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Molecular evidence for dispersal rather than vicariance as the origin of flightless insect species on the Chatham Islands, New Zealand

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Abstract

Aim The aim was to use mitochondrial DNA sequence data to test between vicariance and oversea dispersal explanations for the origin of the Chatham Islands biota.

Location New Zealand and the Chatham Islands, separated by *c.* 800 km in the south-west Pacific Ocean.

Methods DNA sequences from the mitochondrial gene cytochrome oxidase I (COI) were obtained from four genera of relatively large and flightless insects (Coleoptera—*Geodorcus*, *Mecodema*; Orthoptera—*Talitropsis*; Blattoidea—*Celatoblatta*). These were used to test alternative hypotheses for the origin of the Chatham taxa.

Results Phylogenetic analysis revealed the Chatham taxa in each genus to be monophyletic. Genetic distances exhibited by these genera, between taxa found on the Chatham Islands and mainland New Zealand were relatively low (11.2, 2.8, 3.0 and 4.9%, respectively).

Main conclusions Even allowing for variation in molecular evolutionary rates, these genetic distances indicate phylogenetic separation of New Zealand and Chatham insect lineages in the Pliocene (2–6 Ma). Such dates are more than one order of magnitude too recent to be explained by vicariant (tectonic) processes. Oversea dispersal from New Zealand to the Chatham Islands is implicated and this conclusion is in keeping with the taxonomy of the endemic avifauna, flora and fossil molluscan fauna.

Keywords
Chatham Islands, dispersal, insects, mtDNA, New Zealand, phylogeography, vicariance.

INTRODUCTION

In southern hemisphere biology much has been made of patterns of organismal distribution that coincide with the present geographical distributions of fragments of the ancient landmass of Gondwana (e.g. Rosen, 1978; Wiley, 1988; Craw, Grehan & Heads, 1999). The development of plate tectonic theory provided a mechanism for the vicariant origin of biotas and leant much support to vicariance biogeography. Although most modern biogeographers accept a role for both vicariance and dispersal, the vicariance/dispersal debate has been active at least since the time of Charles Darwin and his contemporaries and remains so (Cox, 1998). Only relatively recently have independent molecular data been available and applied to such issues (e.g. Bowen, Meylan & Avise, 1989; Bowen & Grant, 1997; Baum, Small & Wendel, 1998; Waters & Burridge, 1999; Bargelloni *et al.*, 2000). For instance, the plant genus *Sophora* (formerly *Edwardsia*) (Leguminosae), has long been held as evidence of vicariance as it has a classic Gondwanan (southern hemisphere) distribution. However, Charles Darwin thought it could have reached its current range by dispersal and wrote in a letter to Joseph Hooker 'I believe you are afraid to send me a ripe *Edwardsia* pod for fear I sh^{d} float it from N. [ew] Zealand to Chile!!!' (Darwin, 1857). Evidence is now available in the form of molecular data that show the distribution pattern of *Sophora* can be most simply explained by dispersal (Hurr *et al.*, 1999). Similar results have been found for a range of other plant taxa in the New Zealand region (Wagstaff & Garnock-Jones, 1998; Breitwieser *et al.*, 1999; Wagstaff & Wardle, 1999).

Charles Fleming took a phlegmatic approach in his biogeographical synthesis of the New Zealand biota, in proposing

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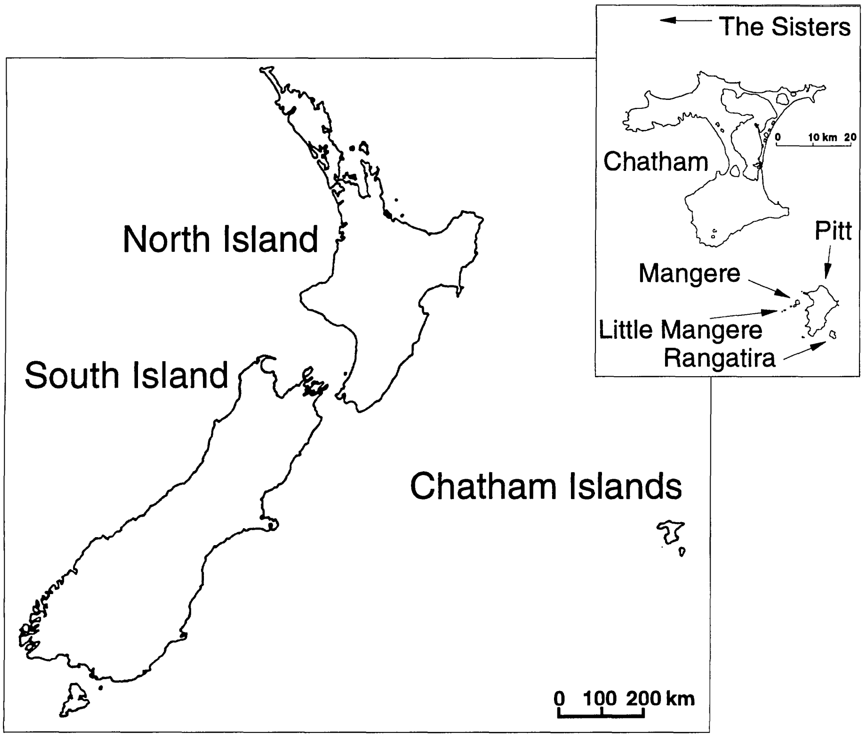

Figure 1 Map showing the relative position of New Zealand and the Chatham Islands, with an inset showing the various islands of the Chatham archipelago.

that some elements probably reflected vicariance while others arrived via dispersal from various sources (Fleming, 1979). Although the debate has often polarized, the fact that New Zealand has geological and biological characteristics of both continental and island systems (Cooper & Millener, 1993; Daugherty, Gibbs & Hitchmough, 1993) makes it an interesting system in which to explore the effects of vicariance and dispersal, and our assumptions about their respective roles.

The Chatham Islands are situated *c.* 800 km east of the New Zealand mainland (hereafter New Zealand) and comprise two relatively large inhabited islands, Pitt and Chatham (Fig. 1). There are also several smaller associated islands including Mangere and Rangatira (near Pitt) and The Sisters to the north of Chatham. The Chatham Islands (hereafter Chathams) lie towards the eastern end of the Chatham Rise that runs eastwards from mid-South Island, New Zealand. Chatham Rise, New Zealand, and other outlying islands are all part of a large continental mass of which only *c.* 10% is above sea-level today (Stevens, 1980).

The Chathams have a distinctive biota with many local and restricted species, of which the Coleoptera are the best studied insect group. The high levels of diversity and the presence of many large flightless coleopteran taxa led Emberson (1995) to suggest that a post-Gondwanan land bridge must have existed linking the Chathams and southern New Zealand. Despite high endemicity, Emberson (1995, 1998) noted that this was primarily at the species level, implying relatively recent biological isolation of the Chathams from New Zealand.

Craw (1988, 1989) applied the panbiogeographical method and identified two elements in the Chatham biota that were related to northern and southern elements of New Zealand. Craw used the 'parallel arcs model' (Heads, 1989) to explain how geological movements had united what he perceived as distinct faunal elements. However, this interpretation is dependant on tectonic activity that probably took place long before the 'New Zealand' region separated from Gondwana (*c.* 140 Ma). Furthermore, the relevant rock strata were probably entirely marine and unlikely to have been capable of transporting terrestrial biota (Cooper, 1989; Lovis, 1989). A more orthodox vicariance hypothesis can be developed from geological evidence that indicates that New Zealand and the Chathams area have not been in direct terrestrial contact since the Pacific and Australasian tectonic plates separated at least 70 Ma (Campbell *et al.*, 1993). Standard vicariance biogeography would therefore expect the biotas of New Zealand and the Chathams to show a similar level of mutual divergence as other Australasian taxa.

