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**Evolutionary lineages  
and the  
diversity of New Zealand true whelks**

A thesis presented in partial fulfilment of  
the requirements for the degree of

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# Abstract

Biological evolution fundamentally operates according to the basic principles of variation, heritability and selection, but it generates the astounding complexity of nature. One of the greatest challenges for evolutionary study is the interpretation of this diversity, and the ability to identify and communicate the underlying biological changes that are responsible. In this thesis, I consider the identification of evolutionary lineages using molecular and morphological data. I address the problem of confusing terminology regarding the evolutionary process, focussing on the concepts of anagenesis and cladogenesis, and the challenge of genetic introgression for taxonomic classification.

I investigate molecular and morphological variation in New Zealand true whelks. There are many species of true whelks described, however their taxonomy is mostly restricted to the traditional examination of shell traits. Evolutionary relationships of true whelks inferred from DNA sequences indicate that neither New Zealand nor Southern Hemisphere true whelks are monophyletic, contradicting taxonomic hypotheses and expectations of geographic isolation. I focus on the siphon whelk genus *Penion* Fischer, 1884, a diverse genus with extant species restricted to New Zealand and Australia. All extant species are genetically sampled for phylogenetic and allelic variation analysis. A monophyletic clade is identified for New Zealand *Penion*. Results suggest the existence of a new species and indicate evolutionary relationships for some taxa not captured by the taxonomy.

Shell shape and size are studied using geometric morphometric analyses, confirming that these traits can distinguish taxa divided by deep evolutionary splits under both informed and naïve analyses. Morphometric variation is hierarchical, with closely related taxa being grouped together within large datasets including samples from multiple evolutionary lineages. Overall, morphometric results show reasonably strong concordance with molecular evidence.

Evolutionary lineages in the fossil record are investigated using morphometric analysis within the context of previous molecular and morphometric findings. Results assist with the identification of fossils from two localities and suggest that multiple extinct species of *Penion* are misclassified. Variation in morphometric traits through

time is fitted to models of evolutionary change, and results indicate that the identification and selection of a lineage has a significant impact upon those results.

## Keywords

anagenesis; benthic; Buccinidae; Buccinulidae; Buccinoidea; Caenogastropoda; cladogenesis; deep sea; dispersal; developmental biology; endemism; evolution; evolutionary biology; evolutionary lineage; evolutionary rate; divergence; diversity; fossil; gastropod; geometric morphometrics; high-throughput sequencing; hybridisation; introgression; lineage split; marine snail; mitochondrial DNA; mollusc; monophyly; morphology; Neogastropoda; next-generation sequencing; nuclear DNA; palaeontology; paraphyly; phylogenetics; RADseq; ribosomal DNA; sexual dimorphism; shell; siphon whelk; snail; speciation; species; systematics; taxonomy; whelk; zoology



A *Penion* Fischer, 1884 siphon whelk from Tasman Bay.



# Preface

The overall aim of this research project, *Evolutionary lineages and the diversity of New Zealand true whelks*, was to investigate the relationship between molecular and morphological variation for the identification of evolutionary lineages. New Zealand true whelks were used as a study system, and I focussed especially on the siphon whelk genus *Penion* Fischer, 1884, which is recognised to be taxonomically diverse. Numerous extant endemic siphon whelk species are recognised in New Zealand, along with a rich fossil record. *Penion* shells exhibit a bewildering level of putative inter- and intraspecific morphological variation. The aim of this project was followed in several stages, which are presented in this thesis as seven independent research chapters (Chapters 1 – 7), with the findings summarised at the end. Most research chapters are followed by supplementary material (including error studies, and additional figures and tables), and taxonomic information is also summarised in Chapter 8 to assist with the interpretation of methods and results.

Research presented in this thesis was produced in collaboration with my supervisors (Mary Morgan-Richards, Steven A. Trewick, and James S. Crampton), but most sampling and laboratory work, and all data analysis and initial drafts of writing were my own work. Within chapters I use the personal pronoun ‘we’, but all work is my own. Mary, Steve and James provided invaluable insight and assistance with conception of the project aims, the design of methods and analyses, discussion of results, editorial guidance, and funding. For writing, I specifically chose many of the topics of research, surveyed the literature and wrote the first drafts of each manuscript with iterative feedback from co-authors. I conducted the majority of molecular sampling, with some assistance from Simon F.K. Hills and Mary. Most DNA extractions, PCR reactions, and necessary clean-up methods were conducted by myself with some assistance from Simon. I worked in cooperation with Michael R. Gemmell to develop the next-generation sequencing method and analytical pipeline. I conducted all shell photography myself. Most specimens were borrowed from museum and university collections acknowledged within chapters, and Mary and I organised the loan of tissue specimens from abroad. High-throughput sequencing was conducted by the Beijing Genomics Institute, Hong Kong or the New Zealand Genomics Limited service. Bruce A. Marshall and Alan G. Beu advised with the taxonomic classification of specimens, as well as the identification of palaeontological provenance and the sex of individual snails.



Chapter 1 is a literature review considering the meaning of the terms ‘anagenesis’ and ‘cladogenesis’ from an evolutionary perspective. These terms are frequently used to discuss speciation and morphological change in the fossil record, and this chapter attempts to clarify the topic. The article was accepted for publication as: Vaux, F., Trewick, S.A., Morgan-Richards, M. (2016). Lineages, splits and divergence challenging the meaning of the terms anagenesis and cladogenesis. *Biological Journal of the Linnean Society* 117, 165 – 176.

