind the former dorsal sclerites, each bearing one rather long seta and sometimes undetectable; segments 2 to 7 similar to segment 1 but with very indistinct dorsal sclerites.

Spiracular atrium (Fig. 32B): Segment 8 with large, oval dorsal plate; plate with four projections on median part of posterior edge, each median projections slightly bifid, with two setae; lateral portion of dorsal plate with three setae each, median one long, remaining two rather long; procercus with one rather short, stout seta and two rather long setae. Segment 9 trilobed; median lobe with one small, incompletely sclerotised projection on each side; two rather short and two moderately short setae on posterior edge of median lobe; each lateral lobe with two long setae on posterior edge.

Second instar. Similar to third instar larva, but more weakly sclerotised.

Head. Antenna: Scape shorter than pedicel (Fig. 31B).

First instar. Similar to second instar larva, but more weakly sclerotised.

Head. Epistomal lobes somewhat asymmetrical; inner part of lobes strongly curved, lateral part slightly rounded (Fig. 29C).

Antenna proportionally short, stout (Fig. 30A). Scape distinctly shorter than pedicel.

Maxilla: Maxillary palpomere 3 slightly shorter than palpomere 4 (Figs. 30D–E).

Labium: Labial palpi longer than mentum (Figs. 30F–G).

Thorax. Mesonotum with six long setae on each posterior dorsal sclerite. Metanotum with six long setae on each dorsal sclerite.

Primary chaetotaxy of head. *Frontale* altogether with 44 sensilla (Figs. 29A, C). FR2 situated more anteriorly and mesally than FR1. FR5 short seta; FR6 moderately long scale-like seta, close to FR7; FR7 moderately short. Nasale with a group of six stout, short setae and three pore-like sensilla (gFR1), the latter sensilla on lateral margin of median two large teeth. Each epistomal lobe with two short setae on inner part, and one short, scale-like seta on median part of outer margin (gFR2). FR10 placed posteriorly to FR9; pore-like sensillum (FR14) situated anteriorly to inner margin of antennal socket. Location of FR11–13 slightly asymmetrical; FR12 situated between FR11 and FR13 but laterally of line connecting them; FR11 situated anteriorly to FR12, close to lateral seta on nasale; sensilla on left lobe more closely aggregated than those on right lobe.

Parietale (Figs. 29A–B): PA1–5 forming irregular row. PA7 very long, trichoid seta; PA12 rather long seta. PA20 rather long seta. PA17 close to PA16, situated more posteriorly and more mesally than PA16; PA16 long, narrow scale-like seta. PA26–28 situated ventrally at midlength and in lateral 0.36 of parietale; PA27 between PA26 and PA28. Two pore-like sensilla (PA29–30) located ventrally on basal fifth of parietale.

Antenna (Fig. 30A): Antennomere 2 with one pore-like sensillum (AN6) situated dorsally close to distal margin of sclerite; five setae (AN7–11) on intersegmentary membrane between antennomeres 2 and 3; AN7 rather short, rounded apically; AN8 rather stout, shorter than AN7; AN9 minute; AN7–9 on outer face of antenna next to sensorium SE1; setae AN10–11 on inner face of antenna; AN10 long, narrow scale-like, AN11 short, both setae situated close to each other.

Mandible (Figs. 30B–C): MN2 between MN1 and MN3, close to MN1; MN4 on lateral face. MN5 pore-like.

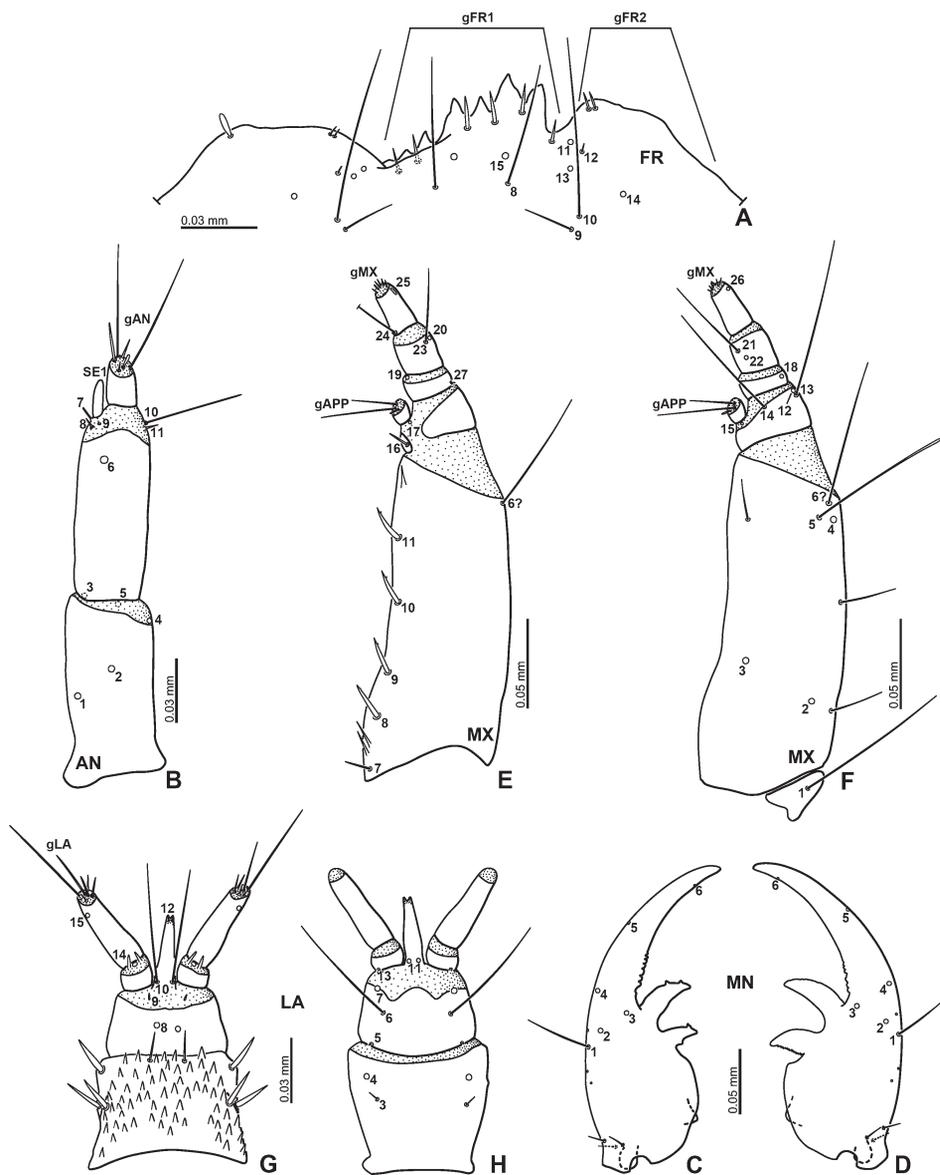


Fig. 31. *Helochares (Helochares) pallens* (MacLeay, 1825), second instar. A – clypeolabrum, dorsal view; B – antenna, dorsal view; C–D – mandibles, dorsal view; E – maxilla, dorsal view; F – maxilla, ventral view; G – labium, dorsal view; H – labium, ventral view.

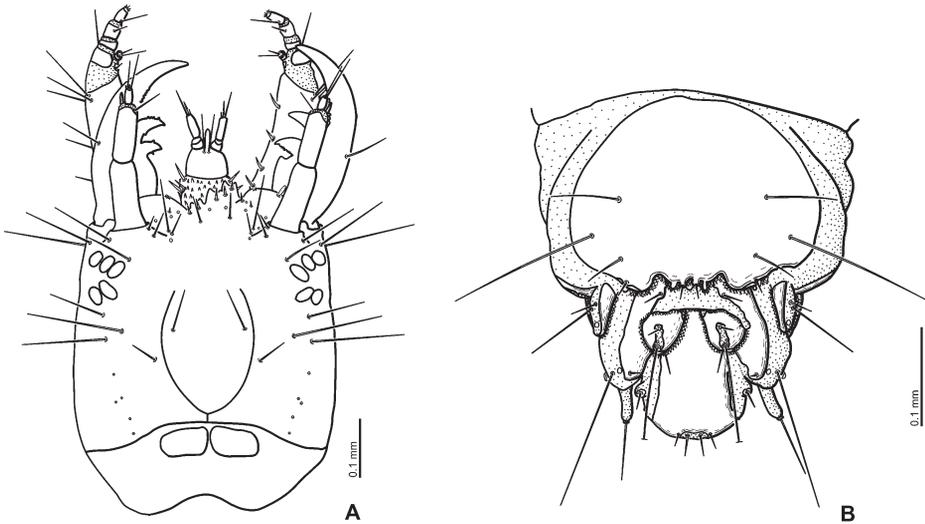


Fig. 32. *Helochares (Helochares) pallens* (MacLeay, 1825), third instar. A – head, dorsal view; B – spiracular atrium, dorsal view.

Maxilla (Figs. 30D–E): One pore-like sensillum (MX12) and one very long seta (MX13) situated dorsally on outer face of palpomere 1, close to distal margin of sclerite; MX13 situated more ventrally than MX12; one long seta (MX14) situated ventrally on median part of distal margin. MX23 on distal part of outer face of sclerite; MX20 behind MX23; MX21 situated ventrally on anterolateral part; MX22 behind MX21. MX24 long seta.

Labium (Figs. 30F–G): LA1 very long.

Secondary chaetotaxy of head. Second instar. Frontale (Fig. 34A): One short secondary seta between FR1 and FR5, close to frontal line.

Parietale (Fig. 34A): One seta located close to frontal line, medially of line connecting PA6 and PA7. Two short secondary setae situated posteriorly to lateral part of antennal socket, one slightly posteriorly to PA9, one slightly laterally of PA8. One pore-like secondary sensillum and one rather short secondary seta close to outer margin of antennal socket, between PA9 and PA19; the seta situated more mesally than pore-like sensillum. One rather short secondary seta behind PA21; one rather short secondary seta situated close to PA14, laterally of line connecting PA13 and PA14; one rather short secondary seta between PA15 and PA16; one rather short secondary seta situated slightly anteriorly to PA17; one short secondary seta close to PA18.

Mandible (Figs. 31C–D): Three pore-like secondary sensilla on medioposterior part of outer face of mandible; three rather short secondary setae located basally on outer part of mandible.

Maxilla (Figs. 31E–F): Outer face of stipes with three trichoid secondary seta; one very long seta on apical part; remaining setae rather long, situated on anterior third and two-thirds

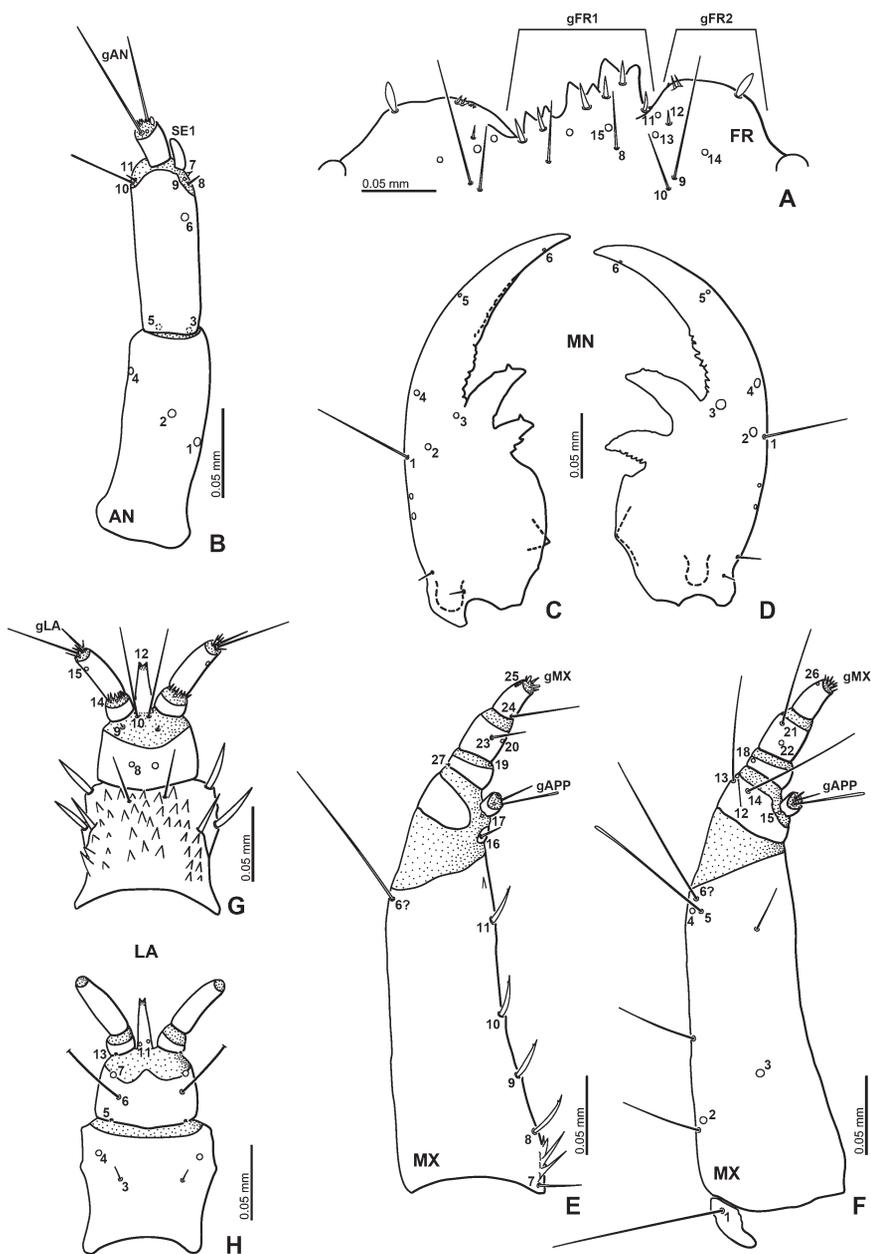


Fig. 33. *Helochares (Helochares) pallens* (MacLeay, 1825), third instar. A – clypeolabrum, dorsal view; B – antenna, dorsal view; C – D – mandibles, dorsal view; E – maxilla, dorsal view; F – maxilla, ventral view; G – labium, dorsal view; H – labium, ventral view.

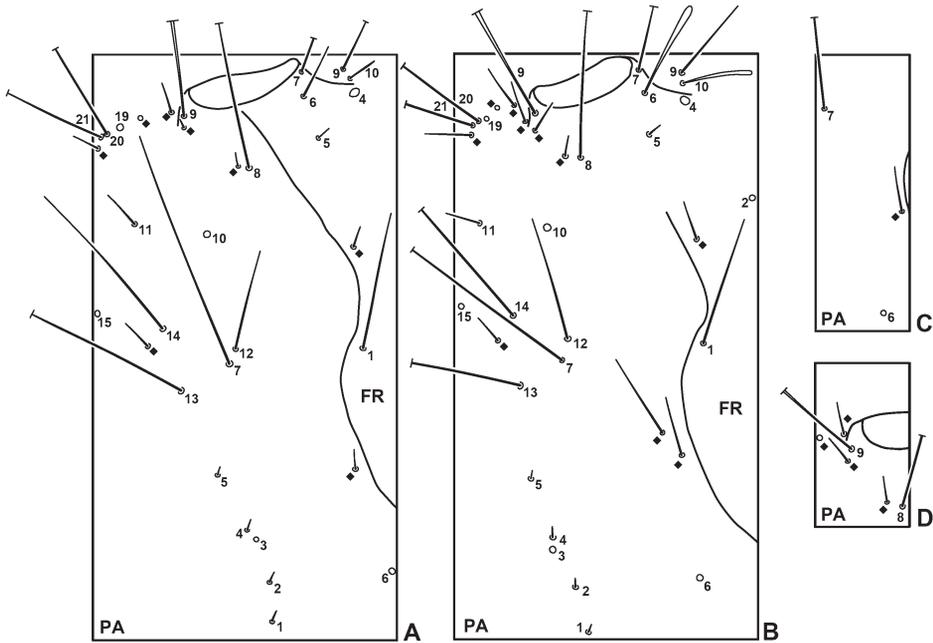


Fig. 34. *Helochares (Helochares) pallens* (MacLeay, 1825), chaetotaxy of head capsule, dorsal view. A – median part of head capsule, second instar. B–D – third instar larva: B – median part of head capsule; C – intraspecific variation of secondary sensilla between PA6 and PA7; D – intraspecific variation of secondary sensilla on outer part of antennal socket. Secondary sensilla are marked by a black rhombus.

respectively; inner part of stipes with one rather long secondary seta situated ventrally on anterior portion of sclerite.

Labium (Figs. 31G–H): Dorsal surface of mentum with three rather short, stout secondary setae on lateral face, one on apical part, two on median part; one pair of rather short, moderately stout setae situated dorsally on median part of anterior margin of mentum.

Third instar. Parietale (Figs. 34B–D): One to two rather long to rather short secondary setae close to frontal line, medially of line connecting PA6 and PA7. One pore-like secondary sensillum and one or two rather short secondary setae close to outer margin of antennal socket, between PA9 and PA19; pore-like sensillum close to PA19, setae close to PA9. One short secondary seta between PA22 and PA26, but sometimes absent; one or two short secondary setae close to PA18 but sometimes absent.

Habitat. Standing water. Larvae were found in water (HAYASHI 2009a).

Identification. First instar larvae were reared from the identified female which carried an egg case underneath the abdomen. Second and third instar larvae were collected in the field and compared with the morphology of the reared first instar larvae; as their morphology matched the first instar larvae in all characters except those known to vary between instars, we identify them as clearly belonging to *H. pallens*.

***Helochaeres (Hydrobaticus) anchoralis* Sharp, 1890**

(Figs. 35–37)

Material examined. JAPAN: Kyūshū: Kagoshima-ken: 35 L1, Kasekenmata, Tatsugō-chō, Amami-ōshima I., I.vii.2008 (fixed) (egg case carried by the adult collected in the field), MH.

General morphology. First instar. Colour. Head and sclerotised parts light yellowish brown; membranous parts milky white.

Head (Fig. 35A). Nasale projecting slightly further than left epistomal lobe, but not projecting further than right lobe (Fig. 36C). Epistomal lobes rounded, asymmetrical; right lobe projecting further than left lobe.

Antenna (Fig. 37A) short, rather stout. Scape slightly shorter than pedicel.

Mandibles (Figs. 37B–C): Distal inner teeth serrate; inner face of mandible serrate.

Maxilla (Figs. 37D–E): Maxillary palpomere 1 about as long as palpomere 4, palpomere 2 the shortest, palpomere 3 slightly longer than palpomere 4; palpomere 1 the widest.

Labium (Figs. 37F–G): Mentum longer and slightly wider than prementum, with small cuticular spines on dorsal surface. Labial palpi about as long as mentum; palpomere 1 much shorter than palpomere 2.

Thorax. Mesonotum with two dorsal sclerites on each side, each with five very long setae. Metanotum with one large dorsal sclerite on each side, each with five very long setae each.

Abdomen. Segment 1 with three visible dorsal sclerites on each side; anterior one narrow, small, posterior two very small, weakly sclerotised; each posterior sclerites with one long seta; segments 2 to 7 similar to segment 1 but dorsal sclerites very indistinct or absent.

Spiracular atrium (Fig. 35B): Segment 8 with large, oval dorsal plate; dorsal plate with four projections on posterior edge, inner two with two setae each; lateral part of dorsal plate

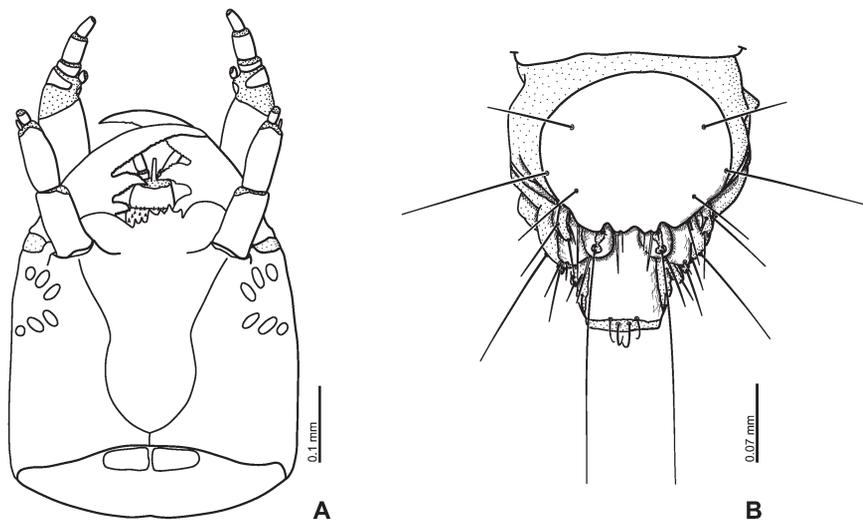


Fig. 35. *Helochaeres (Hydrobaticus) anchoralis* Sharp, 1890, first instar. A – head, dorsal view; B – spiracular atrium, dorsal view.

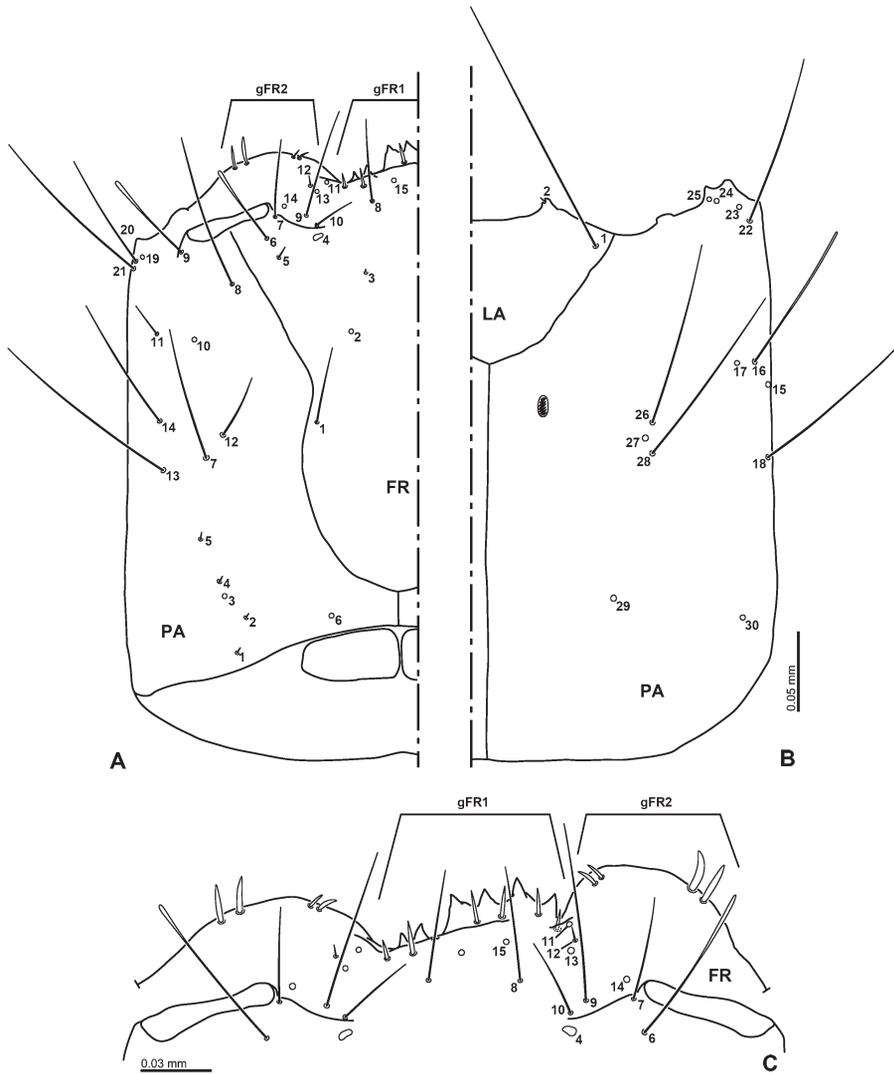


Fig. 36. Head capsule of *Helochares (Hydrobaticus) anchoralis* Sharp, 1890, first instar. A – dorsal view; B – ventral view; C – detail of anterior margin of head capsule, dorsal view.

with three long setae on each side, median one very long; procercus with one rather long stout seta and two rather long setae. Segment 9 trilobed; median lobe with two rather short and two moderately long setae on posterior edge; each lateral lobe with two moderately long setae on posterior edge.

