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Larval morphology of *Liodessus* Guignot, 1939: generic characteristics, descriptions of five species and comparisons with other members of the tribe Bidessini (Coleoptera: Dytiscidae: Hydroporinae).

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Abstract

The larvae of *Liodessus affinis* (Say, 1823), *L. crotchi* Nilsson, 2001, *L. flavofasciatus* (Steinheil, 1869), *L. involucer* (Brinck, 1948), and *L. patagonicus* (Zimmermann, 1923) are described with an emphasis on chaetotaxy of the head capsule, head appendages, legs, last abdominal segment and urogomphi. Larvae of these species are very uniform in terms of larval morphology. Considering all known bidessine larvae, *Liodessus* Guignot, 1939 is more similar to *Hypodessus* Guignot 1939, *Amarodytes* Régimbart, 1900, *Anodocheilus* Babington, 1841, *Glareadessus* Wewalka & Biström, 1998, *Allodessus* Guignot, 1953, and *Neoclypeodytes* Young, 1967, all these genera sharing a short siphon and an elongate first urogomphomere. *Liodessus* differs from *Hypodessus*, *Amarodytes* and *Anodocheilus* by absence of the primary pore PAj whereas it shares with *Anodocheilus* the absence of a ventroapical spinula on the third antennomere.

Key words: Bidessini, *Liodessus*, larval morphology, chaetotaxy

Introduction

Liodessus Guignot, 1939 is a genus of 39 known species mostly distributed in North and South America, Africa, New Zealand and several islands including Tristan da Cunha (Miller 1998; Nilsson 2001, 2003; Nilsson & Fery 2006). Species of this genus are small and generally found in waters with heavy organic debris. *Liodessus* is one of 41 genera of the tribe Bidessini (ca 600 species worldwide) (Nilsson 2001, 2003, 2004; Nilsson & Fery 2006) and is probably polyphyletic (Miller 1998; Larson *et al*. 2000).

Larval morphology of *Liodessus* is practically unknown as the first instar of only one species, *L. affinis* (Say, 1823) has been described (Alarie & Harper 1990; Alarie *et al*. 1990; Alarie 1991). Larval morphology is of great interest in the study of phylogenetic relationships of Holometabola. As different expression of the same genotype, larval characters help to complement adult characters, which have been traditionally the primary basis for classification. A putative phylogenetic hypothesis of relationship based on larval morphology between *Liodessus* and selected genera of Bidessini was formulated recently (Michat & Alarie 2007). This hypothesis should not be viewed as strongly supported, however, as only one species of *Liodessus* (*L. affinis*) was involved.

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The objectives of this paper are: (1) to describe the larvae (including first instar) of five species of *Liodessus* with an emphasis on the morphometry and chaetotaxy and, (2) to compare the ground plan pattern of larval features of *Liodessus* with those of other bidessine genera for which the larvae have been described.

Material and methods

Larvae examined

Description of the larval stages and taxonomic conclusions reported in this paper are based on examination of larvae usually found in association with adults. Larvae of two species (*L. affinis* and *L. crotchi* Nilsson, 2001), however, were identified to species by rearing some larvae *ex ovo*, following the technique described in Alarie *et al*. (1989). The exact locality from which the specimens were obtained is provided with the species description.

Preparation

Larvae were disarticulated and mounted on standard glass slides with Hoyer's medium. Microscopic examination at magnification of 80–800X was done using an Olympus BX50 compound microscope equipped with Nomarsky differential interference optics. Figures were prepared through use of a drawing tube attached to the microscope. Voucher specimens are deposited in the following collections: *L. affinis, L. crotchi* and *L. involucer* (Brinck, 1948) (Department of Biology, Laurentian University, Canada, Y. Alarie; the later also in Albany Museum, Grahamstown, South Africa, H.M. Barber-James); *L. flavofasciatus* (Steinheil, 1869) (Laboratory of Entomology, Buenos Aires University, Argentina, M. C. Michat); *L. patagonicus* (Zimmermann, 1923) (LIESA-CONICET, Universidad Nacional de la Patagonia, Esquel, Argentina, M. Archangelsky).

Descriptions

A complete description applying to all species is provided under the treatment of the genus, but only shorter diagnoses/descriptions and comments on variation are provided under the treatment of each species.

Morphometric and chaetotaxic analyses.

We employed, with minimal modifications and additions, the terms used in previous papers dealing with larval morphology of Bidessini (Alarie & Wewalka 2001; Michat & Alarie 2006, 2007; Michat & Torres 2006). Three specimens of each instar were measured, in which paired structures were considered independently. The following measures were taken. Head length (HL): total head length including the frontoclypeus, measured medially along epicranial stem. Head width (HW): maximum head width. Length of frontoclypeus (FRL): from apex of nasale to posterior margin of ecdysial suture. Occipital foramen width (OCW): maximum width measured along dorsal margin of occipital foramen. Coronal line length (COL). Length of mandible (MN): measured from laterobasal angle to apex. Width of MN: maximum width measured at base. Length of antenna (A), maxillary (MP) and labial (LP) palpi were derived by adding the lengths of the individual articles (e.g., MP1: maxillary palpomere 1; LP1: labial palpomere 1); each article is denoted by the corresponding letter(s) followed by a number (e.g. A1: first antennomere). A3’ is used as an abbreviation for the apical lateroventral process of third antennomere. Length of leg (L) including the longest claw was derived by adding the lengths of the individual articles. Length of trochanter includes only the proximal portion, the length of distal portion is included in the femoral length. Dorsal length of last abdominal segment (LLAS): measured along midline from anterior to posterior margin. Length of urogomphus (U) was derived by adding the lengths of the individual articles; each article is denoted by the letter U followed by a number (e.g. U1: first urogomphomere). U2’ is used as an abbreviation for the length of urogomphomere 2 measured from its proximal mar-

gin to the point of insertion of primary seta UR8. These measurements were used to calculate several ratios, which characterize body shape.

Primary (present in first-instar larva) and secondary (added in later instars) setae and so-called pores were distinguished in the cephalic capsule, head appendages, legs, last abdominal segment, and urogomphus. Sensilla were coded by two capital letters, in most cases corresponding to the first two letters of the name of the structure on which they are located, and a number (setae) or a lower case letter (pores). The following abbreviations were used: AB: abdominal segment VIII, AN: antenna, CO: coxa, FE: femur, FR: frontoclypeus, LA: labium, MN: mandible, MX: maxilla, PA: parietal, PT: pretarsus, TA: tarsus, TI: tibia, TR: trochanter, UR: urogomphus. Setae and pores present in first-instar larva labeled by comparison with the ground plan of chaetotaxy of the subfamily Hydroporinae (Alarie & Harper 1990; Alarie *et al*. 1990; Alarie 1991; Alarie & Michat 2007a). Homologies were established using the criterion of similarity of position (Wiley 1981). Setae located at the apex of maxillary and labial palpi were extremely difficult to distinguish due to their position and small size. Accordingly, they are not well represented.

Color

Description of color is given for all species from ethanol-preserved specimens.

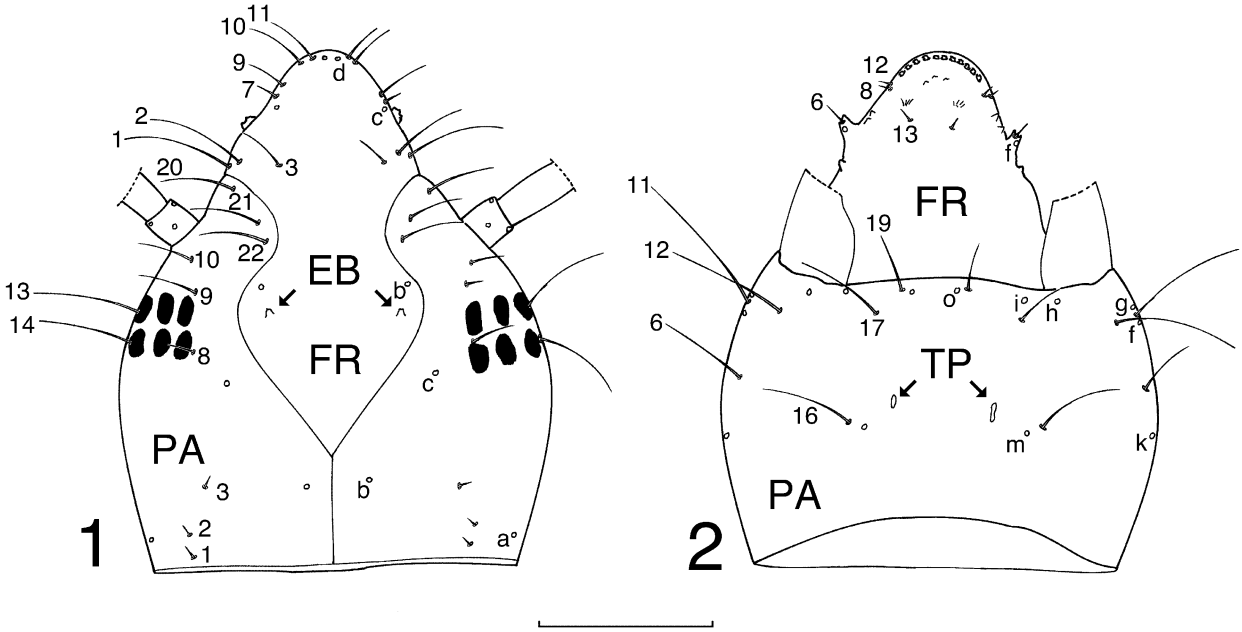
Description of the larvae of *Liodessus* Guignot

Diagnosis.

