Systematics and biology of the endemic water scavenger beetles of Hawaii (Coleoptera: Hydrophilidae, Hydrophilini)

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Abstract. Recent field surveys in the Hawaiian Islands have revealed an adaptive radiation of endemic water scavenger beetles (Coleoptera: Hydrophilidae). Phylogenetic analysis based on 55 adult morphological characters affirms that this endemic hydrophilid fauna is a monophyletic clade that incorporates the first well-supported transformation from an aquatic to terrestrial way of life within any lineage of the subfamily Hydrophilinae. The clade is prescribed to the genus *Limnoxenus* Motschulsky, where described members were previously placed. Five new species are described: *L. waialeale* **sp.n.** (Kauai), *L. kauaiensis* **sp.n.** (Kauai), *L. oahuensis* **sp.n.** (Oahu), *L. punctatostriatus* **sp.n.** (Kauai) and *L. namolokama* **sp.n.** (Kauai). Lectotypes are designated for the two previously described species *L. semicylindricus* (Eschscholtz) and *L. nesiticus* (Sharp). The Hawaiian lineage is a component of a larger clade that also includes the remaining four species of *Limnoxenus* from Europe, South Africa, and Australia, plus the monotypic genera *Limnocyclus* Balfour-Browne of New Caledonia and *Hydramara* Knisch of South America. The majority of the Hawaiian species exhibit vestigial wings, an extremely unusual condition in aquatic beetles. No other island-endemic members of the Hydrophilinae are known to be flightless, suggesting insularity *per se* is not responsible for this condition. *L. nesiticus* of Oahu has not been collected during the past 106 years, suggesting that it has been lost to anthropogenically mediated extinction.

Introduction

The Hydrophilidae (sensu Hansen, 1991) is a large and diverse family of more than 2700 described species, broadly distributed in every major biogeographical region and island group (Hansen, 1999; Short & Hebauer, 2006). Despite the implications of their family group stem and common name of 'water scavenger beetles', this well-defined lineage contains many hundreds of terrestrial species, with the majority concentrated in the subfamily Sphaeridiinae. Conversely, adult and larval lifestyles within the Hydrophilinae, the largest component subfamily with more than 1740 described species, have been reported to be almost exclusively aquatic (Hansen, 1995a).

Recent fieldwork in Hawaii found several new species of Hydrophilinae in semi-aquatic and terrestrial situations (e.g. walking on moss mats, under logs and trail boards) on the islands of Kauai and Oahu. In addition to their collecting circumstances, these new taxa also possessed anatomical features unusual for hydrophilines, including the reduction or absence of natatory setae on the legs, reduced eye size and vestigial flight wings. Only two Hawaiian endemic hydrophilids have been described previously, both of which are fully aquatic (Williams, 1936). Fieldwork conducted in 2005 at the summit of Mt. Waialeale, Kauai – one of the rainiest sites on Earth (United States Geological Survey, 2007) – established that adults and associated larvae of one of these taxa are nocturnally active on wet, vertical rock faces festooned with filamentous cyanobacteria. During that same expedition, an adult female and associated mature larva of a second undescribed species were found together in an arboreal moss mat at Mt. Namolokama, an isolated plateau on Kauai. This species exhibits several morphological features consistent with a terrestrial lifestyle, including ventral brushes of setae on the tarsi.

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We analyse and taxonomically revise the endemic Hawaiian Hydrophilidae within the context of the hydrophiline subtribe Hydrobiusina (sensu Hansen, 1991). Cladistic analysis based on adult morphology supports the hypothesis that the Hawaiian taxa comprise a clade within the Hydrobiusina, but this clade's precise relationships remain ambiguous. We use the phylogenetic hypothesis to examine character transformations within the Hawaiian lineage in tandem with mapped ecological characters, establishing an ecological transformation series for the Hawaiian *Limnoxenus* that is rooted in the aquatic, spans the hygropetric, and terminates in the terrestrial, arboreal microhabitat. The evolution of brachyptery and the origin and pattern of diversification of this remarkable lineage are discussed in the context of the hypothesized phylogenetic relationships. Finally, recent biotic survey results suggest population declines or reduced geographical distributions for several of the taxa, thereby indicating where more intensive assessments of *Limnoxenus* populations should be conducted.

Historical and taxonomic background

The Hawaiian Hydrophilidae

Johann F. Eschscholtz of the University of Tartu (also known as Dorpat) in Estonia collected the first known Hawaiian hydrophilid specimens during an around-the-world voyage aboard the *Rurick* (1815–1818), subsequently describing them as *Hydrophilus semicylindricus* (Eschscholtz, 1822). Originally described from 'Wahu' (Oahu), the species was recorded twice more from the island over the next 60 years by Fairmaire (1849) from a taro (*Arum esculentum*) plantation and by Sharp (1879) from material collected by the Reverend Thomas Blackburn.

Shortly thereafter, Blackburn & Sharp (1885) characterized this seemingly common beetle as, 'Plentiful on all islands, at various elevations, in both stagnant and running waters' (p. 218), and predicted it would 'pretty certainly' be found outside the archipelago (p. 264). They specifically recorded it from the islands of Kauai, Oahu, Maui, Lanai and Hawaii. Contrary to their prediction, it has never been found outside the Hawaiian Islands.

In the first comprehensive treatise on the archipelago's animals, *Fauna Hawaiiensis*, another species, *Hydrobius nesiticus*, was described by Sharp (1908), the second and hitherto last endemic Hawaiian species to be described. No additional specimens of this taxon have been found since the original series was collected by Perkins in 1893. Sharp (1908) also provided a brief mention of *Hydrobius semicylindricus*, but described no additional or specific records. Both species were transferred to the genus *Limnoxenus* Motschulsky, 1853 by Knisch (1924), a placement that has been maintained.

A detailed account of the adult and larval biology of *L. semicylindricus* was given by Williams (1936), who wrote that one would likely encounter the 'mild mannered' species

'if we were to explore even the smallest of our mountain streams for aquatic insects'.

D'Orchymont (1937) and Balfour-Browne (1945) provided checklists of the Hydrophilidae of Oceania that listed both Hawaiian endemic *Limnoxenus* species, but no additional details or specific locality records were given.

Most recently, Hansen (1995b) comprehensively summarized the current status of the Hydrophilidae of Hawaii, which then stood at 21 species. Virtually all of these, however, have been intentionally introduced or are adventive, with up to four species possibly being indigenous. All four of these species, however, are also found outside the Hawaiian Islands, leaving the members of *Limnoxenus* as the only endemic taxa.

Position within Hydrobiusina

The Hydrobiusina (recently emended from Hydrobiina; ICZN, 2003) comprises the smallest of three subtribes recognized by Hansen (1991, 1995a) within the large and diverse tribe Hydrophilini, and currently includes 17 species in five genera. No phylogenetic hypotheses have been proposed regarding any of the generic or species-level relationships within the subtribe.

Two Hawaiian species have hitherto been placed in *Limnoxenus*, which also contains four other species: one each in South Africa and Australia/New Zealand, and two presumed sibling species in Europe and the Mediterranean region (Hansen, 1999). This generic assignment, performed without comment by Knisch (1924), has never been challenged despite the seemingly odd distribution and some differences in body form of the Hawaiian taxa. Apart from *Limnoxenus*, the only other genus in the subtribe with multiple species is the Holarctic *Hydrobius* Leach, 1815 with eight. The three remaining monotypic members of the subtribe include one genus each from Western Australia (*Hybogralius* d'Orchymont, 1942), New Caledonia (*Limnocyclus* Balfour-Browne, 1939) and Argentina (*Hydramara* Knisch, 1925).

Two recent classification changes for the subtribe have been informally proposed, both based on newly available larval data. First, Watts (2002) implied that the monotypic *Hybogralius* from Western Australia is not a member of Hydrobiusina, but he did not propose a definitive, alternative placement. Second, a cladistic study of the Hydrophilinae suggested that the Hydrobiusina forms a sister clade to the Sperchopsini, rather than with the subtribe Hydrophilina of the Hydrophilini (Archangelsky, 2004); this hypothesis is currently under study (A. E. Z. Short, unpublished data).

Materials and methods

Biotic surveys and collecting techniques

Specimens were collected during a series of expeditions by JKL on Kauai, Oahu, Maui, Molokai and Lanai between 1991 and 2004, and by AEZS and JKL on Kauai in 2005.

Aquatic species were usually encountered in mountain streams or pools formed from intermittent or small, head-water tributaries. During the day, beetles can be found clinging to the bottom of rocks and other substrates submerged in the streams. At night, they can be found openly swimming in pools and crawling on algal-covered rocks.

Synthetic pyrethrin insecticide fog was employed in hygropetric habitats, wet rock faces and moss mats along streams, especially on Kauai in 2005. Seep species may also be encountered by looking for suitable habitats during the day and returning at night using a head lamp, as at least one species is known from nocturnally active individuals. Nonetheless, some species were found very serendipitously, whilst looking under boards and logs, or by applying pyrethrin fog to arboreal moss mats.

Several dozen indexed habitat photographs of collecting sites from the 2005 Kauai expedition can be found at http://www.hydrophiloidea.org.

Illustrations

Genitalia were cleared in 10% NaOH at room temperature for 24 h and slide mounted in glycerin for examination. Genitalia were then stored in microvials with glycerin, pinned under each specimen.

Drawings were made with either a camera lucida, or by taking photographs of the given structure and then printing and tracing the image on a light table and modifying it with Adobe Illustrator®. Specimens were prepared for scanning electron microscopy by dehydration in 80% ethanol, 100% ethanol and 99% acetone. Specimens were mounted on stubs with adhesive pads. Most specimens were coated in gold, although the leg of the holotype of *L. namolokama* was left uncoated and re-associated with the specimen. Colour photographs were taken using a Microptics digital imaging system, with multiple exposures at different depths of field merged using Adobe Photoshop®.

Descriptions and terminology

The body length was measured from the anterior margin of the labrum to the posterior margin of the elytra with the head and pronotum reflexed dorsad. The interocular distance was calculated by dividing the narrowest point on the dorsum of the head between the eyes by the width of one eye when viewed dorsally. The 'hind femora ratio' was measured by dividing the length of the femur from the anteroproximal margin to the posterodistal margin by the greatest width, usually near the proximal end.

Lectotypes are designated from the syntype series of both previously described species. Label data for all primary types are given exactly as they appear on the label, with individual labels separated by quotes and lines on a label separated by a single slash (/).

Morphological terminology follows Hansen (1991), with the following exceptions and explanations. The terms 'mesosternum' and 'metasternum', as used in the present work, refer to the entire group of respective sclerites that make up each segment. The terms mesoventrite and metaventrite are used to refer specifically to pre-episterna 2 and 3, respectively, and the term 'process of the mesoventrite' replaces Hansen's use of 'mesosternal process'.

The complex pattern of punctation on the dorsal surface of the Hydrobiusina is composed of three classes of punctures (ground, systematic and serial), which are explained and illustrated here (Fig. 6A, B) to facilitate their recognition and separation. Our homology concept between and within these sets of punctures follows that of Hansen (1991). In species of *Limnoxenus*, as with most hydrobiusines, each elytron contains ten rows of longitudinal serial punctures, which may vary from hardly impressed, to deeply impressed and contiguous, forming deep striae. Frequently, serial punctures are more weakly impressed anteromedially and do not bear hair-like setae. Systematic punctures are found on the labrum, clypeus, frons, pronotum and elytra. They are often the largest dorsal punctures, and almost always bear a single seta, although these can be frequently broken off. On the elytra, they are always present in interstriae 3, 5, 7 and 9.

Taxa examined

In addition to all endemic Hawaiian *Limnoxenus* taxa, all species that currently comprise the Hydrobiusina were examined and included in our analysis, with the exception of three putative Palaearctic synonyms of *Hydrobius fuscipes* (L.). Ten outgroup taxa from the Hydrophiline subtribes Acidocerina and Hydrophilina, as well as the tribe Sperchopsini, were also included.

Hydrophilini: Hydrobiusina. Hybogralius hartmeyeri (Régimbart, 1908); *Limnocyclus puncticeps* Balfour-Browne, 1939; *Hydramara argentina* (Knisch, 1925); *Hydrobius fuscipes* (Linnaeus, 1758); *Hydrobius arcticus* Kuwert, 1890; *Hydrobius tumidus* LeConte, 1855; *Hydrobius melaenus* (Germar, 1824); *Hydrobius convexus* Brullé, 1835; *Limnoxenus niger* (Gmelin, 1790); *Limnoxenus olmoi* Hernando & Fresneda, 1994; *Limnoxenus sjostedti* Knisch, 1924; *Limnoxenus zealandicus* (Broun, 1880).

Hydrophilini: Acidocerina. Cymbiodyta semistriata (Zimmermann, 1869); *Cymbiodyta marginella* (Fabricius, 1792); *Helocombus bifidus* (LeConte, 1855); *Enochrus quadripunctatus* (Herbst, 1797); *Enochrus testaceus* (Fabricius, 1801); *Helochares obscurus* (Müller, 1776).

Hydrophilini: Hydrophilina. Hydrochara obtusata (Say, 1823); *Tropisternus affinis* Motschulsky, 1859.

Sperchopsini. Ametor scabrosus (Horn, 1873); *Sperchopsis tessellata* (Ziegler, 1844).

Coelostomatini. Coelostoma orbiculare (Fabricius, 1775).

Phylogenetic analysis

A character matrix that included all Hawaiian species plus the other taxa listed above, for a total of 30 terminal taxa, was developed using WINCLADA (Nixon, 2002) (Appendix 2). *Coelostoma orbiculare* in the subfamily Sphaeridiinae was used to root the cladogram. No a priori assumptions were made regarding the direction of character evolution and the numbers assigned to character states. A cladistic analysis of 55 adult morphological characters (49 informative) was performed in TNT (Goloboff *et al.*, 2004). Multistate characters 1, 19, 22, 23 and 36 were treated as additive; the remaining characters were binary or treated as non-additive. Characters were coded as a dash ('-') in taxa for which they were inapplicable. A heuristic search was performed, first using a 'traditional' search of 10 000 replications, saving ten trees per replicate. Twenty most parsimonious trees of 158 steps were found. This was followed by a driven search (a 'New Technology search') employing ratchet, tree drifting and tree fusion, which found trees of not more than 158 steps 5000 times. Parsimony bootstrap and jackknife values were found by performing 1000 bootstrap replicates, keeping 100 trees per replicate. Character transformations were examined under unambiguous and ACCTRAN optimizations, with unambiguous transformations used to support classificatory and evolutionary interpretations. The character state matrix can be downloaded from the publicly accessible website of AEZS: www.hydrophiloidea.org.

