BRILL

CONTRIBUTIONS TO ZOOLOGY (2024) 1–23

CTOZ

brill.com/ctoz

Phylogenetic placement of the Neotropical endemic genus *Hydrodessus* J. Balfour-Browne, 1953 (Coleoptera: Dytiscidae) based on larval morphology

Cesar J. Benetti | ORCID: 0000-0001-6795-2194
Departamento de Biodiversidad y Gestión Ambiental, Facultad de Ciencias Biológicas y Ambientales, Universidad de León, Campus de Vegazana, 24071, León, Spain
Coordenação de Biodiversidade, Programa de Pós-Graduação em Entomologia (PPGEnt), Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo 2936, CEP 69067-375, Manaus, AM, Brazil
cjbenetti@gmail.com

Mariano C. Michat | ORCID: 0000-0002-1962-7976
Laboratory of Entomology, IBBEA, CONICET-UBA., DBBE-FCEN,
University of Buenos Aires, Argentina

Yves Alarie | ORCID: 0000-0002-8425-087X
School of Natural Sciences, Laurentian University, Ramsey Lake Road, Sudbury, Ontario, P3E 2C6, Canada

Neusa Hamada | ORCID: 0000-0002-3526-5426
Coordenação de Biodiversidade, Programa de Pós-Graduação em Entomologia (PPGEnt), Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo 2936, CEP 69067-375, Manaus, AM, Brazil

RECEIVED 8 JULY 2024; REVISED 28 AUGUST 2024; ACCEPTED 9 SEPTEMBER 2024; PUBLISHED ONLINE 27 SEPTEMBER 2024; PUBLISHED IN ISSUE
EDITOR: LIZEL HUGO-COETZEE

Abstract

The phylogenetic relationships of members of the hydroporine tribe Bidessini (and particularly of the Neotropical endemic genus *Hydrodessus* J. Balfour-Browne, 1953) are investigated based on a cladistic analysis of larval characteristics, including 26 Hydroporinae species in 25 genera. For this purpose, the larvae of *Hydrodessus latotibialis* Miller, 2016 are described for the first time including detailed morphometric and chaetotaxic analyses of the cephalic capsule, head appendages, legs, last abdominal segment and urogomphi. Larval morphology supports a monophyletic

Published with license by Koninklijke Brill BV | DOI:10.1163/18759866-BJA10072

origin of the Bidessini based on the absence of the primary pore ABc, a unique feature within Hydroporinae. *Hydrodessus* was recovered as sister to other Bidessini studied, being characterized by several unique character states. This result supports a previous hypothesis of a basal position of this genus within Bidessini based on adult characters. The presence of natatory setae on femur, tibia and tarsus could represent an adaption to life in lotic environments.

Keywords

Bidessini – chaetotaxy – cladistics – diving beetles – larvae – natatory setae

Introduction

The neotropical endemic diving beetle genus *Hydrodessus* J. Balfour-Browne, 1953 is currently comprised of 33 species (Nilsson & Hájek, 2024). Whereas the vast majority of these are distributed in the Guiana Shield, some are also known from Paraguay and southern Brazil (Miller, 2016). Very little is known about the biology of these species as the majority of the specimens found in collections were gathered using light traps at night. A few specimens, however, have been collected from forest streams (Miller, 2016).

Hydrodessus is currently included in the very speciose hydroporine tribe Bidessini (ca., 750 species, 49 genera) (Nilsson & Hájek, 2024), which includes some of the smallest known dytiscid species (0.9–4.8 mm) (Miller & Bergsten, 2016). The phylogenetic position of this genus among the Bidessini, however, remains contentious. Originally included within Bidessini (Young, 1967, 1969), *Hydrodessus* was once removed from this tribe (along with *Amarodytes* Régimbart, 1900) owing to the presence of a one-segmented male lateral lobe (Biström, 1988). Miller (2001), however, prompted reinserting both *Hydrodessus* and *Amarodytes* to Bidessini based on the common presence of a spermathecal spine and crusher lobes of the proventriculus with five prominences. More recently, Miller & Bergsten (2014) related *Hydrodessus, Peschetius* Guignot, 1942 and part of *Amarodytes* in a clade sister to the rest of the Bidessini based on morphological and molecular data.

Larval morphology reveals a significant source of characters for the study of the phylogenetic relationships within the Dytiscidae (e.g., Alarie et al., 2009a, b, 2011; Michat et al., 2017; Alarie & Michat, 2023). Moreover, the now generalized larval descriptive format of Dytiscidae, which incorporates detailed chaetotaxic (see Alarie & Michat, 2023 for a comprehensive synthesis) and morphometric analyses has made it possible to standardize descriptions thus facilitating comparisons of species in a phylogenic context. Larval morphology of members of the Bidessini has been the subject of several studies recently. Indeed, 17 of the 49 currently recognized genera (35%) (Nilsson & Hájek, 2024) have been described, most of which according to this descriptive system (Alarie & Wewalka, 2001; Alarie et al., 2007; Michat & Alarie, 2006, 2008; Michat & Torres, 2006, 2013; Michat et al., 2010, 2011, 2012, 2015, 2018, 2022) (cf. table 1).

TABLE 1 Bidessini genera with larvae described and source of descriptions

Genus	Instar	Source
Allodessus Guignot, 1953	I, II, III	Watts (1963), Satô (1964), Michat et al. (2011)
Amarodytes Régimbart, 1900	I, II, III	Michat & Alarie (2006)
Anodocheilus Babington, 1842	I, II, III	Michat & Torres (2006)
Bidessus Sharp, 1880	I, II, III	Richoux (1982), Nilsson (1985)
Brachyvatus Zimmermann, 1919	I, II, III	Michat & Torres (2013)
Glareadessus Wewalka & Biström, 1998	III	Alarie & Wewalka (2001)
Hemibidessus Zimmermann, 1921	II, III	Michat et al. (2022)
Huxelhydrus Sharp, 1882	I, II, III	Michat et al. (2018)
Hydroglyphus Motschulsky, 1853	III	Brasavola de Massa (1930), Meuche (1937), Fukuda et al. (1959), Bertrand (1972), Richoux (1982), Michat et al. (2010)
Hypodessus Guignot, 1939	I, II, III	Michat & Alarie (2008)
Limbodessus Guignot, 1939	I, II, III	Watts (1963), Michat et al. (2012)
Liodessus Guignot, 1939	I, II, III	Watts (1970), Alarie et al. (2007)
Neobidessodes Hendrich & Balke, 2009	I	Michat et al. (2010)
Neoclypeodytes Young, 1967	III	Perkins (1980)
Pachynectes Régimbart, 1903	?	Bertrand (1963, 1972)
Uvarus Guignot, 1939	III	Needham & Williamson (1907), Matta (1983)
Yola Gozis, 1886	II, III	Bertrand (1972), Richoux (1982), Michat et al. (2015)

One of the most distinctive features of diving beetle larvae is the presence of natatory setae on legs (Alarie & Michat, 2023). This feature is commonly present in several groups and is particularly well developed in larvae of the subfamily Dytiscinae (Alarie et al., 2011), which are well-known as very good swimmers, but in some other dytiscid groups, the presence of these setae is rare. Hitherto, larvae of *Brachyvatus* Zimmermann, 1919 and *Hemibidessus* Zimmermann, 1921 are the only known bidessine genera with natatory setae on legs (Michat & Torres, 2013; Michat et al., 2022). The recent discovery of the larvae of *Hydrodessus latotibialis* Miller, 2016 prompted the present study, which is meant to continue the analysis of Bidessini larval morphology with an emphasis on the endemic Neotropical genus *Hydrodessus*.

This paper therefore aims (1) to describe and illustrate for the first time all larval instars of *H. latotibialis* in the context of modern works on Bidessini larvae, which incorporate detailed morphometric and chaetotaxic analyses and, (2) to discuss the phylogenetic relationships of *Hydrodessus* with other Bidessini genera whose larvae have been described in detail. The fact that the larval morphology of *Amarodytes* is known (Michat & Alarie, 2006) gives a most interesting perspective to this article since it makes it possible to test the hypothesis of a close phylogenetic relationship of *Hydrodessus* with this genus (cf. above) under the angle of larval morphology. As a corollary to this objective we intend to test the hypothesis of monophyletic origin of the Bidessini based on larval morphology.

Material and methods

Source of material

One specimen from each of the three larval stages was used for the description. Larvae were collected in association with adults (two males and one female) (fig. 1) at the following locality: **Brazil:** Pará State, Paragominas County (03°46′55″S 048°30′43″W), 22.vii.2011 (instar I); (03°11′32″S 47°31′44″W), 12.vii.2011 (instar II); (03°23′50″S 47°46′38″W), 09.vii.2011 (instar III). The identification is safe as *H. latotibialis* was the only species of *Hydrodessus* found at that locality (see Benetti et al., 2020).

