Zootaxa 5768 (1): 057–072
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5768.1.3
http://zoobank.org/urn:lsid:zoobank.org:pub:47FD3DEC-5078-498D-93D5-91950A1074DA

Larval morphology of *Agnoshydrus* Biström, Nilsson & Wewalka, 1997: description of *A. thailandicus* Okada, 2024 and phylogenetic comparison with other known Hyphydrini (Coleoptera: Adephaga, Dytiscidae)

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Abstract

The three larval instars of the Thailand endemic *Agnoshydrus thailandicus* Okada, 2024 are described for the first time, including a detailed chaetotaxy analysis of the cephalic capsule, head appendages, legs, last abdominal segment, and urogomphi. The phylogenetic position of *Agnoshydrus* Biström, Nilsson & Wewalka, 1997 is studied based on a cladistic analysis of 12 Hyphydrini species (nine genera) and 59 morphological larval characters. Although the phylogenetic relationships of *Agnoshydrus* within the tribe Hyphydrini remain unresolved, it seems reasonable to suggest a closer relationship with *Desmopachria* Babington, 1842, *Hovahydrus* Biström, 1982, and *Microdytes* J. Balfour-Browne, 1946.

Key words: chaetotaxy, Hydradephaga, Hydroporinae, larval morphology, phylogeny, Southeast Asia, taxonomy

Introduction

Agnoshydrus Biström, Nilsson & Wewalka, 1997 is a poorly known Dytiscidae genus (Coleoptera: Adephaga) comprised of small (adult length up to 2.7 mm) and globular beetles. Up to recently, this genus included eight species (Wewalka & Wang 2007) until two new ones, *A. thailandicus* Okada, 2024 and *A. wewalkai* Okada, 2024, were described from Thailand (Okada 2024). *Agnoshydrus* is endemic to Southeast Asia including Taiwan, Sabah and Bali (Miller & Bergsten 2016). Our knowledge of their bionomics, however, remains almost non-existent due to the low number of specimens that have been historically collected (Wewalka 1999; Miller & Bergsten 2016).

Whereas included in the tribe Hyphydrini, subfamily Hydroporinae, the genus *Agnoshydrus* is poorly studied with regards to its phylogenetic position within this group. Ribera & Balke (2007) postulated *Agnoshydrus* as closely related to *Anginopachria* Wewalka, Balke & Hendrich, 2001, *Desmopachria* Babington, 1842, *Allopachria* Zimmermann, 1924, and *Microdytes* J. Balfour-Browne, 1946 based on adult morphological characters, but this hypothesis was not seen as strongly supported (Miller & Bergsten 2016).

This article is part of an effort to improve our knowledge of the larval morphology of Hyphydrini. To date, the larvae of eight of the 15 genera included in this tribe have been described using the now generalized larval descriptive format of aquatic Adephaga, which incorporates chaetotaxic analysis (Alarie & Michat 2023): *Andex* Sharp, 1882 (Alarie & Challet 2006a), *Coelhydrus* Sharp, 1882 (Alarie *et al*. 2017), *Darwinhydrus* Sharp, 1882 (Alarie *et al*. 2017), *Desmopachria* (Alarie *et al*. 1997; Michat & Archangelsky 2007), *Hyphydrus* Illiger, 1802 (Alarie *et al*. 1997; Alarie & Watts 2005), *Hovahydrus* Biström, 1982 (Alarie *et al*. 2022), *Microdytes* (Alarie *et al*. 1997), and *Primospes* Sharp, 1882 (Alarie & Challet 2006b). Obtaining the larvae of the recently described *A. thailandicus* (Okada, 2024) motivated the present study by allowing us to describe these larvae and compare this genus in a phylogenetic context to the other genera of Hyphydrini described with detail at the larval stage.

Accepted by M. Manuel: 24 Jan. 2026; published: 9 Mar. 2026

Material and Methods

The larvae studied (three instar I, two instar II, three instar III) were reared *ex ovo* from adults collected at the *A. thailandicus* type locality: Thailand, Ubon Ratchatani Province, Nam Yuen District, Dom Pradit Station 239, 22.v.2021, leg. R. Okada. Larvae were killed in boiling water and then preserved in 75% ethanol. Specimens were disarticulated and mounted on standard glass slides in Hoyer's medium. Microscopic examination at magnifications up to 1000× and drawings were made using an Olympus BHT and SZX10 compound microscope equipped with Nomarsky differential interference optics. Voucher specimens are deposited in the larval collection of Ryohei Okada, Tokyo, Japan.

The methods for morphometric and chaetotaxic analyses follow those employed in Alarie *et al.* (2022). The reader is referred to that paper for a complete list of abbreviations, terminology, and additional explanations of the terms used here.

Phylogenetic analysis

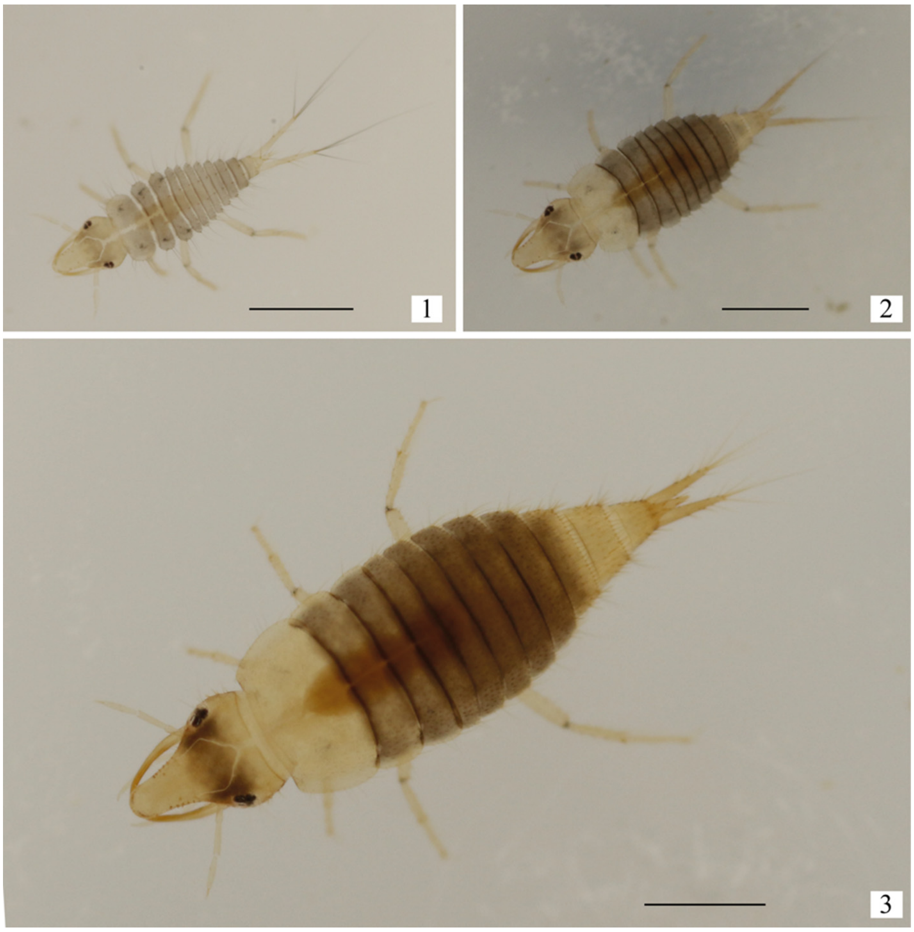
To examine the phylogenetic relationships of the genus *Agnoshydrus* with other Hyphydrini, a cladistic analysis of 12 species of Hyphydrini (nine genera) with sufficiently detailed larval descriptions (*Agnoshydrus* (one species), *Hyphydrus* (two species), *Hovahydrus* (two species), *Microdytes* (one species), *Desmopachria* (two species), *Andex* (one species), *Coelhydrus* (one species), *Darwinhydrus* (one species) and *Primospes* (one species)) was conducted. Consistent with the approach used in the most recent study of Hyphydrini larval morphology (Alarie *et al.* 2022), *Pachydrus* Sharp, 1882 (tribe Pachydrini) and *Laccornis* Gozis, 1914 (tribe Laccornini) were used as out-groups. *Pachydrus* is deemed closely related phylogenetically to the Hyphydrini (Alarie *et al*. 1997), whilst *Laccornis* is recognized as a basal lineage within Hydroporinae (Roughley & Wolfe 1987; Miller *et al*. 2006; Alarie & Michat 2007; Miller & Bergsten 2023).

