

## On the systematic position of the diving-beetle genus *Pachydus* (Coleoptera: Dytiscidae: Hydroporinae): Evidence from larval chaetotaxy and morphology

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**Abstract.** Phylogenetic relationships within the diving-beetle subfamily Hydroporinae are not well understood. Some authors include the genus *Pachydus* Sharp, 1882 in the tribe Hyphydrini, whereas others are in favour of excluding *Pachydus* from the Hyphydrini and placing it in its own tribe, Pachydrini. Larval characters have been underutilised in phylogenetic studies, mainly because the larvae of many taxa within the family are unknown. In this study, the phylogenetic relationships of *Pachydus* are studied based on a cladistic analysis of 34 taxa and 122 morphological larval characters. For this purpose, larvae of *P. obesus* Sharp, 1882 are described and illustrated in detail for the first time, with particular emphasis on morphometry and chaetotaxy. First and second instars for the genus were unknown. The results support a monophyletic origin of the tribe Hyphydrini excluding *Pachydus*, based on four unique character states. On the other hand, *Pachydus* is resolved as the sister group of the Hydrovatini. These results suggest *Pachydus* should not be placed in the Hyphydrini. Given that the Hyphydrini minus *Pachydus* is a distinctive clade, based on this study, it seems useful to recognise this group as Hyphydrini. Including *Pachydus* in Hyphydrini would leave the tribe with a single larval apomorphy, as most characters present in the Hyphydrini and *Pachydus* are also present in the Hydrovatini. However, in the absence of larvae of *Heterhydrus* Fairmaire, 1869 and of a more comprehensive and inclusive analysis, we do not propose a formal exclusion of *Pachydus* from Hyphydrini at this stage. *Pachydus* is a highly distinctive genus within the Hydroporinae and is characterised by several larval apomorphies.

### INTRODUCTION

*Pachydus* Sharp, 1882 is a diving-beetle genus including nine species, all inhabiting the New World (Biström et al., 1997; Nilsson, 2001). The genus includes small-sized individuals of globous shape, and is predominantly Neotropical, with one species [*P. princeps* (Blatchley, 1914)] reaching the Southeast of the Nearctic Region. *Pachydus obesus* Sharp, 1882, the type species of *Pachydus*, is widely distributed in South America, from Venezuela and Brasil to central Argentina (Trémouilles 1995).

*Pachydus* is most commonly included in the tribe Hyphydrini of the subfamily Hydroporinae. Hyphydrini includes 15 genera (Nilsson, 2001) of which only two are present in America, *Desmopachria* Babington, 1841 and *Pachydus*. The phylogenetic position of *Pachydus* has been controversial for many years. The genus was initially included (along with *Heterhydrus* Fairmaire, 1869) in the tribe Bidessini since the adults have the metacoxae fused to the basal abdominal sternite (Sharp, 1882). Zimmermann (1919) transferred both genera to the tribe Hyphydrini, characterised by the metatarsal claws unequal in length (Biström, 1982; Miller, 2001). Young (1980) emphasised that, even though *Pachydus* is commonly included in the tribe Hyphydrini, it is not closely related to the old-world Hyphydrini genera and suggested that the genus should be placed in a new tribe, Pachydrini. Biström et al. (1997), based on a cladistic

analysis including all Hyphydrini genera, found that the clade *Pachydus* + *Heterhydrus* was resolved as the sister group of the remaining Hyphydrini. Biström et al. (1997) postulated that Hyphydrini including *Pachydus* was polyphyletic, formally transferred *Pachydus* and *Heterhydrus* to Pachydrini and proposed several adult apomorphies for the tribe. However, Miller (2001) based on a broad cladistic analysis of adult characters, found that Hyphydrini (including *Pachydus* and *Heterhydrus*) is monophyletic and is supported by two apomorphies: the obliteration of the metacoxal lobes and metatarsal claws of unequal length. Miller (2001) criticised Biström's et al. (1997) analysis, rejected the use of Pachydrini and transferred *Pachydus* and *Heterhydrus* back to Hyphydrini, a synonymy recognised by Nilsson (2001) and supported by Miller et al. (2006). On the other hand, studies based on larval morphology (Alarie et al., 1997; Alarie & Challet, 2006a, b) suggest a monophyletic origin of the tribe Hyphydrini including *Pachydus*, and a position of *Pachydus* (*Heterhydrus* not considered) as the sister group of the remaining Hyphydrini. However, Miller (2001) found that *Pachydus* and *Heterhydrus* are more closely related to *Desmopachria*. All this reflects the differences in opinion regarding the systematic position of *Pachydus* within the Hydroporinae and indicates a need for more studies, including of character sets not so far explored for the genus, such as primary larval chaetotaxy.

The larval morphology of *Pachydrus* is scarcely known, only the third-instar larva is described. The larvae of four species are known: *P. princeps* (Spangler & Folkerts, 1973), *P. obesus* (Crespo, 1996), *P. globosus* (Aubé, 1838) (Alarie et al., 1997) and *P. obniger* (Chevrolat, 1863) (Alarie & Megna, 2006). Also, a short description of the third-instar larva of an unidentified species of *Pachydrus* is presented by Bertrand (1968). Unfortunately, these descriptions include only the mature larva, so the primary chaetotaxy was not studied. Larval chaetotaxy is important in the study of the phylogenetic relationships within Dytiscidae, as reflected in several recent papers presenting phylogenetic hypotheses regarding the different groups within the family (e.g., Michat & Torres, 2005; Alarie & Challet, 2006a, b; Michat, 2006; Shaverdo & Alarie, 2006; Alarie & Michat, 2007b; Michat et al., 2007; Michat & Alarie, 2008). The recent development of a system of nomenclature for the primary sensilla of first-instar larvae of some dytiscid subfamilies, such as the Hydroporinae (Alarie & Harper, 1990; Alarie et al., 1990a; Alarie, 1991a; Alarie & Michat, 2007a), allows the exploration of new sets of characters that are useful in a phylogenetic sense.

The poor knowledge of the larval morphology of *Pachydrus* and the lack of phylogenetic hypotheses about the relationships of this genus based on larval characters, make the discovery of the larvae of *P. obesus* of great interest. The current study had the following goals: (1) description and illustration, for the first time, of the first two larval instars of a species of *Pachydrus* (third instar is redescribed), including detailed morphometric and chaetotaxic analyses of selected structures; and (2) a cladistic study of the phylogenetic relationships of *Pachydrus* within the Hydroporinae based on larval characters.

## MATERIAL AND METHODS

### Source of material

Three specimens of instar I, two of instar II and five of instar III of *P. obesus* were used for the descriptions. Larvae were collected in association with adults at the following locality: Argentina, Corrientes Province, Mburucuyá National Park, 6.–15.xi.1997 and 15.i.2008, large permanent pond with irregular margins, clear water, muddy bottom with organic debris and abundant emergent and floating vegetation (*Salvinia* sp., *Eichhornia* sp.). The identification of the larvae is clear as *P. obesus* was the only *Pachydrus* species found as adults at that locality.

### Methods

Specimens were cleared in lactic acid, dissected and mounted on glass slides in polyvinyl-lacto-glycerol. Observation (at magnifications up to 1000×) and drawings were made using an Olympus CX31 compound microscope equipped with a camera lucida. Drawings were scanned and digitally edited. The material is held in the larval collection of M.C. Michat (Laboratory of Entomology, Buenos Aires University, Argentina).

### Morphometric analysis

We employed, with minimal modifications and additions, the terms used in previous papers dealing with the larval morphology of Hydroporinae (Alarie & Challet, 2006a, b; Alarie & Michat, 2007b; Michat et al., 2007). Paired structures of each

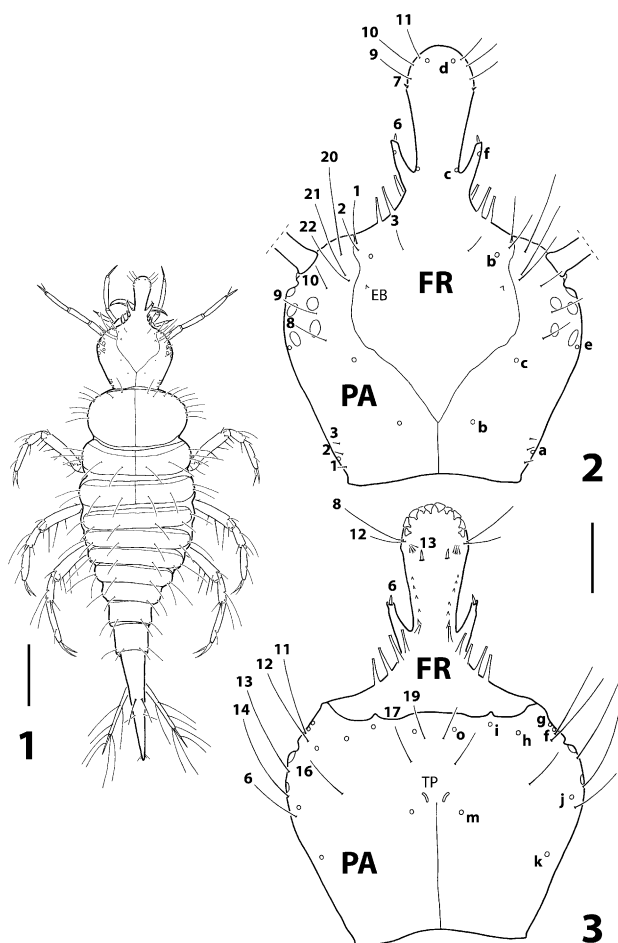
individual were considered independently. The following measurements were taken (with abbreviations shown in parentheses). Total length (excluding urogomphi) (TL); maximum width (MW); head length (HL) (total head length including the frontoclypeus, measured medially along the epicranial stem); maximum head width (HW); length of frontoclypeus (FRL) (from apex of nasale to 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). Lengths of antenna (A), maxillary (MP) and labial (LP) palpi were obtained by adding the lengths of the individual segments; each segment is denoted by the corresponding letter(s) followed by a number (e.g., A1, first antennomere). A3' is used as an abbreviation for the apical lateroventral process of the third antennomere. Length of leg (L), including the longest claw (CL), was obtained by adding the lengths of the individual segments; each leg is denoted by the letter L followed by a number (e.g., L1, prothoracic leg). The length of trochanter includes only the proximal portion, the length of distal portion is included in the femoral length. The legs of the larvae studied were considered as being composed of six segments following Lawrence (1991). Dorsal length of last abdominal segment (LAS) (measured along midline from anterior to posterior margin). Length of urogomphus (U) was derived by adding the lengths of the individual segments; each segment is denoted by the letter U followed by a number (e.g., U1, first urogomphomere). These measurements were used to calculate several ratios that characterise body shape.

