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Phylogeography of the endemic red-tailed cicadas of New Zealand (Hemiptera: Cicadidae: *Rhodopsalta*), and molecular, morphological and bioacoustical confirmation of the existence of Hudson's *Rhodopsalta microdora*

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Why do some genera radiate, whereas others do not? The genetic structure of present-day populations can provide clues for developing hypotheses. In New Zealand, three Cicadidae genera are depauperate [*Amphipsalta* (three species), *Notopsalta* (one species) and *Rhodopsalta* (three species)], whereas two have speciated extensively [*Kikihia* (~30 species/subspecies) and *Maoricicada* (~20 species/subspecies). Here, we examine the evolution of *Rhodopsalta*, the last New Zealand genus to be studied phylogenetically and phylogeographically. We use Bayesian and maximum-likelihood analyses of mitochondrial *cox1* and nuclear *EF1α* gene sequences. Concatenated and single-gene phylogenies for 70 specimens (58 localities) support its monophyly and three described species: *Rhodopsalta cruentata*, *Rhodopsalta leptomera* and *Rhodopsalta microdora*, the last taxon previously regarded as uncertain. We provide distribution maps, biological notes and the first descriptions of diagnostic songs. We show that both *R. cruentata* and *R. microdora* exhibit northern and southern genetic subclades. Subclades of the dry-adapted *R. microdora* clade show geographical structure, whereas those of the mesic *R. cruentata* and sand-dune specialist *R. leptomera* have few discernible patterns. Genetic, bioacoustical and detailed distributional evidence for *R. microdora* add to the known biodiversity of New Zealand. We designate a lectotype for *Tettigonia cruentata* Fabricius, 1775, the type species of *Rhodopsalta*.

ADDITIONAL KEYWORDS: acoustic signals – biodiversity – Cicadettinae – Cicadettini – Cook Strait – morphology – palaeohistory – Pliocene – Zealandia.

INTRODUCTION

As a result of its palaeohistory and geographical isolation, New Zealand (NZ) harbours an abundance of endemic species radiations that have been the focus of numerous phylogeographical studies (reviewed by Wallis & Trewick, 2009; Trewick *et al.*, 2011; Buckley *et al.*, 2015; Craw *et al.*, 2017). In particular, NZ cicadas (Hemiptera: Cicadidae) in the genera *Kikihia* Dugdale, 1972, *Maoricicada* Dugdale, 1972 and *Rhodopsalta* Dugdale, 1972 are a superb example of an island species radiation from a single colonizing ancestor.

All NZ cicadas belong to the subfamily Cicadettinae Buckton, 1890 and tribe Cicadettini (~500 described species), a cosmopolitan group known for its rapid diversification and radiation from Cretaceous–Palaeocene ancestors (Marshall *et al.*, 2016). From two independent colonization events within this tribe, five NZ genera and > 50 endemic NZ species have evolved during the Miocene, Pliocene and Pleistocene epochs (Fleming, 1975a; Arensburger *et al.*, 2004b; Buckley & Simon, 2007; Marshall *et al.*, 2008, 2011, 2012). Both colonization events, one leading to the *Kikihia* + *Maoricicada* + *Rhodopsalta* lineage (Dugdale & Fleming, 1978; Fleming, 1984) and the other forming the *Amphipsalta* Fleming, 1979 + *Notopsalta* Dugdale, 1972 lineage (Marshall *et al.*, 2012), are

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estimated to have occurred within the last 14 Myr (Buckley *et al.*, 2002; Arensburger *et al.*, 2004a; Marshall *et al.*, 2012, 2016).

The majority of NZ cicada species belong to the genera *Kikihia* (16 described species or subspecies plus a similar number not yet described formally; Fleming, 1984; Marshall *et al.*, 2008, 2011) and *Maoricicada* (19 described, with several candidate undescribed taxa; Fleming, 1971; Dugdale & Fleming, 1978; Buckley & Simon, 2007; Hill *et al.*, 2009). *Rhodopsalta* contains only three described species, as does the genus *Amphipsalta*. The genus *Notopsalta*, sister genus to *Amphipsalta*, has only one described NZ species (Larivière *et al.*, 2010; Marshall *et al.*, 2012). The sole Australian species of *Notopsalta* was excluded by Moulds (2012), and only *Notopsalta melanesiana* (Myers, 1926) of New Caledonia (of uncertain relationship) remains outside NZ.

When he constructed four of the current five NZ cicada genera, Dugdale (1972) separated them into two groups based on morphological and genitalic characters. The fact that *Rhodopsalta* shares a 'trifid aedeagus' with the *Amphipsalta–Notopsalta* clade suggested a sister-group relationship. However, molecular data strongly support a *Kikihia–Maoricicada–Rhodopsalta* (KMR) clade, suggesting that the similar genitalic characters represent plesiomorphies or unchanged ancestral states (Buckley *et al.*, 2002; Arensburger *et al.*, 2004b; Marshall *et al.*, 2016). This conclusion is supported further by the large number of related Australian Cicadettini species possessing the trifid aedeagus (Moulds, 2012). A molecular systematic study of the tribe Cicadettini, based on Sanger sequencing of both mitochondrial and nuclear genes, suggests that *Rhodopsalta* is more closely related to *Maoricicada* than to *Kikihia* (Marshall *et al.*, 2016); genomic data currently being analysed might be able to provide a more definitive answer. The absence of an alarm call in both *Rhodopsalta* and *Maoricicada* is consistent with this placement (Dugdale & Fleming, 1978; Arensburger *et al.*, 2004a). Beyond the taxonomic description of *Rhodopsalta* and a few early general studies of NZ cicadas (Myers, 1929a, b; Fleming, 1975a, b), no scientific studies describing the biology of *Rhodopsalta* have been published, in part because of the significant effort focused on their diverse sister genera, *Maoricicada* and *Kikihia* (e.g. Fleming, 1973; Buckley *et al.*, 2001a, 2006; Simon, 2009; Marshall *et al.*, 2011; Ellis *et al.*, 2015; Banker *et al.*, 2017; and other references cited elsewhere in the present paper).

In this study, we use both nuclear and mitochondrial sequence data to examine the phylogenetic relationships, phylogeography and timing of species diversification in the genus *Rhodopsalta*, commonly known as the red-tailed cicadas (Fleming, 1975c; White & Sedcole, 1993; Logan & Connolly, 2005). We find phylogeographical evidence confirming the existence of three monophyletic species including *Rhodopsalta cruentata* (Fabricius, 1775), *Rhodopsalta leptomera* (Myers, 1921) and the previously uncertain species *Rhodopsalta microdora* (Hudson, 1936). We find that *R. cruentata* and *R. microdora* have large distributions represented by both North (NI) and South Island (SI) clades and that *R. leptomera* is restricted to coastal North Island. Subclades of *R. microdora* appear to have phylogeographical structure, whereas *R. cruentata* and *R. leptomera* possess geographically mixed subclades. We discuss dated genetic patterns and hypotheses of evolution for *Rhodopsalta* in response to landscape and climatological changes of palaeo-New Zealand.

Palaeohistory of New ZealaNd

New Zealand (NZ) is well known for its rapidly changing geological history, rugged topography and varied habitats (Cooper & Millener, 1993; Newnham *et al.*, 1999). The continental landmass Zealandia (containing present-day NZ, New Caledonia, Lord Howe Islands and Norfolk Island) separated from the supercontinent Gondwana in the late Cretaceous era (85–80 Mya; Mortimer *et al.*, 2017; Wood *et al.*, 2017). During the Oligocene (~25 Mya), NZ experienced reductions in relief and a marine transgression event that was once proposed to have involved near-total submergence (Pole, 1994; Cooper & Cooper 1995; Landis *et al.*, 2008; but see Mildenhall *et al.* 2014; Kaulfuss *et al.* 2015; Wallis & Jorge, 2018; Buckley *et al.*, 2020).

Molecular clock studies suggest that the ancestors of extant NZ cicadas first became established in NZ during the latter half of the Miocene (Arensburger *et al.*, 2004a; Marshall *et al.*, 2016). Fossil evidence from NZ is known only for distant cicada relatives in the sister-family Tettigarctidae (Kaulfuss & Moulds, 2015), a group now restricted to south-eastern Australia. Throughout the late Miocene, substantial geological changes occurred in NZ, including increased mountain building and volcanic activity, especially on NI (McGlone, 1985; Sutherland, 1994, 1999). Despite an increase in mountain building, Miocene NZ was still predominantly low-lying in relief, and many localities continued to experience warm and wet climates (Wardle, 1968; Wood *et al.*, 2017). The 'climatic optimum' of the Miocene was followed by a decline in temperatures that continued into the Pliocene. Later intensification of cooling led to the ice ages of the Pleistocene epoch (Carter, 2005; Patterson *et al.*, 2014). Glacial periods drive biodiversity change and population extinctions owing to extreme habitat modifications and proliferating ice sheets

(Webb & Bartlein, 1992; Provan & Bennett, 2008; Gavin *et al.*, 2014; Nevado *et al.*, 2018). Orogeny and glaciation are two physical phenomena that can interact with one another, promoting allopatric speciation (Wallis *et al.*, 2016; Craw *et al.*, 2017). Evidence suggests that mountain range formation and subsequent glaciation have mediated shared phylogeographical patterns and genetic discontinuities for terrestrial taxa not only across the Southern Alps of NZ but also across the Pyrenees, southern Andes and southern Himalayas (Wallis *et al.*, 2016).

The Pliocene was a significant period of landscape and climate change, including orogenic creation of rain shadows. Mountain building intensified in the central SI ~5–6 Mya (Batt *et al.*, 2000; Chamberlain & Poage, 2000; Garver & Kamp, 2002). As the height of the axial mountains increased, so too did rain shadow effects along eastern NZ (Craw *et al.*, 2013). Sub-humid interglacial climate in the SI remained relatively stable, but colder periods became more intense throughout the late Pliocene (~2.5 Mya; Wood *et al.*, 2017). A sea strait covered the southern half of the NI for most of this era. Mountain building of the southern NI axial ranges began ~1 Mya, resulting in further rain shadow effects along the south-east coast, while increased volcanic activity, north of the strait, formed multiple microhabitats (Ellis *et al.*, 2015; Fig. 1).

Extreme cycles of warm interglacial and cold glacial periods became prevalent and alternated throughout the Pleistocene, intensifying in the late Pleistocene (Carter & Gammon, 2004; Carter, 2005; Gibbard *et al.*, 2010). Cold periods throughout this era were more extreme than those of the Pliocene, with cooler glacial oceans reducing temperatures by ≤ 8 °C in the south and 4 °C in the north (Ho *et al.*, 2012). Accumulation

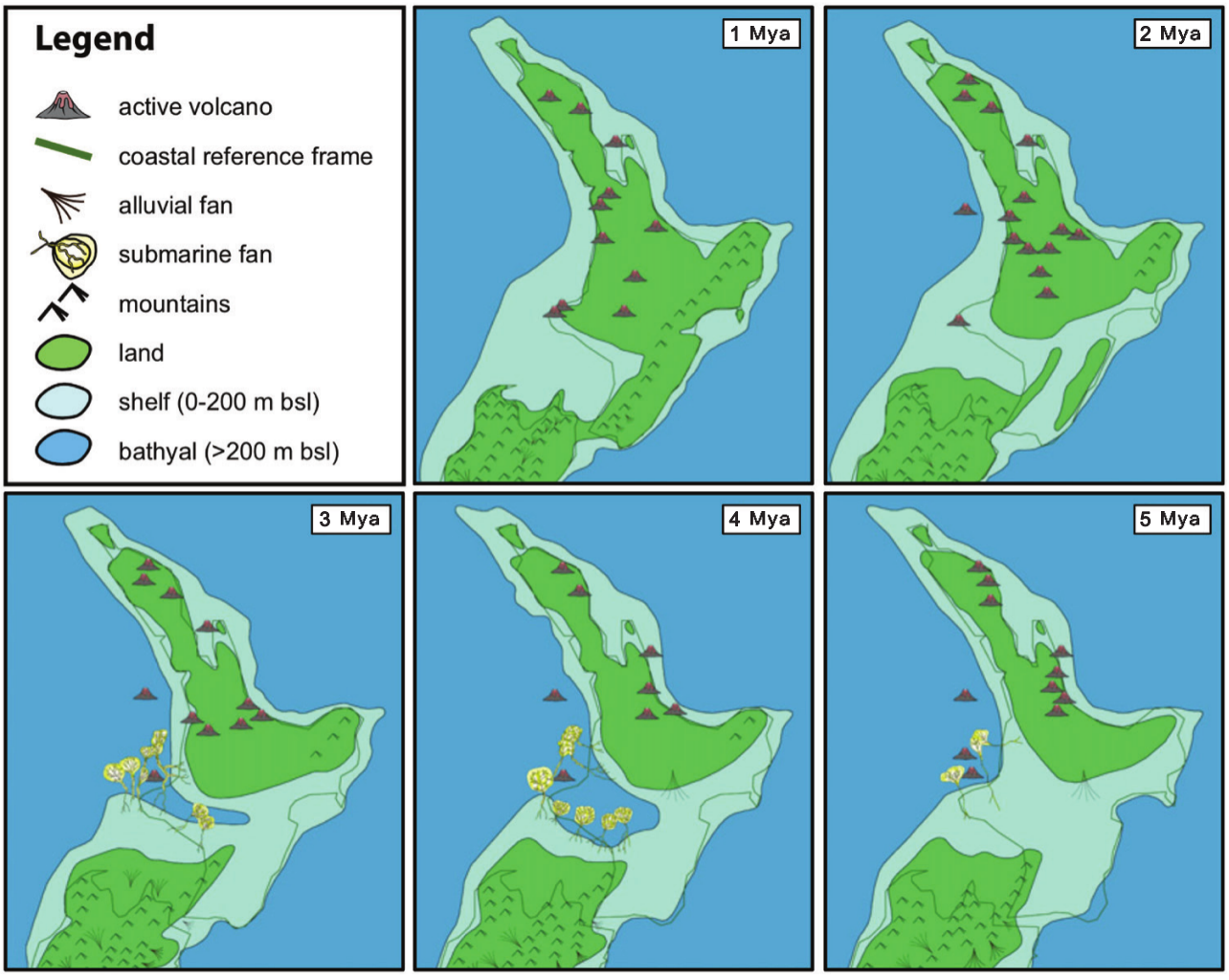

Figure 1. Palaeogeographical maps depicting topographical change in the North Island of New Zealand throughout the Pliocene and Pleistocene epochs. Maps were modified and reprinted from Ellis *et al.* (2015), with permission.

