

THE DIVERSIFICATION, BIOGEOGRAPHY,
AND BODY SIZE EVOLUTION OF
AUSTRALIAN HYLAEINE AND EURYGLOSSINE BEES

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| A | B |
| C | D |
| E | F |
| G | |

- A. *Hylaeus quadratus* (Hylaeinae) head, frontal view
 B. *Hylaeus quadratus* (Hylaeinae) body, lateral view
 C. *Callohesma* sp. (Euryglossinae) body, dorsal view
 D. *Callohesma* sp. (Euryglossinae) head, frontal view
 E. *Hylaeus (Rhodohylaeus)* sp. (Hylaeinae) head, frontal view
 F. *Hylaeus (Rhodohylaeus)* sp. (Hylaeinae) body, lateral view
 G. *Brachyhesma* sp. (Euryglossinae), dorsal view

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SUMMARY

Patterns in diversification, biogeographical histories, and the evolution of body size in euryglossine and hylaeine bees (Colletidae) are the topics of this thesis. Central to the work is the reconstruction of molecular phylogenies, which also enables the evaluation of current taxonomic arrangements within these groups.

Hylaeus (Hylaeinae) is the only globally distributed colletid bee genus, with subgeneric and species-level diversity highest in Australia. I use molecular phylogenetic analyses based on COI, EF-1 α , and 28S genes comprising 3,997 nucleotides and a total of 76 Hylaeinae species and five outgroup species to show that *Hylaeus* originated in Australia about 30 Mya. Log-lineages through time plots indicate high rates of cladogenesis early on in the history of Australian *Hylaeus*, and the phylogeny indicates only two dispersal events out of Australia, both shortly after its crown age. One of these dispersals was into New Zealand, with only a minor subsequent radiation, but a single dispersal event from Australia gave rise to the approximately 450 species of *Hylaeus* outside of Australasia with no evidence for subsequent dispersals from Australia into regions outside of Australasia, nor migration back into Australia. I discuss the possibility that despite a decreasing distance between Australia and Asia over the past 30 My, successful colonisation subsequent to the initial dispersal outside of Australasia would not entail the original benefits of new niche space, but would involve the costs of low genetic variation in colonizing lineages.

The subfamily Euryglossinae is endemic to Australasia, and comprises one of the most speciose bee groups in Australia. I use molecular phylogenetic analyses based on COI, EF-1 α , and 28S genes comprising 3,020 nucleotides and a total of 24 Euryglossinae species and 18 outgroup species to explore evolutionary relationships among the major euryglossine genera and the relationship of Euryglossinae to other colletid subfamilies. My analyses confirm the sister clade relationship between Euryglossinae and the southern African Scapterinae, with a divergence date between the two clades of approximately 50 Mya. I argue that, based on that divergence date, the disjunct distribution of the subfamilies are unlikely to be a legacy of Gondwanan rifting, and I discuss two alternative routes of dispersal between Africa and Australia. A northern

Eurasian route would mean that extensive extinction has taken place throughout Eurasia and northern Africa, and a southern dispersal route is considered more likely, either between Africa and Australia via Antarctica, or with a most recent common ancestor in Antarctica with separate dispersals into Australia and Africa. Two clades within the Euryglossinae that had previously only been recognised from wing morphology are shown to have diverged ca. 45 Mya. Log-lineage through time plots show that diversification in the Australian Euryglossinae has been constant over time, and despite their abundance in Australia (approximately 400 species), only three species of Euryglossinae are known from outside Australia. I discuss the potential influence of nesting substrate (i.e., wood or soil) on dispersal ability and on the distributions and abundance of bees in tropical and Mediterranean climates as one possible explanation for this distribution.

As well as being two of the most abundant groups of bees in Australia, Euryglossinae and Hylaeinae also include some of the smallest species of bees in Australia. A generalised least-squares technique for inferring changes in body size in these two subfamilies found that phylogenetic signal is evident to only a small degree in the body size evolution within these two groups. There is some indication that evolution of body size might be adaptive in both groups, but the results are not strongly supported. It has been suggested that the relatively small size of species in both these subfamilies has led to the loss of pollen-collecting scopae. That Euryglossinae and Hylaeinae are not sister-clades infers that the loss of scopae and internal pollen transport has evolved twice at a higher taxonomic scale (i.e. subfamily) in bees and only within the Colletidae. The thesis discusses an alternative possibility for the loss of scopae, which also provides a possible clue to why these bees are so successful in Australia; that being that the nectar-rich larval provisions utilised by all colletids can easily be collected from the abundant and nectar-rich Myrtaceae species in Australia. It may be that euryglossines and hylaeines have adapted to swallowing both pollen and nectar with the high quantity of nectar used in provisioning allowing for a sufficient amount of liquid for regurgitating both materials back at the nest, thus negating the need for pollen-collecting scopae.

This thesis provides further insight into the evolutionary histories of two of Australia's most diverse and abundant bee groups by highlighting their similarities and differences in diversification and life history.

DECLARATION

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

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