A new species of tree weta from the North Island of New Zealand (Hemideina: Stenopelmatidae: Orthoptera)

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ABSTRACT

Hemideina trewicki, a new species of Stenopelmatidae from Hawkes Bay, is described. Morphologically it differs from H. crassidens only in the colouration of the pronotum but it can be distinguished using two allozyme loci (Ldh-2 and Pgm-1) and the number and gross morphology of the chromosomes. H. trewicki can be sympatric with H. thoracica and although a (probably sterile) F1 hybrid has been found, these two species have four fixed allozyme differences and karyotypes which clearly distinguish them.

Keywords: tree weta, cryptic species, *Hemideina crassidens, Hemideina thoracica, Hemideina trewicki*, Orthoptera, Stenopelmatidae, New Zealand, karyotype, allozyme.

INTRODUCTION

Two species of tree weta are common and widespread in the North Island: Hemideina thoracica White, 1845 (Auckland tree weta) in the north to about 41°S and H. crassidens (Blanchard 1851) (Wellington tree weta) south of Mt Taranaki and Mt Ruapehu (Trewick & Morgan-Richards in press). Much confusion existed over their nomenclature until Ramsay & Bigelow (1978) clarified the situation. Since its original description, H. crassidens has been twice included in revisions where descriptions can be found under different names; Hutton (1897) referred to it as H. megacephala and Salmon (1950) as H. thoracica. Karny (1934), perhaps the last worker to examine the holotype, distinguished H. crassidens from H. thoracica by the presence of abdominal bands and a dark pronotum. In contrast the pronotum of H. thoracica is light yellow/orange with distinct black markings.

Genetic investigation from extensive geographical samples has confirmed Ramsay & Bigelow's (1978) interpretation (Morgan-Richards, Daugherty & Gibbs 1995). For that study Wellington tree weta were obtained from as wide a geographical coverage as possible, including one Hawkes Bay location. This area is especially interesting as it broadly marks the northern limit of *H. crassidens*. When the allozyme characters of the Hawkes Bay weta were examined, it became evident that a discrete species existed there. With the addition of cytogenetic data, this paper describes the species found in that study. More specimens from Hawkes Bay have since been studied using allozyme electrophoresis but as the results do not significantly differ from those described (Morgan-Richards *et al.* 1995) they are not presented here.

Genetics of Hemideina

This recent genetic investigation of weta, and a paper dealing with two South Island Hemideina (Morgan-Richards & Townsend in press), are the first published allozyme electrophoretic studies of this group. The technique has been widely used world-wide and within New Zealand where its application in systematic studies has greatly improved knowledge of the native flora and fauna. Such investigations have: identified cryptic species of skinks (Daugherty, Patterson, Thorn & French 1990), tuatara (Daugherty, Cree, Hay & Thompson 1990) and fish (G. Wallis pers. comm., Smith & Robertson 1981); identified polymorphic species of chafer beetles (Emerson & Wallis 1994) and scree weta (Gibbs & Richards 1991); and described population structure of penguins (Triggs & Dardy 1989), galaxiid fish (T. King pers. comm.) and Nothofagus (Haase 1992). The technique has frequently been used in phylogenetic studies (e.g., marine molluscs (Michaux 1987), geckos (R. Hitchmough pers. comm.) and frogs (Green, Sharbel, Hitchmough & Daugherty 1989)).

For systematic studies, it is important that variation within species be characterised along with the investigation of interspecific variation. Interspecific allozyme variation is frequently characterised by fixed differences whereas conspecific variation is more usually in the form of frequency differences of the same alleles in different populations. Measures of genetic distance should be compared within studies because loci evolve at different rates and some lineages show significant variation from other taxa in their rate of allozyme evolution (Thorpe 1982).

Conspecific variation within *H. crassidens* was described to determine the specific status of *H. crassicruris* Salmon, 1950 and *H. brevaculea* Salmon, 1950 (Morgan-Richards *et al.* 1995). The level of conspecific variation found was similar to that found in similar studies of insects (Berlocher 1984 and references therein) and vertebrates (excluding birds) (Thorpe 1982). *H. thoracica* and *H. femorata* were used to determine the level of interspecific variation in this genus. An investigation of weta from Banks Peninsula that were intermediate in colour between the two species present on the peninsula (*H. femorata* and *H. ricta*), found that first generation hybrids are being produced without any detectable gene flow between these two species (Morgan-Richards & Townsend in press). It was also found that *H. ricta* is polymorphic for the presence of black markings on the tergites and legs. In this situation, colour characters previously used as diagnostic (Ramsay & Bigelow 1978) are not reliable and the ability to produce F1 hybrids persists despite the maintenance of genetic isolation.

