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Larval morphology of *Allodessus* Guignot (Coleoptera: Dytiscidae)

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The three larval instars of the type species of the bidessine genus *Allodessus* Guignot (*A. bistrigatus* (Clark)) are described and illustrated for the first time including detailed morphometric and chaetotaxic analyses of the cephalic capsule, head appendages, legs, last abdominal segment and urogomphi. Larvae of this genus are characterised by the absence of the primary pore ABc, which is a synapomorphy of the tribe Bidessini, and the presence of secondary setae on the urogomphi, which suggest a close phylogenetic relationship with *Amarodytes* Régimbart. *Allodessus* larvae are further characterised by a short last abdominal segment, long urogomphi, absence of colour pattern on the body, presence of a ventroapical spinula on the third antennomere, presence of pore PAk, presence of posterior secondary setae on coxa, presence of a large number of secondary setae on coxa, presence of posteroventral secondary setae on tarsus, and presence of a total of 6–7 (instar II) and 7–11 (instar III) secondary setae on metatarsus. This combination of characters separates larvae of *Allodessus* from those of the other known Bidessini genera.

Keywords: diving beetles; Bidessini; larva; morphometry; chaetotaxy; phylogenetic relationships

Introduction

The genus *Allodessus* Guignot was created to include small diving beetles (adult length < 3.5 mm) previously placed in the genus *Bidessus* Sharp (Watts 1978; Biström 1988). Originally, a single species (*A. bistrigatus* (Clark)) was placed in *Allodessus*, and for a long time the genus was monotypic until Balke and Ribera (2004) transferred four additional species from the genera *Bidessus* and *Liodessus* Guignot, thus increasing to five the number of species included in the genus. As presently defined, *Allodessus* has a wide geographical range, with *A. bistrigatus* being widespread in Australia and Tonga (Watts 1978, 1985; Balke and Ribera 2004) and the remaining species occupying more restricted ranges in the east Palaearctic, central Java, mainland New Zealand, Kermadec Island and Easter Island (Balke and Ribera 2004). It has been suggested that some of the species

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currently included in *Allodessus* may eventually prove to be conspecific (Balke and Ribera 2004).

Allodessus belongs to the subfamily Hydroporinae, and within this assemblage it is placed in the tribe Bidessini (Nilsson 2001). Within the Bidessini, *Allodessus* was hypothesised by Balke and Ribera (2004) to share a sister-group relationship with *Limbodessus* Guignot, which represents a large and morphologically diverse genus including both epi- and hypogaeic species (see Watts and Humphreys 2009 and references therein). Sequence data for *Allodessus* and its relatives were also presented by Leys, Watts, Cooper and Humphreys (2003), Hendrich and Balke (2009) and Hendrich, Hawlitschek and Balke (2009), and confirm a close relationship between *Allodessus* and *Limbodessus*.

Despite the fact that Bidessini represent one of the most significant radiations of diving beetles, with about 40 genera and 600 species (Nilsson 2001, 2003, 2004; Nilsson and Fery 2006), larval morphology of members of this tribe remains very imperfectly known. So far, the larvae of only 13 genera are known (Meuche 1937; Watts 1963; Bertrand 1972; Perkins 1980; Richoux 1982; Matta 1983; Nilsson 1985; Alarie and Wewalka 2001; Michat and Alarie 2006, 2008; Michat and Torres 2006; Alarie, Michat, Archangelsky and Barber-James 2007), some of them very superficially, and the larvae of about 2/3 of the genera are unknown. Regarding *Allodessus*, only a very brief description of the mature larva is available (Watts 1963). As demonstrated recently, larval chaetotaxy is a particularly significant source of characters for the study of the phylogenetic relationships within the Bidessini (Michat and Alarie 2008), and the development of a system of nomenclature to name primary sensilla (setae and pores) in first-instar larvae of the Hydroporinae (Alarie and Harper 1990; Alarie, Harper and Maire 1990; Alarie 1991; Alarie and Michat 2007a) has brought great progress because it allows the exploration of an extensive set of characters that is phylogenetically very useful.

In this context, the finding of all larval instars of *A. bistrigatus* (the type species of *Allodessus*) is of the utmost interest as it allows us to provide, for the first time, detailed descriptions of the morphometry and chaetotaxy of *Allodessus* and to compare the ground plan pattern of larval features of this genus with those of other Bidessini genera for which the larvae have been described. Also, we explore the phylogenetic relationships of *Allodessus* in the context of a previous cladistic analysis of the tribe Bidessini (Michat and Alarie 2008).

Materials and methods

Material

Four specimens of instar I, three of instar II and three of instar III were used for the descriptions. Larvae were collected in association with adults at the following locality: South Australia, Clifton Hills, Stn. 9.7 km W Scorpion Dam, 10-IV-2000.

