ACTA ENTOMOLOGICA MUSEI NATIONALIS PRAGAE
Published 1.vi.2015 Volume 55(1), pp. 47–83 ISSN 0374-1036
http://zoobank.org/urn:lsid:zoobank.org:pub:8CDA7151-FBCD-484B-AF8D-C31EB76E9C67

Description of the larval stages of the berosine genera *Berosus* and *Regimbartia* based on the Japanese species *B. japonicus* and *R. attenuata* (Coleoptera: Hydrophilidae)

Yûsuke N. MINOSHIMA[1] & Masakazu HAYASHI[2]

[1] Natural History Division, Kitakyushu Museum of Natural History and Human History, Higashida 2-4-1, Yahatahigashi-ku, Kitakyushu-shi, Fukuoka, 805-0071 Japan; e-mail: minoshima@kmnh.jp

[2] Hoshizaki Green Foundation, Okinoshima 1659-5, Sono-chô, Izumo-shi, Shimane Pref., 691-0076 Japan; e-mail: hgf-haya@green-f.or.jp

Abstract. Larval morphology and head chaetotaxy are described for two genera of the tribe Berosini, *Berosus* Leach, 1817 and *Regimbartia* Zaitzev, 1908, based on reared and field-collected larvae of *Berosus* (*Berosus*) *japonicus* Sharp, 1873 and *Regimbartia attenuata* (Fabricius, 1801). We describe and illustrate the general morphology and head chaetotaxy of all three instars of both species. We review and discuss an ecological character, which is an adaptation to benthic lifestyle in *Berosus*. *Berosus* larvae do not have air-bubbles in alimentary canal, whereas majority of hydrophilid larvae have air-bubbles. Absence of the bubbles results in loss of buoyancy and would be an adaptation in two different ecological trends: benthic and swimming lifestyles. A detailed comparison of head chaetotaxy of both genera is provided. Chaetotaxy of *Berosus* and *Regimbartia* are not largely different, therefore benthic lifestyle will not strongly affect chaetotaxy. We also provide information of knowledge about immature stages of the tribe Berosini and provide the identification key to larvae of all five genera of the tribe. Biology of both studied species is briefly commented as well.

Key words. Coleoptera, Hydrophilidae, larva, *Berosus*, *Regimbartia*, Berosini, Hydrophilinae, chaetotaxy, Japan, Palaearctic

Introduction

The tribe Berosini represents the second largest tribe in the hydrophilid subfamily Hydrophilinae. It contains over 360 described species assigned to five genera (Short & Fikáček 2011, 2013). The larval morphology of all five genera of the Berosini has been described (see Archangelsky 2008; Table 1). Monophyly of Berosini is well supported with a proposition that one inner projection or seta on antennomere 1 is a larval synapomorphy, and moreover the phylogenetic relationship between the berosine genera was studied based on the morphology and molecular data (Archangelsky 2004, 2008; Short & Fikáček 2013). These trees show a slightly different topology, but two well supported clades are recognised: *Berosus* Leach, 1817 + *Hemiosus* Sharp, 1882 and *Derallus* Sharp,1882 + *Regimbartia* Zaitzev, 1908 + *Allocotocerus* Kraatz, 1883. The former clade has larval morphology adapted to a benthic lifestyle: *Berosus* and *Hemiosus* have highly modified larval head morphology and a reduction of spiracular atrium; *Berosus* larvae have tracheal gills, whereas *Hemiosus* larvae do not (Archangelsky 2008). In contrast, representatives of the latter clade retain the usual morphology of hydrophilid larvae.

Nine species assigned into two genera of Berosini have been recorded from Japan so far: eight species of the genus *Berosus* and one species of the genus *Regimbartia* (Hansen 1999; Short & Hebauer 2006; Short & Fikáček 2011). All of them live in standing waters and are good swimmers. Larvae of two species occurring in Japan were mentioned by previous authors with precise identification (Table 1): the larva of *Berosus japonicus* Sharp, 1873 was only figured in some publications (Table 1), that of *Regimbartia attenuata* (Fabricius, 1801) was described by Watts (2002), but the chaetotaxy of both these species was not described in detail.

The aim of this study is to complete the knowledge of the larval morphology and head chaetotaxy of the berosine genera *Berosus* and *Regimbartia*, including the comparison of all three larval instars, which was not available in the previous papers. In addition, the detailed comparison of larvae of metapneustic *Regimbartia* and apneustic *Berosus* may help us to understand the effect of benthic life style on larval morphology and chaetotaxy.

The authors would like to dedicate this paper to the memory of Dr. Nodoka Hayashi, a pioneer in the field of the immature beetles studies in Japan, who passed away on 29th May, 2013.

Materials and methods

Techniques of larval study. The methods follow those used by Minoshima & Hayashi (2011a). Specimens were fixed in 70% ethanol in the field or in the laboratory. Larvae were preserved in screw-cap vials with ca. 80% ethanol or were mounted on HS-slide (Higgins-Shirayama slide; Shirayama et al. 1993) (Kanto Rika Co., Ltd., Japan) with Euparal (Waldeck GmbH & Co. KG, Germany). Photographs of fixed specimens were taken using a Pentax K-5 digital camera attached to the SZX12 with a MeCan NY-1S digital SLR microscope adapter (MeCan Imaging Inc., Japan), and subsequently adapted in Adobe Photoshop Lightroom 4 and Photoshop CS5. Composite images were created using the focus stacking software CombineZP (Hadley 2010).

Identification of species and instars. *Berosus japonicus*: Some of the larvae were reared from egg-cases laid by identified adults collected in the field by the second author. Remaining specimens collected in the field were associated with co-occurring adults and by the exclusion of the species/genera not occurring in the area. The hydrophilid fauna of the collecting sites has been extensively studied (e.g., Hayashi 2006a,b, 2007, 2008, 2009a,b,c, 2011; Kawano et al. 2006; Hayashi et al. 2008) and is very well known.

Table 1. State of knowledge of the immature stages of the tribe Berosini and source of information. **E** – egg case, eggs; **L1, L2, L3** – larva of first, second, or third instar; **L?** – larval instar unknown; **P** – pupa.

Genus	Species	Stages	Reference
***Allocotocerus* Kraatz, 1883**			
	Allocotocerus punctatus (Blackburn, 1888)	L3	Watts (2002)
***Berosus* Leach, 1817**			
Subgenus *Enoplurus* Hope, 1838			
	Berosus australiae Mulsant et Rey, 1858	L3	Watts (2002)
	Berosus hoplites Sharp, 1887	E, L1, L2, L3, P	Archangelsky (1994)
		E, P	Archangelsky (1997)
	Berosus pugnax LeConte, 1863	E, L1, L2, L3, P	Archangelsky (1994)
		E, L3, P	Archangelsky (1997)
	Berosus spinosus (Steven, 1808)	L?	Schiødte (1862)
		L?	Bøving & Henriksen (1938)
Subgenus *Berosus* Leach, 1817			
	Berosus affinis Brullé, 1835	E	Angus et al. (1994)
		L3	Karaouzas & İncekara (2011)
	Berosus alternans Brullé, 1841	E, L1, L2, L3, P	Fernández & Campos (2002)
	Berosus aulus Orchymont, 1941	E, L1, L3	Archangelsky (1999)
	Berosus auriceps Boheman, 1858	E, L1, L3	Archangelsky (1999)
		P	Archangelsky (2002b)
	Berosus coptogonus Jensen-Haarup, 1910	E, L1, L3	Archangelsky (2002b)
	Berosus cornicinus Knisch, 1922	E, L1, L3	Archangelsky (2002b)
	Berosus corrini Wooldridge, 1964	E, L3, P	Archangelsky (1994)
		E, P	Archangelsky (1997)
	Berosus hispanicus Küster, 1847	E	Angus et al. (1994)
	Berosus japonicus Sharp, 1873	L1, L?	Hayashi (2008)
		E, L1, L?	Hayashi (2009a)
		L?	Hayashi (2011)
	Berosus sp. [?*B. japonicus*]	L?	Fukuda et al. (1959)
	Berosus luridus (Linnaeus, 1761)	E	Angus et al. (1994)
	Berosus metalliceps Sharp, 1882	L?	Spangler (1991)
	Berosus pantherinus LeConte,1855	E, L?, P	Wilson (1923)
	Berosus peregrinus (Herbst, 1797)	L?	Wilson (1923)
		E, L1, L3	Richmond (1920)
	Berosus sp. [?*B. pulchellus* MacLeay, 1825]	L?	Bertrand (1936)
	Berosus sayi Hansen, 1999	L?	Richmond (1920, as *B. striatus*)
		E, L1, L?, P	Wilson (1923, as *B. striatus*)
		L?	Peterson (1951, as *B. striatus*)
	Berosus signaticollis (Charpentier, 1825)	L?, P	Schiødte (1872)
		E, L?	Brocher (1911)
		E, L?, P	Bøving & Henriksen (1938)
	Berosus toxacanthus Oliva, 1989	E, L1, L3	Archangelsky (2002b)

(continues on the next page)

Table 1. Continued from the previous page.

Genus	Species	Stages	Reference
***Derallus* Sharp, 1882**			
	Derallus anicatus Orchymont, 1940	L1?	Bertrand (1968)
	Derallus angustus Sharp, 1882	E, L3, P	Archangelsky & Durand (1992)
		E, L3, P	Archangelsky (1997)
	Derallus paranensis Oliva, 1981	E, L1, L2, L3	Archangelsky & Fernandez (2005)
	Derallus rudis Sharp, 1887	L3	Spangler (1966a)
***Hemiosus* Sharp, 1882**			
	Hemiosus bruchi Knisch, 1924	E, L3, P	Archangelsky (2000)
	Hemiosus dejeanii (Solier, 1849)	L2, L3	Archangelsky & Fernandez (2005)
	Hemiosus multimaculatus (Jansen-Haarup, 1910)	L1, L2, L3	Archangelsky (2002a)
	Hemiosus sp.	L?	Spangler (1966b, as 'Berosinae-?, Genus-?')
***Regimbartia* Zaitzev, 1908**			
	Regimbartia attenuata (Fabricius, 1801)	L3 E, L3?	Watts (2002) Hayashi (2009a)
		L3	Hayashi (2011)
	Regimbartia sp.	L?	Bertrand (1962) (as 'Hydrobiinae genus D')
Undetermined berosine larvae			
	Berosus sp.	L?	Spangler (1966b)
	Berosus sp.	L?	Lawrence & Slipiński (2013)
	Berosini gen. 1	L?	Bertrand (1936)
			Bertrand (1972)
	Berosini gen. 2	L?	Bertrand (1936)
			Bertrand (1972)
	Berosini gen. 4	L?	Bertrand (1962)
			Bertrand (1972)
	Berosini gen. 5	L?	Bertrand (1972)

Regimbartia attenuata (Fabricius, 1801): Some of the larvae were reared from egg-cases laid by identified adults collected in the field by the second author. Remaining specimens collected in the field were associated with co-occurring adults and by the exclusion of the species/genera not occurring in the area. One species of the genus *Regimbartia*: *R. attenuata*, has been recorded from Japan and larval morphology matched that described by Watts (2002) for specimens of the species from Australia; this allowed an independent confirmation of the correctness of our identification.

In both species, instars were identified by the relative size of the head capsule (by sorting the material in one sample into size categories) and the presence/absence of secondary sensilla on head capsule and mouthparts. Larvae that could not be identified with confidence were not used for this study.

Terminology. Morphological terminology follows Archangelsky (1997), Minoshima & Hayashi (2011a) and Minoshima et al. (2013); for the chaetotaxy of the larval head we refer to Fikáček et al. (2008) and Byttebier and Torres (2009). The format of the larval description generally follows that of Minoshima & Hayashi (2011a).

Depository of materials. The examined material is deposited in the following collections:

EUMJ Ehime University Museum, Matsuyama, Ehime, Japan (H. Yoshitomi);
HGF Hoshizaki Green Foundation, Izumo, Shimane, Japan (M. Hayashi);
KMNH Kitakyushu Museum of Natural History and Human History, Kitakyushu, Fukuoka, Japan (Y. Minoshima).

Abbreviations used in description. AN – antenna; **E** – egg-case; **FR** – frontale; **gAN** – group of the antennal sensilla; **gAPP** – group of the sensilla on inner appendage of maxilla; **gFR** – group of the sensilla on frontale; **gLA** – group of the sensilla on labium; **gMX** – group of the sensilla on maxilla; **L1**, **L2**, **L3** – first, second, and third instar; **LA** – labium; **MN** – mandible; **MX** – maxilla; **PA** – parietale; **SE** – sensorium.

Key to the genera of the larvae of the tribe Berosini

Larvae of the Berosini are distinguishable from other hydrophilid larvae by the presence of one inner projection or seta on antennomere 1, which is an autapomorphy of the Berosini.

In the following key, we used our data concerning *Berosus* and *Regimbartia* and combined them with those of the previous authors (see Table 1) for the morphology of the remaining three berosine genera and for the intrageneric variation of *Berosus*. Archangelsky (2008) provided a table comparing larval morphology of all five genera.

1 Abdomen with tracheal gills. .... ***Berosus*** Leach, 1817
– Abdomen without tracheal gills. 2
2 Clypeolabrum strongly asymmetrical; left epistomal lobe strongly projecting anteriorly, bearing a series of stout setae (Figs 3A, 5B); mandibles strongly asymmetrical (Figs 4C–D, 7A–B); abdomen without setiferous projections; spiracular atrium reduced. .... ***Hemiosus*** Sharp, 1882
– Clypeolabrum almost symmetrical (Figs 9C, 13C); epistomal lobe not strongly projecting anteriorly; mandibles symmetrical to slightly asymmetrical (Figs 11A–B, 15A–B); labium with ligula (Figs 11C–D, 15C–D); abdomen with setiferous projections (Fig. 8A–B, D); spiracular atrium well developed (Fig. 12C). 3
3 Antennomere 1 not widened distally. .... ***Derallus*** Sharp, 1882
– Antennomere 1 widened distally (Figs 10A, 14A). 4
4 Inner projection of antennomere 1 pointed apically, spine-like; apex of antennomere 2 with inner extension. .... ***Allocotocerus*** Kraatz, 1883
– Inner projection of antennomere 1 rounded apically (Figs 10A, 14A); apex of antennomere 2 without inner extension. .... ***Regimbartia*** Zaitzev, 1908

Larval morphology

Genus *Berosus* Leach, 1817

(Figs 1–7, 17A–B, 18A)

Diagnosis. Larvae of the genus *Berosus* are easily distinguishable from almost all other Hydrophilidae by the presence of tracheal gills on the abdominal segments (Fig. 1) and the reduction of spiracular atrium (Fig. 5D); *Berosus* larvae often resemble *Laccobius* Erichson, 1837 in head morphology (e.g., Archangelsky 1997), however *Berosus* is distinguishable by the morphology of the clypeolabrum: right epistomal lobe absent in *Berosus* (Figs 3A, 5B) but present in *Laccobius*, and left epistomal lobe bears only stout setae in *Berosus* (Figs 3A, 5B), but bears stout setae and seta-like cuticular projections in *Laccobius* (Y. Minoshima, personal observation).

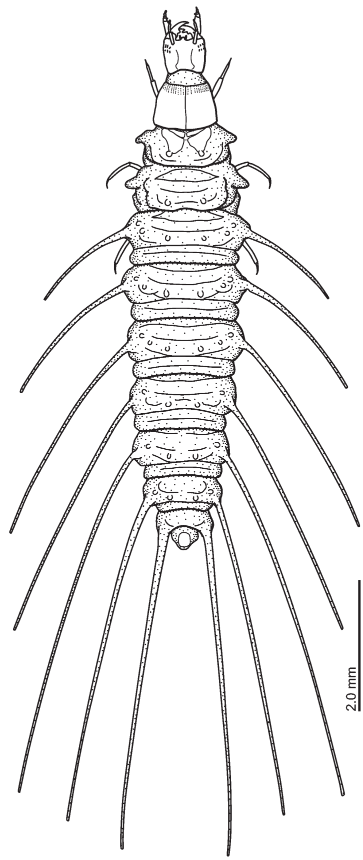

Fig. 1. Habitus of the third instar larva of *Berosus* (*Berosus*) *japonicus* Sharp, 1873.

Within Japanese genera, the genus *Hydrochara* Berthold, 1827 superficially resembles *Berosus* by the presence of lateral projections on the abdomen (but the projections are not tracheal gills) (Minoshima & Hayashi 2011a, Minoshima et al. 2012), the genus *Laccobius* in the head morphology (see above). Larvae of *Berosus* are distinguishable from those by the above mentioned characters, presence of tracheal gills and absence of spiracular atrium. Additional characters also separate *Berosus* from *Hydrochara*: (1) mandibles strongly asymmetrical; (2) labium more or less reduced; (3) clypeolabrum strongly asymmetrical, left lobe strongly projecting anteriorly, right lobe absent; (4) legs without swimming hairs; (5) prostyli absent. See also a key to the genera of Japanese aquatic Hydrophilidae in Minoshima & Hayashi (2011a).