Specimen depositories

Three hundred and twenty-eight specimens were examined in the present study, including 129 collected by us. All material is deposited in the following collections: AEZS, Collection of A. E. Z. Short, Ithaca, NY, U.S.A.; CAS, California Academy of Sciences, San Francisco, CA, U.S.A. (D. H. Kavanaugh); CUIC, Cornell University, Ithaca, NY, U.S.A. (J. K. Liebherr, E. R. Hoebeke); BPBM, Bernice P. Bishop Museum, Honolulu, HI, U.S.A. (G. A. Samuelson); NHML, Natural History Museum, London, U.K. (C. Taylor, M. Barclay); NMW, Naturhistorisches Museum Wien, Vienna, Austria (M. A. Jäch, A. Komarek); SAMA, South Australian Museum, Adelaide, Australia (C. H. S. Watts); UH, University of Hawaii, Manoa, HI, U.S.A. (D. Z. Rubinoff); USNM, United States National Museum of Natural History, Washington DC, U.S.A. (W. E. Steiner); ZMHU, Zoologisches Museum, Berlin, Germany (B. Jäger); ZMUC, Zoological Museum, Copenhagen, Denmark (J. Pedersen).

Results

Phylogenetic analysis

The cladistic analysis resulted in 20 most parsimonious trees [158 steps; consistency index (CI), 0.48; retention index (RI), 0.76] summarizable by strict consensus (Fig. 1). Characters supported under unambiguous optimization, and geographical distributions for the Hawaiian taxa and taxa at the immediately ancestral node (Fig. 2), form the basis for the following presentation.

The Hawaiian species are resolved as a distinct monophyletic group by one unique synapomorphy: a stridulatory file on laterosternite 3 incorporating widely spaced teeth (character 49: state 1). Two other homoplasious synapomorphies are also found in all Hawaiian taxa: procoxae without coarse spines (33: 0; Fig. 8B), which is shared within the Hydrobiusina with *Limnocyclus* and *Hybogralius*, and a weakly impressed depression of the mesoventrite (16: 1; Fig. 5B, C), also shared with *Hybogralius*, a few species of *Hydrobius* and the included acidocerine taxa.

The Hawaiian lineage comprises part of a polytomy that includes the remaining members of *Limnoxenus* and taxa representing the monotypic genera *Limnocyclus* and *Hydramara*. This grouping is supported by five synapomorphies, two uniquely derived: (1) a distinctly tapered laterosternite 3 (47: 1; Fig. 10B–D); and (2) a complex stridulatory file on laterosternite 3 (48: 1; Fig. 10B–D). Because *Limnoxenus* Motschulsky (type species: *Hydrobius niger* Gmelin) would remain the senior name applicable to all Hawaiian taxa under any resolution of the node that includes *Limnoxenus*, *Hydramara* and *Limnocyclus*, we retain this generic assignment for the two previously described species, and use this name in generic combination for all newly described species. Future phylogenetic analysis, including molecular sequence data (A. E. Z. Short, unpublished data), will elucidate the relationships at this node and determine the utility of *Limnocyclus* and *Hydramara* for a cladistic classification.

The basal divergence within the Hawaiian clade is unclear, as the relationships between the three large aquatic species are unresolved. These aquatic taxa form a sister clade to the four non-aquatic taxa, are successively ancestral to these taxa, or a combination of both. The four remaining new taxa, all of which do not have aquatic habits, form a clade well supported by eight synapomorphies (Fig. 2), although each derived character is found in at least one non-Hawaiian hydrobiusine taxon or outgroup. These characters include: (1) a completely setose anepisternum 2 (19: 0; Fig. 5C); (2) a reduced number of systematic punctures (29: 2, 3); (3) a small emargination of the fifth ventrite (52: 0); and (4) a reduced number of ventral spicules on the second metatarsomere (44: 1; Fig. 9C).

The Hawaiian endemic Limnoxenus

Diagnosis. Dorsal ground punctation uniform in size (by contrast with *Limnocyclus* and *Hydramara*, that have dual ground punctation). Mesoventrite with a low carina (Fig. 5B) or a thin but short carina (Fig. 5C) or protuberance [by contrast with other species of *Limnoxenus*, that have a high, linear keel (Fig. 5A) and *Hybogralius* with a flat mesoventrite]. Hind tibiae without long swimming setae as in *Limnocyclus*. Hind femora with pubescence restricted to
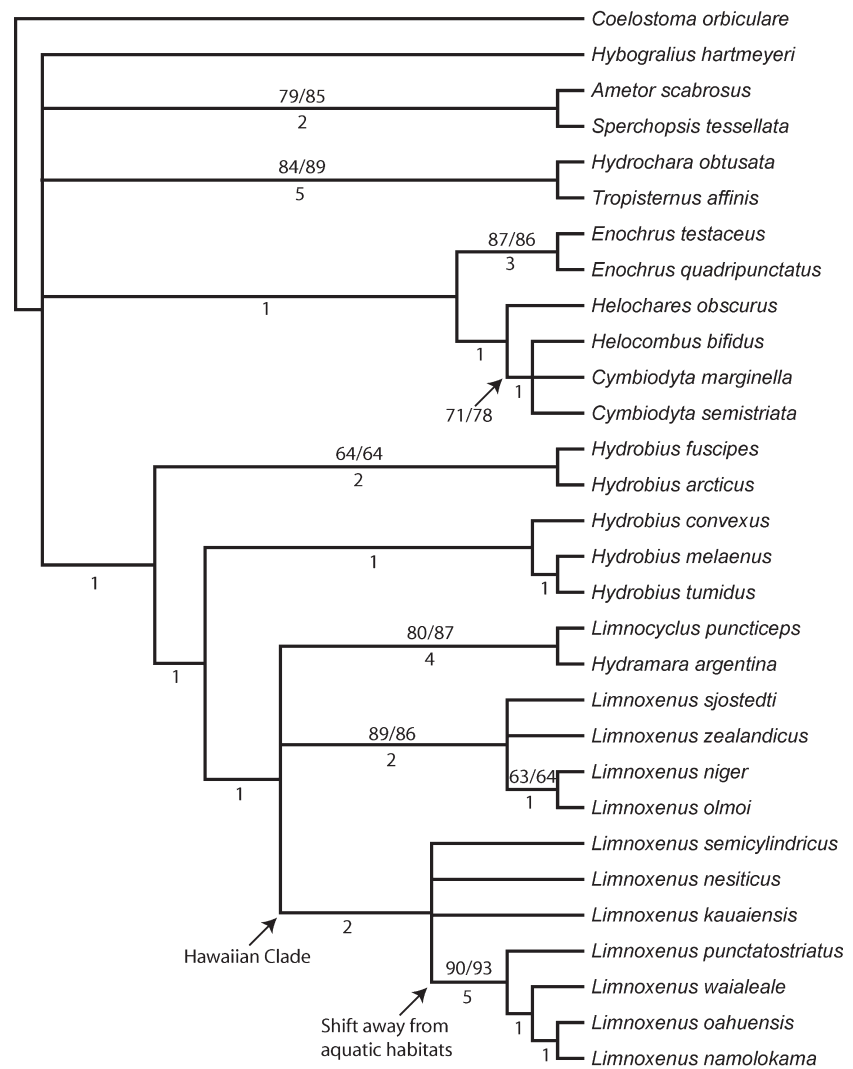
Fig. 1. Strict consensus cladogram. Bootstrap/jackknife values above 50% are indicated above the nodes, Bremer values below the nodes.

extreme base [e.g. Fig. 7C, by contrast with *Hydrobius* (Fig. 7A), which has the pubescence extended distally along the femora far past the trochanter]. File on laterosternite 3 (Fig. 10C–F) with large, coarse teeth [*Hydrobius* and *Hybogralius* lack arranged teeth (Fig. 10A), and they are finer in *Limnocyclus*, other species of *Limnoxenus* (Fig. 10B) and *Hydramara*]. Fifth abdominal ventrite with apicomedial emargination or truncation (by contrast with *Hybogralius* which has the ventrite evenly rounded).

Description. Medium to large beetles, total body length 6.0–12.2 mm (Fig. 3). Coloration. Dorsal body surface usually black to piceous (reddish brown in *L. namolokama*), pronotum and head may have metallic greenish or purplish reflection, pronotal and elytral margins paler, dark brunneous. Head, pronotum and elytra with systematic punctures that are larger than ground punctation, each puncture bearing a seta.

Head. Antennae 9-segmented, including 3-segmented pubescent club. Maxillary palps short to very short; never

much longer than labral width. Anterior margin of clypeus evenly truncate, without emargination. Labrum, clypeus and frons with systematic punctures (e.g. Fig. 4B, C). Mentum generally flat to slightly impressed anteromedially, with very fine to coarse punctures. Eyes ranging from moderately large to small, the distance between eyes varying from *c.* 3.5–7.0× the width of one eye in dorsal view.

Thorax. Pronotum with systematic punctures. Elytra with 10 rows of serial punctures, including a sutural stria, varying in development from lightly impressed, so that the cuticle surface between punctures is coplanar with the elytral disc (e.g. *L. waialeale*; Fig. 6B), to deep and broad, with the intervening cuticle depressed to define a deep stria (e.g. *L. nesiticus*, *L. punctatostriatus*). Elytra with four rows of systematic punctures; plectrum present near inner mediolateral margin (Fig. 6C, D). Prosternum tectiform, with median carina. Process of the mesoventrite varying in form from a low, longitudinal carina (e.g. *L. kauaiensis*; Fig. 5B) to a thick, strongly elevated keel (e.g. *L. namolokama*), which is acuminate in *L. oahuensis*. Hind femoral
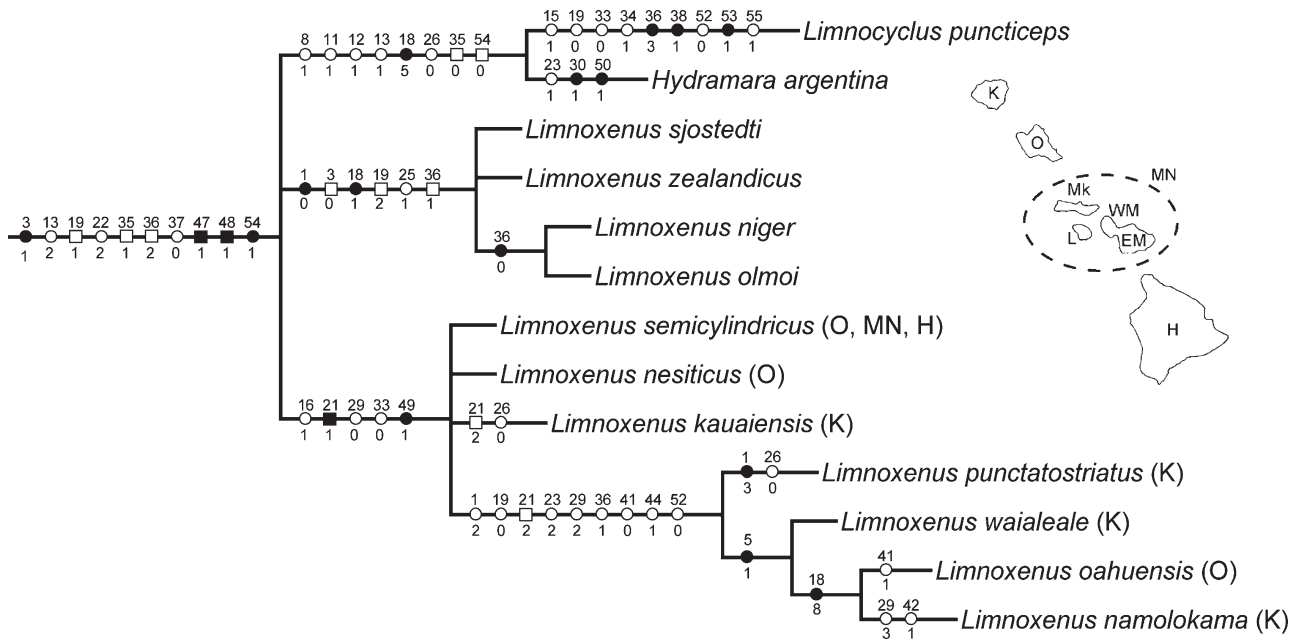
Fig. 2. Strict and collapsed consensus cladogram pruned to show Hawaiian taxa and immediate ancestral node and descendents. Circles on the branches indicate character support under unambiguous optimization; squares represent additional character support under ACCTRAN optimization. Filled symbols represent non-homoplasious, open symbols homoplasious, changes.

microsculpture present, varying from faint to distinct oblique striations (Fig. 7D). Hind femoral pubescence restricted to extreme base, slightly extended on anterior margin to nearly absent (Fig. 7C), never extended distad of trochanter. Tibiae without long setae. Tarsi each with five segments, with two rows of dorsal setae which vary in length from very short (not as long as longer metatibial spur; Fig. 9B) to extremely long (usually much longer than inner metatibial spur; Fig. 9A). Ventral face of tarsi with two rows of short spicules (Fig. 9C) or (in *L. namolokama*) a dense brush of

fine setae (Fig. 9D). Hind wings varying from macropterous with reflexed apex (Fig. 11A) to vestigial, represented by brachypterous flaps that do not extend posterad the third visible abdominal tergite (Fig. 11C).

