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Status of the New Zealand cave weta (Rhaphidophoridae) genera *Pachyrhamma, Gymnoplectron* and *Turbottoplectron*

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Abstract. 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.

Additional keywords: phylogeography, species radiation.

Introduction

As is typical of the Rhaphidophoridae, all New Zealand cave weta[1] 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). 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*a*; Ward 1997). 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*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 1961*a*) 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; Scudder 1869; Brunner von Wattenwyl 1888). Richards (1961*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) in the proposed restitution of *Pachyrhamma*, and follow Kirby (1906) and Karny (1937) 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) and Rhaphidophoridae (usually cave weta), and has the same form for both the singular and plural uses.

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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; Scudder 1869; Walker 1869; Brunner von Wattenwyl 1888). Body lengths range up to 48 mm (Richards 1962*a*), with long hind legs and antennae. *Pachyrhamma* (or *Gymnoplectron sensu* Richards, 1961*a*) has the largest number of described species (13) of the New Zealand genera and some of these are well known denizens of caves and rock tunnels. Within the genus, some species appear to be strongly associated with caves although these species are known to emerge at night to forage, whereas others have been found only away from caves. Although several species of *Pachyrhamma/ Gymnoplectron* at three sites (Richards 1954*b*, 1954*c*, 1961*b*, 1961*c*, 1961*d*, 1962*b*) are the best studied of all New Zealand cave weta, knowledge of the life histories, ecology and distribution of others is very limited. Discussion of their morphological and evolutionary relationships is meagre.

Pachyrhamma occurs widely in North Island, New Zealand, with outlying species on the Poor Knights Islands to the north, and Nelson and Fiordland in the South Island (Fig. 1). Of these 13 species, the only one known to occur exclusively in the South Island is *P. delli* (Richards, 1954*a*), which was described from Fiordland. *Pachyrhamma edwardsii* (Scudder, 1869) (see Hutton 1897; = *Macropathus filifer* of Richards, 1954*a*, 1954*b*) is widespread in patches of native forest from the Nelson region (South Island) to the Waikato (North Island). It is a frequent inhabitant of anthropogenic rock tunnels in the Wellington Region, limestone caves in the Nelson region, dry, stony and steep intermittent stream beds of the mainland and offshore islands of Marlborough Sounds and occurs on small islands off the coast of Wellington (Mana Is. and Kapiti Is.). The largest of the *Pachyrhamma* species, *P. giganteum* (Richards, 1962*a*), is endemic to the Poor Knights Islands, situated off the Northland coast. Other species of *Pachyrhamma* have been found only in the North Island and most apparently have narrow spatial ranges. For example, *P. waitomoense* Richards, 1958*a* (see also Richards 1961*c*) from Waitomo Caves (Waikato), *P. waipuense* Richards, 1960 from the Waipu cave system (Northland), *P. longicaudum* Richards, 1959*a*, from Ohakune and Taumarunui (Tongariro), and *P. spinosum* (Richards, 1961*e*), *P. tuarti* (Richards, 1961*e*) and *P. ngongotahaense* (Richards, 1961*e*) from Rotorua. *Pachyrhamma fuscum* Richards, 1959*b* and *P. uncatum* Richards, 1959*b* are known only from abandoned gold-mining tunnels in Thames and *P. acanthoceras* Milligan, 1926 from old water-works tunnels in the Waitakere Ranges, Auckland. A related species, *Gymnoplectron longipes* (see also Richards 1958*b*), has been recorded in many areas of forest across the central and lower North Island, particularly in the Wellington and Manawatu regions where it overlaps with several other species of *Pachyrhamma* (Fig. 1). Species are distinguished primarily by combinations of colour pattern (e.g. *P. edwardsii* has distinctive banding), linear leg spine number and size, and characters such as pronounced antennal hooks (e.g. male *P. acanthoceras*), and shapes of male parameres and subgenital plate.