Larvae of *Liodessus* can be distinguished from those of other genera of Bidessini that have been well studied (Table 1) by the following combination of characters: HL/HW < 1.30 in instar III (Table 1); occipital suture lacking in instar I (Fig. 1); primary pore PAk present (Fig. 2); antennomere 3 lacking a ventroapical spinula and pore ANf (Figs 3–4); A3'/A4 > 0.80 (Table 1); metathoracic legs > 2.60 times longer than HW in instar III (Table 1); coxae with secondary ventral setae in instar III (Table 2); protarsus with one posterodorsal secondary seta in instar III (Table 2); LAS shorter than HW in instar III (Table 1); urogomphus more than three times as long as LLAS in instar III (Table 1); U1 lacking secondary setae (instars II and III).

First-instar larva (Figs 1–14)

Head. *Head capsule* (Figs 1–2). HL = 0.30–0.33 mm; HW = 0.24–0.26 mm; FCL = 0.24–0.26 mm; longer than broad, HL/HW = 1.20–1.27; maximum width posterior to stemmata, without neck constriction; occipital suture lacking, ecdysial suture well marked, COL short, about 0.20 times HL; occipital foramen emarginated ventrally; posterior tentorial pits visible ventrally; six dorsolateral stemmata arranged in two subparallel rows at each side; FCL elongate, subequal in length to HW, lateral margin sinuate, with two lateral, spine-like egg bursters (*ruptor ovi* of Bertrand (1972)) at the level of stemmata; nasale short, broadly rounded apically, with one short lateral branch on each side generally visible in dorsal view, lateral margin with a variable number of bluntly rounded spine-like processes, anteroventral margin with 12–13 short, spatulate setae (= *lamellae clypeales* of Bertrand (1972)), ventral surface with spinulae. *Antenna* (Figs 3–4). Elongate, composed of four antennomeres, A/HW = 0.77–0.79; A3 > A2 > A4 > A1, A2/A3 = 0.56–0.74; A3'/A4 = 0.70–0.88; A3 without a ventroapical spinula. *Mandible* (Fig. 9). Prominent, broad basally, distal half projected inwards and upwards, sharp apically, about half as long as HL and 3.10–3.30 times as long as broad; mandibular channel present. *Maxilla* (Figs 5–6). Cardo fused to stipes; stipes short, broad; galea and lacinia absent; A/ MP = 1.20–1.31; palpus composed of three palpomeres, MP3 the shortest, MP2 the longest, MP2 1.70–2.00 times longer than MP1. *Labium* (Figs 7–8). Prementum subtrapezoidal, slightly broader than long, indented medially along anterior margin, without lateral spinulae; palpus composed of two palpomeres; MP/LP = 1.20–1.22, LP2 1.90–2.10 times LP1.



FIGURES 1–2. *Liodessus flavofasciatus* (first-instar larva), head capsule: (1) dorsal aspect; (2) ventral aspect. EB, egg bursters: FR, frontoclypeus; PA, parietale; TP, tentorial pits. Numbers and lowercase letters refer to primary setae and pores, respectively. Color pattern not represented. Scale bar = 0.10 mm.

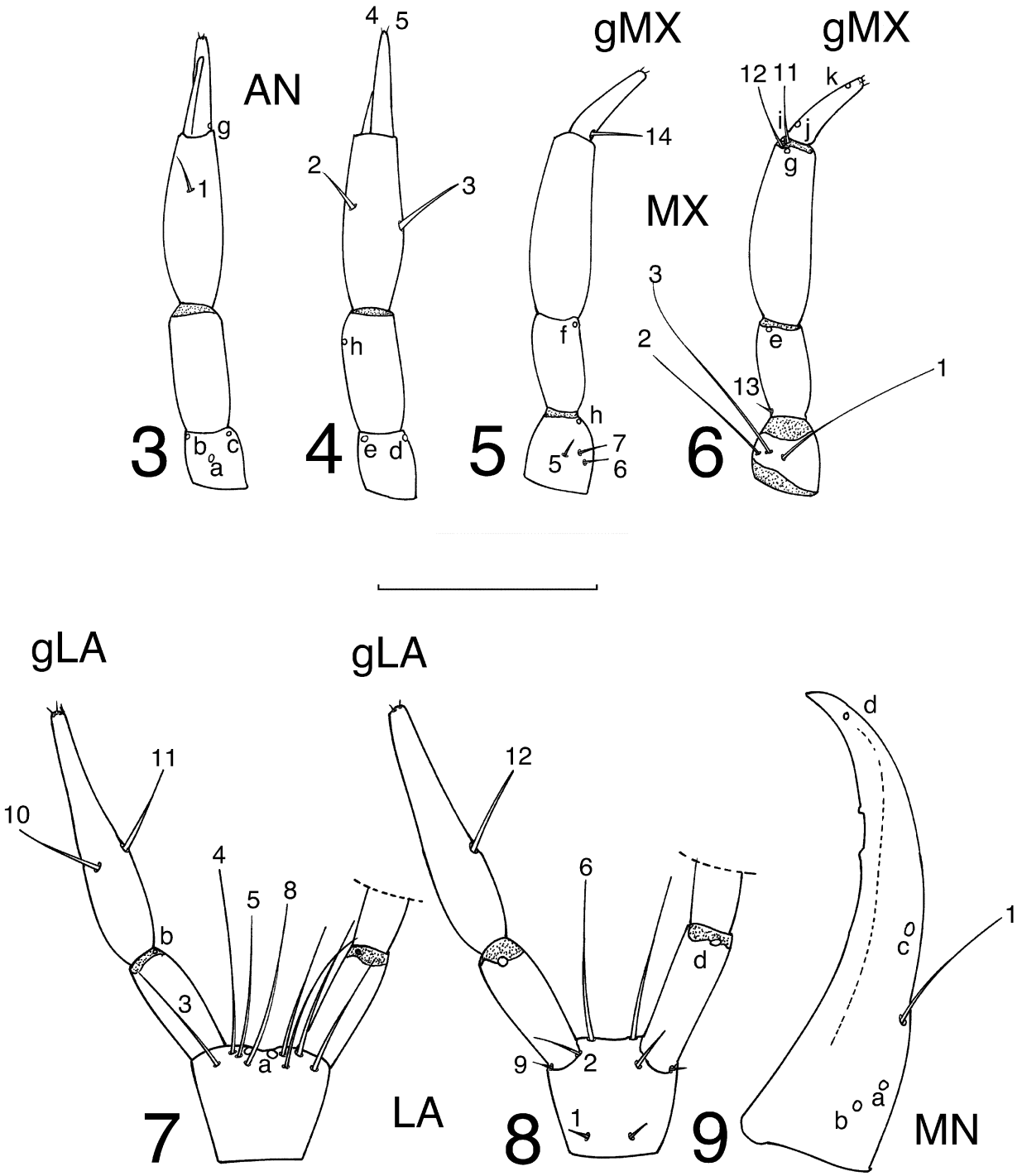
TABLE 1. Measurements and ratios for third instar of selected genera of Bidessini described in detail; *n* = number of species.

Measure	*Liodessus* (*n* = 5)	*Amarodytes*[1] (*n* = 1)	*Anodocheilus*[2] (*n* = 1)	*Hypodessus*[3] (*n* = 1)	*Glareadessus*[4] (*n* = 1)
HL (mm)	0.46–0.62	0.74–0.77	0.49–0.50	0.71–0.73	0.63
HW (mm)	0.37–0.48	0.62–0.65	0.38–0.39	0.36	0.44–0.46
HL/HW	1.23–1.30	1.18–1.20	1.26–1.32	1.27–1.32	1.39–1.44
A/HW	0.63–0.69	0.54–0.57	0.59–0.64	0.60–0.63	0.77–0.78
A2 L/A3	0.83–0.94	0.96–1.00	0.76–0.88	0.92–0.95	0.91–0.94
A3'/A4	0.84–1.00	0.64–0.73	0.89–1.00	0.64–0.78	0.87–0.91
MP2/MP1	0.92–1.06	0.83–0.96	0.95–1.11	0.93–0.96	0.82–0.83
LB2/LB1	1.08–1.22	0.71–0.96	1.14–1.50	1.05–1.09	1.07–1.10
Meta L/HW	2.70–2.98	2.59–2.72	2.69–2.77	3.03–3.12	2.34
LLAS (mm)	0.26–0.37	0.33–0.34	0.39–0.40	0.36	0.19–0.24
LLAS/HW	0.68–0.80	0.52–0.54	1.02–1.04	0.64–0.65	0.44–0.53
U (mm)	0.75–1.28	1.47–1.59	0.71–0.77	1.24–1.34	0.98–1.00*
U/HW	2.14–2.69	2.33–2.46	1.85–2.04	2.22–2.41	2.19–2.20*
U/LLAS	3.04–3.64	4.35–4.77	1.78–1.99	3.49–3.75	4.18–4.36

[1]Michat & Alarie (2006); [2]Michat & Torres (2006); [3]Michat & Alarie (2007); [4]Alarie & Wewalka (2001); *measured as U1 + U2' (cf. Alarie & Wewalka 2001)

Thorax. Terga convex, pronotum about as long as meso- and metanotum combined, meso- and metanotum subequal; protergite subovate, margins rounded, more developed than meso- and metatergite; all tergites without anterotransverse carina; sagittal line visible; thoracic sterna membranous; spiracles absent. *Legs* (Figs 10–11). Long, composed of six articles (sensu Lawrence 1991); prothoracic legs the shortest, metathoracic legs

the longest, 2.80–3.00 times HW; trochanter shortest, transversely divided into two parts, about 0.40 times length of coxa; coxa and femur the longest, coxa robust, elongate, femur, tibia and tarsus slender, subcylindrical, pretarsus with two long, slender, slightly curved claws; posterior claw shorter than anterior one on pro- and mesothoracic legs, posterior claw somewhat longer than anterior one on metathoracic legs; ventrodistal portion of tarsus with a few elongate spinulae; length of longest between setae FE8 and FE9/width of metafemur = 1.14–1.27; length of seta TI4/width of metatibia = 1.47–2.14; length of seta TA2/width of metatibia = 1.30–1.33.