of polar and mountain ice during the Pleistocene glacial maxima reduced sea levels and increased coastal habitats, while development of tundra environments rendered numerous areas of the NI and SI uninhabitable for most species (Trewick & Wallis, 2001; Burge & Schulmeister, 2007). Emergent land connected the main islands of NZ during each major glacial phase (Bunce *et al.*, 2009; Ellis *et al.*, 2015).

Many studies have shown that the NZ flora and fauna were substantially affected by geological and climatic shifts during the Pliocene and Pleistocene (Wallis *et al.*, 2016; Craw *et al.*, 2017); this has been well demonstrated in NZ cicadas (Buckley *et al.*, 2001b, 2006; Buckley & Simon, 2007; Hill *et al.*, 2009; Marshall *et al.*, 2009, 2011, 2012; Ellis *et al.*, 2015; Banker *et al.*, 2017). Drastic geological and climatic shifts posed challenges to a wide variety of NZ fauna and were drivers of both allopatric speciation and extinction events.

MATERIAL AND METHODS

Sample collection

Rhodopsalta specimens were collected throughout mainland NZ. Specimens were coded with typical C. Simon-lab codes. For example, 02.NZ.TO.MGT.04 indicates the year (2002), followed by a two-letter country code (NZ), a two-letter district code (TO, Taupo; Crosby *et al.*, 1998), a three-letter site code (MGT) and a two-digit specimen number. Throughout this paper, we use the codes from the study by Crosby *et al.* (1998) to refer to specific NZ districts, except that we use SI for South Island (SI stands for Stewart Island in the Crosby system, and this location lies beyond the range of *Rhodopsalta*; Fig. 2). Specimens were mostly male, identified by song and captured by net or by hand. Females of all three species were captured opportunistically. Individuals were stored in 95% ethanol upon capture, or one or more legs were removed into ethanol, with the specimen pinned for museum drawer storage. Ethanol-preserved material was stored at −20 °C. Latitude and longitude recordings were taken for collection locations and documented based on the New Zealand Geodetic Datum 1949 (Lee, 1978) or, in some later cases, using WGS84. Global positioning points were then entered in Google Maps (https://www.google.com/maps) to construct a distribution map of the *Rhodopsalta* specimens sampled for the molecular analysis (Supporting Information, Fig. S1; Table S1). Outgroups from *Kikihia* and *Maoricicada* were selected based on past molecular work (Buckley *et al.*, 2002; Arensburger *et al.*, 2004b; Marshall *et al.*, 2008).

Song recording

As in most cicada species, males of the genus *Rhodopsalta* produce a species-specific acoustic signal or 'song' using a pair of specialized abdominal structures called timbals, in order to attract females for mating (Myers, 1929b; Young, 1973; Fleming, 1975d). Owing to their primary role in sexual pair formation, cicada songs are always distinguishable when species are sympatric and synchronic, like acoustic mating signals of other insects (see references in the studies by Otte, 1992 and Hertach, 2021). In the large NZ genera, *Kikihia* and *Maoricicada*, songs are evolutionarily labile and have proved useful in distinguishing even allopatric taxa that are too closely related to have developed diagnostic morphological differences (see Buckley *et al.*, 2006; Hill *et al.*, 2009; Marshall *et al.*, 2008, 2009, 2016). We therefore audio-recorded our collected specimens when possible in order to check for population differences in song that might indicate cryptic species and to provide material for descriptions of the song phenotype produced by each species.

Songs were recorded in the field at 44.1 or 48.0 kHz using one of several models of Marantz (Mahwah, NJ, USA) digital audio recorders (e.g. PMD-670) or a SONY (Park Ridge, NJ, USA) TCD-D8 DAT recorder using a Sennheiser (Old Lyme, CT, USA) ME62 omnidirectional microphone with a windscreen and, in most cases, a Sony PBR-330 parabolic reflector (otherwise, an ME66 short shot gun microphone was used). The microphones were powered by Sennheiser K6 power modules, and they have a frequency response that is approximately flat from 40 Hz to 20 kHz (±2.5 dB). In some cases, male cicadas were recorded while being held in white mesh-fabric cages (Port-A-Bug; Insect Lore, Shafter, CA, USA) placed on the ground in the sunlight or suspended on vegetation. Air temperatures were recorded in most cases with an Omega HH-25KF thermocouple (OMEGA Engineering, Stamford, CT, USA), although cicadas are known to thermoregulate behaviourally via basking; therefore, such temperatures do not necessarily correspond closely to body temperature (Heath, 1967; Sanborn, 2002).

Oscillograms, spectrograms (sonograms) and power spectra were generated using Raven Pro v.1.5.0 (Cornell Bioacoustics Laboratory, Ithaca, NY, USA), with most analysis conducted after exclusion (bandstop filtering) of sound < 10 kHz to minimize background noise from crickets, *Amphipsalta* Dugdale & Fleming, 1969 cicadas and other sources. Summary characteristics of the songs of the three species were determined by examination of the recordings of sequenced males, when available, in Raven Pro, with emphasis on the typical number and patterning of different elements (as opposed to more temperature-dependent details, such

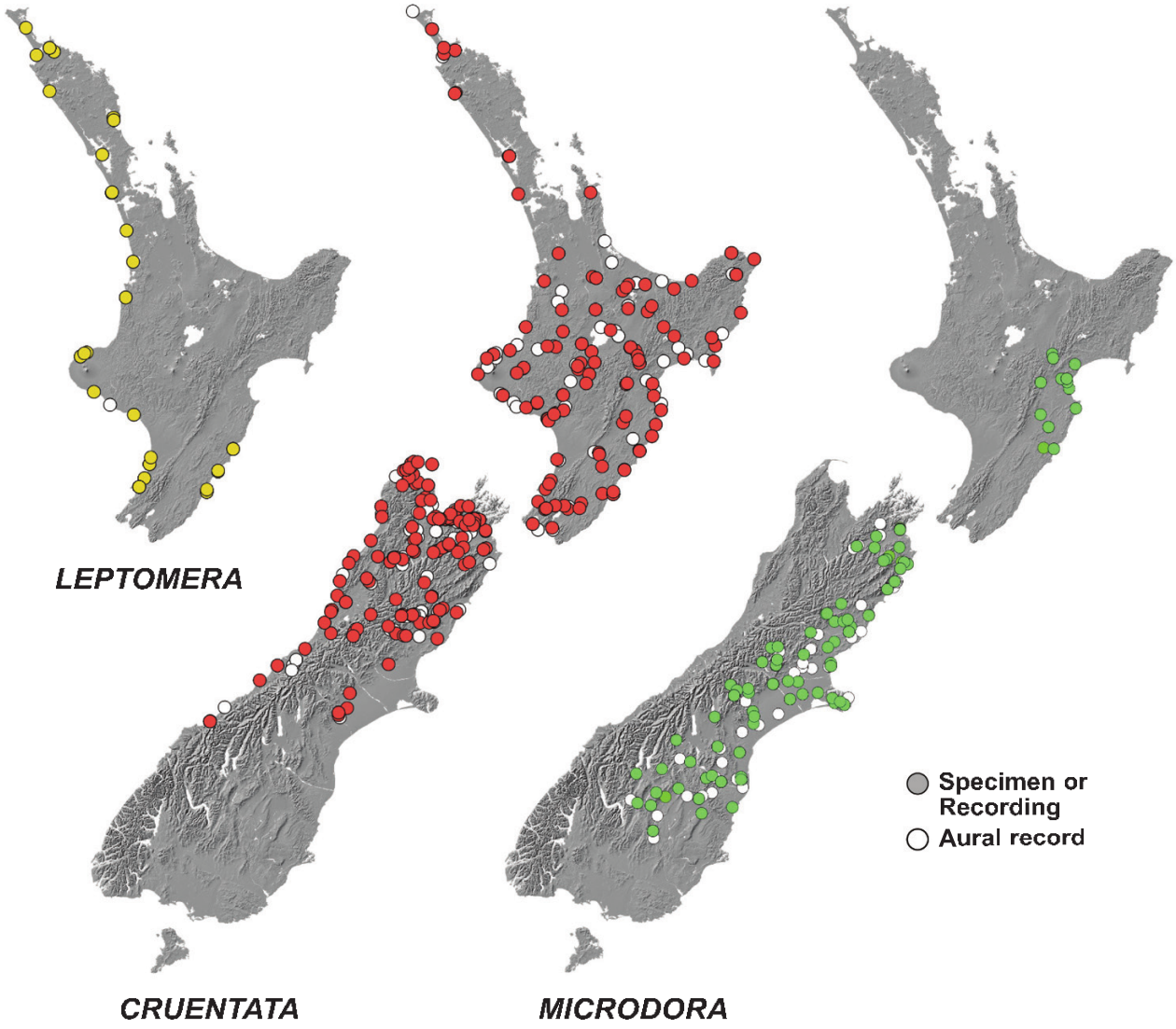

Figure 2. Maps of Simon-lab field records of the three *Rhodopsalta* species.

as rates of production of such elements). Spectrograms were generated with 256-sample Hann windows, 50% overlap, a hop size of 128 samples, a Discrete Fourier Transform size of 256 samples and grid spacing of 128 Hz.

dNa extractioN, amPlificatioN aNd sequeNciNg

Genomic DNA was extracted from leg and thoracic flight tissue using the NucleoSpin Tissue kit and protocol from January 2010 (Macherey-Nagel, Bethlehem, PA, USA). Digestion was conducted at 56 °C overnight. Portions of two genes were amplified: the 5′ (Folmer, 1994) and 3′ halves of the mitochondrial cytochrome *c* oxidase I (*cox1*) gene and the middle region of nuclear elongation factor 1 alpha (*EF1α*), using the primers and annealing temperatures from the Supporting Information (Table S2). Both single-copy genes were chosen for sequencing because of their past usefulness in cicada phylogenetic research (Buckley *et al.*, 2006; Marshall *et al.*, 2008, 2012; Banker *et al.*, 2017).

Approximately 1486 bp of *cox1* (from two sections) and 798 bp of *EF1α* were amplified. Polymerase chain reaction (PCR) recipes used Titanium Taq or EmeraldAmp GT PCR Master Mix (MM), with 25 μL volumes, 1–2 μL of template, 0.13 μL of taq (when using taq), 12.5 μL of GT PCR MM (when using MM), 1.25 or 1.0 μL of primer (10 μM) and 2.5 μL each of 10× buffer and dNTPs. The basic PCR was as follows: (1) initial denaturation at 94 °C for 2 min; (2) denaturation, 30 cycles of 94 °C for 45 s (1 min for *EF1α*); (3) annealing (for temperatures, see Supporting Information, Table S2),

30 cycles of 72 °C for 1 min (1 min 15 s for 3′ *cox1* and *EF1α*); and (4) extension at 72 °C for 5 min.