### Chaetotaxic analysis

Primary (present in first-instar larva) and secondary (added in later instars) setae and so-called pores were distinguished on the cephalic capsule, head appendages, legs, last abdominal segment and urogomphus. Sensilla were coded by two capital letters, in most cases corresponding to the first two letters of the name of the structure on which they are located, and a number (setae) or a lower case letter (pores). The following abbreviations were used: AB – abdominal segment VIII; AN – antenna; CO – coxa; FE – femur; FR – frontoclypeus; LA – labium; MN – mandible; MX – maxilla; PA – parietal; PT – pretarsus; TA – tarsus; TI – tibia; TR – trochanter; UR – urogomphus. Setae and pores present in first-instar larva of *P. obesus* were labelled by comparison with the ground-plan of chaetotaxy of the subfamily Hydroporinae (Alarie & Harper, 1990; Alarie et al., 1990a; Alarie, 1991a; Alarie & Michat, 2007a). Homologies were recognised using the criterion of similarity of position (Wiley, 1981). Setae located at the apices of the maxillary and labial palpi were extremely difficult to distinguish due to their position and small size. Accordingly, they are not well represented in the drawings.

### Cladistic analysis

For the study of the phylogenetic relationships of the genus *Pachydrus* within the subfamily Hydroporinae, *P. obesus* and 27 other species included in eight of the nine hydroporine tribes were analysed using the parsimony program TNT (Goloboff et al., 2003). The tribe Carabhydrini was not included because the larva of *Carabhydrus* Watts, 1978 is unknown. Members of six of the remaining nine dytiscid subfamilies were included as outgroups. All characters were treated as unordered and equally weighted. 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



Figs 1–3. *Pachydrus obesus*, first-instar larva. 1 – habitus, dorsal aspect; 2–3 – cephalic capsule, dorsal and ventral aspects, respectively. EB – egg burster; TP – tentorial pit. Scale bars = 0.30 mm (1), and 0.10 mm (2–3).

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). Jackknife values were calculated with 2000 replicates and P (removal probability) = 36.

## RESULTS

### Description of the larvae of *Pachydrus obesus* Sharp, 1882

#### Diagnosis

Larvae of *Pachydrus* are characterised by the following combination of characters: head capsule without neck constriction and occipital suture; nasale strongly elongate, parallel sided, with well developed lateral branches; basoventral surface of nasale with a row of well developed spinulae on each side; A3 without ventroapical spinula; cardo fused to stipes; galea minute; prementum subquadrate, without lateral spinulae; LP2 narrowing abruptly at distal fourth; abdominal segment VI completely sclerotised, ring-like; siphon elongate, subconical, sharp apically; U2 slender, setiform; seta FR7 short, spiniform; pore PAd absent; pore PAc located on basal half of PA; pore ANh absent; setae MX4 and MX10 absent; setae MX8 and MX9 present; pore MXh absent;

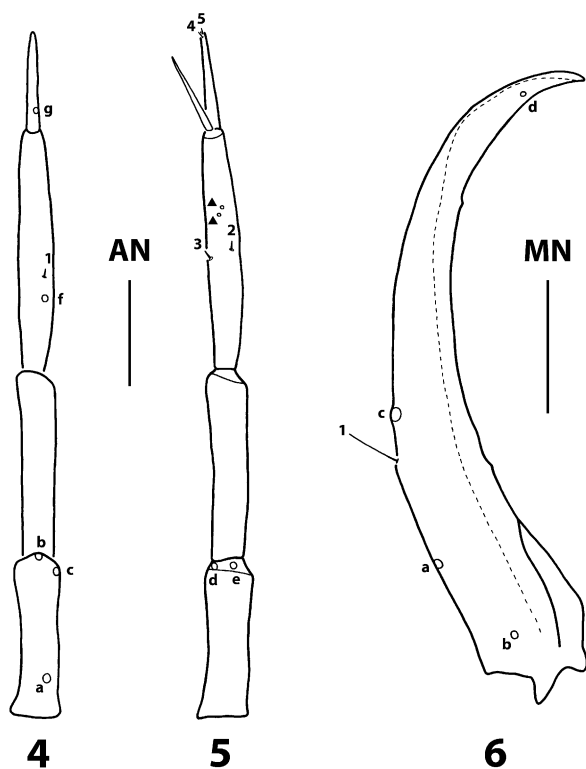
TABLE 1. Measurements and ratios for the three larval instars of *Pachydrus obesus*.

Measure	Instar I (n = 3)	Instar II (n = 2)	Instar III (n = 3)
TL (mm)	2.00–2.70	2.90–3.80	4.80–5.20
MW (mm)	0.50–0.60	0.80–0.90	1.30–1.50
HL (mm)	0.60–0.61	0.78–0.80	1.02–1.07
HW (mm)	0.40–0.42	0.58–0.60	0.80–0.81
FRL (mm)	0.53–0.54	0.67–0.68	0.88–0.92
OCW (mm)	0.21–0.23	0.41–0.42	0.50–0.53
HL/HW	1.46–1.50	1.33	1.29–1.33
HW/OCW	1.79–1.90	1.40–1.47	1.52–1.58
COL/HL	0.10–0.12	0.13–0.15	0.14–0.15
FRL/HL	0.88–0.90	0.85–0.87	0.85–0.86
A/HW	1.11–1.15	0.90–0.93	0.79–0.83
A3/A1	1.50–1.57	1.36–1.41	0.95–1.05
A3/A2	1.22–1.36	1.19–1.22	0.95–1.05
A4/A3	0.33–0.44	0.31–0.34	0.33–0.34
A3'/A4	0.87–0.93	0.85–0.92	0.92–0.93
MNL/MNW	4.40–5.50	4.15–4.47	4.48–4.75
MNL/HL	0.53–0.54	0.51–0.54	0.51–0.55
A/MP	1.24–1.30	1.22–1.24	1.14–1.16
MP2/MP1	1.31–1.42	1.05–1.08	0.83–0.88
MP2/MP3	2.27–2.43	2.60–3.00	2.42–2.53
MP/LP	1.45–1.50	1.41–1.44	1.38–1.46
LP2/LP1	1.22–1.67	0.97–1.07	0.78–0.81
L3 (mm)	1.11–1.17	1.49–1.51	2.01–2.07
L3/L1	1.11–1.13	1.13–1.15	1.16–1.19
L3/L2	1.08–1.09	1.09–1.11	1.12–1.13
L3/HW	2.81–2.82	2.47–2.55	2.50–2.55
L3 (CO/FE)	1.04–1.07	1.04–1.06	1.03–1.11
L3 (TI/FE)	0.51–0.54	0.47–0.48	0.42–0.45
L3 (TA/FE)	0.84–0.86	0.72–0.74	0.57–0.61
L3 (CL/TA)	0.47–0.50	0.41–0.43	0.37–0.41
LAS (mm)	0.63	0.75–0.80	0.97–1.01
LAS/HW	1.52–1.58	1.29–1.32	1.21–1.25
U (mm)	0.49–0.50	0.50–0.51	0.42–0.48
U/LAS	0.77–0.80	0.63–0.68	0.43–0.47
U/HW	1.17–1.20	0.84–0.87	0.52–0.59
U1/U2	2.16–2.27	1.73–1.78	1.33–1.69

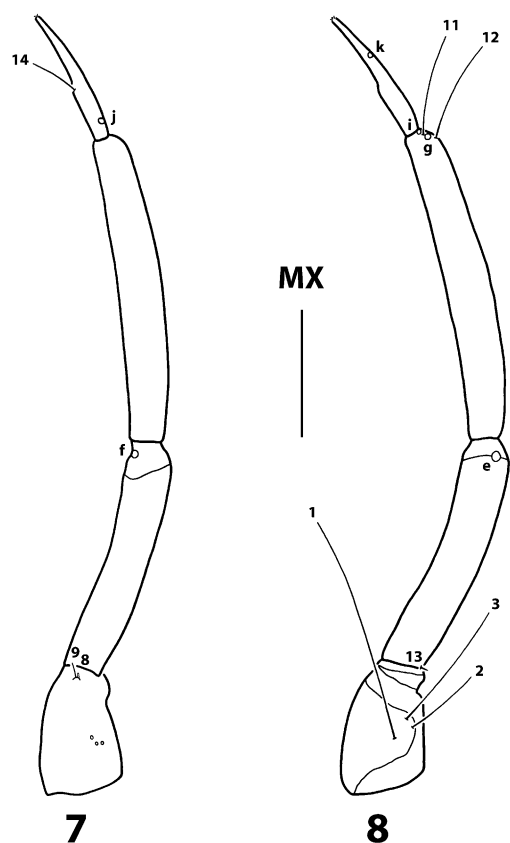
seta LA1 absent; seta LA8 dorsoproximal; pore LAB absent; pore COa absent; seta TR2 absent; pore FEa absent; setae FE2, FE5 and FE6 inserted more proximally; seta TI2 elongate, setiform on L2 and L3, short, spiniform on L1; seta TI7 elongate, setiform; FE with anteroventral natatory setae (instars II–III); pores ABa and ABd absent; sensillum AB2 pore-like; seta AB10 spiniform; ventral surface of siphon with setiform secondary setae; setae UR2 and UR3 arising contiguously; seta UR8 inserted on basal third to basal half of U2; U with 1–3 basal, spiniform, secondary setae (instar III).

