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Larval morphology of the Madagascan endemic diving beetle genus *Hovahydrus* Biström, 1982 (Coleoptera: Dytiscidae) and phylogenetic comparison with other known Hyphydrini

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Abstract

We describe for the first time the instar III larva of the diving beetle genus *Hovahydrus* Biström, 1982, based on *H. praetextus* (Guignot, 1951) and a new species yet to be described (identified here as *Hovahydrus* sp. near *H. minutissimus* (Régimbart, 1903)). We include detailed morphometric and chaetotaxic analyses of the cephalic capsule, head appendages, legs, last abdominal segment and urogomphi in order to discover useful characters for distinguishing *Hovahydrus* larvae from those of other known Hyphydrini (Coleoptera: Dytiscidae, Hydroporinae). A provisional parsimony analysis based on larval characteristics of 11 Hyphydrini species in eight genera was conducted using the program TNT. Larval morphology supports a close relationship between *Hovahydrus*, *Hyphydrus* Illiger, 1802, and the endemic South Africa genera *Andex* Sharp, 1882, *Coelhydrus* Sharp, 1882, *Darwinhydrus* Sharp, 1882 and *Primospes* Sharp, 1882.

Key words: Coleoptera, Dytiscidae, Hydroporinae, Madagascar, larvae, morphometry, chaetotaxy, phylogeny

Introduction

Hovahydrus Biström, 1982 is a dytiscid genus included in the tribe Hyphydrini, subfamily Hydroporinae, which is comprised of tiny (1.9–3.1 mm) and fairly globular diving beetles found largely in highland forest streams of Madagascar (Miller & Bergsten 2016). Although only including four species at this time (Nilsson & Hájek 2022), several new species are known and are in the process of being described (Bergsten, unpublished). With regards to their phylogenetic relationships, the four species actually included in this genus are postulated to share a sister group relationship with the endemic South African monotypic genera *Andex* Sharp, 1882, *Coelhydrus* Sharp, 1882, *Darwinhydrus* Sharp, 1882, *Hydropeplus*, Sharp 1882, and *Primospes* Sharp, 1882 based on molecular data (Ribera & Balke 2007).

Larval morphology of the Hyphydrini has been the subject of several studies recently. Of the 14 genera currently recognized in the tribe (Nilsson & Hájek 2022), seven have described larvae in the context of modern works on aquatic Adephaga larval morphology, which incorporate detailed morphometric and chaetotaxic analyses (Alarie & Michat 2014): *Andex* (Alarie & Challet 2006a), *Coelhydrus* (Alarie *et al*. 2017), *Darwinhydrus* (Alarie *et al*. 2017), *Desmopachria* Babington, 1841 (Alarie *et al*. 1997; Michat & Archangelsky 2007), *Hyphydrus* Illiger, 1802 (Alarie *et al*. 1997; Alarie & Watts 2005), *Microdytes* J. Balfour-Browne, 1946 (Alarie *et al*. 1997), and *Primospes* (Alarie & Challet 2006b).

This article is meant to continue the analysis of Hyphydrini larval morphology with an emphasis on the endemic Madagascar genus *Hovahydrus*. This paper therefore aims to describe and illustrate for the first time the instar III larva of *H. praetextus* (Guignot, 1951) and of a new *Hovahydrus* species yet to be described (here identified as

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Hovahydrus sp. near *H. minutissimus* (Régimbart, 1903)) and to discuss the phylogenetic relationships of *Hovahydrus* with other Hyphydrini genera whose larvae have been described in detail. The fact that the larval morphology of four of the five genera of Hyphydrini endemic to South Africa is known (Alarie & Challet 2006a, 2006b; Alarie *et al*. 2017) gives a most interesting perspective to this article since it makes it possible to test the hypothesis of a close phylogenetic relationship of *Hovahydrus* with these species under the angle of larval morphology.

Material and methods

Larvae were collected at two localities in Marojejy National Park, northeast Madagascar. A tea strainer and a D-frame water net with mesh-size 0.5 mm were used. Larvae were preserved together with adults in 95% ethanol in the field. Matching with adults was by syntopic occurrence of adults and larvae at the same time in small limited localities with few other dytiscid species, the *Hovahydrus* species being the single representative of tribe Hyphydrini present.

Larvae were disarticulated and mounted on standard glass slides in Hoyer's medium. Microscopic examination at magnifications of 80–800× 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). The specimens included in this study are deposited in the larval collection of Y. Alarie (School of Natural Sciences, Laurentian University, Canada).

In the morphometric analysis, the following measurements were taken (with abbreviations shown in parentheses): 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 of occipital foramen); coronal line length (COL); length of mandible (MNL) (measured from laterobasal angle to apex); width of mandible (MNW) (maximum width measured at base). Lengths of antenna (A), maxillary (MP) and labial (LP) palpi were obtained by adding the lengths of the individual segments; each segment is denoted by the corresponding letter(s) followed by a number (e.g., A1, first antennomere). A3' is used as an abbreviation for the apical lateroventral process of the third antennomere. Length of leg (L), including the longest claw (CL), was obtained by adding the lengths of the individual segments; each leg is denoted by the letter L followed by a number (e.g., L1, prothoracic leg). The length of trochanter includes only the proximal portion, the length of distal portion is included in the femoral length. Dorsal length of last abdominal segment (LAS) (measured along midline from anterior to posterior margin). Length of urogomphus (U) was derived for the first urogomphomere (U1) only due to the breakage of urogomphomere 2 (U2) among all the specimens studied. These measurements were used to calculate several ratios that characterize body shape.

In the chaetotaxic analysis, although represented by instar III larvae only, primary sensilla were tentatively identified by comparison with the Hyphydrini ground plan wherever possible (Alarie *et al*. 1997; Alarie & Watts 2005; Alarie & Challet 2006a, 2006b; Alarie *et al*. 2017; Michat & Archangelsky 2007). In these cases, homologies were recognized using the criterion of similarity of position (Wiley 1981). Sensilla were coded by two capital letters, in most cases corresponding to the first two letters of the name of the structure on which they are located, and a number (setae) or a lower-case letter (pores). The following abbreviations were used: 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 located at the apices of the antenna and 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.

The habitus photograph was taken using a Dino-Lite Edge digital microscope.

Phylogenetic analysis

To examine the phylogenetic signal of the larval characters of *Hovahydrus* and to test its relationships with other Hyphydrini, a cladistic analysis of 11 species of Hyphydrini with sufficiently detailed larval descriptions (*Hyphydrus* (two species), *Microdytes* (one species), *Desmopachria* (two species), *Andex* (one species), *Coelhydrus*

(one species), *Darwinhydrus* (one species) and *Primospes* (one species) was conducted. *Pachydrus* Sharp, 1882 (tribe Pachydrini) and *Laccornis* Gozis, 1914 (tribe Laccornini) were used as out-groups. The former sometimes has been suggested to be related phylogenetically to the Hyphydrini (Alarie *et al.* 1997; Michat & Torres 2008), and the latter is generally recognized as a basal lineage within the subfamily Hydroporinae based on adults (Roughley & Wolfe 1987; Miller *et al*. 2006), larvae (Alarie & Michat 2007), and molecules (Miller & Bergsten 2014). All characters were treated as equally weighted. Multistate characters were treated as non-additive. An exact solution algorithm (implicit enumeration) was implemented to find the most parsimonious trees. 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)' 1,000 replicates.

Results

General morphological characteristics of Hyphydrini larvae (based on Alarie *et al.* 2017)

Body fusiform; frontoclypeus elongated, narrow or broad apically; gular sutures fused (visible from instar II), so epicranial plates meet at ventral midline; cardo fused to stipes; primary seta MX1 inserted on stipes; prementum longer than broad, lacking marginal spinulae laterally; without primary pores PAj, ANh, FEa, and ABa, and primary seta TR2; legs of instars II and III with natatory setae; abdominal segments VI–VII sclerotized ventrally; urogomphomere 1 of instars II and III with secondary setae; primary seta UR8 proximally articulated on urogomphomere 2 (Uro2'/Uro2 < 0.50).