Methods

Specimens were cleared in lactic acid, dissected and mounted on glass slides with polyvinyl-lacto-glycerol. Observation (at magnifications up to $1000\times$) and drawings were made using an Olympus CX31 compound microscope equipped with a camera lucida. Drawings were scanned and digitally edited. The material is held in the collection of the South Australian Museum.

Morphometric analysis

We employed, with minimal modifications and additions, the terms used in previous papers dealing with larval morphology of Hydroporinae (Alarie and Michat 2007b; Michat, Alarie, Torres and Megna 2007; Michat and Torres 2008; Alarie, Michat and Watts 2009). Three specimens of each instar were measured. The following measurements were taken (with abbreviations shown in parentheses): total body length (excluding urogomphi) (TL); maximum body width (MW); head length (HL) (total head length including the frontoclypeus, measured medially along the epicranial stem); maximum head width (HW); length of frontoclypeus (FRL) (from apex of nasale to the joint of frontal and coronal sutures); occipital foramen width (OCW) (maximum width measured along dorsal margin of occipital foramen); coronal line length (COL); length of mandible (MNL) (measured from laterobasal angle to apex); width of mandible (MNW) (maximum width measured at base). Lengths of antenna (A), maxillary (MP) and labial (LP) palpi were obtained by adding the lengths of the individual segments; each segment 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 the third antennomere. Length of leg (L), including the longest claw (CL), was obtained by adding the lengths of the individual segments; each leg is denoted by the letter L followed by a number (e.g. L1, prothoracic leg). The length of trochanter includes only the proximal portion, the length of distal portion is included in the femoral length. The legs of the larvae studied were considered as being composed of six segments following Lawrence (1991). Dorsal length of last abdominal segment (LAS) was measured along midline from anterior to posterior margin. Length of urogomphus (U) was derived by adding the lengths of the individual segments; each segment is denoted by the letter U followed by a number (e.g. U1, first urogomphomere). These measurements were used to calculate several ratios that characterise body shape.

Chaetotaxic analysis

Primary (present in first-instar larva) and secondary (added in later instars) setae and pores were distinguished on 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 the first-instar larva of *A. bistrigatus* were labelled by comparison with the ground-plan of chaetotaxy of the subfamily Hydroporinae (Alarie and Harper 1990; Alarie et al. 1990; Alarie 1991; Alarie and Michat 2007a). Homologies were recognised using the criterion of similarity of position (Wiley 1981). Setae located at the apices of the maxillary and labial palpi were extremely difficult to distinguish due to their position and small size. Accordingly, they are not well represented in the drawings.

Results

Description of the larvae of Allodessus bistrigatus (Clark)

Diagnosis

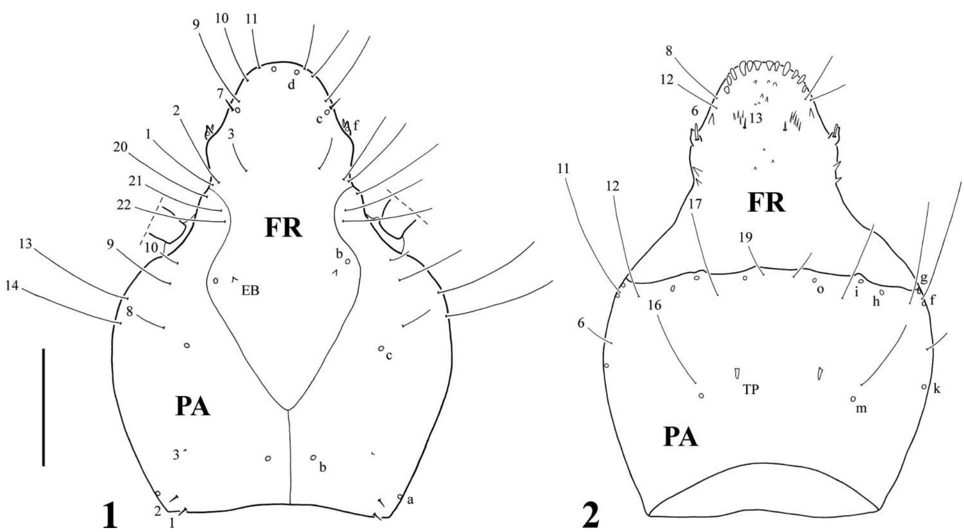
Larvae of *Allodessus* are characterised by the following combination of characters: occipital suture present from instar II (Figure 15); nasale moderately elongate, subtriangular, with small lateral branches (Figures 1–2, 15); A3 with a ventroapical spinula (Figure 4); cardo fused to stipes (Figure 7); galea absent; prementum without lateral spinulae (Figures 8–9); abdominal segment VI membranous ventrally; siphon short (Figures 12–13); pores PAd, PAe and PAj absent (Figures 1–2); pore ANf absent (Figures 3–4); seta TR2 and pore FEa absent (Figures 10–11); seta TI7 short, spine-like (Figure 11); pores ABa and ABc absent (Figure 12); seta AB10 spine-like (Figure 13); setae UR2, UR3 and UR4 inserted far from each other (Figure 14); seta UR8 inserted distally (Figures 14, 18); legs without natatory setae (Figures 10–11, 16–17); U with secondary setae (Figure 18); presence of posterior secondary setae on CO, a large number of secondary setae on CO, posteroventral secondary setae on TA, and a total of 6–7 (instar II) and 7–11 (instar III) secondary setae on metaTA (Table 1); ratios A3/A1, A3/A2, MP2/MP1 and LAS/HW (Table 2).