The character database used in this article is essentially based on that of Alarie *et al.* (2022), to which six new characters were added, and several others redefined (see List at the end). As a result of this effort, a total of 59 characters were incorporated into our study (Table 3). Cladistic analyses were performed in 'Tree Analysis using New Technologies' (TNT) (Goloboff *et al*. 2008). All characters were equally weighted, and multistate characters were treated as unordered. An exact solution algorithm (implicit enumeration) implemented in TNT was used to find the most parsimonious trees. In order to estimate branch support on a cladogram, 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 also calculated, using the following parameters: 'standard (sample with replacement)'; '1000 replicates'.

Results

General morphological characteristics of Hyphydrini larvae (following Alarie *et al*. 2022)

Body fusiform (Figs 1–3); frontoclypeus elongated, narrow or broad apically; gular sutures fused (visible from instar II), so epicranial plates meet at ventral midline (Fig. 19); ventral apical spinula on antennomere 3 present (Fig. 7); cardo fused to stipes (Fig. 9); primary seta MX1 inserted on stipes (Fig. 9); prementum longer than broad, lacking marginal spinulae laterally (Figs 10–11); primary pores ANf, ANh, PAe, PAj, FEa, ABa, and primary setae MX8, MX9, TR2 lacking; seta AB10 spine-like (Fig. 16); secondary natatory setae present on legs (Fig. 21); abdominal segments IV–VI sclerotized ventrally in instars II–III; primary seta UR8 inserted proximally on urogomphomere 2 (Fig. 17).



FIGURES 1–3. Dorsal habitus of larvae of *Agnoshydrus thailandicus* Okada, 2024: **(1)** instar I; **(2)** instar II; **(3)** instar III. Scale bars: 0.5 mm.

Description of larvae of *Agnoshydrus* Biström, Nilsson & Wewalka, 1997

Diagnosis. Not provided for the first two larval stages due to the lack of information for several Hyphydrini genera. Instar III larvae of *Agnoshydrus* can be distinguished from those of other known genera of Hyphydrini (i.e. *Andex*, *Coelhydrus*, *Darwinhydrus*, *Desmopachria*, *Hyphydrus*, *Hovahydrus*, *Microdytes*, and *Primospes*) by the following combination of characters: frontoclypeus not spatulate apically, lateral margin almost parallel-sided to slightly diverging posteriorly, without lateral process (Figs 3–5); maxillary palpus 1.50–1.90 times the length of labial palpus; MNL/MNW > 3.60; LP2/LP1 > 1.50; presence of 1–3 anteroventral secondary spiniform setae on metatarsus (Fig. 20); presence of a variable number of natatory setae along dorsal margin of metafemur and between 14–22 and 13–21 on metatibia and metatarsus, respectively (Fig. 21); ventral surface of abdominal segment II sclerotized; LAS/HW < 0.90; siphon lacking secondary setae on ventral surface (Fig. 23).

Agnoshydrus thailandicus Okada, 2024

Description, instar I (Figs 1, 4–17)

Color (Fig. 1). Head capsule predominantly pale yellow except medial region darker; head appendages pale yellow; thoracic and abdominal tergites I–VII greyish brown; LAS, urogomphi and legs pale yellow.

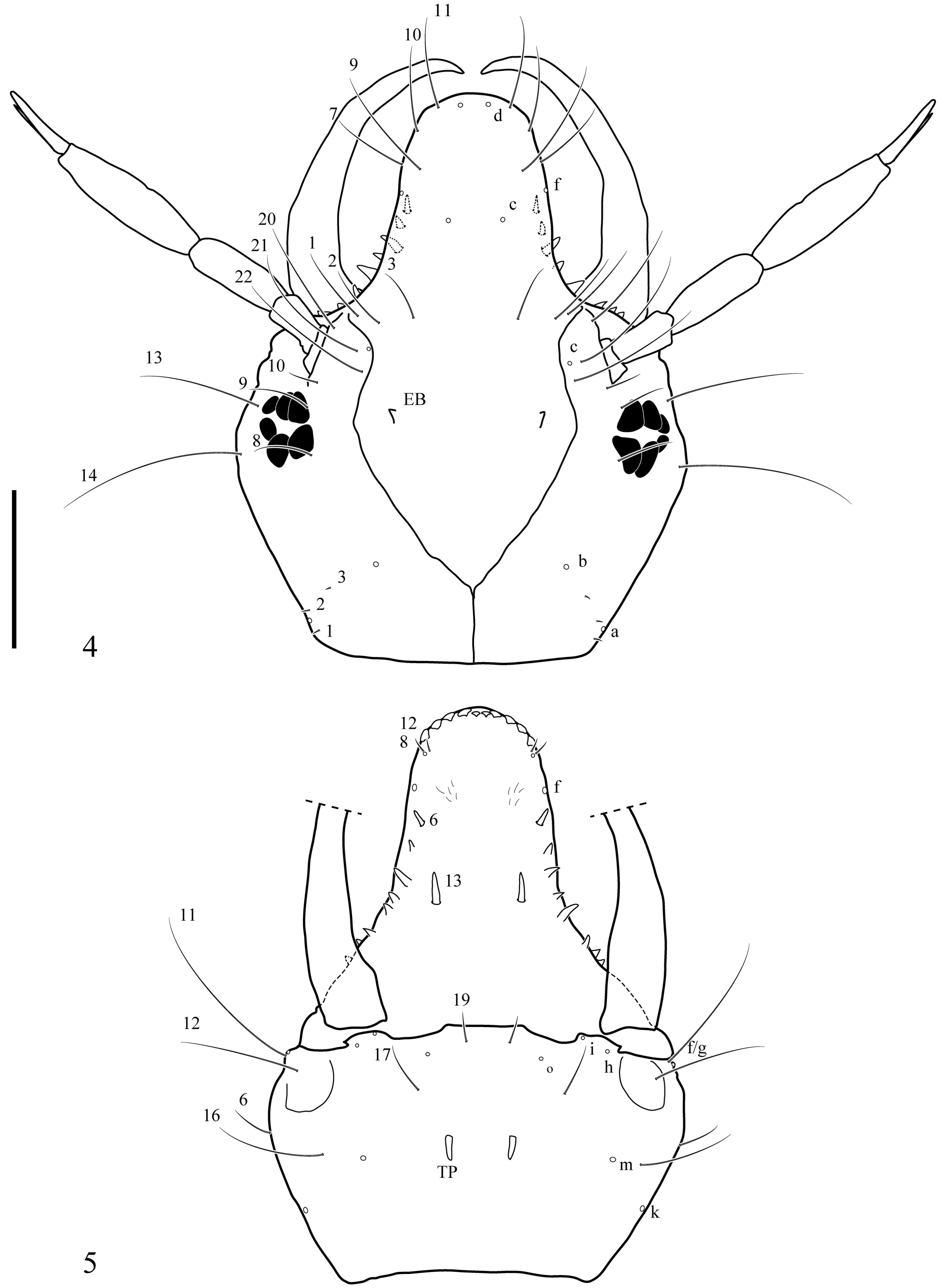
Body. Fusiform, wide (Fig. 1). Measurements and ratios that characterize the body shape are shown in Table 1.

