Systematic
Entomology

Systematic Entomology (2009), DOI: 10.1111/j.1365-3113.2009.00505.x

The phylogenetic placement and biogeographical origins of the New Zealand stick insects (Phasmatodea)

THOMAS R. BUCKLEY[1], DILINI ATTANAYAKE[1], JOHAN A. A. NYLANDER[2] and SVEN BRADLER[3]

[1]Landcare Research, Auckland, New Zealand, [2]Department of Botany, Stockholm University, Stockholm, Sweden and
[3]Johann-Friedrich-Blumenbach-Institut für Zoologie und Anthropologie, Georg-August-Universität Göttingen, Göttingen, Germany

Abstract. The Lanceocercata are a clade of stick insects (Phasmatodea) that have undergone an impressive evolutionary radiation in Australia, New Caledonia, the Mascarene Islands and areas of the Pacific. Previous research showed that this clade also contained at least two of the nine New Zealand stick insect genera. We have constructed a phylogeny of the Lanceocercata using 2277 bp of mitochondrial and nuclear DNA sequence data to determine whether all nine New Zealand genera are indeed Lanceocercata and whether the New Zealand fauna is monophyletic. DNA sequence data were obtained from mitochondrial cytochrome oxidase subunits I and II and the nuclear large subunit ribosomal RNA and histone subunit 3. These data were subjected to Bayesian phylogenetic inference under a partitioned model and maximum parsimony. The resulting trees show that all the New Zealand genera are nested within a large New Caledonian radiation. The New Zealand genera do not form a monophyletic group, with the genus *Spinotectarchus* Salmon forming an independent lineage from the remaining eight genera. We analysed Lanceocercata apomorphies to confirm the molecular placement of the New Zealand genera and to identify characters that confirm the polyphyly of the fauna. Molecular dating analyses under a relaxed clock coupled with a Bayesian extension to dispersal-vicariance analysis was used to reconstruct the biogeographical history for the Lanceocercata. These analyses show that Lanceocercata and their sister group, the Stephanacridini, probably diverged from their South American relatives, the Cladomorphinae, as a result of the separation of Australia, Antarctica and South America. The radiation of the New Caledonian and New Zealand clade began 41.06 million years ago (mya, 29.05–55.40 mya), which corresponds to a period of uplift in New Caledonia. The main New Zealand lineage and *Spinotectarchus* split from their New Caledonian sister groups 33.72 (23.9–45.62 mya) and 29.9 mya (19.79–41.16 mya) and began to radiate during the late Oligocene and early Miocene, probably in response to a reduction in land area and subsequent uplift in the late Oligocene and early Miocene. We discuss briefly shared host plant patterns between New Zealand and New Caledonia. Because *Acrophylla* sensu Brock & Hasenpusch is polyphyletic, we have removed *Vetilia* Stål from synonymy with *Acrophylla* Gray.

Introduction

The New Zealand stick insect fauna currently consists of nine genera and 23 species (Salmon, 1991; Jewell & Brock, 2002). These species occupy a broad range of habitats from the high alpine zone to lowland forest and scrub throughout New Zealand and including almost all offshore

Correspondence: Thomas R. Buckley, Landcare Research, Private Bag 92170, Auckland, New Zealand. E-mail: buckleyt@landcareresearch.co.nz

islands (Salmon, 1948, 1991) with the exception of the subantarctic islands. Parthenogenesis is widespread among stick insects (Bergerard, 1962), and New Zealand harbours species with both obligate and geographical parthenogens (Salmon, 1955a; Morgan-Richards *et al*., 2005; Buckley *et al*., 2008, 2009b, c). All the species are apterous, arboreal and feed on a range of native plants, with preference for species from the Myrtaceae, Cunoniaceae, Rosaceae, Polygonaceae and Podocarpaceae. The genera *Tectarchus* Salmon, *Spinotectarchus* Salmon, *Asteliaphasma* Jewell & Brock are most common in forest, whereas *Micrarchus* Carl, *Clitarchus* Stål, *Acanthoxyla* Uvarov and *Argosarchus* Hutton are common in both forest and scrub. The genus *Niveaphasma* Jewell & Brock can be found from sea level to the high alpine zone (Jewell & Brock, 2002; O'Neill *et al*., 2009), an unusual habitat for a stick insect. The genus *Pseudoclitarchus* Salmon is restricted to the Three Kings Islands, a long-isolated archipelago only 4.86 km^2, off the northern tip of New Zealand (Salmon, 1948). The fauna is in need of revision with both potential synonymies and undescribed species known (e.g. Jewell & Brock, 2002; Trewick *et al*., 2005; Buckley *et al*., 2008, 2009b).

All the New Zealand genera are endemic (see below), although historically, several species were placed in genera that occur in other landmasses. Many early authors (e.g. Hutton, 1899; Brunner, 1908) placed species from the genera *Tectarchus*, *Micrarchus*, *Spinotectarchus* and *Niveaphasma* in the largely Australian genus *Pachymorpha* Gray ('Pachymorphinae'). The first author to apply phylogenetic concepts to the Phasmatodea was Günther (1953), who retained the placement of the above New Zealand taxa in the 'Pachymorphinae', Pachymorphini, along with the Australian genera *Pachymorpha* and *Acanthoderus* Gray. Günther (1953) also placed species now included in the New Zealand genera *Clitarchus*, *Argosarchus* and *Acanthoxyla* in the subfamily 'Phasminae' (='Phasmatinae'), Macracanthiini, along with the Australian genus *Arphax* Stål, although Hennemann & Conle (2008) have doubted the placement of *Arphax* in the Acanthoxylini and instead have hypothesized that it belongs in the Australian tribe Acanthomimini. Günther (1953) also noted that the subfamily 'Pachymorphinae' was probably not a natural group, where taxa from Australia and New Zealand (Pachymorphini) may form an independent group from African 'Pachymorphinae'. Salmon (1954) proposed that *Tectarchus* was related to *Hemipachymorpha* Kirby from South Africa, on the basis of ridged-shaped tergites in both genera. However, Salmon's (1954) hypothesis contradicts the proposed separation of the African 'Pachymorphinae' from the Australasian 'Pachymorphinae' by Günther (1953). Hennemann & Conle (2008) also questioned the monophyly of the Hemipachymorphini.

Despite the uncertainty over the arrangement of genera within the 'Pachymorphinae', all these classifications suggested that the New Zealand fauna is non-monophyletic. A significant problem with the classification of the subfamilies and tribes containing the New Zealand genera is that the arrangement of most genera has not been tested in a formal phylogenetic analysis. Traditional classification is therefore of limited utility for determining whether the New Zealand fauna is of monophyletic or polyphyletic origin or where its closest relatives are to be found.

Bradler (2001, 2009) proposed that the clade Lanceocercata was comprised of Australasian genera that possess four synapomorphies: cerci leaf-like and flattened; vomer absent in males; male claspers formed by a modification to tergum X (functionally replacing the vomer); and during copulation the male clasps the female's operculum (abdominal sternum 8). Using these apomorphies, Bradler (2001, 2009) demonstrated that the Lanceocercata contains genera from the subfamilies 'Pachymorphinae', 'Tropidoderinae', 'Xeroderinae', 'Phasmatinae' and 'Platycraninae'. The monophyly of the Lanceocercata was later supported by the molecular phylogenetic study of Whiting *et al*. (2003).

Trewick *et al*. (2008) constructed a phylogeny for the New Zealand stick insect genera using the nuclear large subunit rRNA gene (28S). On the basis of these analyses, Trewick *et al*. (2008) concluded that, contrary to the assumptions of Salmon (1954) and Günther (1953), New Zealand genera did indeed form a monophyletic group. They also observed, again contrary to Günther (1953), that the Australian *Pachymorpha* was not closely related to any of the New Zealand genera. However, their taxon sampling was insufficient to determine the biogeographical origins of the New Zealand fauna or to rigorously test the monophyly of the fauna. The trees they presented included only one genus from New Caledonia, which has been shown to be an important area in understanding the biogeographical affinities of the New Zealand biota (e.g. Arensburger *et al*., 2004); and only seven Lanceocercata taxa were included.

In an expanded molecular phylogenetic analysis of stick insects from around the Pacific region, and including almost all traditional stick insect subfamilies, Buckley *et al*. (2009a) provided further evidence for the monophyly of the Lanceocercata and demonstrated that this clade contained even more taxa than was suspected previously. In addition to the subfamilies identified by Bradler (2001, 2009), the Lanceocercata was also found to include some members of the 'Eurycanthinae', known as tree lobsters. The studies of Bradler (2001, 2009), Whiting *et al*. (2003) and Buckley *et al*. (2009a) showed that the geographical distribution of the Lanceocercata stretches from the Mascarene Islands in the Indian Ocean, eastwards to Australia, New Guinea, New Caledonia and Pacific Ocean islands such as Fiji. Also included by Buckley *et al*. (2009a) were two New Zealand genera, *Acanthoxyla* and *Clitarchus*, and the phylogenetic analysis demonstrated that these two genera were indeed Lanceocercata and fell within a clade comprised of otherwise New Caledonian stick insects. The New Caledonia stick insect fauna contains approximately 15 genera and 29 species, mostly placed in the 'Xeroderinae' and 'Eurycanthinae' (Carl, 1915; Günther, 1953; Donskoff, 1988; Zompro, 2001) and is highly endemic (Chazeau, 1993). Apart from the biogeographical link proposed by Nakata (1961), based on the erroneous record of New Caledonian *Clitarchus* (see below), the relationship shown between New Zealand and New Caledonia by Buckley *et al.* (2009a) was unsuspected previously. The taxonomic placement of the New Caledonian genera within the polyphyletic 'Xeroderinae' and 'Eurycanthinae' appears to have obscured the phylogenetic link with the New Zealand fauna, which have been placed traditionally in the 'Pachymorphinae' and 'Phasmatinae' (Günther, 1953). Because the study of Buckley *et al*. (2009a) only included two of the nine New Zealand genera, the monophyly of the New Zealand fauna was not established, nor has it been confirmed that all New Zealand genera do indeed belong in the Lanceocercata.

We performed a molecular phylogenetic analysis from two mitochondrial and two nuclear genes of Lanceocercata taxa from all major landmasses on which they are recorded. The key Lanceocercata apomorphies were also examined in representatives of all New Zealand genera and taxa from other regions. The aims of this study were to determine whether the New Zealand genera form a monophyletic group and if they are all members of the Lanceocercata. The phylogenetic trees were then used to reveal the biogeographical origins of the New Zealand stick insect fauna. We also compared host plant patterns between the New Zealand genera and their relatives.

Materials and Methods

Taxon sampling and identification

We sampled Lanceocercata taxa from throughout their known geographical distribution, with dense sampling of New Zealand, New Caledonian and Australian genera (Table 1). New Zealand specimens were collected by TRB and collaborators in the field from various locations throughout New Zealand. The New Caledonian specimens were collected by TRB and collaborators during a field trip in 2007. The Australian material was collected by collaborators or obtained from cultures. Field collected specimens were collected by vegetation beating and by manually searching vegetation, especially at night. Specimens were identified as Lanceocercata on the basis of previously described morphological apomorphies (Bradler, 2001, 2009) and the molecular phylogenetic study of Buckley *et al*. (2009a). The Lanceocercata taxa sampled were drawn from the traditional subfamilies 'Phasmatinae', 'Pachymorphinae', 'Platycraninae', 'Eurycanthinae', 'Tropidoderinae', and 'Xeroderinae'. Subfamilies that have been demonstrated to be non-monophyletic by previous analyses (e.g. Whiting *et al*., 2003; Bradler, 2009; Buckley *et al*., 2009a) are in quote marks. Generic assignments to these subfamilies were based on Günther (1953) for the reasons outlined by Klug & Bradler (2006). The generic nomenclature follows Otte & Brock (2005) and Brock & Hasenpusch (2007), except in those situations where our phylogenetic analyses suggested newly proposed and newly defined genera to be non-monophyletic. Our sampling of the New Zealand fauna included a single species from each genus recognized by Jewell & Brock (2002). The sampling of New Caledonian taxa included all endemic genera recorded from the Grand Terre, except the monotypic *Caledoniophasma* Zompro and *Paracanachus* Carl, the former known only from the holotype and the latter known from very few specimens and almost certainly closely related to *Canachus* Stål. For outgroups we used *Agamemnon* Moxey, *Rhynchacris* Redtenbacher, and *Pterinoxylus* Serville from the Cladomorphinae and *Hermarchus* Stål, *Macrophasma* Hennemann & Conle and *Phasmotaenia* Navas from 'Phasmatinae', Stephanacridini, which were shown by Whiting *et al*. (2003) and Buckley *et al*. (2009a) to be potential sister groups resp. closely related to the Lanceocercata.

The identification of Australasian stick insects is difficult due to the shortage of keys and modern taxonomic descriptions. Furthermore, the fauna of the Australasian region still contains many undescribed taxa (Brock & Hasenpusch, 2007). For these reasons we were unable to identify several specimens to species and in some cases to genus, and these are noted in Table 1. The New Zealand taxa were identified by comparison with type specimens and the keys and descriptions from Salmon (1954, 1955b, 1991). The New Caledonian taxa were identified by comparison with type material and the descriptions of Carl (1913, 1915). The Australian specimens were mostly identified by comparison with type material, cultured specimens of known identity, and the descriptions of Brock & Hasenpusch (2007, 2009).

Genetics laboratory methods

We amplified DNA sequences from two mitochondrial and two nuclear genes. The mitochondrial genes were cytochrome oxidase subunit I (COI) and II (COII) and the nuclear genes were histone subunit 3 (H3) and 28S ribosomal RNA (28S). Primer sequences, polymerase chain reaction and DNA sequencing conditions are given in Buckley *et al*. (2008).

DNA sequence alignment and phylogenetic analysis

Alignment of the COI and H3 genes were trivial as they were both length invariant. The COII gene contained only a few indels, making alignment straightforward. The 28S gene, however, contained substantial length variation. Alignment of this gene was achieved using CLUSTALX (Larkin *et al*., 2007) followed by manual adjustment using the secondary structure motifs described by Gillespie *et al.* (2006). Despite the use of this model, some regions could not be aligned with any confidence and these were excluded prior to phylogenetic analysis. The final size of the concatenated dataset with alignment ambiguous sites excluded was 2277 bp. Stationarity of base frequencies among taxa was tested using the χ^2 test in PAUP*4.0b10 (Swofford, 1998).

Choosing an optimal portioned model from multiple genes is difficult due to the large number of potential ways of partitioning and pooling groups of sites (Nylander *et al*., 2004). We opted for a conservative approach whereby we partitioned the data by gene and then by codon position for the protein-coding genes. We pooled H3 first and second codon positions

Table 1. Taxon sampling.

