ORIGINAL ARTICLE

Evolution and phylogeny of the New Zealand cicada genus *Kikihia* Dugdale (Homoptera: Auchenorrhyncha: Cicadidae) with special reference to the origin of the Kermadec and Norfolk Islands' species

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ABSTRACT

Aim Determine the phylogeny and dispersal patterns of the cicada genus *Kikihia* in New Zealand and the origin of the Norfolk, Kermadec, and Chatham Island cicadas.

Location New Zealand, Norfolk Island, Kermadec Islands and Chatham Island.

Methods DNA sequences from 16 species and four soon to be described species of cicadas from New Zealand and Norfolk Island (Australia) were examined. A total of 1401 base pairs were analysed from whole genome extraction of three mitochondrial genes (cytochrome oxidase subunit II, ATPase6 and ATPase8). These DNA sequences were aligned and analysed using standard likelihood approaches to phylogenetic analysis. Dates of divergences between clades were determined using a molecular clock based on Bayesian statistics.

Results Most species in the genus *Kikihia* diverged between 3 and 5 million years ago (Ma) coincident with a period of rapid mountain building in New Zealand. Cicada species on the Kermadec and Norfolk Islands invaded recently from New Zealand and are closely related to the New Zealand North Island species *Kikihia cutora*.

Main conclusions Speciation in the genus *Kikihia* was likely due in large part to the appearance of new habitats associated with the rise of the Southern Alps, starting *c.* 5 Ma. Dispersal of *Kikihia* species within mainland New Zealand probably occurred gradually rather than through long-distance jumps. However, invasion of Norfolk, the Kermadecs and Chatham Islands had to have occurred through long-distance dispersal.

Keywords

Cicada, New Zealand, phylogeny, *Kikihia*, dispersal, molecular clock.

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INTRODUCTION

New Zealand cicadas are a young group of insects, derived from trans-oceanic dispersal since the Pliocene (Arensburger, 2002; Buckley *et al.*, 2002). They are divided into five genera: *Kikihia* Dugdale (28 estimated species, some not yet described), *Maoricicada* Dugdale (19 estimated species, some not yet described), *Rhodopsalta* Dugdale (three estimated species, one not yet described), *Notopsalta* Dugdale (one species endemic to New Zealand), and *Amphipsalta* Fleming (three species). The evolution of the sub-alpine *Maoricicada* species was examined by Buckley *et al.* (2001a,b,c). Here we focus on the evolution of the genus *Kikihia*. Species in this genus are found throughout the North and South Islands, on surrounding smaller islands (Stewart Island, etc.), and on the more distant outer islands: Norfolk (Australia), the Kermadec (New Zealand), and Chatham (New Zealand) Islands.

The genus *Kikihia* was established by Dugdale (1972) for 11 species previously belonging to the genus *Cicadetta*. Later Fleming (1973, 1984) added four species to this genus (*K. laneorum* Fleming, *K. dugdalei* Fleming, *K. horologium* Fleming and *K. paxillulae* Fleming). In the latter work he divided the genus *Kikihia* into three taxonomic groups based on habitat preference: (i) the 'shade-singing' cicadas [*K. scutellaris* (Walker) and *K. cauta* (Myers)], (ii) the 'green foliage cicadas' [*K. subalpina* (Hudson), *K. laneorum, K. cutora* (Walker), *K. ochrina* (Walker), *K. dugdalei, K. horologium, K. paxillulae* and a suggested species, 'tasmani' identified by Fleming and Dugdale], and (iii) the 'grass and scrub' cicadas [*K. angusta* (Walker), *K. convicta* (Distant), *K. longula* (Hudson), *K. muta* (Fabricius) and *K. rosea* (Walker) plus several suggested species nicknamed 'murihikua'', 'balaena', 'nelsonensis' and 'peninsularis']. The first two groups were treated in a series of publications (Fleming, 1973, 1975a, 1984); however, the third group was referred to in those publications but never treated in detail. The personal correspondence between Charles Fleming and John Dugdale (archives of the New Zealand Arthropod Collection, Mount Albert) makes it clear that they intended to publish descriptions of these suggested species at a later date. These suggested species were included in the present analysis because they represent a significant portion of the species in this genus and have been well defined in the Fleming-Dugdale correspondence. CS is currently planning a revision of the *Kikihia* that will include these suggested species. An additional suggested species collected during the course of this work will be referred as 'NWCM' (D. Marshall, J. Cooley, K. Hill and C. Simon, unpubl. data). One of the most common *Kikihia* species, *K. muta*, was not included in this analysis. Individuals identified as *K. muta* appear to form a complex of several species and/or subspecies. This is the subject of a thorough phylogeographic study currently underway (D. Marshall, K. Hill, J. Cooley and C. Simon, unpubl. data). Because of the complexity and the uncertainty of the identity and distribution of the various members of this group no representative was included here.

Several hypotheses of phylogenetic relationships among *Kikihia* species have been proposed. In his early work Myers (1921, 1929) hypothesized that all New Zealand cicadas were derived from a single invasion of New Zealand. From this single invasion, somewhere in the northern part of the North Island, populations would have moved south, rapidly creating new species as they colonized new habitats. Myers (1929) believed that speciation of New Zealand cicadas occurred very rapidly and viewed each species as having adapted to a particular ecological environment. In this context the geographical distribution of cicada species in New Zealand was primarily influenced by ecological factors. However, as understanding of the geological and climatological history of New Zealand increased, and the influence of this history on New Zealand taxa was recognized, later workers also looked for historical reasons to explain the distribution and speciation of the New Zealand cicada fauna.

Fleming (1975a) emphasized the importance of glaciations on the speciation rate and modern distribution of species in the genus *Kikihia*. The two most ancient *Kikihia* species (*K. cauta* and *K. scutellaris*) were, in Fleming's view, little modified from Tertiary (65–2 Ma) ancestors that had been confined to the North Island following extensive glaciation of the South Island during the Pleistocene (1.8–0.01 Ma). The remaining hypothesized species were the result of two bursts of speciation resulting from Pleistocene climate changes (Fleming, 1973, 1975a, 1984). He supported rapid speciation in the *Kikihia* by noting song similarities and cases of hybridization between species (Fleming, 1973, 1975a,b, 1984; Lane, 1984, 1995). Within these groups he made a number of hypotheses regarding the phylogenetic relationships of several species (Fleming, 1973, 1975a, 1984). In addition to the above-published works, an unpublished tree of phylogenetic relationships among *Kikihia* species was found in the correspondence between Charles Fleming and John Dugdale; this tree is reproduced in Fig. 1. The above hypotheses of *Kikihia* relationships were examined in the light of a *Kikihia* phylogeny derived from molecular data.

MATERIALS AND METHODS

Taxon sampling

All described *Kikihia* species, with the exception of *K. muta*, and cicadas from several suggested *Kikihia* species populations were sampled. Cicadas from suggested species were given the nicknames proposed by Fleming and Dugdale in their correspondence: 'murihikua', 'tasmani', 'nelsonensis', and 'peninsularis'. An additional species, 'NWCM', identified in the Fleming and Dugdale correspondence as a song variant was also added to the analysis. Two outgroup species were also sampled, *Rhodopsalta leptomera* (Myers) and *Maoricicada cassiope* (Hudson), that belong to the two most closely related genera to *Kikihia* (Arensburger et al., 2004).