#### Instar I

Colour. Cephalic capsule with dorsal colour pattern composed of a testaceous to light brown background and several brown maculae centrally on FR and on posterior two-third of PA; head appendages testaceous to light brown except for MN light brown; thoracic and abdominal sclerites I–V with colour pattern composed of



Figs 4–6. *Pachydrus obesus*, first-instar larva. 4–5 – antenna, dorsal and ventral aspects, respectively; 6 – mandible, dorsal aspect. Solid triangle refers to additional pore. Scale bars = 0.07 mm.



Figs 7–8. *Pachydrus obesus*, first-instar larva, maxilla, dorsal and ventral aspects, respectively. Scale bar = 0.07 mm.

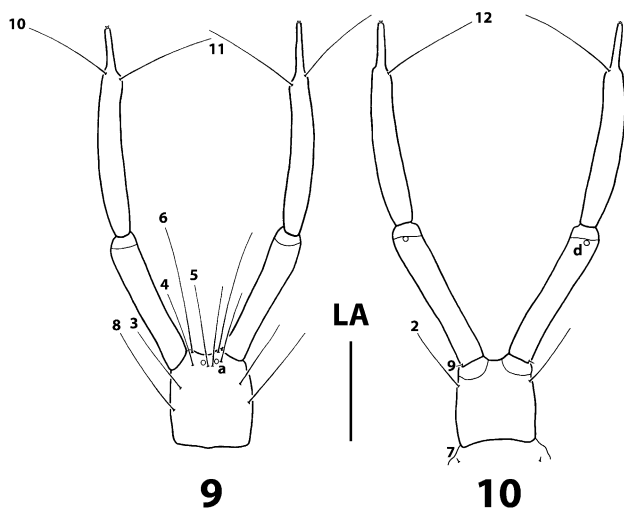
a testaceous to light brown background and brown maculae; abdominal sclerites VI–VIII evenly light brown, distal portion of segment VIII somewhat darker; membranous parts testaceous; legs and U light brown.

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

Head. Head capsule (Figs 2–3). Longer than broad; surface with reticulation; basal half (excluding nasale) subovate, maximum width at stemmata, progressively narrowing towards the occipital foramen, without neck constriction; occipital suture absent; ecdysial line well marked, coronal line short; occipital foramen broadly emarginate ventrally; posterior tentorial pits visible ventrally; FR elongate, subtriangular, slightly convex, lateral margins sinuate, with 2 lateral spiniform egg bursters on anterior third; nasale strongly elongate, parallel sided, rounded apically, with well developed lateral branches; lateroventral surface of nasale with a row of short stout spinulae distal to the lateral branches, and a group of slender pointed spinulae near seta FR13; lateroventral surface of nasale also with a row of robust, elongate, apically truncate spinulae beginning at the base and ending at the level of the lateral branches (Fig. 3); anteroventral margin of nasale with a half circle of 10 short spatulate setae directed downwards, the two anteromedial ones somewhat longer than the others; six subequal lateral stemmata on each side, the four dorsal ones forming a square, the two ventral ones displaced anteriorly with

respect to the others. Antenna (Figs 4–5). Elongate, 4-segmented, somewhat longer than HW; A4 the shortest, A3 the longest, without ventroapical spinula; A3' elongate. Mandible (Fig. 6). Prominent, slender, obliquely oriented, distal half strongly curved inwards and upwards, apex sharp; mandibular channel present. Maxilla (Figs 7–8). Cardo fused to stipes; stipes short, broad, incompletely sclerotised; galea minute; lacinia absent; MP elongate, 3-segmented; MP3 the shortest, MP2 the longest. Labium (Figs 9–10). Prementum subquadrate, about as long as broad, without lateral spinulae; LP elongate, 2-segmented; LP2 longer than LP1, narrowing abruptly on distal fourth.

Thorax. Terga convex, pronotum somewhat shorter than meso- and metanotum combined; meso- and metanotum subequal, wider than pronotum; protergite subovate to subquadrate, margins rounded, more developed than meso- and metatergite; meso- and metatergite transverse, with anterior transverse carina; sagittal line visible on the three tergites; sterna membranous; spiracles absent. Legs (Figs 11–12). Long, 6-segmented; L1 the shortest, L3 the longest; CO robust, elongate, TR divided into 2 parts, FE, TI and TA slender, subcylindrical, PT with 2 long, slender, slightly curved claws; posterior claw shorter than anterior one on L1 and L2, claws subequal in length on L3; surface of TR, FE, TI and TA covered in part with minute spinulae, TI and TA with a ventral row of elongate spinulae.



Figs 9–10. *Pachydrus obesus*, first-instar larva, labium, dorsal and ventral aspects, respectively. Scale bar = 0.07 mm.

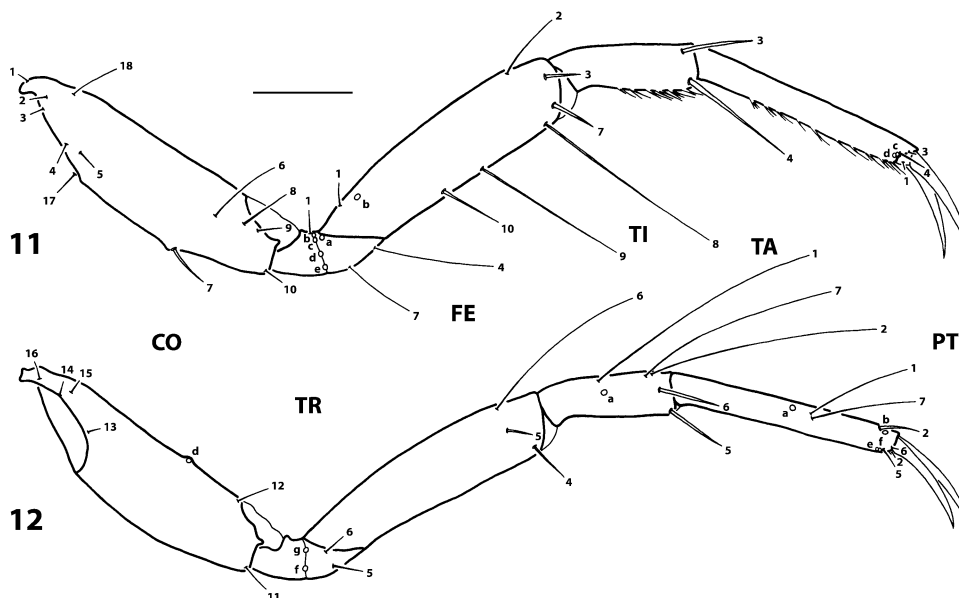
Abdomen. Eight-segmented; segments I–V sclerotised dorsally, membranous ventrally, segments VI–VII completely sclerotised, ring-like; tergites I–VI similar to each other, narrow, transverse; segment VII somewhat longer; spiracles absent on segments I–VII; LAS (Figs 13–14) the longest, completely sclerotised, ring-like; all sclerites with anterior transverse carina, without sagittal line, covered with slender spinulae in transverse rows; siphon elongate, subconical, sharp apically. Urogomphus (Fig. 15). Elongate, 2-segmented; U1 shorter than siphon; U2 slender, setiform, shorter than U1.

Chaetotaxy (Figs 1–15). Similar to that of generalised Hydroporinae larva (Alarie, 1991a; Alarie & Harper, 1990; Alarie et al., 1990a; Alarie & Michat, 2007a) except for the following features: seta FR7 short, spiniform; seta FR13 inserted distally on the nasale; pore PAD absent; pore PAb located basally; pore PAc located on

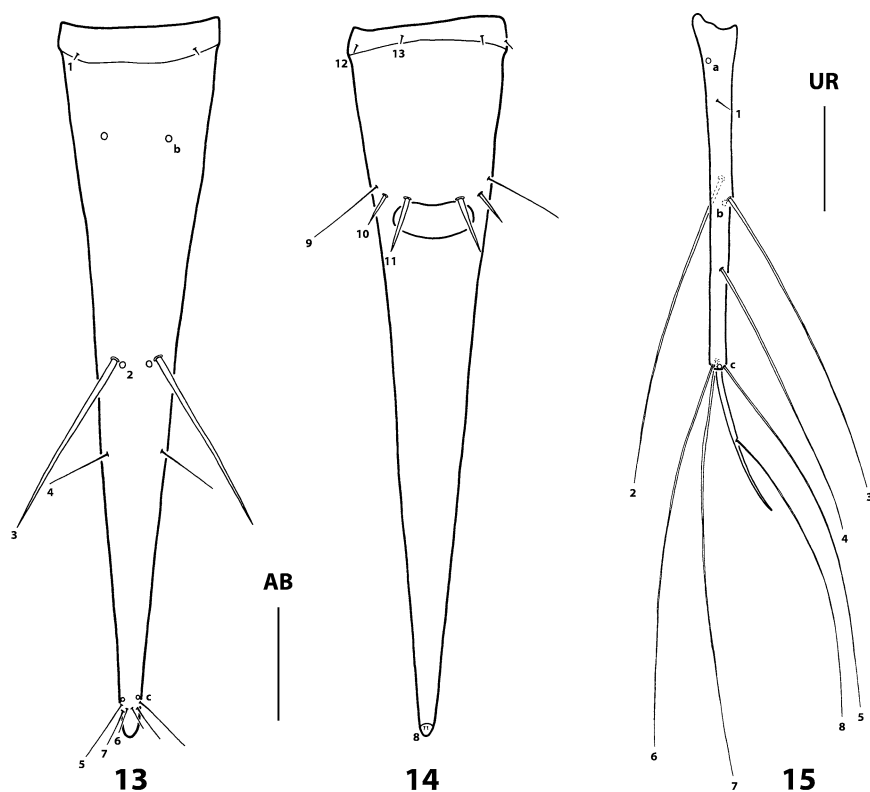
basal half of PA; pore PAg present; pore ANh absent; A3 with two minute structures (possibly additional pores) on ventral surface; seta MX1 inserted on the stipes; setae MX4 and MX10 absent; setae MX5, MX6 and MX7 absent (however, three vestigial structures are present where these setae are commonly located, suggesting that the setae were lost secondarily); setae MX8 and MX9 present; pore MXh absent; seta LA1 absent; seta LA2 inserted marginally; seta LA8 dorsoproximal; pore LAb absent; setae LA10, LA11 and LA12 elongate; pore COa absent; pore COd located more proximally; seta CO12 setiform; seta TR2 absent; pore FEa absent; setae FE2, FE5 and FE6 inserted more proximally; setae FE8 and FE9 elongate; seta TI2 elongate, setiform on L2 and L3, short, spiniform on L1; seta TI7 elongate, setiform; seta TA7 elongate, setiform; the naming of setae and pores on the siphon should be considered tentative, since homologies were difficult to establish due to the different shapes of this structure within Hydroporinae; pores ABa and ABd absent; sensillum AB2 pore-like; seta AB3 strongly developed, spiniform; seta AB8 minute; seta AB10 spiniform; setae UR2 and UR3 arising contiguously; seta UR5 elongate, setiform; seta UR8 inserted on basal third to basal half of U2.

