



Description of the immature stages of the endangered Japanese endemic *Oreodytes kanoi* (Kamiya, 1938) (Coleoptera: Dytiscidae: Hydroporinae) and comparison with the known larvae of *Oreodytes* Seidlitz, 1887

RYOHEI OKADA¹ & YVES ALARIE²¹*Coleopterological Society of Japan. National Museum of Nature and Science, Tsukuba, 3050005 Japan.*✉ wasserinsekt@kub.biglobe.ne.jp; <https://orcid.org/0000-0002-8488-0660>²*Department of Biology, Laurentian University, Ramsey Lake Road, P3E 2C6, Canada.*✉ yalarie@laurentian.ca; <https://orcid.org/0000-0002-8425-087X>

Abstract

The larvae and pupa of the Japanese endemic *Oreodytes kanoi* (Kamiya, 1938) are described and compared with those known of other species of *Oreodytes* Seidlitz, 1887. Larvae of *O. kanoi* and other species of the *alpinus* species-group share the presence of dorsal secondary setae on tarsi, a unique feature amongst *Oreodytes*. The morphology of the pupa of *O. kanoi* is briefly discussed with some information on the ecology of this species.

Key words: Coleoptera, Hydradephaga, Deronectina, *Oreodytes*, chaetotaxy, larvae, pupa

Introduction

The Holarctic dytiscid genus *Oreodytes* Seidlitz, 1887 (*sensu novo*) (Fery & Ribera 2018) contains 14 described species (two of them bitypic) classified in the tribe Hydroporini (subtribe Deronectina) of the subfamily Hydroporinae (Nilsson & Hájek 2020). These small beetles (adult length 3.00–5.65 mm) are adapted to cold habitats and generally occur in rocky streams or along the exposed shorelines of cold lakes (Larson *et al.* 2000). At the present time members of *Oreodytes* can be divided into three informal species groups: the *alaskanus*-group (4 species), the *alpinus*-group (8 species, 1 bitypic), and the *septentrionalis*-group (2 species, 1 bitypic). Among these, two species are found in Japan: *Oreodytes alpinus* (Paykull, 1798) and *O. kanoi* (Kamiya, 1938), both belonging to the *alpinus* species-group. Unlike *O. alpinus*, which is widely distributed from Europe to Far East Russia (Nilsson & Hájek 2020), *O. kanoi* is endemic to Japan where it has only been recorded from Northern Honshu (Mori & Kitayama 2002). The pervasive lack of information on *O. kanoi* associated with the fact that it occupies extremely limited ranges or restricted habitats contributed to the belief that this species might be at risk (Association of Wildlife Research & EnVision 2007; Nakajima *et al.* 2020).

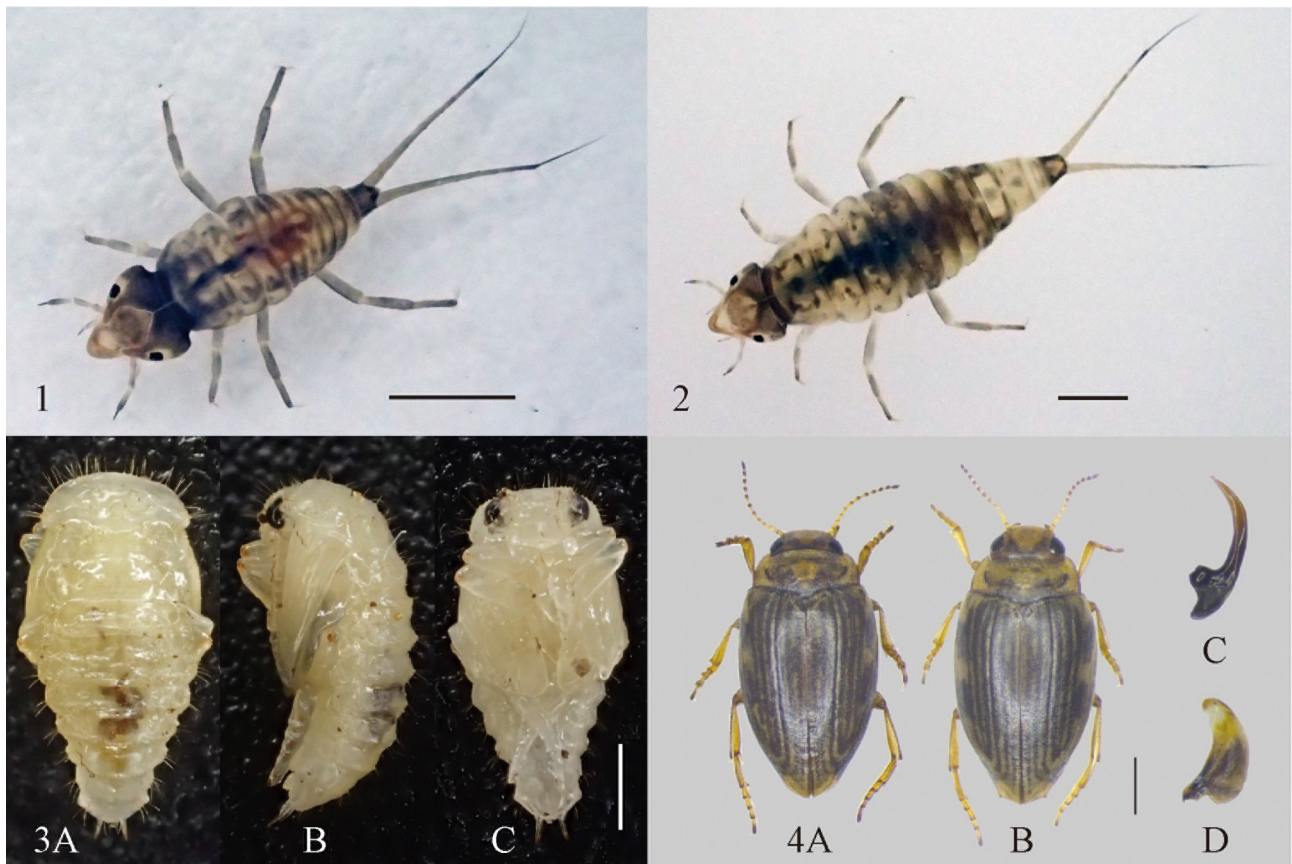
The recent discovery by the senior author of the larvae and pupa of *Oreodytes kanoi* provided the impetus for this study. In addition to offering an opportunity to describe for the first time these two immature stages (prior to this study the larva of *O. kanoi* was only known from a picture (Mitamura *et al.* 2017)), such a discovery should make it possible to identify some ecological and life-history attributes that characterize this species. Furthermore, the description of the larval stages of *O. kanoi* also opens up to important taxonomic considerations, in particular by allowing a comparison with the known larvae of other species of *Oreodytes*. At the present time the larvae of eight *Oreodytes* species are known: the Palaearctic *Oreodytes septentrionalis* (Gyllenhal, 1826) and *O. alpinus* (Nilsson, 1982, 1987), and the Nearctic *Oreodytes alaskanus* (Fall, 1926), *Oreodytes dauricus* (Motschulsky, 1860) (as *O. recticollis* (Fall, 1926)), *Oreodytes laevis* (Kirby, 1837), *Oreodytes productotruncatus* (Hatch, 1944), *Oreodytes scitulus* (LeConte, 1855) (both subspecies), and *Oreodytes snoqualmie* (Hatch, 1933) (Alarie 1997).

This study therefore has the following three goals: (1) to describe in detail the larvae of *Oreodytes kanoi* according to the now-generalized larval descriptive format of Hydradephaga, which incorporates chaetotaxic analysis (e.g., Alarie 1997; Alarie & Michat 2014; Alarie *et al.* 2019); (2) to compare larval features of *O. kanoi* with those of other associated *Oreodytes* species for which the larvae have been described comprehensively (cf. Alarie 1997); and (3) to provide information on the ecology and habitat of this species including the description of its pupal stage.

