

Larvae of four species of the *Hyphydrus lyratus* species-group (Coleoptera: Dytiscidae: Hydroporinae)

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Abstract The third instars of the Australian species *Hyphydrus lyratus* Swartz, *H. contiguus* Wehncke, *H. elegans* (Montrouzier) and *H. decemmaculatus* Wehncke (Coleoptera: Adephaga: Dytiscidae) are described, including a chaetotaxic analysis of the cephalic capsule, head appendages, legs, last abdominal segment and urogomphi. Larvae of these species morphologically resemble other species of *Hyphydrus* Illiger for which the larvae have been described. A key to identify larvae of the Australian species of *Hyphydrus* is provided. Larvae of *H. effeminatus* Watts appear identical to those of *H. decemmaculatus*. A 822 bp fragment of the *COI* gene of larvae and adults of these species showed very slight differences, suggesting the possibility that, in Australia at least, *H. decemmaculatus* is polymorphic.

Key words Australia, chaetotaxy, Hydradephaga, Hyphydrini, *Hyphydrus lyratus* species-group, larvae.

INTRODUCTION

The Hydroporinae genus *Hyphydrus* Illiger contains 133 species worldwide (Nilsson 2001) distributed in Europe, Asia, Africa and Australia (Biström 1982). *Hyphydrus* is included in the tribe Hyphydrini along with 14 other genera (Nilsson 2001). The genus is postulated to be monophyletic based on the shared presence of a well-sclerotised spermatheca and the foremargin of head capsule of adult margined (Biström 1982; Biström *et al.* 1997).

Once subdivided into four subgenera, *Hyphydrus* is now composed of 20 species-groups, the bulk of which are distributed in Africa. One of these, the *Hyphydrus lyratus* species-group comprises six species, *H. contiguus* Wehncke, *H. dani* Biström, Balke & Hendrich, *H. decemmaculatus* Wehncke, *H. effeminatus* Watts, *H. elegans* (Montrouzier) and *H. lyratus* Swartz. Except for *H. lyratus* Swartz, which is distributed all over the Oriental, Palearctic and Australian regions, and *H. dani* from New Guinea, all these species are endemic to Australia (Biström 1982; Nilsson 2001).

Assessment of larval morphology has proven useful in studying phylogenetic relationships among selected groups of the family Dytiscidae (Alarie 1997; Alarie *et al.* 1999, 2000, 2001, 2002). For the Dytiscidae, the use of the positions and shapes of the setae and pores on larvae has proven useful for reconsidering classifications based mainly on adult characteristics. Morphology of the larvae of the genus *Hyphydrus*, however, is poorly known and of unequal value. Only seven

species have been described or illustrated (Bertrand 1928, 1930, 1935, 1948, 1963, 1972, 1976; Kurosa 1959; Wise 1961; Watts 1963; De Marzo 1977; Wichard *et al.* 1995; Alarie *et al.* 1997; Nakanishi 2001). However, except for the descriptions of *H. aubei* (De Marzo 1977), *H. pulchellus* Clark and *H. ovatus* (L.) (Alarie *et al.* 1997) all these descriptions are fairly superficial and do not use chaetotaxy, which hampers any attempt at comparing them.

The recent discovery of the larvae of four species of the *H. lyratus* species-group provided the impetus for this study, which is meant to be a step towards a better knowledge of the larvae of the genus *Hyphydrus*. More specifically it aims at: (i) describing or redescribing the final instar (= third instar) of four Australian species of the *H. lyratus* species-group, namely *H. contiguus*, *H. decemmaculatus*, *H. elegans* and *H. lyratus* with an emphasis on chaetotaxy of the head capsule, head appendages, legs, last abdominal segment and urogomphi; (ii) providing keys and illustrations to facilitate their identifications; and (iii) comparing the ground-plan pattern of larval features of members of the *H. lyratus* group with those of other *Hyphydrus* species for which the larvae have been described.

MATERIALS AND METHODS

Larvae examined

Descriptions of the larval stages and taxonomic conclusions reported in this paper are based on the examination of larvae usually found in association with adults. Some larvae of each species were identified to species by rearing some larvae

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either collected in the field or collected in situations where they could be unequivocally associated with a particular species. To better determine their identity (see under *H. decemmaculatus*), we sequenced a 822 bp fragment of the *COI* gene of larvae and adults of *H. decemmaculatus* and *H. effeminatus* using the method outlined in Leys *et al.* (2003).

Preparation

Larvae were disarticulated and mounted on standard glass slides with Hoyer's medium. Microscopic examination at a magnification of 80–800× was performed using an Olympus BX50 compound microscope equipped with Nomarsky differential interference optics. Figures were prepared with the aid of a drawing tube attached to the microscope. Voucher specimens are deposited in the larval collection of Y Alarie (Department of Biology, Laurentian University, Sudbury, Canada) and in the South Australian Museum (Adelaide, Australia, CHS Watts).

Descriptions

A complete description applying to all species is provided under the treatment of the genus, but only shorter diagnoses/descriptions and comments on variation are provided under the treatments of each species.

