Te Pūtaiao o Tokoriro:

Taxonomy and diversity of New Zealand cave wētā (Orthoptera; Rhaphidophoridae)

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Abstract

Species are the fundamental unit for ecology and evolution. Taxonomy, the naming of species, grabbles with the problem of accurately representing these fundamental units. In this research I targeted a group of understudied and undervalued insects that are common throughout New Zealand. This work focuses on Rhaphidophoridae, a family of Orthoptera found globally, but the diversity in New Zealand is poorly understood and poorly described. I have been the first to use high specimen numbers in order to establish within and between species differences of New Zealand cave wētā. I have established the importance of multiple taxonomic methods. At no stage was the aim to fully resolve all issues, but rather to identify morphological characters that are useful in distinguishing species, and integrating mtDNA sequence data to test species hypotheses.

I focused first on cave wētā specimens that came from a biodiversity studied but had not been identified to genus or species. I was able to identify characters that could distinguish between the taxa present in this sample and developed a method that could be transferred to other locations. Two key findings were that multiple cave wētā species co-exist across a range of habitats and that variation in abundance was species dependent. Of importance was my finding that juveniles cannot be distinguish and placed with their correct adult form due to changes in both subgenital plate shape and apical spines.

From three regions in North Island New Zealand I was able to distinguish and identify fourteen putative cave wētā species. mtDNA sequence data were use to test putative species clusters identified by morphology and allowed me to confidently pair male and female specimens. Combinations of apical leg spines and subgenital plate shape could consistently diagnose most taxa. Many of the species are new to science. Therefore I described three new species in the genus *Neonetus*. I reviewed our current knowledge of the endemic genera *Pleioplectron, Weta* and *Miotopus* and based on evidence from mtDNA sequences and large samples I was able to clarify current species and describe one new *Miotopus* species. As with many insect species, male terminalia are the key to distinguishing among species, and species within the same genus have similar female subgenital plates.

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CHAPTER 1

Introduction to Rhaphidophoridae

Pachyrhamma edwardsii aggregation on wall of a tunnel, Percy's Reserve, Wellington. Photo credit: S. A. Trewick

‘Takoto kau ana te whānau a Tāne”

The descendants of Tāne are laid low

– Tāne is the god of the forest. This is a plea for conservation.

Māori view the natural world with a holistic approach, their beliefs and traditions acknowledge their relationships within the natural environment (Harmsworth & Awatere, 2013). Māori traditional whakapapa (genealogy) places all living flora and fauna within the same family tree. Thus they see themselves as part of the environment and ecosystems rather than being separate from it. This whakapapa or the genealogical sequence from the beginning of time to present is central to Māori perspective of the natural world and their link within it. Central to their belief is the creation myth of the separation of Ranginui (Sky father) and papa-ti-a-nuku (Earth mother) which allowed the birth of their children (wind, forest and plants, sea, rivers and animals). The key thing here is that humans are not separate to other animal and plant species but are included and therefore a key component of a balanced ecosystem. This is reflected in their roles as Kaitiaki (guardians) for carrying out Kaitiakitanga (sustainable resource management and guardianship). Viewing all life as being part of the same whakapapa is compatible with our current understanding of the evolution of life on earth, because all species are linked by a common ancestor (Darwin, 1859; Theobald, 2010).

It has become increasingly more common to take a holistic view of conservation and include indigenous people in planning and monitoring local ecosystems. Through traditional ecological knowledge, tangata whenua (people of the land, or original inhabitants of New Zealand) are well placed to be highly involved in current planning, management and conservation of the environment (Ramstad et al., 2007). This thesis brings the importance of whakapapa to the understanding and conservation of the endemic New Zealand insect species known as cave wētā or Rhaphidophoridae.

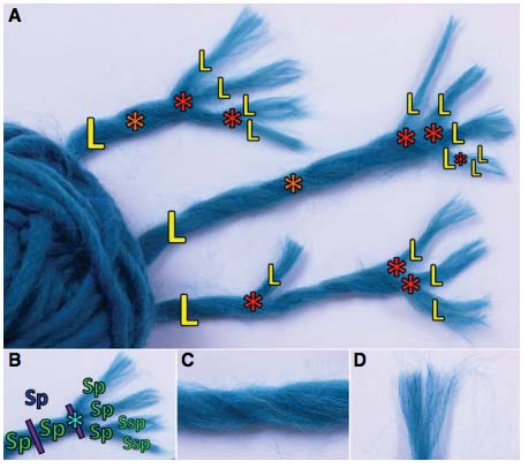
Taxonomy

Taxonomy is the discovery, description, naming and classification of living organisms on earth and the study of their whakapapa (genealogy or evolutionary relationships). Good taxonomy is important in all biological research (Khuroo et al., 2007). As

researchers we need to know what taxonomic units we are considering, whether we study conservation, ecology, phylogenetics, physiology, biochemistry or biomedicine. For the most part we know and have described the large megafauna on earth and have a general understanding of species (see below), but our knowledge of the much greater diversity of smaller life continues to expand (Troia & McManamay, 2016). The diversity of unicellular organisms is only just being realised (Nee, 2004). The discovery of reproductively isolated but morphologically similar taxa (cryptic species) reveals underestimated species diversity. Tools to study the shape and form of plants and animals have resulted in a greater appreciation of the morphological variation that exists. Detailed assessment of morphological differences among specimens can sometimes reveal examples of very subtle patterns of morphological variation, yielding recognition of "pseudo-cryptic" species (Knowlton, 1993). In other situations, morphological variation is found to be within a single lineage, thus for some groups we have overestimated total biodiversity (Bickford et al., 2007). Problems of both underestimation and overestimation are seen in New Zealand cave wētā taxonomy; species diversity has been partitioned into too many genera (Cook et al., 2010), and new species are discovered by combining better sampling and genetic data. For example *Talitropsis* specimens from the Chatham Islands were originally thought to belong to a highly variable single species but are now recognised as two distinct species (Steven A Trewick, 1999).

Taxonomy is limited by poor sampling so that the diversity is not fully represented. But it can also suffer from an excessive number of descriptions where later taxa are recognised as synonymies (Gaston & Mound, 1993). This creates a problem for the biologists who follow, as historical taxonomy must be traced and corrected, before new taxa can be described. In addition, the definition of "species" differs among researchers and this too can lead to conflicts of understanding the literature. The subject of what a species is has been extensively discussed e.g Darwin, 1859; De Queiroz, 2007, 2011; Mallet, 1995; Mayr, 1942. Here I take the view that a 'species' is a taxonomic description of an arbitrarily delineated segment of an evolutionary lineage in time (see Fig. 1 Vaux et al., 2016). However, although a species is artificial, it remains a hypothesis based on empirical observations of an evolutionary lineage and as a hypothesis provides a set of important predictions. In practice, Mallet's genotypic

cluster definition provides a suitable method for identification of “species” using either (or both) morphological and genetic data (Mallet, 1995).



Vaux et al. 2016. (Figure 1) Yarn as a metaphor for evolutionary lineages: lineage-splitting and splitting hairs. A, a piece of yarn represents an evolutionary lineage (yellow L). Like evolutionary lineages, yarn is continuous and consists of many fibres. In both, splits can be identified (red asterisks). The origin of each piece of yarn in the tangled ball of wool represents the unknown common ancestry of lineages as we move backward in time. Many lineage-splits are also missed due to extinction (orange asterisks). B, particular segments of lineages can be classified as species (green Sp, purple lines representing temporal boundaries of segments), relative to the studied organism, the availability of data and the hypotheses under investigation. Segments of lineages can also be classified as subspecies or varieties (green Ssp), or consolidated as intraspecific variation (unlabelled lineages following the designation of a species). The assignment of these taxonomic categories is arbitrary as the size and scale of segments varies. Not all lineage-splits are classified as speciation (cyan asterisk), and species classifications based on ancestral and derived difference without evidence of lineage-splitting (e.g. chronospecies) do not invoke a discrete speciation event. Species may be described based on limited fossil evidence (blue Sp), because variation is novel or of interest, even when there is limited knowledge of the lineage to which it belongs. C, depending upon the scale of observation (limited by the availability of data such as zoom and resolution in photography or sampling in biology) further lineages (fibres) and splits (lineage-splits) can be identified. Many lineages do not persist for a significant length of time and either go extinct or hybridize with the original lineage. D, lineages are made up of individuals within populations and hybridization can unite populations (pieces of yarn that split may recombine soon thereafter). Differentiating lineages (fibres) is easier when divergence has followed a lineage-split.

Biodiversity

Biodiversity is the variation of life among living organisms, and includes the ecological complexes they are part of (Khuroo et al., 2007). Some areas of the world appear to contain a higher density of taxa than others, called 'hotspots'. Approximately 1.5 million species have been described and the total biodiversity on earth is estimated to be between 2-10 million (May, 2011). Estimates of biodiversity are always changing due to changing methods, ongoing extinction and discovery. The science of biodiversity is relatively young but has become one of the most important disciplines in biological science internationally because species extinctions due to human activity are resulting in a rapid loss of global biodiversity (Khuroo et al., 2007). The huge crisis that is facing scientists is the loss of biodiversity before we document its existence. It is important to note that the science of biodiversity relies on the science of taxonomy and systematics, without which we would not have the basis for biodiversity research.

The essence of biodiversity is not always obvious; the greatest numbers of species being invisible without aid (Nee, 2004). Our view of the natural world has often focused on the most visible, forgetting the microscopic diversity that can survive in the deepest oceans, hottest volcanoes, and driest deserts. The diversity of life provides a number of ecological services including air and water purification and pollination (Hoekstra et al., 2005; Mooney, 2010; Turner et al., 2007). The effects of this diversity on some of the ecosystem processes are not all well known; however, it is believed that the loss of species will have a huge impact on ecosystem functioning and services (Hooper et al., 2005; Worm et al., 2006). Loss of locally adapted species and populations disrupts the balance of the ecosystem's stability and functioning, particularly in today's rapid ecological changes (Worm et al., 2006). Having more species that respond to disturbances can stabilize an ecosystem and maintain the important functions that life requires. Our limited understanding of the link between biodiversity and the function of the environment is another reason why it is important to understand taxonomic diversity so we can further learn the role they play in ecosystems.

Cave wētā: Global diversity

Rhaphidophoridae are flightless, nocturnal insects commonly referred to as cave wētā (New Zealand) or cave crickets (rest of the world). Rhaphidophorids are found on every continent except Antarctica (Figure 1.1). Most well known species are found in cave systems throughout the world. Although New Zealand species are found living in crevices in rocks, banks, and tree trunks, it is the cave species that have received the most attention (e.g. Cook et al., 2010; Richards, 1954c, 1962). Some Rhaphidophoridae species live in dry arid environments of North America, for example *Daihinibaenetes giganteus* (Jay & Weissmann, 2011; Weissmann, 1997), whereas some are found in the treeless subantarctic islands, e.g. *Insulanoplectron spinosum* on Snares Island (Richards, 1970). However, most cave cricket species are restricted to cool, moist areas and shelter in forests or cave systems.

The family Rhaphidophoridae is divided into 10 subfamilies (Table 1.1) with 1102 described species distributed within 137 genera and are found worldwide (Eades et al., 2016). Nine subfamilies are found in the Northern hemisphere, with one subfamily, Rhaphidophorinae extending south into Australia. Macropathinae have a southern hemisphere distribution and contain 30 genera in southwestern Australia, Tasmania, New Zealand, South America and Southern Africa (Hubbell et al., 1978). Some subfamilies are restricted to small areas such as Tropidischinnae and Gammarotettiginae, found only in the state of California, North America. Anoplophilinae is a newly erected subfamily of 28 species located in Korea, a relatively small area for so many species. Protroglophilinae is a subfamily that provides insight into the evolutionary history of Rhaphidophoridae with extinct specimens found in Baltic amber from Europe of the Late Eocene (35mya) (Gorochov, 2010). Of all the subfamilies Aemodogryllinae, Macropathinae and Rhaphidophorinae are the most diverse.

It is likely that the known diversity of Rhaphidophoridae will increase as the generation of genetic data becomes cheaper, more readily available, and as we improve our taxonomic tools. One of the most well studied genera of cave crickets is *Dolichopoda,* which is distributed throughout the Mediterranean (Bachmann et

al., 1994; Bernardini & Ketmaier, 2002). This genus is highly diverse with over 40 described species (Eades et al., 2016). Most of these species are restricted to single cave systems between which gene flow is probably limited. *Dolichopoda schiavazzii* for example was found to have gene flow only between cave populations close to each other, creating high genetic subdivision among distant populations (Allegrucci et al., 1997). Evolutionary history of species and genera can be assessed using DNA sequence data from a number of mitochondrial genes such as 12S, 16S and COI, (Allegrucci et al., 2011). The family of *pDo500* satellite DNA has been discovered for the genus *Dolichopoda* and shows its use as a phylogenetic marker (Martinsen et al., 2009).

Species descriptions are usually based on morphological traits. For some species epiphallus and ovipositor type have been used to identify species, especially in *Dolichopoda* (Bernardini et al., 1996). In New Zealand, leg spines and sub-genital plate shapes have been the main traits used to distinguish species (Richards, 1958). Problems have been identified, as some leg spines are variable within species (Cook et al., 2010; Richards, 1958; Ward, 1997). Sub-genital plate shape is often very useful, but does depend on sex and age/maturity of the individual being examined. Thus we see a need for improved sampling and identification of characters to establish which are consistent within species.

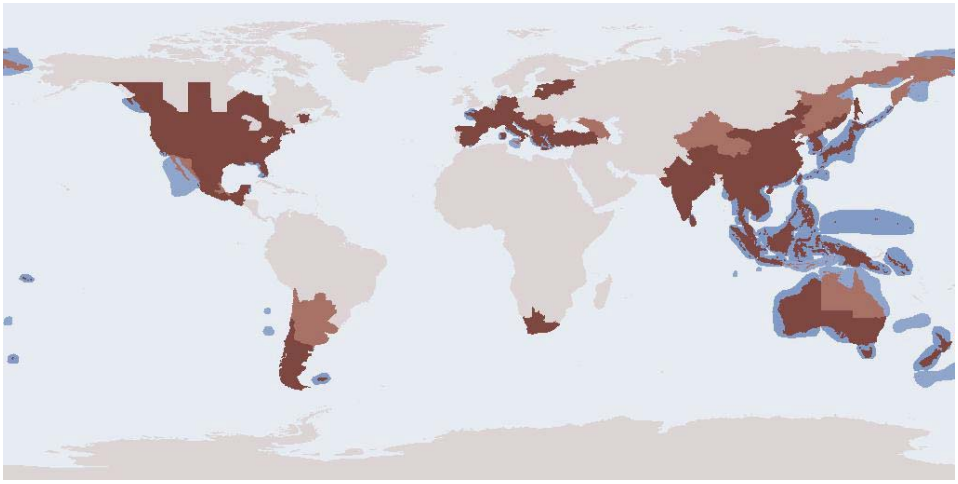


Figure 1.1 Distribution of Rhaphidophoridae around the world. From Orthoptera species file online 29 April 2011 (Eades et al., 2016)

Table 1.1 List of subfamilies within Raphidophoridae, and the number of genera and species and their location. Data from the Orthoptera species file online (Eades 2011).

Subfamily	Genera	Species	Range
Aemodogryllinae (Walker, 1871)	12	93	Asia-tropical/temperate, Europe, NA
Anoplophilinae (Storozhenko & Paik 2010)	2	28	Korea
Ceuthophilinae	24	71	North America
Dolichopainae (Brunner von Wattenwyl 1888)	1	47	South Europe, Asia Minor, Caucasus, Transcaucasia
Gammarotettiginae	1	6	California
Macropathinae (Karny 1929)	29	95	Austral
Protroglophilinae (Gorochov 1999)	2	4	Extinct from Europe
Rhaphidophorinae (Walker 1871)	6	84	Eat Asia, Australia and Samoa
Troglophilinae (Krauss 1879)	1	17	South Europe to Syria
Tropidischiinae (Scudder 1869)	1	1	California

Cave Wētā Ecology

All Rhaphidophoridae are flightless and nocturnal. They hide during the day in dark, humid places seeking refuge from the many avian and mammalian species that eat insects (Jones & Toft, 2006; Murphy et al., 1999; Murphy et al., 2016). Most Rhaphidophoridae are adept at jumping using their long hind legs for springing. They have long antennae useful for detection in the dark. The better-known species of rhaphidophorids are those that tend to dwell in caves. These are usually larger and more easily found than forest species, as they tend to aggregate in caves systems. Our knowledge of the ecology of most species is limited. Cave wēta or cave crickets are often scavengers eating plant, fungi and animal material. Foraging is done after dark when the animals leave their shelter, but how far they go is not known. Rhaphidophorids have been found on the ground and up in trees feeding on leaves and animals. Details of diet relies on observations of cannibalism, and

scavenging on invertebrates, plants and fungi (Richards, 1954, 1962). Some species we know move in and out of caves to feed, in the Mammoth National Park, USA (Lavoie, Helf, & L., 2007; Taylor, Krejca, & Denight, 2005). Aggregation pheromones of *Hadenoecus cumberlandicus* in cave systems in USA have been studied (Yoder et al., 2010). Temperature, moisture and humidity are important for Rhaphidophorids. *Hadenoecus subterraneus* does not leave the cave on cold nights with temperatures below 5°C due to a high evaporative water loss (Lavoie et al., 2007). From these studies we can glimpse the life of some species of cave crickets, however there is still a lot that is not yet understood.

New Zealand Cave wētā

As with most species around the world little is known about the biology of New Zealand rhaphidophorids and only a few taxa have been studied e.g. *Macropathus*. (Richards, 1954a, 1954b, 1954c). New Zealand cave wētā are part of the subfamily Macropathinae and there are 19 genera endemic to New Zealand (see below). New Zealand cave wētā, comprising ~ 56 species (Eades et al., 2016), fall into two tribes within the Subfamily Macropathinae Karny 1930. Macropathini Karny 1930 is the largest tribe with 29 genera found in New Zealand and Australia, while Talitropsini Gorochov 1988 has only one genus endemic to New Zealand and its offshore islands. This higher order classification is not supported by molecular phylogenetics that included five New Zealand genera (Allegrucci et al., 2010). Four of the five New Zealand species (*Talitropsis sedilotti, Pleioplectron simplex, Pachyrhamma edwardsii* and *Pallidoplectron turneri*) formed a monophyletic group sister to the Tasmanian species *Micropathus tasmaniensis*. The New Zealand species *Macropathus filfer* was not part of the fore mentioned clade, suggesting that the Tribe Talitropsini is not a natural group. Some New Zealand genera are endemic to offshore islands. They occupy a range of environments from caves, rotten logs, under stones, human made structures, holes in trees and even bird burrows. Despite being called *cave* wētā they are not restricted to caves, with most species living in forests, grasslands, and alpine rock and scree fields. Listed below are the endemic cave wētā of New Zealand.

Rhapdidophoridae Walker 1869

Subfamily: Macropathinae Karny 1930

Tribe: Macropathini Karny 1930

Genus: *Dendroplectron* Richards 1964

Species: *aucklandensis* Richards 1964

Genus: *Insulanoplectron* Richards 1970

Species: *spinosum* Richards 1970

Genus: *Ischyroplectron* Hutton 1896

Species: *isolatum* Hutton 1895

Genus: *Isoplectron* Hutton 1896

Species: *aciculatum* Karny 1937

armatum Hutton 1896

calcaratum Hutton 1896

cochleatum Karny 1906

Genus: *Macropathus* Walker 1869

Species: *acanthocera* Milligan 1926

filifer Walker 1869

huttoni Kirby 1906

Genus: *Maotoweta* Johns & Cook 2014

Species: *virescens* Johns & Cook 2014

Genus: *Neonetus* Brunner von Wattenwyl 1888

Species: *huttoni* Chopard 1923

pilosus Hutton 1896

variegatus Brunner von wattenwyl 1888

Genus: *Notoplectron* Richards 1964

Species: *campbellensis* Richards 1964

Genus: *Novoplectron* Richards 1958

Species: *serratum* Hutton 1904

Genus: *Pachyrhamma* Brunner von Wattenwyl 1888

Species: *chopardi* Karny 1935
delli Richards 1954
edwardsii Scudder 1869
fusca Richards 1959
giganteum Richards 1962
longicauda Richards 1959
ngongotahaensis Richards 1961
spinosa Richards 1961
tuarti Richards 1961
uncata Richards 1959
unicolor Salmon 1948
wapenensis Richards 1960
waitomoensis Richards 1958

Genus: *Pallidoplectron* Richards 1958
Species *peniculosum* Richards 1960
subterraneum Richards 1965
turneri Richards 1958

Genus: *Paraneonetus* Salmon 1948
Species: *multispinus* salmon 1948

Genus: *Petrottetix* Richards 1972
Species: *cupolaensis* Richards 1972
nigripes Richards 1972
serratus Richards 1972
spinosus Richards 1972

Genus: *Pharmacus* Pictet & Saussure 1893
Species: *brewsterensis* Richards 1972
chapmanae Richards 1972
dumbletoni Richards 1972
montanus Pictet& Saussure 1892

Genus: *Pleioplectron* Hutton 1896
Species: *cavernae* Hutton 1900
diversum Hutton 1896

hudsoni Hutton 1896
pectinatum Hutton 1896
simplex Hutton 1896

Genus: *Setascutum* Richards 1972
Species: *ohauensis* Richards 1972
pallidum Richards 1972

Genus: *Weta* Chophard 1923
Species: *thomsoni* Chopard 1923

Tribe: Tallitropsini Gorochov 1988

Genus: *Talitropsis* Bolivar 1882
Species: *apoduroides* Karny 1930
chopardi Karny 1937
crassicruris Hutton 1896
irregularis Hutton 1896
megatibia Trewick 1999
poduroides Walker 1871
sedillotti Bolivar 1882

The most recent cave wētā description was published just two years ago (Johns & Cook 2014). It is thought that there are many cave wētā species in New Zealand that have not been described (Gordan, 2000), and smaller forest species in particular, such as those belonging to *Isoplectron, Pleioplectron* and *Neonetus*, have not been well described. Species found in forests tend to aggregate less than cave-dwelling species and their cryptic colouration and quick jumping ability make them extremely difficult to find and catch for study purposes. Also, small cave wētā species are often mistaken for juveniles of larger species and not collected. The genus *Pachyrhamma,* although not restricted to caves, has many species that do occupy cave systems making them easier to find and study. This only emphasises why so many species are yet undescribed and undetected.

New Zealand cave wētā, for example suffer from taxonomic misidentification problems (See Appendix 1). Richards (1954c) noted from descriptions of a new

genus erected by Brunner 1888 that *Pachyrhamma* was in-fact the same species that Walker in 1869 described as *Macropathus filifer*. Over the years the genera *Macropathus* and *Pachyrhamma* have been redescribed numerous times, without the authors realizing they were describing the same species. *Pachyhramma edwardsii* (=*Macropathus filifer)* is a common, large and widespread species around New Zealand making it relatively easy to observe and catch. Richards was not hesitant to synonymise many described species under the name *M. filifer* being the most commonly found and observed a great variation in characters that were used to identify species. In one case Walker (see Richards, 1954c) described two species (*M. filifer*, *M. fascifer)* only from male specimens and (*M. altus*) from a single female. Due to natural variation within species it appears that these are male and females of the same species *M. filifer* (Richards, 1954c). However, it is now clear that Richards (1954c) was referring to *Pachyrhamma edwardsii* (Cook et al., 2010). Use of DNA data revealed that the genus *Macropathus* is distinct from *Pachyrhamma* but that some species placed within *Macropathus* are part of the *Pachyrhamma* clade (Cook et al., 2010). For example *Macropathus fascifier* is a synonym of *Pachyrhamma edwardsii.* Ward (1997) distinguished *Macropathus* and *Gymnoplectron (=Pachyrhamma)* by shape of female subgenital plate and apical spine number, but this was based on existing descriptions, not re-evaluation of the specimens. An important note taken from these descriptions is the importance of good preservation and sample size. Many descriptions were based on single individuals and of poor quality, often having parts broken and shrunken.

When Richards (1954, 1958, 1960 etc) re-examined type specimens she often found that the original descriptions were different from the type material she saw, suggesting there is also variation in the way people describe the characters that they see. For example Richards (1954c) noted that Walker (1871) had described the fore part of the head being “nearly horizontal” but Richards saw it as “vertical” and the eyes were recorded as “small” by Walker but “large” by Richards (Richards, 1954c).

It is important at the moment to develop a taxonomic framework of characters and terms that can be used to diagnose species and it is important to clarify what these characters are through photos and drawings. From experience reading

descriptions and trying to find these characters, I have found that it is often difficult to interpret what body part or shape the writer is referring to. In particular spine counts are hard to follow if spines are not accurately and consistently referred to. Often more than one name has been given to the same structure, which adds to the confusion.

As well as the misidentification problems, there is also the problem where specimens cannot be identified to species. There are many examples in published work where rhaphidophorids are identified to the genus or family level. For example, Spurr and Berben (2004a) list species of wētā from other studies where they have been recorded as eating baits. We can see that only one of the eight specimens listed has been identified to species level, the rest to genus and one as "unidentified". Information like this has the potential to add to the repertoire of knowledge for that species, such as where a species is found and the effects baits have on populations, but only if it can be appropriately assigned.

For the general public there is very little information on the descriptions and ecology of species including some basic identification of characters that may help place species into genera. A future goal will be to create a website that contains as much information on these creatures as is available. Wetageta (http://wetageta.massey.ac.nz/) is a searchable website that does just this but only contains the information we have to date.

Table 1.2 Science literature relating to New Zealand cave wētā.

Author	Name	Topic
Allegrucci et al., 2010	*Macropathus filifer* *Pachyrhamma edwardsii* *Pallidoplectron turneri* *Pleioplectron simplex* *Talitropsis sedilotti*	Systematics
Bolivar, 1882	*Talitropsis sedilotti*	
Brunner von Wattenwyl, 1888	*Neonetus variegatus* *Pachyrhamma*	Systematics
Chopard, 1923	*Neonetus variegatus* *Neonetus huttoni* *Weta thomsoni* *Pachyrhamma fascifer* *Pleioplectron cavernae*	Systematics
Cook et al., 2010	*Gymnoplectron longipes* *Macropathus* sp. *Pachyrhamma acanthoceras* *P. delli* *P. edwardsii* *P. fuscum* *P. giganteum* *P. longicaudum* *P. ngonogtahaense* *P. spinosum* *P. tuarti* *P. uncatum* *P. waipuense* *P. waitomoensis* *Pleioplectron cavernae* *P. simplex* *Turbottoplectron cavernae* *T. unicolor* *Weta thomsoni*	Systematics
Gorochov, 1988	Tallitropsini	Systematics
Hutton, 1897	*Talitropsis sedilotti* *T. crassicruris* *T. irregularis* *Ischyroplectron isolatum* *Gymnoplectron longipes* *Pachyrhamma speluncae* *P. novae seelandiae* *P. fascifer* *Pleioplectron simplex* *P. hudsoni* *P. pectinatum* *P. diversum* *Neonetus variegatus* *N. pilosus* *Isoplectron armatum* *I. calcaratum*	Systematics; Hutton attempted to define genera and a number of species. Many he described himself others are redefinitions of existing taxa

	Pharmacus montanus *Macropathus filifer* *M. edwardsii*	
Johns 2014	*Maotoweta virescens*	Systematics
Karny, 1930	*Talitropsis apoduroides*	Systematics; also refers to higher taxonomic levels
Karny 1935	*Pachyrhamma chopardi*	
Karny, 1937	*Isoplectron aciculatum* *Talitropsis chopardi*	Systematics
Kirby, 1906		
Milligan 1926		
Richards, 1954a	*Macropathus filifer*	Ecology Observation
Richards, 1954b	*Macropathus filifer*	Observation
Richards, 1954c	*Macropathus filifer* *Macropathus acathocera*	Systematics Ecology
Richards, 1955		Ecology of general cave weta
Richards, 1958a	*Talitropsis crassicruris* *Novoplectron serratum*	Systematics Ecology
Richards, 1958b	*Macropathus filifer*	Systematics
Richards, 1958c	*Pachyrhamma longipes* *Pachyrhamma waitomoensis* *Pallidoplectron turneri*	Systematics
Richards, 1959a	*Pachyrhamma fusca* *Pachyrhamma uncata*	Systematics
Richards, 1959b	*Pleioplectron simplex* *P. hudsoni* *P. pectinatum* *P. diversum* *P. edwardsii* *P. cavernae*	Systematics
Richards, 1959c	*Pachyrhamma longicauda*	Systematics
Richards, 1960	*Pachyrhamma waipuensis* *Pallidoplectron peniculosum*	Systematics
Richards, 1961a	*Pachyrhamma waitomoensis* *Pallidoplectron turneri*	Ecology
Richards, 1961b		Observations
Richards, 1961c	*Gymnoplectron spinosa* *G. ngongotahaensis*	Systematics

	G. tuarti	
Richards, 1961d	*Gymnoplectron* *Macropathus* *Pachyrhamma*	Systematics and synonym
Richards, 1962a	*Gynmoplectron waitomoensis* *Pallidoplectron turneri*	Ecology
Richards, 1962b	*Gymnoplectron giganteum*	Systematics
Richards, 1964	*Dendroplectron aucklandense* *Notoplectron campbellense*	Systematics
Richards, 1965a		
Richards, 1965b	*Gymnoplectron waitomoensis* *Pallidoplectron turneri*	Ecology
Richards, 1965c	*Pallidoplectron subterraneum*	Systematics
Richards, 1970	*Insulanoplectron spinosum*	Systematics
Richards, 1971	Gymnoplectron Talitropsis Paraneonetus Dendroplectron Novoplectron Turbottoplectron Pleioplectron Insulanoplectron	Biogeography/ Relationships with Australia
Richards, 1972	*Pharmacus montanus* *P. chapmanae* *P. brewsterensis* *P. dumbletoni* *Petrotettix serratus* *P. spinosus* *P. cupolaensis* *P. nigripes* *Setascutum ohauensis* *S. pallidum*	Systematics
Salmon, 1948	*Turbottoplectron unicolor*	Systematics
Thomas et al., 1998	*Pleioplectron simplex*	Ecology
Trewick, 1999	*Talitropsis crassicruris* *T. megatibia* *T. sedilotti*	Systematics
Ward, 1997		Generic key to NZ family

Thesis structure and outline

This thesis is divided into six chapters dealing with the taxonomy and whakapapa of New Zealand cave wētā. The introduction (Chapter 1) is followed by a detailed study of numerous cave wētā specimens from a single location (Te Paki). Four species were identified and the large pitfall trapped collection provided a base for identifying key morphological traits that were consistent within putative species. This work has been published (chapter 2: Fitness J, Morgan-Richards M, Ball O, Godfrey RJA, Trewick SA. 2015. Improved resolution of cave wētā diversity (Orthoptera: Rhaphidophoridae): ecological implications for Te Paki, Far North, New Zealand. *New Zealand Journal of Zoology*). The third chapter compares adult specimens of forest cave weta from three North Island locations. In this work I combine morphological data and mtDNA sequences to study variation within species, delineate species boundaries and determine the distribution of taxa within and between locations. Chapter 4 and Chapter 5 review four genera and provide synonymies, re-describing species and describing five new species of New Zealand cave weta. Chapter 6 brings the results together and makes suggestions for future work.

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CHAPTER 2

Improved resolution of cave wētā diversity (Orthoptera: Rhaphidophoridae): ecological implications for Te Paki, Far North, New Zealand.

Abstract

The New Zealand cave wētā fauna is large and diverse but poorly described. This study aimed to improve the strategies for cave wētā identification and in doing so build an understanding of population dynamics and distribution of the taxon across three habitat types in the Te Paki Ecological District. Species identification used morphological traits and metric analysis of specimens in pitfall traps. Although nearly half the individuals were juveniles (<10mm long) that could not readily be distinguished from one another, four species were identified from the larger specimens. Capture rates of cave wētā varied by species, habitat, month and the interactions of these variables. Nearly half of all identified cave wētā individuals in our sample were *Neonetus variegatus,* which was abundant across all three habitats (pine forest, native forest and shrubland) throughout the year but caught in pitfall traps in greatest numbers in some pine forest sites*.* A species of *Pachyrhamma* was also abundant and showed seasonal variation in capture rate, but no adults were captured by pitfall traps. *Talitropsis* sp. and *Pallidoplectron* sp. were least frequent in our sample. Taxonomic resolution improves ecological inference, but as with other invertebrates, trapping method and design influence sampling outcome among species.