Abdomen. Abdominal ventrites covered with fine, dense pubescence. Laterosternite 3 tapered posteriorly, with lateral margin shorter than mesal margin, and a distinct area of widely spaced teeth, these teeth forming a file (Fig. 10C–F). First ventrite flat. Fifth abdominal ventrite with a median, apical emargination that may be a small,
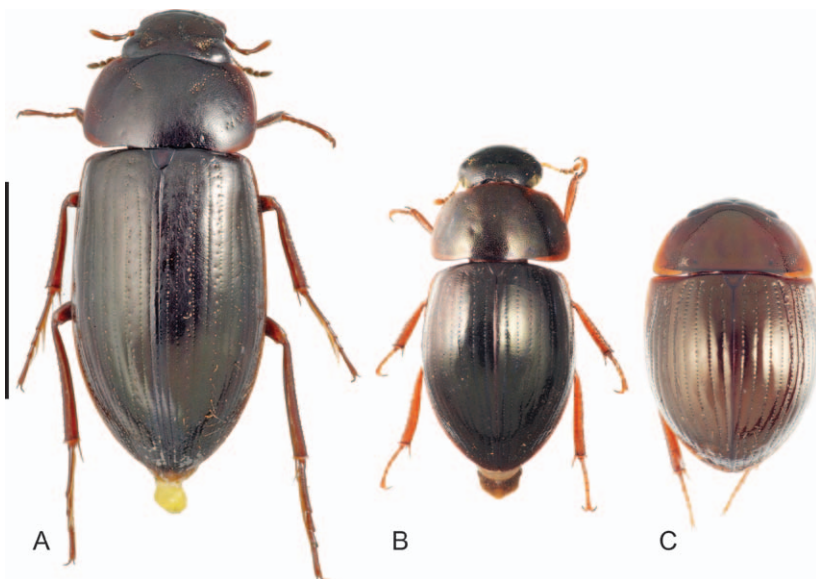

Fig. 3. Hawaiian *Limnoxenus* spp., dorsal habitus. A, *L. kauaiensis*; B, *L. waialeale*; C, *L. namolokama*. Scale bar, 5.0 mm.
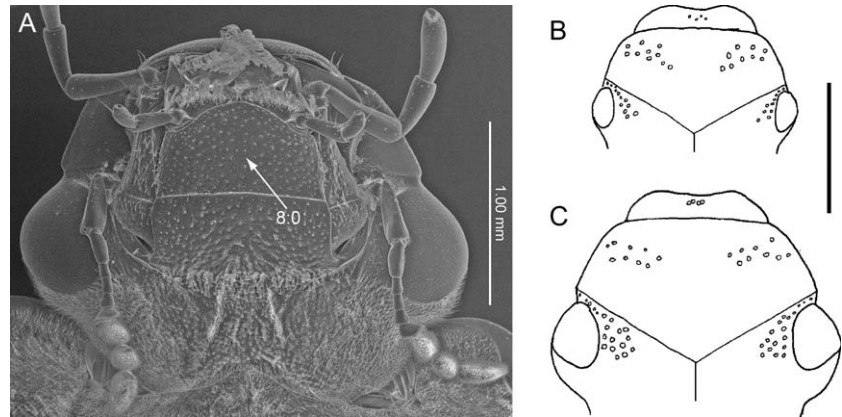
Fig. 4. Heads of Hawaiian *Limnoxenus* spp. A, *L. kauaiensis*, ventral view; B, *L. waialeale*, dorsal view; C, *L. kauaiensis*, dorsal view.

nearly indistinguishable truncation (e.g. *L. waialeale*) or a deep notch (e.g. *L. semicylindricus*). Aedeagus (Figs 12, 13) with basal piece truncate proximally, in some specimens moderately emarginated. Tip of median lobe slightly below the plane created by the apex of the parameres; ventrally with a more sclerotized region that narrows to a blunt point at the apex. Parameres broad basally, gradually narrowing to a round, blunt apex; outer margins usually sinuate near apical third. Despite the significant morphological differences between the species, the aedeagi are remarkably similar and exhibit little discrete interspecific variation.

Limnoxenus semicylindricus (Eschscholtz, 1822)
(Figs 11A, B; 12C; 15; 16)

Hydrophilus semicylindricus Eschscholtz, 1822: 42.
Hydrobius semicylindricus (Eschscholtz) – Fairmaire, 1849: 411.

Limnoxenus semicylindricus (Eschscholtz) – Knisch, 1924: 175.

Type material. **Lectotype** (♂) here designated to preserve the stability of the concept of this species: 'Hist.-Coll. (Coleoptera)/Nr. 10551/Hydrobius semicylindricus/Esch./ Sandwich Ins., v. Chamisso/Zool. Mus. Berlin', 'SYNTYPUS/ Hydrophilus semicylindricus/Eschscholtz, 1822/labelled by MNHUB 2005', 'LECTOTYPE/Hydrophilus/semicylindricus/ Eschscholtz/des. A.E.Z. Short 2006' (ZMHU). **Paralectotypes**: OAHU: 2♀♀, 1♂, same data as Lectotype (ZMHU).

Diagnosis. Total body length 8.4–11.0 mm. Elongate, slightly convex beetles; elytral serial punctures coarse, forming distinct but almost always finely impressed striae; elytral systematic punctures with first row containing at least 35 punctures; process of the mesoventrite moderately to strongly elevated and rounded; dorsal metatarsal setae
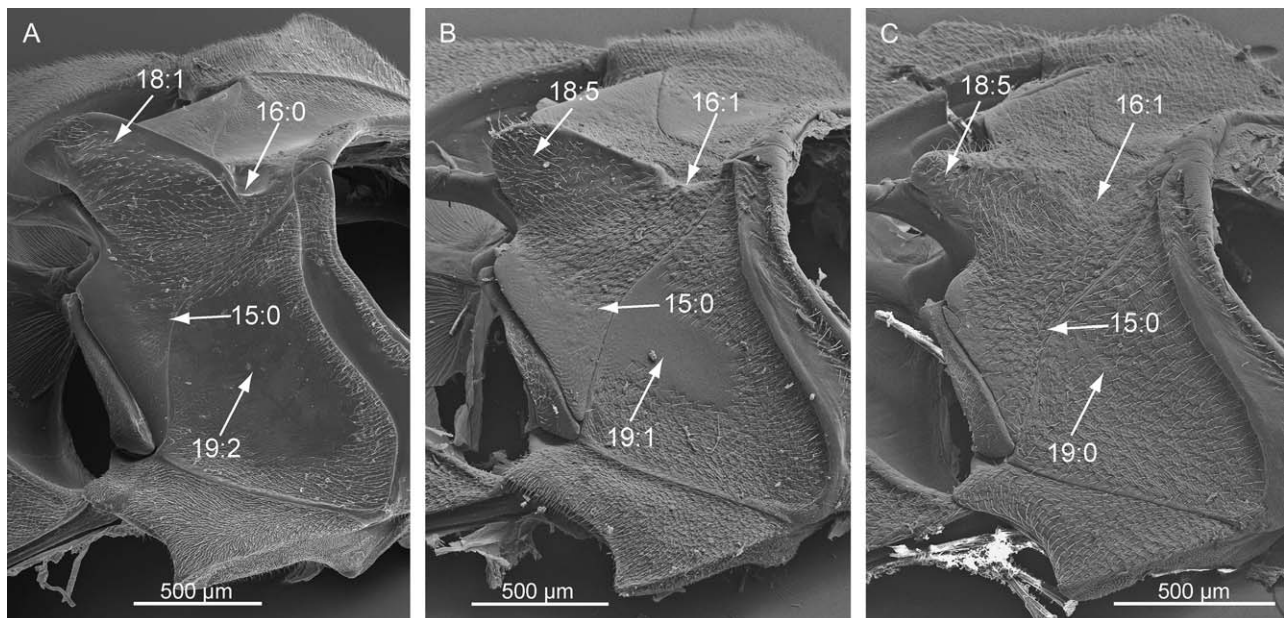
Fig. 5. Mesosterna of *Limnoxenus* spp. A, *L. sjostedti*; B, *L. kauaiensis*; C, *L. waialeale*.
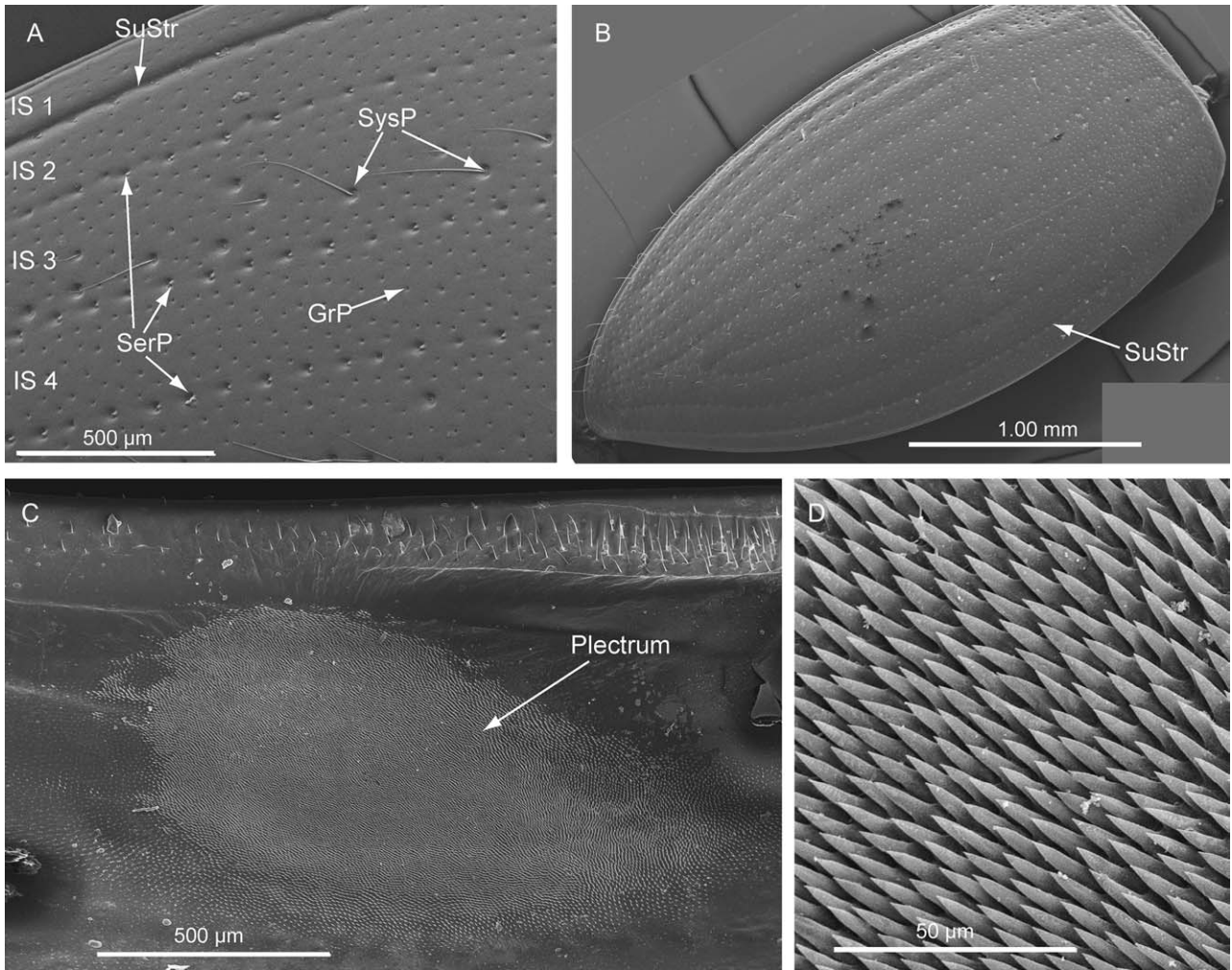
Fig. 6. Elytra of *Limnoxenus* spp. A, *L. zealandicus* dorsal; B, *L. waialeale*, dorsal; C, D, *L. kauaiensis*, ventral and details of plectrum. GrP, ground punctation; IS, interstria; SerP, serial punctures; SuStr, sutural stria; SysP, systematic punctures.
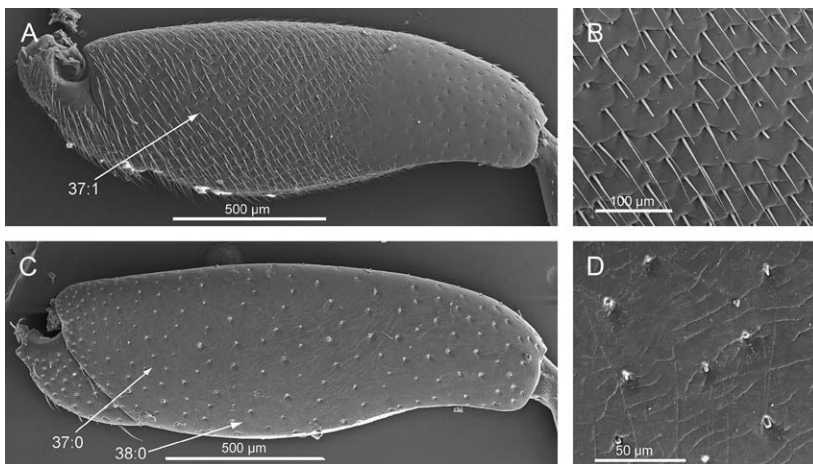
Fig. 7. Metafemora. A, B, *Hydrobius fuscipes*; C, D, *Limnoxenus waialeale*.
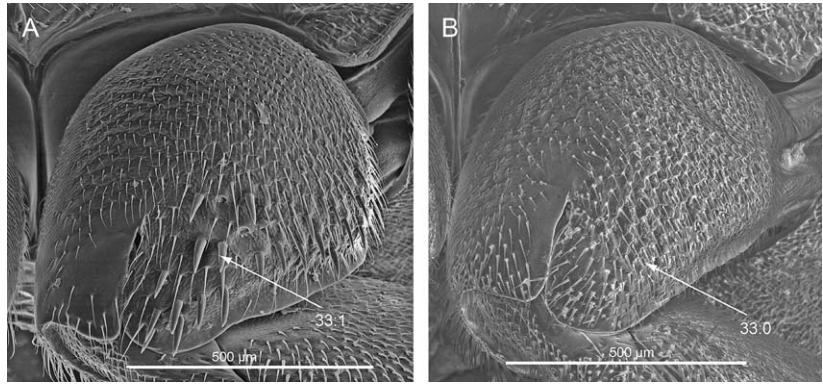
Fig. 8. Procoxae of *Limnoxenus* spp. A, *L. niger*; B, *L. kauaiensis*.

distinctly longer than inner metatibial spur; apical emargination of fifth ventrite as broad to slightly broader than deep.

Description. Coloration. Dorsum of head, pronotum and elytra shiny black; dorsum without coloured or iridescent reflection. Venter of head, centre of prosternum, epipleura, meso- and metasternum and majority of ventrites very dark brown to black; legs and lateral margins of prosternum slightly paler. Each ventrite usually with small but distinct reddish-brown macula on each lateral margin; darker specimens may lack these maculae.

