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Larval morphology of the enigmatic genus *Queda* Sharp, 1882 supports monophyly of Hydrovatini (Coleoptera, Dytiscidae)

Mariano C. Michat[1,2], Yves Alarie[3], Cesar J. Benetti[4,5], Juan I. Urcola[1,2], Georgina Rodriguez[1,2], Patricia L. M. Torres[1,2]

1 *University of Buenos Aires, Faculty of Exact and Natural Sciences, Department of Biodiversity and Experimental Biology, Laboratory of Entomology, Buenos Aires, Argentina*

2 *CONICET-University of Buenos Aires, Institute of Biodiversity and Experimental and Applied Biology (IBBEA), Buenos Aires, Argentina*

3 *School of Natural Sciences, Laurentian University, Ramsey Lake Road, Sudbury, Ontario, Canada*

4 *Departamento de Biodiversidad y Gestión Ambiental, Facultad de Ciencias Biológicas y Ambientales, Universidad de León, Campus de Vegazana, 24071, León, Spain*

5 *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*

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Corresponding author: Mariano C. Michat (marianoide@gmail.com)

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Abstract

A comprehensive phylogenetic analysis of larval characters, including for the first time members of the rare and enigmatic genus *Queda* Sharp, 1882 was conducted to test the hypotheses of monophyly and relationships of the tribe Hydrovatini within the diving-beetle subfamily Hydroporinae. Our results indicate that Hydrovatini (including both *Queda* and *Hydrovatus* Motschulsky, 1853) is monophyletic and unambiguously supported by the absence of the primary pore PAo on the parietal and by the antennal process (commonly identified as A3') arising from the base of the antennomere 4. This result agrees with the original concept of the tribe introduced more than 100 years ago but challenged by some authors. Our study supports the inclusion of Hydrovatini in a clade of ancestral hydroporine lineages together with Laccornini, Laccornellini and Pachydrini. Within this clade, Hydrovatini is sister to Pachydrini based on the shared absence of an occipital suture in instars II–III, although with weak support. The third-instar larva of *Queda* is diagnosed and described. It is characteristic in the broad and semicircular shape of the nasale, the maxillary cardo partially fused to the stipes, the presence of setiferous tubercles on the cephalic capsule and abdominal segment VIII, and the subcylindrical and relatively well-developed galea which, interestingly, is somewhat more developed than those exhibited by other hydroporines.

Key words

Chaetotaxy, diving beetle, larva, Hydroporinae, phylogeny, *Queda hydrovatoides*

1. Introduction

The diving beetle tribe Hydrovatini is composed of two genera, the speciose and cosmopolitan *Hydrovatus* Motschulsky, 1853 with more than 200 species, and the Neotropical *Queda* Sharp, 1882 comprising only three species (Nilsson and Hájek 2025). This last genus was created by Sharp (1882) to place the sole species *Q. compressa* from Brazil. Later, Zimmermann (1921) introduced a second (and much smaller) species, *Q. hydrovatoides*, also from this country. And, finally, Biström (1990) described *Q. youngi*, which has a larger geographical distribution including Panama, Venezuela, and Brazil. This species was later cited from Paraguay and Argentina (Trémouilles et al. 2004; Libonatti et al. 2011). Very little is known about the natural history of *Queda* (Miller and Bergsten 2016). The only available information in this regard relates to the collection of two adults of *Q. youngi* in a slow current stream, associated with floating vegetation (Torres et al. 2012).

The phylogenetic relationships of the tribe Hydrovatini have been the subject of much debate over the years. Since the tribe was created, its classification remained unchallenged until Wolfe (1985, 1988) questioned its monophyly based on morphological differences in the adult abdominal apex and legs between *Queda* and *Hydrovatus* (without suggesting, however, any formal changes). Wolfe also postulated that Hydrovatini is an ancestral lineage within Hydroporinae and considered it sister to the tribe Methlini (see also Désamoré et al. 2018). Biström (1990, 1997) revised the species of *Queda* and *Hydrovatus* respectively, and considered both part of the Hydrovatini. Miller (2001) and Miller et al. (2006), based also on adult morphology (and a few characters from larvae in the latter study), provided a different view and suggested that Hydrovatini is derived within Hydroporinae, sister to Hygrotini. These authors also supported the monophyly of the Hydrovatini including both genera. Michat (2006), based on larval characters, also postulated a derived condition for Hydrovatini, this time more closely related to Hyphydrini (at that time including *Pachydrus* Sharp, 1882). However, *Queda* could not be included in the analysis as the larvae of this genus were unknown. Ribera et al. (2008), based on molecular data, found Hydrovatini sister to Vatellini, although they did not include *Queda* in their analysis. More recently, Miller and Bergsten (2014), in a comprehensive phylogenetic analysis of Dytiscidae combining adult morphological and molecular characters, supported the monophyly of the Hydrovatini and its placement at the base of the Hydroporinae, as sister to the tribe Pachydrini, a relationship later supported by Vasilikopoulos et al. (2021). Finally, Michat et al. (2017), in an extensive analysis of the family based on larval characters but not including *Queda*, supported an ancestral position of Hydrovatini and found it closely related to Laccornellini.

Larval morphology of the Hydrovatini is poorly known. Several descriptions of *Hydrovatus* larvae, which differ greatly in the degree of detail, can be found in the literature (see Michat 2006 for a review and Michat and Alarie 2021). Larvae of *Queda*, however, have been unknown, which hampered considerably the previous hypotheses on the relationships of the Hydrovatini based on larval morphology.

Intensive samplings performed some years ago in the Iberá wetlands, one of the largest wetland ecosystems in South America, located in Argentina's Corrientes province (Neiff and Poi de Neiff 2006), yielded a tiny and strange larva that, at first sight, did not fit any previously known genus, although it was likely attributable to either of the hydroporine tribes Hyphydrini, Pachydrini, or Hydrovatini (see habitus in Fig. 1D, E). A closer inspection under the microscope allowed us to observe that this specimen bears a combination of characters (e.g., absence of an occipital suture; presence of a galea; abdominal segments III–V sclerotized ventrally; absence of the urogomphal seta UR8) that undoubtedly places it in the Hydrovatini. However, other characters, such as a very broad nasale, a cardo only partially fused to the stipes, a robust and clearly longer than broad prementum, and the presence of setiferous tubercles on the head and last

