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A phylogenetic analysis of New Zealand giant and tree weta (Orthoptera : Anostostomatidae : *Deinacrida* and *Hemideina*) using morphological and genetic characters

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Abstract. A phylogenetic analysis of New Zealand weta from the sub-family Deinacridinae is presented. Eighteen species were studied using 27 genetic characters (allozyme and cytogenetic) and 25 morphological characters. The combined data set produced a phylogenetic hypothesis with twelve well-supported nodes. Despite the great diversity of habitats and life styles exhibited by the eleven *Deinacrida* White species a well-supported bipartition separates them from the seven *Hemideina* Walker species. Six of the *Hemideina* species formed a monophyletic clade, with respect to *H. broughi* (Buller). Evolution of stridulatory ridges used for sound production in both defence and intraspecific communication appears to have occurred at least twice. Adaptation to the recent New Zealand alpine environment has also had multiple origins. Biogeographic interpretations from the phylogenetic hypothesis are discussed.

Introduction

Recently, Johns (1997) argued for the use of the family name Anostostomatidae for a group of Southern Hemisphere Orthoptera, previously called Stenopelmatidae, Henicidae or Mimnermidae. In Australasia these insects are commonly known as weta and king crickets. Johns (1997) divided Anostostomatidae into two subfamilies; the smaller of these is Deinacridinae, which includes the two genera (*Deinacrida* White and *Hemideina* Walker) that are the subject of this study. These two genera comprise only eighteen species but form the bulk of the subfamily as described by Johns (1997). Commonly known as tree weta (*Hemideina*) and giant weta (*Deinacrida*), these genera contain species that range from the most familiar to the rarest of insects in New Zealand.

This study is the first phylogenetic analysis of *Deinacrida* and *Hemideina*, although in New Zealand, weta have been much studied by ecologists (Moller 1985; Rufaut 1995; Trewick and Morgan-Richards 1995; Townsend *et al.* 1997), behavioural biologists (Richards 1973; Field 1980; Field and Sandlant 1983), and conservationists (Barrett 1991; Sherley and Hayes 1993; Gibbs 1998). In addition, population genetics has provided a great deal of information about conspecific variation from the study of weta hybrid zones (Morgan-Richards and Townsend 1995; King *et al.* 1996; Morgan-Richards *et al.* 2000) and conspecific chromosome variation (Morgan-Richards and Gibbs 1996; Morgan-Richards 1997, 2000), but little is known about the relationships among species.

All New Zealand weta are nocturnal and flightless and most tree and giant weta are largely herbivorous. However, there is a great deal of behavioural and ecological diversity within this group of eighteen species. Of the eleven species of giant weta, six are restricted to alpine habitats. Their habits vary: *D. connectens* Ander takes refuge during the day under rocks on scree slopes, *D. elegans* Gibbs is specialised to use crevices between rocks on bluffs and cliffs, *D. tibiospina* Salmon shelters under vegetation in the subalpine zone, and *D. talpa* Gibbs lives in underground tunnels. The lowland *Deinacrida* are either ground dwelling like *D. carinata* Salmon and *D. rugosa* Buller or arboreal-like *D. fallai* Salmon, *D. heteracantha* White and *D. mahoenui* Gibbs. Six of the seven tree weta species are arboreal and use holes in trees to seek refuge; the exception is *H. maori* Pictet & Saussure, which is alpine adapted, and takes refuge under rocks. All giant weta species are heavy bodied, with the largest species weighing up to 70 g when gravid. All are now restricted to parts of New Zealand that are relatively free of introduced mammalian predators (off-shore islands or alpine habitats) (Gibbs 1998). However, the smallest of the giant weta are much smaller than the largest tree weta, *H. broughi* (Buller). The smaller tree weta are common over much of the country. Six of the seven tree weta species form ‘harem’ aggregations comprising one male

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with several females within a refuge. The exception, *H. broughi*, has been little studied but the absence of megacephaly in the males suggests it has a different mating system from the other *Hemideina*. The two genera were recently rediagnosed (Gibbs 1999) based on three characters: prosternum spines, superior distal spines of mid-tibia and texture of abdominal tergites (Gibbs 1999).

Weta produce sound by rubbing their abdominal tergites against their hind femora. The resulting scratching sound is used in defence and for intraspecific communication (Field 1993*a*). Sound production is useful in many Orthoptera groups for distinguishing species (for both conspecifics and humans), and provides a mechanism for the maintenance of reproductive isolation. Stridulatory apparatus in weta is quite varied and has been well studied. Most of the *Deinacrida* and *Hemideina* species have a row of stridulatory ridges (which vary in number) on each side of their second abdominal tergite against which pegs on the hind femora are rubbed. Instead of ridges making a file, *H. broughi* and three *Deinacrida* species have patches of minute pegs on the abdominal tergites (Field 1978, 1993*a*). Outgroup analyses suggest that the stridulatory pegs possessed by *H. broughi*, *D. connectens*, *D. tibiospina* and *D. carinata* are ancestral (Field 1993*a*). If the two genera represent natural groupings then there must have been at least two independent origins of stridulatory ridges. Given the diversity within the two genera, the monophyly of each group needs to be confirmed. This study aimed to resolve this question, using both morphological and genetic characters to generate a phylogenetic hypothesis for these distinctive New Zealand orthopterans.

Materials and methods

Insect material

Morphological study of 21 weta species was possible from dried and alcohol-preserved specimens (Table 1), but for genetic study live material of all species of weta in the genera *Hemideina* and *Deinacrida* was collected (Table 2). Only *D. carinata*, a species restricted in distribution to a few small offshore islands south of South Island, was not obtained alive (Salmon 1950; Meads and Notman 1993). Permits to collect eight species of weta, absolutely protected by the 1980 wildlife amendment as endangered species, were provided by the New Zealand Department of Conservation. However, the endangered status of these species limited the number of specimens collected (Table 2). Material of *H. crassidens* (Blanchard), *H. trewicki* Morgan-Richards, *H. thoracica* (White) and *D. connectens* has been used in studies of intraspecific variation and data for these species are published elsewhere (Morgan-Richards 1995; Morgan-Richards *et al.* 1995; Morgan-Richards and Gibbs 1996; Morgan-Richards 1997, 2000). Type material of *D. elegans*, *D. pluvialis* and *D. talpa* was used in this study (Gibbs 1999).