Cicadas were collected in the field using insect nets and by hand. When available, songs of the collected specimens were recorded to help with species identification (songs of most species were available prior to collection from the Fleming tape archive, Museum of New Zealand). Individuals collected in the field were either preserved in 95% ethanol, frozen on dry ice, or both. In the laboratory, specimens were transferred into ultra cold freezers (−70 °C). Identification of all specimens from described species used for molecular sequencing was based on morphology, song and geographical location (Table 1). Specimens belonging to species that have not yet been described were identified based on extensive field notes by Charles Fleming and John Dugdale. In the early stages of this work the identity of many specimens was confirmed by David Lane or John Dugdale. Voucher specimens of each species were deposited in the entomology collection of the Department of Ecology and Evolutionary Biology at the University of Connecticut.
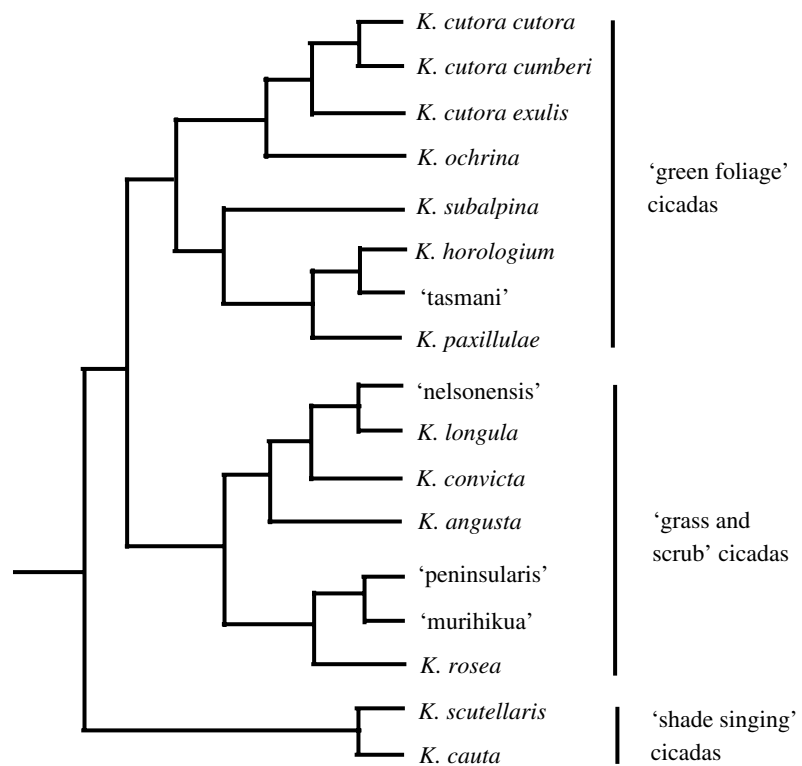
Figure 1 'Intuitive' tree of phylogenetic relationships redrawn from the correspondence of Charles Fleming and John Dugdale. Only taxa included in this analysis are indicated. The 'shade-singing', 'green foliage' and 'grass and scrub' *Kikihia* groups are indicated.

Molecular techniques

DNA samples from two individuals of each species and proposed species were extracted, amplified, and sequenced independently to verify that a contaminant had not been amplified by mistake. Total genomic extractions were performed using the CTAB/DTAB (Gustincich *et al.*, 1991) and 'salting out' (Sunnucks & Hales, 1996) protocols using thoracic and/or ovarian tissue. Sections of three mitochondrial genes were amplified using the polymerase chain reaction (PCR): (i) the entire cytochrome oxidase II gene (COII) (693 bp), (ii) the entire ATPase8 gene (156 bp), and (iii) 552 bp of the ATPase6 gene. The cytochrome oxidase II gene was amplified using primers located in the flanking tRNAs: TL2-J-3034 (AAATATGGCAGATTAGTGCA) and TK-N-3785 (GTTTAAGAGACCAGTACTTG) (Simon *et al.*, 1994). Thermal cycling conditions for amplification of the cytochrome oxidase II gene were: denaturation at 94 °C for 45 s, annealing 50 °C for 45 s and extension at 72 °C for 75 s. The ATPase 8 and 6 regions were amplified using the primer pair: TK-J-3799 (GGCTGAAAGTAAGTAATGGTC-TCT) and A6-N-4570 (AAGACTGAATTATACAAACG-GCTA) (Buckley *et al.*, 2001a,b). Thermal cycling conditions for the ATPase genes were: denaturation at 94 °C for 45 s, annealing 57 °C for 45 s and extension at 72 °C for 75 s (Simon *et al.*, 1994; Buckley *et al.*, 2001a,b,c). DNA products were purified for sequencing using QIAquick PCR Purification Kit (Qiagen, Valencia, CA, USA). Purified PCR products were sequenced using Big Dye[TM] Terminator Cycle Sequencing Ready Reaction Kit (ABI, San Francisco, CA, USA).

Cycle sequencing products were cleaned by ethanol precipitation or by Sephadex spin columns and analysed on an ABI Prism[TM]377 DNA Sequencer. Nucleotide sequence alignments were facilitated by amino acid sequence comparisons. All sequences were deposited into Genbank, accession numbers: AF313498–AF313517 (COII) and AF249888, AF349469–AF349506 (ATPase).

Phylogenetic analyses

Analyses were conducted using PAUP*4.0b2a (Swofford, 1998). Aligned nucleotide sequence data were partitioned into three data sets: (i) the cytochrome oxidase II sequences (COII), (ii) the combined ATPase8 and ATPase6 sequences (ATPase) and (iii) the combined COII and ATPase data sets. Differences in base frequency composition among taxa were examined using a heterogeneity chi-square test as implemented in PAUP*, for all sites and for parsimony-informative sites alone. Phylogenetic analyses were conducted using the maximum likelihood (Felsenstein, 1981), minimum evolution (Kidd & Cavalli-Sforza, 1971; Rzhetsky & Nei, 1992) and maximum parsimony (Fitch, 1971) optimality criteria. Most trees were rooted using the two outgroup species (*M. cassiope* and *R. leptomera*). For each data set the most appropriate model of evolution was determined by comparing the ln-likelihood scores of an initial maximum parsimony tree to a range of substitution models with and without among-site rate variation parameters: Jukes & Cantor (1969) (JC), Kimura (1980) (K2P), Hasegawa *et al.* (1985) (HKY85) and general-time reversible (e.g. Yang,

Table 1 Location and date of collection of New Zealand cicadas in the genus *Kikihia* and two outgroups in the genera *Maoricicada* and *Rhodopsalta*. Two individuals of each species were sequenced. In the case of *K. subalpina* two individuals from the South Island and two from the North Island were sequenced

