

THE EVOLUTION AND DIVERSIFICATION
OF THE ALLODAPINE BEES



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SUMMARY

This thesis investigates the evolution and biogeographical history of the bee tribe *Allodapini*. Examinations of life history traits, nesting patterns, and morphology were the primary methods used to explore allodapine biology, whilst a molecular-based phylogenetic approach was used to explore patterns of speciation and diversification within the tribe. A primary feature of this research is the expansion and revision of the allodapine phylogeny, using DNA sequence techniques. The phylogenetic components of this thesis focus primarily on the earliest divergences and generic-level bifurcations within continentally and environmentally defined allodapine clades. These relationships were used to examine the nature of broader changes in sociality, nesting biology, morphology, and geographic distribution across the tribe as a whole.

Results indicate that the strong benefits social nesting affords in repelling enemies-at-the-nest is implicit in the universal retention of social behaviour within the *Allodapini*, and that this characteristic may also apply to other taxa that show a lack of reversions from social to solitary living. Results also suggest that some of the tribe's farthest-reaching radiations occurred rapidly and relatively early, with some of the foremost involving dispersal events that do not appear to fit with current palaeogeographical reconstructions. The infrequency of major transitions between different environmental biomes within the tribe is indicative of ecological constraints and niche conservatism that appears to have resulted in low adaptive radiation and diversification. These constraints appear ameliorated during periods of climatic and environmental instability; possibly by way of allopatric speciation promoted by habitat fragmentation. Allodapines play a fundamentally important role as pollinators within their ecosystems. As such, these findings highlight the impact that climatic and environmental change, as well as rare and poorly understood mechanisms of dispersal, can have on key components of a biome's constituent taxa and hence the course of an ecosystems future evolution.

DECLARATION

I declare that this thesis does not contain any material previously submitted for any diploma or degree in any university without acknowledgement, and that to the best of my knowledge it does not contain any material previously published by any other person except where due reference is made.

Luke Ballingall Chenoweth

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"In all things of nature there is something of the marvellous."

— Aristotle

GENERAL INTRODUCTION

For species that play pivotal roles in the function of terrestrial ecosystems, such as key pollinators, a better understanding of both biological and biogeographical history has the potential to provide important information about an ecosystem's evolution and development over time. Additionally, understanding how and why certain ecological constraints may restrict an organism's physiology, biology or behaviour can have important ramifications, as the taxonomic composition of an ecosystem is inevitably linked to the frequency or rarity of species' transitions between biomes.

The diversification of the bees is strongly tied in with the sudden and rapid diversification of the angiosperms during the early-mid Cretaceous (Engel 2001). Due to their role as the most diverse and specialised group of angiosperm pollinators (Michener 2007), bees play an integral role in the function of almost every terrestrial environment on Earth. Understanding the history of diversification, speciation, and adaptation of the bees is therefore crucial in better understanding the origins and evolutionary histories of many ecosystems across the globe.

At present, the extant bee lineages are divided into seven families: the "long-tongued" families Apidae and Megachilidae, and the "short-tongued" families Andrenidae, Colletidae, Halictidae, Melittidae, and Stenotritidae. Current understanding of the origins of these families point to the melittids *sensu stricto*, meganomiines and dasypodaiines as the most basal bee taxa (Danforth *et al.*, 2006), followed by the long-tongued lineages Megachilidae and Apidae. Among the Apidae, the subfamily Xylocopinae is situated as the possible sister group to the rest of the family (Roig-Alsina & Michener, 1993), suggesting a relatively early origin for this group amongst the bees. One group of xylocopine bees, the tribe Allodapini, has been the subject of several phylogenetic studies to date. The allodapine bees are largely restricted to the southern hemisphere, where they comprise a significant component of the African, Malagasy, and Australian bee fauna. Despite this relatively widespread intergeneric distribution and habitat range, the allodapine bees frequently show a high level of generic-level conservatism in habitat, nesting biology, life-history traits, and adult morphology (Schwarz *et al.*, 1998; Tierney *et al.*, 2000). Perhaps most notably, social nesting strategies are seemingly present (albeit highly variable) in all but a single species; *Halterapis nigrinervis* (Michener 1969; 1974). The unique attributes this tribe displays, combined with their important functional role in many southern hemisphere ecosystems, means that important insight into the historical ecology of the

southern hemisphere may be gained from a better understanding of diversification and evolution within the allodapines. To date, the biology and phylogenetics of the allodapines is fairly well understood. However, in order to further investigate the history of this group, several key issues still need to be addressed.

This thesis endeavours to address several of these issues in order to better understand the biogeographical and evolutionary history of the allodapines. The components of this thesis are presented in the form of four multi-authored chapters. Versions of chapter I and II have been published in *BMC Evolutionary Biology* (7:246) and *Systematic Entomology* (33(4): 700-710) respectively, and these chapters are presented as copies of the final submitted drafts. Chapter III is currently accepted and awaiting publication in *Journal of Biogeography*, and is also presented as a copy of the final submitted draft. Chapter IV is in the final stages of preparation for submission to *Molecular Phylogenetics and Evolution*, and is presented as the first draft to be submitted to this journal. The following is a summary of each chapter.

CHAPTER I: Social complexity in bees is not sufficient to explain lack of reversions to solitary living over long time scales.

Chapter I investigates the causative factors of the development of social behaviour in the allodapines, focusing chiefly on its maintenance and alteration through speciation.