Berosus (*Berosus*) *japonicus* Sharp, 1873

(Figs 1–7, 17A–B, 18A)

Material examined. JAPAN: Honshû: Shimane Prefecture: 6 L1 (HGF, KMNH), Okinoshima, Sono-chô, Izumo--shi, paddy field, 29.ii.2008 (rearing adults collected in the field), 17.iii.2008 (date of fixation), M. Hayashi leg. & reared; 5 L1(KMNH) , Okinoshima, Sono-chô, Izumo-shi, paddy field, 20.v.2008 (egg-cases collected in the field), 26.v.2008 (date of fixation), M. Hayashi leg.; 20 L3 (HGF, KMNH), Okinoshima, Sono-chô, Izumo-shi, paddy field, 22.vi.2008, M. Hayashi leg.; 6 L1, 5 L2 (HGF, KMNH), Okinoshima, Sono-chô, Izumo-shi, paddy field, 22.v.2009 (egg-cases collected in the field), 31.v.2009 (date of fixation), M. Hayashi leg.

Description. General morphology. Third instar (Figs 1, 5–7). *Body* moderately thick, widest between second and third abdominal segments. *Colour* light brown to light greyish brown, with sclerotised parts darker.

Head (Fig. 5A). Head capsule subquadrate; cervical sclerites small. Frontal lines visible only basally; coronal line absent. Surface of head capsule smooth. Six stemmata on each anterolateral corner of head capsule. Clypeolabrum (Fig. 5B) strongly asymmetrical. Nasale with median projection bearing ca. five small teeth. Lateral lobes of epistome present on left side but absent on right side; left lobe very strongly projecting anteriorly, lateral margin of left lobe partially membranous; anterior margin of right epistome almost straight or very weakly rounded.

Antenna (Figs 6A–B) 3-segmented, short, rather slender. Antennomere 1 longer than antennomeres 2 and 3 combined, with one subapical membranous projection on inner face. Antennomere 2 narrower than antennomere 1. Antennomere 3 the narrowest and shortest. Sensorium slightly shorter than antennomere 3.

Mandibles (Figs 7A–B) strongly asymmetrical; left mandible shorter than right one. Right mandible with three inner teeth on median part; distal one large, with serrated edge; proximal two small, subequal in size. Left mandible with three inner teeth and one strong inner spine posteriorly to inner teeth on dorsal surface; distal tooth large, with a group (usually five) of seta-like projections, apex of projections trifid; median tooth moderately sized, quadrifurcate, with small cuticular projections basally; basal tooth moderately sized, with at least four projections pointed apically, distal one larger than basal ones.

Maxilla (Figs 6C–D) 6-segmented, longer than antenna. Cardo moderate in size, subtriangular. Stipes the longest and widest, longer than palpomeres 1–4 combined; inner face without spine-like cuticular projections; a small cuticular projection subapically on inner face undetectable. Maxillary palpus 4-segmented, palpomere 1 widest, longer than palpomere 2 and 3, palpomere 3 the longest, palpomere 2 the shortest, palpomere 4 narrowest; palpomere 1 may be completely sclerotised but anterior margin of sclerotised part invisible; inner process sclerotised.

Labium (Figs 2B, 7C–D) small, partly reduced. Submentum (e.g., Fig. 2B) fused to head capsule, large, subpentagonal, wider than mentum. Mentum transverse, narrow, cylindrically sclerotised, wider than prementum; dorsal surface bare. Prementum subquadrate. Ligula strongly reduced, very short, completely membranous. Labial palpus long, straight, without cuticular projections; palpomere 1 as wide as palpomere 2 and slightly shorter than prementum, palpomere 2 distinctly longer than palpomere 1.

Thorax (Fig. 1). Thoracic membrane covered with fine cuticular pubescence. Prothorax wider than head capsule. Proscutum formed by one large plate subdivided by fine sagittal line, anterior part rather weakly sclerotised; whole sclerite bearing densely arranged fine cuticular projections. Prosternal sclerite subpentagonal, large, with long and fine sagittal line. Mesonotum with two sclerites on each side; anterior one small, narrow; posterior one large, subtriangular; one small tubercle behind each posterior mesonotal sclerite; lobe-like lateral projection on each side. Mesonotal spiracles situated anteriorly on dorsolateral face. Metanotal sclerites absent; one pair of membranous tubercles present on median part; lobe-like lateral projection on each side. Legs long, slender, visible in dorsal view, 5-segmented; all three pairs similar in shape.

Abdomen (Fig. 1). Ten segmented, tapering posteriad, covered with fine cuticular projections densely arranged; segments 1 to 6 similar in shape and size, segment 7 smaller than others. Lateral sides of segments 1–7 with one long to very long tracheal gill each; dorsal sclerites on segment 1–7 absent. Segments 1–3 with four small tubercles, two on median part, remaining ones laterally behind spiracles; lateral tubercles smaller than median ones. Segments 4–7 with two small tubercles medially. Segment 7 without tubercle.

Spiracular atrium (Fig. 5D) reduced. Segment 8 with oval dorsal plate; segment 9 trilobed, median lobe and each lateral lobe of spiracular atrium very small, hardy visible from dorsal view; procercus, acrocercus, urogomphi and prostyli reduced, undetectable. Ventral surface of spiracular atrium with two bulbous projections.

Second instar. Very similar to third instar larva, slightly more slender than third instar.

Head. Frontal lines clearly visible, nearly straight in median to anterior parts, strongly curved outwards at base.

Antenna proportionally stouter than in third instar; antennomere 1 proportionally shorter than in third instar, slightly longer than or as long as antennomeres 2 and 3 combined.

Maxilla proportionally stouter than third instar.

Mandible. Basal inner tooth on right smaller than median one.

Thorax and abdomen. Arrangements of cuticular projections and pubescence on thorax and abdomen similar to third instar but projections and pubescence finer than in third instar. Lateral tubercles on third abdominal segment indistinct.

First instar (Figs 2–4). Similar to second instar larva; weakly sclerotised than second instar. Spiracles on mesothorax and abdominal segments 1–7 undetectable.

Head. Anterior margin of right epistome almost straight (Fig. 3A). Basal part of frontal line more weakly curved laterally than in second instar (Fig. 2A).

Antenna (Figs 4A–B) proportionally stouter than in second and third instar larvae; antennomere 1 proportionally shorter than in third instar larva, about as long as or slightly shorter than antennomeres 2 and 3 combined.

Maxilla (Figs 4E–F) proportionally stouter than that of second and third instar larva.

Labial palpus (Figs 4G–H) proportionally stouter than third instar; palpomere 1 slightly wider than palpomere 2.

Thorax and abdomen. Arrangements of cuticular projections and pubescence on thorax and abdomen similar to third instar but projections and pubescence finer than in second instar. Prothorax as wide as or slightly wider than head capsule.

Chaetotaxy of head. Primary chaetotaxy (Figs 2–4). *Frontale* (Figs 2A, 3A). Rather long seta FR1 on midlength of frontale close to frontal line. Pore-like sensilla FR2 and FR4 and setae FR5–7 posteromesal to antennal socket, close to anterior end of frontal line; FR5 rather long, FR6 very long (homology of FR5 and FR6 unclear), FR7 short; FR2 and FR6–7 forming a triangular group laterally to FR6–7; FR6 close and lateral to FR5; FR7 anterior to remaining sensilla (FR2, FR4–6), close to inner margin of antennal socket. FR9–13 on epistome, situa-

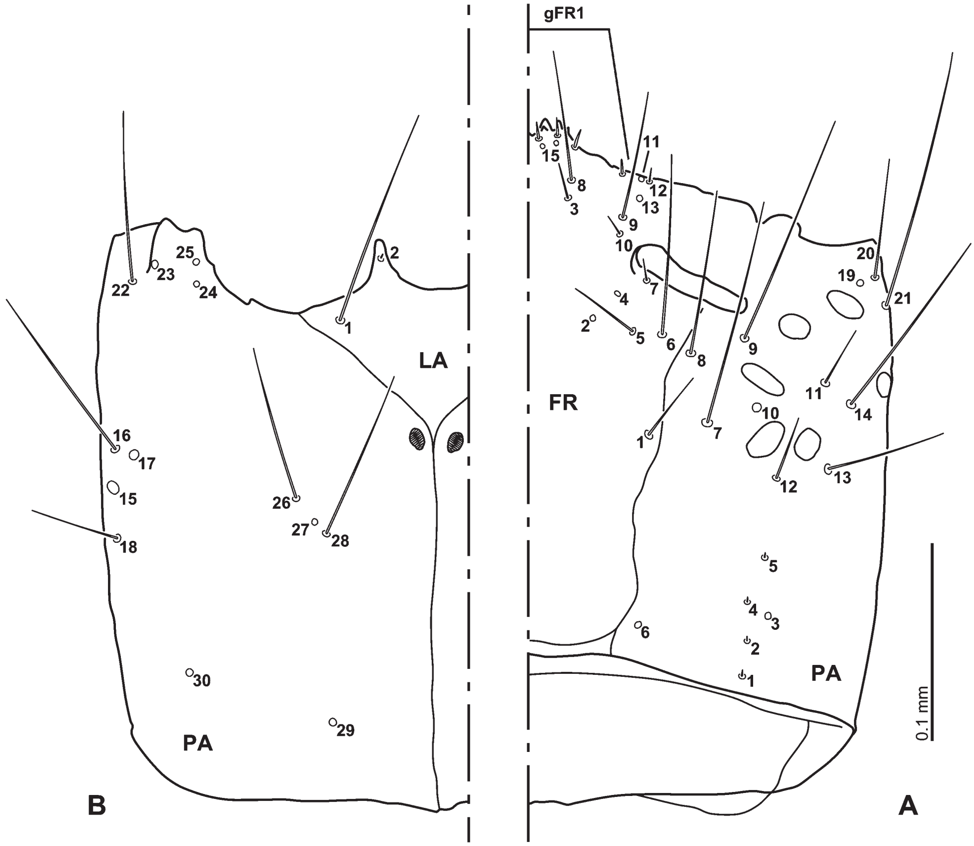

Fig. 2. First instar larva of *Berosus* (*Berosus*) *japonicus* Sharp, 1873, head capsule, dorsal (A) and ventral (B).

ted anteriorly and slightly mesally to antennal socket, forming irregularly longitudinal row; arrangement of FR9–13 slightly asymmetrical; FR10 and FR12 short setae, FR9 long seta, FR11 and FR13 pore-like sensilla; FR12 on right side stouter than left side. FR10 posterior to FR9 and FR11–13, FR9 anterior to FR10, between FR10 and FR13, FR13 between FR9 and FR12; FR11 on anterior margin of epistome, close to FR12; FR12 slightly posterior to FR11. Rather short seta FR3 and long seta FR8 behind nasale, FR3 close and posterior to FR8. Pore-like sensilla FR15 on median part of nasale. Nasale with a group of six equidistant, stout and short setae and with (at least) one pore-like sensillum (gFR1). Left epistomal lobe with a group of about 12 stout setae densely arranged on anterior margin (gFR2), mesal ones strongly bent towards ventrally; gFR2 absent on right side.

Parietale (Figs 2A–B). Dorsal surface with a group of five sensilla (PA1–5) forming irregularly 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 posterior end of frontal line, more distant from posterior margin of head than PA1. Pore-like sensilla PA10 between

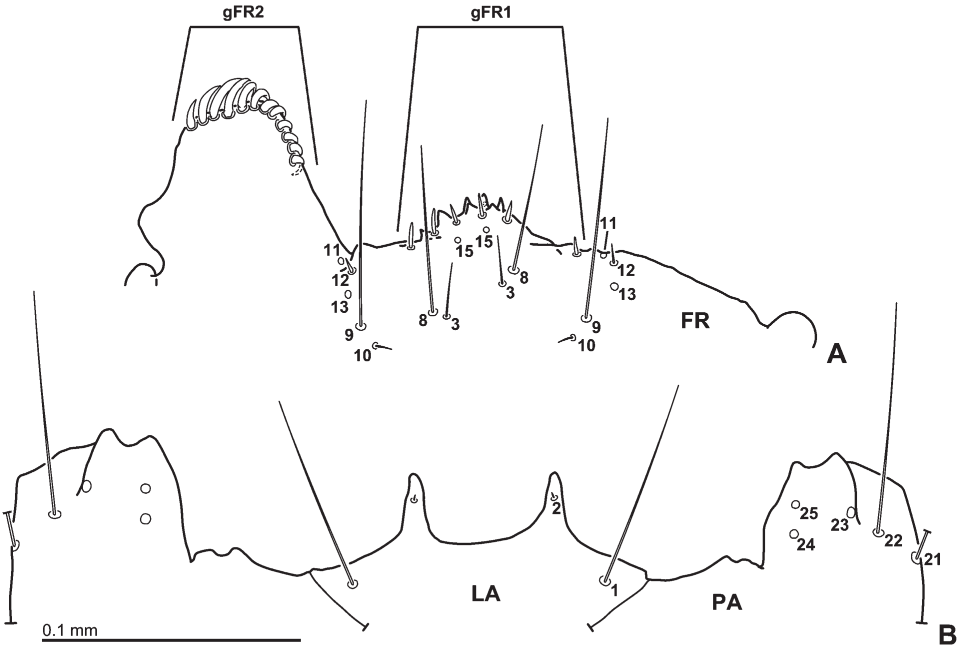

Fig. 3. First instar larva of *Berosus* (*Berosus*) *japonicus* Sharp, 1873, anterior margin of head capsule, dorsal (A) and ventral (B) (both drawn from dorsal).

mesal two stemmata. Setae PA7–9 posterior to antennal socket; PA8 long, PA7 and PA9 very long; PA9 close to lateral margin of antennal socket; PA8 posteromesal to PA9, close to frontal line and FR6; PA7 posterior to PA8 and PA9, mesal to PA10, between FR1 and PA10. Rather long seta PA12 and long seta PA13 close to mesal two stemmata of posterior row; PA12 behind mesal-most one, PA13 posterolateral to median one. Setae PA11 and PA14 in the line connecting lateral four stemmata, PA11 rather long, PA14 very long; PA11 anteromesal to PA14; PA14 between lateral two stemmata of posterior row, anterolateral to PA13. PA19–22 on anterior corner of head capsule, PA19 pore-like, PA20 long seta, PA21 very long seta, PA22 moderately long seta; PA19 dorsal to PA20–22, close to PA20. PA22 ventral to PA19–21, PA20–21 between PA19 and PA22; PA21 behind PA20; PA22 posterolateral to ventral mandibular articulation. Pore-like sensilla PA23–25 close to ventral mandibular articulation; PA23 lateral to PA24–25; PA24 posterior to PA25. PA15–18 situated lateroventrally in midlength of parietale; PA15 and PA17 pore-like, PA16 very long seta, PA18 long seta; PA16 and PA17 anterior to PA15 and PA18, PA17 close and mesal to PA16, PA15 between PA16 and PA18. Two long to very long setae (PA26 and PA28) and pore-like sensillum PA27 situated ventrally on median part of parietale; PA26 posterolateral to PA27 and PA28, PA27 between PA26 and PA28. Two pore-like sensilla (PA29–30) on posterior part of ventral parietale; PA29 mesal to PA30, posterior to PA26–28; PA30 on posterolateral part.