FIGURE 1 *Hydrodessus latotibialis* Miller, 2016, habitus of adult, dorsal aspect. Scale bar = 1 mm

Methods

Specimens were cleared in lactic acid, dissected and mounted on glass slides with polyvinyl-lacto-glycerol. Observations (at magnifications up to 1,000×) and drawings were made using an Olympus CX31 compound microscope equipped with a camera lucida. Drawings were scanned and digitally inked using Adobe Illustrator software version 27.9. The material is held in the collection of the Laboratory of Entomology, Buenos Aires University, Argentina.

Morphometric analysis

We employed the terms used in previous papers dealing with the larval morphology of Bidessini (Michat & Alarie, 2006, 2008; Alarie et al., 2007; Michat & Torres, 2006, 2013; Michat et al., 2010, 2011, 2012, 2015, 2018, 2022). The following measurements were taken (with abbreviations shown in parentheses): total body length (excluding urogomphi, TL); maximum body width (MW); head length (including the frontoclypeus, measured medially along the epicranial stem, HL); maximum head width (HW); length of frontoclypeus (from apex of nasale to the joint of frontal and coronal sutures, FRL); occipital foramen width (maximum width measured along dorsal margin of occipital foramen, OCW); coronal line length (COL); length of mandible (measured from laterobasal angle to apex, MNL); width of mandible (maximum width measured at base, MNW). 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' was 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. Dorsal length of last abdominal segment (measured along midline from anterior to posterior margin, LAS). These measurements were used to calculate several ratios that characterize body shape.

Chaetotaxic analysis

Primary (present in instar I) and secondary (added in instars II–III) setae and pores were distinguished on the cephalic capsule, head appendages, legs, last abdominal segment and urogomphus of the studied larvae according to Alarie & Michat (2023). 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 instar I were labeled by comparison with the ground-plan of chaetotaxy of the subfamily Hydroporinae (Alarie & Harper, 1990; Alarie et al., 1990; Alarie, 1991; Alarie & 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.

Phylogenetic analysis

To examine the phylogenetic signal of the larval characters of *Hydrodessus* and to test its relationships with other Bidessini, a cladistic analysis of 25 Hydroporinae genera including eight Bidessini (nine species) with the three larval stages described (*Allodessus* Guignot, 1953, *Amarodytes* Régimbart, 1900, *Anodocheilus* Babington, 1842, *Brachyvatus* Zimmermann, 1919, *Huxelhydrus* Sharp, 1882, *Hydrodessus*, *Hypodessus* Guignot, 1939, *Liodessus* Guignot, 1939) was conducted using the program TNT (Goloboff & Morales, 2023). We refrain from using bidessine genera without the first larval stages described (cf., table 1) to facilitate better resolution in our phylogenetic analysis. We did not include the genus *Limbodessus* Guignot, 1939 as its first instar was described from a subterranean species (Michat et al., 2012). Subterranean species in general are morphologically somewhat deviated from the more typical morphology shown in their epigean counterparts.

The tree was rooted in *Laccophilus* Leach, 1815 (Laccophilinae) to allow the hydroporine taxa to vary freely, thus testing the relationships of *Hydrodessus* in a broader sense. All characters were treated as equally weighted, and multistate characters were treated as nonadditive. A heuristic search was implemented using 'tree bisection reconnection' as algorithm, with 200 replicates and saving 100 trees per replication (previously setting 'hold 20000'). Bremer support values were calculated using the commands 'hold 20000', 'sub n' and 'bsupport', where 'n' is the number of extra steps allowed. The process was repeated increasing the length of the suboptimal cladograms by one step, until all Bremer values were obtained (Kitching et al., 1998). Bootstrap values were calculated using the following parameters: 'standard (sample with replacement)'; 1000 replicates.

Results

General morphological characteristics of the larvae of the tribe Bidessini

Larvae of Bidessini (all instars) can be distinguished from those of other known Hydroporinae by the following combination of character states: frontoclypeus broad, subtriangular, absence of the primary pores ANf, PAe, PAj, FEa, and ABc, absence of the primary seta TR2, absence of secondary spine-like setae on ventral surface of parietals, and cardo fused to stipes.

General morphological characteristics of the larvae of Hydrodessus J. Balfour-Browne, 1953

Larvae of *Hydrodessus* can readily be distinguished from those of other genera of Bidessini studied (i.e., *Allodessus*, *Amarodytes*, *Anodocheilus*, *Brachyvatus*, *Huxelhydrus*, *Hypodessus*, and *Liodessus*) by the following combination of characters: parietals constricted at level of occipital suture (instars II–III); primary pore MXj and primary seta LA2 absent; secondary posterodorsal natatory setae present on femur, tibia and tarsus; siphon very short, bulge-like, not projecting beyond base of urogomphi (instar III); and, primary seta AB10 hair-like. Useful characters to separate larvae of *Hydrodessus* from those of other bidessine genera are summarized in table 2.

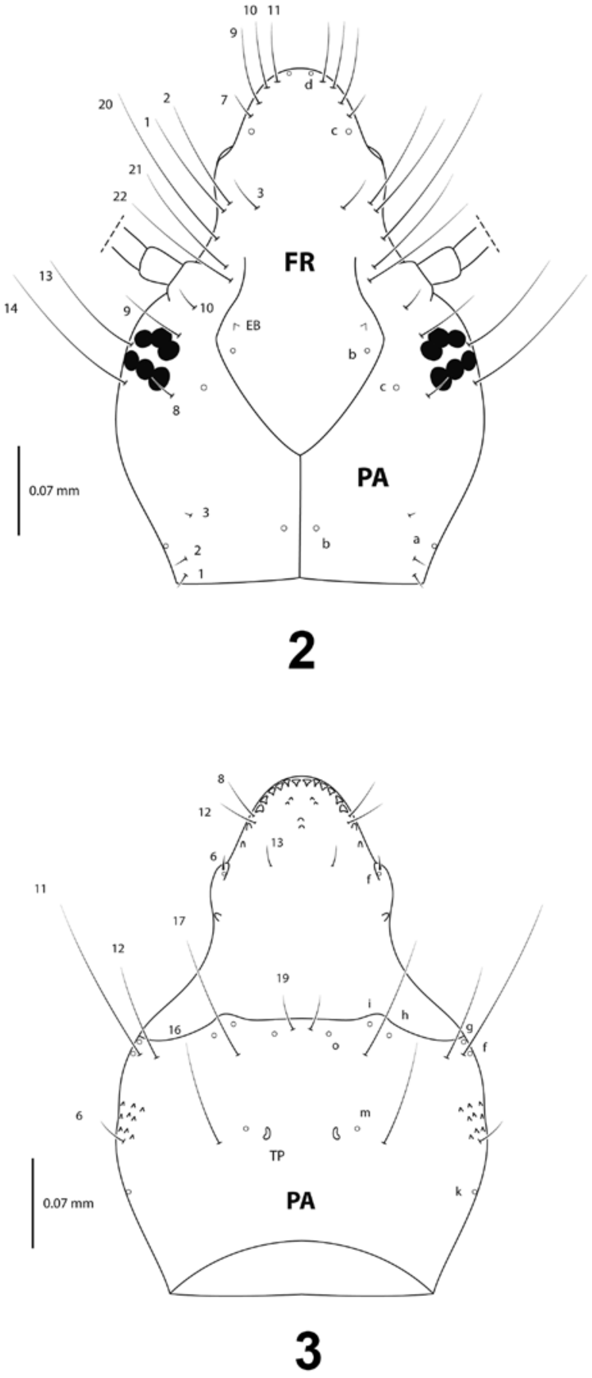
Description of the larvae of Hydrodessus latotibialis Miller, 2016

Instar I (*figs. 2–14*). *Color:* Uniformly testaceous, distal half of mandible somewhat darker. *Body:* Subcylindrical, narrowing towards abdominal apex. Measurements and ratios characterizing body shape shown in table 3. *Head:* Head capsule (figs. 2–3) longer than broad; parietals with reticulation on lateral and ventral surfaces; maximum width posterior to stemmata; with faint neck constriction; occipital suture absent; ecdysial line well marked except anteriorly, coronal line short; occipital foramen broadly emarginate ventrally; posterior tentorial pits visible ventrally at about mid-length; frontoclypeus elongate, lateral margins sinuate, with two lateral, spine-like egg bursters at about mid-length; nasale elongate, subtriangular, rounded anteriorly, with one small branch at each side, slightly visible in dorsal view; ventrodistal surface with very few blunt spinulae; ventrolateral margin with few robust spinulae; six dorsolateral stemmata arranged in two groups at each side. Antenna (figs. 4–5) elongate, somewhat shorter than head width, composed of four antennomeres; antennomeres 1 and 4 shortest, subequal, antennomere 3 longest,