FIGURES 3–9. *Liodessus flavofasciatus* (first-instar larva), head appendages: (3–4) Antenna: (3) dorsal aspect; (4) ventral aspect; (5–6) maxilla, (5) dorsal aspect; (6) ventral aspect; (7–8) labium; (7) dorsal aspect; (8) ventral aspect; (9) mandible, dorsal aspect. AN, antenna; LA, labium; gLA, labium group; MN, mandible; MX, maxilla; gMX, maxilla group. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bar = 0.10 mm.

TABLE 2. Number of secondary setae on the legs of third instars of selected genera of the tribe Bidessini: *Liodessus* Guignot (LIOD), *Amarodytes* Régimbart (AMAR), *Anodocheilus* Babington (ANOD), *Hypodessus* Guignot (HYPO), and *Glareadessus* Wewalka & Biström (GLAR); sensillar series: A = anterior, AD = anterodorsal, AV = anteroventral, PD = posterodorsal, Pr = proximal, PV = posteroventral; *n* = number of species studied.

Segment	Sensillar series	LIOD (*n* = 5)	AMAR[1] (*n* = 1)	ANOD[2] (*n* = 1)	HYPO[3] (*n* = 1)	GLAR[4] (*n* = 1)
ProCO	D	3–6	3–5	3–4	3–6	4
	A	0–1	0–3	0–1	0–1	0
	V	3–8	2–3	3–5	3–6	0
	Total	8–14	7–10	6–8	7–12	4
ProTR	Pr	1	1	0–1	1	0
ProFE	AD	3–6	2–4	5–6	5–7	3
	AV	2–6	4–5	1	1	1
	PD	0	0	0	1–4	0
	PV	1–6	3–4	3–4	3–5	2–3
	Total	7–16	10–12	9–11	12–16	6–7
ProTI	AD	0–1	1	1	0–1	0
	AV	0–2	0–1	0	0	0
	PD	0–2	0	0	0–1	1
	PV	1–3	1–2	1	1–3	1
	Total	3–6	2–4	2	2–4	2
ProTA	AD	0	0	0	0	0
	AV	0–1	0	0	0	0
	PD	1	0	0	0	0
	PV	0	0	0	1–2	0
	Total	1–2	0	0	1–2	0
MesoCO	D	3–7	3–5	2–4	4–5	3–4
	A	0–2	0–1	0–1	1–3	0
	V	1–7	2–4	2–3	2–6	0
	Total	4–13	5–9	5–7	8–12	3–4
MesoTR	Pr	1	1	1	1–2	1
MesoFE	AD	4–7	4–6	5–6	6–9	4
	AV	2–6	4–5	1–2	1	1
	PD	0	0	0	0–2	0
	PV	3–7	5–6	4–5	5–6	2–3
	Total	9–17	14–16	11–12	14–16	7–8
MesoTI	AD	1–2	1	1–2	1	1–2
	AV	1–4	1–3	1	1	1–2
	PD	0–1	1	1	1–2	1
	PV	1–3	2–3	1–2	2–3	1
	Total	5–8	5–7	5–6	5–6	5
MesoTA	AD	0	0	0	0	1
	AV	1–2	2	1	2–3	2

to be continued.

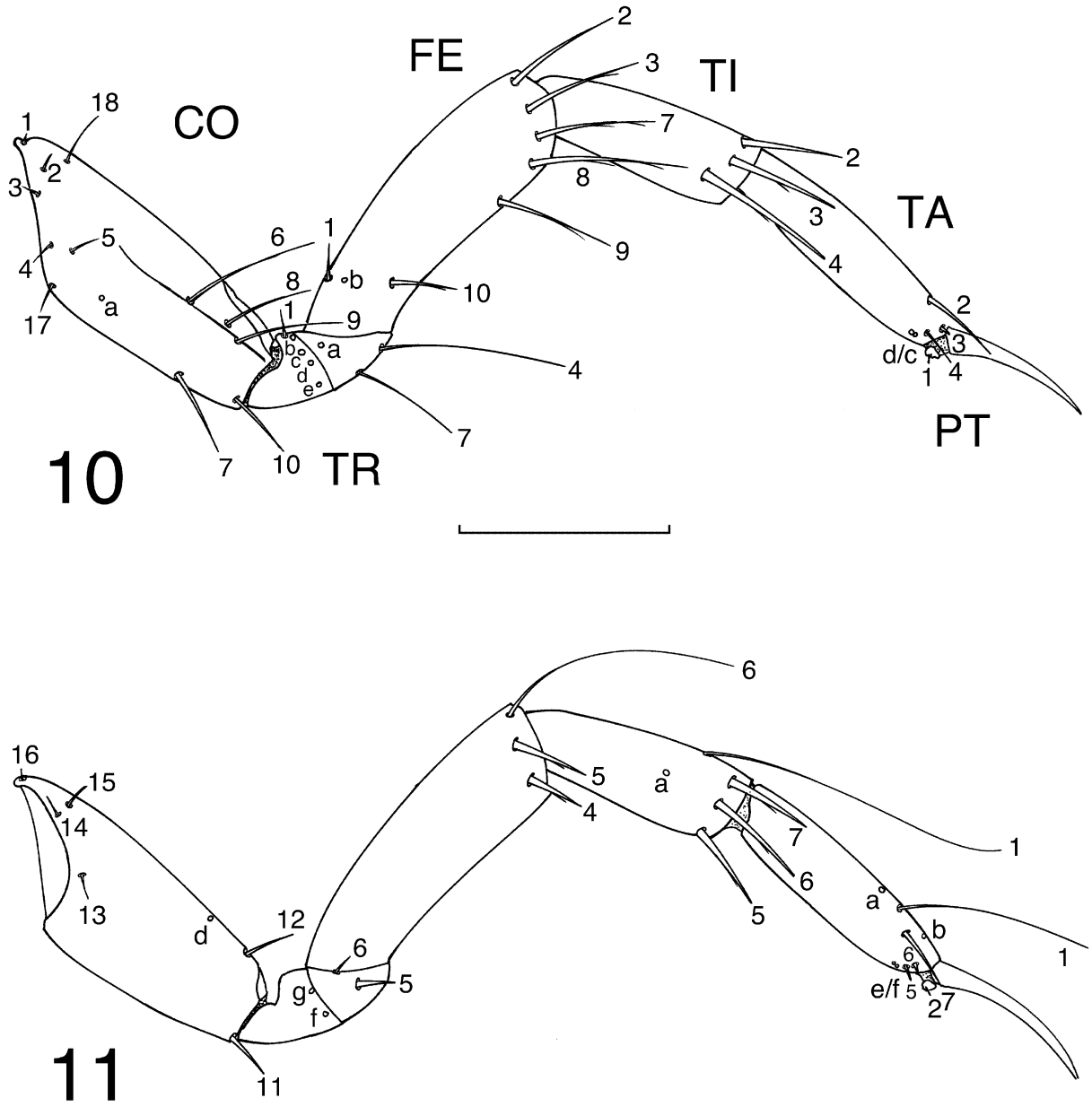
TABLE 2. (continued)

Segment	Sensillar series	LIOD (*n* = 5)	AMAR[1] (*n* = 1)	ANOD[2] (*n* = 1)	HYPO[3] (*n* = 1)	GLAR[4] (*n* = 1)
	PD	1	1	1	1	0
	PV	0–1	0	0	0–1	0
	Total	2–4	3	2	3–4	3
MetaCO	D	3–7	3–5	3–4	2–4	3
	A	0–2	0–2	1–2	1–3	0
	V	2–7	2–4	2–3	2–4	0
	Range	6–14	6–8	6–8	6–9	3
MetaTR	Pr	1–2	1–2	1	1–2	1
MetaFE	AD	5–9	5–8	5–6	6–9	4
	AV	2–6	5–8	1–3	2–4	3
	PD	0	0	0	0	0
	PV	5–8	4–7	5–6	4–7	2–3
	Total	13–22	16–22	13–15	13–18	9–10
MetaTI	AD	1–2	1	3	1–2	1
	AV	2–4	2–3	1	1–3	2
	PD	1–2	0–1	1	1	0
	PV	2–5	2–3	2–3	2–4	0
	Total	7–13	5–8	7–8	6–9	3
MetaTA	AD	0–2	0	0	0	1
	AV	1–3	2–3	1	2–3	2
	PD	1–2	1	1	1	0
	PV	0–2	0	0	0–1	0
	Total	3–7	3–4	2	3–5	3

[1]Michat & Alarie (2006); [2]Michat & Torres (2006); [3]Michat & Alarie (2007); [4] Alarie & Wewalka (2001).

