Sand find New Zealand care we a (Rhaphidophoridae) general *Pachyrhamma, Gymnoplectron* **and** *Turbottoplectron*

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Ab ac. The New Zealand Rhaphidophoridae Walker, 1869 comprise 18 endemic genera (including 8 that are monotypic). Although there are many new species to be described, rationalisation at the genus level is also required due to inconsistencies in their current systematics. Even the largest and best known taxa, including those that occupy cave systems and are the most frequently encountered by people, require taxonomic revision. These cave weta include species assigned to three poorly differentiated genera, *Pachyrhamma* Brunner v*.* Wattenwyl, 1888, *Gymnoplectron* Hutton, 1897 and *Turbottoplectron* Salmon, 1948, that are best known from North Island New Zealand.We used mitochondrial DNA sequence data to examine their relationships using representatives of each genus. The results indicate that a single genus *Pachyrhamma* would be appropriate for all, as *Gymnoplectron* and *Turbottoplectron* nest phylogenetically within it. There are insufficient morphological, spatial or ecological reasons to justify retention of all three. However, we also note that species level diversity does not correlate with genetic or spatial diversity; some species are genetically well partitioned and widespread while others have narrow ranges in single cave systems and are closely related to one another.

Addid a b **e** \mathcal{M} **d**: phylogeography, species radiation.

I o d co

As is typical of the Rhaphidophoridae, all New Zealand cave weta¹ species are nocturnal and flightless. Some of the prominent members of the group live mostly in caves or cave-like structures. However, the majority of species occupy a wide range of environments throughout New Zealand, from rocky shore and lowland forest to the alpine zone. These insects hide by day in small holes and crevices in trees, rocks and rock banks, overhangs and caves, and seabird burrows. Similarly, in Australia, Europe and North America, rhaphidophorid species are frequently known as'cave crickets' even though many species occupy habitats other than caves.

The New Zealand Rhaphidophoridae are dominated by the Macropathinae, one of nine subfamilies. The Macropathinae comprise some 30 genera and 18 of these are endemic to New Zealand. One genus,*Talitropsis*Bolivar, 1883,is currently placed in a tribe of its own (Talitropsini Gorochov, 1988), but the others are assigned to Macropathini Karny, 1929 along with all rhaphidophorids of Australia and Chile (Eades *et al*. [2007\)](#page-6-0). An estimated 50 new species await description (P. M. Johns, unpubl. data).

The taxonomy of cave weta has undergone many adjustments and re-descriptions and this instability has been attributed to the difficulty of finding robust diagnostic characters for both species and genera (Richards [1954](#page-7-0)*a*; Ward [1997\)](#page-7-0). Early taxonomy relied heavily on the number of linear spines on the legs but there is considerable variation among individuals and populations of species. Aola Richards [\(1954](#page-7-0)*a*) recommended that the number of apical leg spines and shape of the subgenital plate be used as characters on which to describe species, as she interpreted these traits as remaining constant within species. However, she $(Richards 1961a)$ $(Richards 1961a)$ $(Richards 1961a)$ also misidentified several species with the result that some formerly within *Pachyrhamma*, *Gymnoplectron*, and *Macropathus* Walker, 1869 are misplaced. Perhaps this is due to four early names being based on just two species that often occur together and have type localities just 3 km apart (von Hochstetter [1867](#page-7-0); Scudder [1869](#page-7-0); Brunner von Wattenwyl [1888](#page-6-0)). Richards [\(1961](#page-7-0)*a*) also argued for the change from her earlier use of *Pachyrhamma* to *Gymnoplectron*, a proposal that is difficult to follow owing to her misidentifications.

Pachyrhamma, Gymnoplectron *and* Turbottoplectron

Here we follow the checklist of Rhaphidophoridae published as the 'Orthoptera Species File Online' (Eades *et al*. [2007\)](#page-6-0) in the proposed restitution of *Pachyrhamma*, and follow Kirby [\(1906](#page-6-0)) and Karny ([1937\)](#page-6-0) in treating *Pachyrhamma* as a neuter noun. We

¹ 'Weta' is a Maori name applied to New Zealand crickets belonging to the Anostostomatidae (more commonly known as the giant, tree, ground and tusked weta)

note that, in terms of taxonomic protocol, *Gymnoplectron longipes* Colenso, 1887 is the only existing species that could be justified as belonging to *Gymnoplectron* and will refer to it as such throughout. We also recognise that *Gymnoplectron* is one of the few widely known New Zealand cave weta names used frequently in popular books and museum displays, so robust justification for its synonymy is warranted. The genus *Pachyrhamma* comprises species justifiably described as the giants of the New Zealand cave weta, which probably explains why they were the first to be discovered and described (von Hochstetter [1867;](#page-7-0) Scudder [1869](#page-7-0); Walker [1869](#page-7-0); Brunner vonWattenwyl [1888](#page-6-0)). Body lengths range up to 48 mm (Richards [1962](#page-7-0)*a*), with long hind legs and antennae. *Pachyrhamma* (or *Gymnoplectron sensu* Richards, [1961](#page-7-0)*a*) has the largest

in current cave weta taxonomy and presents the sort of problem that is tractable using molecular tools. Here we assess the phylogenetic evidence for distinction of *Pachyrhamma*,

Gymnoplectron and *Turbottoplectron* using mitochondrial sequence data. Specifically, is there evidence for phylogenetic distinction of *Gymnoplectron longipes*

are putative *Turbottoplectron* supported as members of a distinct lineage separate from *Pachyrhamma* and *Gymnoplectron*?