General notes on the instar III larvae of *Hovahydrus* Biström, 1982

(Figs 1–16)

Diagnosis. The instar III larvae of *Hovahydrus* can be distinguished from those of other genera of Hyphydrini that have been well studied by the following combination of characters: frontoclypeus with lateral processes visible dorsally (Figs 2, 13); HL = 0.71–1.13 mm; ratio HL/HW = 1.21–1.32; ratio MP/LP = 1.74; ratio A4/A3 < 0.30; ratio LP2/LP1 =1.10–1.50; metathoracic leg < 3.50 times HW; ratio LAS/HW > 0.90; primary setae LA3, LA4, and LA5 articulated distally on prementum; dorsal meso- and metafemoral secondary setae present; siphon elongate, lightly constricted at point of insertion of urogomphi, with a variable number of secondary spine-like setae on ventral surface.

Body (Fig. 1): Fusiform; measurements and ratios that characterize body shape are shown in Table 1.

Head (Figs 2–8, 13): Cephalic capsule either sagittate or pear-shaped, tapering posteriorly, lacking a neck constriction, with reticulation dorsolaterally and ventrally on posterior half; ecdysial suture well-marked, coronal line short; occipital foramen broadly emarginate ventrally; epicranial plates meeting ventrally, posterior tentorial pits visible ventrally on central region; frontoclypeus elongate, bluntly rounded apically, not or slightly spatulate, ventrally with small spinulae on distal region, lateral processes well visible dorsally, margined with a variable number of bluntly rounded notches; six rounded dorsolateral stemmata, at each side. Antenna elongate, shorter than HW; composed of 4 antennomeres, A3 and A2 longest, A1 and A4 subequal in length; A3' elongate, about as long as A4, A3 with a ventroapical spinula. Mandible prominent, broad basally, distal half projected inwards and upwards, apex sharp; mandibular channel present. Maxilla with cardo fused to short, broad stipes; galea absent; palpus elongate, slightly shorter than antenna, composed of three palpomeres, MP1 and MP2 longest, subequal, MP3 shortest. Labium with prementum elongate, subrectangular, much longer than broad, lateral margins curved, lacking spinulae; palpus elongate, composed of two palpomeres, LP2 subfusiform, slightly longer than LP1.

Thorax (Figs 1, 9–10, 15–16): Terga convex, pronotum slightly shorter than meso- and metanota combined, meso- and metanota subequal; protergite subrectangular to subovate, more developed than meso- and metatergites; meso- and metatergites transverse, with anterotransverse carina; sagittal line well-visible on three tergites; sterna membranous; spiracles present on mesothorax. Legs (Figs 9–10, 15–16): long, composed of 6 articles; 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 L3; ventral surface of TI and TA lacking elongate spinulae.

Abdomen (Figs 11–12, 14): Eight-segmented; segment I sclerotized dorsally, membranous ventrally; segments II–VIII sclerotized dorsally and ventrally, all tergites lacking sagittal line, with anterotransverse carina; spiracles present lateroventrally on segments I–VII; segment VIII longest and narrowest, projecting backwards into a long subconical siphon, lightly compressed at point of insertion of urogomphi. Urogomphus very long, composed of 2 urogomphomeres; U1 much shorter than segment VIII; U2 narrower, setiform (length of U2 could not be measured as the structure was broken on every specimen studied).

Chaetotaxy (Figs 2–14, 15–16): Head capsule with numerous secondary setae; lateroventral margin of PA with several secondary spine-like setae (Figs 2–3, 13); anteroventral margin of nasale with half circle of about 30 spatulate lamellae clypeales of different lengths, directed downwards (Fig. 3); AN, MX, and LA lacking secondary setae (Figs 4–8); 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 detailed in Table 2 and Figs 9–10, 15–16; siphon with a variable number of secondary setae on ventral surface (Fig. 12); urogomphomere 1 with secondary setae (Figs 11, 14).

Notes: *Hovahydrus* is a lotic genus whose members inhabit clearwater forest streams and alpine streams and associated side-pools in Madagascar. They are most commonly found in streams with a covering forest canopy, especially in pristine forests. We have never found *Hovahydrus* species in degraded streams in an open agricultural landscape. Adults are often abundant, especially aggregating in backwaters to small chutes in the stream. As to the phenology, there are no studies of the lifecycle of any *Hovahydrus* species, but we hypothesize that larval development takes place during the rainy season based on the current findings of larvae in February.

TABLE 1. Measurements and ratios for the instar III of *Hovahydrus* sp. near *H. minutissimus* (Régimbart, 1903) (HNMI) and *H. praetextus* (Guignot 1951) (HPRA); **, missing data.

Measure	HNMI (n = 4)	HPRA (n = 1)	Measure	HNMI (n = 4)	HPRA (n = 1)
HL (mm)	0.71–0.76	1.13	MP2/MP3	3.49–3.71	**
HW (mm)	0.57	0.93	MP/LP	1.74	**
FRL (mm)	0.53–0.56	0.85	LP2/LP1	1.38–1.48	1.19
OCW (mm)	0.40–0.41	0.56	L3 (mm)	1.73–1.82	2.59
HL/HW	1.28–1.32	1.21	L3/L1	1.27–1.31	1.29
HW/OCW	1.41–1.45	1.65	L3/L2	1.15–1.18	1.15
COL/HL	0.25–0.26	0.25	L3/HW	3.01–3.17	2.78
FRL/HL	0.74–0.75	0.75	L3 (CO/FE)	1.11–1.21	1.02
A/HW	0.77–0.78	0.74	L3 (TI/FE)	0.69–0.71	0.74
A3/A1	2.93–3.80	3.18	L3 (TA/FE)	0.70–0.72	0.78
A3/A2	1.13–1.31	0.98	L3 (CL/TA)	0.36–0.39	0.27
A4/A3	0.30–0.31	0.26	LAS (mm)	0.58–0.63	0.99
A3'/A4	0.85–1.06	0.83	LAS/HW	1.02–1.11	1.06
MNL/MNW	3.06–3.40	3.08	U1 (mm)	0.31–0.36	0.65
MNL/HL	0.50–0.55	0.53	U1/LAS	0.53–0.58	0.66
A/MP	1.07–1.14	**	U1/HW	0.54–0.62	0.70
MP2/MP1	1.06–1.09	**			

TABLE 2. Number and position of secondary setae on the legs of larvae of *Hovahydrus* sp. near *H. minutissimus* (Régimbart, 1903) (HNMI) and *H. praetextus* (Guignot 1951) (HPRA). Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively. A = anterior, AD = anterodorsal, AV = anteroventral, Di = distal, NS = natatory setae, PD = posterodorsal, PV = posteroventral, Pr = proximal, V = ventral, Total = total number of secondary setae on the segment (excluding primary setae).

Segment	Position	HNMI (n = 4)	HPRA (n = 1)*
Coxa	A	2–3 / 3–5/ 5–6	4 / 5 / 5
	PD	6–8 / 5–8/ 7–9	7–8 / 4 / 7
	V	7–8 / 7–9 / 9–10	7 / 10 / 10
	Total	15–18 / 17–21 / 21–24	18–19 / 24 / 23
Trochanter	Pr	1 / 1 / 1	1 / 1 / 1
Femur	AD	6–7 / 6–8 / 8–10	7–8 / 9–10 / 9
	AV	5–6 / 5–6 / 5–7	3–4 / 5–7 / 7
	PD (NS)	10–11 / 11–14 / 5–7	15–17 / 14–15 / 12
	PV	3–4 / 4–5 / 7–9	7 / 8–11 / 13
	Total	24–28 / 26–33 / 28–31	35–37 / 39–40 / 41
Tibia	AD	1–2 / 3 / 3–6	4 / 6 / 13
	AV	1–2 / 3–4 / 3	3–4 / 5–7 / 5
	PD (NS)	11–12 / 12–15 / 14–17	11–13 / 16–19 / 21
	PV	3–4 / 3–4 / 4	5–6 / 6–7 / 9
	Total	16–19 / 22–25 / 25–30	24–26 / 33–39 / 48
Tarsus	AD	1–2 / 1 / 2–3	2–3 / 3 / 7
	AV	1–2 / 1–3 / 1–2	1–3 / 2 / 3
	PD (NS)	6–7 / 9–11 / 13–14	9 / 14–15 / 19
	PV	2–4 / 3–5 / 4–5	4–5 / 7 / 11
	Total	11–13 / 16–18 / 20–22	17–19 / 26–27 / 40

*,both legs considered

Hovahydrus sp. near *H. minutissimus* (Régimbart, 1903)

Source of material. The four instar III larvae studied were associated with adults collected at the following locality: Madagascar: Antsiranana: Sava Marojejy National Park: mid-high altitude rainforest: watersource stream to camp III, 100 m from camp, MAD18-34. 14.4373S, 49.7428E, 1330 m, 11.II.2018. Leg J. Bergsten & T. Ranarilalatiana.