Morphology

A character matrix was constructed for 25 morphological characters from 21 taxa (Table 3). Characters that had more than two states and involved numbers of spines or size were assumed to form an ordered sequence such that one spine is two steps away from three spines, and thus five characters were coded as ordered (mid-tibial superior distal spines, mid-femur apical spines, hind-tibia outer spine row, hind-tibia inner spine row and egg size). Nineteen characters were binary and therefore without order. Stridulatory ridge number varies within species and in fact varies between right and left sides of individual weta. This trait was coded as 15 characters for the 15 possible numbers of ridges an individual could have. The 15 stridulatory ridge characters are not independent and therefore these characters were weighted so that combined, they had the same weight as a single character in the data set. Thus the polymorphic nature of many of the species has been incorporated without biasing the analysis. This coding system was based on Weins' (1995) finding that coding data as discrete states is preferable to coding as polymorphic states. Parsimony analysis was used to construct an evolutionary hypothesis of the group. All characters were parsimoniously informative. An heuristic search, using default settings, for the shortest tree was carried out using PAUP*4.0b (Swofford 1998), and bootstrapped using 1000 replicates. Hillis and Bull (1993) have shown that bootstrap values >70 generally correspond to a 95% probability that the data consistently support a given clade. Trees were rooted using three outgroup taxa from the family Anostostomatidae, two undescribed species of *Hemiandrus* Ander and a new species of *Motuweta* Johns.

List of morphological characters

1. *Stridulatory ridges*: (0) present; (1) absent
   1 Stridulatory ridge: (0) present; (1) absent
   2 Stridulatory ridges: (0) present; (1) absent
   3 Stridulatory ridges: (0) present; (1) absent
   4 Stridulatory ridges: (0) present; (1) absent
   5 Stridulatory ridges: (0) present; (1) absent
   .
   .
   .
   etc. to 15
2. *Mid-tibia superior distal spines*: (1) a single spine; (2) twos spines

Table 1. Sample sizes of adult weta used in the morphological analysis of 21 species of New Zealand Anostostomatidae (*Deinacrida, Hemideina* and outgroups)

Species	Sample size (*n*)
D. heteracantha	4
D. fallai	17
D. mahoenui	29
D. elegans	12
D. rugosa	35
D. parva	30
D. pluvialis	16
D. talpa	2
D. connectens	8
D. tibiospina	2
D. carinata	7
H. broughi	4
H. femorata	5
H. maori	20
H. ricta	3
H. thoracica	4
H. trewicki	5
H. crassidens	20
Motuweta sp.	11
Hemiandrus sp. 1	5
Hemiandrus sp. 2	5

Table 2. Collection details for the 17 species of New Zealand Anostostomatidae (*Deinacrida* and *Hemideina*) used in the genetic analysis

Species	Abbreviation	Location		Region	Latitude	Longitude	*n*
D. heteracantha	*D. het*	Little Barrier Island	Hauraki Gulf	Auckland	36º 13´	175º 05´	3
D. fallai	*D. fal*	Tawhiti Rahi Island	Poor Knight Islands	Northland	35º 27´	174º 44´	3
D. mahoenui	*D. mah*	Mahoenui	Te Kuiti	Waikato	38º 35´	174º 50´	3
D. elegans	*D. ele*	Hapuku River	Seaward Kaikoura Range	Kaikoura	42º 22´	173º 26´	2
D. elegans	*D. ele*	Woolshed Creek	Mt Somers	Mid Canterbury	43º 37´	171º 19´	3
D. rugosa	*D. rug*	Stephens Island		Cook Strait	40º 40´	174º 00´	3
D. rugosa	*D. rug*	Mana Island		Cook Strait	41º 05´	174º 00´	1
D. parva	*D. par*	Long Creek	Hapuku River	Kaikoura	42º 19´	173º 41´	2
D. pluvialis	*D. plu*	Prices Basin	Whitcome catchment	Westland	43º 08´	170º 57´	4
D. pluvialis	*D. plu*	Head Basin	West Matukituki River	West Otago	44º 25´	168º 42´	7
D. talpa	*D. tal*	Mt Faraday	Paparoa Range	Westland	42º 02´	171º 34´	3
D. connectens	*D. con*	see Morgan-Richards & Gibbs 1996					60
D. tibiospina	*D. tib*	Flora hut	Mt Arthur	North west Nelson	41º 12´	172º 44´	1
H. broughi	*H. bro*	Flora Saddle	Mt Arthur	North-west Nelson	41º 12´	172º 44´	2
H. femorata	*H. fem*	Flag Peak	Banks Peninsula	Canterbury	43º 51´	172º 59´	4
H. femorata	*H. fem*	Kowhai Bush	Kaikoura	Kaikoura	42º 23´	173º 36´	5
H. maori	*H. mao*	Mt Percival	Hanmer Range	North Canterbury	42º 29´	172º 56´	1
H. maori	*H. mao*	Maukuratawhai	Clarence Valley	Canterbury	42º 26´	172º 51´	1
H. maori	*H. mao*	Foggy Peak	Torlesse Range	Canterbury	43º 17´	171º 45´	3
H. maori	*H. mao*	Woolshed/Morgan Streams	Mt Somers	Mid Canterbury	43º 35´	171º 19´	8
H. maori	*H. mao*	Hooker River	Hermitage	Mount Cook	43º 44´	170º 07´	2
H. maori	*H. mao*	Harwick Island	Lake Wanaka	Otago Lakes	44º 33´	169º 05´	2
H. maori	*H. mao*	Crescent Island	Lake Wanaka	Otago Lakes	44º 37´	169º 04´	1
H. maori	*H. mao*	Rock & Pillar	Rock and Pillar Range	Otago	45º 28´	170º 00´	4
H. ricta	*H. ric*	Flag Peak	Banks Peninsula	Canterbury	43º 51´	172º 59´	8
H. thoracica	*H. tho*	see Morgan-Richards 1997					141
H. trewicki	*H. tre*	see Morgan-Richards 1995					14
H. crassidens	*H. cra*	see Morgan-Richards *et al.* 1995					84

Table 3. Character matrix for 21 species of weta, 25 morphological characters and 27 genetic characters

