Larval Description and Phylogenetic Placement of the Australian Endemic Genus Barretthydrus Lea, 1927 (Coleoptera: Dytiscidae: Hydroporinae: Hydroporini: Sternopriscina)

Authors: Alarie, Yves, Michat, Mariano C., Hendrich, Lars, and Watts, Chris H. S.

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Larval Description and Phylogenetic Placement of the Australian Endemic Genus *Barretthydrus* Lea, 1927 (Coleoptera: Dytiscidae: Hydroporinae: Hydroporini: Sternopriscina)

Yves Alarie
Department of Biology, Laurentian University
Sudbury, ON P3E 2C6, CANADA
yalarie@laurentian.ca

Mariano C. Michat
Laboratory of Entomology, DBBE-FCEN and IBBEA-CONICET
Universidad de Buenos Aires, Buenos Aires, ARGENTINA

Lars Hendrich
SNSB-Zoologische Staatssammlung, Münchhausenstra*ß*e 21
München, GERMANY

and

Chris H. S. Watts
South Australian Museum, North Terrace
Adelaide, SA 5000, AUSTRALIA

Abstract

The larvae of the Australian endemic species *Barretthydrus tibialis* Lea, 1927 and *Barretthydrus geminatus* Lea, 1927 are described and illustrated for the first time, with detailed morphometric and chaetotaxic analyses of the cephalic capsule, head appendages, legs, last abdominal segment, and urogomphi. A parsimony analysis based on 118 informative larval characteristics of 34 species in all 10 tribes of the subfamily Hydroporinae was conducted using the program TNT. No clear larval morphological synapomorphies support the monophyletic origin of the tribe Hydroporini. Compared to other known larvae of Hydroporini, *Barretthydrus* Lea is postulated to share a closer phylogenetic relationship with *Antiporus* Sharp, which reinforces their inclusion in the subtribe Sternopriscina.

Key Words: morphology, larvae, phylogenetic relationships, biodiversity, evolution, chaetotaxy, Hydradephaga

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Barretthydrus Lea, 1927 is an Australian endemic genus comprised of three species: the more common *B. tibialis* Lea, 1927 and *B. geminatus* Lea, 1927, and the rarely collected *B. stepheni* Watts, 1978. These dyticids are small (adult body length varying from 4.2 mm to 4.5 mm) and mainly live in clear mountain streams in the Great Dividing Range in Victoria and New South Wales (Watts 1978; Miller and Bergsten 2016).

Barretthydrus is included in the tribe Hydroporini (Dytiscidae: Hydroporinae) that consists of a large and diverse group of water beetles mostly distributed in boreal and temperate regions of the northern hemisphere. Worldwide, Hydroporini currently comprises more than 685 species classified in 38 genera (Nilsson 2017). Within Hydroporini, *Barretthydrus* is postulated to belong to the strictly Australian hydroporine radiation Sternopriscina along with *Antiporus* Sharp, 1882, *Brancuporus* Hendrich, Toussaint, and Balke, 2014, *Carabhydrus* Watts, 1978, *Chostonectes* Sharp, 1880, *Megaporus* Brinck, 1943 *Necterosoma* MacLeay, 1871, *Paroster* Sharp, 1882, *Sekaliporus* Watts, 1997, *Sternopriscus* Sharp, 1880, and *Tiporus* Watts, 1985 (Miller and Bergsten 2016).

The larvae of *Antiporus* and *Paroster* were described in much detail recently (Alarie and Watts 2004; Alarie *et al.* 2009). The larval morphology of the other members of the subtribe Sternopriscina are only poorly known, but late instars can be identified to genus using the illustrated keys in Watts (2002). The discovery of the larvae of both *B. tibialis* and *B. geminatus* provided the impetus for this study, which has the following three goals: (1) to describe, in detail, for the first time the larvae of *B. tibialis* and *B. geminatus*; (2) to compare the ground plan of larval features of *Barretthydrus* with those of other associated Sternopriscina genera for which the larvae have been described comprehensively; and (3) to study the phylogenetic relationships of *Barretthydrus* within the tribe Hydroporini based on larval characters.

Material and Methods

Larvae Examined. The descriptions of the larval stages and the taxonomic conclusions reported in this paper are based on the examination of larvae co-occurring with adults. Larvae of each species were identified to species either by rearing some larvae collected in the field (*B. geminatus*) or by collecting in situations where they could unequivocally be associated to either species. The localities from which the specimens were obtained are provided under the individual species descriptions.

Preparation. Larvae were disarticulated and mounted on standard glass slides in Hoyer's medium. Microscopic examination at magnifications of 80–800X was done using an Olympus BX50 compound microscope equipped with Nomarsky differential interference optics. Figures were prepared through use of a drawing tube attached to the microscope. Drawings were scanned and digitally inked using an Intuos 4 professional pen tablet (Wacom Co., Ltd. Kazo, Saitama, Japan). Voucher specimens are deposited in the larval collection of Y. Alarie (Department of Biology, Laurentian University, Canada).

Measurements. All measurements were made with a compound microscope equipped with a micrometer eyepiece. The part to be measured was adjusted so that it was, as nearly as possible, parallel to the plane of the objectives. We employed, with minimal modifications and additions, the terms used in previous papers dealing with larval morphology of Hydroporini (*e.g.*, Alarie and Watts 2004; Alarie *et al.* 2009). The following variables were measured: Head length (HL) = total head length including the frontoclypeus, measured medially along epicranial stem; head width (HW) = maximum head width; length of frontoclypeus (FRL) = from apex of nasale to posterior margin of ecdysial suture; occipital foramen width (OCW) = maximum width measured along dorsal margin of occipital foramen; length of mandible (MN) = measured from laterobasal angle to apex; width of mandible = maximum width measured at base. Lengths of the antenna (A) and maxillary (MP) and labial (LP) palpi were derived 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 the leg (L) including the longest claw was derived 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). Length of trochanter includes only the proximal portion; length of the distal portion is included in the femoral length. Dorsal length of the last abdominal segment (LAS) was measured along the midline from the anterior to the posterior margin. Length of urogomphus (U) was derived by adding the lengths of the individual segments; each segment is denoted by the letter U followed by a number (*e.g.*, U1 = first urogomphomere). These measurements were used to calculate several ratios that characterize the body shape.

Chaetotaxic Analysis. Primary (observed in instar I) and secondary (added throughout ontogenetic development) setae and pores were distinguished on the head capsule, head appendages, legs, last abdominal segment, and urogomphus. The setae and pores were coded according to the system proposed by Alarie (1991) and Alarie and Michat (2007a) for the cephalic capsule and head appendages, Alarie *et al.* (1990) for the legs, and Alarie and Harper (1990) for the last abdominal segment and urogomphi. Setae are coded by two capital letters corresponding to the first two letters of the name of the structure on which the seta is located (AB = abdominal segment VIII; AN = antenna; CO = coxa; FE = femur; FR = frontoclypeus; LA = labium; MN = mandible; MX = maxilla; PA = parietale; TA = tarsus; TI = tibia; TR = trochanter; UR = urogomphus) and a number. Pores are coded in a similar manner except that the number is replaced by a lowercase letter. The position of the sensilla is described by adding the following abbreviations: A = anterior; AD = anterodorsal; AV = anteroventral; D = dorsal; PD = posterodorsal; Pr = proximal; PV = posteroventral.

Color. Description of color is given for all species based on ethanol-preserved specimens.

Cladistic Analysis. To examine the phylogenetic signal of the larval characters of *Barretthydrus* and to test the relationships of this genus with other Hydroporini, a cladistic analyses of 16 species of Hydroporini (nine genera) and 18 species of all other nine tribes of the Hydroporinae was conducted. The genera *Laccornis* Gozis, 1914 (tribe Laccornini), *Laccornellus* Roughley and Wolfe, 1987 and *Canthyporus* Zimmermann, 1919 (tribe Laccornellini), *Celina* Aubé, 1837 (tribe Methlini), *Pachydrus* Sharp, 1882 (Pachydrini), and *Hydrovatus* Motshulsky, 1853 (Hydrovatini), which are generally recognized as basal lineages within the subfamily Hydroporinae based on adults (Roughley and Wolfe 1987; Miller *et al.* 2006), larvae (Alarie and Michat 2007b), and molecules (Miller and Bergsten 2014), and several taxa of Hyphydrini, Bidessini, Vatellini, and Hygrotini were used as outgroups rooting the tree with *Laccornis*. The analysis was performed using the program TNT

(Goloboff *et al.* 2008). A heuristic search was implemented using "tree bisection reconnection" as the algorithm, with 200 replicates and saving 100 trees per replication (previously setting "hold 20000"). Bremer support values were calculated using the commands 'hold 20000', 'sub n' and 'bsupport', where 'n' is the number of extra steps allowed. The process was repeated increasing the length of the suboptimal cladograms by one step, until all Bremer values were obtained (Kitching *et al.* 1998). Bootstrap values were calculated using the following parameters: "standard (sample with replacement)"; 2000 replicates.

