GENERAL INTRODUCTION

Three inter-woven themes run through this book. First, we describe the great diversity in structure, ecology, life-history and behaviour within a single lineage of insects living on plants of a single genus, and how it has evolved. Second, we emphasise the remarkable patterns in host-plant relationships within these insects, whereby some plants support multiple related and unrelated species, most support none, and some insect-plant relationships have evolved independently, in parallel, across different insect clades. Third, we analyse the various ways in which the complex interdependencies among these insect species have driven patterns of insect diversity, behaviour, and host-plant association, through the creation, exploitation, and opportunistic use of niches.

The plant genus involved is *Acacia*, of which more than 1000 species are known across Australia, being referred to by the generalised name of wattles. This genus, together with those quintessentially Australian plants, the gum trees of the genus *Eucalyptus*, dominates the flora and landscape of this ancient landmass. The insects involved are thrips or Thysanoptera, and all are members of a single lineage within one subfamily, the Phlaeothripinae. At least 250 species of phlaeothripines are now known to feed exclusively on the foliage of *Acacia* species, whereas no phlaeothripine is associated with the foliage of any *Eucalyptus*.

Much of this volume is concerned with ‘taxonomy’, a subject area considerably undervalued in modern biological education. Taxonomy has two objectives, to distinguish and provide names for those groups of populations that we call species, and to provide a systematic classification of those species with the aim of reflecting their evolutionary relationships. These two products of taxonomy provide a service to other biologists, facilitating communication about living systems, and give a foundation from which we can consider how these systems have evolved and diversified. If we accept the dictum that in biology nothing makes sense except in the light of evolution, then taxonomy is the process by which we first ignite that light.

Studies in biologically diverse parts of the world, on the ecology, interdependence and evolution of organisms, must overcome extensive scientific and logistic problems—with many of the species unrecognised, undefined and un-named. In taking up a study of the thrips associated with *Acacia* in Australia we faced this problem of high diversity. When these studies first began, less than 10% of the thrips fauna associated with *Acacia* in Australia was recognised. Of the 235 species of thrips named in this volume, 140 are described here for the first time, and a further 58 were described during earlier phases of the current project. Progress in the project has depended on close collaboration between different types of research workers, with the process of descriptive taxonomy considered as an essential element in broader studies on ecology, behaviour, and host-plant use.

The project originated in a descriptive account by a taxonomist (Mound) at the Natural History Museum, London, of 17 genera and 55 species of phlaeothripines found on *Acacia* during fieldwork funded by CSIRO in 1967 and 1968. Observations on intra-specific polymorphism attracted the attention of an insect behaviour specialist (Crespi) who had demonstrated that such polymorphism in some Northern Hemisphere phlaeothripines is related to fighting behaviour. His studies, funded by the National Geographic Society, then led to the discovery of soldier morphs, and the recognition that some species of Australian thrips are thus eusocial. The potential relationship between sociality and haplodiploidy, exhibited by both Hymenoptera and Thysanoptera, attracted Michael Schwarz of Flinders University to join the project, leading to the involvement of a series of graduate and post-graduate students, supported by the Australian Research Council. One of those (Morris) used molecular techniques to examine the relationships between a range of the thrips taxa; subsequently he was supported by the Australian Biological Resources Study to help prepare this volume. Finally, Bruce Maslin, an expert on the diversity of Australian *Acacia*, has prepared a **Botanical Annexe** in which he discusses the phylogenetic relationships between the *Acacia* species used by these thrips.

The diversification of *Acacia* in Australia and the exploitation by insects of the many available species, provide an extraordinarily rich source of evolutionary problems. Thus far, this work has focused primarily on the evolution of social behaviour in this group, their phylogenetics, the evolution of their diverse life histories, and, most recently, the evolution of insect-host plant associations. Future studies of speciation, biogeography, and sex allocation will build upon this broad base of information, as we hope to further develop these insects into a ‘model clade’ for addressing behavioural, ecological, and other questions in the context of complete species-level phylogenies.

Considered as a map to the complex biological relationships between *Acacia* plants and thrips, this volume owes more to the 15th than the 21st Century. Major features are now clear, and some details are established, but the traditional warning, ‘here be demons’ might well appear in the margin, particularly if we consider the bizarre body forms and curious biologies of some of the thrips, and their unexplained distribution patterns across the enormous arid landscape of Australia. May this treatise inspire readers to seek them and learn their secrets.

PART I

ECOLOGY AND EVOLUTION OF AUSTRALIAN ACACIA THRIPS

SYSTEMATIC FOUNDATIONS

In Genesis, light and order were brought forth from chaos, and the world's biota emerged in six metaphorical 'days'. The job of an insect systematist is similar but considerably more laborious: from a complex assemblage of forms with sparse biological information attached, to organise, describe and categorise diversity into more or less natural units that share genes. Most biologists only come to appreciate these labours when they are compelled to study a group whose taxonomy is in a chaotic state. Until then, they might view taxonomy as the purview of specialists using arcane knowledge for dubious return on investment, rather than the domain of the only scientists fulfilling God's instructions to Adam that he name each living thing.

This volume provides a comprehensive treatment of *Acacia* thrips systematics and integrates it with other areas of their biology. As such, the interplay between biology and systematics assumes paramount importance. Non-systematists benefit from systematics in myriad ways. First, without systematics, other biologists remain ignorant not only of what biological units they are studying or seeking to conserve, but what they *could* choose to study. Indeed, the behavioural studies by Crespi (1992a,b) that led to a resurgence of interest in this group were driven by, and wholly dependent upon, Mound's (1970, 1971) systematic work. Second, the morphology that most systematists use in species description provides an initial guide to ecological and behavioural phenomena most worthy of study, since morphology sits at the doorstep into natural history, behaviour, ecology and evolution. Finally, inference of robust phylogenies requires a reasonably complete taxonomy, and morphological data commonly serve as a touchstone and cross-check for the validity of phylogenies inferred with DNA data.

It would be misleading to state that systematists similarly need non-systematic biologists, because most systematists are also accomplished biologists in non-systematic fields. But systematists gain from the studies of other biologists in that non-morphological information collected by others, such as habitat, host plants, phenology, biogeography, and behaviour, can be crucial to delineating species and higher taxa. Moreover, DNA-based phylogenetic and population-genetic studies, motivated largely by evolutionary questions, serve incidentally to improve the quality of species recognition and classification—as has certainly been the case with *Acacia* thrips.

The actual conduct of systematics may seem a mysterious black art to the uninitiated, but it can be surprisingly straightforward in practice. Imagine that a big car has just driven past you. What was it—make and model? You might not know because you have no interest in cars, but many 16-year old boys could have told you it was a Ferrari because of the engine's growl and the prancing horse on the hood. Many boys could even tell you the model name and year of design. How do they do it? Experience, plus the desire to know. That is the way each of us identifies anything, and it is certainly the way that thrips species are identified. Most taxonomists can recognise several hundred species of their charges. Moreover, most of them have learned to take into account the many variants that some of the species exhibit—and extrapolate through experience to predict the variation likely to occur in a species they have seen from only one specimen previously.

But taxonomists not only identify, they also classify: associating an entity with its closest relatives after recognising it. For example, how do you recognise your brother? Can you state how he can be told from the millions of other males on the planet? Species are also 'individuals', with the evolutionary habit of varying in time and space. But now your brother dyes his hair red, grows a beard and eats so much that he doubles his body weight—yet you still recognise him! More problematic is how can he be classified objectively as belonging to a particular family or group? With enough sampling of DNA from other *Homo sapiens*, it might be possible to predict such a relationship. But note the word 'predict'. That is all that can be done.

Similarly, that is all a taxonomist does—*predict* that a specimen belongs to a particular species (that it could breed successfully with other members of that species, in accordance with the biological species concept). Moreover, closest relatives are also *predicted* based on experience with specimens and literature. Every taxon that is described is neither more nor less than a scientific hypothesis that is testable by the collection of further character data, preferably of a different nature, and by collection of more specimens from different localities (Gaston & Mound 1993).

Fundamentally, what taxonomists do in identifying and classifying represents pattern recognition. But although clear and distinct patterns do not always occur in nature, as 'rationalising animals' scientists are often compelled to enforce such patterns, to wring as much presumed order from chaos as possible. That is why so many taxonomists are Platonic 'essentialists', for whom a species or genus must possess a predetermined set of character states. They could not recognise your brother with red hair! Such essentialism is especially problematic when selection has produced continuous or discontinuous polymorphism within populations (as we find in the complex fore leg allometry expressed by many species of the *Acacia* thrips), and among-population variation in any number of traits.

Now let us raise further complications. Perhaps DNA failed to confirm that your brother was actually closely related to you. Why? As a good son or daughter you would hotly deny maternal miscegenation, just as a good professor of biology would probably deny the possibility of a miscegenating thrips—despite the fact that we know that more than 10% of bird species have mated outside their species boundaries (Grant & Grant 1992). We raise this issue because molecular taxonomists tend to be just as 'essentialist' in their approach as morphological taxonomists, whereas evolution requires organisms to be opportunistic.

But ultimately, as biologists, we take a judicial consensus of all our information, and produce predictions (hypotheses) of identity and group membership that can be tested with additional data. Our criterion for assigning generic and higher-taxon status is monophyly, inferred here from DNA-sequence data. And our intended criterion for species is interbreeding, which usually entails monophyly or paraphyly at this lower level (Baum & Shaw 1995; Avise 2000). However, the common absence of molecular-marker or interbreeding data means that in practice, morphology and other aspects of biology serve as surrogates. Moreover, the apparent presence of sets of host-plant-associated sibling species or host races (Drès & Mallett 2002) in many *Acacia* thrips species (e.g. *K. rugosus*, *K. waterhousei*, K. *augonsaxxos*, and *K. schwarzi*) means that some names represent much more hypothetical concepts than others, which should help to target further studies.

Taxonomy is no more a black art than behavioural or evolutionary ecology—it just requires sufficiently deep knowledge of morphology and other aspects of biology for a chosen group, and sufficient dedication to effect organisation from dizzying complexity (Simpson & Cracraft 1995). With this volume we hope to encourage its practice, especially by evolutionary biologists who already appreciate the diversity of variation within and between species, and who come well-supplied with the molecular and analytic tools needed to illuminate biological history and ongoing processes. Indeed, analyses of the causes of speciation, diversification, and adaptive radiation, which remain among the deepest unresolved problems of our generation (Schluter 2000), lend themselves naturally to combined taxonomic and behavioural-ecological-evolutionary approaches. Perhaps only through such increased integration of taxonomy with other biological disciplines can the art of this science be kept alive and vigorous, given its current trend towards extinction.

GEOGRAPHIC AND BIOLOGICAL BACKGROUND

THE CONTINENT OF AUSTRALIA

Australia has a land area similar to that of the United States of America, with the distance between Sydney and Perth on the eastern and western coasts respectively, being about equal to the distance from New York to Los Angeles. The distance between Hobart in the south and Darwin in the north is greater than the distance from Darwin to the capital of Indonesia, Jakarta. The enormous size and latitudinal range of the continent involves many different climatic conditions. Hobart is in a zone of cool moist forest, whereas Darwin is in the tropical monsoon zone. Between these two is one of the most extensive arid zones in the world. These Australian deserts developed over the past 20–30 million years as the continent drifted north and became increasingly arid, whilst the arid zone flora apparently developed from plants that had been adapted to dry habitats in the rain forests (Smith 1982; Barlow 1994; Hill 1994; Johnson & Burrows 1994). As a result of its size, climatic diversity and isolation as an island, Australia is one of the most biologically diverse areas of the world, with, for example, about three times the number of vascular plant species as are found in North America.

THE PLANT GENUS *ACACIA*

About 1000 Australian species are recognised in *Acacia*, the most species-rich plant genus on this continent. The vast majority of these do not, after their juvenile stages, bear the bipinnate leaves that are typical of legume plants of the Mimosaceae. Instead they have leaf-like expansions of the petioles, called phyllodes (Figs 2, 3). The **Botanical Annexe** by Bruce Maslin gives an account of the systematics of *Acacia*, particularly the sections relevant to any study of thrips. Of the three major sections of this plant genus, the Phyllodineae, the Juliflorae, and the Plurinerves, the thrips are associated almost exclusively with members of the second and third sections. The reasons for this asymmetric association are not clear, and there are various possibilities. There may be a simple physical reason. The phyllodes in species of the Phyllodineae have a single vein, and this structure is possibly more difficult to manipulate than the multinerved phyllodes found in species of the other two sections. In addition, there may be a more subtle physiological basis, perhaps as a consequence of the species of *Acacia* varying in their root nodule flora of nitrogen-fixing bacteria. These are subject areas that require investigation.

The main ecological correlate of the *Acacia* species that are utilised by Australian thrips is that nearly all of them are restricted to the arid or semi-arid regions. For the gall-inducing *Acacia* thrips, this pattern is in keeping with other gall-inducing insects, these being disproportionately found on sclerophyllous plants on poor soils in warm climates (Fernandes & Price 1991; Blanche & Westoby 1995; Price *et al.* 1998; Blanche & Ludwig 2001). Such harsh conditions, and the habit of sclerophyllous plants to retain their leaves for long periods, have apparently favoured inducing and living in more or less enclosed domiciles on host plants, where the inhabitants may also be relatively safe from predation and parasitism. In *Acacia* thrips, induction and use of such valuable, long-lived habitats has served as the template to generate much of the behavioural and morphological diversity that we observe. Indeed, since many of the thrips on Australian *Acacia* can be considered as parasites of their hosts (rather than herbivores), the interactions between the two are expected to be complex, intimate, and antagonistic—so understanding the biology of the thrips also necessitates study of the biology of the plants themselves.

THE INSECT ORDER THYSANOPTERA

The insect order Thysanoptera includes approximately 5500 described species worldwide, and possibly as many more undescribed (Mound & Heming 1991; Mound & Teulon 1994; Mound 2002). The order is divided into two suborders and nine families, with eight of these families containing 2300 of the known species and placed in the suborder Terebrantia. The second suborder, the Tubulifera, includes about 3200 species and these are placed in a single family, the Phlaeothripidae. Of these species, 700 feed only on fungal spores and are placed in the subfamily Idolothripinae, with the remaining 2500 comprising the biologically diverse subfamily Phlaeothripinae. All of the thrips species discussed here from *Acacia* are apparently leaf-feeding phlaeothripines, and there is no evidence that any of them are predatory. Indeed, the available molecular evidence suggests that these species represent a single diverse lineage (Morris *et al.* 2001). If the phlaeothripines on Australian *Acacia* constitute a single lineage, then the genus *Acacia* has been invaded by thrips only once. This single invasion suggests some unexplained difficulties for phlaeothripines in colonising these plants, or interspecific competition that has prevented host shifting after the initial radiation. But given that fewer than 800 species of Thysanoptera are currently described from Australia, the 235 species of Phlaeothripinae from *Acacia* recognised here represent 29% of the total thrips fauna of this continent.

The classification of the Phlaeothripinae is very weak above the genus level, with half of the genera worldwide containing only a single species. Within the subfamily, three informal ‘lineages’ have been recognised (Mound & Marullo 1996), based partly on morphology and partly on biology. The *Phlaeothrips* lineage includes almost half the described species, most feeding on fungal hyphae. The *Haplothrips* lineage includes most of the flower-living phlaeothripines, but also a number of predatory species. The *Liothrips* lineage includes a wide range of leaf-feeding species, some of which induce galls (Mound 1994). The phlaeothripines found on Australian *Acacia* appear to fall within the *Liothrips* lineage (Mound & Marullo 1996).

The main genetic and morphological traits of thrips relevant to their ecology and behaviour include: (1) haplodiploidy, which allows facultative sex ratio manipulation and virgin birth, and may favour forms of sociality (Stannard 1968; Crespi 1993; Kranz et al. 2000); (2) piercing-sucking mouthparts, used in *Acacia* thrips to suck cell contents and perhaps also inject gall-inducing compounds; (3) minute size and fringed wings, which facilitate using tiny enclosed spaces, and engender weak powers of flight; (4) wing polymorphism in some species, which can serve as a template for intraspecific divergence in ecology and behaviour; (5) fore leg enlargement and modifications that serve as weaponry or provide means to modify the habitat; (6) accessory gland secretions, used to create domiciles among phyllodes; and (7) dorsoventral flattening, associated with a strong tendency to seek small crevices and enclosed spaces in which to shelter. In the thrips species found on Australian *Acacia* this sheltering tendency is pronounced and is presumably a crucial survival trait under the adverse conditions that usually prevail in the arid and semi-arid areas in which these plants often grow. As with most small insects, thrips require relatively high humidity to survive, and thus in arid environs they must find shelter in any small enclosure that provides a suitable microclimate.

The survival of thrips in arid climates appears to be directly dependent on the availability of galls, bark fissures, and other shelters or crevices to provide sheltered spaces in which to raise their brood. In the lineage of thrips that is found on *Acacia*, the ability to manufacture a suitable shelter has arisen and this, in turn, has led to a proliferation of species, through a number of mechanisms. Not only have the species that build their own shelters proliferated, but a host of other species that also utilise these domiciles have evolved and radiated in concert. This has resulted in the diverse array of thrips species that are now found on *Acacia*.

ANALYSING BIODIVERSITY WITH 'MODEL CLADES'

Many researchers work with so-called 'model systems'—species that are especially useful for addressing particular biological questions. In most cases, such species are amenable to study because they can be bred in the laboratory, their genetics and development are reasonably well-understood, and they are easily observed and manipulated in the field or laboratory. Due to the resultant ease of study, copious information is available on most aspects of the biology of 'model' species, so they can serve as testing grounds for novel hypotheses, and guides to research on species that are less amenable to scientific domestication. The vinegar fly, *Drosophila melanogaster*, provides a prime example, but others include lab mice, the nematode *Caenorhabdites elegans*, *Saccharomyces* yeasts and the bacteria *Escherichia coli* for genetic studies, and *Poecilia* guppies and *Polistes* wasps for analyses of behaviour (Dugatkin 2001).

Model species yield deep insights into mechanisms and provide robust tests of theory, but they have their limits. First, the very traits that make many of them so useful to biologists—especially rapid generation times and simple ecology—may make them unusual and non-representative of the bulk of biodiversity, such that generalisations are difficult to draw. Second, the study of model species sacrifices taxonomic scope for depth, such that we gain detailed knowledge of only very few taxa, far-flung across the tree of life. As a result, such studies cannot provide the evolutionary, phylogenetic, or comparative perspective necessary to draw inferences for entire clades, over both micro- and macroevolutionary timescales.

We suggest that these drawbacks can be overcome by integrating the model systems concept into a systematic, phylogenetic framework, to yield the concept that we call ‘model clades’. Model clades have two main components: (1) robust taxonomy coupled with phylogenies at the species level, including a sufficiently high proportion of taxa to capture extant diversity; and (2) data on biogeography, behaviour, ecology, life history, morphology and other aspects of phenotype and genotype for enough of the species to allow robust, multidisciplinary comparative tests of hypotheses. Large, species-level phylogenies have become easier to assemble each year due to technical advances in DNA sequencing, phylogeny reconstruction, and analytical tools (Hillis *et al.* 1996). Similarly, analyses of phylogenetically structured data have prospered, especially since Felsenstein (1985) introduced the method of independent contrasts; there is now a large suite of methods available to address such issues as adaptive correlated evolution, constraint, inference of ancestral states, and evolutionary dynamics across trophic levels (Ronquist & Nylin 1990; Harvey & Pagel 1991; Maddison & Maddison 1992; Doughty 1996; Ronquist 1997; Garland *et al.* 1999; Martins 2000). Although previous comparative tests of adaptation have often used many species, taxon sampling density is usually low, such that patterns of change are inferred only crudely, and data sets comprise relatively few variables, such that unobserved causal links are difficult to identify and avoid (Ridley 1989). The advantage of a research program based on model clades is that it provides cross-disciplinary depth in an explicitly phylogenetic context, enabling analyses of the evolution and coevolution of diverse traits. Coupled to within-species analyses of functional design and selection measurement (Crespi 2000), studies based on model clades allow fine-scale dissection of interacting macroevolutionary changes, and thus there emerges a much more thorough picture of the evolutionary processes that generate diversity.

One of our main aims in this book is to pioneer a model clades approach for the analysis of behaviour, ecology, and life-history in Australian thrips on *Acacia*. Thus far, we have sufficiently detailed biological data to implement the approach mainly for the species that induce galls, with special focus on the species with soldier castes and their close relatives. For the other groups of thrips on *Acacia*, we hope that the work presented here will serve as a basis and impetus for the data collection needed to implement this approach for them as well.