	D. het	*D. fal*	*D. mah*	*D. ele*	*D. rug*	*D. par*	*D. plu*	*D. tal*	*D. con*	*D. tib*	*D. car*	*H. bro*	*H. fem*	*H. mar*	*H. ric*	*H. tho*	*H. tre*	*H. cra*	*Motu*	*andrus 1*	*andrus 2*
Morphological characters																					
Stridulatory ridges absent	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
1 stridulatory ridge	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 stridulatory ridges	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3 stridulatory ridges	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0
4 stridulatory ridges	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0
5 stridulatory ridges	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0
6 stridulatory ridges	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0
7 stridulatory ridges	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	0	0
8 stridulatory ridges	0	0	0	1	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0
9 stridulatory ridges	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0
10 stridulatory ridges	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0
11 stridulatory ridges	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0
12 stridulatory ridges	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0
13 stridulatory ridges	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0
14 stridulatory ridges	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0
Mid-tibial superior distal spines*	1	1	1	1	1	1	1	1	1	1	1	3	2	2	2	2	2	2	0	1	1
Male megacephaly	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0
Head vertex texture	1	1	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Mandibular 'crest'	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Pronotum texture	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0
Pronotum width	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Prosternum spines	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1
Mesosternum posterior angles	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	1
Fore-femur apical spines	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mid-femur apical spines*	1	1	2	2	2	2	2	0	2	2	1	1	0&1	0	0	0&1	1	0&1	0	0	0
Hind-femur apical spines	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	2	2	2	0	0	1
Hind-femur dorsal surface	1	1	1	0	1	1	0	0	2	2	2	0	0	0	0	0	0	0	0	0	0
Hind-tibia outer spine row*	2	2	2	0	2	1	1	0	3	1	1	2	2	2	2	3	2	2	0	0	0
Hind-tibia inner spine row*	1	1	1	0	1	2	1	1	0	1	1	1	0	0	0&1	0	0&1	1	1	2	0
Hind-tibia distal superior spines	0	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0
Male falci	2	2	2	2	2	2	1	0	2	0	0	0	0	0	0	2	0	2	1	0	1
Male supra-anal setal field	1	1	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Male paranal process	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0
Male paranal process-tooth	3	2	2	1	3	3	1	1	2	2	0	1	0	2	2	1	0	1	0	0	0
Male parannal process-attitude	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	?	?
Male subgenital plate apex	2	2	1	2	2	2	0	1	0	0	0	2	2	2	1	1	1	1	1	0	0
Female subgenital plate apex	1	2	1	1	1	1	2	2	1	1	0	2	1	2	2	1	0	1	0	0	0
Egg size*	1	1	1	2	1	1	2	2	1	0	0	1	0	0	0	0	0	0	?	0	0
Egg shell	2	2	2	1	3	3	1	1	1	4	4	1	1	1	3	5	5	5	0	0	0

	D. het	*D. fal*	*D. mah*	*D. ele*	*D. rug*	*D. par*	*D. plu*	*D. tal*	*D. con*	*D. tib*	*D. car*	*H. bro*	*H. fem*	*H. mar*	*H. ric*	*H. tho*	*H. tre*	*H. cra*	*Motu*	*andrus 1*	*andrus 2*
Genetic characters																					
Ak	1	1	1	0	1		1	1	1	1		0	1	0	0	0	0	0			
Got-1	2	2	2	2	2		0	0	0	0&1		0	0	0	0	0	0	0			
Got-2	1&2	2	2	2	2		3	0	0	?		0	1	1&2	1	0	0	0			
Gp	2	2	2	0	0		0	0	0	0		0	0	0	0	0&1	0	0			
Gpi	3	3	3	3	3		3&4	3	3	3		2	0	0	0	0	1	0			
Hk-1	4	6	6	6	2		6	6	4	?		3	1	2	2	0	0	0			
Hk-2	1	1	1	1	2		5	5	4	?		1	1	1&2&3	2&3	0	0	0			
Icd-1	6	6	6	6	3		0	5	0	4		0	1	3	2	0	0	0			
Icd-2	7	7	2	7	0		5	6	0	0		3	0	0&3&4	0	2	0	0&1			
Ldh-1	3	3&6	3	6	0&3		2	2	2	2		5	1	1	0&1	0	0	0&1&2&3&4			
Ldh-2	?	?	?	2	3		2	2	2	2		1	1	1	1	0	0	1			
Mdh-1	0	0	3	0	0		0	0	0&4	0&3		1	0	2&3	2	0	0	0&1			
Mdh-2	1	1	1	4&7	2		5&6&7&8	2	4&5&6&7	5		6	2&4	4&5	5	3	1	0&1&2			
Mdh-3	2	2	2	1	1		1	1	1	1		1	0	0	0	0	0	0			
Me-1	0	0	0	1	0		1	1	1&2	?		0	0	0	0	0	0	0			
Me-2	0	0	0	4	1		1&4	5	1&4	?		4	1&2&3	1	1	0	0	0			
Me-3	?	0	?	?	0		0	0	?	?		?	0	1	1	0	0	0			
Mnr	0	0	0	0	0		0	0	2	?		0	0	0	0	0&1	0	0			
Pep-1	0	0	0	0	0		0	0	2	0		0	1	1	1	1	1	1			
Pep-2	0	0	0	1	1		3	3	0	1		2	0	1	1	1	1	1			
Pep-3	1	0&1	1	1	0		1	1	1	1		1	0	0	0	1	1	1			
Pep-4	0	0	0	0	0		1	1	0	0		0	0	0	0	0	0	0			
Pgd-1	0	0	0	0&3	0		2	2	1&2&3&5	?		4	2	0&3	0&3	0	0&1	0			
Pgm-1	4	4	4	4	4		4	4	3&4	4		4	1&4	3	3	1&3&4	2	0&1			
Pgm-2	4	4	4	5	4		0	0	1	?		3	0	0	0	1&2&3	0	0&1			
*2n**	5	5	5	8	9	9	6	6	3&4&5	7		7	7	7	7	0&1&2&3 &4&6	3	2&4			
NF*	4	4	4	4	5	5	5	5	4&5	5		5	5	5	5	1&2&3&4	6	4			

Character codes are given in the text. Stridulatory characters (1–14) are weighted so that in total they equal a single character. All characters are unordered except those marked *. 2n = diploid number, NF = number of major chromosome arms.