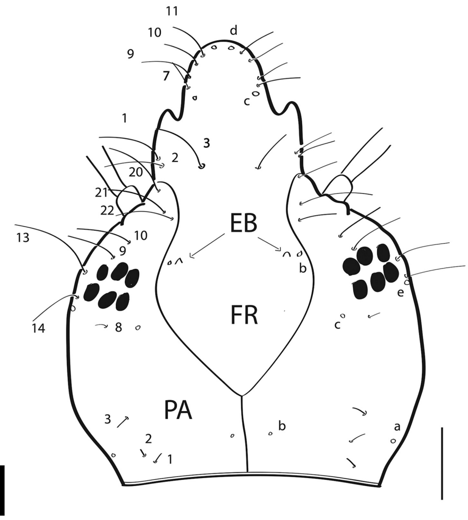
Results

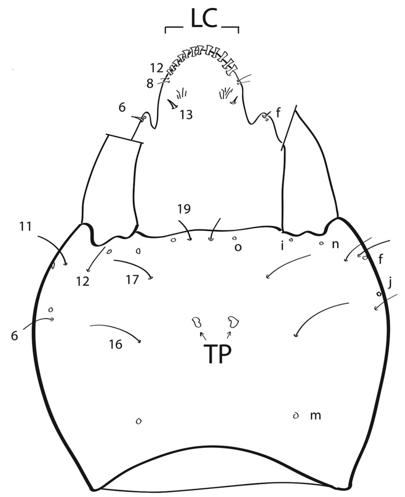
Barretthydrus Lea, 1927
(Figs. 1–19)

Diagnosis. Instar III of *Barretthydrus* can be distinguished from those of other genera of Australian Hydroporini that have been well studied (*i.e.*, *Antiporus* and *Paroster*) by the following combination of characters: HL = 1.24–1.36 mm; HL/HW <1.40; nasale broad, subtriangular, not spatulate apically (Figs. 1, 15–16); parietals constricted at level of occipital suture (Figs. 15–16); primary seta FR7 hair-like (Fig. 1); A4/A3 >0.30; labial palpus composed of two palpomeres (Figs. 5–6); prementum lacking spinulae along lateral margins (Figs. 5–6); L3/HW <3.50; primary seta FE7 present (Fig. 8); natatory setae present on dorsal margin of femora, tibiae, and tarsi (Fig. 18); U1/U2' <3.50; U1/HW <1.70.

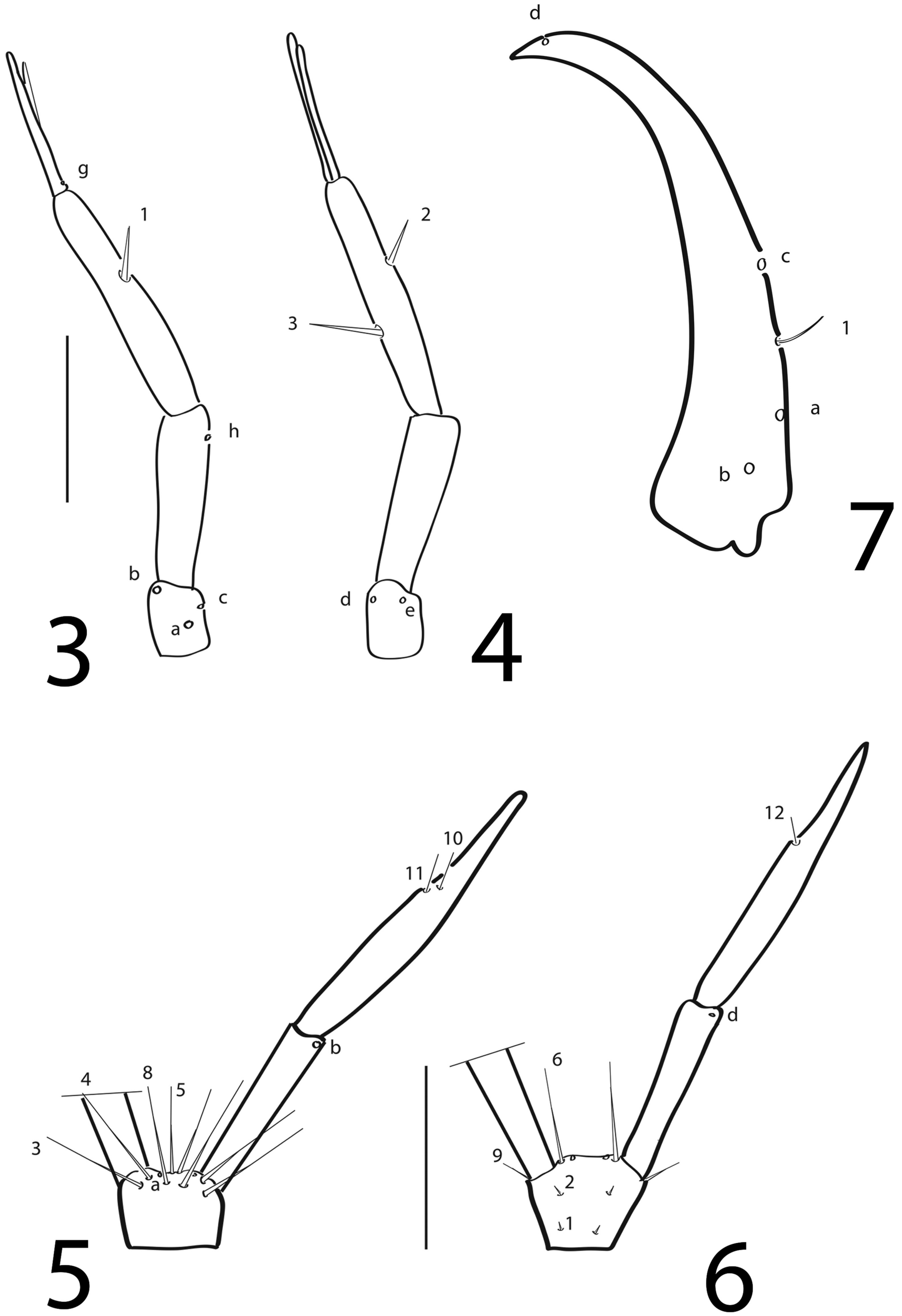
Instar I
(Figs. 1–12)

Description. Body: Subcylindrical, narrowing towards abdominal apex. Measurements and ratios that characterize the body shape are shown in Table 1. **Head:** Head capsule (Figs. 1–2) pear-shaped, tapering posteriorly, not constricted at level of occipital suture; ecdysial suture well-developed, coronal suture short; frontoclypeus elongate, bluntly rounded, subtriangular with well-developed lateral branches, anteroventral margin with 12 ventral lamellae clypeales (Bertrand 1972); dorsal surface with 2 spine-like egg bursters (ruptor ovi of Bertrand 1972) at about mid-length; ocularium present, stemmata not visible ventrally and subdivided into 2 vertical series; epicranial plates meeting ventrally; tentorial pits visible medioventrally at about mid-length. Antenna (Figs. 3–4) elongate, slightly shorter than HW; composed of 4 antennomeres, A2 and A3 longest, A1 shortest; A3' relatively elongate, shorter than A4; A3 lacking ventroapical spinula. Mandible (Fig. 7) prominent, falciform, distal half projecting inwards and upwards, apex sharp; mandibular channel present. Labium (Figs. 5–6), prementum subrectangular, about as long as broad, lacking lateral marginal spinulae; LP elongate, distinctly shorter than MP, composed of 2 palpomeres; LP2 subfusiform, distinctly longer than LP1. Maxilla (Figs. 13–14) with short, thick stipes, incompletely sclerotized ventrally; cardo fused to stipes; galea and lacinia absent; MP elongate, slightly shorter than antenna, composed of 3 palpomeres; MP1 and MP2 longest, MP2 distinctly longer than MP1. **Thorax:** Thoracic terga convex, pronotum slightly shorter than meso- and metanota combined, meso- and metanota

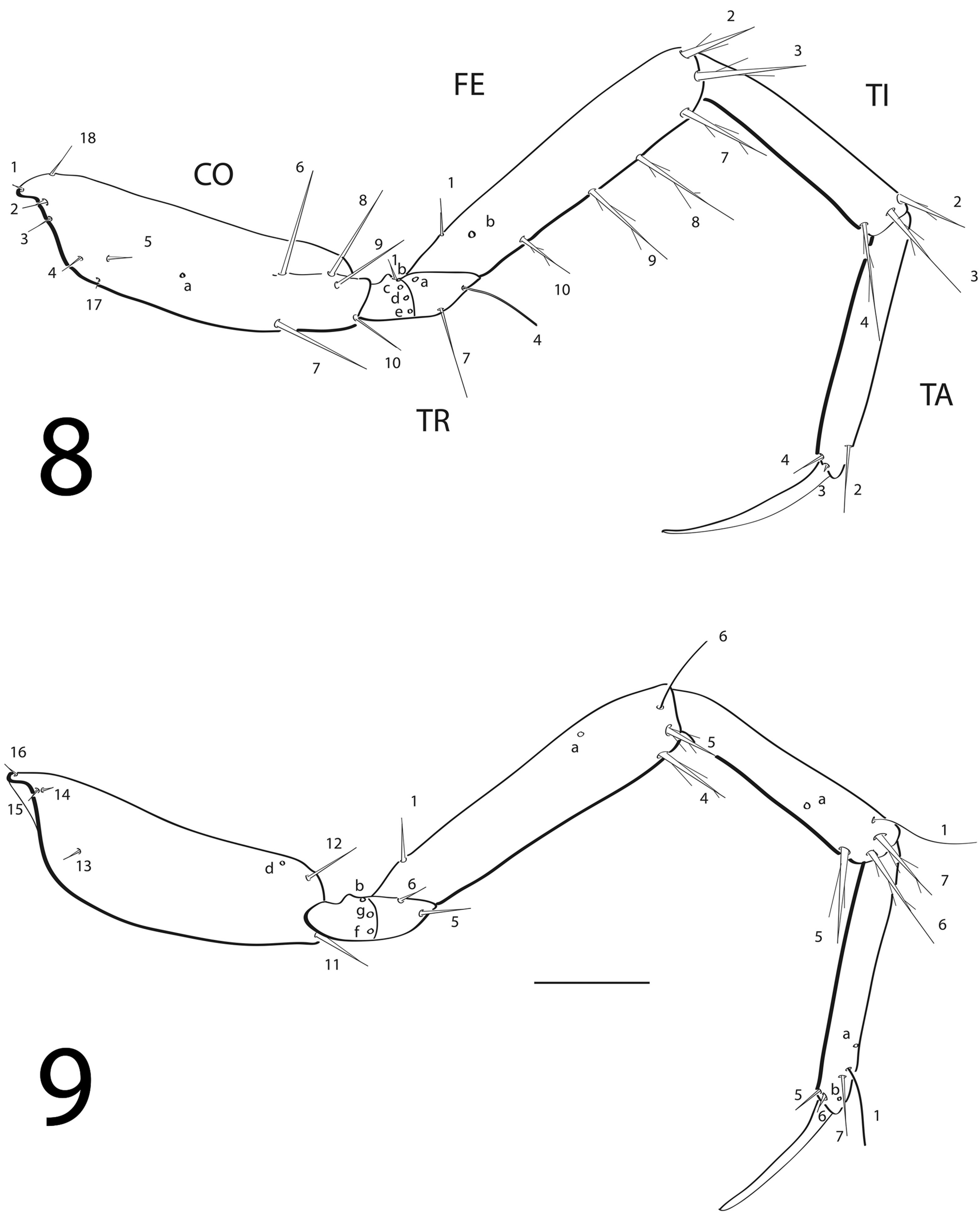
1


2


Figs. 1–2. *Barretthydrus tibialis*, instar I, head capsule. **1)** Dorsal aspect; **2)** Ventral aspect. EB = egg bursters: FR = frontoclypeus; PA = parietale; TP = tentorial pits. Numbers and lowercase letters refer to primary setae and pores, respectively. Color pattern not represented. Scale bar = 0.10 mm.