Introduction

Invertebrates provide a huge range of ecosystem services and functions that are largely unknown to the public or policy makers (Cardoso et al. 2011). Deficiency of ecological information is due in part to inadequate species discovery and classification reliant on scant information from different collecting locations and taxa being confounded. In New Zealand where species-level endemism is high (Trewick & Morgan-Richards 2009) and invertebrate diversity is inadequately characterized (Gordon 2010), studies of the distribution and abundance of forest invertebrates is impeded by lack of taxonomic resolution (Giangrande 2003; Ward & Larivière 2004). It is common practice in studies seeking to contrast biodiversity across habitats or time to taxonomically round-up to family and order level, discarding potentially informative ecological information about habitats, seasons and species (Bowie et al. 2006; Crisp et al. 1998; Moeed & Meads 1992;

Ruscoe et al. 2013). Inadequate taxonomic discrimination can influence all types of downstream biodiversity assessments (Whittaker 1972).

A primary use of biodiversity data is in the establishment of conservation criteria for habitats and areas (Kremen et al. 1993). It is generally assumed that diversity of native invertebrate species is greatest in the least modified areas where the highest diversity of indigenous plants exist (Crisp et al. 1998), but determining the biodiversity of any area, whether natural or modified, is currently intractable at the species level for many invertebrate groups. Similarly, estimation of ecosystem function or community health tends to be dependent on few readily recognized species rather than on the most relevant taxa (Hilty & Merenlender 2000). For example, Australian ants are often used as bio-indicators to assess effects of habitat disturbance (Hoffmann & Andersen 2003), and tree wētā (*Hemideina thoracica* (White, 1846)) abundance to assess the impact of predator control in New Zealand (Ruscoe et al. 2013).

Cave wētā (Orthoptera: Rhaphidophoridae) are abundant, widespread and diverse in most terrestrial New Zealand habitats but few species have been considered in detailed ecological analyses. This is largely because their inadequate taxonomy currently limits their value in comparing regional biodiversity or assessing the effects of habitat modification on biodiversity. There are 55 described New Zealand Rhaphidophoridae species assigned to 16 genera (Eades et al. 2013). Additional diversity certainly exists with many new species awaiting description. At the same time, genus and species level taxonomy needs revision and will involve some synonymy. For example, two genera have recently been discarded (Cook et al. 2010), and this attrition continues a long tradition within the New Zealand literature of revision and synonymy for invertebrates. Most taxonomic work has relied on few individuals from single locations, and the collection of Rhaphidophoridae in general has been limited. In part this is due to the expectation that cave wētā occupy caves. The scarce, locally-distributed large-bodied cave-dwelling species (mostly genus *Pachyrhamma* Brunner von Wattenwyl, 1888) dominate the literature at the expense of the majority that are relatively small, abundant, cryptic forest-dwelling species (e.g. Richards 1958a, b,

1959b, 1960; See also wetageta.massey.ac.nz). In fact, various cave wētā species occupy almost all terrestrial and arboreal habitats in New Zealand from bogs to alpine scree fields, but in most cases this is the limit of our understanding of their biology. Their light-shy nocturnal habit, sexual dimorphism and incomplete metamorphosis all impede taxonomic resolution, but our recent (unpublished) observations indicate that forests in central New Zealand are typically occupied by about six different cave wētā species.

The first task for efficient progress with the taxonomy and complementary ecological analysis of cave wētā is to identify characters and strategies that are useful in detecting differences between taxa. Clarification of terminology is essential to make such tools usable. Here we approach the general problem by explicitly examining how best to detect distinct taxa with the assumption of no prior information about the taxa at a location. Using cave wētā from an extensive sampling programme in Te Paki Ecological District (Far North, New Zealand), we set out to establish an approach to distinguish putative species, determine what taxa exist in the area, and use this information to explore their seasonal distribution and abundance among habitat types and sites.

Methods

Study region & sampling

Te Paki Ecological District in Northland, (Figure 2.1) is regarded as a biodiversity hotspot within New Zealand with a high number of endemic species including herbaceous plants (de Lange 2008), lizards (Chapple et al. 2008), insects (Buckley & Bradler 2010; Winterbourn 2009) and land snail species (Lux et al. 2009; Sherley 1996). The area has a high proportion of native vegetation but most of this is regenerating after anthropogenic fire and agricultural modification (Lux et al. 2009). The range of native habitat types includes kauri (*Agathis australis*) forest, mixed broadleaf-podocarp forest, coastal forest, wetlands, gumlands, and shrublands. There are also extensive plantations of introduced pine (*Pinus radiata*).

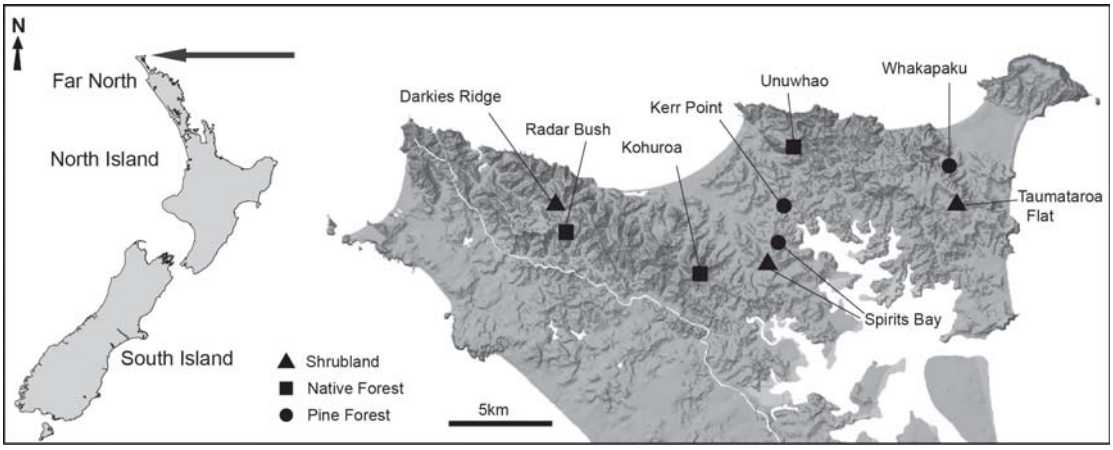

Figure 2.1. Te Paki Ecological District, Far North, New Zealand, showing location of pitfall trap sites that provided cave wētā specimens.

Sampling was carried out in three habitat types from 2006- 2007: native forest (mixed broadleaf-podocarp), pine plantation and shrubland. The latter is dominated by manuka (*Leptospermum scoparium)* and kanuka (*Kunzea ericoides*) but includes sedgeland and gumland elements. Cave wētā and other invertebrates were collected as part of a larger study of Te Paki biodiversity using a stratified design comprising three randomly selected sites in each of the three habitat types. Lethal pitfall trapping at each site, involved a cluster of eight traps placed in two rows of four with each trap 10m from its neighbour. Our sampling sites correspond to sites 18–26 of Ball et al. (2013). The traps consisted of a plastic sleeve 110mm in diameter sunk to just below ground level, inside of which was placed a snug-fitting plastic collecting cup (100mm deep). Approximately 100ml of 100% propylene glycol was used as the killing and preserving agent in each trap. Each trap had a plywood cover (200mm x 200mm x 12mm) raised approximately 30mm above the ground on wooden legs. Traps were reset monthly throughout the survey period from July 2006 until June 2007. The invertebrate samples were rinsed and stored in 80% ethanol and later sorted to family or order. At one site (Unuwhao A) where the rare beetle *Mecodema tenaki* Seldon & Leschen, 2011 was encountered, the sampling was reduced to once every three months to minimise adverse impact on that species.

Morphology and identification

Cave wētā from each site were initially sorted into two groups based on size so that attention could be focused on the morphology of the larger individuals that were more likely to be adult. Most wētā species descriptions rely on characteristics of adults and currently there are no reliable data on morphological variation among juvenile stages within and between species. Our experience and available species descriptions indicate that adult cave wētā are rarely less than about 10mm long (frons to posterior tip of abdomen) so we examined and gathered data from the larger individuals in all time periods and habitats. We expected to encounter large juveniles as well as adults because there is a high degree of variation in adult size among New Zealand cave wētā taxa. Distinguishing between adults and large juveniles relied on the darker sclerotised bodies and fully formed external genitalic structures of the former. In particular the pigmentation, shape and sharpness of ovipositors, sub-genital plates and cerci were informative about developmental stage, although these features differ subtly between adults and sub-adults (the penultimate instar).

Examination of putative adults allowed us to formulate hypotheses about which morphological characters could be used to characterise and distinguish the different taxa present. We subsequently returned to the group of small (<~10mm) individuals in order to determine whether any of these could be classified into one of the putative species inferred from larger specimens.

Specimens were assessed using morphological characters that have previously been considered in cave wētā taxonomy or have been found to be informative in similar arthropods. These characters included the combination of apical spines on the fore, mid and hind femora and tibiae, and shape of sub-genital plate. Altogether, presence/absence of each of 22 apical spines was recorded from one side of the body, although both sides were examined if there was any uncertainty about the absence of a spine, which might have been lost during handling (Table 2.1, Figure 2.2). Measurements were made of pronotum length (Pro), hind-femur length (HF) and hind-tibia length (HT) using electronic callipers. Leg

measurements were taken from the side that had the most complete legs still attached to the body to ensure correct allocation. Pronotum length was preferable to body length, which is variable in living and preserved specimens. The sub-genital plates of males and females were examined and classified into readily recognised types. Pigmentation and pilosity (hairiness) were considered but both are altered or difficult to assess in wet glycol preserved specimens.

Table 2.1. Apical spines used for diagnosis of species and a summary of the presence and absence on each of the four putative species of cave wētā from Te Paki Ecological District: 1= present 0 = absent

	Fore Femur Pro.	Fore Femur Retro.	Mid Femur Pro.	Mid Femur Retro.	Hind Femur Pro.	Hind Femur Retro.	Fore Tibia Superior Pro.	Fore Tibia Superior Retro.	Fore Tibia Inferior Pro.	For Tibia Inferior Retro.	Mid Tibia Superior Pro.	Mid Tibia Superior Retro.	Mid Tibia Inferior Prol.	Mid Tibia Inferior Retro.	Hind Tibia Superior Pro.	Hind Tibia Superior Retro.	Hind Tibia Inferior Pro.	Hind Tibia Inferior Retro.	Hind Tibia Inferior Sub.l Pro.	Hind Tibia Inferior Sub. Retro.	Hind Tibia Superior Sub. Pro.	Hind Tibia Superior Sub. Retro.
Spine Code	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**	**S10**	**S11**	**S12**	**S13**	**S14**	**S15**	**S16**	**S17**	**S18**	**S19**	**S20**	**S21**	**S22**
TPA	1	1	1	1	0	0/1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
TPB	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
TPC	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
TPD	1	0	0	1	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1

Morphometric data for comparative analysis were obtained from a subsample of specimens that represented the range of shapes, sizes and sex of specimens. Most of these were adults or large juveniles and we noted the presence of many males and females that were not adult but were nevertheless large compared to the average size of cave wētā in our sample. All statistical analyses used R v3.0 (R Core Team 2013). Exploratory analysis used Principal Component Analysis (PCA) in the *vegan* package (Oksanen et al. 2013). This analysis included the categorical apical spine and metric data to help determine whether taxa could be separated on the basis of these characters. PCA also examined whether juveniles could be matched to their adult counterparts using this morphological information, and which if any of these traits corresponded on males and females.

With data from adults and large juveniles (i.e. near adults) in the case of one morphotype), t-tests were used to compare size differences between the sexes and the putative species. ANOVA with a Tukey HSD test was used to compare different measured traits among putative taxa. We applied PCA to the metric data (Pro, HF, HT) on their own to assess morphological variation among individuals within the large specimen set. We identified a combination of characters that diagnosed a number of putative species. Alignment of the Te Paki taxa to the existing described cave wētā fauna involved judicious use of existing literature as detailed below.

Abundance

Total counts of all identifiable and unidentified juvenile cave wētā from each sample enabled us to analyse their relative abundance over space and time. All statistical analyses used R v 3.0 (R Core Team 2013). We used Generalised Linear Modelling (GLM) assuming a Poisson distribution of count data to compare cave wētā abundance over time. Site and habitat are nested variables. Strictly "site" is a random effect but was not fitted in this way because we wanted to determine whether there was additional site – site variation and so we added terms sequentially into the model. In general the number of trap-days was constant for all sites in a given month and variation among months was accommodated by including month as a factor in the models. Zero counts were inserted where traps were in use but caught no cave wētā, while traps not in use for a particular month

were coded as NA. We modelled cave wētā abundance with and without data for the unidentified juveniles as a fifth taxon. The response variable was the count for each species. The explanatory variables were site, habitat type (native forest, pine or shrubland) and time (month of the year trapped), and all possible interactions of these variables were considered.

Results

Using the larger cave wētā that were either adults or near adults, we identified four morphotypes from their spination, overall size and appearance. Males and females could be reliably paired based on spine counts and overall size. Despite their size, it was apparent that the largest individuals, all of which were assignable to taxon TPB, included no adults. Females, for instance, had relatively soft, pale and blunt ovipositors whereas adult Rhaphidophoridae ovipositors are sclerotised, dark, and pointed often with fine serrations. The size range of the TPB specimens was greater than the adults of TPA suggesting that a number of instars were included amongst the TPB sample. TPC and TPD were paler than TPA and TPB, and each had a unique spine combination (Table 2.1). TPC was similar in size to TPA and was initially overlooked because its pallid colouration and delicate form made it look like a juvenile of another species. The fourth phenotype, TPD, was the smallest of all of the putative taxa and this species also had a pale, juvenile-like appearance. Careful examination of the ovipositors in the females of TPD specimens revealed otherwise. The unique spine combinations of all four taxa reinforced our hypothesis that they were different species and not just variants of the first morphotypes encountered (Figure 2.3).

Discriminating morphotypes

Initial assessment of the reliability of classifying juveniles into one of the four morphotypes indicated that it was prudent to exclude small juveniles (<~10mm) from subsequent morphological analysis. There was no clear discrimination of juveniles based on size into one of the four putative species (Figure 2.4a). We also found that presence/absence of some spines to be more variable among the small juveniles than adults, suggesting an ontogenetic component to spine development. Juvenile females could usually be distinguished readily from their respective adults

by their pale, soft and blunt ovipositors lacking serrations. Juvenile males were less readily distinguished as late instars were very similar to adults. However, juveniles tended to be smaller, paler, with fewer apical and lateral spines on the legs, and the genitalia were underdeveloped and often difficult to see. Distinguishing penultimate and last instar individuals was the most difficult and in many cases impractical, but also may not be necessary except when secondary sexual characters are expressed only in the final instar. In order for species diagnosis to be as robust as possible we removed all small juvenile and uncertain individuals from the sample sets for each morphotype, excepting those large but not adult individuals of TPB, which could always be reliably distinguished from the other morphotypes.

Males and females within the same species had very different sub-genital plates associated with their different genital structure and function. From examination of adult specimens (and near-adult TPB individuals) collected in this study we were able to identify eight distinct sub-genital plate shapes; four relating to females and four to males (Figure 2.5). To pair the males and females of the same species we used the apical leg spines.

In the TPA specimens, females had a sub-genital plate that was small and triangular, with a notch at the apex, whilst in males it was curved distally with a double keel separated by a shallow groove. TPB females had a triangular sub-genital plate but the males had a long, narrow tongue-like structure indented on the ventral surface. The TPC females' subgenital plate was broad with parallel sides and two distal lobes, while in males it was slightly curved upwards distally with no keel. The female TPD sub-genital plate was broad and short, with the distal margin toothed, and in the male it was narrow at its base but widening as it curved upwards (Figure 2.5).

Four main permutations of apical spines were identified (Table 2.1). In addition we found that the hind femur retrolateral apical spine was sometimes present and sometimes absent in specimens of TPA. This variation showed no consistent pattern in space or time, and was therefore considered to be polymorphic within

this species. The three other apical spine combinations were unvarying among individuals of the same morphogroup including males and females, which allowed them to be matched. Presence/absence of six apical spines varied consistently among the four species; fore-femur retrolateral apical spine, mid-femur prolateral apical spine, fore-tibia superior prolateral apical spine, mid-tibia superior prolateral apical spine, hind-tibia inferior sub-apical prolateral spine, and hind-tibia inferior sub-apical retrolateral spine (Table 2.1 & Figure 2.2). Together these provide a combination of character states that consistently and reliably diagnosed adults and near adults of the four taxa encountered.

Metric analysis

Data from 319 adult TPA, TPC and TPD, 104 large TPB pre-adults and 154 other unidentified small juveniles were used in metric analysis to compare shape and size between sexes and among the four taxa. Only for TPA did we find any significant size difference between the means of adult males and females (t-test, $P<0.0001$, Table 2.2). Although males and females of the other putative species did not differ significantly in size we note that there were quantitative differences between sexes. For instance, the hind-femur of male TPC specimens was longer than the females' (Figure 2.3). Adult TPB may well differ but this could not be tested with the present sample.

Table 2.2. Comparisons using t-tests of male and female mean sizes for three morphological traits in four species of cave wētā (cave wētā) from Te Paki Ecological District. Bold = P<0.05. Standard errors for each mean value are in brackets.

Mean size in mm. (Standard Error)	*Neonetus variegatus* (TPA)		*Pachyrhamma* n.sp (TPB)		*Pallidoplectron* n.sp (TPC)		*Talitropsis* n.sp (TPD)	
	Male n=115	Female n=182	Male n=53	Female n=51	Male n=5	Female n=2	Male n=5	Female n=6
Pronotum	**2.690** (0.023)	**2.980** (0.023)	3.906 (0.185)	4.358 (0.198)	3.190 (0.107)	3.275 (0.215)	2.450 (0.088)	2.384 (0.084)
Hind femora	**8.630** (0.090)	**8.927** (0.074)	12.610 (0.717)	13.293 (0.614)	16.700 (0.175)	10.040 (2.15)	7.120 (0.362)	7.409 (0.467)
Hind tibia	9.346 (0.099)	9.422 (0.078)	13.750 (0.740)	14.508 (0.638)	12.500 (0.196)	11.720 (3.45)	6.880 (0.423)	7.665 (0.679)

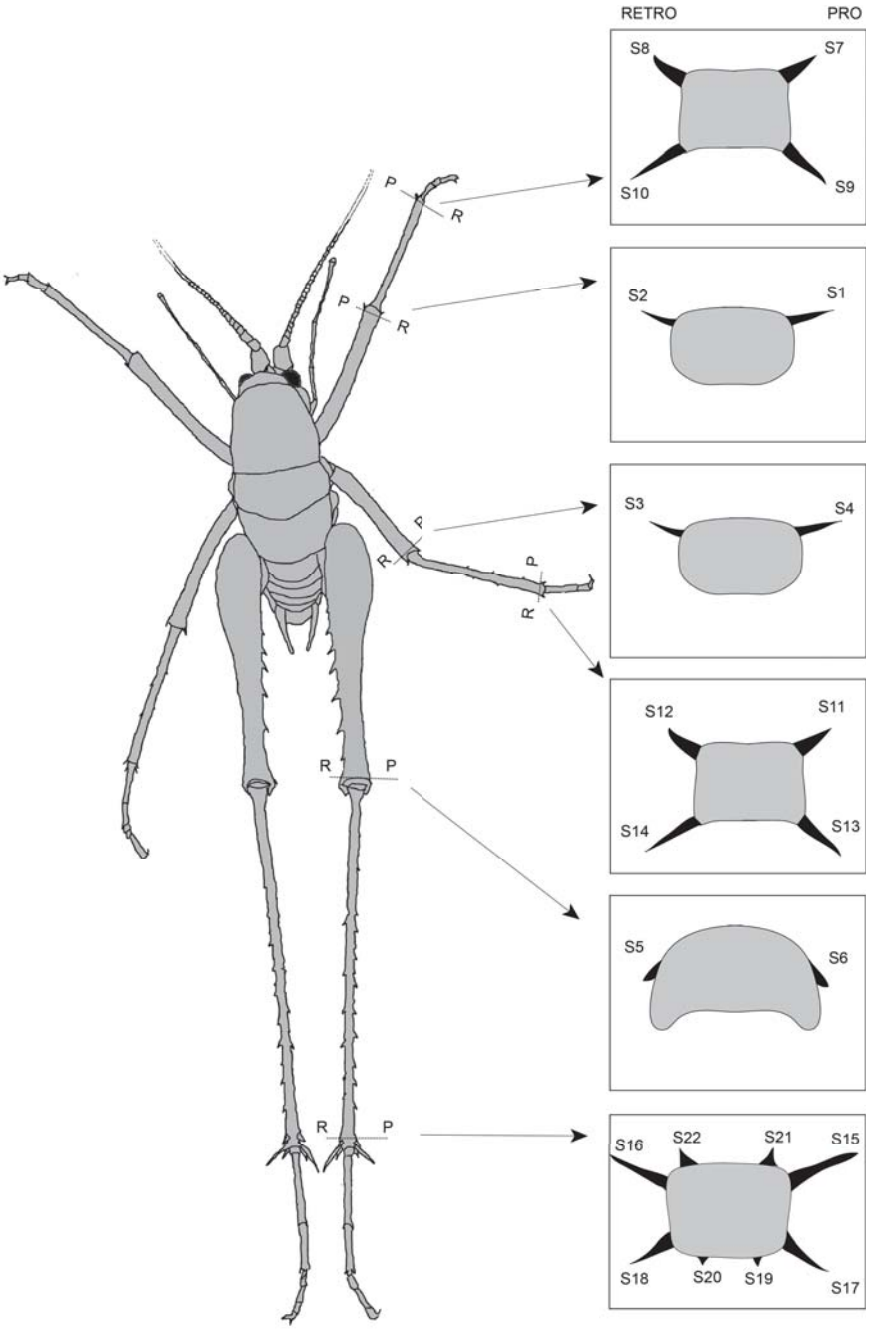

Figure 2.2. Dorsal view of cave wētā showing the location of apical spines. S1) Fore femur prolateral, S2) Fore femur retrolateral, S3) Mid femur prolateral, S4) Mid femur retrolateral, S5) Hind femur prolateral, S6) Hind femur retrolateral, S7) Fore tibia superior prolateral, S8) Fore tibia superior retrolateral, S9) Fore tibia inferior prolateral, S10) Fore tibia inferior retrolateral, S11) Mid tibia superior prolateral, S12) Mid tibia superior retrolateral, S13) Mid tibia inferior prolateral, S14) Mid tibia inferior retrolateral, S15) Hind tibia superior prolateral, S17) Hind tibia inferior prolateral, S19) Hind tibia inferior sub-apical prolateral, S21) Hind tibia superior sub-apical prolateral. Spines S16, S18, S20 and S22 match and appose to S15 S17, S19 and S21 on the retrolateral spine.

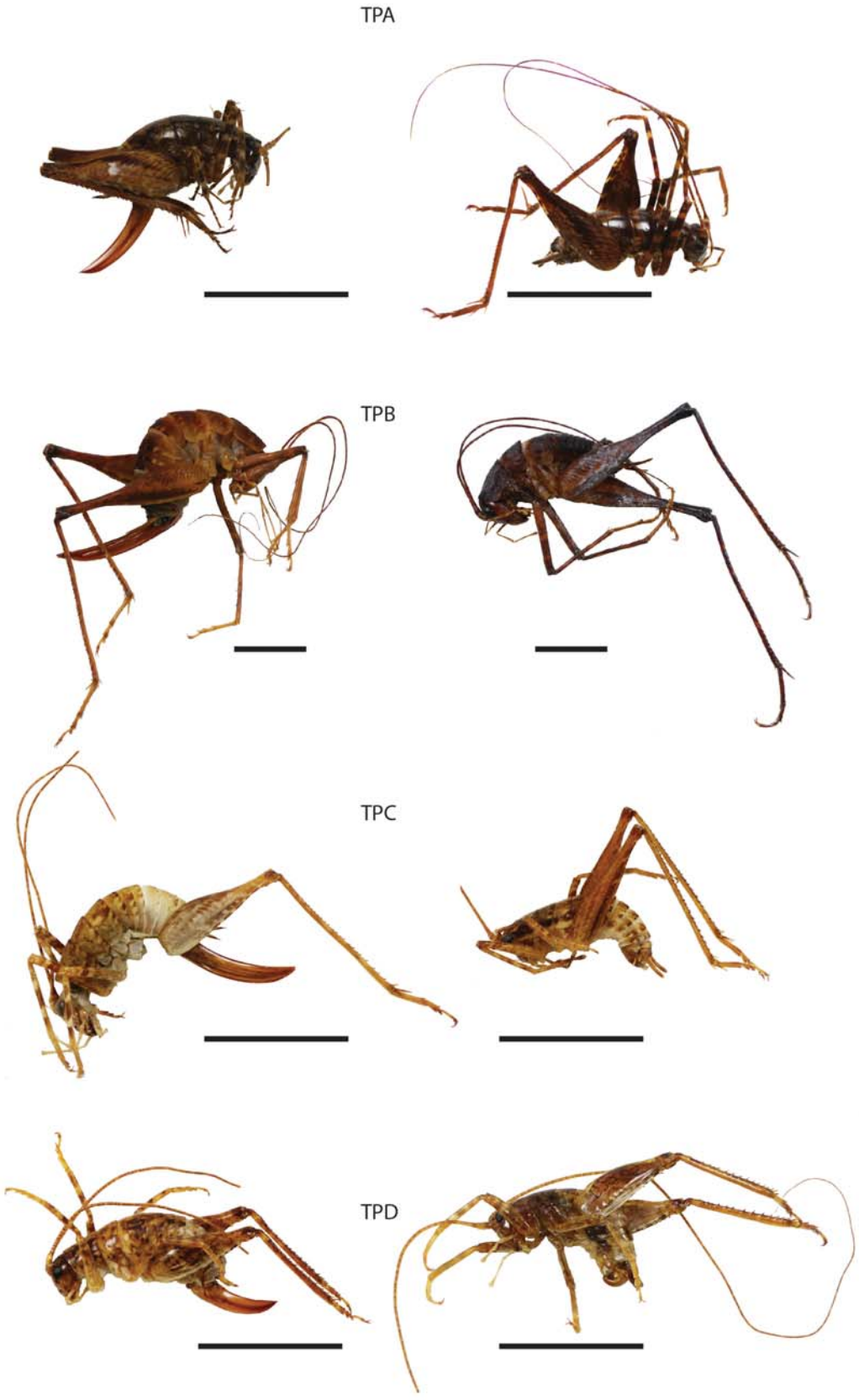

Figure 2.3. Four species of cave wētā identified from Te Paki Ecological District, Females on left, males on right.

Tukey HSD comparison tests showed there were significant differences in size of all three metric variables measured between TPA and TPB (P-value <0.0001), and between TPB and TPD (P-value <0.0001). In all cases TPB was the largest even though no adults of this taxon were present in the sample. However, size alone was not reliable for distinguishing all taxa and the use of spine combination characters and sub-genital plate shape was essential (Table 2.3).

PCA resolved numerous clusters when all spine data and the three metric variables (P, HF and HT) and unidentified juveniles were included (Figure 2.4a). TPA formed a cluster with a relatively large range in male and female sizes, but no discrete clusters indicative of instars or juveniles versus adults. TPB size variation was greatest suggesting the inclusion of several instars, but that these overlapped in size. Excluding unidentified juveniles resulted in the four putative species forming separate arrays (Figure 2.4b). The specimens representing TPA formed two adjacent clusters due to the variable presence/absence of the hind femur retrolateral apical spine. The close proximity of the two clusters strengthened our conclusion that these individuals were conspecific. When spine data were removed from the analysis (Figure 2.4c) we found that metric data alone were not sufficient to distinguish taxa.

Table 2.3. Adjusted P values from Tukey HSD test comparing mean lengths of pronota, hind femura, and hind tibiae of four species of cave wētā from Te Paki Ecological District pitfall traps. Significant differences are underlined (P<0.05) or in bold (P<0.0001). TPA (*Neonetus variegatus*), TPB (*Pachyrhamma* sp.), TPC (*Pallidoplectron* sp.), TPD (*Talitropsis* sp).

	Pronotum Length	**Hind Femur**	**Hind Tibia**
TPA vs TPB	**<0.001**	**<0.001**	**<0.001**
TPA vs TPC	0.543	0.297	0.025
TPA vs TPD	0.174	0.095	0.014
TPB vs TPC	0.014	0.073	0.284
TPB vs TPD	**<0.001**	**<0.001**	**<0.001**
TPC vs TPD	0.089	0.023	**<0.001**

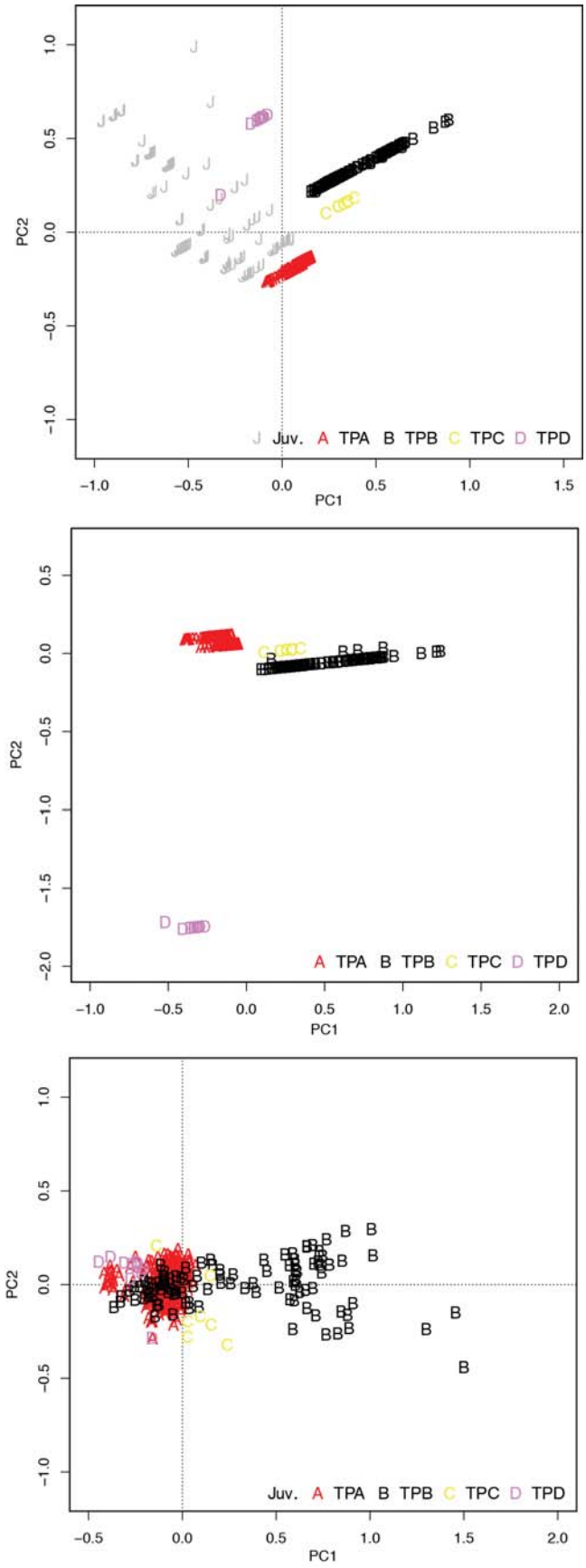

Figure 2.4.

Principal component analysis of Te Paki cave wētā morphology. A) All taxa and juveniles using spine and metric data, B) Four diagnosed taxa using spine and metric data (data from unidentified juveniles excluded), C) Four diagnosed taxa using only metric data. Juveniles (Juv.) were specimens less than 10mm long.

