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The larvae of *Amarodytes duponti* (Aubé) (Coleoptera: Dytiscidae: Hydroporinae), with comments on Bidessini larval morphology and chaetotaxy

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Abstract

Larval morphology of the Neotropical endemic dytiscid genus *Amarodytes* Régimbart is investigated. All three larval instars of *A. duponti* (Aubé) are described and illustrated with particular emphasis on morphometry and chaetotaxy. Larvae of *A. duponti* share with those of other Bidessini studied in detail the absence of the primary pore ABc. Contrary to other first instar Bidessini, *A. duponti* characterizes by the presence of an occipital suture and the absence of pores PAj and PAk. *Amarodytes duponti* is related to *Allodessus bistrigatus* (Clark) by the presence of secondary setae on the first urogomphomere, a unique feature among the Bidessini.

Key words: Diving beetles, Bidessini, *Amarodytes*, larval morphology, chaetotaxy

Introduction

The dytiscid tribe Bidessini is a speciose group of beetles consisting of 43 genera and ca. 600 species (Nilsson 2001, 2003, 2004; Watts & Humphreys 2006). In spite of its great diversity, larval morphology of members of the Bidessini still remains among the most imperfectly known within the Dytiscidae. At the moment, the larvae of only 11 genera (26%) (14 species) have been described, most of them very superficially (Bertrand 1930; Meuche 1937; Watts 1963, 1970; Perkins 1980; Richoux 1982; Matta 1983; Nilsson 1985; Costa *et al.* 1988; Alarie & Wewalka 2001). The lack of detail in existing descriptions is largely due to the small size of these insects, which adults vary from 1.20 to 3.50 mm in length (Alarie & Wewalka 2001).

The present study focuses on the larvae of the Neotropical endemic *Amarodytes* Régimbart, a small genus including 10 species (Nilsson 2001). The placement of

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Amarodytes within the Bidessini remains controversial. Biström (1988) stated that this genus should be excluded from the Bidessini owing to the presence of one-segmented aedeagal lateral lobes in *Amarodytes percosioides* Régimbart, the type species of *Amarodytes*. Benetti and Régil Cueto (2004), however, were of the opinion that *Amarodytes* belongs to the Bidessini as they found two-segmented aedeagal lateral lobes in *A. duponti* (Aubé), in agreement with a previous statement of Miller (2001) based on the shape of the female reproductive tract.

Larval morphology is of great interest in the study of the phylogenetic relationships among Holometabola. As different expressions of the same genotype, larval characters help to complement adult characters that have been traditionally the primary basis for classification. The larval ground plan of the Hydroporinae is well known with detailed descriptions available for several genera (e.g., Alarie & Watts 2005; Alarie & Challet 2006a; Alarie & Challet 2006b; Michat & Torres 2005; Michat in press; Shaverdo & Alarie 2006). The lack of knowledge of the larval morphology of the Bidessini prompted the present study, which aims at describing the larvae of *A. duponti* including for the first time the first two instars. The mature larva of *A. duponti* was described with some detail by Costa *et al.* (1988). However, no reference was made to the chaetotaxy, which prevents any attempt at comparing this species in the context of the chaetotaxy system proposed recently for larval Hydroporinae (Alarie & Harper 1990; Alarie *et al.* 1990; Alarie 1991).

This paper is meant to be a step towards a better understanding of the larval morphology of members of the tribe Bidessini. Here we describe the three larval instars of *A. duponti* with an emphasis on the morphometry and chaetotaxy, and compare the ground plan pattern of larval features of *Amarodytes* with those of other bidessine genera for which the larvae have been described in detail.

Material and methods

Material

Five 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: Argentina, Misiones Province, Iguazú National Park, San Martín island, Feb.–2002, small shallow pool about 5 m long, with clear water, soil bottom and abundant vegetation (mainly grass).