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. The characters and terms used in the morphometric analysis are defined as:

Head length (HL): total head length including the frontoclypeus measured medially along the epicranial stem.

Head width (HW): maximum width measured posterior to the stemmata.

Length of frontoclypeus (FCL): from apex of the nasal to the back of the ecdysial suture.

Spatula width (SpW): maximum width of the rounded and broader apex of the frontoclypeus.

Frontoclypeus narrowest width (FCNW): narrowest distance of the frontoclypeus as measured at about mid-length.

Occipital foramen width (OcW): maximum width measured along the dorsal margin of the occipital foramen.

Length of antenna: derived by adding the length of each individual antennomere; comparison among antennomeres was made using the capital letter A with a number corresponding to the segment considered (e.g. A1 for antennomere I); A3' is used as an abbreviation for the lateral elongation of antennomere III.

Length of maxillary palpus: derived by adding the length of each individual palpomere (e.g. MX1 for palpomere I). The length of the palpomere II was sometimes very difficult to determine with precision owing to its recurved shape.

Length of labial palpus: derived by adding the length of each individual palpomere (e.g. LB1 for palpomere I).

Length of legs: derived by adding the length of each individual segment including the longest claw; the length of each segment was taken at the longest point except for the trochanter which includes only the proximal portion (the length of distal portion being included in the femoral length).

Dorsal length of last abdominal segment (LLAS): includes the whole sclerite measured dorsally along the mid-line from the anterior margin to the posterior margin; siphon refers to the dorsal prolongation of the eighth abdominal segment (= last abdominal segment); the length of the siphon was determined by measuring the difference between the dorsal and ventral lengths of the segment.

Length of urogomphus: derived by adding the length of each individual urogomphomere; comparison between the two urogomphomeres was made using the abbreviation Uro (e.g. Uro1 for urogomphomere I). The length of the second urogomphomere is not included in descriptions owing to difficulty in distinguishing the primary setae UR8 from the urogomphomere.

The individual measurements defined above were used in calculating several ratios aiming at characterising the body shape. Most of the ratios used in this paper are similar to those mentioned in a previous paper dealing with larval morphology of the Hyphydrini (Alarie *et al.* 1997) and, as such, are not defined here. However, one new ratio is introduced in this paper, SpW/FCNW, used for characterising the shape of the apical portion of the frontoclypeus.

Chaetotaxic analysis

Primary (observed in instar I) and secondary (added throughout the ontogenetic development) setae and pores were distinguished on the cephalic capsule, head appendages legs, last abdominal segments and urogomphi. The setae and pores were coded according to the system proposed by Alarie (1991) for the cephalic capsule and head appendages, Alarie *et al.* (1990) for the legs and Alarie and Harper (1990) for the last abdominal segment and urogomphi. The position of leg sensilla is described by adding the following abbreviations: A, anterior; AV, anteroventral; D, dorsal; Di, distal; Pr, proximal; PV, posteroventral.

Colour

Description of colour is given for all species from ethanol-preserved specimens.

SYSTEMATICS

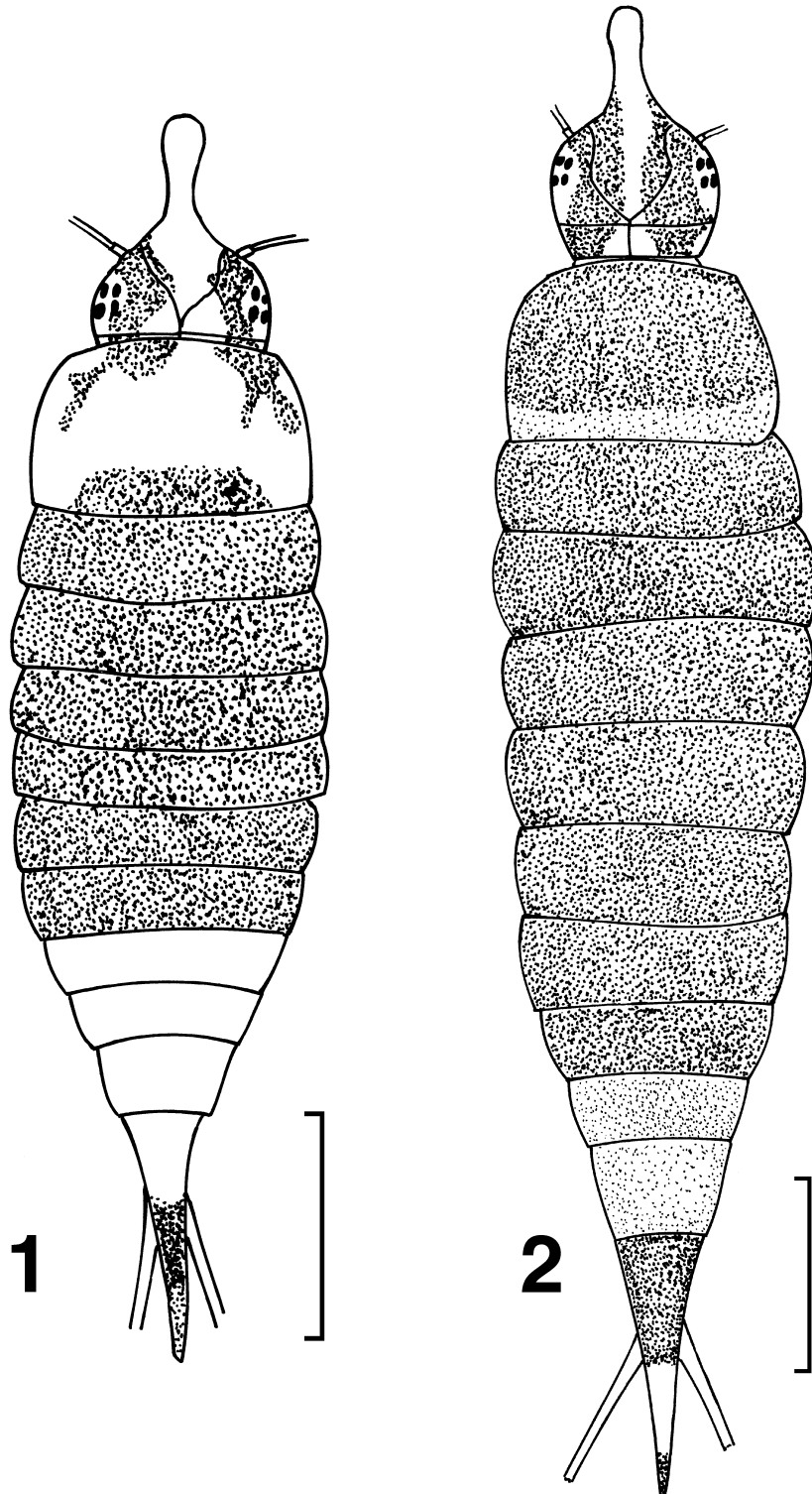
Within Australia, larvae of *Hyphydrus* can be keyed out from other Dytiscidae larvae by the following combination of characters: frontoclypeus extended anteriorly into a frontal projec-