This study has taken a molecular approach to testing the likely origin of the Chathams endemic biota, and in so doing questions the *prima facie* conclusion that vicariance is the major force in southern hemisphere patterns. Specifically, I use DNA sequence data to test alternative hypotheses by phylogeographical analysis of a suite of invertebrate taxa. Candidate taxa include relatively large and flightless insects belonging to exclusively flightless genera. Such taxa are expected to have low vagility over sea, and are thus potentially highly susceptible to vicariance. It is therefore a conservative test of the vicariant hypothesis.

MATERIALS AND METHODS

Hypotheses

Three alternative hypotheses can be proposed for the development of the Chatham biota. (1) Vicariant: a purely vicariant origin would be characterized by ancient divergence between NZ and Chatham taxa (> 70 Ma) with strong phylogeographical structure. This assumes that the Chathams land surface has remained inhabitable since isolation from Gondwana, and that subsequent dispersal has not occurred. (2) Land bridge: an extended period of potential colonization would give rise to a mixture of divergences from New Zealand taxa among different groups, and weak phylogeographical structure within the Chathams. (3) Recent: The biota have shallow divergences (*c.* 4 Ma) from relatives in New Zealand. This assumes that the present Chathams land surface has been exposed above the sea for only *c.* 4 MY (Campbell, 1998).

Sampling

Four flightless insect genera (two beetles, one cave cricket and one cockroach) were selected for the study, each of which is present in the Chathams and New Zealand (Fig. 2). These were *Mecodema* (Coleoptera, Carabidae), *Geodorcus* (Coleoptera, Lucanidae), *Talitropsis* (Orthoptera, Raphidophoridae), *Celatoblatta* (Blattariae, Blattidae). As no phylogenetic hypotheses existed for these genera, it was not possible to specifically target sister taxa representing the two areas (except for *Mecodema alternans*), and the analysis will therefore tend to give a conservative estimate of the relatedness of the respective biotas. All of the genera are endemic to New Zealand, and where the likely sister genera are known, these too are endemics. All species described from the Chathams were represented in the analysis.

Mecodema Blanchard (Coleoptera, Carabidae). Some 58 species occur in New Zealand (Britton, 1949; Townsend, 1971) distributed in a wide range of habitats. The majority of species (*c.* 41) occur only in south island. One species, *Mecodema alternans* is known in the Chathams, and it is also found in southern South Island. Most of the mainland species tend to have relatively narrow distributions. All *Mecodema* and related carabids are flightless.

Geodorcus Holloway (Coleoptera, Lucanidae). Two species of *Geodorcus* are present on the Chathams Islands: *G. capito* on Chatham, Mangere, Pitt, Rangatira and Star Keys, and an undescribed species (*G.* '*sis*') on the Sisters (personal communication, Beverley Holloway). Mainland New Zealand has five species, four of which are scarce and have very restricted ranges, and one, *G. helmsi* is known from west and southern South Island. Holloway (1963) noted that, on the basis of wing morphology, *G. capito* was probably closer to North Island than South Island species. Both fully winged and flightless lucanids are known in New Zealand but *Geodorcus* and its putative sister genus *Paralissotes* are flightless (Holloway, 1963, 1996).

Talitropsis Bolivar (Orthoptera, Raphidophoridae). Four species of this relatively small (body length *c.* 20 mm) cave weta (cricket) are described from New Zealand (Hutton, 1897; Trewick, 1999). Two species are present on the Chathams, *T. crassicruris* on Mangere, Little Mangere, Pitt, Rangatira and The Sisters, and *T. megatibia* on the Chathams (Trewick, 1999). *Talitropsis sedilloti* is abundant and widespread throughout mainland New Zealand. A fourth species occurs within the geographical, and apparently morphological, range of *T. sedilloti* and may be synonymous with it. *Talitropsis* and all New Zealand Raphidophoridae are flightless.

Celatoblatta Johns (Blattariae, Blattidae). Thirteen species are described from New Zealand (Johns, 1966). One 10–14 mm long species (*Celatoblatta brunni*) is described from the Chathams and has been recorded on Chatham, Pitt, Rangatira and The Sisters. Some New Zealand taxa are widespread (e.g. *C. vulgaris*), while others have more restricted geographical ranges (such as *C. quinqemaculata*). Most appear to be habitat specific and all are flightless (Johns, 1966).

Molecular methods

Specimens were collected in the field by the author or sourced from museum collections. Museum material was used with the agreement of curators and was sampled in a manner least likely to detract from the morphological integrity of specimens. All specimens were stored in 80–95% ethanol after capture. In most instances a single leg was removed from specimens, or in the case of *Talitropsis*, muscle tissue was dissected from a hind femur without removing it.

DNA was extracted using a salting-out method (Sunnucks & Hale, 1996). Tissue was macerated and incubated with 5 μL of 10 mg/mL proteinase K in 600 μL of TNES buffer (20 mM EDTA, 50 mM Tris, 400 mM NaCl, 0.5% SDS) at 50 °C. Ten percent 5 M NaCl was added and the extractions shaken vigorously for 20 s, followed by spinning at 14,000 r.p.m. for 5 min. The supernatant was removed and precipitated with an equal volume of cold 100% ethanol. DNA was collected by spinning and washed with 70% ethanol before being dried and dissolved in water.

Segments of the mitochondrial gene cytochrome oxidase I (COI) were amplified using polymerase chain reaction (PCR). COI has been effectively employed in a wide range of intra- and interspecific invertebrate studies (e.g. Szymura, Lunt & Hewitt, 1996; Zhang & Hewitt, 1996; Funk, 1999; Trewick, Wallis & Morgan-Richards, 2000). Two primer combinations were used, targeting different portions of the COI gene, depending on amplification results; C1-J-2195 and L2-N-3014, and/or C1-J-1718 and C1-N-2191 (Simon *et al.*, 1994). PCR was performed in 25 μL volumes (200 μM dNTPs, 2.5 mM $MgCl_2$, 0.25 U Qiagen Taq) and products gel-purified in 2% agarose stained with ethidium bromide. Bands of expected molecular weight were excised and the DNA extracted from the agarose using Qiaquick spin columns (Qiagen). Purified DNA fragments were quantified by eye using agarose electrophoresis with a molecular weight marker. Cycle sequencing used Bigdye chemistry (Perkin Elmer, Long Beach, California, USA) following the manufacturer's protocols. Sequences were aligned manually using SeqEd. v1.0.3 (ABI, PE). Phylogenetic analysis was

