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RESEARCH ARTICLE

Ecology and systematics of the wine wētā and allied species, with description of four new *Hemiandrus* species

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ABSTRACT
Wētā (Orthoptera: Anostostomatidae) are a well-recognised component of New Zealand nocturnal ecology, but much of the diversity remains undescribed and only partly characterised. Species of *Hemiandrus* conceal themselves during the day in soil burrows and most are infrequently encountered, however, one taxon is notorious in some South Island vineyards. We demonstrate that this wētā at unusually high density in some vineyards in the Awatere valley is also found in North Island forests (*Hemiandrus bilobatus*). Here we use morphological and genetic data to identify the wine wētā and examine its ecology in vineyards. We also describe four new species which belong to the same ground wētā clade as the wine wētā. We provide mtDNA analysis and diagnostic morphological characters to distinguish six *Hemiandrus* species that are characterised by adult females having an extremely short ovipositor and maternal care.

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Introduction

As human activity continues to encroach upon native habitats many endemic species continue to suffer population decline, which may eventually cause their extinction (IPBES 2019). Rarely in New Zealand are native animal populations influenced positively by anthropogenic habitat modification, but a conspicuous local example exists within the *Hemiandrus* ground wētā. The wine wētā is a species of orthopteran in the family Anostostomatidae that has been found at high density on Awatere vineyards in Marlborough, New Zealand (Nboyine et al. 2016). Situated in the northeast corner of South Island, the Marlborough region experiences hot sunny days and cool nights, conditions which prolong grape (*Vitis vinifera* L.) ripening times generating the intense wine characteristics (especially in the Sauvignon blanc variety) for which the region is recognised worldwide. Marlborough was once vegetated by native forest but this was replaced by bracken scrub following Polynesian fires (Mcglone and Basher 1995; Perry et al. 2014). Exotic grasslands later developed under European pastoral management with sheep grazing dominating the landscape before the planting of vineyards began in the 1970s.

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The wine wētā has most impact on the grape vines during the spring when it feeds on the new opening buds (Figure 1). Damage to the incipient fruiting bodies early in their development has been identified as reducing grape yield in some instances (Nboyine

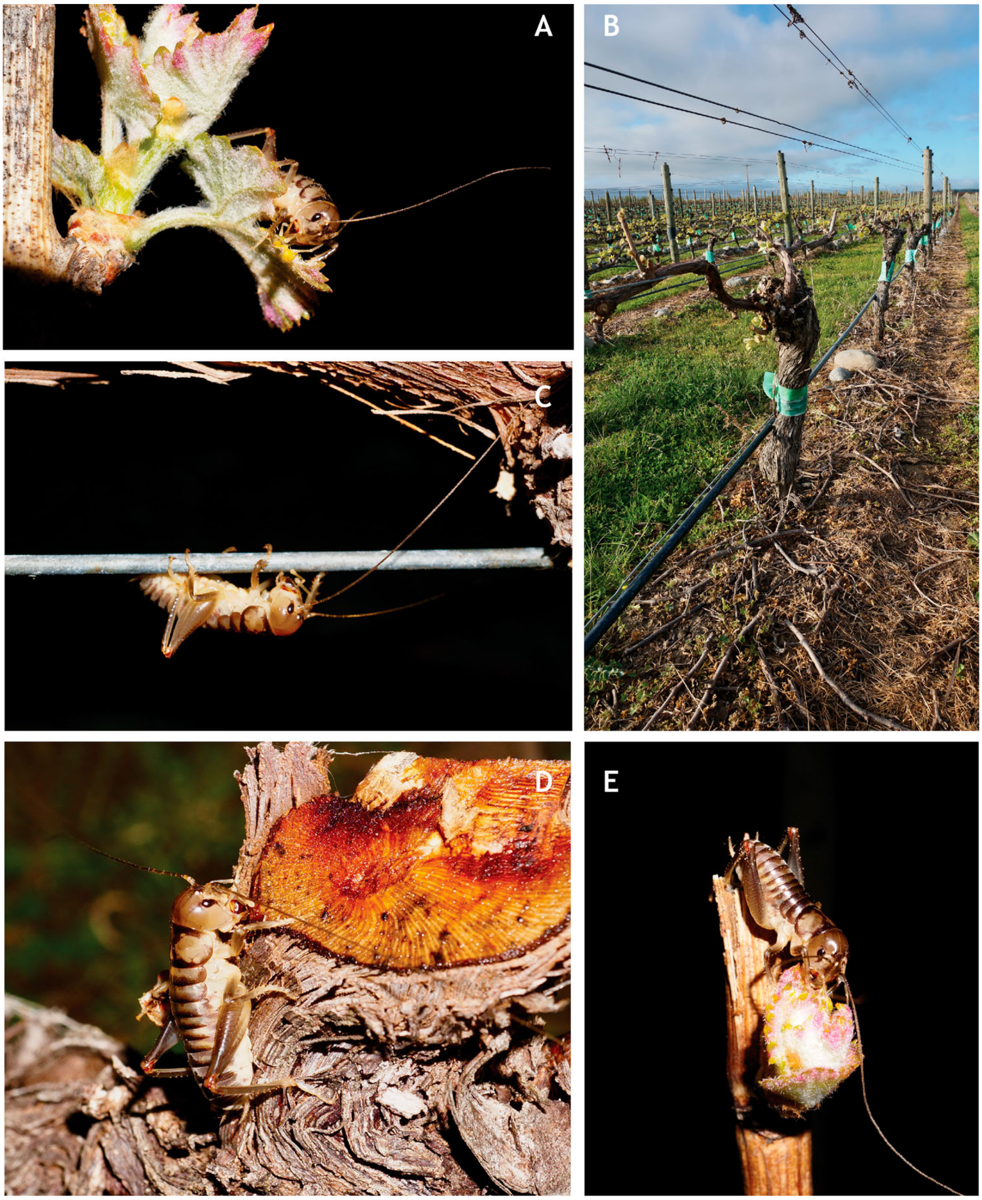


Figure 1. At night *Hemiandrus* ground wētā ascend vines in the seaward Awatere valley near Blenheim, New Zealand. **A,** *Hemiandrus bilobatus* the wine wētā feeding on young vine leaf. **B**, Grape vine rows provide a vertical environment reminiscent of natural forest habitat, with irrigation along rows providing moisture in an otherwise dry spring landscape. **C**, Wine wētā are adept climbers capable of traversing horizontal wires. **D**, Vines provide other foods including sap from freshly pruned stem. **E**, Wine wētā feeding on young vine bud, at the stage when incipient flower buds might be damaged.

et al. 2016). Wētā activity on grape vines is currently managed by attaching plastic sleeves around vine trunks because it is thought this slippery surface makes it difficult for wēta to ascend the stems (Nboyine et al. 2018). Despite several studies directed at identifying the scale of impact on grape harvest and at finding solutions, the identity and behaviour of this wētā has not been addressed. In part this reflects taxonomic uncertainty in the group as a whole, but it is clear that the wētā concerned belongs to the ground wētā genus *Hemiandrus*, which typically reside in closed burrows in soil during the day and emerge only at night.

Although abundant and diverse in native New Zealand habitats, many species of wētā (Insecta: Orthoptera: Anostostomatidae and Rhaphidophoridae) remain undescribed and their biology poorly known (Brockie 1992; Johns 1997; Fitness et al. 2015; Fitness et al. 2018; Hegg et al. 2019). The true wētā of New Zealand belong to the Anostostomatidae, comprising three main lineages; giant and tree wētā (*Deinacrida* White 1842; *Hemideina* White 1846), tusked wētā (*Anisoura* Ander 1938, *Motuweta* Johns 1997) and ground wētā (*Hemiandrus* Ander 1938) (Johns 1997; Trewick and Morgan-Richards 2004; Trewick and Morgan-Richards 2005; Trewick and Morgan-Richards 2019). About 60 species occupy habitats ranging from lowland forest to the alpine herbfields. The ground wētā lineage is the most speciose, with fourteen described species (Johns 1997, 2001; Jewell 2007; Taylor Smith et al. 2013; Taylor-Smith et al. 2016). These 14 *Hemiandrus* species are supplemented by dozens of 'tag-name' entities, including the taxon associated with viticulture (Johns 2001; Jewell 2007; Trewick et al. 2016), representing diversity of uncertain taxonomic rank (Leschen et al. 2009).

Here we provide new data on the natural history of the wine wētā using observations at night in vineyards and examination of gut contents. We identify the wine wētā using diagnostic morphological traits and evidence from DNA sequences, and describe four new species of ground wētā belonging to the same clade of short-ovipositor New Zealand *Hemiandrus* as the wine wētā.

Methods

Field observations of wine wētā were made in the Awatere valley during grape vine bud burst when the wētā are thought to do most damage to the crop (early October 2018 and 2019). The Awatere valley has many vineyards although anecdotally the wine wētā are a concern for growers only in the eastern, seaward part of the valley (Figure 2). Our field site was Cable Bay vineyard (−41.62295, 174.121714) which has a number of grape varieties in close proximity and management includes irrigation and use of plastic sleeves on vine main stem (trunk).

Wine wētā ecology

To estimate the population density of wine wētā we searched the ground at night along vine rows and marked each wētā seen with a spot of nail lacquer on the pronotum (October 2018). On the subsequent night we search the same ground, recorded all wētā seen and whether they had been marked. We estimated population size using the Lincoln-Peterson estimator (Peterson 1896; Lincoln 1930) with the Chapman

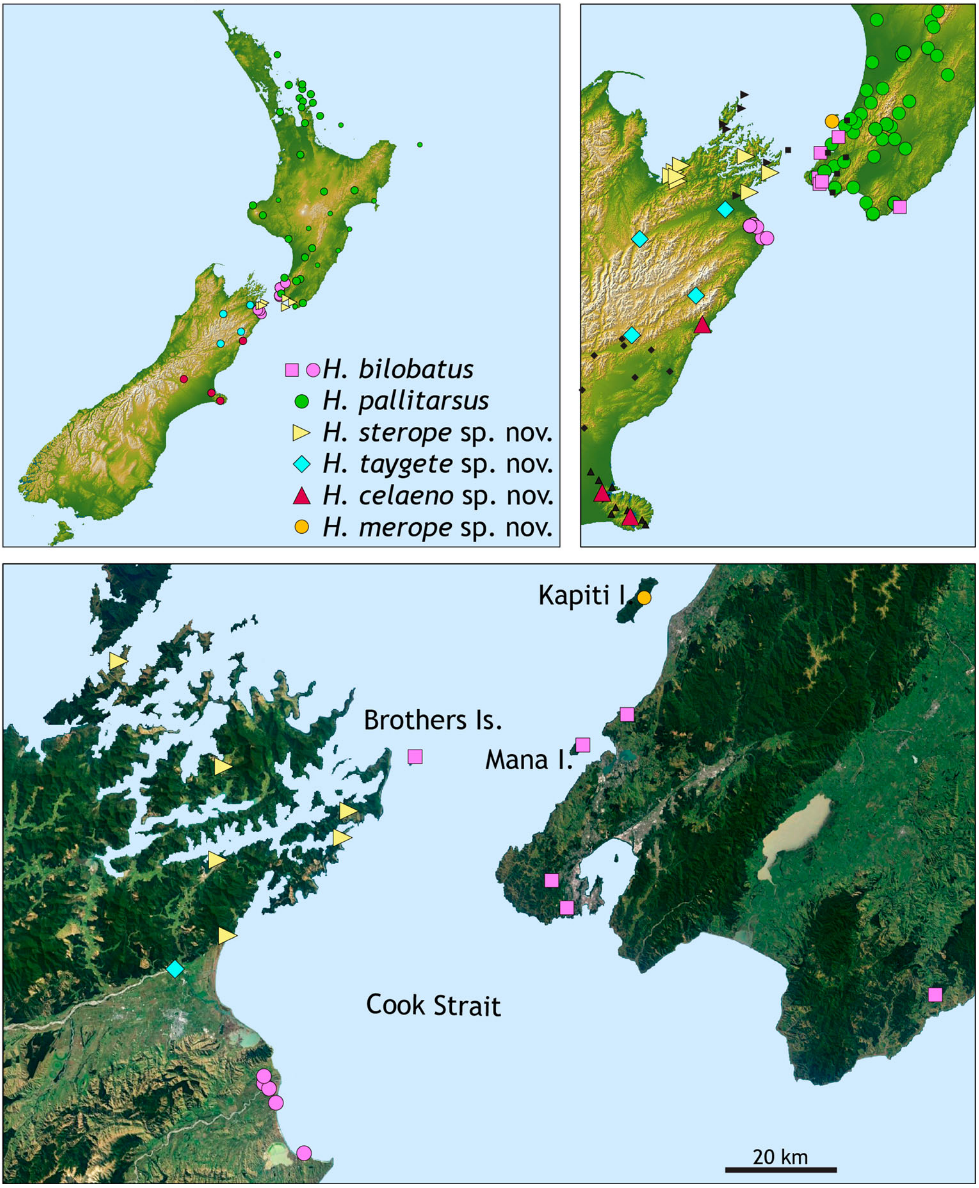


Figure 2. Sampling locations of two described and four new species of short-ovipositor *Hemiandrus* ground wētā near Cook Strait, New Zealand. Symbols are colour-coded by species. Black symbols represent previously reported locations of ground wētā in the region (Johns 2001): *H. bilobatus* square, and undescribed/tag-named *H.* 'onokis' diamond, *H.* 'horomaka' triangle, and *H.* 'vicinus' pennant.

modification which reduces bias associated with small population sizes (Chapman 1951), using the equation:

$$N = \frac{(M+1)(C+1)}{R+1} - 1$$

where N is the estimate of total population size, M is the total number of animals captured and marked on the first night, C is the total number of animals captured on the second night and R is the number of animals captured on the first night that were then recaptured on the second night.