TABLE 1. Measurements and ratios for larvae of *Agnoshydrus thailandicus* Okada, 2024. *n* = number of specimens examined.

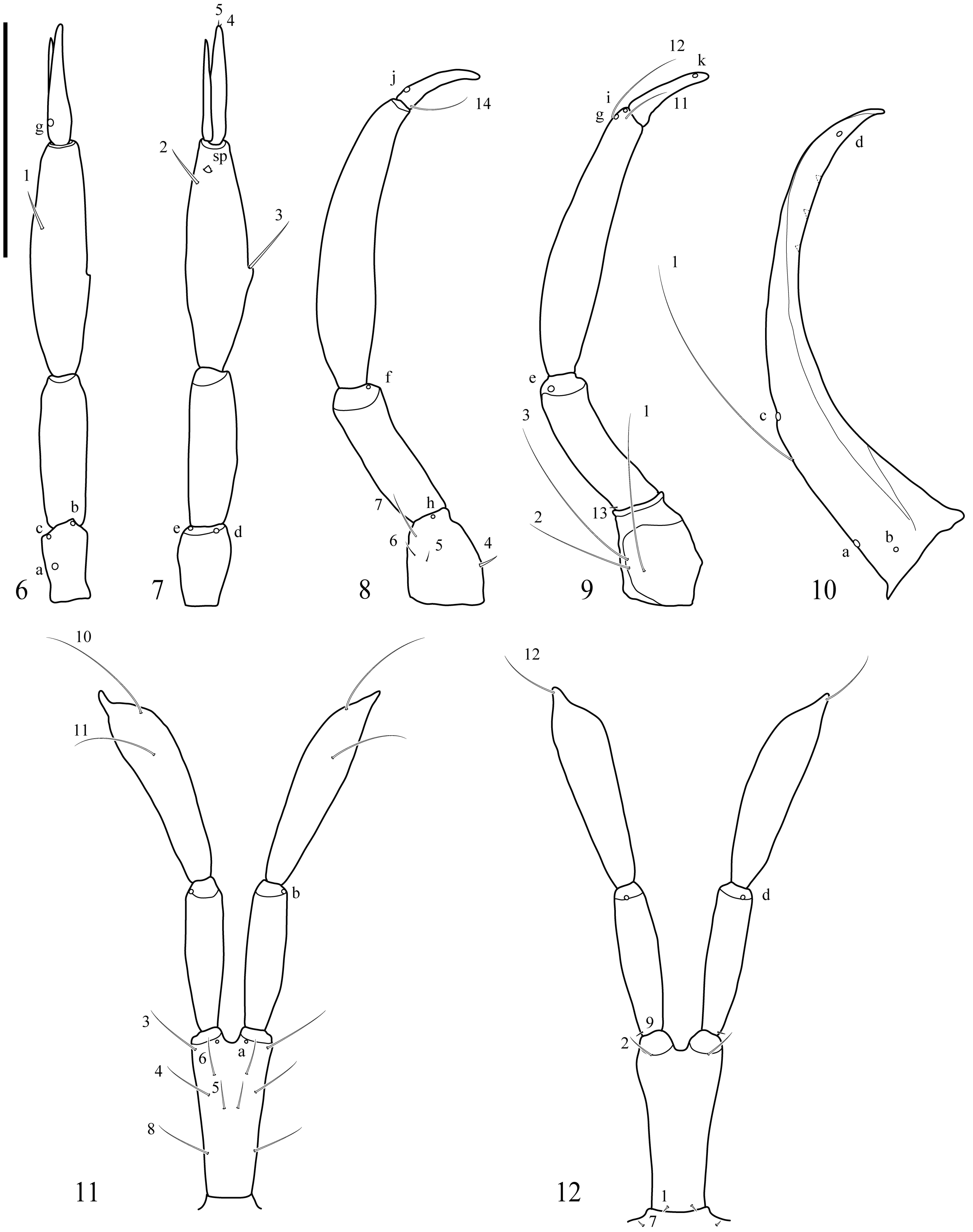
Series	Instar I	Instar II	Instar III	Series	Instar I	Instar II	Instar III
	(*n*=3)	(*n*=2)	(*n*=3)		(*n*=3)	(*n*=2)	(*n*=3)
HL (mm)	0.36	0.49–0.51	0.66–0.68	MP/LP	1.51–1.57	1.49–1.55	1.55–1.67
HW (mm)	0.27	0.37–0.38	0.48–0.50	LP2/LP1	1.41–1.45	1.54–1.66	1.52–1.57
FRL (mm)	0.29–0.30	0.39–0.40	0.52–0.54	L3 (mm)	0.83–0.85	1.09–1.11	1.42–1.47
OCW (mm)	0.18	0.23–0.24	0.29–0.30	L3/L1	1.27–1.30	1.28	1.31–1.37
HL/HW	1.33–1.35	1.33	1.35–1.40	L3/L2	1.14–1.16	1.14–1.16	1.16–1.17
HW/OCW	1.46–1.48	1.59–1.60	1.63–1.67	L3/HW	3.06–3.17	2.90–2.99	2.94–3.01
COL/HL	0.17–0.19	0.19–0.20	0.19–0.22	L3 (CO/FE)	1.20–1.23	1.05–1.08	1.03–1.05
FRL/HL	0.81–0.83	0.80–0.81	0.78–0.81	L3 (TI/FE)	0.78–0.85	0.72–0.76	0.69–0.71
A/HW	0.94–0.97	0.87–0.88	0.77–0.80	L3 (TA/FE)	0.91–0.95	0.81–0.82	0.71–0.77
A3/A1	2.75–2.81	2.05–2.07	1.95–2.09	L3 (CL/TA)	0.66–0.67	0.50–0.51	0.42–0.43
A3/A2	1.63–1.70	1.43–1.44	0.93–0.97	LAS (mm)	0.21–0.22	0.25–0.28	0.33–0.35
A4/A3	0.51–0.53	0.37	0.41–0.47	LAS/HW	0.77–0.83	0.69–0.73	0.66–0.73
A3’/A4	0.81–0.84	0.81–0.82	0.82–0.84	U (mm)	0.53–0.54	0.65–0.69	0.69–0.70
MNL/MNW	3.26–3.37	4.56–4.68	4.10–4.37	U/LAS	2.40–2.61	2.48–2.57	2.02–2.03
MNL/HL	0.56–0.59	0.57–0.58	0.57–0.60	U/HW	1.98–2.02	1.86–1.92	1.46–1.47
A/MP	1.07–1.08	1.11–1.14	0.93–0.96	U1/U2	1.04–1.07	0.78–0.84	0.65–0.75
MP2/MP1	1.86–1.89	1.31–1.33	0.95–1.03	U1/LAS	1.24–1.33	1.19–1.21	0.81–0.89
MP2/MP3	3.35–3.51	3.57–3.58	3.23–3.53	U1/HW	1.01–1.03	0.80–0.82	0.58–0.63