Abdomen (Figs 12–13). Eight segmented; segments I–VI sclerotized dorsally, membranous ventrally; segment VII sclerotized both dorsally and ventrally, ventral sclerite independent from dorsal one; tergites I–VII narrow, transverse, rounded laterally, lacking sagittal line; all sclerites without anterotransverse carina; segment VIII (= LAS) the longest, completely sclerotized, ring-like, constricted at point of insertion of urogomphus; siphon short, 0.53–0.56 LLAS, subconical, rounded apically; LLAS = 0.13–0.15 mm; length seta AB11/LLAS = 0.33–0.40. *Urogomphus* (Fig. 14). Very long, composed of two urogomphomeres; U = 0.69–0.71 mm (U1 = 0.39–0.42 mm); 2.70–3.20 times HW (U1/HW = 1.52–1.71) and 4.70–5.60 times LLAS (U1/LLAS = 2.70–3.00); U1/U2 = 1.20–1.30; U1/U2' = 1.70–1.75; U2'/U2 = 0.69–0.74.

Chaetotaxy (Figs 1–14). Similar to that of generalized Hydroporinae larva (Alarie & Harper 1990; Alarie *et al*. 1990; Alarie 1991; Alarie & Michat 2007a) except for the following features: pores PAd, PAe, and PAj absent; pore FRc submarginal, contiguous to seta FR7; pore PAg present; pore ANf absent; pore ANh distal; seta MX4 absent; seta TR2 absent; pore FEa absent; several setae on FE and TI compound; seta TI7 short, spine-like; setae TA1 and TA7 inserted far from the apex; pores ABa and ABc absent; seta AB10 spine-like; we were unable to find seta AB8 and pore ABd; however, we could not establish if they are really absent due to the presence of dense spinulae on the siphon; setae UR2, UR3 and UR4 inserted far from each other; setae UR5, UR6 and UR7 elongate; seta UR8 inserted sub-apically.



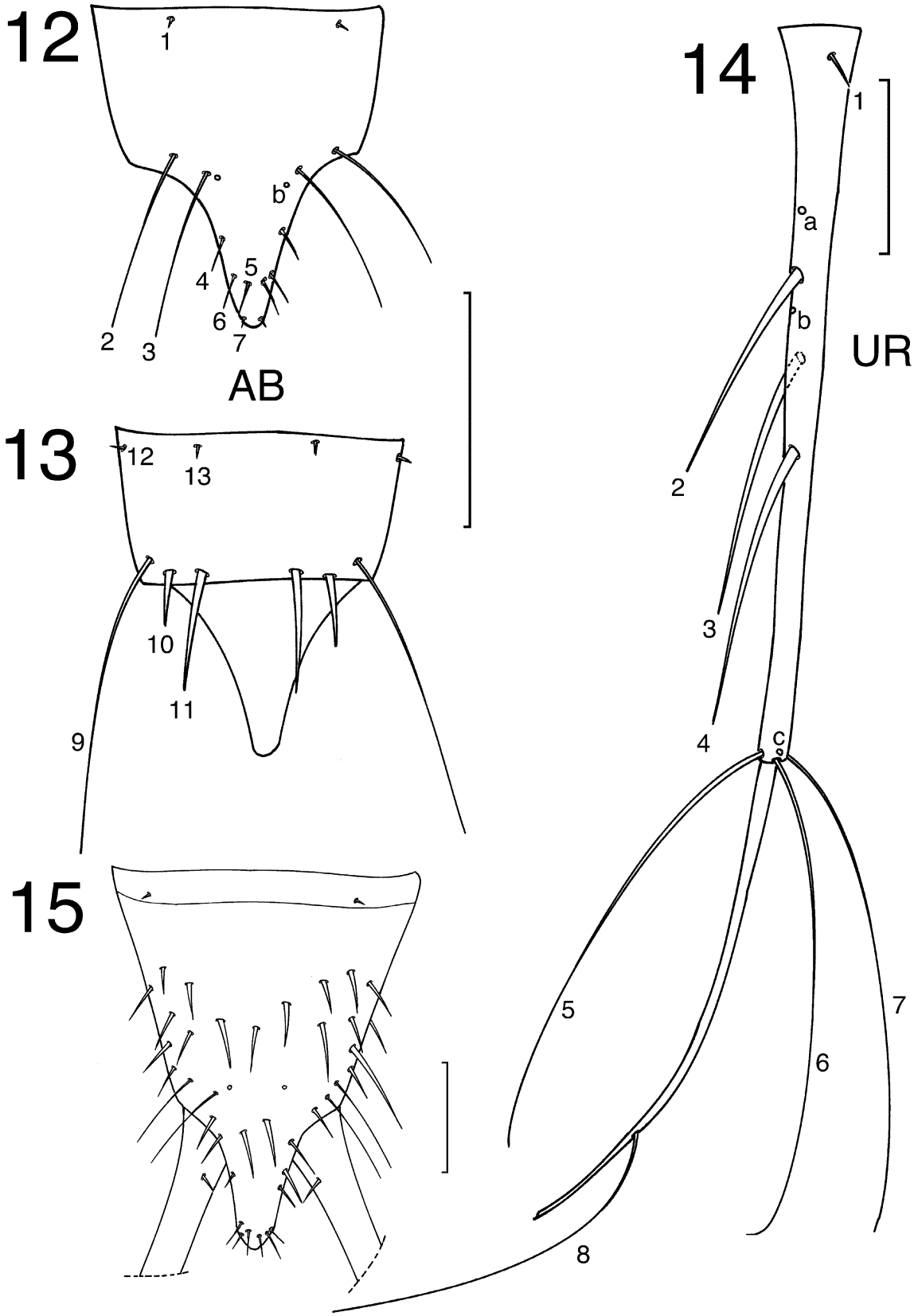
FIGURES 10–11. *Liodessus flavofasciatus* (first-instar larva), metathoracic legs: (10) anterior surface; (11) posterior surface; CO, coxa; FE, femur; TA, tarsus; TI, tibia; TR, trochanter. Numbers and lowercase letters refer to primary setae and pores, respectively; Scale bar = 0.10 mm.

Second-instar larva

As first-instar larva except as follows.

Head. *Head capsule.* HL = 0.42–0.46 mm; HW = 0.33–0.36 mm; FCL = 0.34–0.38 mm; frontoclypeus lacking egg bursters, anterior margin with 23–25 short, spatulate setae. *Antenna***.** A/HW = 0.70–0.72; A1 subequal to A4 in length; A2/A3 = 0.74–0.77; A3'/A4 = 0.62–0.92. *Mandible*. 3.30–3.80 times as long as HL. *Maxilla*. A/MP = 1.12–1.26; MP2 1.24–1.47 times longer than MP1. *Labium*. MP/LP = 1.20–1.32; LP2 1.46–1.51 times LP1.

Thorax. Meso- and metatergite with anterotransverse carina. *Legs.* Metathoracic legs 2.80–2.90 times HW.



FIGURES 12–15. *Liodessus flavofasciatus*: (12–14) (first-instar larva); (12–13) abdominal segment eight; (12) dorsal aspect; (13) ventral aspect; (14) urogomphus, dorsal aspect; (15) (third-instar larva), abdominal segment eight, dorsal aspect; AB, abdominal segment eight; UR, urogomphus. Numbers and lowercase letters refer to primary setae and pores, respectively; Scale bar = 0.10 mm.

Abdomen. LLAS = 0.20–0.23 mm; segment VII completely sclerotized, ring-like; all sclerites with anterotransverse carina; *siphon* 0.40–0.43 times LLAS. *Urogomphus.* U = 0.89–1.06 mm (U1 = 0.47–0.61 mm); 2.47–2.94 times HW (U1/HW = 1.32–1.70) and 4.14–4.75 times LLAS (U1/LLAS = 2.09–2.69); U1/U2 = 1.10–1.25; U1/U2' = 1.35–1.52; U2'/U2 = 0.79–0.86.

Chaetotaxy. Head capsule with secondary setae; lateral margin of parietal lacking temporal spines; mandible with one lateroproximal secondary seta; thoracic and abdominal tergites with numerous secondary setae; position and number of secondary setae on legs (Table 3); urogomphomere 1 lacking secondary setae.