Primary chaetotaxy of head. *Frontale* with 46 sensilla altogether (Figs. 36A, C). FR2 between FR1 and FR3. FR5 short seta. FR6 moderately long scale-like seta situated laterally of line

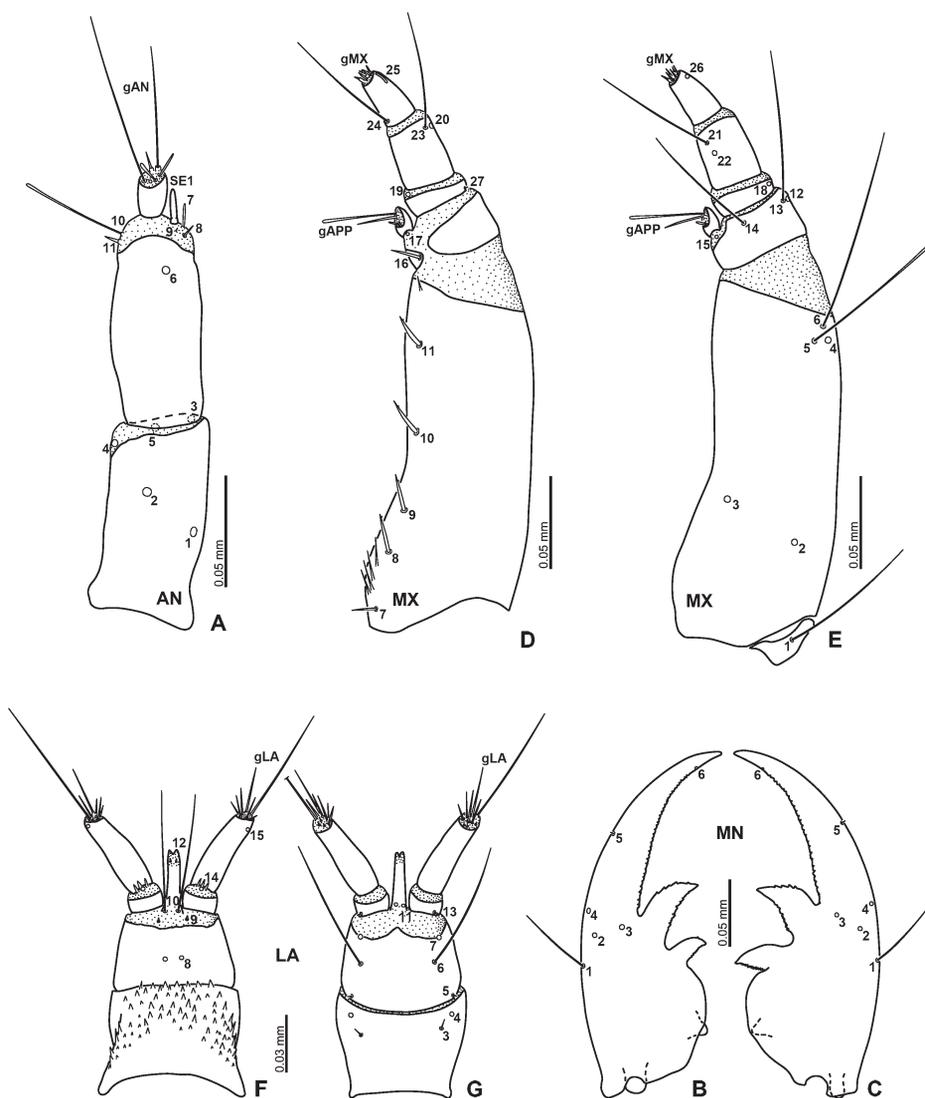


Fig. 37. Head appendages of *Helochares (Hydrobaticus) anchoralis* Sharp, 1890, first instar. A – antenna, dorsal view; B–C – mandibles, dorsal view; D – maxilla, dorsal view; E – maxilla, ventral view; F – labium, dorsal view; G – labium, ventral view.

connecting FR5 and FR7; FR7 moderately long seta. Nasale with a group of six stout, short setae and two small, pore-like sensilla (gFR1). Each epistomal lobe with two short setae on inner part, and two short, scale-like setae mediolaterally (gFR2). FR10 placed between FR4 and FR9, mesally of line connecting FR4 and FR9; one pore-like sensillum (FR14) situated anteriorly to inner margin of antennal socket. Location of FR11–13 slightly asymmetrical.

Right lobe with FR11 situated anteriorly to FR12, close to lateral seta on nasale, FR12 situated between FR11 and FR13, but laterally of line connecting FR11 and FR13. Left lobe with FR12 located more laterally of line connecting FR11 and FR13 than on right lobe.

Parietale (Figs. 36A–B): PA1–5 forming slightly irregular row. PA7 long trichoid seta; PA12 rather long seta. PA20 moderately long seta. PA16 long, narrow scale-like seta situated anteriorly to PA18, and between PA15 and PA17; PA17 close to PA16, situated anteromesally to PA16. PA26–28 situated ventrally on anterior and lateral 0.45 of parietale; PA27 situated mesally of line connecting PA26 and PA28. Two pore-like sensilla (PA29–30) located ventrally on about basal fourth of parietale.

Antenna (Fig. 37A): Antennomere 2 with one pore-like sensillum (AN6) situated dorsally close to distal margin of sclerite, and five setae (AN7–11) on intersegmentary membrane between antennomeres 2 and 3; AN7 rather short, rounded apically, AN8 shorter than AN7, rather stout, AN9 minute; AN7–9 on outer face of antenna next to sensorium SE1; setae AN10–11 on inner face of antenna; AN10 long, narrow scale-like, AN11 short, both setae close to each other.

Mandible (Figs. 37B–C): MN2 located posteriorly to line connecting MN3 and MN4, between MN1 and MN3; MN4 on lateral face. MN5 small seta.

Maxilla (Figs. 37D–E): One pore-like sensillum (MX12) and two very long setae (MX13–14) located ventrally on outer face of palpomere 1; MX12–13 on outer face of distal part of sclerite; MX12 situated more ventrally than MX13; MX14 situated ventrally on median part of distal margin of sclerite. MX23 and MX20 on distal part of outer face of sclerite of palpomere 3; MX20 situated more ventrally than MX23; MX21 situated ventrally on inner part of sclerite of palpomere 3, close to distal margin; MX22 behind MX21; MX24 very long, trichoid seta.

Labium (Figs. 37F–G): LA1 very long.

Habitat. Adults from which the larvae were reared were found in standing water.

Identification. Larvae were reared from an egg case carried by an identified adult female.

Helochares (Hydrobaticus) nipponicus Hebauer, 1995

(Figs. 1F, 6B, 38–43, 44C, 45D, 65C)

Material examined. JAPAN: HONSHŪ: Shimane-ken: 5 L2, 6 L3, San-nōji, Daitō-chō, Un-nan-shi (pond), 17.vii.2008, MH; 1 L3, Shakunouchi-kōen, Kisuki-chō, Un-nan-shi, 24.vi.2007, MH; 1 L1, same locality, 17.vii.2008, MH; 1 L1, 1 L2, 4 L3, same locality, 26.viii.2007, MH; 1 L2, 1 L3, same locality, 23.ix.2007, MH; 1 L2, same locality, 7.v.2008 (fixed), MH; 76 L1, Wadakami, Oku-uga-chō, Izumo-shi (pond), 12.vii.2008 (egg cases carried by adults collected in the field), MH; 13 L2, 6 L3, same locality, 12.vii.2008, MH; 3 L1, 4 L2, 5 L3, same locality, 28.vii.2008, MH; 2 L1, 4 L2, 1 L3, same locality, 19.viii.2008, MH.

General morphology. Third instar. Colour. Head and sclerotised parts light yellowish brown; membranous parts milky white (Fig. 1F).

Head. Nasale projecting slightly further than epistomal lobes (Fig. 42A). Epistomal lobes rounded, asymmetrical; right lobe projecting as far as left lobe.

Antenna short, rather slender (Fig. 42B). Scape longer than pedicel.

Mandibles: Inner teeth serrate (Figs. 42C–D); inner edge of mandibular apex serrate.

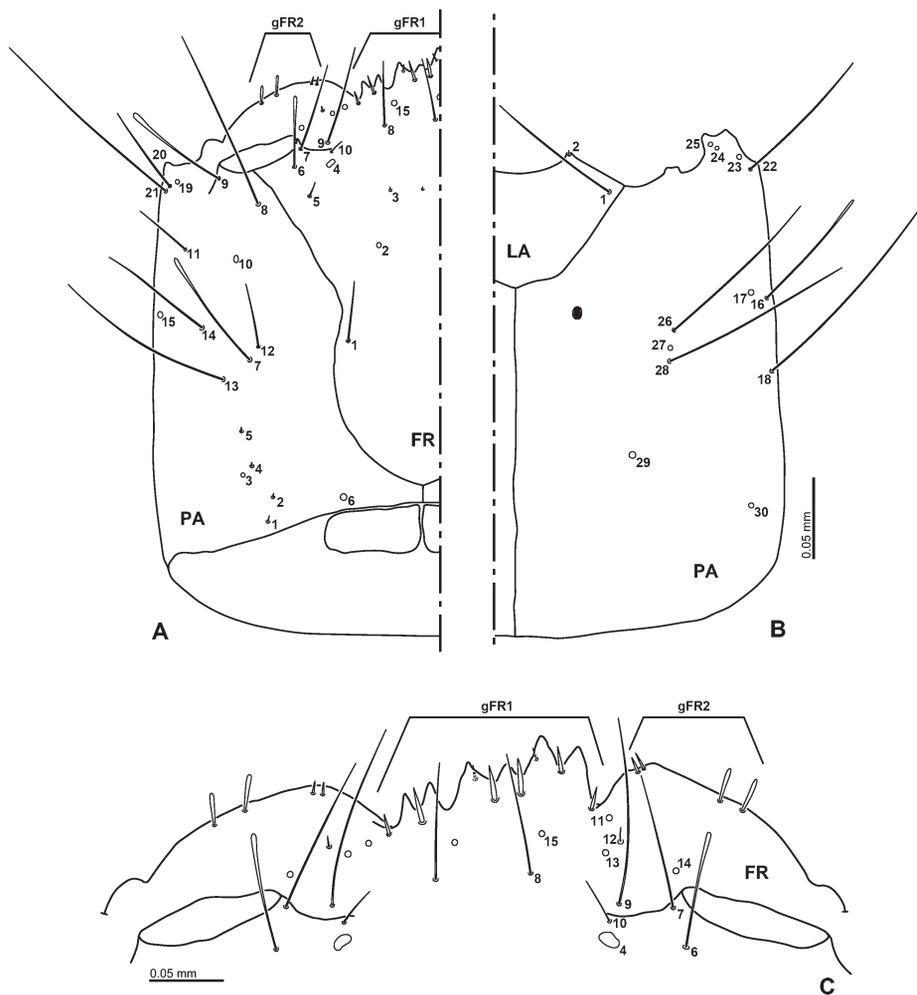


Fig. 38. Head capsule of *Helochaeres (Hydrobaticus) nipponicus* Hebauer, 1995, first instar. A – dorsal view; B – ventral view; C – detail of anterior margin of head capsule, dorsal view.

Maxilla (Figs. 42E–F): Maxillary palpomere 1 slightly shorter than palpomeres 3, palpomere 2 the shortest, palpomere 4 about as long as palpomere 1; palpomere 1 the widest.

Labium (Figs. 42G–H): Mentum bearing small, strong cuticular spines on dorsal surface. Labial palpi shorter than mentum, covered with narrow cuticular spines on dorsal surface of palpomere 2 and intersegmental membrane between palpomeres 1 and 2; palpomere 1 much shorter than palpomere 2.

Abdomen. Segment 1 with four dorsal sclerites on each side; two on anteromedian part, anterior one small, posterior one larger than anterior one; remaining two sclerites very small,

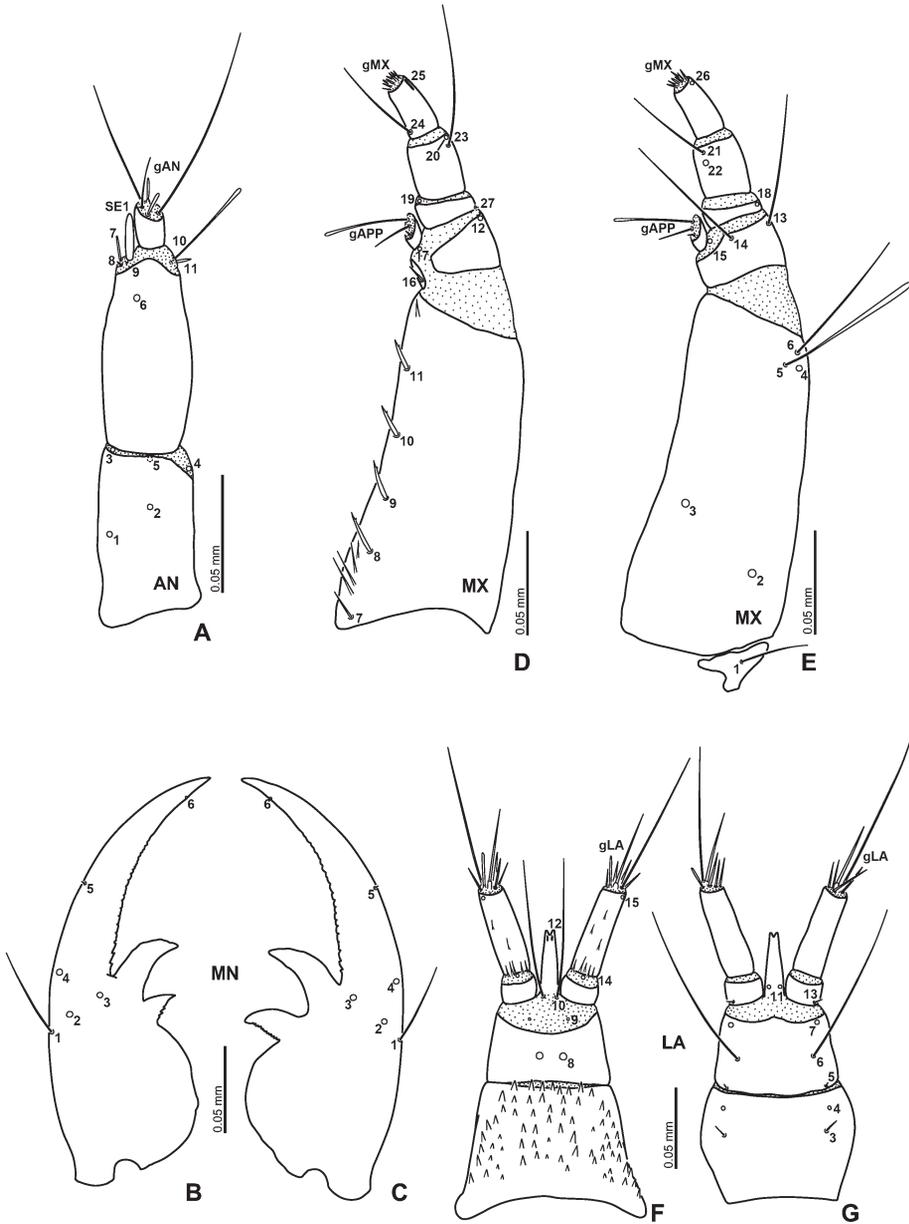


Fig. 39. Head appendages of *Helochaeres (Hydrobaticus) nipponicus* Hebauer, 1995, first instar. A – antenna, dorsal view; B–C – mandibles, dorsal view; D – maxilla, dorsal view; E – maxilla, ventral view; F – labium, dorsal view; G – labium, ventral view.

sometimes undetectable, situated behind former two sclerites, each bearing one rather long seta (Fig. 6B); segments 2 to 7 similar to segment 1 but with three dorsal sclerites on each side, one very small on anteromedian part, two hardly recognisable behind former sclerite.

Spiracular atrium (Fig. 41B): Segment 8 with large, oval dorsal plate; dorsal plate with four projections on posterior edge, each median projection weakly bifid, with two setae; each lateral part of dorsal plate with three long setae, median one longer than remaining ones; posterior part with two long and one short setae; procercus with one rather long stout seta and two rather long setae. Segment 9 trilobed; median lobe with two rather short and two long setae on posterior edge; each lateral lobe with two long setae on posterolateral surface.

Second instar. Similar to third instar, but more weakly sclerotised.

Head. Antenna: Scape about as long as pedicel (Fig. 40B).

Labium: Labial palpi about as long as mentum (Figs. 40G–H).

First instar. Similar to second instar, but more weakly sclerotised.

Head. Epistomal lobes weakly rounded, slightly asymmetrical (Fig. 38C).

Antenna proportionally short, rather stout (Fig. 39A). Scape distinctly shorter than pedicel.

Mandibles: Inner edge of basal tooth serrate (Figs. 39B–C).

Maxilla: Maxillary palpomere 1 slightly shorter than palpomeres 3 and 4 (Figs. 39D–E).

Thorax. Mesonotum with six long setae on each dorsal sclerite; metanotum with five long setae on each dorsal sclerite.

Abdomen. Segment 1 with three visible dorsal sclerites on each side; anterior one narrow, small; posterior two very small, weakly sclerotised, each with one long seta. Segments 2 to 7 similar to segment 1 but without anterior dorsal sclerites.

Spiracular atrium: Segment 8 with large, oval dorsal plate with four projections on posterior edge, each projection bifid at apex, looking like eight projections; procercus with one rather long stout seta and two rather long setae. Segment 9 trilobed; median lobe with two rather short and two moderately long setae on posterior edge of median lobe; each lateral lobe with two moderately long setae on posterior edge.

Primary chaetotaxy of head. *Frontale* altogether with 46 sensilla (Figs. 38A, C). FR2 between FR1 and FR3. FR5 short seta; FR6 moderately long scale-like seta, close to FR7; FR7 moderately long, trichoid. *Nasale* with a group of six stout short setae and two very short setae (gFR1). Each epistomal lobe with two short setae on inner part and two short scale-like setae on mediolateral part (gFR2). FR10 between FR4 and FR9; one pore-like sensillum (FR14) situated anteriorly to inner margin of antennal socket. Location of FR11–13 asymmetrical. Right lobe with FR11 situated anteriorly to FR12 close to lateral seta on nasale, FR12 between FR11 and FR13 but laterally of line connecting FR11 and FR13. Left lobe with FR13 situated between FR11 and FR12, posteriorly to line connecting FR11 and FR12, FR12 situated laterally of FR11.

Parietale (Figs. 38A–B): PA1–5 forming irregular row. PA7 long scale-like seta; PA12 rather long seta. PA20 rather long seta. PA17 close to PA16, situated anteromesally to PA16; PA16 long, narrow scale-like seta. PA26–28 in anterior 0.43 and lateral two-fifths of ventral surface of parietale. Two pore-like sensilla (PA29–30) located ventrally on about basal third of parietale.

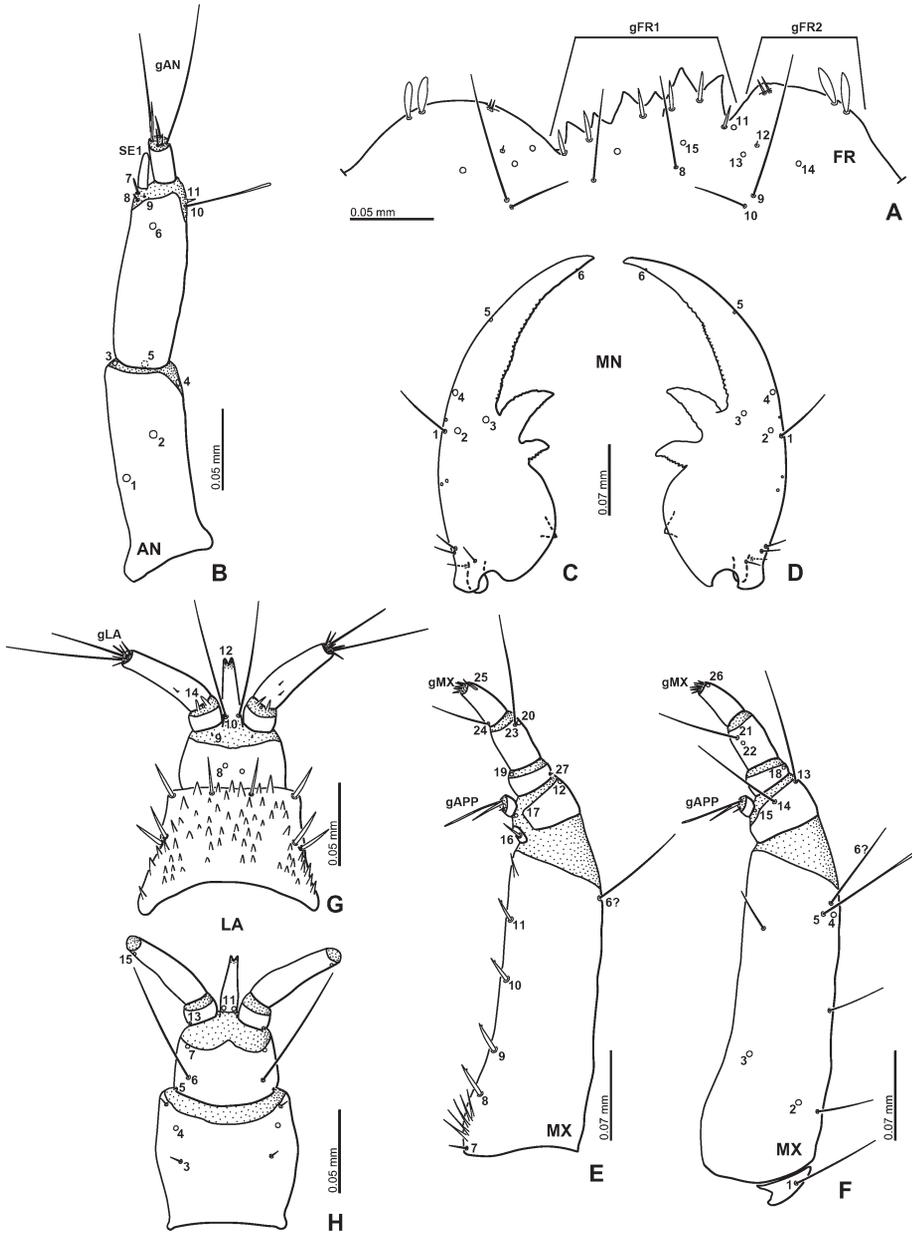


Fig. 40. *Helochares (Hydrobaticus) nipponicus* Hebauer, 1995, second instar. A – clypeolabrum, dorsal view; B – antenna, dorsal view; C–D – mandibles, dorsal view; E – maxilla, dorsal view; F – maxilla, ventral view; G – labium, dorsal view; H – labium, ventral view.



Fig. 41. *Helochares (Hydrobaticus) nipponicus* Hebauer, 1995, third instar. A – head, dorsal view; B – spiracular atrium, dorsal view.

Antenna (Fig. 39A): Antennomere 2 with one pore-like sensillum (AN6) situated dorsally close to distal margin of sclerite and five setae (AN7–11) on intersegmentary membrane between antennomeres 2 and 3. AN7 rather short, AN8 rather stout, shorter than AN7, AN9 minute; AN7–9 on outer face of antenna next to sensorium SE1; setae AN10–11 on inner face of antenna; AN10 long scale-like, AN11 short, both setae close to each other.

Mandible (Figs. 39B–C): MN2 located posteriorly to line connecting MN3 and MN4, between MN1 and MN3; MN4 on lateral face. MN5 small seta.

Maxilla (Figs. 39D–E): One pore-like sensillum (MX12) situated dorsally on outer face, close to distal margin of sclerite; distal part of ventral surface of sclerite with two very long setae (MX13–14); MX13 on outer face, close to MX12; MX14 situated more mesally than MX13. MX23 on distal part of outer face of sclerite; MX20 situated anteriorly to MX23; MX21 situated ventrally close to distal and lateral faces; MX22 behind MX21. MX24 long seta.

Labium (Figs. 39F–G): LA1 long; LA2 short.

Secondary chaetotaxy of head. Second instar. Frontale (Figs. 40A, 43A): One rather short secondary seta between FR1 and FR5 close to frontal line. Scale-like setae of gFR2 wider than those of first instar.

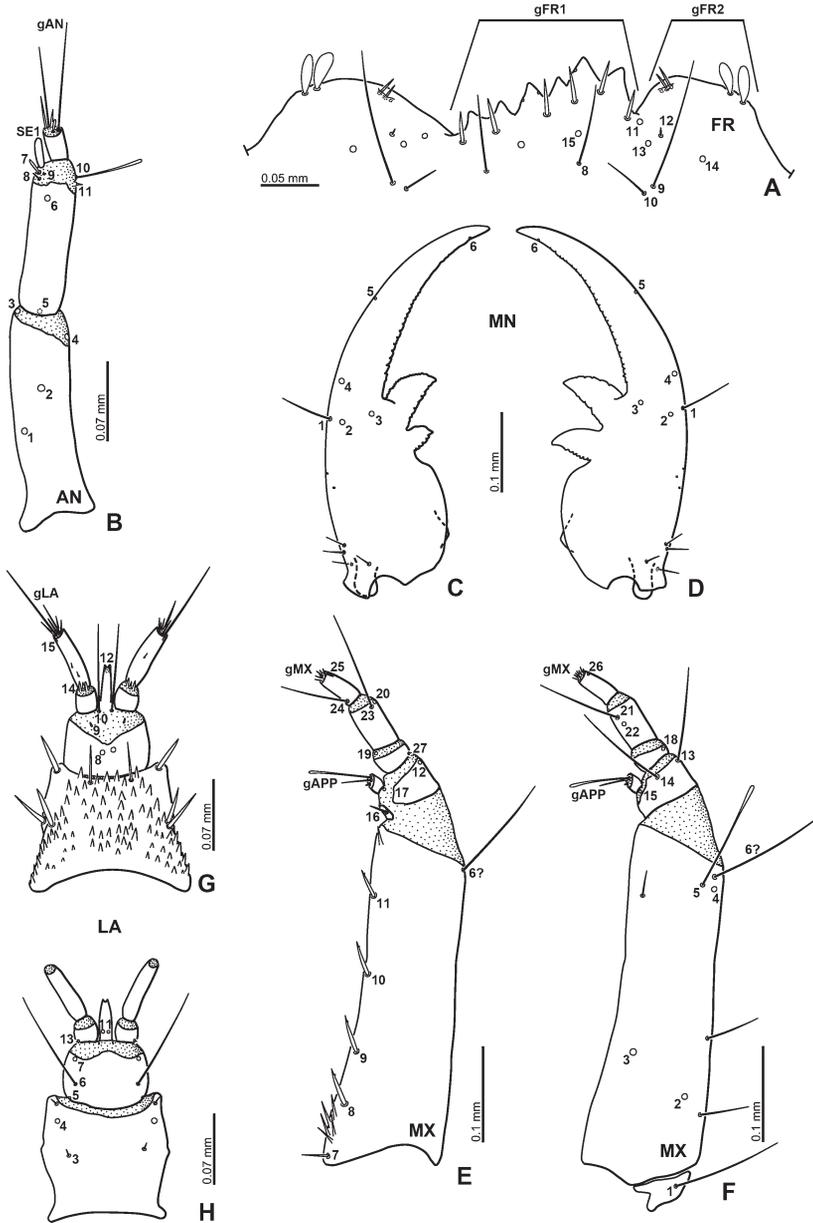


Fig. 42. *Helochaeres (Hydrobaticus) nipponicus* Hebauer, 1995, third instar. A – clypeolabrum, dorsal view; B – antenna, dorsal view; C–D – mandibles, dorsal view; E – maxilla, dorsal view; F – maxilla, ventral view; G – labium, dorsal view; H – labium, ventral view.