tion (= nasale); nasale elongate, narrower than apex at about mid-length and lacking lateral notches.

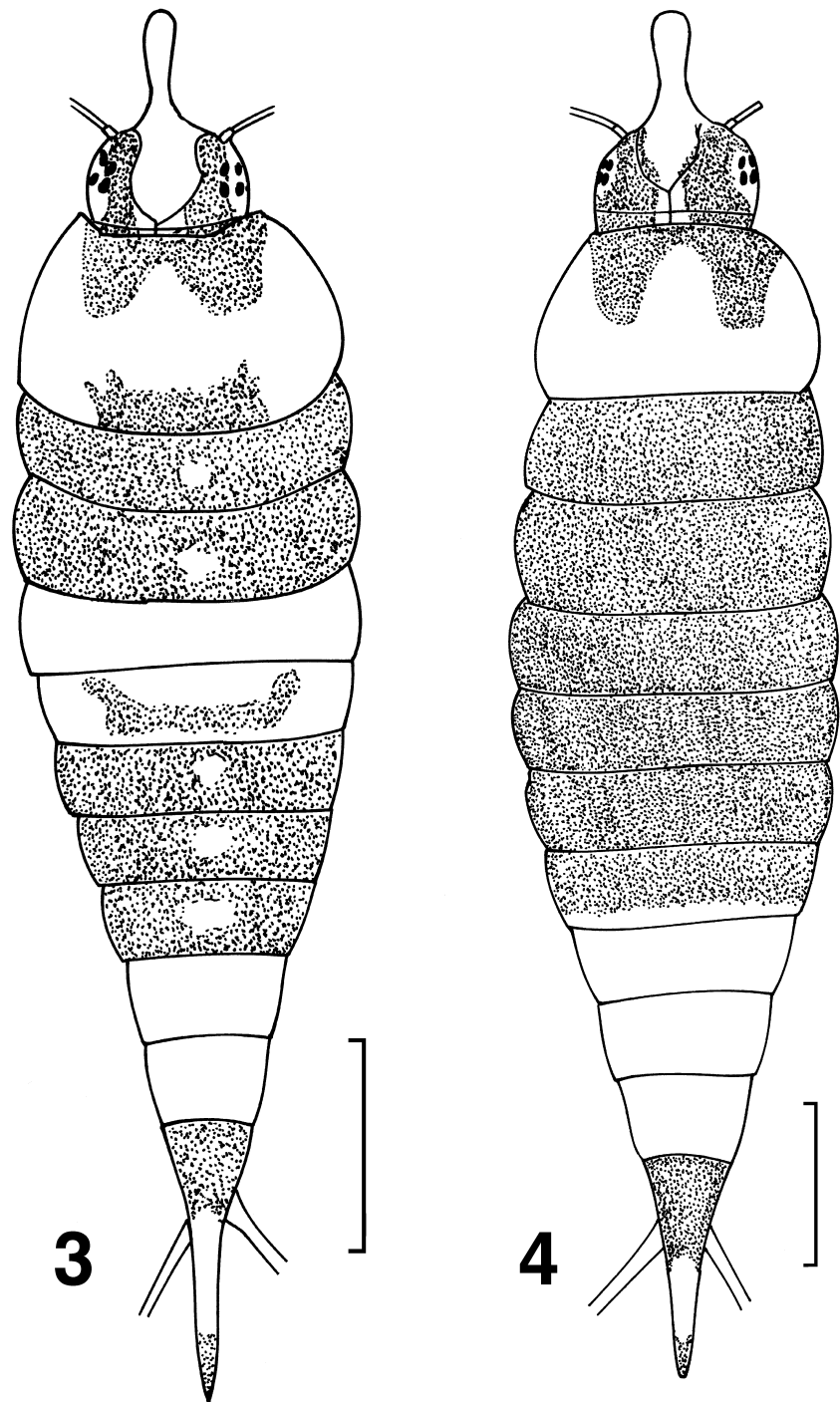
Instar III of *H. lyratus* species-group (Figs 1–4)