Taxon	Subfamily	Code	Geographical locality
Lanceocercata (New Zealand)			
Acanthoxyla geisovii (Kaup, 1866)	'Phasmatinae'	AXG6	Riverton, SL, New Zealand
Argosarchus horridus (White, 1846)	'Phasmatinae'	ARG1	Wilton, WN, New Zealand
Asteliaphasma jucundum (Salmon, 1991)	'Pachymorphinae'	ASJ1	Waitakere Ranges, AK, New Zealand
Clitarchus hookeri (White, 1846)	'Phasmatinae'	CLH19	Wilton, WN, New Zealand
Micrarchus hystriculeus (Westwood, 1859)	'Pachymorphinae'	MIH1	Wellington city, WN, New Zealand
Niveaphasma annulata (Hutton, 1898)	'Pachymorphinae'	NIA1	Dunedin, DN, New Zealand
Pseudoclitarchus sentus (Salmon, 1948)	'Phasmatinae'	PSS1	Three Kings Islands, TH, New Zealand
Spinotectarchus acornutus (Hutton, 1899)	'Pachymorphinae'	SPA1	Okura, AK, New Zealand
Tectarchus huttoni (Brunner, 1908)	'Pachymorphinae'	THE2	Eastbourne, WN, New Zealand
Lanceocercata (New Caledonia)			
Asprenas impennis Carl, 1913	'Eurycanthinae'	ASP2	Road to Canala, New Caledonia
Asprenas sp.	'Eurycanthinae'	ASP5	Mt Panie, New Caledonia
Asprenas sp.	'Eurycanthinae'	ASP7	Col d'Amieu, New Caledonia
Asprenas sp.	'Eurycanthinae'	ASP3	Mt Koghis, New Caledonia
Canachus alligator Redtenbacher, 1908	'Eurycanthinae'	CAN4	Riviere Bleue, New Caledonia
Canachus alligator Redtenbacher, 1908	'Eurycanthinae'	CAA1	New Caledonia (culture)
Canachus sp.	'Eurycanthinae'	CAN2	Mt Panié, New Caledonia
Canachus sp.	'Eurycanthinae'	CAN3	Road to Canala, New Caledonia
Canachus sp.	'Eurycanthinae'	CAN5	Col d'Amieu, New Caledonia
Carlius fecundus (Carl, 1915)	'Eurycanthinae'	ASP8	Mont Koghis, New Caledonia
Carlius sp.	'Eurycanthinae'	ASP10	Mt Panie, New Caledonia
Carlius sp.	'Eurycanthinae'	ASP12	Col d'Amieu, New Caledonia
Carlius sp.	'Eurycanthinae'	ASP11	Mt Panie, New Caledonia
Carlius sp.	'Eurycanthinae'	NC4	Riviere Bleue, New Caledonia
Carlius sp.	'Eurycanthinae'	NC8	Col d'Amieu, New Caledonia
Carlius sp.	'Eurycanthinae'	NC11	Mt Panie, New Caledonia
Cnipsus rachis (Saussure, 1878)	'Xeroderinae'	CR1	Col d'Amieu, New Caledonia
Cnipsus rachis (Saussure, 1878)	'Xeroderinae'	CR3	Mt Panie, New Caledonia
Labidiophasma rouxi Carl, 1915	'Eurycanthinae'	LAR1	New Caledonia
Leosthenes sp.	'Xeroderinae'	NA1	Aoupinié, New Caledonia
Leosthenes sp.	'Xeroderinae'	NA2	Plateau de Dogny, New Caledonia
Microcanachus matileorum Donskoff, 1988	'Eurycanthinae'	MIC1	Mt Panié, New Caledonia
Trapezaspis sp.	'Eurycanthinae'	TRA1	New Caledonia
gen.n. 1	?	NC1	Plateau de Dogny, New Caledonia
gen.n. 1	?	NC2	Riviere Bleue, New Caledonia
gen.n. 2, sp. 1	?	NC6	Aoupinie, New Caledonia
gen.n. 2, sp. 2	?	NC9	Mt Koghis, New Caledonia
gen.n. 2, sp. 2	?	NC7	Riviere Bleue, New Caledonia
gen.n. 2, sp. 3	?	NC10	Aoupinie, New Caledonia
gen.n. 3	?	NC3	Col d'Amieu, New Caledonia
Lanceocercata (Australia)			
Dryococelus australis (Montrouzier, 1855)	'Eurycanthinae'	DRA1	Balls Pyramid, Lord Howe Island (culture)
Acrophylla titan (Macleay, 1826)	'Phasmatinae'	ACP1	Australia (culture)
Acrophylla titan (Macleay, 1826)	'Phasmatinae'	ACP2	Australia
Acrophylla wuelfingi (Redtenbacher, 1908)	'Phasmatinae'	ACT1	Australia (culture)
Acrophylla wuelfingi (Redtenbacher, 1908)	'Phasmatinae'	LAN12	Australia
Anchiale briareus (Gray, 1834)	'Phasmatinae'	LAN6	Airlie Beach, QLD, Australia
Anchiale sp.	'Phasmatinae'	CEB1	Australia (culture)
Ctenomorpha marginipennis Gray, 1833	'Phasmatinae'	CTC2	Australia
Ctenomorpha sp.	'Phasmatinae'	LAN2	Australia
Ctenomorpha sp.	'Phasmatinae'	LAN3	QLD, Australia
Didymuria sp.	'Tropidoderinae'	LAN10	QLD, Australia
Eurycnema goliath (Gray, 1834)	'Phasmatinae'	EYG1	Australia (culture)
Eurycnema goliath (Gray, 1834)	'Phasmatinae'	EYG2	Rubyvale, QLD, Australia
Eurycnema osiris (Gray, 1834)	'Phasmatinae'	EUO2	Australia (culture)
Extatosoma tiaratum bufonium Westwood, 1874	'Tropidoderinae'	EXB1	Australia (culture)
Extatosoma tiaratum tiaratum (Macleay, 1826)	'Tropidoderinae'	EXA2	Australia (culture)
Malandania pulchra Sjöstedt, 1918	'Tropidoderinae'	LAN13	Kuranda, QLD, Australia

Table 1. Continued.

Taxon	Subfamily	Code	Geographical locality
Megacrania batesii Kirby, 1896	'Platycraninae'	MEA1	Australia (culture)
Pachymorpha sp.	'Pachymorphinae'	PAC1	QLD, Australia
Phasma gigas (Linnaeus, 1758)	'Phasmatinae'	PMG1	New Guinea
Podacanthus wilkinsoni Macleay, 1882	'Tropidoderinae'	LAN14	Kuranda, QLD, Australia
Podacanthus wilkinsoni Macleay, 1882	'Tropidoderinae'	POW1	Australia (culture)
Tropidoderus childrenii (Gray, 1833)	'Tropidoderinae'	LAN7	QLD, Australia
Tropidoderus sp.	'Tropidoderinae'	LAN8	Australia
Tropidoderus sp.	'Tropidoderinae'	LAN5	QLD, Australia
Tropidoderus sp.	'Tropidoderinae'	LAN9	QLD, Australia
Vetilia thoon Stål, 1877	'Phasmatinae'	LAN4	Mitchell, QLD, Australia
Xeroderus sp.	'Xeroderinae'	XEK1	Kuranda, QLD, Australia
Lanceocercata sp.	?	STI20	Leeuwin, WA, Australia
Lanceocercata (New Guinea, Pacific Islands)			
Anchiale **sp.n.**	'Phasmatinae'	STI17	Guadacanal, Solomons
Dimorphodes sp.	'Xeroderinae'	DIM1	Papua New Guinea
Dimorphodes mancus Bates, 1865	'Xeroderinae'	DIM2	Papua New Guinea (culture)
Graeffea sp.	'Platycraninae'	GRA1	Russell Islands, Solomons
Graeffea sp.	'Platycraninae'	GRA2	Rarotonga, Cook Islands
Graeffea sp.	'Platycraninae'	FIJ7	Taveuni Island, Fiji
Megacrania phelaus (Westwood, 1859)	'Platycraninae'	MEP1	Malaita, Solomons (culture)
Megacrania batesii Kirby, 1896	'Platycraninae'	MEA1	Australia (culture)
Ophicrania bifasciatus (Redtenbacher, 1908)	'Platycraninae'	OPB1	Eastern Highlands, New Guinea
Lanceocercata (Indian Ocean)			
Monandroptera acanthomera (Burmeister, 1838)	'Tropidoderinae'	MOA1	Mauritius (culture)
Monandroptera acanthomera (Burmeister, 1838)	'Tropidoderinae'	MOA2	La Réunion (culture)
Rhaphiderus scabrosus (Percheron, 1829–1838)	'Tropidoderinae'	RAS1	Mauritius (culture)
Outgroups (Phasmatinae)			
Hermarchus sp.	'Phasmatinae'	HER2	Fiji
Macrophasma biroi (Redtenbacher, 1908)	'Phasmatinae'	HEB1	Papua New Guinea
Phasmotaenia lanyuhensis Huang & Brock, 2001	'Phasmatinae'	PHL1	Taiwan
Phasmotaenia spinosa Hennemann & Conle, 2009	'Phasmatinae'	PHA1	Malaita, Solomon Islands (culture)
Outgroups (Cladomorphinae)			
Pterinoxylus crassus Kirby, 1899	Cladomorphinae	PTC1	Martinique (culture)
Agamemnon cornutus (Burmeister, 1838)	Cladomorphinae	AGC1	West Indies (culture)
Rhynchacris ornata Redtenbacher, 1908	Cladomorphinae	HEL1	Costa Rica (culture)

due to the low number of varied sites. The 28S gene was not partitioned further because there is no biologically meaningful way of separating sets of sites (Simon *et al*., 1994; Pagel & Meade, 2004). This method yielded a nine partition model. We then performed a separate model selection procedure on each partition using the Akaike information criterion (Akaike, 1973) as implemented in MODELTEST 3.7 (Posada & Crandall, 1998) and PAUP*.

We performed a Bayesian phylogenetic analysis using BEAST v.1.4.8 (Drummond & Rambaut, 2007). We ran the dataset under the partitioned model and log normally distributed relaxed clock for 40 million generations with the following prior distributions; exponential priors on the Q-matrix (100), shape parameter for gamma distribution for among-site rate variation ($\lambda = 5$), rate multipliers (100), mean rate (1.0), coefficient of variation (1.0) and covariance (1.0). We used a Jeffrey's prior on the Yule birth rate (1.0). A thinning interval of 1000 was used for sampling from the Markov chain Monte Carlo. We used TRACER v1.4 (Rambaut & Drummond, 2007) to monitor convergence of all parameters from the phylogenetic model, to ensure that all effective sample sizes were greater than 100 and to select appropriate burn-in sizes. Four final runs were completed and concatenated to estimate posterior distributions. The dataset was bootstrapped using maximum parsimony as implemented in PAUP*. We performed 500 pseudoreplicates with 100 stepwise addition trees, with random addition, and steepest descent not in effect.

Molecular dating analyses

Buckley *et al.* (2009a) used two fossil calibrations to obtain minimum divergence dates for the radiation of Phasmatodea lineages. However, neither of these fossils belong to the Lanceocercata or its sister groups, and they provide only lower limits on divergence times. Therefore, we used the arthropod molecular clock rates previously estimated by Brower (1994) to obtain estimates of divergence times within the Lanceocercata. We used BEAST to estimate topology and divergence time jointly, assuming a log normally distributed relaxed clock (Drummond *et al.*, 2006) with mean rate of

Table 2. Sequence statistics and substitution model parameters for the four gene regions.

	COI	COII	H3	28S
Number of sites	762	689	328	498
Frequency A	0.352	0.403	0.236	0.161
Frequency C	0.157	0.151	0.298	0.285
Frequency G	0.147	0.117	0.310	0.348
Frequency T	0.344	0.330	0.155	0.206
Base frequency χ^2 test varied sites	$P = 1.0$	$P = 1.0$	$P = 1.0$	$P = 1.0$
Varied sites	354	400	120	307
Parsimony sites	316	345	111	234

COI, cytochrome oxidase subunit I; COII, cytochrome oxidase subunit II; H3, histone subunit 3; 28S, 28S ribosomal RNA.

0.0115 substitutions/site/million years (Brower, 1994). To account for uncertainty in this rate we assumed a normal distribution centred on 0.0115 with a standard deviation of 10% of the mean. Because the rate we used is applicable only to mitochondrial DNA, only the COI and COII genes were used in the divergence time estimation. We constrained Lanceocercata to be monophyletic and *Dimorphodes* Westwood to be a sister group to the remaining Lanceocercata, because preliminary analyses showed that support for these two nodes was weak when the mitochondrial DNA was analysed in isolation. The prior distributions and Markov chain Monte Carlo settings used were the same as for the analysis of the full data above.

Reconstruction of ancestral geographical areas

We used the dispersal-vicariance method (Ronquist, 1997) implemented in DIVA v1.2 (Ronquist, 2001) to reconstruct ancestral geographical areas. Each taxon was assigned one of eight areas that included New Zealand, New Caledonia, Australia, New Guinea, South America (including Central America and Caribbean islands), Mascarenes, Lord Howe Island and the Pacific Islands. Although some of these areas, such as New Guinea, New Zealand, New Caledonia and the Pacific Islands, are geologically composite (e.g. Michaux & Leschen, 2005; Heads, 2008a; Michaux, 2009), many of the accretion events that formed these areas occurred before the diversification of the Lanceocercata (see below) and in all the above areas most Lanceocercata genera are found distributed across multiple terranes. Furthermore, the distribution of most Lanceocercata genera are too poorly known to be able to be scored for separate terranes within landmasses such as New Guinea and New Caledonia.

To accommodate phylogenetic uncertainty in the ancestral area reconstructions, we used an (empirical) Bayes approach in which the dispersal-vicariance analysis is performed on the posterior tree distribution. More specifically, we sampled 10 000 trees (by thinning, i.e. sampling every *n*th tree) from the BEAST output. In this 'Bayes–dispersal-vicariance' analysis (Nylander *et al*., 2008), the uncertainty in tree reconstruction is integrated out, and the ancestral distributions can be plotted as marginal distributions (probabilities) on nodes in the tree.

Morphological analyses

We investigated Lanceocercata apomorphies in all taxa included in this study. Specimens were studied and illustrations were prepared using Zeiss stereomicroscopes Stemi SV6 and Stemi SV11 at different magnifications and with a drawing tube (camera lucida).