Material and methods

Source of material. Descriptions of larvae and pupa are based on one instar I, three instar II, three instar III and three pupae (Figs 1–3). Larvae and pupae were collected in association with adults (Fig. 4) at the following locality: Tôshichi Onsen, Hôrai-kyo, Hachimantai, Iwate Pref., Japan, 17.VIII.2016, N. Hikida and R. Okada leg. The identification is firm since *Oreodytes kanoi* is the only *Oreodytes* species known at this locality. Comparison with other known larvae of *Oreodytes* was made with reference to the species described in Alarie (1997). Voucher specimens used in this study are deposited in the larval collection of Ryohei Okada (ROLC, Tokyo, Japan) (*O. kanoi* and *O. alpinus* from Japan) and Yves Alarie (Laurentian University, Sudbury, Ontario, Canada) (other *Oreodytes* species).

Methods. The methods and terms included herein to describe the larvae follow those employed in Alarie *et al.* (2018, 2019, 2020) while those used to describe the pupa are drawn from Wolfe & Roughley (1985). The reader is referred to those papers for a complete list and additional explanations of the terms used here.



FIGURES 1–4. *Oreodytes kanoi* (Kamiya, 1938): (1) instar II, dorsal habitus; (2) instar III, dorsal habitus; (3) pupa. A, dorsal aspect; B, lateral aspect; C, ventral aspect; (4) adult. A, male, dorsal habitus; B, female, dorsal habitus; C, median lobe of aedeagus, lateral aspect; D, paramere, lateral aspect. Scale bars = 0.5 mm in (1–2, 4C–D), 1 mm in (3, 4A–B).

Taxonomy

Oreodytes Seidlitz, 1887 (*sensu novo*)

(Figs. 1–25, 28–29)

Diagnosis. Larvae of *Oreodytes* can readily be distinguished from those of other species of Deronectina described in detail (i.e., *Deuteronectes* Guignot, 1945; *Hornectes* Fery & Ribera, 2018; *Nectoporus* Guignot, 1950; *Neonectes* J. Balfour-Browne, 1944) (cf. Alarie & Nilsson 1996; Alarie *et al.* 1996; Alarie 1997) by the following combination of characters: body fusiform, narrow (Figs 1–2); cephalic capsule distinctly constricted posterior to occipital suture; occipital suture present from instar I (Fig 5); parietale lacking pores PAD and PAe (Figs 5–6); temporal spines acute

apically and strongly developed (Fig 19) (instars II and III); lamellae clypeales interrupted medially for a short distance (Fig 6) (instar I); antennomere 2 lacking secondary setae; antennomere 3 with a ventroapical spinula and pore ANf absent (Figs 7–8); primary seta AN2 inserted subapically, either lower or at about level of ventral spinula (Fig 8); maxillary cardo fused to stipes (Fig 10); primary seta MX1 inserted on maxillary stipes (Fig 10); primary seta MX5 present; prementum lacking lateral spinulae (Figs 11–12); legs lacking natatory setae (Figs 20–21); primary seta TR2 of trochanters present (Fig 14); spinulae present on ventral margin of tibiae and tarsi (Figs 14, 20); abdomen segments VII and VIII lacking bluntly rounded secondary setae (Fig 22); abdomen segment VIII strongly constricted posterior to insertion of urogomphi, and short, less than 0.20 times LLAS in instar III (Figs 16, 22); primary seta AB5 short, not extending beyond apex of siphon (Fig 16); urogomphus elongate, more than 1.9 times HW (urogomphomere 1 more than 1.1 times longer than HW) (Figs 18, 23); urogomphomere 1 at least 1.7 times longer than urogomphomere 2, with an additional pore and primary setae UR2, UR3, and UR4 about subequally distant (Fig 18), with secondary spine-like setae (Fig 23).

The *alpinus* species group

Diagnosis. Larvae of the *Oreodytes alpinus* species-group can readily be distinguished from those of both the *alaskanus* and *septentrionalis* species-groups by the following combination of characters: size smaller: HL < 0.65 mm, 0.87 mm, 1.22 mm and FRL < 0.50 mm, 0.68 mm, 0.95 mm (instar I, II, III, respectively); each tarsus with at least one dorsal secondary seta (instars II and III).

Description of the larvae of *Oreodytes kanoi* (Kamiya, 1938)

Diagnosis. Larvae of *Oreodytes kanoi* can be distinguished from other known species of the *alpinus* species-group by the following combination of characters (instar III): U1/HW > 1.65; meso- and metacoxae with less than three secondary setae.

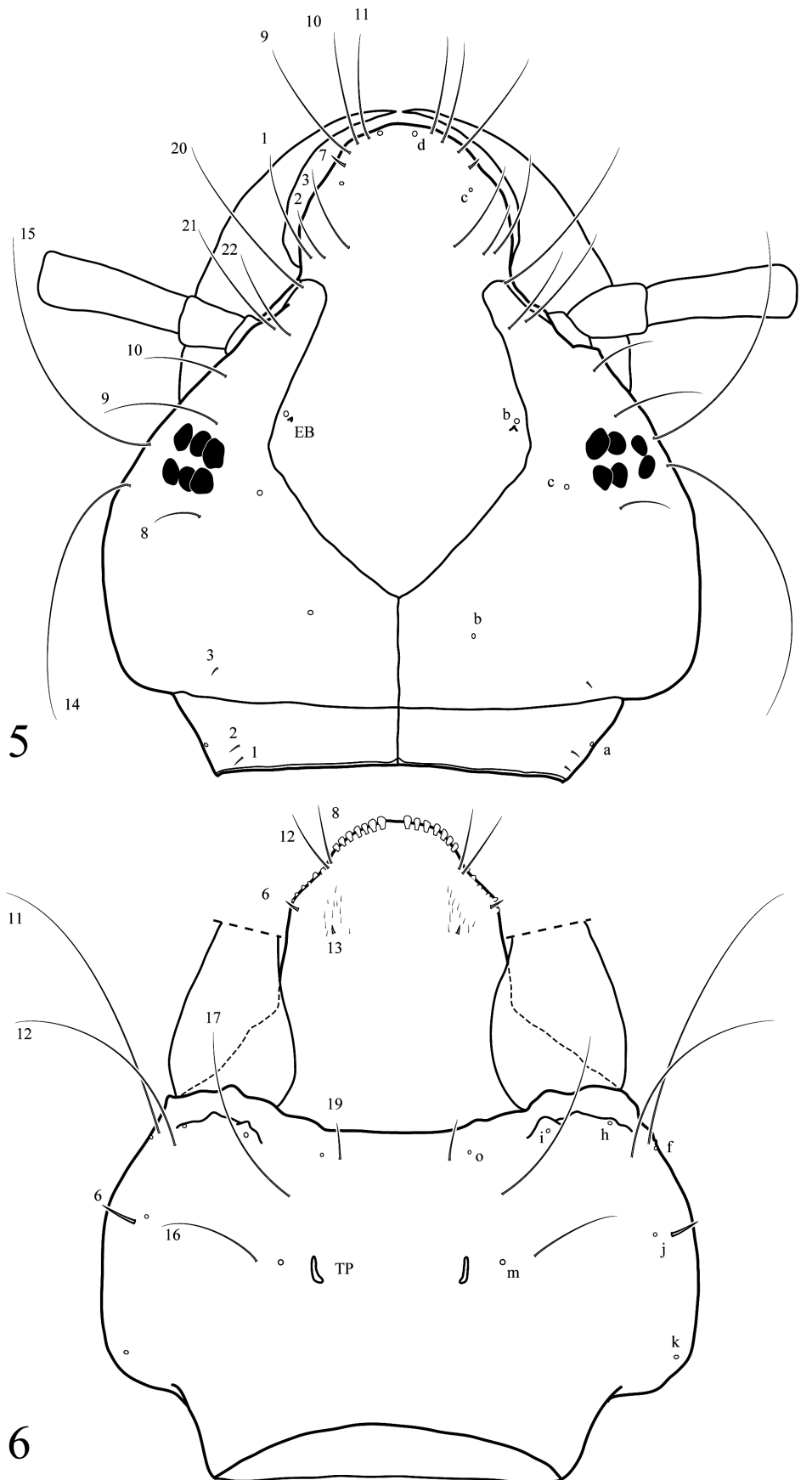
Instar I (Figs 5–18)

Colour (alcohol preserved). Dorsal surface predominantly dark brown except anteromedial region of frontoclypeus and around ocularium pale white; head appendages greyish brown, A4 and apex of A3 infuscate; thoracic and abdominal terga I to VII creamy to greyish brown; LAS dark brown; urogomphus and legs greyish brown.