Head. Head capsule (Figs 4–5). Longer than broad; surface with reticulation; basal half (excluding nasale) subquadrate, maximum width at stemmata, progressively narrowing towards occipital foramen, without neck constriction; occipital suture absent; ecdysial line well-marked, coronal line short; occipital foramen broadly emarginate ventrally; posterior tentorial pits visible ventrally; FR elongate, subtriangular, slightly convex, lateral margins sinuate, with two lateral, spine-like egg bursters at mid length; nasale elongate, rounded apically, not spatulate, without lateral branches; with 7 lateroventral spine-like projections and group of slender pointed spinulae near seta FR6; anteroventral margin of nasale with one half circle of 10 short spatulate setae directed downwards; six rounded dorsolateral stemmata at each side. Antenna (Figs 6–7). Elongate, four segmented, shorter than HW; A1 shortest, A3 longest, with ventroapical spinula; A3’ elongate, slightly shorter than AN4. Mandible (Fig. 12). Prominent, slender, obliquely oriented, distal half strongly curved inwards and upwards, apex sharp, with three minute-dentated structures inside anterior forth; mandibular channel present. Maxilla (Figs 8–9). Cardo fused to stipes; stipes short, broad, incompletely sclerotized; galea and lacinia absent; MP elongate, three segmented; MP3 shortest, MP2 longest, curved inwards and upwards. Labium (Figs 10–11). Prementum subrectangular, about 3.5 times longer than broad, lateral margins slightly curved, without lateral spinulae; LP elongate, two segmented; LP2 broad, robust, longer than LP1, narrowing abruptly on distal fifth, pointed apically.

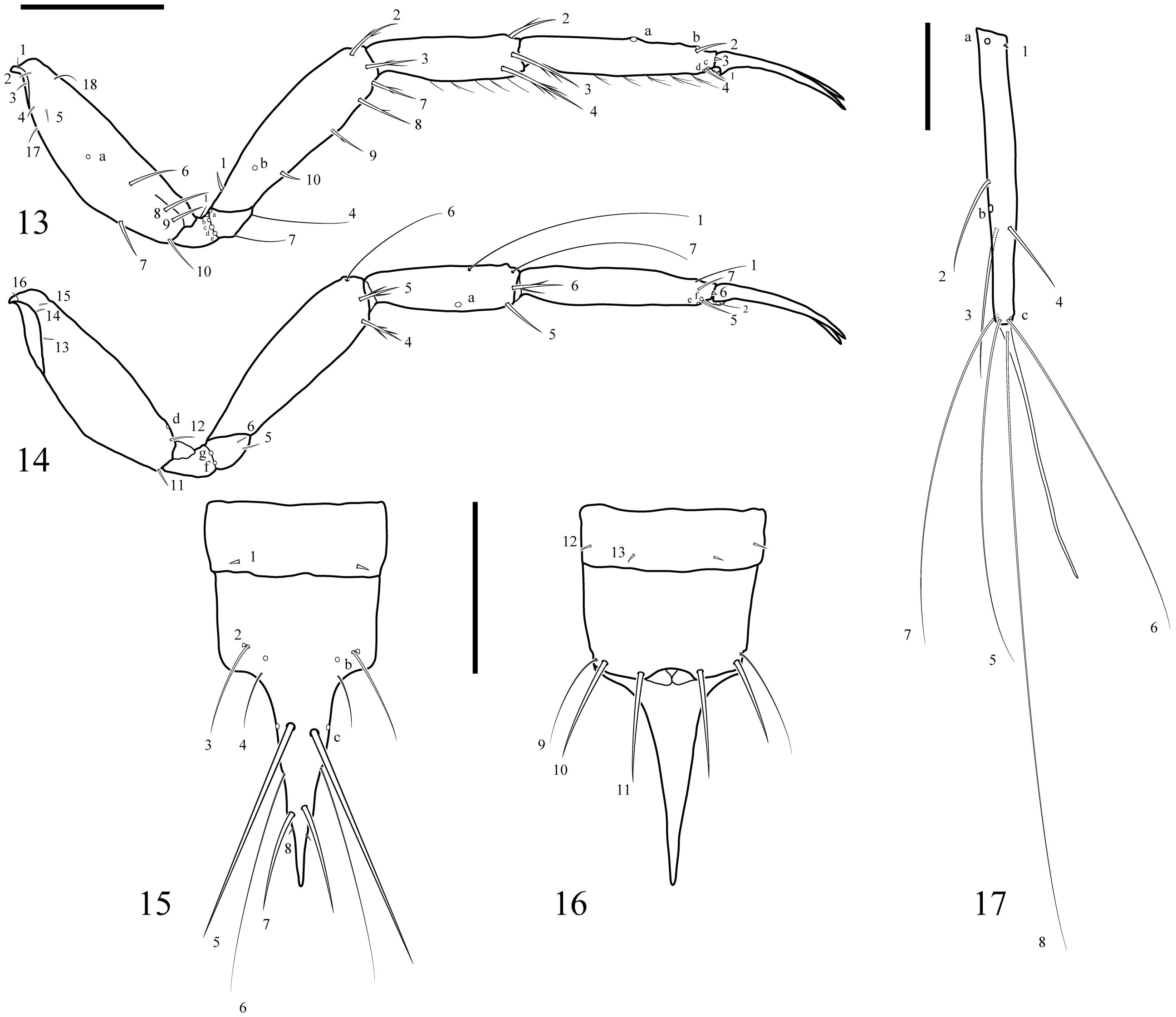
Thorax. Terga convex, pronotum somewhat shorter than meso- and metanotum combined, meso- and metanotum subequal (Fig. 1); protergite subovate, margins rounded, more developed than meso- and metatergite; meso- and metatergite transverse; with anterotransverse carina; sagittal line visible on pro-, meso- and anterior part of metatergite; thoracic sterna membranous; spiracles absent. Legs (Figs 13–14). Long, six segmented, L1 the shortest, L3 the longest; CO robust, elongate, TR divided into 2 parts, FE, TI and TA slender, subcylindrical, PT with two long, slender, slightly curved claws; posterior claw shorter than anterior one on L1 and L2, claws subequal in length on L3; surface of legs in part covered with minute spinulae, TI and TA with a ventral row of elongate spinulae.



FIGURES 4–5. *Agnoshydrus thailandicus* Okada, 2024, instar I: **(4)** head capsule, dorsal aspect (colour pattern not represented); **(5)** head capsule, ventral aspect. EB, egg bursters; TP, tentorial pits. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bar = 0.1 mm.