Results

Patterns of DNA sequence variation

All sequences have been submitted to Genbank under accession numbers GQ927330–GQ927478. Specimens have been accessioned into the New Zealand Arthropod Collection, Landcare Research, New Zealand. Sequence statistics and substitution model parameter estimates are shown in Tables 2 and 3. As expected, the mitochondrial genes had a larger number of varied sites than the nuclear genes and more extreme among-site rate variation (e.g. Lin & Danforth, 2004). The base frequencies were also more skewed at the mitochondrial sites than the nuclear 28S and H3 genes (Table 2); however, all partitions passed the χ^2 test for base frequency stationarity.

Phylogenetic analyses

The Bayesian phylogeny (Fig. 1) was rooted using the three Cladomorphinae genera *Agamemnon*, *Rhynchacris* and *Pterinoxylus* and this rooting implies that *Hermarchus*, *Macrophasma* and *Phasmotaenia* ('Phasmatinae', Stephanacridini) are the sister group to the Lanceocercata, in agreement with Buckley *et al.* (2009a) for *Hermarchus*. Our phylogenetic tree is highly congruent with the more limited taxon sampling of Lanceocercata from Buckley *et al*. (2009a) that sampled the same genes. As in the previous analysis, almost none of the traditional subfamilies with members in the Lanceocercata are monophyletic, including 'Tropoderinae', 'Phasmatinae', 'Eurycanthinae', 'Xeroderinae' and 'Pachymorphinae'. Instead, many of the generic groupings follow geography rather than traditional classification. The 'Platycraninae' are supported by our present study, but appear to be polyphyletic when *Platycrana* is included (Bradler, 2009).

Table 3. Best fit Akaike information criterion (AIC) models and Bayesian parameter estimates for each partition.

	COI 1st	COI 2nd	COI 3rd	COII 1st	COII 2nd	COII 3rd	H3 1st and 2nd	H3 3rd	28S
AIC	TrN + I + Γ	F81 + I + Γ	GTR + I + Γ	HKY + Γ	HKY + I + Γ	K81uf + I + Γ	JC + I	K80 + Γ	GTR + I + Γ
rA-C[a]	0.07039 (0.0353–0.11)	–	0.01357 (0.002878–0.0244)	–	–	0.02555 (0.01052–0.04041)	–	–	0.162 (0.121–0.205)
rA-G	0.165 (0.109–0.228)	–	0.08296 (0.06557–0.102)	–	–	0.09851 (0.08114–0.117)	–	–	0.476 (0.385–0.574)
rA-T	0.215 (0.163–0.268)	–	0.147 (0.12–0.173)	–	–	0.179 (0.156–0.205)	–	–	0.359 (0.292–0.43)
rC-G	0.01252 (0.01872–0.03071)	–	0.0265 (0.00001013–0.05324)	–	–	0.01196 (0.01489–0.0295)	–	–	0.132 (0.09621–0.172)
rG-T	0.05703 (0.03076–0.08472)	–	0.060533 (0.00000002545–0.01401)	–	–	0.02125 (0.01584–0.05877)	–	–	0.331 (0.265–0.397)
Ts/Tv[b]	–	–	–	5.208 (4.426–6.033)	2.437 (1.893–3.013)	–	–	4.145 (3.434–4.839)	–
α[c]	0.685 (0.409–0.973)	0.52 (0.169–1.029)	0.904 (0.776–1.039)	0.242 (0.208–0.276)	0.401 (0.243–0.633)	0.941 (0.824–1.062)	–	1.3 (0.958–1.669)	0.627 (0.446–0.819)
p_{inv}[d]	0.621 (0.532–0.707)	0.793 (0.690–0.882)	0.0162 (0.0002019–0.03598)	–	0.561 (0.445–0.672)	0.01213 (0.0000006855–0.03205)	0.922 (0.884–0.957)	–	0.167 (0.06083–0.265)
μ[e]	0.245 (0.186–0.307)	0.004668 (0.02822–0.0678)	2.568 (2.318–2.819)	0.55 (0.481–0.62)	0.209 (0.154–0.267)	2.179 (1.938–2.415)	0.01461 (0.07223–0.02282)	0.489 (0.407–0.575)	0.249 (0.218–0.283)

[a] Relative rate parameter from the Q-matrix of the GTR nucleotide substitution model.

[b] Transition/transversion rate ratio.

[c] Shape parameter from the discrete gamma distribution for among-site rate variation.

[d] Proportion of invariable sites.

[e] Substitution rate multiplier for each partition.

COI, cytochrome oxidase subunit I; COII, cytochrome oxidase subunit II; H3, histone subunit 3; 28S, 28S ribosomal RNA.

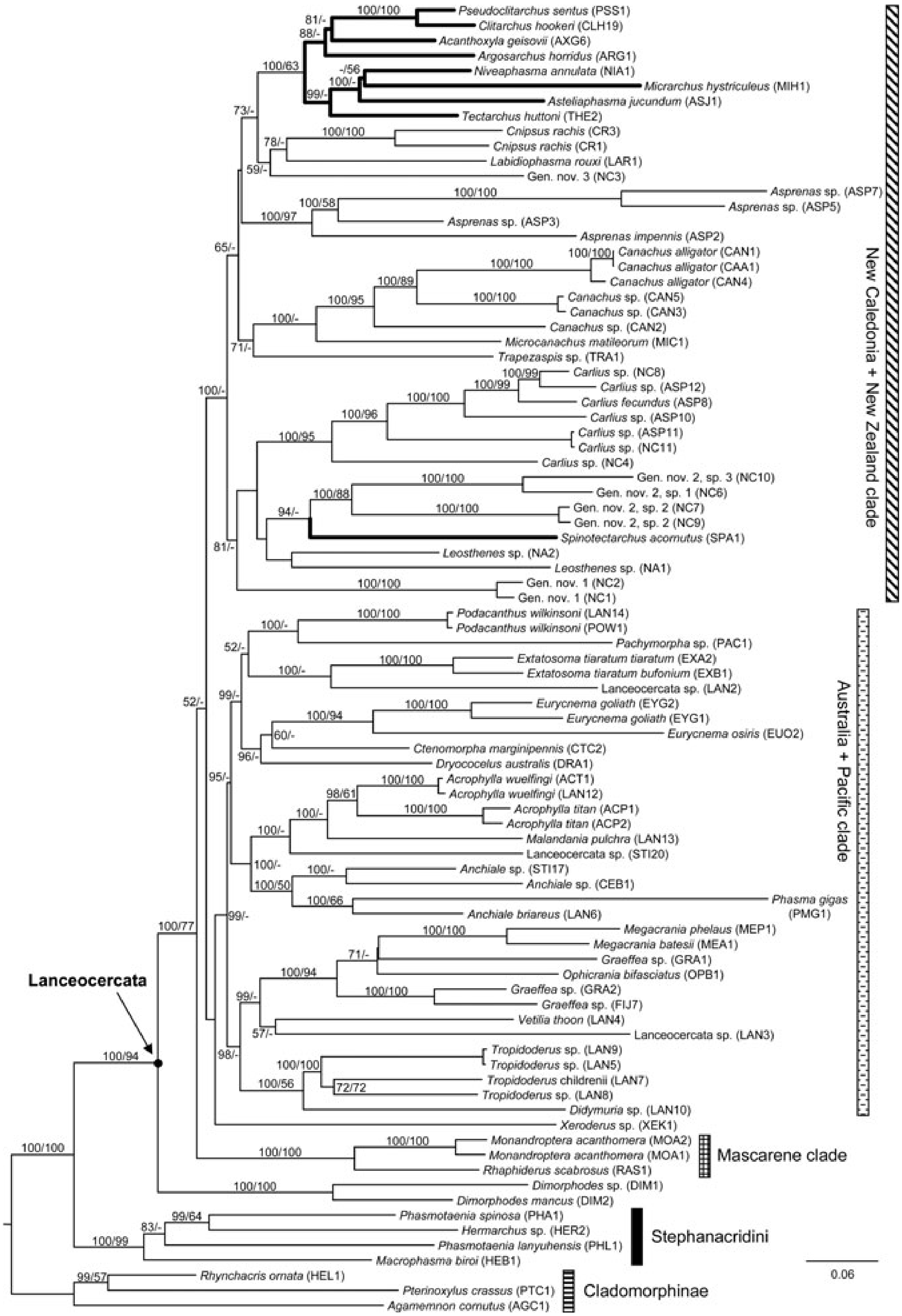


Fig. 1. Bayesian phylogenetic tree with branch lengths drawn proportional to the estimated number of substitutions per site. The numbers above the branches are posterior probabilities followed by maximum parsimony bootstraps, both expressed as percentages. The dashes indicate support less than 50% and nodes that are unmarked received less than 50% from both methods. Thicker branches indicate taxa sampled from New Zealand.

Our phylogenetic analysis has revealed five major lineages within the Lanceocercata, with only partially overlapping geographical distributions. The first clade to split from the root of Lanceocercata is *Dimorphodes*, mainly found in New Guinea, and this is supported with a posterior probability of 1.0 and 94% bootstrap support (Fig. 1). This observation is in agreement with the analysis of Whiting *et al*. (2003) and Buckley *et al*. (2009a). Within the remaining Lanceocercata, the four other clades form an unresolved polytomy. The second major Lanceocercata lineage consists solely of the genus *Xeroderus* Gray, type genus of the 'Xeroderinae', which is recorded from Australia and the Solomon Islands. The third clade contains *Rhaphiderus* Serville and *Monandroptera* Serville and they are restricted to the Mascarene Islands in the Indian Ocean (posterior probability = 1.0, bootstrap = 100%, Fig. 1). These two genera are traditionally placed in the mainly Australian 'Tropidoderinae' (Otte & Brock, 2005). The fourth clade, which contains the greatest number of sampled genera, consists predominantly of Australian taxa and also taxa from New Guinea and the Pacific Islands, including *Phasma* Lichtenstein, type genus of the 'Phasmatinae'. This clade is very well supported under the Bayesian analysis (posterior probability = 0.99, Fig. 1), but not under parsimony (bootstrap <50%, Fig. 1). The genera *Graeffea* Brunner and *Megacrania* Kaup, which have their diversity in New Guinea and associated islands and Oceania (e.g. Hsiung, 2007), and *Ophicrania* Kaup, which are all contained in the 'Platycraninae', form a monophyletic group with a posterior probability of 1.0 and bootstrap support of 94% (Fig. 1).

All the New Zealand and New Caledonian taxa fall into a single fifth clade, as observed by Buckley *et al*. (2009a), with 1.0 posterior probability support, but less than 50% bootstrap support. Within this clade, the New Zealand genera do not form a monophyletic group. The genus *Spinotectarchus* groups with a hitherto undescribed taxon (**gen.n.** 2) (posterior probability = 0.94, bootstrap <50%, Fig. 1). All the remaining New Zealand taxa fall in a separate clade (posterior probability = 1.0, bootstrap = 63%, Fig. 1) and the sister group to this clade is *Cnipsus* Redtenbacher, *Labidiophasma* Carl and **gen.n.** 3 (posterior probability = 0.73, bootstrap <50%, Fig. 1). The New Caledonian tree lobsters *Canachus*, *Microcanachus* Donskoff, and *Trapezaspis* Redtenbacher form a clade with moderate to weak support (posterior probability = 0.71, bootstrap <50%, Fig. 1). These genera are relatively robust, are often ground dwelling, and all are flightless. The second clade contains the New Caledonian *Leosthenes* Stål, *Carlius* Uvarov, **gen.n.** 1 and **gen.n.** 2, in addition to the New Zealand *Spinotectarchus* (posterior probability = 0.81, bootstrap <50%, Fig. 1). The New Caledonian taxa in this clade tend to be more gracile. The genera *Leosthenes*, *Carlius* and **gen.n.** 2 contain species that are fully flighted in the male sex and in fact all flighted New Caledonian taxa are included in this clade.

Within the main New Zealand clade, the Acanthoxylini, which includes *Acanthoxyla*, *Clitarchus*, *Pseudoclitarchus* and *Argosarchus*, is well supported as monophyletic under Bayesian inference (posterior probability = 0.88, Fig. 1), but not under parsimony (bootstrap <50%). The close relationship of *Acanthoxyla*, *Clitarchus* and *Pseudoclitarchus*, to the exclusion of *Argosarchus*, was also observed by Buckley *et al.* (2009a) and Trewick *et al*. (2008). The separation of *Spinotectarchus* from the other New Zealand 'Pachymorphinae' species provides further support for the polyphyly of this subfamily (Günther, 1953; Bradler, 2001, 2009; Trewick *et al*., 2008; Buckley *et al*., 2009a).

Molecular dating analyses

The chronogram estimated from the mitochondrial DNA sequences is shown in Fig. 2. The age of the root of the entire phylogeny was estimated to be 56.89 mya (40.40–80.43 mya), the divergence of the Stephanacridini from the Lanceocercata was estimated at 53.92 mya (38.53–73.62 mya) and the age of the diversification of the Lanceocercata was estimated at 51.76 mya (36.23–69.78 mya). The New Zealand and New Caledonia clade split from its nearest relatives 44.10 mya (31.06–59.44 mya) and began to radiate 41.06 mya (29.05–55.40 mya). The main New Zealand clade diverged from its sister group in New Caledonia 33.72 mya (23.9–45.62 mya) and began to radiate 25.6 mya (16.8–35.5 mya). *Spinotectarchus* diverged from its closest relatives in New Caledonia 29.9 mya (19.79–41.16 mya).

Dispersal-vicariance reconstructions of ancestral areas

Two separate analyses were performed using DIVA, the first was an unconstrained analysis where no limit was placed on the number of areas assigned to each node; in the second, the maximum number of areas was constrained at two. In general, nodes closer to the root were inferred to be distributed across more areas than derived nodes (Ronquist, 1997). The constrained analysis reconstructed the root ancestor as being distributed across five pairs of areas and each of these pairs includes South America and had similar posterior probabilities. The unconstrained analysis reconstructed the root ancestor as being distributed across all areas with the exception of New Zealand and Lord Howe Island with a posterior probability of 0.851. The most support (0.851) for the geographical distribution of the ancestor of the Stephanacridini and Lanceocercata was New Caledonia, Australia, Pacific, New Guinea and Mascarenes under the unconstrained model. The constrained model reconstructed the ancestral distribution as pairs of the above five areas with low support for each pair.