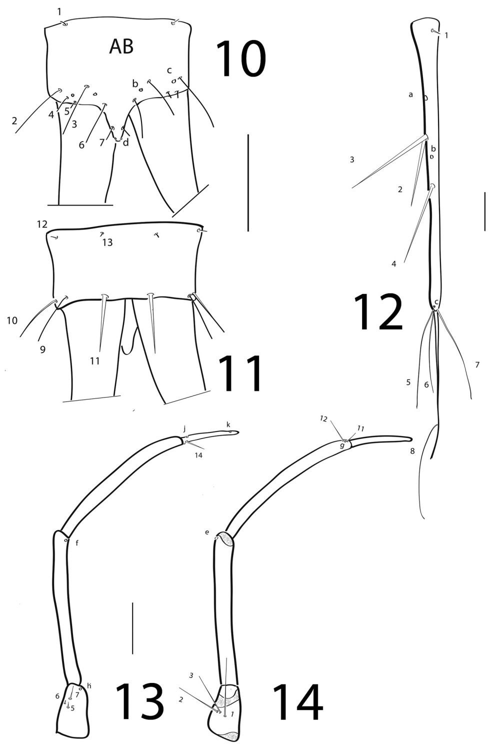


Figs. 3–7. *Barretthydrus tibialis*, instar I, head appendages. Antenna: **3)** Dorsal aspect; **4)** Ventral aspect. Labium: **5)** Dorsal aspect; **6)** Ventral aspect. **7)** mandible, dorsal aspect. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bar = 0.10 mm.

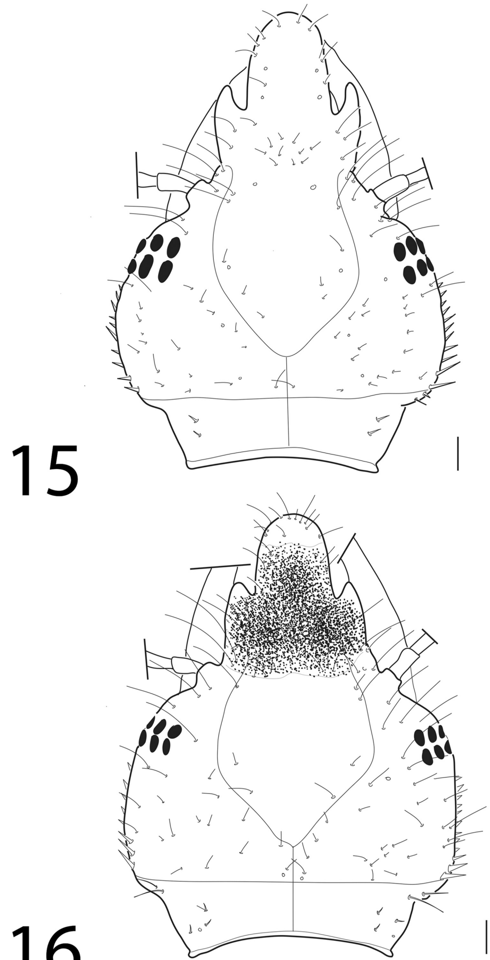


Figs. 8–9. *Barretthydrus tibialis*, instar I, mesothoracic leg. **8)** Anterior surface; **9)** Posterior surface; CO = coxa; FE = femur; TA = tarsus; TI = tibia; TR = trochanter. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bar = 0.10 mm.

subequal; protergite subrectangular to subovate, more developed than meso- and metatergites; [We were unable to determine the presence of an anterotransverse carina owing to the bad condition of the only specimen available.]; thoracic sterna membranous; spiracles absent. **Legs:** Long (Figs. 8–9), composed of 6 articles (*sensu* Lawrence 1991); L1 shortest, L3 longest; CO robust, elongate, TR divided into 2 parts by an annulus, FE, TI, and TA slender, subcylindrical, PT with 2 long, slender, slightly curved claws; posterior claw shorter than anterior claw on L1 and L2, posterior claw longer than anterior claw on



Figs. 10–14. *Barretthydrus tibialis*. Instar I: **10)** Abdominal segment VIII (AB), dorsal aspect; **11)** Abdominal segment VIII, ventral aspect; **12)** Urogomphus, dorsal aspect. Instar III, maxilla: **13)** Dorsal aspect; **14)** Ventral aspect. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bars = 0.10 mm.



Figs. 15–16. *Barretthydrus* species, instar III, dorsal surface of head capsule. **15)** *B. geminatus*; **16)** *B. tibialis*. Scale bars = 0.10 mm.

L3; femora, tibiae, and tarsi lacking spinulae along ventral margin. **Abdomen:** Eight-segmented (Figs 10–11); segments I–VI sclerotized dorsally, membranous ventrally; segment VII sclerotized both dorsally and ventrally, ventral sclerite independent from dorsal one; tergites I–VII narrow, transverse, rounded laterally, lacking sagittal line; [We were unable to determine the presence of an anterotransverse carina owing to the bad condition of the only specimen available.]; segment VIII (=LAS) longest, completely sclerotized, ring-like, strongly constricted at point of insertion of urogomphus; projecting backwards into a very short, subconical siphon; spiracles absent lateroventrally on segments I–VII. Urogomphus very long, composed of 2 urogomphomeres; U1 long, much longer than segment VIII; U2 narrower, setiform, much shorter than U1. **Chaetotaxy:** Similar to that of generalized Hydroporinae larva (Alarie and Harper 1990; Alarie *et al.* 1990; Alarie 1991; Alarie and Michat 2007a) except for the following features (Figs. 1–12): Pores PAd and ANf absent; pore ANh distal; setae MX4 and TR2 absent; pore FEa articulated distally, close to seta FE5; seta TI7 short, spine-like; seta AB10 spine-like; setae UR2 and UR3 contiguous, seta UR4 articulated posteriorly; setae UR5, UR6, and UR7 elongate; seta UR8 inserted subapically. [Pore PAk and seta PA13 could not be located. We are reluctant to consider them as lacking due to the condition of the only instar I specimen available.]

Instar II

No specimens were available for study.

Instar III

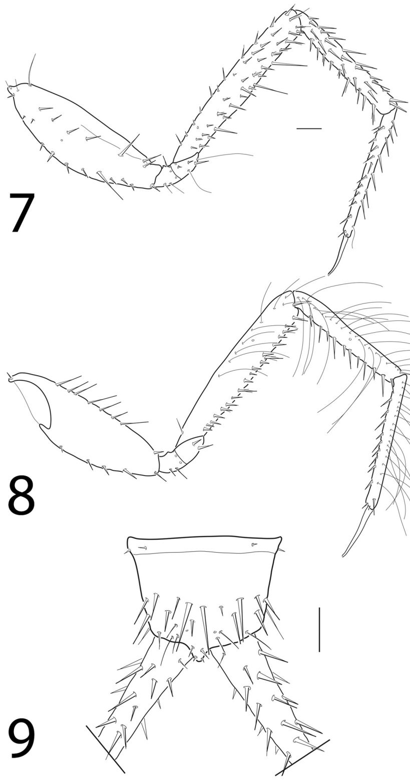
(Figs. 13–19)

Description. As instar I except as follows: **Body:** Measurements and ratios that characterize the body

17

18

19



Figs. 17–19. *Barretthydrus tibialis*, instar III. Metathoracic leg: **17)** Anterior surface; **18)** Posterior surface. **19)** Last abdominal segment, dorsal surface. Scale bars = 0.10 mm.

shape in Tables 1 and 2. **Head:** Head capsule (Figs. 15–16) constricted at level of occipital suture; egg bursters lacking. Antenna elongate, distinctly shorter than HW. LP2 subequal to slightly shorter than LP1. MP subequal in length to antenna, MP1 slightly shorter than MP2 (Figs. 13–14). **Thorax:** Protergum lacking anterotransverse carina; both meso- and metathoracic terga with an anterotransverse carinae; sagittal line visible; mesopleural region with a spiracular opening on each side. **Legs:** Position and number of secondary setae in Table 3; natatory setae present on dorsal margin of femora, tibiae, and tarsi (Figs. 17–18). **Abdomen:** Segment VII completely sclerotized both dorsally and ventrally, all tergites with anterotransverse carina (Fig. 19); mesopleural region of segments I–VII with a spiracular opening on each side. **Chaetotaxy:** Head capsule with numerous secondary setae; lateroventral margin of PA with several secondary spine-like setae (Figs. 15–16); anteroventral margin of nasale with half circle of about 60 lamellae clypeales of different lengths, directed downwards; AN, MX, and LA lacking secondary setae; MN with 1 hair-like secondary seta on basoexternal margin; thoracic and abdominal sclerites I–VIII with numerous secondary setae mainly on posterior half; natatory setae present on dorsal margin of femora, tibiae, and tarsi; secondary leg setation in Tables 3-4 and Figs. 17–18; U with secondary setae (Fig. 19).