Pachyrhamma Brunner v. Wattenwyl, 1888 and *Gymnoplectron* Hutton, 1897 exemplify the taxonomic problems that are widely seen in the New Zealand rhaphidophorids. These genera are distinguished primarily by the presence of both a prolateral and a retrolateral apical spine on each hind femur (Hutton 1897; Richards 1954*a*; Ward 1997). In 1948, John Salmon erected a new genus, *Turbottoplectron*, for a large species from the Three Kings Islands, *T. unicolor*. This description was based on two male specimens and included the statement; 'hind femora with one very small apical spine only on inner margin' (Salmon 1948, p. 303). He considered this genus was 'closest related to *Gymnoplectron* Hutton, from which it is really distinguished from it by having only one small apical spine on the hind femora' (Salmon 1948, p. 304). Although Salmon (1948) did not use the term, examination of the type specimens indicates that the apical spine on the hind femora he referred to on *T. unicolor* was retrolateral. Richards (1961*a*) attempted to clarify taxonomy of this group of cave weta by synonymising *Pachyrhamma* with *Gymnoplectron* with the effect that, in recent years, large, North Island cave weta have usually been referred to as *Gymnoplectron* (notably *G. edwardsii*). Richards (1961*c*) also moved the central North Island species *Pleioplectron cavernae* Hutton, 1900 into *Turbottoplectron*, stating that 'in all its generic characters *Pleioplectron cavernae* agrees with those given for *Turbottoplectron*'. Thus, *Gymnoplectron* (*sensu* Richards, 1961*a*) and *Turbottoplectron* Salmon, 1948, two genera of relatively large weta, are formally distinguished only by the presence or absence of one prolateral apical spine on the hind femora. As *Pachyrhamma* has precedence over *Gymnoplectron*, the same distinction applies.

Many specimens have been collected throughout the North Island before and during the present study that agree with the generic descriptions of *Pachyrhamma* or *Gymnoplectron* in all respects (including leg and body dimensions and sub-genital plate shape) except that they possess only one retrolateral apical spine on the hind femora. Therefore, they have been tentatively assigned to the genus *Turbottoplectron*, although they are probably neither of the two described species of *Turbottoplectron, T. unicolor* or *T. cavernae*.

Richards (1961*a*) may have fallen into the same trap as her predecessors by not realising the full extent of variation that exists within genera and so incorrectly identifying the morphological characteristics that are constant across a genus. Richards (1954*a*) states that number of apical leg spines remain constant across a genus, whereas it is possible that the number of apical spines on the hind femora actually varies among populations and species; putative *Turbottoplectron* species may really be geographical variants of known *Pachyrhamma* (or according to Richards, *Gymnoplectron*) species. Alternatively, apical spination of hind femora may indeed be constant in these genera, meaning the genus *Turbottoplectron* is a 'good' genus that, as Salmon (1948) stated, is very closely related to *Gymnoplectron* (= *Pachyrhamma*). This type of situation whereby two genera are differentiated by few key characters (one character often being number of apical leg spines) is common