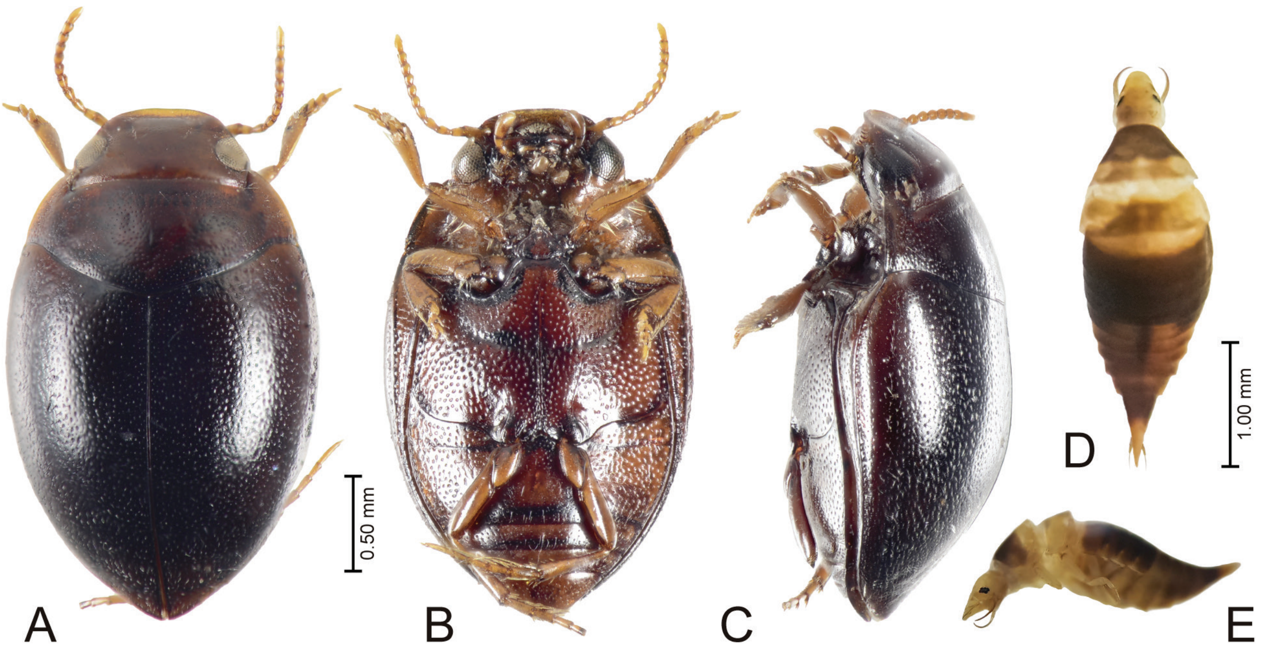

Figure 1. *Queda hydrovatoides* Zimmermann, 1921. **A**–**C** adult male: **A** dorsal aspect; **B** ventral aspect; **C** lateral aspect. **D**, **E** instar III larva: **D** dorsal aspect; **E** lateral aspect.

abdominal segment, exclude it from *Hydrovatus*. Based on this evidence, we pointed to the only other genus in the tribe, i.e., *Queda*. By that time, it was clear that the larva in question was a third instar due to the presence of spiracles on the mesothorax and abdominal segments I–VII. The only member of *Queda* recorded previously from the Iberá wetlands was *Q. youngi*, a large species whose adults range 4.8–6.2 mm in body length. Our tiny larva, however, was too small to be assigned to this species and could only belong to adults about half that size, such as most *Hydrovatus*. Our interest then moved to the large number of adults collected with the larva. Among these there were no *Q. youngi* specimens, but, to our surprise, we found an adult of *Q. hydrovatoides* (Fig. 1A–C), a species so far recorded only from Corumbá in Brazil, and that is half the size of the other two species.

The finding of the larva of *Queda* is very important as it allows to evaluate both the monophyly and relationships of the Hydrovatini based on larval characters and including all the genera in the tribe. For this purpose, we present a comprehensive phylogenetic analysis of the subfamily Hydroporinae, aimed to: (1) test the monophyly of the Hydrovatini; (2) evaluate previous phylogenetic hypotheses on its relationships; and (3) place the genus *Queda* and document its remarkable morphology.

2. Material and methods

2.1. Source and processing of larvae

The description provided in this paper is based on one instar III larva collected at the Iberá wetlands, Corrientes province, Argentina, in December 2019. For a picture of the habitat, see Michat et al. (2024). The specimen was cleared in lactic acid, dissected, and mounted on glass slides in polyvinyl-lacto-glycerol. Observations and drawings were made using an Olympus CX31 microscope equipped with a drawing tube. Drawings were inked digitally with a One by Wacom pen tablet.

The methods and terms used in the morphometric and chaetotaxic analyses follow those employed in previous papers dealing with Hydrovatini larvae (Michat 2006; Michat and Alarie 2021). Despite being an instar III, the primary sensilla of *Queda hydrovatoides* were tentatively identified by comparison with the Hydrovatini ground plan wherever possible. In these cases, homologies were recognized using the criterion of similarity of position (Wiley 1981).

Habitus photographs of the adult were taken with a Nikon D800 digital camera, whereas that of the larva was taken with a Samsung Galaxy S9 cell phone.

2.2. Phylogenetic procedure

For the study of the phylogenetic relationships of Hydrovatini we used a cladistic approach considering the character set provided by the larval morphology and chaetotaxy. A broad taxon sampling of the subfamily Hydroporinae was selected as ingroup, with the purpose of allowing the target taxa to move freely, thus testing relationships in the broadest possible context. Forty-four species were included representing all hydroporine tribes, most of them with multiple genera (except for those that are monotypic) (Table S1). Data for all species were scored directly from the observation of the specimens. Members of all dytiscid subfamilies (except Hydrodytinae which larva is unknown) were selected as the outgroup, rooting the tree in Agabinae, which is considered an ancestral dytiscid lineage and clearly distantly related to the Hydroporinae (e.g., Miller and Bergsten 2014). During character codification, the same instars of each species were compared to avoid the problem of comparing different semaphoronts (Meier and Lim 2009). Exceptions to this rule were *Hydrovatus crassulus* Sharp, 1882 and *Queda hydrovatoides*, for which only instars II–III and Instar III were available, respectively.

The phylogenetic analyses were performed with the program TNT (Goloboff and Morales 2023). All characters were treated as equally weighted, and multistate characters were treated as non-additive. Three search strategies were implemented to find the most parsimonious trees, previously setting “hold 20000” in all cases. Analysis 1: a common heuristic search under “Analize/Traditional search”, using “tree bisection reconnection” (TBR) as algorithm with 200 replicates and saving 100 trees per replication. Analysis 2: involving additional heuristics with 100 random addition sequences and TBR followed by “tree drifting”, using the command “mult 100 =tbr drift ;”. Analysis 3: again 100 random addition sequences and TBR but followed by “ratchet”, using the command “mult 100 = tbr ratchet ;”. Bremer and bootstrap (as implemented in TNT) were used as measures of support for clades. Bremer values were calculated by repeating the commands “hold 20000”, “sub n” and “bsupport”, increasing n (= the length of the suboptimal cladograms) by one step until 10. Values higher than 10 are indicated by the symbol +10. Bootstrap values were calculated using the following parameters: “standard (sample with replacement)”, 1000 replicates.

3. Results

3.1. Characters

In total, 147 characters derived from larval morphology and chaetotaxy were included, of which 112 were coded as binary and 35 as multistate. They are listed in Table S2. All included characters were informative and, therefore, useful to infer relationships of the studied taxa, except characters 20, 28 and 71 which are autapomorphies.

