biologically more like oceanic islands than southern continents (Goldberg *e a*. 2008; Grandcolas *e a*. 2008; Trewick & Morgan-Richards in press).

Evidence for the persistence of land in the New Zealand region throughout the Oligocene has been obscured by the extensive tectonic activity initiated in the early Miocene (Landis *e a*. 2008). The tectonic upheaval that resulted in the formation of New Zealand (as we know it today) began *ca* 24 Ma and still continues (Trewick *e a*. 2007). For example, the major mountain ranges of New Zealand started forming only *ca* 5 Ma. This, and other local geophysical events, may have been more important in the development of the modern biota than ancient vicariant processes. New Caledonia has a similar geological history with tectonic activity forcing a submerged section of Zealandia (and obducted oceanic ultramafic strata) to the sea surface in the late Eocene (*ca* 40 Ma Chardon & Chevillotte 2006; Mortimer *e a*. 2006; Grandcolas *e a*. 2008; Neall & Trewick 2008).

One of the most interesting components of New Zealand's terrestrial fauna, with both taxonomic and ecological diversity, are insects of the orthopteran family Anostostomatidae, known in New Zealand by their Maori name, weta. Of particular biogeographic interest is the presence of the family on all three major Australasian landmasses: Australia, New Caledonia and New Zealand. The group consists of relatively large insects (20–80 mm) that are nocturnal, predominantly flightless and predatory, with a Gondwanan distribution (also found in Central and South America, South Africa, Madagascar and India). In New Zealand, the family is represented by five genera and approximately 56 species. These five genera fall into three distinct groups: (i) nine (plus approx. 30 undescribed) species of *He a d* Ander 1938 (ground weta), (ii) one species of *A a* Ander 1938 and two species of *M e a* Johns 1997 (tusked weta), and (iii) seven *He de a* White 1846 (tree weta) and 11 *De ac da* White 1842 (giant weta) (Trewick & Morgan-Richards 2004, 2005).

The *He de a* and *De ac da* are unusual among Anostostomatidae in that all species are primarily herbivorous. The diversification of *He de a De ac da* dates to the Miocene, with adaptation to diverse habitats following mountain uplift (*ca* 5 Ma Trewick & Morgan-Richards 2005). The three tusked weta species (*A a*/*M e a*), so named owing to the impressive tusk-like structures on the mandibles of mature males, form a monophyletic group among New Zealand taxa (Trewick & Morgan-Richards 2004), although analogous ornamentations are found in some South African species (i.e. *L ba a d a* ; Field & Deans 2001). Within the Australasian anostostomatid genera, *He a d* is the only genus not endemic to a single landmass, being recorded in both Australia and New Zealand (Johns 1997). Of the approximately 40 species

Australasian Anostostomatidae; III—combined 18S and 28S Australasian Anostostomatidae; IV—COI–RY-coded Australasian Anostostomatidae; V—combined COI–RY and 12S Australasian Anostostomatidae; and VI—COI *Hetiana* only.

The COI data were partitioned into three character sets according to the codon position, first, second and third. In order to maximize third codon information, we treated it in three different ways: as four nucleotides (A, G, T, C), Y-coded (Y, A, G) or RY-coded (A and G=R, T and C=Y). In order to avoid potential tree estimation bias due to nucleotide composition or saturation, we used Y or RY coding on the third codon position nucleotides for COI sequences in dataset IV and V. Recoding of this sort has been shown to greatly improve consistency in phylogenetic resolution by reducing bias from differences in nucleotide composition (Phillips & Penny 2003), which is useful when looking at deeper divergences. To assist with tree rooting and thus confirm ingroup status of our sample, we used published Ensifera DNA sequences from both EMBL and NCBI GenBank (see the electronic supplementary material).