Diagnosis. Body fusiformate; frontoclypeus elongated, narrow apically, lacking lateral notches; gular sutures fused, so epicranial plates meets at ventral midline; maxillary cardo

lacking and primary seta MX1 inserted on maxillary stipes; antennomere III with ventroapical spinula; primary pores ANf and ANh lacking; prementum elongated and narrow, primary setae LA3, LA4, LA5 inserted distally; labial palpomere II with primary setae LA10 inserted medially, longer than palpomere I; natatory setae present on dorsal margin of femora, tibiae and tarsi; abdominal segments IV–VIII sclerotised ventrally; siphon elongated, acute apically, with secondary spines



Figs 1,2. Dorsal colour habitus of *Hyphidrus* Illiger, dorsal aspect, third instar: (1) *H. contiguus* Wehncke; (2) *H. decemmaculatus* Wehncke. Scale bar = 1 mm.



Figs 3,4. Dorsal colour habitus of *Hyphydrus* Illiger, dorsal aspect, third instar: (3) *H. lyratus* Swartz; (4) *H. elegans* (Moutrouzier). Scale bar = 1 mm.

over ventral surface; urogomphus two-segmented, longer than last abdominal segment; urogomphomere I subequal or longer than HW, with several secondary setae; primary seta UR8 inserted proximally on urogomphomere II.

Description. Head. HL = 1.03–1.29 mm; HW = 0.74–1.03 mm; FCL = 0.83–1.06 mm. **Cephalic capsule.** Longer than broad (HL/HW = 1.28–1.43), pear-shaped, tapering posteriorly, lacking a constriction posteriorly; ecdysial suture well-developed, coronal suture short about 0.20 times HL; occipital suture present HW/OcW = 1.20–1.55; frontoclypeus bluntly

rounded, narrow apically (SpW/FCNW = 1.34–1.86), elongated (FCL/FCNW = 6.60–9.30), ventroapical margin with several spatulate setae (= lamellae clypeales); stemmata subdivided into two vertical series, stemmata posterior row more widely spaced; tentorial pits visible ventrally on each side of middle at about midlength. **Antenna.** Four-segmented, slightly shorter than head capsule, length of antenna/HW = 0.78–0.82; A2 = A3 > A1 > A4, A2/A3 = 0.87–1.07; A3' slightly or distinctly shorter than antennomere IV (A3'/A4 = 0.69–0.90). **Mandible.** Falciform, narrow, not toothed on inner margin,

curved medially and dorsally apically and elongated, >0.55 times HL. *Maxilla*. Stipes short, thick, incompletely sclerotised ventrally; cardo, lacinia, galea lacking; palpus three-segmented, about as long as antenna; MX1 = MX2 > MX3. *Labium*. Prementum about 3.40–4.60 times longer than broad; palpus two-segmented, distinctly shorter than maxillary palpus (length of maxillary palpus/length of labial palpus = 2.02–2.14), palpomere II, 0.97–1.33 times length of palpomere I. *Thorax*. Pronotum trapezoidal dorsally, ovate laterally, widest at posterior margin; length of pronotum about twice that of mesonotum; metanotum subequal to mesonotum, both slightly wider than pronotum; mesopleural region with spiracular opening on each side. *Legs*. Five-segmented; metathoracic legs longest, 1.30–1.40 times length of prothoracic legs; coxa = femur > tibia = tarsus > trochanter 3.21–3.22 times HW; tarsus with two claws, posterior claw slightly shorter than anterior claw on pro- and mesothoracic legs, slightly longer on metathoracic leg; posterior metathoracic claw 0.30–0.36 times as long as metatarsus; position and number of secondary setae as in Table 1. *Abdomen*. Eight-segmented; maximum

width of body at level of segments I and II; segments I–III sclerotised dorsally, membranous ventrally; segments IV–VIII sclerotised both dorsally and ventrally, segments IV–V with a ventral plate independent of rest of sclerite, segments VI–VIII fully sclerotised; all terga with anterotransverse carina; segments I–VII each with a pair of spiracular openings; segment VIII elongated (LLAS = 1.12–1.48 mm; LLAS/HW = 1.25–1.79); siphon elongated, >0.70 times LLAS, with 8–13 ventral secondary setae. *Urogomphus*. Two-segmented, longer than LLAS; length of Uro1 = 0.83–1.33 mm; length of Uro1/HW = 0.98–1.74; length of Uro1/LLAS = 0.66–1.10; Uro1 with several secondary setae.

