

Taxonomic status of tree weta from Stephens Island, Mt Holdsworth and Mt Arthur, based on allozyme variation

Mary Morgan-Richards, Charles H. Daugherty and George W. Gibbs

Eleven populations of the Wellington tree weta, *Hemideina crassidens* (Blanchard, 1851), were compared with tree weta collected from Stephens Island (*H. crassicruris* Salmon 1950) and from Mt Holdsworth and Mt Arthur (*H. brevaculea* Salmon 1950), using 26 allozyme loci. The level of genetic differentiation is consistent with that found between conspecific populations, supporting the trend in the scientific literature to relegate both *H. brevaculea* and *H. crassicruris* to synonymy with *H. crassidens*. On the basis of morphological data indicating differentiation of the Stephens Island population, we conclude that *H. crassicruris* should be considered a subspecies of *H. crassidens* but *H. brevaculea* a synonym. There is an undescribed cryptic species, defined from the level of genetic differentiation, in Hawke's Bay.

Keywords: Stenopelmatidae, *Hemideina crassidens*, *H. crassicruris*, *H. brevaculea*, weta, systematics, electrophoresis

INTRODUCTION

The tree weta *Hemideina crassidens* (Blanchard, 1851) is found throughout the Wellington region, on the islands of the Cook Strait, and in the north and west of the South Island (Meads 1990). Salmon (1950) described two new species of tree weta, *H. crassicruris* and *H. brevaculea*. Restricted to Stephens Island in Cook Strait, *H. crassicruris* was identified and distinguished from *H. crassidens* by the absence of a retrolateral apical spine on the mid-femur (Salmon 1950, 1954). Tree weta on Stephens Island tend to be more robust and darker than on the mainland (G. Ramsay pers. comm. 1992). *H. brevaculea* was identified from Mt Holdsworth (type locality), Mt Arthur and Motungaratiti (Titi) Island and distinguished by extremely small retrolateral apical mid-femur spines and a relatively short ovipositor (Salmon 1950, 1954).

Salmon's classification has been ignored, to varying degrees, by subsequent workers in this field. Ramsay & Bigelow (1978)'s revision of New Zealand tree weta recognised only five species in this genus and made no reference to either *H. brevaculea* or *H. crassicruris*. Field (1978) recognised *H. crassicruris* as a valid species and in a comparison of the stridulatory apparatus of various *Hemideina* species, revealed a large overlap in the range of abdominal tergal ridge counts of *H. thoracica*, *H. femorata*, *H. crassidens* and *H. crassicruris*. Although there are differences in the mean total ridge count between species, Field (1978: 373) concluded that these species cannot be differentiated on this character. *H. brevaculea* was mentioned but not studied by Field, and *H. crassicruris* was not recognised in later publications (Field 1982, 1993). Moller (1985) showed the diagnostic character used by Salmon for *H. crassicruris* to be unreliable: 66% of weta examined from Stephens Island had no retrolateral apical spine on either mid-femur, 24% of weta examined had a retrolateral apical spine on each mid-femur spine and 10% had the spine on one femur only. Moller concluded "its [*H. crassicruris*] taxonomic status needs to be re-examined" (p 57).

Table 1 – Sample locations of the tree weta used in this study and the sample sizes

Population	Species	Locality	Region ¹	Longitude & Latitude	Sample size
1	<i>H. crassidens</i>	Harihari	WD	170°27' 43°03'	3
2	<i>H. crassidens</i>	Hokitika	WD	171°00' 42°46'	1
3	<i>H. crassidens</i> ²	Mt Arthur	NN	172°46' 41°12'	4
4	<i>H. crassidens</i>	Picton	SD	174°01' 41°18'	2
5	<i>H. crassidens</i>	Maud Island	SD	173°54' 41°02'	4
6	<i>H. crassidens</i>	Wellington	WN	174°48' 41°15'	25
7	<i>H. crassidens</i>	Paremata	WN	174°53' 41°06'	4
8	<i>H. crassidens</i>	Kapiti Island	WN	174°56' 40°51'	5
9	<i>H. crassidens</i>	Lake Pounui	WA	175°07' 41°21'	3
10	<i>H. crassidens</i> ²	Mt Holdsworth	WA	175°29' 40°54'	4
11	<i>H. crassidens</i>	Mangaweka	RI	175°48' 39°49'	1
12	<i>H. crassidens</i>	Mt Taranaki	TK	174°06' 39°16'	8
13	<i>H. c. crassicurvis</i>	Stephens Island	SD	174°00' 40°40'	20
14	<i>H. n. sp.</i>	Raukawa	HB	176°37' 39°44'	4
15	<i>H. thoracica</i>	Mt Taranaki	TK	174°07' 39°20'	3
16	<i>H. thoracica</i>	Lake Taupo	TO	176°04' 38°45'	2
17	<i>H. thoracica</i>	Lake Waihopo	ND	173°03' 34°46'	5
18	<i>H. femorata</i>	Kowhai Bush	KA	173°36' 42°23'	5