FIGURES 6–12. *Agnoshydrus thailandicus* Okada, 2024, instar I, head appendages: **(6–7)** antenna, **(6)** dorsal aspect, **(7)** ventral aspect; **(8–9)** maxilla, **(8)** dorsal aspect, **(9)** ventral aspect; **(10)** mandible, dorsal aspect; **(11–12)** labium, **(11)** dorsal aspect, **(12)** ventral aspect. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bar = 0.1 mm.



FIGURES 13–17. *Agnoshydrus thailandicus* Okada, 2024, instar I: **(13–14)** metathoracic leg, **(13)** anterior aspect, **(14)** posterior aspect; **(15–16)** last abdominal segment, **(15)** dorsal aspect, **(16)** ventral aspect; **(17)** urogomphus, dorsal aspect. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bars = 0.1 mm.

Abdomen. Eight segmented; segments I–V sclerotized dorsally, membranous ventrally, segment VI sclerotized both dorsally and ventrally, ventral sclerite independent from dorsal one, segment VII completely sclerotized, ring-like; tergites I–VII similar to each other, narrow, transverse; all tergites lacking sagittal line, with anterotransverse carina; spiracles absent on segments I–VII; LAS (Figs 15–16) longest, completely sclerotized, ring-like, covered with slender spinulae; siphon elongate, subconical, constricted at point of insertion of urogomphi, sharp apically. Urogomphus (Fig. 17) elongate, two segmented; U1 robust; U2 very slender, setiform, shorter than U1.

Chaetotaxy. Similar to that of generalized Hyphydrini larva (Alarie *et al.* 1997, 2017, 2022; Alarie & Michat 2007) except for the following features: primary seta FR7 elongate, hair-like; primary seta PA3 inserted contiguously to primary setae PA1 and PA2; primary setae MX4, MX5, MX6 present; primary setae LA3, LA4, LA5, LA6 articulated distally on prementum; primary seta LA11 articulated medially on palpomere 2; primary setae UR5, UR6, UR7 elongate, hair-like, equal in length.

Instar II (Fig. 2)

As instar I except as follows:

Color. Prothoracic tergite creamy yellow, meso- and metathoracic tergites and abdominal tergites I–VII greyish brown.

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

Head. Head capsule. Surface without reticulation; occipital suture present dorsally, projecting forwards laterally; anteroventral margin of nasale with 21 short, spatulate setae; egg bursters lacking.

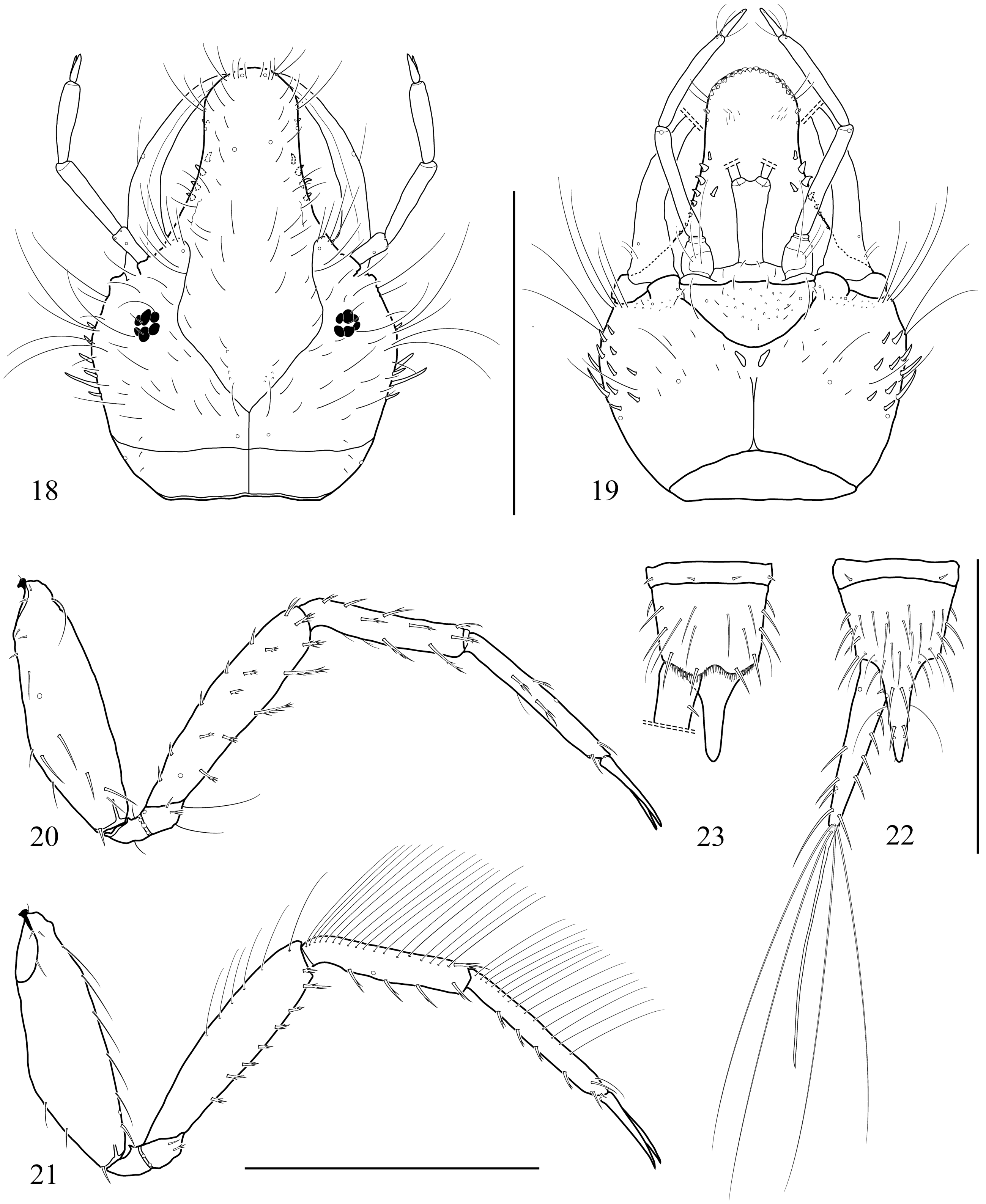
Thorax. Sagittal line visible on the three tergites.

Abdomen. Segments I–II sclerotized dorsally, membranous ventrally; segments III–VI sclerotized dorsally and ventrally, ventral sclerite independent from dorsal one.

Chaetotaxy. Head capsule with a few hair-like, secondary setae; parietale with four spine-like secondary setae along each side of lateral margin; one large secondary pore on dorsal surface of prementum. MN with one hair-like secondary seta on basoexternal margin; thoracic tergites with several elongate secondary setae; secondary leg setation detailed in Table 2; natatory setae present on dorsal margin of FE, TI and TA; abdominal sclerites I–VII with several spine-like secondary setae on posterior half; LAS with several spine-like secondary setae, with dense setae along posterior margin; ventral surface of siphon without hair-like secondary setae. U1 with few spine-like secondary setae.

TABLE 2. Number and position of secondary setae on the legs of instars II and III of larvae of *Agnoshydrus thailandicus* Okada, 2024. A = anterior, AD = anterodorsal, AV = anteroventral, CO = coxa, D = dorsal, PD = posterodorsal, Pr = proximal, PV = posteroventral, V = ventral, NS = natatory setae, n = number of specimens examined, Total = total number of secondary setae on segment. Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively.