Systematic punctation. Labrum with a centromedial row of 4–5 punctures; clypeus with a mediolateral field of 9–13 punctures (most specimens with > 10) on outer
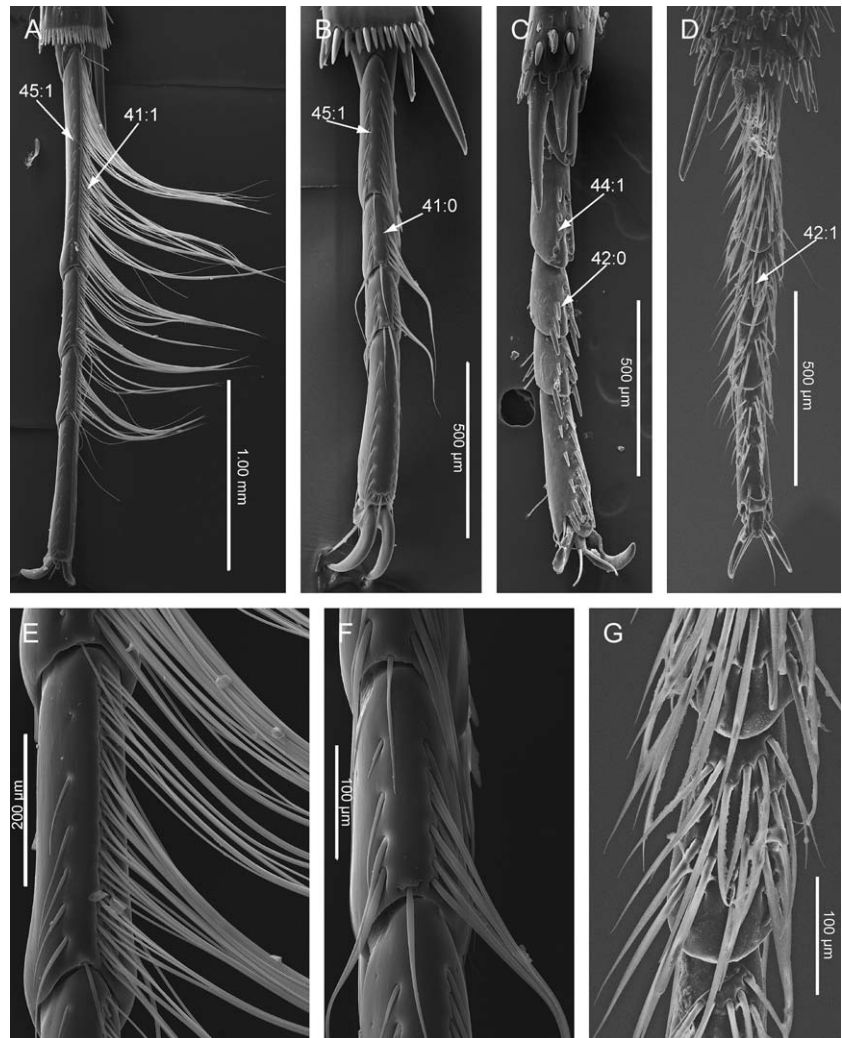
Fig. 9. Hawaiian *Limnoxenus* spp. metatarsi. A, *L. kauaiensis*, dorsal; B, C, *L. waialeale*, dorsal and ventral; D, *L. namolokama*, ventral; E, *L. kauaiensis*, third metatarsomere, dorsal; F, *L. waialeale*, third metatarsomere, dorsal; G, *L. namolokama*, third metatarsomere, ventral.
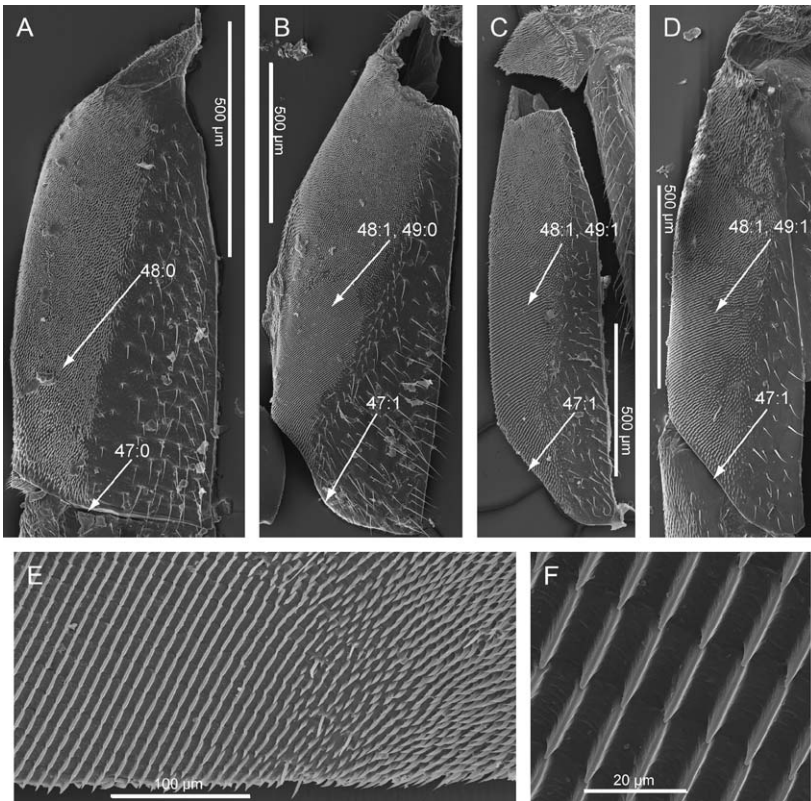
Fig. 10. Right laterosternite 3. A, *Hydrobius fuscipes*; B, *Limnoxenus zealandicus*; C, *L. kauaiensis*; D, *L. waialeale*; E, F, *L. kauaiensis*, details of file.

third of each side that vary in size; frons with cluster of 13–18 very coarse punctures mesad of each eye that define an irregular ovoid fovea, the depressed area narrowed and extended as scattered punctures towards the frontal lateral margin; pronotum with anterolateral series regular and moderately dense, arranged in two semiparallel series in some specimens, posterolateral series forming an irregular row of 12–15 punctures; elytra systematic punctures regular and distinct, sometimes confused with serial punctures that are subequal to slightly smaller, more than 35 punctures comprising the third interstrial row.

Head. Antennal scape slightly shorter than maxillary stipes; combined length of antennomeres 2–6 slightly longer than scape; first two segments of antennal club subequal in length, with apical segment 1.5× as long as penultimate segment. Maxillary palps moderately long, slightly longer than labral width; apical segment and segment 2 subequal in length, segment 3 slightly shorter. Eyes separated by 3.9× the width of one eye. Mentum coarsely punctate, sometimes appearing slightly rugose, with anterolateral portions very slightly elevated. Ground punctation of frons and clypeus moderately coarse, with punctures of uneven size, labral punctation slightly finer.

Thorax. Pronotum with ground punctation moderately impressed, slightly less than head punctation, punctures of disparate size, extremely faint, almost undetectable punctures intermixed with coarser punctures; some small areas of cuticle without detectable punctation. Serial punctures coarse, 3–4× larger than ground punctation and mostly

subequal to elytral systematic punctures, rows denser laterad and posterad. Prosternum highly tectiform, with distinct, narrow median carina. Process of the mesoventrite strongly elevated, apex extended beyond plane defined by anterior third of metaventrite and forming an elongate and rounded protuberance, apically covered with short to moderately long setae. Metaventrite without anteromedial raised process, only narrowly and slightly projected

Fig. 11. Wings of Hawaiian *Limnoxenus* spp. A, *L. semicylindricus*, fully winged (Oahu, Koko Head); B, *L. semicylindricus*, reduced wing (Oahu, Mt. Tantalus); C, *L. waialeale*, vestigial wing (Kauai, Mt. Waialeale).
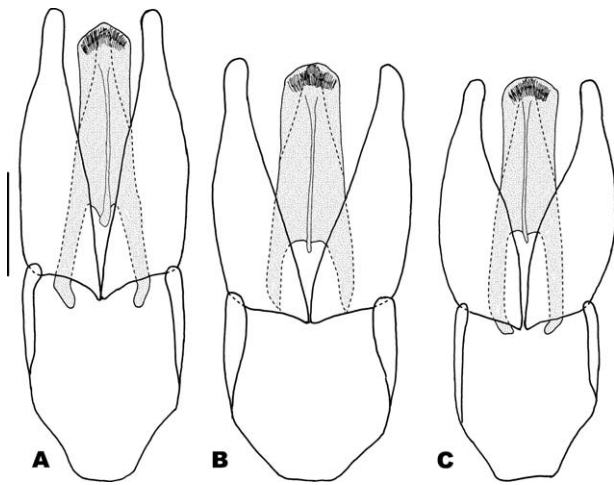
Fig. 12. Hawaiian *Limnoxenus* spp. aedeagi, dorsal views. A, *L. kauaiensis*; B, *L. nesiticus*; C, *L. semicylindricus*. Scale bar, 0.45 mm.

between mesocoxae, narrowed posteromedially into a short, narrow projection between metacoxae. Protibiae with 12–13 spines on dorsal fa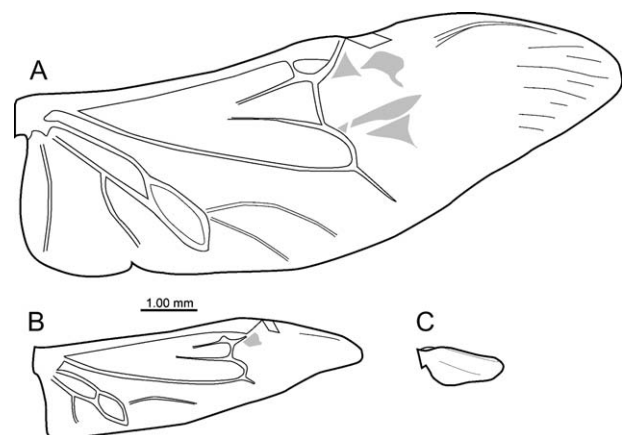ce; protarsi short, with segment 5 slightly shorter than segments 1–4 combined. Meso- and metafemora with microsculpturing forming short, lateral striations. Metafemora almost entirely glabrous, with a small area of pubescence restricted to extreme base along anterior margin. Metafemoral ratio: 3.2. Meso- and meta-tarsi with two dorsal rows of long setae; most setae distinctly longer than inner metatibial spur. Protarsal claws sexually dimorphic, in males, claws more elongate, with a larger, angulate base and sinuate inner face. Hind wings polymorphic, either fully macropterous (Fig. 11A) or partially reduced (Fig. 11B).

Abdomen. Ventrites 1–2 moderately and evenly pubescent; ventrites 3–5 with pubescence progressively denser

medially. Apical emargination of fifth ventrite as broad to slightly broader than deep and fringed with slightly coarser setae. Aedeagus (Fig. 12C) as in the generic description.

Variation. This species shows somewhat broad variation in characters that are relatively stable in other species, although this variation does not appear to be correlated to different island populations. The total length of the maxillary palps is distinctly shorter in a series of specimens from Mt. Kaala, Oahu. The serial punctures of the elytra are set in shallow to moderately impressed striae in most specimens, but these striae are absent in a few specimens from the Waihoi Valley, East Maui.

In 21 specimens examined for the condition of the metathoracic wing, six had fully developed flight wings (Fig. 11A) and 15 had partially reduced flight wings (Fig. 11B). All six fully winged individuals were from various localities on Oahu. Individuals with reduced wings were from Oahu, Molokai, Maui and Hawaii Island.

Distribution (Figs 15, 16). The only species to occur on multiple islands, *L. semicylindricus*, is distributed on Oahu, Maui, eastern Molokai, Lanai, and the northern Kohala Volcano of Hawaii Island. No specimens from Kauai have been found in museum collections, and those listed by Hansen (1995b) are in fact *L. kauaiensis*. We suspect that earlier reports of '*L. semicylindricus*' from Kauai (e.g. Blackburn & Sharp, 1885; Sharp, 1908) refer to *L. kauaiensis* as well.

Bionomics. Generally found actively swimming at night, this species is contemporarily encountered in higher elevation mountain streams and rock pools. Individuals collected under logs and boards away from streams during late April – Molokai: Pepeopae Bog, 24.iv.1991 (CUIC) and Maui: Kipahulu Valley, 30.iv.1991 (CUIC) – indicate that at least
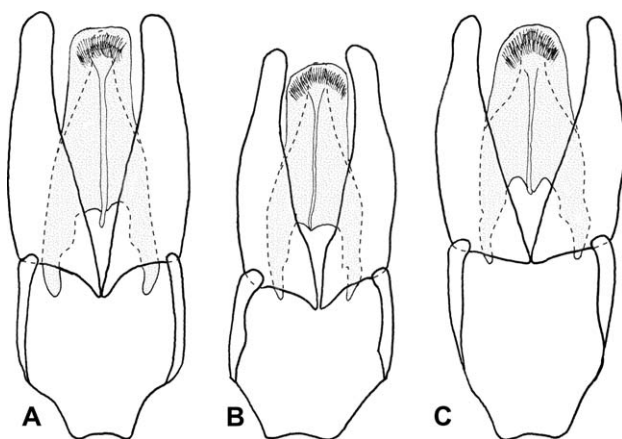

Fig. 13. Hawaiian *Limnoxenus* spp. aedeagi, dorsal views. A, *L. oahuensis*; B, *L. punctatostriatus*; C, *L. waialeale*. Scale bar, 0.45 mm.
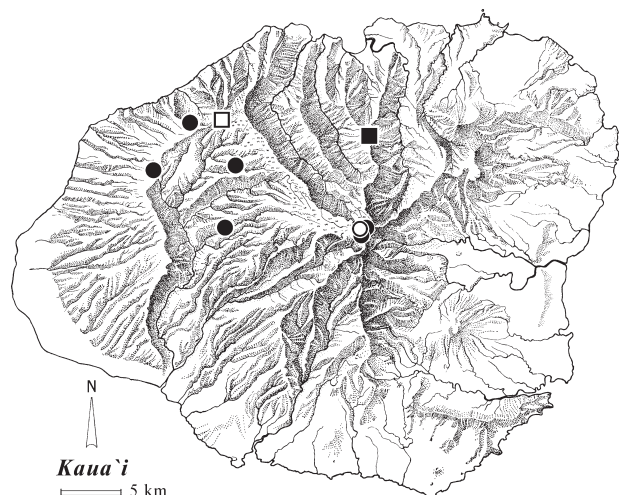
Fig. 14. Distribution of *Limnoxenus* spp. on Kauai: ●, *L. kauaiensis*; ■, *L. namolokama*; □, *L. punctatostriatus*; ○, *L. waialeale*.
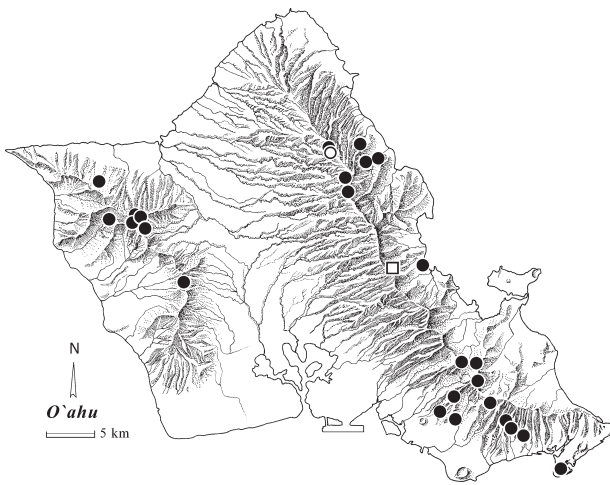
Fig. 15. Distribution of *Limnoxenus* spp. on Oahu: ○, *L. nesiticus*; □, *L. oahuensis*; ●, *L. semicylindricus*.

some individuals overwinter under objects away from streams, most probably to avoid perturbations brought on by winter and early spring floods.

Williams (1936) provides more than seven pages of detailed observations and illustrations regarding the habitats, food sources, larvae and other general biology of this species. Amongst these observations, alimentary canal dissections found that the adults eat filamentous algae, but they would also feed on fruits in captivity. Larvae dig pupal chambers in mud away from the stream. Williams also noted that the species 'flies well', confirming that macropterous individuals are capable of sustained flight.