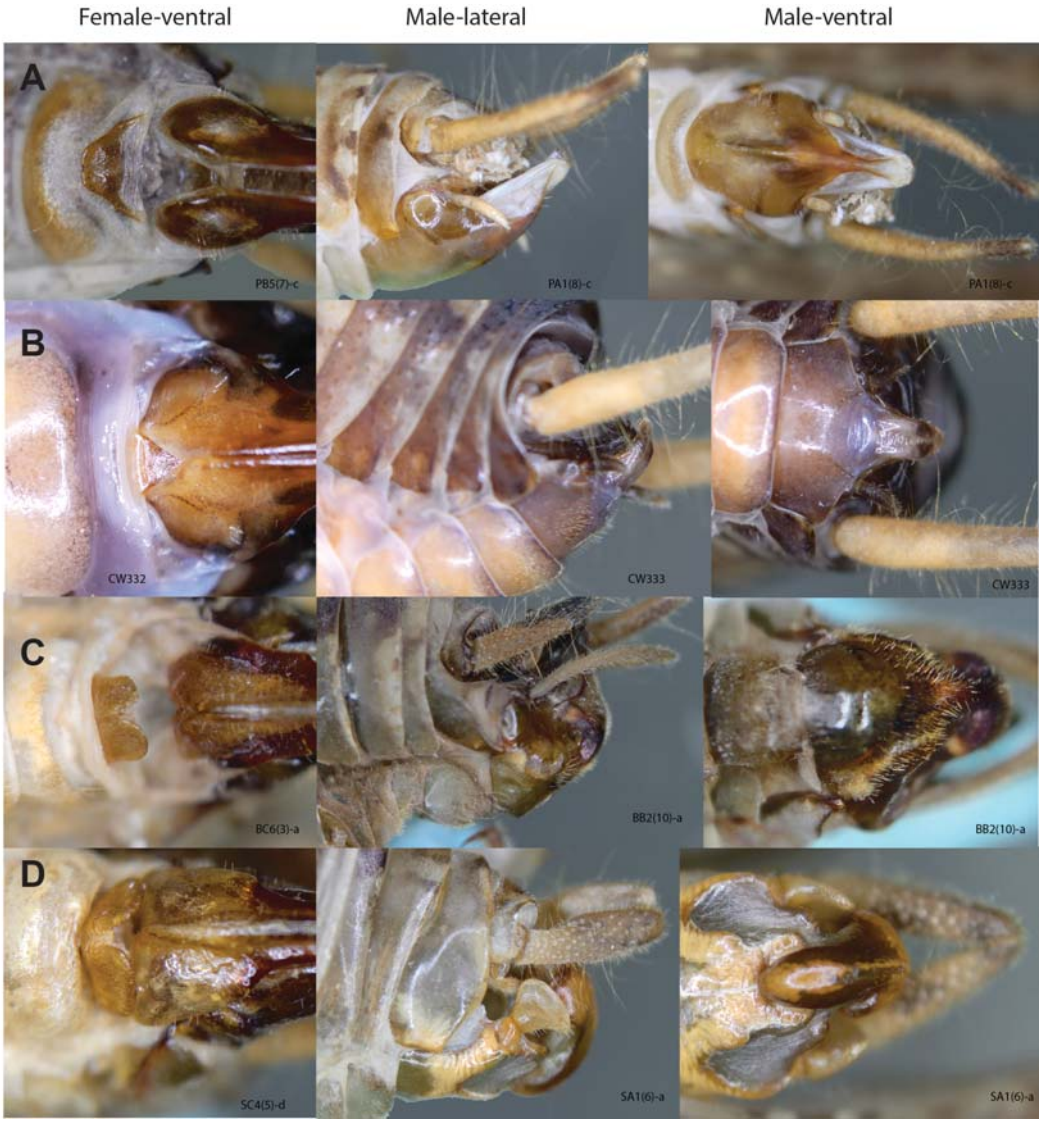

Figure 2.5. Subgenital plates of the four cave wētā species identified from the Te Paki area. Row A: TPA (*Neonetus variegatus*) female ventral (left), male ventral (centre), male lateral (right). Row B: TPB (*Pachyrhamma* sp.) female ventral (left), male ventral (centre), male lateral (right). Row C: TPC (*Pallidoplectron* sp.) female ventral (left), male ventral (centre), male lateral (right). Row D (*Talitropsis* sp.) female ventral (left), male ventral (centre), male lateral (right).

Species abundances

We examined frequency of cave wētā capture in pit fall traps using a generalised linear model and found all explanatory variables significantly affected the fit of the GLM (Table 2.4). From the model we could infer that abundance of cave wētā in pitfall traps depended on time of year, site, habitat, species and interactions of these effects. Including juveniles in the model resulted in the same variables being

significant in determining abundance. In a total sample of 3308 cave wētā in our pitfall data, TPA constituted the majority of the 1880 that were classified into one of four taxa, (83.1%). TPA occurred in all three habitat types sampled (Figure 2.6a) and relative abundance was high in all months, including late winter (August, September) when >100 individuals were caught. At all times of year the highest numbers of TPA were recorded from pine forest. TPB was the next most common species in our sample of cave wētā large enough to be identified (14.4%), and were also found in all three habitats (Figure 2.6b). TPB numbers in pine forest increased from June 2006 until the highest trapping rate in spring (September–October). This spring peak was not observed with the other three cave wētā species, and might be an artefact of adult TPB being under-sampled. Few TPC were found in the pitfall traps (<2% of total), and no specimens of this species were caught between June and October (winter–mid-spring). Although TPC were collected from all three habitats only a single individual adult was collected from native forest and more were sampled from shrubland than pine forest (Figure 2.6c). TPD was also collected in low numbers (<1%) in native forest and pine forest but not shrubland.

Significant interactions of species with month and habitat were detected, and we note significant variation among sites such that cave wētā abundance within habitats was influenced by site. For example, most of the temporal variation in TPB numbers and differences among habitats appears to be derived from the pine forest sites at Kerr Point and Whakapuku. Thus cave wētā abundance at Te Paki requires identification and separate treatment of the four species.

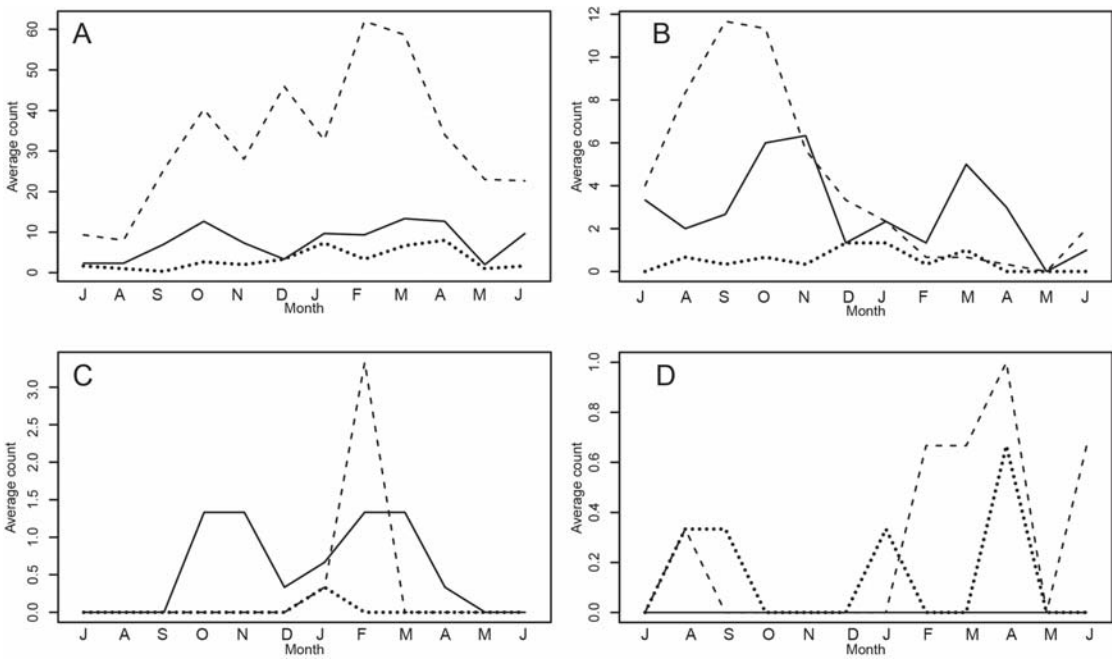

Figure 2.6. Mean monthly counts of four cave wētā species in pitfall traps in Te Paki Ecological District between July 2006 and June 2007. A) TPA, B) TPB, C) TPC, D) TPD. Dashed line = pine forest, dotted line = native forest and full line = shrubland. Note that y axis scales differ.

Taxonomy

We reviewed existing descriptions of New Zealand Rhaphidophoridae in relation to the apical spine data, sub-genital plate shape, other morphological attributes (colour, pattern, hairs etc) and location information. This enabled us to confirm the genus to which each morphotype belonged, and in one case the most likely species name. Thus TPA, the most abundant species in the sample, was most likely *Neonetus variegatus* Brunner von Wattenyl, 1888 according to the description of Chopard (1923). The largest species TPB, of which no adults were found in the pitfall traps, can readily be assigned to *Pachyrhamma* consistent with an adult pair of *Pachyrhamma* previously collected together in a hollow log at Unuwhao (Cook et al. 2010). Although the *Pachyrhamma* from the present study were not adults, their spine counts were consistent with known adult *Pachyrhamma* species from around New Zealand. TPC had numerous small retro and pro lateral spines on the hind femur similar to *Pallidoplectron* Richards, 1958. However, TPC was a much smaller species than the three *Pallidoplectron* currently described (Richards, 1958b, 1960). TPD was most similar to *Talitropsis* Bolivar, 1882, having a combination of spines,

colour and glossy appearance very like *Talitropsis sedilloti* Bolivar, 1882 but the sub-genital plates of males and females clearly distinguished it from that widespread and abundant mainland species.

Table 2.4. Generalised linear model (Poisson, link: log) to explain the variation in cave wētā abundance (response) captured in pitfall traps in Te Paki, New Zealand. Terms added sequentially (first to last). There were eight sites situated in one of three habitats (native forest, pine forest and scrub). Four cave wētā species were identified and juveniles were excluded.

	Df	Deviance	Resid. Df	Resid. Dev	Pr (> Chi)
NULL			431	6461	
Species	3	3177	428	3284	< 0.001
Month	11	336	417	2948	< 0.001
Habitat	2	1260	415	1688	< 0.001
Site	6	448	409	1240	< 0.001
Species:Month	33	260	376	979	< 0.001
Species:Habitat	6	91	370	888	< 0.001
Month:Habitat	22	105	348	783	< 0.001
Species:Month:Habitat	66	86	282	697	0.049

Discussion

Species identification

We found that four species of cave wētā detected in the Te Paki Ecological district could be distinguished just by the presence/absence of apical leg spines. Each spine permutation for adults of the four taxa was associated with a pair of sub-genital plates (male and female). The pitfall trapping method appeared to capture most, if not all, instar stages of the four species, and adults of three of the four species although we found instar sizes were not discrete. Adults of the large *Pachyrhamma* species (TPB) were apparently excluded by the pitfall sampling procedure. This might be due to the physical size of the traps or trap entrances being too small for the adult *Pachyrhamma* sp. to access, or a switch in microhabitat preferences between age classes. Although some species of *Pachyrhamma* are known to frequent caves, they are not limited to this

environment throughout their life cycle, often coming out into the forest to forage on surrounding vegetation at night (Cook et al. 2010; Richards 1954). Furthermore, in caves, adults and juveniles have been observed together (Richards 1962). The present study was limited by the single collection method used. Discovery of full cave wētā diversity, population structure and behavioural shifts would probably be best achieved using a combination of sampling strategies.

It was possible to place the four cave wētā species into genera even though many existing rhaphidophorid descriptions are deficient. *Neonetus* was established by Brunner von Wattenwyl in 1888, but his original description is recognised as being rather vague with respect to species diagnosis (Chopard 1923). Redescription of *N. variegatus* by Chopard (1923) helped reconcile differences between Brunner von Wattenwyl's original description and that of Hutton (1897) and the specimens examined by Chopard (1923) himself. Hutton's description of *N. variegatus* is based on specimens from Auckland, whereas Chopard believed that Brunner's description of *N. variegatus* was closer to Hutton's *N. pilosus* from Wellington. Following Chopard's description, *N. variegatus* is the most likely candidate for the species TPA from Te Paki Ecological District.

Placement of TPB in the genus *Pachyrhamma* stems from particular spine combinations, especially the absence of both the fore-femur retrolateral apical spine and the hind-femur prolateral apical spine (though in some *Pachyrhamma* this spine may be present), and the presence of all the other spines examined (Table 2.1). Geographically, the closest identified species *Pachyrhamma waipuensis* Richards, 1960, was described from the Waipu caves area 280 km south of Te Paki (Cook et al. 2010; Richards 1960). It is possible that our pitfall traps caught an undescribed *Pachyrhamma* species. In order to establish the identity of *Pachyrhamma* sp. in this study we referred to an adult pair collected previously at Unuwhao and included in a phylogenetic study and taxonomic review of *Pachyrhamma* (Cook et al. 2010). The Te Paki specimens have the same spine configuration and subgenital plates as the Unuwhao adult pair that are part of a distinct phylogenetic cluster within the *Pachyrhamma* clade. Neither morphology nor DNA data support the Te Paki *Pachyrhamma* taxon as *P. waipuensis* or any other named species.

The two remaining species of cave wētā recorded in this study appear to be undescribed but are consistent with two existing genera. One can be assigned to *Pallidoplectron* due to the spine combination described by Richards (1958b). This requires reinterpretation of Richards' use of the terms prolateral and retrolateral, which appear to have been transposed in that description. The numerous lateral spines on the hind femur of TPC is a characteristic of this genus that we have recorded in specimens from other parts of North Island (unpublished data). The Te Paki taxon is smaller than the three described species, *Pallidoplectron turneri* Richards 1958, from the Waikato district near Waitomo, *P. peniculosum* Richards 1960, from the Waipu caves and *P. subterraneum* Richards 1965, also from Waikato. Currently there are no other published data on *Pallidpolectron* outside cave environments. The fourth species belongs to the genus *Talitropsis*, and is recognised as a member of this genus by the posterior face of the hind tibia being flattened and the hind femur possessing two small lateral spines on the retrolateral and prolateral sides. Another useful character to distinguish some *Talitropsis* species is that the hind femur is the same length or slightly longer than the hind tibia; the reverse is seen in most other genera. This may relate to the association of *Talitropsis* with small tree-hole roosts. The genitalia show that the Te Paki individuals are not *T. sedilloti*, which is widespread and abundant throughout New Zealand and has been the subject of some morphological and genetic analysis (Trewick 1999, Goldberg and Trewick 2011). There are two species endemic to the Chatham islands but only one other name has been applied to specimens from mainland New Zealand; *Talitropsis irregularis* Hutton, 1896 from Auckland. The brief description *T. irregularis* lacks clarity and no new material has come to light.

Variation in the presence/absence of spines and the size and shape of the cave wētā revealed how challenging identification for this family can be. Initially individuals of similar size were apparently indistinguishable but closer inspection of numerous cave wētā in the Te Paki sample revealed that spine counts alone were sufficient to distinguish four species (when adult or near adult). When dealing with the approximately 55 described species nationwide, apical spine combination will likely need to be combined with details of genitalia, size and

geographic distribution (when better known). Apical spines were shown to be unreliable when dealing with juveniles. There are at least 16 genera of cave wētā in New Zealand and although some revision is required, this classification reflects substantial morphological variation. Although the presence/absence of a single spine has in the past been used for genus description, it is not sufficient. For example *Turbottoplectron* Salmon, 1948 was distinguished from *Pachyrhamma* and *Gymnoplectron* Hutton, 1896 because it did not have the prolateral apical spine on the hind femur that was supposedly present in all species of the other two genera (Salmon 1948). Analysis of morphological and genetic information from representatives of these three genera justifies their synonymy as *Pachyrhamma* (Cook et al. 2010). We observed variation at one apical spine within *N. variegatus* from the Te Paki Ecological District in our study showing that a single character can be misleading and the use of too few specimens in the establishment of cave wētā taxonomy, as has frequently been the case, can overlook intra-specific and intra-population variation and result in unstable systematics.

In some orthopteran families linear spines on leg elements may also be useful to distinguish between species. However, for cave wētā it has been shown that there is too much variation in these linear spines for them to be informative on their own (Richards 1959, 1960). Sub-genital plates proved to be useful in the Te Paki sample. They differ for males and females but once matching pairs are identified using spination, sub-genital plates prove to be the strongest candidate for species distinction. In insect systematics, external genitalic structures are widely used for diagnostic characters as male parts are often more complex than the female equivalent (Eberhard 2010), and this is also true in Orthoptera (e.g. Usmani & Kumar 2011). However, the sub-genital plates in male cave wētā are structurally complex, and their three-dimensional shape is less readily described than the female structure, which can often be characterised in two dimensions.

Species abundance

At least four species of endemic cave wētā are sympatric in the Te Paki region. Adults of *Neonetus variegatus* were caught in all three habitat types surveyed, although they were encountered more often in pine forest than native forest or shrubland. In contrast, adult *Talitropsis* were not caught in any of the shrubland traps although the small sample size of this taxon precludes ecological inferences.

Trap capture rates may not accurately reflect true abundances, as differences including activity levels, trapping vulnerability and habitat heterogeneity are likely to interact to yield final trapping rates. However, capture rates are species-dependent, and species capture rates were found to depend on both habitat and time of year. An interesting observation is that only in *Pachyrhamma* sp. (TPB) did we see a springtime increase in the capture rate. This suggests that when Rhaphidophoridae are combined into a single unit during an analysis, important information is likely to be lost. For example, studies aimed at recording the effects of predator control on cave wētā abundance might produce misleading results when numerous species are treated as one (Ruscoe et al. 2013).

In considering regional biodiversity and its conservation the quality of modified habitats and their capacity to support native species is important. In most instances, native species would be assumed to be more successful in native vegetation, but studies are increasingly showing that many native invertebrates can thrive in disturbed and modified habitats including urban areas (e.g. Blanchon et al. 2011; Brockerhoff et al. 2001). Within *Pinus radiata* plantations at Te Paki we collected the same four species but detected significantly higher numbers of two cave wētā species compared to the native forest or shrubland habitat, providing evidence of the important role pine forest can have in maintaining populations of endemic invertebrates.

Conclusion

Even with an uncertain taxonomy, it is possible to increase resolution of biodiversity analyses using relatively few readily identified morphological characters. Careful treatment allows separation of adult (or near adult) individuals from juveniles, and segregation of distinct taxa among a pool of superficially similar individuals. This then provides the opportunity to glean much more information about spatial and temporal variation in abundance among the different taxa. Using a combination of apical spine and sub-genital plate we were able to distinguish and identify four taxa of cave wētā from the Te Paki Ecological District. Scrutiny of existing descriptions has allowed us to tentatively assign each of the four species to a genus and we consider three are likely to be new undescribed species. Morphological variation observed in *N. variegatus* spine data within populations confirms that some apical spination is not consistent within species. The high capture rate for this species enabled us to establish that this intra-specific variation was independent of sex, habitat or life stage.

With improved systematic resolution, the trapping data provide insights into the distribution of species and indicates species specific spatial, temporal and habitat differences in relative abundances. This indicates that future studies of biodiversity will be more informative and meaningful because distinct taxa with distinct ecologies will each contribute to analyses. Disturbed environments appear not to impede the distribution of *Neonetus variegatus,* and pine forest appears to provide a valuable habitat for at least some endemic invertebrates. It is, however, clear that a single trapping regime will not accurately capture all invertebrates or even all rhaphidophorid diversity.

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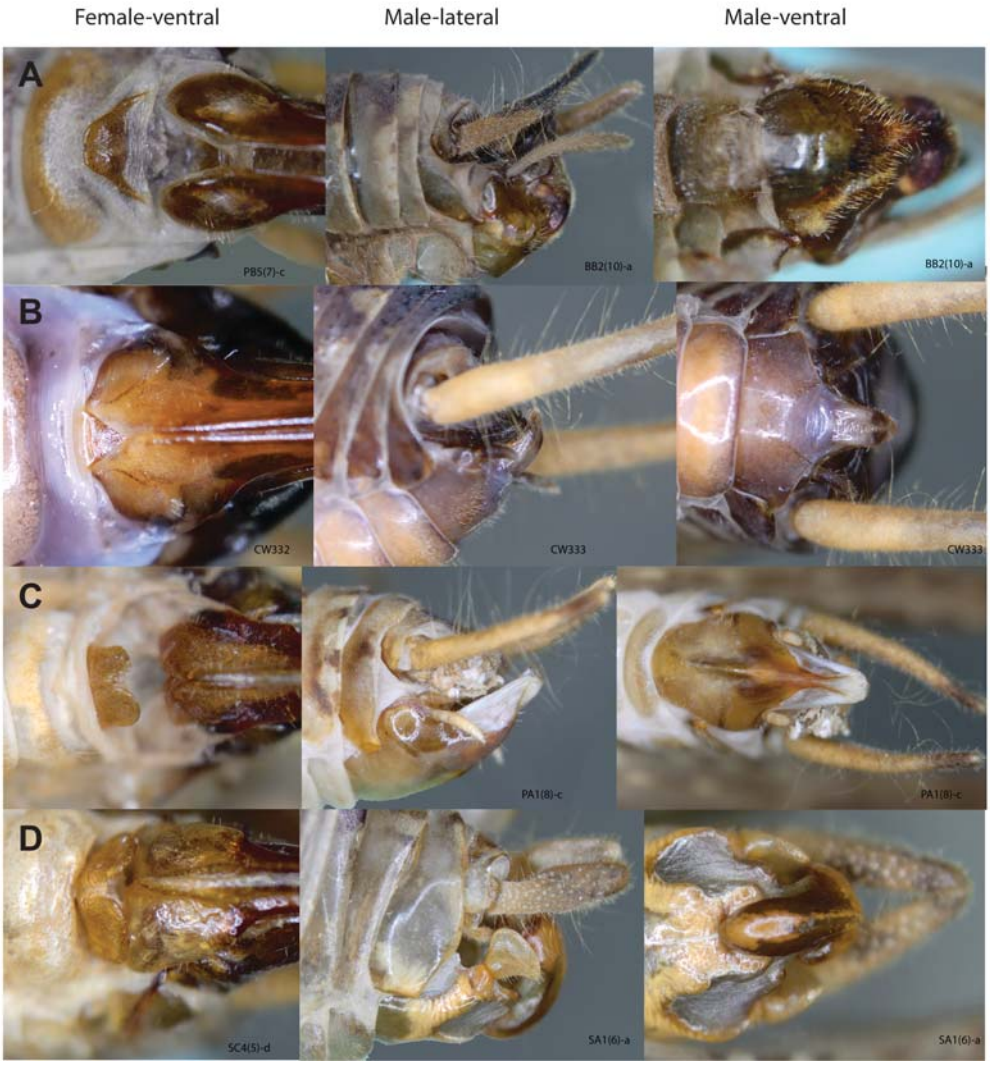
Corrigendum



The above figure is an amendment of figure 2.5 that is in the chapter and was published in the journal article. After publication a mistake has been picked up with photos being placed in the figure in the wrong order. The new version correctly places the photos of male lateral and ventral view for A and C in the right places. These had been switched round in the original version.

DRC 16

MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Josephine Fitness

Name/Title of Principal Supervisor: Dr Steve Trewick

Name of Published Research Output and full reference:

Fitness, J. L., Morgan-Richards, M., Ball, O.-P., Godfrey, A. J. R., & Trewick, S. A. (2015). Improved resolution of cave wētā diversity (Orthoptera: Rhaphidophoridae): ecological implications for Te Paki, Far North, New Zealand. New Zealand Journal of Zoology, 42(1), 1–16.

In which Chapter is the Published Work: Chapter 2

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate: 90%
  and / or
- Describe the contribution that the candidate has made to the Published Work:

Josephine Fitness — Candidate's Signature

25.8.16 — Date

Steve Trewick — Principal Supervisor's signature

21/9/16 — Date

GRS Version 3– 16 September 2011

Chapter 3

Comparing species level diversity of cave wētā among three locations of New Zealand

Introduction

Biodiversity is a term that refers to the diversity or variety of life on Earth. Biodiversity encompasses not only species but the genes they have and the ecosystems they occupy (Gaston, 1998). Variation in the distribution of biodiversity has been recognized among environments and regions (Gaston, 2000), and on a global scale as the latitudinal biodiversity gradient that expresses the tendency for plant and animal species diversity to be greater in the tropics than in temperate zones (Mittelbach et al., 2007). However, our overall understanding of biodiversity is still rudimentary (Nee, 2004). The total number of species for any given region is incomplete given the high level of sampling and labour needed for carrying out this work. Methods for measuring biodiversity are hugely varied and each has its own merits depending on the research purpose.

Biodiversity is usually compared at the level of species (species richness), estimating diversity at any given region (Gotelli & Colwell, 2001). This means the number of species within a region is counted and if similar methods are used at more than one location, numbers can be compared between different regions. If biodiversity levels are compared among locations it may be possible to determine the influence of geology, history, climate, environment, biotic interactions and pressures of human influence on species richness. Regional adaptations to the local climate, ecology and geographical history can strongly influence our understanding of species diversity and its distribution (Mittelbach et al., 2007; Wiens & Donoghue, 2004).

Because the resources required to count all taxa in one location are very large, it is common practice to use particular groups of organisms as proxies (indicator groups) when comparing biodiversity levels (Beccaloni & Gaston, 1995). By using these indicator groups it is hoped that estimates of total species richness for an area can be achieved. Many groups have been used as indicators such as insects (e.g. butterflies (Beccaloni & Gaston, 1995) and tiger beetles (Pearson & Cassola, 1992)) as well as birds and plants (Schulze et al., 2004). For a type of organism to be considered as a potential indicator group they need to have a large number of

species, which are known fairly well. That includes basic taxonomy of the group to be used (Evangelisti et al., 2016). Developing ways to distinguish between similar species has been a major goal for many biologists over the past few decades. Morphological characters combined with genetic data are now widely used to distinguish between closely related species. In taxa that are morphologically identical, DNA markers can be especially valuable and this approach is commonly referred to as DNA barcoding (e.g. Hebert, et al., 2004, but see Moritz & Cicero, 2004; Trewick, 2008).

Species concepts are at the heart of understanding biodiversity and have proliferated since Darwin (Origin of species; Darwin 1859). Each species concept takes slightly different criteria for distinguishing species (Mallet, 2001). From the biological concept (Mayr, 1942), ecological concepts (Van Valen, 1976), evolutionary concept (Simpson, 1951) to genotypic clustering concepts (Mallet, 1995), these ideas have contributed to the continued debate about how to distinguish and define species (Hausdorf, 2011; Mallet, 2001). Applying different criteria to delineate species leads to variations in the number of species recognised and thus variation in estimates of total biodiversity. The issue with 'taxonomic inflation' will depend on which approach is used and what criteria are used by different taxonomists.

The genotypic clustering approach to defining species establishes groups of individuals (and populations) that are broadly similar and part of the same lineage (Mallet, 1995). Genotypic clustering uses multiple data sets to test whether different traits arrive at the same groups (clusters) of individuals. Concordance of characters is key to the approach. The genotypic definition accepts that gene flow can occur between species (but that intermediates are rare), lack of monophyly is not important, and asexual reproduction can be incorporated (Mallet, 1995). Genotypic clustering allows one to use differences in allele frequencies and mtDNA haplotypes in conjunction with morphological characters to determine whether individuals group or cluster together, and provides an hypothesis of species boundaries (Mallet, 2001).

Although cave wētā in New Zealand offer an opportunity for comparing regional diversity via estimates of species richness, the group is poorly known (Fitness et

al., 2015). The New Zealand cave wētā (Rhaphidophoridae) are a diverse group, with ~ 56 species described and many more thought to be undiscovered or/and undescribed (Cook et al., 2010; Eades et al., 2016). A number of factors have made it difficult to accurately identify species and then re-identify when found. This is most often due to vague, brief descriptions (Hutton, 1897), misidentification of juveniles as adults (Richards, 1959), or lack of understanding natural variation leading to males and females being given separate names (Richards, 1954). One outcome of poor taxonomy is that the biodiversity of a group of animals is inaccurately quantified or (more often) simply overlooked due to the inability to identify specimens. Many cave wētā taxa are superficially similar to each other but most are not described or readily identifiable. We cannot guess the species richness of this group or even begin to compare with other species, as we do not have a good understanding of taxonomy, ecology and biology of rhaphidophorids in New Zealand. To the layperson they are long-legged brown jumping cricket-like creatures, but most species are small and cryptic. Often in New Zealand ecological research on different species of Rhaphidophoridae are counted under the family name (Moeed & Meads, 1992; Ruscoe et al., 2013), or just given a genus name i.e. *Pleioplectron* sp., *Isoplectron* sp. (Spurr & Berben, 2004a). Not knowing or understanding the species that exist can place pressure on conservation efforts on a particular species. In addition, invertebrates are often overlooked but important prey species of threatened vertebrates.

Here I extend the work of the previous chapter (Fitness et al., 2015) looking at diagnosis and identification of species. In the previous chapter I developed some basic morphological measures to assess the morphological difference between different groups of individuals and determine whether species could be distinguished using morphology. Expanding this approach to a different area that might contain more and different species, I use mitochondrial DNA sequences to test species hypotheses and provide additional information to explore biodiversity and establish taxonomy. In this case sampling effort will target three North Island New Zealand regions with similar general environmental conditions that will allow comparison of species level diversity among locations.

Before the arrival of humans, lowland forest was extensive in North Island New Zealand, with effectively contiguous habitat that could have enabled individuals of many species to have ranges extended throughout North Island. Unless there was local adaptation or extremely low rates of gene flow we would expect little regional microendemism, and species would be widespread. This predicts that adjacent regions in North Island will share a set of taxa. Alternatively, encountering assemblages unique to specific regions will suggest the spatial scale over which partitioning occurs (Figure 3.1). Even where different regions have distinct taxa, it would be expected that adjacent regions would have related species. To test predictions about the relationship between space and diversity I use a combination of morphological and genetic information for a sample of cave wētā from three regions of southern North Island New Zealand.

Methods

Three regions in the southern half of North Island New Zealand were selected for study on the basis of their accessibility, broad environmental similarity, and terrestrial connectivity (Taranaki; Manawatū; Hawke's Bay; Figure 3.1). Previous collecting over many years ensured that many taxa would be available for examination. Most of the cave wētā from the three regions came from forested areas although the vegetation type varied from mixed native broadleaf and podocarp at various stages of regeneration to exotic pine plantation. Within the three regions, numerous sites were visited in order to maximize representation of rhaphidophorid diversity. In Taranaki, collections ranged from the slopes of Mt Taranaki to gardens within New Plymouth suburbs. The Hawke's Bay wētā specimens came mostly from Mohi Bush (a regenerating native forest reserve) a private reserve at Cape Kidnappers, and other forest remnants between the two. In the Manawatū the majority of wētā came from forest in the vicinity of the Palmerston North water catchment reserve in the Turitea Valley and Kahuterawa Valley, in the northern foothills of the Tararua Range.

Cave wētā specimens were obtained using a combination of hand collecting at night, extraction from roost holes during the day and pitfall traps. Pitfall trapping was carried out using a standard method with traps consisting of a plastic round container (110mm diameter and 90mm deep) buried into the ground. The rim of the container was flush with the ground. Propylene glycol was used as the preservative and the containers were half filled with it. A tin cover was placed over the trap about 3cm above the ground. This allowed invertebrates to move under and into the trap without being impeded but prevented larger animals, rain and debris from entering into the trap. Pitfall traps were collected and reset every month during the summer of 2011/2012, while the insects were active. Preserved cave wētā were sorted out of the glycol and placed in 100% ethanol. Daytime collecting involved lifting decaying logs where cave wētā often roost during the day or searching hollows in trees and banks. Artificial tree wētā cavities (wētā motels) were searched where available (Trewick & Morgan-Richards, 2000).