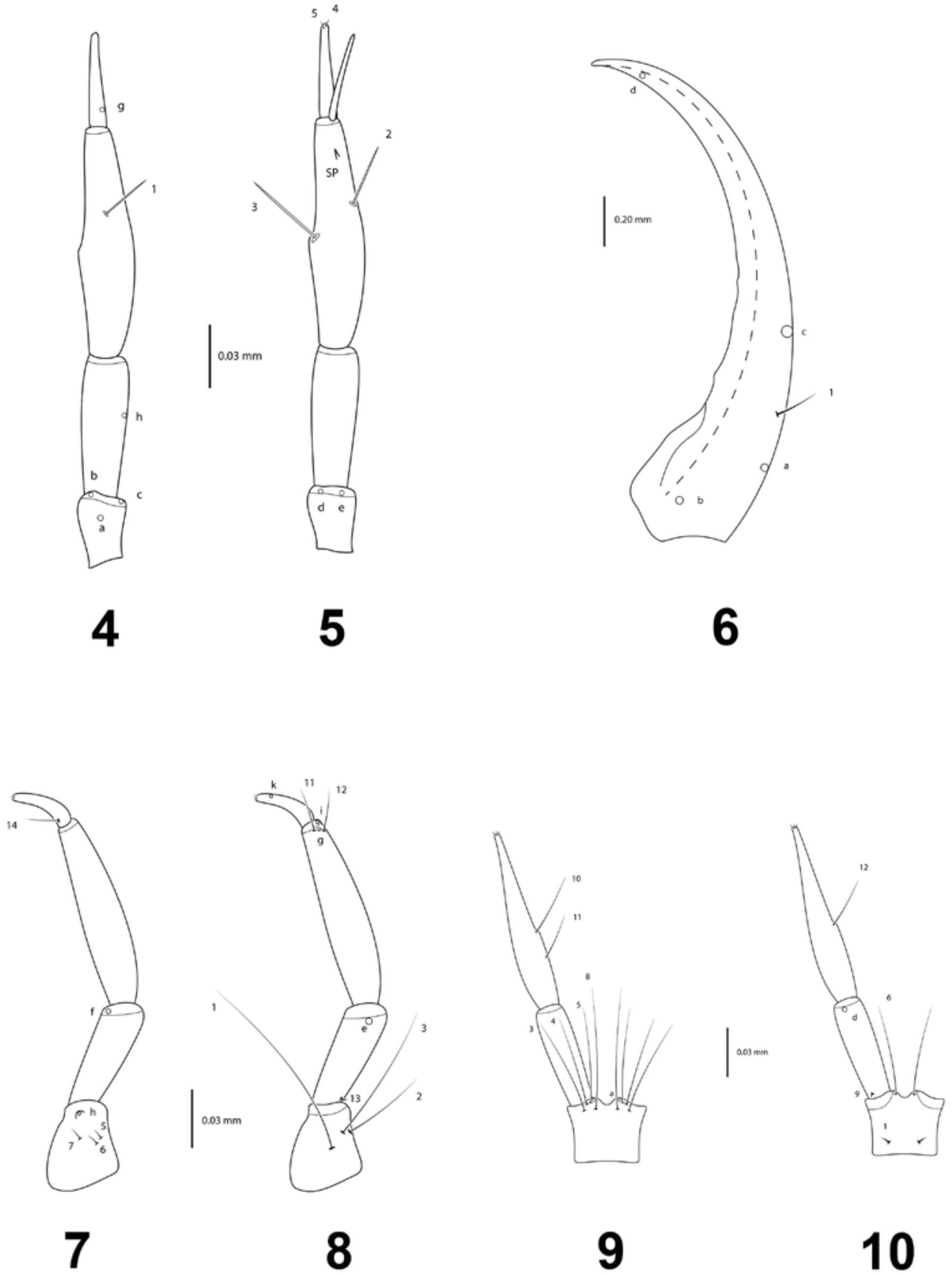
TABLE 2 Summary of characters useful to distinguish larvae of *Hydrodessus* from those of other Bidessini genera

	Ventro-apical spinula on antennomere 3	Ratio MNL/ MNW > 4.3 (instar III)	Parietals constricted at level of occipital suture (instars II–III)	Pore MXj (instar I)	Seta LA2 (instar I)	Natatory PD setae on femur (instars II–III)	Natatory PD setae on tibia (instars II–III)	Natatory PD setae on metatarsus (instars II–III)	Siphon moderately/ very elongate (instar III)	Seta AB10 spine-like (instar I)
ALL	+	–	–	+	+	–	–	–	+	+
AMA	+	–	–	+	+	–	–	–	+	+
ANO	–	–	–	+	+	–	–	–	+	+
BRA	–	–	–	+	+	–	+	–	+	+
GLA	+	+	–	?	+	–	–	–	+	?
HEM	–	–	–	+	+	+	+	–	+	+
HUX	+	–	–	+	+	–	–	–	+	+
HYG	+	–	–	+	+	–	–	–	+	+
HYD	+	+	+	–	–	+	+	+	–	–
HYP	+	–	–	+	+	–	–	–	+	+
LIM	+	–	–	+	+	–	–	–	+	+
LIO	–	–	–	+	+	–	–	–	+	+
YOL	–	–	–	+	+	–	–	–	+	+

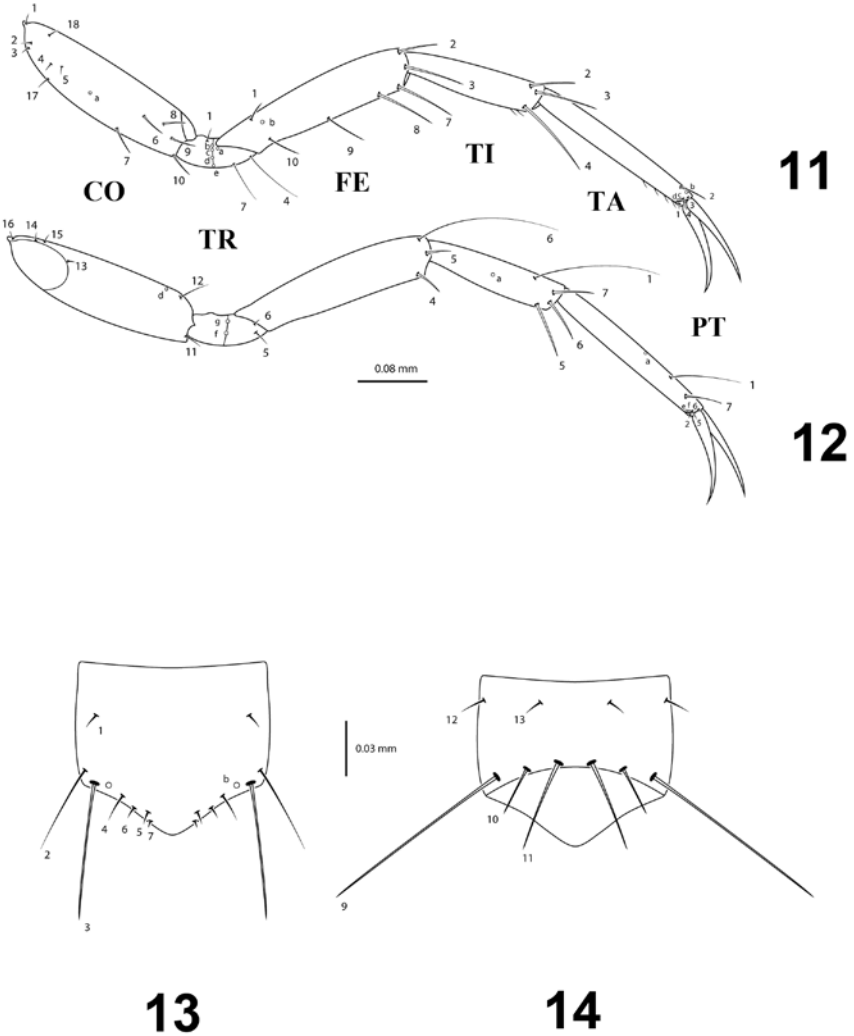
ALL: *Allodessus bistrigatus* (Clark, 1862); AMA: *Amarodytes duponti* (Aubé, 1838); ANO: *Anodocheilus maculatus* Babington, 1842; BRA: *Brachyvatus acuminatus* (Steinheil, 1869); GLA: *Glareadessus stocki* Wewalka and Biström, 1998; HEM: *Hemibidessus conicus* (Zimmermann, 1921); HUX: *Huxelhydrus syntheticus* Sharp, 1882; HYD: *Hydrodessus latotibialis* Miller, 2016; HYG: *Hydroglyphus balkei* Hendrich, 1999; HYP: *Hypodessus cruciatus* (Régimbart, 1903); LIM: *Limbodessus shuckardii* (Clark, 1862); LIO: *Liodessus* (two species: *L. affinis* (Say, 1823), *L. flavofasciatus* (Steinheil, 1869); YOL: *Yola wraniki* Wewalka, 2004; +: present; –: absent.