BEHAVIOURAL-ECOLOGICAL DIVERSITY

The thrips on Australian *Acacia* are similar in that all feed on plant cell contents, but this similarity belies tremendous diversity in morphology, behaviour, ecology and life-history. Mound and Moritz (2000) proposed categorising this diversity into six distinct ‘suites’, based on the way in which the thrips create or utilise domiciles: (1) ‘gall-inducers’; (2) ‘domicile-constructers’ (that glue phyllodes together); (3) ‘kleptoparasites’ (that usurp galls or glued phyllodes); (4) ‘inquilines’ (that cohabit domiciles without usurpation); (5) ‘opportunists’ (that live in abandoned or old domiciles); and (6) ‘squatters’ (that live in cavities not generated by other thrips, mainly on young stems). Subsequently, Morris *et al.* (2002a) condensed this list of six suites to four, by incorporating the kleptoparasitic and inquiline species into a single 'parasitic' suite (here called 'exploiters'), and combining the opportunists and squatters into 'opportunists'.

These four suites constitute alternative adaptive peaks with regard to utilisation of enclosed spaces on *Acacia*. Associated with each peak is a large set of behavioural and life-history traits that are driven by the nature of the domicile—its size, shape, dispersion, duration, defensibility, expansibility, quality as food, and how it is obtained. The high behavioural-ecological diversity represented by these four suites means that the thrips on Australian *Acacia* can be considered as a microcosm or model for the diversity found among all phytophagous insects. As such, analysing the diversification of this group should provide insights into how these, the most speciose of all animals, have evolved.

THE FOUR ECOLOGICAL-BEHAVIOURAL SUITES

Suite 1: Gall-inducers

The gall-inducing suite contains all of the species of thrips known to induce galls on phyllodes of Australian *Acacia* (Table 1). This currently includes 22 described thrips species from approximately 50 different *Acacia* species; several putative species from *Ac. aneura*, *Ac. nyssophylla*, *Ac. colletioides*, *Ac. mackeyana*, and *Ac. masliniana* whose recognition requires DNA data; also numerous apparent host-plant specific sibling species in the nominal species *K. rugosus*, *K. waterhousei*, *K. augonsaxxos*, and *K. schwarzi* (Crespi *et al.* 1998). These gall-inducing thrips include all of the species that were treated under the generic names, *Kladothrips*, *Oncothrips* and *Onychothrips* in previous work on these insects. However, we now recognise that these genera do not represent natural groups, and the relationships between the species are more accurately represented by a single monophyletic genus *Kladothrips* (Morris *et al.* 2001).

Gall induction and form:- The exact mechanism of galling is not well understood in these thrips. However, gall-induction has been studied in other galling insects, and it is believed to be a plant response triggered by a chemical or physical stimulus delivered by the insect (Ananthakrishnan 1984; Weis *et al.* 1988; Shorthouse & Rohfritsch 1992; Ananthakrishnan & Gopichandran 1993; Williams 1994; Mound & Kranz 1997). In thrips, unlike most galling insects, galls result from feeding activity (and possibly also injection of chemicals) of an adult female foundress, rather than oviposition behaviour (Crespi *et al.* 1997). The gall-inducing thrips on *Acacia* are among the few thrips species that are capable of causing a fully enclosed gall to be produced by a plant. The feeding activity of thrips on the phyllodes of certain *Acacia* species causes the tissues adjacent to the site to proliferate, and results in localised rapid growth of the phyllode tissues (Crespi 1992a; Mound 1994; Crespi *et al.* 1997; Mound & Kranz 1997; Crespi & Worobey 1998). A female thrips typically feeds near the centre of a phyllode on the dorsal surface, and the abnormal expansion of the tissues in the centre of the developing phyllode causes a bubble-like outgrowth that quickly forms a pouch within which the foundress is sealed (Figs 4–8). In some species, the effect of feeding by a thrips spreads along the length of the phyllode causing an elongate pouch, or even giving the impression that the phyllode has been rolled laterally (Fig. 12; Crespi & Worobey 1998).

Table 1. Ecological, behavioral, and life history traits of gall-inducing thrips on Australian *Acacia*.

Species	Host plant	Gall size and shape	Male present at founding?	Micropterae present?	Pupation	Physogastry?
K. acaciae	*Ac. harpophylla*	large, fat elongate pouch	often	no	in soil	yes
K. antennatus	*Ac. aneura, paraneura, ramulosa, adsurgens,* related form on *aff. citrinoviridis*	large, fat elongate cylinder	no	no	in gall	partial
K. arotrum	*Ac. aneura*	large and spherical	no	no	in gall	yes
K. augonsaxxos	*Ac. aprepta, grasbyii, kempeana, resinimarginea, rhodophloia, stowardii*	large and spherical	no	no	in gall?	yes
K. ellobus	*Ac. cambagei, georginae*	medium-sized, flat round disk	often	no	in soil	yes
K. habrus	*Ac. melvillei, pendula*	small, lens shape	no	yes	in gall	no
K. hamiltoni	*Ac. cambagei, georginae*	medium-sized, skinny elongate cylinder	very rarely	yes	in gall	no
K. harpophyllae	*Ac. harpophylla*	medium-sized, skinny elongate cylinder	often	yes (hemi-macropterous)	in gall	no
K. intermedius	*Ac. oswaldii*	small, lens-shape	no	yes (hemi-macropterous)	in gall	no
K. maslini	*Ac. orites*	medium-sized conical pouch	unknown	no	in gall?	unknown
K. morrisi	*Ac. calcicola*, related forms on *Ac. carneorum and Ac. aff. cuthbersoni* (‘gizzard wattle’)	very large, fat elongate cylinder	no	yes	in gall	no
K. pilbara	*Ac. citrinoviridis*	large, fat elongate cylinder	no	no	in gall	partial
K. rodwayi	*Ac. melanoxylon*	small, lens-shape	no	no	in gall	no
K. rugosus	*Ac. ammophila, cana, enervia, loderi, maranoensis, melvillei, microcephala microsperma, omalophylla, papyrocarpa, pendula, sibilans, tephrina*	large elongate pouch or spherical, sometimes with ribs or spikes on the exterior surface of the gall	often	no	in soil	yes
K. schwarzi	*Ac. aprepta, kempeana, resinimarginea, rhodophloia, stowardii*, related forms on *grasbyi, sibina*	small, skinny elongate cylinder	no	no	in gall	no
K. sterni	*Ac. aneura, catenulata, ramulosa*	large, spherical, multilocular	no	apterous gall-morph (non-soldier)	in gall	yes
K. tepperi	*Ac. aneura, paraneura*	large, spherical	no	no	in gall	yes
K. torus	*Ac. citrinoviridis*	large, spherical	no	no	in gall?	yes
K. waterhousei	*Ac. ammophila, ancistrophylla, cana, enervia, inceana, loderi, maranoensis, microcephala, microsperma, omalophylla, papyrocarpa, sibilans, tephrina*	small, skinny elongate cylinder, or lens shape	no	yes	in gall	no
K. yalgoo	*Ac. masliniana, mackeyana, nyssophylla*	small, elongate cylinder	no	no	in gall	no
K. xiphius	*Ac. xiphophylla*	large, fat elongate cylinder	often	no	in gall	unknown
K. zygus	*Ac. pickardii*	large, fat elongate cylinder	no	no	unknown	unknown

In other gall-inducing thrips species, the galling stimulus remains more localised and the pouch expands at right angles to the surface of the phyllode forming a cone or balloon-shaped gall (Figs 13, 14).

In most species of Australian *Acacia* thrips, feeding by a single adult female, the foundress, induces a gall, but in some species, such as *Kladothrips rugosus*, *K. acaciae*, *K. ellobus*, and *K. harpophyllae*, an adult male is also found in up to 50% of newly induced galls (Fig. 14). Founding by both sexes has also been noted at a much lower frequency in *K. hamiltoni*, and has also been observed rarely in *K. intermedius* (formerly *Oncothrips tepperi*) (Kranz, unpubl. data) (Table 1).

The galls induced by thrips on *Acacia* are usually highly species-specific. However, in some nominal species such as *K. waterhousei* and *K. rugosus*, gall form will vary across host plant species, and also sometimes the same apparent species of gall thrips will produce two different gall forms on the same host (Crespi & Worobey 1998). Gall morphology varies from simple rolled phyllodes, to elongate pouches, to hollow spheres or irregular shapes (Table 1, Figs 4–14). Additionally, some galls exhibit further complexities, being covered with spikes, hairs, or ridges, whereas others have internal structures such that the inside of the gall is divided into numerous interconnected compartments.

Behaviour:- The behavioural diversity of the gall-inducers centres on the gall habitat, which serves as food, shelter, and nursery. *Acacia* thrips, like other galling insects, enjoy only a narrow window for gall induction, when the plant produces a flush of young phyllodes. Since this resource is severely restricted spatially as well as temporally, phyllodes suitable for galling, and incipient galls, are extremely valuable. Many species of gall-inducers have evolved intraspecific fighting morphology and behaviour to compete for this valuable resource. Thus, during the gall initiation period, females of *Kladothrips arotrum*, *K. intermedius*, *K. rugosus* on *Ac. pendula*, and *K. tepperi*, have been observed to fight one another, using their enlarged, armed fore legs, in defence of galling sites or developing galls (Crespi 1992a). These fights are often lethal, as evidenced by a considerable number of dead bodies of vanquished rivals in young galls containing a single live foundress (Crespi 1992a). Intraspecific female fighting can also be inferred as highly probable for most other species of gall-inducers that have similar fore leg modifications. Similarly, in species with bisexual founding, the males fight one another during gall initiation, leading to high rates of mortality. Among gall-inducing aphids, such fighting over galling sites has evolved convergently, apparently in response to the same selective pressures (Whitham 1979; Aoki & Makino 1982; Akimoto 1989, 1996; Akimoto & Yamaguchi 1997).

Foundresses will not only fight one another during gall initiation, they will also fight invading kleptoparasitic *Koptothrips* that attempt to usurp the gall after it is formed. Such interspecific fighting has been observed in *Kladothrips intermedius* and *K. habrus* (Crespi 1992b), and, given the fatal consequences of a *Koptothrips* invasion, we hypothesise that it occurs in all of the gall-inducers that are beset by these enemies to any substantial degree.

Intraspecific and interspecific fighting by foundresses may have served as a crucial preadaptation for the evolution of within-gall morphs, which we refer to as ‘soldiers’, that also attack invading *Koptothrips*. In *Kladothrips hamiltoni*, *K. harpophyllae*, *K. morrisi*, *K. waterhousei*, *K. intermedius*, and *K. habrus*, some or all of the foundresses’ first-brood females and males eclose within the gall in a distinct cohort, well before the developing brood that will later disperse. These soldiers exhibit reduced wings, enlarged fore legs (relative to foundresses), pale cuticle, and short antennae (Fig. 22). When the gall is breached by a *Koptothrips*, soldiers will attack it, attempting to grasp and hold it with their fore legs, driving their sharp fore tarsal teeth into its cuticle. The *Koptothrips* fights back using its fore legs, and either is killed, or succeeds in killing off all of the gall inhabitants, after which it produces a brood of its own within the gall.

Life histories:- The life histories of nearly all of the gall-inducers can be characterised into four modes, each representing a set of traits that together comprise a coordinated strategy for survival and reproduction.

Species with soldiers, which we refer to as 'fighters', have two full or partial generations within the gall, and the galls are relatively long-lived (Crespi & Mound 1997), some persisting for a year. These species have small brood sizes and large eggs compared to other gall-inducers on *Acacia*, and they inhabit galls that are relatively small and have high ratios of inner surface area to inner volume (Crespi & Worobey 1998; Kranz *et al.* 2001a,b; 2002; Crespi, unpubl. data). In most species, emergence from the gall occurs at the second-instar stage, as fully grown larvae apparently leave via small openings at each end of the gall lips, drop to the ground, and pupate in cracks in the soil. The one exception is *Kladothrips intermedius*, in which the adults eclose within the gall, and disperse from it only when new phyllodes are available for gall induction (Crespi 1992a).

At the opposite end of the life-history spectrum are what we call 'fliers', species that lack soldiers and inhabit relatively large, spherical, short-lived galls. These species include *K. acaciae*, *K. ellobus*, and *K. rugosus*, and they all have bisexual founding, very large brood sizes, commonly extreme physogastry (Figs 14, 343), small eggs, and dispersal from the gall by second-instar larvae. Whereas the fighter species have evolved to repel *Koptothrips* via soldier defence, fliers apparently seek to escape in time, leaving only a narrow window of vulnerability and investing little in defence. We hypothesise that their life history strategy involves lower survivorship of their galls, and that this is counterbalanced by their much higher fecundity (e.g. Kranz *et al.* 2002). The divergences between fighter and flier thrips is paralleled in the gall aphids, where species with soldiers inhabit galls that are longer-lived than those of their soldierless relatives (Crespi & Mound 1997; Stern & Foster 1996, 1997).

In contrast to fighters and fliers, 'hiders' inhabit galls that are tightly closed and have a very low incidence (or an absence) of invasion by *Koptothrips*. These species, which include *Kladothrips antennatus*, *K. arotrum*, *K. augonsaxxos*, *K. pilbara*, *K. tepperi*, *K. schwarzi*, *K. torus*, and *K. zygus*, tend to inhabit the highly arid interior of Australia, and most of them make relatively large spherical or elongate galls that support large broods (Figs 1, 9). The progeny apparently all eclose within the gall, and appear to remain there for some, perhaps long, period of time, until the gall drops to the ground, dries, and opens.

The fourth life-history mode, found only in *Kladothrips sterni* and *K. morrisi*, can be termed 'expanders', because both of these species induce very large galls that contain a wingless within-gall morph that is relatively highly fecund, and whose breeding appears necessary to fully utilise the gall's capacity. In *K. morrisi*, this within-gall morph has enlarged fore legs, and although it helps to defend the gall against *Koptothrips*, its propensity to defend is low compared to the other species with soldiers (Perry *et al.* 2002), and its fecundity is high and comparable to that of the foundress (Kranz *et al.* 2001b, 2002; Chapman *et al.* 2002). By contrast, the within-gall morph of *K. sterni* is unarmed, appears larviform and neotenic, and is unlikely to defend (Fig. 23), especially since *Koptothrips* are not known to invade its galls.

Table 2. Ecological, behavioural, and life-history traits of phyllode-glueing thrips on Australian *Acacia*.

Species	**Host plant**	**Domicile type**	**Pleometrosis**	**Colony structure**	**Behaviour**
Carcinothrips					
tania	*Ac. stowardii*	2 phyllode, webbing, sealed	no	single generation	
leai	*Ac. kempeana, torulosa*				
Dunatothrips					
aneurae	*Ac. aneura*	multi-phyllode, webbing, open or sealed	most	multiple generations	de-alation in some species
armatus	*Ac. aneura*				
aulidis	*Ac. catenulata*				
chapmani	*Ac. ramulosa*				
gloius	*Ac. lysiphloia,*				
skene	*Ac. catenulatea*				
vestitor	*Ac. aneura*				
Lichanothrips					
albus	*Ac. harpophylla*	2 phyllode, glue, open or sealed	no	single generation	
calcis	*Ac. calcicola*				
curvatus	*Ac. harpophylla*				
magnificus	*Ac. harpophylla*				
metopus	*Ac. harpophylla*				
pastinus	*Ac. cambagei, georginae*				
pulchra	*Ac. harpophylla*				
semifuscipennis	*Ac. harpophylla*				
triquetus	*Ac. harpophylla*				
xouthus	*Ac. argyrodendron*				
Panoplothrips					
australiensis	*Ac. shirleyi*	2 phyllode, webbing, open	no	single generation	
Paracholeothrips					
calcicolae	*Ac. calcicola*	multi-phyllode, glue, open or sealed	no	single generation	group foraging outside the domicile in some species
clavisetae	*Ac. ammophila, cana, maranoensis, melvillei, microcephala, omalophylla, papyrocarpa, pendula, sibilans, tephrina*				
gracilis	*Ac. 'aff' citrinoviridis*				
mulgae	*Ac. aneura*				
validus	*Ac. ramulosa*				
Sartrithrips					
areius	*Ac. citrinoviridis*	2 phyllode, webbing, sealed	no	single generation	de-alation in some species
bapto	*Ac. adsurgens*				
luctator	*Ac. stowardii*				
mars	*Ac. rhodophloia*				
popinator	*Ac. aprepta, kempeana, torulosa*				
pyctus	*Ac. grasbyi*				
vesper	*Ac. kempeana*				
Truncatothrips					
terryae	*Ac. kempeana*	2 phyllode, webbing, sealed	no	single generation	

Both species inhabit galls that are voluminous but have shapes that lead to an increased ratio of inner surface area to volume, elongate in *K. morrisi* but with a lobed interior in *K. sterni*. Such a gall form may help in providing sufficient food for a large and persistent population.

Suite 2: Domicile-builders (phyllode-gluers)

Inducing a gall is not the only way to create an enclosed space using one or more *Acacia* phyllodes. The thrips that we refer to as domicile-builders, or phyllode-gluers, construct a living space using an anal secretion to bind two or more phyllodes together (Table 2). The ability to construct domiciles in this manner appears to be unique and has not been observed in any other thrips species worldwide. The genera of thrips whose species characteristically construct glandular-secretion domiciles include *Carcinothrips*, *Dunatothrips*, *Lichanothrips*, *Panoplothrips*, *Paracholeothrips*, *Sartrithrips* and *Truncatothrips* (Mound & Morris 1999, 2000, 2001; Morris *et al.* 2002a,b). The majority of *Acacia* species that are hosts to gall-inducing thrips are also utilised by one or more species of these domicile-building thrips. Indeed, there are only four incidences of domicile-building thrips species known from an *Acacia* that is not known also to host gall-inducing thrips (*Ac. shirleyi*, *Ac. lysiphloia*, *Ac. torulosa* and *Ac. argyrodendron*).

Domicile construction and form:- As with the galls induced by *Acacia* thrips, there is considerable variation in the architecture of the domiciles that are constructed by thrips on *Acacia* (Table 2). Domiciles may consist of a pair of phyllodes glued together, such that the ventral surface of one is attached to the dorsal surface of the other, with the thrips living in the shallow space between (Figs 16–19). Alternatively, three or more phyllodes are attached by their edges to create an elongate space that is tubular or triangular in cross section (Figs 20, 21). Some species of domicile-builders have even managed to eliminate the need for multiple phyllodes, and simply spread a layer of 'silk' across a single phyllode, and live beneath this. In addition, while the architecture of some domiciles may appear to be similar, different lineages of thrips utilise what appear to be different types of adhesive for constructing domiciles. For example, *Lichanothrips* and *Paracholeothrips* 'glue' phyllodes together using secretion not unlike rubber cement, whereas other domicile-builders draw out their secretion into slender threads that are overlaid between phyllodes to create a woven sheet that binds the domicile together.

The nature of domicile architecture appears to be dependent on a number of factors, including the species of thrips involved, the size and shape of the phyllodes of the host *Acacia*, and the arrangement of the phyllodes on the host. Among the species that glue phyllodes together flatly or by their edges, the domiciles may be completely sealed until the brood are ready to disperse (as in *Lichanothrips*), or they may be only partially sealed (as in *Panoplothrips*) such that there is movement of individuals in and out. In the sealed domiciles, the founding thrips and developing brood must gain all of their nourishment from the inner surfaces of the phyllodes that form the domicile, and their feeding activity often discolours the phyllode in this area, making it yellowish or purple (Fig. 18).

The actual process of domicile creation has been observed in *Dunatothrips aulidis*. A foundress in this species weaves a tent-like covering over herself on the surface of an *Ac. catenulata* phyllode by waving the abdomen side to side whilst secreting thin, silky threads from the anus. The kleptoparasitic species *Koptothrips dyskritus* uses a similar behaviour to enclose partially open galls: we have observed a female of this species, in a half-open gall induced by *Kladothrips rugosus* on *Ac. papyrocarpa*, close off the opening by secreting threads of sticky fluid across it with back and forth abdominal movements, and gradually, overnight, filling in the lattice to form a cellophane-like, fully enclosing cover.

Table 3. Ecological, behavioural, and life-history traits of opportunist thrips on Australian *Acacia*.

Genus	**Host plant Section**	**Habitat types**	**Behaviour**
Akainothrips	Botrycephalae, Juliflorae, Phyllodinae, Plurinerves	empty galls, glues or lepidopteran cocoons	
Brakothrips	Juliflorae, Plurinerves		
Corroboreethrips	Juliflorae, Plurinerves	empty galls, glues or lepidopteran cocoons, splits and cracks in stems and bark	
Csirothrips	Juliflorae	empty galls	block open lips with exuviae
Dactylothrips	Botrycephalae, Juliflorae, Phyllodinae, Plurinerves	empty galls, glues or lepidopteran cocoons, splits and cracks in stems and bark	some defend domicile with abdominal pincers
Domeothrips	Juliflorae	empty galls, glues or lepidopteran cocoons	
Grypothrips	Plurinerves	empty galls, glues or lepidopteran cocoons	some apparently defend their domiciles
Heptadikothrips	Plurinerves		
Hexadikothrips	Plurinerves		
Katothrips	Juliflorae, Phyllodinae, Plurinerves	empty galls, glues or lepidopteran cocoons, splits and cracks in stems and bark	some defend domicile chemically
Kellyia	Botrycephala, Juliflorae, Phyllodinae, Plurinerves	empty galls, glues or lepidopteran cocoons	
Ostlingothrips	Juliflorae, Phyllodinae, Plurinerves		
Rhopalothripoides	Botrycephalae, Juliflorae, Phyllodinae, Plurinerves	empty galls, glues or lepidopteran cocoons, splits and cracks in stems and bark	
Warithrips	Juliflorae	empty galls, glues or lepidopteran cocoons	some have micropterae and multiple generations in old gall

The similarity of domicile-creation in these two divergent species suggests that other phyllode-glueing species use comparable behaviours. Moreover, these observations imply that the ability to adapt accessory gland secretions, which presumably originated in the context of glueing eggs to the substrate, to use in forms of construction has evolved convergently in *Acacia* thrips.