Segment	Position	Instar II	Instar III
		(*n*=2)	(*n*=3)
Coxa	D	1/1/1	5–6/5–6/6
	A	0/0/0	2/2/2
	V	0–1/0–1/0	1/2–3/2–4
	Total	4–7/4–6/4–6	8–9/9–11/10–12
Trochanter	Pr	0–1/1/1	0/0–1/0–1
Femur	NS (PD)	1–3/2–3/0	9–10/9–10/3–7
	AD	2/2–3/3–4	3–4/4–5/3–4
	AV	1/1/2–3	4–5/4/5–6
	PV	0/2–3/4	3–4/5/6
	Total	4–76/8–9/10	20–22/22–24/18–22
Tibia	NS (PD)	3/4–6/5	10–12/13–14/15–16
	AD	1/2/3	1–2/2–3/3–4
	AV	0/1/1	1/3–4/2–4
	PV	0/2–3/0	2/2/3–5
	Total	4/7–9/9	14–17/8–12/25–27
Tarsus	NS (PD)	1–4/4/5	7–8/8–12/13–16
	AD	1/1/1–2	1/1/1
	AV	0/0–1/1	1/1/2
	PV	0/0–1/1	2/3/3–4
	Total	2–5/6/8–9	11–12/13–17/19–23



FIGURES 18–23. *Agnoshydrus thailandicus* Okada, 2024, instar III: **(18–19)** head capsule, **(18)** dorsal aspect (color pattern not represented), **(19)** ventral aspect; **(20–21)** prothoracic leg, **(20)** anterior aspect, **(21)** posterior aspect; **(22–23)** last abdominal segment, **(22)** dorsal aspect with urogomphus represented, **(23)** ventral aspect. Scale bars = 0.5 mm.

Instar III (Figs 3, 18–23)

As instar II except as follows:

Color. Posterior half of abdominal tergites VI to VII creamy yellow.

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

Head. Head capsule (Figs 18–19). Anteroventral margin of nasale with 22–24 spatulate setae.

Thorax. Spiracular openings present on mesothorax. Legs. Ventral row of spinulae on TI and TA reduced in number.

Abdomen. Spiracles present on segments I–VII, that on segment VII very small, indistinct. Segment I sclerotized dorsally, membranous ventrally; segments II–VI sclerotized dorsally and ventrally, ventral sclerite independent from dorsal one.

Chaetotaxy. Parietale with 12–16 spine-like secondary setae on lateroventral margin; MN with two hair-like secondary setae on basoexternal margin; thoracic tergites with numerous hair-like secondary setae; secondary leg setation detailed in Table 2; abdominal sclerites I–VIII with numerous spine-like secondary setae all over the surface.

Results of the parsimony analysis

The analysis of the data matrix using the "implicit enumeration" algorithm in TNT resulted in three most parsimonious trees of 102 steps (CI = 0.72, consistency index; RI = 0.75, retention index). All genera of Hyphydrini studied found themselves as a strongly supported clade, inside which *Hyphydrus*, *Coelhydrus*, *Primospes*, *Darwinhydrus*, and *Andex* share a monophyletic origin (Fig. 24). All other hyphydrine genera studied (*Desmopachria*, *Microdytes*, *Agnoshydrus*, *Hovahydrus*) are recovered as part of a polytomy. Character state changes are mapped onto one of the most parsimonious trees (Fig. 25).

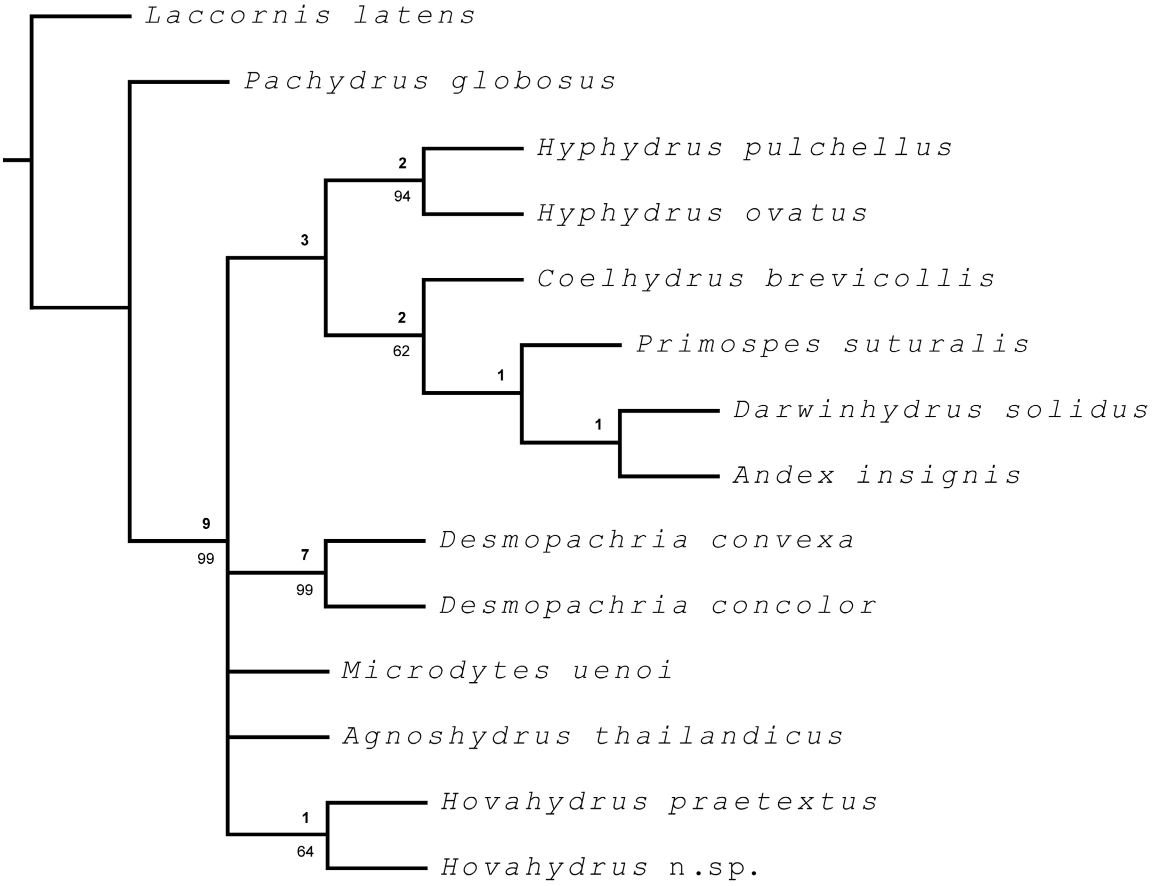


FIGURE 24. Strict consensus cladogram obtained from the cladistic analysis of 59 morphological characters scored for 12 terminal taxa of Hyphydrini and two outgroups, with Bremer support values indicated above branches and Bootstrap support values higher than 50 indicated below branches.