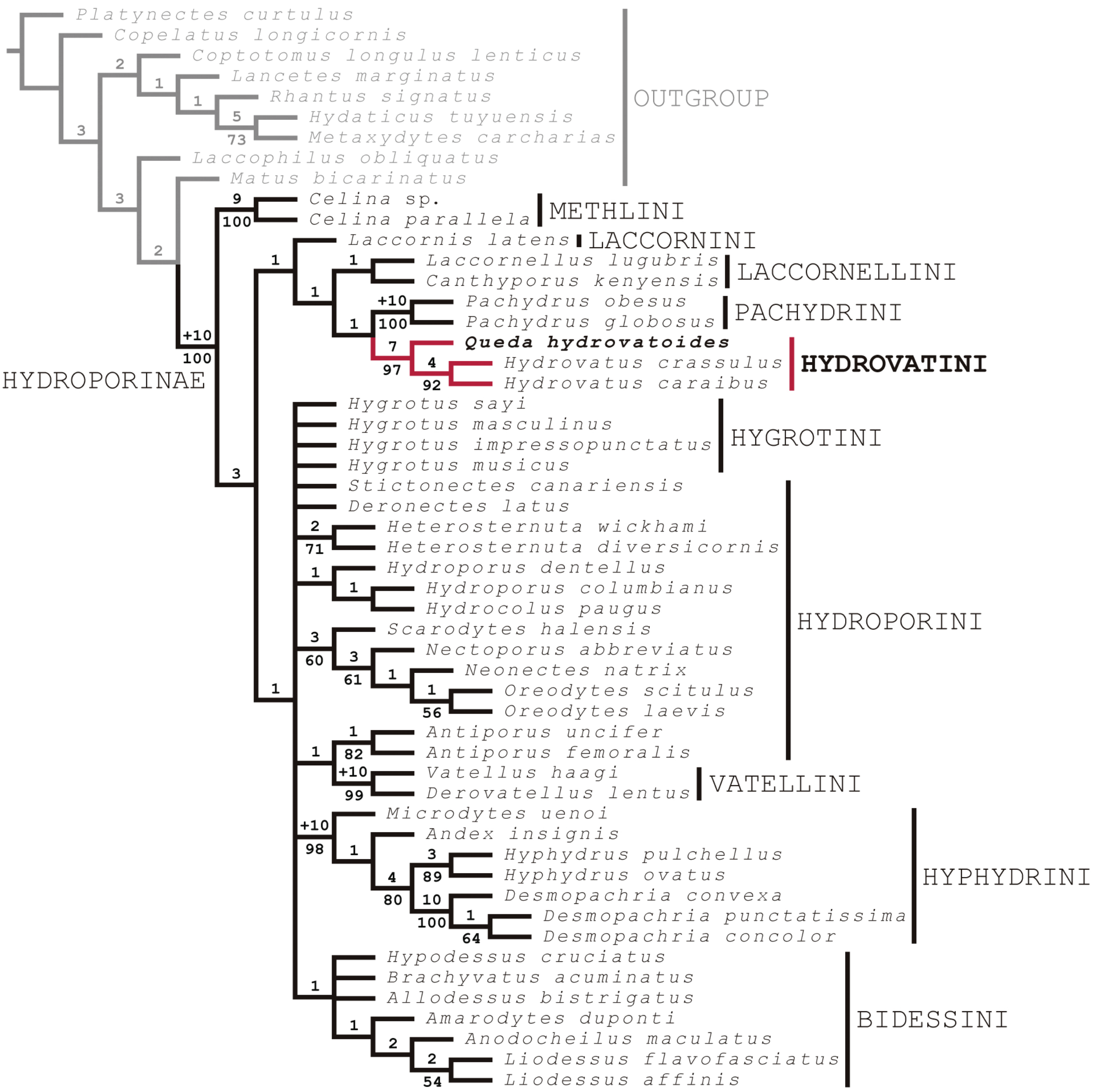

Figure 2. Strict consensus cladogram with Bremer support values indicated above branches and bootstrap values higher than 50 indicated below branches. Clade Hydrovatini indicated in red.

3.2. Results of the phylogenetic analysis

The data matrix is shown in Table S3. The searches with TNT using different parameters (Analyses 1–3, see above) converged to 31 most parsimonious trees of 485 steps (CI = 0.40; RI = 0.78). The strict consensus (of similar topology in the three analyses) is well resolved and informative, except for a large polytomy that involves several genera of Hygrotini and Hydroporini and the tribes Vatellini, Hyphydrini, and Bidessini (Fig. 2). Within a strongly supported Hydroporinae, the tribe Methlini is sister to the remainder of the subfamily, in agreement with some previous analyses based on larval morphology and molecular data (Michat et al. 2017; Vasilikopoulos et al. 2021) but not with others based on adults or molecules (e.g., Wolfe 1985; Miller 2001; Miller and Bergsten 2014). The remaining tribes are separated into two large sister clades, one of them comprising the monophyletic Vatellini, Hyphydrini, and Bidessini, the first two strongly supported and the third one showing weak support, and members of Hygrotini and Hydroporini, which are not recovered as monophyletic groups. The other large clade involves the tribes Laccornini, Laccornellini, Pachydrini and Hydrovatini, all resolved as monophyletic with moderate to high support, except for the weakly supported Laccornellini. Of this grouping, Laccornini is sister to the rest, and Laccornellini is sister to Pachydrini and Hydrovatini, which are resolved as sister groups with low support. The tribe Hydrovatini, with its two genera *Queda* and *Hydrovatus*, is robustly supported and well defined by several characters (see below). Characters were ACCTRAN optimized in one of the most parsimonious trees and character state changes were mapped (Figs 3, 4).

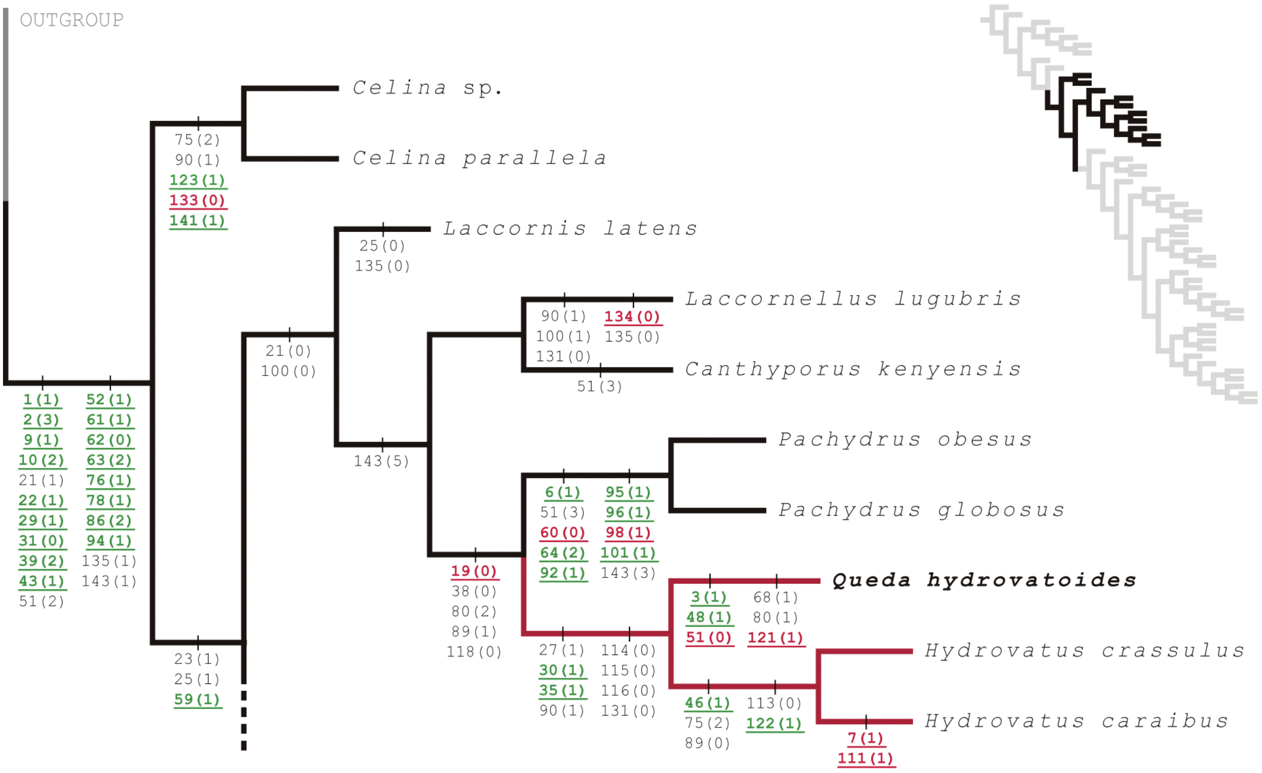

Figure 3. Portion of one of the most parsimonious cladograms with selected character state changes mapped for each clade. Clade Hydrovatini indicated in red. Green numbers indicate character state changes that are unique within Dytiscidae; red numbers indicate character state changes that are unique within the subfamily Hydroporinae.