Third-instar larva (Figs 15–22)

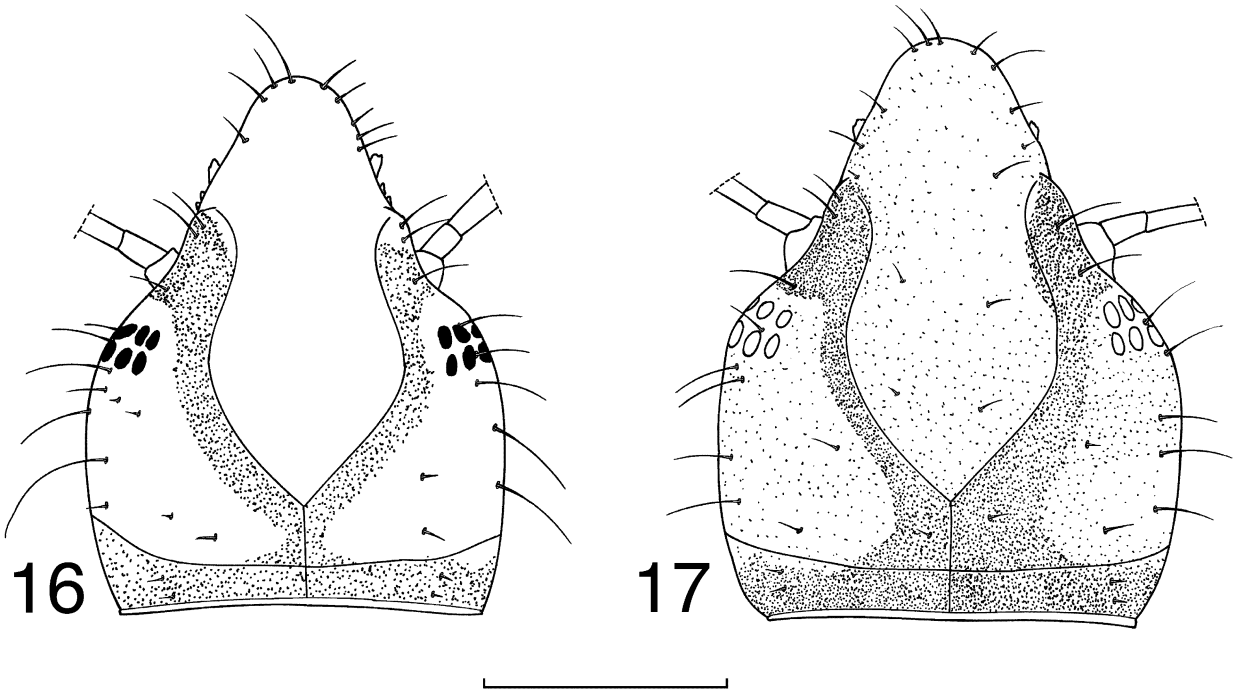
As second-instar larva except as follows.

Head. *Head capsule* (Figs 16–20). HL = 0.46–0.62 mm; HW = 0.37–0.48 mm; FCL = 0.37–0.48 mm; anterior margin of frontoclypeus with 42–50 short, spatulate setae. *Antenna***.** A/HW = 0.63–0.69; A4 shorter than A1; A2/A3 = 0.83–0.96; A3'/A4 = 0.84–1.00. *Mandible*. 3.30–3.80 times as long as HL. *Maxilla*. A/MP = 1.07–1.15; MP2 0.89–1.08 times longer than MP1. *Labium*. MP/LP = 1.25–1.32; LP2 1.08–1.22 times LP1.

Thorax. Spiracles present on mesothorax. *Legs* (Figs 21–22). Metathoracic legs 2.70–3.00 times HW.

Abdomen (Fig. 15). Spiracles present on segments I–VII; LLAS = 0.26–0.37 mm; *siphon* 0.32–0.42 times LLAS. *Urogomphus.* U = 0.81–1.28 mm (U1 = 0.45–0.76 mm); 2.10–2.87 times HW (U1/HW = 1.10–1.67) and 3.00–3.07 times LLAS (U1/LLAS = 1.55–2.14); U1/U2 = 1.28–1.44; U1/U2' = 1.28–1.49; U2'/U2 = 0.91–0.96.

Chatetotaxy. Position and number of secondary setae on legs (Table 3).



FIGURES 16–17. Head capsule of selected species of *Liodessus*, third-instar larva, dorsal aspect: (16) *L. affinis*; (17) *L. crotchi*; not every secondary seta represented. Scale bar = 0.25 mm.

Key to instar III of five species of the genus *Liodessus*

Instar III of Dytiscidae are distinguished from previous instars by the absence of egg bursters on the frontoclypeus and the presence of spiracles on each side of mesothorax and abdominal segments I to VII.

1. Small size, HL < 0.50 mm, profemur with less than 9 ventral secondary setae ..... *L. involucer*
- Larger size, HL > 0.50 mm, profemur with more than 11 ventral secondary setae 2
2. Urogomphomere 1 > 1.40 times HW, Nearctic 3
- Urogomphomere 1 < 1.30 times HW, Neotropical 4
3. Antenna less than 1.30 times as long as labial palpus; procoxa at most with 10 secondary setae; metacoxa at most with 9 secondary setae; metatibia at least with 3 anteroventral secondary setae ..... *L. crotchi*
- Antenna more than 1.30 times as long as length of labial palpus; procoxa at least with 11 secondary setae; metacoxa at least with 10 secondary setae; metatibia with 2 anteroventral secondary setae ..... *L. affinis*
4. Protarsus with 1 ventral secondary seta; metatibia with 9 secondary setae or less; metatarsus with 4 secondary setae or less ..... *L. flavofasciatus*
- Protarsus lacking ventral secondary setae; metatibia with more than 11 secondary setae; metatarsus with more than 5 secondary setae ..... *L. patagonicus*

Description of the larvae of *Liodessus affinis* (Say, 1823)

Source of material

The larvae studied were reared *ex ovo* from adults collected at the following localities: **Canada: Québec,** Trois-Rivières, cattail pond off Boulevard des Récollets, 1km N. boulevard Royal, 10.V.1986; Louiseville, cattail pond at Lac St- Pierre, off Hwy 40, 03.V.1988; **Ontario,** ephemeral pond, 50 km E. Port Perry, 08.V.1990.

Diagnosis (instar III)

Instar III larvae of *L. affinis* are characterized by the following combination of characters: larger size, HL larger than 0.50 mm; antenna more than 1.40 times longer than length of labial palpus; procoxa at least with 11 secondary setae; profemur at least with 11 secondary setae; mesotibia with two anteroventral secondary setae; metacoxa at least with 10 secondary setae; metatibia at most with nine secondary setae; metatarsus at most with four secondary setae; urogomphomere 1 more than 1.40 times as long as HW; Nearctic.

First-instar larva (n = 3).

Color. Larva entirely brown except around stemmata and apical portion of frontoclypeus yellow to pale brown.

Head. HL = 0.31–0.33 mm (mean = 0.32 mm); HW = 0.24–0.26 mm (mean = 0.25 mm); FCL = 0.24–0.26 mm (mean = 0.24 mm); antenna 1.20–1.23 times as long as LP; MN 3.24–3.40 times as long as broad.

Legs. Longest of either primary seta FE8 or FE9 1.16–1.18 times as long as maximum width of metafemur; primary seta TI4 1.47 times as long as maximum width of metatibia.

Abdomen. LLAS = 0.13–0.16 mm (mean = 0.14 mm); siphon 0.50–0.56 times length of last abdominal segment; primary seta AB11 0.33–0.38 times as long as LLAS.

Urogomphus. U = 0.75–0.77 mm (mean = 0.74 mm) (U1 = 0.41–0.42 mm [mean = 0.41 mm]); 3.06–3.18 times as long as HW (U1/HW = 1.66–1.71) and 5.59–5.62 times as long as LLAS (U1/LLAS = 3.01–3.07).

Second-instar larva (n = 3)

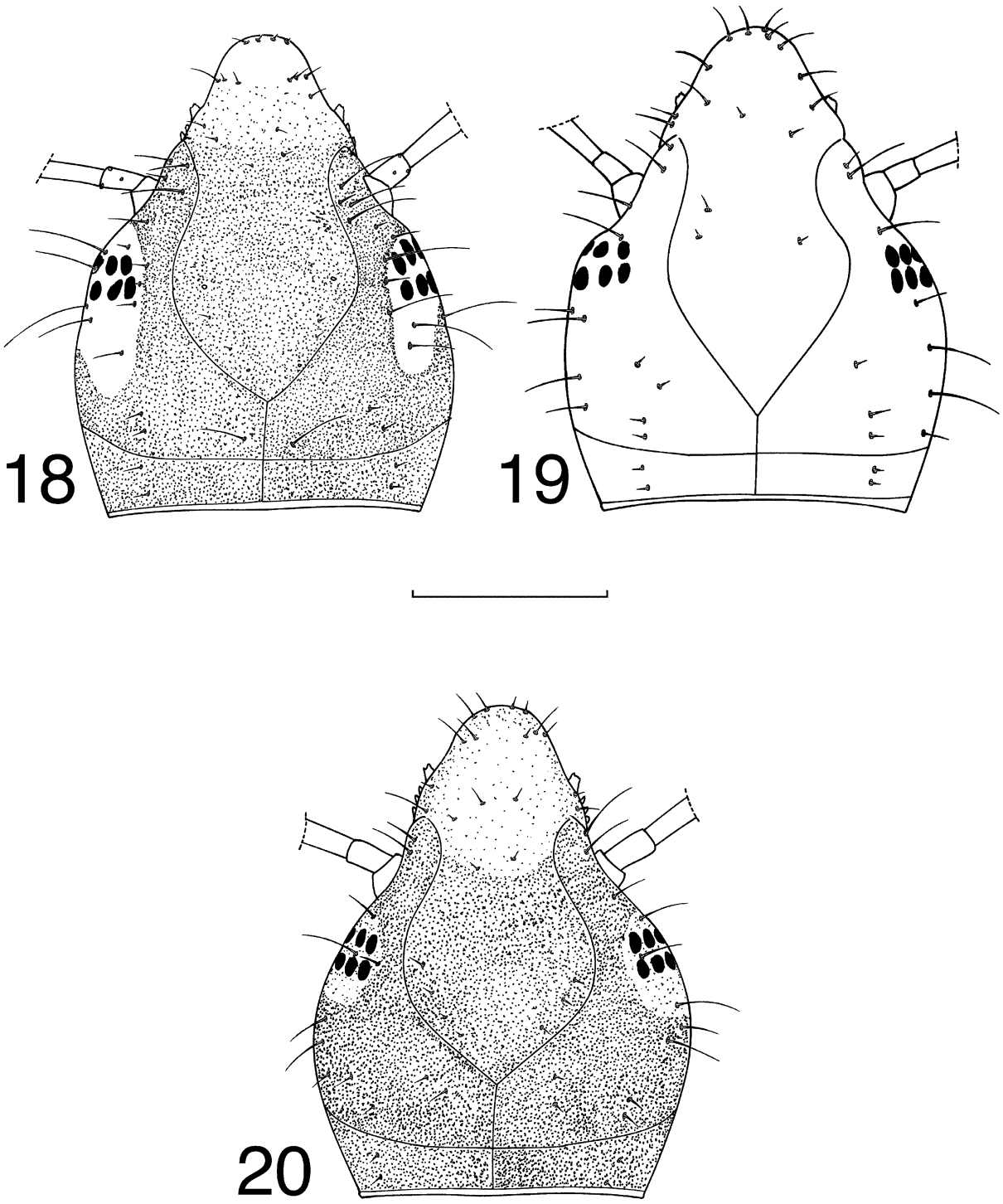
Color. As for first instar, except as follows; head capsule pale brown, parietal with a U-shape dark brown macula along epicranial stem, darker mesally over parietale and occiput; legs creamy white to pale yellow except coxae brownish.