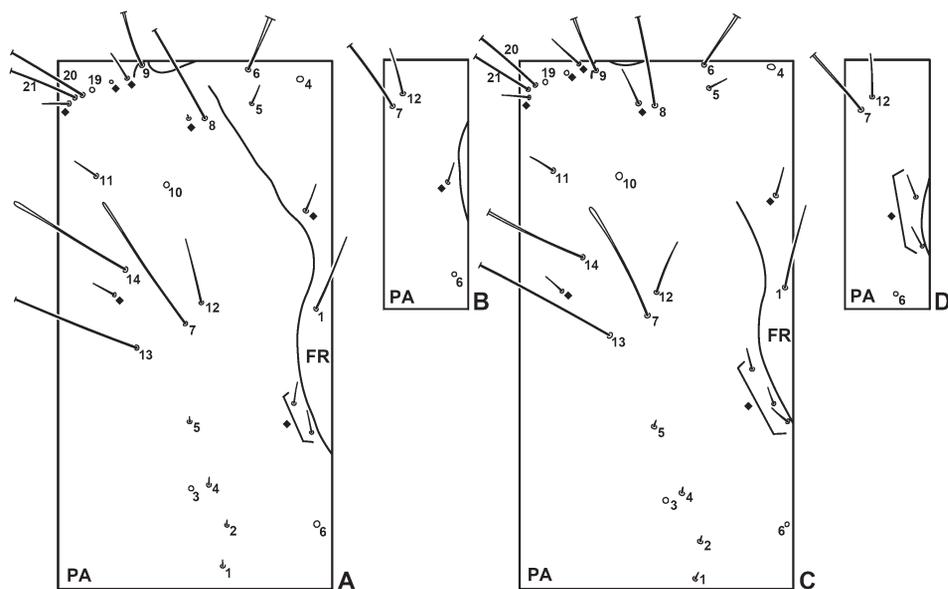


Fig. 43. *Helochaeres (Hydrobaticus) nipponicus* Hebauer, 1995, chaetotaxy of head capsule, dorsal view. A–B – second instar larva: A – median part of head capsule; B – intraspecific variation of secondary sensilla between PA6 and PA7. C–D – third instar larva: C – median part of head capsule; D – intraspecific variation of secondary sensilla between PA6 and PA7. Secondary sensilla are marked by a black rhombus.

Parietale (Figs. 43A–B): One to two secondary setae close to frontal line, mesally of line connecting PA6 and PA7. One short secondary seta close to PA8, more laterally than PA8. One pore-like secondary sensillum and one rather short secondary seta between PA9 and PA19, seta situated more mesally than pore-like sensillum. One rather short secondary seta close to PA21. One rather short secondary seta located close to PA14, posterolaterally to PA14. One short secondary seta situated on lateral surface of parietale close to PA16, more dorsally than PA16. Lateroventral surface with three secondary setae; one rather long seta close to PA17, situated anterolaterally to PA16; one seta close to PA18, situated anterolaterally to PA16; remaining sensilla moderately long, between PA16 and PA30, situated mesally of line connecting PA16 and PA30.

Mandible (Figs. 40C–D): Three secondary sensilla situated medioposteriorly on outer face of mandible, one close to MN1, remaining sensilla behind MN1; basal part of mandible bearing four rather short secondary setae on outer part.

Maxilla (Figs. 40E–F): Outer face of stipes with three rather long to long secondary setae; one long seta on apical part; rather long seta on anterior third and two-thirds respectively; inner part of stipes with one rather long secondary seta on distal fourth of ventral surface of sclerite.

Labium (Figs. 40G–H): Dorsal surface of mentum with three rather short, stout secondary setae on each lateral part, one on apical part, two on median part; one pair of rather short

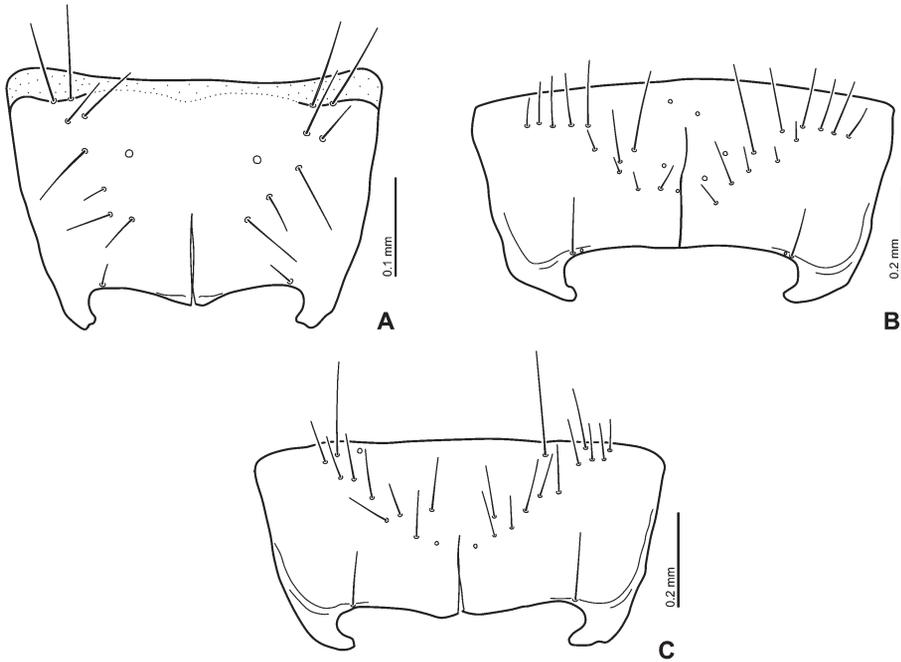


Fig. 44. Prosterna of Acidocerini species, third instar, ventral view. A – *Agraphydrus narusei* (Satô, 1960); B – *Enochrus umbratus* Sharp, 1884; C – *Helochares nipponicus* Hebauer, 1995.

moderately stout setae at midwidth of distal margin of mentum; one short secondary seta situated ventrally on each anterior corner.

Third instar. Similar to second instar larvae.

Frontale: Scale-like setae of gFR2 proportionally wider than those of second instar (Fig. 42A).

Parietale (Figs. 43C–D): Two to three rather short secondary setae close to frontal line, mesally of line connecting PA6 and PA7. Short secondary setae between PA16 and PA18, more close to PA18 than those of second instar, sometimes situated mesally to PA18.

Mandible (Figs. 42C–D): Three to four secondary sensilla in medioposterior part of outer face of mandible, one close to MN1, remaining sensilla behind MN1.

Maxilla (Figs. 42E–F): Outer face of stipes with three secondary setae, one long on distal part, two rather long in basal half.

Habitat. Standing water. Larvae were found in water (HAYASHI 2009a).

Identification. First instar larvae of this species were reared from the egg case carried by an identified female. Second and third instar larvae were collected in the field and compared with the reared first instar larvae.

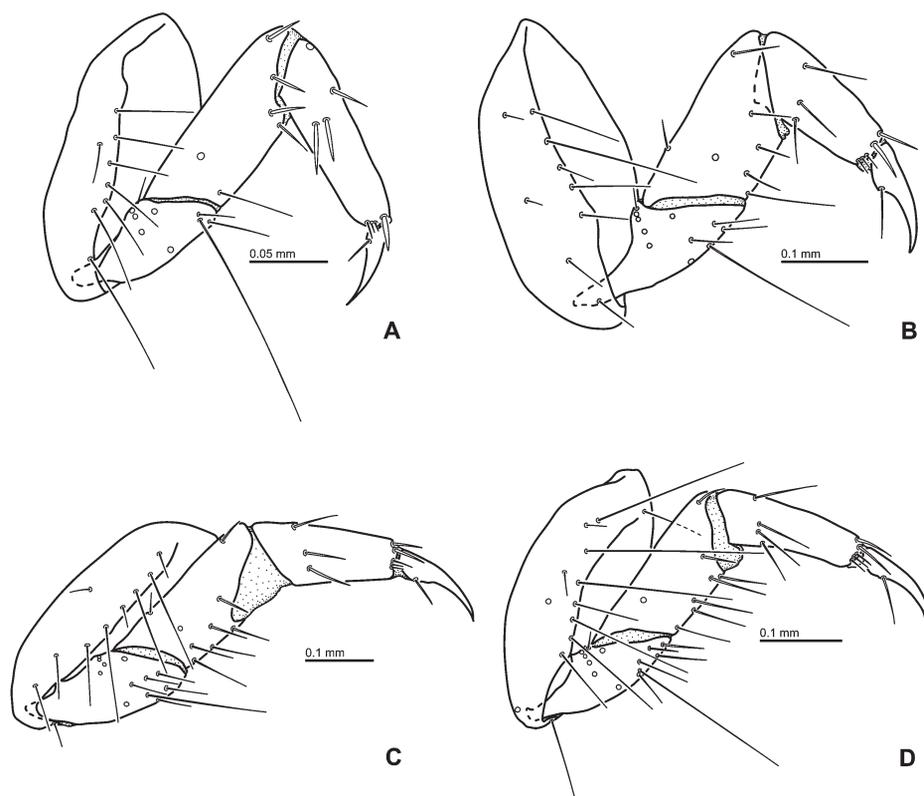


Fig. 45. Mesothoracic legs of Acidocerini species, third instar, anterior view. A – *Agraphydrus narusei* (Satô, 1960); B – *Enochrus umbratus* Sharp, 1884; C – *Enochrus japonicus* (Sharp, 1873); D – *Helochares nipponicus* Hebauer, 1995.

4.2. Tribe Hydrobiusini

Diagnosis. Dorsal surface of head capsule smooth, without densely arranged, strong tooth-like cuticular projections (Fig. 48A). Frontal lines V-shaped, converging towards base of head capsule (Figs. 46A, 48A); coronal line present. Epistomal lobes rounded, almost symmetrical, with four (or more) rather short, stout setae (Figs. 46C, 48C). Nasale with five teeth, never with a single median tooth (Figs. 46C, 48C). Inner face of scape bare, without inner projection or seta (Figs. 47A, 49A). Sensorium (SE1) on intersegmental membrane between scape and pedicel (Fig. 49A). Mandibles symmetrical, with three inner teeth (Figs. 49B–C). Apex of inner face of stipes with a spine-like cuticular projection (Fig. 49D). Labium without well developed hypopharyngeal lobe; mentum less than twice as wide as prementum (Figs.

47B, 49F); anterior corners of mentum not projecting anteriorly (Figs. 47B, 49F). Ligula well developed (e.g., Figs. 8F, 21F, 30F, 47B–C, 49F). Anterior margin of proscutum without fringe of long setae (e.g., Figs. 6, 51). Proscutum without lateral lobes (e.g., Figs. 6, 51). Legs rather long, well developed, without fringes of long swimming hairs (e.g., Figs. 45, 50C). Abdominal segments without tracheal gills (e.g., Figs. 3, 6). Ventral surface of abdominal segments without spinose prolegs. Median lobe of spiracular atrium simple, entire; prostyli reduced (Fig. 48B).

Genus *Hydrobius* Leach, 1815

Hydrobius pauper Sharp, 1884

(Figs. 1G, 6C, 46–50)

Material examined. JAPAN: HOKKAIDŌ: 2 L2, 1 L3, Sarobetsu-gen-ya, Toyotomi-chō, 12.–13.vii.2008, YM; 1 L2, Shinoro, Sapporo-shi, 26.vi.2009, YM.

General morphology. *Third instar.* *Body* rather slender, widest between abdominal segments 3 and 4 (Figs. 1G, 6C). *Colour* (Fig. 1G). Dorsal surface of head light brown, darker in posterolateral part, paler in anterolateral part. Proscutum light brown medially and laterally; dorsal surface of meso- and metathorax, and abdominal segments with two darker brown longitudinal lines, brown to light brown on sclerites, greyish white on membranous parts, paler medially. Ventral surface of thorax and abdomen greyish white, proscutum pale yellowish brown.

Head (Figs. 48A, C). Head capsule subquadrate. Frontal lines almost V-shaped, fused at base of head capsule, coronal line short. Six stemmata on each anterolateral portion of head capsule. Clypeolabrum slightly asymmetrical. Nasale with five teeth, two on right more closely aggregated and projecting further anteriorly than two on left side. Epistomal lobes rounded, almost symmetrical, not projecting further than nasale, with small spine-like cuticular projection on inner margin.

Antenna (Fig. 49A) 3-segmented, rather slender. Scape the longest, distinctly longer than pedicel. Flagellum the shortest.

Mandibles (Figs. 49B–C) symmetrical, each with three inner teeth; distal two teeth large, basal one small; inner face of mandibular apex smooth.

Maxilla (Figs. 49D–E) 6-segmented (including cardo), distinctly longer than antenna. Cardo small, irregularly shaped. Stipes the longest, longer than palpomeres 1–4 combined; distal margin of stipes with spine-like cuticular projection on inner face; base of inner face bearing small cuticular projections. Maxillary palpus 4-segmented, palpomere 2 the shortest, palpomere 3 the longest, palpomere 1 slightly shorter than palpomere 4; palpomere 1 the widest, incompletely sclerotised on dorsal surface; inner process sclerotised.

Labium (Fig. 49F) well developed. Submentum fused to head capsule, large, subpentagonal, wider than mentum (e.g., Fig. 46B). Mentum trapezoidal in dorsal view, wider than prementum, bearing small, strong cuticular spines dorsally. Prementum subquadrate, slightly wider than long. Ligula distinctly shorter than labial palpi, largely sclerotised. Membrane between sclerite of prementum and palpi bear short cuticular spines laterally. Labial palpi longer than prementum, covered with narrow cuticular spines on palpomere 2 and intersegmental membrane between palpomeres 1 and 2.

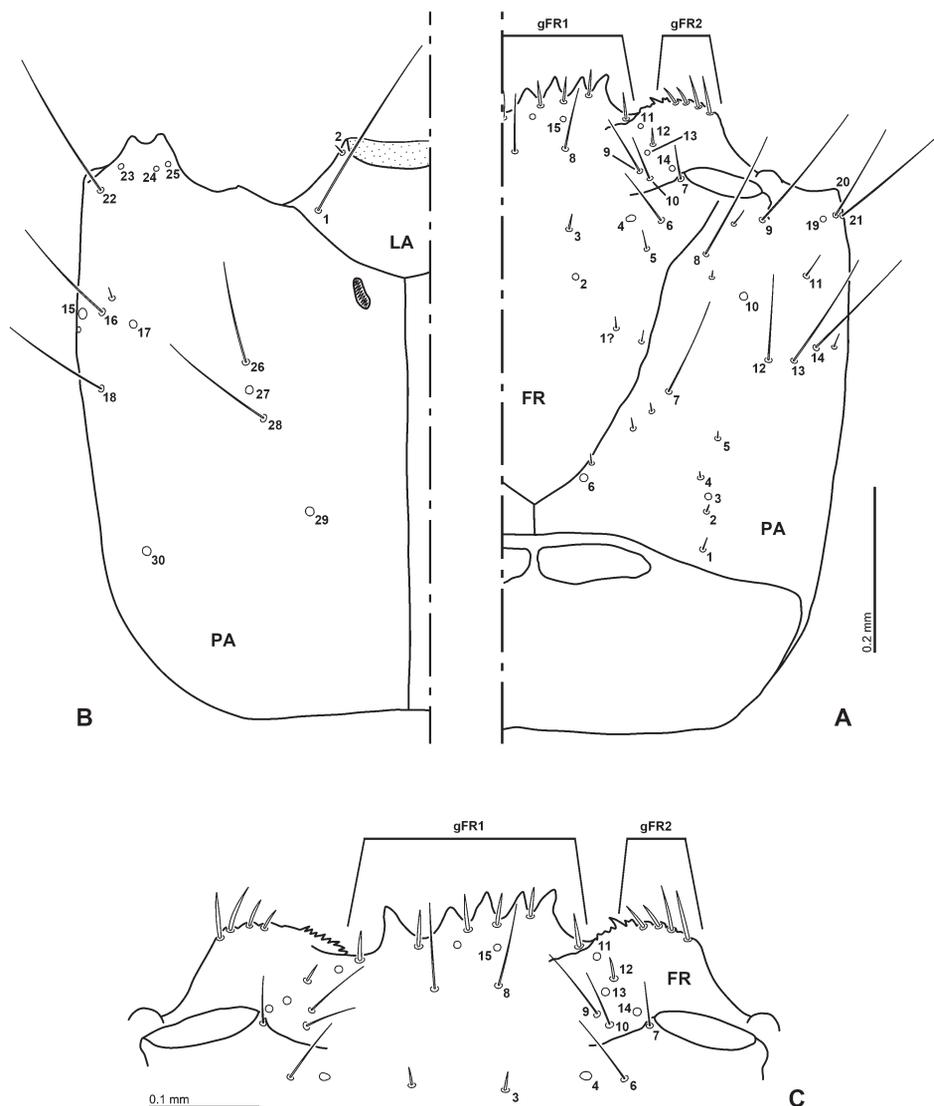


Fig. 46. Head capsule of *Hydrobius pauper* Sharp, 1884, second instar. A – dorsal view; B – ventral view; C – detail of anterior margin of head capsule, dorsal view.

Thorax. Prothorax wider than head capsule (Fig. 6C). Proscutum formed by large plate subdivided by fine sagittal line, bearing densely arranged short to rather long setae and minute hair-like cuticular projections (Fig. 50A). Prosternum rectangular, with almost complete sagittal line (Fig. 50B). Mesothoracic tergum with two sclerites on each side, anterior one narrow, posterior one large; metathoracic tergum with two sclerites, anterior one large,

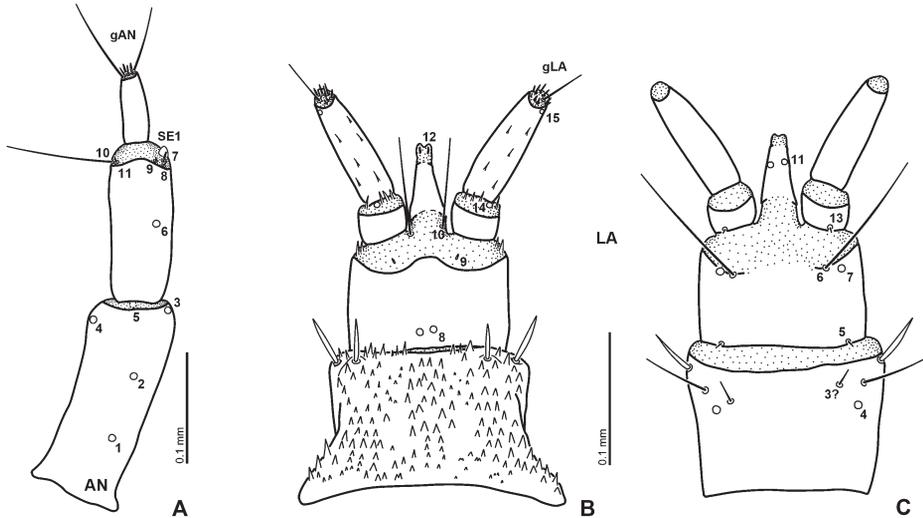


Fig. 47. Head appendages of *Hydrobius pauper* Sharp, 1884, second instar. A – antenna, dorsal view; B – labium, dorsal view; C – labium, ventral view.

posterior one small (Fig. 6C). Legs (Fig. 50C) rather short, weakly visible in dorsal view, 5-segmented, all pairs similar in shape.

Abdomen. Abdomen 10-segmented, tapering towards posterior end, segments 8 to 10 forming spiracular atrium (Fig. 6C); segments 1 to 7 similar in shape and size. Segment 1 with three dorsal sclerites on each side; anterior one oval, small; posterior two very small, weakly sclerotised, each with one long seta; segments 2 to 7 similar to segment 1 but anterior sclerites smaller (Fig. 6C).

Spiracular atrium (Fig. 48B): Segment 8 with large, oval dorsal plate; posterior edge of dorsal plate with three emarginations medially; dorsal surface of plate bearing numerous rather short setae; procercus incompletely sclerotised, with one rather long and two short setae. Segment 9 trilobed, partially sclerotised; median lobe almost as large as lateral lobes, with two long and two short apical setae; each lateral lobe with one long seta and three short to rather short apical setae; acrocerci undetectable; urogomphi short, one segmented; prostyli reduced.

Second instar. Very similar to third instar.

Head. Antenna (Fig. 47A) rather slender, proportionally shorter than in third instar. Scape slightly longer than pedicel.

Labium (Figs. 47B–C): Labial palpi slightly wider than in third instar. Anterior margin of mentum slightly wider than prementum.

Chaetotaxy of head. Second instar. *Frontale* altogether with 44 primary sensilla and two secondary sensilla (Figs. 46A, C). Central part with four pairs of sensilla divergent posteriad; FR1 and one short secondary seta at midlength and close to frontal line; FR2 pore-like situated

anteromesally to FR1, between FR1 and FR3; FR3 short and rather stout seta at midwidth and in anterior third of frontale. Two setae (FR5 and FR6) and one pore-like sensillum FR4 situated posteromesally to antennal socket, forming a triangular group; FR5 rather short; FR6 moderately long. Seta FR7 rather short close to inner margin of antennal socket. Nasale with a group of six almost equidistant, stout and rather short setae (gFR1). Each epistomal lobe with a group of four short to moderately long setae (gFR2), two mesal setae distinct shorter than lateral ones. Pore-like sensillum FR15 placed posteriorly to median setae of nasale; seta FR8 situated posteriorly to FR15. Two moderately long trichoid setae (FR9 and FR10) situated between FR7 and FR8, slightly anteromesally to antennal socket. Four sensilla (FR11–14) on epistomal lobe, forming an irregular row; FR11 on anteromesal margin of epistomal lobe, close to gFR1; FR12 and FR13 at midlength between FR11 and FR14; FR14 situated close to inner margin of antennal socket, anteriorly to FR7; FR11 and FR13–14 pore-like sensilla, FR12 short and rather stout seta.

Parietale with 30 sensilla and seven secondary sensilla each (Figs. 46A–B). Dorsal surface with a group of five posterior sensilla (PA1–5) forming a slightly irregular longitudinal row at midwidth; PA3 pore-like between PA2 and PA4; remaining sensilla short setae. PA6 pore-like, situated anterolaterally to joint of frontal and coronal lines. Three short secondary setae between PA6 and PA7. PA7 long seta, situated anteromesally to PA5, equidistant from PA6 and PA8 as well as PA5 and FR1. Seta PA8 long, behind antennal socket close to frontal line; one short secondary seta situated posterolaterally to PA8. Seta PA9 long, close to outer margin of antennal socket; one rather short secondary seta located behind antennal socket, mesally of PA9. Two sensilla (PA10 and PA11) behind antennal socket, between PA9 and PA12–14; PA10 pore-like sensillum, PA11 rather short seta. Three long setae (PA12–14) at about midlength of parietale, behind PA10 and PA11; one short secondary seta situated slightly laterally of PA14. Anterior corner of epicranium with one pore-like sensillum (PA19) and three moderately long to long setae, PA19 situated dorsally to remaining setae; PA20 between PA19 and PA21; PA22 situated ventrally to remaining sensilla; PA20 and PA21 moderately long setae, PA22 long seta. Two pore-like sensilla (PA15 and PA17) and two long setae (PA16 and PA18) on anterior third of lateroventral surface of parietale; PA16 between PA15 and PA17; PA18 behind PA15–17. Ventral surface with three pore-like sensilla (PA23–25) on anterior margin close to mandibular acetabulum; PA23 on outer part, PA24 and PA25 on inner part; PA24 between PA23 and PA25. Two long setae (PA26 and PA28) and one pore-like sensillum (PA27) situated ventrally on median part of parietale; PA27 between PA26 and PA28. Two pore-like sensilla (PA29 and PA30) situated ventrally on basal third; PA30 on lateral portion; PA29 close to gular sulcus.

Antenna (Fig. 47A): Antennomere 1 with five pore-like sensilla (AN1–5); AN1 on basal third; AN2 on basal 0.67; AN3–5 on distal margin, AN3 and AN4 on outer and inner face of sclerite respectively; AN5 situated ventrally. Antennomere 2 with seven sensilla (AN6–11 and SE1); AN6 pore-like, located dorsally at midlength of sclerite; AN7–11 on intersegmentary membrane between antennomeres 2 and 3; small setae AN7–9 on outer part of antenna, behind and close to SE1; long seta AN10 and short seta AN11 on outer face of antenna; SE1 small, about as long as AN7. Antennomere 3 with apical sensilla (gAN) on apical membranous area; gAN with two rather long and several short setae.

