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Phylogenetics of New Zealand's tree, giant and tusked weta (Orthoptera: Anostostomatidae): evidence from mitochondrial DNA

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Abstract

The evolutionary relationships of the New Zealand representatives of the family Anostostomatidae were examined using DNA sequence data. All species of giant weta (*Deinacrida*), tree weta (*Hemideina*) and tusked weta (*Anisoura, Motuweta*) were included in the study plus 4 taxa from the large genus of New Zealand ground weta (*Hemiandrus*). Sequence data from 2 mitochondrial genes (COI and 12S) were analysed to obtain a hypothesis of the evolution of these species. The 3 New Zealand tusked weta species formed a monophyletic clade with respect to the ground weta and to the giant and tree weta clade. We found no support for the placement of *Anisoura nicobarica* Ander within Deinacridinae as has previously been suggested. The giant and tree weta (Deinacridinae) consistently formed a monophyletic clade with respect to the tusked and ground weta. However, we found little support in our data for the reciprocal monophyly of the tree and giant weta genera. The tree weta *Hemideina broughi* (Buller) appears to be more closely related to *Deinacrida pluvialis* Gibbs and *D. talpa* Gibbs than to any other *Hemideina* species. The deinacridine radiation of leaf-eating weta comprises at least 6 comparatively ancient lineages (*Hemideina* and *Deinacrida*). Habitat-specialisation in South Island appears to have evolved in response to habitat diversification associated with Pliocene mountain building.

Key words

molecular systematics, New Zealand, phylogeography, COI, 12S, *Deinacrida, Hemideina, Motuweta*

Introduction

New Zealand has been geographically isolated from other land masses since the Cretaceous when it broke away from Gondwana. Many New Zealand endemics belong to groups with distributions restricted to the Southern Hemisphere and are assumed to be of ancient vicariant origin (*e.g.*, Onycophora, and *Nothofagus*; Stevens 1980, Cooper & Millener 1993, but see Knapp *et al.* 2005). The Anostostomatidae (Orthoptera) comprises taxa with a predominantly Southern Hemisphere (Gondwanan) distribution (Johns 1997), and the majority of species are flightless nocturnal predators that hunt on the ground and burrow to conceal themselves. The family is represented in New Zealand by 4 groups of weta: tree (*Hemideina* Walker), giant (*Deinacrida* White), ground (*Hemiandrus* Ander) and tusked weta (*Anisoura* Ander, *Motuweta* Johns). *Hemideina* and *Deinacrida* comprise most (Johns 1997) or all (Gorochov 2001) of the species of the small subfamily Deinacridinae, which are distinguished by stridulatory ridges, the musculature of their hind femur and their herbivorous diet. *Hemideina* and *Deinacrida* are closely allied, and indeed finding support for the reciprocal monophyly of the 2 genera has so far proven difficult (Morgan-Richards & Gibbs 2001). One species in particular [*H. broughi* (Buller)] shares characteristics of both genera and it has been suggested that it represents the nearest form to the deinacridine common ancestor (Field 1993, Gibbs 2001). It has been suggested that *H. broughi* might appropriately be placed in a separate genus (Field 2001). However, at least one morphological character does allow consistent diagnosis of the 2 genera as they are currently known (Gibbs 1999). The ground weta (*Hemiandrus*) and tusked weta (*Anisoura, Motuweta*) of New Zealand have a predatory diet and burrowing habit (with one exception) more typical of the family. *Hemiandrus* and *Motuweta* are placed in the tribe Anostostomatini with 13 other genera from Australia, Southern Africa, Madagascar and South America (Johns 1997).

In New Zealand, the tree weta (*Hemideina*) are the best known and most commonly encountered species because they are large, often frequent human habitats (especially in North Island), and possess impressive spines on their hind legs that are used in defensive displays. The adult males of most species of *Hemideina* have enlarged heads and mandibles (Field & Deans 2001). Most tree weta species are abundant and have wide distributions (Fig. 1). They conceal themselves by day in tree holes or, in one instance, beneath stones. The giant weta (*Deinacrida*) include some very large species. Females of the largest, *D. heteracantha* White, usually weigh over 40 g (gravid females can attain a weight of 70 g), and can reach more than 80 mm in length. All but one of the 11 species are the subject of conservation efforts, having suffered the effects of introduced mammalian predators (Gibbs 1998, Sherley 2001, McGuinness 2001). Curiously, one rare species, *D. mahoenui* Gibbs, appears to have survived extinction, gaining protection from introduced predators among the spines of the introduced plant gorse (*Ulex europeus*), browsed by introduced goats (Richards 1994, Sherley & Hayes 1993). Several species are now restricted to offshore island refuges (Fig. 1, Table 1), where mammalian predators are absent. All tree and giant weta will scavenge invertebrate food (usually dead) but they are distinctive among Anostostomatids in that they are primarily herbivores that feed on the foliage, flowers and fruit of trees and shrubs. This contrasts with, for example, the weta fauna of Australia, most of which forage on the forest floor, eating decaying material, or are predatory (Monteith & Field 2001).

The prehuman distribution of some weta, and in particular now rare species of *Deinacrida*, was very probably wider than that observed today. Early collections of weta indicate that *D. heteracantha*, which is now restricted to one offshore island, once occurred throughout North Island (Watt 1963), and *D. rugosa* Buller which is now restricted to 3 islands in Cook Strait was found in southern North Island (Fig. 1B). Together with the disjunct distribution of *D. elegans* Gibbs in South Island, and the presence of *D. carinata* Salmon