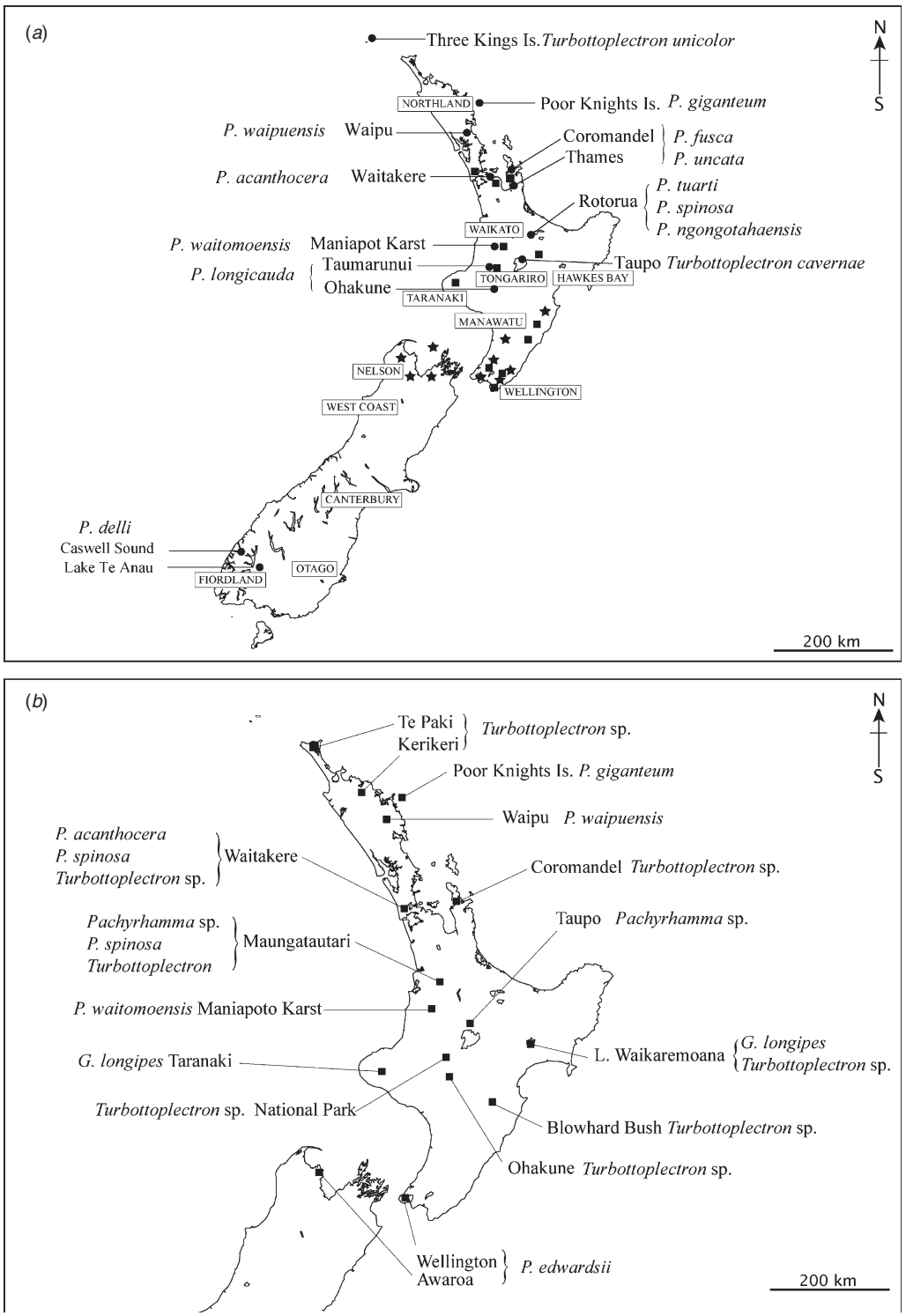

Fig. 1. The Rhaphidophoridae (cave weta) *Pachyramma* Brunner v. Wattenwyl, 1888, *Gymnoplectron* Hutton, 1897 and *Turbottoplectron* Salmon, 1948 in New Zealand. (*a*) Type locations of described taxa (circles), and recorded sites for *P. edwardsii* (stars) and *G. longipes* (squares); (*b*) site locations for samples used in the present study.

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* from *Pachyrhamma*, and

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

Methods

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 of *Turbottoplectron* spp. and *Gymnoplectron longipes*. We include specimens with and without prolateral apical spines on the hind femora from the same location. *Pachyrhamma tuarti* and *P. ngongotahaense* have not been found since their original descriptions (Richards 1961*d*) and we found that their type localities no longer exist (due to deforestation and development). Furthermore, no specimens of *Pachyrhamma* were found in the regenerated forest that presently surrounds Rotorua. *Pachyrhamma spinosum* was however collected from other North Island locations (Table 1). No specimens fitting the description of *P. longicaudum* were found from the type localities at Ohakune or Taumarunui although other *Pachyrhamma* and putative *Turbottoplectron* were found. The type locality for *T. cavernae*, in fumarole cavities at Lake Taupo, is now a major tourist attraction and geothermal power station and specimens collected elsewhere near Lake Taupo fit better the description of *Pachyrhamma/Gymnoplectron* rather than of *Turbottoplectron*. There has been no record of either *P. longicaudum* or *T. cavernae* since their original descriptions (Richards 1959*a* and Richards 1961*c*, respectively) and this appears to be the case for many of the apparent local endemics. However, species that we have not located are, according to the original descriptions, closely allied to species we have found. For example, *P. longicaudum* is close to *G. longipes* (Richards 1959*a*), *P. fuscum* is close to *P. waitomoense*, and *P. uncatum* close to *P. acanthoceras* (Richards 1959*b*). We did not obtain *T. unicolor* from the offshore Three Kings Islands conservation reserve, and only type material is available in museum collections.