Head. HL = 0.42–0.46 mm (mean = 0.44 mm); HW = 0.33–0.36 mm (mean = 0.35 mm); FCL = 0.34–0.38 mm (mean = 0.36 mm); antenna 1.39–1.46 times as long as LP; mandible 3.12–3.54 times as long as broad.

Legs. Number and position of secondary setae as in Table 3.

Abdomen. LLAS = 0.21–0.23 mm (mean = 0.22 mm); siphon 0.38–0.42 times LLAS.

Urogomphus. U = 1.00–1.02 mm (mean = 1.01 mm) (U1 = 0.55–0.56 mm [mean = 0.55 mm]), 2.82–2.93 times as long as HW (U1/HW = 1.56–1.66) and 4.50–4.64 times as long as LLAS (U1/LLAS = 2.48–2.64).



FIGURES 18–20. Head capsule of selected species of *Liodessus*, third-instar larva, dorsal aspect: (18) *L. flavofasciatus*; (19) *L. involucer*; (20) *L. patagonicus*; not every secondary seta represented. Scale bar = 0.25 mm.

TABLE 3. Number of secondary setae on the legs of second and third instars of *Liodessus affinis* (Say) (AFF), *L. crotchi* Nilsson (CRO), *L. flavofasciatus* (Steinheil) (FLA), *L. involucer* (Brinck) (INV), and *L. patagonicus* (Zimmerman) (PAT); segments of legs: CO = coxa, FE = femur, TA = tarsus, TI = tibia, TR = trochanter; sensillar series: A = anterior, AD = anterodorsal, AV = anteroventral, PD = posterodorsal, Pr = proximal, PV = posteroventral.

		AFF (n = 3)	PAT (n = 3)	FLA (n = 3)	AFF (n = 4)	CRO (n = 5)	PAT (n = 3)	FLA (n = 4)	INV (n = 3)
Segment	Sensillar series	Second Instar			Third Instar				
ProCO	D	2–3	2	2–3	4–6	4–6	3–4	4–5	4–6
	A	0	0	0	0–1	0–1	0–1	0–1	0–1
	V	1	1	1–2	6–7	3–5	6–9	3–6	4–8
	Total	3–4	3	3–5	11–14	8–10	10–14	9–11	10–14
ProTR	Pr	1	1	1	1	1	1	1	1
ProFE	AD	2	2	2	4–5	4–6	5	4–5	3–4
	AV	1	1	1	4–6	3–4	4–5	3–4	2–3
	PD	0	0	0	0	0	0	0	0
	PV	1	1–2	1–2	3	3–4	4–6	3–4	1–3
	Total	4	4–5	4–5	11–14	11–14	13–16	11	7–9
ProTI	AD	0–1	0	0	0–1	0–1	1	0	1
	AV	0	0	0	1	1–2	2	1	0–1
	PD	0	0	0	1–2	1	0	1–2	0–1
	PV	1	1	1	1–2	1–3	2–3	1–3	1–2
	Total	1–2	1	1	4–5	4–5	5–6	4	3–4
ProTA	AD	0	0	0	0	0	0	0	0
	AV	0	0	1	0	0	0	1	0
	PD	1	1	1	1	1	1	1	1
	PV	0	0	0	0	0	0	0	0
	Total	1	1	2	1	1	1	2	1
MesoCO	D	2–3	3–4	2	6–7	4–5	4–6	4–5	3–6
	A	0	0	0	1–2	0	1–2	0–2	0
	V	1–2	1–3	1–2	4–5	4–6	6–7	3–5	1–4
	Total	4	5–6	3–4	11–13	8–11	12–13	7–10	4–9
MesoTR	Pr	1	1	1	1	1	1	1	1
MesoFE	AD	2	2–3	2	4–6	5–6	5–6	4–7	4–5
	AV	1	1	0–1	2–6	2–4	4–5	3	2–4
	PD	0	0	0	0	0	0	0	0
	PV	1–2	2	2	4–5	3–5	5–7	4–5	3–4
	Total	4–5	5–6	4–5	12–15	11–14	15–17	11–15	9–12
MesoTI	AD	1	1	1	1	1–2	1–2	1	1
	AV	1	1	1	2	3–4	2–3	2–3	1–2
	PD	0–1	0	0	1	0–1	1	1	1
	PV	0–1	1	0–1	1–2	2	2–3	1–2	2
	Total	2–4	3	2–3	5–6	6–8	7–8	5–7	5–6
MesoTA	AD	0	0	0	0	0	0	0	0

to be continued.

TABLE 3. (continued)

Segment	Sensillar series	AFF (*n* = 3)	PAT (*n* = 3)	FLA (*n* = 3)	AFF (*n* = 4)	CRO (*n* = 5)	PAT (*n* = 3)	FLA (*n* = 4)	INV (*n* = 3)
		Second Instar			Third Instar				
	AV	0–1	1	1	1	1	1–2	1–2	1
	PD	0–1	1	1	1	1	1	1	1
	PV	0	0–1	0	0	0	1	0	0
	Total	0–2	2–3	2	2	2	3–4	2–3	2
MetaCO	D	2	1–3	1–2	4–7	3–5	4–7	4–5	4–5
	A	0	0	0	1–2	0	0–2	0–1	0
	V	1	1	1–2	5–6	2–5	6–7	4–5	2–5
	Total	3	2–4	3	10–14	6–9	11–14	9–10	6–10
MetaTR	Pr	1	1	1	1–2	1	1–2	1–2	1
MetaFE	AD	2–3	2–3	2–3	6–8	5–8	5–7	6–9	5–6
	AV	2	1–2	1–2	2–6	3–5	4–5	2–5	3–4
	PD	0	0	0	0	0	0	0	0
	PV	2–3	2–3	2–3	5–8	5–6	7–8	6	5–6
	Total	7	6	6–7	14–22	14–17	17–18	15–20	13–15
MetaTI	AD	1–2	1	1	1–2	1–2	1–2	1–2	1–2
	AV	0–2	1	1	2–3	2–3	3–4	2–4	2–3
	PD	1	0	0	1–2	1	2	1–2	1–2
	PV	0–2	1	1	2–3	2–3	4–5	2–3	2
	Total	2–7	3	3	7–9	7–8	11–13	8–9	7–8
MetaTA	AD	0	0	0	0	0	0–2	0	0
	AV	1	1	1–2	2	2	1–2	2–3	2
	PD	1	1	1–2	1	1	1–2	1	1
	PV	0	0–1	0	0–1	0	2	0	0–1
	Total	2	2–3	2–4	3–4	3	5–7	3–4	3–4

Third-instar larva (n = 4) (Fig. 16)

Color. As for second instar.

Head. HL = 0.53–0.56 mm (mean = 0.54 mm); HW = 0.42–0.47 mm (mean = 0.44 mm); FCL = 0.43–0.44 mm (mean =0.43 mm); antenna 1.42–1.49 times as long as LP; mandible 3.40–3.73 times as long as broad.

Legs. Number and position of secondary setae as in Table 3.

Abdomen. LLAS = 0.35–0.37 mm (mean = 0.38 mm); siphon 0.42–0.47 times LLAS.

Urogomphus. U = 1.11–1.21 mm (mean = 1.16 mm) (U1 = 0.62–0.70 mm [mean = 0.66 mm]); 2.64–2.77 times as long as HW (U1/HW = 1.50–1.61) and 3.13–3.30 times as long as LLAS (U1/LLAS = 1.74–1.92).