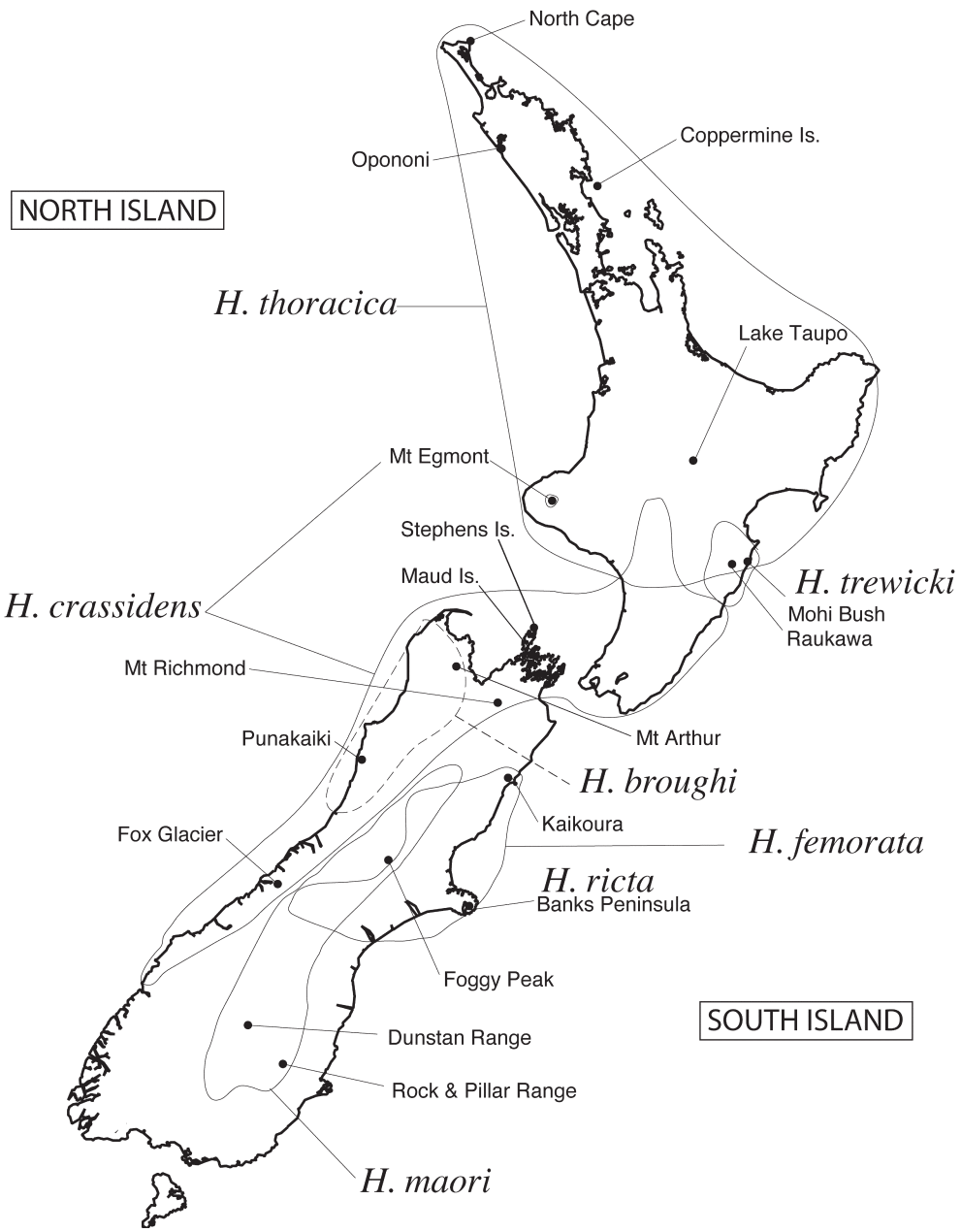

Fig. 1A. Distribution and sampling locations in New Zealand of tree weta species, *Hemideina*, used in this study.

on islands in Foveaux Strait and *Hemideina crassidens* (Blanchard) in Cook Strait, these early records indicate once broader distributions of these species, consistent with previous land connections during the Pleistocene.

Although the tusked weta group comprises just 3 species, their classification is unresolved. They are united by the presence in males of prominent, curved tusks protruding from the mandibles. Salmon (1950) placed the smallest (~21 mm long), and at that time, only species, with the ground weta as *Hemiandrus monstrosus*. However, unlike the ground weta, all 3 tusked weta have auditory pits on fore tibiae. Johns (1997) placed the small tusked weta with the Deinacridinae (*i.e.*, tree and giant weta), and renamed it, by precedent, *Anisoura nicobarica*. However, the species does not occur in the Nicobar Islands (in the Bay of Bengal) and the origin of the type specimen appears to have been incorrectly recorded. The largest species of New Zealand tusked weta, *Motuweta islolata* Johns (~65 mm), discovered in 1975, was placed in the much larger subfamily, Anostostomatinae (Johns 1997). Gorochov (2001) accepted *Motuweta* in Anostostomatinae but considered that the placement of *Anisoura* and *Hemiandrus* (ground weta) was unclear. The most recently discovered and described species, *Motuweta riparia* Gibbs (2002), shares diagnostic features with *M. isolata*, but the 3 species are morphologically well differentiated. The tusked weta are predators, the larger species (*Motuweta*) being active mostly on the ground, and sheltering in burrows, while *Anisoura* is active in trees

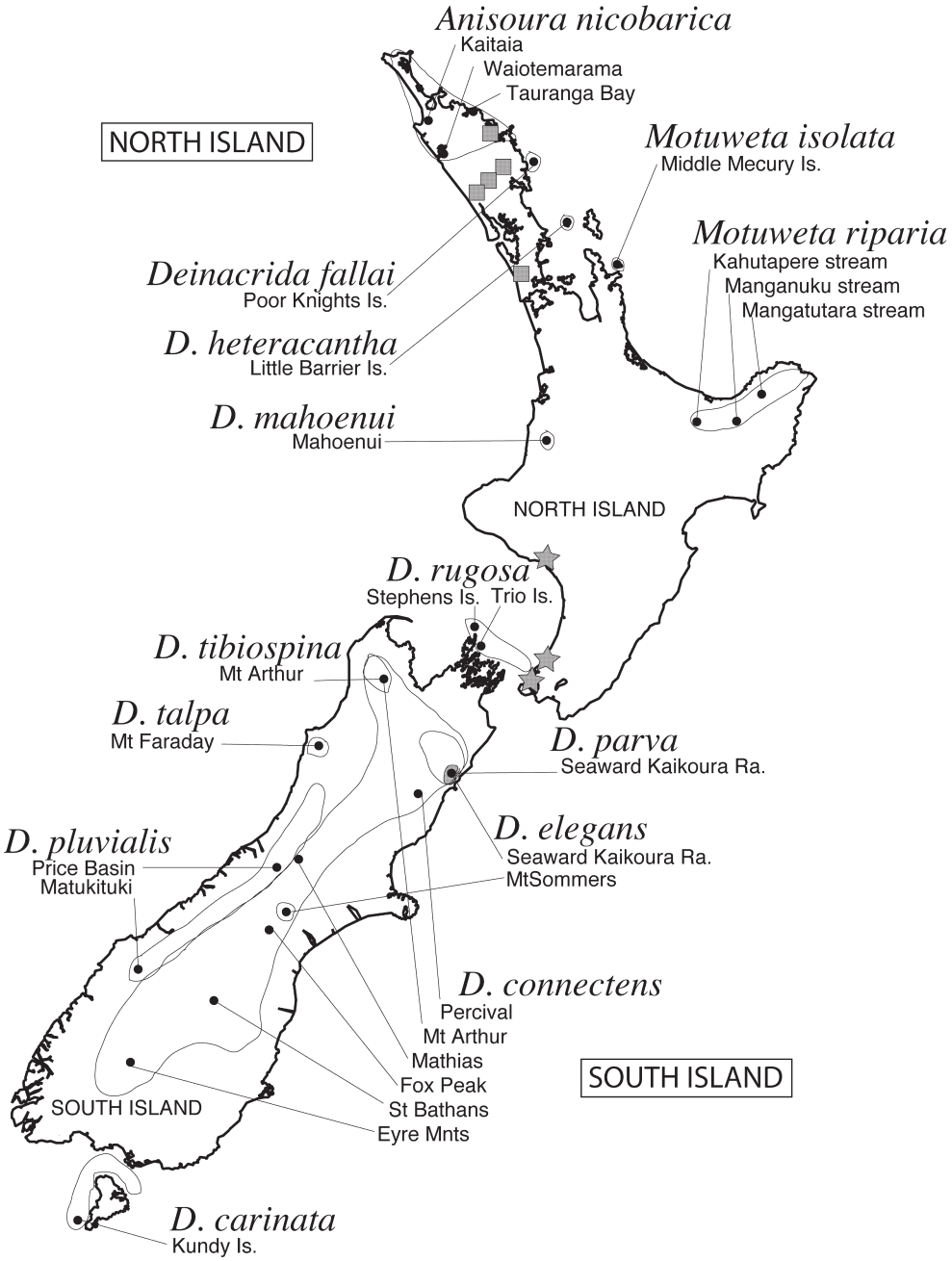

Fig 1B. Distribution and sampling locations in New Zealand of Giant weta, *Deinacrida* and tusked weta. The locations of early records of *D. heteracantha* and *D. rugosa* are indicated by grey squares and grey stars respectively.

and shrubs and occupies tree holes. All ground weta are terrestrial predators and shelter in burrows.