Diagnosis (instar III). The instar III larvae of *Hovahydrus* sp. can easily be distinguished from those of *H. praetextus* by the following combination of characters: smaller size, HL = 0.71–0.76 mm; head capsule sagittate, frontoclypeus broad, subquadrate apically (Fig. 2); parietale with a reduced number of temporal spines in dorsal view (Fig. 2); metathoracic leg elongate, > 3.00 times HW; femora, tibiae and tarsi with a lesser number of secondary setae (Figs 9–10; Table 2); abdominal segment VIII distinctly constricted at point of insertion of urogomphi (Fig. 11).

Description, instar III (Figs 1–12)

Color (Fig. 1): Head capsule creamy white; head appendages creamy white except mandible light brown (somewhat darker on distal fourth); thoracic and abdominal sclerites I–III and VIII dark brown (although abdominal segment III lightly paler); abdominal sclerites IV–VII creamy white; legs creamy white except coxae, dark brown; urogomphus dark brown.

Body: Measurements and ratios aimed to characterize body shape are shown in Table 1.

Head (Figs 2–8): HL = 0.71–0.76 mm; head capsule sagittate; anterior margin of frontoclypeus subquadrate and lightly convex apically; HW/OCW = 1.41–1.45.

Thorax (Figs 9–10): L3 = 1.73–1.82 mm; L3/HW = 3.01–3.17.

Abdomen (Figs 11–12): LAS = 0.58–0.63 mm; LAS distinctly constricted at point of insertion of urogomphi. Urogomphus: U1 = 0.31–0.36 mm; U1/HW = 0.54–0.62.

Chaetotaxy: Position and number of secondary setae on legs are shown in Table 2 and Figs 9–10.

Notes: Larvae were found in a side-pool associated to a small clearwater forest stream in medium-high altitude rainforest (1330m) (Figure 17). The lentic side-pool was filled with rocks and dead leaves. The larvae were observed foraging around after patient observations of the pool and could be collected with a small tea-sieve. We also collected one larva from a backwater in the lotic section of the same stream together with many adults with a D-frame water-net. The side-pool was co-inhabited by *Laccophilus alluaudi* species group and Madagascan endemic *Madaglymbus* sp. adults.

Hovahydrus praetextus (Guignot, 1951)

(Figs 13–16)

Source of material. The only instar III larva studied was associated with adults collected at the following locality: Madagascar: Antsiranana: Sava Marojejy National Park: alpine, above treeline: small clearwater stream with knee-deep pools, below summit: MAD18-31. 14.4506S, 49.7318E, 2060 m, 10.II.2018. Leg J. Bergsten & T. Ranarilalatiana.

Diagnosis (instar III). The instar III larvae of *Hovahydrus praetextus* can easily be distinguished from those of *Hovahydrus* sp. by the following combination of characters: larger size, HL = 1.13 mm; head capsule pear-shaped, frontoclypeus narrower, rounded apically (Fig. 13); parietale with a large number of temporal spines in dorsal view (Fig. 13); metathoracic leg shorter, < 2.90 times HW; femora, tibiae and tarsi with a larger number of secondary setae (Figs 15–16; Table 2); abdominal segment VIII lightly constricted at point of insertion of urogomphi (Fig. 14).

Description, instar III (Figs 13–16)

Color: Head capsule yellow, with cloudy pale brown maculae mesally; head appendages yellow except mandible light brown (somewhat darker on distal fourth); prothoracic sclerite yellow with a dark brown macula mesally; meso- and metathoracic sclerites dark brown; abdominal sclerites I–III dark brown gradually yellow laterally; abdominal segments IV–VIII yellow; legs creamy white except coxae, dark brown; urogomphus creamy white.

Body: Measurements and ratios aimed to characterize body shape are shown in Table 1.

Head (Fig. 13): HL = 1.13 mm; head capsule pear-shaped; anterior margin of frontoclypeus rounded and convex apically; HW/OCW = 1.65.

Thorax (Figs 15–16): L3 = 2.59 mm; L3/HW = 2.78.

Abdomen (Fig. 14): LAS = 0.99 mm; LAS lightly constricted at point of insertion of urogomphi. Urogomphus: U1 = 0.65 mm; U1/HW = 0.70.

Chaetotaxy: Position and number of secondary setae on legs are shown in Table 2.

Notes: Two larvae (one instar II and one instar III) were found together with adults in a clearwater alpine stream at high altitude (2060m) above the treeline in Marojejy National Park (Figure 18). The second-stage larva was not the subject of our study because of its poor preservation condition. The vegetation here is a unique and original alpine bush vegetation, unaltered by fire in contrast to most of other higher massifs in Madagascar. The stream formed narrow channels and at a couple of places, knee-deep pools in the alpine landscape; it was in one of these pools that larvae and adults of *H. praetextus* were found.

Results of the parsimony analysis

In total 53 characters were included in the parsimony analysis, of which four were uninformative (autapomorphies) (see Table 3 and the List at the end). The analysis of the data matrix with TNT resulted in a single most parsimonious tree of 80 steps (CI = 0.75; RI = 0.78) (Fig. 19). The support for the monophyly of the Hyphydrini is high (Bremer > 10; Bootstrap = 99), with *Microdytes* sister to a large and well supported clade including all the other Hyphydrini studied (Bremer = 3; Bootstrap = 50). *Desmopachria* stands as strongly monophyletic (Bremer = 6; Bootstrap = 99) sister to *Hovahydrus*, *Hyphydrus*, *Coelhydrus*, *Primospes*, *Darwinhydrus* and *Andex*. Among these, the four Cape genera occur to form another well supported clade (Bremer = 3; Bootstrap = 72). With low support (Bremer = 2; Bootstrap = <50) *Hyphydrus* and the Cape genera are monophyletic to the exclusion of *Hovahydrus*.

TABLE 3. Data matrix used for the cladistic analysis. Missing data coded '?'. *Hovahydrus* sp. near *H. minutissimus* abbreviated to *Hovahydrus* n. sp.

Species	0 0	0 1	0 2	0 3	0 4	0 5	0 6	0 7	0 8	0 9	1 0	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2	2 3	2 4	2 5	2 6
Laccornis latens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachydrus globosus	1	1	1	0	1	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1	0	2	0	1	0	0	0
Andex insignis	1	2	1	0	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	2	0	0	0
Coelhydrus brevicollis	1	0	1	0	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1	2	2	1	0	0
Darwinhydrus solidus	1	2	1	0	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	2	0	0	0
Desmopachria concolor	0	0	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	1	1	1	1	0	2	1	1	1
Desmopachria convexa	0	0	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	1	1	1	1	0	2	1	1	1
Hovahydrus n.sp.	0	1	1	1	1	?	?	?	?	?	0	0	0	1	1	1	1	0	1	0	1	1	1	2	1	0	0
Hovahydrus praetextus	0	1	1	1	1	?	?	?	?	?	0	0	0	1	1	1	1	0	1	0	1	1	1	2	1	0	0
Hyphydrus ovatus	1	0	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	0	1	1	2	2	1	0	0
Hyphydrus pulchellus	1	0	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	0	1	1	2	2	1	0	0
Microdytes uenoi	0	2	1	1	1	1	0	1	1	1	0	0	0	1	0	1	1	0	1	0	1	1	1	2	0	0	0
Primospes suturalis	1	0	1	0	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1	2	2	0	0	0

