

Horelophus walkeri rediscovered: adult morphology and notes on biology (Coleoptera: Hydrophilidae)

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Abstract. *Horelophus walkeri* Orchymont, 1913, the single representative of the enigmatic hydrophilid subfamily Horelophinae, is redescribed and illustrated based on recently collected specimens and its external morphology is briefly compared with other groups of Hydrophilidae. The species is hygropetric, inhabiting the spray zone and still waters along streams and waterfalls; its habitat preferences are discussed based on direct observation. A list of known specimens of *H. walkeri* is presented and its distribution is summarized.

Key words. Hydrophilidae, Horelophinae, *Horelophus*, endemics, morphology, biology, New Zealand

Introduction

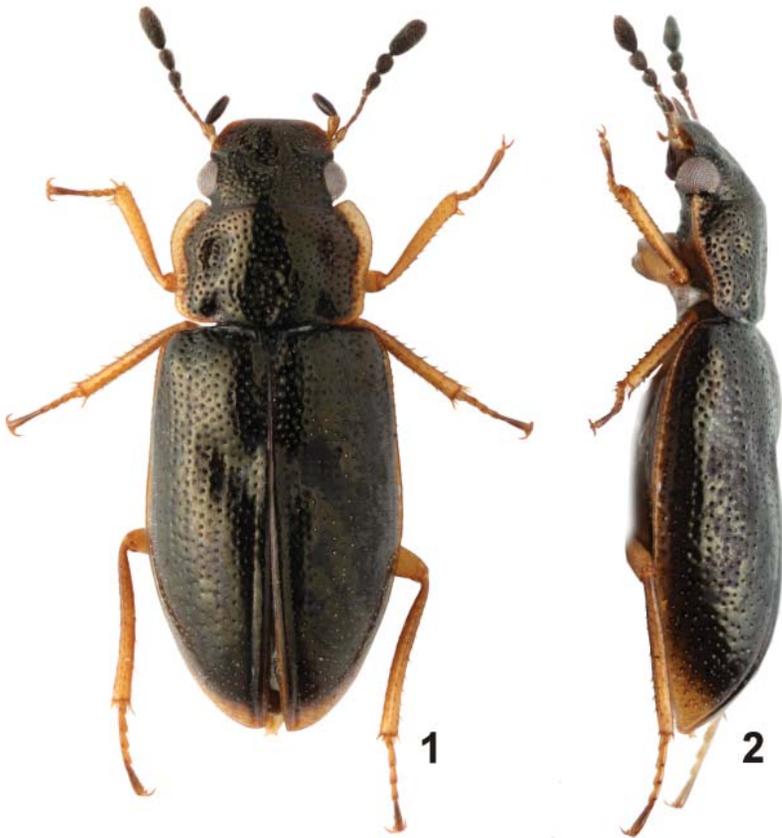
Horelophus walkeri Orchymont, 1913 was one of the first hydrophiloid species which A. d'Orchymont, one of the masters of hydrophiloid taxonomy, described nearly 100 years ago at the beginning of his career. The species was described based on two specimens collected in the South Island of New Zealand in 1902, and placed in the tribe Helophorini (i.e. what is today the family Helophoridae) (ORCHYMONT 1913). Since that time, no additional specimens became available for a long time and the species became a mystery considering both its taxonomic placement and biology. After the original description, the position of *Horelophus* Orchymont, 1913 was discussed by several authors. SHARP (1915) reexamined

its placement and expressed ‘little doubt that *Horelophus* will prove to be more nearly allied to *Ochthebius* than to *Helophorus*’. This comment was apparently the reason why *Horelophus* was excluded from the Helophoridae and placed in the staphylinoid family Hydraenidae, at that time considered as closely related to Hydrophilidae, by some subsequent authors (e.g., BALFOUR-BROWNE 1958, SMETANA 1985). ORCHYMONT (1924) commented on SHARP’s (1915) removal of *Horelophus* from Helophorini and admitted that *Horelophus* may well not belong near *Helophorus* Fabricius, 1775, but strongly disagreed with the placement of the genus with *Ochthebius* Leach, 1815 (Hydraenidae). He suggested that *Horelophus* might be best placed among the primitive Rygmodini, the tribe of terrestrial hydrophilids that was then known to be distributed in Australia and New Zealand. Later, ORCHYMONT (1937) formally listed *Horelophus* in the tribe Rygmodini, which was followed by MALCOLM (1981). Ten years later, HANSEN (1991) performed the first formal phylogenetic analysis of the Hydrophiloidea, in which *Horelophus* was revealed as the sister-group of the hydrophilid subfamilies Hydrophilinae + Sphaeridiinae, based on many characters shared with these subfamilies, but at the same time bearing supposedly plesiomorphic characters shared with some basal hydrophiloid families (e.g. lateral margin of pronotum not forming a continuous curve with elytra, pronotal surface bearing depressions, and femora lacking tibial grooves). Consequently, HANSEN (1991) established the monotypic subfamily Horelophinae and considered it as the basal-most hydrophilid clade. Since then, no additional information on *Horelophus walkeri* has been published, the two syntypes remain the only known specimens with precise locality data published, and its biology has remained nearly unknown, except for the note by HANSEN (1991) mentioning label data of two unspecified specimens.

As the sole representative of a separate subfamily, *Horelophus* has become crucial for ongoing projects focused on resolving the phylogeny of the Hydrophiloidea (a project by A. Short) or beetles as a whole (HUNT et al. 2007, LAWRENCE et al. 2011) on the basis of molecular and morphological data. For that reason, we have first summarized the few available (largely unpublished) data on the species, and then we conducted a short survey of the South Island of New Zealand in order to rediscover the species, collect fresh material for DNA studies and discover some basic data on its biology. The aim of this paper is to summarize these unpublished and new data concerning the distribution and biology of *H. walkeri*, and provide detailed morphological data which will be necessary for further analyses when the results of the molecular studies become available.

Material and methods

We have examined one syntype and 121 additional specimens collected between 1902 and 2012. The study on external morphology is based on dry mounted specimens examined using an Olympus SZ61 binocular microscope, slide mounted specimens examined using an Olympus BX41 compound microscope (mounted in Euparal or Canada balsam, deposited in FMNH and NMPC) and gold-coated specimens examined by JEOL 6380 LV electron microscope in the Laboratory of Electron Microscopy, Faculty of Science, Charles University, Prague. Habitus photographs were taken using a Canon MP-E 65 mm macro lens attached to a Canon EOS 550D camera and stacked from multiple layers using the Helicon Focus 5.1



Figs. 1–4. *Horelophus walkeri* Orchymont, 1913. 1–2 – general habitus in dorsal and lateral view (photo M. Fikáček); 3–4 – individuals on the wet rock surfaces at Dead Horse Creek, Marlborough (photo R. Leschen).