1. Region codes: HB = Hawkes Bay, KA = Kaikoura, ND = Northland, NN = Nelson, RI = Rangitikei, SD = Marlborough Sounds, TK = Taranaki, TO = Taupo, WA = Wairapa, WD = Westland, WN = Wellington.

2. Collected from a location where Salmon (1950) identified *H. brevaculea*

We therefore undertook an analysis of allozyme variation of tree weta from thirteen sites including Stephens Island, with the aim of establishing whether the weta on Stephens Island should be viewed as a separate species, and also to determine whether *H. brevaculea* exists as a distinct entity, parapatric or sympatric with *H. crassidens*, at the sites from which Salmon (1950) described it.

MATERIALS AND METHODS

Between 1989 and 1994 a total of 103 weta were collected from 17 locations (Table 1). Five purported species of *Hemideina* were sampled, including *H. thoracica* and *H. femorata* which were used as out-groups. Sample sizes were usually small (1–8); generally large numbers of individuals are not required to determine species status using allozyme data even between closely related species such as chimpanzees and humans, so long as a reasonably large number of genetic loci are used (Sarich 1977).

Tree weta were collected from Mt Holdsworth (Taranaki Ranges) and from near Mt Arthur in the hope of obtaining specimens of *H. brevaculea*. Weta from these localities fit the descriptions for both *H. crassidens* and *H. brevaculea*, the only distinctions being that females of the latter have “very short [ovipositors], only about one-fifth length of body” and minute retrolateral apical mid-femur spines (Salmon 1950). Since all immature female tree weta comply with this description, we deemed them to be *H. crassidens* until proven otherwise. Thus in the following text all specimens from the *H. brevaculea* locations are referred to as *H. crassidens*. The most northern population of *H. crassidens* sampled was Mt Taranaki where it is sympatric with *H. thoracica* (Fig. 1). One of the populations we initially assumed to be *H. crassidens* proved, unexpectedly, to be so highly differentiated genetically that it is clearly an undescribed species and will be treated separately for the remainder of the paper.