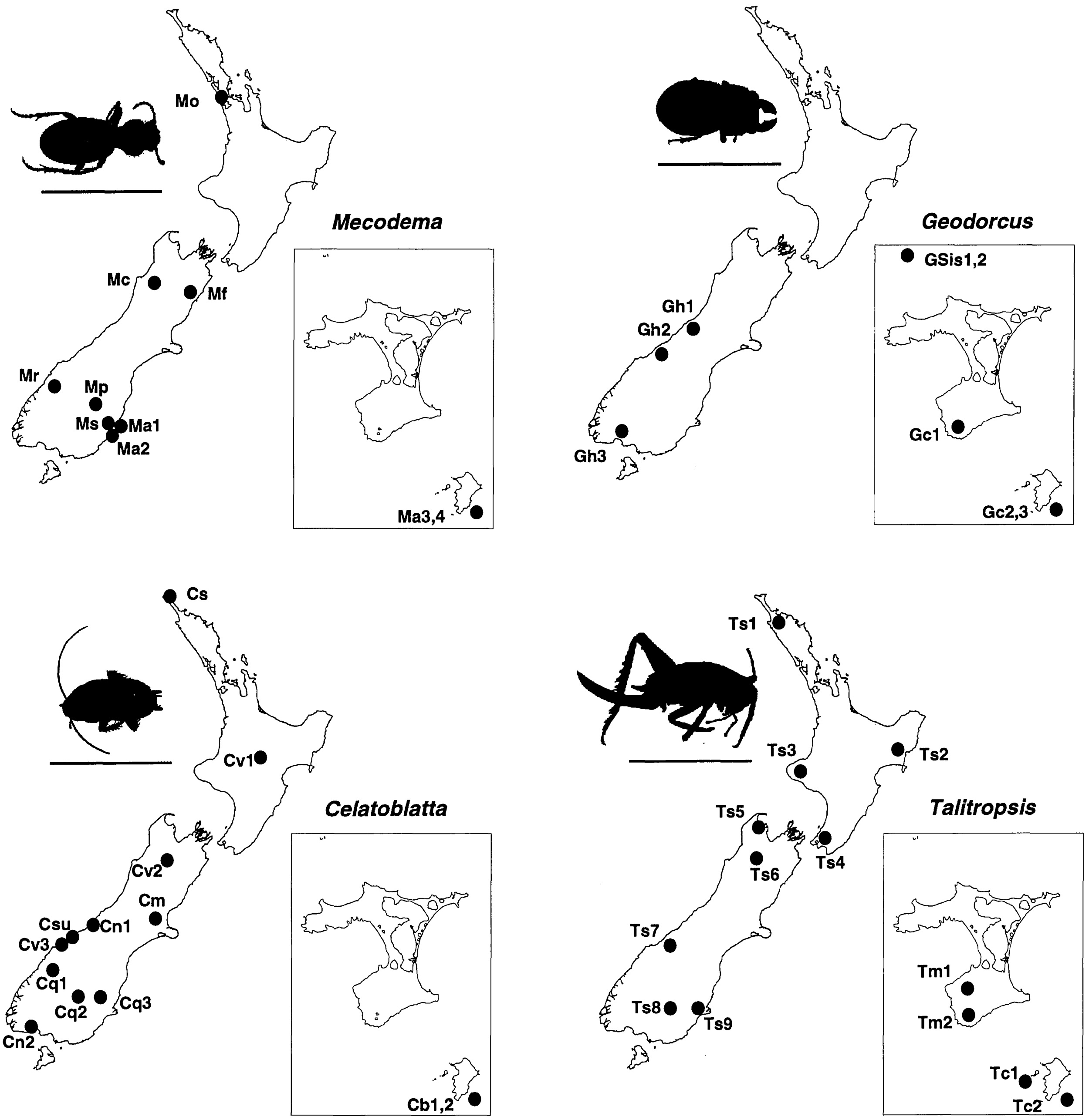

Figure 2 Sampling locations for four insect genera surveyed from New Zealand and the Chatham Islands. New Zealand and Chatham Islands are not to scale. A silhouette and 20 mm scale bar is given for each genus.

performed using PAUP*4.01b (Swofford, 1998). Primers were sourced from the insect mtDNA primer set (John Hobbs, Nucleic Acid—Protein Service, NAPS Unit, University of British Columbia, Vancouver, B.C., Canada).

RESULTS

Each genus (*Mecodema*, *Geodorcus*, *Celatoblatta* and *Talitropsis*) was sampled from sites in New Zealand and the Chathams. The range and number of taxa obtained for each genus was largely dependent on its diversity and the availability of individuals of each species (Fig. 2, Table 1).

Sequence data

Fragments of the mtDNA COI gene, varying in length from 480 to 650 bp, were sequenced for the four genera. DNA from *Mecodema*, *Geodorcus* and *Celatoblatta* was sequenced for

Table 1 Details of sampling sites for representatives of four genera of insects surveyed from New Zealand and the Chatham Islands.

Taxon group	Species	Location	Island*	Latitude, longitude†
Mecodema				
Mo	*M. occiputale*	Waitakere	NI	36°54′ S, 174°33′ E
Mc	*M. crenicolle*	Shenandoah	SI	41°52′ S, 172°14′ E
Mf	*M. fulgidum*	Mt Fyffe	SI	42°20′ S, 173°38′ E
Mr	*M. rugiceps*	Harris Saddle	SI	44°43′ S, 168°10′ E
Mp	*M. punctatum*	Rock and Pillars	SI	45°25′ S, 170°04′ E
Ms	*M. sculpturatum*	Swampy Summit	SI	45°48′ S, 170°29′ E
Ma1	*M. alternans*	Sandfly Bay	SI	45°53′ S, 170°38′ E
Ma2	*M. alternans*	Taieri Mouth	SI	46°03′ S, 170°12′ E
Ma3	*M. alternans*	Rangatira	RI	45°20′ S, 176°11′ W
Ma4	*M. alternans*	Rangatira	RI	45°20′ S, 176°11′ W
Geodorcus				
Gh1	*G. helmsi*	Rough Creek	NZ	43°34′ S, 169°48′ E
Gh2	*G. helmsi*	L. Paringa	NZ	43°42′ S, 169°25′ E
Gh3	*G. helmsi*	Riverton	NZ	46°21′ S, 167°58′ E
Gc1	*G. capito*	Taiko Camp	CI	44°04′ S, 176°38′ W
Gc2	*G. capito*	Rangatira	RI	45°20′ S, 176°11′ W
Gc3	*G. capito*	Rangatira	RI	46°20′ S, 177°11′ W
Gsis1	*G. 'sis'*	The Sisters	Sis	43°33′ S, 176°48′ W
Gsis2	*G. 'sis'*	The Sisters	Sis	44°33′ S, 177°48′ W
Celatoblatta				
Cv1	*C. vulgaris*	L. Taupo	NI	38°47′ S, 176°04′ E
Cv2	*C. vulgaris*	Mt Roberts	SI	42°49′ S, 172°48′ E
Cv3	*C. vulgaris*	Okuru	SI	43°54′ S, 168°55′ E
Cs	*C. sedilloti*	Cape Reinga	NI	34°25′ S, 172°40′ E
Cn1	*C. notialis*	L. Matheson	SI	43°26′ S, 169°57′ E
Cn2	*C. notialis*	Riverton	SI	46°21′ S, 167°58′ E
Csu	*C. subcorticaria*	North Haast	SI	43°49′ S, 169°03′ E
Cm	*C. montana*	Fog Peak	SI	44°43′ S, 168°10′ E
Ca	*C. anisoptera*	Mt St Bathans	SI	44°46′ S, 169°48′ E
Cq1	*C. quinqemaculata*	Conical Peak	SI	44°43′ S, 168°10′ E
Cq2	*C. quinqemaculata*	Obelisk	SI	45°19′ S, 169°12′ E
Cq3	*C. quinqemaculata*	Rock & Pillars	SI	45°25′ S, 170°04′ E
Cb1	*C. brunni*	Rangatira	RI	45°20′ S, 176°11′ W
Cb2	*C. brunni*	Rangatira	RI	45°20′ S, 176°11′ W
Talitropsis				
Ts1	*T. sedilloti*	Whatitiri	NI	35°47′ S, 174°09′ E
Ts2	*T. sedilloti*	Matawai	NI	38°21′ S, 177°32′ E
Ts3	*T. sedilloti*	Mt Taranaki	NI	39°16′ S, 174°05′ E
Ts4	*T. sedilloti*	Mt Kauwau	NI	41°13′ S, 174°46′ E
Ts5	*T. sedilloti*	The Grove	SI	40°50′ S, 172°52′ E
Ts6	*T. sedilloti*	Mt Roberts	SI	42°49′ S, 172°48′ E
Ts7	*T. sedilloti*	North Haast	SI	43°49′ S, 169°03′ E
Ts8	*T. sedilloti*	Piano Flat	SI	45°34′ S, 169°01′ E
Ts9	*T. sedilloti*	Fraser's Gully	SI	45°50′ S, 170°29′ E
Tm1	*T. megatibia*	Whangamerino	CI	44°01′ S, 176°39′ W
Tm2	*T. megatibia*	Taiko Camp	CI	44°04′ S, 176°38′ W
Tc1	*T. crassicruris*	Little Mangere	LM	44°16′ S, 176°19′ W
Tc2	*T. crassicruris*	Rangatira	RI	45°20′ S, 176°11′ W

