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THE UNKNOWN LARVA OF THE MINUTE DIVING BEETLE GENUS *BRACHYVATUS* ZIMMERMANN, 1919 (COLEOPTERA: DYTISCIDAE: BIDESSINI)¹

Mariano C. Michat² and Patricia L. M. Torres²

ABSTRACT: The three larval instars of *Brachyvatus acuminatus* (Steinheil, 1869) (the type species of the bidessine genus *Brachyvatus* Zimmermann, 1919) 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 characterized by the absence of the primary pore ABc, which is a synapomorphy of the tribe Bidessini. *Brachyvatus* larvae can be separated from those of all other known Bidessini genera by the following combination of characters: very small size; lateral branches of nasale well visible in dorsal view; ventroapical spinula on third antennomere absent; meso- and metatergite of instar I with anterotransverse carina; siphon short; long urogomphi with secondary setae; seta PA3 absent; setae UR2 and UR4 inserted contiguously; natatory setae present on tibiae in instars II-III.

KEY WORDS: Hydroporinae; Brachyvatus acuminatus; larvae; morphometry; chaetotaxy

Among the smallest known diving beetles are the members of *Brachyvatus* Zimmermann, 1919, which adults barely reach 1.5 mm in length. The genus includes four species (Nilsson, 2001) and is distributed in America approximately from the latitude of Florida in the US to central Argentina. *Brachyvatus acuminatus* (Steinheil, 1869), the type species, is commonly found in water bodies covered with dense masses of floating vegetation, and is distributed in southern Brazil and the northern half of Argentina (Bruch, 1927; Trémouilles, 1988; Torres et al., 2007, 2012). It most probably occurs also in Uruguay, Paraguay and Bolivia.

Brachyvatus is included in the hydroporine tribe Bidessini, which represents a significant radiation of small diving beetles with about 40 genera and more than 600 species (Nilsson, 2001, 2003, 2004; Nilsson and Fery, 2006). Larval morphology of members of this tribe, however, remains imperfectly known, with only 16 described genera (see Michat et al., 2011, 2012). Larval chaetotaxy is a significant source of characters both for diagnosis of genera and species and for phylogenetic analyses (Alarie et al., 2011; Michat and Torres, 2011). The development of a system of nomenclature to name primary sensilla in first-instar larvae of the Hydroporinae (Alarie and Harper, 1990; Alarie et al., 1990; Alarie, 1991; Alarie and Michat, 2007) provides a template that allows the exploration of this extensive set of characters in a comparative way.

The larvae of *Brachyvatus* have been unknown. Therefore, the recent discovery of all larval instars of *B. acuminatus* allows us to provide, for the first time, a detailed description of this genus in the context of modern works on Bidessini

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larvae, which incorporate detailed morphometric and chaetotaxic analyses (Michat and Alarie, 2006, 2008; Michat and Torres, 2006; Michat et al., 2010, 2011, 2012). We also provide a diagnosis of the genus and discuss the most relevant characters to separate it from the other Bidessini genera for which the larvae have been described in detail.

METHODS

Eight specimens of instar I, four of instar II and five of instar III were used for the descriptions. The larvae were collected in association with adults at the following locality: Argentina, Entre Ríos Province, Pre-Delta National Park, 23-XI-2010, large pond of moderate depth, with rushes and water not visible from above due to the presence of a dense cover of floating aquatic macrophytes (duckweeds).

Specimens were cleared in lactic acid, dissected and mounted on glass slides with polyvinyl-lacto-glycerol. Observation (at magnifications up to 1000x) 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 M. C. Michat (Laboratory of Entomology, Buenos Aires University, Argentina).

In the morphometric analysis, the terms used in previous papers dealing with larval morphology of Bidessini (Michat et al., 2010, 2011, 2012) were applied. 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 characterize body shape.

In the 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 B. acuminatus were labeled 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, 2007). Homologies were recognized 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.