The ancestor of the Lanceocercata was inferred to be distributed across New Guinea and Australia (0.529) or New Guinea and the Mascarenes (0.276) or New Guinea and New Caledonia (0.203). Under the constrained analysis, this ancestor was reconstructed as being distributed across New Caledonia, Australia, New Guinea and the Mascarenes, with a posterior probability of 0.851. The other three reconstructions

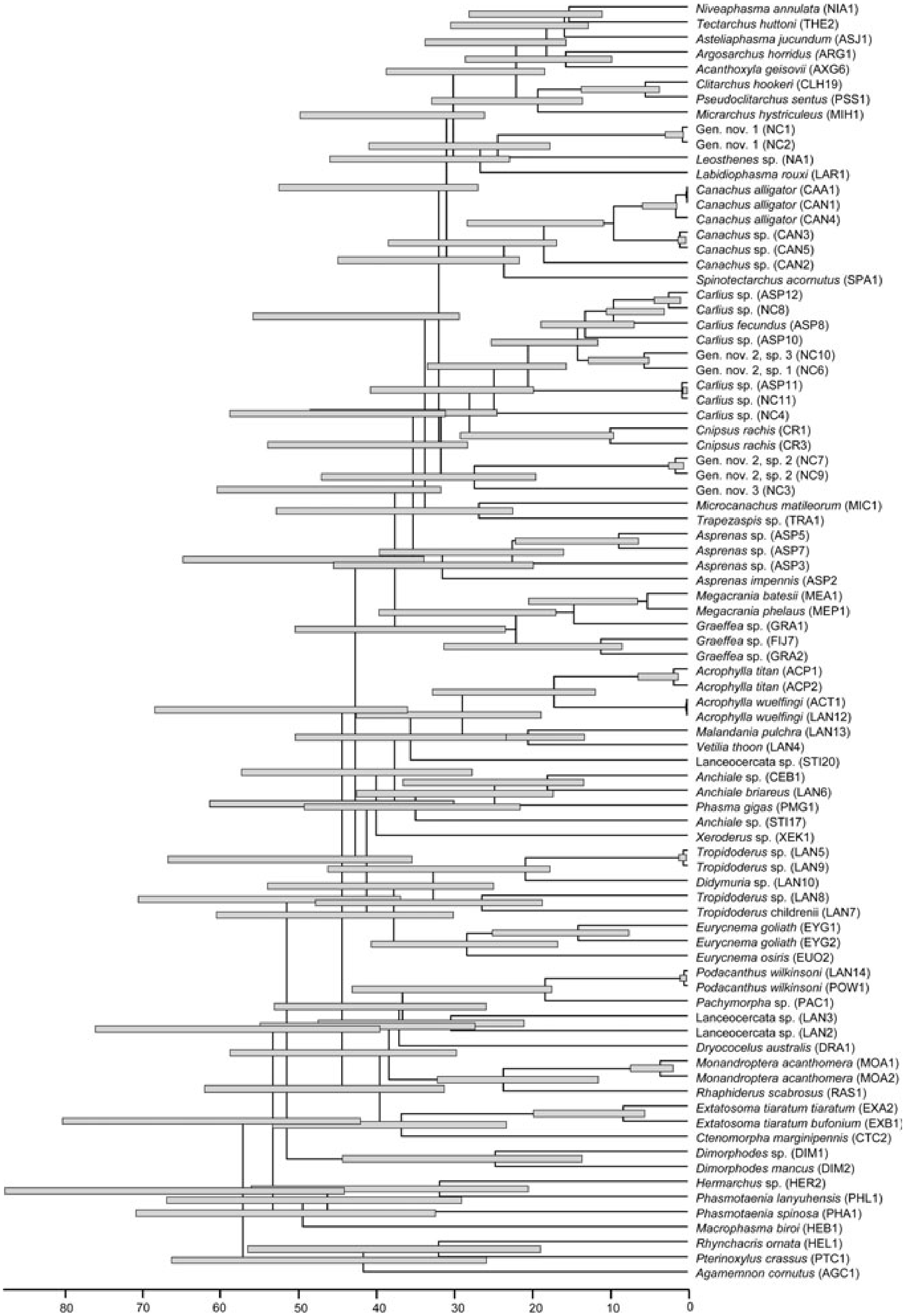


Fig. 2. Bayesian phylogenetic tree estimated from the mitochondrial data only. Branch lengths are drawn proportional to time and 0.95 posterior intervals are indicated for all nodes by horizontal grey bars. The horizontal scale bar measures time in millions of years.

received less support, but all included Australia and New Guinea and only one included New Zealand, with a posterior probability of 0.01. Both analyses reconstructed the distribution of the ancestor of the Australian/Pacific clade as being Australian only, with posterior probabilities of 1.0.

The ancestor of the New Zealand and New Caledonian clade was inferred to be distributed in New Caledonia only, with posterior probabilities of 0.999 and 0.989 for the constrained and unconstrained analyses, respectively. The ancestor of the main New Zealand clade and its sister group of *Cnipsus*, *Labidiophasma* and **gen.n.** 3 was inferred to be distributed in both New Zealand and New Caledonia (posterior probability = 0.58) or New Caledonia only (posterior probability = 0.42) under both analyses. The ancestor of *Spinotectarchus* and New Caledonia **gen.n.** 2 was reconstructed as being distributed across New Zealand and New Caledonia, with a posterior probability of 1.0 under both analyses. Reconstructions of all nodes are given in Figs S1, S2.

Morphological analyses

All examined stick insects of New Caledonia and New Zealand exhibit the character states proposed to be synapomorphic for the Lanceocercata clade (see above). No Lanceocercata male included in our study bears a vomer, a sclerotized and hook-like movable clasper on the venter of abdominal segment 10 (Fig. 3A, D, F). The cerci are flattened laterally, but less leaf-like or lanceolate than in many Australian members such as *Acrophylla* and *Eurycnema* (Bradler, 2009). The female abdominal sternum 8 (operculum) is keeled in most taxa, allowing for the derived copulatory position of the Lanceocercata, in which the males grasp sternum 8 instead of the hind margin of sternum 7. Even taxa without a keeled operculum, e.g. *Micrarchus*, show the derived mode (Fig. 3C). In this case, a saddle-like appendage on the operculum, an opercular organ (Bradler, 2009), serves as a grasping structure for the male. The male abdominal tergum 10 of the euphasmatodean stick insect usually bears a pair of rigid thorn pads (Wedmann *et al*., 2007; Bradler, 2009). The thorns are directed ventrally in most euphasmatodeans, but in Lanceocercata males these are directed medially against each other. The thorn pads can consist of several spines arranged in species-specific patterns (e.g. Fig. 3B) or of a single pair as in *Cnipsus* (Fig. 3I). The midline of abdominal tergum 10 is weakly developed and serves as a pivot for the movable hemitergites forming the typical roof-like tergum as seen from behind (Fig. 3B, E, G–J). The spines are usually situated near the lateral margins of the tergum, forming an effective clasper. In *Spinotectarchus*, however, the thorn pads lie near the tergal median line in close vicinity (Fig. 3G, H). This unusual arrangement of narrowly situated thorn pads is also present in the New Caledonian **gen.n.** 2 (Fig. 3H) and must be interpreted as a synapomorphic character state supporting the sister-group relationship of both taxa and the polyphyletic origin of the New Zealand phasmid fauna.

Discussion

Higher level phylogeny and taxonomy of the Lanceocercata

The results of this study and those of Bradler (2001, 2009), Whiting *et al*. (2003) and Buckley *et al*. (2009a) strongly suggest that the higher level taxonomy of the Phasmatodea is in need of extensive revision. Every subfamily that was sampled in this study, with the exceptions of the outgroup Cladomorphinae and the 'Platycraninae', was found to be polyphyletic. Furthermore, even some of the genera were observed to be non-monophyletic, including some newly described and some new combinations. For example, Brock & Hasenpusch (2007) synonymized the genera *Acrophylla* Kirby and *Vetilia* Stål, with the latter being the junior synonym. Our analyses show this expanded definition of *Acrophylla* to be polyphyletic, with *Malandania* Sjöstedt the sister group to *Acrophylla titan* + *Acrophllya wuelfingi* and *Vetilia thoon* closely related to the Pacific 'Platycraninae'. Therefore, we have removed *Vetilia* from synonymy with *Acrophylla*. Further examples of paraphyletic genera include *Anchiale* Stål, which has *Phasma* nested within it, and possibly *Graeffea*, which has *Megacrania* nested within it. *Phasmotaenia*, as revised by Hennemann & Conle (2009), appears to be paraphyletic in respect of *Hermarchus*. Much work remains to revise generic boundaries within the Lanceocercata and Euphasmatodea in general, although we recommend that any further nomenclatural changes to the genera are made only after a phylogenetic analysis of all relevant species and identification and critical analysis of morphological synapomorphies.

Phylogenetic placement and polyphyly of the New Zealand stick insect fauna

Clitarchus includes *C. multidentatus* Brunner from New Caledonia, *C. magnus* Brunner from Thailand and *C. longipes* Brunner from Australia. We have examined the holotype of *C. multidentatus*, and it is identical to *C. hookeri*. We believe the specimen was mislabelled and was in fact collected from New Zealand. Hennemann *et al*. (2008) examined the type of *C. magnus* and reported that it does not resemble *C. hookeri* and appears to be more closely related to *Ramulus* Saussure, from 'Phasmatinae', Clitumnini. The species *C. longipes* Brunner was also recorded from Australia by Brunner (1907), but Vickery (1983) reported that this species almost certainly belongs in another genus and in fact was placed in *Candovia* Stål (Necrosciinae) by Brock & Hasenpusch (2007). Salmon (1991) reported that *Micrarchus hystriculeus* Carl was also found in Australia and Papua New Guinea, although this species is unknown from collections taken from outside New Zealand (Jewell & Brock, 2002) and Salmon (1991) gave no details regarding these specimens. We regard this record as an error and conclude that all New Zealand genera are endemic.

The phylogenetic analyses presented here and those of Buckley *et al*. (2009a) demonstrate clearly that the New Zealand stick insect fauna is polyphyletic. The polyphyly of the fauna was suggested by previous authors, given that the New Zealand genera have always been split into two subfamilies, both of which contain taxa in Australia, among other areas (e.g. Günther, 1953; Salmon, 1991; Jewell & Brock, 2002; Otte & Brock, 2005). Therefore, our finding of polyphyly is not in itself surprising; however, what is surprising is the identity of the genera that render the New Zealand fauna polyphyletic. Previous classifications had predicted a close relationship between Australian 'Pachymorphinae' and at least some New Zealand genera, but this has been disproved in this study and those of Buckley *et al*. (2009a) and Trewick *et al*. (2008). Whiting *et al*. (2003), Bradler (2009) and Buckley *et al*. (2009a) sampled the genus *Clonaria* Stål from South Africa and found that this 'Pachmorphinae' genus was unrelated to the Lanceocercata. If we assume that the African 'Pachymorphinae' genera *Clonaria* and *Hemipachymorpha* are related, then this finding is inconsistent with any relationship between *Hemipachymorpha* and the New Zealand *Tectarchus*, as proposed by Salmon (1955a).

Trewick *et al*. (2008) reconstructed a phylogeny from the 28S gene in which all nine New Zealand genera formed a monophyletic group. The taxon sampling and outgroup

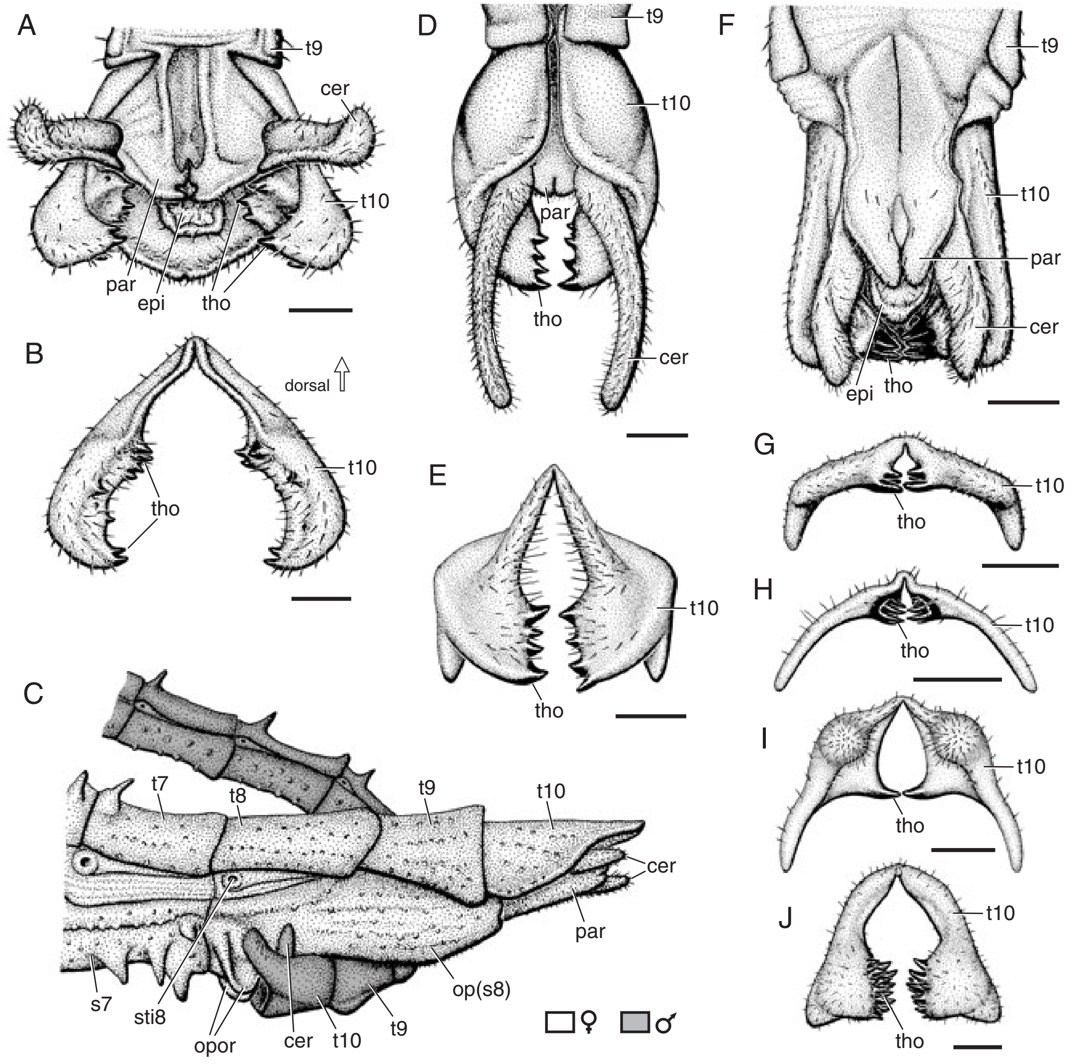


Fig. 3. Morphological details of New Caledonian and New Zealand stick insects. (A–C) *Micrarchus hystriculeus* ('Pachymorphinae', New Zealand), male terminal region, ventral view (A), abdominal tergum 10, posterior view (B), male and female terminal region during copulation, lateral view (C); (D, E) *Clitarchus hookeri* ('Phasmatinae', New Zealand), male terminal region, ventral view (D) and abdominal tergum 10, posterior view (E); (F, G) *Spinotectarchus acornutus* ('Pachymorphinae', New Zealand), male terminal region, ventral view (F) and abdominal tergum 10, posterior view (G); (H) **gen.n.** 2, male abdominal tergum 10, posterior view; (I) *Cnipsus rachis* ('Xeroderinae', New Caledonia), male abdominal tergum 10, posterior view; (J) *Canachus alligator* ('Eurycanthinae', New Caledonia), male abdominal tergum 10, posterior view. All abdominal terga 10 are oriented as indicated by the white arrow in (B). cer, cercus; epi, epiproct; op, operculum; opor, opercular organ; par, paraproct; s7, s8, abdominal sternum 7, 8; sti8, abdominal stigmum 8; t7–t10, abdominal tergum 7–10; tho, thorns resp. thorn pads. Scale: 0.5 mm.