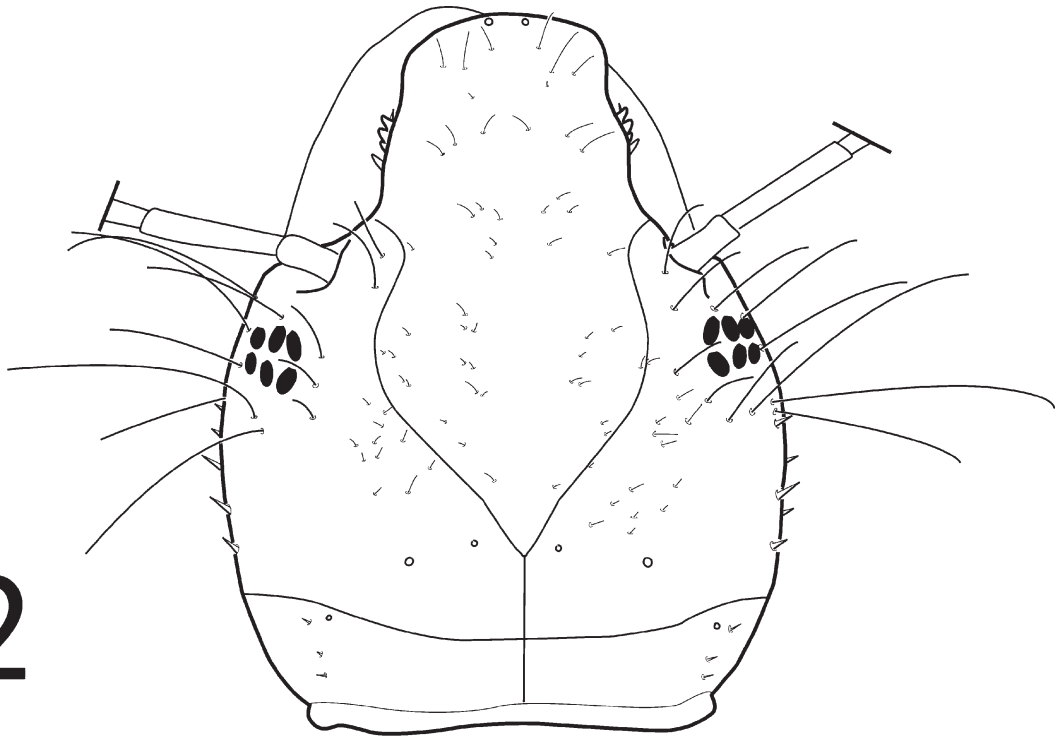
Continued.

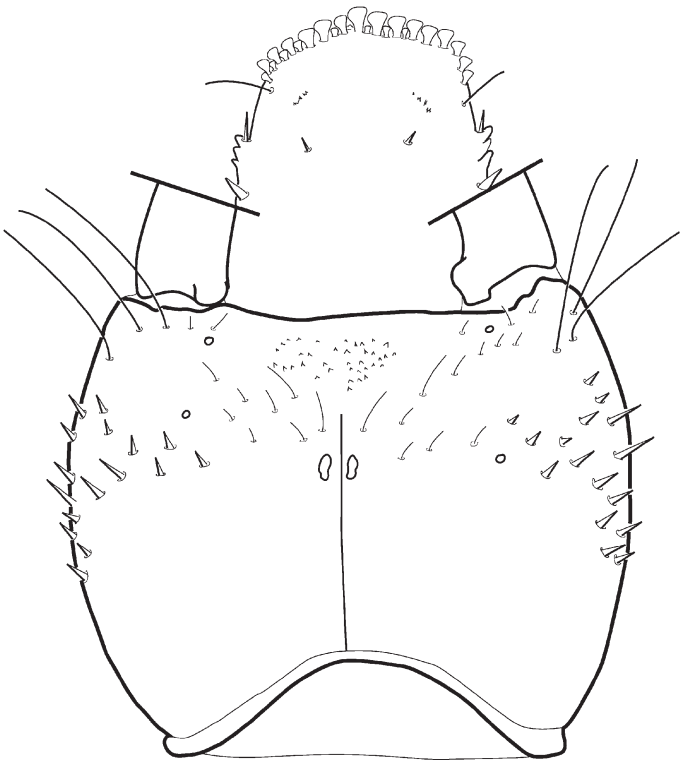
Species	2 7	2 8	2 9	3 0	3 1	3 2	3 3	3 4	3 5	3 6	3 7	3 8	3 9	4 0	4 1	4 2	4 3	4 4	4 5	4 6	4 7	4 8	4 9	5 0	5 1	5 2
Laccornis latens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachydrus globosus	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0
Andex insignis	0	0	2	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	1	1	0	1	1	2	1	2
Coelhydrus brevicollis	0	0	0	1	1	1	1	0	1	0	1	1	1	0	1	1	1	1	1	1	0	1	?	?	1	2
Darwinhydrus solidus	0	1	0	1	1	1	1	0	1	0	1	1	1	0	1	1	1	1	1	1	0	1	?	?	1	2
Desmopachria concolor	1	1	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	1	1	1	0	1	2	1	0
Desmopachria convexa	1	1	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	1	1	1	0	1	2	1	0
Hovahydrus n.sp.	0	0	0	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	?	1	1	0	?	?	1	0
Hovahydrus praetextus	0	0	0	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	?	1	1	0	?	?	1	0
Hyphydrus ovatus	0	0	0	1	1	1	1	0	1	0	1	1	0	0	0	1	1	0	1	1	1	0	1	2	1	1
Hyphydrus pulchellus	0	0	1	1	1	1	1	0	1	0	1	1	0	0	0	1	1	0	1	1	1	0	1	2	1	1
Microdytes uenoi	0	0	0	1	1	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	1	0	2	1	0
Primospes suturalis	0	0	0	1	1	1	1	0	1	0	1	1	1	0	1	1	1	1	1	1	0	1	?	2	1	?

Discussion

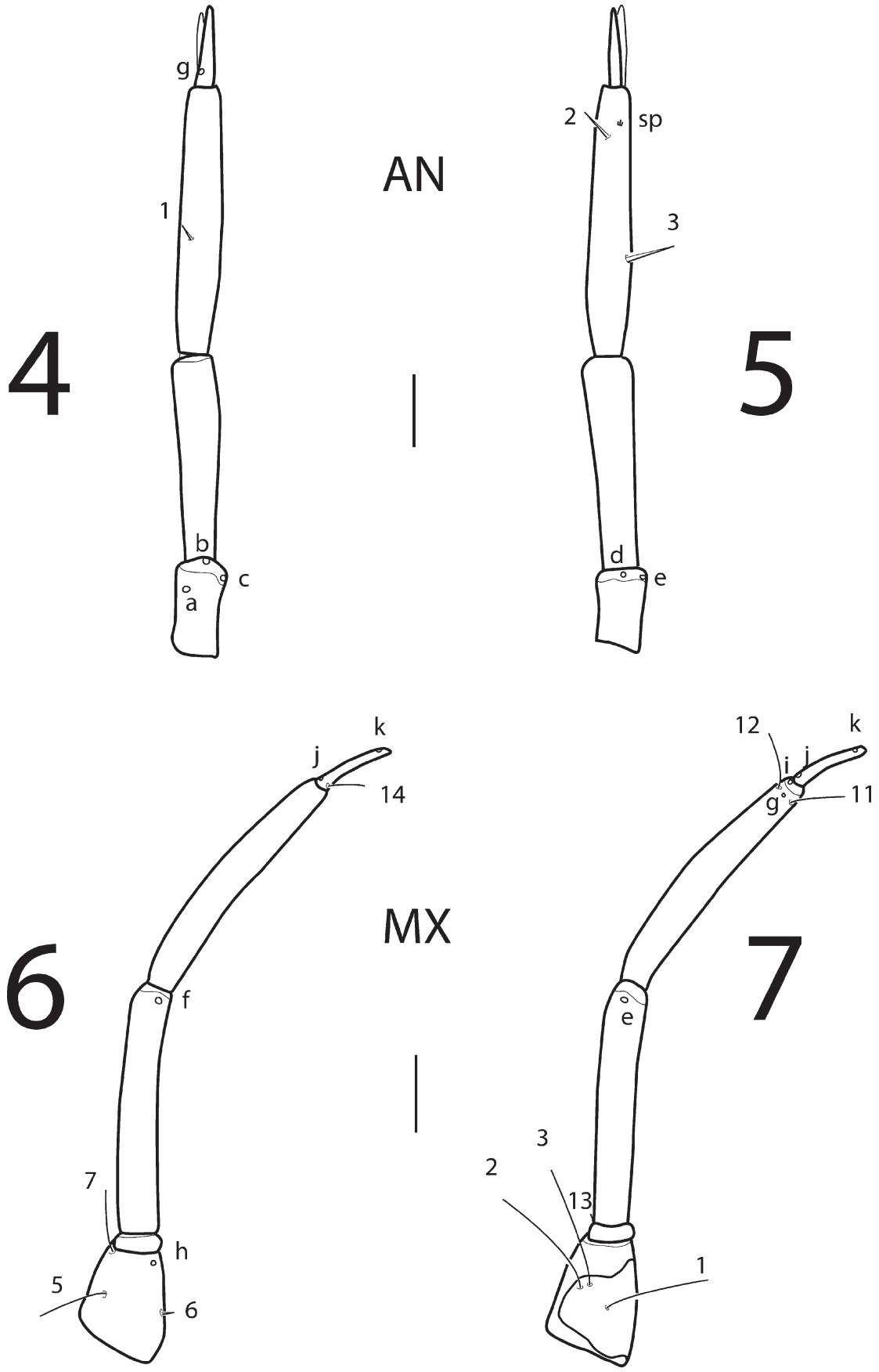
The description of *Hovahydrus* presented in this article brings to eight the number of genera of the tribe Hyphydrini whose larval morphology has been studied in detail, which allows an interesting comparison of their phylogenetic relationships under the angle of larval morphology. Several recent studies (Alarie *et al.* 1997; Alarie & Challet 2006a, 2006b; Alarie *et al.* 2017; Michat & Archangelsky 2007) have made it possible to depict a basic pattern for these larvae. Adding *Hovahydrus* to this group reinforces the monophyletic origin of the Hyphydrini (Fig. 19). Although the absence of first stage larvae and the poor condition of the larvae studied prevent us from asserting with certainty that some characteristics specific to the first-stage larvae of Hyphydrini are indeed present in *Hovahydrus* (e.g., absence of the primary pores FRb, PAe, and PAj; primary pore PAc inserted anteriorly to stemmata; primary setae AB6 and AB7 elongate; proximal articulation of the primary seta UR8 on urogomphomere 2), there is no doubt that the two species studied belong to this group. Like other known Hyphydrini, both species are characterized by: the presence of a ventroapical spinula on antennomere 3 (character 13; Fig. 5), the presence of the primary setae MX8 and MX9 (character 20; Fig. 6), the insertion of the primary pore MXh on stipes (character 21; Fig. 6), the prementum longer than broad (character 23; Fig. 8), the presence of posterodorsal natatory setae on tibiae and tarsi (characters 37, 38; Figs 10, 16), and, the sclerotization of the ventral surface of abdominal segments IV–V (character 42). Surprisingly, the shape of the head capsule is considerably different in the two species described (Figs 2, 13). Being, however, very similar for all the other morphological characters, there is no doubt that the two species belong to the current concept of the genus.