Species	Collection date	Collection location	NZ district	Notes
Kikihia angusta	Feb 5, 1998	Lake Sedgemere	Marlborough	
Kikihia angusta	Feb 12, 1994	Old Man range, Symes Road	Otago	
'murihikua'	Feb 14, 1994	Route 94	Fiordland	Species not yet described, see text
'murihikua'	Feb 14, 1994	Route 94	Fiordland	Species not yet described, see text
'tasmani'	Jan 26, 1996	Cobb River Reservoir	Nelson	Species not yet described, see text
'tasmani'	Jan 26, 1996	Cobb River Reservoir	Nelson	Species not yet described, see text
'NWCM'	Jan 18, 1993	Hwy 63 NE of Rainbow Ski Field turnoff	Nelson	Species not yet described, see text
'NWCM'	Jan 18, 1993	Hwy 63 NE of Rainbow Ski Field turnoff	Nelson	Species not yet described, see text
Kikihia subalpina	Feb 26, 1998	12-mile Delta, Lake Wakatipu	Otago	
Kikihia subalpina	Feb 20, 1998	Broad bay, Dunedin	Otago	
Kikihia subalpina	Feb 23, 1994	Rimutaka Summit	Wellington	Specimen provided by D. Lane
Kikihia subalpina	Feb 23, 1994	Rimutaka Summit	Wellington	Specimen provided by D. Lane
Kikihia longula	Jan 7, 1994	Chatham Islands	Chatham	Specimen provided by S. Trewick
Kikihia longula	Jan 7, 1994	Chatham Islands	Chatham	Specimen provided by S. Trewick
'nelsonensis'	Feb 22, 1994	Havelock, 12 km S. of Canvastown	Marlborough	Species not yet described, see text
'nelsonensis'	Feb 22, 1994	Havelock, 12 km S. of Canvastown	Marlborough	Species not yet described, see text
Kikihia paxillulae	Feb 1, 1997	Puhipuhi reserve	Kaikoura	
Kikihia paxillulae	Feb 1, 1997	Puhipuhi reserve	Kaikoura	
Kikihia cutora cutora	Feb 5, 1993	Bullock Track, Warkworth	North Auckland	
Kikihia cutora cutora	Feb 5, 1993	Bullock Track, Warkworth	North Auckland	
Kikihia cutora exulis	Jan 10, 1997	Raoul island, Kermadec Islands	Kermadec	Specimen provided by Chris Green, NZ DOC
Kikihia cutora exulis	Jan 10, 1997	Raoul island, Kermadec Islands	Kermadec	Specimen provided by Chris Green, NZ DOC
Kikihia cutora cumberi	Feb 23, 1994	Rimutaka Summit	Wellington	Specimen provided by D. Lane
Kikihia cutora cumberi	Feb 10, 1999	Tongariro National Park, Whakapapa	Tongariro	
Kikihia convicta	Mar 1, 1997	Norfolk Island, Australia		Specimen provided by M. Jowett
Kikihia convicta	Mar 1, 1997	Norfolk Island, Australia		Specimen provided by M. Jowett
Kikihia ochrina	Jan 25, 1994	164 Nevay Rd., Miramar, Wellington	Wellington	
Kikihia ochrina	Feb 19, 1994	164 Nevay Rd., Miramar, Wellington	Wellington	
'peninsularis'	Feb 16, 1998	Road to Port Levy, Banks Peninsula	Canterbury	Species not yet described, see text
'peninsularis'	Feb 16, 1998	Road to Port Levy, Banks Peninsula	Canterbury	Species not yet described, see text
Kikihia rosea	Feb 10, 1998	Broad Bay, Dunedin	Otago	Specimen provided by G. Wallis
Kikihia rosea	Feb 10, 1994	Silverstream Road, Dunedin	Otago	Specimen provided by D. Gwynne
Kikihia horologium	Mar 3, 1999	Mt Fyffe, Kaikoura	Marlborough	
Kikihia horologium	Jan 22, 1993	Mt Sebastopol, Mt Cook National Park	Westland	
Kikihia scutellaris	Jan 28, 1997	Johnston's Hill, Kakore	Wellington	
Kikihia scutellaris	Jan 28, 1997	Johnston's Hill, Kakore	Wellington	
Kikihia cauta	Feb, 23, 1994	Rimutaka Summit	Wellington	
Kikihia cauta	Feb, 23, 1994	Rimutaka Summit	Wellington	
Maoricicada cassiope	Jan 26, 1997	Mt Ruapehu, Tongariro National Park	Tongariro	
Maoricicada cassiope	Jan 26, 1997	Mt Ruapehu, Tongariro National Park	Tongariro	
Rhodopsalta leptomera	Feb 23, 1994	Waikanae Beach	Wellington	Specimen provided by D. Lane
Rhodopsalta leptomera	Feb 23, 1994	Waikanae Beach	Wellington	Specimen provided by D. Lane

1994) (GTR) as in Frati *et al.* (1997). Among-site rate variation was accommodated in three different ways: (i) assuming a proportion of sites were invariable (e.g. Hasegawa *et al.*, 1985), (ii) all sites free to vary with rates among sites following a discrete approximation to the gamma distribution (Yang, 1994) and (iii) assuming that a proportion of sites were invariable with the remainder free to vary following a gamma distribution (Gu *et al.*, 1995). Tree topologies obtained from the molecular data were compared with alternative topologies suggested from the literature (see discussion) using the SOWH parametric bootstrap (Swofford *et al.*, 1996; Goldman *et al.*, 2000) and Shimodaira-Hasegawa (SH) (Shimodaira & Hasegawa, 1999) tests.

Table 2 Sequence statistics for COII, ATPase 8 and ATPase 6 gene sequences. 'Nucleotide' is abbreviated 'nt'

	COII				ATPase 6				ATPase 8				All sites
	1st	2nd	3rd	All	1st	2nd	3rd	All	1st	2nd	3rd	All	
No. of nt sites	231	231	231	693	184	184	184	552	52	52	52	156	1401
No. of varied nt sites	36	13	125	174	46	14	111	171	15	12	29	56	401
No. of parsimony-informative nt sites	19	6	70	95	24	3	62	89	8	2	15	25	209
Varied nt sites (%)	16	6	54	25	25	8	60	31	29	23	56	36	29
Parsimony-informative nt sites (%)	8	3	30	14	13	2	34	16	15	4	29	16	15

Estimating dates of divergence

Dates of divergence were estimated through the use of a method based on Bayesian statistics developed by Thorne *et al.* (1998). KH developed a wrapper script to facilitate the input of data and output of results. A single outgroup taxon (*R. leptomera*) was used in these analyses to simplify calculations. The following 'priors' were specified: the age of the tree root, the rate of evolution at the tree root and the amount of variation in evolutionary rate allowed from node to node. The age of the tree root was estimated from a single calibration point within the genus *Kikihia,* the age of the node linking the Norfolk Island cicada (*K. convicta*) from its sister species and verified by comparison with a *Maoricicada* calibration point (as described in Simon, C., D. Vanderpool, T. Buckely, D. Marshall, P. Arensburger, K. Holsinger, unpubl. data). The Norfolk Island cicada is endemic to this volcanic island and is likely to have evolved there from New Zealand colonists. The age of the node separating this species from its sister species is not known exactly but can be reasonably estimated from the geological age of the island (between 3.05 and 2.3 Ma; Jones & McDougall, 1973) and the number of substitutions the Norfolk Island cicada has accumulated. In this study, the age of this node was set to be between 1.0 and 1.5 Ma based on a comparative Bayesian analysis of *Maoricicada* and *Kikihia* (Simon *et al.*, in prep.). Evolutionary distances were estimated using an HKY85 model with among-site rate variation accommodated using a discrete gamma distribution. The more sophisticated models of molecular evolution used in the phylogenetic analyses (e.g. GTR with among-site rate variation model) could not be used with the Thorne *et al.* (1998) program because such models have not yet been incorporated into the technique. However, results from the HKY85 model were not expected to deviate substantially from the GTR model because the more sophisticated models did not differ significantly from the HKY85 model with among-site rate variation for the data presented here (see Results).

RESULTS

A total of 1401 base pairs were sequenced from the three mitochondrial genes: (i) the entire cytochrome oxidase II, (ii) the entire ATPase 8 and (iii) 552 base pairs of the ATPase 6 gene (Table 2). These genes did not contain any insertions or

deletions and were unambiguously aligned using amino acid sequences. PAUP* chi-square tests of homogeneity of base frequencies across taxa revealed no significance differences when uninformative sites were excluded ($P > 0.05$) and when genes were analysed individually and in combination. Phylogenetic analyses were conducted using the combined COII and ATPase genes. This was justified because genes analysed individually or in combination produced mostly identical topologies suggesting that all genes had the same underlying pattern of evolution (Bull *et al.*, 1993; Hillis *et al.*, 1996). The few topological differences between trees from the COII gene and the combined ATPase genes were near the branch tips and all differing nodes had weak bootstrap support (< 66%). The combined data set supported similar topologies regardless of optimality criterion (consensus topology shown in Fig. 2). Dates of divergence, estimated using the modified Thorne *et al.* (1998) program, are summarized in Fig. 3 along with standard deviations. The *Kikihia* were estimated to have diverged from the genus *Rhodopsalta* 9.33 Ma (SD 2.98) (node 18, Fig. 3). The two early branching *Kikihia* species, *K. cauta* and *K. scutellaris*, were estimated to have originated 5.87 Ma (SD 1.74) and 5.44 Ma (SD 1.63) respectively. The remaining species and undescribed taxa originated after 3.7 Ma. Only eight taxa shared their most recent common ancestor during the Pleistocene (1.8–0.01 Ma): *K. angusta*, 'murihikua', 'tasmani', 'NWCM', *K. cutora exulis* (Hudson), *K. cutora cutora* (Walker), *K. convicta*, 'nelsonensis' and *K. longula*.