Separately we observed ground wētā during the night (after 20:30h) on the trunk, stems, branches and leaves of grape vines. We recorded whether each vine examined had a plastic sleeve on its trunk or not. The plastic sleeves attached to grape vine trunks are an attempt to reduce wētā access and some had dropped off vines (apparently at random) and not been replaced. We analysed presence/absence of wētā and sleeves.

To gauge the range of food types consumed by wine wētā in the spring we used direct observations at night when the insects were active, including on artificial feeding arenas provided with protein (either thawed beetle larva or cat biscuit), carbohydrate (rolled oats), and fruit (apricot pieces; see Taylor Smith et al. 2013 for details of this approach). We also examined crop contents of wine wētā collected by hand at night, in pitfall traps, and opportunistically during digging holes for vineyard trellis posts. Wētā preserved in ethanol were dissected so that contents of the gut could be examined. We used stereomicroscopy to identify any large particles including fragments of invertebrate exoskeleton, and then bleached and stained (with basic Fuchsin) smaller particles mostly comprising plant matter. We scored positive presence of animal and vine material in the diet and documented other material seen.

Systematics and taxonomy

We used a combination of field observation, morphology and phylogenetic analysis to establish the systematic position of the wine wētā and its allies. Specimens examined came primarily from the Phoenix Lab insect collection at Massey University, Palmerston North (MPN) with additional material from Department of Conservation (DOC) pitfall trap survey samples (Sherley & Stringer 2016). All specimens were dry or preserved in 70%–95% ethanol. Sample locations were mapped using the R project (R core team 2013) package MAPS (Becker and Wilks 2018), and regional occurrence documented using the New Zealand entomological area codes (Crosby et al. 1976). Specimens were examined and anatomical features photographed using an Olympus SZX7 Zoom Stereomicroscope with an attached SC100 digital camera and Cellsens software.

Males were considered to be adults if dark, sclerotized hooks (falci) were present on the tenth abdominal tergite, whereas females were assessed as adults based on the shape of the subgenital plate and ovipositor (Cary 1981). Measurements were made using digital callipers accurate to 0.01mm. Anatomical features were assessed (Taylor Smith et al. 2013) including BL, partial body length; HW, head width; HL, head length; PL, pronotum length; PW, pronotum width; FW, femur width; FL, femur length; OV, ovipositor length; SG, subgenital plate length; T1, first abdominal tergite; T2, second abdominal tergite; T3, third abdominal tergite; T7, seventh abdominal tergite; T8, eighth abdominal tergite; T9, ninth abdominal tergite; T10, tenth abdominal tergite; MP3, third segment of the maxillary palps; MP4, fourth segment of the maxillary palps; MP5, fifth segment of the maxillary palps (Figure 3).

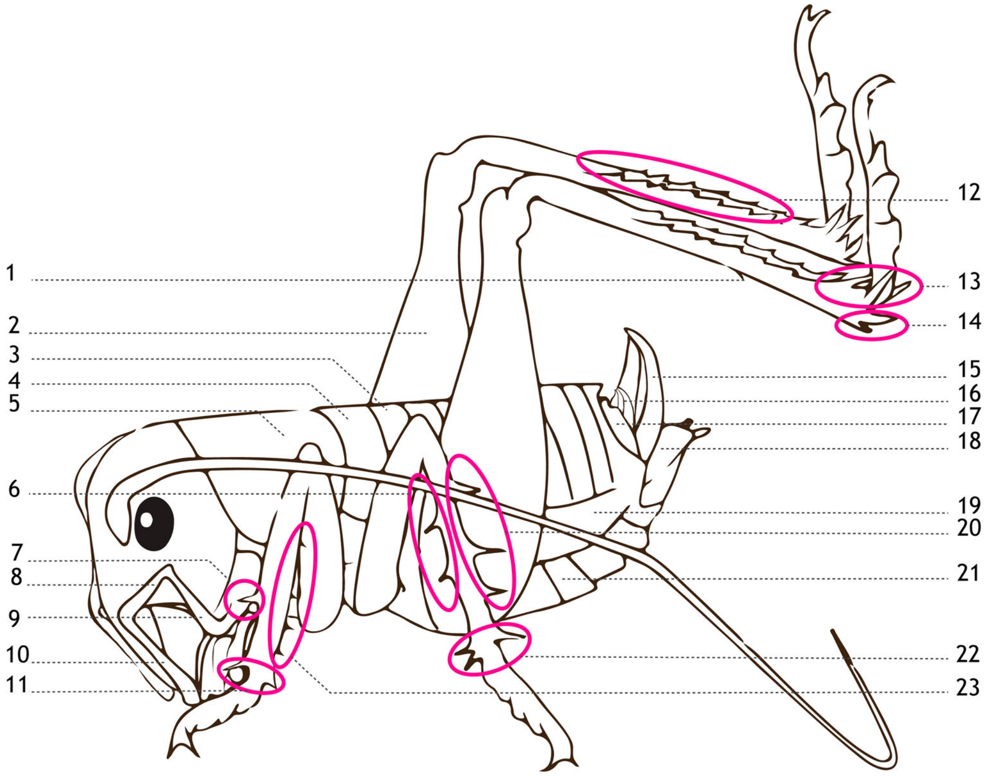


Figure 3. Morphological features of *Hemiandrus* anatomy useful in taxonomy: (1) Hind tibia inferior articulated spines; (2) Hind femur retrolateral surface; (3) Metanotum; (4) Mesonotum; (5) Pronotum; (6) Mid tibia superior prolateral spines; (7) Fore tibia superior prolateral spine; (8) Fourth segment of maxillary palp MP4; (9) MP3; (10) MP5; (11) Fore tibia apical spines; (12) Hind tibia superior fixed spines; (13) Hind tibia subapical spines; (14) Hind tibia apical spines; (15) Cerci; (16) Paranal processes; (17) 10th abdominal tergite T10 with falci; (18) Subgenital plate; (19) Pleural membrane; (20) Mid tibia retrolateral spines; (21) Abdominal sternites; (22) Mid tibia apical spines; (23) Fore tibia inferior retrolateral spines.

Hemiandrus mitochondrial DNA cytochrome oxidase subunit I sequences were generated for representative outgroup taxa and individuals and populations of the ingroup (Table 1) using standard polymerase chain reaction (PCR) conditions (Trewick and Morgan-Richards 2005). We used PCR primers C1-J–2195 (TTG ATT TTT TGG TCA TCC AGA AGT) (Simon et al. 1994) and mtd12_wetaR (ATT GCA CTT ATC TGC CAT ATT AG) which is a modified version of L2-N–3014 targeting the 3' portion of COI (Bulgarella et al. 2014). Previously published sequences (Pratt et al. 2008; Chappell et al. 2012) were obtained from Genbank. DNA sequence checks, data alignment and analysis used Geneious v10.2 (Kearse et al. 2012). Phylogenetic analysis was implemented in Geneious v10.2 using, (A) Bayesian inference with chain length of 4 million and burnin of 400,000 generations and GTR + I+G model of DNA evolution, and (B) Neighbor-Joining of Tamura-Nei genetic distances. A median spanning network was generated in PopArt (Leigh and Bryant 2015).

Table 1. Sample location and details of *Heminadrus* ground wētā included in genetic analysis of the short-ovipositor clade using mtDNA COI sequence data.

Hemiandrus species	Location	Entomological area	Sample code	COI GenBank accession	Latitude	Longitude	Date collected
H. bilobatus	Newtown, Wellington	WN	GW025	EU676794	−41.31536	174.77633	20/03/96
	Tinakori, Wellington	WN	GW240	JF895562	−41.28329	174.76707	29/09/07
	Tinakori, Wellington	WN	GW241	JF895563	−41.28329	174.76707	29/09/07
	Mana Island	WN	GW650	MT623091	−41.089961	174.785528	14/12/10
	Mana Island	WN	GW652	MT623094	−41.089961	174.785528	14/12/10
	Mana Island	WN	GW654	MT623096	−41.089961	174.785528	14/12/10
	Mana Island	WN	GW657	MT623095	−41.089961	174.785528	14/12/10
	Tora near Martinborough	WA	GW1308	MT641250	−41.464791	175.523157	08/11/19
	Tora near Martinborough	WA	GW1306	MT641252	−41.464791	175.523157	08/11/19
	Tora near Martinborough	WA	GW1312	MT641251	−41.464791	175.523157	08/11/19
	Paekakariki, Kapiti Coast	WN	GW965	MT623093	−40.976464	174.965	20/11/13
	Paekakariki, Kapiti Coast	WN	GW967	MT623092	−40.976464	174.965	20/11/13
	Cable Bay Vineyard, Awatere	MB	GW1153	MT623089	−41.62295	174.121714	03/10/18
	Cable Bay Vineyard, Awatere	MB	GW1164	MT623079	−41.62295	174.121714	03/10/18
	Cable Bay Vineyard, Awatere	MB	GW1176	MT623081	−41.62295	174.121714	03/10/18
	Cable Bay Vineyard, Awatere	MB	GW1177	MT623080	−41.62295	174.121714	03/10/18
	Cable Bay Vineyard, Awatere	MB	GW1184	MT623087	−41.62295	174.121714	02/10/19
	Cable Bay Vineyard, Awatere	MB	GW1189	MT623076	−41.62295	174.121714	20/08/19
	Cable Bay Vineyard, Awatere	MB	GW1194	MT623082	−41.62295	174.121714	20/08/19
	Cable Bay Vineyard, Awatere	MB	GW1196	MT623078	−41.62295	174.121714	20/08/19
	Boundary Creek, Awatere	MB	GW3Const	MT623083	−41.62295	174.128680	14/03/19
	Boundary Creek, Awatere	MB	GW1Const	MT623088	−41.62295	174.128680	14/03/19
	Boundary Creek, Awatere	MB	GW2Const	MT623090	−41.607654	174.128680	14/03/19
	Lower Awatere Valley	MB	GW581	MT623084	−41.634433	174.086952	28/10/10
	Lower Awatere Valley	MB	GW584	MT623077	−41.634433	174.086952	28/10/10
	Lower Awatere Valley	MB	GW585	MT623086	−41.634433	174.086952	28/10/10
	Lower Awatere Valley	MB	GW586	MT623085	−41.634433	174.086952	28/10/10
	Marfells Beach, Clifford Bay	KA	GW055	EU676789	−41.725974	174.204283	11/03/00
	Marfells Beach, Clifford Bay	KA	GW122	EU676777	−41.725974	174.204283	11/03/00
	Marfells Beach, Clifford Bay	KA	GW193	JF895564	−41.644504	174.156904	19/11/06
H. celaeno sp. nov.	Wainui, Banks Peninsula	MC	GW880	MT623118	−43.815454	172.900257	30/11/12
	Wainui, Banks Peninsula	MC	GW881	MT623125	−43.815454	172.900257	30/11/12
	Wainui, Banks Peninsula	MC	GW882	MT623123	−43.815454	172.900257	30/11/12
	Wainui, Banks Peninsula	MC	GW883	MT623124	−43.815454	172.900257	30/11/12
	Wainui, Banks Peninsula	MC	GW884	MT623119	−43.815454	172.900257	30/11/12
	Wainui, Banks Peninsula	MC	GW886	MT623121	−43.815454	172.900257	30/11/12

(*Continued*)

Table 1. Continued.