selection for this study was based on a BLAST (Altschul *et al*., 1990) method called sequence similarity sieve (SeqSSi). This method led the authors to discard the two Lanceocercata genera *Ophicrania* Kaup and *Leosthenes* as suitable taxa to include in the analysis. SeqSSi also indicated that *Cnipsus* was the optimal outgroup from all the taxa sampled in that study and those from Whiting *et al*. (2003), which included representatives from most major Euphasmatodea lineages. The genital morphology of male *Cnipsus* (Fig. 3I) clearly indicates its phylogenetic placement in Lanceocercata, which was disregarded by Trewick *et al.* (2008), who consequently chose an ingroup member as an outgroup. The taxon sampling and rooting scheme of Trewick *et al*. (2008) led to a non-monophyletic Lanceocercata, which is clearly at odds with the more extensive sampling in this study, and the studies of Bradler (2001, 2009), Whiting *et al*. (2003) and Buckley *et al*. (2009a). The method also led to the incorrect reconstruction of the New Zealand fauna as monophyletic. The 28S gene shows marked changes in substitution rate in lineages such as *Asprenas*, *Micrarchus* and *Phasma* (data not shown) and therefore genetic distance is unlikely to be a good predictor of phylogenetic relationship for this gene.

Biogeographical history of the Lanceocercata and origins of the New Zealand stick insect genera

We have constructed a biogeographical scenario for the evolution of the Lanceocercata by reconciling information from geographical distributions, phylogenetic analysis, dispersal-vicariance analysis and molecular dating. Some regions of the tree are poorly supported, such as the basal radiation of the Lancerocercata, but we have accounted for this uncertainty by integrating over topology in the estimation of divergence times and reconstruction of ancestral areas. A concern with the dispersal-vicariance analyses is the well-known property of this method to reconstruct ancestors as being increasingly widespread at deeper nodes (e.g. Clark *et al*., 2008). We have partially accounted for this by performing reconstructions where the number of areas at internals nodes was limited to two. This did not affect the reconstruction of the geographical range of the ancestors of the New Zealand lineages, which is our primary interest.

We have accounted for uncertainty in the rate of evolution by estimating divergence times using a relaxed clock and by placing a prior on the rate. The divergence dates we recovered are deep, indicating model misspecification is potentially a concern (Arbogast *et al*., 2002) and we have attempted to account for the high rate of change in the mitochondrial genes by applying parameter-rich partitioned models. Verification of these dates will await future Phasmatodea fossils that can be placed confidently on extant crown groups to calibrate the tree. Further sampling of Lancerocercata within Australasia will allow more accurate reconstruction of ancestral areas once the geographical distributions of all the relevant taxa are known.

The analyses of Whiting *et al.* (2003) and Buckley *et al.* (2009a) indicate that the sister group to the Lanceocercata and Stephanacridini clade is the Cladomorphinae, which are restricted today to South and Central America, including the Caribbean. The sampled Stephanacridini genera, *Hermarchus*, *Macrophasma* and *Phasmotaenia*, are distributed in New Guinea, Fiji, Solomon Islands, Vanuatu, Taiwan and the Philipines (Huang & Brock, 2001; Eusebio *et al*., 2004; Hennemann & Conle, 2006, 2009) and so have a distribution that is overlapped almost completely by the Lanceocercata. Therefore, the root of our phylogeny links two clades, the Lanceocercata + Stephanacridini restricted to Australasia, the Mascarenes, New Guinea some Pacific islands, Borneo, Malaysia, the Philippines and southern China, and the Cladomorphinae restricted to Central and South America. All the dispersal-vicariance reconstructions had the common ancestor of Cladomorphinae and Lanceocercata + Stephanacridini distributed across South America and at least some areas currently inhabited by the Lanceocercata and Stephanacridini. Seafloor spreading began between Australia and Antarctica during the Cretaceous, but land connections were not totally lost until about 35 mya during the Eocene (Li & Powell, 2001). Connections between South America and Antarctica also existed until 28–32 mya, during the Oligocene at the latest (Lawver & Gahagan, 1998; McLoughlin, 2001). Our divergence dates for the split between the South/Central American Cladomorphinae and the Australasian Stephanacridini and Lanceocercata clade is 56.89 mya (40.40–80.43 mya), which predates the completion of the continental splits. However, the movement of biota between South America and Australia may have been impeded before these dates or the ancestral taxon may have diverged before the breakup of this region of Gondwana. This latter possibility is not unexpected given the large geographical distance between Australia and South America within Gondwana.

The sister group to the Lanceocercata are the Stephanacridini genera *Hermarchus*, *Macrophasma* and *Phasmotaenia*, and these are distributed to the north and east of Australia. These genera split from the Lanceocercata 53.92 mya (38.53–73.62 mya), and may be the result of rifting of parts of New Guinea from Australia 55.5–63.5 mya (Veevers & Li, 1991; McLoughlin, 2001). This hypothesis assumes that the Stephanacridini split from the Cladomorphinae before the breaking of the last possible land connections between Australia and South American via Antarctica during the Oligocene. The ancestor of Lanceocercata and Stephanacridini was reconstructed as being widespread under the unconstrained dispersal-vicariance analysis and in pairs of areas in the constrained analysis that always included the Pacific and either New Guinea, Australia, Mascarenes or New Caledonia. Therefore, many of these reconstructions are consistent with a vicariant split across the Coral Sea.

The deepest split within the Lanceocercata is between *Dimorphodes*, which is largely restricted to New Guinea (Van Herwaarden, 1998), and the remaining taxa, dated at 51.76 mya (36.23–69.78 mya). There were repeated land connections interspersed with marine inundation between New Guinea and Australia during the Cenozoic, and an early connection or dispersal facilitated that separation of *Dimorphodes* from the rest of the Lanceocercata.

At 39.53 mya (27.19–53.88 mya), the age of the Mascarene clade is old. The geology of the Indian Ocean is complex and volcanism is recorded from islands and seamounts to the north of the Mascarenes and in the Seychelles, at 65 mya (Sheth *et al*., 2003). Previous research (Braby *et al*., 2005) indicated that the Kerguelen Plateau, a deeply submerged, large igneous province in the Southern Ocean, may have acted as a land bridge between Antarctica and Indian Ocean landmasses such as Madagascar. However, more recent reconstructions show that the Kerguelen Plateau was probably never emergent (Ali & Aitchison, 2009). Therefore, beyond invoking dispersal we can provide no convincing mechanism for explaining the origin of the Mascarene clade. The long-term survival and speciation of the Mascarene clade was probably facilitated by dispersing among islands groups as they formed. A possible example of this is seen in *Monandroptera acanthomera*, which we have sampled from Mauritius and La Réunion. Both these islands are volcanic and have never been connected by land. The oldest known lava flows on La Réunion are dated at 2.08 mya (McDougall, 1971; Malengreau *et al*., 1999), which places a lower limit on the age of the island. Our estimated divergence date for the Mauritius and La Réunion populations of *M. acanthomera* is 3.91 mya (1.68–6.67 mya), which is consistent with dispersal from Mauritius to La Réunion following its formation at least 2.08 mya.

To our knowledge, no Lanceocercata species have been recorded from Madagascar or India. Our divergence dates are consistent with this observation because the India–Madagascar block split from Australia approximately 132 mya (McLoughlin, 2001) or perhaps even later during the Late Cretaceous 80–100 mya (Braby *et al*., 2005), which is earlier than our estimated age for the diversification of the Lanceocercata. Therefore, the absence of Lanceocercata from India and Madagascar provides independent evidence in support of our dates. If the Lanceocercata were older than early Cretaceous, which is not supported by our dating, then we would expect them to be present in India and Madagascar.

The ancestor of the major Australian clade was inferred to have inhabited Australia under both constrained and unconstrained dispersal-vicariance analyses. The dating analyses indicate that this clade began to radiate approximately 47.83 mya (33.78–64.70 mya). Within this clade there are subclades, such as *Anchiale*/*Phasma*, *Ctenomorpha* and *Eurycnema*, that have representatives outside Australia in New Guinea, South East Asia and some Pacific Islands, although they are not found as far north as mainland China (Hennemann *et al*., 2008). Although the Lanceocercata has been recorded from Borneo (*Ophicrania*, *Megacrania* and possibly *Pachymorpha*; Bragg, 2001) and Singapore and Malaysia (*Ophicrania* and *Eurycnema*; Brock, 1999), all these genera are relatively widely distributed, suggestive of a recent colonization of this region from Australia. As mentioned above, there have been repeated land connections between New Guinea and Australia (e.g. Ladiges *et al*., 2003) that would have allowed the movement of Lanceocercata taxa. De Jong (2001) argued that faunal exchange would have become increasingly likely 10 mya, although our dates are somewhat older than this with *Phasma gigas* from New Guinea and *Anchiale* sp. from the Solomon Islands having diverged from their Australian sister groups 27.02 mya (15.8–38.96 mya) and 31.70 mya (19.67–45.14 mya), respectively.

Of note are the Pacific 'Platycraninae' genera of *Megacrania*, *Graeffea* and *Ophicrania*, which have almost all of their diversity outside Australia (e.g. Hsiung, 2007). The Tertiary geological history to the north of Australia is complex, but there have been periodic land connections with New Guinea and movement of island arcs and terranes (Hall, 2002), which coupled with dispersal would have facilitated the diversification of the Lanceocercata into the Pacific Ocean. A further possible example of dispersal is the Lord Howe stick insect, *Dryococelus*. Although the distribution of the ancestor of *Dryococelus* and its sister group *Eurycnema* was inferred to be either Australia only or Lord Howe Island and Australia, nodes deeper in the tree were reconstructed as Australia only, which predicts a dispersal out of Australia to Lord Howe Island. As with the dating study of Buckley *et al.* (2009a), we inferred the age of *Dryococelus* to be 36.70 mya (25.02–50.35 mya) which greatly predates the age of Lord Howe Island (6.4–6.9 mya; McDougall *et al*., 1981) and this is consistent with this species migrating down now-drowned seamounts along the Lord Howe Rise. The Lord Howe tree lobster provides an interesting example of a taxon being much older than the land it currently inhabits (e.g. Heads, 2008a).

Although we sampled many Australian Lanceocercata genera that cover most of the observed morphological diversity, there are still some potential Lanceocercata genera not included in our study and that have not been examined for Lanceocercata apomorphies. Further sampling of Australian genera will reveal the complete diversity of this clade and the processes that have led to the large diversity in Australia and allow reconciliation with the diversification patterns in other taxa (e.g. Cracraft, 1991; Jennings *et al*., 2002; Byrne *et al*., 2008; Oliver & Sanders, 2009).

The New Caledonia and New Zealand clade split from the other main Lanceocercata clades 44.10 mya (31.06–59.44 mya) and this date range is consistent with land connections between Australia and New Caledonia that may have persisted as late as the Eocene (34–56 mya; Ladiges & Cantrill, 2007) and have been implicated in biogeographical patterns in other taxa (e.g. Oliver & Sanders, 2009). The geology of New Caledonia is complex and this landmass was formed by the accretion of several different terranes (Heads, 2008a), but the relationship of the New Caledonia and New Zealand clade to clades found to the west in Australasia suggests a western origin. Although several largely Grand Terre genera are shared with the Loyalty Islands (*Leosthenes*, *Carlius* and *Asprenas*), the Loyalty Islands are somewhat distinctive in their phasmatodean fauna also having genera, such as *Cladomimus* Carl, *Gigantophasma* Sharp and *Graeffea*, that are more closely associated with New Guinea, and Pacific Islands such as the Solomon Islands, a pattern shared with other taxa (e.g. Heads, 2008a). The radiation of the New Caledonian genera began 41.06 mya (29.05–55.40 mya) and this corresponds well with a period of intensive crustal deformation in the New Caledonia region in the Middle–Late Eocene due to emplacement of older oceanic crust on top of the New Caledonia basement (∼34–44 mya; Aitchison *et al.*, 1995; Schellart *et al.*, 2006), which caused regional uplift. Our future studies will investigate patterns of diversification more thoroughly within the New Caledonian phasmids and reconcile this with the geology of the Grand Terre and inferences from other taxa [reviewed in Grandcolas *et al.* (2008) and Heads (2008b)].

The main New Zealand clade and *Spinotectarchus* diverged from their New Caledonian sister groups 25.6 mya (16.8–35.5 mya) and 29.9 mya (19.79–41.16 mya), respectively, and therefore the two New Zealand lineages are of a very similar age. The dispersal-vicariance analyses reconstructed the ancestor of the New Zealand and New Caledonia clade as being restricted to New Caledonia only. Therefore, we can say with certainty that the New Zealand stick insects are derived both phylogenetically and biogeographically from the New Caledonian stick insects. The geological history of the region between New Zealand and New Caledonia is complex. It is well established that extensive marine transgression occurred along the Lord Howe Rise and Norfolk Ridge in the Late Cretaceous and at best these ridges probably comprised only a few emergent islands (Herzer *et al.*, 1997). However, uplift occurred on the Norfolk–Three Kings composite ridge in the Oligocene from New Caledonia southwards, but not as far as New Zealand, which may have supported a terrestrial biota. Formation of an island arc on the Norfolk–Three Kings composite ridge, which crossed the Reinga ridge and ran through the Reinga basin in the early Miocene, may have then allowed movement of this biota to New Zealand via island hopping (Herzer *et al.*, 1997). Ladiges & Cantrill (2007) suggested that there may have been emergent land along the Lord Howe Rise, allowing biotic connections between New Caledonia and New Zealand until the Late Eocene (34 mya). Schellart *et al*. (2009) have also provided evidence for a chain of emergent volcanoes between New Caledonia and New Zealand. This chain of volcanoes was part of a continuous island arc running from the Loyalty Islands, then southwards along the Loyalty Ridge, then the Three Kings Ridge and finally the Northland Plateau just north of Northland. These geological reconstructions are uncertain, as are our date estimates, but the two overlap and propose a possible mechanism for the movement of ancestors of the New Zealand stick insects from New Caledonia.