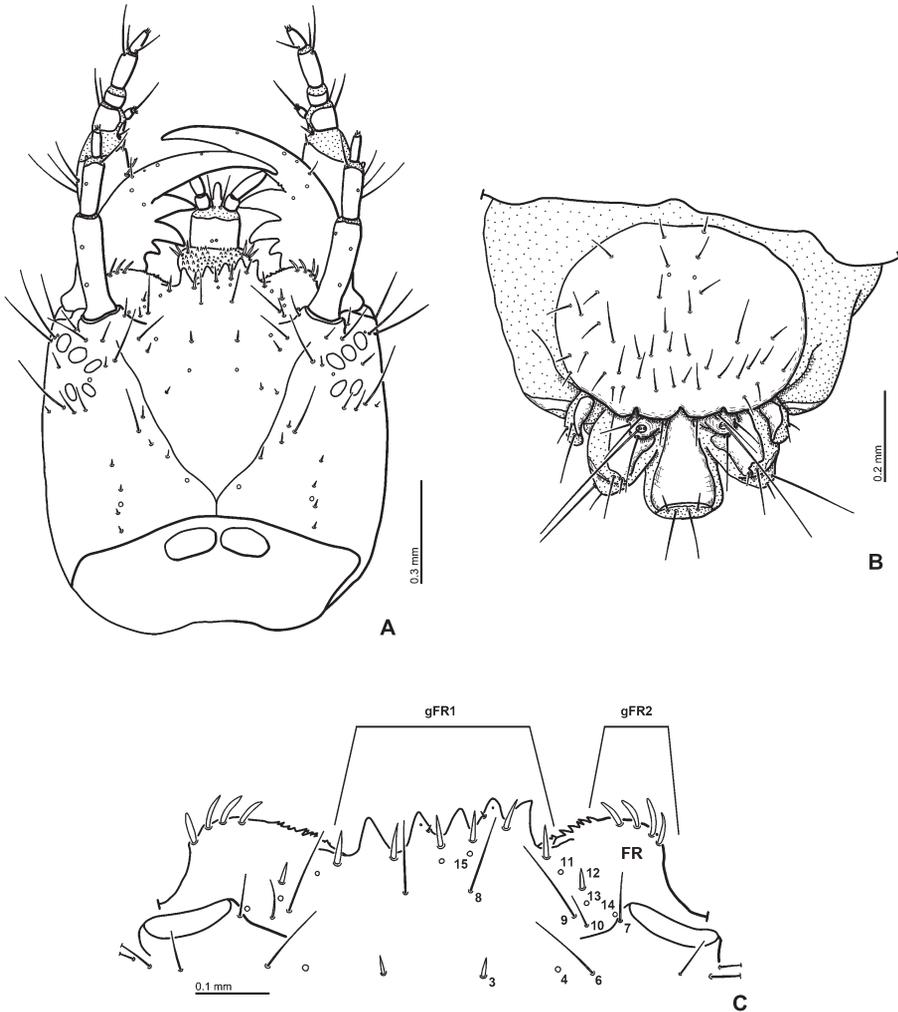


Fig. 48. *Hydrobius pauper* Sharp, 1884, third instar. A – head, dorsal view; B – spiracular atrium, dorsal view; C – detail of anterior margin of head capsule, dorsal view.

Mandible (e.g., Figs. 49B–C) with two setae (MN1 and MN5) and four pore-like sensilla (MN2–4 and MN6), and with small secondary setae in basal half of outer face. MN1 moderately long, at midlength of outer face of mandible. MN2–4 on median part of dorsal surface; MN2 at midlength between MN1 and MN3; MN4 situated on outer face, anteriorly to MN1. Seta MN5 minute, on outer face of subapical part of mandible. MN6 situated subapically on inner face of mandible.

Maxilla (e.g., Figs. 49D–E) Cardo with one moderately long ventral seta (MX1). Stipes with a row of five rather short stout setae (MX7–11) situated dorsally along inner face; MX7–11

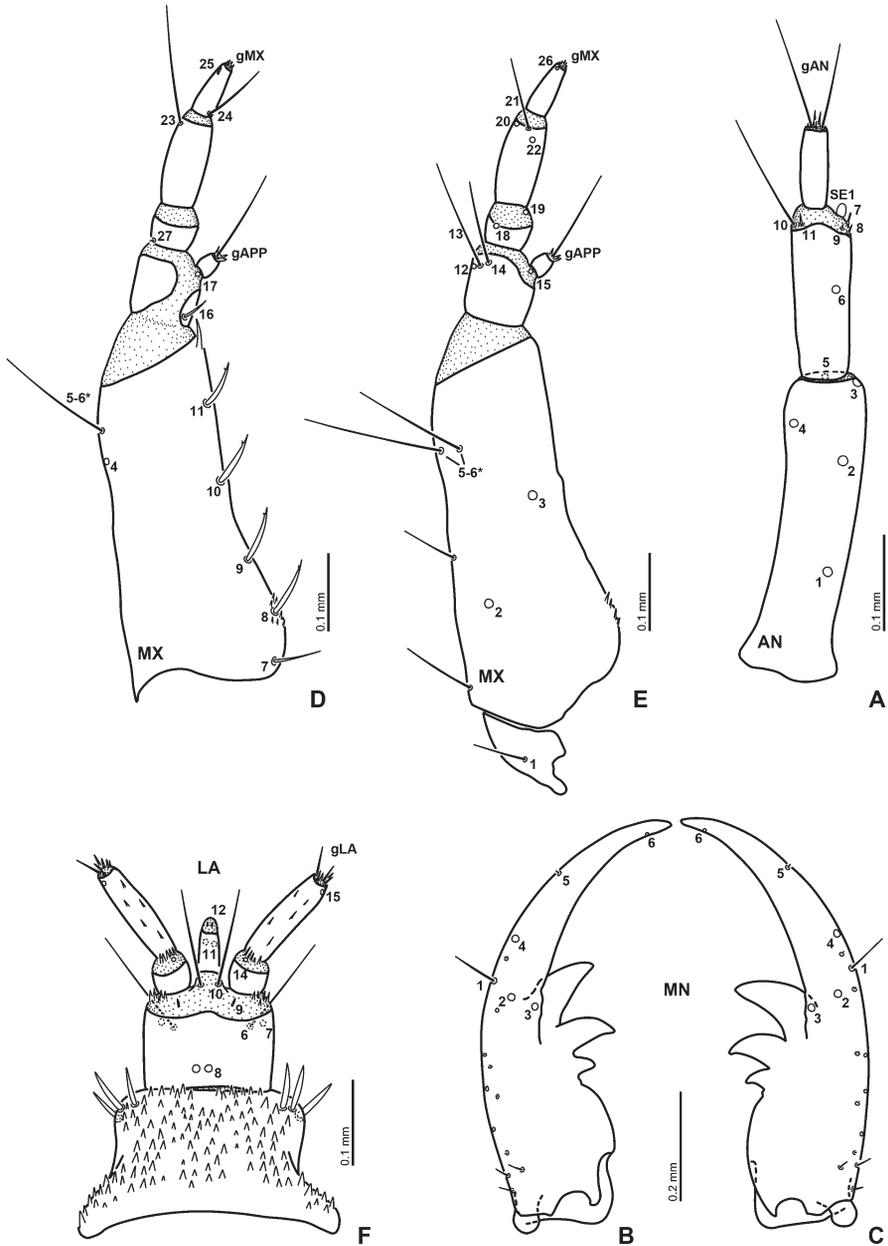


Fig. 49. Head appendages of *Hydrobius pauper* Sharp, 1884, third instar. A – antenna, dorsal view; B–C – mandibles, dorsal view; D – maxilla, dorsal view; E – maxilla, ventral view; F – labium, dorsal view.

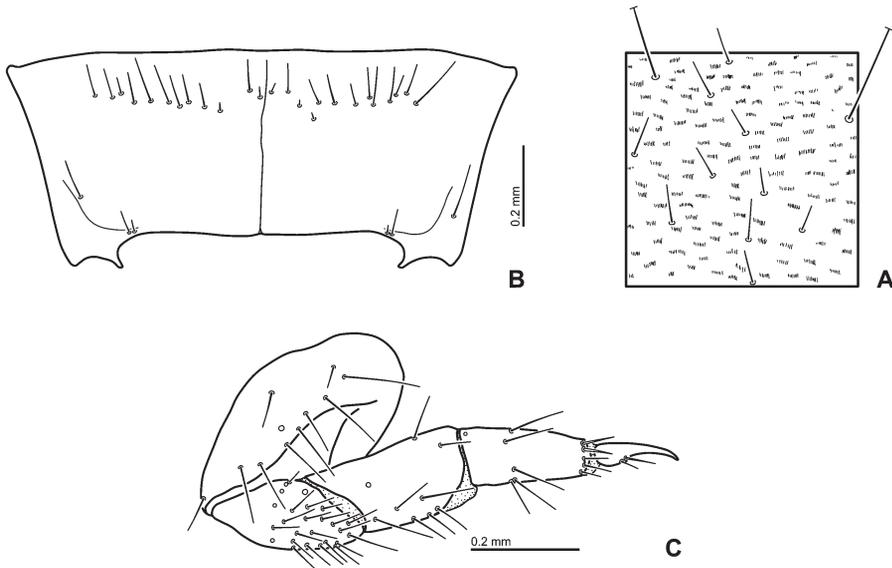


Fig. 50. Thoracic structures of *Hydrobius pauper* Sharp, 1884, third instar. A – surface of proscutum; B – prosternum, ventral view; C – mesothoracic leg, anterior view.

almost equidistant; MX8–11 with subapical tooth. Ventral surface of stipes with three pore-like sensilla (MX2–4), two long setae (MX5–6), and three secondary setae; MX2 on basal fourth of sclerite; MX3 on apical two-fifths of sclerite; MX4–6 on outer face of apical part of sclerite; three moderately long secondary setae on outer face, one situated basally, one at midlength of sclerite, one situated distally; distal one close to MX4–6. Palpomere 1 with four sensilla on sclerite (MX12–14 and MX16); one moderately short spiniform seta (MX16) situated dorsally on base of inner face; MX12 pore-like, situated subapically on outer face of sclerite; MX13–14 long setae situated subapically close to and mesally of MX12; MX13 between MX12 and MX14. Two pore-like sensilla (MX15 and MX17) on membrane behind inner appendage, MX17 dorsal, MX15 ventral. Inner appendage with one rather long trichoid seta and rather to very short setae (gAPP). Palpomere 2 with two pore-like sensilla (MX18–19) and one minute seta (MX27); MX18 situated ventrally on outer part of sclerite; MX19 on inner face of intersegmental membrane between palpomeres 2 and 3; MX27 on outer face of basal margin of sclerite. Palpomere 3 with two long setae (MX21 and MX23) and two pore-like sensilla (MX20 and MX22); MX20 and MX23 situated distally on outer face of sclerite; MX21 at midwidth of ventral surface, on borderline of sclerite and intersegmental membrane between palpomeres 3 and 4; MX22 located posteriorly to MX21. Palpomere 4 with one long seta (MX24) situated basally on inner face of sclerite, and with digitiform sensillum (MX25) and pore-like sensillum (MX26) situated subapically on outer face, MX25 dorsal, MX26 ventral. Apical membranous area of palpomere 4 with minute setae (gMX).

Labium (Figs. 47B–C): Submentum with two pairs of setae (LA1–2); LA1 very long, in lateral corners, LA2 short on anterior margin. Anterolateral face of mentum with three rather long, stout secondary setae, two on dorsal, one on ventral. Ventral surface of mentum with two primary sensilla (LA3 and LA4) and one secondary seta on anterolateral part of sclerite; rather short seta (LA3), pore-like sensillum (LA4) and one rather long secondary seta forming a triangular group; LA3 situated more mesally than remaining sensilla, LA4 situated slightly lateroposteriorly to LA3; one rather short, stout secondary seta on anterior corner of sclerite. Dorsal surface of prementum with a pair of pore-like sensilla (LA8) at midwidth of sclerite close its posterior margin. Ventral surface of prementum with three pairs of sensilla (LA5–7) on outer part; seta LA5 short on posterior margin; LA6 and LA7 close to or on distal margin of sclerite; LA6 long seta; LA7 pore-like. Membrane between sclerite of prementum and palpi with a pair of pore-like sensilla (LA9) and moderately long setae (LA10) dorsally; LA9 close to basal margin of sclerite; LA10 at base of ligula. Ligula with two pairs of subapical pore-like sensilla (LA11 and LA12); LA12 situated dorsally on apical membranous area; LA11 situated ventrally on sclerite. Palpomere 1 with one minute seta (LA13) situated ventrally on basal margin of sclerite; LA14 pore-like, on dorsal surface of intersegmentary membrane between palpomeres 1 and 2. Palpomere 2 with one pore-like sensillum (PA15) situated subapically on outer face of sclerite. Apical membranous area of palpomere 2 with several short setae (gLA).

Third instar. Very similar to second instar larva.

Antenna: AN4 situated in subapical part of antennomere 1 (Fig. 47A).

Habitat. Standing water. Larvae were found in water.

Identification. The larvae of the genus *Hydrobius* are known and therefore may be easily recognised (RICHMOND 1920, BØVING & HENRIKSEN 1938, BERTRAND 1972, ARCHANGELSKY 1997, FIKÁČEK et al. 2008). Only one species of *Hydrobius*, *H. pauper*, is distributed in Japan and the larval material collected in the field may therefore be clearly assigned to this species. The Japanese record of *Hydrobius fuscipes* (Linnaeus, 1758) by HANSEN (1999) is doubtful and *H. fuscipes* is not considered a part of the Japanese fauna.

4.3. Tribe Hydrophilini

Diagnosis. Dorsal surface of head capsule without densely arranged, strong tooth-like cuticular projections (Figs. 54A, 58A, 62A). Frontal lines V- or U-shaped, converging towards base of head capsule (Figs. 54A, 58A, 62A); coronal line present. Epistomal lobes not or moderately extended anteriorly, setation of the lobes on both sides more or less the same (Figs. 52C, 55A, 56C, 60C, 62B). Shape of nasale variable (straight, weakly rounded, serrate, or with at least two teeth, never with a single median tooth; Figs. 52C, 55A, 56C, 60C, 62B). Scape with numerous setae at least in the second and third instars (Figs. 55B, 59A–B, 63A) (all instars of *Hydrophilus* bear numerous setae on scape; Fig. 57A). Stipes with one to several cuticular projections, never with densely arranged cuticular projections on most of inner face (Figs. 55F–G; 57D–E; 63E–F). Labium without well developed hypopharyngeal lobe; mentum at

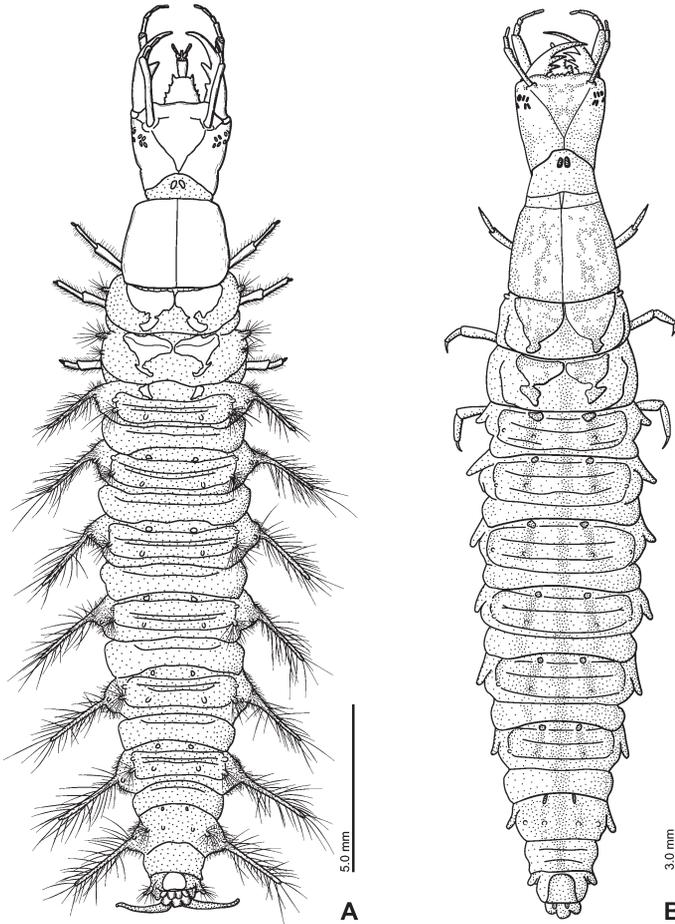


Fig. 51. Habitus of Hydrophilini species, third instar, dorsal view. A – *Hydrochara affinis* (Sharp, 1873); B – *Sternolophus rufipes* (Fabricius, 1792).

least twice as wide as prementum (Figs. 55H, 61F, 63G); anterior corners of mentum strongly projecting anteriorly (Figs. 57F, 63G); prementum with one pair of small membranous areas completely surrounded by sclerite (Figs. 53F, 57F, 63G). Ligula well developed (Figs. 55H, 57F–G, 61F). Anterior margin of proscutum without fringe of long setae (Fig. 51). Proscutum without lateral lobes (Fig. 51). Legs moderately long, well developed, with fringes of long swimming hairs (Figs. 64B–D). Abdominal segments without tracheal gills (Fig. 51). Ventral surface of abdominal segments without spinose prolegs. Median lobe of spiracular atrium simple, entire; prostyli reduced (*Sternolophus*) to long (*Hydrochara* and *Hydrophilus*) (Figs. 54B, 58B, 62C).

Key to the genera of the tribe Hydrophilini from Japan (all instars)

1. Frontal lines U-shaped (Fig. 58A); mandibles strongly asymmetrical, left mandible with one inner tooth, right mandible with two closely aggregated inner teeth (Figs. 57B–C).
..... *Hydrophilus* Geoffroy, 1762
- Frontal lines V-shaped (Fig. 54A); mandibles almost symmetrical, both mandibles similar in shape and with the same number of inner teeth (Figs. 53B–C). 2
2. Nasale with five distinct teeth (Figs. 60C, 62B); each mandible with three inner teeth, distal two large, basal one small (Figs. 61B–C, 63C–D); abdominal segments with short lateral projections (Fig. 51B). *Sternolophus* (Fabricius, 1792)
- Nasale without distinct teeth, almost straight or slightly serrate (Figs. 52C, 55A); mandibles with two inner teeth, distal one large, basal one small (Figs. 53B–C, 55D–E); abdominal segments with long lateral projections (Fig. 51A). *Hydrochara* Berthold, 1827

Genus *Hydrochara* Berthold, 1827

(Figs. 2A–B, 51A, 52–55, 64A–B, 65B, 67B)

Diagnosis. This genus is distinguished from Japanese Hydrophilini by the following combination of characters: (1) frontal lines V-shaped (Fig. 54A); (2) nasale without distinct teeth, slightly serrate (Figs. 52C, 55A); (3) inner face of scape strongly serrate in first instar (Fig. 53A); (4) three setae (AN7–9) close to antennal sensorium (SE1) (Fig. 53A); (5) mandibles symmetrical, with two inner teeth (Figs. 53B–C, 55D–E); (6) abdominal segments with long setiferous projections on each side (Figs. 2A–B, 51A).

***Hydrochara affinis* (Sharp, 1873)**

(Figs. 2A–B, 51A, 52–55, 64A–B, 65B, 67B)

Material examined. JAPAN: HONSHŪ: Shimane-ken: 29 L1, Nakanosu, Nadabun-chô, Izumo-shi, 26.v.2008 (egg cases collected in the field), 28.v.2008 (fixed), MH; 1 L3, Midami-chô, Izumo-shi (paddy field), 31.v.2008, MH; 1 L1, Nakanosu, Nadabun-chô, Izumo-shi, 14.v.2008, MH; 1 L3, same locality, 22.v.2008, MH; 2 L3, same locality, 24.v.2008, MH; 1 L3, Nakanosu, Nadabun-chô, Izumo-shi (paddy field), 26.v.2008, MH; 2 L3, same locality, 1.vi.2008, MH; 1 L1, 4 L3, same locality, 11.vi.2008, MH; 1 L3 (HGF), Okinoshima, Sono-chô, Izumo-shi (paddy field), 10.vi.2007, MH.

General morphology. Third instar. *Body* rather thick (Figs. 2B, 51A). *Colour.* Head and sclerotised parts yellowish brown; non-sclerotised parts greyish white to light yellowish brown (e.g., Figs. 2A–B).

Head. Head capsule subtrapezoidal, widest anteriorly (Fig. 54A). Frontal lines almost V-shaped, fused at base of head capsule, coronal line very short. Surface of head capsule smooth. Six stemmata on each anterolateral portion of head capsule. Clypeolabrum almost symmetrical (Fig. 55A). Nasale weakly rounded, slightly serrate. Epistomal lobes almost symmetrical, rounded, not projecting anteriorly.

Antenna (Figs. 55B–C) 3-segmented, long, slender. Scape longer than pedicel and flagellum combined; inner face smooth. Pedicel with outer membranous area completely surrounded by sclerite, situated at midlength of sclerite. Flagellum slightly longer than pedicel.

Mandibles (Figs. 55D–E) symmetrical, with two inner teeth, distal one larger than basal one; inner teeth and inner edge of mandibular apex slightly serrate.

Maxilla (Figs. 55F–G) 6-segmented (including cardo), slightly longer than antenna. Cardo small, irregularly shaped. Stipes the longest, longer than palpomeres 1–4 combined; inner face bearing tiny spine-like cuticular projections between two basal-most setae. Maxillary palpus 4-segmented, palpomere 1 about as long as palpomere 3, palpomeres 1 and 3 each the longest, palpomere 2 the shortest, palpomere 4 slightly longer than palpomere 2; palpomere 1 the widest, completely sclerotised; inner process sclerotised.

Labium (Figs. 55H–I) well developed. Submentum fused to head capsule, large, subpentagonal, wider than mentum (e.g., Fig. 52B). Mentum subtrapezoidal in dorsal view, distinctly wider than prementum, dorsal surface bearing densely arranged, tiny cuticular projections on basal two-fifths and sparsely arranged, small tooth-like cuticular projections; lateral surface serrate. Prementum subrectangular; dorsal surface of sclerite with one pair of small membranous areas situated on anterior portion. Ligula stout, distinctly shorter than labial palpi, longer than labial palpomere 1, largely sclerotised, apical membranous area slightly bifid. Labial palpi shorter than mentum.

Thorax. Prothorax slightly wider than head capsule (Fig. 51A). Proscutum formed by one large plate subdivided by fine sagittal line, anterior part rather weakly sclerotised; whole sclerite bearing densely arranged setae of variable length. Prosternum subpentagonal, with incomplete sagittal line (Fig. 64A). Mesonotum with two sclerites on each side; anterior one small, narrow; posterior one large, anterior part larger than posterior part. Metanotum with one large sclerite each, anterior part subdivided by transverse ridge, posterior part smaller than anterior part. Legs (Fig. 64B) long, visible in dorsal view, 5-segmented, bearing numerous long swimming hairs; all three pairs similar in shape.

Abdomen. Abdomen 10-segmented, tapering posteriad, covered with fine pubescence on membranous parts; segments 1 to 7 similar in shape and size (Fig. 51A). Segment 1 with four small dorsal sclerites and two setiferous tubercles dorsally; two sclerites situated anteromedially, remaining two behind the latter; two setiferous tubercles on posterior portion behind sclerites, each bearing very long setae; lateral part of segment 1 with one setiferous tubercle and very long setiferous projection on each side. Segments 2 to 7 similar to segment 1, but with three small dorsal sclerites each, one on anterior part, two on posterior part; the sclerites smaller than those on first segment.

Spiracular atrium (Fig. 54B): Segment 8 with oval dorsal plate; median part of posterior edge of plate with four strong projections, inner two larger than lateral ones; procercus incompletely sclerotised, with one long and two short setae. Segment 9 trilobed, partially sclerotised; each lateral lobe with short, incompletely sclerotised acrocercus; urogomphi short, one-segmented; prostyli very long.

First instar. Similar to third instar larva, more weakly sclerotised than second third (Fig. 2A).

Head. Nasale almost straight.

Antenna: Inner face of scape with large cuticular teeth (Fig. 53A). Flagellum about as long as pedicel.

Maxilla distinctly longer than antenna. Maxillary palpomere 4 the longest, slightly longer than palpomere 3 (Figs. 53D–E).

Labium: Mentum bearing small, strong cuticular spines on basal half of dorsal surface (Figs. 53F–G).

Thorax. Prothorax narrower than head capsule (Fig. 2A).

Abdomen. *Spiracular atrium*: Segment 8 with oval dorsal plate, posterior edge of plate with two projections.

Primary chaetotaxy of head. *Frontale* altogether with 44 sensilla (Figs. 52A, C). Central part with three pairs of sensilla divergent posteriad; FR1 short seta, rather close to frontal line; FR2 pore-like, situated more anteriorly and more mesally, between FR1 and FR3; FR3 short and rather stout seta, situated more anteriorly and slightly more mesally than FR2. Three rather short setae (FR5–7) and one pore-like sensillum (FR4) close to antennal socket; FR4 located mesally to antennal socket, FR5–6 situated posteromesally to antennal socket; FR5 behind FR6; FR7 close to inner margin of antennal socket. Nasale with a group of six equidistant, stout and short setae (gFR1). Each epistomal lobe with a group of four setae; lateral two short, stout, mesal two small (gFR2). Pore-like sensillum FR15 placed posteriorly to median part of nasale; rather long seta FR8 behind FR15. Two setae (FR9–10) situated anteromesally to antennal socket; FR10 shorter than FR9, behind FR9; pore-like sensillum FR14 situated anteriorly to antennal socket. Pore-like sensilla FR11 and FR13 and short seta FR12 close to base of epistomal lobe; FR11–12 close to lateral seta of nasale; FR12 situated anteriorly and laterally to FR11; FR13 at midlength between FR11 and FR14.

