Phylogenetic Relationships of the Tribe Vatellini Based on Larval Morphology, With Description of *Derovatellus lentus* (Coleoptera: Dytiscidae: Hydroporinae)

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ABSTRACT The phylogenetic relationships and putative monophyly of the diving-beetle tribe Vatellini are explored based on a cladistic analysis of 37 taxa and 122 chaetotaxic and morphological characters from larvae. For this purpose, larvae of the genus *Derovatellus* Sharp are described and illustrated in detail, with particular emphasis on morphometry and chaetotaxy, with the later being unexplored until now. The results strongly support the monophyly of the Vatellini based on several unique larval characters. The terminal insertion of the primary seta UR8 on the second urogomphomere in members of Vatellini represents a reversal from the derived condition. Vatellini was recovered as the sister group of the Australian genus *Antiporus* Sharp (Hydroporini) based on the presence of: a spatulate nasale, pore PAe and elongate lateral spinulae on prementum. These characters, however, have a reduced value because all of them seem to have evolved several times independently within the Hydroporinae. The tribe Vatellini and its genera are diagnosed and compared with other hydroporine taxa, and interesting features are discussed. *Vatellus* Aubé is unique within Hydroporinae in the presence of secondary setae on the first antennomere and the first maxillary palpomere, and the one-segmented labial palpus. *Derovatellus* can be separated from almost every other Hydroporinae by the absence of seta LA1 on prementum and of secondary anterodorsal setae on femur.

KEY WORDS diving beetles, larvae, phylogenetic relationships, chaetotaxy

The vatellines are a distinctive group among diving beetles in which the adults have evolved certain morphological characters that make them unique (Miller 2005). The larvae are considerably less known than adults, but not less interesting judging from certain morphological features such as the disproportionately long and curious nasale and the extremely elongate abdominal siphon (Michat and Torres 2005). Members of this group are small, the adults range from ≈3.0 to 7.5 mm in length and occur in ponds, marshes and slow streams with considerable emergent vegetation (Miller 2005). The larvae are found in the same habitats, but in general are much more difficult to locate than adults, and considerable sampling and sorting effort is needed before collecting a significant number of specimens.

In terms of classification, the vatellines form a tribe within the subfamily Hydroporinae, and after Miller (2005) only two extant genera are recognized: *Vatellus* Aubé including the largest species and *Derovatellus* Sharp including the smallest species. *Derovatellus* is composed of 42 species and has a large distributional range comprising the Afrotropical, Nearctic, Neotropical, and Oriental regions (Nilsson 2001). In the Neotropics, *Derovatellus* includes six species, the most common and widespread of which is *D. lentus* (Wehncke), distributed from central Argentina to the Caribbean (Miller 2005).

The phylogenetic relationships and putative monophyly of the Vatellini were studied recently, considering different sets of characters. Miller (2001) and Miller et al. (2006) based on adult characters, and Ribera et al. (2008) based on molecular characters found evidence for the monophyly of the Vatellini. With respect to the position of the tribe within Hydroporinae, however, there is no general agreement among studies using different data sets. Miller (2001) and Miller et al. (2006) found Vatellini more related to members of Hydroporini. Ribera et al. (2008) found Vatellini sister to Hydrovatini. Ribera and Balke (2007) (based on molecular data, and including only *Derovatellus*) found a sister-group relationship between Vatellini and the rest of the Hydroporinae. Finally, several studies that were based on larval characters (including only *Vatellus*) found Vatellini to be closely related to Hyphydrini or to the Australian

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genus *Antiporus* Sharp (Hydroporini) (Michat and Torres 2005, 2008; Michat 2006; Alarie and Michat 2007a; Michat et al. 2007; Michat and Alarie 2008). Immatures have been underutilized in phylogenetic studies though there is considerable evidence for the utility of characters from larvae (Meier and Lim 2009). As demonstrated over the past recent years, larval chaetotaxy is a particularly significant source of characters for the study of the phylogenetic relationships within Hydroporinae (Michat and Torres 2005, 2008; Michat 2006; Alarie and Michat 2007a; Michat et al. 2007; Michat and Alarie 2008). The development of a system of nomenclature to name primary sensilla (setae and pores) in first-instar larvae of that subfamily has brought great progress because it allows for exploration of an extensive set of characters that is phylogenetically very useful.

Descriptions of larvae of Vatellini are extremely rare in the literature. A fossil Vatellini larva was illustrated by Koch and Berendt (1854), the third instar larvae of *V. mexicanus* (Sharp) and *D. floridanus* Fall (as *D. ibarrai* Spangler) were described by Spangler (1963, 1966), and all instars of *V. haagi* Wehncke were described by Michat and Torres (2005). Except for the last one, existing descriptions have not emphasized the chaetotaxy. Therefore, this set of characters remains unexplored for *Derovatellus*, and the hypotheses on the relationships of Vatellini remain untested using this source of information. The recent finding of the larvae of *D. lentus* gives the opportunity to study in detail, for the first time, the larval chaetotaxy of a member of *Derovatellus*, and to conduct a detailed morphometric analysis of selected structures. A cladistic analysis is also included, with the objective of testing previous hypotheses on the phylogenetic relationships of Vatellini and to identify the larval characters potentially useful in studying relationships within the group.

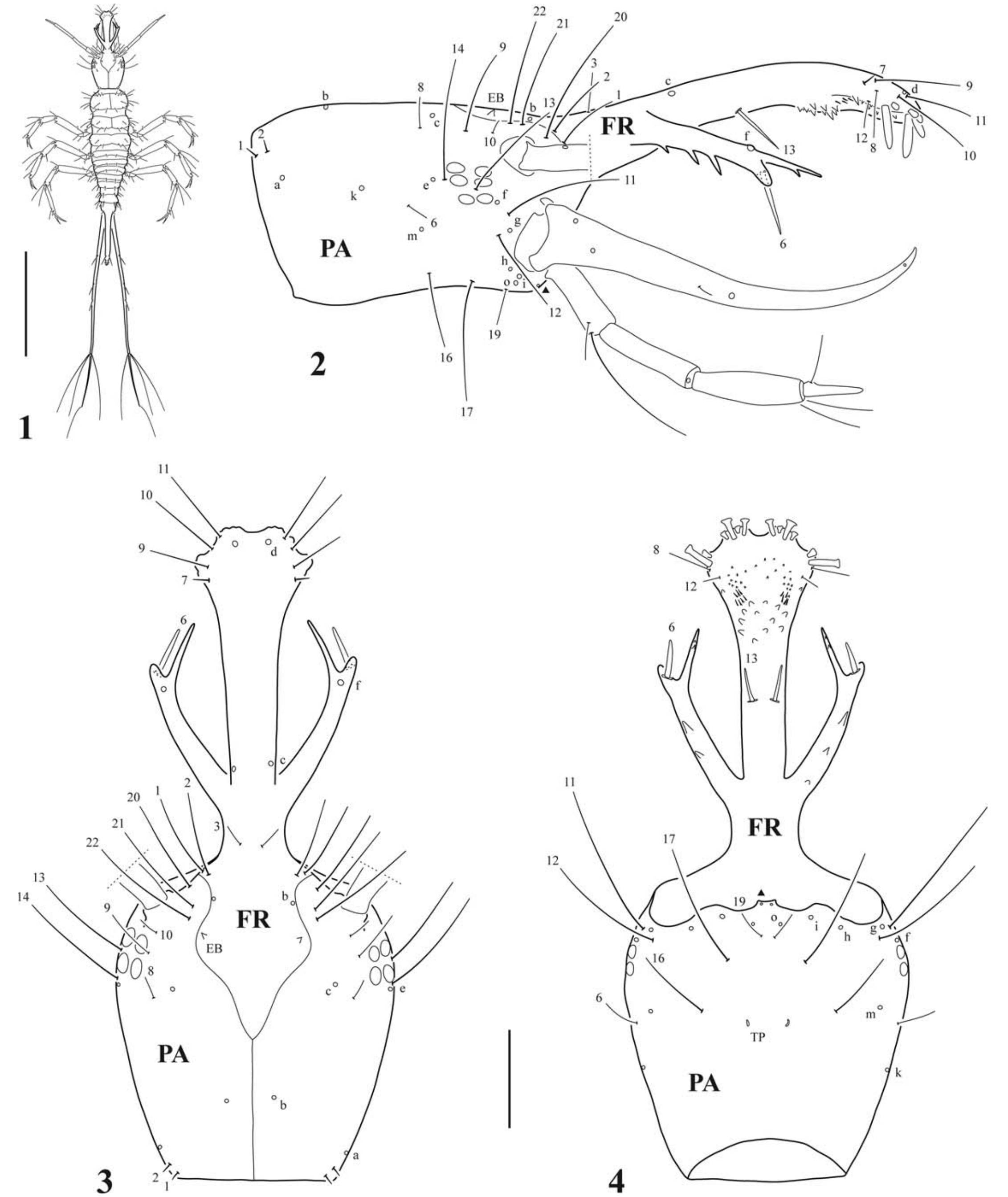
Materials and Methods

Material Examined. Seven specimens of instar I and two of instar II were used for the descriptions. Larvae were collected in association with adults at the following locality: ARGENTINA, Chaco Province, El Cachapé refuge, 4-XII-2008, small semipermanent pond about 15 m in length, 5 m in width, and 70 cm in depth, with vegetated margins. The association is firm because larvae and adults of *D. lentus* were taken together from the collecting site and also *D. lentus* is the only species present in Chaco Province; the distributional range of the other two *Derovatellus* species present in Argentina (*D. bruchi* Zimmermann and *D. spangleri* Miller) is at least 800 km away (Miller 2005).