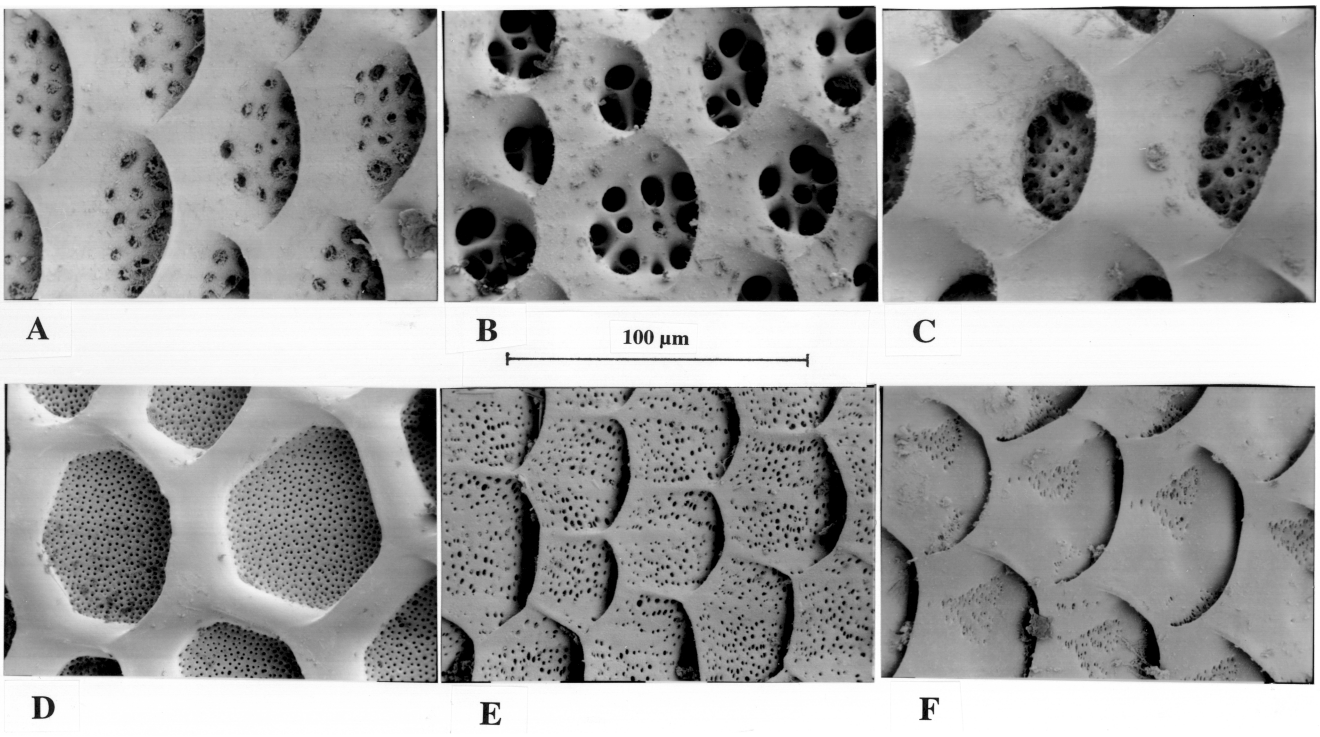

Fig. 1. Examples of the five egg shell character states as seen under a scanning electron microscope (character 25): *A*, *H. broughi*, shallow primary pits, with up to 20 large aeropyle pores (score 1); *B*, *D. pluvialis*, as *A* (score 1); *C*, *D. heteracantha*, deep oval primary pits with 20–40 small aeropyle pores (score 2); *D*, *D. parva*, deep hexagonal primary pits, with about 500 fine pores (score 3); *E*, *D. carinata*, oblique crescentic depressions with overall pattern of fine pores (score 4); *F*, *H. thoracica*, oblique crescentic depressions with distinctive linear patterns of extremely fine aeropyle pores (score 5). Scale bar = 0.1 mm.

3. *Male megacephaly*: (0) absent; (1) present
4. *Head vertex texture*: (0) smooth; (1) sculptured/punctures
5. *Mandibular 'crest'*: (0) absent; (1) present
6. *Pronotum texture*: (0) smooth/shiny; (1) rugose
7. *Pronotum width*: (0) same as head; (1) wider than head
8. *Prosternum spines*: (0) without spines; (1) with spines
9. *Mesosternum posterior angles*: (0) not pronounced; (1) forming a blunt spine
10. *Fore-femur apical spines*: (0) spines absent; (1) single spine
11. *Mid-femur apical spines*: (0) spines absent; (1) single spine; (2) two spines
12. *Hind-femur apical spines*: (1) single spine; (2) two spines
13. *Hind-femur dorsal surface*: (0) smooth; (1) rugose; (2) with spines
14. *Hind-tibia outer spine row*: (0) six or more; (1) five; (2) four; (3) fewer than four
15. *Hind-tibia inner spine row*: (0) greater than outer; (1) same as outer; (2) fewer than outer
16. *Hind-tibia distal superior spines*: (0) articulated; (1) fused
17. *Male falci*: (0) simple lobe; (1) hooked; (2) crest-like
18. *Male supra-anal setal field*: (0) absent; (1) dense patch of long setae
19. *Male paranal process in cross section*: (0) flattened; (1) circular
20. *Male paranal process-tooth*: (0) lacking apical tooth; (1) apical tooth; (2) tooth apical on lateral corner; (3) tooth subapical
21. *Male paranal process- attitude*: (0) upright position; (1) more or less horizontal
22. *Male subgenital plate apex*: (0) straight; (1) concave; (2) V-notched
23. *Female subgenital plate apex*: (0) straight; (1) concave; (2) V-notched
24. *Egg size*: (0) small (3–6mm); (1) medium (6–9mm); (2) large (9–12mm)
25. *Egg shell*: (1) shallow primary pits, with up to 20 large aeropyle pores; (2) deep oval primary pits, with 20–40 small aeropyle pores; (3) deep hexagonal primary pits, with about 500 fine pores; (4) oblique crescentic depressions, with overall pattern of fine pores; (5) oblique crescentic depressions, with distinctive linear patterns of extremely fine aeropyle pores (Fig. 1).