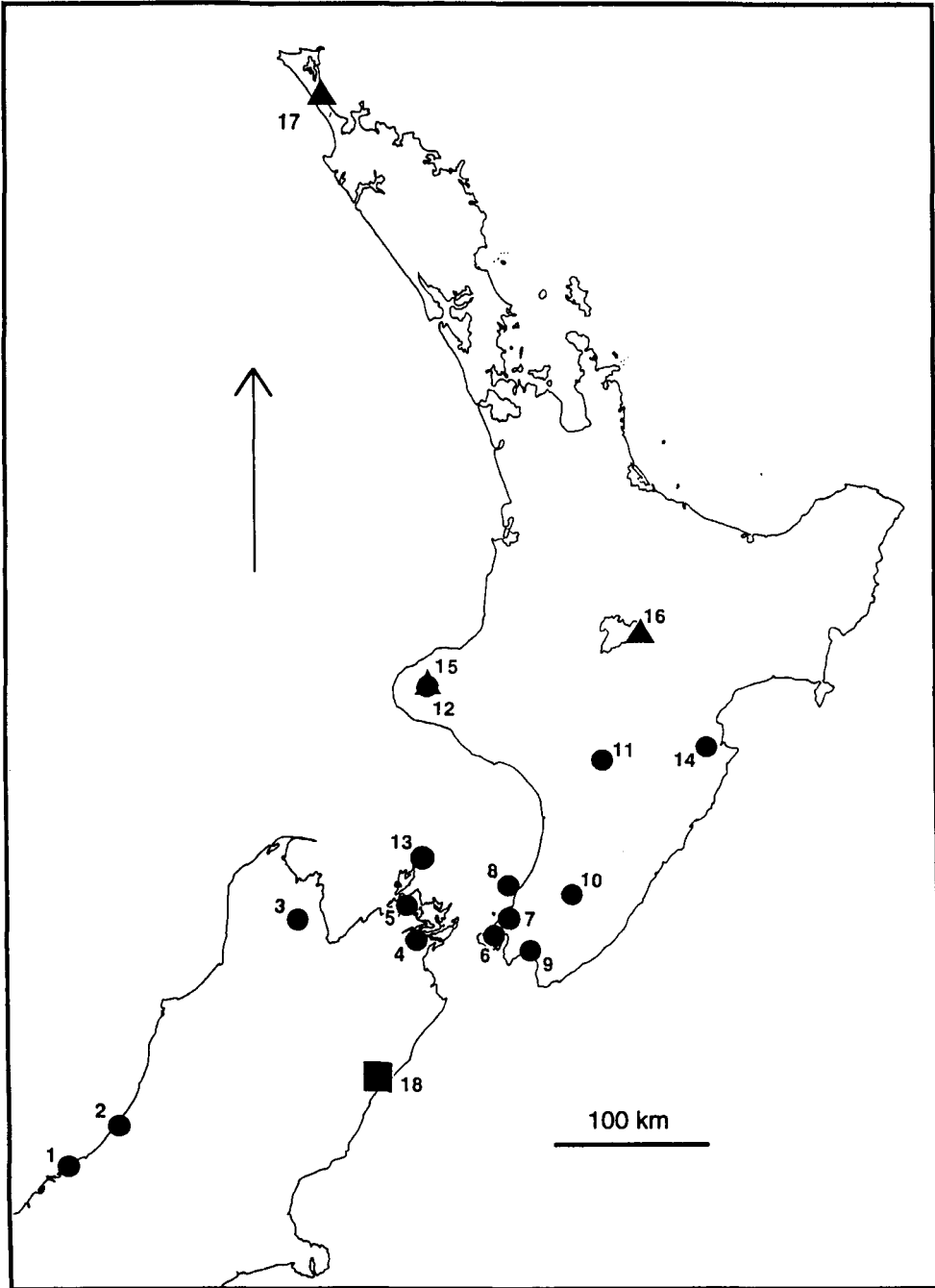


Fig. 1 – New Zealand localities where tree weta were collected for this study. Two species were collected from Mt Taranaki, numbers are those used in table 1. ● = *H. crassidens*, ▲ = *H. thoracica*, ■ = *H. femorata*)

Weta were killed using ether and immediately dissected. Tissue from the malpighian tubules and femur muscles was removed, blended with an equal quantity of distilled water, and stored at -80°C until required for electrophoresis. All specimens were stored in ethanol and those from Stephens Island lodged with the Museum of New Zealand Te Papa Tongarewa.

Starch gel electrophoresis techniques followed those of Allendorf et al. (1977). Tissue was transferred by a filter paper wick to a 12.5% horizontal starch gel. Direct current was applied to the gel for 2–4 h. All combinations of four gel/electrode buffer systems and 15 different protein stains were examined for electrophoretic activity and resolution.

The BIOSYS-1 program (Swofford & Selander 1981) was used to calculate allelic frequencies for each population and for estimating average unbiased heterozygosity per locus (Nei 1978). Genetic distances between populations were calculated according to the methods of Nei's (1978) unbiased genetic distance and Cavalli-Sforza & Edwards' (1967) arc distance. Phenograms were constructed by the WPGMA (Sneath & Sokal 1973) method and by the neighbor-joining (Saitou & Nei 1987) method using the computer program MEGA (Kumar et al. 1993). Nei's genetic distance was used to compare these weta because it is quoted extensively in the literature and so comparisons with similar studies can be made. The scale of the Cavalli-Sforza & Edwards arc distance incorporates an angular transformation; its advantages as a measure of genetic distance are summarised in Wright (1978) and by Swofford & Olsen (1990). Nei's genetic distance is influenced by within-taxon heterozygosity, but the arc distance of Cavalli-Sforza & Edwards is not. Furthermore, the arc distance depends on more realistic assumptions, because the transformation has the effect of standardising the distance with respect to random drift so that the rate of increase in genetic distance under drift is nearly independent of the initial gene frequencies.

