

Descriptions of larvae of the North American endemic stygobiontic *Ereboporus naturaconservatus* Miller, Gibson & Alarie and *Haideoporus texanus* Young & Longley (Coleoptera: Dytiscidae)

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The larvae of the North American stygobiontic dytiscid species *Ereboporus naturaconservatus* Miller, Gibson & Alarie, 2009 and *Haideoporus texanus* Young & Longley, 1976 are described with an emphasis on chaetotaxy of the head capsule, head appendages, legs, last abdominal segment and urogomphi. Both of these species share the presence of a nasale and the absence of the primary pores MXd and LAc, which have been recognized as synapomorphies for members of the subfamily Hydroporinae. Out of the common convergent characteristics associated with hypogaean living, no synapomorphies were found that could relate *Haideoporus texanus* and *Ereboporus naturaconservatus*, which reinforces the hypothesis that these species evolved independently within the subfamily Hydroporinae. In terms of morphological adaptations, *E. naturaconservatus* stands as a remarkable hydroporine in that its larvae evolved a truncated last abdominal segment and a very elongate urogomphomere 1 relative to urogomphomere 2.

Keywords: Adepaga, Dytiscidae, Hydroporini, stygobiontic, larval chaetotaxy.

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Introduction

Stygobiontic aquatic Coleoptera represent a heterogeneous and fascinating grouping of taxa associated with underground waters. In hypogean or subterranean habitats, these beetles not only are found in bed sediments but also in caves, wells and deep aquifers (Castro & Delgado 2001). Compared to epigeal or surface-dwelling species, these beetles generally have small geographic ranges and high levels of endemism, making their biogeography dis-

tinct (Porter 2007). Most stygobiontic beetles are placed within the coleopteran suborder Adepaga, and a great number of them in the dytiscid subfamily Hydroporinae of the Dytiscidae (Castro & Delgado 2001). Groundwater adapted Dytiscidae were known only sporadically (cf., Miller et al. (2009) for a literature review) until a recent discovery of more than 100 species in Australia (Watts & Humphreys 2006, Watts et al. 2007, Leys & Watts 2008) sug-

gests that stygobiontic dytiscids may be more diverse and widespread than previously thought.

Until this century *Morimotoa phreatica* Uéno, 1957, *Phreatodessus hades* Ordish, 1976, *Haideoporus texanus* Young & Longley, 1977, and *Siئتitia avenionensis* Guignot, 1925 were the only stygobiontic dytiscid species for which larvae had been described (Uéno 1957, Ordish 1976, Longley & Spangler 1977, Richoux 1980), although these descriptions were generally superficial. More recently, however, larvae of *Glareadessus stocki* Wewalka & Biström, 1998 (Alarie & Wewalka 2001), *Neobidessodes limestoneensis* (Watts & Humphreys, 2003) (Michat et al. 2010), seven species of *Paroster* Sharp, 1882 (Alarie et al. 2009a) and 25 species of *Limbodessus* Guignot, 1939 (Michat et al. 2012) were described, all of which included chaetotaxy (Alarie & Michat 2007a, Alarie et al. 2009a, 2009b, 2011, Michat & Torres 2005, Michat et al. 2007).

Five subterranean species of Dytiscidae are recognized in North America: *Ereboporus naturaconservatus*, *Haideoporus texanus*, *Stygoporus oregonensis* Larson & Labonte, 1994, *Psychopomporus felipi* Jean, Telles & Miller, 2012 and *Comaldessus stygius* Spangler & Barr, 1995 (Miller et al. 2009), all of which belong to the large and diverse subfamily Hydroporinae. The purpose of this paper is to describe the second and third instar larvae of both *E. naturaconservatus* and to redescribe the larvae of *H. texanus* with emphasis on morphometry and chaetotaxy and to compare these species with larvae of other Hydroporinae.

Material and methods

Larvae examined. This project is based on specimens collected in drift nets (mesh size 300–500 μm) over two spring orifices of Caroline Springs, the headwaters of Independence Creek, Terrel County, TX, USA, 22 June 2007. The only subterranean diving beetle species known to occur in Caroline Springs is *E. naturaconservatus*, and we assume the larvae belong to that species. Larvae assumed to be *H. texanus* were collected in association with adults of that species from Comal Springs, Comal County, TX, USA, 8 November 2006. The only other diving beetle species known from this spring system is *Comaldessus stygius*, which is much smaller and clearly a member of the tribe Bidessini. Thus we are confident that these larvae represent the species *E. naturaconservatus* and *H. texanus*. Voucher specimens are deposited in the larval collection of Y Alarie (Department of Biology, Laurentian University, Sudbury, ON, Canada).

Preparation. Larvae were disarticulated and mounted on standard glass slides with Hoyer's medium. Mi-

croscopic examination at magnifications of 80–800 \times 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.

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 Hydroporinae (Michat & Torres 2005, Michat et al. 2007, Michat & Alarie 2008, Alarie et al. 2009a). The following measurements were taken. 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 MN: maximum width measured at base. 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 third antennomere. Length of 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, the length of the distal portion is included in the femoral length. 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, which characterize the body shape.

Chaetotaxic analysis. The setae and pores were coded according to the system proposed by Alarie (1991) and Alarie & Michat (2007b) for the cephalic capsule and head appendages, Alarie et al. (1990) for the legs, and Alarie & 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 (AN, antenna; AB, abdominal segment VIII; CO, coxa; FE, femur; FR, frontoclypeus; LA, labium; MN, mandible; MX, maxilla; PA, parietal; TA, tarsus; TI, tibia; TR, trochanter; UR, urogom-

phus) and a corresponding number. Pores are coded in a similar manner except that the number is replaced by a lower case 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.