Methods

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 camera lucida. Drawings were scanned and digitally edited. The material is held in the larval collections of M. C. Michat (Laboratory of Entomology, Buenos Aires University, Argentina) and Y. Alarie (Department of Biology, Laurentian University, Sudbury, Ontario, Canada).

Morphometric and chaetotaxic analyses

We employed, with minimal modifications and additions, the terms used in previous papers dealing with larval morphology of Hydroporinae (Alarie & Harper 1990; Alarie *et al.* 1990; Alarie 1991). Three specimens of each instar were measured, in which paired structures were considered independently. The following measures were taken. Total length (excluding urogomphi) (TL). Maximum width (MW). 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 (MNL): measured from laterobasal angle to apex. Width of mandible (MNW): 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; 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 (CL) was derived by adding the lengths of the individual articles; each leg is denoted by the letter L followed by a number (e.g., L1: prothoracic leg). 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 articles following Lawrence (1991). Dorsal length of last abdominal segment (LAS): 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). 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 head 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 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 of *A. duponti* were labeled by comparison with the ground plan of chaetotaxy of the subfamily Hydroporinae (Alarie & Harper 1990; Alarie *et al.* 1990; Alarie 1991). 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.

Description of the larvae of *Amarodytes duponti* (Aubé)

Diagnosis

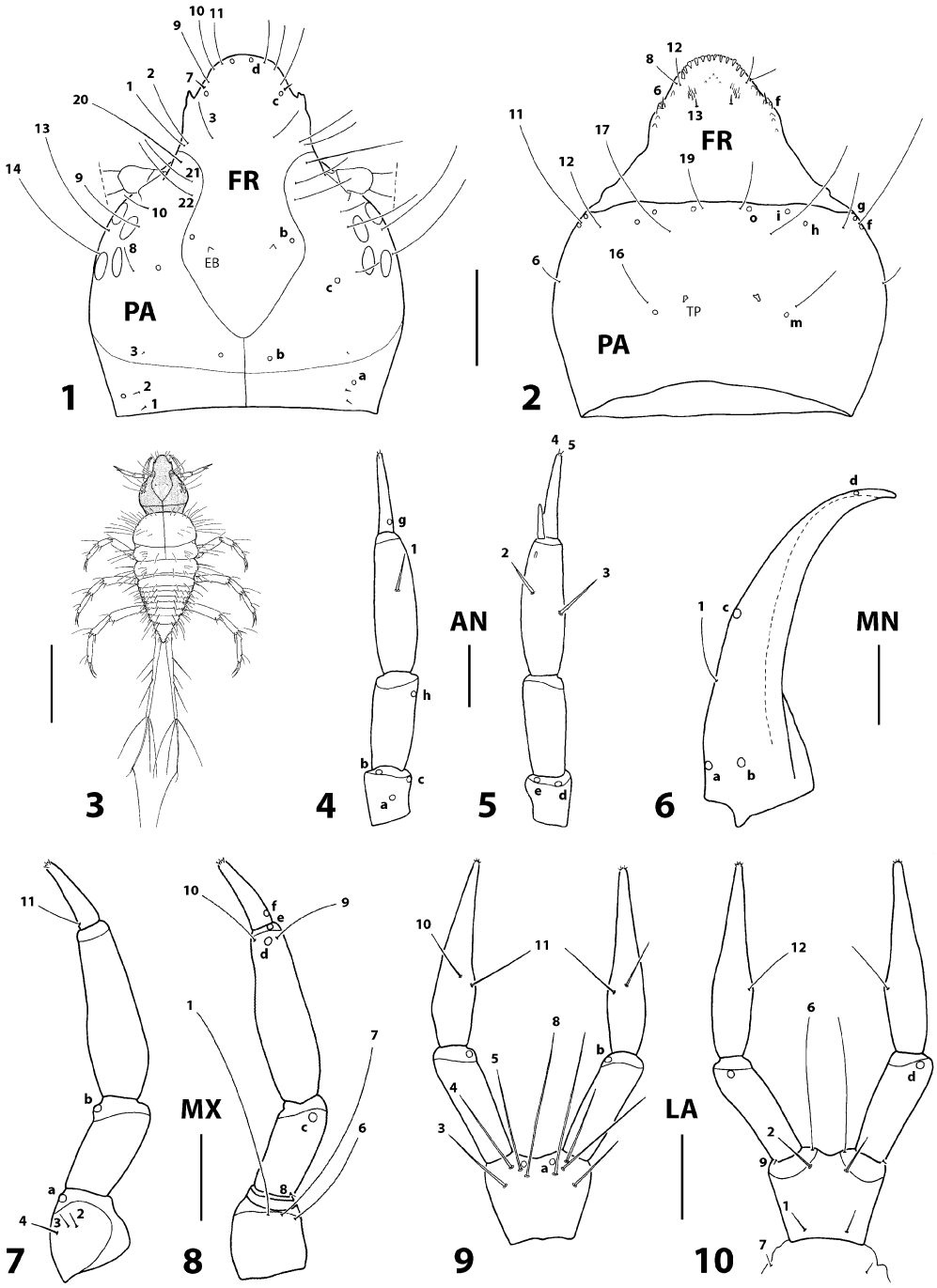
Larvae of all instars of *A. duponti* are characterized by the following combination of characters: occipital suture present (Figs. 1, 16); nasale short, subtriangular, with short lateral branches (Figs. 1–2, 16); A3 with a ventroapical spinula (Fig. 5); cardo fused to stipes (Fig. 8); galea absent; prementum without lateral spinulae (Figs. 9–10); abdominal segment VI membranous ventrally; siphon short (Figs. 13–14); urogomphus very long (Figs. 15, 19); pores PAd, PAe, PAj and PAk absent (Figs. 1–2); pore ANf absent (Figs. 4–5); seta MX5 absent (Figs. 7–8); seta TR2 and pore FEa absent (Figs. 11–12); seta TI7 short, spine-like (Fig. 12); legs without natatory setae (Figs. 11–12, 17–18); pores ABa and ABc absent (Fig. 13); seta AB10 spine-like (Fig. 14); setae UR2, UR3 and UR4 inserted far from each other (Fig. 15); seta UR8 inserted distally (Figs. 15, 19); U1 with numerous spine-like, secondary setae (instars II-III) (Fig. 19).