Figs. 5–10. Habitats of *Horelophus walkeri* Orchymont, 1913. 5–6 – Marlborough, Dead Horse Creek, 30.xi.2010 (5 – R. Leschen collecting specimens walking on rock steps; 6 – general view of the exposed part of Dead Horse Creek where *H. walkeri* occurred); 7–9 – Nelson, Deepwater Creek, 2.xii.2010 (7 – general view of the small streamlet on which side the specimens were found, see black arrows; 8–9 – details of the microhabitats where *H. walkeri* occurred); 10 – Marlborough, Pelorus Bridge, 28.xii.1984, A. Newton collecting *H. walkeri* at the side of the waterfall. Photos by M. Fikáček (5–9) and M. Thayer (10).

Pro software. Drawings were prepared using a drawing tube attached to the above compound microscope.

Morphological terminology largely follows HANSEN (1991), KOMAREK (2004) and LAWRENCE et al. (2010), and wing venation nomenclature follows KUKALOVÁ-PECK & LAWRENCE (1993, 2004) and LAWRENCE et al. (2010). Comparisons with other genera are based on the material deposited in the collections of the National Museum, Prague, Czech Republic (NMPC). Taxonomy and nomenclature follow HANSEN (1991, 1999) and SHORT & FIKÁČEK (2011).

Voucher specimens are deposited in the following collections:

ANIC	Australian National Insect Collection, Canberra, Australia (A. Šlipiński);
BMNH	The Natural History Museum, London, U.K. (M. Barclay);
FMNH	Field Museum of Natural History, Chicago, U.S.A. (A. Newton);
IRSN	Institut Royal des Sciences Naturelles, Bruxelles, Belgium (P. Limbourg);
IZAS	Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing, China (K.-Q. Song);
LUNZ	Entomology Research Museum, Lincoln University, Christchurch, New Zealand (J. Marris);
NHMW	Naturhistorisches Museum, Wien, Austria (M. Jäch);
NMPC	National Museum, Prague, Czech Republic (M. Fikáček);
NZAC	New Zealand Arthropod Collection, Auckland, New Zealand (R. Leschen);
SEMC	Natural History Museum, University of Kansas, Lawrence, U.S.A. (A. Short);
YMSJ	Yūsuke Minoshima collection, Sapporo, Japan;
ZMUC	Zoological Museum, University of Copenhagen, Denmark (A. Solodovnikov).

Results

Horelophus Orchymont, 1913

Horelophus Orchymont, 1913: 94. Type species: *Horelophus walkeri* Orchymont, 1913 (by monotypy).

Horelophus: SHARP (1915: 2, transferred to Hydraenidae); ORCHYMONT (1916: 237, compared with Rygmodini); KNISCH (1924: 94, catalogue, in Helophorinae); ORCHYMONT (1924: 93, comments on taxonomic placement); ORCHYMONT (1937: 155, listed under Rygmodini); BALFOUR-BROWNE (1958: 88, as in Hydraenidae); MALCOLM (1981: 6, in Rygmodini); SMETANA (1985: 11, in Hydraenidae); HANSEN (1991: 105, placed in Hydrophilidae: Horelophinae); KLIMASZEWSKI & WAIT (1997: 23, 130, summary on New Zealand hydrophilids, habitus illustration); HANSEN (1999: 67, catalogue); LESCHEN et al. (2003: 19, list of genera); SHORT & FIKÁČEK (2011: 85, list of genera).

Horelophus walkeri Orchymont, 1913

(Figs. 1–4, 11–51)

Horelophus walkeri Orchymont, 1913: 97.

Type locality. New Zealand, South Island, Buller district, Reefton.

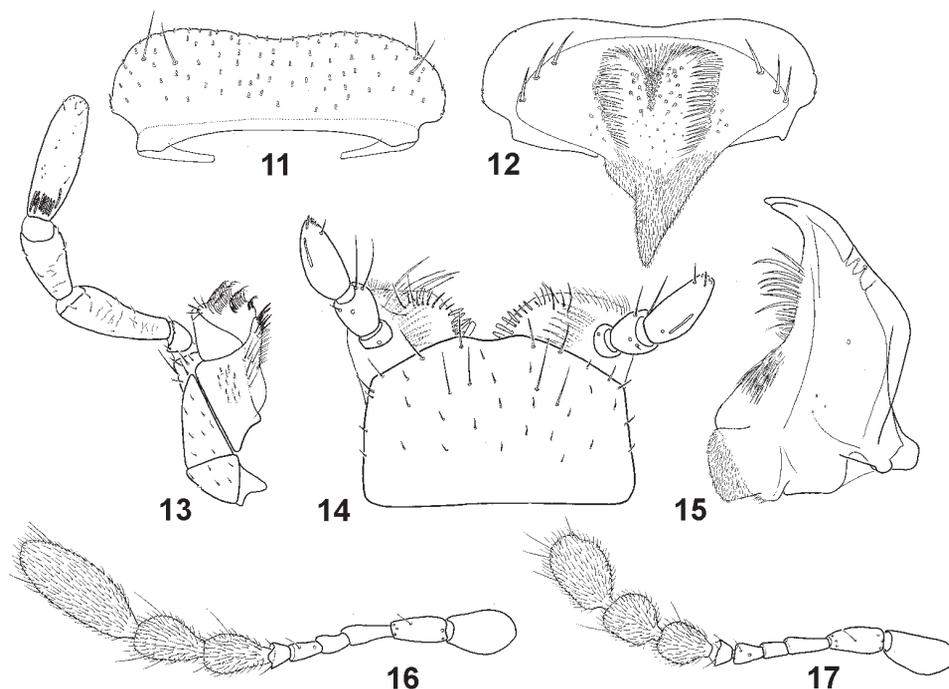
Type material examined. SYNTYPE: 1 spec. (IRSN): ‘Coll. R. I. Sc. N. B. / Nouvelle Zelande // [label glued on the previous:] Reefton / N.Z. 12 1902 / J. J. Walker // det. d’Orchymont / *Horelophus* Walkeri / d’Orch. / Cotype’.