Behaviour and Life History:- Whereas the *Acacia* gall-inducing thrips establish their habitation with either a single female or a female-male pair, the domicile-builders engage in founding with either a single female, multiple females (referred to here as pleometrosis, as found in many other social insects) (Keller 1993; Choe & Crespi 1997), or one or more adults of both sexes (Table 2). Pleometrosis is, however, never obligatory, and females of all of these species are capable of colony-founding alone. Domiciles of some species last for a single generation, while in others the domiciles are expanded over two or more generations and thus sometimes include up to 70 individuals.

Table 4. Ecological, behavioural, and life-history traits of exploitative thrips on Australian *Acacia.*

Exploiter genus	**Species**	**Host thrips**	**Host plant**
Advenathrips	*inquilinus*	*Dunatothrips vestitor* (maybe *aneurae* but not confirmed)	*Ac. aneura*
Crespithrips	*enigmaticus*	*Sartrithrips luctator, popinator, mars*	*Ac. kempeana, stowardii, rhodophloia*
	hesperus	*Sartrithrips pyctus*	*Ac. grasbyii*
Glaridothrips	*koptus*	*Panoplothrips australiensis*, on *aneura* and *catenulata* not certain, maybe *Paracholeothrips* and/or *Domeothrips*	*Ac. aneura, catenulata, shirleyi*
Koptothrips	*dyskritus*	gall inducers on Plurinerves, especially *K. rugosus,* also *K.antennatus*	*Ac. aneura, maranoensis, melvillei, omalophylla, papyrocarpa, pendula, ramulosa, rhodophloia, sibilans, tephrina*
	flavicornis	gall inducers on Plurinerves, especially *K. habrus, intermedius, morrisi, rodwayi, rugosus, waterhousei*	*Ac. calcicola, maranoensis, melanoxylon, melvillei, omalophylla, oswaldii, papyrocarpa, pendula, sessiliceps*
	xenus	*K. ellobus* and *hamiltoni*	*Ac. cambagei*
	zenus	*K. acaciae* and *harpophyllae*	*Ac. harpophylla*
Schwarzithrips	*glyphis*	*Dunatothrips skene*	*Ac. catenulata* (Qld*)*
	zammit	*Dunatothrips aulidis*	*Ac. catenulata* (WA*)*
Triadothrips	*arckaringa*	*Paracholeothrips calcicolae*	*Ac. calcicola*
	briga	*Lichanothrips* spp.	*Ac. harpophylla*
	hesmus	*Paracholeothrips clavisetae*	*Ac. ammophila, cana, melvillei, microcephala, pendula, papyrocarpa, sibilans, tephrina*
Turmathrips	*apistus*	*Kladothrips schwarzi*	*Ac. grasbyi*
	dyspistus	*Kladothrips schwarzi*	*Ac. kempeana, stowardii*
Vicinothrips	*bullatus*	*Dunatothrips skene*	*Ac. catenulata*
Xaniothrips	*eremus*	*Sartrithrips popinator*	*Ac. kempeana, stowardii, aprepta*
	foederatus	*Paracholeothrips mulgae*	*Ac. aneura*
	leukandrus	*Lichanothrips* spp.	*Ac. harpophylla*
	mulga	*Dunatothrips* spp. *(aneurae* and *vestitor)*	*Ac. aneura*
	rhodopus	*Sartrithrips mars*	*Ac. rhodophloia*
	xantes	*Lichanothrips* spp.	*Ac. harpophylla, argyrodendron, cambagei*
	zophus	*Dunatothrips* spp. *(aneurae, armatus)*	*Ac. aneura, ramulosa*

The behaviour of domicile-builders is difficult to observe, due to the difficulty of reconstituting their enclosed environment for microscopic viewing. However, their remarkable fore leg enlargements and modifications (Figs 24–26), which exhibit considerable among-species diversity, provide testimony to fighting behaviour by comparison with other thrips genera such as *Kladothrips*, *Elaphrothrips*, *Hoplothrips*, and *Sporothrips* (Crespi 1986; 1988, 1992a).

Such fighting may involve within-species, within-sex combat over ownership of domiciles, presumably only in haplometrotic species, and presumably mainly between females, which show notably larger body sizes, and more-pronounced armature, than do males (Figs 456, 457). Alternatively, females or both sexes may fight against attempted usurpation by klepto-parasites, as do female *Kladothrips*. Finally, enlarged fore legs may, in some domicile-builders such as *Carcinothrips* (Fig. 15), be used to pull juxtaposed phyllodes together into position for glueing.

Suite 3: Opportunists

The opportunistic suite encompasses a range of thrips species that inhabit galls and glued-phyllode domiciles, as well as other crevices that are available on *Acacia* (Table 3). As the name of this suite implies, these species opportunistically inhabit a wide variety of small, enclosed spaces, and, unlike the members of the exploitative suite, they are not reliant on other thrips species to provide refuges for them. Suitable crevices include fissures and splits in the bark, phyllodes that have been bound together by lepidopteran larvae or spiders, phyllodes that have been mined by lepidopteran and coleopteran larvae, and galls that have been caused by thrips, other insects or fungal infection on the host *Acacia*. This suite includes a large number of species that occur on *Acacia* species that are not hosts to gall-inducing or domicile-building thrips.

The opportunistic species can be subdivided by body size, which is associated with the type of enclosed space that they can utilise. The large opportunists include genera such as *Domeothrips*, *Grypothrips*, and *Warithrips* whose species tend to inhabit galls that have been abandoned by gall-inducers or phyllode domiciles created by thrips or lepidopteran larvae. The small opportunists include species from genera such as *Brakothrips*, *Corroboreethrips*, *Dactylothrips*, *Katothrips* and *Rhopalothripoides*. Most of these species are small to minute, and they can be found in almost any crevice on the host *Acacia*. The opportunistic species tend to be collected infrequently, because of their patchy distribution, and as such, details on their biology are as yet poorly known.

Suite 4: Exploiters

The exploiter suite of thrips includes ‘kleptoparasites’ that invade the galls or domiciles created by other thrips and kill or otherwise displace the original occupants, and a number of ‘inquiline’ or ‘commensal’ species that cohabit but apparently cause no harm (Table 4). The kleptoparasitic species invade a gall or domicile and then use the residence to house and feed their own brood until maturity. These species have developed a number of morphological and behavioural traits that apparently enhance their ability to successfully invade a gall or other domicile.

The genus *Koptothrips* contains species that have become specialised to invade galls and lay their own eggs within them, thus gaining all the protective benefits of the gall without the difficulties involved in inducing it. *Koptothrips* appear unusual among kleptoparasitic thrips in that females of three of the four species, *Ko. dyskritus*, *Ko. xenus*, and *Ko. zelus*, can use anal secretions to close off any openings in a gall (in *Ko. dyskritus*), or form an enclosed substructure within a gall that has been invaded by multiple *Koptothrips* foundresses, each with its own small cavity for rearing brood (in *Ko. zelus* and *Ko. xenus*) (Crespi & Mound 1997).

In a similar fashion, species of *Xaniothrips* and *Glaridothrips* can be found within glued phyllode domiciles, from which they have evicted the domicile-building thrips and in which they are raising their own offspring. Although the invasion of a gall or domicile is rarely observed, *Xaniothrips* species can be seen to thrash their abdomen laterally, and presumably the vigour of this activity drives out the original domicile-builder. In contrast, *Koptothrips* species usually kill the gall-inducers within a gall. This difference in the interaction between host and parasite may be related to the value of the resource, because phyllodes suitable for glueing together are presumably available year-round, and an evicted species can thus create another domicile. In contrast, for a gall-inducing thrips eviction is likely to result in death, because suitable young phyllodes for galling are not likely to be available elsewhere.

The inquiline species include a number of morphologically diverse thrips that are found only within the domiciles created by other thrips species. A single species, *Advenathrips inquilinus*, is considered a true inquiline, in that it enters another thrips' domicile and then raises its own offspring without undue disturbance to the host (Morris *et al.* 2000). Species of *Triadothrips* are often found inhabiting domiciles that have been abandoned by their original builders (usually when all of their brood has matured and dispersed), but it also can often be found in domiciles that still contain adults of the domicile-building species. As such, the species in this genus are also regarded as inquilines.

There is also a range of other species that are only found within glued-phyllode domiciles, but for lack of behavioural observations (or other evidence) cannot be categorised readily as either kleptoparasites or inquilines (Mound & Morris 2000). Because each of these species is found only in thrips-built domiciles (and not in other similar crevices on the *Acacia*), and they appear to be specific to certain species of domicile-building thrips, it is assumed that they are obligately linked to the host domicile-building thrips. However, in most cases these species are substantially smaller than their host species, and thus it is assumed that they would be unlikely to be able to kill the host. These species are often found alone in domiciles, usually with some remaining evidence of occupation by the original domicile-building species, but with no indication of what might have happened to the host thrips, or how the parasite might have gained entry to the domicile. Thus, species from the genera *Crespithrips*, *Schwarzithrips* and *Vicinothrips* appear to be exploiters, but the nature of their interaction with their hosts requires further study.

Finally, an additional interaction between domicile-creating thrips and exploitative forms may blur the line between opportunism and exploitation. Thus, *Csirothrips watsoni* exclusively inhabits relatively old galls of *Kladothrips arotrum*, from which all or most of the gall-inducer brood has left. However, if this invading species is placed experimentally in a half-gall together with live *K. arotrum* then the two species will fight, and *C. watsoni* adults have been observed to kill those of *K. arotrum* (Crespi 1992a). Other taxa, such as *Warithrips aridum* and *Turmathrips* species, also form colonies in relatively old galls, but whether they overlap with live gall-inducers early in their occupation is unknown.

VARIATION AMONG THE SUITES IN MORPHOLOGICAL-TAXONOMIC DIVERSITY

The Australian *Acacia* thrips comprise 30 genera and 235 species, but their distribution among the four behavioural-ecological suites is remarkably uneven (Table 5). Thus, the gall-inducers exhibit striking morphological uniformity among the 22 species in their single genus *Kladothrips*. The opportunists include many more genera, some but not all of which are highly species-rich (*Akainothrips*, *Dactylothrips*, *Katothrips*). The phyllode-gluers comprise seven similarly species-rich genera, and the parasites have run taxonomically rampant, with nine genera for only 23 species reflecting tremendous morphological divergence.

Table 5. Numbers of genera and species in the four behavioral-ecological suites of Australian *Acacia* thrips. The four suites vary in the number of species per genus (ANOVA, F = 3.21, P < 0.05).

Behavioural-ecological suite	Number of genera	Number of species	Species/ genus (SE)
Gall inducers	1	22	22 (0)
Phyllode gluers	7	33	4.7 (1.3)
Opportunists	13	140	10.8 (3.2)
Exploiters	9	23	2.6 (0.6)

We suggest that much of this morphological-taxonomic variation among behavioural-ecological suites is a result of variation in habitat stability, and the nature of interspecific interactions, over macroevolutionary time. Thus, the gall-inducers all inhabit a highly homogeneous environment, well-buffered from the external world, and their ecology, behaviour and life-histories are quite similar compared to the extent of variation observed in the other three suites. This similarity could be expected to engender morphological conservatism. By contrast, the opportunists include some species-rich genera with many species that inhabit abandoned galls (*Dactylothrips*, *Katothrips),* but also many genera that live in other habitats—indeed, any habitat that provides a suitable shelter on *Acacia*—and such habits might select for morphological divergence. Phyllode-glueing species all create domiciles in fundamentally the same way, but these domiciles exhibit striking variation in size, shape, duration, and their degree of interface with the external world. We believe that, in consequence, the morphology of these species has been subject to a considerable degree of diversifying selection. Finally, parasites inhabit a wide range of environments in galls or phyllode glues, which they exploit in remarkably different ways, from benevolent cohabitation through to expulsion or killing of their hosts. Moreover, most of their life-history strategies involve strongly selected antagonistic interspecific interactions that could be expected to drive behavioural and morphological diversification.

These hypotheses for the generation of morphological diversity via divergence in habitat and behaviour can be evaluated through analyses of this question in comparable groups of insects, such as wasps associated with figs or cynipid galls. More generally, ecological shifts are well known to drive morphological and behavioural change (e.g. Harrison & Crespi 1999; Brown *et al.* 2000), and they may be responsible for much of the phenotypic variation that we observe among insects and other animals.

CREATING, EXPLOITING AND DEFENDING DOMICILES

The thrips on Australian *Acacia* create and modify domiciles in two main ways: gall induction (in *Kladothrips*), and phyllode enclosure using adhesive or silky secretions (in *Carcinothrips*, *Dunatothrips*, *Lichanothrips*, *Panoplothrips*, *Paracholeothrips*, *Sartrithrips* and *Truncatothrips*). Gall shape and size vary considerably between species, and as described in detail below, gall form appears to be related adaptively to brood size, number of generations in the gall (one or two), and, perhaps, crypsis and defence against natural enemies (Crespi & Worobey 1998). The structure of adhesive and silky domiciles also differs notably between species, apparently in part as a function of thrips size in relation to phyllode size. Thus, large, broad phyllodes glued flat together (Figs 18, 19), or terete phyllodes glued together to form a tube (Figs 20, 21), can each support a group of up to several dozen large-bodied thrips (e.g. in *Lichanothrips* on *Ac. harpophylla*). By contrast, smaller phyllodes (e.g. those of *Ac. lysiphloia*, *Ac. aneura*, and *Ac. catenulata*) are more commonly enclosed partially or completely with tent-like silken material, and they tend to contain smaller species of thrips (e.g. *Dunatothrips*).

Gall-inducers differ from domicile-builders in that multiple females never induce galls jointly—in most species they fight, sometimes to the death, in defence of incipient galls. By contrast, facultative pleometrosis, the founding of domiciles by either one or multiple females, is common in the domicile-building genus *Dunatothrips* (Table 2). We hypothesise that this difference is due to the ease of creation and temporal features of their respective domiciles. Gall-inducing females have only a narrow temporal window in which to start a gall on a developing phyllode; a single female can induce a gall, and she, perhaps in conjunction with her daughters, is fully capable of filling it to capacity with offspring. However, domicile-builders must generate quantities of secretion (Figs 16, 17), which may be physiologically costly, and they are probably quite vulnerable to predation by ants before they are enclosed. Moreover, if one or more females die during domicile creation then the others can complete the task, and their domiciles can, in many species, be expanded over several generations. These four factors may favour pleometrosis, as the benefits to females of starting domiciles quickly are considerable, and the reproductive costs of sharing the domicile would be low. Similar factors have been proposed or demonstrated to help explain pleometrotic colony founding in spiders, embiids, wasps, bees, and ants (Keller 1993), and further studies of pleometrotic *Acacia* thrips will show how well they apply here. Indeed, it would be especially illuminating to compare the haplometrotic and pleometrotic *Acacia* thrips, to assess the roles of ecological and genetic selective pressures in the evolution of colony founding.

The creation of a resource by one species is almost always followed closely in evolutionary time by exploitation of this resource by other species, and the galls and other domiciles of *Acacia* thrips are no exception. Exploitative *Acacia* thrips usurp galls or other domiciles and evict the original inhabitants (e.g. *Koptothrips* and *Xaniothrips*), what we call inquilines cohabit with them (e.g. *Advenathrips*, *Triadothrips*) and what we call opportunists (e.g. *Grypothrips*, *Katothrips*, *Warithrips*) use thrips-created habitations facultatively, after the original inhabitants have left. All of these must compete with a hoard of other creatures that also exploit thrips habitations, such as the flies, Lepidoptera, spiders and ants that invade *Kladothrips* galls (Mound 1971; Crespi 1992a; Mound & Kranz 1997).

Against such a panoply of enemies, the domicile creators, as well as the invaders themselves, have evolved diverse defences to prevent usurpation or predation. Among these are structural, behavioural, morphological, and chemical adaptations to reduce the impacts of exploiters. Structural defences include aspects of the morphology of galls, such as tiny ostioles in some species (e.g. *K. waterhousei*), tight closure in others (e.g. *K. arotrum*), paralleled by the morphology of glued domiciles, which display either narrow, single openings (e.g. *Panoplothrips*) or complete closure (e.g. *Lichanothrips*, *Carcinothrips*). Structural defence may also involve gall protuberances such as the ridges and spikes found on galls of *K. rugosus* on various *Acacia* species (Crespi & Worobey 1998), and small size, as galls of some species such as *Kladothrips waterhousei* are minute and phyllode-shaped, which may make them not only difficult to find, but a less profitable resource due to their tiny volume. Some invading thrips themselves 'man the barricades', as *Csirothips* use cast exuviae to plug the open gall lips of old *Kladothrips arotrum* galls, and *Koptothrips dyskritus* uses an anal secretion to cover holes in invaded or abandoned galls of *Kladothrips rugosus*.

Behavioural and morphological defences evolve together closely. Foundresses of some species of gall-inducers have enlarged fore legs, armed with sharp fore tarsal teeth, which they use not just to fight one another but also to repel invading *Koptothrips* (Crespi 1992a,b; Crespi & Mound 1997). Even more pronounced fore leg enlargement and modification is found among the soldiers of *K. habrus*, *K. hamiltoni*, *K. harpophyllae*, *K. morrisi*, *K. intermedius*, and *K. waterhousei*, all of which fight only to drive off invading *Koptothrips*. In *K. habrus*, soldiers have been shown to exhibit a higher propensity to attack invaders than does the foundress (i.e. a division of labour), and a trend for this pattern, albeit non-significant, is also found in *K. intermedius* (Crespi 1992b; Perry *et al.* 2002). Most species of domicile gluers also exhibit enlarged, armed fore legs, which likewise are used presumably in intraspecific fights, interspecific defence, or both—although observations are sorely needed to document such inference. Moreover, the large fore legs of some exploitative thrips, such as *Koptothrips xenus*, *Ko. dyskritus*, *Ko. zelus*, may also be used to defend a usurped gall against con-specifics, as it is not uncommon to find recently dead *Koptothrips* foundresses (plus one live *Koptothrips* foundress) within galls where the inducer has long since perished and dried (Crespi, pers. obs.).

Although fore leg diversity represents a primary axis of morphological defence in *Acacia* thrips, several genera show abdominal modifications that apparently are used aggressively. Thus, *Dactylothrips aenictus*, a large opportunistic species that inhabits holes in old, dry Hymenoptera galls, has abdominal tergite projections that, together with the modified tube, form pincers (Fig. 124). This thrips positions itself in its hole with the abdomen towards the opening (Crespi & Mound 1997), and the pincers are used to grasp and squeeze threatening items such as paintbrushes wielded by curious entomologists. By contrast, the exploitative *Xaniothrips* have slender, unarmed, fore legs but sport offensive weaponry on the abdomen that comprises many stout spines (Fig. 27). These species have been observed to thrash the abdomen laterally, expelling *Lichanothrips* from their glued phyllodes.

Chemical defences have been detected in one species of *Acacia* thrips, and probably occur in others. The opportunist, *Katothrips flindersi*, lives in groups within abandoned, hollow, blister-shaped phyllode mines created by a weevil on *Acacia acradenia* (Crespi & Mound 1997). One to several adult thrips remain near the weevil exit hole with the apex of their abdomen pointing out. When stimulated with a brush, the anus of each thrips was seen to pulsate, and a pungent smell reminiscent to that of pentatomid bugs was detected at the hole (Crespi & Mound 1997). We also suspect a second example of chemical warfare in *Acacia* thrips: the parasitic species *Koptothrips flavicornis* has a fore-femoral gland and pointed fore tarsal teeth but, unlike the other three species of *Koptothrips*, its fore legs are not notably enlarged. If a *Ko. flavicornis* grasps a foundress or soldier of a gall inducing species, even briefly, the attacked individual dies within a few minutes at most, having suffered no damage visible to the eye. We suspect that it is no coincidence that both of these species with apparent chemical weapons are small and exhibit little or no morphological adaptation for offence or defence (Figs 234, 235).

The presence of four distinct and diverse behavioural-ecological suites in a single clade, all centred around the use of domiciles, immediately raises questions concerning the frequency and nature of evolutionary trajectories between the suites, the selective pressures driving such transitions, and the adaptive significance of the traits exhibited by species in each suite. Moreover, analysis of the selective pressures that drive evolution in this group bears directly on fundamental issues in evolutionary ecology, including the evolution of social behaviour, sex allocation, parasitism, host-plant use, and life history. Consideration of the macroevolutionary aspects of such problems requires robust phylogenies, and the use of these phylogenies to infer evolutionary events and processes.