First-instar larva

Colour. Uniformly pale, unpigmented.

Body. Subcylindrical, narrowing towards abdominal apex. Measurements and ratios that characterise the body shape are shown in Table 2.

Head. Head capsule (Figures 1–2). Longer than broad; posterolateral surface covered with minute spinulae; maximum width posterior to stemmata, without neck constriction; occipital suture absent; ecdysial line well marked, coronal line short;



Figures 1–2. *Allodessus bistrigatus*, first-instar larva: (1) cephalic capsule, dorsal aspect; (2) cephalic capsule, ventral aspect. EB, egg burster; TP, tentorial pit. Scale bar = 0.10 mm.

Table 1. Number and position of secondary setae on the legs of larvae of *Allodessus bistrigatus*. Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively.

Segment	Position	Instar II ($n = 3$)	Instar III ($n = 3$)
Coxa	A	0–1 / 1–4 / 2–4	5–9 / 8–10 / 6–10
	AD	0 / 0 / 0	5–7 / 7–11 / 6–11
	P	0 / 0–1 / 1–4	1–3 / 5–11 / 9–16
	PD	4 / 4–5 / 4–6	6–13 / 5–15 / 6–13
	V	2–3 / 2–4 / 1–4	6–8 / 6–11 / 8–13
	Total	6–8 / 8–13 / 13–15	25–36 / 33–54 / 47–56
Trochanter	Pr	0 / 1 / 1	0 / 1 / 1–2
	Total	0 / 1 / 1	0 / 1 / 1–2
Femur	AD	1–2 / 2 / 2–3	2 / 2 / 2–3
	AV	3–4 / 3–4 / 3–5	7–8 / 7 / 8–11
	PV	0 / 1–3 / 5	1–5 / 5–6 / 9–12
	Total	5 / 6–8 / 10–13	11–14 / 14–15 / 22–24
Tibia	AD	0 / 1 / 1–2	0 / 1–2 / 1–3
	AV	0 / 1–2 / 1–2	0 / 1–3 / 3–4
	PD	0 / 1 / 1	1 / 2 / 2–3
	PV	0 / 1–2 / 1–2	1 / 3 / 3–4
	Total	0 / 4–5 / 4–6	2 / 8–9 / 11–12
Tarsus	AV	0 / 1 / 2	0 / 1–2 / 2–4
	PD	0 / 1 / 2	0 / 1–2 / 2–3
	PV	1 / 1 / 2–3	1 / 1–2 / 2–4
	Total	1 / 3 / 6–7	1 / 4–6 / 7–11

A = anterior, D = dorsal, P = posterior, Pr = proximal, V = ventral. Total = total number of secondary setae on the segment (excluding primary setae).

occipital foramen broadly emarginate ventrally; posterior tentorial pits visible ventrally; FR elongate, lateral margins sinuate, with two lateral, spine-like egg bursters at mid-length; nasale moderately elongate, subtriangular, rounded apically, sinuate laterally, with one small branch at each side; ventrodistal surface with spinulae of different shapes, ventrolateral margin with robust spinulae (Figure 2); anteroventral margin of nasale with a half circle of 12 short spatulate setae of different lengths, directed downward; we were unable to see the stemmata though they most probably are present. Antenna (Figures 3–4). Elongate, composed of four antennomeres, shorter than HW; A1 the shortest, A3 the longest, with a ventroapical spinula; A3' relatively short. Mandible (Figure 5). Prominent, broad basally, distal half projected inwards and upwards, apex sharp; mandibular channel present. Maxilla (Figures 6–7). Cardo fused to stipes; stipes short, broad; galea and lacinia absent; MP elongate, composed of three palpomeres, MP3 the shortest, MP2 the longest. Labium (Figures 8–9). Prementum small, subtrapezoidal, about as long as broad, without lateral spinulae, anterior margin slightly indented medially; LP elongate, composed of two palpomeres; LP2 longer than LP1.