#### Instar II

As first-instar larva except for the following features. Colour. Distal portion of segment VIII of similar colour as the rest of the segment. Body. Measurements and ratios that characterise the body shape are shown in Table 1. Head. Head capsule. Basal half (excluding nasale) subquadrate; anteroventral margin of nasale with 20–21 short spatulate setae. Antenna. Somewhat shorter than HW. Maxilla. MP1 and MP2 the longest, subequal. Labium. LP1 and LP2 subequal in length. Thorax. Legs. Spinulae restricted to ventral surface of FE, TI and TA, rows on TI and TA elongate. Chaetotaxy. Head capsule with numerous minute or setiform secondary setae, and



Figs 11–12. *Pachydrus obesus*, first-instar larva, metathoracic leg, anterior and posterior aspects, respectively. Scale bar = 0.10 mm.



Figs 13–15. *Pachydrus obesus*, first-instar larva. 13–14 – abdominal segment VIII, dorsal and ventral aspects, respectively; 15 – urogomphus, dorsal aspect. Scale bars = 0.10 mm.

7–8 spiniform secondary setae on each lateral margin of PA; MN with 1 setiform secondary seta on basoexternal margin; prementum with one secondary seta on each lateral margin; thoracic tergites with numerous setiform secondary setae; secondary leg setation detailed in Table 2; FE with a row of natatory setae on anteroventral margin; abdominal sclerites I–VIII with numerous setiform secondary setae; ventral surface of siphon with several setiform secondary setae.

#### Instar III

As second-instar larva except for the following features. Colour. Colour pattern more diffusely delimited. Body. Measurements and ratios that characterise the body shape are shown in Table 1. Head (Fig. 16). Head capsule. Anteroventral margin of nasale with 42 short spatulate setae. Antenna. A1, A2 and A3 the longest, subequal. Maxilla. MP1 the longest. Labium. LP1 longer than LP2. Thorax. Spiracles present on mesothorax. Legs. Spinulae absent on meso- and metaFE. Abdomen. Spiracles present on segments I–VII, those on segments V–VII very small, indistinct. Chaetotaxy. PA with 9–11 spiniform secondary setae on each lateral margin; secondary leg setation detailed in Table 2 and Figs 17–18; secondary setation on LAS and U detailed in Fig. 19; U with 1–3 basal, spiniform, secondary setae.

#### Comparative notes

The third-instar larva of *P. obesus* described here is very similar morphometrically to that described by Crespo (1996). The seta TR2 and the pore FEa, reported

as absent by Crespo (1996) are also absent in our material. However, Crespo (1996) reported the absence of pore URc. This pore is present in our larvae, located terminally on the dorsal surface of the first urogomphomere. Due to the terminal location of URc, and the presence of setae on that region of the urogomphus, this pore is difficult to see and may be easily overlooked.

The descriptions of Bertrand (1968) and Spangler & Folkerts (1973) are superficial, making in-depth comparisons with the larvae described here difficult. Nevertheless, *P. princeps* and *P. obesus* seem to be structurally similar. We did not find reliable characters to

TABLE 2. Number and position of secondary setae on the legs of larvae of *Pachydrus obesus*. Numbers between slash marks refer to pro-, meso- and metathoracic legs, respectively. A – anterior, D – dorsal, P – posterior, Pr – proximal, V – ventral, Total – total number of secondary setae on the segment (excluding primary and natatory setae).

Segment	Position	Instar II (n = 2)	Instar III (n = 3)
Coxa	PD	4 / 3–4 / 2–4	5–7 / 5–8 / 4–6
	Total	4 / 3–4 / 2–4	5–7 / 5–8 / 4–6
Trochanter	Pr	1 / 1 / 1	1 / 1 / 1–2
	Total	1 / 1 / 1	1 / 1 / 1–2
Femur	AV	0 / 4 / 3–6	0–1 / 10–15 / 11–13
	PV	2 / 4 / 5–6	7–10 / 9–10 / 10–12
	Total	2 / 8 / 8–12	7–10 / 20–24 / 21–24
Tibia	AV	2 / 3–4 / 4	2–3 / 5–6 / 6–7
	Total	2 / 3–4 / 4	2–3 / 5–6 / 6–7
Tarsus	AV	5 / 4–6 / 5–6	5–7 / 5–7 / 6–8
	Total	5 / 4–6 / 5–6	5–7 / 5–7 / 6–8

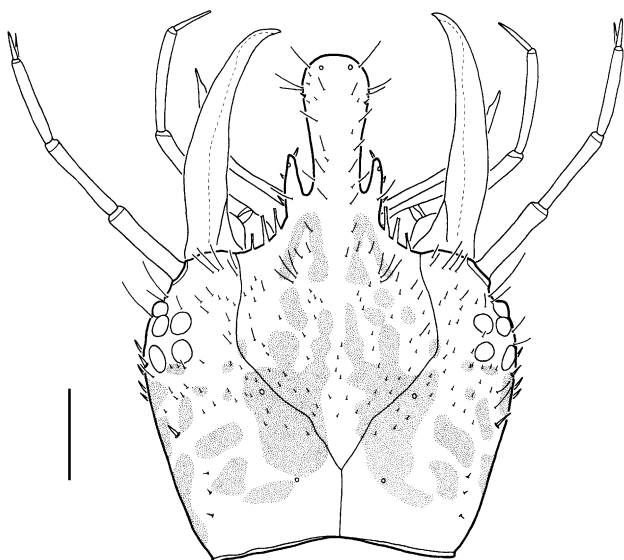


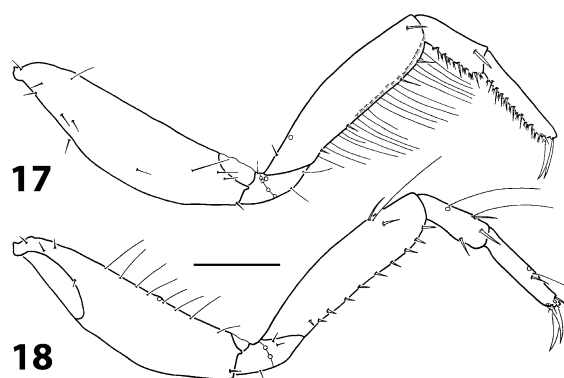
Fig. 16. *Pachydrus obesus*, third-instar larva, head, dorsal aspect. Scale bar = 0.20 mm.

separate these species. In their description of *P. princeps*, Spangler & Folkerts (1973) report the presence of 4-segmented maxillary palpi, 3-segmented labial palpi and 1-segmented urogomphi. In *P. obesus*, the maxillary palpi are 3-segmented, the labial palpi are 2-segmented, and the urogomphi are 2-segmented. The characteristics observed in *P. obesus* are common within the subfamily Hydroporinae (Bertrand, 1972; Alarie & Delgado, 1999; Michat & Torres, 2005). Based on this evidence and the drawings of Spangler & Folkerts (1973), it is likely that the whole stipes was considered as a palpomere, the distal constriction of the second labial palpomere was interpreted as an articulation and the second urogomphomere was overlooked.

According to Alarie & Megna (2006) third-instar larvae of *P. globosus* and *P. obniger* are very similar morphologically, and no differences were found to separate them. The third instar of *P. obesus* is also very similar to those of *P. globosus* and *P. obniger*, in morphometry as well as chaetotaxy, suggesting a marked structural homogeneity within the genus. The seta identified as LA1 in *P. globosus* (Alarie et al., 1997) is secondary in *P. obesus*. Alarie et al. (1997) and Alarie & Megna (2006) report the absence of secondary setae on the ventral surface of the siphon in *P. globosus* and *P. obniger*. These setae are present in *P. obesus*, which may constitute a diagnostic difference. However, we have not seen material of *P. globosus* and *P. obniger*, so these setae may have been overlooked.