Allozyme electrophoresis

Malpighian tubules and femur muscle were used for starch gel electrophoresis; the technique followed that of Richardson *et al*. (1986). Twenty-eight presumed genetic loci were suitable for analysis (*Ak*, *Got* (2), *Gp*, *Gpi*, *Gus*, *Hk* (2), *Icd* (2), *Ldh* (2), *Mdh* (3), *Me* (3), *Mnr*, *Pep* (4), *Pgd* (2), *Pgm* (2), *Sod*). The loci were coded as characters and the alleles as unordered character states (Table 3). For a full discussion on the merits of this approach see Murphy (1993). In summary, this coding system avoids unequal weight being given to more rapidly evolving loci, avoids the separate loss of ancestral alleles being treated as synapomorphies, avoids the theoretical problem of the non-independence of the characters (invalidating a basic assumption of parsimony methods), and avoids the formation of ancestral taxa that have no alleles at some loci. A phylogenetic tree was constructed using the parsimony algorithm of the computer program PAUP* (Swofford 1998). *Deinacrida parva* Buller and *D. tibiospina* were left out of the genetic analysis because of failure to resolve alleles for a number of

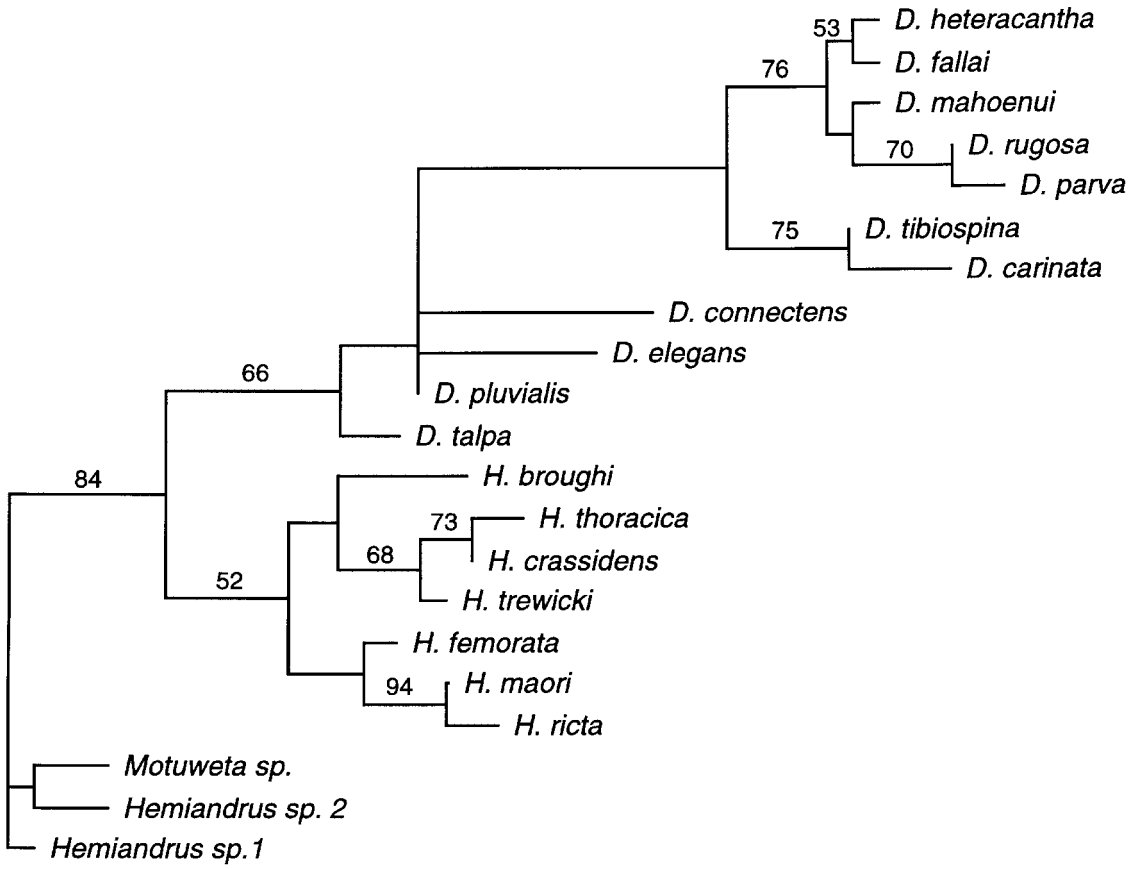

Fig. 2. Concensus tree from two equally parsimonious trees produced for 21 New Zealand weta species (*Deinacrida* and *Hemideina*) from the morphological character matrix (Table 2) and rooted with three outgroup taxa (*CI* = 0.52, *RI* = 0.718). Branch lengths are proportional to the number of steps and numbers above branches are bootstrap values (>70) obtained from 1000 replicates.

loci. Support for the bipartitions within the tree were explored with the use of bootstrapping and Bremer indices (Bremer 1988, 1994). Bremer indices were calculated using inverse-constraints in separate heuristic searches and bootstrapping was performed with 1000 replicates.

Outgroup analysis was not possible with the allozyme data set due to the degree of divergence of the taxa available as outgroups. An undescribed *Hemiandrus* species from Poor Knights Islands, and two New Zealand tusked weta (*Motuweta isolata* Johns, *Anisoura nicobarica* Ander) were included in the electrophoresis study, but their great divergence from the ingroup species meant that the characters were saturated (alleles present at the majority of loci differed, and some loci could not be resolved).

A partition-homogeneity test was performed on the combined morphological and genetic data (without *D. carinata*, *D. parva* and the three outgroup taxa) using 1000 replicates. From the partition-homogeneity test a *P*-value of 0.1 was obtained and therefore the combined data (50 characters) were used to search for the most parsimonious tree (see Huelsenbeck *et al.* 1996 for a discussion of the merits of combining data sets). The stridulatory ridge characters were removed from the combined character matrix so that the evolution of this character could be mapped onto an independent tree. We regard removing this character as a more conservative approach than leaving the character in the data matrix when studying character evolution (De Queiroz 1996). Bootstrapping and Bremer indices were used to explore levels of support for the bipartitions within the most parsimonious tree.

Chromosomes

Reproductive tissue was taken from freshly killed weta, fixed and used to make chromosome preparations. Air-dried slides were plain stained in 8% Giemsa, and examined under a light microscope. The chromosomes were counted from at least ten mitotic spreads for each individual, (for more detail see Morgan-Richards and Gibbs 1996; Morgan-Richards 1997). Chromosome data were coded in two ways: *(1)* diploid numbers for males or *(2)* number of major chromosome arms (NF) as suggested by Cameron (1996). Chromosome numbers vary among populations of some species so chromosome data was coded as polymorphic for *H. thoracica*, *H. crassidens*, *D. connectens*, and *D. elegans* (Table 3). Diploid numbers are coded thus: (0) 2n(X0)=11; (1) 13; (2) 15; (3) 17; (4) 19; (5) 21; (6) 23; (7) 25; (8) 27; (9) 29. NF coded: (1) 22; (2) 24; (3) 26; (4) 28; (5) 30; (6) 32.