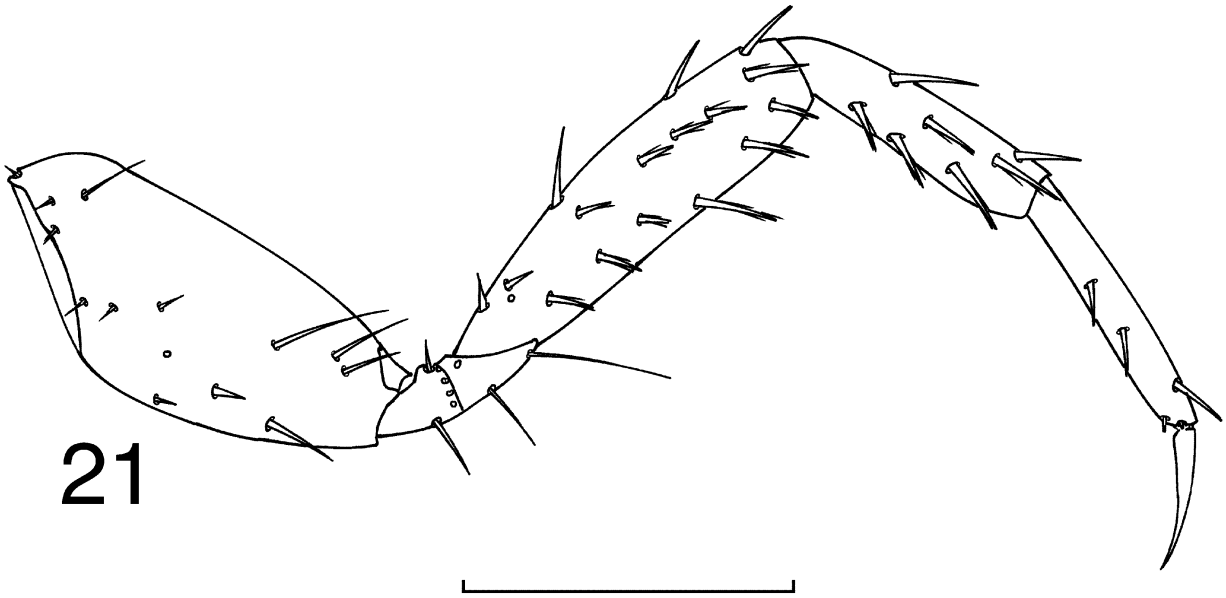
Distribution

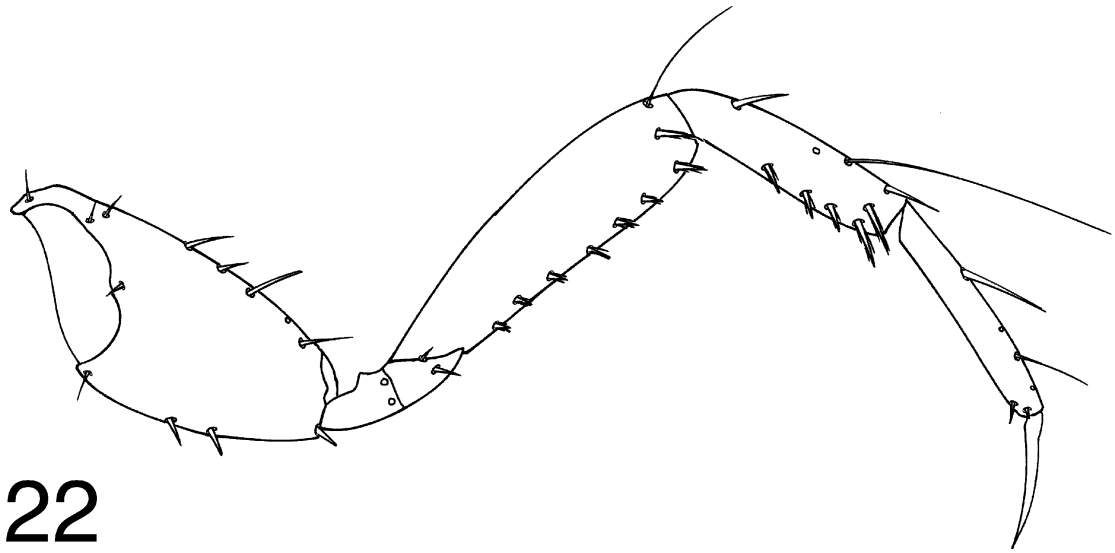
The observed distribution of *Liodessus affinis* is in eastern North America, from Newfoundland south to southwestern Virginia west to eastern Minnesota with sporadic records as far west as Iowa and Kansas (Miller 1998)

Remarks

Superficially instar III larvae of *L. affinis* are likely to be confounded with those of *L. crotchi* because of the similar head capsule color pattern. Larvae of *L. affinis* are distinguished from those of *L. crotchi* by lighter

coloration, shorter antenna when compared to length of labial palpus, and by differences in the number of secondary setae of selected leg articles (Table 3). Matta (1983) compared larvae of *Uvarus granarius* (Aubé) with what may be *L. affinis* larvae from Virginia. However, the larva of *L. affinis* has not been described in adequate detail, and according to Miller (1998), Matta's larvae may have been those of *L. noviaffinis* Miller, 1998.





FIGURES 21–22. *Liodessus flavofasciatus* (third-instar larva), metathoracic legs: (21) anterior surface; (22) posterior surface. Scale bar = 0.25 mm.

Description of the larvae of *Liodessus crotchi* Nilsson, 2001

Source of material

The larvae studied were reared *ex ovo* from adults collected at the following localities: **Canada: Québec,** Saint-Louis de France, Toubière des Grandes Prairies, *Sphagnum* bog covered with *Cassandra calyculata* (L.) and *Carex oligosperma* (Michx.), 26.V.1986, 18.V.1987.

Diagnosis (instar III)

Instar III larvae of *L. crotchi* are characterized by the following combination of characters: larger size, HL larger than 0.50 mm; antenna less than 1.30 times as long as labial palpus; procoxa at most with 10 secondary setae; profemur at least with 11 secondary setae; mesotibia at least with three secondary setae; metacoxa at most with nine secondary setae; metatibia at most with eight secondary setae; metatarsus at most with three secondary setae; urogomphomere 1 more than 1.40 times as long as HW; Nearctic.

First-instar larva

No specimen available for study.

Second-instar larva

No specimen available for study.

Third-instar larva (n = 5) (Fig. 17)

Color. Larva uniformly brown; head capsule predominantly pale brown with a U-shaped dark brown macula along the epicranial stem, dark brown macula mesally over parietale and occiput; head appendages pale brown; legs predominantly dark yellow to pale brown; urogomphus dark brown, urogomphomere 1 yellow proximally, over a short distance.

Head. HL = 0.59–0.62 mm (mean = 0.60 mm); HW = 0.47–0.48 mm (mean = 0.47 mm); FCL = 0.47–0.48 mm (mean = 0.48 mm); antenna 1.25–1.26 times as long as LP; MN 3.25–3.65 times as long as broad.

Legs. Number and position of secondary setae as in Table 3.

Abdomen. LLAS = 0.35–0.37 mm (mean = 0.36 mm); siphon 0.40–0.43 times LLAS.

Urogomphus. U = 1.22–1.28 mm (mean = 1.26 mm) (U1 = 0.69–0.76 mm [mean = 0.73 mm]); 2.60–2.73 times as long as HW (U1/HW = 1.51–1.59) and 3.41–3.70 times as long as LLAS (U1/LLAS = 1.89–2.14).

Distribution

Nearctic. This species has a wide distribution in forested areas of eastern North America, from the boreal regions of Labrador to Saskatchewan, south to Florida and Texas (Miller 1998; Larson *et al*. 2000).

Remarks

See under *L. affinis*.

Description of the larvae of *Liodessus flavofasciatus* (Steinheil, 1869)

Source of material

The larvae studied were collected in association with adults at the following localities: **Argentina:** Jujuy Province: PN Calilegua, 16.XI.2003; Alto Queñoa, 23.XI.2003.

Diagnosis (instar III)

Instar III larvae of *L. flavofasciatus* are characterized by the following combination of characters: larger size, HL larger than 0.50 mm; antenna more than 1.40 times longer than labial palpus; procoxa at most with 11 secondary setae; profemur with 11 secondary setae; mesotibia with at most three anteroventral secondary setae; metacoxa at most with 10 secondary setae; metatibia at most with nine secondary setae; metatarsus at most with four secondary setae; urogomphomere 1 about 1.20 times as long as HW; Neotropical.

First-instar larva (n = 3) (Figs 1–14)

Color. Larva entirely dark brown; head capsule yellow around ocularium; head appendages brown, paler proximally; urogomphus brown, urogomphomere 1 paler proximally over a short distance.

Head (Figs 1–9). HL = 0.30–0.31 mm (mean = 0.31 mm); HW = 0.25–0.26 mm (mean = 0.25 mm); FCL = 0.24 mm; antenna 1.53–1.62 times as long as LP; MN 3.08–3.16 times as long as broad.

Legs (Figs 10–11). Longest of either primary seta FE8 or FE9 1.14–1.27 times as long as maximum width of metafemur; primary seta TI4 2.00–2.14 times as long as maximum width of metatibia.

Abdomen (Figs 12–13). LLAS = 0.14–0.15 mm (mean = 0.14 mm); siphon 0.50–0.63 times LLAS; primary seta AB11 0.38–0.40 times as long as LLAS.