Hemiandrus species	Location	Entomological area	Sample code	COI GenBank accession	Latitude	Longitude	Date collected
	Wainui, Banks Peninsula	MC	GW887	MT623120	−43.815454	172.900257	01/12/12
	Wainui, Banks Peninsula	MC	GW888	MT623122	−43.815454	172.900257	01/12/12
	Kennedy’s Reserve, Banks Peninsular	MC	GW120	EU676771	−43.62942	172.62071	26/12/05
	Porters Pass, Foggy Peak stream	MC	GW127	EU676778	−43.29663	171.74187	09/03/06
	Porters Pass, Foggy Peak stream	MC	GW129	MT623117	−43.29663	171.74187	09/03/06
	Kowhai Bush, Kowhai River, Kaikoura	KA	GW251	MT623116	−42.3763	173.612781	19/12/07
H. merope sp. nov.	Rangatira track, Kapiti Island	WN	GW674	MT623126	−40.852124	174.931355	14/11/11
	Rangatira track, Kapiti Island	WN	GW682	MT623127	−40.852124	174.931355	14/11/11
H. taygete sp. nov.	Goose Flat, Middle clarence valley	KA	GW491	MT623112	−42.15105	173.55123	29/01/09
	Upper Clarence Valley	KA	GW869	MT623114	−42.446261	172.914848	02/02/12
	Upper Clarence Valley	KA	GW871	MT623113	−42.446261	172.914848	02/02/12
	Renwick, Marlborough	MB	GW958	MT623111	−41.513591	173.842335	30/08/11
	Redhills Hut, Mt Richmond	MB	GW1031	MT623115	−41.731425	172.992037	31/12/13
H. sterope sp. nov.	Whites Bay track, Rarangi	SD	GW054	EU676788	−41.384923	174.057169	07/01/04
	Whites Bay, Rarangi	SD	GW1200	MT623097	−41.384923	174.057169	12/12/18
	Te Rua Bay, Tory Channel	SD	GW596	MT623100	−41.2395	174.27135	11/11/10
	Te Rua Bay, Tory Channel	SD	GW602	MT623101	−41.2395	174.27135	11/11/10
	Branford Reserve, Nelson.	NN	GW1033	MT623110	−41.272033	173.304746	24/02/14
	Branford Reserve, Nelson.	NN	GW1036a	MT623109	−41.272033	173.304746	24/02/14
	Branford Reserve, Nelson.	NN	GW1036b	MT623107	−41.272033	173.304746	25/02/14
	Maitai Valley, Nelson.	NN	GW1037	MT623104	−41.296766	173.342838	24/02/14
	Wakapuaka Cemetery, Atawhai, Nelson	NN	GW1038	MT623106	−41.254908	173.302957	24/02/14
	Wakapuaka Cemetery, Atawhai, Nelson	NN	GW1040	MT623105	−41.254908	173.302957	24/02/14
	Dodson’s Valley, Nelson	NN	GW1043	MT623108	−41.24592	173.323759	25/02/14
	Marybank Reserve, Nelson	NN	GW1044c	MT623098	−41.228815	173.321227	25/02/14
	Marybank Reserve, Nelson	NN	GW1044d	MT623099	−41.228815	173.321227	26/02/14
	Cable Bay track, Nelson	NN	GW1047	MT623103	−41.186065	173.377949	25/02/14
	Manaroa, Kenepuru Sound	SD	GW717	MT623102	−41.117125	174.035969	14/01/12
H. pallitarsis	Lake Waikaremoana, Black Beech track	GB	GW066	EU676740	−38.7522	177.15870	27/03/04
	Newlands, Wellington	WN	GW082	JF895552	−41.232864	174.826941	06/06/04
	Newlands, Wellington	WN	GW097	EU676797	−41.232864	174.826941	20/08/05
	Newlands, Wellington	WN	GW176	JF895561	−41.232864	174.826941	16/04/06
	Tora near Martinborough	WA	GW1206	MT623131	−41.464791	175.523157	08/11/19
	Tora near Martinborough	WA	GW1214	MT623130	−41.464791	175.523157	08/11/19
	Tora near Martinborough	WA	GW1215	MT623128	−41.464791	175.523157	08/11/19
	Tora near Martinborough	WA	GW1216	MT623129	−41.464791	175.523157	08/11/19
	Tora near Martinborough	WA	GW1217	MT623132	−41.464791	175.523157	08/11/19
	Tora near Martinborough	WA	GW1307	MT641253	−41.464791	175.523157	08/11/19
	East Holdsworth Track, Tararua Range	WA	GW091	EU676768	−40.88090	175.44090	06/02/05

	Little Barrier Island (Te Hauturu-o-Toi)	CO	GW226	JF895542	−36.212147	175.068512	17/05/07
	Little Barrier Island (Te Hauturu-o-Toi)	CO	GW227	JF895541	−36.212147	175.068512	17/05/07
	Moehau, Stony Bay	CO	GW348	JF895551	−36.530571	175.417714	27/01/07
	Moehau, Stony Bay	CO	GW352	JF895550	−36.530571	175.417714	27/01/07
	Cuvier Island (Repanga)	CO	GW371	JF895553	−36.43706	175.77106	16/01/07
	Ruamahuanui Island, Aldermen islands	CO	GW271	JF895546	−36.952841	176.095819	24/01/07
	Ruamahuanui Island, Aldermen islands	CO	GW270	JF895545	−36.952841	176.095819	24/01/07
	Ruamahuanui Island, Aldermen islands	CO	GW269	JF895547	−36.952841	176.095819	24/01/07
	Kauaeranga Valley	CO	GW382	JF895543	−37.120154	175.630188	21/01/07
	Kaueranga Valley	CO	GW384	JF895544	−37.120154	175.630188	21/01/07
	Atiu, Mercury islands	CO	GW399	JF895548	−36.63633	175.861416	22/01/07
	Atiu, Mercury islands	CO	GW396	JF895549	−36.63633	175.861416	22/01/07
	Pohangina	RI	GW087	JF895554	−40.130525	175.845966	18/10/04
H. nox	Awakari Valley, Buller	BR	GW076	EU676766	−41.938775	171.509757	15/03/97
H. maculifrons	Franz Josef, Westland	WD	GW150	EU676786	−43.411782	170.176506	10/01/06

Results

Ecology of wine wētā

From night time mark-recapture observations within an area of 480 m^2 of an Awatere vineyard we calculated there were approximately 1700 ground wētā (Figure 4). This yields an estimated ground wētā density of 3.4 individuals per square metre. In October 2018 the sex ratio of a small randomly harvested sample of night-active individuals was 1:1 (n = 8 males, n = 8 females). However, the majority of these ground wētā were not adults; one or two instars from maturity. At the same time of the year we observed adult females with eggs by digging burrows during the day. In contrast, 12 individuals opportunistically collected from vines after dark in November (2019) comprised 10 adult males and 2 adult females.

Although ground wētā density is high near vines, most of the active wētā we observed at night were on the ground. For example on one night in the vineyard, of 163 wētā observed along vine rows only 6 (3.7%) were on vine plants. However, direct observation confirmed that ground wētā do climb vines and we saw some wētā eating buds, while others were feeding on sap or were moving and not feeding

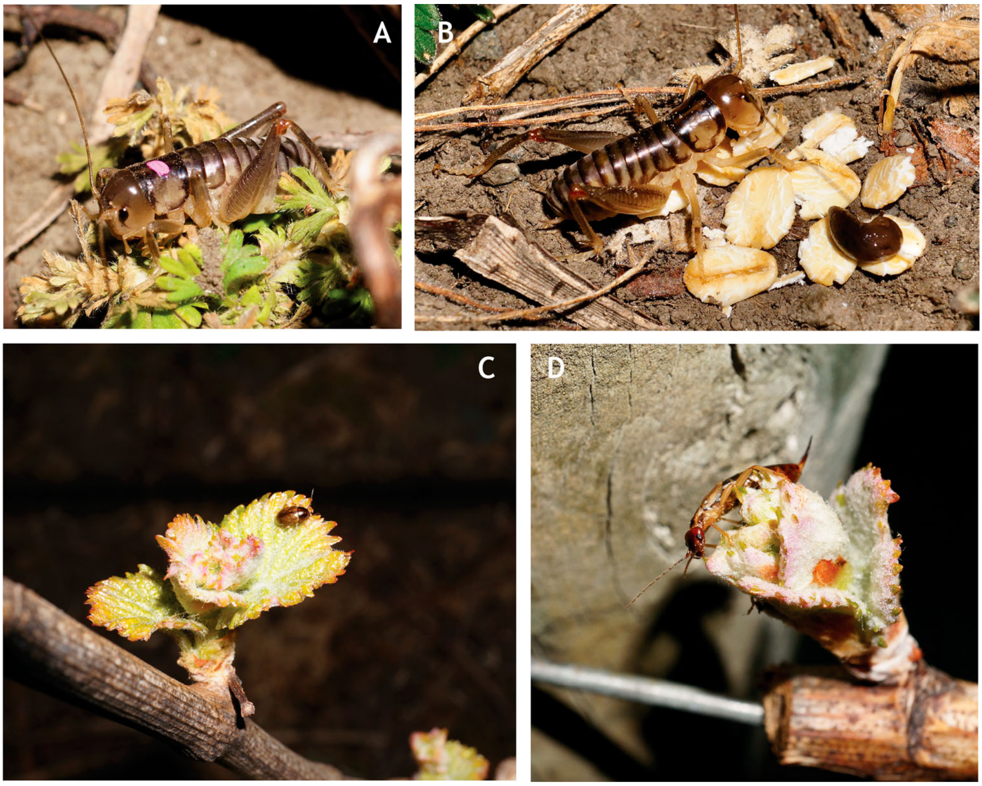


Figure 4. Invertebrate activity on Awatere grape vines at night. **A**, *Hemiandrus bilobatus* ground wētā marked for mark-recapture population density estimate. **B**, *H. bilobatus* (and introduced slug) visiting rolled oats at experimental feeding station. **C**, Native chrysomelid leaf beetle *Eucolaspis brunnea* (Eumolpinae) feeding on vine leaf. **D**, European earwig *Forficula auricularia* feeding on vine leaf.

(Figure 1). We also observed ground wētā at night eating food provided. Only four of 19 experimental replicates had all three food items available when observed at 20:30h, however we directly observed ground wētā eating each of the three food items provided (cat biscuits, oats, apricot; Figure 4). In addition, slugs, earwigs and harvestmen were seen on the food.

We examined the gut contents of seven wētā collected directly from vines (November 2019), and 11 from pitfall traps placed at the ends of vine rows (October–November 2018). Of these 18 gut samples, 12 contained fragments of invertebrate exoskeleton as well as plant material (Figure 5). Of 10 samples with sufficient material that were stained and examined with a compound microscope, five contained trichomes and/or leaf cuticles that were characteristic of vine leaves (*Vitis vinifera*). These and others contained cuticle fragments representing several other plant taxa but we did not attempt to identify these.

At night we observed ground wētā on the trunks, stems and branches of grape vines. We recorded whether the vine on which wētā were observed had a plastic sleeve on its trunk or not. On 5th October 2018 the rows we examined had a ratio of about 12 plants with sleeves to every plant without a sleeve (358:29). We observed 24 ground wētā on these 387 vines, 21 were on plants with sleeves, 3 on plants without sleeves, which did not differ significantly from random occurrence (expected 22.2 and 1.8; Chi-squared = 0.865; $P = 0.352$). On 2nd and 3rd October 2019 we repeated our observations. During the 2019 observations, air temperature was low on both observation nights and frost formed by the following mornings. Despite this, ground wētā were active on the soil and on vines and we saw a total of 128 wētā on vines. Again, we found many wētā climbing over plastic sleeves, but time and grape variety made a significant difference to the number of wētā observed and, possibly, the effect of sleeves. We examined 888 Pinot noir vines and recorded 11.4% of these had a wētā. Pinot noir vines with plastic sleeves were equally likely to have wētā as those without (Figure 6; Chi-squared = 0.820; $P = 0.365$). We looked at 1224 Sauvignon blanc vines and recorded wētā on 2.2% of these. In this case plants with plastic sleeves were statistically less likely to have a wētā than those without. Together the Sauvignon blanc data for 2018 (5th Oct) and 2019 (2nd, 3rd Oct) comprised observation of 1611 vines on which 51 wētā were seen (28 on plants with sleeves, 23 on plants without). Thus, although more than half the wētā observed were climbing up vines with plastic sleeves, there were fewer than expected by chance given the ratio of vines with and without sleeves (expected 40.75 and 10.25; Chi-squared = 19.849; $P < 0.0001$).

Systematics

We found that mtDNA COI sequences supported a clade of New Zealand *Hemiandrus* ground wētā comprising six lineages (Figure 7). The evolutionary relationships inferred for haplotypes from 93 specimens revealed six clusters corresponding to six morphologically differentiated taxa. Two of these lineages correspond to formally named species: *Hemiandrus pallitarsis* (Walker 1871) (=*H. furcifer* Ander 1938) and *H. bilobatus* Ander 1938. Adult female wētā in this group share the characteristic of having an extremely short ovipositor and being equipped with a modified structure on the 6th sternite. In these two species the structure is well developed and is associated with transfer of sperm