***Ereboporus naturaconservatus* Miller, Gibson & Alarie**

Figs 1–6

Diagnosis (third instar larva)

Body lightly sclerotized; stemmata absent (Fig. 1); frontoclypeus very broad with lateral margins strongly inflated and with several spine-like protuberances, abruptly constricting anteriorly to form a rounded and narrow spatula (Fig. 1); HL/HW > 1.50; A3 about 1.60 times as long as A2; maxillary palpus about 1.70 times as long as labial palpus; primary seta FR6 strongly developed; primary

setae MX4 and TR2 present; last abdominal segment truncated along posterior margin, not extending into a siphon (Fig. 2); U1 more than 10 times as long as U2 (Fig. 3); primary setae UR2, UR3 and UR4 not contiguous, apart from each other; U1 with one secondary seta.

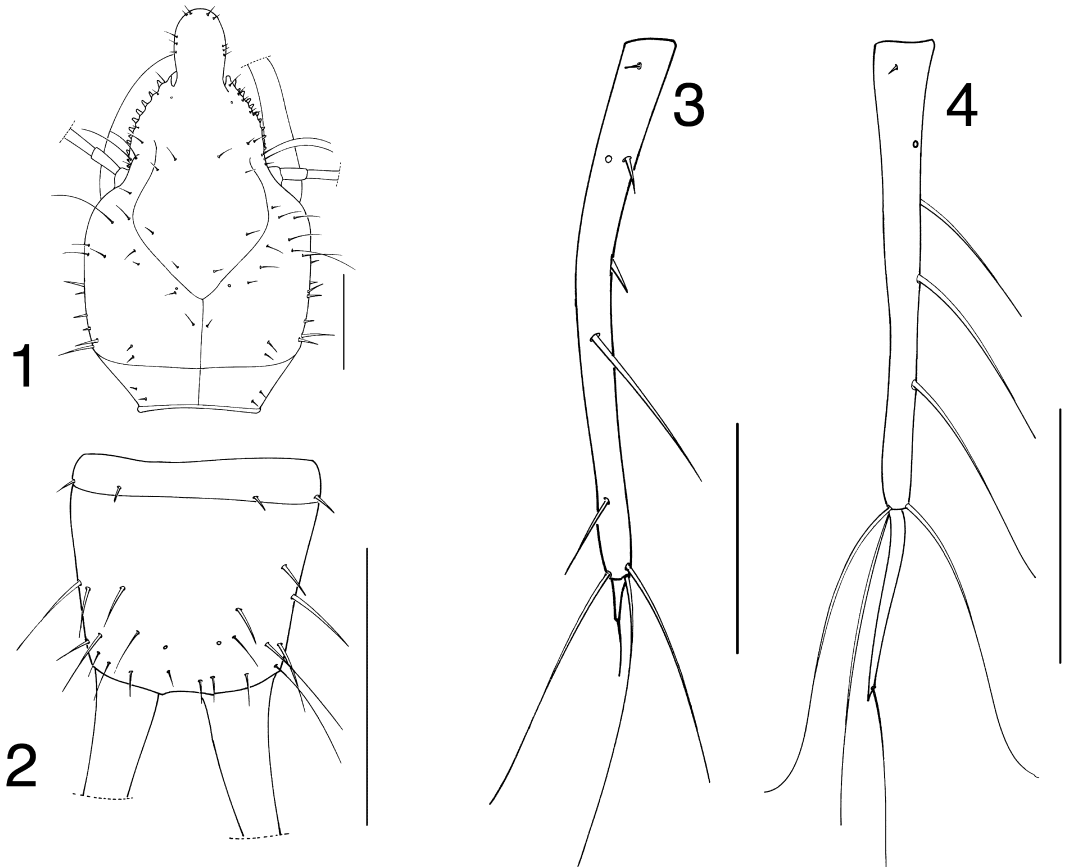
First-instar larva

No specimens were available for study.

Second-instar larva ($n = 1$) (Figs 1–2, 4)

Color: Uniformly pale, unpigmented, distal half of mandible light brown. Body. Lightly sclerotized, subcylindrical, narrowing towards abdominal apex. Measurements and ratios that characterize the body shape are shown in Table 1.

Head: Head capsule with stemmata absent (Fig. 1), longer than broad; maximum width at about mid-length, slightly constricted at level of occipital suture; ecdysial line slightly visible, coro-



Figs 1–4. *Ereboporus naturaconservatus*, dorsal aspect. – 1–2, second-instar larva; 1, head capsule; 2, abdominal segment VIII; 3–4, urogomphus; 3, third-instar larva; 4, second-instar larva. Scale bars: 0.20 mm.

Table 1. Measurements and ratios for the second- and third-instar larvae of *Ereboporus naturoconservatus* (EREB) and *Haideoporus texanus* (HAID); l = length; w = width; ? = missing data; ** = not applicable.

