Systematics and phylogeography of the large land snail *Powelliphanta*

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Image previous page: *Powelliphanta hochstetteri hochstetteri* by Rob Suisted

Abstract

Without a generally accepted name, a species is less likely to receive conservation effort. For the large, colourful and carnivorous land snails in the New Zealand genus *Powelliphanta,* doubts about the validity of the existing morphologically-based nomenclature, and the absence of taxonomic assessment for many late-discovered taxa, have been hindering conservation efforts. *Powelliphanta* have been in decline due to continuing loss of habitat and a suite of predators recently introduced to New Zealand, but scarce conservation resources are targeted to formally described taxa. The aim of this study was to review and if appropriate revise the taxonomy of the genus to remove any taxonomic impediment to conservation action. Like other Pacific Ocean archipelagos, the fauna and flora of New Zealand is characterised by a small number of families with extensive radiations. Understanding of relationships is often hindered by the recency of lineage separations and requires multiple lines of evidence. Allozymes and mitochondrial sequences were used to identify genotypic clusters in *Powelliphanta* and to assess the relationship with presumed sister taxa *Victaphanta*. A matrix of morphological characters was assembled for multivariate analysis. These characters included for the first time in *Powelliphanta*, features of the soft body and Fourier coefficients describing subtle shape differences. Intraspecific variation within one of the species, *P. lignaria*, received detailed distributional, morphological and genetic evaluation to investigate the use of subspecies in the genus. *Powelliphanta fiordlandica* was found to be a sister taxon to all other *Powelliphanta*, with a deep genetic divergence and differences in morphology indicating it should be placed within its own monotypic genus. Allozymes, mtDNA and morphology all identified similar clusters, many of which equated to the already described taxa and to taxa which had been tag-named but remained undescribed. Shell colour, pattern and size, which show environmental plasticity in some molluscs, were found in *Powelliphanta* to be genetically-based and shape also proved informative. The described subspecies of *Powelliphanta lignaria* were found to be morphologically diagnosable, largely allopatric, and with gene flow limited to the extent that the integrity of each subspecies has been maintained. A recently discovered and critically threatened species was described as *Powelliphanta augusta*, and a new classification for the genus comprising 20 species and 59 subspecies (including the existing *P. lignaria* subspecies) was proposed.

"For a moment she rediscovered the purpose of her life.
She was here on earth to grasp the meaning of its wild enchantment,
and to call each thing by its right name"

"Dr Zhivago" by Boris Pasternak

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Chapter 1.
General Introduction

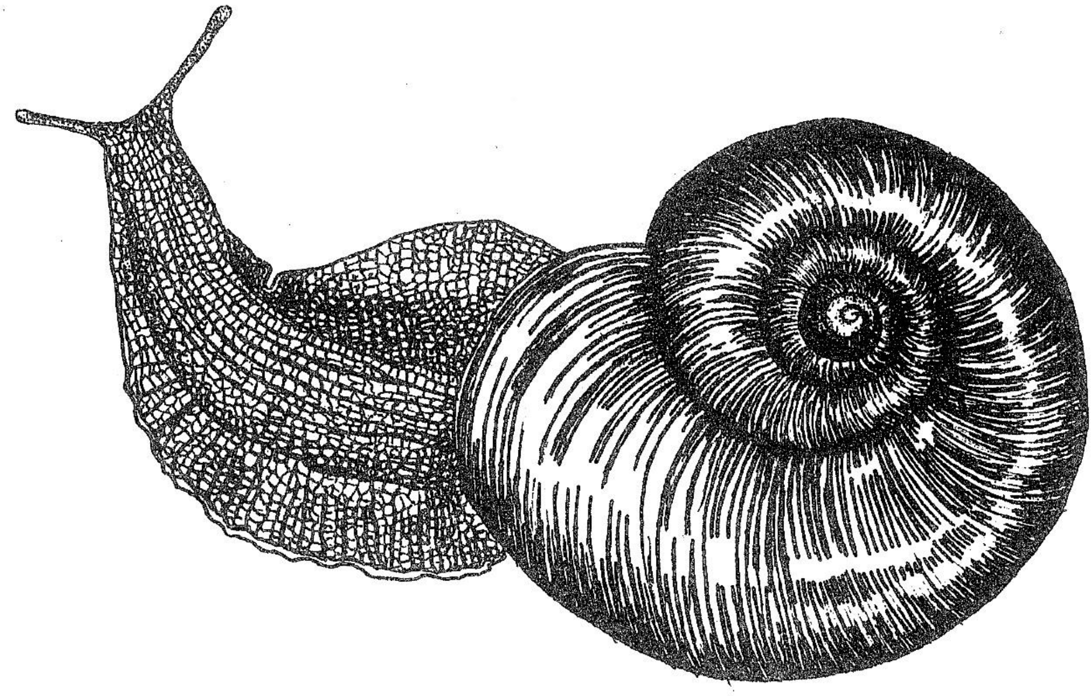

Image previous page*: Powelliphanta superba superba*; artist Pauline Morse

General Introduction

Why names matter

It is a truth universally acknowledged, that a species without a proper name, must be of lesser value. This misquote of Jane Austen's famous opening line is only partially said in jest, as sadly, research has shown taxonomic splitting tends to lead to increased conservation effort, whereas taxonomic "lumping' tends to lead to reduced conservation effort (Morrison et al. 2009). However, when the species in question is beautiful, charismatic, iconic or of economic importance, neither a reduction nor an increase in taxonomic status appear to alter the amount of conservation attention received (Morrison et al. 2009).

This is disheartening when considered in relation to invertebrates, specifically non-marine molluscs, which are amongst the most threatened and under-described animal groups on the planet (Lydeard et al. 2004). Of the 693 recorded extinctions of animal species since 1500 AD, 42% are molluscs, 99% of these non-marine molluscs, but its estimated between 11,000 to 40,000 species of terrestrial mollusc remain to be described (Lydeard et al. 2004). If having a name increases chances of conservation effort being applied, then more work urgently needs to be done to clarify the taxonomic status of terrestrial molluscs.

The reasons so many living organisms, including terrestrial molluscs, remain nameless despite names being so integral to their conservation, are complex. They stem in part from the decimation of taxonomic resources in recent decades (Dubois 2003), with traditional taxonomy on the verge of extinction (Cardosa et al. 2011). Much has been written on the causes of this decline (Wheeler 2004, 2007) which in brief relate to a comprehensive underrating of taxonomy relative to other aspects of biology and systematics (Dubois 2003). It is ironic that this decline has happened when taxonomic effort has never been more urgent. With the ever-growing and accelerating mass extinction of species due to human activities (Cardosa et al. 2011 and references therein) a new discipline "conservation biology" has developed, focussing most of its effort on evaluation of current threats and to finding the causes of and solutions to those threats.

> *"However, one major problem of this endeavour is that such evaluations are necessarily incomplete, if not fully wrong, as their starting point, the inventory of the living species of our planet, is largely unsatisfactory, both regarding taxonomic* ***completeness*** *and taxonomic* ***accuracy****: ... the so-called 'taxonomic impediment'"* (Dubois 2003).

The "taxonomic impediment" to species conservation—that gaping canyon between the number of taxa needing systematic assessment and the number receiving it—has been widely discussed (Franz 2005, Grimaldi & Engel 2007), from ways to re-evaluate the importance of taxonomic activity in conservation (Dubois 2003, Mace 2004), warnings of gross underestimation of the scale of the problem (Delic et al. 2017) and credibility issues with the current taxonomic process (Garnett & Christidis 2017). As the vast majority of biodiversity losses belong to understudied taxa, such as certain groups of invertebrates (the 'little things that run the world" Evan 1993, Wilson 1987), others have focused on ways to overcome the Linnean shortfall (Wheeler 2007, Padial et al. 2010, Cardosa et al. 2011). What seems agreed is that conservation depends on good taxonomy, that many extinctions are now inevitable and that while it's still possible, taxonomic effort on those living organisms still present must be accelerated, given the impossibility of discovering this information after extinction (Dubois 2003).

The land snail fauna of New Zealand—an isolated island archipelago in which molluscs have come to occupy every ecosystem—is large, diverse and predominantly unnamed, especially its micro-snails. The subject of this thesis, *Powelliphanta* (O'Connor 1945) is a genus of terrestrial mollusc endemic to New Zealand and a member of the southern hemisphere family Rhytididae. Most species and subspecies are considered threatened (Hitchmough 2007), mainly because of habitat loss, habitat degradation and predation by animals introduced to New Zealand (Walker 2003) and require conservation effort if they are to survive. However, while the first-discovered *Powelliphanta* were large, attractive forest-dwellers which were easy to find and received comparatively thorough systematic attention, many of the smaller, less colourful and less accessible alpine *Powelliphanta* were not discovered till much later and most remain unnamed.

This thesis is a first step towards enabling the conservation of *Powelliphanta.* It aims to synthesize the genetic, morphological and geographic distinctiveness of newly discovered but still undescribed *Powelliphanta* populations, to re-examine described taxa to see if those earlier designations on simple conchology stand up to more comprehensive morphological and genetic assessment, and to see whether the evolutionary history of *Powelliphanta* is captured in its current taxonomy.

While some *Powelliphanta*, with their large and attractive shells, have become as near to an icon in New Zealand as any invertebrate is likely to be, a lack of taxonomic assessment and formal description for almost a third of putative species, and questions as to the validity of the assessments made in the 1930s and 1940s for those which are described, leaves a gap that urgently needs filling. That names do indeed matter, is for *Powelliphanta,* abundantly clear.

When an apparently new *Powelliphanta* was discovered in 2004 on the edge of a large open-cast coal mine on the Stockton Plateau, its lack of formal description nearly derailed efforts to protect the population and its last remaining fragment of unmined habitat. Was it something different or was it not? In the heated court of public opinion as to whether a revenue-generating coal mine should be hindered from mining the last habitat of a snail, it mattered greatly whether the snail was just a variant of a more abundant subspecies or species of *Powelliphanta*, or something genuinely different, yet that information did not exist.

I found that snail in the Stockton coal mine, and to my eye it appeared on morphological grounds to be related to *Powelliphanta lignaria* but was quite distinct from it. It was an uncomfortable experience maintaining that view through Environment Court hearings without the assurance that would have come had a comprehensive comparative morphological and molecular assessment been available before a very public argument broke out. Long after mining had resumed, most of the snails remaining habitat had been lost, and the snails moved to a new uncertain life outside their range, the science caught up and a mitochondrial DNA (mtDNA) study confirmed *P. augusta* as a new species, sister to *P. lignaria* (Trewick et al. 2008). Later still another mtDNA and nuclear gene study came to the same conclusion (Buckley et al. 2014). The present thesis is a direct result of that experience and is intended to ensure the systematics of *Powelliphanta* can be properly evaluated in a less heated environment.

History of Powelliphanta speciation studies

For an animal with a comparatively high profile today, a surprisingly small amount of systematic work has been carried out over the last century. The saga of the snail in the Stockton Mine brought *Powelliphanta* attention and fame of a sort; predominantly notoriety and outrage that protection of such a "lowly creature" could threaten the economic well-being of a community, but also widespread adoption as a symbol of the New Zealand fauna, along-side more familiar symbols such as the kiwi (Figure 1). While the strong impact this story made was perhaps due more to growing concern over the climate impact of burning coal than to concern for loss of biodiversity, it did draw attention to the poor understanding of evolutionary relationships even within some of New Zealand's most prominent land snails.

Figure 1. From 2007, *Powelliphanta* snails began to appear in cartoons published in newspapers along-side other immediately recognizable endemic fauna such as kiwi, used as code for "New Zealand wildlife", as in this cartoon by Trace Hodgson.

It seems unlikely that such large animals as *Powelliphanta* were unknown to the Polynesian people who settled New Zealand around 1300 AD, so presumably they were not distinguished by them from the large “Pupurangi” *(Paryphanta)* land snails of Northland forests as no separate word for them survives in te reo Maori. The chronology of Linnaean *Powelliphanta* nomenclature, will be described in Chapter 2.

Not long after European settlement of New Zealand, geologists, botanists and land surveyors started encountering *Powelliphanta* with the type species *Powelliphanta hochstetteri* named after the geologist Ferdinand Van Hochstetter in1862. However, the hey-day of *Powelliphanta* classification was the 1930s and 1940s, when the malacologist at the Auckland Institute and Museum at the time, AWB Powell, investigated in detail their distribution and “hypothetical ancestry” (Powell 1930). He found *P. traversi, P. gilliesi, P. superba, P. lignaria* and *P. hochstetteri* each showed great variation in shell colour and pattern which was strongly geographically distributed, with shells of each “type” confined to discrete areas. He later formed a long association with cousins Frederick and Albert Prouse who helped refine his knowledge of *P. traversi* and *P. gilliesi* distributions in the lowland forests and flax swamps they were milling in both the North Island’s Horowhenua Plains and the western coast of the South Island’s Golden Bay, and with Harry Johnston who came across *P. lignaria* snails amidst the forest logging and coal mining near Mokihinui in North Westland (Powell 1944–1975, in lit).

The first *Powelliphanta* map Powell published (1930) showed the distribution of *P. hochstetteri*, *P. traversi* and *P. gilliesi* as formerly connected across Cook Strait, the seaway separating New Zealand’s two main islands (Figure 2). As the sea forms a conspicuous barrier to land snail dispersal, the close relationship Powell hypothesized of snails either side of Cook Strait was subsequently used by geologists to estimate dates for proposed land-bridges between New Zealand's two major islands (Te Punga 1953). In addition to envisaging snail speciation through recent isolation on real islands, Powell's (1930) descriptions of subspecies of *Powelliphanta hochstetteri* isolated on mountain tops as “islands” in a "virtual sea" of unfavourable habitat was also evocative and caught public attention. The idea was subsequently repeated in many publications by the influential geologist and biologist Sir Charles Fleming (1949, 1962, 1979), though he was of the view "the vigorous race-formation in *Paryphanta* dates from the post-glacial re-colonization of the South Island mountains, and not from the Miocene as Powell originally suggested" (Fleming 1949).

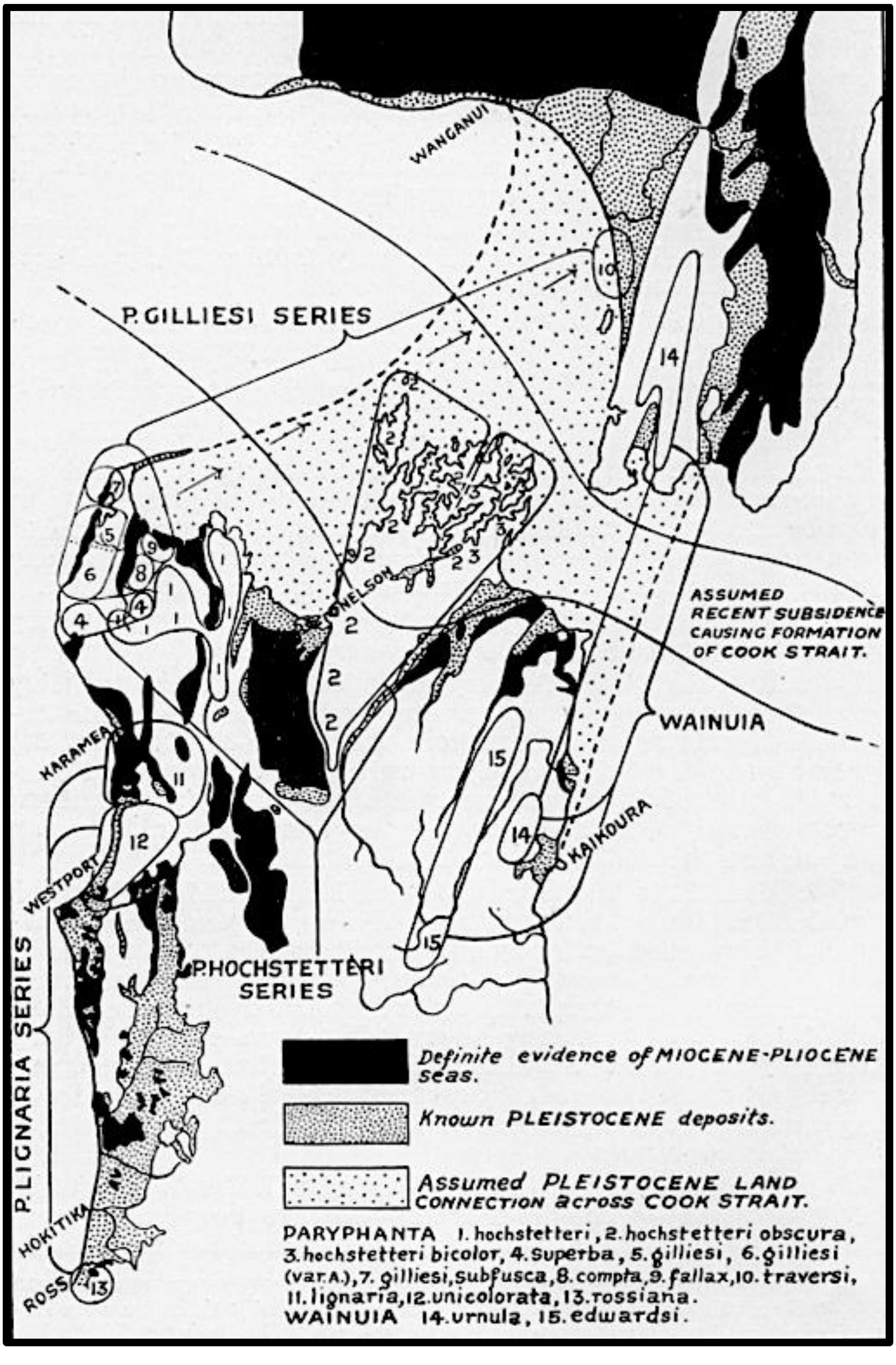

Figure 2: The "Hypothetical geological map of the Cook Strait region, illustrating the distribution of *Paryphanta* and *Wainuia*" published by Powell (1930) which made a strong

impression on biologists of the day, and helped general understanding of the comparatively young nature of Cook Strait and the close relationships between species on either side. These ideas lingered in public consciousness of *Powelliphanta* “species” for another 30 years, but both Te Punga's and Fleming's examples actually related mostly to the close relationships of the morphologically and geographically distinct “forms” which Powell had described as sub-species, rather than of the species themselves. In 1971 the malacologist at the National Museum of New Zealand, FM Climo, described the first new species of *Powelliphanta* to be found in nearly 40 years, *Powelliphanta fiordlandica,* then in 1977 he elevated *Powelliphanta* from subgeneric to genus status. In 1978, nearly 50 years after Powell’s original *Powelliphanta* publications, Climo shifted the focus firmly from intra to inter-specific variation, with an alternative evolutionary hypothesis for *Powelliphanta*. He suggested the intra-specific variation described in *Powelliphanta* was “morphological minutiae, devoid of phyletic meaning" (Climo 1978). In the belief most of Powell’s species merged clinally with one another, he proposed all previously named species and subspecies were part of one complex ring species, formed comparatively recently from southward movement of North Island *Powelliphanta* across a Cook Strait land bridge during the past glacial period (~20,000 years ago) and hybridization there with glacially disjunct South Island populations (Climo 1978). Little geological or distributional information was provided to support this model, which never-the-less stimulated much interest and further work.

Parkinson (1979) reviewed the paper, noting the paucity of data presented in support of Climo's hypothesis. While rejecting Climo’s model of a north to south invasion, Parkinson was also unsupportive of Powell’s theory of a **very recent** migration of South Island species northwards over a Cook Strait land bridge (Parkinson 1979), as he thought the widely separated locations they occupied in the North Island precluded this. He raised the prospect that *P. fiordlandica* may not belong in the genus. He presented an alternative classification, retaining most of Powell’s species but amalgamating *P. hochstetteri* and *P. superba* based only on their equally large size: he subsumed one or two of the subspecies in the species *hochstetteri*, *superba*, *lignaria* and *spedeni* and all of those in *gilliesi*; and moved Marlborough Sounds *Powelliphanta* from *hochstetteri* into *traversi*, along with wider North Island snails formerly in *marchanti*. While ignorant, as indeed Powell and Climo were, of the complexities within the still-barely known southern alpine “*rossiana*” series and excepting the simplistic size-driven amalgamation of *superba* and *hochstetteri,* this was a more thoughtful and reasonable revision. Unfortunately, it was self-published in inflammatory language and was not widely distributed.

A large publication by Powell in an unspecified month in 1979, in which his original descriptions were reiterated in a summarized form, included reference to Climo's relatively slight 1978 classification (though not to Parkinson's equally slim March 1979 publication). This meant Powell's classification was technically more recent than Climo's, and probably also than Parkinson's, though it was clearly written earlier than either. As a result, the taxonomic status of many *Powelliphanta* populations was unclear, and was left in this unsatisfactory state for many years, with some authors continuing to use Powell's nomenclature (Meads et al. 1984, Walker 2003) while the National Museum of New Zealand followed Climo's 1978 taxonomy. Climo's paper had created a perception that the group was over-split. The arrival of more powerful taxonomic tools finally makes it possible to test this perception and is the subject of this thesis.

Morphometric study of molluscs

Molluscs have a particularly long and august history in morphometric study, due to the persistence of their calcified shells, and their conspicuous variability. Variations in the shell patterns of land snails have been the subject of evolutionary study for over 100 years, due to the light they shed on the action of natural selection in shaping present-day phenotypic diversity (Davison 2002). This has become more potent with the recent widespread adoption of molecular methods, allowing a separate account of the history of populations to compare with that gauged from shell patterns (Chiba 1999, Douris et al. 1998, Davison & Clarke 2000, Goodacre 2002).

As the taxonomy of fossil molluscs—an essential component of the record of the earth's pre-history (Monnet et al. 2009)—depends almost exclusively on morphological study of their shells, much effort has gone into refining techniques to measure shell shape and size (Van Bocxlaer & Schultheiβ 2010). While paleontology has been one of the main drivers and beneficiaries in a recent "revolution in morphometrics" (Rolf & Marcus 1993) made possible by improved computing power, the value of this revolution to the study of extant molluscs is also high. Since the 1970s when multivariate statistical tools first became widely used, the traditional measurement of shells has steadily become more accurate and comprehensive, with area finally able to be measured through computer-assisted measurement of digital shell images. This has expanded into the capture of shape through the use of landmarks and outlines to provide mathematical description and reproduction of the geometry of the shell structures being studied (Crampton 1995, Haines & Crampton 2000, Adams et al. 2004, Monnet et al. 2009, Van Bocxlaer & Schultheiβ 2010, Vaux et al. 2017).

The expansion of methods available for capturing morphological differences has been important in improving the usefulness of morphology in species delimitation, as such expansion helps resolve the problem of differing levels of morphological complexity among taxa (Van Bocxlaer & Schultheiβ 2010). The fewer the morphological features used to characterize a higher taxon, the fewer the lower-level taxa expected to be assigned to it (Schopf et al. 1975, Schopf 1982), simply because there are not enough characters for finer-scale differentiation to be expressed. Classifications based on morphology alone can thus reflect differences in perceived morphological complexity, not necessarily underlying biological relationships (Van Bocxlaer & Schultheiβ 2010).

Despite its widespread use in paleontology, and in the classifications of many extant taxa, shell morphology is often viewed as too “plastic” to be a reliable guide to phylogeny, presumably because the external shells of molluscs can be subject to strong environmental selection. However, this apparent plasticity is also due to the enthusiastic naming and description in early 18th and 19th century classifications of every different shell form encountered, however minor. In the 1980s many systematic revisions gloried in a wholesale collapse of these early over-inflated nomenclatures. Gould & Woodruff (1986), who dropped *Cerion* on New Providence Island from 71 “species” to “2 hybridizing semi-species”, quoted favourably Dall (1896) noting the original over-splitting based on shell characters to be “noxious and stupefying”.

However, both the over-splitting and the triumphant contractions are extremes, which malacologists today attempt to avoid by integrating morphological with molecular and ecological evidence in delimiting species, and by reducing the variability in morphological approaches by focussing on utilising as many quantifiable morphometric characters as possible. The New Zealand genus *Powelliphanta* has undergone the classification pendulum so common in molluscs, from Powell's expansive taxonomy in the 1930s and 1940s to the very sparse one of Climo (1978). This thesis attempts the modern integrative approach by increasing the range of morphological characters used in *Powelliphanta* classifications, describing each morphological character in numeric terms, and supplementing morphologic data with molecular and ecological information.

Species concepts used in this study

The unified species concept (de Queiroz 1998, 2007) is used here due to its focus on "*separately evolving lineages*" as assessed by general progression on many speciation fronts, rather than simply on indisputably achieving one or more of the contingent properties acquired by those lineages during divergence (e.g. either reproductive isolation, or diagnosability or monophyly) as older species concepts do. The unified species concept is particularly applicable because the main purpose of this examination of *Powelliphanta* is to look for evidence of genotypic and morphological clusters. Focussing only on a specific line of evidence such as monophyly in this group is unlikely to be successful in delineating species, as the radiation may be of comparatively recent origin (Fleming 1949), as is much of the diversity in the New Zealand flora and fauna (Trewick et al. 2007; Trewick 2008). Many lines of evidence will probably be needed for an understanding of *Powelliphanta* systematics as incomplete lineage sorting could be common, given that Pleistocene glacial cycling of barely 20,000 years ago has been suggested as the primary cause of the diversity in *Powelliphanta* (Powell 1949, Climo 1978). As it often takes millions of years for alleles from a common ancester to die out in a descendant species after a lineage split, it is likely not enough time has elapsed for gene trees to be identical to species trees.

Genotypic clusters are an updated version of Darwin's view of species as [morphologically] "distinguishable groups of individuals that have few or no intermediates when in contact" (Mallet 1995). Genotypic clusters are likewise distinguishable when there is a "deficit of intermediates at both single loci (heterozygote deficits) and at multiple loci" when two populations are being examined (Mallet 1995). It is of course much easier to apply these definitions to populations in contact, where any possible interaction can be seen and measured, yet many putative *Powelliphanta* species are allopatric. For Darwin when dealing with allopatric populations "*the opinion of naturalists having sound judgement and wide experience seems the only guide to follow*" (Darwin 1859). To try and limit unconscious (or conscious) bias that can operate when relying on expert opinion, set criteria will need to be met before a cluster can reasonably be considered a distinct taxon, particularly in the case of the early stages in divergence represented by intraspecific variation. However, it is recognized that systematics inevitably involves decisions by an individual taxonomist that might be made differently by another (Hey 2001).

Scope of the thesis

Powelliphanta is such a large genus that examining the case for each putative taxon, and formally describing in sufficient detail those which are distinct enough to warrant recognition, is not possible within the time and space constraints of a PhD. Accordingly, in this thesis I focus on establishing the genetic, morphological and ecological evidence supporting or rejecting existing or newly proposed (Walker 2003) species and subspecies, speculate on ways that diversity may have arisen, and describe one of the most endangered taxa—that from the Stockton coal mine—as a guide to how I will subsequently treat the remainder.

Thesis Outline

Excluding this introduction and the final synthesis, there are 4 stand-alone chapters forming the body of the thesis, 3 of them intended for publication, and the 4th has been published. This paper format means there is some repetition in both the introductory and reference sections of each chapter, though this has been avoided wherever possible. The thesis has a nested structure, moving from the broadest scale to the finest. It starts with an examination of the genetic relationship of *Powelliphanta* to presumed sister genera and looks at the pattern of neutral genetic variation across the whole genus. It then moves to a modern examination of morphological variation of the described or tag-named species in *Powelliphanta*, followed by a study of the nature of subspecies in *Powelliphanta* through detailed investigation of the intraspecific variation within one species, *P. lignaria*. Finally, *P. augusta*, the first species to be investigated using a combination of genetic, morphological and ecological evidence, is described.

In chapter 2 evidence of genotypic clusters in *Powelliphanta* is examined using 2 types of genetic data; allozymes to look indirectly at the nuclear genome, and the mitochondrial Cytochrome Oxidase subunit 1 gene, which is particularly useful for detecting species-level differences. The relationship of the Australian rhytidid genus *Victaphanta* to *Powelliphanta* is briefly examined using allozymes, as it was suggested on morphological grounds they may be sister taxa. The genetic relationship of the morphologically distinctive *Powelliphanta fiordlandica* to all other *Powelliphanta* is also explored, using both allozymes and mtDNA. Genotypic clusters in *Powelliphanta* are identified and possible reasons for the lack of resolution in south-western alpine clusters are suggested.

In chapter 3 the morphology of *Powelliphanta* is examined through analysis of shape, linear and area measures and categorical colour and pattern characters of the shell and soft body. It concludes with speculation about the origin of colour and pattern in the shells of *Powelliphanta*.

In chapter 4 the criteria to be met before subspecies status is conferred are described. The intraspecific diversity within *P. lignaria* is examined in detail and genetics, morphology, ecology and distribution are used to assess the validity of the seven previously-described subspecies.

In chapter 5 the first “modern” (ie comprehensive) description is made of a *Powelliphanta* species. The habitat which formerly supported *P. augusta* before it was lost to opencast coal mining is described in detail, along with the life history of the species as determined from salvaged snails kept in captivity.

In conclusion, the molecular, morphological, ecological and geographic information collected in this study is synthesized to produce a proposed classification.

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Chapter 2.

Phylogeography of *Powelliphanta*: genotypic clusters in a radiation of predatory landsnails

Image previous page: A distinctive but undescribed form of *Powelliphanta gilliesi*, tag-named "Iwituaroa" after its location in the headwaters of Moutere Stream in western Kahurangi National Park. Photographer Rod Morris.

Introduction

Giant carnivorous land snails in the genus *Powelliphanta*, endemic to New Zealand, display a great range of coloured and patterned shells within comparatively small geographic distances. The genetic basis of this diversity has become a matter of urgent conservation interest, as many forms occupy only small areas and so are particularly vulnerable to ongoing habitat loss. *Powelliphanta* are also susceptible to the exotic predators which relatively late human settlement of New Zealand brought, with most taxa now considered threatened and declining (Hitchmough et al. 2007). With these strong pressures, and funds for biodiversity conservation scarce, it has become important to see how much of the genetic diversity in *Powelliphanta* has been recognized and protected within the current morphologically-based classification.

Powelliphanta O'Connor, 1945 belongs to the carnivorous southern hemisphere family Rhytididae Pilsbry, 1893, which has a South African, Australasian–Austronesian distribution (Herbert & Moussalli 2010). Though briefly classified in the northern European genus *Helix* Linnaeus, 1758, the large New Zealand rhytidids were subsequently all placed in the endemic genus *Paryphanta* Albers, 1850. However, for a long period from the mid 1900's it was recognized, though unpublished, that the plain dark green *Paryphanta* snails of northern New Zealand were distinct from the brightly coloured and patterned southern *Paryphanta* (*Powelliphanta*) snails, with the only obvious character in common their large size (Climo 1977). Using strong anatomical differences, particularly in reproductive anatomy, they were each elevated to generic status by Climo in 1977.

AWB Powell, after whom the genus is named, described 10 species and 27 subspecies in a classification based largely on detailed examination of shell size, colour and pattern (Powell 1930, 1932, 1936, 1938, 1946, 1949). His field studies found intense localization of *Powelliphanta*, "with colour forms constant within their respective distributional areas which are segregated by definite topographical boundaries" (Powell 1936). He gave sub-specific status to what he considered the most significant of those forms, noting their value in determining modes of speciation and in answering questions as to how geographic barriers shaped the intra-specific variation present (Powell 1930, 1936, 1947). Using general shell similarities Climo (1978) proposed an alternative classification comprising a ring species with only one or two species and five subspecies, but this was contentious (Parkinson 1979), and failed to gain acceptance (Powell 1979, Walker 2003). While their approaches led Powell and Climo to very different inferences about the taxonomic diversity in *Powelliphanta*, a modern approach focusses on mixed evidence for genotypic clusters (Mallet 1995). This has the advantage that attention is given to agreement amongst a variety of data types, and consistency with an evolutionary framework. To this end, both nuclear-based allozymes and mitochondrial DNA are used here to assess the monophyly of *Powelliphanta,* and to examine any genetic clustering within the genus, while the following chapter examines morphological clustering.

Several aspects of the biology of *Powelliphanta* are likely to be having a large impact on their genetic structure: they are hermaphrodites who routinely cross-fertilize but are probably capable of self-fertilization or sperm storage as they continue to lay fertile eggs years after being kept in isolation (Walker et al. 2008); they are predators, and therefore live at relatively low densities; and they are relatively sedentary and have specific habitat requirements so their distribution within a diverse landscape tends to be patchy (Walker 2003).

Methods

Material examined

Tissue samples were taken from live snails in at least one population of each of Powell's species, subspecies, and forms (Powell 1979), and from other populations that might represent new taxa (Walker 2003) (Table 1). Collection sites represent the distribution of *Powelliphanta* diversity (Figure 1). In addition, as Smith (1968) and Climo (1977) had suggested on the basis of reproductive anatomy that *Victaphanta* was sister to *Powelliphanta,* 4 species of the Australian rhytidid genus *Victaphanta* Iredale, 1933 and several New Zealand rhytidids from the genera *Wainuia*, *Rhytida* and *Paryphanta* were used as outgroups in both the allozyme and mtDNA studies (Table 2), including some published (Spencer et al. 2006) mitochondrial sequences from GenBank. Tissue samples collected between 1987 and 2002 for allozyme study were from common species and comprised whole animals, killed by freezing. The soft parts of these snails were removed and held at $^{-}80^{0}$C while the shells were stored dry at ambient temperatures. Initially 6—10 individuals were collected from each location, but allozyme diversity within populations was found to be low, so only 1—3 individuals were subsequently collected from each site. During 2004—2013 tissue sampling was extended to rare or threatened *Powelliphanta.*

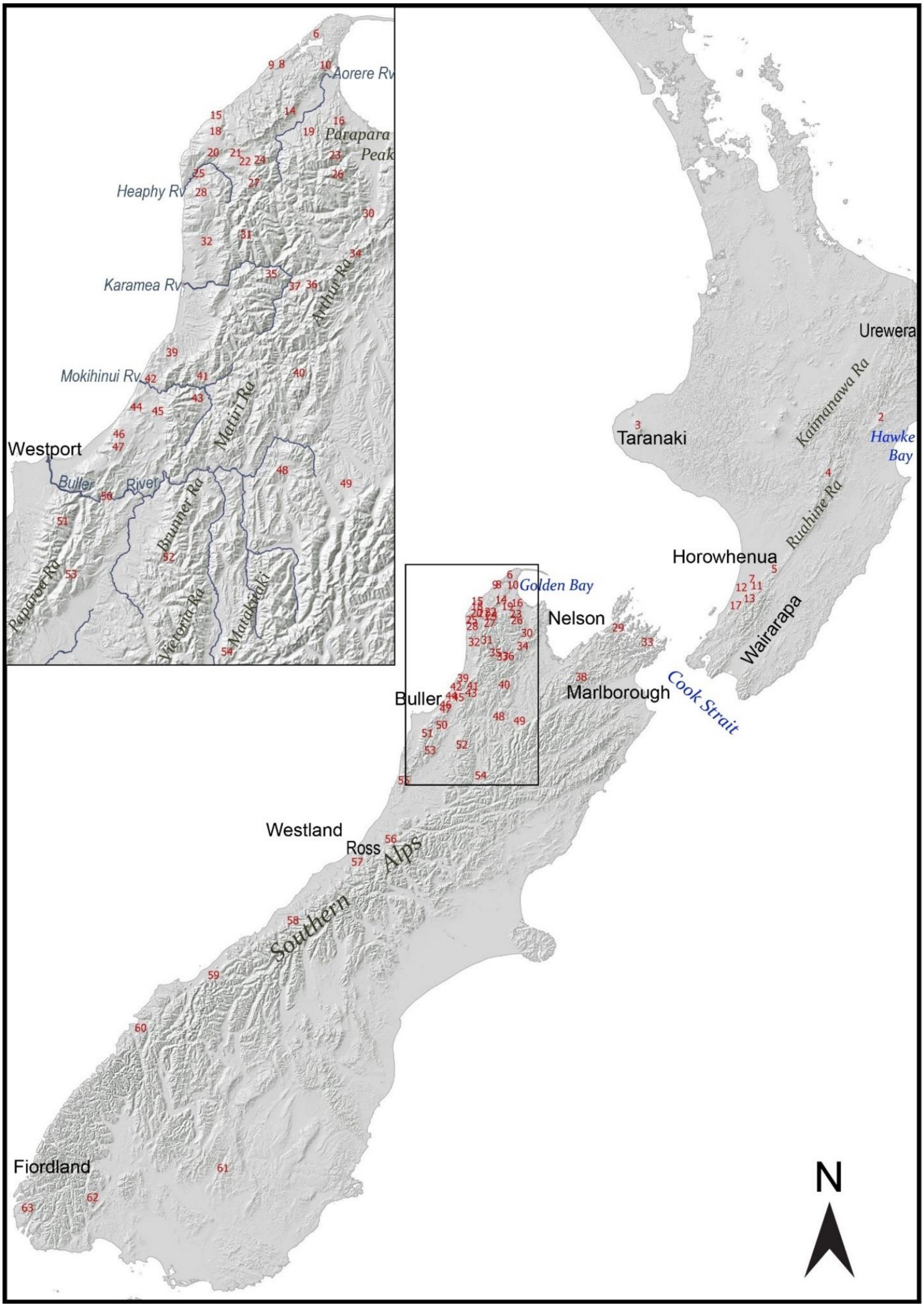

Figure 1. Places mentioned in the text and the averaged location of genetic sample collections (see Table 1 for the specific site names, and the number and types of samples collected at each site).

Table 1. Sampling of *Powelliphanta* for genetic analysis. Numbers of individuals of each named species (Powell 1979) and tag-named population (Walker 2003) that provided nuclear (allozymes) and mitochondrial DNA. Sampling locations are numbered and mapped in Figure 1.

Taxon	**Genotype cluster**	**Location**	***N* allozyme**	***N mtDNA***	***N* sites**	**Map ID**
P. annectens	*superba*	Oparara Valley, Karamea	5	3	1	32
P. augusta	*augusta*	Mt Augustus, Stockton Plateau	0	43	2	46
P. fiordlandica	*fiordlandica*	Kakapo Range & Resolution Id, Fiordland	5	2	2	63
P. fletcheri	*fletcheri*	Mt Tuhua, mid Westland	5	4	1	56
P. gagei	*gagei*	Croesus Knob - Mt Davy, south Paparoa Rng	4	8	4	55
P. gilliesi gilliesi	*gilliesi*	Mt Burnett, Wakamarama Range	5	5	1	10
P. gilliesi aurea	*gilliesi*	Maungarakau Scenic Reserve	5	5	1	8
P. gilliesi brunnea	*gilliesi*	Paturau River mouth	0	5	1	9
P. gilliesi compta	*gilliesi*	The Castles & Moonlight Flat, Aorere Valley	1	5	2	19
P. gilliesi fallax	*gilliesi*	Pupu Rv - Parapara Inlet	8	9	3	16
P. gilliesi jamesoni	*gilliesi*	Gouland Downs, Heaphy Track	6	6	2	22
P. gilliesi kahurangica	*gilliesi*	Kahurangi Point	5	6	1	15
P. gilliesi montana	*gilliesi*	Bock Peak, Wakamarama Range	1	5	1	14
P. gilliesi subfusca	*gilliesi*	Kaihoka Lakes, Golden Bay	3	3	1	6
“Haidinger”	*gilliesi*	Mt Haidinger, Wakamarama Range	0	4	1	N/A
“Heaphy”	*gilliesi*	Gunner River, Heaphy Valley	1	1	1	25
P. hochstetteri hochstetteri	*hochstetteri*	Canaan & Flora Stm, Arthur Range	4	4	2	30
P. hochstetteri anatokiensis	*hochstetteri*	Parapara Peak - Walker Ridge & Anatoki Forks, Golden Bay	7	12	4	23
P. hochstetteri bicolor	*hochstetteri*	Blumine Id, Mt Stokes & Curious Cove Marlborough Sounds	5	10	3	33
P. hochstetteri consobrina	*hochstetteri*	Mt Maungatapu & Mt Fell, Richmond Ranges	1	5	2	38
P. hochstetteri obscura	*hochstetteri*	D’Urville Id, Editor Hill & Maud Id, Marlborough Sounds	1	4	3	29
P. lignaria lignaria	*lignaria*	Gentle Annie Pt, Karamea Bluff, Sawyers Ck, Mokihinui mth	5	10	4	42
P. lignaria johnstoni	*lignaria*	Upper & mid-Charming Ck, & mouth Ngakawau Rv.	5	12	3	44
P. lignaria lusca	*lignaria*	Mouth & mid Glasseye Ck, Lake Hanlon, Four Mile Ck mth	5	13	4	39
P. lignaria oconnori	*lignaria*	Wilkinson Track & Slippery Ck, Karamea Rv, Kahurangi NP	1	2	2	37
P. lignaria rotella	*lignaria*	St Andrews Stm & State Mine Hill, Mokihinui,, Seddonville	5	6	2	45
P. lignaria ruforadiata	*lignaria*	Maori Gully & Pakihi Ck, TL Mokihinui River	1	8	2	41
P. lignaria unicolorata	*lignaria*	Mokihinui Rv: mouth of Gorge, Forks, Sth Branch (Goat Ck)	2	8	3	43
P. marchanti	*hochstetteri*	Ruahine, Kaimanawa & Kaweka Ranges	1	11	3	4
P. patrickensis	“Kawatiri”	Stockton–Denniston Plateaux	6	58	11	47
P. rossiana rossiana	*rossiana*	Mt Rangitoto	0	2	1	57
“Fox”	*rossiana*	Mt Fox, Fox Glacier	5	4	1	58
“Haast”	*rossiana*	Mark Range, Haast	8	8	1	59
P. spedeni spedeni	*spedeni*	Argyle Burn, Umbrella Mtns, Southland	5	4	1	61
P. spedeni lateumbilicata	*spedeni*	Green Lake Track, Lake Monowai	5	5	1	62
P. superba superba	*superba*	Cedar Rdge & Haupiri Ra (E Aorere); Bock Peak (W Aorere)	4	6	3	31
P. superba harveyi	*superba*	Mackay Hut, Heaphy Track	4	3	1	20
P. superba mouatae	*superba*	Saxon Rv, Heaphy Track	5	4	2	21
P. superba prouseorum	*superba*	upper Moutere Rv, Mackay Downs, Heaphy Track	1	4	2	18
P. superba richardsoni	*superba*	Perry Saddle, Gouland Range	5	4	1	24
“Gouland Range”	*superba*	Mt Goul, Gouland Range	1	1	1	27
“Gunner River”	*superba*	Gunner Downs & Gunner Rv, Heaphy Valley	1	2	2	28
P. traversi traversi	*hochstetteri*	Lake Papaitonga, Manawatu	5	8	1	12
P. traversi florida	*hochstetteri*	Kimberley SR, Manawatu	2	1	1	13
P. traversi koputaroa	*hochstetteri*	Koputaroa, Manawatu	0	6	1	7
P. traversi latizona	*hochstetteri*	Greenaway’s Bush, mid & nth Shannon Heights, Manawatu	5	10	3	11
P. traversi otakia	*hochstetteri*	Rahui Rd & Hutton’s Bush, Otaki	0	9	2	17
P. traversi tararuaensis	*hochstetteri*	Kahuterawa Stream, Palmerston North	5	5	1	5
“Egmont”	*hochstetteri*	Mt Taranaki	4	7	2	3
“Maungaharuru”	*hochstetteri*	Taraponui & Cashes Bush, Maungaharuru Range	1	5	2	2
“Urewera”	*hochstetteri*	Mt Manuoha, Urewera National Park	5	5	1	1
“Buller River”	“Kawatiri”	Berlin’s Bluff & Ten Mile Ck, Buller Gorge	5	7	2	50
“Baton”	“Kawatiri”	Baton Saddle, Arthur Range	3	2	1	36
“Garabaldi”	“Kawatiri”	Garabaldi Plateau, Kahurangi NP	4	3	1	35
“Matiri”	“Kawatiri”	Matiri Plateau, Braeburn Tops & Nardoo, Buller	3	7	3	48
“Matakitaki”	“Kawatiri”	Baldy, Springs Junction	4	4	1	54
. “North Paparoas”	“Kawatiri”	Buckland Peaks, Three Sisters, Mt Bovis	0	10	3	51
“East Paparoas”	“Kawatiri”	Mts Epping-McHardy, North Brunner Range	0	5	4	53
“Kirwin’s”	“Kawatiri”	Kirwin’s Hill & South Brunner Range	4	6	3	52
“Anatoki Range”	“alpine”	Anatoki Peak, Golden Bay	4	4	1	26
“Lodestone”	“alpine”	Mt Lodestone, Arthur Range	4	3	1	34
“Owen”	“alpine”	Billie’s Knob, Mt Owen	5	5	1	40
“Nelson Lakes”	“alpine”	Mt Murchison, Mt Robert & St Arnaud Ranges	3	6	3	49
“vitattus”	“vittatus”	Yates Pt & Haast Range, Northern Fiordland	5	7	2	60
TOTALS			**219**	**449**	140	

Table 2. Number of *Victaphanta*, *Wainuia*, *Rhytida* and *Paryphanta* individuals collected whose nuclear (allozymes) or mitochondrial DNA were examined, and the location of those collecting sites.

Taxon	**Location**	***N* allozyme**	***N* mtDNA**	***N* sites**
Paryphanta busbyi busbyi	Whangaruru	3	1	1
Wainuia urnula urnula	Otaki Forks, west Tararua Ranges	3	3	1
Rhytida greenwoodi greenwoodi	Matai Flat, Clarence Rv, Marlborough	1	1	1
Victaphanta lampra	Scotsdale, NE Tasmania	4	1	1
Victaphanta milligani	NW Tasmania	4		1
Victaphanta compacta	Marts Rest, Otway Ranges, Victoria, Australia	4	4	1
Victaphanta atramentaria	Gentle Annie camp, West Gippsland, Victoria	4	1	1
TOTALS		**28**	**11**	**10**

populations for mitochondrial DNA study using biopsies from live snails in the wild (Trewick *et al.* 2008).

Allozyme electrophoresis

Samples of foot muscle and digestive gland were dissected out of thawed snails, homogenised with an equal volume of water, and subjected to horizontal 12% Sigma starch-gel electrophoresis (Allendorf et al. 1977, Selander et al. 1991). Samples were tested on all combinations of four buffers and 24 enzyme-specific stains and a subset which produced consistent results was used for this study (Table 3). Stained gels were scored immediately by eye and photographed for later re-examination and independent assessment of alleles. Line-up gels were used to confirm allele identity among populations.

The number of genetically distinct clusters within the *Powelliphanta* genotypes was assessed without priors using a Bayesian assignment approach implemented in the programme STRUCTURE v.2.3.3 (Pritchard et al. 2000). This assigns individuals probabilistically to genetic clusters (K) by calculating membership coefficients per individual per cluster (Q). Support for potential hypothetical clusters (K) between 10 and 20 was searched for in separate runs with 10 iterations of each. The clusters consistently identified in this process—some of which had formal names and some to which tag-names were applied—were then used as "populations" in subsequent genetic diversity comparisons and analyses (Table 1).

The APE package (Paradis et al. 2004) in R (R core team 2015) was used to calculate allele frequencies, genetic distances, and diversity and to construct Neighbour Joining trees. Nei's (1978) unbiased genetic distance (D), Rogers (Wright, 1978) modified genetic distance (R) and Cavalli-Sforza & Edwards (1967) arc distance were calculated to evaluate their influence on tree topologies. To test whether input order affected tree topology as can occur from "ties" in the distance matrix (Farris et al 1996), data were randomly re-ordered 100 times and compared. To test for long-branch attraction, genotypes associated with long branches were temporarily removed and the dataset reanalysed to identify changes in topology. The number of fixed differences between each pair of populations was determined by direct count. To compare genetic diversity among species, genotype scores were pooled from all populations within each described or presumed species and estimated overall species-level values of allelic richness (A_r) and observed and expected heterozygosity (H_e & H_r) were made. Intraspecific distances were estimated by calculating F_{ST} between each pair of populations.

Table 3. Enzymes assayed and loci scored in this study, and the tissues and buffer conditions which allowed the clearest discrimination of each loci. The Est-2 loci was not consistently scorable and was left out of the final analysis

EC number	Enzyme/protein	Loci scored	Tissue	Buffer
3.1.3.2	Acid cell phosphatase	ACP-1	Digestive gland	AC
		ACP-2	Digestive gland	AC
3.1.3.1	Alkaline phosphatase	ALP-1	Digestive gland	PK
		ALP-2	Digestive gland	PK
3.2.1.23	*B*-Galactosidase	B-Gal	Digestive gland	RW
3.1.1.1	Esterase	EST-1	Foot muscle	AC
3.1.1.1	Esterase	EST-2	Digestive gland	RW
2.6.1.1	Glutamate oxaloacetate transamihase	GOT-1	Digestive gland	AC
		GOT-2	Digestive gland	AC
5.3.1.9	Glucose-phosphate isomerase	GPI	Foot muscle	RW
1.1.1.42	Isocitrate dehydrogenase	IDH-1	Digestive gland	PH
		IDH-2	Digestive gland	PH
1.1.1.27	Lactate dehydrogenase	LDH	Digestive gland	PK
1.1.1.37	Malate dehydrogenase	MDH-1	Foot muscle	AC
		MDH-2	Foot muscle	AC
		MDH-3	Foot muscle	AC
3.4.11	Peptidase	PEP-1	Foot muscle	RW
		PEP-2	Foot muscle	RW
2.7.5.3	Phosphoglucomutase	PGM	Digestive gland	PK

Buffer

AC	Acid: Citric acid 16.8; pH 6.1
PK	Poulik: Tris 18.42, Citric acid 2.1; pH 8.7
RW	Ridgeway: Tris 7.27, Citric acid 2.10: pH 8.5
PH	Phosphate: KH_2PO_4 37.56, NaOH 4.96; pH 6.7

Mitochondrial DNA

Genomic DNA was extracted using incubation at 55°C with Proteinase K and a CTAB buffer (2% Hexadecyltrimethylammonium bromide, 100 mM Tris-HCl pH 8.0, 1.4 M NaCl, 20 mM EDTA), followed by a combined phenol-chloroform-isoamyl alcohol (25: 24: 1) cleanup based on previously described methods (Thomaz et al. 1996; Stine 1989; Terrett 1992). Extracted DNA was re-suspended in TE buffer (10 mM Tris, 0.1 mM EDTA) or water. Several primer combinations were trialled but the most reliable amplification over all samples was obtained using two pairs of primers that target part of the mitochondrial Cytochrome Oxidase subunit I gene (COI) using primers 1490 and 2198 for COI (Folmer et al. 1994).

Polymerase chain reactions were performed in 10 µl volumes with Red Hot® Taq polymerase under the cycling conditions: initial denaturation at 94°C for 2 min, followed by 35 cycles of 94°C for 30 sec, annealing at 50°C for 30 sec, extension at 72°C for 45 sec, with a final extension at 72°C for 3 min. PCR products were purified using SAP/EXO (Shrimp Alkaline Phosphatase/Exonuclease) enzymatic digest (USB corporation), and cycle sequenced using Perkin Elmer Bigdye® chemistry following the manufacturer's protocols, and read on a ABI ABI3730 genetic analyzer. Sequences were checked, trimmed, and aligned using GENEIOUS v 6.1.7 (Biomatters Ltd).

Three overlapping datasets were used in the analysis as follows: (1) the full ingroup of 424 individual *Powelliphanta* whose sequence lengths varied between 500 and 850 bp (2) a subset of 86 representatives of each described or tag-named *Powelliphanta* from the full ingroup, selected for relatively long sequence length (15 snails = 625 bp, 61 snails = 738 bp, 10 snails = 810 bp) and (3) 49 of the 86 *Powelliphanta* from the group above with sequence lengths of 738 bp, plus 11 out-group rhytidids with sequence lengths of either 820 or 912 bp. The phylogenetic analyses were performed with APE (Paradis et al. 2004) and PHANGORN (Schliep 2011) in R (R core team 2016) for Maximum Likelihood (ML) searches and bootstrapping, whereas MrBayes (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003) was used for Markov-chain Monte-Carlo (MCMC) Bayesian analysis. For visualization purposes, the outgroup was defined in the first and second datasets as *Powelliphanta fiordlandica* and in the third dataset as *Victaphanta compacta*. The model of sequence evolution was selected using Modeltest (Posada and Crandall, 1998) with the ML tree for dataset 2 constructed using GTR+G+I corrected distances, while that for dataset 3 used

HKY+G+I. Bootstrap support for each node was assessed using 100 replicates under ML optimality criteria, implemented in Phangorn for dataset 2 and Geneious for dataset 3. Bayesian analyses used the same evolutionary models as in ML for each dataset, with gamma distributed rate variation across sites (with 4 categories), a proportion of invariant sites and default priors. Each analysis of 105 generations used two independent simultaneous runs with 2 heated chains and a sample frequency of 100 generations. For burnin, 25,000 samples were discarded.

Results

In total, allozymes of 219 *Powelliphanta* snails were examined, and part of the mitochondrial CO1 gene in 449 snails was sequenced. A large number of sequences (93) represented just two taxa suffering extensive habitat loss—58 *P. patrickensis* and 41 *P. augusta* (Table 1). Of the 476 individuals from which some form of molecular data was obtained, 196 individuals had both nuclear-based allozymes and mitochondrial DNA data available for analysis.

Allozyme variation in putative outgroup

Consistent results were obtained from 10 loci. At five of these, all *Rhytida* samples lacked information, and at one all *Wainuia*, *Paryphanta* and *Victaphanta* samples lacked information. All outgroup taxa differed at every scorable locus and were unscorable at several loci where *Powelliphanta* are readily scorable, indicating that relationships are very distant. Allozyme electrophoresis is therefore not an optimal tool for examining the deeper relationships within the former Paryphantididae, however the analyses confirmed that *Victaphanta* and *Wainuia* are sister to *Powelliphanta.*

Due to uncertainty that homologous loci were being scored, *Victaphanta* samples were subsequently scored independently of *Powelliphanta*. Six of the 8 loci which could be reliably scored were found to be polymorphic. All individuals from the 4 populations of *Victaphanta* were genetically identical to the other individuals at the same location, and no heterozygosity was detected. The 4 species of *Victaphanta* examined were each genetically distinctive, particularly *V. lampra* which had 3 private alleles. The two species endemic to Tasmania, *V. lampra* and *V. milligani*, were separated by 3 fixed differences from each other while the 2 species endemic to Victoria, *V. compacta* and *V. atramentaria* were separated by 2 fixed differences from each other. The 2 Tasmanian species were separated from the 2 Victorian species by 3 fixed differences (Table 4).

Table 4. Genetic distance within the Australian genus *Victaphanta*, with Nei's (1978) uncorrected genetic distance above the diagonal and the number of fixed differences below it.

Species	*V. lampra*	*V. milligani*	*V. compacta*	*V. atramentaria*
V. lampra	******	0.470	0.981	1.386
V. milligani	3	******	0.470	0.981
V. compacta	5	3	******	0.288
V. atramentaria	6	5	2	******

Allozyme variation in Powelliphanta

Information was obtained for 19 loci from 64 populations. Two of the loci, ALP-2 and B-Gal, were monomorphic and provided no useful data for taxon differentiation. Several samples lacked information for several of the loci, and a few populations were represented by single individuals. Where these sampling deficiencies coincided, calculation of genetic distance was not possible and some samples were discarded at the outset. In total 16 variable loci from 210 individual snails in 54 populations were available, but this was reduced further to 168 individuals and 51 populations for genetic distance estimates and tree building, both to make tree-size more manageable and to remove all individuals with missing data, as gaps were found to produce ambiguous population assignments.

The allozyme data showed some evidence of saturation, with too few loci scored to adequately separate those taxa with some to many fixed differences from those which clearly had a high frequency of fixed differences. Conversely in a few taxa sample size was inadequate to capture rare alleles, resulting in a slight inflation of the number of fixed differences. The first deficiency probably only dampened a little the scale of the distinctiveness of *P. fiordlandica*, while the second only slightly enhanced the extent of fixed differences in a few subspecies (identified in Appendix 1).

Allozyme markers displayed moderate levels of polymorphism with 2–10 alleles per locus for a total of 76 variable alleles. Most species and many subspecies recognized à priori were separated by loci fixed for different alleles (Appendix 1). Most individuals from the same population were genetically very similar to each other, and there was markedly low heterozygosity; of the 3702 genotypes encountered across all loci, only 169 (5%) were heterozygotes (Appendix 2).

Genetic diversity within species is summarized in Table 5. Sample sizes for many species were too small for high confidence in these estimates, but though they are not ideal, they are included as the best available in otherwise unknown threatened species, as recommended by Pruett & Winker (2008).

In almost all cases observed heterozygosity was lower than expected, with only "Parapara" (*fallax*) and "vitattus" exceeding that expected. Estimates of allelic diversity in *P. lignaria* from allozyme markers were lower than those recorded in *P. lignaria* from microsatellite markers (Buckley et al. 2014), unsurprisingly given the latter's much faster mutation rate.

Table 5. Summary statistics for 16 allozyme loci in 9 described and 11 potential species

	N	N_a	A_r	H_o	H_e
P. hochstetteri	13.4	1.4	1.2	0.05	0.15
P. traversi	9	1.2	1.1	0.04	0.13
"Urewera"	2	1.1	1.1	0.03	0.09
"Egmont"	3.9	1	1	0	0
P. gilliesi	24.2	1.6	1.1	0.03	0.10
"Parapara"	2.8	1.3	1.1	0.15	0.12
"Anatoki Range"	3	1.1	1.0	0.04	0.04
"alpine"	5.7	1.6	1.2	0.02	0.19
P. superba	17.9	1.5	1.1	0.04	0.09
P. annectens	4.7	1.4	1.1	0.10	0.14
P. lignaria	12.6	1.4	1.1	0.04	0.12
"Buller River"	4.5	1.1	1.1	0.05	0.05
"Kawatiri"	14.4	1.6	1.2	0.03	0.18
" Matiri"	5.8	1.3	1.1	0.03	0.09
P. fletcheri	4.8	1.1	1.0	0.01	0.03
P. gagei	4.8	1.2	1.1	0.04	0.07
P. rossiana	8.3	1.3	1.1	0.03	0.13
"vittatus"	5	1.1	1.1	0.08	0.04
P. spedeni	10	1.1	1.0	0.03	0.04
P. fiordlandica	2	1.1	1.1	0.06	0.05

N = mean number of individuals genotyped, N_a = mean number of alleles per locus, A_r = allelic richness, H_o = expected heterozygosity, H_e = observed heterozygosity

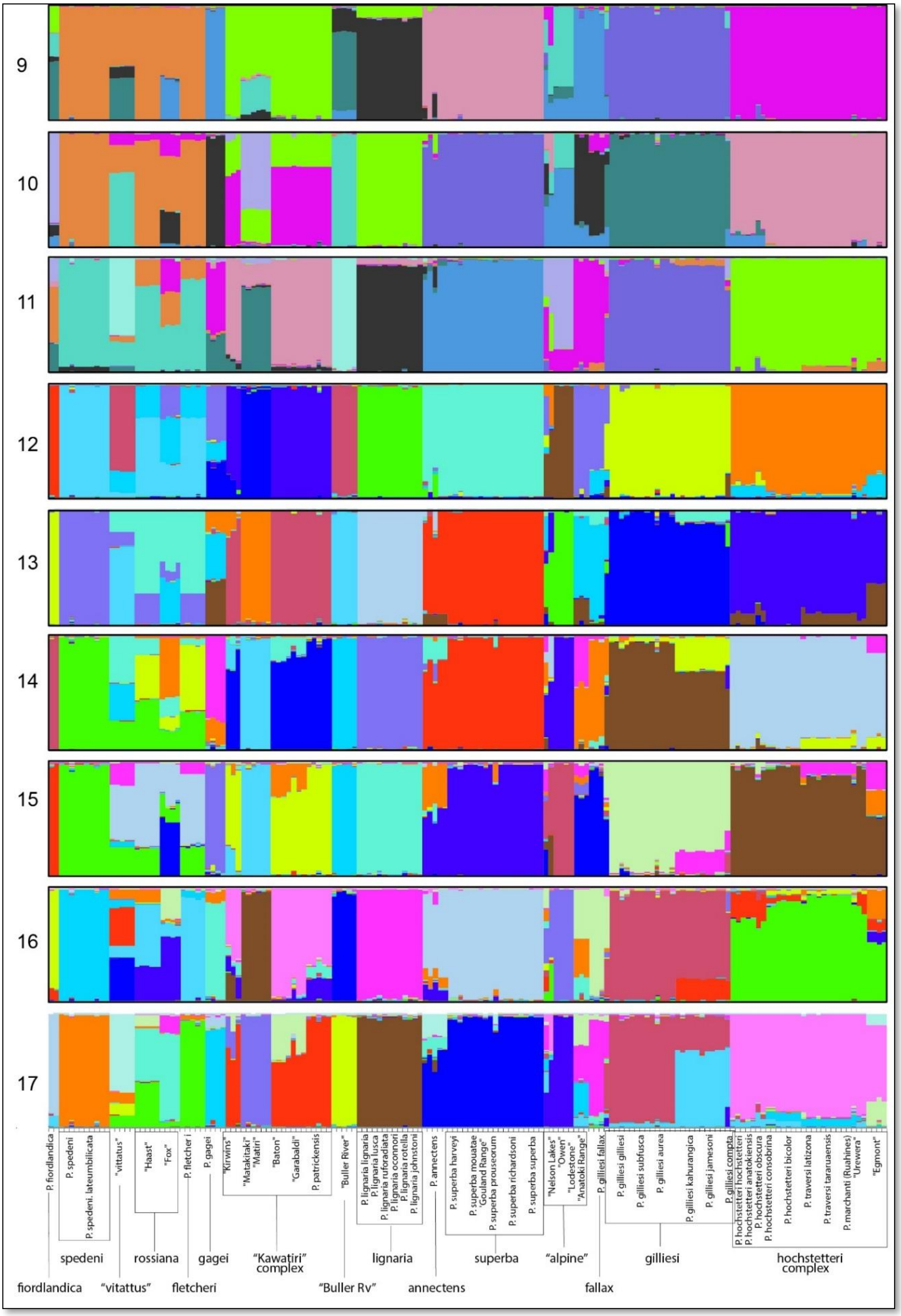

Figure 2. Proportional membership of 166 *Powelliphanta* to genetic clusters (K) as estimated using STRUCTURE when K=9 to K=17. Each vertical bar represents a single individual and individuals are ordered by name or sampling location.

Evidence for at least 17 genetically distinct groups (Figure 2) was inferred from the Bayesian assignments of individual genotypes from STRUCTURE. Genetic assignments corresponded well with geographic sampling location. Thereafter, these 17 groups were identified by name if previously described, or by tag-name or geographic location. To facilitate easy reference to related clusters, an unofficial tag-name of "Kawatiri complex" was used to indicate all montane snails in the Buller region, and "alpine" to indicate all alpine snails in the Nelson region.

Mitochondrial DNA variation

MtDNA sequences were obtained from *Powelliphanta* snails representing 42 described and 22 undescribed taxa. Sequence lengths varied so subsets of the data were subjected to different types of phylogenetic analyses. As the subsets were found to vary from the full dataset only in minor aspects of terminal tip branch length, only results from the smaller representative dataset are described.

Maximum Likelihood and Bayesian analysis

Relatively long CO1 sequences from 49 ingroup *Powelliphanta* and 11 outgroup taxa were initially analysed revealing strong support for *Powelliphanta* as a monophyletic group (Figure 3). Subsequently COI sequences from 86 *Powelliphanta* representing each described or putative taxa were analysed, with 13 main clusters supported in all ML and Bayesian trees. These were *P. fiordlandica,* "vittatus", *P superba/annectens, P. lignaria, P. augusta, P. gagei, P. fletcheri,* the "Kawatiri" complex, the *rossiana* complex, *P. spedeni, P. gilliesi,* "alpine" and the *hochstetter*i complex (Figure 4). Maximum likelihood and Bayesian phylogenies produced from this representative mtDNA dataset were assessed and later visually compared with that produced by Neighbour-Joining analyses of the allozyme dataset (Figure 5). Tree topology was generally concordant among analyses, and those relationships which differed were only in those areas where neither ML or BI provided strong support for any particular relationship. Most discordant was “vittatus”, placed on a long branch of its own in maximum likelihood analyses and with the globose southern species of *Powelliphanta* (*rossiana*, *spedeni, superba* and *lignaria*) in Bayesian analyses. Both placements received low support, but the latter is more likely to be correct as the dataset of the former comprised a greater proportion of relatively short sequences (to ensure all putative taxa were included). Notably, neighbour-joining analyses of nuclear markers also placed “vittatus” with other small rounded southern *Powelliphanta* (Figure 5).

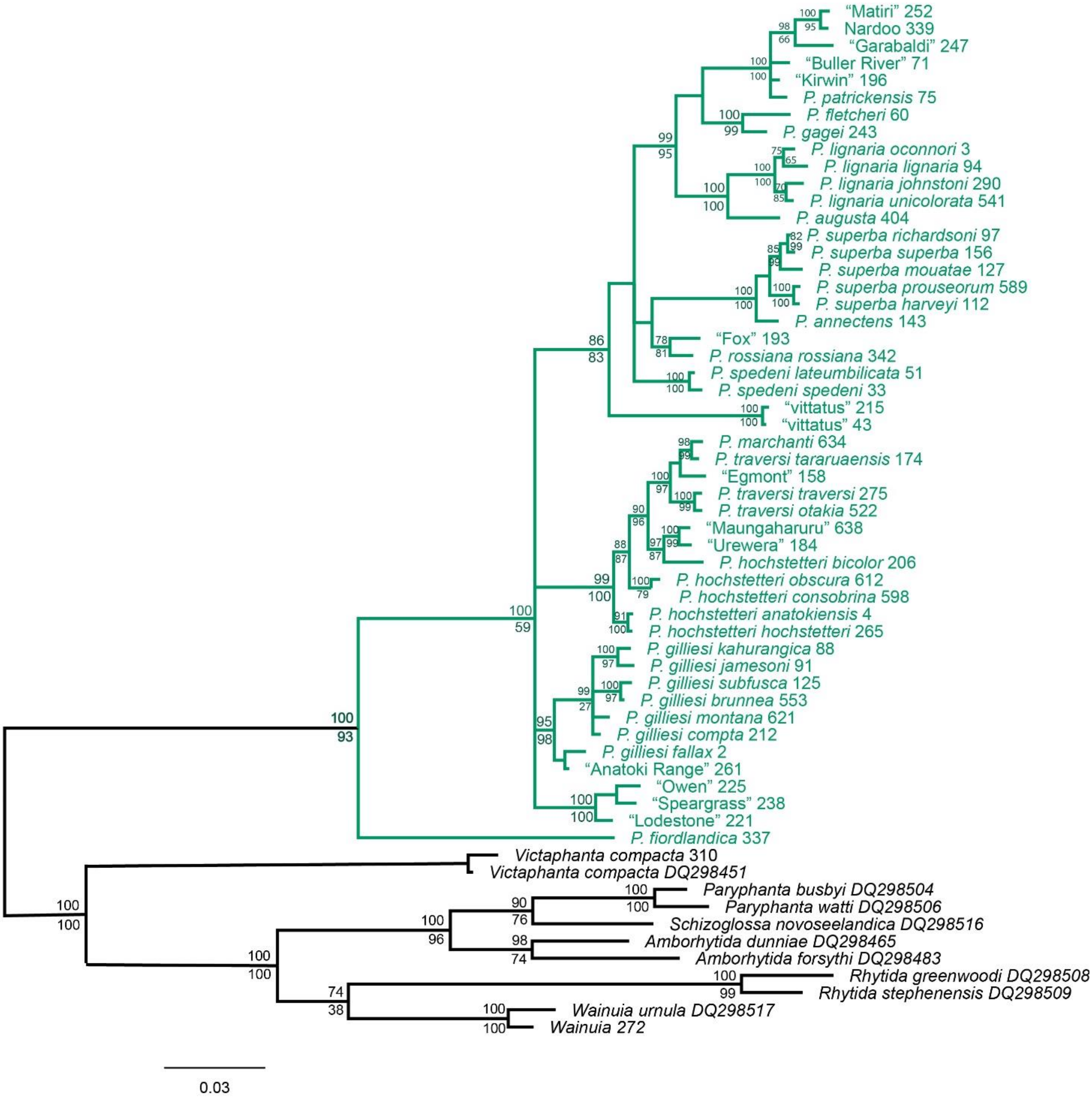

Figure 3. Evolutionary hypothesis from a Bayesian analysis of mtDNA CO1 sequences of 730 bp length from 49 *Powelliphanta* snails and of 810 and 910 bp length from 11 outgroup rhytidids. Posterior probabilities are shown above the nodes and maximum-likelihood bootstrap support values below. Numbers after taxon names are sample codes and alpha numerics are Genbank ascession numbers.

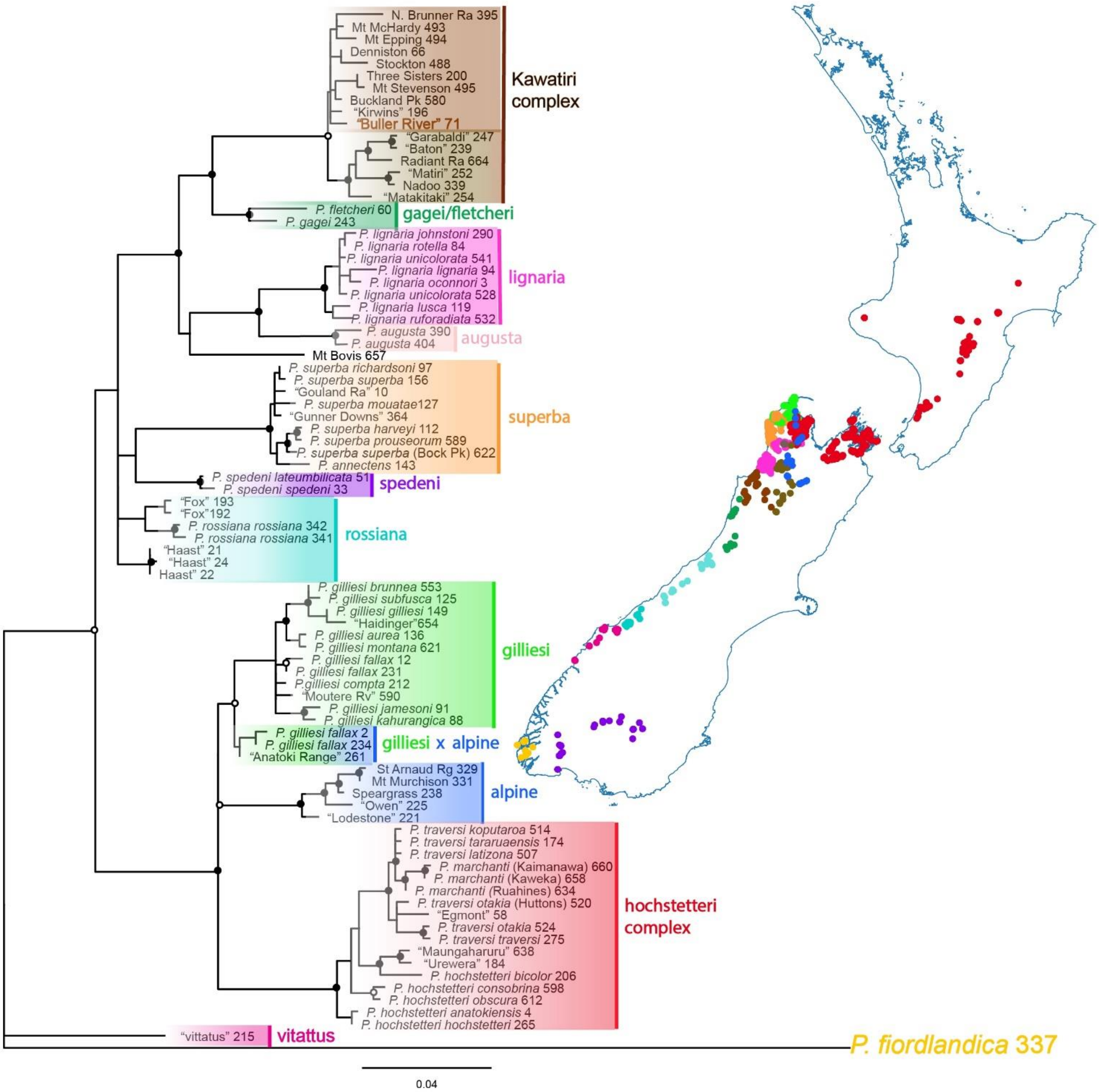

Figure 4. Evolutionary hypothesis from a maximum-likelihood analysis of 86 mtDNA CO1 sequences (61 of them 738 bp long, 10 of them 810 bp long and 15 of them 625 bp long) from *Powelliphanta* snails. A solid black circle indicates nodal support values greater than 90% for ML bootstraps and greater than 0.95 for BI posterior probabilities. An empty circle represents significant BI support (>0.95) but mediocre (<90%) bootstrap support. The distribution of *Powelliphanta* snails in the North and South Islands of New Zealand are colour-coded according to the clade they fall within. The number following each taxon name is each individual's unique sample code.

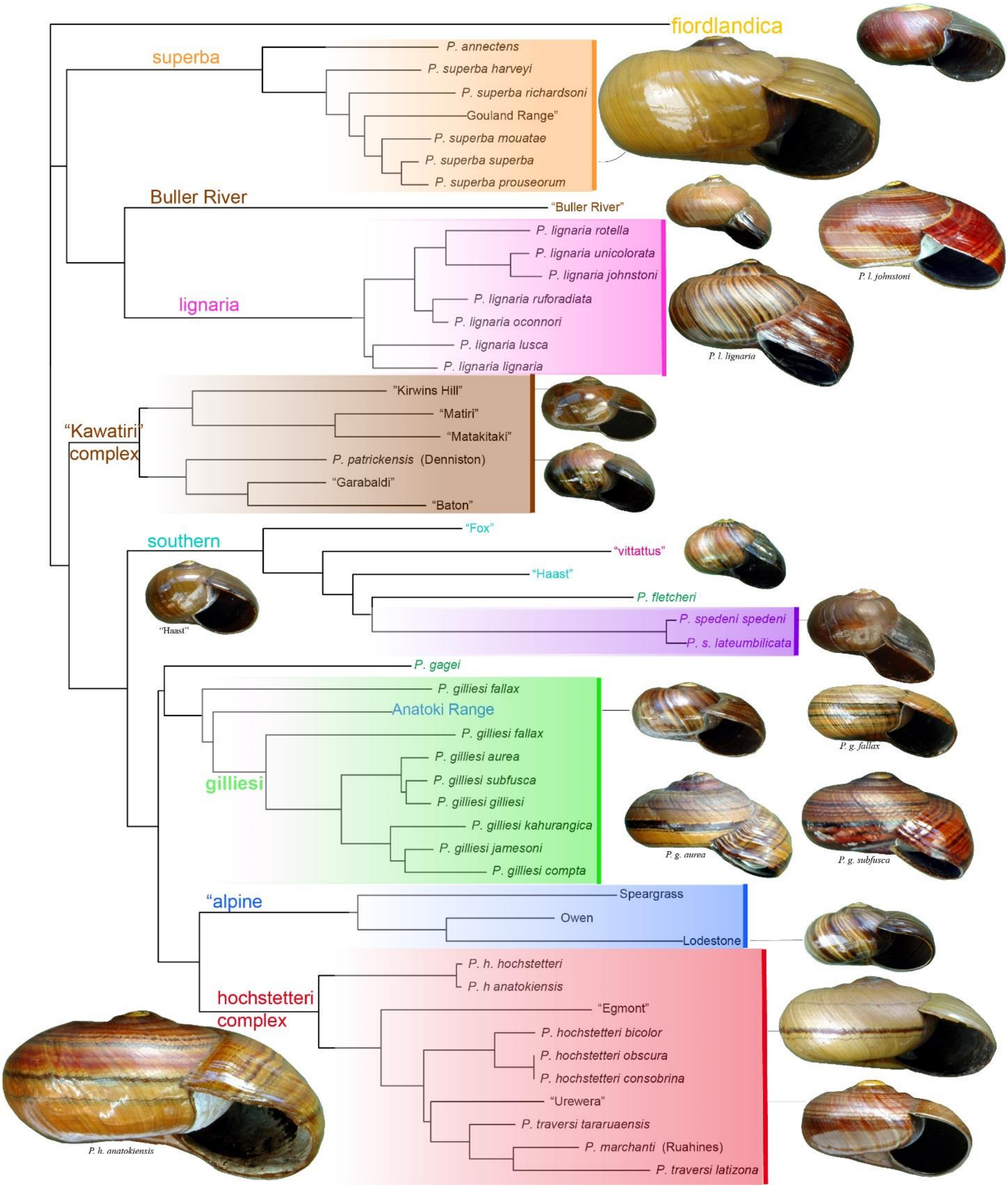

Figure 5. Neighbour-joining phenogram using Rogers (Wright 1978) modified genetic distance from 16 allozyme loci for 51 described or tag-named groups of *Powelliphanta.* The relative size and shape of snails in each clade is illustrated by a shell from at least one taxon within the clade, positioned immediately adjacent to the clade and labelled when more than one taxon is present. The geographic location of clades can be found by matching their colour-codes with that used in Figure 4. For sample sizes for each taxon, see Table 1.

Genotypic clusters within Powelliphanta

Allozyme and mtDNA data were consistent (Figures 4 & 5) in their support of the major groups within *Powelliphanta*, several of which were divided into distinct lineages. Most (8 of the 9 known at the time) of Powell's species names correlated with genetic clusters. There were 3 major divisions (1) the morphologically highly distinctive ***P. fiordlandica*** (2) the **northern** spirally striped and flattened snails of the top of the South Island and the North Island (3) the **southern** axially-striped or uni-coloured rounded snails of the western South Island, though the smaller alpine southern snails in this group varied in their internal position between trees.

P. fiordlandica

There was deep allozyme divergence between *P. fiordlandica*, and all other *Powelliphanta*. It differed by an average 10 fixed differences (range 8-13) including 11 and 13 fixed differences respectively from its nearest geographical neighbours “vittatus” and *P. spedeni* and had private alleles at 4 of the 16 loci. *P. fiordlandica* was separated by an average Nei's genetic distance D = 1.07 (range 0.75 - 1.67) from all other *Powelliphanta* (Figure 5, Appendix 1). There was equally deep mtDNA divergence with a mean 36% sequence divergence between *P. fiordlandica* and all other *Powelliphanta* (Figure 4, Appendix 3). Within P. *fiordlandica* there was almost no genetic difference between the population on mainland New Zealand and that on Resolution Island.

Northern Snails

Within the northern spirally-striped flattened snails there were 3 major clades (1) the large to very large *P hochstetteri* in west and east Nelson, plus all the North Island's *Powelliphanta*; *P. traversi, P. marchanti,* "Urewera", "Maungaharuru" and "Egmont" - hereinafter referred to as the *hochstetteri* complex (2) the medium-sized *P. gilliesi,* including "Parapara" and the small alpine "Anatoki Range" from western Golden Bay and (3) the small "alpine" snails from the St Arnaud and Arthur Ranges near Nelson.

The monophyly of both the *hochstetteri* complex and "alpine" was well supported, as was *P. gilliesi* sensu stricto. The phylogenetic status of *P. gilliesi* was complicated however, by what seemed to be an ancient hybridization with neighbouring "alpine" on the summit of Parapara Peak. On and near the summit a form of *P. gilliesi* dubbed "Parapara" which was intermediate morphologically between *P. g. fallax* and "Anatoki Range", sat between both in all allozyme trees. "Anatoki Range" is morphologically and ecologically strongly aligned to "alpine" but shared no haplotypes with it, though this is likely to be due in part to a lack of sampling in the suitable habitat between the two. In all allozyme trees "alpine" was sister to *P. hochstetteri* but in all mtDNA trees it was sister to *P. gilliesi*.

Within the *hochstetteri* complex in both allozymes and mtDNA (Figures 4 & 5) there was shallow but consistent structuring, with moderate to high support for 8 clusters (1) Golden Bay *P. h. hochstetteri* and *P. h. anatokienisis* (2) western Marlborough Sounds *P. h. obscura* and *P. h. consobrina*, (3) eastern Marlborough Sounds *P. h. bicolor* (4) lowland Horowhenua Plains *P. traversi traversi, P. t. florida, P. t. otakia* (5) upland Horowhenua *P. t. latizona, P. t. koputaroa, P. t. tarauaensis* (6) *P. marchanti* on the Ruahine, Kaimanawa and Kaweka Ranges (7) "Egmont" on Mt Taranaki and (8) 'Maungaharuru" and "Urewera" in upland Hawkes Bay. The genetic distances between these 8 clusters were low, with the relationship between *P. marchanti* and the upland Horowhenua group in particular close. However, despite low genetic distances, across analyses these 8 clusters were monophyletic and largely stable in phylogenetic position.

Southern snails

South Island rounded and axially-striped or uni-coloured snails form 9 well supported monophyletic clades (Figure 4) in mtDNA (1) *P. superba* and *P. annectens* (2) *P. lignaria* (3) *P. augusta* (4) the "Kawatiri" complex (5) *P. gagei* (6) *P. fletcheri* (7) *P. spedeni* (8) *P. rossiana* (9) "vitattus". The latter four formed a single clade in allozyme analyses (Figure 5), albeit with each taxon on a separate long branch, and *P. augusta* was unknown at the time of the allozyme study, but beyond these small differences nDNA retrieved the same clades.

The "Kawatiri" complex comprised almost entirely small thin-shelled alpine snails. The exception was the heavy-shelled lowland snail "Buller River" which is morphologically most similar to lowland heavy-shelled *P. lignaria unicolorata*, whose range it nearly abuts. In allozymes (figure 5) it was deeply divergent from all other *Powelliphanta* including the "Kawatiri" complex (D = 0.8, mean of 7.8 fixed differences); in allozyme trees it was usually sister to *P. lignaria* though occasionally suffered long branch attraction to other highly differentiated clades. In mtDNA analyses however, the monophyletic "Buller River" was genetically closest to the alpine snails within the "Kawatiri" complex (Figure 4) whose distributions near the mouth of the lower Buller Gorge it bisects. With differing parentage indicated by nuclear-based allozymes and mitochondrial DNA, "Buller River" is presumed to be the result of ancient hybridization between *lignaria* and "Kawatiri" stock.