We used mitochondrial DNA sequences from 3 prominent groups of New Zealand weta. Our phylogenetic analyses utilise data from previously published studies that explored within-species phylogeography, supplemented by data from the taxa not previously studied. We address the issue of the monophyly of the tree, giant and tusked weta.

Methods and Materials

Sampling—. We sampled all species of tree (*Hemideina*; 7 species), giant (*Deinacrida*; 11 species) and tusked weta (*Anisoura*, *Motuweta*; 3 species), plus representative ground weta (*Hemiandrus*) for comparison. The *Hemiandrus* sample consisted of both distinct ovipositor forms; *H. focalis*, *H. maculifrons* (long ovipositor) and 2 undescribed species from Haast (long) and Dunedin (short ovipositor; Johns 2001). A number of species have been sampled fairly extensively throughout their respective ranges, and their population genetics reported in detail (Trewick *et al.* 2000, Morgan-Richards *et al.* 2001, Morgan-Richards 2002, Trewick 2001, King *et al.* 2003). For the present study we obtained data from individuals of the remaining *Hemideina* and *Deinacrida* and tusked species, utilising, wherever possible, specimens collected for studies of morphology, allozymes and cytogenetics (Morgan-Richards 1995, Morgan-Richards & Townsend 1995, Cameron 1996, Gibbs 1999,

Morgan-Richards & Gibbs 1996, Morgan-Richards & Gibbs 2001, Trewick & Wallis 2001, Morgan-Richards 2002). Other taxa were collected in the field during the course of the present study, or were provided to us by researchers engaged in ecological studies (including captive rearing) of the rare species. Sample sizes are, for the most part, small, reflecting the rarity and conservation status of many of the species and include type material for recently described species. Where possible we obtained specimens and data from several individuals to provide an indication of minimum within-species genetic diversity across geographical ranges, but this was not a priority of the study. In all instances, appropriate authority to collect and use specimens was obtained from the New Zealand Department of Conservation. Most specimens, and in particular those of the rare species have been the subject of several different studies and have thus been efficiently employed (References in Table 1).

Molecular methods.— Specimens were anaesthetised by chilling and preserved by freezing or in 95% ethanol. Muscle tissue from fresh, frozen or alcohol-preserved specimens was removed from hind femora or other leg elements for DNA extraction. Whole genomic DNA was extracted using a salting-out method (Sunnucks & Hale 1996). Tissue was macerated and incubated with 5 µL of 10 mg/mL proteinase-K in 600 µL of TNES buffer (20 mM EDTA, 50 mM Tris, 400 mM NaCl, 0.5% SDS) at 50°C for 1 to 4 h. Ten percent 5 M NaCl was added and the extractions shaken vigorously for 60 s followed by spinning at 14,000 rpm for 5 min. The supernatant was removed and precipitated with an equal volume of cold 100% ethanol. DNA was collected by spinning and washed with 70% ethanol, then dried and dissolved in water.

Molecular analysis used mitochondrial DNA sequences obtained using primers that target part of cytochrome oxidase I (COI) and the third domain of the small ribosomal subunit (12S). Both of these gene fragments have been widely used in phylogenetic studies of invertebrates.

PCR (polymerase chain reaction) was performed in 25 µL reactions (200 µM dNTPs, 2.5 mM $MgCl_2$, 0.25 U Qiagen Taq), treated to 40 cycles of 94°C for 15 s, 50°C for 30 s, 72°C for 90 s with an initial denaturation of 94°C for 60 s. We used primer pairs C1-J-2195 and L2-N-3014, and SR-N-14588 and LR-J-13417 (Simon *et al.* 1994) to amplify COI and 12S respectively. Amplification products were either gel-purified using Qiaquick spin columns (Qiagen) or cleaned directly using High Pure purification columns (Roche). Cycle sequencing employing primers C1-J-2195 and SR-N-14588, used Bigdye chemistry (Perkin Elmer) following the manufacturer's protocols. Sequences were aligned manually using SeqEd. v1.0.3 (ABI, PE).

One species [*H. femorata* (Hutton)] consistently yielded COI sequences with ambiguous calls indicating the presence of one or more nuclear copies (Bensasson *et al.* 2001). PCR with primers that amplify a larger fragment comprising adjacent parts of the COI and COII genes produced products of 2 sizes that were separable by gel electrophoresis. Sequencing of the product of expected size produced an unambiguous sequence that aligned appropriately with reference COI and COII genes.

Phylogenetic analysis employed neighbor-joining (NJ), maximum parsimony (MP) and maximum likelihood (ML) methods implemented by PAUP* v.4.0b10 (Swofford 1998). NJ trees were initially obtained using observed distances and compared with results produced with more complex distance estimations. MP analysis used either unweighted and unordered data or one of a range of transition/transversion weightings, and we explored the effects of weighting among codon positions for the COI data. For ML analyses, permutations of alternative nucleotide substitution and among-site rate variation models (I- invariable sites, and Γ- gamma distribution) were first assessed by comparing likelihood scores for a suite of models in order to achieve the best compromise between parameter richness and likelihood scores (Sullivan *et al.* 1997). We used either the shortest unweighted MP tree or a NJ tree as starting points for these searches and compared the resulting log likelihood scores using χ^2 tests. All ML analyses used empirical base frequencies and in ML tree searches we obtained an initial tree by stepwise addition followed by TBR branch swapping.We examined support for nodes using nonparametric bootstrapping with 1000 replications for MP and NJ searches, and 200 or 500 replications for ML searches, depending on the number of taxa involved.

Results

Our analyses utilised 52 COI and 25 12S sequences with aligned lengths of 510 and 440 bp respectively. We sequenced 64 individuals from 21 ingroup taxa and 4 outgroup *Hemiandrus* for COI, and 23 individuals of the same ingroup taxa (with each species represented once except *H. maori* Pictet & Saussure and *H. femorata*) plus 2 *Hemiandrus* for 12S. Our data therefore comprise one or more representatives of each of 11 giant weta (*Deinacrida*), 7 tree weta (*Hemideina*), 3 tusked weta (*Anisoura*, *Motuweta*), plus 4 ground weta (*Hemiandrus*). The provenance of ingroup samples is indicated in Fig. 1, with details referenced in Table 1. A combined COI/12S data set was created that comprised 25 sequences of 950 bp representing each species in our analysis.

As is typical for insects, these sequences were AT rich. The COI sequences comprised 28.5% A, 35.5% T, 19% C and 16.6% G overall, but third codon positions were the most heavily AT biased (41.6% A, 35% T, 17.8% C, 5.4% G). The set of 25 combined COI/12S sequences had a mean composition of 30.4% A, 35.6% T, 12.4% C, 21.7% G. Using χ^2 tests implemented by PAUP*, we accepted the hypothesis of base frequency homogeneity among all sequences for all sites. However, we had to reject this hypothesis for COI third codon sites alone (χ^2 =293.7, df=165, p< 0.001), and because most informative sites are at third codon positions, we had to reject the hypothesis of base homogeneity for parsimony-informative sites too (χ^2 =304.5, df=165, p<0.001). We also found that for the combined COI/12S data set, including all taxa and all sites, we could accept the hypothesis of base homogeneity (χ^2 =42.3, df=72, p>0.05), although this was not the case for informative sites only (χ^2 =142.6, df=72, p<0.0001). Comparisons of base frequencies for each sequence revealed that the tusked weta had the highest AT content. Among the tree and giant weta with these data, base composition at parsimony-informative sites was apparently less heterogeneous: COI- χ^2 =159.7, df=129, p=0.035, COI/12S χ^2 =84.55, df=57, p>0.01. Compared to other weta, *Hemideina thoracica* has the lowest AT content (58% *vs* the next lowest 62%) and the disparity is more pronounced at third codon positions (61% *vs* 70%). When *Hemideina thoracica* was excluded from our COI data, we could accept the hypothesis of base homogeneity for informative sites (χ^2 =75.3, df=117, p>0.05).