Fixed karyotypes are characteristic of many species although chromosome variation within species is also well documented from many animals and plants. The significance of chromosome variation needs to be studied in the light of the cytogenetic characteristics of the taxa under investigation. Chromosome variation frequently causes abnormal products of meiosis in chromosome heterozygotes thus lowering fertility. The chromosome rearrangements involved and the taxa exhibiting them will determine the extent of the infertility; it may vary from undetectable to complete sterility of heterozygous individuals. In some species, chromosome rearrangements behave like neutral variations and occur in Hardy-Weinberg equilibrium within populations (Porter & Sites 1985). From the extremes of sterile hybrids to neutral mutations, the chromosome rearrangements provide additional characters for population genetics and systematic studies and, like other genetic characters, fixation in sympatry will indicate absence of gene flow. Variation in karyotypes has been found within both H. thoracica and H. crassidens (unpublished data) and so karyotype variation, in this group, on its own is unlikely to be enough to diagnose a separate species. The key strength of this study lies in the fact that the populations sampled are either sympatric or adjacent. Specific status can be determined due to fixed character differences in an area where continuous weta habitat recently existed. Sampling for this study is limited to the Hawkes Bay district and adjacent areas.

MATERIAL AND METHODS

Weta Collection Sites

Weta were collected from ten locations in or adjacent to the Hawkes Bay region as follows.

H. thoracica: Esk Forest (39° 20'S, 176° 44'E), Hastings (39° 38'S, 176° 49'E), Mohi Bush Scenic Reserve (39° 51'S, 176° 53'E) and Kaweka ranges (39° 24'S, 176° 23'E). Sample size = 6.

H. crassidens: Webber Rd (40° 24'S, 176° 17'E), Tiritea (40° 25'S, 175° 39'E), Mangaweka (39° 49'S, 175° 48'E), Mt Holdsworth (40° 54'S, 175° 29'E). Sample size = 8.

H. trewicki n. sp.: Raukawa (39° 44′S, 176° 37′E), Hastings (39° 40′S, 176° 49′E), Mohi Bush Scenic Reserve (39° 51′S, 176° 53′E), Blowhard Bush (39° 23′S, 176° 23′E), Porangahau (40° 10′S, 176° 36′E). Sample size = 16.

Cytogenetics

Air dried chromosome preparations (Webb 1976) were made from the reproductive tissue of male and female weta and plain stained with 10% Giemsa's stain in phosphate

buffer. Female weta were injected with a 0.05% colchicine solution in insect saline (1% KH₂PO₄, 0.8% Na₂HPO₄) 17 hours before being killed. After hypotonic treatment the reproductive tissue was fixed in 3:1 methanol:acetic acid for at least an hour before being used for chromosome preparations. For each weta, slides were scanned until the chromosomes of 15 mitotic cells had been counted. The chromsome spreads were photographed under oil immersion on T-max film with a Zeiss photomicroscope.

In common with the majority of orthopteran species studied (White 1973), female tree weta have two sex chromosomes (XX) and males have one (XO) (Richards 1989), thus diploid numbers quoted for males are odd. Plain stained chromosomes provide information about their gross morphology as well as the diploid number. The position of the centromere determines whether the chromosome is metacentric (the two arms of equal length), submetacentric (one arm substantially shorter than the other) or acrocentric (the short arm absent or not visible under a light microscope). This information is summarised by the fundamental number (NF) which is the number of chromosome arms in the complement.

Chromosome slides made from the weta in this study including the holotype and paratypes will be deposited with the type material at the Museum of New Zealand Te Papa Tongarewa, Wellington.

Allozyme electrophoresis

The methods and results are described in detail elsewhere (Morgan-Richards et al. 1995). Eighteen populations of weta were sampled including eleven from the North Island and 99 weta were examined using standard starch gel electrophoresis. 26 presumed genetic loci were analysed and used to resolve the taxonomy and produce an unrooted phylogenetic tree of the three North Island *Hemideina* species.