Within the "Kawatiri" complex a second monophyletic group was distinguished by both allozymes and mtDNA (Figures 4 & 5). These were the eastern-most snail populations of the complex, with 3, 5 and 8 fixed differences between the "Matiri" snails and "Kirwins", *P. patrickensis* and "Baton" respectively. "Garabaldi" and "Baton" in the north-east are sister to the “Matiri”/ “Matakitaki” clade, and together with it formed a monophyletic group, reasonably homogenous morphologically over a substantial area, and distinct from the remainder of the "Kawatiri" complex snails to the west. This division into eastern and western clades, while shallow, is well supported.

Western "Kawatiri" populations showed substantial diversity and structure in the mtDNA analyses but their relationships remained largely unresolved. Populations on the Brunner and the northern Paparoa Ranges were unknown at the time of the allozyme study so no nuclear data was available to assist interpretation.

P. gagei and *P. fletcheri* formed a well supported clade in mtDNA but in nuclear markers the more distinctive *P. gagei* suffered long-branch attraction to other highly differentiated clades (Figure 5). The genetic distance between *P. gagei* and *P. fletcheri* was high in allozymes (D = 0.7, with 8 fixed differences) but less in mtDNA (3.1% sequence divergence). *P. gagei* occupies the south western Paparoa Ranges, while snails of the "Kawatiri" complex occupy the northern and western Paparoa Ranges. In the gap between the two, a single specimen sequenced from Mt Bovis in the mid-west Paparoa Ranges was highly distinctive but its wider distribution is unknown and its phylogeny remained unresolved.

Discussion

A mean 36% sequence divergence and 11–13 fixed allozyme differences, combined with the observation that *P. fiordlandica* differs in shell/body organization from all other *Powelliphanta* and shares characters with other rhytidids not seen in *Powelliphanta*, including eggshell structure (Chapter 3), indicates it should be in its own monotypic genus. It is sister to *Powelliphanta s.s.* and closer to it than to any of the other Rhytididae examined.

It was not possible to measure the relative genetic distance of *Powelliphanta* to other New Zealand rhytidids and Australian *Victaphanta* with allozymes as the differences proved too great for results to be comparable. However, using mtDNA and when scored separately using allozymes, the four described species of *Victaphanta* showed considerable genetic distance from each other, with *V. lampra* from north-east Tasmania particularly distinctive. The deep divergence between *V. lampra* and the other 3 species was unexpected as *V. lampra*, *V. milligani*, and *V. atramentaria* have similar body colour (bright orange), while *V. compacta* does not. *Victaphanta compacta* also differs—at least from *V. atramentaria*—in shell, radula and reproductive anatomy (Smith 1968).

Climo's (1978) proposal that *Powelliphanta* comprises only one or two species is not supported by the molecular data which indicates instead that, even without *fiordlandica*, there are at least 12 distinct lineages. If clades in the *hochstetteri* and "kawatiri" complexes are included, at least 16 distinct lineages within the genus are supported by this data. Little evidence was found of the "clinal merging" Climo argued existed between Powell's (1979) described species, and instead genetic distances between lineages were found to be at levels typically associated with species. Allozyme distances between described *Powelliphanta* species (*hochstetteri*, *superba*, *gilliesi*, *lignaria*, *traversi*, *spedeni*) at a mean D = 0.71 (0.17–1.1) are comparable to the distance between two New Zealand species of large *Placostylus* land snail, *P. ambagiosus* and *P. hongi* (D = 0.60, Triggs & Sherley 1993); to the mean distance between 25 congeneric species of mollusc reported as D = 0.113 by Davis (1984); and to the range of between-species distances of 0.2–0.6 in 23 genera of snail reported by Woodruff et al. (1988). Corrected genetic distances (GTR+G+I) between mtDNA sequences of the same described *Powelliphanta* species at a mean 11.4% (3%–17.7%) are likewise comparable to the mean between-species distance of 11.8% reported by Davison et al. (2009) in 97 species of land snail. In general, there is congruence between mtDNA and allozymes in identification of monophyletic clades.

Strong support for species classification was provided for Powell's *P. superba*, *P. lignaria*, *P. gilliesi*, and *P. hochstetteri* with lesser support for *P. marchanti*, *P. traversi* and *P. spedeni*. Although monophyletic, *P. annectens* is genetically so close to *P. superba* it could be described as a highly distinctive subspecies of the latter. Conversely, the south-western alpine snails loosely described by Powell as *P. rossiana* include at least 3 additional highly divergent lineages, "alpine", "Kawatiri" and *P. gagei / fletcheri*. Three additional *Powelliphanta* species or putative species from the South Island's west coast—"Buller River", "vitattus" and *P. augusta*—were discovered late and were unknown to Powell. Recently discovered *Powelliphanta* populations in the North Island at Urewera, Maungaharuru and Mt Taranaki are also genetically distinct, possibly at species level.

Intra-specific differences

While levels of intra-specific genetic distances vary greatly, Powell's division of most of these species into subspecies (as defined in Chapter 4) gains some molecular support from this study. The described subspecies of *P. gilliesi* mostly occupy continuous forest habitat but within this are geographically and genetically discrete, though usually only by 1–2 fixed differences at allozyme loci. Conversely, most of the described subspecies of *P. superba* have distributions that abut at least one other subspecies, and most subspecies share some haplotypes. Unexpectedly, there was a 1.7% mtDNA sequence divergence between eastern and western Aorere /Heaphy Valley population samples of *P. superba*, though this separation was not obvious in allozymes. The populations within the linear ranges of alpine specialists *P. rossiana*, *P. gagei*, *P. fletcheri* and "alpine" are each confined to separate mountain ranges and have high intraspecific genetic distances. In contrast, "Matiri" within the “Kawatiri” complex has populations with little genetic differentiation over a wide but contiguous area of mountain ranges. Little or no genetic difference was detected between several of Powell's subspecies *i.e. P. hochstetteri hochstetteri* and *P. h. anatokiensis*; *P. spedeni spedeni* and *P. s. lateumbilicata*; *P. traversi traversi*, *P. t. florida* and *P. t. koputaroa.* However, *P. h. hochstetteri* and *P. h. anatokiensis* are easily distinguished morphologically and occupy discrete geographical areas making them good candidates for sub-specific status. The failure to find significant genetic differences within some species and monophyly in other subspecies is likely due in part to the tools used here; while allozymes and mtDNA are ideal for identifying species-level differences, faster-evolving microsatellites would be more suitable for measuring genetic structure within species.

Most *Powelliphanta* subspecies are allopatric, have at least 1 fixed diagnosable character state as they are morphologically readily separable. This study suggests that at least some of those easily observed morphological differences between many *Powelliphanta* subspecies reflect genetic structure. Within species, most of the large-shelled *Powelliphanta* subspecies have 1–3 fixed differences and mean intraspecific mtDNA divergences of 1.2%–2%, with higher levels of both between most small-shelled alpine tag-named taxa. The intra-specific genetic distances found in this study within *P. lignaria* will be explored in more detail and combined with morphological and ecological characters in Chapter 4, and in subsequent papers focussing on the classification and description of each *Powelliphanta* species.

Divergence estimates

The timing of land connections between the North and South Islands provides one of the few potential ways to calibrate mutation rates in *Powelliphanta*, thanks to the close relationship between South and North Island members of the *hochstetteri* complex, and recent improvements in geological knowledge of the timing of tectonically-driven land emergence in central New Zealand (Trewick and Bland 2012) and the structure (Nodder 1995) and opening of Cook Strait (Lewis et al. 1994). However, there are still too many imponderables to make this a valid approach. Instead a range of calibrated rates from marine molluscs (0.7–1.2% substitutions per million years Marko 2002; 2.4% per Ma, Hellberg and Vaquier 1999) are used to produce coarse estimates of the approximate timing of divergence, against which consistency with current geological understanding is assessed.

Most sequence divergences between pairs of South Island and North Island populations in the "*hochstetteri* complex" are around 3.3%. While mitochondrial DNA indicated the far-eastern lineage *bicolor* separated from all more-western stock earlier than this (4.1% sequence divergence), nuclear-based allozyme genetics did not, indicating instead that *hochstetteri* in Golden Bay (western South Island) and "Egmont" in Taranaki (western North Island) were the earliest lineages to diverge. This incongruence between mtDNA and nDNA suggests that separation is of comparatively recent origin. Applying the standard range of marine molluscan rates to *Powelliphanta* implies a separation time for most South and North Island *hochstetteri* stock of between 1.4–4.7 (mean 2.2) Ma. So how well does this crude estimate relate to *Powelliphanta* biogeography and today's understanding of land connections in central New Zealand?

It was previously thought the most likely time *Powelliphanta* "crossed" Cook Strait was at the height of the last glaciation only ~20,000 years ago when sea levels were ~120 m lower than today. This late timing led both Te Punga (1953) and Climo (1978) to propose fast speciation rates in *Powelliphanta.* However, it is now considered that opportunities for land connections during glacial maxima after Cook Strait opened ~450 kya were limited (Lewis et al. 1994), but that other land connections, albeit tenuous and perhaps fleeting in geological time, existed much earlier (Trewick & Bland 2012, Figure 6). As early as 3 Ma some land in the modern Wellington region (North Island) which today supports *Powelliphanta traversi* was probably part of Marlborough (South Island), and from early to mid-Pleistocene 2.4–1 Ma opportunities for land connections or rafting across shallow tidal waters existed (Trewick & Bland 2012). Current knowledge of the timing of Cook Strait formation is thereby reasonably consistant with the timing of separation of the "*hochstetteri* complex" determined through use of the calibrated mutation rate for some marine molluscs.

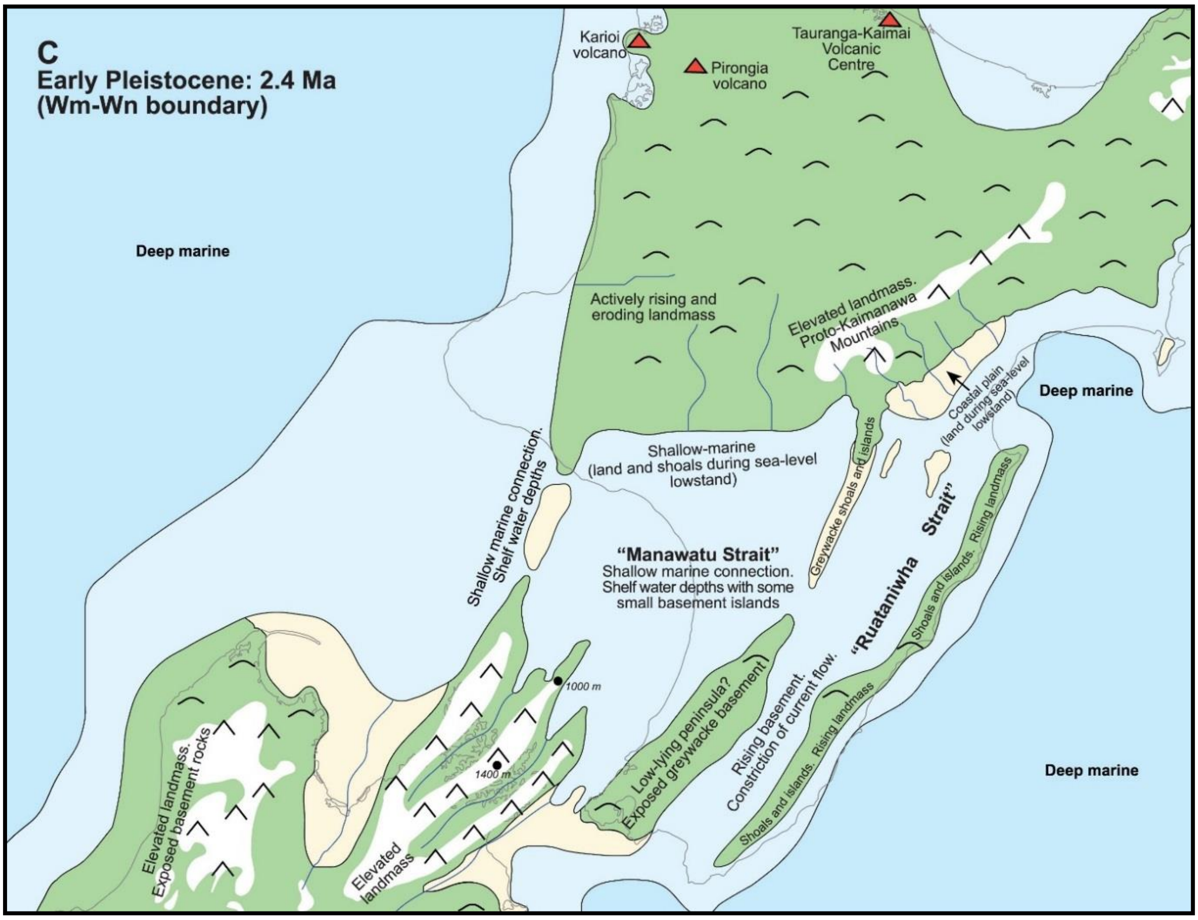

Figure 6. Simplified palaeogeographic reconstruction of the central New Zealand region as it is now thought likely to have appeared 2.4 Ma, reproduced from Trewick & Bland (2012) who compiled it from many geological sources (see references therein).

Some authors have suggested extreme levels of molecular diversity in some pulmonate land snails may be the result of exceptionally fast mutation rates (Thomaz et al. 1996, Chiba 1999), casting doubt on the wisdom of using the relatively slow rates found in marine molluscs for land snail divergence estimates. However, the vegetarian pulmonates in those studies, *Cepaea nemoralis* and *Mandarina* snails respectively, differ in important ways from carnivorous *Powelliphanta*. *Cepaea nemoralis* forms large populations in many discrete demes, with very fast generation times, giving rise to their description as a “molluscan weed” (Jones et al. 1977). By contrast predatory *Powelliphanta* live at comparatively low densities, occur patchily but not at the habitat micro-scale of *Cepaea*, and have a long generation time (Walker 2003). Avise et al. (1984, 1987) noted the time to monophyly of lineages in the latter situation is likely to be long, with relatively slow mutation rates. Genetic studies of other Rhytididae also tend to support the application of marine molluscan mutation rates to *Powelliphanta*. When used to estimate divergence dates for Rhytididae in northern New Zealand, Spencer et al. (2006) preferred a rate at the low end (0.65% per Ma) to tie in with geological evidence on the timing of separation of Three Kings Islands from mainland New Zealand. Mousalli and Herbert (2016) also selected a comparatively slow rate of 0.85%/lineage/million years for South African Rhytididae using a single biogeographic calibration (an assumed east-west Gondwanan split of basal Rhytidoidea 120 Mya).

At 0.7–2.4% mean substitution rate for molluscan CO1 per million years, ancestral *P. fiordlandica* may have separated from all other *Powelliphanta* around 15–30 mya in the mid Miocene; separation of the 2 major groups of *Powelliphanta*, the northern axially–striped snails and the southern spirally striped or uni-coloured snails may have occurred around 10–12 mya in the late Miocene; separation within these two groups into most of today's species around 6–9 mya in the early Pliocene, continuing into the early to mid-Pleistocene 1–2 mya with the spread of *hochstetteri* stock into the southern North Island as it was uplifted from the sea, and rapid and recent expansion once there into western, central and eastern stocks.

Limits to phylogenetic resolution

Relationships within both *P. rossiana* and the "Kawatiri" complex are poorly resolved in likelihood analyses of the mitochondrial dataset. While frequently due to insufficient data, it is possible given their biogeographic position these polytomies are real. This would imply ancestral species gave rise to several new taxa almost simultaneously through rapid fragmentation of a widespread ancestral species.

The estimated timing of the *P. rossiana* divergences at 1.9—1.5 mya coincides with early Pleistocene cold temperature minima at 1.79 and 1.53 Ma (Carter 2010). *Powelliphanta rossiana* snails now occur in a long, narrow, north-south strip just west of the heavily glaciated Southern Alps in central to south Westland, where they are confined to the ridges between westward-flowing glaciated valleys. As a treeline specialist they may have formerly been widespread across the region when it supported low tussock and shrub vegetation in the cooling early Pleistocene, but as the temperatures dropped, may have become trapped at essentially the same time in separate parts of Westland as glaciers filled the intervening valleys. Detailed chronology of glacier formation and mountain uplift supporting this timing comes from glacial deposits from Mt Greenland —the type locality of *P. rossiana* —near Ross, upon which the description of the Ross Glacial climate period, the first Pleistocene ice advance in New Zealand (Gage 1960, Carter 2010) was based.

Similarly, divergence estimates within the "Kawatiri" complex during the Pleistocene imply snail populations north of Ross in the Buller (Kawatiri) region separated at a time of cyclical environmental change. By the late Pliocene, sediments from the Southern Alps blanketed the entire low-lying Buller region, but in the early Quaternary intense faulting began, causing rapid uplift and the present topography of NNE-trending mountain ranges and intervening depressions (Nathan, quoted in Anderson 1981, Nathan *et al*. 1986, Ghisetti et al. 2014, Suggate 2015). In the Buller region this rapid uplift coincided with the onset of the first glacial advances of the Pleistocene and with the final expulsion of the sea from north Westland (Gage 1960). The scale and speed of all these changes suggest near synchronous lineage formation in the "Kawatiri" complex may be a reasonable interpretation of the observed polytomy. Further support that the separation may be related to topographical changes comes from the strongly NNE-geographic trend to both the landscape of the Kawatiri region and the genetic relationships within the "Kawatiri" complex.

The biology of *Powelliphanta*, with its propensity towards rapid fixation of alleles on the margins of low density populations through selfing, may make polytomies more likely. If there is patchy but near simultaneous habitat loss across the range of a species with many geographically separate subpopulations, each remaining population would capture a different subset of the parental species genetic variation, making identification of branching pattern very difficult (Hoelzer & Melnick 1994). The absence of polytomies in *Powelliphanta* further south, which experienced even colder Pleistocene conditions, might be explained by glacial ice covering virtually all of the landscape there and a post-glacial invasion of *Powelliphanta*. This theory is given some support from the fact that both *P. spedeni* and "vitattus" are, unlike snails in the “Kawatiri” and *rossiana* complexes, genetically identical across their relatively large geographic ranges. The absence of polytomies in the warmer north might be explained by the fact that there, glacial ice was confined to central north-west Nelson, leaving large contiguous areas in the coastal north-west where lineage sorting could continue.

Conclusions

The morphology of *Powelliphanta* should be re-evaluated considering the genotypic clusters identified in this study, and a taxonomic revision of the genus incorporating both molecular and morphological evidence undertaken. The divergent shell and body organization of *P. fiordlandica* combined with the molecular data presented here supports its treatment as a separate genus. It is sister to *Powelliphanta*, which is shown here to be a monophyletic genus. The relationship between *Powelliphanta*, other New Zealand rhytidids and the Australian genus *Victaphanta* is distant, while within *Victaphant*a large genetic distances were found between *V. lampra* in NE Tasmanian and those species in NW Tasmania and Victoria. Both allozymes and mitochondrial DNA data support most species described by Powell (1979) but a significant number of more recently discovered populations are also genetically distinctive and require description as species. These include 2 poorly resolved species complexes in Westland whose rapid separation may be related to abrupt climatic and tectonic change in the early Pleistocene.

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Appendix 1. Nei's 1978 unbiased genetic distances (above the diagonal) and the number of allozyme loci (out of 16) with no shared alleles (below the diagonal) among 54 *Powelliphanta* taxa. An * marks those taxa where low sample size may have led to a slightly inflated fixed difference score

	P. fiordlandica	"Garabaldi"	"Baton"	*P. patrickensis*	"Kirwin's"	"Haast"	"Matakitaki"	"Matiri"	*P. fletcheri*	"Fox"	"Anatoki Range"	*P. gagei*	*P. s. spedeni*	*P. s. lateumbilicata*	"Nelson Lakes"	"Owen"	"Lodestone"	"Buller River"
P. fiordlandica	****	0.766	0.94	0.967	0.851	1.044	0.778	0.732	1.257	1.05	1.121	0.868	1.658	1.617	1.091	1.312	1.651	1.221
"Garabaldi"	9	****	0.145	0.131	0.165	0.662	0.444	0.527	0.935	0.672	0.441	0.38	0.901	0.939	0.78	0.676	0.705	0.668
"Baton"	10	2	****	0.231	0.365	0.453	0.537	0.659	0.795	0.624	0.597	0.502	0.926	0.953	0.66	0.625	0.763	0.611
P. patrickensis	9	1	1	****	0.197	0.6	0.312	0.396	0.744	0.703	0.354	0.397	0.973	1.024	0.778	0.743	0.794	0.806
"Kirwin's"	9	2	4	2	****	0.761	0.273	0.266	0.822	0.694	0.548	0.531	1.001	1.047	0.88	0.819	0.832	0.951
"Haast"	10	8	6	7	8	****	0.581	0.522	0.333	0.235	0.675	0.646	0.367	0.363	0.811	0.776	0.981	0.957
"Matakitaki"	8	5	6	4	2	7	****	0.118	0.686	0.679	0.544	0.443	1.002	0.983	0.957	0.922	1.155	1.126
"Matiri"	9	7	8	5	3	6	2	****	0.593	0.579	0.54	0.46	0.938	0.931	0.894	0.913	1.146	1.345
P. fletcheri	11	10	9	8	8	4	8	7	****	0.371	0.793	0.691	0.428	0.43	0.893	0.915	1.148	1.124
"Fox"	10	8	7	8	8	2	8	7	5	****	0.43	0.439	0.344	0.349	0.729	0.575	0.841	1.008
"Anatoki Range"	11	5	7	4	6	8	6	7	9	6	****	0.295	0.813	0.846	0.593	0.558	0.69	0.737
P. gagei	9	5	6	5	6	7	6	6	8	6	4	****	0.869	0.909	0.592	0.474	0.748	0.671
P. s. spedeni	12	9	9	9	9	5	10	9	5	4	8	8	****	0	1.026	0.99	1.098	0.776
P. s. lateumbilicata	12	10	10	10	9	5	10	9	5	4	9	9	0	****	1.041	1.005	1.152	0.806
"Nelson Lakes"	10	9	8	9	9	9	10	9	8	8	6	7	10	10	****	0.183	0.454	0.653
"Owen"	12	7	7	8	8	8	9	9	9	7	5	5	9	9	1	****	0.279	0.676
"Lodestone"	12	8	8	9	9	10	11	11	11	9	8	8	10	11	6	4	****	0.657
"Buller River"	10	6	6	7	8	9	9	11	10	9	8	6	7	8	8	7	6	****
P. l. lignaria	8	7	7	6	6	7	5	4	8	6	6	7	8	8	10	10	11	7
P. l. lusca	10	7	7	6	6	8	6	6	9	7	7	8	9	9	10	10	11	7
*P. l. oconnori**	9	7	7	6	6	7	5	5	8	8	9	8	9	9	10	10	11	7
P. l. johnstoni	8	7	7	6	5	8	5	5	9	8	9	8	9	9	10	10	11	7
*P. l. ruforadiata**	9	7	7	6	5	8	5	5	8	8	9	8	9	9	10	10	11	7
P. l. unicolorata	8	8	8	7	4	9	5	5	9	9	10	9	9	9	11	10	11	7
P. l. rotella	9	8	6	7	6	7	6	6	8	7	10	9	8	8	9	9	10	6
P. s. superba	10	7	8	5	7	7	5	6	7	7	6	6	9	10	11	10	10	8
P. s. richardsoni	11	9	8	7	9	6	7	7	6	6	8	7	8	9	10	9	9	7

	P. l. lignaria	*P. l. lusca*	*P. l. oconnori*	*P. l. johnstoni*	*P. l. ruforadiata*	*P. l. unicolorata*	*P. l. rotella*	*P. s. superba*	*P. s. richardsoni*	"Gouland Range"	*P. s. prouseorum*	*P. s. harveyi*	*P. s. mouatae*	*P. annectens*	*P. g. gilliesi*	*P. g. aurea*	*P. g. subfusca*	*P. g. kahurangica*
P. fiordlandica	0.992	1.129	0.874	0.81	0.903	0.741	0.924	1.058	1.245	1.075	1.075	0.995	0.971	1	0.931	0.917	0.942	0.951
"Garabaldi"	0.554	0.538	0.528	0.611	0.544	0.616	0.756	0.656	0.844	0.641	0.689	0.634	0.682	0.692	0.354	0.332	0.36	0.456
"Baton"	0.569	0.552	0.543	0.595	0.558	0.692	0.525	0.842	0.763	0.818	0.894	0.833	0.888	0.782	0.601	0.557	0.625	0.629
P. patrickensis	0.478	0.487	0.5	0.579	0.515	0.614	0.721	0.463	0.63	0.5	0.5	0.491	0.485	0.552	0.381	0.337	0.378	0.3
“Kirwin's"	0.444	0.486	0.466	0.431	0.447	0.407	0.542	0.663	0.832	0.657	0.678	0.688	0.643	0.63	0.453	0.427	0.454	0.555
"Haast"	0.61	0.64	0.617	0.773	0.693	0.847	0.657	0.596	0.47	0.742	0.617	0.551	0.58	0.605	0.667	0.682	0.683	0.687
"Matakitaki"	0.421	0.509	0.434	0.452	0.45	0.434	0.542	0.425	0.581	0.498	0.459	0.572	0.457	0.594	0.555	0.514	0.571	0.575
"Matiri"	0.361	0.484	0.388	0.388	0.389	0.373	0.476	0.517	0.635	0.64	0.524	0.529	0.483	0.613	0.532	0.535	0.548	0.552
P. fletcheri	0.788	0.868	0.87	0.96	0.856	1.001	0.815	0.637	0.528	0.775	0.644	0.639	0.633	0.711	0.786	0.803	0.801	0.806
"Fox"	0.644	0.676	0.826	0.882	0.787	0.902	0.748	0.644	0.54	0.78	0.648	0.604	0.644	0.566	0.447	0.461	0.463	0.539
"Anatoki Range"	0.62	0.556	0.792	0.906	0.808	0.946	1.094	0.534	0.675	0.648	0.541	0.505	0.537	0.536	0.26	0.248	0.259	0.252
P. gagei	0.615	0.699	0.71	0.759	0.677	0.797	0.925	0.481	0.606	0.597	0.485	0.526	0.519	0.517	0.382	0.392	0.395	0.399
P. s. spedeni	0.834	0.836	0.947	1.047	0.938	1.053	0.894	0.905	0.772	1.082	0.906	0.883	0.917	1.043	0.751	0.763	0.762	0.899
P. s. lateumbilicata	0.828	0.816	0.937	1.053	0.937	1.05	0.894	0.953	0.815	1.136	0.954	0.931	0.966	1.101	0.789	0.806	0.805	0.947
"Nelson Lakes"	1.03	1.023	1.083	1.137	1.052	1.237	1.005	1.13	0.965	0.949	1.131	1.109	1.152	0.905	0.651	0.666	0.667	0.553
"Owen"	1.094	1.083	1.096	1.21	1.112	1.289	1.062	1.095	0.93	0.914	1.096	1.074	1.117	0.724	0.591	0.606	0.607	0.72
"Lodestone"	1.145	1.135	1.147	1.261	1.163	1.31	1.113	0.964	0.827	0.811	0.965	0.943	0.977	0.775	0.692	0.682	0.683	0.806
"Buller River"	0.661	0.584	0.653	0.714	0.669	0.783	0.633	0.8	0.682	0.801	0.801	0.86	0.86	0.745	0.866	0.853	0.851	0.869
P. l. lignaria	****	0.021	0.45	0.055	0.033	0.077	0.128	0.545	0.686	0.594	0.546	0.55	0.533	0.531	0.633	0.644	0.649	0.653
P. l. lusca	0	****	0.091	0.143	0.095	0.172	0.22	0.623	0.77	0.649	0.624	0.617	0.625	0.593	0.613	0.629	0.629	0.634
*P. l. oconnori**	0	1	****	0.055	0.016	0.084	0.128	0.506	0.617	0.516	0.516	0.514	0.497	0.471	0.784	0.802	0.8	0.805
P. l. johnstoni	0	1	0	****	0.037	0.005	0.05	0.625	0.739	0.626	0.626	0.651	0.58	0.536	0.898	0.893	0.914	0.918
*P. l. ruforadiata**	0	1	0	0	****	0.065	0.108	0.558	0.693	0.559	0.559	0.58	0.557	0.529	0.8	0.818	0.816	0.82
P. l. unicolorata	0	2	1	0	1	****	0.068	0.66	0.811	0.661	0.661	0.687	0.6	0.571	0.898	0.885	0.914	0.955
P. l. rotella	1	2	1	0	1	1	****	0.77	0.657	0.771	0.771	0.803	0.72	0.628	1.086	1.078	1.102	1.106
P. s. superba	6	7	6	7	7	8	8	****	0.07	0.066	0.01	0.055	0.005	0.165	0.555	0.531	0.548	0.552
P. s. richardsoni	7	8	7	8	8	9	7	1	****	0.154	0.083	0.122	0.075	0.207	0.692	0.682	0.683	0.687

	P. g. jamesoni	*P. g. compta*	"Parapara"	*P. h. hochstetteri*	*P. h. anatokiensis*	*P. h. bicolor*	*P. h. obscura*	*P. h. consobrina*	*P. t. traversi*	"Urewera"	*P. t. latizona*	*P. t. tararuaensis*	*P. marchanti*	"Egmont"	"vittatus"	"Maungaharuru"	*P. t. florida*	*P. g. fallax* "PI"	*P. g*"Pupu"
P. fiordlandica	0.948	0.957	1.204	1.111	1.116	1.113	1.286	1.286	1.031	1.126	0.882	1.084	0.941	1.363	1.298	1.124	1.044	1.083	1.124
"Garabaldi"	0.366	0.374	0.448	0.565	0.575	0.647	0.728	0.728	0.649	0.683	0.763	0.59	0.711	0.796	0.689	0.6	0.646	0.403	0.398
"Baton"	0.629	0.635	0.536	0.679	0.691	0.641	0.6	0.6	0.796	0.776	0.92	0.711	0.868	0.81	0.501	0.725	0.794	0.401	0.388
P. patrickensis	0.382	0.437	0.55	0.486	0.497	0.564	0.645	0.645	0.586	0.627	0.755	0.515	0.645	0.725	0.714	0.527	0.584	0.419	0.422
"Kirwin's"	0.458	0.464	0.562	0.732	0.74	0.792	0.907	0.907	0.782	0.836	0.775	0.751	0.78	0.95	0.77	0.756	0.733	0.544	0.561
"Haast"	0.687	0.827	0.553	0.77	0.783	0.562	0.505	0.505	0.534	0.576	0.844	0.627	0.617	0.575	0.351	0.677	0.617	0.519	0.559
"Matakitaki"	0.575	0.685	0.660	0.581	0.593	0.641	0.751	0.751	0.687	0.733	0.779	0.611	0.685	0.837	1.106	0.624	0.685	0.583	0.566
"Matiri"	0.552	0.676	0.576	0.647	0.653	0.676	0.77	0.77	0.622	0.677	0.761	0.643	0.62	0.81	1.057	0.66	0.6	0.62	0.66
P. fletcheri	0.806	0.966	0.661	0.921	0.943	0.706	0.644	0.644	0.756	0.749	1.09	0.778	0.825	0.812	0.498	0.796	0.727	0.622	0.662
"Fox"	0.467	0.582	0.316	0.525	0.515	0.581	0.531	0.531	0.612	0.627	0.931	0.648	0.704	0.554	0.456	0.656	0.595	0.328	0.36
"Anatoki Range"	0.252	0.345	0.274	0.325	0.322	0.466	0.532	0.532	0.438	0.469	0.659	0.425	0.487	0.468	0.798	0.387	0.436	0.286	0.292
P. gagei	0.399	0.507	0.33	0.409	0.415	0.458	0.521	0.521	0.412	0.447	0.638	0.416	0.461	0.544	0.809	0.422	0.374	0.457	0.5
P. s. spedeni	0.766	0.922	0.696	1.069	1.085	0.858	0.784	0.784	0.9	0.921	1.349	0.938	1.026	0.705	0.489	0.882	0.915	0.61	0.638
P. s. lateumbilicata	0.809	0.97	0.718	1.084	1.1	0.873	0.8	0.8	0.915	0.936	1.364	0.953	1.041	0.707	0.529	0.889	0.937	0.641	0.666
″Nelson Lakes"	0.553	0.454	0.671	0.648	0.654	0.479	0.438	0.438	0.664	0.644	0.666	0.66	0.726	0.617	0.9	0.631	0.631	0.41	0.544
"Owen"	0.661	0.547	0.497	0.428	0.436	0.307	0.275	0.275	0.454	0.416	0.438	0.432	0.486	0.524	0.906	0.433	0.433	0.499	0.566
"Lodestone"	0.687	0.575	0.633	0.798	0.803	0.737	0.677	0.677	0.813	0.793	0.815	0.81	0.885	0.827	0.682	0.811	0.811	0.547	0.505
"Buller River"	0.855	0.861	0.908	0.832	0.853	0.647	0.592	0.592	0.72	0.7	0.865	0.717	0.787	0.608	0.657	0.653	0.718	0.716	0.772
P. l. lignaria	0.653	0.712	0.718	0.777	0.773	0.947	1.049	1.049	0.876	0.94	1.054	0.872	0.923	1.027	0.773	0.857	0.811	0.74	0.781
P. l. lusca	0.634	0.665	0.738	0.755	0.747	0.992	1.079	1.079	0.906	0.97	1.123	0.903	0.988	0.975	0.779	0.851	0.877	0.713	0.754
*P. l. oconnori**	0.805	0.811	0.825	0.936	0.942	1.005	1.083	1.083	0.871	0.957	1.059	0.915	0.949	1.147	0.752	0.949	0.869	0.908	0.949
P. l. johnstoni	0.918	0.924	0.928	1.074	1.079	1.11	1.245	1.245	1.089	1.158	0.998	1.086	1.039	1.29	0.781	1.087	0.994	0.998	1.039
*P. l. ruforadiata**	0.82	0.827	0.841	0.952	0.957	1.058	1.147	1.147	0.967	1.034	1.152	0.964	1.052	1.163	0.733	0.965	0.885	0.924	0.965
P. l. unicolorata	0.918	0.924	0.948	1.118	1.124	1.162	1.355	1.355	1.134	1.219	0.954	1.13	1.036	1.37	0.9	1.131	1.036	1.048	1.083
P. l. rotella	1.106	1.113	0.961	1.297	1.303	1.141	1.097	1.097	1.313	1.293	1.181	1.309	1.241	1.326	0.696	1.31	1.198	0.88	0.921
P. s. superba	0.552	0.676	0.727	0.746	0.754	0.796	0.868	0.868	0.705	0.781	1.022	0.728	0.77	0.964	0.665	0.77	0.747	0.646	0.681
P. s. richardsoni	0.687	0.827	0.72	0.952	0.957	0.823	0.742	0.742	0.813	0.837	1.193	0.899	0.885	0.981	0.562	0.965	0.885	0.561	0.617

	P. fiordlandica	"Garabaldi"	"Baton"	*P. patrickensis*	"Kirwin's"	"Haast"	"Matakitaki"	"Matiri"	*P. fletcheri*	"Fox"	"Anatoki Ra"	*P. gagei*	*P. s. spedeni*	*P. s. lateumbilicata*	"Nelson Lakes"	"Owen"	"Lodestone"	"Buller River"
"Gouland Range"*	10	7	8	6	7	8	6	7	8	8	7	6	10	11	10	9	9	8
*P. s. prouseorum**	10	8	9	6	8	7	6	6	7	7	7	5	9	10	11	10	10	8
P. s. harveyi	10	8	8	6	8	7	7	6	7	6	6	4	9	10	11	10	10	7
P. s. mouatae	9	7	8	5	7	7	5	6	6	7	6	5	9	10	11	10	10	8
P. annectens	9	8	8	6	7	6	7	7	7	4	7	5	8	9	8	7	8	6
P. g. gilliesi	10	6	7	5	6	8	7	7	9	6	4	5	8	9	8	6	8	7
P. g. aurea	10	4	6	4	5	8	6	7	9	6	3	5	8	9	8	6	8	7
P. g. subfusca	9	4	7	5	6	8	7	7	9	6	4	5	8	9	8	6	8	7
P. g. kahurangica	10	5	7	4	6	8	7	7	9	6	3	5	8	9	7	6	8	7
P. g. jamesoni	9	4	7	5	6	8	7	7	9	6	3	5	8	9	7	6	8	7
*P. g. compta**	10	5	7	6	6	9	8	8	9	7	4	6	9	10	6	5	7	7
"Parapara"	11	6	7	7	7	6	8	7	7	4	4	4	7	7	6	4	6	7
P. h. hochstetteri	11	7	8	7	8	8	7	8	9	6	4	6	9	9	8	5	9	8
P. h. anatokiensis	11	7	8	6	8	8	7	8	10	7	4	6	10	10	8	5	9	8
P. h. bicolor	9	7	7	6	8	6	7	7	7	6	5	5	9	9	6	3	8	6
*P. h. obscura**	11	8	7	7	9	6	8	8	7	6	6	6	9	9	6	3	8	6
P. h. consobrina	11	8	7	7	9	6	9	9	7	7	7	6	9	9	7	4	8	6
P. t. traversi	11	9	10	8	10	7	9	8	9	7	7	6	10	10	8	5	9	8
"Urewera"	11	8	10	8	10	8	9	8	9	8	7	6	11	11	8	5	9	8
P. t. latizona	10	9	10	9	9	10	9	9	11	10	8	9	13	13	8	5	9	9
P. t. tarauaensis	11	8	9	7	9	8	8	8	9	8	6	6	11	11	8	5	9	8
*P. marchanti**	10	8	9	8	9	8	8	7	8	7	6	5	11	10	9	6	10	7
P. "Egmont"	13	9	9	9	10	8	9	9	9	7	6	7	9	8	8	7	10	7
"vittatus"	11	8	7	8	8	5	10	11	6	5	10	9	5	6	10	10	8	7
"Maungaharuru"*	11	7	7	6	8	7	7	8	8	7	5	6	8	8	6	4	8	6
P. t. florida	10	8	8	7	8	6	8	7	7	6	6	5	8	8	6	4	8	6
P. g. fallax "PI"	10	4	5	4	5	7	6	8	8	5	1	5	7	8	5	5	6	6
P. g. fallax "Pupu"	10	4	5	4	5	7	6	7	8	5	2	5	8	8	7	6	6	7

	P. l. lignaria	*P. l. lusca*	*P. l. oconnori*	*P. l. johnstoni*	*P. l. ruforadiata*	*P. l. unicolorata*	*P. l. rotella*	*P. s. superba*	*P. s. richardsoni*	"Gouland Range"	*P. s. prouseorum*	*P. s. harveyi*	*P. s. mouatae*	*P. annectens*	*P. g. gilliesi*	*P. g. aurea*	*P. g. subfusca*	*P. g. kahurangica*	*P. g. jamesoni*
"Gouland Range"*	7	8	6	7	7	8	8	1	2	****	0.084	0.139	0.084	0.1	0.676	0.641	0.667	0.671	0.671
*P. s. prouseorum**	6	7	6	7	7	8	8	0	1	1	****	0.062	0.014	178	0.539	0.547	0.549	0.553	0.553
P. s. harveyi	6	7	6	7	7	8	8	0	1	1	0	****	0.014	0.2	0.515	0.511	0.513	0.517	0.517
P. s. mouatae	6	8	6	7	7	7	8	0	1	1	0	0	****	0.153	0.551	0.535	0.547	0.551	0.551
P. annectens	5	5	5	5	5	5	5	2	2	1	2	2	2	****	0.679	0.66	0.668	0.672	0.672
P. g. gilliesi	7	7	9	9	9	9	10	7	8	8	6	5	6	7	****	0.007	0.002	0.13	0.071
P. g. aurea	7	7	9	9	9	9	10	6	8	7	7	6	6	7	0	****	0.004	0.133	0.073
P. g. subfusca	7	7	9	9	9	9	10	7	8	8	7	6	7	7	0	0	****	0.121	0.063
P. g. kahurangica	7	7	9	9	9	9	10	7	8	8	7	6	7	7	1	1	1	****	0.052
P. g. jamesoni	7	7	9	9	9	9	10	7	8	8	7	6	7	7	1	1	1	0	****
*P. g. compta**	8	8	9	9	9	9	10	8	9	7	8	7	8	6	2	2	2	1	1
"Parapara"	7	7	9	9	9	9	9	8	8	9	8	7	8	6	4	5	5	3	3
P. h. hochstetteri	8	8	10	10	10	11	11	8	10	9	9	8	8	9	5	4	5	5	5
P. h. anatokiensis	8	8	10	10	10	11	11	8	10	9	9	8	8	9	4	4	4	5	5
P. h. bicolor	9	10	9	10	10	10	10	8	8	9	9	8	8	8	6	5	6	7	7
*P. h. obscura**	10	10	10	10	11	12	10	9	8	10	9	9	9	8	7	6	7	7	7
*P. h. consobrina**	11	10	11	12	12	13	10	10	9	11	10	10	10	10	8	7	8	9	8
P. t. traversi	10	10	10	11	11	10	12	9	10	10	9	9	9	9	7	7	7	8	8
"Urewera"	10	10	10	11	11	11	12	9	10	10	9	9	9	9	7	7	6	8	7
P. t. latizona	11	12	11	11	12	10	12	11	12	10	11	11	10	8	9	7	9	10	10
P. t. tarauaensis	10	10	10	11	11	11	12	9	10	10	9	9	9	9	7	6	7	8	8
P. marchanti	9	10	9	11	10	11	12	8	9	9	9	8	8	8	6	6	7	8	8
"Egmont"	9	10	10	12	11	13	12	10	10	11	11	10	10	10	8	8	9	8	8
"vittatus"	9	8	8	8	9	10	7	9	8	9	9	9	9	7	9	8	9	7	7
"Maungaharuru"*	8	8	10	10	10	11	10	8	9	9	9	9	8	9	6	5	6	7	7
P. t. florida	8	8	9	9	9	10	9	8	8	9	8	8	8	8	6	6	6	7	7
P. g. fallax "PI"	7	7	9	9	9	9	9	6	7	7	7	6	6	7	2	1	1	0	0
P. g. fallax "Pupu"	7	7	9	9	9	9	9	6	7	7	7	6	6	7	2	1	2	2	2

	P. g. compta	*P.* "Parapara"	*P. h. hochstetteri*	*P. h. anatokiensis*	*P. h. bicolor*	*P. h. obscura*	*P. h. consobrina*	*P. t. traversi*	"Urewera"	*P. t. latizona*	*P. t. tararuaensis*	*P. marchanti*	"Egmont"	"vittatus"	"Maungaharuru"	*P. t. florida*	*P. g. fallax "PI"*	*P. g"Pupu"*
"Gouland Range"*	0.559	0.838	0.875	0.885	0.852	1.036	1.036	0.871	0.957	0.874	0.868	0.949	1.147	0.666	0.908	0.908	0.772	0.795
*P. s. prouseorum**	0.677	0.739	0.782	0.787	0.838	0.908	0.908	0.728	0.799	1.059	0.766	0.795	0.965	0.666	0.795	0.76	0.669	0.726
P. s. harveyi	0.639	0.679	0.744	0.747	0.792	0.856	0.856	0.657	0.739	0.983	0.723	0.72	0.943	0.643	0.773	0.712	0.63	0.687
P. s. mouatae	0.679	0.723	0.777	0.783	0.803	0.886	0.886	0.691	0.774	0.938	0.745	0.723	0.977	0.667	0.794	0.743	0.665	0.716
P. annectens	0.555	0.641	0.792	0.796	0.792	0.844	0.844	0.695	0.769	0.641	0.765	0.72	0.966	0.571	0.819	0.745	0.759	0.819
P. g. gilliesi	0.144	0.316	0.322	0.319	0.469	0.533	0.533	0.455	0.461	0.656	0.427	0.479	0.667	0.766	0.428	0.428	0.14	0.205
P. g. aurea	0.146	0.348	0.309	0.308	0.453	0.525	0.525	0.469	0.475	0.636	0.416	0.482	0.682	0.765	0.421	0.441	0.135	0.184
P. g. subfusca	0.135	0.351	0.334	0.331	0.485	0.549	0.549	0.471	0.472	0.671	0.443	0.495	0.683	0.748	0.444	0.444	0.147	0.22
P. g. kahurangica	0.12	0.428	0.42	0.411	0.603	0.671	0.671	0.555	0.593	0.809	0.552	0.61	0.687	0.741	0.553	0.553	0.148	0.299
P. g. jamesoni	0.065	0.34	0.422	0.414	0.603	0.671	0.671	0.555	0.589	0.809	0.552	0.61	0.687	0.747	0.553	0.553	0.092	0.225
*P. g. compta**	****	0.41	0.53	0.519	0.737	0.811	0.811	0.68	0.724	0.682	0.676	0.742	0.827	0.747	0.677	0.677	0.17	0.314
"Parapara"	3	****	0.436	0.438	0.45	0.455	0.455	0.431	0.426	0.635	0.459	0.481	0.497	0.804	0.481	0.428	0.251	0.226
P. h. hochstetteri	6	6	****	0	0.151	0.212	0.212	0.105	0.107	0.321	0.128	0.202	0.328	0.047	0.062	0.039	0.446	0.451
P. h. anatokiensis	6	6	0	****	0.17	0.231	0.231	0.12	0.124	0.34	0.146	0.219	0.338	0.059	0.08	0.105	0.441	0.461
P. h. bicolor	8	5	1	2	****	0.015	0.015	0.113	0.102	0.218	0.082	0.114	0.257	0.861	0.099	0.107	0.517	0.523
*P. h. obscura**	9	5	2	3	0	****	0	0.159	0.132	0.303	0.137	0.176	0.272	0.787	0.157	0.157	0.475	0.49
*P. h. consobrina**	10	6	3	3	1	0	****	0.159	0.132	0.303	0.137	0.176	0.272	0.787	0.157	0.157	0.475	0.49
P. t. traversi	8	5	2	2	1	3	3	****	0.021	0.218	0.092	0.086	0.253	0.902	0.052	0.019	0.623	0.664
"Urewera"	8	5	2	2	1	3	3	0	****	0.238	0.099	0.106	0.254	0.923	0.049	0.025	0.603	0.644
P. t. latizona	8	6	4	4	2	5	5	3	3	****	0.146	0.085	0.363	1.128	0.252	0.228	0.896	0.921
P. t. tarauaensis	8	5	2	2	1	3	3	1	1	2	****	0.038	0.191	0.94	0.08	0.087	0.583	0.588
P. marchanti	9	6	4	4	2	3	3	2	2	2	1	****	0.231	1.028	0.138	0.102	0.685	0.726
"Egmont"	10	7	5	5	5	5	5	4	5	5	4	4	****	0.802	0.231	0.272	0.636	0.677
"vittatus"	9	9	9	9	10	9	9	10	11	12	11	11	10	****	0.941	0.9	0.636	0.724
"Maungaharuru"*	8	5	1	1	1	1	1	1	1	3	1	2	2	9	****	0.033	0.59	0.601
P. t. florida	8	4	2	2	1	1	1	0	0	3	1	1	3	8	1	****	0.621	0.661
P. g. fallax "PI"	1	2	5	5	6	6	6	7	7	8	6	7	7	7	6	7	****	0.052
P. g. fallax "Pupu"	3	1	5	5	6	6	6	7	7	8	6	7	7	8	6	7	2	****

Appendix 2. Allele frequencies within *Powelliphanta* taxa for 16 polymorphic loci. Alleles are labelled alphabetically from A, closest to the origin. Where more than one allele at a locus was encountered per taxa, the number of individuals which were heterozygotes and the total number of individuals sampled at that locus are given in parentheses (-/-)

	P. h. hochstetteri	*P. h. anatokiensis*	*P. h. obscura*	*P .h. consobrina*	*P. h. bicolor*	*P. t. traversi*	*P. t. florida*	*P. t. tararuaensis*	*P. t. atizona*	*P. marchanti*	"Egmont"	"Urewera"	Maungaharuru"	*P. g. gilliesi*	*P. g. subfusca*	*P. g. aurea*	*P. g. kahurangica*	*P. g. jamesoni*	*P. g. compta*	"Parapara"	*P. g.* "P. inlet"	*P. g.* "Pupu"	*P. s. superba*	*P. s. richardsoni*	*P. s. prouseorum*	*P. s. harveyi*
n	4	7	1	1	5	4	2	5	5	1	4	5	1	5	3	5	5	7	2	3	4	1	4	5	2	4
Acp-1						-	-	-	-											(1/3)						
A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C	1	1	1	1	1	1	1	1	-	1	1	1	1	1	1	1	1	1	-	0.83	1	1	1	1	1	1
D	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-		-	-	1	0.17	-	-	-	-	-	-
Acp-2					(3/5)																					
A	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B	1	1	-	-	0.5	1	1	1	1	1	-	0.5	1	1	1	1	1	1	1	-	-	-	1	-	1	1
C	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
E	-	-	1	1	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-
Alp-1	(1/2)	(1/5)	(1/1)	(1/1)			(1/1)	(4/5)	(2/5)			(1/5)	(1/1)	(3/5)	(1/3)			(1/5)		(3/3)	(1/1)		(2/3)		(1/1)	(1/4)
A	0.25	0.3	-	-	-	-	-	-	-	-	-	-	-	0.7	0.8	1	1	0.9	1	-	0.5	-	-	-	-	-
B	-	-	0.5	0.5	0.4	1	0.5	0.4	0.8	1	-	0.7	-	-	-	-	-	-	-	0.5	-	-	0.67	1	0.5	0.88
C	-	-	-	-	-	-	-	-	-	-	1	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-
D	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	0.2	-	-	0.1	-	-	-	-	-	-	-	-
E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F	0.75	0.7	0.5	0.5	0.6	-	-	-	0.2	-	-	-	0.5	-	-	-	-	-	-	-	0.5	1	0.33	-	-	-
G	-	-	-	-	-	-	0.5	0.6	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-
H	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	0.5	0.13
I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	P. h. hochstetteri	*P. h. anatokiensis*	*P. h. obscura*	*P .h. consobrina*	*P. h. bicolor*	*P. t. traversi*	*P. t. florida*	*P. t. tararuaensis*	*P. t. atizona*	*P. marchanti*	"Egmont"	"Urewera"	"Maungaharuru"	*P. g. gilliesi*	*P. g. subfusca*	*P. g. aurea*	*P. g. kahurangica*	*P. g. jamesoni*	*P. g. compta*	"Parapara"	*P. g.* "P. inlet"	*P. g.* "Pupu"	*P. s. superba*	*P. s. richardsoni*	*P. s. prouseorum*	*P. s. harveyi*
Est																	(1/5)				(1/4)					(2/4)
A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.88
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	0.13
E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.13	-	-	-	-	-
H	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	0.1	1	1	1	0.88	1	-	-	-	-
I	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	0.9	-	-	-	-	-	-	-	-	-
J	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Got-1																										
A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-
Got-2														(2/5)							(3/4)	(1/1)				
A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	1	1	1	1	1	-	0.63	0.5	1	1	1	1
E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-	1	0.38	0.5	-	-	-	-
G	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
H	1	1	-	-	-	1	1	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
J	-	-	-	-		-	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	P. h. hochstetteri	*P. h. anatokiensis*	*P. h. obscura*	*P .h. consobrina*	*P. h. bicolor*	*P. t. traversi*	*P. t. florida*	*P. t. tararuaensis*	*P. t. atizona*	*P. marchanti*	"Egmont"	"Urewera"	"Maungaharuru"	*P. g. gilliesi*	*P. g. subfusca*	*P. g. aurea*	*P. g. kahurangica*	*P. g. jamesoni*	*P. g. compta*	"Parapara"	*P. g.* "P. inlet"	*P. g.* "Pupu"	*P. s. superba*	*P. s. richardsoni*	*P. s. prouseorum*	*P. s. harveyi*
GPI																										
A	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	-	1	1	-	-	-	-
B	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	1	-	-	-	-	-	-
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1
D	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Idh-1																										
A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Idh-2					(1/5)					(1/1)						(1/5)										
A	1	1	1	1	0.8	1	1	1	-	0.5	1	1	1	1	1	0.9	1	1	1	1	1	1	1	1	1	1
B	-	-	-	-	0.2	-	-	-	1	0.5	-	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ldh																										
A	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mdh-1																										
A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

	P. h. hochstetteri	*P. h. anatokiensis*	*P. h. obscura*	*P .h. consobrina*	*P. h. bicolor*	*P. t. traversi*	*P. t. florida*	*P. t. tararuaensis*	*P. t. atizona*	*P. marchanti*	"Egmont"	"Urewera"	.Maungaharuru"	*P. g. gilliesi*	*P. g. subfusca*	*P. g. aurea*	*P. g. kahurangica*	*P. g. jamesoni*	*P. g. compta*	"Parpara"	*P. g.* "P. inlet"	*P. g.* "Pupu"	*P. s. superba*	*P. s. richardsoni*	*P. s. prouseorum*	*P. s. harveyi*
Mdh-2																										
A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-	-
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1
Mdh-3	(1/4)																			(2/3)						(1/4)
A	0.88	1	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	0.67	1	1	-	-	-	0.13
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	0.88
D	0.13	-	1	1	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	0.33	-	-	-	-	-	-
E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pep-1																										
A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pep-2																										
A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1
D	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-		-	-
Pgm	(1/4)	(2/7)				(2/4)														(1/3)	(2/4)					(2/4)
A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.83	0.25	1	-	-	-	-
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	0.17	0.75	-	-	-	-	-
C	0.88	0.86	1	1	1	0.75	1	1	1	1	-	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-
D	0.13	0.14	-	-	-	0.25	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	0.75
F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25

	P. s. mouatae	"Gouland Ra"	*P. annectens*	*P. l. lignaria*	*P. l. lusca*	*P. l. connori*	*P. l. johnstoni*	*P. l. rotella*	*P. l. ruforadiata*	*P. l. unicolorata*	*P. s. spedeni*	*P. s.*	"Anatoki Rg"	"Lodestone"	"Owen"	"Nelson Lakes"	*P. patrickensis*	"Garibaldi"	"Baton"	"Matiri"	"Matakitaki"	"Kirwins"	*P. gagei*	*P. fletcheri*	" Fox"	"Haast"	"vittatus"	"Buller River"	*P. fiordlandica*
n	5	1	5	5	5	1	4	5	1	2	5	5	4	4	5	4	6	4	3	3	4	4	4	5	4	5	5	5	5
Acp-1																					(1/4)								
A	-	-	-	1	0.8	1	1	1	1	1	-	-	-	-	-	-	1	1	1	-	0.1	1	-	-	-	-	1	1	1
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C	1	-	-	-	0.2	-	-	-	-	-	1	1	1	-	-	-	1	-	-	1	0.9	-	1	1	1	1	-	-	-
D	-	1	1	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Acp-2			(2/5)				(1/4)																						
A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B	1	1	0.8	1	1	1	0.88	-	1	1	-	-	1	-	-	-	1	1	-	1	1	1	1	-	-	-	-	-	1
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E	-	-	0.2	-	-	-	0.13	1	-	-	1	1	-	1	1	1	-	-	1	-	-	-	-	1	1	1	1	1	-
Alp-1	(2/5)	(1/1)	(1/4)										(1/3)							(2/3)			(1/4)		(1/4)				(3/3)
A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
B	0.8	0.5	0.88	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	0.33	-	-	0.13	-	0.13	1	-	-	0.5
C	-	-	-	-	0.67	-	-	-	-	-	1	1	0.83	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-
D	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	0.17
E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F	0.1	0.5	-	-	-	-	-	-	-	-	-	-	0.17	-	-	-	1	0.8	1	-	1	0.33	-	-	-	-	-	-	-
G	-	-	0.13	1	0.33	1	1	1	1	1	-	-	-	-	-	1	-	-	-	0.67	-	0.67	0.88	1	0.88	-	1	-	0.33
H	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	P. s. mouatae	"Gouland Ra"	*P. annectens*	*P. l. lignaria*	*P. l. lusca*	*P. l. connori*	*P. l. johnstoni*	*P. l. rotella*	*P. l. ruforadiata*	*P. l. unicolorata*	*P. s. spedeni*	*P. s. lateumbilicata*	"Anatoki Range"	"Lodestone"	"Owen"	"Nelson Lakes"	*P. patrickensis*	"Garibaldi"	"Baton"	"Matiri"	"Matakitaki"	"Kirwins"	*P. gagei*	*P. fletcheri*	" Fox"	"Haast"	"vittatus"	"Buller River"	*P. fiordlandica*
Est	(1/4)									(1/2)					(1/5)										(2/4)				
A	0.38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
D	0.63	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	1	-
E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
F	-	-	0	1	1	1	1	1	1	0.75	-	-	-	-	-	-	-	-	1	-	-	-	-	-	0.25	1	1	-	-
G	-	-	-	-	-	-	-	-	-	-	-	-	1	-	0.5	1	-	-	-	-	-	-	-	-	-	-	-	-	-
H	-	-	-	-	-	-	-	-	-	0.25	1	1	-	1	0.5	-	-	1	-	-	-	1	-	-	0.75	-	-	0	-
I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
J	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Got-1																													
A	1	1	1	1	1	1	1	1	1	1	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
B	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Got-2							(2/4)								(2/3)			(2/3)	(2/3)				(1/3)						
A	-	-	-	-	-	-	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C	-	-	-	1	1	1	0.75	1	1	1	1	1	-	-	-	-	-	-	-	1	1	0.3	-	1	1	1	-	-	1
D	1	1	1	-	-	-	-	-	-	-	-	-	1	1	-	-	1	0.67	0.33	-	-	0.8	0.33	-	-	-	1	1	-
E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.33	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-
F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.33	0.67	-	-	-	0.17	-	-	-	-	-	-
G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.67	1	-	-	-	-	-	-	-	-	-	-	-	-	-
H	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
J	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	P. s. mouatae	"Gouland Ra"	*P. annectens*	*P. l. lignaria*	*P. l. lusca*	*P. l. connori*	*P. l. johnstoni*	*P. l. rotella*	*P. l. ruforadiata*	*P. l. unicolorata*	*P. s. spedeni*	*P. s. lateumbilicata*	"Anatoki Range"	"Lodestone"	"Owen"	"Nelson Lakes"	*P. patrickensis*	"Garibaldi"	"Baton"	"Matiri"	"Matakitaki"	"Kirwins"	*P. gagei*	*P. fletcheri*	" Fox"	"Haast"	. "vittatus"	"Buller River"	*P. fiordlandica*
GPI																													
A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	1
B	-	-	1	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	1	-	1	-	-	1	-
C	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
E	-	-	-	1	1	1	1	1	1	1	-	-	-	-	-	-	1	1	1	1	1	1	-	-	-	1	-	-	-
F	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Idh-1																													
A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	1	1	1	1	1
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	1	-	-	-	-	-
Idh-2	(1/2)		(3/5)																										
A	0.75	1	0.7	1	1	1	0.25	0	1	-	1	1	1	1	1	1	1	1	1	-	-	-	1	1	1	1	1	1	-
B	0.25	-	0.3	-	-	-	0.75	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-
Ldh																													
A	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	1	-
B	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-	1	1	1	1	1	1	1	1	1	1	1	-	-
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Mdh-1																													
A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
B	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-

	P. s. mouatae	"Gouland Ra"	*P. annectens*	*P. l. lignaria*	*P. l. lusca*	*P. l. connori*	*P. l. johnstoni*	*P. l. rotella*	*P. l. ruforadiata*	*P. l. unicolorata*	*P. s. spedeni*	*P. s. lateumbilicata*	"Anatoki Range"	"Lodestone"	"Owen"	"Nelson Lakes"	*P. patrickensis*	"Garibaldi"	"Baton"	"Matiri"	"Matakitaki"	"Kirwins"	*P. gagei*	*P. fletcheri*	" Fox"	"Haast"	"vittatus"	"Buller River"	*P. fiordlandica*
Mdh-2																													
A	-	-	-	1	1	1	1	1	1	1	-	-	1	1	1	1	1	1	1	1	1	1	1	-	-	-	-	1	-
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
C	1	1	1	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	-	-
Mdh-3			(2/5)																										
A	-	-	0.1	1	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
B	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	1	-	-	-	-	-	-
C	1	1	0.8	-	-	1	1	1	1	1	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	1
D	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	1	-
E	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	1	-	-	-	-	-	-	-
Pep-1																													
A	-	-	-	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
B	1	1	1	-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	1
Pep-2																													
A	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C	1	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
D	-	-	-	-	-	-	-	-	-	-	1	1	1	-	1	1	1	1	1	1	1	1	1	1	1	1	-	-	1
Pgm													(1/4)		(3/5)		(1/6)												
A	-	-	-	-	-	-	-	-	-	-	-	-	0.9	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-	-	-	-	0.1	-	0.3	1	-	-	-	-	-	-	-	-	-	-	-	-	-
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-
E	1	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	0.75	-	-	1	1	1	-	1	-	-	-	-	-
F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	1	1	-	-	-	1	-	-	-	-	1	1

Appendix 3. Corrected pairwise genetic distances among samples based on 86 representative mtDNA CO1 sequences below the diagonal. ML distances were calculated using the bestfit model (GTR+G+I) identified using AIC implemented by ModelTest. Boxed values indicate pairwise distances within samples of described or presumed species.

	"Lodestone" 221	"Arnaud Range" 329	"Speargrass" 238	"Mt Murchison" 331	"Owen" 225	"Anatoki Range" 261	*P. g. aurea* 136	*P. g brunnea* 553	*P. g. compta* 212	*P. g. fallax* 2	*P. g. fallax* 12	*P. g. fallax* 231	*P. g. fallax* 234	*P. g. gilliesi* 149	"Haidinger"654	*P. g. jamesoni* 91	*P. g. kahurangica* 88	*P. g. montana* 621	"Moutere Rv"590	*P. g. subfusca* 125
"Lodestone" 221		0.024	0.018	0.023	0.020	0.038	0.058	0.059	0.052	0.046	0.057	0.052	0.043	0.065	0.070	0.062	0.061	0.058	0.054	0.062
"Arnaud Range" 329	0.024		0.010	0.002	0.020	0.052	0.072	0.073	0.066	0.060	0.071	0.066	0.057	0.079	0.085	0.077	0.075	0.072	0.068	0.077
"Speargrass" 238	0.018	0.010		0.008	0.014	0.045	0.066	0.067	0.059	0.054	0.065	0.060	0.050	0.072	0.078	0.070	0.068	0.066	0.061	0.070
"Mt Murchison" 331	0.023	0.002	0.008		0.019	0.050	0.071	0.072	0.064	0.059	0.070	0.065	0.055	0.077	0.083	0.075	0.074	0.071	0.067	0.075
"Owen" 225	0.020	0.020	0.014	0.019		0.048	0.068	0.069	0.062	0.056	0.067	0.062	0.053	0.075	0.080	0.073	0.071	0.068	0.064	0.073
"Anatoki Range" 261	0.038	0.052	0.045	0.050	0.048		0.024	0.025	0.017	0.008	0.022	0.018	0.005	0.030	0.036	0.028	0.026	0.024	0.019	0.028
P. g. aurea 136	0.058	0.072	0.066	0.071	0.068	0.024		0.013	0.012	0.032	0.017	0.012	0.029	0.018	0.024	0.023	0.021	0.004	0.014	0.016
P. g brunnea 553	0.059	0.073	0.067	0.072	0.069	0.025	0.013		0.013	0.033	0.018	0.013	0.029	0.006	0.011	0.024	0.022	0.013	0.015	0.003
P. g. compta 212	0.052	0.066	0.059	0.064	0.062	0.017	0.012	0.013		0.026	0.011	0.006	0.022	0.019	0.024	0.016	0.015	0.012	0.008	0.016
P. g. fallax 2	0.046	0.060	0.054	0.059	0.056	0.008	0.032	0.033	0.026		0.031	0.026	0.003	0.038	0.044	0.036	0.035	0.032	0.028	0.036
P. g. fallax 12	0.057	0.071	0.065	0.070	0.067	0.022	0.017	0.018	0.011	0.031		0.005	0.027	0.024	0.030	0.022	0.020	0.017	0.013	0.022
P. g. fallax 231	0.052	0.066	0.060	0.065	0.062	0.018	0.012	0.013	0.006	0.026	0.005		0.023	0.019	0.025	0.017	0.015	0.012	0.008	0.017
P. g. fallax 234	0.043	0.057	0.050	0.055	0.053	0.005	0.029	0.029	0.022	0.003	0.027	0.023		0.035	0.041	0.033	0.031	0.029	0.024	0.033
P. g. gilliesi 149	0.065	0.079	0.072	0.077	0.075	0.030	0.018	0.006	0.019	0.038	0.024	0.019	0.035		0.006	0.029	0.028	0.018	0.021	0.009
"Haidinger"654	0.070	0.085	0.078	0.083	0.080	0.036	0.024	0.011	0.024	0.044	0.030	0.025	0.041	0.006		0.035	0.033	0.024	0.026	0.015
P. g. jamesoni 91	0.062	0.077	0.070	0.075	0.073	0.028	0.023	0.024	0.016	0.036	0.022	0.017	0.033	0.029	0.035		0.008	0.023	0.019	0.027
P. g. kahurangica 88	0.061	0.075	0.068	0.074	0.071	0.026	0.021	0.022	0.015	0.035	0.020	0.015	0.031	0.028	0.033	0.008		0.021	0.017	0.025
P. g. montana 621	0.058	0.072	0.066	0.071	0.068	0.024	0.004	0.013	0.012	0.032	0.017	0.012	0.029	0.018	0.024	0.023	0.021		0.014	0.016
"Moutere Rv"590	0.054	0.068	0.061	0.067	0.064	0.019	0.014	0.015	0.008	0.028	0.013	0.008	0.024	0.021	0.026	0.019	0.017	0.014		0.018
P. g. subfusca 125	0.062	0.077	0.070	0.075	0.073	0.028	0.016	0.003	0.016	0.036	0.022	0.017	0.033	0.009	0.015	0.027	0.025	0.016	0.018	
P. h. anatokiensis 4	0.074	0.088	0.082	0.087	0.084	0.050	0.070	0.071	0.064	0.058	0.069	0.064	0.055	0.077	0.082	0.074	0.073	0.070	0.066	0.074
P. h. bicolor 206	0.094	0.108	0.101	0.106	0.104	0.069	0.090	0.091	0.083	0.078	0.089	0.084	0.074	0.096	0.102	0.094	0.093	0.090	0.086	0.094
P. h. consobrina 598	0.082	0.097	0.090	0.095	0.093	0.058	0.078	0.079	0.072	0.066	0.077	0.072	0.063	0.085	0.091	0.083	0.081	0.078	0.074	0.083
P. h. hochstetteri 265	0.072	0.087	0.080	0.085	0.083	0.048	0.068	0.069	0.062	0.056	0.067	0.062	0.053	0.075	0.081	0.073	0.071	0.068	0.064	0.073
P. h. obscura 612	0.081	0.095	0.089	0.094	0.091	0.057	0.077	0.078	0.071	0.065	0.076	0.071	0.062	0.084	0.089	0.081	0.080	0.077	0.073	0.081
P. t. koputaroa 514	0.087	0.102	0.095	0.100	0.098	0.063	0.083	0.084	0.077	0.071	0.082	0.077	0.068	0.090	0.096	0.088	0.086	0.083	0.079	0.088

	P. h. anatokiensis 4	*P. h. bicolor* 206	*P. h. consobrina* 598	*P. h. hochstetteri* 265	*P. h. obscura* 612	*P. t. koputaroa* 514	*P. t. latizona* 507	*P. t. otakia* (Huttons)520	*P. t. otakia* 524	*P. t. traversi* 275	*P. t. tararuaensis* 174	"Egmont" 158	"Kaimanawa" 660	"Kaweka" 658	"Maungaharuru" 638	*P. marchanti* 634	"Urewera" 184	*P. annectens* 143	"Gouland Ra" 10	*P. s. harveyi* 112
"Lodestone" 221	0.074	0.094	0.082	0.072	0.081	0.087	0.087	0.090	0.096	0.096	0.087	0.096	0.096	0.095	0.090	0.089	0.090	0.135	0.127	0.132
"Arnaud Range" 329	0.088	0.108	0.097	0.087	0.095	0.102	0.102	0.104	0.110	0.111	0.102	0.110	0.111	0.109	0.104	0.103	0.105	0.149	0.142	0.147
"Speargrass" 238	0.082	0.101	0.090	0.080	0.089	0.095	0.095	0.097	0.104	0.104	0.095	0.103	0.104	0.102	0.098	0.097	0.098	0.143	0.135	0.140
"Mt Murchison" 331	0.087	0.106	0.095	0.085	0.094	0.100	0.100	0.102	0.109	0.109	0.100	0.109	0.109	0.108	0.103	0.102	0.103	0.148	0.140	0.145
"Owen" 225	0.084	0.104	0.093	0.083	0.091	0.098	0.098	0.100	0.106	0.107	0.098	0.106	0.107	0.105	0.100	0.099	0.101	0.145	0.138	0.143
"Anatoki Range" 261	0.050	0.069	0.058	0.048	0.057	0.063	0.063	0.065	0.072	0.072	0.063	0.071	0.072	0.070	0.066	0.065	0.066	0.111	0.103	0.108
P. g. aurea 136	0.070	0.090	0.078	0.068	0.077	0.083	0.083	0.086	0.092	0.092	0.083	0.092	0.092	0.091	0.086	0.085	0.086	0.131	0.123	0.128
P. g brunnea 553	0.071	0.091	0.079	0.069	0.078	0.084	0.084	0.087	0.093	0.093	0.084	0.093	0.093	0.092	0.087	0.086	0.087	0.132	0.124	0.129
P. g. compta 212	0.064	0.083	0.072	0.062	0.071	0.077	0.077	0.079	0.086	0.086	0.077	0.086	0.086	0.084	0.080	0.079	0.080	0.125	0.117	0.122
P. g. fallax 2	0.058	0.078	0.066	0.056	0.065	0.071	0.071	0.074	0.080	0.080	0.071	0.080	0.080	0.079	0.074	0.073	0.074	0.119	0.111	0.116
P. g. fallax 12	0.069	0.089	0.077	0.067	0.076	0.082	0.082	0.085	0.091	0.091	0.082	0.091	0.091	0.090	0.085	0.084	0.085	0.130	0.122	0.127
P. g. fallax 231	0.064	0.084	0.072	0.062	0.071	0.077	0.077	0.080	0.086	0.086	0.077	0.086	0.087	0.085	0.080	0.079	0.081	0.125	0.117	0.123
P. g. fallax 234	0.055	0.074	0.063	0.053	0.062	0.068	0.068	0.070	0.077	0.077	0.068	0.076	0.077	0.075	0.071	0.070	0.071	0.116	0.108	0.113
P. g. gilliesi 149	0.077	0.096	0.085	0.075	0.084	0.090	0.090	0.092	0.099	0.099	0.090	0.098	0.099	0.097	0.093	0.092	0.093	0.138	0.130	0.135
"Haidinger"654	0.082	0.102	0.091	0.081	0.089	0.096	0.096	0.098	0.104	0.105	0.096	0.104	0.105	0.103	0.098	0.097	0.099	0.143	0.136	0.141
P. g. jamesoni 91	0.074	0.094	0.083	0.073	0.081	0.088	0.088	0.090	0.096	0.097	0.088	0.096	0.097	0.095	0.090	0.089	0.091	0.135	0.128	0.133
P. g. kahurangica 88	0.073	0.093	0.081	0.071	0.080	0.086	0.086	0.088	0.095	0.095	0.086	0.095	0.095	0.094	0.089	0.088	0.089	0.134	0.126	0.131
P. g. montana 621	0.070	0.090	0.078	0.068	0.077	0.083	0.083	0.086	0.092	0.092	0.083	0.092	0.092	0.091	0.086	0.085	0.086	0.131	0.123	0.128
"Moutere Rv'590	0.066	0.086	0.074	0.064	0.073	0.079	0.079	0.081	0.088	0.088	0.079	0.088	0.088	0.087	0.082	0.081	0.082	0.127	0.119	0.124
P. g. subfusca 125	0.074	0.094	0.083	0.073	0.081	0.088	0.088	0.090	0.096	0.097	0.088	0.096	0.097	0.095	0.090	0.089	0.091	0.135	0.128	0.133
P. h. anatokiensis 4		0.032	0.021	0.002	0.019	0.026	0.026	0.028	0.035	0.035	0.026	0.034	0.035	0.033	0.028	0.028	0.029	0.147	0.139	0.144
P. h. bicolor 206	0.032		0.032	0.031	0.030	0.032	0.032	0.034	0.041	0.041	0.032	0.041	0.041	0.039	0.021	0.034	0.022	0.167	0.159	0.164
P. h. consobrina 598	0.021	0.032		0.019	0.005	0.025	0.025	0.028	0.034	0.034	0.025	0.034	0.035	0.033	0.028	0.027	0.029	0.155	0.148	0.153
P. h. hochstetteri 265	0.002	0.031	0.019		0.018	0.024	0.024	0.027	0.033	0.033	0.024	0.033	0.033	0.032	0.027	0.026	0.027	0.145	0.138	0.143
P. h. obscura 612	0.019	0.030	0.005	0.018		0.024	0.024	0.026	0.033	0.033	0.024	0.032	0.033	0.031	0.027	0.026	0.027	0.154	0.146	0.151
P. t. koputaroa 514	0.026	0.032	0.025	0.024	0.024		0.003	0.010	0.016	0.016	0.003	0.016	0.012	0.011	0.028	0.005	0.029	0.160	0.153	0.158

	P. s. mouatae 127	*P. s. prouseorum* 589	*P. s. richardsoni* 97	*P. s. superba* (Bock)622	*P. s. superba* 156	"Gunner Downs" 364	*P. l. johnstoni* 290	*P. l. lignaria* 94	*P. l. lusca* 119	*P. l. oconnori* 3	*P. l. rotella* 84	*P. l. ruforadiata* 532	*P. l. unicolorata* 541	*P. l. unicolorata* 528	"Buller River" 71	*P. s. lateumbilicata* 51	*P. s. spedeni* 33	"Fox" 193	"Fox" 192	"Haast" 21
"Lodestone" 221	0.130	0.132	0.126	0.131	0.127	0.126	0.149	0.156	0.147	0.151	0.146	0.148	0.146	0.146	0.146	0.102	0.106	0.092	0.092	0.086
"Arnaud Range" 329	0.145	0.147	0.140	0.145	0.142	0.140	0.164	0.170	0.162	0.165	0.160	0.163	0.160	0.161	0.161	0.116	0.120	0.106	0.106	0.100
"Speargrass" 238	0.138	0.140	0.134	0.139	0.135	0.134	0.157	0.163	0.155	0.158	0.154	0.156	0.154	0.154	0.154	0.110	0.113	0.100	0.100	0.093
"Mt Murchison" 331	0.143	0.145	0.139	0.144	0.140	0.139	0.162	0.168	0.160	0.164	0.159	0.161	0.159	0.159	0.159	0.115	0.118	0.105	0.105	0.099
"Owen" 225	0.141	0.143	0.136	0.141	0.138	0.136	0.160	0.166	0.158	0.161	0.156	0.159	0.156	0.157	0.157	0.112	0.116	0.102	0.102	0.096
"Anatoki Range" 261	0.106	0.108	0.102	0.107	0.103	0.102	0.125	0.131	0.123	0.126	0.122	0.124	0.122	0.122	0.122	0.078	0.081	0.068	0.068	0.061
P. g. aurea 136	0.127	0.128	0.122	0.127	0.123	0.122	0.145	0.152	0.143	0.147	0.142	0.144	0.142	0.143	0.142	0.098	0.102	0.088	0.088	0.082
P. g brunnea 553	0.128	0.129	0.123	0.128	0.124	0.123	0.146	0.153	0.144	0.148	0.143	0.145	0.143	0.144	0.143	0.099	0.103	0.089	0.089	0.083
P. g. compta 212	0.120	0.122	0.116	0.121	0.117	0.116	0.139	0.145	0.137	0.141	0.136	0.138	0.136	0.136	0.136	0.092	0.095	0.082	0.082	0.076
P. g. fallax 2	0.114	0.116	0.110	0.115	0.111	0.110	0.133	0.140	0.131	0.135	0.130	0.132	0.130	0.130	0.130	0.086	0.090	0.076	0.076	0.070
P. g. fallax 12	0.125	0.127	0.121	0.126	0.122	0.121	0.144	0.151	0.142	0.146	0.141	0.143	0.141	0.141	0.141	0.097	0.101	0.087	0.087	0.081
P. g. fallax 231	0.121	0.122	0.116	0.121	0.117	0.116	0.139	0.146	0.138	0.141	0.136	0.139	0.136	0.137	0.137	0.092	0.096	0.082	0.082	0.076
P. g. fallax 234	0.111	0.113	0.107	0.112	0.108	0.107	0.130	0.136	0.128	0.131	0.127	0.129	0.127	0.127	0.127	0.083	0.086	0.073	0.073	0.066
P. g. gilliesi 149	0.133	0.135	0.128	0.134	0.130	0.129	0.152	0.158	0.150	0.153	0.149	0.151	0.149	0.149	0.149	0.105	0.108	0.095	0.095	0.088
"Haidinger"654	0.139	0.141	0.134	0.139	0.136	0.134	0.158	0.164	0.156	0.159	0.154	0.157	0.154	0.155	0.155	0.110	0.114	0.100	0.100	0.094
P. g. jamesoni 91	0.131	0.133	0.126	0.131	0.128	0.126	0.150	0.156	0.148	0.151	0.146	0.149	0.146	0.147	0.147	0.102	0.106	0.092	0.092	0.086
P. g. kahurangica 88	0.129	0.131	0.125	0.130	0.126	0.125	0.148	0.154	0.146	0.150	0.145	0.147	0.145	0.145	0.145	0.101	0.104	0.091	0.091	0.085
P. g. montana 621	0.127	0.128	0.122	0.127	0.123	0.122	0.145	0.152	0.143	0.147	0.142	0.144	0.142	0.143	0.143	0.098	0.102	0.088	0.088	0.082
"Moutere Rv'590	0.122	0.124	0.118	0.123	0.119	0.118	0.141	0.147	0.139	0.143	0.138	0.140	0.138	0.138	0.138	0.094	0.097	0.084	0.084	0.078
P. g. subfusca 125	0.131	0.133	0.126	0.131	0.128	0.126	0.150	0.156	0.148	0.151	0.146	0.149	0.146	0.147	0.147	0.102	0.106	0.092	0.092	0.086
P. h. anatokiensis 4	0.143	0.144	0.138	0.143	0.139	0.138	0.161	0.168	0.159	0.163	0.158	0.161	0.158	0.159	0.159	0.114	0.118	0.104	0.104	0.098
P. h. bicolor 206	0.162	0.164	0.158	0.163	0.159	0.158	0.181	0.187	0.179	0.183	0.178	0.180	0.178	0.178	0.178	0.134	0.137	0.124	0.124	0.118
P. h. consobrina 598	0.151	0.153	0.146	0.151	0.148	0.146	0.170	0.176	0.168	0.171	0.166	0.169	0.166	0.167	0.167	0.123	0.126	0.112	0.112	0.106
P. h. hochstetteri 265	0.141	0.143	0.136	0.141	0.138	0.136	0.160	0.166	0.158	0.161	0.156	0.159	0.156	0.157	0.157	0.112	0.116	0.102	0.102	0.096
P. h. obscura 612	0.149	0.151	0.145	0.150	0.146	0.145	0.168	0.175	0.166	0.170	0.165	0.167	0.165	0.165	0.165	0.121	0.125	0.111	0.111	0.105
P. t. koputaroa 514	0.156	0.158	0.151	0.156	0.153	0.151	0.175	0.181	0.173	0.176	0.171	0.174	0.171	0.172	0.172	0.128	0.131	0.117	0.117	0.111