Data were obtained from 14 specimens representing at least seven *Pachyrhamma*/*Gymnoplectron* species (*P. giganteum*, *P. edwardsii, P. spinosum, P. acanthoceras, P. waipuense, P. waitomoense* and *G. longipes*), plus nine individuals consistent with *Turbottoplectron* on the basis of their apical spination. Individuals (adults and late instars) were identified to species level using species descriptions and with reference to the most recent taxonomic keys (Richards 1961*c*, 1961*e*; Ward 1997) and type material. Holotypes and/or paratypes for *P. giganteum*, *P. fuscum*, *P. uncatum*, *P. waitomoense*, *P. longicaudum* and *P. spinosum* were examined at the Auckland Museum. Identified material of *T. unicolor*, *G. longipes, P. acanthoceras* and *P. edwardsii* was examined at the Museum of New Zealand Te Papa Tongarewa, Wellington, and the types of *T. cavernae* and *G. longipes* and other material at the Canterbury Museum, Christchurch. The relevant type material of Brunner von Wattenwyl (*Pachyrhamma novaeseelandiae*), Scudder (*Hadenoecus edwardsii*) and

Table 1. Identity, habitat and source of New Zealand Rhaphidophoridae (cave weta) used in this study
Habitat indicates specific locality in which specimen was found, if known. Approximate location of sampling sites is given in Fig. 1

Species	Sample no.	Location	Habitat
Gymnoplectron longipes	CW197	Lake Waikaremoana, Urewera	Cave
G. longipes	CW721	Manaia Road, Taranaki	Tree hole by day
Pachyrhamma acanthocera	CW485	Nihotopu Stm, Waitakare Ra.	Cave
P. edwardsii	CW68	Khandallah Reserve, Wellington	Mine tunnel
P. edwardsii	CW70	Awaroa, Golden Bay	Outhouse
P. giganteum	CW239	Poor Knights Islands	Cave
P. spinosa	CW149	Aratati Reserve, Waitakere Ra.	Under bark
P. spinosa	CW369	Maungatautari Ecological Island	On tree at night
P. spinosa	CW763	Little Barrier Island, Hauraki Gulf	On tree at night
Pachyrhamma sp.	CW380	Maungatautari Ecological Island	On tree at night
Pachyrhamma sp.	CW142	Ohakune, Tongariro	Tree hole by day
Pachyrhamma sp.	CW482	Ohakuri Power Dam, Taupo	Inspection tunnel
P. waipuensis	CW418	Abbey Caves, Whangarei.	Cave
P. waitomoensis	CW318	Ruakuri Reserve, Waitomo Caves	Cave
Turbottoplectron sp.	CW198A	Lake Waikaremoana, Urewera	Cave
Turbottoplectron sp.	CW53	Blowhard Bush, Hawkes Bay	Cave
Turbottoplectron sp.	CW69	National Park, Tongariro	Fire hydrant in road
Turbottoplectron sp.	CW151	Sharp Bush, Auckland	Tree hole by day
Turbottoplectron sp.	CW333	Te Paki, Unuwhao	not known
Turbottoplectron sp.	CW55A	Kerikeri, Northland	Tree hole by day
Turbottoplectron sp.	CW338	Ohakune, Tongariro	Tree hole by day
Turbottoplectron sp.	CW367	Maungatautari Ecological Island	On tree at night
Turbottoplectron sp.	CW494	Coromandel	not known
Macropathus sp.	CW86B	Charleston, West Coast	Cave
Macropathus sp.	CW442	Piopio, Waikato	Cave
Pleioplectron simplex	CW306	Dunedin, Otago	Hole in bank
Weta thomsoni	CW146	Raincliffe, South Canterbury	Cave

Walker (*Macropathus fascifer, M. filifer*) 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) designed for fresh tissue, but used successfully for preserved orthopteran tissue (Trewick and 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 *et al*. 1994), C1-J-1718, C1-N-2191, C1-J-2195 and L2-N-3014 (Simon *et al*. 1994).

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 using SEQUENCHER ver. 4.2 sequence editor (Gene Codes Corp., Michigan), and aligned using SEAL V2.0 (Rambaut 1996). 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.