Thorax. Terga convex, pronotum slightly shorter than meso- and metanotum combined, meso- and metanotum subequal; protergite subovate, margins rounded, more developed than meso- and metatergite; meso- and metatergite transverse; all sclerites without anterotransverse carina; sagittal line not visible; sterna membranous; spiracles absent. Legs (Figures 10–11). Long, composed of six articles, L1 the shortest, L3 the longest; CO robust, elongate, TR divided into two parts, FE, TI and

Table 2. Measurements and ratios for the three larval instars of *Allodessus bistrigatus*.

Measure	Instar I ($n = 3$)	Instar II ($n = 3$)	Instar III ($n = 3$)
HL (mm)	0.37–0.38	0.54–0.58	0.79–0.81
HW (mm)	0.27–0.29	0.42–0.43	0.60–0.62
FRL (mm)	0.30	0.44–0.47	0.62–0.64
OCW (mm)	0.17–0.19	0.28–0.31	0.45–0.48
HL/HW	1.31–1.39	1.28–1.39	1.29–1.30
HW/OCW	1.46–1.66	1.39–1.52	1.29–1.40
COL/HL	0.19–0.21	0.18–0.22	0.20–0.22
FRL/HL	0.79–0.81	0.78–0.82	0.78–0.80
A/HW	0.78–0.89	0.71–0.75	0.63–0.67
A3/A1	2.13–2.57	2.00–2.30	1.73–2.00
A3/A2	1.31–1.50	1.05–1.15	0.90–0.93
A4/A3	0.47–0.61	0.43–0.50	0.41–0.46
A3'/A4	0.36–0.50	0.40–0.50	0.67–0.73
MNL/MNW	3.45–3.80	3.80–4.21	3.81–4.10
MNL/HL	0.50–0.51	0.50–0.51	0.50–0.52
A/MP	1.32–1.45	1.20–1.31	1.15–1.19
MP2/MP1	1.45–1.70	1.05–1.22	0.81–0.90
MP2/MP3	2.29–2.43	2.10–2.63	2.36–2.60
MP/LP	1.17–1.26	1.26–1.31	1.31–1.36
LP2/LP1	1.80–2.00	1.29–1.53	1.08–1.13
L3 (mm)	0.87–0.92	1.28–1.31	1.78–1.85
L3/L1	1.29–1.31	1.34–1.38	1.37–1.42
L3/L2	1.12–1.17	1.15–1.17	1.17–1.20
L3/HW	3.03–3.45	3.05–3.08	2.86–3.05
L3 (CO/FE)	1.05–1.10	0.97–1.02	1.00
L3 (TI/FE)	0.68–0.70	0.65–0.67	0.65–0.67
L3 (TA/FE)	0.78–0.81	0.71–0.74	0.65–0.67
L3 (CL/TA)	0.63–0.68	0.57–0.59	0.51–0.55
LAS (mm)	0.14–0.16	0.24–0.25	0.41–0.45
LAS/HW	0.52–0.55	0.58	0.66–0.71
U (mm)	0.85–0.92	1.18–1.26	1.49–1.51
U/LAS	5.38–6.61	4.78–5.20	3.38–3.73
U/HW	2.97–3.43	2.78–3.00	2.41–2.51
U1/U2	1.46–1.53	1.68–1.81	1.85–2.00