First-instar larva (Figs. 1–15)

Color. Larva entirely light brown except around stemmata, on frontoclypeus (near egg bursters), distal portion of coxa and proximal portion of trochanter pale yellow.

Body. Navicular, narrowing towards abdominal apex (Fig. 3). Measurements and ratios that characterize the different structures are shown in Table 1.

Head. *Head capsule* (Figs. 1–2). Longer than broad; posterodorsal and ventral surfaces with reticulated microsculpture; maximum width posterior to stemmata, without neck constriction; occipital suture present, weakly marked; 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 level of stemmata; nasale short, subtriangular, rounded apically, slightly sinuate laterally, with one short lateral branch at each side; lateral and ventral surfaces of nasale with spinulae of different shapes (Fig. 2), anteroventral margin with a half circle of 12–13 short, spatulate setae directed downwards; six dorsolateral stemmata arranged in two subparallel rows at each side. *Antenna* (Figs. 4–5). Elongate, composed of four antennomeres, shorter than HW; A1 the shortest, A3 the longest, with a ventroapical spinula; A3' short. *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 to subquadrate, about as long as broad, without lateral spinulae, anterior margin slightly indented medially; LP elongate, composed of two palpomeres; LP2 longer than LP1.



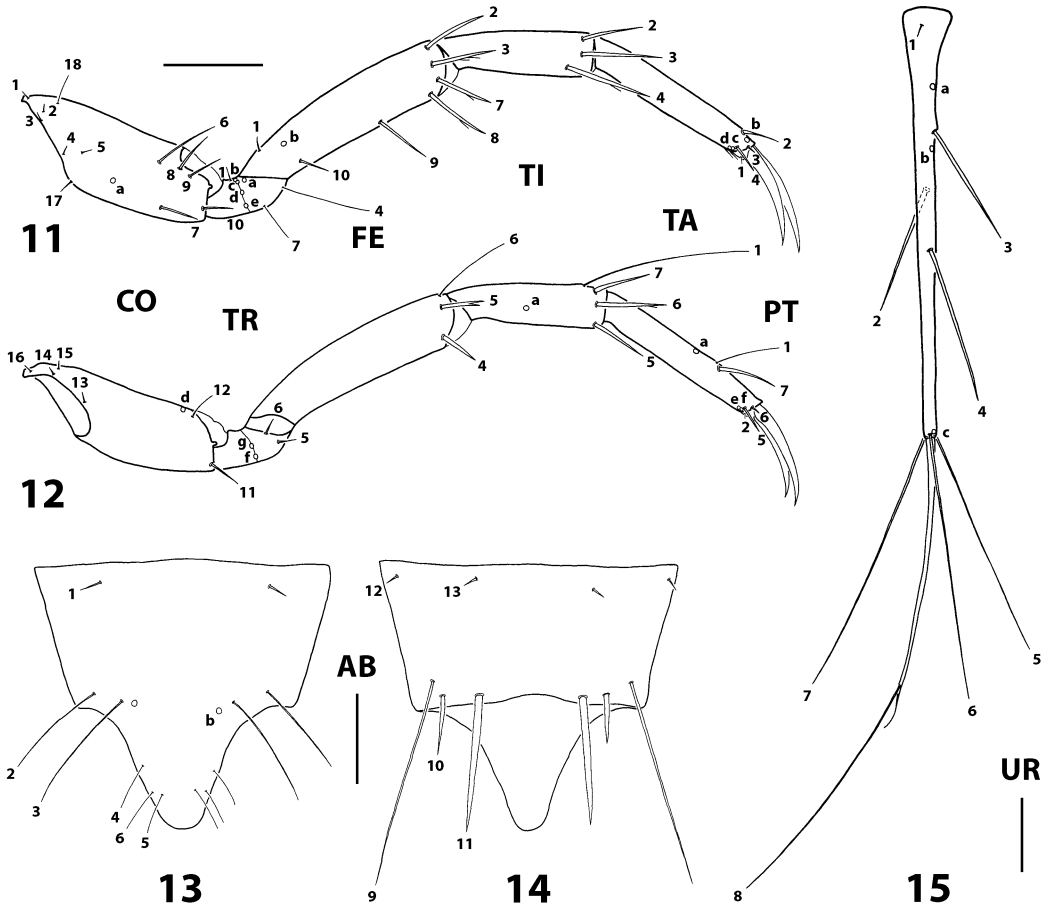
FIGURES 1–10. *Amarodytes duponti* (first-instar larva). 1—cephalic capsule, dorsal aspect; 2—cephalic capsule, ventral aspect; 3—habitus, dorsal aspect; 4—right antenna, dorsal aspect; 5—right antenna, ventral aspect; 6—left mandible, dorsal aspect; 7—right maxilla, dorsal aspect; 8—left maxilla, ventral aspect; 9—labium, dorsal aspect; 10—labium, ventral aspect. Numbers and lower case letters refer to primary setae and pores, respectively. Scale bars: Figs. 1–2 = 0.10 mm, Fig. 3 = 0.40 mm, Figs. 4–10 = 0.04 mm.

TABLE 1. Measurements and ratios for the three larval instars of *Amarodytes duponti*.