FIGURES 2–3
Hydrodessus latotibialis Miller, 2016, instar I larva, head capsule. 2, dorsal view. 3, ventral view. EB, egg burster. FR, frontoclypeus. PA, parietal. TP, tentorial pit



FIGURES 4–10 *Hydrodessus latotibialis* Miller, 2016, instar I larva. 4, antenna, dorsal view. 5, antenna, ventral. 6, mandible, dorsal view. 7, maxilla, dorsal view. 8, maxilla, ventral view. 9, labium, dorsal view. 10, labium, ventral view. SP, spinula



FIGURES 11–14 *Hydrodessus latotibialis* Miller, 2016, instar I larva. 11, metathoracic leg, anterior view. 12, metathoracic leg, posterior view. 13, abdominal segment VIII, dorsal view. 14, abdominal segment VIII, ventral view. CO, coxa. FE, femur. PT, pretarsus. TA, tarsus. TI, tibia. TR, trochanter

with a ventroapical spinula; A3' elongate. Mandible (fig. 6) prominent, projected inwards and upwards; broadest basally, progressively narrowing to pointed apex; mandibular channel present. Maxilla (figs. 7–8): cardo fused to stipes; stipes short, broad; galea and lacinia absent; maxillary palpus elongate, composed of three palpomeres, palpomeres 1 and 3 shortest, subequal, palpomere 2 longest. Labium (figs. 9–10): prementum small, subtrapezoidal, about as long as broad, anterior margin slightly indented, lateral margins lacking spinulae; labial palpus elongate, composed

TABLE 3 Measurements and ratios for the larvae of *Hydrodessus latotibialis* Miller, 2016

Measure	**Instar II (n = 1)**	**Instar II (n = 1)**	**Instar III (n = 1)**	**Measure**	**Instar I (n = 1)**	**Instar II (n = 1)**	**Instar III (n = 1)**
TL (mm)	–	–	2.30	MNL/HL	0.50	0.49	0.49
MW (mm)	–	–	0.50	A/MP	1.31	1.30	1.19
HL (mm)	0.40	0.57	0.74	MP2/MP1	1.87	1.20	0.88
HW (mm)	0.29	0.44	0.60	MP2/MP3	2.58	2.67	2.80
FRL (mm)	0.32	0.47	0.60	MP/LP	1.16	1.10	1.15
OCW (mm)	0.20	0.27	0.40	LP2/LP1	1.83	1.18	0.85
HL/HW	1.36	1.30	1.24	L3 (mm)	0.99	1.39	1.80
HW/OCW	1.48	1.62	1.51	L3/L1	1.36	1.37	1.39
COL/HL	0.20	0.19	0.19	L3/L2	1.15	1.19	1.20
FRL/HL	0.81	0.81	0.81	L3/HW	3.39	3.16	3.00
A/HW	0.88	0.78	0.69	L3 (CO/FE)	0.94	0.94	0.94
A3/A1	3.14	2.45	1.93	L3 (TI/FE)	0.71	0.71	0.67
A3/A2	1.57	1.29	1.04	L3 (TA/FE)	0.88	0.83	0.71
A4/A3	0.41	0.37	0.38	L3 (CL/TA)	0.52	0.43	0.33
A3'/A4	0.89	0.80	0.87	LAS (mm)	0.09	0.12	0.16
MNL/MNW	4.00	4.38	4.35	LAS/HW	0.32	0.28	0.27

of two palpomeres; palpomere 2 longer than palpomere 1. *Thorax:* Terga convex, pronotum slightly shorter than meso- and metanotum combined, meso- and metanotum subequal; protergite subrectangular, margins rounded, more developed than transverse meso- and metatergite; sterna membranous; spiracles absent. Legs (figs. 11–12) long, composed of six articles, prothoracic leg shortest, metathoracic leg longest; coxa elongate, trochanter divided into two parts by an annulus, femur, tibia and tarsus slender, subcylindrical, pretarsus with two long, slender, slightly curved claws; posterior claw shorter than anterior claw on pro- and mesothoracic legs, posterior claw longer than anterior claw on metathoracic leg; surface of legs lacking minute spinulae; ventrodistal surface of tarsus and to a lesser extent tibia with elongate spinulae (more developed on prothoracic leg). *Abdomen:* Eight-segmented; tergites I–VII transverse, lacking spiracles; segment VIII (figs. 13–14) completely sclerotized, ring-like, lacking anterotransverse carina, covered with minute spinulae; siphon very short. Urogomphus not described (broken). *Chaetotaxy* (*figs. 2–14*)*:* Similar to that of a generalized Hydroporinae larva (Alarie & Harper, 1990; Alarie et al., 1990; Alarie, 1991; Alarie & Michat, 2007) except for following features: anteroventral margin of nasale with a half circle of 12 short lamellae clypeales directed downwards; pore FRc submarginal, contiguous to seta FR7; pores PAd, PAe and PAj absent; pore

PAg present; pore ANf absent; setae MX4, MX8, MX9 and MX10 absent; pore MXj absent; seta LA2 absent; we were unable to find pore LAb, but could not establish if it is really absent; seta TR2 absent; pore FEa absent; seta TI7 short, spine-like; pores ABa and ABc absent; seta AB10 hair-like.

Instar II (*figs. 15–18*). As for instar I except for following features: *Body:* Measurements and ratios characterizing body shape shown in table 3. *Head* (*fig. 15*)*:* Egg bursters absent; lateral branches of nasale well visible in dorsal view; parietals without reticulation; neck constriction well marked; occipital suture present; maxillary palpomere 1 relatively more elongate, slightly shorter than palpomere 2; labial palpomere 1 relatively more elongate, slightly shorter than palpomere 2. *Thorax:* Tarsal ventral spinulae more developed, present all along the segment. *Abdomen:* Urogomphomere 1 long, with two fractures along its length (fig. 16). Urogomphomere 2 not described (broken). *Chaetotaxy:* Anteroventral margin of nasale with 22 lamellae clypeales; head capsule with numerous hair-like secondary setae; parietal with three short spine-like secondary setae on each lateroventral margin; mandible with one hair-like secondary seta on basoexternal margin; thoracic tergites with several secondary setae, mainly on posterior and lateral margins; secondary leg setation detailed in table 4 and figs. 17–18; abdominal sclerites I–VIII with some secondary setae on posterior half (fig. 16); U1 lacking secondary setae (fig. 16).

Instar III (*figs. 19–22*). As for instar II except for following features: *Body:* Measurements and ratios characterizing body shape shown in table 3. *Head* (*fig. 19*)*:* Antennomere 4 shortest, antennomeres 2 and 3 longest, subequal; maxillary palpomere 1 longest, somewhat more elongated than palpomere 2; labial palpomere 1 longest, somewhat more elongated than palpomere 2. *Thorax:* Spiracles present on mesothorax. *Abdomen:* Spiracles present on segments I–VII. *Chaetotaxy:* Anteroventral margin of nasale with 46 lamellae clypeales; parietal with seven short spine-like secondary setae on each lateroventral margin; secondary setation on cephalic capsule, thoracic and abdominal sclerites more abundant; secondary leg setation detailed in table 4 and figs. 20–21; secondary setation on abdominal segment VIII detailed in fig. 22.

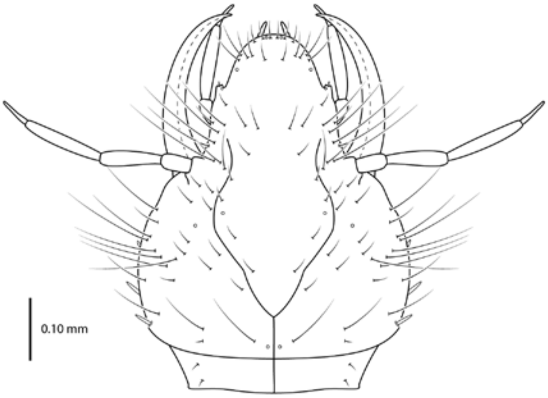
Habitat

Adults and larvae were collected in shaded forest streams, at 90–110 m a.s.l.

Results of the parsimony analysis

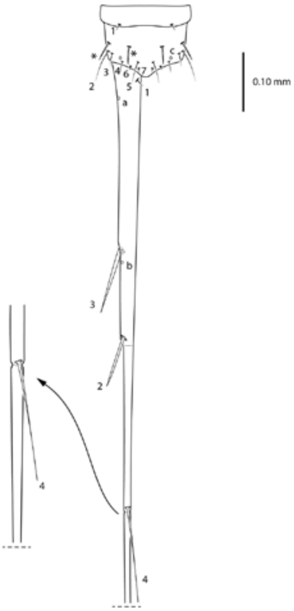
In total, 94 informative characters (60 binary and 34 multistate) were coded for larvae of 26 species of Hydroporinae and one outgroup, *Laccophilus obliquatus* Régimbart, 1889 (supplementary table S1).