3.3. Diagnosis of the genus Queda

Within Hydroporinae, the larva of *Queda* is characterized by the combination of the following characters: cephalic capsule pear-shaped (Fig. 5A); nasale very broad, semicircular, without lateral branches (Fig. 5A, B); coronal line very short (Fig. 5A); parietal lacking occipital suture (Fig. 5A); occipital foramen somewhat reduced (Fig. 5B); A3' arising from base of A4 (Fig. 6B); mandible very slender (Fig. 6C); cardo partially fused to stipes (Fig. 7B); galea present, relatively well developed (Fig. 7A); prementum longer than broad (Fig. 8A, B); abdominal segments V–VIII completely sclerotized, ring-like (Fig. 1D, E); cephalic capsule and abdominal segment VIII bearing setiferous tubercles (Figs 5A, B, 10A); seta MX4 present (Fig. 7A); setae LA2 and UR8 absent (Figs 8B, 11).

3.4. Description of Queda hydrovatoides

Color (Fig. 1D, E)**:** Cephalic capsule light brown; antenna, maxilla and labium testaceous; mandible brown; protergite light brown laterally and on posterior third, brown on anterior two thirds; mesotergite light brown; metatergite and abdominal tergites I–II brown; abdominal tergite III brown except central portion light brown with brown macula in middle; abdominal sternite III brown; abdominal sclerites IV–VII light brown with dorsal brown macula in middle; abdominal sclerite VIII brown except siphon light brown; legs testaceous; urogomphus light brown.

Body (Fig. 1D, E)**:** Broad, fusiform; measurements and ratios that characterize body shape are shown in Table S4.

Head (Fig. 5A, B)**:** Cephalic capsule pear-shaped, longer than broad, maximum width posterior to stemmata; ecdysial line well marked but diffuse on anterior portion, coronal line very short, weakly marked; occipital foramen somewhat reduced, broadly emarginate ventrally; frontoclypeus very elongate, convex, lateral margins sinuate; nasale very broad, semicircular, sides converging anteriorly to rounded apex, without lateral branches; parietal lacking neck constriction and occipital suture, with six subcircular stemmata on each side, arranged in two parallel vertical rows; lateroventral surface with reticulation; posterior tentorial pits visible ventrally on central portion. Antenna (Fig. 6A, B). Shorter than head width, composed of four antennomeres; A3 longest, without ventroapical spinula, A2 slightly shorter than A3, A1 and A4 shortest, subequal in length; A3' elongate, arising from base of A4. Mandible (Fig. 6C). Prominent, very slender, oriented obliquely, distal half strongly curved inwards and upwards, apex sharp; mandibular channel present. Maxilla (Fig. 7A, B). Cardo partially fused to stipes; stipes short, broad, incompletely sclerotized; galea elongate, subcylindrical; lacinia absent; MP elongate, composed of three palpomeres, MP1 and MP2 longest, subequal in length, MP3 shortest. Labium (Fig. 8A, B). Prementum large, subrectangular, 1.5 times longer than broad, anteri-

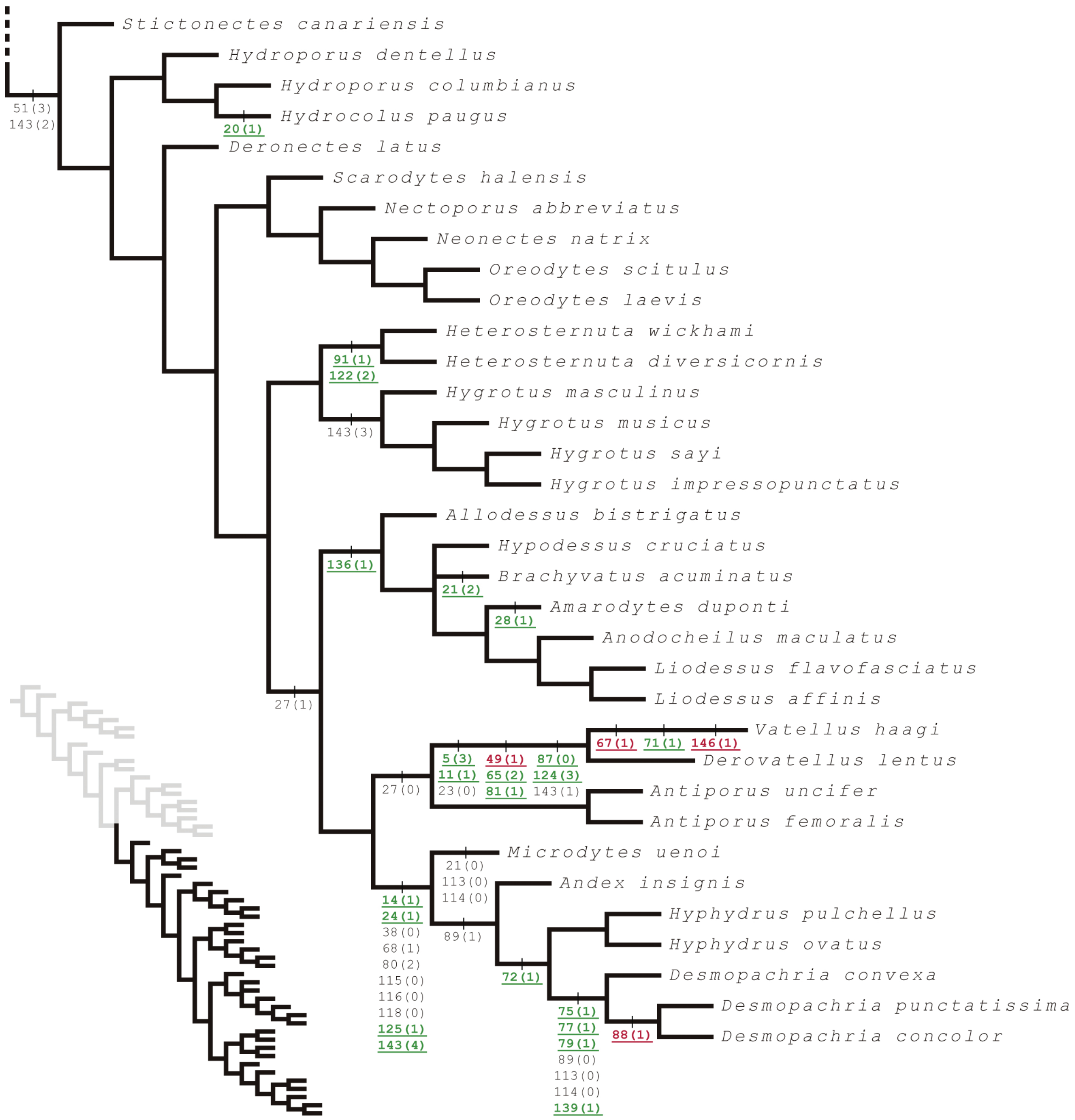

Figure 4. Portion of one of the most parsimonious cladograms with selected character state changes mapped for each clade. Green numbers indicate character state changes that are unique within Dytiscidae; red numbers indicate character state changes that are unique within the subfamily Hydroporinae.

or margin slightly indented medially; LP relatively short, composed of two palpomeres, LP2 longer than LP1.