Results

Morphology

Heuristic searches for the most parsimonious tree using the morphological character matrix resulted in two shortest trees with the same consistency index (*CI* = 0.462) and retention index (*RI* = 0.707). These two trees differed only in the arrangment of three *Deinacrida* species (*D. elegans*,

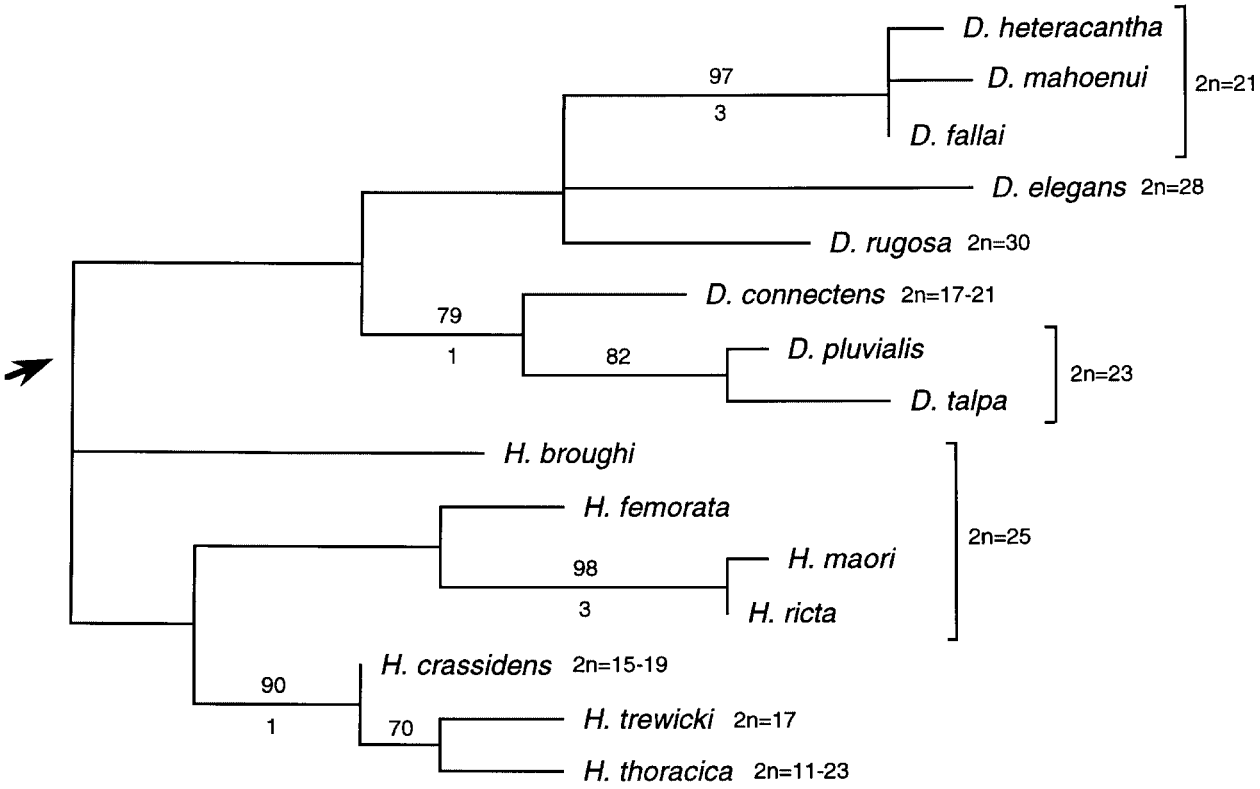

Fig. 3. Consensus of the two most parsimonious trees for 15 New Zealand weta species (*Deinacrida* and *Hemideina*) produced from 27 genetic characters (Table 2) with mid-point rooting (*CI* = 0.881, *RI* = 0.814). Arrow indicates where root is in morphological-based phylogeny. Branch lengths are proportional to the number of steps. Numbers above branches are bootstrap values (>70) obtained from 1000 replicates and below branches are Bremer indices.

D. pluvialis Gibbs, *D. connectens*) and their consensus is shown in Fig. 2. A bipartition separates the eleven *Deinacrida* species from the seven *Hemideina* species. The five characters that distinguish these two groups are: *(1)* number of mid-tibia distal spines, *(2)* male megacephaly (exception of *H. broughi*), *(3)* texture of the pronotum, *(4)* presence of prosternum spines and *(5)* prothorax wider than head. Within *Deinacrida* there is good support for a sister-species relationship between *D. tibiospina* and *D. carinata* and a clade of five northern species is well supported (*D. heteracantha, D. fallai, D. mahoenui, D. rugosa* and *D. parva*). Within *Hemideina* two bipartitions have reasonable support: one forms a clade of two southern species (*H. maori* and *H. ricta* Hutton) and one forms a clade of two northern species (*H. thoracica* and *H. crassidens*). Bootstrapping provides support (>70%) (Hillis and Bull 1993) for just a minority (five) of the nodes in this evolutionary hypothesis (Fig. 2).

Genetic data

Of the twenty-eight genetic loci suitable for analysis only three were monomorphic: *Gus, Sod* and *Pgd*-2. Variable loci had between two and seven alleles. Pairwise genetic distances (Nei's *D* (Nei 1978)) varied from the minimum of 0.07 (between *H. maori* and *H. ricta*) to 1.56 (between *H. ricta* and *D. talpa*). The pairwise distances among *Hemideina* species and among *Deincrida* species were as high as pairwise distances between members of the two genera (data available on request). It should be noted that values of Nei's *D* >1 indicate that more than one allelic substitution per locus has probably occurred and therefore the data set is reaching saturation.

Diploid numbers ranged from 11 in *H. thoracica* to 30 in *D. parva* and *D. rugosa* (Table 3). NF (number of major chromosome arms) ranged from 22 (*H. thoracica*) to 32 (*H. trewicki*). In all species males had a single large metacentric X-chromosome, which was paired in females. Thus, odd numbers refer to the male diploid number (X0) and even numbers refer to females (XX).

Two most parsimonious trees were found using the genetic character matrix (160 steps, *CI* = 0.881, *RI* = 0.814, Fig. 3). Bootstrapping of the data set reveals five well-supported nodes (bootstrap >70). The smallness of this data set is highlighted by the low Bremer indices, but it provides some support for two of the bipartitions in the tree: *(1)* the sister-species relationships of the three northern giant weta (*D. heteracantha, D. fallia* and *D. mahoenui*) and *(2)* two southern tree weta (*H. maori* and *H. ricta*). One allozyme allele appears to differentiate the two genera: *Gpi* has an allele found in all *Deinacrida* but no *Hemideina* species.