Remarks. Larvae of *Barrethydrus* can readily be distinguished from those of other Australian Hydroporini described in detail (*i.e.*, *Paroster* and *Antiporus*) by the presence of natatory setae on the dorsal margins of the femur, tibia, and tarsi and metric characters presented in Table 2, and, superficially, from the less well-studied genera by the strong, dark yellow banding on the body.

Distribution. Endemic to Australia.

Barretthydrus tibialis Lea, 1927
(Figs. 1–14, 16–19)

Source of Material. Larvae were collected in association with adults at the following localities: **Australia, New South Wales**, 20 km North of Nelligan, 15-VIII.1997, coll. C. H. S. Watts; Sardine Creek, 30 km North of Orbost V, 30-XI-1998, C. H. S. Watts leg.

Diagnostic Combination (Instar III). The third instar of *B. tibialis* can easily be distinguished from that of the closely similar *B. geminatus* by the presence of a broad, blackish macula on the anterior portion of the frontoclypeus (Fig. 16) in addition to a relatively shorter head capsule compared to the length of abdominal segment VIII (HL/LAS <4.50 compared to >4.60) and a larger total number of secondary setae on selected leg articles (Table 3).

Instar I
(Figs. 1–12)

Description. Color: [Not available owing to the bad state of preservation of the only specimen available.] **Body:** Measurements and ratios that characterize the body shape in Table 1. **Head:** Head capsule as in Figs. 1–2, HL = 0.60 mm, HL/LAS = 4.61. **Abdomen:** As in Figs. 10–11, U1 = 0.75 mm; U1/HW = 1.55.

Instar II
No specimen available for study.

Instar III
(Figs. 13–14, 16–19)

Description. Color: Head capsule predominantly yellow; frontoclypeus with a broad, black, subapical macula (Fig. 16); head appendages dark yellow; thoracic tergites dark brown; abdominal tergites I, IV–VII dark brown, II and III dark yellow to pale brown and VIII pale yellow; urogomphi dark yellow to pale brown; legs dark brown proximally, pale yellow distally. **Body:** Measurements and ratios that characterize the body shape in Table 1. **Head:** Head capsule as in

Table 1. Measurements and ratios for the larvae of *Barretthydrus tibialis* (BATI) and *Barretthydrus geminatus* (BAGE). *n* = number of specimens studied; ** = missing values. See text for definitions of variable codes.

	BATI		BAGE
Variables	**Instar I (*n* = 1)**	**Instar III (*n* = 12)**	**Instar III (*n* = 4)**
HL (mm)	0.60	1.24–1.30	1.27–1.36
HW (mm)	0.49	0.96–1.02	0.94–1.02
FRL (mm)	0.48	0.97–0.99	1.01–1.05
OCW (mm)	0.34	0.56–0.65	0.56–0.63
HL/HW	1.23	1.24–1.35	1.33–1.35
HL/LAS	4.61	3.91–4.47	4.63–4.66
HW/OCW	1.44	1.57–1.70	1.60–1.69
A/HW	0.83	0.70–0.73	0.75–0.77
A3/A2	1.33	0.84–1.00	0.87–0.88
A4/A3	0.62	0.31–0.38	0.30–0.35
A3'/A4	0.81	0.76–0.92	0.76–0.98
MNL/MNW	3.78	3.74–4.31	3.95–4.74
MNL/HL	0.53	0.50–0.56	0.52–0.59
A/MP	1.13	1.02–1.07	1.00–1.02
MP2/MP1	1.48	0.86–1.00	0.90–0.92
MP/LP	1.24	1.20–1.24	1.16–1.25
LP2/LP1	1.60	0.81–0.95	0.81–0.94
L1 (mm)	1.15	2.09–2.19	2.03–2.13
L2(mm)	1.33	2.51–2.69	2.41–2.53
L3 (mm)	**	2.94–3.09	2.80–2.96
L3/L1	**	1.37–1.42	1.36–1.39
L3/L2	**	1.11–1.18	1.15–1.17
L3/HW	**	2.98–3.15	2.96–3.05
L3(CO/FE)	**	0.90–0.94	0.91–0.92
L3(TI/FE)	**	0.73–0.77	0.70–0.75
L3(TA/FE)	**	0.70–0.80	0.71–0.76
L3(PC/TA)	**	0.34–0.38	0.35–0.36
LAS (mm)	0.13	0.28–0.34	0.28–0.30
LAS/HW	0.27	0.28–0.35	0.29
U1 (mm)	0.75	1.51–1.69	1.29–1.45
U1+U2'(mm)	1.05	1.99–2.19	**
U1+U2 (mm)	1.14	**	**
U1/U2'	2.53	2.87–3.33	**
U1/LAS	5.79	4.63–6.08	4.56–5.12
U1/HW	1.55	1.56–1.67	1.37–1.49
U1+U2'/LAS	8.08	6.68–7.90	**
U1+U2'/HW	2.17	2.11–2.13	**
U1+U2/LAS	8.76	**	**
U1+U2/HW	2.35	**	**

Fig. 16, HL = 1.24–1.30, HL/LAS <4.50. **Abdomen:** U1 = 1.51–1.69 mm, U1/HW = 1.56–1.67 (Fig. 19). **Chaetotaxy:** ProFE with more than 52 secondary setae; mesoFE with more than 56 secondary setae; mesoTI with more than 47 secondary setae; mesoTA with more than 34 secondary setae; metaCO with more than 26 secondary setae; metaFE with more than 66 secondary setae; metaTI with more than 50 secondary setae; metaTA with more than 43 secondary setae.

Barretthydrus geminatus Lea, 1927
(Fig. 15)

Source of Material. Larvae were collected in association with adults at the following locality: **Australia, New South Wales**, 13 km NNW Dungog, Williams River, Tillegra Bridge, 109 m., 19. X.2006, 32.19.078S 151.41.250E, L. Hendrich leg. (NSW 84).

Diagnostic Combination (Instar III). The third instar of *B. geminatus* can easily be distinguished from that of the closely similar *B. tibialis* by the absence of maculae on the dorsal surface of the head capsule (Fig. 15), in addition to a relatively longer head capsule compared to the length of abdominal segment VIII (HL/LAS >4.60 compared to <4.50) and a lower total number of secondary setae on selected leg articles (Table 3).

Table 2. Measurements and ratios for instar III of selected genera of Australian Hydroporini: ANTI = *Antiporus*; BARR = *Barretthydrus*; PARO = epigaeic *Paroster*. *n* = number of species; **, missing values. See text for definitions of variable codes.

Variables	ANTI (*n* = 7)	BARR (*n* = 2)	PARO (*n* = 6)
HL (mm)	1.43–2.12	1.24–1.36	0.69–0.93
HW (mm)	0.73–1.20	0.94–1.02	0.55–0.75
FRL (mm)	1.08–1.65	0.97–1.05	0.55–0.75
OCW (mm)	0.54–0.64	0.56–0.65	0.45–0.60
HL/HW	1.60–2.00	1.24–1.35	1.18–1.43
HL/LAS	3.40–5.30	3.91–4.66	2.05–2.45
HW/OCW	1.40–1.67	1.57–1.70	1.09–1.33
A/HW	0.90–1.36	0.70–0.77	0.50–0.67
A3/A2	0.86–1.16	0.84–1.00	0.87–1.22
A4/A3	0.16–0.22	0.30–0.38	0.39–0.51
A3’/A4	0.60–0.96	0.76–0.98	0.66–0.91
MNL/MNW	4.24–5.99	3.74–4.74	3.32–4.40
A/MP	1.00–1.20	1.00–1.07	0.82–1.09
MP2/MP1	0.74–1.01	0.86–1.00	0.82–1.24
MP/LP	1.31–1.79	1.16–1.25	1.16–1.45
LP2/LP1	0.74–1.09	0.81–0.95	0.81–1.10
L1 (mm)	2.33–3.48	2.03–2.19	1.16–1.58
L3 (mm)	3.05–4.92	2.80–3.09	1.52–2.25
L3/L1	1.28–1.40	1.36–1.42	1.25–1.50
L3/HW	3.83–4.40	2.96–3.15	2.41–3.52
LAS (mm)	0.31–0.54	0.28–0.34	0.34–0.43
LAS/HW	0.36–0.56	0.28–0.35	0.49–0.68
U1 (mm)	2.34–3.65	1.29–1.69	1.12–2.30
U1+U2’ (mm)	2.89–4.43	1.99–2.19	1.62–2.26
U1/U2’	3.98–6.54	2.87–3.33	4.00–6.46
U1/LAS	5.24–9.39	4.56–6.08	3.14–6.28
U1/HW	2.59–3.59	1.37–1.67	1.80–4.00

Instar I

No specimen available for study.

Instar II

No specimen available for study.

Instar III
(Fig. 15)

Description. Color: Head capsule testaceous (Fig. 15); head appendages pale yellow; thoracic tergites dark brown; abdominal tergites I–III brown mesally, broadly yellow laterally, IV–VII dark brown, VIII pale yellow; urogomphi dark yellow; legs predominantly dark yellow except coxae brownish. **Body:** Measurements and ratios that characterize the body shape in Table 1. **Head:** Head capsule as in Fig. 15, HL = 1.27–1.36, HL/LAS >4.60. **Abdomen:** U1 = 1.29–1.45 mm, U1/HW = 1.37–1.49. **Chaetotaxy:** ProFE with less than 45 secondary setae; mesoFE with less than 51 secondary setae; mesoTI with less than 45 secondary setae; mesoTA with less than 30 secondary setae; metaCO with less than 18 secondary setae; metaFE with less than 53 secondary setae; metaTI with less than 46secondary setae; metaTA with less than 38 secondary setae.