PHYLOGENETIC FOUNDATIONS

Whereas taxonomy ignites the light of evolutionary insight, phylogeny focuses it through the dimension of time. Phylogenies are essential in principle, if rare in practice, to robust classifications. But they also serve as the context for inferences concerning biological history, most notably the history of diversity among species and their adaptations. In turn, comparative, phylogeny-based tests of adaptive significance and the causes of species diversity complement and strengthen tests of evolutionary hypotheses that are based on other methods, such as functional design, analysis of selection, and experimentation (Losos 1996; Crespi 2000; Martins 2000; Webb *et al.* 2002).

In keeping with the challenge of developing these insects into a model clade for evolutionary analyses, our ultimate goal is a species-level phylogeny, plus extensive biological information, for all of the species. The development of a species-level tree for a large group such as the *Acacia* thrips normally proceeds from the top down, via inference of genus-level relationships followed by bottom-up backfill of phylogenetic data from all the species into this framework. By contrast, this project began with an emphasis on assembling data for all of the gall-inducing species, to infer the evolution of soldier castes (Crespi *et al.* 1997), and it has only recently expanded to include phylogenetic analysis of representatives from most of the other genera (Morris *et al.* 2002a).

Our strategy for phylogeny inference has been threefold. First, we have sought to infer trees from as many different sources of data, especially different genes, as possible. If the phylogenies from independently evolving genes concur, then the results are much more robust because locus-specific or gene-specific effects such as long-branch attraction or gene-species tree differences have been precluded (Hillis *et al.* 1996). Moreover, the use of multiple genes tends to increase resolution and support throughout the tree, because the different genes, which evolve at different rates, will provide information on relationships in different parts of the tree (in different clades, or near the tips vs the base).

Second, we have used maximum parsimony and maximum likelihood algorithms for phylogeny inference. We have done so not just because we view these as the only methods that are epistemologically justifiable, but also because they make different assumptions, so concordance in results across the methods means that the phylogeny is robust to violation of their various assumptions. Parsimony is also uniquely useful in allowing combination of qualitatively different data sets, such as DNA with morphology (Crespi *et al.* 1997), whereas likelihood provides a solid grounding in molecular-evolutionary processes, through choice of the optimal model for base-pair changes (Posada & Crandall 2001).

Third, as species names are hypotheses of gene flow and reproductive isolation, we regard our phylogenies as more or less well-supported hypotheses of relationships. Current phylogenies also serve as guides to what genes and which species will best extend and test the hypotheses of relationship, leading ultimately to an essentially complete species-level tree, and perhaps even one that extends to the population level, that is as well resolved and supported as the genomes involved will permit.

RELATIONSHIP BETWEEN *ACACIA* THRIPS, OTHER PHLAEOTHRIPIDAE AND OTHER INSECTS

The bauplan of Australian *Acacia* thrips derives from their legacy of evolution with regard to other insects in general, and the order Thysanoptera in particular. DNA-sequence evidence divides the thrips into two main lineages that correspond to the suborders Terebrantia and Tubulifera (Crespi *et al.* 1996). Tubulifera comprises one family, the Phlaeothripidae, containing the Idolothripinae, which are mainly large species that feed on fungal spores, and the Phlaeothripinae, which include many smaller species that feed either on fungal mycelium or plant cell contents (Mound & Marullo, 1996). It is this subfamily that includes the phytophagous thrips on Australian *Acacia*.

The monophyly of this host-plant-associated assemblage is difficult to ascertain as so little is known about the relationships among any other genera or lineages of Australian thrips. The available evidence suggests that the phytophagous thrips on *Acacia* are a monophyletic group (Fig. 28). However, this thesis must be approached with caution, as sequence data for only a small number of other Australian thrips are available to test this hypothesis. One of the problems that arises when attempting to establish the monophyly of this group is a lack of reasonable alternatives. Thus, it is difficult to know what other thrips species might be related to the *Acacia* thrips such that they might compromise the monophyly of the group. Some alternative hypotheses that we examined include: (a) evolution of the *Acacia* thrips from another lineage of gall-inducing thrips; and (b) evolution of *Acacia* thrips from another lineage of phytophagous thrips on a different Australian host plant. To this end we included in an analysis a small number of thrips species from other Australian host plants that also induce galls or are found in them. The other taxa included in our analyses were *Teuchothrips*, a genus of thrips whose species form simple galls on a range of Australian plants (including *Myoporum*, *Pittosporum*, and *Callistemon*), and *Thaumatothrips* and *Phallothrips* species that live in woody stem galls on *Casuarina* species. The outgroup used for this analysis was *Gynaikothrips*, the species of which induce galls on *Ficus* species in Australia. None of the species tested thus far has disrupted the monophyly of the *Acacia* thrips.

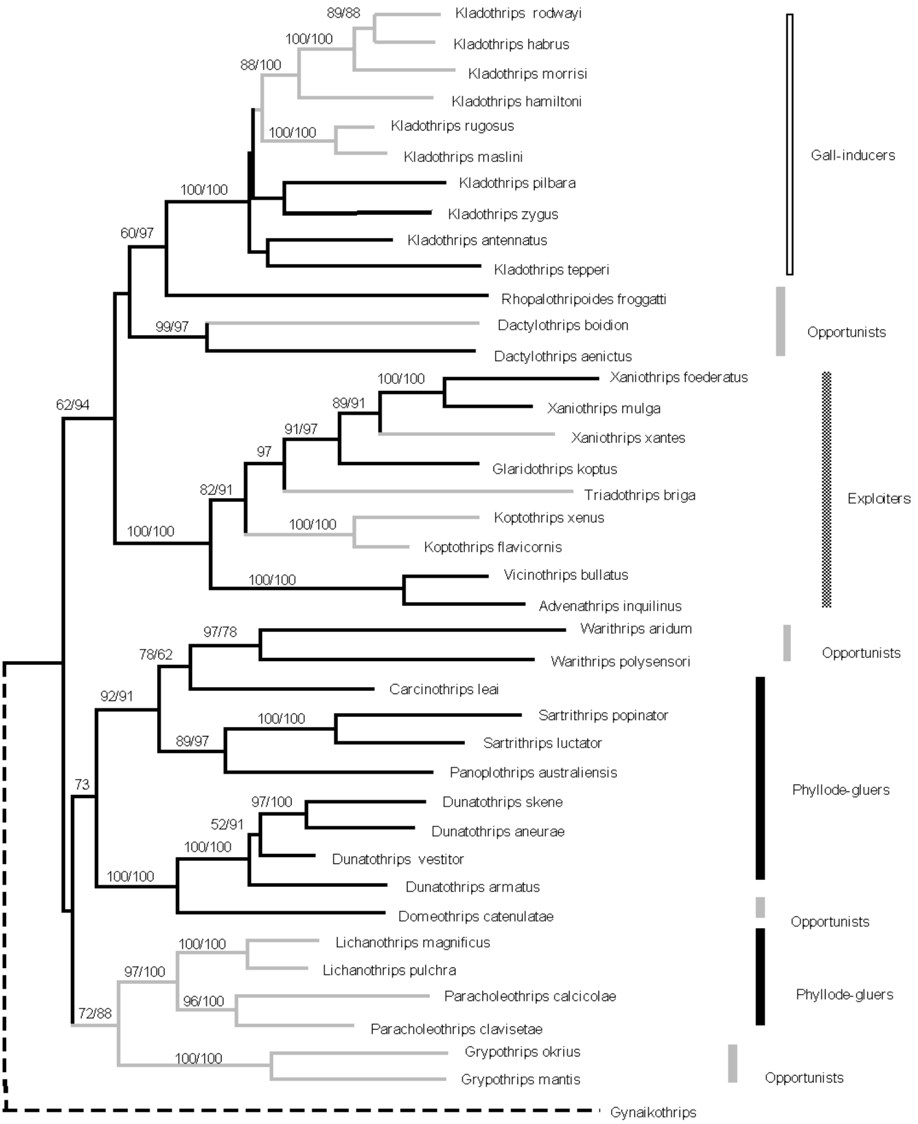

Fig. 28. A phylogeny for *Acacia* thrips based on maximum likelihood analysis of *elongation factor-1a* and *wingless* gene regions, with behavioural/ecological suite indicated (see text). Black branches indicate thrips from *Acacia* Section Juliflorae; grey bars indicate thrips from *Acacia* Section Plurinerves. Numbers by branches indicate parsimony bootstrap values (1000 replicates).

RELATIONSHIPS AMONG GENERA OF *ACACIA* THRIPS

One of the most fundamental levels of diversity involves variation in how organisms utilise resources: whether they generate them, purloin them from others, or use them opportunistically as encountered. Australian *Acacia* thrips span this spectrum in their use of habitations on the host plant, from gall-induction, to domicile-building with glue, to parasitism, to opportunism. These thrips thus provide a useful system for analysing the patterns and causes of such major transitions in the evolution of life-history and behaviour.

The phylogeny for most of the genera of thrips on *Acacia* has been inferred using the combined data from the genes elongation factor 1-alpha, wingless, and cytochrome oxidase I (Morris *et al.* 2002a; Fig. 28). Maximum parsimony and maximum likelihood analyses of these data, plus statistical tests of monophyly vs alternative hypotheses, indicate that:

(1) the gall-inducing genus *Kladothrips* is monophyletic, and its sister-taxon is either *Dactylothrips* or *Rhopalothripoides*, both of which are opportunistic species;

(2) the genera of exploitative thrips, *Advenathrips*, *Koptothrips*, *Triadothrips*, *Vicinothrips* and *Xaniothrips*, clearly form a monophyletic group, despite the tremendous diversity in morphology across and within these genera;

(3) domicile creation through phyllode-glueing has evolved once, although this habit has been lost in *Grypothrips*, *Warithrips* and *Domeothrips*, the species of which are opportunistic;

(4) the opportunistic species are polyphyletic, there being at least several independent origins of this trait, and at least two losses.

The diversity in evolutionary patterns of behavioural, ecological, and morphological conservatism represented by these four behavioural-ecological groups is remarkable and requires hypotheses for its causes, and comparison with patterns found in other organisms.

The monophyly of the gall-inducers, and the absence of any loss of this habit within the lineage, suggests that the process of gall induction does not evolve readily, and that once it has evolved it is difficult to lose. We hypothesise that the evolution of gall induction may begin with simple leaf distortion and curling (Crespi *et al.* 1997; Crespi & Worobey 1998), and that it rapidly comes to involve an intimate biochemical, physiological, and phenological interaction with the host plant. Moreover, some of the morphological adaptations of the gall-inducers, such as physogastry and relatively large, tubular bodies, would probably be highly maladaptive, if not fatal, outside of the protective gall environment.

Among other insects, the only possible escape from gall induction appears to be the evolution of gall parasitism, whereby a species usurps or cohabits the gall of an inducer, usually a related one (e.g. Akimoto 1988b; Akimoto & Yamaguchi 1997; Yang *et al.* 2001; Miller & Crespi 2003), but remains an obligate gall inhabitant. Thus, whereas gall induction may be a ‘key’ evolutionary innovation that can result in a rapid radiation (Price & Roininen 1993; Givnish & Sytsma 1997), gall habitation may represent an irreversible transition (Bull & Charnov 1995). Such irreversibility would be the result of the myriad adaptations to life within the specialised habitat of the enclosed gall, coupled with the difficulty of the evolutionary transition from intraspecific to interspecific usurpation. But given the tremendous species diversity of gall-inducing insects (e.g. Cecidomyiidae: Gagné 1989; Cynipidae: Stone *et al.* 2002), it appears that such irreversibility seldom engenders an evolutionary dead end in terms of species numbers.

The single origin of domicile creation by glueing phyllodes together suggests that this habit is also difficult to achieve. However, the use of apparently similar anal secretions to create an enclosure within a gall, or to close off a broken invaded gall, is also known from *Koptothrips dyskritus*, *Ko. xenus*, and *Ko. zelus*, as well as from the *Casuarina* gall-inducer *Iotatubothrips* and its kleptoparasite, *Phallothrips houstoni* (Mound *et al.* 1998). Thus, this form of building may arise more readily than gall induction. Moreover, our phylogeny indicates that phyllode-glueing has probably been lost at least several times in the branches leading to *Warithrips*, *Grypothrips*, and *Domeothrips*, with species opportunistically inhabiting old galls or glued phyllodes. We hypothesise that these patterns may arise for at least four reasons. First, producing a domicile with anal secretions probably involves a less-intimate insect-plant interaction than galling, because phyllode growth is not modified, and for all of the genera except *Dunatothrips* (which glues relatively young phyllodes, is monophyletic, and shows no losses of glueing), there appears to be no strong phenological link to the plant. Second, some glued-phyllode domiciles resemble lepidopteran leaf-ties or the old galls of some gall-inducing species (e.g. *Kladothrips ellobus*), such that behavioural transitions from building to opportunism may be relatively simple. Third, plausible selective pressures for a loss of building include the difficulty of finding phyllodes suitable for glueing together, and the likely physiological costs of producing the secretion. Fourth, domicile-builders appear less morphologically specialised for their habitat than are the gall-inducers, as their most notable adaptation to the domicile is strong dorsoventral flattening, which is probably adaptive in other situations.

Our DNA-based phylogeny also shows strong support for monophyly of the group that contains *Advenathrips*, *Koptothrips*, *Triadothrips*, *Vicinothrips*, and *Xaniothrips*. Of these, all are exploitative but in different ways, with *Koptothrips* usurping galls and the other genera using glued-phyllode domiciles, either usurping them (*Xaniothrips*) or cohabiting with the hosts (*Advenathrips*, *Triadothrips* and *Vicinothrips*). The monophyly of this group of five genera is remarkable given the tremendous diversity in morphology that they exhibit, with some species tiny but others among the largest species on *Acacia*, some with fore legs that are greatly enlarged and modified in different ways, and some with fore legs slender but the abdomen with stout spines.

Behavioural variations on the exploitative theme parallel this morphological variation. Examples are single females of some species killing the host thrips and raising a brood in the gall or glued domicile; multiple females invading and using an anal secretion to each form an enclosure within a gall; apparent use of a venom to kill the host by one species; and apparent mimicry of a host thrips to facilitate cohabitation, as in some ants. Such diversity appears to attest to strong diversifying selection on exploiter morphology, behaviour and life-history strategies, as the parasites radiated to attack hosts with different types of domicile and defensive adaptations. Moreover, the absence of losses of parasitism suggests that it engenders close morphological, behavioural, and phenological adaptation to particular types of host insects, even though some parasite lineages (e.g. *Xaniothrips*) have clearly retained sufficient evolutionary flexibility to shift between more or less related host insects and host plants. The most central adaptation leading to the irreversibility of parasitism is probably a requirement for fresh domiciles within which to breed.

The opportunistic genera of thrips on *Acacia*, in contrast to the gall-inducers, domicile gluers and parasites, are inferred to be polyphyletic, with at least three origins of this type of life history or, perhaps, fewer origins but many losses. This evolutionary lability possibly follows from the wide range of domiciles used by these thrips, including old galls of thrips, other insects or fungi, glued phyllodes, hollow leaf mines, phyllode glands, lepidopteran ties, and presumably any other cavity of convenient size on the plant.

We hypothesise that opportunism provides an evolutionary bridge between the three other behavioural-ecological suites. Thus, feeding in a small cavity or depression on a young phyllode may have developed into gall induction; glueing of eggs on the inner phyllode surface of a lepidopteran leaf tie, or two parallel phyllodes, may lead to the glueing together of phyllodes as an obligate strategy; loss of glueing may lead to use of similar domiciles that are already present; and opportunistic use of an old gall or glued phyllode may create conditions favouring the origin of parasitism. These four hypotheses can be tested via future analyses of species-rich opportunistic genera such as *Katothrips* and *Akainothrips*, the tiny opportunists in the genera *Ostlingothrips*, *Brakothrips*, *Hexadikothrips*, *Heptadikothrips* and *Corroboreethrips*, and parasites in the genera *Crespithrips*, *Schwarzithrips*, and *Turmathrips*.

The main selective pressures involved in the evolution of transitions between behavioural-ecological modes in *Acacia* thrips appear to include predation risk (especially from ants); phenological adaptation to the host insect and host plant; ecological opportunity to utilise a novel type of domicile or food source (i.e. gall tissue); and behavioural opportunity whereby transitions are easier between similar types of domicile. Further study of the patterns and causes of transitions between the modes requires denser taxon sampling in the DNA data set; the addition of data from a more slowly evolving gene, such as 18S, to help in providing resolution and support to the basal regions of the phylogeny; and behavioural and ecological tests of the hypothesised causes of transitions between modes.

RELATIONSHIPS AMONG SPECIES OF GALL-INDUCERS

Phylogenetic hypotheses for all of the described gall-inducing species have been inferred by Morris *et al.* (2001) (Fig. 29), using data from COI, 16S, EF 1-alpha, and wingless. These genes provide generally well-resolved and well-supported maximum parsimony and maximum likelihood trees that are identical in topology, and allow robust inferences to be drawn concerning the evolution of diversity within this group.

We focus on the evolution of six key traits: foundress physogastry, the presence of males at the founding stage, gall morphology, eclosion in the gall or in soil, the presence of soldier morphs, the presence of *Koptothrips* invaders, and the taxonomic section of *Acacia* inhabited (Juliflorae or Plurinerves) (Tables 1 and 6). Given the completeness and strength of the phylogeny for this clade, we are able to infer the joint evolution of these traits as the gall-inducers diversified.

Plesiotypic gall-inducers

The species that branch earliest from the base of the tree, including *Kladothrips zygus*, *K. schwarzi*, *K. pilbara*, and *K. antennatus*, all appear morphologically ‘primitive’ (i.e. lacking specialised, derived morphology), and inhabit galls that are also ‘primitive’, resembling elongate, modified, simple leaf rolls (Crespi & Worobey 1998) (Fig. 29). They inhabit host plants in the section Juliflorae (or the Phyllodinae, for *K. zygus*) mostly

Table 6. Behavioural, ecological, population-genetic, and life history traits of gall-inducing thrips on Australian *Acacia*.

Social species	**Gall volume (mm^3) total/inner**	**Number of soldiers**	**Number of dispersers**	**Soldier % male**	**Disperser % male**	**Soldier eclosion by sex**	**Female soldier relatedness**	**Foundress inbreeding level Fis**	**Soldier inbreeding level Fis**	**Skew, msat**	**% *Koptothrips***	**% galls with male founder**
K. habrus (*Ac. melvillei*)	135/31	10	105	16	51	females first	0.60	0.31	0.30	0.16	23	0
K. hamiltoni	246/89	25	115	52	6	males first	0.83	0.70	0.63	0.38	25	6
K. harpophyllae	--/65						1.0		1.0		25	50
K. intermedius	136/54	15	60	21	15	no sex difference	0.72	0.34	0.31	0.07	31	0
K. morrisi	1020/337	38	619	25	41	no sex difference	0.62	0.45	0.31	0.45	29	0
K. waterhousei (*Ac.papyrocarpa*)	50/16	7	79	9	47	females first	0.65	0.02	-0.13	0.35	32	0
Solitary species	**Gall volume**		**Number of dispersers**		**Disperser % male**		**Female disperser relatedness**	**Foundress inbreeding level Fis**			**% *Koptothrips***	**% galls with male founder**
K. rodwayi	172/58		37		12						7	0
K. xiphius								0.67				0
K. rugosus (*Ac.papyrocarpa*)	338/139		375		51			0.09–0.59				42
K. ellobus	403/128		460		41						40	45
K. arotrum	--/266		433		6		0.73	0.54			0	0
K. antennatus	--/132		313		5		0.21	0.52			2	0
K. acaciae	--/286										35	
K. schwarzi	--/30											

in highly arid regions of the Australian interior, and all eclose within the domicile, as do species in the other behavioural-ecological suites, and as do gall-inducing thrips on other plant genera (Ananthakrishnan 1984). These considerations suggest that these species are similar in their biology to the ancestral *Acacia* gall thrips (Crespi & Worobey 1998).

Derived lineage A: Arid-zone ball-galling, 'hiders'

This lineage includes five species that also inhabit highly arid regions, and Juliflorae host-plants (Fig. 29). Of these, *Kladothrips augonsaxxos* apparently represents a sibling species or host race complex, as forms that key to this species have been found in morphologically similar galls on *Acacia aprepta*, *Ac. grasbyi*, *Ac. kempeana*, *Ac. resinimarginea*, *Ac. rhodophloia*, and *Ac. stowardii*.