DISCUSSION

Phylogenetic analyses

Similar topologies were supported by the COII, ATPase and combined COII and ATPase data sets. Trees from the individual COII and ATPase genes disagreed primarily with regard to the position of *K. horologium*, *K. rosea* and 'peninsularis'. All three taxa were collapsed into a larger polytomy in the combined tree (Fig. 2), and the resulting tree topology was identical to that of a strict consensus of the COII and ATPase trees. The combined COII and ATPase data set can therefore be reasonably assumed to represent the best estimate of phylogenetic relationships within the genus *Kikihia*, based on the molecular data presented here. New data for additional taxa and genes are being collected and will provide
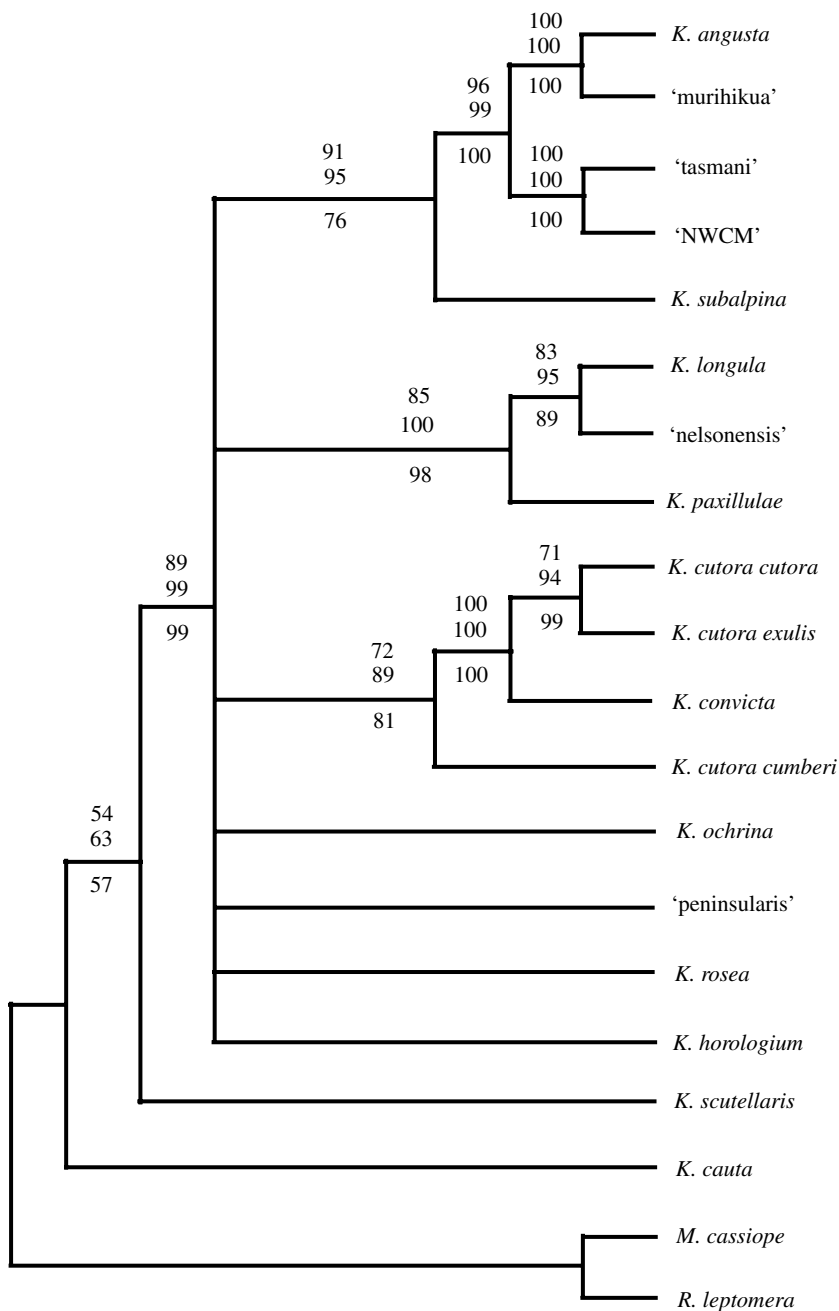
Figure 2 Consensus topology of cicadas with the combined COII and ATPase data set using three optimality criteria. Numbers next to each node indicate percent bootstrap support from 100 replicates; each column of bootstrap values corresponds to following optimality criteria, from top to bottom: maximum likelihood, minimum evolution and unweighted maximum parsimony. The model of evolution used for both maximum likelihood and minimum evolution criteria is a GTR model with among-site rate variation accommodated using a gamma distribution (alpha = 0.19).

more resolution in the future (D. Marshall, K. Slon, K. Hill,, J. Cooley and C. Simon, in prep.). The single polytomy in Fig. 2 was associated with very short internal branches and very short time intervals (Fig. 3 nodes 3, 8, 13, 14 and 15). These results are consistent with a rapid burst of speciation 3–5 Ma. A similar burst of speciation was found in another New Zealand cicada genus (*Maoricicada*) estimated to have occurred between 2.6 and 5.0 Ma (Buckley *et al.*, 2001c). The idea of a species explosion in the genus *Kikihia* was already advanced by Fleming (1975a, 1984). He remarked on the similarities in morphology, song and cases of hybridization within the 'green foliage' and 'grass and scrub' cicada groups and hypothesized that, with the exception of *K. cauta* and *K.*

scutellaris, all *Kikihia* species had originated within a very short period of time during the Pleistocene (1.8–0.01 Ma). The results of this study appear to confirm Fleming's hypothesis of a species explosion, but disagree with him on the age of this event. Possible reasons for these dating differences are examined below.

The shade-singing cicadas (*K. cauta* and *K. scutellaris*)