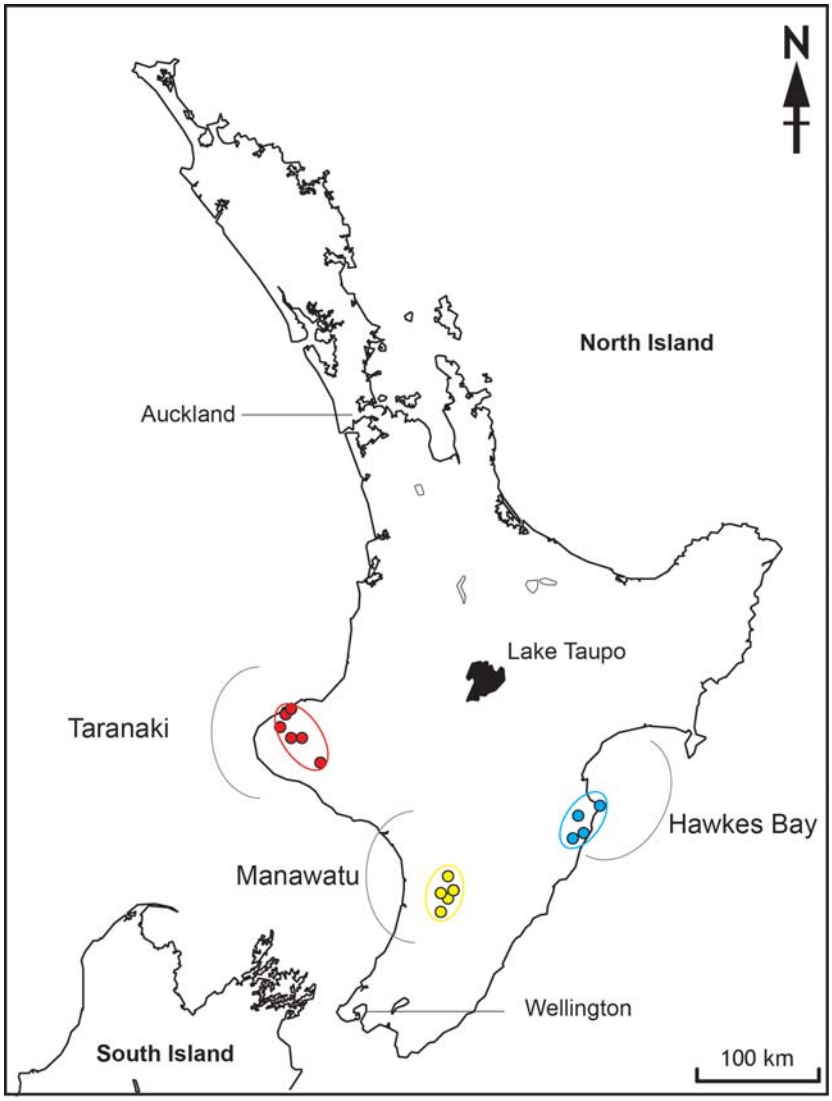


Figure 3.1. North Island, New Zealand, showing the locations from which cave wētā were collected.

Specimens belonging to the genus *Pachyrhamma* were not included in the present analysis for two reasons. 1. Adult *Pachyrhamm*a are often too large to be trapped in pitfall traps (see chapter 2). 2. Many *Pachyrhamma* species are usually found in caves (Richards, 1959), and equivalent cave habitats were not available for each of the three regions. Cave wētā were identified as *Pachyrhamma* based on characteristic spine combinations and subgenital plate (Cook et al., 2010) and excluded from further analysis (6 specimens).

Morphology

Specimens were examined under a dissecting microscope and adults, juveniles, males and females identified. Presence/absence of each of the 22 apical leg spines (see chapter 2/Fitness et al., 2015) were recorded for each adult individual (Appendix 1). Each spine combination was recorded with a spine type number so that each specimen could be assigned to a spine type (Refer to Table 3.2 for spine types). The subgenital plates of adult males and females were recorded and each different subgenital plate was assigned an SB number, so that each specimen could be classified. Each combination of spine type and subgenital plate was treated as a separate phenotype and each specimen classified into one of these phenotypes. Grouping of phenotypes allowed males and females to be assigned the same Operational taxonomic unit (OTU; a unique letter code) based on whether they were deemed to be the same species. Based on evidence presented in the previous chapter I considered some apical leg spines likely to be variation within species (particular those of the hind tibia and hind femur), therefore OTUs incorporated some spine type variation.

mtDNA extraction, amplification and sequencing

Whole genomic DNA extractions were performed using a 'salting out' protocol (Sunnucks & Hales, 1996) designed for fresh tissue, but used successfully for preserved Orthopteran tissue (Trewick & Morgan-Richards, 2004). For each sample, a ~1500 base pair (bp) fragment spanning most of the cytochrome *c* oxidase I (COI) gene of the mitochondrial genome was amplified using polymerase chain reaction (PCR) and a combination of universal invertebrate primers: LCO1490 (Folmer O, Black M, Hoeh W, Lutz R, 1994), C1-J-1718, C1-N-2191, C1-J-2195 and L2-N-3014 (Simon et al., 1994). Where possible a representative of each phenotype from each location was sequenced but not all specimens provided DNA that could be successfully amplified.

Successful PCR products were prepared using the SAP/EXO1 digest protocol (USB Corp., Cleveland, OH) and sequenced with Bigdye chemistry and an ABI 3730

genetic analyser (Applied Biosystems Inc., Carlsbad, CA). Nucleotide sequences were assembled and aligned using Geneious v8 (Kearse et al., 2012). No insertions/deletions were detected and sequences were translated to confirm that there were no stop codons or frame shifts that would indicate the presence of nuclear paralogs.

Haplotypes were clustered based on sequence similarity (HKY pairwise distances) using the Neighbor-Joining algorithm (Saitou & Nei, 1987) implemented in Geneious v8. New Zealand cave wētā COI sequences associated with previous studies were available for the following species: *Talitropsis sedilotti* (Goldberg et al., 2008), *Talitropsis megatiba, T. crassicruris* (Trewick, 2000), *Macropathus* sp. (Cook et al., 2010); *Macropathus filifer, Pallidoplectron turneri, Pleioplectron simplex* (Allegrucci et al., 2010).

Species hypotheses based on morphology (OTUs) were tested with the mtDNA data. Pairwise genetic distances were calculated and used to assess potential OTU identified by morphology. Species Delimitation tools in Geneious were used to calculate the average genetic distance within a cluster (clade), and the mean genetic distance between the nearest haplotype clade. The ratio of within and between cluster distances (Intra/Inter) can be used to identify "gaps" between the COI sequence similarity that might correspond to species level differences (Hebert, Stoeckle, et al., 2004). My criteria for confirmation of species required pairwise genetic distances to be low (less than ~4%) and concordance of mtDNA clusters for specimens from the same morphological OTU. If no morphological difference could be identified, mtDNA sequences difference on its own was not enough to establish a unique OTU. If morphology differed but mtDNA sequences were similar this meant my species hypothesis was not supported. DNA sequences for four putative species that had been collected from all three regions were used to infer haplotype networks using the minimum spanning approach (Bandelt et al., 1999) using the software POPART (Leigh & Bryant, 2015) and coded by collection location.

Results

In total, 163 individual adult cave wētā were included in the analysis. Specimens were catalogued into the Phoenix collection in the Ecology Group, Massey University. The sample included 57 adult cave wētā from Hawke's Bay, 56 from Manawatū and 50 from Taranaki. The use of pitfall traps in Manawatū and Taranaki increased the sample size for these regions, however many of the cave wētā caught were juveniles. In the previous chapter (this thesis) juveniles were shown to be difficult to assess morphologically into species and so are not included in this study.

Table 3.1. Cave wētā diversity recorded as number of distinct phenotypes and operational taxonomic units (OTUs) at each of three North Island, New Zealand regions

Location	Number of Phenotypes	Number of OTUs
Hawke's Bay	18	8
Manawatū	26	11
Taranaki	28	10

There were 18 distinct cave wētā phenotypes found in the Hawke's Bay, 26 in Manawatū and 28 in Taranaki (Table 3.1, Figure 3.2). The phenotypes found in the sample set were made up from 23 spines types (Table 3.2) and 23 male and female subgenital plates (Table 3.2 & Figure 3.3). The combination of the spine types and subgenital plate types made 49 distinct phenotypes that separated males and females into different groups (Table 3.2). Examination of the male and female phenotypes using the following characters: spines, size, shape and general pattern and colouration were used to match pairs of phenotypes into the same putative species. In addition, information on whether males and female individuals were found together when caught was used to determine operational taxonomic unit (OTU). By pairing males and females and grouping specimens with the same subgenital plate together (and spine variation considered minor) I reduced the overall groups from 49 distinct phenotypes to 15 operational taxonomic units.

Pairing males with females was easier for some taxa than others due to minor apical spine variation. Phenotypes with spine types T10 and T11 are always found with SB plates SB3 or SB31 (sex dependent; Table 3.2). No other phenotype has these spine types, reinforcing the idea that these characters are for male and female of the same species. In some cases the spine type (i.e. T3) is found in a number of taxa for both males and females making the use of spines impossible to distinguish species alone. Spine type T3 is found in taxa that appear to be from distinct genera, including *Miotopus* and *Neonetus,* as well as taxa considered to be the same genus, (see chapter 4*)*. Where matching was not possible, males and female specimens were left in separate OTUs. Thus, for some taxa only one sex was represented in the total specimen sample set (i.e. OTU: K, P, M, R & U).

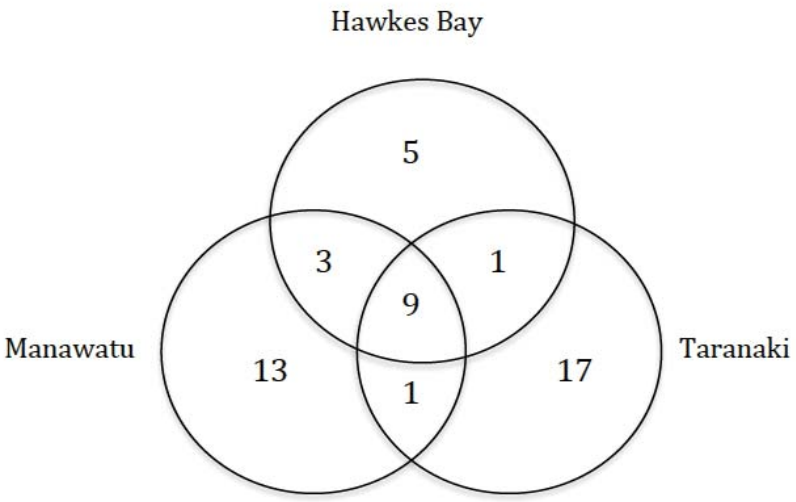


Figure 3.2. Number of cave wētā phenotypes observed at each of the three New Zealand locations.

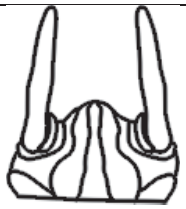
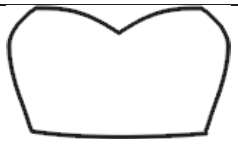
Table 3.2. Cave wētā phenotypes found in the three regions, with the data used to formulate each one including the spines (Refer to Figure 2.2 chapter 2), subgenital plate and sex**.**

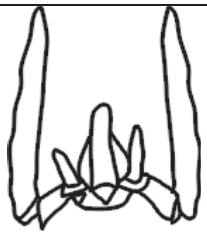
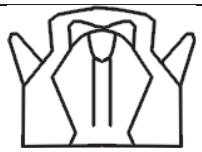
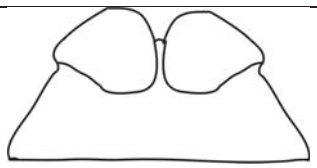
Phenotype	Sex	Location	Subgenital Plate	Spine type	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	OTU
P1	M	HB, T, M	SB22	T11	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1	A
P2	M	HB, T	SB22	T22	0	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1	A
P3	M	T	SB22	T17	0	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1	A
P4	M	T	SB22	T14	0	0	0	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1	A
P5	F	HB, T, M	SB16	T11	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1	A
P6	M	M	SB15	T1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	C
P7	M	M	SB15	T20	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	C
P8	M	M	SB15	T16	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	C
P9	M	M	SB15	T19	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	C
P10	F	M	SB19	T1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	C
P11	F	HB	SB19	T21	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	C
P12	F	T	SB23	T3	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	B
P13	M	HB, T, M	SB3	T9	1	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	G
P14	M	HB, M	SB3	T10	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	G
P15	M	T	SB3	T5	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1	G
P16	F	T	SB21	T9	1	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	G

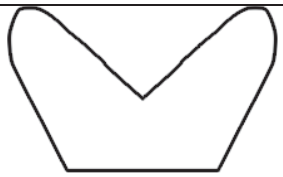
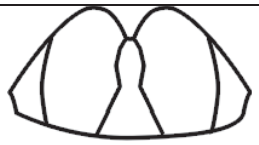
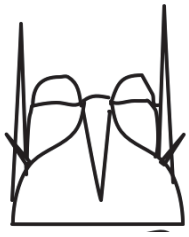
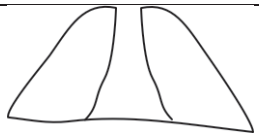
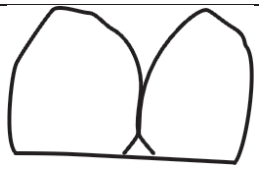
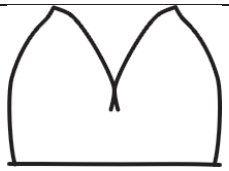
P17	F	HB, T, M	SB21	T10	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	G
P18	M	T	SB2	T26	1	1	1	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	D
P19	M	HB, T, M	SB2	T21	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	D
P20	M	HB, T, M	SB2	T3	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	D
P21	M	M	SB2	T7	1	0	0	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	1	D
P22	F	T	SB9	T1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	E
P23	F	T	SB9	T20	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	E
P24	M	T	SB10	T1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	E
P25	M	T	SB10	T20	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	E
P26	M	M, T	SB11	T3	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	H
P27	F	HB, T, M	SB14	T3	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	H
P28	F	T	SB14	T21	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	H
P29	M	HB, T, M	SB12	T4	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	F
P30	M	HB, M	SB12	T24	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	F
P31	F	HB, T, M	SB6	T4	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	F
P32	F	T	SB6	T24	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	F
P33	M	HB, M	SB4	T3	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	B
P34	M	HB	SB4	T21	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	B
P35	F	HB	SB20	T21	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	D
P36	F	T	SB26	T3	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	D
P37	M	T	SB1	T16	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	L

P38	F	T	SB1	T16	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	L
P39	F	T	SB13	T6	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	K
P40	M	M	SB5	T12	0	0	0	1	0	0	1	0	1	0	1	0	1	0	1	1	1	1	1	1	1	1	I
P41	M	HB	SB5	T13	0	0	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	1	1	1	1	1	I
P42	F	M	SB17	T12	0	0	0	1	0	0	1	0	1	0	1	0	1	0	1	1	1	1	1	1	1	1	I
P43	F	M	SB19	T25	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	C
P44	F	M	SB24	T14	0	0	0	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1	P
P45	F	M	SB19	T16	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	C
P46	F	T	SB26	T18	1	0	0	1	0	0	0	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	M
P49	F	HB	SB16	T22	0	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1	A
P51	F	M	SB19	T8	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	C
P53	F	M	SB23	T21	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	U

Table 3.3 Line drawings of the different types of cave wētā subgenital plates represent by specimens from three North Island New Zealand locations.

Subgenital Plate Type	Ventral View	Lateral View
SB1		
SB2		
SB3		
SB4		
SB5		
SB6		
SB9		

SB10		
SB11		
SB12		
SB13		
SB14		
SB15		
SB16		
SB17		

SB18		
SB19		
SB20		
SB21		
SB22		
SB23		
SB24		
SB26		
SB27		

Most taxa are comprised of at least two different phenotypes with a male and female combined to make an operational taxonomic unit (OTU). Only 1 or 2 individuals represent some of the phenotypes. When the only difference between specimens was a different spine type due to a single apical spine differences these wētā were usually placed in the same OTU if subgenital plate matched. However, some individuals had an unusual phenotype where one character was unique. For example, CW466 and CW950 (both females, from Taranaki and the Manawatū, respectively) each had a short stumpy ovipositor unlike any other cave wētā specimen examined. These two specimens (CW466, CW950) had slightly different subgenital plate shape and different spine combinations (T18, SB18 and T14, SB24 respectively) and therefore are considered as separate OTUs, (P and M respectively). No matching male specimen for either OTU P or M was found in my sample.

mtDNA

DNA sequences of COI (~1500 bp) from 76 individuals resulted in 75 unique haplotypes identified. Analysis of 76 individuals included 35 phenotypes and all 15 OTUs. Pairwise genetic distances among mtDNA sequences were used to identify clusters of genetically similar wētā specimens (Table 3.4; Appendix 2). When mtDNA haplotypes are clustered using Neighbor-joining (NJ; Figure 3.3) most cave wētā specimens are part of a cluster of similar sequences, each representing a different OTU. Using the previously published DNA sequence data some haplotypes can be assigned to sampled genera (for example *Macropathus* and *Pleioplectron*). One species can be assigned based on genetic similarity with published data: *Talitropsis sedilotti* (OTU A in Figure 3.3). Eleven clusters and four single specimens are recognized by comparing within and between group distances (Table 3.4), and these are colour coded in the NJ tree (Figure 3.3). Thirteen of the putative species identified based on morphology are supported by genetic evidence (OTU: A, B, C, D, E, F, G, H, I, K, L, T, U). The OTU M and P were each represented by single individuals, and although morphologically distinct these two specimens were genetically similar with pairwise distance of only 0.011 (Table 3.4; Appendix 2). Four cave wētā specimens from OTU E were sequenced and they

form two clusters of two individuals each, although morphologically very similar they differed by a maximum genetic distance of 0.084 (mean within clade genetic distance = 5.6%; Table 3.4). Four haplotypes did not belong to clusters in the NJ tree (Figure 3.3), and three of these represented the only specimens of a particular OTU that was sequenced (CW1403 OTU=L; CW141 OTU=T; CW1345 OTU=U) and therefore genetics and morphology agree. The fourth distinct haplotype was from CW817, which had the same subgenital plate as OTU A (*Talitropsis sedilotti*), but a different spine combination (T14). CW817, collected from high elevation on Mt Taranaki had a mtDNA sequence that differed by 7.8% from other *Talitropsis* taxa (Table 3.4). All other mtDNA sequences formed haplotype clusters of between two and 15 sequences. The mtDNA data provides independent confirmation of the cave wētā species diversity that exists in the three regions (Figure 3.3). There was concordance of morphology and genetic information for the majority of specimens (13/15 OTUs). Most OTUs (i.e. morphological character combinations) appeared in a single mtDNA clusters with a single OTU (e.g. D, E, F, H, I). A single OTU (A) occurred in two mtDNA clusters. Eight mtDNA clusters have cave wētā from 2-4 phenotypes. The phenotypes represent different sexes and minor apical spinal variation.

Table 3.4 Cave wētā species delimitation using mtDNA sequences from 15 putative taxa and their closest clade. Also refer to figure 3.3

Putative Species	Closest Species	Monophyletic?	Intra Dist	Intra Dist	Inter Dist-Closest	Intra/Inter
morphotype (O.T.U)	nearest clade (O.T.U)		Mean within clade genetic distance	Mean within clade genetic distance (%)	Mean genetic distance between nearest clades	
D	T	yes	0.007	0.7	0.085	0.08
C	U	yes	0.006	0.6	0.086	0.06
B	*Talitropsis*	yes	0.005	0.5	0.098	0.05
I	*Talitropsis*	yes	0.001	0.1	0.094	0.01
A	*Talitropsis*	yes	0.007	0.7	0.038	0.17
G	M	yes	0.013	1.3	0.092	0.14
F	*Pleioplectron simplex*	yes	0.016	1.6	0.094	0.17
Pleioplectron simplex	F	yes			0.094	
H	L	yes	0.014	1.4	0.109	0.13
L	*Pleioplectron simplex*	yes			0.108	
K	*Pleioplectron simplex*	yes	0.036	3.6	0.119	0.3
Talitropsis	A	yes	0.014	1.4	0.038	0.37
CW817	*Talitropsis*	yes			0.078	
Pallidoplectron turneri	M	yes			0.092	
T	D	yes			0.085	
U	C	yes			0.086	
E	U	yes	0.056	5.6	0.105	0.53
P	M	yes			0.011	
M	P	yes			0.011	

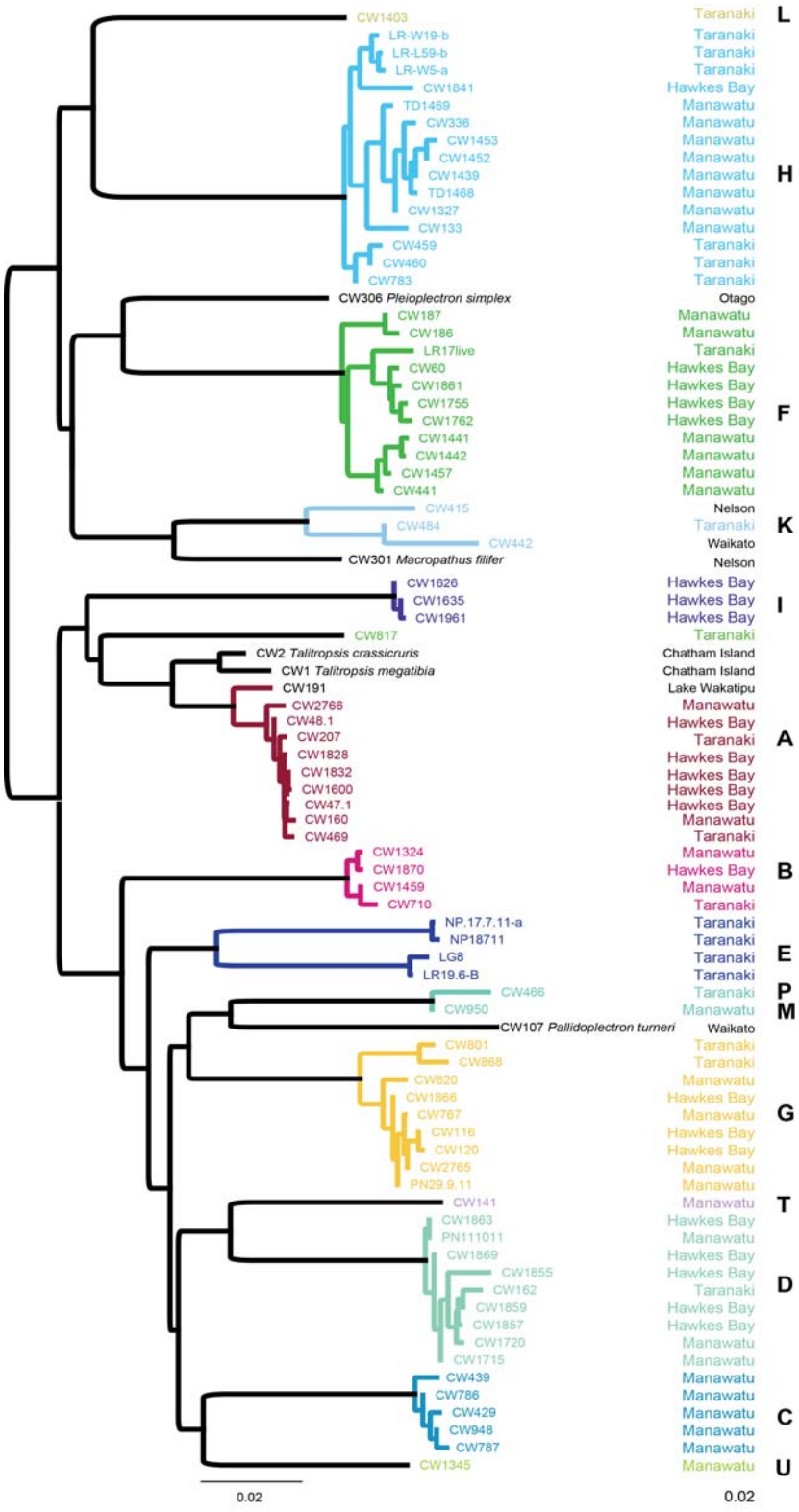


Figure 3.3 Neighbour-Joining clustering of mtDNA COI sequences of cave wētā sampled from three New Zealand regions. Letter codes on right refer to operating taxonomic units assigned based on morphology.

Some of the OTUs were found in all three regions and included individuals that were indistinguishable morphologically. i.e. OTU F, H, G, D, and A (Figure 3.3). All individuals of the same sex that are subscribed to a putative species based on mtDNA data share the same subgenital plate no matter where they were collected. There is within these species spinal variation where one or more apical spines on legs may be present or absent within the population, but this is not regional differentiation. Networks of mtDNA sequences from four species (Figure 3.4) show that some haplotypes are shared by more than one individual and sometimes by specimens from more than one location, although some taxa had distinct haplotypes associated with a region.

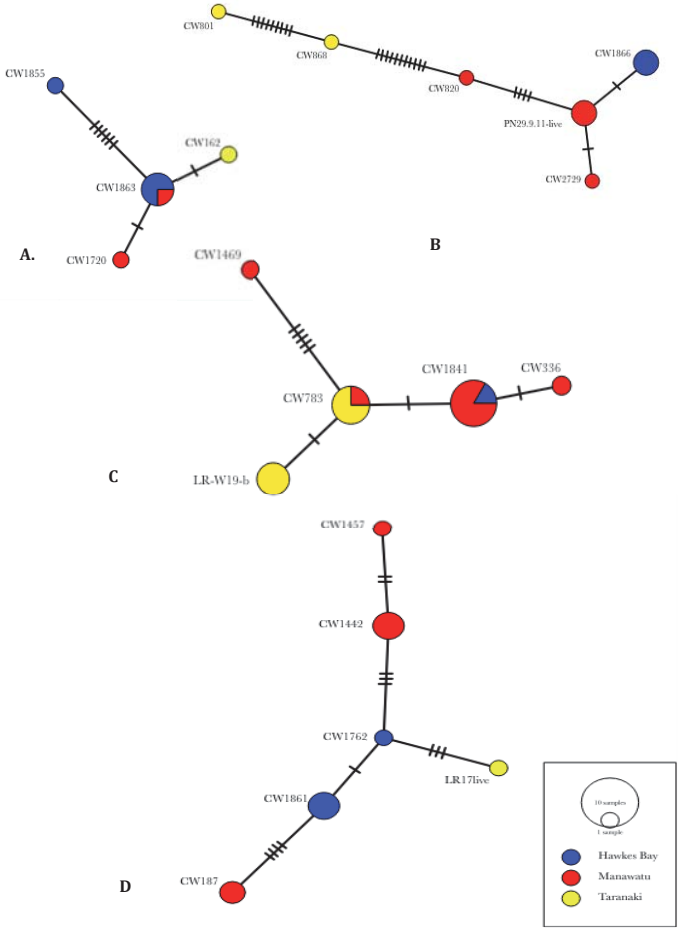


Figure 3.4 Minimum-spanning network from MtDNA sequences of four cave weta species that were encountered in all three regions. A is *Neonetus varigatus* (OTU = D), B is a new species of *Neonetus* (OTU = G). C is *Miotopus diversus* (OTU = H); D is *Pleioplectron* sp. (OTU = F).

The species detected varied among regions. Some species were found in just one location. Taranaki had the smallest sample size (n = 50) but more regionally restricted species. For example, in Taranaki I found a species of *Macropathus* (OTU=K) that was not collected from either Hawke's Bay or Manawatū, as well two new species from the genus *Neonetus* OTU M & E.

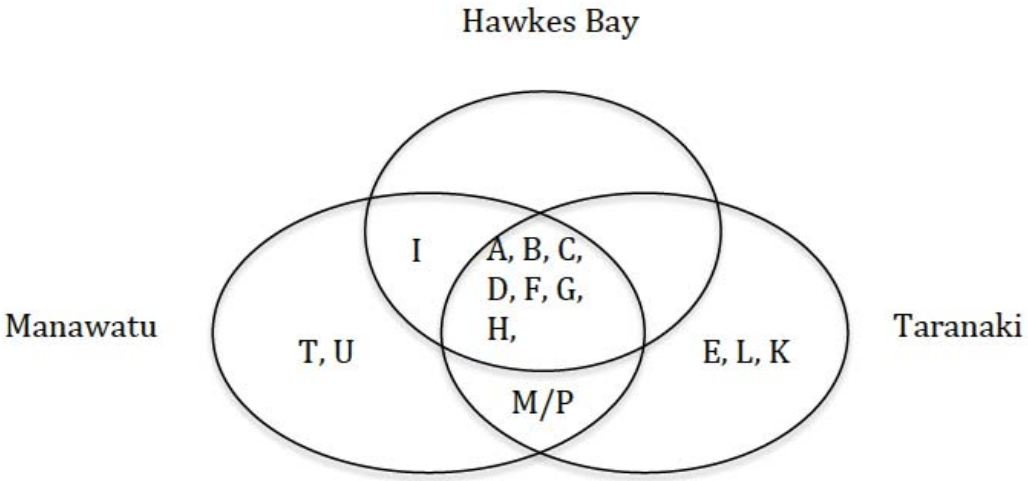


Figure 3.5 Cave wētā species diversity in each of three North Island regions using combined morphological and mtDNA characters. Each letter is a putative species (OTU).

The number of species distinguished at each of the three regions, using a combination of morphology and mtDNA data, varied from 8 to 12 (Figure 3.5). No unique species were collected from Hawke's Bay, all eight species from there are also found in either Taranaki or Manawatū or both. Based on morphology OTU P & M are separated but this is not supported by genetic evidence and therefore they are likely to be the same species (found in Taranaki and the Manawatū).

Discussion

To use species for understanding the diversity of life we need to apply an approach to establishing the identity of these (Mallet, 2001). In this study I adopted the genotypic clustering approach (Mallet, 1995, 2001). This allows me to use a combination of data sets of morphology and mitochondrial COI sequences, requiring concordance of traits to define and distinguish separate species. Here I explored diversity in cave wētā by testing the clustering of variation in abundant sampling at three separate geographic regions. Clustering by similarity across spatially separate samples provides a strong test of species status. I was able to distinguish putative species (OTUs) morphologically where characters varied among the sampling, in particular the subgenital plate and some combinations of apical spines. Using mtDNA data I was able to confirm that specimens that had a strong morphological similarity were placed together to form a genetic cluster, and matching males and females into the same OTU was valid. Spatially distinct sampling gave me the opportunity to assess how widespread species were, and contrast differences between sympatric species and allopatric populations of the same species. Gene flow, although somewhat limited today, must have at one point been possible between populations in the three regions before humans cleared the forest in southern North Island. As can be seen in figure 3.4 above, individuals collected from different regions share some of the mtDNA haplotypes.

The use of genitalia structures is important in the taxonomy of many insect groups. Male genitalia evolve rapidly due to sexual selection and closely related species often have divergence in sexual morphological traits (Arnqvist, 1997; Song & Bucheli, 2010). Genital structure helps us to see how species are remaining separated. Many insect species are identified on genitalia (e.g. Nagarkatti & Nagaraja, 1971); it is unsurprising that genitalia morphology is also important for the taxonomic and systematics of Cave wētā. The apparent sympatry of many species of cave wētā in New Zealand forest would favour reproductive character displacement for the divergence of both physical and behavioural traits.