### Character analysis

One hundred and twenty-two characters (100 binary and 22 multistate) were coded for larvae of 28 species of Hydroporinae and six outgroups (Table 3). The characters used and their states are listed in Appendix 1. The analysis of the data matrix (Appendix 2) using TNT resulted in 13 most parsimonious cladograms of length 350. In all trees, *Pachydrus* was resolved as the sister



Figs 17–18. *Pachydrus obesus*, third-instar larva, prothoracic leg, anterior and posterior aspects, respectively. Scale bar = 0.20 mm.

group of *Hydrovatus* Motschulsky, 1853. The trees differed largely in outgroup topology and/or in the relative positions of several Hydroporini genera. For this reason, the strict consensus was calculated, in which several taxa collapsed in polytomies (Fig. 20). In the consensus, the clade Hyphydrini minus *Pachydrus* was recovered as monophyletic and well supported, as part of a polytomy along with Vatelini and the genus *Antiporus* Sharp, 1882 (Hydroporini), whereas *Pachydrus* was recovered as sister to *Hydrovatus*, and more closely related to *Canthyporus* Zimmermann, 1919, *Laccornellus* Roughley & Wolfe, 1987 and *Laccornis* Gozis, 1914 than to other Hyphydrini genera. Characters of interest were mapped (using ACCTRAN optimization) in one of the most parsimonious cladograms (Fig. 21). The support obtained was

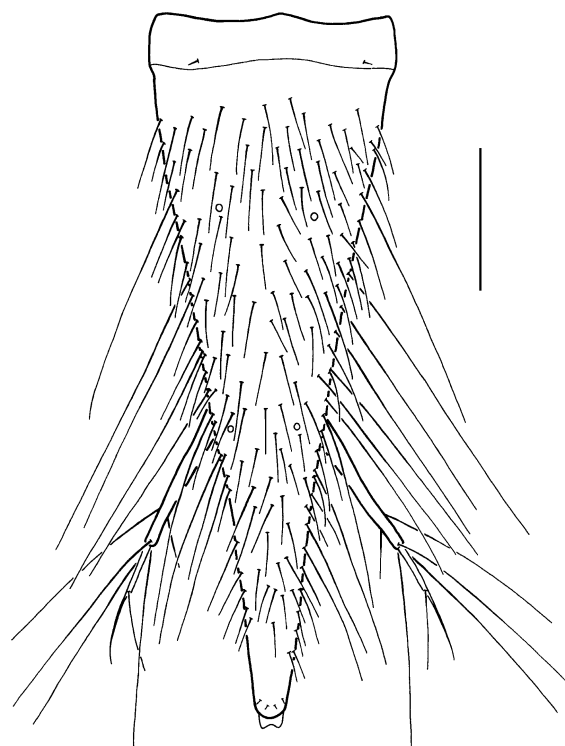


Fig. 19. *Pachydrus obesus*, third-instar larva, abdominal segment VIII and urogomphi, dorsal aspect. Scale bar = 0.20 mm.

TABLE 3. Taxa coded for parsimony analysis.

Taxon	Species	Source
AGABINAE		
Agabini	<i>Agabus anthracinus</i> Mannerheim, 1852	Alarie (1995, 1998)
COLYMBETINAE		
Colymbetini	<i>Rhantus signatus</i> (Fabricius, 1775)	M.C. Michat collection
DYTISCINAE		
Hydaticini	<i>Hydaticus tuyuensis</i> Trémouilles, 1996	Michat & Torres (2006a)
HYDROPORINAE		
Bidessini	<i>Amarodytes duponti</i> (Aubé, 1838)	Michat & Alarie (2006)
	<i>Anodocheilus maculatus</i> Babington, 1841	Michat & Torres (2006b)
	<i>Hypodessus cruciatus</i> (Régimbart, 1903)	Michat & Alarie (2008)
	<i>Liodessus flavofasciatus</i> (Steinheil, 1869)	Alarie et al. (2007)
Hydroporini	<i>Antiporus uncifer</i> Sharp, 1882	Alarie & Watts (2004)
	<i>Canthyporus kenyensis</i> Bilardo & Sanfilippo, 1979	Shaverdo & Alarie (2006)
	<i>Deronectes latus</i> (Stephens, 1829)	Alarie et al. (1999)
	<i>Heterosternuta wickhami</i> (Zaitzev, 1908)	Alarie & Harper (1990); Alarie et al. (1990a); Alarie (1991a, b)
	<i>Hydrocolus paugus</i> (Fall, 1923)	Alarie & Harper (1990); Alarie et al. (1990a); Alarie (1991a, b)
	<i>Hydroporus columbianus</i> Fall, 1923	Alarie & Harper (1990); Alarie et al. (1990a); Alarie (1991a, b)
	<i>Laccornellus lugubris</i> (Aubé, 1838)	Alarie & Michat (2007b)
	<i>Neoporus undulatus</i> (Say, 1823)	Alarie & Harper (1990); Alarie et al. (1990a); Alarie (1991a, b)
	<i>Oreodytes scitulus</i> (LeConte, 1855)	Alarie (1997)
	<i>Scarodytes halensis</i> (Fabricius, 1787)	Alarie et al. (1999)
	<i>Stictonectes canariensis</i> Machado, 1987	Alarie & Nilsson (1997)
Hydrovatini	<i>Hydrovatus caraibus</i> Sharp, 1882	Michat (2006)
Hygrotini	<i>Coelambus impressopunctatus</i> (Schaller, 1783)	Alarie & Harper (1990); Alarie et al. (1990a, b); Alarie (1991a)
	<i>Herophydrus musicus</i> (Klug, 1834)	Alarie et al. (2001a)
Hyphydrini	<i>Hygrotus sayi</i> J. Balfour-Browne, 1944	Alarie & Harper (1990); Alarie et al. (1990a, b); Alarie (1991a)
	<i>Andex insignis</i> Sharp, 1882	Alarie & Challet (2006b)
	<i>Desmopachria concolor</i> Sharp, 1882	Michat & Archangelsky (2007)
	<i>Desmopachria punctatissima</i> Zimmermann, 1923	Michat & Archangelsky (2007)
	<i>Hyphydrus ovatus</i> (Linnaeus, 1761)	Alarie et al. (1997)
	<i>Microdytes uenoi</i> Satô, 1972	Alarie et al. (1997)
	<i>Pachydrus obesus</i> Sharp, 1882	This paper
	<i>Laccornis latens</i> (Fall, 1937)	Alarie & Harper (1990); Alarie et al. (1990a); Alarie (1989, 1991a)
Methlini	<i>Celina parallela</i> (Babington, 1841)	Michat et al. (2007)
Vatellini	<i>Vatellus haagi</i> Wehncke, 1876	Michat & Torres (2005)
LACCOPHILINAE		
Laccophilini	<i>Laccophilus maculosus</i> Say, 1823	Alarie et al. (2000)
LANCETINAE		
Lancetini	<i>Lancetes marginatus</i> (Steinheil, 1869)	Michat et al. (2005)
MATINAE		
Matini	<i>Matus bicarinatus</i> (Say, 1823)	Alarie et al. (2001b)

variable throughout the tree, with some clades well supported and others showing lower values.

## DISCUSSION

The results of the cladistic analysis are interesting with regard to the phylogenetic position of the genus *Pachydrus* within Hydroporinae. The analysis supports a polyphyletic origin of the tribe Hyphydrini as long as *Pachydrus* is included. In fact, whereas *Pachydrus* appears among the ancestral groups of Hydroporinae, more closely related to Hydrovatini, the clade formed by the remaining Hyphydrini genera appears as monophyletic and well supported (Fig. 20). Though the identity of the sister group of Hyphydrini remains obscure based on the results of this analysis, the tribe appears to be more closely related to Vatellini and the genus *Antiporus*. The

results obtained here are in agreement with previous studies that suggest that *Pachydrus* is a strange element within the Hyphydrini and may be improperly placed in that tribe (Young, 1980; Biström et al., 1997).

In this study, Hyphydrini (excluding *Pachydrus*) is well supported and characterised by four apomorphies: absence of pore FRb (character 14.1), pore PAc inserted distally (anterior to the stemmata) (character 19.1), prementum longer than broad (character 55.1) and seta UR8 inserted proximally on second urogomphomere (character 118.3) (Figs 20–21). Hyphydrini is also supported by several homoplastic characters including: absence of pore PAj (character 22.1, homoplastic in Bidessini and *Hydrovatus*), absence of pore ANh (character 34.1, homoplastic in *Pachydrus* and *Hydrovatus*), seta LA8 inserted proximally (character 67.1, homoplastic in *Pachydrus* and



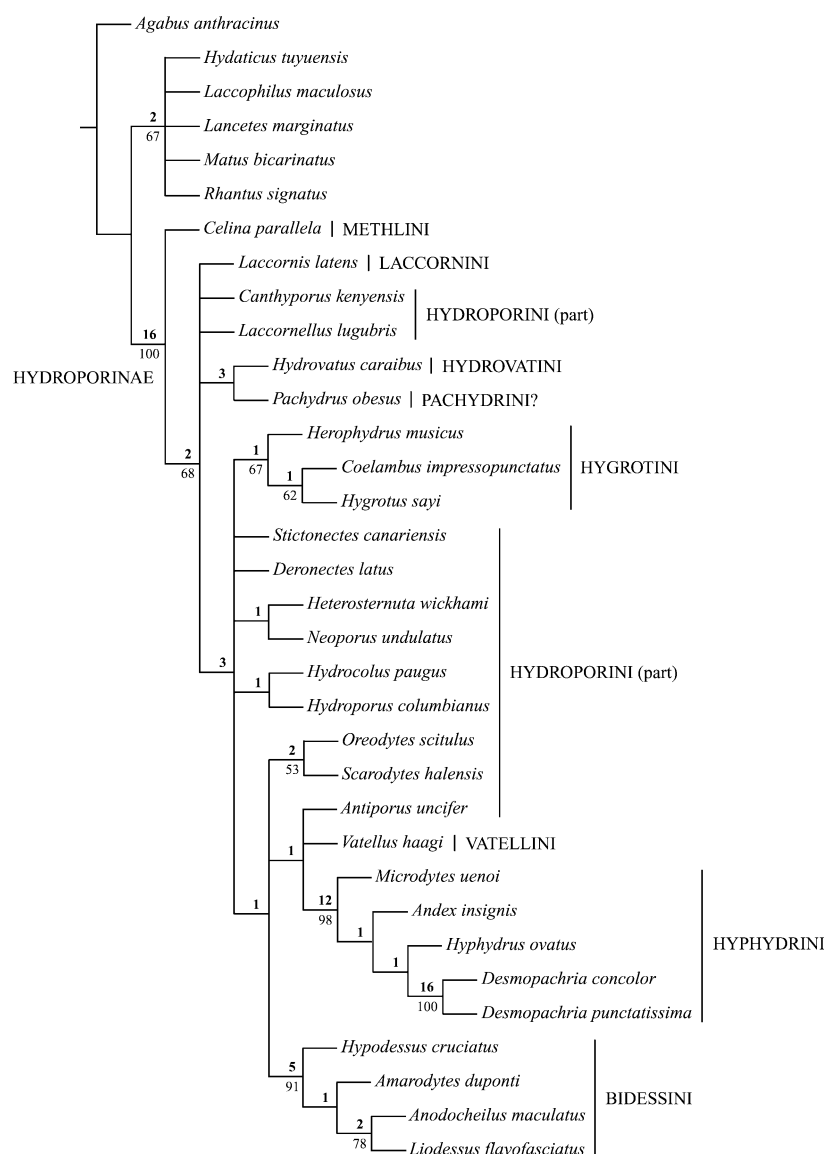


Fig. 20. Strict consensus cladogram of 34 terminal taxa of Dytiscidae. Bremer support values are indicated above branches; jack-knife values above 50 are indicated below branches.