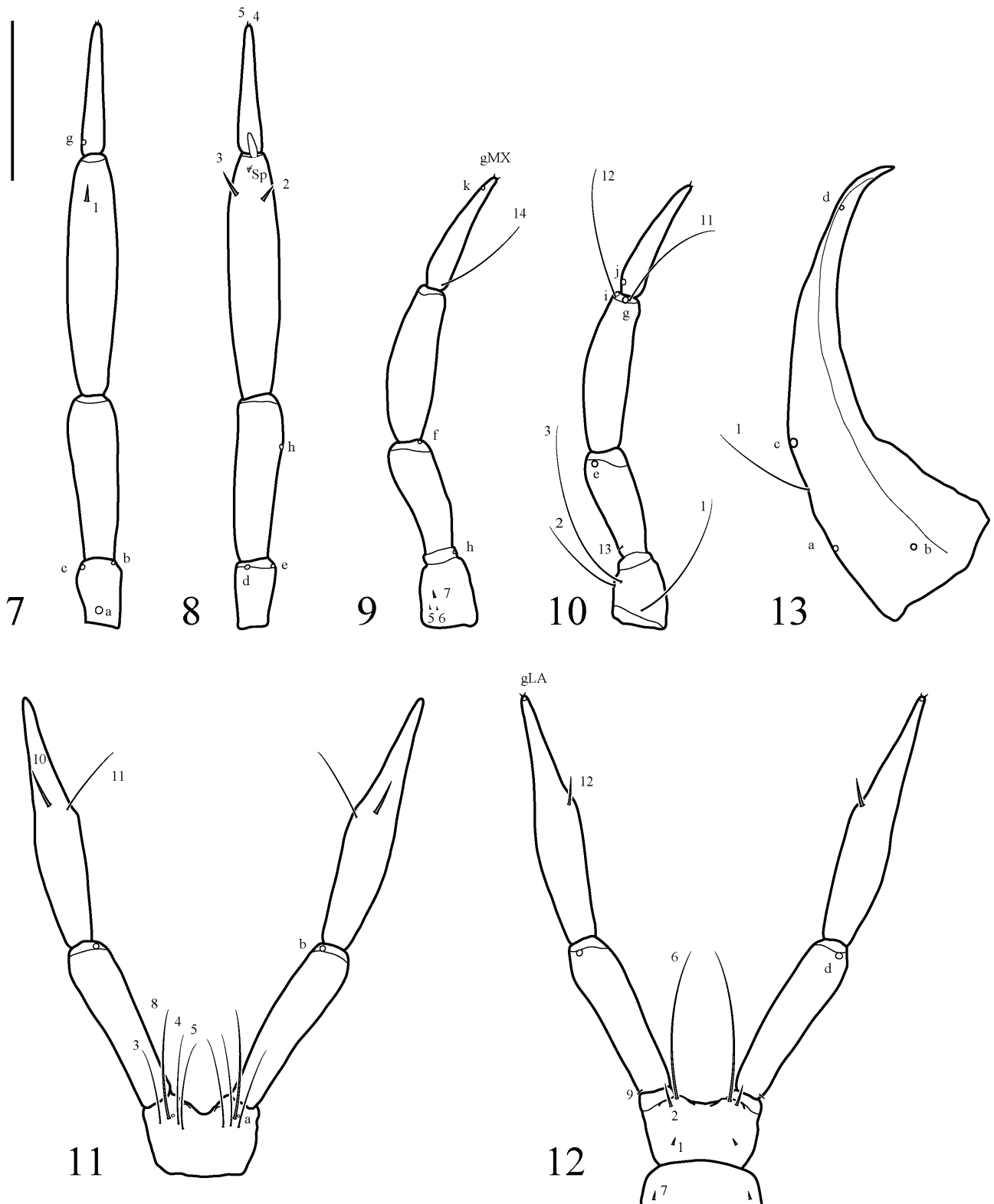
Body. Fusiform, narrow. Measurements and ratios that characterize the body shape are shown in Table 1.

Head. Head capsule (Figs 5–6). Pear-shaped, about as broad as long, maximum width posterior to stemmata, with neck constriction distinctly delimited; occipital suture present; ecdysial line well marked, coronal line short; occipital foramen broadly emarginate ventrally; frontoclypeus bluntly rounded, lateral margin slightly sinuate; dorsal surface with two egg bursters; ventroapical margin of frontoclypeus with 14–15 spatulate setae [= lamella clypeales of Bertrand (1972)], interrupted medially for a short distance; ocularium present, stemmata not visible ventrally; tentorial pits visible medioventrally. Antenna (Figs 7–8). Elongate, four-segmented, shorter than HW; A1 the shortest, A3 the longest, with a ventroapical spinula; A3' short. Mandible (Fig 13). Falciform, curved inward and upward apically; mandibular channel present. Maxilla (Figs 9–10). Cardo fused to stipes; stipes short, broad; galea and lacinia absent; MP elongate, three segmented, shorter than antenna, MP2 the longest, MP3 the shortest. Labium (Figs 11–12). Prementum small, subtrapezoidal, broader than long, without lateral spinulae, anterior margin slightly indented medially; LP elongate, two segmented, LP2 longer than LP1.

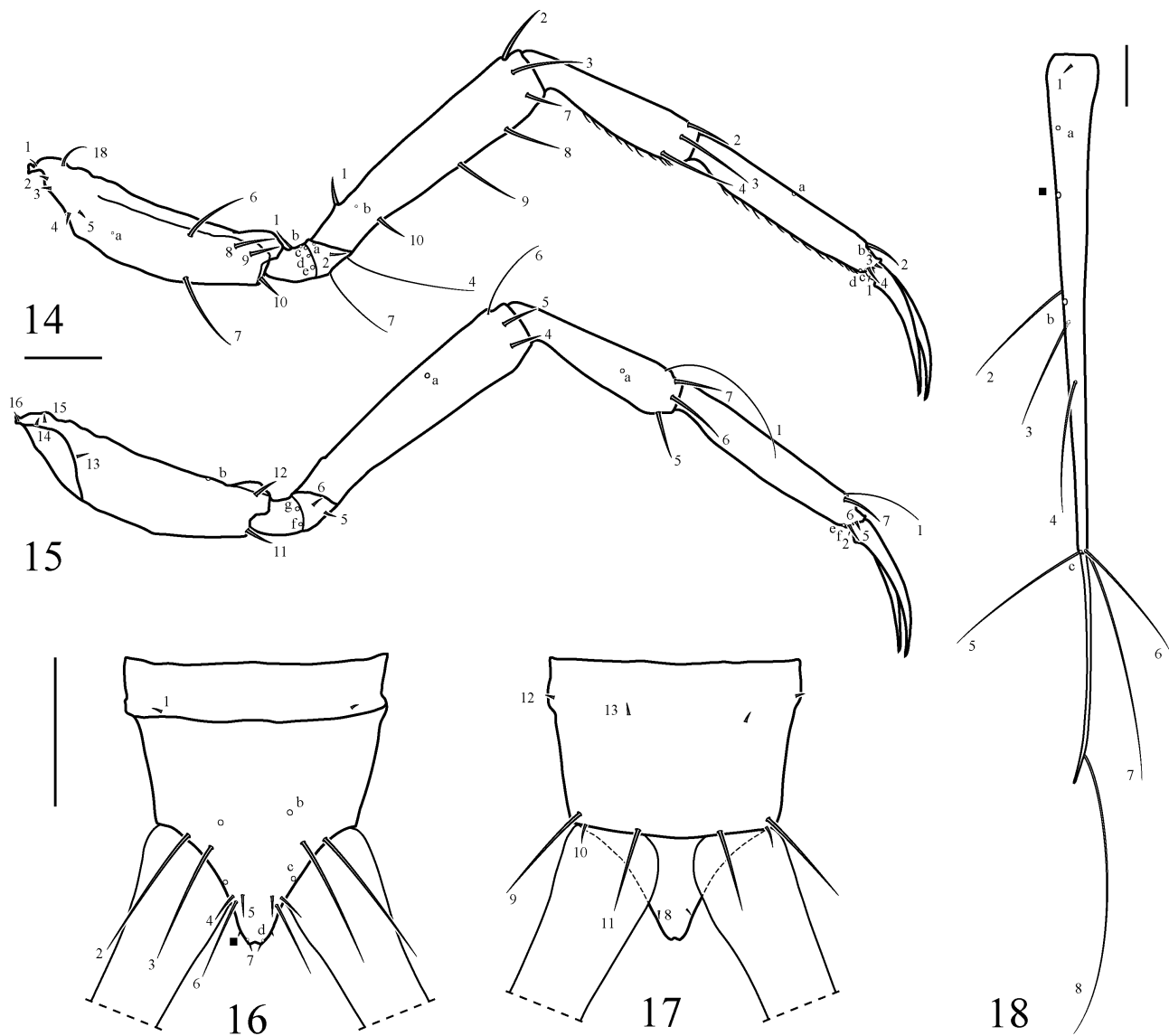
Thorax. Pronotum trapezoidal dorsally, ovate laterally, widest at posterior margin; subequal to meso- and metanotum combined; pronotum without anterotransverse carina; both meso- and metathoracic terga with an anterotransverse carina; sagittal line visible on the three tergites; thoracic sterna membranous; spiracles absent. Legs (Figs 14–15). Long, composed of six segments (including pretarsus), L1 the shortest, L3 the longest; CO robust, elongate, TR divided into two parts, FE, TI and TA slender, subcylindrical; pretarsus with two long, slender, slightly curved claws, posterior claw shorter than anterior one on L1 and L2, claws subequal in length on L3; claws lacking basoventral spinulae; TI and TA with ventral spinulae.