FIGURE 1. *Hovahydrus* sp. near *H. minutissimus* (Régimbart, 1903): habitus of instar III, dorsal aspect. Scale bar = 0.2 mm.

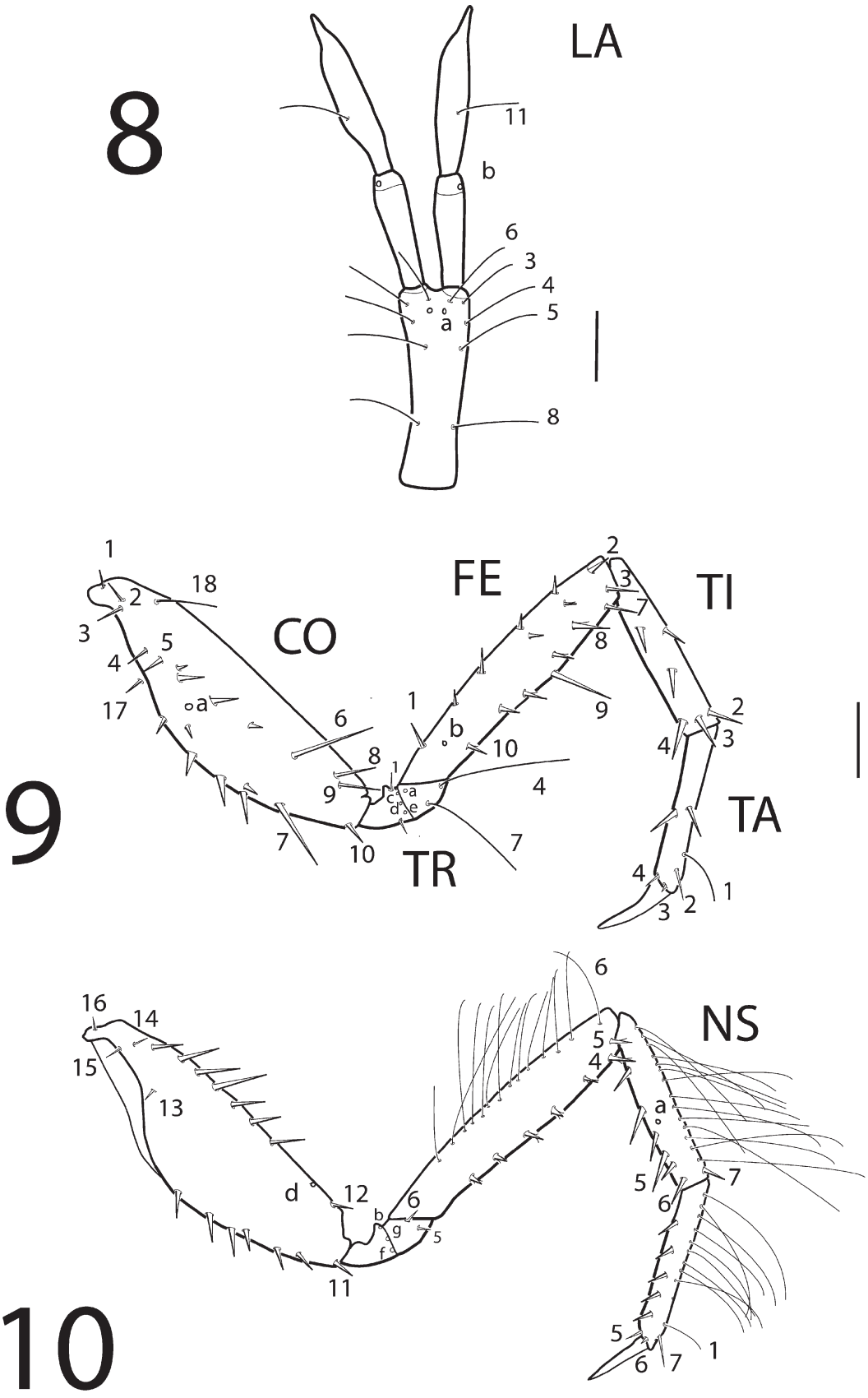




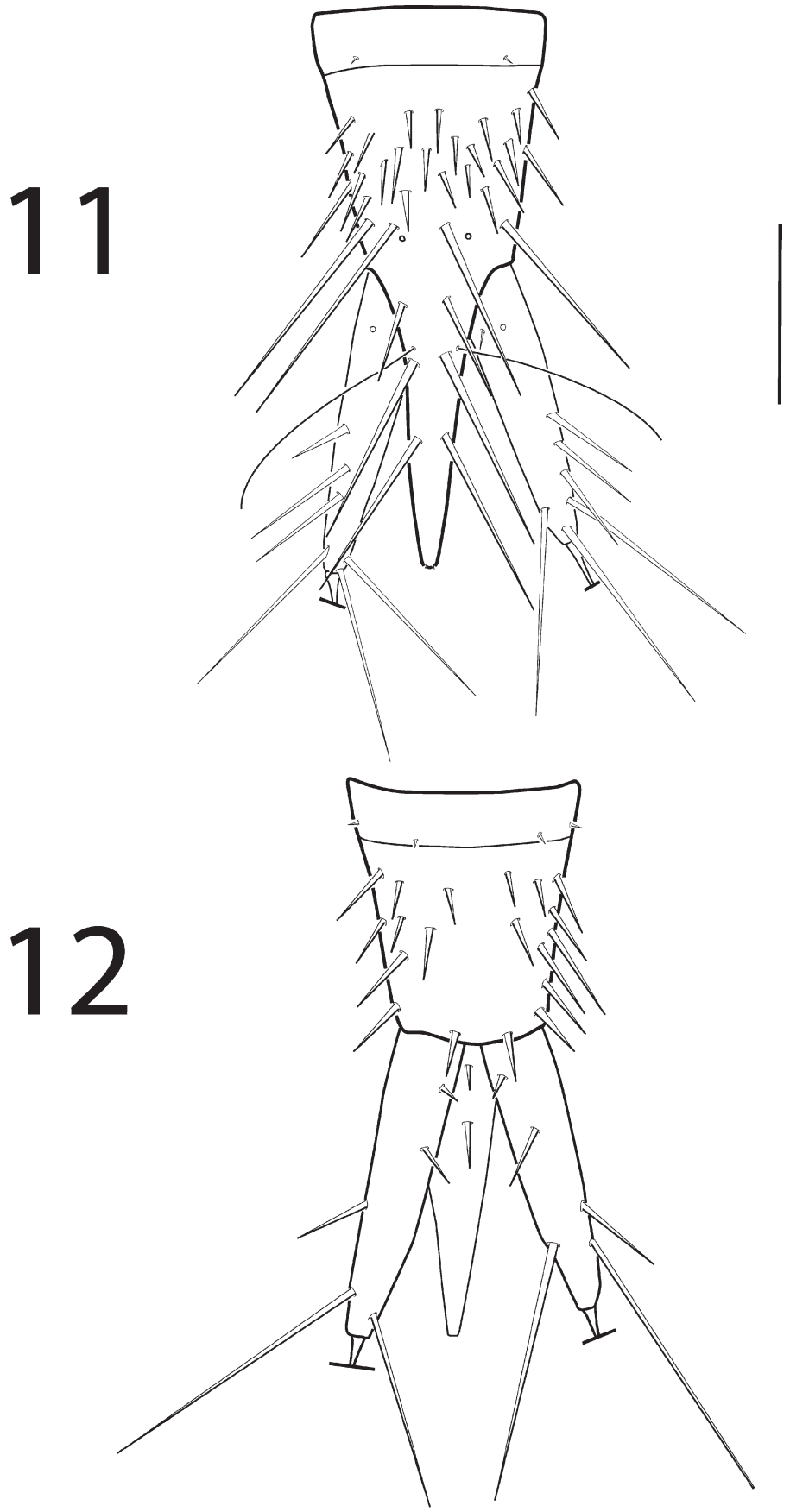
FIGURES 2–3. *Hovahydrus* sp. near *H. minutissimus* (Régimbart, 1903), instar III: (2) head capsule, dorsal aspect; (3) head capsule, ventral aspect. Scale bar = 0.2 mm.