Measure	Instar I	Instar II	Instar III	Measure	Instar I	Instar II	Instar III
TL (mm)	0.90–1.10	1.90–2.60	2.05–3.30	MP2/MP1	1.70–1.78	1.17–1.33	0.83–0.96
MW (mm)	0.25–0.30	0.40–0.55	0.60–0.90	MP2/MP3	2.00–2.43	2.44–2.86	2.60–3.13
HL (mm)	0.37–0.39	0.57–0.59	0.74–0.77	MP/LP	1.10–1.14	1.15–1.21	1.16–1.29
HW (mm)	0.32–0.33	0.47–0.50	0.62–0.65	LP2/LP1	1.73–1.82	1.24–1.28	0.71–0.96
FRL (mm)	0.30	0.45–0.46	0.59–0.60	L3 (mm)	0.92–0.98	1.22–1.35	1.64–1.72
OCW (mm)	0.23–0.27	0.31–0.34	0.43–0.50	L3/L1	1.31–1.35	1.27–1.36	1.33–1.37
HL/HW	1.10–1.20	1.18–1.22	1.18–1.20	L3/L2	1.15–1.18	1.17–1.19	1.17–1.18
HW/OCW	1.22–1.38	1.49–1.53	1.32–1.47	L3/HW	2.81–3.04	2.68–2.81	2.59–2.72
COL/HL	0.18–0.23	0.22–0.23	0.21–0.22	L3 (CO/FE)	0.84–0.88	0.83–0.87	0.80–0.88
FRL/HL	0.77–0.82	0.77–0.78	0.78–0.79	L3 (TI/FE)	0.67–0.73	0.67–0.69	0.60–0.65
A/HW	0.69–0.75	0.58–0.59	0.54–0.57	L3 (TA/FE)	0.75–0.79	0.77–0.78	0.64–0.69
A3/A1	2.43–2.83	2.44–2.75	2.09–2.27	L3 (CL/TA)	0.56–0.62	0.47–0.51	0.42–0.48
A3/A2	1.21–1.42	1.11–1.16	1.00–1.04	LAS (mm)	0.14–0.15	0.22–0.24	0.33–0.34
A4/A3	0.56–0.61	0.45–0.50	0.42–0.48	LAS/HW	0.44–0.45	0.48–0.51	0.52–0.54
A3'/A4	0.40–0.50	0.50	0.64–0.73	U (mm)	0.92–1.01	1.37–1.40	1.47–1.59
MNL/MNW	3.08–3.55	3.38–3.63	3.60–4.17	U/LAS	6.41–7.07	5.75–5.88	4.35–4.77
MNL/HL	0.49–0.50	0.48–0.50	0.48–0.51	U/HW	2.82–3.15	2.73–2.79	2.33–2.46
A/MP	1.35–1.44	1.22–1.26	1.05–1.17	U1/U2	1.45–1.57	1.64–1.65	1.28–1.55