Identification of species, whether described or not, is necessary for estimating and comparing diversity levels. One aim of this research was to extend the technique used to distinguish between taxa in the previous chapter in other regions where potentially more species are present. Distinguishing separate taxa of cave wētā using morphology is possible when both subgenital plates and apical spines are considered together. Difficulty comes when small samples result in just one or two specimens, which show variation in traits that are not yet understood at the intraspecific level. It is normal for species to show natural morphological variation across populations. Spine traits alone are frequently not adequate to identify a particular species, due to both similarity between species and variation within species. However, apical spines will frequently eliminate many potential taxa. Subgenital plate does distinguish species but only if the specimen is an adult (of course, males and females differ). Morphological traits used to diagnose a species are not reliable before the last moult. Using the spines and subgenital plate I was able to estimate 15 putative species. About half (nine) of these taxa were collected from more than one of the three regions. The combined data of morphology and sequencing shows that CW817 although morphologically very similar to *Talitropsis sedilotti* specimens is genetically distinct. This highlights the importance of using multiple methods and data sets to develop species boundaries.

The use of mitochondrial DNA sequencing is useful to test species hypotheses and resolve issues of taxonomic significance. On its own, mtDNA sequencing is a controversial tool (Moritz & Cicero 2004; Trewick, 2008), but it provides independent evidence to support or refute groupings of specimens based on phenotypic similarity. The same mitochondrial region (COI) has been studied in many different types of organisms (e.g. fish (Hubert et al., 2008; R. D. Ward et al., 2005), birds (Kerr et al., 2007), bats (Clare et al., 2007) and invertebrates (Herbert et al. 2004)). Such work provides evidence of the success of mtDNA sequencing in distinguishing between taxa when used in combination with other characters. In this study 14 putative species of forest cave wētā can be recognized based on a combination of morphology and mtDNA sequence evidence.

Many of the cave wētā OTUs are made up from individuals with the same subgenital plates but vary in spine type (Table 3.2). One spine in particular is seen to be either present or absent in a number of putative taxa that share the same subgenital plate. For example in OTU=F there are 2 phenotypes that represent males for this species and the only difference is a single spine; the hind femur retro lateral apical spine. We see this spine varying in many different taxa, thus I consider it to be natural intraspecific variation. Presence or absence of the hind femur retro lateral apical spine is not useful for diagnosis. Thus specimens of OTU=F, have a similar apical spine combination where all spines are the same except for that single spine. As well as this, there are two different types of subgenital plates; a male one and a female one. All males in the OTU=F have the same subgenital plate no matter which of the three regions they are from. This is the same for the females.

Developing a clear and reliable taxonomy for species is important for many reasons. The use of morphospecies or RTUs (recognisable taxonomic units) has lead to debate about benefits and problems of this approach (D. F. Ward & Stanley, 2004). Although, some studies show that using morphospecies taxonomy can work (Oliver & Beattie, 1996) it will be taxon dependent and work for some groups of invertebrates but not others. More importantly is whether it will be possible to identify species extinction if recognisable taxonomic units are used instead of traditional species descriptions. Where taxonomy has not yet been fully developed for a group of species it may well be better to use morphospecies or phenotypes to distinguish between taxa but as we see in this chapter that can lead to over estimation of species. Natural variation is common in all species. Some species are wide spread and many have slight phenotypic variations (adaptive or neutral). These trait may be use to separated taxa and therefore suggest two or more species when in fact it is only one species. Studies using morphospecies will always be hard to replicate in new regions or at different times and make the job of comparisons of biodiversity levels problematic.

Understanding the distribution of taxa is vital for ecological monitoring and conservation programs. They often rely on the biodiversity of an area and the

status of the taxa within that area. If species are grouped under the same banner as being a rhaphidophorid sp. but not clearly defined as any particular species a possible under estimation of the cave wētā biodiversity will result. This could suggest large numbers of cave wētā but in fact the region includes a number of species that are rare and possibly threatened. Many species in the past have been described from a single location only to have another specimen described from another location as another species. Better morphological techniques and DNA sequencing allows us to synonomise species that have been previously separated because of collecting location. It would be reasonable to assume that some cave wētā species will be widespread and sufficiently abundant, but also some species would have evolved in isolation. The number of cave wētā species observed in each of the three regions was similar, but eight species were not found everywhere. Despite the scale of samples, only 1 – 3 individuals represented six of the putative species, and this suggests that fewer of the taxa are really regionally restricted. Notably, no fewer than 11 different cave wētā species can occur in the same forest fragment in New Zealand. What limits the distribution and abundance of all these species awaits further study.

The remaining difficulty is that many of the existing species descriptions are so poor that they could refer to more than one of the taxa identified, and holotypes are frequently missing or damaged. Assigning names to the putative species recognized here will be addressed in the following chapters. Cave wētā give us an opportunity to work through historical descriptions and the present specimens will help to resolve some of the issues that have arisen from this poor understanding of New Zealand cave wētā. It is readily apparent how combining morphology and mtDNA sequencing can help clarify species' boundaries.

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Chapter 4

The cave wētā genus Neonetus, including description of three new species

Neonetus new species Turitea, Palmerston North, NZ.
Photo credit: S. A. Trewick

DISCLAIMER: This chapter includes draft taxonomic descriptions of three proposed new species. I do not however consider this thesis chapter to constitute formal publication, which will await further peer reviewed and publication in an appropriate and widely accessible journal. At such time the proposed names will be formatted appropriately and museum catalogue codes for voucher specimens will be appended etc, in accordance with Article 8 of the International Commission on Zoological Nomenclature Code of Zoological Nomenclature.

Introduction

Identifying the ~56 New Zealand Rhaphidophoridae species has been problematic (Aola M Richards, 1959b). This was due to the poor condition (or loss) of type specimens, the lack of detail in many early descriptions, and the naming of the same species several times (Chopard, 1923; Hutton, 1897; Aola M Richards, 1959b). Not all species names applied to New Zealand cave wētā are currently recognised as valid taxa and many putative species have not been found or collected since their original descriptions. Reviews of past descriptions indicate inconsistency in the formal language used to describe species, in particular the terms used to identify spines has varied among authors. Cave wētā descriptions vary in the terminology used for particular traits such as the apical spines on the legs (see chapter 2). Here I clarify the terms used to identify characteristics and the structures used to describe Rhaphidophoridae species. Having a common language means that biologists can correctly identify species without having to send specimens to taxonomists for identification. Taxonomists play an important role but the ubiquity and great species diversity within New Zealand cave wētā make them excellent for future ecological and biodiversity studies (see chapter 3) and citizen science projects, but this requires that species-level identification is possible by non-experts. Research output would be increased if a common set of terms were accepted and used and it is hoped that online tools such as the wētā-geta website (http://wetageta.massey.ac.nz/) will facilitate biodiversity studies.

Many New Zealand cave wētā species are small as adults (less than 11mm body length) and forest dwelling. In the past, collecting small individuals from forests has been neglected and so museum collections and species descriptions are lacking. Only a minority of small specimens in my studies can be placed into known species as most belong to undescribed species. This chapter focuses on the genus *Neonetus,* which was first described by Brunner von Wattenwyl in 1888*. Neonetus* is a genus of small cave wētā found predominately in forested areas (Hutton, 1897), and neither of the described species has been recorded from cave systems. Hutton took the species he found most commonly to be *Neonetus variegatus*, without looking at Brunner's type material, and described *Neonetus pilosus* as a

new species from Wellington. He distinguished *N. pilosus* from *N. variegatus* by the hairiness of *N. pilosus*. After examining type material (held in European museums), Chopard 1923 determined that *Neonetus pilosus* was a synonym of *N. variegatus*. *Neonetus huttoni* Chopard, 1923 was established to correct Hutton's mistake. So Chopard's *N. huttoni* is described in Hutton 1897 under the name *N. variegatus.* Unfortunately Hutton's type specimens are now missing. Here I redefine *N. variegatus* on recently collected specimens that (with the exception of some terminology changes) match Brunner von Wattenwyl's (1888) original description and Hutton's (1897) redescription under the name *pilosus*. Examination of modern material representing *N. variegatus* reveals it to be more common and widespread than most other *Neonetus* species. I also redescribe *Neonetus huttoni* here and illustrate the key characteristics of the male subgenital plate that distinguishes the five *Neonetus* species.

The genus *Neonetus* might include the species *Talitropsis poduroides* (Walker, 1869), which was described from a single female specimen (held at the British Natural History Museum London). It has no hind legs, and was thought to be from Australia (Walker 1871). Originally placed in *Hadenoecus,* Karny (1937) reassigned it *Talitropsis*, but due to the poor condition of the type specimen establishing correct placement can probably never be done with confidence.

Cave wētā specimens from the Far North of New Zealand (Chapter 2) were found to be consistent with Chopard's (1923) re-description of Brunner's species *N. variegatus* originally collected from Auckland. I have found specimens matching the morphological characters of this species in urban Taranaki, Hawkes Bay and Manawatu (Chapter 3, OTU D = *N. variegatus*). In the Far North one *Neonetus* taxon was defined as Te Paki species A (TPA), recorded from three different forest habitats and was more common in pitfall traps than any of the other cave wētā taxon in this region. However, since publishing that work, I have established that TPA infact consisted of two distinct *Neonetus* species. The specimens photographed in Figure 2.3 (TPA) are *Neonetus huttoni*. The male specimen (BB2(10)-a) in Figure 2.5 is incorrectly labelled as TPC (Te Paki species C) is

Neonetus variegatus. The female specimen in Figure 5 (incorrectly labelled as TPC) is *Neonetus huttoni*.

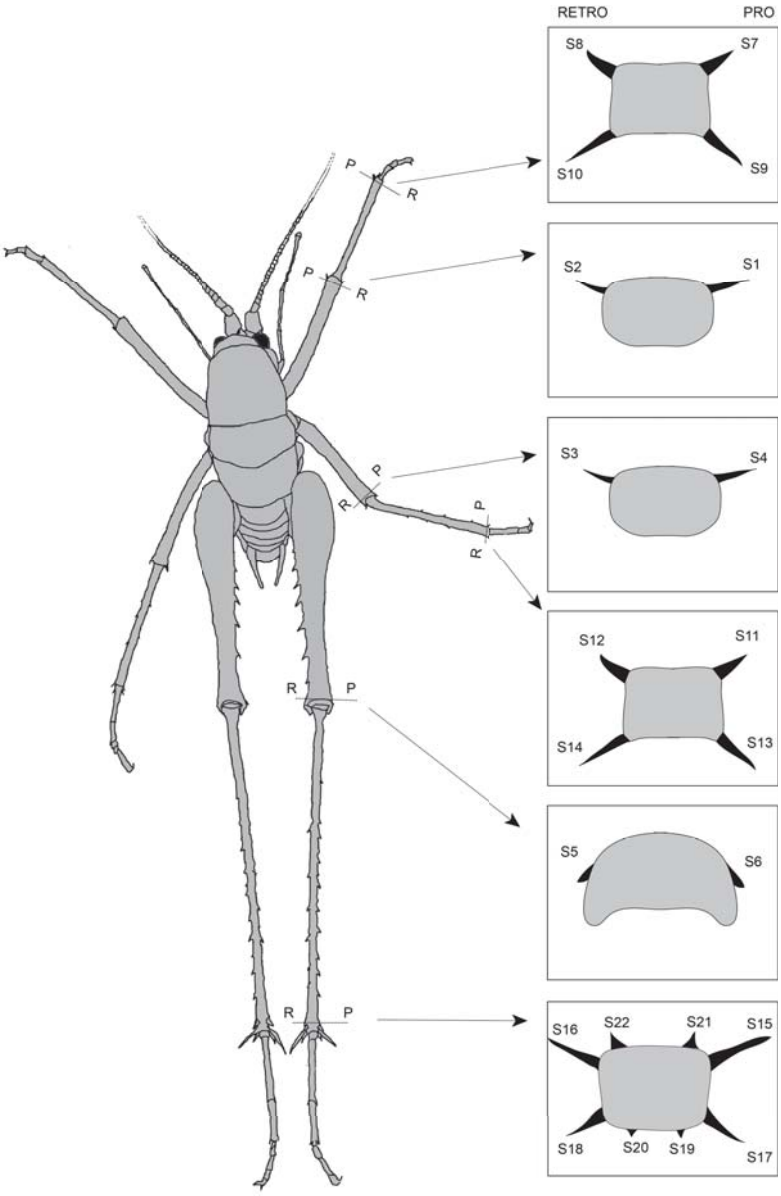


Figure 4.1. Dorsal view of cave wētā showing the location of apical spines. S1) Fore femur prolateral S2) Fore femur retrolateral S3) Mid femur prolateral S4) Mid femur retrolateral, S5) Hind femur prolateral S6) Hind femur retrolateral S7) Fore tibia superior prolateral S8) Fore tibia superior retrolateral S9) Fore tibia inferior prolateral S10) Fore tibia inferior retrolateral S11) Mid tibia superior prolateral S12) Mid tibia superior retrolateral S13) Mid tibia inferior prolateral S14) Mid tibia inferior retrolateral S15) Hind tibia superior prolateral S17) Hind tibia inferior prolateral S19) Hind tibia inferior sub-apical prolateral S21) Hind tibia superior sub-apical prolateral. Spines S16, S18, S20 and S22 match and appose to S15 S17, S19 and S21 on the retrolateral spine.

In figure 2.5 the specimens labelled as TPA were TPC specimens (correctly labelled in Figure 2.3) and identified as *Pallidoplectron* n sp*.* A specimen of this undescribed *Pallidoplectron* species was collected in the Manawatu (CW141) and identified as OTU = T (part of the *Neonetus* mtDNA clade, Chapter 3).

Combining morphology and mtDNA evidence I showed in chapter 3 that at least seven small cave wētā belong to undescribed species. These specimens were collected from multiple locations in Hawkes Bay, Manawatu, and Taranaki, and additional sampling from other North Island regions have now also been examined. Using spine counts, subgenital plate shape and mtDNA sequence data I was able to clearly group specimens and differentiate species (Chapter 3). In this chapter the three most common species that were found throughout the central and southern North Island will be formerly described. These descriptions are based on observations of at least eight adult specimens for each putative species and mtDNA sequencing confirmed the pairing of male and female specimens.

Methods

Genetic analysis

Whole genomic DNA extractions were performed using a 'salting out' protocol (Sunnucks & Hales, 1996) designed for fresh tissue, but used successfully for preserved Orthopteran tissue (Trewick & Morgan-Richards, 2004). Cave wētā specimens from pitfall traps that were killed and initially preserved in 100% propylene glycol yielded low quality DNA quantities. For fresh samples, a ~1500 base pair (bp) fragment spanning most of the Cytochrome *c* Oxidase I (COI) gene of the mitochondrial genome was amplified using polymerase chain reaction (PCR) and a combination of universal invertebrate primers: LCO1490 (Folmer O, Black M, Hoeh W, Lutz R, 1994), C1-J-1718, C1-N-2191, C1-J-2195 and L2-N-3014 (Simon et al., 1994). Nucleotide sequences were assembled and aligned using GENEIOUS v.8 (Kearse et al., 2012). Haplotypes were clustered based on sequence similarity (HKY pairwise distances) using the Neighbor-Joining algorithm (Saitou & Nei, 1987).

An initial survey with sequence data from 320 individuals representing all New Zealand Rhapidophoridae genera and locations throughout the country and on offshore islands allowed identification of a suitable phylogenetic outgroup for the "*Neonetus*" ingroup (Appendix II). The alignment extended over the entire COI gene (1545 bp) although sequence lengths for many individuals were shorter than this (~800 bp). Phylogenetic relationships were inferred from the mtDNA sequences using the Maximum Likelihood (ML) approach with the PhyML algorithm implemented in Genieous v.9 applying a GTR+I+G model, and 100 bootstrap replicates. Bayesian analysis with MrBayes used a GTR+G model with four heated MCMC chains of 5 million generations and a burnin of 100 thousand.

Morphology

After the initial phylogenetic analysis (Chapter 3) an ingroup sample of 119 specimens that represented the broad *Neonetus* clade from North Island, New Zealand, were identified (Table 4.1). Many of these specimens also provided morphological data ('yes' in Table 4.1) but 20 were either in poor condition or were juveniles and provided DNA sequence only.

Morphological data were collated and supplemented for specimens representing each of the best-sampled genetic clades within the *Neonetus* group. Spine count information that was recorded included the presence/absence of each of the 22 apical leg spines (see chapter 2/Fitness et al., 2015) (Appendix I). Each spine combination was designated a spine type number so that each specimen could be assigned to a spine type (Refer to previous chapter; Table 3.2 for spine types). The subgenital plates of adult males and females were recorded with each different subgenital plate shape being assigned a subgenital plate (SB) number, so that each specimen could be classified. Each combination of spine type and subgenital plate was treated as a separate phenotype and each specimen classified into one of these phenotypes. Grouping of phenotypes allowed males and females to be assigned the same Operational Taxonomic Unit (OTU; a unique letter code) based on whether they were deemed to be the same species. Based on evidence presented in the previous chapter, some apical leg spines were considered to vary within species

(in particular those of the hind tibia and hind femur), therefore OTUs incorporated some spine type variation (Table 4.1).

Results and Discussion

Data were obtained from 119 specimens identified as being part of the broad *Neonetus* clade (Table 4.1). Morphological and genetic data were not obtained from all specimens but reciprocal data were obtained from representatives of each phenotype.

Phylogenetic analysis of cave wētā mtDNA haplotypes revealed 10 clusters or clades (Figure 4.2), most of which could be assigned Operational Taxonomic Unit codes (OTUs) designated previously (Chapter 3). Several of these included additional specimens representing additional North Island regions (Northland; Waikato; Bay of Plenty; Gisborne; Taupo; Wellington). Of the 10 genetic clusters representing distinct phenotypically distinct forms, only three of these have previously been described: *Neonetus variegatus* (OTU D)*; N. huttoni* (OTU E)*; Pallidoplectron turneri*.

Specimens of the scarce (n = 7) Te Paki taxon TPC (Chapter 2) clustered phenotypically and genetically with specimens from Manawatu and Wanganui (OTU T). Te Paki TPC specimens had earlier been inferred as being morphologically most similar to *Pallidoplectron*. Te Paki taxon TPD had been inferred as belonging to the genus *Talitropsis* (Chapter 2), however analysis of mtDNA COI sequence data showed that TPD clustered within the broad *Neonetus* group rather than with *Talitropsis* (Appendix II). Specimens of taxon TPD have a hind femur / hind tibia ratio of 1, that is more typical of *Talitropsis* than *Neonetus*, so describing this species may require redefinition of *Talitropsis*. This species was represented by only seven specimens collected at Te Paki and its phenotype has not been observed elsewhere in the country. Mitochondrial COI data indicated a sister relationship between TPD and *Pallidoplectron turneri* in the present data set. Within the well-supported *Neonetus* clade only two sister species relationships are resolved: Te Paki taxon C is sister to *N. variegatus*; Te Paki taxon D is sister to *P. turneri*.

Table 4.1 Cave wētā specimens in the *Neonetus* group summarising phenotypic variation identified. For a subset of specimens mtDNA sequence was generated (sequence = yes).

Wētā code	Sex	Location	Spine	SB Plate	Phenotype	O.T.U	DNA Sequence
CW710	Female	Taranaki	T3	SB23	12	B	yes
CW375	Female	Waikato	T3			B	yes
CW1839	Male	Hawkes Bay	T3	SB4	33	B	
CW1849	Male	Hawkes Bay	T3	SB4	33	B	
CW1870	Male	Hawkes Bay	T21	SB4	34	B	yes
CW1324	Male	Manawatu	T3	SB4	33	B	yes
CW918	Male	Manawatu	T3	SB4	33	B	
CW1459	Male	Manawatu	T3	SB4	33	B	yes
CW1864	Female	Hawkes Bay	T21	SB19	11	C	
CW439	Female	Manawatu	T8	SB19	51	C	yes
CW2729	Female	Manawatu	T16	SB19	45	C	yes
CW431	Male	Manawatu	T1	SB15	6	C	
CW786	Male	Manawatu	T20	SB15	7	C	yes
CW291	Male	Manawatu	T20	SB15	7	C	
CW948	Male	Manawatu	T16	SB15	8	C	yes
CW787	Male	Manawatu	T19	SB15	9	C	yes
CW429	Female	Manawatu	T1	SB19	10	C	yes
CW785	Female	Manawatu	T1	SB19	10	C	
CW788	Female	Manawatu	T1	SB19	10	C	yes
CW290	Female	Manawatu	T3	SB19	12	C	
CW1389	Female	Manawatu	T25	SB19	43	C	
CW433	Female	Manawatu	T16	SB19	45	C	

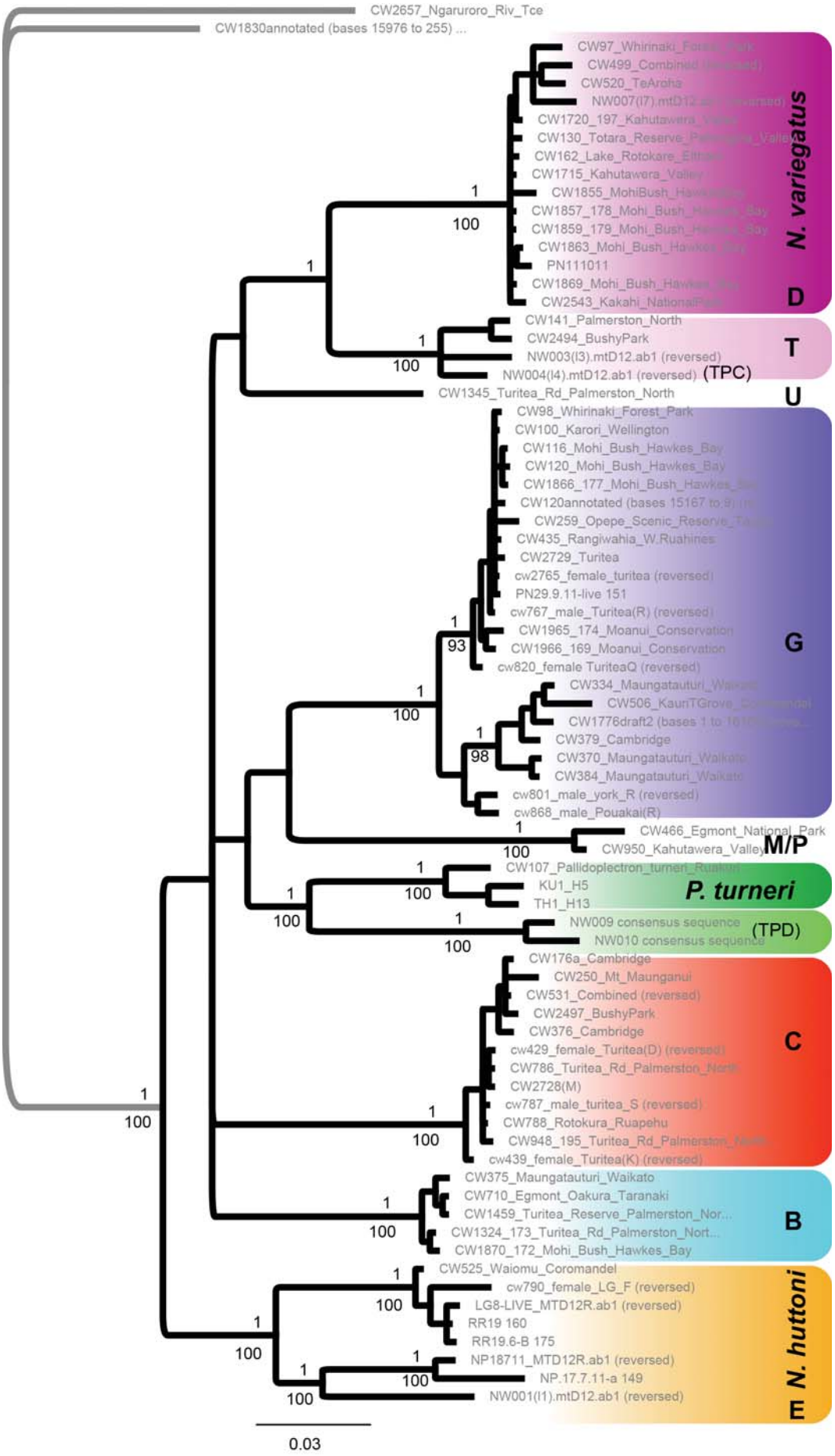
CW250	Female	Tauranga	T3			C	Yes
CW176a	Male	Waikato	T21			C	Yes
CW376	Female	Waikato	T3			C	Yes
CW1855	Male	Hawkes Bay	T21	SB2	19	D	yes
CW1863	Male	Hawkes Bay	T21	SB2	19	D	yes
CW1869	Male	Hawkes Bay	T21	SB2	19	D	yes
CW1865	Male	Hawkes Bay	T21	SB2	19	D	
CW1857	Male	Hawkes Bay	T3	SB2	20	D	yes
CW1851	Male	Hawkes Bay	T3	SB2	20	D	
CW581	Male	Hawkes Bay	T3	SB2	20	D	
CW1859	Female	Hawkes Bay	T21	SB20	35	D	yes
CW1763	Female	Hawkes Bay	T21	SB20	35	D	
CW130	Male	Manawatu	T21	SB2	19	D	yes
PN11/10/11-a	Female	Manawatu	T3	SB26	36	D	yes
CW687	Male	Manawatu	T21	SB2	19	D	
CW1720	Male	Manawatu	T3	SB2	20	D	yes
CW1715	Female	Manawatu	T21	SB20	35	D	yes
CW162	Male	Taranaki	T26	SB2	18	D	yes
CW467	Male	Taranaki	T21	SB2	19	D	
CW468	Male	Taranaki	T21	SB2	19	D	
CW471	Male	Taranaki	T21	SB2	19	D	
CW755	Male	Taranaki	T21	SB2	19	D	
CW1397	Male	Taranaki	T3	SB2	20	D	
CW473	Male	Taranaki	T3	SB2	20	D	
CW757	Male	Taranaki	T3	SB2	20	D	
CW815	Male	Taranaki	T3	SB2	20	D	

CW758	Female	Taranaki	T3	SB26	36	D	
CW97	Male	Whirinaki	T3			D	Yes
NP18/7/11-a	Male	Taranaki	T1	SB10	22	E	yes
CW790	Male	Taranaki	T20	SB10	23	E	yes
NP21/7/11-a	Female	Taranaki	T20	SB10	23	E	
NP10/7/11-a	Female	Taranaki	T1	SB9	24	E	
NP11/7/11-a	Female	Taranaki	T20	SB9	25	E	
LG8-live	Female	Taranaki	T20	SB9	25	E	yes
LG3(4)-live	Female	Taranaki	T20	SB9	25	E	
CW1761	Male	Hawkes Bay	T9	SB3	13	G	
CW574	Male	Hawkes Bay	T9	SB3	13	G	
CW575	Male	Hawkes Bay	T9	SB3	13	G	
CW1866	Male	Hawkes Bay	T10	SB3	14	G	yes
CW573	Male	Hawkes Bay	T10	SB3	14	G	
CW576	Male	Hawkes Bay	T10	SB3	14	G	
CW577	Male	Hawkes Bay	T10	SB3	14	G	
CW578	Male	Hawkes Bay	T10	SB3	14	G	
CW579	Male	Hawkes Bay	T10	SB3	14	G	
CW116	Male	Hawkes Bay	T10	SB3	14	G	yes
CW580	Female	Hawkes Bay	T10	SB21	17	G	yes
CW1845	Female	Hawkes Bay	T10	SB21	17	G	
CW1862	Female	Hawkes Bay	T10	SB21	17	G	
CW571	Female	Hawkes Bay	T10	SB21	17	G	
CW767	Male	Manawatu	T9	SB3	13	G	yes
CW430	Male	Manawatu	T10	SB3	14	G	
CW820	Female	Manawatu	T10	SB21	17	G	yes

CW1363	Male	Taranaki	T9	SB3	13	G	
CW868	Male	Taranaki	T10	SB3	14	G	yes
CW801	Male	Taranaki	T5	SB3	15	G	yes
CW867	Female	Taranaki	T9	SB21	16	G	
CW802	Female	Taranaki	T10	SB21	17	G	
CW2765		Manawatu				G	yes
CW334	Male	Waikato	T9			G	Yes
CW120	Female	Hawkes Bay				G	yes
CW466	Female	Taranaki	T18	SB18	46	M	yes
CW950	Female	Manawatu	T14	SB24	44	P	yes
CW141	Male	Manawatu	T7	SB27	21	T	yes
CW1345	Female	Manawatu	T21	SB23	53	U	yes
PN29.9.11		Manawatu					Yes
CW2728		Manawatu					yes
CW379	Female	Waikato	T9			G	Yes
CW370	Male	Waikato	T9			G	Yes
SA1(6)a	Male	Far North	T27				yes
SC4(5)d	Female	Far North	T27				Yes
PA1(9)-e	Female	Far North	T1			E	Yes
BB2(10)a	Male	Far North	T3			D	Yes
PA1(8)c	Male	Far North					Yes

Figure 4.2 Phylogenetic relationships within the New Zealand cave wētā genus *Neonetus* inferred from MtDNA sequences (COI) using maximum likelihood (numbers above nodes are posterior probabilities, below nodes are bootstrap values). Main clades are labelled with either existing species name, Te Paki codes from Chapter 2, or letters referenced in the text. Clade G: *Neonetus* ~~CIRRATUS~~ sp. nov.; Clade C *Neonetus* ~~UNCINUS~~ sp. nov.; Clade B *Neonetus* ~~PATERLONGIPES~~ sp. nov.

[Following page]


CW2657_Ngaruroro_Riv_Tce
CW1830annotated (bases 15976 to 255) ...
CW97_Whirinaki_Forest_Park
CW499_Combined (reversed)
CW520_TeAroha
NW007(I7).mtD12.ab1 (reversed)
CW1720_197_Kahutawera_Valley
CW130_Totara_Reserve_Palmerston_Valley
CW162_Lake_Rotokare_Eltham
CW1715_Kahutawera_Valley
CW1855_MohiBush_Hawkes_Bay
CW1857_178_Mohi_Bush_Hawkes_Bay
CW1859_179_Mohi_Bush_Hawkes_Bay
CW1863_Mohi_Bush_Hawkes_Bay
PN111011
CW1869_Mohi_Bush_Hawkes_Bay
CW2543_Kakahi_NationalPark
N. variegatus
D
CW141_Palmerston_North
CW2494_BushyPark
NW003(I3).mtD12.ab1 (reversed)
NW004(I4).mtD12.ab1 (reversed)
T
(TPC)
CW1345_Turitea_Rd_Palmerston_North
U
CW98_Whirinaki_Forest_Park
CW100_Karori_Wellington
CW116_Mohi_Bush_Hawkes_Bay
CW120_Mohi_Bush_Hawkes_Bay
CW1866_177_Mohi_Bush_Hawkes_Bay
CW120annotated (bases 15167 to 9) (re...
CW259_Opepe_Scenic_Reserve_Taupo
CW435_Rangiwahia_W.Ruahines
CW2729_Turitea
cw2765_female_turitea (reversed)
PN29.9.11-live 151
cw767_male_Turitea(R) (reversed)
CW1965_174_Moanui_Conservation
CW1966_169_Moanui_Conservation
cw820_female TuriteaQ (reversed)
G
CW334_Maungatauturi_Waikato
CW506_KauriTGrove_Coromandel
CW1776draft2 (bases 1 to 1619) (reve...
CW379_Cambridge
CW370_Maungatauturi_Waikato
CW384_Maungatauturi_Waikato
cw801_male_york_R (reversed)
cw868_male_Pouakai(R)
CW466_Egmont_National_Park
CW950_Kahutawera_Valley
M/P
CW107_Pallidoplectron_turneri_Ruakuri
KU1_H5
TH1_H13
P. turneri
NW009 consensus sequence
NW010 consensus sequence
(TPD)
CW176a_Cambridge
CW250_Mt_Maunganui
CW531_Combined (reversed)
CW2497_BushyPark
CW376_Cambridge
cw429_female_Turitea(D) (reversed)
CW786_Turitea_Rd_Palmerston_North
CW2728(M)
cw787_male_turitea_S (reversed)
CW788_Rotokura_Ruapehu
CW948_195_Turitea_Rd_Palmerston_North
cw439_female_Turitea(K) (reversed)
C
CW375_Maungatauturi_Waikato
CW710_Egmont_Oakura_Taranaki
CW1459_Turitea_Reserve_Palmerston_Nor...
CW1324_173_Turitea_Rd_Palmerston_Nort...
CW1870_172_Mohi_Bush_Hawkes_Bay
B
CW525_Waiomu_Coromandel
cw790_female_LG_F (reversed)
LG8-LIVE_MTD12R.ab1 (reversed)
RR19 160
RR19.6-B 175
NP18711_MTD12R.ab1 (reversed)
NP.17.7.11-a 149
NW001(I1).mtD12.ab1 (reversed)
N. huttoni
E
0.03

Taxonomy of *Neonetus* and descriptions of new species.