The 'shade-singing' cicadas are remarkable for their habit of often singing in the deep forest rather than in full sun. These species have long been separated from the other *Kikihia* species. Myers (1929) believed all New Zealand cicadas to be
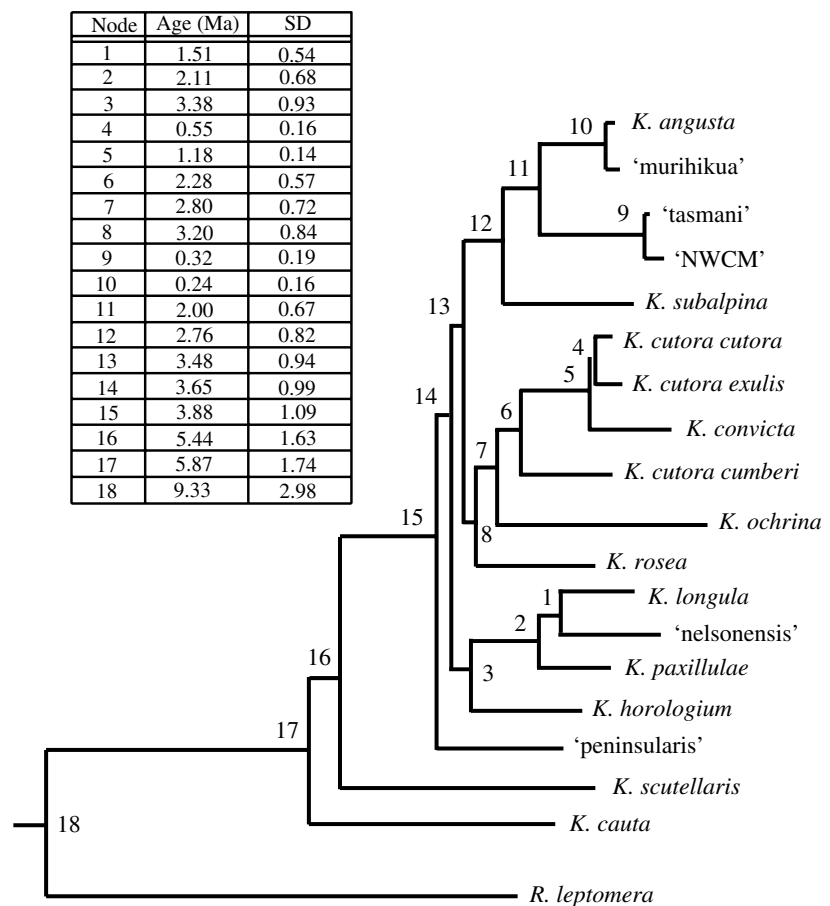
Node	Age (Ma)	SD
1	1.51	0.54
2	2.11	0.68
3	3.38	0.93
4	0.55	0.16
5	1.18	0.14
6	2.28	0.57
7	2.80	0.72
8	3.20	0.84
9	0.32	0.19
10	0.24	0.16
11	2.00	0.67
12	2.76	0.82
13	3.48	0.94
14	3.65	0.99
15	3.88	1.09
16	5.44	1.63
17	5.87	1.74
18	9.33	2.98

Figure 3 Age estimates of nodes on the maximum likelihood *Kikihia* tree using a modified Thorne *et al.* (1998) program. The age of each node is indicated along with its standard deviation. Molecular clock estimates are based on a divergence date of *K. convicta* from *K. cutora cutora* and *K. cutora exulis* between 1.0 and 1.5 Ma (see text for details).

derived from a hypothetical xerophytic ancestor from New Caledonia. He singled out *K. cauta* and *K. scutellaris* from the remaining New Zealand cicadas, noting the differences in habitat and singing station preference (forest dwelling and shade singers) and aedeagal structure. He placed these two species basal to all the species described at that time that would later be placed into the genus *Kikihia* (*ochrina*, *cutora*, *subalpina* and *muta*); he identified *K. cauta* as the sister species to all other *Kikihia*. Fleming (1975a, 1984) also believed that the 'shade-singing' cicadas were the oldest *Kikihia* species, dating back to the Tertiary, before the speciation explosion that gave rise to the remaining *Kikihia* species.

The molecular tree strongly supported the 'shade singers' as the earliest branching extant species in the genus *Kikihia* (bootstrap support between 89% and 99% in Fig. 2). The antiquity of the divergence of these old apparently unbranched lineages was also supported by the large sequence divergence between *K. cauta* and *K. scutellaris* (0.13 corrected distance, Table 3), which was nearly the same as the divergence of *K. cauta* and *K. scutellaris* from the remainder of the *Kikihia* (corrected distances ranged from 0.11 to 0.16, Table 3) and similar in depth to the earliest divergence in *Maoricicada*, *Rhodopsalta* and *Amphipsalta* (Arensburger, 2002; Buckley *et al.*, 2002 and T.R. Buckley, unpubl. data). These results suggest that the two shade-singing species diverged from other *Kikihia* early in the evolution of this genus, *c.* 5.6 Ma (nodes 16

and 17, Fig. 3). It is possible that these two lineages gave rise to other species that have subsequently gone extinct but due to a poor fossil record, we are unlikely to ever know this.

The Norfolk cicadas

Norfolk Island (Australia) is located 800 km north of the northern tip of New Zealand. It was formed 3.05–2.3 Ma from several volcanic episodes (Jones & McDougall, 1973). Its volcanic origin and the absence of nearby islands requires that its biota be the descendants of long-distance dispersing ancestors (Holloway, 1977; Pole, 1994). During the warmer months (October–March) winds on Norfolk Island are primarily influenced by the south-east trade winds (Tomlinson, 1973). The fauna of Norfolk Island could only have developed after volcanic activity ceased, probably within the last 2.3 million years (Holloway, 1977). It is composed of endemic elements as well as of taxa with outside affinities. Holloway (1977) reported that of the 98 species of macro-Lepidoptera found on Norfolk Island, only 22 species and subspecies were endemic. Of the endemic species only two appeared to have New Zealand affinities, the rest having affinities primarily with Australia and New Caledonia (two species may have affinities with New Hebrides and Samoa).

The single cicada species found on Norfolk Island, *K. convicta* is endemic to this island. It was placed in the

Table 3 Corrected and uncorrected sequence divergence between *Kikihia* species and two outgroup taxa (*Maoricicada cassiope* and *Rhodopsalta leptomera*), from the combined COII and ATPase data set. Numbers below the diagonal are uncorrected sequence divergence (expected number of substitutions per site), above the diagonal divergence values are corrected for multiple hits using the model with the lowest ln-likelihood not significantly different from the ln-likelihood of the best fitting model (GTR + G model)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1 *Kikihia angusta*	–	0.00	0.04	0.04	0.07	0.10	0.11	0.10	0.09	0.10	0.10	0.10	0.12	0.07	0.10	0.09	0.13	0.14	0.28	0.28
2 'murihikua'	0.00	–	0.04	0.04	0.08	0.10	0.11	0.10	0.09	0.10	0.10	0.10	0.12	0.07	0.10	0.10	0.13	0.14	0.28	0.29
3 'tasmani'	0.03	0.03	–	0.01	0.07	0.09	0.10	0.09	0.09	0.10	0.09	0.10	0.11	0.08	0.09	0.08	0.12	0.14	0.28	0.29
4 'NWCM'	0.03	0.03	0.01	–	0.08	0.09	0.11	0.09	0.10	0.10	0.10	0.11	0.11	0.08	0.10	0.08	0.12	0.13	0.28	0.28
5 *Kikihia subalpina*	0.05	0.05	0.05	0.05	–	0.10	0.10	0.09	0.10	0.10	0.11	0.10	0.13	0.07	0.10	0.09	0.16	0.15	0.31	0.31
6 *Kikihia longula*	0.06	0.06	0.06	0.06	0.06	–	0.05	0.05	0.12	0.13	0.12	0.11	0.14	0.08	0.11	0.08	0.14	0.13	0.28	0.31
7 'nelsonensis'	0.07	0.07	0.07	0.07	0.07	0.04	–	0.06	0.12	0.13	0.13	0.11	0.14	0.09	0.11	0.09	0.15	0.14	0.29	0.33
8 *Kikihia paxillulae*	0.06	0.06	0.06	0.06	0.06	0.04	0.05	–	0.10	0.11	0.12	0.10	0.13	0.08	0.10	0.08	0.15	0.15	0.29	0.29
9 *Kikihia cutora cutora*	0.06	0.06	0.06	0.06	0.06	0.07	0.07	0.06	–	0.01	0.03	0.06	0.10	0.08	0.09	0.09	0.17	0.15	0.29	0.34
10 *Kikihia cutora exulis*	0.06	0.06	0.06	0.06	0.07	0.07	0.08	0.07	0.01	–	0.03	0.06	0.10	0.09	0.09	0.09	0.18	0.16	0.30	0.35
11 *Kikihia convicta*	0.06	0.06	0.06	0.06	0.07	0.07	0.08	0.07	0.02	0.03	–	0.07	0.12	0.09	0.11	0.10	0.18	0.17	0.31	0.36
12 *Kikihia cutora cumberi*	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.06	0.04	0.04	0.05	–	0.10	0.08	0.09	0.09	0.16	0.14	0.30	0.33
13 *Kikihia ochrina*	0.07	0.07	0.07	0.07	0.07	0.08	0.08	0.07	0.06	0.06	0.07	0.06	–	0.11	0.11	0.11	0.17	0.17	0.29	0.32
14 'peninsularis'	0.05	0.05	0.06	0.06	0.05	0.06	0.06	0.05	0.06	0.06	0.06	0.06	0.07	–	0.07	0.07	0.13	0.12	0.24	0.27
15 *Kikihia rosea*	0.06	0.06	0.06	0.06	0.06	0.07	0.07	0.06	0.06	0.06	0.06	0.06	0.07	0.05	–	0.09	0.15	0.16	0.30	0.33
16 *Kikihia horologium*	0.06	0.06	0.06	0.06	0.06	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.07	0.05	0.06	–	0.14	0.15	0.27	0.28
17 *Kikihia scutellaris*	0.07	0.07	0.07	0.07	0.09	0.08	0.08	0.08	0.09	0.09	0.09	0.08	0.09	0.07	0.08	0.08	–	0.15	0.25	0.27
18 *Kikihia cauta*	0.08	0.08	0.08	0.07	0.08	0.07	0.08	0.08	0.08	0.08	0.09	0.08	0.09	0.07	0.08	0.08	0.08	–	0.25	0.29
19 *Maoricicada cassiope*	0.11	0.11	0.11	0.11	0.12	0.11	0.12	0.12	0.11	0.12	0.12	0.12	0.11	0.10	0.12	0.11	0.11	0.10	–	0.26
20 *Rhodopsalta leptomera*	0.11	0.12	0.11	0.11	0.12	0.12	0.12	0.11	0.12	0.13	0.13	0.12	0.12	0.11	0.12	0.11	0.11	0.11	0.11	–