Measure	EREB		HAID	
	Instar II (n = 1)	Instar III (n = 1)	Instar II (n = 1)	Instar III (n = 1)
HL (mm)	0.84	1.03	0.87	1.13
HW (mm)	0.48	0.67	0.66	0.88
FRL (mm)	0.60	0.76	0.68	0.94
OCW (mm)	0.25	?	0.44	0.44
HL/HW	1.77	1.53	1.31	1.28
HL/LAS	5.01	4.32	2.75	?
HW/OCW	3.40	?	1.81	2.02
A/HW	0.77	0.57	0.65	0.59
A3/A2	1.59	1.64	1.12	0.97
A4/A3	0.39	0.38	0.51	0.41
A3'/A4	1.00	0.90	0.74	0.86
MN (l/w)	4.73	4.74	4.12	4.18
A/MP	0.91	0.80	1.11	0.95
MP2/MP1	1.15	1.05	1.00	0.79
MP/LP	1.68	1.71	1.04	1.08
LP2/LP1	0.96	1.04	0.95	0.78
L1 (mm)	1.01	1.26	1.28	1.71
L3 (mm)	1.09	1.42	1.49	2.02
L3/HW	2.30	2.11	2.25	2.29
L3(PC/TA)	0.42	0.29	0.35	0.30
L3/L1	1.09	1.13	1.16	1.18
LAS (mm)	0.17	0.24	0.32	?
LAS/HW	0.35	0.35	0.48	?
U1 (mm)	0.37	0.49	0.63	?
U1 + U2' (mm)	0.52	**	0.872	?
U1 + U2 (mm)	0.53	0.53	0.916	?
U1/U2'	2.47	**	2.66	?
U1/LAS	2.21	2.04	2.00	?
U1/HW	0.78	0.72	0.96	?
U1 + U2'/LAS	3.10	**	2.75	?
U1 + U2'/HW	1.10	**	1.32	?
U1 + U2/LAS	3.13	2.21	2.89	?
U1 + U2/HW	1.11	0.78	1.38	?

nal line relatively short; occipital foramen small, broadly emarginate ventrally; posterior tentorial pits visible ventrally; FR elongate, with lateral margins strongly inflated with several lateral spine-like protuberances, abruptly constricting anteriorly to form a rounded narrow spatula. Antenna elongate, composed of four antennomeres, shorter than HW; A4 the shortest, A3 the longest, A1 and A2 subequal in length, A3 with a ventroapical spinula; A3' elongate. Mandible. Elongate, slender, distal half projected inwards and upwards, apex sharp; mandibular channel present. Maxilla. Cardo present, not fused to stipes; stipes short, broad; galea and lacinia absent; MP longer than antenna, composed of three palpomeres, MP3 the shortest, MP2 slightly longer than MP1. Labium. Prementum small, subtrapezoidal, somewhat broader than long, without lateral spinulae, anterior margin slightly indented medially; LP elon-

gate, composed of two palpomeres; LP1 about as long as LP2.

Thorax: Terga convex, pronotum slightly shorter than meso- and metanotum combined, meso- and metanotum subequal; protergite subovate, more developed than meso- and metatergite; sterna membranous; spiracles absent. Legs elongate, composed of six articles (*sensu* Lawrence 1991), L1 the shortest, L3 the longest; CO elongate, TR short, divided into two parts, FE, TI and TA slender, subcylindrical, PT with two short, robust, slightly curved claws; posterior claw shorter than anterior claw on L1 and L2, posterior claw slightly longer than anterior claw on L3; FE, TI and TA without spinulae along ventral margin.

Abdomen (Fig. 2): Eight-segmented; segments I–VI sclerotized dorsally, membranous ventrally; segment VII completely sclerotized, ring-like (difficult to assess due to the lightly sclerotized body); tergites I–VI narrow, transverse, rounded laterally, sagittal line not visible; spiracles absent on segments I–VII; LAS subconical, completely sclerotized, ring-like, siphon absent. Urogomphus (Fig. 3) long, composed of two urogomphomeres; U1 longer than LAS; U2 narrow, shorter than U1.