	"Haast" 22	"Haast" 24	*P. r. rossiana* 342	*P. r. rossiana* 341	*P. fletcheri* 60	*P. gagei* 243	"Mt Bovis" 657	"Garabaldi" 247	"Baton" 239	"Radiant Ra" 664	"Matiri" 252	"Nardoo" 339	"Matakitaki" 254	*P. augusta* 390	*P. augusta* 404	"Buckland Pk" 580	"N. Brunner Ra" 395	"Denniston" 66	"Kirwins" 196	"Three Sisters" 200
"Lodestone" 221	0.086	0.088	0.095	0.097	0.134	0.125	0.133	0.162	0.162	0.160	0.163	0.161	0.154	0.136	0.150	0.145	0.158	0.145	0.145	0.150
"Arnaud Range" 329	0.100	0.102	0.109	0.111	0.148	0.139	0.148	0.176	0.176	0.175	0.177	0.175	0.168	0.150	0.165	0.159	0.172	0.159	0.159	0.164
"Speargrass" 238	0.093	0.095	0.102	0.104	0.142	0.133	0.141	0.170	0.170	0.168	0.170	0.169	0.162	0.143	0.158	0.152	0.165	0.153	0.153	0.158
"Mt Murchison" 331	0.099	0.101	0.108	0.109	0.147	0.138	0.146	0.175	0.175	0.173	0.176	0.174	0.167	0.149	0.163	0.158	0.170	0.158	0.158	0.163
"Owen" 225	0.096	0.098	0.105	0.107	0.144	0.135	0.144	0.172	0.172	0.171	0.173	0.171	0.164	0.146	0.161	0.155	0.168	0.155	0.155	0.160
"Anatoki Range" 261	0.061	0.063	0.070	0.072	0.110	0.101	0.109	0.138	0.138	0.136	0.138	0.137	0.130	0.111	0.126	0.120	0.133	0.121	0.121	0.126
P. g. aurea 136	0.082	0.084	0.091	0.093	0.130	0.121	0.129	0.158	0.158	0.156	0.159	0.157	0.150	0.132	0.146	0.141	0.154	0.141	0.141	0.146
P. g brunnea 553	0.083	0.085	0.092	0.094	0.131	0.122	0.130	0.159	0.159	0.157	0.160	0.158	0.151	0.133	0.147	0.142	0.155	0.142	0.142	0.147
P. g. compta 212	0.076	0.077	0.085	0.086	0.124	0.115	0.123	0.152	0.152	0.150	0.153	0.151	0.144	0.126	0.140	0.135	0.147	0.135	0.135	0.140
P. g. fallax 2	0.070	0.072	0.079	0.081	0.118	0.109	0.117	0.146	0.146	0.144	0.147	0.145	0.138	0.120	0.134	0.129	0.142	0.129	0.129	0.134
P. g. fallax 12	0.081	0.083	0.090	0.092	0.129	0.120	0.128	0.157	0.157	0.155	0.158	0.156	0.149	0.131	0.145	0.140	0.153	0.140	0.140	0.145
P. g. fallax 231	0.076	0.078	0.085	0.087	0.124	0.115	0.123	0.152	0.152	0.150	0.153	0.151	0.144	0.126	0.140	0.135	0.148	0.135	0.135	0.140
P. g. fallax 234	0.066	0.068	0.075	0.077	0.115	0.105	0.114	0.143	0.142	0.141	0.143	0.142	0.135	0.116	0.131	0.125	0.138	0.126	0.126	0.131
P. g. gilliesi 149	0.088	0.090	0.097	0.099	0.137	0.127	0.136	0.165	0.164	0.163	0.165	0.164	0.157	0.138	0.153	0.147	0.160	0.147	0.147	0.153
"Haidinger"654	0.094	0.096	0.103	0.105	0.142	0.133	0.142	0.170	0.170	0.169	0.171	0.169	0.162	0.144	0.158	0.153	0.166	0.153	0.153	0.158
P. g. jamesoni 91	0.086	0.088	0.095	0.097	0.134	0.125	0.134	0.162	0.162	0.161	0.163	0.162	0.154	0.136	0.151	0.145	0.158	0.145	0.145	0.150
P. g. kahurangica 88	0.085	0.087	0.094	0.095	0.133	0.124	0.132	0.161	0.161	0.159	0.162	0.160	0.153	0.135	0.149	0.144	0.156	0.144	0.144	0.149
P. g. montana 621	0.082	0.084	0.091	0.093	0.130	0.121	0.129	0.158	0.158	0.156	0.159	0.157	0.150	0.132	0.146	0.141	0.154	0.141	0.141	0.146
"Moutere Rv'590	0.078	0.080	0.087	0.088	0.126	0.117	0.125	0.154	0.154	0.152	0.155	0.153	0.146	0.128	0.142	0.137	0.149	0.137	0.137	0.142
P. g. subfusca 125	0.086	0.088	0.095	0.097	0.134	0.125	0.134	0.162	0.162	0.161	0.163	0.161	0.154	0.136	0.151	0.145	0.158	0.145	0.145	0.150
P. h. anatokiensis 4	0.098	0.100	0.107	0.109	0.146	0.137	0.145	0.174	0.174	0.172	0.175	0.173	0.166	0.148	0.162	0.157	0.170	0.157	0.157	0.162
P. h. bicolor 206	0.118	0.119	0.127	0.128	0.166	0.157	0.165	0.194	0.194	0.192	0.195	0.193	0.186	0.168	0.182	0.177	0.189	0.177	0.177	0.182
P. h. consobrina 598	0.106	0.108	0.115	0.117	0.154	0.145	0.154	0.182	0.182	0.181	0.183	0.182	0.174	0.156	0.171	0.165	0.178	0.165	0.165	0.170
P. h. hochstetteri 265	0.096	0.098	0.105	0.107	0.144	0.135	0.144	0.172	0.172	0.171	0.173	0.171	0.164	0.146	0.161	0.155	0.168	0.155	0.155	0.160
P. h. obscura 612	0.105	0.107	0.114	0.116	0.153	0.144	0.152	0.181	0.181	0.179	0.182	0.180	0.173	0.155	0.169	0.164	0.177	0.164	0.164	0.169
P. t. koputaroa 514	0.111	0.113	0.120	0.122	0.159	0.150	0.159	0.187	0.187	0.186	0.188	0.187	0.179	0.161	0.176	0.170	0.183	0.170	0.170	0.175

	"Mt Epping" 494	"Mt Stevenson" 495	*P. patrickensis* 488	"Mt McHardy" 493	"vittatus" 215	*P. fiordlandica* 337
"Lodestone" 221	0.149	0.152	0.153	0.145	0.147	0.358
"Arnaud Range" 329	0.164	0.166	0.167	0.160	0.161	0.373
"Speargrass" 238	0.157	0.160	0.161	0.153	0.154	0.366
"Mt Murchison" 331	0.162	0.165	0.166	0.158	0.160	0.371
"Owen" 225	0.160	0.162	0.163	0.156	0.157	0.369
"Anatoki Range" 261	0.125	0.128	0.129	0.121	0.122	0.334
P. g. aurea 136	0.145	0.148	0.149	0.141	0.143	0.354
P. g brunnea 553	0.146	0.149	0.150	0.142	0.144	0.355
P. g. compta 212	0.139	0.142	0.143	0.135	0.137	0.348
P. g. fallax 2	0.133	0.136	0.137	0.129	0.131	0.342
P. g. fallax 12	0.144	0.147	0.148	0.140	0.142	0.353
P. g. fallax 231	0.139	0.142	0.143	0.135	0.137	0.349
P. g. fallax 234	0.130	0.132	0.134	0.126	0.127	0.339
P. g. gilliesi 149	0.152	0.154	0.155	0.148	0.149	0.361
"Haidinger"654	0.158	0.160	0.161	0.154	0.155	0.367
P. g. jamesoni 91	0.150	0.152	0.153	0.146	0.147	0.359
P. g. kahurangica 88	0.148	0.151	0.152	0.144	0.146	0.357
P. g. montana 621	0.145	0.148	0.149	0.141	0.143	0.354
"Moutere Rv'590	0.141	0.144	0.145	0.137	0.139	0.350
P. g. subfusca 125	0.150	0.152	0.153	0.146	0.147	0.359
P. h. anatokiensis 4	0.161	0.164	0.165	0.157	0.159	0.371
P. h. bicolor 206	0.181	0.184	0.185	0.177	0.179	0.390
P. h. consobrina 598	0.170	0.172	0.173	0.166	0.167	0.379
P. h. hochstetteri 265	0.160	0.162	0.163	0.156	0.157	0.369
P. h. obscura 612	0.168	0.171	0.172	0.164	0.166	0.377
P. t. koputaroa 514	0.175	0.177	0.178	0.171	0.172	0.384

	"Lodestone" 221	"Arnaud Range" 329	"Speargrass" 238	"Mt Murchison" 331	"Owen" 225	"Anatoki Range" 261	*P. g. aurea* 136	*P. g brunnea* 553	*P. g. compta* 212	*P. g. fallax* 2	*P. g. fallax* 12	*P. g. fallax* 231	*P. g. fallax* 234	*P. g. gilliesi* 149	"Haidinger"654	*P. g. jamesoni* 91	*P. g. kahurangica* 88	*P. g. montana* 621	"Moutere Rv"590	*P. g. subfusca* 125
P. t. latizona 507	0.087	0.102	0.095	0.100	0.098	0.063	0.083	0.084	0.077	0.071	0.082	0.077	0.068	0.090	0.096	0.088	0.086	0.083	0.079	0.088
P. t. otakia (Huttons)520	0.090	0.104	0.097	0.102	0.100	0.065	0.086	0.087	0.079	0.074	0.085	0.080	0.070	0.092	0.098	0.090	0.088	0.086	0.081	0.090
P. t. otakia 524	0.096	0.110	0.104	0.109	0.106	0.072	0.092	0.093	0.086	0.080	0.091	0.086	0.077	0.099	0.104	0.096	0.095	0.092	0.088	0.096
P. t. traversi 275	0.096	0.111	0.104	0.109	0.107	0.072	0.092	0.093	0.086	0.080	0.091	0.086	0.077	0.099	0.105	0.097	0.095	0.092	0.088	0.097
P. t. tararuaensis 174	0.087	0.102	0.095	0.100	0.098	0.063	0.083	0.084	0.077	0.071	0.082	0.077	0.068	0.090	0.096	0.088	0.086	0.083	0.079	0.088
"Egmont" 158	0.096	0.110	0.103	0.109	0.106	0.071	0.092	0.093	0.086	0.080	0.091	0.086	0.076	0.098	0.104	0.096	0.095	0.092	0.088	0.096
"Kaimanawa"660	0.096	0.111	0.104	0.109	0.107	0.072	0.092	0.093	0.086	0.080	0.091	0.087	0.077	0.099	0.105	0.097	0.095	0.092	0.088	0.097
"Kaweka" 658	0.095	0.109	0.102	0.108	0.105	0.070	0.091	0.092	0.084	0.079	0.090	0.085	0.075	0.097	0.103	0.095	0.094	0.091	0.087	0.095
"Maungaharuru" 638	0.090	0.104	0.098	0.103	0.100	0.066	0.086	0.087	0.080	0.074	0.085	0.080	0.071	0.093	0.098	0.090	0.089	0.086	0.082	0.090
P. marchanti (Ruahine)634	0.089	0.103	0.097	0.102	0.099	0.065	0.085	0.086	0.079	0.073	0.084	0.079	0.070	0.092	0.097	0.089	0.088	0.085	0.081	0.089
"Urewera" 184	0.090	0.105	0.098	0.103	0.101	0.066	0.086	0.087	0.080	0.074	0.085	0.081	0.071	0.093	0.099	0.091	0.089	0.086	0.082	0.091
P. annectens 143	0.135	0.149	0.143	0.148	0.145	0.111	0.131	0.132	0.125	0.119	0.130	0.125	0.116	0.138	0.143	0.135	0.134	0.131	0.127	0.135
"Gouland Ra" 10	0.127	0.142	0.135	0.140	0.138	0.103	0.123	0.124	0.117	0.111	0.122	0.117	0.108	0.130	0.136	0.128	0.126	0.123	0.119	0.128
P. s. harveyi 112	0.132	0.147	0.140	0.145	0.143	0.108	0.128	0.129	0.122	0.116	0.127	0.123	0.113	0.135	0.141	0.133	0.131	0.128	0.124	0.133
P. s. mouatae 127	0.130	0.145	0.138	0.143	0.141	0.106	0.127	0.128	0.120	0.114	0.125	0.121	0.111	0.133	0.139	0.131	0.129	0.127	0.122	0.131
P. s. prouseorum 589	0.132	0.147	0.140	0.145	0.143	0.108	0.128	0.129	0.122	0.116	0.127	0.122	0.113	0.135	0.141	0.133	0.131	0.128	0.124	0.133
P. s. richardsoni 97	0.126	0.140	0.134	0.139	0.136	0.102	0.122	0.123	0.116	0.110	0.121	0.116	0.107	0.128	0.134	0.126	0.125	0.122	0.118	0.126
P. s. superba (Bock)622	0.131	0.145	0.139	0.144	0.141	0.107	0.127	0.128	0.121	0.115	0.126	0.121	0.112	0.134	0.139	0.131	0.130	0.127	0.123	0.131
P. s. superba 156	0.127	0.142	0.135	0.140	0.138	0.103	0.123	0.124	0.117	0.111	0.122	0.117	0.108	0.130	0.136	0.128	0.126	0.123	0.119	0.128
"Gunner Downs" 364	0.126	0.140	0.134	0.139	0.136	0.102	0.122	0.123	0.116	0.110	0.121	0.116	0.107	0.129	0.134	0.126	0.125	0.122	0.118	0.126
P. l. johnstoni 290	0.149	0.164	0.157	0.162	0.160	0.125	0.145	0.146	0.139	0.133	0.144	0.139	0.130	0.152	0.158	0.150	0.148	0.145	0.141	0.150
P. l. lignaria 94	0.156	0.170	0.163	0.168	0.166	0.131	0.152	0.153	0.145	0.140	0.151	0.146	0.136	0.158	0.164	0.156	0.154	0.152	0.147	0.156
P. l. lusca 119	0.147	0.162	0.155	0.160	0.158	0.123	0.143	0.144	0.137	0.131	0.142	0.138	0.128	0.150	0.156	0.148	0.146	0.143	0.139	0.148
P. l. oconnori 3	0.151	0.165	0.158	0.164	0.161	0.126	0.147	0.148	0.141	0.135	0.146	0.141	0.131	0.153	0.159	0.151	0.150	0.147	0.143	0.151
P. l. rotella 84	0.146	0.160	0.154	0.159	0.156	0.122	0.142	0.143	0.136	0.130	0.141	0.136	0.127	0.149	0.154	0.146	0.145	0.142	0.138	0.146
P. l. ruforadiata 532	0.148	0.163	0.156	0.161	0.159	0.124	0.144	0.145	0.138	0.132	0.143	0.139	0.129	0.151	0.157	0.149	0.147	0.144	0.140	0.149

	P. h. anatokiensis 4	*P. h. bicolor* 206	*P. h. consobrina* 598	*P. h. hochstetteri* 265	*P. h. obscura* 612	*P. t. koputaroa* 514	*P. t. latizona* 507	*P. t. otakia* (Huttons)520	*P. t. otakia* 524	*P. t. traversi* 275	*P. t. tararuaensis* 174	"Egmont" 158	"Kaimanawa" 660	"Kaweka" 658	"Maungaharuru" 638	*P. marchanti* 634	"Urewera" 184	*P. annectens* 143	"Gouland Ra" 10	*P. s. harveyi* 112
P. t. latizona 507	0.026	0.032	0.025	0.024	0.024	0.003		0.010	0.016	0.016	0.003	0.016	0.012	0.011	0.028	0.005	0.029	0.160	0.153	0.158
P. t. otakia (Huttons)520	0.028	0.034	0.028	0.027	0.026	0.010	0.010		0.013	0.014	0.010	0.013	0.019	0.017	0.031	0.011	0.031	0.163	0.155	0.160
P. t. otakia 524	0.035	0.041	0.034	0.033	0.033	0.016	0.016	0.013		0.004	0.016	0.019	0.025	0.023	0.037	0.018	0.037	0.169	0.161	0.167
P. t. traversi 275	0.035	0.041	0.034	0.033	0.033	0.016	0.016	0.014	0.004		0.016	0.020	0.025	0.024	0.037	0.018	0.038	0.169	0.162	0.167
P. t. tararuaensis 174	0.026	0.032	0.025	0.024	0.024	0.003	0.003	0.010	0.016	0.016		0.016	0.012	0.011	0.028	0.005	0.029	0.160	0.153	0.158
"Egmont" 158	0.034	0.041	0.034	0.033	0.032	0.016	0.016	0.013	0.019	0.020	0.016		0.025	0.023	0.037	0.017	0.037	0.169	0.161	0.166
"Kaimanawa"660	0.035	0.041	0.035	0.033	0.033	0.012	0.012	0.019	0.025	0.025	0.012	0.025		0.002	0.037	0.008	0.038	0.169	0.162	0.167
"Kaweka" 658	0.033	0.039	0.033	0.032	0.031	0.011	0.011	0.017	0.023	0.024	0.011	0.023	0.002		0.036	0.006	0.036	0.168	0.160	0.165
"Maungaharuru" 638	0.028	0.021	0.028	0.027	0.027	0.028	0.028	0.031	0.037	0.037	0.028	0.037	0.037	0.036		0.030	0.006	0.163	0.155	0.160
P. marchanti (Ruahine)634	0.028	0.034	0.027	0.026	0.026	0.005	0.005	0.011	0.018	0.018	0.005	0.017	0.008	0.006	0.030		0.030	0.162	0.154	0.159
"Urewera" 184	0.029	0.022	0.029	0.027	0.027	0.029	0.029	0.031	0.037	0.038	0.029	0.037	0.038	0.036	0.006	0.030		0.163	0.156	0.161
P. annectens 143	0.147	0.167	0.155	0.145	0.154	0.160	0.160	0.163	0.169	0.169	0.160	0.169	0.169	0.168	0.163	0.162	0.163		0.016	0.017
"Gouland Ra" 10	0.139	0.159	0.148	0.138	0.146	0.153	0.153	0.155	0.161	0.162	0.153	0.161	0.162	0.160	0.155	0.154	0.156	0.016		0.014
P. s. harveyi 112	0.144	0.164	0.153	0.143	0.151	0.158	0.158	0.160	0.167	0.167	0.158	0.166	0.167	0.165	0.160	0.159	0.161	0.017	0.014	
P. s. mouatae 127	0.143	0.162	0.151	0.141	0.149	0.156	0.156	0.158	0.165	0.165	0.156	0.164	0.165	0.163	0.158	0.158	0.159	0.019	0.009	0.017
P. s. prouseorum 589	0.144	0.164	0.153	0.143	0.151	0.158	0.158	0.160	0.166	0.167	0.158	0.166	0.167	0.165	0.160	0.159	0.161	0.017	0.014	0.003
P. s. richardsoni 97	0.138	0.158	0.146	0.136	0.145	0.151	0.151	0.154	0.160	0.160	0.151	0.160	0.160	0.159	0.154	0.153	0.154	0.015	0.005	0.012
P. s. superba (Bock)622	0.143	0.163	0.151	0.141	0.150	0.156	0.156	0.159	0.165	0.165	0.156	0.165	0.166	0.164	0.159	0.158	0.160	0.016	0.012	0.007
P. s. superba 156	0.139	0.159	0.148	0.138	0.146	0.153	0.153	0.155	0.161	0.162	0.153	0.161	0.162	0.160	0.155	0.154	0.156	0.016	0.006	0.014
"Gunner Downs" 364	0.138	0.158	0.146	0.136	0.145	0.151	0.151	0.154	0.160	0.160	0.151	0.160	0.161	0.159	0.154	0.153	0.155	0.015	0.005	0.012
P. l. johnstoni 290	0.161	0.181	0.170	0.160	0.168	0.175	0.175	0.177	0.183	0.184	0.175	0.183	0.184	0.182	0.177	0.176	0.178	0.132	0.125	0.130
P. l. lignaria 94	0.168	0.187	0.176	0.166	0.175	0.181	0.181	0.183	0.190	0.190	0.181	0.189	0.190	0.188	0.184	0.183	0.184	0.139	0.131	0.136
P. l. lusca 119	0.159	0.179	0.168	0.158	0.166	0.173	0.173	0.175	0.181	0.182	0.173	0.181	0.182	0.180	0.175	0.174	0.176	0.131	0.123	0.128
P. l. oconnori 3	0.163	0.183	0.171	0.161	0.170	0.176	0.176	0.178	0.185	0.185	0.176	0.185	0.185	0.184	0.179	0.178	0.179	0.134	0.126	0.131
P. l. rotella 84	0.158	0.178	0.166	0.156	0.165	0.171	0.171	0.174	0.180	0.180	0.171	0.180	0.181	0.179	0.174	0.173	0.175	0.129	0.122	0.127
P. l. ruforadiata 532	0.161	0.180	0.169	0.159	0.167	0.174	0.174	0.176	0.183	0.183	0.174	0.182	0.183	0.181	0.176	0.175	0.177	0.132	0.124	0.129

	P. s. mouatae 127	*P. s. prouseorum* 589	*P. s. richardsoni* 97	*P. s. superba* (Bock)622	*P. s. superba* 156	"Gunner Downs" 364	*P. l. johnstoni* 290	*P. l. lignaria* 94	*P. l. lusca* 119	*P. l. oconnori* 3	*P. l. rotella* 84	*P. l. ruforadiata* 532	*P. l. unicolorata* 541	*P. l. unicolorata* 528	"Buller River" 71	*P. s. lateumbilicata* 51	*P. s. spedeni* 33	"Fox" 193	"Fox" 192	"Haast" 21
P. t. latizona 507	0.156	0.158	0.151	0.156	0.153	0.151	0.175	0.181	0.173	0.176	0.171	0.174	0.171	0.172	0.172	0.128	0.131	0.117	0.117	0.111
P. t. otakia (Huttons)520	0.158	0.160	0.154	0.159	0.155	0.154	0.177	0.183	0.175	0.178	0.174	0.176	0.174	0.174	0.174	0.130	0.133	0.120	0.120	0.113
P. t. otakia 524	0.165	0.166	0.160	0.165	0.161	0.160	0.183	0.190	0.181	0.185	0.180	0.183	0.180	0.181	0.181	0.136	0.140	0.126	0.126	0.120
P. t. traversi 275	0.165	0.167	0.160	0.165	0.162	0.160	0.184	0.190	0.182	0.185	0.180	0.183	0.180	0.181	0.181	0.136	0.140	0.126	0.126	0.120
P. t. tararuaensis 174	0.156	0.158	0.151	0.156	0.153	0.151	0.175	0.181	0.173	0.176	0.171	0.174	0.171	0.172	0.172	0.127	0.131	0.117	0.117	0.111
"Egmont" 158	0.164	0.166	0.160	0.165	0.161	0.160	0.183	0.189	0.181	0.185	0.180	0.182	0.180	0.180	0.180	0.136	0.139	0.126	0.126	0.120
"Kaimanawa"660	0.165	0.167	0.160	0.166	0.162	0.161	0.184	0.190	0.182	0.185	0.181	0.183	0.181	0.181	0.181	0.137	0.140	0.127	0.127	0.120
"Kaweka" 658	0.163	0.165	0.159	0.164	0.160	0.159	0.182	0.188	0.180	0.184	0.179	0.181	0.179	0.179	0.179	0.135	0.138	0.125	0.125	0.119
"Maungaharuru" 638	0.158	0.160	0.154	0.159	0.155	0.154	0.177	0.184	0.175	0.179	0.174	0.176	0.174	0.174	0.174	0.130	0.134	0.120	0.120	0.114
P. marchanti (Ruahine)634	0.158	0.159	0.153	0.158	0.154	0.153	0.176	0.183	0.174	0.178	0.173	0.175	0.173	0.174	0.173	0.129	0.133	0.119	0.119	0.113
"Urewera" 184	0.159	0.161	0.154	0.160	0.156	0.155	0.178	0.184	0.176	0.179	0.175	0.177	0.174	0.175	0.175	0.131	0.134	0.121	0.121	0.114
P. annectens 143	0.019	0.017	0.015	0.016	0.016	0.015	0.132	0.139	0.131	0.134	0.129	0.132	0.129	0.130	0.130	0.074	0.078	0.075	0.075	0.069
"Gouland Ra" 10	0.009	0.014	0.005	0.012	0.006	0.005	0.125	0.131	0.123	0.126	0.122	0.124	0.122	0.122	0.122	0.067	0.070	0.068	0.068	0.061
P. s. harveyi 112	0.017	0.003	0.012	0.007	0.014	0.012	0.130	0.136	0.128	0.131	0.127	0.129	0.127	0.127	0.127	0.072	0.075	0.073	0.073	0.066
P. s. mouatae 127		0.017	0.008	0.015	0.009	0.008	0.128	0.134	0.126	0.129	0.125	0.127	0.125	0.125	0.125	0.070	0.073	0.071	0.071	0.064
P. s. prouseorum 589	0.017		0.012	0.007	0.014	0.012	0.130	0.136	0.128	0.131	0.127	0.129	0.127	0.127	0.127	0.072	0.075	0.073	0.073	0.066
P. s. richardsoni 97	0.008	0.012		0.011	0.002	0.003	0.123	0.130	0.121	0.125	0.120	0.123	0.120	0.121	0.121	0.065	0.069	0.066	0.066	0.060
P. s. superba (Bock)622	0.015	0.007	0.011		0.012	0.011	0.128	0.135	0.127	0.130	0.125	0.128	0.125	0.126	0.126	0.070	0.074	0.071	0.071	0.065
P. s. superba 156	0.009	0.014	0.002	0.012		0.005	0.125	0.131	0.123	0.126	0.122	0.124	0.122	0.122	0.122	0.067	0.070	0.068	0.068	0.061
"Gunner Downs" 364	0.008	0.012	0.003	0.011	0.005		0.124	0.130	0.122	0.125	0.120	0.123	0.120	0.121	0.121	0.065	0.069	0.066	0.066	0.060
P. l. johnstoni 290	0.128	0.130	0.123	0.128	0.125	0.124		0.016	0.017	0.011	0.003	0.018	0.006	0.007	0.106	0.100	0.103	0.090	0.089	0.083
P. l. lignaria 94	0.134	0.136	0.130	0.135	0.131	0.130	0.016		0.023	0.011	0.013	0.024	0.013	0.013	0.113	0.106	0.109	0.096	0.096	0.090
P. l. lusca 119	0.126	0.128	0.121	0.127	0.123	0.122	0.017	0.023		0.018	0.014	0.011	0.013	0.014	0.104	0.098	0.101	0.088	0.088	0.081
P. l. oconnori 3	0.129	0.131	0.125	0.130	0.126	0.125	0.011	0.011	0.018		0.008	0.019	0.008	0.008	0.108	0.101	0.105	0.091	0.091	0.085
P. l. rotella 84	0.125	0.127	0.120	0.125	0.122	0.120	0.003	0.013	0.014	0.008		0.015	0.003	0.004	0.103	0.096	0.100	0.086	0.086	0.080
P. l. ruforadiata 532	0.127	0.129	0.123	0.128	0.124	0.123	0.018	0.024	0.011	0.019	0.015		0.015	0.015	0.105	0.099	0.102	0.089	0.089	0.082

	"Haast" 22	"Haast" 24	*P. r. rossiana* 342	*P. r. rossiana* 341	*P. fletcheri* 60	*P. gagei* 243	"Mt Bovis" 657	"Garabaldi" 247	"Baton" 239	"Radiant Ra" 664	"Matiri" 252	"Nardoo" 339	"Matakitaki" 254	*P. augusta* 390	*P. augusta* 404	"Buckland Pk" 580	"N. Brunner Ra" 395	"Denniston" 66	"Kirwins" 196	"Three Sisters" 200
P. t. latizona 507	0.111	0.113	0.120	0.122	0.159	0.150	0.159	0.187	0.187	0.186	0.188	0.187	0.179	0.161	0.176	0.170	0.183	0.170	0.170	0.175
P. t. otakia (Huttons)520	0.113	0.115	0.122	0.124	0.162	0.153	0.161	0.190	0.190	0.188	0.190	0.189	0.182	0.163	0.178	0.173	0.185	0.173	0.173	0.178
P. t. otakia 524	0.120	0.122	0.129	0.131	0.168	0.159	0.167	0.196	0.196	0.194	0.197	0.195	0.188	0.170	0.184	0.179	0.192	0.179	0.179	0.184
P. t. traversi 275	0.120	0.122	0.129	0.131	0.168	0.159	0.168	0.196	0.196	0.195	0.197	0.196	0.188	0.170	0.185	0.179	0.192	0.179	0.179	0.184
P. t. tararuaensis 174	0.111	0.113	0.120	0.122	0.159	0.150	0.159	0.187	0.187	0.186	0.188	0.187	0.179	0.161	0.176	0.170	0.183	0.170	0.170	0.175
"Egmont" 158	0.120	0.122	0.129	0.131	0.168	0.159	0.167	0.196	0.196	0.194	0.197	0.195	0.188	0.170	0.184	0.179	0.191	0.179	0.179	0.184
"Kaimanawa"660	0.120	0.122	0.129	0.131	0.169	0.159	0.168	0.196	0.196	0.195	0.197	0.196	0.189	0.170	0.185	0.179	0.192	0.179	0.179	0.184
"Kaweka" 658	0.119	0.121	0.128	0.129	0.167	0.158	0.166	0.195	0.195	0.193	0.196	0.194	0.187	0.169	0.183	0.178	0.190	0.178	0.178	0.183
"Maungaharuru" 638	0.114	0.116	0.123	0.125	0.162	0.153	0.161	0.190	0.190	0.188	0.191	0.189	0.182	0.164	0.178	0.173	0.186	0.173	0.173	0.178
P. marchanti (Ruahine)634	0.113	0.115	0.122	0.124	0.161	0.152	0.160	0.189	0.189	0.187	0.190	0.188	0.181	0.163	0.177	0.172	0.185	0.172	0.172	0.177
"Urewera" 184	0.114	0.116	0.123	0.125	0.163	0.153	0.162	0.190	0.190	0.189	0.191	0.190	0.183	0.164	0.179	0.173	0.186	0.173	0.173	0.178
P. annectens 143	0.069	0.071	0.078	0.080	0.117	0.108	0.116	0.145	0.145	0.143	0.146	0.144	0.137	0.119	0.133	0.128	0.141	0.128	0.128	0.133
"Gouland Ra" 10	0.061	0.063	0.070	0.072	0.110	0.100	0.109	0.138	0.137	0.136	0.138	0.137	0.130	0.111	0.126	0.120	0.133	0.120	0.120	0.125
P. s. harveyi 112	0.066	0.068	0.075	0.077	0.115	0.105	0.114	0.143	0.142	0.141	0.143	0.142	0.135	0.116	0.131	0.125	0.138	0.125	0.125	0.131
P. s. mouatae 127	0.064	0.066	0.073	0.075	0.113	0.104	0.112	0.141	0.141	0.139	0.142	0.140	0.133	0.115	0.129	0.124	0.136	0.124	0.124	0.129
P. s. prouseorum 589	0.066	0.068	0.075	0.077	0.115	0.105	0.114	0.143	0.142	0.141	0.143	0.142	0.135	0.116	0.131	0.125	0.138	0.125	0.125	0.130
P. s. richardsoni 97	0.060	0.062	0.069	0.071	0.108	0.099	0.107	0.136	0.136	0.134	0.137	0.135	0.128	0.110	0.124	0.119	0.132	0.119	0.119	0.124
P. s. superba (Bock)622	0.065	0.067	0.074	0.076	0.113	0.104	0.112	0.141	0.141	0.140	0.142	0.140	0.133	0.115	0.129	0.124	0.137	0.124	0.124	0.129
P. s. superba 156	0.061	0.063	0.070	0.072	0.110	0.100	0.109	0.138	0.137	0.136	0.138	0.137	0.130	0.111	0.126	0.120	0.133	0.120	0.120	0.125
"Gunner Downs" 364	0.060	0.062	0.069	0.071	0.108	0.099	0.108	0.136	0.136	0.135	0.137	0.135	0.128	0.110	0.125	0.119	0.132	0.119	0.119	0.124
P. l. johnstoni 290	0.083	0.085	0.092	0.094	0.094	0.085	0.086	0.122	0.122	0.120	0.123	0.121	0.114	0.046	0.060	0.105	0.117	0.105	0.105	0.110
P. l. lignaria 94	0.090	0.092	0.099	0.100	0.100	0.091	0.093	0.128	0.128	0.126	0.129	0.127	0.120	0.052	0.067	0.111	0.124	0.111	0.111	0.116
P. l. lusca 119	0.081	0.083	0.090	0.092	0.092	0.083	0.084	0.120	0.120	0.118	0.121	0.119	0.112	0.044	0.059	0.103	0.115	0.103	0.103	0.108
P. l. oconnori 3	0.085	0.087	0.094	0.096	0.095	0.086	0.088	0.123	0.123	0.122	0.124	0.122	0.115	0.047	0.062	0.106	0.119	0.106	0.106	0.111
P. l. rotella 84	0.080	0.082	0.089	0.091	0.091	0.081	0.083	0.118	0.118	0.117	0.119	0.118	0.111	0.043	0.057	0.101	0.114	0.101	0.101	0.106
P. l. ruforadiata 532	0.082	0.084	0.091	0.093	0.093	0.084	0.085	0.121	0.121	0.119	0.122	0.120	0.113	0.045	0.060	0.104	0.117	0.104	0.104	0.109

	"Mt Epping" 494	"Mt Stevenson" 495	*P. patrickensis* 488	"Mt McHardy" 493	"vittatus" 215	*P. fiordlandica* 337
P. t. latizona 507	0.175	0.177	0.178	0.171	0.172	0.384
P. t. otakia (Huttons)520	0.177	0.180	0.181	0.173	0.174	0.386
P. t. otakia 524	0.183	0.186	0.187	0.179	0.181	0.393
P. t. traversi 275	0.184	0.186	0.187	0.180	0.181	0.393
P. t. tararuaensis 174	0.175	0.177	0.178	0.171	0.172	0.384
"Egmont" 158	0.183	0.186	0.187	0.179	0.181	0.392
"Kaimanawa"660	0.184	0.186	0.187	0.180	0.181	0.393
"Kaweka" 658	0.182	0.185	0.186	0.178	0.180	0.391
"Maungaharuru" 638	0.177	0.180	0.181	0.173	0.175	0.386
P. marchanti (Ruahine)634	0.176	0.179	0.180	0.172	0.174	0.385
"Urewera" 184	0.178	0.180	0.181	0.174	0.175	0.387
P. annectens 143	0.132	0.135	0.136	0.128	0.144	0.356
"Gouland Ra" 10	0.125	0.127	0.128	0.121	0.136	0.348
P. s. harveyi 112	0.130	0.132	0.133	0.126	0.141	0.353
P. s. mouatae 127	0.128	0.131	0.132	0.124	0.139	0.351
P. s. prouseorum 589	0.130	0.132	0.133	0.126	0.141	0.353
P. s. richardsoni 97	0.123	0.126	0.127	0.119	0.135	0.347
P. s. superba (Bock)622	0.129	0.131	0.132	0.125	0.140	0.352
P. s. superba 156	0.125	0.127	0.128	0.121	0.136	0.348
"Gunner Downs" 364	0.124	0.126	0.127	0.120	0.135	0.347
P. l. johnstoni 290	0.109	0.112	0.113	0.105	0.158	0.370
P. l. lignaria 94	0.115	0.118	0.119	0.112	0.165	0.376
P. l. lusca 119	0.107	0.110	0.111	0.103	0.156	0.368
P. l. oconnori 3	0.111	0.113	0.114	0.107	0.160	0.371
P. l. rotella 84	0.106	0.108	0.109	0.102	0.155	0.367
P. l. ruforadiata 532	0.108	0.111	0.112	0.104	0.157	0.369

	"Lodestone" 221	"Arnaud Range" 329	"Speargrass" 238	"Mt Murchison" 331	"Owen" 225	"Anatoki Range" 261	*P. g. aurea* 136	*P. g brunnea* 553	*P. g. compta* 212	*P. g. fallax* 2	*P. g. fallax* 12	*P. g. fallax* 231	*P. g. fallax* 234	*P. g. gilliesi* 149	"Haidinger"654	*P. g. jamesoni* 91	*P. g. kahurangica* 88	*P. g. montana* 621	"Moutere Rv"590	*P. g. subfusca* 125
P. l. unicolorata 541	0.146	0.160	0.154	0.159	0.156	0.122	0.142	0.143	0.136	0.130	0.141	0.136	0.127	0.149	0.154	0.146	0.145	0.142	0.138	0.146
P. l. unicolorata 528	0.146	0.161	0.154	0.159	0.157	0.122	0.143	0.144	0.136	0.130	0.141	0.137	0.127	0.149	0.155	0.147	0.145	0.143	0.138	0.147
"Buller River" 71	0.146	0.161	0.154	0.159	0.157	0.122	0.142	0.143	0.136	0.130	0.141	0.137	0.127	0.149	0.155	0.147	0.145	0.143	0.138	0.147
P. s. lateumbilicata 51	0.102	0.116	0.110	0.115	0.112	0.078	0.098	0.099	0.092	0.086	0.097	0.092	0.083	0.105	0.110	0.102	0.101	0.098	0.094	0.102
P. s. spedeni 33	0.106	0.120	0.113	0.118	0.116	0.081	0.102	0.103	0.095	0.090	0.101	0.096	0.086	0.108	0.114	0.106	0.104	0.102	0.097	0.106
"Fox" 193	0.092	0.106	0.100	0.105	0.102	0.068	0.088	0.089	0.082	0.076	0.087	0.082	0.073	0.095	0.100	0.092	0.091	0.088	0.084	0.092
"Fox" 192	0.092	0.106	0.100	0.105	0.102	0.068	0.088	0.089	0.082	0.076	0.087	0.082	0.073	0.095	0.100	0.092	0.091	0.088	0.084	0.092
"Haast" 21	0.086	0.100	0.093	0.099	0.096	0.061	0.082	0.083	0.076	0.070	0.081	0.076	0.066	0.088	0.094	0.086	0.085	0.082	0.078	0.086
"Haast" 22	0.086	0.100	0.093	0.099	0.096	0.061	0.082	0.083	0.076	0.070	0.081	0.076	0.066	0.088	0.094	0.086	0.085	0.082	0.078	0.086
"Haast" 24	0.088	0.102	0.095	0.101	0.098	0.063	0.084	0.085	0.077	0.072	0.083	0.078	0.068	0.090	0.096	0.088	0.087	0.084	0.080	0.088
P. r. rossiana 342	0.095	0.109	0.102	0.108	0.105	0.070	0.091	0.092	0.085	0.079	0.090	0.085	0.075	0.097	0.103	0.095	0.094	0.091	0.087	0.095
P. r. rossiana 341	0.097	0.111	0.104	0.109	0.107	0.072	0.093	0.094	0.086	0.081	0.092	0.087	0.077	0.099	0.105	0.097	0.095	0.093	0.088	0.097
P. fletcheri 60	0.134	0.148	0.142	0.147	0.144	0.110	0.130	0.131	0.124	0.118	0.129	0.124	0.115	0.137	0.142	0.134	0.133	0.130	0.126	0.134
P. gagei 243	0.125	0.139	0.133	0.138	0.135	0.101	0.121	0.122	0.115	0.109	0.120	0.115	0.105	0.127	0.133	0.125	0.124	0.121	0.117	0.125
"Mt Bovis" 657	0.133	0.148	0.141	0.146	0.144	0.109	0.129	0.130	0.123	0.117	0.128	0.123	0.114	0.136	0.142	0.134	0.132	0.129	0.125	0.134
"Garabaldi" 247	0.162	0.176	0.170	0.175	0.172	0.138	0.158	0.159	0.152	0.146	0.157	0.152	0.143	0.165	0.170	0.162	0.161	0.158	0.154	0.162
"Baton" 239	0.162	0.176	0.170	0.175	0.172	0.138	0.158	0.159	0.152	0.146	0.157	0.152	0.142	0.164	0.170	0.162	0.161	0.158	0.154	0.162
"Radiant Ra" 664	0.160	0.175	0.168	0.173	0.171	0.136	0.156	0.157	0.150	0.144	0.155	0.150	0.141	0.163	0.169	0.161	0.159	0.156	0.152	0.161
"Matiri" 252	0.163	0.177	0.170	0.176	0.173	0.138	0.159	0.160	0.153	0.147	0.158	0.153	0.143	0.165	0.171	0.163	0.162	0.159	0.155	0.163
"Nardoo" 339	0.161	0.175	0.169	0.174	0.171	0.137	0.157	0.158	0.151	0.145	0.156	0.151	0.142	0.164	0.169	0.162	0.160	0.157	0.153	0.161
"Matakitaki" 254	0.154	0.168	0.162	0.167	0.164	0.130	0.150	0.151	0.144	0.138	0.149	0.144	0.135	0.157	0.162	0.154	0.153	0.150	0.146	0.154
P. augusta 390	0.130	0.144	0.138	0.143	0.140	0.107	0.127	0.128	0.121	0.115	0.126	0.121	0.112	0.133	0.139	0.131	0.130	0.127	0.123	0.131
P. augusta 404	0.136	0.150	0.143	0.149	0.146	0.111	0.132	0.133	0.126	0.120	0.131	0.126	0.116	0.138	0.144	0.136	0.135	0.132	0.128	0.136
"Buckland Pk" 580	0.145	0.159	0.152	0.158	0.155	0.120	0.141	0.142	0.135	0.129	0.140	0.135	0.125	0.147	0.153	0.145	0.144	0.141	0.137	0.145
"N. Brunner Ra" 395	0.158	0.172	0.165	0.170	0.168	0.133	0.154	0.155	0.147	0.142	0.153	0.148	0.138	0.160	0.166	0.158	0.156	0.154	0.149	0.158
"Denniston" 66	0.145	0.159	0.153	0.158	0.155	0.121	0.141	0.142	0.135	0.129	0.140	0.135	0.126	0.147	0.153	0.145	0.144	0.141	0.137	0.145

	P. h. anatokiensis 4	*P. h. bicolor* 206	*P. h. consobrina* 598	*P. h. hochstetteri* 265	*P. h. obscura* 612	*P. t. koputaroa* 514	*P. t. latizona* 507	*P. t. otakia* (Huttons)520	*P. t. otakia* 524	*P. t. traversi* 275	*P. t. tararuaensis* 174	"Egmont" 158	"Kaimanawa" 660	"Kaweka" 658	"Maungaharuru" 638	*P. marchanti* 634	"Urewera" 184	*P. annectens* 143	"Gouland Ra" 10	*P. s. harveyi* 112
P. l. unicolorata 541	0.158	0.178	0.166	0.156	0.165	0.171	0.171	0.174	0.180	0.180	0.171	0.180	0.181	0.179	0.174	0.173	0.174	0.129	0.122	0.127
P. l. unicolorata 528	0.159	0.178	0.167	0.157	0.165	0.172	0.172	0.174	0.181	0.181	0.172	0.180	0.181	0.179	0.174	0.174	0.175	0.130	0.122	0.127
"Buller River" 71	0.159	0.178	0.167	0.157	0.165	0.172	0.172	0.174	0.181	0.181	0.172	0.180	0.181	0.179	0.174	0.173	0.175	0.130	0.122	0.127
P. s. lateumbilicata 51	0.114	0.134	0.123	0.112	0.121	0.128	0.128	0.130	0.136	0.136	0.127	0.136	0.137	0.135	0.130	0.129	0.131	0.074	0.067	0.072
P. s. spedeni 33	0.118	0.137	0.126	0.116	0.125	0.131	0.131	0.133	0.140	0.140	0.131	0.139	0.140	0.138	0.134	0.133	0.134	0.078	0.070	0.075
"Fox" 193	0.104	0.124	0.112	0.102	0.111	0.117	0.117	0.120	0.126	0.126	0.117	0.126	0.127	0.125	0.120	0.119	0.121	0.075	0.068	0.073
"Fox" 192	0.104	0.124	0.112	0.102	0.111	0.117	0.117	0.120	0.126	0.126	0.117	0.126	0.127	0.125	0.120	0.119	0.121	0.075	0.068	0.073
"Haast" 21	0.098	0.118	0.106	0.096	0.105	0.111	0.111	0.113	0.120	0.120	0.111	0.120	0.120	0.119	0.114	0.113	0.114	0.069	0.061	0.066
"Haast" 22	0.098	0.118	0.106	0.096	0.105	0.111	0.111	0.113	0.120	0.120	0.111	0.120	0.120	0.119	0.114	0.113	0.114	0.069	0.061	0.066
"Haast" 24	0.100	0.119	0.108	0.098	0.107	0.113	0.113	0.115	0.122	0.122	0.113	0.122	0.122	0.121	0.116	0.115	0.116	0.071	0.063	0.068
P. r. rossiana 342	0.107	0.127	0.115	0.105	0.114	0.120	0.120	0.122	0.129	0.129	0.120	0.129	0.129	0.128	0.123	0.122	0.123	0.078	0.070	0.075
P. r. rossiana 341	0.109	0.128	0.117	0.107	0.116	0.122	0.122	0.124	0.131	0.131	0.122	0.131	0.131	0.129	0.125	0.124	0.125	0.080	0.072	0.077
P. fletcheri 60	0.146	0.166	0.154	0.144	0.153	0.159	0.159	0.162	0.168	0.168	0.159	0.168	0.169	0.167	0.162	0.161	0.163	0.117	0.110	0.115
P. gagei 243	0.137	0.157	0.145	0.135	0.144	0.150	0.150	0.153	0.159	0.159	0.150	0.159	0.159	0.158	0.153	0.152	0.153	0.108	0.100	0.105
"Mt Bovis" 657	0.145	0.165	0.154	0.144	0.152	0.159	0.159	0.161	0.167	0.168	0.159	0.167	0.168	0.166	0.161	0.160	0.162	0.116	0.109	0.114
"Garabaldi" 247	0.174	0.194	0.182	0.172	0.181	0.187	0.187	0.190	0.196	0.196	0.187	0.196	0.196	0.195	0.190	0.189	0.190	0.145	0.138	0.143
"Baton" 239	0.174	0.194	0.182	0.172	0.181	0.187	0.187	0.190	0.196	0.196	0.187	0.196	0.196	0.195	0.190	0.189	0.190	0.145	0.137	0.142
"Radiant Ra" 664	0.172	0.192	0.181	0.171	0.179	0.186	0.186	0.188	0.194	0.195	0.186	0.194	0.195	0.193	0.188	0.187	0.189	0.143	0.136	0.141
"Matiri" 252	0.175	0.195	0.183	0.173	0.182	0.188	0.188	0.190	0.197	0.197	0.188	0.197	0.197	0.196	0.191	0.190	0.191	0.146	0.138	0.143
"Nardoo" 339	0.173	0.193	0.182	0.171	0.180	0.187	0.187	0.189	0.195	0.196	0.187	0.195	0.196	0.194	0.189	0.188	0.190	0.144	0.137	0.142
"Matakitaki" 254	0.166	0.186	0.174	0.164	0.173	0.179	0.179	0.182	0.188	0.188	0.179	0.188	0.189	0.187	0.182	0.181	0.183	0.137	0.130	0.135
P. augusta 390	0.142	0.161	0.150	0.140	0.149	0.155	0.155	0.158	0.164	0.164	0.155	0.164	0.164	0.163	0.158	0.157	0.158	0.114	0.107	0.112
P. augusta 404	0.148	0.168	0.156	0.146	0.155	0.161	0.161	0.163	0.170	0.170	0.161	0.170	0.170	0.169	0.164	0.163	0.164	0.119	0.111	0.116
"Buckland Pk" 580	0.157	0.177	0.165	0.155	0.164	0.170	0.170	0.173	0.179	0.179	0.170	0.179	0.179	0.178	0.173	0.172	0.173	0.128	0.120	0.125
"N. Brunner Ra" 395	0.170	0.189	0.178	0.168	0.177	0.183	0.183	0.185	0.192	0.192	0.183	0.191	0.192	0.190	0.186	0.185	0.186	0.141	0.133	0.138
"Denniston" 66	0.157	0.177	0.165	0.155	0.164	0.170	0.170	0.173	0.179	0.179	0.170	0.179	0.179	0.178	0.173	0.172	0.173	0.128	0.120	0.125

	P. s. mouatae 127	*P. s. prouseorum* 589	*P. s. richardsoni* 97	*P. s. superba* (Bock)622	*P. s. superba* 156	"Gunner Downs" 364	*P. l. johnstoni* 290	*P. l. lignaria* 94	*P. l. lusca* 119	*P. l. oconnori* 3	*P. l. rotella* 84	*P. l. ruforadiata* 532	*P. l. unicolorata* 541	*P. l. unicolorata* 528	"Buller River" 71	*P. s. lateumbilicata* 51	*P. s. spedeni* 33	"Fox" 193	"Fox" 192	"Haast" 21
P. l. unicolorata 541	0.125	0.127	0.120	0.125	0.122	0.120	0.006	0.013	0.013	0.008	0.003	0.015		0.004	0.103	0.096	0.100	0.086	0.086	0.080
P. l. unicolorata 528	0.125	0.127	0.121	0.126	0.122	0.121	0.007	0.013	0.014	0.008	0.004	0.015	0.004		0.104	0.097	0.100	0.087	0.087	0.080
"Buller River" 71	0.125	0.127	0.121	0.126	0.122	0.121	0.106	0.113	0.104	0.108	0.103	0.105	0.103	0.104		0.097	0.100	0.087	0.087	0.080
P. s. lateumbilicata 51	0.070	0.072	0.065	0.070	0.067	0.065	0.100	0.106	0.098	0.101	0.096	0.099	0.096	0.097	0.097		0.005	0.042	0.042	0.036
P. s. spedeni 33	0.073	0.075	0.069	0.074	0.070	0.069	0.103	0.109	0.101	0.105	0.100	0.102	0.100	0.100	0.100	0.005		0.046	0.046	0.040
"Fox" 193	0.071	0.073	0.066	0.071	0.068	0.066	0.090	0.096	0.088	0.091	0.086	0.089	0.086	0.087	0.087	0.042	0.046		0.003	0.026
"Fox" 192	0.071	0.073	0.066	0.071	0.068	0.066	0.089	0.096	0.088	0.091	0.086	0.089	0.086	0.087	0.087	0.042	0.046	0.003		0.026
"Haast" 21	0.064	0.066	0.060	0.065	0.061	0.060	0.083	0.090	0.081	0.085	0.080	0.082	0.080	0.080	0.080	0.036	0.040	0.026	0.026	
"Haast" 22	0.064	0.066	0.060	0.065	0.061	0.060	0.083	0.090	0.081	0.085	0.080	0.082	0.080	0.080	0.080	0.036	0.040	0.026	0.026	0.000
"Haast" 24	0.066	0.068	0.062	0.067	0.063	0.062	0.085	0.092	0.083	0.087	0.082	0.084	0.082	0.082	0.082	0.038	0.041	0.028	0.028	0.002
P. r. rossiana 342	0.073	0.075	0.069	0.074	0.070	0.069	0.092	0.099	0.090	0.094	0.089	0.091	0.089	0.089	0.089	0.045	0.049	0.018	0.018	0.029
P. r. rossiana 341	0.075	0.077	0.071	0.076	0.072	0.071	0.094	0.100	0.092	0.096	0.091	0.093	0.091	0.091	0.091	0.047	0.050	0.020	0.020	0.031
P. fletcheri 60	0.113	0.115	0.108	0.113	0.110	0.108	0.094	0.100	0.092	0.095	0.091	0.093	0.091	0.091	0.070	0.084	0.088	0.074	0.074	0.068
P. gagei 243	0.104	0.105	0.099	0.104	0.100	0.099	0.085	0.091	0.083	0.086	0.081	0.084	0.081	0.082	0.061	0.075	0.079	0.065	0.065	0.059
"Mt Bovis" 657	0.112	0.114	0.107	0.112	0.109	0.108	0.086	0.093	0.084	0.088	0.083	0.085	0.083	0.084	0.090	0.084	0.087	0.074	0.073	0.067
"Garabaldi" 247	0.141	0.143	0.136	0.141	0.138	0.136	0.122	0.128	0.120	0.123	0.118	0.121	0.118	0.119	0.027	0.112	0.116	0.102	0.102	0.096
"Baton" 239	0.141	0.142	0.136	0.141	0.137	0.136	0.122	0.128	0.120	0.123	0.118	0.121	0.118	0.119	0.027	0.112	0.116	0.102	0.102	0.096
"Radiant Ra" 664	0.139	0.141	0.134	0.140	0.136	0.135	0.120	0.126	0.118	0.122	0.117	0.119	0.117	0.117	0.025	0.111	0.114	0.101	0.101	0.094
"Matiri" 252	0.142	0.143	0.137	0.142	0.138	0.137	0.123	0.129	0.121	0.124	0.119	0.122	0.119	0.120	0.028	0.113	0.117	0.103	0.103	0.097
"Nardoo" 339	0.140	0.142	0.135	0.140	0.137	0.135	0.121	0.127	0.119	0.122	0.118	0.120	0.118	0.118	0.026	0.111	0.115	0.101	0.101	0.095
"Matakitaki" 254	0.133	0.135	0.128	0.133	0.130	0.128	0.114	0.120	0.112	0.115	0.111	0.113	0.111	0.111	0.019	0.104	0.108	0.094	0.094	0.088
P. augusta 390	0.110	0.112	0.105	0.110	0.107	0.106	0.046	0.052	0.043	0.047	0.043	0.044	0.043	0.043	0.090	0.082	0.085	0.072	0.072	0.066
P. augusta 404	0.115	0.116	0.110	0.115	0.111	0.110	0.046	0.052	0.044	0.047	0.043	0.045	0.043	0.043	0.093	0.086	0.090	0.076	0.076	0.070
"Buckland Pk" 580	0.124	0.125	0.119	0.124	0.120	0.119	0.105	0.111	0.103	0.106	0.101	0.104	0.101	0.102	0.008	0.095	0.099	0.085	0.085	0.079
"N. Brunner Ra" 395	0.136	0.138	0.132	0.137	0.133	0.132	0.117	0.124	0.115	0.119	0.114	0.117	0.114	0.115	0.021	0.108	0.111	0.098	0.098	0.092
"Denniston" 66	0.124	0.125	0.119	0.124	0.120	0.119	0.105	0.111	0.103	0.106	0.101	0.104	0.101	0.102	0.008	0.095	0.099	0.085	0.085	0.079

	"Haast" 22	"Haast" 24	*P. r. rossiana* 342	*P. r. rossiana* 341	*P. fletcheri* 60	*P. gagei* 243	"Mt Bovis" 657	"Garabaldi" 247	"Baton" 239	"Radiant Ra" 664	"Matiri" 252	"Nardoo" 339	"Matakitaki" 254	*P. augusta* 390	*P. augusta* 404	"Buckland Pk" 580	"N. Brunner Ra" 395	"Denniston" 66	"Kirwins" 196	"Three Sisters" 200
P. l. unicolorata 541	0.080	0.082	0.089	0.091	0.091	0.081	0.083	0.118	0.118	0.117	0.119	0.118	0.111	0.043	0.057	0.101	0.114	0.101	0.101	0.106
P. l. unicolorata 528	0.080	0.082	0.089	0.091	0.091	0.082	0.084	0.119	0.119	0.117	0.120	0.118	0.111	0.043	0.058	0.102	0.115	0.102	0.102	0.107
"Buller River" 71	0.080	0.082	0.089	0.091	0.070	0.061	0.090	0.027	0.027	0.025	0.028	0.026	0.019	0.093	0.107	0.008	0.021	0.008	0.008	0.013
P. s. lateumbilicata 51	0.036	0.038	0.045	0.047	0.084	0.075	0.084	0.112	0.112	0.111	0.113	0.111	0.104	0.086	0.101	0.095	0.108	0.095	0.095	0.100
P. s. spedeni 33	0.040	0.041	0.049	0.050	0.088	0.079	0.087	0.116	0.116	0.114	0.117	0.115	0.108	0.090	0.104	0.099	0.111	0.099	0.099	0.104
"Fox" 193	0.026	0.028	0.018	0.020	0.074	0.065	0.074	0.102	0.102	0.101	0.103	0.101	0.094	0.076	0.091	0.085	0.098	0.085	0.085	0.090
"Fox" 192	0.026	0.028	0.018	0.020	0.074	0.065	0.073	0.102	0.102	0.101	0.103	0.101	0.094	0.076	0.090	0.085	0.098	0.085	0.085	0.090
"Haast" 21	0.000	0.002	0.029	0.031	0.068	0.059	0.067	0.096	0.096	0.094	0.097	0.095	0.088	0.070	0.084	0.079	0.092	0.079	0.079	0.084
"Haast" 22		0.002	0.029	0.031	0.068	0.059	0.067	0.096	0.096	0.094	0.097	0.095	0.088	0.070	0.084	0.079	0.092	0.079	0.079	0.084
"Haast" 24	0.002		0.031	0.033	0.070	0.061	0.069	0.098	0.098	0.096	0.099	0.097	0.090	0.072	0.086	0.081	0.093	0.081	0.081	0.086
P. r. rossiana 342	0.029	0.031		0.005	0.077	0.068	0.076	0.105	0.105	0.103	0.106	0.104	0.097	0.079	0.093	0.088	0.101	0.088	0.088	0.093
P. r. rossiana 341	0.031	0.033	0.005		0.079	0.070	0.078	0.107	0.107	0.105	0.108	0.106	0.099	0.081	0.095	0.090	0.102	0.090	0.090	0.095
P. fletcheri 60	0.068	0.070	0.077	0.079		0.026	0.078	0.086	0.086	0.084	0.087	0.085	0.078	0.080	0.095	0.069	0.081	0.069	0.069	0.074
P. gagei 243	0.059	0.061	0.068	0.070	0.026		0.069	0.077	0.076	0.075	0.077	0.076	0.069	0.071	0.086	0.059	0.072	0.059	0.059	0.065
"Mt Bovis" 657	0.067	0.069	0.076	0.078	0.078	0.069		0.106	0.106	0.104	0.107	0.105	0.098	0.073	0.087	0.089	0.101	0.089	0.089	0.094
"Garabaldi" 247	0.096	0.098	0.105	0.107	0.086	0.077	0.106		0.003	0.016	0.026	0.024	0.021	0.108	0.123	0.025	0.038	0.025	0.025	0.030
"Baton" 239	0.096	0.098	0.105	0.107	0.086	0.076	0.106	0.003		0.016	0.026	0.024	0.021	0.108	0.123	0.025	0.038	0.025	0.025	0.030
"Radiant Ra" 664	0.094	0.096	0.103	0.105	0.084	0.075	0.104	0.016	0.016		0.024	0.023	0.020	0.107	0.121	0.024	0.036	0.024	0.024	0.029
"Matiri" 252	0.097	0.099	0.106	0.108	0.087	0.077	0.107	0.026	0.026	0.024		0.005	0.022	0.109	0.124	0.026	0.039	0.026	0.026	0.031
"Nardoo" 339	0.095	0.097	0.104	0.106	0.085	0.076	0.105	0.024	0.024	0.023	0.005		0.020	0.107	0.122	0.024	0.037	0.024	0.024	0.030
"Matakitaki" 254	0.088	0.090	0.097	0.099	0.078	0.069	0.098	0.021	0.021	0.020	0.022	0.020		0.100	0.115	0.017	0.030	0.017	0.017	0.022
P. augusta 390	0.066	0.068	0.075	0.077	0.079	0.070	0.068	0.105	0.105	0.104	0.106	0.104	0.097		0.006	0.088	0.101	0.088	0.088	0.093
P. augusta 404	0.070	0.072	0.079	0.081	0.080	0.071	0.073	0.108	0.108	0.107	0.109	0.107	0.100	0.000		0.091	0.104	0.091	0.091	0.096
"Buckland Pk" 580	0.079	0.081	0.088	0.090	0.069	0.059	0.089	0.025	0.025	0.024	0.026	0.024	0.017	0.091	0.106		0.019	0.007	0.007	0.008
"N. Brunner Ra" 395	0.092	0.093	0.101	0.102	0.081	0.072	0.101	0.038	0.038	0.036	0.039	0.037	0.030	0.104	0.118	0.019		0.019	0.019	0.024
"Denniston" 66	0.079	0.081	0.088	0.090	0.069	0.059	0.089	0.025	0.025	0.024	0.026	0.024	0.017	0.091	0.106	0.007	0.019		0.007	0.012

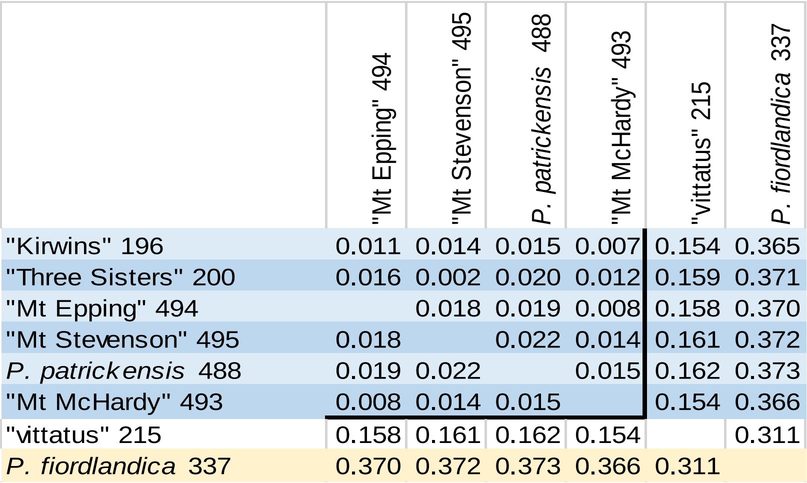
	"Mt Epping" 494	"Mt Stevenson" 495	*P. patrickensis* 488	"Mt McHardy" 493	"vittatus" 215	*P. fiordlandica* 337
P. l. unicolorata 541	0.106	0.108	0.109	0.102	0.155	0.367
P. l. unicolorata 528	0.106	0.109	0.110	0.102	0.155	0.367
"Buller River" 71	0.013	0.015	0.016	0.009	0.155	0.367
P. s. lateumbilicata 51	0.100	0.102	0.103	0.096	0.111	0.323
P. s. spedeni 33	0.103	0.106	0.107	0.099	0.114	0.326
"Fox" 193	0.090	0.092	0.093	0.086	0.101	0.313
"Fox" 192	0.090	0.092	0.093	0.086	0.101	0.313
"Haast" 21	0.083	0.086	0.087	0.079	0.095	0.306
"Haast" 22	0.083	0.086	0.087	0.079	0.095	0.306
"Haast" 24	0.085	0.088	0.089	0.081	0.097	0.308
P. r. rossiana 342	0.092	0.095	0.096	0.088	0.104	0.315
P. r. rossiana 341	0.094	0.097	0.098	0.090	0.106	0.317
P. fletcheri 60	0.073	0.076	0.077	0.069	0.143	0.355
P. gagei 243	0.064	0.066	0.067	0.060	0.134	0.345
"Mt Bovis" 657	0.093	0.096	0.097	0.089	0.142	0.354
"Garabaldi" 247	0.030	0.032	0.033	0.026	0.171	0.383
"Baton" 239	0.030	0.032	0.033	0.026	0.171	0.382
"Radiant Ra" 664	0.028	0.031	0.032	0.024	0.169	0.381
"Matiri" 252	0.031	0.033	0.034	0.027	0.172	0.383
"Nardoo" 339	0.029	0.031	0.032	0.025	0.170	0.382
"Matakitaki" 254	0.022	0.024	0.025	0.018	0.163	0.375
P. augusta 390	0.093	0.095	0.096	0.089	0.139	0.341
P. augusta 404	0.096	0.098	0.099	0.092	0.145	0.356
"Buckland Pk" 580	0.011	0.010	0.015	0.007	0.154	0.365
"N. Brunner Ra" 395	0.020	0.026	0.027	0.016	0.167	0.378
"Denniston" 66	0.011	0.014	0.008	0.007	0.154	0.365

	"Lodestone" 221	"Arnaud Range" 329	"Speargrass" 238	"Mt Murchison" 331	"Owen" 225	"Anatoki Range" 261	*P. g. aurea* 136	*P. g brunnea* 553	*P. g. compta* 212	*P. g. fallax* 2	*P. g. fallax* 12	*P. g. fallax* 231	*P. g. fallax* 234	*P. g. gilliesi* 149	"Haidinger"654	*P. g. jamesoni* 91	*P. g. kahurangica* 88	*P. g. montana* 621	"Moutere Rv"590	*P. g. subfusca* 125
"Kirwins" 196	0.145	0.159	0.153	0.158	0.155	0.121	0.141	0.142	0.135	0.129	0.140	0.135	0.126	0.147	0.153	0.145	0.144	0.141	0.137	0.145
"Three Sisters" 200	0.150	0.164	0.158	0.163	0.160	0.126	0.146	0.147	0.140	0.134	0.145	0.140	0.131	0.153	0.158	0.150	0.149	0.146	0.142	0.150
"Mt Epping" 494	0.149	0.164	0.157	0.162	0.160	0.125	0.145	0.146	0.139	0.133	0.144	0.139	0.130	0.152	0.158	0.150	0.148	0.145	0.141	0.150
"Mt Stevenson" 495	0.152	0.166	0.160	0.165	0.162	0.128	0.148	0.149	0.142	0.136	0.147	0.142	0.132	0.154	0.160	0.152	0.151	0.148	0.144	0.152
P. patrickensis 488	0.153	0.167	0.161	0.166	0.163	0.129	0.149	0.150	0.143	0.137	0.148	0.143	0.134	0.155	0.161	0.153	0.152	0.149	0.145	0.153
"Mt McHardy" 493	0.145	0.160	0.153	0.158	0.156	0.121	0.141	0.142	0.135	0.129	0.140	0.135	0.126	0.148	0.154	0.146	0.144	0.141	0.137	0.146
"vittatus" 215	0.147	0.161	0.154	0.160	0.157	0.122	0.143	0.144	0.137	0.131	0.142	0.137	0.127	0.149	0.155	0.147	0.146	0.143	0.139	0.147
P. fiordlandica 337	0.358	0.373	0.366	0.371	0.369	0.334	0.354	0.355	0.348	0.342	0.353	0.349	0.339	0.361	0.367	0.359	0.357	0.354	0.350	0.359

	P. h. anatokiensis 4	*P. h. bicolor* 206	*P. h. consobrina* 598	*P. h. hochstetteri* 265	*P. h. obscura* 612	*P. t. koputaroa* 514	*P. t. latizona* 507	*P. t. otakia* (Huttons)520	*P. t. otakia* 524	*P. t. traversi* 275	*P. t. tararuaensis* 174	"Egmont" 158	"Kaimanawa" 660	"Kaweka" 658	"Maungaharuru" 638	*P. marchanti* 634	"Urewera" 184	*P. annectens* 143	"Gouland Ra" 10	*P. s. harveyi* 112
"Kirwins" 196	0.157	0.177	0.165	0.155	0.164	0.170	0.170	0.173	0.179	0.179	0.170	0.179	0.179	0.178	0.173	0.172	0.173	0.128	0.120	0.125
"Three Sisters" 200	0.162	0.182	0.170	0.160	0.169	0.175	0.175	0.178	0.184	0.184	0.175	0.184	0.184	0.183	0.178	0.177	0.178	0.133	0.125	0.131
"Mt Epping" 494	0.161	0.181	0.170	0.160	0.168	0.175	0.175	0.177	0.183	0.184	0.175	0.183	0.184	0.182	0.177	0.176	0.178	0.132	0.125	0.130
"Mt Stevenson" 495	0.164	0.184	0.172	0.162	0.171	0.177	0.177	0.180	0.186	0.186	0.177	0.186	0.186	0.185	0.180	0.179	0.180	0.135	0.127	0.132
P. patrickensis 488	0.165	0.185	0.173	0.163	0.172	0.178	0.178	0.181	0.187	0.187	0.178	0.187	0.187	0.186	0.181	0.180	0.181	0.136	0.128	0.133
"Mt McHardy" 493	0.157	0.177	0.166	0.156	0.164	0.171	0.171	0.173	0.179	0.180	0.171	0.179	0.180	0.178	0.173	0.172	0.174	0.128	0.121	0.126
"vittatus" 215	0.159	0.179	0.167	0.157	0.166	0.172	0.172	0.174	0.181	0.181	0.172	0.181	0.181	0.180	0.175	0.174	0.175	0.144	0.136	0.141
P. fiordlandica 337	0.371	0.390	0.379	0.369	0.377	0.384	0.384	0.386	0.393	0.393	0.384	0.392	0.393	0.391	0.386	0.385	0.387	0.356	0.348	0.353

	P. s. mouatae 127	*P. s. prouseorum* 589	*P. s. richardsoni* 97	*P. s. superba* (Bock)622	*P. s. superba* 156	"Gunner Downs" 364	*P. l. johnstoni* 290	*P. l. lignaria* 94	*P. l. lusca* 119	*P. l. oconnori* 3	*P. l. rotella* 84	*P. l. ruforadiata* 532	*P. l. unicolorata* 541	*P. l. unicolorata* 528	"Buller River" 71	*P. s. lateumbilicata* 51	*P. s. spedeni* 33	"Fox" 193	"Fox" 192	"Haast" 21
"Kirwins" 196	0.124	0.125	0.119	0.124	0.120	0.119	0.105	0.111	0.103	0.106	0.101	0.104	0.101	0.102	0.008	0.095	0.099	0.085	0.085	0.079
"Three Sisters" 200	0.129	0.130	0.124	0.129	0.125	0.124	0.110	0.116	0.108	0.111	0.106	0.109	0.106	0.107	0.013	0.100	0.104	0.090	0.090	0.084
"Mt Epping" 494	0.128	0.130	0.123	0.129	0.125	0.124	0.109	0.115	0.107	0.111	0.106	0.108	0.106	0.106	0.013	0.100	0.103	0.090	0.090	0.083
"Mt Stevenson" 495	0.131	0.132	0.126	0.131	0.127	0.126	0.112	0.118	0.110	0.113	0.108	0.111	0.108	0.109	0.015	0.102	0.106	0.092	0.092	0.086
P. patrickensis 488	0.132	0.133	0.127	0.132	0.128	0.127	0.113	0.119	0.111	0.114	0.109	0.112	0.109	0.110	0.016	0.103	0.107	0.093	0.093	0.087
"Mt McHardy" 493	0.124	0.126	0.119	0.125	0.121	0.120	0.105	0.112	0.103	0.107	0.102	0.104	0.102	0.102	0.009	0.096	0.099	0.086	0.086	0.079
"vittatus" 215	0.139	0.141	0.135	0.140	0.136	0.135	0.158	0.165	0.156	0.160	0.155	0.157	0.155	0.155	0.155	0.111	0.114	0.101	0.101	0.095
P. fiordlandica 337	0.351	0.353	0.347	0.352	0.348	0.347	0.370	0.376	0.368	0.371	0.367	0.369	0.367	0.367	0.367	0.323	0.326	0.313	0.313	0.306

	"Haast" 22	"Haast" 24	*P. r. rossiana* 342	*P. r. rossiana* 341	*P. fletcheri* 60	*P. gagei* 243	"Mt Bovis" 657	"Garabaldi" 247	"Baton" 239	"Radiant Ra" 664	"Matiri" 252	"Nardoo" 339	"Matakitaki" 254	*P. augusta* 390	*P. augusta* 404	"Buckland Pk" 580	"N. Brunner Ra" 395	"Denniston" 66	"Kirwins" 196	"Three Sisters" 200
"Kirwins" 196	0.079	0.081	0.088	0.090	0.069	0.059	0.089	0.025	0.025	0.024	0.026	0.024	0.017	0.091	0.106	0.007	0.019	0.007		0.012
"Three Sisters" 200	0.084	0.086	0.093	0.095	0.074	0.065	0.094	0.030	0.030	0.029	0.031	0.030	0.022	0.096	0.111	0.008	0.024	0.012	0.012	
"Mt Epping" 494	0.083	0.085	0.092	0.094	0.073	0.064	0.093	0.030	0.030	0.028	0.031	0.029	0.022	0.096	0.110	0.011	0.020	0.011	0.011	0.016
"Mt Stevenson" 495	0.086	0.088	0.095	0.097	0.076	0.066	0.096	0.032	0.032	0.031	0.033	0.031	0.024	0.098	0.113	0.010	0.026	0.014	0.014	0.002
P. patrickensis 488	0.087	0.089	0.096	0.098	0.077	0.067	0.097	0.033	0.033	0.032	0.034	0.032	0.025	0.099	0.114	0.015	0.027	0.008	0.015	0.020
"Mt McHardy" 493	0.079	0.081	0.088	0.090	0.069	0.060	0.089	0.026	0.026	0.024	0.027	0.025	0.018	0.092	0.106	0.007	0.016	0.007	0.007	0.012
"vittatus" 215	0.095	0.097	0.104	0.106	0.143	0.134	0.142	0.171	0.171	0.169	0.172	0.170	0.163	0.145	0.159	0.154	0.167	0.154	0.154	0.159
P. fiordlandica 337	0.306	0.308	0.315	0.317	0.355	0.345	0.354	0.383	0.382	0.381	0.383	0.382	0.375	0.356	0.371	0.365	0.378	0.365	0.365	0.371



	"Mt Epping" 494	"Mt Stevenson" 495	*P. patrickensis* 488	"Mt McHardy" 493	"vittatus" 215	*P. fiordlandica* 337
"Kirwins" 196	0.011	0.014	0.015	0.007	0.154	0.365
"Three Sisters" 200	0.016	0.002	0.020	0.012	0.159	0.371
"Mt Epping" 494		0.018	0.019	0.008	0.158	0.370
"Mt Stevenson" 495	0.018		0.022	0.014	0.161	0.372
P. patrickensis 488	0.019	0.022		0.015	0.162	0.373
"Mt McHardy" 493	0.008	0.014	0.015		0.154	0.366
"vittatus" 215	0.158	0.161	0.162	0.154		0.311
P. fiordlandica 337	0.370	0.372	0.373	0.366	0.311	

Chapter 3.

Appearances do matter: morphology supports genotypic clustering in *Powelliphanta*.

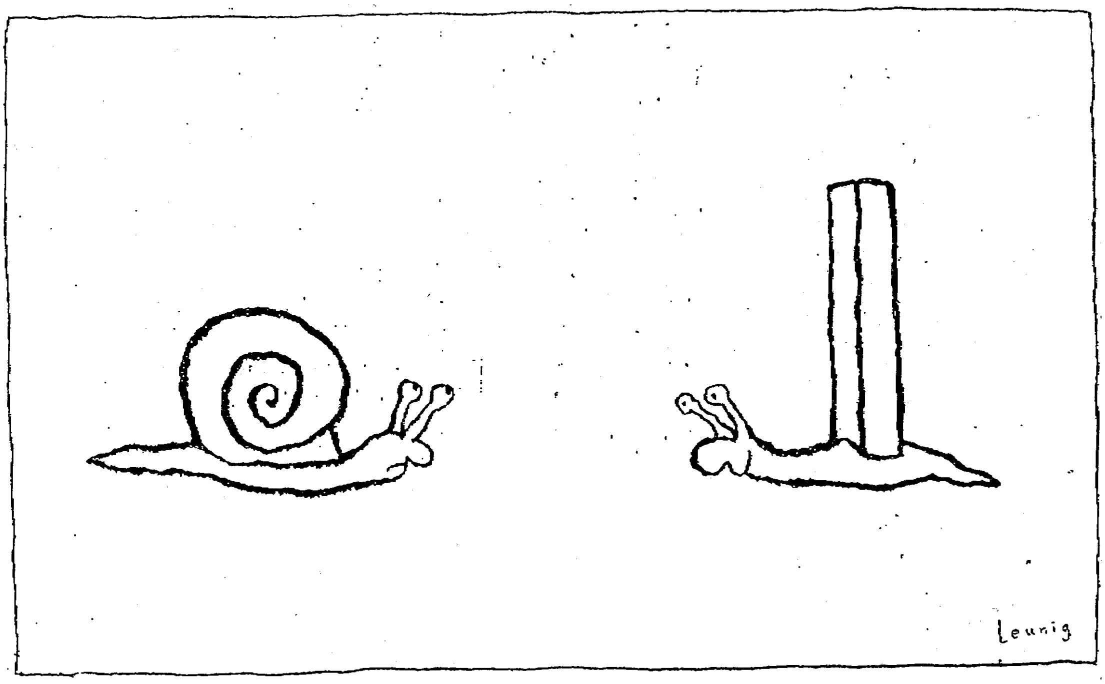


Image previous page: Cartoon by Michael Leunig, reproduced from "The Age" newspaper

Introduction

In a tsunami of molecular approaches to species recognition, morphology remains a rich and reliable source of information about systematic, evolutionary, and ecological relationships (McLellan & Endler 1998). Knowledge of morphological characters remains the usual way potential species are initially identified and tested, described and subsequently recognised (Wheeler 2007). The extent to which phylogeny can be inferred from morphology is still being examined, with land snails particularly useful subjects due to the longevity of their shells (Hills et al. 2012). A few lineages of the southern land snail family Rhytididae (Pilsbry 1883) are morphologically diverse, including shell colour and pattern, while most are not, providing fertile ground for such study.

The Rhytididae (Mollusca; Gastropoda; Pulmonata) are a group of small to very large carnivorous land snails with a southern hemisphere distribution (South Africa, Australia, New Zealand and islands in the south west Pacific) and a particularly rich fauna in New Zealand (Spencer 2006). The relatively high taxonomic diversity in New Zealand may however, be an artifact of early identification of taxa there due to conspicuous shell diversity. Recent studies have shown the morphologically-conservative South African rhytidids do in fact contain significant genetic diversity (Moussalli et al. 2009; Moussalli & Herbert 2016).

Within New Zealand rhytidids, morphological diversity is most conspicuous in *Powelliphanta,* a genus of medium to large snails. Other New Zealand genera such as the small to medium-sized *Rhytida* and *Wainuia* snails are nearly as morphologically-conservative as South African rhytidids, but like them, have recently been found to be taxonomically rich (Efford et al. 2002; Fred Brook pers. comm.). It is not clear why *Powelliphanta* are so much more morphologically diverse than other New Zealand rhytidids occupying similar habitats and, in the absence of any explanation, *Powelliphanta* taxonomy has suffered from a persistent view that morphology may have been a misleading guide to phylogenetic and taxonomic diversity in the genus (Climo 1978, Parkinson 1979, Buckley et al. 2014).

The most striking feature of *Powelliphanta* is their large size (up to 90 mm shell diameter) and strongly patterned and coloured shells, so conchology was the basis for early classification into 10 species and 27 subspecies (Powell 1930, 1932, 1936, 1938, 1946). However, shell variation as the basis for classification is treated cautiously by some, as shells—being external—are considered particularly susceptible to selective processes and can therefore be more homoplastic than other characters (Kool 1993, Robertson 1996, but see Schander & Sundberg 2001 and references therein). Others have argued that with careful use of sufficient morphological characters, adult shells provide useful information on evolutionary relationships (Wagner 2001, Papadopoulos et al. 2004). Since the 1980s many new populations of *Powelliphanta* have been discovered (Walker 2003) but their assessment and classification has awaited further information on the relationship of morphology to phylogeny in the whole group. Recent molecular study provided evidence of a strong genetic basis to at least some of the morphological diversity (Trewick et al. 2008).

Powelliphanta occur in small spatially separate populations in the wetter western or mountainous parts of New Zealand from the middle of the North Island to the south of the South Island (Figure 1). Many of Powell's species are allopatric but the medium-sized *P. gilliesi* is sympatric in north-west Nelson with large *P. superba*. Overlaps of other species of more similar size occur on a smaller scale (~1^2 km) in some places in north-west Nelson: eg. Parapara Peak (*P. hochstetteri* and *P. superba*; *P. gilliesi fallax* and "Anatoki Range") and on Mt Owen ("Owen" and "Matiri"). These instances of sympatry provide strong evidence of an inherited rather than an environmental basis to the shell diversity within *Powelliphanta*.

Many described or tag-named species of *Powelliphanta* are threatened (Hitchmough et al. 2007) but need taxonomic stability for conservation planning. A more comprehensive examination of morphological variation in *Powelliphanta* than has previously been undertaken could (1) improve understanding of the nature and possible causes of morphological diversity in *Powelliphanta* (2) help determine the validity of species and subspecies within *Powelliphanta,* and (3) provide useful ways of identifying and defining them.

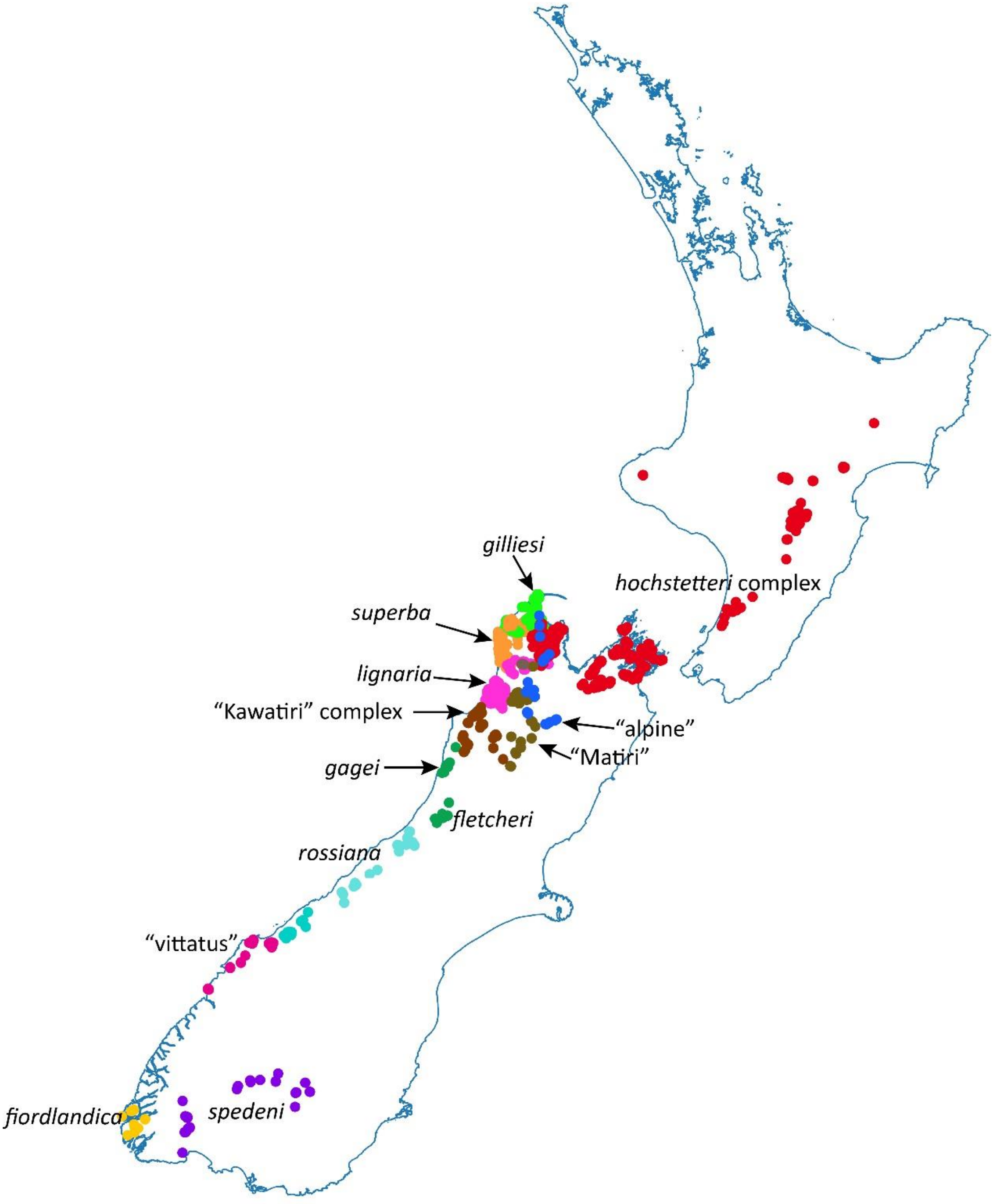


Figure 1. Distribution of *Powelliphanta* species or species complexes described in chapter 2 which were examined (including their subspecies—not shown) in the morphological study.

This study aims to complement a molecular study of the whole genus (Chapter 2) by assessing the morphological distinctiveness of currently described (Climo 1978, Powell 1979) and proposed (Walker 2003; Chapter 2) species and subspecies of *Powelliphanta* and their validity as separate taxa. A key part of this is the identification of additional taxonomically informative morphological characters whose measurement can consistently be undertaken by a variety of observers.

Three questions are addressed: (1) can the addition of modern morphometrics improve taxonomic resolution and lend support to the genotypic clusters identified in the molecular study? (2) does use of a broad suite of morphological characters resolve the intra-specific diversity into convincing subspecies? (3) What is behind the strikingly high levels of morphological diversity in *Powelliphanta* given morphological conservatism in most Rhytididae?

To investigate these matters, computer-assisted non-linear measures, external soft body morphology and fourier shape analysis are added to traditional conchological characters (colour and pattern) to develop a numerical matrix representing morphological traits. These are used to create a phenogram whose topology is compared with molecular-based *Powelliphanta* phylogenies. As the distribution of *Powelliphanta* is well known, the nature of the physical environment around identified phenotypic and genotypic clusters will be considered and suggestions made as to possible relationships.