genus *Kikihia* by Dugdale (1972), a genus that is endemic to New Zealand, the Kermadec and Chatham Islands. Within this genus Fleming (1973) placed *K. convicta* within the 'green foliage' species group based on habitat preference. However, in latter publications describing the 'green foliage' cicadas, Fleming (1975a, 1984) makes no mention of this species. In their unpublished tree of phylogenetic relationships (Fig. 1) Charles Fleming and John Dugdale grouped *K. convicta* with *K. longula* (from the Chatham Islands, see below), and an undescribed species they nicknamed 'nelsonensis'.

The Norfolk Island cicada (*K. convicta*) shared a recent common ancestor with *K. c. cutora* and *K. c. exulis*. The node uniting these three taxa had very high bootstrap values, 100% of replicates supported this grouping when all the available molecular data were used (Fig. 2). This result was unexpected because it broke up the monophyly of the *K. cutora* species (i.e. *K. c. cumberi* was not the closest relative of the other two *K. cutora* subspecies). Furthermore, alternative topologies with a monophyletic *K. cutora* group were strongly rejected by parametric bootstrap and SH tests (all *P* < 0.01). These results suggest that *K. cutora* is not a monophyletic species. Arensburger (2002) compared the species descriptions of *K. cutora* subspecies and *K. convicta* and found no taxonomically significant morphological differences (autaporphies) that could be used to separate these two species.

The apparent paraphyletic status of *K. cutora* may warrant re-examination of the taxonomy of this species, depending on the preferred species concept. Many species concepts require monophyly (in the sense of Holloway, 1977) of species (reviewed in de Pinna, 1999). If monophyly is a requirement then the present study would not support *K. cutora* as a proper species. Possible solutions might include placing *K. convicta* as a subspecies of *K. cutora*, or giving specific status to the three *K. cutora* subspecies. Given a choice between lumping *K. convicta* into *K. cutora* or splitting taxa into separate species (i.e. retaining *K. cutora cutora* and *K. cutora* exulis as subspecies and making a new species *K. cumberi*) the unique song of *K. convicta*, the polyphyly of the *K. cutora* species and the molecular distances (similar to the divergences between other full species of *Kikihia*, e.g. *K. longula* and *K. paxillulae*) appear to favour ranking *K. cutora cumberi* as a distinct species. However, species concepts that use the ability to interbreed as a species identifier can lead to recognition of paraphyletic species (e.g. Bremer & Wanntrop, 1979). Therefore, if this kind of species concept is used, one might *a priori* accept current taxonomy. Too little is currently known about the ecology of these organisms to know whether a species concept based on interbreeding would retain the current taxonomy. Finally, most evolutionary and phylogenetic species concepts (reviewed in Wheeler & Meier, 2000) would recognize *K. cutora* as a valid paraphyletic species if *K. convicta* evolved from a recently isolated population of *K. cutora*.

Regardless of the species concept, these results should not be interpreted as the deciding factor between competing taxonomic schemes. *Kikihia* species have been defined on the basis of morphological, song and ecological characteristics, so

revision of individual species should be done at least in part on the same basis. We prefer to follow Mayden & Wood (1995) and urge that the molecular evidence be used in conjunction with more traditional taxonomic methods rather than as an alternative set of markers.

Kermadec Island cicada

Lying about 1000 km north-east of New Zealand, the Kermadec Islands are of volcanic origin and late Pliocene (3–1.8 Ma) in age, similar to Norfolk Island (Watt, 1975). The biota of the Kermadecs comprises endemic elements as well as Australian and New Zealand taxa. A few taxa are shared with Tonga, Fiji and Polynesia. Dugdale (1973) found that 18% of the lepidopteran fauna was endemic and only one species (of a total of 51) was shared exclusively with New Zealand. However, Watt (1975) reported that among the Coleoptera the New Zealand element was quite strong on the Kermadec Islands (e.g. Klimaszewski & Crosby, 1997). Alexander (1973) found that two of the five crane fly species (Tipulidae) had New Zealand affinities. Several species in the heteropteran family Miridae are also found both in New Zealand and Kermadecs (Eyles, 1999), as well as several proturan species (Tuxen, 1986). Overall species diversity appears to be quite low and is derived from chance trans-oceanic dispersal (Watt, 1975).

The single endemic cicada subspecies in the Kermadecs is found on Raoul Island, *Kikihia cutora exulis* (Fleming, 1973). This subspecies is part of a subspecies group that also includes *K. cutora cutora* and *K. cutora cumberi*. These last two have parapatric ranges covering the entire North Island of New Zealand. In the North Island *K. cutora* is partially sympatric with *K. subalpina* and *K. laneorum*. Fleming (1973, 1984) postulated a close phylogenetic relationship between *K. cutora*, *K. subalpina* and *K. laneorum*. These three species were examined in detail by Lane (1984), who concluded on the basis of morphological and behavioural characters that these species indeed formed a monophyletic group, but that the sister relationships could not be resolved using the available morphological and behavioural data.

Our results support a close phylogenetic relationship of *K. c. exulis* and *K. c. cutora*. Fleming (1973) stated that *K. c. exulis* was 'very clearly related to and certainly derived from the populations of *K. c. cumberi* (…) not from *K. c. cutora*'. However, the molecular results were in conflict with this statement (Fig. 2). This conclusion was also supported by song analysis which confirm similar song patterns between *K. c. exulis* and *K. c. cutora* that are distinct from *K. c. cumberi* (D. Marshall, pers. comm.).†

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†Fleming (1973) stated that the songs of *K. c. cumberi* and *K. c. cutora* were identical and different from *K. c. exulis*. This conclusion has not been supported by more recent song recordings and is likely to have been made in error (D. Marshall, pers. comm.).