FIGURES 5–6. *Oreodytes kanoi* (Kamiya, 1938), instar I, head capsule: (5) dorsal aspect (colour pattern not represented); (6) 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 7–13. *Oreodytes kanoi* (Kamiya, 1938), instar I, head appendages: (7–8) antenna, (7) dorsal aspect; (8) ventral aspect; (9–10) maxilla, (9) dorsal aspect; (10) ventral aspect; (11–12) labium, (11) dorsal aspect; (12) ventral aspect; (13) mandible, dorsal aspect. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bar = 0.1 mm.



FIGURES 14–18. *Oreodytes kanoi* (Kamiya, 1938), instar I: (14–15) metathoracic leg, (14) anterior aspect; (15) posterior aspect; (16–17) last abdominal segment, (16) dorsal aspect; (17) ventral aspect; (18) urogomphus, dorsal aspect. Numbers and lowercase letters refer to primary setae and pores, respectively; filled squares refer to additional setae and pores. Scale bars = 0.1 mm.

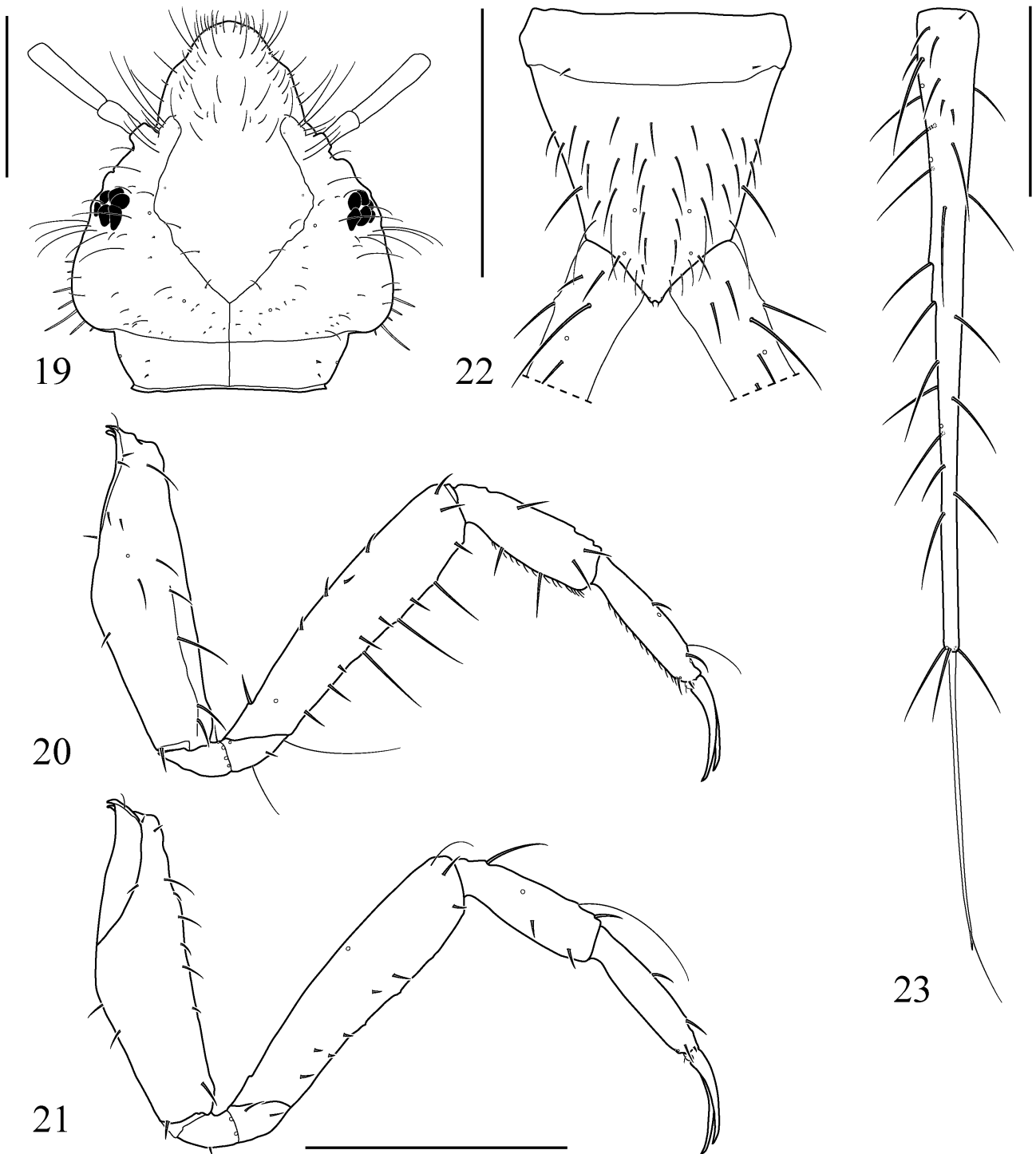
Abdomen. Eight-segmented; segments I–VI sclerotized dorsally, membranous ventrally; segment VII sclerotized both dorsally and ventrally, ventral sclerite demarcated from dorsal one; tergites I–VII narrow, transverse, rounded laterally, without sagittal line, with anterotransverse carina, with long setae along lateral and posterior margins; spiracles absent on segments I–VII; LAS (Figs 16–17). Short, subtrapezoidal, lateral margins subparallel, slightly converging from base to point of insertion of urogomphi, abruptly converging thereafter; completely sclerotized, ring-like, with anterotransverse carina dorsally and laterally; siphon short, bluntly rounded to acute apically. Urogomphus (Fig 18). Elongate, two-segmented; U1 much longer than LAS and U2.

Chaetotaxy. Similar to that of generalized *Oreodytes* larva (Alarie 1997) except for following features: AN2 inserted subapically, lower than ventral spinula.

Instar II (Fig 1)

As instar I except as follows:

Colour. Thoracic and abdominal terga III, IV and VII creamy yellow, abdominal terga I, II, V and VI greyish brown.



FIGURES 19–23. *Oreodytes kanoi* (Kamiya, 1938), instar III: (19) head capsule, dorsal aspect (colour pattern not represented); (20–21) prothoracic leg, (20) anterior aspect; (21) posterior aspect; (22) last abdominal segment, dorsal aspect; (23), urogomphus, dorsal aspect. Scale bars = 0.5 mm.