RESULTS

Cytogenetics

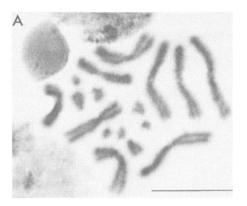
Three distinct karyotypes were observed. At Mohi Bush Scenic Reserve and in Hastings, both *H. thoracica* and the new species were collected and thus variation for chromosome complement at single locations were observed. At Mohi Bush one hybrid specimen was discovered for which karyotype data coincided with allozyme data and external colour, identifying this weta as a first generation hybrid. All other samples were monomorphic for karyotypes. With the exception of the hybrid individual, the three species showed fixed karyotype differences.

- H. thoracica (Fig. 1a): X-chromosome large and metacentric, indistinguishable from four pairs of large metacentric autosomes; four pairs of small acrocentric autosomes decreasing in size, the largest smaller than the arms of the metacentric chromosome (Table 1).
- H. crassidens (Fig. 1b): X-chromosome large and metacentric; five pairs of large metacentric autosomes decreasing in size; two small autosome pairs, one pair metacentric and one pair acrocentric (Table 1).
- H. trewicki n. sp. (Fig. 1c): X-chromosome large and metacentric; three pairs of metacentric autosomes; three pairs of medium submetacentric autosomes; one pair medium metacentric and one small pair acrocentric (Table 1).

Hybrid male: 2n = 17 (XO), NF = 29. Large metacentric X-chromosome, eight large metacentric autosomes, three medium submetacentric, one medium metacentric and five small acrocentric autosomes.

Allozyme electrophoresis

Fixed differences separate the three species. The alleles observed in these species for six polymorphic loci are defined based on their comparative speed (Table 1). *H. thoracica* has nine private alleles, *H. crassidens* has four and the new species has one. The minimum number of fixed allozyme differences between any pairwise comparison is two; between





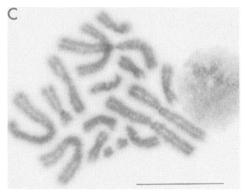


Fig. 1: The chromosomes during mitosis from testicular tissue of adult tree weta. A: *Hemideina thoracica* from Hastings, 2n = 17 (XO). B: *Hemideina crassidens* from Mt Holdsworth, 2n = 15 (XO). C: *Hemideina trewicki* n. sp. preparation made from the holotype from Mohi Bush Scenic Reserve. 2n = 17 (XO). (Scale line in each case $= 20\mu m$).

Table 1: Characters that distinguish the three tree weta species in Hawkes Bay, (characteristic alleles at each of the loci given: vS = very slow; S = slow: M = medium; F = fast; vF = very fast).

Character	H. thoracica	H. crassidens	H. trewicki
Pronotum light yellow/orange with black			
markings (Fig. 2)	yes	no	ye
Abdominal segments strongly banded	no	yes	ye
Abdominal tergites with mottled pigment	yes	no	no
2n (XO)	17	15	17
NF (number of chromosome arms)	26	28	32
Submetacentric autosomes present	no	no	ye
<i>Idh</i> - 2 alleles	vS, S	M, F	F
Ldh- 2 alleles	F	M	F
Mdh-2 alleles	M, F	S	S
Pgd alleles	M, S	S, F	S, F
Pgm-l alleles	F , vF	S, F	M
Pgm-2 alleles	vS, S, M	S, F	F

H. crassidens and the new species. Frequency differences at three loci also reveal differentiation between H. crassidens and the new species.

DESCRIPTION

Hemideina trewicki, new species

Figs 1c & 2

Diagnosis

Colour: Unique combination of (1) the presence of black or brown bands on the anterior and posterior edge of each abdominal tergite and (2) the pronotum light yellow/orange with dark brown or black markings in the grooves of the dorsal surface.

Allozymes: Two fixed differences from *H. crassidens*: lactate dehydrogenase-2 (*Ldh*-2) allele migrates at a faster rate (more positively charged); phosphoglucomutase-1 (*Pgm*-1) allele migrates faster than common North I. *H. crassidens* allele. Four fixed differences from *H. thoracica*: isocitrate dehydrogenase-2 (*Idh*-2) faster, malate dehydrogenase (*Mdh*-2) slower, *Pgm*-1 slower and *Pgm*-2 faster (Table 1).

Karyotype: Diploid number in male is 17 (XO) and in female 18 (XX). Fundamental number 32 (XO) and 34 (XX). Three pairs of large metacentric autosomes, three pairs of submetacentric autosomes, one pair of medium metacentrics, one pair of very small acrocentric autosomes.

Male and Female

Head: Antennae long, with 250-340 segments per antenna. Mandibles slightly keeled but not with blade; elongated, longer in adult males than in adult females.