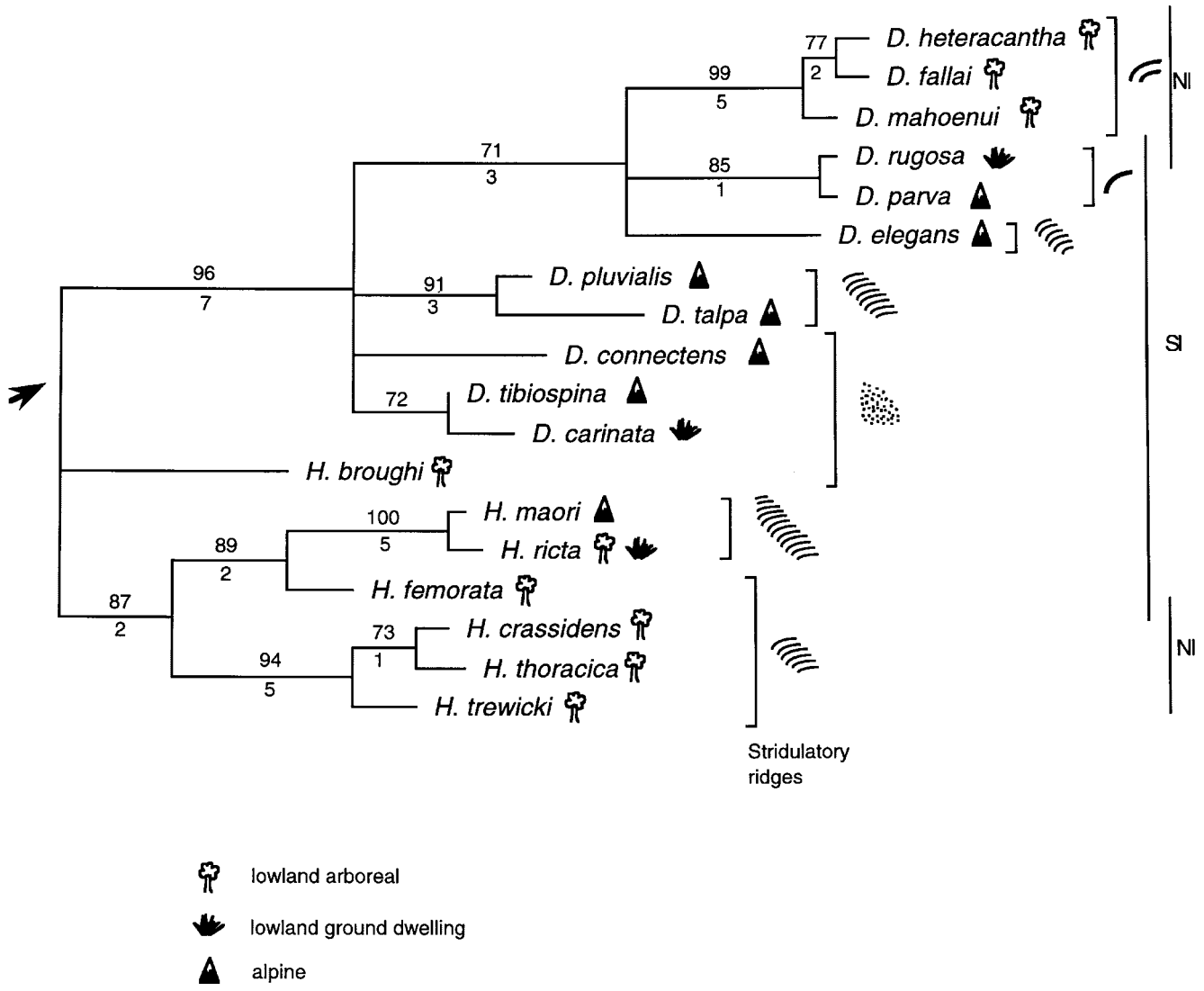

Fig. 4. Phylogeny for 18 New Zealand weta species (*Deinacrida* and *Hemideina*) using a combined morphological and genetic data set, with mid-point rooting (*CI* = 0.738, *RI* = 0.739). Arrow indicates where root is in morphological-based phylogeny. Branch lengths are proportional to the number of steps. Numbers above branches are bootstrap values (>70) obtained from 1000 replicates and below branches are Bremer indices. The clade consisting of *D. tibiospina* and *D. carinata* did not occur in the shortest tree. NI = North Island, SI = South Island.

Combined

The combined data set, with 50 parsimonously informative characters, resulted in a single shortest tree of 255 steps (*CI* = 0.738, *RI* = 0.739). Although only five nodes had good support in either the morphological or genetic trees, twelve nodes with bootstrap values above 70 were recovered from the combined data. The most parsimonous tree from the combined data differed slightly from the bootstrap consensus tree from the combined data. One clade (*D. carinata* and *D. tibiospina*), absent from the shortest tree, had a bootstrap support of 72% (Fig. 4). In the shortest tree these two species are basal to the *Deinacrida* clade, *D. carinata* being the closest to the *Hemideina* clade. The basal placement of these two species is probably a result of missing data (there was no genetic data for *D. carinata* and only partial genetic data for *D. tibiospina*). However, it is also possible that all the characters that unite these two species (see Table 3) are, in fact, ancestral to the *Deinacrida* clade. The stridulatory structures and habitat of each species were mapped onto the combined-data tree.

The twelve clades that the combined-data tree resolves are:

1. A bipartition separating *Deinacrida* from *Hemideina.* Although the morphological analyses places the root between *Deinacrida* and *Hemideina*, a suitable genetic outgroup to root the combined tree would strengthen the case for monophyly of both *Deinacrida* and *Hemideina*.