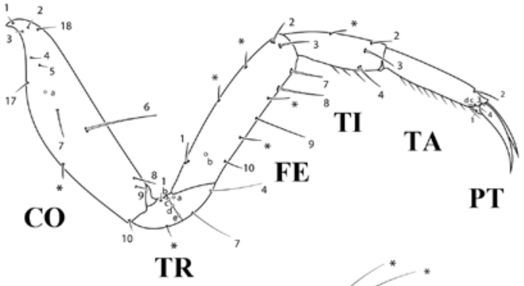
The analysis of the data matrix (supplementary table S2) with TNT resulted in 19 most parsimonious trees of 267 steps (CI = 0.42; RI = 0.61) (fig. 23). The strict consensus tree (fig. 24) supports the monophyletic origin of the tribe Bidessini and the placement of *Hydrodessus latotibialis* as sister to the other Bidessini studied. If we except *Liodessus* and *Anodocheilus* which emerge as a distinct clade with low support, all the other genera studied are part of an unresolved polytomy.



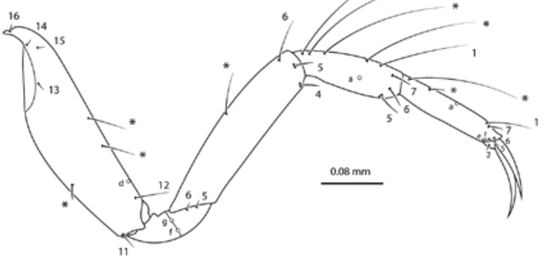
15

16





17



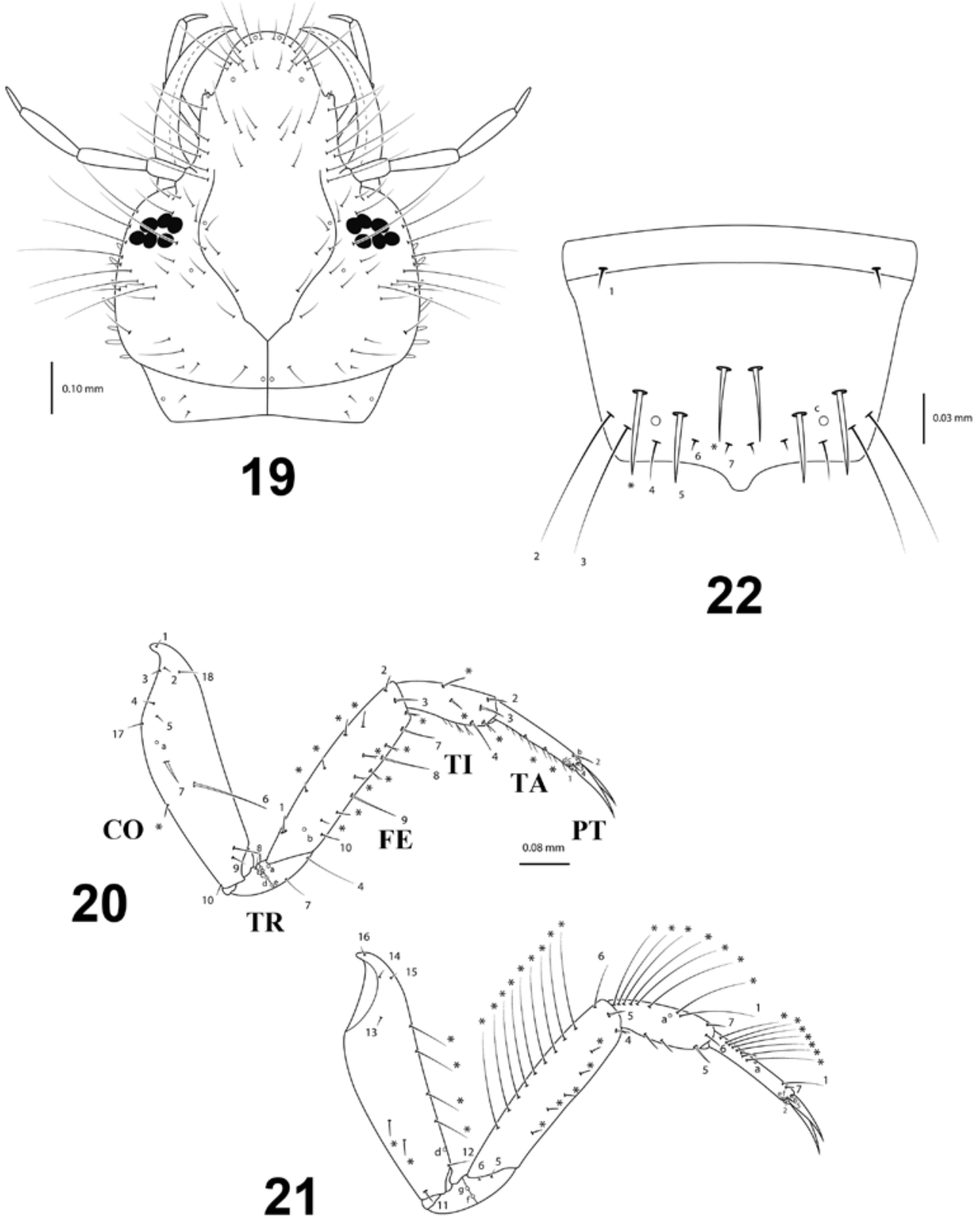
18

FIGURES 15–18 *Hydrodessus latotibialis* Miller, 2016, instar II larva. 15, head capsule, dorsal view. 16, abdominal segment VIII and urogomphus, dorsal view. 17, prothoracic leg, anterior view. 18, prothoracic leg, posterior view. CO, coxa. FE, femur. PT, pretarsus. TA, tarsus. TI, tibia. TR, trochanter. (*), secondary setae

TABLE 4 Number and position of secondary setae on the legs of larvae of *Hydrodessus latotibialis* Miller, 2016

Segment	Position	Instar II (n = 1)	Instar III (n = 1)
Coxa	A	0 / 0 / 0	0 / 2 / 2
	PD	2 / 3 / 3–4	4 / 4–5 / 4–5
	V	1–2 / 1 / 2	3 / 1–2 / 2
	Total	3–4 / 4 / 5–6	7 / 8 / 8–9
Trochanter	Pr	0 / 1 / 1	0 / 1 / 1
	Total	0 / 1 / 1	0 / 1 / 1
Femur	A	0 / 0 / 0	1 / 1–2 / 4
	AD	2 / 3 / 3–4	4 / 5–6 / 6–7
	AV	1–2 / 2 / 2	6 / 4–5 / 3
	PD (NS)	1 / 0 / 0	9 / 10 / 7
	PV	0 / 3 / 4–5	5 / 5–6 / 7–9
	Total	4–5 / 8 / 9–11	25 / 26–28 / 27–30
Tibia	A	0 / 0 / 0	1 / 2 / 1–4
	AD	1 / 2 / 4	1 / 2 / 4
	AV	0 / 1 / 2	1 / 2 / 2–4
	PD (NS)	3–4 / 5–6 / 5	7 / 12–13 / 10–12
	PV	0 / 1 / 1–3	2 / 4–5 / 6
	Total	5–4 / 9–10 / 12–14	12 / 22–24 / 23–30
Tarsus	AD	1 / 1 / 1	1 / 1–2 / 1–2
	PD (NS)	1 / 2–3 / 4–5	7 / 7 / 9–12
	PV	0 / 0–1 / 1	2 / 4 / 5
	Total	2 / 4 / 6–7	10 / 12–13 / 15–19

Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively. A = anterior, AD = anterodorsal, AV = anteroventral, NS = natatory setae, PD = posterodorsal, Pr = proximal, PV = posteroventral, V = ventral, Total = total number of secondary setae on the segment (excluding primary and natatory setae).