DESCRIPTION OF THE LARVAE OF *BRACHYVATUS ACUMINATUS* (STEINHEIL, 1869)

Diagnosis. Larvae of Brachyvatus are characterized by the following combination of characters: small size (instar III: HL 0.47-0.49 mm); lateral branches of nasale well visible in dorsal view (Figs. 2, 16); ventroapical spinula on A3 absent (Fig. 5); meso- and metatergite with anterotransverse carina from instar I (Fig. 1); siphon short, subconical (Figs. 13-14, 19); U very long (ratio U/HW 3.11-3.91 mm) (Figs. 1, 19); setae PA3, MX4, MX8, MX9, MX10, TR2 and AB7 absent (Figs. 2, 7-8, 11, 13-14); pores PAd, PAe, PAj, ANf, FEa, ABa and ABc absent (Figs. 2-5, 12-13); seta AB10 spine-like (Fig. 14); setae UR2 and UR4 inserted contiguously (Fig. 15); seta UR8 inserted distally (Fig. 15); natatory setae present on TI (instars II-III) (Fig. 18); U1 with secondary setae (Fig. 19).

First-instar larva (Figs. 1-15). Color. Uniformly pale, lacking distinct color pattern.

Body (Fig. 1). Subcylindrical, narrowing towards abdominal apex. Measurements and ratios that characterize the body shape are shown in Table 1.

Head. Head capsule (Figs. 2-3). Longer than broad; parietals with reticulation; maximum width at stemmata, without neck constriction; occipital suture absent; ecdysial line well marked, coronal line short; 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, with one small branch at each side, well visible in dorsal view; ventrodistal surface with a few spinulae of

different shapes; lateral margin relatively straight, with 1-2 robust ventrolateral spinulae not visible in dorsal view; anteroventral margin with a half circle of 12 short lamellae clypeales directed downward; six dorsolateral stemmata arranged in two groups at each side. Antenna (Figs. 4-5). Elongate, composed of four antennomeres, somewhat shorter than HW; A1 the shortest, A3 the longest, without a ventroapical spinula; A3' elongate. Mandible (Fig. 6). Prominent, broad basally, distal half projected inwards and upwards, apex sharp; mandibular channel present. Maxilla (Figs. 7-8). Cardo fused to stipes; stipes short, broad; galea and lacinia absent; MP elongate, composed of three palpomeres, MP3 the shortest, MP2 the longest. Labium (Figs. 9-10). Prementum small, subtrapezoidal, about as long as broad, without lateral spinulae; 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, with anterotransverse carina; sagittal line visible on pro- and mesotergite; sterna membranous; spiracles absent. Legs (Figs. 11-12). Long, composed of six articles, L1 the shortest, L3 the longest; CO robust, elongate, TR divided into two parts, FE, TI and 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 sclerotized dorsally, membranous ventrally; segment VII sclerotized 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 (Figs. 13-14) the longest, completely sclerotized, ring-like, covered with minute spinulae in transverse rows; siphon short, subconical. Urogomphus (Fig. 15). Very long, composed of two urogomphomeres; U1 long, much longer than LAS, basal half covered with minute spinulae; U2 narrow, setiform, shorter than U1.

Chaetotaxy (Figs. 1-15). Similar to that of generalized 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; seta PA3 absent; 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 TR2 absent; pore FEa absent; some setae on FE multi-branched; seta TI7 short, spine-like; seta AB7 absent; pores ABa and ABc absent; seta AB10 spine-like; we were unable to find pore ABd and seta AB8; however, we could not establish if they are really absent due to the presence of spinulae on the siphon; setae UR2 and UR4 inserted contiguous; setae UR5, UR6 and UR7 elongate; seta UR8 inserted distally.

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

Color. Somewhat darker in general; parietals posterior to occipital suture and distal half of mandible light brown.

Body. Measurements and ratios that characterize the body shape are shown in Table 1.

Head. Head capsule. Occipital suture present; egg bursters absent; anteroventral margin of nasale with 21 lamellae clypeales. Antenna. A1 and A4 the shortest, subequal. Labium. LP2 slightly longer than LP1.

Thorax. Sagittal line visible on the three tergites. Legs. Elongate ventral spinulae restricted to distal portion of TI and TA.