*Hydrovatus*), seta LA12 inserted distally (character 70.1, homoplastic in *Pachydrus* and *Celina* Aubé, 1837), ventral surface of abdominal segments IV–V sclerotised in instar III (character 95.1, homoplastic in *Hydrovatus*), ventral surface of abdominal segment VI sclerotised (character 96.1, homoplastic in *Pachydrus* and *Hydrovatus*), sensillum AB2 pore-like (character 102.1, homoplastic in *Pachydrus*), seta AB5 strongly developed (character 105.1, homoplastic in *Canthyporus* and *Hydrovatus*) and seta AB7 well developed (character 107.1, homoplastic in *Vatellus* Aubé, 1837) (Fig. 21). Characters 14.1, 22.1, 34.1, 96.1 and 118.3 were previously proposed as synapomorphies for Hyphydrini including *Pachydrus* by Alarie et al. (1997) and Alarie & Challet (2006a, b), who also regard the epicranial plates meeting on the ventral midline (a character not included in this study) as synapomorphic. However, as mentioned above, characters 22.1, 34.1 and 96.1 are homoplastic in the cladogram obtained in this study. Only one character, the

pore-like aspect of the sensillum AB2 (character 102.1), is shared exclusively by Hyphydrini and *Pachydrus* and may indicate a closer relationship between these taxa than that hypothesised here.

*Pachydrus* is a highly distinctive genus within Hydroporinae, characterised by 10 apomorphies: presence of a row of elongate spinulae on basoventrolateral surface of nasale (character 9.1), galea minute (character 42.2), pore MXh absent (character 52.2), seta LA1 absent (character 60.1), pore COa absent (character 75.1), seta FE2 inserted subdistally (character 77.1), presence of natatory ventral setae on femur (character 81.1), seta TI2 elongate, setiform on meso- and metatibia (character 83.1), abdominal segment VII completely sclerotised in instar I (character 97.2) and seta AB3 spiniform (character 103.1) (Fig. 21). It is interesting to note that some of these characters (9.1, 60.1, 75.1, 77.1 and 83.1) are not found in any other dytiscid for which the larvae are known in detail, which indicates *Pachydrus* is a very distinctive diving-beetle

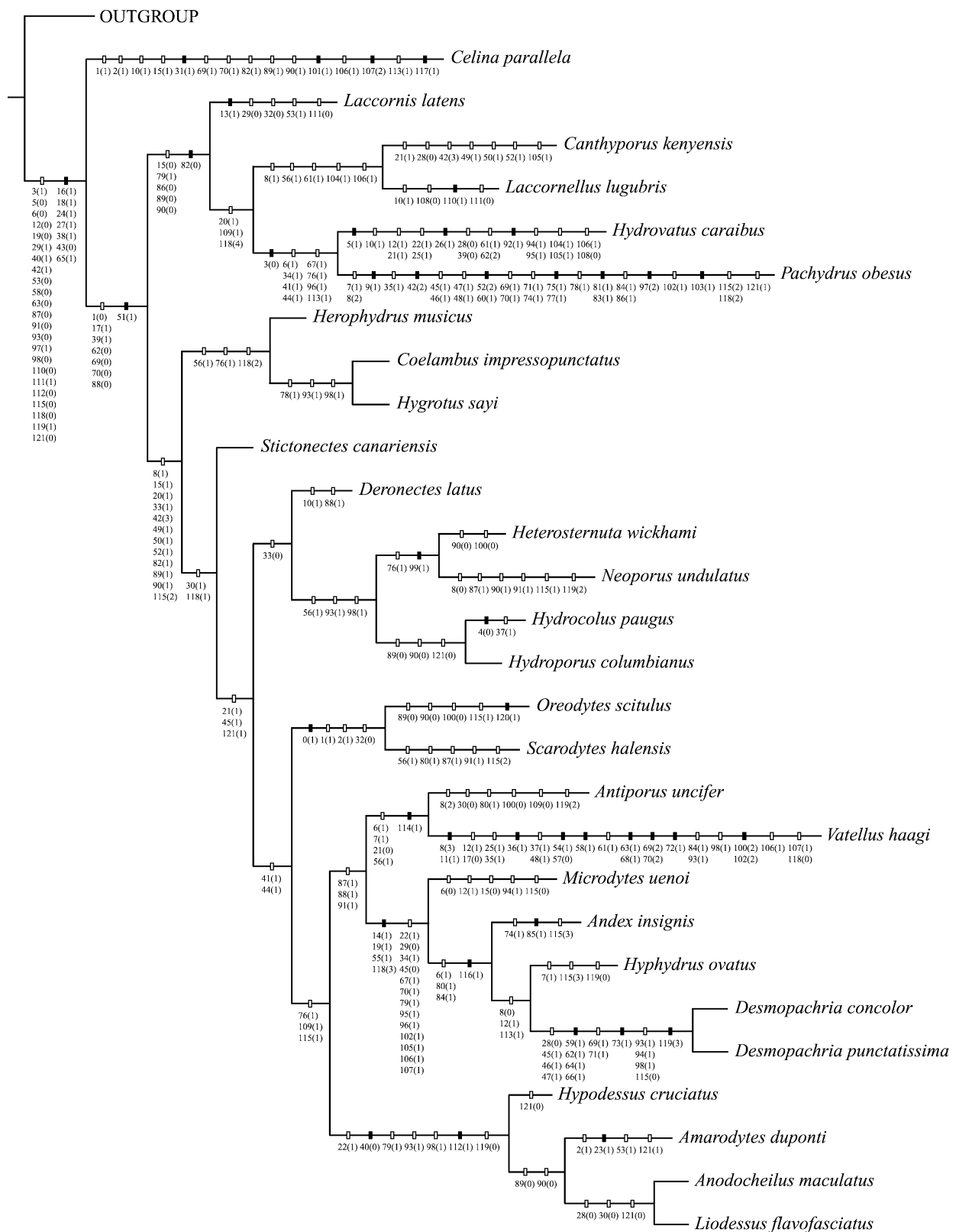


Fig. 21. One of the most parsimonious cladograms of 34 terminal taxa of Dytiscidae, with character changes mapped for the clades of Hydroporinae. Solid rectangles indicate unique character state transformations; open rectangles indicate homoplastic character state transformations.

genus. *Pachydrus* is resolved as the sister group of Hydrovatini (Fig. 20). Both taxa share a unique character within Hydroporinae: the absence of an occipital suture in

instars II and III (character 3.0). As mentioned above, both taxa are characterised by some other characters also present in Hyphydrini (Fig. 21).

On the basis of the results presented here, the evidence for a monophyletic origin of Hyphydrini excluding *Pachydrus* is strong. Given that Hyphydrini minus *Pachydrus* is a highly distinctive group supported by several larval apomorphies, it seems useful to recognise this group as Hyphydrini. Including *Pachydrus* within Hyphydrini would leave the tribe with a single larval apomorphy (the pore-like aspect of the sensillum AB2), as most characters present in Hyphydrini including *Pachydrus* are also present in Hydrovatini. Even if future evidence supports that *Pachydrus* and Hyphydrini are sister groups, as sometimes regarded in the past (Biström et al., 1997; Alarie et al., 1997; Alarie & Challet, 2006a, b), larval characters argue in favour of a placement of *Pachydrus* outside the Hyphydrini. These results follow Young (1980) and Biström et al. (1997), who based on adult characters supported the inclusion of *Pachydrus* in Pachydrini, and contradict the results of Miller (2001) and Miller et al. (2006) based on adults and Alarie et al. (1997) and Alarie & Challet (2006a, b) based on larvae, who support the inclusion of *Pachydrus* in Hyphydrini. However, although this study indicates that *Pachydrus* should be excluded from Hyphydrini, we do not formally propose exclusion at this stage. On the one hand, a placement of *Pachydrus* within Hydrovatini (a possible scenario based on our results) seems inconvenient given that Hydrovatini as presently conceived is a well defined tribe based on adult morphology (Miller, 2001; Miller et al., 2006). On the other hand, the reinstatement of Pachydrini may be premature in the absence of larvae of *Heterhydrus* and a more comprehensive study including more species and characters. Therefore, we prefer to formally retain *Pachydrus* in Hyphydrini (the placement given by Nilsson, 2001) until future analyses, including adult and larval characters as well as molecular data, improve the resolution of the phylogeny under study.