Me **h** d

Sampling and identification

We obtained representatives of *Pachyrhamma* spanning spatial and morphological diversity of the genus, plus individuals consistent with Richards' descriptions and identified material

Walker (*Macropathus fascifer, M. lifer*) has also been examined. Those specimens possessing only one apical spine (retrolateral) on the hind femora were classified as *Turbottoplectron*, and those possessing a retrolateral and a prolateral apical spine on the hind femora were classed as *Pachyrhamma/Gymnoplectron*. *Gymnoplectron longipes* is the only species that can be confidently separated from the others due to the nature of its hind tibial 'rose thorn'spination, though how consistent this is in the smaller instars is not known.

mtDNA extraction, amplification and sequencing

Whole genomic DNA extractions were performed using a 'salting out' protocol (Sunnucks and Hales [1996\)](#page-7-0) designed for fresh tissue, but used successfully for preserved orthopteran tissue (Trewick and Morgan-Richards

would be unusual for species distinction, let alone generic distinction.

Genetic diversity between *P. edwardsii* and other ingroup taxa was high (up to 0.21 using ML distances). This is high compared with the average mtDNA sequence divergence of 0.113 given by Hebert *et al*. ([2003\)](#page-6-0) from a survey of congeneric invertebrate species pairs, and higher than estimates of divergence found between the other ingroup taxa sampled in this study. Morphologically and ecologically though, there is no justi

hide important information on the morphology, preferred habitats and geographic distribution of these taxa that are likely indicators of reproductive isolation, local adaptation and thus biodiversity. Clade V may represent a species complex that has diverged much more recentlythan the other sampled*Pachyrhamma* lineages and, as a result of rapid radiation, exhibit low genetic diversity but high morphological diversity. Similarly, European and American rhaphidophorid phylogenies based on molecular data are not always concordant with phylogenies based on morphology (Caccone and Powell, 1987; Caccone and Sbordoni, 1987; Allegrucci *et al*. 2005).

This analysis, which included *Macropathus* in the outgroup (sample codes CW442, CW86, see Table [1\)](#page-3-0), does not support its synonymy with *Pachyrhamma* proposed by Richards [\(1961](#page-7-0)*e*). It also fails to support *G. longipes* (Colenso 1887) as separate from other species that have been included in *Gymnoplectron* (*sensu* Richards [1961](#page-7-0)*a*), especially *Pachyrhamma novaeseelandiae* (now *P. edwardsii*) – the type species of *Pachyrhamma.* Based on albeit unidentified members, *Turbottoplectron* is almost certainly part of this *Pachyrhamma/Gymnoplectron* complex. Until other, more compelling evidence based on the type specimens, well preserved modern material and genetic analysis is forthcoming, *Gymnoplectron* and *Turbottoplectron* are thus formally synonymised with the prior and valid *Pachyrhamma* Brunner v. Wattenwyl, 1888.

Pachyrhamma Brunner von Wattenwyl, 1888

Type species: *Pachyrhamma novaeseelandiae* by subsequent designation of Hutton, 1900. (= *Hadenoecus edwardsii* Scudder, [1869](#page-7-0); = *Macropathus fascifer* Walker, [1869](#page-7-0)) (not = *Macropathus lifer* Walker, 1869)

Gymnoplectron Hutton, 1897: 229.

Type species: *Hemideina longipes* Colenso, 1887, by monotypy.

Turbottoplectron Salmon, [1948](#page-7-0): 303.

Type species: *Turbottoplectron unicolor* Salmon, 1948, by original designation.

Undoubtedly, the view that these 'cave' weta are predominantly cave dwellers is driven by the relative ease with which they are found in cave habitat. The occupation by some species of various human constructions including mine tunnels and outhouses (pers. obs.) demonstrates that these taxa are also present in the surrounding forest, whereas other taxa do appear to be more restricted. Although molecular phylogenetics provides a powerful tool for evolutionary inference, comparison of DNA sequence similarity (DNA barcodes) is a tenuous basis for species determination as it assumes that rates of both molecular evolution and speciation are clocklike (Rubinoff *et al*. [2006;](#page-7-0) Trewick [2008](#page-7-0)). Here we demonstrate that generic synonymy is required if taxonomy is to reflect evolutionary relationships among these Rhaphidophoridae, but, at the species level, patterns of subdivision reflect differing degrees of population cohesion. Ongoing study using ecological, morphological and population genetic tools will help to clarify the interaction between local adaptation and gene flow, and clarify the spatial and genetic limits of these 'cave' weta.

Ac^{λ} **Q** w edge e

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Refe e ce

- Allegrucci, G., Todisco, V., and Sbordoni, V. (2005). Molecular phylogeography of *Dolichopoda* cave crickets (Orthoptera, Rhaphidophoridae): A scenario suggested by mitochondrial DNA. *Molecular Phylogenetics and Evolution* **37**, 153–164. doi[:10.1016/](dx.doi.org/10.1016/j.ympev.2005.04.022) [j.ympev.2005.04.022](dx.doi.org/10.1016/j.ympev.2005.04.022)
- Brunner von Wattenwyl, C. (1888). Monographie der Stenopelmatiden und Gryllacriden. *Verhandlungen zoologische-botanische Gesellschaft, Wien* **38**, 247–394. [also issued separately and repaginated 1–149]
- Caccone, A., and Powell, J. R. (1987).^{*I. a*Widecular evolutionary divergence} among North American cave crickets. II. DNA-DNA hybridization. *Evolution* **41**, 1215–1238. doi[:10.2307/2409089](dx.doi.org/10.2307/2409089)
- Caccone, A., and Sbordoni, V. (1987). Molecular evolutionary divergence among North American cave crickets. I. Allozyme variation. *Evolution* **41**, 1198–1214. doi:[10.2307/2409088](dx.doi.org/10.2307/2409088)
- Colenso, W. (1887). A description of a large and new species of Orthopterous insect of the genus *Hemideina* Walker.*38*