Thorax: Terga convex, pronotum somewhat shorter than meso- and metanotum combined, meso- and metanotum subequal; protergite trapezoid-shaped in dorsal view, more developed than meso- and metatergite; meso- and metatergite transverse, with anterotransverse carina; sagittal line visible on three tergites; venter membranous except for a small central plate on prothorax; spiracles present on mesothorax. Legs (Fig. 9A, B). Long, six-segmented, L1 shortest, L3 longest; CO robust, elongate, TR divided into two parts by a transverse annulus, FE, TI and TA slender, subcylindrical, PT with two long, slender, slightly curved claws; posterior claw shorter than anterior claw on L1 and L2, claws subequal in length on L3; FE with a short row of comb-like spinulae (pecten) on anteroventral surface; TA and to a lesser extent TI with a ventral row of bifid or trifid elongate spinulae, more developed on L1.

Abdomen: Eight-segmented, with segments progressively narrower and longer to apex; sagittal line visible on segments I–IV; segments I–II sclerotized dorsally, membranous ventrally; segments III–IV sclerotized both dorsally and ventrally, with ventral sclerite independent from dorsal sclerite; segments V–VIII completely sclerotized, ring-like; all sclerites with anterotransverse carina; spiracles present lateroventrally on segments I–VII, terminal-

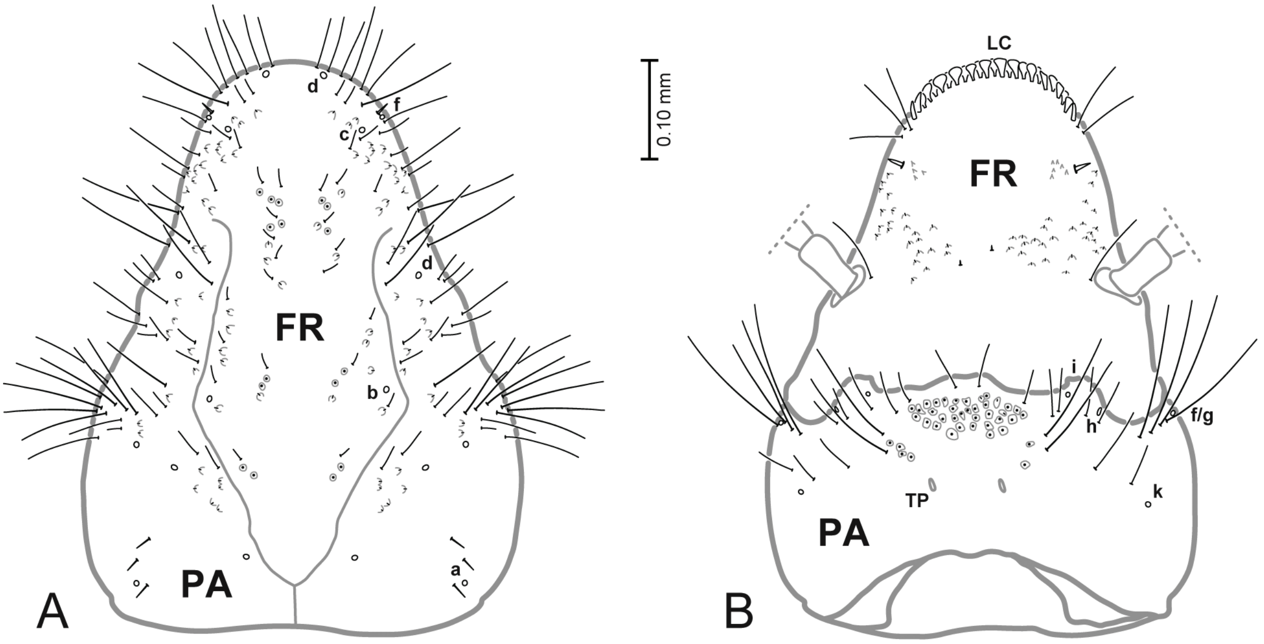

Figure 5. *Queda hydrovatoides* Zimmermann, 1921, instar III, cephalic capsule: **A** dorsal aspect (stemmata not represented); **B** ventral aspect. Lowercase letters indicate primary pores. Abbreviations: FR, frontoclypeus; LC, lamellae clypeales; PA, parietal; TP, tentorial pit.

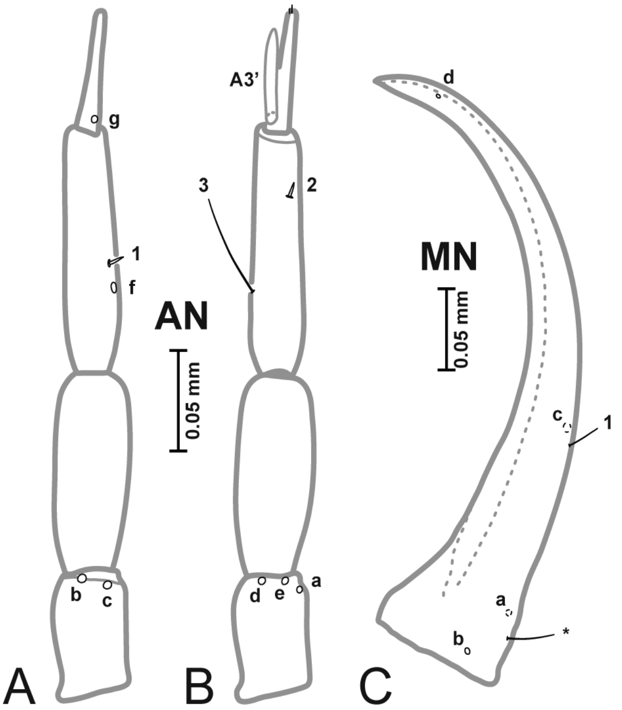

Figure 6. *Queda hydrovatoides* Zimmermann, 1921, instar III. **A** right antenna, dorsal aspect; **B** left antenna, ventral aspect; **C** right mandible, dorsal aspect. Numbers and lowercase letters indicate primary setae and pores, respectively. Abbreviations: A3', apical lateroventral process of antennomere 3; AN, antenna; MN, mandible.

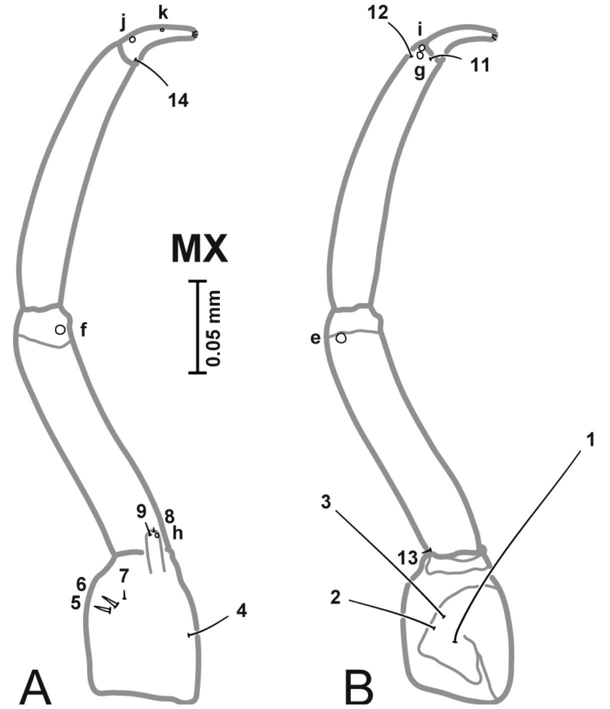

Figure 7. *Queda hydrovatoides* Zimmermann, 1921, instar III. **A** left maxilla, dorsal aspect; **B** right maxilla, ventral aspect. Numbers and lowercase letters indicate primary setae and pores, respectively. Abbreviations: MX, maxilla.

ly on segment VIII; segment VIII (= LAS) the longest, cone-shaped; siphon elongate, sharp apically (Fig. 10A, B). Urogomphus (Fig. 11). Short, two-segmented; U1 robust, not extending beyond siphon; U2 very slender, setiform, twice longer than U1.