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

Head. Reticulation of head capsule reduced. Anteroventral margin of frontoclypeus with 24–26 short, spatulate setae, medial gap lacking; egg bursters lacking. Labium. LP2 and LP1 subequal in length.

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

Abdomen. Segment VII completely sclerotized, ring-like; U2 much shorter than U1.

Chaetotaxy. Head capsule with a few hair-like, secondary setae; parietale with 8 spine-like secondary setae along lateral margin; MN with one hair-like, secondary seta on basoexternal margin; abdominal tergites I–VII with

several secondary setae along posterior margin; LAS with some spine-like, secondary setae; U1 with numerous acute, secondary setae.

TABLE 1. Measurements and ratios of larvae of *Oreodytes kanoi* (Kamiya, 1938). *n* = number of specimens examined.

Series	Instar I	Instar II			Instar III		
	(<i>n</i> =1)	(n=3)			(n=3)		
HL (mm)	0.50	0.81	-	0.83	1.14	-	1.16
HW (mm)	0.47	0.72	-	0.74	1.00	-	1.01
FRL (mm)	0.35	0.63	-	0.64	0.87	-	0.88
OCW (mm)	0.26	0.40	-	0.43	0.57	-	0.63
HL/HW	1.06	1.12	-	1.13	1.14	-	1.15
HW/OCW	1.78	1.71	-	1.81	1.60	-	1.75
A/HW	0.80	0.64	-	0.69	0.60	-	0.62
A4/A1	1.14	0.70	-	0.82	0.62	-	0.65
A3/A2	1.44	1.04	-	1.13	0.90	-	0.99
A4/A3	0.54	0.38	-	0.42	0.29	-	0.33
A3'/A4	0.23	0.26	-	0.27	0.29	-	0.30
MN/HL	0.57	0.47	-	0.48	0.49	-	0.50
A/MP	1.41	1.33	-	1.49	1.27	-	1.34
MP3/MP2	0.57	0.52	-	0.58	0.43	-	0.55
MP3/MP1	0.63	0.48	-	0.57	0.33	-	0.39
MP/LP	1.05	1.01	-	1.06	0.96	-	1.06
LP2/LP1	1.25	0.96	-	0.99	0.72	-	0.81
L3 (mm)	1.53	2.11	-	2.15	2.98	-	3.03
L3/HW	3.26	2.86	-	2.97	2.98	-	3.02
L3/L1	1.46	1.34	-	1.45	1.41	-	1.42
L3 (CO/FE)	0.94	0.78	-	0.89	0.86	-	0.91
L3 (TI/FE)	0.69	0.63	-	0.69	0.64	-	0.66
L3 (TA/FE)	0.79	0.67	-	0.76	0.64	-	0.68
L3 (CL/TA)	0.67	0.50	-	0.57	0.48	-	0.50
LAS (mm)	0.18	0.28	-	0.32	0.45	-	0.54
LAS/HW	0.37	0.38	-	0.45	0.45	-	0.54
U (mm)	1.17	1.76	-	1.78	2.43	-	2.55
U1 (mm)	0.81	1.20	-	1.22	1.69	-	1.76
U/HW	2.48	2.38	-	2.47	2.44	-	2.51
U1/HW	1.72	1.65	-	1.67	1.69	-	1.74
U1/LAS	4.61	3.71	-	4.36	3.15	-	3.81
U/LAS	6.65	5.48	-	6.41	4.61	-	5.45

Instar III (Figs 2, 19–23)

As instar II except as follows:

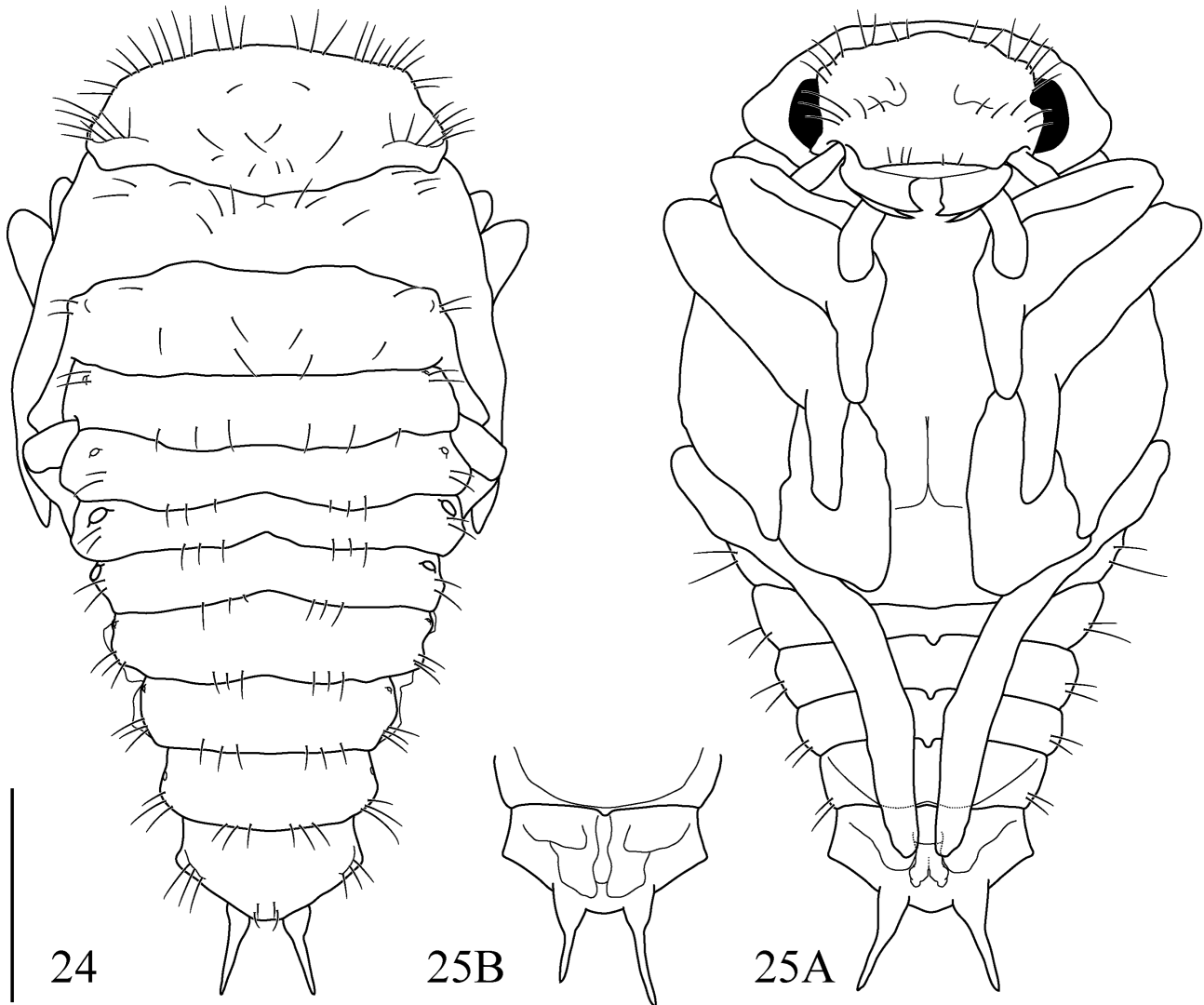
Colour. Abdominal terga VI and VIII obviously creamy yellow.

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

Head. Head capsule (Fig 19). Frontoclypeus with 27–28 short, spatulate setae. Parietal with 13–15 spine-like setae along lateroventral margin. Antenna. A4 the shortest, A2 and A3 the longest, subequal in length. Maxilla. MP1 the longest, MP3 the shortest. Labium. LP2 shorter than LP1.

Thorax. Spiracular openings present on mesothorax. Position and number of secondary setae on legs are shown in Table 2.

Abdomen. Spiracular openings present on segments I–VII.