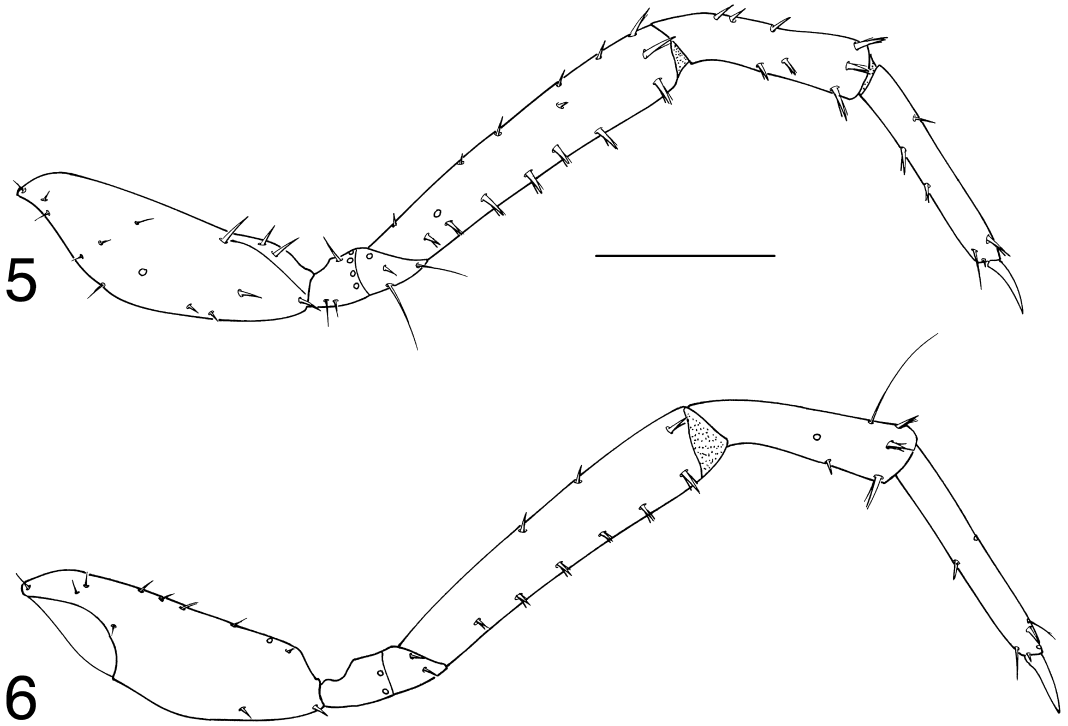
Chaetotaxy. Head capsule with numerous secondary setae; frontoclypeus with 34 spatulate lamellae clypeales: parietal with 11–12 short, spine-like, secondary setae on each lateroventral margin; MN with one spine-like, secondary seta on basoexternal margin; thoracic and abdominal sclerites I–VIII with several secondary setae, mainly on posterior half; legs lacking natatory setae; secondary leg setation detailed in Table 2. Primary chaetotaxy of second instar larva similar to that of generalized Hydroporinae larva (Alarie & Harper 1990, Alarie et al. 1990, Alarie 1991, Alarie & Michat 2007b): pore PAd absent; we were unable to locate either pore PAj or PAg; pore ANf absent; setae MX8, MX9 and MX10 absent; seta MX1 inserted distally on the stipes; seta TI7 short, spine-like; pore ABa absent; seta AB10 short and hair-like; we were unable to find pore ABd and setae AB7 and AB8; however, we could not establish if they are really absent owing to the absence of siphon; setae UR2, UR3 and UR4 inserted far from each other; setae UR5, UR6 and UR7 elongate; seta UR8 inserted subapically (Fig. 3).

Third-instar larva (n = 1) (Figs 3, 5–6)

Similar to second-instar except as follows:

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

Thorax: Legs (Figs 5–6). Number and position of secondary setae are shown in Table 2.



Figs 5, 6. *Ereboporus naturaconservatus*, metathoracic leg, third-instar larva. – 5, anterior surface; 6, posterior surface. Scale bar: 0.20 mm.

Abdomen: Urogomphus (Fig. 3). U1 with one secondary seta; U2 minute; seta UR8 inserted apically. We were unable to determine if the thoracic and abdominal spiracles are present owing to the bad condition of the specimen studied.

Haideoporus texanus Young & Longley

Figs 7–11

Diagnosis (third instar larva)

Body lightly sclerotized; stemmata absent (Fig. 7); frontoclypeus subtriangular anteriorly, slightly inflated laterally, lacking lateral processes, broadly rounded apically; HL/HW < 1.40; A3 and A2 subequal in length; maxillary palpus about as long as labial palpus; primary seta FR6 not distinctly developed; primary setae MX4 and TR2 absent; posterior margin of last abdominal segment extending into a short siphon; U1 less than 3 times as long as U2; primary setae UR2 and UR3 contiguously articulated, not contiguous to seta UR4; U1 lacking secondary setae.