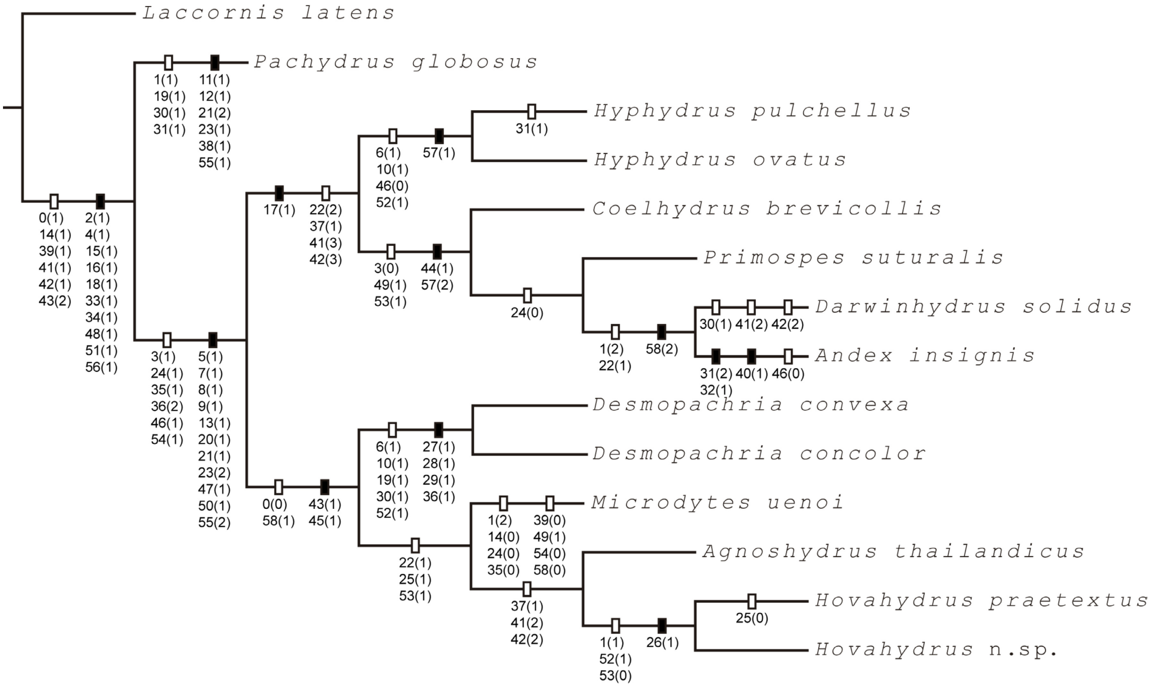


FIGURE 25. One of the most parsimonious trees obtained from the cladistic analysis, with character state changes mapped for each clade. Solid rectangles indicate unique character state transformations; open rectangles indicate homoplasious character state transformations.

Discussion

Study of larval morphology of aquatic Adephaga has experienced considerable progress in recent decades by the adoption of chaetotaxic analyses (Alarie & Michat 2023). Given the great diversity of the Dytiscidae, however, progress in this regard could only be made punctually, often resulting in partial representation in most lineages. Hyphydrini stands out in this regard given that the description of *Agnoshydrus* provided in this paper brings to nine (= 60 %) the number of the genera in this tribe for which larval morphology has been studied in detail.

The first observation of our study is that the tribe Hyphydrini including *Agnoshydrus* has a monophyletic origin (Fig. 24) which agrees with a recent study on the genus *Hovahydrus* (Alarie *et al.* 2022). Such a result should not be surprising given the fact that the data matrix used in our study is based on that developed in Alarie *et al.* (2022). As reflected in Fig. 25, no less than 11 unique synapomorphic characters support this hypothesis (Table 3; see List). The topology of the strict consensus tree obtained in this study, however, differs slightly from that obtained in Alarie *et al.* (2022) being less well-resolved. This is explained by the addition of the genus *Agnoshydrus*, as well as by the inclusion of some new characters and the redefinition of others, with the aim of refining relationships among taxa. With this in mind, *Andex*, *Coelhydrus*, *Darwinhydrus*, *Primospes*, and *Hyphydrus* still stand out as a relatively well-supported clade (Bremer support = 3) (Fig. 24). Such a relationship is supported by the shared presence of a shorter antennomere 4 relative to antennomere 3 (character 17). Except for *Andex*, members of this clade are also characterized by the presence of a significantly larger number of secondary natatory setae on instar III metatibia and metatarsus, which could possibly be seen as an adaptation improving swimming. Within this clade, *Hyphydrus* is recovered sister to the other four genera, all South African (Fig. 24).

TABLE 3. Data matrix used for the cladistic analysis. Missing data coded '?'. *Hovahydrus* sp. near *H. minutissimus* abbreviated to *Hovahydrus* n. sp (cf. Alarie *et al.* 2022).

Species	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
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	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	0	0	0
Agnoshydrus thailandicus	0	0	1	1	1	1	0	1	1	1	0	0	0	1	1	1	1	0	1	0	1	1	1	2	1	1	0	0	0	0
Andex insignis	1	2	1	0	1	1	0	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	2	0	0	0	0	0	0
Coelhydrus brevicollis	1	0	1	0	1	1	0	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1	2	2	1	0	0	0	0	0
Darwinhydrus solidus	1	2	1	0	1	1	0	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	2	0	0	0	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	0	0	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	0	0	1	1	1
Hovahydrus n.sp.	0	1	1	1	1	?	0	?	?	?	0	0	0	1	1	1	1	0	1	0	1	1	1	2	1	1	1	0	0	0
Hovahydrus praetextus	0	1	1	1	1	?	0	?	?	?	0	0	0	1	1	1	1	0	1	0	1	1	1	2	1	0	1	0	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	0	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	0	0	0
Microdytes uenoi	0	2	1	1	1	1	?	1	1	1	0	0	0	1	0	1	1	0	1	0	1	1	1	2	0	1	0	0	0	0
Primospes suturalis	1	0	1	0	1	1	0	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1	2	2	0	0	0	0	0	0

TABLE 3. (Continued)

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

The remaining four genera studied (*Desmopachria*, *Microdytes*, *Hovahydrus*, *Agnoshydrus*) are part of an unresolved polytomy (Fig. 24). Although a clear relationship among these genera could not be determined in the context of this study, some morphological evidence suggests a possible affinity of *Agnoshydrus* with *Desmopachria*, *Microdytes*, and *Hovahydrus*. Indeed, larvae of these genera are characterized by two unique character states: presence of 1–3 anteroventral secondary spiniform setae on instar III metatarsus (character 43; Fig. 20) and sclerotized ventral surface of abdominal segment II in instars II and III (character 45). Ribera & Balke (2007) postulated that *Agnoshydrus* could possibly be related to *Desmopachria* and *Microdytes* based on adult morphological characters. Compared to *Desmopachria*, however, larvae of *Agnoshydrus* clearly differ in several characters, including the primary seta PA3 inserted contiguously to primary setae PA1 and PA2 (character 06; Fig. 4), the presence of secondary spine-like setae on the lateral margin of parietals (character 10; Figs 18–19), the presence of the primary setae MX4, MX5, MX6 (character 19; Figs 8–9) and the primary pore LAb (character 30; Fig. 10), the distal position of the primary setae LA3, LA4, LA5, LA6 on the prementum and the medial articulation of the primary seta LA11 on the palpomere 2 (characters 27–29; Fig. 10), as well as the presence of more than nine natatory setae along the dorsal margin of the instar III mesofemur (character 36). Furthermore, instar III of *Agnoshydrus* shares with those of *Microdytes* and *Hovahydrus* a maxillary palpus 1.50–1.90 times as long as the labial palpus (character 22), a more elongate labial palpomere II relative to labial palpomere I (LP2/LP1 > 1.50) (character 25), and a shorter last abdominal segment (LAS/HW < 0.90) (character 53). Any inferred relationship among these genera remains speculative at this stage, given that these characters are homoplastic within Hyphydrini . Clearly, sampling additional Hyphydrini genera and species would be necessary to help clarify the phylogenetic position of the genus *Agnoshydrus* within this tribe.