Larval morphology of members of Hyphydrini is in need of further study. The larvae of most genera within the tribe (e.g., *Agnoshydrus* Biström, Nilsson & Wewalka, 1997, *Allopachria* Zimmermann, 1924, *Coelhydrus* Sharp, 1882, *Darwinhydrus* Sharp, 1882, *Dimitshydrus* Uéno, 1996, *Hovahydrus* Biström, 1982, *Hydropeplus* Sharp, 1882, *Hyphovatus* Wewalka & Biström, 1994) are still unknown, and few species of other, speciose genera (e.g., *Desmopachria*, *Hyphydrus* Illiger, 1802, *Microdytes* J. Balfour-Browne, 1946) are known in detail. In particular, detailed studies (including chaetotaxy) of the larvae of *Heterhydrus* would be of great interest. With the very deficient knowledge of the larval morphology of *Heterhydrus* that we have at present (Bertrand, 1972) little can be said about whether larval characters support a close relationship of this genus with *Pachydrus* or the placement of *Heterhydrus* within Hyphydrini.

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APPENDIX 1. Characters and states used for the parsimony analysis of 34 terminal taxa of Dytiscidae.

- (000) Parietal (at level of occipital suture) (instar I): (0) not constricted; (1) constricted.
- (001) Parietal (at level of occipital suture) (instars II–III): (0) not constricted; (1) constricted.
- (002) Occipital suture (instar I): (0) absent; (1) present.
- (003) Occipital suture (instars II–III): (0) absent; (1) present.
- (004) Stemmata (instars I–II): (0) absent; (1) present.
- (005) Egg bursters (instar I): (0) located submedially; (1) located basally.
- (006) Nasale (instars I–III): (0) broad, subtriangular; (1) narrow, more or less parallel sided; (2) absent.
- (007) Apex of nasale (instars I–III): (0) not spatulate; (1) spatulate.
- (008) Lateral projections of nasale (instars I–III): (0) absent; (1) very small, inconspicuous; (2) well developed, short, not bifid apically; (3) strongly developed, bifid apically.
- (009) Row of elongate spinulae on basoventrolateral surface of nasale (instars I–III): (0) absent; (1) present.
- (010) Seta FR2 (instar I): (0) inserted close to frontal line; (1) inserted far from frontal line.
- (011) Seta FR6 (instar I): (0) not distinctly developed; (1) strongly developed.
- (012) Seta FR7 (instar I): (0) spiniform; (1) setiform.
- (013) Seta FR13 (instar I): (0) present; (1) absent.
- (014) Pore FRb (instar I): (0) present; (1) absent.
- (015) Seta PA3 (instar I): (0) inserted contiguously to setae PA1 and PA2; (1) inserted far from setae PA1 and PA2.
- (016) Seta PA7 (instar I): (0) present; (1) absent.
- (017) Seta PA18 (instar I): (0) present; (1) absent.
- (018) Pore PAb (instar I): (0) inserted contiguously to seta PA3; (1) inserted far from seta PA3, close to coronal line or to frontal line.
- (019) Pore PAc (instar I): (0) inserted medially (not passing the level of stemmata); (1) inserted distally (anterior to the stemmata); (2) absent.
- (020) Pore PAd (instar I): (0) present; (1) absent.
- (021) Pore PAe (instar I): (0) present; (1) absent.
- (022) Pore PAj (instar I): (0) present; (1) absent.
- (023) Pore PAk (instar I): (0) present; (1) absent.
- (024) Pore PAI (instar I): (0) present; (1) absent.
- (025) Pore PAm (instar I): (0) present; (1) absent.
- (026) Pore PAo (instar I): (0) present; (1) absent.
- (027) Pore PAp (instar I): (0) present; (1) absent.
- (028) Secondary spiniform setae on lateral margin of parietal (instars II–III): (0) absent; (1) present.
- (029) Secondary spiniform setae on ventral surface of parietal (instars II–III): (0) present; (1) absent.
- (030) Ventoapical spinula on antennomere 3 (instars I–III): (0) absent; (1) present.
- (031) Seta AN1 (instar I): (0) inserted medially or distally; (1) inserted proximally.
- (032) Seta AN3 (instar I): (0) inserted distally; (1) inserted submedially.
- (033) Pore ANf (instar I): (0) present; (1) absent.
- (034) Pore ANh (instar I): (0) present; (1) absent.
- (035) Additional ventroapical pores on antennomere 3 (instar I): (0) present; (1) absent.
- (036) Secondary setae on antennomere 1 (instars II–III): (0) absent; (1) present.
- (037) Secondary setae on antennomere 2 (instars II–III): (0) absent; (1) present.
- (038) Mandible (instars I–III): (0) not oriented obliquely; (1) oriented obliquely.
- (039) Sensillum MN2 (instar I): (0) setiform; (1) pore-like.
- (040) Pore MNa (instar I): (0) inserted at about the same level as pore MNb; (1) inserted distal to pore MNb.
- (041) Cardo (instars I–III): (0) not fused to the stipes; (1) fused to the stipes.
- (042) Galea (instars I–III): (0) well developed, subconical; (1) very short, subconical; (2) minute; (3) absent.
- (043) Palpifer (instars I–III): (0) inconspicuous, not clearly differentiated from the stipes; (1) palpomere-like, clearly differentiated from the stipes.
- (044) Seta MX1 (instars I–III): (0) inserted on the cardo; (1) inserted on the stipes.
- (045) Seta MX4 (instar I): (0) present; (1) absent.
- (046) Seta MX5 (instar I): (0) present; (1) absent.
- (047) Seta MX6 (instar I): (0) present; (1) absent.
- (048) Seta MX7 (instar I): (0) present; (1) absent.
- (049) Seta MX8 (instar I): (0) present; (1) absent.
- (050) Seta MX9 (instar I): (0) present; (1) absent.
- (051) Seta MX10 (instar I): (0) present; (1) absent.
- (052) Pore MXh (instar I): (0) inserted on the galea; (1) inserted on the stipes; (2) absent.
- (053) Pore MXk (instar I): (0) present; (1) absent.
- (054) Secondary setae on maxillary palpomere 1 (instars II–III): (0) absent; (1) present.
- (055) Prementum (instars I–III): (0) broader than long or as long as broad; (1) longer than broad.
- (056) Elongate lateral spinulae on prementum (instars I–III): (0) absent; (1) present.
- (057) Labial palpus (instars I–III): (0) composed of one palpomere; (1) composed of two palpomeres.
- (058) Ratio MP/LP (instar III): (0) less than 1.90; (1) more than 2.30.
- (059) Labial palpomere 2 (instars I–III): (0) normal shape; (1) broad, robust, rounded apically (2) inapplicable.
- (060) Seta LA1 (instar I): (0) present; (1) absent.
- (061) Seta LA2 (instar I): (0) present; (1) absent.
- (062) Seta LA3 (instar I): (0) inserted distally or subdistally; (1) inserted proximally; (2) absent.
- (063) Seta LA5 (instar I): (0) setiform; (1) spiniform.
- (064) Setae LA4 and LA5 (instar I): (0) inserted distally or subdistally; (1) inserted proximally; (2) absent.
- (065) Setae LA4 and LA8 (instar I): (0) short, spiniform; (1) elongate, setiform; (2) elongate, spiniform.
- (066) Seta LA6 (instar I): (0) inserted distally or subdistally; (1) inserted medially; (2) absent.
- (067) Seta LA8 (instar I): (0) inserted distally or subdistally; (1) inserted proximally; (2) absent.
- (068) Seta LA9 (instar I): (0) present; (1) absent.
- (069) Seta LA10 (instar I): (0) inserted submedially; (1) inserted distally; (2) absent.
- (070) Seta LA12 (instar I): (0) inserted submedially; (1) inserted distally; (2) absent.
- (071) Pore LAb (instar I): (0) present; (1) absent.
- (072) Pore LAd (instar I): (0) present; (1) absent.
- (073) Additional setae on dorsal surface of prementum (instar I): (0) absent; (1) present.
- (074) Secondary setae on prementum (instars II–III): (0) absent; (1) present.
- (075) Pore COa (instar I): (0) present; (1) absent.
- (076) Seta TR2 (instar I): (0) present; (1) absent.
- (077) Seta FE2 (instar I): (0) inserted distally; (1) inserted subdistally.
- (078) Seta FE6 (instar I): (0) inserted distally; (1) inserted subdistally; (2) absent.
- (079) Pore FEa (instar I): (0) present; (1) absent.
- (080) Natatory dorsal setae on femur (instars II–III): (0) absent; (1) present.
- (081) Natatory ventral setae on femur (instars II–III): (0) absent; (1) present.
- (082) Secondary anterodorsal setae on femur (instars II–III): (0) absent; (1) present.
- (083) Seta TI2 on meso- and metatibia (instar I): (0) short, spiniform; (1) elongate, setiform; (2) inapplicable.
- (084) Seta TI7 (instar I): (0) short, spiniform; (1) elongate, setiform.
- (085) Pore TIa (instar I): (0) present; (1) absent.
- (086) Secondary setae on tibia (instars II–III): (0) absent; (1) present.
- (087) Natatory dorsal setae on tibia (instars II–III): (0) absent; (1) present.
- (088) Secondary setae on anterodorsal margin of protarsus (instars II–III): (0) absent; (1) present.
- (089) Secondary setae on posteroventral margin of protarsus (instar III): (0) absent; (1) present.