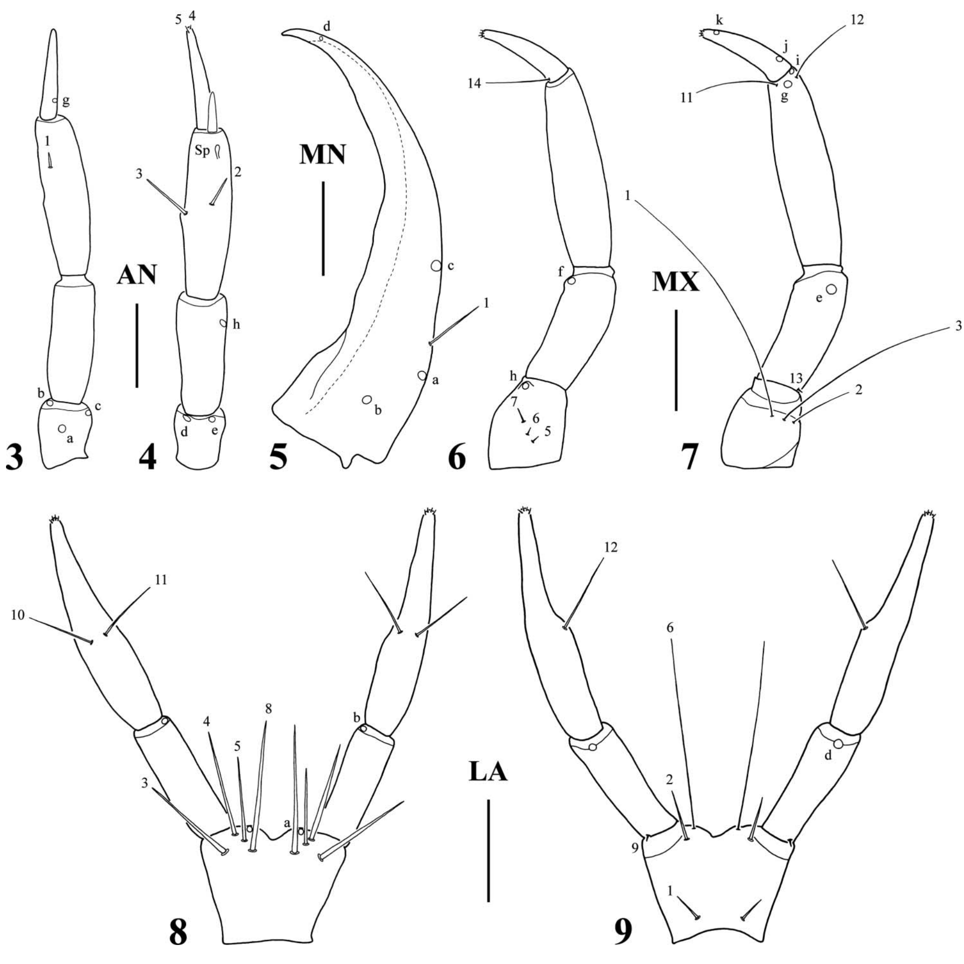
TA slender, subcylindrical, PT with two long, slender, slightly curved claws; posterior claw shorter than anterior claw on L1 and L2, posterior claw longer than anterior claw on L3; most surface of legs covered with minute slender spinulae in transverse rows; ventral surface of TA and to a lesser extent TI with elongate spinulae.

Abdomen. Eight-segmented; segments I–VI sclerotised dorsally, membranous ventrally; segment VII sclerotised both dorsally and ventrally, with ventral sclerite independent from dorsal sclerite; tergites I–VII narrow, transverse, rounded laterally, without sagittal line; all sclerites without anterotransverse carina, covered with minute spinulae in transverse rows; spiracles absent on segments I–VII; LAS (Figures 12–13) the longest, completely sclerotised, ring-like, covered with minute spinulae in transverse rows; siphon short, subconical. Urogomphus (Figure 14). Very long, composed of two urogomphomeres; U1 long, much longer than LAS, covered with minute spinulae except on distal portion; U2 narrow, setiform, shorter than U1.

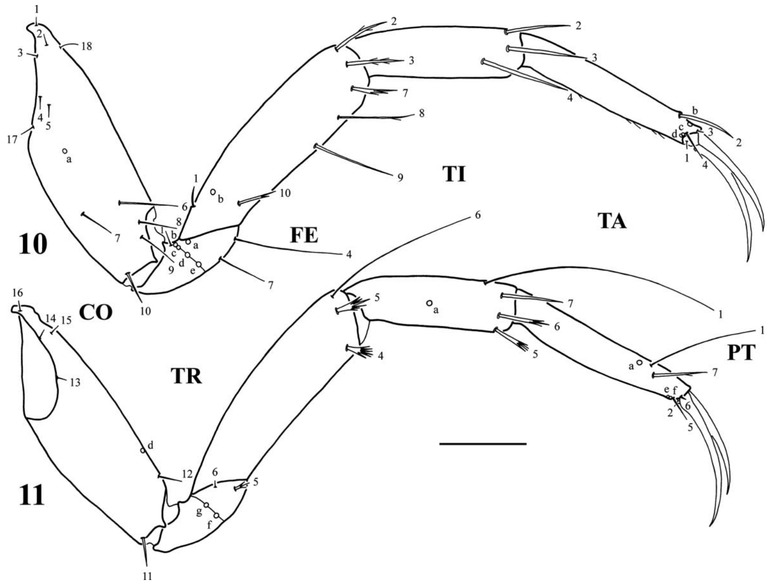
Chaetotaxy. Similar to that of generalised Hydroporinae larva (Alarie and Harper 1990; Alarie et al. 1990; Alarie 1991; Alarie and Michat 2007) except for the following features: pore FRc submarginal, contiguous to seta FR7; pores PAd, PAe and PAj absent; pore PAg present; pore ANf absent; pore ANh distal; setae MX4, MX8, MX9 and MX10 absent; seta MX1 inserted distally on the stipes; seta LA7 absent; seta TR2 absent; pore FEa absent; several setae on FE and TI multi-branched; seta TI7 short, spine-like; pores ABa and ABc absent; seta AB10 spine-like; we were unable to find pore ABd and setae AB7 and AB8; however, we could not establish if they are really absent due to the presence of spinulae on the siphon; setae UR2, UR3 and UR4 inserted far from each other; setae UR5, UR6 and UR7 elongate; seta UR8 inserted distally.