Thorax: Prosternum without spines but with two rounded projections. Mesosternum and metasternum bilobed without spines.

Legs: Fore-tibia with 1-2 dorsal apical spines and 10-11 ventral spines. Fore-femur without spines. Mid-tibia with one small dorsal spine near tarsus and 8-11 ventral spines. Mid-femur with a single small retrolateral apical spine. Hind-tibia with 10-12 dorsal spines and 6-9 ventral spines. Hind femur with 0-10 dorsal spines, 2-11 ventral spines and 2 apical spines. Second joint of hind tarsus with single blunt projection above. Last tarsal segment as long as first 3 tarsi combined.

Abdomen: Second abdominal tergite with a file of 4-10 stridulatory ridges on each side, against which fine pegs on the inner hind femoral surface are rubbed.

Genitalia: Male: apex of sub-genital plate slightly concave between styles, strongly concave in juveniles. Female: sub-genital plate triangular, apex notched strongly.

Colour: Head dark brown or black. Pronotum light yellow/orange (Revised Standard Soil Color Charts, Oyama & Takekara (1967)) with dark brown or black markings as in Fig. 2. Metanotum and mesonotum dull yellow/orange with black markings. Abdominal tergites transversely banded light yellow/orange with dark brown or black posterior and anterior margins. Ventral surface of abdomen pale brown. Pigmentation of abdomen not mottled. Femora pale yellow/orange with dark brown or black markings. Hind tibia brown with darker dorsal spines, fore and mid tibia light yellow/orange. Male subgenital plate reddish brown.

Measurements of holotype: Head width 8.9mm, head length 10.8mm. Pronotum width 8.2mm, pronotum length 5.9mm. Fore tibia 10.9mm, mid tibia 10.0mm, hind tibia 17.2mm, hind femora 15mm long respectively. Ridges per tergite file: right 7, left 8.

Material examined

Holotype: Adult \circ plus three chromosome slide preparations. Mohi Bush Scenic Reserve (39° 52′S, 176° 52′E), February 1994, S. A. Trewick & M. Morgan-Richards. Deposited with the Museum of New Zealand Te Papa Tongarewa, Wellington (MONZ).

Paratypes: 1♀, 3♂♂, Mohi Bush, February 1994, S.A. Trewick & M. Morgan-Richards (MONZ). 2 ♂♂, same data (New Zealand Arthropod Collection, Auckland).

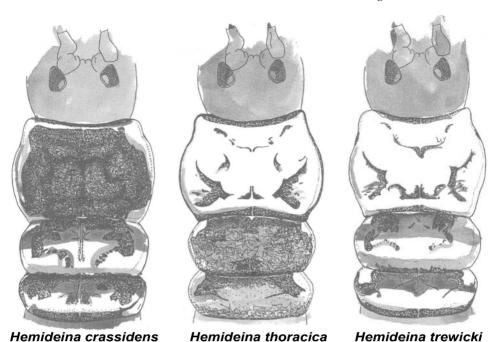


Fig. 2: The distinguishing colour pattern on the pronotum of the three North Island tree weta (Hemideina).

Other material: 11 ♀, 3 ♂ ♂, Raukawa, Hawkes Bay, August 1993, S. A. Trewick & M. Morgan-Richards (MONZ). 1 ♂, Hastings, in apricot tree, February 1994, S. A. Trewick & M. Morgan-Richards. 1 ♂, Blowhard bush, Kaweka Range, May 1994, M. Morgan-Richards, S. A. Trewick & J. Trewick. 1 ♀, 1 ♂, Porangahau, May 1994, S. A. Trewick & M. Morgan-Richards.

Each paratype and non-type specimen is accompanied by one chromosome slide preparation.

Distribution

Collected from five locations in Hawkes Bay: Raukawa, Mohi Bush Scenic Reserve, Blowhard Bush, Porangahau, and Hastings city. It is likely that it is found throughout the Hawkes Bay district. Northerly extent of distribution unknown (but see Trewick & Morgan-Richards in press). *H. trewicki* has a limited distribution in a region where native bush is not common. The species survives in urban gardens and bush remnants. Scenic reserve status affords protection at Mohi Bush.

Etymology

This species is named after the collector.