FIGURES 24–25. *Oreodytes kanoi* (Kamiya, 1938), pupa: (24) dorsal aspect; (25) ventral aspect. A, male; B, female. Scale bar = 1 mm.

Description of pupa (Figs 3, 24–25)

Colour. Creamy white, except for the eyes black and distal half of cerci dark brown.

Body. Length (including cerci) = 4.45–4.66 mm, maximum width at level of abdominal segment II = 1.79–1.90 mm.

Head. Trapezoidal, mediodorsally concave, broadest at level of middle of eyes.

Thorax. Wing pads extending posteroventrally between mid and hind legs.

Abdomen. Segments IV, V and VI ventrally with medial, appressed, posteriorly projected, triangular process (TP). Ventral end of abdomen showing sexual dimorphism: male gonopods, three short genital lobes protruding caudally, outer ones similar, middle one longer and with bifid apex (Fig 25A); female gonopods, two slightly diverging subequal genital lobes protruding caudally, with apices well-rounded, both lobes shorter than outer male lobes (Fig 25B). Spiracles I–VI well-developed, functional, slightly decreasing in size from III to VI. Cerci short (0.30–0.40 mm), symmetrical or asymmetrical (individual variation), conical, tapered and slightly diverging in distal half, acute at apex, without lateral setae.

Chaetotaxy. Position and number of setae are shown in Table 3.

TABLE 2. Number and position of secondary setae on the legs of larvae of *Oreodytes kanoi* (Kamiya, 1938). A = anterior, AD = anterodorsal, AV = anteroventral, CO = coxa, D = dorsal, FE = femur, PD = posterodorsal, Pr = proximal, PV = posteroventral, TA = tarsus, TI = tibia, TR = trochanter, V = ventral, *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 (<i>n</i> =3)	Instar III (<i>n</i> =3)
CO	D	3-4/2-4/2-4	4-6/3-5/3-4
	A	0/0/0	0-3/1-2/0-2
	V	1-2/1-2/2	2-6/4-5/4-6
	Total	4-7/4-6/4-6	8-11/9-10/8-11
TR	Pr	1/1/1	1-2/1-2/2-3
FE	AD	2-3/3-5/5-7	4-5/7-8/7-9
	AV	3-4/4-6/5-8	5-7/6-9/8-10
	PV	4-5/5-6/5-6	6/6-8/6-9
	Total	9-11/12-17/15-19	15-18/20-24/21-28
TI	AD	1/2/2-4	1-2/2/3-6
	AV	0/1-2/3	0-1/1-4/2-4
	PD	1/0-2/1-2	1/0-2/2-4
	PV	1-2/2/1-2	1/2-3/3-4
	Total	3-4/5-8/9-11	4/7-9/11-12
TA	PD	1-2/1-2/2-3	1/2-3/3-5
	PV	0-1/1/1-2	0/1-2/1-2
	Total	1-3/2-3/4	1/3-4/5-6



FIGURES 26–29. Habitats of larvae and pupae of *Oreodytes kanoi* (Kamiya, 1938): (26) Tōshichi Onsen, Iwate Prefecture, small stream; (27) habitat of pupae; (28) prepupa; (29) pupa in case. Scale bars = 1 mm.

TABLE 3. Number and position of setae on head, thorax and abdomen segments of pupae of *Oreodytes kanoi* (Kamiya, 1938) and *Nebrioporus ceresyi* (Aubé, 1838). A = anterior, AL = anterolateral, CL = clypeal, DI = discal, DL = dorsolateral, DM = dorsomedial, DM = dorsomedial, DPL = dorsopleural, L = lateral, LB = labral, ML = mediolateral, M = medial, P = posterior, VPL = ventropleural. *n* = number of specimens examined, Total = total number of setae.

Segment	Position	<i>O. kanoi</i> (<i>n</i> = 3)		<i>N. ceresyi</i> * (<i>n</i> = 1)		Segment	Position	<i>O. kanoi</i> (<i>n</i> = 3)		<i>N. ceresyi</i> * (<i>n</i> = 1)	
		left/right	Total	left/right	Total			left/right	Total	left/right	Total
Head	DL	4/4	8	6/6	12	SegI	DPL	2/2	4	2/2	4
	DM	4/4	8	1/1	2		P	3-4/3-4	6-8	3/3	6
	M	0-1/1	1-2	2/2	4		Total	5-6/5-6	10-12	5/5	10
	ML	5-6/5-6	10-12	2/2	4	SegII-VI	DPL	2-3/2-3	4-6	3/3	6
	CL	2/3-4	5-6	2/2	4		P	3/3	6	4/4	8
	LB	0	0	0	0		VPL	1-2/2	3-4	2/2	4
	Total	15-17/17-19	32-36	13/13	26		Total	7-8/7-8	15-16	9/9	18
Pronotum	A	11-12/11	22-23	8/10	18	SegVII	DPL	3/3	6	4/4	8
	AL	1/1-2	2-3	NA	NA		P	3/3-4	6-7	4/4	8
	DI	3-5/3-5	8-10	2/2	4		VPL	2/2	4	2/2	4
	P	7-8/7	14-15	5/4	9		Total	8/8-9	16-17	10/10	20
	Total	23-25/23-24	47-48	15/16	31	SegVIII	DPL	3/3	6	1/1	2
Mesonotum	A	1/1	2	1/1	2		P	2/2	4	4/4	8
	L	2/2	4	2/2	4		Total	5/5	10	5/5	10
	P	3/3	6	3/3	6						
Metanotum	Total	6/6	12	6/6	12						
	A	1/1	2	1/1	2						
	L	2/2	4	2/2	4						
	P	3/3	6	3/2	5						
Total	6/6	12	6/5	11							

* from Giulio & Nardi (2006).

TABLE 4. Measurements and ratios for the instar III of selected species of *Oreodytes* Seidlitz, 1887: *O. alpinus* (Paykull, 1798) (OALP), *O. alaskanus* (Fall, 1926) (OALA), *O. dauricus* (Motschulsky, 1860) (ODAU), *O. laevis* (Kirby, 1837) (OLAE), *O. kanoi* (Kamiya, 1938) (OKAN), *O. productotruncatus* (Hatch, 1944) (OPRO), *O. scitulus* (LeConte, 1855) (OSCI), *O. septentrionalis* (Gyllenhal, 1826) (OSEP), *O. snoqualmie* (Hatch, 1933) (OSNO). l = length, w = width, n = number of specimens examined, ? = missing data.