Parietale with 30 sensilla each (Figs. 52A–B). Dorsal surface with a group of five sensilla (PA1–5) forming longitudinal row at midwidth in posterior part of parietale; PA1–2 and 4–5 short setae, PA3 pore-like. PA6 pore-like, located posteromesally close to joint of coronal and frontal lines, more distant from posterior margin of head than PA1. PA7 rather long seta, situated anteriorly to PA5, in about posterior two-fifths of parietale; two rather long setae (PA12–13) and one long seta (PA14) on median part of parietale, forming a triangular group; PA12 situated medially of line connecting FR13 and FR14; FR 14 situated anteriorly to remaining sensilla. Seta PA8 rather long, behind antennal socket close to frontal line; seta PA9 long, situated posterolaterally to antennal socket. Pore-like sensillum PA10 situated laterally of line connecting PA8 and 14, rather close to PA8. PA11 long seta, located slightly laterally of line connecting PA9 and PA18. Pore-like sensillum PA15 and rather long seta PA18 in anterior third of lateral surface; PA18 behind PA15; moderately long seta PA16 and pore-like sensillum PA17 on lateral surface of parietale, located anteriorly to PA15; PA17 situated mesally of PA16. Anterior corner of epicranium with one pore-like sensillum (PA19) and three long setae (PA20–22); PA19 situated dorsally to remaining setae; PA20 between PA19 and PA21; PA22 situated ventrally to remaining sensilla. Three pore-like sensilla (PA23–25) on anterior margin close to ventral mandibular acetabulum; PA23 on outer face; PA24 and PA25 closely aggregated, on inner face; PA24 behind PA25. Two long setae (PA26 and PA28) and one pore-like sensillum (PA27) situated ventrally on median part of parietale; PA27 between PA26 and PA28, close to PA28. Two pore-like sensilla (PA29–30) close to basal margin of ventral parietale; PA29 situated mesally to PA30; PA30 on posterolateral corner.

Antenna (Fig. 53A): Antennomere 1 with five pore-like sensilla (AN1–5), AN1 situated dorsally on basal 0.27, AN2 dorsally on basal 0.35, AN3–5 on distal margin; AN3 and AN4 lateral, AN5 ventral. Antennomere 2 with one pore-like sensillum (AN6) situated dorsally

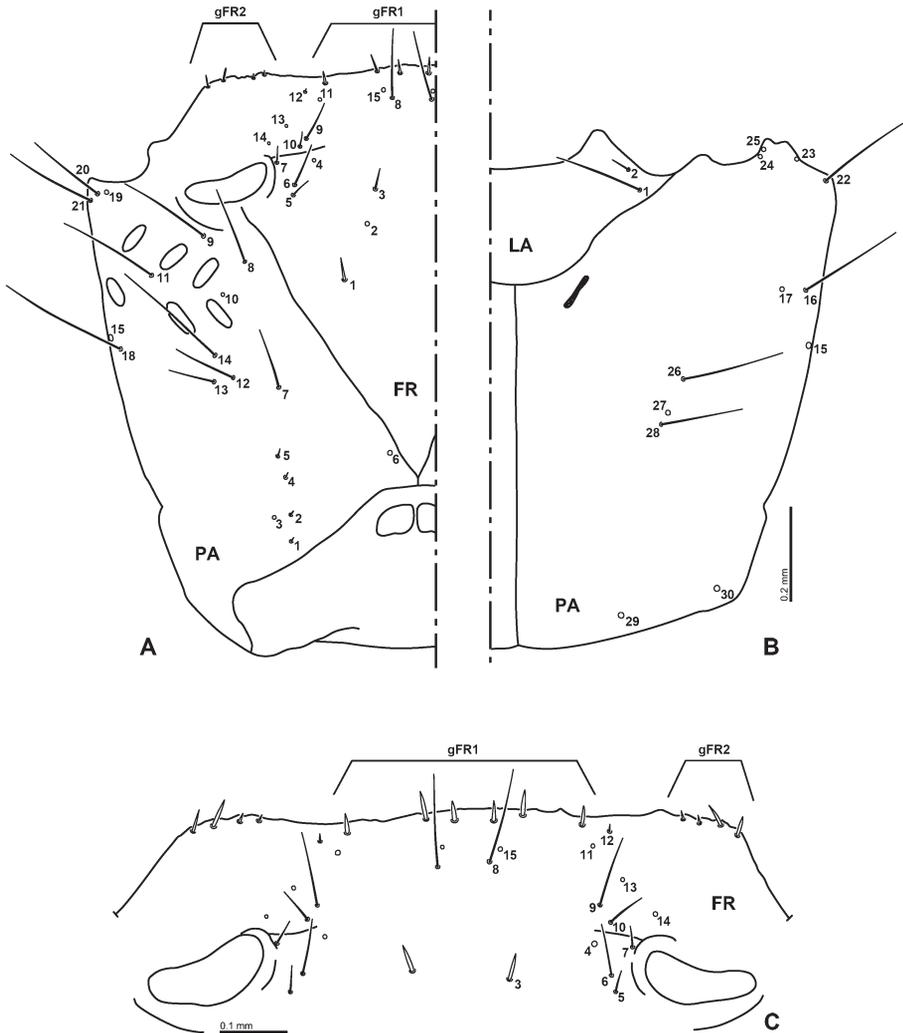


Fig. 52. Head capsule of *Hydrochara affinis* (Sharp, 1873), first instar. A – dorsal view; B – ventral view; C – detail of anterior margin of head capsule, dorsal view.

on basal 0.36 of sclerite; three setae (AN7–9) and sensorium SE1 on small membranous area completely surrounded by sclerite and situated at midlength of antennomere 2; AN7 short, stout; AN8 short, between AN7 and AN9; AN9 small; SE1 behind remaining sensilla; AN10–11 on inner face of intersegmentary membrane between antennomeres 2 and 3, AN10 rather short, AN11 short, stout, both setae close to each other. SE1 small, rounded. Antennomere 3 with apical sensilla (gAN) in apical membranous area; gAN with two rather long setae and a few short setae.

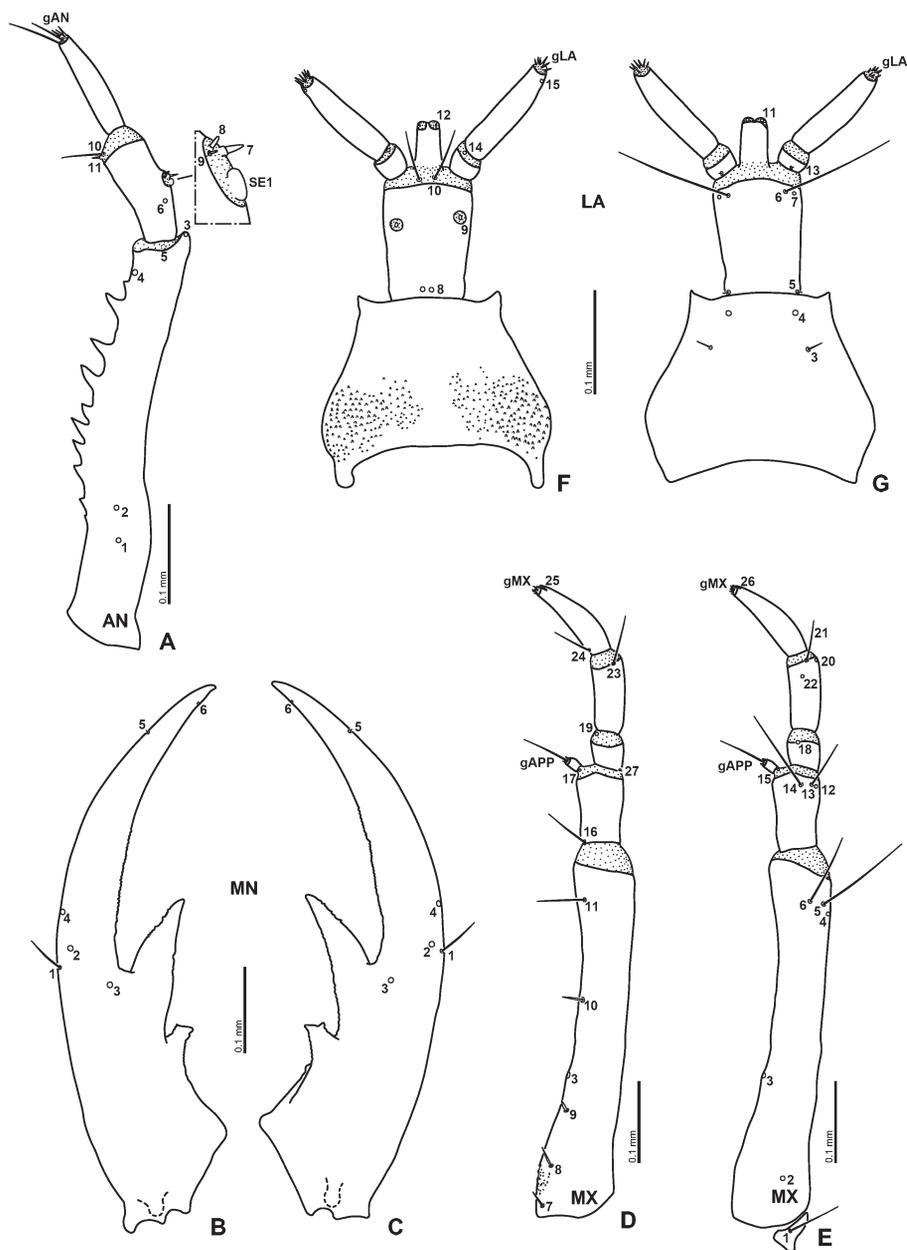


Fig. 53. Head appendages of *Hydrochara affinis* (Sharp, 1873), first instar. A – antenna, dorsal view; B–C – mandibles, dorsal view; D – maxilla, dorsal view; E – maxilla, ventral view; F – labium, dorsal view; G – labium, ventral view.

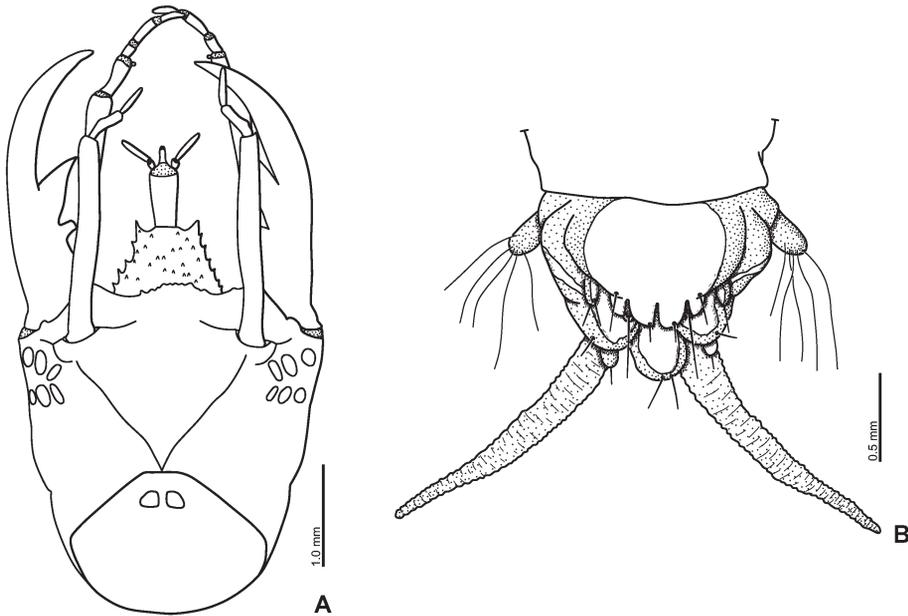


Fig. 54. *Hydrochara affinis* (Sharp, 1873), third instar. A – head, dorsal view; B – spiracular atrium, dorsal view.

Mandible (Figs. 53B–C) with two setae (MN1 and MN5) and four pore-like sensilla (MN2–4 and MN6). MN1 rather short, on outer face of mandible. Sensilla MN2–4 pore-like, on midlength of dorsal surface; MN2 located laterally of line connecting MN3 and MN4, close to MN1; MN4 on lateral face. MN5 minute, situated subapically on outer face of mandible; MN6 situated subapically on inner face of mandible.

Maxilla (Figs. 53D–E): Cardio with one rather short ventral seta (MX1). Stipes with a row of five short to rather long setae (MX7–11) situated dorsally along inner face; MX7–9 and MX9–11 equidistant from each other; MX7–8 short, rather stout; MX9 shorter than MX8, stout; MX10 slightly longer than MX8, stout; MX11 the longest, trichoid. Pore-like sensillum MX2 situated ventrally on basal 0.14 of sclerite; pore-like sensillum MX3 on basal two-fifths of inner face; one pore-like sensillum (MX4) and two rather long setae (MX5–6) located ventrally on outer face of apical part of sclerite; MX4 situated on lateral face; MX5 between MX4 and MX6, longer than MX6. Dorsal surface of palpomere 1 with one moderately long seta (MX16) situated basally on dorsal inner face; ventral surface of sclerite of palpomere 1 with three sensilla (MX12–14) close to distal margin of sclerite; MX12 pore-like, MX13 rather short seta, MX14 moderately long seta; MX12 on lateral face; MX13 between MX12 and MX14; MX14 mesally. Two pore-like sensilla (MX15 and MX17) on membrane behind inner appendage; MX17 dorsal, MX15 ventral. Inner appendage with one rather 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 part of distal margin of sclerite;

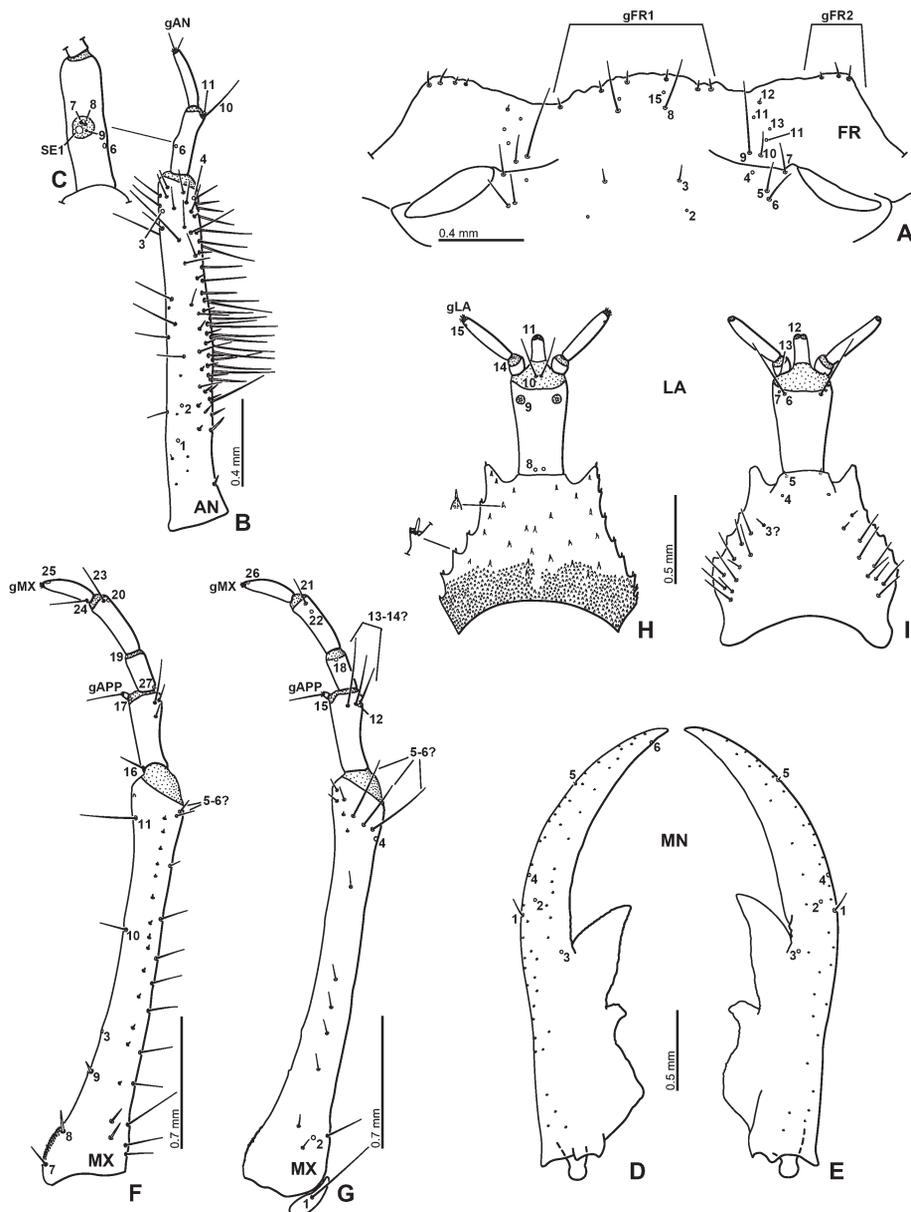


Fig. 55. *Hydrochara affinis* (Sharp, 1873), third instar. A – clypeolabrum, dorsal view; B – antenna, dorsal view; C – antenna, detail of outer membranous area on pedicel; D–E – mandibles, dorsal view; F – maxilla, dorsal view; G – maxilla, ventral view; H – labium, dorsal view; I – labium, ventral view.

MX19 situated dorsally on inner part of intersegmental membrane between palpomeres 2 and 3; MX27 on base of outer face. Palpomere 3 with two rather short setae (MX21 and MX23) and two pore-like sensilla (MX20 and MX22); MX20 on outer face close to distal margin of sclerite; MX21 situated ventrally on distal margin of sclerite; MX22 behind MX21; MX23 situated dorsally on outer part close to distal margin. Palpomere 4 with one rather short seta (MX24) situated basally on inner face, and with digitiform sensillum (MX25) and pore-like sensillum (MX26) situated subapically on outer face; MX25 dorsal, MX26 ventral. Apical membranous area of palpomere 4 with several minute setae (gMX).

Labium (Figs. 52B, 53F–G): Submentum with two pairs of setae (LA1–2); LA1 moderately long, in each lateral corner, LA2 short, situated anteromesally to LA1 (Fig. 52B). Ventral surface of mentum with one pair of rather short setae (LA3) and pore-like sensilla (LA4) on distal part; LA3 behind LA4, LA4 close to distal margin. Dorsal surface of prementum with two pairs of pore-like sensilla (LA8–9); LA8 at midwidth of prementum close to basal margin; LA9 on small membranous area completely surrounded by sclerite of prementum. Ventral surface of prementum with three pairs of sensilla (LA5–7) on lateral portion; seta LA5 very short on basal margin of sclerite; long seta LA6 and pore-like sensillum LA7 on distal margin of sclerite; LA6 situated mesally to PA7. Membrane between prementum and palpi with one pair of rather long setae (LA10) close to base of ligula. Ligula with two pairs of pore-like sensilla on apical membranous area; LA12 dorsal, LA11 ventral. Palpomere 1 with one minute seta (LA13) situated ventrally on basal margin of sclerite; LA14 on dorsal face of intersegmentary membrane between palpomeres 1 and 2. Palpomere 2 with one subapical pore-like sensillum (LA15) on outer face. Apical membranous area of palpomere 2 with several short setae (gLA).

Secondary chaetotaxy of head. Third instar. *Parietale* bearing numerous, rather long secondary setae on lateral surface.

Antenna: Antennomere 1 bearing moderately long to small, densely arranged secondary setae, setation more dense in distal two-thirds of inner face (Fig. 55B).

Mandible: Outer part of mandible bearing numerous small secondary setae (Figs. 55D–E).

Maxilla (Figs. 55F–G): Outer face of stipes with a row of long to rather short secondary setae; one long secondary seta close to MX5–6; dorsal surface of sclerite of stipes with a longitudinal row of secondary setae; basal two rather short, stout, remaining setae very short; ventral surface of sclerite of stipes with rather irregular row of moderately long to short secondary setae. Palpomere 1 with three to four short to rather long secondary setae on distal end of sclerite.

Labium (Figs. 55H–I): Dorsal surface of mentum with about 25 short secondary setae below tooth-like cuticular projections; lateral face of mentum with about six to nine small secondary setae on each lateral projection; ventral surface of mentum with about 6 to 11 rather short, secondary setae on each lateromedian part of ventral surface, LA3 undistinguishable.

Biology. Larvae were found in standing water (HAYASHI 2009a). The biology of the species has been reported by previous studies (e.g., for the life history see HOSOI (1947); for the construction of the egg case see YOSHIMURA (1992); and for the construction of egg case in

regards to leaf preference during case construction in paddy fields see JINGUJI & TSUYUZAKI (2008)). HOSOI (1947) reported a fourth larval instar of *H. affinis*, however in the present study we consider the species as having three instars as it is usual for other hydrophilids. Three instars are also present in the western Palaearctic *Hydrochara caraboides* (Linnaeus, 1758) (M. FIKÁČEK, pers. comm. 2011).

Identification. No other closely related species occurs in the collecting sites where the examined larvae were collected; hence, the larvae clearly belong to *H. affinis*.

Genus *Hydrophilus* Geoffroy, 1762

(Figs. 2C, 56–59, 64C, 66D)

Diagnosis. Larvae of this genus are easily distinguishable from other Japanese genera of the Hydrophilini by their large body size; additional diagnostic characters are: (1) frontal lines U-shaped, forming a straight line in posterior part of the head (Fig. 58A); (2) nasale smooth (Fig. 56C); (3) epistomal lobes almost symmetrical, rounded (Fig. 56C); (4) mandibles asymmetrical, right mandible with two inner teeth, left mandible with one inner tooth (Figs. 57B–C); (5) abdominal segments with short setiferous projections on each side.

***Hydrophilus (Hydrophilus) acuminatus* Motschulsky, 1854**

(Figs. 2C, 56–59, 64C, 66D)

Material examined. JAPAN: HOKKAIDŌ: 5 L1, Tôge-shita, Rumoi, vi.2008, H. Yoshitomi leg.; 8 L1, 6 L2, 2 L3, same locality, vii.2008, H. Yoshitomi leg.; 2 L1, same locality, 6.-11.vi.2009 (fixed) (egg cases collected in the field), YM.

General morphology. Third instar. *Body* rather thick (Fig. 2C). *Colour.* Brown to light yellowish brown, sclerotised parts darker (Fig. 2C).

Head. Head capsule (Fig. 58A) semicircular. Frontal lines U-shaped, transverse posteriorly, fused at base of head capsule, coronal line short. Surface of head capsule smooth. Six stemmata on each anterolateral portion of head capsule. Clypeolabrum (e.g., Fig. 56C) almost symmetrical. Nasale smooth, slightly rounded. Epistomal lobes rounded, almost symmetrical, projecting further than nasale.

Antenna (Figs. 59A–C) 4-segmented, slender, long. Scape the longest, longer than pedicel and flagellum combined. Pedicel subdivided by narrow membranous area; basal segment small, apical segment longer than basal segment. Flagellum about as long as pedicel.

Mandibles strong asymmetrical (e.g., Figs. 57B–C, 58A); right mandible with two closely aggregated inner teeth, basal tooth slightly larger than distal one; left mandible with one inner tooth.

Maxilla (Figs. 59D–E) 6-segmented (including cardo), slender, distinctly longer than antenna. Cardo small, irregularly shaped. Stipes the longest, slightly longer than palpomeres 1–4 combined. Maxillary palpus 4-segmented, palpomere 1 the longest and widest, palpomere 4 the shortest and narrowest; inner process sclerotised.

Labium (e.g., Figs. 56B, 57F–G) well developed. Submentum fused to head capsule, large, subpentagonal, wider than mentum (Fig. 56B). Mentum subtrapezoidal in dorsal view, more

than twice wider than prementum, densely bearing small cuticular projections on dorsal surface, anterior corners strongly projecting anteriorly. Prementum subquadrate; dorsal surface of sclerite with one pair of small membranous areas completely surrounded by sclerite. Ligula distinctly shorter than labial palpi, median part sclerotised. Labial palpi shorter than mentum.

Thorax. Membranous parts of thoracic segments with densely arranged small cuticular asperities and small stout setae. Prothorax wider than head capsule (Fig. 2C). Proscutum with two large, irregularly shaped subrectangular plates, each bearing numerous short to rather long setae; the plates closely attached to each other medially (Fig. 2C). Prosternum subtrapezoidal, rather narrow. Mesonotum with two sclerites on each side; anterior one on medioanterior part, small, narrow; posterior one on median part, large but smaller than those on proscutum, subtriangular, bearing sparsely arranged setae of variable length. Metanotum with one subtriangular sclerite on each side, sclerite smaller than mesothoracic tergum, bearing sparsely arranged setae. Legs (e.g., Fig. 64C) long, visible in dorsal view, 5-segmented; trochanter and femur bearing long, densely arranged swimming hairs; all three pairs similar in shape.

Abdomen. Abdomen 10-segmented, tapering posteriorly (Fig. 2C); membranous area covered with densely arranged small cuticular asperities and small stout setae as those on membranous areas of thorax. Segments 1 to 7 similar in shape, with four small tubercles bearing long seta on posterior portion of each segment; segments 1 to 8 with one short setiferous projection on each side, projection on segment 8 smaller than those on segments 1 to 7.

Spiracular atrium (Fig. 58B): Segment 8 with two dorsal sclerites, sclerites rather slender, subtriangular, widest posteriorly; segment 9 trilobed, partially sclerotised; each lateral lobe with two sclerites, one on inner part, one on outer face, and with short incompletely sclerotised acrocercus; median lobe smaller than lateral lobe, with two sclerites; urogomphi short, one segmented; prostyli long, membranous.

Second instar. Very similar to third instar.

First instar. Similar to second instar, but more weakly sclerotised.

Head. Antenna 3-segmented, long (Fig. 57A). Scape about as long as pedicel and flagellum combined. Flagellum longer than pedicel.

Maxilla: Maxillary palpus 4-segmented, all palpomeres subequal in length; palpomere 1 the widest (Figs. 57D–E).

Labium: Ligula mostly membranous (Figs. 57F–G).

Thorax. Mesothoracic tergum bearing dense and fine pubescence. Membranous area covered by fine pubescence without cuticular asperities.

Abdomen. Abdomen covered by fine pubescence as on thorax, without cuticular asperities.