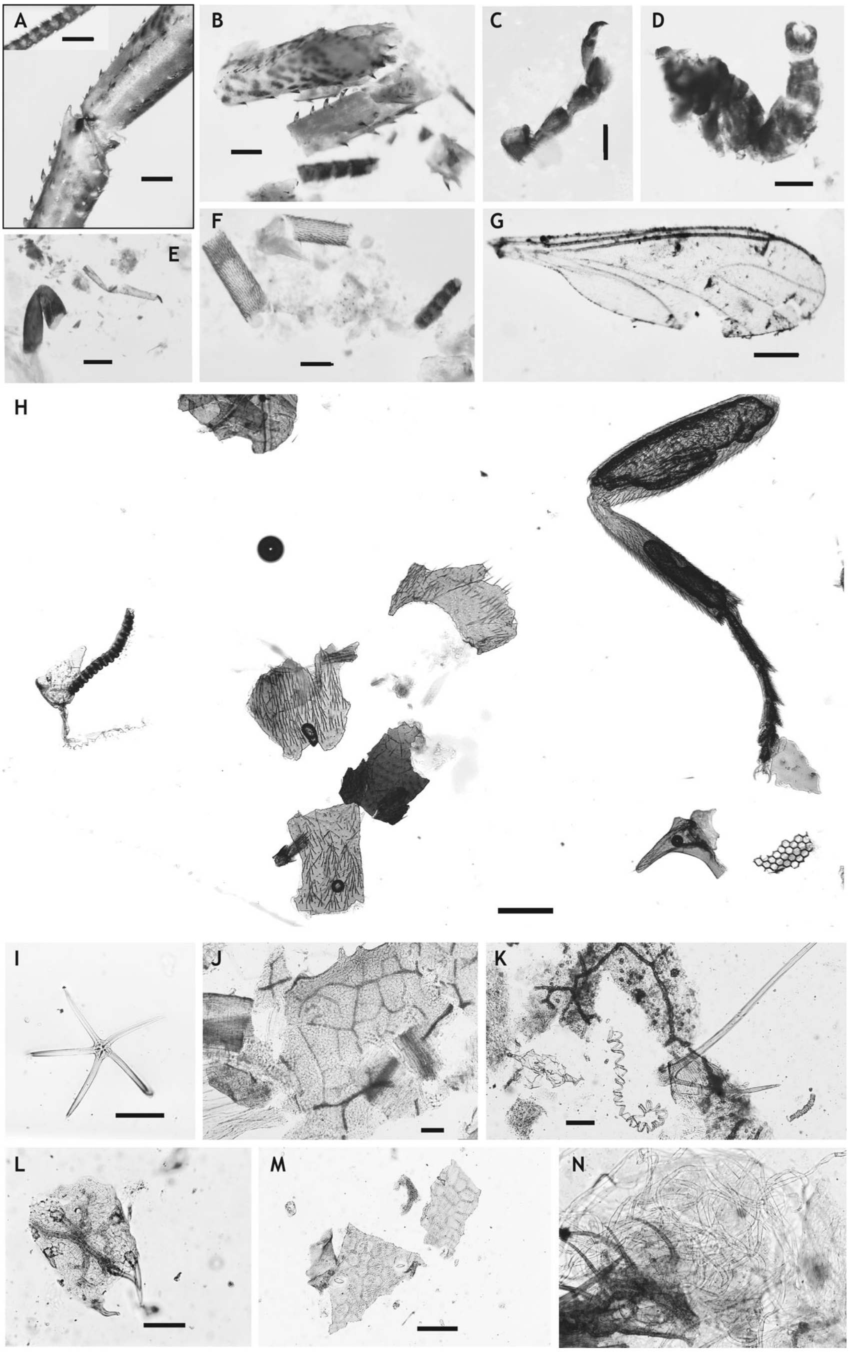


Figure 5. Fragmentary remains of food items consumed by *Hemiandrus bilobatus* collected among Awatere valley grape vines. **A**, Leg and antennal fragments of European harvestman *Phalangium opilio* collected in pitfall trap at Awatere for comparison (Cf. B). **B–H,** Chitinous structures from invertebrate prey including spider (**E–F**) and fly (**G**). Scale bar 100 µm. **I–N,** Plant cuticles and internal structures including sclereids (**I**), stomata (**L–M**), and woolly trichomes typical of vine leaves (**N**).

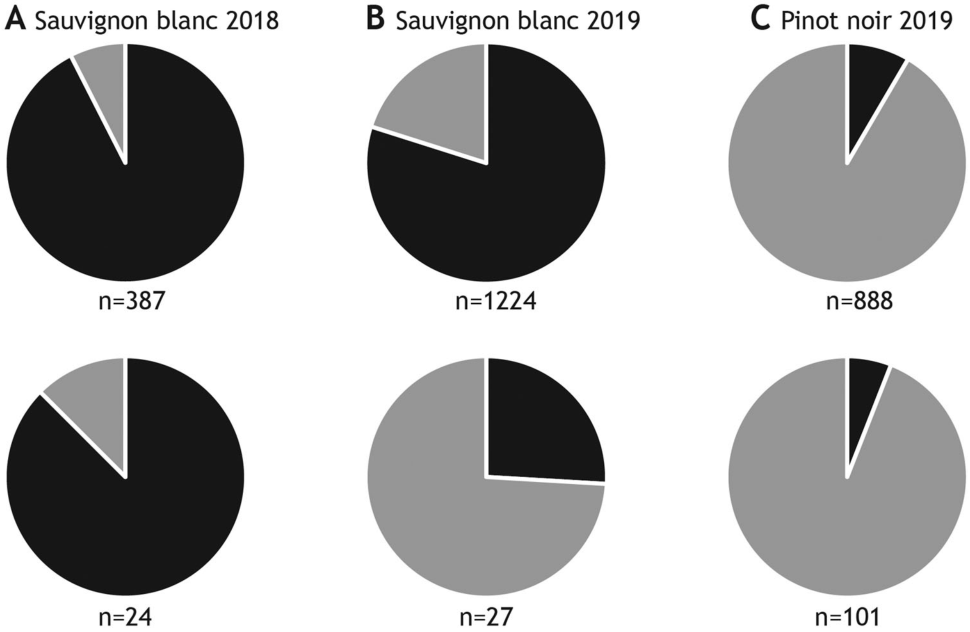


Figure 6. Relative abundance of *Hemiandrus bilobatus* observed at night on grape vines with and without plastic sleeves on trunks during spring bud-burst in an Awatere vineyard. The proportion of vines examined with (black) and without (grey) plastic sleeves is shown for all vines examined (above) and the subset of these that had wētā on them (below). **A,** Sauvignon blanc plants 5/OCT/2018. **B,** Sauvignon blanc plants 2–3/OCT/2019. **C,** Pinot noir 2–3/OCT/2019.

and nuptial gifts during copulation (Gwynne 2002, 2005). The shortness of the ovipositor was the basis for the genus name *Hemiandrus* alluding to the resulting similarity of males and females, which contrasts with females of other Anostostomatidae including other ground wētā that have long curved ovipositors (formerly referred to as *Zealandosandrus;* Salmon 1950). The name Ander (1938) chose for the type species (*furcifer*) referred to the unusual forked structure on the 6th sternite of the females in this species (Figure 8). We found that the prominence of an analogous structure differed among adults of each lineage within this clade and also differs among instars. As is usual with secondary sexual characteristics, the modified 6th sternite of females is only fully developed, and thus diagnostic, in adult specimens. At sexual maturity the valves of the short ovipositor, which are not sclerotised, are largely covered (in ventral view) by the, acuminate to triangular subgenital plate (Figure 8).

Ander (1938) encountered the problem of ontogenetic change of the sternite structure when describing a third species of his new genus, *Hemiandrus similis,* for which the only female examined was a juvenile, as he recognised. Subadult instars of female *H. pallitarsis* are similar in terms of the 6th sternite structure to adult *H. bilobatus* and so could be confused. Unbeknown to Ander (1938), *H. pallitarsis* (*H. furcifer* as he called it) and *H. bilobatus* co-occur in Wellington which is where the material for *H. similis* originated. Ander's (1938) description of *H. similis* emphasises that this putative species was very similar to *H. furcifer* (i.e. *H. pallitarsis*), 'but a little smaller'. Critically, the unique male

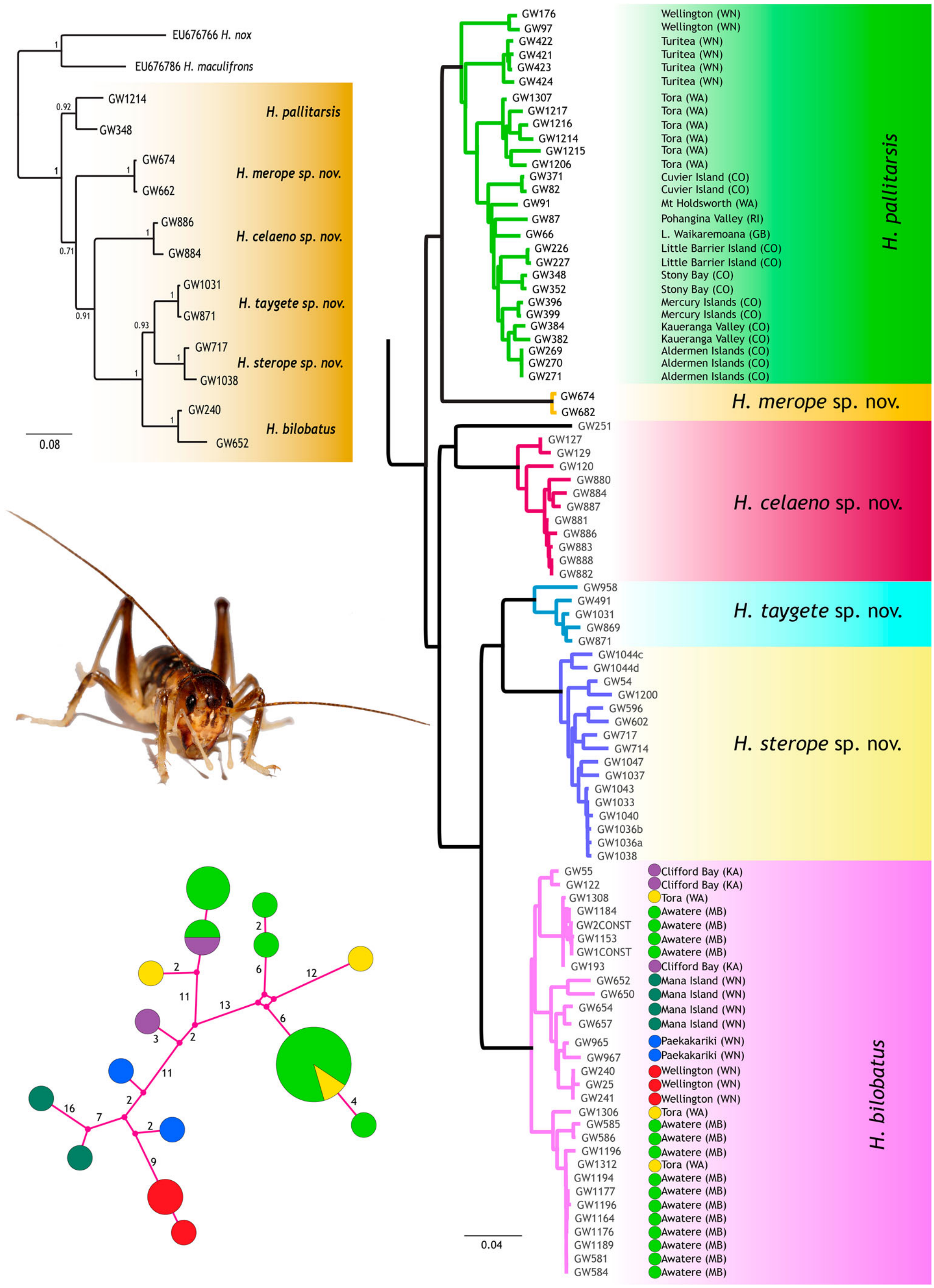


Figure 7. Phylogeny of the short-ovipositor clade of *Hemiandrus* ground wētā based on mitochondrial COI (757bp) DNA sequences, representing two described and four new species. Haplotype analysis of data from multiple individuals using Neighbor-Joining with Tamura-Nei distances is colour coded to show clusters identified as species based on morphology. Collecting locations (with Crosby regions) are included for two widespread species, *H. pallitarsis* and *H. bilobatus*. Upper inset: Bayesian analysis of lineage representatives and outgroup New Zealand *Hemiandrus* using GTR model with posterior probabilities shown. Lower inset: Median joining network of *H. bilobatus* mtDNA haplotypes showing their geographic distribution (colour spots shown on clade in main tree).

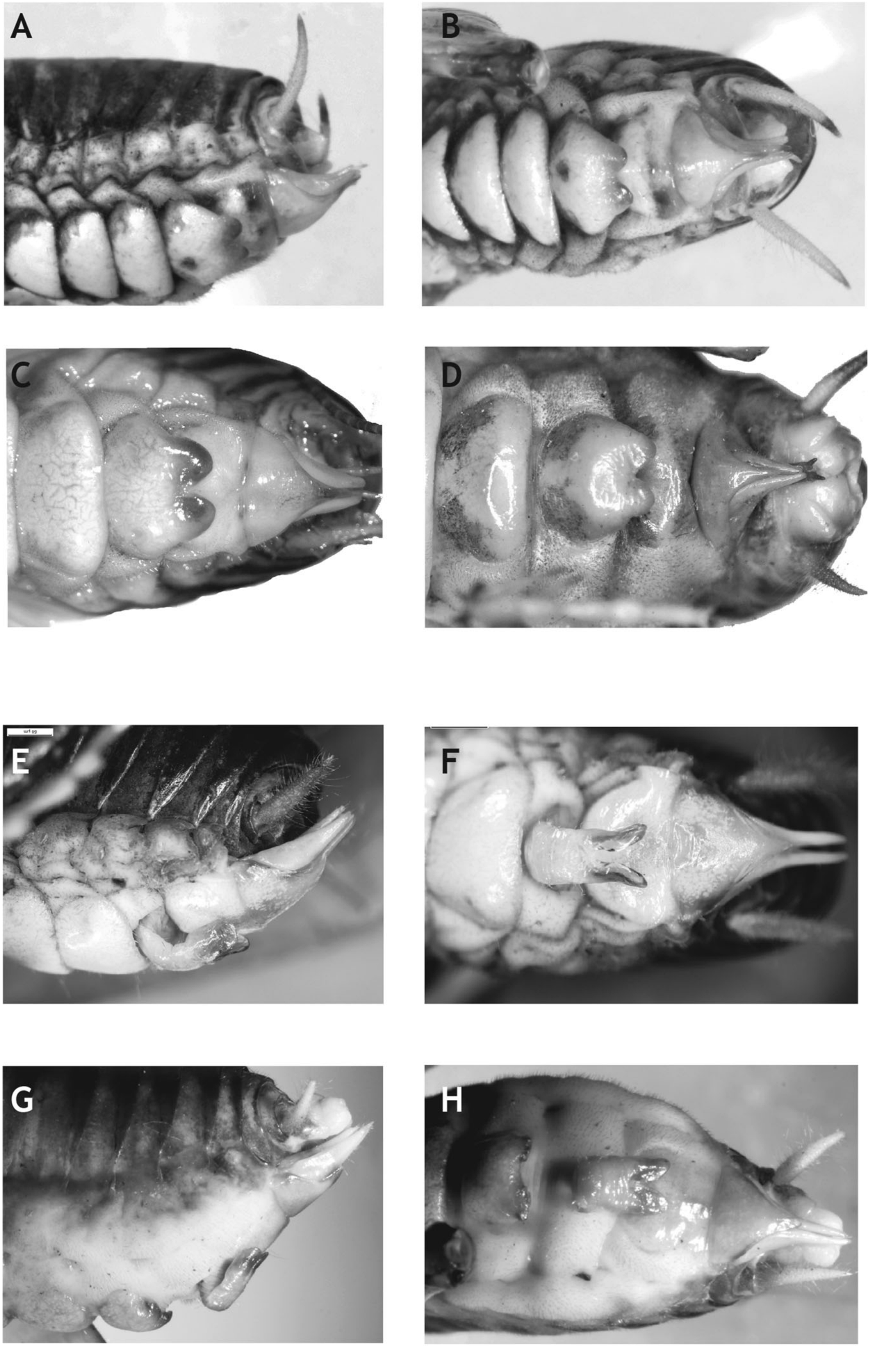


Figure 8. Modification of sternite 6 (S6) in adult females of two described short-ovipositor *Hemiandrus* ground wētā. *Hemiandrus bilobatus*: **A–B,** Awatere (GW1160); **C,** Mana (GW652); **D,** Awatere (GW1225). *Hemiandrus pallitarsis*: **E–F,** Karori Wellington with typical S6 (GW1140); **G–H,** Karori with unusual additional S5 modification (GW1139).