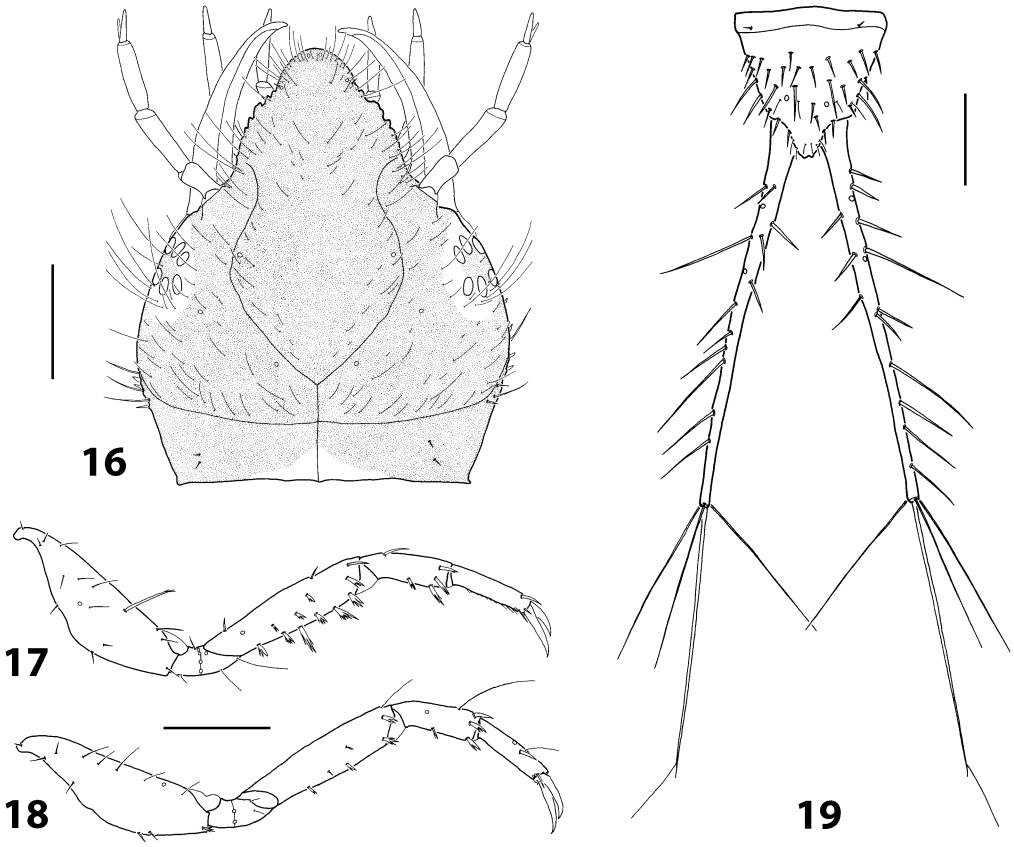
Thorax. Terga convex, pronotum about as long as meso- and metanotum combined, meso- and metanotum subequal; protergite subovate, margins rounded, more developed than meso- and metatergite; meso- and metatergite transverse; all tergites without anterotransverse carina; sagittal line visible; thoracic sterna membranous; spiracles absent. *Legs* (Figs. 11–12). Long, composed of six articles, L1 the shortest, L3 the longest; CO robust, elongate, TR transversely divided into two parts, FE, TI and TA slender, subcylindrical, PT with two long, slender, slightly curved claws; posterior claw shorter than anterior one on L1 and L2, posterior claw somewhat longer than anterior one on L3; most surface of legs covered with minute, slender spinulae in transverse rows; ventrodistal portion of TA with a few elongate spinulae.

Abdomen. 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, without sagittal line; all sclerites without anterotransverse carina; spiracles absent on segments I–VII; LAS (Figs. 13–14) the longest, completely sclerotized, ring-like, covered with minute, slender spinulae in transverse rows; siphon short, subconical, rounded apically. *Urogomphus* (Fig. 15). Very long, composed of two urogomphomeres; U1 long, much longer than LAS, covered with minute, slender spinulae; U2 narrow, shorter than U1.



FIGURES 11–15. *Amarodytes duponti* (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. Numbers and lower case letters refer to primary setae and pores, respectively. Scale bars: Figs. 11–12, 15 = 0.10 mm, Figs. 13–14 = 0.05 mm.

Chaetotaxy (Figs. 1–15). Similar to that of generalized Hydroporinae larva (Alarie & Harper 1990; Alarie *et al.* 1990; Alarie 1991) except for the following features. Pores PAd, PAe, PAj and PAk absent. Pore FRc submarginal, contiguous to seta FR7; pore PAg present; pore ANf absent; pore ANh distal; seta MX5 absent (possibly replaced by a minute structure that may be interpreted as a rudimentary seta); seta MX1 distal; seta TR2 absent; seta CO12 hair-like; pore FEa absent; several setae on FE and TI multi-branched; seta TI7 short, spine-like; setae TA1 and TA7 inserted far from the apex; pores ABa and ABc absent; seta AB10 spine-like; setae AB7 and AB8 and pore ABd not distinguishable, possibly 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 distally.



FIGURES 16–19. *Amarodytes duponti* (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 = 0.20 mm.

Second-instar larva

As first-instar larva except for the following features:

Color. Without pale yellow maculae on frontoclypeus.