Morphological comparisons were limited to three characters. R. Bigelow (unpublished) has studied the stridulatory apparatus and leg spination of 724 specimens of *H. crassidens*, and found the same range of geographical variation in all characters except the number of stridulatory ridges (G. Ramsay pers. comm. 1992). Given the apparent larger size of *H. crassicruris*, we measured the hind tibia width and length of all weta in our samples in addition to a count of the stridulatory ridges.

RESULTS

Allozyme variation

A total of twenty-six presumed genetic loci was suitable for analysis (Table 2), seventeen of which were polymorphic. Variable loci possessed between two and five alleles. Unbiased estimates of average heterozygosity varied from 0–0.078 (Table 3). Where loci were polymorphic within populations, heterozygotes were detected in 25 cases out of 27: the two samples where heterozygotes were not detected were small ($n=2$ and 4). Excluding *H. femorata* eleven loci were polymorphic, and within the *H. crassidens* populations 1–13 (Table 1) eight loci were polymorphic. Four fixed differences separated *H. thoracica* from the thirteen *H. crassidens* populations. No fixed differences were detected that separated the Stephens Island, Mt Holdsworth or Mt Arthur weta from any of the *H. crassidens* populations. The sample of weta from Raukawa, Hawke's Bay, had three fixed differences from the *H. crassidens* populations and five fixed differences from *H. thoracica* (Table 3).

Cavalli-Sforza & Edwards' arc distance among *H. crassidens* populations ranges from 0.0 to 0.34 (Table 4); among the *H. thoracica* populations the range is from 0.16 to 0.33. For interspecific comparisons between *H. femorata*, *H. thoracica* and *H. crassidens* arc distances range from 0.44 to 0.76 and between *H. thoracica* and *H. crassidens* range from 0.44 to 0.52. The arc genetic distances between 0.06 and 0.34 separating *H. crassicruris* from the *H. crassidens* populations fall within the conspecific range seen here. The same pattern of genetic distances is seen when Nei's unbiased genetic distances are compared between and within species. Greater variation was found within *H. crassidens* than between *H. crassicruris* and *H. crassidens*.

This pattern of relationships is summarised in the unrooted tree (Fig. 2) produced by the

Table 2 – Enzymes, number of loci, tissue source and electrophoretic conditions for stain systems used in this study.

Enzyme system	Abbreviation and EC number	No. of loci	Tissue	Buffer system
Aspartate aminotransferase	<i>Aat</i> 2.6.1.1	2	T	B
Adenylate kinase	<i>Ak</i> 2.7.4.3	1	M	A
General protein	<i>Gp</i> nonspecific	1	M	A
Glucose-phosphate isomerase	<i>Gpi</i> 5.3.1.9	1	M	A
b-Glucuronidase	<i>Gus</i> 3.2.1.31	1	M	A
Hexokinase	<i>Hk</i> 2.7.1.1	2	M	A
Isocitrate dehydrogenase	<i>Idh</i> 1.1.1.27	2	T	B
Lactate dehydrogenase	<i>Ldh</i> 1.1.1.27	2	T	B & C
Malate dehydrogenase	<i>Mdh</i> 1.1.1.37	2	T	B
Malic enzyme	<i>Me</i> 1.1.1.40	2	T	D
Menadione reductase	<i>Mnr</i> 1.6.5.2	1	T	C
Peptidase	<i>Pep</i> 3.4.-.-	4	M	A
Phosphogluconate dehydrogenase	<i>Pgd</i> 1.1.1.44	2	T	D
Phosphoglucomutase	<i>Pgm</i> 5.4.2.2	2	T	B
Superoxide dismutase	<i>Sod</i> 1.15.1.1	1	M	B

Tissue: M = muscle; T = malpighian tubule.