Models of DNA evolution were optimized separately for each dataset using MODELTEST v. 3.7 (Posada & Crandall 1998) and Akaike Information Criterion was preferred to the hierarchical likelihood ratio test (Posada & Buckley 2004). Maximum-likelihood (ML) analyses were implemented using the programs PAUP* (Swofford 2003), GARLI v. 0.951 (Zwickl 2006) and PHYML (Guindon & Gascuel 2003). Model parameters from MODELTEST were implemented using a general time-reversible model with invariable sites and a gamma distribution for variable rate sites (GTR+I+G) model with a heuristic search under the likelihood criterion with trees obtained from stepwise addition.

Bayesian analyses were implemented using MRBAYES v. 3.1 (Huelsenbeck & Ronquist 2001). We specified nst=2 (HKY) and nst=6 (GTR) with a proportion of invariant sites and gamma distribution of rate variation. Analyses of datasets III (18S+28S), IV (COI) and V (COI +12S) were undertaken with (parameters unlinked) and without character set partitions. We used two runs of four Markov chains (each with one cold chain) with $1–10\times10^6$ generations and default priors, sampling every thousandth tree. A 'burn-in' of 10 per cent was removed after examination of log-likelihood scores and average standard deviation of the split frequencies. Trees saved below the burn-in generation were discarded and a majority rule consensus of the remaining trees was calculated. Multiple replicates of the Bayesian runs were carried out to insure convergence of the posteriors.

(c) Tree comparisons

We assessed the degree of conflict between our phylogenetic estimates by using tree comparison tests, to see if one topology was significantly better at explaining the molecular data than alternative phylogenies. We used the SH tests (Shimodaira & Hasegawa 1999) implementing a RELL distribution derived from 1000 bootstrap replicates as executed in PAUP*. For dataset IV (COI), we carried out multiple analyses manipulating the third codon position so that it was; four states, Y-coded and RY coded. To observe the effect of this simple noise reduction technique, we compared ML topologies obtained from PHYML for each state using either a simple model (HKY85) or a parameter-rich model (GTR +I+G). We also used constraint analysis to test the likelihood of alternative tree topologies for the monophyly of New Zealand taxa and the genus *Hetiana* (New Zealand and Australia).

(d) Divergence estimates

We compared the likelihood scores obtained from ML analysis both with and without the implementation of a molecular clock in PAUP* for dataset II (18S Australasia) and dataset IV (COI–RY-coded Australasia). This was carried out both with and without the inclusion of taxa we suspected of having a rate shift due to long branches observed in initial analyses. SH tests were applied to resulting trees to determine whether there was rate heterogeneity and therefore if the data were acting in a clock-like manner to determine whether to use a strict or relaxed molecular clock in BEAST v. 1.4.6 (Drummond & Rambaut 2007).

As there are no suitable fossils for molecular dating, we used geological events as points of reference to test the plausibility of vicariant versus dispersal explanations for the New Zealand weta diversification (figure 1*a*). In order to explicitly examine the alternative hypotheses for patterns of diversity, we calibrated trees using initial separation of Zealandia from Gondwana (less than 82 Ma as applied by avian evolutionists, see Ericson *et al.* 2002; Baker *et al.* 2005) and emergence of New Caledonian (less than 40 Ma). The two dating constraints were separately applied to the nuclear dataset II (18S Australasia) and mitochondrial dataset IV (COI–RY-coded Australasia). We removed a clade of five taxa (clade A plus New Caledonian taxa), shown by initial analyses to have long branches and a substantially elevated rate of molecular evolution (indicated by BEAST rates). First, if Zealandia and Australia parted *ca* 82 Ma, we assumed vicariance and constrained the most basal split of Anostostomatidae to more than 82 Ma (BEAST

Ensifera (Flook *e a*. 1999; Terry & Whiting 2005; Jost & Shaw 2006). We confirm the monophyly of Anostostomatidae in our sample and found the Gryllacrididae to be sister to Anostostomatidae with Stenopelmatidae sister to the Anostostomatidae–Gryllacrididae clade. Both of these families have previously been suggested as close relatives to Anostostomatidae (figure 3).