Chapter 2 is a reply to a comment written in response to the published version of Chapter 1. The chapter discusses the treatment of species as arbitrary concepts, and it addresses the significance of genetic introgression for the process of biological speciation and taxonomic classification. The chapter was published as: Vaux, F., Trewick, S.A., Morgan-Richards, M. (2016). Speciation through the looking-glass. *Biological Journal of the Linnean Society* (early access).

Chapter 3 is a molecular phylogenetic investigation of true whelks (Neogastropoda: Buccinidae or Buccinulidae) from the Southern Hemisphere. The aim of the chapter was to determine whether true whelks from the Southern Hemisphere, or at least New Zealand, are monophyletic and separate from lineages distributed in the Northern Hemisphere. The findings also provide new insight towards timing of speciation and dispersal in the siphon whelk genera *Antarctoneptunea* Dell, 1972, *Kelletia* Bayle, 1884 and *Penion*. The dataset contains newly sequenced mitochondrial genomes and nuclear ribosomal DNA sequences from numerous species of marine snail. I am hoping to submit an abbreviated version of this chapter to a peer-reviewed journal soon.

Chapter 4 is a molecular phylogenetic and restriction site associated DNA (RAD) sequencing investigation of the siphon whelk genus *Penion*. The aim was to produce a comprehensive hypothesis for the evolutionary relationships of all recognised, extant species of *Penion* from Australia and New Zealand (Chapter 3 contains a subset of species). Analysis of single nucleotide polymorphic (SNP) variation for anonymous nuclear loci was used to investigate species delimitation, and to test phylogenetic concordance between mitochondrial and nuclear DNA. The dataset contains newly sequenced mitochondrial genomes and nuclear ribosomal DNA sequences from all

species of *Penion*. Results from this chapter are intended to be merged with those of Chapter 6, and will be submitted to a peer-reviewed journal for publication.

Chapter 5 is an investigation for evidence of secondary sexual dimorphism in the shells of *Penion chathamensis* (Powell, 1938) using geometric morphometric analysis. Neogastropod molluscs such as *Penion* are dioecious, but sexual dimorphism is an understudied topic of research. Our analysis of shell shape and size variation used a two dimensional, landmark-based geometric morphometric approach with sampling across the entire range of *P. chathamensis*. For comparison I also sampled shells across the entire range of *P. sulcatus* (Lamarck, 1816). This chapter was published as: Vaux, F., Crampton, J.S., Marshall, B.A., Trewick, S.A., Morgan-Richards, M. (2017). Geometric morphometric analysis reveals that the shells of male and female siphon whelks *Penion chathamensis* are the same size and shape. *Molluscan Research* (early access).

Chapter 6 is an investigation of variation in the shell morphology of all extant species of *Penion*. The aim was to establish if variation in shell morphology in *Penion* is concordant with the evolutionary relationships among species estimated from the molecular results of Chapter 4. The same two dimensional, landmark-based geometric morphometric method as in Chapter 5 was used to analyse shell shape and size. All extant species of *Penion* from Australia and New Zealand were sampled. Results from this chapter are intended to be merged with those of Chapter 4, and will be submitted to a peer-reviewed journal for publication.

Chapter 7 utilises the combined results of Chapters 3 – 6 as a context to analyse the fossil record of *Penion* in Australia and New Zealand. The chapter investigates variation in the shell morphology of fossils classified as extinct and extant species in comparison to modern shell sampling (covered in Chapter 6). The analysis follows the same framework to consider evolutionary lineages and speciation discussed in Chapters 1 and 2, and the method considers the concordance between molecular phylogeny and shell morphological variation in *Penion* (Chapters 3 and 4, 6), and the apparent absence of secondary sexual dimorphism in at least some species (Chapter 5). Since findings from every previous chapter are synthesised, Chapter 7 almost acts as a conclusion of the thesis. The same two dimensional, landmark-based geometric morphometric method as in Chapters 5 and 6 was used to analyse shell shape and size. Shells from all extinct

species of *Penion* from Australia were sampled, as well as a number of fossil species from New Zealand. This chapter has been prepared for publication but will not be submitted until the previous chapters have been published.

Chapter 8 summarises the taxonomy of living and fossil *Antarctoneptunea*, *Kelletia* and *Penion*, which were three genera of key interest for this thesis. Specifically, this section summarises the current, published taxonomy of the group and also suggests revisions based on the results of Chapters 3 – 7. Importantly, this section also specifies the operative taxonomic units (OTUs) used for this thesis. Some taxa were not considered for this study as the examination of shells suggested that numerous fossil taxa were conspecific. These decisions were made independent of geometric morphometric and molecular results. This chapter should be read for reference when the taxonomy and available fossil material for the three genera requires clarification in Chapters 3 – 7. The revisions summarised in this chapter are planned to be converted into a formal taxonomic review that will be submitted for publication.

At the end of this thesis I provide a brief summation of the overall results of Chapters 1 – 8. I also suggest future research topics based on the results of this thesis.

Results from Chapters 1 – 6 were also included within conference presentations listed in Appendix I.





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Two shells of *Penion mandarinus* (Duclos, 1832) from waters off of Australia.

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