Phylogenetic analyses

Preliminary analyses using a larger dataset including representatives of 15 New Zealand cave weta genera resulted in the selection of an outgroup consisting of data from the four cave weta taxa that appear to be closest relatives of *Pachyrhamma*. Maximum Likelihood (ML) using PAUP* 4.0b 10 (Swofford 2002) and PHYMYL (Guindon and Gascuel 2003), and Bayesian analysis using MrBAYES V3.1 (Ronquist and Huelsenbeck 2003) were implemented though GENEIOUS V4.6.4 (Drummond *et al*. 2009). Akaike Information Criteria as implemented by MODELTEST V3.6 (Posada and Crandall 1998) were used to select the appropriate substitution model to apply in ML analyses. Bayesian analyses used two parallel runs of six million generations, sampling every 1000th tree, with a 10% burn-in. Maximum Likelihood bootstrapping with 500 replicates was undertaken using PHYML. Genetic distances were calculated for the complete dataset using observed distance (uncorrected) and the ML model selected with Modeltest.

Results

The resulting dataset comprised 26 accessions with aligned sequences of 1200-bp. This included sequences from 22 individuals of *Pachyrhamma/Gymnoplectron* and *Turbottoplectron* plus four outgroup taxa (*Pleioplectron simplex* Hutton, 1897, *Weta thomsoni* Chopard, 1923, two *Macropathus* Walker, 1869 spp.). All phylogenetic analyses resulted in trees with the same clades although some variation in local topology was reflected in weak support values for some nodes. In no analysis were *Pachyrhamma* and *Turbottoplectron* reciprocally monophyletic. In all analyses *P. edwardsii* was sister to the rest of our *Pachyrhamma* and *Turbottoplectron* specimens (Fig. 2). Sequences from specimens identified as *Turbottoplectron* fell into three different clades (IV, V, VI). Two of these clades (V, VI) also included samples of *Pachyrhamma*. *Gymnoplectron longipes* was nested within *Pachyrhamma*.

Using a GTR + I + G model, genetic divergence between *P. edwardsii* (Clade I) and all other ingroup taxa ranged from 0.11 to 0.21. The highest divergence between species (0.18–0.21) was found between *P. edwardsii* (Clade I) and Clade VI *Pachyrhamma* sp./*Turbottoplectron* sp. individuals. In contrast, genetic distances among the genetically closest species, *P. waitomoense, P. waipuense* and *P. acanthoceras* in Clade V, were as low as 0.01.

Discussion

Of the 18 genera of Rhaphidophoridae in New Zealand, the large cave-dwelling species of *Pachyrhamma/Gymnoplectron* are the best known with the greatest described species diversity. However, even within this familiar genus there are many undescribed species and the limits of the group are not well resolved. The representatives of *Pachyrhamma*, *Gymnoplectron* and *Turbottoplectron* included in this study form a monophyletic clade with respect to the four species of the outgroup (and other genera not shown), with *P. edwardsii* sister to the rest of the ingroup.

Pachyrhamma/Gymnoplectron can be distinguished from all other cave weta genera by the presence of one prolateral and one retrolateral apical spine on the hind femora (Richards 1961*a*; Ward 1997). Nine specimens in this study have body and leg dimensions, and sub-genital plate shape, that fall within the *Pachyrhamma/Gymnoplectron* range, but differ from the generic description in the absence of a prolateral apical on the hind femora (Table 1). The absence of the prolateral apical hind femur spine places these specimens in the closely related genus, *Turbottoplectron*, but our phylogenetic analyses did not support this separation (i.e. lack of reciprocal monophyly of *Pachyrhamma* and *Turbottoplectron*) (Fig. 1). From this we infer that the number of apical spines on the hind femur is not consistent with the evolutionary history of the taxa, and is not an appropriate basis for partitioning species into genera. It remains possible that *Turbottoplectron unicolor* is itself a distinct genus, but the present molecular, phylogenetic and morphological evidence based on other species does not support this. Either way, the presence of apical femur spines is insufficient evidence to diagnose a separate rhaphidophorid clade. Not only does apical spine number fail to differentiate monophyletic generic clades, but the number of apical spines on the hind femora varies even within populations. For example, clades V and VI (Fig. 2) each represent specimens of *Pachyrhamma* and *Turbottoplectron* collected at the same locations, which are otherwise morphologically identical to one another and have little mtDNA genetic difference (<0.01). This low level of variation