Methods. Specimens were cleared in lactic acid, dissected, and mounted on glass slides with polyvinyl-lacto-glycerol. Observation (at magnifications up to 1,000×) and drawings were made using an Olympus CX31 compound microscope equipped with a camera lucida. Drawings were scanned and digitally edited. The material is stored in the collection of M.C.M. (Laboratory of Entomology, Buenos Aires University, Buenos Aires, Argentina).

Morphometric Analysis. We employed, with minimal modifications and additions, the terms used in previous papers dealing with the larval morphology of Hydroporinae (Michat and Torres 2005, 2008). 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 the joint of frontal and coronal sutures); occipital foramen width (OCW) (maximum width measured along dorsal margin); coronal line length (COL); length of mandible (MNL) (measured from laterobasal angle to apex); width of mandible (MNW) (maximum width measured at base); length of stipes (STL). Length of antenna (A), 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 leg (L), including the longest claw (CL), 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). The length of trochanter includes only the proximal portion, considered from the base to the beginning of the femur. The legs were considered as being composed of six articles following Lawrence (1991). Dorsal length of last abdominal segment (LAS) (measured along midline from anterior to posterior margin). Length of urogomphus (U) was derived by adding the lengths of the individual 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 body shape.

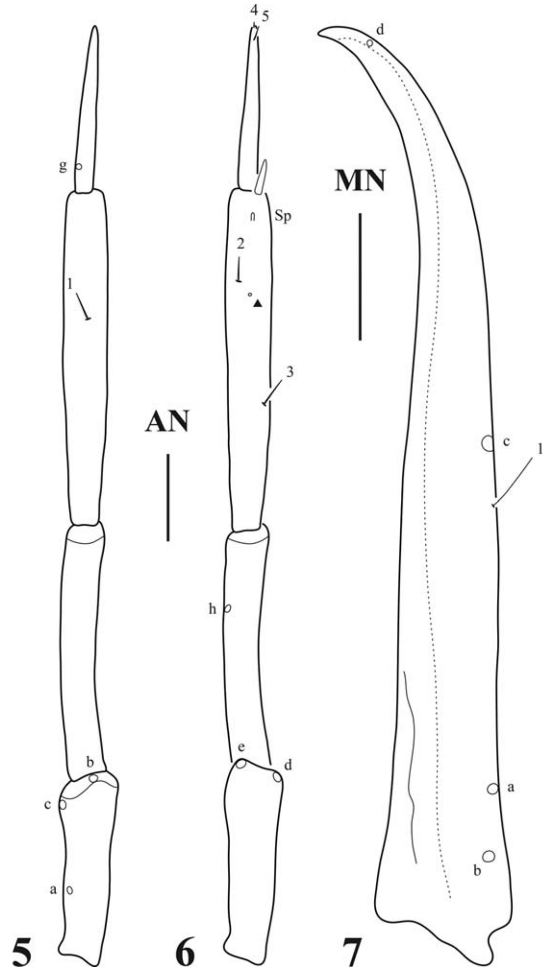
Chaetotaxic Analysis. Primary (present in first-instar larva) and secondary (added in later instars) setae and so-called pores were distinguished in the cephalic capsule, head appendages, legs, last abdominal segment and urogomphus. Sensilla were coded by two capital letters, in most cases corresponding to the first two letters of the name of the structure on which 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 were labeled by comparison with the ground-plan of chaetotaxy of the subfamily Hydroporinae (Alarie and Harper 1990, Alarie et al. 1990, Alarie 1991, Alarie and Michat 2007b). Homologies were recognized using the criterion of similarity of position (Wiley 1981). Setae located at



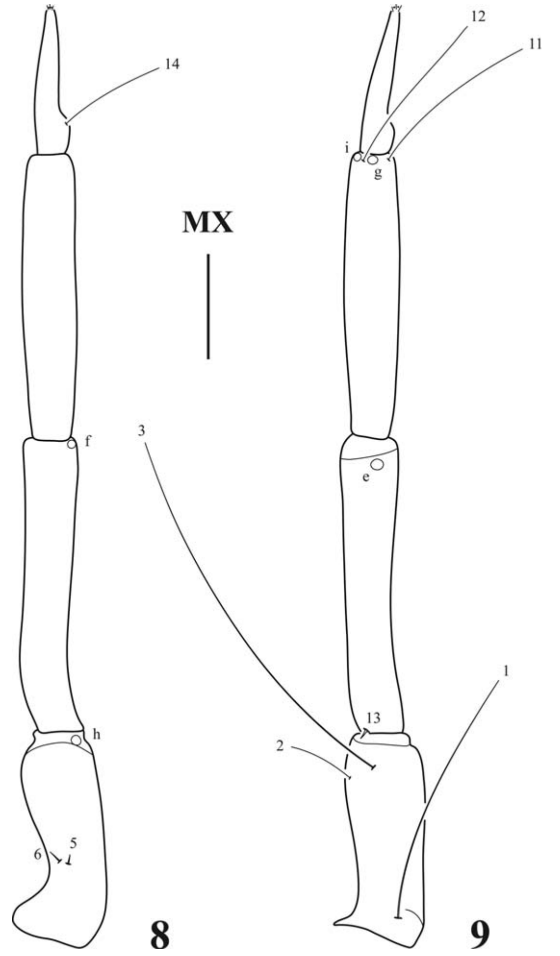
Figs. 1–4. *Derovatellus lentus*, first-instar larva. (1) Habitus, dorsal aspect. (2) Cephalic capsule, lateral aspect. (3) Cephalic capsule, dorsal aspect. (4) Cephalic capsule, ventral aspect. EB, egg burster; TP, tentorial pit. Solid triangle refers to additional pore. Scale bars = 1.00 mm for 1 and 0.10 mm for 2–4.

the apices of the maxillary and labial palpi were extremely difficult to distinguish due to their position and small size. Accordingly, they are not well represented in the drawings.

Phylogenetic Analysis. The phylogenetic relationships and putative monophyly of the tribe Vatellini were analyzed cladistically using the program TNT (Goloboff et al. 2008) and considering the character set provided by the larval morphology and chaetotaxy. A broad taxon sampling was included comprising members of all tribes of Hydroporinae. Members of seven subfamilies of Dytiscidae were included as outgroups, the remaining two subfamilies were not included because their larvae are unknown (Hy-

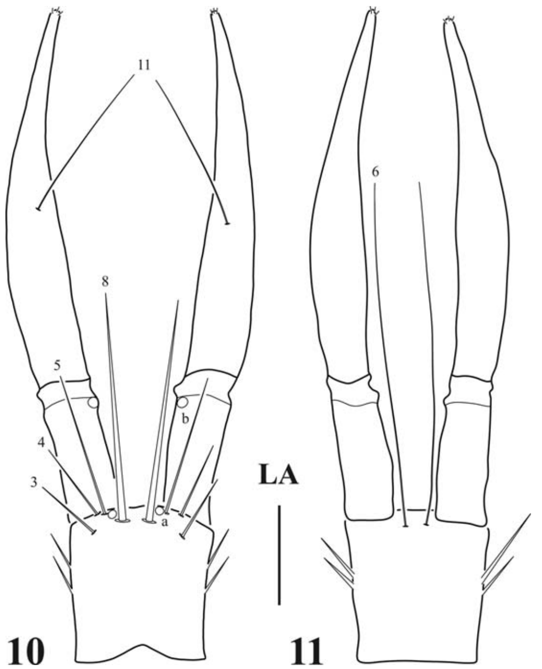


Figs. 5–7. *Derovatellus lentus*, first-instar larva. (5) Left antenna, dorsal aspect. (6) Right antenna, ventral aspect. (7) Right mandible, dorsal aspect. SP, spinula. Solid triangle refers to additional pore. Scale bars = 0.05 mm.