Amplified PCR products were run on a 1% agarose gel to check bands before cleaning with ExoSAP-IT (USB Corp., Cleveland, OH, USA). Cycle sequencing was conducted with Big Dye v.1.1 (Applied Biosystems, Foster City, CA, USA), cleaned by Sephadex filtration (GE Healthcare, Piscataway, NJ, USA) and then sequenced on an ABI 3100 capillary sequencer. Sequences were analysed using the ABI Prism Sequencing Analysis 3.7 software (Applied Biosystems), manually aligned (using default parameters), edited in geNeious (Biomatters, Auckland, NZ, USA) and checked for errors. Sequences were monitored for double-peaked chromatograms, length variants and stop codons, all of which can indicate amplification of non-functional nuclear copies of mitochondrial DNA (mtDNA) genes or numts (Lopez *et al.*, 1994; Bensasson *et al.*, 2001; Song *et al.*, 2008). A total of 68 *Rhodopsalta* individuals, four outgroup taxa and 2284 concatenated bases were sequenced successfully.

PhylogeNetic aNalysis

Individual gene trees for *EF1α* and mitochondrial *cox1* were constructed using both maximum-likelihood (ML) and Bayesian inference (BI) methods. Data partitioning schemes and models of evolution were determined initially by using the greedy algorithm, Phyml v.3.0 and the Bayesian information criterion within the program PartitioNfiNder2 using PythoN v.2.7 (Supporting Information, Table S3; Burnham & Anderson, 2003; Guindon *et al.*, 2010; Python Software Foundation, 2010; Lanfear *et al.*, 2012, 2016). Amplicons of *cox1* (5′ and 3′ halves) and the mid-section of nuclear *EF1α* were concatenated using sequeNcematrix v.1.8 (Vaidya *et al.*, 2011). Partitions included individual codon positions for both *cox1* and *EF1α* (data treated separately for concatenated sets) and a combined intron dataset for *EF1α*. Indel characters from the intron subset were coded with the simple coding option using seqstate v.1.0 (Simmons & Ochoterena, 2000)

Bayesian phylogenetic analyses were run in mrBayes v.3.2.6 (Ronquist *et al.*, 2012) using the CIPRES Science Gateway v.3.3 (www.phylo.org), with paired runs and four chains. The branch length prior was set to *unconstrained:exp(100)*, and the among-partition rate parameter was set to *variable*. The topology and branch lengths were linked across partitions. Otherwise, default parameter settings were used. Analyses were run until the average standard deviation of split frequencies reached a value < 0.01. Maximum-likelihood analyses were constructed with raxml-HPC v.8117 on a Macintosh MacBook Pro, using the rapid non-parametric bootstrap option and 1000 bootstrap pseudoreplicates (Stamatakis, 2014). Given that raxml does not allow assignment of models simpler than GTR (as recommended by PartitioNfiNder for *cox1* data partitions) and because early results suggested that the single-gene analyses were consequently overparameterized (see Discussion), the raxml analysis of the *cox1* gene was conducted under a single partition modelled with GTRGI. The raxml analysis of the *EF1α* dataset was conducted under a two-partition model, with the DNA analysed under GTRG with empirical base frequencies and the indels as binary-state characters in the MkV model with Lewis ascertainment bias correction (Lewis, 2001). Inferred tree topologies were visualized using figtree v.1.4.4. Model-corrected pairwise distances were obtained in the form of patristic distances (summed branch lengths) generated in mesquite v.3.51 (Maddison & Maddison, 2018) from the *cox1* Bayesian tree.

divergeNce time estimatioN

We used starBeast v.2.5.2 (*Beast; http://beast2.org/; Bouckaert *et al.*, 2019) to estimate divergence times for the *Rhodopsalta* radiation, both interspecific population divergence dates and intraspecific *cox1* subclade dates (the latter providing approximate dates for splits of geographically coherent populations). This analysis was performed with the combined genetic dataset (without indels) and calibrated with an empirical *cox1* molecular clock prior following the approach described by Marshall *et al.* (2016). The genetic data were partitioned and modelled as in the mrBayes phylogenetic analysis, but with all *cox1* sites combined into a single data partition under a GTRIG substitution model and estimated base frequencies. A Yule tree prior was used with a one over *x* prior on the *birth rates* and *popmean* parameters. All data partitions were assigned lognormal relaxed clocks, separately estimated, with time information derived only from a lognormal prior on the *ucld.mean* parameter for *cox1* (M = 0.01172, S = 0.288, with *mean in real space* selected; for the empirical data behind this calibration, see Marshall *et al.*, 2016). All other parameters were given uniform priors. The population function of the multispecies coalescent was set to *linear_with_constant_root*. *Automatic set clock rate* and *automatic set fix mean substitution rate flag* were deselected. Species-level taxon sets were defined according to specimen song phenotypes or, when the song was unavailable, by morphology. The *Beast Markov chain Monte Carlo procedure was run for 1×10^8 generations, and a 10% burn-in was used, resulting in effective sample sizes > 450 for all parameters, according to tracer v.1.7.1 (Rambaut & Drummond, 2007).

RESULTS

Species names, specimen codes, locality data and gene regions sequenced are shown for each specimen in the Supporting Information (Table S1). All three gene regions were sequenced for 56 of the 68 specimens. For four specimens, one *cox1* section and the *EF1α* region were amplified, and for the remaining nine specimens only one region was obtained. Sequences were submitted to GenBank under accession numbers MZ470285–MZ470348 (*cox1* 5′), MZ470358–MZ470418 (*cox1* 3′) and MZ488336–MZ488403 (*EF1α*). Locality records for all *Rhodopsalta* specimens collected or recorded during Simon-lab expeditions are mapped in Figure 2 by species in accordance with the results below.

SoNgs

Song structure in Rhodopsalta

Fleming (1975d) showed that the basic unit within most *R. cruentata* and *R. leptomera* timbal songs is a rapid sequence of three pulses (forming an ~10 ms 'pulse group' in Fleming's terminology) created by one in–out movement from each of the timbals (left and right), with the in-clicks synchronous and the out-clicks asynchronous. Thus, the first pulse, formed by overlapping left and right timbal actions, is normally stronger. As shown below, our recordings confirm this pattern for those species (although variations exist, as discussed by Fleming) and for songs of *R. microdora*, which was not previously discussed. In the summaries of song structure of the three species below, we use the term 'click' in place of Fleming's (1975d) 'pulse group' for simplicity, because the three pulses within a group are created by one coordinated timbal action and because they occur too quickly to be distinguished by the human ear. Groups of clicks of different combinations are referred to here as types of echemes.

While observing *Rhodopsalta* pair-forming behaviour in the field, we confirmed that females signal mating receptivity with wing-flicks that are produced in response to a particular element of the song of the male, as in other NZ genera (see Discussion). In the figures, the approximate positions of female wing-flick replies are marked by stars. We observed that the male song can be divided into introductory and cueing sections (see Marshall *et al.*, 2008), with the latter containing the cues that trigger the female response. Males alternate between these sections while singing, sometimes spending ≥ 1 min producing a single song section (as also observed especially in *Amphipsalta*, see Discussion).

Individual species songs

We documented three *Rhodopsalta* song phenotypes in the field, corresponding to the three described species (see 'Taxonomic and individual species notes', which include a lectotype designation for *R. cruentata*). Diagnostic differences between the songs of these species are found mainly in the temporal pattern of song elements. The three species produce overlapping frequency spectra, more or less unmodulated, with most sound energy > 10 kHz and peak frequencies (sound pitch with highest intensity) ranging from 12 to 18 kHz (Fig. 3), although the peak frequencies of *R. leptomera* and *R. microdora* tend to be higher on average. We describe the temporal patterns of the introductory and cueing sections of each species separately below.

Rhodopsalta cruentata: The introductory section of *R. cruentata* (Fig. 3A) comprises continuously repeated echemes produced at ~3–5/s, with each echeme containing a set of two to six (typically four or five) approximately evenly spaced single clicks (having a repetition rate of 20–40/s), followed immediately by a single pair of closely set clicks having a gap less than half the duration of the gaps separating the preceding clicks. The echemes are separated by silent gaps of ~0.05–0.20 s. The number of clicks within the introductory section echemes usually varies as the individual sings, as can the rate of production of the echemes (depending on temperature and other factors), but the gaps between the echemes typically remain shorter than the lengths of the echemes. The cueing section (Fig. 3B) contains repeated echemes of the same structure (although with a higher average number of clicks, more typically six or seven) that alternate with short echemes comprising two clicks produced with a rate similar to or slower than that of the single clicks within the larger echemes. Notably, the shorter two-click cueing echeme is preceded by a gap ~1.5–2.0 times the length of that found between introductory section echemes, and the gap following the shorter echeme is similar in length to that found between introductory echemes. We were able to attract males of *R. cruentata* by clicking with fingers after the shorter cueing echeme. We did not notice any diagnostic differences between the songs of NI and SI *R. cruentata*.

Rhodopsalta leptomera: The introductory section of *R. leptomera* (Fig. 3C) comprises continuously repeated echemes that are shorter than those of *R. cruentata*, each containing two clicks followed by a close-set click-pair (the latter, with an internal gap of only ~0.005 s, resembles the click-pair that terminates each echeme in *R. cruentata*). The gaps between the single clicks and between these and the click-pair are all equal, at ~0.04–0.06 s. Therefore, the introductory song might also be conceptualized as one long echeme of indefinite length. The cueing section (Fig. 3D, G) contains sets of usually three to five of these short echemes produced

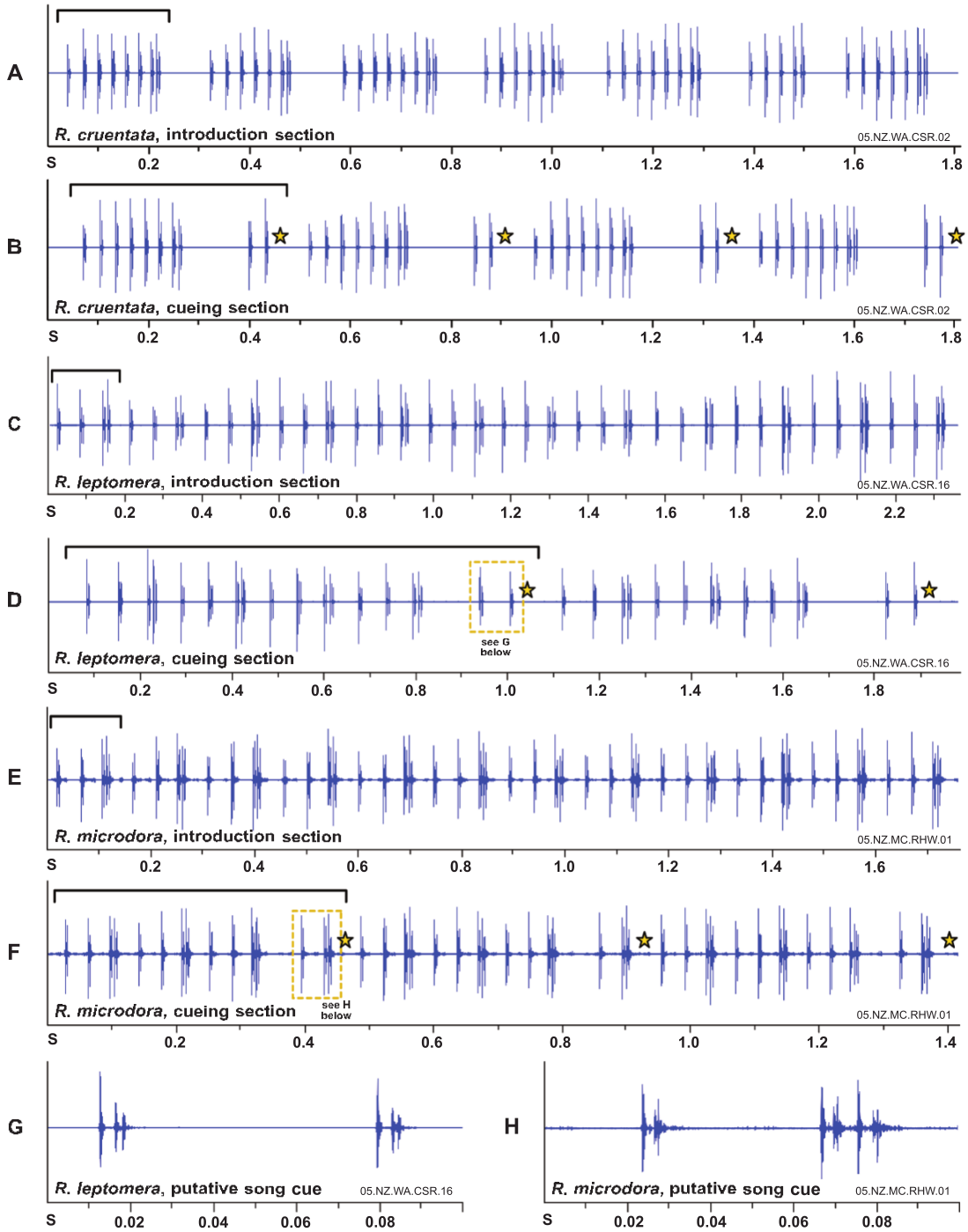

Figure 3. Waveforms illustrating song phenotypes of the three *Rhodopsalta* species. All fully developed *Rhodopsalta* songs consist of repeated phrases, the first one of which is indicated by a bracket in graphs A–F. Stars indicate the observed or inferred (*Rhodopsalta microdora*) positions of wing-flick responses produced by sexually receptive females.

as in the introductory section, alternating with a pair of clicks, the latter being the putative song cue based on the observed position of female responses. The clicks in the putative cue are not closely set, but separated by a gap equal to that observed between single clicks in the introductory section. However, the cue is preceded and followed by gaps that are longer than these, at ~0.06–0.10 s.