Buffer systems A: Gel – 0.03M Tris, 0.005M citric acid, pH 8.5; Electrode – 0.06M lithium hydroxide, 0.3M boric acid, pH 8.1; gels made with 99% gel buffer and 1% electrode buffer. B: Gel – 0.002M citric acid, pH 6.0; Electrode – 0.04M citric acid, pH 6.1. pH of both buffers adjusted with N-(3-aminopropyl)-morpholine. C: Gel – 0.076M Tris, 0.005M citric acid, pH 8.7; Electrode – 0.3M boric acid, 0.06M NaOH, pH 8.2. D: Gel – 0.069M KH₂PO₄-NADP, pH 6.7; Electrode – 0.138M KH₂PO₄, pH 6.7.

neighbor-joining method of phylogenetic tree reconstruction using the arc distance; *H. crassicuris* is placed within the *H. crassidens* clade. A similar branching pattern was obtained using WPGMA cluster analysis of Nei's unbiased genetic distance (not illustrated). The sample from Mt Arthur was placed within the predominantly South Island *H. crassidens* clade and the sample from Mt Holdsworth was placed within the predominantly North Island *H. crassidens* clade.

The undescribed species from Raukawa, Hawke's Bay, is genetically differentiated from all other tree weta studied. The pairwise genetic distances separating this sample from the Mangaweka and Mt Taranaki *H. crassidens* samples (0.46 and 0.44, respectively) were equivalent to the pairwise distances separating *H. thoracica* samples from the *H. crassidens* samples. The Raukawa sample was fixed for alternate alleles at three loci (*Gpi*, *Ldh-2* and *Pgm-1*), and had different frequencies, from other *H. crassidens* samples, for the same alleles at two loci (*Pgd-1* and *Ldh-1*). In the neighbor-joining tree the Hawke's Bay population branches at almost the same point that *H. thoracica* and *H. crassidens* separate; our data cannot resolve this trichotomy (Fig 2).

Morphological variation

The mean hind tibia length, width and the number of stridulatory ridges were compared in weta from Wellington and Stephens Island. Samples are sometimes small, and consist of males and females, adults and juveniles. The mean number of stridulatory ridges did not vary between different ages or between the sexes (Table 5). Data for all individuals from Stephens Island were compared with all from Wellington (Table 5) and they did differ significantly; specimens collected from Wellington have fewer stridulatory ridges, on average, than those collected from Stephens Island.

Although the tibia of immature weta were shorter than those of adult weta they did not

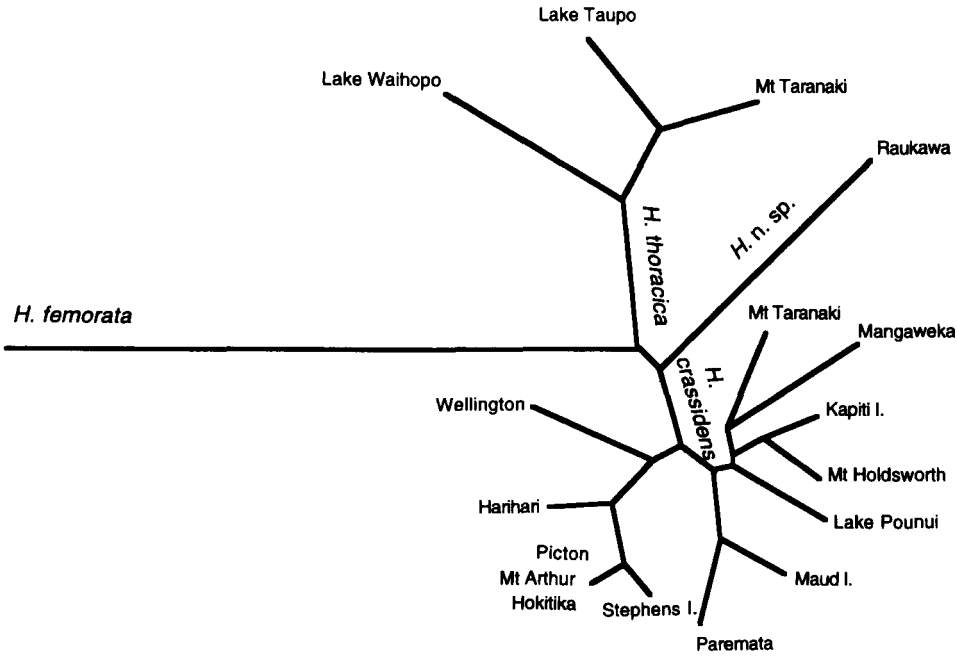


Fig. 2 – Neighbor-joining tree (Saitou and Nei 1987) using Cavalli-Sforza and Edwards (1967) arc distance from 26 loci for 18 populations of *Hemideina*. Branch lengths are proportional to genetic distances.