The lower limits on the divergence of the two New Zealand lineages and their sister taxa are close to or overlap with the peak of the late Oligocene marine transgression in New Zealand (Cooper & Cooper, 1995). The mean estimate for the start of the radiation of the main New Zealand clade (24.3, 17.3–31.8 mya) falls on the peak of the New Zealand Oligocene marine transgression. This correlation is consistent with an increased speciation rate following the emergence of land after the marine transgression (Cooper & Cooper, 1995) or an increased speciation rate during the transgression on isolated islands (Hickson *et al.*, 2000).

The finding of a monophyletic New Zealand and New Caledonian stick insect clade in this study and that of Buckley *et al*. (2009a) was not assumed from the taxonomic arrangement of the genera. However, this finding accords well with phylogenetic studies of other organisms (e.g. Gaskin, 1970; Leigh *et al*., 2007), including cicadas (e.g. Arensburger *et al*., 2004), caddisflies (Ward *et al.*, 2004), Scarabaeinae beetles (Monaghan *et al.*, 2007), weta (Pratt *et al.*, 2008), *Placostylus* land snails (Ponder *et al*., 2003), geckos (Chambers *et al*., 2001), parakeets (Boon *et al*., 2001), skinks (Bauer, 1988; Smith *et al*., 2007), *Corynocarpus* (Corynocarpaceae; Wagstaff & Dawson, 2000) and *Metrosideros* (Myrtaceae; Wright *et al*., 2000), which all show strong evidence of biogeographical links between New Zealand and New Caledonia.

Host plant patterns between New Zealand and New Caledonia

The New Zealand stick insects are all polyphagous and are especially common on species from the families Cunoniaceae (*Weinmannia*), Polygonaceae (*Muehlenbeckia*), Rosaceae (*Rubus*, *Acaenea*), Malvaceae (*Hoheria*), Ericales (*Dracophyllum*, *Cyathodes*), Asteliaceae (*Astelia*) and especially Myrtaceae (e.g. *Kunzea*, *Leptospermum*, *Metrosideros*, *Lophomyrtus*) (Salmon, 1991; Trewick *et al*., 2005; Buckley *et al*., 2008, 2009b, c; O'Neill *et al*., 2009). Many genera from these families that are favoured by the New Zealand species, and other host genera, are present in New Caledonia (e.g. *Leptospermum*, *Metrosideros*, *Weinmannia*, *Muelhenbeckia*, *Dracophyllum* and *Cyathodes*). Unfortunately, the information on host plants from the New Caledonian stick insect fauna is very poor, but our field observations indicate that they feed on similar plants, including species of *Metrosideros* (e.g. *Carlius*) and Cunoniaceae (e.g. *Canachus*; Buckley, unpublished data). Therefore, the close phylogenetic relationship of the two faunas is reflected in their host plant preferences. One notable exception is the preference of some New Caledonian species for ferns, including *Cnipsus* and *Asprenas*, yet no New Zealand species feed on ferns to our knowledge. This lack of fern feeding in the New Zealand fauna is peculiar, especially given the close relationship between the major New Zealand clade and *Cnipsus* and given the long history, high diversity and abundance of ferns in the New Zealand flora (Mildenhall, 1980; Brownsey, 2001; Perrie & Brownsey, 2007).

All of the above plant families have a long history in New Zealand, where fossils are recorded from the Miocene (*Lophomyrtus* and *Muehlenbeckia*), Oligocene (*Weinmannia*), Eocene (*Hoheria* and *Dracophyllum*) and Paleocene (*Metrosideros* and *Lepterspermum*) (Lee *et al*., 2001). The genus *Acanthoxyla* is often found on *Podocarpus* and *Dacrydium* from the Podocarpaceae, and this family has been present in New Zealand since the Cretaceous (Mildenhall, 1980; Pole, 1995). Therefore, at whatever point in geological time the ancestors of the New Zealand genera arrived in New Zealand from New Caledonia, no significant host shift would have been required for their survival.

Supporting Information

Additional Supporting Information may be found in the online version of this article under DOI: 10.1111/j.1365-3113.2009.00505.x.

Fig. S1 Bayesian consensus tree with dispersal-vicariance analysis reconstructions of ancestral areas under the constraints of maxareas = 2. Tip labels use codes from Table 1 and are followed by geographical area codes (A = New Zealand; B = New Caledonia; C = Australia; D = Pacific; E = New Guinea; F = South/Central America; G = Lord Howe Island). Nodes are labelled with the proportion of trees (marginal distributions) in which a certain reconstruction was optimal

Fig. S2 Bayesian consensus tree with dispersal-vicariance analysis reconstructions of ancestral areas with no constraints on the maximum number of ancestral areas. All labelling as in Fig. S1

Acknowledgements

The authors would like to thank the following people for providing specimens and assisting with field work; Martin Brinkert, Chris Carlton, Sylvie Cazeres, Trevor Crosby, Neal Evenhuis, George Gibbs, Grace Hall, Kristien Rabaey, Kathy Hill, Robert Hoare, Margaret Humphries, Tony Jewell, Bruno Kneubühler, Rich Leschen, David Marshall, Nicholas Martin, Christian Millé, Peter Miller, Geoff Monteith, Rod Morris, Max Moulds, Daniel Otte, Dave Seldon, Rob Simoens, Karlijn Vandervennet, Kipling Will and the late Henri Blafard. Laboratory work was aided by Julia Allwood, Robyn Howitt and Duckchul Park. Permits for New Caledonia were issued by David Paulaud and Jean-Jérôme Cassan. Special thanks to Christian Millé for his enthusiastic support of the New Caledonian research. Rich Leschen, Wouter Schellart, Peter Cranston and two anonymous reviewers gave comments on the manuscript. Funding was provided by the New Zealand Foundation for Research Science and Technology through the Defining New Zealand's Land Biota OBI, Royal Society of New Zealand Marsden fund (LCR302), the National Geographic Society (7906-05), and an Ernst Mayr Travel Award from Harvard University (to TRB).

References

Aitchison, J.C., Clarke, G.L., Meffre, S. & Cluzel, D. (1995) Eocene-continent collision in New Caledonia and implications for regional southwest Pacific tectonic evolution. *Geology*, **23**, 161–164.

Akaike, H. (1973) Information theory as an extension of the Maximum Likelihood principle. *Second International Symposium on Information Theory* (ed. by B. N. Petrov and F. Csaki), pp. 267–281. Akademiai Kiado, Budapest.

Ali, J.R. & Aitchison, J.C. (2009) Kerguelen Plateau and the Late Cretaceous southern-continent bioconnection hypothesis: tales from a topographic ocean. *Journal of Biogeography*, **36**, 1778–1784.

Altschul, S.F., Gish, W., Miller, W., Myers, E.W. & Lipman, D.J. (1990) Basic local alignment search tool. *Journal of Molecular Biology*, **215**, 403–410.

Arbogast, B.S., Edwards, S.V., Wakeley, J., Beerli, P. & Slowinski, J.B. (2002) Estimating divergence times from molecular data on phylogenetic and population genetic timescales. *Annual Review of Ecology and Systematics*, **33**, 707–740.

Arensburger, P.A., Buckley, T.R., Simon, C., Moulds, M.S. & Holsinger, K.E. (2004) Biogeography and phylogeny of the New Zealand cicada genera based on nuclear and mitochondrial DNA data. *Journal of Biogeography*, **31**, 557–569.

Bauer, A.M. (1988) Reptiles and the biogeographic interpretation of New Caledonia. *Tuatara*, **30**, 39–50.

Bergerard, J. (1962) Parthenogenesis in the Phasmidae. *Endeavour*, **21**, 137–143.

Boon, W.M., Daugherty, C.H. & Chambers, G.K. (2001) The Norfolk Island green parrot and New Caledonian red-crowned parakeet are distinct species. *Emu*, **101**, 113–121.

Braby, M.F., Trueman, J.W.H. & Eastwood, R. (2005) When and where did troidine butterflies (Lepidoptera: Papilionidae) evolve? Phylogenetic and biogeographic evidence suggests an origin in remnant Gondwana in the Late Cretaceous. *Invertebrate Systematics*, **19**, 113–143.

Bradler, S. (2001) The Australian stick insects, a monophyletic group within the Phasmatodea? *Zoology*, **104** (Suppl. IV) (DZG 94.1), 69.

Bradler, S. (2009) Phylogeny of the stick and leaf insects (Insecta: Phasmatodea). *Species, Phylogeny and Evolution*, **2**, 3–139.

Bragg, P.E. (2001) *Phasmids of Borneo*. Natural History Publications (Borneo), Kota Kinabalu.

Brock, P.D. (1999) *Stick and Leaf Insects of Peninsular Malaysia and Singapore*. Malaysian Nature Society, Kualar Lumpur.

Brock, P.D. & Hasenpusch, J. (2007) Studies on the Australian stick insects (Phasmida), including a checklist of species and bibliography. *Zootaxa*, **1570**, 1–81.

Brock, P.D. & Hasenpusch, J.W. (2009) *The Complete Field Guide to Stick and Leaf Insects of Australia*. CSIRO Publishing, Victoria.

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

Brownsey, P.J. (2001) New Zealand's Pteridophyte flora–plants of ancient lineage but recent arrival? *Brittonia*, **53**, 284–303.

Brunner von Wattenwyl, K. & Redtenbacher, J. (1906–1908) *Die Insekten familie der Phasmiden*. Wilhelm Englemann, Leipzig.

Buckley, T.R., Attanayake, D. & Bradler, S. (2009a) Extreme convergence in stick insect evolution: phylogenetic placement of the Lord Howe Island tree lobster. *Proceedings of the Royal Society of London, Series B*, **276**, 1055–1062.

Buckley, T.R., Attanayake, D., Park, D-C., Ravindran, S., Jewell, T.R. & Normark, B.B. (2008) Investigating hybridization in the parthenogenetic New Zealand stick insect *Acanthoxyla* (Phasmatodea) using single-copy nuclear loci. *Molecular Phylogenetics and Evolution*, **47**, 335–349.

Buckley, T.R., Marske, K. & Attanayake, D. (2009b) Phylogeography and ecological niche modelling of the New Zealand stick insect *Clitarchus hookeri* (White) support survival in multiple coastal refugia. *Journal of Biogeography*, in review.

Buckley, T.R., Marske, K. & Attanayake, D. (2009c) Identifying glacial refugia in a geographic parthenogen using palaeoclimate modeling and phylogeography: the New Zealand stick insect *Argosarchus horridus* (White). *Molecular Ecology*, **18**, 4650–4663.

Byrne, M., Yeates, D.K., Kearney, M. *et al.* (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology*, **17**, 4398–4417.

Carl, J. (1913) Phasmides nouveaux ou peu connus du Museum de Geneve. *Annales de la Societe Zoologique Suisse et du Museum d'Histoire Naturelle de Geneve*, **21**, 1–56.

Carl, J. (1915) Phasmiden von Neu-Caledonien und den Loyalty-Inseln. *Nova Caledonia, Recherches scientifiques en Nouvelle-Calédonie et aux îles Loyalty, Zoologie A* (ed. by F. Sarasin and J. Roux), Vol. 2, 173–178.

Chambers, G.K., Boon, W.M., Buckley, T.R. & Hitchmough, R.A. (2001) Using molecular methods to understand the Gondwanan affinities of the New Zealand biota: three case studies. *Australian Journal of Botany*, **49**, 377–387.

Chazeau, J. (1993) Research on New Caledonia terrestrial fauna: achievements and prospects. *Biodiversity Letters*, **1**, 123–129.

Clark, J.R., Ree, R.H., Alfaro, M.E., King, M.G., Wagner, W.L. & Roalson, E.H. (2008) A comparative study in ancestral range reconstruction methods: retracing the uncertain histories of insular lineages. *Systematic Biology*, **57**, 693–707.

Cooper, A. & Cooper, R.A. (1995) The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *Proceedings of the Royal Society, Biological Sciences*, **261**, 293–302.

Cracraft, J. (1991) Patterns of diversification within continental biotas: hierarchical congruence among areas of endemism of Australian vertebrates. *Australian Systematic Botany*, **4**, 211–227.

De Jong, R. (2001) Faunal exchange between Asia and Australia in the Tertiary as evidenced by recent butterflies. *Faunal and Floral Migrations and Evolution in SE Asia-Australasia* (ed. by I. Metcalfe, J. M. B. Smith, M. Morwood and I. Davidson), pp. 133–146. Balkema Publishers, Rotterdam.

Donskoff, M. (1988) Phasmatodea de Nouvelle-Calédonie 1. Nouvelle signialisations et description de *Microcanachus* n. gen. *Zoologica Neocaledonica*, Vol. 1 (ed. by S. Tillier). *Mémoires, Museum National d'Histoire Naturelle, Paris (A)*, **142**, 53–60.

Drummond, A.J., Ho, S.Y.W., Philips, M.J. & Rambaut, A. (2006) Relaxed phylogenetics and dating with confidence. *Public Library of Science (Biology)*, **4**, e88.

Drummond, A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7**, 214.

Eusebio, O.L., Lit, I.L. Jr & Vörkel, I. (2004) First description of the male of *Phasmotaenia elongata* Zompro & Eusebio (Phasmatodea: Phasmatidae) with notes on its host plants and a revised key to the species of *Phasmotaenia navas*. *The Philippine Agricultural Scientist*, **87**, 191–195.

Gaskin, D.E. (1970) The origins of the New Zealand fauna and flora: a review. *Geographical Review*, **60**, 414–434.

Gillespie, J.J., Johnson, J.S., Cannone, J.J. & Gutell, R.R. (2006) Characteristics of the nuclear (18S, 5.8S, 28S, and 5S) and mitochondrial (12S and 16S) rRNA genes of *Apis mellifera* (Insecta: Hymenoptera): structure, organization, and retrotransposable elements. *Insect Molecular Biology*, **15**, 657–686.