Rhodopsalta microdora: The introductory section of the song of *R. microdora* (Fig. 3E) is not distinguishable consistently from that of *R. leptomera*. In many specimens (especially from SI), the gap that precedes each closely set click-pair is slightly shorter than the gap following, but the difference is subtle and not present in all of our samples. Overall, the gap durations (and therefore the echeme repetition rates) appear slightly smaller, but without controlled temperature observations this difference remains uncertain. The cueing section (Fig. 3H) is also extremely similar to that of *R. leptomera*, but with one consistent difference: the putative cue consists of a single click followed by a closely set click-pair (of the form observed within the introductory section echemes) rather than another single click as in *R. leptomera*.

PhylogeNetics

The Supporting Information (Table S3) shows the dataset statistics and model-fitting results for each sequenced gene region and/or data partition. Figure 4 shows the tree from the Bayesian combined data analysis partitioned by gene and codon position, with Bayesian posterior probabilities and raxml bootstraps supports shown. We considered posterior probabilities of ≥ 0.95 and bootstrap percentages of ≥ 60–70% as representing moderate to strong support for a branch. Figure 5 shows the Bayesian trees from analyses of the separate *cox1* and *EF1α* amplicons.

The *cox1* + *EF1α* combined data tree (Fig. 4) and single-amplicon *EF1α* (Fig. 5B) trees show the three species of *Rhodopsalta* as monophyletic, although the bootstrap support for the *R. cruentata* clade is only moderate in the combined data analysis. The *cox1* data alone (Fig. 5A) also recover three monophyletic species, but with considerably lower support, especially for *R. microdora*. *Rhodopsalta microdora* was not recovered as monophyletic when we analysed *cox1* with the three-partition model recommended by PartitioNfiNder (not shown), but we disregarded this outcome as an effect of overparameterization, because there was strong discordance between the ML topology and the patterns across the bootstrap replicates (not shown). The concordant positions of the few taxa with missing data suggest that missing data did not greatly affect the analysis.

Rhodopsalta cruentata and *R. leptomera* are strongly supported as sister taxa (with *R. microdora* sister to both) by the combined data tree (Fig. 4) and the individual *cox1* tree (Fig. 5A), for both Bayesian and raxml analyses. The *EF1α* tree suggests a sister-group relationship between *R. microdora* and *R. leptomera*, but with essentially no support. Preliminary analyses of nuclear genomic data (C. Simon *et al.*, in preparation) agree with the structure of the combined gene tree.

Nuclear coPies of mitochoNdrial dNa *cox1*

In preliminary analyses of the genetic dataset, we found that sequences from seven specimens of *R. microdora*, obtained from the 3′ end of *cox1*, contained an 18 bp insertion and formed a distinct clade that fell in a position sister to the *R. cruentata* + *R. leptomera* clade (Supporting Information, Fig. S2). The presence of the insertion and the two TAA stop codons contained within it suggest that these haplotypes represent a non-functional nuclear copy (numt). The sequences were also of poor quality; in some cases, a 1 bp length-variant allele was possibly present at low frequency (allele not shown). We removed these presumed numt sequences from the preceding analysis, but we have included them at the end of the Supporting Information. We were unable to infer the true mtDNA copy from these individuals.

During the same preliminary phylogenetic analyses, we found that *cox1* sequences from eight specimens of *R. leptomera*, obtained only with the C1-J-1490 primer, formed a separate clade of identical haplotypes in a position sister to the main *R. cruentata* + *R. leptomera* clade (Supporting Information, Fig. S2), the same position as the presumed *R. microdora* 3′ numt clade (Supporting Information, Fig. S2). This group of identical sequences was characterized by high-quality chromatograms, and the sequences showed no indels or in-frame stop codons. However, they did share six amino-acid changes, in four cases caused by single mutations (three in the first position and one in the second) and two caused by multiple mutations (one second + third and one first + third change), whereas the remainder of the dataset showed few amino acid-changing substitutions, suggesting that the clade of identical sequences was a numt clade. Some re-amplification and resequencing attempts for these individuals yielded double-peaked chromatograms, with one set of peaks matching the character states of the presumed numt. In these cases, we subtracted the presumed numt states to obtain what we believed to be the true mtDNA haplotype. Nuclear mitochondrial copies that produce unambiguous chromatograms with no signs of non-functionality have been discovered before in divergent arthropod groups, such as crayfish and grasshoppers (Song *et al.*, 2008). Cicadas are known for their large genome sizes (Hanrahan & Johnston, 2011), a trait which has been linked positively to high levels of numts in other insect groups, such as Orthoptera. We have included the presumed 5′ *cox1* numt sequences at the end of the Supporting Information.

Rhodopsalta sPecies PhylogeograPhy

treetomaP (Maya-Lastra, 2020), an interactive program used to explore phylogeny and biogeography, was used to plot a map of the primary *Rhodopsalta*

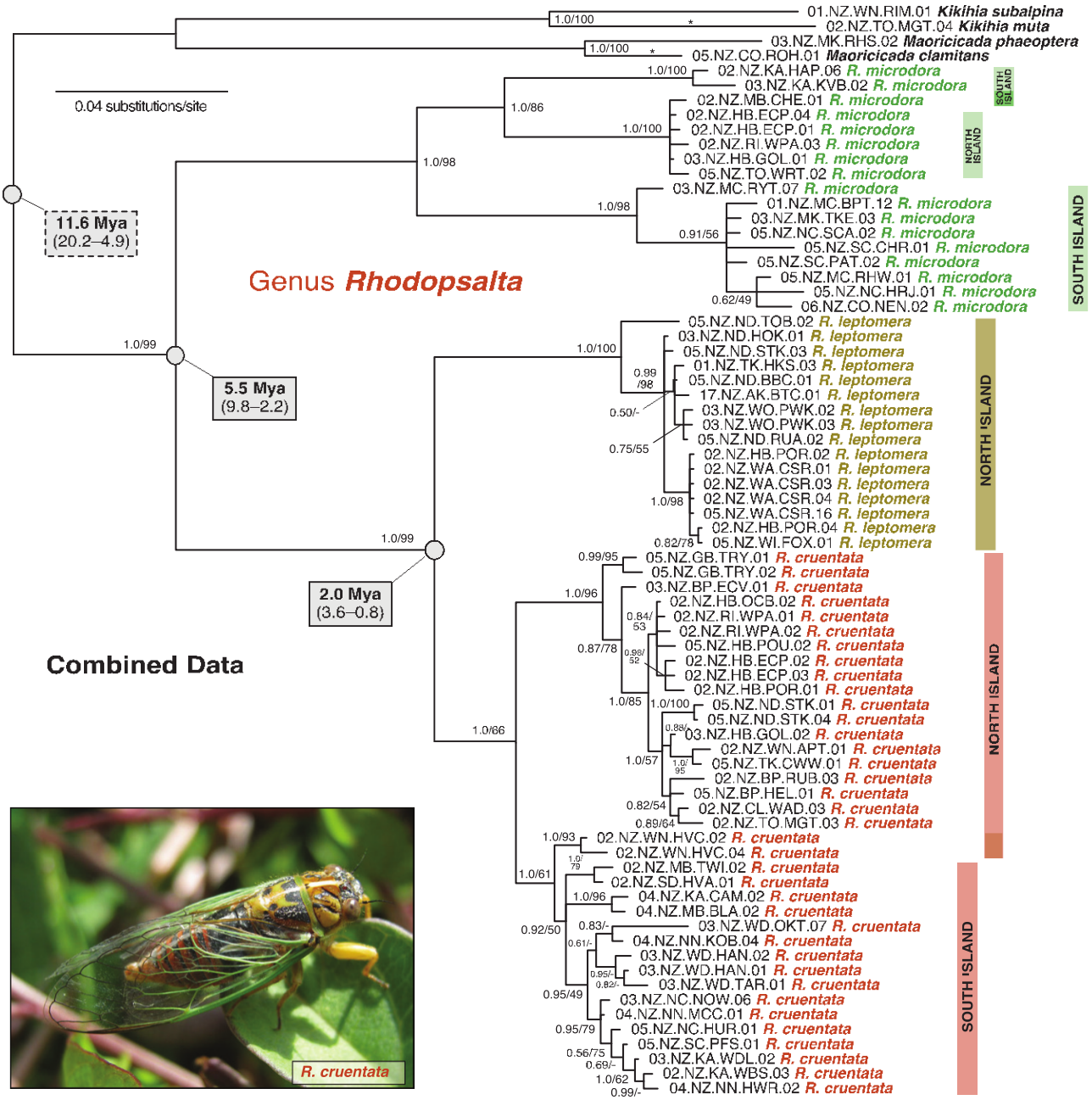

Figure 4. Bayesian phylogenetic tree based on 2284 bp of concatenated genes (5′ and 3′ *cox1* and *EF1α*). Six partition subsets were used (by gene and codon position for each gene, respectively). Branch support values represent Bayesian posterior probabilities and raxml bootstrap percentages from 1000 non-parametric pseudoreplicates. The number of parsimony-informative sites is 300. Grey boxes show mean divergence time estimates and 95% confidence intervals from the *Beast analysis.

geographical subclades within each species (Fig. 6). These patterns are described below.

Rhodopsalta cruentata

A sister-group relationship is found between NI and SI *R. cruentata*, with the exception of two Wellington specimens that group within the SI clade (Figs 4, 5A). These relationships are informed primarily by the *cox1* gene. Some weak geographical concordance is present. The earliest splits in the NI *R. cruentata* clade divide a set of samples from north-eastern NI from the remainder, and the majority of south-eastern NI individuals, specifically from Hawkes Bay (HB)