FIGURES 19–22 *Hydrodessus latotibialis* Miller, 2016, instar III larva. 19, head capsule, dorsal view. 20, prothoracic leg, anterior view. 21, prothoracic leg, posterior view. 22, abdominal segment VIII, dorsal view. CO, coxa. FE, femur. PT, pretarsus. TA, tarsus. TI, tibia. TR, trochanter. (*), secondary setae

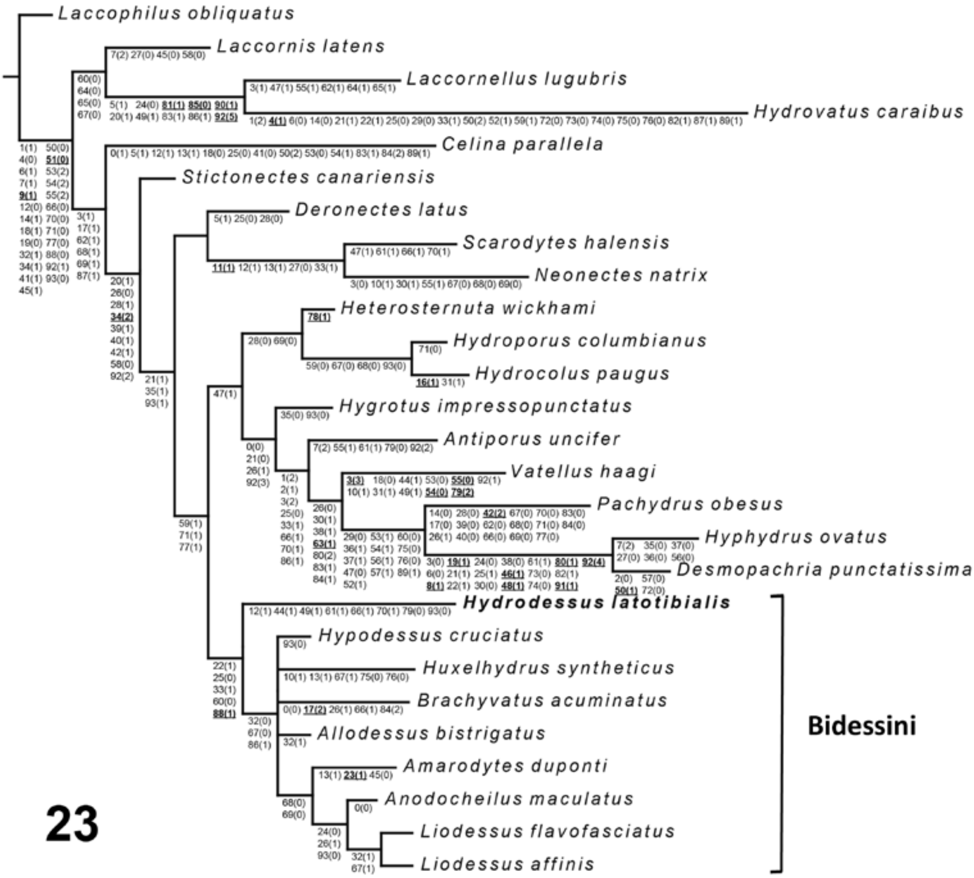


FIGURE 23 One of most parsimonious cladograms of 26 terminal taxa of Hydroporinae, with characters mapped for each clade

Discussion

Phylogenic relationship of Hydrodessus within Bidessini

Despite the low number of genera representing several tribes, our study supports previous results on suprageneric relationships within Hydroporinae based on larval morphology (Michat et al., 2017). In particular, an ancestral condition of Laccornini, Hydrovatini, Pachydrini and Methlini, a close relationship of Hyphydrini, Pachydrini and Vatellini, and a largely polyphyletic Hydroporini, with several genera more related to other tribes than to each other, are supported by our analysis.

The description of *Hydrodessus latotibialis* larvae presented in this article brings to 18 the number of Bidessini genera whose larval morphology is known (table 1), most of which according to the now generalized descriptive format that

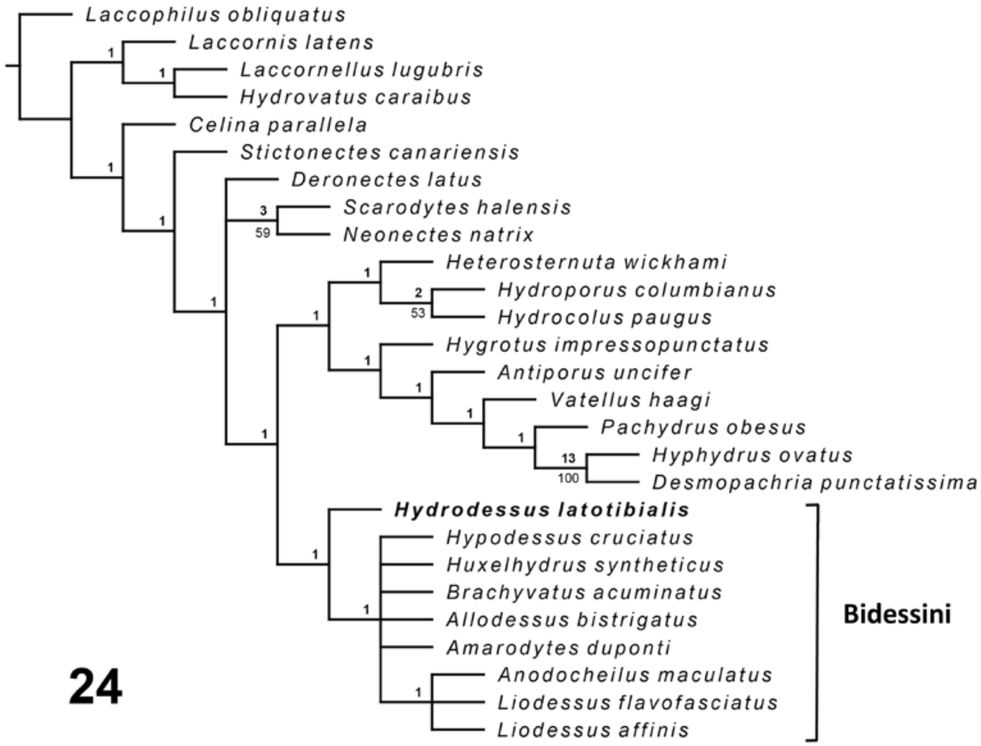


FIGURE 24 Strict consensus cladogram of most parsimonious cladograms of 26 terminal taxa of Hydroporinae based on larval characters, using *Laccophilus obliquatus* as outgroup

includes chaetotaxy (Alarie & Michat, 2023). Although weakly supported, our analysis confirms the monophyletic origin of the Bidessini genera studied which are characterized by a unique character among the Hydroporinae, namely the shared absence of the primary pore ABc on the dorsal surface of the last abdominal segment (character 88). This feature was previously proposed as a synapomorphy of the Bidessini (Michat & Alarie, 2008; Michat et al., 2010) and distinguishes the members of this tribe from the remaining Hydroporinae. This was later confirmed by Michat et al. (2017) in a comprehensive phylogenetic analysis of Dytiscidae. Based on adult morphology and molecular data, Miller & Bergsten (2014) also recovered Bidessini as monophyletic in line with larvae data.

When compared to other Bidessini studied, larvae of *Hydrodessus* are distinguished by several character states: parietals constricted at level of occipital suture in instars II–III (character 12; figs. 15, 19); primary pore MXj absent (character 44); primary seta LA2 absent (character 49; fig. 9); presence of secondary natatory setae on femora (character 61), tibiae (character 66), and tarsi (character 70) (figs. 18, 21); and, siphon very short, bulge-like, not projecting beyond bases of urogomphi in instar III (character 79; fig. 22). As previously noted by Miller & Bergsten (2014), the internal phylogeny of Bidessini needs considerable phylogenetic revisionary work because of the difficulty of many morphological character combinations defining the various genera and many uncomfortably placed taxa and potentially paraphyletic groups.

According to our results, *Hydrodessus* is recovered as the sister group to the other Bidessini genera studied, in agreement with a previous hypothesis of a basal position of this genus based on adult characters (Miller & Bergsten, 2014). *Hydrodessus* was placed as *incerta sedis* with respect to tribe (Miller, 2001) until Miller & Bergsten (2014) placed it back into Bidessini. According to their analysis *Hydrodessus* may be closely related to *Amarodytes* Régimbart, 1900 and *Peschetius* Guignot, 1942, which are part of a clade (except for a species of *Amarodytes*) that is sister to the other Bidessini (Miller & Bergsten, 2014).

An underlying objective of this study was to compare the *Hydrodessus* larva with that of *Amarodytes* given the suggested sister-group relationship between these two genera (Miller, 2001; Miller & Bergsten, 2014). In our analysis, *A. duponti* (Aubé, 1838), the only *Amarodytes* species with known larva, is recovered in a clade with other Bidessini, apart from *Hydrodessus* (fig. 24). The larvae of *Amarodytes* stand out as quite different morphologically from those of *Hydrodessus* in several characters, such as the occipital suture present in instar I (character 13), the absence of pore PAk (character 23), the pore MNa inserted approximately at the same level as pore MNb (character 32), the absence of pore MXk (character 45), the seta AB10 spine-like (character 86), and the presence of secondary setae on urogomphus in instars II and III (character 93), apart from the unique characters that define *Hydrodessus* within Bidessini (see above). One should keep in mind, however, that previous studies based on adult morphology and molecular data (Miller & Bergsten, 2014; Miller et al., 2023) suggested that *Amarodytes* as currently defined may not be monophyletic. In this sense, the study of larvae of other *Amarodytes* species could help to better understand the phylogenetic position of ancentral Bidessini. Obviously, sampling larvae of more Bidessini species and genera is needed to ascertain whether the hypothesis of non-monoplyly of *Amarodytes* is supported, as well as to shed light on the relationships of *Hydrodessus* with other Bidessini genera.