Figs. 8–9. *Derovatellus lentus*, first-instar larva. (8) Left maxilla, dorsal aspect. (9) Right maxilla, ventral aspect. Scale bar = 0.04 mm.

drodytinae) or well known but without sufficient chaetotaxic detail (Coptotominae). Data for most species [*Leuronectes curtulus* Régimbart, *Copelatus longicornis* Sharp, *Hydaticus tuyuensis* Trémouilles, *Laccophilus obliquatus* Régimbart, *Lancetes marginatus* (Steinheil), *Rhantus signatus* (F.), *Allodessus bistrigatus* (Clark), *Amarodytes duponti* (Aubé), *Anodocheilus maculatus* Babington, *Hypodessus cruciatus* (Régimbart), *Liodessus flavofasciatus* (Steinheil), *Laccornellus lugubris* (Aubé), *Hydrovatus caraibus* Sharp, *Desmopachria concolor* Sharp, *Desmopachria punctatissima* Zimmermann, *Pachydrus obesus* Sharp, *Celina parallela* (Babington), *Derovatellus lentus, Vatellus haagi*] were scored directly from the observation of the specimens, and data for the remaining species [*Matus bicarinatus* (Say), *Antiporus uncifer* Sharp, *Canthyporus kenyensis* Bilardo and Sanfilippo, *Deronectes latus* (Stephens), *Heterosternuta wickhami* (Zaitzev), *Hydrocolus paugus* (Fall), *Hydroporus columbianus* Fall, *Neoporus undulatus* (Say), *Oreodytes scitulus* (LeConte), *Scarodytes halensis* (F.), *Stictonectes canariensis* Machado, *Coelambus impressopunctatus* (Schaller), *Herophydrus musicus* (Klug), *Hygrotus sayi* J. Balfour-Browne, *Andex insignis* Sharp, *Hyphydrus ovatus* (L.), *Microdytes uenoi* Sató, *Laccornis latens* (Fall)] were scored from the literature (Michat and Torres 2008, and references therein). The tree was rooted in *L. curtulus* (Agabinae) to allow the hydroporine taxa to vary freely, thus testing the relationships of Vatellini with the other tribes. All characters were treated as unordered and equally weighted. Multistate characters were treated as nonadditive. A heuristic search was implemented using "tree bisection reconnection" as algorithm, with 200 replicates and saving 100 trees per replication (previously setting "hold 20000"). Bremer support values were calculated using the commands "hold 20000", "sub n" and "bsupport," where "n" is the number of extra steps allowed. The process was repeated increasing the length of the suboptimal cladograms by one step,



Figs. 10–11. *Derovatellus lentus*, first-instar larva. (10) Labium, dorsal aspect. (11) Labium, ventral aspect. Scale bar = 0.03 mm.

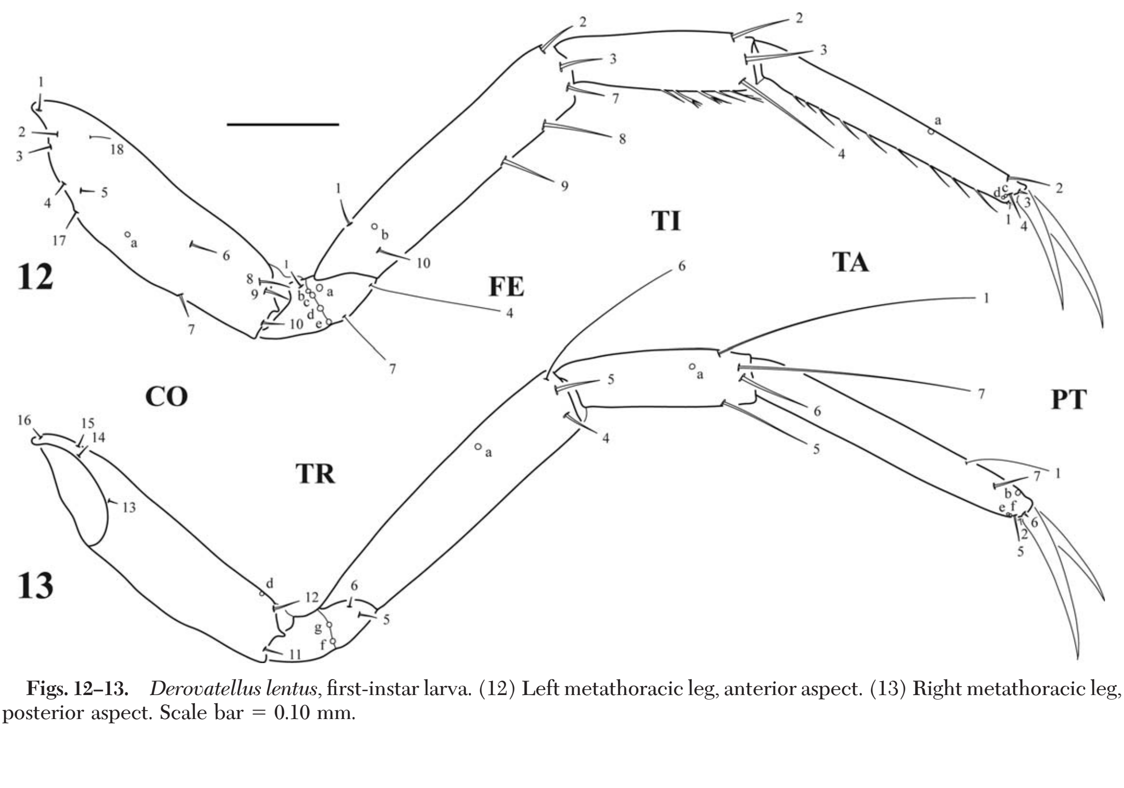
until all Bremer values were obtained (Kitching et al. 1998). Jackknife values were calculated with 2,000 replicates and P (removal probability) = 36.

Results

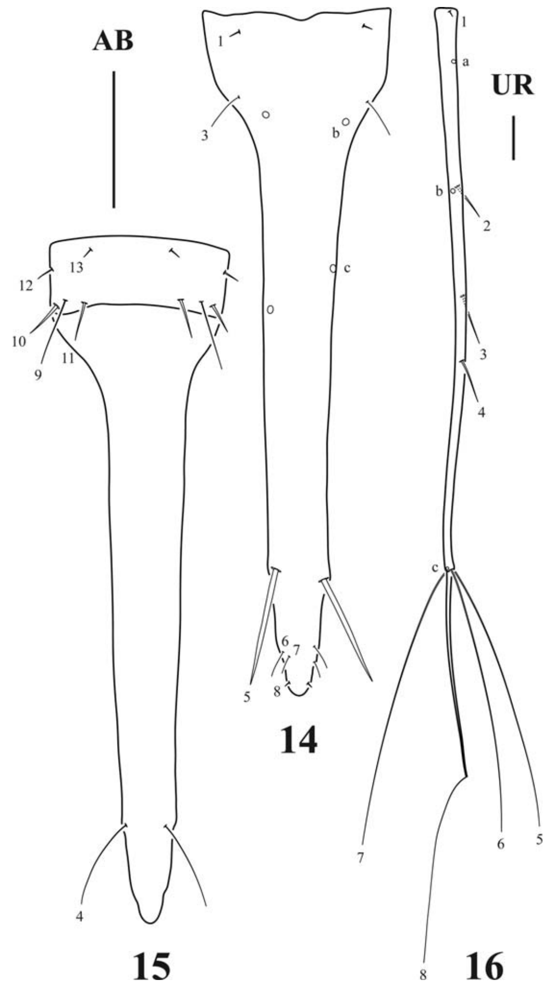
Diagnosis of Tribe Vatellini and Its Genera

Vatellini. Neck constriction absent; occipital suture absent in instar I, present in instars II-III; nasale strongly developed, trifurcate, median branch long, narrow, spatulate apically, lateral branches long, bifid apically; A3 with a ventroapical spinula; cardo fused to stipes; stipes elongate, palpomere-like, curved at base; galea absent; prementum with long spinulae on lateral margin; siphon strongly elongate, parallel-sided; urogomphus very long; setae FR6 and FR13 strongly developed; pores PAd and PAj absent; A3 with an additional pore on ventral surface; setae MX4, MX7, MX8, MX9, MX10, LA2, LA9, LA10 and LA12 absent; pores MXj, MXk and LAd absent; seta TR2 absent; pore FEa present; seta TI7 elongate, setiform; seta AB2 and pores ABa and ABd absent; setae UR2, UR3 and UR4 inserted far from each other; seta UR5 elongate, setiform; seta UR8 inserted apically on U2; lateral branches of nasale with four secondary setae (instars II-III); TI and TA with posterodorsal natatory setae (instars II-III); U1 with secondary setae (instars II-III).