Abdomen. Segment VII completely sclerotized, ring-like; all sclerites with anterotransverse carina. Urogomphus. Minute spinulae restricted to base.

Chaetotaxy. Head capsule with numerous secondary setae; PA with one short, spine-like, secondary seta 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 2; TI with a row of natatory setae on posterodorsal margin; abdominal sclerites I-VIII with several secondary setae on posterior half (absent on ventral surface of LAS); U1 with several spine-like and hair-like secondary setae.

Third-instar larva (Figs. 16-19). As for second-instar larva except for the following features:

Color. Somewhat darker in general; predominantly light brown, parietals posterior to occipital suture and distal half of mandible darker, rest of head appendages lighter; CO somewhat darker than rest of leg.

Body. Measurements and ratios that characterize the body shape are shown in Table 1.

Head (Fig. 16). Head capsule. Lateral margin of nasale sinuate; robust spinulae on ventrolateral margin of nasale visible in dorsal view; anteroventral margin of nasale with 35-39 lamellae clypeales. Antenna. A4 the shortest. Maxilla. MP1 and MP2 the longest, subequal.

Thorax. Spiracles present on mesothorax.

Abdomen. Spiracles present on segments I-VII.

Chaetotaxy. Secondary setation on cephalic capsule, thoracic and abdominal sclerites more abundant; secondary leg setation detailed in Table 2 and Figs. 17-18; natatory setae on posterodorsal margin of TI more abundant; secondary setation on LAS and U detailed in Fig. 19.

DISCUSSION

Larvae of *Brachyvatus* are characterized by the absence of the primary pore ABc on the last abdominal segment, which has been proposed as a synapomorphy of the Bidessini (Michat and Alarie, 2008) and distinguishes the members of this tribe from the remaining Hydroporinae. The absence of pore PAj on the ventral surface of the parietals and the seta UR8 inserted distally on the second uro-

gomphomere are also distinctive features of Bidessini larvae. However, these two character states should not be viewed as strong evidence of a monophyletic origin of the Bidessini since they are present also in the tribes Hydrovatini and Hyphydrini and in several genera of the tribe Hydroporini respectively.

Within the Bidessini, *Brachyvatus* is highly characteristic in that the larvae of instars II and III bear natatory setae on the tibiae. This feature is not found in any other Bidessini known so far, and probably represents an adaptation to improve swimming ability. Natatory setae are commonly present in several groups of diving beetles (Michat et al., 2008), and are particularly well developed in larvae of the subfamily Dytiscinae (Alarie et al., 2011), which are well known as very good swimmers. It is curious, however, that the larvae of *Brachyvatus* studied here were found in a particular habitat that apparently gives little chance for swimming, as the water surface is covered by a dense carpet of floating macrophytes (mainly duckweeds). According to our observations in recent years, that certainly appears to be the habitat of the species as adults of *B. acuminatus* were found repeatedly in situations similar to that described here.

Another highly distinctive feature of *Brachyvatus* larvae is the presence of secondary setae on the urogomphi. Within the Bidessini, a similar character state is known to occur in *Amarodytes* Régimbart, 1900 (Michat and Alarie, 2006), *Allodessus* Guignot, 1953 (Michat et al., 2011), and some *Limbodessus* Guignot, 1939 (Michat et al., 2012), suggesting a close phylogenetic relationship of these genera. However, except for *Allodessus* and *Limbodessus*, which appear to be closely related to each other (Hendrich et al., 2009; Leys et al., 2012), there is not strong evidence that *Brachyvatus* could be related neither to those genera nor to *Amarodytes* (Miller et al., 2006). According to Michat et al. (2011, 2012), the shared presence of urogomphal secondary setae should not be interpreted as a synapomorphy for *Amarodytes* and *Limbodessus-Allodessus*. Therefore, it is reasonable to assume that the development of secondary setae on the urogomphus in *Brachyvatus* larvae has occurred independently from those in the other genera.