Historical records suggest that this species was once commonly found in a broader range of aquatic situations, including standing waters and coastal areas (e.g. Fairmaire, 1849; Blackburn & Sharp, 1885). Not enough specimen data are available to accurately quantify if or when a population decline occurred, but anecdotal evidence is suggestive: All early authors consider the species as a 'common' or 'abundant' element of the Hawaiian riparian fauna (e.g. Blackburn & Sharp, 1885; Sharp, 1908;

Williams, 1936). This is in stark contrast to recent observations and collections, which have found it to be rarely collected outside of certain higher elevation mountain streams (e.g. Hansen, 1995b; M. Hansen, personal observation).

Additional material examined. Appendix S1 (see 'Supplementary material').

Limnoxenus kauaiensis Short & Liebherr sp.n.
(Figs 3A, 4A, C, 5B, 6C, D, 8B, 9A, E, 10C, E–F, 12A, 14)

Type locality. U.S.A.: Hawaii: Kauai Island: Summit of Mt. Waialeale, 22°04.355′N, 159°30.054′W, 1520 m asl.

Type material. **Holotype** (♂): 'USA: HAWAII: Kauai/ Waialeale summit; gulch stream/at night; 18.v.2005, A.E.Z. Short/& J.Liebherr, AS-05-170, 5000 ft [1520 m]/N 22°04.355′, W 159°30.054′', 'HOLOTYPE/Limnoxenus/ kauaiensis/Short & Liebherr 2006' (CUIC). **Paratypes**: KAUAI: 6, Halemanu, 9.ix.1919 (*Cooke*) (BPBM); 1, Kalalan [sic Kalalau] Ridge, 26.ix.1919, Van Dyke Collection (CAS); 1, Waialae River, 1220 m, 14.iv.1920 (*Kusche*) (BPBM); 1, NaPali-Kona Forest Reserve, Mohihi-Waialae Trail, 1030–1060 m, 13.v.1991 (*Liebherr*) (CUIC); 6, Waialeale summit, gulch 1 at night, AS-05-168, 1534 m, 18.v.2005 (*Short*) (AEZS, CUIC); 1, Waialeale summit, under logs/ rocks/moss stream, lot 4, 1520–1540 m, 18.v.2005 (*Liebherr*) (CUIC); 8, Waialeale summit, under rocks in stream, lot 6, 1545 m, 18.v.2005 (*Liebherr*) (CUIC); 1, Waialeale summit, along stream at night, lot 9, 1520 m, 18.v.2005 (*Liebherr*) (CUIC); 10, Waialeale summit, gulch stream at night, AS-05-170, 1520 m, 18.v.2005 (*Short & Liebherr*) (CUIC); 14, Waialeale summit, gulch 2 waterfall pool, AS-05-172, 1515 m, 19.v.2005 (*Short & Polhemus*) (BPBM, CUIC, NHML, NMW); 14, Waialeale summit, gulch 2, side waterfall pool, AS-05-173, 1515 m, 19.v.2005 (*Short & Polhemus*) (AEZS, CUIC); 11, Waialeale summit, gulch 3, AS-05-175, 1490 m, 18.v.2005 (*Short*) (CUIC).

Diagnosis. Total body length 9.6–12.2 mm. Elongate, slightly convex beetles (Fig. 3A); elytral serial punctures

Fig. 16. Distribution of *Limnoxenus semicylindricus* on Maui Nui and Hawaii Island. A, Molokai; B, Lanai; C, Maui; D, Mt. Kohala of Hawaii Island.

coarse, forming distinct but usually finely impressed striae; elytral systematic punctures with first row composed of at least 35 punctures. Process of the mesoventrite slightly elevated and rounded, distinctly lower than in *L. semicylindricus*; metatarsal setae distinctly longer than inner metatibial spur; fifth ventrite with deep emargination, depth usually greater than width.

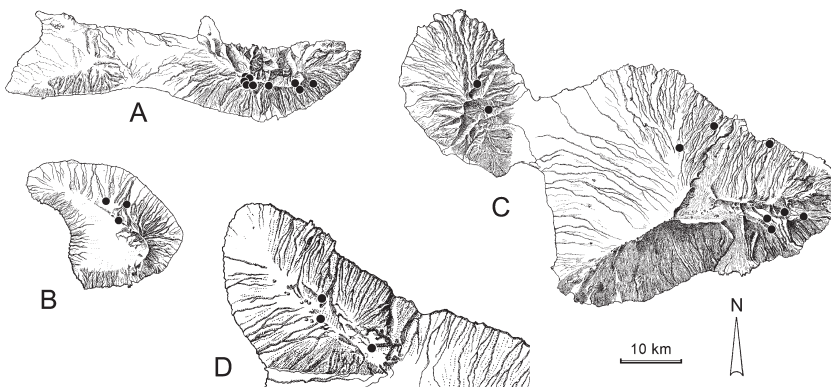*Description.* Coloration. Dorsum of head, pronotum and elytra shiny black; dorsum without coloured or iridescent reflection. Venter of head, centre of prosternum, epipleura, meso- and metasternum and majority of ventrites very dark brown to black; legs and prosternal lateral margins slightly paler. Each ventrite usually with small but distinct reddish-brown macula each side on lateral margin.

Systematic punctation, Labrum with a centromedial row of 4–5 punctures; clypeus with a mediolateral field of 6–15 punctures (most specimens with > 10) on each side that are not uniform in size; frons with a cluster of 15–20 very coarse punctures mesad each eye, cluster narrowed and extended as a few single punctures towards the frontal lateral margin; pronotum with anterolateral series regular and moderately dense, in some specimens arranged as two semiparallel series, posterolateral series forming a more or less regular row of 12–15 punctures; on elytra regular and distinct, sometimes confused with serial punctures that are slightly larger.

Head. Antennal scape and maxillary stipes subequal in length; combined length of antennomeres 2–6 slightly longer than scape; first two segments of antennal club subequal in length, apical segment 1.5× length of penultimate segment. Maxillary palps moderately long, slightly longer than labral width, with apical segment and segment 2 subequal in length, segment 3 slightly shorter. Eyes separated by *c*. 3.7× the width of one eye. Mentum very coarsely punctate, appearing moderately rugose in some specimens, antero-lateral portions very slightly elevated. Ground punctation of frons and clypeus moderately coarse, with punctures of uneven sizes, labral punctation slightly finer.

Thorax. Pronotum with ground punctation moderately impressed, not as coarse as on head, disparately sized, with very faint, almost undetectable punctures intermixed with coarser punctures; some small areas of cuticle without detectable punctation. Serial punctures moderately coarse, at least 2× diameter of ground punctation; rows denser laterally and posteriorly. Prosternum highly tectiform, with distinct median carina, but usually with a small tooth or angular ridge at anteromedial and posteromedial margins. Process of the mesoventrite a moderately elevated, elongate and rounded ridge, apex rising to nearly the same plane as anterior third of metaventrite (Fig. 5B), covered apically with short to moderately long setae. Metaventrite without anteromedial raised process, only narrowly and slightly projected between mesocoxae, narrowed posteromedially into a short, narrow projection between metacoxae. Protibiae with 14–15 spines on dorsal face; protarsi short, with segment 5 slightly shorter than segments 1–4 combined. Meso- and metafemora with distinct microsculpturing

forming short, lateral striations. Metafemora almost entirely glabrous, with a small pubescent area at extreme base along anterior margin. Metafemoral ratio: 3.5. Meso- and metatarsi with two dorsal rows of long setae (Fig. 9A); most setae distinctly longer than inner metatibial spur. Protarsal claws sexually dimorphic, in males, claws more elongate; inner face sinuate. Hind wings partially reduced in all specimens examined (e.g. Fig. 11B).

Abdomen. Ventrites moderately and evenly pubescent. Fifth ventrite with a narrow, deep emargination that is usually slightly deeper than broad and fringed with slightly coarser setae. Aedeagus (Fig. 12A) as in the generic description.

Distribution. Distributed at higher elevations on Kauai, including the Waialeale summit, Kalalau Ridge, Alakai Swamp and Waialae River (Fig. 14). Historically, as with *L. semicylindricus*, it may have been more widespread at lower elevations. Although abundant in the summit streams of Mt. Waialeale in May 2005, no specimens were found that year in streams in and around Kokee State Park, including Kokee, Kawaikoi and Awaawapuhi.

Bionomics. During the day, adult and associated larval specimens were found on the undersides of cobbles that were partially or entirely submerged in streambeds and the plunge pools of small waterfalls. At night, adults were observed actively swimming in pools of the same streams. On Mt. Waialeale, this species was frequently collected with *Rhantus pseudopacificus* Balke (Coleoptera: Dytiscidae) (M. Balke, personal communication).

Etymology. Named after the island of Kauai, to which this species is endemic.

Limnoxenus nesiticus (Sharp, 1908)
(Figs 12B, 15)

Hydrobius nesiticus Sharp, 1908: 578.
Limnoxenus nesiticus (Sharp) – Knisch, 1924: 174.

Type material. **Lectotype** (♂) here designated to preserve the concept of this species: '65/H. nesiticus/Oahu. Far up/ Kawailoa Gulch. 14.I.1893. Perkins', 'Fauna Hawaiiensis/ Collection', 'Limnoxenus/nesiticus', '[yellow disc]', 'LEC-TOTYPE/Hydrobius/nesiticus/Sharp/des. A.E.Z. Short 2006' (BPBM). **Paralectotypes**: OAHU: 2♀♀, same data as Lectotype (NHML).

Diagnosis. Total body length 10.6 mm. Larger, elongate, slightly convex beetles; elytral serial punctures extremely coarse, forming distinct and coarse striae, distinctly coarser than *L. semicylindricus* or *L. kauaiensis*; elytral systematic punctures with first row composed of at least 35 punctures. Process of the mesoventrite moderately elevated and rounded; metatarsal setae distinctly longer than inner metatibial spur; fifth ventrite with shallow emargination that is distinctly broader than deep.

Description. Coloration. Dorsum of head, pronotum and elytra black; dorsum without coloured or iridescent reflection. Venter of head, prosternum, epipleura, meso- and metasternum and the majority of ventrites and legs very dark brown to black. Each ventrite with an indistinct, faintly reddish-brown macula on each lateral margin.

Systematic punctation. Labrum with a centromedial row of 4–5 punctures; clypeus with a mediolateral field of 6–15 punctures on each side that are not uniform in size; frons with a cluster of 15–20 very coarse punctures mesad each eye defining a fovea that is narrowly extended to the frontal lateral margin; pronotum with anterolateral series regular and moderately dense, sometimes appearing to form two semiparallel series, posterolateral series arranged in a more or less regular row of 12–15 punctures; on elytra regular and distinct, sometimes confused with serial punctures that are slightly larger.

Head. Antennal scape and maxillary stipes subequal in length; combined length of antennomeres 2–6 slightly longer than scape; first two segments of antennal club subequal in length, apical segment 1.5× length of penultimate segment. Maxillary palps moderately, slightly longer than labral width, with apical segment and segment 2 subequal in length, segment 3 slightly shorter. Eyes separated by *c.* 3.9× the width of one eye. Mentum very coarsely punctate, appearing moderately rugose, with anterolateral portions very slightly elevated. Ground punctation of frons and clypeus moderately coarse, with punctures of uneven size; labral punctation slightly finer in size.

Thorax. Pronotum with ground punctation moderately impressed, not as coarse as on head, of disparate size, with very faint, almost undetectable punctures intermixed with coarser punctures; some small areas of cuticle without detectable punctation. Serial punctures moderately coarse, at least 2× size of ground punctation, with rows denser laterally and posteriorly. Prosternum highly tectiform, with distinct median carina and a small tooth or angular ridge at anteromedial margin. Process of the mesoventrite moderately elevated, elongate and rounded at apex, extended to nearly the same plane as defined by anterior third of metaventrite, apex covered with short to moderately long setae. Metaventrite without anteromedial raised process, only narrowly and slightly projected between mesocoxae, narrowed posteromedially into a short, narrow projection between metacoxae. Protibiae with 14–15 spines on dorsal face; protarsi short, with segment 5 slightly shorter than segments 1–4 combined. Meso- and metafemora with distinct microsculpturing forming short, lateral striations. Metafemora almost entirely glabrous, with small area of pubescence restricted to extreme base. Metafemoral ratio: 3.3. Meso- and metatarsi with two dorsal rows of long setae; most setae distinctly longer than inner metatibial spur. Protarsal claws sexually dimorphic, in male, claws more elongate, with a larger, angulate base and sinuate inner face. Hind wings reduced in the lectotype; not examined in the paralectotypes.

Abdomen. Ventrites moderately and evenly pubescent. Fifth ventrite with a broad, moderately shallow emargination that is distinctly broader than deep, fringed with slightly coarser setae. Aedeagus (Fig. 12B) as in the generic description.

Distribution. Oahu (Fig. 15), 'Far up' Kawailoa Gulch.

Bionomics. This species has not been seen since its first and only collection in 1893. Based on the previous collection record and its morphology, it was presumably a stream-inhabiting species. It is presumed to be extinct, although this should be confirmed by additional survey efforts at the type locality.

Limnoxenus waialeale Short & Liebherr sp.n.
(Figs 3B, 4B, 5C, 6B, 7C, D, 9B, C, F, 10D, 11C, 13C, 14)

Type locality. U.S.A.: Hawaii: Kauai Island: Summit of Mt. Waialeale, 22°04.354′N, 159°30.056′W, 1520 m asl.

Type material. **Holotype** (♂): 'HI: Kauai Waialeale summit/ gulch 18-V-2005 lot 07/22°04.354′N, 159°30.056′W/el. 1520 m vertical algal/surface/night J.K. Liebherr', 'HOLOTYPE/ Limnoxenus/waialeale/Short & Liebherr 2006' (CUIC). **Paratypes**: KAUAI: 1, Waialeale summit, mossy creekbank at night, lot 5, 1515–1530 m, 17.v.1995 (*Liebherr*) (CUIC); 2, Waialeale summit, on algae at night, lot 7, 1520 m, 18.v.2005 (*Liebherr*) (CUIC); 7, Waialeale summit gulch, fog seep faces, lot 1, 1520 m, 19.v.2005 (*Liebherr*) (CUIC); 4, Waialeale summit, gulch 2, in algae, AS-05-171b, 1520 m, 19.v.2005 (*Short*) (AEZS, CUIC); 5, Waialeale summit, gulch 2 waterfall pool, AS-05-172, 1515 m, 19.v.2005 (*Short & Polhemus*) (CUIC); 17, Waialeale summit, gulch 2, side waterfall pool, AS-05-173, 1515 m, 19.v.2005 (*Short & Polhemus*) (AEZS, BPBM, CUIC, NHML, NMW).

Diagnosis. Total body length 6.8–7.8 mm. Smaller, very convex beetles (Fig. 3B); elytral serial punctures moderately coarse but not joined in striae; elytral systematic punctures sparse, first row not containing more than 15 punctures; process of the mesoventrite low and rounded; metatarsal ventral setae shorter than inner metatibial spur; fifth ventrite with very shallow apical emargination or only appearing truncate apically.