'processes of the 9th tergite [are] as in *furcifer*'. It is clear that *H. similis* is not just similar to *furcifer* but is *furcifer*, simply representing variation within *furcifer* (i.e. *H. pallitarsis*), and rendering *H. similis* nomen nudum.

Taxonomy

Class Insecta
Order Orthoptera
Suborder Ensifera
Superfamily Stenopelmatoidea
Family Anostostomatidae Saussure (1859)
Genus *Hemiandrus* Ander (1938)

Type species: *Hemiandrus furcifer* Ander 1938, = *Hemiandrus pallitarsis* (Walker 1871) (combination proposed by Johns 2001).

The elegant and informative description translated from Ander (1938) makes it clear that the genus name applies to only some of the New Zealand ground wētā, specifically those species considered here. As it stands our genetic data indicates that the genus *Hemiandrus* should be retained for these species potentially resulting in resurrection of *Zealandosandrus* Salmon 1950 for some of the ground wētā with females bearing developed ovipositors.

> Similar to the genus *Onosandrus* Stål in general body shape and leg armament, but the anterior tibia with 1 or 2 dorsal linear spines on the inside, additional to the 2 apical spines. Fastigium at most twice as wide as the 1st segment of the antenna. Prosternum with blunt humps. Side lobes of the mesosternum are acute-angled but bluntly extended, those of the metasternum are approximately right-angled. Unarmed hind (femora). ♂ The 9th tergite is extended at the posterior end; this part bears 2 dorsal, close-fitting finger-like extensions protruding backwards on the dorsal surface. The 10th tergite has 2 brown, rather long, pointed, upward teeth. Paraprocts extended in a gradually thinner process that ends with a sharp tooth. Subgenital plate significantly longer than broad. Styli short, cylindrical. ♀ Tergites without extension. The 6th sternite has a flattened formation, bilobed at the apex, at the posterior margin, or 2 short protuberances orientated backwards. The gonapophyses are present as valves pointed towards the back, but do not form a true ovipositor. Superior valves at the apex with very small styli. Subgenital plate triangular, tapering sharply at the apex. Type species: *Hemiandrus furcifer* n. sp.

Ander's (1938) descriptions of two species within this genus were similarly explicit and clear about the difference between 6th sternite structures of adult females (Figure 8).

Hemiandrus pallitaris

> ♂ Narrow, rounded projection of the 9th tergite to the rear; the finger-shaped attachments do not reach to the edge. Paraproctal processes pressed against each other, their distal part very straight. Subgenital plate as wide as long, the margins weakly S-shaped. The front part is arched, the rear part is about 1/3 narrower and the bottom is excavated in the middle of the trailing edge. ♀ The 6th sternite is missing, there is a significantly narrower, backward formation in its place, divided into two at the tip, hard sclerotized. Subgenital plate is wider than long, extended to the rear in a latex, the edges of the sides weakly S-shaped. (Ander 1938)

In fact the female 6th sternite was not 'missing', but supplemented by a novel process that emerges from its surface and bends abruptly 'backward' where it forms the two sclerotized points described by Ander (1938). On either side of the stem of this structure is a stout curved hair. Similarly, the male 9th tergite is medially convex forming a distinct tongue, but this is supplemented above by a novel structure consisting of a pair of finger-like projections that overlay the sclerotized dorsal surface of the 9th tergite. The 8th tergite is simple with a slight medial bulge in dorsal view.

Distribution: The type locality of Ander 1938 (male and female) is Palmerston North, and the species is recorded throughout North Island New Zealand, as far north as Omaha Bay (https://inaturalist.nz/observations/4792461), and on numerous offshore islands including Tawhiti Rahi/Poor Knights, Hauturu/Little Barrier, Aotea/Great Barrier, Repanga/Cuvier, Atiu/Middle Mercury, and Ruamahuanui (Aldermen Islands) in the Tīakapa Moana/Hauraki Gulf (Chappell et al. 2012).

Material examined: Tora, Martinborough (WA) ♀GW1216,♂GW1307, ♂GW1310, ♂GW1313, ♀GW1206; Bledisloe Park, Massey University (WN) ♂GW794a, ♂GW794b, ♂GW794c, ♂GW794d; Boundary Stream Reserve (HB) ♀GW872a, ♂GW872b, ♂GW872c, ♂GW872d; Coromandel Town (CL) ♂GW517; Newlands, Wellington (WN) ♂GW506, ♂GW512, ♂GW961; Te Mata, Havelock North (HB) ♀GW957; Orongorongo Valley, Wairarapa (WA) ♀GW659; Sledge Track, Kahuterawa Valley (WN) ♀GW891; Atene, Whanganui (WI) ♂GW640; Karamatura farm, Waitakere Ranges (AK) ♀GW889; Karori, Wellington (WN) ♀GW1140, ♂GW1143, ♂GW1138; Seaview Road, New Plymouth (TK) ♂GW855; Turitea Valley, Palmerston North (WN) ♀GW1297, ♂GW1296.

Hemiandrus bilobatus **(which includes the wine wētā)**

'♀ The 6th sternite is just as wide as the 7th, its rear edge is somewhat extended with 2 broadly rounded lobes that do not cover half of the 7 sternite' (Ander 1938). Each lobe bears one or two stout, outward-leaning hairs near the base of the outer margin of each lobe.

Ander 1938 did not have a male for this species and as it is sympatric with *H. pallitarsis* in Wellington, from where the female holotype of *H. bilobatus* came, confusion was likely. However, our field observations of mating pairs in locations of sympatry and allopatry as well as genetic data allow confirmation. Male *H. bilobatus* are very different from male *H. pallitarsis* with respect to the margin of the 8th tergite which is medially concave with a broad, smooth medial U, and the margin forms a distally projecting point on either side of this (Figure 9, Table 2, supplementary). The 9th tergite forms a blunt triangular structure, shorter than in *H. pallitaris*, and having a shallow notch at the tip. In *H. bilobatus* there is no supplementary structure between the 8th and 9th tergites as seen in male *H. pallitarsis*.

Voucher data: Adult female, under vines at Cable Bay wines, Redwood Pass Road, Awatere River valley, Marlborough, New Zealand (Lat. −41.615282, Long. 174.12931) by Mary Morgan-Richards, 20 August 2019 (NMNZ AI.041976; previously GW1191). Adult male, on vine at Cable Bay wines, Redwood Pass Road, Awatere River valley, Marlborough, New Zealand (Lat. −41.615282, Long. 174.12931) by Steve Trewick, 2 October 2019 (NMNZ AI.041977; previously GW1184).

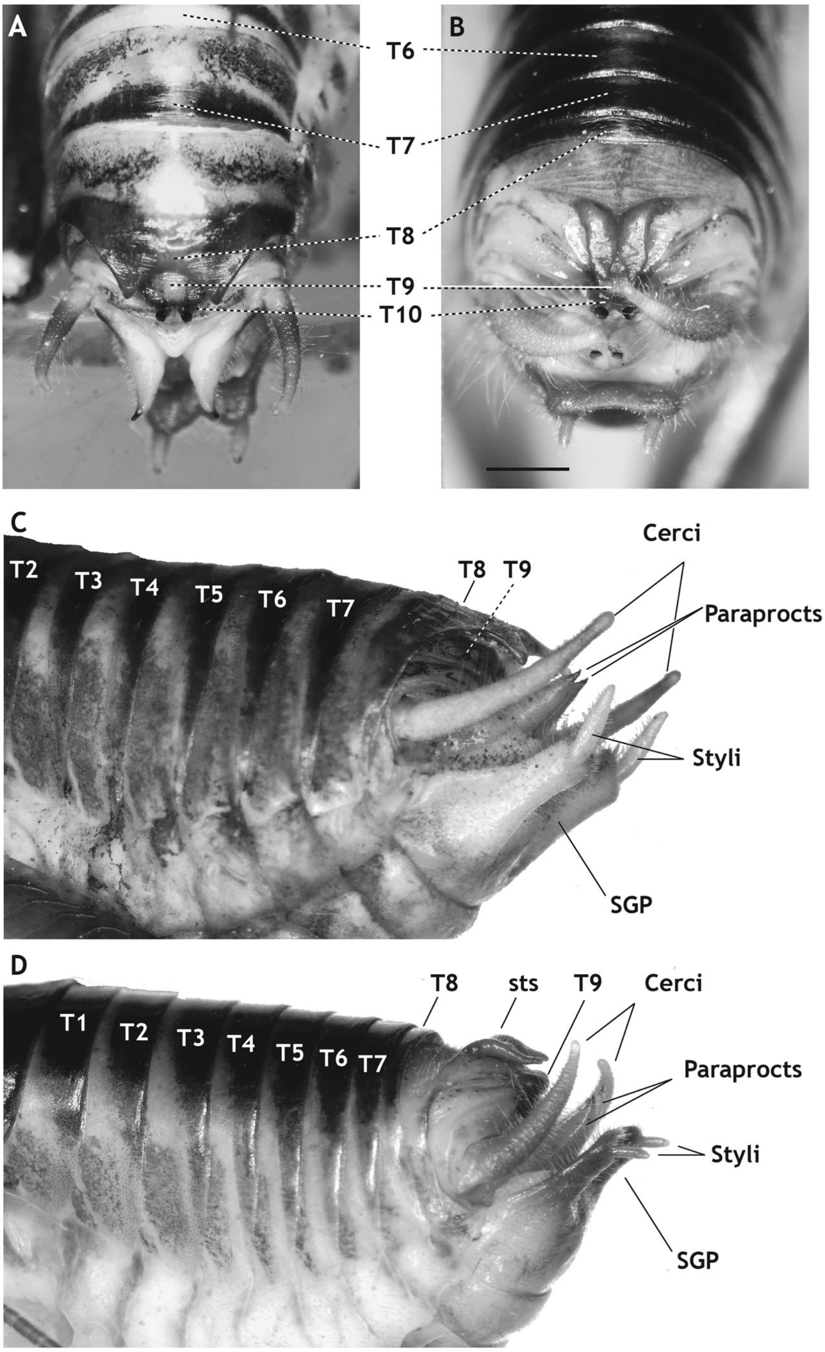
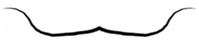
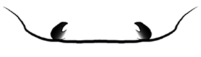
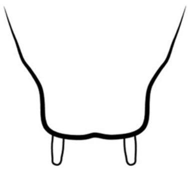
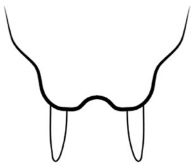
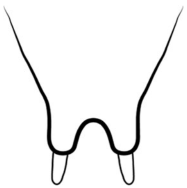
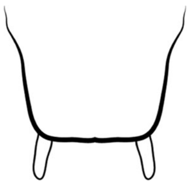
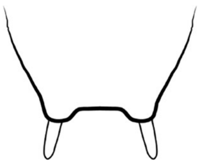
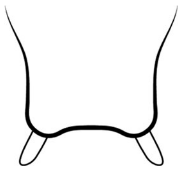
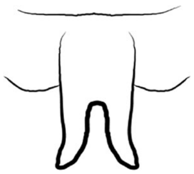
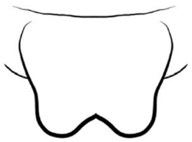
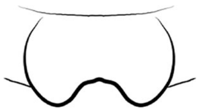
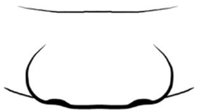


Figure 9. Male terminalia of adult *Hemiandrus bilobatus* and *H. pallitarsis* showing tergite numbers and structures. Posterior view: **A,** *H. bilobatus* Awatere (GW1229); **B,** *H. pallitarsis* Tora (GW1307). Lateral view: **C,** *H. bilobatus* Tora (GW1306); **D,** *H. pallitarsis* Tora (GW1307). T – tergite number starting behind the metanotum, SGP – subgenital plate, sts – supplementary tergite structure.