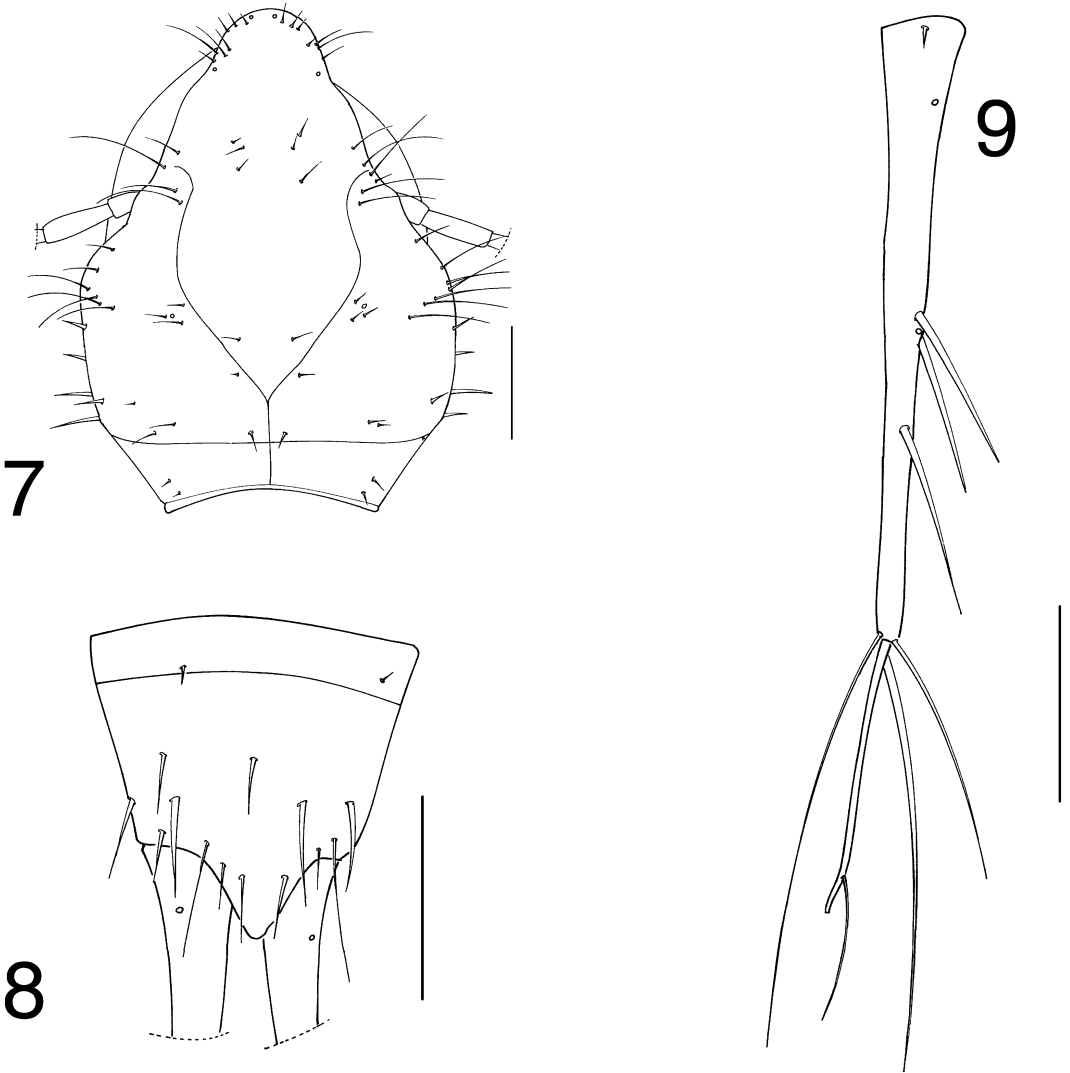
First-instar larva

No specimens were available for study.

Second-instar larva ($n = 1$) (Figs 7–9)

Color: Uniformly pale, unpigmented, distal half of mandible light brown. Body. Relatively soft, lightly sclerotized, subcylindrical, narrowing towards abdominal apex. Measurements and ratios that characterize the body shape are shown in Table 1.

Head: Head capsule (Fig. 7) longer than broad; maximum width at about mid-length, not constricted at level of occipital suture; ecdysial line visible, coronal line relatively short; occipital foramen broad, broadly emarginate ventrally; posterior tentorial pits visible ventrally; FR elongate, subtriangular anteriorly, broadly rounded apically, lateral margins slightly inflated, lateral process not visible dorsally; stemmata absent. Antenna elongate, composed of four antennomeres, shorter than HW; A4 the shortest subequal to A1 in length, A3 the longest, with a ventroapical spinula; A3' elongate. Mandible. Elongate, slender, distal half projected inwards and upwards, apex sharp; mandibular channel present. Maxilla. Cardo present, not fused to stipes; stipes short, broad; galea and lacinia absent; MP shorter than antenna, composed of three palpomeres, MP3 the shortest, MP1 as long as MP2. Labium. Prementum small, subtrapezoidal, somewhat broader than long, without lateral spinulae, anterior margin



Figs 7–9. *Haideoporus texanus*, second-instar larva, dorsal aspect. – 7, head capsule; 8, abdominal segment VIII; 9, urogomphus. Scale bar: 0.20 mm.

slightly indented medially; LP elongate, composed of two palpomeres; LP2 about as long as LP1.

Thorax: Terga convex, pronotum slightly shorter than meso- and metanotum combined, meso- and metanotum subequal; protergite subovate, more developed than meso- and metatergite; sterna membranous; spiracles absent. Legs. Long, composed of six articles (*sensu* Lawrence 1991), L1 the shortest, L3 the longest; CO elongate, TR short, divided into two parts, FE, TI and TA slender, subcylindrical, PT with two short, robust, slightly curved claws; posterior claw shorter than anterior claw on L1 and L2, posterior claw slightly longer than anterior claw on

L3; ventral marginal spinulae lacking, faintly developed on protarsus.

Abdomen (Fig. 8): Eight-segmented; segments I–VI sclerotized dorsally, membranous ventrally; segment VII completely sclerotized, ring-like (difficult to assess due to the lightly sclerotized body); tergites I–VI narrow, transverse, rounded laterally, sagittal line not visible; spiracles absent on segments I–VII; LAS subconical, completely sclerotized, ring-like, extended posteriorly into a short siphon. Urogomphus (Fig. 9) long, composed of two urogomphomeres; U1 longer than LAS; U2 narrow, shorter than U1.

Table 2. Number of secondary setae on the legs (both legs were considered) of second and third instars of *Ereboporus naturaconservatus* (EREB) and *Haideoporus texanus* (HAID); segments of legs: CO = coxa, FE = femur, TA = tarsus, TI = tibia, TR = trochanter; sensillar series: A = anterior, AD = anterodorsal, AV = anteroverventral, PD = posterodorsal, Pr = proximal, PV = posteroventral; ? = missing data.