Methods

Material examined

Empty *Powelliphanta* shells were collected from at least the type locality but usually from many additional populations of each of Powell's species, subspecies and forms, and from any presumed new taxa, discovered after Powell's time and informally tag-named by Walker (2003). The empty shells were compared to type material held at the AIM and NMNZ, assigned to one of Powell's taxa on their morphological similarity to the described types and geographic location, and held at the New Zealand Department of Conservation, Nelson (DOCNn). This collection, comprising c.45,000 individuals in c.6,000 lots, was the source of shells selected for morphometric study. For each previously described subspecies (Powell 1979) and tag-named taxa (Walker 2003)—a total of 73 à priori groups—between 4 and 6 specimens were selected for detailed analysis. As most of Powell's species were identified by conchology and contained 5 to 9 subspecies, between 30 and 54 specimens of each previously described species were examined, which accordingly included the range of conchological variation within each of those species.

Shells for measurement were selected for size and intactness. Shell growth in *Powelliphanta* continues throughout life. This indeterminate growth makes it difficult to separate size and shape variation attributable to ontogeny from that attributable to variation among individuals, and this complicates efforts to distinguish taxa by morphometrics. Nonetheless, growth in *Powelliphanta* does slow greatly in “old age”, and from breeding studies the size at which each taxon becomes reproductive is known (K. Walker, unpubl. data). Further, in old age the last portion of the body whorl descends more relative to the proceeding whorl (ie. the point of insertion of the upper aperture rim on the body whorl descends from the horizontal plane), so that its certain in those individuals that growth has all but ceased. In some species the descent from the horizontal plane is very pronounced, while in other species it is very limited. To increase the likelihood that shell characteristics of adults of a similar age were compared, only shells which had reached the standard adult 4.5-5.0 whorls, were amongst the largest, and/or had the greatest last-whorl-descent within each collection, were selected for measurement. As comparatively few of the shells from snails in old age were intact, choices within each of the 73 groups were constrained and essentially random.

The soft bodies of live snails captured for tissue sampling for molecular study (Chapter 2) were examined and photographed when the snails emerged from their shells, so that the appearance of live snails from different locations could be compared. Usually 3-6 snails from each described or tag-named *Powelliphanta* species and subspecies were examined, but often more and occasionally fewer (see Table 1 and Figure 1 in Chapter 2 for details). Photographs of incidentally found additional live snails, whose DNA was not sampled but whose exact location was known, were also examined and recorded in this way.

In the text, tables and phenograms *Powelliphanta* snails are referred to in a standardized format, with formally described taxa in italics, and informal tag-named taxa (usually the name of the place they were found, hence capitalized) within quotation marks in regular font. The genus name is omitted in figures to aid clarity. For analyses the taxa are grouped into the genotypic clusters suggested by Walker (2003). Those clusters which comprise subspecies and presumed new subspecies of described taxa are referred to by the relevant species name, while those clusters comprising undescribed taxa are referred to by newly-coined cluster tag-names, that is “Kawatiri” for all the small alpine snails of the Buller area and “Alpine” for all the small alpine snails of the Nelson area (see colour-coded dots for location of these clusters in Figure 1).

Morphometric matrix

A morphological dataset was assembled comprising (1) categorical characters (external soft body and egg characters, shell colour, texture, pattern, structure, sculpture and form) scored from live snails (or photos of live snails) and the large collection of empty shells, and (2) metric data (computer-assisted measures of shell dimensions, area and shape) scored from digital images of the 328 shells in the 73 à priori groups.

For each of the 73 groups, 3 digital images of all 4–6 shells in each group were taken; the dorsal surface, the ventral surface, and the shells in profile. In profile, all shells were orientated such that an imaginary horizontal line along the top of the body whorl to the suture and a horizontal line along the bottom of the body whorl to the umbilicus were parallel to each other with both the suture and umbilicus equally visible at the same time (Figure 2).

As advised by Collins & Gazley (2017) all imaging was undertaken by the same photographer, in the same light conditions with the same camera and lens to limit the introduction of variation to the measurement through the photographic process. A Nikon F90 SLR camera with a 70–100 mm lens was set on a tripod 1 m above the shells which were grouped in the centre of view to reduce parallax. Focal length was kept constant between most groups but was adjusted for photographing groups of very large snails to ensure all in the group were well away from the edge of the image, and very small sized snails to ensure there was enough depth and detail in the image. ImageJ (Rasband 2008) was used to standardize the scale between photographs.

Categorical character states

Categorical character states thought to be useful in differentiating between taxa were identified by a careful examination of the variation within *Powelliphanta* (Figure 2), and each à priori taxon was scored for each character. Care was taken in selection of characters to avoid redundancies and character dependence which might over-weight some characters. Almost all characters had more than two states and absence was treated as a separate character and as carefully delimited as the other character states, as advised by Jenner (2002).

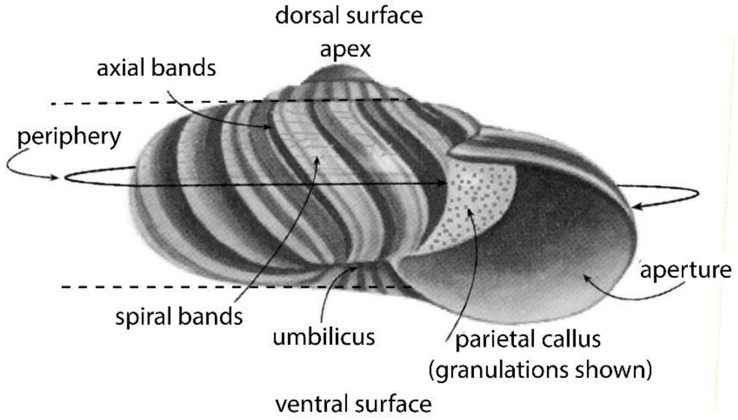


Figure 2. Names and location of some of the *Powelliphanta* shell features that provided categorical characters, including shell colour, pattern and texture. Dashes indicate 2 imaginary lines which were kept parallel when positioning shells for profile photography.

Seventeen categorical characters were used: 3 soft-body attributes (mantle/mucous colour, foot fringe colour and texture; Figure 3), an egg descriptor (colour/texture/shape), 12 features of the shell (whorl number and expansion rate, suture shape, umbilicus depth, shell colour and pattern, colour and texture of the parietal callus, shell sculpture and appearance), and 1 structural attribute (shell position during locomotion; Figure 4). The states defined for each of these categorical characters are listed in Appendix 1.

Linear and area measures

ImageJ (Rasband 2008) was used to make many computer-assisted standard linear and area measures on each photographed shell. After initial assessment of results these were reduced to a smaller number of measures for which principal components analysis explained most of the variation between groups. Size is often considered to be more sensitive to environmental variation than shape, so size and shape were separated by transforming the linear measures by dividing them by maximum shell diameter and excluding any other direct measures of size. The measures used in the final analysis are shown in Figure 5.

Figure 3. Some of the states in two of the soft-body characters thought to be useful in discriminating taxa, as illustrated in (clockwise from top) *P. superba superba*, *P. gilliesi montana* and *P. lignaria lignaria*): **(1) foot fringe colour** is "white" (top snail) or is "same as body" (bottom two snails), and **(2) foot colour/texture** is "slate-grey background, fine black reticulation" (top and bottom right snails) or "pinkish-white background, coarse black reticulation (bottom left snail). All the snails in this image, are sexually mature, illustrating the large differences in size between the described species, though size per sé was not used as an input to the character matrix.

Figure 4. The 2 states for the character "shell position during locomotion", with *P. lignaria lignaria* (left image) illustrating state (1) "towards rear, covering tail", and *P. fiordlandica* (right image) illustrating state (2) "central, with tail exposed".

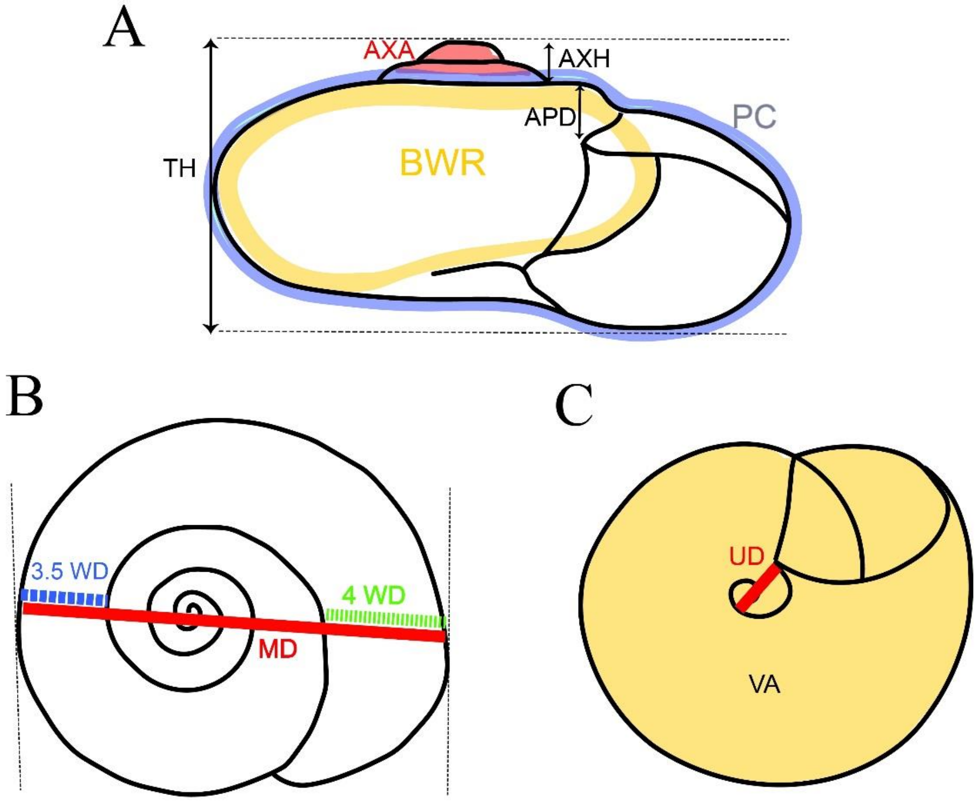


Figure 5. Placement of shell measurements on *Powelliphanta*. (A) Profile: **TH**, total height; **AXH***, apex height; **AXA***, apex area; **APD***, aperture drop, the distance the point of insertion of the upper aperture rim on the body whorl has descended from the horizontal plane; **BWR**, body whorl roundness; **PC**, profile circularity from outline digitization, when 0=infinitely elongated polygon & 1=perfect circle (B) Upper Surface: **MD**, maximum diameter; **3.5WD***, diameter of 4th (last) whorl at mid-point in the whorl, measured along the straight line of the shell's maximum diameter; **4WD***, diameter of 4th (last) whorl at aperture (C) Lower Surface: **UD**, umbilicus diameter: **VA***, ventral area. Those measures marked with * were used as ratios in the analysis: in A by division by MD; in B by division of 3.5WD/4WD; in C by division of UD/VA, to remove size from shape as far as possible, as the effects of size, if not removed, will dominate any analysis of shape (Crampton & Maxwell 2000).

While the assistance of a computer to take such measures is known to increase their accuracy (Alonso et al. 2006), it was found sensitive to small variations in the tilt of the shell in profile and shadow (particularly in the umbilicus) within the photographs, so images with shadow or where shells were not clearly parallel to the lens were repeated. This was considered important as initial screening found the measures that separated the groups most dramatically, aperture drop, apex height and umbilicus diameter, were those most difficult to measure in a standard repeatable manner.

Outline shape

Fourier shape analysis was used to capture subtle shape differences of the photographed *Powelliphanta* shells, as outline is recognized as particularly significant for visual recognition in taxonomy (Scott 1980). Fourier outline shape analysis is a technique for generating from landmark-poor outlines a set of shape-representing variates that are suitable for use in statistical comparisons between samples (Crampton 1995). The outline of each shell in profile was finely digitally traced using ImageJ to create a polygon of digitised xy-cordinates from which Fourier coefficients were derived using the computer programme Hangle (Crampton and Haines 1996). These coefficients describe the size, shape and orientation of each harmonic ellipse and form the input into subsequent multivariate statistical analysis. Finally, the outline of each shell was reconstructed according to the Fourier descriptors using HCURVE (Crampton and Haines 1996).

Analysis

The programme Hangle (Crampton and Haines 1996) was used to generate 17 Fourier Coefficients (FC) for each of the 328 individuals whose shells were digitised. For analysis, these individuals were placed into 16 groups: the existing 12 described species plus the 4 tag-named groups “alpine’, “Buller River”, “Kawatiri” and “vittatus” identified in Walker (2003), confirmed as appropriate clusters to test through principal component analysis of the categorical measure dataset. The first harmonic was discarded because it contained size information (Crampton 1995), while the 2nd to 11th harmonics were retained for the analysis as they were found to contain most of the variation in the data. PCA on the remaining 10 harmonics found the first 7 principal components explained 93% of the variance and were subjected to Discriminant Function Analysis (DFA). While most population samples had 25–45 individuals, a few included only 5 individuals, and it is generally recommended for effective DFA that the number of individuals be greater than the number of PCs (Crampton & Maxwell 2000). However, the higher number of PCs made little difference in the discrimination of those groups with small sample-sizes but did improve resolution of the large sample-size groups and, as these were the majority, the analysis was completed with 7 PCs. 95% confidence ellipses were drawn around the group means of the first two canonical variates using the R package ellipse (Murdoch & Chow 2013) and the likelihood that the Mahalanobis distances between the group means of all canonical variates was due to chance was estimated using a 1000 iteration permutation test.

Principal components analysis (PCA) was used to examine the combined dataset generated from shell measurements, Fourier shape coefficients and categorical characters. The whole dataset of ungrouped individuals was used in this analysis, with each type of data first assessed separately, before all were assessed jointly. In case its large size obscured finer patterns, PCA was subsequently used on subsets of the data. A simple scatter diagram showing total height versus maximum diameter of all the measured shells was generated and those species which overlapped in basic size were subsequently compared only with each other using PCA to more clearly resolve which morphological features best separated them and their subspecies.

Finally, a phenogram based on all *Powelliphanta* morphological characters (measures with ratios, categorical data and Fourier coefficients) measured in 328 individuals was created by naive clustering of unweighted scores using Ward's (1963) method and Euclidian distances in the statistical package R (R core team 2015).

Results

The scores of 328 individuals on 12 linear and area measures, 16 categorical character states and 10 Fourier coefficients are given in Appendix 2.

Shell size by itself (maximum diameter x height) spread the 328 shells along a continuum from small to large, which roughly ordered them into the previously described species and tag-named clusters (Figure 6). Additionally, there was a shape component which spread the shells along a second continuum, orthogonal to the first, between oblong and conical. Those snails which are more oblong ("alpine", *P. hochstetteri*, *P. marchanti*, *P. traversi*, *P. superba*) fell below the size continuum while those which are more conical (*P. gilliesi* and *P. lignaria*) fell above it. Small-shelled taxa were the most difficult to distinguish on size alone, because there were a large number and extensive overlap in morphospace. Much of the variation in size within species was found to correlate with the characteristic size range of their subspecies (not shown).

Confidence intervals around the group means of the canonical variates of the Fourier coefficients were tightest in those *Powelliphanta* species with multiple subspecies where large numbers of individuals were, as a matter of course sampled, such as *lignaria* (41 individuals) and *gilliesi* (53), compared to monotypic *fiordlandica*, “Buller River”, *gagei* and *augusta* where only 6 individuals were sampled in each. Fourier analysis of shell outline shape found highly significant differences between most group means (Table 1). While these differences were obvious when only a few groups were compared at a time (not shown), it was difficult to detect visually when all 16 groups were displayed together due to crowding of the morphospace (Figure 7).

The least different means were those of the medium-sized *Powelliphanta*, *gilliesi* and *traversi*, which Powell had initially classified as a single species, presumably in part due to a similarity in shape. Medium-sized *Powelliphanta lignaria* and small "Buller River"—which molecular data suggested arose from the same stock—also had non-significant differences between their group means.

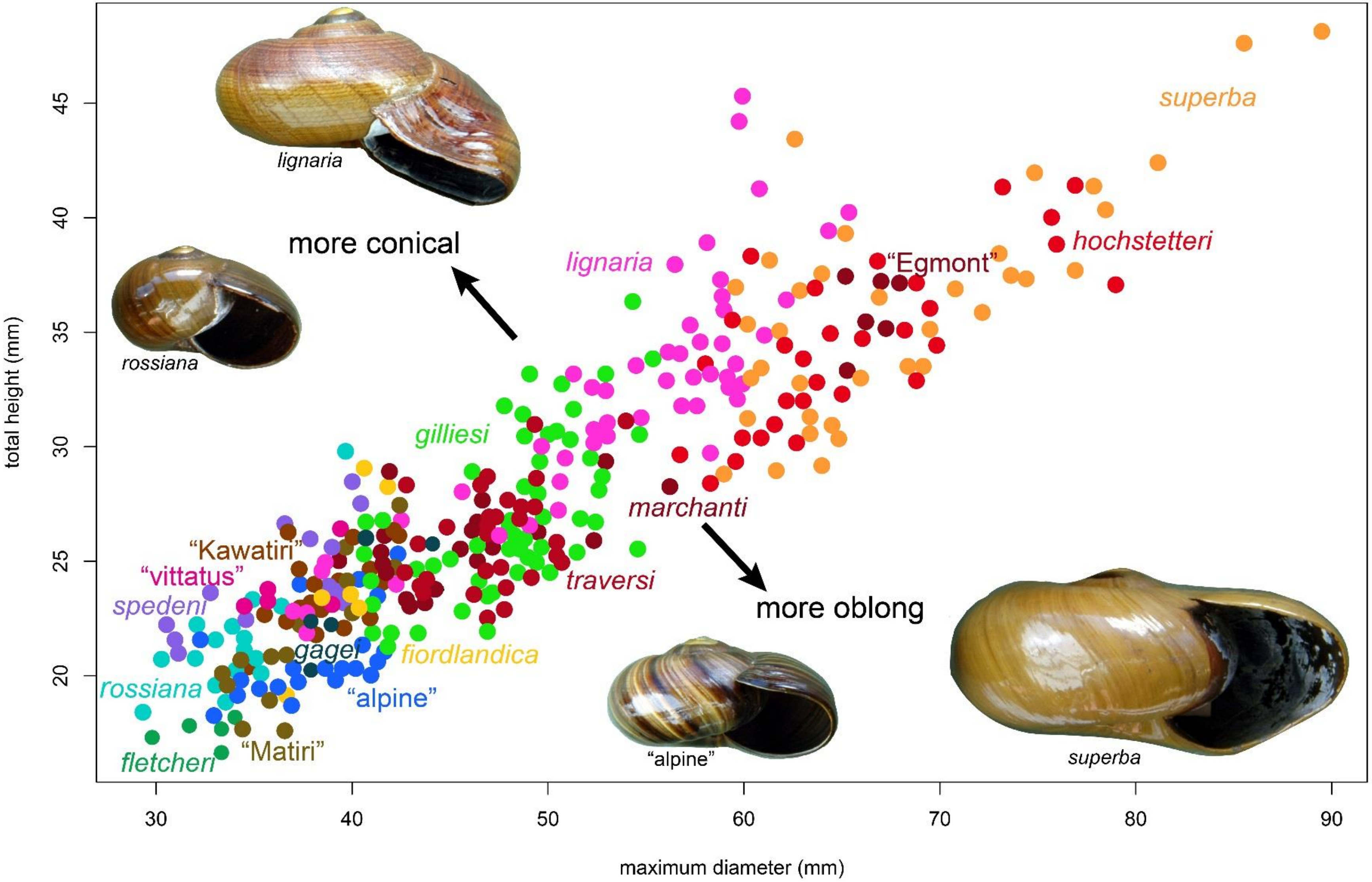


Figure 6. Scatter plot of size of all 328 shells used in the morphometric study, colour-coded by species/cluster.

Table 1. Mahalanobis distances between the *Powelliphanta* Fourier Coefficient group means (above the diagonal) and pairwise permutation test probabilities (below the diagonal), in alphabetical order. * P < 0.001

	“alpine”	*P. augusta*	“Buller_River”	*P. fiordlandica*	*P. fletcheri*	*P. gagei*	*P. gilliesi*	*P. hochstetteri*	“Kawatiri “compex	*P. lignaria”*	*P. marchanti*	*P. rossiana*	*P. spedeni*	*P. superba*	*P. traversi*	“vittatus”
“alpine”	—	2.26	2.84	2.36	1.91	1.63	2.26	2.30	1.03	1.79	1.13	3.24	3.91	1.82	2.45	3.59
P. augusta	0.002	—	3.48	3.98	2.77	3.45	3.55	4.08	2.00	2.84	2.62	2.78	3.15	3.91	3.76	3.20
“Buller_River”	*	0.001	—	3.28	4.08	3.03	1.73	3.18	3.12	1.48	2.49	4.86	4.94	3.70	1.91	4.87
P. fiordlandica	0.002	*	*	—	3.49	1.04	2.98	3.19	2.71	2.65	2.86	4.15	4.99	2.64	3.25	4.22
P. fletcheri	0.017	*	*	0.006	—	2.96	3.66	3.51	1.45	3.21	1.89	2.31	2.92	2.98	3.61	2.87
P. gagei	0.128	*	*	0.953	0.019	—	2.55	2.64	2.20	2.34	2.29	3.91	4.74	2.14	2.81	4.05
P. gilliesi	*	*	0.025	*	*	*	—	1.54	2.96	1.05	1.87	5.08	5.45	2.54	0.55	5.15
P. hochstetteri	*	*	*	*	*	*	*	—	3.18	2.13	2.07	5.38	5.94	1.64	1.54	5.55
“Kawatiri” complex	0.051	0.002	*	0.001	0.206	0.009	*	*	—	2.25	1.46	2.35	2.94	2.58	3.09	2.77
P. lignaria	*	*	0.161	*	*	0.012	*	*	*	—	1.49	4.33	4.66	2.53	1.37	4.45
P. marchanti	0.043	0.003	0.002	*	0.047	0.015	*	*	*	*	—	3.56	3.95	2.07	1.86	3.90
P. rossiana	*	*	*	*	0.017	*	*	*	*	*	*	—	1.36	4.72	5.16	1.41
P. spedeni	*	0.001	*	*	0.002	*	*	*	*	*	*	0.167	—	5.43	5.47	1.84
P. superba	*	*	*	0.005	*	0.099	*	*	*	*	*	*	*	—	2.70	5.11
P. traversi	*	*	0.009	*	*	*	0.542	*	*	*	*	*	*	*	—	5.19
“vittatus”	*	*	*	0.005	0.025	0.003	*	*	*	*	*	0.341	0.178	*	*	—

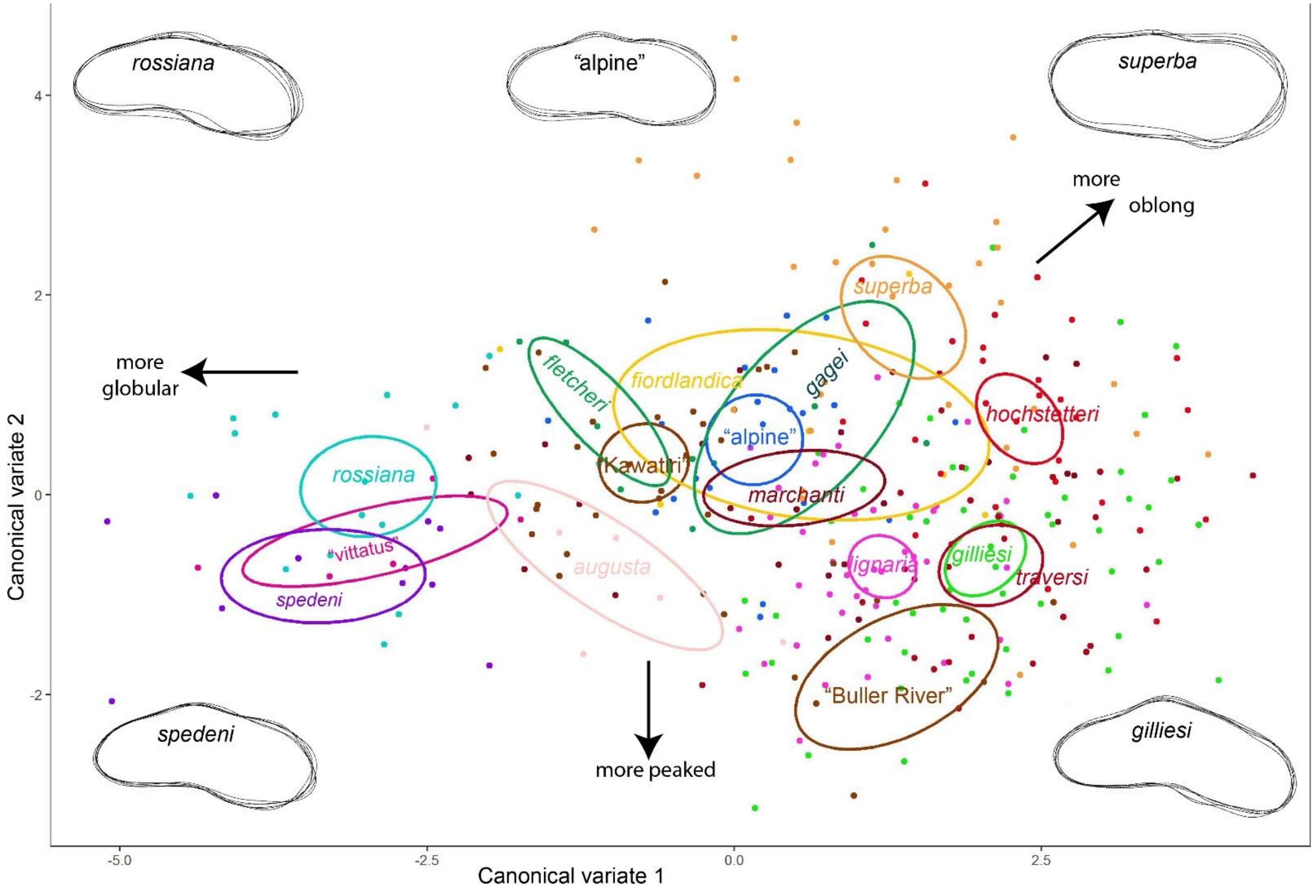


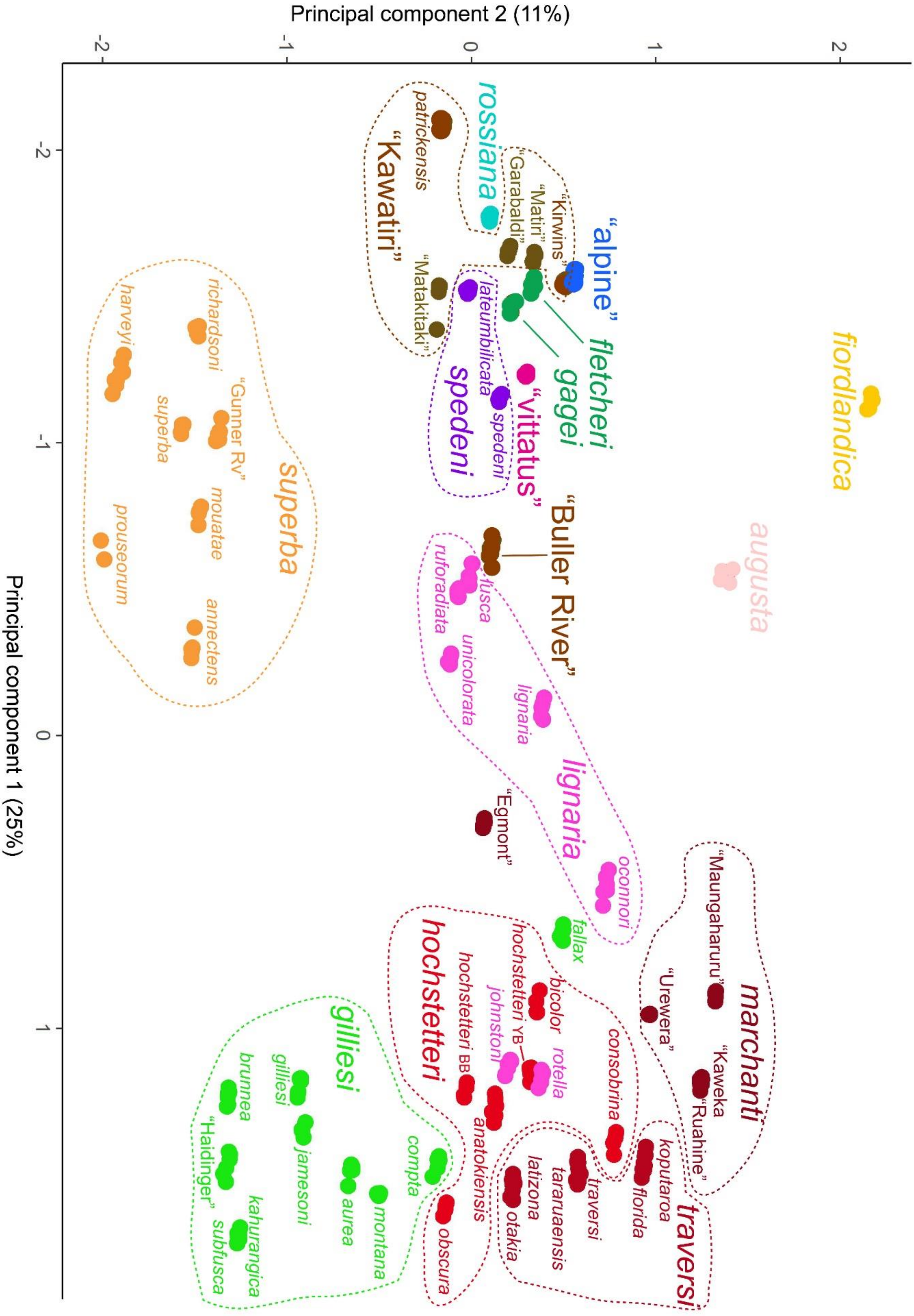
Figure 7. Discriminant function analysis plot based on the Fourier coefficients of the outline shape of 328 shells used in the morphometric study and placed in *à priori* groupings of described or tag-named taxa for this analysis. Ellipses indicate the 95% confidence regions on the group means which are at the centre of their ellipses. While there is overlap, most pairwise comparisons of means differ at >99.9% level of confidence (see Table 1 for details). At the edge of the figure, the synthetic shapes of *rossiana*, *spedeni*, "alpine", *superba* and *gilliesi* snails generated from the mean of each groups Fourier descriptors illustrate the more extreme shapes detected in this analysis.

When direct size was excluded and only ratios used, PCA of categorical, metric and outline shape measures separated almost all the sampled *Powelliphanta* into discrete groups corresponding to the currently described and tag-named species and subspecies (Figure 8). The most informative morphological characters were found to be the categorical measures, and these were also the simplest to observe. On their own, neither linear/area measures (not shown) or Fourier coefficients could separate the groups cleanly without overlap.

Powelliphanta lignaria johnstoni and *P. l. rotella,* which alone amongst the mainly axially-striped species *P. lignaria* have strong spiral stripes, grouped on the first 2 principal components near to the spirally-striped *P. hochstetteri hochstetteri* whose shell has a similar colour and pattern but a different shape. However, plotting 3 principal components separated *P. hochstetteri* from all *P. lignaria*, including the subspecies *rotella* and *johnstoni* (Figure 9). Similarly, most small-sized snails lay close together when only 2 principal components were plotted (Figure 8) but were more clearly separated with 3 principal components (Figure 9). *Powelliphanta fiordlandica,* which was well separated on principal component 1 and 2, was such an outlier on principal component 3 that it was necessary to zoom in to see these finer-scale separations (Figure 9).

A phenogram of the whole morphological dataset reflected the results of the PCA, with division into the described and tag-named taxa (Figure 10), similar to molecular phylogenies (Chapter 2). One main split separated *P. gilliesi* and the *hochstetteri* complex from *P. superba*, *P. lignaria* and all the small snails. The main difference between the morphological phenogram and molecular phylogenies was the placement of "alpine" and *P. fiordlandica* with other small snails in the *superba*/*lignaria* clade, whereas the former clustered closely with *P. gilliesi* on all molecular trees and the latter on its own separate branch.

Figure 8 (Next page). Principal components analysis based on all 69 morphological characters (metric, categorical and outline shape) measured in 328 adult individuals, with each individual colour-coded by taxon-name, with dashed lines surrounding all or most of those of similar colour to highlight the large groups described in the study.


Principal component 2 (11%)
-2
-1
0
1
2
Principal component 1 (25%)
-2
-1
0
1
fiordlandica
augusta
"alpine"
fletcheri
gagei
"Kirwins"
"Matiri"
"Garabaldi"
rossiana
patrickensis
"Kawatiri"
"Matakitaki"
lateumbilicata
spedeni
spedeni
"vittatus"
"Buller River"
fusca
ruforadiata
unicolorata
lignaria
lignaria
"Egmont"
oconnori
superba
richardsoni
harveyi
"Gunner Rv"
superba
mouatae
prouseorum
annectens
fallax
marchanti
"Maungaharuru"
"Urewera"
"Kaweka"
"Ruahine"
hochstetteri
hochstetteri YB
hochstetteri BB
bicolor
johnstoni
rotella
consobrina
anatokiensis
obscura
traversi
koputaroa
florida
traversi
tararuaensis
latizona
otakia
gilliesi
gilliesi
brunnea
"Haidinger"
jamesoni
compta
aurea
montana
kahurangica
subfusca

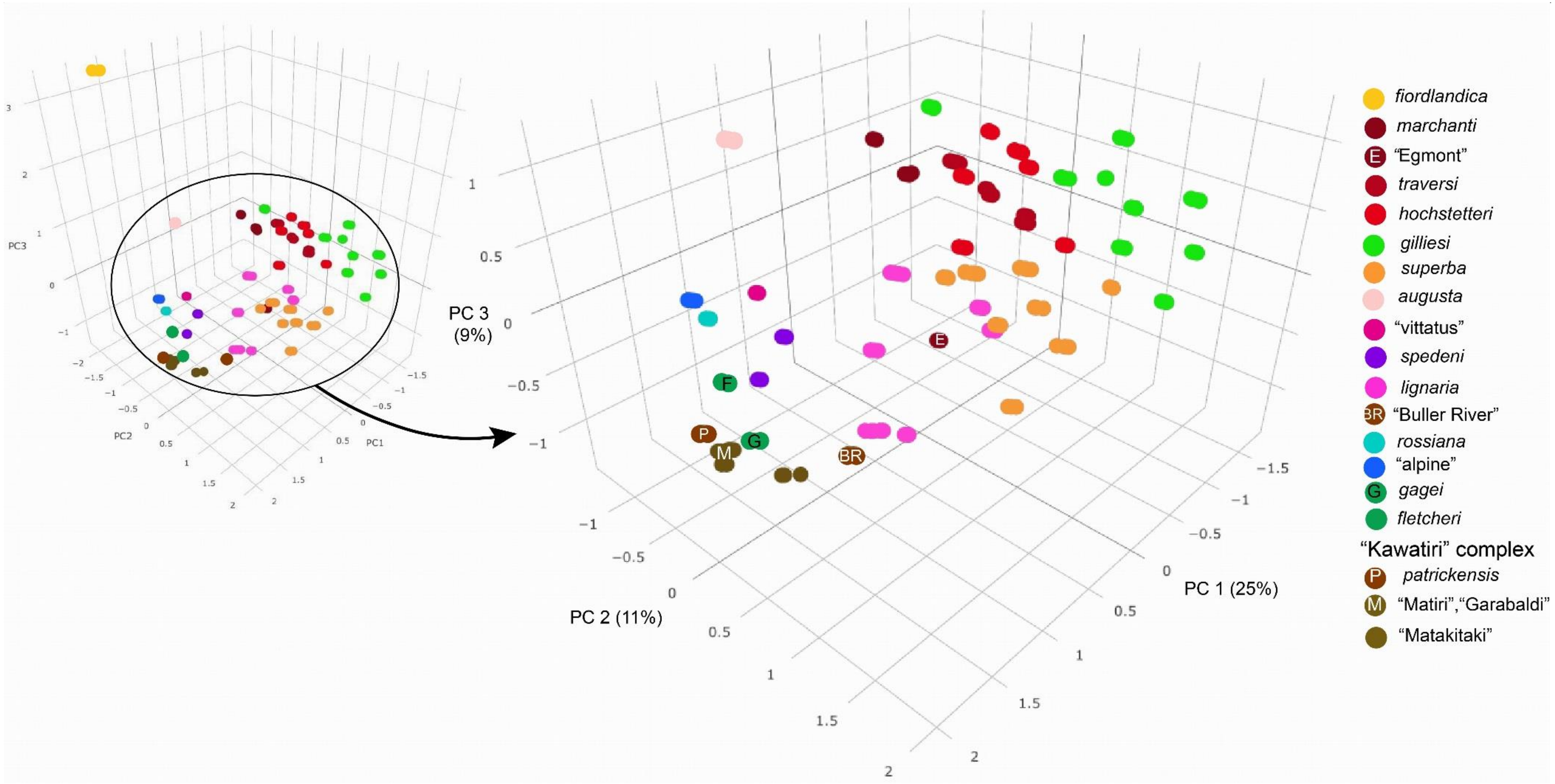


Figure 9. Three-dimensional principal components analysis based on the scores obtained from 389 individual adult *Powelliphanta* snails for 69 morphological characters

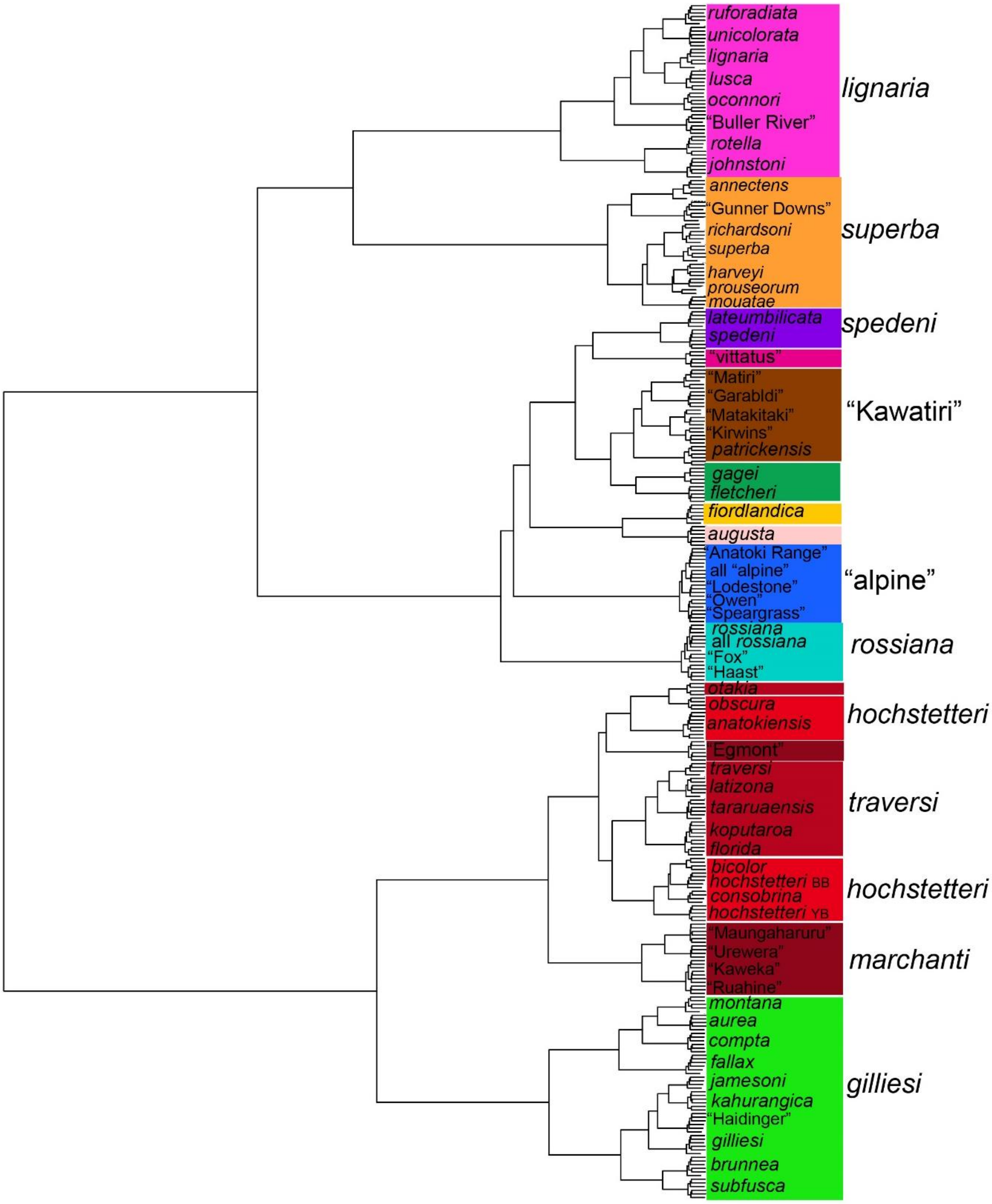


Figure 10. Phenogram generated in the statistical package R using Ward's linkage algorithm with Euclidian distances for hierarchical clustering of 69 morphological *Powelliphanta* characters (measures with ratios, categorical data and Fourier Coefficients). All individuals on the terminal tips belong to the same named clade as all other individuals with the same colour in the same clade, with the following exceptions: some admixture between named forms of *rossiana*; some admixture between named forms of "alpine" and the cluster labelled *florida* and *koputaroa* is an integrated mixture of the two.

Discussion

The use of measurable characters, numerical descriptions of shape, and a broad range of morphological characters including mucous colour and head/foot colour and texture—not previously described—provided a reproducible morphological dataset which mostly separated *Powelliphanta* into the same species and subspecies groups as earlier, simpler, morphometric study did.

There are some similarities between the phenogram of morphological characters and phylogenies based on molecular data (Chapter 2). Most striking is the mutual support of the genotypic clusters identified therein. The separate but close morphological relationship between "Buller River" and *P. lignaria* evident from morphology supports the molecular hypothesis that "Buller River" arose from an ancient hybridization between snails of the "Kawatiri" complex and *P. lignaria* (Chapter 2). However, morphology failed to support the sister relationship of “alpine” snails to *P. gilliesi*. While, *P. fiordlandica* was recognized as a separate group in the phenogram, its phylogenetic distinctiveness from all other *Powelliphanta* is not obvious there, though it is strongly apparent in the PCA analysis of the same morphological data (Figure 9). This suggests the phenogram approach is not as reliable in detecting evolutionary relationships as other forms of morphological analysis.

Principal components analysis of each morphological dataset separately found both linear/area measures and outline shape to be less powerful in separating the groups than characters of shell and body colour and pattern. While the categorical dataset readily discriminated groups, it also produced some uninformatively tight clusters due to fixed differences in a few characters. Shape and linear measures helped spread those clusters. Individuals could be difficult to identify if shape and linear measures were the only tools available, due to the extent of overlap between some groups. In combination however, morphology in *Powelliphanta* supported and improved the resolution of the purely molecular phylogeny described in Chapter 2 and also provided better resolution of intraspecific variation.

The sympatric *P. superba* and *P. gilliesi* are the only species with a granulated parietal callus in some of their subspecies, though on almost every other morphological measure these two species are highly distinctive. There is no known adaptive advantage to granules on the parietal callus as the granules are too small to act as a shield against water loss or predator entry, the two functions most often suggested for apertural dentricles (Goodfriend 1986, Vermeij 2015). While they are genetically distantly related (Chapter 2), the presence of callused apertures in only the western-most populations of both species suggests ancient hybridization between them or convergent evolution of an adaptive trait, with either explanation equally plausible.

Causes of morphological diversity

Most Rhytidids are small with plain shells and white limy eggs. *Powelliphanta* were initially elevated to sub-genus status within *Paryphanta* because their eggs had a membranous cuticle, were glossy and a pale buff colour, whereas *Paryphanta*, along with other New Zealand rhytidids *Wainuia*, *Rhytida* and *Schizoglossa* had rough, white, limy eggs without cuticle (O'Connor 1945). It is now known that South African *Natalina* (Herbert & Moussalli 2010) and Australian *Victaphanta* (Smith 1970) as well as *P. fiordlandica* (this study) also lay non-cuticled white limy eggs, suggesting limy eggs and plain shells equate to the ancestral condition, from which the glossy cuticled eggs and large varied shells of *Powelliphanta* may have derived.

The basic rhytidid template may be the outcome of achieving relative safety through small adult size and cryptic colouration. Moussalli & Herbert (2016) suggested these two qualities were intertwined, noting a tendency to less variable shell form and simplified anatomy—in essence a simpler "body plan"—with decreasing size. They described an exceptional morphological stasis in South African dwarf rhytidid genera, and noted this morphological conservatism also dominated many Australian and New Zealand rhytidid genera (Moussalli & Herbert 2016). They suggested the "low-spired, relatively broadly umbilicate, rather uniformly yellowish-brown, weakly sculptured and often glossy" form of all these small rhytidids had proved particularly suitable to a carnivorous mode of life, being also found in many unrelated families through convergent evolution (Herbert & Moussalli 2016).

However, there are clearly some advantages in being big. It is likely, for example, that large snails are at less risk of dessication than small snails as they have a smaller surface area to volume ratio (Goodfriend 1986). All rhytidids are carnivorous and possession of a larger shell allows bigger prey to be taken. The two large New Zealand rhytidids *Powelliphanta* and *Paryphanta*, feed primarily on earthworms (Walker 2003; Stringer et al. 2003) many of them much larger than themselves, pulling them whole into their bodies for digestion and requiring significant internal space to do so, whereas many smaller rhytids are restricted to either feeding on animals smaller than themselves (Efford 2000) or to tearing off small pieces of flesh from larger items (Herbert & Moussalli 2010). However, being big also requires that to reach maturity, more prey need to be consumed, and it also makes a snail more conspicuous to other predators.

Paryphanta and *Powelliphanta*—two very large Rhytidids—appear to have solved this problem in quite different ways, though no evidence is available to differentiate cause and effect here. *Paryphanta* has retained the cryptic colouration of small rhytidids, such that the genetic diversity within the genus is not obvious from its plain shell (Spencer et al. 2006), but substantially thickened the calcareous lining of its shell to make it less permeable and harder for a predator to break into. In contrast, *Powelliphanta* is only 65% the weight of a *Paryphanta* shell, but has adopted shell colour and pattern, presumably for camouflage. *Powelliphanta* reach a greater overall size than *Paryphanta* (90 mm cf 80 mm diameter) suggesting the latter strategy is the most successful, perhaps because it has the added benefits of reducing the amount of calcium required to build a shell and requiring less energy to carry it around.

This idea is speculative, but supported somewhat by the observation that the bright patterning and colouring for which *Powelliphanta* is best known is most conspicuous in the larger species, with smaller species tending towards the dark brown colouration typical of the rest of the family. From the basal position of "small brown" *Powelliphanta* in all molecular trees (Chapter 2) its apparent that large size and strong colouring and patterning are derived features even within *Powelliphanta*. Furthermore, the same morphological change from small-plain to large-coloured-patterned appears to have evolved separately up to three times, in all the major large-shelled lineages (ie with the "alpine" group sister to *gilliesi*/*hochstetteri*; *P. augusta* sister to *lignaria*; and *rossiana/spedeni* sister to *superba*). Other possible explanations for this repeated evolution from small and plain to large and coloured/patterned are discussed in turn below.

Size

Though size is often regarded as particularly susceptible to environmental control (particularly moisture levels, temperature and calcium availability) there are surprisingly few studies convincingly demonstrating many of these direct effects, and shell size in land snails generally has a large genetic component (Goodfriend 1986). Size does appear to be genetically based in *Powelliphanta* (Chapter 2) and it is consistent within both species (Figure 6) and subspecies (not illustrated). Size appears to be used in *Powelliphanta* as a way to reduce competition between species. *P. superba* and *P. gilliesi*, the only two species whose distributions overlap extensively, have very different body sizes. *P. superba* is one of the largest snails, weighing up to 90 g and its last whorl and aperture is wide and open, allowing growth of a very big animal, whereas the medium-sized *P. gilliesi* weighs only 24 g and the upper part of the body is squeezed into a high-spired apex and its aperture drops sharply in old age and nearly closes (Figure 11). These volume differences must affect the maximum size of earthworms each species can ingest, thereby limiting direct competition to the short period *P. superba* are juveniles. The shape differences may also allow exploitation of differing ecological niches, as only *P. gilliesi* snails with their small and twisted shells that may reduce moisture loss, inhabit free-draining sandy environments at sea level in the drier north and east of the region.

In a similar fashion the large *P. hochstetteri hochstetteri* and very small "alpine" overlap extensively on the Arthur Range, and the very large *P. h. anatokiensis* and medium-sized *P. gilliesi* on Parapara Peak (see figure 1 in Chapter 2 for these locations). However, also on Parapara Peak is the very large *P. superba superba* but its distribution only overlaps that of equally large *P. h. anatokiensis* along a narrow band of ~50-100 m width on the south-western and north-eastern slopes of the peak. The area of overlap is so small because presumably they directly compete. Likewise, in all other cases where the ranges of *Powelliphanta* coincide but the species involved are the same adult size as each other, the overlap zone is very narrow.

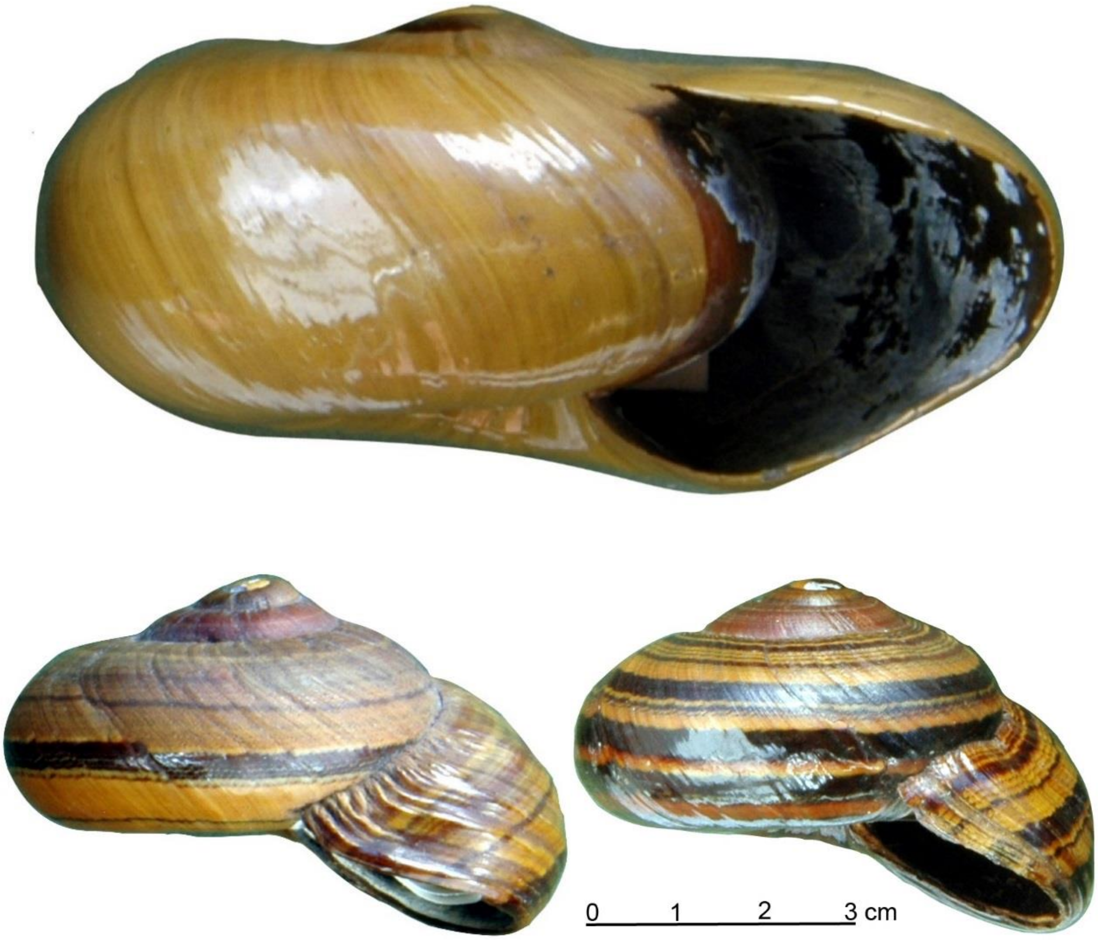


Figure 11. Differences in the shape and size of the sympatric species *Powelliphanta superba* (top) and *Powelliphanta gilliesi* which may be acting to reduce competition between the two species. The shell of *P. superba* is very large with a wide, open aperture and body-whorl presumably to accommodate big earthworms but providing little barrier to moisture loss, whereas *P. gilliesi* has a narrowed aperture, high apex and steep descent of the last body whorl, which may limit the size of prey it can ingest but also reduce water-loss, enabling it to live in drier sand dune country.

Colour and pattern

Synthesis of pigment is likely to be energetically costly (Williams 2016), so is usually inferred to confer some benefits on those which invest heavily in it. In many animals suggested reasons for coloration include species recognition (Couldridge & Alexander 2002), temperature control (Heath 1975, Savazzi & Sasaki 2013) or camouflage (Cain & Shepard 1954, Kobluk & Mapes 1989, Vermeij 2015).

Most (but not all) shelled molluscs are thought to have poor vision (Williams 2016), being capable of little more than recognizing light from which they need to hide (Chase 2001), though New Zealand *Wainuia urnula* are thought to recognize their amphipod prey by visual cues (Efford 2000). It is unlikely any can see in colour (Kobluk & Mapes 1989, Nilsson 2013) so shell pattern and colour are likely to be of little value to *Powelliphanta* for signalling or communication within species.

It has been suggested that shell colouration might be under abiotic selection with lighter coloured shells more common in hot dry environments inferred to reduce internal temperatures (Williams 2016) because such shells strongly reflect radiation (Savazzi & Sasaki 2013). Dark shelled *Mytilus* mussels can heat up in the sun 2-3°C more than lighter morphs (Mitten 1977) and darker-pigmented *Cepaea nemoralis* land-snail shells were almost always hotter than lighter-coloured shells (Heath 1975). However, while light-coloured shells can keep cooler and any camouflaging shell pattern is obvious in visible light and of high contrast in near ultra-violet (NUV) light, they become completely translucent in near infra-red (NIR) and would be very conspicuous against soil on a forest floor which is usually dark in NIR (Savazzi & Sasaki 2013).

Unlike many tropical snails, the shells of *Powelliphanta* absorb visible and NIR light (visibility in NUV hasn't been tested; Savazzi & Sasaki 2013) which means their shell colour and pattern are still visible in low light situations, perhaps providing camouflage even at dawn and dusk. *Powelliphanta* can probably afford to absorb rather than reflect NIR as they live under dense vegetation and only emerge at night or on grey misty days and live in areas where moisture is plentiful and temperatures cool (Walker 2003).

While mate recognition and temperature control appear to play little part in the development of coloured and patterned shells in *Powelliphanta*, camouflage may, as discussed earlier. The dominant colours in *Powelliphanta* shells, though strikingly varied compared to the dark olive or tan-colour of other rhytids, comprise a fairly restrained palette of reds, yellows, browns and black arranged in either spiral or radial bands, or a uniform gold colour. These are not only the colours of dead leaves on the forest floor but are all long wave-length colours near the infra-red end of the spectrum. Such colours are less visible to birds, which were the main predators of *Powelliphanta* throughout its evolution due to the absence of land mammals in New Zealand since at least the Miocene. Birds have excellent vision in light visible to human eyes and in UV radiation, but not in NIR (Savazzi & Sasaki 2013). Many New Zealand bird species became extinct following the arrival of humans and other mammals about 800 years ago so it is not possible to know just how important to the evolution of *Powelliphanta* shells bird predation may have been. However, crepuscular birds such as weka (*Gallirallus australis*), are still important predators of *Powelliphanta* today (Walker 2003), suggesting the impact of at least some species was possibly significant.

A weakness in the theory of predation as the causal factor in *Powelliphanta* shell ornamentation is that when the snails are alive, their shells appear a near-uniform dark brown, just like other rhytidids, as the moisture from their body permeates the thin shells (Figure 12). Only when a part of the shell is exposed to heat does it dry out and the colour and pattern become visible. It is possible that shell colour in *Powelliphanta* has no function and is selectively neutral, as has been hypothesized for colourful and patterned marine gastropods that live buried in sediments which renders their shells almost entirely invisible (Comfort 1951, Luttikhuizen & Drent 2008, Williams 2016). However, this is probably not the case in *Powelliphanta*. Camouflage, especially during daylight when parts of the shell may dry out if the snail is incompletely hidden, seems likely to be the main reason for their investment in complex shell colouring and patterning.

While the thickness of the calcium carbonate layer has been reduced in *Powelliphanta* so the shell is relatively light and the snail presumably speedier, the remaining colourful periostracum may also have compensatory functions. The protein-rich periostracum which holds the colour and pattern, probably provides not just these but also some strength, as pigments such as melanin have been shown to strengthen and reduce the effects of abrasion in insect cuticles (Burtt 1977, 1981; Bonser 1996; True 2003) and may serve a similar function in mollusc shells (Williams 2016).

Figure 12. The usual dark colour of all *Powelliphanta* whilst the snail is alive is illustrated in the top photo of a *P. patrickensis* snail active in the daytime due to overcast rainy conditions; the bright colours of *Powelliphanta* shells is only seen once the shell surface dries out (bottom photo of *P. patrickensis*). When a shell has dried out to this extent, the life of the snail inside is at great risk, as the snail's body too will be drying out, forcing the snail to immediately seek shade and moisture to re-hydrate. The reasons *Powelliphanta* spend energy building colourful patterned shells when those colours are rarely seen are complex and not fully understood.

Conclusion

This chapter addressed the question of whether the addition of morphometrics improves taxonomic resolution in *Powelliphanta*, and whether it lends support to the genotypic clusters identified in Chapter 2. That it does both is clear, through the similarities between morphological and genotypic clusters, and through the provision of information on infraspecific diversity missing from molecules due to incomplete lineage sorting. It also advanced speculation as to possible causes of the high levels of morphological diversity in *Powelliphanta*.

A perhaps controversial aspect of *Powelliphanta* taxonomy is the attribution of subspecific rank to morphologically distinct populations within species. While this study clarified which morphological characters differentiated populations the most, and better defined the measures used, the decision to formally recognize the identified morphological diversity remains reliant on the total weight of evidence for each subspecies.

Differences in shell morphology seem to appear in *Powelliphanta* almost as soon as gene flow slows and become fixed when it ceases entirely. This is presumably because these snails are sedentary and their habitat preferences particular, so they can quickly become confined to small areas, especially in New Zealand's highly varied topography and climate over small distances. In the north-west corner of the South Island where the intra-specific diversity is most concentrated, land has been above the sea and free of glacial ice, for longer than in the rest of New Zealand so more time has been available there than elsewhere for chance and genetic drift to separate populations.

Shell pigment and pattern come from gene expression in the mantle tissue of molluscs and there is some evidence that genes in the secreted mantle proteins (secretomes) are rapidly evolving (Jackson et al 2007), making it more likely that changes in shell colour and pattern occur at a comparatively fast evolutionary rate.

This may be the reason *Powelliphanta* appear to be "painted on the landscape" in a way which no other land snails in New Zealand are. It is possible to identify just where a *Powelliphanta* has come from, from examination of its shell alone. In the biogeographical patterns the morphological (and genetic) relatedness of *Powelliphanta* taxa make, the history of the last several million years of climatic, geologic and topographic change in New Zealand find a reflection. For this reason if no other, subspecies should be retained as the main way the conspicuous intra-specific diversity in *Powelliphanta* is described.

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Appendix 1

Categorical character states

1. Number of whorls

2. Whorl type
    1 4 - 4.9 (rapidly expanding, resulting in fewer whorls)
    2 5 – 6 (slowly expanding, resulting in more whorls)

3. Mucous/mantle colour
    1 clear in all individuals in population
    2 clear, except rarely in population some juveniles blue
    3 blue, except rarely in population some adults clear
    4 purple
    5 reddish-yellow

4. Foot fringe colour
    1 same as body
    2 white
    3 tan

5. Foot colour/texture
    1 Pinkish-white background, coarse black reticulation
    2 Light grey background, coarse black reticulation
    3 Slate grey background, fine black reticulation
    4 Dark bluish-black foot, fine black reticulation

6. Suture in body whorl
    1 Flat - not impressed
    2 Slightly impressed
    3 depressed; suture lower than body whorl

7. Umbilicus
    1 closed
    2 narrowly umbilicate
    3 widely umbilicate

8. Axial stripes
    1 None
    2 Very few, sparse, mostly on dorsal surface
    3 Moderate number
    4 Abundant

9. Spiral stripes on dorsal surface
    1 None
    2 Few, narrow

3 Many, variable width, conspicuous

10. Spiral stripes on ventral surface
 1 None
 2 Few, narrow, inconspicuous
 3 Variable width, conspicuous

11. Bi-coloured striped shell
 1 Uni-coloured and/or predominantly radially striped
 2 Spiral stripes on entire shell
 3 Spiral stripes and plain contrasting umbilicus patch
 4 Spiral stripes on top, plain coloured base from periphery

12 Parietal callus texture
 1 Smooth
 2 Sparsely covered in exceedingly fine granulations
 3 Finely but distinctly granulated
 4 Strongly, densely & coarsely granulated

13 Parietal callus colour in live snails
 1 Transparent: glaze so thin, colour same as bodywhorl base colour
 2 Bluish-white
 3 Chocolate brown
 4 Purple of varying shades
 5 Pale grey
 6 Dark brown-black

14. Shell sculpture
 1 Smooth & glossy all over
 2 smooth & glossy below periphery, faintly striated above
 3 smooth & glossy below periphery, strongly sculptured above

15. Shell appearance
 1 bright, smooth, opaque, sturdy
 2 dull, crumpled-tissue texture, thin & hollow

16. Eggshell colour and texture
 1 pearly pink with smooth, glossy, membranous cuticle
 2 white with rough calcareous surface, no cuticle

17 Shell position during locomotion
 1 towards rear, covering tail
 2 central, with tail exposed

Appendix 2: Character matrix. **Linear, area, shape and categorical character scores for adult *Powelliphanta* snails in old age**

sample number	taxon	total height	max diam	apex height	apex area	aperture drop	BW roundness	circularity	diam last whorl	diam 3.5 whorl	umbilicus diam	dorsal area	whorl no.	whorl type	mucous	fringe	foot colour	suture	umbilicus	axial stripes	dorsal stripes	ventral stripes	bicolor stripes	callus texture	callus colour	sculpture	appearance	egg type
RA1	"Anatoki Range"	19.67	35.31	2.71	20.24	4.99	0.5	0.78	12.54	7.34	5.34	828.33	4.4	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
RA2	"Anatoki Range"	19.86	37.2	2.04	12.87	5.6	0.56	0.77	13.43	8.56	4.09	849.71	4.4	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
RA3	"Anatoki Range"	19.29	36.3	2.21	16.11	5.09	0.54	0.79	13.03	9.06	6.06	832.47	4.4	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
RA4	"Anatoki Range"	20.25	38.63	2.55	18.86	5.94	0.51	0.77	13.71	8.02	5.37	915.2	4.4	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
RA5	"Anatoki Range"	20.05	40.92	3.06	23.25	6.62	0.5	0.75	15.42	8.6	6.35	1025.09	4.4	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
LO1	"Lodestone"	18.77	36.84	2.23	17.16	3.93	0.55	0.78	13.91	7.67	5.96	873.39	4.4	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
LO2	"Lodestone"	20.88	41.51	1.89	11.29	6.67	0.51	0.74	14.29	10.27	6.92	1070.41	4.4	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
LO3	"Lodestone"	20.36	40.09	2.23	16.56	4.77	0.53	0.76	14.21	7.53	6.31	1005.48	4.4	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
LO4	"Lodestone"	21.32	41.7	2.02	13.34	9.97	0.5	0.74	15.3	7.54	6.46	1079.49	4.4	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
LO5	"Lodestone"	21.37	40.53	1.86	12.81	5.59	0.53	0.78	13.98	10.87	5.73	1051.55	4.4	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
NL1	"Speargrass"	19.94	39.34	2.87	21.58	5.66	0.54	0.75	15.99	6.44	4.77	945.68	4.5	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
NL2	"Speargrass"	24.02	37.18	2.91	24.72	7.04	0.53	0.79	13.77	7.19	4.4	939.96	4.5	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
NL3	"Speargrass"	20.14	39.52	3.64	28.8	5.58	0.49	0.76	16.18	9.78	5.32	993.55	4.5	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
NL4	"Speargrass"	23.53	41.14	3.47	24.98	8.09	0.51	0.77	13.64	7.01	4.74	1051.76	4.5	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
NL5	"Speargrass"	25.51	42.26	3.71	28.62	11.5	0.55	0.75	14.5	8.44	5.58	1123.31	4.5	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
NL6	"Speargrass"	24.08	39.92	3.24	26.27	9.22	0.51	0.76	13.68	8.29	4.2	1014.24	4.5	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
OW1	"Owen"	18.07	32.95	3.14	21.06	4.71	0.53	0.8	12.05	5.69	4.06	671.33	4.5	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
OW2	"Owen"	21.47	32.3	2.17	19.31	7.85	0.58	0.77	9.68	6.61	5	736.81	4.5	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
OW3	"Owen"	19.8	34.07	2.65	17.89	7.82	0.55	0.78	11.81	6.06	3.52	755.21	4.5	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
OW4	"Owen"	20.22	36.97	1.55	20.59	7.36	0.54	0.78	11.89	8.37	4.88	894.65	4.5	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
OW5	"Owen"	19.1	33.89	2.07	13.35	2.99	0.56	0.8	11.71	8.7	4.87	727.42	4.5	1	1	1	4	3	2	4	1	1	1	1	6	3	1	1
FI1	*fiordlandica*	23.58	39.75	1.94	18.96	5.98	0.49	0.75	15.19	6.23	7.64	989.64	4.25	1	5	3	2	3	3	2	2	2	1	1	6	3	2	2
FI2	*fiordlandica*	19.18	36.65	1.59	10.57	4.05	0.51	0.76	12.71	7.3	5.99	809.27	4.25	1	5	3	2	3	3	2	2	2	1	1	6	3	2	2
FI3	*fiordlandica*	23.05	40.37	2.29	20.01	7.39	0.49	0.75	13.74	6.61	7.98	1028.18	4.25	1	5	3	2	3	3	2	2	2	1	1	6	3	2	2
FI4	*fiordlandica*	29.04	40.64	2.99	21.39	8.45	0.53	0.74	16.74	5.25	7.89	1000.08	4.25	1	5	3	2	3	3	2	2	2	1	1	6	3	2	2
FI5	*fiordlandica*	23.41	39.03	2.82	26.2	6.16	0.46	0.76	11.48	7.59	7.52	984.38	4.25	1	5	3	2	3	3	2	2	2	1	1	6	3	2	2

sample number	taxon	shell position	fourier coeff 2	fourier coeff.3	fourier coeff 4	fourier coeff 5	fourier coeff 6	fourier coeff 7	fourier coeff 8	fourier coeff 9	fourier co 10	fourier co 11
RA1	"Anatoki Range"	1	0.212	-0.085	-0.028	0.006	-0.034	-0.014	-0.021	0.006	-0.016	0.007
RA2	"Anatoki Range"	1	0.212	-0.044	-0.028	-0.023	-0.049	-0.007	0.002	0.010	-0.019	-0.024
RA3	"Anatoki Range"	1	0.201	-0.050	-0.051	-0.036	-0.019	0.017	-0.021	0.004	-0.021	-0.015
RA4	"Anatoki Range"	1	0.221	-0.068	-0.016	0.000	-0.026	-0.004	-0.009	0.004	-0.048	-0.023
RA5	"Anatoki Range"	1	0.218	-0.061	-0.046	-0.023	-0.038	0.009	-0.006	-0.005	-0.052	-0.007
LO1	"Lodestone"	1	0.202	-0.063	-0.045	-0.007	-0.023	-0.003	-0.036	-0.016	-0.040	-0.029
LO2	"Lodestone"	1	0.219	-0.075	-0.013	0.000	-0.012	0.003	-0.032	0.012	-0.042	-0.016
LO3	"Lodestone"	1	0.220	-0.073	-0.027	0.001	-0.036	-0.005	-0.012	-0.002	-0.041	-0.018
LO4	"Lodestone"	1	0.222	-0.075	-0.032	-0.025	-0.002	0.004	-0.034	0.017	-0.045	-0.017
LO5	"Lodestone"	1	0.223	-0.069	-0.003	0.005	-0.010	-0.007	-0.020	0.006	-0.032	-0.012
NL1	"Speargrass"	1	0.214	-0.061	-0.057	-0.028	-0.018	0.022	0.004	0.000	-0.068	-0.019
NL2	"Speargrass"	1	0.188	-0.084	-0.055	0.007	-0.021	-0.007	-0.053	-0.003	-0.039	-0.018
NL3	"Speargrass"	1	0.209	-0.078	-0.049	-0.007	-0.022	0.030	0.004	0.003	-0.046	-0.013
NL4	"Speargrass"	1	0.207	-0.085	-0.042	0.002	-0.050	-0.018	0.005	0.012	-0.072	-0.016
NL5	"Speargrass"	1	0.215	-0.095	-0.058	0.012	-0.007	0.013	-0.013	-0.001	-0.062	-0.018
NL6	"Speargrass"	1	0.210	-0.097	-0.025	0.003	-0.037	0.013	-0.025	-0.010	-0.036	0.013
OW1	"Owen"	1	0.187	-0.057	-0.060	0.010	-0.038	-0.026	-0.049	-0.001	-0.040	-0.012
OW2	"Owen"	1	0.206	-0.078	-0.068	0.018	0.000	0.002	-0.031	-0.024	-0.018	-0.009
OW3	"Owen"	1	0.201	-0.069	-0.068	-0.018	-0.038	-0.022	-0.025	-0.007	-0.028	-0.022
OW4	"Owen"	1	0.215	-0.067	-0.012	-0.020	-0.029	0.006	0.010	0.001	-0.062	0.007
OW5	"Owen"	1	0.206	-0.061	-0.016	0.008	-0.041	-0.023	-0.012	0.014	-0.023	-0.012
FI1	*fiordlandica*	2	0.212	-0.089	-0.070	-0.026	-0.050	-0.015	-0.022	0.010	-0.012	-0.020
FI2	*fiordlandica*	2	0.231	-0.079	-0.031	-0.014	-0.020	-0.019	0.010	0.012	-0.019	-0.014
FI3	*fiordlandica*	2	0.204	-0.084	-0.036	-0.025	-0.063	0.003	0.056	0.028	-0.064	-0.035
FI4	*fiordlandica*	2	0.227	-0.124	-0.060	0.037	-0.015	0.009	-0.009	-0.007	-0.037	0.006
FI5	*fiordlandica*	2	0.203	-0.107	-0.056	-0.026	-0.039	0.002	-0.003	0.012	0.005	-0.013

sample number	taxon	total height	max diam	apex height	apex area	aperture drop	BW roundness	circularity	diam last whorl	diam 3.5 whorl	umbilicus diam	dorsal area	whorl no.	whorl type	mucous	fringe	foot colour	suture	umbilicus	axial stripes	dorsal stripes	ventral stripes	bicolor stripes	callus texture	callus colour	sculpture	appearance	egg type
FI6	*fiordlandica*	28.51	41.83	2.64	27.37	7.74	0.43	0.75	10.33	8.96	8.46	1173.3	4.25	1	5	3	2	3	3	2	2	2	1	1	6	3	2	2
AU1	*P. g. aurea*	33.18	49.11	5.89	72.53	15.79	0.44	0.72	12.06	7.29	6.16	1683.84	5	2	1	1	3	1	2	1	2	2	4	4	4	3	1	1
AU2	*P. g. aurea*	30.61	50.28	5.95	69.83	15.73	0.47	0.75	13.28	8.35	8.28	1678.67	5	2	1	1	3	1	2	1	2	2	4	4	4	3	1	1
AU3	*P. g. aurea*	33.06	53.02	6.06	67.52	15.84	0.45	0.72	13.43	10.6	9.03	1922.19	5	2	1	1	3	1	2	1	2	2	4	4	4	3	1	1
AU4	*P. g. aurea*	32.92	50.95	5.51	72.47	17.8	0.45	0.74	9.95	8.68	6.86	1796.5	5	2	1	1	3	1	2	1	2	2	4	4	4	3	1	1
AU5	*P. g. aurea*	30.51	54.83	7.02	101.15	16.48	0.43	0.72	12.76	11.81	8.46	2045.04	5	2	1	1	3	1	2	1	2	2	4	4	4	3	1	1
BN1	*P. g. brunnea*	24.52	48.69	3.61	36.38	10.23	0.49	0.77	15.53	9.57	8.84	1456.29	5	2	1	1	3	2	2	1	3	1	4	4	4	3	1	1
BN2	*P. g. brunnea*	29.38	49.47	5.1	54.07	9.1	0.46	0.74	15.08	9.2	9.2	1562.19	5	2	1	1	3	2	2	1	3	1	4	4	4	3	1	1
BN3	*P. g. brunnea*	30.69	49.01	4.85	54.78	12.25	0.5	0.75	14.21	10.52	9.16	1555.37	5	2	1	1	3	2	2	1	3	1	4	4	4	3	1	1
BN4	*P. g. brunnea*	29.46	52.36	4.17	43.39	11.49	0.45	0.73	14.42	10.96	10.95	1904.1	5	2	1	1	3	2	2	1	3	1	4	4	4	3	1	1
BN5	*P. g. brunnea*	25.69	49.75	3.64	35.6	8.98	0.48	0.72	13.69	10.4	9.91	1626.37	5	2	1	1	3	2	2	1	3	1	4	4	4	3	1	1
BN6	*P. g. brunnea*	25.58	54.64	3.16	32.55	6.46	0.44	0.73	18.3	13.51	10.65	1890.16	5	2	1	1	3	2	2	1	3	1	4	4	4	3	1	1
CO1	*P. g. compta*	25.62	46.51	3.81	39.28	7.52	0.52	0.77	17.75	8.76	6.9	1424.4	5	2	1	1	3	2	2	1	2	2	3	2	4	3	1	1
CO2	*P. g. compta*	26.63	48.12	3.4	33.5	8.79	0.54	0.77	16.85	10.6	5.57	1408.49	5	2	1	1	3	2	2	1	2	2	3	2	4	3	1	1
CO3	*P. g. compta*	26.99	49.82	3.93	38.08	8.54	0.5	0.74	16.68	12.21	6.71	1587.13	5	2	1	1	3	2	2	1	2	2	3	2	4	3	1	1
CO4	*P. g. compta*	26.08	49.08	4.45	40.81	9.98	0.51	0.75	16.09	9.21	6.58	1492.06	5	2	1	1	3	2	2	1	2	2	3	2	4	3	1	1
CO5	*P. g. compta*	31.39	48.58	4.82	48.68	11.75	0.49	0.75	14.58	10.33	6.18	1519.65	5	2	1	1	3	2	2	1	2	2	3	2	4	3	1	1
CO6	*P. g. compta*	31.86	47.72	4.98	53.71	12.25	0.48	0.73	9.91	11.85	8.55	1638.78	5	2	1	1	3	2	2	1	2	2	3	2	4	3	1	1
FA1	*P. g. fallax*	21.76	41.92	2.74	20.81	5.63	0.49	0.77	12.54	10.47	5.63	1147.44	4.5	1	1	1	3	1	2	1	2	2	2	1	4	3	1	1
FA2	*P. g. fallax*	24.35	41.93	3.76	31.23	8.07	0.51	0.76	13.26	8.34	6.31	1093.17	4.5	1	1	1	3	1	2	1	2	2	2	1	4	3	1	1
FA3	*P. g. fallax*	21.46	41.81	1.6	10.97	3.8	0.46	0.74	14.38	10.89	5.84	1109.06	4.5	1	1	1	3	1	2	1	2	2	2	1	4	3	1	1
FA4	*P. g. fallax*	21.81	43.39	2.54	18.7	6.85	0.49	0.8	13.51	9.75	6	1232.42	4.5	1	1	1	3	1	2	1	2	2	2	1	4	3	1	1
FA5	*P. g. fallax*	22.02	40.98	2.74	17.62	5.63	0.5	0.78	12.5	10.03	5.08	1107.69	4.5	1	1	1	3	1	2	1	2	2	2	1	4	3	1	1
FA6	*P. g. fallax*	23.13	40.81	2.64	21.91	5.28	0.51	0.78	10.61	11.03	5.72	1089.28	4.5	1	1	1	3	1	2	1	2	2	2	1	4	3	1	1
GI1	*P. g. fallax*	23.62	46.8	3.27	30.61	9.58	0.47	0.73	15.86	9.05	7.13	1392.52	4.75	1	1	1	3	2	2	1	3	3	4	4	4	3	1	1
GI2	*P. g. gilliesi*	28.74	46.23	4.7	48.5	15.22	0.45	0.72	11.07	9.26	7.19	1516.7	4.75	1	1	1	3	2	2	1	3	3	4	4	4	3	1	1
GI3	*P. g. gilliesi*	24.19	46.47	3.56	42.44	10.81	0.44	0.71	13.63	10.73	8.05	1445.37	4.75	1	1	1	3	2	2	1	3	3	4	4	4	3	1	1
GI4	*P. g. gilliesi*	25.61	48.52	3.13	28.03	9.39	0.47	0.72	15.65	9.22	7.04	1506.83	4.75	1	1	1	3	2	2	1	3	3	4	4	4	3	1	1
GI5	*P. g. gilliesi*	25.04	49.35	3.13	27.9	6.73	0.48	0.73	15.26	11.08	8.19	1546.74	4.75	1	1	1	3	2	2	1	3	3	4	4	4	3	1	1
GI6	*P. g. gilliesi*	26.18	48.25	3.13	44.85	7.3	0.48	0.74	14.98	12.04	7.82	1495.11	4.75	1	1	1	3	2	2	1	3	3	4	4	4	3	1	1
HA1	″ Haidinger"	30.43	50.99	4.21	44.85	7.81	0.48	0.78	14.82	7.6	8.44	1646.57	5	2	1	1	3	1	2	1	3	3	4	3	4	3	1	1
HA2	″ Haidinger"	27.85	49.41	3.26	37.16	6.25	0.48	0.78	14.82	9.97	7.19	1598.26	5	2	1	1	3	1	2	1	3	3	4	3	4	3	1	1

sample number	taxon	shell position	fourier coeff 2	fourier coeff.3	fourier coeff 4	fourier coeff 5	fourier coeff 6	fourier coeff 7	fourier coeff 8	fourier coeff 9	fourier co 10	fourier co 11
FI6	*fiordlandica*	2	0.199	-0.123	-0.075	-0.041	-0.019	-0.001	-0.018	0.009	0.015	-0.009
AU1	*P. g. aurea*	1	0.195	-0.137	-0.118	-0.034	-0.033	0.015	-0.047	-0.006	-0.024	0.007
AU2	*P. g. aurea*	1	0.207	-0.118	-0.085	0.009	-0.046	0.000	-0.031	-0.023	-0.043	0.017
AU3	*P. g. aurea*	1	0.216	-0.130	-0.086	-0.010	-0.043	-0.004	-0.046	0.002	-0.031	-0.006
AU4	*P. g. aurea*	1	0.214	-0.116	-0.066	-0.025	-0.046	0.011	-0.014	-0.009	-0.077	0.016
AU5	*P. g. aurea*	1	0.218	-0.119	-0.087	-0.036	-0.041	-0.002	-0.049	0.000	-0.033	0.000
BN1	*P. g. brunnea*	1	0.221	-0.060	-0.025	-0.007	-0.015	-0.016	-0.064	-0.012	-0.045	-0.017
BN2	*P. g. brunnea*	1	0.210	-0.109	-0.076	0.003	-0.042	-0.020	-0.079	-0.011	-0.034	-0.005
BN3	*P. g. brunnea*	1	0.205	-0.109	-0.079	0.011	-0.027	-0.013	-0.056	-0.008	-0.036	-0.004
BN4	*P. g. brunnea*	1	0.227	-0.094	-0.057	-0.023	-0.028	-0.022	-0.047	-0.015	-0.045	-0.012
BN5	*P. g. brunnea*	1	0.230	-0.067	-0.065	-0.040	-0.023	-0.009	-0.041	-0.022	-0.045	-0.020
BN6	*P. g. brunnea*	1	0.238	-0.055	-0.027	-0.044	-0.024	-0.018	-0.022	0.016	-0.042	-0.038
CO1	*P. g. compta*	1	0.199	-0.071	-0.078	-0.035	-0.033	-0.014	-0.034	0.005	-0.046	-0.036
CO2	*P. g. compta*	1	0.209	-0.071	-0.053	-0.022	-0.010	0.000	-0.014	0.005	-0.052	-0.038
CO3	*P. g. compta*	1	0.217	-0.075	-0.072	-0.038	-0.025	-0.010	-0.022	0.006	-0.052	-0.026
CO4	*P. g. compta*	1	0.223	-0.085	-0.045	-0.010	-0.032	-0.010	-0.032	0.007	-0.048	-0.016
CO5	*P. g. compta*	1	0.200	-0.095	-0.083	0.001	-0.056	-0.007	-0.048	-0.016	-0.068	-0.005
CO6	*P. g. compta*	1	0.217	-0.109	-0.080	-0.012	-0.016	0.005	-0.052	-0.013	-0.059	-0.012
FA1	*P. g. fallax*	1	0.208	-0.073	-0.068	-0.045	-0.020	-0.022	-0.009	0.010	-0.025	-0.022
FA2	*P. g. fallax*	1	0.197	-0.113	-0.067	0.000	-0.036	-0.009	-0.015	0.022	-0.047	-0.034
FA3	*P. g. fallax*	1	0.240	-0.071	-0.028	-0.015	-0.006	-0.019	-0.026	0.005	-0.018	-0.020
FA4	*P. g. fallax*	1	0.203	-0.040	-0.038	-0.039	-0.012	0.001	-0.054	-0.033	-0.039	-0.021
FA5	*P. g. fallax*	1	0.193	-0.064	-0.076	-0.036	-0.044	0.004	-0.046	-0.018	-0.027	-0.025
FA6	*P. g. fallax*	1	0.192	-0.081	-0.072	-0.040	-0.018	-0.006	-0.023	-0.001	-0.038	-0.005
GI1	*P. g. fallax*	1	0.217	-0.053	-0.075	-0.048	-0.040	-0.011	-0.046	-0.014	-0.030	0.004
GI2	*P. g. gilliesi*	1	0.201	-0.123	-0.092	-0.054	-0.004	0.002	-0.029	0.001	-0.053	-0.005
GI3	*P. g. gilliesi*	1	0.233	-0.063	-0.050	-0.039	-0.025	-0.013	-0.043	0.002	-0.049	-0.014
GI4	*P. g. gilliesi*	1	0.225	-0.088	-0.068	-0.038	-0.017	-0.006	-0.044	-0.009	-0.058	-0.014
GI5	*P. g. gilliesi*	1	0.223	-0.066	-0.052	-0.025	-0.027	-0.038	-0.030	0.016	-0.047	-0.028
GI6	*P. g. gilliesi*	1	0.215	-0.056	-0.050	-0.043	-0.028	-0.005	-0.033	0.001	-0.048	-0.029
HA1	″Haidinger"	1	0.193	-0.095	-0.065	-0.015	-0.048	-0.025	-0.048	-0.016	-0.013	0.001
HA2	″Haidinger"	1	0.203	-0.082	-0.053	-0.027	-0.034	-0.010	-0.046	-0.011	-0.023	-0.021