- (090) Secondary setae on posteroventral margin of metatarsus (instar III): (0) absent; (1) present.
- (091) Natatory dorsal setae on tarsus (instars II–III): (0) absent; (1) present.
- (092) Basoventral spinulae on claw (instar I): (0) absent; (1) present.
- (093) Abdominal tergites I–VI (instar I): (0) with anterior transverse carina; (1) without anterior transverse carina.
- (094) Ventral surface of abdominal segments II–III (instar III): (0) membranous; (1) sclerotised.
- (095) Ventral surface of abdominal segments IV–V (instar III): (0) membranous; (1) sclerotised.
- (096) Ventral surface of abdominal segment VI (instars I–III): (0) membranous; (1) sclerotised.
- (097) Abdominal segment VII (instar I): (0) sclerotised dorsally, membranous ventrally; (1) sclerotised dorsally and ventrally, with ventral sclerite separate from dorsal sclerite; (2) completely sclerotised except for a narrow, longitudinal, ventral band; (3) completely sclerotised.
- (098) Abdominal sclerite VII (instar I): (0) with anterior transverse carina; (1) without anterior transverse carina.
- (099) Spiracles on mesothorax and abdominal segments I–VII (instar III): (0) present; (1) absent.
- (100) Siphon (instars I–III): (0) very short; (1) short to moderately long; (2) very long, urogomphomere-like.
- (101) Tracheal trunks (instars I–III): (0) not protruding from the apex of siphon; (1) protruding from the apex of siphon.
- (102) Sensillum AB2 (instar I): (0) setiform; (1) pore-like; (2) absent.
- (103) Seta AB3 (instar I): (0) setiform; (1) spiniform.
- (104) Seta AB4 (instar I): (0) not distinctly developed; (1) very elongate, strongly developed.
- (105) Seta AB5 (instar I): (0) not distinctly developed; (1) strongly developed.
- (106) Seta AB6 (instar I): (0) short (1) elongate.
- (107) Seta AB7 (instar I): (0) small; (1) well developed to strongly developed; (2) absent.
- (108) Seta AB9 (instar I): (0) inserted dorsolaterally; (1) inserted ventrolaterally.
- (109) Seta AB10 (instar I): (0) setiform; (1) spiniform.
- (110) Seta AB15 (instar I): (0) absent; (1) present.
- (111) Pore ABa (instar I): (0) present; (1) absent.
- (112) Pore ABc (instar I): (0) present; (1) absent.
- (113) Secondary ventral setae on siphon (instar III): (0) absent; (1) present.
- (114) Ratio U/HW (instar III): (0) less than 3.00; (1) more than 3.60.
- (115) Setae UR2, UR3 and UR4 (instar I): (0) inserted contiguously; (1) not inserted contiguously; (2) only UR2 and UR3 inserted contiguously; (3) only UR3 and UR4 inserted contiguously.
- (116) Seta UR5 (instar I): (0) elongate, setiform; (1) short, spiniform.
- (117) Seta UR6 (instar I): (0) elongate; (1) short.
- (118) Seta UR8 (instar I): (0) inserted terminally on urogomphomere 2; (1) inserted subapically on urogomphomere 2; (2) inserted submedially on urogomphomere 2; (3) inserted proximally on urogomphomere 2; (4) absent; (5) inserted on urogomphomere 1.
- (119) Pore URb (instar I): (0) proximal to seta UR2; (1) contiguous to seta UR2; (2) distal to seta UR2; (3) absent.
- (120) Additional pores on urogomphus (instar I): (0) absent; (1) present.
- (121) Secondary setae on urogomphus (instars II–III): (0) absent; (1) present.

APPENDIX 2. Data matrix of 122 larval characters for 34 terminal taxa of Dytiscidae. “?” – missing data.

Species	Character												
	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000001	1111111111	1111111111
	00000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888889	9999999990	0000000001	1111111112	1111111112
	01234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12345678901
<i>Agabus anthracinus</i>	01001020000	01700000000	00000000171	00001000000	00100000000	00100001000	00100000011	00000000000	07000010777	00700007770	00000000101	00070005200	00000000001
<i>Hydaticus tuyuensis</i>	11111020000	01700000000	00000000101	0100110001	00100000000	00100010000	00100000011	00010000201	1101011100	1100002000	00000000001	00002005200	00000000001
<i>Laccophilus maculosus</i>	00001120000	01700000020	00000000100	01001000000	00100000000	00100011000	0210000022	00000000000	0000011100	1010000101	0000000101	00001005001	00001005001
<i>Lancetes marginatus</i>	11001020000	01700000000	00000000101	11000000000	00100000000	00100010000	00100000001	00100000000	0001011000	1010000100	00000000001	00001005011	00001005011
<i>Matus bicarinatus</i>	00111020000	01700000000	00000000171	1000011000	00100000000	00110010000	0010200011	00010000001	0120011111	1000001001	00000000001	00002005201	00002005201
<i>Rhantus signatus</i>	11111020000	01700000000	00000000101	10000000000	00100000000	00100010000	00100000011	00110000001	0101011101	1100000000	00000000001	00001005001	00001005001
<i>Amarodytes duponti</i>	00111000100	0000111101	1111001111	0110100110	1301100011	1100001000	00001000000	0000010010	0100010000	0010001101	0000007110	11001001001	11001001001
<i>Anodocheilus maculatus</i>	00011000100	0000111101	1101001010	0110100110	1301100011	1100001000	00001000000	0000010010	0100010000	0010001101	0000007110	11001001000	11001001000
<i>Hypodessus cruciatus</i>	00011000100	0000111101	1101001111	0110100110	1301100011	1170001000	00001000000	0000010010	0100010011	0010001101	0000007110	11001001000	11001001000
<i>Liodessus flavofasciatus</i>	00011000100	0000111101	1101001010	0110100110	1301100011	1100001000	00001000000	0000010010	0100010000	0010001101	0000007110	11001001000	11001001000
<i>Antiporus uncifer</i>	00011011200	0000111101	0001001170	0110100111	1301100011	1100011000	00001000000	0000010001	0100011111	1000001000	0000000100	10011001201	10011001201
<i>Canthyporus kenyensis</i>	00011000100	0000011101	1001001070	0100100111	0300000011	1100011000	10001000000	0000000010	0000000000	00700077701	0001110110	10070004100	10070004100
<i>Deronectes latus</i>	00011000101	0000111101	1001001171	7100100117	0300100011	1100001700	00001000000	00000000000	0100010111	00000001001	00000000100	10072001701	10072001701
<i>Heterosternuta wickhami</i>	00011000100	0000111101	1001001171	0100100117	0300100011	1100011000	00001000000	0000010000	0100010010	0010001110	00000000100	10002001101	10002001101
<i>Hydrocolus paugus</i>	00010000100	0000111101	1001001171	0100101117	0300100011	1100011000	00001000000	00000000000	0100010000	0010001101	00000000100	10002001100	10002001100
<i>Hydroporus columbianus</i>	00011000100	0000111101	1001001171	0100100117	0300100011	1100011000	00001000000	00000000000	0100010000	0010001101	00000000100	10002001100	10002001100
<i>Laccornellus lugubris</i>	07071000101	0000001101	0001001770	0100177111	01000000000	1007011700	10001000000	0007000017	7700077777	7007701071	0001010011	00770004107	00770004107
<i>Neoporus undulatus</i>	00011000000	0000111101	1001001171	0100100117	0300100011	1100011000	00001000000	0000010000	0100011011	1010001111	00000000100	10001001201	10001001201
<i>Oreodytes scitulus</i>	11111000100	0000111101	1001001171	0010100111	1301100011	1100001000	00001000000	00000000000	0100010000	0000000100	00000000100	10001001711	10001001711
<i>Scarodytes halensis</i>	11111000100	0000111101	1001001171	7010100117	1301100011	1100011700	00001000000	00000000001	0100011011	10000001001	0000000700	10002001701	10002001701
<i>Stictonectes canariensis</i>	00011000100	0000111101	0001001171	7110100117	03000000011	1100001000	00001000000	00000000000	0100010011	00000001001	00000000100	10072001100	10072001100
<i>Hydrovatus caraibus</i>	00001110001	0100011101	1101111010	0101100101	1101000000	1000001000	1200101000	0000010010	0000000000	0101111001	0001110010	10100004100	10100004100
<i>Coelambus impressopunctatus</i>	00011000100	0000111101	0001001170	0110100117	03000000011	1100011700	00001000000	0000010100	0100010011	0010001101	00000000100	10002002100	10002002100
<i>Herophydrus musicus</i>	00011000100	0000111101	0001001170	7210100117	03000000011	1100011000	0000700000	0000010000	0100010011	00777077701	00000000100	10002002700	10002002700
<i>Hygrotus sayi</i>	00011000100	0000111101	0001001170	0110100117	03000000011	1100011700	00001000000	0000001000	0100010011	0010001101	00000000100	10002002100	10002002100
<i>Andex insignis</i>	00011010100	0001111111	1101001101	0111100011	1301000011	1170101000	00000101001	0001010011	0101111111	1000117001	0100111110	10003103101	10003103101
<i>Desmopachria concolor</i>	00011010000	0101111111	1101001001	0111100011	1301111011	1100101010	0101111011	1010010011	0101011111	1011111101	0100111110	10100103301	10100103301
<i>Desmopachria punctatissima</i>	00011010000	0101111111	1101001001	0111100011	1301111011	1100101010	0101111011	1010010011	0101011111	1011111101	0100111110	10100103301	10100103301
<i>Hyphydrus ovatus</i>	00011011000	0101111111	1101001101	7711100117	1301000011	1100101000	0000101001	0000010011	0101011111	1000111001	0100111110	10103103001	10103103001
<i>Microdytes uenoi</i>	00011000100	0101011111	1101001101	7711100117	1301000011	1100101000	0000101001	0000010010	0100011111	1001111001	0100111110	10000003101	10000003101
<i>Pachydrus obesus</i>	00001011210	0000001101	0001001110	0101000011	1201111100	1200001001	0000101011	1001111110	1011010000	0000012001	0110000010	10102002101	10102002101
<i>Laccornis latens</i>	00011000000	0010001100	0001001100	0000100117	01000000000	1010001700	00001000000	00000000010	0000000000	00000001001	00000000100	00000000100	00000000100
<i>Celina parallela</i>	01111000001	0000101000	0001001110	1100100101	01000000000	0000001000	0200100011	0000000000	0100010111	00000001001	1000012100	10100010100	10100010100
<i>Vatellus haagi</i>	00011011300	1100101001	0001001111	0110111111	1301100111	1171010120	1010100122	0100010000	0101011111	1010001102	0200011110	10011000010	10011000010