Genetic distance.—We estimated genetic diversity using observed distance, and Kimura 2 parameter (K2p) and ML GTR+I+G models. In all instances genetic distances using the same mode were higher for COI data compared to the combined COI/12S data (Table 2). In the COI data set, which comprised more individuals than the combined COI/12S data, the genetically closest pair of tree weta

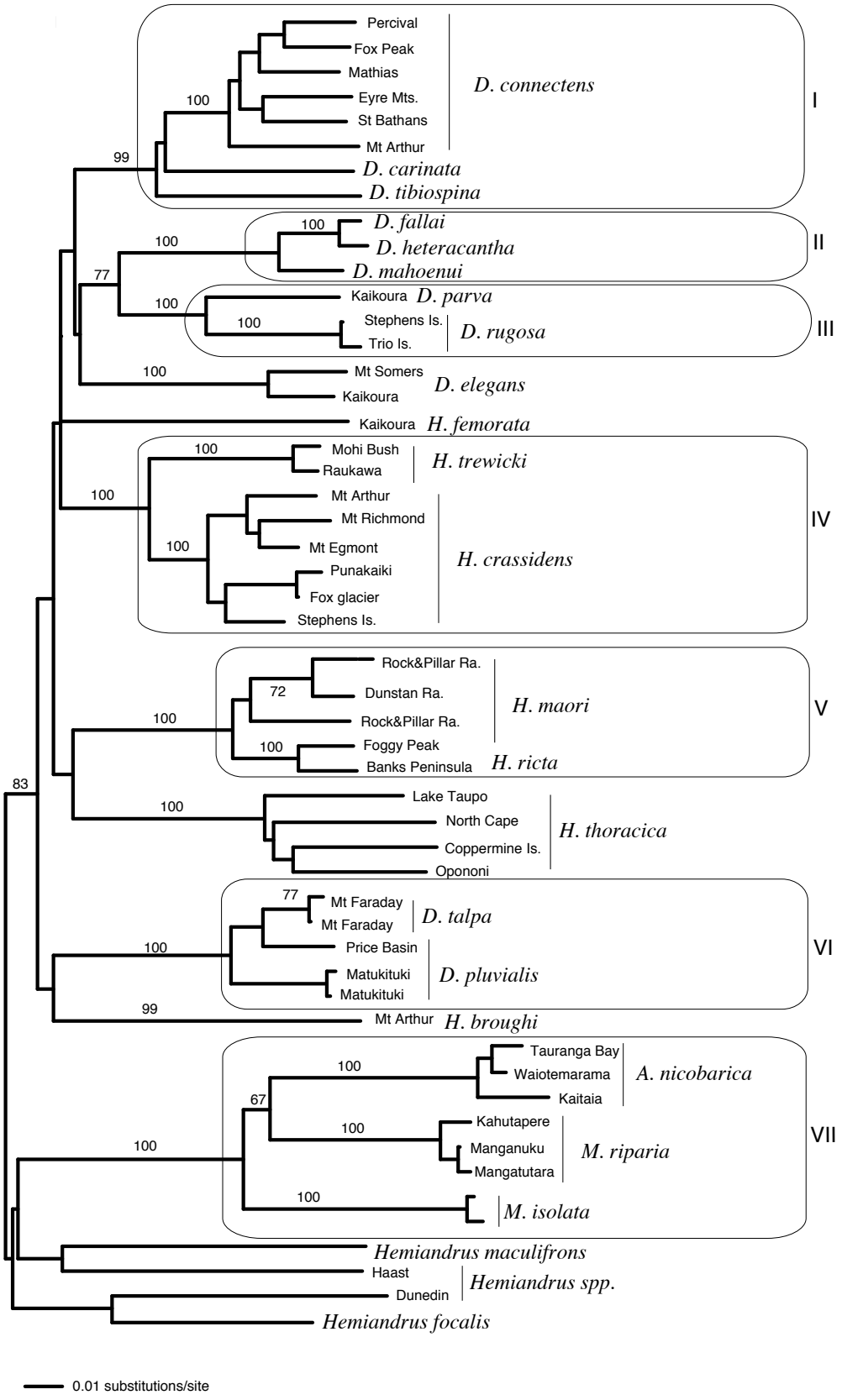

Fig. 2. Neighbor-joining tree using observed distances, comprising all individuals sequenced for COI included in the present study. Numbers above edges indicate bootstrap support using NJ (observed distance).

Table 1. Summary of ecological features of weta. Source references for details of location sampling are as follows (Source Refs.): 1 Morgan-Richards 1995; 2 Morgan-Richards *et al.* 1995, Morgan-Richards 2002; 3 Morgan-Richards & Gibbs 2001; 4 Morgan-Richards & Townsend 1995; 5 Morgan-Richards 1997, Morgan-Richards *et al.* 2001; 6 Morgan-Richards & Gibbs 1996, Trewick *et al.* 2000, Trewick 2001.

Species	Group	Region	North Island/ South Island	Altitude	Habitat	Roost	Diet	Source Refs.
H. trewicki Morgan-Richards	tree	Hawkes Bay (mideast)	NI	lowland	arboreal	in tree holes	Herbivore	1
H. crassidens (Blanchard)	tree	Southern NI, northwest SI	NI+SI	lowland	arboreal	in tree holes	Herbivore	2
H. maori *Pictet & Saussure*	tree	Southern & central	SI	sub/alpine	terrestrial	under rocks	Herbivore	3
H. ricta Hutton	tree	Bank's Peninsula	SI	lowland	arboreal	under rocks/ in tree holes	Herbivore	3, 4
H. femorata Hutton	tree	Northeastern	SI	lowland	arboreal	in tree holes	Herbivore	3
H. thoracica (White)	tree	central & north NI	NI	lowland	arboreal	in tree holes	Herbivore	5
H. broughi (Buller)	tree	Northwest South Island	SI	subalpine	arboreal	in tree holes	Herbivore	3
D. talpa Gibbs	giant	Paparoa Range	SI	subalpine	terrestrial	excavates burrows	Herbivore	3
D. pluvialis Gibbs	giant	West coast mountains	SI	subalpine	terrestrial	under stones	Herbivore	3
D. connectens Ander	giant	Southern Alps	SI	alpine	terrestrial	lives in scree	Herbivore	6
D. tibiospina Salmon	giant	Nelson area	SI	subalpine	terrestrial	in vegetation.	Herbivore	3
D. carinata Salmon	giant	Foveaux Strait islands	SI	lowland	terrestrial	in vegetation	Herbivore	
D. heteracantha White	giant	Little Barrier Island	NI	lowland	arboreal	in vegetation	Herbivore	3
D. mahoenui Gibbs	giant	Mahoenui (midwest)	NI	lowland	arboreal	in vegetation	Herbivore	3
D. fallai Salmon	giant	Poor Kniqhts Islands	NI	lowland	arboreal	in vegetation	Herbivore	3
D. parva Buller	giant	Seaward Kaikoura Ra.	SI	subalpine	terrestrial	in vegetation/ under rocks	Herbivore	3
D. rugosa Buller	giant	Cook Strait islands	between	lowland	terrestrial	in vegetation	Herbivore	3
D. elegans Gibbs	giant	Central and northeast (disjunct)	SI	subalpine	terrestrial	rock crevices	Herbivore	3
Anisoura nicobarica Ander	tusk	Northland	NI	lowland	terrestrial	excavates burrows	Predator	
Motuweta isolata Johns	tusk	Middle Mercury Is.	NI	lowland	terrestrial	excavates burrows	Predator	
M.riparia Gibbs	tusk	Northeast	NI	lowland	arboreal	in tree holes	Predator	