Discussion

The dytiscid subfamily Hydroporinae is generally recognized as monophyletic (Burmeister 1976; Wolfe 1985; Miller 2001; Ribera *et al.* 2002; Miller *et al.* 2006; Michat *et al.* 2007, 2017; Miller and Bergsten 2014). This subfamily is presently composed of 10 tribes (Miller and Bergsten 2016), including the very speciose Hydroporini. Hydroporini remains a difficult group to diagnose, and, as shown in this study (Fig. 20), no really clear larval morphological synapomorphies yet support the monophyletic origin of this group.

Our results, however, posit *Barretthydrus* as closely related to *Antiporus* and members of the tribe Vatellini. Larvae of these three lineages are characterized by the presence of well-developed lateral branches on the frontoclypeus (Figs. 1, 15–16; character 003.2), the cardo fused to the stipes (Fig. 14, character 036.1), the primary setae LA10 and LA12 short (Figs. 5–6; character 063.1), the presence of natatory posterodorsal setae on the femur (character 076.1), tibia (character 082.1), and tarsus (ch. 087.1) (Fig. 18), a very short siphon (Figs. 10, 19; character 097.0), and the seta AB10 spine-like (Fig. 11; character 105.1). All these features, however, are homoplasious within the

Table 3. Number of secondary setae on the legs of third instars of *Barretthydrus geminatus* (BAGE) and *Barretthydrus tibialis* (BATI). Four specimens of each species were studied. CO = coxa; FE = femur; TA = tarsus; TI = tibia; TR = trochanter. Sensillar series: A = anterior; AD = anterodorsal; Adi = anterodistal; AV = anteroventral; D = dorsal; NS = natatory setae; PD = posterodorsal; Pr = proximal; PV = posteroventral; V = ventral. Total is the total number of secondary setae on the segment.

Segment	Sensillar series	BAGE	BATI	Segment	Sensillar series	BAGE	BATI
ProCO	D	4–5	6–8	MesoTI	NS(PD)	18–22	19–20
	A	2–3	2–3		AD	6–8	9–11
	V	5–7	7–10		AV	5–9	10–13
	Total	11–15	15–21		PV	6–7	7–10
ProTR	Pr	1	1		Total	36–45	47–51
	ADi	0–2	0–1	MesoTA	NS(PD)	16–19	14–16
	Total	1–3	1–2		AD	3–4	6–7
ProFE	NS(PD)	9–12	11–14		AV	4–5	6–8
	AD	6–10	11–12		PV	2–4	6–7
	AV	13–16	18–20		Total	26–30	34–37
	PV	7–10	12–14	MetaCO	D	5–7	7–10
	Total	35–45	52–58		A	5	7–9
ProTI	NS(PD)	12–17	14–15		V	4–6	11–14
	AD	3–4	4–5		Total	14–18	26–32
	AV	2–3	1–4	MetaTR	Pr	2	2–3
	PV	2–5	6–7		ADi	2–3	2–2
	Total	19–27	27–31		Total	4–5	4–5
ProTA	NS(PD)	9–12	10–11	MetaFE	NS(PD)	6–9	8–12
	AD	2	2–3		AD	10–18	15–16
	AV	0	0		AV	14–18	18–24
	PV	4	4–6		PV	8–13	19–22
	Total	15–18	17–19		Total	43–53	66–69
MesoCO	D	6–10	9–13	MetaTI	NS(PD)	20–22	18–22
	A	2–5	4–6		AD	8–11	14–16
	V	5–6	7–11		AV	6–8	7–10
	Total	15–21	21–29		PV	6	9–11
MesoTR	Pr	1–3	0–2		Total	40–46	50–55
	ADi	1–2	1–2	MetaTA	NS(PD)	19–22	19–21
	Total	2–5	2–3		AD	4–5	7–10
MesoFE	NS(PD)	11–16	12–14		AV	5–8	8–10
	AD	7–14	12–17		PV	3–5	7–9
	AV	13–16	16–18		Total	31–38	43–47
	PV	11–14	14–19				
	Total	44–51	56–64				

Hydroporinae, which results in weak support for this clade. In our study, the tribe Vatellini is recovered as monophyletic with strong support (Fig. 20; Bremer support >10, Bootstrap value = 99). Larvae of Vatellini have evolved a large number of synapomorphies (Fig. 21), which reinforces the hypothesis that Vatellini is a natural group (*e.g.*, Miller 2001, 2005; Michat and Torres 2005, 2011; Miller *et al.* 2006; Ribera *et al.* 2008; Michat *et al.* 2017). The sister group relationship of Vatellini with *Antiporus*, however, is only supported by scarce and homoplasious characters. Larvae of this clade share a narrow, more or less parallel-sided (character 001.1) and spatulate (character 002.1) nasale as well as the absence of secondary spine-like setae on the parietals (Alarie and Watts 2004). The phylogenetic relationship between the Vatellini and *Antiporus* deserves to be further tested using a larger data set that include more taxa.

Although weakly supported, the close relationship of *Barethydrus* with *Antiporus* is worth noting knowing that both genera were included in the subtribe Sternopriscina by Miller and Bergsten (2016). Larvae of *Barretthydrus* differ from those of *Antiporus* by the presence of a hair-like seta FR7 (Fig. 1; character 008.0) (spine-like in *Antiporus*), the parietals constricted at the level of the occipital suture in instars II–III (Figs. 15–16; character 013.1), and the absence of spinulae along the lateral margin of the prementum (Figs. 5–6; character 051.0).

This paper is the third of a series of articles aiming to study the larvae of the strictly Australian radiation Sternopriscina. Along with *Antiporus* (Alarie and

Table 4. Number of secondary setae on the legs of third instars of selected genera of Australian Hydroporini: *Antiporus* (ANTI); *Barretthydrus* (BARR); epigaeic *Paroster* (PARO). *n* = number of species studied. CO = coxa; FE = femur; TA = tarsus; TI = tibia; TR, trochanter. Sensillar series: A = anterior; AD = anterodorsal; Adi = anterodistal; AV = anteroventral; D = dorsal; NS = natatory setae; PD = posterodorsal; Pr = proximal; PV = posteroventral; V = ventral. Total is the total number of secondary setae on the segment.

Segment	Sensillar series	ANTI (*n* = 7)	BARR (*n* = 2)	PARO (*n* = 6)	Segment	Sensillar series	ANTI (*n* = 7)	BARR (*n* = 2)	PARO (*n* = 6)
ProCO	D	5-19	4-8	3-8	MesoTI	NS(PD)	17-39	18-22	0
	A	1-12	2-3	0-3		AD	6-19	6-11	1-4
	V	3-19	5-10	0-4		AV	5-17	5-13	1-4
	Total	10-43	11-21	3-14		PD	0	0	0-1
ProTR	Pr	1-6	1	0		PV	6-16	6-10	1-9
	ADi	0-3	0-2	0		Total	43-83	36-51	3-13
	Total	1-8	1-3	0	MesoTA	NS(PD)	15-40	16-19	0
ProFE	NS(PD)	14-28	9-12	0		AD	4-10	3-7	0-1
	AD	12-21	6-12	2-6		AV	6-13	4-8	0-1
	AV	15-28	13-20	6-13		PD	0	0	0-1
	PD	0-1	0	0-3		PV	6-13	2-7	1-3
	PV	6-16	7-14	2-7		Total	37-69	26-37	3-5
	Total	50-84	35-58	1-5	MetaCO	D	5-30	5-10	3-9
ProTI	NS(PD)	14-28	12-17	0		A	0-18	5-9	1-6
	AD	4-13	3-5	0-1		V	3-25	4-14	0-8
	AV	3-10	2-4	0-2		Total	10-63	14-32	5-23
	PV	4-8	2-7	0-2	MetaTR	Pr	1-8	2-3	0-3
	Total	31-57	19-31	1-5		ADi	0-6	2-3	0
ProTA	NS(PD)	11-27	9-12	0		Total	1-13	4-5	0-3
	AD	2-10	2-3	0-1	MetaFE	NS(PD)	9-29	6-12	0
	AV	5-12	0	0-1		AD	15-26	10-18	3-9
	PD	0	0	0-1		AV	10-29	14-24	5-14
	PV	5-9	4-6	0-2		PD	0-4	0	0-1
	Total	27-56	15-19	1-4		PV	12-31	8-22	6-31
MesoCO	D	4-24	6-10	1-4		Total	54-105	43-69	14-55
	A	0-14	2-6	0-4	MetaTI	NS(PD)	17-41	20-22	0
	V	2-21	5-11	0-6		AD	7-18	8-16	0-5
	Total	8-54	15-29	4-17		AV	5-15	6-10	1-4
MesoTR	Pr	1-7	1-3	0-2		PD	0	0	0-3
	ADi	0-5	1-2	0		PV	7-18	6-11	1-12
	Total	1-12	2-5	0-2		Total	46-84	40-55	5-20
MesoFE	NS(PD)	13-31	11-16	0	MetaTA	NS(PD)	17-42	19-22	0
	AD	13-24	7-17	3-8		AD	5-14	4-10	0-1
	AV	16-26	13-18	6-14		AV	6-14	5-10	1-3
	PD	0-2	0	0-2		PD	0	0	0-4
	PV	10-25	11-19	6-23		PV	7-15	3-9	2-7
	Total	56-101	44-64	14-42		Total	42-73	31-47	4-10

Watts 2004) and *Barretthydrus* (this paper), *Paroster* is the only other genus that has been studied in much detail (Alarie *et al.* 2009). One may wonder why *Paroster* was not included in our data matrix. (Tables 5–6). The first instar of only one *Paroster* species (the hypogaeic *Paroster darlotensis* Watts and Humphries) has been described to date. Hypogaeic *Paroster* are morphologically strongly modified (Alarie *et al.* 2009) and exhibit some parallelisms (*e.g.*, absence of stemmata) with other subterranean dytiscids that we judged would interfere with the larval phylogenetic signal and, therefore, hamper the phylogenetic resolution. Thus, the genus was excluded from the analysis.