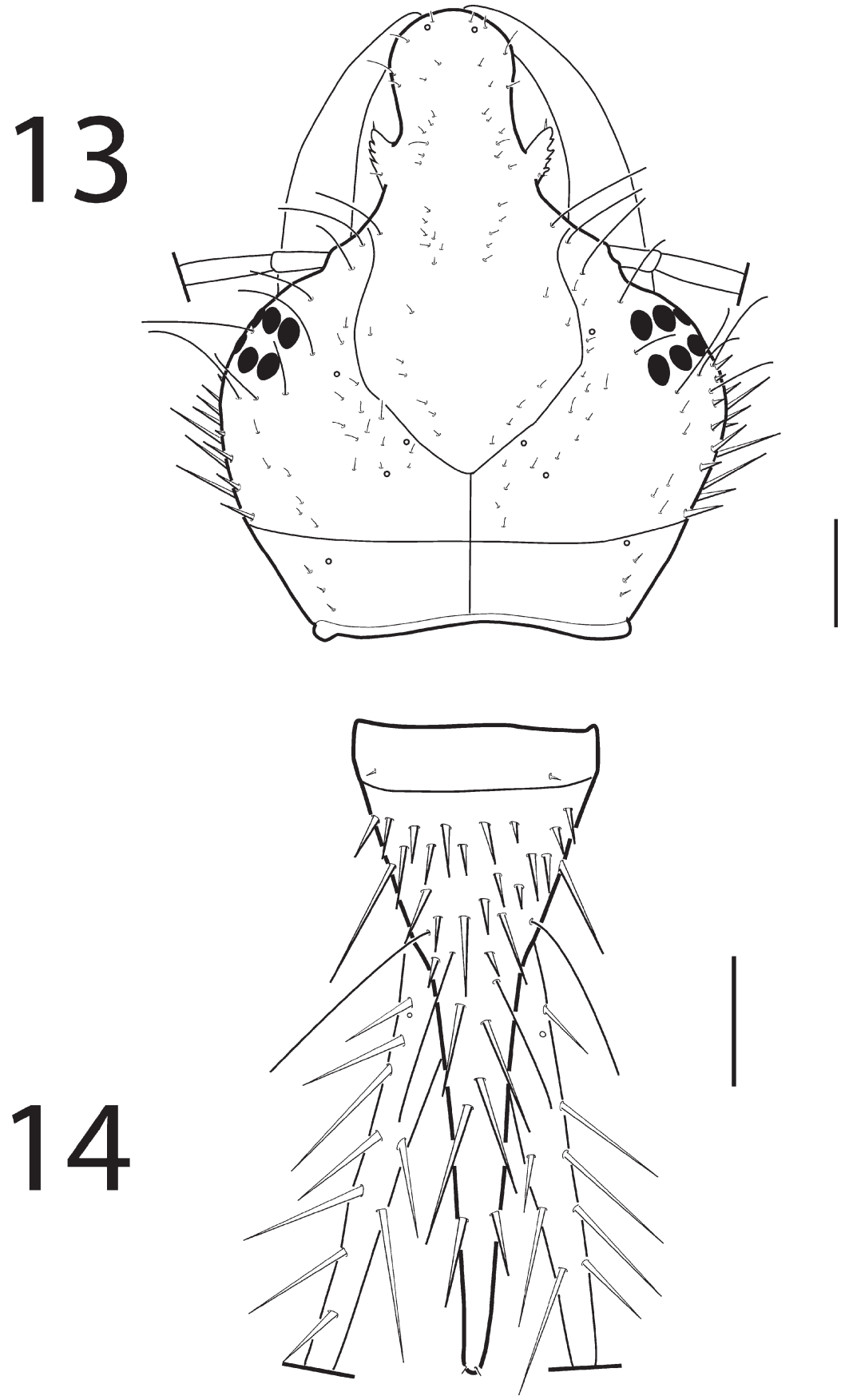
FIGURES 4–7. *Hovahydrus* sp. near *H. minutissimus* (Régimbart, 1903), instar III: (4) antenna, dorsal aspect; (5) antenna, ventral aspect; (6) maxilla, dorsal aspect; (7) maxilla, ventral aspect. Numbers and lowercase letters indicate primary setae and pores, respectively. AN: antenna; MX: maxilla; sp: spinula. Scale bars = 0.05 mm.



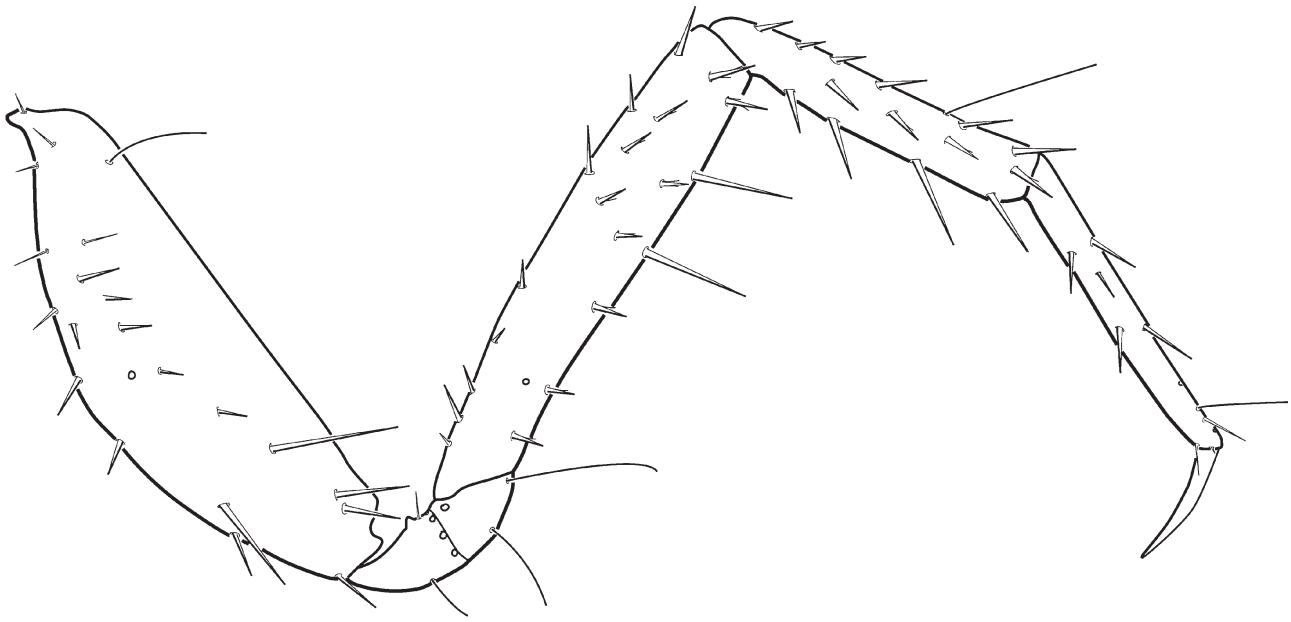
FIGURES 8–10. *Hovahydrus* sp. near *H. minutissimus* (Régimbart, 1903), instar III: (8) labium, dorsal aspect; (9) mesothoracic leg, anterior aspect; (10) mesothoracic leg, posterior aspect. CO: coxa; FE: femur; LA: labium; NS: natatory setae; TA: tarsus; TI: tibia; TR: trochanter. Numbers and lowercase letters indicate primary setae and pores, respectively; others are secondary setae. Pore TRb not represented. Scale bars: 8 = 0.05 mm; 9–10 = 0.1 mm.