Table 2. Diagnostic morphological characteristics for six species of short-ovipositor *Heminadrus* ground wētā, with the margins of abdominal tergites (T) of males and modification of sternites (S) of females illustrated.

			H. pallitarsis	*H. bilobatus*	*H. taygete* sp. nov.	*H. celaeno* sp. nov.	*H. sterope* sp. nov.	*H. merope* sp. nov.
Linear leg spines	Superior prolateral angle of fore tibia		1	2	1	1	1	1
	Superior prolateral angle of mid tibia	excluding apical spines	2	1 (2*)	1	2	1	1
	Superior retrolateral angle of mid tibiae		3	3	3	2	3	3
Male	T8							
	T9	dorsal view, posterior margins						
	T10 & falci							
	Subgenital plate	ventral view, posterior margin						
Female	Modification of S6 (margins of S5 and S7 shown)	ventral view, posterior margin						

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* Mana island specimens.

Distribution: The type locality is Wellington. Morphological and genetic data show that the same species also occurs in Martinborough and across Cook Strait in Marlborough and Marlborough Sounds. This species is broadly sympatric with *H. pallitarsis* in Wellington, but only *H. bilobatus* is reported on Mana Island, while Matiu-Somes island in Wellington harbour has a population of *H. pallitarsis*.

Material examined: Tora, Martinborough (WA) ♀GW1308, ♀GW1313, ♂GW1306; Lower Awatere Valley (MB) ♀GW581, ♀GW584, GW585, ♀GW586; Redwood Pass Road, Awatere Valley (MB) ♂GW1157,♀GW1159, ♀GW1160, ♂GW1165, ♂GW1167, GW1172, ♀GW1191, ♀GW1217, ♀GW1219, ♀GW1225, ♂GW1229; Tinakori, Wellington (WN) ♀GW242, GW240, GW241; Mana Island (WN) ♂GW648, ♀GW658, ♀GW652, ♂GW657, ♂GW654; Marfell's Beach, Clifford Bay (KA) GW055, ♂GW122; Muritai Reserve, Clifford Bay (KA) ♀GW194, GW193; Newtown, Wellington (WN) ♂GW025; Paekakariki (WN) GW965, GW966, GW967, GW968; Raphiti Road, Pukerua Bay (WN)♀GW098; Takapu Valley, Porirua (WN) ♂GW179, ♂GW181.

Comments: MtDNA haplotype diversity within the *H. bilobatus* clade had a mean of 0.03 K2P (Kimura 2 parameter), and differed from the next clade by 0.09. Haplotypes within *H. bilobatus* were shared by individuals on both sides of Cook Strait (Figure 7).

The tag-named entity *H.* 'promontorius' proposed from specimens collected at Cape Campbell (Johns 2001) and subsequently collected more widely in the vicinity (Figure 2) has the same morphological characteristics as *H. bilobatus* (Ander 1938) and is thus clearly conspecific.

New species

The following proposed species represent lineages of New Zealand ground wētā in a monophyletic mtDNA clade that includes the described species *H. pallitarsis* and *H. bilobatus*. In accordance with the genus description (Ander 1938) the females share the characteristic of having the valves of the genital opening aligned and they 'do not form a true ovipositor' (Ander 1938). Adult females of all six species in this clade also have a modified 6th sternite although in one this is only barely apparent (Figure 10). The new species are named for their females as daughters of Pleione (and Atlantis).

Hemiandrus taygete sp. nov.

Etymology: The golden horns of the doe, into which the Pleiad Taygete was transformed by Artemis, resemble the sternite lobes of females in this species.

Diagnosis: A small to medium-sized ground wētā found on the east coast of the South Island, New Zealand, with hairs absent from the 3rd apical segment of the maxillary palps and the 4th segment only partially clothed in fine hairs; the superior prolateral angle of the fore tibiae with one articulated spine positioned medially and an apical spine; the superior prolateral angle of the mid tibiae with one spine positioned medially and an apical spine; the superior retrolateral angle of the mid tibiae usually with three spines distributed along the leg and an apical spine; females with a very short ovipositor and the sixth abdominal sternite with two sclerotized lobes extending distally over much of the seventh abdominal sternite; male subgenital plate with U-shaped posterior margin.

Description: Size. Adult male (n = 3): PL 3.7–4.0 mm; PW 4.1–4.4 mm; FL 9.3–9.9 mm; FW 2.8–3.0 mm; HL 6.3–6.8 mm; HW 4.2–4.5 mm; full BL 15.3–16.3 mm; partial

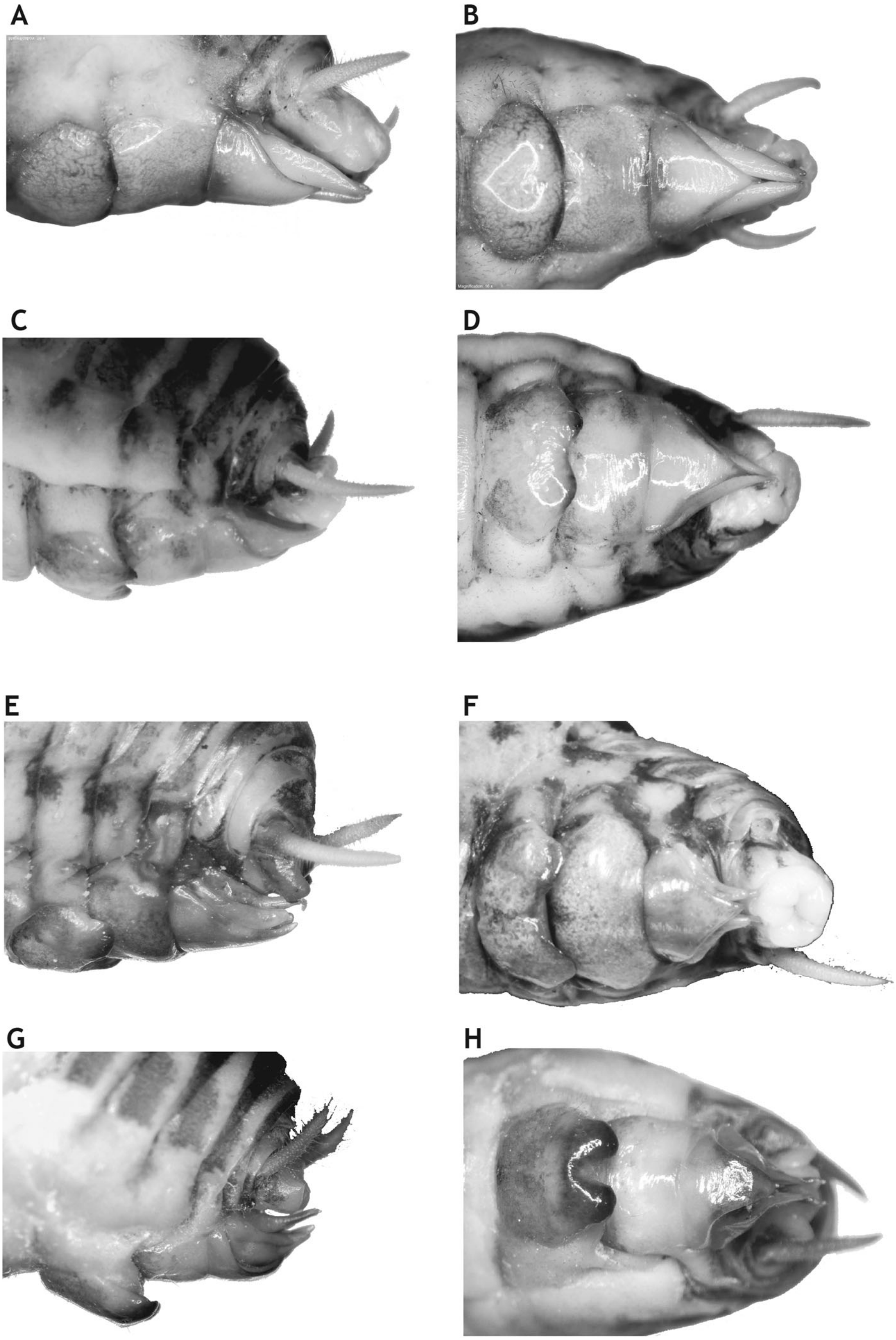

Figure 10. Modification of sternite 6 in adult females of four new species of short-ovipositor *Hemiandrus* ground wētā. Posterior portion of abdomen in lateral (left) and ventral (right) view. **A–B,** *Hemiandrus merope* sp. nov., Kapiti Island (GW849); **C–D,** *H. sterope* sp. nov., Manaroa, Marlborough Sounds (GW714); **E–F,** *H. celaeno* sp. nov., Wainui, Banks Peninsula (GW882, GW880); **G–H,** *H. taygete* sp. nov., Upper Clarence valley (GW869).

BL 8.7–10.3 mm; SG 2.5–2.8 mm; SG/PL 0.7; FL/HW 2.1–2.2. Adult female (n = 3): PL 4.2–4.7 mm; PW 4.6–5.3 mm; FL 9.4–11.3 mm; FW 2.9–3.4 mm; HL 7.0–7.9 mm; HW 4.7–5.7 mm; full BL 13.6–19.7 mm; partial BL 8.3–11.1 mm; FL/HW 2.0–2.1.

Head. Antennal flagella proximally smooth (7–12 antennomeres); maxillary palps with widely spaced setae and with short fine microsetae partially covering the 4th apical segment and the entire 5th segment.

Thorax. Pronotum slightly wider than long, with large lateral pale patches and the dorsal midline with a yellow stripe.

Legs. Short (hind femora 2.0–2.2 times head width). The superior prolateral angle of the fore tibiae with a medial articulated spine and one apical one. The superior prolateral angle of the mid tibiae with a medial articulated spine and one apical spine. The superior retrolateral angle of the mid tibiae with three (rarely four) articulated spines distributed along the leg and one apical spine (Figure 11). Hind tibiae with six to eight fixed spines along the superior prolateral angle, seven to nine fixed spines along the superior retrolateral angle, two to five small articulated spines on the ventral side. The inner side of the hind femora with 45–95 min pegs.

Males. Ninth abdominal tergite (T9) with a median lobe with two dark, sclerotized patches on the apical margin and two more adjacent patches anterior of this; T10 with two widely spaced dark hooks; subgenital plate approximately 70% of pronotum length (mean 2.66 mm), smooth, narrowing distally with deep U-shaped posterior margin (Figure 9); styli short; conical paraprocts with sclerotized tips; cerci very long (Supplementary).

Females. Very short ovipositor; 6th abdominal sternite with two slightly elongated lobes with rounded sclerotized edges, protruding ventrally, and projecting part way across S7 positioned towards the midline (space between lobes is less than the width of each lobe where they cross S7) (Figure 10; Supplementary).

Type data: Holotype: adult female at Goose Flat hut, Waiau Toa/ Clarence River valley, Marlborough, New Zealand (Lat. −42.151346, Long. 173.551111), 29 January 2009 by Jan Clayton-Greene (NMNZ AI.041945; previously MPN GW491). Paratype: adult male in beech forest near Mitchells Cutting, Upper Clarence Valley, Canterbury (Lat. −42.448288, Long. 172.918968) 2 February 2012, by Troy Watson (NMNZ AI.041946; previously MPN GW867).

Distribution: MB, KA, NN. Found on the east coast of the South Island, New Zealand from Renwick and Mt Richmond Forest Park south to Hanmer Range (Figure 2).

Material examined: Upper Clarence Valley (MB) ♀GW869, ♂GW867, ♂GW871a, ♂GW871b; Red Hills, Mt Richmond Forest Park (NN) ♀GW1031; Goose Flat, Clarence Valley (KA) GW491; Renwick (MB) GW958; Cape Campbell (MB) GW186.

Comments: MtDNA haplotype diversity within the *H. taygete* sp. nov. clade had a mean of 0.02 (K2P), and differed from the next clade by 0.10.

Hemiandrus taygete sp. nov. is probably the same entity represented by the tag-name *Hemiandrus* 'onokis' (Johns 2001), referred to in discussion of *Hemiandrus* reproductive behaviour (Gwynne 2004, 2005).

Hemiandrus sterope sp. nov.

Etymology: Sterope (lightning), one of the Pleiades sisters. The males of this species produce the most rapid premating drumming of all species of this genus studied (Gwynne 2004).