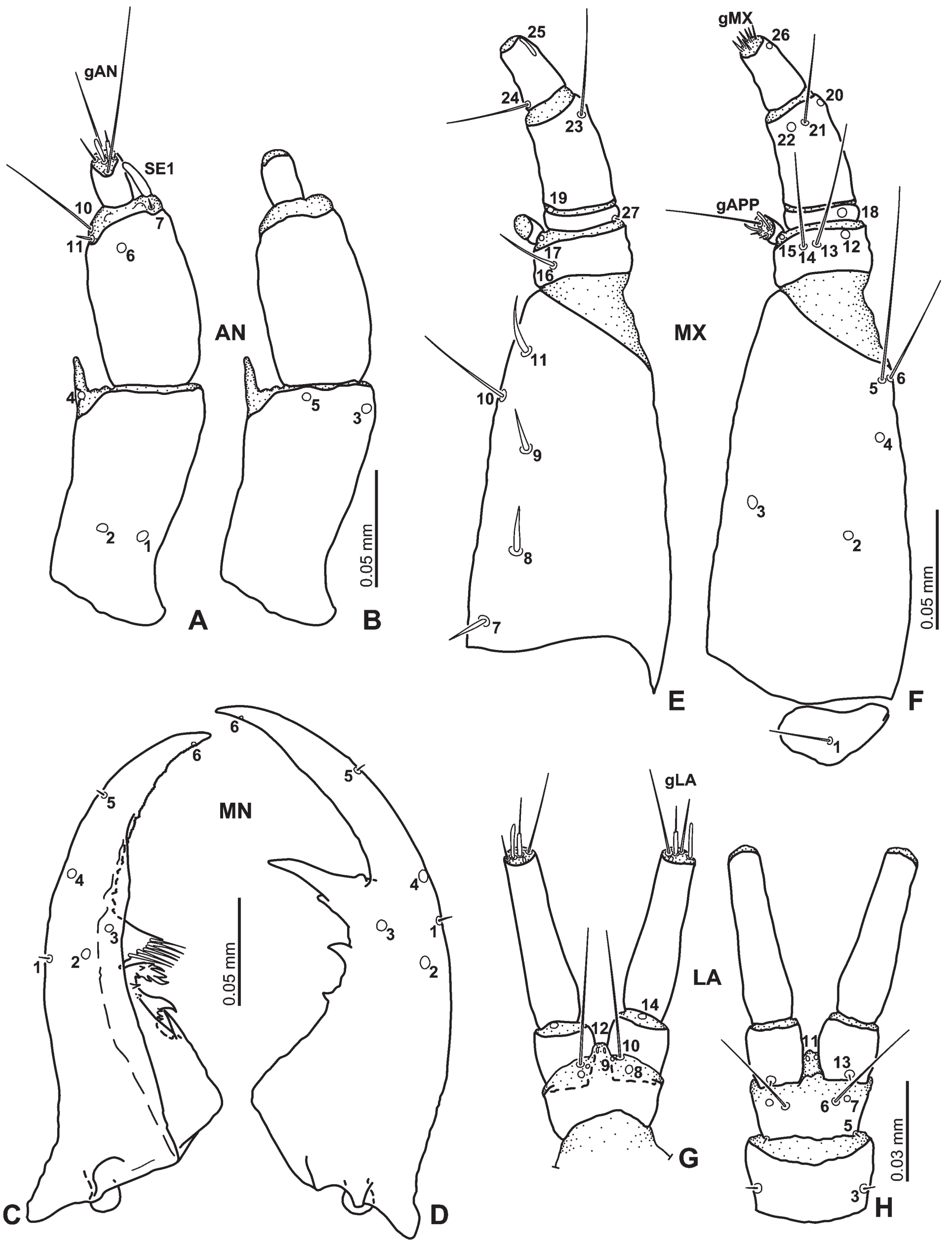

Fig. 4. First instar larva of *Berosus* (*Berosus*) *japonicus* Sharp, 1873, head appendages. A–B – antenna, dorsal (A) and ventral (B); C–D – left and right mandible, dorsal; E–F – maxilla, dorsal (E) and ventral (F); G–H – labium, dorsal (G) and ventral (H).

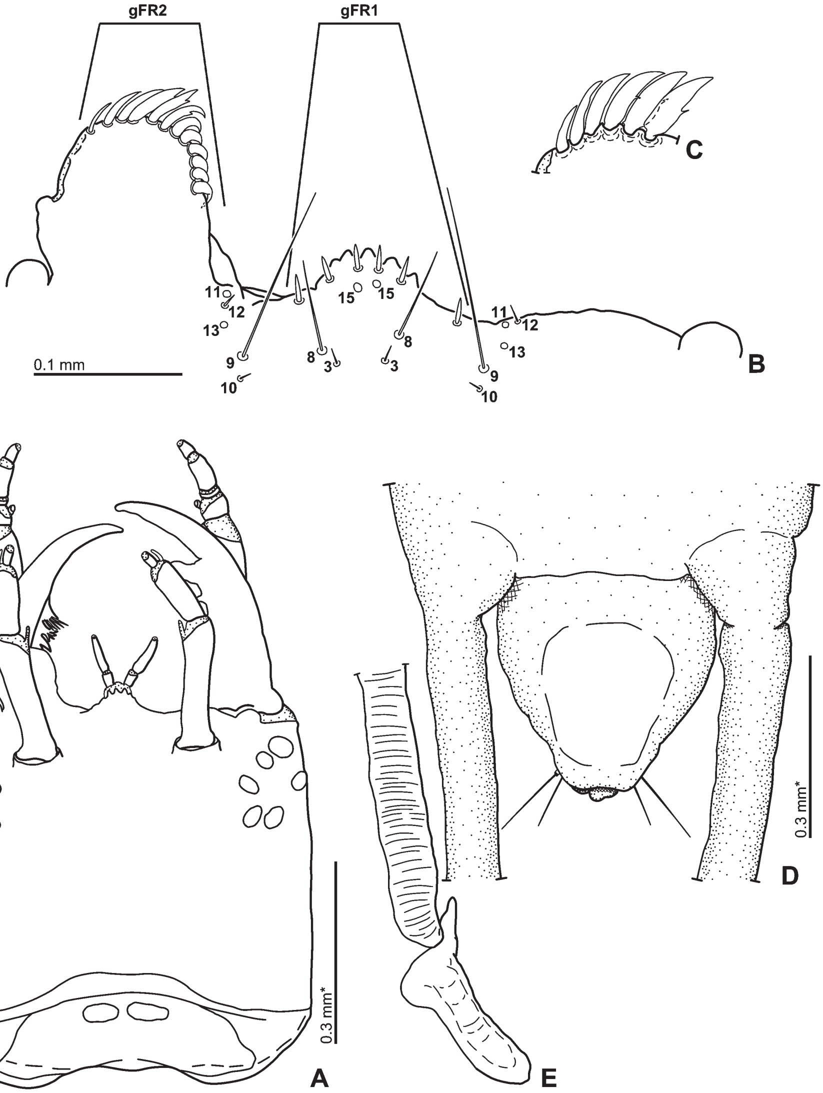

Fig. 5. Third instar larva of *Berosus* (*Berosus*) *japonicus* Sharp, 1873, dorsal; A – head capsule; B – anterior margin of head capsule; C – detail of setae of gFR2; D – spiracular atrium; E – spiracle in spiracular atrium.

Antenna (Figs 4A–B). Antennomere 1 with five pore-like sensilla (AN1–5); AN1–2 situated dorsally on posterior third, AN1 laterally to AN2, AN3 subapically on lateral face, AN4 on base of inner projection, AN5 ventrally on median portion of anterior margin of sclerite. Antennomere 2 with one pore-like sensillum (AN6) situated dorsally on subapical part of sclerite; minute seta AN7 and sensorium SE1 on lateral face of intersegmental membrane

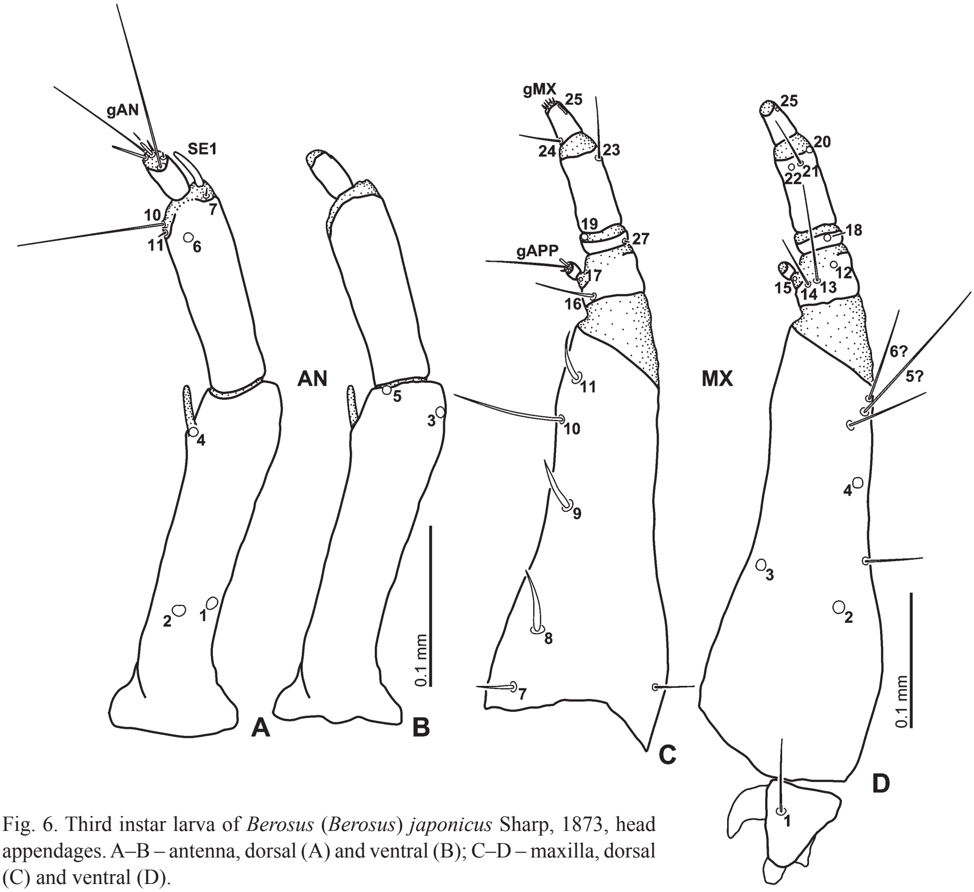

Fig. 6. Third instar larva of *Berosus* (*Berosus*) *japonicus* Sharp, 1873, head appendages. A–B – antenna, dorsal (A) and ventral (B); C–D – maxilla, dorsal (C) and ventral (D).

between antennomeres 2 and 3, AN8–9 absent; SE1 slender, about as long as antennomere 3; setae AN10–11 on inner face of intersegmental membrane between antennomeres 2 and 3, AN10 long, AN11 short, both setae close to each other. Antennomere 3 with apical sensilla (gAN) in apical membranous area; gAN with two rather long setae and a few (at least four) short setae of variable shape.

Mandibles (Figs 4C–D). Mandible with two setae (MN1 and MN5) and three pore-like sensilla (MN2–4). Pore-like sensillum MX6 situated on apical part of incisors area. Very short seta MN1 on midlength of lateral face of mandible. MN2–3 on median part of mandible; MN3 mesal to MN1–2, MN2 posterior to line connecting MN1 and MN3, MN2 on right mandible more distant than left. MN4 and minute seta MN5 on lateral face anteriorly to MN1; MN5 subapical; MN4 at midlength between MN1 and MN5 on left, closer to MN1 on right.

Maxilla (Figs 4E–F). Cardo with one moderately short ventral seta (MX1). Stipes with irregular row of five setae (MX7–11) situated dorsally along inner face; MX7–9 and MX11

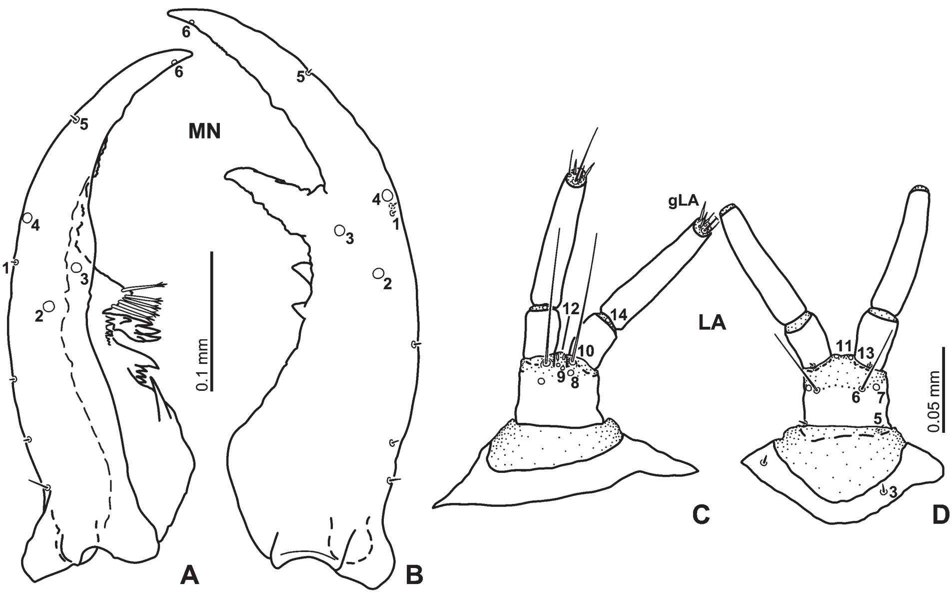

Fig. 7. Third instar larva of *Berosus* (*Berosus*) *japonicus* Sharp, 1873, head appendages. A–B – mandible, dorsal; C–D – labium, dorsal (C) and ventral (D).

stout, moderately short, MX10 trichoid, long; MX7–9 and MX11 almost equidistant from each other; MX10 between MX9 and MX11 but situated more ventrally. Two setae (MX5–6) situated apically on outer face of sclerite; MX5 very long, MX6 long; MX5 very close and dorsal to MX6. Pore-like sensilla MX2–3 situated ventrally on median part of sclerite; MX2 on outer part, MX3 on inner part; pore-like sensillum MX4 behind MX5–6, between MX2 and MX5. Dorsal surface of palpomere 1 with one rather long, slightly stout seta (MX16) on inner face; ventral surface of sclerite with three sensilla (MX12–14) close to distal margin of sclerite; MX12 pore-like on lateral part, MX13 long seta between MX12 and MX14, MX14 long seta on inner part, close to MX13. Rather small pore-like sensilla (MX15 and MX17) on membrane behind inner appendage; MX17 dorsal, MX15 ventral. Inner appendage with one long seta and a few short setae (gAPP). Palpomere 2 with two pore-like sensilla (MX18 and MX19) and one minute seta (MX27); MX18 situated ventrally on outer part of sclerite; MX19 on inner face of intersegmental membrane between palpomeres 2 and 3; MX27 at base of outer face of sclerite. Palpomere 3 with two setae (MX21 and MX23) and two pore-like sensilla (MX20 and MX22); MX21 rather long, MX23 long; MX20 on outer face very close to distal margin of sclerite; MX21–22 on median part of sclerite close to distal margin of sclerite; MX21 lateral to MX22; MX23 dorsal on outer face close to distal margin. Palpomere 4 with one rather long seta (MX24) situated basally on inner face, and with digitiform sensillum (MX25) and pore-like sensillum (MX26) apically on outer face of sclerite; MX25 dorsal, MX26 ventral. Apical membranous area of palpomere 4 with several minute setae (gMX).

Labium (Figs 2B, 3B, 4G–H). Submentum with two pairs of setae (LA1–2); LA1 very long, in each lateral corner, LA2 minute, on anterior margin. Ventral surface of mentum with one pair of short setae (LA3) situated on median part of outer face; LA4 absent. Prementum with three pairs of sensilla (LA8–10) on dorsal surface and with three pairs of sensilla (LA5–7) on ventral surface. LA8–10 on anterior membranous area of prementum, close to each other; arrangement of LA8–10 vary, LA8–9 sometimes absent; LA8–9 pore-like, LA10 long seta; LA9–10 at basal part of ligula, LA8 behind LA9–10. Minute seta LA5 at base of outer face; long seta LA6 and pore-like sensillum LA7 on anterior part, close to borderline between sclerite and membrane of prementum; LA6 close and mesally to LA7. Ligula with two pairs of pore-like sensilla (LA11–12) apically; LA12 dorsal, LA11 ventral. One minute seta (LA13) situated ventrally on basal margin of palpomere 1; pore-like sensillum LA14 on dorsal surface of intersegmental membrane between palpomeres 1 and 2. LA15 absent. Apical membranous area of palpomere 2 with several setae of variable length and shape (gLA).

Second instar. Primary sensilla similar to first instar, and secondary chaetotaxy similar to third instar.

Parietale with four rather short secondary setae. Two dorsal setae close to frontal line, one between PA6 and PA7, one between PA8 and PA9; one seta lateroventral, anterior to PA16; one seta on median part of lateral face, between PA13 and PA15–18.

Mandible (e.g., Figs 7A–B). Outer face of mandible bearing a few short to minute secondary setae.

Maxilla (e.g., Figs 6C–D). Stipes bearing three secondary setae; one moderately short seta situated dorsally on basal part of outer face, one moderately long seta on median portion of outer face, one long seta ventrally on subapical part of sclerite, close to and behind MX5.

Third instar (Figs 5B–C, 6–7). Similar to second instar.

Egg-case. Egg-cases were laid on substrate (Figs 17A–B; Hayashi 2009a).