Second-instar larva

As for first-instar larva except for the following features:



Figures 3–9. *Allodessus bistrigatus*, first-instar larva: (3) antenna, dorsal aspect; (4) antenna, ventral aspect; (5) mandible, dorsal aspect; (6) maxilla, dorsal aspect; (7) maxilla, ventral aspect; (8) labium, dorsal aspect; (9) labium, ventral aspect. Sp, spinula. Scale bars = 0.04 mm.



Figures 10–11. *Allodessus bistrigatus*, first-instar larva: (10) metathoracic leg, anterior aspect; (11) metathoracic leg, posterior aspect. Scale bar = 0.07 mm.

Body. Measurements and ratios that characterise the body shape are shown in Table 2.

Head. Head capsule. Spinulae restricted to lateral margins; occipital suture present; egg bursters absent; nasale slightly sinuate laterally; anteroventral margin of nasale with 25 short, spatulate setae; six dorsolateral stemmata at each side forming a circle. Antenna. A1 and A4 the shortest, subequal, A2 and A3 the longest, subequal. Maxilla. MP1 and MP2 the longest, subequal.

Thorax. Meso- and metatergite with anterotransverse carina; sagittal line slightly visible. *Legs*. Elongate ventral spinulae restricted to proTA and distal portion of mesoTA.

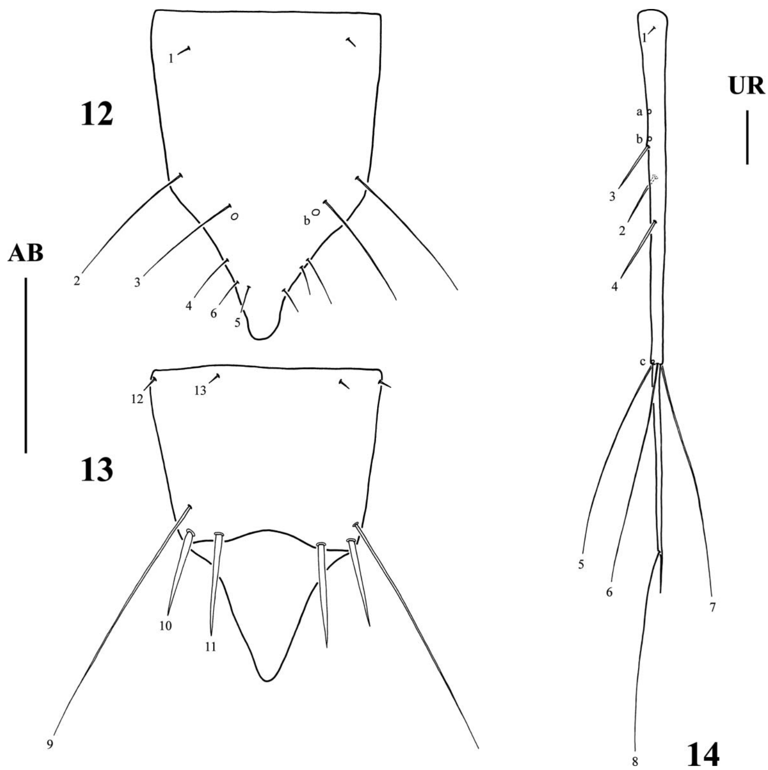
Abdomen. Segment VII completely sclerotised, ring-like; all sclerites with anterotransverse carina.

Chaetotaxy. Head capsule with numerous secondary setae; parietal with 1–4 short, spine-like, secondary setae on each lateroventral margin; MN with one hair-like, secondary seta on basoexternal margin; thoracic tergites with numerous secondary setae; secondary leg setation detailed in Table 1; abdominal sclerites I–VII with several secondary setae on posterior half; LAS and U1 with several spine-like secondary setae.

Third-instar larva

As for second-instar larva except for the following features:

Colour. Somewhat darker in general, mandible light brown.



Figures 12–14. *Allodessus bistrigatus*, first-instar larva: (12) abdominal segment VIII, dorsal aspect; (13) abdominal segment VIII, ventral aspect; (14) urogomphus, dorsal aspect. Scale bars = 0.08 mm.

Body. Measurements and ratios that characterise the body shape are shown in Table 2.

Head (Figure 15). Head capsule. Anteroventral margin of nasale with 48–50 short, spatulate setae. Antenna. A3' more elongate. Maxilla. MP1 the longest. Labium. LP1 and LP2 subequal in length.