Larvae of *Paroster* are unique within the Hydroporinae in that their labial palpus is composed of three palpomeres (in comparison to two in every other hydroporine species) (Alarie *et al.* 2009). They also strongly differ from larvae of *Antiporus* and *Barretthydrus* by the absence of natatory setae on their legs (Table 4). On the other hand, *Paroster* larvae share with these two Sternopriscina genera the presence of well-developed lateral branches on the frontoclypeus, the cardo fused to the stipes, the primary setae LA10 and LA12 short, a very short siphon, and the seta AB10 spine-like, which would support their inclusion within the Sternopriscina. A more thorough study

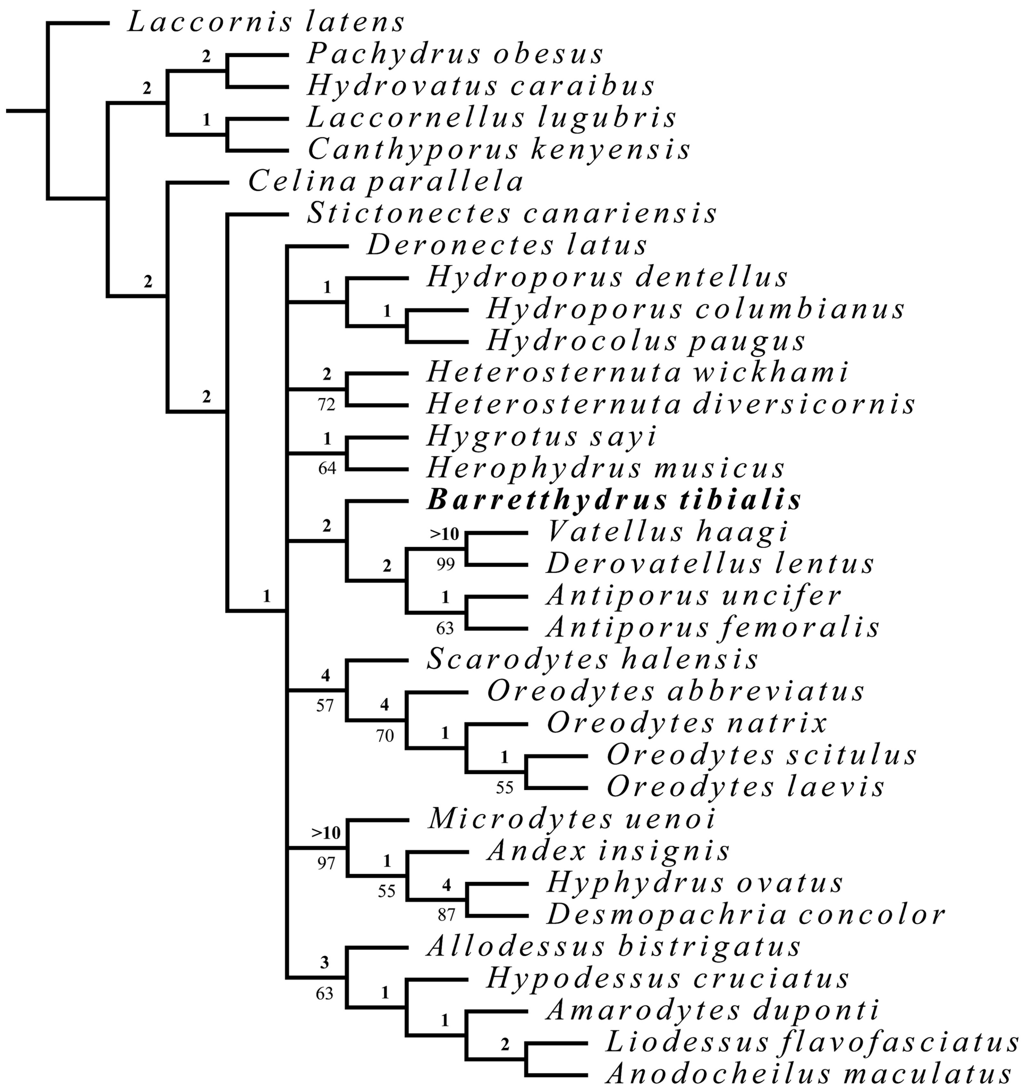


Fig. 20. Strict consensus cladogram obtained from the cladistic analysis of 34 terminal taxa of Hydroporinae, with Bremer support values indicated above branches and Bootstrap values higher than 50 indicated below branches.

including the larvae of additional Sternopriscina genera would be needed to confirm and refine such hypotheses.

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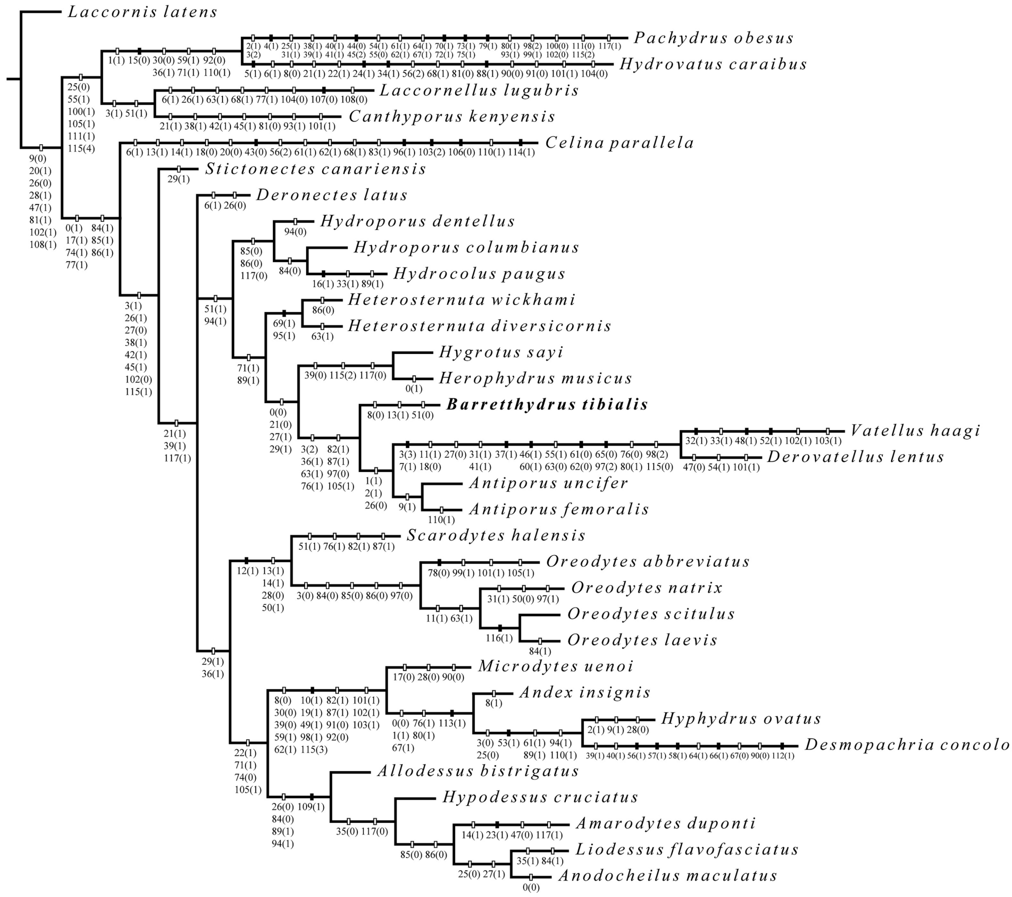

Fig. 21. One of the most parsimonious trees obtained from the cladistics analysis of 34 terminal taxa of Hydroporinae, with character changes mapped for each clade (using ACCTRAN optimization). Solid rectangles indicate unique character state transformations; open rectangles indicate homoplasious character state transformations.

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Table 5. Characters used for the cladistic analysis and the coding of states using selected genera of Hydroporinae as outgroup.