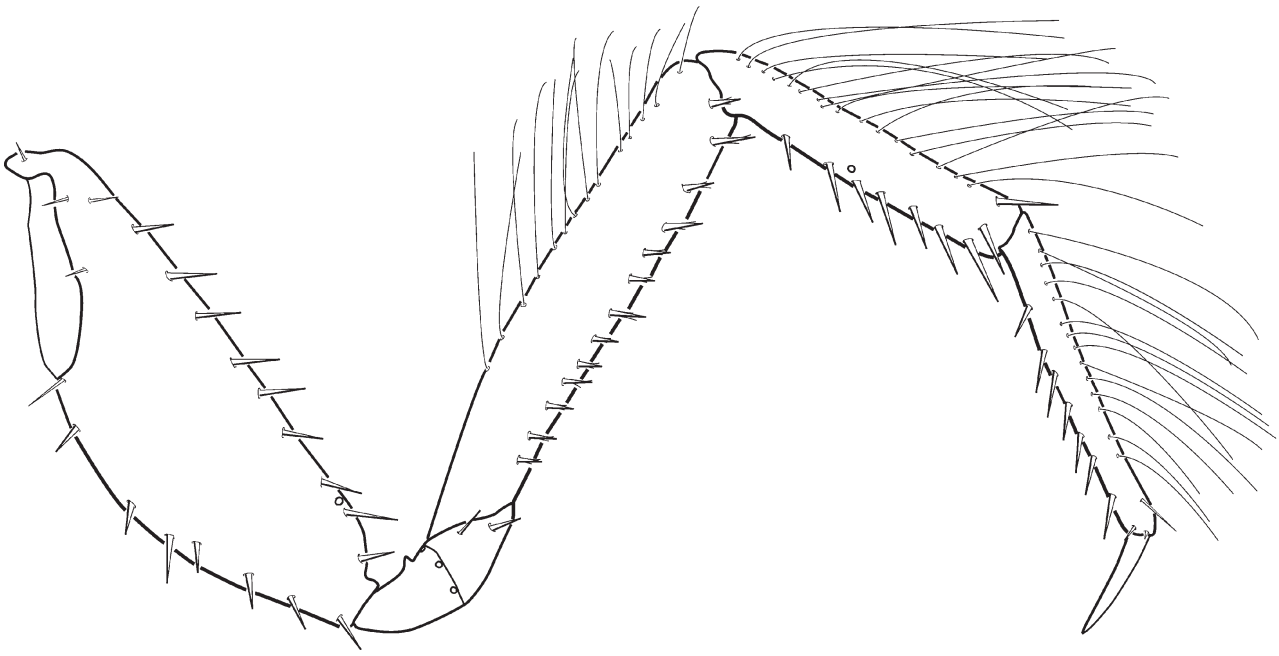
FIGURES 11–12. *Hovahydrus* sp. near *H. minutissimus* (Régimbart), 1903, instar III: (11) abdominal segment VIII, dorsal aspect; (12) abdominal segment VIII, ventral aspect. Scale bar = 0.2 mm.



FIGURES 13–14. *Hovahydrus praetextus* (Guignot, 1951), instar III: (13) head capsule, dorsal aspect; (14) abdominal segment VIII, dorsal aspect. Scale bars = 0.15 mm.



15



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FIGURES 15–16. *Hovahydrus praetextus* (Guignot, 1951), instar III: (9) mesothoracic leg, anterior aspect; (10) mesothoracic leg, posterior aspect. Scale bar = 0.1 mm.

FIGURE 17. Side-pool to small forest stream in medium-high altitude rainforest in Marojejy National Park, Madagascar where *Hovahydrus* sp. near *H. minutissimus* (Régimbart, 1903) instar III larvae were collected. Photo J. Bergsten.

Some recent studies dealing with the phylogenetic relationships of the Hyphydrini based on molecular data (Ribera & Balke 2007; Ribera *et al.* 2008) suggested the existence of four well supported groups among 10 of the 14 genera included in these analyses: (1) *Hyphydrus*, (2) the five South African genera (*Andex*, *Coelhydrus*, *Primospes*, *Darwinhydrus*, *Hydropeplus* Sharp, 1882) plus the Madagascan *Hovahydrus*, (3) *Desmopachria*, and (4) *Microdytes* + *Allopachria* Zimmermann, 1924. It would seem that larval morphology is somewhat consistent with this hypothesis. As reflected in the single most parsimonious tree obtained in this study (Fig. 19), *Microdytes* stands out as a distinct lineage sister to all the other Hyphydrini. Larvae of this genus differ from all other Hyphydrini by the more distal position of the primary seta AN3 on the antenna and the spiniform aspect of the primary seta TI7 on tibiae (Alarie *et al.* 1997). Similarly, *Desmopachria* emerges as another independent lineage, larvae of this group being characterized by the proximal insertion of the primary setae LA3, LA4, and LA5 and the submedial position of seta LA6 on the prementum and by the distal articulation of seta LA10 on the second labial palpomere (Alarie *et al.* 1997; Michat & Archangelsky 2007). At the present time, larval morphology suggests a sister-group relationship of *Desmopachria* with *Hyphydrus*, *Hovahydrus* and the four Cape genera known as larvae (*Andex*, *Coelhydrus*, *Primospes*, and *Darwinhydrus*). Although weakly supported in our analysis, the presence of natatory setae on the metafemur of these genera (character 33; Figs 10, 16), a unique character state among the Hyphydrini, appears to us to be a serious argument supporting the monophyletic origin of this larger clade, excluding *Desmopachria*.

Like the observations made on the basis of molecular analyses, our study strengthens the hypothesis of a monophyletic origin for the four South African genera studied whose larvae share the presence of elongate metathoracic legs, elongate urogomphi and a very short siphon (Alarie & Challet 2006a, 2006b; Alarie *et al.* 2017). The relative position of the genera *Hyphydrus* and *Hovahydrus* with respect to this group, however, remains uncertain. *Hyphydrus* is sister to the Cape lineage genera in our analysis owing to the shared presence of a shorter antennomere IV relative to antennomere III (character 17), and the homoplastic presence of spatulate frontoclypeus (character 0) and membranous ventral surface of abdominal segment II (character 40) (Alarie *et al.* 1997; Alarie & Watts 2005). Some might also see in the relative length of urogomphi an evolutionary transition between the very short condition observed in *Hovahydrus* and the very long urogomphi found in the Hyphydrini larvae of South Africa,

FIGURE 18. Alpine stream above the treeline near the peak of Marojejy National Park, Madagascar where one instar II and one instar III larvae of *Hovahydrus praetextus* (Guignot, 1951) were collected. Photo J. Bergsten.

the condition in *Hyphydrus* being intermediate. The arrangement of *Hyphydrus* as the closest relative to the Cape clade is in conflict with previous molecular studies that found rather strong support for *Hovahydrus* in this position using two mitochondrial and two nuclear markers (Ribera & Balke 2007; Ribera *et al.* 2008). What seems obvious in the light of our study, however, and in agreement with molecular data, is that larval morphology does suggest a relatively close relationship between *Hovahydrus*, *Hyphydrus* and the endemic Cape Hyphydrini.