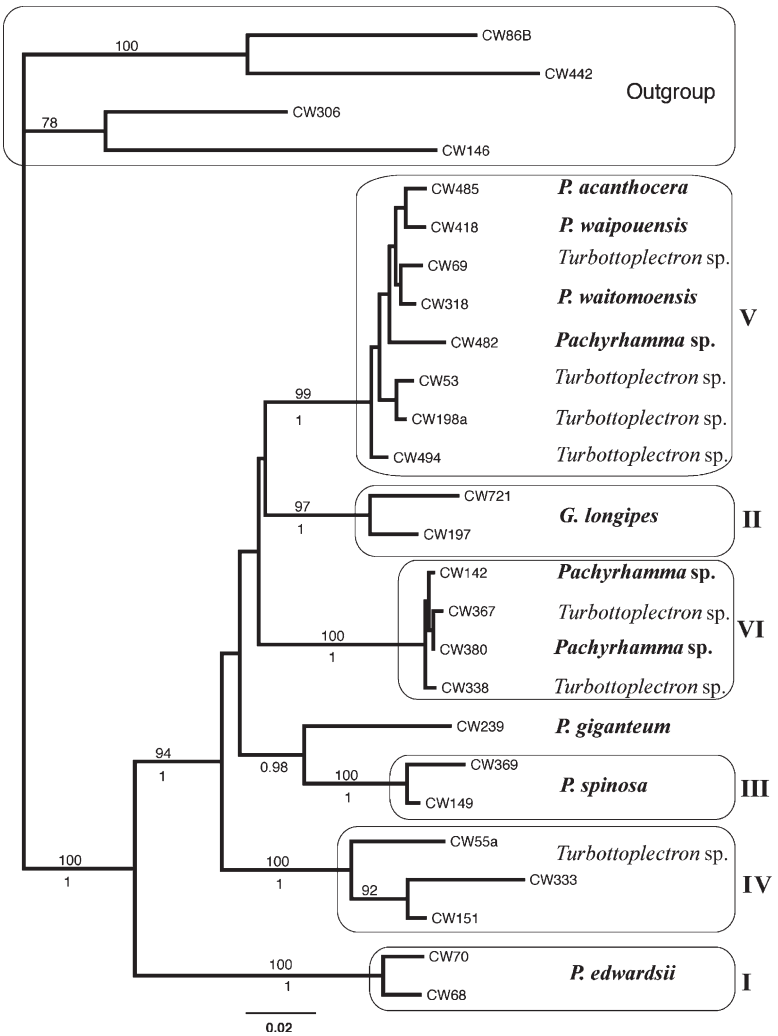

Fig. 2. Maximum likelihood analysis of COI mtDNA sequences from New Zealand Rhaphidophoridae: *Pachyrhamma*, *Gymnoplectron*, *Turbottoplectron*. Values at nodes are results of ML bootstrap resampling (above), and posterior probabilities from Bayesian analysis (below) using GTR+I+G model.

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) 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 justification for generic separation of *P. edwardsii* from the other ingroup taxa.

Specimens of species within Clade V (*P. waitomoense, P. waipuense*, and *P. acanthoceras*, plus unidentified taxa) vary in colour patterns, leg spine numbers, leg and body dimensions and sub-genital plate structure that are not only consistent with the described diversity but may be indicative of several new species. For example, male *P. acanthoceras* and *P. waipuense* exhibit impressive spines (fused setae) on their antennae and male *P. waipuense* have a distinctive lobe between the apical spines of the hind tarsi (Richards 1960). Unidentified taxa might represent hitherto undescribed species, but it is reasonable to assume for the time being that they might also represent existing poorly characterised species, which will be resolved with further morphological analysis. The three described species within Clade V appear to occupy narrow geographic ranges: *P. acanthoceras*, *P. waipuense* and *P. waitomoense* are known only from the Waitakere Ranges, Waipu Caves and Maniapoto Karst Area respectively (see Fig. 1), although further searching may extend their known distributions.

The low genetic divergence and high taxonomic diversity found within Clade V taxa highlights the importance of morphological and ecological information in phylogenetic studies. On the basis of their COI sequences using Hebert *et al.*'s (2003) DNA barcoding guidelines, *P. waitomoense, P. waipuense* and *P. acanthoceras* could be treated as populations of a single species. To do this, however, would

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 recently than 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), does not support its synonymy with *Pachyrhamma* proposed by Richards (1961*e*). It also fails to support *G. longipes* (Colenso 1887) as separate from other species that have been included in *Gymnoplectron* (*sensu* Richards 1961*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; = *Macropathus fascifer* Walker, 1869) (not = *Macropathus filifer* Walker, 1869)

Gymnoplectron Hutton, 1897: 229.

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

Turbottoplectron Salmon, 1948: 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; Trewick 2008). 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.

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