Segment	Sensillar series	Second-Instar		Third-Instar	
		EREB (n = 2)	HAID (n = 2)	EREB (n = 2)	HAID (n = 2)
ProCO	D	2	2	?	5-7
	A	1	0	?	1-2
	V	0	1	?	2-3
	Total	3	3	?	8-12
ProTR	Pr	1	1	2	1
ProFE	AD	3	1	4	3-5
	AV	1	4-6	6	7-8
	PD	0	0	3-4	0-1
	PV	4	3	4-5	6-8
Total	8	7-10	17-19	19	
ProTI	AD	0	0	0-1	0-1
	AV	0	0	0-1	2
	PD	0	1	1-2	0-1
	PV	0-1	2	2	1-2
Total	0-1	3	4	4-5	
ProTA	AD	0	1	0	1-2
	AV	0	2	0	2
	PD	0	0	1	0
	PV	2	3	3	3-4
Total	2	6	4	6-8	
MesoCO	D	1	2	3	5-6
	A	0	0	1	3-5
	V	0	0	0	1-4
	Total	1	2	4	11-13
MesoTR	Pr	1	1	1-2	1
MesoFE	AD	1	2-3	4-6	5-6
	AV	1	4-5	3-5	6-10
	PD	0	0	2-3	0
	PV	3	3-4	6	9
Total	5	10-11	17-18	21-24	
MesoTI	AD	1	1	0-1	1
	AV	1	4	1-2	3-5
	PD	0	0	3	0-2
	PV	0	0	1	2
Total	2	5	6	6-10	
MesoTA	AD	0	2	2	0
	AV	1	5	2	7
	PD	0	0	0	2-3
	PV	0	0	0-1	0
Total	1	7	4-5	9-10	
MetaCO	D	1	2	4	4
	A	0	0	1	3
	V	0	0	1-3	1
	Total	1	2	6-8	8
MetaTR	Pr	1	1	1-2	1-2
MetaFE	AD	2	2-4	6	7
	AV	1	5	3	9-10
	PD	0	0	2	0
	PV	2	3-4	5	7-8
Total	5	11-12	16	24	
MetaTI	AD	1	1-2	1-3	2
	AV	1	3	2	4-5
	PD	0	0	2	1-2

Table 2. (Continued.)

Segment	Sensillar series	Second-Instar		Third-Instar	
		EREB (n = 2)	HAID (n = 2)	EREB (n = 2)	HAID (n = 2)
MetaTA	PV	0	0	1	1-2
	Total	2	4-5	6	9-10
	AD	0	2-3	1	0
	AV	2	4-5	2	5-7
	PD	0	0	0	3-5
	PV	0	0	1	0
Total	2	7	4	8-10	

Chaetotaxy: Head capsule with numerous secondary setae; frontoclypeus with 19 spatulate lamellae clypeales; parietal with 4-5 short, spine-like, secondary setae on each lateroventral margin; MN with one hair-like, secondary seta on basoexternal margin; thoracic and abdominal sclerites I-VIII with several secondary setae, mainly on posterior half; legs lacking natatory setae; secondary leg setation detailed in Table 2; LAS with several spine-like secondary setae. Primary chaetotaxy of second instar larva similar to that of generalized Hydroporinae larva (Alarie & Harper 1990, Alarie et al. 1990, Alarie 1991, Alarie & Michat 2007b), except for the following features: pores PAD, PAe and PAj absent; we were unable to determine if pore PAg is present; pore ANf absent; setae MX4, MX8, MX9 and MX10 absent; seta MX1 inserted on the cardo; seta TR2 absent; seta TI7 short, spine-like; pore ABa absent; seta AB10 short and spine-like; we were unable to find pore ABD and setae AB7 and AB8; however, we could not establish if they are really absent on the siphon; setae UR2 and UR3 contiguously articulated apart from seta UR4; setae UR5, UR6 and UR7 elongate; seta UR8 inserted subapically (Fig. 9).

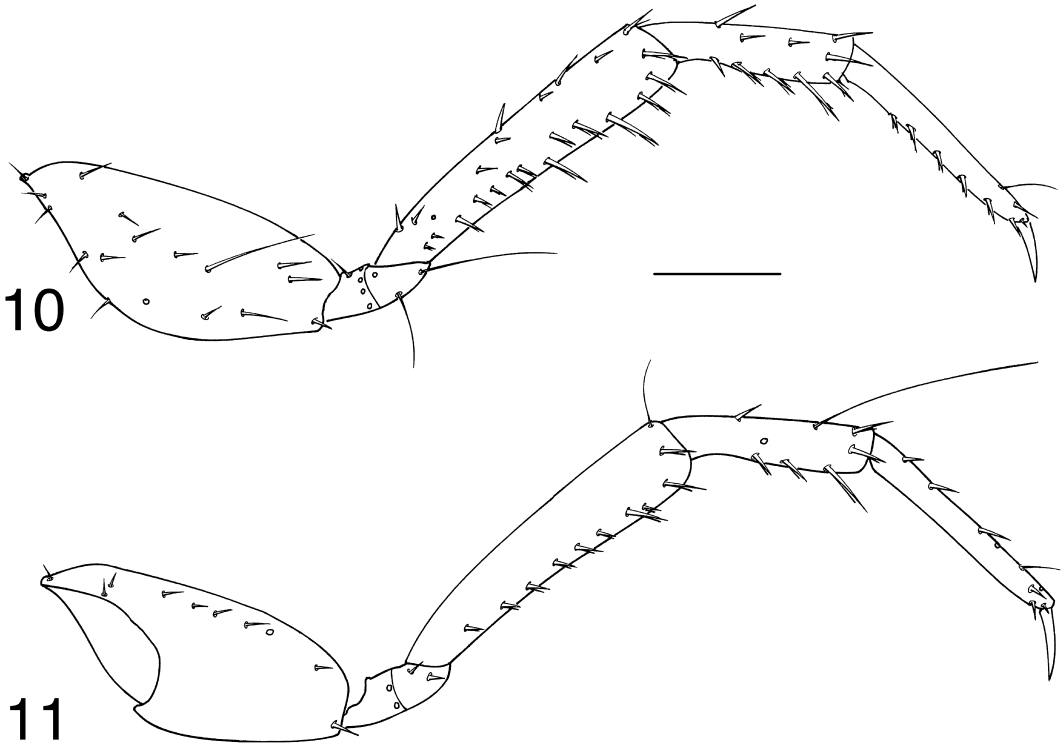
Third-instar larva (n = 1) (Figs 10-11)

Similar to second-instar except as follows:

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

Head: A2 and A3 the longest, subequal in length. MP longer than antenna, MP1 longer than MP2. LP1 longer than LP2.