Body. Measurements and ratios that characterize the different structures are shown in Table 1.

Head. Occipital suture well marked; anteroventral margin of nasale with 23–24 short, spatulate setae.

Thorax. Meso- and metatergite with anterotransverse carina.

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

Chaetotaxy. Head capsule with numerous secondary setae; lateral margin of parietal with 4–6 spine-like, secondary setae; MN with one basal, hair-like, secondary seta on external margin; thoracic tergites with numerous secondary setae; secondary leg setation

detailed in Table 2; abdominal sclerites I–VIII with several spine-like, secondary setae on posterior margin; U1 with numerous spine-like, secondary setae.

TABLE 2. Number and position of secondary setae on the legs of larvae of *Amarodytes duponti*. Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively. A = anterior, D = dorsal, P = posterior, Pr = proximal, V = ventral, range = total number of secondary setae on the article (excluding primary and natatory setae).

Article	Position	Instar II	Instar III
Coxa	A	0 / 0 / 0	0–3 / 0–1 / 0–2
	PD	1 / 1 / 1–2	3–5 / 3–5 / 3–5
	V	1 / 1 / 1	2–3 / 2–4 / 2–4
	Range	2 / 2 / 2–3	7–10 / 5–9 / 6–8
Trochanter	Pr	1 / 1 / 1	1 / 1 / 1–2
	Range	1 / 1 / 1	1 / 1 / 1–2
Femur	AD	0–1 / 1–2 / 2–3	2–4 / 4–6 / 5–8
	AV	3 / 2–3 / 2–4	4–5 / 4–5 / 5–8
	PV	0–1 / 2–4 / 3–4	3–4 / 5–6 / 4–7
	Range	3–5 / 6–8 / 7–10	10–12 / 14–16 / 16–22
Tibia	AD	0 / 1 / 1	1 / 1 / 1
	AV	0 / 1 / 1–2	0–1 / 1–3 / 2–3
	PD	0 / 0 / 0	0 / 1 / 0–1
	PV	0–1 / 0–1 / 1	1–2 / 2–3 / 2–3
	Range	0–1 / 2–3 / 3–4	2–4 / 5–7 / 5–8
Tarsus	AV	0 / 0–1 / 1–2	0 / 2 / 2–3
	PD	0 / 1–2 / 1	0 / 1 / 1
	Range	0 / 2 / 2–3	0 / 3 / 3–4

Third-instar larva (Figs. 16–19)

As second-instar larva except for the following features:

Color. Larva entirely light brown except around stemmata, dorsomedially near occipital suture, proximal and distal portions of coxa, trochanter, and 3–4 ring-like maculae on distal half of urogomphomere 1 pale yellow.

Body. Measurements and ratios that characterize the different structures are shown in Table 1.

Head. *Head capsule* (Fig. 16). Anteroventral margin of nasale with 41–46 short, spatulate setae. *Antenna*. A1 and A4 the shortest, subequal, A2 and A3 the longest, subequal; A3' somewhat more elongate. *Maxilla*. MP1 the longest, MP2 slightly shorter than MP1. *Labium*. LP1 slightly longer than LP2.

Thorax. Spiracles present on mesothorax.

Abdomen. Spiracles present on segments I–VII.

Chaetotaxy. Secondary setation on cephalic capsule, thoracic and abdominal sclerites more abundant; lateral margin of parietal with 8–10 spine-like, secondary setae; secondary leg setation detailed in Table 2 and Figs. 17–18; secondary setation on LAS and U detailed in Fig. 19.

Discussion

The mature larva of *A. duponti* was described in detail by Costa *et al.* (1988). A comparison of that description with our material reveals that the larvae are very similar, both in coloration and general morphology. The somewhat greater length of the larvae described by Costa *et al.* (1988) (4,0 mm) with respect to our larvae (Table 1) may be due to the fact that, when fixed and preserved, the body may become more or less contracted. Alternatively, Costa *et al.* (1988) may have included the urogomphi in their measure (which was not specified). Costa *et al.* (1988) included *A. duponti* within the tribe Hydroporini. However, most workers (e.g., Miller 2001; but see Biström 1988 for an alternative hypothesis) consider that *Amarodytes* belongs to the Bidessini.