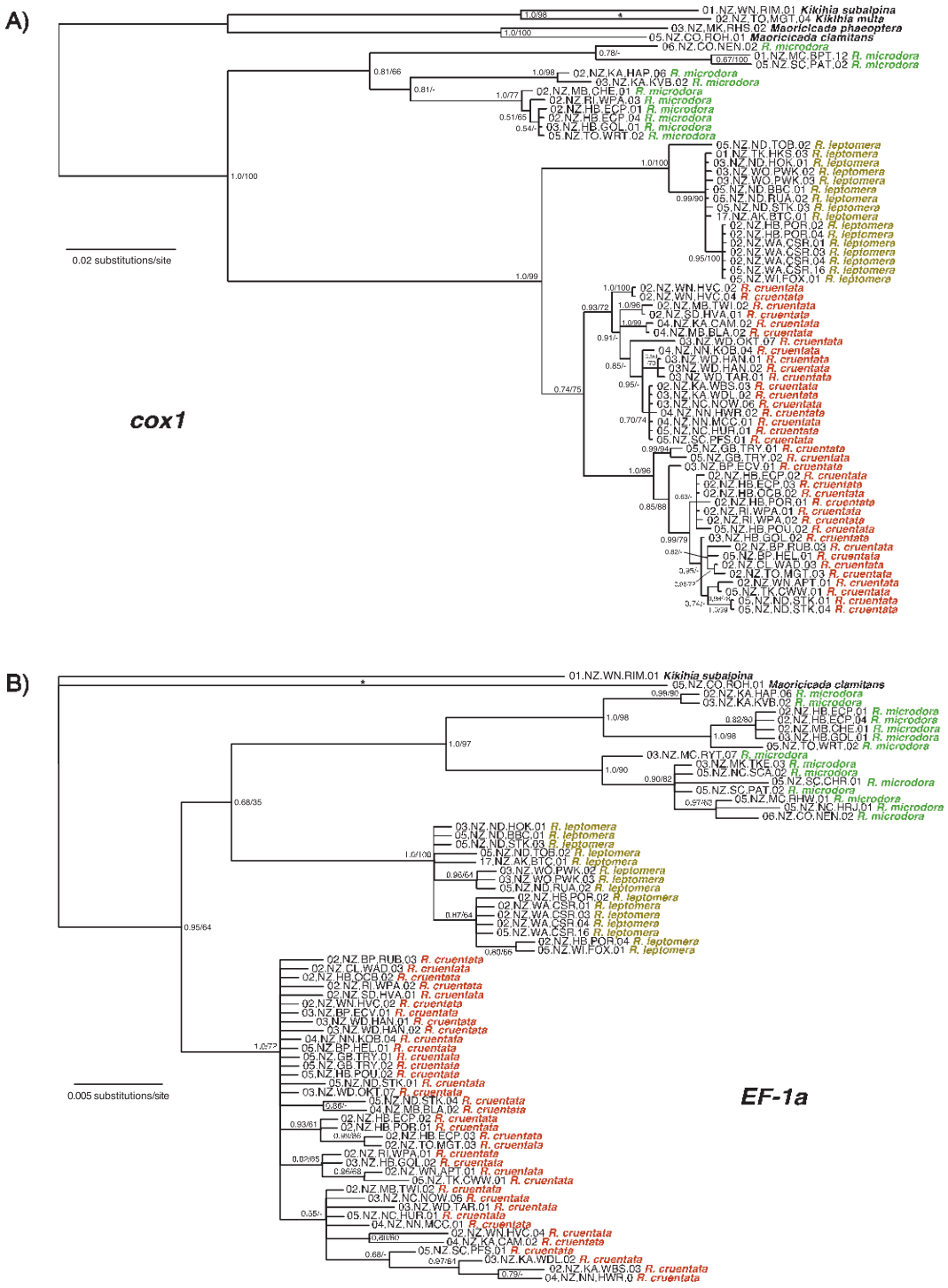

Figure 5. Single-gene Bayesian phylogenetic trees based on mitochondrial *cox1* (1486 bp; A) and nuclear *EF1α* (798 bp; B) using CIPRES v.3.3. Branch support values represent Bayesian posterior probabilities and raxml bootstrap percentages from 1000 non-parametric pseudoreplicates. The number of parsimony informative sites is 239 for *cox1* and 61 for *EF1α*.

and Rangitikei (RI), form a weakly supported subclade distinct from the rest of the NI specimens. Within the mainly SI *R. cruentata* clade, the earliest splits separate samples from the northern part of the range of the clade [Wellington (WN), Marlborough Sounds (SD) and northern Kaikoura (KA)].

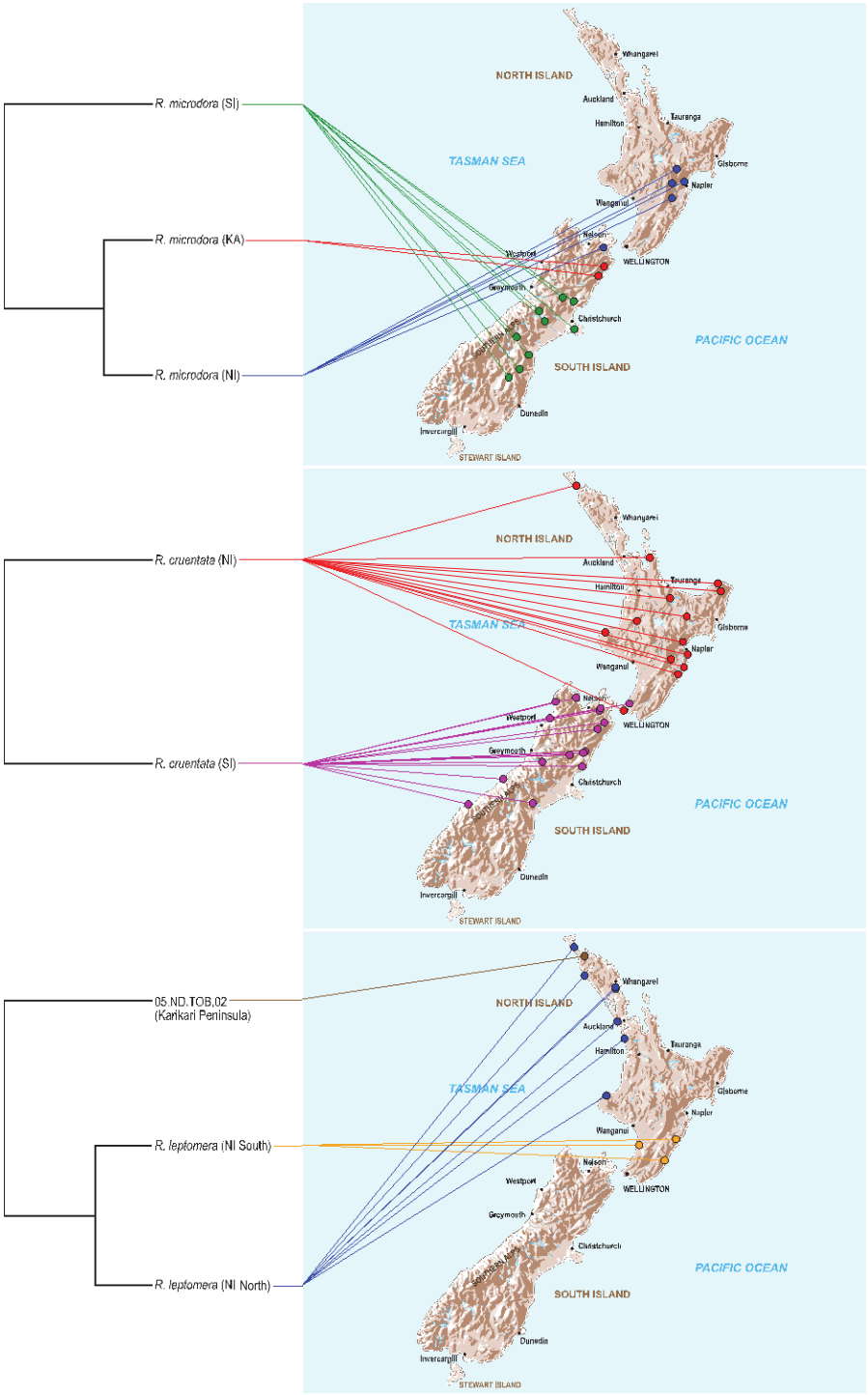

Figure 6. Primary geographical subclades found for the sequenced specimens, mapped for each *Rhodopsalta* species.

Rhodopsalta leptomera

The trees reveal strong support for a split between *R leptomera* along the northern coasts of NI, including Northland (ND), Auckland (AK), Taranaki (TK) and Waikato (WO), vs. the eastern and southern coasts of NI, including Hawkes Bay, Wairarapa (WA) and Wanganui (WI) (Figs 4, 5A). Both individual *cox1* and combined gene trees show one *R. leptomera* specimen from the far north (05.NZ.ND.TOB.02; Karikari Peninsula) as sister to the rest of the clade (Figs 4, 5A).

Rhodopsalta microdora

This species comprises three main clades. The southern SI clade is composed of specimens from North Canterbury (NC), Mid Canterbury (MC), South Canterbury (SC), Mackenzie region (MK) and Central Otago (CO). It is sister to an eastern clade made up of a Kaikoura group (SI) + mixed SI/NI clade composed of specimens from Marlborough (MB) (SI) and Rangitikei, Taupo and Hawkes Bay (NI) districts (Figs 4, 5A).

genetic distances

Corrected (patristic) and uncorrected genetic distances from the *cox1* locus are presented in the Supporting Information (Table S4). Average uncorrected distances between the three species groups are as follows: *Rhodopsalta cruentata–R. leptomera*, 0.031; *R. cruentata–R. microdora*, 0.047; and *R. microdora–R. leptomera*, 0.047. Average uncorrected intraspecific distances were near zero among populations of eastern NI *R. leptomera* and largest among populations of SI *R. microdora* (≤ 0.040). As a whole, *R. microdora* had the greatest intraspecific average distance (0.019) and *R. leptomera* the least (0.003) (Supporting Information, Table S5).

molecular clock dating

The *Beast multispecies coalescent analysis estimated that *Rhodopsalta* diverged from its sister genera, *Maoricicada* and *Kikihia*, between ~5 and 20 Mya (mean 11.6 Mya; see interspecific divergence dates plotted in Fig. 4). The wide confidence interval reflects the uncertainty encoded in the *cox1* molecular clock prior. The earliest split in the *Rhodopsalta* clade is the split between *R. microdora* and the ancestor of *R. cruentata* and *R. leptomera*, with a mean estimate of 5.5 Mya (Fig. 4). *Rhodopsalta leptomera* diverged from *R. cruentata* between 0.8 and 3.6 Mya (mean 2.0 Mya).

Although *Beast cannot be used to estimate dates within assumed populations (species), we present the dated mtDNA gene tree from this analysis (Fig. 7), which can be used to obtain approximate divergence times for geographically coherent intraspecific clades that might correspond to diverging, isolated populations (keeping in mind that this violates the *Beast model assumptions, as discussed later in this paper). Note that mtDNA clade divergence dates necessarily overestimate any corresponding population splits to an unknown degree, which adds to the uncertainty (Edwards & Beerli, 2000). The three deepest *cox1* subclades within *R. microdora* diverged during the Pliocene to early Pleistocene (Fig. 7). The mean estimated divergence date for the split of the central-eastern SI clade from the ancestor of the Kaikoura and Hawkes Bay clades is 2.8 Mya, and the mean estimated date for the Kaikoura/Hawkes Bay split is 2 Mya, about the time *R. leptomera* split from *R. cruentata*. North Island *R. cruentata* split from SI *R. cruentata* between 0.5 and 2.5 Mya (mean 0.9 Mya). These date estimates involve additional uncertainty, which is not reflected in the wide confidence intervals, owing to choice of priors and potential violations of model assumptions (see Discussion).

DISCUSSION

Molecular phylogenetic analysis of *Rhodopsalta*, confirmed by acoustic and morphological data, strongly supports the presence of three monophyletic groups that correspond to the three described species, *R. cruentata*, *R. leptomera* and *R. microdora* (Figs 4, 5). Note that we fix the identity of *R. cruentata* with a lectotype designation in the 'Taxonomic and individual species notes' section below. *Rhodopsalta cruentata* and *R. microdora* occur on both NI and SI, whereas *R. leptomera* resides solely on NI (Fig. 2; Supporting Information, Fig. S1). *Rhodopsalta microdora* ranges along the drier eastern sides of NI (from central Hawkes Bay to Cape Turnagain) and SI (from the Marlborough Sounds to Central Otago and Dunedin regions). *Rhodopsalta cruentata* is more widely distributed, found throughout NI and the northern half of SI from coast to coast. *Rhodopsalta cruentata* and *R. microdora* are generally found living on woody shrubs, with *R. cruentata* ranging from sea level up to ~1200 m a.s.l. and *R. microdora* from low elevation to ~800 m a.s.l. (although we have not sampled many higher-elevation areas of north-eastern SI where *R. microdora* might be found). *Rhodopsalta leptomera* is distributed patchily along the NI coasts in sand dune grass (Fig. 2; Supporting Information, Fig. S1).

The species were previously described primarily on colour pattern and size. Early species descriptions are often incomplete relative to modern species descriptions, (especially in lacking description of genitalic attributes). Given that the descriptions by Fabricius and Hudson have no illustrations and that the hand-drawn colour plates of Myers (1921) are not true to life, we have included photographs of these species taken in the field (Supporting Information, Figs S3–S5) and refer the reader to the well-illustrated field guide by Hills (2018). The male and female genitalia of *R. cruentata* were illustrated by Dugdale (1972) as part of the generic description. At the end of the Discussion, we include 'species notes' to enrich the original descriptions of all three species. In the Supporting Information (Supplementary Materials), we translate the Latin description written by Fabricius (1775) and reproduce the brief formal descriptions created by Myers (1921) and Hudson (1936).