Thorax: Legs (Figs 10-11). Protarsus lacking marginal spinulae. Number and position of secondary setae as in Table 2. We were unable to determine if the thoracic and abdominal spiracles are present owing to the bad condition of the specimen studied. Chaetotaxy: Head capsule with 35 spatulate lamellae clypeales; parietal with 12-15 short, spine-like, secondary setae on each lateroventral margin.



Figs 10, 11. *Haideoporus texanus*, metathoracic leg, third-instar larva. – 10, anterior surface; 11, posterior surface. Scale bar: 0.20 mm.

Discussion

Beetle larvae found living underground generally display characteristic attributes that are likely to be adaptive to a subterranean existence. Among these are reduced pigmentation and lesser sclerotization, and reduction or loss of eyes, all of which are observed in *Haideoporus texanus* and *Ereboporus naturaconservatus*. As shown in this study, both species share the presence of a nasale (Figs 1 and 7) and the absence of the primary pores MXd, LAc, which are considered as synapomorphies for members of the subfamily Hydroporinae (Alarie & Michat 2007a, Michat et al. 2007).

Haideoporus texanus and *Ereboporus naturaconservatus* have been traditionally included within the tribe Hydroporini (Hydroporinae) (Nilsson 2001), which has since been postulated to be polyphyletic based on larval morphology (Alarie & Michat 2007a, Michat et al. 2007). Within the Hydroporini *sensu lato* adult morphology and molecular data suggest that *Haideoporus* could be related phylogenetically to *Neoporus* Guignot, 1931 and *Heterosternuta* Strand, 1935, while *Ereboporus* was deemed to be the only North American member of the otherwise Mediter-

ranean *Graptodytes*-group of genera (Miller et al. 2012).

Study of larval morphology provides another line of evidence to test phylogenetic hypotheses. As different expressions of the same genotype, larval characters help to complement adult characters, which have been traditionally the primary basis for classification. Recent studies have demonstrated the importance of chaetotaxy in elucidating taxonomic and phylogenetic relationships among larval Hydroporinae (e.g., Alarie & Michat 2007a, Michat et al. 2007). The relative phylogenetic position of *Haideoporus texanus* and *Ereboporus naturaconservatus* within the Hydroporinae, however, could not be tested in this study due to absence of first instar specimens, the character of which represents the bulk of the characters used in the context of previous studies of Hydroporinae larval morphology.

Despite the common convergent characteristics associated with hypogaeic living no synapomorphies were found that could relate *Haideoporus texanus* and *Ereboporus naturaconservatus*, which reinforces the hypotheses formulated by Miller et al. (2012) that these species evolved independently. Indeed both species are deemed to have evolved independently as

many as ten character states: (1) apex of the nasale: spatulate vs not spatulate; (2) seta FR6: not distinctly developed vs strongly developed; (3) seta AN1: inserted medially or distally vs proximally; (4) seta MX4: present vs absent; (5) seta TR2: present vs absent; (6) last abdominal segment: truncate vs moderately elongate; (7) urogomphomere 1, 3 times vs 10 times longer than urogomphomere 2; (8) secondary setae on urogomphus: present vs absent; (9) setae UR2 and UR3: not inserted contiguous vs contiguous; and (10) the frontoclypeolabrum: short vs elongate. In terms of morphological adaptation, *Erebo-
porus naturaconservatus* larvae stand as unique among the Hydroporinae as its larvae evolved a truncate last abdominal segment (Fig. 2) and a very elongate urogomphomere 1 (more than 10 times longer than urogomphomere 2). Additional collections and descriptions of subterranean hydroporine larvae may shed light on the phylogenetic relationships of these unique beetles.