Derovatellus. Median branch of nasale (posterior to spatulate apex) widening toward apex; ratio A4/A3 > 0.35; A1, A2, and MP1 without secondary setae (instar II); seta LA1 absent; coxa without posterodorsal secondary setae (instar II); femur without anterodorsal secondary setae (instar II); distal portion of siphon with a single long spiniform seta (instar I).



Figs. 12–13. *Derovatellus lentus*, first-instar larva. (12) Left metathoracic leg, anterior aspect. (13) Right metathoracic leg, posterior aspect. Scale bar = 0.10 mm.



Figs. 14–16. *Derovatellus lentus*, first-instar larva. (14) Abdominal segment VIII, dorsal aspect. (15) Abdominal segment VIII, ventral aspect. (16) Right urogomphus, dorsal aspect. Scale bars = 0.10 mm.

Vatellus. Median branch of nasale (posterior to spatulate apex) parallel-sided; ratio A4/A3 < 0.35; A1, A2 and MP1 with secondary setae (instar II); seta LA1 present; coxa with posterodorsal secondary setae (instar II); femur with anterodorsal secondary setae (instar II); distal portion of siphon with two long spiniform setae (instar I).

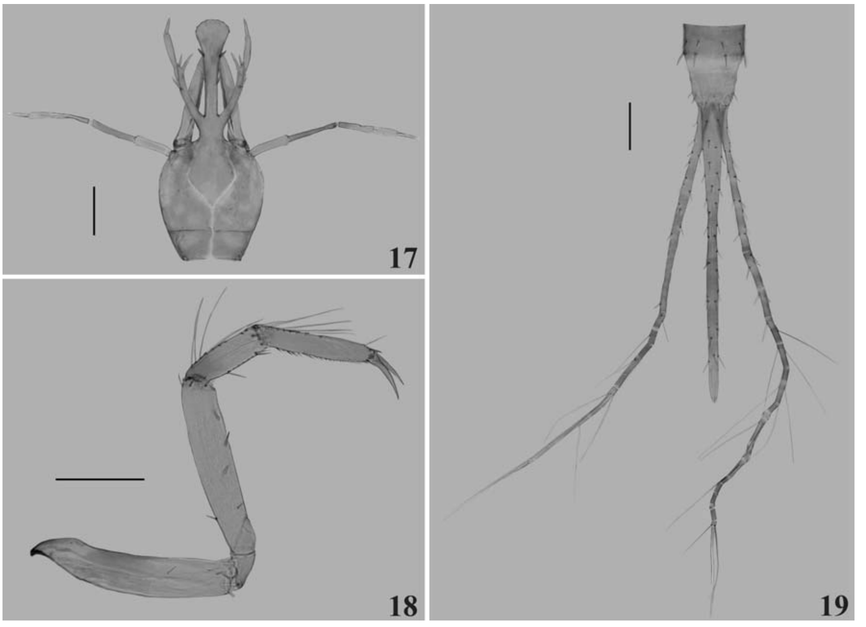
Description of Larvae of *Derovatellus lentus* (Wehncke) (Figs. 1–19)

First Instar, Description. *Color.* Cephalic capsule light brown except ocularium and area near ecdysial and coronal sutures creamy white; nasale paler, testaceous at the apex; A2 and basal half of A3 light brown, rest of antenna testaceous; MN testaceous, inner margin and apex light brown; maxilla and labium testaceous; thoracic and abdominal sclerites light brown, siphon somewhat darker except distal fourth testaceous; membranous parts creamy white; legs testaceous to light brown with basal portions of articles somewhat darker; U1 light brown, middle third with three testaceous bands, U2 creamy white.

Body. Subcylindrical, maximum width at metathorax, narrowing toward abdominal apex (Fig. 1). Measurements and ratios that characterize the body shape are shown in Table 1.

Head. Cephalic Capsule (Figs. 2–4). Markedly longer than broad; surface of basal third with reticulation; basal half (excluding nasale) subovate, maximum width at stemmata, progressively narrowing toward the occipital foramen, without neck constriction; occipital suture absent; ecdysial line well marked, coronal line moderately long; occipital foramen broadly emarginate ventrally; posterior tentorial pits visible ventrally; FR elongate, subtriangular, slightly convex, lateral margins sinuate, with two lateral spiniform egg bursters at about mid-length; nasale strongly developed, trifurcate; median branch long, narrow, slightly widening toward apex, spatulate and slightly curved downward apically, ventral surface of anterior half with spinulae of different shapes, anterior margin with 12 spatulate setae directed downward, arranged in clusters along lateral and apical margins, six of them longer (one seta on each lateral and four on anterior margin), remaining setae short; lateral branches of nasale long, oblique, bifid apically, shorter than median branch, each with a ventral row of two to three bulges progressively more robust to the apex; six subequal lateral stemmata arranged in two vertical series. *Antenna* (Figs. 5 and 6). Elongate, composed of four antennomeres, much longer than HW; A3 the longest, with a ventroapical spinula, A4 the shortest, A1 slightly longer than A4, A2 somewhat longer than A1; A3′ short. *Mandible* (Figs. 2 and 7). Prominent, slender, obliquely oriented, distal half strongly curved inward and upward, apex sharp; with longitudinal striae on dorsal surface of distal half; mandibular channel present. *Maxilla* (Figs. 8 and 9). Cardo fused to stipes; stipes elongate, palpomere-like, completely sclerotized, markedly curved at base; galea and lacinia absent; MP elongate, much shorter than antenna, composed of three palpomeres, MP1 the longest, MP2 somewhat shorter than MP1, MP3 the shortest. *Labium* (Figs. 10 and 11). Prementum subquadrate, with two long spinulae on lateral margin; LP slender, much shorter than MP, composed of two palpomeres, LP2 much longer than LP1, narrowing to apex in distal half.

Thorax. Terga convex, pronotum somewhat longer than mesonotum, metanotum subequal in length to mesonotum, both somewhat wider than pronotum; tergites transverse, laterally rounded, protergite somewhat more developed than meso- and metatergite; pro- and mesotergite with sagittal line; tergites without anterior transverse carina; sterna membranous; spiracles absent (Fig. 1). *Legs* (Figs. 12 and 13). Long, composed of six articles; L1 the shortest, L3 the longest; CO robust, elongate, TR divided into two parts, FE, TI and TA slender, sub-



Figs. 17–19. *Derovatellus lentus*, second-instar larva. (17) Head, dorsal aspect. (18) Prothoracic leg, anterior aspect. (19) Abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.20 mm.

Table 1. Measurements and ratios for the larvae of *D. lentus*

Measure	Instar I (n = 3)	Instar II (n = 2)
TL (mm)	2.00–2.90	4.00–4.50
MW (mm)	0.30–0.35	0.45–0.50
HL (mm)	0.66–0.67	0.95–0.98
HW (mm)	0.29	0.41–0.43
FRL (mm)	0.52	0.73–0.76
OCW (mm)	0.17	0.23–0.24
HL/HW	2.31–2.34	2.28–2.34
HW/OCW	1.66–1.71	1.78
COL/HL	0.21–0.22	0.22–0.23
FRL/HL	0.78–0.79	0.77–0.78
A/HW	1.90–2.03	1.74–1.75
A3/A1	1.74–1.83	1.52–1.56
A3/A2	1.40–1.43	1.25–1.26
A3/(A1+A2)	0.78–0.80	0.68–0.70
A4/A3	0.48–0.55	0.40–0.43
A3'/A4	0.23–0.27	0.22–0.30
MNL/MNW	6.00–7.40	6.44–6.73
MNL/HL	0.54–0.55	0.52–0.53
A/MP	1.83–2.00	1.74–1.83
STL/MP1	0.69–0.75	0.63–0.66
MP2/MP1	0.85–0.92	0.79
MP3/MP2	0.55–0.59	0.47–0.50
MP/LP	1.84–1.97	2.13–2.28
LP2/LP1	2.44–2.75	2.25–2.27
L3 (mm)	1.24–1.28	1.77–1.84
L3/L1	1.15–1.20	1.21–1.24
L3/L2	1.08–1.10	1.11–1.24
L3/HW	4.30–4.44	4.25–4.37
L3 (CO/FE)	0.94–0.98	0.90–0.92
L3 (TI/FE)	0.56–0.61	0.55–0.57
L3 (TA/FE)	0.89–0.95	0.83–0.85
L3 (CL/TA)	0.48–0.51	0.40–0.41
LAS (mm)	0.48–0.54	1.36–1.45
LAS/HW	1.66–1.90	3.35–3.36
U (mm)	1.73–1.76	2.28–2.29
U/LAS	3.18–3.23	1.58
U/HW	6.03–6.12	5.30–5.31
U1/U2	2.76–2.86	3.91–3.96

cylindrical, PT with two long, slender, slightly curved claws; posterior claw shorter than anterior claw on L1 and L2, posterior claw longer than anterior claw on L3; surface of CO and FE covered in part with minute spinulae, TI and TA with a ventral row of elongate spinulae.