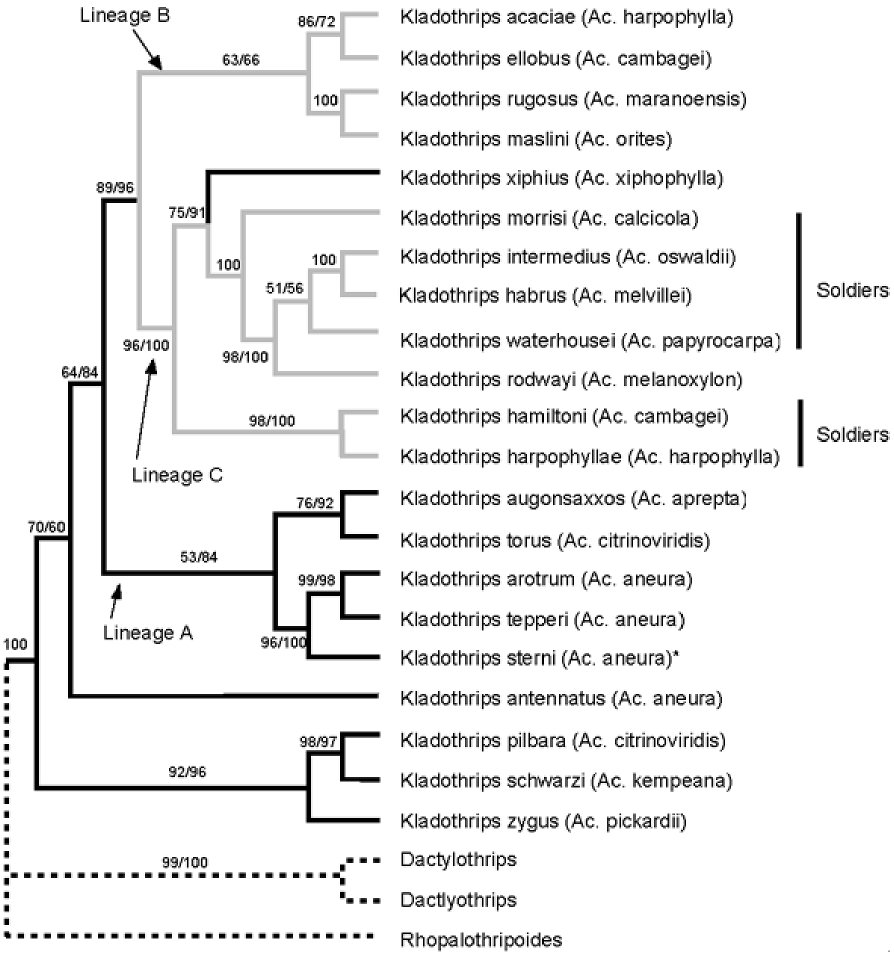

Fig. 29. A phylogeny for species of gall-inducing thrips on *Acacia*, adapted from Morris *et al.* (2001). Lineages indicated are: A, 'hiders'; B, 'fighters'; C, 'fliers'.

The species in this lineage have evolved a combination of relatively spherical galls and pronounced foundress physogastry (Tables 1 and 6). This combination of traits appears to have been driven by selection for high fecundity: physogastry allows large numbers of eggs to be produced rapidly, and a large, spherical gall presumably maximises the volume available for developing brood, though the intraspecific relationship between brood size and gall size has yet to be quantified.

Eclosion within the gall, apparently inherited from the basal lineages, has been recorded from *Kladothrips tepperi* and *K. arotrum*, and it may also occur in *K. augonsaxxos*, *K. sterni*, and *K. torus*. This trait may be adaptive in the context of the high aridity and unpredictable rainfall of the areas inhabited by these species, as brood may remain within the gall until conditions are relatively suitable for dispersal and gall induction, such as after rains.

Derived lineage B: Semi-arid zone 'fliers'

This lineage is paraphyletic, branching off after derived lineage A. It retains relatively spherical galls, physogastry, and large brood sizes, but it is characterised by a large suite of derived traits: (1) gall induction on *Acacia* in the section Plurinerves, in semi-arid or mesic regions; (2) departure of second-instar larvae from the gall followed by eclosion apparently in the soil; (3) the presence of males with foundresses, during gall-induction and afterwards, in up to 50% of galls; and (4) attack by *Koptothrips*, which is absent or very infrequent in all lineages basal to these (Fig. 29, Table 6). All of these traits are known from *Kladothrips acaciae*, *K. ellobus*, and *K. rugosus*, but *K. maslini,* which lives in a mesic area and has been infrequently collected, requires further study. Moreover, *K. rugosus* also appears to represent a large suite of sibling species or host races, as it has been collected from galls on *Acacia ammophila*, *Ac. ancistrophylla*, *Ac. cana*, *Ac. enervia*, *Ac. loderi*, *Ac. maranoensis*, *Ac. melvillei*, *Ac. microcephala*, *Ac. microsperma*, *Ac. omalophylla*, *Ac. papyrocarpa*, *Ac. pendula*, *Ac. sibilans*, and *Ac. tephrina*.

We suspect that the changes in habitat, kleptoparasite attack, and life-history that define this lineage are not coincidental. Thus, living in a less arid region, with more predictable, seasonal flushes of new phyllodes for gall-induction in spring and summer, may lead to maintenance of larger, more stable populations of these species, which could consequently support viable populations of kleptoparasites (Wcislo 1987). In turn, the presence of *Koptothrips* may have selected for departure from the gall by the gall-inducers as early as possible, to minimise the period of vulnerability—and living in a less arid region might allow pupation in the soil (as is common among Thysanoptera) rather than the gall. The presence of males during founding may also be related to the higher temporal predictability of gall induction and less harsh habitat in these species, as location of gall-inducing females would be easier. Moreover, eclosion outside of the gall presumably leads to mating after dispersal and thus to a more or less unbiased adult sex ratio (as has been shown for *K. rugosus* and *K. ellobus*) (Kranz *et al.* 2000, 2002). Such a lack of sex-ratio bias increases the operational sex ratio (Emlen & Oring 1977) and favours male mate-guarding. The hypotheses described above can be tested using data on phenology, demography, sex ratio, and parasitism rates among and within species.

Derived lineage C: 'Fighters' and their relatives

This monophyletic group contains the species of gall-inducing thrips with soldier morphs, also their close relatives, *Kladothrips xiphius* and *K. rodwayi*, whose lineages have apparently lost soldiers (Fig. 29). The origin of this group is characterised by the origin of soldiers, the loss of foundress physogastry, and the evolution of relatively elongate galls, which in all species except *K. morrisi* are considerably smaller than those in lineage B and support substantially smaller brood sizes (Kranz *et al.* 2001a,b; Table 6). However, all of the species in this clade have retained life on *Acacia* in the section Plurinerves, and eclosion in the soil, except for *K. intermedius* and *K. rodwayi*, which eclose in the gall.

Species with soldiers include *K. hamiltoni*, *K. harpophyllae*, *K. morrisi*, *K. habrus*, *K. tepperi*, and *K. waterhousei*, and this latter nominal species appears to comprise a sibling species or host race complex, being found on nearly all of the same *Acacia* species that host *K. rugosus*. Of these, the species *K. hamiltoni* and *K. harpophyllae* are somewhat atypical in that they have retained some degree of cofounding with males (Kranz *et al.* 1999, Table 6). Moreover, *K. morrisi* is unusual in having a relatively large gall, very large disperser brood sizes, and soldiers with high fecundity (Kranz *et al.* 2001a) that appear to be less defensive than those in other species (Perry *et al.* 2002).

RELATIONSHIPS WITHIN THE SPECIES/HOST RACE COMPLEXES

Four described species, *Kladothrips rugosus*, *K. waterhousei*, *K. schwarzi* and *K. augonsaxxos*, all inhabit many host plants. The former two species are both found on 14 species of *Acacia* in the section Plurinerves, and the latter two are both found on seven species of *Acacia* in the Juliflorae. Two lines of evidence suggest that these species each represents a set of sibling species or host races: (1) previous work has shown that the host-associated forms differ in mtDNA (COI) from one another to a degree consistent with species status (Crespi *et al.* 1997, 1998; but see Ferguson 2002); and (2) aside from these forms, all of the gall-inducing thrips species on *Acacia* are host-plant specific, and indeed, in other insects host-plant specificity is the rule among gall-inducers.

We have inferred a phylogeny that includes a large sample of the *K. rugosus*, *K. waterhousei*, *K. schwarzi* and *K. augonsaxxos* species complexes, augmenting the data sets of Morris *et al.* (2001) with data from 16S and additional data from COI (Crespi & Abbot 1999; unpublished data) (Fig. 30). This phylogeny shows that each of the four species complexes forms a monophyletic or paraphyletic group, that some lineages centred in Western Australia form monophyletic groups on related hosts (*Ac. enervia* + *Ac. ancistrophylla*; *Ac. rhodophloia* + *Ac. grasbyi*), and that, as described in detail below, patterns of host-plant use have evolved in parallel across lineages. However, increased sampling, resolution and support is needed before this phylogeny can be used directly for robust tests of hypotheses regarding biogeography, the evolution of host-plant use, sociality, and exploitative behaviour. Moreover, we have only begun to uncover the extent of biological diversity within the apparent sibling species. When resolved, these should greatly increase sample sizes for comparative tests, and provide useful insights into the processes of speciation among gall-inducing *Acacia* thrips.

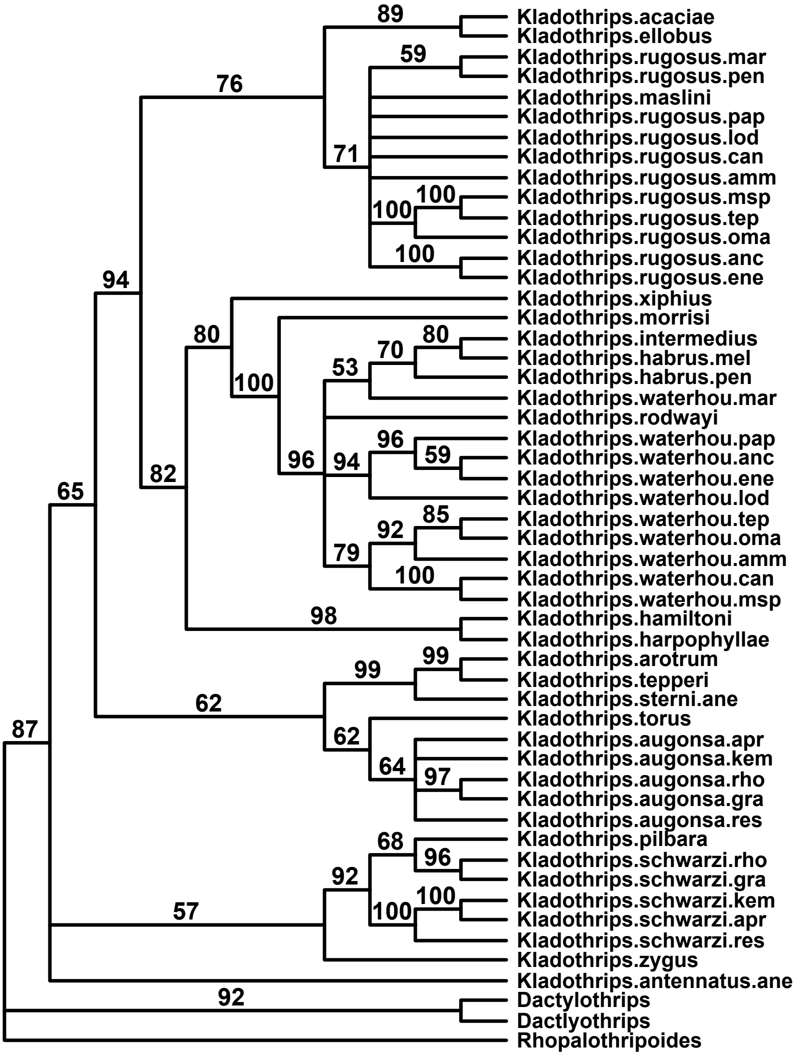

Fig. 30. Bootstrap majority-rule maximum-parsimony phylogeny (200 replicates) of gall-inducing thrips, including many of sibling species or host races. *Acacia* hosts indicated as follows: mar = *maranoensis*, pen = *pendula*, pap = *papyrocarpa*, lod = *loderi*, can = *cana*, amm = *ammophila*, msp = *microsperma*, tep = *tephrina*, oma = *omalophylla*, anc = *ancistrophylla*, ene = *enervia*, mel = *melvillei*, apr = *aprepta*, kem = *kempeana*, rho = *rhodophloia*, gra = *grasbyi*, res = *resinimarginea*, ane = *aneura*. Phylogeny inferred from data in Morris *et al.* (2001), augmented with data for the sibling species from mitochondrial genes COI and 16S (about 400 base pairs) (Crespi, unpublished data).

EVOLUTIONARY-ECOLOGICAL APPLICATIONS

The striking biological variation displayed by the thrips on Australian *Acacia* represents in miniature all of life's diversity. Thus, a single lineage has radiated across a huge landmass to produce forms strikingly divergent in habitat, ecology, morphology, and behaviour, driven by the forces of selection and the vagaries that help to promote reproductive isolation. To understand the evolutionary processes behind this radiation, we must apply our taxonomic, phylogenetic, geographic, and biological-diversity information in the context of the relevant theory and findings available from other taxa.

The radiation of thrips on *Acacia* bears directly on three of the outstanding questions in evolutionary-ecological theory: the evolution of host-plant use, the evolution of social behaviour, and the evolution of resource exploitation. Indeed, for *Acacia* thrips these three questions turn out to be closely linked, as selective processes fostering diversification appear to span the three trophic and interactive levels involved. For each of these questions, we apply our nascent model clades approach as a framework for testing theory. Moreover, we make extensive comparisons with other taxa, to maximise the generality of our inferences. Our proximate goal is a comprehensive understanding of the diversification of the Australian *Acacia* thrips, and through this to gain insights into how all of biodiversity evolves.

EVOLUTION OF HOST PLANT USE

Study of the evolution of trophic relationships between plants and animals has its roots in the work of Darwin, who emphasised the importance of interactions between species and the role that these interactions play in the process of evolution by natural selection (Thompson 1994). Understanding the roles of plant-insect cospeciation, host-plant shifting and other macroevolutionary processes in the generation of biodiversity is an important unresolved question in evolutionary theory, one with implications that extend from speciation, to conservation of biodiversity, to the management of host-shifting agricultural pests (Mitter *et al.* 1991; Paterson & Banks 2001; Singer *et al.* 1993). Some of the best natural systems for analysing the dynamics of across-trophic level evolution are provided by plant-feeding insects, the most species-rich of all animals (Farrell 1998; Farrell & Mitter 1990, 1998).

Understanding the causes of diversity among phytophagous insects requires an analysis of their evolutionary history in relation to that of their host plants. Four primary mechanisms have been proposed to explain the macroevolution of insect host-plant use: (a) cospeciation, or strict association by descent; (b) host-shifting, where an insect lineage becomes established on a new host-plant via host-range expansion followed by splitting; (c) speciation of insects independent of host-plant speciation or patterns of host plant use; and (d) lineage sorting as a result of extinctions of insects or host-plants (Mitter *et al.* 1991; Weintraub *et al.* 1995).

Cospeciation between phytophagous insects and their hosts, parasites, or mutualists has been demonstrated clearly in a number of cases (Ronquist & Nylin 1990; Barker 1996; Herre *et al.* 1996; Machado *et al.* 1996; Roderick 1997; Roderick & Metz 1997; Burckhardt & Bassett 2000; Clark *et al.* 2000; Itino *et al.* 2001; Weiblen & Bush 2002). The majority of studies, however, indicate that congruence between insect and host plant phylogenies is partial or nonexistent, and thus host-shifting appears to be the more prevalent mechanism in determining the associations of insects and their hosts (Humphries *et al.* 1986; Weintraub

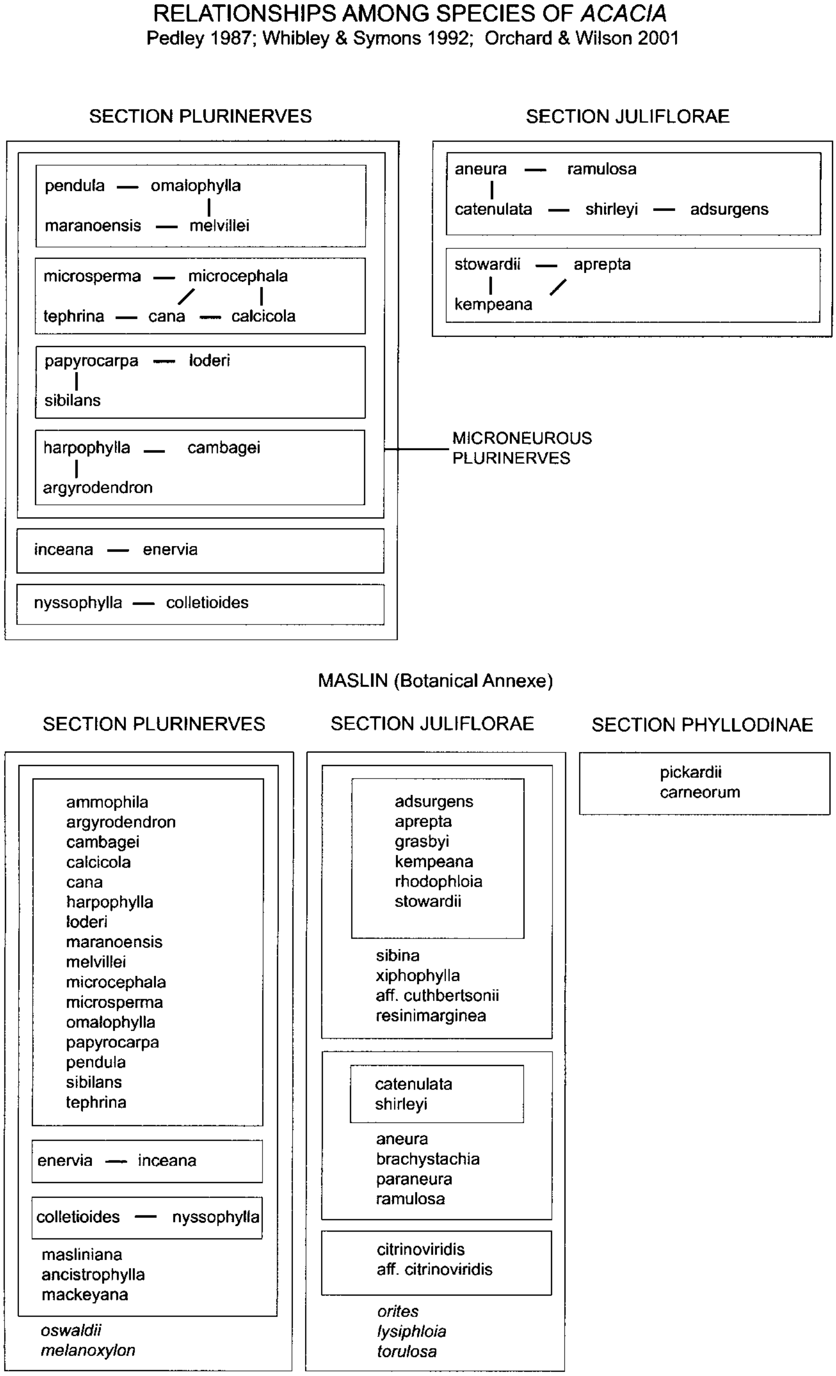

Fig. 31. Relationships among Australian *Acacia* utilised by some thrips species. (a) Based on taxonomy (Pedley 1987; Whibley & Symon 1992; Maslin 2001). A link between a pair of species indicates that they are noted as being closely related in one or more publication, and boxes surround sets of closely related species. (b) Based on Maslin (see Botanical Annexe), where a box around a set of species represents an hypothesised relatively close phylogenetic relationship. Five species in italics at the bottom are not closely related to the others.

et al. 1995; Janz & Nylin 1998; Dobler & Farrell 1999; Janz *et al.* 2001; Jones 2001; Lopez-Vaamonde *et al.* 2001; Ronquist & Liljeblad 2001). Consequent to host shifting, fitness tradeoffs between hosts, or ecological divergence of derived, host-shifted populations, may spur the evolution of reproductive isolation (Joshi & Thompson 1997; Hawthorne & Via 2001; Nosil *et al.* 2002). Moreover, colonisation of new host-plant lineages may provide opportunities to diversify rapidly (Ehrlich & Raven 1964; Mitter *et al.* 1988; Mitter & Farrell 1991).

Thus far, the bulk of evidence for the primacy and phenotypic effects of host-plant shifts in insect diversification is based on taxonomic information rather than robust species-level insect phylogenies. Moreover, for most insect-plant assemblages, little or no phylogenetic information is available for the plants. As a result, it has been difficult to assess the prevalence, roles, and causes of cospeciation and independent speciation in diversification, and to pinpoint the circumstances and effects of host-shifting events. Such analyses are critical to understanding the phylogenesis of diversity, and to making connections between microevolutionary processes and the patterns of macroevolutionary change (Futuyma 1983, 1991; Mitter *et al.* 1991; Thompson 1994).

The main questions addressed in this research area are as follows.

(1) To what extent do related insect species utilise related species of plants (Ehrlich & Raven 1964; Janz *et al.* 2001), and how common are cospeciation and host-plant shifting in insect diversification?

(2) What aspects of plants, insects, and their ecological interactions favour co-speciation, and when does cospeciation involve coevolution?

(3) What are the causes and consequences of host-plant shifting?

(4) How and why do host-plant specialisation and generalisation evolve, and how are they related to patterns of species diversity?

