LAB SCHWARZ

EVOLUTIONARY DIVERSIFICATION OF AUSTRALIAN GALL-INDUCING THRIPS

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B.Sc. Hons.

A THESIS SUBMITTED FOR THE DEGREE DOCTOR OF PHILOSOPHY

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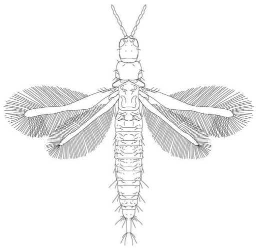
August 2006



CONTENTS

SUMMARY

This work further elucidates processes involved in promoting and sustaining evolutionary diversification within the gall-inducing thrips that specialise on Australian *Acacia*. A phylogenetic approach was taken to determine modes of diversification available to these insects. The extension and revision of the gall-thrips phylogeny is central to the work and primarily focuses on cryptic populations of the *Kladothrips rugosus* and *Kladothrips waterhousei* species complexes. Parallel diversification, where the radiation of the *K. rugosus* and *K. waterhousei* lineages broadly mirror one another, offered a rare opportunity to test hypotheses of coevolution between gall-thrips and their *Acacia* hosts. In the absence of a reliable host *Acacia* phylogeny, indirect inference of insect/plant cospeciation can be arrived at as these two complexes share the same set of host species. The expectation is that if the phylogenies for the gall-thrips complexes show a significant level of concordance, then cospeciation between insect and host-plant can be inferred. Results indicate that the *K. rugosus* species complex comprise populations at species level. A significant level of phylogenetic concordance between the two species complexes is consistent with gall-thrips lineages tracking the diversification of their *Acacia* hosts. Given the less than strict form of insect/host cospeciation, factors impacting host diversification become important to gall-thrips diversification. Gall-thrips radiated over a period during the expansion of the Australian arid-zone. Cycles of host range expansion and fragmentation during the Quaternary could have played a major role in gall-thrips diversity. An interesting feature of resourse sharing amongst the *K. rugosus* and *K. waterhousei* complex members is the apparent absence of competitive exclusion between them. The persistence of this sympatry over millions of years is an unusual feature and merits further investigation.

DECLARATION

I certify that this thesis does not incorporate without acknowledgement 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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“So listen well and hear the call,
and long life to those
who keep the jungle law.”

Rudyard Kipling, 1894.

GENERAL INTRODUCTION

Conspicuous absence of surface water, oscillating drought and flood, extreme temperature, nutrient deficient saline soils, strongly weathered landforms, and millions of years – is the setting of the research presented here. The taxonomic foci are the *Acacia* (Leguminosae), a dominant feature of arid Australia and host to specialist gall-inducing thrips (Insecta: Thysanoptera). Evolutionary conservation of affinities bonding such plant and phytophagous insect groups offer a means of untangling mechanisms driving evolutionary diversification. The theory of coevolution put forward by Ehrlich and Raven (1964) has been one of the more influential explanations for the enormous diversity of phytophagous insects and is a central theme in this work.

Four manuscripts are presented as chapters addressing the following broad questions: (i) is there a reproductive boundary defining two morpho-types that specialise on the same host species; (ii) what systematics describe two species complexes comprising other morpho-types inhabiting different host species and to what extent do insect and insect-plant groups codiverge; (iii) to what degree does host plant diversification facilitate gall-thrips diversification; and (iv) what ecological processes maintain diversity among gall-thrips on *Acacia*?

About 5500 described species of thrips are known throughout the world either living on fungi or green plants exploiting leaves, buds, flowers and some with the ability to form galls. Of these species, approximately 3200 belong to the family Phlaeothripidae in the sub-order Tubulifera. The subfamily Phlaeothripinae comprises approximately 2500 species and at least 250 of these species feed exclusively on *Acacia* foliage (Crespi *et al*., 2004). This group is distributed mainly in Australia, India, and Southeast Asia. Before this work, 22 described thrips species induce galls on phyllodes of Australian *Acacia* (Morris *et al*., 2001). Gall-inducing *Acacia* thrips represent a monophyletic group (Morris *et al*., 2002) implying that the ability to induce galls (see Appendix I) has arisen once. Gall-thrips induce galls on young, actively growing phyllodes (a flat dilated petiole functioning as a leaf) of *Acacia* by the feeding activity of females and fully enclose the founder within a few days after initiation. The number of individuals that develop in the gall varies between species and can be more than one thousand or as few as twenty. All thrips develop through two mobile larval stages, two or three mobile pupal stages, and eclose as adults (Crespi & Mound, 1997).

Acacia gall-thrips comprise cryptic populations at undefined intermediate stages between polymorphism and full species margins. Polymorphisms, cryptic species, host races, biotypes, and ecological races are various stages in differentiation in a continuum from single to separate species (Bush, 1969). Differentiating between them remains a contiguous area. Cryptic species cannot be distinguished on the basis of morphology and might indicate recently diverged taxa (Walker, 1964; Jaenike, 1981). The *Kladothrips rugosus* (Froggatt) species complex is not grossly distinguishable at the morphological level (Crespi & Worobey, 1998; Mound *et al*., 1996). However, variation in gall morphology within the *K. rugosus* complex rivals interspecific gall-form variation. Gall morphology is not strictly unique at the species level. Evidence of divergence, derived from gall measurements (Crespi & Worobey, 1998) among some of these cryptic populations, raises the question of the degree of differentiation among populations in the *K. rugosus* species complex. To identify important factors propagating diversification in this group, species delimitation, host affiliation, historical biogeography, and ecological considerations are explored using phylogenetic approaches.

Taxonomic formalisation of sympatric gall-thrips morpho-types that belong to the *K. rugosus* species complex and specialise on the same host species, establishes a systematic perspective for these taxa. Phylogenetic inference is used as a platform to test hypotheses of cospeciation and convergence between gall-thrips and *Acacia* hosts. Climatic processes impacting the expansion of Australian arid-zone biomes provide background to explaining gall-thrips diversification in terms of host diversification. Resource sharing among gall-thrips taxa specialising on the same host is then explored using a phylogenetic approach to explain the maintenance of gall-thrips diversity across evolutionary and ecological timeframes. Phylogenetic inferences made in each chapter are generated from varying numbers of taxa depending on the objective pursued in each case.

This thesis presents work in the form of multi-authored manuscripts. The Candidate wholly contributed to the laboratory, analysis, and discussion components presented. The following contributions were made by various co-authors: Chapter I drew on the taxonomic expertise of Dr. Laurence Mound, providing explanations of morphological variation in the focal thrips taxa; elements of the literature review in the Introduction and general discussion in Chapter II were written with some helpful commentary from Professor Bernard Crespi. The first two chapters, as with Chapters III and IV, were written with commentary from my supervisor Associate Professor Michael Schwarz and co-supervisor Dr. Tom Chapman. Funding from grants awarded to Schwarz and Chapman was also recognised by their inclusion as authors.

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