Measure	<i>alpinus</i> group					<i>alaskanus</i> group					<i>septentrionalis</i> group		
	OALP (n = 2)	OKAN (n = 3)	OLAE (n = 5)	OSNO (n = 4)	ODAU (n = 2)	OPRO (n = 4)	OSCI (n = 12)	OSEP (n = 2)	OSCI (n = 12)	OSEP (n = 2)	OSCI (n = 12)	OSEP (n = 2)	OSCI (n = 12)
HL (mm)	1.14–1.18	1.14–1.16	1.07–1.21	1.09–1.14	1.29–1.34	1.23–1.35	1.01–1.17	0.97	1.01–1.17	1.01–1.17	1.01–1.17	1.01–1.17	1.01–1.17
HW (mm)	0.99–1.10	1.00–1.01	0.95–1.13	0.97–1.00	1.18–1.30	1.18–1.25	0.99–1.11	0.85–0.86	0.99–1.11	0.99–1.11	0.99–1.11	0.99–1.11	0.99–1.11
FRL (mm)	0.89–0.9	0.87–0.88	0.82–0.93	0.85–0.87	1.00–1.02	0.96–1.03	0.81–0.89	0.73–0.74	0.81–0.89	0.81–0.89	0.81–0.89	0.81–0.89	0.81–0.89
OCW (mm)	0.56–0.67	0.57–0.63	0.62–0.80	0.62–0.63	0.77–0.84	0.70–0.80	0.61–0.73	0.47–0.50	0.61–0.73	0.61–0.73	0.61–0.73	0.61–0.73	0.61–0.73
HL/HW	1.07–1.14	1.14–1.15	1.01–1.17	1.09–1.16	1.02–1.09	1.04–1.11	0.97–1.08	1.13–1.14	0.97–1.08	0.97–1.08	0.97–1.08	0.97–1.08	0.97–1.08
HW/OCW	1.63–1.76	1.60–1.75	1.41–1.60	1.52–1.58	1.49–1.60	1.52–1.68	1.47–1.61	1.70–1.85	1.47–1.61	1.47–1.61	1.47–1.61	1.47–1.61	1.47–1.61
A/HW	0.57–0.58	0.60–0.62	0.56–0.63	0.62–0.64	0.58–0.62	0.61–0.68	0.56–0.63	0.58–0.63	0.56–0.63	0.56–0.63	0.56–0.63	0.56–0.63	0.56–0.63
A4/A1	0.55–0.58	0.62–0.65	0.51–0.68	0.65–0.66	0.46–0.52	0.50–0.56	0.50–0.58	0.68–0.80	0.50–0.58	0.50–0.58	0.50–0.58	0.50–0.58	0.50–0.58
A3/A2	0.86–0.91	0.90–0.99	0.84–0.98	0.92–1.00	0.89–0.94	0.86–0.89	0.80–1.02	0.88–1.00	0.80–1.02	0.80–1.02	0.80–1.02	0.80–1.02	0.80–1.02
A4/A3	0.33–0.35	0.29–0.33	0.29–0.35	0.35–0.38	0.28–0.30	0.29–0.33	0.27–0.37	0.39–0.51	0.27–0.37	0.27–0.37	0.27–0.37	0.27–0.37	0.27–0.37
A3/A4	0.26–0.33	0.29–0.30	0.34–0.43	0.26–0.32	0.30–0.36	0.32–0.34	0.41–0.56	0.32–0.36	0.41–0.56	0.41–0.56	0.41–0.56	0.41–0.56	0.41–0.56
MNL/HL	0.49*	0.49–0.50	0.52–0.53	0.50–0.52	0.53–0.54	0.52–0.57	0.49–0.53	?	0.49–0.53	0.49–0.53	0.49–0.53	0.49–0.53	0.49–0.53
A/MP	1.24*	1.27–1.34	1.18–1.29	1.27–1.30	1.20–1.30	1.21–1.29	1.25–1.35	?	1.25–1.35	1.25–1.35	1.25–1.35	1.25–1.35	1.25–1.35
MP3/MP2	0.49*	0.43–0.55	0.38–0.48	0.39–0.42	0.42–0.44	0.42–0.49	0.37–0.56	?	0.37–0.56	0.37–0.56	0.37–0.56	0.37–0.56	0.37–0.56
MP3/MP1	0.36*	0.33–0.39	0.31–0.39	0.33–0.34	0.30–0.34	0.30–0.37	0.32–0.41	?	0.32–0.41	0.32–0.41	0.32–0.41	0.32–0.41	0.32–0.41
MP/LP	1.09*	0.96–1.06	1.08–1.16	1.10–1.12	1.04–1.07	1.04–1.09	1.02–1.11	?	1.02–1.11	1.02–1.11	1.02–1.11	1.02–1.11	1.02–1.11
LP2/LP1	0.70–0.74	0.72–0.81	0.70–0.79	0.76–0.82	0.68–0.78	0.71–0.82	0.67–0.76	0.82	0.67–0.76	0.67–0.76	0.67–0.76	0.67–0.76	0.67–0.76
L3 (mm)	2.84*	2.98–3.03	2.87–3.33	2.82–2.92	3.13–3.40	3.28–3.36	2.41–2.63	?	2.41–2.63	2.41–2.63	2.41–2.63	2.41–2.63	2.41–2.63
L3/L1	1.42*	1.41–1.42	1.32–1.40	1.39–1.43	1.35–1.41	1.36–1.38	1.32–1.39	?	1.32–1.39	1.32–1.39	1.32–1.39	1.32–1.39	1.32–1.39
L3/HW	2.86*	2.98–3.02	2.89–3.02	2.85–3.03	2.53–2.71	2.70–2.73	2.41–2.82	?	2.41–2.82	2.41–2.82	2.41–2.82	2.41–2.82	2.41–2.82
L3(CO/FE)	0.88*	0.86–0.91	0.85–0.92	0.81–0.84	0.83–0.85	0.84–0.86	0.83–0.94	?	0.83–0.94	0.83–0.94	0.83–0.94	0.83–0.94	0.83–0.94

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TABLE 4. (Continued)

Measure	<i>alpinus</i> group				<i>alaskanus</i> group				<i>septentrionalis</i> group		
	OALP (n = 2)	OKAN (n = 3)	OLAE (n = 5)	OSNO (n = 4)	OALA (n = 5)	ODAU (n = 2)	OPRO (n = 4)	OSCI (n = 12)	OSEP (n = 2)		
L3(TI/FE)	0.60*	0.64-0.66	0.61-0.68	0.63-0.67	0.61-0.64	0.65-0.67	0.62-0.64	0.62-0.69			?
L3(TA/FE)	0.61*	0.64-0.68	0.57-0.60	0.65-0.67	0.57-0.60	0.63-0.65	0.60-0.62	0.64-0.69			?
L3(C/TA)	0.55*	0.48-0.50	0.45-0.70	0.53-0.58	0.54-0.58	0.53	0.57-0.59	0.45-0.50			?
LAS (mm)	0.43*	0.45-0.54	0.46-0.52	0.40-0.44	0.52-0.53	0.46-0.49	0.50-0.52	0.36-0.39			0.31-0.38
LAS/HW	0.44*	0.45-0.54	0.45-0.49	0.40-0.44	0.40-0.44	0.38-0.41	0.40-0.44	0.35-0.38			0.36-0.44
U1 (mm)	1.38*	1.69-1.76	1.72-2.02	1.72-1.76	1.72-1.99	1.71-1.90	1.75-1.91	1.22-1.69			1.31-1.35
U1+U2 (mm)	2.09*	2.43-2.55	2.50-2.81	2.49-2.58	2.43-2.90	2.63-2.73	2.62-2.91	1.84-2.61			2.04-2.13
U1/LAS	3.17*	3.15-3.81	3.48-4.02	3.95-4.44	3.35-3.86	3.53-3.12	3.40-3.86	3.65-4.21			3.42-4.37
U1/HW	1.38*	1.69-1.74	1.63-1.93	1.58-1.63	1.46-1.61	1.45-1.56	1.48-1.57	1.23-1.57			1.51-1.58
U1+U2/LAS	4.81*	4.61-5.45	4.92-5.95	6.44-6.50	6.24-6.28	5.42-5.77	5.10-5.88	5.17-6.08			5.34-6.91
U1+U2/HW	2.10*	2.44-2.51	2.35-2.86	2.32-2.38	2.12-2.31	2.23-2.28	2.23-2.34	1.86-2.42			2.37-2.50

* data from n = 1.

TABLE 5. Number of secondary setae on the legs of instar III of selected species of *Oreodytes* Seidlitz, 1887: *O. alpinus* (Paykull, 1798) (OALP), *O. alaskanus* (Fall, 1926) (OALA), *O. dauricus* (Motschulsky, 1860) (ODAU), *O. laevis* (Kirby, 1837) (OLAE), *O. kanoi* (Kamiya, 1938) (OKAN), *O. productotruncatus* (Hatch, 1944) (OPRO), *O. scitulus* (LeConte, 1855) (OSCI), *O. septentrionalis* (Gyllenhal, 1826) (OSEP), *O. snoqualmie* (Hatch, 1933) (OSNO). A = anterior, AD = anterodorsal, Di = distal, AV = anteroventral, D = dorsal, NS = natatory setae, PD = posterodorsal, Pr = proximal, PV = posteroventral, V = ventral, n = number of specimens examined, Total = total number of secondary setae on segment.