(*H. ricta* Hutton and Foggy Peak *H. maori*), and giant weta (*D. heteracantha* and *D. fallai* Salmon) had observed distances of 0.031 and 0.014 respectively. Within species K2p distances for COI were highest (0.097) in *H. thoracica* (White). Haplotypes representing the 2 disjunct populations of *D. elegans* (Fig. 1.) differed by 0.039.

Kimura 2 parameter (K2p) distances between combined COI/12S species haplotypes reached 0.19 ($\bar{x}$ = 0.14) between tree and giant weta species (*H. thoracica* and *H. broughi*), and had a maximum of 0.25 ($\bar{x}$ = 0.22) in comparisons of tusked weta and tree/giant weta (Table 2). K2p distance among the tusked weta species averaged 0.11. Estimates using methods that incorporate more complex nucleotide substitution and among site-variation models were, as expected, much higher. For example GTR+I+G distance among tree and giant weta reached 0.27, and between tree/giant and tusked weta 0.72 (Table 2).

Phylogenetic relationships.— All NJ and MP analyses of our total COI data set resulted in trees with similar topologies, irrespective of substitution model and character weighting used (Fig. 2). The 3 tusked weta species (*Motuweta isolata*, *M. riparia*, *Anisoura nicobarica*) always formed a monophyletic group, with ground weta (*Hemiandrus*) basal to these (see below). Similarly, the tree and giant weta formed a monophyletic group with respect to the tusked weta (*Motuweta* and *Anisoura*) and ground weta (*Hemiandrus*). The ground weta with long ovipositors were not monophyletic with respect to the single short-ovipositor species sampled.

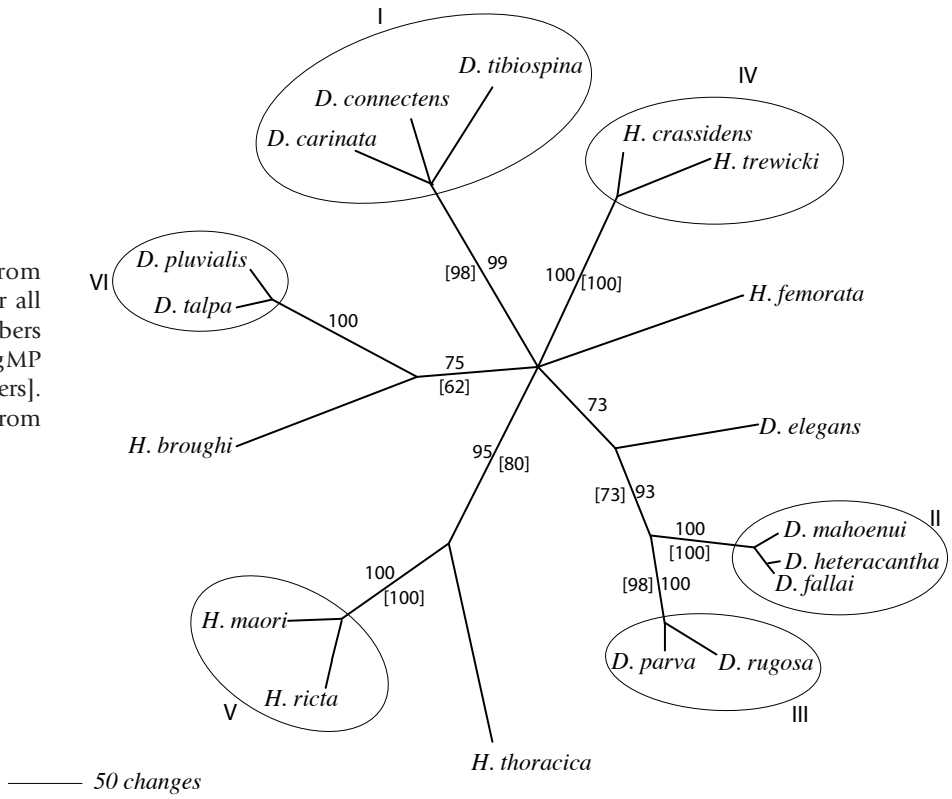

Fig. 3. Maximum parsimony tree from COI/12S, using Tv:Ti 5:1 weighting for all *Deinacrida* and *Hemideina* species. Numbers on edges indicate bootstrap support using MP with Tv:Ti 5:1 and [unordered characters]. Clades (in ellipses) and clade labels from Fig. 2 are shown.

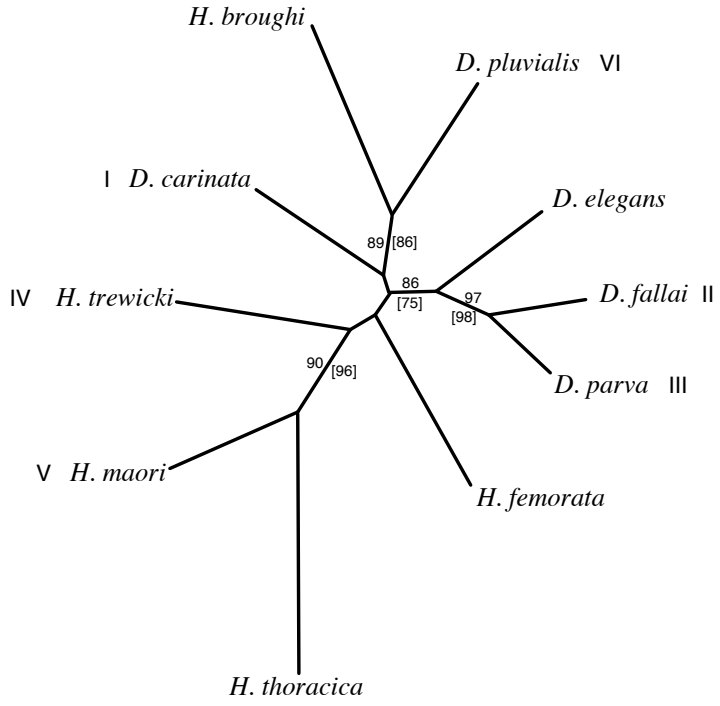

Fig. 4. Maximum likelihood tree from COI/12S data using GTR+I+Γ for species representative of *Deinacrida* and *Hemideina* clades/lineages. Clade labels from Fig. 2 are shown. Numbers on edges indicate bootstrap support under ML GTR+I+Γ model and [MP with Tv:Ti 5:1].

Table 2. Summary of genetic diversity among New Zealand tree, giant and tusked weta based on COI and combined COI/12S mtDNA sequence data. Above the diagonal are pairwise genetic distances calculated using GTR+I+G and combined COI/12S; below the diagonal are Kimura 2 parameter distances (combined COI and 12S, and the COI alone in the left and right, respectively, of each column).