Table 3 (contd)

locus	<i>H. crassidens</i>										<i>H. c. n. sp</i>		<i>H. thoracica</i>	<i>H. fem-orata</i>				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Pep-3																		
(a)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	–
(b)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.00
Pgd-1																		
(a)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.87	1.00	1.00	1.00	0.25	1.00	0.50	1.00	–
(b)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.50	–	–
(c)	–	–	–	–	–	–	–	–	–	0.13	–	–	–	0.75	–	–	–	–
(d)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.00
Pgm-1																		
(a)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.00	1.00	0.75	0.25
(b)	1.00	1.00	1.00	1.00	–	1.00	–	–	–	–	–	–	1.00	–	–	–	0.25	0.75
(c)	–	–	–	–	–	–	–	–	–	–	–	–	–	1.00	–	–	–	–
(d)	–	–	–	–	1.00	–	1.00	1.00	1.00	1.00	1.00	1.00	–	–	–	–	–	–
Pgm-2																		
(a)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.00	1.00	–	1.00
(b)	0.50	–	–	–	–	1.00	–	0.17	0.50	0.50	1.00	1.00	–	–	–	–	–	–
(c)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.00	–
(d)	0.50	1.00	1.00	1.00	1.00	–	1.00	0.83	0.50	0.50	–	–	1.00	1.00	–	–	–	–
H																		
	0.058	0.00		0.033		0.029		0.078		0.00		0.013		0.00		0.016		
		0.00		0.00		0.023		0.032		0.052		0.015		0.019		0.045		0.018

Table 4 – Pairwise genetic distances between 18 populations of tree weta, Cavalli-Sforza and Edwards' (1967) arc distance below the diagonal and Nei's (1978) unbiased genetic distance above the diagonal, (populations as in table 1)

Populations	<i>H. crassidens</i>										<i>H. c. c.</i>		n.sp.	<i>H. thoracica</i>			<i>H. fem- orata</i>	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 Harihari		0.010	0.010	0.010	0.052	0.022	0.048	0.060	0.047	0.053	0.081	0.073	0.011	0.183	0.230	0.232	0.260	0.545
2 Hokitika	0.118		0.000	0.000	0.043	0.070	0.040	0.066	0.064	0.080	0.123	0.115	0.001	0.192	0.262	0.265	0.292	0.548
3 Mt Arthur	0.118	0.000		0.000	0.043	0.070	0.040	0.066	0.064	0.080	0.123	0.115	0.001	0.192	0.262	0.265	0.292	0.548
4 Picton	0.118	0.000	0.000		0.043	0.070	0.040	0.066	0.064	0.080	0.123	0.115	0.001	0.192	0.262	0.265	0.292	0.548
5 Maud I	0.246	0.217	0.217	0.217		0.107	0.002	0.020	0.018	0.031	0.063	0.066	0.044	0.187	0.258	0.261	0.302	0.583
6 Wellington	0.151	0.259	0.259	0.259	0.333		0.104	0.079	0.063	0.048	0.072	0.056	0.070	0.197	0.216	0.217	0.244	0.603
7 Paremata	0.230	0.212	0.212	0.212	0.121	0.310		0.020	0.012	0.030	0.076	0.068	0.041	0.183	0.241	0.244	0.284	0.613
8 Kapiti I	0.240	0.256	0.256	0.256	0.182	0.257	0.161		0.008	0.006	0.057	0.026	0.067	0.174	0.236	0.238	0.278	0.650
9 Lake Pounui	0.253	0.267	0.267	0.267	0.199	0.269	0.168	0.149		0.007	0.032	0.015	0.065	0.191	0.222	0.224	0.265	0.640
10 Mt Holdsworth	0.247	0.298	0.298	0.298	0.233	0.230	0.203	0.095	0.183		0.038	0.017	0.080	0.155	0.209	0.207	0.250	0.647
11 Mangaweka	0.294	0.340	0.340	0.340	0.245	0.280	0.285	0.243	0.232	0.224		0.032	0.122	0.240	0.262	0.265	0.305	0.674
12 Mt Taranaki	0.281	0.340	0.340	0.340	0.285	0.223	0.276	0.155	0.162	0.138	0.196		0.116	0.228	0.250	0.252	0.293	0.667
13 Stephens I	0.131	0.057	0.057	0.057	0.218	0.261	0.219	0.262	0.272	0.302	0.333	0.344		0.194	0.256	0.258	0.286	0.543
14 Raukawa	0.399	0.413	0.413	0.413	0.419	0.420	0.399	0.393	0.432	0.372	0.458	0.442	0.417		0.240	0.223	0.283	0.832
15 Mt Taranaki	0.458	0.480	0.480	0.480	0.485	0.444	0.464	0.460	0.480	0.447	0.480	0.465	0.480	0.458		0.026	0.082	0.734
16 Lake Taupo	0.468	0.490	0.490	0.490	0.495	0.455	0.474	0.470	0.490	0.458	0.490	0.476	0.490	0.464	0.163		0.113	0.711
17 Lake Waihopo	0.476	0.498	0.498	0.498	0.523	0.463	0.504	0.500	0.519	0.489	0.519	0.505	0.498	0.498	0.285	0.328		0.891
18 Kowhai Bush	0.654	0.654	0.654	0.654	0.667	0.672	0.684	0.697	0.696	0.707	0.707	0.707	0.654	0.760	0.719	0.719	0.762	