Michener (1971) described *Halterapis nigrinervis* as nesting in a subsocial manner with each nest containing a single inseminated female and any additional females described as newly emerged callows preparing to disperse. However, the possibility of alloparental care or the presence/absence of size-based reproductive hierarchies within nests has never been fully investigated. A study by Chenoweth (2005) was the first to show reproductive skew based loosely on size, strong female bias in sex ratio, and increased per capita brood production in multifemale nests, suggesting benefits of social nesting do exist in *H. nigrinervis*. As a result, no solitary allodapine species would be known to exist despite a potentially ancient origin of sociality. Unlike other taxonomic groups where social behaviour is ubiquitous such as ants and termites, the Allodapini do not display any of the key behavioural, physiological, or genetic traits which have been traditionally associated with highly social nesting strategies (Wilson & Hölldobler 2005). This leaves an intriguing avenue for further study.

CHAPTER II: *Hasinamelissa*: a new genus of allodapine bee from Madagascar revealed by larval morphology and DNA sequence data.

Chapter II examines the relationship between the African and Malagasy species of the allodapine genus *Halterapis*, and explores how this relationship fits with current hypotheses of biotic interchange between Africa and Madagascar. Recent studies into the social biology of the African+Malagasy genus *Halterapis* suggest the presence well-established sociality and highly unique brood rearing strategies restricted to the genus' Malagasy taxa (Schwarz *et al.* 2005; Chenoweth & Schwarz 2007.). Whilst the African and Malagasy taxa are currently assigned as congeneric, lack of information on larval characteristics or a well-resolved phylogeny renders the placement of the Malagasy and African taxa together unpersuasive. Madagascar has one of the highest levels of species endemism in the world, and this also applies to its bee fauna (Pauly *et al.* 2001). Determining the historical connection between the Malagasy *Halterapis* and the remainder of the tribe could provide important insight into not only the biogeographical history of the allodapines, but also the greater history of biotic interchange between Madagascar and Africa.

CHAPTER III: Biogeographical origins and diversification of the exoneurine allodapine bees of Australia (Hymenoptera, Apidae).

Chapter III explores the geographical hypothesis of the Australian 'exoneurine' clades' dispersal into Australia, and its subsequent history of diversification within the continent. Two distinct clades of allodapines are known to exist in Australia. The first are members of the largely African genus *Braunsapis* and provide a typical example of dispersal into Australia via the Indian Ocean Rim after the collision between the Australian and Laurasian plates (Fuller *et al.* 2005). The history of the second allodapine group in Australia is more puzzling. The Australian allodapine genera *Exoneura*, *Brevineura*, *Exoneurella*, and the parasitic *Inquilina* form an endemic, continentally defined clade that primarily inhabits the southern semiarid and temperate regions of Australia (Michener 1965; Schwarz *et al.* 2006). Schwarz *et al.* (2003) showed that the Australian clade is monophyletic among the allodapines and Bull *et al.* (2003) showed this divergence to be very early in the tribe's history. Current palaeogeographical models rebuke a Gondwanan origin for the clade, and Schwarz *et al.* (2006) approximated the initial radiation of the exoneurines dating back at least 25-30 My, making the notion of dispersal of the exoneurines into Australia through Asia also unlikely. Despite these findings, very little can be substantiated about either the means by which the clade reached Australia, or their

subsequent history of diversification and speciation. Australia has the most unusual complement of bee fauna in the world (Michener 1965, 2007), of which the allodapines comprise a relatively archaic and basal group. A better understanding of the origin and diversification of the exoneurines can thus provide a greater understanding of the biogeographical history of what may be some of the oldest members of the Australian bee fauna.

CHAPTER IV: Biogeographical history of the African allodapine bees (Hymenoptera, Apidae).

Chapter IV looks at the major speciation events within the African allodapines and the factors that have influenced tribe's radiation both within and out of Africa. The continent of Africa holds an important position as the likely origin of the Allodapini (Bull et al. 2003; Schwarz et al. 2004) and the African taxa are rendered paraphyletic to both the Australian and Malagasy clades. The African taxa are composed of a basal '*Macrogalea*' clade and a more derived clade containing the remainder of the African taxa. This latter 'African' clade spans a broad range of habitats across the Afrotropic zone of sub-Saharan Africa, and is unique as it also contains two major dispersals into other regions of the world. One of these dispersals resulted in the genus *Exoneuridia*: a rare montane genus present in the Arabic peninsula, Iran, and southern Turkey (Terzo 1999). The second, involving *Braunsapis*, is thought to have its origins in tropical Africa and subsequently spread throughout Asia and into northern Australia (Schwarz *et al.* 2006). Whilst both these genera are thought to have diverged from the remainder of the African taxa at similar times, they differ radically in their current distribution and habitat ranges. At present the topological placement of these genera within the African clade remain poorly defined. This is primarily due to the fact that despite strong phylogenetic support in a majority of the clade, certain areas require a much larger taxonomic set in order to confidently infer phylogenetic relationships. A better understanding of the history of the African taxa is fundamental to understanding the broader trends of diversification within the Allodapini as a whole. Additional phylogenetic examination of the African allodapine taxa, using an expanded data set, is essential to more accurately infer these divergences and explore the earliest stages of diversification within the Allodapini.

Finally, the overall conclusions and broader implications of these studies, as well as important avenues for further research, are examined in a General Discussion following Chapter IV.

The candidate is primarily responsible for all data collection, analysis, laboratory work, interpretation/discussion of the results, as well as production and formatting of published material. The following contributions were made by various co-authors: Chapter I drew on data collection assisted by Jaclyn A Smith and the analytical expertise of Dr Steven JB Cooper. Chapters I and II drew from substantial data collection and sequence data assisted by Simon M Tierney. Chapter II also drew from sequence data obtained by Yung C Park and Susan Fuller. Chapter IV drew from the field collections and analytical expertise of Michael J McLeish. All four chapters were written with commentary from the candidate's supervisor, Associate Professor Michael P Schwarz. Funding from grants awarded to Michael Schwarz are also recognised by his inclusion as author.

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