Chaetotaxy (Figs 5–11)**:** Cephalic capsule with several hair-like secondary setae of different lengths (Fig. 5A, B); cephalic capsule also with setiferous tubercles (i.e., small bulges bearing a minute seta) sparsely distributed on dorsal surface of frontoclypeus and parietal (Fig. 5A),

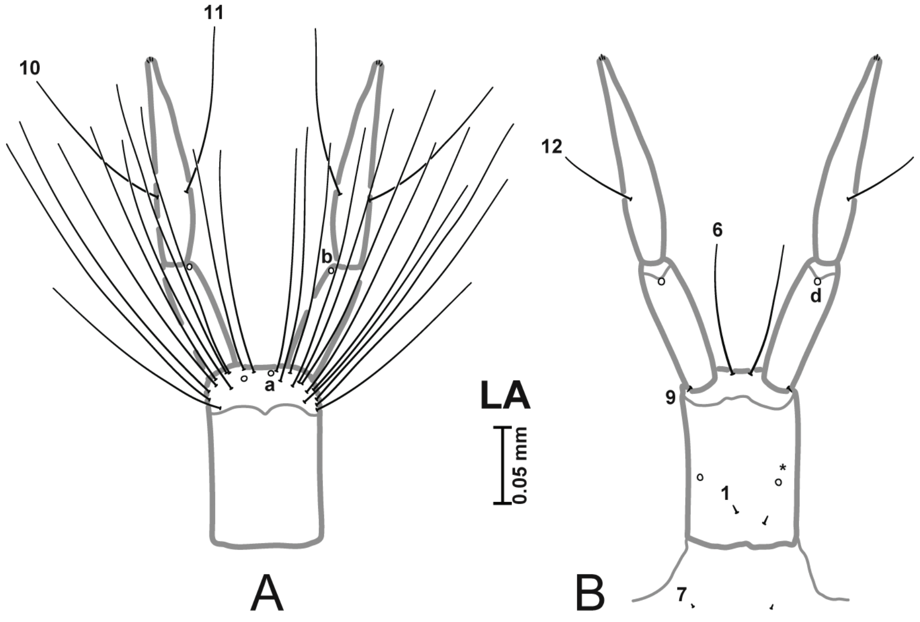

Figure 8. *Queda hydrovatoides* Zimmermann, 1921, instar III. **A** labium, dorsal aspect; **B** labium, ventral aspect. Numbers and lowercase letters indicate primary setae and pores, respectively. Asterisk indicates presumably secondary pore. Abbreviations: LA, labium.

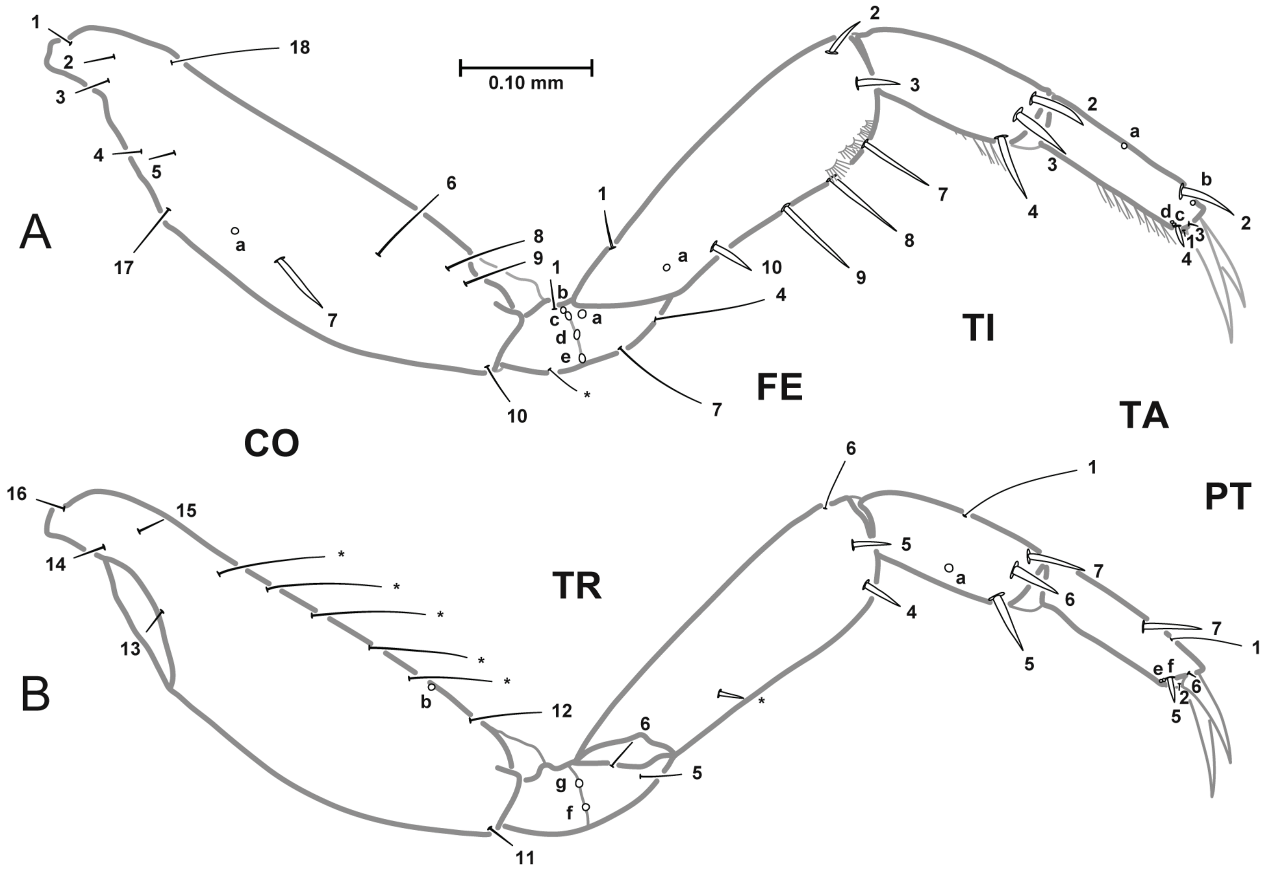

Figure 9. *Queda hydrovatoides* Zimmermann, 1921, instar III. **A** left prothoracic leg, anterior aspect; **B** right prothoracic leg, posterior aspect. Numbers and lowercase letters indicate primary setae and pores, respectively. Asterisks indicate secondary setae. Abbreviations: CO, coxa; FE, femur; PT, pretarsus; TA, tarsus; TI, tibia; TR, trochanter.

and more densely distributed on ventral surface of nasale (anteriorly to antennal bases) and on anteroventral surface of parietal (Fig. 5B); anteroventral margin of nasale with a half circle of 49 lamellae clypeales (Fig. 5B); MN with one hair-like secondary seta on basoexternal margin (Fig. 6C); apical sensillum of MN with the shape of a pore (labelled MNd) (Fig. 6C); prementum with one secondary pore on each side of ventral surface (Fig. 8B); thoracic tergites with several secondary setae; secondary leg setation detailed in Table S5; abdominal sclerites I–VII with several secondary setae on posterior half, these setae changing from hair-like on anterior segments to spine-like on posterior segments; LAS with numerous hair-like secondary setae, mostly on dorsal surface, and with se-