		H. tre	*H. cras*	*H. mao*	*H. ric*	*H. fem*	*H. tho*	*H. bro*	*D. tal*	*D. plu*
MOHI522	*H. trewicki*		0.07	0.27	0.32	0.28	0.37	0.32	0.29	0.30
SI55	*H. crassidens*	0.06/0.09	IV	0.26	0.30	0.26	0.34	0.29	0.26	0.27
DUN1	*H. maori*	0.14/0.17	0.14/0.16		0.06	0.31	0.28	0.33	0.34	0.35
HR320	*H. ricta*	0.16/0.18	0.15/0.17	0.05/0.07	V	0.32	0.29	0.36	0.31	0.33
Hf181	*H. femorato*	0.14/0.17	0.14/0.17	0.15/0.18	0.16/0.18		0.43	0.36	0.33	0.32
TA440	*H. thoracica*	0.17/0.19	0.16/0.18	0.16/0.19	0.15/0.18	0.18/0.22		0.45	0.37	0.36
HB254	*H. broughi*	0.16/0.19	0.15/0.18	0.16/0.18	0.17/0.19	0.17/0.20	0.19/0.24		0.26	0.27
PAP822	*D. talpa*	0.14/0.17	0.13/0.15	0.16/0.21	0.15/0.19	0.15/0.19	0.17/0.21	0.14/0.18		0.05
MTK844	*D. pluvialis*	0.15/0.17	0.14/0.17	0.17/0.22	0.16/0.20	0.15/0.18	0.17/0.20	0.14/0.19	0.05/0.06	VI
TKT959	*D. connectens*	0.13/0.16	0.12/0.15	0.15/0.19	0.15/0.19	0.13/0.18	0.16/0.20	0.15/0.20	0.13/0.18	0.13/0.18
Dtib160	*D. tibiospina*	0.15/0.18	0.14/0.17	0.16/0.20	0.17/0.20	0.14/0.18	0.16/0.19	0.17/0.21	0.14/0.17	0.14/0.18
Kundy	*D. carinata*	0.15/0.19	0.12/0.15	0.15/0.18	0.16/0.19	0.13/0.18	0.16/0.18	0.15/0.19	0.15/0.19	0.15/0.20
220.00	*D. heteracantha*	0.13/0.16	0.12/0.15	0.16/0.20	0.15/0.20	0.17/0.21	0.17/0.20	0.16/0.21	0.13/0.17	0.13/0.18
DF620	*D. fallai*	0.14/0.16	0.13/0.15	0.16/0.20	0.15/0.19	0.16/0.20	0.17/0.20	0.16/0.20	0.13/0.17	0.14/0.18
180	*D. mahoenui*	0.13/0.16	0.12/0.15	0.15/0.18	0.15/0.18	0.15/0.18	0.17/0.20	0.16/0.20	0.13/0.17	0.14/0.18
DP15	*D. parva*	0.14/0.17	0.12/0.15	0.14/0.17	0.13/0.16	0.14/0.18	0.16/0.19	0.16/0.21	0.13/0.17	0.14/0.18
DR29	*D. rugosa*	0.13/0.17	0.13/0.16	0.15/0.20	0.15/0.18	0.14/0.17	0.17/0.22	0.16/0.20	0.14/0.17	0.14/0.18
SO611	*D. elegans*	0.14/0.16	0.12/0.15	0.16/0.18	0.16/0.20	0.14/0.17	0.16/0.19	0.16/0.20	0.16/0.23	0.14/0.19
NTW300	*A. nicobarica*	0.23/0.28	0.22/0.26	0.23/0.30	0.22/0.28	0.22/0.27	0.25/0.31	0.24/0.30	0.22/0.29	0.22/0.27
RTW100	*M. riparia*	0.21/0.23	0.20/0.24	0.23/0.26	0.22/0.25	0.21/0.25	0.24/0.29	0.23/0.27	0.21/0.25	0.21/0.26
MI100	*M. isolata*	0.22/0.25	0.21/0.24	0.22/0.26	0.21/0.25	0.22/0.28	0.21/0.25	0.23/0.26	0.22/0.27	0.22/0.27

Haplotypes from individuals of the same species formed monophyletic clades, with the exception of 2 instances of paraphyly. As previously reported, *Deinacrida pluvialis* sampled from 2 sites was paraphyletic with respect to *D. talpa* (Trewick & Wallis 2001), and *Hemideina maori* was paraphyletic with respect to *H. ricta* (King *et al.* 2003). In constrast, *Deinacrida parva*, which is sometimes regarded as a population of *D. rugosa*, was well differentiated based on mtDNA sequence (Fig. 2).

Although *Hemideina* and *Deinacrida* were not reciprocally monophyletic, several species associations were evident and supported in all our analyses: Clade I- *Deinacrida tibiospina* Salmon, *D. carinata* Salmon and *D. connectens* Ander; II- *D. fallai*, *D. heteracantha* and *D. mahoenui*; III- *D. rugosa* and *D. parva* Buller; IV- *H. crassidens* and *H. trewicki* Morgan-Richards; V- *H. maori* and *H. ricta;* VI- *D. talpa* Gibbs and *D. pluvialis* Gibbs (Fig. 2). These same groupings were found in our analysis of the 12S data, although we additionally found support for nodes grouping clades II and III (MP bootstrap support with unweighted and Tv:Ti weighted 5:1 were 71% and 78% respectively), and for clade V with *H. thoracica* (69% and 75% respectively; not shown).

For a subset of weta representing all tree, giant and tusked weta, plus 2 ground weta, we combined COI and 12S data for further analysis in an attempt to resolve deeper level relationships. Analysis of 25 sequences (of 950 bp) using NJ and MP, supported our findings from separate analysis of COI and 12S. We subsequently divided this data set into 2 parts comprising the tree and giant weta, and the tusked and ground weta. We attempted to resolve the relationships among the 3 tusked weta species using MP and ML searches with a range of substitution and rate variation models. MP bootstrapping gave negligible support breaking the trichotomy, although a single shortest tree (unordered and 5:1 Tv:Ti) grouped the 2 *Motuweta* species *vs A. nicobarica*. However, the MP tree with unordered characters with this topology was just one step shorter than the tree grouping *M. riparia* with *Anisoura nicobarica*. Most ML analyses produced similarly equivocal results. For instance, ML bootstrap analysis under the HKY model gave just 51% support to the grouping of *M. riparia* with *Anisoura nicobarica*, although under the GTR+I+ this support was elevated to 93% (not shown). Conservatively, although there appears to be insufficient signal to break the trichotomy, there is also no support for *A. nicobarica* as sister to *Motuweta*.

With the combined COI/12S data for the tree and giant weta group reduced to one representative per species, all analyses resulted in polyphyletic trees as before (Fig. 3). We found support for a clade comprising *H. broughi* and Clade VI (*D. talpa*, *D. pluvialis*), which had been indicated in other trees (*e.g.*, Fig. 2). We also found support for the grouping of *D. elegans*, and the northern *Deinacrida* of clades II and III in MP analysis using a Tv:Ti weighting of 5:1. We examined the effect of constraining tree topology to make tree and giant weta monophyletic using MP. In all cases constrained trees were longer than unconstrained trees. For instance, with unordered characters using 18 taxa, MP yielded one tree of length 898; constraining the search to make *Hemideina* monophyletic resulted in 2 trees of 907 steps. However, constraining the search to keep *Hemideina*, except *H. broughi*, monophyletic, resulted in a single tree 6 steps shorter (901; mean random tree length 1240).