Table 5 – Comparison of tree weta from Stephens Island with those from Wellington using three morphological characters using Student t-tests for separate populations (separate variances), P = probability that the mean of the two population samples do not differ significantly, $P > 0.05$ = not significant (n.s.).

Character	Comparison	(n)	Mean	Significance (P)
Number of stridulatory ridges	All adults	(41)	13.610	n.s.
	All juveniles	(14)	13.786	
	All females	(27)	13.296	
	All males	(28)	14.000	
	Wellington	(13)	12.769	
	Stephens I.	(31)	14.548	0.038
Hind-tibia length (mm)	All adults	(40)	21.333	0.000
	All juveniles	(14)	17.011	0.000
	Adult females	(18)	22.569	
	Adult males	(18)	20.247	
	Wellington females	(9)	21.878	
	Stephens I. females	(9)	23.261	
	Wellington males	(4)	21.438	
Stephens I. males	(14)	19.907		
Hind-tibia width (mm)	All adults	(40)	2.103	n.s.
	All juveniles	(14)	2.064	0.001
	All females	(26)	2.240	
	All males	(28)	1.955	
	Wellington females	(9)	2.050	
	Stephens I. females	(14)	2.421	
	Wellington males	(4)	1.650	
Stephens I. males	(16)	2.153		

differ significantly in width, therefore the juveniles were taken out of the analysis only for comparisons of tibia length. Females had, on average, both longer and wider hind-tibia than males. The width of the tibia, but not the length, differed between the Wellington sample and the Stephens Island sample ($P < 0.003$). The specimens from Stephens Island had on average wider but not longer hind-tibia.

DISCUSSION

The taxonomic interpretation of geographical variation depends upon the choice of species concepts. The Biological Species Concept of Mayr (1963) defines species on the basis of reproductive isolation, a criterion that cannot be tested directly among allopatric populations such as those on islands (Mckittrick & Zink 1988), and thus is not applicable to the Stephens Island population. The Evolutionary Species Concept (Wiley 1978) which identifies species on the basis of their independent evolutionary tendencies and fate can be criticised for requiring forecasting of the future. The Phylogenetic Species Concept (Cracraft 1983) identifies species on the basis of cladistic analysis: a species is the smallest monophyletic unit with at least one diagnostic character or a unique combination of characters. The Phylogenetic Species Concept has been criticised as leading to an unwarranted proliferation of species; in principle even a single laboratory *Drosophila* culture could be a species. And it has been shown that some biological and evolutionary species are paraphyletic, indicating that monophyly is not a necessary character (Patton & Smith 1989). The Cohesion Species Concept (Templeton 1989) defines species as groups of populations that are (1) genetically cohesive because of gene flow and (2) demographically exchangeable in the sense of sharing a fundamental niche or ecological role in biological communities. For rare species the second requirement (demographic exchangeability) of the Cohesion Species Concept will often be impossible to assess.