At the moment, the Bidessini genera for which the larvae are known in detail are: *Allodessus* (Michat et al., 2011), *Amarodytes* (Michat and Alarie, 2006), *Anodocheilus* Babington, 1841 (Michat and Torres, 2006), *Glareadessus* Wewalka and Biström, 1998 (Alarie and Wewalka, 2001), *Hydroglyphus* Motschulsky, 1853 (only instar III) (Michat et al., 2010), *Hypodessus* Guignot, 1939 (Michat and Alarie, 2008), *Limbodessus* (Michat et al., 2012), *Liodessus* Guignot, 1939 (Alarie et al., 2007) and *Neobidessodes* Hendrich and Balke, 2009 (only instar I) (Michat et al., 2010). Apart from the characters mentioned above, the following characters are useful to distinguish *Brachyvatus* from the other Bidessini larvae: (1) smaller size (only the larvae of *Anodocheilus* are close in size, but still larger); (2) absence of a ventroapical spinula on the third antennomere (present in *Allodessus*, *Amarodytes*, *Glareadessus*, *Hydroglyphus*, *Hypodessus*, *Limbodessus*, *Liodessus* and *Neobidessodes*); (3) presence of an anterotransverse carina on meso- and metathorax in instar I (absent in all the genera except *Anodo-*