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References

- Alarie, Y., 1991. Primary setae and pores on the cephalic capsule and head appendages of larval Hydroporinae (Coleoptera: Dytiscidae). – *Canadian Journal of Zoology* 69: 2255–2265.
- Alarie, Y. & P.P. Harper, 1990. Primary setae and pores on the last abdominal segment and the urogomphi of larval Hydroporinae (Coleoptera: Adepaga: Dytiscidae), with notes on other dytiscid larvae. – *Canadian Journal of Zoology* 68: 368–374.
- Alarie, Y., P.P. Harper & A. Maire, 1990. Primary setae and pores on legs of larvae of Nearctic Hydroporinae (Coleoptera: Dytiscidae). – *Questiones Entomologicae* 26: 199–210.
- Alarie, Y. & M.C. Michat, 2007a. Phylogenetic analysis of Hydroporinae (Coleoptera: Dytiscidae) based on larval morphology, with description of first-instar of *Laccornellus lugubris*. – *Annals of the Entomological Society of America* 100: 655–665.
- Alarie, Y. & M.C. Michat, 2007b. Primary setae and pores on the maxilla of larvae of the subfamily Hydroporinae (Coleoptera: Adepaga: Dytiscidae): ground plan pattern reconsidered. – *The Coleopterists Bulletin* 61: 310–317.
- Alarie, Y., M.C. Michat & K.B. Miller, 2011. Notation of primary setae and pores on larvae of Dytiscinae (Coleoptera: Dytiscinae), with phylogenetic considerations. – *Zootaxa* 3087: 1–55.
- Alarie, Y., M.C. Michat & C.H.S. Watts, 2009a. Larval morphology of *Paroster* Sharp, 1882 (Coleoptera: Dytiscidae: Hydroporinae): reinforcement of the hypothesis of monophyletic origin and discussion of phenotypic accommodation to a hypogaic environment. – *Zootaxa* 2274: 1–44.
- Alarie, Y., M.C. Michat, A.N. Nilsson, M. Archangelsky & L. Hendrich, 2009b. Larval morphology of *Rhantus* Dejean, 1833 (Coleoptera: Dytiscidae: Colymbetinae): descriptions of 22 species and phylogenetic considerations. – *Zootaxa* 2317: 1–102.
- Alarie, Y. & G. Wewalka, 2001. Description of the mature larva of *Glareadessus stocki* Wewalka and Biström (Coleoptera: Dytiscidae), a stygobiontic Bidessini from the Persian Gulf region. – *The Coleopterists Bulletin* 55: 144–151.
- Castro, A. & J.A. Delgado, 2001. *Hydrochus aljibensis* sp. n. una nueva especie del sur del la Peninsula Ibérica (Coleoptera: Hydrochidae). – *Aquatic Insects* 23: 25–28.
- Lawrence, J.F., 1991. Order Coleoptera. Introduction. – In: F.W. Stehr (ed.), *Immature Insects*, Vol. 2: 144–184. Kendall/Hunt, Dubuque, Iowa.
- Leys, R. & C.H.S. Watts, 2008. Systematics and evolution of the Australian hypogaic hydroporine diving beetles (Dytiscidae: Coleoptera). – *Invertebrate Systematics* 22: 1–9.
- Longley, G. & P.J. Spangler, 1977. The larva of a new subterranean water beetle, *Haideoporus texanus* (Coleoptera: Dytiscidae: Hydroporinae). – *Proceedings of the Biological Society of Washington* 90: 532–535.
- Michat, M.C., Y. Alarie, P.L.M. Torres & Y.S. Megna, 2007. Larval morphology of the diving beetle *Celina* and the phylogeny of ancestral hydroporines (Coleoptera: Dytiscidae: Hydroporinae). – *Invertebrate Systematics* 21: 239–254.
- Michat, M.C. & Y. Alarie, 2008. Morphology and chaetotaxy of larval *Hypodessus cruciatus* (Régimbart) (Coleoptera: Dytiscidae: Hydroporinae), and analysis of the phylogenetic relationships of the Bidessini based on larval chaetotaxy. – *Studies on Neotropical Fauna and Environment* 43: 135–146.
- Michat, M.C., Y. Alarie & C.H.S. Watts, 2010. Descriptions of the first instar larva of the hypogaic species *Neobidessodes limestoneensis* (Watts & Humphreys) and of the third instar larva of *Hydroglyphus balkei* Hendrich (Coleoptera: Dytiscidae: Bidessini) with phylogenetic considerations. – *Zootaxa* 2658: 38–50.
- Michat, M.C., Y. Alarie & C.H.S. Watts, 2012. Phylogenetic relationships and comparative larval morphology of epigeal and stygobitic species of *Limbodessus* Guignot (Coleoptera: Dytiscidae: Bidessini). – *Zootaxa* (in press).

- Michat, M.C. & P.L.M. Torres, 2005. Larval morphology of *Macrovatellus haagi* (Wehncke) and phylogeny of Hydroporinae (Coleoptera: Dytiscidae). – *Insect Systematics & Evolution* 36: 199–217.
- Miller, K.B., J.R. Gibson & Y. Alarie, 2009. North American stygobiontic diving beetles (Coleoptera: Dytiscidae: Hydroporinae) with description of *Ereboporus naturaconservatus* Miller, Gibson and Alarie, new genus and species, from Texas, U.S.A. – *The Coleopterists Bulletin* 63: 191–202.
- Nilsson, A.N., 2001. Dytiscidae (Coleoptera). – In: *World Catalogue of Insects* 3: 1–395. Apollo Books, Stenstrup, Denmark.
- Ordish, R.G., 1976. Two new genera and species of subterranean water beetles from New Zealand (Coleoptera: Dytiscidae). – *New Zealand Journal of Zoology* 3: 1–10.
- Porter, M.L., 2007. Subterranean biogeography: what have we learned from molecular techniques. – *Journal of Caves and Karst Studies* 69: 179–186.
- Richoux, P., 1980. Les larves du Coléoptère Dytiscide phréatobie: *Siettitia avenionensis* Guignot. – *Mémoire de Biospéléologie* 7: 195–200.
- Uéno, S.-I., 1957. Blind aquatic beetles of Japan, with some accounts of the fauna of Japanese subterranean waters. – *Archiv für Hydrobiologie* 53: 250–296.
- Watts, C.H.S. & W.F. Humphreys, 2006. Twenty-six new Dytiscidae (Coleoptera) of the genera *Limbodessus* Guignot and *Nirripiriti* Watts and Humphreys, from underground waters in Australia. – *Transactions of the Royal Society of South Australia* 130: 123–185.
- Watts, C.H.S., P.J. Hancock & R. Leys, 2007. A stygobitic *Carabhydrus* Watts (Dytiscidae, Coleoptera) from the Hunter Valley in New South Wales, Australia. – *Australian Journal of Entomology* 46: 56–59.

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