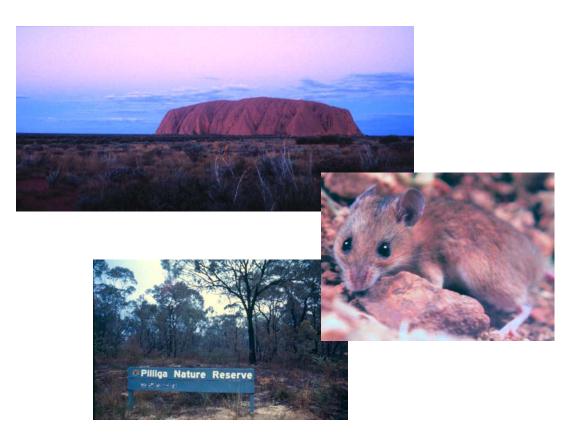
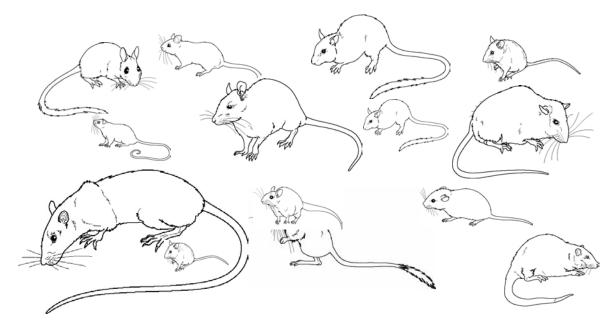
Conilurine Rodent Evolution:

The role of ecology in modifying evolutionary consequences of environmental change



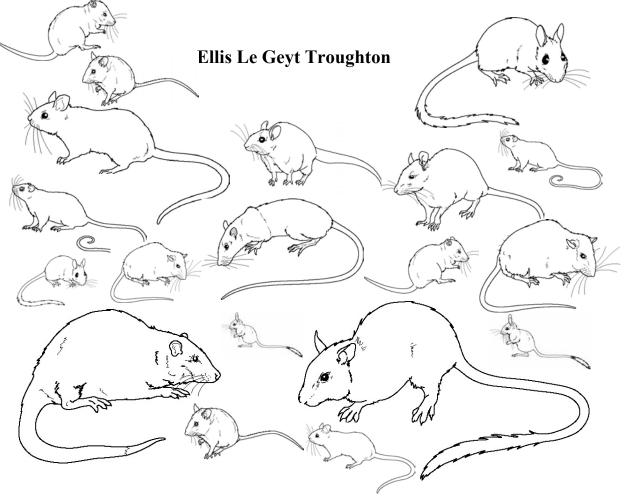
Thesis submitted by Frederick David Ford BSc (Hon) ANU In June 2003

for the degree of Doctor of Philosophy in Zoology and Tropical Ecology within the School of Tropical Biology James Cook University



"Some of these exhibit the close similarity arising from their common ancestry abroad; others have evolved as peculiar types during prolonged

isolation."



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Abstract

Conilurine rodents are the most speciose and ecologically diverse rodent group within Australia. Previous research has demonstrated that conilurines are members of a larger Australasian Murid tribe, the Hydromyini, and are generally thought to be an endemic Australian radiation with a fossil history dating to the mid Pliocene. However, monophyly of conilurines is not well established due to the distant placement of some genera in recent systematic studies. I investigated the evolution of conilurine rodents using a combination of molecular and ecological techniques. I examined phylogenetic relationships among all Australian rodent genera using the mitochondrial control region and a nuclear intron (DHFR 1). These results suggested that conilurines are monophyletic, and that unresolved generic relationships within the group are the product of an early savannah radiation. Building on the results of systematic studies, I examined patterns of speciation and population divergence in model species and species groups. Bioclimatic range modelling and some ecological studies were performed to aid interpretation of molecular evolution within these groups. The overall goal of this thesis is to provide a detailed account of some evolutionary processes affecting an interesting group for which such information is lacking, and to highlight the potential of conilurines for evolutionary study in an Australian context. A more specific goal is to investigate the effect that species ecology has on altering the evolutionary response of different species to the same environmental stimuli.