Class: **Insecta**

Order: **Orthoptera**

Suborder: **Ensifera**

Superfamily: **Tettigoniodea**

Family: **Rhaphidophoridae**

Genus: *Neonetus*

Type species: *variegatus* Brunner von wattenwyl 1888

Neonetus Brunner von Wattenwyl 1888 (Type species *variegatus*)

variegatus Brunner von wattenwyl 1888 (syntypes: MHNG, Geneva Museum; NMW, Vienna Museum)

pilosus [syn.] Hutton 1896

huttoni Chopard 1923 (holotype: missing)

Table 4.2. Spine characters for two recognized and three new species of *Neonetus,* cave wētā from New Zealand

Species	Fore femur	Mid femur	Hind femur	Fore tibia	Mid tibia	Hind tibia	Authority
N. variegatus	2	2	0	2	2	4	Brunner 1888
N. huttoni	2	2	0	2	2	4	Chopard 1923
N. ~~CIRRATUS~~ sp. nov.	2	2	0–1	4	4	8	This thesis
N. ~~UNCINUS~~ sp. nov	2	2	0–1	4	4	6–8	This thesis
N. ~~PATERLONGIPES~~ sp. nov	2	2	0–1	4	4	8	This thesis

Species redescription: *Neonetus variegatus* Brunner von Wattenwyl 1888

This is a redefinition of Brunner's *N. variegatus* (1888). Hutton took what he considered the most common species he found to be *N. variegatus*. Later Chopard examined type specimens of both Brunner (1888) and Hutton (1897) and redefined Brunner's *N. variegatus* (Chopard, 1923). Chopard also pointed out that the species Hutton had referred to as *N. variegatus* was in need of a new name and so proposed *Neonetus huttoni* stating only that it was *"*absolutely different from Brunner's *N. variegatus."* (page 239, Chopard 1923). Fortunately Hutton included figures (pl 13, 16-16c) when he thought he was re-describing *N. variegatus* (Hutton, 1897), which has allowed us to identify *N. huttoni* in our collections despite the loss of Hutton's type material. Below is a redefinition of *Neonetus variegatus* Brunner 1888 using the same terminology as other species described in this chapter. (Table 4.1 & Figure 4.1).

Diagnosis

A small cave wētā found throughout North Island New Zealand, with the following traits: absence of the hind femora retrolateral spine and distinguished by male and female genitalia (Figure 4.4).

Description

Adult Body Length: males: 9.2 mm (n=6) females: 10.7 mm (n=4).

Head: Head small; almost vertical; vertex tawny brown; frons and mandibles are pale with brown tips; peduncle and scape pale; flagellum tawny brown; antennae longer than body; eyes black and ovoid.

Thorax: Pronotum equal long as wide; medium brown with pale speckles; the edge of the pronotum and metanotum pale with a slightly thickened edge; sternum light cream colour.

Legs: Moderately long. Hind femora shorter than tibiae; coxae and trochanters cream; femora and tibiae with cream and brown bands.

Fore femora compressed with 1 prolateral apical spine, 1 retrolateral apical spine and numerous short gold setae.

Fore tibiae with 2 pairs of long spines positioned in the mid to lower portion of the tibiae, spines are pale with dark tips, 1 prolateral superior apical spine, 1 short and pale with retrolateral superior apical spine dark tip that is almost hidden amongst the setae, 1 prolateral inferior apical spine, 1 retrolateral inferior apical spine. Inferior apical spines are longer than superior spines, articulate, pale with dark tip and longer and thicker than the surrounding setae.

Mid femora compressed with 1 articulated prolateral apical spine, 1 long articulated retrolateral apical spine.

Mid tibiae with 2 pairs of long spines positioned in the middle to lower portion of the tibia with prolateral side spines longer than the retrolateral spine, 1 prolateral superior apical spine, 1 retrolateral superior apical spine that is pale with dark tip, 1 retrolateral inferior apical spine, 1 prolateral inferior apical spine, and inferior spines longer than superior spine.

Hind femora with 0 or 1 retrolateral apical spine. (no prolateral apical spine). 4 to11 small slightly dark retrolateral spines that get progressively larger from proximal to distal position, 0 to 14 slightly dark prolateral spines that get progressively larger from proximal to distal end.

Hind tibiae longer than hind femora with small brown alternate spines along the length of the tibiae on superior surface, a pair (1 prolateral and 1 retrolateral) of superior subapical spines, a pair (1 prolateral and 1 retrolateral) of superior apical spines that are twice as long as superior subapical spines, a pair (1 prolateral and 1 retrolateral) of inferior apical spines that are 2/3 length of superior apical spines, 2 short inferior subapical spines that are hidden amongst the thick setae on the inferior surface of the tibiae.

Tarsae with 4 segments, 1st and 2nd segment with a pair of spine on distal end, 4th segment almost equal in length as 1st segment.

Abdomen: Shiny medium brown with dappled pattern. Edges of the tergites pale. There is a distinct contrasting lateral margin between the brown dorsal surface

and pale underside.

Males: (Figure 4.4). Cerci long and rounded, golden in colour with few darker brown markings, pilose with long golden hairs. Styli narrow, half the length of cerci, golden colour with short golden setae. Subgenital plate forms a large curved thick and sclerotised structure, with a slight keel and base of the plate is wide and long before it curves dorsally. At its curve it is almost black in colour, and the upward structure tapers to the blunt point as it rounds up between the styli and cerci to sit above the last tergites.

Females: (Figure 4.4). Subgenital plate is bilobed with closely-spaced lobes forming an 'M' like apex with a shallow indent between the lobes. The subgenital plate is lightly pilose with hairs of a light golden colour, and is often flat against the base of the ovipositor hidden by the last sternite. Ovipositor golden, long and serrated on the ventral margin near the apex.

Figure 4.3 Neotype of *Neonetus variegatus* (Left) male, (right) female. Scale bar 10mm.

Figure 4.4 Subgenital plate of *Neonetus variegatus* (Left) male lateral view, (centre) male ventral view, (right) female.

Distribution: NZ: Wellington, Manawatu, Taranaki, Hawke's Bay, Waikato, Taupo, Te Paki, Northland, Auckland, Coromandel (Figure 4.13).

Type material:

Neotype: Adult male (Figure 4.3): 9.39mm, collected 24/9/06 Waiwhakaio, Burgess Hill, New Plymouth (39° 5'51.18"S; 174° 6'30.02"E) Collected by Steve Trewick & Mary Morgan-Richards. Museum accession number (MONZxxx and CW473). Other material examined: adult female (Figure 4.3): 10.96mm, collected 8/10/12 Mohi Bush, Hawkes Bay (39°51'33.03"S; 176°54'23.00"E) Collected by M. Lusk. Museum accession number (MONZxxx and Phoenix code CW1859).

Additional material examined: Hawke's Bay (HB) (CW 581, 1763, 1851, 1855, 1857, 1863, 1865, 1869); Manawatu (M) (CW130, 687, 1715, 1720, PN11/10/11-a); Taranaki (T) (CW 162, 467, 468, 471, 755, 757, 758, 815, 1397). These specimens are held in the Phoenix collection at Massey University, New Zealand.

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Species redefinintion: *Neonetus huttoni* Chopard 1923

Chopard (1923) does not give a clear definition of *Neonetus huttoni*, only coming up with the new name given to Hutton's (1987) *Neonetus variegatus.* Here is a redefinition of Chopard's *Neonetus huttoni.*

Diagnosis

A small cave wētā found in North Island New Zealand, with the following traits: Absence of the hind tibia inferior subapical spine; male external genitalia has distinctive hooked structure.

Most similar to *Neonetus variegatus* found in the North Island and distinguished by male and female genitalia, absence of the hind tibial inferior sub-apical retrolateral and prolateral spines, (Table 4.2, Figure 4.5).

Description

Adult BL: males 8.4mm (n= 3) females 8.89mm (n= 4) (Figure 4.11) number of individuals examined.

Head: Head small; almost vertical; vertex is a tawny brown; frons and mandibles are pale; tip of mandibles brown; peduncle and scape pale flagellum slightly darker brown; antennae longer than body; eyes black and ovoid.

Thorax: Pronotum equally long as wide; medium to dark brown with pale speckles; Sternum golden to dark brown.

Legs: Moderately long. Hind femora shorter than tibiae. Coxae and trochanters golden or dark brown. Femora and tibiae brown and speckled.

Fore femora compressed with 1 prolateral apical spine, 1 retrolateral apical spine, short setae present.

Fore tibiae with 2 pairs of long, brown with dark tipped spines positioned in the middle to distal portion of the tibiae, 1 prolateral superior apical spine that is shorter than other spines, pale with dark tip and almost hidden amongst the setae. A pair (1 prolateral and 1 retrolateral) of longer inferior apical spines are articulated, pale with dark tip and longer and thicker than the surrounding setae.

Mid femora compressed with 1 prolateral apical spine and 1 long articulated retrolateral apical spine.

Mid tibiae with 2 pairs of long spines position in the middle to distal portion of the tibiae, prolateral side spines longer than the retrolateral spines. 1 retrolateral superior apical spine, pale with dark tip. A pair (1 prolateral and 1 retrolateral) of longer inferior apical spines, pale with dark tip.

Hind femora with 1 or 0 retrolateral apical spine, but never with a prolateral apical spine, 3 to 5 small slightly dark spines along retrolateral ventral edge at the distal end , but no prolateral spines.

Hind tibiae longer than femora with small brown spines along the length of the tibiae on superior surface, a pair (1 prolateral and 1 retrolateral) superior subapical spines, a pair (1 prolateral and 1 retrolateral) of superior apical spines that are twice as long as superior subapical spines, a pair (1 prolateral and 1 retrolateral) of inferior apical spines that are 2/3 the length of superior apical spines above.

Tarsae with 4 segments, 1st and 2nd segments with a pair of spines on distal end, 4th segment almost equal in length as 1st segment.

Abdomen: Shiny brown with small pale speckles. Male paler than female with each tergite the same pattern and colour. Sternites almost the same colour as tergites becoming paler toward the ventral midline and slightly pilose towards the anterior end.

Males: (Figure 4.6). Cerci compressed, wide and blunt, brown and cream in a speckled pattern and pilose. Stylus narrow, half the length of cerci and pale in colour. Subgenital plate is a 'hooked' structure strengthened by a double keel that runs from base to apex and terminates above the terminal tergite.

Females: (Figure 4.6). Subgenital plate is bilobed, almost triangular in shape with a slightly concave tip, gold setae present.

Distribution: NZ: Taranaki, Coromadel, Auckland, Northland (Figure 4.13).

Type material:

Lectotype Adult male (Figure 4.5): 8.3mm, collected 31/3/07 Lucy's Gully, Mt Egmont National Park, Tarnaki by SAT & MMR. Museum accession number (MONZxxx and CW790). Other material examined: adult female (Figure 4.5): 8.9mm, collected 11/7/11 Seaview Road, New Plymouth, Museum accession number (MONZxxx and phoenix code NP11/7/11-a).

Figure 4.5 Lateral view of *Neonetus huttoni* (Left) male, (right) female. Scale bars 10mm.

Figure 4.6 Subgenital plates of *Neonetus huttoni* (Left) male lateral view, (centre) male ventral view, (right) female venteral view.

Additional material examined: Taranaki (T) (LG8-live, LG3(4)live, NP18/7/11-a, NP21/7/11-a, NP10/7/11-a). These specimens are held in the Phoenix collection at Massey University, New Zealand.

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Species description: *Neonetus* ~~CIRRATUS~~ sp. nov.

Figure 4.7 Holoypes of species *Neonetus* ~~CIRRATUS~~ sp. nov. (Left) male holotype CW574, (right) female holotype CW802. Scale bars 10mm.

A combination of morphological structures provides diagnostic characters for *Neonetus* (Figure 4.7)

Diagnosis

A small cave wētā found in central North Island New Zealand, with the following traits: Absence of the fore femur retrolateral apical spine and mid femur prolateral apical spine; male external genitalia has distinctive 'curled' structure.

Most similar to *Neonetus variegatus* found in the North Island and distinguished by male and female genitalia, absence of the fore femoral retrolateral apical spine and present of the hind tibial inferior sub-apical retrolateral and prolateral spines, (Figures 4.7, 4.8, Table 4.2).

Etymology: Latin cirratus- curled. This name is given to this species references the strongly curled shape of the male subgenital plate.

Description

Adult Body Length: males 9.02 mm (n= 7) females 9.94 mm (n= 4).

Head: Head small, almost vertical, vertex is tawny brown. Frons and mandibles are pale, tip of mandibles brown, peduncle and scape pale flagellum slightly darker brown, antennae longer than body, eyes black and ovoid.

Thorax: Pronotum equally long as wide, medium to dark brown with pale speckles. Sternum light cream colour.

Legs: Moderately long, hind femora shorter than tibiae, coxae and trochanters cream, femora and tibiae cream and brown speckled.

Fore femora compressed with 1 prolateral apical spine, short gold setae, but retrolateral apical spine absent.

Fore tibiae with 2 pairs of long spines positioned in the middle to distal portion of the tibiae, spines are pale with dark tips, 1 prolateral superior apical spine and is shorter than other spines, pale with dark tip and almost hidden amongst the setae, a pair (1 prolateral and 1 retrolateral) of articulated inferior apical spines that are longer than superior spine, pale with dark tip and longer and thicker than the surrounding setae.

Mid femora compressed with 1 long articulated l retrolateral apical spine but no prolateral apical spine.

Mid tibia with 2 pairs of long spines positioned in the middle to distal portion of the tibiae, with prolateral side spines longer than the retrolateral spines. 1 retrolateral superior apical spine that is pale with dark tip, a pair (1 prolateral and I retrolateral) inferior apical spines that are longer than superior spine, pale with dark tip.

Hind femora with 1 or 0 retrolateral apical spine, but never with a prolateral apical spine, 3 to 6 small slightly dark spines along the retrolateral ventral edge at the distal end, and getting progressively larger toward the distal end. 1 to 7 slightly dark prolateral spines becoming progressively larger from proximal to distal end.

Hind tibiae longer than femora with small brown alternate spines distributed along the superior surface, a pair (1 prolateral and 1 retrolateral) of superior subapical spines, a pair (1 prolateral and 1 retrolateral) of superior apical spines that are twice as long as superior subapical spines, a pair (1 prolateral and 1 retrolateral) of inferior apical spines that are 2/3 length of superior

apical spines above, a pair of short inferior subapical spines are typically hidden amongst the thick setae on the inferior surface of the tibiae.

Tarsae with 4 segments, 1st and 2nd segment with a pair of spine on distal end, 4th segment almost equal in length as 1st segment.

Abdomen: Shiny tawny brown with pale speckles, becoming paler laterally. Each tergite of the same pattern and colour. Sternites cream and slightly pilose towards the anterior end.

Males (Figure 4.8): Cerci compressed, wide and blunt, brown and cream in a banded pattern, pilose. Stylus narrow, half the length of cerci and pale colour. Subgenital plate is a strongly curved structure consisting of a thin solid outer margin with connective tissue extending toward the body of the animal. The subgenital plate terminates with a blunt trianglular tubercle on the upper (strictly ventral) margin, held above the last tergite.

Females (Figure 4.8): Subgenital plate is bilobed, with a minute projection on the tip of each lobe, slightly pilose and pale.

Distribution: NZ: Manawatu, Taranaki, Taupo, Hawke's Bay, Waikato, Wellington, Rotorua, Gisborne.

Figure 4.8 Details of subgenital plates of male and female *Neonetus* ~~CIRRATUS~~. (Left) male lateral view, (centre) male ventral view, (right) female ventral view.

Type material

Holotype: Adult male (Fig 4.7): 9.01mm. Collected 8/8/2004 Mohi Bush, Hawke's Bay (39°51'33.03"S; 176°54'23.00"E) Collected by Steve Trewick, Mary Morgan-Richards. Museum accession number (MONZxxx and CW574). Allotype adult female (Fig 4.7): 9.98mm collected 22/10/2007 York Rd, Taranaki (39°17'17.71"S: 174°10'31.29"E) collected by Steve Trewick, Mary Morgan-Richards. Museum accession number (MONZxxx and phoenix code CW802).

Additional material examined: Hawke's Bay (HB) (CW 116, 571, 573, 575, 576, 577, 578, 579, 580, 1761, 1802, 1845); Manawatu (M) (CW 430, 767, 820); Taranaki (T) (CW 802, 867, 868, 1363). These specimens are held in the Phoenix collection, Massey University, New Zealand.

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Species description: *Neonetus* ~~UNCINUS~~ sp. nov.

Diagnosis

A small cave wētā found in central North Island New Zealand, with the following trait: underside of abdomen pale in contrast to upper surface. Most similar to *Neonetus variegatus* found in the North Island and distinguished by male and female terminalia (Table 4.1, Figures 4.9, 4.10).

Etymology: Latin uncinus- hooked. This refers to the shape of the male subgenital plate.

Description

Adult BL: males: 7.5mm (n=3) females: 9.4 (n=3).

Head: Head small, almost vertical. Vertex brown, frons with brown markings,

mandibles are pale with brown tips. Peduncle and scape pale with brown markings, flagellum golden brown. Antennae longer than body. Eyes black and ovoid.

Thorax: Edges of pronotum rounded, medium brown with dappled pattern with slightly thickened margin.

Legs: Moderately long, hind femora shorter than tibiae, coxae and trochanters cream, femora and tibiae with irregular bands of cream and brown.

Fore femora compressed, with a pair (1 prolateral and 1 retrolateral) apical spines, short gold setae.

Fore tibiae with 2 pairs of long spines positioned in the middle to distal portion of the tibiae, spines are pale with dark tips. A pair (1 prolateral and 1 retrolateral) of superior apical spines shorter than other spines, pale with dark tips, almost hidden amongst the setae, a pair (1 prolateral and 1 retrolateral) of articulated prolateral inferior apical spines longer than superior spines, pale with dark tip, longer and thicker than the surrounding setae.

Mid femora compressed with 1 articulated prolateral apical spine and 1 long articulated retrolateral apical spine.

Mid tibiae with 2 pairs of long spines positioned in the middle to distal portion of the tibia, prolateral side spines longer than the retrolateral spines, a pair (1 prolateral and 1 retrolateral) superior apical spines, a pair (1 prolateral and 1 retrolateral) of retrolateral inferior apical spines longer than superior spines, pale with dark tip.

Hind femora with 0 or 1 retrolateral apical spine, but prolateral apical spine absent, 1 to 4 small retrolateral spines, slightly dark, becoming progressively larger toward distal end, 0 to 14 slightly dark prolateral spines becoming progressively larger toward the distal end of femora.

Hind tibiae longer than femora with two rows of small brown spines along the length of the superior surface, a pair (1 prolateral and 1 retrolateral) of subapical spines, a pair (1 prolateral and 1 retrolateral) of superior apical spines, twice as long as superior subapical spines, a pair (1 prolateral and 1 retrolateral) of inferior apical spines 2/3 the length of superior apical spines above. Presence/absence of prolateral and retrolateral inferior subapical

spines varies among individuals.

Tarsae with 4 segments, 1st and 2nd segment with a pair of spine on distal end, 4th segment almost equal in length as 1st segment.

Abdomen: Shiny medium brown with dappled pattern on dorsal surface and extending to edges of the sternites; sternites golden colour with brown markings and slightly pilose.

Males. (Figure 4.10): Cerci thick and rounded; golden colour with few darker brown markings; pilose with long golden hairs; stylus narrow and pale; more than half the length of the cerci; subgenital plate forms a large bent structure, that ascends for a bit before bending upwards in an sublinear line tapering to a blunt apex; an 'ear'-like structure protrudes on either side of the lower portion; blunt point reaches beyond the tergites between the styli and cerci.

Females. (Figure 4.10): Subgenital plate is bilobed; the lobes form an 'Y' like apex; the indent between the lobes is deep; the subgenital plate is lightly pilose and light gold; it is small and has a slight dent in the middle creating a subtle three deminsional shape; the structure has a slight globular appearance; ovipositor golden in colour; long with a few serrated teeth near the apex.

Figure 4.9 Holotype of species *Neonetus* ~~UNCINUS~~ sp. nov. (Left) male holotype CW786, (right) paratype female CW788.

Figure 4.10 Subgenital plate of male and female *Neonetus* ~~UNCINUS~~ A) Male lateral view B) Male ventral view C) Female.

Distribution: NZ: Manawatu, Hawke's Bay, Taranaki, Taupo, Bay of Plenty, Whanganui, Waikato (Figure 4.13).

Type material

Holotype: Adult male (Figure 4.9 & 4.10): 7.16mm, collected 24.2.07 Turitea Rd, Palmerston North (40°24'54.15"S; 175°39'50.28"E) Collected by EXM Trewick. Museum accession number (MONZxxx and CW786). Allotype adult female (Figure 4.10): 11.15mm collected 24.2.07 Turitea Rd, Palmerston North (40°24'54.15"S; 175°39'50.28"E) Collected by EXM Trewick. Museum accession number (MONZxxx and phoenix code CW788).

Additional material examined: Hawke's Bay (HB) (CW 1864); Manawatu (M) (CW 290, 291, 429, 431, 433, 439, 785, 786, 787, 788, 948, 1389, 2729). These specimens are held in the Phoenix collection at Massey University, New Zealand.

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Species description: *Neonetus* ~~PATERLONGIPES~~ sp. nov.

Diagnosis

A small-bodied cave wētā found in southern North Island New Zealand, with the following traits: long hind legs. Most similar to a *Neonetus* species discovered in the Far North and sequenced to show it belonging to this genus; distinguished by male and female terminalia (Table 4.2, Figures 4.11, 4.12).

Etymology: Latin *pater*-father, *longipes*- long foot. Adult males of this species have significantly longer hind tibiae and tarsae than adult females.

Description

Adult BL: males: 12.90mm (n=4), females: 13.12mm (n=1).

Head: Head small; almost vertical; vertex is brown; frons pale; mandibles pale with brown tips; peduncle and scape pale with brown markings; flagellum golden brown; antennae longer than body; eyes black and ovoid.

Thorax: Edges of pronotum rounded; medium brown with dappled pattern; edge of pronotum slightly thickened at sides.

Legs: Twice as long as other *Neonetus* sp.; hind femora shorter than tibiae; coxae and trochanters cream; femora and tibiae brown with pale bands. Fore femora compressed; 1 prolateral apical spine; 1 retrolateral apical spine; short gold setae; fore tibiae with 2 pairs of spines positioned in the mid to lower portion of the tibia; spines are pale with dark tips sometimes hidden among setae; apical spines as follows: 1 fore tibia prolateral superior apical spine; 1 fore tibia retrolateral superior apical spine; shorter than other spines; pale with dark tip; almost hidden amongst the setae; 1 fore tibia prolateral inferior apical spine; 1 fore tibia retrolateral inferior apical spine; inferior apical spines longer than superior spines; articulate; pale with dark tip; longer and thicker than the surrounding setae; mid

femora compressed with 1 articulate prolateral apical spine; 1 articulate long retrolateral apical spine; mid tibia with 2 pairs of long spines positioned in the mid to lower portion of the tibia; mid tibiae apical spines as follows: 1 mid tibia prolateral superior apical spine; 1 mid tibia retrolateral superior apical spine; pale with dark tip; 1 mid tibia retrolateral inferior apical spine; 1 mid tibia prolateral inferior apical spine; inferior spines longer than superior spine; pale with dark tip; hind femora apical spines with 0–1 retrolateral apical spine present; hind femora with 6 (females) or 30+ (male) of retrolateral spines, small; dark; 0 (female) or 30+ in males of prolateral spines; slightly dark; hind tibiae longer than femora; small brown alternate spines running up the length of the tibia on superior surface; hind apical tibia spines as follows: 2 superior subapical spines, 1 prolateral and 1 retrolateral; 2 superior apical spines, 1 prolateral and 1 retrolateral; spines twice as long as superior subapical spines; 2 inferior apical spines, 1 prolateral and 1 retrolateral; 2/3 length of superior apical spines above; hind tibia prolateral and retrolateral inferior subapical spines being either present or absent; tarsus with 4 segments, 1st and 2nd segment with a pair of spine on distal end, 4th segment almost equal in length as 1st segment.

Abdomen: Shiny medium brown with dappled pattern, pattern continuing round to the sternites; sternites golden colour with brown markings; slightly pilose.

Figure 4.11 Holotype of species *Neonetus* ~~PATERLONGIPES~~ sp. nov. (Left) male, (right) female. Scale bar 10mm.

Males (Figure 4.12): Cerci long and thin, golden in colour with few darker brown markings and numerous long golden hairs. Stylus narrow and pale, more than half

the length of the cerci. Subgenital plate longer in length than it is broad, flat with a central keel and pointed apex.

Females. (Figure 4.12): Subgenital plate is bilobed and the lobes are parallel finger-like projections. Ovipositor golden in colour, long and serrated near the apex on the ventral edge.

Distribution: NZ: Manawatu, Taranaki, Hawke's Bay, Waikato (Figure 4.13)

Figure 4.12 Subgenital plate of male and female *Neonetus* ~~PATERLONGIPES~~ sp. nov. Above (left) male lateral view, (centre) male ventral view, (right) female.

Type material:

Holotype: Adult male (Figure 4.11): 12.90mm, collected 1.11.09 Turitea Rd, Palmerston North (40°24'54.15"S; 175°39'50.28"E) by E.X.M. Trewick. Museum accession number (MONZxxx and CW1324). Allotype adult female (Figure 4.11): collected Davies track, Egmont N.P. Oakura, Taranaki (Kaitaki Ranges), 14/11/06 Collected by SAT. Museum accession number (MONZxxx and phoenix code CW710).

Additional material examined: Hawke's Bay (HB) (CW 1839, 1849, 1870); Manawatu (M) (CW 918, 1324, 1459); Taranaki (T). These specimens are held in the Phoenix collection at Massey University, New Zealand.

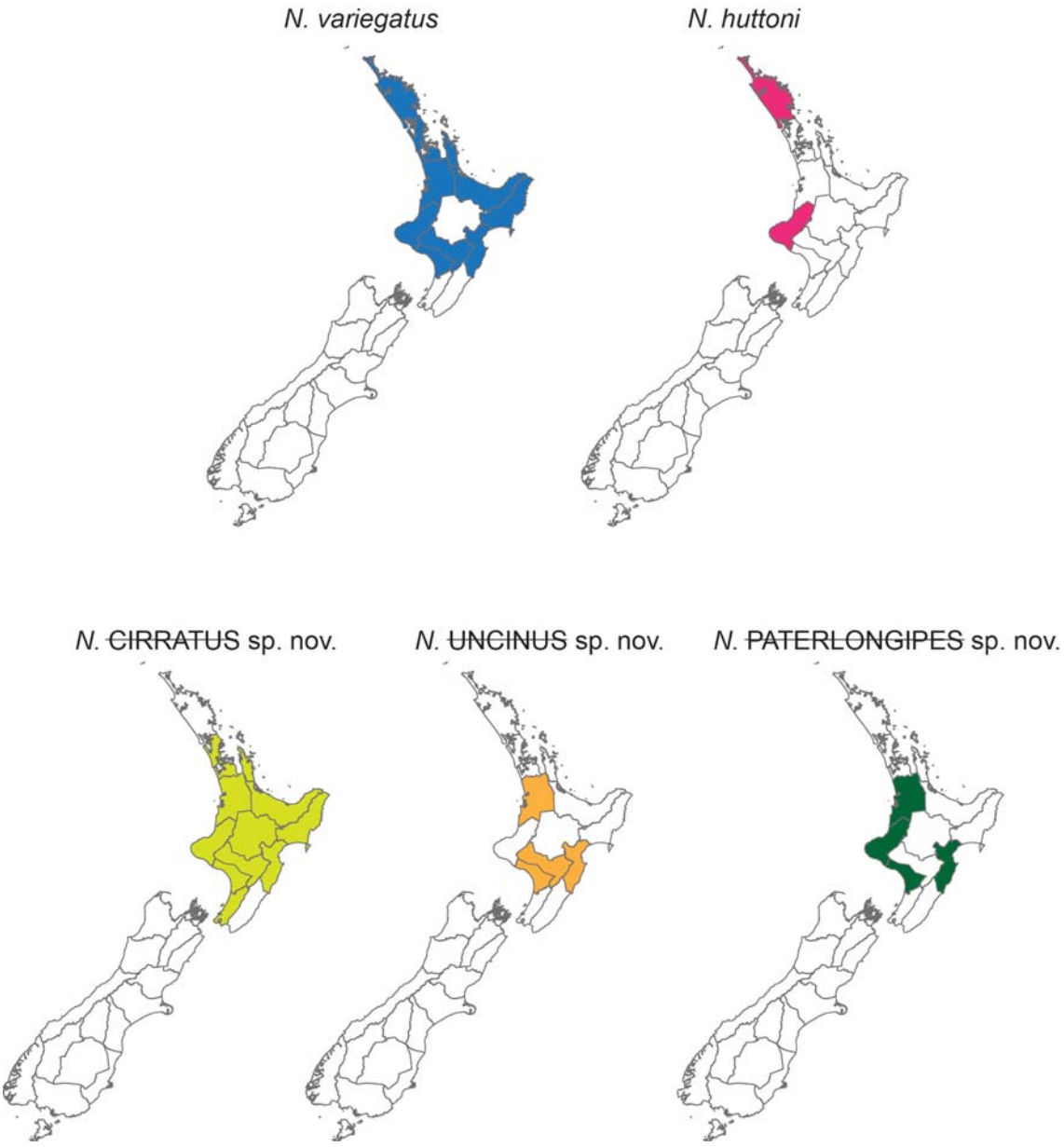

Figure 4.13 Known distributions of *Neonetus* species recorded by New Zealand entomological (Crosby) regions.

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Chapter 5

Clarification of the genera Pleioplectron, Weta, Miotopus and the species within.

DISCLAIMER: This chapter includes draft taxonomic descriptions of three proposed new species. I do not however consider this thesis chapter to constitute formal publication, which will await further peer reviewed and publication in an appropriate and widely accessible journal. At such time the proposed names will be formatted appropriately and museum catalogue codes for voucher specimens will be appended etc, in accordance with Article 8 of the International Commission on Zoological Nomenclature Code of Zoological Nomenclature.

Introduction

Identifying cave wētā specimens to genus level is made difficult by absence of diagnostic characters (Cook et al., 2010) and many of the nineteen currently recognised genera of New Zealand Rhaphidophoridae are poorly described. The most recent attempt to provide a diagnostic key to New Zealand genera was based purely on the available published material from many years earlier but provides the best summary of subgenital plate variation (D. F. Ward, 1997). When there is only one or two species per genus such keys are valuable, but as more species are described the variation within genera that becomes apparent reduces some of their value. In the case of New Zealand cave wētā variation within species has seldom be recognised and this further reduces the utility of such keys.

Three genera and sixteen species of New Zealand Rhaphidophoridae were proposed by F. W. Hutton (1897). When Hutton named new species of Orthoptera his descriptions were usually brief, and many appear to have been based on single specimens. Working 60 years later, Aola Richards attempted to readdress this problem by returning to the original specimens (if she could find them) and re-describing many species (Aola M Richards, 1959b). Richards noted some discrepancies between her observations and Hutton's descriptions. Using improved microscopes, larger insect collections and a better understanding of taxonomic characters, Richards was able to improve earlier work. Unfortunately, Richards focused on large cave dwelling species and did not consult a wide range of specimens representing the smaller species that do not aggregate in caves. Two genera of these relatively small Rhaphidophoridae are the focus of this chapter: *Pleioplectron* and *Miotopus*.