Biology and ecology

Although little is known about the biology of Bidessini larvae, available data suggest that most of them do not swim and that they are associated to bed sediments of water bodies (Alarie et al., 1990; Galewski, 1971; Alarie, 1995; Michat & Alarie, 2008). In this regard, a highly distinctive feature of *Hydrodessus* larvae is the presence of natatory setae on legs. Whereas present in *Brachyvatus* (tibia only) (Michat & Torres, 2013) and *Hemibidessus* (femur and tibia only) (Michat et al., 2022), larvae of *Hydrodessus* remain the only known Bidessini with natatory setae on all femora, tibiae and tarsi.

Natatory setae are generally associated with an enhanced swimming ability (Michat et al., 2022; Alarie et al., 2021).

Their presence on femur, tibia and tarsus, therefore, would suggest that *Hydrodessus* larvae are more efficient swimmers compared to other known Bidessini. On the other hand, it seems to be a correlation between presence of natatory setae on legs and utilization of more vegetated microhabitats, as suggested by Galewski (1971). Larvae of *Brachyvatus* and *Hemibidessus*, the only other known bidessine genera with natatory setae on legs, were observed living in association with the aquatic vegetation (Michat & Torres, 2013; Michat et al., 2022), which gives support to Galewski's hypothesis. Larval swimming ability, and its associated morphological structures, may have evolved in response to transitions to novel microhabitats, such as those structured by the aquatic vegetation, by larvae primitively inhabiting less complex microhabitats such as the sediments of water bodies (Michat et al., 2017).

Little is known about the biology and habitat of *Hydrodessus* species, mainly because most specimens deposited in collections were found using light traps (Miller, 2016; Spangler, 1985). The few specimens collected in their habitat were mostly found in running waters (e.g., Benetti et al., 2020). However, knowing that the larvae studied in this paper are stream dwellers, we suggest that the extensive presence of natatory setae on legs may also be interpreted as an adaptation to survive in lotic environments.

Acknowledgements

We wish to thank all the people who contribute in the field works and data acquisition. Special thanks to Janaina Brito for collecting beetle specimens. CJB thanks CNPq and FAPEAM for a post-doctoral fellowship (processes 302031/2015-4, 104231/2018-1, and 160666/2019-8) and Spain Ministry of Universities and NextGenerationEU (María Zambrano Program). NH is CNPq research fellow (308970/2019-5). We also thank the two anonymous reviewers for their supportive remarks.

Author contributions

CJB and MCM conceptualization and designed the study, CJB sorted, processed and determined the specimens, and wrote the manuscript draft. MCM prepared, and mounted specimens in glass slides and observed characters, and performed the phylogenetic analyses. CJB and MCM made the drawings and prepared figures.

All authors contributed to the discussion, reviewed the text and have read and agreed to the published version of the manuscript.

Funding

The following projects supported this study: CNPq 401866/2022-0/ Chamada 26/2021; PROTAX/CNPq 440616/2015-8; CNPq/MCTI/F5P/PROTAX-FAPEAM (Fundação de Amparo à Pesquisa do Estado do Amazonas); PRONEX (SECTI/FAPEAM/CNPq); FAPEAM POSGRAD; INCT ADAPTA II funded by CNPq – Brazilian National Research Council (465540/2014-7), FAPEAM – Amazonas State Research Foundation (062.1187/2017). Some specimens were collected under the "Rede Amazônia Sustentável (RAS)" project

(CNPq; 574008/2008-0), Empresa Brasileira de Pesquisa Agropecuária (SEG: 02.08. 06.005.00), the UK Darwin Initiative (17-023), The Nature Conservancy, and the Natural Environment Research Council (NE/F01614X/1 and NE/G000816/1) and SEPLANCTI, FAPEAM-PRONEX (Governo do Estado do Amazonas).

Supplementary material

Supplementary material is available online at:
https://doi.org/10.6084/m9.figshare.27003514

References

Alarie, Y. (1991) Primary setae and pores on the cephalic capsule and head appendages of larval Hydroporinae (Coleoptera: Dytiscidae: Hydroporinae). *Can. J. Zool.*, 69, 2255–2265.

Alarie, Y. (1995) Primary setae and pores on the legs, the last abdominal segment, and the urogomphi of larvae of Nearctic Colymbetinae (Coleoptera: Adephaga: Dytiscidae) with an analysis of their phylogenetic relationships. *Can. Entomol.*, 127, 913–943.

Alarie, Y. & Harper, P.P. (1990) Primary setae and pores on the last abdominal segment and the urogomphi of larval Hydroporinae (Coleoptera: Adephaga: Dytiscidae), with notes on other dytiscid larvae. *Can. J. Zool.*, 68, 368–374.

Alarie, Y., Harper, P.P. & Maire, A. (1990) Primary setae and pores on legs of larvae of Nearctic Hydroporinae (Coleoptera: Dytiscidae). *Quaest. Entomol.*, 26, 199–210.

Alarie, Y. & Michat, M.C. (2007) Primary setae and pores on the maxilla of larvae of the subfamily Hydroporinae (Coleoptera: Adephaga: Dytiscidae): ground plan pattern reconsidered. *The Coleopt. Bull.*, 61, 310–317.

Alarie, Y. & Michat, M.C. (2023) Larval chaetotaxy of world Dytiscidae (Coleoptera: Adephaga) and implications for the study of Hydradephaga. In: D.A. Yee (Ed.) *Ecology, Systematics, and the Natural History of Predaceous Diving Beetles* (*Coleoptera: Dytiscidae*), pp. 17–53. Springer, Cham. https://doi.org/10.1007/978-3-031-01245-7_2.

Alarie, Y., Michat, M.C., Archangelsky, M. & Barber-James, H.M. (2007) Larval morphology of *Liodessus* Guignot, 1939: generic characteristics, descriptions of five species and comparisons with other members of the tribe Bidessini (Coleoptera: Dytiscidae: Hydroporinae). *Zootaxa*, 1516, 1–21. https://doi.org/10.11646/zootaxa.1516.1.1.

Alarie, Y., Michat, M.C. & Miller, K.B. (2011) Notation of primary setae and pores on larvae of Dytiscinae (Coleoptera: Dytiscidae), with phylogenetic considerations. *Zootaxa*, 3087, 1–55.

Alarie, Y., Michat, M.C., Nilsson, A.N., Archangelsky, M. & Hendrich, L. (2009a) Larval morphology of *Rhantus* Dejean, 1833 (Coleoptera: Dytiscidae: Colymbetinae): descriptions of 22 species and phylogenetic considerations. *Zootaxa*, 2317, 1–102.

Alarie, Y., Michat, M.C. & Watts, C.H.S. (2009b) Larval morphology of *Paroster* Sharp, 1882 (Coleoptera: Dytiscidae: Hydroporinae): reinforcement of the hypothesis of monophyletic origin and discussion of phenotypic accommodation to a hypogaeic environment. *Zootaxa*, 2274, 1–44.

Alarie, Y., Michat, M.C. & Watts, C.H.S. (2021) Description of the mature larva of four species of the Australasian endemic genus *Sternopriscus* Sharp, 1882 (Coleoptera: Dytiscidae) with phylogenetic considerations. *Aquat. Insects*, 42, 197–215. http://doi.org/10.1080/01650424.2021.1919716.

Alarie, Y. & Wewalka, G. (2001) Description of the mature larva of *Glareadessus stocki* Wewalka and Biström (Coleoptera: Dytiscidae), a stygobiontic Bidessini from the Persian Gulf region. *Coleopt. Bull.*, 55, 144–151. https://doi.org/10.1649/0010-065X(2001)055[0144:DOTMLO]2.0.CO;2.

Benetti, C.J., Michat, M.C. & Hamada, N. (2020) *Hydrodessus ducke* sp.n. and new records of other species of the genus (Coleoptera, Dytiscidae, Bidessini). *Zootaxa*, 4743, 047–060. http://doi.org/10.11646/zootaxa.4743.1.4.

Bertrand, H. (1963) Contribution à l'étude des premiers états des coléoptères aquatiques de la région éthiopienne (5° note). Families: Haliplidae, Dytiscidae, Gyrinidae (Hydrocanthares). *Bull. I.F.A.N.* (*A*), 25, 389–466.

Bertrand, H. (1972) *Larves et nymphes des coléoptères aquatiques du globe*. F. Paillart, Abbeville, Paris.

Biström, O. (1988) Generic review of the Bidessini (Coleoptera, Dytiscidae). *Acta Zool. Fenn.*, 184, 1–41.

Brasavola de Massa, A. (1930) Note coleotterologiche. *Stud Trent. Sci. Nat.*, 2, 3–6.