Australian *Acacia* thrips provide excellent opportunities to test hypotheses on the causes of the evolution of host plant use, because they have been reasonably well characterised taxonomically and ecologically, and considerable information is available on relationships among their host plants. In this section, we use a combination of taxonomic and phylogenetic data, on both the *Acacia* and the insects, to address these questions. We present our evidence for the patterns and processes in the evolution of host-plant use for each of the four behavioural-ecological suites of *Acacia* thrips, with reference to the relationships among their *Acacia* host plants described in Figures 31, 32, and the **Botanical Annexe**.

PATTERNS OF HOST-PLANT USE

Gall-inducers

Analysis of the host plant relationships of this group is facilitated by a more or less complete sampling of the species, a robust among-species phylogeny (Fig. 29), and a larger phylogeny that also includes samples of each of the nominal species that are found on multiple host plants, *Kladothrips rugosus*, *K. waterhousei*, *K. augonsaxxos*, and *K. schwarzi* (Fig. 30). As a result, it is possible to interpret the host-plant relationships of this group in an explicitly phylogenetic context.

Several lines of evidence indicate that related species of gall-inducing thrips are found on related species of *Acacia*.

(1) The gall-inducing thrips of *Acacia* Section Plurinerves form a monophyletic group that is derived from within the lineage that contains the thrips of *Acacia* Section Juliflorae.

(2) The galling thrips on Plurinerves form two lineages, one of which includes species inducing round galls, whereas the other includes species inducing elongate galls. Each of these groups contains one lineage on *Acacia harpophylla* and *Ac. cambagei*, and another lineage on a large suite of 'microneurous' *Acacia* species that are grouped together taxonomically and phylogenetically (Pedley 1987; Maslin & Stirton 1997; Maslin 2001) (Fig. 31, **Botanical Annexe**).

(3) *Acacia harpophyll*a and *Ac. cambagei* are sister-taxa by our cpDNA data and by taxonomic data (Figs 31, 32), and they bear two sister-species pairs of gall thrips species (*Kladothrips ellobus* + *K. acaciae*, and *K. hamiltoni* + *K. harpophyllae*) (Figs 29, 30).

(4) Each of 15 species of microneurous *Acacia* Section Plurinerves harbours two species of thrips, one morphologically indistinguishable from *Kladothrips rugosus* and inducing a more or less round gall, and the other indistinguishable from *K. waterhousei (*or the very similar *K. habrus)* and inducing a more or less elongate gall. Mitochondrial DNA divergences of over 3% between the *K. rugosus* forms on different *Acacia* species, and between the *K. waterhousei* forms on the exact same set of *Acacia* species, suggest that each of these named species represents a suite of host-plant specific sibling species. Such an inference would be consistent with evidence that other gall-inducing insects are virtually always host-plant specific (Ananthakrishnan 1984; Shorthouse & Rohfritsch 1992; Williams 1994; Abrahamson *et al.* 1998).

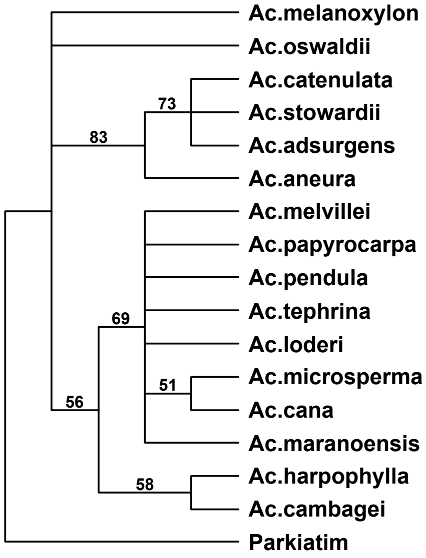

Fig. 32. Bootstrap majority-rule maximum-parsimony *Acacia* phylogeny (200 replicates), inferred from the analysis of 47 unambiguous insertion-deletion characters (Simmons & Ochoterena 2000) derived from 1152 base pairs of sequence of the gene regions psbA-trnH and trnL-trnF. Data for *Ac. oswaldii*, *Ac. melanoxylon* and *Parkia timoriana* (as *Parkiatim*) are from Murphy *et al.* (2000), and data for the other taxa are from Crespi (unpublished). The analysis yielded 273 most-parsimonious trees of length 55, and 20 of the 47 characters were parsimony-informative.

(5) The thrips on Juliflorae form two lineages; in one of them all of the species induce spherical galls (*Kladothrips arotrum*, *K. augonsaxxos*, *K. sterni*, and *K. torus*), and in the other the species induce elongate, tubular galls (*K. antennatus*, *K. pilbara*, and *K. schwarzi*).

(6) Each of these two lineages on Juliflorae comprises two monophyletic groups, one on a set of *Acacia* species of which some are known to be closely related (*Ac. aprepta*, *Ac. kempeana*, and *Ac. stowardii*) and the other on the three closely related species *Ac. aneura*, *Ac. catenulata*, and *Ac. ramulosa* (Fig. 32).

Table 7. Parallel patterns in host-plant use among Australian *Acacia* thrips. Host plants used are shown just below each thrips lineage (see Figs 29, 30 and 31). Each 'cluster' comprises four independently evolved lineages of gall-inducers and phyllode-gluers, each of which uses an overlapping set of related host plants, with only a few exceptions (in italics). These data show that related thrips species use related host plants, and that these patterns of conservatism in thrips host-plant use have evolved multiple times in parallel.

CLUSTER A: Plurinerves

Phyllode-gluers and opportunists			**Gallers**	
***Lichanothrips* lineage**	***Paracholeothrips* lineage 1**	***Grypothrips* lineage**	***Kladothrips* lineage 1-round**	***Kladothrips* lineage 2-elongate**
harpophylla		*harpophylla*	*harpophylla*	*harpophylla*
cambagei		*cambagei*	*cambagei*	*cambagei*
calcicola	*calcicola*		*calcicola*	
argyrodendron		*argyrodendron*		
	ammophila	*ammophila*	*ammophila*	*ammophila*
	cana	*cana*	*cana*	*cana*
	maranoensis	*maranoensis*	*maranoensis*	*maranoensis*
	melvillei	*melvillei*	*melvillei*	*melvillei*
	microcephala	*microcephala*	*microcephala*	*microcephala*
	omalophylla	*omalophylla*	*omalophylla*	*omalophylla*
	papyrocarpa	*papyrocarpa*	*papyrocarpa*	*papyrocarpa*
	pendula	*pendula*	*pendula*	*pendula*
	sibilans	*sibilans*	*sibilans*	*sibilans*
	tephrina	*tephrina*	*tephrina*	*tephrina*
			ancistrophylla	*ancistrophylla*
		loderi	*loderi*	*loderi*
			enervia	*enervia*
		microsperma	*microsperma*	*microsperma*
			orites	*inceana*
		oswaldii		*oswaldii*
		longifolia		*aff. cuthbertsoni*
		stenophylla		*carneorum*
				melanoxylon
				xiphophylla

CLUSTER B: Juliflorae

Phyllode-gluers and opportunists		**Gallers**	
***Dunatothrips* + *Domeothrips* lineage**	***Paracholeothrips* lineage 2**	***Kladothrips* lineage 1-round, *K. arotrum, K. terni, K. tepperi***	***Kladothrips* lineage 4-elongate, *K. antennatus***
aneura	*aneura*	*aneura*	*aneura*
catenulata		*catenulata*	
ramulosa	*ramulosa*	*ramulosa*	*ramulosa*
lysiphloia			
	aff. citrinoviridis	*aff. citrinoviridis*	*aff. citrinoviridis*
			adsurgens

Table 7, contd.

CLUSTER C: Juliflorae

Phyllode-gluers and opportunists		**Gallers**	
***Carcinothrips* + *Warithrips* lineage**	***Sartrithrips* + *Panoplothrips* + *Truncatothrips* lineage**	***Kladothrips* lineage 5-round, *K. augonsaxxos, K. torus***	***Kladothrips* lineage 6-elongate, *K. schwarzi, K. pilbara***
kempeana	*kempeana*	*kempeana*	*kempeana*
stowardii	*stowardii*	*stowardii*	*stowardii*
torulosa	*torulosa*		
	aprepta	*aprepta*	*aprepta*
citrinoviridis	*citrinoviridis*	*citrinoviridis*	*citrinoviridis*
	grasbyi	*grasbyi*	*grasbyi*
rhodophloia	*rhodophloia*	*rhodophloia*	*rhodophloia*
adsurgens	*adsurgens*	*resinimarginea*	*resinimarginea*
shirleyi		*sibina*	*sibina*
tumida		*pickardii*	
aneura			

(7) Seven species of *Acacia* in these two Juliflorae lineages each harbour two species of thrips, one morphologically indistinguishable or very similar to *Kladothrips augonsaxxos* and inducing a more or less round gall, and the other morphologically indistinguishable or very similar to *K. schwarzi* and inducing a more or less elongate gall (Fig. 9). As in *K. rugosus* and *K. waterhousei*, mtDNA divergences strongly indicate that *K. augonsaxxos* and *K. schwarzi* each represents a set of sibling species. A comparable sibling species complex also occurs in *K. antennatus* on *Ac. aneura*, *Ac. ramulosa*, and *Ac. aff. citrinoviridis*.

These patterns, summarised in Table 7, indicate that related thrips species tend to induce galls on related species of *Acacia* to a striking degree. Moreover, different thrips lineages show remarkably parallel patterns of host plant use. Thus, in the thrips on Plurinerves, ((*Kladothrips ellobus* + *K. acaciae*) (*K. rugosus* complex)) parallels ((*K. hamiltoni* + *K. harpophyllae*)(*K. waterhousei* complex)), and in the thrips on Juliflorae, (*K. augonsaxxos* complex + *K. torus*) parallels (*K. schwarzi* complex + *K. pilbara*), and (*K. antennatus* complex) parallels (*K. arotrum* + *K. tepperi* + *K. sterni*).

The parallel range of host-plant affinities of these independently evolving thrips lineages is explicable by postulating either cospeciation between the thrips and the *Acacia*, or parallelisms and convergences on the same sets of host plant species. An hypothesis of cospeciation makes three unique predictions: the phylogenies of the presumptive parallel thrips lineages should mirror one another; the phylogeny of the relevant thrips lineages should each mirror the phylogeny of the *Acacia* host plants; and the parallel speciation events among the thrips lineages, and between the thrips and the *Acacia*, should be contemporaneous. Table 7 provides some evidence suggestive for such parallel patterns of host-plant associated phylogenesis: in *Kladothrips rugosus* and *K. waterhousei*, samples from *Ac. loderi*, *Ac. ancistrophylla*, and *Ac. enervia* form a monophyletic group for each nominal species, and the samples from *Ac. microcephala*, *Ac. tephrina*, and *Ac. omalophylla* are each closely related. Moreover, in *K. schwarzi* and *K. augonsaxxos,* the samples from *Ac. grasbyi* and *Ac. rhodophloia* each comprise strongly supported sister-taxa.

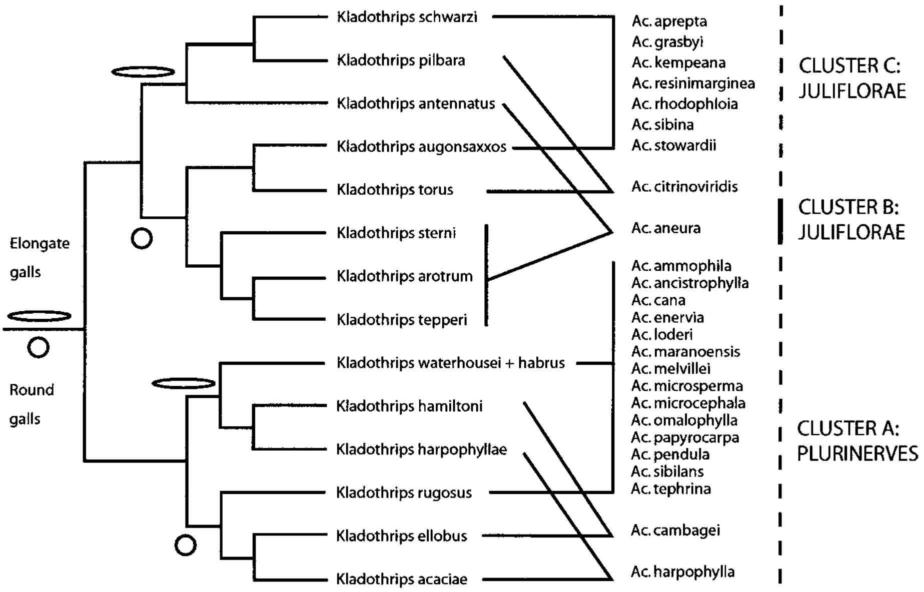

Fig. 33. Idealised depiction of the parallel cospeciation hypothesis, in which thrips in two lineages, one inducing round galls the other elongate galls, track host plant speciation. Patterns in the diversification of thrips host plant use are parallel among the two main lineages on *Acacia* in the Plurinerves, and among the two main lineages on *Acacia* in the Juliflorae. This thrips phylogeny differs in only a few branches from the phylogeny in Fig. 29. Clusters A, B, and C refer to the *Acacia* species in Table 7.

However, some evidence appears to contravene a cospeciation hypothesis: for example, the *K. waterhousei* on *Ac. cana* and *Ac. microsperma* are closely related, but the *K. rugosus* on these two plants clearly are not.

In contrast to an hypothesis of cospeciation, under an hypothesis of convergence or parallelism only certain *Acacia* species are amenable to gall induction by *Kladothrips*, due for example to their large monospecific stands and wide distributions (Pedley 1987; Whibley & Symons 1992), phyllode physiology or morphology, phenology, or other factors. Thus, although related thrips species tend to inhabit related *Acacia* species, they do so only because host-plant shifts tend to occur more readily between such plants. This hypothesis predicts a lack of strict concordance between plant and insect phylogenies, or between the phylogenies of the *K. waterhousei* species complex with the *K. rugosus* complex, and the *K. schwarzi* complex with the *K. augonsaxxos* complex. Finally, *Acacia*-thrips phylogenesis may involve a mix of cospeciation and host-shifting among related plants, which could be indicated by statistical significance in tests of cospeciation coupled with clear examples of host shifts. Rigorous statistical testing of these hypotheses requires better-resolved and better-supported phylogenies than are available at present, especially for the sibling species complexes.

Under a model involving extensive cospeciation, the apparent complexity of the patterns described above belies great simplicity of presumed evolutionary processes of thrips-*Acacia* phylogenesis (Fig. 33). Imagine that two ancestral gall-inducing thrips species, one of which induced an elongate gall, and the other a spherical gall, inhabited an ancestral species of *Acacia*. The diversification of the *Acacia* involved splitting into one lineage of species in the Juliflorae, and one lineage of species in the Plurinerves. As this diversification proceeded, the two thrips species simply tracked the speciation of their host plants and remained upon the lineages that could support them, such that each plant lineage retained an elongate-galler and a spherical-galler.

The thrips on *Acacia* in the Juliflorae inhabited (*Ac. aneura* + *Ac. catenulata* + *Ac. ramulosa*) and a sister-lineage including (*Ac. citrinoviridis* + *Ac. stowardii* + *Ac. kempeana* + *Ac. aprepta* + *Ac. grasbyi* + *Ac. rhodophloia* + *Ac. resinimarginea* + *Ac. sibina*). The thrips on *Acacia* in the Plurinerves likewise radiated by tracking the speciation of their host plants, giving rise to species on ((*Ac. harpophylla* + *Ac. cambagei*) + (other microneurous *Acacia* species)), all of which also retained one species inducing a round gall, and one inducing an elongate gall. This hypothesis is also supported by the presence of morphologically distinct thrips species in the apparently older thrips lineages (on *Ac. harpophylla* and *Ac. cambagei*) and the parallel evolution of two morphologically distinct species on *Ac. citrinoviridis*. The main evidence against the cospeciation hypothesis is that it appears to contradict the best currently available phylogeny of the gall-inducing thrips at several basal nodes (Fig. 29). However, these nodes exhibit such low bootstrap support that we cannot reject an hypothesis of cospeciation based on phylogenetic criteria alone.

The evidence described above implicates cospeciation as a possible factor involved in plant-insect macroevolutionary associations of the gall-inducing Australian *Acacia* thrips. This pattern, however, is overlaid by several instances where host-plant shifts appear to have led to colonisation of new *Acacia* lineages. In all of these cases, as described below, the relevant host-plant species bears only one species of gall thrips (in contrast to the elongate/spherical gall species pairs found on all other *Acacia*), and it is not closely related to the set of *Acacia* species used as host by the most-closely related gall thrips (Figs 31, 32).

(1) *Kladothrips intermedius*, which is paraphyletic with respect to the *K. waterhousei* species group, lives on *Ac. oswaldii*, an *Acacia* that is not closely related to the host plants of *K. waterhousei* (Pedley 1987; Maslin 2001; **Botanical Annexe**).

(2) *K. rodwayi* lives only on *Ac. melanoxylon*, a species phylogenetically distant from the microneurous *Acacia* species inhabited by thrips to which it is most-closely related (Pedley 1987; Maslin 2001; **Botanical Annexe**).

(3) *K. xiphius* induces galls on *Ac. xiphophylla*, which is grouped in the Juliflorae, although the relatives of *K. xiphius* are all on *Acacia* in the Plurinerves.

(4) *K. maslini* is apparently derived from within the *K. rugosus* complex, but it lives on *Ac. orites*, an *Acacia* not closely related to the microneurous Plurinerves that harbour *K. rugosus* (Pedley, 1987; Maslin 2001; **Botanical Annexe**).

(5) *K. zygus* lives on *Acacia pickardii*, which is classified in the Section Phyllodinae, though it is related to thrips species on *Acacia* in the Juliflorae.

(6) *Ac. calcicola*, *Ac. carneorum*, and *Ac. aff. cuthbertsonii* each bear one species of gall-inducing thrips; these appear to be closely related, but only *K. morrisi* from *Ac. calcicola* has been described. Although *Ac. calcicola* appears to be related to the microneurous Plurinerves that bear gall thrips, the latter two *Acacia* species are highly divergent from this group.

All of these cases of apparent host-plant shift, with the possible exception of *K. morrisi*, involve movement to an *Acacia* species that is phylogenetically removed from the host-plants used by all of their close thrips relatives. Moreover, all of them also involve phenotypic divergence, with morphological species differences evolving in each case, and striking differences in life cycles and behaviour evolving in some species (e.g. in *K. intermedius, K. xiphius,* and *K. rodwayi*) (Table 6). Such notable divergences are not observed across thrips lineages that have remained on closely related host plants, as best evidenced by the apparent sibling species complexes on closely related plants in *K. rugosus*, *K. waterhousei*, *K. augonsaxxos*, *K. schwarzi*, and *K. antennatus*. These data provide strong evidence that host-plant shifting leads to phenotypic divergence and novel adaptations. Indeed, this pattern, if supported further (e.g. Singer *et al.* 1993), implies that the generation of phenotypic diversity in phytophagous insects is driven by shifting to phylogenetically divergent host-plants, presumably as a result of strong selection subsequent to colonisation (e.g. Price & Willson 1976; Feder *et al.* 1993, 1999; Brown *et al.* 1995; Bush & Smith 1997; Crespi & Sandoval 2000; Berlocher & Feder 2002). If so, then the ability of a group of insects to shift to plants that are more or less phylogenetically distant from their current host may ultimately determine the degree of diversity within that lineage, and the factors limiting and facilitating host plant shifts assume paramount importance in explaining cross-taxon variation in phytophagous insect phenotypic and species diversity.

Phyllode-gluers

Our phylogeny that includes the phyllode-glueing species demonstrates our less complete taxon sampling for this group than for gall-inducers (Fig. 28). Consequently, our inferences regarding host plant use in this group are based primarily on a combination of genus-level phylogeny and taxonomic information. We assume that the genera *Carcinothrips*, *Domeothrips*, *Dunatothrips*, and *Sartrithrips* are each monophyletic, as all of the available evidence suggests, such that species not represented in the phylogeny can still be included in the analysis of the phylogenesis of host plant use.

At the broad level of *Acacia* section, the *Acacia* gluers exhibit a similar high degree of host plant conservatism to the gall-inducers: there are two lineages, one on *Acacia* in Juliflorae and one on *Acacia* in Plurinerves (Fig. 34). One lineage is paraphyletic with respect to the other, but in this case the ancestral host plant section cannot be inferred with confidence, although we suspect that it is the Juliflorae.

At a finer level, there are three main lineages among the gluers:

(1) (*Paracholeothrips* + *Lichanothrips* + the opportunistic *Grypothrips*);
(2) (*Dunatothrips* + the apparently opportunistic *Domeothrips*); and
(3) (*Carcinothrips* + *Panoplothrips* + *Satrithrips* + the opportunistic *Warithrips*) (Fig. 34).

Each of these lineages, as outlined below, exhibits a strong pattern of related thrips species on related *Acacia* species, and in many cases these patterns coincide with those uncovered for the gall-inducers.