cheilus, in which a weakly delimited anterotransverse carina is present); (4) very long urogomphi relative to other parts of the body (ratio U/HW in instar III more than 3.1 compared to less than 2.6 in the other genera); and (5) presence of secondary setae on the protarsus (absent in *Amarodytes* and *Anodocheilus*). *Brachyvatus* larvae also differ from *Uvarus* Guignot, 1939 larvae (Matta, 1983) in having a short last abdominal segment and long urogomphi, and from *Neoclypeodytes* Young, 1967 larvae (Perkins, 1980) in the lack of a color pattern on the head and abdomen.

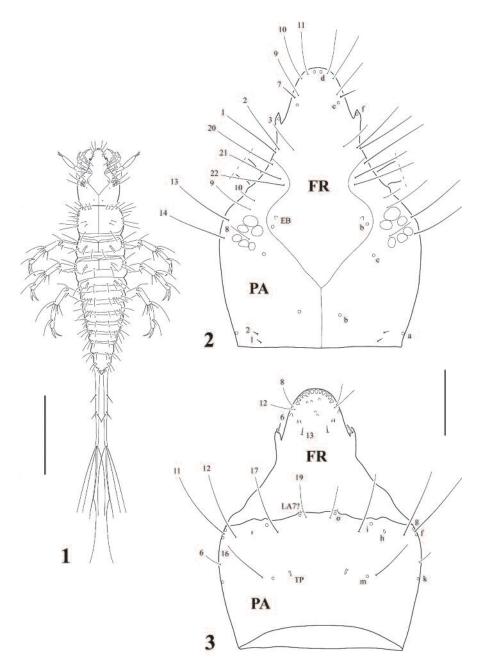
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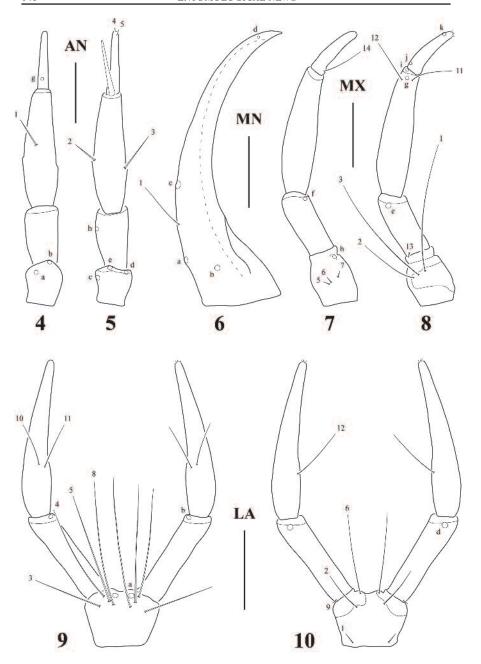
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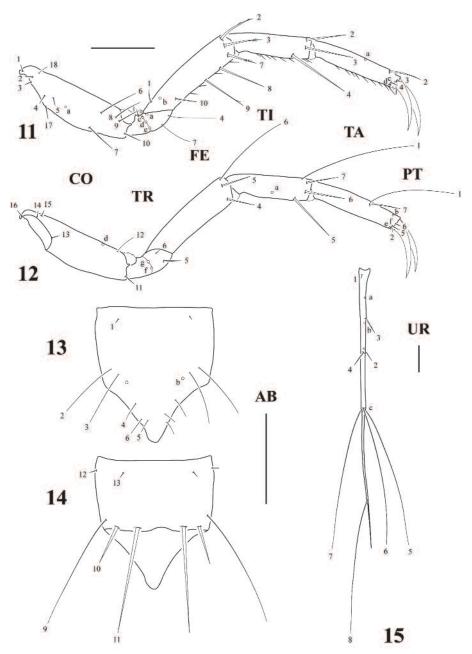
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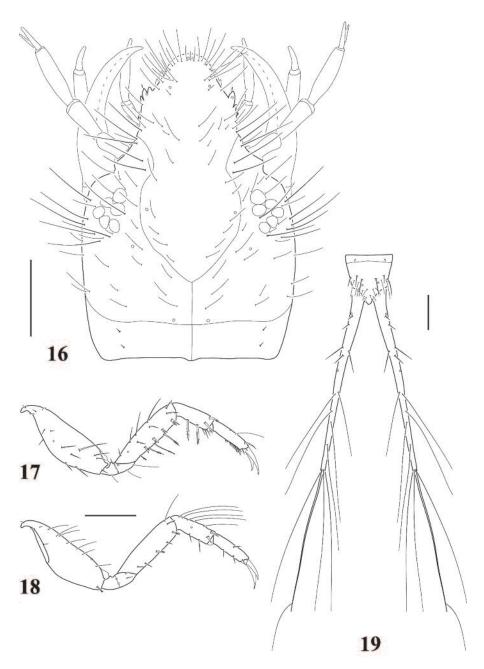
Figs. 1-3. *Brachyvatus acuminatus*, first-instar larva: (1) habitus, dorsal aspect; (2) cephalic capsule, dorsal aspect; (3) cephalic capsule, ventral aspect. EB, egg burster; TP, tentorial pit. Scale bars = 0.40 mm (Fig. 1) and 0.07 mm (Figs. 2-3).