Key to instar III of known Australian species of *Hyphydrus*

- 1 Abdominal terga I and II yellow (Fig. 3); urogomphomere I subequal or longer than LLAS and >1.40 times HW; length of metathoracic leg >3.40 HW..... *H. lyratus*

Table 1 Number of secondary setae on the legs of instar III of selected species of Hyphydrini

Segment	Sensillar series	Species				Segment	Sensillar series	Species				
		CON (n = 4)	EFF (n = 7)	LYR (n = 4)	ELE (n = 5)			CON (n = 4)	EFF (n = 7)	LYR (n = 4)	ELE (n = 5)	
ProCO	D	6–8	6–11	4–10	7–10	MesoTI	NS	32–35	26–34	35–48	35–41	
	A	3–5	4–7	4–8	4–6		AD	6–8	6–9	6–8	5–10	
	V	6–8	7–14	9–16	9–14		AV	7–8	9–11	8–9	8–12	
	Total	15–20	17–28	17–32	22–27		PV	4–5	7–8	5–8	5–8	
ProTR	Pr	1–2	1–2	1	2	MesoTA	Total	50–55	51–59	55–71	60–70	
ProFE	NS (D)	23–25	22–27	21–29	24–29		NS	20–26	21–27	23–26	20–29	
	AD	7–8	7–9	6–9	8–12		AD	1–2	2	2–3	3–4	
	AV	9–13	9–14	8–12	9–15		AV	4–5	3–6	2–5	4–7	
	PD	0	0	0	0	PV	6–8	9–11	10–12	8–10		
	PV	3–6	4–6	3–5	5–7	Total	32–39	38–41	37–45	36–50		
ProTI	Total	44–51	44–53	40–54	47–58	MetaCO	D	10–13	9–16	15–19	11–17	
	NS	25–31	24–29	26–35	27–34		A	4–6	7–10	6–8	7–12	
	AD	5–6	5–7	4–6	4–7		V	7–11	12–20	19–25	14–20	
	AV	6–9	9–12	6–8	9–11		Total	23–30	28–43	40–50	35–44	
	PV	3–4	4–7	4	5–6	MetaTR	Pr	2–3	2–3	1–2	2–5	
Total	42–49	45–52	42–51	47–55	MetaFE		NS (D)	12–18	12–20	13–18	18–25	
ProTA	NS	15–21	15–19	14–18			15–22	AD	9–12	11–18	12–16	14–21
	AD	1–2	1	1			1–2	AV	8–10	10–15	10–12	10–12
	AV	4	5–7	5–7			5–7	PD	0	0–1	0–2	1–2
	PV	4–5	4–6	5–7		5–6	PV	7–10	11–16	14–19	11–19	
	Total	25–31	25–31	27–32	26–36	Total	38–48	49–69	55–63	57–76		
MesoCO	D	8–9	10–12	10–16	10–13	MetaTI	NS	30–37	29–36	33–45	34–44	
	A	4–5	4–7	5–8	3–6		AD	10–12	11–13	7–11	9–14	
	V	6–8	8–17	15–19	10–15		AV	7–9	7–11	9–12	11–15	
	Total	19–21	23–35	32–41	24–32		PV	5–7	8–11	8–11	8–13	
MesoTR	Pr	2	1–3	2	1–2		Total	53–63	61–69	57–75	67–80	
MesoFE	NS (D)	20–25	20–26	21–27	21–29	MetaTA	NS	23–29	23–30	26–33	27–37	
	AD	8–9	7–13	8–9	9–13		AD	2–3	1–3	3–4	3–5	
	AV	6–8	6–13	8–9	6–13		AV	4–6	4–7	4–5	5–7	
	PD	0	0	0	0–1		PV	8–11	11–13	12–15	11–12	
	PV	6–8	7–10	8–11	7–11		Total	38–49	42–51	46–55	48–60	
	Total	43–47	43–56	47–55	47–63							

Leg segments: CO, coxa; FE, femur; TA, tarsus; TI, tibia; TR, trochanter; sensillar series: A, anterior; AD, anterodorsal; AV, anteroventral; D, dorsal; PD, posterodorsal; Pr, proximal; PV, posteroventral; NS, natatory setae; V, ventral; species studied: CON, *Hyphydrus contiguus*; EFF, *H. effeminatus*, ELE, *H. elegans*, LYR, *H. lyratus*; n, number of specimens studied.