(1) This first lineage comprises a polyphyletic genus, *Paracholeothrips*. This includes a relatively basal lineage with species on several *Acacia* species in Section Juliflorae, and a second lineage comprising two species on microneurous Plurinerves: *P. clavisetae*, found on ten such *Acacia* species, and *P. calcicola*e, found only on *Ac. calcicola*. This second lineage forms a monophyletic assemblage together with two genera that are

also restricted to Plurinerves: *Lichanothrips*, with seven species on *Ac. harpophylla*, one each on the related plants *Ac. argyrodendron* and *Ac. cambagei*, one species on *Ac. calcicola*, and the genus of opportunists *Grypothrips*.

(2) *Dunatothrips* + *Domeothrips* are found on two closely related *Acacia* species, *Ac. aneura* and *Ac. catenulata*, as well as on *Ac. lysiphloia*. The presence of numerous, related thrips species on the former two host plants matches the situation in the gall-inducing species on *Ac. aneura* and *Ac. catenulata*, which include *Kladothrips antennatus*, *K. arotrum*, *K. sterni*, and *K. tepperi*.

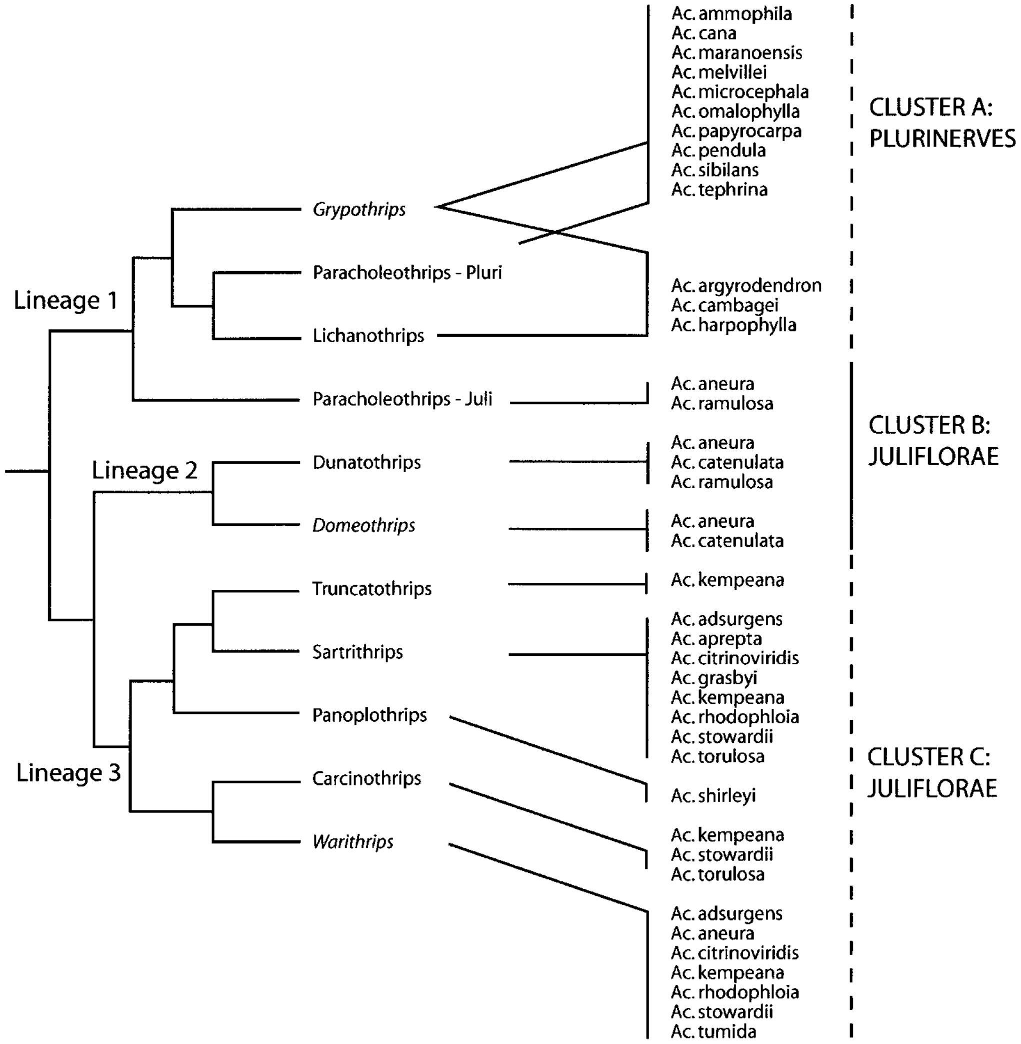

Fig. 34. Diversification of host plant use in the Australian *Acacia* thrips that glue phyllodes, and in the genera and species of opportunists that are closely related to them (with opportunist genus names in italics). The evolution of host plant use is highly conservative with regard to the section of *Acacia* utilised, and with regard to the sets of related *Acacia* within Juliflorae used. Each lineage of phyllode-glueing species has apparently given rise to a lineage of opportunistic species that uses an overlapping set of host plants. The phylogeny is from Fig. 28, with the addition of the hypothesised position of the lineage of *Paracholeothrips* on *Acacia* in the Juliflorae. Clusters A, B, and C refer to the *Acacia* species in Table 7.

(3) Species in the third lineage are found on *Ac. kempeana*, *Ac. stowardii*, *Ac. rhodophloia*, *Ac. grasbyi*, *Ac. aprepta*, *Ac. citrinoviridis*, as well as *Ac. adsurgens*, *Ac. shirleyi*, and *Ac. torulosa*. The former five species harbour members of the *K. augonsaxxos* and *K. schwarzi* complexes; *Ac. citrinoviridis* bears two species of gall-inducers related to these; *Ac. adsurgens* supports a species resembling *K. schwarzi* and *K. antennatus*; and *Ac. shirleyi* and *Ac. torulosa* do not bear gall-inducing thrips, probably because they are found in monsoonal areas. As such, the patterns of host plant use in this lineage also generally correspond well between the gluers and gall-inducers.

Paracholeothrips also includes species on *Ac. ramulosa* and *Ac. aff. citrinoviridis*, which we expect will be found to be related to the species *P. mulgae* on *Ac. aneura*. If these relationships bear true, then this genus will provide another example of related thrips on these three Juliflorae species, and related thrips on microneurous Plurinerves. Similarly, *Lichanothrips* are restricted to a small set of closely related Plurinerves, and show an additional remarkable pattern of seven congeners on the same host plant species.

These findings demonstrate that closely related phyllode-glueing thrips tend to inhabit closely related host plants, which implicates restricted host shifting or cospeciation in the evolution of their host plant use. Moreover, this group also shows two apparent cases of host-plant shifting leading to notable phenotypic divergence, and habitation of the host plant by only a single species. First, *Dunatothrips gloius* lives on *Ac. lysiphloia*, which is in the Juliflorae but phylogenetically removed from the set of closely related Juliflorae species *Ac. aneura*, *Ac. catenulata*, and *Ac. ramulosa* that harbour all of the other *Dunatothrips* (Fig. 31 and **Botanical Annexe**). *D. gloius* differs strikingly from the other *Dunatothrips* in morphology and behaviour (exhibiting a lack of pleometrosis, and a domicile different in form), as well as apparently not being subject to any of the myriad exploitative thrips species that attack the other *Dunatothrip*s. Second, *Panoplothrips* is most closely related to the thrips genera (*Sartrithrips* and *Carcinothrips*) that inhabit *Ac. kempeana*, *Ac. stowardii*, *Ac. aprepta*, *Ac. grasbyi*, *Ac. rhodophloia*, *Ac. adsurgens* and *Ac. torulosa*, but its host plant, *Ac. shirleyi*, appears to be related to the set of plants that includes *Ac. aneura*, *Ac. catenulata*, and *Ac. ramulosa* (as well as *Ac. adsurgens)*. Thus, the lineage leading to *Panoplothrips* may have host-shifted to a relatively divergent *Acacia*, which would accord with its monospecific status, its divergent morphology, and its unusual, open domiciles. Such a shift may also have led to the attack on *Panoplothrips* by *Glaridothrips*, a genus of exploiters that also inhabit *Ac. aneura* and *Ac. catenulata*.

Opportunists

Our inferences for the evolution of host plant use in the opportunists are based almost entirely on taxonomic information, in particular the patterns of host use for genera and for species that have been recorded from multiple hosts.

Dactylothrips species show strong, though not complete, restriction to *Acacia* sections, or closely related species within sections, in some species. Thus, *D. aneura*e has been found on the closely related Juliflorae species, *Ac. aneura* and *Ac. catenulata*, and *D. aenictus* has been recorded from the Juliflorae species, *Ac. adsurgens*, *Ac. aprepta*, *Ac. kempeana*, *Ac. tarculensis*, *Ac. grasbyi*, *Ac. xiphophylla*, and *Ac. citrinoviridis* (but also apparently from the Plurinerves species *Ac. tephrina*). Thus, the differences in host plant use between these two species parallel those found in the gall-inducing *Kladothrips* on Juliflorae

(Table 7), and the gluer genera *Dunatothrips*, *Domeothrips*, and *Carcinothrips*. By contrast, *D. turba* and *D. junix* are found only on species of microneurous Plurinerves, except for the curious presence of *D. turba* on *Ac. pickardii* as well.

Katothrips shows a similar division between species on Juliflorae and Plurinerves, though only in a small subset of the many species in this genus. Thus, two species inhabit only Juliflorae: *Ka. spinosus* from the closely related *Ac. grasbyi* and *Ac. rhodophloia*, *Ac. biconus* from the closely related *Ac. aneura* and *Ac. ramulosa*. Two species, *Ka. pendulae* and *Ka. brigalowi*, each live on several species of microneurous Plurinerves, and a third, *Ka. tityrus*, inhabits two closely related Plurinerves species *Ac. melanoxylon* and *Ac. implexa* (Maslin 2001).

The genus *Grypothrips* is almost entirely limited to *Acacia* species in the Section Plurinerves, with *G. mantis* on nine microneurous species (plus *Ac. longifolia*, in the Juliflorae), *G. curiosus* on the closely related *Ac. harpophylla* and *Ac. argyrodendron*, and *G. okrius* and *G. darlingi* each recorded from three species of microneurous Plurinerves.

Akainothrips species display less strong host-plant conservatism than the other genera of opportunists, but related species still tend to use sets of related plants. Four species, *Ak. dubitalis*, *Ak. gremius*, *Ak. irenae*, and *Ak. bipictus*, are each found on two or more *Acacia* in the Juliflorae, and *Ak. polysetulus* is recorded from four species of microneurous Plurinerves, as well as from the related *Ac. mackeyana* and *Ac. masliniana*. By contrast, *Ak. citritarsus* has been recorded from 20 *Acacia* species across the Plurinerves and Juliflorae, but this nominal species appears to constitute two forms, one with and one without postocular setae, each of which is largely restricted to one of the *Acacia* sections. Finally, the more catholic *Ak. herbae* and *Ak. tosofagi* have each been recorded from apparently unrelated *Acacia* in two plant sections.

A considerable number of opportunist species utilise *Acacia* species that are not hosts to gallers or gluers, eg. *Ac. paradoxa*. Many of these opportunists have been able to move onto a much broader range of hosts than the majority of *Acacia* thrips, perhaps because they are not constrained by the requirement of being able to induce galls or glue phyllodes together. These include some of the genera for which DNA sequence data are not yet available, and so it is possible that some (e.g. *Katothrips*, *Akainothrips* and *Kellyia*) may not be of the same lineage as the other *Acacia* thrips, although morphology would suggest that this is unlikely.

Exploiters

Host plant use by the exploiter genera and species (Fig. 35) tends to mirror that of their host thrips, although the exploiters may sometimes be restricted to a subset of the host plants used by their host thrips.

Among *Koptothrips* species, *Ko. flavicornis* is found only on various microneurous Plurinerves, attacking the gall-inducers on these plants, whereas *Ko. dyskritus* has been recorded from such Plurinerves as well as from the Juliflorae species *Ac. aneura*, *Ac. ramulosa*, and *Ac. rhodophloia*, though at very low frequency. By contrast, the other two *Koptothrips* species are specialised, attacking *Kladothrips acaciae* and *K. ellobus* on the closely related host plants *Ac. harpophylla* and *Ac. cambagei*. Thus they match the pattern observed in the gall-inducers, where each of these two plants also bears specialised, morphologically differentiated species, the sister-taxon pairs (*K. acaciae* + *K. ellobus*) and (*K. harpophyllae* + *K. hamiltoni*).

Crespithrips shows notable host plant conservatism, being found only on a subset of the plants of their *Sartrithrips* hosts, *Ac. aprepta*, *Ac. kempeana*, *Ac. rhodophloia*, and *Ac. stowardii* (*C. enigmaticus*) and *Ac. grasbyi* (*C. hesperus*). Similarly, *Triadothrips* are limited to microneurous Plurinerves, with *T. hesmus* recorded from eight species of microneurous Plurinerves, *T. briga* from *Ac. harpophylla*, and *T. arkaringa* from *Ac. calcicola*, where it parasitises the specialist *Paracholeothrips calcicola*e. We note, however, that the restricted host distributions of these exploiters may be due in part to limited sampling, as some of the host species are rarely collected and exploiters only tend to affect a small proportion of host populations.

All of the exploiter genera above attack either gall-inducers, or only one of the three lineages of phyllode-gluers, (*Dunatothrips*), (*Carcinothrips* + *Panoplothrips* + *Sartrithrips*), and (*Lichanothrips* + *Paracholeothrips*). By contrast, *Xaniothrips* is unique among exploitative *Acacia* thrips in that, considered at the genus level, it parasitises all three lineages of gluers, and thus utilises the full range of Plurinerves-Juliflorae host plant diversity (Fig. 35). We suspect that the relative ecological success of this genus may be attributable to its unique abdominal spine morphology, which provides it with a novel, and presumably effective, mechanism for invasion of host domiciles. At the species level, however, *Xaniothrips* shows evidence of the same pattern of host plant and host thrips affinities as the other *Acacia* thrips: the related species *X. eremus* and *X. rhodopus* both attack *Sartrithrips* species on the related *Acacia* species *Ac. kempeana*, *Ac. stowardii* and *Ac. rhodophloia*; the related pair of species *X. mulga* and *X. zophus* attack *Dunatothrips* on the related plants *Ac. aneura* and *Ac. ramulosa*; and the related *X. leukandrus* and *X. xantes* attack *Lichanothrips* on the related Plurinerves species *Ac. harpophylla*, *Ac. cambagei* and *Ac. argyrodendron*. Indeed, we predict that phylogenetic evidence will show that *Xaniothrips* comprises three lineages, each limited to a set of related thrips and *Acacia*.

HOST PLANT USE, SPECIALISATION, AND SPECIES DIVERSITY

Elucidation of the selective forces that drive the evolution of ecological relationships is one of the outstanding unresolved questions in evolutionary biology (Mayr 1942; Levins & MacArthur 1969; Futuyma 1976, 1983, 1991; Futuyma & Moreno 1988; Jaenike 1990; Thompson 1994). This question remains challenging because it requires connecting selective processes with historical patterns, in relation to the ecology and genetic architecture unique to particular lineages (e.g. Via 1984; Futuyma & McCafferty 1990). Many studies have used comparative approaches to infer correlates of specialisation, generalisation, and patterns of host-plant use (e.g. Otte & Joern 1977; Bernays & Chapman 1994), or inferred patterns of evolutionary transition between specialisation and generalisation (Benson 1950; Holloway & Hebert 1979; Mitter & Brooks 1983; Strong *et al.* 1984; Futuyma & Moreno 1988; Thompson 1994; Kelley & Farrell 1998; Nosil 2002). Evolutionary transitions in host use may be driven by selective pressures and tradeoffs at the trophic level above, below, or at the level of the taxon of interest, and by historical contingencies, such as opportunities for host-range expansion or extinction of specialist hosts (Levins & MacArthur 1969; Futuyma 1976; Via 1984; Bernays & Graham 1988; Jermy 1988; Fry 1990; Jaenike 1990; Bernays & Chapman 1994; Mackenzie 1996; Pellmyr *et al.* 1997; Crespi & Sandoval 2000; Hawthorne & Via 2001). To understand how ecological range evolves, we must assess how selection and non-deterministic processes are involved in the generation and maintenance of ecological diversity.

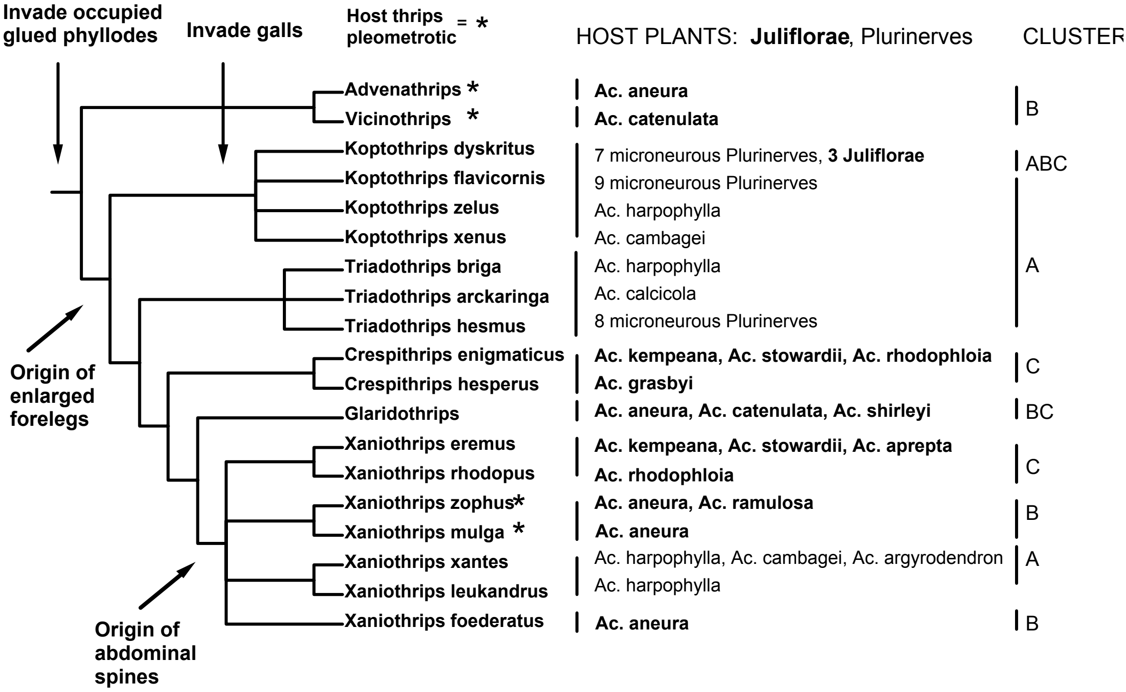

Fig. 35. Diversification of host plant use, morphology, and behaviour in thrips that exploit the galls or glued phyllodes created by other species. The evolution of host plant use is conservative within all of the genera except *Xaniothrips*, but among genera, and within *Xaniothrips*, it exhibits a high degree of evolutionary lability. The phylogeny is derived from Fig. 5, with the addition of *Crespithrips* in its hypothesised position. Clusters A, B, and C refer to the *Acacia* species in Table 7.

Analysis of the evolution of specialisation is intimately connected to the determinants of species diversity, since at least in insects, specialisation normally engenders higher species numbers. The Australian *Acacia* thrips provide a useful system for the analysis of these questions because they comprise a large set of diverse lineages, which use a largely overlapping set of host plants. As a result, aspects of diversity in host-plant use can be compared across species, genera, and the four behavioural-ecological suites, to detect patterns that may be indicative of the causal factors at work.

The main limitations on our analyses of the evolution of host plant use in *Acacia* thrips are twofold. First, inferences concerning evolutionary patterns are based predominantly on host plant records, which are more or less incomplete and prone to sampling effort biases; and taxonomy, which currently provides polytomies rather than a resolved phylogeny. Sampling effort is especially an issue for the small opportunist thrips, such as *Dactylothrips*, *Katothrips*, and the *Rhopalothipoides* group, which probably comprise many more species per genus than have been collected and described thus far. Second, apparently polyphagous species of *Acacia* thrips may sometimes represent a set of globally or locally monophagous species (Fox & Morrow 1981). For example, all of the gall-inducers appear to be monophagous, with four large sets of sibling species on related host plants. We suspect, however, that sibling species complexes or host races may be especially common in, or nearly restricted to, the gall-inducers, due to their high morphological similarity and the evolutionary conservatism of their enclosed environments—though in other genera there are sometimes morphological hints of monophagy in putatively polyphagous species.

We can use our database on the associations between *Acacia* thrips and their host plants, in conjunction with the taxonomy and available phylogenies, to evaluate two hypotheses regarding the evolution of specialisation and the generation and maintenance of diversity in host plant use.