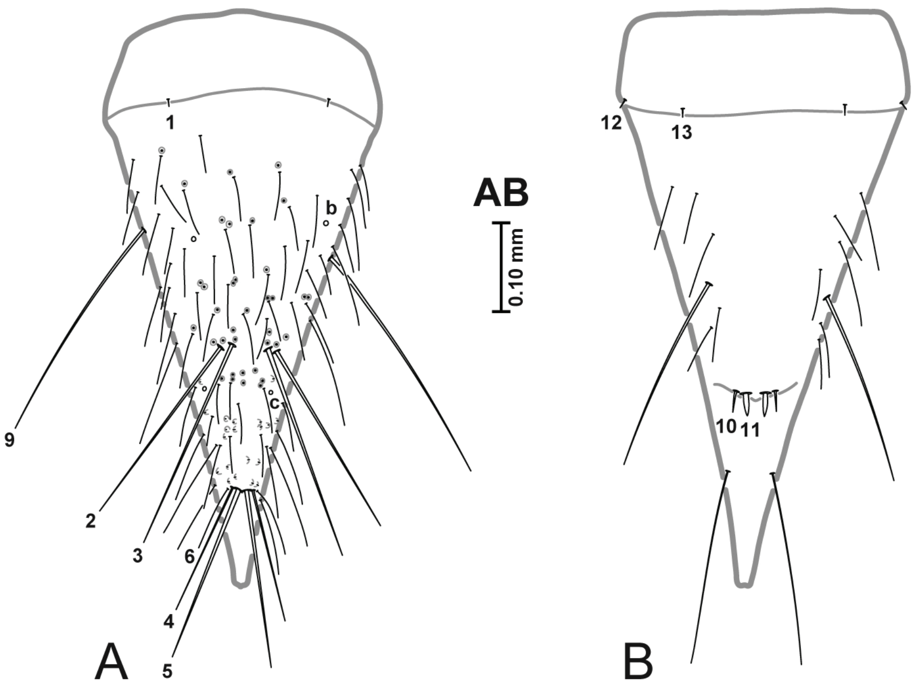

Figure 10. *Queda hydrovatoides* Zimmermann, 1921, instar III. **A** abdominal segment VIII, dorsal aspect; **B** abdominal segment VIII, ventral aspect. Numbers and lowercase letters indicate primary setae and pores, respectively. Abbreviations: AB, abdominal segment VIII.

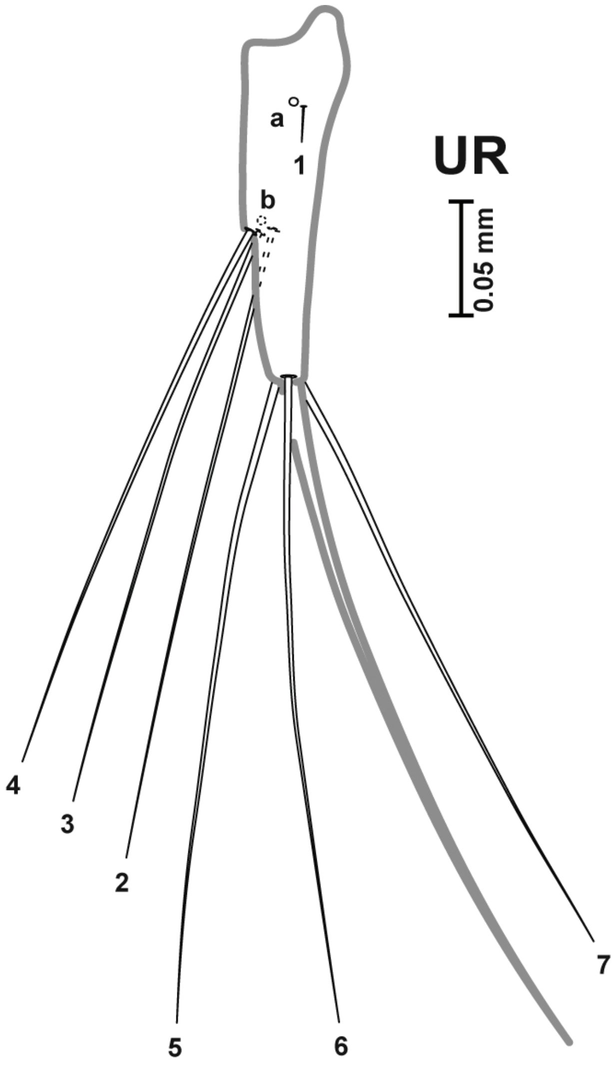

Figure 11. *Queda hydrovatoides* Zimmermann, 1921, instar III, left urogomphus, dorsal aspect. Numbers and lowercase letters indicate primary setae and pores, respectively. Abbreviations: UR, urogomphus.

tiferous tubercles (as those present on cephalic capsule) sparsely distributed over dorsal surface (Fig. 10A); we were unable to find pore URc, but we cannot determine if it is really absent.

4. Discussion

4.1. Identification of Hydrovatini larvae

According to Michat et al. (2017) the tribe Hydrovatini is diagnosed by the proximal position of the egg bursters on the frontoclypeus, the absence of the primary pores PAj and PAo on the ventral surface of the parietal, the hair-like appearance of the mandibular sensillum MN2, the presence of basoventral spinulae on the claws in instar I, and the sclerotized ventral surface of the abdominal segments II–V in instar III. At that time, however, only the larvae of selected species of *Hydrovatus* were known. The study of the larvae of *Queda*, the only other genus in the tribe, allows us to revise this diagnosis in light of the new evidence.

Despite being a third instar, primary chaetotaxy is (with few exceptions) evident in the studied larva of *Queda*. In particular, the parietal pores PAj and PAo are absent, two conditions also found in *Hydrovatus* (Michat 2006; Michat and Alarie 2021). Within Hydroporinae, PAj is also absent in the tribes Bidessini and Hyphydrini, whereas the absence of PAo is unique. Therefore, the absence of these two pores is a good diagnostic feature for the tribe Hydrovatini.

An interesting character exhibited by Hydrovatini larvae is the position of the so-called “apical lateroventral process of antennomere 3” (generally abbreviated as A3’). This process is variously shaped in Dytiscidae, from a rounded and not protruding structure (such as in some Agabinae and Dytiscinae, and in many Colymbetinae) to an elongate and subcylindrical process that ranges from much shorter to almost as long as antennomere 4 (like in most dytiscids) (Alarie et al. 2011, 2024; Michat et al. 2017). In all cases, however, it arises from the apical portion of the antennomere 3 (as its name indicates). In the larvae of *Queda* and *Hydrovatus*, A3’ is somewhat transposed from its typical position and arises from the base of the antennomere 4 (Fig. 6B). This characteristic is rather difficult to see, which likely explains why in previous descriptions of *Hydrovatus* larvae (Michat 2006; Michat and Alarie 2021) A3’ is drawn in its usual position. A close inspection of these larvae, however, allowed us to corroborate that A3’ originates in the same position as in *Queda* larva.

The small sensillum near the apex of the mandible is generally described as a pore or minute seta in Dytiscidae. In *Hydrovatus*, however, it has the shape of a short hair-like seta (Michat 2006; Michat and Alarie 2021). This sensillum is generally labelled MNd when it has a pore-like appearance, or MN2 if it is a seta, either minute or more elongate. In *Queda* larva this sensillum has the shape of a pore, similar to the condition found in all hydroporines except *Hydrovatus*. Therefore, this character is not useful as diagnostic for Hydrovatini, although it remains a good character for distinguishing genera in this tribe.

A secondary pore is usually present on each side of the ventral surface of the prementum in non-hydroporine Dytiscidae (exceptions: Matinae, some Laccophilinae). Within Hydroporinae, however, the presence of these pores is a rare feature restricted to some ancestral lineages such as Methlini and *Laccornellus* Roughley & Wolfe, 1987. The larvae of both *Queda* and *Hydrovatus* have these secondary pores (Fig. 8B), which are therefore a useful diagnostic character for the tribe Hydrovatini.