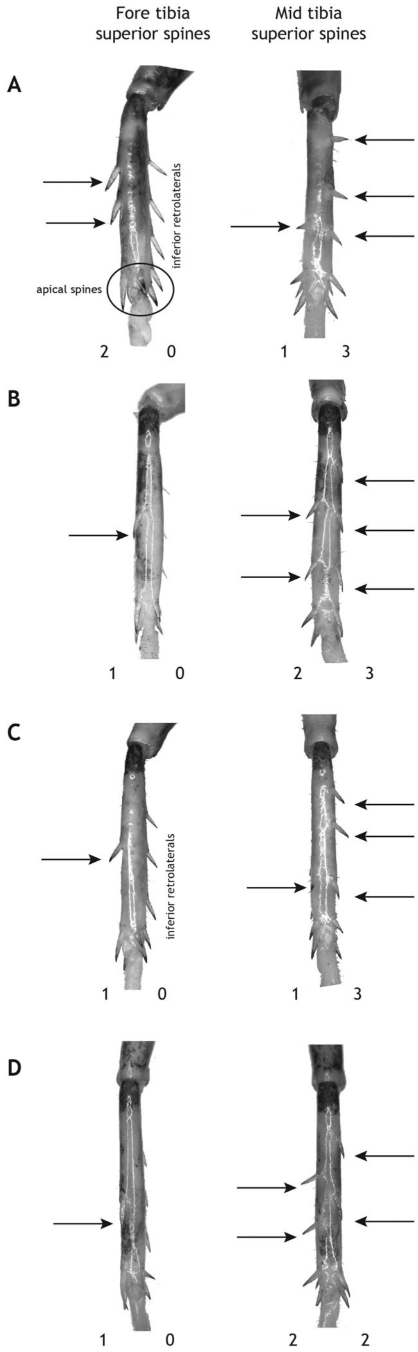

Figure 11. Spines on superior prolateral and retrolateral angles of fore and mid tibiae of representative *Hemiandrus* ground wētā in the short-ovipositor clade. Number configurations are as in Table 2. **A,** *H. bilobatus*, Awatere (GW1159); **B,** *H. pallitarsis*, Tora (GW1310); **C,** *H. sterope* sp. nov., Atawhai, Nelson (GW1051); **D,** *H. celaeno* sp. nov., Upper Clarence valley (GW880).

Diagnosis: A medium-sized ground wētā found in north-eastern South Island, New Zealand, with hairs absent from the 3rd apical segment of the maxillary palps and the 4th segment only partially clothed in fine hair; the superior prolateral angle of the fore tibiae with one medial articulated spine and one apical spine; the superior prolateral angle of the mid tibiae with one medial spine and one apical spine; the superior retrolateral angle of the mid tibiae usually with three articulated spines distributed along the leg and an apical spine; females with a very short ovipositor and the sixth abdominal sternite with two sclerotized lobes projecting slightly over the seventh abdominal sternite.

Description: Size. Adult male (n = 10): PL 4.0–5.2 mm; PW 4.5–7.9 mm; FL 10.2–12.7 mm; FW 3.1–3.8 mm; HL 6.2–7.7 mm; HW 4.2–5.5 mm; full BL 16.1–19.5 mm; partial BL 8.6–11.9 mm; SG 2.1–2.6 mm; SG/PL 0.5–0.6; FL/HW 2.3–2.4. Adult female (n = 17): PL 4.4–5.6 mm; PW 5.1–6.3 mm; FL 11.2–13.8 mm; FW 3.5–4.4 mm; HL 7.1–8.9 mm; HW 5.0–6.3 mm; full BL 17.2–25.1 mm; partial BL 10.2–12.6 mm; FL/HW 2.2–2.3.

Head. Antennal flagella proximally smooth (7–13 antennomeres); maxillary palps with widely spaced setae and with short fine microsetae partially covering the 4th apical segment and the entire 5th segment.

Thorax. Pronotum slightly wider than long, with large lateral pale patches and the dorsal midline with a yellow stripe (Supplementary).

Legs. Short (hind femora 2.2–2.4 times head width). The superior prolateral angle of the fore tibiae with one (rarely two) medial and one apical articulated spines. The superior prolateral angle of the mid tibiae with two one medial and one apical articulated spines. The superior retrolateral angle of the mid tibiae with three (rarely two) articulated spines distributed along the leg one apical spine (Figure 11). Hind tibiae with seven to nine fixed spines along the superior prolateral angle, eight or nine fixed spines along the superior retrolateral angle, one to three small articulated spines on the ventral side. The inner side of the hind femora with 55–110 min pegs.

Males. Eighth abdominal tergite (T8) bilobed; T9 lobed with two dark sclerotized patches on the posterior margin and two more adjacent patches more anteriorly positioned; T10 with two widely spaced dark hooks; subgenital plate 50%–60% of pronotum length (mean 2.33 mm), with shallow indentation on distal margin between styli; styli medium-length; conical paraprocts with sclerotized tips; cerci medium-length.

Females. Very short ovipositor; 6th sternite with two sclerotized lobes extending distally slightly over S7 (Figure 10).

Type data: Holotype: adult female under native scrub near Manaroa, Kenepuru Sound, Marlborough, New Zealand (Lat. −41.129732, Long. 174.04335), 14 January 2001 by Steve Trewick (NMNZ AI.041947; previously MPN GW712). Paratype: adult male under scrub Branford Park, Matai Valley Road, Nelson, New Zealand (Lat. −41.272194, Long. 173.302975), 24 February 2014 by Noel Smith (NMNZ AI.041948; previously MPN GW1034).

Distribution: NN, SD, MB. Found in north-east South Island, New Zealand (Figure 2).

Material examined: Wakapuaka Cemetary, Atawhai (NN) ♀GW1038, ♂GW1039, ♂GW1040, ♂GW1041; Te Rua Bay (SD) GW596, GW597, GW598, GW599, GW600, GW601, ♀GW602, GW603, GW604, GW605, ♀GW606, ♀GW607; Maitai Valley (NN) ♀GW1037; Manaroa (SD) GW712, ♀GW713, ♀GW714, ♀GW715, ♀GW716, ♀GW717; Cable Bay (NN) DOCORD056445; Cable Bay track (NN) ♀GW1045, ♀GW1046, ♂GW1047; Branford Reserve, Nelson (NN) ♀GW1032, ♂GW1033, ♂GW1034,

♂GW1035; Marybank Reserve, Nelson (NN) ♀GW1044A, ♂GW1044B; Maud Island (SD) ♀GW458, ♂GW459; Dodson's Valley (NN) GW1042, GW1043; Whites Bay (SD) GW054; Esson Valley (NN) DOCORD047771; Opouri (SD) DOCORD047957; Pelorus Bridge (MB) GW853.

Comments: MtDNA haplotype diversity within the *H. sterope* sp. nov. clade had a mean of 0.03 (K2P), and differed from the next clade by 0.10.

Hemiandrus sterope sp. nov. is probably the same entity represented by the tag-name *Hemiandrus* 'vicinus' (Johns 2001) and 'vicinius' [*sic*] referred to in discussion of *Hemiandrus* reproductive behaviour (Gwynne 2004, 2005).

Hemiandrus merope sp. nov.

Etymology: Merope, faintest of the Pleiades (sometimes referred to as the 'lost Pleiad' because she was at first not seen by astronomers or charted like her sister stars). The female of this species has the faintest (missing) structures on her sixth sternite.

Diagnosis: A medium-sized ground wētā found on Kapiti Island, New Zealand, with hairs absent from the 3rd apical segment of the maxillary palps and the 4th segment only partially clothed in fine hairs; the superior prolateral angle of the fore tibiae with one articulated spine positioned medially an apical spine; the superior prolateral angle of the mid tibiae with one spine positioned medially and an apical spine; the superior retrolateral angle of the mid tibiae usually with three articulated spines distributed along the leg and an apical spine; females with a very short ovipositor and a pair of sclerotised cusps on the posterior margin of the sixth abdominal sternite.

Description. Size. Adult male (n = 8) (Figure 1): PL 4.3–4.9 mm; PW 4.6–5.3 mm; FL 11.4–12.8 mm; FW 3.4–3.8 mm; HL 6.3–6.9 mm; HW 4.1–4.6 mm; full BL 16.3–20.5 mm; partial BL 9.5–10.7 mm; SG 1.7–1.9 mm; SG/PL 0.4; FL/HW 2.7–2.8. Adult female (n = 1): PL 5.4 mm; PW 6.3 mm; FL 13.9 mm; FW 4.2 mm; HL 8.4 mm; HW 5.7 mm; partial BL 12.4 mm; FL/HW 2.5.

Head. Antennal flagella proximally smooth (9–17 antennomeres); maxillary palps with widely spaced setae and with short fine microsetae partially covering the 4th apical segment and the entire 5th segment.

Thorax. Pronotum slightly wider than long, with large lateral pale patches and the dorsal midline with a yellow stripe.

Legs. Short (hind femora 2.5–2.8 times head width). The superior prolateral angle of the fore tibiae with one (rarely two) medial articulated spines and one apical spine. The superior prolateral angle of the mid tibiae with one medial articulated spine and one apical spine (Figure 11). The superior retrolateral angle of the mid tibiae with three (rarely four) articulated spines distributed along the leg and one apical spine. Hind tibiae with seven or eight fixed spines along the superior prolateral angle, eight or nine fixed spines along the superior retrolateral angle, one to four small articulated spines on the ventral side. The inner side of the hind femora with 65–120 min pegs.

Males. T9 lobed with two dark sclerotized patches on the apical margin and two more adjacent patches more anteriorly positioned; T10 with two widely spaced dark hooks; subgenital plate approximately 40% of pronotum length (mean 1.81 mm), with a slightly concave posterior margin; styli medium-length; conical paraprocts with sclerotized tips; cerci medium-length.

Females. Very short ovipositor; 6th abdominal sternite with two scelortised cusps on the posterior margin (Figure 10).

Type data. Holotype: adult female in regenerating forest Rangatira loop Track, Kapiti island, Wellington, New Zealand (Lat. −40.852514, Long. 174.930925), 14 November 2011 by Briar Taylor-Smith (NMNZ AI.041949; previously MPN GW849). Paratype: adult male in regenerating forest Rangatira loop track, Kapiti island, Wellington, New Zealand (Lat. −40.852514, Long. 174.930925), 31 March 2011 by Steve Trewick (NMNZ AI.041950; previously MPN GW846).

Distribution: WN. Recorded only on Kapiti Island, New Zealand.

Material examined: Kapiti Island (WN) ♀GW671, ♂GW672, GW673, ♀GW674, ♀GW675, ♀GW676, ♀GW677, ♀GW678, GW679, ♂GW680, ♂GW681, ♂GW682, ♂GW683, ♀GW684, ♂GW685, GW843, ♂GW844, ♂GW845, ♂GW846, ♂GW847, ♂GW848, ♀GW849, ♂GW850, ♂GW851, ♂GW852, ♂GW854, ♀GW1102, ♂GW1103, ♀GW1104, ♀GW1105.

Comments: This species is probably the same entity represented by the tag-name *Hemiandrus* ‘kapiti’ (Johns 2001). Although female *Hemiandrus* on Kapiti island were recorded by Johns (2001) as having long ovipositors, repeated intensive searching on several separate occasions has failed to reveal any long-ovipositor *Hemiandrus* on Kapiti Island; all had very short ovipositors but otherwise match *H.* ‘kapiti’ in fore and mid tibial spine number.

Hemiandrus celaeno sp. nov.

Etymology. Celaeno, the dark one of the Pleiades sisters.

Diagnosis: A small to medium-sized ground wētā on the east coast of the South Island, New Zealand, with hairs absent from the 3rd apical segment of the maxillary palps and the 4th segment only partially covered; dorsal midline of pronotum lacking a yellow stripe; the superior prolateral angle of the fore tibiae with one medial spine and an apical spine; the superior prolateral angle of the mid tibiae usually with two spines distributed along the leg and an apical spine; the superior retrolateral angle of the mid tibiae usually with two spaced along the leg and an apical spine; males with very long cerci; females with a very short ovipositor and a bilobed 6th abdominal sternite.

Description.

Size. Adult male (n = 9): PL 3.5–4.6 mm; PW 4.1–5.3 mm; FL 9.5–12.1 mm; FW 2.5–3.6 mm; HL 5.9–7.6 mm; HW 3.9–5.1 mm; full BL 14.9–19.0 mm; partial BL 6.7–11.4 mm; SG 1.7–2.3 mm; SG/PL 0.4-0.6; FL/HW 2.1–2.6. Adult female (n = 7): PL 4.2–5.1 mm; PW 4.6–5.9 mm; FL 10.5–12.5 mm; FW 2.9–3.7 mm; HL 7.0–8.2 mm; HW 4.6–5.6 mm; full BL 19.6–20.7 mm; partial BL 9.4–11.0 mm; FL/HW 2.2–2.4.

Head. Antennal flagella proximally smooth (8–13 antennomeres); maxillary palps with widely spaced setae and with short fine microsetae partially covering the 4th apical segment and the entire 5th segment.

Thorax. Pronotum slightly wider than long, with large lateral pale patches and dorsal midline lacking a yellow stripe.

Legs. Short (hind femora 2.1–2.6 times head width). The superior prolateral angle of the fore tibiae with one medial articulated spine and one apical spine. The superior prolateral angle of the mid tibiae with two (rarely one) three articulated spines spaced along the leg and one apical spine (Figure 11). The superior retrolateral angle of the mid tibiae usually with two articulated spines spaced along the leg and one apical spine. Hind tibiae with five to nine fixed spines along the superior prolateral angle, seven to nine fixed spines along the superior retrolateral angle, zero to five small articulated spines on the ventral side. The inner side of the hind femora with 55–110 min pegs.

Males. T9 lobed with two dark sclerotized patches on the apical margin and two more adjacent patches more anteriorly positioned; T10 with two widely spaced dark hooks; subgenital plate approximately 40%–60% of pronotum length (mean 1.78 mm), smooth with a flat posterior margin; styli short; conical paraprocts with sclerotized tips; cerci very long.

Females. Very short ovipositor; 6th abdominal sternite with two widely spaced, barely protruding (ventrally), rounded lobes with sclerotized margins projecting over S7 (distance between lobes is greater than the width of each lobe where they cross S7)(Figure 10). A stout, inward slanted hair at the base of each lobe on each side of the gap between them.