Fukuda, A., Kurosa, K. & Hayashi, N. (1959) Coleoptera. In: A. Kawada, T. Esaki, T. Ishii, T. Shiraki & H. Yuasa (Eds) *Illustrated Insect Larvae of Japan*, pp. 392–545. The Hokuryukan Co. Ltd., Tokyo.

Galewski, K.A. (1971) Study on morphobiotic adaptations of European species of the Dytiscidae (Coleoptera). *Pol. Pis. Entomol.*, 41, 487–702.

Goloboff, P.A. & Morales, M.E. (2023) TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. *Cladistics*, 39, 144–153. https://doi.org/10.1111/cla.12524.

Kitching, I.J., Forey, P.L., Humphries, C.J. & Williams, D.M. (1998) *Cladistics, second edition. The Theory and Practice of Parsimony Analysis. Systematics Association Publications, 11.* Oxford University Press, New York.

Matta, J.F. (1983) Description of the larva of *Uvarus granarius* (Aubé) (Coleoptera: Dytiscidae) with a key to the Nearctic Hydroporinae larvae. *Coleopt. Bull.*, 37, 203–207.

Meuche, A. (1937) Der Käfer *Bidessus hamulatus* Gyll. in Ostholstein. *Entomol. Blätter*, 33, 427–436.

Michat, M.C. & Alarie, Y. (2006) The larvae of *Amarodytes duponti* (Aubé) (Coleoptera: Dytiscidae: Hydroporinae), with comments on Bidessini larval morphology and chaetotaxy. *Zootaxa*, 1351, 1–13. https://doi.org/10.11646/zootaxa.1351.1.1.

Michat, M.C. & Alarie, Y. (2008) Morphology and chaetotaxy of larval *Hypodessus cruciatus* (Régimbart) (Coleoptera: Dytiscidae: Hydroporinae), and analysis of the phylogenetic relationships of the Bidessini based on larval characters. *Stud. Neotrop. Fauna E.*, 43, 135–146. https://doi.org/10.1080/01650520701430553.

Michat, M.C., Alarie, Y. & Benetti, C.J. (2022) Larval morphology of the Neotropical diving beetle genus *Hemibidessus* Zimmermann, 1921 (Coleoptera: Dytiscidae: Bidessini). *Zootaxa*, 5168, 388–400. https://doi.org/10.11646/zootaxa.5168.3.9.

Michat, M.C., Alarie, Y. & Hájek, J. (2015) Larval morphology of *Yola* Gozis, 1886 (Coleoptera: Dytiscidae: Bidessini) and comparison with other genera of the tribe Bidessini. *Coleopt. Bull.*, 69, 489–497. https://doi.org/10.1649/0010-065X-69.3.489.

Michat, M.C., Alarie, Y. & Hájek, J. (2018) Larvae of *Huxelhydrus syntheticus* Sharp, 1882 (Coleoptera: Dytiscidae: Bidessini). *Zootaxa*, 4524, 121–131. https://doi.org/10.11646/zootaxa.4524.1.9.

Michat, M.C., Alarie, Y. & Miller, K.B. (2017) Higher-level phylogeny of diving beetles (Coleoptera: Dytiscidae) based on larval characters. *Syst. Entomol.*, 42, 734–767. https://doi.org/10.1111/syen.12243.

Michat, M.C., Alarie, Y. & Watts, C.H.S. (2010) Descriptions of the first-instar larva of the hypogaeic species *Neobidessodes limestoneensis* (Watts & Humphreys) and of the third-instar larva of *Hydroglyphus balkei* Hendrich (Coleoptera: Dytiscidae: Bidessini) with phylogenetic considerations. *Zootaxa*, 2658, 38–50. https://doi.org/10.11646/zootaxa.2658.1.2.

Michat, M.C., Alarie, Y. & Watts, C.H.S. (2011) Larval morphology of *Allodessus* Guignot (Coleoptera: Dytiscidae). *Aquat. Insects*, 33, 27–40. https://doi.org/10.1080/01650424.2011.574228.

Michat, M.C., Alarie, Y. & Watts, C.H.S. (2012) Phylogenetic relationships and comparative larval morphology of epigean and stygobitic species of *Limbodessus* Guignot, 1939 (Coleoptera: Dytiscidae: Bidessini). *Zootaxa*, 3584, 1–110. https://doi.org/10.11646/zootaxa.3584.1.1.

Michat, M.C. & Torres, P.L.M. (2006) The unknown larva of *Anodocheilus* Babington (Coleoptera: Dytiscidae: Hydroporinae: Bidessini): description of *A. maculatus* Babington and chaetotaxic considerations. *T. Am. Entomol. Soc.*, 132, 431–444. https://doi.org/10.3157/0002-8320(2006)132[431:TULOAB]2.0.CO;2.

Michat, M.C. & Torres, P.L.M. (2013) The unknown larva of the minute diving beetle genus *Brachyvatus* Zimmermann, 1919 (Coleoptera: Dytiscidae: Bidessini). *Entomol. News*, 123, 139–153. https://doi.org/10.3157/021.123.0205.

Miller, K.B. (2001) On the phylogeny of the Dytiscidae (Insecta: Coleoptera) with emphasis on the morphology of the female reproductive system. *Insect Syst. Evol.*, 32, 45–92.

Miller, K.B. (2016) Revision of the Neotropical diving beetle genus *Hydrodessus* J. Balfour-Browne, 1953 (Coleoptera, Dytiscidae, Hydroporinae, Bidessini). *ZooKeys*, 580, 45–124. https://doi.org/10.3897/zookeys.580.8153.

Miller, K.B., Benetti, C.J. & Michat, M.C. (2023) *Miradessus* gen. nov. from South America described for two species previously in *Amarodytes* Régimbart, 1900 and two new species (Arthropoda, Insecta, Coleoptera, Adephaga, Dytiscidae, Hydroporinae, Bidessini). *ZooKeys*, 1176, 13–28. https://doi.org/10.3897/zookeys.1176.104980.

Miller, K.B. & Bergsten, J. (2014) The phylogeny and classification of predaceous diving beetles. In: D.A. Yee (Ed.) *Ecology, Systematics, and the Natural History of Predaceous Diving Beetles* (*Coleoptera: Dytiscidae*), pp. 49–171. Springer, New York.

Miller, K.B. & Bergsten, J. (2016) *Diving Beetles of the World. Systematics and Biology of the Dytiscidae*. Johns Hopkins University Press, Baltimore.

Needham, J.G. & Williamson, H.V. (1907) Observations on the natural history of diving beetles. *Am. Nat.*, 41, 477–494.

Nilsson, A.N. (1985) The larvae of the predaceous diving beetles *Bidessus grossepunctatus, Graptodytes granularis* and *G. pictus*

(Coleoptera: Dytiscidae). *Aquat. Insects*, 7, 165–172.

Nilsson, A.N. & Hajek, J.A. (2024) *A World Catalogue of the Family Dytiscidae, or the Diving Beetles* (*Coleoptera, Adephaga*). Version 1.I.2024. Available at: http://www.waterbeetles.eu/documents/W_CAT_Dytiscidae_2024_new.pdf (accessed 24 June 2024).

Perkins, P.D. (1980) Larval and pupal stages of a predaceous diving beetle, *Neoclypeodytes cinctellus* (LeConte) (Dytiscidae: Hydroporinae: Bidessini). *P. Entomol. Soc. Wash.*, 82, 474–481.

Richoux, P. (1982) Introduction pratique à la systématique des organismes des eaux continentales françaises. 2. Coléoptères aquatiques (genres: adultes et larves) (Suite). *Bull. Mens. Soc. Linn. L.*, 51 (8), 257–272.

Satô, M. (1964) Studies on the marine beetles in Japan, II. Study on the dytiscid-beetle dwelling in the tide-pool. *J. Nagoya J. Coll.*, 10, 60–71.

Spangler, P.J. (1985) Five new species of the predacious water beetle genus *Hydrodessus* from Guyana and a key to the species (Coleoptera: Dytiscidae). *P. Acad. Nat. Sci. Phila.*, 137, 80–89.

Watts, C.H.S. (1963) The larvae of Australian Dytiscidae. *T. Roy. Soc. South Aust.*, 87, 23–40.

Watts, C.H.S. (1970) The larvae of some Dytiscidae (Coleoptera) from Delta, Manitoba. *Can. Entomol.*, 102, 716–728.

Wiley, E.O. (1981) *Phylogenetics. The theory and practice of phylogenetic systematics*. John Wiley & Sons, New York.

Young, F.N. (1967) A key to the genera of American bidessine water beetles, with descriptions of three new genera (Coleoptera: Dytiscidae, Hydroporinae). *Coleopt. Bull.*, 21, 75–84.

Young, F.N. (1969) A checklist of the American Bidessini (Coleoptera: Dytiscidae–Hydroporinae). *Smith. C. Zool.*, 33, 1–5. https://doi.org/10.5479/si.00810282.33.