Pleioplectron Hutton 1897 (Type species: *simplex)*

Weta [syn.] Chopard (1923) (Type species: *thomsoni*) new synonymy

simplex Hutton 1897

pectinatum[syn.] Hutton 1897 new synonymy

hudsoni Hutton 1897

thomsoni **(**Chopard 1923)

Miotopus Hutton 1899 (Type species: *diversus* by monotype)

diversus Hutton 1897

~~RICHARDSI~~ new species, this work.

Hutton (1897) erected the genus *Pleioplectron* and described four new species, two species each from the South and North islands of New Zealand.

South Island

Pleioplectron simplex - North Canterbury and Banks Peninsula

Pleioplectron pectinatum - Banks Peninsula

North Island

Pleioplectron hudsoni - Wellington

Pleioplectron diversum – Upper Wanganui

In 1900 Hutton described *Pleioplectron cavernae* from Karapiti, Taupo, North Island. Richards (1959b) was able to examine Hutton's (1900) type specimen of *Pleioplectron cavernae*. Despite the holotype being immature and damaged she was able to conclude that it was closer to the genus *Pachyrhamma* than it was to *Pleioplectron.* Richards (1959b) redefined the genus *Pleioplectron* following examination of the original type material of *Pleioplectron simplex* (1 male specimen held CMNZ, Canterbury). The re-description by Richards differs from Hutton's original description in that it is more detailed and better matches the current observation of *Pleioplectron* species observed in the present research. However, it should be noted that Richards stated that the number of apical spines were constant within species, but further research (see chapters II & III) shows that presence/absence of the hind femur retrolateral apical spine varies within a species (and thus within the genus). South Island cave wētā specimens in our collections can readily be identified as *Pleioplectron simplex* using the Richards' (1959) redefinition of the species.

Pleioplectron hudsoni was described by Hutton from a single male specimen collected in Wellington. The female is not formally known at this stage. Richards (1959) stated that the loss of the original material and poor description by Hutton

made identification of this species difficult. Hutton did, however provide information to distinguish the two *Pleioplectron* species: *P. simplex* fore and hind tibiae with two or three spines in the inner row; *P. hudsoni* fore and hind tibiae with one spine in the inner row.

According to Hutton (1897), *Pleioplectron pectinatum* differs from *Pleioplectron diversum* (now *Miotopus diversus*) in "mid tibiae [being] unarmed above", "narrow keel" rather than "slightly keeled" subgenital plate of male. The number of spines on hind tibiae "about twenty-five spines in each row" cf. *P. simplex* "about twenty-nine spines in the outer (anterior) and about seventeen in the inner (posterior) row". Richards (1959b) was able to examine the holotype of *P. pectinatum*, and although she noted that it was in poor condition this specimen was used to redefine the species. As a result the type basis of the description is one damaged individual representing one sex at one location.

Chopard (1923) described a new species and monotypic genus; *Weta thomsoni.* Chopard's description is detailed but there are reasons to consider that this species belongs in *Pleioplectron* not *Weta.* Although seemingly distinguished by being found only in caves, female *Weta thomsoni* have a sub-genital plate similar to that of *Pleioplectron* species; in all there is a sinuous posterior margin creating a subtle tri-lobed effect. This differs from the summary of Ward (1997), which did not consult the original material.

Hutton (1899) proposed that his species *Pleioplectron diversum* belonged in a new genus, *Miotopus.* However, Richards (1959) disagreed and returned *Miotopus diversus* to *Pleioplectron* stating that the differences in spination identified by Hutton (1899) to establish *Miotopus* were the result of natural congeneric variation. Here I review the status of *Pleioplectron, Miotopus* and *Weta* in order to identify both common and diagnostic traits of the putative genera and species.

Methods

Cave wētā material held in the Phoenix lab collection at Massey University were examined. Specimens were identified based on the descriptions of Hutton (1897), Richards (1959) and Chopard (1923). Specimens that did not match with existing species descriptions become the subject of further examination and proposal for new species.

Fifty-three cave wētā specimens from the North Island and South Island were identified as *Pleioplectron, Weta* or *Miotopus* (See Appendix 2). All apical spines, sub-genital plate and three body measurements were recorded (Table 5.1). Measurements consisted of pronotum length (Pro), hind femur length (HF) and hind tibia length (HT) as these have been shown in previous research in this thesis to be informative. Although the majority of specimens were adult, sub-adult individuals were also examined.

A scatterplot between pronotum and hind femur was done to display the size relationship between these two body parts. This was also done using pronotum and hind tibia and hind femur and hind tibia but there was no significant different between the relationship. Using Rstudio (Rstudio Team, 2015), I was able so conduct this display and group according to the specimens spine data. Using size and apical spines a Principle Component Analysis was performed.

Results

Although a scatterplot of pronotum and hind femur lengths (Figure 5.1) shows differences among species, there are extremely few diagnostic traits separating the six putative species examined (Table 5.1). *Miotopus* and *Pleioplectron simplex* and *Weta thomsoni* are similar in spines and size, while the smaller *Pleioplectron hudsoni* has fewer apical spines (Figure 5.1). Specimens assigned to a particular species based on shape, size and spines tend to cluster together in a Principle Component Analysis as expected. These morphological traits need to be used

together with subgenital plate shape of males to distinguish species of the three putative genera *Miotopus, Weta* and *Pleioplectron*.

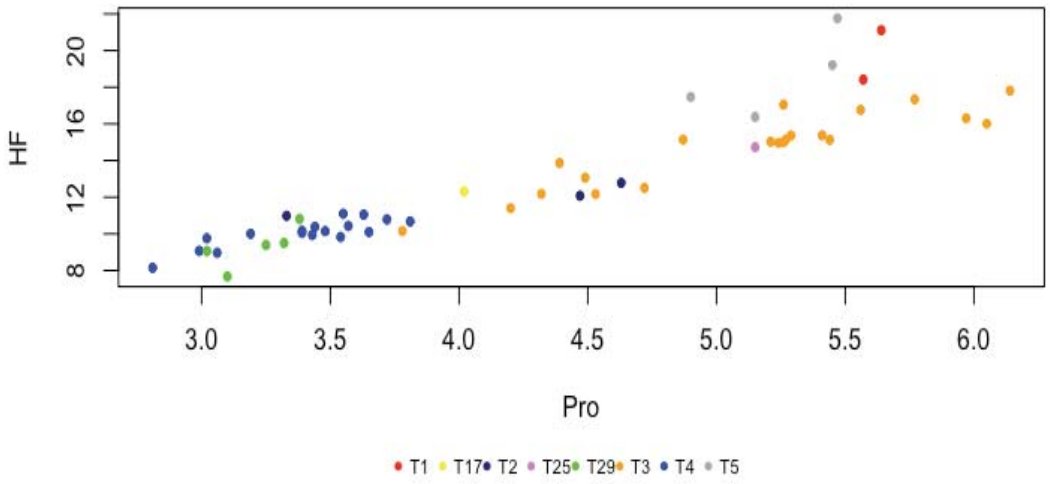

Figure 5.1 Size variation of adult cave wētā can help differentiate species. Scatterplot of the length of pronotum and hind femur of 54 specimens of *Pleioplectron* and *Miotopus*. Apical leg spine combinations are given distinguishing colours: *Pleioplectron simplex* (T2, dark blue); *P. hudsoni* (T4 & T29, blue & green); *P. thomsoni* (T1, red); *Miotopus diversus* (T3 & T17 & T25, orange, green, purple); *M.* ~~RICHARDSI~~ sp. nov. (T5, black)(Table 5.1).

Phylogenetic clustering of mtDNA haplotypes (Chapter III) did not group *Miotopus diversus* specimens (OTU = H) with *Pleioplectron simplex* or *P. hudsoni* (OTU = F) (Figure 3.4). Although *Miotopus* specimens are broadly similar in morphology to *Pleioplectron* species they are probably not sister genera according to mitochondrial data. Taken together with morphological details identified when examining specimens from southern North Island (Taranaki, Manawatu and Hawkes Bay; Chapter III) this indicates that Hutton's original treatment of *Miotopus diversus* was valid and should be resurrected. Hutton (1897) was correct to separate *P. diversum* into the new genus *Miotopus*, which is distinguished from *Pleioplectron* by distinctive apical spine count, subgenital plate shape and large size of adults. In the North Island, *Miotopus* specimens have two apical spines on their fore femora while *Pleioplectron hudsoni* individuals have just one (Table 5.1). The relatively widespread North Island species is consistent with Hutton's

Miotopus diversus, and a new South Island species of *Miotopus* has been identified. *Miotopus* is redefined and a new species described below.

In contrast to the situation with *Miotopus*, the specimens of the monotypic genus *Weta* had mtDNA haplotypes that clustered within the diversity of *Pleioplectron* collected from the South Island*. Weta thomsoni* is also morphologically more similar to *Pleioplectron* than *Miotopus* in the absence of the inferior subapical spines on the hind tibia. In addition, the male subgenital plate of *Weta thomsoni* is flat and disc-like, similar to *Pleioplectron.* As *Weta* and *Pleioplectron* are shown to be morphologically and genetically so similar and as *Pleioplectron* has chronological precedence over *Weta*, this species should now be defined as *Pleioplectron thomsoni*. Although Hutton described two *Pleioplectron* species from Banks Peninsular I found no evidence from examination of morphology or mtDNA variation in the available sample to indicate that Banks Peninsular and nearby Canterbury contain more than one species of *Pleioplectron*.

Table 5.1 Specimens representing *Pleioplectron* and *Miotopus* from which morphological data were obtained. Measurements are in mm. Spine codes are as given in Figure 4.1. Pro = Pronotum length, HF = Hind femur length, HT = Hind tibia length, Location codes T = Taranaki, M = Manawatu, HB = Hawkes Bay

Code	Species	Sex	Location		S2	S5	S6	S19	S20	Pro	HF	HT
CW1403	*Miotopus diversus*	Female	T	T17	1	0	1	1	0	4.02	12.31	14.75
CW133	*Miotopus diversus*	Male	M	T3	1	0	1	1	1	4.39	13.87	15.87
CW1439	*Miotopus diversus*	Male	M	T3	1	0	1	1	1	5.77	17.34	19.79
CW1327	*Miotopus diversus*	Female	M	T3	1	0	1	1	1	5.41	15.38	17
CW1837	*Miotopus diversus*	Female	HB	T3	1	0	1	1	1	5.26	15.01	16.65
CW1841	*Miotopus diversus*	Female	HB	T3	1	0	1	1	1	4.49	13.06	14.23
CW460	*Miotopus diversus*	Female	T	T3	1	0	1	1	1	5.24	14.97	16.48
CW462	*Miotopus diversus*	Female	T	T3	1	0	1	1	1	5.44	15.13	16.15
CW783	*Miotopus diversus*	Female	T	T3	1	0	1	1	1	4.53	12.17	12.7
LR-L3-A	*Miotopus diversus*	Female	T	T3	1	0	1	1	1	5.29	15.37	17.16
LR-W19-A	*Miotopus diversus*	Female	T	T25	1	0	0	1	1	5.15	14.73	16.63
CW1459	*Miotopus diversus*	Male	M	T3	1	0	1	1	1	5.56	16.77	20.46
CW1467	*Miotopus diversus*	Male	M	T3	1	0	1	1	1	6.14	17.81	21.66
CW461	*Miotopus diversus*	Male	T	T3	1	0	1	1	1	4.87	15.14	17.19
cw465	*Miotopus diversus*	Male	T	T3	1	0	1	1	1	4.32	12.18	13.58
TD19(1)-b	*Miotopus diversus*	Male	M	T3	1	0	1	1	1	3.78	10.15	11.67
CW1452	*Miotopus diversus*	Male	M	T3	1	0	1	1	1			
CW1469	*Miotopus diversus*	Male	M	T3	1	0	1	1	1			
CW1468	*Miotopus diversus*	Female	M	T3	1	0	1	1	1			
CW336	*Miotopus diversus*	Female	M	T3	1	0	1	1	1			
LR-L59-b	*Miotopus diversus*	Male	T	T3	1	0	1	1	1			

LR-W19-b	*Miotopus diversus*	Female	T	T3	1	0	1	1	1			
CW345	*Miotopus* ~~RICHARDSI~~ sp. nov.	Male	C	T5	1	1	1	1	1	4.9	17.47	22.56
CW302	*Miotopus* ~~RICHARDSI~~ sp. nov.	Female	C	T5	1	1	1	1	1	5.15	16.38	19.96
CW2617	*Miotopus* ~~RICHARDSI~~ sp. nov.	Male	GB	T5	1	1	1	1	1	5.45	19.21	21.72
CW2567	*Miotopus* ~~RICHARDSI~~ sp. nov.	Female	GB	T5	1	1	1	1	1	5.47	21.76	26.62
CW1440	*Pleioplectron hudsoni*	Male	M	T29	0	0	0	0	0	3.1	7.68	10.22
CW1442	*Pleioplectron hudsoni*	Male	M	T29	0	0	0	0	0	3.38	10.81	12.16
CW1464	*Pleioplectron hudsoni*	Male	M	T29	0	0	0	0	0	3.32	9.5	10.79
CW1609	*Pleioplectron hudsoni*	Male	HB	T4	0	0	1	0	0	3.39	10.05	11.12
CW187	*Pleioplectron hudsoni*	Male	M	T4	0	0	1	0	0	3.65	10.1	11.2
CW60	*Pleioplectron hudsoni*	Male	HB	T4	0	0	1	0	0	3.06	8.97	10.55
LR19(6)-live	*Pleioplectron hudsoni*	Male	T	T4	0	0	1	0	0	2.99	9.07	10.46
TD17(1)-a	*Pleioplectron hudsoni*	Male	M	T4	0	0	1	0	0	3.02	9.76	10.56
TD19(1)-a	*Pleioplectron hudsoni*	Male	M	T4	0	0	1	0	0	3.19	10	12.15
CW1759	*Pleioplectron hudsoni*	Male	HB	T29	0	0	0	0	0	3.02	9.06	10.13
CW1441	*Pleioplectron hudsoni*	Female	M	T4	0	0	1	0	0	3.72	10.79	11.91
CW1454	*Pleioplectron hudsoni*	Female	M	T4	0	0	1	0	0	3.57	10.43	12.01
CW1465	*Pleioplectron hudsoni*	Female	M	T4	0	0	1	0	0	3.39	10.16	11.79
CW1755	*Pleioplectron hudsoni*	Female	HB	T29	0	0	0	0	0	3.25	9.39	10.41
CW1762	*Pleioplectron hudsoni*	Female	HB	T4	0	0	1	0	0	3.43	9.94	11.23
CW186	*Pleioplectron hudsoni*	Female	M	T4	0	0	1	0	0	3.44	10.38	11.65
CW1861	*Pleioplectron hudsoni*	Female	HB	T4	0	0	1	0	0	3.54	9.83	11.12
CW434	*Pleioplectron hudsoni*	Female	M	T4	0	0	1	0	0	3.81	10.68	11.6
LR-L5-b	*Pleioplectron hudsoni*	Female	T	T4	0	0	1	0	0	3.55	11.1	12.57
LR17-live-a	*Pleioplectron hudsoni*	Female	T	T4	0	0	1	0	0	3.48	10.15	11.61
CW1457	*Pleioplectron hudsoni*	Male	M	T3	1	0	1	0	0			

CW131	*Pleioplectron hudsoni*	Male	M	T4	0	0	1	0	0			
CW161	*Pleioplectron hudsoni*	Female	M	T4	0	0	1	0	0			
CW306	*Pleioplectron simplex*	Female	C	T2	0	0	1	1	1	4.63	12.78	14.69
CW328	*Pleioplectron simplex*	Male	C	T2	0	0	1	1	1	3.33	10.98	12.19
CW361	*Pleioplectron simplex*	Female	C	T2	0	0	1	1	1	4.47	12.08	12.92
CW1877	*Weta thomsoni*	Male	C	T1	1	0	1	0	0	5.64	21.11	22.77
CW1878	*Weta thomsoni*	Female	C	T1	1	0	1	0	0	5.57	18.42	21.41

Table 5.2 Summary of species and their authority, spine and subgenital plate description.

Name	Date	Collection Location	Author	Apical Spines – Pairs						Sub-genital plate	
				Femora			Tibiae			Female	Male
				Fore	Mid	Hind	Fore	Mid	Hind		
Pleioplectron simplex	1897	North Canterbury, Banks Peninsula. South Island	Hutton 1897, redefined by Richards 1959	1	2	1	4	4	8	Tri-lobed	
Pleioplectron hudsoni	1897	Wellington. North Island.	Hutton 1897	1	2	0	4	4	6	Tri-lobed	Cupsidate plate with small keel
Pleioplectron pectinatum	1897	Banks Peninsula. South Island	Hutton 1897, redefined by Richards 1959	1	2	0	4	4	6		
Miotopus diversus Syn. *Pleioplectron diversum*	1897	Upper Wanganui. North Island	Hutton 1897	2	2	1/0	4	4	8	Tri-lobed with the apex of outer two lobes slightly higher than the middle lobe	
Miotopus ~~RICHARDSI~~ sp. nov.		South Island	Fitness 2016, this work	2	2	1/0	4	4	8	Tri-lobed; less defined than *M. diversus*	Small, tongue-like
Pleioplectron thomsoni Syn. *Weta thomsoni*	1923	South Island	Chopard 1923	2	2	1	4	4	6		

Species

My examination of Rhaphidophoridae specimens from the North Island has identified a common species of small, dark, forest dwelling cave wētā. This species is consistent in morphology at all locations. Adult males and females are often found together and they have the same spine count (Table 5.1). The spines from the North Island species are similar to Hutton's original description of the genus. The difference being that *P. simplex* has four pairs of hind tibia apical spines and the North Island species (*P. hudsoni*) has only three pairs. Female subgenital plates within the genus *Pleioplectron* are similar, having a large plate-like structure that may have a tri-apex or flat looking apex. Male subgenital plates have species distinctions. MtDNA sequences of wētā from various North Island specimens (OTU = F) are sister to *Pleioplectron simplex* from South Island locations including Canterbury (Appendix 2). Thus I consider that the widespread North Island morph represents Hutton's species *Pleioplectron hudsoni.* Because of the paucity of Hutton's description of *P. hudsoni* (and lack of females) I have redefined it below:

Pleioplectron hudsoni is a little smaller than *P. simplex* (Figure 5.1) and is a little darker in colour. Subgenital plate of females has three points, which are nearly in a line, and ovipositor of adult females has about 5 serrations on the lower margin at the tip. In contrast, male subgenital plates are slightly longer than broad in a cuspidate shape. There is a slight keel down the centre of the plate. *Pleioplectron simplex* subgenital plate of adult males has three apical bulges, the middle resulting from a keel.

***

Pleioplectron hudsoni Hutton 1897

Diagnosis: A small cave wētā found in forested areas of the North Island, New Zealand. It is brown speckled. Most similar to *Pleioplectron simplex* based on the similarity of the tri-lobed female subgenital plate and apical spines (Figure 5.3, Table 5.2), but distinguished by absence of hind femora apical spines. Male subgenital plates are slightly longer than broad with cuspidate shape and slight keel down centre of plate.

Description: Body Length: Male: 9.18mm (n=6), Female = 10.21mm (n=8).

Head: Head slightly variegated colouring with a medium brown and golden light brown; covered in fine setae; palps are light golden brown and covered with fine setae; fastigium medium brown with minor golden light brown; eyes black; antennae long and medium brown with setae; scape and peduncle light golden brown.

Thorax: Pronotum round anteriorly and slightly posteriorly; lateral sides are rounded with a slight 'lip' coming outwards; coloured in a medium brown with a slight variegated pattern if light brown.

Legs: Moderately long; hind femora shorter than tibia; coxae and trochanters cream; femora and tibia dark brown with cream bands; fore femora compressed; 1 prolateral apical spine present and 1 retrolateral apical spine absent; short gold setae present; fore tibiae with 2 pairs of long spines position in the mid to lower portion of the tibia; spines are pale almost transparent; apical spines as follows: 1 fore tibia prolateral superior apical spine;1 fore tibia retrolateral superior apical spine; shorter than other spines; pale with dark tip; almost hidden amongst the setae; 1 fore tibia prolateral inferior apical spine; 1 fore tibia retrolateral inferior apical spine; inferior apical spines longer than superior spine; articulate; pale with dark tip; longer and thicker than the surrounding setae; mid femora compressed with 1 articulate long prolateral apical spine; 1 articulate long retrolateral apical

spine; mid tibia with 2 pairs of long spines position in the mid to lower portion of the tibia; prolateral side spines longer than the retrolateral spine; mid tibiae apical spines as follows: 1 mid tibia prolateral superior apical spine; 1 mid tibia retrolateral superior apical spine; pale with dark tip; 1 mid tibia prolateral inferior apical spine; 1 mid tibia retrolateral inferior apical spine; inferior spines longer than superior spine; pale with dark tip; hind femora with 1-7 retrolateral spines, small; slightly dark; size gets progressively larger from proximal to distal; 3-7 prolateral spines; slightly dark; size gets progressively larger from proximal to distal end; hind tibiae longer than femora; small brown alternate spines running up the length of the tibia on superior surface; hind apical tibia spines as follows: 2 superior subapical spines, 1 prolateral and 1 retrolateral; 2 superior apical spines, 1 prolateral and 1 retrolateral; spines twice as long as superior subapical spines; 2 inferior apical spines, 1 prolateral and 1 retrolateral; 2/3 length of superior apical spines above; no inferior subapical spines; tarsus with 4 segments, 1st and 2nd segment with a pair of spine on distal end, 4th segment almost equal in length as 1st segment.

Abdomen: Shiny, brown coloured. Short setae covering both turgites and sternites; sterum pale brown colour.

Male (Figure 5.3): Cerci long, round; brown colour; clothed in setae; styli short, not extending beyond the end of the sub-genital plate; sub-genital plate is as wide as long in a triangular shape; terminates to a blunt point between the styli; a gentle keel down the middle of the plate ending is a blub at the apex.

Female (Figure 5.3): Sub-genital plate is trilobed; outer two lobes higher than the middle lobe; apex rounded and blunt; ovipositor brown with a few serrations at the tip on the bottom edge.

Distribution: NZ: Wellington, Waiarapa, Mangaweka, Manawatu, Taranaki, Hawke's Bay, Whanganui, Kaweka Ranges, Waikato (Figure 5.8).

Type material:

Neotype: Adult male (Figure 5.2): collected 15/08/2010 Turitea, Manawatu

(40°25'48.64" S: 175°40'24.00" E) Collected by S.A. Trewick. Museum accession number (MONZxxx and CW1442). Also examined: adult female (Figure 5.2): collected 19/11/2010 Turitea, Manawatu (40°25'48.64"S: 175°40'24.00" E) by S.A. Trewick. Museum accession number (MONZxxx and CW1465).

Figure 5.2 *Pleioplectron hudsoni.* Lateral view, (left) male, (right) female. Scale bars 10mm

Figure 5.3 Subgenital plate of *Pleioplectron hudsoni.* (Left) male lateral view, (centre) male ventral view, (right) female ventral view.

Additional material examined: Hawke's Bay (HB) (CW 60, 1609, 1759, 1762, 1861, 1755); Manawatu (M) (CW 1457, 187, 131, 1442, 1440, 1464, 1441, 186, 1454, 1465, 434, 161, TD17(1)-a, TD19(1)-a); Taranaki (T) (LR19(6)-live, LR17-live-a, LR-L5-b). These specimens are held in the Phoenix collection at Massey University, New Zealand.

Miotopus diversus Hutton 1989

Diagnosis: A medium sized cave wētā found in forested areas around the North Island, New Zealand. Described by Hutton in 1989 but male was unknown. Spine and subgenital plate defines and separates this species from *Pleioplectron.* Redefinition as follows:

Description: Body Length: Male: 13.65mm (n=11), Female = 13.19mm (n=11).
Head: Head with vertical brown and pale stripes; covered in fine setae; palps light brown with fine setae; fastigium light brown; eyes black and ovoid; antennae long and dark brown; male antennae thick with thick covering of setae tapering to a thin thread; female uniform thin shape from end to end; scape and peduncle pale.

Thorax: Pronotum round anteriorly and slightly posteriorly; lateral sides are rounded with a slight 'lip' coming outwards; dark brown – red brown with occasional pale markings.

Legs: Moderately long; hind femora shorter than tibia; coxae and trochanters cream; femora and tibia dark brown with cream bands; fore femora compressed; 1 prolateral apical spine present and 1 retrolateral apical spine present; short dark setae present; fore tibiae with 2 pairs of long spines position in the mid to lower portion of the tibia; spines are pale almost transparent; apical spines as follows: 1 fore tibia prolateral superior apical spine;1 fore tibia retrolateral superior apical spine; shorter than other spines; pale with dark tip; almost hidden amongst the setae; 1 fore tibia prolateral inferior apical spine; 1 fore tibia retrolateral inferior apical spine; inferior apical spines longer than superior spine; articulate; pale with dark tip; longer and thicker than the surrounding setae; mid femora compressed with 1 articulate long prolateral apical spine; 1 articulate long retrolateral apical spine; mid tibia with 2 pairs of long spines position in the mid to lower portion of the tibia; prolateral side spines longer than the retrolateral spine; mid tibiae apical spines as follows: 1 mid tibia prolateral superior apical spine; 1 mid tibia retrolateral superior apical spine; pale with dark tip; 1 mid tibia prolateral inferior apical spine; 1 mid tibia retrolateral inferior apical spine; inferior spines longer

than superior spine; pale with dark tip; hind femora with 0-1 retrolateral apical spine, small; slightly dark; hind tibiae longer than femora; small brown alternate spines running up the length of the tibia on superior surface; hind apical tibia spines as follows: 2 superior subapical spines, 1 prolateral and 1 retrolateral; 2 superior apical spines, 1 prolateral and 1 retrolateral; spines twice as long as superior subapical spines; 2 inferior apical spines, 1 prolateral and 1 retrolateral; 2/3 length of superior apical spines above; no inferior subapical spines; tarsus with 4 segments, 1st and 2nd segment with a pair of spine on distal end, 1st segment has 3 small spines up from the end in alternate fashion; on the underside of the 1st segments minute brown spines run up the length of the segment on the retrolateral and prolateral side; the 2nd segment has 1 pair of minute spines the underside of the tarsi; 4th segment half the length of the 1st segment.

Abdomen: Shiny, brown coloured. Short setae covering both turgites and sternites; sterum light brown colour.

Male: Cerci long, round; brown colour; clothed in setae; styli short, not extending beyond the end of the sub-genital plate; sub-genital plate is a finger-like protrusion.

Female: Sub-genital plate is trilobed; outer two lobes slightly higher than the middle lobe; apex rounded and blunt; ovipositor brown with a few serrations at the tip on the bottom edge.

Figure 5.4 Lateral view of *Miotopus diversus*. (Left) male, (right) female.

Figure 5.5 Subgenital plate of *Miotopus diversus.* (Left) male lateral view (centre) male ventral view, (right) female ventral view.

Distribution: NZ: Wellington, Manawatu, Taranaki, Hawke's Bay (Figure 5.8).

Type maerial:

Holotype: Adult male (Figure 5.4, 5.5): 13.65mm, collected 25/09/06, Lucy's Gully, Kaitake Range, Egmont National Park. (grid ref, -39.14904: 173.94254) Collected by SAT/MMR. Museum accession number (MONZxxx and CW461). Neotype adult female (Figure 5.4, 5.5): 12.48mm, collected 2009, Kahutarawa valley stream bed, Manawatu (grid ref, -40.47318: 175.61604) Collected by graduate student. Museum accession number (MONZxxx and CW1327).

Additional material examined: Hawke's Bay (HB) (CW 1841, 1837); Manawatū (M) (CW 133, 1439, 1452, 1469, 1467, 1327, 1468, 336, TD19(1)-b); Taranaki (T) (CW 461, 465, 460, 783, 462, LR-L59-b, LR-W19-A, LR-L3-A, LR-W19-A)

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New species *Miotopus* ~~RICHARDSI~~ sp. nov.

Diagnosis: A medium sized cave wētā found in forested areas of the South Island, New Zealand with a variegated colour pattern. Similar to *Miotopus diversus* based on apical spines with the exception of the presence of hind femur prolateral apical spine. Similar female subgenital plate but differs in male genital terminalia (Figure 5.6 & 5.7).

Etymology: Named for Aola Richards who studied New Zealand cave wētā and published many important systematics papers from 1954 until 1972.

Description: Body Length: Male: 13.31 (n=3), Female = 17.06mm (n=1).

Head: Head slightly variegated colouring with a medium brown and golden light brown; covered in fine setae; palps are light golden brown and covered with fine setae; fastigium medium brown with minor golden light brown; eyes black; antennae long and medium brown with setae; scape and peduncle light golden brown.

Thorax: Pronotum round anteriorly and slightly posteriorly; lateral sides are rounded with a slight 'lip' coming outwards; coloured in a medium brown with a pale 'V' shaped pattern.

Legs: Moderately long; hind femora shorter than tibia; coxae and trochanters cream; femora and tibia dark brown with cream bands; fore femora compressed; 1 prolateral apical spine present and 1 retrolateral apical spine absent; short dark setae present; fore tibiae with 2 pairs of long spines position in the mid to lower portion of the tibia; spines are pale almost transparent; apical spines as follows: 1 fore tibia prolateral superior apical spine; 1 fore tibia retrolateral superior apical spine; shorter than other spines; pale with dark tip; almost hidden amongst the setae; 1 fore tibia prolateral inferior apical spine; 1 fore tibia retrolateral inferior apical spine; inferior apical spines longer than superior spine; articulate; pale with dark tip; longer and thicker than the surrounding setae; mid femora compressed

with 1 articulate long prolateral apical spine; 1 articulate long retrolateral apical spine; mid tibia with 2 pairs of long spines position in the mid to lower portion of the tibia; prolateral side spines longer than the retrolateral spine; mid tibiae apical spines as follows: 1 mid tibia prolateral superior apical spine; 1 mid tibia retrolateral superior apical spine; pale with dark tip; 1 mid tibia prolateral inferior apical spine; 1 mid tibia retrolateral inferior apical spine; inferior spines longer than superior spine; pale with dark tip; hind femora with 1 retrolateral spines, small; slightly dark; hind tibiae longer than femora; small brown alternate spines running up the length of the tibia on superior surface; 4 pairs are spur like and 3 times the length of the other small spines; hind apical tibia spines as follows: 2 superior subapical spines, 1 prolateral and 1 retrolateral; 2 superior apical spines, 1 prolateral and 1 retrolateral; spines twice as long as superior subapical spines; 2 inferior apical spines, 1 prolateral and 1 retrolateral; 2/3 length of superior apical spines above; no inferior subapical spines; tarsus with 4 segments, 1st and 2nd segment with a pair of spine on distal end, 1st segment has 3 small spines up from the end in alternate fashion; on the underside of the 1st segments minute brown spines run up the length of the segment on the retrolateral and prolateral side; the 2nd segment has 1 pair of minute spines the underside of the tarsi; 4th segment half the length of the 1st segment.

Abdomen: Shiny, brown coloured. Short setae covering both turgites and sternites; sterum pale brown colour.

Male: Cerci long, round; brown colour; clothed in setae; styli short, not extending beyond the end of the sub-genital plate; almost invisible; sub-genital plate is short and tongue shape; apex curls up slightly, fleshy structure; a small spine near the rounded part on either side.

Female: Sub-genital plate is slightly trilobed; outer two lobes slightly higher than the middle lobe but plate curves with body appears almost straight across the top; apex rounded and blunt; ovipositor brown with a few serrations at the tip on the bottom edge.

Distribution: NZ: Taranaki, Golden Bay, Southland, Fiordland (Figure 5.8).