Biology. *Berosus japonicus* inhabits paddy fields in the locality of Shimane prefecture; larvae prefer masses of algae, possibly *Spirogyra* or *Zygnema* (Zygnemataceae). Nearly one hundred larvae were occasionally found in such masses of algae, together with larvae of *Peltodytes intermedius* (Sharp, 1873) (Coleoptera: Haliplidae) (Hayashi, personal observation). This habitat preference might be the reason for confusion about the diet of larval *Berosus*, which was considered to consist of algae (Wilson 1923, Bøving & Henriksen 1938, Peterson 1951). As Bøving & Henriksen (1938) and Archangelsky (1997, 2008) questioned, *Berosus* larvae will be carnivorous.

Genus *Regimbartia* Zaitzev, 1908

(Figs 8–16, 17C–D)

Diagnosis. The larva of *Regimbartia* is very similar to those of genera *Allocotocerus* and *Derallus*. Larvae of these genera are distinguishable from other hydrophilid larvae by the following combination of characters: (1) almost symmetrical clypeolabrum (Figs 9C, 13C); (2) the presence of an inner projection on antennomere 1 (autapomorphy of Berosini; Figs 10A–B, 15A–B), (3) almost symmetrical to slightly asymmetrical mandibles (Figs 11A–B); (4) elongated prementum (Figs 11C–D, 15C–D); and (5) presence of short to long setiferous abdominal projections on the dorsal to lateral surface (e.g., Fig. 8D). *Regimbartia* is distinguishable from *Allocotocerus* and *Derallus* by antennal characters: apex of inner projection on antennomere 1 rounded; antennomere 2 widened distally, without inner extension apically.

Within the Japanese aquatic Hydrophilidae, the larva may superficially resemble those of *Amphiops* Erichson, 1843, *Hydrochara*, and *Sternolophus* Solier, 1834 in the head morphology: i.e., elongate antennae, mandibles, and maxilla (e.g., Minoshima & Hayashi 2011a, 2012; Minoshima et al. 2012; Watts 2002); however *Regimbartia* is easily distinguishable from them by the aforementioned characters. See also a key to the genera of Japanese aquatic Hydrophilidae in Minoshima & Hayashi (2011a).

Regimbartia attenuata (Fabricius, 1801)

(Figs 8–16, 17C–D)

Material examined. JAPAN: Honshû: Shimane Prefecture: 9 L1 (HGF, KMNH), Wadakami, Oku-uga-chô, ponding fallow field, 16.vi.2008 (date of fixation), M. Hayashi leg. & reared; 1 L1 (KMNH), Wadakami, Oku-uga-chô, ponding fallow field, 13.vi.2008 (date of fixation), M. Hayashi leg. & reared; 2 L3 (KMNH), Wadakami, Oku-uga-chô, ponding fallow field, 12.vii.2008, M. Hayashi leg.; 1 L1, 3 L2 (HGF, KMNH), Okinoshima, Sono-chô, Izumo-shi, paddy field, 19.vi.2008, M. Hayashi leg.; 1 L1 (KMNH), Wadakami, Oku-uga-chô, ponding fallow field, 25.vi.2008 (date of fixation), M. Hayashi leg. & reared; 2 L1 (KMNH), Nozato-chô, Izumo-shi, 3.vi.2008 (date of fixation), M. Hayashi leg. & reared. **Nansei Islands: Okinawa Prefecture:** 2 L3 (EUMJ), Sonai, Yonaguni-jima I., 1.viii.1962, M. Satô leg.

Description. General morphology. Third instar (Figs 8, 12–15, 16B). Larva metapneustic. Body (Figs 8A–B) rather slender with strong setiferous projections, nearly parallel-sided; thorax and abdomen bear short to long, membranous projections. Colour greyish white with sclerotised parts brownish, head capsule yellowish brown. One pair of spiracles on mesothorax; eight pairs of spiracles on abdominal segments; spiracles on mesothorax and abdominal segments 1–3 strongly protuberant; those on abdominal segments 4–7 hardly detectable, seem to be reduced; posterior one pair enclosed in spiracular atrium, very large, annular; anterior eight pairs non-functional, posterior pair functional.

Head (Figs 12A, 13). Head capsule subquadrate, attenuated posteriad; cervical sclerites large, subrectangular. Frontal line straight and slightly lyriform, but almost invisible in third instar; posterior end of frontal lines U-shaped; coronal line absent. Surface of head capsule smooth. Six stemmata on each anterolateral corner of head capsule. Clypeolabrum nearly symmetrical (Fig. 13C). Nasale weakly convex with strongly serrate anterior margin (bearing many small cuticular teeth on ventral surface of anterior margin). Epistomal lobe very weakly rounded; both lobes with a few to several small cuticular teeth.

Antenna (Figs 14A–B) 3-segmented, long, slender. Antennomere 1 longer than antennomeres 2 and 3 combined, with one projection on subapical part of inner face; apical part of projection membranous. Antennomere 2 attenuated basally, narrower than antennomere 1 at base, about as wide as antennomere 1 at apex; apical part of inner face of antennomere 2 weakly projecting anteriorly. Antennomere 3 the narrowest and shortest.

Mandibles (Figs 15A–B) rather slender, slightly asymmetrical. Right mandible with two inner teeth, apical one large, projecting apically, and basal one small; basal inner tooth of left mandible with one, closely aggregated associated tooth.

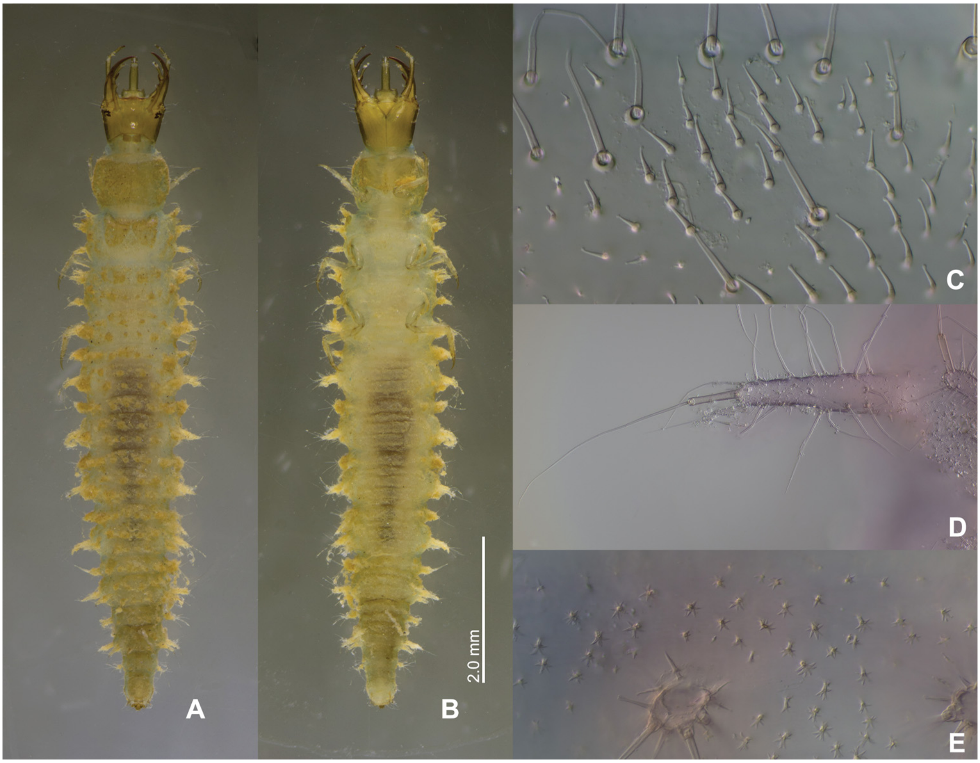

Fig. 8. Third instar larva of *Regimbartia attenuata* (Fabricius, 1801). A–B – habitus, dorsal (A) and ventral (B); C – cuticular projection on pronotum, dorsal; D – lateral setiferous projection, dorsal; E – cuticular projections on abdominal segment, dorsal.

Maxilla (Figs 14C–D) 6-segmented, slightly longer than antenna. Cardo small, subtriangular. Stipes the longest and widest, about twice as long as palpomeres 1–4 combined; inner face with few cuticular spines basally; a small cuticular projection present subapically on inner face. Maxillary palpus 4-segmented, palpomere 1 widest, dorsal surface completely sclerotised; palpomere 2 shortest and wider than palpomere 3; palpomere 3 the longest; palpomere 4 narrowest; inner process small, sclerotised.

Labium (Figs 13B, 15C–D) well developed. Submentum (Fig. 13B) fused to head capsule, large, subpentagonal or subtriangular, wider than mentum. Mentum transverse subrectangular, lateral face weakly convex, widest medially, each anterior corner weakly but distinctly projecting anteriorly; dorsal surface covered with small cuticular spines posterolaterally. Prementum very narrow and long, about two-fifths as width of mentum, and about 2.7 times as wide as long; basal part close to LA8 sensilla partially membranous. Ligula stout, shorter than or as long as labial palpus, weakly curved dorsally; dorsal part of ligula mostly membranous excluding basal margin, ventral surface of ligula sclerotised but lateral part membranous. Labial palpus short, palpomere 1 shorter and slightly wider than palpomere 2.

Thorax. Thoracic membrane covered with fine cuticular pubescence, each apex multi-furcate (e.g., Fig. 8E) excluding anterior margin which bears fine cuticular pubescence of simple shape; thoracic sclerites bearing densely arranged fine cuticular projections; apex of projections expanded circularly (Fig. 8C). Prothorax wider than head capsule. Proscutum formed by one large plate subdivided by fine sagittal line, anterior part rather weakly sclerotised. Prosternal sclerite (Fig. 12B) subpentagonal, with long and fine indistinct sagittal line; anterior margin of sclerite with densely arranged short setae. Mesonotum with two sclerites on each side; anterior two narrow, weakly sclerotised and indistinct; posterior sclerites large, subtriangular, both posterior sclerites jointing at anterior margin. Five pairs of setiferous, membranous projections present on dorsal and lateral surfaces; one small on posterior mesonotal sclerite; one small laterodorsal at midlength; three long (e.g., Fig. 8D) on lateral face. Metanotum with apparently two metanotal sclerites; sclerites very weakly sclerotised and indistinct, subrectangular. One short membranous projection bearing apical seta present posteromesally to lateral sclerite. Eight pairs of setiferous, membranous projections present on dorsal and lateral surfaces; one small very close and posteromesally to metanotal sclerite; three long on lateral surface; remaining ones forming a transverse row behind metanotal sclerite; from mesal to lateral, bearing small, short setiferous projections. Legs (Fig. 16B) long, visible in dorsal view, 5-segmented; all three pairs similar in shape.

Abdomen. Abdomen 10 segmented, tapering posteriad (Figs 8A–B); segments 1 to 7 similar in shape and size. Abdominal membrane covered with fine cuticular pubescence, each apex multi-furcate (Fig. 8E) excluding anterior margin of dorsal surface, ventral surface, and membrane on segment 8, which bears fine cuticular pubescence of simple shape. Segment 1 without dorsal sclerite. Twelve setiferous, membranous projections (e.g., Fig. 8D) present on each side of dorsal and lateral surfaces; four small on anterior part of segment; two small and four long behind anterior four, mesal pair small, lateral two pairs long; these projections situated between spiracles; two pairs of long projections on lateral surface, ventrally to spiracles, one laterally, one lateroventrally; five pairs forming a transverse row on posterior part; dorsal four pairs small, lateral pair long. Two small setiferous, membranous projections present laterally on ventral surface, one on anterior part, one on posterior part. Segments 2 to 7 similar to segment 1, but dorsal and lateral projections on segment 6 and 7 differ from segment 1. Segment 6 with 11 pairs of setiferous, membranous projections on dorsal and lateral surfaces; four pairs forming a transverse row on posterior part, behind remaining projection on segment 6; dorsal three pairs small, lateral pair long. Segment 7 with nine pairs of setiferous, membranous projections on dorsal and lateral surfaces; four pairs of projections forming a transverse row present at midlength, behind anterior four projections, median two rather short, lateral three long; three pairs of projections forming transverse row in posterior part, lateral pair long, remaining pairs on dorsal surface, small.

Spiracular atrium (Fig. 12C). Segment 8 with large oval dorsal plate covered with fine cuticular projections and setae of variable length; dorsal surface of segment 8 tetralobate, median two lobes very large, covered with short pubescence, lateral ones small, indistinct. Segment 9 trilobed, partially sclerotised; urogomphus large, bearing one very long seta and a few short setae; procercus rather long, partially sclerotised, with one long and two short setae apically; median lobe of spiracular atrium partially sclerotised, with four long setae on posterior margin; lateral lobe of spiracular atrium partially sclerotised composed by inner sclerite and outer sclerite, bearing several setae of variable length; acrocercus and prostylus undetectable, absent.

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

Head. *Head capsule*. Frontal lines clearly visible. Epistomal lobe very weakly projecting anteriorly, similar to that of first instar (Fig. 9C). Ventral cuticular teeth on nasale much sparsely arranged than in third instar, rather similar to those in first instar.

Antenna (e.g., Figs 14A–B) proportionally stouter than in third instar.

Labium (e.g., Figs 15C–D). Mentum subtrapezoidal, widest basally; lateral face of mentum slightly convex; anterior corners of mentum slightly projecting anteriorly.

Thorax and abdomen. Arrangement of cuticular projections and pubescence on thorax and abdomen similar to but finer than in third instar. Apex of cuticular pubescence and projections similar to but more simple than in third instar; setiferous, membranous projections on thoracic and abdominal segments proportionally smaller than in third instar, but more similar to third instar than to first instar.

First instar (Figs 9–11, 16A). Similar to second instar larva; sclerites on meso- and metathorax more weakly sclerotised than in second instar.

Head. Head capsule (Fig. 9). Epistomal lobe hardly detectable or absent (Fig. 9C). Nasale very weakly convex anteriorly, nearly straight; ventral cuticular teeth on nasale sparsely arranged.

Antenna (Figs 10A–B) proportionally stouter than in second and third instars.

Maxilla (Figs 10C–D) proportionally stouter than in third instar.

Labium (Figs 11C–D). Anterior margin of mentum rounded in dorsal view, without anterior corners and projection; prementum about 3.1 times as long as wide but about half the width of mentum.

Thorax and abdomen. Arrangements of cuticular projection and pubescence on thorax and abdomen similar to third instar but projection and pubescence finer than in second instar. Apex of cuticular pubescence or projections simple; setiferous, membranous projections on thoracic and abdominal segments proportionally smaller than in second instar, the number of the projections less than in third instar. Prothorax as wide as or slightly wider than head capsule.