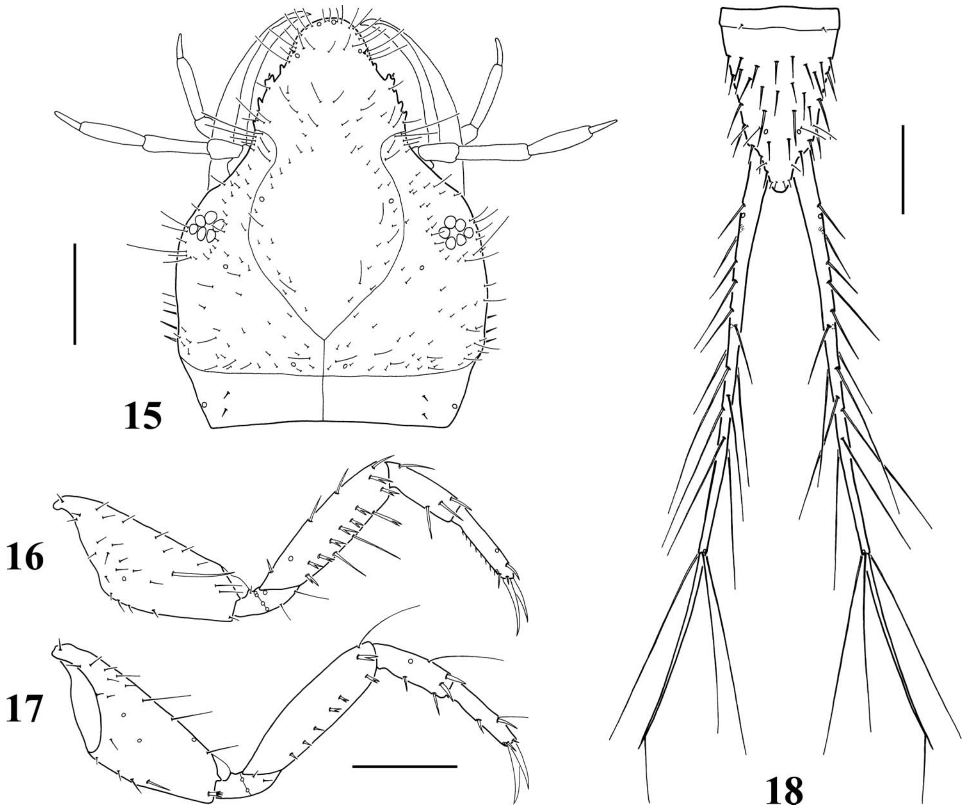
Thorax. Sagittal line well visible on pro- and mesotergite; spiracles present on mesothorax.

Abdomen. Spiracles present on segments I–VII.

Chaetotaxy. Secondary setation on cephalic capsule, thoracic and abdominal sclerites more abundant; parietal with 3–5 short, spine-like, secondary setae on each lateroventral margin; secondary leg setation detailed in Table 1 and Figures 16–17; secondary setation on LAS and U detailed in Figure 18.

Discussion

Larvae of *Allodessus* are characterised by the absence of the primary pore ABc on the last abdominal segment. This character state is unique within the subfamily



Figures 15–18. *Allodessus bistrigatus*, third-instar larva: (15) head, dorsal aspect; (16) prothoracic leg, anterior aspect; (17) prothoracic leg, posterior aspect; (18) abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.20 mm.

Hydroporinae and has been proposed as a synapomorphy of the tribe Bidessini (Michat and Alarie 2008). The urogomphal setae UR2, UR3 and UR4 inserted far from each other on the first urogomphomere and the seta UR8 inserted subapically on the second urogomphomere are also distinctive of *Allodessus* and the remaining Bidessini genera known in detail. However, these two latter character states should not be viewed as strong evidence of a monophyletic origin of the Bidessini since they are present also in several genera of the tribe Hydroporini (Michat and Alarie 2008).

A highly distinctive feature of *Allodessus* larvae is the presence of secondary setae on the urogomphi (see also Watts 1963). Within Bidessini, a similar character state is present only in *Amarodytes* Régimbart (Michat and Alarie 2006), thus favouring the hypothesis of a close phylogenetic relationship of both genera. To explore this hypothesis in more detail, we reanalysed the data matrix of Michat and Alarie (2008) with exactly the same parameters but including *Allodessus* in the ingroup. The topology of the consensus tree (Figure 19) remained unaltered, with the obvious inclusion of *Allodessus*, and the support values were increased for several nodes but not for the Bidessini clade which remained poorly supported. In this tree, Bidessini was monophyletic and *Allodessus* was resolved as part of a basal polytomy along with *Amarodytes* and a clade formed by the genera *Glareadessus* Wewalka and Biström, *Hypodessus* Guignot, *Liodessus* and *Anodocheilus* Babington. *Allodessus*