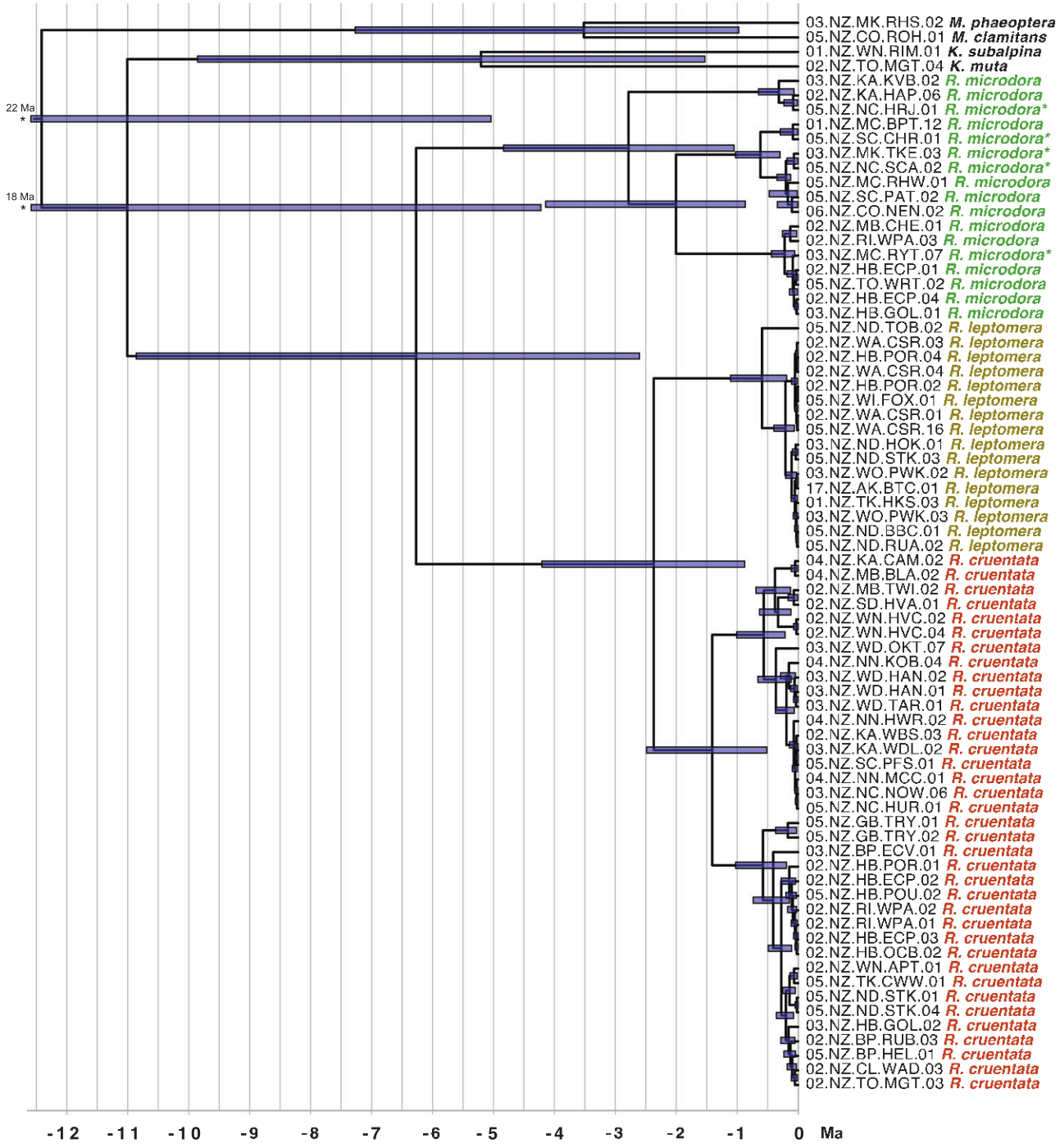

Figure 7. *cox1* chronogram from the *Beast multispecies coalescent analysis, showing divergence times for intraspecific haplotype clades as bars indicating the 95% highest posterior density intervals. Taxa with asterisks were missing *cox1*, and their positions within the species clades are determined by the *EF1α* gene tree.

Colour variation

Rhodopsalta cruentata and *R. microdora* show similar colour variation across the majority of individuals, including green coloration in the proximal half of the fore- and hindwings and along the collar of the pronotum. A minority of individuals are coloured with a more uniform yellow–gold hue rather than green in these areas. Single populations typically have both green and gold wing-vein morphs. Collected specimens suggest that colour variation is minimal within overlap

zones for these two taxa (populations from NC, HB and TO; see Supporting Information (Supplementary Materials). *Rhodopsalta cruentata* specimens from drier north-eastern districts of NI tend to exhibit more orange/red colour compared with their relatives from northwest NI. Specimens of *R. microdora* from southern SI (CO, DN, MK and OL) typically display darker coloration on the thorax, with prominent yellow colouring along the costal margin and abdomen. We hypothesize that the darker coloration amongst these *R. microdora* individuals might be a selective response to the cooler and wetter climate of southern SI. A more thorough morphometric analysis integrating discrete and continuous characters might be a useful avenue for future study, to test this hypothesis, as done in other insect quantitative studies (Sasakawa, 2016; Sontigun *et al.*, 2017; Phanitchant *et al.*, 2019).

Molecular clock dating in relation to palaeogeography

We attempted to incorporate uncertainty in the assumed *cox1* molecular clock rate in our divergence time analysis. No independently estimated *cox1* clock rate exists for *Rhodopsalta* or other NZ cicadas. The wide confidence intervals observed in the estimates partly reflect the broad lognormal prior placed on the substitution rate, reflecting a range of estimates observed in insect *cox1* studies (see Papadopoulou *et al.*, 2010; Marshall *et al.*, 2016). New Zealand cicadas probably all have multiple-year life cycles [e.g. 3–4 years in *Kikihia ochrina* (Walker, 1858) and *Amphipsalta zelandica* (Boisduval, 1835); Logan, 2006 and Logan *et al.*, 2014, respectively] and they live in a cool-temperate climate; therefore, their *cox1* substitution rates could differ from those observed in insects that have shorter life cycles or live in warmer climates (Bromham & Penny, 2003).

Some potentially large sources of error are not accommodated formally by our analysis. The *Beast multispecies coalescent analysis converged on one solution, yielding large effective sample sizes in 1×10^7 generations. However, in preliminary standard relaxed clock analysis of the mtDNA dataset conducted in Beast (unpublished data), we noticed dependence of the outcome on the choice of priors, especially the tree prior (Yule vs. birth–death), with some analyses estimating much younger trees. Large differences between solutions estimated under alternative priors have been observed in analyses calibrated solely by molecular clocks, probably attributable, in part, to the presence of alternative branch-length solutions with similar maximum-likelihood scores (Marshall, 2010; Marshall *et al.*, 2016). Preliminary trials with *Beast suggested less effect of the tree prior for the *Rhodopsalta* analysis. It might be that the multiple-gene coalescent model is less influenced by tree prior choice or that the small number of species-level lineages in the tree is involved. Additional uncertainty is caused by likely violations of the assumptions of the coalescent model. For example, random mating within the assumed species is unlikely because intraspecific spatial genetic structure is apparent (especially in *R. microdora*). Lastly, when considering the mtDNA clade splits as a proxy for intraspecific population divergences, an unknown amount of error is present, because gene tree splits necessarily precede population splits (Edwards & Beerli, 2000). This can be observed by comparing the date of the *R. cruentata–R. leptomera* mtDNA gene tree split (2.4 Mya; Fig. 7) with that of the corresponding species tree split (2.0 Mya; plotted in Fig. 4).

Rhodopsalta evolutionary scenarios

Rhodopsalta microdora split from its congeners ~5.5 Mya according to the *Beast analysis (see Fig. 4), at the beginning of the Pliocene epoch. At this time, NI was separated from SI by a wide sea strait, the Manawatu Strait (Fig. 1). We suggest a few hypotheses to shed light on the potential evolutionary scenarios for *Rhodopsalta*. These scenarios are based on mean date estimates, but alternative scenarios might be supported if the true dates are substantially different for reasons noted above.

Evolutionary scenario 1

The *Rhodopsalta* ancestor originated on NI. Later, ~5.5 Mya, the ancestor of *R. microdora* colonized SI across the strait, while *R. cruentata* and *R. leptomera* diverged on NI. The Kaikoura *R. microdora* clade separated from other SI populations after 2.8 Mya and then spread back to NI after ~2 Mya, creating the NI Hawkes Bay clade. Repeated NI–SI splits with Pliocene/Pleistocene dates have been observed in other NZ cicada clades. The NI–SI split for *Maoricicada cassiope* (Hudson, 1891) is at ~2 Mya (range ~1–4 Mya, based on other intervals given in the study; Buckley & Simon, 2007), whereas the *Maoricicada campbelli* (Myers, 1923) NI clade split from its SI relatives ~1 Mya (range ~0.5–2.0 Mya; Hill *et al.*, 2009). The split between *Kikihia subalpina* (Hudson, 1891) (NI) and *Kikihia* 'flemingi' (SI) was estimated to be ~0.5–1.0 Mya (Marshall *et al.*, 2009), when rising sea levels in interglacial periods of the Mid-Pleistocene Transition (Wood *et al.*, 2017) narrowed the land bridge connecting NI and SI (Lewis *et al.*, 1994) (see also Fig. 1).

Evolutionary scenario 2

The *Rhodopsalta* ancestor originated on SI, and then ~5.5 Mya the ancestor of *R. cruentata* + *R. leptomera*

colonized NI. In the early Pliocene, *R. microdora* might have adapted to the drier eastern sides of the Southern Alps as mountain formation intensified. Although there was mountainous terrain in NI during the late Miocene–early Pliocene, NI was still predominantly low lying (Wood *et al.*, 2017). Given the lack of a tall axial mountain range along the eastern portion of NI before 1 Mya (Fig. 1), it seems more plausible that *R. microdora* evolved on SI. The ancestor of the *R. microdora* Kaikoura (SI) and Hawkes Bay (NI) clades might have occupied eastern regions of SI between 5.5 and 2.8 Mya, when it finally diverged from the rest of SI *R. microdora* and later colonized NI when the current south-east coast of NI was uplifted, probably recently, given the low genetic divergence of the NI *R. microdora* clade.

In either scenario, we suggest that *R. cruentata* and *R. leptomera* diverged from each other on NI ~2 Mya, before the southern sea strait was obliterated by uplift (Fig. 1). *Rhodopsalta cruentata* might have invaded the SI during the Pleistocene when both islands were connected owing to low sea levels. The NI and SI *R. cruentata* clades might have diverged from each other later in the Pleistocene, ~0.5–1.0 Mya. The fact that there is little geographical structuring in *R. cruentata* on NI and SI might reflect a rapid spread, with intermittent ice-age habitat changes limiting refugia during cold climate periods, leading to population bottlenecks.

dispersal theories

Most interesting within the *R. cruentata* SI clade is the presence of NI Wellington individuals, strongly supported as members of the SI clade and weakly supported as sister to the rest of the SI specimens in the combined data tree. At some point in the past, individuals might have flown from NI to SI, or vice versa, or they might have been blown over during storms (similar to cases of probable *Kikihia* dispersal to the Norfolk, Kermadec and Chatham Islands; Marshall *et al.*, 2008, 2011; Arensburger *et al.*, 2004b).

Alternatively, *Rhodopsalta* individuals might have dispersed through human transportation. Fleming (1975b) hypothesized that NI *Kikihia scutellaris* (Walker, 1850) was transported to SI by the Wellington ferry, upon discovering specimens from Picton collected by A. D. McEwen in 1966 (Fleming, 1967). Pairwise genetic distances between the Wellington and SI *R. cruentata* individuals argue against recent transport as hypothesized for *K. scutellaris* by Hill *et al.* (2005). However, more likely might be a migration event that occurred during the Last Glacial Maximum (LGM; ~31–16 kya) or one of the previous Late Pleistocene cold phases. Cold temperatures and glaciers were at their most extreme during the LGM, exposing vast areas of the continental shelf of Zealandia when sea levels became 100 m lower than what they are today (McSaveney, 2007). The Cook Strait gap, which typically divides NI and SI, was substantially narrowed (Lewis *et al.*, 1994), increasing the possibility of *Rhodopsalta* overwater dispersal between islands.

The split between the *R. microdora* SI Kaikoura clade and its NI sister clade occupying the Hawkes Bay region dates to perhaps 1–2 Mya (keeping in mind that the gene tree divergence pre-dates the population split), a period when the south-east of NI was connected to the Kaikoura region of SI via an eastern land bridge (Fig. 1). However, given that the eastern NI *R. microdora* samples are all genetically similar and closely related to a specimen from far north-eastern SI (02.MB.CHE.01), the NI populations of this species might be derived recently from SI, perhaps even post-LGM.

divergence levels, sympatry and hybridization

Rhodopsalta cruentata and *R. microdora* overlap in parts of their ranges (Fig. 2; Supporting Information, Fig. S1) and sometimes sing in close proximity, as do *R. cruentata* and *R. leptomera*, implying the potential for interspecific mating and hybridization. *Rhodopsalta microdora* and *R. leptomera* do not occur in sympatry, but they do exist in close geographical proximity, < 1 km, near Porangahau. Both current and past hybridization in *Kikihia* contact zones have been documented in the form of intermediate song phenotypes and conflicts between nuclear and mitochondrial phylogenies (Marshall *et al.*, 2011, 2016; Banker *et al.*, 2017). More ancient introgression events have been inferred in *Maoricicada* (Buckley *et al.*, 2006), the 'M' of the KMR radiation. No evidence of hybridization between *Rhodopsalta* taxa has been recorded, but songs from *Rhodopsalta* contact zones have not been examined as carefully as in *Kikihia*.