Chaetotaxy of head. ***Primary chaetotaxy*** (Figs 9–11). *Frontale* (Figs 9A, C). Very short seta FR1 on about midlength of frontale rather close to frontal line. Pore-like sensillum FR2 anteromesal to FR1, posteromesal to inner margin of antennal socket. Short seta FR5 and rather long seta FR6 posteromesal to antennal socket, lateral to FR2; FR5 mesal to FR6. Pore-like sensillum FR4 mesal to antennal socket, anterior to FR5–6. Three sensilla (FR3, FR8, FR15) situated mesally behind nasale, FR3 rather short, stout seta, FR8 long seta, FR15 pore-like; FR3 mesal to FR8, FR8 posterior to FR15. Short seta FR10 between FR7 and FR8. Four sensilla (FR7, FR9, FR12–13) forming longitudinal row between inner margin of antennal socket to lateral portion of nasale; FR7 very short seta, FR9 very long seta, FR12 rather short and stout seta, FR13 pore-like sensillum; FR7 mesal and close to inner margin of antennal socket, FR9 between FR7 and FR13, FR13 between FR9 and FR12, FR12 anterior to remaining sensilla

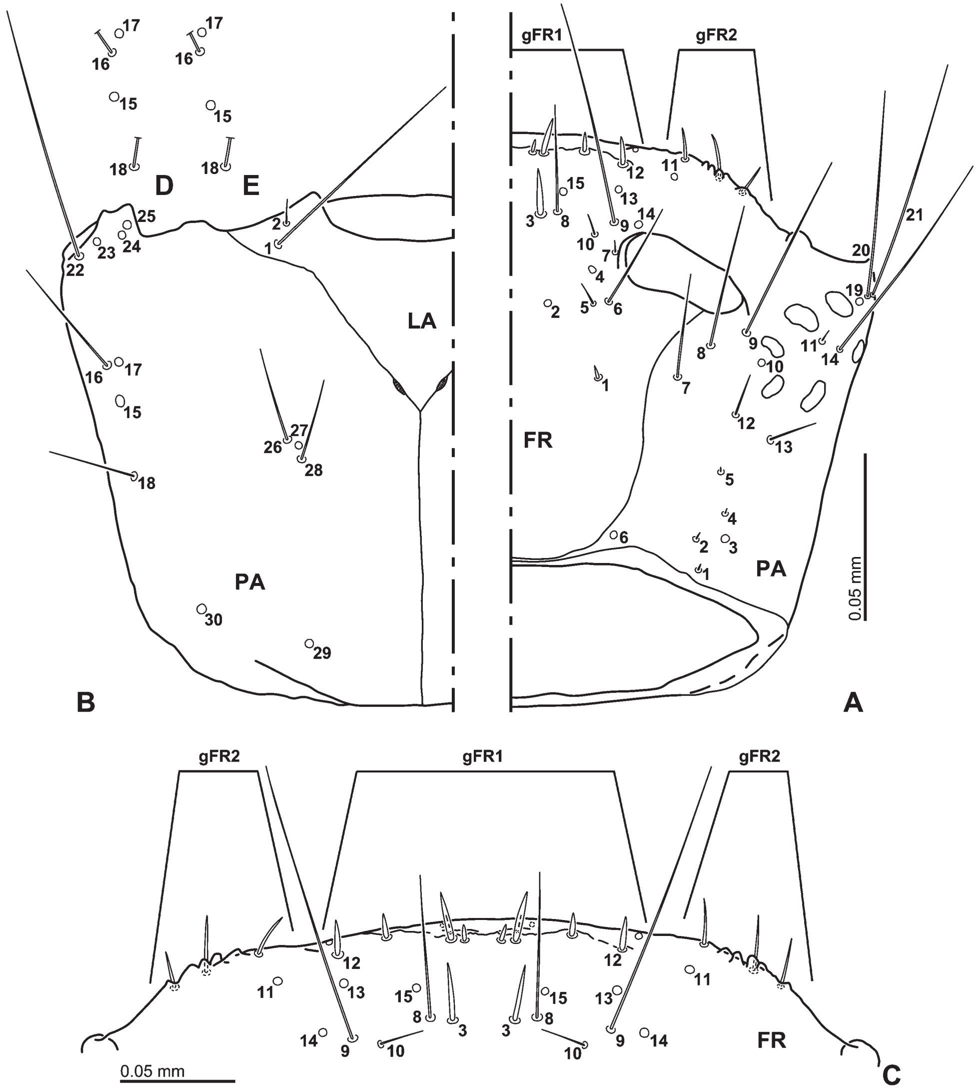

Fig. 9. First instar larva of *Regimbartia attenuata* (Fabricius, 1801), head capsule. A–B – head capsule, dorsal (A) and ventral (B); C – anterior margin of head capsule, dorsal; D–E – variation of sensilla PA15–18, ventral.

(FR7, FR9, FR13). Pore-like sensillum FR11 on anteromesal portion of epistome, posterior to mesal-most seta of gFR2. Pore-like sensillum FR14 lateral and close to FR9. Nasale with group of six short setae, and with (at least) two short ventral seta and four small pore-like sensilla (gFR1) (Fig. 9C); median two dorsal setae very short, shorter than other ones, next ones rather short, longer than other ones, lateral ones short; median two pairs of dorsal setae

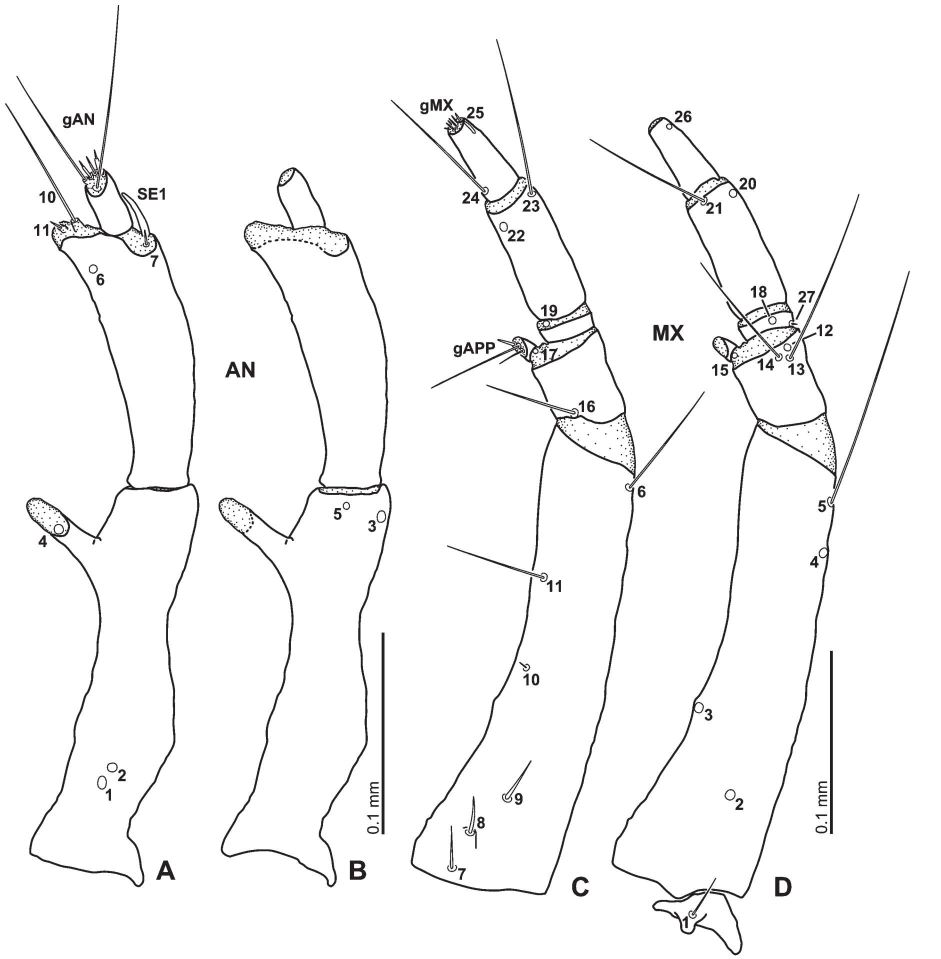

Fig. 10. First instar larva of *Regimbartia attenuata* (Fabricius, 1801), head appendages. A–B – antenna, dorsal (A) and ventral (B); C–D – maxilla, dorsal (C) and ventral (D).

closely aggregated. Pore-like sensillum on lateral part of nasale, close to FR12; a pair of ventral setae and ventral pore-like sensilla situated mesally close to median four setae of gFR1. Each epistomal lobe with three rather short, stout but somewhat slender setae (gFR2).

Parietale (Figs 9A–B, D–E). Dorsal surface with a group of five sensilla (PA1–5) forming irregularly 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 posterior end of frontal line, close to posterior margin of head capsule. Very long seta PA9 behind lateral margin of antennal socket; long setae PA7–8 close to frontal line, posterior to lateral part of antennal socket; PA8 posterolateral to PA7, between PA9. Pore-like sensillum PA10 between mesal

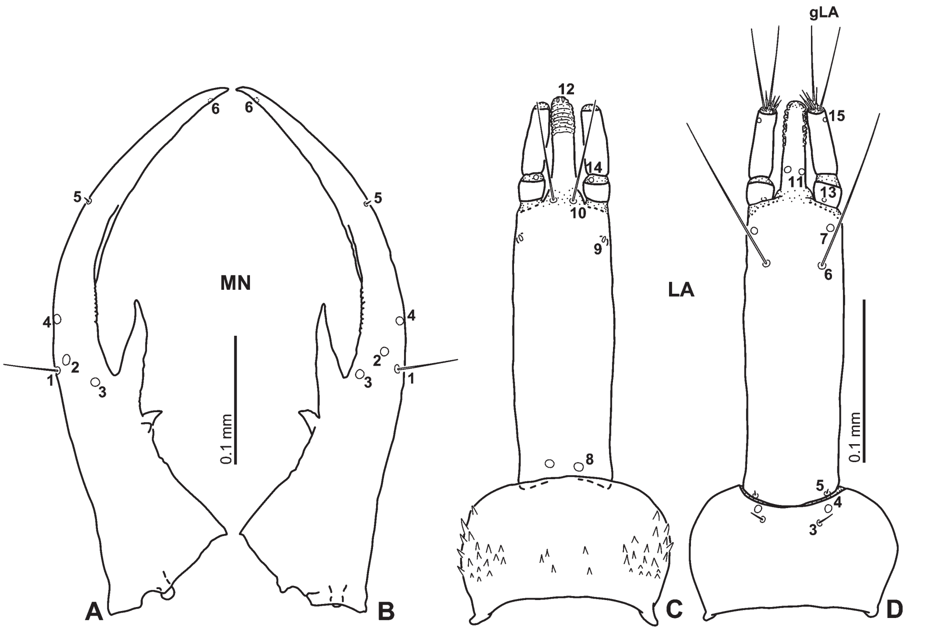

Fig. 11. First instar larva of *Regimbartia attenuata* (Fabricius, 1801), head appendages. A–B – mandible, dorsal; C–D – labium, dorsal (C) and ventral (D).

stemmata of anterior and posterior rows. Two rather short setae (PA12–13) posterior to PA9–10, PA12 between PA5 and PA9, PA13 posterolateral to PA12. Short seta PA11 and very long seta PA14 located inside of line connecting stemmata; PA14 lateral to PA11. PA19–22 in anterior corner of head capsule; PA19 pore-like sensillum, PA20–22 very long setae; PA19–21 very closely aggregated on laterodorsal face, PA19 dorsal to PA20–21; PA20 between PA19 and PA21; PA21 ventral to PA19–20; PA22 lateroventral. Pore-like sensilla PA23–25 situated behind ventral mandibular articulation, PA23 lateral to PA24–25, close to PA22; PA24–25 very close to each, PA25 anterior to PA24. Four sensilla (PA15–18) on lateroventral surface (Figs 9B, D–E), PA15–17 on anterior third, PA18 slightly posterior to midlength; PA16 and PA18 long setae, PA15 and PA17 pore-like sensilla; PA16 and PA17 anterior to PA15, closely aggregated, PA17 mesal to PA16; PA15 between PA16 and PA18. Two long setae (PA26 and PA28) and pore-like sensillum PA27 aggregated on median part of ventral surface of parietale, slightly more mesal to midwidth; PA26 anterior to PA27–28, PA27 between PA26 and PA28, PA28 posterior to PA26–27. Two pore-like sensilla (PA29–30) in posterior portion of ventral surface of parietale; PA30 close to posterior corner, PA29 mesal to PA30, on about midlength between PA30 and gular sulcus.

Antenna (Figs 10A–B). Antennomere 1 with five pore-like sensilla (AN1–5); AN1–2 situated dorsally on posterior fourth to fifth, AN1 posteriorly to AN2, AN3 subapically on lateroventral face, AN4 on inner projection, AN5 ventrally on median portion of anterior margin of sclerite. Antennomere 2 with one pore-like sensillum (AN6) situated dorsally on subapical part of sclerite; very short seta AN7 and sensorium SE1 on lateral face of inter-

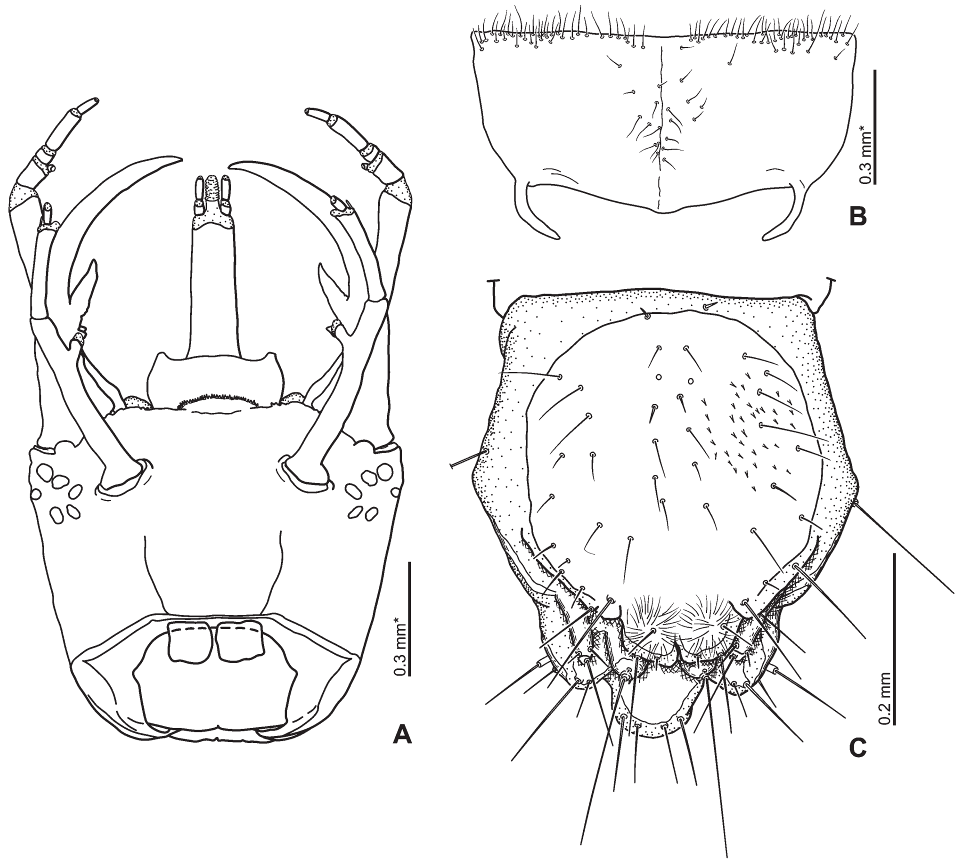

Fig. 12. Third instar larva of *Regimbartia attenuata* (Fabricius, 1801). A – head, dorsal; B – prosternal sclerite, ventral; C – spiracular atrium, dorsal.

segmental membrane between antennomeres 2 and 3, AN8–9 absent. SE1 slender, about as long as antennomere 3. Setae AN10–11 aggregated on inner face of intersegmental membrane between antennomeres 2 and 3, AN10 very long, AN11 short. Antennomere 3 with apical sensilla (gAN) in apical membranous area; gAN with two very long setae and a few short setae of variable shape.

Mandibles (Figs 11A–B). Mandible with two setae (MN1 and MN5) and four pore-like sensilla (MN2–4 and MX6). MN1 and MN4 on median part of outer face; MN1 rather short, posterior to MN4. MN2–3 on median part of mandible; MN3 posteromesal to MN1–4, MN2 between MN3 and MN4; minute seta MN5 on apical third of outer face; MN6 very small and indistinct, subapical on inner face.