Abdomen. Eight-segmented (Fig. 1); segments I–VI sclerotized dorsally, membranous ventrally; tergites I-IV similar to each other, narrow, transverse, tergites V-VI somewhat longer, extending to ventrolateral margin; segment VII sclerotized both dorsally and ventrally, ventral sclerite independent from dorsal sclerite; spiracles absent on segments I-VII; LAS (Figs. 14 and 15) the longest, completely sclerotized, ring-like; all sclerites without anterior transverse carina, without sagittal line, covered with minute spinulae in transverse rows; siphon strongly elongate, parallel-sided, sharp apically. *Urogomphus* (Fig. 16). Very long, much longer than HW, composed of two urogomphomeres; U1 longer than siphon; U2 slender, setiform, much shorter than U1.

Chaetotaxy. Similar to that of generalized Hydroporinae larva (Alarie 1991, Alarie and Harper 1990, Alarie et al. 1990, Alarie and Michat 2007b; Figs. 1–16) except for the following features: seta FR6 strongly developed; seta FR13 marginal, strongly developed; pores PAd and PAj absent; pore PAg present; pore FRb anterior to the egg burster; PA with two minute structures (possibly pores) on anteroventral margin, anterior to pore PAo; we were unable to find seta PA3, but we could not establish whether it is really absent because a minute structure is present in the place where PA3 is usually located; A3 with a minute structure (possibly an additional pore) on ventral surface;

seta MX1 inserted on the stipes; setae MX4, MX7, MX8, MX9 and MX10 absent; pores MXj and MXk absent; setae LA1, LA2, LA9, LA10 and LA12 absent; pore LAd absent; seta TR2 absent; seta TI7 elongate, setiform; seta AB2 absent; pores ABa and ABd absent; seta AB10 spiniform; setae UR2, UR3 and UR4 inserted far from each other, UR3 somewhat nearer to UR4 than to UR2; seta UR5 elongate, setiform; seta UR8 inserted apically on U2.

Second Instar, Description. As for instar I except for the following features.

Color. Light brown area of dorsal surface of cephalic capsule with several testaceous maculae; U1 light brown with several testaceous bands.

Body. Measurements and ratios that characterize the body shape are shown in Table 1.

Head. Reticulation of cephalic capsule (Fig. 17) restricted to posteroventral portion; occipital suture present; egg bursters absent; median branch of nasale with a long, spine-like, lateral projection posterior to the spatulate apex; anterior margin of median branch with 19–21 spatulate setae (six of them longer) directed downward, covering the anterior and lateral margins of the spatulate apex; lateral branches of nasale with a ventral row of four to six bulges. *Antenna.* A1 considerably longer than A4. *Labium.* Prementum with one to three long spinulae on lateral margin.

Thorax. Meso- and metatergite with anterior transverse carina. *Legs* (Fig. 18). Surface of CO and FE without minute spinulae, metaFE with a posteroventral row of elongate spinulae on middle third.

Abdomen. Tergites I–V (Fig. 19) similar to each other, tergite VI extending to ventrolateral margin; segment VII completely sclerotized, ring-like; sclerites I–VII with anterior transverse carina.

Chaetotaxy. Head capsule with numerous minute or setiform secondary setae anterior to occipital suture; lateral margin of PA with four spiniform secondary setae; median branch of nasale with several minute or setiform secondary setae on dorsal surface; each lateral branch of nasale with four secondary setae (two spiniform, strongly developed, and two setiform); mandible with one setiform secondary seta on basoexternal margin, proximal to pore MNa; secondary leg setation detailed in Table 2; TI and TA with a row of natatory setae on posterodorsal margin; LAS with two secondary spiniform setae on laterodistal portion; siphon with numerous secondary spiniform setae on dorsal and lateral surfaces; U1 with numerous secondary setae that are spiniform on basal half and setiform on distal half.

Table 2. Number and position of secondary setae on the legs of the second-instar larva of *D. lentus*

Segment	Position	Instar II ($n = 2$)
Trochanter	Pr	1/1/1
	Total	1/1/1
Femur	AV	1–2/1/1–2
	PV	0/1/2–3
	Total	1–2/2/3–5
Tibia	AV	0/1–2/1
	PD	0/2/2–3 (NS)
	PV	1/0/0
	Total	1/3–4/3–4
Tarsus	AD	1/1/1
	AV	0/1/1
	PD	0/0/0 (NS)
	PV	1/0/0
	Total	2/2/2

Numbers between slash marks refer to pro-, meso-, and metathoracic leg, 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). The presence of natatory setae (NS) is indicated in parentheses.

Comparative Notes

The instar of the larva of *D. floridanus* described by Spangler (1966) was not specified. However, he mentioned the presence of spiracles on the mesothorax and abdominal segments I–VII. This character added to the length of the specimen (7.5 mm), leads to suppose that it was probably a third instar. Because this is the only instar that we did not have the opportunity to examine in *D. lentus*, comparisons become difficult. Also, because the description of *D. floridanus* was restricted mainly to general morphological characters, and morphometric and chaetotaxic details were not emphasized, we experienced difficulties in finding reliable characters to separate this species from *D. lentus.*

In our comparison of larvae of *Derovatellus* and *Vatellus* (Michat and Torres 2005), we gave the ratio MP2/MP1 and the absence of lateral spinulae on the prementum (among other characters) as diagnostic for *Derovatellus*, based on the description of *D. floridanus* made by Spangler (1966). These two differences are not corroborated when *D. lentus* is examined, because larvae of this species bear lateral spinulae on the prementum and have a ratio MP2/MP1 not significantly different from that observed in *Vatellus.* We suspect that larvae of *D. floridanus* bear lateral spinulae on the prementum, and that this feature was overlooked in the description. The characters that separate larvae of *Derovatellus* and *Vatellus* are summarized above (see diagnosis of the genera).

The labial palpus shows interesting differences within the Vatellini. In the two known species of *Derovatellus* (*D. floridanus* and *D. lentus*) it is two-segmented, which is similar to that of almost every known dytiscid larvae (Bertrand 1972). Within *Vatellus*, however, there are at the moment two larval descriptions which differ in the number of labial palpomeres. Indeed, a one-segmented and a three-segmented palpus were reported for *V. haagi* and *V. mexicanus*, respectively (Spangler 1963, Michat and Torres 2005). The description of *V. mexicanus* is dubious, however, and we suspect that the labial palpus in that species bear less than three palpomeres. Whereas the labial palpus of *D. lentus* is clearly two-segmented, the articulation between palpomeres is rather weak in comparison with those of

Table 3. Characters and states used for the cladistic analysis

	Character and state
(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 PAl (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)	Ventroapical 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)	Stipes (instar I): (0) short, robust; (1) elongate, palpomere-like.
(043)	Galea (instars I–III): (0) well developed, subconical; (1) very short, subconical; (2) minute; (3) absent.
(044)	Palpifer (instars I–III): (0) inconspicuous, not clearly differentiated from the stipes; (1) palpomere-like, clearly differentiated from the stipes.
(045)	Seta MX1 (instars I–III): (0) inserted on the cardo; (1) inserted on the stipes.
(046)	Seta MX4 (instar I): (0) present; (1) absent.
(047)	Seta MX5 (instar I): (0) present; (1) absent.
(048)	Seta MX6 (instar I): (0) present; (1) absent.
(049)	Seta MX7 (instar I): (0) present; (1) absent.
(050)	Seta MX8 (instar I): (0) present; (1) absent.
(051)	Seta MX9 (instar I): (0) present; (1) absent.
(052)	Seta MX10 (instar I): (0) present; (1) absent.
(053)	Pore MXh (instar I): (0) inserted on the galea; (1) inserted on the stipes; (2) absent.
(054)	Pore MXk (instar I): (0) present; (1) absent.
(055)	Secondary setae on maxillary palpomere 1 (instars II–III): (0) absent; (1) present.
(056)	Prementum (instars I–III): (0) broader than long or as long as broad; (1) longer than broad.
(057)	Elongate lateral spinulae on prementum (instars I–III): (0) absent; (1) present.
(058)	Labial palpus (instars I–III): (0) composed of one palpomere; (1) composed of two palpomeres.
(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)	Seta LA6 (instar I): (0) inserted distally or subdistally; (1) inserted medially; (2) absent.
(066)	Seta LA8 (instar I): (0) short, spiniform; (1) elongate, setiform; (2) elongate, spiniform.
(067)	Seta LA8 (instar I): (0) inserted distally or subdistally; (1) inserted proximally; (2) absent.
(068)	Seta LA9 (instar I): (0) present; (1) absent.