There are several differences among the three larval instars of *A duponti*. They can be easily separated by using some measures mentioned in Table 1 (e.g., the relative head width). On the other hand, with the present knowledge on Bidessini larvae, morphometry is of little comparative value as most known larvae have not been measured thoroughly. Considering the head length (the only measure that was included in most descriptions), *Amarodytes* is among the largest genera, being comparable to *Allodessus* Guignot (0.76 mm) and *Liodessus amabilis* (Clark) (0.78 mm) (Watts 1963).

Larval morphology of Bidessini is poorly known. The only detailed treatments (including chaetotaxic analysis) of members of this tribe are those dealing with the larvae of *Liodessus affinis* (Say) (Alarie & Harper 1990; Alarie *et al.* 1990; Alarie 1991) and *Glareadessus stocki* Wewalka & Biström (Alarie & Wewalka 2001). Larvae of *A. duponti* differ from those of *L. affinis* and *G. stocki* in the presence of secondary setae on the first urogomphomere. This character also distinguishes *A. duponti* from other Bidessini larvae known with less detail, as *Neoclypeodytes cinctellus* (LeConte) (Perkins 1980), *Uvarus granarius* (Aubé) (Matta 1983) and *Bidessus grossepunctatus* Vorbringer (Nilsson 1985). The only other Bidessini larva that is known to possess secondary urogomphal setae is that of *Allodessus bistrigatus* (Clark) (Watts 1963). *Amarodytes duponti* also differs from *L. affinis* in the presence of an occipital suture in first-instar larva and in the absence of pores PAj and PAk. However, these characters could not be determined for the other known bidessine species due to either lack of detail or not inclusion of first-instar larva in the descriptions. *Liodessus affinis* is characterized by the absence of a ventroapical spinula on third antennomere; in *A. duponti* and *G. stocki* this spinula is present. On the other hand, the presence of elongate urogomphi and a short siphon is common to every Bidessini

species studied except *U. granarius*, in which shorter urogomphi and a longer siphon are present. *B. grossepunctatus* and *L. amabilis* also have a somewhat elongate siphon.

Amarodytes duponti, *L. affinis* and *G. stocki* share the absence of seta TR2, pores ANf and FEa, and lateral spinulae on prementum, and have the maxillary cardo fused to the stipes. However, none of these character states should be viewed as strong evidence to group members of Bidessini since they are also present in members of other hydroporine tribes (Alarie *et al.* 1997, 1999). At this point, only one character (the absence of pore ABc) relates the species of Bidessini studied in detail. Pore ABc is consistently present in larvae of the remaining Hydroporinae. On the other hand, as mentioned above, other characters as the absence of pore PAj, the presence of an occipital suture in first-instar larva, and the presence of secondary setae on the first urogomphomere differ between *A. duponti* and *L. affinis*, and argue in favour of a great diversity of larval features within Bidessini as presently defined. However, the lack of detailed descriptions of most genera within the tribe (and consequently of a cladistic analysis based on larval characters) makes it impossible at this time to evaluate rigurously the hypotheses on the phylogenetic position of *Amarodytes* based on adult features (Biström 1988; Miller 2001).

Detailed descriptions (including chaetotaxic analysis) of members of Bidessini, especially of the large amount of genera that are still unknown, are much needed. With regard to *Amarodytes*, a study of the larvae of the type species, *A. percosioides*, would be very interesting. It has been reported (Biström 1988) that males of this species have one-segmented lateral lobes of aedeagus, an unusual feature within Bidessini. Also, a detailed comparison of the larvae of *A. percosioides* and those described here would be of the utmost interest with regard to the monophyly of *Amarodytes* as presently defined.

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