Figs. 4-10. *Brachyvatus acuminatus*, first-instar larva: (4) left antenna, dorsal aspect; (5) right antenna, ventral aspect; (6) left mandible, dorsal aspect; (7) left maxilla, dorsal aspect; (8) right maxilla, ventral aspect; (9) labium, dorsal aspect; (10) labium, ventral aspect. Scale bars = 0.04 mm.



Figs. 11-15. *Brachyvatus acuminatus*, first-instar larva: (11) left metathoracic leg, anterior aspect; (12) right metathoracic leg, posterior aspect; (13) abdominal segment VIII, dorsal aspect; (14) abdominal segment VIII, ventral aspect; (15) right urogomphus, dorsal aspect. Scale bars = 0.08 mm.



Figs. 16-19. *Brachyvatus acuminatus*, third-instar larva: (16) head, dorsal aspect; (17) left prothoracic leg, anterior aspect; (18) right prothoracic leg, posterior aspect; (19) abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.12 mm.

Table 1. Measurements and ratios for the three larval instars of *Brachyvatus acuminatus*.

Measure	Instar I $(n = 3)$	Instar II (n = 3)	Instar III (n = 3)
TL (mm)	1.15-1.20	1.40-1.60	2.00-2.70
MW (mm)	0.15-0.20	0.25-0.30	0.40-0.50
HL (mm)	0.30	0.38-0.39	0.47-0.49
HW (mm)	0.21-0.23	0.29-0.30	0.34
FRL (mm)	0.23-0.24	0.29-0.30	0.36
OCW (mm)	0.15-0.19	0.23-0.24	0.27-0.28
HL/HW	1.30-1.45	1.27-1.34	1.38-1.44
HW/OCW	1.22-1.36	1.20-1.26	1.23-1.24
COL/HL	0.21-0.23	0.21-0.24	0.24-0.31
FRL/HL	0.77-0.79	0.76-0.79	0.74-0.76
A/HW	0.86-0.93	0.77-0.80	0.78-0.82
A3/A1	2.50-2.68	2.33-2.38	1.75-1.87
A3/A2	1.78-1.84	1.63-1.70	1.30-1.37
A4/A3	0.49-0.51	0.42-0.48	0.40-0.41
A3'/A4	0.88-1.00	0.78-0.82	0.90-1.00
MNL/MNW	3.80-4.13	3.51-3.82	3.82-4.00
MNL/HL	0.54-0.56	0.53-0.54	0.49-0.53
A/MP	1.24-1.28	1.22-1.25	1.20-1.25
MP2/MP1	1.84-1.90	1.37-1.42	1.06
MP2/MP3	2.42-2.52	2.13-2.54	2.35-2.38
MP/LP	1.08-1.15	1.10-1.13	1.12-1.17

Table 1 (continued). Measurements and ratios for the three larval instars of *Brachyvatus acuminatus*.

Measure	Instar I $(n = 3)$	Instar II (n = 3)	Instar III (n = 3)
LP2/LP1	1.45-1.55	1.19-1.24	1.02-1.11
L3 (mm)	0.65-0.67	0.82-0.87	1.02-1.07
L3/L1	1.24-1.30	1.29-1.35	1.36
L3/L2	1.11-1.13	1.11-1.16	1.17-1.19
L3/HW	2.89-3.09	2.77-2.97	3.00-3.18
L3 (CO/FE)	1.00-1.08	0.99-1.03	0.98-1.00
L3 (TI/FE)	0.74-0.76	0.73-0.76	0.70-0.76
L3 (TA/FE)	0.83-0.86	0.73-0.78	0.66-0.70
L3 (CL/TA)	0.58-0.63	0.55-0.59	0.54
LAS (mm)	0.11-0.12	0.14-0.15	0.16-0.17
LAS/HW	0.50-0.55	0.47-0.51	0.48-0.50
U (mm)	0.73-0.85	0.98-0.99	1.06-1.32
U/LAS	6.28-7.48	6.94-7.14	6.48-8.06
U/HW	3.48-3.74	3.28-3.39	3.11-3.91
U1/U2	1.10-1.30	1.30-1.46	1.09-1.43

Table 2. Number and position of secondary setae on the legs of larvae of *Brachyvatus acuminatus*. 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 / 0 / 0	0-2 / 2 / 1-5
	PD	2-3 / 2-3 / 2-3	2-5 / 3-4 / 2-4
	V	1 / 1 / 1	1-3 / 2-3 / 2-4
	Total	3-4 / 3-4 / 3-4	4-8 / 7-8 / 6-10
Trochanter	Pr	1 / 1 / 1	1 / 1 / 1
	Total	1 / 1 / 1	1 / 1 / 1
Femur	AD	2 / 2-4 / 4-5	3-4 / 5-7 / 6-10
	AV	2-3 / 1-3 / 1-3	1-3 / 2-4 / 2-5
	PV	1-3 / 2 / 2-3	2-3 / 3-5 / 4-6
	Total	6-7 / 6-8 / 8-11	7-10 / 11-15 / 13-20
Tibia	AD	0 / 1-2 / 1-2	0 / 1-2 / 2-3
	AV	1 / 1 / 1-2	0-1 / 1-2 / 2-3
	PD (NS)	1-2 / 3 / 3-4	2-4 / 6-8 / 8-10
	PV	0 / 1 / 1	0-1 / 1-2 / 2-3
	Total	1 / 3-4 / 3-4	1-2 / 3-6 / 7-8
Tarsus	AD	0 / 1 / 1	0 / 1 / 1
	AV	0 / 1-2 / 2	0-1 / 2-3 / 2-3
	PV	1 / 1-2 / 1-2	1-2 / 1-3 / 3-4
	Total	1 / 3-4 / 4-5	1-3 / 4-6 / 6-8

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