Continued on following page

Table 3. Continued

	Character and state
(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 TR3 (instar I): (0) present; (1) absent.
(078)	Seta FE2 (instar I): (0) inserted distally; (1) inserted subdistally.
(079)	Seta FE6 (instar I): (0) inserted distally; (1) inserted subdistally; (2) absent.
(080)	Pore FEa (instar I): (0) present; (1) absent.
(081)	Natatory dorsal setae on femur (instars II–III): (0) absent; (1) present.
(082)	Natatory ventral setae on femur (instars II–III): (0) absent; (1) present.
(083)	Secondary anterodorsal setae on femur (instars II–III): (0) absent; (1) present.
(084)	Seta TI2 on meso- and metatibia (instar I): (0) short, spiniform; (1) elongate, setiform; (2) absent.
(085)	Seta TI7 (instar I): (0) short, spiniform; (1) elongate, setiform.
(086)	Pore TIa (instar I): (0) present; (1) absent.
(087)	Secondary setae on tibia (instars II–III): (0) absent; (1) present.
(088)	Natatory dorsal setae on tibia (instars II–III): (0) absent; (1) present.
(089)	Secondary setae on anterodorsal margin of protarsus (instars II–III): (0) absent; (1) present.
(090)	Secondary setae on posteroventral margin of protarsus (instar III): (0) absent; (1) present.
(091)	Secondary setae on posteroventral margin of metatarsus (instar III): (0) absent; (1) present.
(092)	Natatory dorsal setae on tarsus (instars II–III): (0) absent; (1) present.
(093)	Basoventral spinulae on claw (instar I): (0) absent; (1) present.
(094)	Abdominal tergites I–VI (instar I): (0) with anterior transverse carina; (1) without anterior transverse carina.
(095)	Ventral surface of abdominal segments II–III (instar III): (0) membranous; (1) sclerotized.
(096)	Ventral surface of abdominal segments IV–V (instar III): (0) membranous; (1) sclerotized.
(097)	Ventral surface of abdominal segment VI (instars I–III): (0) membranous; (1) sclerotized.
(098)	Abdominal segment VII (instar I): (0) sclerotized dorsally, membranous ventrally; (1) sclerotized dorsally and ventrally, with ventral sclerite separate from dorsal sclerite; (2) completely sclerotized except for a narrow, longitudinal, ventral band; (3) completely sclerotized.
(099)	Abdominal sclerite VII (instar I): (0) with anterior transverse carina; (1) without anterior transverse carina.
(100)	Spiracles on mesothorax and abdominal segments I–VII (instar III): (0) present; (1) absent.
(101)	Siphon (instars I–III): (0) very short; (1) short to moderately long; (2) very long, urogomphomere-like.
(102)	Tracheal trunks (instars I–III): (0) not protruding from the apex of siphon; (1) protruding from the apex of siphon.
(103)	Sensillum AB2 (instar I): (0) setiform; (1) pore-like; (2) absent.
(104)	Seta AB3 (instar I): (0) setiform; (1) spiniform.
(105)	Seta AB4 (instar I): (0) not distinctly developed; (1) very elongate, strongly developed.
(106)	Seta AB5 (instar I): (0) not distinctly developed; (1) strongly developed.
(107)	Seta AB6 (instar I): (0) short (1) elongate.
(108)	Seta AB7 (instar I): (0) small; (1) well developed to strongly developed; (2) absent.
(109)	Seta AB9 (instar I): (0) inserted dorsolaterally; (1) inserted ventrolaterally.
(110)	Seta AB10 (instar I): (0) setiform; (1) spiniform.
(111)	Seta AB15 (instar I): (0) absent; (1) present.
(112)	Pore ABa (instar I): (0) present; (1) absent.
(113)	Pore ABc (instar I): (0) present; (1) absent.
(114)	Secondary ventral setae on siphon (instar III): (0) absent; (1) present.
(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.

other members of the subfamily Hydroporinae (Michat 2006, Alarie and Michat 2007a, Michat et al. 2007, Michat and Alarie 2008, Michat and Torres 2008). Also, the pore LAd, considered to be part of the ancestral system of the Hydroporinae (Alarie 1991) is absent in *D. lentus* and *V. haagi.* Pores in the region of articulation are in general related to the sense of movements between palpomeres (McIver 1975, Zacharuk and Shields 1991, Keil 1997). Therefore, the absence of LAd may indicate a decreased importance of the articulation between the palpomeres, reflected in a less conspicuous articulation in *D. lentus* and a complete absence in *V. haagi.* Larvae of more species of Vatellini will have to be examined before attempting more comprehensive generalizations on the evolution of the labial palpus within the tribe.

We find worth mentioning that our interpretation in the naming of some setae on the prementum of *D. lentus* is somewhat different from that previously

Table 4. Data matrix used for the cladistic analysis. Missing data coded "?"

Species	Character											
	00000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000001	1111111111	11111111111
	00000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888889	9999999990	0000000001	11111111122
	01234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12345678901
Leuronectes curtulus	11001020000	01?0000000	0000000101	0000000000	0001000000	0001000100	0010000011	0000000000	0010000000	0000000000	0000000000	10000005000
Copelatus longicornis	11011020000	01?0000000	0000000001	0000100000	0001000100	0001000100	0010000011	0010000000	0000000000	0001000010	0000000000	10000001000
Hydaticus tuyuensis	11111020000	01?0000000	0000000101	0100110001	0101000000	0001000100	0010000011	0001000020	1110101110	0110000200	0000000000	10002005200
Laccophilus obliquatus	01001120000	01?0000020	0000000100	0100100000	0001000000	0001000100	0210000022	0000000000	0000001110	0101000010	1000000010	10101005001
Lancetes marginatus	11001020000	01?0000000	0000000101	1100000000	0001000000	0001000100	0010000001	0010000000	0000101100	0101000010	0000000000	10001005011
Matus bicarinatus	00111020000	01?0000000	00000001?1	1000011000	0001000000	0001100100	0010020011	0001000000	1012001111	1100000100	1000000000	10002005201
Rhantus signatus	11111020000	01?0000000	0000000101	1000000000	0001000000	0001000100	0010000011	0011000000	1010101110	1110000000	0000000000	10001005001
Allodessus bistrigatus	00011000100	0000111101	1101001111	0110100111	1030110001	1110000100	0010020000	0000011001	0010001001	1001000110	1000000?11	01101001001
Amarodytes duponti	00111000100	0000111101	1111001111	0110100110	1030110001	1111000100	0000010000	0000011001	0010001000	0001000110	1000000?11	01101001001
Anodocheilus maculatus	00011000100	0000111101	1101001010	0110100110	1030110001	1110000100	0000010000	0000011001	0010001000	0001000110	1000000?11	01101001000
Hypodessus cruciatus	00011000100	0000111101	1101001111	0110100110	1030110001	111?000100	0000010000	0000011001	0010001001	1001000110	1000000011	01101001000
Liodessus flavofasciatus	00011000100	0000111101	1101001010	0110100110	1030110001	1110000100	0000010000	0000011001	0010001000	0001000110	1000000011	01101001000
Antiporus uncifer	00011011200	0000111101	00010011?0	0110100111	1030110001	1110001100	0000010000	0000011000	1010001111	1100000100	0000000010	01001001201
Canthyporus kenyensis	00011000100	0000011101	10010010?0	0100100111	0030000001	1110001100	1000010000	0000001001	0000000000	000?000??0	1000111011	01000004100
Deronectes latus	00011000101	0000111101	10010011?1	?10010011?	0030010001	1110000100	0000010000	0000001000	0010001011	1000000100	1000000010	01002001?01
Heterosternuta wickhami	00011000100	0000111101	10010011?1	010010011?	0030010001	1110001100	0000010000	0000011000	0010001001	0001000111	0000000010	01002001101
Hydrocolus paugus	00010000100	0000111101	10010011?1	010010111?	0030010001	1110001100	0000010000	0000001000	0010001000	0001000110	1000000010	01002001100
Hydroporus columbianus	00011000100	0000111101	10010011?1	010010011?	0030010001	1110001100	0000010000	0000001000	0010001000	0001000110	1000000010	01002001100
Laccornellus lugubris	0?0?1000101	0000011101	0001001??0	01001??111	0010000000	0100?01100	1000010000	000?001001	???000????	??00??010?	1000101001	100?000410?
Neoporus undulatus	00011000000	0000111101	10010011?1	010010011?	0030010001	1110001100	0000010000	0000011000	0010001101	1101000111	1000000010	01001001201
Oreodytes scitulus	11111000100	0000111101	10010011?1	0010100111	1030110001	1110000100	0000010000	0000001000	0010001000	0000000100	0000000010	01001001?11
Scarodytes halensis	11111000100	0000111101	10010011?1	?01010011?	1030110001	1110001100	0000010000	0000001000	1010001101	1100000100	10000000?0	01002001?01
Stictonectes canariensis	00011000100	0000111101	00010011?1	?11010011?	0030000001	1110000100	0000010000	0000001000	0010001001	1000000100	1000000010	01002001100
Hydrovatus caraibus	00001110001	0100011101	1101111010	0101100101	1010100000	0100000100	1200011000	0000011001	0000000000	0010111100	1000111001	01010004100
Coelambus impressopunctatus	00011000100	0000111101	00010011?0	011010011?	0030000001	1110001100	0000010000	0000011010	0010001001	1001000110	1000000010	01002002100
Herophydrus musicus	00011000100	0000111101	00010011?0	??1010011?	0030000001	1110001100	00000?0000	0000011000	0010001001	100???0??0	1000000010	01002002?00
Hygrotus sayi	00011000100	0000111101	00010011?0	011010011?	0030000001	1110001100	0000010000	0000011010	0010001001	1001000110	1000000010	01002002100
Andex insignis	00011010100	0001111111	1101001101	0111100111	1030100001	111?010100	0000011001	0001011001	1010111111	1100011?00	1010011111	01003103101
Desmopachria concolor	00011010000	0101111111	1101001001	0111100111	1030111101	1110010110	0101111011	1010011001	1010101111	1101111110	1010011111	01010103301
Desmopachria punctatissima	00011010000	0101111111	1101001001	0111100111	1030111101	1110010110	0101111011	1010011001	1010101111	1101111110	1010011111	01010103301
Hyphydrus ovatus	00011011000	0101111111	1101001101	??1110011?	1030100001	1110010100	0000011001	0000011001	1010101111	1100011100	1010011111	01013103001
Microdytes uenoi	00011000100	0101011111	1101001101	??1110011?	1030100001	1110010100	0000011001	0000011001	0010001111	1100111100	1010011111	01000003101
Pachydrus obesus	00001011210	0000011101	0001001110	0101000111	1020111110	0120000101	0000011011	1001111111	0101101000	0000001200	1011000011	01012002101
Laccornis latens	00011000000	0010011100	0001001100	000010011?	0010000000	0101000100	0000010000	0000001001	0000000000	0000000100	1000000010	00000000100
Celina parallela	01111000001	0000110100	0001001110	1100100101	0010000000	0000000100	0200010011	0000001000	0010001011	1000000100	1100001210	01010010100
Derovatellus lentus	00011011300	1000?11101	0101001111	0110000111	1130110011	1111001101	1000020122	0100011000	0000101111	010100011?	2020010011	01001000101
Vatellus haagi	00011011300	1000111101	0101001111	0110011111	1130110011	111?101020	1000020122	0100011000	0010101111	1101000110	2020001111	01001000101