- Abdominal terga I and II brown (Figs 1,2,4); urogomphomere I shorter than LLAS and <1.20 times HW; length of metathoracic leg <3.30 HW..... 2
- 2 Length of mentum/width of mentum <3.90; pronotum predominantly yellowish, with a brown macula along posterior margin (Fig. 1); protarsus with 4 AV secondary spines; metatibia with <7 PV secondary spines..... *H. contiguus*
- Length of mentum/width of mentum >4.10; pronotum either predominantly yellowish, lacking a brown macula along posterior margin (Fig. 4), or dark brown (Fig. 2); protarsus with >5 AV secondary spines; metatibia with >8 PV secondary spines..... 3
- 3 Abdominal tergum V dark brown (Fig. 2); mesotibia with <34 natatory setae; mesotarsus with 2 AD secondary spines..... *H. decemmaculatus/H. effeminatus*
- Abdominal tergum V predominantly yellow (Fig. 4); mesotibia with >35 natatory setae; mesotarsus with >3 AD secondary spines..... *H. elegans*

***Hyphydrus contiguus* Wehncke (Fig. 1)**

Material examined. *Queensland.* 20 km W Petford, 28.iii.1996; 8 km S Greenvale, 27.iii.1996; 2 km N Mt Molloy, 5.ii.1997. *Northern Territory.* Georgetown Billabong, Kakadu N.P., 19.iii.1998.

Diagnosis. Mentum less than 3.90 times as long as broad; metathoracic legs less than 3.30 times HW; Uro1 shorter than LLAS and less than 1.20 times HW; abdominal terga I and II brown; abdominal tergum V yellow.

Description. Colour. Cephalic capsule. Dorsal surface predominantly pale yellow with dark brown longitudinal stripes. **Head appendages.** Predominantly creamy white to pale yellow, antennomeres I–III lightly infusate apically. **Thorax.** Pronotum predominantly pale yellow, except for a brown macula each side of anterior margin and mesally along posterior margin; meso- and metaterga predominantly brown. **Legs.** Creamy white to pale brown. **Abdomen.** Terga I–IV brown; terga V–VII yellow to pale brown; tergum VIII yellow over anterior region, brownish posteriorly, slightly paler over siphon. **Urogomphus.** Brown, paler proximally over a short distance. **Head.** HL = 1.03–1.08 mm (mean = 1.05 mm, $n = 4$); HW = 0.78–0.81 mm (mean = 0.80 mm, $n = 4$); FCL = 0.83–0.87 mm (mean = 0.85 mm, $n = 4$); SpW/FCNW = 1.47–1.70; length of mentum/width of mentum = 3.20–3.80. **Legs.** Metathoracic leg about 3.00 times as long as HW; position and number of secondary setae as in Table 1. **Abdomen.** LLAS = 1.12–1.23 mm (mean = 1.16 mm, $n = 4$). **Urogomphus.** Length of Uro1 = 0.83–0.90 mm (mean = 0.91 mm, $n = 4$); length of Uro1/HW = 1.10–1.23; length of Uro1/LLAS = 0.71–0.89.

Distribution. *Hyphydrus contiguus* is found in the wetter tropical areas of northern Australia from the Kimberly to Cape York and at least as far south as Bundaberg on the eastern coast.

***Hyphydrus decemmaculatus* Wehncke (Fig. 2)**

Material examined. *Queensland.* 5 km NE Mt Molloy, 30.iii.1996; 2 km N Mt Molloy, 5.ii.1997; Eubenangee Swamp nr Babinda 1.iv.1996 and 4.ii.1997; 10 km S Cardwell, 7.ii.1997; Nardello's Lagoon, 6.ii.1997. *Northern Territory.* Manton Dam, 23.iii.1998, 2.ii.1999.

Diagnosis. Mentum more than 4.10 times as long as broad; metathoracic legs less than 3.30 times HW; Uro1 shorter than LLAS and less than 1.20 times HW; abdominal terga I, II and V brown.

Description. Colour. Cephalic capsule. Dorsal surface predominantly dark brown, paler over frontoclypeus and posteromesal region of parietale. **Head appendages.** Yellow to pale brown. **Thorax.** Pronotum predominantly dark brown, yellow to pale brown along posterior margin; meso- and metatergum predominantly dark brown. **Legs.** Predominantly brown. **Abdomen.** Terga I–VIII dark brown; terga VI–VII paler; tergum VIII yellow to pale brown over prescutum and siphon. **Urogomphus.** Dark brown, paler distally over a short distance.

Head. HL = 1.14–1.24 mm (mean = 1.18 mm, $n = 7$); HW = 0.82–0.91 mm (mean = 0.87 mm, $n = 7$); FCL = 0.90–0.99 mm (mean = 0.95 mm, $n = 7$); SpW/FCNW = 1.52–1.86; length of mentum/width of mentum = 4.16–4.72. **Legs.** Metathoracic leg about 3.20 times as long as HW; position and number of secondary setae as in Table 1. **Abdomen.** LLAS = 1.22–1.46 mm (mean = 1.32 mm, $n = 7$). **Urogomphus.** Length of Uro1 = 0.86–1.00 mm (mean = 0.92 mm, $n = 6$); length of Uro1/HW = 0.98–1.14; length of Uro1/LLAS = 0.66–0.73.