Grandcolas, P., Murienne, J., Robillard, T., Desutter-Grandcolas, L., Jourdan, H., Guilbert, E. & Deharveng, L. (2008). New Caledonia: a very old Darwinian island? *Philosophical Transactions of the Royal Society B*, **363**, 3309–3317.

Günther, K. (1953) Über die taxonomische Gliederung und geographische Verbreitung der Insektenordnung der Phasmatodea. *Beiträge zur Entomologie, Berlin*, **3**, 541–563.

Hall, R. (2002) Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences*, **20**, 353–431.

Heads, M. (2008a) Panbiogeography of New Caledonia, southwest Pacific: basal angiosperms on basement terranes, ultramafic endemics inherited from volcanic island arcs and old taxa endemic to young islands. *Journal of Biogeography*, **35**, 2153–2175.

Heads, M. (2008b) Biological disjunction along the West Caledonian fault, New Caledonia: a synthesis of molecular phylogenetics and panbiogeography. *Biological Journal of the Linnean Society*, **158**, 470–488.

Hennemann, F.H. & Conle, O.V. (2006) Studies on New Guinean giant stick-insects of the tribe Stephanacridini Günther, 1953, with the descriptions of a new genus and three new species of *Stephanacris* Redtenbacher, 1908 (Phasmatodea: "Anareolatae"). *Zootaxa*, **1283**, 1–24.

Hennemann, F.H. & Conle, O.V. (2008) Revision of Oriental Phasmatodea: the tribe Pharnaciini Günther, 1953, including the description of the world's longest insect, and a survey of the family Phasmatidae Gray, 1853 with keys to the subfamilies and tribes (Phasmatodea: "Anareolatae": Phasmatidae). *Zootaxa*, **1906**, 1–316.

Hennemann, F.H. & Conle, O.V. (2009) Studies on the genus *Phasmotaenia* Navás, 1907, with the descriptions of five new species from the Solomon Islands, a revised key to the species and notes on its geographic distribution (Phasmatodea: "Anareolatae": Phasmatidae *s.l.*: Stephanacridini). *Zootaxa*, **2011**, 1–46.

Hennemann, F.H., Conle, O.V. & Zhang, W. (2008) Catalogue of the stick and leaf-insects (Phasmatodea) of China, with a faunistic analysis, review of recent ecological and biological studies and bibliography (Insects: Orthoptera: Phasmatodea). *Zootaxa*, **1735**, 1–77.

Herzer, R.H., Chaproniere, G.C.H., Edwards, A.R. *et al.* (1997) Seismic stratigraphy and structural history of the Reinga Basin and its margins, southern Norfolk Ridge system. *New Zealand Journal of Geology and Geophysics*, **40**, 425–451.

Hickson, R.E., Slack, K.E. & Lockhart, P. (2000) Phylogeny recapitulates geography, or why New Zealand has so many species of skink. *Biological Journal of the Linnean Society*, **70**, 415–433.

Hsiung, C.-C. (2007) Revision of the genus *Megacrania* Kaup (Cheleutoptera, Phasmatidae). *Journal of Orthoptera Research*, **16**, 207–221.

Huang, Y.S.-F. & Brock, P.D. (2001) A new species of *Phasmotaenia* Navas (Phasmida: Phasmatidae) from Taiwan. *Journal of Orthoptera Research*, **10**, 9–14.

Hutton, F.W. (1899) Revision of the New Zealand Phasmidae. *Transactions of the New Zealand Institute*, **31**, 50–59.

Jennings, W.B., Pianka, E.R. & Donnellan, S. (2002) Systematics of lizard family Pygopodidae with implications for the diversification of Australian temperate biotas. *Systematic Biology*, **52**, 757–780.

Jewell, T. & Brock, P.D. (2002) A review of the New Zealand stick insects: new genera and synonymy, keys, and a catalogue. *Journal of Orthoptera Research*, **11**, 189–197.

Klug, R. & Bradler, S. (2006) The pregenital abdominal musculature in phasmids and its implications for the basal phylogeny of Phasmatodea (Insecta: Polyneoptera). *Organisms, Diversity and Evolution*, **6**, 171–184.

Ladiges, P.Y. & Cantrill, D. (2007) New Caledonia-Australia connections: biogeographic patterns and geology. *Australian Systematic Botany*, **20**, 383–389.

Ladiges, P.Y., Udovicic, F. & Nelson, G. (2003) Australian biogeographical connections and the phylogeny of large genera in the plant family Myrtaceae. *Journal of Biogeography*, **30**, 989–998.

Larkin, M.A., Blackshields, G., Brown, N.P. *et al.* (2007) Clustal W and Clustal X version 2.0. *Bioinformatics*, **23**, 2947–2948.

Lawver, L.A. & Gahagan, L.M. (1998) Opening of Drake Passage and its impact on Cenozoic ocean circulation. *Tectonic Boundary Conditions for Climate Reconstructions* (ed. by T. J. Crowley and K. Burke), pp. 212–223. Oxford University Press, Oxford.

Lee, D.E., Lee, W.G. & Mortimer, N. (2001) Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Australian Journal of Botany*, **49**, 341–356.

Leigh, E.G., Hladik, A., Hladik, C.M. & Jolly, A. (2007) The biogeography of large islands, or how does the size of the ecological theatre affect the evolutionary play. *Revue d'Écologie (La Terre et la Vie)*, **62**, 105–168.

Li, Z.X. & Powell, C.Mc.A. (2001) An outline of the paleogeographic evolution of the Australasian region since the beginning of the Neoproterozoic. *Earth-Sciences Reviews*, **53**, 237–277.

Lin, C.P. & Danforth, B.N. (2004) How do insect nuclear and mitochondrial gene substitution patterns differ? Insights from Bayesian analyses of combined datasets. *Molecular Phylogenetics and Evolution*, **30**, 686–702.

Malengreau, B., Lénat, J-F. & Froger, J-L. (1999) Structure of Réunion Island (Indian Ocean) inferred from the interpretation of gravity anomalies. *Journal of Volcanology and Geothermal Research*, **88**, 131–146.

McDougall, I. (1971) The geochronology and evolution of the young volcanic island of Réunion (Indian Ocean). *Geochimica et Cosmochimica Acta*, **35**, 261–288.

McDougall, I., Embleton, B.J.J. & Stone, D.B. (1981) Origin and evolution of Lord Howe Island, southwest Pacific Ocean. *Journal of the Geological Society of Australia*, **28**, 155–176.

McLoughlin, S. (2001) The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany*, **49**, 271–300.

Michaux, B. (2009) Reciprocality between biology and geology: reconstructing polar Gondwana. *Gondwana Research*, **16**, 655–668.

Michaux, B. & Leschen, R.A.B. (2005) East meets west: biogeology of the Campbell Plateau. *Biological Journal of the Linnaean Society*, **86**, 95–115.

Mildenhall, D.C. (1980) New Zealand late Cretaceous and Cenozoic plant biogeography: a contribution. *New Zealand Journal of Botany*, **23**, 723–749.

Monaghan, M.T., Inward, D.J.G., Hunt, T. & Vogler, A.P. (2007) A molecular phylogenetic analysis of the Scarabaeinae (dung beetles). *Molecular Phylogenetics and Evolution*, **45**, 674–692.

Morgan-Richards, M. & Trewick, S.A. (2005) Hybrid origin of a parthenogenetic genus? *Molecular Ecology*, **14**, 2133–2142.

Nakata, S. (1961) Some notes on the occurrence of Phasmatodea in Oceania. *Pacific Insects Monographs*, **2**, 107–121.

Nylander, J.A.A., Olsson, U., Alström, P. & Sanmartín, I. (2008) Accounting for phylogenetic uncertainty in biogeography: a Bayesian approach to dispersal-vicariance analysis of the thrushes (Aves: *Turdus*). *Systematic Biology*, **57**, 257–268.

Nylander, J.A.A., Ronquist, F., Huelsenbeck, J.P. & Nievea-Aldrey, J.L. (2004) Bayesian phylogenetic analysis of combined data. *Systematic Biology*, **53**, 47–67.

Oliver, P.M. & Sanders, K.L. (2009) Molecular evidence for Gondwanan origins of multiple lineages within a diverse Australasian gecko radiation. *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2009.02149.x.

O'Neill, S.B., Buckley, T.R., Jewell, T. & Ritchie, P.A. (2009) Phylogeographic history of the New Zealand stick insect *Niveaphasma annulata* (Phasmatodea) estimated from mitochondrial and nuclear loci. *Molecular Phylogenetics and Evolution*, **53**, 523–536.

Otte, D. & Brock, P.D. (2005) *Phasmida Species File: A Catalog to the Stick Insects of the World* (The Orthopterists Society).

Pagel, M. & Meade, A. (2004) A phylogenetic mixture model for detecting pattern-heterogeneity in gene sequence or character-state data. *Systematic Biology*, **53**, 571–581.

Pagel, M., Meade, A. & Barker, D. (2004) Bayesian estimation of ancestral character states on phylogenies. *Systematic Biology*, **53**, 673–684.

Perrie, L. & Brownsey, P. (2007) Molecular evidence for long-distance dispersal in the New Zealand pteridophyte flora. *Journal of Biogeography*, **34**, 2028–2038.

Pole, M. (1995) Late Cretaceous macrofloras of Eastern Otago, New Zealand: gymnosperms. *Australian Systematic Botany*, **8**, 1067–1106.

Ponder, W.F., Colgan, D.J., Gleeson, D.M. & Sherley, G.H. (2003) Relationships of *Placostylus* from Lord Howe Island: an investigation using the mitochondrial cytochrome *c* oxidase 1 gene. *Molluscan Research*, **23**, 159–178.

Posada, D. & Crandall, K.A. (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics*, **14**, 817–818.

Pratt, R.C., Morgan-Richards, M. & Trewick, S.A. (2008) Diversification of New Zealand weta (Orthoptera: Ensifera: Anostostomatidae) and their relationships in Australasia. *Philosophical Transactions of the Royal Society B*, **363**, 3427–3437.

Rambaut, A. & Drummond, A.J. (2007) Tracer v1.4 [WWW document]. URL http://beast.bio.ed.ac.uk/Tracer [accessed in 2009].

Ronquist, F. (1997) Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, **46**, 195–203.

Ronquist, F. (2001) *DIVA version 1.2. Computer program for MacOS and Win32*. Evolutionary Biology Centre, Uppsala University [WWW document]. URL http://www.ebc.uu.se/systzoo/research/diva/diva.html. [accessed in 2009].

Salmon, J.T. (1948) New genera, species and records of Orthoptera from the Three Kings Islands New Zealand. *Records of the Auckland Institute and Museum*, **3**, 291–311.

Salmon, J.T. (1954) A new genus and species of Phasmidae from New Zealand. *Transactions of the Royal Society of New Zealand*, **82**, 161–168.

Salmon, J.T. (1955a) Parthenogenesis in New Zealand stick insects. *Transactions of the Royal Society of New Zealand*, **82**, 1189–1192.

Salmon, J.T. (1955b) The genus *Acanthoxyla* (Phasmidae). *Transactions of the Royal Society of New Zealand*, **82**, 1149–1156.

Salmon, J.T. (1991) *The Stick Insects of New Zealand*. Reed, Auckland.

Schellart, W.P., Kennett, B.L.N., Spakman, W. & Amaru, M. (2009) Plate reconstructions and tomography reveal a fossil lower mantle slab below the Tasman Sea. *Earth and Planetary Science Letters*, **278**, 143–151.

Schellart, W.P., Lister, G.S. & Toy, V.G. (2006) A late Cretaceous and Cenozoic reconstruction of the Southwest Pacific region: tectonics controlled by subduction and slab rollback processes. *Earth-Science Reviews*, **76**, 191–233.

Sheth, H.C., Mahoney, J.J. & Baxter, A.N. (2003) Geochemistry of lavas from Mauritius, Indian Ocean: mantle sources and petrogenesis. *International Geology Review*, **45**, 780–797.

Simon, C., Frati, F., Crespi, B., Liu, H. & Flook, P.K. (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved PCR primers. *Annals of the Entomological Society of America*, **87**, 651–701.

Smith, A.S., Sadlier, R.A., Bauer, A.M., Austin, C.C. & Jackman, T. (2007) Molecular phylogeny of the scincid lizards of New Caledonia and adjacent areas: evidence for a single origin of the endemic skinks of Tasmantis. *Molecular Phylogenetics and Evolution*, **43**, 1151–1166.

Swofford, D.L. (1998) *PAUP*. Phylogenetic Analysis Using Parsimony (* and Other Methods). Version 4*. Sinauer Associates, Sunderland, Massachusetts.

Trewick, S.A., Goldberg, J. & Morgan-Richards, M. (2005) Fewer species of *Argosarchus* and *Clitarchus* stick insects (Phasmida: Phasmatinae): evidence from mitochondrial and nuclear DNA sequences. *Zoologica Scipta*, **34**, 483–491.

Trewick, S.A., Morgan-Richards, M. & Collins, L.J. (2008) Are you my mother? Phylogenetic analysis reveals orphan hybrid stick insect genus is part of a monophyletic New Zealand clade. *Molecular Phylogenetics and Evolution*, **48**, 799–808.

Van Herwaarden, H.C.M. (1998) A guide to the genera of stick- and leaf-insects (Insecta: Phasmida) of New Guinea and the surrounding islands. *Science in New Guinea*, **24**, 55–114.

Veevers, J.J. & Li, Z.X. (1991) Review of seafloor spreading around Australia. II. Marine magnetic anomaly modeling. *Australian Journal of Earth Sciences*, **38**, 391–408.

Vickery, V.R. (1983) *Catalogue of Australian Stick Insects (Phasmida, Phasmatodea, Phasmatoptera, or Cheleutoptera)*. Technical Paper No. 20. CSIRO Australian Division of Entomology, Canberra, 1–19.

Wagstaff, S.J. & Dawson, M.I. (2000) Classification, origin, and patterns of diversification of *Corynocarpus* (Corynocarpaceae) inferred from DNA sequences. *Systematic Botany*, **25**, 134–149.

Ward, J.B., Leschen, R.A.B., Smith, B.J. & Dean, J.C. (2004) Phylogeny of the caddisfly (Trichoptera) family Hydrobiosidae using larval and adult morphology, with the description of a new genus and species from Fiordland, New Zealand. *Records of the Canterbury Museum*, **18**, 23–43.

Wedmann, S., Bradler, S. & Rust, J. (2007) The first fossil leaf insect: 47 million years of specialized cryptic morphology and behavior. *Proceedings of the National Academy of Sciences USA*, **104**, 565–569.