The strong similarity of the songs of *R. leptomera* and *R. microdora*, which differ consistently by only one click in the cueing section, is unexpected given their ~5.5 Myr of divergence, especially considering the much greater difference observed between *R. leptomera* and its sister species *R. cruentata*. The degree of song divergence of *R. leptomera* and *R. microdora* is similar to that observed between parapatric subspecies-level pairs of *Kikihia*, most of which are estimated to have diverged in the last 2 Myr (Fleming, 1973; Marshall *et al.*, 2008, 2011). Further exploration of the potential contact zone between these two species near Porangahau would be interesting.

phylogeographical structure

Although *R. microdora* subclades possess some geographical structure, the phylogeographical

structure of both *R. cruentata* and *R. leptomera* appears minimal. This might be related to the fact that *R. microdora* occurs in drier shrubby habitats that might have had greater persistence during late Pleistocene climate cycles. Other species of NZ cicadas that share similar dry-adapted shrub ecologies show more geographical structure than their relatives inhabiting wetter environments. For example, the eastern NI *Kikihia cutora cumberi* Fleming, 1973 clades possess more structure than their sister western clade (Ellis *et al.*, 2015), and the grass species *Kikihia* 'aotea east', which is co-distributed with *K. c. cumberi*, displays structured northern and southern clades on NI, suggesting minimal migration between them in the past (Marshall *et al.*, 2011; Ellis *et al.*, 2015). In the *Amphipsalta–Notopsalta* radiation, the two species that live on exposed banks [*Notopsalta sericea* (Walker, 1850)] and dry eastern hillsides [*Amphipsalta strepitans* (Kirkaldy, 1891)] show clear geographical structure, whereas the two species from mesic forest habitats do not [*Amphipsalta cingulata* (Fabricius, 1775) and *A. zelandica*] (Marshall *et al.*, 2012). *Amphipsalta cingulata* prefers forest edges and scrubby slope vegetation but, like *A. zelandica*, it could be limited by large body size, requiring warm temperatures for flight. This explanation would not be applicable to any of the *Rhodopsalta* species because none occurs in forest habitats.

The lack of genetic structure in *R. leptomera* is surprising because it is a small-bodied species, presumably with limited dispersal ability, and because it is restricted to isolated patches of dune vegetation. Two hypotheses could explain the lack of structure. Large population sizes could slow allopatric divergence, but comparative demographic data are not available for testing this possibility. Alternatively, Late Pleistocene cold phases (Carter & Gammon, 2004; Carter, 2005) might have forced *R. leptomera* populations into one or two small refugia, resulting in population bottlenecks, as has been proposed for other NZ cicadas, such as *A. cingulata* and *A. zelandica* (Marshall *et al.*, 2012). True *Kikihia muta* (Fabricius, 1775) is suggested to have spread down the east coast of the SI after the LGM, leaving widely distributed populations across both islands with little genetic differentiation (Marshall *et al.*, 2011; Ellis *et al.*, 2015). Furthermore, recent dispersal along the coasts during expansion from refugia could have been facilitated in *R. leptomera* by lower sea levels, which would have increased coastal plains and perhaps connected sandy beach habitats around NI. The populations of *R. leptomera* we see today might be remnants of a larger recent distribution.

Aside from one *R. leptomera* individual from the Karikari peninsula (05.NZ.ND.TOB.02) that is sister to all others, the molecular phylogenies suggest a shallow division separating southern and eastern populations in Hawkes Bay, Wairarapa and Wanganui from populations in western regions (Figs 4, 5). An east–west division was found in NI *Kikihia* by Ellis *et al.* (2015), suggesting a biogeographical boundary, which they named 'Cockayne's Line'. This line was first noted by the botanist Leonard Cockayne (1911), in reference to the axial mountain range that splits plant communities of the southern NI into western and eastern divisions. Axial mountain uplift began ~2 Mya and continues today (Te Punga, 1954; Bunce *et al.*, 2009). This line also demarcates genetic breaks for a variety of NZ organisms, such as the parasitic plant *Dactylanthus taylorii* Hook.f. (Balanophoraceae) (Holzapfel *et al.*, 2002), the stick insect *Clitarchus hookeri* (White, 1846) (Buckley *et al.*, 2010) and other NZ cicadas, such as *Kikihia cutora*, *Kikihia* 'aotea east' and *Kikihia* 'aotea west' (Marshall *et al.*, 2011) and *N. sericea* (Marshall *et al.*, 2012; Ellis *et al.*, 2015).

Songs and Pair-formation Behaviour

Published observations show that species in the NZ genera *Amphipsalta* (Dugdale & Fleming, 1969), *Kikihia* (Fleming, 1973; Lane, 1984, 1995) and *Maoricicada* (Buckley *et al.*, 2006; Hill *et al.*, 2009) exhibit a 'duet' pair-formation process, in which a receptive female responds with a rapid, audible flick of the wings to a particular element or echeme in a conspecific song of the male, which we call the song cue. Males perceiving these responses then attempt to locate the female (in North American *Magicicada* Davis, 1925, the male searches aurally and visually for the female response; Cooley & Marshall, 2001). We have recorded anecdotal evidence of such timed, species-specific female wing-flick signalling in all known described and undescribed NZ cicada species, now including all three *Rhodopsalta* species, along with many Australian and American relatives in the tribe Cicadettini (e.g., Gwynne, 1987; Marshall & Hill, 2009; Popple & Marshall, 2016). In some species, we have made direct observations of female wing-flick replies to male song, along with the resulting copulation, and in most species we have attracted males with finger-snaps produced after a suspected cueing element.

While illustrating the species-specific songs of *Kikihia* species, Marshall *et al.* (2008) distinguished introductory and cueing song sections, between which the male alternates regularly (usually several times per minute; also see examples in the papers by Fleming, 1973; Lane, 1995). The cueing section contains the song cue, which is usually repeated one or more times and sometimes alternated with short additional echemes. The introduction, which in *Kikihia* is often more structurally complex, presumably primes the female

and contributes to mate recognition, although these functions have not been tested carefully. Introductory and cueing components are also observed in songs of the other large NZ genus, *Maoricicada*, except that in many species only one cueing echeme is produced before returning to the introduction (see oscillograms in the paper by Buckley *et al.*, 2006). The acoustic behaviour of *Rhodopsalta* resembles, in part, that of the *Amphipsalta* species *A. zelandica* and *A. cingulata*, in that males may produce one song section for ≥ 1 min at a time. To a lesser degree, extended introductory phase singing is also observed in some *Kikihia* species, such as *K. ochrina* and *K. cutora cutora* (Marshall *et al.*, 2008).

why only three species?

It is remarkable that *Rhodopsalta* contains only three taxa but belongs to the species-rich KMR clade. In terms of diversity, the genus has more in common with the small *Amphipsalta–Notopsalta* radiation. Interestingly, *Amphipsalta* and *Rhodopsalta* are absent from southernmost SI and *Notopsalta* is found only on NI, as is *R. leptomera*. Extinction events were much greater on the SI throughout glacial periods, given the drastic changes in both temperature and habitat. Intense vegetational shifts are apparent from marine pollen records gathered off the eastern coast of NZ (Wright *et al.*, 1995; Ryan *et al.*, 2012; Sikes *et al.*, 2013).

At the time of the LGM, the southern SI was dominated by grass and shrublands, with central regions characterized by mixed conifer–shrubland–herbaceous communities and northern areas (NI included) experiencing drastic shifts in forest types (conifers and broadleaves), with grasslands being sparse (Heusser & Van de Geer, 1994; Mildenhall, 2003; Alloway *et al.*, 2007). It might be that genera such as *Rhodopsalta* and *Notopsalta* exhibit lower physiological tolerance to cool temperatures than either *Kikihia* or *Maoricicada*. *Kikihia* and *Maoricicada* inhabit greater ranges in latitude and elevation than *Rhodopsalta*, *Amphipsalta* and *Notopsalta*. Although we have found *R. cruentata* on Mount Ruapehu at an elevation of 1200 m a.s.l., this location sits at a relatively low latitude. *Kikihia* species are known to reach elevations of 1500–1600 m a.s.l., even in some central SI regions, and some *Maoricicada* reach 1900 m a.s.l. as far south as Treble Cone (Buckley & Simon, 2007). *Kikihia* and *Maoricicada* each have at least one species that apparently survived the LGM in the far south (*Kikihia* 'murihikua' and *Maoricicada otagoensis maceweni* Dugdale & Fleming, 1978). Limited climatic tolerance in *Rhodopsalta* would imply greater population extinctions in central and southern NZ during Pleistocene cold shocks, increasing the chance of Pleistocene bottlenecks; both *Kikihia* and *Maoricicada* are hypothesized to have survived in many different Pleistocene refugia (Buckley & Simon, 2007; Marshall *et al.*, 2009).

taxonomic and individual species notes

Rhodopsalta cruentata *(Fabricius, 1775)* *(Supporting Information, Figs S3, S4, S8)*

Rhodopsalta cruentata was described by I. C. Fabricius in 1775 as *Tettigonia cruentata* (see translation of the original Latin in the Supporting Information, Supplementary Materials). The description was based on specimens collected during Cook's first *Endeavour* voyage by the naturalist Joseph Banks or one of his associates, as indicated by 'Mus. Banks' in the original description (see also Radford, 1981). *Rhodopsalta cruentata* possesses, among other features listed in that description, a prominent yellow midline stripe on the head, yellow forewing costa, and prominent red bands on the margins of all but the first or second abdominal segments. In addition, the proximal wing veins are green, the cruciform elevation is uniformly pale yellow–green to red in colour, and a broken silvery midline stripe is usually present from the head to at least the first abdominal segments.

Zimsen (1964: 290) and Larivière *et al.* (2010: 54) state that two syntypes of this species are lodged at The Natural History Museum in London (NHM). This matches the NHM entomology register from 1863, which records the transfer of two types from the Linnean Society (B. Price, pers. comm.). The two specimens are kept in a separate drawer together with other Banks collection material, and they are accompanied by an unattached outlined label that reads, on two lines, 'Tettigonia cruentata / Fab. Entomol. p. 680 n.10' and a second unattached small underlined label reading 'Type'. The outlined label text resembles other labels attributed to Fabricius by Radford (1981).

Both syntypes were photographed for us by B. Price. One of them, number BMNH(E)#668764 (Supporting Information, Fig. S6), is a poor match to the description and current concept of *R. cruentata*. This specimen is ~13.5 mm in body length (tip of head to tip of abdomen). In addition to its NHM code label, it bears handwritten labels reading 'New Zealand.' and '63 / 47'. (The latter numbers are written one above the other and indicate entry 47 for 1863 in the NHM specimen register mentioned above.) It has a black ground colour, a small, partial midline stripe on the pronotum, a dark midline stripe through the cruciform elevation and metanotum, and muted, narrow yellow bands on the abdomen, all features that are consistent with *N. sericea* rather than *R. cruentata*.

The other NHM syntype, male specimen BMNH(E)#668765 (Fig. 8), bears a red-circled round label that reads 'Type' and a handwritten round label ambiguously reading either '63 / 47' or (less likely) '69 / 47', in addition to its NHM specimen code label. The specimen has a body length of ~16 mm, has only one (left) antenna protruding anteriorly (the other is tucked beneath the head) and is missing the left forewing. The features of this specimen are consistent with the current concept of *R. cruentata*, especially the prominent red bands on the margins of the abdominal segments, the prominent yellow midline stripe on the pronotum and the yellow forewing costa. In addition, the specimen possesses a declivous, unflanged pronotum and a subacute, subascending upper pygofer lobe, which is a combination of attributes reported for *Rhodopsalta* but not the other NZ genera (for illustrations of the male and female genitalia of *R. cruentata*, see Dugdale, 1972).

Andrews & Gibbs (1989: 105–106) reported finding an unlabelled male of *N. sericea* pinned alongside an *R. cruentata* specimen that they inspected in Fabricius' personal collection now kept at the Zoologisk Museum, Copenhagen. We believe that the Copenhagen specimens are the two indicated by Zimsen (1964: 290) with the parenthetical phrase 'Kiel 2 specimens', because the Zoological Museum in Kiel now holds no material of *Tettigonia cruentata* (M. Kuhlmann, pers.