Additional material examined. NEW ZEALAND: MARLBOROUGH: 31 spec. (FMNH, ZMUC): 0.9 km SW of Pelorus Bridge, 60 m a.s.l., 41°18'17.64"S, 173°34'2.89"E, 28.xii.1984, on rocks in spray zone of falls, lgt. A. Newton & M. Thayer; 13 spec. (NMPC, NZAC, ANIC, SEMC): S of Canvastown, Dead Horse Creek, ca. 30 m a.s.l., wet stones with algae and moss along exposed stream, 41°19.59'S, 173°39.57'E, 30.xi.2010, lgt. Fikáček & Leschen (RL1511) [2 spec. in pure alcohol in NMPC]; 2 spec. (SEMC): same label data [voucher specimens to DNA isolates SLE132 and SLE133, isolated deposited in SEMC]; 2 spec. (NMPC): same label data [voucher specimens to DNA isolates COL1799 and COL1834, isolates deposited in ANIC]; 1 spec. (NZAC): same label data, dip net (RL1512). NELSON: 6 spec. (NZAC): Lyell Walkway, Deepwater Creek, 130 m a.s.l., 41°47'39.35"S, 172°3'20.37"E, 2.xii.2010, lgt. Fikáček & Leschen (RL1525); 2 males (NMPC): same label data [voucher specimens to DNA isolates COL1790 and COL1823, isolates deposited in ANIC]; 3 spec. (IZAS): same label data [1 spec. is voucher specimen to DNA isolate A31 deposited

in IZAS]; 4 spec. (NMPC, BMNH): same locality, exposed small stream and waterfall (surface scraping in splash zone), 2.xii.2010, lgt. Fikáček & Leschen (RL1527); 7 spec. (NMPC, BMNH, ANIC): same locality, exposed small stream and waterfall (ex mosses), 2.xii.2010, lgt. Fikáček & Leschen (RL1526) [3 spec. in pure alcohol in NMPC]; 14 spec. (NMPC, NZAC, NHMW, YMSJ): same locality, 2.xii.2010, exposed hygropetric along small stream and waterfall (pyrethrum spraying rock surface), lgt. Fikáček & Leschen (RL1533); 1 spec. (NMPC): Lyell Walkway, past cemetery, 110 m a.s.l., 41°47'49.43"S, 172°3'3.97"E, rock surface, 2.xii.2010, lgt. Fikáček & Leschen (RL1531); 3 spec. (NMPC, ANIC): Lyell Walkway, small creek at track junctions, 115 m a.s.l., 41°47'42.59"S, 172°3'20.1"E, 2.xii.2010, ex rock surfaces, lgt. Fikáček & Leschen (RL1530); 1 spec. (NMPC): NE of Owen River, Sunrise Bridge track, Halfway creek, ca. 440 m a.s.l., 41°35.993'S, 172°32.236'E, 1.xii.2010, at rock along the stream, lgt. Fikáček & Leschen (RL1519) [voucher specimen to DNA isolate COL1835 deposited in ANIC]; 8 spec. (NZAC): Nelson, Cawthron Park, ca. 30 m a.s.l. (coordinates ca. 41°18'S, 173°13'E), 4.xii.1924, lgt. E. S. Gourlay; 2 spec. (NZAC): same locality, 9.xii.1924, lgt. E. S. Gourlay; 11 spec. (LUNZ): Owen River env., 460 m a.s.l. (coordinates ca. 41°41'S, 172°27'E), 2.i.1984, on tent in *Nothofagus* forest ca. 10–15 m from Owen River, lgt. R. M. Emberson [collected in late afternoon in bright sunshine, sitting or landing on a dome tent with alternating panels of dark green and pale beige color; the tent was pitched in a clearing in *Nothofagus* forest within 10–15 m of the bank of the Owen River, which at that point is a small fast-flowing river with lots of protruding rocks and little cascades overhung with beech trees (R. Emberson, in litt. 1986 to A. Newton)]; 7 spec. (NZAC): Courthouse Flat, Nuggety Cr, Lutine Pool, 25.i.2012, R. Leschen, 41.473360°S, 172.560224°E, along edges of still water (RL1632); 2 spec. (NZAC): same locality, 26.i.2012 (RL1634). **BULLER**: 1 spec. (BMNH): Greymouth, Ten Mile Creek [as '10 mile creek'], lgt. Helms [mouth of Ten Mile Creek where it meets the west coast is at ca. 42°20'05"S, 171°15'38"E].

Redescription. Body elongate, strongly depressed (Figs. 1–2); total length 2.1–3.1 mm, maximum width of pronotum 0.8–1.0 mm, maximum width of elytra 1.0–1.5 mm. General coloration of dorsal surface piceous brown to black often with greenish tinge, lateral margins of pronotum and elytra with wide pale reddish stripe, anterolateral margins of clypeus vaguely dark reddish; ventral parts dark brown to black, only gular area and prosternum paler brown and epipleura pale reddish; head appendages dark reddish, maxillary palpomere 4 and antennal club dark brown; legs with brownish coxae, pale reddish femora, tibiae and basal tarsomeres, and distal tarsomeres darkened.

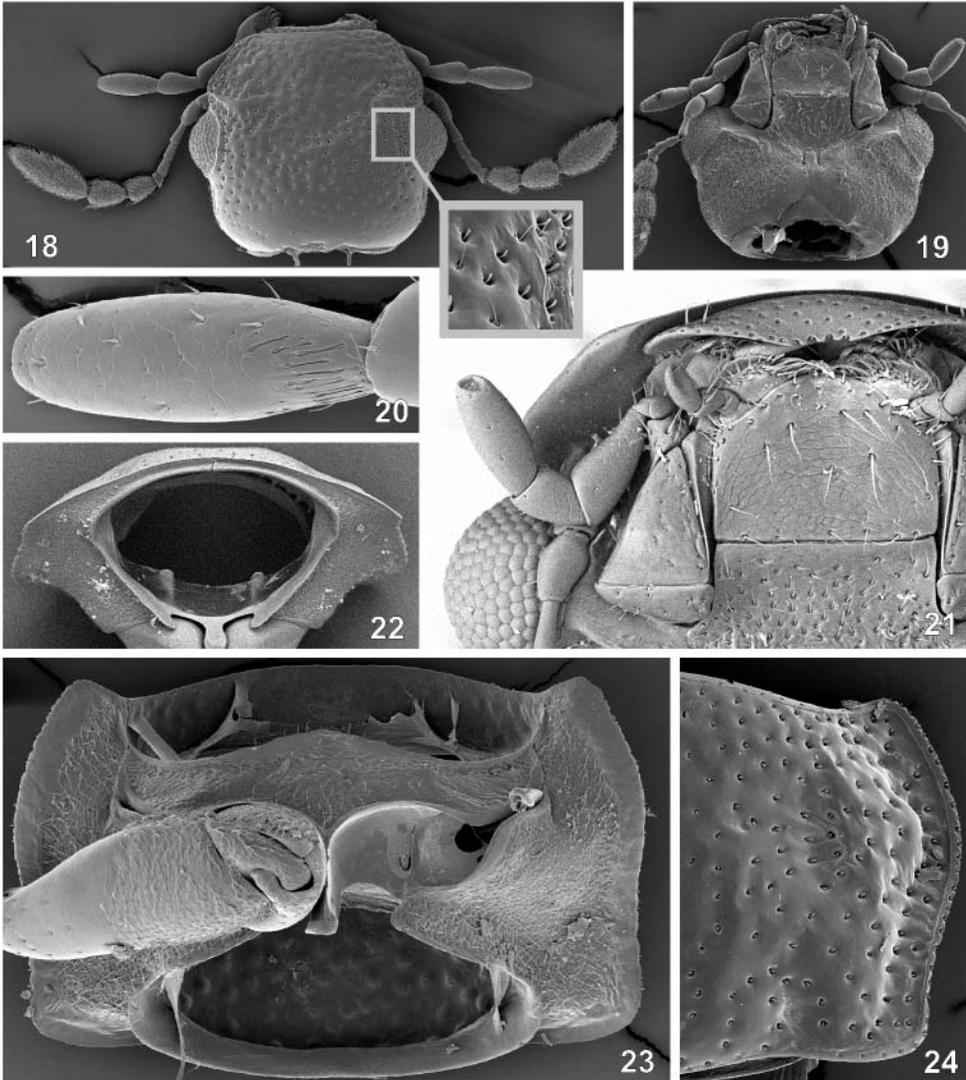
Head. *Clypeus and frons* (Fig. 18) with sparse but rather coarse punctation, each puncture bearing a short apically widened seta, frons with several trichobothria, clypeus without trichobothria; frontoclypeal suture only distinct laterally, arising closely before eyes; clypeus slightly expanded laterally, covering bases of antennae, anteromedian margin shallowly concave. *Eyes* small, protruding from outline of head, separated by 6× width of one eye. *Labrum* (Figs. 11–12) largely exposed dorsally, only slightly retracted under clypeus, widest subbasally, strongly narrowed basally and arcuately narrowing anteriorly, shallowly bisinuate on anterior margin; dorsal surface bearing two pairs of long sublateral setae and the ground punctation similar to that on clypeus; epipharynx with a lateral row of three stout setae on each side, median portion with two vertical rows of long cuticular spines and cone-shaped group of similar spines anteriorly, basal portion with densely pubescent membranous cone. *Mandibles* (Fig. 15) symmetrical, with distinct mandibular angle, mandibular apex bifid; mediobasal portion with a group of long cuticular projections, medioproximal portion with very fine setae, mola rather small, bearing numerous backwards directed setae on median face. *Maxilla* (Fig. 13) with a simple subtriangular cardo lacking trichobothria; basistipes triangular, bearing few fine setae only; mediostipes rather vaguely delimited from lacinia, the latter membranous, bearing fine hair-like setae mesally and few stouter and longer setae distally; galea short, with distal setae arranged into well-defined rows; palpifer rather small,