* Island codes: CI, Chatham; LM, Little Mangere; RI, Rangatira; Sis, The Sisters; SI, South Island; NI, North Island.
† Longitudes given are east of the Greenwich meridian, except for those relating to the Chatham Islands, which are west.

the portion of COI downstream from the primer C1-J-2195, while *Talitropsis* COI was sequenced from primer C1-J-1718. Summary statistics for COI sequences from each genus are given in Table 2. As is typical for COI in insects, all the taxa showed an AT bias of 65–72% overall, with third codon positions comprising 89–95% AT (Table 2). A χ^2-test (PAUP*) indicated no significant base composition heterogeneity among taxa within each genus. The majority of substitutions were at third codon positions (79.5–81.5%), with fewer at first (9.4–19%) and second positions (1.6–3.7%). Sequence data were deposited on GenBank (AF320644–AF320687).

Genetic distance

Genetic distances among taxa within each genus were calculated using the Kimura 2 parameter (K2P) model (Kimura, 1980) (Table 3). The highest genetic distances within a genus were among *Geodorcus* individuals (maximum 13.7%). High intraspecific genetic distances were also found among *Geodorcus* in New Zealand (*G. helmsi* 7.2%) and the Chathams (*G. capito* 6.6%). In contrast, maximum intraspecific distances in *Talitropsis sedilloti* were lower (maximum 4.4%), despite greater geographical distances between the individuals sampled (Fig. 2). Seven species were surveyed from both *Mecodema* and *Celatoblatta*, and these revealed interspecific genetic distances of 3.2–6.8% and 4.6–8.6%, respectively (Table 3).

In *Mecodema* and *Celatoblatta*, the genera for which several New Zealand species were sampled, the highest K2P distances were not those between Chatham and New Zealand taxa. Mean genetic distances between the most closely related Chatham and New Zealand taxa for each genus were 2.8% (*Mecodema*), 3.0% (*Talitropsis*), 4.9% (*Celatoblatta*) and 11.2% (*Geodorcus*). Genetic distances between populations/species on separate islands of the Chatham group for those taxa sampled in this way were 4.8–6.8% (*Geodorcus*) and 1.5–2.6% (*Talitropsis*). Individuals of each genus sampled from separate Chatham populations were not identical. Genetic distances among *Geodorcus* individuals and species were consistently the highest in the study, despite the fact that this genetic diversity was represented by few species.

Phylogenetic analysis

Phylogenetic analysis was performed using unweighted maximum parsimony (MP). The use of transition : transversion weighting did not alter tree topologies or improve bootstrap values. In all cases, the edges of interest (linking Chatham and New Zealand taxa) were well supported by bootstrap analysis (91–100%) (Fig. 3). Neighbour-joining analysis using K2P distance data produced trees with the same topologies.

In all genera, haplotypes from Chatham taxa were monophyletic (Fig. 3). In the Chatham genera that included two described species, *Talitropsis* and *Geodorcus*, *T. megatibia* and *T. crassicruris* were reciprocally monophyletic, but *G. capito* and *G.* '*sis*' were not. *Geodorcus capito* (from Taiko Camp and Rangatira) was paraphyletic with respect to its sister species on the Sisters, *Geodorcus* '*sis*'. But, for all genera,

Table 2 Summary statistics of cytochrome oxidase I mtDNA sequences from four insect genera. Information on proportional base composition by codon position and overall, percentage A + T, number of sites (N), number and percentage of informative sites, and transition to transversion ratios (TI : TV) are given.

	A	C	G	T	A + T%	N	Substitutions (%)	Informative sites %	N	TI : TV
Mecodema										
1	0.286	0.113	0.276	0.325	61.1	217	14.7			
2	0.176	0.245	0.159	0.420	59.6	217	3.7			
3	0.459	0.310	0.015	0.496	95.5	216	81.6			
Overall	0.305	0.131	0.151	0.413	71.8	650		6	39	2
Geodorcus										
1	0.330	0.124	0.282	0.264	59.4	167	9.4			
2	0.189	0.218	0.148	0.445	63.4	166	3.5			
3	0.409	0.070	0.032	0.479	88.8	167	87.1			
Overall	0.309	0.138	0.154	0.399	70.8	500		13.6	68	1.7
Celatoblatta										
1	0.252	0.137	0.300	0.315	56.7	203	18.9			
2	0.191	0.237	0.162	0.410	60.1	204	1.6			
3	0.496	0.040	0.012	0.452	94.8	203	79.5			
Overall	0.313	0.138	0.158	0.391	70.4	610		11.3	69	1.5
Talitropsis										
1	0.232	0.189	0.300	0.279	51.1	160	18.2			
2	0.137	0.307	0.157	0.400	53.7	160	2.3			
3	0.455	0.059	0.022	0.464	91.9	160	79.5			
Overall	0.274	0.185	0.160	0.381	65.5	480		4.1	20	1.6

Table 3 Genetic distances (calculated using the Kimura 2 parameter model) among taxa of four insect genera. Bold text indicates lowest distances between Chatham and New Zealand taxa

Mecodema	Ma3	Ma4	Ma2	Ma1	Mr	Mo	Ms	Mp	Mf	Mo
Ma3										
Ma4	0.9									
Ma2	**2.8**	**2.8**								
Ma1	**2.7**	**2.9**	0.0							
Mr	5.6	5.6	4.8	4.8						
Mo	6.5	6.1	6.8	6.9	6.8					
Ms	5.1	5.4	4.8	4.8	5.8	6.5				
Mp	4.8	5.0	5.0	5.0	5.5	6.0	3.2			
Mf	5.9	6.0	5.7	5.7	6.0	6.7	4.5	3.9		
Mc	6.6	6.4	6.1	6.2	7.5	6.8	5.6	4.7	4.7	

Geodorcus	Gsis1	Gsis2	Gc2	Gc3	Gc1	Gh3	Gh1	Gh2
Gsis1								
Gsis2	0.2							
Gc2	5.4	5.2						
Gc3	5.1	4.8	0.4					
Gc1	6.8	6.6	6.6	6.6				
Gh3	**11.7**	**11.5**	**10.8**	**10.9**	10.9			
Gh1	14.2	13.9	13.7	13.8	13.5	7.2		
Gh2	13.7	13.4	12.7	13.0	12.3	6.1	1.6	