Maxilla (Figs 10C–D). Cardo with one moderately short ventral seta (MX1). Stipes with five setae (MX7–11) situated dorsally along inner face; MX7–9 moderately short and stout, MX10 very short, MX11 long and trichoid; MX7–9 in basal fourth, MX10 at midlength of

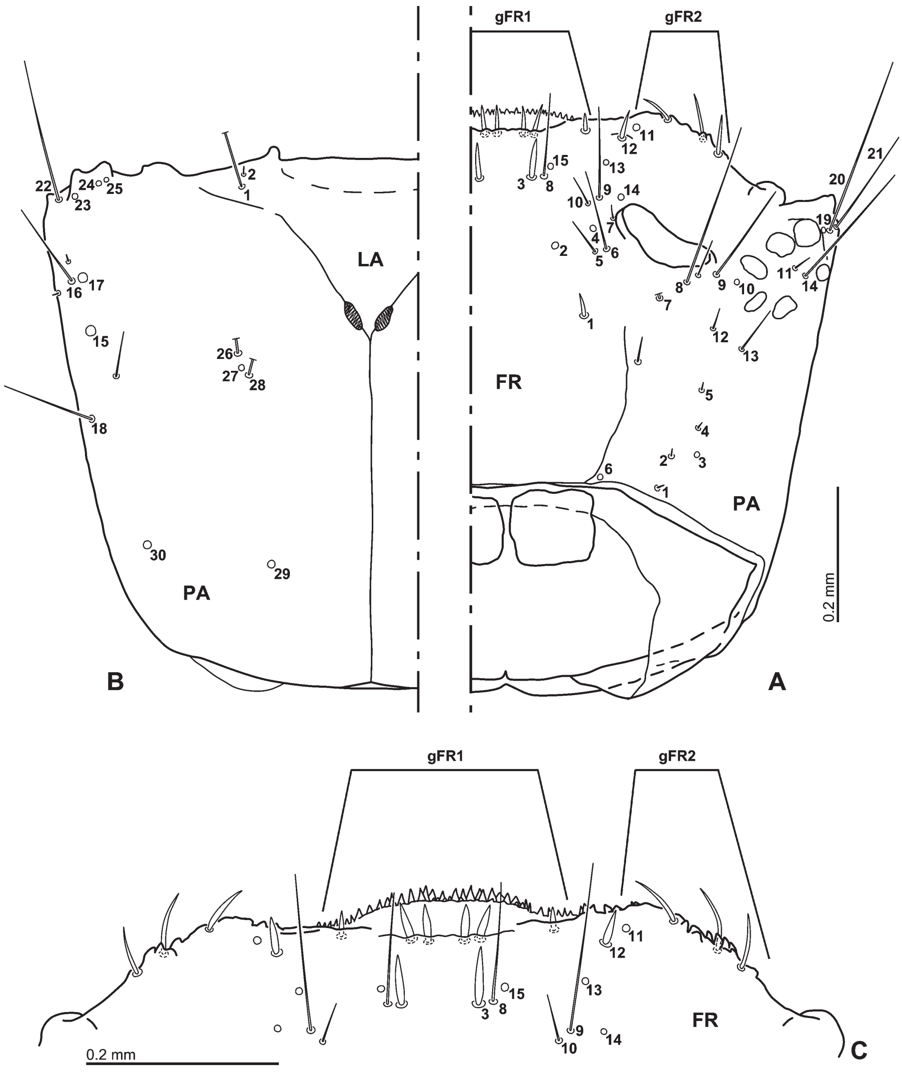

Fig. 13. Third instar larva of *Regimbartia attenuata* (Fabricius, 1801), head capsule. A–B – head capsule, dorsal (A) and ventral (B); C – anterior margin of head capsule, dorsal.

sclerite, MX11 on apical fourth. Two setae (MX5–6) on subapical portion of outer face of sclerite; MX5 very long, MX6 long; MX6 anterior and dorsal to MX5. Pore-like sensillum MX4 posterior to MX5–6. Pore-like sensilla (MX2–3) on ventral surface, MX2 on posterior fourth, MX3 on posterior two-fifths. Dorsal surface of palpomere 1 with one long, slightly stout, trichoid seta (MX16) situated basally on inner face; ventral surface of sclerite with

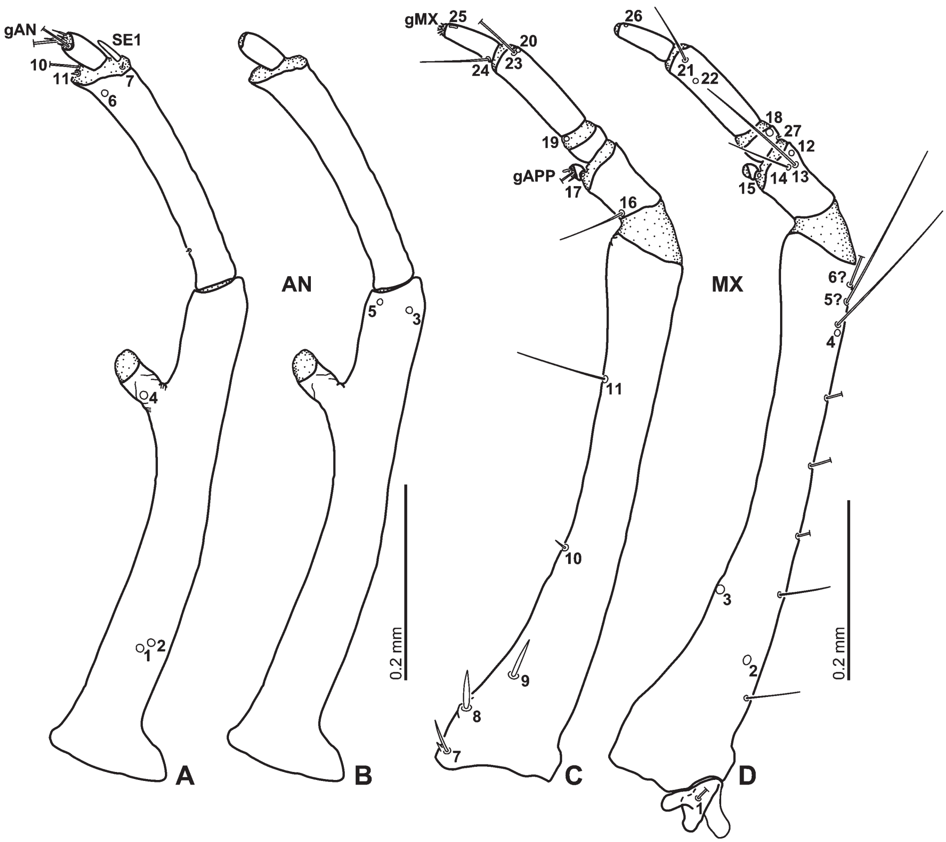

Fig. 14. Third instar larva of *Regimbartia attenuata* (Fabricius, 1801), head appendages. A–B – antenna, dorsal (A) and ventral (B); C–D – maxilla, dorsal (C) and ventral (D).

three sensilla (MX12–14) close to distal margin of sclerite; MX12 pore-like on lateral part, MX13 very long seta posterior to MX12, MX14 long seta mesal to MX12–13. Pore-like sensilla (MX15 and MX17) on membrane behind inner appendage; MX17 dorsal, MX15 ventral. Inner appendage with one long seta and a few short setae (gAPP). Palpomere 2 with two pore-like sensilla (MX18 and MX19) and one minute seta (MX27); MX18 situated ventrally on median part of sclerite; MX19 on inner face of intersegmental membrane between palpomeres 2 and 3; MX27 at base of outer face of sclerite. Palpomere 3 with two very long setae (MX21 and MX23) and two pore-like sensilla (MX20 and MX22); MX20 and MX23 on outer face close to distal margin of sclerite, MX20 ventral to MX23; MX21 on lateral to median part of ventral surface, closer to distal margin of sclerite or on borderline between sclerite and intersegmental membrane; MX22 situated dorsally on lateral part close to distal margin of sclerite. Palpomere 4 with one long seta (MX24) situated basally on inner face, and with digitiform (MX25) and pore-like (MX26) sensilla apically on outer face of sclerite;

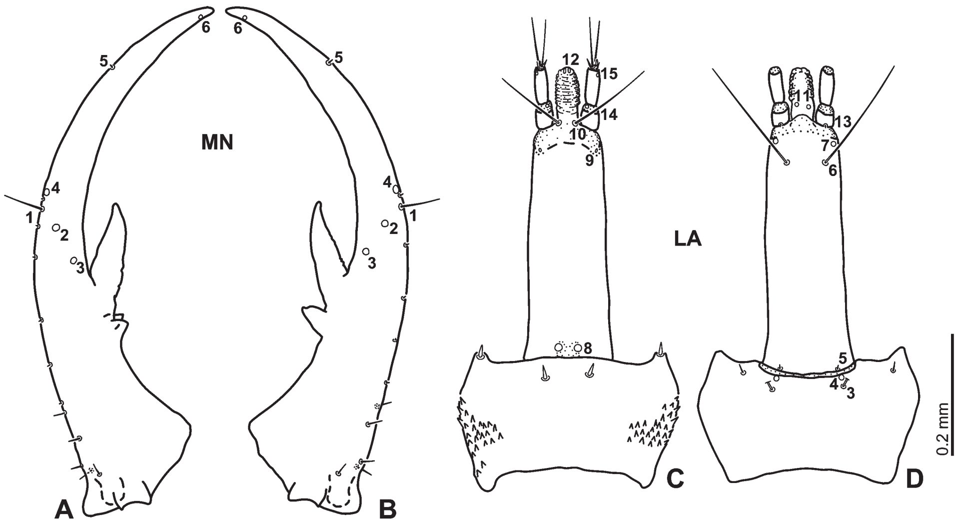

Fig. 15. Third instar larva of *Regimbartia attenuata* (Fabricius, 1801), head appendages. A–B – mandible, dorsal; C–D – labium, dorsal (C) and ventral (D).

MX25 dorsal, MX26 ventral. Apical membranous area of palpomere 4 with several minute setae (gMX).

Labium (Figs 11C–D). Submentum with two pairs of setae (LA1–2) on each lateral portion; LA1 very long, LA2 short; LA2 anterior to LA1. Ventral surface of mentum with one pair of rather long setae (LA3) and pore-like sensillum (LA4) on anterior margin of sclerite; LA4 posterolateral and close to LA3. Prementum with three pairs of sensilla (LA8–10) situated dorsally and three pairs of sensilla ventrally (LA5–7). LA8 pore-like, situated basally; LA9 pore-like but weakly projecting sensillum, situated subapically on dorsolateral face; LA10 long seta, at base of ligula. LA5 minute seta, situated basally on lateral part, closer to basal margin of sclerite; very long seta LA6 and pore-like sensillum LA7 subapical on lateral part, LA6 posterior to LA7. Ligula with two pairs of pore-like sensilla (LA11–12); LA12 apical, LA11 ventral and basal. LA13 minute seta situated ventrally on basal margin of sclerite of palpomere 1; pore-like sensillum LA14 situated dorsally on intersegmental membrane between palpomeres 1 and 2, LA15 subapically on outer face of palpomere 2. Apical membranous area of palpomere 2 with several setae of variable length and shape (gLA).

Second instar. Primary sensilla similar to first instar.

Parietale (e.g., Figs 13A–B) with five secondary setae, two dorsal, three lateral. One short between PA6 and PA7, close to frontal line; one short between PA8 and PA9; one short lateral to PA16; one short close to PA16; one rather short mesal to PA15 and PA18.

Antenna (e.g., Figs 14A–B). SE1 shorter than antennomere 3.

Mandibles (e.g., Figs 15A–B). Basal half of outer face of mandibles with about 10 secondary sensilla; basal five sensilla short, remaining ones minute.

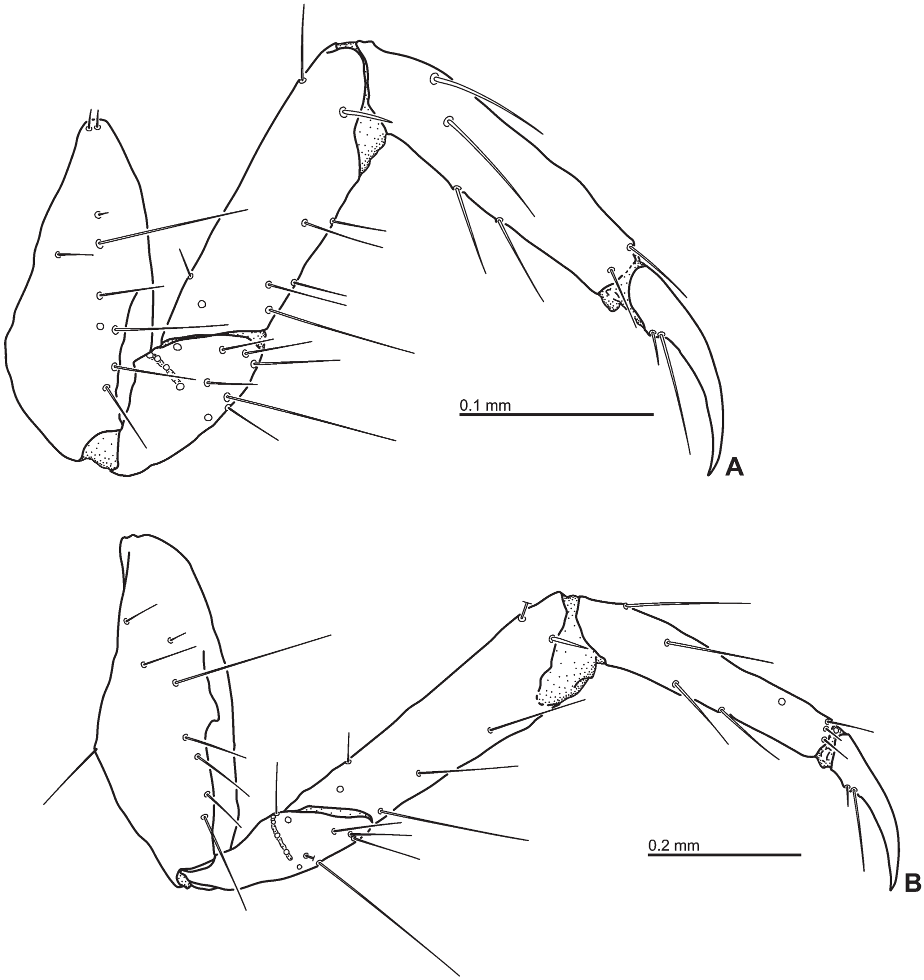

Fig. 16. *Regimbartia attenuata* (Fabricius, 1801), mesothoracic leg, anterior view. First (A) and third (B) instar.

Maxilla (e.g., Figs 14C–D). Stipes with six long to rather short secondary setae on outer surface; one long situated apically close to MX4–6; four rather short setae situated latero-ventrally on median to posterior portions.

Labium (e.g., Figs 15C–D). Dorsal surface of mentum with two pairs of short, stout secondary sensilla along anterior margin, one pair on median part, another pair on anterior corner; ventral surface with one short secondary seta on each lateral part.

Third instar (Figs 13–15). Similar to second instar.

Antenna (Figs 14A–B). Antennomere 2 with one minute secondary sensillum situated subbasally on inner face, often absent.

Mandibles (Figs 15A–B). MN2 situated on or slightly anteriorly to the line connecting MN1 and MN3.

Egg-case. Egg-cases were laid on substrate (Fig. 17C; Hayashi 2009a).

Gopalaswamy and Hanumantha Rao (1975) reported the egg-laying behaviour of *R. attenuata* and mentioned that the specimens carried egg-cases under their abdomen. However, *R. attenuata* lays egg-case on substrate such as leaves (Hayashi 2009a; Fig. 17C) like other Berosini (e.g., Archangelsky 1997, 2004, 2008; Figs 17A–B). This confusing observation of Gopalaswamy and Hanumantha Rao (1975) seems to be actually caused by a misidentification, as they likely observed specimens of the genus *Helochares* Mulsant, 1844. The carrying of the egg-case under abdomen has been observed in the species of the genera *Helochares*, *Helobata* Bergroth, 1888, and *Radicitus* Short & García, 2014 (all Hydrophilidae: Acidocerinae), and in hydrophiloid families Epimetopidae and Spercheidae (Bøving & Henriksen 1938, Archangelsky 1997, Hansen 2000, Short & García 2014). This behaviour is not known for any genus within the Hydrophilinae, including all berosine genera.

Discussion

Morphological and ecological characters. Most aquatic hydrophilid larvae are metapneustic. Gas exchange is accomplished through the eighth pair of abdominal spiracles enclosed in a spiracular atrium, i.e., they breathe by exposing the tip of the abdomen at the water surface. Therefore, they must stay close to the water surface (e.g., in riparian habitats, on vegetation), or reach the water surface if they are submerged. Contrary to this, some larvae have lost the functionality of the spiracular atrium and are considered apneustic, this has evolved independently in the tribes Berosini and Hydrobiusini: the genera *Berosus* and *Hemiosus* (Berosini), and *Hybogralius* Orchymont, 1942 (Hydrobiusini) (Watts 2002, Archangelsky 2004). *Berosus* larvae have abdominal tracheal gills for respiration, whereas *Hemiosus* and *Hybogralius* lack gills, and their respiratory mechanisms are unknown (Watts 2002; Archangelsky 2008, 2004).

The apneustic hydrophilid larvae have unusual head morphology within the Hydrophilidae, especially in the structure of the anterior margin of the head capsule, mandibles, and labium (Archangelsky 1997, 2004, 2008; Watts 2002; Figs 3–4, 5A–B, 7). Exceptionally, larvae of the genus *Laccobius* have very similar head morphology (e.g., Archangelsky 1997). They have a well-developed spiracular atrium but some behaviour resemble those of apneustic larvae (see below). In addition, the hydrophiloid genus *Epimetopus* Lacordaire, 1854 (Epimetopidae), does not have a spiracular atrium, but has functional spiracles and membranous abdominal projections, and slightly similar head morphology to *Berosus* (Archangelsky 1997, Fikáček et al. 2011). These characters have evolved independently in each clade within Hydrophiloidea (Short & Fikáček 2013).

Relationships between their lifestyles and morphology of hydrophilid larvae have been discussed in previous studies; they concluded that modifications in the morphology of head capsule and its appendages are an adaptation to a benthic lifestyle (Archangelsky 2008). Larvae of Hydrophilidae are predatory and carry out external digestion. While feeding, most aquatic hydrophilid larvae move close to the water surface and raise their head above the

Fig. 17. A–B – Egg-case of *Berosus* (*Berosus*) *japonicus* Sharp, 1873, wild (A) and rearing (B); C – egg-case of *Regimbartia attenuata* (Fabricius, 1801), rearing; D – egg of *R. attenuata*. Figs A, C modified after Hayashi (2009a). Photos by M. Hayashi.

surface to prevent outflow and dilution of digested body fluids of the prey, but apneustic larvae and *Laccobius* larvae exceptionally do not raise their head (Archangelsky 2008; Y. Minoshima, personal observation). Feeding behaviour of *Hybogralius* is unknown so far. Their head morphology prevents outflow and dilution of digested prey and allows them to perform the external digestion under the water surface (Archangelsky 2008).