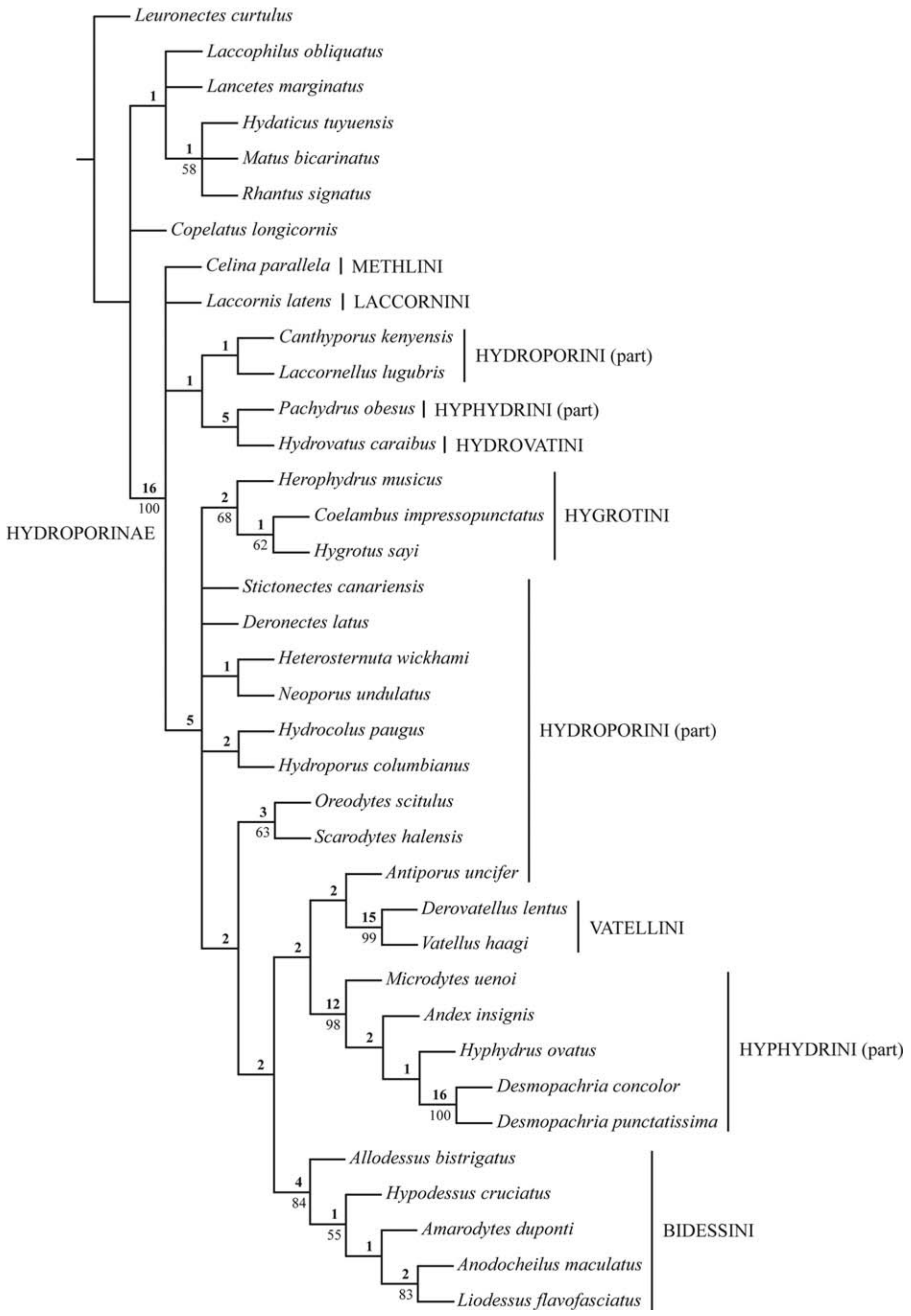


Fig. 20. Strict consensus cladogram. Bremer support values are indicated above branches; jackknife values above 50 are indicated below branches.

made by us for *V. haagi* (Michat and Torres 2005). In our opinion, setae originally labeled LA3, LA4, LA5 and LA8 in *V. haagi* should better be labeled LA4, LA5, LA8 and LA3 respectively.

Character Analysis

In total, 122 characters derived from the larval morphology and chaetotaxy were included, of which 100 were coded as binary and 22 as multistate (Table 3). The analysis of the data matrix (Table 4) by using TNT resulted in six most parsimonious trees of 364 steps (CI = 0.41; RI = 0.73). In all trees the tribe Vatellini was recovered as monophyletic with high support, as the sister group of the Australian genus *Antiporus* (Hydroporini), this clade being sister to the tribe Hyphydrini (except *Pachydrus* Sharp) (Fig. 20). The equally par-