Celatoblatta	Cb1	Cb2	Cq1	Cq2	Cq3	Cm	Cn2	Cn1	Csu	Cs	Cv3	Cv2
Cb1												
Cb2	0.8											
Cq1	**5.5**	**5.1**										
Cq2	**5.1**	**4.8**	2.0									
Cq3	**4.6**	**4.6**	2.2	2.2								
Cm	7.8	7.4	7.1	6.7	7.0							
Cn2	7.4	7.1	6.0	6.9	6.8	7.3						
Cn1	7.3	6.9	6.2	7.1	6.9	8.2	2.7					
Csu	5.8	5.6	6.5	6.9	6.8	6.2	6.5	7.3				
Cs	7.1	6.9	6.3	6.3	6.4	7.3	7.1	7.3	4.8			
Cv3	6.5	6.1	5.9	5.7	5.6	5.6	6.1	6.6	6.4	5.5		
Cv2	6.9	6.5	6.7	6.9	6.7	6.4	8.0	8.4	6.3	6.9	2.6	
Cv1	7.1	6.9	6.9	6.0	6.6	6.4	7.8	8.6	7.4	7.5	2.7	4.4

Talitropsis	Tc1	Tc2	Tm1	Tm2	Ts1	Ts2	Ts3	Ts4	Ts5	Ts6	Ts7	Ts8
Tc1												
Tc2	0.9											
Tm1	2.1	2.6										
Tm2	1.5	1.7	0.4									
Ts1	**3.0**	**3.5**	**2.6**	**2.3**								
Ts2	**3.0**	**3.5**	**2.6**	**2.4**	0.4							
Ts3	**3.4**	**3.9**	**3.0**	**2.8**	0.4	0.4						
Ts4	**3.0**	**3.5**	**2.6**	**2.4**	0.6	0.2	0.6					
Ts5	2.6	3.1	2.8	2.1	1.5	1.1	1.5	0.8				
Ts6	3.6	4.1	3.2	3.0	2.1	1.7	2.1	1.5	0.8			
Ts7	3.9	4.4	3.6	3.4	2.1	1.7	2.1	1.3	1.0	2.1		
Ts8	3.6	4.1	3.4	3.2	1.9	1.5	1.9	1.5	0.8	1.9	0.6	
Ts9	3.4	3.9	3.7	3.0	2.1	1.7	2.1	1.7	0.6	2.1	0.8	0.6

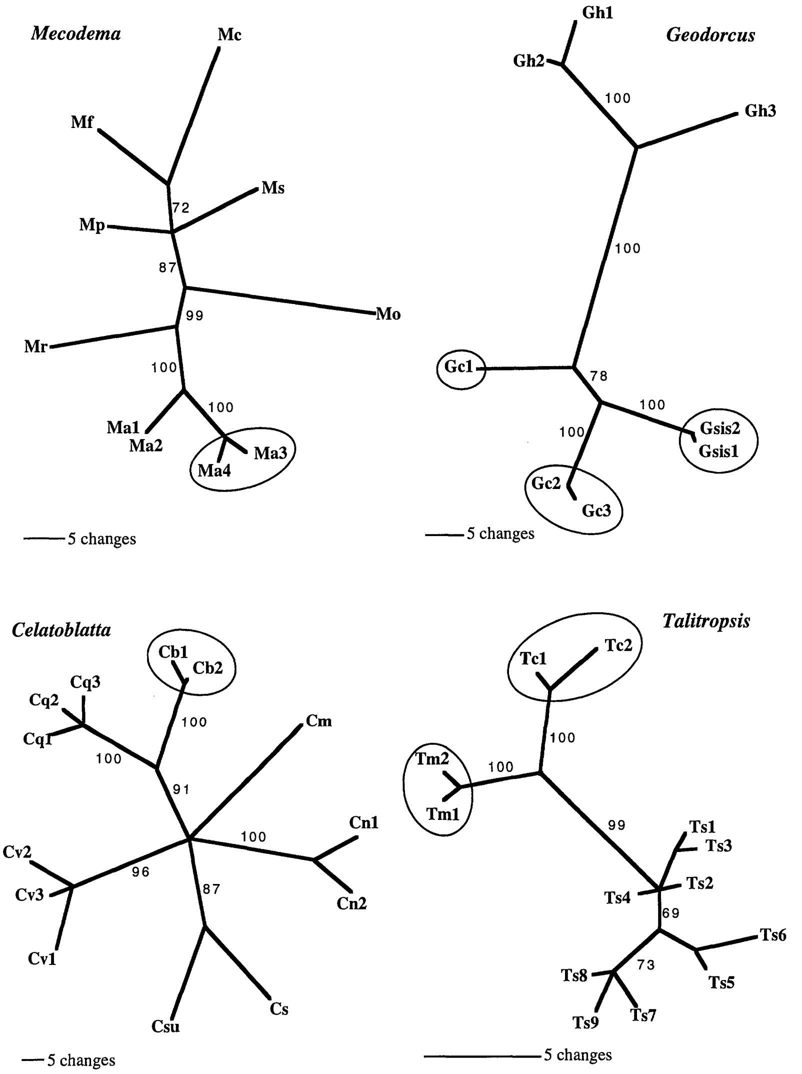

Figure 3 Unrooted networks derived from unweighted maximum parsimony analysis of cytochrome oxidase I mtDNA sequences from four insect genera. Values on internal edges are scores from 500 bootstrap replicates performed using the heuristic search option of PAUP*. Taxon codes are as given in Table 1. Elipses indicate chatham taxa.

each of the Chatham island populations is supported as monophyletic.

DISCUSSION

Chatham taxa are closely related to New Zealand taxa and in *Mecodema*, are not morphologically separable as distinct species. Chatham diversity appears to be a subset of New Zealand diversity, as previously noted (Emberson, 1998). Each of the four genera appears to have colonized the Chathams only once, although it is feasible (especially in case of *Geodorcus*) that lineages of New Zealand taxa not encountered in this study may share a closer ancestor with the Chatham lineages. On the basis of morphological evidence, it is likely that the closest extant New Zealand relative of Chathams *Geodorcus* was not included in the present study (Holloway, 1963). However, although genetic distances among *Geodorcus* were high, suggesting a relatively earlier split of New Zealand/Chatham taxa in this genus compared with the others studied, this pattern could alternatively have resulted from an elevated mutation rate in this genus. This interpretation is consistent with the observations that genetic distances within *G. helmsi* in New Zealand, and among the Chatham taxa were all high, and that the Chatham species were paraphyletic. Although paraphyletic species do occur (e.g. Arias *et al.*, 1996; Crespi *et al.*, 1997), they are expected to become less frequent with increasing genetic divergence.

All four genera examined here show levels of genetic divergence that are consistent with colonization of the Chathams from New Zealand within the last *c.* 6 Ma (< 3 Ma if *Geodorcus* is excluded), using the standard calibrations of 2–2.3% sequence divergence per million years (Brown, George Jr & Wilson, 1979; DeSalle *et al.*, 1987; Brower, 1994). This estimate is, of course, dependent on the applicability of an averaged rate calibration based on different taxa and genes, and whether or not the most closely related New Zealand and Chatham taxa have been compared. However, a 2% sequence divergence rate has also been identified for COI among congeneric beetle species of the Canary Islands (Juan, Oromi & Hewitt, 1995) and similar mtDNA rates have been found among Hawaiian invertebrates (Fleischer, McIntosh & Tarr, 1998), both calibrations based on geological ages of volcanic islands. Although the 2% divergence rate estimated for COI sequence data is expected to increasingly underestimate separation time as sequences become more different, this rate appears to remain a reliable estimate for uncorrected genetic distances up to 10 or 12% (i.e. as found with *Geodorcus*) (Juan, Oromi & Hewitt, 1996).