2. Placement of *H. broughi* outside the main *Hemideina* clade
3. Two *Hemideina* clades; one southern (*H. femorata* Hutton, *H. maori*, *H. ricta*), and
4. One northern (*H. crassidens*, *H. thoracica*, *H. trewicki*)
5. A giant weta clade of six species (*D. heterocantha*, *D. fallai*, *D. mahoenui*, *D. parva*, *D. rugosa* and *D. elegans*)
6. A clade of the three northern giant weta (*D. heterocantha*, *D. fallai*, *D. mahoenui*)

Sister-species status of:

7. Two west coast alpine giant weta *D. pluvialis* and *D. talpa*
8. Two central NZ giant weta *D. parva* and *D. rugosa*
9. Two southern giant weta *D. tibiospina* and *D. carinata*
10. Two northern giant weta *D. heteracantha* and *D. fallai*
11. Two southern tree weta *H. ricta* and *H. maori*.
12. Two northern tree weta *H. crassidens* and *H. thoracica*

Discussion

Alpha taxonomy

Most currently recognised species were supported by the allozyme data. However, estimates of genetic distances between two pairs of recognised species were low (*H. ricta* and *H. maori*; *D. fallai* and *D. heteracantha*). In fact, the intraspecific distances observed within *D. connectens* (Morgan-Richards and Gibbs 1996) and *H. thoracica* (Morgan-Richards 1997) are as great as the distance between these two congeneric species pairs. The colour character distinguishing *H. ricta* and *H. maori* (Ramsay and Bigelow 1978; Field 1993*b*) has been shown to be polymorphic within *H. ricta* (Morgan-Richards and Townsend 1995), suggesting that these two species share a recent common ancestor or that *H. maori* is polyphyletic with respect to *H. ricta*. In contrast, two additional morphological characters were identified as differentiating these two species: the shape of the male subgenital plate (concave in *H. ricta* and V-notched in *H. maori*), and the egg shell surface (pitted in *H. ricta* in a unique manner).

Chromosomes

Few cytogenetic studies of Anostostomatidae have been published. In 1987 John and Rentz presented new data and a summary of results to date. To their list of six species from Australia and South America can now be added 17 New Zealand species (Morgan-Richards 1995; Cameron 1996; Morgan-Richards and Gibbs 1996; Morgan-Richards 1997, 2000 and this study). Diploid numbers range from 11 to 46. Six of the 23 species studied show intraspecific karyotype variation, and, as the majority of the species have been studied from a single location, this is probably an under representation of variation. Clearly this family is karyotypically variable. This leads to two points: *(1)* differences in number and morphology of chromosomes between species should be treated with caution by taxonomists until extensive intraspecific studies are carried out, and *(2)* similarity of karyotype among distinct species such as *H. femorata, H. maori,* and *H. broughi* is worth noting in contrast to the diversity of karyotypes in the other three *Hemideina* species. The rate of chromosome evolution is far from clock-like in many organisms (Baker and Bickham 1980; Eldridge and Close 1993; Nachman and Searle 1995) and similarity of karyotype is as likely to indicate a conservative rate of evolution as it is to indicate phylogenetic proximity.

Phylogenetics

The phylogenetic hypothesis generated from the combined data agrees in general with the species groups identified by studies of the stridulata (Field 1978, 1993*a*). Within the genus *Deinacrida* the three northern species with two stridulatory ridges form a clade (*D. heteracantha, D. fallai, D. mahoenui*). Within *Hemideina, H. maori* and *H. ricta* form a clade and share the character of 10–14 ridges per tergite file. The South Island tree weta *H. femorata* was placed by Field (1993*a*) in a group with *H. crassidens* and *H. thoracica,* but the combined analyses placed *H. femorata* with *H. maori* and *H. ricta* (Fig. 4). The stridulatory character state that is shared by *H. femorata, H. crassidens* and *H. thoracica* (4–8 tergite ridges) can be interpreted as ancestral. The southern *Hemideina* species all have a heavy ridge on their mandibles, which is absent in the northern species, a character that is apparently derived, as it is absent in *H. broughi*. In the bootstrapped combined-data tree (Fig. 4) stridulatory ridges have two independent origins: once in the *Hemideina* clade and at least once in the *Deinacrida* clade.

Alpine weta do not form a monophyletic group in this phylogeny. Although many of the species at the base of the *Deinacrida* clade are alpine adapted, there are two reasons for thinking this is the result of multiple origins rather than retention of an ancestral trait. First, the alpine zone in New Zealand is a very recent phenomenon, being no more than 2–7 million years old (Whitehouse and Pearce 1992), and the level of genetic diversity within a single alpine species (*D. connectens*) is compatible with the age of the alpine zone (Trewick *et al.* 2000). Therefore, the majority of species in our study must have differentiated before the alpine zone existed. Second, freeze tolerance has arisen independently many times within Orthoptera (Sinclair 1999): evidence that multiple origins are possible. An alternative explanation for the lack of monophyly in alpine weta is that there was a single origin of alpine adaptation and multiple loss of this trait, but this requires that weta

were pre-adapted to alpine living prior to the development of alpine habitats in New Zealand. The existance of two sister-species pairs, which comprise taxa with contrasting ecologies, confirm that shifts from lowland to alpine habitats (or vice-versa) have had more than one origin in the recent past (*D. parva* and *D. rugosa; H. maori* and *H. ricta*), and the ability to survive freezing has been found in lowland *Hemideina* species as well as alpine species (Sinclair *et al.* 1999). Lowland or alpine adaptation can therefore be viewed as quite a plastic character.

Biogeography

Geographic proximity is a feature with phylogenetic concordance within our evolutionary hypothesis. Eight of the ten terminal or subterminal clades, which have good support in our weta phylogeny, involve species with adjacent or slightly overlapping distributions. In contrast, one clade contains a pair of widely separated species (*D. tibiospina* and *D. carinata*) in northwest Nelson and on Foveaux Strait islands respectively, suggesting their present distributions are a relic of a former pattern. Relic populations on islands are likely to be the result of introduced predators and habitat disturbance by humans obliterating populations on the mainland. The *Deinacrida* and *Hemideina* lineages each have a well-supported three-species clade of arboreal forest weta reaching to the far north of North Island (Fig. 4). However, apart from these, all remaining species-richness is on South Island (including islands in the central Cook Strait). Many of the southern weta taxa tend to be adapted to open grass, shrub or rock habitats. In the South Island both alpine and lowland species exhibit east–west separation on either side of the axial mountains: *D. connectens*, *D. elegans*, *H. maori*, *H. ricta* and *H. femorata* to the east and *D. pluvialis*, *D. talpa*, *H. broughi* and *H. crassidens* to the west. The two western alpine species *D. pluvialis* and *D. talpa*, occur on either side of the alpine fault, with the former widespread species on the east of the fault-line, and the latter species confined to the Paparoa Range west of the fault. The patterns of geographical and evolutionary proximity seen in the weta phylogeny are generally consistent with cladogenesis being associated with geophysical barriers that have subdivided populations facilitating allopatric speciation.

Although twelve bipartitions are well supported in our evolutionary hypothesis of the New Zealand Deinacridinae, the absence of a suitable outgroup in the combined analysis leaves two important phylogenetic questions unanswered. Is *H. broughi* a member of the *Hemideina* clade (Ramsay and Bigelow 1978) and are the two genera reciprocally monophyletic?

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