sample number	taxon	total height	max diam	apex height	apex area	aperture drop	BW roundness	circularity	diam last whorl	diam 3.5 whorl	umbilicus diam	dorsal area	whorl no.	whorl type	mucous	fringe	foot colour	suture	umbilicus	axial stripes	dorsal stripes	ventral stripes	bicolor stripes	callus texture	callus colour	sculpture	appearance	egg type
HA3	"Haidinger"	31.79	51.41	4.75	60.09	8.83	0.48	0.78	12.94	10.71	9.29	1872.3	5	2	1	1	3	1	2	1	3	3	4	3	4	3	1	1
HA4	"Haidinger"	30.57	50.59	4.08	50.48	9.92	0.47	0.75	15.47	8.26	8.72	1646.04	5	2	1	1	3	1	2	1	3	3	4	3	4	3	1	1
HA5	"Haidinger"	36.41	54.35	6.25	85.73	15.21	0.45	0.75	11.98	8.95	10.32	2073.12	5	2	1	1	3	1	2	1	3	3	4	3	4	3	1	1
HA6	"Haidinger"	33.83	55.34	5.17	69.48	8.42	0.44	0.75	10.86	12.77	11.31	2187.1	5	2	1	1	3	1	2	1	3	3	4	3	4	3	1	1
JA1	*P. g. jamesoni*	25.23	45.02	3.67	29.29	7.26	0.53	0.78	16.83	8.19	8.21	1260.25	5	2	1	1	3	1	2	1	3	3	4	1	4	3	1	1
JA2	*P. g. jamesoni*	24.16	40.99	3.79	35.52	3.44	0.52	0.8	13.33	9.4	7.24	1052.44	5	2	1	1	3	1	2	1	3	3	4	1	4	3	1	1
JA3	*P. g. jamesoni*	26.65	41.72	4.74	43.73	11.61	0.52	0.74	13.41	8.04	6.31	1176.77	5	2	1	1	3	1	2	1	3	3	4	1	4	3	1	1
JA4	*P. g. jamesoni*	24.52	43.48	3.67	33.89	9.48	0.53	0.77	12.39	10.57	7.37	1232	5	2	1	1	3	1	2	1	3	3	4	1	4	3	1	1
KA1	*P. g. kahurangica*	22.14	46.92	3.48	25.61	6.09	0.48	0.74	17.8	10.96	8.35	1335.32	5	2	1	1	3	2	2	1	3	3	4	4	4	3	1	1
KA2	*P. g. kahurangica*	22.74	45.65	3.52	32.74	5.09	0.48	0.75	16.59	10.52	8.97	1274.94	5	2	1	1	3	2	2	1	3	3	4	4	4	3	1	1
KA3	*P. g. kahurangica*	24.65	44.02	3.6	29.61	7.3	0.49	0.75	13.77	9.88	7.82	1246.91	5	2	1	1	3	2	2	1	3	3	4	4	4	3	1	1
KA4	*P. g. kahurangica*	23.69	47.33	4.12	39.94	7.47	0.49	0.76	16.18	10.78	8.72	1426.73	5	2	1	1	3	2	2	1	3	3	4	4	4	3	1	1
KA5	*P. g. kahurangica*	25.23	48.87	4.72	45.96	7.47	0.44	0.72	14.51	11.84	8.3	1535.64	5	2	1	1	3	2	2	1	3	3	4	4	4	3	1	1
KA6	*P. g. kahurangica*	25.58	48.24	4.12	36.9	7.12	0.47	0.74	15.33	12.18	8.8	1478.33	5	2	1	1	3	2	2	1	3	3	4	4	4	3	1	1
MN1	*P. g. montana*	26.76	52.4	3.85	45.81	6.71	0.46	0.75	15.75	11.95	9.98	1831.23	5	2	1	1	3	2	2	1	2	2	4	3	4	3	1	1
MN2	*P. g. montana*	28.9	52.74	4.42	44.33	10.7	0.48	0.74	14.02	10.71	8.12	1826.59	5	2	1	1	3	2	2	1	2	2	4	3	4	3	1	1
MN3	*P. g. montana*	28.11	52.45	4.57	42.37	14.98	0.52	0.75	16.46	11.32	7.27	1770.17	5	2	1	1	3	2	2	1	2	2	4	3	4	3	1	1
MN4	*P. g. montana*	26.82	51.61	4.07	44.72	7.31	0.45	0.73	14.4	11.69	8.23	1804	5	2	1	1	3	2	2	1	2	2	4	3	4	3	1	1
MN5	*P. g. montana*	24.42	50.18	3.84	38	3.01	0.47	0.76	14.47	14.6	7.54	1665.26	5	2	1	1	3	2	2	1	2	2	4	3	4	3	1	1
SB1	*P. g. subfusca*	23.8	44.56	3.79	38.46	7.4	0.46	0.75	13.79	8.41	6.22	1318	5	2	1	1	3	2	2	1	3	3	4	4	4	3	1	1
SB2	*P. g. subfusca*	26.57	40.59	3.17	30.33	8.89	0.48	0.76	10.81	7.19	5.56	1197.93	5	2	1	1	3	2	2	1	3	3	4	4	4	3	1	1
SB3	*P. g. subfusca*	28.16	48.73	4.49	44.2	13.12	0.46	0.72	11.73	9.76	8.3	1583.8	5	2	1	1	3	2	2	1	3	3	4	4	4	3	1	1
SB4	*P. g. subfusca*	25.11	40.67	3.3	31.4	10.9	0.5	0.75	10.77	8.02	6.38	1109.56	5	2	1	1	3	2	2	1	3	3	4	4	4	3	1	1
SB5	*P. g. subfusca*	26.8	48.2	3.78	35.66	12.87	0.44	0.71	13.02	9.31	8.6	1581.31	5	2	1	1	3	2	2	1	3	3	4	4	4	3	1	1
SB6	*P. g. subfusca*	25.44	51.21	3.47	32.84	7.43	0.45	0.75	14.04	12.57	10.01	1717.02	5	2	1	1	3	2	2	1	3	3	4	4	4	3	1	1
AR1	*P. h. anatokiensis* (RF)	33.05	68.96	3.02	36.8	7.34	0.47	0.76	22.02	15.76	14.84	3103.67	5.5	2	1	1	4	3	2	1	3	3	2	1	4	3	1	1
AR2	*P. h. anatokiensis* (RF)	34.41	69.83	1.96	21.69	7.39	0.49	0.78	22.1	18.68	15.1	2961.05	5.5	2	1	1	4	3	2	1	3	3	2	1	4	3	1	1
AR3	*P. h. anatokiensis* (RF)	37.12	68.51	5.73	80.15	7.34	0.47	0.75	21.77	14.17	13.96	3083.97	5.5	2	1	1	4	3	2	1	3	3	2	1	4	3	1	1
AR4	*P. h. anatokiensis* (RF)	35.99	69.54	4.38	53.19	7.04	0.46	0.73	18.14	18.8	14.45	3212.08	5.5	2	1	1	4	3	2	1	3	3	2	1	4	3	1	1
AY1	*P. h. anatokiensis* (YF)	40.07	75.59	4.28	54.02	15.3	0.45	0.73	24.82	14.7	15.89	3646.17	5.5	2	1	1	4	3	2	1	3	3	2	1	4	3	1	1
AY2	*P. h. anatokiensis* (YF)	41.44	76.87	3.08	34.74	13.81	0.46	0.76	24.66	18.66	18.39	3761.13	5.5	2	1	1	4	3	2	1	3	3	2	1	4	3	1	1
AY3	*P. h. anatokiensis* (YF)	38.81	75.95	5.48	74.47	11.64	0.46	0.75	25.91	15.29	17.48	3595.46	5.5	2	1	1	4	3	2	1	3	3	2	1	4	3	1	1

sample number	taxon	shell position	fourier coeff 2	fourier coeff.3	fourier coeff 4	fourier coeff 5	fourier coeff 6	fourier coeff 7	fourier coeff 8	fourier coeff 9	fourier co 10	fourier co 11
HA3	"Haidinger"	1	0.194	-0.093	-0.069	-0.023	-0.053	-0.013	-0.043	-0.019	-0.017	0.001
HA4	"Haidinger"	1	0.208	-0.122	-0.066	-0.010	-0.027	-0.014	-0.045	-0.008	-0.014	-0.002
HA5	"Haidinger"	1	0.188	-0.135	-0.097	-0.026	-0.019	0.022	-0.040	-0.011	-0.008	0.016
HA6	"Haidinger"	1	0.198	-0.118	-0.072	-0.044	-0.031	-0.008	-0.020	0.007	-0.011	0.014
JA1	*P. g. jamesoni*	1	0.183	-0.058	-0.093	-0.052	-0.025	-0.004	-0.063	-0.016	-0.045	-0.024
JA2	*P. g. jamesoni*	1	0.189	-0.069	-0.057	0.004	-0.039	-0.024	-0.072	-0.020	-0.027	0.000
JA3	*P. g. jamesoni*	1	0.187	-0.124	-0.105	-0.008	-0.026	0.009	-0.047	-0.007	-0.066	-0.024
JA4	*P. g. jamesoni*	1	0.201	-0.069	-0.067	-0.022	-0.012	-0.021	-0.017	0.008	-0.050	-0.033
KA1	*P. g. kahurangica*	1	0.228	-0.055	-0.045	-0.032	-0.030	0.014	-0.031	-0.010	-0.056	-0.024
KA2	*P. g. kahurangica*	1	0.213	-0.065	-0.062	-0.034	-0.036	-0.005	-0.043	-0.002	-0.024	-0.038
KA3	*P. g. kahurangica*	1	0.200	-0.065	-0.081	-0.052	-0.050	-0.020	-0.057	-0.007	-0.033	-0.015
KA4	*P. g. kahurangica*	1	0.225	-0.068	-0.037	-0.010	-0.005	-0.006	-0.030	0.005	-0.048	-0.014
KA5	*P. g. kahurangica*	1	0.235	-0.070	-0.049	-0.036	-0.031	-0.017	-0.045	0.009	-0.062	-0.023
KA6	*P. g. kahurangica*	1	0.228	-0.065	-0.036	-0.019	-0.038	-0.014	-0.041	-0.011	-0.064	-0.020
MN1	*P. g. montana*	1	0.231	-0.064	-0.043	-0.014	-0.028	-0.014	-0.051	-0.017	-0.037	-0.028
MN2	*P. g. montana*	1	0.223	-0.110	-0.032	0.018	-0.034	-0.031	-0.028	0.008	-0.050	0.009
MN3	*P. g. montana*	1	0.227	-0.082	-0.031	-0.009	-0.001	0.007	-0.033	0.002	-0.035	0.009
MN4	*P. g. montana*	1	0.241	-0.080	-0.043	-0.018	-0.002	-0.001	-0.024	-0.014	-0.063	-0.024
MN5	*P. g. montana*	1	0.231	-0.048	-0.020	-0.036	-0.020	-0.010	-0.003	0.003	-0.023	-0.026
SB1	*P. g. subfusca*	1	0.211	-0.083	-0.058	-0.027	-0.024	-0.013	-0.055	-0.008	-0.056	-0.008
SB2	*P. g. subfusca*	1	0.203	-0.111	-0.047	0.027	-0.034	-0.014	-0.061	0.003	-0.023	-0.007
SB3	*P. g. subfusca*	1	0.214	-0.095	-0.074	-0.045	-0.028	-0.008	-0.072	-0.001	-0.045	-0.016
SB4	*P. g. subfusca*	1	0.215	-0.104	-0.056	0.005	-0.012	-0.003	-0.070	-0.035	-0.042	-0.013
SB5	*P. g. subfusca*	1	0.232	-0.108	-0.076	-0.016	-0.002	0.010	-0.033	-0.011	-0.057	-0.025
SB6	*P. g. subfusca*	1	0.230	-0.046	-0.026	-0.031	-0.004	-0.007	-0.057	-0.023	-0.040	-0.020
AR1	*P. h. anatokiensis* (RF)	1	0.236	-0.045	-0.029	-0.023	-0.011	-0.003	-0.024	-0.028	-0.005	-0.019
AR2	*P. h. anatokiensis* (RF)	1	0.235	-0.027	-0.003	-0.011	-0.018	-0.013	-0.009	-0.024	-0.013	-0.016
AR3	*P. h. anatokiensis* (RF)	1	0.225	-0.081	-0.045	-0.015	-0.015	0.004	-0.041	-0.015	-0.047	-0.035
AR4	*P. h. anatokiensis* (RF)	1	0.241	-0.057	-0.040	-0.032	-0.010	-0.016	-0.037	-0.019	-0.050	-0.028
AY1	*P. h. anatokiensis* (YF)	1	0.236	-0.078	-0.028	-0.015	-0.017	-0.009	-0.024	0.013	-0.034	-0.022
AY2	*P. h. anatokiensis* (YF)	1	0.230	-0.049	-0.020	-0.030	-0.012	0.003	-0.023	0.020	-0.031	-0.033
AY3	*P. h. anatokiensis* (YF)	1	0.228	-0.066	-0.033	-0.019	0.000	0.003	-0.006	0.013	-0.042	-0.027

sample number	taxon	total height	max diam	apex height	apex area	aperture drop	BW roundness	circularity	diam last whorl	diam 3.5 whorl	umbilicus diam	dorsal area	whorl no.	whorl type	mucous	fringe	foot colour	suture	umbilicus	axial stripes	dorsal stripes	ventral stripes	bicolor stripes	callus texture	callus colour	sculpture	appearance	egg type
AY4	*P. h. anatokiensis* (YF)	36.99	79.04	4.68	67.57	11.99	0.45	0.74	22.5	19.53	18.41	4191.08	5.5	2	1	1	4	3	2	1	3	3	2	1	4	3	1	1
BI1	*P. h. bicolor*	30.93	61.5	3.11	31.05	7.01	0.49	0.77	21.34	12.59	12.08	2404.74	5.25	2	1	1	4	2	2	1	2	1	3	1	4	3	1	1
BI2	*P. h. bicolor*	30.22	62.72	3.61	46.77	6.55	0.46	0.74	18.19	15.81	12.11	2571.68	5.25	2	1	1	4	2	2	1	2	1	3	1	4	3	1	1
BI3	*P. h. bicolor*	33.96	63	5.08	67.68	8.56	0.46	0.74	16.44	12.12	9.99	2637.86	5.25	2	1	1	4	2	2	1	2	1	3	1	4	3	1	1
BI4	*P. h. bicolor*	31.9	62.23	5.15	68.25	10.74	0.46	0.74	17.76	12.26	10.6	2387.34	5.25	2	1	1	4	2	2	1	2	1	3	1	4	3	1	1
CN1	*P. h. consobrina*	36.88	63.4	2.7	35.76	12.63	0.49	0.76	17.46	12.42	13.01	2703.74	5.25	2	1	1	4	2	2	1	2	2	3	1	4	3	1	1
CN2	*P. h. consobrina*	35.62	59.31	3.87	41.51	12.04	0.49	0.75	15.89	11.81	11.58	2427.02	5.25	2	1	1	4	2	2	1	2	2	3	1	4	3	1	1
CN3	*P. h. consobrina*	38.4	60.49	5.05	71.35	17.51	0.49	0.76	14.38	10.83	10.94	2600.18	5.25	2	1	1	4	2	2	1	2	2	3	1	4	3	1	1
CN4	*P. h. consobrina*	34.61	62.07	3.87	49.68	13.14	0.47	0.72	15.33	14.82	10.42	2641.54	5.25	2	1	1	4	2	2	1	2	2	3	1	4	3	1	1
HB1	*P. h. hochstetteri* (BB)	32.89	63.49	3.96	51.66	11.27	0.48	0.75	19.42	15.41	13.52	2606.63	5.25	2	1	1	4	3	2	1	2	3	3	1	4	3	1	1
HB2	*P. h. hochstetteri* (BB)	34.94	66.07	5.02	71.64	16.85	0.5	0.75	20.05	13.75	13.6	2766.96	5.25	2	1	1	4	3	2	1	2	3	3	1	4	3	1	1
HB3	*P. h. hochstetteri* (BB)	30.38	60.88	4.57	53.17	6.09	0.51	0.78	20.68	12.92	11.33	2366.84	5.25	2	1	1	4	3	2	1	2	3	3	1	4	3	1	1
HB4	*P. h. hochstetteri* (BB)	32.2	65	3.81	44.3	12.69	0.5	0.77	20.63	14.73	13.37	2682.18	5.25	2	1	1	4	3	2	1	2	3	3	1	4	3	1	1
HB5	*P. h. hochstetteri* (BB)	32	62.95	2.89	39.18	11.27	0.48	0.75	17.25	16.52	11.84	2533.1	5.25	2	1	1	4	3	2	1	2	3	3	1	4	3	1	1
HY1	*P. h. hochstetteri* (YB)	29.25	59.59	4.27	38.61	9.24	0.48	0.76	19.33	11.33	11.64	2232.66	5.25	2	1	1	4	3	2	1	3	3	3	1	4	3	1	1
HY2	*P. h. hochstetteri* (YB)	29.55	56.76	3.61	28.59	6.61	0.53	0.78	19.68	12.13	10.16	1984.71	5.25	2	1	1	4	3	2	1	3	3	3	1	4	3	1	1
HY3	*P. h. hochstetteri* (YB)	33.77	57.89	3.89	51.38	8.79	0.51	0.79	16.13	12.47	11.02	2204.46	5.25	2	1	1	4	3	2	1	3	3	3	1	4	3	1	1
HY4	*P. h. hochstetteri* (YB)	28.5	58.36	3.7	37.81	8.19	0.51	0.77	19.78	11.9	11.1	2219.83	5.25	2	1	1	4	3	2	1	3	3	3	1	4	3	1	1
HY5	*P. h. hochstetteri* (YB)	30.49	59.92	4.08	48.06	8.66	0.47	0.75	17.57	14.97	13.06	2418.28	5.25	2	1	1	4	3	2	1	3	3	3	1	4	3	1	1
OB1	*P. h. obscura*	35.06	67.92	4.87	75.3	14.15	0.49	0.75	21.54	12.21	15.49	2953.44	5.25	2	1	1	4	2	2	1	3	3	4	1	4	3	1	1
OB2	*P. h. obscura*	34.81	64.5	5.54	77.29	8.78	0.5	0.76	19.61	12.78	13.6	2710.46	5.25	2	1	1	4	2	2	1	3	3	4	1	4	3	1	1
OB3	*P. h. obscura*	38	66.77	5.94	85.62	16.33	0.48	0.75	18.84	11.85	11.41	2958.13	5.25	2	1	1	4	2	2	1	3	3	4	1	4	3	1	1
OB4	*P. h. obscura*	41.28	73.24	7.08	105.33	13.25	0.47	0.73	19.93	16.12	13.88	3408.74	5.25	2	1	1	4	2	2	1	3	3	4	1	4	3	1	1
AG1	*P. augusta*	24.12	42.18	3.27	26.11	8.1	0.54	0.78	16.04	7.71	6.86	1066.55	4.5	1	2	1	2	3	2	4	2	2	1	1	5	3	1	1
AG2	*P. augusta*	24.48	38.42	2.72	22.11	10.03	0.51	0.76	12.11	7.87	5.57	973.38	4.25	1	2	1	2	3	2	4	2	2	1	1	5	3	1	1
AG3	*P. augusta*	25.02	38.72	2.54	22.05	8.46	0.56	0.78	11.49	8.5	6.86	992.18	4.25	1	2	1	2	3	2	4	2	2	1	1	5	3	1	1
AG4	*P. augusta*	22.85	36.89	3.45	24.49	8.7	0.54	0.78	13.34	6.69	5.84	861	4.25	1	2	1	2	3	2	4	2	2	1	1	5	3	1	1
AG5	*P. augusta*	26.65	42.31	3.45	28.14	11.36	0.55	0.77	13.18	8.5	6.64	1204	4.25	1	2	1	2	3	2	4	2	2	1	1	5	3	1	1
AG6	*P. augusta*	21.94	37.52	3.63	26.06	6.65	0.54	0.77	10.77	9.01	6.52	970.77	4.25	1	2	1	2	3	2	4	2	2	1	1	5	3	1	1
JO1	*P. l. johnstoni*	31.5	54.72	4.25	45.37	4.85	0.49	0.79	17.67	10.5	8.92	1843.01	5.25	2	2	1	1	2	2	1	3	3	3	1	2	3	1	1
JO2	*P. l. johnstoni*	32.85	56	4.38	55.1	9.29	0.47	0.76	15.2	12.24	9.34	2042.18	5.25	2	2	1	1	2	2	1	3	3	3	1	2	3	1	1
JO3	*P. l. johnstoni*	33.65	54.62	4.58	62.95	10.3	0.46	0.75	11.53	12.62	7.59	2095.78	5.25	2	2	1	1	2	2	1	3	3	3	1	2	3	1	1

sample number	taxon	shell position	fourier coeff 2	fourier coeff.3	fourier coeff 4	fourier coeff 5	fourier coeff 6	fourier coeff 7	fourier coeff 8	fourier coeff 9	fourier co 10	fourier co 11
AY4	*P. h. anatokiensis* (YF)	1	0.238	-0.083	-0.029	-0.010	0.000	0.001	-0.022	0.009	-0.030	-0.012
BI1	*P. h. bicolor*	1	0.219	-0.029	-0.024	-0.013	-0.017	-0.017	-0.061	-0.031	-0.021	-0.037
BI2	*P. h. bicolor*	1	0.235	-0.049	-0.039	-0.054	-0.016	0.000	-0.033	-0.021	-0.026	-0.033
BI3	*P. h. bicolor*	1	0.221	-0.080	-0.067	-0.045	-0.015	-0.028	-0.042	-0.022	-0.042	-0.019
BI4	*P. h. bicolor*	1	0.215	-0.052	-0.041	-0.050	-0.070	-0.034	-0.013	0.011	-0.055	-0.029
CN1	*P. h. consobrina*	1	0.226	-0.087	-0.032	0.007	-0.008	-0.025	-0.025	0.000	-0.026	-0.032
CN2	*P. h. consobrina*	1	0.209	-0.094	-0.074	-0.035	0.004	-0.009	-0.011	0.002	-0.041	-0.046
CN3	*P. h. consobrina*	1	0.207	-0.104	-0.073	-0.017	-0.030	-0.012	-0.027	-0.006	-0.014	-0.028
CN4	*P. h. consobrina*	1	0.234	-0.091	-0.061	-0.032	0.017	-0.008	-0.015	0.009	-0.047	-0.027
HB1	*P. h. hochstetteri* (BB)	1	0.224	-0.064	-0.055	-0.037	-0.012	-0.006	-0.045	-0.022	-0.050	-0.027
HB2	*P. h. hochstetteri* (BB)	1	0.217	-0.073	-0.047	-0.019	-0.021	0.000	-0.039	-0.029	-0.064	-0.014
HB3	*P. h. hochstetteri* (BB)	1	0.229	-0.035	-0.020	-0.019	-0.016	-0.012	-0.032	-0.033	-0.052	-0.019
HB4	*P. h. hochstetteri* (BB)	1	0.222	-0.057	-0.025	-0.016	0.003	-0.010	-0.029	0.000	-0.031	-0.021
HB5	*P. h. hochstetteri* (BB)	1	0.228	-0.056	-0.035	-0.021	0.002	-0.007	-0.037	-0.008	-0.041	-0.036
HY1	*P. h. hochstetteri* (YB)	1	0.229	-0.052	-0.044	-0.030	-0.006	0.003	-0.036	-0.021	-0.049	-0.024
HY2	*P. h. hochstetteri* (YB)	1	0.208	-0.053	-0.044	-0.018	-0.003	-0.009	-0.026	-0.007	-0.049	-0.019
HY3	*P. h. hochstetteri* (YB)	1	0.196	-0.058	-0.069	-0.054	-0.042	-0.016	-0.013	-0.023	-0.014	-0.010
HY4	*P. h. hochstetteri* (YB)	1	0.229	-0.059	-0.027	-0.009	0.003	-0.007	-0.008	-0.014	-0.032	-0.009
HY5	*P. h. hochstetteri* (YB)	1	0.233	-0.042	-0.032	-0.045	-0.012	-0.005	-0.021	-0.012	-0.039	-0.025
OB1	*P. h. obscura*	1	0.226	-0.058	-0.057	-0.035	-0.035	-0.016	-0.047	-0.024	-0.051	-0.021
OB2	*P. h. obscura*	1	0.211	-0.063	-0.065	-0.049	-0.031	-0.015	-0.030	-0.012	-0.031	-0.023
OB3	*P. h. obscura*	1	0.211	-0.083	-0.072	-0.036	-0.027	-0.020	-0.062	-0.003	-0.038	-0.014
OB4	*P. h. obscura*	1	0.221	-0.089	-0.065	-0.027	-0.034	-0.003	-0.044	-0.003	-0.047	-0.021
AG1	*P. augusta*	1	0.194	-0.085	-0.042	0.003	-0.028	0.002	-0.019	0.016	-0.063	-0.015
AG2	*P. augusta*	1	0.208	-0.105	-0.046	0.021	-0.031	-0.004	-0.054	-0.004	-0.054	0.015
AG3	*P. augusta*	1	0.203	-0.093	-0.038	0.014	-0.010	0.017	0.009	-0.005	-0.065	0.008
AG4	*P. augusta*	1	0.195	-0.092	-0.056	0.014	-0.029	0.022	-0.040	-0.007	-0.067	-0.012
AG5	*P. augusta*	1	0.200	-0.084	-0.055	-0.003	-0.026	0.004	-0.025	-0.016	-0.083	-0.009
AG6	*P. augusta*	1	0.197	-0.078	-0.053	-0.007	-0.020	0.025	-0.023	-0.008	-0.060	0.008
JO1	*P. l. johnstoni*	1	0.203	-0.061	-0.023	0.016	-0.040	-0.019	-0.060	-0.025	-0.046	-0.038
JO2	*P. l. johnstoni*	1	0.208	-0.093	-0.058	-0.005	-0.028	-0.004	-0.068	-0.031	-0.026	-0.016
JO3	*P. l. johnstoni*	1	0.212	-0.107	-0.052	-0.003	-0.044	0.001	-0.035	0.005	-0.047	0.009

sample number	taxon	total height	max diam	apex height	apex area	aperture drop	BW roundness	circularity	diam last whorl	diam 3.5 whorl	umbilicus diam	dorsal area	whorl no.	whorl type	mucous	fringe	foot colour	suture	umbilicus	axial stripes	dorsal stripes	ventral stripes	bicolor stripes	callus texture	callus colour	sculpture	appearance	egg type
JO4	*P. l. johnstoni*	31.77	57.4	4.31	51.13	9.69	0.48	0.76	18.74	9.54	9.34	2026.32	5.25	2	2	1	1	2	2	1	3	3	3	1	2	3	1	1
JO5	*P. l. johnstoni*	30.15	52.33	4.31	46	8.68	0.49	0.75	13.76	12.05	8.07	1846.19	5.25	2	2	1	1	2	2	1	3	3	3	1	2	3	1	1
JO6	*P. l. johnstoni*	32.58	52.66	4.85	58.93	8.48	0.51	0.78	11.68	12.29	8.38	1922.55	5.25	2	2	1	1	2	2	1	3	3	3	1	2	3	1	1
LI1	*P. l. lignaria*	32.06	59.84	3.17	34	10.16	0.51	0.78	20.9	12.25	9.01	2157.7	5.25	2	1	1	1	2	2	4	2	1	1	1	2	3	1	1
LI2	*P. l. lignaria*	32.74	59.75	3.16	41.1	11.06	0.51	0.76	17.46	13.2	9.53	2371.84	5.25	2	1	1	1	2	2	4	2	1	1	1	2	3	1	1
LI3	*P. l. lignaria*	36.58	62.32	4.06	48.09	11.74	0.5	0.74	17.13	14.22	8.55	2664.97	5.25	2	1	1	1	2	2	4	2	1	1	1	2	3	1	1
LI4	*P. l. lignaria*	40.42	65.4	5.42	77.97	14.45	0.49	0.75	20.3	10.77	9.4	2711.16	5.25	2	1	1	1	2	2	4	2	1	1	1	2	3	1	1
LI5	*P. l. lignaria*	41.32	60.88	4.74	65.51	16.94	0.51	0.76	16.36	11.87	9.09	2524.13	5.25	2	1	1	1	2	2	4	2	1	1	1	2	3	1	1
LI6	*P. l. lignaria*	34.55	58.84	4.97	60.47	11.06	0.51	0.77	16.89	13.2	8.5	2295.17	5.25	2	1	1	1	2	2	4	2	1	1	1	2	3	1	1
LU1	*P. l. lusca*	35.74	59.24	3.8	41.17	13.92	0.5	0.73	18.61	9.56	7.53	2235.94	5.25	2	1	1	1	2	2	4	1	1	1	1	2	3	1	1
LU2	*P. l. lusca*	34.16	56.55	6.17	71.97	11.7	0.48	0.75	17.54	11.21	8.99	2088.8	5.25	2	1	1	1	2	2	4	1	1	1	1	2	3	1	1
LU3	*P. l. lusca*	37.9	56.48	4.49	54.46	12.73	0.53	0.76	15.13	12.5	8.75	2164.14	5.25	2	1	1	1	2	2	4	1	1	1	1	2	3	1	1
LU4	*P. l. lusca*	33.06	58.88	3.7	39.51	12.28	0.52	0.76	19.84	11.65	7.54	2232.92	5.25	2	1	1	1	2	2	4	1	1	1	1	2	3	1	1
LU5	*P. l. lusca*	32.66	59.56	5.39	62.58	14.08	0.48	0.73	17.16	12.4	9.52	2325	5.25	2	1	1	1	2	2	4	1	1	1	1	2	3	1	1
LU6	*P. l. lusca*	33.53	59.53	5.69	68.16	10.91	0.47	0.74	16.58	13.66	10.59	2265.9	5.25	2	1	1	1	2	2	4	1	1	1	1	2	3	1	1
OC1	*P. l. o'connori*	34.94	61.38	4.1	41.79	12.16	0.52	0.77	20.46	11.83	9.79	2427.7	5	2	1	1	1	2	2	3	2	2	1	1	2	3	1	1
OC2	*P. l. o'connori*	44.18	59.65	4.84	70.36	18.75	0.48	0.72	11.17	11.58	7.75	2552.81	5	2	1	1	1	2	2	3	2	2	1	1	2	3	1	1
OC3	*P. l. o'connori*	32.97	57.41	4.1	47.13	10.7	0.53	0.77	16.71	13.6	10.94	2319.65	5	2	1	1	1	2	2	3	2	2	1	1	2	3	1	1
OC4	*P. l. o'connori*	39.56	64.35	6.15	80.54	14.36	0.49	0.75	19.05	10.81	9.69	2625.42	5	2	1	1	1	2	2	3	2	2	1	1	2	3	1	1
OC5	*P. l. o'connori*	36.7	58.87	5.13	63.85	14.94	0.52	0.76	16.71	11.07	9.22	2278.52	5	2	1	1	1	2	2	3	2	2	1	1	2	3	1	1
OC6	*P. l. o'connori*	45.49	60.01	6.45	96.57	15.97	0.46	0.75	12.36	10.74	11.28	2609.75	5	2	1	1	1	2	2	3	2	2	1	1	2	3	1	1
RT1	*P. l. rotella*	34.6	57.74	3.1	33.86	12.51	0.48	0.68	20.36	9.98	10.27	2040.23	5	2	2	1	1	2	2	1	3	2	4	1	2	3	1	1
RT2	*P. l. rotella*	29.7	58.25	4.48	47.45	10.67	0.45	0.73	20.61	12.94	6.99	2038.72	5	2	2	1	1	2	2	1	3	2	4	1	2	3	1	1
RT3	*P. l. rotella*	37.18	58.85	4.25	44.77	12.97	0.48	0.72	17.75	11.56	8.29	2168.09	5	2	2	1	1	2	2	1	3	2	4	1	2	3	1	1
RT4	*P. l. rotella*	31.76	57.01	3.79	34.62	10.9	0.49	0.75	19.1	11.16	9.01	2024.69	5	2	2	1	1	2	2	1	3	2	4	1	2	3	1	1
RT5	*P. l. rotella*	34.09	56.23	2.52	24.54	14.12	0.52	0.75	16.27	11.85	8.26	2003.07	5	2	2	1	1	2	2	1	3	2	4	1	2	3	1	1
RT6	*P. l. rotella*	35.26	57.24	4.2	51.74	11.75	0.46	0.74	13.42	12.22	9.35	2264.45	5	2	2	1	1	2	2	1	3	2	4	1	2	3	1	1
RU1	*P. l. ruforadiata*	30.71	52.62	3.02	30.4	8.53	0.56	0.77	17.56	9.47	7	1621.21	5	2	1	1	1	2	2	3	1	1	1	1	2	3	1	1
RU2	*P. l. ruforadiata*	27.27	50.42	3.1	27.2	5.03	0.54	0.77	18.77	11.51	8.36	1525.9	5	2	1	1	1	2	2	3	1	1	1	1	2	3	1	1
RU3	*P. l. ruforadiata*	28.48	50.57	3.64	32.94	7.27	0.51	0.76	16.88	12.58	6.77	1534.78	5	2	1	1	1	2	2	3	1	1	1	1	2	3	1	1
RU4	*P. l. ruforadiata*	32.55	52.71	3.81	41.53	7.22	0.54	0.8	17.42	9.84	7.96	1759.4	5	2	1	1	1	2	2	3	1	1	1	1	2	3	1	1
RU5	*P. l. ruforadiata*	38.99	58.22	3.91	42.69	15.89	0.49	0.71	15.86	11.03	7.94	2289.42	5	2	1	1	1	2	2	3	1	1	1	1	2	3	1	1

sample number	taxon	shell position	fourier coeff 2	fourier coeff.3	fourier coeff 4	fourier coeff 5	fourier coeff 6	fourier coeff 7	fourier coeff 8	fourier coeff 9	fourier co 10	fourier co 11
JO4	*P. l. johnstoni*	1	0.216	-0.094	-0.042	0.009	-0.024	-0.009	-0.027	-0.002	-0.060	-0.007
JO5	*P. l. johnstoni*	1	0.221	-0.090	-0.042	0.011	0.000	0.007	-0.032	0.004	-0.055	-0.004
JO6	*P. l. johnstoni*	1	0.202	-0.075	-0.045	-0.002	-0.025	-0.019	-0.053	-0.012	-0.069	-0.007
LI1	*P. l. lignaria*	1	0.207	-0.069	-0.026	-0.007	-0.033	-0.002	-0.047	0.011	-0.045	-0.013
LI2	*P. l. lignaria*	1	0.218	-0.077	-0.055	-0.016	-0.023	-0.005	-0.030	0.004	-0.045	-0.029
LI3	*P. l. lignaria*	1	0.214	-0.087	-0.060	-0.019	-0.026	-0.005	-0.036	0.001	-0.052	0.002
LI4	*P. l. lignaria*	1	0.199	-0.115	-0.076	-0.019	-0.067	-0.005	-0.016	0.008	-0.042	-0.008
LI5	*P. l. lignaria*	1	0.205	-0.110	-0.051	0.026	-0.033	-0.001	-0.067	0.006	-0.039	0.007
LI6	*P. l. lignaria*	1	0.201	-0.072	-0.056	-0.014	-0.046	-0.012	-0.075	-0.007	-0.046	-0.015
LU1	*P. l. lusca*	1	0.213	-0.104	-0.071	-0.007	-0.017	0.012	-0.044	-0.007	-0.032	0.005
LU2	*P. l. lusca*	1	0.190	-0.090	-0.093	-0.054	-0.044	-0.011	-0.060	-0.010	-0.034	-0.014
LU3	*P. l. lusca*	1	0.192	-0.112	-0.089	-0.014	-0.031	-0.007	-0.043	-0.009	-0.027	-0.015
LU4	*P. l. lusca*	1	0.229	-0.096	-0.038	0.011	-0.007	-0.011	-0.035	0.012	-0.012	-0.004
LU5	*P. l. lusca*	1	0.236	-0.094	-0.037	0.004	-0.007	-0.012	-0.040	0.006	-0.064	-0.005
LU6	*P. l. lusca*	1	0.233	-0.092	-0.027	0.007	0.010	-0.001	-0.025	0.009	-0.042	0.005
OC1	*P. l. o'connori*	1	0.212	-0.086	-0.039	0.003	-0.011	-0.006	-0.032	0.012	-0.024	-0.001
OC2	*P. l. o'connori*	1	0.195	-0.182	-0.091	0.002	0.005	-0.020	-0.009	0.053	-0.011	0.012
OC3	*P. l. o'connori*	1	0.202	-0.078	-0.061	-0.024	0.000	-0.006	-0.032	0.010	-0.049	-0.027
OC4	*P. l. o'connori*	1	0.210	-0.116	-0.058	-0.001	-0.028	-0.006	-0.036	0.017	-0.044	0.005
OC5	*P. l. o'connori*	1	0.193	-0.121	-0.062	0.002	-0.040	-0.009	-0.019	0.037	-0.050	-0.037
OC6	*P. l. o'connori*	1	0.190	-0.148	-0.092	0.008	-0.015	-0.011	-0.035	0.007	-0.015	0.022
RT1	*P. l. rotella*	1	0.244	-0.108	-0.068	-0.005	0.002	0.011	-0.071	-0.026	-0.042	0.014
RT2	*P. l. rotella*	1	0.226	-0.074	-0.020	-0.019	-0.069	0.015	-0.033	0.004	-0.088	0.007
RT3	*P. l. rotella*	1	0.200	-0.118	-0.082	-0.021	-0.046	0.019	-0.048	0.003	-0.061	0.019
RT4	*P. l. rotella*	1	0.223	-0.079	-0.035	0.012	-0.034	-0.009	-0.052	0.006	-0.055	-0.007
RT5	*P. l. rotella*	1	0.207	-0.084	-0.087	-0.035	-0.022	0.006	-0.029	-0.042	-0.042	0.001
RT6	*P. l. rotella*	1	0.210	-0.101	-0.057	-0.002	-0.042	0.000	-0.061	0.005	-0.039	-0.010
RU1	*P. l. ruforadiata*	1	0.191	-0.092	-0.078	-0.026	-0.008	-0.009	-0.032	0.023	-0.040	-0.021
RU2	*P. l. ruforadiata*	1	0.210	-0.068	-0.044	-0.003	-0.020	0.006	-0.025	-0.001	-0.032	-0.010
RU3	*P. l. ruforadiata*	1	0.218	-0.068	-0.041	-0.009	-0.047	-0.011	-0.032	0.008	-0.045	-0.031
RU4	*P. l. ruforadiata*	1	0.187	-0.099	-0.065	0.004	-0.023	-0.021	-0.049	0.013	-0.018	-0.015
RU5	*P. l. ruforadiata*	1	0.209	-0.141	-0.092	-0.045	0.019	-0.003	-0.024	0.004	-0.017	0.027

sample number	taxon	total height	max diam	apex height	apex area	aperture drop	BW roundness	circularity	diam last whorl	diam 3.5 whorl	umbilicus diam	dorsal area	whorl no.	whorl type	mucous	fringe	foot colour	suture	umbilicus	axial stripes	dorsal stripes	ventral stripes	bicolor stripes	callus texture	callus colour	sculpture	appearance	egg type
RU6	*P. l. ruforadiata*	30.71	52.95	2.96	28.59	11.58	0.5	0.75	16.49	13.18	10.39	1848.03	5	2	1	1	1	2	2	3	1	1	1	1	2	3	1	1
UN1	*P. l. unicolorata*	31.06	52.9	3.26	29.37	9.77	0.48	0.73	17.18	9.57	7.34	1781.77	5	2	1	1	1	2	2	1	1	1	1	1	2	3	1	1
UN2	*P. l. unicolorata*	33.06	51.04	4.26	35.99	12.77	0.48	0.75	15.42	9.92	6.7	1740.04	5	2	1	1	1	2	2	1	1	1	1	1	2	3	1	1
UN3	*P. l. unicolorata*	30.05	49.69	4.13	42.49	8.64	0.47	0.79	14.46	8.61	7.33	1601.31	5	2	1	1	1	2	2	1	1	1	1	1	2	3	1	1
UN4	*P. l. unicolorata*	29.55	50.87	3.51	30.74	8.64	0.48	0.74	17.78	9.65	6.6	1705.44	5	2	1	1	1	2	2	1	1	1	1	1	2	3	1	1
UN5	*P. l. unicolorata*	26.3	47.61	3.51	35.04	8.77	0.46	0.75	15.66	9.54	7.68	1454.36	5	2	1	1	1	2	2	1	1	1	1	1	2	3	1	1
UN6	*P. l. unicolorata*	28.05	45.58	3.76	32.88	7.51	0.54	0.8	14.11	11.75	6.29	1377.5	5	2	1	1	1	2	2	1	1	1	1	1	2	3	1	1
EG1	"Egmont"	37.21	68.15	4.17	58.4	13.1	0.48	0.73	20.84	13.11	12.1	2854.56	5.25	2	1	1	4	2	2	1	1	1	4	1	5	3	1	1
EG2	"Egmont"	35.27	67.31	3.99	51.84	11.93	0.49	0.75	20.04	15.39	14.42	2895.41	5.25	2	1	1	4	2	2	1	1	1	4	1	5	3	1	1
EG3	"Egmont"	35.38	66.33	4.17	61.13	10.39	0.47	0.74	19.52	16.08	15.05	2898.13	5.25	2	1	1	4	2	2	1	1	1	4	1	5	3	1	1
EG4	"Egmont"	33.37	65.39	3.73	48.19	8.56	0.5	0.77	21.25	15.07	12.87	2860.29	5.25	2	1	1	4	2	2	1	1	1	4	1	5	3	1	1
EG5	"Egmont"	37.29	67	4.39	62.63	7.61	0.48	0.74	20.82	14.91	15.94	2965.58	5.25	2	1	1	4	2	2	1	1	1	4	1	5	3	1	1
EG6	"Egmont"	37.5	65.12	4.39	63.63	12.15	0.48	0.73	17.69	14.16	12.62	2817.7	5.25	2	1	1	4	2	2	1	1	1	4	1	5	3	1	1
KW1	"Kaweka"	25.2	41.36	2.63	25.39	8.58	0.57	0.79	15.36	8.3	7.46	1124.73	5	2	1	1	4	2	2	1	2	2	2	1	5	3	1	1
KW2	"Kaweka"	26.25	41.78	2.54	22.94	6.91	0.58	0.83	13.51	7.72	7.96	1145.83	5	2	1	1	4	2	2	1	2	2	2	1	5	3	1	1
KW3	"Kaweka"	28.71	41.87	2.88	28.3	8.26	0.54	0.81	15.66	9.05	5.24	1201.41	5	2	1	1	4	2	2	1	2	2	2	1	5	3	1	1
KW4	"Kaweka"	24.95	39.2	2.75	23.78	6.17	0.54	0.81	12.35	7.75	6.48	1044.08	5	2	1	1	4	2	2	1	2	2	2	1	5	3	1	1
KW5	"Kaweka"	24.77	41.45	3.88	37.39	8.07	0.52	0.81	12.97	8.52	6.27	1138.11	5	2	1	1	4	2	2	1	2	2	2	1	5	3	1	1
KW6	"Kaweka"	24.58	41.57	3	25.76	6.5	0.54	0.81	13.55	10.44	6.48	1142.49	5	2	1	1	4	2	2	1	2	2	2	1	5	3	1	1
MU1	"Mangaharuru"	25.59	46.94	3.95	44.26	5.86	0.51	0.8	15.63	8.9	7.78	1437.05	5	2	1	1	4	2	2	2	2	2	2	1	5	3	1	1
MU2	"Mangaharuru"	25.11	46.3	3.35	29.86	5.98	0.5	0.76	15.84	9.23	6.7	1388.91	5	2	1	1	4	2	2	2	2	2	2	1	5	3	1	1
MU3	"Mangaharuru"	27.75	46.72	3.5	31.26	5.2	0.5	0.8	15.03	9.54	7.04	1447.09	5	2	1	1	4	2	2	2	2	2	2	1	5	3	1	1
MU4	"Mangaharuru"	25.59	45.44	3.61	37.82	4.53	0.48	0.77	16.89	9.08	7.41	1337.38	5	2	1	1	4	2	2	2	2	2	2	1	5	3	1	1
MU5	"Mangaharuru"	26.66	46.7	3.4	31.91	4.28	0.51	0.79	15.7	10.23	6.32	1420.89	5	2	1	1	4	2	2	2	2	2	2	1	5	3	1	1
MU6	"Mangaharuru"	23.2	42.87	3.35	31.57	5.02	0.5	0.78	13.6	8.97	6.71	1208.13	5	2	1	1	4	2	2	2	2	2	2	1	5	3	1	1
UR1	"Urewera"	23.73	43.87	3.44	30.88	6.65	0.51	0.8	14.9	8.61	7.27	1230.61	5	2	1	1	4	2	2	2	3	2	2	1	5	3	1	1
UR2	"Urewera"	26.31	46.34	2.95	29.95	6.11	0.51	0.76	14.97	11.57	8.27	1424.05	5	2	1	1	4	2	2	2	3	2	2	1	5	3	1	1
UR3	"Urewera"	23.31	43.75	3.57	31.03	4.84	0.49	0.79	15.14	8.54	8.11	1211.28	5	2	1	1	4	2	2	2	3	2	2	1	5	3	1	1
UR4	"Urewera"	23.36	42.61	2.89	28.55	5.36	0.52	0.78	14.65	8.63	7.61	1149.61	5	2	1	1	4	2	2	2	3	2	2	1	5	3	1	1
MA1	*P. marchanti*	26.12	49.25	2.89	28.4	4.03	0.53	0.8	17.86	9.81	8.26	1550.8	5	2	1	1	4	2	2	1	2	2	2	1	5	3	1	1
MA2	*P. marchanti*	28.27	56.22	3.31	31.53	7.39	0.5	0.79	17.86	13.98	9.98	1995.3	5	2	1	1	4	2	2	1	2	2	2	1	5	3	1	1
MA3	*P. marchanti*	29.41	52.66	3.68	40.12	8.5	0.49	0.76	18.75	9.23	8.11	1827.17	5	2	1	1	4	2	2	1	2	2	2	1	5	3	1	1

sample number	taxon	shell position	fourier coeff 2	fourier coeff.3	fourier coeff 4	fourier coeff 5	fourier coeff 6	fourier coeff 7	fourier coeff 8	fourier coeff 9	fourier co 10	fourier co 11
RU6	*P. l. ruforadiata*	1	0.217	-0.092	-0.037	-0.019	-0.001	0.023	-0.032	-0.004	-0.043	-0.003
UN1	*P. l. unicolorata*	1	0.211	-0.106	-0.086	-0.042	-0.018	0.001	-0.007	0.009	-0.031	-0.019
UN2	*P. l. unicolorata*	1	0.197	-0.112	-0.066	-0.001	-0.053	-0.042	-0.024	0.049	-0.052	-0.015
UN3	*P. l. unicolorata*	1	0.186	-0.090	-0.068	-0.056	-0.047	-0.005	-0.004	0.012	-0.005	-0.002
UN4	*P. l. unicolorata*	1	0.222	-0.090	-0.060	-0.005	-0.043	-0.010	-0.023	0.013	-0.051	-0.019
UN5	*P. l. unicolorata*	1	0.218	-0.072	-0.052	-0.030	-0.030	0.003	-0.047	-0.004	-0.060	-0.027
UN6	*P. l. unicolorata*	1	0.188	-0.054	-0.058	-0.033	-0.016	-0.014	-0.018	0.006	-0.072	-0.043
EG1	"Egmont"	1	0.229	-0.099	-0.063	-0.021	-0.019	-0.019	-0.025	0.005	-0.031	-0.003
EG2	"Egmont"	1	0.235	-0.071	-0.035	-0.003	-0.002	-0.018	-0.037	-0.004	-0.012	-0.017
EG3	"Egmont"	1	0.237	-0.072	-0.031	-0.020	0.002	0.003	-0.028	-0.004	-0.031	-0.034
EG4	"Egmont"	1	0.230	-0.067	-0.025	0.007	-0.012	-0.005	-0.028	-0.020	-0.029	-0.013
EG5	"Egmont"	1	0.235	-0.096	-0.034	-0.002	-0.017	-0.004	-0.044	0.000	-0.029	-0.020
EG6	"Egmont"	1	0.220	-0.086	-0.071	-0.027	-0.043	-0.025	-0.031	-0.007	-0.026	0.011
KW1	"Kaweka"	1	0.191	-0.097	-0.043	0.011	-0.006	0.019	-0.031	0.015	-0.025	-0.001
KW2	"Kaweka"	1	0.172	-0.077	-0.039	0.026	-0.005	0.001	-0.045	-0.004	-0.038	-0.031
KW3	"Kaweka"	1	0.186	-0.098	-0.017	0.057	-0.018	-0.006	-0.032	0.007	-0.020	-0.005
KW4	"Kaweka"	1	0.180	-0.100	-0.045	0.017	0.001	0.012	-0.015	0.017	-0.016	-0.009
KW5	"Kaweka"	1	0.178	-0.086	-0.047	0.012	-0.004	0.009	-0.051	0.004	-0.037	-0.022
KW6	"Kaweka"	1	0.190	-0.075	-0.039	0.009	0.012	0.020	-0.022	0.000	-0.036	-0.035
MU1	"Mangaharuru"	1	0.184	-0.062	-0.049	-0.014	-0.048	-0.015	-0.037	-0.001	-0.035	-0.029
MU2	"Mangaharuru"	1	0.199	-0.081	-0.075	-0.031	-0.045	0.016	-0.035	0.004	-0.051	-0.040
MU3	"Mangaharuru"	1	0.186	-0.071	-0.059	-0.027	-0.038	0.003	-0.057	-0.018	-0.029	-0.018
MU4	"Mangaharuru"	1	0.207	-0.082	-0.062	-0.018	-0.045	0.005	-0.029	-0.014	-0.038	-0.027
MU5	"Mangaharuru"	1	0.193	-0.067	-0.052	-0.010	-0.035	-0.004	-0.049	-0.010	-0.032	-0.024
MU6	"Mangaharuru"	1	0.208	-0.072	-0.032	-0.013	-0.030	0.010	-0.019	0.002	-0.025	-0.001
UR1	"Urewera"	1	0.193	-0.061	-0.047	-0.009	-0.032	-0.004	-0.034	-0.017	-0.035	-0.007
UR2	"Urewera"	1	0.220	-0.078	-0.039	0.004	-0.023	-0.015	-0.045	-0.002	-0.011	-0.019
UR3	"Urewera"	1	0.195	-0.047	-0.037	-0.030	-0.052	-0.006	-0.042	-0.017	-0.028	-0.028
UR4	"Urewera"	1	0.199	-0.066	-0.051	-0.018	-0.034	0.016	-0.015	0.002	-0.030	-0.017
MA1	*P. marchanti*	1	0.203	-0.050	-0.028	-0.006	-0.032	0.002	-0.026	-0.017	-0.047	-0.012
MA2	*P. marchanti*	1	0.199	-0.033	-0.031	-0.047	-0.020	0.014	-0.013	0.010	-0.053	-0.029
MA3	*P. marchanti*	1	0.217	-0.083	-0.045	0.003	-0.029	-0.002	-0.023	0.013	-0.055	-0.018

sample number	taxon	total height	max diam	apex height	apex area	aperture drop	BW roundness	circularity	diam last whorl	diam 3.5 whorl	umbilicus diam	dorsal area	whorl no.	whorl type	mucous	fringe	foot colour	suture	umbilicus	axial stripes	dorsal stripes	ventral stripes	bicolor stripes	callus texture	callus colour	sculpture	appearance	egg type
MA4	*P. marchanti*	25.93	52.25	3.38	35.52	5.63	0.48	0.77	16.18	12.04	10.9	1774.87	5	2	1	1	4	2	2	1	2	2	2	1	5	3	1	1
BR1	"Buller River"	22.65	35.56	4.25	38.5	8.64	0.49	0.74	8.16	6.23	4.5	886.33	5	2	3	1	1	2	2	1	1	1	1	1	6	3	1	1
BR2	"Buller River"	22.11	39.67	3.86	33.64	8.06	0.49	0.75	9.43	7.83	5.35	1071.5	5	2	3	1	1	2	2	1	1	1	1	1	6	3	1	1
BR3	"Buller River"	26.45	36.69	4.54	40.02	13.13	0.49	0.75	7.3	7.61	6.87	933.88	5	2	3	1	1	2	2	1	1	1	1	1	6	3	1	1
BR4	"Buller River"	22.85	37.17	3.2	27.93	7.95	0.52	0.76	9.72	6.03	5.22	930.81	5	2	3	1	1	2	2	1	1	1	1	1	6	3	1	1
BR5	"Buller River"	22.52	36.96	4.81	32.55	9.21	0.53	0.75	8.74	8.93	4.97	939.51	5	2	3	1	1	2	2	1	1	1	1	1	6	3	1	1
BR6	"Buller River"	24.07	39.51	2.87	22.24	7.18	0.5	0.77	10.31	8.63	5.96	1057.12	5	2	3	1	1	2	2	1	1	1	1	1	6	3	1	1
FT1	*P. fletcheri*	17.82	31.72	2.1	13.71	2.91	0.58	0.84	12.33	6.09	4.78	639.54	4.4	1	1	1	4	2	2	2	1	1	1	1	1	2	1	1
FT2	*P. fletcheri*	17.27	29.76	1.7	10.86	3.31	0.58	0.83	10.74	6.47	4.32	558.72	4.4	1	1	1	4	2	2	2	1	1	1	1	1	2	1	1
FT3	*P. fletcheri*	17.82	33.29	2.34	14.48	3.15	0.57	0.81	12.05	7.29	4.97	685.57	4.4	1	1	1	4	2	2	2	1	1	1	1	1	2	1	1
FT4	*P. fletcheri*	18.06	34	2.5	13.33	5.17	0.54	0.81	11.36	6.46	5.68	720.1	4.4	1	1	1	4	2	2	2	1	1	1	1	1	2	1	1
FT5	*P. fletcheri*	16.61	33.19	2.99	21.61	3.39	0.56	0.81	11.49	8.13	5.75	681.21	4.4	1	1	1	4	2	2	2	1	1	1	1	1	2	1	1
GG1	*P. gagei*	26.15	40.59	1.71	11.78	10.77	0.53	0.75	12.77	7.99	4.08	1110.84	4.5	1	4	1	2	2	2	1	1	1	1	1	1	2	1	1
GG2	*P. gagei*	22.31	38.92	1.62	9.99	5.98	0.53	0.78	10.27	9.79	5.06	1004.67	4.5	1	4	1	2	2	2	1	1	1	1	1	1	2	1	1
GG3	*P. gagei*	22.11	37.83	2.65	20.3	5.38	0.54	0.77	11.78	8.89	5.03	981.02	4.5	1	4	1	2	2	2	1	1	1	1	1	1	2	1	1
GG4	*P. gagei*	25.77	43.96	1.2	10.72	9.83	0.52	0.76	12.56	9.19	5.96	1304.34	4.5	1	4	1	2	2	2	1	1	1	1	1	1	2	1	1
GG5	*P. gagei*	20.38	37.9	2.22	16.12	6.67	0.54	0.76	11.08	10.01	5.83	921.09	4.5	1	4	1	2	2	2	1	1	1	1	1	1	2	1	1
GA1	"Garibaldi"	21.04	31.17	1.7	9.19	3.1	0.55	0.81	12.08	6.55	5.42	628.75	4.5	1	3	1	2	2	2	1	1	1	1	1	6	1	1	1
GA2	"Garibaldi"	17.45	36.55	1.79	12.66	3.53	0.53	0.78	14.92	9.05	5.99	801.33	4.5	1	3	1	2	2	2	1	1	1	1	1	6	1	1	1
GA3	"Garibaldi"	19.86	33.44	1.47	8.12	2.87	0.58	0.79	13.37	6.19	4.81	692.17	4.5	1	3	1	2	2	2	1	1	1	1	1	6	1	1	1
GA4	"Garibaldi"	20.76	35.56	1.8	11.96	2.14	0.6	0.8	11.27	8.09	4.86	825.86	4.5	1	3	1	2	2	2	1	1	1	1	1	6	1	1	1
GA5	"Garibaldi"	19.54	33.57	2.31	14.99	2.98	0.56	0.8	11.18	8.3	4.51	721.04	4.5	1	3	1	2	2	2	1	1	1	1	1	6	1	1	1
KI1	"Kirwins"	24.03	37.98	3.25	25.78	8.12	0.48	0.74	12.65	6.65	5.06	933.72	4.25	1	3	1	4	2	2	1	1	1	1	1	6	2	1	1
KI2	"Kirwins"	20.3	34.6	2.76	20.47	4.38	0.55	0.8	11.74	8.29	5.21	750.2	4.25	1	3	1	4	2	2	1	1	1	1	1	6	2	1	1
KI3	"Kirwins"	21.92	37.93	3.25	22.77	5.2	0.56	0.79	14.9	8.56	5.36	871.42	4.25	1	3	1	4	2	2	1	1	1	1	1	6	2	1	1
KI4	"Kirwins"	22.57	40.88	2.44	18.72	6.66	0.54	0.78	16.12	8.9	5.95	1004.14	4.25	1	3	1	4	2	2	1	1	1	1	1	6	2	1	1
KI5	"Kirwins"	24.68	41.12	2.28	17.55	8.45	0.54	0.75	12.15	10.04	5.13	1143.62	4.25	1	3	1	4	2	2	1	1	1	1	1	6	2	1	1
MK1	"Matakitaki"	25.7	39.47	2.93	20.99	8.68	0.55	0.77	11.05	8.18	6.53	1042.53	4.3	1	3	1	3	2	2	1	1	1	1	1	6	2	1	1
MK2	"Matakitaki"	22.64	37.6	2.56	22.95	3.17	0.57	0.85	14.44	9.59	5.77	855.08	4.3	1	3	1	3	2	2	1	1	1	1	1	6	2	1	1
MK3	"Matakitaki"	24.12	39.84	2.14	74.23	6.65	0.58	0.77	14.82	7.05	6.18	1018.54	4.3	1	3	1	3	2	2	1	1	1	1	1	6	2	1	1
MK4	"Matakitaki"	27.5	42.45	3.04	24.78	8.57	0.55	0.75	12.67	8.24	5.86	1186.24	4.3	1	3	1	3	2	2	1	1	1	1	1	6	2	1	1
MK5	"Matakitaki"	24.59	41.82	3.41	30.76	7.43	0.54	0.77	12.85	8.83	6.99	1154.01	4.3	1	3	1	3	2	2	1	1	1	1	1	6	2	1	1

sample number	taxon	shell position	fourier coeff 2	fourier coeff.3	fourier coeff 4	fourier coeff 5	fourier coeff 6	fourier coeff 7	fourier coeff 8	fourier coeff 9	fourier co 10	fourier co 11
MA4	*P. marchanti*	1	0.215	-0.060	-0.034	-0.019	-0.006	0.022	-0.042	-0.011	-0.033	-0.015
BR1	"Buller River"	1	0.190	-0.129	-0.086	0.001	-0.047	-0.005	-0.060	-0.007	-0.041	-0.004
BR2	"Buller River"	1	0.207	-0.086	-0.061	-0.018	-0.059	-0.014	-0.053	-0.005	-0.061	-0.012
BR3	"Buller River"	1	0.189	-0.134	-0.096	-0.007	-0.033	-0.009	-0.037	-0.007	-0.024	0.000
BR4	"Buller River"	1	0.196	-0.104	-0.073	0.005	-0.041	0.002	-0.049	-0.007	-0.030	-0.016
BR5	"Buller River"	1	0.208	-0.095	-0.065	-0.019	-0.041	-0.038	-0.040	0.010	-0.047	-0.003
BR6	"Buller River"	1	0.200	-0.078	-0.065	-0.005	-0.048	-0.020	-0.042	-0.014	-0.033	-0.006
FT1	*P. fletcheri*	1	0.184	-0.037	-0.027	0.002	0.011	0.004	-0.017	-0.001	-0.033	-0.017
FT2	*P. fletcheri*	1	0.183	-0.057	-0.051	-0.003	0.006	0.002	-0.029	-0.027	-0.019	0.005
FT3	*P. fletcheri*	1	0.196	-0.068	-0.043	0.016	-0.009	-0.010	-0.023	-0.004	-0.057	-0.010
FT4	*P. fletcheri*	1	0.189	-0.051	-0.038	-0.018	-0.041	-0.017	-0.011	0.024	-0.053	-0.025
FT5	*P. fletcheri*	1	0.199	-0.051	-0.042	0.000	-0.026	-0.005	0.007	-0.001	-0.026	-0.005
GG1	*P. gagei*	1	0.203	-0.105	-0.070	-0.019	-0.024	0.005	-0.001	0.000	-0.055	-0.007
GG2	*P. gagei*	1	0.203	-0.069	-0.044	-0.017	-0.047	-0.035	-0.023	-0.014	-0.016	-0.001
GG3	*P. gagei*	1	0.200	-0.072	-0.055	-0.014	-0.023	0.002	-0.018	-0.012	-0.032	0.000
GG4	*P. gagei*	1	0.219	-0.081	-0.051	-0.028	-0.026	-0.030	0.030	-0.019	-0.001	-0.007
GG5	*P. gagei*	1	0.215	-0.066	-0.029	-0.012	-0.040	-0.033	0.005	0.037	-0.073	-0.019
GA1	"Garibaldi"	1	0.187	-0.078	-0.007	0.039	-0.068	-0.043	-0.003	0.035	-0.031	-0.028
GA2	"Garibaldi"	1	0.218	-0.065	-0.035	-0.016	-0.009	0.016	-0.018	-0.018	-0.021	-0.012
GA3	"Garibaldi"	1	0.212	-0.073	0.002	0.037	-0.052	-0.012	0.009	0.017	-0.043	-0.019
GA4	"Garibaldi"	1	0.189	-0.076	-0.043	0.001	-0.025	-0.004	0.016	0.027	-0.028	-0.010
GA5	"Garibaldi"	1	0.200	-0.076	-0.033	0.008	-0.019	-0.008	-0.007	0.015	-0.039	-0.030
KI1	"Kirwins"	1	0.211	-0.099	-0.079	0.005	-0.054	-0.004	-0.011	0.018	-0.057	-0.017
KI2	"Kirwins"	1	0.195	-0.074	-0.032	0.018	-0.033	0.007	-0.006	0.009	-0.045	-0.015
KI3	"Kirwins"	1	0.204	-0.072	-0.037	0.007	-0.029	-0.019	-0.008	0.013	-0.040	-0.009
KI4	"Kirwins"	1	0.204	-0.056	-0.048	-0.011	-0.029	-0.010	-0.007	0.008	-0.054	-0.026
KI5	"Kirwins"	1	0.223	-0.087	-0.032	-0.013	-0.005	0.001	0.002	-0.014	-0.062	-0.003
MK1	"Matakitaki"	1	0.195	-0.101	-0.050	0.017	-0.010	0.002	-0.043	0.001	-0.043	-0.022
MK2	"Matakitaki"	1	0.165	-0.036	-0.042	0.004	-0.023	-0.005	-0.041	-0.009	-0.040	-0.029
MK3	"Matakitaki"	1	0.209	-0.102	-0.040	0.014	-0.005	0.010	-0.010	-0.006	-0.050	-0.016
MK4	"Matakitaki"	1	0.213	-0.112	-0.048	0.029	-0.018	0.019	-0.023	0.001	-0.058	0.022
MK5	"Matakitaki"	1	0.205	-0.075	-0.045	0.001	-0.024	-0.005	-0.044	0.001	-0.052	-0.025

sample number	taxon	total height	max diam	apex height	apex area	aperture drop	BW roundness	circularity	diam last whorl	diam 3.5 whorl	umbilicus diam	dorsal area	whorl no.	whorl type	mucous	fringe	foot colour	suture	umbilicus	axial stripes	dorsal stripes	ventral stripes	bicolor stripes	callus texture	callus colour	sculpture	appearance	egg type
MT1	"Matiri"	20.66	34.31	2.53	18.47	2.74	0.6	0.84	13.64	6.13	5.64	735.89	4.5	1	3	1	2	2	2	1	1	1	1	1	6	2	1	1
MT2	"Matiri"	20.96	36.55	3.16	25.95	3.45	0.54	0.82	12.77	8.4	5.57	853.8	4.5	1	3	1	2	2	2	1	1	1	1	1	6	2	1	1
MT3	"Matiri"	17.68	34.44	3.28	21.84	2.95	0.54	0.84	12.44	7.97	6.02	736.74	4.5	1	3	1	2	2	2	1	1	1	1	1	6	2	1	1
MT4	"Matiri"	19.06	35.87	2.21	15.16	1.19	0.58	0.81	13.21	8.09	4.72	820.62	4.5	1	3	1	2	2	2	1	1	1	1	1	6	2	1	1
MT5	"Matiri"	22.12	37.46	2.11	15.15	6.04	0.57	0.79	12.78	8.35	5.75	900.75	4.5	1	3	1	2	2	2	1	1	1	1	1	6	2	1	1
MT6	"Matiri"	22.98	40.1	3.41	25.82	7.49	0.48	0.77	12.98	10.07	6.25	1020.71	4.5	1	3	1	2	2	2	1	1	1	1	1	6	2	1	1
PT1	*P. patrickensis*	26.56	41.86	2.22	19.87	8.61	0.53	0.78	12.82	8.63	6.61	1108.72	4.25	1	3	1	3	1	2	4	1	1	1	1	6	2	1	1
PT2	*P. patrickensis*	23.12	38.09	2.46	18.07	5.04	0.59	0.8	14.76	7.1	6.01	906.88	4.25	1	3	1	3	1	2	4	1	1	1	1	6	2	1	1
PT3	*P. patrickensis*	24.59	37.42	2.83	23.6	7.99	0.56	0.78	11.1	8.17	4.96	953.34	4.25	1	3	1	3	1	2	4	1	1	1	1	6	2	1	1
PT4	*P. patrickensis*	26.19	39.79	2.71	23.84	8.12	0.58	0.81	14.76	7.28	5.23	1022.05	4.25	1	3	1	3	1	2	4	1	1	1	1	6	2	1	1
PT5	*P. patrickensis*	24.22	41.19	2.23	15.83	8.98	0.55	0.78	13.44	8.17	6.11	1080.47	4.25	1	3	1	3	1	2	4	1	1	1	1	6	2	1	1
PT6	*P. patrickensis*	22.99	38.43	2.58	20.98	4.3	0.56	0.8	12.45	9.57	6.66	961.2	4.25	1	3	1	3	1	2	4	1	1	1	1	6	2	1	1
FO1	"Fox"	20.01	34.15	2.03	10.56	5.54	0.57	0.78	15.13	6.65	5.11	679.9	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
FO2	"Fox"	20.26	35.4	2.11	12.61	6.58	0.59	0.78	14.81	8.03	5.39	766.68	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
FO3	"Fox"	18.99	33.75	2.38	14.85	4.72	0.6	0.8	14.87	6.71	4.42	666.07	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
FO4	"Fox"	21.65	34.41	2.45	17.2	8.74	0.59	0.77	13.03	6.62	4.08	756.31	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
FO5	"Fox"	23	36.38	2.24	15.12	7.89	0.64	0.74	13.93	8.38	6.62	824.49	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
FO6	"Fox"	29.97	39.64	2.37	17.88	10.86	0.55	0.75	13.33	7.55	5.4	1008.18	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
HS1	"Haast"	18.33	29.36	1.95	11.45	2.49	0.65	0.87	12.84	5.86	2.85	519.7	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
HS2	"Haast"	21.61	33.01	2.19	12.71	5.99	0.57	0.8	13.65	6.31	4	665.13	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
HS3	"Haast"	20.67	31.97	2.4	15.55	4.38	0.61	0.85	11.83	6.23	3.44	645.54	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
HS4	"Haast"	20.83	30.35	2.19	11.67	2.99	0.61	0.86	11.81	5.2	2.73	600.88	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
HS5	"Haast"	20.52	35.19	1.73	10.8	6.27	0.62	0.82	14.75	6.84	3.79	761.72	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
HS6	"Haast"	22.24	32.05	2.37	13.17	5.06	0.62	0.82	12.12	6.5	3.68	654.47	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
RO1	*P. r. rossiana*	19.69	33.35	2.51	16.06	4.86	0.56	0.8	12.75	6.87	5	754.25	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
RO3	*P. r. rossiana*	22.19	33.91	2.23	13.1	5.19	0.63	0.84	13.64	6.22	4.45	721.69	4.5	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
RO4	*P. r. rossiana*	23.16	34.93	2.12	11.49	6.78	0.59	0.81	12.09	7.23	4.41	812.58	4.5	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
RO5	*P. r. rossiana*	20.96	34.52	2.02	11.31	4.38	0.6	0.84	11.59	8.03	4.76	711.5	4.25	1	1	1	4	1	2	2	1	1	1	1	1	1	1	1
AN1	*P. annectens*	30.44	64.84	1.08	5.69	1.41	0.51	0.8	26.02	16.57	13.61	2514.15	5.4	2	1	2	3	2	2	4	1	1	1	4	4	3	1	1
AN2	*P. annectens*	35.07	69.34	3.9	45.74	7.25	0.47	0.73	23.35	16.47	13.66	3129.85	5.4	2	1	2	3	2	2	4	1	1	1	4	4	3	1	1
AN3	*P. annectens*	31.24	63.42	4.3	46.8	2.44	0.51	0.78	23.57	17.6	11.37	2494.76	5.4	2	1	2	3	2	2	4	1	1	1	4	4	3	1	1
AN4	*P. annectens*	37.02	70.79	4.55	43.35	10.61	0.46	0.73	20.86	15.16	12.25	3259.16	5.4	2	1	2	3	2	2	4	1	1	1	4	4	3	1	1

sample number	taxon	shell position	fourier coeff 2	fourier coeff.3	fourier coeff 4	fourier coeff 5	fourier coeff 6	fourier coeff 7	fourier coeff 8	fourier coeff 9	fourier co 10	fourier co 11
MT1	"Matiri"	1	0.167	-0.050	-0.059	-0.019	-0.028	-0.002	-0.015	-0.007	-0.039	-0.033
MT2	"Matiri"	1	0.183	-0.060	-0.037	-0.002	-0.027	-0.001	-0.035	-0.004	-0.029	-0.023
MT3	"Matiri"	1	0.182	-0.031	-0.038	-0.011	-0.029	0.003	-0.024	-0.023	-0.025	-0.021
MT4	"Matiri"	1	0.204	-0.032	-0.014	-0.001	-0.035	-0.010	-0.004	-0.019	-0.016	-0.018
MT5	"Matiri"	1	0.201	-0.091	-0.037	0.011	-0.004	-0.004	-0.017	0.019	-0.018	-0.016
MT6	"Matiri"	1	0.209	-0.083	-0.039	0.000	-0.040	-0.001	-0.001	0.025	-0.050	-0.026
PT1	*P. patrickensis*	1	0.197	-0.115	-0.050	0.003	-0.022	-0.003	-0.007	0.010	-0.032	-0.006
PT2	*P. patrickensis*	1	0.182	-0.077	-0.057	0.009	-0.024	0.011	-0.036	-0.004	-0.035	-0.011
PT3	*P. patrickensis*	1	0.196	-0.096	-0.075	0.001	-0.033	-0.024	-0.008	-0.011	-0.027	0.015
PT4	*P. patrickensis*	1	0.199	-0.084	-0.031	0.023	-0.009	0.008	-0.028	-0.018	-0.063	0.010
PT5	*P. patrickensis*	1	0.220	-0.095	-0.012	0.019	0.005	-0.024	-0.012	0.009	-0.057	0.012
PT6	*P. patrickensis*	1	0.187	-0.062	-0.048	-0.012	-0.037	0.009	-0.022	0.014	-0.047	-0.009
FO1	"Fox"	1	0.207	-0.085	-0.034	0.028	-0.018	0.023	0.013	-0.004	-0.049	-0.012
FO2	"Fox"	1	0.212	-0.102	-0.040	0.024	-0.009	0.002	0.028	0.005	-0.046	-0.014
FO3	"Fox"	1	0.173	-0.067	-0.069	0.007	-0.045	0.015	-0.016	-0.011	-0.057	-0.021
FO4	"Fox"	1	0.195	-0.124	-0.037	0.046	-0.008	0.030	0.014	0.009	-0.075	0.023
FO5	"Fox"	1	0.208	-0.120	-0.065	0.023	0.030	0.021	-0.017	0.002	-0.024	0.001
FO6	"Fox"	1	0.197	-0.114	-0.097	0.010	-0.040	0.038	0.003	-0.010	-0.061	0.006
HS1	"Haast"	1	0.150	-0.056	-0.035	0.018	-0.029	-0.021	-0.023	0.004	-0.038	-0.003
HS2	"Haast"	1	0.185	-0.085	-0.041	0.044	-0.040	0.000	-0.008	-0.003	-0.021	0.014
HS3	"Haast"	1	0.153	-0.059	-0.047	0.015	-0.015	-0.012	0.009	0.011	-0.038	-0.005
HS4	"Haast"	1	0.157	-0.077	-0.034	0.023	-0.028	-0.006	0.008	-0.002	-0.019	0.007
HS5	"Haast"	1	0.177	-0.071	-0.049	0.016	-0.024	0.013	0.019	0.012	-0.037	-0.021
HS6	"Haast"	1	0.158	-0.079	-0.060	0.008	-0.029	0.011	-0.009	0.006	-0.048	-0.003
RO1	*P. r. rossiana*	1	0.183	-0.077	-0.055	-0.007	-0.032	0.011	-0.002	0.000	-0.040	-0.034
RO3	*P. r. rossiana*	1	0.159	-0.083	-0.056	0.020	-0.032	0.001	-0.010	0.008	-0.031	-0.021
RO4	*P. r. rossiana*	1	0.168	-0.078	-0.053	0.016	-0.042	-0.004	0.000	0.009	-0.036	-0.028
RO5	*P. r. rossiana*	1	0.165	-0.046	-0.030	0.009	-0.041	-0.023	-0.004	0.031	-0.018	-0.024
AN1	*P. annectens*	1	0.216	-0.025	0.003	-0.003	0.021	0.001	-0.014	-0.010	-0.029	0.005
AN2	*P. annectens*	1	0.244	-0.080	-0.034	-0.004	-0.006	-0.025	-0.039	-0.007	-0.052	-0.007
AN3	*P. annectens*	1	0.225	-0.029	-0.015	-0.033	-0.006	0.005	-0.014	-0.035	-0.044	-0.014
AN4	*P. annectens*	1	0.242	-0.078	-0.032	-0.008	-0.004	-0.014	-0.060	-0.009	-0.031	-0.016

sample number	taxon	total height	max diam	apex height	apex area	aperture drop	BW roundness	circularity	diam last whorl	diam 3.5 whorl	umbilicus diam	dorsal area	whorl no.	whorl type	mucous	fringe	foot colour	suture	umbilicus	axial stripes	dorsal stripes	ventral stripes	bicolor stripes	callus texture	callus colour	sculpture	appearance	egg type
AN5	*P. annectens*	33.45	68.48	5.03	62.79	5.2	0.47	0.76	22.68	16.44	13.5	3031.61	5.4	2	1	2	3	2	2	4	1	1	1	4	4	3	1	1
AN6	*P. annectens*	30.93	64.43	3.9	42.08	3.41	0.49	0.76	22.25	17.82	12.87	2581.41	5.4	2	1	2	3	2	2	4	1	1	1	4	4	3	1	1
GD1	"Gunner Downs"	31.31	60.24	4.53	50.46	5.07	0.47	0.77	20.47	13.77	9.34	2363.66	5	2	1	2	3	3	2	2	1	1	1	1	4	2	1	1
GD2	"Gunner Downs"	34.95	61.56	4.21	37.95	2.91	0.51	0.78	23.54	15.75	14.55	2511.75	5	2	1	2	3	3	2	2	1	1	1	1	4	2	1	1
GD3	"Gunner Downs"	28.89	61.59	3.73	41.16	2.27	0.48	0.76	22.21	18.27	11.77	2426.25	5	2	1	2	3	3	2	2	1	1	1	1	4	2	1	1
GD4	"Gunner Downs"	29.13	63.98	2.27	16.41	2.81	0.5	0.79	26.27	15.9	11.51	2576	5	2	1	2	3	3	2	2	1	1	1	1	4	2	1	1
GD5	"Gunner Downs"	33.01	60.29	3.56	36.98	7.44	0.5	0.79	22.25	15.09	12.16	2383.24	5	2	1	2	3	3	2	2	1	1	1	1	4	2	1	1
GD6	"Gunner Downs"	30.58	63.14	4.1	50.28	3.99	0.46	0.73	18.3	18.57	12.37	2589.7	5	2	1	2	3	3	2	2	1	1	1	1	4	2	1	1
HK1	*P. s. harveyi*	35.35	60.19	4.15	49.71	13.44	0.57	0.77	17.78	11.2	10.22	2313.38	5.5	2	1	2	3	3	2	2	1	1	1	3	3	1	1	1
HK2	*P. s. harveyi*	39.34	65.07	3.82	50.68	10.95	0.51	0.74	15.77	15.99	13.62	2884.3	5.5	2	1	2	3	3	2	2	1	1	1	3	3	1	1	1
HK3	*P. s. harveyi*	37.6	76.85	2.66	25.53	5.48	0.52	0.77	26.69	18.91	15.9	3597.91	5.5	2	1	2	3	3	2	2	1	1	1	3	3	1	1	1
HK4	*P. s. harveyi*	36.85	62.85	3.15	28.33	9.29	0.54	0.77	16.42	16.54	11.98	2660.84	5.5	2	1	2	3	3	2	2	1	1	1	3	3	1	1	1
HM1	*P. s. harveyi*	41.89	74.89	3.27	32.74	13.64	0.5	0.72	19.15	15.28	15.98	3878.12	5.5	2	1	2	3	3	2	3	1	1	1	3	3	1	1	1
HM2	*P. s. harveyi*	36.01	72.12	2.29	17.17	11.98	0.49	0.72	17.55	18.55	13.59	3457.54	5.5	2	1	2	3	3	2	3	1	1	1	3	3	1	1	1
HM3	*P. s. harveyi*	40.42	78.51	2.78	26.56	8.17	0.51	0.76	23.37	18.37	14.06	3810.83	5.5	2	1	2	3	3	2	3	1	1	1	3	3	1	1	1
HM4	*P. s. harveyi*	41.4	77.85	4.38	46.56	10.67	0.5	0.75	19.39	22.91	15.67	4132.14	5.5	2	1	2	3	3	2	3	1	1	1	3	3	1	1	1
MO1	*P. s. mouatae*	36.94	59.57	4.36	44.62	11.73	0.54	0.77	19.3	10.42	10.93	2405.34	5	2	1	2	3	2	2	1	1	1	1	1	3	1	1	1
MO2	*P. s. mouatae*	38.2	61.19	4.36	50.77	15.58	0.56	0.78	17.61	12.88	10.39	2502.27	5	2	1	2	3	2	2	1	1	1	1	1	3	1	1	1
MO3	*P. s. mouatae*	43.48	62.57	6.03	76.38	15.75	0.52	0.73	16.78	11.57	10.67	2593.11	5	2	1	2	3	2	2	1	1	1	1	1	3	1	1	1
MO4	*P. s. mouatae*	37.44	63.84	5.03	55.51	12.57	0.5	0.73	18.58	14.12	12.36	2680.74	5	2	1	2	3	2	2	1	1	1	1	1	3	1	1	1
PR1	*P. s. prouseorum*	47.63	85.72	6.19	82.79	5.37	0.46	0.75	27.37	16.87	15.31	4774.16	6	2	1	2	3	3	2	1	1	1	1	3	4	1	1	1
PR2	*P. s. prouseorum*	48.12	89.41	1.63	22.75	13.57	0.47	0.71	17.55	22.52	18.59	5809.42	6	2	1	2	3	3	2	1	1	1	1	3	4	1	1	1
RI1	*P. s. richardsoni*	28.73	58.79	1.75	13.69	1.67	0.51	0.8	22.34	14.18	12.12	2185.65	5.5	2	1	2	3	3	2	2	1	1	1	1	3	1	1	1
RI2	*P. s. richardsoni*	32.83	62.96	3.04	24.5	1.98	0.53	0.82	22.6	18.4	13.4	2447.25	5.5	2	1	2	3	3	2	2	1	1	1	1	3	1	1	1
RI3	*P. s. richardsoni*	33.06	65.9	3.65	35.04	5.78	0.48	0.76	24.88	14.26	13.07	2762.28	5.5	2	1	2	3	3	2	2	1	1	1	1	3	1	1	1
RI4	*P. s. richardsoni*	36.48	66.82	2.43	22.62	2.58	0.55	0.82	22.54	17.87	13.78	2775.7	5.5	2	1	2	3	3	2	2	1	1	1	1	3	1	1	1
RI5	*P. s. richardsoni*	33.52	60.86	1.22	9.8	3.34	0.54	0.8	17.4	18.85	12.08	2430.36	5.5	2	1	2	3	3	2	2	1	1	1	1	3	1	1	1
SU1	*P. s. superba*	42.35	81.29	3.1	37.15	11.42	0.5	0.77	28.92	19.21	16.75	4167.2	5.4	2	1	2	3	3	2	1	1	1	1	1	3	1	1	1
SU2	*P. s. superba*	37.32	74.49	4.45	51.16	7.22	0.5	0.76	24.05	19.72	17.04	3488.97	5.4	2	1	2	3	3	2	1	1	1	1	1	3	1	1	1
SU3	*P. s. superba*	38.41	72.97	3.2	37.21	6.06	0.55	0.8	24.44	19.87	13.97	3337	5.4	2	1	2	3	3	2	1	1	1	1	1	3	1	1	1
SU4	*P. s. superba*	37.4	73.63	3.03	30.23	9.94	0.51	0.75	23.38	20.36	15.23	3565.84	5.4	2	1	2	3	3	2	1	1	1	1	1	3	1	1	1
SU5	*P. s. superba*	33.36	69.17	3.54	44.7	2.03	0.49	0.76	22.69	19.44	15	2854.85	5.4	2	1	2	3	3	2	1	1	1	1	1	3	1	1	1