Figs. 11–17. Mouthparts and head appendages of *Horelophus walkeri* Orchymont, 1913. 11 – labrum, dorsal view; 12 – labrum, ventral view (epipharynx); 13 – maxilla; 14 – mentum and prementum; 15 – mandible; 16–17 – antenna (16 – male, 17 – female).

with few rather long setae; maxillary palpus with 4 palpomeres, palpomere 1 minute, palpomeres 2 and 4 subequal in length, ca. twice length of palpomere 3; base of palpomere 4 with a group of 10–11 digitiform sensilla on dorsolateral surface. **Labium** (Figs. 14, 20–21) with submentum ca. as long and wide as mentum, bearing sparsely arranged setae; mentum transverse, ca. 1.5× wider than long, with continually convex anterior margin, its surface bearing a few larger setae and very weak and sparse mesh-like microsculpture, lateral margins without rows of setae; prementum subdivided into two membranous lobes bearing anteromedian row of fine setae (becoming spoon-like medially) and a dorsal sublateral row of setae, palpifer vaguely sclerotized; labial palpus with three palpomeres, palpomere 1 minute, palpomere 2 ca. half as long as palpomere 3; palpomere 3 with one subbasal digitiform sensillum and few minute apical sensilla. **Antenna** (Figs. 16–17) with 9 antennomeres, scapus conical, ca. as long as pedicel, pedicel widest proximally, bearing a few pore-like sensilla and one tiny seta, antennomere 3 ca. as long as antennomeres 4–5 combined, cupula small, antennomeres 7–9 forming a distinct, loosely segmented and densely pubescent antennal club; length of antennae slightly sexually dimorphic, slightly longer (and antennomeres slightly more elongate) in males than in females, proportions of antennomere 9 strongly sexually dimorphic, ca. 3× as long as wide in males and 1.5× as long as wide in females, bearing numerous small conical

sensilla on ventral surface (intermixed with trichoid setae on whole surface in male, more accumulated in subapical group in female). **Gula** (Fig. 19) narrow, gular sutures narrowly separated at midlength, slightly diverging at tentorial pits, the latter distinct, elongate. **Temporae** with short but distinct ridge arising from inner margin of each eye.