DISCUSSION

Sympatric taxa

Sympatric species are easy to define if assortative mating results in fixed character differences between the members of the two populations. A single character, whether genetic or morphological, can be enough to show that individuals belong to two or more gene pools. *H. thoracica* and *H. trewicki* are known to be sympatric at Hastings, Mohi Bush and in the Kaweka ranges. They can be distinguished externally by the presence in the latter of bold transverse black and light yellow/orange bands on the abdominal tergites, and genetically by five characters (Table 1).

One male was found to be morphologically intermediate between the two species. It

was also genetically intermediate, being heterozygous for chromosome complement and at those loci where the two species show fixed differences. The only exception was the sex linked locus Pgm-1, a locus at which H. thoracica and H. trewicki differ in their alleles. The hybrid was male and therefore hemizygous expressing a single allele at this locus, as seen in the tree weta hybrids found on Banks Peninsula (Morgan-Richards & Townsend in press). The single allele present in the hybrid was that characterising H. thoracica and so the weta is presumed to be a first generation hybrid between a female H. thoracica and a male H. trewicki. Studies of meiosis in this individual suggest that it would have been infertile due to failure of homologous chromosomes to align. These data are consistent with the presence of four fixed allozyme differences and fixed colour and karyotype differences between these sympatric species, indicating that they retain discrete gene pools.

Parapatric taxa

In the case of parapatry, in order to resolve taxonomic questions, extensive examinations of closely related taxa occupying different geographic ranges have been undertaken, often without a final taxonomic solution. Where the ranges of two similar forms meet, clines or hybrid zones may result, as for example those seen in mice (Mus musculus domesticus, (Sage, Atchley & Cappanno 1993)), grasshoppers (Caledia captiva (Shaw, Marchant, Contreras, Arnold, Groeters & Kohlmann 1993)) and pocket gophers (Thomomys (Patton & Smith 1990)). In such situations the species concepts used by the authors influence the nomenclature they decide to use.

The weta described here has apparently remained undetected due to its overall similarity to *H. crassidens*. It can be clearly separated from this species by two allozyme loci (Morgan-Richards et al. 1994), karyotype and colouration of the pronotum (Table 1). The light yellow/orange pronotum of the new *Hemideina* resembles more closely that of *H. thoracica* and the South Island species, rather than the dark pronotum of *H. crassidens*. Colouration and patterns are not good characters to distinguish *H. ricta* from other *Hemideina* species (Morgan-Richards & Townsend in press) because of variation within *H. ricta*; it is possible that variation within *H. crassidens* will make the only visible character distinguishing *H. trewicki* from *H. crassidens* problematical. A colour polymorphism has also been noted in the Mahoenui giant weta (*Deinacrida* sp) where about a third of the population is dark yellow rather than the more common dark tan-brown (Sherley & Hayes 1993).

Further searching is required to determine whether H. trewicki is purely parapatric with H. crassidens or sympatric in part of its range as only 30km separate the two sites where these species have been found to approach most closely. Patchiness of the remaining habitat in the highly-modified landscape makes assessment of the natural distribution of H. trewicki very difficult. The closest sites where H. crassidens has been collected are Mangaweka (38° 49'S, 175° 48'E) (to the west) and Webber Rd (40° 24'S, 175° 17'E) (to the south). An additional record of *H. crassidens* comes from Blowhard Bush (Moeed & Meads 1992), the most northerly location west of Mt Ruapehu of H. crassidens but this weta may be H. trewicki; efforts to obtain this material for verification have failed. The genetic investigation of the samples collected suggests that, although geographically proximal, the two species are maintaining discrete gene pools. It appears that these two species although parapatric are genetically distinct and thus are capable of maintaining separate evolutionary fates, and so under the evolutionary species concept (Wiley 1978) would be considered separate species. With fixed colour and genetic characters that are diagnostic and monophyly (suggested by allozyme analysis (Morgan-Richards et al. 1995), H. trewicki satisfies the criteria set out by the phylogenetic species concept (Cracraft 1983). The cohesion species concept (Templeton 1989) requires that separate species are neither genetically nor demographically exchangeable with any other taxa. My data support the view that H. trewicki, with unique genetic characters, is not genetically exchangeable with any other weta species. There is no information about the ecology of this species to know if it is demographically exchangeable. The genetic differentiation described suggests that H. trewicki has in the past been reproductively isolated from all other Hemideina populations. Whether it is currently completely reproductively isolated from H. crassidens so that they cannot produce fertile off-spring, as required by the biological species concept (Mayr 1963), requires further investigation. In my view there is adequate evidence that *H. trewicki* is genetically isolated from the other two described North Island *Hemideina* and therefore should be regarded as a separate species.

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