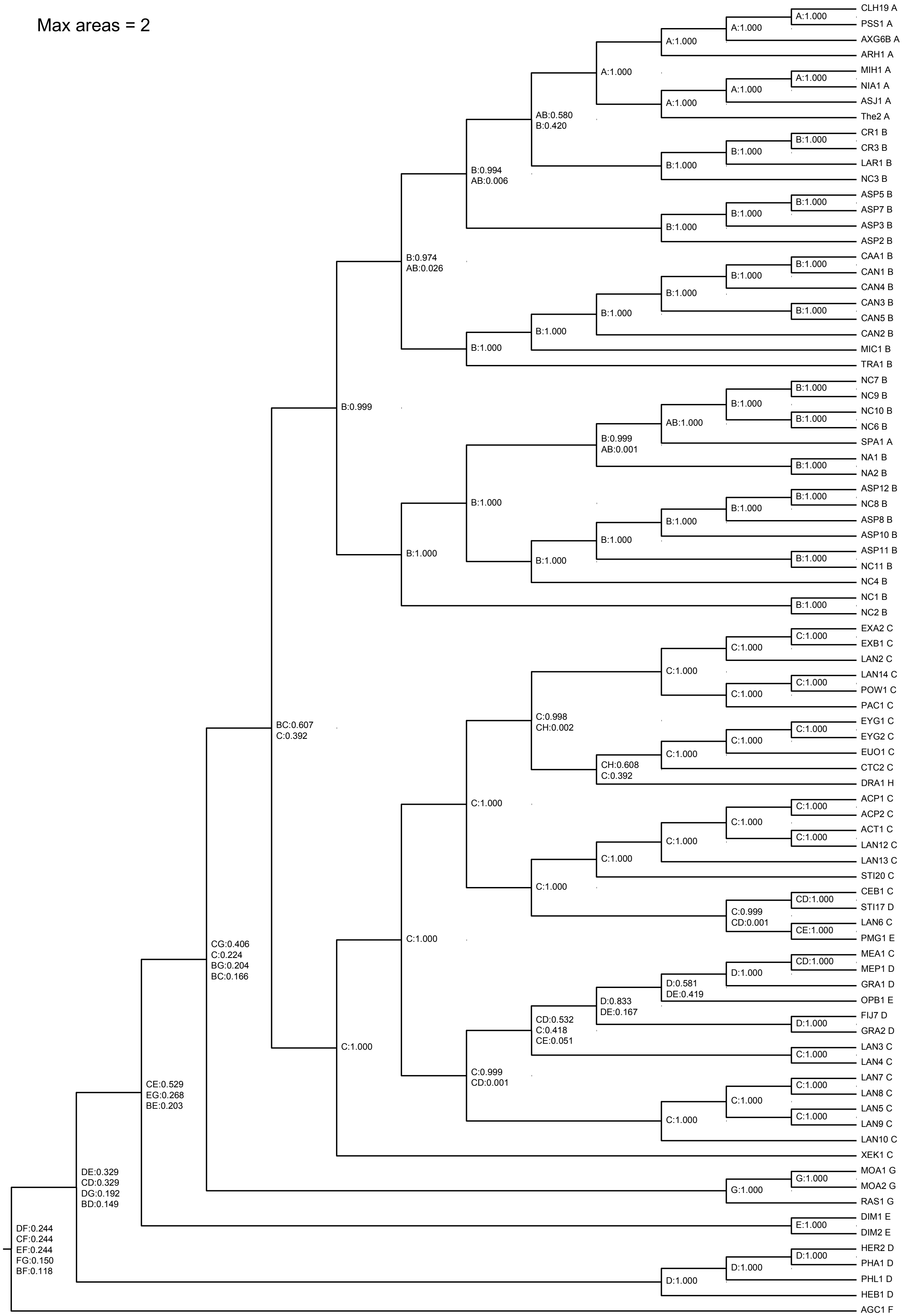
Whiting, M.F., Bradler, S. & Maxwell, T. (2003) Loss and recovery of wings in stick insects. *Nature*, **421**, 264–267.

Wright, S.D., Yong, C.G., Dawson, J.W., Whittaker, D.J. & Gardner, R.C. (2000) Riding the ice age El Nino? Pacific biogeography and evolution of *Metrosideros* subg. *Metrosideros* (Myrtaceae) inferred from nuclear ribosomal DNA. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 4118–4123.

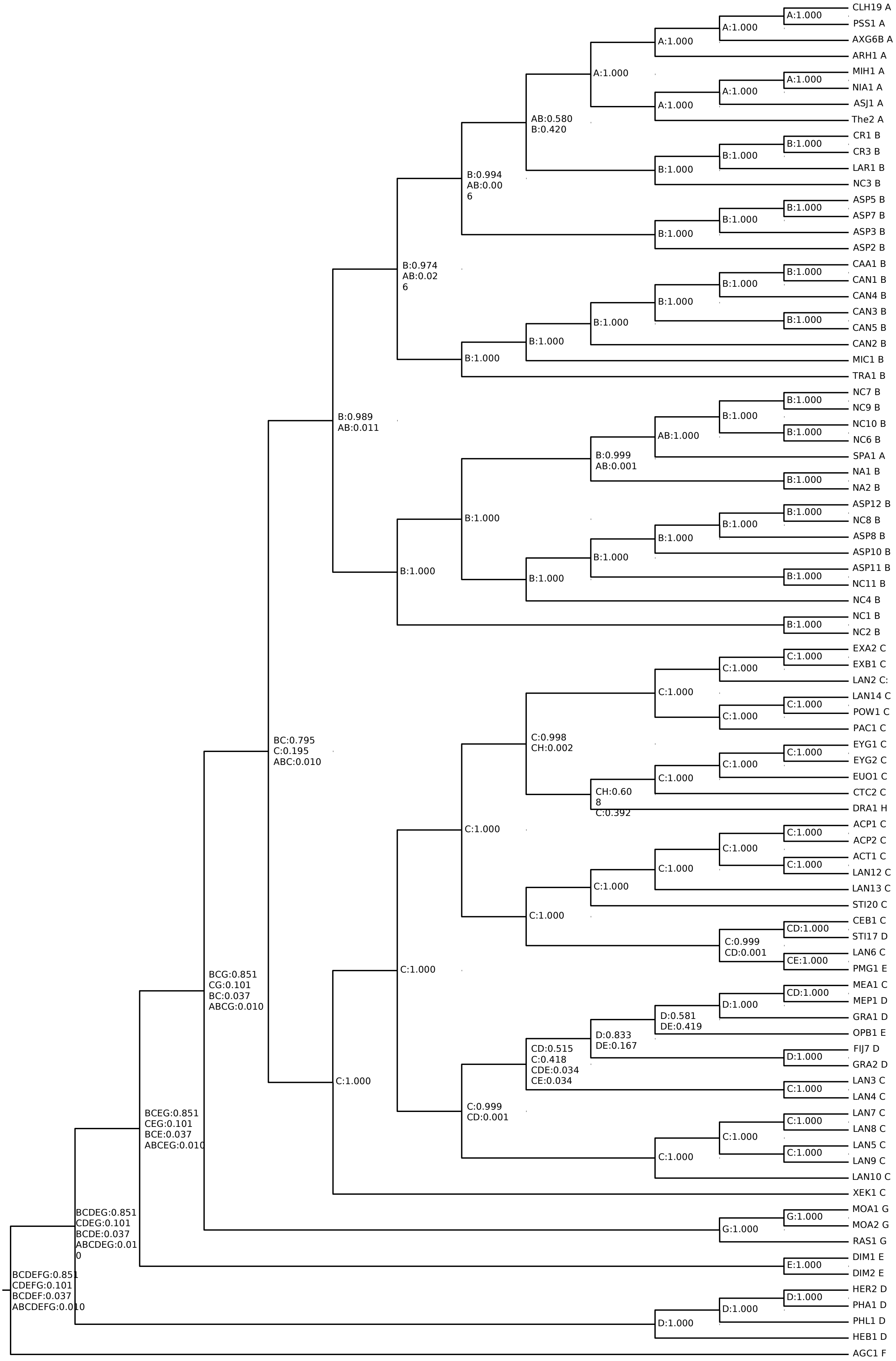
Zompro, O. (2001) A review of Eurycanthinae: Eurycanthini, with a key to genera, notes on the subfamily and designation of type species. *Phasmid Studies*, **10**, 19–23.

Accepted 17 August 2009

Max areas = 2



CLH19 A
A:1.000
PSS1 A
A:1.000
AXG6B A
A:1.000
ARH1 A
MIH1 A
A:1.000
A:1.000
NIA1 A
A:1.000
ASJ1 A
A:1.000
AB:0.580
B:0.420
The2 A
CR1 B
B:1.000
CR3 B
B:1.000
LAR1 B
B:1.000
B:0.994
AB:0.006
NC3 B
ASP5 B
B:1.000
ASP7 B
B:1.000
ASP3 B
B:1.000
ASP2 B
CAA1 B
B:0.974
AB:0.026
B:1.000
CAN1 B
B:1.000
CAN4 B
B:1.000
CAN3 B
B:1.000
B:1.000
CAN5 B
B:1.000
CAN2 B
B:1.000
MIC1 B
TRA1 B
NC7 B
B:1.000
NC9 B
B:1.000
B:0.999
NC10 B
B:1.000
AB:1.000
NC6 B
B:0.999
AB:0.001
SPA1 A
NA1 B
B:1.000
NA2 B
ASP12 B
B:1.000
B:1.000
NC8 B
B:1.000
ASP8 B
B:1.000
ASP10 B
B:1.000
ASP11 B
B:1.000
B:1.000
B:1.000
NC11 B
NC4 B
NC1 B
B:1.000
NC2 B
EXA2 C
C:1.000
EXB1 C
C:1.000
LAN2 C
C:1.000
LAN14 C
C:1.000
POW1 C
C:1.000
PAC1 C
C:0.998
CH:0.002
EYG1 C
BC:0.607
C:0.392
C:1.000
EYG2 C
C:1.000
EUO1 C
C:1.000
CH:0.608
C:0.392
CTC2 C
DRA1 H
ACP1 C
C:1.000
C:1.000
ACP2 C
C:1.000
ACT1 C
C:1.000
C:1.000
LAN12 C
C:1.000
LAN13 C
STI20 C
C:1.000
CEB1 C
CD:1.000
STI17 D
C:0.999
CD:0.001
LAN6 C
CE:1.000
PMG1 E
C:1.000
CG:0.406
C:0.224
BG:0.204
BC:0.166
MEA1 C
CD:1.000
MEP1 D
D:1.000
D:0.581
DE:0.419
GRA1 D
OPB1 E
D:0.833
DE:0.167
FIJ7 D
CD:0.532
C:0.418
CE:0.051
D:1.000
GRA2 D
LAN3 C
C:1.000
C:1.000
LAN4 C
C:0.999
CD:0.001
LAN7 C
CE:0.529
EG:0.268
BE:0.203
C:1.000
LAN8 C
C:1.000
LAN5 C
C:1.000
C:1.000
LAN9 C
LAN10 C
XEK1 C
MOA1 G
DE:0.329
CD:0.329
DG:0.192
BD:0.149
G:1.000
MOA2 G
G:1.000
RAS1 G
DIM1 E
E:1.000
DF:0.244
CF:0.244
EF:0.244
FG:0.150
BF:0.118
DIM2 E
HER2 D
D:1.000
PHA1 D
D:1.000
PHL1 D
D:1.000
HEB1 D
AGC1 F


CLH19 A
A:1.000
PSS1 A
A:1.000
AXG6B A
A:1.000
ARH1 A
A:1.000
MIH1 A
A:1.000
NIA1 A
A:1.000
ASJ1 A
A:1.000
The2 A
AB:0.580
B:0.420
CR1 B
B:1.000
CR3 B
B:1.000
LAR1 B
B:1.000
B:0.994
AB:0.00
6
NC3 B
ASP5 B
B:1.000
ASP7 B
B:1.000
ASP3 B
B:1.000
ASP2 B
B:0.974
AB:0.02
6
CAA1 B
B:1.000
CAN1 B
B:1.000
CAN4 B
B:1.000
CAN3 B
B:1.000
B:1.000
CAN5 B
B:1.000
CAN2 B
B:1.000
MIC1 B
TRA1 B
NC7 B
B:1.000
NC9 B
B:1.000
B:0.989
AB:0.011
NC10 B
B:1.000
AB:1.000
NC6 B
SPA1 A
B:0.999
AB:0.001
NA1 B
B:1.000
NA2 B
ASP12 B
B:1.000
NC8 B
B:1.000
B:1.000
ASP8 B
B:1.000
ASP10 B
B:1.000
ASP11 B
B:1.000
B:1.000
NC11 B
B:1.000
NC4 B
NC1 B
B:1.000
NC2 B
EXA2 C
C:1.000
EXB1 C
C:1.000
LAN2 C:
C:1.000
LAN14 C
C:1.000
POW1 C
C:1.000
PAC1 C
C:0.998
CH:0.002
BC:0.795
C:0.195
ABC:0.010
EYG1 C
C:1.000
EYG2 C
C:1.000
EUO1 C
C:1.000
CTC2 C
CH:0.60
8
C:0.392
DRA1 H
ACP1 C
C:1.000
C:1.000
ACP2 C
C:1.000
ACT1 C
C:1.000
LAN12 C
C:1.000
LAN13 C
C:1.000
STI20 C
C:1.000
CEB1 C
CD:1.000
STI17 D
C:0.999
CD:0.001
LAN6 C
CE:1.000
PMG1 E
C:1.000
BCG:0.851
CG:0.101
BC:0.037
ABCG:0.010
MEA1 C
CD:1.000
D:1.000
MEP1 D
D:0.581
DE:0.419
GRA1 D
D:0.833
DE:0.167
OPB1 E
CD:0.515
C:0.418
CDE:0.034
CE:0.034
FIJ7 D
D:1.000
GRA2 D
C:1.000
LAN3 C
C:1.000
LAN4 C
C:0.999
CD:0.001
BCEG:0.851
CEG:0.101
BCE:0.037
ABCEG:0.010
LAN7 C
C:1.000
C:1.000
LAN8 C
C:1.000
LAN5 C
C:1.000
LAN9 C
LAN10 C
XEK1 C
BCDEG:0.851
CDEG:0.101
BCDE:0.037
ABCDEG:0.01
0
MOA1 G
G:1.000
G:1.000
MOA2 G
RAS1 G
DIM1 E
E:1.000
DIM2 E
BCDEFG:0.851
CDEFG:0.101
BCDEF:0.037
ABCDEFG:0.010
HER2 D
D:1.000
D:1.000
PHA1 D
D:1.000
PHL1 D
HEB1 D
AGC1 F