The degree of sclerotization of the ventral surface of the abdominal segments varies greatly in Dytiscidae. In general, segments I–VI are ventrally membranous, with some exceptions in the subfamilies Laccophilinae and Hydroporinae (Michat et al. 2017). The larva of *Queda* studied here has the segment II membranous ventrally, thus differing from *Hydrovatus* where this part is sclerotized (Michat 2006; Michat and Alarie 2021). Segments III–V, on their part, are similarly sclerotized in both genera, which represents a good diagnostic character for the tribe as it is relatively easily seen under the microscope.

The urogomphal primary seta UR8 exhibits a considerable variation in position among diving-beetle larvae. It is generally inserted at the apex of the urogomphomere 1 in none-hydroporine dytiscids, but within Hydroporinae this seta is inserted on the urogomphomere 2 and varies from apical in Methlini and Vatellini, distal in Bidessini and Hydroporini, submedial in Hygrotini and Pachydrini, to proximal in Hyphydrini, and in a few taxa it is absent, such as members of the Laccornellini. Like in this last tribe, the larvae of both *Queda* and *Hydrovatus* lack seta UR8 (Fig. 11), differing in this way from most hydroporines.

With all this information at hand, the diagnosis of the larvae of the tribe Hydrovatini can be updated as follows: primary pore PAj absent on ventral surface of parietal (shared with Bidessini and Hyphydrini); primary pore PAo absent on ventral surface of parietal; A3’ arising from base of antennomere 4; secondary pores present on ventral surface of prementum (shared with Methlini and *Laccornellus*); ventral surface of abdominal segments III–V sclerotized in instar III (shared with Hyphydrini); primary seta UR8 absent (shared with Laccornellini). The position of the egg bursters on the frontoclypeus and the presence/absence of basoventral spinulae on the claws, also mentioned as diagnostic for Hydrovatini in Michat et al. (2017), are characters restricted to the instar I and therefore could not be evaluated in *Queda*. They remain as potential diagnostic characters for the tribe but need to be corroborated when the first instar of *Queda* is discovered.

4.2. Differentiation of Hydrovatini genera

Despite sharing several characters, the larvae of *Queda* and *Hydrovatus* also present some conspicuous differences, at least in the third instar (compare this study with Michat 2006 and Michat and Alarie 2021). As mentioned above, both genera differ in the shape of the sensillum placed at the apex of the mandible (MNd/MN2) and in the sclerotization of the ventral surface of the abdominal segment II. Apart from these, other significant features can be mentioned. In *Queda* the nasale is broad and progressively narrows to the apex (Fig. 5A), whereas in *Hydrovatus* it is much narrower and parallel sided. The primary setae AN1 and AN2 are shaped as short spines in *Queda* (Fig. 6A, B), whereas in *Hydrovatus* they are elongate and slender. The cardo is completely fused to the stipes in *Hydrovatus* but only partially fused to the stipes in *Queda* (Fig. 7B). The galea is somewhat more developed in *Queda* (Fig. 7A) than in *Hydrovatus*. The prementum is small, subquadrate, and does not bear secondary setae in *Hydrovatus*, whereas in *Queda* it is large, clearly longer than broad, and bears several very long, hair-like, most likely secondary setae (Fig. 8A). The abdominal spiracles in *Queda* larva are all well developed and located in the typical position found in Dytiscidae, i.e. laterally on segments I–VII and terminally on segment VIII. In *Hydrovatus*, however, the segments I–III and VIII bear well developed spiracles but the segments IV–VII have the spiracles obliterated yet still visible (erroneously considered as well developed in Michat 2006). Finally, the cephalic capsule and the abdominal segment VIII of *Queda* larva bear setiferous tubercles (Figs 5A, B, 10A) which are absent in those of *Hydrovatus*.

4.3. Phylogenetic relationships of the Hydrovatini

Our study supports a monophyletic Hydrovatini including both *Queda* and *Hydrovatus*, with high Bremer and bootstrap values (Fig. 2). The tribe is unambiguously supported by the absence of the primary pore PAo on the parietal (character 30.1) and by the process A3' arising from the base of the antennomere 4 (character 35.1) (Fig. 6B). Other characters sustaining this relationship are homoplasious and include the absence of the primary pore PAj on the parietal (character 27.1, also absent in Bidessini and Hyphydrini), the presence of a secondary pore on each side of the ventral surface of the prementum (character 90.1, shared with Methlini and *Laccornellus*) (Fig. 8B), and the sclerotized ventral surface of the abdominal segments III–V in instar III (characters 114.0, 115.0 and 116.0, convergent with Hyphydrini) (Fig. 3). This result agrees with the original concept of the tribe introduced by Sharp (1882) and supported by Biström (1990, 1997), Miller (2001), Miller et al. (2006), and Miller and Bergsten (2014).

Our study also supports the inclusion of Hydrovatini in a clade of taxa generally considered ancestral within the large subfamily Hydroporinae, such as the tribes Laccornini, Laccornellini and Pachydrini (Figs 2, 3). Within this clade, the sister group of the Hydrovatini was found to be the tribe Pachydrini, in agreement with Miller and Bergsten (2014) and Vasilikopoulos et al. (2021). Although the support for this relationship was low, larvae of both tribes share a unique feature within Hydroporinae, the absence of an occipital suture in instars II–III (character 19.0; Fig. 5A). Other characters supporting this grouping are homoplasious, among which are the absence of the pore ANh on the second antennomere (character 38.0) and the sclerotized ventral surface of the abdominal segment VI in instar III (character 118.0), both shared with the tribe Hyphydrini.

In our analysis, the larvae of *Queda* are characteristic within Dytiscidae in the broad and semicircular shape of the nasale (character 3.1; Fig. 5A) and in the cardo partially fused to the stipes (character 48.1; Fig. 7B). Also, they are unique within Hydroporinae in the presence of setiferous tubercles on the cephalic capsule and on the abdominal segment VIII (character 121.1; Figs 5A, B, 10A) and in having a subcylindrical and relatively well developed galea (character 51.0; Fig. 7A). According to Michat et al. (2017), the presence of a galea is characteristic of ancestral hydroporines, which have retained this structure as a plesiomorphic condition. The galea found in *Queda* larva therefore reinforces the hypothesis of an ancestral condition of the Hydrovatini within Hydroporinae. Interestingly, the galea of *Queda* larva is somewhat more developed than those exhibited by other genera of Hydroporinae (i.e., *Celina* Aubé, 1837, *Laccornis* Gozis, 1914, *Laccornellus* and *Hydrovatus*).

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Supplementary Material 1

Tables S1–S5

Authors: Michat MC, Alarie Y, Benetti CJ, Urcola JI, Rodriguez G, Torres PLM (2025)

Data type: .pdf

Explanation notes: Table S1. Species of Dytiscidae examined for phylogenetic analysis. Taxon marked “*” was observed only as instars II and III, taxon marked “**” was observed only as instar III. Classification of subfamilies and tribes of Dytiscidae follows Nilsson & Hájek (2025). — **Table S2.** Characters used for phylogenetic analysis. — **Table S3.** Data matrix used for phylogenetic analysis. Missing data coded “?”. — **Table S4.** Measurements and ratios for the instar III of *Queda hydrovatoides* Zimmermann, 1921. Abbreviations: see Material and methods. — **Table S5.** Number and position of secondary setae on the legs of instar III of *Queda hydrovatoides* Zimmermann, 1921. Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively. Abbreviations: PD, posterodorsal; Pr, proximal; PV, posteroventral.

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