We further reduced the size of the COI/12S data set by including only a single representative of each clade supported in other analy-

Table 2. continued.

D. con	*D. tib*	*D. car*	*D. het*	*D. fal*	*D. mah*	*D. par*	*D. rug*	*D. ele*	*A. nic*	*M.rip*	*M. iso*
0.26	0.31	0.31	0.26	0.27	0.26	0.26	0.26	0.26	0.78	0.67	0.71
0.21	0.27	0.23	0.23	0.24	0.23	0.22	0.23	0.21	0.73	0.61	0.65
0.29	0.36	0.31	0.33	0.32	0.31	0.28	0.31	0.33	0.77	0.77	0.68
0.32	0.38	0.33	0.31	0.31	0.30	0.26	0.29	0.34	0.71	0.70	0.63
0.25	0.27	0.26	0.35	0.35	0.31	0.29	0.28	0.27	0.74	0.71	0.70
0.36	0.37	0.34	0.37	0.38	0.39	0.35	0.39	0.35	0.89	0.80	0.68
0.31	0.37	0.31	0.34	0.33	0.33	0.34	0.32	0.32	0.89	0.80	0.78
0.25	0.29	0.30	0.24	0.25	0.25	0.27	0.28	0.32	0.79	0.66	0.70
0.26	0.30	0.31	0.25	0.27	0.27	0.28	0.30	0.28	0.77	0.65	0.72
	0.10	0.08	0.27	0.27	0.26	0.23	0.21	0.25	0.71	0.68	0.67
0.08/0.12		0.11	0.31	0.31	0.30	0.25	0.26	0.28	0.79	0.73	0.78
0.06/0.10	0.08/0.13	I	0.28	0.28	0.26	0.23	0.24	0.26	0.79	0.72	0.74
0.14/0.20	0.14/0.18	0.14/0.19		0.02	0.03	0.15	0.14	0.21	0.72	0.72	0.69
0.14/0.19	0.14/0.18	0.14/0.18	0.01/0.01		0.03	0.14	0.14	0.20	0.74	0.73	0.71
0.13/0.19	0.14/0.18	0.14/0.17	0.03/0.04	0.03/0.04	II	0.13	0.14	0.20	0.71	0.72	0.67
0.12/0.17	0.13/0.16	0.12/0.16	0.10/0.15	0.10/0.14	0.09/0.14		0.06	0.20	0.66	0.65	0.66
0.12/0.16	0.13/0.17	0.12/0.16	0.09/0.13	0.09/0.13	0.09/0.14	0.05/0.08	III	0.20	0.67	0.70	0.71
0.13/0.18	0.14/0.17	0.13/0.17	0.12/0.17	0.12/0.16	0.12/0.16	0.12/0.17	0.12/0.16		0.76	0.70	0.70
0.22/0.29	0.22/0.28	0.23/0.29	0.22/0.29	0.22/0.29	0.22/0.28	0.20/0.27	0.20/0.28	0.22/0.28		0.18	0.22
0.22/0.27	0.22/0.26	0.22/0.25	0.21/0.28	0.22/0.28	0.21/0.28	0.20/0.24	0.20/0.25	0.21/0.26	0.11/0.14		0.16
0.22/0.27	0.23/0.28	0.22/0.26	0.22/0.29	0.22/0.29	0.22/0.29	0.21/0.27	0.22/0.28	0.22/0.27	0.12/0.17	0.10/0.13	VII

ses. This resulted in a set of 10 taxa (5 *Hemideina* and 5 *Deinacrida*). Tree searches using these data with NJ, MP and ML returned similar topologies. Nonparametrc bootstrapping with MP (Tv:Ti 5:1), NJ (pdistance, K2p, LogDet) and ML (HKY, GTR+I+Γ) all yielded support for the same 4 nodes within this topology and resolution of 3 clades (*H. broughi* with *D. talpa*; *D. elegans* with *D. fallai* and *D. parva; H. thoracica* with *H. maori*). Internal edges between these clades were short, implying little signal at this level (Fig. 4).

Discussion

Tusked weta.— We found consistent support in our data for a monophyletic group comprising the 3 species of New Zealand tusked weta. Our data indicated that the smallest species (*Anisoura nicobarica*) is not closer to the Deinacridinae (*Hemideina* and *Deinacrida*), as suggested by Johns (1997), than the other tusked weta (*Motuweta*). Nor is there evidence that *A. nicobarica* is nearer the ground weta (*Hemiandrus*) as initially suggested (Salmon 1950). Genetic distances among the 3 tusked weta species are similar to those among species in 2 of the giant weta clades, but interclade distances between the tusked weta and all other taxa in the analysis are high. We were unable to resolve the relationships among the 3 tusked weta species further, primarily because there is no sufficiently close outgroup among the New Zealand taxa studied. It is possible that a closer living relative exists among the weta faunas of neighboring Australia or New Caledonia.

Despite substantial differences in size and a number of other morphological characteristics, it appears that mandibular tusks of these species are indeed synapomorphic. On the available phylogenetic evidence and similarity of the male secondary sexual head structures (tusks), we feel placement of the 3 tusked weta in a single genus would more accurately describe their relationships. Although the tusks of these weta are structurally similar, their phylogenetic significance has in the past been de-emphasised because a number of anostostomatid genera appear to have independently evolved similar (but distinct) secondary sexual head structures in males (Johns 1997, Field & Deans 2001). In addition, other morphological characters, in particular the muscle insertion pattern of the hind femora in *A. nicobarica*, appear to be inconsistent with monophyly (Johns 1997). The association of the Nicobar Islands with the monotypic genus *Anisoura* is apparently the result of mislabelling of an early specimen described by Ander in 1938 and attributed to the Nicobar Islands (see Johns 1997). We feel placement of *A. nicobarica* in *Motuweta* as *M. monstrosus* (Salmon 1950) would better reflect the provenance of this and its sister species to New Zealand. However, such a move would require the approval of the International Commission on Zoological Nomenclature as the *Anisoura nicobarica* couplet, although misleading, has priority.

Tree and giant weta.— In our analyses, the tree and giant weta are monophyletic with respect to the ground and tusked weta, and are genetically diverse. This is consistent with many morphological and behavioral traits. Similarly, 6 clades (I-VI) revealed in our analyses of COI sequence data are consistent with those indicated by allozyme and morphological evidence (Morgan-Richards & Gibbs 2001, Field 2001). The combined morphological and allozyme

character analyses supported a bipartition separating *Deinacrida* from *Hemideina* (minus *H. broughi;* Morgan-Richards & Gibbs 2001). However, the majority of the 25 morphological traits studied were not diagnostic for either genus. We did not find support for the reciprocal monophyly of the tree and giant weta with the present data. This is interesting because in terms of morphology and ecology the tree weta (*Hemideina*) form a homogenous group with little variation among species (with the exception of *H. broughi*), and so we expected their mtDNA to form a monophyletic group too. With the exception of *H. maori*, which shows distinctive ecological features associated with alpine habitat, the group comprises generalist, arboreal, allopatric species.