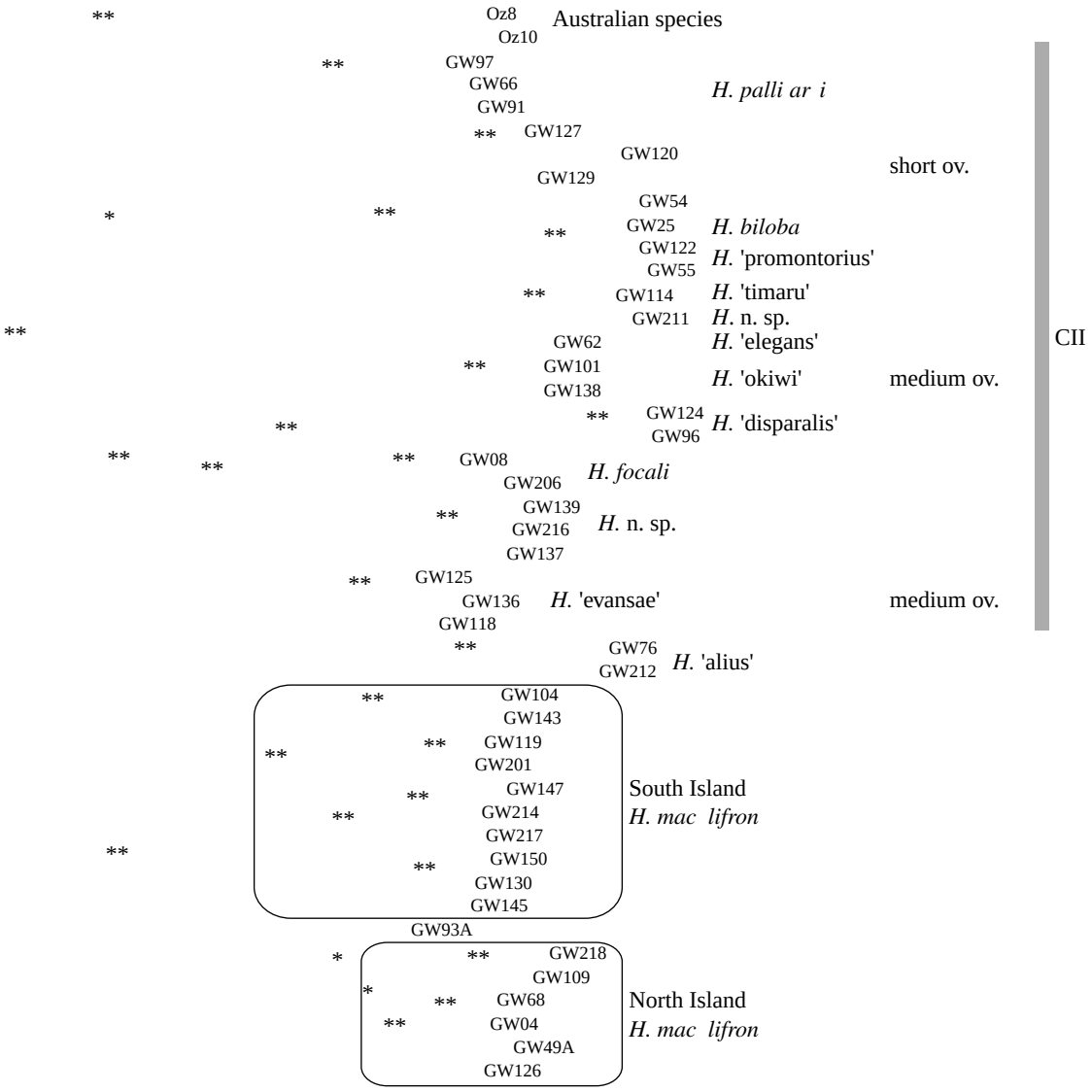
Dataset II-18S Australasian Anostostomatidae: After establishing support for monophyly of the Anostostomatidae, we turned our focus to the relationships within the family. We included more representatives from the Australasian region and a slightly shorter fragment of 18S (29 taxa, 1746 bp), again excluding the problematic indel region. Bayesian and ML analyses yielded similar topologies (figure 4). We observed that the New Zealand tusked weta (*A a/M e a*; clade A) and New Caledonian taxa (*A* and *Ca c*) formed long branches in the phylogeny. Long branches like these can result in misleading results even without rate differences (Hendy & Penny 1989) that affect all further tree selection criteria. We explored the effect of these long branches by subjecting the dataset to identical analyses with the inclusion or exclusion of either or both the