sample number	taxon	shell position	fourier coeff 2	fourier coeff.3	fourier coeff 4	fourier coeff 5	fourier coeff 6	fourier coeff 7	fourier coeff 8	fourier coeff 9	fourier co 10	fourier co 11
AN5	*P. annectens*	1	0.225	-0.062	-0.035	-0.032	-0.012	0.004	-0.038	-0.028	-0.053	-0.025
AN6	*P. annectens*	1	0.236	-0.050	-0.006	0.007	-0.020	-0.011	-0.017	-0.007	-0.036	-0.020
GD1	"Gunner Downs"	1	0.214	-0.049	-0.051	-0.038	-0.059	-0.017	-0.048	-0.021	-0.040	-0.013
GD2	"Gunner Downs"	1	0.206	-0.080	-0.009	0.029	-0.051	-0.052	-0.001	0.037	-0.048	-0.019
GD3	"Gunner Downs"	1	0.239	-0.005	0.009	-0.033	-0.029	-0.021	-0.005	-0.005	-0.028	-0.014
GD4	"Gunner Downs"	1	0.228	-0.060	0.017	0.005	-0.003	-0.014	0.008	0.014	-0.004	-0.016
GD5	"Gunner Downs"	1	0.215	-0.057	0.000	0.017	-0.033	-0.008	-0.040	0.002	-0.044	-0.029
GD6	"Gunner Downs"	1	0.250	-0.060	-0.027	-0.025	-0.028	-0.003	-0.025	-0.018	-0.054	-0.031
HK1	*P. s. harveyi*	1	0.186	-0.076	-0.098	-0.045	-0.012	-0.027	0.002	-0.011	-0.040	-0.010
HK2	*P. s. harveyi*	1	0.209	-0.096	-0.085	-0.057	0.034	-0.013	-0.014	0.005	-0.060	-0.027
HK3	*P. s. harveyi*	1	0.231	-0.036	0.004	-0.001	-0.013	-0.021	0.013	0.018	-0.037	-0.017
HK4	*P. s. harveyi*	1	0.202	-0.064	-0.066	-0.031	-0.020	-0.026	0.004	-0.001	-0.035	-0.013
HM1	*P. s. harveyi*	1	0.240	-0.096	-0.045	-0.006	0.033	-0.021	-0.001	-0.005	-0.023	0.008
HM2	*P. s. harveyi*	1	0.233	-0.065	-0.045	-0.014	0.022	-0.011	0.018	0.005	-0.056	-0.034
HM3	*P. s. harveyi*	1	0.235	-0.056	-0.015	0.007	0.001	-0.026	-0.014	0.006	-0.038	-0.031
HM4	*P. s. harveyi*	1	0.230	-0.049	-0.043	-0.027	0.019	-0.016	-0.005	0.013	-0.024	-0.036
MO1	*P. s. mouatae*	1	0.207	-0.103	-0.031	0.024	-0.032	-0.029	-0.041	0.002	-0.036	0.015
MO2	*P. s. mouatae*	1	0.204	-0.089	-0.059	-0.009	-0.015	-0.025	-0.014	-0.005	-0.058	0.007
MO3	*P. s. mouatae*	1	0.205	-0.132	-0.086	-0.008	-0.005	-0.026	-0.049	-0.006	-0.045	-0.002
MO4	*P. s. mouatae*	1	0.221	-0.082	-0.084	-0.039	-0.008	-0.019	0.009	-0.003	-0.041	-0.022
PR1	*P. s. prouseorum*	1	0.235	-0.083	-0.032	-0.003	-0.026	-0.001	0.001	0.001	-0.056	-0.014
PR2	*P. s. prouseorum*	1	0.251	-0.079	-0.039	-0.031	0.018	-0.043	-0.001	-0.005	0.022	0.029
RI1	*P. s. richardsoni*	1	0.221	0.012	0.018	-0.015	-0.032	-0.011	0.005	-0.012	-0.009	-0.009
RI2	*P. s. richardsoni*	1	0.204	-0.026	0.048	0.024	-0.023	-0.037	0.003	0.014	-0.037	-0.037
RI3	*P. s. richardsoni*	1	0.237	-0.033	0.006	-0.004	-0.004	-0.015	-0.008	-0.002	-0.032	-0.016
RI4	*P. s. richardsoni*	1	0.211	-0.007	0.044	0.023	-0.024	-0.046	0.001	-0.001	0.017	-0.012
RI5	*P. s. richardsoni*	1	0.212	-0.009	-0.006	0.006	-0.012	-0.018	-0.025	-0.014	-0.024	-0.032
SU1	*P. s. superba*	1	0.231	-0.101	-0.021	0.014	0.028	-0.027	0.002	0.008	-0.013	-0.002
SU2	*P. s. superba*	1	0.233	-0.051	-0.036	-0.014	-0.016	-0.005	-0.036	-0.027	-0.037	-0.038
SU3	*P. s. superba*	1	0.221	-0.081	0.033	0.051	-0.035	-0.029	0.014	0.001	-0.032	-0.010
SU4	*P. s. superba*	1	0.235	-0.069	-0.025	-0.006	0.006	-0.017	-0.022	0.012	-0.026	-0.008
SU5	*P. s. superba*	1	0.237	-0.008	0.001	-0.014	-0.063	-0.032	-0.002	-0.005	-0.027	-0.041

sample number	taxon	total height	max diam	apex height	apex area	aperture drop	BW roundness	circularity	diam last whorl	diam 3.5 whorl	umbilicus diam	dorsal area	whorl no.	whorl type	mucous	fringe	foot colour	suture	umbilicus	axial stripes	dorsal stripes	ventral stripes	bicolor stripes	callus texture	callus colour	sculpture	appearance	egg type
LA1	*P. s. lateumbilicata*	22.15	30.53	1.95	12.71	2.59	0.66	0.87	12.85	4.69	3.71	583.08	4	1	1	1	4	1	2	1	1	1	1	2	6	2	1	1
LA2	*P. s. lateumbilicata*	23.76	32.74	2.59	16.13	5.5	0.62	0.83	13.35	5.79	4.4	712.93	4	1	1	1	4	1	2	1	1	1	1	2	6	2	1	1
LA3	*P. s. lateumbilicata*	21.02	31.09	1.81	11.52	4.42	0.62	0.84	9.56	7.84	4.6	660.55	4	1	1	1	4	1	2	1	1	1	1	2	6	2	1	1
LA4	*P. s. lateumbilicata*	23.44	39.11	2.75	20.32	8.3	0.56	0.78	15.9	6.76	4.64	878.65	4	1	1	1	4	1	2	1	1	1	1	2	6	2	1	1
LA5	*P. s. lateumbilicata*	22.31	34.46	2.59	18.58	4.85	0.58	0.83	12.61	7.14	5.14	759.05	4	1	1	1	4	1	2	1	1	1	1	2	6	2	1	1
SP1	*P. s. spedeni*	23.91	38.75	2.49	19.92	8.97	0.57	0.77	15.99	7.39	5.43	938.19	4.35	1	1	1	4	1	2	1	1	1	1	2	6	3	1	1
SP2	*P. s. spedeni*	25.57	38.96	2.5	21.45	8.3	0.61	0.8	13.22	9.37	4.95	979.96	4.35	1	1	1	4	1	2	1	1	1	1	2	6	3	1	1
SP3	*P. s. spedeni*	28.56	40.08	3.15	25.35	10.29	0.6	0.77	13.28	8.14	4.52	1002.49	4.35	1	1	1	4	1	2	1	1	1	1	2	6	3	1	1
SP4	*P. s. spedeni*	27.56	40.43	2.49	19.71	8.3	0.58	0.8	17.34	6.26	4.78	1047.78	4.35	1	1	1	4	1	2	1	1	1	1	2	6	3	1	1
SP5	*P. s. spedeni*	26.57	36.6	2.99	20.67	8.47	0.62	0.81	12.65	8.22	4.46	907.4	4.35	1	1	1	4	1	2	1	1	1	1	2	6	3	1	1
SP6	*P. s. spedeni*	26.07	37.82	2.33	18.12	8.47	0.62	0.81	13.25	8.34	5.06	961.88	4.35	1	1	1	4	1	2	1	1	1	1	2	6	3	1	1
FD1	*P. t. florida*	24.01	43.51	3.82	33.6	5.99	0.5	0.77	14.14	9.22	6.39	1225.62	5	2	1	1	4	2	2	1	2	2	2	1	4	3	1	1
FD2	*P. t. florida*	25.77	43.55	3.3	29.48	11.63	0.49	0.74	12.32	9.48	8.22	1251.83	5	2	1	1	4	2	2	1	2	2	2	1	4	3	1	1
FD3	*P. t. florida*	27.36	48.61	4.93	51.27	9.51	0.47	0.73	15.14	9.48	7.8	1541.27	5	2	1	1	4	2	2	1	2	2	2	1	4	3	1	1
FD4	*P. t. florida*	25.25	50.36	4.23	38.89	11.39	0.47	0.73	15.42	11.38	9.71	1651.8	5	2	1	1	4	2	2	1	2	2	2	1	4	3	1	1
FD5	*P. t. florida*	28.65	46.66	4.58	50.19	11.51	0.48	0.73	12.05	9.39	7.39	1484.78	5	2	1	1	4	2	2	1	2	2	2	1	4	3	1	1
KO1	*P. t. koputaroa*	22.91	47.74	2.44	24.5	8.39	0.5	0.76	15.83	11.12	9.26	1481.03	5	2	1	1	4	2	2	1	2	2	2	1	4	3	1	1
KO2	*P. t. koputaroa*	26.57	47.04	5.78	62.66	9.63	0.45	0.77	11.77	10.41	9.53	1519.48	5	2	1	1	4	2	2	1	2	2	2	1	4	3	1	1
KO3	*P. t. koputaroa*	25.03	50.4	5.13	60.18	7.45	0.48	0.77	16.16	10.4	8.56	1646.02	5	2	1	1	4	2	2	1	2	2	2	1	4	3	1	1
KO4	*P. t. koputaroa*	28.5	46.41	4.36	43.64	13.61	0.49	0.75	10.89	9.07	8.14	1510.81	5	2	1	1	4	2	2	1	2	2	2	1	4	3	1	1
KO5	*P. t. koputaroa*	24.45	49.14	4.81	54.67	6.85	0.45	0.74	14.15	11.91	8.75	1556.61	5	2	1	1	4	2	2	1	2	2	2	1	4	3	1	1
LZ1	*P. t. latizona*	24.52	46.54	4.07	41.6	7.27	0.51	0.77	15.35	9.08	7.69	1361	5	2	1	1	4	2	2	1	3	3	2	1	4	3	1	1
LZ2	*P. t. latizona*	26.37	46.73	3.08	32.88	8.63	0.51	0.75	13.82	8.5	8.28	1455.83	5	2	1	1	4	2	2	1	3	3	2	1	4	3	1	1
LZ3	*P. t. latizona*	27.45	49.49	2.86	27.2	8.24	0.5	0.77	15.86	11.16	9.68	1588.82	5	2	1	1	4	2	2	1	3	3	2	1	4	3	1	1
LZ4	*P. t. latizona*	23.54	43.76	3.33	35.01	6.41	0.53	0.78	16.02	8.71	7.53	1212.51	5	2	1	1	4	2	2	1	3	3	2	1	4	3	1	1
LZ5	*P. t. latizona*	28.43	49.25	5.45	57.27	10.21	0.46	0.74	11.68	9.26	8.11	1676.26	5	2	1	1	4	2	2	1	3	3	2	1	4	3	1	1
LZ6	*P. t. latizona*	23.76	47.53	3.5	33.78	6.58	0.5	0.77	15.83	11.84	7.68	1457.01	5	2	1	1	4	2	2	1	3	3	2	1	4	3	1	1
OT1	*P. t. otakia*	24.36	43.71	3.19	29.61	7.33	0.52	0.77	13.44	8.29	6.54	1208.86	5	2	1	1	4	2	2	1	3	2	4	1	4	3	1	1
OT2	*P. t. otakia*	28.37	42.7	3.6	35.66	11.41	0.51	0.75	10.9	8.67	6.12	1254.03	5	2	1	1	4	2	2	1	3	2	4	1	4	3	1	1
OT3	*P. t. otakia*	27.6	48.03	5.04	54.35	11.62	0.51	0.75	15.42	9.57	7.14	1458.85	5	2	1	1	4	2	2	1	3	2	4	1	4	3	1	1
OT4	*P. t. otakia*	24.72	42.83	3.69	36.02	6.33	0.5	0.78	13.76	10.48	7.03	1248	5	2	1	1	4	2	2	1	3	2	4	1	4	3	1	1
TA1	*P. t. tararuaensis*	22.41	46.87	3.52	32.57	7.3	0.51	0.76	16.67	9.86	6.96	1415.27	5	2	1	1	4	2	2	1	3	2	2	1	4	3	1	1

sample number	taxon	shell position	fourier coeff 2	fourier coeff.3	fourier coeff 4	fourier coeff 5	fourier coeff 6	fourier coeff 7	fourier coeff 8	fourier coeff 9	fourier co 10	fourier co 11
LA1	*P. s. lateumbilicata*	1	0.123	-0.060	-0.021	0.039	-0.013	-0.002	-0.035	0.035	-0.016	-0.001
LA2	*P. s. lateumbilicata*	1	0.137	-0.089	-0.076	0.038	-0.020	0.025	-0.032	-0.003	-0.038	-0.010
LA3	*P. s. lateumbilicata*	1	0.151	-0.068	-0.036	0.037	-0.038	-0.019	-0.002	0.025	-0.036	0.000
LA4	*P. s. lateumbilicata*	1	0.173	-0.072	-0.064	-0.009	-0.067	0.020	0.012	0.011	-0.063	0.004
LA5	*P. s. lateumbilicata*	1	0.172	-0.060	-0.043	0.016	-0.054	-0.010	-0.009	0.005	-0.042	-0.018
SP1	*P. s. spedeni*	1	0.184	-0.090	-0.073	-0.002	-0.021	0.043	-0.018	-0.008	-0.043	-0.018
SP2	*P. s. spedeni*	1	0.181	-0.088	-0.052	0.025	-0.031	-0.006	-0.011	0.006	-0.042	0.011
SP3	*P. s. spedeni*	1	0.178	-0.096	-0.085	0.014	-0.045	-0.011	-0.003	0.012	-0.070	-0.033
SP4	*P. s. spedeni*	1	0.182	-0.102	-0.038	0.055	-0.031	0.001	-0.033	0.002	-0.023	0.022
SP5	*P. s. spedeni*	1	0.165	-0.098	-0.052	0.047	-0.009	0.017	-0.021	0.019	-0.055	-0.012
SP6	*P. s. spedeni*	1	0.171	-0.091	-0.045	0.042	-0.009	0.008	-0.040	0.022	-0.031	-0.005
FD1	*P. t. florida*	1	0.196	-0.080	-0.076	-0.022	-0.049	-0.005	-0.054	-0.013	-0.027	-0.032
FD2	*P. t. florida*	1	0.206	-0.100	-0.076	-0.026	-0.020	-0.017	-0.047	0.019	-0.036	-0.032
FD3	*P. t. florida*	1	0.215	-0.093	-0.088	-0.032	-0.054	-0.014	-0.040	-0.009	-0.038	-0.025
FD4	*P. t. florida*	1	0.233	-0.057	-0.062	-0.055	-0.026	-0.014	-0.044	-0.027	-0.038	-0.021
FD5	*P. t. florida*	1	0.203	-0.099	-0.099	-0.021	-0.041	0.003	-0.044	-0.004	-0.018	-0.001
KO1	*P. t. koputaroa*	1	0.231	-0.061	-0.024	-0.007	-0.006	0.004	-0.033	-0.006	-0.035	-0.022
KO2	*P. t. koputaroa*	1	0.196	-0.087	-0.070	-0.018	-0.046	-0.015	-0.061	-0.016	-0.052	-0.014
KO3	*P. t. koputaroa*	1	0.226	-0.088	-0.042	0.009	-0.032	-0.017	-0.043	-0.008	-0.030	-0.017
KO4	*P. t. koputaroa*	1	0.217	-0.099	-0.050	0.013	-0.019	-0.012	-0.055	0.000	-0.041	0.024
KO5	*P. t. koputaroa*	1	0.225	-0.061	-0.055	-0.049	-0.023	0.004	-0.037	-0.023	-0.039	-0.034
LZ1	*P. t. latizona*	1	0.197	-0.054	-0.072	-0.053	-0.029	-0.009	-0.068	-0.030	-0.053	-0.027
LZ2	*P. t. latizona*	1	0.217	-0.079	-0.061	-0.016	-0.026	-0.017	-0.039	-0.018	-0.034	-0.008
LZ3	*P. t. latizona*	1	0.214	-0.067	-0.060	-0.032	-0.017	-0.020	-0.034	-0.016	-0.033	-0.029
LZ4	*P. t. latizona*	1	0.204	-0.062	-0.050	-0.009	-0.041	-0.020	-0.052	-0.005	-0.036	-0.015
LZ5	*P. t. latizona*	1	0.193	-0.104	-0.091	-0.052	-0.037	-0.013	-0.064	-0.005	-0.030	0.006
LZ6	*P. t. latizona*	1	0.213	-0.048	-0.049	-0.037	-0.020	-0.003	-0.037	-0.006	-0.065	-0.041
OT1	*P. t. otakia*	1	0.203	-0.082	-0.071	-0.007	-0.037	-0.003	-0.040	-0.006	-0.032	-0.031
OT2	*P. t. otakia*	1	0.180	-0.139	-0.101	-0.030	-0.018	0.018	-0.024	-0.001	-0.032	-0.010
OT3	*P. t. otakia*	1	0.175	-0.089	-0.095	-0.055	-0.051	-0.016	-0.036	0.045	-0.029	-0.033
OT4	*P. t. otakia*	1	0.196	-0.067	-0.047	-0.025	-0.046	0.014	-0.027	0.000	-0.034	-0.031
TA1	*P. t. tararuaensis*	1	0.220	-0.056	-0.036	-0.030	-0.007	0.005	-0.034	-0.003	-0.045	-0.014

sample number	taxon	total height	max diam	apex height	apex area	aperture drop	BW roundness	circularity	diam last whorl	diam 3.5 whorl	umbilicus diam	dorsal area	whorl no.	whorl type	mucous	fringe	foot colour	suture	umbilicus	axial stripes	dorsal stripes	ventral stripes	bicolor stripes	callus texture	callus colour	sculpture	appearance	egg type
TA2	*P. t. tararuaensis*	26.81	48.61	3.74	35.39	9.02	0.48	0.75	14.22	11.27	8.44	1574.73	5	2	1	1	4	2	2	1	3	2	2	1	4	3	1	1
TA3	*P. t. tararuaensis*	30.75	49.18	3.91	35.45	12.12	0.46	0.72	10.33	11.29	7.91	1796	5	2	1	1	4	2	2	1	3	2	2	1	4	3	1	1
TA4	*P. t. tararuaensis*	26.88	47.59	4.25	39.61	10.91	0.49	0.74	12.75	9.48	8.27	1565.27	5	2	1	1	4	2	2	1	3	2	2	1	4	3	1	1
TA5	*P. t. tararuaensis*	25.8	50.24	4.17	46.48	8.6	0.47	0.75	14.42	12.05	9.85	1627.71	5	2	1	1	4	2	2	1	3	2	2	1	4	3	1	1
TA6	*P. t. tararuaensis*	24.76	47.65	2.61	25.01	7.82	0.52	0.74	14.04	12.21	7.62	1535.06	5	2	1	1	4	2	2	1	3	2	2	1	4	3	1	1
TR1	*P. t. traversi*	26.44	44.82	4	37.35	12.79	0.49	0.78	12.62	8.57	7.75	1329.02	5	2	1	1	4	2	2	1	2	3	2	1	4	3	1	1
TR2	*P. t. traversi*	23.7	46.46	3.65	31.8	5.48	0.5	0.8	15.53	11.12	9.28	1372.84	5	2	1	1	4	2	2	1	2	3	2	1	4	3	1	1
TR3	*P. t. traversi*	31.14	54.15	5.48	55.54	14.53	0.47	0.72	16.97	10.22	8.45	1822.25	5	2	1	1	4	2	2	1	2	3	2	1	4	3	1	1
TR4	*P. t. traversi*	26.93	46.87	4.06	36.7	11.31	0.53	0.75	12.97	10.39	8.86	1430.57	5	2	1	1	4	2	2	1	2	3	2	1	4	3	1	1
VH1	"vittatus" (HR)	23.33	35.49	2.83	16.63	7.13	0.62	0.83	11.88	6.47	2.58	793.32	4.4	1	4	1	3	1	1	4	1	1	2	1	6	3	1	1
VH2	"vittatus" (HR)	26.42	39.26	3.17	22.84	7.54	0.56	0.81	13.55	7.24	2.68	914.7	4.4	1	4	1	3	1	1	4	1	1	2	1	6	3	1	1
VH3	"vittatus" (HR)	23.53	35.68	2.49	20.14	8.14	0.58	0.81	10.26	7.25	2.87	828.19	4.4	1	4	1	3	1	1	4	1	1	2	1	6	3	1	1
VH4	"vittatus" (HR)	23.34	39.03	2.83	22.31	6.75	0.57	0.78	13.76	8.41	1.73	946.36	4.4	1	4	1	3	1	1	4	1	1	2	1	6	3	1	1
VH5	"vittatus" (HR)	22.95	34.58	2.74	16.42	6.49	0.59	0.83	10.35	8.85	1.81	773.14	4.4	1	4	1	3	1	1	4	1	1	2	1	6	3	1	1

sample number		taxon	shell position	fourier coeff 2	fourier coeff.3	fourier coeff 4	fourier coeff 5	fourier coeff 6	fourier coeff 7	fourier coeff 8	fourier coeff 9	fourier co 10	fourier co 11
TA2	*P. t. tararuaensis*		1	0.211	-0.070	-0.073	-0.042	-0.029	-0.015	-0.056	-0.001	-0.025	-0.019
TA3	*P. t. tararuaensis*		1	0.224	-0.123	-0.087	-0.049	0.034	0.008	-0.028	-0.002	-0.047	-0.028
TA4	*P. t. tararuaensis*		1	0.219	-0.099	-0.067	-0.027	-0.018	0.001	-0.029	0.008	-0.040	-0.040
TA5	*P. t. tararuaensis*		1	0.230	-0.078	-0.049	-0.021	-0.013	-0.018	-0.048	-0.015	-0.027	-0.030
TA6	*P. t. tararuaensis*		1	0.225	-0.074	-0.064	-0.028	-0.002	-0.003	-0.021	-0.005	-0.059	-0.023
TR1	*P. t. traversi*		1	0.187	-0.067	-0.060	-0.034	-0.047	0.002	-0.077	-0.035	-0.009	-0.002
TR2	*P. t. traversi*		1	0.201	-0.038	-0.030	-0.007	-0.056	-0.023	-0.044	-0.005	-0.029	-0.034
TR3	*P. t. traversi*		1	0.220	-0.105	-0.057	0.000	-0.016	0.002	-0.074	0.014	-0.048	-0.001
TR4	*P. t. traversi*		1	0.211	-0.082	-0.062	-0.015	-0.019	-0.006	-0.045	-0.003	-0.051	0.011
VH1	"vittatus" (HR)		1	0.153	-0.094	-0.068	0.004	-0.011	0.010	-0.014	0.018	-0.035	-0.004
VH2	"vittatus" (HR)		1	0.156	-0.089	-0.052	0.011	-0.064	0.007	0.015	0.036	-0.054	-0.012
VH3	"vittatus" (HR)		1	0.168	-0.091	-0.070	-0.004	-0.044	-0.006	0.011	0.001	-0.058	-0.006
VH4	"vittatus" (HR)		1	0.189	-0.076	-0.063	-0.014	-0.037	0.007	0.009	0.022	-0.070	-0.031
VH5	"vittatus" (HR)		1	0.170	-0.076	-0.055	0.002	-0.002	0.002	-0.010	0.014	-0.040	-0.006

Chapter 4.

Subspecies in the large landsnail *Powelliphanta lignaria*: are they valid?

Image previous page: *Powelliphanta lignaria lusca*. Photographer Rod Morris.

Introduction

Amongst the most striking elements of the invertebrate fauna of New Zealand are the giant land snails in the genus *Powelliphanta* O'Connor, 1945 as their shells are not only large but colourful and patterned and vary in an intriguing fashion across the landscape. They were mostly described in the 1930s and 1940s, and as was customary at the time for such radiations, classified on morphological grounds as polytypic species. Their conspicuous intra-specific diversity was described as subspecies (Powell 1930, 1932, 1936, 1938, 1946, 1949).

Subspecies have since fallen out of fashion as a taxonomic unit (Wilson & Brown 1953, Mallet 2001). While subspecies were conceived to document geographical variation, principally through assessment of morphology, the category was applied unevenly as standardized diagnostic criteria were lacking (Patten & Unitt 2002). Along with a lack of consistency, many taxa described as subspecies failed to reflect distinct evolutionary units (Braby et al. 2012). In the 1980s an alternative category for the recognition of intra-specific diversity—evolutionary significant units (ESU's)—was devised in which evolutionary history (and potential) were to be the main guide for biodiversity conservation (Ryder 1986). While ESU's were initially identified on multiple strands of evidence, they were later defined simply as monophyletic groups (Moritz 1994). Improving genetic techniques also brought the rise of the phylogenetic species concept (PSC), in which subspecies have no place, as below the generic level in the PSC "a taxon is either a species or it is nothing" (Patten 2015). Reliance on genetic difference threshold values for identifying ESU's led to a rise in the number of intra-specific and specific units which were based only on reproductive isolation without differing in any other attributes (Braby 2012), and to inflation of the number of species recognized (Isaac et al. 2004, Mallet 2008). Such thresholds could imply a species as much as an ESU (Braby 2012). More recently there has been a return of interest in geographical variation and the use of subspecies (eg Sackett et al. 2014) amidst urgings to "consider both phenotype and genotype [in species/subspecies boundary determination], even in the face of an overwhelming push to consider only the latter" (Patten 2015).

The history of *Powelliphanta* taxonomy is an example of these changing "fashions". Powell initially described 10 species and 27 subspecies in the 1930s and 1940s. However, it was proposed that they be collapsed into 2 species with 4 subspecies on the assumption that all merged in a clinal fashion (Climo 1978). None-the-less Powell's classification continued to hold sway (Parkinson 1979, Meads et al. 1984, Walker 2003) until recently when a genetic study of *P. lignaria* cast doubts on the morphological characters used by Powell to classify *Powelliphanta* (Buckley et al. 2014). That study found that several subspecies of *P. lignaria* shared alleles, and on this basis recommended the subspecies be replaced by a smaller number of monophyletic ESU's (Buckley et al. 2014).

Many of the problems around recognition of subspecies have stemmed from the last half century of disagreement around species concepts and boundaries, as the criteria used to define subspecies hinge very much on the species concept used (Braby et al. 2012, Sackett et al. 2014, Schwartz & Boness 2017). The emergence of the genotypic cluster definition of species (Mallet 1995, 2008), and a unified species concept (de Queiroz 1998, 2007) in which species are diverging lineages based on one or many lines of evidence, has arguably reduced disagreement around species concepts and it has become possible to usefully re-visit subspecies. However, "if defining and delimiting species is complex, defining subspecies is tortuous" (Schwartz & Boness 2017).

Braby et al. (2012) suggested incorporation of defined criteria and an evolutionary perspective under the general lineage (unified) species concept in the following definition:

> *"subspecies comprise evolving populations that represent partially isolated lineages of a species that are allopatric, phenotypically distinct, have at least one fixed diagnosable character state, and that these character differences probably correlate with evolutionary independence*".

So how well do *Powelliphanta* subspecies conform to this definition? A recent population genetic study of *Powelliphanta lignaria* concluded "not all of Powell's subspecies meet all of these criteria" and further, that the morphological characters used by Powell to differentiate species did not reflect the underlying evolutionary patterns (Buckley et al. 2014). On the strength of this the authors suggested the subspecies of other *Powelliphanta* species described by Powell needed critical reassessment and nuclear gene analysis, and that the effects of substrate on shell phenotype should be examined to see if the differing shell morphologies reported by Powell were under environmental rather than genetic control.

Powelliphanta lignaria has long been used to investigate speciation processes; Powell himself said it was crucial in shaping his views on "the species problem" in New Zealand land snails (Powell 1947). Not only are *P. lignaria* shells large and striking but they differ greatly over comparatively short distances. Six of the seven subspecies are distributed in a semi-circle around the Mokihinui River catchment in north Westland, in New Zealand's South Island, with each subspecies most like its neighbour on the same side of the river (Figure 1). Those *P. lignaria* subspecies near the mouth of the Mokihinui River at either end of the semi-circle but on opposite banks, *lignaria* and *johnstoni,* are geographically close but very different from each other in shell pattern and ecological niche. Indeed, so different did they appear that they were originally described as two different species, with *unicolorata*, *johnstoni* and *rotella* on the south bank considered one species and the north bank *lignaria* and *lusca* another (Powell 1930, 1932, 1938). It took a further decade and discovery of a population of intermediate appearance in the headwaters of the Mokihinui River (*ruforadiata*) and the discovery of hybrid populations where they were washed against each other down the Mokihinui River before the current taxonomy emerged (Powell 1949). As the only species of *Powelliphanta* considered from here on in this chapter is *P. lignaria*, for readability all seven of its described subspecies are referred to henceforth only by their subspecific names; *lignaria*, *lusca*, *ruforadiata*, *oconnori*, *unicolorata*, *rotella* and *johnstoni*.

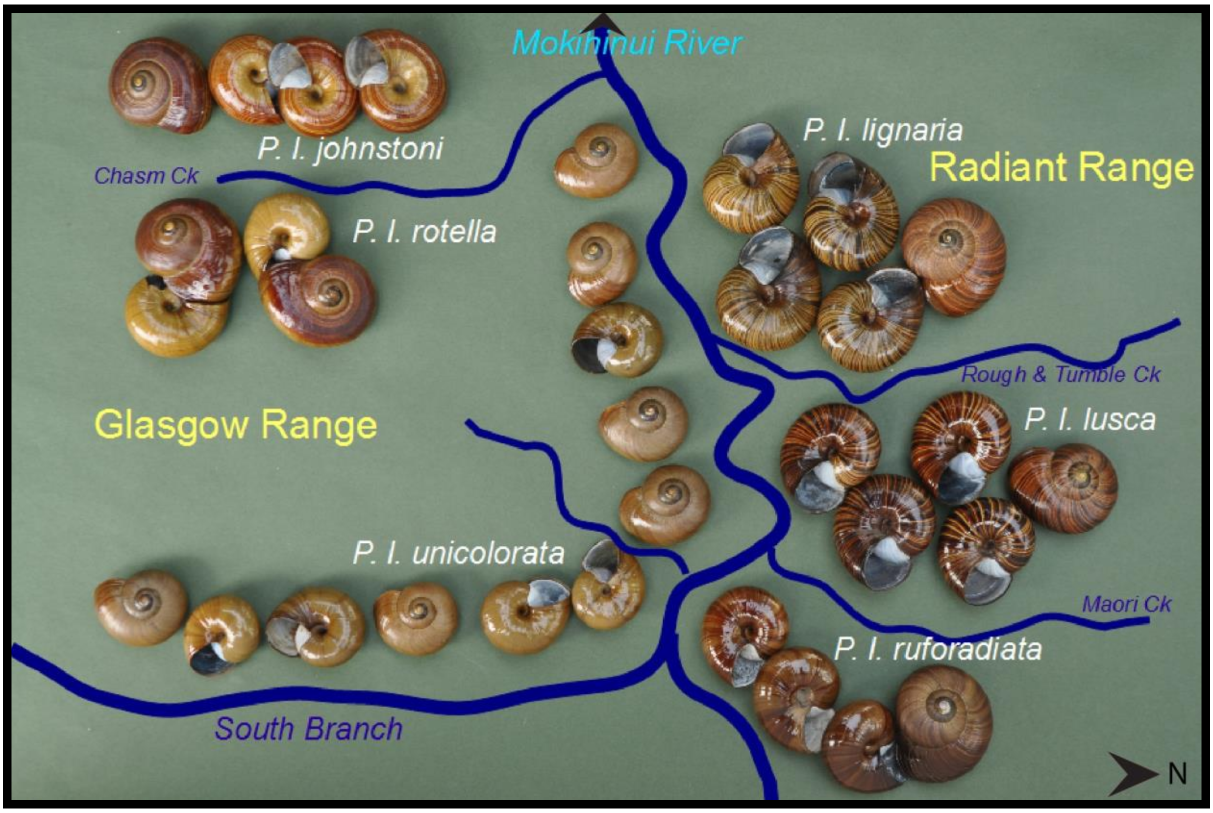


Figure 1. *Powelliphanta lignaria* subspecies distribution in relation to the Mokihinui River mouth (top centre)

The interaction of geography, climate and *Powelliphanta* biology most probably explains the formation of the putative hybrid colonies beside the Mokihinui River. The river drains extensive upper catchments in its north and south branches and the accumulated large volume of water is subsequently funnelled through a long, winding, antecedent gorge before exiting onto lowland plains at Seddonville (Figure 2) and spilling out to sea (Williams 2012). The area is tectonically active (Laird 1968) with frequent earthquakes, which in combination with the high rainfall, means flooding and landslips are common (Williams 2012). *Powelliphanta* snails drown if they fall into water, but not immediately, so although snails cannot normally cross the wide, swiftly-flowing Mokihinui River, they occasionally survive being washed down and across it (Powell 1947). The intense 1929 Buller earthquake caused major landslides (Henderson 1938), one of which blocked the Mokihinui River at the top of the gorge for 2 weeks. An extensive lake (Lake Perrine) formed behind the dam (Adams 1981a), flooding parts of the habitat of the *P. lignaria* subspecies *unicolorata* and *ruforadiata*. When the dam finally broke, the resulting torrent of water presumably carried these live snails with it down the gorge. The torrent was such it flooded the town of Seddonville and the entire lowland plain, even pouring through a nearby railway tunnel (Benn 1990).

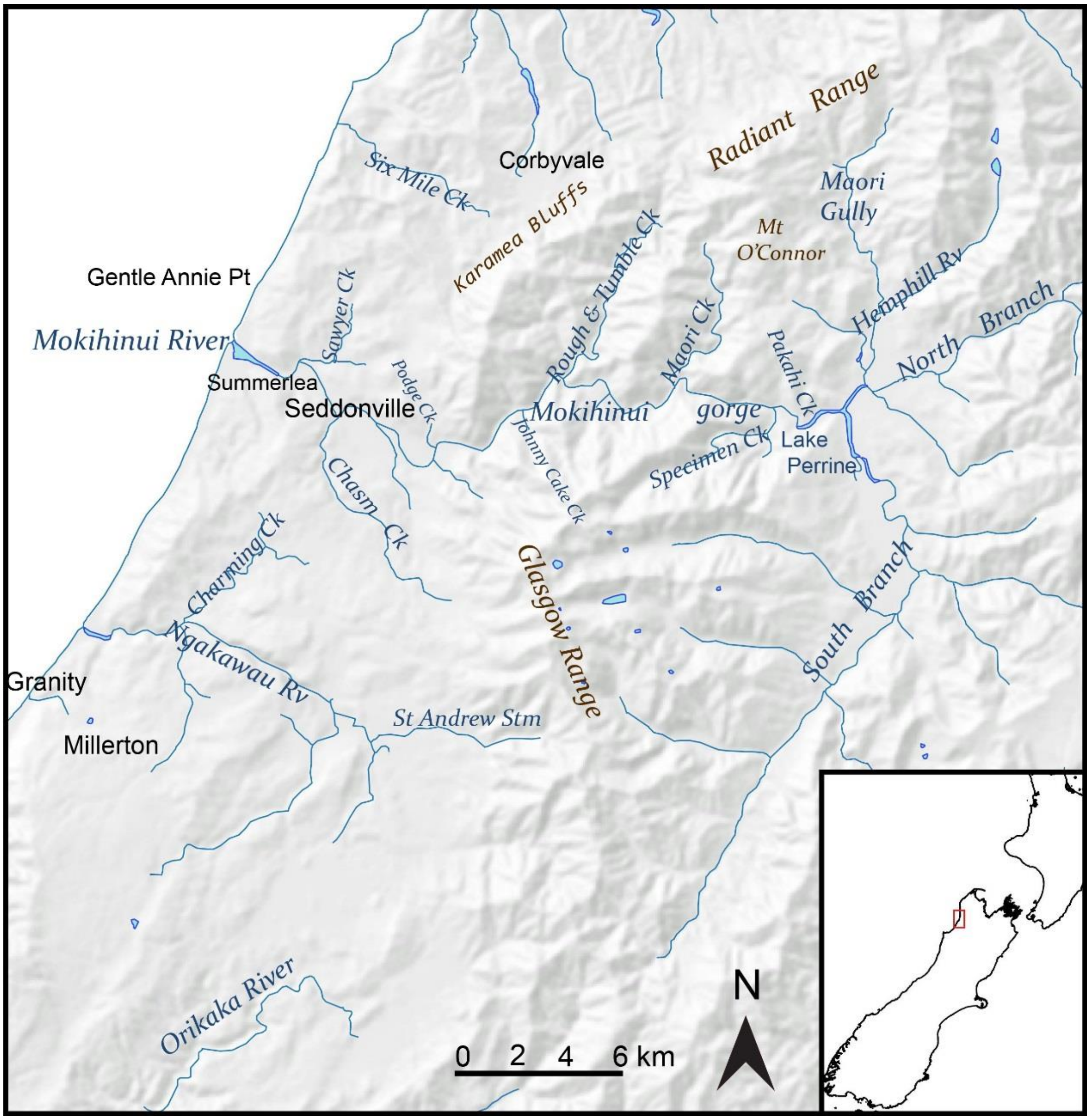


Figure 2: The location of the Mokihinui River which flows into the Tasman Sea, 50 km north of Westport in New Zealand's South Island.

Floods of similar scale will have occurred previously in geological-time (Adams 1981b); the biological significance of the 1929 flood is in the formation of hybrid snail colonies still conspicuous today. Hybrid colonies are most obvious where the river slows at bends and flood debris accumulate. These colonies predominantly involve *unicolorata* and/or *ruforadiata* influencing whichever *P. lignaria* subspecies occupied the land the flood-washed snails ended up against (Powell 1947). Near the river mouth on its south bank where there were no resident *Powelliphanta*, the flood-derived colony is a unique mix of upstream subspecies (Powell 1947). Powell viewed the latter colony as an exceptional chance event which could eventually lead to a new form, as no single subspecies dominated the mix, whereas he thought the immigrants at most of the other hybrid populations likely to be rapidly absorbed by the numerical strength of the resident populations.

Despite Powell's interest in hybridization within *P. lignaria,* no hybrids were reported from sites distant from the Mokihinui River, though the distribution and characteristics of snails on the north bank was poorly known until 2011 when it was mapped in some detail (Walker 2012). Limited genetic data for *P. lignaria* suggest Powell may have underestimated the amount of gene flow among populations (Buckley et al. 2014) and implies the river could be more accurately viewed as a conduit than the semi-permeable barrier Powell thought it was. Addressing the processes and outcomes involved in *P. lignaria* requires a detailed examination of intra-specific morphological diversity using repeatable well-defined morphological characters accompanied by representative genetic sampling. This would not only clarify the situation with this species but shed light on the reliability of morphology in subspecies recognition in the rest of the genus. To this end, this study adopts Braby et al.'s (2012) recommended criteria for sub-specific recognition and seeks clarity on four aspects:

1) Are subspecies of *P. lignaria* allopatric, and if not, what is the nature of the snail populations in areas of overlap? To address this, the distribution of shell morphotypes will be mapped in detail: if *P. lignaria* subspecies are allopatric, the null hypothesis is that shell character will be constant within a defined geographic area, and $\leq$ 2% of snails with differing phenotypes will be found $\leq$ 2 km from the boundary of each subspecies.

2) Are subspecies of *P. lignaria* phenotypically distinct; do at least 75% of the population possess those distinctive phenotypic character/s, and does each subspecies possess at least 1 fixed diagnosable character state? Numerical assessment of shell morphology will be undertaken to investigate this aspect.

3) Is there any evidence that phenotypic differences do not have a genetic basis? To see if the differing shell morphologies reported by Powell are under environmental rather than genetic control, the geology of the Mokihinui-Karamea area will be overlain with the distribution of each subspecies (as determined from shell examination): if shell phenotype is related to substrate as Buckley et al. (2014) suggested it might be, the null hypothesis is that the geology and substrate under each *P lignaria* subspecies is distinct from that under all other subspecies.

4) Are the patterns of diversity within *P. lignaria* congruent with the recent geological history of north Westland? If the morphological diversity within *P. lignaria* is not caused by selection acting on environmental variables such as substrate, the null hypothesis is that the inferred age of subspecific diversification from a molecular clock analysis will match the timing of major ecological, climatic and geomorphic changes in the area.

Methods

Distribution survey

Between 1980 and 2017 the range of *P. lignaria* was identified using exploratory walking transects. Sites initially visited included all locations mentioned in the original description of each subspecies, followed by searches of the surrounding areas until land without snails was encountered (Walker 1982, 2003, 2012; Meads et al. 1984). The transects involved mapping of snail distribution, collection of empty shells and recording of vegetation and substrate. This information was supplemented in 2006–2011 by data from additional transects surveyed by contractors (Buckingham 2006, 2007, 2011).

Morphological data

All shells seen on transects and plots were collected, along with a grid reference and a habitat description of the site they came from, and stored at the Department of Conservation, Nelson (DOCNn). Each of 10,761 shells collected was assigned to one of Powell's subspecies based on its similarity to type specimens using Powell's 1949 key and descriptions, which related largely to shell colour and pattern. This was straightforward as the shell of each subspecies is distinctive (see Figure 1) and shells were consistent in these distinctive characteristics across their range. However, large numbers of shells were an advantage to this process as colour and pattern were found to be expressed in numerous different ways whilst still holding true to the general form described by Powell. Being able to view numerous shells assigned to one subspecies against those assigned to another, allowed trivial differences and those due to snail age or shell condition to be taken into account.

Of the 10,761 *P. lignaria* shells collected, 1,022 were assigned to the subspecies *lignaria*, 667 to *lusca*, 2,151 to *oconnori*, 967 to *ruforadiata*, 2,698 to *unicolorata*, 1,112 to *rotella*, 1,928 to *johnstoni* and 216 had shell characters with aspects of two or more of Powell’s types and were deemed hybrids. The shells in these subspecies groupings were then re-examined and the distinguishing colour/pattern characters were translated into 5 “categorical” states that could be described numerically. All individuals in each described group therefore had the same score as other members of that subspecies for four categorical states. A 5th categorical character (mantle and mucous colour) was scored from examination of 58 live snails caught and used for DNA tissue collection. A 6th categorical character (whorl number) was described from a smaller subset of shells, selected as described below. The states defined for each of the 6 categorical characters are listed in Appendix 1.

Nine linear and area morphometric measures, along with the whorl number, were scored from a subsample of 6 shells from each of the 7 subspecies groupings described above (42 shells in total). These 42 shells representing each subspecies were selected for maturity and intactness, as some of the most informative shell characters develop fully only in old age (which is positively correlated to large size) and others cannot be measured unless the shell is intact. As a large majority of shells collected had sustained some damage from attack by predators and few snails survive to old age, the number of shells available for detailed morphometric study was much smaller than the total numbers available for the (more powerful) colour/pattern assessment of categorical characters described above but was still substantial. Selection of 6 examples from within the subset of large/ intact shells in each subspecies focussed on capturing the full range of diversity seen within that subspecies and on the broadest possible geographic spread of samples.

For linear and area measurement of the 42 shells, each individual shell was photographed in dorsal, ventral and profile view (i.e. 126 images) and computer-assisted measures were made using the public domain image analysis software ImageJ (Rasband 2008) as this form of measurement increases accuracy (Alonso et al. 2006). Size is more closely related to age and to environmental conditions than is shape, so size and shape were converted to ratios by dividing them by maximum shell diameter. The measures taken are listed in Table 1 and described in more detail in Chapter 3 (Figures 2 & 5).

Molecular data

Twenty-three tissue samples collected in the 1980's and 1990's from near the centre of each subspecies' described range comprised whole animals, killed by freezing. The soft parts of these snails were removed and held at minus 80°C while the shells were stored at dry ambient temperatures at DOCNn. An additional 35 tissue samples (total = 58) were collected from more distant parts of each subspecies range in 2004–2017 as biopsies from live snails (Trewick et al.

2008). Searches for snails for genetic sampling were done during daylight, and all empty shells found at the same site during these live snail searches were collected and stored at DOCNn, as described above. In addition, photographs were taken of some of the live snails from which biopsies were taken before the snails were released to the wild, to match shell morphology to genetic profile. Live snails from which DNA was collected were identified to subspecies by the similarity of their shells to type specimen descriptions. An additional 38 published *P. lignaria* mtDNA CO1 sequences (Buckley et al. 2014) were obtained from Genbank. Geographic location of all sites from which DNA was collected is given in Appendix 2 & 3 and illustrated in Figure 3.

Allozymes

Allozyme genotypes at 6 polymorphic enzyme loci (*ACP-1*, *ALP-1*, *Est*-1, *GOT-2*, *IDH-2* and *MDH-3*) from 14 snails from all 7 *P. lignaria* subspecies were identified by starch gel electrophoresis (see Chapter 2). The genotypes from an additional 9 *P. lignaria* individuals, and for all individuals at a 7th locus (*Est-2*) not used in the study described in Chapter 2 were also identified. The APE package (Paradis et al. 2004) in R (R core team 2015) was used to calculate Cavalli-Sforza & Edwards (1967) arc genetic distance and to visualize relationships using neighbour-joining. The phenogram was rooted using data from *Powelliphanta superba*, which had previously been found using allozymes to be sister to *P. lignaria* (Walker 2003; Chapter 2). The number of fixed differences between each pair of subspecies was determined by direct count.

Mitochondrial DNA

Mitochondrial DNA cytochrome *c* oxidase subunit I (CO1) sequences from 57 *P. lignaria* (Chapter 2), plus 37 additional published *P. lignaria* sequences (Buckley et al. 2014), were aligned and analysed. Methods of DNA extraction, PCR sequencing and alignment were as described in Chapter 2. The most appropriate model of sequence evolution was determined using the AIC selection criterion of jMODELTEST v.2.1.1 (Darriba et al 2012) and corrected pairwise genetic distance among subspecies was calculated with the HKY+I model using PHANGORN (Schliep 2011) in R. Sequences of equal length (650 bp) were used in this calculation as both variation in sequence length and use of sequences much shorter than this are known to affect the reliability of genetic distance estimation (Roe & Sperling 2007, Fregin et al. 2012). Statistical analyses of sequences were performed in DnaSP v. 6. (Rozas et al. 2017) with genetic diversity within each subspecies measured by nucleotide diversity (π) and haplotype diversity (*h*). For visualization of evolutionary relationships, a haplotype network of phylogeographic structure was produced in PopArt (Leigh & Bryant 2015).

Microsatellite data

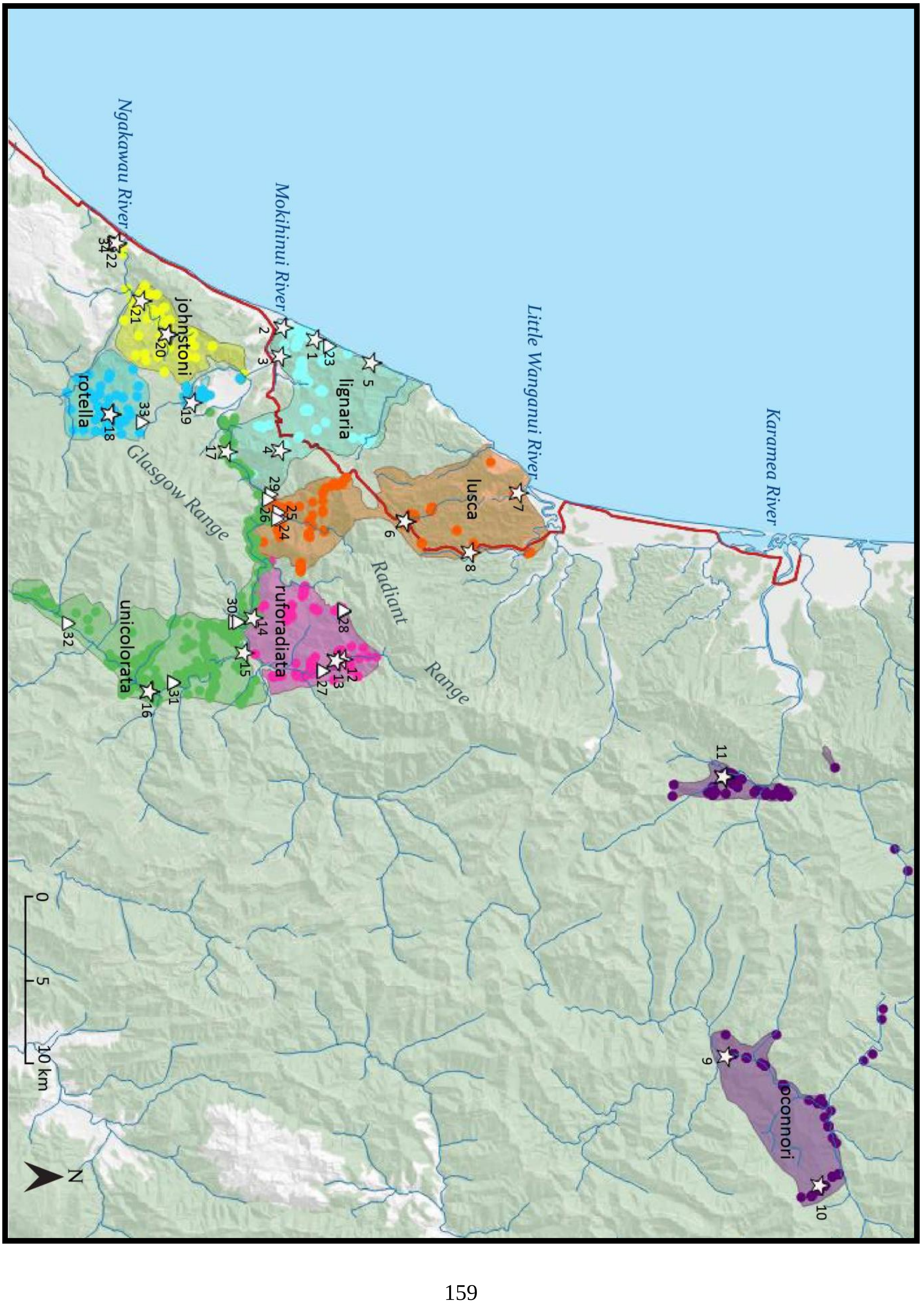
Sites that had provided samples for microsatellite data (Buckley et al. 2014) were revisited and searched for snails and empty shells. All shells found were collected and assigned to a *P. lignaria* subspecies according to their similarity to the type specimens and Powell's 1949 descriptions.

Results

Distribution

The range of each subspecies was mapped using all available information (Figure 3). Those places where the limits of a subspecies range were known precisely can be identified by a lack of shell records immediately adjacent to the subspecies boundary, whereas shell records were common on the occupied side of the boundary (Figure 3). In other places the boundary was inferred by assuming habitat types which had been found to contain snails in sampled areas would also support snails in un-sampled areas, unless there was clear evidence they were absent. In this case the edge of the range is shown as a smoothed polygon, drawn along landscape features thought likely to limit gene flow.

Figure 3 (next page). Location of *P. lignaria* subspecies. Solid coloured dots indicate sites where shells were collected for morphological assessment and smoothed polygons show the extent of each subspecies known range. White stars and reference numbers indicate where allozyme and mtDNA samples were collected in this study (see Appendix 2 for details). White triangles and reference numbers indicate where DNA samples collected by Buckley et al. (2014) and referred to in this study were collected (see Appendix 3 for details).


Ngakawau River
Mokihinui River
Little Wanganui River
Karamea River
johnstoni
rotella
lignaria
lusca
ruforadiata
unicolorata
oconnori
Glasgow Range
Radiant Range
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
0
5
10 km
N

The distribution of *P. lignaria oconnori* was found to comprise disjunct ranges of more than one contiguous area. *P. lignaria rotella* and *P. l. johnstoni* were allopatric in respect of other subspecies but parapatric to each other. The remaining *lignaria* subspecies shared one or more parapatric boundaries with at least one other neighbouring subspecies (Figure 3).

The distributions of *P. l. johnstoni* and *P. l. rotella* met on a <1 km long stretch of habitat in the headwaters of Chasm Creek but elsewhere there was a snail-free gap between them of at least 100 m. Judging from the character of the vegetation within these distributions, *P. l. johnstoni* and *P. l. rotella* occur on poorly drained, infertile and acidic coal measures supporting low yellow-silver pine (*Lepidothamnus intermedius*), manuka (*Leptospermum scoparium*) and mountain beech (*Nothofagus solandri cliffortiodes*) forest (Figure 4).

Some prehistoric mixing probably occurred following secondary (probably flood-derived) contact between *P. lignaria* subspecies *johnstoni* and *unicolorata* at the mouth of Chasm Creek and between *rotella* and *unicolorata* on the eastern Seddonville flats where their ranges formerly met (Powell 1949). However, the extent of overlap was unclear, as the area was drained and logged last century, making it difficult to determine how much of the area was originally able to support snails.

Powelliphanta lignaria lignaria was found to share a north-south border with *lusca*, and *lusca* a west-east border with *ruforadiata*. Snails were rare or absent on drier ridges and mid-slopes between the valleys north of the Mokihinui River, presumably because such ridges usually did not support their preferred habitat of moist, fertile northern rata (*Metrosideros robusta*) dominated forest (Figure 5). In the Karamea Bluffs area Powell (1949) found that subspecies *lignaria* on the 6 Mile flats was separated from *lusca* on the Corbyvale flats by about 1600 m of unoccupied transverse ridge. The present study identified similar uninhabited zones on the true left of Maori Creek separating *lusca* and *ruforadiata*. However, all three subspecies were found to have some parapatric boundaries near the stream mouths where the ridges terminated and those habitat differences disappeared.

Powelliphanta lignaria unicolorata was found to occur beside the Mokihinui River from the South Branch down the length of the Mokihinui gorge. On the south bank through the gorge *unicolorata* had spread upslope, but had only a toehold on the north bank, where it came into contact with the subspecies *ruforadiata*, and down-river, with *lusca* and *lignaria* (Figure 6).

Powelliphanta lignaria unicolorata was probably in closest contact with *ruforadiata* above the gorge as there, water barriers were reduced.

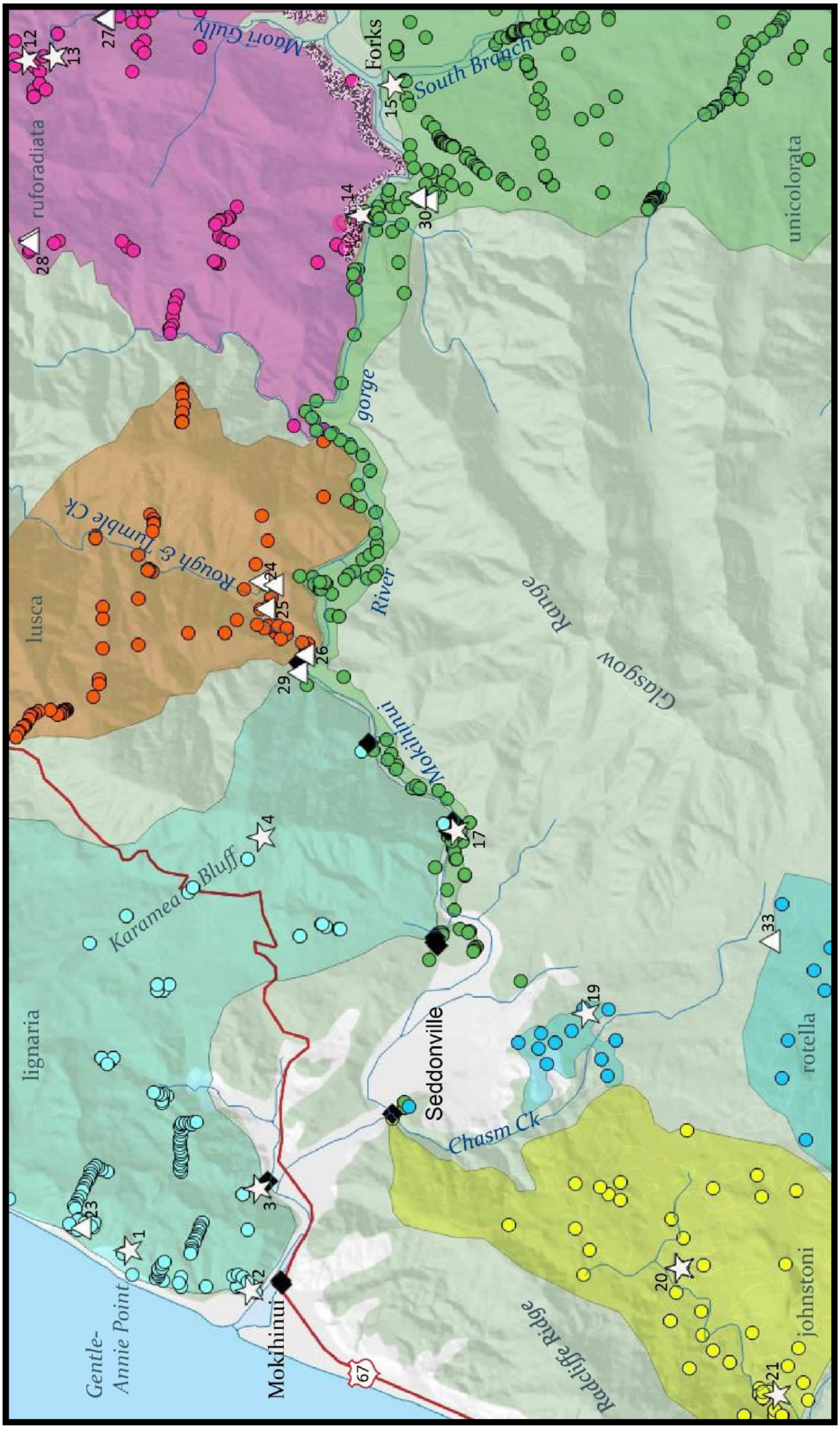
There was a narrow and apparently stable *unicolorata* x *ruforadiata* overlap zone about 1.5 km wide and 6 km long on the north bank just above the gorge entry and on the flood plain above it. At the west end of this zone at Pakahi Creek, all snails looked like a form of *P. l. unicolorata,* with shells of small to medium size with no obvious axial striping, but uniquely, a very fine reddish-orange hue to the entire shell in place of the normal *unicolorata* khaki colour. At Pakihi Creek no snails had typical *P. l. ruforadiata* or *P. l. unicolorata* shell character, nor did snail shells show mixtures of those characters; rather it appeared a new steady state form had emerged, with likely origins from reddish-brown streaked *ruforadiata* stock and small plain *unicolorata* stock. East of Pakihi Creek, 0.5 km above Mokihinui Forks and in the centre of the mixing zone, the population was a variable mix of *unicolorata* and *ruforadiata* shell character, with the latter more dominant. Further east and upstream again, on the Hemphill River-North Branch Mokihinui River flats, *P. lignaria* snails were readily identifiable as *ruforadiata* but some introgression of *unicolorata* stock was also indicated, as at Pakihi Creek, by a more even reddish colour and a reduction in the number and strength of axial stripes (Figure 7).

On the north bank in the lower part of the gorge just below the mouth of Rough and Tumble Creek, there were *P. lignaria* snails with mixtures of *unicolorata* and *lusca* shell character, and at the mouth of the gorge itself and just below it at Podge Creek, mixtures of *unicolorata* and *lignaria* (Figure 7). At sharp bends where the river slows near the mouth of the Mokihinui River at Chasm Creek, Sawyers Creek, Summerlea and Waimarie, the small colonies of conspicuously mixed ancestry described by Powell (1949) (Figure 6) had been reduced though roading expansion, river erosion, vegetation clearance and predation to tiny populations.

Figure 4. Looking west across Charming Creek to Radcliffe Ridge, with stunted shrubland and rimu forest on infertile acidic Brunner Coal Measures and Kaiata mudstones in the foreground (top photo), the main habitat of *P. lignaria johnstoni* (bottom left). *Powelliphanta lignaria rotella* (bottom right) occupies a similar environment in a separate area east of Charming Creek on the flanks of the Glasgow Range (not illustrated).

Figure 5. *Powelliphanta lignaria lignaria* with its favoured northern rata forest habitat on fertile soils on the true left of the lower Mokihinui River gorge.

Figure 6 (next page). Distribution of *P. lignaria* subspecies near the Mokihinui River gorge where their ranges abut. The sites where shells were collected for morphological examination are shown as solid colour-coded circles, with shells of mixed morphological character shown as solid black diamonds. The number of coloured circles does not directly equate to the number of shells collected: in the absence of accurate GPS, shells within ~100 m were aggregated into collections with a single grid reference, but later each shell was given an individual GPS location, conspicuous here as multiple circles in close proximity. Stippling shows the stable hybrid zone between *ruforadiata* and *unicolorata*. The sites where tissue samples were collected for allozyme and mtDNA analysis by this study are identified as white stars with a reference number (Appendix 2) while those collected by Buckley et al. (2014) for microsatellite and mtDNA study are shown by white triangles and a reference number (Appendix 3).


ruforadiata
lusca
lignaria
unicolorata
rotella
johnstoni
Maori Gully
Forks
South Branch
gorge
River
Rough & Tumble Ck
Mokihinui
Glasgow Range
Karamea Bluff
Seddonville
Chasm Ck
Radcliffe Ridge
Gentle-Annie Point
Mokihinui
67
1
2
3
4
12
13
14
15
17
19
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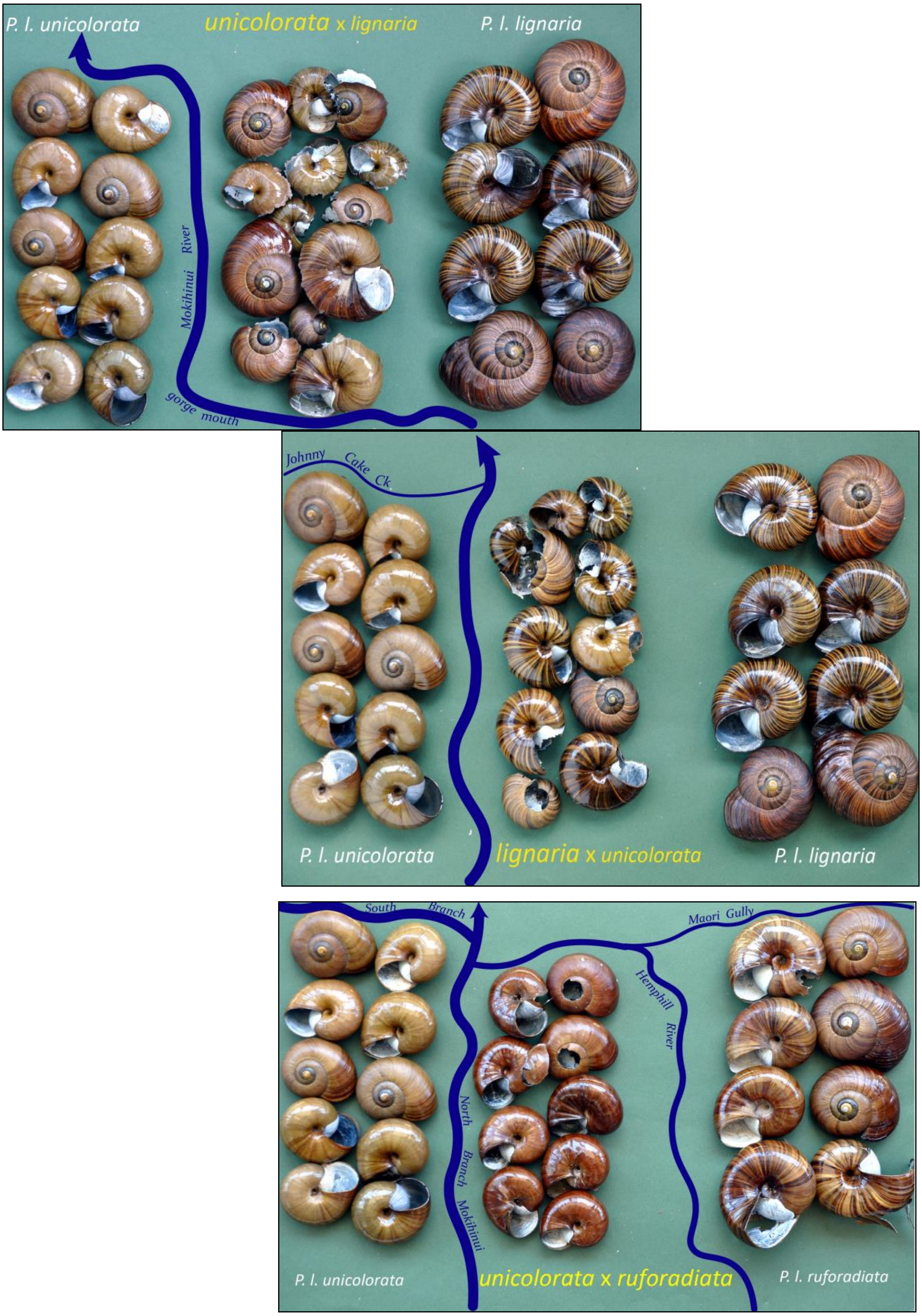


Figure 7. Shells in the narrow zones of subspecies mixing (yellow font) on the north bank of the Mokihinui River at (**top**) the mouth of the gorge (**centre**) in the lower gorge opposite Johnny Cake Creek mouth, and (**bottom**) between Hemphill River and the Mokihinui North Branch. Note the *unicolorata* and *lignaria* shells shown are representative of the morphologies seen in those areas, rather than specifically from those areas.

The distribution survey found that shell morphology was consistent within defined geographical areas with snails of mixed appearance only occurring at or immediately adjacent to (ie within ~0.5–1 km of) the boundary between *P. l. unicolorata* and other subspecies. As a result, the null hypothesis of the first question could be accepted and the distributions of *P. lignaria* subspecies considered allopatric.

Morphology

Principal components analysis (PCA) of the 15 morphological shell and soft body characters separated the snails within *P. lignaria* into non-overlapping groups which corresponded to the described subspecies (Figure 8). Size alone was sufficient to separate some pairs of subspecies but there was considerable overlap between others (Figure 9). When linear and area measures were analysed on their own (not shown) there was considerable overlap between subspecies. Coefficient of variance found the size-adjusted apex height, apex area and aperture drop the most influential of the metrics, and shell pattern had the most discriminating power of the categorical shell characters (Table 1). Fixed differences in some categorical characters caused tight clustering in the groups.

The subspecies were readily distinguishable from each other using non-overlapping and readily-observable shell characters (Figure 8, and also see Figures 1, 4, 5, 11 & 12 for comparisons of shell profiles and dorsal and ventral surfaces). The shells of all *P. lignaria* north of the Mokihinui River had axial bands while shells of south bank *johnstoni*, *rotella* and *unicolorata* had none (Figure 1). There were strong red spiral bands of variable width on the dorsal shell surface of *johnstoni* and *rotella* but in *johnstoni* the red bands continued over the entire shell while in *rotella* there was a sharp demarcation just above the periphery into a red upper shell and a yellow base (Figure 4). Unlike all other *P. lignaria*, *unicolorata* appeared unbanded with a plain coloured shell and only faint traces of narrow red spiral bands on the upper surface of some shells. *Powelliphanta lignaria lignaria* (Figure 5) was distinguishable from its neighbour *P. l. lusca* by its generally larger size (Figure 9 and Table 1), less sunken suture and the colour of its shell: *lignaria* had many narrow dark axial bands over a yellow base while *lusca* had fewer yellow axial bands over a dark red base. *P. l. ruforadiata* was distinguishable from all other axially-banded *P. lignaria* in possessing only broad, irregular and very sparse brown axial bands, while *oconnori*, alone of all *P. lignaria*, had a shell with narrow red spiral stripes underlying a few occasional narrow red axial bands.

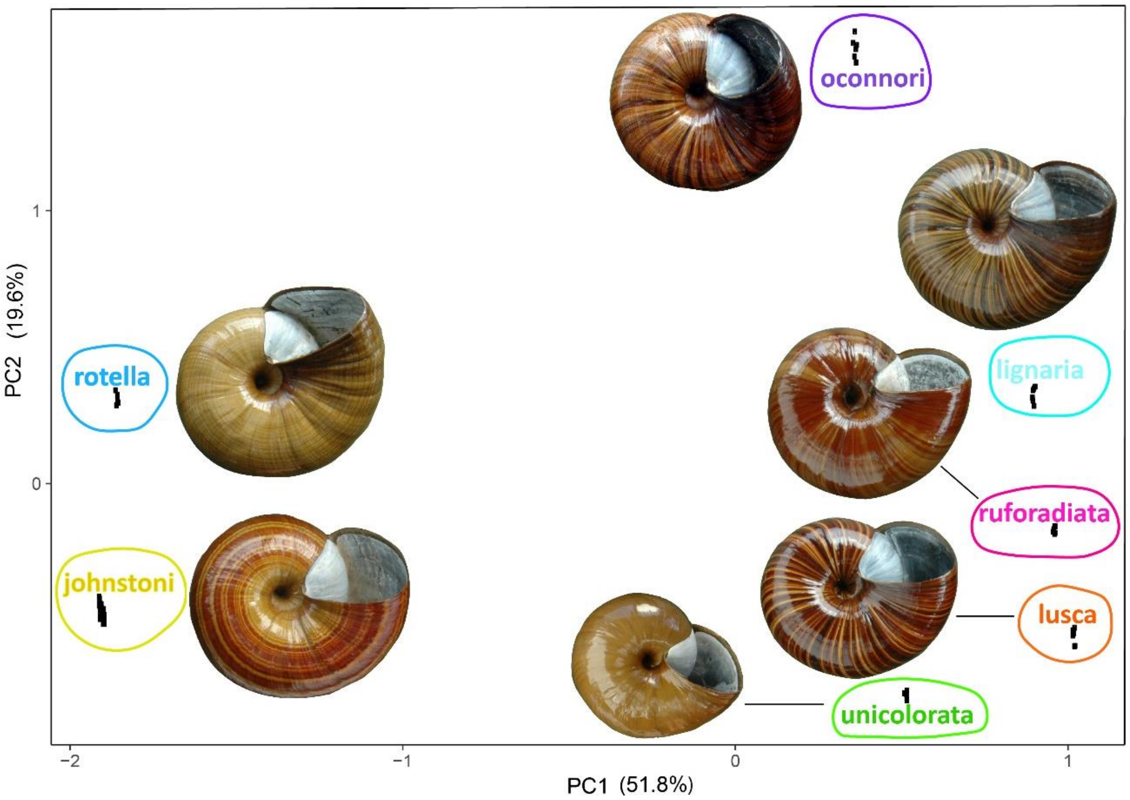


Figure 8. Projection of the morphological variables on the principal plane of the size-constrained PCA on the *P. lignaria* shell data set. The first two axes explain 71% of the variation. Representative shells are shown in ventral view.

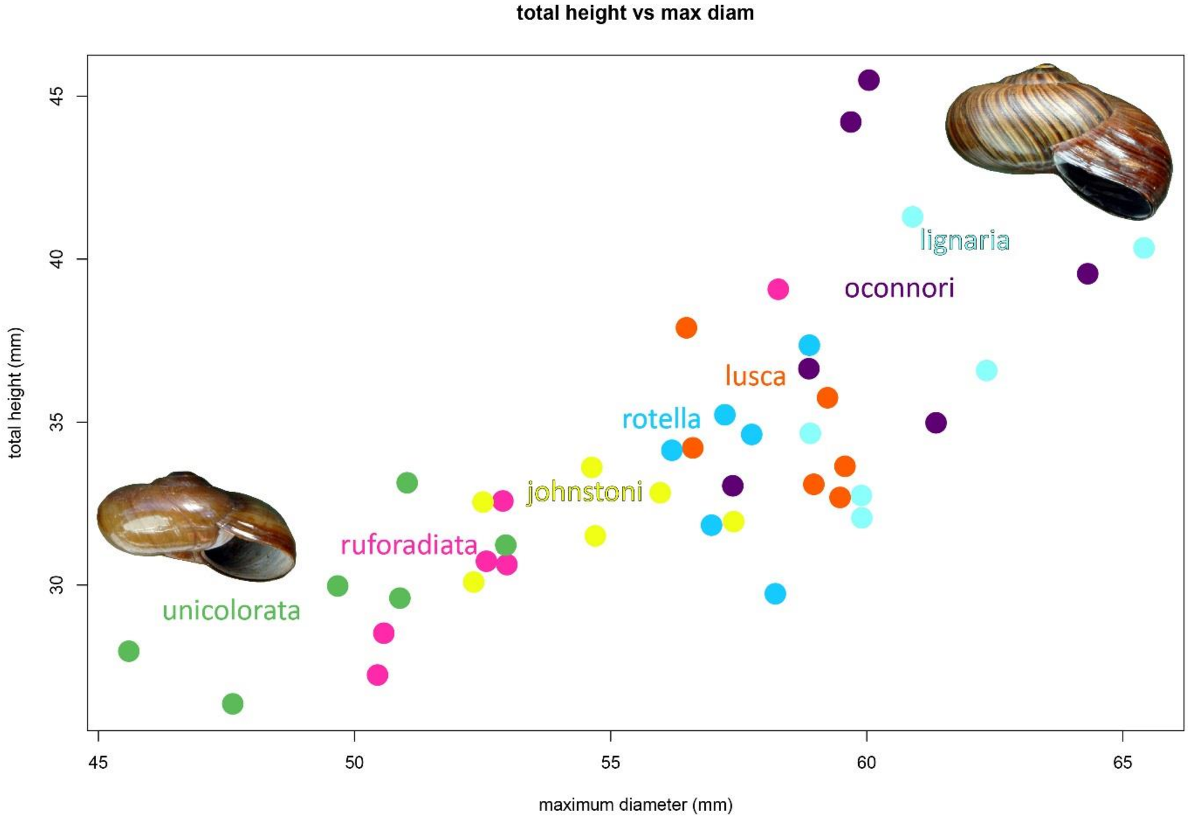


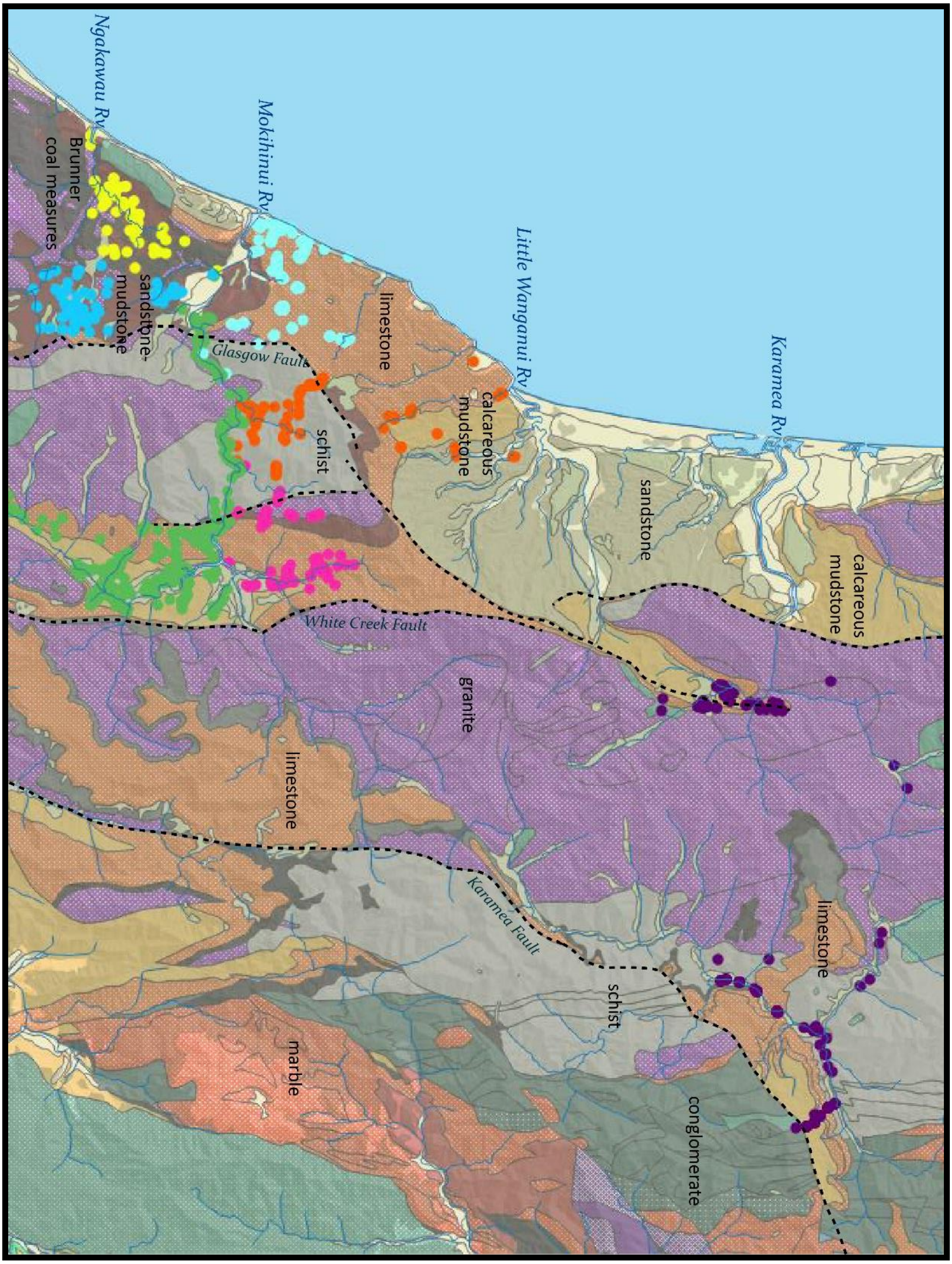
Figure 9: Scatter plot of the relative size of the 6 representatives of each *Powelliphanta lignaria* subspecies in old age, whose shells were used for detailed morphometric analyses.

Relationship between shell morphology and substrate

It had been suggested (Buckley et al. 2014) that the phenotypic differences between subspecies might derive from non-heritable environmental factors, particularly substrate, but no evidence in support of this was found. When the distribution of each subspecies of *P. lignaria* was laid over a geological map (Figure 10) their distributional boundaries were not coincident with substrate boundaries, though the species was found to be confined to areas with fine-grained rocks which break down to moisture-retentive soils. The subspecies *lignaria, lusca*, *ruforadiata*, *unicolorata* and *oconnori* were all found to occur predominantly on Nile Group limestones and Lower Blue Bottom Group calcareous mudstones and muddy sandstones, but the shell of each subspecies was morphologically distinct from each of the other subspecies, despite sharing the same substrate. Further, shell morphology was consistent across the range of each subspecies, even though the substrate varied, including in the most extreme case of *lusca* from calcareous rocks to schist. Likewise, Brunner sandstone coal measures and younger Kaiata mudstones were found to underlie all the habitat of the subspecies *johnstoni* and *rotella* and no change of substrate marked the sharp change in shell morphology where *rotella* gave way to *johnstoni*, nor was there any change in shell morphology in either subspecies where coal measures gave way to mudstones.

The null hypothesis that the geology and substrate supporting each *P. lignaria* subspecies is distinctive and that substrate differences are the cause of differing shell morphologies is thus rejected.

Figure 10 (next page). Geology of the Mokihinui area (simplified from Rattenbury et al. 1998), overlain by the distribution of *Powelliphanta lignaria* subspecies, indicated by solid circles (colour-coded as in Figure 2) indicating where shells of each subspecies were collected. Black dashed lines indicate major fault lines, though many additional changes between different geological units are also fault-bounded.


Ngakawau Rv
Brunner coal measures
Mokihinui Rv
sandstone-mudstone
Glasgow Fault
limestone
Little Wanganui Rv
calcareous mudstone
schist
Karamea Rv
sandstone
calcareous mudstone
White Creek Fault
granite
limestone
Karamea Fault
limestone
schist
marble
conglomerate

Molecular Data

Allozymes

The phenogram of *P. lignaria* allozyme genotypes indicated 2 major sub-species groups, with *lignaria* and *lusca* on the north bank of the Mokihinui River in one and *rotella*, *johnstoni* and *unicolorata* from the south bank in the other. Specimens of each subspecies formed monophyletic clusters. The single specimens of *oconnori*, *ruforadiata* and *lignaria* from the Sawyers Creek hybrid colony formed a second cluster in the south bank group (Figure 11). There was a fixed allelic difference between these two groupings at *Est-2*, a near-fixed difference at *Mdh-3* and a pronounced allelic frequency difference at *Idh-2*. Within the north and south bank clusters there were 1–2 fixed allelic differences, near-fixed differences and allele frequency difference between subspecies samples (Tables 1 & 2). In Chapter 2 the observed heterozygosity for 16 loci within *P. lignaria* was found to be lower than expected (H_o = 0.04; H_e = 0.1) if the population was a single undifferentiated population. One potential explanation for this is that gene flow is not uniform across the range of *P. lignaria* and is instead partitioned into several populations.