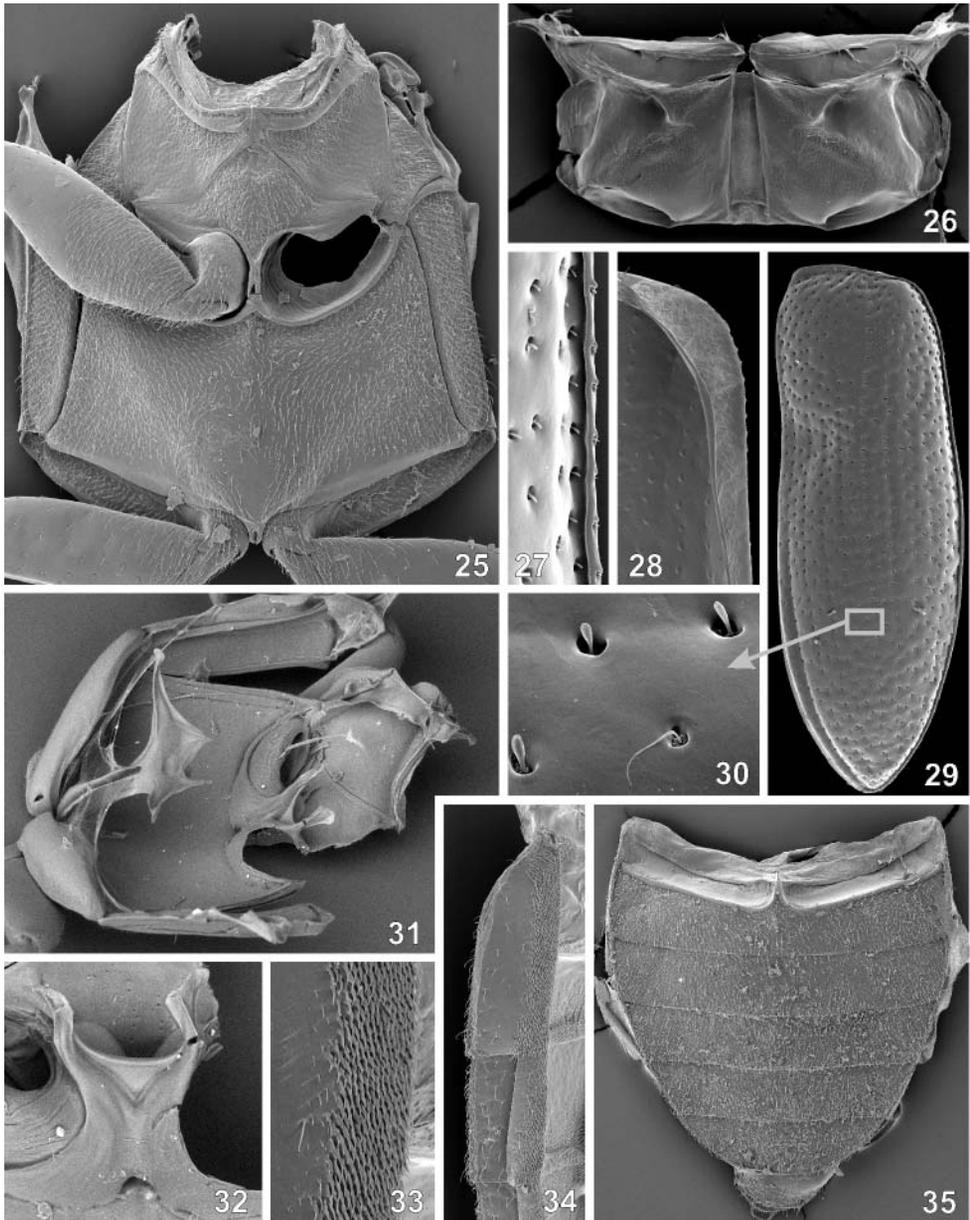


Figs. 18–24. Morphology of *Horelophus walkeri* Orchymont, 1913. 18 – head, dorsal view (inset: detail of punctation of frons); 19 – head, ventral view; 20 – maxillary palpomere 4, dorsal view; 21 – detail of mouthparts; 22 – prothorax, posterior view; 23 – prothorax, ventral view; 24 – right side of pronotum.

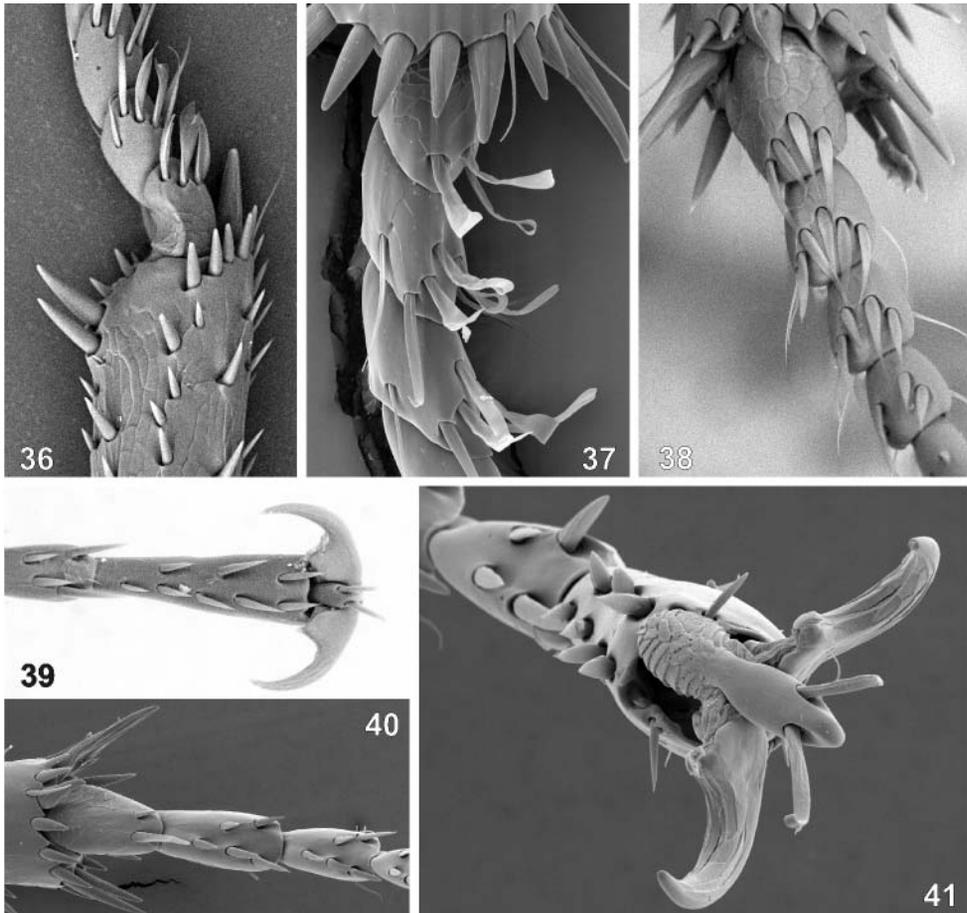
Prothorax. Pronotum (Fig. 1, 24) subrectangular, widest in anterior third, with weakly projecting anterior corners, lateral margins not forming continuous curve with lateral margins of elytra; surface with one posteromedian and two sublateral depressions, ground punctation sparse and rather coarse, similar to that of clypeus, trichobothria missing; lateral edges slightly sinuate, with fine marginal bead extending onto anterior edge. **Hypomeron** (Fig. 22–23) with rather narrow lateral glabrous portion and densely pubescent median portion, portions not divided by a ridge, hypomeral process large, rounded mesally. **Prosternum** (Fig. 23) rather long anterior to procoxae, ca. 0.6× as long as procoxa, without longitudinal or transverse ridges or impressions, slightly convex on anterior margin, prosternal process indistinct, concealed between procoxae. **Coxal cavities** closed internally, open posteriorly, coxal fissure rather long, closed, notopleural suture distinct. Accessory ridge below posterior pronotal margin, laterally obliterated, recognizable as short and indistinct ‘transverse fold’. **Profurca** (Fig. 22) short, profurcal arms widely separated, in the form of slightly asymmetrical plate-like extensions.

Mesothorax. Scutum (Fig. 46) with finely microsculptured median portion, bearing sparsely arranged setae; scutellar shield exposed, triangular, pointed posteriorly, slightly longer than wide, with a few fine setae present on its surface. **Elytron** (Figs. 27–30) elongate, with a distinct mesal depression in anterior third; sutural stria present, reaching ca. midlength of elytron; elytral series irregular, formed of the punctures of the same size and morphology as subserially arranged interval punctation, hence elytron seemingly bears ca. 18 more or less irregular series of punctures; scutellary stria absent (not visible even in slide-mounted elytron); alternate elytral intervals each with a few short trichobothria, punctures of elytral series and intervals each bearing a short club-like seta; lateral edge with a narrow bead, finely crenulate; epipleuron moderately wide anteriorly, gradually narrowing from level of metaventrite posteriorly, reaching subapically, median pubescent portion not delimited from lateral bare one by a line or ridge; ventral elytral surface without any elevated ridges, only with a narrow longitudinal field of fine spines situated sublaterally between anterior fourth and midlength. **Mesoventrite** (Fig. 25) distinctly divided from mesanepisternum by distinct anapleural suture; mesoventrite subtriangular in shape in anterior two thirds, widely extended laterad in posterior third, lateral extensions bearing distinct coxal lobes; whole mesoventrite nearly flat, without distinct protuberances or ridges, whole surface except for the lateral wings bearing sparse pubescence; mesoventral process narrow. **Mesanepisterna** not meeting anteromesally, very narrowly divided by anterior portion of mesoventrite; anterior collar well-defined, moderately wide; mesal portion of each mesanepisternum pubescent, large lateral portions bare. **Mesepimeron** with large ventral portion, not reaching anterior collar or mesanepisternum anteriorly, forming lateral margin of coxal cavity; its whole surface pubescent. **Coxal cavities** obliquely transverse, ca. 1.5× wider than long, very narrowly separated from each other by mesoventral and metaventral processes; internal postcoxal wall moderately wide mesally and posteriorly. **Mesofurca** (Figs. 31–32) well-developed but short, arising as two widely separate plate-like extensions from posterior wall of coxal cavities.