Distribution. Based on specimens in the South Australian Museum, *H. decemmaculatus* is patchily distributed in wetter areas of northern Australia, with specimens from the Kimberly, Cairns region and near Brisbane. No specimens are known from the Northern Territory. The species also occurs in Papua New Guinea (Biström 1982). *Hyphydrus effeminatus* (see below) occurs in the Darwin/Kakadu area of the Northern Territory, and on Cape York Peninsula as far south as Townsville.

Remarks. Larval specimens from Eubenangee swamp were associated with *H. decemmaculatus* owing to the abundance of adults and larvae of only that species at that locality. We cannot separate these as larvae of *H. effeminatus* from Manton Dam (identified by rearing). A preliminary DNA sequence analysis showed very slight differences between *H. decemmaculatus* and *H. effeminatus* (three substitutions in 828 bp, = sequence divergence of 0.36%). This, together with our failure to differentiate the larvae morphologically, suggests that they could represent one species showing an extreme polymorphism at the adult stage (i.e. males with narrower tarsi and females with shiny surface (*effeminatus* facies) compared with males with greatly enlarged tarsi and females with rugose surface (*decemmaculatus* facies)). Further DNA study is needed to verify this hypothesis. Since the larvae of the two species could not be separated morphologically (nor biochemically), the larvae of *H. effeminatus* from the Northern Territory have been included in the above description of *H. decemmaculatus*.

***Hyphydrus lyratus* Swartz (Fig. 3)**

Material examined. *Queensland.* Emu Ck, 5 km NE Petford, 29.iii.1996; 8 km S Greenvale, 27.iii.1996; 2 km S Mt Molloy, 30.iii.1996; 8 km N Bluewater, 3.ii.1997. *Northern Territory.* 1 km W Gubara, Kakadu, 17.iii.1998; Manton Dam, 2.ii.1999.

Diagnosis. Mentum more than 4.10 times as long as broad; metathoracic legs more than 3.40 times HW; Uro1 subequal or longer than LLAS and more than 1.40 times HW; abdominal terga I and II yellow; abdominal tergum V brown.

Description. *Colour.* *Cephalic capsule.* Dorsal surface predominantly creamy white to pale yellow, with a longitudinal brown stripe on each side. *Head appendages.* Creamy white. *Thorax.* Pronotum predominantly creamy white to pale yellow, with a U-shape and a transversal narrow brownish macula along anterior and posterior margin, respectively; meso- and metaterga predominantly brownish, with a small yellowish macula mesally. *Legs.* Pale yellow to pale brown. *Abdomen.* Terga I–II yellow, tergum II with a brownish macula mesally; terga III–V brown with a small yellowish macula mesally; tergum VI–VII yellow; tergum VIII predominantly brown, yellowish posteriorly over siphon. *Urogomphus.* Dark brown, paler proximally over a short distance. **Head.** HL = 1.03–1.07 mm (mean = 1.05 mm, $n = 4$); HW = 0.74–0.80 mm (mean = 0.77 mm, $n = 4$); FCL = 0.84–0.87 mm (mean = 0.86 mm, $n = 4$); SpW/FCNW = 1.34–1.53; length of mentum/width of mentum = 4.20–4.86. **Legs.** Metathoracic leg about 3.60 times as long as HW; position and number of secondary setae as in Table 1. **Abdomen.** LLAS = 1.19–1.31 mm (mean = 1.24 mm, $n = 4$). **Urogomphus.** Length of Uro1 = 1.21–1.33 mm (mean = 1.27 mm, $n = 4$); length of Uro1/HW = 1.55–1.74; length of Uro1/LLAS = 0.97–1.10.

Distribution. A very common northern species occurring as far south as the Pilbara, Central Australia and Brisbane. The species is also widespread in India, China and south-east Asia east to Fiji (Biström 1982; South Australian Museum collection).

Remarks. The mature larva of *H. lyratus* has been described by Bertrand (1935) and Nakanishi (2001). Nakanishi (2001) indicated that the urogomphomere I of *H. lyratus* is about 27 times as long as urogomphomere II (compared with 2.9 times in this paper) which appears to be a mistake. It is possible that Nakanishi (2001) measured the urogomphomere II from the point of insertion of the primary setae UR8 which is inserted proximally, fairly close to urogomphomere I (Alarie *et al.* 1997).

***Hyphydrus elegans* (Montrouzier) (Fig. 4)**

Material examined. *Australia. New South Wales.* 2 km N Batemans Bay, 2.xi.1997. *Queensland.* Star River, 1.xi.1995; Cunninghams Gap, 24.xi.1995; Alligator R., 20 km S Townsville; 2 km S Mt Molloy, 30.iii.1996; 2 km S Greenvale, 29.iii.1996; Nadello's Lagoon nr Mareeba, 29.iii.1996. *South Australia.* Inglewood, i.1993. *Victoria.* Healesville, xii.1968. *Western Australia.* Mt Pongo, 5.i.1988; 24 km W Gin Gin, 15.x.1996; 10 km S Yallingup, 22.x.1996; 30 km N Perth,

14.x.1996. *New Zealand. Auckland.* Water tank, Mangere, 25.ix.1959.