The Chatham Island cicada

These islands lie 820 km east of New Zealand on the Chatham rise. Unlike Norfolk and the Kermadec Islands, these are not of volcanic origin, but instead separated from Gondwanaland 82 Ma, at approximately the same time as New Zealand (Cooper & Millener, 1993). There does not appear to have been a land connection between New Zealand and these islands since the separation from Gondwanaland. The Chatham Islands were submerged by a marine transgression in the mid-Oligocene wiping out any terrestrial organisms (Watt, 1975; Cooper & Cooper, 1995; Herzer *et al.*, 1997). Therefore, present day terrestrial organism must have arrived there via long-distance dispersal (Pole, 1994). The biota of the Chatham Islands includes many endemic elements derived from New Zealand species, including some Lepidoptera (Gaskin, 1975; Craw, 1988), beetles (Emberson, 1998, 2002) parakeets (Nixon, 1982) and a moss (Vitt, 1983). They also share elements with Australia (Dugdale, 1989). Craw (1988) found that many of the endemic Chatham taxa had as their closest relatives widespread New Zealand taxa.

The single New Zealand cicada species from the Chatham Islands, *K. longula* was found by Hudson (1950) to be 'extremely similar' to *K. angusta* which is endemic to South Island tussock lands. He also found that the Chatham and Kermadec Island cicadas were dissimilar enough from mainland New Zealand species to merit separate species status. In their unpublished 'intuitive' evolutionary tree (Fig. 1), John Dugdale and Charles Fleming suggested that the sister species of *K. longula* was the undescribed species 'nelsonensis' and the sister species to that group was *K. convicta* (Fig. 1).

Our phylogenetic analyses suggest that the Chatham Island cicada is most closely allied to the 'nelsonensis' group on the South Island but further species sampling especially including the *muta* group complex may alter these conclusions (a close phylogenetic relationship of *K. longula* to North Island *K. muta* is supported by a recent study, D. Marshall, unpubl. data).

Island cicadas and long-distance dispersal

The very young age of the *K. c. exulis* species begs the question why it took so long to colonize the Kermadec Islands. Both Norfolk and the Chatham Islands had been colonized much earlier and both islands are at similar distances to the New Zealand mainland. As both the Kermadec and Norfolk Island cicadas share a very recent common ancestor (Fig. 2) it is unlikely that differences in morphology or behaviour can account for the late arrival of the Kermadec Island cicadas. The answer may lie instead in the transport mechanism. Wind dispersal has usually been used to explain dispersal of New Zealand cicadas over water (Myers, 1929; Fleming, 1973). Westerly winds predominate through this portion of the Southern Hemisphere, particularly during the winter season (Struman & Tapper, 1996). These 'prevailing westerlies' are associated with the absence of land over a large portion of the southern hemisphere and

have probably existed since the opening of the Drake passage 23.5 ± 2.5 Ma (Barker & Burrel, 1982). These currents provide a reasonable mechanism for wind dispersal from New Zealand to the Chatham Islands. However, there is also considerable evidence that the direction of the dominant winds over New Zealand has been quite variable. The last 10,000 years have been particularly well studied (reviewed in Shulmeister, 1999). These shifts in dominant wind direction appear to be associated primarily with periods of climate change. Two well-documented phenomena, the El Niño-Southern Oscillation and the Quasi-biennial Oscillation are associated with changes in wind direction over New Zealand to predominantly south-westerly and north-easterly winds, respectively (Struman & Tapper, 1996). Such climatic anomalies, along with the south-east trade winds (October–March; Tomlinson, 1973) might provide a possible dispersal route from New Zealand to Norfolk Island. Wind dispersal between New Zealand and the Kermadecs is more difficult to trace. Water and associated wind currents between New Zealand and the Kermadec Islands are traced indirectly as a north-easterly flow from New Zealand to the Norfolk Ridge and an easterly flow from there to the Kermadecs (Ridgway & Heath, 1975). There is evidence of water dispersal along this route, as well as possible movement from Norfolk Island to Raoul Island (Oliver, 1910; Sykes & Godley, 1968; Nelson & Adams, 1984). Therefore, while the record of specific wind directions over the past several million years is still very speculative, it is clear that wind directions between New Zealand and the outer islands are quite variable on a millennial scale and above. Therefore there is no reason to doubt that wind dispersal routes between New Zealand and all three outer islands have existed in the past.

The young age of all three outer island cicadas along with the geological history of the islands leaves little doubt that cicadas arrived there via long-distance dispersal. This result may be surprising because cicadas have previously been thought to be poor dispersers (e.g. Myers, 1929). This view was reiterated by de Boer & Duffels (1996) who found very strong correlations between the geographical distributions of a tribe and subtribe of Indo-Australian tropical cicadas and geotectonic terrane movements in that area. They concluded that present day cicada distributions reflected past terrane movements rather than widespread dispersal patterns. However, de Boer & Duffels (1996) did not exclude dispersal entirely. They recognized localized instances of cicada dispersal, particularly in the *Baeturia bloetei* species group which apparently dispersed several thousands of miles to numerous islands surrounding (and including) New Guinea (de Boer, 1989; Duffels & de Boer, 1990) as well as in the *Baeturia viridis* and *Diceropyga subapicalis* species groups (Duffels, 1977; de Boer, 1995). Holloway (1998) reanalysed the de Boer & Duffels (1996) data using sophisticated biogeographic techniques and concluded that localized dispersal events must have occurred to explain present day distribution and phylogenetic patterns of these cicadas. These conclusions are consistent with the present results for New

Zealand cicadas. Long-range dispersal appears to be rare among New Zealand cicadas. Of the 40+ species of New Zealand cicadas, there is evidence that only three taxa from a single genus have successfully been able to colonize the outer islands, and of these three taxa, two appear to be very closely related.

The green foliage cicadas (*K. cutora*, *K. ochrina*, *K. subalpina*, *K. horologium*, 'tasmani' and *K. paxillulae*)

Myers (1929) segregated a group of bright green cicadas (often found in tops of short trees and shrubs) from other New Zealand cicadas based primarily on their singing station. This group was composed of the modern *K. subalpina*, *K. cutora* and *K. ochrina*. Fleming (1975a, 1984) maintained this grouping naming it the 'green foliage' group for the habit of its members of singing on forest evergreen foliage or forest-edge shrubs. He also added four species to this group [which were described after the Myers (1929) publication], *K. horologium*, *K. paxillulae*, *K. laneorum* and *K. dugdalei* (the last two species were unavailable for the present study). In their correspondence, Charles Fleming and John Dugdale added an eighth undescribed *Kikihia* species referred to in their correspondence as 'tasmani' (Fig. 1). In the Fleming-Dugdale unpublished tree (Fig. 1) 'green foliage' cicadas were specified as having wholly green venters, and mesonotum with posterior spots distant from outer lozenges. Myers, Fleming and Dugdale most likely considered that these cicadas shared a single most recent common ancestor. Charles Fleming and John Dugdale grouped these species into a monophyletic clade on their unpublished tree (Fig. 1), and Myers (1929), who envisioned a gradual colonization of successive habitats as cicadas spread throughout New Zealand, believed these species were all derived from *K. muta*. However, the 'green foliage' cicadas did not form a well-supported monophyletic clade on the molecular tree (Fig. 2). Three species, *K. cutora*, *K. ochrina* and *K. horologium*, shared a most recent common ancestor only because they all came off the only polytomy on the tree (which included other species as well). The remaining three species were spread across the tree. These data clearly reject consideration of the 'green foliage' group as a valid phylogenetic clade. It is also unlikely that the 'green foliage' cicadas represent an ancestral type from which the remaining non-'shade-singing' cicadas had evolved. Such a hypothesis would not only require multiple losses and at least two gains of the 'green foliage' characters, but would require these to have occurred on some very short branches (e.g. the branch separating 'nelsonensis' and *K. longula* from *K. paxillulae*, see Fig. 3).