(000)	Cephalic capsule (instar I): (0) maximum width at level of stemmata; (1) maximum width posterior to stemmata.
(001)	Nasale (instars I–III): (0) broad, subtriangular; (1) narrow, more or less parallel-sided.
(002)	Apex of nasale (instars I–III): (0) not spatulate; (1) spatulate.
(003)	Lateral branches of nasale (instars I–III): (0) absent; (1) very small, inconspicuous; (2) well developed, short, not bifid apically; (3) strongly developed, bifid apically.
(004)	Row of elongate robust spinulae on basoventrolateral surface of nasale (instars I–III): (0) absent; (1) present.
(005)	Egg bursters (instar I): (0) located submedially on the frontoclypeus, close to frontal suture; (1) located proximally on the frontoclypeus.
(006)	Seta FR2 (instar I): (0) inserted close to frontal suture; (1) inserted far from frontal suture.
(007)	Seta FR6 (instar I): (0) not strongly developed; (1) strongly developed.
(008)	Seta FR7 (instar I): (0) hair-like; (1) spine-like.
(009)	Seta FR13 (instar I): (0) inserted submedially; (1) inserted proximally.
(010)	Pore FRb (instar I): (0) present; (1) absent.
(011)	Row of lamellae clypeales (instar I): (0) continuous in the middle; (1) discontinuous in the middle.
(012)	Parietals (at level of occipital suture) (instar I): (0) not constricted; (1) constricte.d
(013)	Parietals (at level of occipital suture) (instars II–III): (0) not constricted; (1) constricted.
(014)	Occipital suture (instar I): (0) absent; (1) present.
(015)	Occipital suture (instars II–III): (0) absent; (1) present.
(016)	Stemmata (instars I–II): (0) present; (1) absent.
(017)	Seta PA3 (instar I): (0) inserted contiguously to setae PA1 and PA2; (1) inserted far from setae PA1 and PA2.
(018)	Seta PA18 (instar I): (0) present; (1) absent.
(019)	Pore PAc (instar I): (0) not inserted anteriorly to stemmata; (1) inserted anteriorly to stemmata.
(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 PAo (instar I): (0) present; (1) absent.
(025)	Secondary spine-like setae on lateral margin of parietals (instars II–III): (0) absent; (1) present.
(026)	Secondary spine-like setae on ventral surface of parietals (instars II–III): (0) absent; (1) present.
(027)	Ventroapical spinula on antennomere 3 (instars I–III): (0) present; (1) absent.
(028)	Seta AN3 (instar I): (0) inserted distally; (1) inserted submedially.
(029)	Pore ANf (instar I): (0) present; (1) absent.
(030)	Pore ANh (instar I): (0) absent; (1) present.
(031)	Additional ventroapical pores on antennomere 3 (instar I): (0) absent; (1) present.
(032)	Secondary setae on antennomere 1 (instars II–III): (0) absent; (1) present.
(033)	Secondary setae on antennomere 2 (instars II–III): (0) absent; (1) present.
(034)	Sensillum MN2 (instar I): (0) with the appearance of a pore or minute seta; (1) with the appearance of a short hair-like seta.
(035)	Pore MNa (instar I): (0) inserted approximately at the same level as pore MNb; (1) inserted distally to pore MNb.
(036)	Cardo (instars I–III): (0) not fused to stipes; (1) fused to stipes.
(037)	Stipes (instar I): (0) short, robust, subtrapezoidal; (1) elongate, narrow, subcylindrical.
(038)	Second galeomere (instars I–III): (0) poorly developed, thin and very short; (1) absent, at most a minute bulge.
(039)	Seta MX4 (instar I): (0) present; (1) absent.
(040)	Setae MX5 and MX6 (instar I): (0) present; (1) absent.
(041)	Seta MX7 (instar I): (0) present; (1) absent.
(042)	Setae MX8 and MX9 (instar I): (0) present; (1) absent.
(043)	Seta MX10 (instar I): (0) present; (1) absent.
(044)	Seta MX14 (instar I): (0) inserted submedially; (1) inserted at basal third or more basally.
(045)	Pore MXh (instar I): (0) inserted on the galea; (1) inserted on the stipes; (2) absent.
(046)	Pore MXj (instar I): (0) present; (1) absent.
(047)	Pore MXk (instar I): (0) absent; (1) present.
(048)	Secondary setae on maxillary palpomere 1 (instars II–III): (0) absent; (1) present.
(049)	Prementum (instars I–III): (0) broader than long or about as long as broad; (1) clearly longer than broad.

Continued on next page

Table 5. Continued.

(050)	Prementum (instar III): (0) completely sclerotized ventrally; (1) not sclerotized ventromedially.
(051)	Elongate spinulae on lateral margin of prementum (instar I): (0) absent; (1) present.
(052)	Labial palpus (instars I–III): (0) composed of two palpomeres; (1) composed of one palpomere.
(053)	Labial palpomere 2 (instars I–III): (0) narrow, subcylindrical, narrowing to apex; (1) robust, broadest at mid length.
(054)	Seta LA1 (instar I): (0) present; (1) absent.
(055)	Seta LA2 (instar I): (0) present; (1) absent.
(056)	Seta LA3 (instar I): (0) inserted distally; (1) inserted proximally; (2) absent.
(057)	Setae LA4 and LA5 (instar I): (0) inserted distally or subdistally; (1) inserted proximally.
(058)	Seta LA6 (instar I): (0) inserted distally; (1) inserted submedially.
(059)	Seta LA8 (instar I): (0) inserted distally; (1) inserted proximally.
(060)	Seta LA9 (instar I): (0) present; (1) absent.
(061)	Seta LA10 (instar I): (0) absent; (1) inserted distally; (2) inserted submedially.
(062)	Seta LA12 (instar I): (0) absent; (1) inserted distally; (2) inserted submedially.
(063)	Setae LA10 and LA12 (instar I): (0) absent; (1) short or very short; (2) long.
(064)	Pore LAb (instar I): (0) present; (1) absent.
(065)	Pore LAd (instar I): (0) absent; (1) present.
(066)	Additional setae on dorsal surface of prementum (instar I): (0) absent; (1) present.
(067)	Secondary setae on prementum (instars II–III): (0) absent; (1) present.
(068)	Secondary pores on ventral surface of prementum (instars II–III): (0) absent; (1) present.
(069)	Spiracles on mesothorax (instar III): (0) present; (1) absent.
(070)	Pore COa (instar I): (0) present; (1) absent.
(071)	Seta TR2 (instar I): (0) present; (1) absent.
(072)	Seta FE2 (instar I): (0) inserted apically; (1) not inserted apically.
(073)	Seta FE6 (instar I): (0) inserted apically; (1) not inserted apically.
(074)	Pore FEa (instar I): (0) absent; (1) present.
(075)	Natatory anteroventral setae on femur (instars II–III): (0) absent; (1) present.
(076)	Natatory posterodorsal setae on femur (instars II–III): (0) absent; (1) present.
(077)	Secondary anterodorsal setae on femur (instars II–III): (0) absent; (1) present.
(078)	Spinulae on ventral surface of protibia (instar III): (0) absent or few small disperse. spinulae that do not form a distinct row; (1) present, forming a distinct row although sometimes short and weakly developed.
(079)	Seta TI2 on meso- and metatibia (instar I): (0) short, spine-like; (1) long, hair-like.
(080)	Seta TI7 (instar I): (0) short, spine-like; (1) long, hair-like.
(081)	Secondary setae on tibia (instars II–III): (0) absent; (1) present.
(082)	Natatory posterodorsal setae on tibia (instars II–III): (0) absent; (1) present.
(083)	Seta TA1 on metatarsus (instar I): (0) inserted distally; (1) inserted submedially.
(084)	Secondary dorsal setae on protarsus (instars II–III): (0) absent; (1) present.
(085)	Secondary posteroventral setae on protarsus (instar III): (0) absent; (1) present.
(086)	Secondary posteroventral setae on metatarsus (instar III): (0) absent; (1) present
(087)	Natatory posterodorsal setae on tarsus (instars II–III): (0) absent; (1) present.
(088)	Basoventral spinulae on claws (instar I): (0) absent; (1) present.
(089)	Abdominal tergites I–VI (instar I): (0) with anterotransverse carina; (1) without anterotransverse carina.
(090)	Ventral surface of abdominal segments II–III (instar III): (0) sclerotized; (1) membranous.
(091)	Ventral surface of abdominal segments IV–V (instar III): (0) sclerotized; (1) membranous.
(092)	Ventral surface of abdominal segment VI (instars I–III): (0) sclerotized; (1) membranous.
(093)	Abdominal segment VII (instar I): (0) sclerotized dorsally and ventrally, with ventral sclerite independent from dorsal sclerite; (1) completely sclerotized, ring-like.
(094)	Abdominal sclerite VII (instar I): (0) with anterotransverse carina; (1) without anterotransverse carina.
(095)	Spiracles on abdominal segments I–VII (instar III): (0) present; (1) absent.
(096)	Principal abdominal tracheal trunks (instars I–III): (0) not protruding from the apex of siphon; (1) protruding backward from the apex of siphon.
(097)	Siphon (instars I–III): (0) very short; (1) short to moderately elongate; (2) very elongate, urogomphomere-like.
(098)	Sensillum AB2 (instar I): (0) seta-like; (1) pore-like; (2) absent.
(099)	Seta AB3 (instar I): (0) hair-like; (1) spine-like.
(100)	Seta AB4 (instar I): (0) not strongly developed; (1) strongly developed.
(101)	Seta AB5 (instar I): (0) not strongly developed; (1) strongly developed.

Continued on next page

Table 5. Continued.

(102)	Seta AB6 (instar I): (0) short; (1) long.
(103)	Seta AB7 (instar I): (0) short; (1) long; (2) absent.
(104)	Seta AB9 (instar I): (0) inserted dorsolaterally; (1) inserted ventrolaterally.
(105)	Seta AB10 (instar I): (0) hair-like; (1) spine-like.
(106)	Seta AB11 (instar I): (0) hair-like; (1) spine-like.
(107)	Seta AB15 (instar I): (0) present; (1) absent.
(108)	Pore ABa (instar I): (0) present; (1) absent.
(109)	Pore ABc (instar I): (0) present; (1) absent.
(110)	Secondary ventral setae on siphon (instar III): (0) absent; (1) present.
(111)	Number of primary setae on urogomphus (excluding natatory setae) (instar I): (0) eight; (1) seven.
(112)	Number of primary pores on urogomphus (instar I): (0) three or more; (1) two.
(113)	Seta UR5 (instar I): (0) long, hair-like; (1) short, spine-like.
(114)	Seta UR6 (instar I): (0) long, hair-like; (1) short, spine-like.
(115)	Seta UR8 (instar I): (0) inserted apically on urogomphomere 2; (1) inserted distally on urogomphomere 2; (2) inserted submedially on urogomphomere 2; (3) inserted proximally on urogomphomere 2; (4) absent.
(116)	Additional pores on urogomphus (instar I): (0) absent; (1) present.
(117)	Secondary setae on urogomphus (instars II–III): (0) absent; (1) present.

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Table 6. Data matrix used for the cladistic analysis. Missing data coded '?'. See Table 5 for characters used for the cladistic analysis and the coding of states.