New35.2(in31;1ro)-0n3(s)-9.4(h)-42o2.8(t-1.15 TD0 T.277ole)-4.7sscl4-110 -1.1t6(can)-f27.2(as)-4dp.42o2311i -6.9(a)]

He a d ac f

nodes. This is consistent with the short branch lengths obtained at the base of the tree.

Dataset IV (COI–RY-coded Australasia; figure 5) returned three Australian clades of interest: (i) winged *T a ae* sister to the non-winged Australian *He a d* and genus B, (ii) winged *E g ac* sister to the non-winged *H c h de* and *Pe a a*, and (iii) winged *G a* sister to the non-winged *A a* and genus A. These three Australian clades were not resolved in the analysis of dataset II (18S Australasia; figure 4



diverged before the separation of Zealandia from Australia but also that dispersal has since occurred. The phylogenetic placement of *A , Ca c* and *A a/M e a* as sister to *He de a De ac da* suggests genetic exchange between New Zealand and New Caledonia after separation of Zealandia.

4. DISCUSSION

Despite comprehensive morphological studies, phylogenetic relationships within the Ensifera are poorly understood (Gwynne 1995; Whiting 2002*b*; Desutter-Grandcolas 2003). Johns (1997) removed taxa from Stenopelmatidae to form Anostostomatidae, a separation subsequently supported by molecular analyses (Jost & Shaw 2006). Although we are not concerned here with deeper Ensiferan relationships, it is important to know that our taxon set comprises a true ingroup. We found support for the monophyly of Anostostomatidae in our analysis (0.96 BPP) and for the close relationship with the Gryllacrididae and Stenopelmatidae (figure 3), supporting previous inferences (Jost & Shaw 2006; P. M. Johns 2007, personal communication). However, we did not find evidence of a sister relationship of Deinacridinae (*He de a* and *De ac da*) and Anostostomatidae (rest of the family; Johns 1997; Gorochov 2001).

For the first time, we have shown that members of the family Anostostomatidae are not monophyletic in New Zealand or Australia. To explain the phylogenetic diversity of the New Zealand weta by vicariance requires that at least four distinct clades of Anostostomatidae were already present in Gondwana before Zealandia split from Australia, and that some of these subsequently went extinct in Australia. On the face of it, this seems an unlikely scenario, given the small size and geological activity of New Zealand compared with Australia, and indeed this has been shown to be a poor explanation for the distribution of *N h fag* beech in the region (Cook & Crisp 2005*a*). Although we found some variation in node dates inferred from COI and 18S data, we have to reject the hypothesis that all

New Zealand lineages arose before continental break-up (*ca* 82 Ma). However, relaxed molecular clock calibrated phylogenies do suggest that some New Zealand clades may have formed before continental separation. These inferred early splits are consistent with a vicariant origin and survival of some Anostostomatidae lineages on Zealandia throughout the Oligocene marine transgression. Taxa missing from analyses (owing to extinction) will always result in long unbroken branches in phylogenetic trees and thus the inference of great age since common ancestors (Cook & Crisp 2005*b*) whereas recent splits (short branches) cannot be made older by the inclusion of 'missing taxa'.

Colonization of New Zealand from the Australian biota, which includes three separate winged lineages, might have been facilitated by increasing land area after the Oligocene (less than 22 Ma). Dispersal events continue today, and include the establishment of an Australian Gryllacridid in recent years (Green & Ramsay 2003). The current study suggests that the two New Caledonia genera are more closely related to one of the New Zealand lineages but not to any Australian taxa. This is despite the comparatively close physical proximity and more similar climate of New Caledonia and Queensland, Australia. Despite

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