Type material:

Holotype: Adult male (Figure 5.6, 5.7): size, collected Jan 2014, Cleddau Valley, Fiordland (grid ref, -44.70383:167.95894) Collected by Tony Jewell. Museum accession number (MONZxxx and CW2617). Paratype adult female (Figure 5.6, 5.7): SIZE collected 2013, Longwoods Range, Southland (grid ref, -46.20240:167.82265) Collected by Tony Jewell. Museum accession number (MONZxxx and CW2567).

Additional material examined: Takaka (CW 302, 303)

Figure 5.6 Holotype of *Miotopus* ~~RICHARDSI~~ (Left) male, (right) female. Scale bars 10mm.

Figure 5.7 Subgenital plate of *Miotopus* ~~RICHARDSI~~. (Left) male lateral view, (centre) male ventral view, (right) female ventral view.

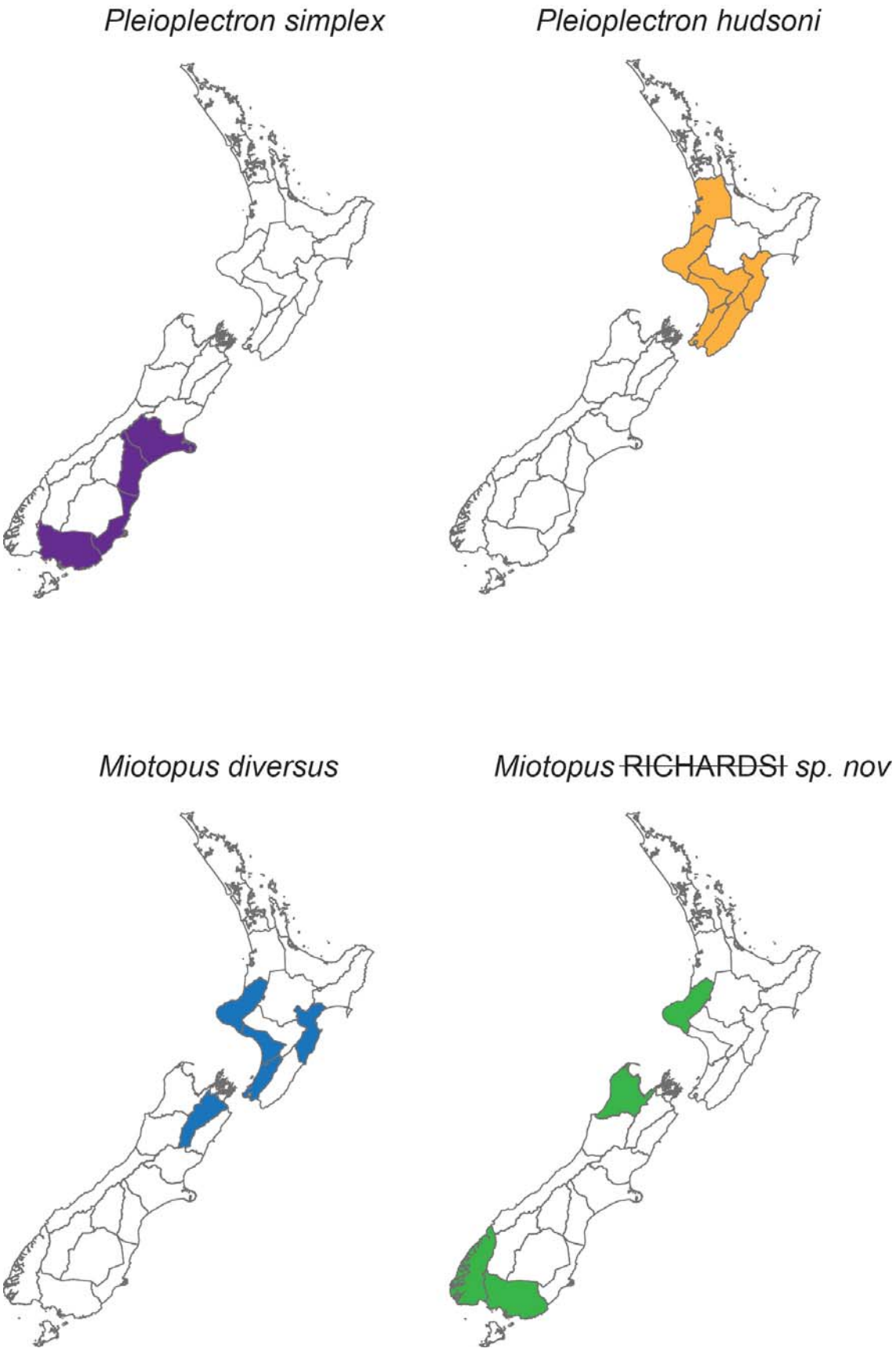

Figure 5.8 Known distributions of *Pleioplectron* and *Miotopus* species recorded by New Zealand entomological (Crosby) regions.

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Chapter 6

A step towards understanding New Zealand Rhaphidophoridae

Ko ahau te taiao, ko te taiao, ko ahau

The ecosystem defines my quality of life

Introduction

The aim of this study was to explore the diversity of rhaphidophorids in New Zealand and try to take the first steps to understand their whakapapa. Taxonomy and systematics are fundamental to our understanding of biodiversity and meaningful identification of species needs an understanding of their relationships with one another. Unfortunately this key component is frequently undervalued. An analysis of publications in the field of community ecology found that where more than one species was involved 62% of studies did not include taxonomic justification for their treatment identification as species (Bortolus, 2008). By excluding this step our ability to repeat studies and our ability to compare findings will be hindered. New Zealand biologists have largely ignored rhaphidophorid diversity; species commonly referred to simply as 'cave wētā' or by one or two known genera (Moeed & Meads, 1985, 1992; Spurr & Berben, 2004b). The issue with '*poor taxonomy*' and the '*taxonomic impediment*' is becoming more pronounced as taxonomy is carried out by researchers with a wide range of backgrounds often relying on simplistic DNA barcoding approaches.

In this work I have been able to show that many forest cave wētā species can be identified, and many new species should be described. Assigning names to specimens has required careful scrutiny and comparison of scientific papers from 120 years of New Zealand cave wētā taxonomy (Chapter 1, Table 1.2). Unfortunately the historical literature has sometimes formed a barrier to easy identification and revision of cave wētā taxonomy in New Zealand. In my research I have sought to summarize this work and find a path through the maze of names, traits and synonymies towards providing clear tools to identify some of the commonest forest cave wētā species. The challenges are highlighted by the difficulties involved even in distinguishing between sympatric species; many

species are superficially similar in appearance and overlap in habitat. The challenges of identifying the boundaries between groups of individuals in such circumstances that are well recognised in species level taxonomy (De Queiroz, 2007; Mallet, 1995) are prominent in the rhaphidophorids. Modern genetic methods have been invaluable in testing hypotheses based on morphological characters including spines and subgenital plate shape. By comparing the morphology and mtDNA data I was able to confidently identify species' boundaries, contrast species level diversity and identify trait variation with putative species.

Failure to recognise systematic diversity (Hebert, Penton, et al., 2004; Williams et al., 2006) can cause underestimation of biodiversity, however cryptic species are readily distinguished using comparisons of neutral DNA sequences (Williams et al., 2006). Using multiple methods in distinguishing species and to accurately describe them is an increasingly accepted approach (Carstens et al., 2013). The value of this is readily apparent in the instances where morphology alone has not accurately distinguished taxa. For example, the Taranaki *Talitropsis* (CW817) was genetically distinct but morphologically almost indistinguishable from *Talitropsis sedilloti* (OTU=A). Interestingly, the morphological characters examined were not always sufficient for determining species whakapapa. Many examples have been identified where species that look very different are genetically similar; for example the *Neonetus* species from Te Paki (TPD) with relatively short legs is genetically sister to *Pallidoplectron turneri* who has long legs (Chapter 4). In contrast, morphologically similar species are not always closely related, e.g. *Miotopus diversus* is not genetically sister to *Pleioplectron* species (see Chapter 5). In chapter 4 of this thesis the genus *Neonetus* was found to comprise a large number of species, many of which are similar in appearance. One of the most obvious similarities of *Neonetus* species is that they are small (compared to the large and robust *Pachyrhamma*, or medium robust *Miotopus*), and most are common in forest environments. In general, the spine counts for the nine putative species I identified in *Neonetus* were rather similar with only nine minor variations. Presence or absence of an apical spine on a leg might be diagnostic for a species or might reflect conspecific variation. Without further evidence the significance of

presence / absence of these apical spines is not easily interpreted. Distinguishing these taxa is mostly dependent on features of the genitalia. Males and females differ (of course) and pairing the two sexes together is often difficult. However, the subgenital plate differences between males of each species (chapter 3 table 3.3) are quite pronounced and important for distinguishing species. Females of the different *Neonetus* species tend to have similar shaped subgenital plates, i.e. *Neonetus* females tend to have bi-lobed structures. Mitochondrial DNA sequence aided in pairing male and females and tested putative species boundaries but was also hugely important in our understanding of their whakapapa (genealogy or evolutionary relationships at the species and genus level). MtDNA sequencing provides a first study of the whakapapa of many of the North Island cave wētā. I found that species that are part of the genus *Pallidoplectron* erected by Richards (1958c) fit nicely into the genetic diversity of *Neonetus*. The genus *Neonetus* has a huge morphological diversity within it and it makes it almost impossible to say that the genus *Pallidoplectron* is not in fact *Neonetus.* I observed that one of the major defining character with *Pallidoplectron* from other *Neonetus* species is its size but that could equally be an adaptation to cave dwelling. Richards (1965) found another species of *Pallidoplectron* from a cave system west of Huntley. This species has not been identified since. The similarities between the newly described species in chapter 4 *Neonetus* ~~PATERLONGIPES~~ and *Pallidoplectron turneri* are notable (although mtDNA indicates they are not sister taxa, see chapter 4). Both are long legged, small bodied but one is a cave dweller and the smaller one is found in forest. I suggest that the genus *Pallidoplectron* should be synonymized into *Neonetus* as cave dwelling species.

The genus *Neonetus* has been a large part of this research project. It is a widespread genus and has gone from 3 described species to 5 described, 3 of which are newly described in this research, and *Neonetus pilosus* described by Hutton (1897) has been synonymized with *Neonetus variegatus*. There are at least four more *Neonetus* species yet to be described and as these species are probably fairly widespread (if not locally common). Museums probably hold material of these species that can be used as additional specimens for descriptions in the future.

New Zealand genera

I have only dealt with a few of the common North Island species and two genera that are found in both North and South Island. I have concentrated on forest species as Richards (1958) focused on cave dwelling genera. My recommendations reduce the number of valid genera, recognizing *Miotopus* but synonymizing *Pallidoplectron* (with *Neonetus*) and *Weta* (with *Pleioplectron*). We now have a good basis to consider the generic level taxonomy of New Zealand cave wētā.

A rhaphidophorid whakapapa is emerging with the six monotypic genera of New Zealand cave wētā that are restricted to islands (*Dendroplectron* (Auckland Is.), *Insulanoplectron* (Snares I.), *Ischyroplectron* (Bounty I.), *Novoplectron* (Chatham Is.), *Notoplectron* (Campbell Is.), *Paraneonetus* (Great I. Three Kings)) being readily classified geographically and mainland genera being partitioned by the presence/absence of particular leg spines. With the addition of details of subgenital plate shape and structure of terminal abdominal tergites in males especially it will be possible to gain further resolution (Figure 6.1).

As understanding of the generic relationship of putative species improve, assisted by molecular data, it becomes increasingly apparent that genus level classification is sensitive to the number of species within each genus. Monotypic genera tend to be readily separable using simple leg spine characteristics, but as the number of species attributed to a given genus increases the degree of interspecific variation reduces the diagnostic power of some of these charater states at the genus level. In particular, recognition of the number of putative species in *Neonetus* (including at least one formerly assigned to *Pallidoplectron*) has resulted in more permutations of leg spine presence/absence. Further challenges to a robust systematics of Rhaphidophoridae in New Zealand come from the number of new species that are being discovered that bear trait combinations that are inconsistent with existing genera.

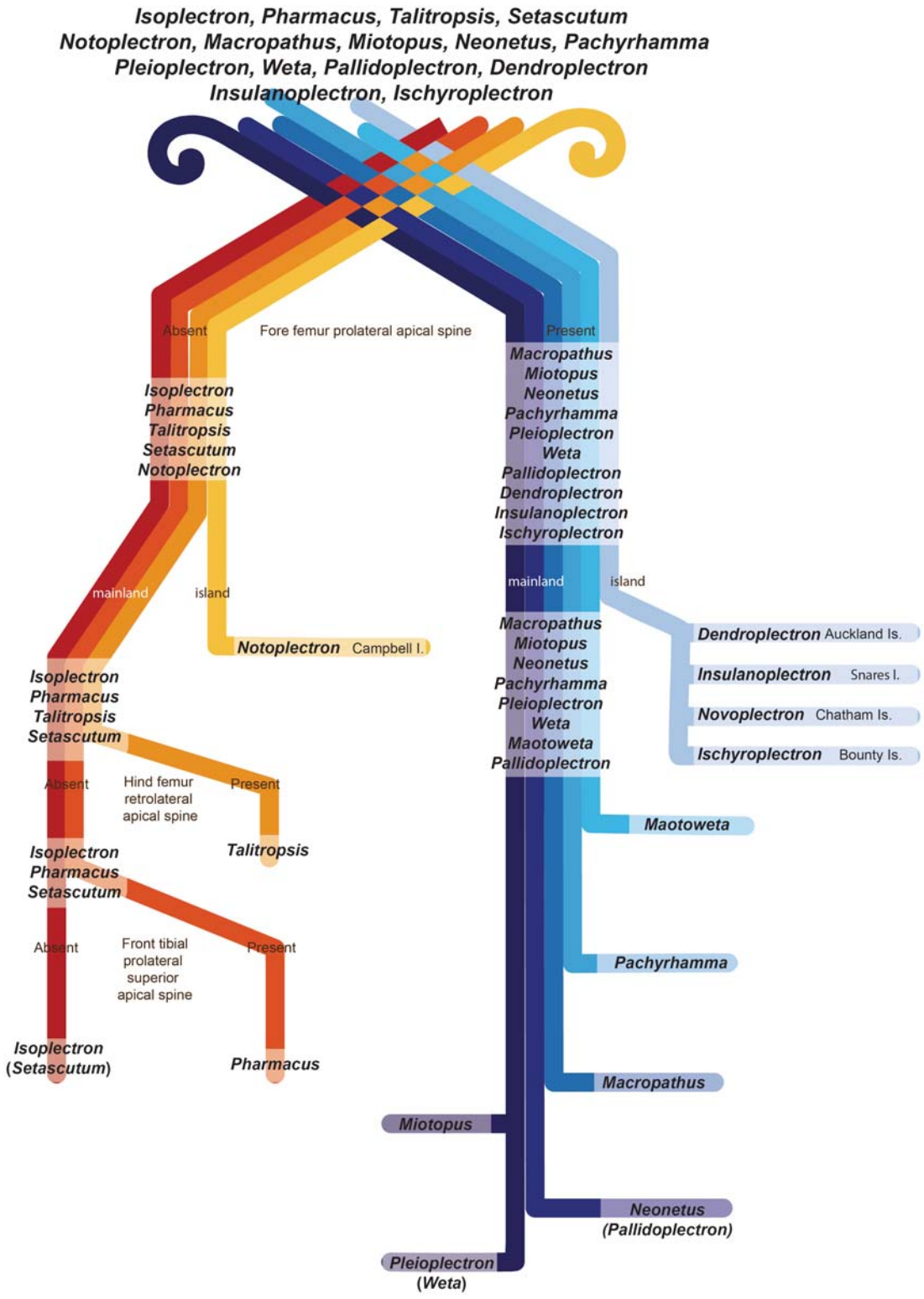

Figure 6.1 A developing whakapapa of New Zealand rhaphidophorid genera.

Future Work

A number of species I have identified as new to science await formal description because of the low numbers of specimens that represent them; single specimens, or material representing only one sex. Data in chapters 2, 3 & 4 reveal that there are at least four more *Neonetus* species to describe from the North Island. In addition there is at least one *Isoplectron* species, one *Talitropsis* and one *Macropathus* species to characterise. My conservative approach to describing species, which endeavored to avoid some of the problems of encountered by previous authors, was to always observe specimens of both sexes, and include enough specimens to accurately describe most aspects of that species, including any variation in apical spines that exists.

Many species of cave wētā exist in sympatry. Further work on this capacity to partition resources is needed to properly understand the world of cave wētā. Basic information such as diet, where eggs are laid, the numbers of instars from hatching to sexual maturity and mate locating methods are all lacking. However we do know that many vertebrates eat cave wētā. Cave wētā are important prey for native nocturnal native animals such as lizards, kiwi (*Apteryx*) and owl (*Ninox*) (Colbourne & Powlesland, 1988; Haw et al., 2001; Shapiro, 2005), but wētā populations are also impacted on by pest species such as rats, cats and hedgehogs (Smith and Jamieson 2003; Watts et al. 2011). What are the long-term effects of this predation? Some cave wētā have been observed to canabilise (Richards, 1954), but how much does this behaviour occur and in what circumstances? Closer observation has revealed a huge diversity of genitalic structure on male cave wētā. How are these put to use and what mechanisms of sexual selection have driven their evolution? To improve our knowledge of cave wētā behaviour and ecology we need to be able to focus on single species and not group all forest Rhaphidophoridae into the same analysis (Fitness et al. 2015).

There is much work still to do. For example little is know about the genus *Isoplectron* Hutton 1897. Specimens of cave wētā that have been collected around the Hawke's Bay area can be identified as *Isoplectron calcaratum* based on the long single spine on the underside of the hind femur. Four species of *Isoplectron* are

currently described with the other three being from the South Island. There is some indication that there are possibly species undescribed in collections that may be *Isoplectron* from the Wellington region. One question raised by the preliminary mtDNA sequences data is whether there is a close relationship between the species within *Isoplectron* and *Talitropsis*. Morphologically speaking it is not clear that these two genera should be combined as one, although Figure 6.1 shows that they share the absence of fore femur apical spines. Male subgenital plates of both *I. calcaratum* and *T. sedilotti* are large, wider at the base and narrowing to a smaller apex, with a keel. The keel of *T. sedilotti* is bigger than *I. calcaratum* but is this morphological similarity evidence of a recent common ancestor? Additional DNA sequencing will help us understand these genera. *Talitropsis* is a robust cave wētā with two species found on Chatham Islands and a single species named on the mainland. A similar *Talitropsis* species was also collected from Mt Taranaki, but mtDNA revealed it was probably a distinct taxa (see chapter 3). More specimens are required to confirm small spine differences are diagnostic for this taxa.

Macropathus spp. has often been used in the past for study (Richards, 1954a, 1954b) but has also had taxonomic problems that have tentatively been resolved. It is my belief that this genus may still require work and that there may be unknown species. For example a specimen was collected on Mt Taranaki that is possibly *Macropathus* but the species is undescribed. I believe we should focus more on *Macropathus* as it was the first genus to be described but has also had a lot of species come and go from the genus and it is full of synonyms. It would be nice to see that this group have a little more clarity and maybe there are more species in it.

My research did not focus on the South Island cave wētā species. There are currently four cave wētā genera that are known only from the South Island. These genera consist of *Setascutum* Richards, 1972, with two described species from Canterbury, *Petrotettrix* Richards, 1972, with four species from Canterbury and Marlbourgh areas, *Pharmacus* Pictet & Saussure, 1893, which includes four species from mountains ranges in the Canterbury, Otago and Nelson areas and a recently erected genus *Maotoweta* Johns & Cook, 2014 with a single species from

Canturbury. It is likely that these genera will benefit from investigations using morphology of museum specimens, new fresh specimens and DNA sequencing.

For the next scientist attempting to look at cave wētā, my advice is to have an open mind in terms of previous work done. Large samples and multiple tools are necessary to fully grasping cave wētā diversity and taxonomy today. This is a highly diverse group of nocturnal elusive insects that require the use of genetic data and the acceptance that variation is high in some species. What I have aimed to do here is to lay out a guide that can used for any species observed such as counting spines, and provide an idea of the diversity of subgenital plates in the North Island. This is a work in progress and any further information will no doubt increase our understanding of both biodiversity and the whakapapa of New Zealand's biota.

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Appendix I

Wētā Code	Species	Sex	Location	Spine type	Phenotype	O.T.U.	Subgenital plate type	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22
CW113	*Talitropsis sedilloti*	M	HB	T11	1	A	SB22	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW1438	*T. sedilloti*	M	T	T11	1	A	SB22	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW1600	*T. sedilloti*	M	HB	T11	1	A	SB22	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW1813	*T. sedilloti*	M	HB	T11	1	A	SB22	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW1814	*T. sedilloti*	M	HB	T11	1	A	SB22	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW1816	*T. sedilloti*	M	HB	T11	1	A	SB22	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW1817	*T. sedilloti*	M	HB	T11	1	A	SB22	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW1818	*T. sedilloti*	M	HB	T11	1	A	SB22	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW1829	*T. sedilloti*	M	HB	T11	1	A	SB22	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW1832	*T. sedilloti*	M	HB	T11	1	A	SB22	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW1437	*T. sedilloti*	M	T	T11	1	A	SB22	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW472	*T. sedilloti*	M	T	T14	4	A	SB22	0	0	0	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW817	*T. sedilloti*	M	T	T17	3	A	SB22	0	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1
CW1836	*T. sedilloti*	M	HB	T22	2	A	SB22	0	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1
CW806	*T. sedilloti*	M	T	T22	2	A	SB22	0	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1
CW1815	*T. sedilloti*	F	HB	T22	5	B	SB16	0	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1
CW1828	*T. sedilloti*	F	HB	T11	49	B	SB16	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW1833	*T. sedilloti*	F	HB	T11	49	B	SB16	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW1708	*T. sedilloti*	F	T	T22	5	B	SB16	0	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1
CW1819	*T. sedilloti*	F	HB	T11	49	B	SB16	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1

CW816	*T. sedilloti*	F	T	T11	49	B	SB16	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW1604	*T. sedilloti*	F	HB	T22	5	B	SB16	0	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1
CW1870	*Neonetus* ~~PATERLONGIPES~~	M	HB	T21	34	B	SB4	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1324	*N.* ~~PATERLONGIPES~~	M	M	T3	33	B	SB4	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1849	*N.* ~~PATERLONGIPES~~	M	HB	T3	33	B	SB4	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW918	*N.* ~~PATERLONGIPES~~	M	M	T3	33	B	SB4	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1839	*N.* ~~PATERLONGIPES~~	M	HB	T3	33	B	SB4	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW710	*N.* ~~PATERLONGIPES~~	F	T	T3	12	B	SB23	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW429	*Neonetus* ~~UNCINUS~~	F	M	T1	10	C	SB19	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW788	*N.* ~~UNCINUS~~	F	M	T1	10	C	SB19	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW785	*N.* ~~UNCINUS~~	F	M	T1	10	C	SB19	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW431	*N.* ~~UNCINUS~~	M	M	T1	6	C	SB15	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW291	*N.* ~~UNCINUS~~	M	M	T20	7	C	SB15	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW786	*N.* ~~UNCINUS~~	M	M	T20	7	C	SB15	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW948	*N.* ~~UNCINUS~~	M	M	T16	8	C	SB15	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
CW787	*N.* ~~UNCINUS~~	M	M	T19	9	C	SB15	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1389	*N.* ~~UNCINUS~~	F	M	T25	43	C	SB19	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1
CW439	*N.* ~~UNCINUS~~	F	M	T8	51	C	SB19	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
CW1864	*N.* ~~UNCINUS~~	F	HB	T21	11	C	SB19	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW290	*N.* ~~UNCINUS~~	F	M	T3	12	C	SB19	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1863	*Neonetus variegatus*	M	HB	T21	19	D	SB2	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1865	*N. variegatus*	M	HB	T21	19	D	SB2	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1869	*N. variegatus*	M	HB	T21	19	D	SB2	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW467	*N. variegatus*	M	T	T21	19	D	SB2	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW468	*N. variegatus*	M	T	T21	19	D	SB2	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW471	*N. variegatus*	M	T	T21	19	D	SB2	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

CW687	*N. variegatus*	M	M	T21	19	D	SB2	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW755	*N. variegatus*	M	T	T21	19	D	SB2	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1855	*N. variegatus*	M	HB	T21	19	D	SB2	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1397	*N. variegatus*	M	T	T3	20	D	SB2	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1720	*N. variegatus*	M	M	T3	20	D	SB2	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1851	*N. variegatus*	M	HB	T3	20	D	SB2	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1857	*N. variegatus*	M	HB	T3	20	D	SB2	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW473	*N. variegatus*	M	T	T3	20	D	SB2	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW581	*N. variegatus*	M	HB	T3	20	D	SB2	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW757	*N. variegatus*	M	T	T3	20	D	SB2	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW815	*N. variegatus*	M	T	T3	20	D	SB2	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW162	*N. variegatus*	M	T	T26	18	D	SB2	1	1	1	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1
CW1763	*N. variegatus*	F	HB	T21	35	D	SB20	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1859	*N. variegatus*	F	HB	T21	35	D	SB20	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW758	*N. variegatus*	F	T	T3	36	D	SB26	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
PN11/10/11-a	*N. variegatus*	F	M	T3	36	D	SB26	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1715	*N. variegatus*	F	M	T21	35	D	SB2	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
NP18/7/11-a	*Neonetus huttoni*	F	T	T1	22	E	SB10	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW790	*N. huttoni*	F	T	T20	23	E	SB10	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
NP21/7/11-a	*N. huttoni*	F	T	T20	23	E	SB10	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
NP10/7/11-a	*N. huttoni*	M	T	T1	24	E	SB9	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
LG3(4)-live	*N. huttoni*	M	T	T20	25	E	SB9	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
LG8-live	*N. huttoni*	M	T	T20	25	E	SB9	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
NP11/7/11-a	*N. huttoni*	M	T	T20	25	E	SB9	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1

CW1440	*Pleioplectron hudsoni*	M	M	T24	30	F	SB12	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW1442	*P. hudsoni*	M	M	T24	30	F	SB12	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW1464	*P. hudsoni*	M	M	T24	30	F	SB12	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW1759	*P. hudsoni*	M	HB	T24	30	F	SB12	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW1609	*P. hudsoni*	M	HB	T4	29	F	SB12	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW187	*P. hudsoni*	M	M	T4	29	F	SB12	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW60	*P. hudsoni*	M	HB	T4	29	F	SB12	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
LR19(6)-live	*P. hudsoni*	M	T	T4	29	F	SB12	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
TD17(1)-a	*P. hudsoni*	M	M	T4	29	F	SB12	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
TD19(1)-a	*P. hudsoni*	M	M	T4	29	F	SB12	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW1755	*P. hudsoni*	F	HB	T24	32	F	SB6	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW1441	*P. hudsoni*	F	M	T4	31	F	SB6	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW1454	*P. hudsoni*	F	M	T4	31	F	SB6	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW1465	*P. hudsoni*	F	M	T4	31	F	SB6	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW1762	*P. hudsoni*	F	HB	T4	31	F	SB6	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW186	*P. hudsoni*	F	M	T4	31	F	SB6	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW1861	*P. hudsoni*	F	HB	T4	31	F	SB6	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW434	*P. hudsoni*	F	M	T4	31	F	SB6	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
LR-L5-b	*P. hudsoni*	F	T	T4	31	F	SB6	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
LR17-live-a	*P. hudsoni*	F	T	T4	31	F	SB6	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW867	*Neonetus* ~~CIRRATUS~~	F	T	T9	16	G	SB21	1	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW1862	*N.* ~~CIRRATUS~~	F	HB	T10	17	G	SB21	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW580	*N.* ~~CIRRATUS~~	F	HB	T10	17	G	SB21	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW1845	*N.* ~~CIRRATUS~~	F	HB	T10	17	G	SB21	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW571	*N.* ~~CIRRATUS~~	F	HB	T10	17	G	SB21	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1

CW802	*N. ~~CIRRATUS~~*	F	T	T10	17	G	SB21	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW820	*N. ~~CIRRATUS~~*	F	M	T10	17	G	SB21	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW1363	*N. ~~CIRRATUS~~*	M	T	T9	13	G	SB3	1	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW1761	*N. ~~CIRRATUS~~*	M	HB	T9	13	G	SB3	1	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW574	*N. ~~CIRRATUS~~*	M	HB	T9	13	G	SB3	1	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW575	*N. ~~CIRRATUS~~*	M	HB	T9	13	G	SB3	1	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW767	*N. ~~CIRRATUS~~*	M	M	T9	13	G	SB3	1	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW573	*N. ~~CIRRATUS~~*	M	HB	T10	14	G	SB3	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW577	*N. ~~CIRRATUS~~*	M	HB	T10	14	G	SB3	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW1866	*N. ~~CIRRATUS~~*	M	HB	T10	14	G	SB3	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW430	*N. c-~~CIRRATUS~~*	M	M	T10	14	G	SB3	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW576	*N. ~~CIRRATUS~~*	M	HB	T10	14	G	SB3	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW578	*N. ~~CIRRATUS~~*	M	HB	T10	14	G	SB3	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW579	*N. ~~CIRRATUS~~*	M	HB	T10	14	G	SB3	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW801	*N. ~~CIRRATUS~~*	M	T	T5	15	G	SB3	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1
CW868	*N. ~~CIRRATUS~~*	M	T	T10	14	G	SB3	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
CW116	*N. ~~CIRRATUS~~*	F	HB	T10	14	G	SB21	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
LR-W19A	*Miotopus diversus*	F	T	T21	28	H	SB14	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1327	*M. diversus*	F	M	T3	27	H	SB14	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1837	*M. diversus*	F	HB	T3	27	H	SB14	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1841	*M. diversus*	F	HB	T3	27	H	SB14	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW460	*M. diversus*	F	T	T3	27	H	SB14	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW462	*M. diversus*	F	T	T3	27	H	SB14	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW783	*M. diversus*	F	T	T3	27	H	SB14	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
LR-L3-A	*M. diversus*	F	T	T3	27	H	SB14	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW133	*M. diversus*	M	M	T3	26	H	SB12	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

CW1439	*M. diversus*	M	M	T3	26	H	SB12	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1459	*M. diversus*	M	M	T3	26	H	SB12	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1467	*M. diversus*	M	M	T3	26	H	SB12	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW461	*M. diversus*	M	T	T3	26	H	SB12	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
cw465	*M. diversus*	M	T	T3	26	H	SB12	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
TD19.1.b	*M. diversus*	M	M	T3	26	H	SB12	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1452	*M. diversus*	M	M	T3	26	H	SB12	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1468	*M. diversus*	F	M	T3	26	H	SB14	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1469	*M. diversus*	M	M	T3	26	H	SB12	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
LR-W19b	*M. diversus*	F	T	T3	26	H	SB14	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
LR-L59-b	*M. diversus*	M	T	T3	26	H	SB12	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1626	*Isoplectron*	M	HB	T12	40	I	SB5	0	0	0	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1
CW438	*Isoplectron*	M	M	T13	41	I	SB5	0	0	0	1	0	0	1	0	1	0	1	0	1	0	1	1	1	1	1	1	1	1
CW115	*Isoplectron*	F	HB	T12	42	I	SB17	0	0	0	1	0	0	1	0	1	0	1	0	1	0	1	1	1	1	0	1	1	1
CW484	*Macropathus*	F	T	T6	39	K	SB13	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW433		F	M	T16	38	L	SB1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
CW466	*Neonetus sp*	F	T	T18	46	M	SB18	1	0	0	1	0	0	0	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1
CW950	*Neonetus sp*	F	M	T14	44	P	SB24	0	0	0	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1
CW141	*Neonetus sp*	M	M	T7	21	T	SB27	1	0	0	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1
CW1345	*Neonetus sp*	F	M	T21	53	U	SB23	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW1403	*Miotopus*	F	T	T16			0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
CW1457	*Miotopus*	M	M	T3			0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CW697			T	T16			0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
CW1398		M	T	T16			0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1

Appendix II

Neighbor joining phylogeny of mtDNA Cytochrome Oxidase I sequences for mainland New Zealand Rhapidophoridae genera. Branches are transformed so lengths are not proportional to genetic distance.