Description. Coloration: dorsum of head, pronotum and elytra black; head and pronotum with faint but distinctive dark green reflection. Venter of head, centre of prosternum, metasternum and majority of ventrites black; legs, epipleura and lateral margins of pronotum, and mesosternum reddish brown. Each ventrite usually with small but distinct reddish-brown macula on each lateral margin.

Systematic punctation. Labrum with a centromedial row of 4–5 punctures; clypeus with a mediolateral arc of five punctures on each side; frons with a cluster of 7–10 very coarse punctures mesad of each eye, and a row of smaller punctures extending from anterior of each eye to the frontal lateral margin; pronotum with anterolateral series sparse

and widely spaced, posterolateral series arranged in a more or less regular row of eight punctures; on elytra very sparse and indistinct (Fig. 6B), sometimes confused with serial punctures that are slightly larger.

Head. Antennal scape and maxillary stipes subequal in length; combined length of antennomeres 2–6 subequal in length to scape; first two antennal club segments subequal in length, apical segment 1.5× length of penultimate segment. Maxillary palps short, about two-thirds as long as labral width, with apical segment almost as long as segments 2 + 3. Eyes separated by 4.8× width of one eye. Mentum moderately to extremely rugose, with anterolateral portions slightly elevated. Ground punctation of frons and clypeus moderately coarse, with punctures of uneven size, labral punctation slightly finer.

Thorax. Pronotum with ground punctation moderately coarse and uneven in size and distribution, punctation may comprise very faint, smaller punctures intermixed with coarser punctures; some areas of cuticle may be smooth or without detectable punctation. Serial punctures coarse, at least 2× size of ground punctation, with rows denser laterally and posteriorly. Prosternum highly tectiform, but without distinct median carina, at most with small tooth at anteromedial and posteromedial margins. Process of the mesoventrite low and rounded (Fig. 5B), forming a short, broad tubercle, without distinct long setae at apex. Metaventrite without anteromedial raised process, only narrowly and slightly projected between mesocoxae, narrowed posteromedially into a short, narrow projection between metacoxae. Protibiae with 10 spines on dorsal face; protarsi short, with segment 5 as long as segments 1–4 combined. Meso- and metafemora with faint microsculpture comprising short, lateral striations. Metafemora almost entirely glabrous (Fig. 7C), with a small area of pubescence restricted to extreme base along anterior margin. Metafemoral ratio: 2.9. Meso- and metatarsi with two dorsal rows of short, sparse setae; all setae shorter than longest metatibial spur. Protarsal claws sexually dimorphic, in males, claws slightly more elongate, with a larger, angulate base and sinuate inner face. Hind wings vestigial in all specimens (Fig. 11C).

Abdomen. Ventrites moderately and evenly pubescent. Fifth ventrite with very shallow medial emargination (often appearing truncate). Aedeagus (Fig. 13C) as in the generic description.

Distribution. Summit of Mt. Waialeale, Kauai (Fig. 14).

Bionomics. A single specimen of this species was found walking on moss in a small gulch at night on the summit area of Mt. Waialeale in 1995. A subsequent trip to the summit in 2005 found this species associated with algal-covered hygropetric areas on the sidewalls of the gulches and in the spray zones of waterfalls in a stream dropping off the summit. At night, specimens were found actively crawling on algal mats of the filamentous cyanobacteria *Phormidium retzii* that were hanging from the walls of the gulch. The same area was examined the next day, but no specimens were visible. Portions of the algal-covered walls were then fogged with synthetic pyrethrin the following, third day, yielding more than 30 additional specimens. Because no specimens were observed prior to fogging, it is likely that adults burrow into the algae or mud during the day and are active only at night. Other regions of the gulch that lacked algal growth were examined and fogged, but no specimens were found. Samples of the algae from the gulch walls were taken back to the laboratory, in which two small hydrophilid larvae were found and putatively associated with *L. waialeale*. A photograph of the microhabitat can be found in Liebherr & Short (2006).

Etymology. Named after the mountain summit to which this species is endemic.

Limnoxenus punctatostriatus Short & Liebherr sp.n.
(Figs 13B, 14)

Type locality. U.S.A.: Hawaii: Kauai Island: Kokee State Park, Pihea Trail, *c.* 1200 m asl.

Type material. **Holotype** (♂): 'HI: Kauai NaPali-Kona/For. Res. Pihea Tr./el. 1180–1210 m J.K./Liebherr on ground/ under logs on trail 16-V-1991', 'HOLOTYPE/Limnoxenus/ punctatostriatus/Short & Liebherr 2006' (CUIC). **Paratype**: KAUAI: 1♀, same locality but 19.iii.1991 (CUIC).

Diagnosis. Total body length 6.8 mm. Smaller, moderately convex beetles; elytral serial punctures very coarse, forming shallow elytral striae; elytral systematic punctures sparse, first row not containing more than 15 punctures; Process of the mesoventrite low and rounded; metatarsal setae shorter than inner metatibial spur; fifth ventrite with very shallow apical emargination or only appearing truncate apically. Very similar to *L. waialeale* but with much coarser elytral serial punctures, longer maxillary palps and smaller eyes.

Description. Coloration. Dorsum of head, pronotum and elytra black; head and pronotum with a very faint, almost undetectable, dark green reflection. Venter of head, sternum and ventrites nearly uniformly dark brown, with legs slightly reddish brown.

Systematic punctation. Labrum with a centromedial row of five punctures; clypeus with a mediolateral arc of seven punctures on each side; frons with a cluster of 10–12 very coarse punctures mesad of each eye, and a row of smaller punctures extending from anterior of each eye to the frontal lateral margin; pronotum with anterolateral series sparse and widely spaced, posterolateral series arranged in a more or less regular row of 6–8 punctures; on elytra very sparse and indistinct, sometimes confused with serial punctures that are slightly larger.

Head. Antennal scape and maxillary stipes subequal in length; combined length of antennomeres 2–6 subequal in length to scape; first two segments of antennal club subequal in length, apical segment 1.5× length of penultimate

segment. Maxillary palps of moderate length, *c*. as long as labral width, segments 2 and 4 subequal in length. Eyes separated by 6.9× the width of one eye. Mentum slightly to moderately rugose, nearly flat. Ground punctation of frons and clypeus coarse, with punctures not entirely uniform in size; labral punctation slightly finer.

Thorax. Pronotum with ground punctation moderately coarse and disparately sized, extremely faint, smaller punctures intermixed with regular, coarser punctures; unevenly distributed, some small areas of cuticle without detectable punctation. Serial punctures very coarse, at least 4–5× size of ground punctation, often larger, with rows denser laterally and posteriorly. Prosternum highly tectiform, with indistinct median carina, and a small tooth at anteromedial and posteromedial margins. Process of the mesoventrite moderately elevated, forming a broad, elongate tubercle, without distinct long setae at apex. Metaventrite without anteromedial raised process, only narrowly and slightly projected between mesocoxae, narrowed posteromedially into a short, narrow projection between metacoxae. Protibiae with 9–10 spines on dorsal face; protarsi short, with segment 5 as long as segments 1–4 combined. Meso- and metafemora with very faint microsculpturing forming short, lateral striations. Metafemora almost entirely glabrous, with a small area of pubescence restricted to extreme base along anterior margin. Metafemoral ratio: 2.6. Meso- and metatarsi with two dorsal rows of short, sparse setae; all setae shorter than longest metatibial spur. Protarsal claws sexually dimorphic, in male, claws more elongate, with a larger, angulate base and sinuate inner face. Hind wings vestigial in the paratype; not examined in the holotype.

Abdomen. Ventrites moderately and evenly pubescent. Fifth ventrite with very narrow medial truncation that is fringed with slightly coarser setae. Aedeagus (Fig. 13B) as in the generic diagnosis.

Distribution. Alakai Swamp, Kauai (Fig. 14).

Bionomics. The two known specimens were collected under logs on rain-soaked ground along the Pihea Trail. The soil was clay with a thin layer of organic humus above. The morphology is very similar to that of *L. waialeale*, suggesting a similar hygropetric lifestyle.

Etymology. Named after the deeply sulcate elytral striae.

Limnoxenus oahuensis Short & Liebherr sp.n.
(Figs 13A, 15)

Type locality. U.S.A.: Hawaii: Oahu Island: Koolau Mountains, Eleao massif, 805 m asl.

Type material. **Holotype** (♂): 'HI: Oahu Koolau Mts./ Eleao massif, N peak/8-V-1995 lot 04/805 m in creekbed at/night J.K. Liebherr', 'HOLOTYPE/Limnoxenus/ oahuensis/Short & Liebherr 2006' (CUIC). *Paratype*: OAHU: 1♀, same data as holotype (CUIC).

Diagnosis. Total body length 7.4–7.6 mm. Moderately sized, convex beetles; elytral serial punctures moderately coarse, forming very shallow striae; elytral systematic punctures sparse, with first row containing not more than 18 punctures. Process of the mesoventrite strongly elevated into a mostly glabrous central tubercle; metatarsal setae as long to slightly longer than inner metatibial spur; fifth ventrite with shallow apical emargination.

Description. Coloration. Dorsum of head, pronotum and elytra black; head and pronotum with very faint dark green reflection. Venter of head, centre of prosternum, metasternum and majority of ventrites dark brown to black; legs, epipleura and lateral margins of pronotum reddish brown. Each ventrite with small but distinct reddish-brown macula on each lateral margin.

Systematic punctation. Labrum with an apparent centromedial row of 3–5 punctures, although the punctures are not much larger than the coarse ground punctation making them difficult to discern; clypeus with a mediolateral field of 9–14 punctures on each side; frons with a cluster of 9–10 very coarse punctures mesad of each eye, and row of smaller punctures extending from anterior of each eye to the frontal lateral margin; pronotum with anterolateral series sparse and widely spaced, posterolateral series arranged in a more or less regular row of 8–10 punctures; on elytra very sparse and indistinct, sometimes confused with serial punctures that are slightly larger.

Head. Antennal scape and maxillary stipes subequal in length; combined length of antennomeres 2–6 subequal in length to scape; first two segments of antennal club subequal in length, apical segment 1.5× length of penultimate segment. Maxillary palps moderately short, about four-fifths as long as labral width, with apical segment slightly longer than penultimate. Eyes separated by 5.2× the width of one eye. Mentum extremely rugose, with anterolateral portions very slightly elevated. Ground punctation of frons and clypeus coarse, with punctures of uneven size; labral punctation slightly finer but still coarse.

Thorax. Pronotum with ground punctation moderately coarse and generally of similar size; unevenly distributed, some small areas of cuticle without detectable punctation. Serial punctures coarse, with ground punctation appearing fine to extremely fine. Prosternum highly tectiform, with indistinct median carina and small tooth at anteromedial and posteromedial margins. Process of the mesoventrite strongly elevated, raised above the plane of the metaventrite and forming a thick, mostly glabrous tubercle. Metaventrite with broad, bluntly rounded anteromedial process, distinctly projected between mesocoxae, narrowed posteromedially into a short, moderately narrowed projection between metacoxae. Protibiae with 9–13 spines on dorsal face; protarsi short, with segment 5 as long as segments 1–4 combined. Meso- and metafemora with microsculpturing forming short, lateral striations. Metafemora appearing entirely glabrous, with a few sparse setae at extreme base. Metafemoral ratio: 2.5. Meso- and metatarsi with two dorsal rows of moderately long setae; longest setae equal

to slightly longer than inner metatibial spur. Protarsal claws sexually dimorphic, in male, claws more elongate, with a larger, angulate base and sinuate inner face. Hind wings vestigial in the paratype; not examined in the holotype.

Abdomen. Ventrites moderately and evenly pubescent. Fifth ventrite with shallow medial emargination that is fringed with slightly coarser setae. Aedeagus (Fig. 13A) as in the generic diagnosis.

Distribution. Koolau Mountains, Oahu (Fig. 15).

Bionomics. The two specimens were collected at night from a clay face in an open stream bed near the summit ridge of Eleao massif.

Etymology. Named after the island of Oahu, to which this species is endemic.

Limnoxenus namolokama Short & Liebherr sp.n.
(Figs 3C, 9D, 9G, 14)

Type locality. U.S.A.: Hawaii: Kauai Island: Namolokama Mountain, 1325 m asl.

Type material. **Holotype** (♀): 'USA: HAWAII: Kauai/ Namolokama Mt./21-V-2005, lot 4/elev. 1325 m, J.K. Liebherr/pyr. fog mossy ohia', 'HOLOTYPE/Limnoxenus/ namolokama/Short & Liebherr 2006' (CUIC).

Diagnosis. Total body length 6.5 mm. Smaller, very convex species (Fig. 3C); elytral serial punctures moderately coarse but not forming striae; elytral systematic punctures sparse, first row containing less than 10 punctures. Process of the mesoventrite raised into a broad, blunt tubercle; dorsal metatarsal setae shorter than inner metatibial spur; all tarsi with ventral brush of fine setae. Fifth ventrite with very shallow apical emargination, almost appearing truncate.

Description. Coloration. Dorsum of head, pronotum and elytra medium chestnut brown. Venter, including epipleura, ventrites and legs similar in colour to dorsum, with extreme margins of thoracic sclerites slightly darker.

Systematic punctation. Labrum with a centromedial row of six punctures; clypeus with a mediolateral arc of *c.* 5 punctures on each side; frons with a cluster of 7–10 very coarse punctures mesad of each eye, and row of smaller punctures extending from anterior of each eye to the frontal lateral margin; pronotum with anterolateral series sparse and widely spaced, posterolateral series arranged as more or less regular row of *c.* 8 punctures; punctures very sparse and indistinct on elytra, sometimes confused with serial punctures that are slightly larger.

Head. Antennal scape and maxillary stipes subequal in length; combined length of antennomeres 2–6 subequal in length to scape; first two segments of antennal club subequal in length, apical segment 1.5× length of penultimate seg-

ment. Maxillary palps short, about two-thirds as long as labral width, with apical segment almost as long as segments 2 + 3. Eyes separated by 5.1× the width of one eye. Mentum smooth, largely flat with a row of moderately long setae along anterior margin. Ground punctation of frons and clypeus moderately coarse; labral punctation slightly finer.

Thorax. Pronotum with ground punctation moderately coarse and unevenly distributed, some small areas of cuticle without detectable punctation. Serial punctures very coarse, at least 4× size of ground punctation, with rows generally uniform in density. Prosternum tectiform, but with median carina. Process of the mesoventrite strongly elevated, raised above the plane of the metaventrite and defining a thick, mostly glabrous tubercle, which is slightly higher on anterior end. Metaventrite with broad anteromedial process, distinctly and broadly projected between mesocoxae, narrowed posteromedially into a short, moderately broad but acute projection between metacoxae. Protibiae with 11 spines on dorsal face; protarsi short, with segment 5 as long as segments 1–4 combined. Meso- and metafemora with faint microsculpturing forming short, lateral striations. Metafemora almost entirely glabrous, with a small area of pubescence restricted to extreme base along anterior margin. Metafemoral ratio: 2.6. Meso- and metatarsi with two dorsal rows of short, sparse setae; all setae shorter than inner metatibial spur. Ventral face of all tarsi with dense brush of moderately long setae (Fig. 9D). Hind wings vestigial (e.g. Fig. 11C).