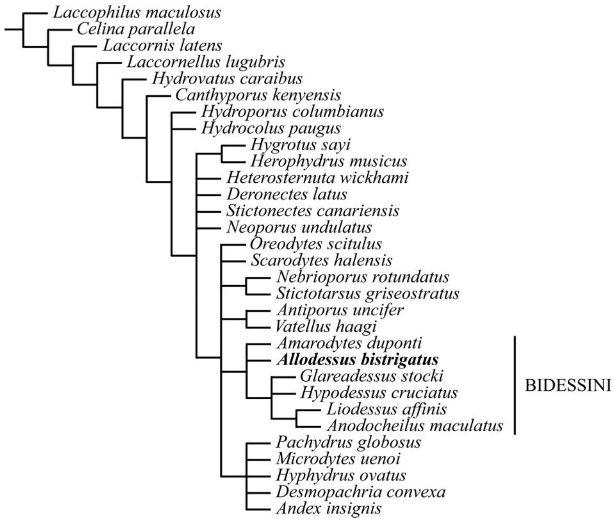


Figure 19. Strict consensus cladogram of 100 most parsimonious cladograms obtained through the reanalysis of the data matrix presented by Michat and Alarie (2008), with the objective of showing the phylogenetic position of *Allodessus* (in bold lettering).

and *Amarodytes* did not form a clade and therefore the shared presence of urogomphal secondary setae (character 39 in Michat and Alarie 2008) should not be interpreted as a synapomorphy for both genera. However, the unresolved basal position of these genera leaves open the question of whether or not to consider them more closely related, and therefore the relationships of *Allodessus* would benefit from being tested in a future, more comprehensive analysis including more characters and taxa. The presence of a ventroapical spinula on the third antennomere (character 12 in Michat and Alarie 2008) separates *Allodessus* from *Anodocheilus* and *Liodessus* (Michat and Torres 2006; Alarie et al. 2007), and the presence of pore PAk on the parietal (not included in Michat and Alarie 2008 because it is uninformative) separates *Allodessus* from *Amarodytes* (Michat and Alarie 2006).

The sequence data place *Allodessus* as either the sister group to *Limbodessus* (Leys et al. 2003; Balke and Ribera 2004; Hendrich and Balke 2009) or possibly within this genus (Hendrich et al. 2009). Unfortunately, little is known of the larval morphology of *Limbodessus* except for a brief description of *L. amabilis* (Clark) (Watts 1963). Despite the brief description, *Allodessus* clearly differs from *Limbodessus* in the presence of secondary setae on the urogomphi, suggesting a sister-group relationship rather than being subordinated within *Limbodessus*.

Some genera (such as *Neoclypeodytes* Young and *Uvarus* Guignot) could not be included in the cladistic analysis of Michat and Alarie (2008) because their larvae are known with less detail. On the other hand, several characters are difficult to evaluate cladistically due to their gradational nature or because they are difficult to code. Therefore, the following comments are not cladistically based but still include useful characteristics to distinguish genera. Within Bidessini, *Allodessus* belongs to the group of genera in which the larvae bear a short last abdominal segment and long urogomphi (*Amarodytes*, *Glareadessus*, *Hypodessus*, *Liodessus*, *Neoclypeodytes*) (Perkins 1980; Alarie and Wewalka 2001; Michat and Alarie 2006, 2008; Alarie et al. 2007). These characters distinguish the genus from *Uvarus* (Matta 1983) and

Anodocheilus (Michat and Torres 2006). On the other hand, the lack of a colour pattern on the head and abdomen distinguishes *Allodessus* from *Neoclypeodytes* (Perkins 1980). The presence of posterior secondary setae on the coxa, a large number of total secondary setae on the coxa, and a total of 6–7 (instar II) and 7–11 (instar III) secondary setae on the metatarsus distinguish *Allodessus* from *Amarodytes*, *Hypodessus*, *Glareadessus*, *Anodocheilus* and *Liodessus* (Alarie and Wewalka 2001; Michat and Alarie 2006, 2008; Michat and Torres 2006; Alarie et al. 2007). Finally, the presence of posteroventral secondary setae on the tarsus separates *Allodessus* from *Amarodytes*, *Hypodessus* (instar II only), *Glareadessus*, *Anodocheilus*, and most *Liodessus*.

As mentioned above, the species composition of the genus *Allodessus* has changed recently owing to the inclusion of four additional species and the putative conspecificity of some of them (Balke and Ribera 2004). Larval morphology could be useful in providing characters at the species and genus levels that could help to generate a better picture of both the relationships among the *Allodessus* species and the relationship of *Allodessus* to its presumed sister group *Limbodessus*. However, larvae of most genera and species of Bidessini are still unknown, and therefore future work should focus on finding more species/genera and providing detailed descriptions (including chaetotaxy) of larvae of this tribe.

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