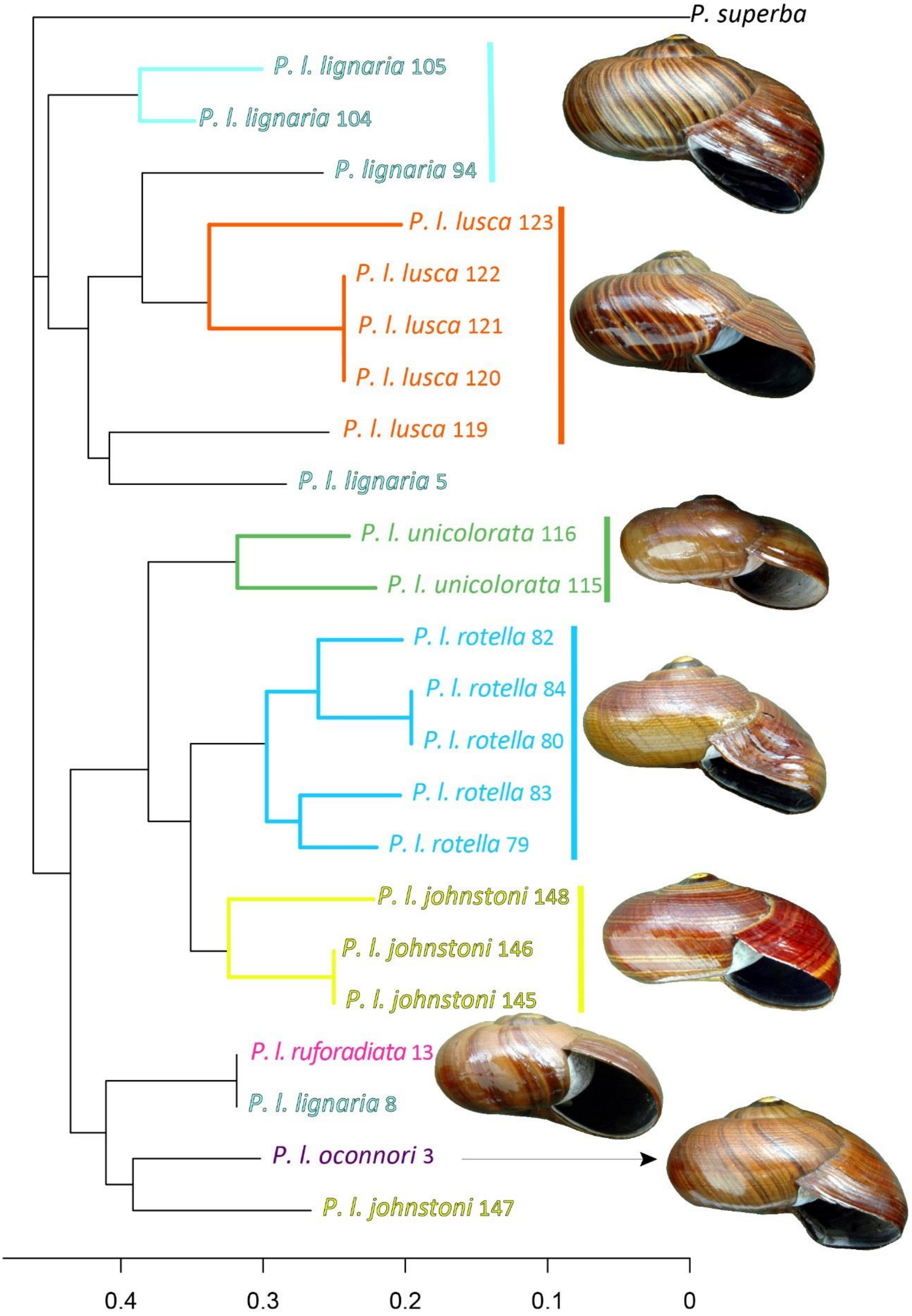


Figure 11. Neighbour-joining phenogram using Edward and Cavelli-Sforza's (1967) genetic distances from 8 allozyme loci in 23 individuals representing 7 *P. lignaria* subspecies. Numbers with names are sample codes relating to voucher specimens.

Table 1. Characteristics of *Powelliphanta lignaria* subspecies. None of the shells used in this morphometric assessment are from the narrow zones of mixing where shells of hybrid appearance occur, but some of the mtDNA samples came from those sites (see Figure 6). * identifies characters used in Powell's original descriptions. Abbreviated shell dimension categories are apex height (AH), maximum diameter (MD), apex area (AA, in mm^2), aperture drop (AD), umbilicus diameter (UD), ventral area (VA, in mm^2), body-whorl roundness (BWR). Abbreviated mtDNA haplotype genetic diversity statistics are *n*=number of individuals, *k*=average number of differences, H= number of haplotypes, *h*=haplotype diversity, π=nucleotide diversity.

Character	***lignaria***	***lusca***	***oconnori***	***ruforadiata***	***unicolorata***	***rotella***	***johnstoni***
Dimensions mm (CV)	*n*=6	*n*=6	*n*=6	*n*=6	*n*=6	*n*=6	*n*=6
Total height* (9.26)	36.28	34.51	38.97	31.45	29.68	33.77	32.08
Max Diameter * (7.40)	61.17	58.37	60.28	52.92	49.62	57.55	54.62
AH/MD x 100 (11.81)	6.94	8.36	8.49	6.44	7.56	6.46	8.15
AA/MD x 10 (20.99)	8.87	9.66	11.04	6.38	6.96	6.85	9.76
AD/MD x 10 (14.28)	2.05	2.16	2.40	1.72	1.88	2.11	1.56
UD/VA x 1000 (7.43)	3.67	3.98	3.96	4.58	4.35	4.16	4.39
Circularity x 10 (1.68)	7.60	7.45	7.53	7.60	7.60	7.28	7.65
BWR x 10 (3.06)	5.05	4.97	5.00	5.23	4.85	4.80	4.83
4th whorl Diam (7.49)	18.17	17.48	16.08	17.16	15.77	17.92	14.76
Categorical measures							
Whorl number	5.25	5.25	5	5	5	5	5.25
Mucous colour	1	1	1	1	1	2	2
Axial stripes*	4	4	3	3	1	1	1
Dorsal spiral stripes*	2	1	2	1	1	3	3
Ventral spiral stripes*	1	1	2	1	1	2	3
Bicoloured striped*	1	1	1	1	1	4	3
Allozymes	*n*=5	*n*=5	*n*=1	*n*=1	*n*=2	*n*=5	*n*=4
Est-1	F	F	F	F	F 0.75 H 0.25	F	F
Est-2	C 0.1 J 0.9	I	B 0.5 J 0.5	J	C 0.75 E 0.25	B 0.6 I 0.4	B
Got-2	C	C	C	C	C	C	A 0.25 C 0.75
Mdh-3	A 0.6 C 0.4	A	C	C	C	C	C
Idh-2	A 0.8 B 0.2	A	A	A	B	A 0.2 B 0.8	A 0.25 B 0.75
Acp-1	A 0.6 C 0.4	A 0.8 C 0.2	A	A	A	A	A
Acp-2	B	B	B	B	B	E	B 0.88 E 0.13
Alp-1	C 0.2 G 0.8	C 0.2 G 0.8	B 0.5 G 0.5	G	G	G	G
mtDNA haplotypes	*n*=14 *k*=2.53 H=5 *h*=0.78 π=0.0045	n=13 *k*=4.95 H=11 *h*=0.88 π=0.0087	*n*=3 *k*=0.53 H=2 *h*=0.53 π=0.0009	*n*=13 *k*=4.51 H=9 *h*=0.87 π=0.0079	*n*=18 *k*=2.40 H=10 *h*=0.81 π=0.0042	*n*=16 *k*=1.08 H=4 *h*=0.65 π=0.0019	*n*=18 *k*=1.50 H=5 *h*=0.71 π=0.0026

Mitochondrial DNA

Mitochondrial DNA COI haplotypes were obtained from 96 individual snails (59 collected in this study and 37 from Genbank) from 34 separate locations (Appendices 2 & 3). There were 34 haplotypes in *P. lignaria*. One haplotype was found only in the hybrid zone at Pakihi Creek mouth at the top of the gorge, and in the Genbank sample of uncertain identity from the mixing zone at Rough and Tumble Creek mouth in the lower gorge . When the latter is excluded from consideration, of the snails north of the Mokihinui River, three *P. lignaria* subspecies (*lignaria*, *lusca* and *oconnori*) each had a unique suite of haplotypes, while a fourth, *ruforadiata*, shared just one haplotype with *unicolorata.* In contrast, the *P. lignaria* subspecies south of the Mokihinui River, *rotella* and *johnstoni,* shared 3 haplotypes, with 2 additional unique haplotypes in *johnstoni*. *Powelliphanta lignaria unicolorata*, whose range straddles both sides of the Mokihinui River, encountering almost all the other *P. lignaria* subspecies, shared one haplotype with *ruforadiata* and another with *rotella* and *johnstoni*, and had in addition 6 unique haplotypes (Figure 12). For most subspecies there was little overlap in haplotypes between sample locations, and considerable diversity even at single sites.

Excluding *oconnori*, whose sample size was too small for meaningful results, mitochondrial gene diversity within *P. lignaria* subspecies as measured by the number of haplotypes each possessed, the average number of nucleotide differences between haplotypes, and haplotype diversity and nucleotide diversity, was moderate (*unicolorata* and *lignaria*) to high (*lusca* and *ruforadiata* (Table 1). However, *rotella* and *johnstoni*, with by far the smallest and most disturbed ranges of any of the subspecies (> 80% of habitat lost or substantially modified last century), were comparatively depauperate genetically.

Genetic distances between subspecies of *P. lignaria* and the extent of allozyme loci sharing are shown in Table 2. The highest corrected mean pairwise distances were those between *lignaria* and *lusca* and between *lignaria* and *ruforadiata* at 2.1% and the smallest distances those between *rotella* and *johnstoni* at 0.4% (Table 2).

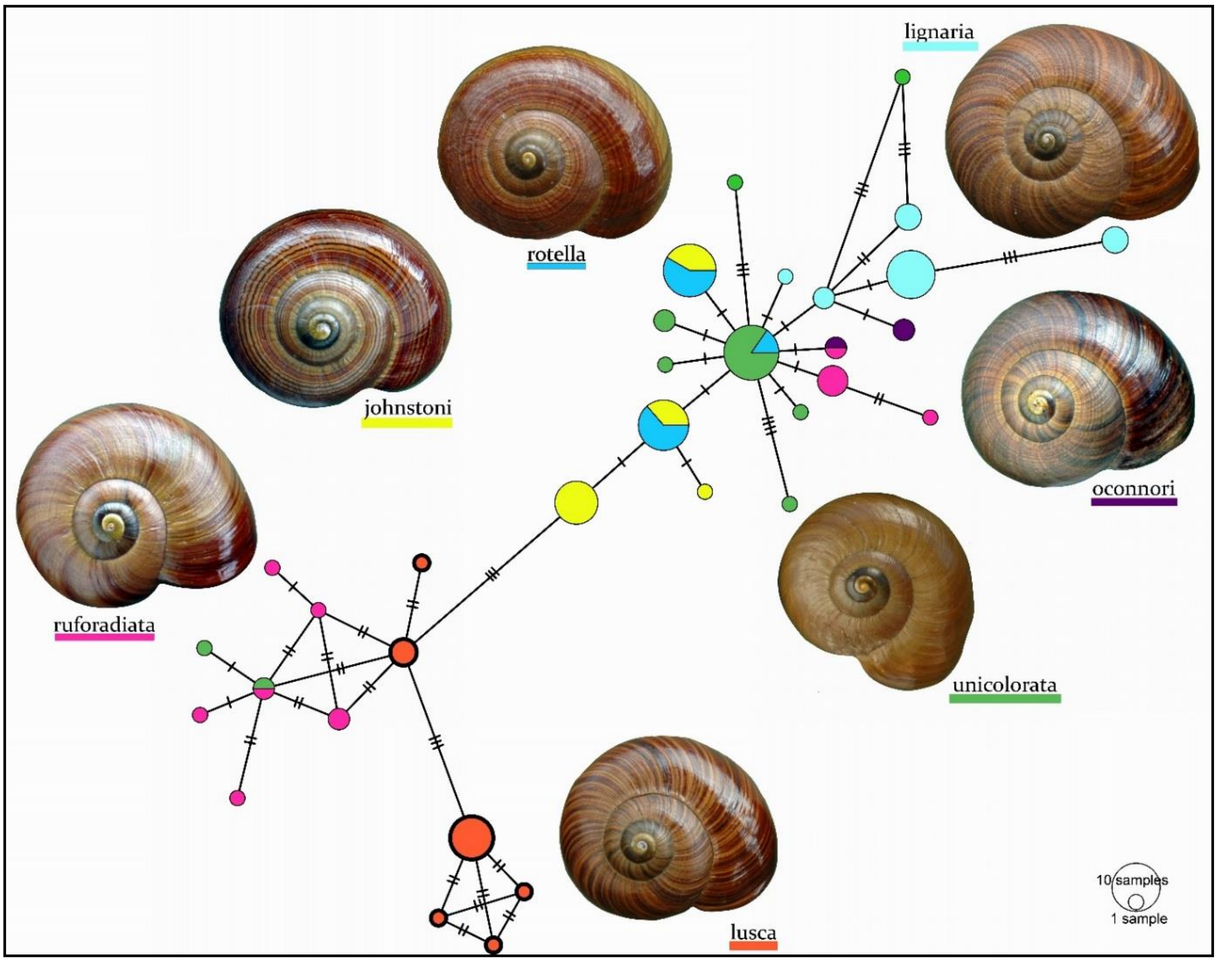


Figure 12. Median-joining haplotype network of the COI gene in *P. lignaria*.

Table 2. Above the diagonal, the number of allozyme loci (out of 8) with no shared alleles in 23 individual snails (Appendix 2) within 7 subspecies of *Powelliphanta lignaria*, and below the diagonal, estimates of HKY + I corrected mean pairwise genetic distance among 86 individual snails (Appendices 2 & 3) in 7 *P. lignaria* subspecies based on mtDNA CO1 sequences 650 bp long.

subspecies (*P. lignaria*)	*johnstoni*	*rotella*	*unicolorata*	*ruforadiata*	*lusca*	*oconnori*	*lignaria*
johnstoni	***	-	1	1	2	-	1
rotella	0.4	***	2	2	2	1	2
unicolorata	0.8	0.5	***	2	3	2	-
ruforadiata	1.6	1.4	1.3	***	2	-	-
lusca	1.7	1.3	1.3	1.0	***	2	1
oconnori	1.1	0.9	0.9	1.7	1.7	***	-
lignaria	1.5	1.3	1.3	2.1	2.1	1.1	***

Powelliphanta lignaria individuals found on the edge of the small settlements of Millerton, Granity and Birchfield south of the Mokihinui River were genetically identical on mtDNA to others from the same site and their haplotypes matched those of *lignaria*, *lusca* and *oconnori* respectively, though all are otherwise confined to land north of the Mokihinui River. Their proximity to houses and their small distributions far from the rest of the range of their subspecies, suggests all are likely to have originated by people moving live snails by hand. The limited extent of the colonies further suggests this occurred not long ago, probably early in the 20th century when *Powelliphanta* were first being discovered and when the area was more densely populated. Due to their likely artificial origins, individuals from these translocated populations were removed from further consideration.

Microsatellites

Collection and examination of shells from the sites sourced for microsatellite genotypes (Buckley et al. 2014) indicates 4 groups of snails were probably mis-assigned to subspecies in that study. These were:

1) Snails from near Mt O'Connor match the type specimen and Powell's (1949) description of *P. l. ruforadiata* so the 3 DNA samples collected from there and previously labelled "*P. lignaria* sp" (KF981916, KF981918 & KF981919) were re-categorized *P. l ruforadiata*.

2) Snails on the north bank of the Mokihinui River just below its junction with Rough and Tumble Stream have mixtures of *P. l. unicolorata* x *P. l. lusca* shell character so the DNA sample described as "*P. lignaria* sp" (KF981917) was re-categorized as a *lusca*/*unicolorata* hybrid.

3) Snails just up from the mouth of Rough and Tumble Stream appear to be *P. lignaria lusca* so 3 DNA samples (KF981910, KF981911, KF981912,) previously attributed to "*P. l. lignaria"* were re-categorized as *P. l. lusca*. However, these 3 snails are very near the boundary of *P. l. lusca* with *P. l. unicolorata*, so some introgression with *unicolorata* is possible and in the absence of the shells from the sampled snails themselves, there remains some uncertainty as to the identity of these snails.

4) Snails on the true-left of Rough and Tumble Stream at its junction with the Mokihinui River appear to be *P. l. unicolorata* so sample KF981929 previously attributed to *P. l. lignaria* was re-categorized as *unicolorata*.

When the corrected subspecies names are applied, those populations with mixed ancestry according to the microsatellite data are all very close to the Mokihinui River through its gorge.

This is illustrated in a reproduction of figures in Buckley et al. (2014) with the reassigned samples labelled and the position of the river relative to those samples indicated (Figure 13).

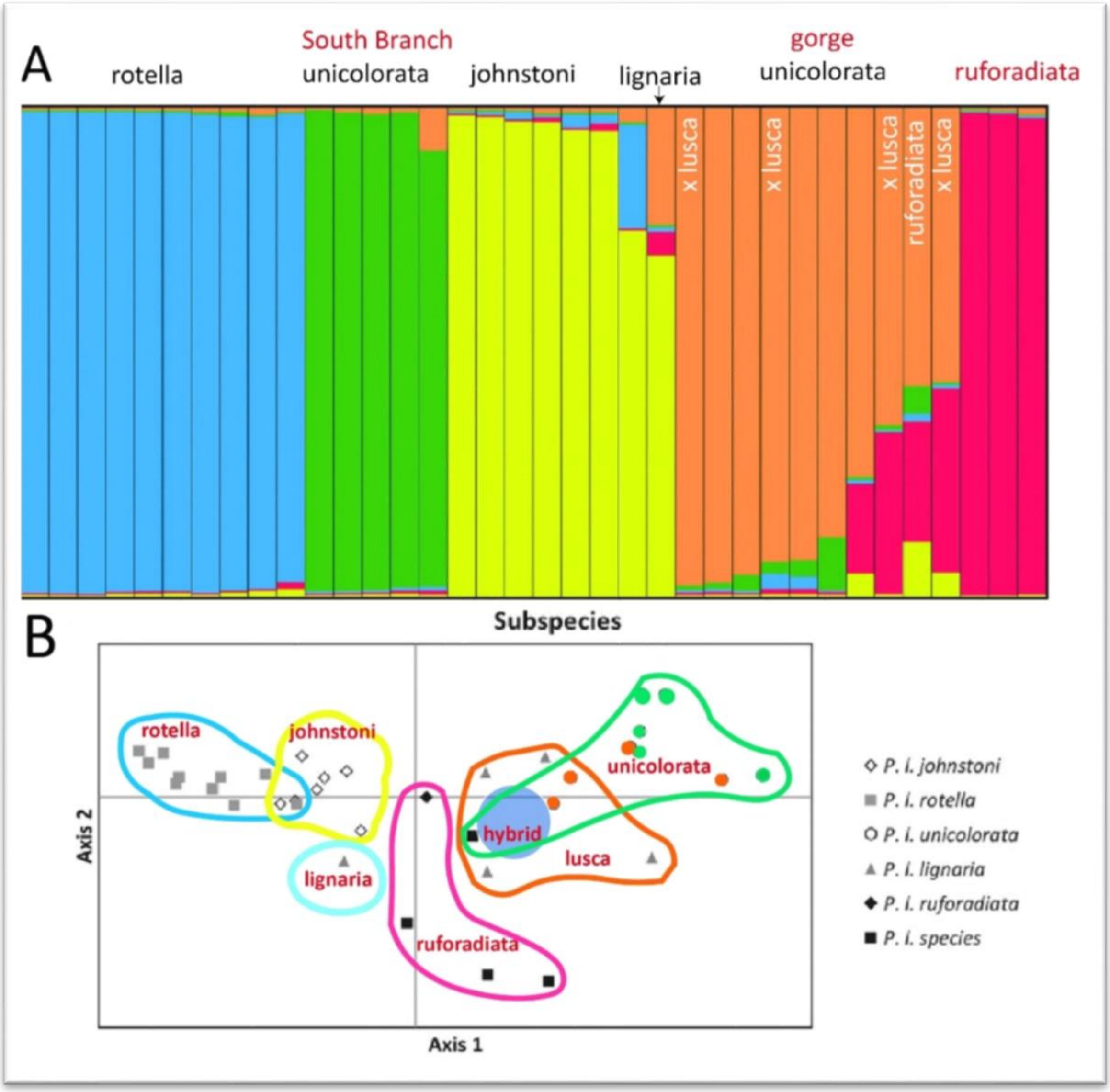


Figure 13. Re-analysis of micro-satellite data presented by Buckley et al (2014), with red or white text and colour-coded polygons indicating new subspecies identifiers which have been placed on the original figures using shell morphology information presented in this study. Figure **13A** is a reproduction of a STRUCTURE plot of assignment of individuals to populations, while **13B** is a reproduction of PCA of subspecies classification, with the grey key showing the original study's identifications. In 13B those *P. l. unicolorata* samples in the Mokihinui gorge close to other subspecies are coloured orange and those isolated from other subspecies are coloured green to illustrate more clearly the proximity of sampled individuals to the Mokihinui River (blue circle) in the gorge.

Unsurprisingly, given there was only 1 individual of *P. l. lignaria* and only 3 *lusca* in the original study—all of which were physically very close to the *unicolorata* colonies along the north bank of the Mokihinui River-—the *lignaria* and *lusca* micro-satellite samples in the study of Buckley et al. 2014 showed mixtures from all clusters in STRUCTURE.

Replication of the original STRUCTURE analysis for each *k* between 3 and 5 found *k*=4 to be the optimum clustering, rather than *k*=5 reported by Buckley et al. (2014). When *k*=4 all samples of *P. l. unicolorata* clustered together, instead of in two separate geographical clusters (Mokihinui gorge and South Branch) as they did when *k*=5 (Figure 14). Samples from the contact zone between *unicolorata* and *lusca* near Rough and Tumble Stream in the lower Mokihinui gorge remained an admixture whether *k*=4 or *k*=5. No conclusions were reached as to the assignment of the subspecies *lignaria* and *lusca* to clusters as they were too poorly represented in terms of both numbers of individuals and geographic spread of sampling effort.

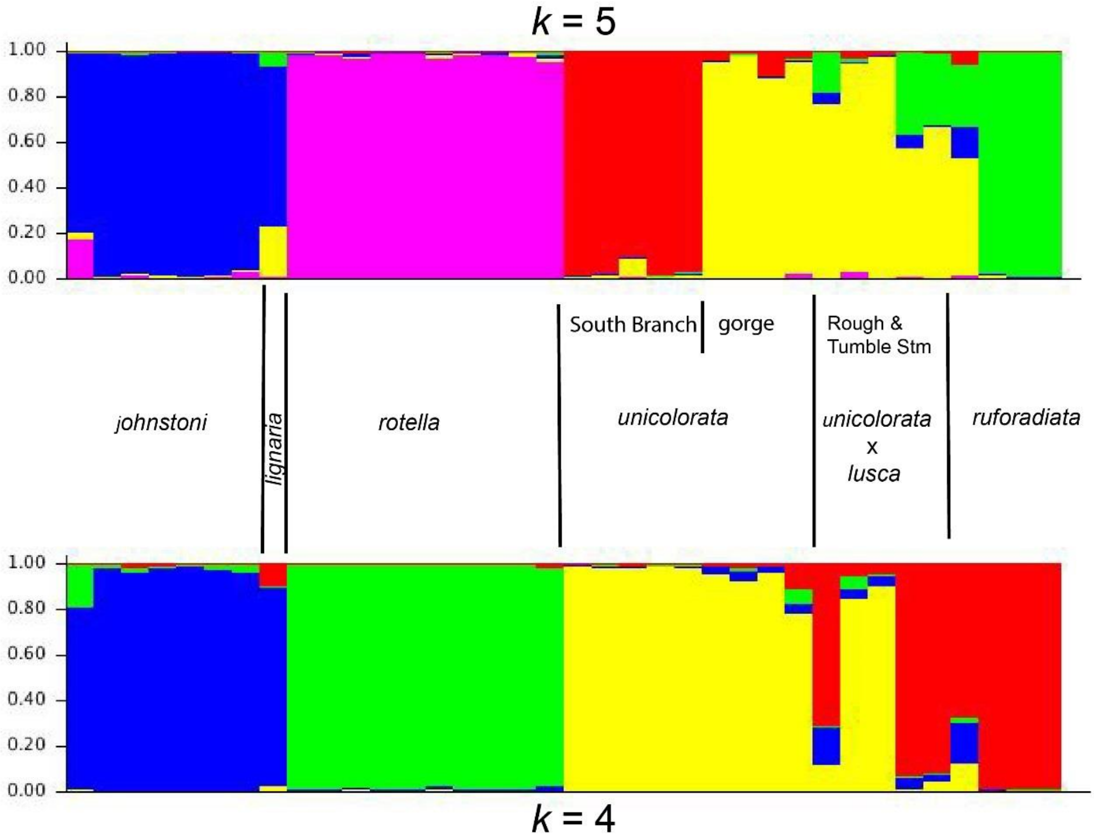


Figure 14. Population structure based on microsatellite allele frequencies showing the proportion of ancestry of 37 *Powelliphanta lignaria* individuals from Genbank (Appendix 3) as estimated by STRUCTURE when *k*=5 (top) and when *k*=4 (bottom).

Discussion

Weighing the evidence

This study has shown that the described subspecies of *P. lignaria* differ morphologically from each other, that these differences align with mostly separate geographic ranges rather than underlying geology and appear to be genetically based. However, is this differentiation sufficient to rank them as separate subspecies? The more strands of supporting evidence available, the greater the reliability of a diagnosis of species rank (de Quieroz 2007) and this logic also applies to subspecies (Haig et al. 2006, Sackett et al. 2014). In *P. lignaria* the strength of evidence and its nature varies between the subspecies.

Powelliphanta lignaria oconnori

Limited genetic data were gathered from *P. l. oconnori* (allozyme data from only 1 individual and mtDNA sequences from only 3, though these were from both major parts of their range). It comprises 2 unique mitochondrial haplotypes with 1 or 2 fixed allelic differences in allozymes from *P. l. rotella*, *P. l. unicolorata* and *P. l. lusca*. Its geographic distribution is entirely separate from the rest of the group so presumably there is now no gene flow. This subspecies has disjunct—possibly flood-derived—populations. While shells of snails in the western population have notably stronger axial banding, they appear genetically indistinguishable to those in the east. *P. l. oconnori* is morphologically distinct and readily diagnosable on shell pattern so easily fulfils the criteria for sub-species rank.

Powelliphanta lignaria johnstoni and *P. l. rotella*

These two subspecies are ecologically and morphologically differentiated from all other *P. lignaria* and are mostly geographically separate from them. It could be argued that *rotella* and *johnstoni* together represent a separate species. In nuclear markers they have 1-2 fixed allelic differences from almost all other *P. lignaria*, they have 4 unique mtDNA haplotypes and share a 5th with *unicolorata*, and in STRUCTURE analysis of microsatellite data (Buckley et al. 2014) cluster separately from both *P. augusta* and other *P. lignaria*. However, the level of sequence divergence between *rotella/johnstoni* and all other *P. lignaria* is very low in comparison with that between other well-supported species, with a mean corrected pair-wise distance of between 0.5% to 1.6%, whereas inter-specific distances for many other land snail species range between 2 and 10% (Walker et al. 2008 and references therein). The original taxonomic treatment of *rotella* and *johnstoni* as subspecies of a separate *unicolorata* species, and as distinct from axially striped snails north of the Mokihinui River, gains some support from the molecular data reported here. The lowest genetic distances recorded in all *P. lignaria* are those between *rotella*, *johnstoni* and *unicolorata*. Morphologically the picture is less compelling, as shadows of the strong narrow red spiral banding which make *rotella* and *johnstoni* so distinctive within *P. lignaria,* do occur in all its other subspecies, albeit in highly reduced form. In addition, while *rotella* and *johnstoni* appear to share the same ecological niche, ecologically *unicolorata* is closer to the *P. lignaria* populations north of the Mokihinui River. On balance there seems insufficient reason to elevate *rotella* and *johnstoni,* with or without *unicolorata,* to specific status, despite their marked ecological and morphological differences.

P. l. rotella and *P. l. johnstoni* are clearly a well-differentiated group within *P. lignaria*, but are there sufficient differences between them for each to qualify for sub-species status? They are readily separable and diagnosable and their distributions abut but do not overlap. They cluster separately in nuclear DNA (Buckley et al. 2014; Figure 13), but in the slower-evolving mtDNA markers used here share 3 haplotypes, with 2 additional unique haplotypes in *P. l. johnstoni*. While clearly from the same ancestral stock, their distinctive phenotypes relate to separate geographic areas, and nuclear DNA shows these reflect different, albeit recent, evolutionary histories, thus fitting the criteria for separate subspecies.

Powelliphanta lignaria subspecies *lusca, ruforadiata, and unicolorata*

The *P. lignaria* subspecies *lignaria*, *lusca*, *ruforadiata* and *unicolorata* cluster near each other in the morphological PCA but are phenotypically separable on shell pattern, as well as on colour and size (Figures 8 & 9). Though occupying large separate geographic areas over which their morphologies are consistent, with sea, river or simply unoccupied forest habitat on most sides, they also share some parapatric boundaries (Figures 3 & 6). Those between *lignaria* and *lusca* and particularly between *lusca* and *ruforadiata* occur where habitat is poor and snail density low. The beachhead *unicolorata* has made on the north bank of the Mokihinui River seems secondary, being narrow with pockets of conspicuous morphological hybrids between *unicolorata* and *lusca* and *lignaria* in the immediate vicinity of the river (figure 7). Interaction between *ruforadiata* and *unicolorata* is more extensive, presumably because it occurs just beyond the top of the gorge in good quality snail habitat where densities of both subspecies are high. An apparently stable tension zone has formed there, about 1.5 km wide and 6 km long with obvious hybrids in the centre and a relatively uniform intermediate phenotype in the west and in the east (Figure 7).

It is thought inadvisable to erect subspecies when geographic variation is clinal due to the difficulty of identifying steps or fixed character states, though exceptions can be made for parapatric subspecies connected by a narrow hybrid zone through secondary contact (Braby et al. 2012). Molecular evidence sheds some light on the amount of gene flow occurring between these north bank snail populations that helps guide whether an exception should be made in this case. In north bank *P. lignaria* there is 1 fixed allelic difference between *lignaria* and *lusca*, 2 between *lusca* and *ruforadiata*, 2 between *ruforadiata* and *unicolorata* and 3 between *unicolorata* and *lusca* (Table 2). Each of these *P. lignaria* subspecies has a large, diverse and unique set of mtDNA haplotypes (Table 1) and *lignaria*, *lusca* and *ruforadiata* each form largely distinct clusters in the mtDNA network (Figure 12). Corrected genetic distances are comparatively high (2.1%) between neighbouring *P. lignaria* subspecies pairs, *lignaria–lusca* and *lusca–ruforadiata* as well as between *P. l. unicolorata* and these three north-bank *P. lignaria* (1.3%) indicating persistent partitioning of populations in close geographical proximity. Given their diagnosability, limited geographic overlap, low gene flow, and the consistency of their differing morphologies across a large area, sub-species recognition is warranted for each.

Evidence of sufficient weight for subspecies status

The morphologically distinctive populations of *P. lignaria* fulfil the criteria for subspecies recognition suggested by Braby et al. (2012). That is, the distributions of the described subspecies of *P. lignaria* are essentially allopatric, even though some closely abut. Each subspecies is separable in PCA on a suite of morphological characters and is readily diagnosable on at least 1 non-overlapping shell colour/pattern character. The morphological differences are not associated with differing substrates and are probably genetically-based. The subspecies have adapted to differing local conditions, with *johnstoni* and *rotella* confined to acidic coal measures and the remainder to alkaline fertile soils. While lineage sorting is incomplete, most of each subspecies alleles are unique, as assessed by still relatively limited allozyme, microsatellite and mtDNA data. Despite the presence of small hybrid colonies in the lower reaches of the Mokihinui River which seem to have arisen through disturbance, each subspecies is maintaining its essential genetic and morphological integrity.

Biogeography

Using estimates of genetic distance between *P. lignaria* subspecies and employing a standard calibration rate for *Powelliphanta* of 1% sequence divergence per million years as a coarse guide (Chapter 2), segregation into the current subspecies may have begun in the early Pleistocene. Such timing coincides with a period of rapid geomorphic and climatic change in the region, due to tectonic movement along the Alpine Fault. About 6 Ma (early Pliocene) folding and reverse faulting occurred in north-west Nelson on a network of interconnected NNE–SSW trending faults which splay off the Southern Alps, causing high rates of deformation in one of the most active oblique margins in the world (Ghisetti & Sibson 2006, Ghisetti et al. 2014). In the mid-Pliocene the Mokihinui River would have meandered across a relatively gentle landscape cloaked in deep layers of tertiary sediments, without the concentrated power it has today. However, from around 2 Ma (late Pliocene) tectonic folding, faulting, compression and rapid uplift occurred on the previously subdued relief, leading to the up-thrust of the Glasgow and Radiant Ranges, and a deepening gorge as the Mokihinui River down-cut through the rising ranges (Nathan et al. 1986, Williams 2012). Alternating cold and warm phases during the Pleistocene likely accelerated erosion of the uplifted ranges and stripped away the tertiary siltstones, sandstones, limestones and mudstones which formerly covered them. Older and coarser granite basement rocks were exposed (Nathan et al. 1986), and these effectively separated into fault-bounded remnants tertiary sediments which support *P. lignaria*.

Those *P. lignaria* subspecies separated by the highest levels of mtDNA sequence divergence and greatest number of fixed allelic differences in nuclear DNA, *ruforadiata* and *lusca* are geographically close to each other today but separated by faults These faults have been very active through the Quaternary and their movement has caused horizontal shortening of up to 3 km (Ghisetti & Sibson 2006). Tectonic activity on these faults may have not only separated *P. lignaria* into eastern and western populations by uplift of the Glasgow and Radiant Ranges, and into southern and northern populations by incision of the Mokihinui Gorge but caused some horizontal displacement of the northern-most populations in relation to each other through shifts in the location of favoured habitat, and on-going landslides which destroy snail habitat and fragment their populations.

Conclusions

The conclusions reached here differ from those of Buckley et al. (2014). The earlier study of sub-species variation in *P. lignaria* was, as noted by the authors, hampered by limited sampling of snails on the north-west side of the Mokihinui River with only 1 specimen of *lignaria* sampled. There was no sampling of *lusca* away from its boundary with *unicolorata*, and indeed no recognition that the snails they had sampled there were morphologically *lusca* not *lignaria*. This was due to the related problem in their study that there was no formal examination of shells.

Despite the significant genetic structuring they found in *P. lignaria* (Figure 13), lack of reciprocal monophyly led Buckley et al. (2014) to dismiss the use of subspecies in this species and potentially in all *Powelliphanta*, suggesting that "the occurrence of gene flow between populations is inconsistent with the usual taxonomic usage of the rank of subspecies". This is incorrect and an unexpected conclusion, especially as they used in support of it a quote from Braby et al. (2012) that "subspecies be **partially** isolated lineages" (emphasis added). Indeed, the latter authors specifically noted:

> "*Subspecies are populations within species that, although they are distinct in certain heritable phenotypic and molecular characters, should not be expected to be reciprocally monophyletic according to mtDNA phylogeography"*

Others have noted the same point.

> *"Whilst some nuclear genes under natural selection are expected to differ, given that subspecies characters are assumed to have a genetic basis, the generally accepted definition of subspecies is that gene flow has not been completely severed, so it makes no sense to expect clusters of genes or reciprocal monophyly among groups, at least with respect to neutral markers"* (Patten 2015).

Reciprocal monophyly may not hold at the species level, let alone within species due to, amongst other things, introgression, incomplete lineage sorting and recent speciation events (Funk & Omland 2003, Knowles & Carstens 2007, Braby et al. 2012). Reciprocal monophyly should not be a necessary criterion for identifying units below the level of species (James 2010, Braby et al. 2012). Incomplete lineage-sorting is particularly likely in recently-diverged populations with large effective population sizes (Knowles and Carstens 2007) such as *Powelliphanta lignaria*

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While a subspecies—a collection of populations occupying a distinct breeding range and diagnosably distinct from other such populations—may not be isolated reproductively from these populations, and indeed have possibly persistent gene flow between parapatric populations, this must not be of a scale to swamp phenotypic diagnosability (Patten 2010). It is the extent of any overlap in morphology, ecology and range which matters (Patten 2010), and was the focus in this study.

One of the main reasons for documenting intraspecific variation is to identify those units which need to be protected for maintenance of biological diversity. While ESU's have come to be equated almost solely with reproductively isolated units due to advances in molecular techniques which can measure this readily, it was not how they were initially conceived or should now be selected (Moritz 1994, Crandall et al. 2000). A focus on monophyly in either ESU's or subspecies at the expense of adaptability would be a mistake since adaptability is arguably a more important attribute in efforts to conserve diversity (Crandall et al. 2000, but see Moritz 2002). *Powelliphanta lignaria* has been able to exploit the wide range of very different habitats available within a small geographic area courtesy of the tilting, uplifting and exposure of differing layers of sediments, through its apparent ecological specializations. That this is genetically-based appears highly likely: patches of low rimu forest on coal measures east of Gentle Annie within the range of alkaline-adapted *lignaria* support almost no snails and likewise acid-adapted *johnstoni* are absent in fertile free-draining beech forest on the upper slopes of Radcliffe Ridge though there are dense colonies only a hundred metres away on coal measures. Such differing capacities could be lost if all *P. lignaria* were to be represented by just one population on the basis that gene flow still occurred within the group.

Almost more remarkable than the strong habitat niche specialization in *P. lignaria* is the close geographic proximity of the north bank subspecies; what processes have kept them apart? By identifying this diversity, questions as to the nature of the physical environment in the recent past which could have produced such diversity can be formulated. The detailed descriptive mapping started by Powell (1930, 1949), and the genetic work in Buckley et al. (2014) and expanded here demonstrate that shell morphology in *Powelliphanta* can be a reliable and useful guide to taxonomy, and to understanding of a tempestuous biogeographic past.

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Appendix 1

Categorical character states

1. Number of whorls

2. Mucous/mantle colour
    1 clear in all individuals in population
    2 clear, except rarely in population some juveniles blue

3. Axial stripes
    5 None
    6 Very few, sparse, mostly on dorsal surface
    7 Moderate number
    8 Abundant

4. Spiral stripes on dorsal surface
    4 None
    5 Few, narrow
    6 Many, variable width, conspicuous

6. Spiral stripes on ventral surface
    1 None
    2 Few, narrow, inconspicuous
    3 Variable width, conspicuous

7. Bi-coloured striped shell
    1 Uni-coloured and/or predominantly radially striped
    2 Spiral stripes on entire shell
    3 Spiral stripes and plain contrasting umbilicus patch
    4 Spiral stripes on top, plain coloured base from periphery

Appendix 2

Sampling localities of 59 *Powelliphanta lignaria* snails caught in this study, from which DNA samples were taken and mantle and mucous colour scored. Reference number is that shown on the map in Figure 2 to illustrate sampling locality. The haplotype of each individual snail at each sampling location is immediately adjacent to it

Subspecies	**Ref no.**	**Individuals' sample no. (prefix KJW)**	**Haplo-type**	**Location**	***N* allozyme**	***N* mtDNA**	**Easting (NZMG)**	**Northing (NZMG)**
P. l. lignaria	1	94, 95,104	27	Gentle Annie Point	3	4	2422475	5966180
		105	26					
P. l. lignaria	2	624	26	TR Mokihinui River mouth		1	2421841	5964140
P. l. lignaria	3	5, 8	26	Sawyers Bend	2	2	2423400	5963900
P. l. lignaria	4	615, 616	18	Karamea Bluffs		3	2429346	5963912
		617	28					
P. l. lignaria	5	630, 631, 632	30	Four Mile Creek mouth		3	2423506	5969435
P. l. lusca	6	119	5	Glasseye Ck/ Karamea Highway junction	5	5	2433500	5971700
		120, 121,	6					
		122	12					
		123	13					
P. l. lusca	7	533,	11	Glasseye Ck mouth		2	2431726	5978323
		534	10					
P. l. lusca	8	606,	31	Lake Hanlon Track		3	2435200	5975500
		607, 608	10					
P. l. oconnori	9	3	29	Slippery Creek, Karamea Rv	1	1	2465700	5990900
P. l. oconnori	10	258	29	Wilkinson Track to Leslie Rv		1	2473500	5996500
P. l. oconnori	11	668	29	Kakapo Valley		1	2448631	5490896
P. l. ruforadiata	12	13	20	mid Maori Gully	1	1	2441790	5967990
P. l. ruforadiata	13	529	9	mid Maori Gully		4	2441840	5967539
		530	21					
		531	2					
		532	8					
P. l. ruforadiata	14	535	15	Pakihi Creek mouth		2	2439294	5962399
		537	20					
P. l. unicolorata	15	115	2	Mokihinui Forks	2	2	2440400	5961600
		116	1					
P. l. unicolorata	16	525,528	24	Goat Ck, South Branch		4	2443708	5956333
		526, 527	14					
P. l. unicolorata	17	541	16	TL, mouth Mokihinui Gorge		2	2429117	5960928
		542	17					
P. l. rotella	18	79, 80	14	St Andrews Stream	5	5	2427002	5954016
		83	19					
		82, 84	32					
P. l. rotella	19	600	14	Hydro Hill		1	2426400	5958500
P. l. johnstoni	20	286, 288	34	Mumm's Mill		5	2422199	5957428
		287, 289	14					
		290	33					
P. l. johnstoni	21	145, 146, 148	34	Charming Creek Bridge	4	4	2420172	5955691
		147	14					
P. l. johnstoni	22	365,366,367	34	Under Ngakawau cableway		3	2416700	5954300
TOTAL					**23**	**59**		

Appendix 3

Sampling localities of 37 *Powelliphanta lignaria* snails from which mtDNA sequences were obtained from Genbank. Reference number is that shown on the map in Figure 2 to illustrate sampling locality. The haplotype of each individual snail at each sampling location is given. The subspecies identification for 5 individuals has been corrected from the Genbank label as described in the results.

subspecies	**Ref no.**	**Genbank number (prefix KF)**	**Haplo-type**	**Location**	***N* mt DNA**	**Easting (NZMG)**	**Northing (NZMG)**
P. l. lignaria	23	981935	26	Gentle Annie Pt	1	2422858	5967059
P. l. lusca	24	981910	22	Near Rough & Tumble Ck mouth	2	2433280	5963950
		981911	10				
P. l. lusca	25	981912	6	Near Rough & Tumble Ck mouth	1	2432927	5963906
P. l. lusca?	26	981929	15	At Rough & Tumble Ck mouth	1	2432258	5963298
P. l. ruforadiata	27	981913	7	mid Maori Gully	2	2442452	5966719
		981914	7				
P. l. ruforadiata	27	981915	3	mid Maori Gully	1	2442457	5966690
P. l. ruforadiata	28	981916	20	SE of Mt O'Connor	1	2438826	5967917
P. l. ruforadiata	28	981918	20	SE of Mt O'Connor	1	2438897	5967918
P. l. ruforadiata	28	981919	4	SE of Mt O'Connor	1	2438880	5967919
P. l. unicolorata	29	981917	16	Just below Rough & Tumble Ck	1	2431861	5963374
P. l. unicolorata	30	981926	25	Specimen Creek	1	2439561	5961646
P. l. unicolorata	30	981927	16	Specimen Creek	1	2439561	5961646
P. l. unicolorata	30	981928	16	Specimen Creek	1	2439499	5961458
P. l. unicolorata	31	981925	23	South of Mokihinui Forks	1	2439581	5951472
P. l. unicolorata	32	981920 to 981924	14	Mountain Creek, South Branch	5	2443215	5957736
P. l. rotella	33	981936	19	Mt Glasgow Track	1	2427545	5955675
P. l. rotella	33	981937	32	Mt Glasgow Track	1	2427538	5955682
P. l. rotella	33	981938	32	Mt Glasgow Track	1	2427536	5955682
P. l. rotella	33	981939	32	Mt Glasgow Track	1	2427535	5955680
P. l. rotella	33	981940	32	Mt Glasgow Track	1	2427539	5955678
P. l. rotella	33	981941	19	Mt Glasgow Track	1	2427539	5955675
P. l. rotella	33	981942	32	Mt Glasgow Track	1	2427535	5955674
P. l. rotella	33	981943	19	Mt Glasgow Track	1	2427542	5955676
P. l. rotella	33	981944	19	Mt Glasgow Track	1	2427540	5955675
P. l. rotella	33	981945	19	Mt Glasgow Track	1	2427537	5955674
P. l. johnstoni	34	981930	19	Ngakawau coal cableway	1	2416691	5954294
P. l. johnstoni	34	981931	32	Ngakawau coal cableway	1	2416653	5954269
P. l. johnstoni	34	981933	19	Ngakawau coal cableway	1	2416719	5954404
P. l. johnstoni	34	981932	32	Ngakawau coal cableway	1	2416720	5954355
P. l. johnstoni	34	981934	32	Ngakawau coal cableway	1	2416719	5954440
P. l. johnstoni	34	981946	32	Ngakawau coal cableway	1	2416731	5954487
TOTALS					**37**		

Chapter 5.

Powelliphanta augusta, a new species of land snail with a description of its former habitat, Stockton coal plateau, New Zealand.

The content of this chapter is the same as the following published paper:

> Walker KJ, Trewick SA, Barker GM 2008**.** *Powelliphanta augusta*, a new species of land snail, with a description of its former habitat, Stockton coal plateau, New Zealand. *Journal of the Royal Society of New Zealand* **38**:163–186.

I conducted the research and wrote the manuscript. SAT supervised my research, carried out the genetic work reproduced in Figure 2 and provided comments on the manuscript. GMB dissected *P. augusta* and prepared the Appendix detailing its reproductive anatomy and provided comments on the manuscript.

Image previous page: the northern escarpment of Mt Augustus where *Powelliphanta* snails were discovered living in 2004 (top), and the deconstruction of the escapment in 2008 (centre) and 2009 (bottom).

Abstract

A recently discovered and threatened large land snail, *Powelliphanta augusta* n. sp. is described from Mount Augustus on the western scarp of the Stockton Plateau, North Westland. On shell characters it is readily distinguishable from all other *Powelliphanta*, with narrow red spiral lines underlying irregular and variable dark reddish-brown axial bands, a small adult size and sculptured dorsal surface. Differences in the shell morphology of *P. augusta,* its closest phylogenetic relative *P. lignaria*, and its closest geographic neighbour *P. patrickensis*, were investigated using principal components analysis. *P. lignaria* is much larger than either *P. augusta* or *P. patrickensis*, but there are significant differences in shell shape as well as size between the 3 taxa. Earlier mitochondrial DNA sequencing data, which supported specific status of *P. augusta,* is discussed. The snail's only habitat on the Mt Augustus ridgeline is described, but most has now been removed by coal mining. Snails salvaged before the destruction of their habitat have been taken into captivity or released in the wild outside their natural range.

Introduction

Powelliphanta O'Connor, 1945 is a genus of large, predatory land snails endemic to New Zealand. The shells of many taxa are strongly patterned and brightly coloured and have been used as the primary tool in identification. Most taxa were described on the basis of shell morphology in the 1930s and 1940s (Powell 1930, 1932, 1936, 1938, 1946), producing a taxonomy of 10 species and 27 subspecies. Later, Climo (1978) proposed an alternative classification reducing the number of species to 2 with 4 subspecies, but this was considered contentious (Parkinson 1979, Powell 1979) and failed to gain wide acceptance. More recently, molecular studies (Walker 2003, Trewick 2008) provided substantial support for the original morphologically-based classification (Powell 1979).

Almost all taxa of *Powelliphanta* occupy small ranges. This restricted distribution pattern has made *Powelliphanta* particularly vulnerable to habitat loss and degradation, and these snails are afforded high conservation status (Walker 2003). The recent discovery of an unknown *Powelliphanta* in a small part of a large open-cast coal mine at Stockton led to intense interest in its taxonomic status and long-term prospects.

In April 1996 members of the Nelson Botanical Society collected 6 *Powelliphanta* shells on the north-eastern slopes of Mt Augustus, the southern-most of 3 high points which collectively form the Augustus massif, on the western scarp of the Stockton Plateau, north of Westport, South Island, New Zealand (Figure 1). The Stockton and adjacent Denniston coal plateaux are an elevated and exposed former peneplain where very acid and infertile soil parent materials (Brunner coal measures), montane to subalpine altitude (400-1106 m above sea level (asl)), poor drainage, low sunshine hours, high wind exposure, and a very high rainfall have produced dramatic and unique landscapes and biota (Overmars et al. 1998). It is a somewhat unlikely habitat for large land snails which normally need alkaline, well-drained conditions supporting abundant earthworms as their primary prey, and high levels of available calcium for shell and egg formation. However, one species was already well known from the plateau, *Powelliphanta patrickensis* (Powell, 1949), and initially the shells found on Mt Augustus were assumed to be this species. In apparent response to the harsh conditions, *P. patrickensis* is relatively small, has a thin and fragile shell, and is patchily and sparsely though widely distributed on the plateau. The Mt Augustus shells were also small, but their shape and colour patterning were very different from the glossy *P. patrickensis*. The shells of the Mt Augustus snails appeared most similar to those of *P. lignaria* (Hutton 1880), a large, thick-shelled lowland species with 7 described subspecies found just north of Stockton Plateau, but there were sufficient differences to conclude that while *P. lignaria* and the Mt Augustus snails probably shared a common ancestry, the latter was a distinct taxon.

By the time the Mt Augustus shells were critically examined in late 2003, the site they had been collected from had been destroyed by coal mining, but in March 2004 KJW found a surviving population on the north peak of the Augustus massif. The shells of the north peak snails differed slightly in colour and banding from the original 6 but were still recognisably members of the same taxon. Subsequent further searches found that the extant population was restricted to about 8.5 ha in the immediate vicinity of the Augustus ridgeline between 900-1011 m. Most surviving snails were on the north peak, but a small number referable to the southern morph collected by the Botanical Society were still present on the north-western and south-eastern flanks of Mt Augustus (Figure 1).

In 2005 the taxonomic status of the snails on Mt Augustus and their phylogenetic relationship with other *Powelliphanta* was assessed using COI mitochondrial DNA sequence data (Trewick 2005). This study found the Mt Augustus snails to be a distinctive evolutionary lineage and concluded on genetic and other evidence that they comprised a specialized local endemic species with a phylogenetic sister-taxon relationship to *P. lignaria* (Trewick 2005; Trewick et al. 2008, Figure 2). It found two haplotypes, differing by 0.5%, which were distributed along the same spatial lines as the shell differences already noted, with all individuals from the ridge south of Mt Augustus (="southern-morph") having one haplotype, and those from the north peak having the other.

In 2006 and 2007, subsequent to the discovery of the snail population on Mt Augustus and its confirmation as a distinct taxon, all remaining snail habitat above the escarpment on the Augustus massif was destroyed by coal mining, leaving only a sliver of snail habitat on the stump of the north peak. Before mining began, the area was searched for live snails, 6139 of which were taken into captivity, and during this process many empty shells were also found and collected. This provided a ready source of tissue biopsies for genetic analysis and shells for morphological analysis, but of course also left the new species without its habitat.

The purpose of this chapter is to describe the Mt Augustus snail as *P. augusta* n.sp., to quantify the shell characteristics which distinguish it from its closest relatives and neighbours, and to characterise the environment the snails formerly occupied.

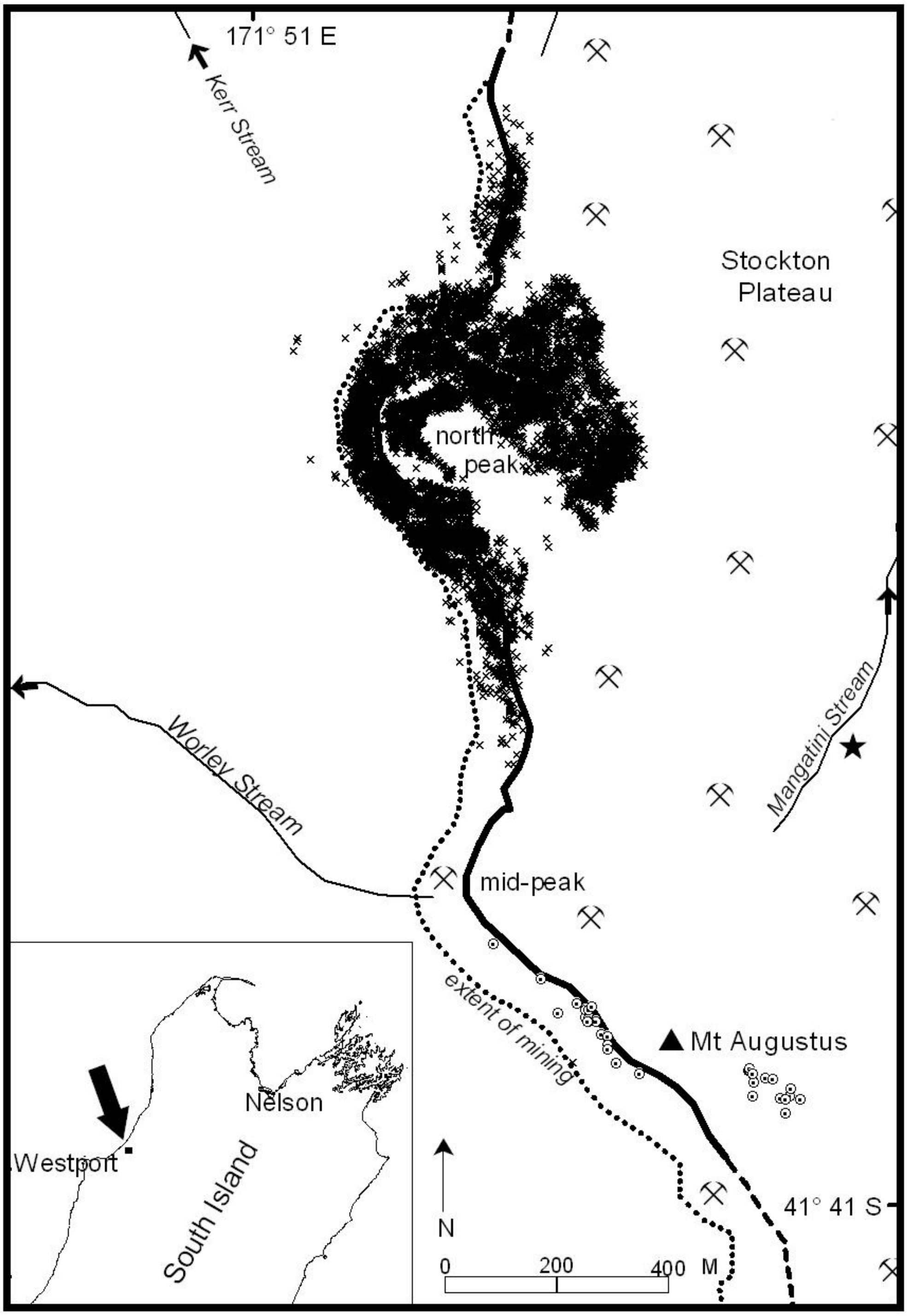


Figure 1. Distribution of live *Powelliphanta augusta* n. sp. snails in the period 2004-2007. Crosses indicate where snails of the northern morph were seen (and 6319 collected) and solid circles nested within an open circle where 26 snails of the southern morph were seen and collected. A black star indicates the site where 6 shells were collected by the Botanical Society in 1996. The western escarpment of the Stockton Plateau where high cliffs form the Augustus massif is shown by a solid black line, with dashed lines indicating the ridgeline north and south of the massif. The sharp edges of the snail's distribution east of the ridgeline are not natural boundaries but rather indicate the presence of bulldozed roads and mine pits. By late 2007 coal mining had removed all the snails and snail habitat east of the dotted line.

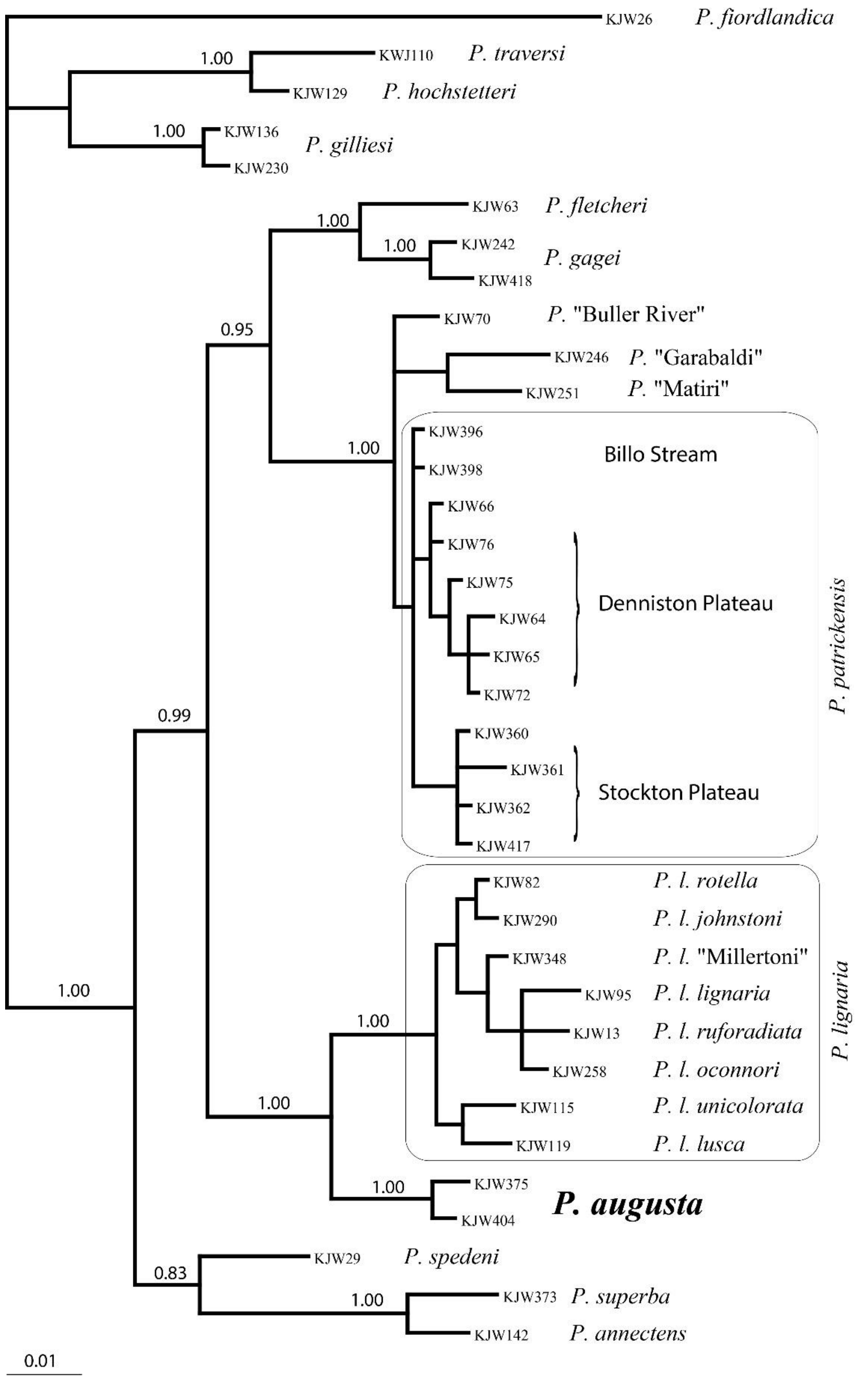


Figure 2. Evolutionary hypothesis from a Bayesian analysis of 36 mtDNA COI sequences up to 800bp long from *Powelliphanta* snails. Numbers at nodes are Bayesian credibility values, with maximum support indicated by highest value (1.0). Reproduced with minor changes from Trewick et al. 2008.

Materials and Methods

Powell's nomenclature, with additions and revisions as proposed by Walker (2003) on the basis of allozyme analysis and wider field studies, is adopted here.

Materials examined

Between 1980 and 1990 the extensive collections of *Powelliphanta* shells held at the National Museum of New Zealand Te Papa Tongarewa (NMNZ) were examined by KJW. Much of the material held at NMNZ had been collected at or near type localities, but shell-examination was not restricted to type material. Between 1987 and 1994 KJW visited all sites where *Powelliphanta* were at that time known or thought to occur and collected shells and examined live snails as part of a study into the taxonomy of the genus. Shells collected at that time formed the basis of a large collection presently held at the Department of Conservation, Nelson (DoCNn). Since then the collection has been expanded to include shells collected in the period 1995-2007 from newly discovered snail populations, and from more intensive sampling within the range of well-known taxa (K. Walker, unpub. data). The type specimens of most *Powelliphanta*, held at the Auckland Institute and Museum (AI&M), were examined by KJW in 2000 to confirm that identifications afforded by the extensive NMNZ and DoCNn collections were consistent with typological material.

KJW examined 8057 *Powelliphanta* shells (including those from ca. 1000 freshly-dead "mature" animals) received by DoCNn in 2006/07 as a result of the searches for live snails on Mt Augustus that preceded mining activities. In addition, about 100 live snails collected from all parts of the snail population on the north peak of the Augustus massif (New Zealand Map Series 260, map L29, between grid co-ordinates 147easting-476northing and 146-480; L29/145-478 to 148-478) and 24 live snails from the southern ridgeline near Mt Augustus (L29/147-473 and L29/149-472) were examined while they were in captivity during parts of 2005-2007. The 6 shells collected by the Nelson Botanical Society east of Mt Augustus (L29/150-475) in 1996, presently in DoCNn, were also examined.

The anatomy of six specimens of *P. augusta* from the north peak of the Augustus massif (L29/146-480) was examined by GMB. A further 8 snails representing a range of *Powelliphanta* taxa were also examined anatomically by GMB for comparative purposes. These were: *P. superba superba* (Powell, 1930) and *P. hochstetteri anatokiensis* (Powell 1938), both from the Haupiri Range, western Golden Bay, M26/367-837 (1 specimen each); *P. gilliesi aurea* (Powell 1946) from the type locality at Mangarakau, 200 m asl ca. M25/658-630, collector FM Climo 1967 (1 specimen); *P. patrickensis*, mid Waimangaroa Valley L29/145-395 (1 specimen); *P. l. lignaria*, Gentle Annie Point, L28/222-663 (1 specimen); *P. l. johnstoni* (Powell 1946) behind Ngakawau, L28/167-543 (3 specimens).

Morphometric analyses of shell morphology

The shells of 90 large adult snails were measured: 30 *P. augusta* from the north peak of the Augustus massif, 30 *P. patrickensis* from sites across the Denniston and Stockton Plateau (Mt Rochfort, mid-Waimangaroa Valley, Happy Valley and the western escarpment north of Mt Frederick), and 30 *P. l. johnstoni* from the mid-reaches of Charming Creek in Mokihinui Forest at L28/202-558. *P. l. johnstoni* was selected to represent *P. lignaria* as its shell morphology was the most similar of all the *P. lignaria* subspecies to that of *P. augusta*, and its range was the closest.

Shells for measurement were selected on the basis of size and intactness. Shell growth in *Powelliphanta* continues throughout life. This indeterminate growth makes it difficult to separate size and shape variation attributable to ontogeny from that attributable to variation among individuals, and thus complicates efforts to distinguish taxa on the basis of morphometrics. Nonetheless, growth in *Powelliphanta* does slow greatly in “old age”, and we know from breeding studies the size at which each taxon becomes reproductive (K. Walker, unpubl. data). Further, in old age the last portion of the body whorl descends more relative to the proceeding whorl (ie. the point of insertion of the upper aperture rim on the body whorl descends from the horizontal plane), so that we can be certain in those individuals that growth has all but ceased. In some species, including *P. augusta,* the descent from the horizontal plane is very pronounced, while in other species, such as *P. patrickensis*, it is very limited. To increase the likelihood that shell characteristics of adults of a similar age were compared, only shells which had reached the standard adult 4.5-5.0 whorls, were amongst the largest, and/or had the greatest last-whorl-descent within each collection, were selected for measurement.

Twelve point to point measures were taken from each shell using digital display callipers. The measurements (Figure 3) were chosen because they encompassed the obvious sources of phenotypic variation amongst *Powelliphanta*, and they included the standard biometric variables of many molluscan studies (Gould & Woodruff 1986).

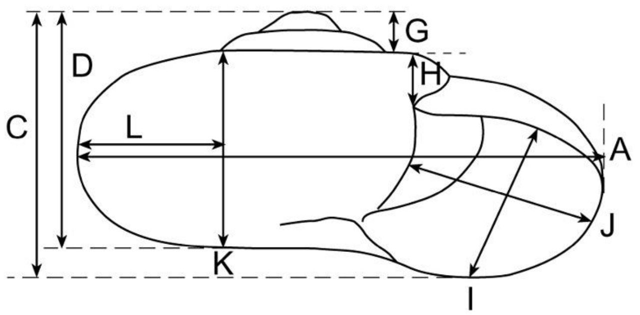


Figure 3. Dimensions of *Powelliphanta* shells used for morphometric analyses. ***A***, maximum diameter ***C***, total height of shell with last whorl ***D***, total height of shell without last whorl ***G***, spire height, from the last whorl to the apex, measured above the aperture ***H***, descent in aperture incision: the distance from the top of the aperture to the top of the previous whorl ***I***, height of the aperture at its widest point ***J***, width of the aperture, from midway up to its widest point ***K***, height of the last whorl opposite the aperture ***L***, width of the last whorl opposite the aperture. Not visible in this view are ***B***, minimum diameter ***E***, umbilicus depth and ***F***, umbilicus width.

Multivariate analysis was used to determine whether *P. augusta* could be consistently distinguished from its closest phylogenetic and spatial neighbours on quantifiable shell shape characters, in addition to its unique shell banding and colour pattern. Relationships between individuals were examined with principal components analysis (PCA) of the log-transformed variables. The log transformation was performed to minimise deviations from normality and distortion effects caused by allometric relationships of the raw variables, and to find shape components that were independent of size effects. After preliminary PCA analysis indicated substantial amounts of variation still related to size, a new set of variables was created that expressed each measure as proportions of maximum diameter (Table 2), to identify similarities and differences between the taxa that related to shape alone and not to size. Comparisons of these new variables between the taxa were made using the Tukey Test (Zar, 1996).

Results

The banding-pattern, colour and size displayed in *P. augusta* shells forms a combination unique to that species. *P. augusta* is always distinguishable from its near geographic neighbour *P. patrickensis* by the consistent presence of narrow red spiral lines on the former, underlying any axial banding (Figure 4). While *P. patrickensis* occasionally has sculpturing on the dorsal surface that might be mistaken for spiral lines, it never has spiral lines. Several subspecies of *P. lignaria* have red spiral lines, but they are always distinguishable from those on *P. augusta* by their variable width, colour and much greater prominence (*P. l. johnstoni* (Fig 4) and *P. l. rotella* (Powell 1938)), or by the additional presence of dominant, strong and very regular axial bands (*P. l. oconnori* (Powell 1938)); always on much larger and heavier shells.

PCA found that while there was some overlap in shape of *P. augusta* and *P. patrickensis*, shape on its own was also diagnostic (Figure 5). The shell shape principal component 1, which accounted for 72% of the total variance, was primarily a reflection of descent in the last whorl, and to a lesser extent umbilicus depth and width; these were both expressions of differences in the extent of the descent in the last whorl. The second principal component incorporated 16.7% of the remaining variation and was largely an expression of descent in the last whorl, with spire height and aperture height of secondary importance.

Shell minimum and maximum diameter, and height were all significantly greater in *P. l. johnstoni* than in *P. augusta* or *P. patrickensis* (Table 1). Once size differences had been removed and only ratios used, *P. augusta* still had a significantly greater descent in the last whorl, wider aperture, wider and shallower umbilicus and proportionally lower spire than its closest phylogenetic relative *P. l johnstoni*. It also had a significantly greater descent in the last whorl, wider umbilicus, narrower aperture and proportionally smaller-diameter whorl profile than the similarly-sized but genetically distant *P. patrickensis* (Table 2, Figure 2).

While this morphometric analysis shows the taxa can be distinguished by shell shape measurement, they are easy to separate without resorting to measurement.

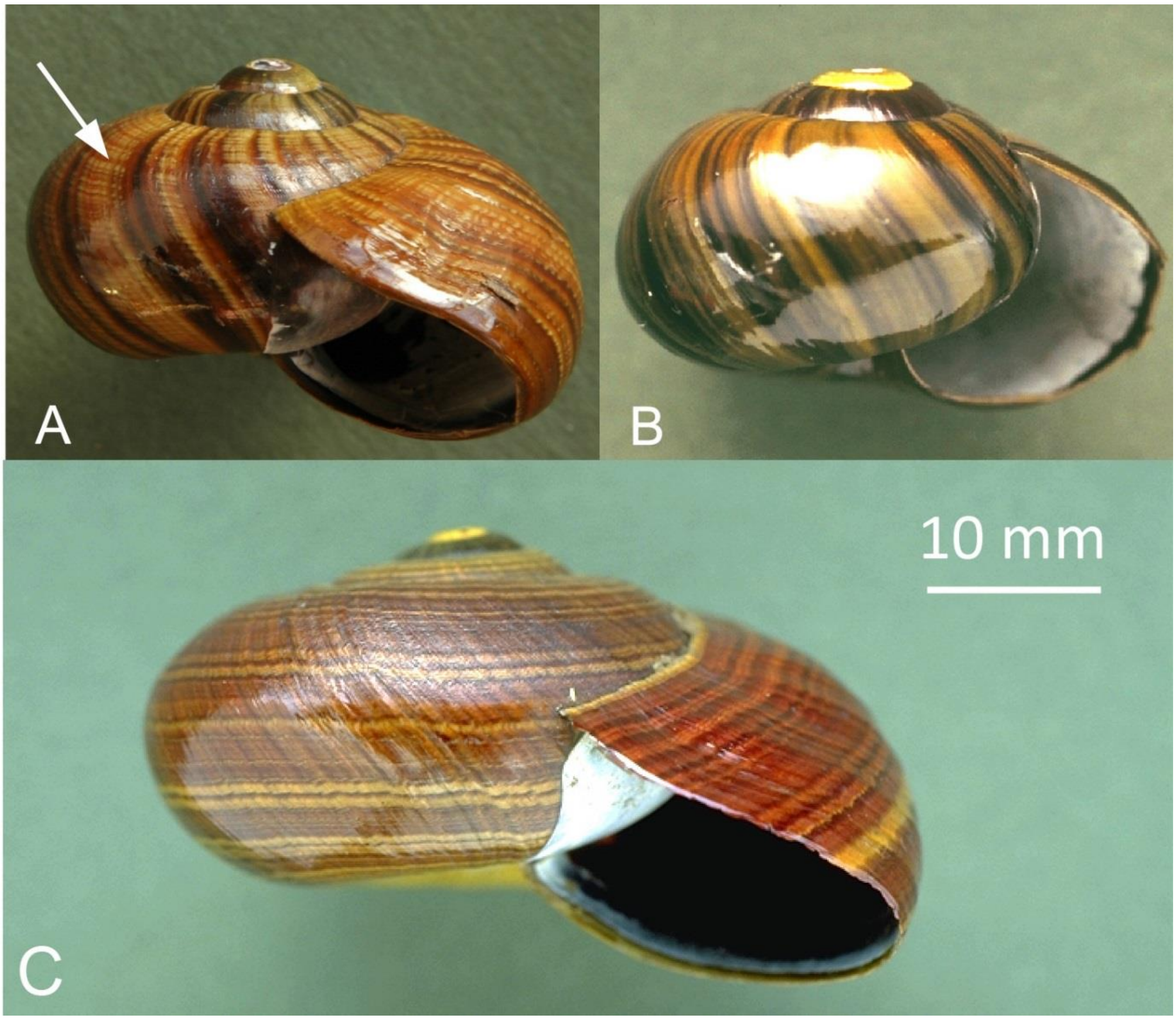


Figure 4. Banding pattern differences between ***A***, *Powelliphanta augusta* n. sp. ***B***, *Powelliphanta patrickensis* ***C***, *Powelliphanta lignaria johnstoni*. Arrow on *P. augusta* shell indicates the diagnostic narrow red spiral lines which underlie more conspicuous dark radial bands. Spiral lines are absent in the similarly-sized *P. patrickensis* and are present but much more dominant and abundant in *P. l. johnstoni*. All *P. lignaria* snails, including the illustrated *P. l. johnstoni*, have much larger and heavier shells than *P. augusta.*

Systematics

Family Rhytididae Pilsbry, 1893

Genus *Powelliphanta* O'Connor, 1945

Powelliphanta O'Connor, 1945: 55 (erected as a subgenus of *Paryphanta* Albers, 1850).

Type species: *Helix hochstetteri* Pfeiffer, 1862 by original designation.

Table 1 Morphometric shell variation in *Powelliphanta* (all measures in mm).

	P. augusta					*P. lignaria johnstoni*				*P. patrickensis*			
	NMNZ 277582	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
Maximum diameter	37.97	37.9	34.0	44.3	2.8	52.3	47.5	55.8	2	36.4	32.5	43.6	2.2
Minimum diameter	31.84	31.0	27.6	36.1	2.2	42.9	38.6	46.0	1.6	29.1	27.0	36.9	1.8
Height + last whorl	25.08	22.9	20.5	27.8	2.0	30.4	25.8	33.6	1.9	21.0	18.1	26.1	1.6
Height – last whorl	18.84	17.7	15.8	20.1	1.0	23.9	21.9	25.5	0.9	17.6	16.1	20.7	0.9
Umbilicus depth	5.8	4.7	3.7	6.5	0.7	7.3	5.5	9.0	0.9	4.4	3.3	5.9	0.7
Umbilicus width	7.69	7.6	6.0	9.9	1.2	9.8	6.5	12.1	1.1	5.8	4.6	7.8	0.7
Spire height	2.96	2.6	2.0	3.0	0.3	3.9	3.1	5.0	0.5	2.3	1.6	3.1	0.3
Aperture drop	9.32	7.3	2.7	11.9	2.3	7.6	3.6	12.2	2.0	4.1	2.1	9.4	1.4
Aperture height	15.04	15.5	12.7	18.4	1.3	21.5	18.4	25.0	1.4	15.6	12.2	19.9	1.9
Aperture width	16.33	16.8	8.2	22.4	2.6	21.4	18.6	23.8	1.3	15.9	13.0	19.1	1.6
Last whorl width	15.48	14.7	12.8	17.2	1.0	19.5	16.9	21.0	0.8	14.8	13.7	17.7	0.8
Last whorl depth	9.75	8.7	6.6	11.2	1.2	11.7	9.7	12.8	0.7	8.5	6.5	9.9	0.8

Table 2 Tukey multiple comparisons of differences in morphometric measures between *Powelliphanta lignaria johnstoni* and *P. augusta*, *P. patrickensis* and *P. augusta*, and *P. patrickensis* and *P. l. johnstoni*.

	P. l. johnstoni – P. augusta		*P. patrickensis – P. augusta*		*P. patrickensis – P. l. johnstoni*	
	Difference (mm)	*P*	Difference (mm)	*P*	Difference (mm)	*P*
Maximum diameter (MD)	14.39	<0.001	–1.51	0.037	–15.90	<0.001
Minimum diameter	11.90	<0.001	–1.86	0.001	–13.76	<0.001
Total height incl. last whorl	7.50	<0.001	–1.96	<0.001	–9.46	<0.001
Aperture drop/MD	–0.05	<0.001	–0.08	<0.001	–0.03	0.005
Aperture width/MD	–0.04	0.001	–0.01	0.801	0.03	0.009
Umbilicus depth/MD	0.02	<0.001	–0.00	0.736	–0.02	<0.001
Umbilicus width/MD	–0.01	0.039	–0.04	<0.001	–0.03	<0.001
Spire height/MD	0.00	0.260	–0.01	0.019	–0.01	<0.001
Aperture height/MD	0.00	1.000	0.02	0.196	0.02	0.196
Height without last whorl/height with LW	0.01	0.617	0.07	<0.001	0.06	<0.001
Last whorl width/MD	0.23	0.026	0.22	0.011	0.24	0.017
Last whorl depth/MD	–0.02	0.009	0.02	0.002	0.04	<0.001

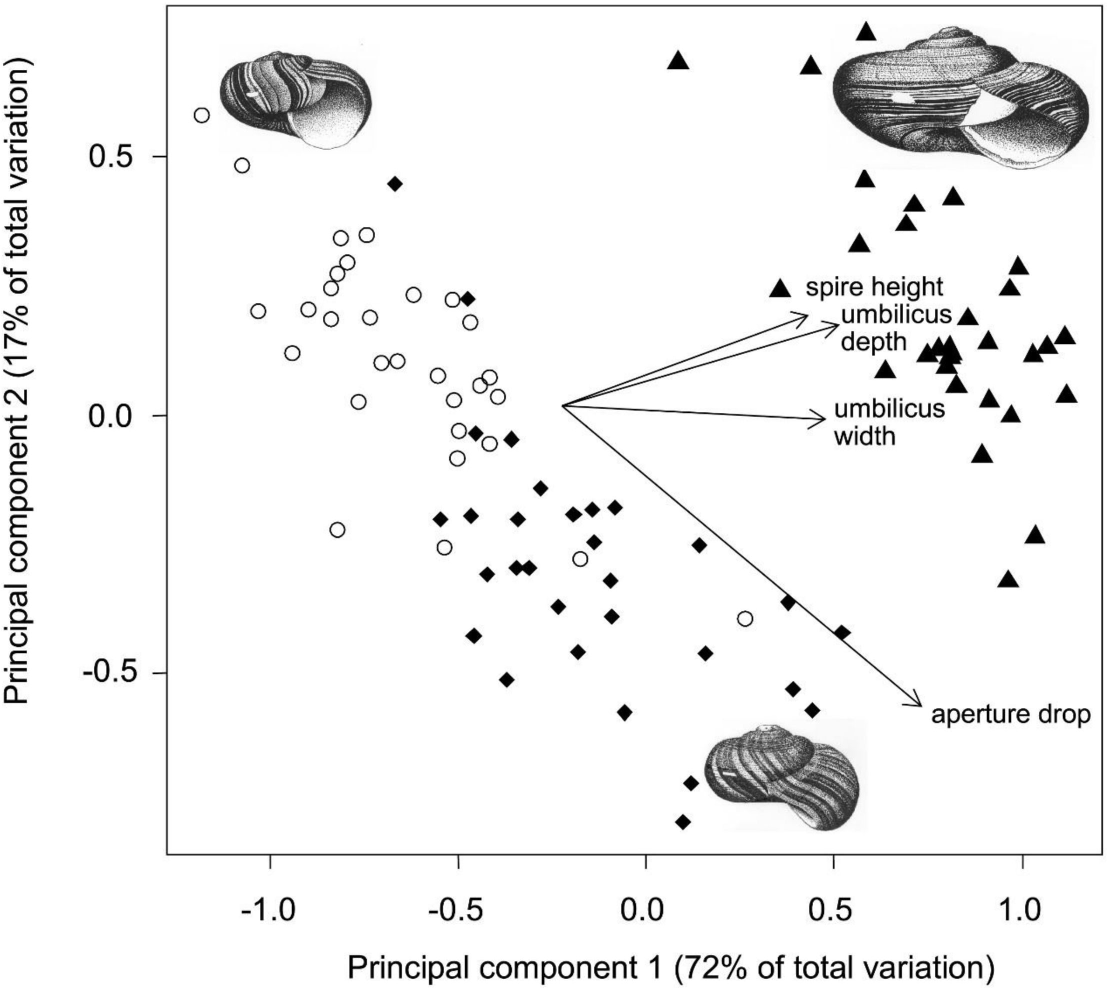


Figure 5. Plot of the first two principal components of the log-transformed shell measures of *Powelliphanta augusta* n. sp. (black diamonds), its phylogenetically closest related lineage *Powelliphanta lignaria johnstoni* (black triangles) and its spatially and ecologically closest neighbour, *Powelliphanta patrickensis* (open circles).

DIAGNOSIS: Land snails, with a shell capable of fully housing the retracted animal. Shells large, moderately to strongly depressed, tightly coiled, with whorl periphery well rounded and wide umbilicus; aperture ovate, the opening without teeth, the margin simple. Shell with reduced calcareous content, but with thick periostracum, usually brightly coloured, often with either spiral or radial lines or zones of alternating and contrasting yellow, brown, red and black hue, ventral surface always glossy and dorsal surface sometimes matt due to sculpture of spirally arranged short wrinkles and crescent-shaped malleations. Genitalia characterised with long, thin penis, dark grey to black due to pigmentation of internal epithelium and connective tissue; with the retractor muscle attached apically, and with the vas deferens bound to the side of the organ by fibrous connective tissue to open more or less distant from the penial apex. Bursa copulatrix a large ovate sac, on a short stout duct. No epiphallus, penial sheath or accessory glands on the genitalia. Secondary ureter enclosed. Carnivorous, with enlarged pharynx accommodating a radula with V-shaped rows of large, sharply-pointed aculeate teeth, protrusible for impalement and capture of earthworms and slugs; radula with or (rarely) without a rachidian tooth, and with 50 to 70 lateral-marginal teeth. Jaw absent.

North, South, Stephens, D'Urville, Arapawa, Maud, Secretary and Resolution Islands, New Zealand.