Acknowledgements

The authors would like to warmly thank Weeyawat Jaitrong (Pathum Thani, Thailand) for giving the opportunity to conduct field survey of Thailand dytiscid beetles. Financial support was provided by Agencia Nacional de Promoción Científica y Tecnológica under Grant PICT-I-INVI-00460 and by Universidad de Buenos Aires under Grants UBACyT-20020190100240BA and UBACyT-20020220400253BA to M.C.M.

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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 (instars I–III)*: (0) not spatulate, lateral margin almost parallel-sided to slightly diverging posteriorly; (1) spatulate, lateral margin strongly attenuate posteriorly.
01. *Frontoclypeus (instars I–III)*: (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 (instars I–III)*: (0) separate at the ventral midline; (1) meet on the ventral midline.
03. *Primary seta FR7 (instar I)*: (0) spine-like; (1) hair-like.
04. *Primary seta FR13 (instar I)*: (0) absent; (1) present.
05. *Primary pore FRb (instar I)*: (0) present; (1) absent.
06. *Primary seta PA3 (instar I)*: (0) inserted contiguously to primary setae PA1 and PA2; (1) inserted far from primary setae PA1 and PA2.
07. *Primary pore PAc (instar I)*: (0) not inserted anteriorly to stemmata; (1) inserted anteriorly to stemmata.
08. *Primary pore PAe (instar I)*: (0) present; (1) absent.
09. *Primary pore PAj (instar I)*: (0) present; (1) absent.
10. *Secondary spine-like setae on lateral margin of parietals (instars II–III)*: (0) present; (1) absent.
11. *Antennomere 2 (instar III)*: (0) longer than antennomere 1; (1) subequal in length to antennomere 1.
12. *Antennomere 3 (instar III)*: (0) longer than antennomere 1; (1) subequal in length to antennomere 1.
13. *Ventral apical spinula on antennomere III (instars I–III)*: (0) absent; (1) present.
14. *Primary seta AN3 (instars I–III)*: (0) inserted distally; (1) inserted at about midlength.
15. *Primary pore ANf (instars I–III)*: (0) present; (1) absent.
16. *Primary pore ANh (instars I–III)*: (0) present; (1) absent.
17. *Antennomere 4 (instar III)*: (0) A4/A3 > 0.30; (1) A4/A3 < 0.30.
18. *Cardo (instars I–III)*: (0) not fused to stipes: (1) fused to stipes.
19. *Primary setae MX4, MX5, MX6 (instars I–III)*: (0) present; (1) absent.
20. *Primary setae MX8 and MX9 (instars I–III)*: (0) present; (1) absent.
21. *Primary pore MXh (instars I–III)*: (0) inserted on the galea; (1) inserted on the stipes; (2) absent.
22. *Maxillary palpus (instar III)*: (0) < 1.40 times the 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 (instars I–III)*: (0) broader than long; (1) as broad as long; (2) longer than broad.
24. *Labial palpomere II (instars I–III)*: (0) narrow, subcylindrical, narrowing at apex; (1) robust, broadest at midlength.
25. *Labial palpomere II (instar III)*: (0) LP2/LP1 < 1.30; (1) LP2/LP1 > 1.50.
26. *Mandible (instar III)*: (0) MNL/MNW > 3.60; (1) MNL/MNW < 3.40.
27. *Primary setae LA3, LA4, LA5 (instars I–III)*: (0) articulated distally on prementum; (1) articulated proximally on prementum.
28. *Primary seta LA6 (instars I–III)*: (0) articulated distally; (1) articulated submedially.
29. *Primary seta LA10 (instars I–III)*: (0) articulated medially; (1) articulated distally.
30. *Primary pore LAb (instars I–III)*: (0) present; (1) absent.
31. *Prementum (instars II–III)*: (0) lacking secondary setae; (1) with one secondary seta; (2) with several secondary setae.
32. *Metatrochanter (instar III)*: (0) 0–1 ADi secondary seta; (1) > 2 ADi secondary setae.
33. *Primary seta TR2 (instars I–III)*: (0) present; (1) absent.
34. *Primary pore FEa (instars I–III)*: (0) present; (1) absent.
35. *Dorsal profemoral secondary natatory setae (instar III)*: (0) absent; (1) present.
36. *Dorsal mesofemoral secondary natatory setae (instar III)*: (0) absent; (1) 1–5; (2) > 9.
37. *Dorsal metafemoral secondary natatory setae (instar III)*: (0) absent; (1) present.
38. *Ventral femoral secondary natatory setae (instars II–III)*: (0) absent; (1) present.
39. *Primary seta TI7 (instar I)*: (0) short, spine-like; (1) elongate, hair-like.
40. *Primary pore TIa (instars I–III)*: (0) present; (1) absent.
41. *Dorsal natatory setae on metatibia (instar III)*: (0) absent; (1) 1–9; (2) 14–22; (3) > 27.

42. *Dorsal natatory setae on metatarsus (instar III)*: (0) absent; (1) 1–9; (2) 13–21; (3) > 23.
43. *Anteroventral secondary spiniform setae on metatarsus (instar III)*: (0) absent; (1) 1–3; (2) > 4.
44. *Metathoracic legs (instar III)*: (0) shorter, < 3.30 times as long as HW; (1) longer, > 3.50 times as long as HW.
45. *Ventral surface of abdominal segment II (instars II–III)*: (0) membranous; (1) sclerotized.
46. *Ventral surface of abdominal segment III (instars II–III)*: (0) membranous; (1) sclerotized.
47. *Ventral surface of abdominal segments IV–V (instars II–III)*: (0) membranous; (1) sclerotized.
48. *Ventral surface of abdominal segment VI (instars II–III)*: (0) membranous; (1) sclerotized.
49. *Abdominal segment VIII (instars II–III)*: (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.
50. *Primary setae AB6 and AB7 (instar I)*: (0) short; (1) elongate.
51. *Primary pore ABa (instar I)*: (0) present; (1) absent.
52. *Siphon (instars II–III)*: (0) lacking secondary setae on ventral surface; (1) with a variable number of secondary setae on ventral surface.
53. *Abdominal segment VIII (instar III)*: (0) LAS/HW > 1.00; (1) LAS/HW < 0.90.
54. *Primary seta UR5 (instar I)*: (0) short, spine-like; (1) elongate, hair-like.
55. *Primary seta UR8 (instar I)*: (0) inserted apically on urogomphomere 2; (1) inserted submedially on urogomphomere 2; (2) inserted proximally on urogomphomere 2.
56. *Urogomphomere 1(instars II–III)*: (0) lacking secondary setae; (1) with secondary setae.
57. *Urogomphomere 1 (instar III):* (0) U1/HW < 0.80; (1) U1/HW = 1.00–1.80; (2) U1/HW > 2.00.
58. *Urogomphomere 1 (instar III)*: (0) U1/U2 = 1.00–3.00; (1) U1/U2 < 1.00; (2) U1/U2 > 4.00.