Metathorax. Metanotum (Fig. 26) weakly sclerotized, ca. 2× wider than long, with rather wide anterior membranous area, alacristae slightly diverging posteriorly. **Metaventrite** (Fig. 25) ca. 1.5× longer than mesoventrite, evenly convex, without defined median portion,



Figs. 25–35. Morphology of *Horelophus walkeri* Orchymont, 1913. 25 – meso- and metathorax, ventral view; 26 – metanotum; 27 – elytral margin, dorsal view; 29 – elytron, dorsal view; 30 – detail of elytral punctation; 31 – meso- and metafurca, lateral view (part of mesoventrite broken off); 32 – mesofurca, posterior view; 33 – detail of projections of laterotergite 3; 34 – abdominal laterotergites 3–4; 35 – abdomen, ventral view



Figs. 36–41. Legs of *Horelophus walkeri* Orchymont, 1913. 36 – male, apex of protibia and basal part of protarsus; 37 – male, mesotarsomeres 1–3; 38 – female, mesotarsomeres 1–3; 39 – male, metatarsomere 5 and pretarsus in relaxed condition; 40 – male, metatarsomeres 1–3; 41 – male, metatarsomere 5 and pretarsus with exposed unguis and unguitactor.

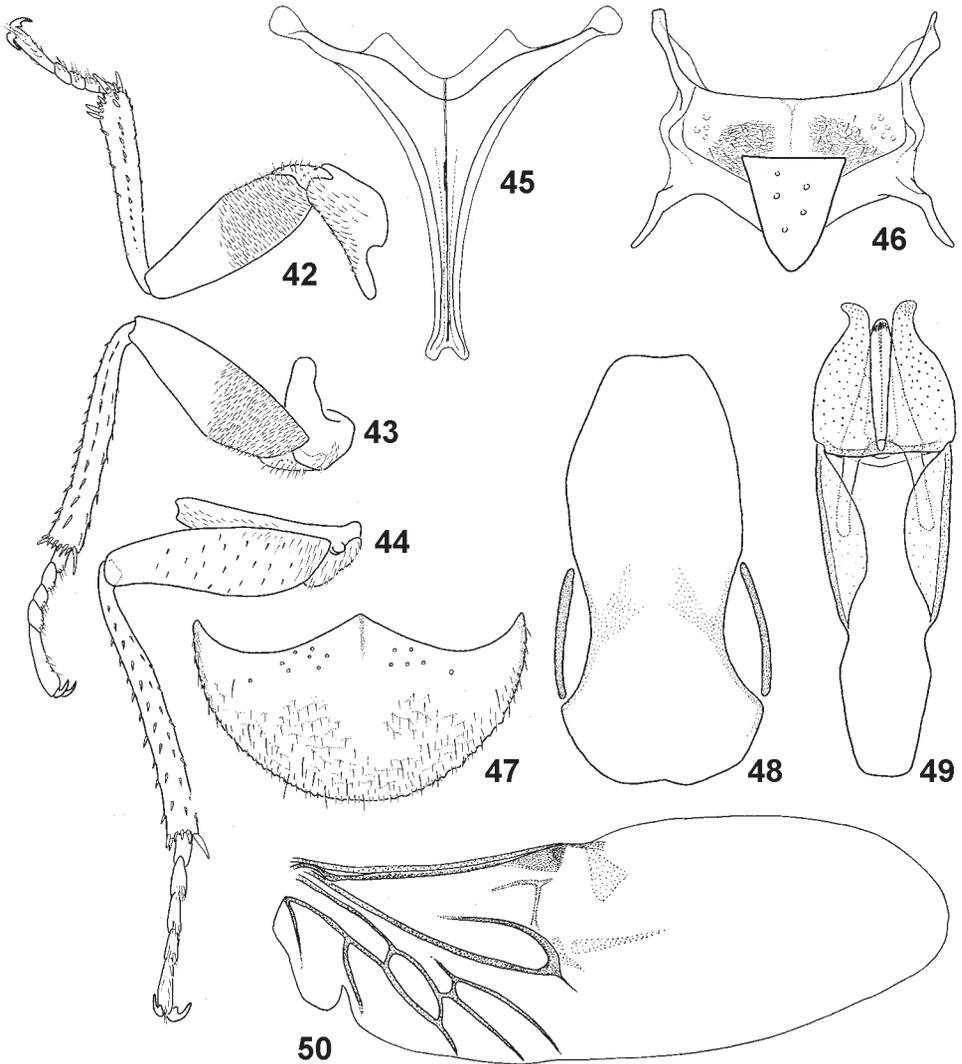
whole surface (except for a small posteromedian area) bearing dense pubescence; katepisternum narrowly exposed, metacoxal process short but distinctly exposed. Postcoxal ridge very narrow but well-defined. *Metanepisternum* ca. 6× longer than wide, with an obliquely transverse strengthened ridge anteriorly; whole surface pubescent. *Metepimeron* with minute but distinct ventral portion. *Metafurca* (Figs. 31, 45) rather large, Y-shaped; stalk grooved medially, without basal extensions; lateral arms rather long, with large anterobasal extensions, apical portions roundly plate-like. *Hind wing* (Fig. 50) well developed, ca. 2× longer than elytron, venation well-developed in basal half, absent in distal half; anal lobe rather large, well-defined by anal notch; RA tightly attached to ScA except of subbasally, both reaching to triangular radial cell, RP_{3+4} rather long, cross vein r4 arising from its distal portion; MP_{1+2}

strong, forming a loop with distal portion of RP, the latter reaching midlength between the loop and wing base, median spur short but distinct; vein complex of $MP_4+Cu+AA$ well developed, not connected to MP_{1+2} by cross veins, with well-defined and completely closed basal and wedge cells; AA_4 , CuA_2 and MP_4 reaching posterior margin of wing in basal third, branching of CuA_2 and MP_4 slightly variable between specimens or even within the specimen, forming a continuous series between X-shaped and H-shaped branching pattern; AA_4 well developed, nearly reaching posterior wing margin; AP_{1+2} well developed, reaching ca. midlength of anal lobe.