Species	000	001	002	003	004	005	006	007	008	009	010	011	012	013	014	015	016	017	018	019	020	021	022	023	024	025	026	027	028	029
Laccornis latens	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0
Allodessus substrigatus	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	1	0	0	1	0	0	1	1
Amarodytes duponti	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	1	1	1	1	0	1	0	0	1	1
Anodocheilus maculatus	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	1	0	0	0	0	1	1	1
Hypodessus cruciatus	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	1	0	0	1	0	0	1	1
Liodessus flavofasciatus	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	1	0	0	0	0	1	1	1
Antiporus femoralis	0	1	1	2	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	0	1	1	1
Antiporus uncifer	0	1	1	2	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	0	1	1	1
Barretthydrus tibialis	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	1	0	0	?	0	1	1	1	1	1
Deronectes latus	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	0	0	1	0
Heterosternuta diversicornis	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	1	0	1	0
Heterosternuta wickhami	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	1	0	1	0
Hydrocolus paugus	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	1	1	0	1	0
Hydroporus columbianus	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	1	0	1	0
Hydroporus dentellus	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	1	0	1	0
Oreodytes abbreviatus	1	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	1	1	0	1	1	0	0	0	1	1	0	0	1
Oreodytes laevis	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	1	1	0	0	0	1	1	0	0	1
Oreodytes natrix	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	1	1	0	0	0	1	1	0	0	1
Oreodytes scitulus	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	1	1	0	0	0	1	1	0	0	1
Scarodytes halensis	1	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	0	1	1	0	1	1	0	0	0	1	1	0	0	1
Stictonectes canariensis	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1	0	1	1
Hydrovatus caraibus	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	1	1	0

Continued on next page

Table 6. Continued.

Species	000	001	002	003	004	005	006	007	008	009	010	011	012	013	014	015	016	017	018	019	020	021	022	023	024	025	026	027	028	029
Herophydrus musicus	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1	1	1	1
Hygrotus sayi	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1	1	1	1
Andex insignis	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	1	1	1	1	0	0	1	1	0	1	1
Desmopachria concolor	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	1	1	1	0	0	0	1	0	1	1
Hyphydrus ovatus	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	1	1	1	1	1	0	0	0	1	0	0	1
Microdytes uenoi	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	1	1	0	0	1	1	0	0	1
Canthyporus kenyensis	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1	1	0
Laccornellus lugubris	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	1	1	0
Celina parallela	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0
Pachydrus obesus	0	1	1	2	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0
Derovatellus lentus	0	1	1	3	0	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	1
Vatellus haagi	0	1	1	3	0	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	1

Table 6. Continued.

Species	030	031	032	033	034	035	036	037	038	039	040	041	042	043	044	045	046	047	048	049	050	051	052	053	054	055	056	057	058	059
Laccornis latens	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Allodessus substrigatus	1	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Amarodytes duponti	1	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anodocheilus maculatus	1	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Hypodessus cruciatus	1	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0
Liodessus flavofasciatus	1	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Antiporus femoralis	1	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Antiporus uncifer	1	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Barretthydrus tibialis	1	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Deronectes latus	1	0	0	0	0	1	0	0	1	1	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Heterosternuta diversicornis	1	0	0	0	0	1	0	0	1	1	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Heterosternuta wickhami	1	0	0	0	0	1	0	0	1	1	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Hydrocolus paugus	1	0	0	1	0	1	0	0	1	1	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Hydroporus columbianus	1	0	0	0	0	1	0	0	1	1	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Hydroporus dentellus	1	0	0	0	0	1	0	0	1	1	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Oreodytes abbreviatus	1	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Oreodytes laevis	1	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Oreodytes natrix	1	1	0	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Oreodytes scitulus	1	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Scarodytes halensis	1	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0
Stictonectes canariensis	1	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Hydrovatus caraibus	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	2	0	0	1

Continued on next page

Table 6. Continued.

Species	030	031	032	033	034	035	036	037	038	039	040	041	042	043	044	045	046	047	048	049	050	051	052	053	054	055	056	057	058	059
Herophydrus musicus	1	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Hygrotus sayi	1	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Andex insignis	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Desmopachria concolor	0	0	0	0	0	1	1	0	1	1	1	0	1	1	1	1	0	1	0	1	0	0	0	1	0	0	1	1	1	1
Hyphydrus ovatus	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1
Microdytes uenoi	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Canthyporus kenyensis	1	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0
Laccornellus lugubris	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0
Celina parallela	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0
Pachydrus obesus	0	1	0	0	0	1	1	0	1	1	1	1	0	1	0	2	0	1	0	0	0	0	0	0	1	0	0	0	0	1
Derovatellus lentus	1	1	?	?	0	1	1	1	1	1	0	1	1	1	1	1	1	0	?	0	0	1	0	0	1	1	0	0	0	0
Vatellus haagi	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	?	1	0	0	1	1	0	0	1	0	0	0	0

Table 6. Continued.

Species	060	061	062	063	064	065	066	067	068	069	070	071	072	073	074	075	076	077	078	079	080	081	082	083	084	085	086	087	088	089
Laccornis latens	0	2	2	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Allodessus substrigatus	0	2	2	2	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	1	1	0	0	1
Amarodytes duponti	0	2	2	2	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1
Anodocheilus maculatus	0	2	2	2	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1
Hypodessus cruciatus	0	2	2	2	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	1	1	0	0	1
Liodessus flavofasciatus	0	2	2	2	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	1
Antiporus femoralis	0	2	2	1	0	1	0	0	0	0	0	1	0	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	0	1
Antiporus uncifer	0	2	2	1	0	1	0	0	0	0	0	1	0	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	0	1
Barretthydrus tibialis	0	2	2	1	0	1	0	0	0	0	0	1	0	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	0	1
Deronectes latus	0	2	2	2	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	1	1	0	0	0
Heterosternuta diversicornis	0	2	2	1	0	1	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0	0	1	1	1	0	0	1
Heterosternuta wickhami	0	2	2	2	0	1	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0	0	1	1	0	0	0	1
Hydrocolus paugus	0	2	2	2	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1
Hydroporus columbianus	0	2	2	2	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0
Hydroporus dentellus	0	2	2	2	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0
Oreodytes abbreviatus	0	2	2	2	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Oreodytes laevis	0	2	2	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0
Oreodytes natrix	0	2	2	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0
Oreodytes scitulus	0	2	2	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0
Scarodytes halensis	0	2	2	2	0	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	0	0
Stictonectes canariensis	0	2	2	2	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	1	1	0	0	0
Hydrovatus caraibus	0	2	2	2	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0

Continued on next page

Table 6. Continued.

Species	060	061	062	063	064	065	066	067	068	069	070	071	072	073	074	075	076	077	078	079	080	081	082	083	084	085	086	087	088	089
Herophydrus musicus	0	2	2	2	0	1	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	1	1	1	0	0	1
Hygrotus sayi	0	2	2	2	0	1	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	1	1	1	0	0	1
Andex insignis	0	2	1	2	0	1	0	1	0	0	0	1	0	0	0	0	1	1	1	0	1	1	1	0	1	1	1	1	0	0
Desmopachria concolor	0	1	1	2	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	0	1	1	1	0	1	1	1	1	0	1
Hyphydrus ovatus	0	1	1	2	0	1	0	1	0	0	0	1	0	0	0	0	1	1	1	0	1	1	1	0	1	1	1	1	0	1
Microdytes uenoi	0	2	1	2	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	1	1	1	1	0	0
Canthyporus kenyensis	0	2	2	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Laccornellus lugubris	0	2	2	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0
Celina parallela	0	1	1	2	0	1	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0
Pachydrus obesus	0	1	1	2	1	1	0	1	0	0	1	1	1	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0
Derovatellus lentus	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	?	1	0	1	1	1	0	1	1	?	1	0	1
Vatellus haagi	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	1	1	0	1	1	1	1	0	1

Table 6. Continued.

Species	090	091	092	093	094	095	096	097	098	099	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117
Laccornis latens	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Allodessus substrigatus	1	1	1	0	1	0	0	1	0	0	0	0	0	?	1	1	1	1	1	1	0	0	0	0	0	1	0	1
Amarodytes duponti	1	1	1	0	1	0	0	1	0	0	0	0	0	?	1	1	1	1	1	1	0	0	0	0	0	1	0	1
Anodocheilus maculatus	1	1	1	0	1	0	0	1	0	0	0	0	0	?	1	1	1	1	1	1	0	0	0	0	0	1	0	0
Hypodessus cruciatus	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	0	0
Liodessus flavofasciatus	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	0	0
Antiporus femoralis	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	1	0	1
Antiporus uncifer	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	1
Barretthydrus tibialis	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	1
Deronectes latus	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	1
Heterosternuta diversicornis	1	1	1	0	1	1	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	1
Heterosternuta wickhami	1	1	1	0	1	1	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	1
Hydrocolus paugus	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0
Hydroporus columbianus	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0
Hydroporus dentellus	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0
Oreodytes abbreviatus	1	1	1	0	0	0	0	0	0	1	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	1
Oreodytes laevis	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	1	1
Oreodytes natrix	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	1
Oreodytes scitulus	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	1	1
Scarodytes halensis	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	1
Stictonectes canariensis	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0
Hydrovatus caraibus	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	1	1	1	0	1	1	0	0	0	4	0	0
Herophydrus musicus	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	2	0	0
Hygrotus sayi	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	2	0	0
Andex insignis	1	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	0	3	0	1
Desmopachria concolor	0	0	0	0	1	0	0	1	1	0	0	1	1	1	1	1	1	1	1	0	1	0	1	1	0	3	0	1
Hyphydrus ovatus	1	0	0	0	1	0	0	1	1	0	0	1	1	1	1	1	1	1	1	0	1	0	0	1	0	3	0	1
Microdytes uenoi	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	3	0	1
Canthyporus kenyensis	1	1	1	1	0	0	0	1	0	0	1	1	1	0	1	1	1	1	1	0	0	1	0	0	0	4	0	0
Laccornellus lugubris	1	1	1	0	0	0	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	0	4	0	0
Celina parallela	1	1	1	0	0	0	1	1	0	0	0	0	1	2	1	0	0	1	1	0	1	0	0	0	1	0	0	0
Pachydrus obesus	1	1	0	1	0	0	0	1	2	1	0	0	0	0	1	1	1	1	1	0	1	0	0	0	?	2	0	1
Derovatellus lentus	1	1	1	0	1	0	0	2	2	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1
Vatellus haagi	1	1	1	0	1	0	0	2	2	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1