Allozyme variation is conservative, reflecting at most 30% of the underlying DNA variation (Lewontin 1974). Thus the data obtained in this study are conservative and almost certainly underestimate the level of divergence among study populations. We make our assessments below by analysing the level and pattern of divergence in allozyme variation, realising that no single species definition is sufficient to deal with every population.

Hemideina crassidens

Levels of population divergence among all populations now assigned to *H. crassidens* are consistent with the normal level of variation among conspecific populations. Although the majority of samples are small, more than half of the clusters in the neighbor-joining tree (Fig. 2) group samples from geographically proximate locations together, a result which gives us confidence in this analysis. The Stephens Island population and those from Mt Holdsworth and Mt Arthur fit into the geographical structure of *H. crassidens*. All genetic variation in these populations is in the form of allele frequency differences. The parapatric populations of *H. crassidens* show in many cases less divergence from the Stephens Island tree weta than they do from each other.

The Stephens Island weta

The Stephens Island weta shows limited morphological divergence from other populations of *H. crassidens* (this study, Field 1978; Ramsay pers. comm. 1992). For this reason, some workers (e.g., Barrett 1991) continue to regard the Stephens population as specifically distinct. This view could be supported by the Evolutionary Species Concept, but because no diagnostic characters have been found (as required by the Phylogenetic Species Concept) and because the Stephens Island weta appears to occupy the same ecological niche as other populations of *H. crassidens* (in line with requirements of the Cohesion Species Concept), we do not support specific status for this population. The Stephens Island population shows no greater divergence in allozymes than do other populations of *H. crassidens*.

On the other hand, we believe that the morphological distinctiveness identified in the Stephens Island population is sufficiently great to warrant taxonomic recognition. We recommend that the Stephens Island population be recognised as *Hemideina crassidens crassicruris* because (1) many entomologists have believed that this population possesses recognisable morphological differentiation, however limited; (2) the Stephens Island population is apparently not part of a cline in colour and shape found among other populations; and (3) the Stephens Island population may represent an opportunity for sustained evolutionary divergence (Hammond 1985; Patton & Smith 1990) which might give it specific status under the Evolutionary Species Concept. The latter point acknowledges that speciation is a process rather than an event, and that recognition can be warranted for populations distinctive enough to indicate that they may be incipient species.

Mt Holdsworth and Mt Arthur weta

The remote possibility that a sympatric form of *H. brevaculea* co-exists with *H. crassidens* cannot be excluded on the basis of our findings, but if it does, it was not represented in our samples. The tree weta collected from Mt Holdsworth and Mt Arthur (original localities of *Hemideina brevaculea*) could be neither morphologically nor genetically distinguished from *H. crassidens*. Although sample sizes from both these locations were small, any genetic variation of the level found in the Hawke's Bay sample that did exist would almost certainly have been detected. Therefore we conclude, with the evidence we have, that *H. brevaculea* Salmon 1950 refers to immature specimens of *H. crassidens* Blanchard, 1851. The specimens in the Museum of New Zealand Te Papa Tongarewa labelled by Salmon as *H. brevaculea*, including the holotype, are not distinguishable from immature *H. crassidens* (pers. obs.).

Hawke's Bay tree weta

The Raukawa population from Hawke's Bay was the only sample of *H. crassidens* we found

that had genetic characters significantly different from those of all the other populations of *H. crassidens* studied. It came from the most eastern collection site, and from initial searches it now appears to be isolated from other *H. crassidens* populations. The extent of the genetic differentiation of this weta from *H. crassidens* is equivalent to the differentiation separating *H. thoracica* and *H. crassidens*. The differentiation includes three fixed differences and unique alleles, which we believe warrant its recognition as a separate species under both the Evolutionary and Phylogenetic Species Concept. Despite apparent opportunity in the recent past for interbreeding with *H. crassidens*, this species has maintained a high level of genetic differentiation and therefore may also be a separate species under the Biological Species Concept. It is formally described by Morgan-Richards (in press).

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