Legs (Figs. 36–44). **Coxae**: procoxae subglobular, narrowly transverse, sparsely pubescent ventrally; mesocoxae transverse, rather robust mesally, narrowly separated, finely pubescent ventrally; metacoxae narrowly transverse, subrectangular in ventral view, sparsely pubescent on whole ventral surface. **Trochanters** with proximal parts concealed by coxae, distal subtriangular parts exposed ventrally, pubescent. **Femora** attached to trochanters by their posteromesal (in meso- and metafemora) or anteromesal (on profemora) portions only, anteromesal (in meso- and metafemora) or posteromesal bases (in profemora) free, angulate; pro- and mesofemora densely pubescent in their basal portion, metafemora bearing such pubescence only on extreme basoanterior portions, most of their surface bearing sparsely arranged spine-like setae; tibial grooves not defined on any femora. **Tibiae** slightly longer than femora, slightly widening distad; each tibia with three dorsal and three lateral series of spines, distal portion with a group of enlarged spines and two rather short but stout tibial spurs; protibia with two large closely associated spines subdistally on outer margin, outermost series of spines closely aggregated. **Tarsi** with 5 tarsomeres, basal tarsomere short, subequal in length to each of tarsomeres 2–4, tarsomere 5 as long as tarsomeres 2–4 (in pro- and mesotarsus) or 3–4 (in metatarsus) combined. Ventral setae of pro- and mesotarsomeres 1–3 sexually dimorphic, in shape of long wide plates in males (Fig. 36–37), shorter, spine-like in females (Fig. 38), ventral setae of pro- and mesotarsomeres 4–5 and metatarsomeres 1–5 of both sexes spine-like (Figs. 39–41); claws rather large, arcuate, bearing a subbasal tooth, shape of claws the same in all three pairs of legs and in both sexes; empodium moderately large, with rather massive and sculptured unguitactor plate concealed within distal part of tarsomere 5 in relaxed position (Figs. 39, 41), exposed portion of empodium bearing a pair of stout subapical setae.

Abdomen (Figs. 33–35) with five exposed ventrites; ventrite 1 with moderately large bare coxal grooves, remaining portion densely pubescent, median portion without longitudinal carina; ventrites 2–5 subequal in length, densely pubescent on whole surface, with a few larger setae scattered among ground pubescent in posterior portion of ventrite 3–4 and especially ventrite 5; posterior margin of ventrite 5 without median emargination or group of enlarged setae; laterotergite 3 simple, dorsal portion not divided from ventral one by a ridge, bearing an area of goose-head-shaped cuticular projections, without any kind of organized stridulatory file; laterotergites 4–6 step-like, subdivided into elevated ventral and depressed dorsal portion, ventral portion with cuticular projections similar to laterotergite 3; tergites weakly sclerotized, densely pubescent posterolaterally.

Genitalia. Male genitalia (Figs. 47–49). Aedeagus of simply trilobed type; parameres short, ca. $0.4\times$ as long as phallobase, wide basally, arcuately narrowing to apical fifth on outer margin, mesal margin nearly straight, apices rounded, bent laterad, whole paramere bearing numerous pore-like sensilla; median lobe ca. $1.5\times$ as long as parameres, subtrian-



Figs. 42–50. Morphology of *Horelophus walkeri* Orchymont, 1913. 42–44 – legs, ventral view (42 – anterior leg; 43 – middle leg; 44 – posterior leg); 45 – metafurca; 46 – scutellum; 47 – male sternite 8; 48 – male sternite 9; 49 – aedeagus; 50 – hind wing.

gular apically, with rather long straight apodemes reaching into phallobase, apex narrowly rounded, gonoporus apical; phallobase with extremely enlarged symmetrical manubrium ca. 0.8× as long as main portion of phallobase. Sternite 9 widely tongue-like, with very short subbasal lateral struts. Sternite 8 crescent-like, finely serrate on posterior margin, with low and wide anterior projection. **Female genitalia** examined only externally, with long peg-like gonoxocites 9 and gonostyli 9.

Variation. The species is rather constant in all characters examined, with slight variation observed only in the shape of lateral margins of parameres which may be nearly subangular instead of rounded in some specimens. Specimens from Deepwater Creek and Dead Horse Creek exhibit both subangular and circular lateral portions of parameres (and even intermediate states) and we failed to find any other character by which the specimens would differ from each other, for which reason we consider this variation as intraspecific. Moreover, the variation may be possibly partly an artifact of the preparation of the aedeagus, i.e., the shape of the parameres may partly depend on the precise orientation of the aedeagus on the slide. Slight variation was also found in the precise branching of wing veins CuA_2 and MP_4 as mentioned directly in the description.

Biology. Longer series of *H. walkeri* were first collected in 1984 at Pelorus Bridge by A. Newton & M. Thayer on wet rock in the spray zone of an exposed waterfall (Fig. 10), but no specimens were found later at this site during visits in late November 2005 (by Newton & Thayer) and in December 2010 (by Leschen & Fikáček), possibly because the waterfall is much less sun-exposed at present than it was in 1984. In 2010, we found multiple specimens on sun-exposed wet rocks at sides of streams at Dead Horse Creek (Marlborough; Figs. 5–6, rocks with algal film) and three localities at Lyell walkway (Nelson; Figs. 7–9, rocks without algae), whereas single specimens were collected on a wet algae-covered stone on side of the Halfway Creek or just beyond the spray zone of an unnamed water fall at Lyell walkway. On two consecutive days in 2012 individuals were observed at Nuggety Creek (Nelson) at mid-day on exposed smooth rock surfaces, much like that shown in Fig. 6, but with less moss and in an area of high scouring. Individuals hide in wet moss (Fig. 9), damp rock cracks and crevices (Fig. 10), or along shaded margins of still water and can be extracted from field-collected moss scrapings or collected on rock surfaces sprayed with pyrethrum. Individuals were usually found walking on the surface of the wet rock (Figs. 3–4, see also the video mentioned below), and were never seen closely attached to the rock and therefore submerged in the surface water film as is normally the case for other hygropetric hydrophilids (e.g., *Laccobius* Erichson, 1837 and *Oocyclus* Sharp, 1882). Individuals observed for a period of 2.5 hours at Nuggety Creek were resting or walking along the edges of still water without entering (see the video at <http://www.youtube.com/watch?v=g03QtbXUCMI>), and were not generally active or observed to feed. Rowan Emberson collected a series of *H. walkeri* landing in the bright afternoon sunshine on a tent built in a clearing ca. 10–15 m from the Owen river in 1984 (see under Material examined for details). We observed that when submerged (examined by putting live specimens in a dish of water), the specimens bear a thin film of air on their ventral surfaces, but cannot swim. Complete records of each collecting event are listed in Material examined when known.