In addition to these morphological adaptations, we bring additional observations of an ecological character of hydrophilid larvae, which was observed in a few old studies but has been neglected afterwards (e.g., Richmond 1920, Takahashi 1922, Bøving & Henriksen 1938). Larvae of *Berosus japonicus* do not swallow air into the alimentary canal, therefore they lack air bubbles in the intestine (Takahashi 1922; Fig. 18A); air bubbles are usually present in the majority of aquatic hydrophilid larvae observed so far (Richmond 1920, Takahashi 1922, Bøving & Henriksen 1938; Fig. 18B). The bubbles may increase buoyancy, and help them to float on the water surface for respiration, and transfer via water surface. Richmond (1920) wrote this behaviour as 'the first duty of the aquatic larvae' in the paper; however, he did not specify which species did it. Takahashi (1922) mentioned that the bubbles were absent in larvae of good swimmers (*Sternolophus* – Hydrophilinae: Hydrophilini) and ben-

Fig. 18. Living individuals of the hydrophilid larvae. A – *Berosus* (*Berosus*) *japonicus* Sharp, 1873; B – *Enochrus* (*Methydrus*) *japonicus* (Sharp, 1873); C – *Laccobius* (*Laccobius*) *kunashiricus* Shatrovskiy, 1984. Photo A by M. Hayashi, B–C by Y. Minoshima.

thic larvae (*Berosus*), whereas they were present in *Helochares* (Acidocerinae), *Amphiops* (Hydrophilinae: Amphiopini), and *Enochrus* (Enochrinae). He observed the behaviour of *Helochares pallens* (MacLeay, 1825) in detail, and mentioned that the bubbles are often absent when they were not submerged (e.g., on wet paper); and once they were submerged, they start to swallow air. The first author confirmed this behaviour based on the observation of *Enochrus haroldi* (Sharp, 1884). Bøving and Henriksen (1938) noted that 'many' aquatic larvae (but did not specify) have the bubbles; they only mentioned presence of air bubbles in *Enochrus* and '*Paracymus*' (probably misidentification of *Anacaena* Thomson, 1859, see Archangelsky & Fikáček 2004) in the description of respective taxa. We observed this ecological character within the Hydrophilidae: *Laccobius* (*Microlaccobius*) *fragilis* Nakane, 1966 and *L.* (*Laccobius*) *kunashiricus* Shatrovskiy, 1984 (Hydrophilinae: Laccobiini) did not have the bubbles (Fig. 18C), whereas *Enochrus haroldi*, *E. japonicus* (Sharp, 1873) and *E. simulans* (Sharp, 1873) (Enochrinae) have the bubbles (Fig. 18B). Up to now, absence of the bubbles has been observed only in the subfamily Hydrophilinae, in which presence of the bubbles was observed only in *Amphiops* by Takahashi (1922), and the behaviour of the remaining taxa (*Paracymus*-group of Laccobiini and Hydrobiusini) remains unknown. This makes unclear the evolutionary process of the behaviour.

Table 2. Difference of qualitative characters of head chaetotaxy between *Berosus japonicus* Sharp, 1873 and *Regimbartia attenuata* Fabricius, 1801.

	Berosus japonicus	***Regimbartia attenuata***
FR1	Rather long, trichoid seta	Short, stout seta
FR3	Trichoid seta	Stout seta
Left FR14	Absent	Present
Left gFR2	With a series of stout setae	With three stout setae
Right gFR2	Absent	Present
MX10	Long	Very short
MX11	Rather short, stout	Long, trichoid
LA15	Absent	Present
Number of secondary setae on outer face of mandibles	3–4	10–11
Number of secondary setae on outer face of stipes	2	5
Number of secondary setae on mentum	0	6

Increasing buoyancy resists benthic life style or highly-developed swimming behaviour. Benefit of the absence of the bubbles is the loss of buoyancy in two different life styles: benthic lifestyle in the clades Berosini and Laccobiini, and swimming life style in the clade Hydrophilini.

Comparison of head chaetotaxy between *B. japonicus* and *R. attenuata*. Despite large differences between their lifestyles in the larval stages, chaetotaxy of the head capsule of *B. japonicus* and *R. attenuata* are very similar (Figs 2, 9A–B). Although head appendages are more or less modified in *Berosus* (Fig. 4), especially in the mandibles and labium, *Berosus* bear nearly all the hydrophilid primary sensilla (*B. japonicus* bears 13 of 15 primary sensilla on the labium excluding gLA, and bears all the primary sensilla on the mandibles) (Figs 4G–H).

Head capsule. Both genera bear all the primary sensilla, exceptionally FR14 is absent in *B. japonicus*. Positions of the primary sensilla on the head capsule seem to be different due to modification of the head capsule shape, i.e. the head capsule of *R. attenuata* is more transverse than that of *B. japonicus* (Figs 5A, 12A). However, relative positions and morphology of the primary sensilla on the head capsule are not largely different in both genera; these are therefore identical between *B. japonicus* and *R. attenuata*. Relative positions and morphology of the sensilla on the frontale are more different than those on the parietale (Figs 9A, 12A). FR1 is a rather long trichoid seta close to the frontal line in *Berosus*, whereas it is a short seta, more distant from the frontal line in *Regimbartia*. FR3 is a short trichoid seta situated behind FR8 in *B. japonicus*, whereas it is a short, stout seta situated mesally to FR8 in *Regimbartia*. FR4–7 and FR9–10 are more closely aggregated in *R. attenuata* than in *B. japonicus*. FR14 is absent in *B. japonicus* but present in *Regimbartia* (Figs 3A, 9C); the absence of FR14 is rare in the Hydrophilidae (e.g., Fikáček et al. 2008, Minoshima & Hayashi 2011a). gFR1 consists of short setae in *B. japonicus*, whereas these setae are longer and stouter in *R. attenuata*; gFR2 in *B. japonicus* consists of a series of stout setae on the left, and no setae on the right, whereas in

R. attenuata it consists of three stout setae on each side (Figs 3A, 9C). Difference of position and shape of the primary sensilla on the clypeolabrum will be due to the modification of clypeolabrum in *Berosus*, but they are almost identical (Figs 3A, 9C).

Head appendages. A few sensilla are absent on the head appendages of *B. japonicus*: AN8–9, LA4, and LA15 are absent, whereas only antennal sensilla AN8–9 are absent in *R. attenuata*. Absence of AN8 and/or AN9 is a common trend in hydrophilid larvae (Fikáček et al. 2008, 2013, 2014; Torres et al. 2011, 2014; Minoshima & Hayashi 2012). Absence of LA4 and LA15 seems rare in the Hydrophilidae (Fikáček et al. 2008, Minoshima & Hayashi 2012) and that of LA15 was also observed in *Laccobius striatulus* (Fabricius, 1801) and *Amphiops mater mater* Sharp, 1873, which have modified labium (Fikáček et al. 2008, Minoshima & Hayashi 2012). The reduction of labial sensilla is known in several hydrophilid larvae, which have a modified labium (Fikáček et al. 2008). The morphology of primary sensilla, MX9–10 are distinctly different: MX9 is a short, stout seta and MX10 is a long trichoid seta in *B. japonicus* (Fig. 4E), in *R. attenuata* (Fig. 10C) they are very short and long, respectively.

When comparing third instar larvae, *R. attenuata* bears more secondary setae on the base of the outer face of the mandibles than *Berosus*. The outer face of the stipes bears few secondary setae in *B. japonicus*, whereas more secondary setae are present in *R. attenuata* (Figs 6C–D, 14C–D). *Berosus japonicus* does not bear any secondary sensilla on the mentum (Figs 7C–D), but *R. attenuata* bears two pairs of short, stout secondary setae on the anterior margin of the dorsal face and one pair of short secondary setae on the anterior margin of the ventral face (Figs 15C–D). The latter case is common in the secondary chaetotaxy of aquatic hydrophilid larvae (e.g., Minoshima & Hayashi 2011a,b, 2012). Thus, absence of secondary sensilla on the mentum can be considered a result of the reduction of the labium.

Consequently, chaetotaxy of the head capsule and its appendages of both genera are similar, excluding the modified clypeolabrum and labium in *B. japonicus*. This similarity of chaetotaxy between *B. japonicus* and *R. attenuata* indicates that the benthic lifestyle of *Berosus* does not strongly affect the presence/absence of primary sensilla.

Comparison of head chaetotaxy within *Berosus*. Fikáček et al. (2008) summarised characters of hydrophilid larval head chaetotaxy, including *B. signaticollis* (Charpentier, 1825), the only other Berosini with chaetotaxy known in detail. According to the study, head chaetotaxy of *B. japonicus* differs from that of *B. signaticollis* in (1) gFR2 consists of 12 setae in *B. japonicus*, whereas there are 11 setae in *B. signaticollis*; (2) FR11 is present in *B. japonicus*, whereas it is absent in *B. signaticollis*; (3) the additional pore on antennomere 1 is absent in *B. japonicus*, whereas it is present in *B. signaticollis*; (4) LA11 is present in *B. japonicus*, whereas it is absent in *B. signaticollis*.

Acknowledgements

This study is based on a part of Minoshima's PhD thesis at the Graduate School of Agriculture, Hokkaido University, Sapporo, Japan. Minoshima (YM) thanks the members of the laboratory of Systematic Entomology, Hokkaido University, particularly Masahiro Ôhara, Kazunori Yoshizawa, and Shin'ichi Akimoto, for their support, and critical reading and helpful comments to the draft of the thesis; Hideki Takahashi (Hokkaido University Museum, Sapporo, Japan) for his critical reading to the draft of the thesis. YM is especially deeply grateful to M. Ôhara for his kindness during the supervising YM's PhD thesis. We thank Martin Fikáček (National Museum, Prague, Czech Republic) for his critical reading and helpful comments to the draft; Miguel Archangelsky (CONICET, LIESA, Universidad Nacional de la Patagonia San Juan Bosco, Argentina) for his comments on the behaviour of the hydrophilid larvae and his constructive criticism to the manuscript. YM also thanks the staff and volunteers of the Hokkaido University Museum for their kindness. This study was partly supported by the Grant-in-Aid for JSPS Fellows (10J03421) to YM (2010–2012).

References

ANGUS R. B., AOUAD N. & SHAARAWI F. A. I. 1994: The karyotypes of Berosus (s. str.) affinis Brulle and B. (s. str.) hispanicus Kuster, with notes on the egg cocoons. (Coleoptera: Hydrophilidae). *Koleopterologische Rundschau* **64**: 133–139.

ARCHANGELSKY M. 1994: Description of the immature stages of three Nearctic species of the genus Berosus Leach (Coleoptera: Hydrophilidae). *Internationale Revue der Gesamten Hydrobiologie* **79(3)**: 357–372.

ARCHANGELSKY M. 1997: Studies on the biology, ecology, and systematics of the immature stages of New World Hydrophiloidea (Coleoptera: Staphyliniformia). *Bulletin of the Ohio Biological Survey, New Series* **12**: 1–207.

ARCHANGELSKY M. 1999: Larvae of Neotropical Berosus (Coleoptera, Hydrophilidae): B. aulus Orchymont, 1941 and B. auriceps Boheman, 1859. *Tijdschrift voor Entomologie* **142**: 1–8.

ARCHANGELSKY M. 2000: Immature stages of Neotropical Hydrophilidae (Coleoptera): Hydramara argentina (Knisch, 1925) and Hemiosus bruchi Knisch, 1924. *Proceedings of the Entomological Society of Washington* **10**: 280–291.

ARCHANGELSKY M. 2002a: Nuevas larvas de Hydrophilidae (Coleoptera: Hydrophiloidea): Hemiosus multimaculatus y Chaetarthria bruchi. *Revista de la Sociedad Entomológica Argentina* **61**: 89–97.

ARCHANGELSKY M. 2002b: Immature stages of Neotropical Berosus (Coleoptera, Hydrophilidae): B. toxacanthus Oliva, 1989, B. coptogonus Jensen-Haarup, 1910, B. cornicinus Knisch, 1922 and B. auriceps Boheman, 1859. *Tijdschrift voor Entomologie* **145**: 19–28.

ARCHANGELSKY M. 2004: Higher-level phylogeny of Hydrophilinae (Coleoptera: Hydrophilidae) based on larval, pupal and adult characters. *Systematic Entomology* **29**: 188–214.

ARCHANGELSKY M. 2008: Phylogeny of Berosini (Coleoptera: Hydrophilidae, Hydrophilinae) based on larval and adult characters, and evolutionary scenarios related to habitat shift in larvae. *Systematic Entomology* **33**: 635–650.

ARCHANGELSKY M. & DURAND M. E. 1992: Description of the preimaginal stages of Derallus angustus Sharp, 1882 (Coleoptera, Hydrophilidae, Berosinae). *Aquatic Insects* **14**: 169–178.

ARCHANGELSKY M. & FERNANDEZ L. A. 2005: Description of new neotropical Berosini larvae: Derallus paranensis and Hemiosus dejeanii (Coleoptera : Hydrophilidae). *Coleopterists Bulletin* **59**: 211–220.

ARCHANGELSKY M. & FIKÁČEK M. 2004: Descriptions of the egg case and larva of Anacaena and a review of the knowledge and relationships between larvae of Anacaenini (Coleoptera: Hydrophilidae: Hydrophilinae). *European Journal of Entomology* **101**: 629–636.

BERTRAND H. 1936: Larves de Coléopteres aquatiques de l'Expédition Limnologique Allemande en Insulinde. *Archiv für Hydrobiologie, Supplement Band XIV "Tropische Binnengewässer"* **6**: 193–285, pls. I–XI.

BERTRAND H. 1962: Contribution à l'étude des premiers états des Coléoptères aquatiques de la région éthiopienne (4e note). Famille: Hydrophilidae s.lat. (Palpicornia auct.). *Bulletin de l'Institut Français de l'Afrique Noire, Serie A* **24**: 1065–1114.

BERTRAND H. 1968: Larves de Coléoptères aquatiques recueillies au Brésil par M. G. Marlier. *Bulletin de la Société Entomologique de France* **73**: 8–21.

BERTRAND H. 1972: *Larves et nymphes des Coléoptères aquatiques du globe*. Imprimerie F. Paillart, Abbeville, 804 pp.

BLACKBURN T. 1888: Notes on Australian Coleoptera with descriptions of new species. *Proceedings of the Linnean Society of New South Wales, Second Series* **3** (1889): 805–875.

BOHEMAN C. H. 1858: Coleoptera. In: *Kongliga Svenska Fregatten Eugenies Resa Omkring Jorden Under Befäl af C. A. Virgin Åren 1851-1853. Vetenskapliga Iakttagelser II. Zoologi. 1. Insecta.* P. A. Norstedt & Söner, Stockholm, 218 pp + 2 pls.

BØVING A. G. & HENRIKSEN K. L. 1938: The developmental stages of the Danish Hydrophilidae (Ins., Coleoptera). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i København* **102**: 27–162.

BROCHER F. 1911: Observations biologiques sur quelques insectes aquatiques. *Annales de Biologie Lacustre* **4** (1909–1911): 367–379.

BRULLÉ A. 1835: *Histoire Naturelle des Insectes, 5. Coléoptères II*. F. D. Pillot, Paris, 436 pp.

BRULLÉ A. 1841: Tribu des Palpicornes. Pp. 52–61. In: d'ORBIGNY A. (ed.): *Voyage dans l'Amérique Méridionale: (le Brésil, la République Orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivia, la République du Pérou), Exécuté Pendant les Années 1826, 1827, 1828, 1829, 1830, 1831, 1832, et 1833, Tome Sixième, 2e Partie: Insectes*. Strasbourg, Paris (continued from 1837).

BYTTEBIER B. & TORRES P. L. M. 2009: Description of the preimaginal stages of Enochrus (Hugoscottia) variegatus (Steinheil, 1869) and E. (Methydrus) vulgaris (Steinheil, 1869) (Coleoptera: Hydrophilidae), with emphasis on larval morphometry and chaetotaxy. *Zootaxa* **2139**: 1–22.

CHARPENTIER T. DE 1825: *Horae Entomologicae, Adjectis Tabulis Novem Coloratis*. A. Gosohorsky, Wratislaviae, xvi + 254, 9 pls. pp.