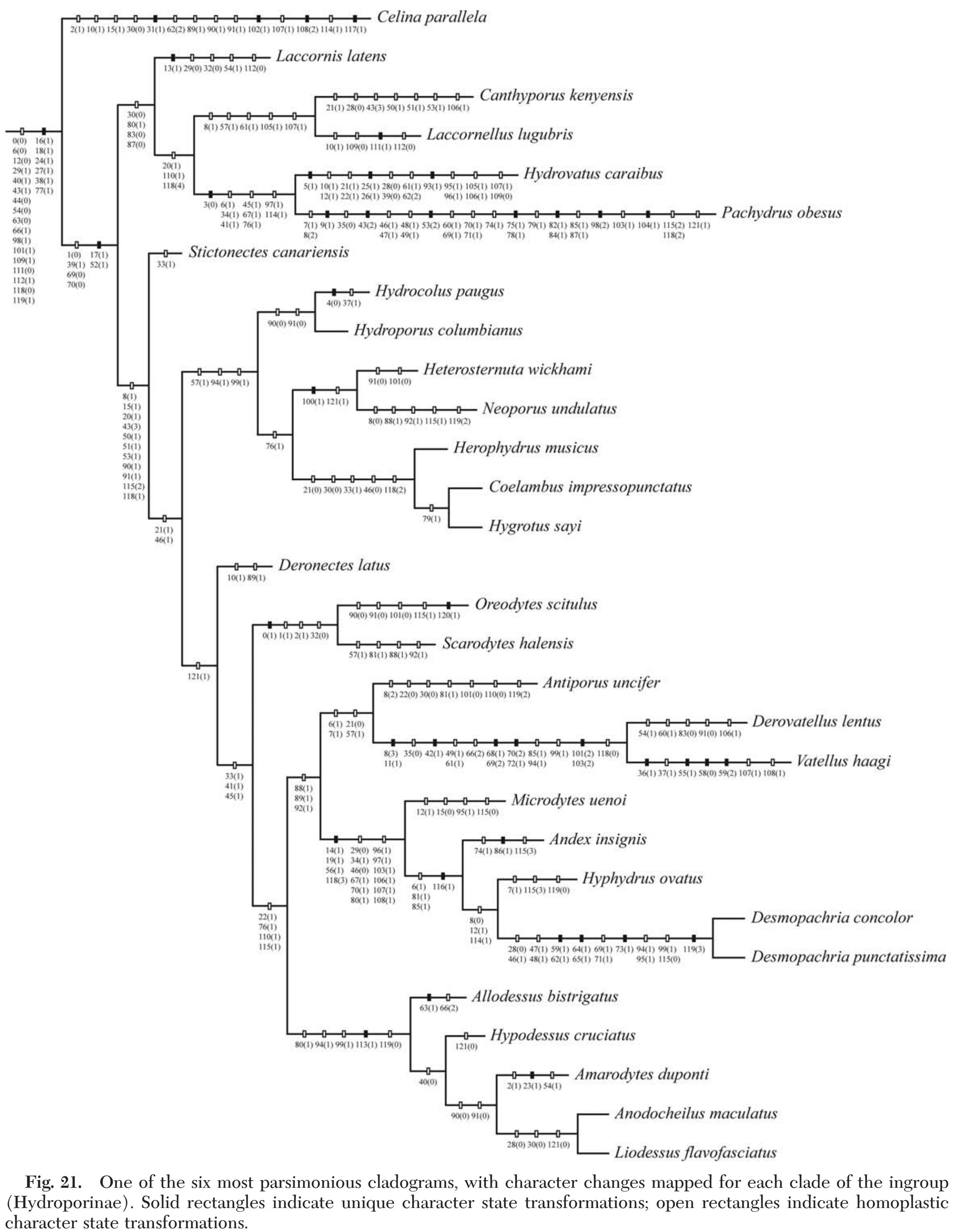


Fig. 21. One of the six most parsimonious cladograms, with character changes mapped for each clade of the ingroup (Hydroporinae). Solid rectangles indicate unique character state transformations; open rectangles indicate homoplastic character state transformations.

simonious trees differed in outgroup topology and in the relative positions of some groups within the ingroup. The strict consensus (Fig. 20) shows polytomies in the basal nodes of the Hydroporinae clade. Characters were mapped in one of the most parsimonious cladograms (Fig. 21).

Discussion

The current study brings considerable evidence for monophyly of the tribe Vatellini based on several unique larval character states: 1) lateral projections of nasale strongly developed, bifid apically (character

8.3); 2) seta FR6 strongly developed (character 11.1); 3) stipes elongate, palpomere-like (character 42.1); 4) seta LA9 absent (character 68.1); 5) seta LA10 absent (character 69.2); 6) seta LA12 absent (character 70.2); 7) pore LAd absent (character 72.1); 8) siphon very long, urogomphomere-like (character 101.2); and 9) sensillum AB2 absent (character 103.2) (Fig. 21). The support obtained for this clade was among the highest within the analysis (Fig. 20). The monophyly of Vatellini also received support from studies based on adult (Miller 2001, Miller et al. 2006) and molecular (Ribera et al. 2008) characters, and this group of beetles is certainly one of the most characteristic within the subfamily Hydroporinae.

Vatellini is supported by other characters that are also present in other hydroporine lineages. For example, the presence of additional ventroapical pores on the third antennomere (character 35.0) and the absence of seta MX7 (character 49.1) are shared only with *Pachydrus;* the elongate and setiform aspect of seta TI7 is shared with *Pachydrus* and Hyphydrini (except *Microdytes* J. Balfour-Browne); and the absence of seta LA2 (character 61.1) is shared with *Canthyporus* Zimmermann, *Laccornellus* Roughley & Wolfe, and *Hydrovatus* Motschulsky. Interestingly, these characters relate the Vatellini with presumably ancestral hydroporine lineages (also see Michat et al. 2007, Michat and Torres 2008). Larvae of the tribe Vatellini also are characterized by the terminal insertion of the primary seta UR8 on the second urogomphomere (character 118.0). This character state is present only in the tribes Methlini and Laccornini, considered to be the most ancestral lineages within the subfamily Hydroporinae (Alarie 1991, Alarie and Michat 2007a, Michat et al. 2007). According to the derived position of Vatellini obtained in our analysis (Fig. 20), however, it has to be assumed that the terminal insertion of UR8 in members of this tribe represents a reversal from the derived condition.

Vatellini was recovered as the sister group of the Australian genus *Antiporus.* However, this relationship did not receive strong support in our analysis (Fig. 20), and we were unable to find characters that unambiguously support this grouping (Fig. 21). Both taxa share a spatulate apex of the nasale (character 7.1, present also in *Pachydrus* and *Hyphydrus* Illiger), the presence of pore PAe (character 21.0, shared with Hygrotini, *Stictonectes* Brinck, *Pachydrus, Laccornellus, Laccornis* Gozis, and *Celina* Aubé) and the presence of elongate lateral spinulae on prementum (character 57.1, shared with Hygrotini and several Hydroporini genera). According to the topology obtained, these characters have a reduced value because all of them seem to have evolved several times independently within the Hydroporinae. In absence of unambiguous support the hypothesis of a clade Vatellini + *Antiporus* seems unlikely. Moreover, previous analyses based on other data sets do not support such hypothesis, which reinforces the idea that the grouping is not natural. For example, Miller (2001) and Miller et al. (2006) found Vatellini more related to other members of Hydroporini, Ribera et al. (2008) found Vatellini sister of Hydrovatini, and Ribera and Balke (2007) found a sister-group relationship of Vatellini with the remaining Hydroporinae.

The clade Vatellini + *Antiporus* was resolved as the sister group of the tribe Hyphydrini (excluding *Pachydrus*). This relationship, however, was only weakly supported (Fig. 20) by three characters: the presence of natatory setae on the dorsal surface of tibia and tarsus in instars II–III (characters 88.1 and 92.1 respectively, both shared with *Neoporus* Guignot and *Scarodytes* Gozis); and the presence of secondary setae on the anterodorsal margin of protarsus in instars II–III (character 89.1, shared with *Deronectes* Sharp and *Celina*) (Fig. 21). A sister-group relationship between Vatellini and Hyphydrini was hypothesized by Michat and Torres (2005) based on the shared absence of pore PAj, the antennomeres 1 and 2 subequal in length, the setiform aspect of seta TI7 and the strong development of setae AB6 and AB7. However, based on the topology obtained in the current study these characters are not unambiguous synapomorphies for the clade Vatellini + *Antiporus* + Hyphydrini because pore PAj is present and seta TI7 is spiniform in *Antiporus,* and setae AB6 and AB7 are not strongly developed in *Antiporus* and *Derovatellus.* The relative length of antennomeres 1 and 2 was not included as a character in this study owing to its continuous nature.

Larvae of *Vatellus* bear several unique characters within Hydroporinae including the presence of secondary setae on antennomere 1 and maxillary palpomere 1 (characters 36.1 and 55.1 respectively) and the labial palpus composed of one palpomere (character 58.0) (but see Comparative Notes for discussion about this character). However, no characters were discovered that separate the larvae of *Derovatellus* from those of all other Hydroporinae studied, although the genus is distinct by the absence of seta LA1 on the prementum (character 60.1, shared with *Pachydrus*) and the absence of anterodorsal secondary setae on femur (character 83.0, shared with some presumably ancestral lineages) (Fig. 21).

Whereas the hypothesis of monophyletic origin of the Vatellini seems beyond dispute, the phylogenetic relationships of this tribe within the Hydroporinae are contentious. The studies based on larval characters (Michat and Torres 2005, 2008; Michat 2006; Alarie and Michat 2007a; Michat et al. 2007; Michat and Alarie 2008; this study) always link the Vatellini to Hyphydrini and/or *Antiporus,* in different combinations. Adult characters, however, are in favor of a close relationship of Vatellini with members of Hydroporini (Miller 2001, Miller et al. 2006). Finally, molecular data suggest a close relationship with Hydrovatini (Ribera et al. 2008) or with the remaining Hydroporinae (Ribera and Balke 2007). These disparate results evidence the need of broader studies, including more taxa and characters and combining different data sets.

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