Though we did not systematically check all creeks in the Nelson, Marlborough, and Buller regions, all *H. walkeri* localities we visited were first-order and second-order streams in the Pelorus River (Dead Horse Creek and Pelorus Bridge), Buller River (Owen River and Lyell Creek area), and Motueka River (Nuggety Creek) catchments. Locations were with clear cool waters with high gradients flowing on grey-wackes, fine-clastic, or metasedimentary rocks, often with small pools or seams with still waters. Other streams examined in Nelson with streambeds composed of sandstones, or of moderate to coarse clastics did not have *H. walkeri*. Stream sections that were enclosed by a canopy did not yield specimens, and most



Fig 51. Distribution of *Horelophus walkeri* Orchymont, 1913 in New Zealand.

localities were dominated by beech trees (*Nothofagus*) apart from Dead Horse Creek which was surrounded by rejuvenating forest and adjacent to a *Pinus radiata* plantation.

Summarizing all of these data, we conclude that *H. walkeri* is a hygropetric species inhabiting exposed wet rocks along streams and waterfalls, and is most common in areas with extensive smooth surfaces. The specimens seem to hide in moss and rock crevices normally, and move to the rock surface probably for feeding on algae (but guts that we dissected were empty). The polarized light reflected from the wet rock surface may be used for finding suitable habitats (as it is in many other hydrophilids; KRISKA et al. 2006) which might explain the finding of the specimens on the tent by R. Emberson. This would also indicate that *H. walkeri* is a good flier, which is congruent with its long, well-developed wings.

Immature stages. Unknown. During the trip in the beginning of December 2010, we collected mosses and brushed the algal film from the microhabitats where adults were found at Dead Horse

Creek (Marlborough) and Deepwater Creek (Nelson), and these samples were carefully examined later that day in the laboratory. However, the only larvae which were obtained by this way belong to *Cylomissus* Broun, 1903 (associated by *cox1*, 16S and 28S DNA sequences). Likewise, Newton and Thayer in December 1984 and November 2005 collected and berlesed damp debris and mosses from the waterfall where the series of *H. walkeri* was found in 1984, but also found only *Cylomissus* larvae and no likely candidates for larvae of *Horelophus*. A single larva collected at Nuggety Creek also agrees with those of *Cylomissus* even though no hydrophilids other than *Horelophus walkeri* were collected or observed at the locality.

Distribution (Fig. 51). *Horelophus walkeri* is endemic to the northern part of the South Island of New Zealand, so far known only from the districts of Marlborough, Nelson and Buller west and north of the Alpine fault.

Discussion

In the phylogenetic analysis by HANSEN (1991), the position of *Horelophus* within the family Hydrophilidae was strongly supported by a number of synapomorphies shared with other hydrophilid taxa. This allowed him to reject definitely the original hypotheses by ORCHYMONT (1913) and SHARP (1915) assigning *Horelophus* close to Helophoridae or Hydraenidae, and supported the later idea of ORCHYMONT (1937) who considered *Horelophus* as an aberrant hydrophilid. The characters unusual for the Hydrophilidae, i.e. lateral margin of the pronotum

not forming a continuous curve with margin of elytra, femora without tibial grooves and pronotal surface with depressions, were evaluated as plesiomorphic in the analysis by HANSEN (1991) which made *Horelophus* a supposed sister taxon to the remaining Hydrophilidae. However, HANSEN (1991) also realized that the same character states which were supposed as plesiomorphic or autapomorphic in *Horelophus* also occur in some derived groups of the Hydrophilidae (e.g., depressions on pronotum are found in some Megasternini genera, extremely long legs and antennae are also found in *Rygmodes*, etc.). Hence, the position of *Horelophus* as derived inner group of Hydrophilidae (as proposed by ORCHYMONT (1937) and MALCOLM (1981)) was not totally excluded. Preliminary results of a multigene phylogenetic analysis of the Hydrophilidae (SHORT et al., in prep.) also support the latter view.

Of the inner groups of the Hydrophilidae, *Horelophus* shares some of its peculiar characters with the basal Sphaeridiinae (Rygmomini and Tormissini) and also with some basal Anacaenini (Hydrophilinae). When compared with the New Zealand endemic genus *Rygmodes* White, 1846 (tribe Rygmomini), it shares the long legs and antennae, protruding eyes, flat mesoventrite and sexual dimorphism in the size of the antennomere 9. Of other New Zealand taxa, some Tormissini (especially *Tormissus* Broun, 1893) have the enlarged manubrium of the aedeagus that we found in *Horelophus*. The large manubrium of the aedeagus is also found in some *Crenitis* Bedel, 1881 (tribe Anacaenini), which may also bear depressions on the pronotum and in which the lateral pronotal margin does not form a continuous curve with the elytra. Alternatively, the elytral punctation of the east Australian genus *Notohydus* Balfour-Browne, 1939 (tribe Anacaenini) bears club-like setae similar to those of *Horelophus*, and this genus also seems to exhibit sexually dimorphic ventral tarsal setae of the pro- and mesotarsus. However, a detailed morphological comparison is best postponed until the results of molecular analyses are available, and all relevant characters are examined in the supposed relatives of *Horelophus*. The morphological study of *Horelophus* provided in this paper should make this comparison with other hydrophilid taxa rather easy and straightforward.

The known distribution of *H. walkeri* is within a band adjacent to and north/northwest of the Alpine Fault, the active boundary of the Australasian and Pacific plates (KING 2000), and it is sympatric with other terrestrial arthropods on the Buller Terrane, which may indicate that it may be a Gondwanan relic (see LIEBHERR et. al 2011). The phylogenetic placement of *Horelophus* as shown by HANSEN (1991) as sister taxon to the remaining hydrophilids supports this contention, but the similarities to *Rygmodes*, *Tormissus* and some Anacaenini as stated above may indicate a different hypothesis, and a comprehensive phylogenetic analysis of hydrophilids is required for further speculation.

Surveys of aquatic beetles in New Zealand are lacking, particularly of lotic waters and hygropteric habitats, where *H. walkeri* is found. Queries about *H. walkeri* catches in samples for water quality assessments were negative (Paul Lambert, pers. comm.), indicating that *H. walkeri* may not tolerate urban development or may be found in high-order streams. We did not locate suitable habitats in Nelson City, and we assume that Gourlay's Cawthron Park collections were located within the hilly area surrounding the urban areas to the southeast, much of which drains into the Maitai River catchment. We also did not survey Ten Mile Creek catchment draining a portion of the southwestern flank of the Paparoa Range. Intensive searches in urban areas, like Nelson, and a broader survey of the northern tier of the South

Island would verify our geographic observations. Detailed studies of streambeds may also help to determine the habitat preferences of *H. walkeri*.

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