Primary chaetotaxy of head. *Frontale* with 50 sensilla altogether (Figs. 56A, C). Seta FR1 rather short in basal third of frontale; one pore-like sensillum (FR2) and one rather short seta (FR3) on distal third of frontale, FR2 between FR1 and FR3, FR3 more medially and more anteriorly than FR2. Two rather short setae (FR5–6) situated posteromesally to antennal socket; FR6 behind FR5. Pore-like sensillum (FR4) and short seta (FR7) close to inner margin of antennal socket; FR7 behind FR4. Nasale with a group of six equidistant, short setae and

two small setae; small setae situated mesally (gFR1). Each epistomal lobe with a group of six sensilla; lateral three short setae, median two minute setae, inner one pore-like sensillum (gFR2). Pore-like sensillum FR15 located posteriorly to median setae of nasale; short seta FR8 situated posterolateral to FR15. Two setae (FR9–10) and one pore-like sensillum (FR13) placed anteromesally to antennal socket. FR9 rather short but longer than FR10; FR10 situated slightly laterally of FR9; position of FR10 slightly asymmetrical; pore-like sensillum FR11 at about midlength between FR13 and FR8; FR13 situated anterolaterally to PA10, mesally of line connecting FR12 and FR14. Pore-like sensillum (FR14) located anteriorly to antennal socket; short seta (FR12) close to groove between nasale and epistomal lobe.

Parietale with 33 sensilla each (Figs. 56A–B). Dorsal surface with group of five sensilla (PA1–5) situated posteriorly at midwidth, forming slightly irregular longitudinal row; PA1–2 and 4–5 short setae, PA3 pore-like. Pore-like sensillum PA6 located posteromesally close to frontal line. PA7 rather short seta, at midlength between basal margin of parietale and antennal socket, close to frontal line; one rather short additional seta between PA6 and PA7, close to PA7. Two setae (PA12–13) on median part of parietale; PA12 rather long, situated mesally to PA13; PA13 rather short. Seta PA8 rather long, behind antennal socket, between PA7 and PA9, close to frontal line; seta PA9 rather long, placed posterolaterally to antennal socket. Pore-like sensilla PA10 situated at midlength between PA9 and PA12 but laterally of line connecting PA9 and PA12. Two rather long setae (PA11 and PA14) and one pore-like sensillum (PA15) located on about anterior fifth of lateral surface of parietale; PA15 situated laterally of PA11 and PA14; PA14 behind PA11 and PA15. Anterior corner of epicranium with one pore-like sensillum (PA19) and two rather long setae (PA20–21) dorsally; PA20 between PA19 and PA21; PA21 placed laterally of PA20 and PA19; ventral surface with one rather long seta (PA22) and three pore-like sensilla (PA23–25) close to mandibular acetabulum; PA22 and PA23 on lateral margin of mandibular acetabulum, PA22 behind PA23; PA24 between PA22 and PA25, close to PA25; PA25 on inner margin of mandibular acetabulum. Two long setae (PA16 and PA18), one rather short additional seta, and one pore-like sensillum (PA17) situated ventrally behind PA21, forming a row; PA18 on lateral surface; PA16 between PA17 and PA18; PA17 between additional setae and PA16; PA16–18 and one additional seta equidistant. Two rather long setae (PA26 and PA28) and one pore-like sensillum (PA27) situated ventrally on median part of parietale, divergent posteriad, PA28 behind PA27, closer to PA27 than to PA26; PA26 more anteriorly and more laterally than PA27 and PA28. Two pore-like sensilla (PA29–30) on basal part of ventral surface of parietale; PA30 on lateral surface; one pore-like additional sensilla situated ventrally on lateral surface of posterior 0.24 of parietale.

Antenna (Fig. 57A): Antennomere 1 with five pore-like sensilla (AN1–5), bearing numerous short to moderately long additional setae on inner face; AN1 on basal 0.25; AN2 on basal 0.36, AN3–5 on distal margin; AN1–4 dorsal, AN5 ventral. Antennomere 2 with one pore-like sensillum (AN6) situated dorsally on basal 0.18 of sclerite, and four setae (AN7–8 and AN10–11) on intersegmentary membrane between antennomeres 2 and 3; AN7–8 on outer face of antenna next to sensorium SE1; AN7 short, AN8 shorter than AN7; setae AN10–11 on inner face of antenna; AN10 rather short; AN11 short, both setae close to each other. SE1 small, rounded. Antennomere 3 with one pore-like additional sensillum situated dorsally on

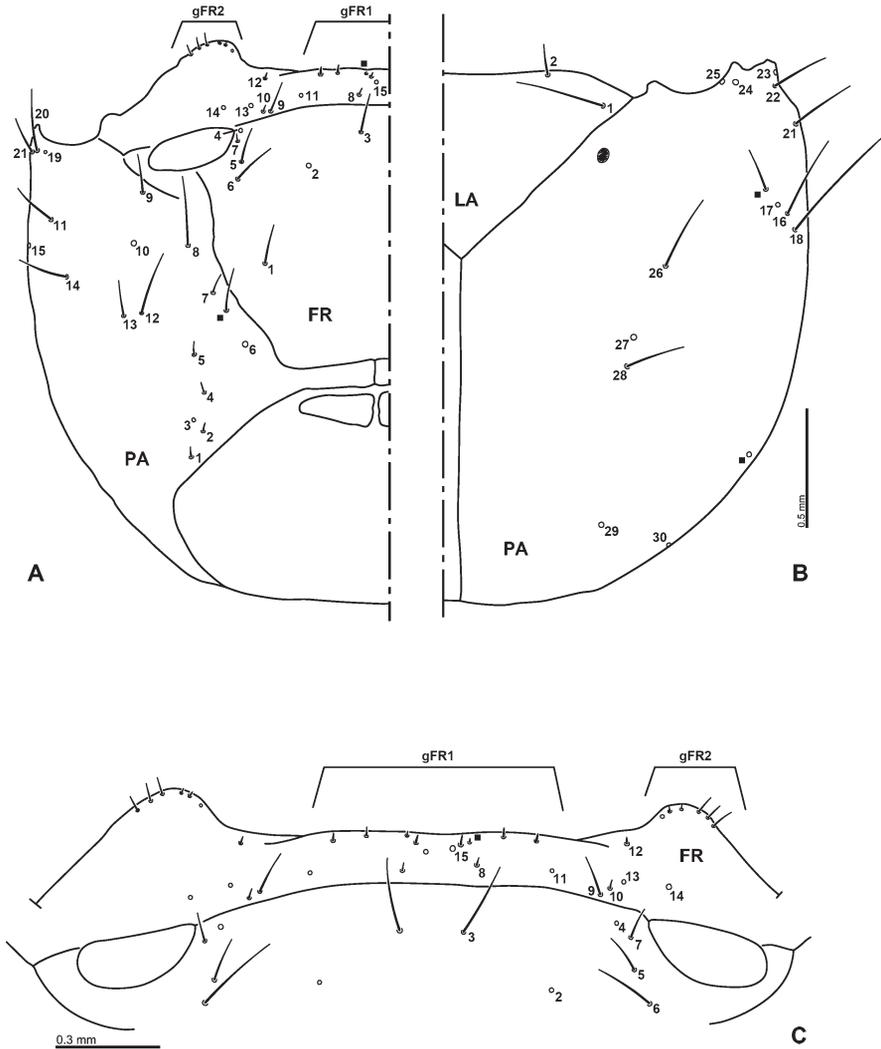


Fig. 56. Head capsule of *Hydrophilus acuminatus* Motschulsky, 1854, first instar. A – dorsal view; B – ventral view; C – detail of anterior margin of head capsule, dorsal view.

distal 0.39; apical sensilla (gAN) in apical membranous area; gAN with two rather long setae and a few short to minute setae.

Mandible (Figs. 57B–C) with two setae (MN1 and MN5) and three pore-like sensilla (MN2–4 and MN6), sparsely covered with very small pore-like additional sensilla on outer face. MN1 rather short, on outer face of mandible. Sensilla MN2–4 situated dorsally on median part; MN2 at midlength of line connecting MN3 and MN4; MN4 on outer face close

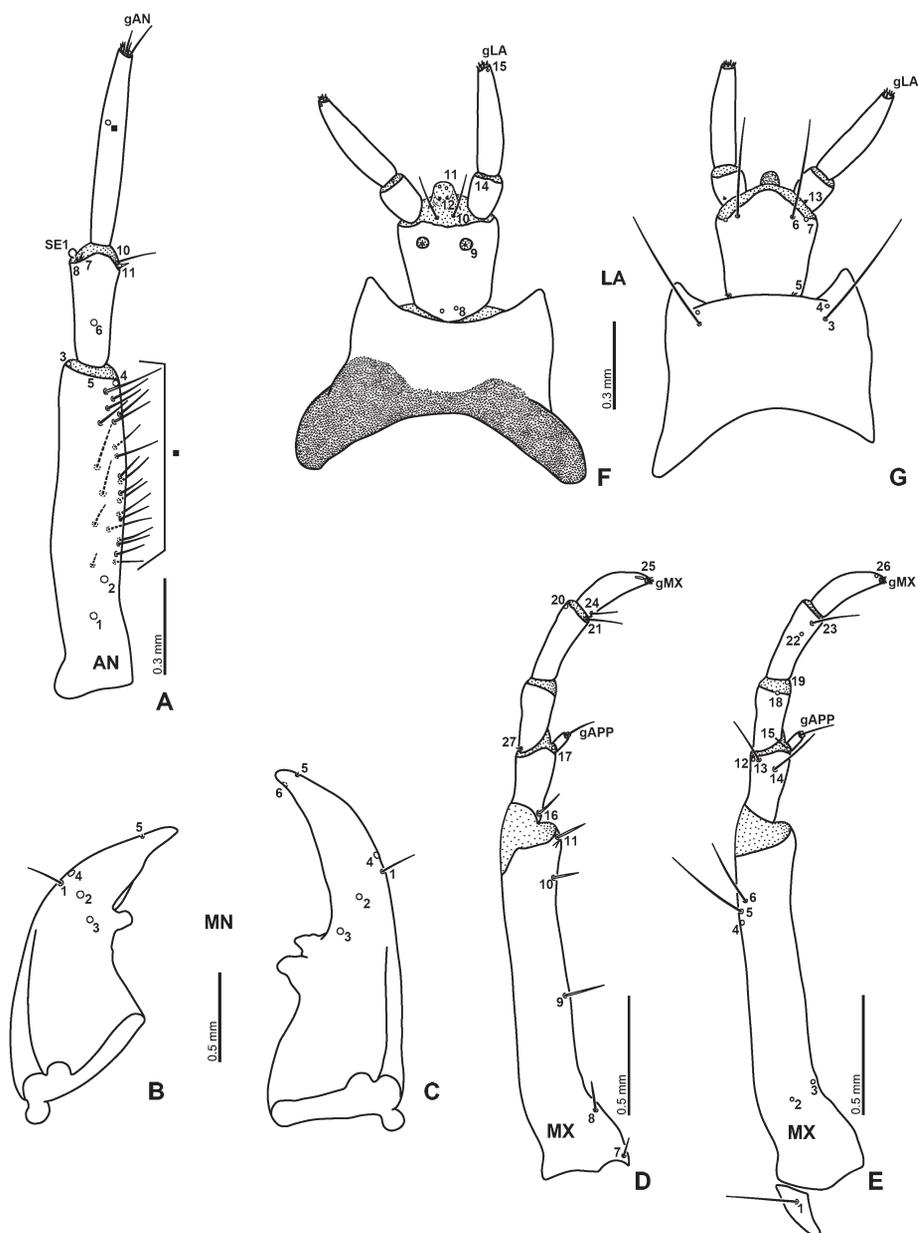


Fig. 57. Head appendages of *Hydrophilus acuminatus* Motschulsky, 1854, first instar. A – antenna, dorsal view; B–C – mandibles, dorsal view; D – maxilla, dorsal view; E – maxilla, ventral view; F – labium, dorsal view; G – labium, ventral view.

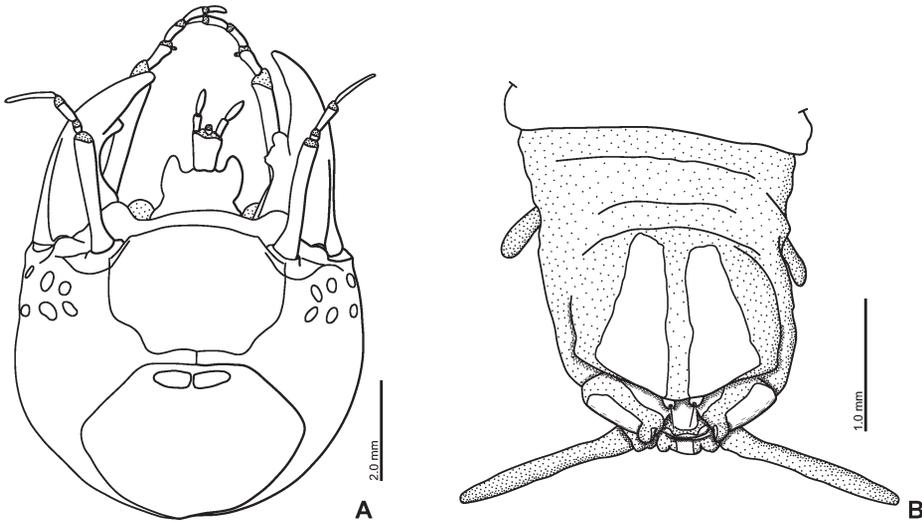


Fig. 58. *Hydrophilus acuminatus* Motschulsky, 1854, third instar. A – head, dorsal view; B – spiracular atrium, dorsal view.

to MX1. Seta MN5 minute, situated subapically on outer face. Pore-like sensillum MN6 situated subapically on inner face.

Maxilla (Figs. 57D–E): Cardio with one rather long ventral seta (MX1). Stipes with a row of five moderately short, rather stout setae (MX7–11) situated dorsally on inner face; MX8–10 equidistant, separated by distance larger than between MX7 and MX8 and between MX10 and MX11; MX7 the shortest; MX9 the longest. Ventral surface of stipes with three pore-like sensilla (MX2–4) and two rather long setae (MX5–6); MX2 located mesally on basal 0.25; MX3 on basal 0.30 of inner face; MX4–6 located lateroventrally on distal 0.15 of sclerite; MX6 situated posteriorly to remaining sensilla, MX5 between MX6 and MX4. Dorsal surface of palpomere 1 with one moderately short spiniform seta (MX16) situated basally on dorsal inner face; ventral surface of palpomere 1 with one pore-like sensillum (MX12) and two rather long setae (MX13–14); MX12–13 on outer face, close to distal margin of sclerite; MX13 close to MX12, situated mesally of MX12; MX14 situated mesally on distal fourth. Two pore-like sensilla (MX15 and MX17) on membrane behind inner appendage; MX17 dorsal, MX15 ventral. Inner appendage with one rather long seta and a few short setae (gAPP). Palpomere 2 with two pore-like sensilla (MX18–19) and one minute seta (MX27); MX18 situated ventrally on middle of borderline between sclerite and intersegmental membrane between palpomeres 2 and 3; MX19 on lateroventral surface of intersegmental membrane between palpomeres 2 and 3; MX27 situated basally on outer surface. Palpomere 3 with two rather long setae (MX21 and MX23) and two pore-like sensilla (MX20 and MX22); MX20 on outer face of distal margin of sclerite; MX21 on inner face of intersegmental membrane between palpomeres 3

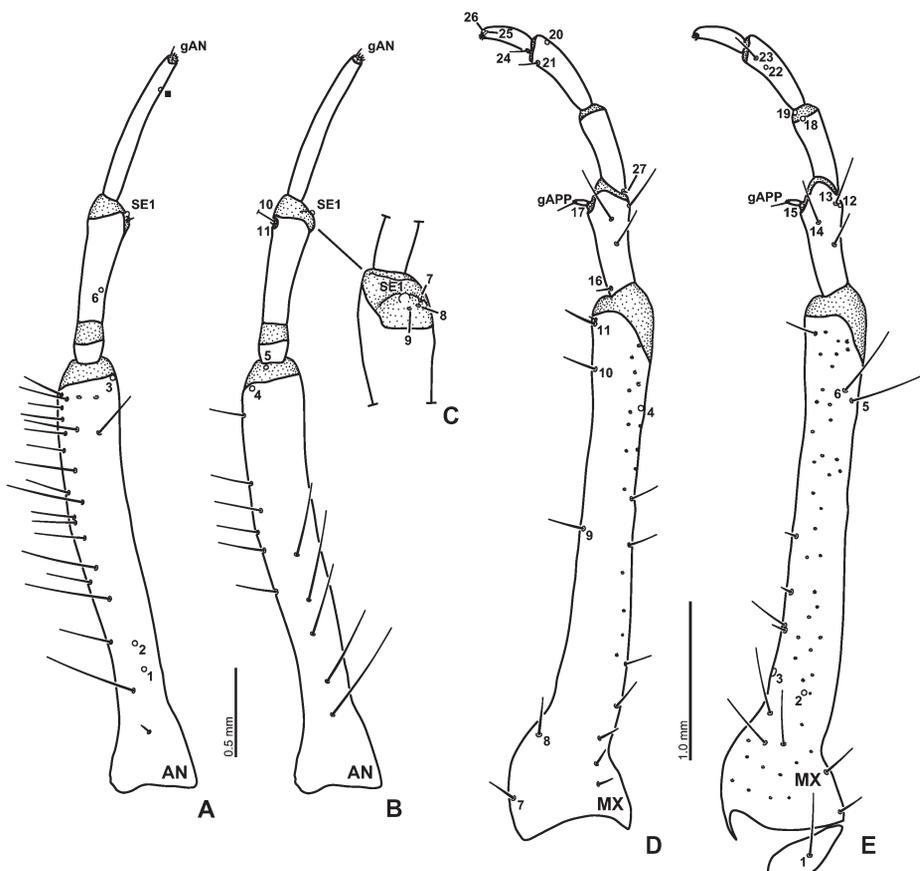


Fig. 59. Head appendages of *Hydrophilus acuminatus* Motschulsky, 1854, third instar. A – antenna, dorsal view; B – antenna, ventral view; C – detail of inner surface of intersegmental membrane between pedicel and flagellum; D – maxilla, dorsal view; E – maxilla, ventral view.

and 4; MX22 at midwidth of anterior third of ventral surface of sclerite; MX23 on inner part close to distal margin of ventral surface of sclerite. Palpomere 4 with one rather short seta (MX24) situated basally on inner face, and with digitiform sensillum (MX25) and pore-like sensillum (MX26) situated subapically on outer face; MX25 dorsal, MX26 ventral. Apical membranous area of palpomere 4 with several minute setae (gMX).

Labium: (Figs. 56B, 57F–G): Submentum (Fig. 56B) with two pairs of setae (LA1–2); LA1 long in lateral corners, LA2 short on anterior margin. Ventral surface of mentum with one pair of long setae (LA3) and one pair of pore-like sensilla (LA4) close to distal margin; LA3 behind LA4. Dorsal surface of prementum with two pairs of sensilla (LA8–9); pore-like sensillum LA8 situated basally at midwidth of prementum; small seta LA9 in small membranous area

completely surrounded by sclerite of prementum. Ventral surface of prementum with three pairs of sensilla (LA5–7) on lateral part; seta LA5 short, on basal portion; LA6 long, situated close to distal margin of sclerite and LA7, laterally of LA7; LA7 pore-like, on borderline between sclerite and membranous area between prementum and palpi. Membrane between sclerite of prementum and palpi with one pair of rather long setae (LA10) close to base of ligula. Ligula with two pairs of pore-like sensilla (LA11 and LA12) situated apically; LA12 dorsal, LA11 ventral. Palpomere 1 with one minute seta (LA13) situated ventrally close to basal margin of sclerite; LA14 situated dorsally on intersegmental membrane between palpomeres 1 and 2. Palpomere 2 with one pore-like sensillum (LA15) situated subapically on laterodorsal face of sclerite. Apical membranous area of palpomere 2 with several short setae (gLA).

Secondary chaetotaxy of head. Second instar. *Frontale* bearing about 50 secondary sensilla on anterior two-thirds of median part, between FR1 and gFR1.

Parietale bearing numerous secondary sensilla.

Mandible: Mandibles with numerous small secondary sensilla on outer face.

Maxilla: (e.g., Figs. 59D–E): Stipes covered with small secondary setae, the setae on ventral surface denser than those on dorsal surface; inner face with four short, stout secondary setae; outer face bearing five rather long trichoid secondary setae; three long secondary setae situated ventrally on basal part, behind MX2–3; four rather short, stout setae located basally on outer part of dorsal surface of sclerite. Palpomere 1 with four rather long secondary setae. Two setae situated dorsally at midwidth of sclerite, one on anterior third, one at midlength. One seta situated subapically on outer face of sclerite, close to MX12, the seta forming a group of setae with MX12–13 situated dorsally to MX12. One seta situated ventrally on median part of sclerite.

Labium: Mentum with sparsely arranged rather long secondary setae on lateral faces; dorsal surface of mentum covered with rather densely arranged small secondary setae.

Third instar. Very similar to second instar.

Antenna (Figs. 59A–C): Minute seta AN9 present, on intersegmental membrane between palpomeres 2 and 3, close to AN7–8 and SE1.

Biology. Larvae are found in standing water (HAYASHI 2009a). The biology of this species has been reported by previous studies. HOSOI (1939) studied the life history of the species. INODA et al. (2003) reported on the feeding effectiveness of asymmetrical mandibles of *H. acuminatus* in different prey: larvae preferred the right-handed shells of the snail, *Austropeplea ollula* (Gould, 1859) (Gastropoda: Lymnaeidae), to the left-handed shells of *Physa acuta* Draparnaud, 1805 (Gastropoda: Physidae). They demonstrated that asymmetrical mandibles of *H. acuminatus* evolved as an adaptation for handling the right-handed snails.

Identification. Two species of *Hydrophilus* are known from Hokkaidō, Japan: *Hydrophilus acuminatus* and *Hydrophilus dauricus* Mannerheim, 1852. However, *H. dauricus* is only distributed in eastern Hokkaidō, whereas the collecting sites are situated in western Hokkaidō where only *H. acuminatus* occurs. Hence, we identified the examined larvae as *H. acuminatus*.

Genus *Sternolophus* Solier, 1834

(Figs. 2D–E, 51B, 60–63, 64D, 65D)

Diagnosis. Larvae of this genus are distinguished from other Japanese Hydrophilini by the following combination of characters: (1) frontal lines V-shaped (Fig. 62A); (2) nasale with distinct teeth (Figs. 60C, 62B); (3) epistomal lobes rounded, projecting as far as or only slightly further than nasale (Figs. 60C, 62B); (4) mandibles symmetrical, with two large and one small inner teeth (Figs. 61B–C, 63C–D); (5) abdominal segments with rather short setiferous projections on each side (Fig. 51B).

***Sternolophus (Sternolophus) rufipes* (Fabricius, 1792)**

(Figs. 2D–E, 51B, 60–63, 64D, 65D)

Material examined. JAPAN: HONSHŪ: Shimane-ken: 1 L1, 13 L2, 1 L3, mouth of Kando-gawa river, Izumo-shi, 10.ix.2007, MH; 1 L2, 1 L3, Nakanosu, Nadabun-chô, Izumo-shi (ponding fallow field), 23.viii.2007, MH; 3 L3, Nakanosu, Nadabun-chô, Izumo-shi, 10.ix.2007, MH; 7 L2, 1 L3, Okinoshima, Sono-chô, Izumo-shi (paddy field), 10.vi.2007, MH; 2 L2, 2 L2, Okinoshima, Sono-chô, Izumo-shi (artificial pond for conservation purpose), 11.vi.2007, MH; 1 L2, 1 L3, same locality, 13.ix.2007, MH; 1 L3, Shakunouchi-kôen, Kisuki-chô, Un-nan-shi, 23.ix.2007, MH.

General morphology. Third instar. *Body* rather thick (Fig. 51B). *Colour.* Head and sclerotised parts yellowish brown; non-sclerotised parts greyish white to light yellowish brown (Figs. 2D–E).

Head. Head capsule (Fig. 62A) subtrapezoidal, widest anteriorly. Frontal lines almost V-shaped, fused at base of head capsule, coronal line short. Surface of head capsule smooth. Six stemmata on each anterolateral portion of head capsule. Clypeolabrum (Fig. 62B) slightly asymmetrical. Nasale with five teeth, four on right side more closely placed and projecting further than left one. Epistomal lobes almost symmetrical, weakly rounded, projecting as far as nasale; lateral part of anterior margin of epistomal lobes weakly serrate.

Antenna (Figs. 63A–B) 3-segmented, long, slender. Scape the widest, longer than pedicel and flagellum combined. Pedicel with outer membranous area completely surrounded by sclerite, situated on subapical part of outer face. Flagellum the narrowest, about as long as pedicel.

Mandibles (Figs. 63C–D) symmetrical, with three inner teeth, distal two large, basal one small; inner face of distal two teeth slightly serrate; basal half of inner face of mandibular apex serrate, apical portion smooth.

Maxilla (Figs. 63E–F) 6-segmented (including cardo), long, slender, distinctly longer than antenna. Cardo small, subtriangular. Stipes the longest, slightly longer than palpomeres 1–4 combined; one subapical spine-like cuticular projection on inner face; base of inner face bearing numerous small cuticular projections, between MX7 and MX8. Maxillary palpus 4-segmented; dorsal surface of palpomere 1 completely sclerotised; palpomere 1 about as long as palpomere 3; palpomere 2 the shortest; palpomere 4 slightly shorter than palpomere 3; palpomere 1 the widest; inner process sclerotised.

Labium (Figs. 63G–H) well developed. Submentum (e.g., Fig. 60B) fused to head capsule, large, subpentagonal, apically rounded, wider than mentum. Mentum more than twice as wide

as prementum, subquadrate, each anterior corner strongly projecting anteriorly; dorsal surface of mentum bearing densely arranged small cuticular spines except for anterior-most part. Prementum subquadrate, longer than wide; dorsal surface of sclerite with one pair of small membranous areas completely surrounded by sclerite. Ligula distinctly shorter than labial palpi, longer than labial palpomere 1, partly sclerotised, basal and apical parts membranous. Labial palpi about as long as prementum.