There is no support in these data for the insect genera surveyed in the present study to have arrived in the Chathams through tectonic vicariant processes. This would mean that the data and/or calibration were in error by more than one order of magnitude for all four genera. It also seems clear that they arrived as a result of dispersal from New Zealand some time during the Pliocene (2–6 Ma). Lower sea level during the Pleistocene may have facilitated greater movement among the islands of the Chatham group, providing opportunities for isolation on the current archipelago and lineage sorting.

Genetic distances between Chatham and New Zealand congenerics are substantially lower than those observed in a study of flightless *Pimelia* and *Hegeter* beetles on the Canary Islands using COI (Juan *et al.*, 1995, 1996). This is despite the relatively small geographical distances between the Canary archipelago and mainland Africa. However, the islands nearest Africa (*c.* 120 km away) are relatively old (15–20 MY) so there has been opportunity for greater divergence of island and mainland taxa. By contrast, despite their greater geological age, it seems that submergence by marine inundation (*c.* 4 Ma) may best explain the absence of deeply divergent lineages in the Chathams (Campbell, 1998). Finston & Peck (1995) noted similarly low genetic differences among island species of darkling beetles in the Galápagos archipelago, which date from *c.* 3 Ma (Hickman & Lipps, 1985), but DNA data for comparison with mainland taxa are not available.

Taxonomic evidence also indicates a close relationship between New Zealand and the Chathams. The avifauna of the Chathams is dominated by seabirds (e.g. Tennyson & Millener, 1994 and references therein), subspecies and sister species of New Zealand mainland forest birds (Fleming, 1979; Turbott, 1990), and flightless derivatives of widely dispersing Pacific taxa (mostly Rails now extinct, Millener, 1991; 1997b; Trewick, 1997a). A single lizard is known (*Oligosoma nigriplantare nigriplantare*; Rodney Hitchmough, personal communication), and the beetles (Emberson, 1995, 1998) and Diptera (Macfarlane, 1979) show close affinity with New Zealand. The flora is also closely allied to that of the New Zealand mainland and endemism is restricted to the species level or below (Given & Williams, 1984). The most distinctive feature of the flora is the absence of divarication, a character common to many New Zealand plants that probably relates to their defence against browsing by moa, which were also absent from the Chathams (Greenwood, 1992). The intertidal fauna and flora show close affinities with New Zealand (Knox, 1954).

A large proportion of the New Zealand biota is not represented on the Chathams (e.g. *Leiopelma* frogs, *Sphenodon* tuatara, *Powelliphanta* snails, Anostostomatid crickets, *Simulid* midges, Onychophora). The stochastic effects of extinction or colonization might equally explain their absence, but the predominant shallowness of taxonomic distinction between the two extant biotas indicates recent association between the Chatham and New Zealand, rather than ancient isolation. The fact that the Recent fossil molluscan fauna of the Chathams is more closely allied to the New Zealand fauna than the Chatham Tertiary fauna further supports Pliocene colonization (Finlay, 1928). The panbiogeographical 'analysis', which indicated ancient patterns in the biotas, has apparently not been effective in elucidating processes in the development of the Chatham biota, specifically, the claim that the dispersal model could be statistically rejected (Craw, 1989), suggests that the method is flawed.

The current study targeted taxa with little potential for active migration over water. However, it may be that they have a relatively high susceptibility to passive dispersal. Bell (1979) argued that Rhysodini beetles were amenable to passive dispersal in floating logs because both adults and larvae live inside dead wood. In the present study, *Mecodema* and *Geodorcus* beetles similarly have their larval stage within decaying logs, and *Talitropsis* and *Celatoblatta* also often have their daytime roosts in logs. It is therefore possible that these insects travelled to the Chathams in floating logs, and this is more probable than aerial transport. Emberson (1995) argued for land-bridging to explain the presence of large flightless beetles in the Chathams, but geology has so far failed to reveal evidence of any such structure in the relevant time-frame (*c.* 6 Ma). Similar land-bridging proposed for the Galápagos has also remained unsupported by geological evidence (Peck & Kukalová-Peck, 1990).

Direct observation of successful oversea dispersal events are, not surprisingly, rare (but see for example Wheeler, 1916; Heatwole & Levins, 1972; Censky, Hodge & Dudley, 1998). However, many studies have shown that there is aerial and sea-surface (pleuston) 'plankton' of terrestrial invertebrates that represent potential colonisers (e.g. Holzapfel & Harrel, 1968; Ashmole & Ashmole, 1988; 1994b; Peck, 1994a), and there is much indirect evidence for dispersal among Pacific islands (Gressitt, 1956). Even in the short time since its destructive eruption, Krakatau has been colonized by a variety of invertebrates (Thornton & New, 1988), and colonization is presumed to have been in operation for much longer in the Galápagos, Hawaiian and Canary islands, etc. The infrequency of successful dispersal of large and flightless invertebrates to oceanic islands is not evidence that the process is not a significant one in biogeographical terms given the time frame involved. Similarly, close affinity of taxa on neighbouring land masses (New Zealand and Chathams in this case) is not in itself evidence of vicariance, as the probability of successful dispersal will be highest between nearer rather than further locations.

There is increasing evidence that dispersal has played a significant role in the development of local biotas. The emergence of phylogeography (Avise *et al.*, 1987; Avise, 1998) has marked a renaissance in biogeography because it provides an independent means to both develop biogeographical scenarios (e.g. Thorpe *et al.*, 1994; Schneider-Broussard *et al.*, 1998) and test existing geology-based hypotheses (Bowen *et al.*, 1989; Lessios *et al.*, 1999). In New Zealand, such evidence strongly indicates that both dispersal and recent radiation have impacted on the New Zealand flora (Wagstaff & Garnock-Jones, 1998; Breitwieser *et al.*, 1999; Wagstaff & Wardle, 1999; Winkworth *et al.*, 1999), and the present study suggests a similar role among invertebrate groups. This is not to say that dispersal has been the only or even primary source of endemic lineages (Winkworth *et al.*, 1999), but that it should be accepted as a relevant one, irrespective of the impressions drawn from distribution patterns and the appeal of tectonic-based vicariance.

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REFERENCES

Arias, M. C., Tingek, S., Kelitu, A. & Sheppard, W. S. (1996) *Apis nulesnsis* Tingek, Koeniger and Koeniger, 1996 and its genetic relationship with sympatric species inferred from DNA sequences. *Apidologie*, **27**, 415–422.

Ashmole, N. P. & Ashmole, M. J. (1988) Insect dispersal on Tenerife, Canary Islands: high altitude fallout and seaward drift. *Arctic and Alpine Research*, **20**, 1–12.

Avise, J. C. (1998) The history and purview of phylogeography: concepts a personal reflection. *Molecular Ecology*, **7**, 371–379.

Avise, J. C., Arnold, J., Ball, R. M., Bermingham, E., Lamb, T., Neigel, J. E., Reeb, C. A. & Saunders, N. C. (1987) Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics*, **18**, 489–522.

Baum, D. A., Small, R. L. & Wendel, J. F. (1998) Biogeography and floral evolution of Baobabs (*Adansonia*, Bombacaceae) as inferred from multiple data sets. *Systematic Biology*, **47**, 181–207.

Bargelloni, L., Marcato, S., Zane, L. & Patarnello, T. (2000) Mitochondrial phylogeny of Notothenioids: a molecular approach to Antarctic fish evolution and biogeography. *Systematic Biology*, **49**, 114–129.