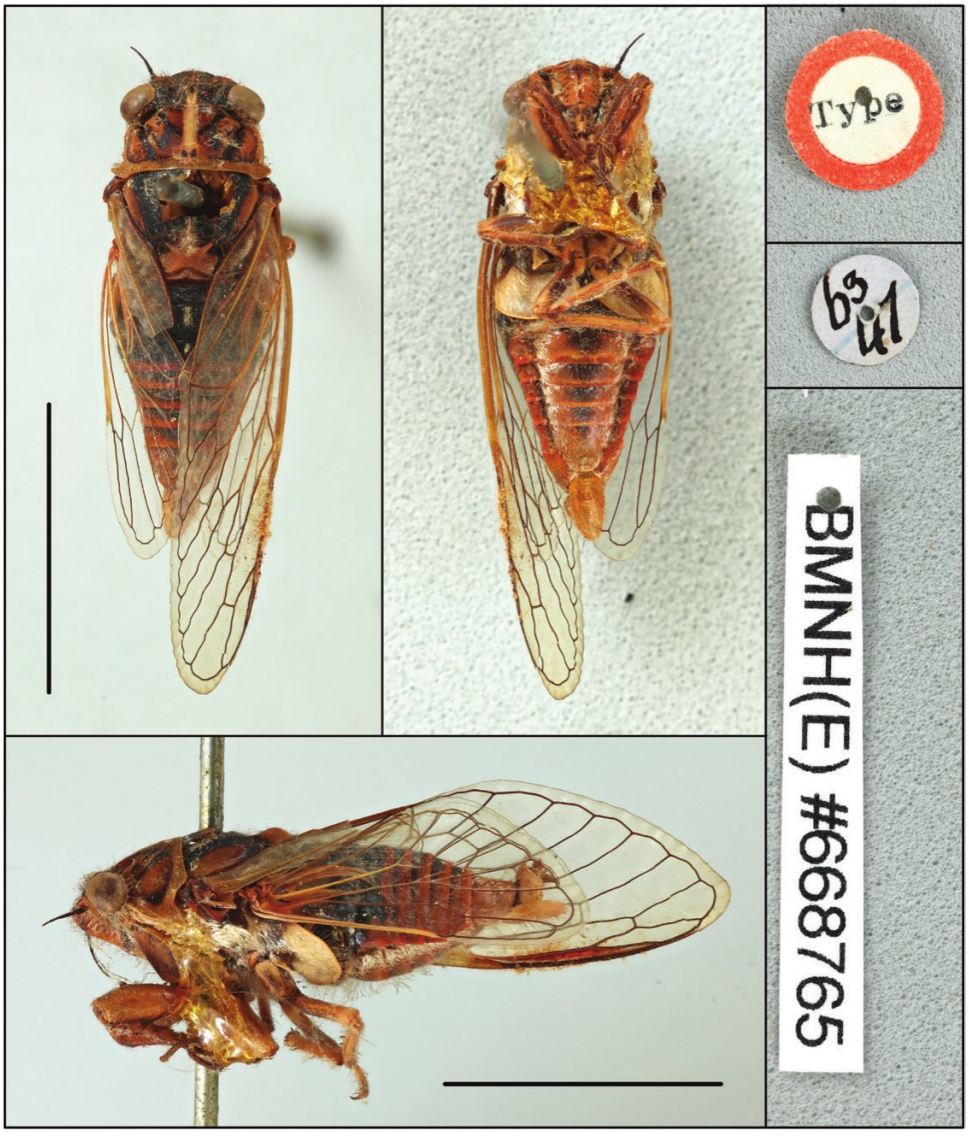

Figure 8. Lectotype of *Tettigonia cruentata* Fabricius, 1775, type species of genus *Rhodopsalta* Dugdale, 1972, with attached labels shown. Scale bars: 1 cm. Photographs by B. Price.

comm.). Photographs of these two specimens sent to us by L. Vilhelmsen confirm the report by Andrews and Gibbs. One specimen is clearly an *N. sericea* male and bears only a determination label from J. S. Dugdale dated 1987. The other matches the description of *R. cruentata* and bears a small handwritten label with what looks like the species epithet 'cruentata', consistent with other labels made by Fabricius (Zimsen, 1964: 10). Not being part of the Banks collection in London, the two Copenhagen specimens are not regarded as syntypes.

To eliminate the uncertainty caused by the heterogeneous syntype series for the identity of *R. cruentata* and for genus *Rhodopsalta*, of which *R. cruentata* is the type species, we designate NHM specimen BMNH(E)#668765 as the lectotype for *Tettigonia cruentata* Fabricius, 1775 in accordance with Article 74.7 of the Code of Zoological Nomenclature (ICZN, 1999). Given that the other NHM syntype is not a *R. cruentata* specimen, we designate no paralectotype.

Rhodopsalta cruentata is the most widely distributed species of the genus, and it can be found singing on a wide range of vegetation types, ranging from grasses and sedges, including those on sand dunes, to native manuka myrtle (*Leptospermum scoparium* J.R.Forst. & G.Forst.) to introduced species, such as common alder (*Alnus glutinosa* L.) and kiwifruit (Chinese gooseberry, *Actinidia* Lindl.). Adults are active from November to April (Myers, 1929b; Larivière *et al.*, 2010).

Rhodopsalta microdora *(Hudson, 1936) (Supporting Information, Figs S4, S7, S8)*

Rhodopsalta microdora was described by G. V. Hudson as *Melampsalta microdora* from two female specimens collected at Cape Kidnappers on the NI (see Supporting Information, Supplementary Materials); the smaller of these two syntypes was designated as the lectotype by Fleming & Ordish (1966). No male specimens were discussed by Hudson, who referred to the species as a diminutive version of *Kikihia scutellaris* Walker, 1850 without mentioning *R. cruentata*. Dugdale (1972) omitted mention of *R. microdora* while listing *R. cruentata* and *R. leptomera* for his description of genus *Rhodopsalta*, and Larivière *et al.* (2010) discussed the uncertainty of the status of *R. microdora*. In many NZ cicadas, females are substantially different in appearance from males of the same species, and they are generally paler, often lacking well-defined aspects of species-specific coloration commonly observed in males. This has probably contributed to the neglect of Hudson's taxon.

We examined a large series of *Rhodopsalta* specimens from Cape Kidnappers, the type location of *R. microdora*, collected after the description of *R. microdora* and kept at the National Museum of New Zealand Te Papa Tongariro (also discussed by Larivière *et al.*, 2010). *Rhodopsalta microdora* and *R. cruentata*, as here defined, are broadly sympatric in that region (but not *R. leptomera*). Our findings suggest that Hudson's selection of a female syntype series might be attributable to clearer differentiation from *R. cruentata* in that sex. The male *Rhodopsalta* specimens from Cape Kidnappers range from larger ones tending to possess a prominent silvery midline stripe, as in *R. cruentata*, to smaller males with often subtler or nearly absent stripes, as described for Hudson's female *R. microdora* specimens, but there is no large break in size to separate the males of the two species, and the silvery pubescence varies considerably throughout the series, perhaps owing to wear. In contrast, the nine female specimens group into two distinct clusters (see Supporting Information, Supplementary Materials), the smaller one with dimensions accommodating those of the *R. microdora* lectotype and paralectotype, which are also lodged at Te Papa. We provide photographs of the *R. microdora* lectotype (Supporting Information, Fig. S7), in addition to a comparison of *R. cruentata* and *R. microdora* females from the Cape Kidnappers series (Supporting Information, Fig. S8). Therefore, we are confident that the smaller-bodied *Rhodopsalta* species that we are calling *R. microdora*, which we have collected from Ocean Beach south of Cape Kidnappers, is indeed Hudson's species.

We note that the path taken by the *Endeavour* on its first voyage also helps to show that the *R. cruentata* lectotype specimen is unlikely to belong to the species we have identified as *R. microdora*. According to Banks's journal (Banks, 1896), on the NI the *Endeavour* anchored at Poverty Bay, Anaura Bay, Tolaga Bay, Mercury Bay, the Thames River tidal portion and the Bay of Islands. *Endeavour* then sailed along the northernmost point of NI and down the west coast without stopping until arriving at the Marlborough Sounds (SI) and anchoring at Ship Cove in Queen Charlotte Sound. Although *Endeavour* circumnavigated the SI, it did so without stopping until it returned to the Marlborough Sounds and anchored in Low Neck Bay, D'Urville Island. Based on our records (Fig. 2), none of these locations is within the range of the taxon we have identified as *R. microdora*. We have not surveyed D'Urville Island, but this location lies ~50 km north of the nearest known populations of *R. microdora*, and it was visited by Banks in late March, which is late in the season for that species, based on our records.

Rhodopsalta microdora inhabits drier scrub environments along the eastern sides of NI and SI. We have often found this species singing on matagouri shrubs (*Discaria toumatou* Raoul).

Rhodopsalta leptomera *(Myers, 1921) (Supporting Information, Fig. S5)*

The largest of the three species in this genus, *R. leptomera*, is readily distinguished by its straw-to orange–yellow-coloured legs and forewing costal margins. The species has a longer, more slender body and wings (on average) than its congeners and more abundant short silvery pubescence (Myers, 1921). *Rhodopsalta leptomera* is restricted to the NI (Fig. 2; Supporting Information, Fig. S1), where it uses dune grass and sedge species such as the introduced marram [*Ammophila arenaria* (L.) Roem. & Schult.] and endemic pingao [*Ficinia spiralis* (A.Rich.) Muasya & de Lange] (Myers, 1929a). *Rhodopsalta leptomera* is unique among NZ cicadas in its apparent dependence upon coastal dune habitat. Other, unrelated cicadas inhabiting saline environments can be found in the south-eastern USA (genus *Diceroprocta* Sta□l, 1870), Argentina (*Derotettix* Berg, 1882; Simon *et al.* 2019), South Africa [*Azanicada zuluensis* (Villet, 1987); Villet & Van Noort, 1999], Queensland, Australia [*Arunta perulata* (Gue□rin-Me□neville, 1831); Sanborn, 1996; Sanborn *et al.*, 2004], south-eastern Australia [the 'sand fairy', *Sylphoides arenaria* (Distant, 1907); (Moulds, 1990, 2012)] and NZ (*Kikihia* 'tuta' along SI saline mud flat sedges and grasses). Adults are active from November to March (Myers, 1929b).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Google map depicting New Zealand localities for the 70 *Rhodopsalta* specimens in this study. Coloured dots signify the following: green, *Rhodopsalta microdora*; red, *Rhodopsalta cruentata*; black, *Rhodopsalta leptomera*. Source: https://www.google.com/maps

Figure S2. Bayesian *cox1* (A) 5′ and (B) 3′ segment trees with numt sequences included, and with Bayesian and maximum-likelihood branch supports shown.

Figure S3. Field photograph of *Rhodopsalta cruentata* from the Cam River crossing on the Molesworth/Awatere Valley Road. Photograph: C. Simon.

Figure S4. Upper image: *Rhodopsalta microdora* (left) and *Rhodopsalta cruentata* from Pine Valley Stream at Wairau River, South Island. Lower image: *R. microdora* (top) and *R. cruentata* (bottom) from the same location.

Figure S5. Upper image: male *Rhodopsalta leptomera* from Porangahau Beach, south of Napier (HB.POR). Lower image: male from Oakura Beach, Taranaki (TK.OAK) with unusually blue eyes. Photographs: K. Hill.

Figure S6. Specimen BMNH(E)#668764, syntype of *Tettigonia cruentata* Fabricius, 1775, now identified as *Notopsalta sericea*. Scale bar: 1 cm. Photograph: B. Price.

Figure S7. Photograph of *Rhodopsalta microdora* lectotype specimen taken at the National Museum of New Zealand Te Papa Tongariro. Photograph: D. Marshall.

Figure S8. Photograph comparing size difference between probable *Rhodopsalta cruentata* (left) and *Rhodopsalta microdora* (right) females taken from the type location for *R. microdora* (Cape Kidnappers series, National Museum of New Zealand Te Papa Tongariro). Photograph: D. Marshall.

Table S1. *Rhodopsalta* specimens, locality, collection data and loci sequenced for each individual. Asterisked taxa represent outgroups from *Kikihia* and *Maoricicada*. Loci sequenced successfully for a given specimen are marked with an 'x'.

Table S2. Primers and polymerase chain reaction annealing temperatures used.

Table S3. Dataset statistics for nuclear and mitochondrial genes, excluding outgroups and including partition-specific substitution models from PartitioNfiNder2.

Table S4. Uncorrected and model-corrected (patristic, derived from the mrBayes tree) *cox1* genetic distance matrix of *Rhodopsalta* specimens. The uncorrected matrix is displayed by the lower-left triangle, and the corrected matrix is displayed by the upper-right triangle.

Table S5. Average uncorrected intraspecific and interspecific genetic distances of *Rhodopsalta* clades from mitochondrial *cox1*.