Abdomen. Ventrites moderately and evenly pubescent. Fifth ventrite with very shallow medial emargination, almost appearing truncate, that is fringed with slightly coarser setae. Male unknown.

Distribution. Summit of Namolokama Mountain, Kauai (Fig. 14).

Bionomics. The single adult specimen and associated larva were fogged from a moss mat on an Ohia lehua tree (*Metrosideros polymorpha*) on the summit plateau of Namolokama. This technique has been used by JKL on over a dozen expeditions in Hawaii, and no other hydrophilids have been found using this technique on arboreal moss mats. The summit of Namolokama is an isolated, extremely wet plateau with an average rainfall of 630–760 cm per year (Wood, 2000). Not accessible by foot, it was not biologically explored until 1988 (K. Wood, personal communication), and had never previously been comprehensively surveyed for arthropods.

Etymology. Named after the mountain summit to which this species is endemic.

Key to the Hawaiian Limnoxenus

1.   Body elongate, length more than 8.0 mm (e.g. Fig. 3A). Eyes separated by less than 4.5× the width of one eye (Fig. 4C). Metatarsi with row of long setae on

dorsal face, each seta longer than inner metatibial spur (Fig. 9A).. 2
–   Body shorter, compact, length less than 8.0 mm (e.g. Fig. 3B, C). Eyes separated by at least 4.5× the width of one eye (Fig. 4B). Metatarsi with row of setae on dorsal face, each seta shorter to as long as inner metatibial spur, except *L. oahuensis* (Fig. 9B) 4
2 (1).   Hind femora ratio less than 3.5. Elytra with serial punctures contiguously joined by depressed areas forming shallow to deep striae. Oahu, Molokai, Lanai, Maui, Hawaii 3
–   Hind femora ratio 3.5 or greater. Elytral serial punctures not forming striae, or striae only lightly impressed. Kauai .... *L. kauaiensis* **sp.n.**
3 (2).   Elytra with serial punctures forming deep striae. Oahu .... *L. nesiticus* (Sharp)
–   Elytra with serial punctures not set in distinct stria or set in shallow striae. Oahu, Molokai, Lanai, Maui, Hawaii .... *L. semicylindricus* (Eschscholtz)
4 (1).   Meso- and metatarsi ventrally bearing two rows of spicules (e.g. Fig. 9C) 5
–   Meso- and metatarsi ventrally bearing fine setae(Fig. 9 D,G).Kauai .... *L. namolokama* **sp.n.**
5 (4).   Rows of serial punctures on elytra not set in striae (e.g. Fig. 6B). Maxillary palps very short, no more than two-thirds as long as labral width 6
–   Rows of serial punctures on elytra strongly impressed and set in shallow striae. Maxillary palps longer, subequal in length to labral width. Kauai .... *L. punctatostriatus* **sp.n.**
6 (5).   Mesoventrite with low, rounded linear elevation (Fig. 5C). Meso- and metatarsi dorsally with only short setae (Fig. 9B). Kauai .... *L. waialeale* **sp.n.**
–   Mesoventrite elevated into broad, thick tubercle. Meso- and metatarsi dorsally with moderately long setae. Oahu .... *L. oahuensis* **sp.n.**

Discussion

Several species of Hawaiian *Limnoxenus* exhibit attributes unusual for the Hydrophilinae, including: (1) monomorphically brachypterous or vestigial metathoracic flight wings; and (2) occupation of terrestrial microhabitats. The former is only known in a handful of other hydrophiline species, whereas the latter has never been adequately documented within the subfamily.

Brachyptery

Flight wing reduction is extremely rare in Hydrophilidae (Spangler, 1979), as the occupied aquatic habitats appear unstable in time and space, requiring the retention of macroptery to maintain populations via winged dispersal (Southwood, 1977). Amongst Hawaiian *Limnoxenus* species, there are three wing configurations, i.e. fully macropterous wings on individuals capable of flight (known only in

some specimens of *L. semicylindricus*), individuals with reduced wings that are smaller and less developed than the macropterous condition, but still folded posteriorly (observed in *L. kauaiensis* and the majority of *L. semicylindricus*), and individuals bearing completely vestigialized wings which are reduced to functionless pads lacking veins (e.g. *L. waialeale*, *L. namolokama*, *L. punctatostriatus* and *L. oahuensis*).

Two primary factors thought to favour flightlessness are habitat persistence and habitat isolation (e.g. Harrison, 1980; Zera & Denno, 1997), both factors exemplified by the Hawaiian Islands (Zimmerman, 1948). The high incidence of flightlessness in Hawaiian *Limnoxenus* is probably a combination of both of these factors, as each situation taken independently can be found repeatedly in other hydrophilid taxa, without an associated reduction in dispersal capacity.

Given the historical pre-eminence of the view that oceanic islands offer a specific form of habitat isolation (Darwin, 1859), it is tempting to explain the loss of dispersal ability in Hawaiian *Limnoxenus* by the very presence of the species on islands. However, no statistical correlation has been found between oceanic islands and flightlessness when accounting for other factors, such as latitude and altitude (Roff, 1990). Moreover, despite numerous examples of insular aquatic hydrophilids, including others occurring on oceanic islands, such as the Galapagos, none are known to be flightless. Therefore, a connection between flightlessness and island endemism cannot be established for the family.

A more unique level of isolation for flightless Hawaiian taxa is found at the microhabitat level. For *L. waialeale* (and probably most of the other vestigially winged species), there are no other comparable habitats on the island outside the wind- and rain-swept gulches inhabited near the summit of Mt. Waialeale. The headwater gulches that support the hygropetric habitat drop sharply hundreds of metres in elevation shortly downstream of the type locality, thereupon emptying into the Pacific Ocean. Dispersal off the summit would place any surviving beetles in a completely different life zone with regard to rainfall, elevation and level of disturbance.

Ecomorphological shifts

Within the Hydrophilinae, there are no other species with demonstrably terrestrial adults and larvae, nor any hypotheses about how this condition might have evolved. The only other potential example concerns a handful of species in the genus *Anacaena* Thomson. Individuals of several of these species have been collected in forest litter as adults, leading to anecdotal suggestions that the species are 'terrestrial' (e.g. Hansen, 1995a; Komarek, 2004). However, in several instances, individuals of these same *Anacaena* species (e.g. *A. parvula* Sharp) have been reported living in aquatic environments (Komarek, 2004; A. E. Z. Short, personal observation). No supporting

morphological adaptations or breeding data have been reported.

When mapped onto the cladogram (Fig. 1), the ancestor of Hawaiian *Limnoxenus* is unambiguously optimized to be aquatic and to have common adaptations for such habitats, such as natatory setae on the legs (e.g. Fig. 9A). The condition has been maintained in the three aquatic Hawaiian taxa (e.g. *L. semicylindricus*), which all occur in streams and stream pools, and are well adapted to such habitats. In contrast, four derived Hawaiian taxa have moved away from true aquatic habitats, and all have a suite of morphological modifications that indicate a shift away from typical aquatic lifestyles.

Within the clade of non-aquatic Hawaiian taxa, a two-step transformation into a fully terrestrial habitat (e.g. tree moss) can be inferred. In the first step, fully aquatic ancestors transformed to occupy a hygropetric zone. Dorsal natatory setae became partially to fully reduced, body size became shorter and the wings became fixed for a vestigial state. This condition is found in *L. punctatostriatus*, *L. waialeale* and *L. oahuensis*. This shift did not require a change in food sources for either adults or larvae; adults were still able to feed on algae and the predatory larvae had access to endemic chironomid and other Diptera larvae that also lived in these seeps. In the second shift, these hygropetric species moved further away from the streambed to occupy damp arboreal moss lacking any flow of water, possibly with the exception of very heavy rain. With the dorsal setae already lost, the ventral tarsal spicules became dense setal brushes (as in *L. namolokama*; Fig. 9D, G), a common adaptation to arboreal and other terrestrial habitats (e.g. Liebherr, 2003).

The Hawaiian endemic damselfly genus *Megalagrion* also exhibits a nearly identical habitat shift (Polhemus, 1993, 1997). The immature stages of species in this genus are found in a variety of aquatic habitats, as well as on rock seeps, the leaf axils of plants and in damp fern litter (Williams, 1936). A phylogenetic hypothesis of the group based on morphological characters suggested that hygropetric habitats served as an intermediate stage between fully aquatic and fully terrestrial taxa (Polhemus, 1997). However, this habitat transition was ambiguous in a subsequent study that included molecular data (Jordan *et al.*, 2003). By contrast with *Megalagrion*, the habitat shift in Hawaiian *Limnoxenus* involves both adult and larval life stages, whereas only the immatures of *Megalagrion* have undergone such a shift.

Age, origin and pattern of diversification

Within Hawaii, single-island endemic *Limnoxenus* species are found on the oldest two islands: Kauai (*c.* 5.0 million years old; Clague & Dalrymple, 1987) has four and Oahu (*c.* 3.7 million years old) has two. The one widespread species, *L. semicylindricus*, is found on the younger islands of Maui Nui and Hawaii (*c.* 2.0 and 0.5 million years old, respectively; Carson & Clague, 1995). These dates represent the estimated emergence of these islands, and not the cessation of volcanic activity required to initiate substantial development of the biota. This suggests two initial colonization scenarios for Hawaii: an initial Kauai colonization with subsequent dispersal to younger islands as they evolved suitable habitat, or a pre-Kauai colonization on an island now submerged.

The lack of resolution at the ancestral Hawaiian node (Fig. 2) limits our ability to make well-supported hypotheses about the pattern of diversification of the lineage after its initial foothold in the islands was established. As all possible ancestors of the Hawaiian lineage are aquatic, it is probable that the Hawaiian aquatic taxa represent an ancestral habitat preference. The fact that three of the four non-aquatic taxa are found on Kauai, including the two oldest species of that lineage, with the two youngest being on Kauai and Oahu, respectively, suggests a Kauai origin of a non-aquatic lifestyle, with subsequent dispersal down the island chain [e.g. following the 'progression' pattern of Funk & Wagner (1995)].

The evolutionary origin of the Hawaiian *Limnoxenus* remains somewhat unclear, as our analysis did not resolve a particular adelphotaxon to the Hawaiian lineage. Within the 'file' lineage, two members are found in Oceania, the most common origin of Hawaiian lineages with Miocene to Pliocene ages of Hawaiian colonization (Zimmerman, 1948: 95–97): *L. zealandicus* of Australia and New Zealand, and *Limnocyclus puncticeps* of New Caledonia. The latter is strongly supported as adelphotaxon to the Argentinian *Hydramara argentina*. Any vicariant event involving both New Caledonia and austral South America would have occurred far earlier (Sanmartín & Ronquist, 2004) than the 28 million years before present currently proposed for the duration of continuously exposed high islands in the Hawaiian archipelago (Carson & Clague, 1995; Price & Clague, 2004). Consequently, an Australian *Limnoxenus* ancestor seems more likely; however, until a sister group is definitively established, conclusions concerning the geographical origin of the Hawaiian taxa must remain somewhat speculative.

Conservation

Five of the seven Hawaiian *Limnoxenus* species are known from single localities, and six are restricted to single islands. On Kauai, all taxa are known from established state parks or forest reserves. The sheer remoteness and inaccessibility of the Waialeale and Namolokama summits afford their respective localized endemics protection from human development pressures for the time being. These high-altitude riparian habitats also provide insulation from invasive species, such as ants (Gillespie & Reimer, 1993), that have negatively impacted arthropod species in lower or drier habitats (e.g. Cole *et al.*, 1992; LaPolla *et al.*, 2000).

The situation on Oahu, however, is of greater concern. Here, an endemic species is probably extinct, and a second

species is in apparent decline: *L. nesiticus*, known only from its original type series collected in 1893, was suggested to be extinct (Hansen, 1995b), and its continuing absence from recent collections affirms this conclusion. Its absence is made more conspicuous as it is a putatively aquatically active taxon similar to *L. kauaiensis* and *L. semicylindricus*, both of which can be reliably collected in stream habitats. Survey efforts around the type locality of Kawailoa Gulch are needed to bolster the conclusion that this species has been extirpated.

Early authors (e.g. Blackburn & Sharp, 1885; Williams, 1936) described *L. semicylindricus* on Oahu as 'plentiful' and occurring in a wide range of aquatic habitats from 'near sea level' to 'the smallest mountain streams'. However, the number of successful collecting events has noticeably dropped in recent decades. The species has been recorded on Oahu by five collecting events in the past 30 years, compared with 13 events during 1946–75, and 17 instances during 1916–45. Habitat degradation on Oahu, as a result of stream capture for irrigation and the pumping of groundwater over the 190 years since the species was first observed, is a probable cause of the overall decline. Introduced poeciliid and other fish may be another contributing factor to the decline and subsequent general restriction to higher elevations. Originally introduced to control mosquito populations, these fish have been implicated in the decline of populations of other low-elevation endemic aquatic arthropods, including *Megalagrion* damselflies (Polhemus, 1997; Englund, 1999).

Supplementary material

The following material is available at www.Blackwell-Synergy.com under the DOI reference doi:10.1111/j.1365-3113.2007.00403.x

Appendix S1. Additional material examined of *L. semicylindricus* (Eschscholtz).

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Appendix 1. Characters and character states used in the cladistic analysis

1. *Inter-ocular distance* [narrowest width between eyes divided by the width of one eye when viewed dorsally]: (0) less than 3.50; (1) 3.50–4.49; (2) 4.50–5.49; (3) greater than 5.49.

2. *Labrum*: (0) partially or entirely membranous; (1) completely sclerotized (e.g. Fig. 4A).

3. *Labrum*: (0) with a transverse row of eight or more systematic punctures; (1) with a short row or medial cluster of six or fewer systematic punctures (e.g. Fig. 4C). In some taxa (e.g. most outgroup Acidocerina), these punctures cannot easily be differentiated from the general punctation, although their presence is affirmed by small setae. In those cases of uncertainty regarding the exact number, the character state was coded as missing.

4. *Labial palps*: (0) without row of setae on inner face; (1) with row of setae on inner face (e.g. Fig. 4A).

5. *Maxillary palps*: (0) longer than posterior margin of labrum (e.g. Fig. 4A); (1) equal to or shorter than posterior margin of labrum.

6. *Second segment of maxillary palps*: (0) slightly to distinctly bowed inward; (1) bowed outward. An outwardly bowed maxillary palp is uncommon in the Hydrophilidae; in the taxa included, it is only observed in *Enochrus*.