Urogomphus (Fig. 14). U = 0.69–0.71 mm (mean = 0.70 mm) (U1 = 0.39–0.40 mm [mean = 0.39 mm]); 2.70–2.76 times as long as HW (U1/HW = 1.52–1.57) and 4.66–5.04 times as long as LLAS (U1/LLAS = 2.71–2.81).

Second-instar larva (n = 3)

Color. As for first instar except creamy white macula around ocularium broader and frontoclypeus paler apically.

Head. HL = 0.44–0.45 mm (mean = 0.44 mm); HW = 0.35–0.36 mm (mean = 0.35 mm); FCL = 0.35–0.36 mm (mean = 0.35 mm); antenna 1.47–1.53 times as long as LP; MN 3.38–3.85 times as long as broad.

Legs. Number and position of secondary setae as in Table 3.

Abdomen. LLAS = 0.21–0.22 mm (mean = 0.22 mm); siphon 0.40–0.44 times LLAS.

Urogomphus. U = 0.89–0.92 mm (mean = 0.92 mm) (U1 = 0.47–0.50 mm [mean = 0.43 mm]); 2.47–2.62 times as long as HW (U1/HW = 1.32–1.42) and 4.14–4.29 times as long as LLAS (U1/LLAS = 2.09–2.38).

Third-instar larva (n = 4) (Figs 15, 18, 21–22)

Color. As for second instar except as follows: creamy white macula around ocularium larger, expanding posteriorly to level of occipital suture; frontoclypeus pale yellow over anterior half; head appendages predominantly pale yellow, darker over distal articles; legs dark yellow to pale brown; thoracic and abdominal terga paler; urogomphus predominantly yellow to pale brown.

Head (Fig. 18). HL = 0.56–0.59 mm (mean = 0.57 mm); HW = 0.45–0.48 mm (mean = 0.46 mm); FCL = 0.43–0.45 mm (mean =0.44 mm); antenna 1.46–1.50 times as long as LP; MN 3.69–3.80 times as long as broad.

Legs (Figs 21–22). Number and position of secondary setae as in Table 3.

Abdomen. LLAS = 0.32–0.33 mm (mean = 0.32 mm); siphon 0.37–0.40 times LLAS.

Urogomphus. U = 0.97–0.99 mm (mean = 0.98 mm) (U1 = 0.53–0.60 mm [mean = 0.56 mm]); 2.10–2.14 times as long as HW (U1/HW = 1.16–1.33) and 3.03–3.10 times as long as LLAS (U1/LLAS = 1.67–1.86).

Distribution

Neotropical, endemic to Argentina (Young 1969; Nilsson 2001).

Description of the larvae of *Liodessus involucer* (Brinck, 1948)

Source of material

The larvae studied were collected in association with adults at the following locality: **South Atlantic,** Inaccessible Island, 23.X.1989.

Diagnosis (instar III)

Instar III larvae of *L. involucer* are characterized by the following combination of characters: smaller size, HL less than 0.50 mm; antenna more than 1.40 times as long as labial palpus; procoxa at least with 10 secondary setae; profemur at most with nine secondary setae; mesotibia at most with two secondary setae; metacoxa

at most with 10 secondary setae; metatibia at most with eight secondary setae; metatarsus at most with four secondary setae; urogomphomere 1 less than 1.30 times as long as HW; Neotropical.

First-instar larva

No specimen available for study.

Second-instar larva

No specimen available for study.

Third-instar larva (n = 3) (Fig. 19)

Color. Uniformly creamy white to pale yellow.

Head (Fig. 19). HL = 0.46–0.48 mm (mean = 0.47 mm); HW = 0.37–0.38 mm (mean = 0.37 mm); FCL = 0.37–0.39 mm (mean = 0.37 mm); antenna 1.42–1.44 times as long as LP; MN 3.04–3.41 times as long as broad.

Legs. Number and position of secondary setae as in Table 3.

Abdomen. LLAS = 0.26–0.27 mm (mean = 0.27 mm); siphon 0.30–0.39 times LLAS.

Urogomphus. U = not available (U1 = 0.42–0.45 mm [mean = 0.43 mm]); U1/HW = 1.15–1.19; U1/LLAS = 1.55–1.74.

Distribution

Neotropical, endemic to Tristan da Cunha island group (Young 1969; Nilsson 2001).

Remarks

Larvae of *L. involucer* are unique among the species studied by its smaller size and presence of less than nine secondary setae on the profemur.

Description of the larvae of *Liodessus patagonicus* (Zimmermann, 1923)

Source of material

The larvae studied were collected in association with adults at the following locality: **Argentina:** Chubut Province, road to Los Cipreses, km 58, 375 masl, 12.II.2004.

Diagnosis (instar III)

Instar III larvae of *L. patagonicus* are characterized by the following combination of characters: larger size, HL larger than 0.50 mm; antenna more than 1.40 times longer than labial palpus; procoxa at least with 10 secondary setae; profemur with at least 13 secondary setae; mesotibia with at most three anteroventral secondary setae; metacoxa at least with 11 secondary setae; metatibia at least with 11 secondary setae; metatarsus at least with five secondary setae; urogomphomere 1 less than 1.40 times as long as HW; Neotropical.

First-instar larva

No specimen available for study.

Second-instar larva (n = 3)

Color. Uniformly dark brown except as follows: head capsule dark yellow to pale brown around ocularium; antenna slightly paler apically; urogomphus dark brown, urogomphomere 1 slightly paler proximally over a short distance.

Head. HL = 0.46–0.47 mm (mean = 0.46 mm); HW = 0.35–0.36 mm (mean = 0.35 mm); FCL = 0.35–0.36 mm (mean =0.35 mm); antenna 1.45–1.54 times as long as LP; MN 3.47–3.63 times as long as broad.

Legs. Number and position of secondary setae as in Table 3.

Abdomen. LLAS = 0.22–0.23 mm (mean = 0.22 mm); siphon 0.40–0.45 times LLAS.

Urogomphus. U = 1.02–1.06 mm (mean = 1.05 mm) (U1 = 0.53–0.61 mm [mean = 0.57 mm]); 2.89–2.94 times as long as HW (U1/HW = 1.58–1.71) and 4.65–4.75 times as long as LLAS (U1/LLAS = 2.41–2.69).

Third-instar larva (n = 3) (Fig. 20)

Color. As for second instar.

Head (Fig. 20). HL = 0.58–0.60 mm (mean = 0.59 mm); HW = 0.45–0.47 mm (mean = 0.46 mm); FCL = 0.45–0.47 mm (mean = 0.46 mm); antenna 1.43–1.52 times as long as LP; MN 3.52–3.94 times as long as broad.

Legs. Number and position of secondary setae as in Table 3.

Abdomen. LLAS = 0.30–0.32 mm (mean = 0.31 mm); siphon 0.32–0.33 times LLAS.

Urogomphus. U = 0.97–1.02 mm (mean = 1.01 mm) (U1 = 0.56–0.63 mm [mean = 0.60 mm]); 2.14–2.27 times as long as HW (U1/HW = 1.25–1.33) and 3.20–3.29 times as long as LLAS (U1/LLAS = 1.87–1.98).

Distribution

Neotropical, endemic to Argentina (Young 1969; Nilsson 2001).

Remarks

Third instar larvae of *L. patagonicus* are unique among the species studied by the larger number of secondary setae both on metatibia and metatarsus (Table 3).

Discussion

Knowledge of bidessine larvae is poor. In part because of this, and also to develop a system useful for phylogenetic analysis, a system of nomenclature of larval chaetotaxy was devised (Alarie 1991; Alarie *et al.* 1990; Alarie & Harper 1990; Alarie & Michat 2007a). Such a framework was particularly useful in studies of larval morphology of the bidessine genera *Liodessus* (this paper), *Amarodytes* Régimbart, 1900 (Michat & Alarie 2006), *Anodocheilus* Babington, 1841 (Michat & Torres 2006), *Glareadessus* Wewalka & Biström, 1998 (Alarie & Wewalka 2001), and *Hypodessus* Guignot, 1939 (Michat & Alarie 2007) and has contributed towards the formulation of several hypotheses of phylogeny. At the present time, only one character (the absence of the primary pore ABc) supports a monophyletic origin of these genera (Michat & Alarie 2007). Pore ABc is consistently present in larvae of the remaining Hydroporinae (Alarie & Michat 2007b; Michat *et al*. 2007). Within this group, *Liodessus* differs from other genera by absence of the primary pore PAj. Moreover, larvae of *Liodessus* share with those of *Anodocheilus* the absence of a ventroapical spinula on the third antennomere (Michat & Torres 2006).

Other Bidessini genera are known as larvae [*Allodessus* Guignot, 1953 (Watts 1963); *Bidessus* Sharp, 1882 (Nilsson 1985), *Limbodessus* Guignot, 1939 (Watts 1963), *Neoclypeodytes* Young, 1967 (Perkins 1980), and *Uvarus* Guignot 1939 (Matta 1983); brief descriptions of some other genera are summarized in Bertrand (1972) and references therein]. However, only the third instar larvae of these genera were described, and lack of detail of chaetotaxic characters does not allow making in-depth comparisons with *Liodessus*. Considering all known bidessine larvae, however, *Liodessus* is more similar to *Hypodessus*, *Amarodytes*, *Glareadessus*, *Allodessus*, and *Neoclypeodytes*, all these genera sharing a short siphon and an elongate first urogomphomere.

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