Recent evolutionary history of the Australian freshwater turtles *Chelodina expansa* and *Chelodina longicollis*.

by

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Kate Hodges with *Chelodina (Macrochelodina) expansa* from upper River Murray.

Photo by David Thorpe, Border Mail.

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Publications associated with this thesis

Chapter 2 – Phylogeography of Chelodina expansa

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Chapter 3-Phylogeography of Chelodina longicollis

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The above publications are reproduced in this thesis without change apart for formatting.

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Summary

Of all the global biomes, freshwater ecosystems are the most degraded and freshwater taxa suffer the highest extinction rates on record. Given the degradation of river basins in Australia specifically, there is a pressing need to characterise Australian freshwater biodiversity and the evolutionary processes that maintain it. In this thesis I examine Australian freshwater biodiversity by integrating across multiple disciplines of biogeography, phylogeography, ecology, and phylogenetics. I address questions in each of these disciplines using two Australian freshwater turtles in the genus *Chelodina*. The patterns, diversity, and evolutionary processes I uncover scale to the broader freshwater community and can facilitate effective conservation and better understanding of Australian freshwater ecosystems.

Chapter 2 presents a mitochondrial phylogeographic investigation of *C. expansa*. I uncovered two divergent haplogroups representing discrete regional populations each with independent evolutionary trajectories. One haplogroup is found in the inland Murray-Darling Basin, and on the east coast south of the Conondale Range and on southern Fraser Island. The other is found only on the east coast north of the Conondale Range and on northern Fraser Island. Few studies have explicitly examined relationships among inland and coastal bioregions and I show that with extensive sampling, complex and cryptic patterns can emerge that are concordant across a range of other freshwater taxa. This chapter improves understanding of how taxa respond to regional scale biogeographic boundaries, and highlights new and important phylogeographic breaks and centres of diversity within regions. I conclude with a call to uncover and recognise cryptic microbiogeographic regions for more directed freshwater conservation and biodiversity management.

In Chapter 3 I investigate the phylogeographic structure of *C. longicollis*. I predicted this species would have highly connected populations and would show insensitivity to biogeographic barriers owing to its strong capacity for overland dispersal and specific adaptions to terrestriality. Contrary to expectations, and in a pattern similar to low vagility freshwater vertebrates, *C. longicollis* revealed two ancient mitochondrial haplogroups with clear geographic partitioning either side of the Great Dividing Range. This pattern is overlayed with signatures of recent gene flow over the longstanding biogeographic barrier, likely facilitated by late Pleistocene and ongoing anthropogenic landscape change. I discuss how evolutionary and biogeographic processes can dominate at different times in freshwater species to create complex patterns of population divergence and connectivity. I demonstrate that even in a highly vagile freshwater species, the divergent effects of landscape history and hydrological boundaries often overwhelm the homogenising effects of life history.

Chapter 4 examines the nature and extent of mitochondrial gene tree – species tree discordance within *Chelodina*. I was drawn to investigate this issue as phylogeographic exploration of *C. expansa* and *C. longicollis* revealed three instances of mitochondrial haplotype exchange between the two species. A multilocus phylogenetic approach of the broader species tree revealed extensive mitonuclear discordance and high levels of mitochondrial paraphyly. I found that the mitochondrial genome of *C. expansa* is completely replaced with that of either *C. longicollis* or *C. canni*. This chapter adds to a small but growing set of case studies demonstrating complete mitochondrial replacement. It is the second only reported case of dual mitochondrial genome capture and the first reported case in a reptile. The *C. longicollis* mitochondrial genome has also been partially replaced with that of *C. canni*. Estimates of common ancestry for mitochondrial and nuclear lineages, plus coalescent simulations of gene flow suggest these patterns are not a

result of deep coalescence but rather multiple and ancient asymmetric introgressive events within and between subgenera. In Chapter 5 I use palaeodistribution and ecological niche modelling to explore the biogeographic, ecological, and climatic arena that led to ancient introgression. I support inferences made earlier in favour of neutral demographic disparity driving introgression from the common into the rare species during Plio/Pleistocene glacial aridity.

This thesis significantly improves our knowledge of southeast Australian freshwater biogeography. The pervasive yet equivocal influence of the Great Dividing Range on the evolutionary history of freshwater species is emphasised. Life history characteristics such as strong dispersal capacity and adaptations for terrestriality are shown to be unreliable predictors of population connectivity, and phylogeographic concordance among species illustrates broad-scale biogeographic processes that reach beyond taxonomy, life history, and ecology.

This thesis also reframes our understanding of the relationships and historic interactions among freshwater turtles in *Chelodina*. In synthesising evidence from multiple disciples I show that phylogeographic patterns have been shaped by complex evolutionary and ecological interactions between each species, and with *C. canni*. Molecular dating of *C. longicollis* and *C. expansa* haplogroups indicate that signals of expansion and diversification track recent post-hybridisation events and demographic histories unique to each species. Deeper mitochondrial genetic structure however reflects repeated and temporally separated episodes of mitochondrial genome capture during Plio/Pleistocene glacial aridity. The patterns I uncover of ancient, repeated, asymmetric introgression among Australian freshwater turtles is unique and of great biogeographic, evolutionary, and ecological interest. I conclude this thesis by highlighting future directions to better

understand the biogeography of freshwater systems, and the cause and extent of introgression in *Chelodina*.