Segment	Sensillar series	alpinus-group				alaskanus-group				septentrionalis-group	
		OALP (n = 3)	OKAN (n = 3)	OLAE (n = 5)	OSNO (n = 4)	OALA (n = 5)	ODAU (n = 2)	OPRO (n = 4)	OSCI (n = 12)		
ProCO	D	4-7	4-6	4-10	6-7	7-14	7-8	9-12	4-8		
	A	0-3	0-3	2-5	1-2	3-6	3-4	2-7	1-3		
	V	1-7	2-6	2-6	2-3	3-9	2-3	2-3	1-5		
	Total	6-15	8-11	8-18	6-13	16-25	13-14	15-19	6-13		
ProTR	Pr	1-2	1-2	1-3	1-2	1-3	1	1	1-2		
	AD	2-3	4-5	1-5	4-5	2-5	2-4	2-3	2-6		
ProFE	AV	5-8	5-7	5-8	7-9	4-6	3-5	3-5	3-6		
	PV	4-9	6	5-6	4-7	4-6	4-5	4-5	3-5		
ProTI	Total	11-20	15-18	12-19	15-20	11-16	10-14	9-12	10-15		
	AD	1-2	1-2	1-3	1-2	1-3	1	1	0-2		
	AV	1-2	0-1	1	1	1-2	1-2	1	0-1		
	PD	1-2	1	1	1	1	1	1	1		
ProTA	PV	1	1	1-2	1	1	1	1	0-2		
	Total	4-7	4	4-6	4-5	4-7	4-5	4	2-5		
	AV	0	0	0	0	0	1-2	0	0		
	PD	1	1	1-2	1-2	0	0	0	0		
MesoCO	PV	0	0	0	0	0	0-1	0	0		
	Total	1	1	1-2	1-2	0	1-2	0	0		
	D	3-4	3-5	4-8	4	7-12	4-6	7-11	3-8		
	A	2-5	1-2	3-7	2-5	4-7	3-5	4-6	2-4		
MesoTR	V	1-9	4-5	3-6	4-6	4-8	2-4	3-5	1-5		
	Total	6-18	9-10	11-18	10-14	15-26	10-13	15-22	8-14		
	Pr	1-2	1-2	1-4	1-3	1-4	1-2	1-3	1-3		
	AD	5-7	7-8	4-9	6-9	4-7	5-7	5	5-9		
MesoFE	AV	6-8	6-9	6-9	7-10	6-8	5	5-6	4-8		
	PV	6-9	6-8	6-8	8-10	6-7	5-6	6-8	6-8		

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TABLE 5. (Continued)

Segment	Sensillar series	<i>alpinus</i> -group				<i>alaskanus</i> -group			<i>septentrionalis</i> -group
		OALP (<i>n</i> = 3)	OKAN (<i>n</i> = 3)	OLAE (<i>n</i> = 5)	OSNO (<i>n</i> = 4)	OALA (<i>n</i> = 5)	ODAU (<i>n</i> = 2)	OPRO (<i>n</i> = 4)	OSCI (<i>n</i> = 12)
	Total	17–23	20–24	19–26	22–27	18–22	16–18	16–19	16–24
MesoTI	AD	3–4	2	4	3–5	2–6	2–3	2–3	2–6
	AV	1–3	1–4	1–2	2–3	1–3	1–2	1–2	1–3
	PD	1–3	0–2	1–3	1–4	1–2	1	1	1–3
	PV	2–3	2–3	2–3	2–3	2–3	2	1–2	0–2
	Total	8–12	7–9	10–12	9–12	7–14	6–8	6–8	4–11
MesoTA	AV	0	0	0	0–1	0	0–1	0	0
	PD	1–2	2–3	2–3	2	0	0	0	0
	PV	0–2	1–2	1	0–1	0	0–2	0	0
	Total	1–4	3–4	3–4	3	0	1–2	0	0
MetaCO	D	2–3	3–4	3–6	3–5	4–8	3–5	5–6	3–6
	A	1–4	0–2	4–7	2–4	4–6	2–4	5–8	3–5
	V	2–7	4–6	3–9	4–6	6–11	3–4	5–6	2–6
	Total	8–13	8–11	12–19	10–13	16–22	9–13	16–20	8–15
MetaTR	Pr	1–2	2–3	3–4	2	2–5	1–2	2–3	1–3
MetaFE	AD	5–7	7–9	6–9	8–9	6–7	5–6	6–7	5–11
	AV	7–11	8–10	7–10	8–9	7–8	5–7	5–8	6–12
	PV	9–10	6–9	8–10	10–11	7–8	5–8	8–11	6–10
	Total	22–29	21–28	24–27	27–28	21–23	17–19	21–25	18–28
MetaTI	AD	4–5	3–6	3–6	4–6	3–6	3	3–5	4–7
	AV	2–3	2–4	2–4	3–4	3–5	3	3–4	2–3
	PD	1–3	2–4	1–3	1–3	1–2	1	1–3	1–3
	PV	2–4	3–4	2–4	1–3	3–4	2–4	2–4	1–3
	Total	9–14	11–12	11–15	12–16	10–15	9–11	9–15	9–13
MetaTA	AD	0	0	0	1–2	0	0	0	0
	AV	0	0	0	1	0–1	1–2	0	0
	PD	2–4	3–5	2–3	1–4	0	0	0	0
	PV	1–2	1–2	1–2	0–1	0	0–1	0	0
	Total	3–6	5–6	3–6	4–6	0–1	1–2	0	0

Ecology. The specimens studied were collected in a small stream characterized by the presence of sulphurous sediments at an altitude of 1400 m (Fig 26). *Oreodytes kanoi* larvae were observed swimming among the sediments as well as among the roots of dried grasses. On several occasions we observed larvae feeding on mosquito larvae in our sampling tray. Pupae and prepupae were collected on gradual slope along river bank, within one meter above the water level (Fig 27). After turning over numerous stones along the littoral zone, we found they were more abundant under larger flat stones, where they grouped more densely (Fig 28). The minimum stone size diameter over pupal chambers was 15 mm, 3.5 times as large as pupa. Pupal chambers were built into peculiar mounds, consisted of fine damp sands, usually with a small opening at the top (Fig 28). Mounds were about 5–6 mm in diameter basally. In each pupal chamber, the pupa was found upward, on its back in a suspended position (Fig 29). According to our observations, the larvae and pupae were more active and abundant during the months of July and August which suggests a life cycle of type I, i.e., univoltine with overwintering adults and larval development in summer (Nilsson 1986).

Discussion

The description of the larvae of *Oreodytes kanoi* presented in this study increased to nine the number of species of *Oreodytes* (sensu novo) known to date, which makes this group of Hydroporinae one of the best known in terms of larval morphology. What is surprising when comparing these species, however, is the great resemblance between the described larvae both morphometrically (Table 4) and chaetotaxically (Table 5). Considering this great homogeneity between the known species, it is all the more surprising that each of the species groups established informally by Fery & Ribera (2018) can be easily distinguished by the combination of relative size and presence or absence of secondary setae on the tarsi (Tables 4–5).

Like the other species included in the *alpinus* species-group, larvae of *Oreodytes kanoi* are distinguished from those of the other species of *Oreodytes* by the unique presence of secondary setae on the dorsal margin of the tarsi (Figs 20–21; Table 5). Such a characteristic suggests that these species form a natural group.

Unlike larvae, knowledge of the pupal morphology of Hydroporinae is scanty. Amongst *Oreodytes*, only *O. scitulus* had its pupa described but very superficially (Matheson 1914). At a larger taxonomic scale, the pupa of another Deronectina, *Nebrioporus ceresyi* (Aubé, 1838), was recently described (Giulio & Nardi 2006). In comparison to this species, the pupa of *O. kanoi* differentiates by its larger size (TL > 4.4 mm compared to 3.7 mm) as well as by the presence of larger number of setae on the head capsule, especially on ML (10–12 compared to 4) (Table 3).

Regarding the habitat of Dytiscidae pupa, field observations remain scarce. As for *Oreodytes kanoi*, mature larvae were found building mounds made of fine sand, under flat stone of the river bank, which is similar to observations made for *O. scitulus* (Matheson 1914). It is worth noting that pupae and prepupae could only be found over narrower portion of the river margin where the humidity level of sand was kept moderate. Interestingly pupal chambers could not be found along steeper portion of the littoral zone as well as under rocks leaving little space with the ground, which suggests that the pupation process can only be undertaken under specific conditions. More in-depth studies would be needed to better understand the pupation environment of *O. kanoi*.

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