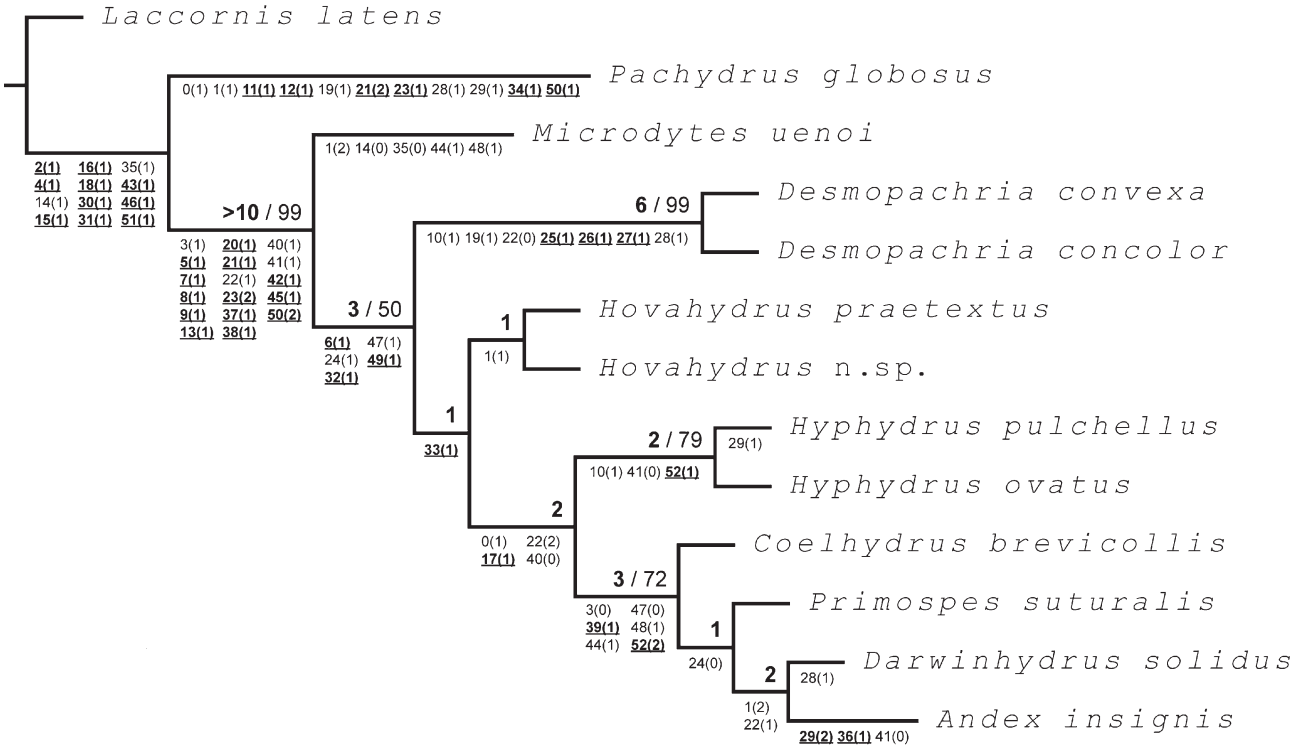

FIGURE 19. Single most parsimonious cladogram obtained from the cladistic analysis, with Bremer (in bold) and Bootstrap (higher than 50) support values indicated above branches. Character changes are mapped for each clade, with numbers in bold underlined indicating unique character state transformations. *Hovahydrus* sp. near *H. minutissimus* (Régimbart, 1903) is abbreviated to *Hovahydrus* n.sp. in the cladogram.

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List. Characters used for the phylogenetic analysis and the coding of states using the genera *Laccornis* Gozis, 1914 and *Pachydrus* Sharp, 1882 as outgroups.

00. Apex of nasale: (0) not spatulate, lateral margin almost parallel-sided to slightly diverging posteriorly; (1) spatulate, lateral margin strongly attenuate posteriorly.
01. Frontoclypeus: (0) lateral process lacking, if present barely visible in dorsal view; (1) one lateral process well visible in dorsal view; (2) several short lateral processes well visible in dorsal view.
02. Epicranial plates: (0) separate at the ventral midline; (1) meet on the ventral midline.
03. Primary seta FR7: (0) spine-like; (1) hair-like.
04. Primary seta FR13: (0) absent; (1) present.
05. Primary pore FRb: (0) present; (1) absent.
06. Primary seta PA3: (0) inserted contiguously to primary setae PA1 and PA2; (1) inserted far from primary setae PA1 and PA2.
07. Primary pore PAc: (0) not inserted anteriorly to stemmata; (1) inserted anteriorly to stemmata.
08. Primary pore PAe: (0) present; (1) absent.
09. Primary pore PAj: (0) present; (1) absent.
10. Secondary spine-like setae on lateral margin of parietals: (0) present; (1) absent.
11. Antennomere II: (0) longer than antennomere I; (1) subequal in length to antennomere I.
12. Antennomere III: (0) longer than antennomere I; (1) subequal in length to antennomere I.
13. Ventral apical spinula on antennomere III: (0) absent; (1) present.
14. Primary seta AN3: (0) inserted distally; (1) inserted submedially.
15. Primary pore ANf: (0) present; (1) absent.
16. Primary pore ANh: (0) present; (1) absent.
17. Antennomere IV: (0) > 0.30 times as long as antennomere III; (1) < 0.20 times as long as antennomere III.
18. Cardo: (0) not fused to stipes: (1) fused to stipes.
19. Primary setae MX4, MX5, MX6: (0) present; (1) absent.
20. Primary setae MX8 and MX9: (0) present; (1) absent.
21. Primary pore MXh: (0) inserted on the galea; (1) inserted on the stipes; (2) absent.
22. Maxillary palpus: (0) < 1.40 times length of labial palpus; (1) 1.50–1.90 times the length of labial palpus; (2) > 2.00 times the length of labial palpus.
23. Prementum: (0) broader than long; (1) as broad as long; (2) longer than broad.
24. Labial palpomere II: (0) narrow, subcylindrical, narrowing at apex; (1) robust, broadest at midlength.
25. Primary setae LA3, LA4, LA5: (0) articulated distally on prementum; (1) articulated proximally on prementum.
26. Primary seta LA6: (0) articulated distally; (1) articulated submedially.
27. Primary seta LA10: (0) articulated medially; (1) articulated distally.
28. Primary pore LAb: (0) present; (1) absent.
29. Prementum: (0) lacking secondary setae; (1) with one secondary seta; (2) with several secondary setae.
30. Primary seta TR2: (0) present; (1) absent.
31. Primary pore FEa: (0) present; (1) absent.
32. Dorsal mesofemoral natatory setae: (0) absent; (1) present.
33. Dorsal metafemoral natatory setae: (0) absent; (1) present.
34. Ventral femoral natatory setae: (0) absent; (1) present.
35. Primary seta TI7: (0) short, spine-like; (1) elongate, hair-like.
36. Primary pore TIa: (0) present; (1) absent.
37. Dorsal natatory setae on tibiae: (0) absent; (1) present.
38. Dorsal natatory setae on tarsi: (0) absent; (1) present.
39. Metathoracic legs: (0) shorter, < 3.30 times as long as HW; (1) longer, > 3.50 times as long as HW.
40. Ventral surface of abdominal segment II: (0) membranous; (1) sclerotized.
41. Ventral surface of abdominal segment III: (0) membranous; (1) sclerotized.
42. Ventral surface of abdominal segments IV–V: (0) membranous; (1) sclerotized.
43. Ventral surface of abdominal segment VI: (0) membranous; (1) sclerotized.
44. Abdominal segment VIII: (0) not or at most very slightly constricted posteriorly at point of insertion of urogomphi;

(1) strongly constricted posteriorly at point of insertion of urogomphi.

45. *Primary setae AB6 and AB7*: (0) short; (1) elongate.
46. *Primary pore ABa*: (0) present; (1) absent.
47. *Siphon*: (0) lacking secondary setae on ventral surface; (1) with a variable number of secondary setae on ventral surface.
48. *Abdominal segment VIII*: (0) longer, LAS/HW > 1.00; (1) shorter, LAS/HW < 0.90.
49. *Primary seta UR5*: (0) short, spine-like; (1) elongate, hair-like.
50. *Primary seta UR8*: (0) inserted apically on urogomphomere 2; (1) inserted submedially on urogomphomere 2; (2) inserted proximally on urogomphomere 2.
51. *Urogomphomere 1*: (0) lacking secondary setae; (1) with secondary setae.
52. *Urogomphomere 1*: (0) very short, < 0.80 times HW; (1) longer, 1.00 to 1.80 times HW; (2) very long, > 2.00 times HW.