Bell, R. T. (1979) Zoogeography of Rhysodini—do beetles travel on driftwood? *Carabid beetles: their evolution, natural history and classification* (ed. by T. L. Erwin, G. E. Ball and D. R. Whitehead), pp. 331–342. Junk, The Hague.

Bowen, B. W., Meylan, A. B. & Avise, J. C. (1989) An odyssey of the green sea turtle: ascension Island revisited. *Proceedings of the National Academy of Sciences of the U.S.A.*, **86**, 573–576.

Bowen, B. W. & Grant, W. S. (1997) Phylogeography of the sardines (*Sardinops* spp.): assessing biogeographic models and population histories in temperate upwelling zones. *Evolution*, **51**, 1601–1610.

Breitwieser, I., Glenn, D. S., Thorne, A. & Wagstaff, S. J. (1999) Phylogenetic relationships in Australasian *Gnaphaliaea* (Compositae) inferred from ITS sequences. *New Zealand Journal of Botany*, **37**, 399–412.

Britton, E. B. (1949) The Carabidae (Coleoptera) of New Zealand. Part III: a revision of the tribe Broscini. *Transactions of the Royal Society of New Zealand*, **77**, 533–581.

Brower, A. V. Z. (1994) Rapid morphological radiation and convergence among races of the butterfly *Helioconius erato* inferred from patterns of mitochondrial DNA evolution. *Proceedings of the National Academy of Sciences of the U.S.A.*, **91**, 6491–6495.

Brown, W. M., George, M. Jr & Wilson, A. C. (1979) Rapid evolution of animal mitochondrial DNA. *Proceedings of the National Academy of Sciences of the U.S.A.*, **76**, 1967–1971.

Campbell, H. J., Andrews, P. B., Beu, A. G., Maxwell, P. A., Edwards, A. R., Laird, M. G., de Hornibrook, N. B., Mildenhall, D. C., Watters, W. A., Buckeridge, J. S., Lee, D. E., Strong, C. P., Wilson, G. J. & Hayward, B. W. (1993) Cretaceous-Cenozoic geology and biostratigraphy of the Chatham Islands, New Zealand. *Institute of Geological & Nuclear Sciences Monograph*, **2**, IGNS, Lower Hutt.

Campbell, H. J. (1998) Fauna and flora of the Chatham Islands: less than 4 m.y. old? Geology and Genes. *Geological Society of New Zealand Miscellaneous Publishers*, **97**, 15–16.

Censky, E. J., Hodge, K. & Dudley, J. (1998) Over-water dispersal of lizards due to hurricanes. *Nature*, **395**, 556.

Cooper, R. A. (1989) New Zealand tectonostratigraphic terranes and panbiogeography. *New Zealand Journal of Zoology*, **16**, 699–712.

Cooper, R. A. & Millener, P. R. (1993) The New Zealand biota: historical background and new research. *Trends in Ecology and Evolution*, **8**, 429–433.

Cox, C. B. (1998) From generalized tracks to ocean basins—how useful is Panbiogeography? *Journal of Biogeography*, **25**, 813–828.

Craw, R. (1988) Continuing the synthesis between panbiogeography, phylogenetic systematics and geology as illustrated by empirical studies on the biogeography of New Zealand and the Chatham Islands. *Systematic Zoology*, **37**, 291–310.

Craw, R. (1989) New Zealand biogeography: a panbiogeographic approach. *New Zealand Journal of Zoology*, **16**, 527–547.

Craw, R. C., Grehan, J. R. & Heads, M. J. (1999) *Panbiogeography: tracking the history of life*. Oxford University Press, New York, NY.

Crespi, B. J., Carmean, D., Mound, L. A., Worobey, M. & Morris, D. (1997) Phylogenetics of social evolution in Australian gall-forming thrips: evidence from mitochondrial DNA sequence, adult morphology, and gall morphology. *Molecular Phylogenetics and Evolution*, **9**, 163–180.

Daugherty, C. H., Gibbs, G. W. & Hitchmough, R. A. (1993) Mega-island or micro-continent? New Zealand and its fauna. *Trends in Ecology and Evolution*, **8**, 437–442.

Darwin, C. (1857) Letter to J. D. Hooker. *The correspondence of Charles Darwin* Vol. 6 (ed. by F. Burkardt and S. Smith), pp. 408–410 (1990). Cambridge University Press, Cambridge.

DeSalle, R., Freedman, T., Praager, E. M. & Wilson, A. C. (1987) Tempo and model of sequences evolution in mitochondrial

DNA of Hawaiian *Drosophila*. *Journal of Molecular Evolution*, **26**, 157–164.

Emberson, R. M. (1995) The Chathams Islands beetle fauna and the age of separation of the Chatham Islands from New Zealand. *New Zealand Entomologist*, **18**, 1–7.

Emberson, R. M. (1998) The beetle (Coleoptera) fauna of the Chatham Islands. *New Zealand Entomologist*, **21**, 25–64.

Finlay, H. J. (1928) The recent mollusca of the Chathams Islands. *Transactions of the New Zealand Institute*, **59**, 232–286.

Finston, T. L. & Peck, S. B. (1995) Population structure and gene flow in *Stomion*: a species swarm of flightless beetles of the Galápagos Islands. *Heredity*, **75**, 390–397.

Fleischer, R. C., McIntosh, C. E. & Tarr, C. I. (1998) Evolution on a volcanic conveyor belt: using phylogeographic reconstructions and K-Ar-based ages of the Hawaiian Islands to estimate molecular evolutionary rates. *Molecular Ecology*, **7**, 533–545.

Fleming, C. A. (1979) *The geological history of New Zealand and its Life*. Auckland and Oxford University Presses, Auckland.

Funk, D. J. (1999) Molecular systematics of cytochrome oxidase I and 16S from *Neochlamisus* leaf beetles and the importance of sampling. *Molecular Biology and Evolution*, **16**, 67–82.

Givens, D. R. & Williams, P. A. (1984) *Conservation of Chatham Island flora and vegetation*. Botany Division, Department of Scientific and Industrial Research, Christchurch.

Greenwood, R. M. (1992) Some differences between plants of the Chatham Island and the New Zealand mainland. *New Zealand Journal of Ecology*, **16**, 51–52.

Gressitt, J. L. (1956) Some distribution patterns of Pacific island faunae. *Systematic Zoology*, **5**, 11–33.

Heads, M. (1989) Integrating earth and life sciences in New Zealand natural history: the parallel arcs model. *New Zealand Journal of Zoology*, **16**, 549–585.

Heatwole, M. & Levins, R. (1972) Biogeography of the Puerto Rican Bank: flotsam transport of terrestrial animals. *Ecology*, **53**, 112–117.

Hickman, C. S. & Lipps, J. M. (1985) Geological youth of Galápagos Islands confirmed by marine stratigraphy and paleontology. *Science*, **227**, 1579–1580.

Holzapfel, E. P. & Harrel, J. C. (1968) Transoceanic dispersal studies of insects. *Pacific Insects*, **10**, 115–153.

Holloway, B. A. (1963) Wing development and evolution of New Zealand Lucanidae (Insecta: Coleoptera). *Transactions of the Royal Society of New Zealand*, **3**, 99–116.

Holloway, B. A. (1996) Two new genera of New Zealand stag beetles previously placed in *Dorcus* Macleay and *Lissotes* Westwood (Coleoptera: Lucanidae). *New Zealand Journal of Zoology*, **23**, 61–66.