7. *Apical segment of maxillary palps*: (0) longer than penultimate segment; (1) shorter than penultimate segment.

8. *Mentum*: (0) flat, at most slightly depressed anteromedially (Fig. 4A); (1) strongly depressed medially; (2) slightly convex medially. *Hydrobius fuscipes* and *Hydrobius arcticus* share a rather unusual hydrophilid

condition in which the central region of the mentum is slightly convex centrally.

9. *Dorsal surface*: (0) without shagreening; (1) with at least faint shagreening. In all ingroup taxa and some outgroup taxa, a distinct but sometimes faint iridescent green shagreening is present on the dorsum, including the head, pronotum and thorax. It is best viewed at a slight angle under a directed light source.

10. *Pronotum*: (0) without systematic punctures; (1) with systematic punctures.

11. *Ground punctation on pronotum*: (0) generally uniform in size; (1) composed of two distinct sizes.

12. *Scutellum*: (0) with punctation uniform in size and similar to ground punctation on elytra; (1) with at least several punctures that are much larger than elytral ground punctation, often the size of elytral serial or systematic punctures.

13. *Prosternum*: (0) without carina; (1) with low median carina; (2) with strongly elevated carina; (3) nearly divided into two halves by anterior projection of the mesoventrite.

14. *Accessory ridge below posterior pronotal margin*: (0) not produced laterally into a small dentiform process; (1) produced laterally into a small bluntly dentiform process.

15. *Mesoventrite*: (0) trapezoidal (Fig. 5A–C); (1) triangular; (2) with anapleural sutures forming acute curve. In most taxa examined, the anapleural sutures are obtusely arcuate, which results in the lateral portions of the mesoventrite appearing 'winged'. In *Hybogralius* and *Limnocyclus*, the anopleural sutures are nearly straight, giving the mesoventrite a triangular appearance. In some outgroup taxa (*Enochrus*), this suture is recurved, forming an acute curve.

16. *Mesoventrite depression*: (0) distinct, well differentiated (e.g. Fig. 5A); (1) less differentiated or not distinguishable (e.g. Fig. 5B, C). In *Hydrochara* and *Tropisternus*, the highly modified mesoventrite obscures this character, and so this character was coded as missing for these taxa.

17. *Mesoventrite*: (0) elevated into a keel or tubercle; (1) flat, without distinct elevation.

18. *Mesoventrite elevation*: (0) a high, laminar keel which is fused posteriorly with the metaventrite; (1) a high rectangular keel which is not fused with the metaventrite (e.g. Fig. 5A); (2) a low, transverse ridge with is densely and finely pubescent; (3) a transverse glabrous ridge; (4) an elevated, longitudinal, glabrous carina; (5) a low, granular elevation with both transverse and longitudinal components; (6) a low, longitudinal and pubescent ridge (e.g. Fig. 5B, C); (7) a strongly elevated and glabrous tubercle with transverse and longitudinal elements; (8) a strongly elevated blunt and broad glabrous tubercle.

19. *Anepisternum 2*: (0) uniformly pubescent (Fig. 5C); (1) not uniform in sculpturing, with a glabrous or differentiated medial area (Fig. 5B); (2) mostly glabrous, setiferous only around margins (Fig. 5A).

20. *Meso- and metasternum*: (0) not fused into a common keel (e.g. Fig. 5); (1) fused into a common keel.

21. *Metathorax*: (0) macropterous (Fig. 11A); (1) with reduced wings (Fig. 11B); (2) with vestigial wings (Fig. 11C). In the examined taxa with reduced wings, a nearly full complement of veins is present in the basal half, whereas, in the vestigial wings, no veins are present except for the costal margin and a presumed remnant of the cubitus. This character was coded for *L. semicylindricus* as a partial polymorphism (0, 1).

22. *Metasternal projection*: (0) absent; (1) with a pointed projection between metacoxae but not surpassing (overlapping) condyles; (2) with a pointed projection between metacoxae overlapping condyles.

23. *Metaventrite ratio (posterior width/median length)*: (0) less than 3.49; (1) 3.50–4.20; (2) greater than 4.20.

24. *Elytral serial punctures*: (0) absent; (1) present.

25. *Elytral serial punctures*: (0) uniform along entire length; (1) distinct on posterior half, becoming more diffuse or indistinguishable on anterior half.

26. *Elytral serial punctures*: (0) set in distinct striae; (1) not set in striae (e.g. Fig. 6B) (excluding sutural row).

27. *Elytra*: (0) with sutural stria (Fig. 6A); (1) without sutural stria.

28. *Elytral systematic punctures*: (0) absent; (1) present (Fig. 6A).

29. *First row of elytral systematic punctures*: (0) composed of 35 or more punctures; (1) with 20–30 punctures; (2) with 10–19 punctures; (3) with fewer than ten punctures.

30. *Elytral systematic punctures*: (0) without cuticular elevation on anterior margin (e.g. Fig. 6A); (1) with cuticular elevation on anterior margin.

31. *Elytra*: (0) with smooth margins (e.g. Fig. 6B); (1) with serrated margins.

32. *Epipleura*: (0) glabrous in posterior half; (1) with marginal row or band of fine setae.

33. *Procoxae*: (0) without spines (e.g. Fig. 8B); (1) with short spines scattered among pubescence (e.g. Fig. 8A).

34. *Metatibia*: (0) without row of hair-like setae; (1) with row of hair-like setae.

35. *Metafemora*: (0) without detectable microsculpture in apical glabrous region; (1) with detectable microsculpture in apical glabrous region.

36. *Metafemoral ratio*: (0) less than 2.50; (1) 2.50–2.99; (2) 3.00–3.99; (3) 4.00 or greater.

37. *Metafemora*: (0) glabrous or with pubescence not extending on posterior margin distad of trochanter (Fig. 7C); (1) with dense pubescence extending on posterior margin past trochanter (Fig. 7A).

38. *Metafemora*: (0) with posterior margin evenly curved (Fig. 7C); (1) with posterior margin angulate.

39. *Tarsi*: (0) 5-5-5; (1) 5-4-4.

40. *Meso- and metatarsi*: (0) without two rows of dorsal hairs; (1) with two rows of dorsal hairs, the inner row often reduced (Fig. 9A, B).

41. *Dorsal metatarsal hairs*: (0) shorter than length of inner metatibial spur (Fig. 9B); (1) as long or longer than length of metatibial spur (Fig. 9A).

42. *Meso- and metatarsi*: (0) with two rows of short, pointed spicules on ventral face (Fig. 9C); (1) with a brush of hair-like setae on ventral face (Fig. 9D).
43. *Metatarsi*: (0) normal, not rotated; (1) rotated 90° so that ventral face is directed inward.
44. *Second metatarsomere*: (0) with six or more ventral spicules; (1) with five or fewer ventral spicules (Fig. 9C).
45. *Second metatarsomere*: (0) as long or longer than basal metatarsomere (Fig. 9A, B); (1) shorter than basal metatarsomere.
46. *Laterosternite 3*: (0) flat, without longitudinal division (e.g. Fig. 10); (1) longitudinally divided by a distinct ridge.
47. *Laterosternite 3*: (0) quadrate in posterior half (Fig. 10A); (1) distinctly tapered in posterior half (Fig. 10B–D).
48. *Laterosternite 3*: (0) without cuticular projections arranged into a linearly arranged file in posterior half (Fig. 10A); (1) with cuticular projections arranged into a linearly arranged file in posterior half (Fig. 10B–D).
49. *File on laterosternite 3*: (0) with fine teeth (Fig. 10B); (1) with coarse teeth (Fig. 10C, D).
50. *File on laterosternite 3*: (0) composed of rows without gaps (Fig. 10); (1) composed of rows with gaps. In all taxa that contain an organized file, teeth are arranged in regular, aligned rows. In *Hydramara*, there are distinct gaps between each row of teeth.
51. *Fifth abdominal ventrite*: (0) evenly rounded; (1) with an apicomedial emargination or truncation.
52. *Emargination of fifth abdominal ventrite*: (0) narrow, deep; (1) narrow, shallow; (2), broad, shallow.
53. *Aedeagus*: (0) with parameres normal, not divided; (1) with parameres divided into two lobes. Most taxa examined possess a typical hydrophiloid-like paramere, with the exception of *Hydramara*, in which each paramere is deeply split into an inner and outer lobe that, together with the median lobe, make it appear to have five projections apically.
54. *Median lobe*: (0) without median carina dorsally; (1) with median carina dorsally. In the genus *Limnoxenus*, including all Hawaiian taxa, the median lobe possesses a median raised ridge in the dorsal third. This character is best observed in uncleared aedeagi.
55. *Gonopore*: (0) at apex of dorsal sclerite (e.g. Figs 12, 13); (1) distinctly shorter than dorsal sclerite.

Appendix 2.

Taxon	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
Coelostoma orbiculare	1	0	–	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	–	2	1	0	0	0	0	1	1	0	–	0	0	1	1	1	1	1	1	1	0	0	–	1	0	–	1	1	0	0	–	0	0	0	0	0	–
Ametor scabrosus	2	1	?	1	0	0	0	0	0	0	1	1	0	1	1	0	1	2	1	–	1	1	1	0	1	1	0	0	?	1	1	0	0	1	1	1	1	1	0	0	1	1	0	–	0	0	0	0	–	0	0	0	0	0	0
Sperchopsis tessallata	1	1	?	1	0	0	0	0	0	1	1	0	0	1	0	1	1	2	1	–	0	0	0	0	0	0	0	0	?	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	–	0	0	0	0	0	0
Hydrochara obtusata	1	0	1	1	0	1	0	0	1	1	0	0	2	0	0	0	1	2	0	–	1	0	2	0	0	0	0	1	?	1	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	–	0	0	0	0	0	0
Tropisternus affinis	1	1	0	1	0	0	1	0	0	0	0	0	1	0	–	0	0	1	1	0	1	0	0	0	–	1	1	1	?	0	0	1	1	0	1	1	0	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	1
Cymbiodyta semistriata	2	1	?	1	0	0	1	0	0	1	0	0	3	0	0	1	0	1	1	0	2	0	0	0	1	1	0	0	?	1	1	0	0	1	0	1	1	0	0	1	0	1	0	0	0	1	1	0	–	1	0	0	0	0	1
Helocombus bifidus	1	1	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	3	2	0	0	0	0	0	0	1	0	?	1	0	1	1	0	1	1	0	1	0	1	0	0	0	0	1	1	0	0	–	0	0	0	0	0	0
Cymbiodyta marginella	1	1	?	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	3	2	0	0	0	0	0	0	1	0	?	1	1	1	1	0	1	0	1	1	0	1	0	0	0	*	1	1	0	0	–	0	0	0	0	0	0
Enochrus testaceus	1	1	?	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	4	1	0	0	0	0	1	1	0	?	1	0	0	0	0	1	0	1	1	0	0	1	0	0	0	1	1	0	0	–	0	0	0	0	0	1
Enochrus quadripunctattus	1	1	?	1	0	1	0	0	0	0	0	0	0	0	0	0	2	1	1	4	0	0	0	0	0	1	1	0	?	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	–	0	0	0	0	0	1
Helochares obscurus	1	1	?	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	3	0	0	0	0	0	1	1	0	?	1	1	0	0	0	1	0	1	1	0	0	1	0	0	0	1	1	0	0	–	0	1	1	0	0	?
Hybogralius hartmeyeri	2	1	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	2	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	0	0	1
Limnocyclus puncticeps	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	0	0	5	0	0	0	2	0	1	0	0	1	0	2	0	1	0	1	0	0	3	0	1	0	1	0	0	0	0	0	0	1	1	0	1	0	1	0	1	1
Hydramara argentina	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	0	0	5	1	0	0	2	0	1	0	0	0	0	2	0	0	0	0	0	0	2	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	0	0
Hydrobius fuscipes	1	1	0	1	0	0	0	0	2	1	0	0	0	1	0	0	0	6	2	0	1	0	1	0	0	1	1	0	1	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	–	1	0	0	0	0	0
Hydrobius arcticus	2	1	0	1	0	0	0	0	2	1	0	0	0	0	0	0	0	6	2	0	1	0	0	0	0	1	1	0	2	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	–	1	0	0	0	0	0
Hydrobius melaenus	1	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	7	2	0	1	0	1	0	0	1	1	0	1	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	–	1	0	0	0	0	0
Hydrobius tumidus	1	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	7	2	0	1	0	0	0	0	1	1	0	1	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	–	1	0	0	0	0	0
Hydrobius convexus	1	1	0	1	0	0	0	0	2	1	0	0	0	1	0	0	0	6	2	0	1	0	1	0	0	1	1	0	2	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
Limnoxenus niger	0	1	0	1	0	0	0	0	1	1	0	0	2	1	0	0	0	1	2	0	2	0	0	0	1	1	1	0	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Limnoxenus olmoi	0	1	0	1	0	0	0	0	2	1	0	0	2	1	0	0	0	1	2	0	2	0	0	0	1	1	1	0	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Limnoxenus sjostedti	0	1	0	1	0	0	0	0	1	1	0	0	2	1	0	0	0	1	2	0	2	0	0	0	1	1	1	0	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Limnoxenus zealandicus	0	1	0	1	0	0	0	0	1	1	0	0	2	1	0	0	0	1	2	0	2	0	0	0	1	1	1	0	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Limnoxenus kauaiensis	1	1	1	1	1	0	0	0	2	1	0	0	2	1	0	0	0	6	1	1	0	1	0	1	1	0	1	0	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0
Limnoxenus semicylindricus	1	1	1	1	1	0	0	0	2	1	0	0	2	1	0	1	0	6	1	0	$	2	0	1	0	*	0	1	0	0	0	0	0	1	2	0	0	1	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0
Limnoxenus nesiticus	1	1	1	1	1	0	0	0	2	1	0	0	2	1	0	1	0	6	1	0	0	2	0	1	1	0	1	0	1	0	0	0	0	1	2	0	0	1	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0
Limnoxenus waialeale	2	1	1	1	1	0	0	0	2	1	0	0	2	2	0	1	0	8	0	0	2	2	1	0	1	1	0	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	?
Limnoxenus oahuensis	2	1	1	1	1	0	0	0	2	1	0	0	2	2	0	1	0	8	0	0	2	2	–	1	1	1	0	1	0	0	0	0	1	1	0	0	1	1	0	1	0	0	1	–	0	1	1	0	0	1	0	1	0	0	?
Limnoxenus namolokama	2	1	1	1	1	0	0	0	1	1	0	0	2	2	0	1	0	8	0	0	2	2	2	0	1	1	0	1	3	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	0	1	1	0	0	1	0	1	0	0	?
Limnoxenus punctatostriatus	3	1	1	1	0	0	0	0	1	1	0	0	2	1	0	1	0	6	0	0	2	2	2	0	1	0	0	1	2	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	0	1	1	0	0	1	0	1	0	0	0