FABRICIUS J. C. 1801: *Systema Eleutheratorum secundum ordines, genera, species adiecticis synonymis, locis, observationibus, descriptionibus. Tomus I.* Impensis Bibliopolii Academici Novi, Kiliae, 24 + 506 pp.

FERNÁNDEZ L. A. & CAMPOS R. E. 2002: Description of immature stages of Berosus alternans Brullé (Coleoptera: Hydrophilidae). *Transactions of the American Entomological Society* **128**: 255–263.

FIKÁČEK M., ARCHANGELSKY M. & TORRES P. L. M. 2008: Primary chaetotaxy of the larval head capsule and head appendages of the Hydrophilidae (Coleoptera) based on larva of Hydrobius fuscipes (Linnaeus, 1758). *Zootaxa* **1874**: 16–34.

FIKÁČEK M., BARCLAY M. V. L. & PERKINS P. D. 2011: Two new species of the Epimetopus mendeli species group and notes on its adult and larval morphology (Coleoptera: Hydrophiloidea: Epimetopidae). *Acta Entomologica Musei Nationalis Pragae* **51**: 477–504.

FIKÁČEK M., MINOSHIMA Y., VONDRÁČEK D., GUNTER N. & LESCHEN R. A. B. 2013: Morphology of adults and larvae and integrative taxonomy of southern hemisphere genera Tormus and Afrotormus (Coleoptera: Hydrophilidae). *Acta Entomologica Musei Nationalis Pragae* **53**: 75–126.

FIKÁČEK M., MINOSHIMA Y. N. & NEWTON A. F. 2014: A review of Andotypus and Austrotypus gen. nov., rygmodine genera with an austral disjunction (Hydrophilidae: Rygmodinae). *Annales Zoologici* (Warszawa) **64**: 557–596.

FUKUDA A., KUROSA K. & HAYASHI N. 1959: Coleoptera. Pp. 392–545. In: KAWADA A., ESAKI T., ISHII T., SHIRAKI T. & YUASA H. (eds.): *Illustrated Insect Larvae of Japan*. The Hokuryukan Co. Ltd., Tokyo (in Japanese with English title; descriptions and illustrations of the Hydrophiloidea by K. Kurosa).

GOPALASWAMY G. & HANUMANTHA RAO K. 1975: Studies on the feeding and breeding habits of Dineutes indicus (Aube) (Gyrinidae) and Regimbartia attenuata (Fabr.) found in the brackish waters of Visakhapatnam (S. India). *Bulletin of the Department of Marine Sciences (Cochin University)* **7(3)**: 569–582.

HADLEY A. 2010: CombineZP (6th June, 2010). Available online at http://www.hadleyweb.pwp.blueyonder.co.uk/.

HANSEN M. 1999: *World Catalogue of Insects 2: Hydrophiloidea (s. str.) (Coleoptera)*. Apollo Books, Amsterdam, 416 pp.

HANSEN M. 2000: Observations on the immature stages of Georissidae (Coleoptera: Hydrophiloidea), with remarks on the evolution of the hydrophiloid egg cocoon. *Invertebrate Taxonomy* **14**: 907–916.

HAYASHI M. 2006a: Aquatic insects of Syakunouchi park, Un'nan city, Shimane prefecture, Japan. *Bulletin of Hoshizaki Green Foundation* **9**: 113–119 (in Japanese with English title and abstract).

HAYASHI M. 2006b: Aquatic insects observed from biotope in western coast area of Shinjiko lake, Shimane, Japan (2004–2005). *Bulletin of Hoshizaki Green Foundation* **9**: 193–202 (in Japanese with English title and abstract).

HAYASHI M. 2007: Distributional records and ecological notes on aquatic Coleoptera of Shimane prefecture. *Bulletin of Hoshizaki Green Foundation* **10**: 77–113 (in Japanese with English title and abstract).

HAYASHI M. 2008: Distributional records and ecological notes on aquatic Coleoptera of Shimane prefecture, Part II. *Bulletin of Hoshizaki Green Foundation* **11**: 61–91 (in Japanese with English title and abstract).

HAYASHI M. 2009a: Aquatic Hydrophilidae of Shimane prefecture. *Bulletin of Hoshizaki Green Foundation* **12**: 87–121 (in Japanese with English title and abstract).

HAYASHI M. 2009b: Distributional records and ecological notes on aquatic Coleoptera of Shimane prefecture, Part III. *Bulletin of Hoshizaki Green Foundation* **12**: 235–258 (in Japanese with English title and abstract).

HAYASHI M. 2009c: Reproduction of aquatic beetles on paddies in eastern Shimane prefecture, Japan. *Bulletin of Hoshizaki Green Foundation* **12**: 289–298 (in Japanese with English title and abstract).

HAYASHI M. 2011: Aquatic Coleoptera of Shimane Prefecture. *Special Bulletin of the Hoshizaki Green Foundation* **1**: 1–117 (in Japanese with English title).

HAYASHI M., SASAKI K., NAKANO H., TERAOKA S., YAMAGUCHI K. & KOSHIKAWA T. 2008: Records on invertebrate and vertebrate of rivers and streams in Hirata area, Izumo city, Shimane prefecture, Japan. *Bulletin of Hoshizaki Green Foundation* **11**: 1–60 (in Japanese with English title and abstract).

HERBST J. F. W. 1797: *Natursystem Aller Bekannten In- und Ausländischen Insekten als Eine Fortsetzung der von Buffonschen Naturgeschichte, der Käfer, 7*. J. Pauli, Berlin, 346 + xi pp., 26 pls.

JENSEN-HAARUP A. 1910: New species of Coleoptera from West Argentina. *Deutsche Entomologische Zeitschrift* **1910(5)**: 541–554.

KÜSTER H. C. 1847: *Die Käfer Europas, nach der Natur beschrieben. Heft 12*. Bauer & Raspe, Nürnberg, 2 + 100 pp., 2 pls.

KARAOUZAS I. & İNCEKARA Ü. 2011: First record of the genus Berosus (Coleoptera: Hydrophilidae) in Crete island, Greece. *Entomologia Hellenica* **20(2)**: 69–74.

KAWANO K., NAKANO H., HAYASHI M. & YAMAUCHI T. 2006: Aquatic insects in the ponds of Hirata area (Izumo city) in Shimane prefecture, Japan. *Bulletin of Hoshizaki Green Foundation* **9**: 13–37 (in Japanese with English title and abstract).

KNISCH A. 1922: Hydrophiliden-Studien. (Op. 10.). *Archiv für Naturgeschichte, Abteilung A* **88(5)**: 87–126.

KNISCH A. 1924: Neue neotropische Palpicornier. (Col. Hydrophilidae. Op. – 16). *Wiener Entomologische Zeitung* **41**: 114–140.

LAWRENCE J. F. & ŚLIPIŃSKI A. 2013: *Australian Beetles Volume 1. Morphology, Classification and Keys*. CSIRO Publishing, Melbourne, viii + 561 pp.

LECONTE J. L. 1855: Synopsis of the Hydrophilidæ of the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia* **7(9)**: 356–375.

LECONTE J. L. 1863: New species of North American Coleoptera. Part I. *Smithsonian Miscellaneous Collections* **6(167)**: 1–177 (1863–66; only pp. 1–86 issued in 1863; pp. 87–177 in 1866).

LINNAEUS C. 1761: *Fauna Svecica, Sistens Animalia Sveciæ Regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes, Distributa per Classes & Ordines, Genera & Species, cum Differentiis Specierum, Synonymis Auctorum, Nominibus Incolarum, Locis Natalium, Descriptionibus Insectorum, Editio Altera, Auctior*. Laurentii Salvii, Stockholmiæ, 46 + 578 pp., 2 pls.

MACLEAY W. S. 1825: *Annulosa Javanica or an attempt to illustrate the natural affinities and analogies of the Insects collected in Java by Thomas Horsfield, M.D. F.L. & G.S. and deposited by him in the Museum of the Honourable East-India Company*. Kingsbury, Parbury, and Allen, London, 1 pl., 50 pp.

MINOSHIMA Y. & HAYASHI M. 2011a: Larval morphology of the Japanese species of the tribes Acidocerini, Hydrobiusini and Hydrophilini (Coleoptera: Hydrophilidae). *Acta Entomologica Musei Nationalis Pragae* **51(supplementum)**: 1–118.

MINOSHIMA Y. & HAYASHI M. 2011b: Larval morphology of the genus Hydrocassis Fairmaire (Coleoptera: Hydrophilidae). *Journal of Natural History* **45**: 2757–2784.

MINOSHIMA Y. & HAYASHI M. 2012: Larval morphology of Amphiops mater mater Sharp (Coleoptera: Hydrophilidae: Chaetarthriini). *Zootaxa* **3351**: 47–59.

MINOSHIMA Y., HAYASHI M., KOBAYASHI N. & YOSHITOMI H. 2013: Larval morphology and phylogenetic position of Horelophopsis hanseni Satô et Yoshitomi (Coleoptera, Hydrophilidae, Horelophopsinae). *Systematic Entomology* **38**: 708–722.

MINOSHIMA Y., IWATA Y. & HAYASHI M. 2012: Morphology of the immature stages of Hydrochara libera (Sharp) (Coleoptera, Hydrophilidae). *Elytra, New Series* **2(2)**: 285–302.

MULSANT E. & REY C. 1858: Description de quelques espèces nouvelles de Coléoptères du genre Bérose. *Annales des Sciences Physiques et Naturelles, d'Agriculture et d'Industrie, Publiées par la Société Impériale* *d'Agriculture de Lyon, Troisième Série* **2**: 316–320. [The same article issued in MULSANT E. 1859: *Opuscules Entomologique* **9**: 58–62].

NAKANE T. 1966: New or little-known Coleoptera from Japan and its adjacent regions. XXIII. *Fragmenta Coleopterologica Japonica* **14–15**: 55–59 [continued from 1965 (part 13): 51–54; pp. 55–58 in part 14, 59 in part 15].

OLIVA A. 1981: El genero Derallus Sharp en la Argentina (Coleoptera, Hydrophilidae). *Revista de la Sociedad Entomológica Argentina* **40**: 285–296.

OLIVA A. 1989: El genero Berosus (Coleoptera: Hydrophilidae) en America del Sur. *Revista del Museo Argentino de Ciencias Naturales, Entomología* **6**: 57–236.

ORCHYMONT A. d' 1940: Contribution à l'étude des Palpicornia XIV. *Bulletin et Annales de la Société Entomologique de Belgique* **80**: 157–197.

ORCHYMONT A. d' 1941: Palpicornia (Coleoptera). Notes diverses et espèces nouvelles II. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* **17**: 1–5.

PETERSON A. 1951: *Larvae of Insects. An Introduction to Nearctic Species. Part II. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera*. Edwards Brothers, Inc., Columbus, Ohio, v + 416 pp.

RICHMOND E. A. 1920: Studies on the biology of the aquatic Hydrophilidae. *Bulletin of the American Museum of Natural History* **42**: 1–94, pls. 1–16.

SCHIØDTE J. C. 1862: De metamorphosi eleutheratorum observationes: bidrag til insekternes udviklingshistorie. *Naturhistorisk Tidsskrift* **1(2)**: 199–232, Tab. VI–X.

SCHIØDTE J. C. 1872: De metamorphosi eleutheratorum observationes: bidrag til insekternes udviklingshistorie. Pars IV Carabi (Suppl.), Dytisci (Suppl.), Gyrini (Suppl.), Hydrophili (Suppl.). *Naturhistorisk Tidsskrift* **8**: 165–226, Tab. I–IX.

SHARP D. 1873: The water beetles of Japan. *Transactions of the Entomological Society of London* **1873**: 45–67.

SHARP D. 1882: Insecta. Coleoptera. Vol. 1, part 2. Pp. xv + 824, 19 pls. In: GODMAN F. D. & SALVIN O. (eds.): *Biologia Centrali-Americana*. Taylor and Francis, London [1882–87; only pp. 1–144 issued in 1882].

SHARP D. 1884: The water-beetles of Japan. *Transactions of the Entomological Society of London* **1884**: 439–464.

SHARP D. 1887: Insecta. Coleoptera. Vol. 1, part 2. Pp. xv + 824, 19 pls. In: GODMAN F. D. & SALVIN O. (eds.): *Biologia Centrali-Americana*. Taylor and Francis, London [1882–87; only pp. i–xv, and 673–824 (= suppl.) issued in 1887].

SHATROVSKIY A. G. 1984: Obzor vodolyubov roda Laccobius Er. (Coleoptera, Hydrophilidae) fauny SSSR. [Revision of the genus Laccobius Er. of the Soviet Union (Coleoptera, Hydrophilidae)]. *Entomologicheskoe Obozrenie* **63**: 301–325 (in Russian with English title and abstract).

SHIRAYAMA Y., KAKU T. & HIGGINS R. P. 1993: Double-sided microscopic observation of meiofauna using an HS-slide. *Benthos Research* **44**: 41–44 (in Japanese with English title and abstract).

SHORT A. E. Z. & FIKÁČEK M. 2011: World catalogue of the Hydrophiloidea (Coleoptera): additions and corrections II (2006–2010). *Acta Entomologica Musei Nationalis Pragae* **51**: 83–122.

SHORT A. E. Z. & FIKÁČEK M. 2013: Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). *Systematic Entomology* **38**: 723–752.

SHORT A. E. Z. & GARCÍA M. 2014: A new genus of egg case-carrying water scavenger beetle from the Guiana Shield (Coleoptera: Hydrophilidae: Acidocerinae). *Zootaxa* **3835**: 251–262.

SHORT A. E. Z. & HEBAUER F. 2006: World catalogue of Hydrophiloidea – additions and corrections, 1 (1999–2005) (Coleoptera). *Koleopterologische Rundschau* **76**: 315–359.

SOLIER A. J. J. 1849: Coleoptera. Pp. 105–511. In: GAY C. (ed.) *Historia fisica y Politica de Chile. Zoologia. Tomo Cuarto*. C. Gay, Paris.

SPANGLER P. J. 1966a: A description of the larva of Derallus rudis Sharp (Coleoptera, Hydrophilidae). *Coleopterists Bulletin* **20**: 97–100.

SPANGLER P. J. 1966b: The Catherwood foundation Peruvian-Amazon Expedition. XIII – Aquatic Coleoptera (Dytiscidae; Noteridae; Gyrinidae; Hydrophilidae; Dascillidae; Helodidae; Psephenidae; Elmidae). *Monographs of the Academy of Natural Sciences of Philadelphia* **14**: 377–443.

SPANGLER P. J. 1991: Hydrophilidae (Hydrophiloidea). Pp. 355–358. In: STEHR F. E. (ed.) *Immature Insects, Volume 2*. Kendall / Hunt Publishing Co., Dubuque, Iowa.

STEVEN C. V. 1808: [Descriptions of new species]. Pp. 3, 8. In: SCHÖNHERR C. J. (ed.) *Synonymia Insectorum, oder: Versuch einer Synonymie aller bisher bekannten Insecten, nach Fabricii Systema Eleutheratorum & c.*

geordnet, Erster Band (Vol. 1). Eleutherata oder Käfer. Zweiter Theil (Part 2). Spercheus--*Cryptocephalus*. Carl Friedr Marquard, Stockholm, x + 424 pp + 1 pl.

TAKAHASHI R. 1922: [Observations of the hydrophilid beetles and introduction to the ecology of aquatic insects]. *Zoological Magazine* **34(405)**: 691–700 (in Japanese).

TORRES P. L. M., MICHAT M. C. & ARCHANGELSKY M. 2011: The immature stages of Tropisternus (Pleurhomus) sahlbergi (Sharp) (Coleoptera: Hydrophilidae), with considerations on the primary chaetotaxy of Tropisternus Solier. *Zootaxa* **2777**: 25–40.

TORRES P. L. M., MICHAT M. C., ARCHANGELSKY A. & FERNÁNDEZ L. A. 2014: Description of immatures of the genus Tropisternus Solier, subgenus Pristoternus Orchymont (Coleoptera: Hydrophilidae), with emphasis on the chaetotaxy and morphometry of larval forms. *Zootaxa* **3790**: 380–398.

WATTS C. H. S. 2002: The larvae of some Australian aquatic Hydrophilidae (Coleoptera: Insecta). *Records of the South Australian Museum* **35**: 105–138.

WILSON C. B. 1923: Water beetles in relation to pondfish culture, with life histories of those found in fishponds at Fairport, Iowa. *Bulletin of the Bureau of Fisheries* **39**: 231–345.

WOOLDRIDGE D. P. 1964: Two new species of Berosus from the southeastern United States (Coleoptera: Hydrophilidae). *Coleopterists Bulletin* **18(4)**: 97–100.