Thorax. Prothorax wider than head capsule, widest at posterior end (Fig. 51B). Proscutum formed by one large plate subdivided by fine sagittal line, anterior and posterior margins weakly sclerotised; proscutum bearing numerous, rather short, fine setae. Prosternum subpentagonal, with fine, almost complete sagittal line. Mesonotum with two dorsal sclerites on each side; anterior one small, narrow; posterior one large, subtriangular, its anterior part subdivided by fine transverse ridge. Metanotum with one dorsal sclerite on each side, anterior part subtriangular, large, subdivided by fine transverse ridge, posterior part small. Legs (Fig. 64D) long, visible in dorsal view, 5-segmented, bearing long swimming hairs; all three pairs similar in shape.

Abdomen. Abdomen 10-segmented, tapering posteriorly, densely covered with fine pubescence on membranous parts; segments 1 to 7 similar in size and shape (Fig. 51B). Segment 1 with one small dorsal sclerite on anteromedian part on each side, and with small setiferous projections laterally; segments 2 to 7 similar to segment 1 but dorsal sclerites smaller than those on segment 1.

Spiracular atrium (Fig. 62C): Segment 8 with large suboval dorsal plate, plate wider than long; posterior edge of segment 8 with four setiferous, stout and lobe-like almost membranous projections; procercus incompletely sclerotised, with three setae; urogomphi short, one segmented, with three setae, two long on median part, one very long on apex. Segment 9 trilobed, partially sclerotised; each lateral lobe with small, incompletely sclerotised acrocercus.

Second instar. Similar to third instar larva (Fig. 2D). Pubescence covering membranous parts of thoracic and abdominal segments sparser than in third instar. Swimming hairs of legs denser than in first instar.

First instar. Similar to third instar larva but more weakly sclerotised.

Head. *Antenna* long, rather slender (Fig. 61A).

Mandibles: Inner face of mandibles almost smooth (Figs. 61B–C).

Maxilla: Maxillary palpomere 4 the longest, slightly longer than palpomere 3 (Figs. 61D–E).

Labium: Labial palpi longer than prementum (Figs. 61F–G).

Primary chaetotaxy of head. *Frontale* altogether with 50 sensilla (Figs. 60A, C). Central part with three pairs of sensilla divergent posteriorly; FR1 short seta, rather close to frontal line; FR2 pore-like, situated more anteriorly and more mesally than FR1, between FR1 and FR3; FR3 short and rather stout seta, situated even more anteriorly and slightly more mesally than FR2. Two moderately short setae (FR5 and FR6) and one pore-like sensillum (FR4) situated posteromesally to antennal socket; FR5 and FR6 more laterally than FR4; FR5 situated slightly posteriorly and laterally to FR6. FR7 rather long seta close to inner margin of antennal soc-

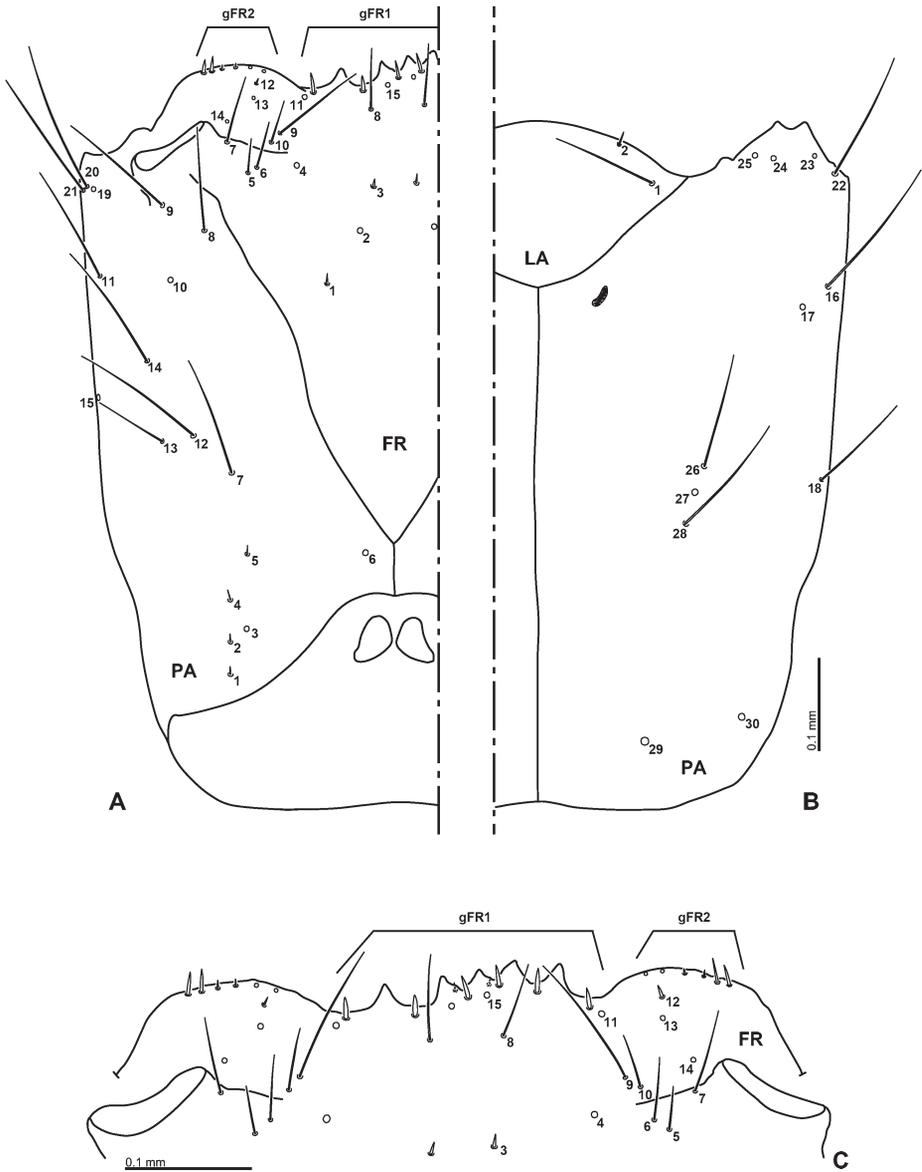


Fig. 60. Head capsule of *Sternolophus (Sternolophus) rufipes* (Fabricius, 1792), first instar. A – dorsal view; B – ventral view; C – detail of anterior margin of head capsule, dorsal view.

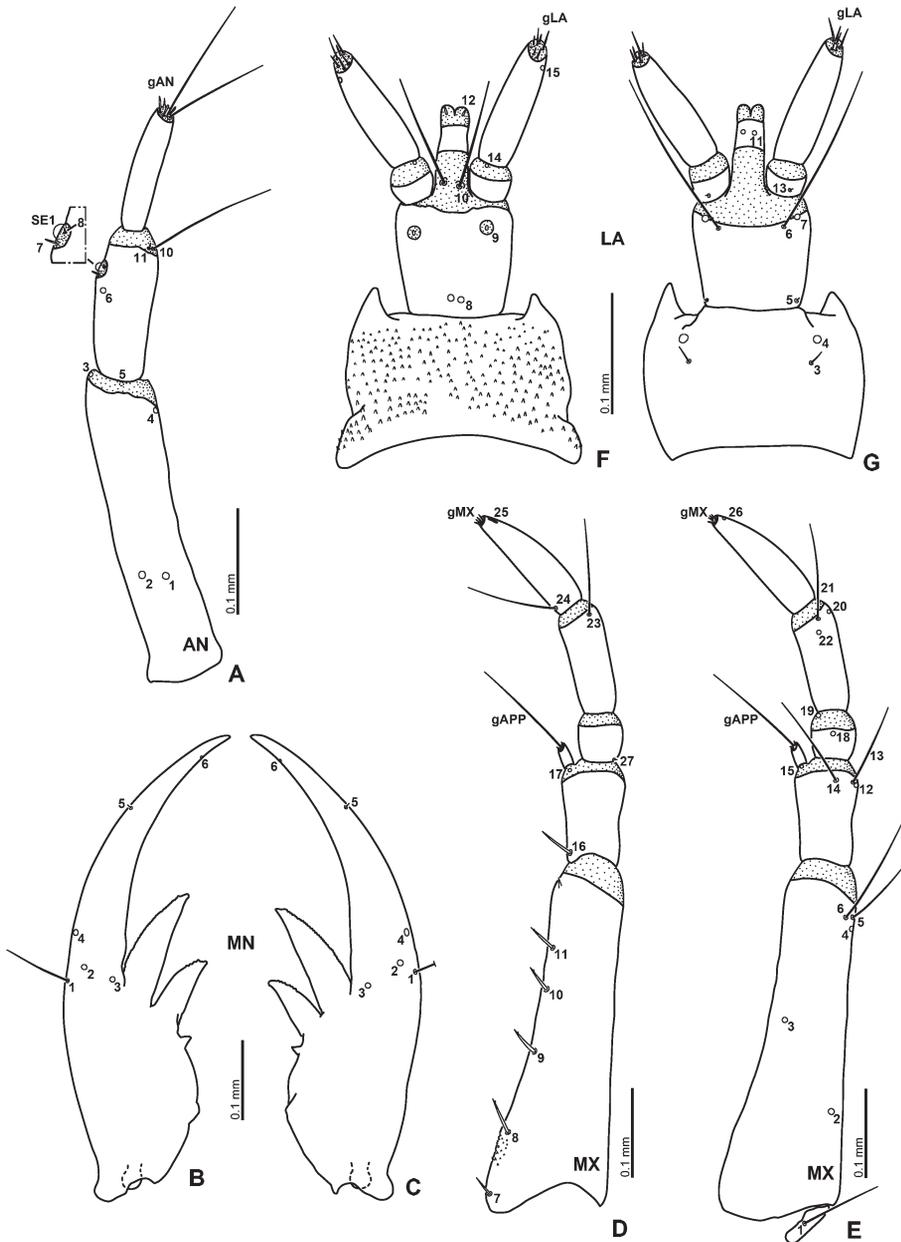


Fig. 61. Head appendages of *Sternolophus* (*Sternolophus*) *rufipes* (Fabricius, 1792), first instar. A – antenna, dorsal view; B–C – mandibles, dorsal view; D – maxilla, dorsal view; E – maxilla, ventral view; F – labium, dorsal view; G – labium, ventral view.

ket. Nasale with a group of six equidistant stout and short setae and with two small setae on middle of ventral surface (gFR1), lateral-most seta of gFR1 on each side located in grooves between nasale and epistomal lobe. Each epistomal lobe with a group of six sensilla (gFR2); lateral two short and rather stout setae, middle two small setae, inner two pore-like. FR15 pore-like, behind median setae of nasale; seta FR8 rather long, situated posteriorly to FR15. Two setae (FR9–10) situated mesally to antennal socket; FR10 shorter than FR9, behind FR9; pore-like sensillum FR14 situated medioanteriorly to antennal socket, posteriorly to FR7. Pore-like sensilla FR11 and FR13, and short seta FR12 on inner part of each epistomal lobe; FR11 close to lateral seta of nasale, FR12 close to FR13; FR13 behind FR12.

Parietale with 30 sensilla each (Figs. 60A–B). Dorsal surface with a group of five sensilla (PA1–5) situated posteriorly at midwidth, forming a slightly irregular longitudinal row; PA1–2 and 4–5 short setae, PA3 pore-like; PA6 pore-like sensilla, located posteromesally close to joint of coronal and frontal lines, slightly more distant from posterior margin of head than PA1. Long setae PA7 and PA12 and rather long seta PA13 situated dorsally on median part of parietale; PA7 located medially to remaining sensilla; PA12 situated anteriorly to line connecting PA7 and PA13, more close to PA13 than PA7. Seta PA8 long, behind antennal socket close to frontal line. Seta PA9 long, close to outer margin of antennal socket. Long setae PA11 and PA14 and pore-like sensillum PA10 in about anterior fourth of dorsal surface of parietale, forming rather large triangular group; PA10 between PA8 and PA14; PA11 on lateral surface; PA14 between PA7 and PA11. Pore-like sensillum FR15 and rather long seta PA18 situated laterally on median part of parietale; PA18 behind PA15. Moderately long seta PA16 and pore-like sensillum PR17 on lateroventral surface of parietale close to PA11; PA17 situated posteromesally to PA16. Anterior corner of epicranium with one pore-like sensillum (PA19) and three long setae (PA20–22); PA19 situated dorsally to the remaining setae; PA20 between PA19 and PA21; PA22 situated ventrally to remaining sensilla. Ventral surface with three pore-like sensilla (PA23–25) on anterior margin close to ventral mandibular acetabulum; PA23 on outer face; PA24 and PA25 on inner part; PA24 between PA23 and PA25. Two long setae (PA26 and PA28) and one pore-like sensillum (PA27) situated ventrally on median part of parietale, almost equidistant, PA26 situated anteriorly to remaining sensilla, PA27 between PA26 and PA28. Two pore-like sensilla (PA29–30) located ventrally on basal part of parietale; PA29 situated mesally to PA30.

Antenna (Fig. 61A): Antennomere 1 with five pore-like sensilla (AN1–5); AN1–2 in basal 0.35, AN3–5 on distal margin; AN1–4 dorsal, AN5 ventral. Antennomere 2 with one dorsal pore-like sensillum (AN6) in distal 0.37 of sclerite, two setae (AN7–8) and sensorium SE1 in small lateral membranous area completely surrounded by sclerite situated in distal 0.22 of sclerite; AN7 short, behind AN8 and SE1; AN8 minute; AN10–11 on inner face of intersegmentary membrane between antennomeres 2 and 3, AN10 long, AN11 short, stout, both setae close to each other. SE1 small, rounded. Antennomere 3 with apical sensilla (gAN) in apical membranous area; gAN with two long setae and a few short setae.

Mandible (Figs. 61B–C) with two setae (MN1 and MN5) and four pore-like sensilla (MN2–4 and MN6). MN1 rather long on outer face of mandible. Sensilla MN2–4 pore-like, at midlength of dorsal surface; MN2 located laterally of line connecting MN3 and MN4,

close to MN1; MN4 on lateral face. Seta MN5 minute, situated subapically on outer face of mandible. MN6 situated subapically on inner face of mandible.

Maxilla (Figs. 61D–E): Cardo with one rather long ventral seta (MX1). Stipes with a row of five rather short, stout setae (MX7–11) situated dorsally along inner face; MX7–11 equidistant, MX8–11 with subapical tooth; MX7 shorter than others. Ventral surface of stipes with three pore-like sensilla (MX2–4) and two rather long setae (MX5–6); MX2 close to outer face in basal 0.30 of sclerite; MX3 close to inner face in distal 0.42 of sclerite; MX4–6 subapical, on outer face of sclerite; MX5 and MX6 more distally than MX4, MX4–5 more laterally than MX6. Dorsal surface of palpomere 1 with one moderately short spiniform seta (MX16) on base of inner face; ventral surface of palpomere 1 with one pore-like sensillum (MX12) and two rather long setae (MX13–14) close to distal margin of sclerite; MX12 on lateral face; MX13 close to MX12, between MX12 and MX14; MX14 situated medially. Two pore-like sensilla (MX15 and MX17) on membrane behind inner appendage; MX17 dorsal, MX15 ventral. Inner appendage with one rather long seta and a few short setae (gAPP). Palpomere 2 with two pore-like sensilla (MX18–19) and one minute seta (MX27); MX18 situated ventrally at midwidth of palpomere 2, on borderline between sclerite and intersegmental membrane between palpomeres 2 and 3; MX19 on inner face of intersegmental membrane between palpomeres 2 and 3; MX27 at base of outer face. Palpomere 3 with two rather long setae (MX21 and MX23) and two pore-like sensilla (MX20 and MX22); MX20 situated laterodorsally on distal margin of sclerite; MX21 on middle of dorsal surface, on distal margin of sclerite; MX22 behind MX21; MX23 on laterodorsal surface of sclerite, close to distal margin. Palpomere 4 with one rather long seta (MX24) on base of inner face, and with digitiform sensillum (MX25) and pore-like sensillum (MX26) situated subapically on outer face; MX25 dorsal, MX26 ventral. Apical membranous area of palpomere 4 with several minute setae (gMX).

Labium (Figs. 60B, 61F–G): Submentum (Fig. 60B) with two pairs of setae (LA1–2); LA1 moderately long, in lateral corners; LA2 short on anterior margin. Ventral surface of mentum with one pair of rather short setae (LA3) and one pair of pore-like sensilla (LA4) close to distal margin; LA3 behind LA4. Dorsal surface of prementum with two pairs of pore-like sensilla (LA8–9); LA8 situated basally at midwidth; LA9 in small membranous area completely surrounded by sclerite of prementum. Ventral surface of prementum with three pairs of sensilla (LA5–7) on lateral portion; seta LA5 short, on basal margin of sclerite; LA6 long seta, situated on distal margin of sclerite but more mesally than LA7; LA7 pore-like, on borderline between sclerite and membranous area between prementum and palpi. Membrane between prementum and palpi with one pair of long setae (LA10) at base of ligula. Ligula with two pairs of pore-like sensilla; LA12 dorsal, on apical membranous area, LA11 subapical, on ventral surface of sclerite. Palpomere 1 with one minute seta (LA13) located ventrally, close to basal margin of sclerite; LA14 situated dorsally on intersegmental membrane between palpomeres 1 and 2. Palpomere 2 with one pore-like sensillum (LA15) situated laterally on subapical margin. Apical membranous area of palpomere 2 with short to minute setae (gLA).

Secondary chaetotaxy of head. *Second instar.* *Frontale* with one short secondary seta close to FR1, more posterolaterally than FR1.

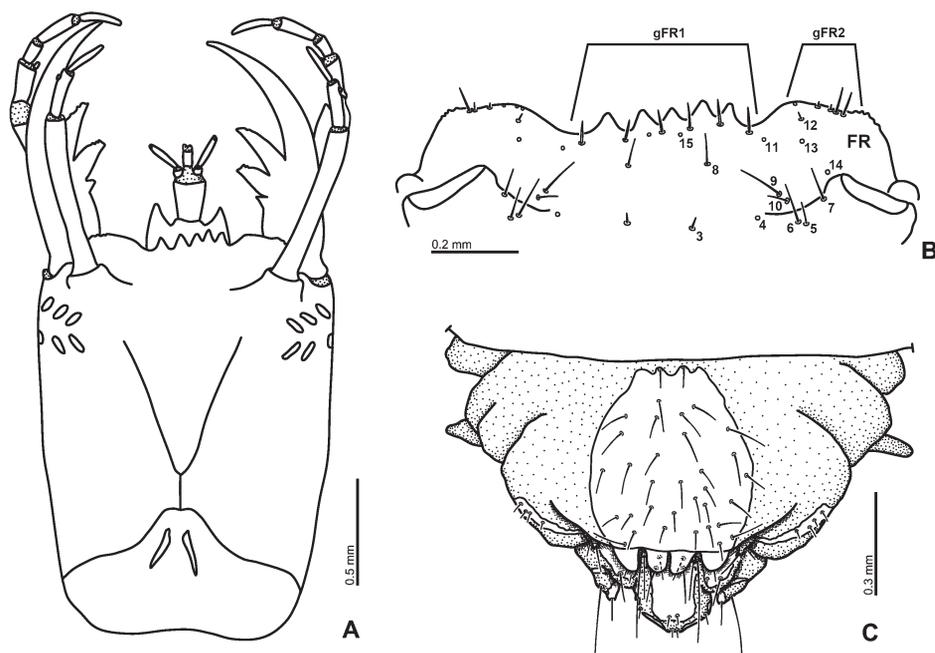


Fig. 62. *Sternolophus* (*Sternolophus*) *rufipes* (Fabricius, 1792), third instar, dorsal view. A – head; B – detail of anterior margin of head capsule; C – spiracular atrium.

Parietale: Two to seven short secondary setae between PA6 and PA8 along frontal line. Three short secondary setae close to PA7 and PA13, situated laterally of line connecting PA5 and PA13. Two short secondary setae situated posteriorly to antennal socket close to PA9 and PA10; one more mesally than PA9; the other more mesally than PA10. One rather short secondary seta close to outer margin of antennal socket. One rather short secondary seta between PA11 and PA15. Lateral part bearing nine to eleven rather short secondary setae. One short secondary seta situated ventrally, rather close but more mesally than PA17. PA26 situated more anteriorly than that of first instar.

Antenna: Scape with a transverse row of setae formed by ca. seven rather long secondary setae, and four rather long secondary setae on subapical portion, behind AN3–5 (e.g., Fig. 63A).

Mandible (e.g., Figs. 63C–D): Outer face of mandible bearing numerous small setae; base of mandible without or with one to two short secondary setae.

Maxilla (e.g., Figs. 63E–F): Stipes with nine rather long secondary setae on outer face, and two short, stout secondary setae on basal part of outer face; one rather long seta on subapical part of ventral surface of sclerite.

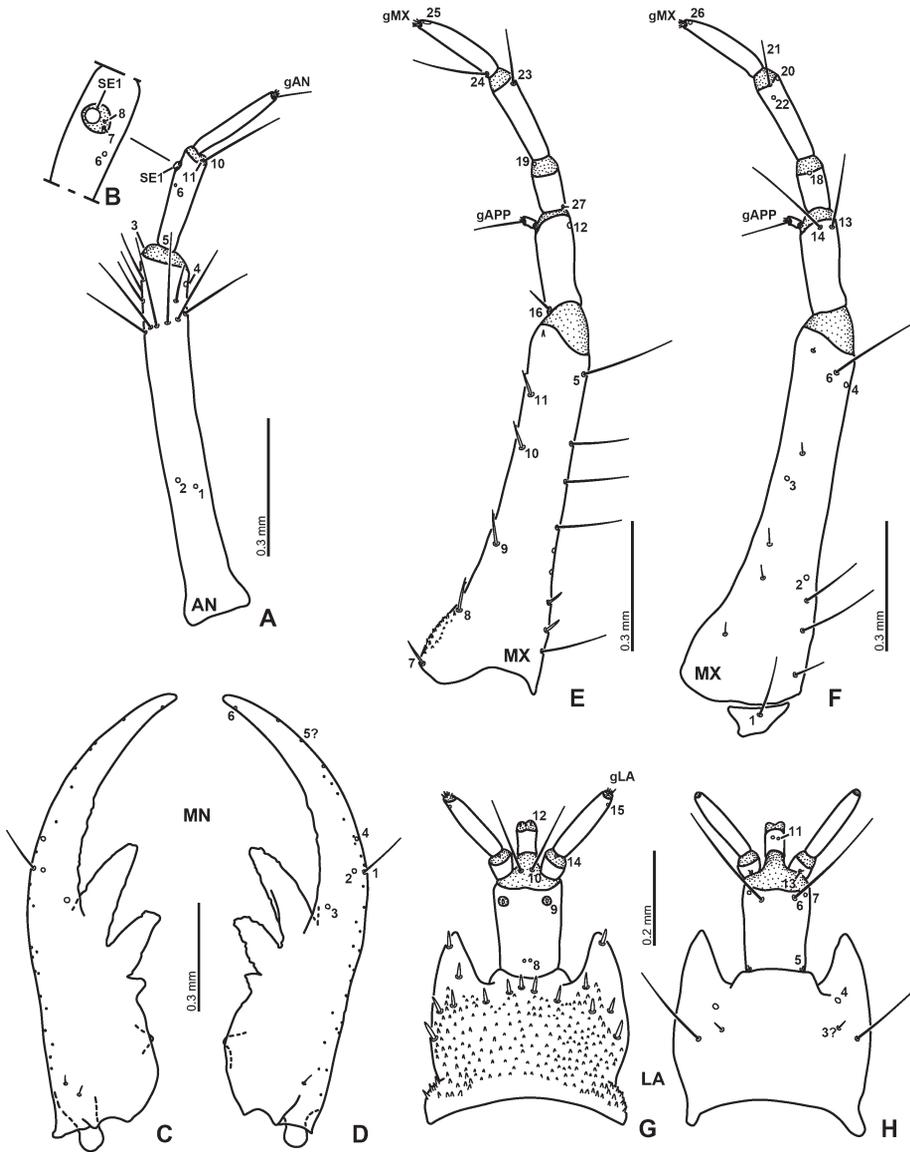


Fig. 63. Head appendages of *Sternolophus* (*Sternolophus*) *rufipes* (Fabricius, 1792), third instar. A – antenna, dorsal view; B – detail of outer surface of pedicel, lateral view; C–D – mandibles, dorsal view; E – maxilla, dorsal view; F – maxilla, ventral view; G – labium, dorsal view; H – labium, ventral view.

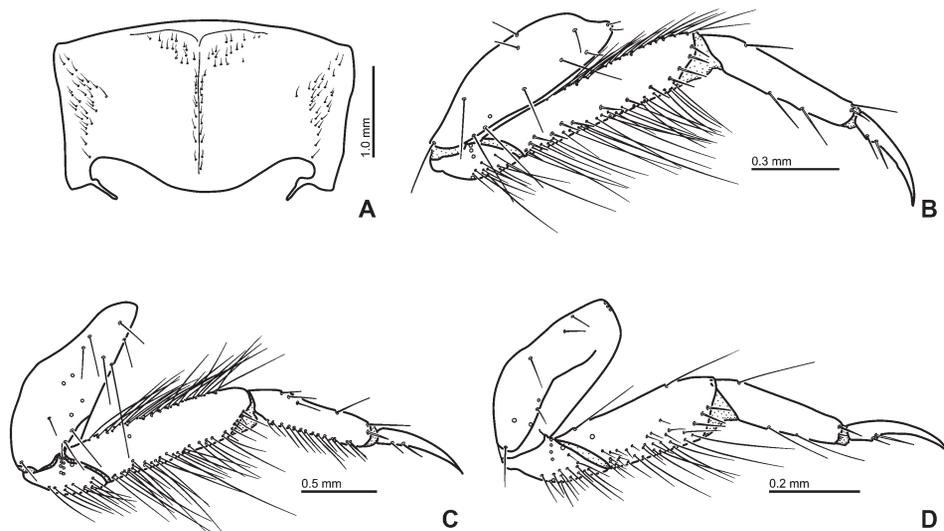


Fig. 64. Prothoracic sternum and mesothoracic legs of Hydrophilini species. A – prothoracic sternum of *Hydrochara affinis* (Sharp, 1873), third instar, ventral view. B–D – mesothoracic legs, first instar, anterior view: B – *Hydrochara affinis* (Sharp, 1873); C – *Hydrophilus acuminatus* Motschulsky, 1854; D – *Sternolophus rufipes* (Fabricius, 1792).