Hurr, K. A., Lockhart, P. J., Heenan, P. B. & Penny, D. (1999) Evidence for the recent dispersal of *Sophora* (Leguminosae) around the Southern Oceans: Molecular data. *Journal of Biogeography*, **26**, 565–578.

Hutton, F. W. (1897) The Stenopelmatidae of New Zealand. *Transactions of the New Zealand Institute*, **29**, 223–240.

Johns, P. M. (1966) The cockroaches of New Zealand. *Records of the Canterbury Museum*, **8**, 93–136.

Juan, C., Oromi, P. & Hewitt, G. M. (1995) Mitochondrial DNA phylogeny and sequential colonization of Canary Islands by darkling beetles of the genus *Pimelia* (Tenebrionidae). *Proceedings of the Royal Society, London, Series B*, **261**, 173–180.

Juan, C., Oromi, P. & Hewitt, G. M. (1996) Phylogeny of the genus *Hegeter* (Tenebrionidae, Coleoptera) and its colonization of the Canary Islands deduced from cytochrome oxidase I mitochondrial DNA sequences. *Heredity*, **76**, 392–403.

Kimura, M. (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, **16**, 111–120.

Knox, G. A. (1954) The intertidal flora and fauna of the Chatham Islands. *Nature*, **174**, 871–873.

Lessios, H. A., Kessing, B. D., Robertson, D. R. & Paulay, G. (1999) Phylogeography of the pantropical sea urchin *Eucidaris* in relation to land barriers and ocean currents. *Evolution*, **53**, 806–817.

Lovis, J. D. (1989) Timing, exotic terranes, angiosperm diversification, and panbiogeography. *New Zealand Journal of Zoology*, **16**, 713–729.

Macfarlane, R. P. (1979) Notes on insects of the Chatham Islands. *New Zealand Entomologist*, **7**, 64–70.

Millener, P. R. (1991) The Quaternary avifauna of New Zealand. *Vertebrate Palaeontology of Australasia* (ed. by P. Vickers-Rich, J. M. Mohaghan, R. F. Baird, and T. H. Rich), pp. 1317–1339. Pioneer Design/Monash University, Melbourne.

Peck, S. B. (1994a) Aerial dispersal of insects between and to islands in the Galápagos archipelago, Ecuador. *Annals of the American Entomology Society*, **87**, 218–224.

Peck, S. B. (1994b) Sea-surface (plueston) transport of insects between island in the Galápagos archipelago, Ecuador. *Annals of the American Entomology Society*, **87**, 576–582.

Peck, S. B. & Kukalová-Peck, J. (1990) Origin and biogeography of the beetles (Coleoptera) of the Galápagos archipelago, Ecuador. *Canadian Journal of Zoology*, **68**, 1617–1638.

Rosen, D. R. (1978) Vicariant patterns and historical explanation in biogeography. *Systematic Zoology*, **27**, 159–188.

Schneider-Broussard, R., Felder, D. L., Chlan, C. A. & Neigel, J. E. (1998) Tests of phylogeographic models with nuclear and mitochondrial DNA sequence variation in the stone crabs, *Menippe adina* and *Menippe mercenaria*. *Evolution*, **52**, 1671–1678.

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. & Flook, P. (1994) Evolution, weighting and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the American Entomology Society*, **87**, 651–701.

Stevens, G. (1980) *New Zealand adrift*. Reed, Wellington.

Sunnucks, P. & Hale, D. F. (1996) Numerous transposed sequences of mitochondrial cytochrome oxidase I–II in aphids of the genus *Sitobion* (Hemiptera: aphididae). *Molecular Biology and Evolution*, **13**, 510–524.

Swofford, D. (1998) *Phylogenetic analysis using parsimony (and other methods) PAUP* 4.01 beta version*. Sinauer Associates, Sunderland, MA.

Szymura, J. M., Lunt, D. H. & Hewitt, G. M. (1996) The sequence and structure of the meadow grasshopper (*Chorthippus parallelus*) mitochondrial srRNA, ND2, COI, COII, ATPase8 and 9 tRNA genes. *Insect Molecular Biology*, **5**, 127–139.

Tennyson, A. J. D. & Millener, P. R. (1994) Birds extinctions and fossil bones from Mangere Island, Chatham Islands. *Notornis*, **41** (Suppl.), 165–178.

Thornton, I. W. B. & New, T. R. (1988) Krakatau invertebrates: the 1980s fauna in the context of a century of recolonization. *Philosophical Transactions of the Royal Society, London, Series B*, **322**, 493–522.

Thorpe, R. S., Mcgregor, D. P., Cumming, A. M. & Jordan, W. C. (1994) DNA evolution and colonization sequence of island lizards in relation to geological history: mtDNA RFLP, cytochrome b, cytochrome oxidase, 12S rRNA sequence, and nuclear RAPD analysis. *Evolution*, **48**, 230–240.

Townsend, J. I. (1971) Entomology of the Aucklands and other islands south of New Zealand: Coleoptera: Carabidae: Broscini. *Pacific Island Monographs*, **27**, 173–184.

Trewick, S. A. (1997a) Flightlessness and phylogeny amongst endemic rails (Aves: Rallidae) of the New Zealand region. *Philosophical Transactions of the Royal Society, London, Series B*, **352**, 429–446.

Trewick, S. A. (1997b) Sympatric flightless rails *Gallirallus dieffenbachii* and *G. modestus* on the Chatham Islands, New Zealand; morphometrics and alternative evolutionary scenarios. *Journal of the Royal Society of New Zealand*, **27**, 451–464.

Trewick, S. A. (1999) A new weta from the Chatham Islands (Orthoptera: Raphidophoridae) *Journal of the Royal Society of New Zealand*, **29**, 165–173.

Trewick, S. A., Wallis, G. P. & Morgan-Richards, M. (2000) Phylogeographic pattern correlates with Pliocene mountain-building in the alpine scree weta (Orthoptera, Anostostomatidae). *Molecular Ecology*, **9**, 657–666.

Turbott, E. G. (1990) *Checklist of the birds of New Zealand and the Ross Dependency, Antarctica* 3rd edn. Random Century/ Ornithological Society of New Zealand Inc., Auckland.

Wagstaff, S. J. & Garnock-Jones, P. J. (1998) Evolution and biogeography of the *Hebe* complex (Scrophylariaceae) inferred from ITS sequences. *New Zealand Journal of Botany*, **37**, 425–437.

Wagstaff, S. J. & Wardle, P. (1999) Whipcord Hebes-systematics, distribution, ecology and evolution. *New Zealand Journal of Botany*, **37**, 17–39.

Waters, J. M. & Burridge, C. P. (1999) extreme intraspecific mitochondrial DNA divergence in *Glaxias maculatus* (Osteichthyes: Galaxiidae), one of the world's most widespread freshwater fish. *Molecular Phylogenetics and Evolution*, **11**, 1–12.

Wheeler, W. N. (1916) Ants carried in a floating log from the Brazilian coast to San Sebastian Island. *Psyche*, **28**, 180.

Wiley, E. O. (1988) Vicariance biogeography. *Annual Review of Ecology and Systematics*, **19**, 153–542.

Winkworth, R. C., Robertson, A. W., Ehrendorfer, F. & Lockhart, P. J. (1999) The importance of dispersal and recent speciation in the flora of New Zealand. *Journal of Biogeography*, **26**, 1323–1325.

Zhang, D.-Z. & Hewitt, G. M. (1996) Assessment of the universality and utility of a set of conserved mitochondrial COI primers in insects. *Insect Molecular Biology*, **6**, 143–150.

BIOSKETCH

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