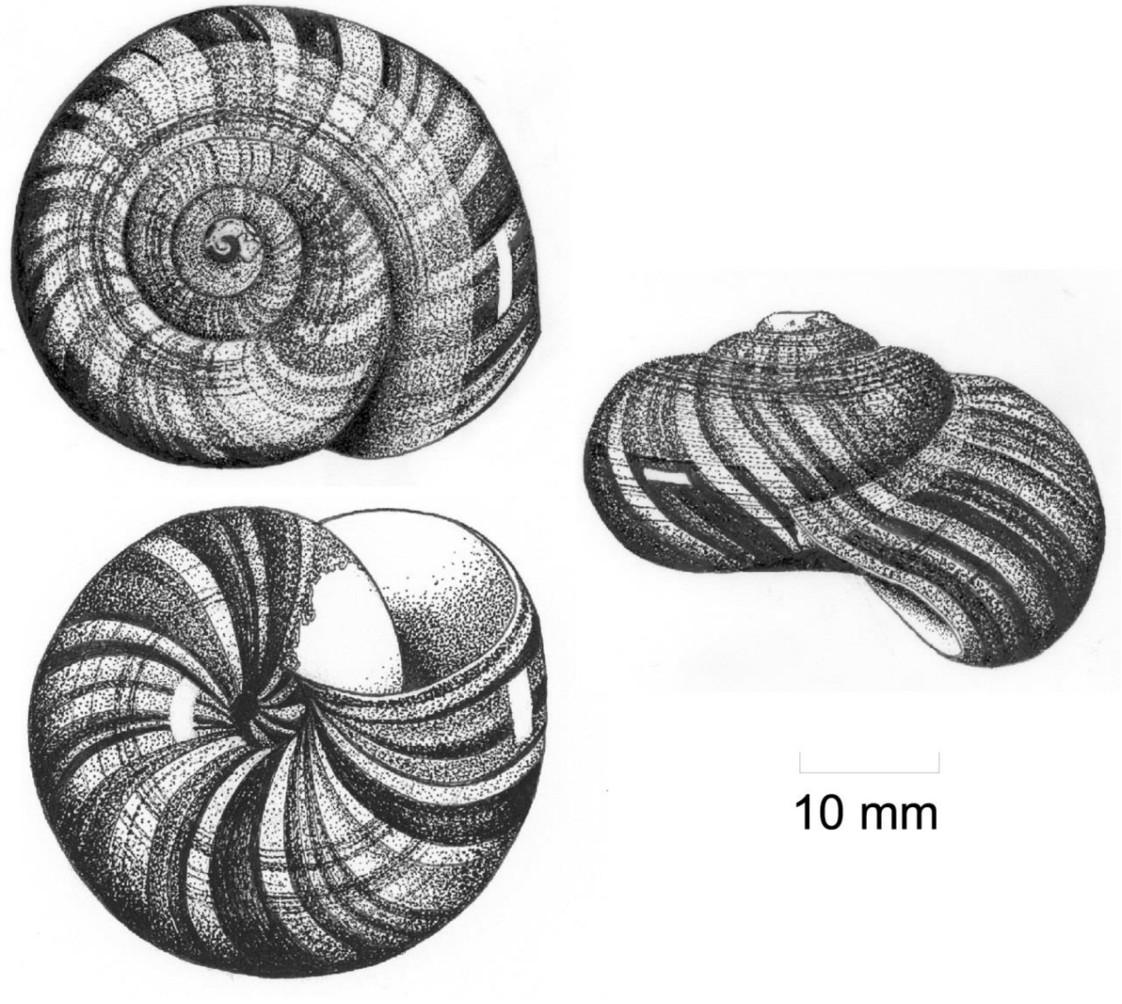


Figure 6. *Powelliphanta augusta* n. sp. holotype (NMNZ M.277582), actual size 38 mm diameter x 25 mm height. Illustration by Cathy Jones.

***Powelliphanta augusta* n.sp.** (Figs 6-7; Table 1)

Powelliphanta "Mt Augustus" Hitchmough et al., 2007: 35.

Powelliphanta "Augustus" Trewick et al. 2008.

HOLOTYPE: NMNZ M.277582, shell (Figure 6) collected on 12 March 2007: type locality; snail-search Area 8c, NNE of north peak of Mt Augustus massif, 955 m elevation, Stockton Plateau, north Westland, New Zealand, L29/E 2414704, N 5947941, in shrubland of low mountain beech (*Nothofagus solandri* var *cliffortioides*) and manuka (*Leptospermum scoparium*).

PARATYPES: 21 in total, all from north peak of the Augustus massif: NMNZ M.277583 (4 shells) and AI&M AK73318 (2 shells) from L29/2414630-5947675 to 2414650-5947570 in snail-search Areas 3a, 10d & 10c under litter in low mountain beech and leatherwood (*Olearia colensoi*) scrub, and under prostrate manuka and wire rush (*Empodisma minus*) on western escarpment, 950 m elevation; NMNZ M.277584 (4 shells, and 3 dissected reproductive tracts) and AI&M AK73319 (2 shells) from L29/ 2414580-5947760 in snail-search Areas 5a, 5b, 6d & 6c under flax (*Phormium cookianum*) and low manuka and wire rush on flat ridge top with scattered small tarns just east of western escarpment, 980 m elevation; NMNZ M.277585 (4 shells) and AI&M AK73320 (2 shells) from L29/2414610-5947940 to 2414800-5947800 in snail-search Areas 4c & 8 under low manuka on gentle slopes east of the ridgeline, 945-955 m elevation.

DIAGNOSIS: *Powelliphanta augusta* can be distinguished from all other *Powelliphanta* by the presence of underlying narrow red spiral lines over the entire shell (most clearly seen on the shell’s dorsal surface) on a small shell (adult size ≤44 mm) which in old age has a rapidly descending last whorl.

The diagnostic red spiral lines on *P. augusta* shells has some similarity to that on *P. l. johnstoni*, *P. l. rotella* and *P. l. oconnori*. However, the spiral lines on *P. augusta* are weaker, narrower and more regular in width than that on *P. l. johnstoni* and *P. l. rotella*, and there are conspicuous axial bands on *P. augusta* which are entirely absent in *P. l. johnstoni* (Figure 4) and *P. l. rotella*. The spiral lines on *P. augusta* shells are more pronounced and redder that those on the strongly-axially banded *P. l. oconnori*. The shells of all *P. lignaria* subspecies are significantly larger and heavier than those of *P. augusta*.

P. patrickensis is similar in size to P. *augusta*, but it lacks the diagnostic red spiral lines of *P. augusta*, has a more glossy shell (normally glossy on the dorsal as well as the ventral surface), and a more globose and lower-spired shell.

DESCRIPTION: **Shell** medium to small for genus (maximum diameter 44 mm), subdiscoidal, with elevated but rounded spire, without the spire nearly rectangular in lateral profile, in mature adults a corkscrew-appearance with pronounced descent of the last whorl from the horizontal plane, about 4 to 5 whorls including protoconch of about 1 whorl, rapidly expanding, slightly inflated, bluntly-shouldered. Final suture impressed; keeled ridge above suture in last whorl. Umbilicus comparatively wide, about 0.2 of maximum diameter, but shallow, revealing only the previous whorl. Shell only weakly calcareous, thin, but with strong, flexible periostracum. From protoconch to periphery, shell microscopically sculptured with close spiral striae, giving the upper surface a matt appearance. Ventral surface glossy and smooth. Aperture elongated oval, with smooth thin edge; parietal callus smooth when viewed macroscopically and pale greyish-white.

Shell ground colour old-gold (Ridgeway 1912, Pl. 16), with narrow reddish-brown spiral lines always present over the whole shell, faint and sparse below the periphery, but much more conspicuous on dorsal surface. Spiral lines overlain by broad, irregular, mahogany-red (Ridgeway 1912, Pl. 2) axial streaks, occasionally so comprehensive above the periphery as to appear a diffuse wash over the entire dorsal surface. Below the periphery, the axial streaks are more dominant and are alternately warm brown shades (mars brown Pl. 15, chestnut Pl. 2; Ridgeway 1912) and old gold (Figure 7).

Figure 7 (next page). *Powelliphanta augusta* n. sp. shells and live animal ***A***, some of the first recorded shells (36-38 mm diameter) found, collected by Botanical Society in 1996 from the north-east flanks of Mt Augustus showing the characteristics of the "southern" morph of the species. ***B***, profile and dorsal view of an old adult (37 mm diameter) "southern" morph snail found alive on the south-eastern flanks of Mt Augustus (Mining Block A11b). ***C***, large (43 mm diameter) old adult "southern" morph snail collected from the ridgeline just west of Mt Augustus (Mining Block A12) and now held in captivity. Note erosion pits on the shell apex, the rapidly descending last whorl, and the fleshy pink colour of the foot between widely-spaced reticulated dark-pigmentation. ***D***, "northern" morph snail shells from all parts of the north peak of the Mt Augustus ridgeline (Mining Blocks A10 and A14). Note the stronger axial banding and overall redder shell colour of the "northern" morph (largest shell 38 mm diameter).


A
B
C
D

Considerable variability in shell colour and banding and in overall size between individuals (Figure 7d). Notably smaller and darker shells on snails just north of the north peak of the Augustus massif, with the mahogany red axial streaks tending to be replaced by alternate black, chestnut, antique brown (Ridgeway 1912, Pl. 3) and old gold axial bands. Snails just south-west of the north peak are larger and lighter coloured than those further north. Snails on Mt Augustus itself ("southern" morph) have only sparse mars brown axial bands, narrow reddish-brown spiral lines, and occasionally a small circular zone of plain yellow around the umbilicus, free of spiral lines (Figure 7a-c)

Animal: Foot fleshy-pink to light grey (Ridgeway 1912, pallid purplish gray Pl. 53) with dark slate grey (Ridgeway 1912, Pl. 53) pigmentation forming regular but widely spaced reticulation (Fig. 7c). Mantle usually pale and mucus clear, but particularly in juveniles the mantle and mucus are sometimes a deep inky blue colour. Short wide tail protruding only a little behind the shell when the animal is active.

REMARKS: Dentition and reproductive anatomy have not previously been used to separate species within *Powelliphanta*, and these characters also proved taxonomically uninformative in separating *P. augusta* from its closest relative, *P. lignaria* (Appendix A).

Powell described (1930, 1932, 1946) and illustrated (1930) the radula of various *Powelliphanta* based on light microscopy. While no information was presented on variation among individuals, Powell's descriptions indicate taxon differences to be subtle and to involve primarily the relative size of the rachidian tooth and numbers of the transverse rows. In this study we found the radula of the very large snails *P. h. anatokiensis* and *P. s superba* could only be distinguished from that of the smaller snails *P. augustus*, *P. patrickensis*, *P. gilliesi*, and *P. lignaria* by the number of teeth in the transverse rows, which is consistent with scaling of the width of the radula with animal size.

The anatomy of the type species for the genus, *P. h. hochstetteri* (Pfeiffer, 1862) is known from the published works of Godwin-Austen (1893), Collinge (1901), Beutler (1901), Powell (1930, 1979), and Schileyko (2000). Our dissection of the subspecies, *P. h. anatokiensis* (not illustrated) generally confirmed these earlier descriptions of the type species. Our dissections of a limited number of individuals from several other species of *Powelliphanta* (not illustrated) found that, in addition to variation among species in size of the genitalia that scale with animal size, there were a few further differences. *P. h. anatokiensis* and *P. s. superba* could be distinguished anatomically from *P. l. lignaria* by possession of a longer vagina, and a longer penis in which the proximal region is lined with scale-like, uniformed-size and distally-oriented papillae, as opposed to upright papillae decreasing in size toward the junction of proximal and distal penis sections. *P. h. anatokiensis* was distinguishable from both *P. s. superba* and *P. l. lignaria* in that the length of the proximal caecum above the entry to the vas deferens was considerably longer. *P. patrickensis* and *P. g. aurea* were very similar in genitalia to *P. l. lignaria*, differing primarily in a slightly longer vagina and slightly shorter penis (relative to the female genitalia) and more strongly developed vas deferens in its proximal sections in the former, and the vas deferens opening closer to the penial apex in the latter. Vaginal length, penis length and degree of dilation of the vas deferens in *P. augusta* varied slightly to that of *P. lignaria,* but these genital differences on their own would not be sufficient to differentiate the taxa.

If these subtle differences in reproductive anatomy are due to more than stage of maturity/activity and preservation artifacts (this is likely, but confirmation requires a much larger sample of dissected animals), then the existing *Powelliphanta* taxonomy based on shell morphology (Powell 1979, Walker 2003) and molecular genetics (Walker 2003, Trewick et al 2008) is generally mirrored by reproductive anatomy (this study). Using genitalia the species *P. hochstetteri*, *P. superba* and *P. lignaria* were distinguishable, and the close relationship of *P. lignaria* and *P. augusta* was supported. On anatomical grounds the closest relative of *P. augusta* was *P. l. lignaria,* but they were not identical. In contrast, the subspecies of *P. lignaria* appeared to have identical genitalia (with *P. l. johnstoni* indistinguishable from *P. l. lignaria* in this study).

The differences in reproductive anatomy appear less marked than those in shell, animal external morphology, allozymes and mtDNA. Minimal differences were found between the genitalia of *P. g. aurea* and *P. lignaria, P. augusta* and *P. patrickensis*, or between *P. s. superba* and *P. h. anatokiensis,* yet these taxa have discrete and distinctive shell morphologies, and the latter pair occur in sympatry with no evidence of interbreeding.

They also differ substantially genetically: between *P. g. aurea* and *P. lignaria* there are fixed-differences at 6 allozyme loci, and mtDNA sequences differ by 11.8%; between *P. augusta* and *P. patrickensis* mean mtDNA sequence divergence is 7.7%; between *P. s. superba* and *P. h. anatokiensis* there are fixed-differences at 7 allozyme loci, and mtDNA sequences differ by 9.2% divergence (K. Walker unpubl. data; Trewick et al. 2008).

Given the level of genetic and conchological differentiation, the absence of substantial genital differentiation within *Powelliphanta* perhaps indicates uncoupling of, or different rates of evolution in these characters, as has been noted in other molluscan studies (Chiba 1999, Giokas et al. 2006, Alonso et al. 2006). It has been hypothesised (Giorkas et al. 2006, Thomaz et al. 1996) that both the hermaphrodite reproductive system of many land snails and the spatial structure of their populations (small, isolated, sedentary, "stepping stones") means there may be little pressure to develop strong sexual isolating mechanisms. In *Powelliphanta* genital morphology appears to be conserved and is therefore not informative about reproductive isolation.

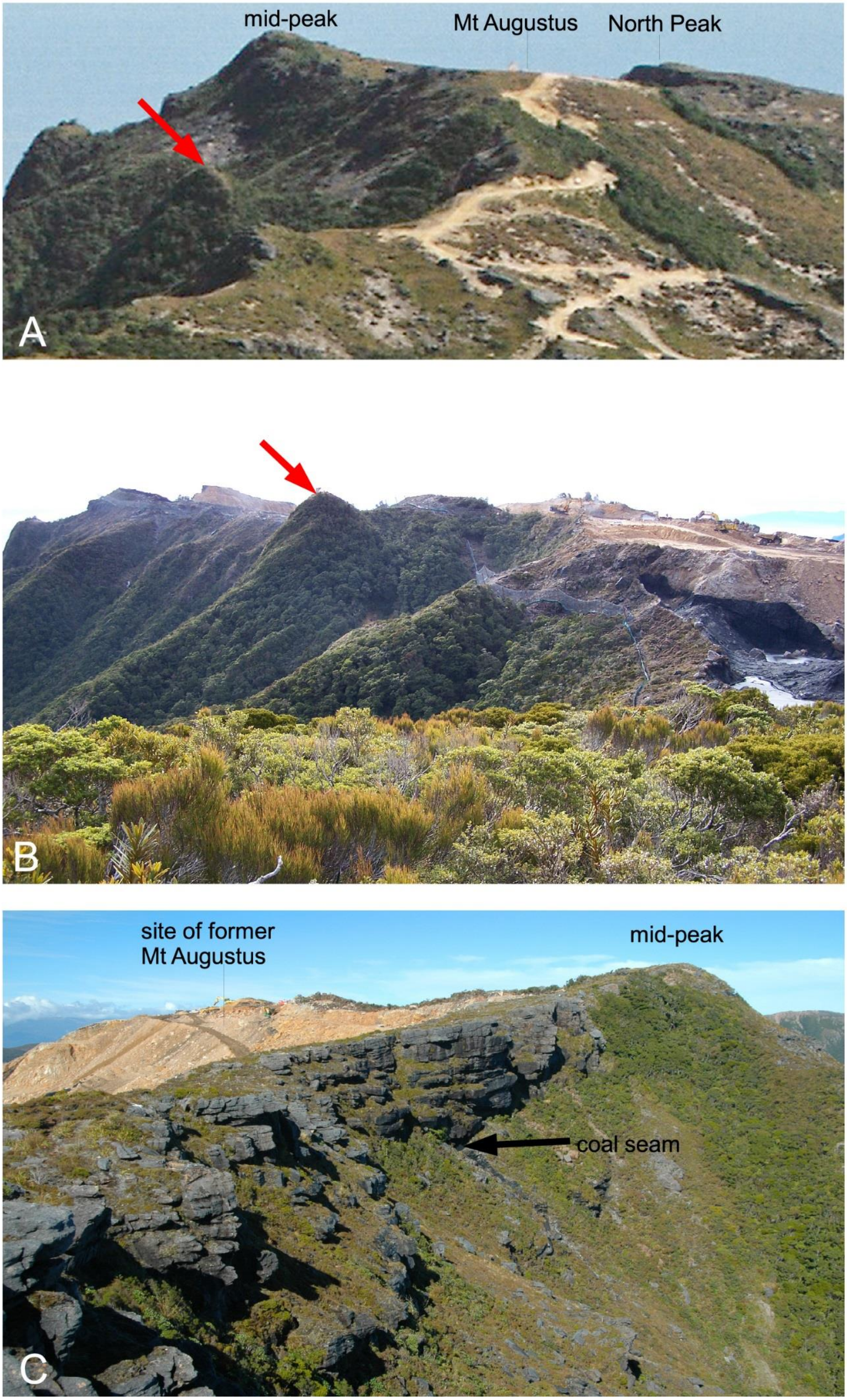
ETYMOLOGY: The species epithet *augusta* is a reference to the Mount Augustus massif, the site this species was apparently naturally confined to. The feminine form, august*a* was selected for use in conjunction with the feminine genus name Powelliphant*a*. From the Latin adjective *augustus* or French *auguste* meaning "consecrated, venerable", "Augustus" has come to mean "inspiring reverence and admiration, eminent, dignified" (Brown 1993), which seems apt as a memorial for both the mountain and the snail, since the mountain and snail habitat have now been destroyed by mining.

DISTRIBUTION: Whilst most of the land *P. augusta* formerly occupied has now gone, its distribution was studied in some detail just after the taxon was recognised (2004-05) but before the remaining ridgeline was removed by mining in 2006-07. *P. augusta* was most common at high altitude (940 – 980 m asl) on the north peak of the Augustus massif. It also occurred at the same altitudes at the south end of the massif on the ridge just north-west of Mt Augustus, and on the slopes south-east of it. The summit of Mt Augustus and all the north-eastern faces had been destroyed by 2004, but as there were snails on its remaining flanks, they probably also formerly occurred on the summit itself at 1011 m.

The 3 high peaks which together formed the Augustus massif lay on the western escarpment of the Stockton Plateau, and towered on cliffs above the headwaters of Worley Stream and Kerr Stream (Figures 1 & 8). Except for a narrow ridgeline about 10-15 m wide and the north peak, all the land east of the ridge had been mined before the snail surveys began, so it is unclear to what extent the snail populations on Mt Augustus and on the north peak were formerly connected. There was an apparent gap in distribution at and just north of mid-peak (L29/2414620-5947470 to 2414630-5947330), and snails were sparse on the ridgeline either side of this gap. However, the shells found in 1995 by the Botanical Society came from about this latitude but on the eastern side of the ridge, so the two populations may have been continuous on the eastern side but not the west.

On the long ridgeline which forms the western escarpment, snails occurred only on the highest protruding rocky portion here described as the Augustus massif. Snails were absent north of L29/2414685-5948150 and south of about L29/2414885-5947120 where the altitude dropped and the nature of the landform and vegetation changed. To the west, snail densities dropped off sharply with decreasing altitude, with snails absent below about 900 m. To the east, at north peak snails were still present in high numbers up to the point where the unmodified land met the mined land, at about 940 m. Old pre-mining photos show a topography and vegetation on the rest of the eastern side of the massif similar to snail habitat at north peak. It therefore seems probable that the eastern side of the ridgeline formerly provided much of the species' habitat, particularly as the comparatively gentle slopes meant much more land lay above 900 m than on the steep western slopes.

Figure 8 (next page). Location of *Powelliphanta augusta* n. sp. habitat. ***A***, the south-end of the Augustus massif in 1994 when damage to Mt Augustus had just begun (photo: Lloyd Homer, GNS Science). ***B***, the south end of the Augustus massif in 2007 when much of the massif had been removed to access the coal seam visible in the right middle-distance (photo: Pete Lusk). The amount of snail habitat removed can be seen by lining up the distinctive knob (arrowed) in both A & B. The fence line in the middle-distance indicates what the final height of the ridge will be once habitat-stripping is completed. ***C***, the western escarpment of the Augustus massif in 2006, looking south-east from north peak to the stump of Mt Augustus. Snails lived in the runnels of vegetation down and just below the cliffs. The entire escarpment is being removed to access the, just visible, seam of coal.


mid-peak
Mt Augustus
North Peak
A
B
site of former Mt Augustus
mid-peak
coal seam
C


A
B
C
D

Figure 9 (previous page). Habitat types of *Powelliphanta augusta* n. sp. on north peak in 2004-05 ***A***, flax, manuka and inaka shrubland on the edge of low mountain beech and southern rata forest on the north-eastern slopes, with overburden piles in the Stockton open cast coal mine in the middle-distance and the Glasgow Range on the far horizon. ***B***, rush-tussockland with flax, *inaka* and scattered emergent manuka amidst small tarns on the summit ***C***, shrubby ecotone between the mountain beech and rata forest and clearings of wire-rush and tussock on the northern slopes ***D***, mixed shrubland on the western slopes. The tall forest on the steep land just below the snail colony (right of picture) does not support snails. Westport is just visible at the left-hand end of the coastal flats below.

Since the Augustus massif was mined, the species' natural range has shrunk to a sliver of land (~ 1 ha) below the western escarpment under north peak. Salvaged snails have been artificially transferred to three other sites: to the ridgeline 500-1000 m north of the Augustus massif between L29/2414615-5948190 and 2414580-5948840; to the summit of Mt Rochfort at K29/053-357; and to a small basin just south-west of Mt Rochfort at K29/045-355, about 16 km from the Augustus massif.

HABITAT: Preferred habitat of *P. augusta* was moist soil under dense knee-high vegetation which maintained high levels of ground humidity and supplied comparatively abundant litter material, on and above the outcrops of sandstone forming the Augustus massif. The snails lived only on the highest peaks in an altitudinally demarcated cool microclimate with persistent cloud, and frequent rain and fog.

Powelliphanta augusta lived under the litter in all parts of a mosaic of vegetation types just at and above the tree line, though snail density was very patchy. Field workers searching and retrieving snails before the ridgeline was destroyed reported that plant diversity was a good indication of snail density, with more snails found in complex than in simple vegetation communities. They appeared to prefer the ecotones between subalpine forest and shrubland and between shrubland and low rush-tussockland more than large expanses of either community on its own (Figure 9). The dominant species of the shrubland were manuka, leatherwood, tussock (*Chionochloa flavescens*, *C. rubra*), mountain flax, *Astelia fragans*, *Dracophyllum uniflorum*, *Pseudopanax lineare* and *Gahnia procera*. The rush-tussockland largely comprised wire rush, *Chionochloa juncea*, *Celmisia dubia* and manuka, either prostrate or emergent. The forest comprised variable amounts of low stunted mountain beech, pink pine (*Halocarpus biformis*), southern rata (*Metrosideros umbellata*), *Dracophyllum longifolium*, and leatherwood.

Plant species diversity over the whole snail colony was significantly higher (*P*=<0.001) than on nearby land without snails just north of the Augustus massif, with a mean 28 species (SD=5.611) per 100m^2 plot within the snail colony compared to 18 (SD=5.059) species per plot just outside it (Bartlett 2006; Walker 2006).

The substrate in the snail colony was hard gritty quartz-rich sandstone with a mean soil pH of 4.3 (SD=0.199), mean C/N ratio of 27.1, and mean levels of exchangeable calcium of 2.0 me/100 g (SD=3.264), magnesium 2.7 me/100 g (SD=2.658) and potassium 0.5 me/100 g (SD=0.351) (Bartlett 2006; Gruner & Bartlett unpubl. data). While the soils in *P. augusta* habitat were thus acidic, they were significantly more alkaline (*P*=0.021) and had a lower C/N ratio (P=<0.001) than the soils outside the snail's range just north of the Augustus massif, where mean pH is 4.1 (SD = 0.145) and mean C/N is 43.3 (SD=4.892). Just beyond the snail's range exchangeable calcium was lower, but not significantly so (1.8 me/100 g; SD=1.420, *P*=0.788), whilst magnesium and potassium levels were similar inside and just outside the snails' range (Bartlett 2006; Gruner & Bartlett unpubl. data).

Long-term mean rainfall recorded at Downertown on the Stockton Plateau, 1.5 km east of the Mt Augustus snail colony is 6.116 m per year with little seasonality (Anderson 2006). As there are strong rainfall gradients (6 mm per m asl) in this region (Anderson 2006), it is estimated rainfall in the snail colony, 100-200 m above the Downertown Station, was 6.716-7.316 m per year. Even within the snail colony a strong rainfall gradient existed, with about a metre more rain per annum on the top of north peak where most snails lived than just below the western escarpment where snail habitation ceased (Walker 2006). The steep rainfall gradient occurred as the predominant, moisture-laden westerly winds coming off the Tasman Sea were forced up and over the Augustus massif. These physical conditions also caused regular and persistent cloud formation over the Augustus massif, even in otherwise dry sunny weather when lower parts of the ridgeline north and south of the massif were still clear.

The mean daily air temperature at 900 m just below the main snail colony was about 3ºC in the winter months (Jun-Aug) and 11-13ºC in summer (Jan-Mar). Temperatures would have been 1ºC colder at 1000 m at the top of the snail colony, so most of the snails lived in slightly colder temperatures than those at 900 m at the ambient weather station shown in Table 3. For about 3 months of the year, exposed parts of the ground were frequently frozen with frost or, less commonly, snow.

LIFE HISTORY: *Powelliphanta augusta* is evidently normally an out-crossing hermaphrodite, but individuals kept separately in captivity have laid eggs from either stored sperm or self-fertilisation. The fertility of these eggs is as yet unknown. In captivity, breeding *P. augusta* laid on average 2-3 hard-shelled eggs in spring, mostly between late September and October, though some eggs were laid throughout the spring and summer from August to March. Five eggs laid in late October/early December 2005 by snails which had mated shortly after being taken into captivity hatched in December 2006 and January 2007 (i.e. after 12-15 months incubation). Mean size of eggs laid in the wild on north peak was 8.02 (6.99-8.58) x 6.76 (5.50-7.48) mm (*n* = 40) (Department of Conservation, unpubl. data). Snails were sexually mature at about 36 mm shell diameter, but productivity seemed to decline in older animals, with more snails in the 36-39 mm shell-size range laying eggs than those over 40 mm. Growth rates and longevity in the wild are unknown, but as *P. augusta* eggs in captivity took about 12-15 months to hatch, compared to 2-6 months for lowland species of *Powelliphanta* in captivity (KJW, pers. obs.), *P. augusta* snails may grow more slowly and live longer than their lowland relatives.

Table 3 Air temperature, humidity and rainfall recorded under the western escarpment at the bottom of the snail colony on north peak during the 6 months from July 2006 to February 2007 before the Augustus massif was removed.

Month (2006/07)	No. of days	Rainfall (mm)	Mean monthly humidity(%)	Monthly extremes in temp.(Cº)	Mean daily min air temp (Cº)	Mean daily max air temp(Cº)	Mean daily air temp(Cº)
Jul 06	23	76.2	80	-1.4 - 12.1	2.0	5.7	3.8
Aug	31	137.2	90	-2.7 – 8.5	1.6	5.3	3.2
Sept	30	230.4	93	-0.3 – 11.3	3.9	7.6	5.7
Oct	31	256.2	90	¯2.1 – 12.9	3.3	7.9	5.5
Nov	30	445.8	95	¯0.7 – 13.1	4.1	9.1	6.6
Dec	31	205.4	89	1.4 – 14	4.9	10.0	7.2
Jan 07	31	372.2	94	5.4 – 17.7	9.0	12.7	10.8
Feb	24	165.0	87	7.9 – 20.5	10.8	15.3	12.8

Prey items seen being eaten in the wild were unidentified species of native earthworm. In captivity snails grew on a diet of exotic earthworms, particularly the pasture worms *Lumbricus rubellus* and *Aporrectodea caliginosa* and the compost worm *Eisenia andrei.* In the wild snails were most active in late spring (October/November); during winter months (June-August) when the ground was frozen, snails apparently retreated up to 5 cm underground and buried themselves in litter and soil in crevices formed by large rocks, or in the bases of *Gahnia* or tussocks, and moved very little. Surface activity was greatest on comparatively warm wet nights after a dry spell.

Invariably by the time adults were “middle-aged”, the periostracum had worn from the apex of their shell, and the conchin was pitted (Figure 7c). In “old age” the erosion was sometimes so extensive that small holes formed right through the shell. While these pits and holes are probably a consequence of reduced shell density from the low-calcium environment the snails were living in, such erosion was almost never found in *Powelliphanta patrickensis*, which similarly has a thin fragile shell and lives in equally or even lower calcium-environments on the Stockton-Denniston coal plateau.

Powelliphanta augusta on the Augustus massif were preyed on by the native weka (*Gallirallus australis*), and also by introduced possums (*Trichosurus vulpecula*), ship rats (*Rattus rattus*) and song-thrushes (*Turdus philomelos clarkei*). However, rates of predation were comparatively low: in a sample of 883 fresh shells collected in 2006 from north peak, 72% were intact and these snails probably died of natural causes. Of the rest, 7% had been killed by weka, 10% had been crushed, presumably by people during the preliminary mining activities, and only 11% had been preyed on by exotic pests (5% by possums, 3% by thrushes and 3% by rats).

Discussion

This study found that, using easily visible characters, the large land-snail here described as *Powelliphanta augusta* is distinct from all other *Powelliphanta*, with a unique combination of shell-banding pattern, colour, size and shape. A more detailed comparison of shell shape in *P. augusta* and its closest phylogenetic neighbour (*P.*

lignaria) and geographic neighbour (*P. patrickensis*) found simple measures of shape alone were sufficient to separate most individuals from these adjacent species.

Shell form can be influenced by environmental selection or by the vagaries of population establishment and genetic drift (Goodfriend 1986, Thomaz et al. 1996, Davison 2002) so caution is required in erecting new snail taxa on the basis of shell morphology alone. An independent, but complementary study using COI mtDNA sequence data supports recognition of *P. augusta* as a monophyletic lineage (Trewick et al. 2008). That study found *P. augusta* differed from *P. lignaria* (its closest extant relative) by an average genetic distance of 3.6%. This is consistent with, though towards the low end of the range of species-level differences observed in molluscs and indicates a comparatively recent separation. If an accelerated sequence evolution rate of 5%/my is applied (fast rates of mtDNA evolution have been inferred in some pulmonates; Chiba 1999), *P. augusta* may have diverged from *P. lignaria* about 700,000 years ago. More conventional calibration rates of change for molluscan COI (ranging from 0.7 – 2.4%/my; Hellberg & Vacquier 1999; Marko 2002), imply divergence occurred about 1.5 million years ago, but also within the Pleistocene. The restricted distribution to a single mountain range suggests that *P. augusta* evolved in this region: regional speciation with subsequent local persistence seems to be typical for this genus. The phylogenetic sister relationship of *P. augusta* with *P. lignaria,* rather than with *P. patrickensis*, the closest neighbour geographically and ecologically, suggests independent occupation of the Denniston-Stockton Plateau by *P. augusta* and *P. patrickensis*.

With both shell characters and DNA sequences indicating *P. augusta* is more closely related to *P. lignaria* than to other *Powelliphanta*, why should this taxon not be regarded as a highly distinctive subspecies of *P. lignaria* rather than as a distinct species? Firstly, the level of sequence divergence between these two taxa is, at 3.6%, within the range of genetic distances between other pairs of well-differentiated land-snail species. The genetic distance between long-established *Powelliphanta* species ranges from 1.9% between P. *hochstetteri* and *P. traversi* to 13.7% between *P. lignaria* and *P. traversi* (Trewick et al. 2008); the New Zealand rhytidid species *Amborhytida forsythia* and *A. duplicata* differ by 4.6% (Spencer et al. 2005); and species in the Hawaiian subfamily Achatinellinae have a mean divergence among all species of 5.9%, ranging from 0.9%

between *Partulina semicarinata* and *Partulina variabilis* to 9.7% between *Achatinella lila* and *Partulina redfieldi* (Holland & Hadfield 2004). The Hawaiian land snail *Succinea quadrata* differs from *Succinea konaensis* by only 2.5% (Rundell et al. 2004), and Douris et al. (1998) studying Cretan land snail radiations also report quite low interspecific differences (eg 3.9-4.5% and 2.1-5.1%) for some *Albinaria* species.

Secondly, the differences in shell morphology between *P. augusta* and *P. lignaria* are far more marked than are any of the differences between the existing well-supported subspecies within *P. lignaria*. (Within *P. lignaria* the described subspecies have easily recognisable constant shell morphology within their respective distributional areas and differ in environmental preferences). Whilst a reduction in shell size and thickness in *P. augusta* could reasonably be assumed to be a response to the low pH/low Ca environment of the Stockton coal plateau, other *P. lignaria* subspecies confined to similarly acidic and mineral-depleted environments (ie *P. l. rotella* and *P. l. johnstoni* in wire-rush and yellow-silver pine pakihi bogs) have retained their large and heavy shells. This evidence suggests that *P. augusta* is not simply an extreme ecological variant within the *P. lignaria* lineage.

Powelliphanta augusta seems none-the-less to be a specialist of an unusual niche. It survived within an inhospitably acidic and infertile environment by exploitation of the one part which was slightly but significantly more fertile, less acidic, wetter, and with more continuous and extensive pockets of deeper-soil than the surrounding landscape. Probably as a consequence of these characteristics, the flora of the snail habitat was also significantly more diverse than that on land without snails nearby. With so much of the Stockton Plateau including Mt Augustus mined before the snails were discovered, and with the loss of most of the rest of the snail's habitat only a couple of years after this, knowledge of this species' environment, gleaned in the brief interlude between discovery and demise, is irreplaceable. For this reason, and because some of the snails but not their habitat were retained, this environment has been described here at length.

In the absence of other habitat of the same character and quality but lacking competing *P. patrickensis* populations, the best chance for survival of this species in the wild probably lies in the sliver of habitat left under the western escarpment on completion of coal mining. This is low quality habitat on the margins of the former north peak snail colony and is fragmented by the intrusion of barren unsuitable habitat. Further, it may become drier with the removal of the Augustus massif above it as the landform itself appeared in large part responsible for the creation of the local cloud cover which formerly characterised it.

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Appendix A: Anatomy of *Powelliphanta augusta* n. sp.

Reproductive system: (Figures 10, 11) Ovotestis consisting of 3 clusters of claviform lobes, embedded on dorsocolumellar side of the digestive gland. Hermaphrodite duct rather long, for the greater part highly convoluted and modestly distended, but narrowing to its entry to carrefour which has a vesicular seminalis as short bulbous-headed diverticulum. Albumen gland linguiform, varying considerably in size with phase in reproductive activity. Male and female pallial gonoducts fused and thus of spermoviduct condition, rather long, slender; female part with weak transversal folds; prostatic part a ribbon of acini along entire length. Free oviduct rather short. Bursa copulatrix duct short, stout; bursa copulatrix reservoir an oval sac, bound to the spermoviduct by fine connective tissue that extends to the vicinity of the pericardium. Vagina moderately long, with numerous muscle strands connecting the organ with the body wall. Vas deferens proximally convoluted and modestly distended, narrowing distally to run around oviduct-penial junction and extending along penis, bound to side of the latter by fibrous connective tissue, to open below penial apex. In life, the phallus lies across the pharynx, the right tentacular retractor muscle crossing over it at the distal end. Phallus rather long, dark grey to black due to colouration of the luminal epithelium and the underlying connective tissues; proximal part slightly bulbous, internally with the epithelium thrown into numerous, upright conical to scale-like papillae that decrease in size towards distal penis; these papillae are enlarged around the perimeter of a furrow leading a short distance from the opening of the vas deferens toward the penial apex; distal penis more-or-less cylindrical, with the internal epithelium produced as longitudinal folds which are initially weakly papillate and reticulated, but become more-or-less smooth towards genital opening. Atrium very short, essentially a shallow vesicle via which the male and female open more-or-less separately to the body exterior. Genital opening on the right side mid-way between the pneumostome and the base of the right ocular peduncle.

Penial retractor muscle long, arising from diaphragm at posterior of pallial cavity. No spermatophore produced. Seminal material, comprising a multi-layered ovoid mass, evidently deposited directly into bursa copulatrix during mating.

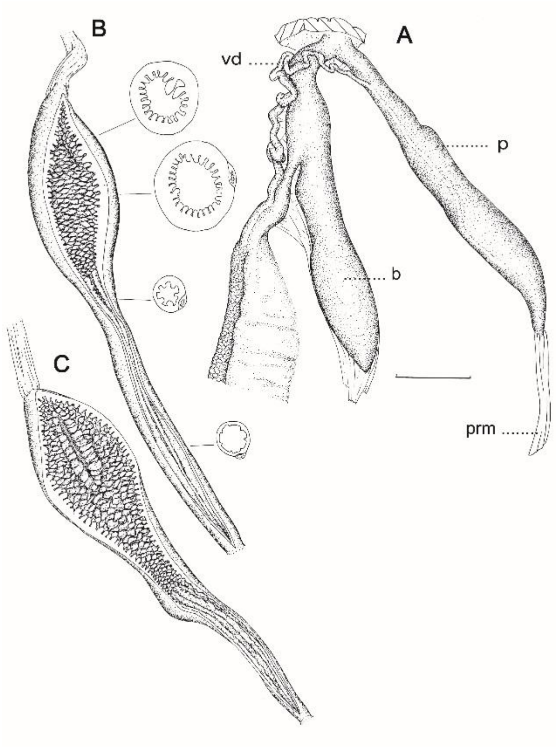


Figure 10. Genitalia of *Powelliphanta augusta* n. sp. ***A***, General view (paratype NMNZ M.277584). Note that the numerous muscle strands that bind the vagina to the right body wall in life are not illustrated. Scale line 5 mm. ***B***, ***C***, (paratype NMNZ M.277584) Penis, opened longitudinally to show internal structure. Note the papillae lining the proximal penis, which are elaborated around the furrow running from the opening of the vas deferens towards the penial apex. b, bursa copulatrix; p, penis; prm, penial retractor muscle; vd, vas deferens.

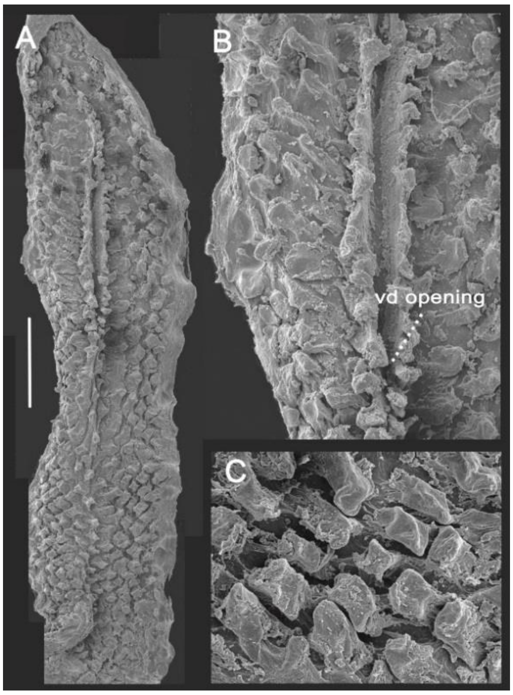


Fig. 11 Scanning electron micrographs of the papillae lining the proximal penis in *Powelliphanta augusta* n. sp., topotype. ***A***, Overview of apical region of the penis, with surface covered in papillae and elaborated around the furrow running from the opening of the vas deferens towards the penial apex. Scale line 1mm. ***B***, ***C***, Close-up views of the furrow and papillae from the general penial wall. vd, vas deferens.

Digestive tract: (Figure 12). Pharynx enlarged, long, cylindrical, occupying almost all the cephalic space, with massive retractor muscles attached to posterior, and weaker retractors attached mid-laterally; radular sac weakly protruding from posterior of pharynx. Oesophagus slender, long, arising from the dorso-anterior aspect of the pharynx, abruptly giving rise to a dilated stomach. Intestine extending in a short anteriorly-directed loop to abut the kidney, then producing a short posteriorly-directed loop before running forwards to anus in mantle collar. Salivary glands flanking the oesophagus, unequal in size with the right gland small.

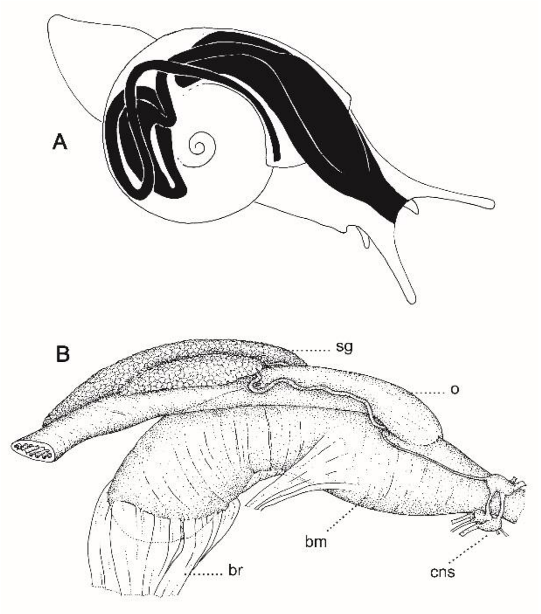


Figure 12. Digestive tract of *Powelliphanta augusta* n. sp. topotype. ***A***, Layout of digestive tract (schematic). ***B***, Right lateral view of the pharynx and associated oesophagus and salivary glands. bm, buccal mass; br, buccal retractor; cns, central nervous system; o, oesophagus; sg, salivary gland.

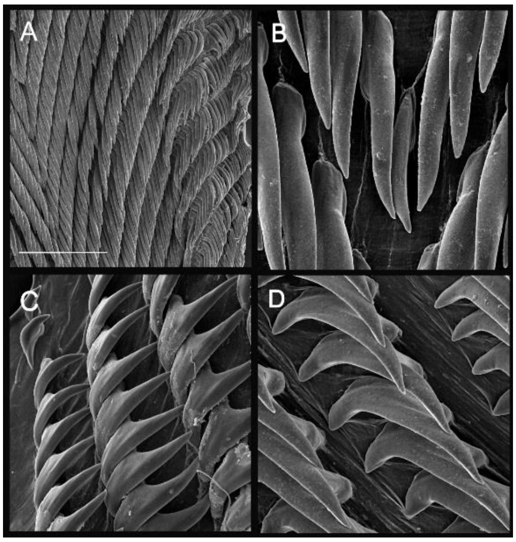


Fig. 13 Scanning electron micrographs of the radular dentition of *Powelliphanta augusta* n. sp. topotype. ***A***, Overview of the radular dentition, showing V-shaped rows of teeth. Scale line 500 µm. ***B-D***, Detail of central tooth and adjacent lateral teeth, marginal teeth, lateral teeth, respectively.

Radula: (Figure 13) with V-shaped transverse rows of unicuspid, sharply-pointed, aculeate teeth, each row with formula 59-60 + 1 + 59-60. The rachididian tooth is about half the size of the lateral teeth. There is no clear differentiation between lateral and marginals, just a simple gradation from elongate lanceolate form to small, more or less triangular form. The teeth increase in size from the centre to a maximum at about tooth 50, then decrease gradually towards the radular margin.

Pallial complex: Pulmonary cavity deep, extending to about 0.5 of the body whorl; venation of the roof modestly developed. Kidney triangular, extending to about 0.25 to 0.3 of pulmonary cavity, with pericardium extending along the greater part of its left wall. Ureter sigmoid, closed to the excretory orifice adjacent to the pneumostome, rather broad in its primary arm along the anterior face of the kidney, more slender in its secondary part along the rectum.

Free muscle system: Columellar muscle extending forwards as a broad fan, attaching to pedal and lateral body walls, and near its origin giving rise to paired tentacular retractors, each of which divides anteriorly into branches to ocular peduncle, inferior tentacle, and cephalic body wall. Right ocular retractor passing across phallus. Buccal retractors originating from columellar stem adjacent to and immediately in front of tentacular muscles, extending anteriorly as a broad ribbon to attachment to posterior and posterior-lateral aspects of the pharynx.

Chapter 6. Synthesis

“*Whoever wants to hold firm rules, should give up taxonomic work. Nature is too disorderly for such a man*” Stresemann (1936)

Image previous page: Morphological variation in *Powelliphanta*.

Synthesis

Summary of Major Findings

In this thesis I have identified genetic and morphological clusters in the genus *Powelliphanta* which in many cases relate closely to already described species and subspecies. I also determined that the sister genus of *Powelliphanta* is not *Victaphanta* as previously suggested but rather the taxon formerly described as *Powelliphanta fiordlandica*, and described a new species of *Powelliphanta*. This thesis constitutes the first genetic study of the genus throughout its range, and the first to define its shell morphology in numeric terms and to include outline shape and external soft body characters in morphometric assessment. The questions posed relate directly to the taxonomic and hence to the evolutionary and conservation status of the many threatened members of the genus.

Taxonomic relationships

The most recent classification of *Powelliphanta* as a two-species ring (Climo 1978) is not supported by either genetic or morphological data and needs to be formally replaced. The suggestion by Parkinson (1979) that *P. fiordlandica* may not be in the right genus proved correct, with the finding of a high level of genetic divergence from the remainder of the genus, and an egg character, shell/body organization, and shell morphology which distinguishes it from all other *Powelliphanta*. The relationship of *Powelliphanta* to *Victaphanta* is distant.

Nuclear and mitochondrial genetic markers identified similar genetic clusters, most of which equated to the species that were described prior to 1972. More predictably, given that those original designations were based on simple morphology, detailed morphometric study largely recovered those same clusters. In addition, tag-named smaller *Powelliphanta* discovered after 1972 and not referable to any described species were found to be genetically and morphologically distinct. The biggest cluster of these form a species complex tag-named “Kawatiri” whose relationships were not well resolved with the techniques and sampling design available.

Biogeography

Powelliphanta had previously been characterized as an ancient group whose ancestors survived along with the tuatara (*Spenodon*), frogs (*Leipelma)* and kakapo (*Strigops habroptilus*) on a proto-New Zealand landmass following the separation of Zealandia from Gondwanaland about 83 million years ago (Stevens et al. 1988). This study did not address deep-time phylogeny so cannot shed light on whether ancestral rhytids survived the Oligocene sinking of Zealandia or arrived by long-range dispersal subsequently. However, it did determine that the diversity seen today in *Powelliphanta* is of much younger origin than popularly thought, though just how much younger is not clear as only coarse estimates from genetic distances were possible. Ironically, given geologists earlier reliance on *Powelliphanta* relationships to estimate timing of Cook Strait land bridges, the estimates made here of *Powelliphanta* divergence rates now depend on (improved) geophysical knowledge of the formation of Cook Strait (Lewis et al. 1994, Trewick & Bland 2012).

In Chapter 2 it was estimated that two major lineages of *Powelliphanta* thought to be present in the late Miocene—northern, “oblong-shaped”, sculptured and axially-striped snails, and southern, more conical, glossy and spirally-striped or uni-coloured snails—may have begun separating into today’s species in the early Pliocene around 6–9 mya. Infraspecific divergence of southern snails, and the spread to and rapid expansion of eastern *hochstetteri* stock into the southern North Island were estimated to occur around 1–2 mya, during the fluctuating climate, sea-level and vegetation cover of the Pleistocene glacial cycles. This is earlier than Powell (1930), Fleming (1949) and Climo (1978) suggested and more in line with the timing suggested by Parkinson (1979) but is still predicated on the same close relationships within the *hochstetteri* complex which led those authors to their theories of *Powelliphanta* speciation.

Systematics

The recentness of the spread into the North Island, and the rapid and widespread segregation of snail populations on the South Island’s West Coast during the upheavals of the late Plicene and Pleistocene make any classification in those parts of the genus tentative. Nevertheless, delimitation of species in this comparatively youthful radiation remains an essential conservation task, as it is in such radiations that much of New

Zealand's biodiversity resides, even more than in its better-known archaic oddities. Recognition of the infraspecific diversity is equally important in terms of biodiversity conservation because it represents evolutionary potential (Haig et al. 2006). While identifying genetic and morphological clusters was the main aim of this thesis, synthesis of this information involves more explicit systematic conclusions, and is the ultimate goal.

With the inexorable rise in molecular approaches to systematics in recent decades, there has been a corresponding decrease in the more laborious (and hence expensive) traditional forms of classification based on a search for synapomorphies in (mostly morphological) characters (Mooi & Gill 2010). An unfortunate outcome has been a trend toward constructing branching diagrams divorced from formal Linnean names and classifications (Franz 2005) and divorced from serious thought and analysis of complex characters, most notably morphology (Wheeler 2007). A tribute to Robert MacArthur expresses well what needs to accompany molecular approaches:

> "*a wide and quite deep understanding of organisms, past and present, is as basic a requirement as anything else…….it may best be self-taught, but how often is this difficult task made harder by a misplaced emphasis on a quite specious modernity. Robert MacArthur really knew his warblers"* (Hutchinson 1975)

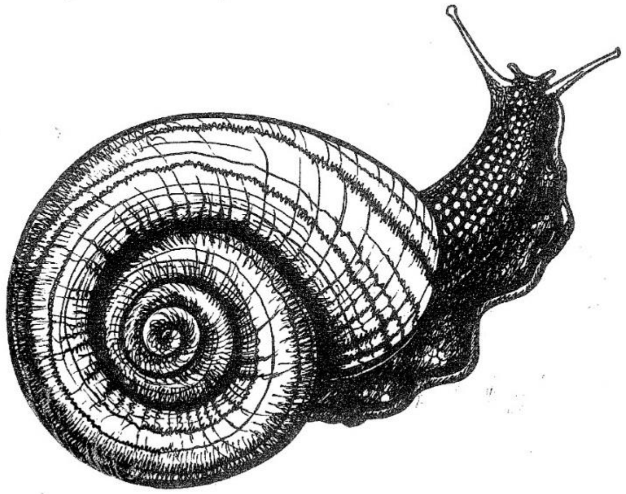
While this thesis has attempted to investigate the morphology of *Powelliphanta* in as much depth as its molecules, much remains to be done to ensure this revision of *Powelliphanta* does not simply contribute to the growing pile of papers the above authors decry, which fail to translate insights from molecular study to Linnean nomenclature. Accordingly, a synthesis of the molecular, morphological and distributional information found in this study is attempted below, to provide a working list of proposed genera, species and subspecies for *Powelliphanta*, along with some initial supplementary notes, as a first step towards making this a reality and the foundation of a formal classification.

Proposed re-classification of *Powelliphanta*

The classification proposed here is informal on two accounts. Firstly, only *Powelliphanta lignaria* has received detailed examination of intraspecific variation, and until this is done for other species, the subspecific designations presented here remain tentative. The taxonomic status of closely-related and/or poorly-known species such as those in the species “complexes” are also tentative as they are likely to be affected by improved sampling in the near future.

Secondly, it is informal in that any undescribed taxa (that is, taxa not yet described and represented by a type specimen deposited in a recognized taxonomic facility) are referred to in the table below by “tag name”. A “tag” name is an unofficial name that exists outside the International Codes of Nomenclature, given as a temporary label to indicate an entity that is thought to represent a putative taxonomic unit until it can be formally assessed and described. Tag names are usually distinguished from formally described taxa by placement in regular font inside inverted commas, a practice which is followed here.

In the following table, the “current” nomenclature and all references to taxa in the comments section follow Powell (1979), or for undescribed taxa, Walker (2003), whilst the names in the yellow row above each section and those in red-font are the proposed nomenclature suggested by this study. Comments are only provided for those taxa which have not already been discussed in some detail. While levels of molecular distinctiveness are often summarized in the comments section, for details of differences in morphological character see Chapter 3, Appendix 2.



Powelliphanta hochstetteri

P. hochstetteri hochstetteri

Currently: ***P. hochstetteri hochstetteri* (brown-based)**

The yellow & brown based forms of *P. h. hochstetteri* (sensu stricta) are allopatric and meet at a sharp boundary with no overlap or sign of intermediates, are always diagnosable & retain their distinct characters over their (separate) large ranges, warrenting subspecific recognition.

Original type lost, pleisiotype is from Mt Campbell (ie brown-based), so this would become the nominate type for the species.

P. hochstetteri "Canaan"

Currently: ***P. hochstetteri hochstetteri*(yellow-based)**

P. hochstetteri anatokiensis

Currently: ***P. hochstetteri anatokiensis***

Includes a red-shelled population ("Anatoki") and a yellow-shelled population ("Parapara") whose distributions are allopatric, without a contact zone. The morphological differences are probably of insufficient magnitude for subspecies designation but represent consistant diversity which should be recognized and retained.

("Parapara" profile far-left photo; "Anatoki" base near-left photo)

Powelliphanta “bicolor”

The morphologically distinctive snails of the east Nelson ranges differ genetically from other snails in the “*hochstetteri* complex” in the west Nelson Ranges, with pairwise sequence divergences between *P. h. obscura*, *P. h. consobrina* and *P. h. hochstetteri* of 1.8%, and between *P. h. bicolor* and *P. h. hochstetteri* of 3.1%, having presumably been separated by rapid mountain uplift and Moutere Depression widening and deepening from around 3 Ma. This is within the range of genetic distances between other pairs of well-differentiated land snail species, though towards its low end, as are all the distances between genotype clusters within the relatively recently-derived “*hochstetteri* complex”. Either no differences are recognized in this complex, or an attempt is made to distinguish the more closely-related groups and untangle their origins. The latter course has been chosen due to the stability of the groupings in all tree topologies, their discrete distributions and diagnosability.

The ancestral form of the east Nelson *Powelliphanta* may have been *consobrina*-like, with later geographic separation along the north-south trending Marlborough mountain ranges which were uplifted then eroded, drowned and separated by deep valleys during the Pliocene-Pleistocene (Trewick & Bland 2012). The extremes of the *“consobrina”* form, *obscura* and *bicolor*, now occur separately in the NW and NE sectors of the Marlborough Sounds respectively, but re-combine in a narrow (~500 m) zone of secondary contact at Mt Kiwi/Bob’s Knob with snails there of hybrid appearance. Eastern *bicolor* appears to have been the more isolated as it is now genetically distinct from the *consobrina*/*obscura* cluster (3.2% sequence divergence), to the extent that it could be considered a separate species, with closer eastern-North Island relatives (2.1% sequence divergence with “Maungaharuru”). However, morphological intergradation of *bicolor* with *consobrina* suggests specific status for *bicolor* is unwarranted. DNA testing of snails near the boundary of *bicolor* and *consobrina* (SH6) might resolve this conflict.

Powelliphanta **“bicolor”**

P. “bicolor” *bicolor*

Currently: ***P. hochstetteri bicolor***

P. “bicolor” *consobrina*

Currently: ***P. hochstetteri consobrina***

P. “bicolor” *obscura*

Currently: ***P. hochstetteri obscura***

Powelliphanta traversi

Lowland snails north of Levin (*P. traversi tararuaensis*, *P. t. latizona* and *P. t. koputaroa*) are more closely related genetically to each other than to those just south of Levin (*P. t. traversi* and *P. t. florida*), with *P. t. otakia* forming a third equally genetically distinct group. Pairwise sequence divergences between these 3 clusters average 1.6% compared to within-cluster divergences of only 0.3%.

P. traversi traversi

Currently: ***P. traversi traversi***

P. traversi traversi “florida”

Currently*:* ***P. traversi traversi* fa florida**

While “forms” are no longer recognized in zoological nomenclature, the distinctive population known earlier as *P. traversi florida* or *P. traversi traversi* fa florida should continue to be recognised. It can be referred to as the florida population of *P. t. traversi*, or via the common name, the florida *Powelliphanta*.

P. traversi otakia

Currently*:* ***P. traversi otakia***

Allopatric, morphologically & genetically distinctive from other *P. traversi*, with the 2 surviving colonies also genetically distinct from each other.

Powelliphanta traversi (continued)

P. traversi tararuaensis

Currently: ***P. traversi traversi* fa tararuaensis**

As *P. t. tararuaensis* was described earlier than either *P. t. latizona* or *P. t. koputaroa*, it becomes the subspecific name by which all three should be known, albeit with the names of their distinctive "populations" attached.

P. traversi tararuaensis "latizona"

Currently: ***P. traversi traversi* fa. latizona**

While "forms" are no longer recognized in zoological nomenclature, the distinctive population known earlier as *P. traversi latizona* or *P. traversi traversi* fa latizona should continue to be recognised. It can be referred to as the latizona population of *P. t. tararuaensis*, or via the common name, the latizona *Powelliphanta*

P. traversi tararuaensis "Koputaroa"

Currently*:* ***P. traversi traversi* fa Koputaroa**

While "forms" are no longer recognized in zoological nomenclature, the distinctive population known earlier as *P. traversi koputaroa* or *P. traversi traversi* fa koputaroa should continue to be recognised. It can be referred to as the Koputaroa population of *P. t. tararuaensis*, or via the common name, the Koputaroa *Powelliphanta*

Powelliphanta marchanti

The populations of *P. marchanti* in the Ruahine Ranges are genetically very close to *P. traversi* (sequence divergence from the northern *P. traversi* cluster only 0.5%, and from the southern *P. traversi* cluster 1.8%) though the distances between *P. marchanti* populations in the Kaimanawa Ranges and northern and southern *P. traversi* are higher (1.2% and 2.5% respectively). There are ecological differences between them with *P. marchanti* essentially a species of higher altitude forest and tussockland while *P. traversi* is confined to lowland forest. Outline shape distinguished *P. marchanti* from *P. traversi* in this study as to a lesser extent did shell pattern and colour. There is a wide variation in overall size with snails in the Kaimanawa Range population consistently smaller than those in the Ruahine Ranges and snails in the Kaweka Ranges smaller again. Recognition of intraspecific differences in shell shape, colour and pattern are proposed.

P. marchanti "marchanti"

Currently: ***P. marchanti***

Refers to both the *P. marchanti* population on the Ruahine Ranges and that on the Kaimanawa Ranges. While each population clustered separately, inter-population genetic distances were very low. While these 2 populations are allopatric and Kaimanawa Range snails reach a smaller adult size, no detailed comparative morphometric study of the latter was undertaken. On current data both are considered members of what would become the nominotypical subspecies of *P. marchanti*

P. marchanti "Kaweka"

Currently: ***P. marchanti***

Refers to the *P. marchanti* population on the Kaweka Ranges. While clustering separately from Ruahine and Kaimanawa Range snails in genetic analyses, genetic distances are very low. The snails in this allopatric population reach a smaller adult size than do snails in the Kaimanawa and Ruahine Range populations, have a more patterned shell and are separable in PCA's from the Ruahine Range population in outline shape.

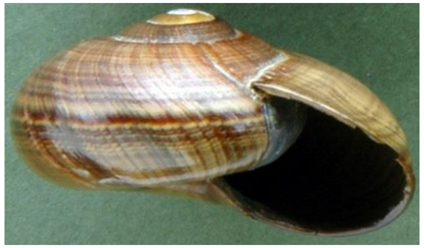
Powelliphanta “pupu”

Small colourful spirally and axially striped snails, genetically and morphologically distinct from *P. marchanti*, in which it was rather arbitrarily placed in 1979 after its late discovery. Pairwise sequence divergences range from 2.1% with *P. h. bicolor* to 3–3.8% with P. *t. traversi* and Kaimanawa Range *P. marchanti*. While mtDNA indicates their origins lie with larger eastern Marlborough “bicolor” stock, morphological similarities with *P. traversi* and Kaweka Ranges *P. marchanti* suggest the rapidly changing topography of the lower North Island from the early Pleistocene (Trewick & Bland 2012) allowed some gene flow between eastern and western North Island *Powelliphanta*. Subfossil *Powelliphanta* in limestone caves from Wairarapa to Hawkes Bay considered intermediate in shell size and shape between *hochstetteri* and *traversi* (Dell 1953) are smaller even than the Maungaharuru and Urewera Range snails and fill the present *Powelliphanta* distribution gap. Given their geographic proximity to extant *Powelliphanta* populations on Maungaharuru Range, they likely represent an early form of “Pupu” (interim tag-name from the Maori word for snail).

P. “pupu Urewera”

Currently: ***P. marchanti***

P. “pupu Maungaharuru”



Currently: **undescribed**

Powelliphanta “Egmont”

Recognition of the snails on Mt Taranaki as a separate species is a marginal call genetically as while there are 4 fixed allele differences between *P. traversi* and “Egmont”, pairwise sequence divergences are low (mean 2.2% from Ruahines, Kaimanawa and Kaweka populations of *P. marchanti* and mean 1.7% from *P. traversi*). However, these allopatric snails are always distinguishable morphologically from either *P. marchanti* or *P. traversi,* not just because they are much larger and more oblong in shape, but because unlike the latter, or indeed unlike any others in the “*hochstetteri* complex”, they have almost no spiral colour bands. The existance of similar (probably subfossil) shells from Waitotara Valley bridge the gap between *marchanti*/*traversi* and the Egmont snail populations, supporting genetic evidence suggesting they originated from a westward spread of *traversi* stock. Subfossil *Powelliphanta* remains in limestone caves near Te Kuiti (Powell 1946) may indicate a wider distribution of “Egmont” or at least its ancesters in the Pleistocene. Their present confinement to lava flows only 10,000 years old on a recent volcano suggests upslope migration in quite recent times as the tussock grasslands in the lower surrounding country in the cool dry conditions of the Holocene gave way to tall forest.

P. “Egmont”

Currently: ***P. marchanti***

Powelliphanta gilliesi

Each of the morphologically distinct described subspecies of *P. gilliesi* is, with the exception of *fallax*, allopatric and monophyletic. However, they cluster genetically into 3 geographic groupings with a mean 2.2% sequence divergence between groups and mean 0.6% within groups. These groups are north-west (*gilliesi*, *subfusca*, "Haidinger", *brunnea*); central (*montana*, *aurea*, *fallax*, *compta*); southern (*jamesoni*, *kahurangica*), indicating previous continuities across the mid-Aorere Valley. Subfossil shells found behind Collingwood on the eastern bank of the Aorere River at its mouth resemble *P.g. gilliesi* from the western bank, adding weight to this conclusion. The Aorere and Heaphy River valleys occupied by *P. gilliesi* have a complicated recent geological past, which is likely to have assisted separation into the many distinct taxa seen today. However, other factors must also be involved as even in continuous forest habitat their individual ranges are in many cases very small, and much smaller than those of the *P. superba* subspecies which they share their habitat with. The exception is *P. g. fallax*, whose alleles are still found in several other subspecies to the west and whose eastern distribution overlaps that of small alpine snails, with hybridization giving rise to a new species "Parapara". Several newly-discovered morphologically distinctive *P. gilliesi* populations in the Heaphy River catchment are, like populations of the existing subspecies, localized and allopatric. Their genetic affinities have not been examined but judging from morphological similarity, are most likely to fall into the southern *jamesoni-kahurangica* cluster. While the genetic distances between subspecies are very low, their allopatry and the distinctiveness of their morphology in terms not just of colour, pattern and shape of the shell but in colour and granulation of the parietal callus supports subspecific status.

P. gilliesi gilliesi

Currently: ***P. gilliesi gilliesi***

P. gilliesi subfusca

Currently: ***P. gilliesi subfusca***

P. gilliesi "Haidinger"

Currently: **undescribed**

P. gilliesi brunnea

Currently: ***P. gilliesi brunnea***

P. gilliesi aurea

Currently: ***P. gilliesi aurea***

P. gilliesi montana

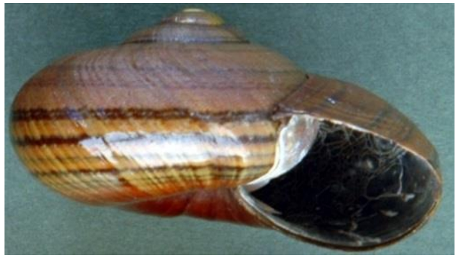
v

Currently: ***P. gilliesi montana***

P. gilliesi compta

Currently**: *P. gilliesi compta***

P. gilliesi kahurangica



Currently: ***P. gilliesi kahurangica***

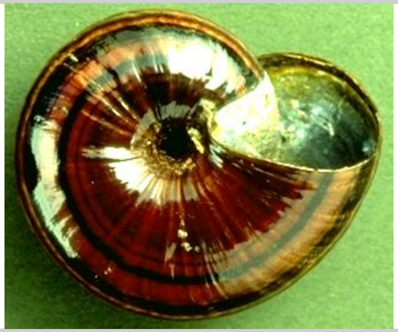
***P. gilliesi jameson*i**

Currently: ***P. gilliesi jamesoni***

***P. gilliesi* “Iwituaroa”**

Currently: **Undescribed**

***P. gilliesi* “Heaphy”**



Currently: **Undescribed**

P. gilliesi fallax

Currently: ***P. gilliesi fallax***

The appearance of the type specimen suggests it lacks “Parapara” hybrid influence so this name remains valid for use for the lowland snails of Parapara Peak

Powelliphanta “Parapara”

P. “Parapara”

Currently**: Undescribed**

A cryptic species apparently originating from an ancient hybridization between sub-alpine “Anatoki Range” and forest-dwelling *P. g. fallax*. Genetically distinctive (3.3% sequence divergence from *P. gilliesi*, and 3–5 fixed allozyme differences) but morphologically allied to *P. gilliesi*, with which it is likely to hybridize.

Powelliphanta “Anatoki Range”

P. “Anatoki Range”

Currently: **Undescribed**

Monophyletic and genetically sister to “Parapara” (4 fixed allozyme loci differences; 0.7% sequence divergence) but morphologically aligned to the proposed new species “alpine”. The genetic distance between “Anatoki Range” and the geographically closest population of “alpine” snails (that on Mt Lodestone) appears relatively large (8 fixed allozyme loci differences; 3.8% sequence divergence). However, there are likely to be other geographically closer populations still undiscovered which could narrow this genetic gap and resolve the apparent conflict of genetics with morphology.

Powelliphanta “Alpine”

P. “alpine Lodestone”

Currently: **Undescribed**

P. “alpine Owen

”

Currently: **Undescribed**

P. “alpine Nelson Lakes”

Currently: **Undescribed**

Powelliphanta superba

P. superba populations form a complex mosaic with great diversity of shell colour, parietal callus granulation and size. Mitochondrial DNA indicates the *P. superba* populations on the nor-eastern side of the Heaphy and Aorere Rivers (*harveyi, superba, prouseorum*) are distinct (mean sequence divergence 1.4%) from those on the south-western side ("Gunner River", "Gouland Range", *mouatae, richardsoni, superba*), with the divergence of the 2 different groups starting in the south near the mouth of the Heaphy River. However, this division is not evident with allozymes, suggesting the separation is comparatively recent. The eastern and western-sides of tectonic Heaphy/Aorere Depression were separated by a marine seaway in the Tertiary (Cotton 1915, Rattenbury et al. 1998) and there remains today a strong northeast/southwest grain to the fault-bounded blocks along which the Heaphy and Aorere Rivers flow, so some topographical barrier to gene flow was probably involved in the marked divergence within *P. superba* into northeastern and southwestern stocks. The south-eastern populations are each allopatric and morphologically distinct, but the morphology of the north-western populations varies in a more clinal fashion. *P. s. superba,* which occurs in both groups, is morphologically but not genetically identical in its populations at the northern extremities of both the eastern and western groups, supporting evidence from *P. gilliesi* relationships that the eastern and western sides of the mid-lower Aorere Valley were joined at some stage. On their boundary on the Slate Range *P. s. mouatae* from the eastern group and *P. s. superba* from the western group overlap by ~100 m, with no obvious hybrids. Identification of infraspecific diversity is problematic due to very low sequence divergences between each subspecies in both the western and eastern sectors (mean 0.5 % and 0.6 % respectively), the narrow hybrid zone between eastern and western stocks in the Heaphy catchment, and complicated mixing, perhaps clinal variation, between western *harveyi*, *prouseorum* and *superba*. However, whilst acknowledging the genetic evidence of distinct intra-specific taxa is rather weak, the morphological differences in each of the described or tag-named taxa are large in comparison to those in other *Powelliphanta* species, all except *prouseorum* and *harveyi* occupy an essentially separate geographical range, are readily diagnosable, and evidence from their contact zones suggests these differences are genetically-based, so the original subspecific categories are retained here.

Powelliphanta. superba (continued)

P. s. superba

Currently: ***P. s. superba***

P. s. prouseorum

Currently: *P. s. prouseorum*

P. s. harveyi

Currently: ***P. s. harveyi***

P. s. "Gouland Range"

Currently: **Undescribed**

P. s. mouatae

Currently: ***P. s. mouatae***

Powelliphanta superba (continued)

P. s. richardsoni

Currently: ***P. s. richardsoni***

P. s. "Gunner River"

Currently: **Undescribed**

Powelliphanta annectens

Monophyletic and morphologically highly distinctive at the southern end of its range, at its type locality on Bellbird Ridge *P. annectens* seems to merge in clinal fashion with *P. superba* “Gunner River” over a short distance, though it is allopatric in the rest of its range. When originally described as a separate species *P. annectens* was presumed to be related to *P. lignaria* snails on the basis if its strong axial stripes (Powell 1936). However, the white fringe to its foot connects it instead to *P. superba*, a relationship confirmed by both mtDNA and nDNA in this study. However, the closeness of the relationship isn’t entirely clear as no genetic sampling has been undertaken at the contact zone on Bellbird Ridge between *P. superba* and *P. annectens*. The shell of *P. annectens* is sculptured on the upper surface giving it a matt appearance whilst all *P. superba* shells lack such sculpture and are entirely glossy, and the white fringe to their foot is only a faint reminder of that on *P. annectens*. There are 2 fixed allozyme loci differences between *P. annectens* and *P. superba*, with a mean sequence divergence of 1.6%, towards the lowest levels usually found between pairs of well differentiated species. While it could on this basis be regarded as a highly distinctive subspecies of *P. superba*, retention of separate species status is proposed due to the strong diagnosability of *P. annectens* and the consistency of its distinct morphology over a large range separate from that of *P. superba*. The complex mosaic of striped and plain, granulated and smooth callused morphotypes in *P. superba* in the Heaphy catchment may represent a hybrid zone where *P. annectens* from the south (red, strongly axially-striped shell and heavily granulated parietal callus) meets the *P. superba* (plain yellow shell with a smooth callus) lineage from the north.

P.annectens

Currently: ***P. annectens***

Powelliphanta lignaria

P. l. lignaria

Currently: ***P. l. lignaria***

P. l. lusca

Currently: ***P. l. lusca***

P. l. oconnori

Currently: ***P. l. oconnori***

P. l. ruforadiata

Currently: ***P. l. ruforadiata***

P. l. unicolorata

Currently: ***P. l. unicolorata***

P. l. rotella

Currently: ***P. l. rotella***

P. l. johnstoni

Currently: ***P. l. johnstoni***

Powelliphanta augusta

Although the geographic and genetic distances between the northern and southern forms of *P. augusta* are small, both forms are allopatric with a sharp genetic and morphological boundary of about 50 m (Chapter 5). Each form is readily diagnosable, and the morphological differences between them correlates with evolutionary independence, thus easily fitting the criteria for subspecific recognition. The holotype and all paratypes are from the more numerous northern form which would thereby become the nominate type species, while it is suggested the subspecific name of the nearly-exterminated southern form could be a latinized version of the Maori word “morehu”, meaning “survivor”.

P. augusta augusta

Currently*:* ***P. augusta*** **(Northern form)**

P. augusta **“Morehu”**

Currently: ***P. augusta*** **(Southern form)**

Powelliphanta patrickensis

A micro-satellite study (Trewick & Daly 2012) found *Powelliphanta* on the Stockton Plateau to be genetically distinct from those on the Denniston Plateau, with almost no overlap either genetically or geographically. There are also morphological differences between the Stockton and Denniston populations (Walker 2003) so separate subspecies status is proposed. *Powelliphanta* populations on the northern Paparoa Ranges, the Brunner Range and (particularly) the Victoria Range (ie the snails in the south west of the "Kawatiri complex") are less well known and more detailed geographic sampling may affect the subspecies divisions suggested here on genetic and morphological grounds. Unlike the snails of the eastern "Kawatiri complex", snails in most western populations are specialists of low fertility substrates, most notably on the acidic coal-measures of the Buller Plateaux.

P. "patrickensis" patrickensis

Currently: ***P. rossiana patrickensis***

P. "patrickensis Denniston"

Currently: ***P. rossiana patrickensis***

P. "patrickensis Brunner"

Currently: **Undescribed**

P. "patrickensis N Paparoa"

Currently: **Undescribed**

P. "patrickensis E Paparoa"

Currently: **Undescribed**

Powelliphanta "Calci"

The eastern snails in the "Kawatiri complex" are genetically, morphologically and ecologically separable from those in the western part of the complex, though both nDNA and mtDNA suggest a relatively recent shared past (5 fixed allozyme loci differences and a mean sequence divergence of 3.2% with *P. p. patrickensis* on Stockton Plateau). The eastern snails are themselves separable on these grounds into northern ("Garibaldi", "Baton" and snails from the Radiant Range) and southern ("Matiri", "Matakitaki") clusters. The eastern snails all occupy alkaline fertile substrates, many on limestone, and it is suggested this uniting character be incorporated into the species name eventually selected.

P. "calci Matiri"

Currently: **Undescribed**

P. "calci Garabaldi"

Currently: **Undescribed**

P. "calci Baton"

Currently: **Undescribed**

P. "calci "Radiant"

Currently: **Undescribed**

P. "calci Matakitaki"

Currently: **Undescribed**

Powelliphanta “Buller River”

P. “Buller River”

Currently: **Undescribed**

Powelliphanta “vitattus”

In morphology and both mtDNA and nDNA “vittatus” is distinct from all other small southern *Powelliphanta*. There is a pairwise sequence divergence between “vittatus” and “Haast” of 11.5%, despite their occupation of adjacent mountain ranges, and a sequence divergence of 9.6% with the geographically more distant *P. spedeni*. There are 5 fixed allozyme loci differences between “vittatus” and both “Haast” and *P. spedeni*. Sequence data found no genetic differentiation between the northern and southern populations of “vittatus”, despite this comprising a considerable geographic distance. Morphologically there are obvious differences between the (smaller) southern and (more colourful) northern populations with intermediate forms found in the centre of the range. However, too little is known of how the observed morphological diversity is geographically partitioned for proper assessment of infra-specific diversity within “vittatus“at this stage.

***P.* “vittatus”**

Currently: **Undescribed**

Powelliphanta gagei

While initially described as separate species (Powell 1938), both were later relegated to subspecific status under *P. rossiana* (Powell 1949) due to their conservative morphology. However, this study has shown that genetically they are strongly differentiated from *P. rossiana* (mean 7.3% sequence divergence), and while mtDNA suggests *gagei* and *fletcheri* are relatively closely related (2.6% sequence divergence), both nDNA (8 fixed differences) and morphology indicate the relationship is more distant so restoration of each as species is proposed. While varying in size and shape, the most conspicuous morphological difference is not shell pattern but mucous and mantle colour which is purple in *P. gagei* and clear in *P. fletcheri*. Wider geographic sampling on the separate mountain ranges between the type localities is needed to see if the genetic distances found in this study are maintained.

P. gagei

Currently: ***P. rossiana gagei***

Powelliphanta fletcheri

P. fletcheri

Currently: ***P. rossiana fletcheri***

Powelliphanta rossiana

Described from Mt Greenland behind Ross (Powell 1930), all the small alpine snails from mid to north Westland were subsequently placed within *P. rossiana* ss (Powell 1949). However, this study has shown that none of the snails north of Mt Greenland belong to this species, but that all the small alpine snails subsequently discovered from mid to south Westland probably do. Snails referable to *P. rossiana* have now been found on the most westerly ends of most of the mountains along the Southern Alps from Ross to Haast but only snails from 3 populations in the north, south and central parts of this zone were examined genetically in this study. Each of the 3 populations sampled are genetically and to a lesser extent morphologically distinct (mostly in shape), with corrected pairwise sequence divergences between 1.8—3.1% and 2 fixed allele differences between the Fox and Haast populations, suggesting at least subspecific recognition is warrented. There are conspicuous impediments to easy gene flow in the form of geologically recent glacial ice flows which presumably are behind the considerable population structuring observed, and most populations remain isolated today on their (separate) mountain tops, with deep valleys of forest, river and in places glacial ice between them. More detailed genetic sampling of geographically intermediate populations may alter the conclusions reached here.

P. rossiana rossiana

Currently: ***P. rossiana rossiana***

***P. rossiana* “Fox”**

Currently: **Undescribed**

***P. rossiana* “Haast”**

Currently: **Undescribed**

Powelliphanta spedeni

Limited genetic and morphological differences were found within *P. spedeni*. However only the most-northerly population of *P. s. lateumbilicata* (ie that geographically closest to *P. s. spedeni*) was examined genetically and morphologically. Until more representative sampling of *P. s. lateumbilicata* occurs, the current taxonomy in this species should remain.

P. spedeni spedeni

Currently: ***P. s. spedeni***

P. spedeni lateumbilicata

Currently: ***P. s. lateumbilicata***

“new.genus” *fiordlandica*

“N gen” *fiordlandica*

Currently: ***Powelliphanta fiordlandica***

Future Research

While eventually encompassing most of the genus, the molecular study has some limitations. In the study of allozymes through electrophoresis which required large quantities of tissue, a few taxa were not sampled due to their scarcity, samples mostly came from type localities rather than more broadly from throughout each taxon's range, and some very recently-discovered taxa missed being sampled at all. The mitochondrial DNA study—while much broader in the range of taxa and number of populations within those taxa which were sampled—focussed on only one gene, CO1, and the sequence lengths achieved by today's standards, when sampling the whole genome has become a real possibility, were sometimes relatively short; each of these limitations could be improved by future research. It would also be useful to apply genetic techniques more suited to population study of intraspecific variation in the *hochstetteri* complex, and also in those *Powelliphanta* species where many subspecies have been described such as *superba* and *gilliesi*. Inclusion of DNA from a greater part of the range of smaller alpine *Powelliphanta*, particularly "Anatoki Range", *gagei, fletcheri, rossiana,* and the western "Kawatiri" group might improve their phylogenetic resolution.

While external morphological characters were explored exhaustively, internal morphology was not, as it was considered insufficently informative to justify the sacrifice of live snails. While radula measurements are included in many of the original descriptions made by Powell, they do not serve to discriminate between taxa, often varying instead in proportion to the differing size of each taxa. A pilot comparison of *Powelliphanta* internal organs in *augusta, hochstetteri, superba* and *lignaria* made by Dr Gary Barker found differences between each of these species in reproductive anatomy (Chapter 5). However, the differences were subtle, so large numbers of individuals would have been required to separate variation caused by maturity of specimens or inperfect curation from morphological variation, and this was not practical given the threat status of many *Powelliphanta.* As larger differences in anatomy would be anticipated between genera, a comparison of the internal anatomy of *fiordlandica* and *Powelliphanta* is a high priority for future research, particularly given the readily observable difference in the way *fiordlandica* carries its shell.

The most urgent future work at this stage however, is not improved molecular or morphological study but rather the translation of the information presented here into the formal description of new taxa, to provide a working taxonomy with which to tackle current conservation problems. From this a better understanding of species geographical range and abundance can be developed, knowledge essential for assessment of population size and eventually, conservation status.

Final words

At the beginning of this thesis it was asserted that names matter. Now at its end, with one new species described but 10 proposed new species and 21 subspecies still tag-named, the matter of naming needs some reflection or perhaps simply a qualification: some names matter more than others.

Some argue that tag-names are actually a backward step due to the confusion they can cause, particularly if they change over time (Leschen et al. 2009). Others would probably consider this a minor inconvenience given the benefits they bring: tag names provide a way to think about, to talk about and to investigate possible new taxa, and could be considered a necessary evil, given the scale of the biodiversity crisis and the lack of taxonomists (Dubois 2003, Boero 2010).

When it comes to conservation, having the “right” name may be nearly as important as having a name at all (Barron et al. 2015) particularly for invertebrates and other groups not usually considered charismatic (New 2008). The use of common rather than scientific names has been suggested as one way to give “the conservation mission [for invertebrates] warmth and familiarity” (Samways 2005). While scientific names have been regarded as “the keys to biodiversity” (Thompson 1997), common names may be the “keys to conservation success” (New 2008). This is because they are likely to be the only names recognised by the general public (Braby et al. 2007) and recognition is an essential part in overcoming impediments to invertebrate conservation (Cardoso et al. 2011).

Powelliphanta provide good examples of both views. The taxon referred to throughout this thesis as “vittatus” was initially dubbed *Powelliphanta* “Wolf River” after the first place it was found. It was subsequently also found about 500 km away, which made the name a little less relevant, then later still Wolf River was recognised as a cartographic error and the river was re-named Professor Creek. The tag-name was later changed to *Powelliphanta* "vittatus" to avoid further geographic embarrassment and with the intention of limiting subsequent name change problems when it is finally formally described, but such latinized tag names are more likely to cause confusion if not very carefully identified as informal (Leschen et al 2009). All the problems of tag names identified by Leschen et al. (2009) illustrated in just one example!

Public interest in protecting *Powelliphanta* has probably suffered from their lack of a common name, as without one it is much harder "to communicate beyond the scientific community to stimulate the interest of the many people who may participate in practical conservation" (New 2008). A rather opaque common name coined for the group ("woodformed snails"; Meads 1990) perhaps breached one of the guidelines (Braby et al. 1997) for "good" common names—being short and easy to pronounce—and failed to catch on.

In New Zealand, as on many oceanic islands where species have small ranges and have evolved in isolation from competitors and predators, molluscan extinction is a real possibility. Regnier et al. (2008) found 70% of known mollusc extinctions occurred on oceanic islands and suggested part of the reason for this high toll was that narrow-range endemics are more easily affected by environmental changes brought by humans. They attributed the IUCN red-data-listing process overlooking these high rates to an inverse relationship between the rich molluscan diversity on such islands and a scarcity of the invertebrate taxonomists who might notice such extinctions (Regnier et al. 2009). One might reasonably conclude they became extinct partly because they did not have a name, and nobody recognised them or their imminent departure.

Names do matter: Even tag names can help conservation by drawing attention to biodiversity. Well-chosen common names in conjunction with scientific names remains the ultimate goal, and here the stage has finally been set for progress for *Powelliphanta*.

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