The grass and scrub cicadas ('peninsularis', 'murihikua', *K. rosea*, *K. angusta*, *K. muta*, 'nelsonensis', 'balaena', *K. longula*, *K. convicta*)

The 'grass and scrub' cicada group was proposed by Fleming (1975a, 1984) to describe a group of mainly South Island

cicadas that had resulted from a burst of speciation concurrent with the 'green foliage' cicadas. This group includes several undescribed species ('peninsularis', 'murihikua' and 'balaena'), and was never treated in as much detail as the 'shade-singing' and 'green foliage' cicadas Fleming (1975a, 1984). John Dugdale and Charles Fleming indicated that members of this group all had 'posterior spots (on the dorsal first thoracic segment) fused or contiguous with outer lozenges'. However, the molecular tree clearly does not support such a group as a monophyletic clade.

Impact of climatological and tectonic forces on *Kikihia* speciation and geographical distribution

When *Kikihia* species distributions are compared with the molecular phylogeny in Fig. 2, it becomes apparent that closely related species in mainland New Zealand are likely to have contiguous or overlapping distributions (e.g. *K. angusta* and 'murihikua', species distribution maps in Arensburger, 2002). This is consistent with a long-held belief that cicadas are generally poor dispersers (e.g. Myers, 1929; de Boer & Duffels, 1996). However, two *Kikihia* species and one subspecies (*K. convicta*, *K. longula* and *K. cutora exulis*) have been able to colonize the outer islands of New Zealand through long-distance dispersal. The ability of these three taxa to disperse over long stretches of ocean does not necessarily mean that other *Kikihia* species could have established new populations by long-distance dispersal over land. The outer island cicadas invaded lands that were presumably uninhabited by cicadas, while migrants over land would eventually have had to compete with other cicada species. Furthermore, all three outer island taxa share at least one apparent adaptation to long-distance dispersal (unusually long wings), a character not shared by other *Kikihia*. The absence of this character in mainland species suggests that this putative adaptation to long-distance dispersal carries either a fitness cost or is rare enough to be lost by genetic drift. Furthermore, the taxa on Norfolk (*K. convicta*) and the Kermadec (*K. cutora exulis*) Islands are very closely related to *K. cutora cutora* although both islands are over 1000 km. distant. The estimated date of divergence of these two species, based on the relaxed-clock method we employed, was only 1.2 Ma. This suggests that the ability for long-distance dispersal is confined to only a few taxa. Therefore, in the absence of any evidence for long-distance dispersal in mainland New Zealand (such as closely related taxa with clearly disjunct distributions) it is likely that dispersal in mainland New Zealand was gradual and that modern *Kikihia* distributions reflect to some extent past environmental modifications.

Cycles of glacial advances and retreats during the Pleistocene (1.8–0.01 Ma) have been hypothesized to have had a major impact on *Kikihia* speciation rates and geographical distributions. Fleming (1975a, 1984) dated the major burst of speciation in the *Kikihia* (which he believed gave rise to the 'green foliage' and 'grass and scrub' groups) to the Pleistocene. However, the results of the molecular clock analysis

(Fig. 3) indicate that the large majority of speciation events in this genus occurred well before the start of that epoch. Other than the island speciation events, only the *K. angusta* – 'murihikua' split and the 'tasmani' – 'NWCM' split appears to be Pleistocene in age. Speciation in many *Kikihia* is therefore unlikely to have been strongly influenced by glaciers and associated phenomena, but the molecular clock results do not exclude the possibility that Pleistocene climate changes influenced modern geographical distributions. Fleming (1975a) explained the absence of the shade-singing cicadas (*K. cauta* and *K. scutellaris*) from the South Island by the presence of massive ice sheets during the last glaciation (100,000–10,000 years ago). More generally, proponents of the 'glacial refuge' hypothesis (Wardle, 1963) have suggested that most species were excluded from the center of the South Island and the southern tip of the North Island by inhospitable environments between 14,000 and 10,000 years ago. However, evidence that glaciers have had a major influence on modern *Kikihia* distributions is thin. Previously glaciated areas do not appear to have fewer *Kikihia* species, as might be expected if these areas were recolonized from non-glaciated regions.

In response to the 'glacial refuge' hypothesis, other hypotheses emphasizing the importance of geological events have been proposed. The importance of fault displacement on disjunct distribution patterns (Heads, 1998) does not seem to be well supported (Wallis & Trewick, 2001). However, a combination of Pliocene mountain building and glaciation has been used to explain the distribution patterns of some species (Trewick *et al.*, 2000; McGlone *et al.*, 2001; Trewick & Wallis, 2001). The rise of the Southern Alps started about 10 Ma, intensified around 5 Ma, and continues to this day (Katz, 1979; Witehouse & Pearce, 1992). The age of the *Kikihia* species explosion, *c.* 3.6 Ma, is concurrent with this rapid uplift across the South Island. Furthermore the capacity of members of this genus for rapid morphological evolution is evident in a few very short branches on the molecular phylogenetic tree (e.g. the branches separating *K. angusta* and 'murihikua' in Fig. 3; these two taxa can very easily be distinguished in the field by morphology and song). If species in this genus are capable of such rapid speciation in recent times it would not be surprising that the dramatic environmental changes caused by the formation of a mountain range would lead to rapid evolution of new species.

CONCLUSIONS

The New Zealand biota appears to have resulted from a combination of descendants from ancient Gondwanan events and more recent dispersal (e.g. Winkworth *et al.*, 1999, 2002; Stockler *et al.*, 2002) with recent arrivals predominating. The results of this study are in general agreement with the conclusions reached for many other island species – arrival followed by rapid radiation (Hurr *et al.*, 1999; Price & Clague, 2002; Winkworth *et al.*, 2002). The genus *Kikihia* evolved within the last 10 million years with its two oldest modern

species (*K. cauta* and *K. scutellaris*) probably the sole survivors of possibly one but probably two older lineages. The remaining *Kikihia* are descended from a species explosion 3–5 Ma.

This species explosion coincided with a period of rapid mountain building in the South Island, suggesting that tectonic forces, rather than glaciers, were associated with the appearance of many new species. As the *Kikihia* species are typically found in specific habitats (e.g. *K. horologium* are mostly found on subalpine shrubs) it is likely that new species are formed by adaptation to new habitat types. The formation of the Southern Alps probably opened many new habitats in a short period of time. However, not all species date back to this species explosion and the cause of the more recent speciation events must be found by close examination of smaller scale changes in the New Zealand environment.

The outer island cicadas (*K. longula*, *K. convicta* and *K. cutora exulis*) are young species, diverging from their New Zealand ancestors within the last 2 million years. In the absence of any recent land connection between New Zealand and the outer islands the young age and very close phylogenetic relationship of these species to New Zealand taxa can only be explained if these species had arrived on the outer islands via long-distance dispersal. The same conclusion was reached for several other New Zealand insect species (Trewick, 2000). The transport mechanism cannot be known with certainty but wind dispersal has generally been favoured for cicadas and is consistent with the pattern of dispersal observed here (i.e. Norfolk and the Chatham Islands, which have consistent winds blowing towards them from New Zealand, were colonized first). Furthermore, all three outer island species have longer wings (in proportion to body length) than species on the New Zealand mainland which also suggests wind dispersal by adults. The three outer islands were colonized only by members of the genus *Kikihia*. This suggests that this genus may be better adapted to long-distance dispersal and/or survival than other New Zealand genera.

ACKNOWLEDGMENTS

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BIOSKETCHES

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