Resolution of *Hemideina* relationships was poor. Three species pairings were revealed, and 2 of these (*H. crassidens* with *H. trewicki*, and *H. maori* with *H. ricta*) are consistent with evidence from morphology and allozymes (Morgan-Richards & Gibbs 2001). *H. maori* is paraphyletic with respect to *H. ricta* which, on the basis of mtDNA sequence, is a very recent isolate of the more widespread species (King *et al*. 2003). It is interesting to note therefore, that *H. maori* is, among tree weta, unusual in seeking refuge beneath rocks (trees being absent in its subalpine habitat). The use of tree holes as well as rocks by *H. ricta* appears to be a reversal to the ancestral state. Inconsistency in the placement of *H. thoracica* with respect to *H. maori*, *ie.*, tree weta not forming southern and northern clades as indicated by morphological and allozyme evidence (Morgan-Richards & Gibbs 2001), could represent a true discordance of the mitochondrial gene tree and the organismal tree, due perhaps, to introgression. Alternatively, the unusual AT:GC ratio of *H. thoracica* may be misleading the analysis, and this is the subject of ongoing research.

Paraphyly was also detected in the west coast giant weta where *D. pluvialis* is paraphyletic with respect to *D. talpa*. *Deinacrida talpa* is restricted to the Paparoa Ranges while *D. pluvialis* enjoys a much larger range on the wet western flanks of the Southern Alps (Fig. 1B). The soil of the Paparoa Ranges is distinctive and *D. talpa* shelters in burrows in this soil, unlike *D. pluvialis* which hides under rocks (Gibbs 1999). From our small samples it appears that there is more diversity within *D. pluvialis* than within *D. talpa*, such that the northern populations of *D. pluvialis* are genetically more similar to *D. talpa* than to southern populations of *D. pluvialis*, a common pattern seen in recently evolved species complexes (Patton & Smith 1994). In this instance natural selection appears to have rapidly produced an ecologically and morphologically distinct species with little change to mtDNA sequence, although an alternative possibility is that there has been mitochondrial introgression from *D. pluvialis* to *D. talpa*.

In some instances pairwise genetic distances between species (*e.g.*, *D. heteracantha* and *D. mahoenui*) are lower than genetic distances within other species (*e.g.*, *D. connectens*, *H. crassidens* and *H. thoracica*). The level of genetic diversity detected within these wide ranging species is high compared to studies of northern hemisphere invertebrates using this gene region, possibly due to the very different impact of Pleistocene glaciation in the north compared to the south (Trewick *et al*. 2000, Trewick & Wallis 2001). This aside, the observation that some species can be genetically more similar to each other than are populations of a different species, simply reflects the much less clock-like nature of morphological evolution compared to molecular evolution and the independence of the 2 markers (Wilson *et al*. 1977).

In contrast to the tree weta, the giant weta (*Deinacrida*) comprise a diverse group with 7 of the 11 species in South Island. The geographic bias in diversity reflects a dichotomy between the arboreal species that predominate in North Island (which are in this respect similar to the tree weta), and the habitat-specialised taxa of montane South Island. Species in the south seem to be substrate adapted for concealment although their diet remains that of the generalist herbivore. Within *Deinacrida*, the speciose clade (*D. elegans*, *D. rugosa*, *D. parva*, *D. mahoenui*, *D. fallai*, *D. heteracantha*) spanning North and South islands, supported by the present mtDNA data, was also apparent in a combined analysis of allozyme and morphological characters (Morgan-Richards & Gibbs 2001).

We found signal in our data indicating a close association of the aberrant tree weta *H. broughi* and *Deinacrida* species (Figs 3 & 4), and this is consistent with at least some morphological characteristics. For example, most tree weta (*Hemideina*) show secondary sexual dimorphism, with males having enlarged heads and mandibles (as in some other genera of the Anostostomatidae, Field & Deans 2001). *Hemideina broughi* males do not have enlarged heads and in this respect the species is more like *Deinacrida*. Similarly, *H. broughi* does not possess abdominal stridulatory ridges, whereas all other tree weta have ridges, but 3 *Deinacrida* species do not (Morgan-Richards & Gibbs 2001). Such inconsistencies have long been recognized, and the species has been referred to as the stem species of living Deinacridinae (Field 1993, Gibbs 2001, Morgan-Richards & Gibbs 2001). Our DNA sequence data suggest *H. broughi* is sister to the 2, geographically neighboring, western alpine *Deinacrida (D. pluvialis* and *D. talpa*). The morphological characters that unite these 3 species are similarity of body shape and color and details of their leg spines and genitalia, such as the male paranal apical-process tooth. These characters may have been considered shared ancestral traits, in the past, rather than synapomorphies. Our results could be interpreted to suggest changes be made to the current classification: for example mtDNA monophyletic clades could be given separate generic status, or *broughi* moved (back) into the genus *Deinacrida*. However, the lack of resolution at the base of the Deinacridinae clade would mean that reciprocal monophyly was not assured for all of the 6 clades/genera. Therefore, a reduction to a single genus would be a more logical conclusion based on our molecular data. On the other hand, morphological and ecolological data support *Hemideina* (without *broughi*) as a monophyletic group and we feel there would be a loss of information should this genus be consumed.

Further resolution of the relationships of these tree and giant weta taxa might be achieved using data from more slowly evolving genes and/or longer sequences, but our analyses might also indicate a rapid radiation of lineages, as implied by the inconsistency of morphological and genetic characters. The only New Zealand taxa available as outgroups (ground and tusked weta) do not help resolve relationships among the tree and giant weta. The 6 principal lineages indicated in our analyses (*H. broughi* and clade VI (*D. talpa, D. pluvialis*); *D. elegans* and clades II (*D. fallai, D. heteracantha, D. mahoenui*) and III (*D. rugosa, D. parva*); *H. femorata; H. thoracica* and clade V (*H. maori, H. ricta*); clade I (*D. connectens, D. carinata, D. tibiospina*); clade IV (*H. trewicki, H. crassidens*), may represent the initial products of this radiation. The extent of genetic diversity among species indicates that the primary radiation is ancient. Phylogeographic data from *D. connectens* (Trewick *et al.* 2000) and *H. thoracica* (Morgan-Richards *et al.* 2001) correlate with mountain

building in South Island and the formation of an archipelago in North Island during the Pliocene (7-2 mya). This indicates that the majority of speciation in *Deinacrida* took place in the Pliocene or earlier, and that radiation of the Deinacridinae probably dates from the Miocene. From this we can infer that separation of the ground weta, tusked weta and the Deinacridinae is older still, and may indeed date to before the isolation of New Zealand.

The Deinacridinae (*Hemideina* and *Deinacrida*) are unusual in the Anostostomatidae in that they feed primarily on the leaves of trees and shrubs. While the taxonomic distinctiveness of New Zealand is well documented, the ecological and evolutionary implications of this are less well understood (Daugherty *et al*. 1993). For instance, the Deinacridinae have been referred to as the New Zealand invertebrate equivalent of rodents, even "invertebrate mice" (Fleming 1977, Ramsay 1978). The characteristics used to justify this analogy are nocturnal foraging, use of daytime refuges (linked traits), polygamy and large droppings, and they are said to "fill the niches of mice and rats" (Daugherty *et al.* 1993). While this characterisation is catchy, it is superficial and conceals much of the ecological and evolutionary distinctiveness of the group. The "invertebrate mouse" analogy would be positive if it led to research into the diet and role of weta as fruit and seed eaters, seeds being an important component of the diet of many rodents.

Morphological, behavioral, allozyme and mtDNA data reveal that, with the tusked and ground weta, the Deinacridinae constitute an ancient and complex radiation of the endemic New Zealand biota, without parallel among the extant vertebrate fauna.

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