Diagnosis. Mentum more than 4.10 times as long as broad; metathoracic legs less than 3.30 times HW; Uro1 shorter than LLAS and less than 1.20 times HW; abdominal terga I and II brown; abdominal tergum V yellow.

Description. *Colour.* *Cephalic capsule.* Dorsal surface predominantly creamy white to pale yellow, with a longitudinal brown stripe on each side; frontoclypeus with a few pale brown maculae posteriorly. *Head appendages.* Predominantly pale yellow, A4 infuscate apically. *Thorax.* Pronotum predominantly yellow, with a large dark brown macula over anterior region; meso- and metaterga brown. *Legs.* Pale brown. *Abdomen.* Terga I–IV dark brown, tergum IV narrowly yellowish along posterior margin; terga V–VII predominantly yellow; tergum VIII dark brown over anterior half, yellowish over siphon. *Urogomphus.* Dark brown, paler proximally over a short distance. **Head.** HL = 1.25–1.29 mm (mean = 1.27 mm, $n = 5$); HW = 0.97–1.03 mm (mean = 1.00 mm, $n = 4$); FCL = 1.00–1.06 mm (mean = 1.04 mm, $n = 5$); SpW/FCNW = 1.35–1.62; length of mentum/width of mentum = 4.08–4.35. **Legs.** Metathoracic leg about 3.10 times as long as HW; position and number of secondary setae as in Table 1. **Abdomen.** LLAS = 1.32–1.48 mm (mean = 1.38 mm, $n = 4$). **Urogomphus.** Length of Uro1 = 1.03–1.15 mm (mean = 1.08 mm, $n = 4$); length of Uro1/HW = 1.04–1.18; length of Uro1/LLAS = 0.76–1.82.

Distribution. *Hyphydrus elegans* occurs commonly over much of Australia with the apparent exception of Tasmania and the northern coastal region. It has a more southerly distribution than the other species and is the only species found south of 26°S latitude. Outside Australia it occurs in Papua New Guinea, New Caledonia and New Zealand (Biström 1982).

Remarks. The mature larva of *H. elegans* has been described by Wise (1961) and Watts (1963) (as *H. australis* Clark).

DISCUSSION

The larvae of the *H. lyratus* species-group that we describe and document in detail are very uniform in terms of larval morphology. All these species are fairly similar morphologically and resemble those of other species of the genus recently described. Like other species of *Hyphydrus*, third instars of the *H. lyratus* species-group are characterised by: (i) a narrower frontoclypeus lacking frontoclypeal spine-like projections and lateral notches; (ii) the absence of the primary pore ANf and of a ventral spinula on antennomere III; (iii) the prementum longer than broad with primary setae LA3, LA4 and LA5 inserted distally; (iv) the presence of natatory setae on dorsal margin of femora, tibiae and tarsi; (v) the abdominal segments IV–VIII sclerotised ventrally; (vi) the presence of secondary spine-like setae on the ventral surface of the siphon; and (vii) the elongate urogomphus with secondary setae. Such a close similarity between the larvae of the *H. lyratus* species group and those of other species of *Hyphydrus* for which the larvae

have been described reinforces the hypothesis that *Hyphydrus* is monophyletic (Biström 1982; Alarie *et al.* 1997).

Based on knowledge of the larval morphology of the tribe Hyphydrini, Alarie *et al.* (1997) suggested that *Hyphydrus* shares a monophyletic origin with *Macrodytes* Balfour–Browne and *Desmopachria* Babington. This is based on the shared presence of: (i) a very elongated prementum; (ii) a more proximal articulation of the primary setae UR8 in instar I and; (iii) the absence of the primary pore ANf on antennomere III. Among these genera, *Desmopachria* and *Hyphydrus* are deemed to be closely related based on the absence of lateral notches on frontoclypeus and by the presence of at least one secondary seta on the siphon venter. Another putative larval synapomorphy in support of the monophyly of this clade is the presence of a short and spiniform seta UR5 in instar I (Alarie *et al.* 1997). We were unable to determine whether this feature occur among the species of the *H. lyratus* species-group studied owing to absence of first instars in our study. Larvae of *Hyphydrus* may readily be distinguished from those of *Desmopachria* by the relative position of the primary setae LA3, LA4, and LA5 on the prementum (apical compared with proximal) and LA10 on labial palpomere II (medial compared with apical) and by the larger number of natatory setae on legs (Alarie *et al.* 1997).

The genus *Hyphydrus* is composed of 20 species-groups (Biström 1982). Whereas adult structures indicate that these species could be subdivided into putative monophyletic assemblages (Biström 1982), knowledge of the larval morphology of the genus *Hyphydrus* does not allow to determine whether larval features would support any of these groupings. A broader analysis including the larvae of more species would be needed to improve resolution.

Our study suggests that, in Australia at least, *H. decemmaculatus* is polymorphic, with one form having males with strongly expanded pro- and mesotarsi and females with a mat dorsal surface (the typical form), and a second form with males with narrow female-like tarsi and female with a shiny dorsal surface (*H. effeminatus*). Further work is required to determine whether this is correct.

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