Labium (e.g., Figs. 63G–H): Dorsal surface of mentum with 12–17 short, stout secondary setae on anterior part of sclerite (e.g., Fig. 63G); ventral surface of mentum with one long secondary seta close to but more laterally than LA3.

Third instar. Similar to second instar.

Parietale: Five to seven rather short secondary setae between PA6 and PA8. Nine to 12 rather long secondary setae on lateral part.

Antenna (Fig. 63A): Antennomere 1 with 13–14 rather long secondary setae on apical part, behind AN3–5.

Biology. Larvae are found in standing water (HAYASHI 2009a). The life history of this species has been reported by HOSOI (1952) and HUANG & PU (1984).

Identification. Two species of the *Sternolophus* are known in Japan, but only one of them, *S. rufipes*, is distributed in Honshū. Hence we identified examined larvae as *S. rufipes*.

Remarks. YOSHIMURA (1959) described a Japanese hydrophilid larva collected in the field as *Hydrocylus* sp. B. Judging from the description, figures, and the locality where the specimens were collected, the larvae described by him belong to *Sternolophus rufipes*.

4.4. Key to the known genera of the aquatic Hydrophilidae from Japan

Here we provide a preliminary generic key to all known larvae of the aquatic Japanese Hydrophilidae (i.e., representatives of the subfamily Hydrophilinae and the genus *Coelostoma* Brullé, 1835 of the subfamily Sphaeridiinae). This key presumably works for all instars. The larvae of the genus *Megagraphydrus* Hansen, 1999 are unknown; larvae of the Japanese species of the tribe Anacaenini and of the genera *Pelthydrus* d'Orchymont, 1919 (Laccobiini) and *Chasmogenus* are also unknown. For *Anacaena* and *Chasmogenus*, we refer to previous studies (RICHMOND 1920; WINTERBOURN 1973; ANDERSON 1976; ARCHANGELSKY 1997, 1999; ARCHANGELSKY & FIKÁČEK 2004). The knowledge on the larva of the genus *Pelthydrus* is based on the larva described by BERTRAND (1936) as Hydrophilidae genus 1 and only later assigned to *Pelthydrus* by BERTRAND (1974); moreover, as the larva does not fit other known Laccobiini larvae based on its morphology, its identification is doubtful and the genus *Pelthydrus* is therefore not included in the key.

1. Labium with well developed hypopharyngeal lobe; legs more or less reduced. Mostly terrestrial species. Subfamily **Sphaeridiinae (part.)**
- Labium without well developed hypopharyngeal lobe; legs sometimes short, but well developed. 2
2. Both mandibles similar in shape and with same number of inner teeth (Figs. 33C–D, 49B–C, 61B–C). 3
- Mandibles strongly asymmetrical, with different number of inner teeth on each mandible (Figs. 11B–C, 15D–E, 57B–C). 14
3. Median lobe of spiracular atrium deeply bifurcate (HAYASHI 1986: Pl. 8I, HANSEN & RICHARDSON 1998: Fig. 12). Terrestrial species. Subfamily **Sphaeridiinae (part.)**
- Median lobe of spiracular atrium simple, entire (Fig. 5). 4
4. Nasale with only one large tooth medially (HAYASHI 2009a: Fig. 6A). *Coelostoma* Brullé, 1835
- Shape of nasale variable (straight, weakly rounded, serrate, or with variable number of teeth; e.g., Figs. 13C, 29C, 46C, 55A, 56C), never with a single median tooth. 5
5. Nasale with several distinct teeth (Figs. 36C, 46C, 60C, 62B). 6
- Nasale without distinct teeth, straight or slightly serrate (Figs. 52C, 55A). 13
6. Ligula reduced, indistinct. *Amphiops* Erichson, 1843
- Ligula well developed (e.g., Figs. 8F, 21F, 30F, 55H, 57F). 7
7. Anterior corners of mentum strongly projecting anteriad (Figs. 61F, 63G); legs long, with fringes of long swimming hairs (Fig. 64D). *Sternolophus* Solier, 1834
- Anterior corners of mentum not projecting anteriad (Fig. 30F, 47B); legs rather short to moderately long, without fringes of long swimming hairs (Figs. 45, 50C). 8
8. Proscutum with lateral lobes (ARCHANGELSKY & FIKÁČEK 2004: Figs. 9, 11); posterior margin of dorsal plate of abdominal segment 8 slightly to strongly trifold (ARCHANGELSKY & FIKÁČEK 2004: Figs. 10, 12). 9
- Proscutum without lateral lobes (Figs. 3, 6); posterior margin of dorsal plate of abdo-

- minal segment 8 straight to sinuate (Figs. 32B, 41B, 48B). 10
 9. Inner edge of antennal socket with fringe-like seta (ARCHANGELSKY & FIKÁČEK 2004: Fig. 3); proscutum with rounded lateral lobes (ARCHANGELSKY & FIKÁČEK 2004: Fig. 9); abdominal segments without finger-like lateral projections (ARCHANGELSKY & FIKÁČEK 2004: Fig. 1). *Anacaena* Thomson, 1859
 – Inner edge of antennal socket with trichoid seta; proscutum with flat lateral lobes (ARCHANGELSKY & FIKÁČEK 2004: Fig. 11); abdominal segments with finger-like lateral projections (ARCHANGELSKY 1997: Fig. 37A). *Crenitis* Bedel, 1881
 10. Frontal lines not converging towards base of head capsule (the lines widely separated at the base of head capsule) or widely U-shaped (ARCHANGELSKY 1997: Fig. 34B; WINTERBOURN 1973: Fig. 4). *Paracymus* Thomson, 1867
 – Frontal lines converging towards base of head capsule, V-shaped or lyriiform (Figs. 29A, 35A, 48A). 11
 11. Nasale strongly asymmetrical (Figs. 38C, 42A); mandibles with two inner teeth, distal one large, basal one smaller (Figs. 42C–D); head capsule with long scale-like setae (Figs. 29, 36, 38). *Helochares* Mulsant, 1844
 – Nasale slightly asymmetrical (Fig. 46C); mandibles with three inner teeth, distal two large, basal one smaller (Figs. 49B–C); head capsule without long scale-like setae (Fig. 46). 12
 12. Dorsal and lateral surface of head capsule with densely arranged, strong tooth-like cuticular projections; abdominal segments with transverse rows of tubercles.
 *Hydrocassis* Fairmaire, 1878
 – Dorsal and lateral surface of head capsule smooth, without densely arranged, strong tooth-like cuticular projections (Fig. 48A); abdominal segments without transverse rows of tubercles (Figs. 1G, 6C). *Hydrobius* Leach, 1815
 13. Abdominal segments with long lateral projections (Fig. 51A); spiracular atrium with long prostyli (Fig. 54B). *Hydrochara* Berthold, 1827
 – Thoracic and abdominal segments with several pairs of long setiferous projections (HAYASHI 2009a: Figs. 10A–B); spiracular atrium without distinct prostyli (e.g., Figs. 5, 32B). *Regimbartia* Zaitzev, 1908
 14. Abdominal segments with long lateral tracheal gills (HAYASHI 2009a: Figs. 10C–D); spiracular atrium reduced. *Berosus* Leach, 1817
 – Abdominal segments without tracheal gills; spiracular atrium developed (e.g., Fig. 5). 15
 15. Epistomal lobes strongly extended anteriorly; left lobe with dense series of stout setae on anterior margin, right lobe without setae (ARCHANGELSKY 1997: Fig. 45A).
 *Laccobius* Erichson, 1837
 – Epistomal lobe not or moderately extended anteriorly, setation of both lobes more or less the same (Figs. 10C, 20C, 56C). 16
 16. Nasale almost straight, without distinct teeth or serrate margin (Fig. 56C); frontal lines U-shaped (Fig. 58A); anterior corners of mentum strongly projecting anteriad (Fig. 57F); abdominal segments without spinose prolegs.
 *Hydrophilus* Geoffroy, 1762

- Nasale not straight, with distinct teeth or serrate margin (Figs. 10C, 15A); frontal lines V-shaped to lyriform (Figs. 9A, 25A); anterior corners of mentum not projecting anteriorly (Fig. 26G); abdominal segments with spinose prolegs (Figs. 12A–B, 28). 17
- 17. Nasale serrate, with only one or two teeth (Figs. 17A, 22C).
..... *Enochrus* Thomson, 1859
- Nasale with several distinct teeth, without serrate margin (Figs. 7C, 10C). 18
- 18. Nasale almost symmetrical (ANDERSON 1976: Fig. 9). *Chasmogenus* Sharp, 1882
- Nasale strongly asymmetrical (Figs. 7C, 10C). *Agraphydrus* Régimbart, 1903

5. Conclusions

5.1. Chaetotaxy of the larval head

The taxonomic significance of chaetotaxy in hydrophilid larvae is demonstrated by FIKÁČEK et al. (2008) for the Hydrophilidae in general, by BYTTEBIER & TORRES (2009) for the genus *Enochrus*, and by TORRES et al. (2011) for the genus *Tropisternus* Solier, 1834. FIKÁČEK et al. (2008) pointed out that the primary sensilla of the Hydrophilidae are rather stable in number and position. Our observations support this opinion. The presence of additional sensilla or the absence of some primary sensilla are generally rare, with only a few primary sensilla (e.g., positions of PA1–5) showing slight intraspecific variation.

BYTTEBIER & TORRES (2009) and TORRES et al. (2011) studied the secondary chaetotaxy of the larval head of two species of *Enochrus* and one species of *Tropisternus* respectively, including the intraspecific variation in number and position of secondary sensilla. Our study brings data on the secondary head chaetotaxy for a wider spectrum of species. We confirm that it is easily possible to distinguish almost all primary sensilla even in second or third instar larvae, only with an exception of a few species that bear numerous secondary sensilla in the second and third instars (e.g., parietale in *Hydrochara* and *Hydrophilus*). Secondary chaetotaxy shows some intraspecific variation in all species treated in this study (e.g., Figs. 18, 27, 34, 43), but seems to be rather stable in the position and the presence or absence of some secondary sensilla or within the groups within genera or subtribes in many cases. These results demonstrate that we can use later instar larvae for studies of primary chaetotaxy. The presence or absence of secondary sensilla is mostly stable among taxa, and their number and position usually do not change even between second and third instars (see e.g. the characters mentioned below). This indicates that there likely is homology between some secondary sensilla of the second and third instars of the same species, as well as between different taxa. This would allow treatment (and possibly even the naming) these secondary sensilla in the same way as primary ones and the use of them more or less as subprimary sensilla.

The shape of setae shows variation. The most considerable character state is presence of long scale-like setae. All examined species of *Agraphydrus* and *Helochares* in this study have long scale-like setae on the head capsule, antenna, and maxilla (e.g., Figs. 10, 12C–D, 38). These setae are also present on the thoracic and abdominal segments (Fig. 12D). Only long trichoid setae have been reported for most genera in previous studies,

with the exception of the long fringe-like setae in *Anacaena* Thomson, 1859 (Hydrophilinae: Anacaenini) (ARCHANGELSKY & FIKÁČEK 2004) and long trifold setae of PA21 and PA26 of *Coelostoma* Brullé, 1835 (Sphaeridiinae, Coelostomatini) (FIKÁČEK 2006). The long scale-like setae reported for *Helochaeres* and *Agraphydrus* in this study seem to even differ in shape between both of the genera: they are much narrower in *Helochaeres* than in *Agraphydrus*.

In the chaetotaxy of the head capsule, the additional sensilla on the nasale, which were recognised as presumably being homologous in the genera *Hydrophilus* and *Tropisternus* (FIKÁČEK et al. 2008) (Fig. 56C) seem to be, in fact, present in all examined taxa of the tribes Acidocerini, Hydrobiusini and Hydrophilini except for *Enochrus* species. TORRES et al. (2011) considered these sensilla, together with stout setae on the nasale in the genus *Tropisternus*, as being gFR1. These additional sensilla are generally situated on margins of the median teeth of the nasale, but are also often situated on the ventral side in many cases. Even though it seems therefore possible to homologise at least some sensilla of gFR1 between hydrophilid taxa, we follow the way introduced by FIKÁČEK et al. (2008) for the genus *Hydrophilus* (as additional sensilla) and follow TORRES et al. (2011) for the remaining genera (as gFR1). Additional studies of a wider spectrum of taxa are needed to confirm these homologies.

On the secondary sensilla on head capsule, *Hydrochara* and *Hydrophilus* bear numerous secondary sensilla on the parietale. The remaining taxa generally bear secondary sensilla on (1) the lateral part of the frontale, between FR1 and FR5; (2) the posteromesal portion of the parietale, along frontal line; (3) the anterolateral part of the parietale, close to antennal socket, PA8 and PA9; and (4) the lateral surface of the parietale (Figs. 10A–B, 20A–B, 46A–B). The number of sensilla is rather variable but the positions of the sensilla are stable among taxa (Figs. 18, 27, 34, 43).

Antennal chaetotaxy shows little variation among taxa and instars in the Acidocerini and Hydrobiusini species (e.g., Fig. 65A) (FIKÁČEK et al. 2008, TORRES et al. 2011). Species of the Hydrophilini bear numerous secondary sensilla on the stipes in the second and third instars (Figs. 55B, 59A–B, 63A, 65B) (HOSOI 1947, ARCHANGELSKY 1997, TORRES et al. 2011). However, larvae of *Hydrophilus* bear many additional sensilla on the scape already present in the first instar, but these sensilla are also present in later instars (Figs. 57A, 59A–B) (BØVING & HENRIKSEN 1938, HOSOI 1939b, BERGE HENEGOUWEN 1982, FIKÁČEK et al. 2008). For this reason, the primary and secondary sensilla cannot be distinguished in second and third instar larvae of *Hydrophilus*.

The mandibles bear sparse to dense secondary sensilla on the outer face (Figs. 65C–D), which are usually small to minute setae (e.g., Figs. 26C–D, 49B–C, 55D–E). Several secondary sensilla are located in the basal part of the mandible and close to the mandibular acetabulum (Figs. 11B–C, 24C–D, 33C–D, 49B–C, 63C–D). The secondary sensilla are easily distinguishable from the primary sensilla, only MN5 is occasionally scarcely detectable.

Chaetotaxy of the maxillae varies among taxa. Only *Enochrus* (*Methydrus*) *japonicus* bears stout secondary sensilla on the inner face of the stipes in the examined species of the Acidocerini (Figs. 24E, 26E, 66B). The remaining Acidocerini species examined bear

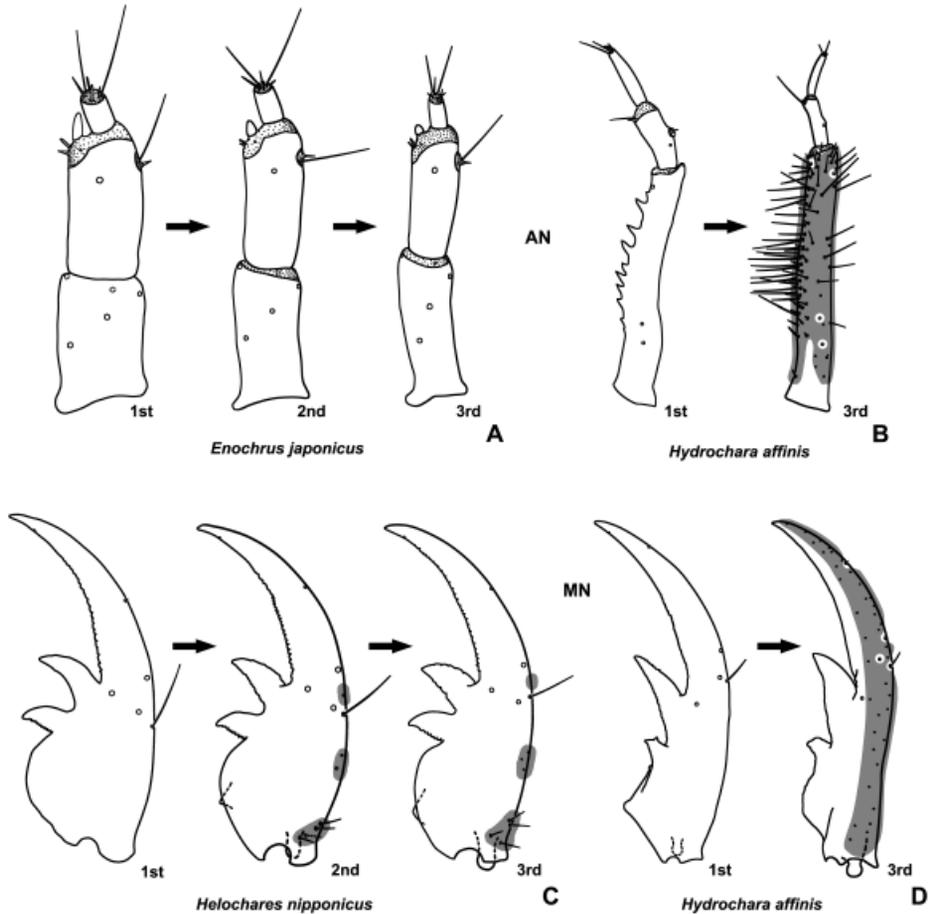


Fig. 65. Examples of morphological transformations between instars in the Acidocerini and Hydrophilini larvae. A–B – antennae, dorsal view; C–D – mandibles, dorsal view. A – *Enochrus (Methyrus) japonicus* (Sharp, 1873), B – *Hydrochara affinis* (Sharp, 1873), C – *Helochares (Hydrobaticus) nipponicus* Hebauer, 1995, D – *Hydrochara affinis*.

only several secondary sensilla on the lateral and ventral surfaces of the stipes (Figs. 66A, C). The Hydrophilini species bear numerous to several, minute to long secondary sensilla on the stipes (Figs. 55F–G, 59D–E, 63E–F) (ARCHANGELSKY 1997, WATTS 2002, TORRES et al. 2008). Moreover, *Hydrochara* and *Hydrophilus* bear secondary setae on palpomere 1 (Figs. 55F–G, 59D–E).

On the labium, Acidocerini and Hydrobiusini species bear several secondary sensilla on the mentum (e.g., Figs. 11F–G, 17G–H, 33G–H, 47B–C, 49F, 67A) (ARCHANGELSKY 1997, 2002, FERNÁNDEZ 2004, BYTTEBIER & TORRES 2009), in contrast to the Hydrophilini species which bear numerous secondary sensilla (Figs. 55H–I, 63G–H, 67B) (ARCHANGELSKY 1997,

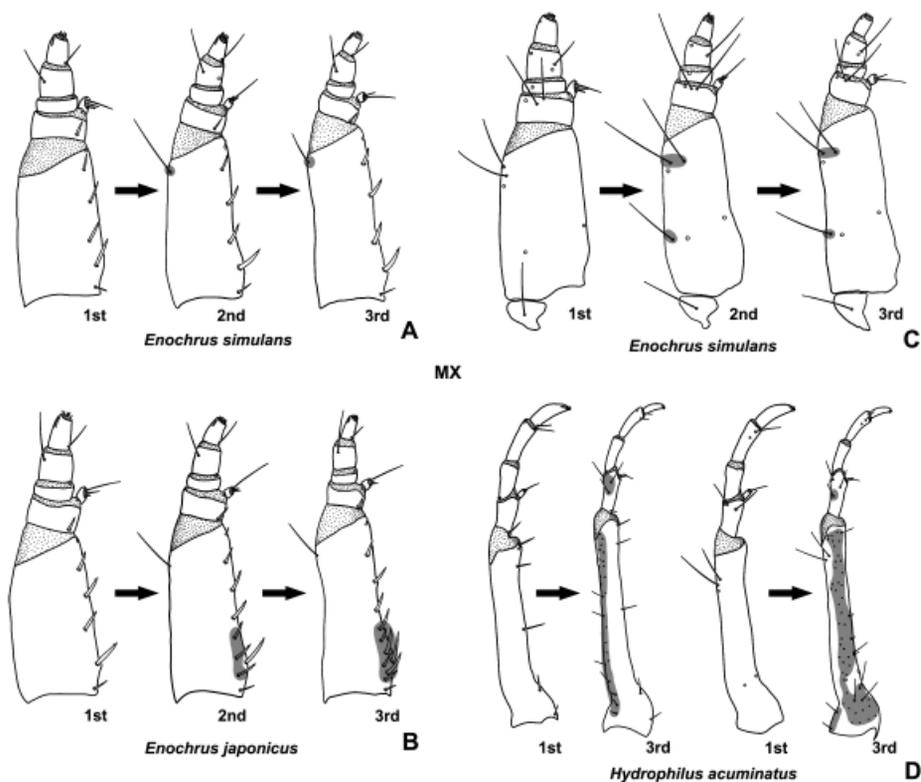


Fig. 66. Examples of morphological transformations between instars in the maxilla of the Acidocerini and Hydrophilini larvae. A–B – dorsal view, C – ventral view, D – dorsal (left side) and ventral (right side) views. A – *Enochrus (Holcophilydrus) simulans* (Sharp, 1873), B – *Enochrus (Methydrus) japonicus* (Sharp, 1873), C – *E. simulans*, D – *Hydrophilus (Hydrophilus) acuminatus* Motschulsky, 1854.

WATTS 2002; TORRES et al. 2008, 2011). The presence and absence of these secondary sensilla on the mentum may be used for the identification of instars in the genus *Enochrus* (BYT-TEBIER & TORRES 2009) and *Helochares* (FERNÁNDEZ 2004). We confirm that the number of secondary sensilla on the mentum can be used for the identification of instars in examined *Enochrus* species, however, the number of secondary sensilla on the mentum does not differ between the second and third instars in the examined species of *Helochares*.

5.2. Morphological transformations

Hydrophilid larvae generally have three instars and the morphology changes throughout their growth stages. The shape of the head capsule and its appendages are generally stable, showing little difference between instars, except for a few exceptional cases.

The antennae of most of the taxa examined for this study are stout in the first instar, becoming gradually more slender in the later instars (Figs. 65A–B). The most drastic

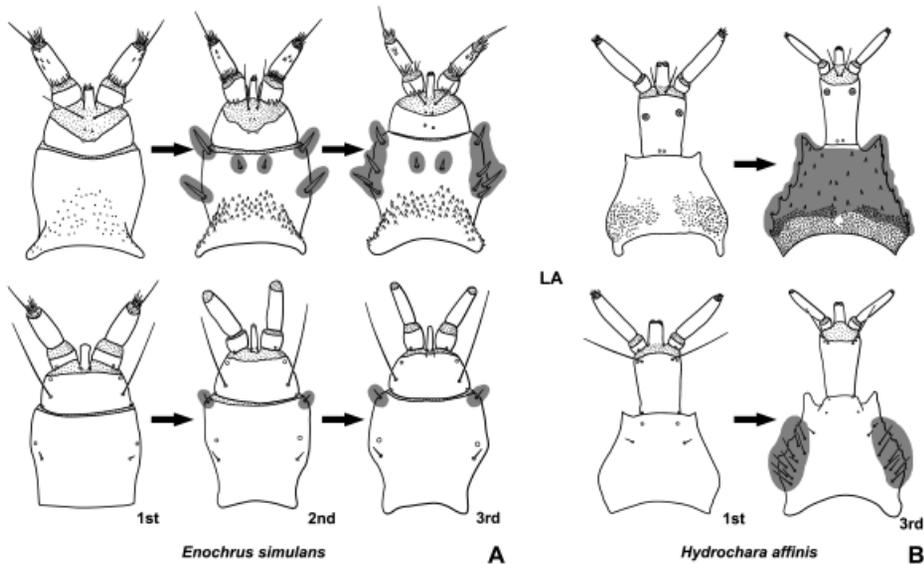


Fig. 67. Examples of morphological transformations between instars in the labium of the Acidocerini and Hydrophilini larvae. A–B – dorsal (upper side) and ventral (lower side) views. A – *Enochrus (Holcophilydrus) simulans* (Sharp, 1873), B – *Hydrochara affinis* (Sharp, 1873).

changes in the antennae occur between the first and the second instars of *Hydrochara*. We examined only first and third instar larvae of *Hydrochara affinis* in this study, but the information about the second instar published by HOSOI (1947) may be of use to complete our data. The inner face of the scape is smooth and bears secondary sensilla in the second and third instars, but is strongly denticulate and bare in the first instar (Fig. 65B) (HOSOI 1947). The number of antennal segments is stable among instars in all taxa examined except in *Hydrophilus*, in which it increases in the second instar with the first instar larvae having three-segmented antenna (Fig. 57A) (BØVING & HENRIKSEN 1938, HOSOI 1939b, BERGE HENEGOUWEN 1982, ARCHANGELSKY 1997), whereas the second and third instar larvae have four-segmented antennae (e.g., Figs. 59A–B) (HOSOI 1939b). The additional segment is situated between the scape and the pedicel and seems to belong to the pedicel according to the position of the primary sensilla (Figs. 57A, 59A–C). The relative size of sensorium SE1 gradually decreases slightly to distinctly in later instar (e.g., Figs. 23A, 24B, 26B).

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