Molecular studies identified a number of taxonomic issues within the group. The genera *Notomys, Mastacomys* and *Pseudomys* formed a monophyletic group identified by previous studies. *Mastacomys* was placed within *Pseudomys*, with which it was recently synonymised, and *Notomys* was not clearly separable from *Pseudomys*. Both *Notomys* and *Mastacomys* should be recognised as genera. As a result, *Pseudomys* was split into several smaller genera. These included resurrection of the genus *Thetomys* for *P. gracilicaudatus* and *P. nanus*, and creation of a new genus *Phorolithomys* for the recently described pebblemound mice. A further three groups are apparent within *Pseudomys*, but splitting of these at the generic level is contingent on further resolving the placement of several species among them. Some individuals previously described as *P. delicatulus* from north-western Australia

appear to be a morphologically cryptic species, and were placed outside the *P. delicatulus/ novaehollandiae* group in phylogenetic trees. The subspecies *P. delicatulus mimulus* has no genetic basis. *Pseudomys laborifex* is probably a subspecies of *P. johnsoni*, which is an unexpected result given the distribution of *P. laborifex* in the Kimberley, a region anticipated to contain the sib-taxon to the Top End *P. calabyi*.

Phylogeographic studies of variation in the mitochondrial control region revealed significant differences in the evolution of species groups as result of their differing ecologies. This contrast centres on the morphologically similar pebble-mound mice and delicate mouse group. These are the largest species groups within the current genus *Pseudomys*. Pebble-mound mice are characterised by the fact that they require pebbly habitat for breeding, and have therefore speciated in allopatry due to erosion and fragmentation of that habitat. Climatic change has also affected pebble-mound mice, and has driven recurrent extinction processes, in part re-enforced by the inability of pebble-mound mice to track climatic change across pebble-free habitats.

The delicate mouse group have distributions primarily determined by climate. This means they are periodically isolated and bottlenecked, but also experience secondary contact when conditions permit range expansion. A major finding was that there is no taxon corresponding to *Pseudomys pilligaensis*, and that individuals of both *P. delicatulus* and *P. novaehollandiae* have been included within that species. The genetic distinctness of *P. novaehollandiae* from *P. delicatulus* was no greater than that among individuals of *P. delicatulus*. Whether *P. delicatulus* and *P. novaehollandiae* represent sib-species or subspecies was not resolved, but evidence of clinal morphology and probable interbreeding suggests that they have not yet speciated. *Pseudomys hermannsburgensis*, an arid zone member of the delicate mice, showed little genetic variability, and no geographical structuring across a very large distribution. This result is consistent with ecological studies that show the species possesses morphological adaptations to aridity and exists in relatively mobile populations. A similar result was found for the co-distributed *P. desertor*.

Patterns of genetic structuring are not predictable based on crude habitat preference. It was thought *a priori* that *Zyzomys argurus* was a taxon with a similar habitat preference to pebble-mound mice and that it would also exhibit deep genetic structuring between allopatric populations found in rocky habitats across northern Australia. Previous isozyme studies did not find such a relationship, and this was confirmed by mtDNA sequencing. Unlike most other study species, there was no signal from the last glacial maximum, despite the fact that *Z. argurus* would not have been able to track climate change as many species did. A broad climatic tolerance and good dispersal ability seem to explain the lack of population structuring.

Amplification of nuclear copies of the mitochondrial control region hampered efforts to study the chestnut mice, *P. gracilicaudatus* and *P. nanus*. However, three clean control region sequences were obtained that apparently confirmed currently recognised species boundaries. Nuclear copies were also amplified from the pebble-mound mice, but primers were designed that prevented their hindrance of phylogeographic studies.

The characterisation of evolution among conilurine rodents presented here reveals that species ecology clearly accounts for many differences in patterns of population divergence and speciation. I suggest that ecological interpretation of evolutionary pattern can be extended to a general contrast between the entire conilurine assemblage and marsupials.

Acknowledgements

It is not hard to find those willing to travel the wilder parts of northern Australia, but it is often a struggle to find people who will embrace the reality of early mornings bashing through charcoal coated scrub just to scribe a few numbers and catch fleeting glimpses of small furry creatures. It is even more difficult to find people who will come back for more. Repeat offenders who provided invaluable help during field trips included Jane Antrobus, Zoe Baron, Mathu, Laura Inman, Ben Collins, Tabitha Lloyd, Allen McIllwee and Euan Ritchie. Others proved stoic enough to overcome both the hardships of fieldwork in remote locations and prolonged exposure to my rambling and sometimes (often?) demanding ways on long field trips- special thanks to Kathy Tsang, Dave Shevill, Chris Parker, Bob Wong, Daniel Keating and Kelli Gowland.

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¹ and generally ignored

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Statement on Sources Declaration

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from published or unpublished work of others has been acknowledged in the text and a list of references is given.

Frederick David Ford