Type data. Holotype: adult female at YMCA Wainui Park Camp, Wainui Valley Road, Banks Peninsula, Canterbury, New Zealand (Lat. −43.813101, Long. 172.893391), 30 November 2012 by Mary Morgan-Richards (NMNZ AI.041951; previously MPN GW884). Paratype: adult male YMCA Wainui Park Camp, Wainui Valley Road, Banks Peninsula, Canterbury, New Zealand (Lat. −43.813101, Long. 172.893391), 30 November 2012 by Briar Taylor-Smith (NMNZ AI.041952; previously MPN GW888).

Distribution: KA, MC, NC. Found on the east coast of the South Island, New Zealand from Kaikoura south to Banks Peninsula, and west to Porters Pass (Figure 2).

Material examined: Kaikoura (KA) ♀GW251, ♀GW252, GW253, GW254, ♀GW470A; YMCA Wainui, Banks Peninsula (MC) ♀GW879, ♀GW880, ♀GW882, ♀GW884, ♀GW887, GW878, ♂GW888; Akaroa (MC) ♂GW523, ♂GW524; Foggy Peak Stream, Porters Pass (MC) ♂GW127, ♂GW129; Omihi, Pegasus Bay (NC) DOCORD069320; Kennedy's Bush scenic reserve, Governors Bay (MC) ♂GW120; Limestone creek, (KA) DOCORD069744, DOCORD053418.

Comments: MtDNA haplotype diversity within the *H. celeano* sp. nov. clade had a relatively high mean of 0.07 (K2P) with inclusion of a well diverged haplotype (GW251) from specimens near Kaikoura (Kowhai bush, Kowhai river), 0.02 K2P without Kaikoura haplotype. Specimens from Kaikoura (GW251–GW255) could not be distinguished morphologically from others in the clade (Figure 7) and mean distance to next clade was higher (0.15 K2P).

Hemiandrus celeano sp. nov. may be the same entity represented by the tag-name *Hemiandrus* 'horomaka', but it differs in the number of spines on the superior prolateral angle of the mid tibiae reported by Johns (2001). Judging by comparison of photographs showing pronotum and female sternite appendage, and spatial distribution, *Hemiandrus* sp. reported feeding on plantation apricots in Horotane, Christchurch (Wahid 1978) was very probably this species. Referred to as *Hemiandrus* 'horomaka' and *Hemiandrus* 'peninsularis' in Gwynne (2004, 2005).

Discussion

Diversity

Ground wētā found amongst grape vines in the lower Awatere Valley in Marlborough, New Zealand belong to the species *Hemiandrus bilobatus* described by Ander 1938 and formerly thought to occur only in the southern tip of North Island, New Zealand (Johns 2001).

Heminadrus bilobatus belongs to a clade (Figure 7) of endemic ground wētā distinguished by the adult females lacking ovipositors, and thus appearing superficially similar to males. Ander's (1938) genus is particularly apt for this set of species. Adult females of most of the species in this group also bear distinctive secondary sexual structures on the 6th abdominal sternite associated with sperm transfer during mating (Gwynne 2004). The two original species placed in *Hemiandrus* are now supplemented by four new species that share morphological and genetic characters that could be considered diagnostic for the clade and hence genus name as originally established (Ander 1938). Each of the six species appear to have predominantly separate geographic distributions although there is some sympatry with long ovipositor *Hemiandrus* species. In particular, across much of its North Island range *H. pallitaris* co-occurs with *H. luna* and/or *H. brucei* (Taylor-Smith et al. 2016).

This group of six ground wētā species with reduced ovipositors are a monophyletic lineage with shared physical and behavioural reproductive traits. Females lay eggs within their own burrow and remain with them, in a departure from the predominant habit among Anostostomatidae and other Ensifera of disregarding eggs injected singularly into soil or plants (Gwynne 1995, 2004). Adult females with broods have been observed in *H. bilobatus* (North Island and South Island 'promontorius' populations), *H. sterope* sp. nov., *H. celaeno* sp. nov., and *H. taygete* sp. nov. (Gwynne 2004; with the tag names 'vicinius' [*sic*], 'horomaka' and 'onokis') and *H. merope* sp. nov. (Pers. Comm. Darryl Gwynne). The behaviour displayed by these species appears to have independently evolved in another *Hemiandrus* lineage (Taylor Smith et al. 2013) and also in some other Ensifera (Alexander and Otte 2009) including the aptly named short-tailed gryllid crickets *Anurogryllus* (Walker 1973). The clade represents an informative system in which to examine the adaptive links between maternal care, sexual selection, male provisioning and expression of secondary sexual characters.

The six species in the wine wētā clade can be distinguished from one another using a combination of terminalia, sternite structures and leg spines (Table 2). Notably, we can confirm a pattern of close parapatry between *H. pallitarsis* and *H. bilobatus* in southern North Island in and around Wellington, although typically only one species is recorded per location. It is likely that population density of the two lineages varies in a mosaic, but further data are needed to confirm the dynamics of competition. We did however, extend the known range of *H. bilobatus* into the Wairarapa and eastern coast of North Island, where we found it in sympatry with *H. pallitarsis*; males and females of both species were collected at the same location on the same night.

The geographic distribution of *H. bilobatus* spanning the Cook Strait most likely represents dispersal opportunity during one or more periods of lowered sea level during Pleistocene glacial phases. A global drop in sea level of 100–120 m is estimated for the last glacial maximum (LGM) and this would have resulted in land connection between the two main islands of New Zealand (Trewick and Bland 2012). Although many New Zealand species have range limits that are marked by the Cook Strait (Trewick & Olley 2016; Trewick et al. 2017), a number of counter examples including the Wellington tree wētā *Hemideina crassidens* are known (Trewick and Morgan-Richards 1995; Bulgarella et al. 2014). *Hemiandrus pallitarsis* shows a pattern of regional partitioning with distinct mitochondrial DNA haplogroups associated with

Figure 12. The eggs of *Hemiandrus bilobatus* develop within the mother's burrow. These eggs (GW1160) at Awatere were in an advanced stage of development on 3rd October 2018 at the time of vine bud burst.

different places (Chappell et al. 2012), but its range does not extend across Cook Strait. In contrast, *H. bilobatus* mtDNA diversity (Figure 7) is shared across the strait (Figure 2).

Wine wētā ecology

Our estimate of ground wētā density in an Awatere vineyard of 3.4 individuals per square metre from mark-recapture data is very similar to estimates determined using daytime digging of burrows in the soil (3.3 individuals/m^2; Nboyine et al. 2016). During the spring some adult females have eggs (Nboyine et al. 2016) and therefore they might not come out at night. Our digging of burrows confirmed that adult females with eggs were present at the time we estimated population size (Figure 12). However, most active insects we observed at night were not adult. In contrast, 12 individuals gathered opportunistically on vines after dark at spring/summer boundary (28th November) were all adult (10 males, 2 females). Although our November sample suggests there might be fewer adult females active at this time, the proportion of brooding females is highest in winter (July; Nboyine et al. 2016).

From direct observations at night in vineyards we can confirm that these ground wētā are omnivores. Our analysis of gut contents of individuals active in the vineyard

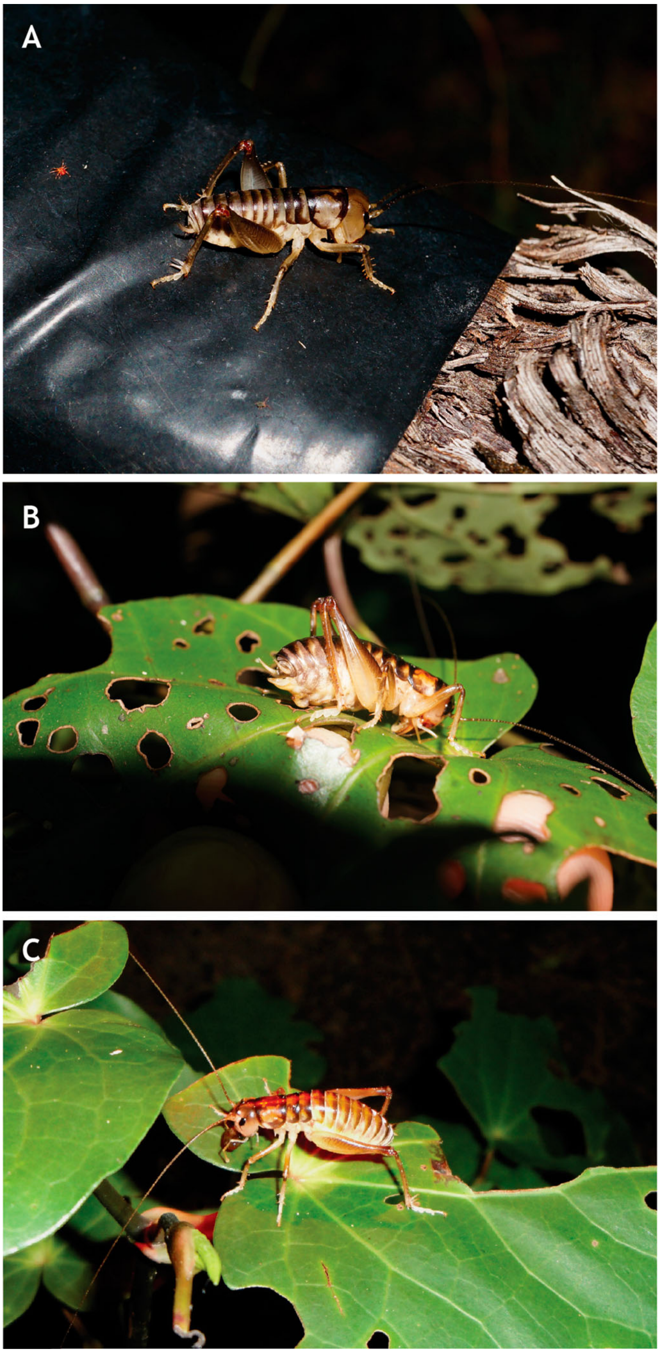

Figure 13. Short-ovipositor wētā at night. **A,** *Hemiandrus bilobatus* on grape vine sleeve, Awatere; **B,** *H. pallitarsis* female with 6th sternite structure visible, on leaf of kawakawa *Piper excelsum*, Turitea, Palmerston North; **C,** *H. merope* sp. nov. female eating nuptial gift after mating, on kawakawa, Kapiti Island.

found most had eaten a mixture of plants and invertebrates. Half the sample had vine (*Vitis vinifera*) and two-thirds of our sample had invertebrate exoskeleton in their gut. This species is known to eat a large range of plant species (Nboyine et al. 2019) but by using primers to amplify plant DNA from their frass all the invertebrate components of their diet has, until now, largely been ignored. Because protein is known to improve growth rate of this species (Smith 2014), and observations of many *Hemiandrus* species suggest a diet described as primarily carnivore, scavenger or omnivore (Cary 1983; Gwynne 2004; Morgan-Richards et al. 2008; Taylor Smith et al. 2013), the potential role of wine wētā as predators of other pest species should not be ignored.

Although wine wētā density is high near vines, most of our night observations were of wētā on the ground. At night in early October, few vines (~6%) have wētā feeding on the buds. Although over the course of the season it can be expected that the cumulative number of wine wētā/vine interactions could be high, damage to leaves that are protected by masses of woolly hairs (trichomes) is likely of limited consequence.

We found little evidence that the plastic sleeves wrapped around the trunk of grape plants reducing the rate at which wine wētā climb vine trunks. Direct observations confirmed that the wētā do climb vines and we saw some wētā eating buds (Figure 1), while others were feeding on sap. In addition to seeing wine wētā walking up plastic sleeves, we also saw them traversing trellis wires between vine plants (Figure 1). These are typical of the activity displayed by related ground wētā in native forests. From our direct nocturnal observations of wine wētā on plastic sleeves, including sleeves attached to smooth, cylindrical, vertical trellis posts, we can conclude that the plastic does not prevent these insects from accessing vines plants. Any benefit of plastic sleeves might, however, be influenced by the age of the plastic, the growth stage of the vines, the local density of wētā, or temperature. Further work is required because each grape variety has slightly different phenology and differing foliage characteristics (Konlechner and Sauer 2016; Ma et al. 2016) which might influence food availability to wētā.

We can confirm from direct observation that *Hemiandrus bilobatus* ground wētā do climb grape vines in the Awatere valley, something that has not previously been documented. We can also confirm that they do forage on vine buds, but ground wētā spend time in vegetation for many reasons including hunting, premating signalling (drumming) and mating (Gwynne 2004; Chappell et al. 2012). Even when ground foraging is commonplace, *Hemiandrus* can be observed on leaves (Figure 13) at night, and trunk traps on trees in the Orongorongo forest showed a high level of vertical commuting (Brockie 1992). When most female *H. bilobatus* (and other short-ovipositor ground wētā) are mature, mated and with eggs in their burrows, adult males remain active on vegetation as we observed of wine wētā in the Awatere.

Finding ground wētā on vines is not surprising given that vines represent the only large plants in the area. Rarely in New Zealand are native animal populations influenced positively by anthropogenic habitat modification but in the Awatere Valley the irrigation of vines seems to provide *Hemiandrus bilobatus* with suitable conditions to thrive. Further work on the biology of this species throughout the year would be useful to elucidate its role as predator within this system, and indeed to learn about the evolution, ecology and resilience of endemic biodiversity in a rapidly changing world.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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