First, we can evaluate the degree to which different *Acacia* species support different numbers of thrips species, and different numbers of specialists. We can then relate this variation in thrips diversity to variation in characteristics of the *Acacia*, such as geographic range and local abundance (i.e. the size of the resource base). Moreover, we can determine if the variation in thrips diversity among host plant species is correlated across the four thrips behavioural-ecological modes, as it may be, given that opportunists and exploiters often rely on resources and niches generated by gall-inducers and phyllode-gluers. Second, we can explore the connections between specialisation, phylogeny, ecological habits, and species diversity to evaluate the extent to which the diversification of these insects has involved ecological determinism driven by niche availability and structure, as opposed to the vagaries of chance events and history (Gould 1989; Ricklefs & Schluter 1993; Losos et al. 1998). These two analyses provide a starting point for a full-scale assault on the causes of species diversity in *Acacia* thrips, which will require species-level phylogenies for the entire group, coupled with more complete information on host-plant use.

The *Acacia* resource base

Considered as a whole, the *Acacia* thrips utilise many dozens of species of host plants. However, their species diversity is distributed in a highly non-random pattern across plant species. A few *Acacia* species, notably *Ac. harpophylla*, *Ac. cambagei*, *Ac. papyrocarpa* among the Plurinerves, and *Ac. aneura*, *Ac. catenulata*, and *Ac. kempeana* among the Juliflorae, support strikingly large numbers of thrips species. What characteristics of such plants might foster such high diversity? We will evaluate two non-exclusive hypotheses: first that a broad geographic range in an *Acacia* species fosters speciation, the maintenance of high species diversity, or both; and second, that species diversity amplifies across ecological modes of thrips, generating between-species interactions that make some plant species hyperdiverse.

A broad geographic range for a given *Acacia* species, if it is associated with high local abundance, results in a larger resource base for the thrips species using this plant. Consequently, plant species with larger ranges may support different insect species in different areas, and geographic isolation may foster allopatric speciation if the range of a species becomes fragmented (Blanche & Westoby 1996). Plant population subdivision is common among Australian *Acacia* species, many of which occur in mosaic stands on particular soil types (Maslin 2001). Moreover, a larger geographic range is also more likely to provide a relatively stable resource over time on a landscape (metapopulation) scale, since unpredictable, local fluctuations in rainfall mean that only a subset of the total population of an *Acacia* species may be suitable for thrips survival and reproduction (e.g. producing new phyllodes in a given year). Such rainfall fluctuations are especially important in arid-zone Australia, with precipitation under the capricious influence of the Southern Oscillation. During drought conditions, we have driven and searched for several days at a time through vast stands of *Ac. aneura*, *Ac. harpophylla*, and *Ac. cambagei*, unable to find a single *Acacia* thrips until we reached an area where rain had fallen in the previous few months. Temporal, metapopulation stability should be especially important in the maintenance of specialist thrips populations, since otherwise occasional downward fluctuations in resource levels on a single *Acacia* species might drive them to extinction (Bernays & Chapman 1994).

According to the geographic range hypothesis, *Acacia* species that have larger geographic ranges, high local abundances, or both should host more species of thrips overall, and a larger proportion of these should be specialised (i.e. on a single *Acacia* species). Moreover, if the spatial-isolation component of large *Acacia* range drives speciation, then we should see cases of multiple, closely related and ecologically similar species, either in allopatry or sympatry on the same host plant. Such correlations between plant geographic range and insect species richness have been reported in a wide variety of insect and plant groups (Fowler & Lawton 1982; Cornell 1985; Leather 1986; Blanche & Westoby 1996; Kelly & Southwood 1999), though their causes, which include differentiation among widespread sites in insect species present (Blanche & Westoby 1996), local plant abundance (Fowler & Lawton 1982; Kelly & Southwood 1999), age of the plant lineages (Leather 1986), and numbers of habitats occupied by the plants (Fowler & Lawton 1982) are not always easy to discern.

In Australian *Acacia* thrips, tests of the geographic range hypothesis make various assumptions regarding whether collecting effort is similar across *Acacia* species and the behavioural-ecological suites of thrips, whether allopatric speciation occurs more commonly for species on *Acacia* with larger ranges, whether the range of an *Acacia* species is correlated with its local abundance, whether a given *Acacia* species actually represents a set of closely related species, and whether factors that might be causally associated with species range, such as age of *Acacia* lineages, confound the interpretation. However, the data provide useful indicators of pattern, made stronger by the independence and diversity of the thrips lineages involved. In addition, we are confident that we have sampled at least the great majority of the gall-inducing and phyllode-glueing species, these being relatively easy to discover on their host plants.

We tested the resource base-geographic range hypothesis by extracting estimates of *Acacia* geographic range from the distribution maps in Maslin (2001), and testing for correlations of geographic range with numbers of species, and with the proportion of species that are host-plant specialists, for the thrips in each of the four behavioural-ecological modes (Table 8). For the gall-inducers, we assume, based on the available DNA evidence (Crespi et al. 1997) and evidence from other gall-inducing insects (Ananthakrishnan 1984; Shorthouse & Rohfritsch 1992; Williams 1994; Abrahamson *et al.* 1998), that each morphospecies recorded from different host plants actually represents a set of host-plant specific, sibling species. Under this assumption, all of the *Acacia* species used by gall-inducing thrips support either zero, one, or two species of thrips, except *Ac. aneura*, which harbours four species (Table 8). For these gall-inducing species, there was no correlation between *Acacia* geographic range and numbers of thrips species (Spearmann's rho= -0.08, P > 0.5, N = 24).

The lack of pattern appears to arise in part because almost all the *Acacia* with gall-inducing thrips host two species, such that there is little variance in this variable. Moreover, some of the *Acacia* species with only one gall thrips, such as *Ac. oswaldii* and *Ac. melanoxylon*, have large geographic ranges, but their abundances are relatively low because they do not form extensive monospecific stands. By contrast, *Ac. aneura* is one of the most common and widespread of all Australian *Acacia* species used by thrips, and it hosts a striking four gall-inducing species, three of which, *K. arotrum*, *K. tepperi*, and *K. sterni*, are closely related to one another (Fig. 29); this pattern suggests a role for within-host plant speciation in the gall-inducer species diversity on this plant. This interpretation remains subject only to the reservation that *Ac. aneura* is highly variable in phyllode form and has been split into multiple varieties (Maslin 2001), although at least some of the thrips involved (e.g. *K. arotrum* and *K. antennatus*) are known to inhabit multiple such forms.

An important caveat to interpreting these results for gall-inducers is that, as described above, the host plants with single gall-inducing thrips appear to be inhabited as a result of host-plant shifts to less related species. Shifting of this kind may be rare, such that species numbers on such *Acacia* are determined more strongly by historical events than by ecological factors. However, if we exclude the *Acacia* species subject to the clearest thrips gall-inducer host-plant shifts, *Ac. oswaldii* and *Ac. melanoxylon*, the results are the same (rho = 0.053, P > 0.5, N = 22).

In contrast to the gall-inducers, in the phyllode-glueing species the highest thrips species diversity is found on the *Acacia* with the largest geographic ranges (rho = 0.49, P < 0.025, N = 27), and this pattern remains if the *Acacia* subject to host-plant shifts by thrips are excluded (rho = 0.46, P < 0.05, N = 25). Moreover, for this set of species, *Acacia* geographic range is also correlated positively with the proportion of thrips species that are specialised on a single *Acacia* species, for the full data set (rho = 0.39, P < 0.05, N = 27) and for the data that exclude cases of host-shifting (rho = 0.50, P < 0.025, N = 25). High phyllode-gluer diversity and specialisation are especially notable for the gluers on *Ac. aneura*, *Ac. kempeana*, *Ac. cambagei*, and *Ac. harpophylla* (Table 8). These phyllode-glueing species also exhibit numerous cases of closely related species on the same host plant: seven species of *Lichanothrips* live on *Ac. harpophylla*, three species of *Dunatothrips* inhabit *Ac. aneura* and two are on *Ac. catenulata*, and two species of *Sartrithrips* live on *Ac. kempeana*. For the latter two genera, vicariant splits between eastern and western Australia have apparently generated some of these species, but for *Lichanothrips* the species appear, at least currently, to be sympatric. For *Lichanothrips* on *Ac. harpophylla* in particular, and phyllode-gluers in general, phyllodes that are wide and flat, and at high density in the canopy, appear to support a relatively high diversity and abundance of species—these aspects of plant morphology create the best conditions for joining phyllodes together into a domicile. However, in some cases the phyllode-gluers have overcome this constraint, by creating expansible 'tents' on single phyllodes (e.g. *Dunatothrips aulidis* and *D. skene*), or enclosing sets of small terminal phyllodes in a webbing-like enclosure (e.g. *Dunatothrips gloius* and *D. vestitor*).

Table 8. Numbers of species, and numbers of specialised species (on a single host plant), in the four behavioural-ecological suites, in relation to their *Acacia* host plant and its geographic range (from Orchard & Wilson 2001).

Acacia species	Number of gall inducer species (specialised)	Number of phyllode-gluer species (specialised)	Number of opportunist species (specialised)	Number of exploiter species (specialised)	Estimated geographic range (km^2 x 10^6)
Section Plurinerves					
cambagei	2 (2)	1 (1)	15 (8)	2 (1)	2.5
harpophylla	2 (2)	7 (7)	16 (11)	4 (3)	1.8
pendula	2 (2)	1 (0)	10 (3)	3 (0)	1.2
omalophylla	2 (2)	1 (0)	5 (0)	3 (0)	1
calcicola	1 (1)	1 (1)	6 (3)	1 (1)	1
papyrocarpa	2 (2)	1 (0)	14 (10)	3 (0)	0.9
melvillei	2 (2)	1 (0)	2 (0)	3 (0)	0.8
microcephala	2 (2)	1 (0)	3 (0)	3 (0)	0.06
tephrina	2 (2)	1 (0)	10 (2)	3 (0)	0.5
cana	2 (2)	1 (0)	2 (0)	3 (0)	0.25
argyrodendron	0 (0)	1 (1)	3 (0)	1 (0)	0.08
ammophila	2 (2)	1 (0)	1 (0)	3 (0)	0.00001
maranoensis	2 (2)	1 (0)	2 (0)	3 (0)	0.00001
*melanoxylon**	1 (1)	0 (0)	3 (0)	2 (0)	0.9
*oswaldii**	1 (1)	1 (0)	3 (1)	2 (0)	4.5
Section Juliflorae					
aneura	4 (4)	4 (4)	15 (6)	6 (5)	3
stowardii	2 (2)	2 (2)	3 (1)	1 (0)	2.8
adsurgens	1 (1)	1 (1)	4 (1)	0 (0)	2.6
kempeana	2 (2)	4 (2)	8 (1)	2 (0)	2.2
ramulosa	2 (2)	2 (2)	5 (2)	1 (0)	2
torulosa	0 (0)	2 (0)	0 (0)	0 (0)	1.6
shirleyi	0 (0)	1 (1)	4 (1)	1 (0)	1.5
rhodophloia	2 (2)	1 (1)	3 (0)	1 (1)	1
grasbyi	2 (2)	1 (1)	5 (3)	1 (1)	0. 8
catenulata	1 (1)	2 (2)	9 (4)	2 (2)	0.7
citrinoviridis	2 (2)	1 (1)	7 (0)	0 (0)	0.3
aprepta	2 (2)	1 (0)	2 (0)	2 (0)	0.15
*lysiphloia**	0 (0)	1 (1)	1 (0)	0 (0)	1.3

*indicates divergent *Acacia* to which the thrips have apparently host-shifted. Only *Acacia* species inhabited by one or more gall-inducing or phyllode-glueing species are included. Other *Acacia* species that harbour gall-inducers or phyllode-gluers were excluded due to relatively limited sampling effort or relative uncertainty regarding the presence of some thrips species on these plants.

Limitations on the quality of host-plant data due to variable sampling effort are likely to be highest among the many species of opportunists with small body size, since many of these have been collected rarely and only in small numbers. However, the same patterns of species diversity also appear to hold for these species. Thus, among the opportunist thrips, *Acacia* geographic range is marginally non-significantly correlated with the numbers of species on a given plant species (rho = 0.35, P = 0.07, N = 28), but the relationship becomes significant if the *Acacia* involved in host-shifting are omitted (rho = 0.46, P < 0.05, N = 25). In addition, *Acacia* geographic range is correlated with the proportion of opportunists that are host-plant specialised, for the full data set (rho = 0.54, P < 0.01, N = 27) and the reduced one (rho = 0.58, P < 0.01, N = 24).

Opportunist thrips, like the phyllode-gluers and gall-inducers, exhibit notable cases of multiple specialist species on the same host plant. Four *Akainothrips* species live on *Ac. papyrocarpa* and two on *Ac. aneura*; two *Domeothrips* species inhabit *Ac. catenulata*; five *Dactylothrips* species live on *Ac. cambagei*, five on *Ac. harpophylla* and three on *Ac. papyrocarpa*; two *Katothrips* species inhabit *Ac. ramulosa*, and there are three *Kellyia* species on *Ac. harpophylla* and two on *Ac. papyrocarpa*. At least in some of these cases, the thrips species on the same host plant appear to be closely related. However, robust tests of the hypothesis that thrips speciation within widespread host-plant species generates species diversity requires well-supported phylogenies for the taxa involved.

Among exploitative thrips, species diversity is high on *Ac. aneura* and *Ac. harpophylla*. However, overall there is no relationship between *Acacia* geographic range and either numbers of species (full data set: rho = -0.21, P > 0.2, N = 27; reduced data set: rho = -0.19, P > 0.3, N = 25) or proportion of thrips species specialised on one *Acacia* species (full data set: rho = 0.20, P > 0.3, N = 24; reduced data set: rho = 0.26, P > 0.2, N = 22). We suspect that this subset of the data may be subject to substantial sampling variation, since exploitative species can be rare and we are not yet confident that we have sampled thoroughly from each of the *Acacia* species that harbours their host thrips. Despite this lack of association, we note that there are also several cases of apparent within plant-host speciation among exploitative thrips. Thus, two of the three *Xaniothrips* species on *Ac. aneura* are apparently closely related, and the product of an eastern-western Australia split followed by speciation in their thrips hosts, as are the two *Schwarzithrips* species on *Ac. catenulata* (see Eubanks *et al.* 2003 for a parallel case of speciation in gall-inducing flies associated with speciation in their specialist beetle predators).

The patterns of high thrips species diversity on the more widespread *Acacia* species may be due not only to effects of host plant traits on the insects, but also to interactions among the insect groups themselves. In particular, since many of the opportunist species, and all of the exploiters, use domiciles created by the gall-inducers and phyllode-gluers, higher diversity of these resource generators should create ecological space for the resource exploiters and usurpers. We can test this 'diversity amplification' hypothesis by calculating the correlations, across host plant species, between numbers of species in the various behavioural-ecological suites of thrips. For the host plants that support at least one gall-inducer or phyllode-gluer, the number of opportunist species on a plant species is positively correlated with the number of gall-inducers on that plant (Spearmann's rho = 0.44, P < 0.05, N = 28 for all), the number of phyllode-gluers (rho = 0.47, P < 0.05), and the total number of domicile-creators combined (rho = 0.49, P < 0.05). In addition, the number of exploiter species on a plant species is also positively correlated with the number of gall-inducers (rho = 0.68, P < 0.01), and with the total number of domicile-creators (rho = 0.56, P < 0.05), though not significantly with the number of phyllode-glueing species (rho = 0.27, P > 0.05). By contrast, the number of opportunist species on a given plant species is not significantly correlated with the number of exploiters there (rho = 0.31, P > 0.05). These results are consistent with the idea that the primary direction of causation is from the species diversity of domicile creators to the diversity of the species that use them secondarily, and not just from the geographic range of *Acacia* species to the diversity of each behavioural-ecological set of thrips species independently.

The diversity amplification hypothesis can be tested further for gall thrips using more-detailed information on whether the associations are strongest for the opportunist genera and species that use galls and phyllode-glues more commonly. However, the evidence to date supports it, as does simple ecological logic. Indeed, such amplification effects are apparent in other insect groups with forms of sociality and domicile creation, such as Hymenoptera and Isoptera, though they have yet to be quantified or evaluated formally as engines of diversification for inquilines, exploiters, specialist predators, and mutualists.

PARALLEL PATTERNS OF DIVERSIFICATION IN RESOURCE USE

The hallmark of deterministic processes in diversification is parallel evolution of ecological patterns, and subsequent predictability of species diversity and ecological diversity in particular clades (e.g. Losos *et al.* 1998; Schluter 2000). Such patterns indicate that diversity is guided and constrained by ecology, rather than just by the opportunity for speciation, sexual selection, or other non-ecological processes. Notably predictable relationships and patterns of specialisation are apparent within and across several lineages of *Acacia* thrips, as itemized below.

(1) All of the gall-inducers are apparently host-plant specialised, and as described above, the same large set of related host plants is shared between the members of the *Kladothrips rugosus* complex and the *K. waterhousei* complex, and between the *K. augonsaxxos* and *K. schwarzi* complexes. All told, each of 24 species of arid-zone *Acacia* are known to bear one inducer of a round gall, and one inducer of an elongate gall. To the extent that this pattern is not due to history (i.e. cospeciation), it must be due to ecological predictability, or we would see more *Acacia* species in these groups that bear one, or three or more, species of gall-inducers, and fewer instances of the round/elongate gall pairs.

(2) There are three lineages of thrips that glue phyllodes, each of which uses a set of host plants (*Ac. harpophylla* and *Ac. cambagei*, plus other microneurous Plurinerves), (*Ac. aneura* + *Ac. catenulata* + *Ac. ramulosa*), and (*Ac. kempeana* + *Ac. aprepta* + *Ac. stowardii* + *Ac. grasbyi* + *Ac. rhodophloia*) that corresponds to the three sets of host plants used by the main lineages of gall-inducers (Table 7). Thus, two behaviourally divergent lineages, gall-inducers and gluers, have converged independently on use of the same subsets of related *Acacia*. Presumably, these *Acacia* species each exhibits some suite of characteristics that makes them amenable to both gall-induction and phyllode-glueing. Still, each lineage of galling and phyllode-glueing thrips is also predictably restricted to its subset of related *Acacia*, and such a parallel pattern can only be due to ecological aspects of the thrips-plant relationship unless cospeciation has been rampant in both gall-inducers and phyllode-gluers. Such patterns appear considerably less evident among many of the genera of opportunistic thrips, whose biology may be less closely keyed to particularities of their host plants.

(3) Each of the three main lineages of phyllode-gluers appears to have spawned a lineage of opportunistic thrips that uses glued phyllodes as well as other types of domicile, on a subset of the same host plants (Fig. 34). Thus, *Dunatothrips* is sister-taxon to *Domeothrips*, (*Carcinothrips* + *Panoplothrips* + *Sartrithrips*) is related to *Warithrips*, and (*Paracholeothrips* + *Lichanothrips*) is sister-taxon to *Grypothrips*. Assuming that phyllode-glueing originated only once, this strikingly parallel pattern suggests that in each case, a lineage of phyllode-gluers abandoned domicile creation, and evolved to opportunistically use glued phyllodes formed by other thrips of the same or related species. Subsequently, *Warithrips* and *Grypothrips* presumably diversified to use other types of domicile on this set of host plants, such as lepidopteran ties or old thrips galls. Such parallel evolution of behavioural-ecological suites indicates that ecology, in the form of domiciles on the same host plants that can be used opportunistically, can drive diversification.

(4) All of the gall-inducing *Acacia* thrips in the section Plurinerves, and virtually all of the phyllode-glueing species, are beset by species of exploitative thrips, usually with a single such enemy species but rarely with two (e.g. *Koptothrips dyskritus* and *Ko. flavicornis* invading *Kladothrips rugosus* galls, *Schwarzithrips* and *Vicinothrips* invading *Dunatothrips skene* domiciles). The presence of such natural enemies, as well as the genus represented, is thus highly predictable, and the diversity of their host thrips clearly constrains the diversification of the exploiters. The only clear exception to this pattern is the phyllode-glueing genus *Carcinothrips*, which is apparently not parasitised; the two species in this genus also exhibit the most massive and formidable fore leg armature of any *Acacia* thrips, or indeed, for their size, of all animals of which we are aware.

(5) Host plant use patterns of the two phyllode-glueing species *Paracholeothrips clavisetae* and *P. calcicola*e mirror those of the two gall-inducers *Kladothrips waterhousei* and *K. morrisi*, and the two exploitative species *Triadothrips hesmus* and *T. arckaringa*. In each of these three diverse lineages, the former species inhabits the same set of related microneurous *Acacia* in the Plurinerves, and the latter is specialised on *Ac. calcicola*. This pattern suggests that parallel host-plant shifts or cospeciation patterns have occurred in three highly divergent groups. Moreover, the *Lichanothrips* species on *Ac. calcicola* is highly divergent morphologically from its congeneric relatives, which also suggests that adoption of this plant is associated with divergent selection and speciation.

In contrast to the patterns above, several lines of evidence appear to contravene ecologically deterministic influences on the tritrophic relations between plants, host thrips, and exploiters in *Acacia* thrips.

(1) A number of gall-inducing thrips species are found on *Acacia* species that are relatively distant, phylogenetically, from the *Acacia* that bear the bulk of the gall-inducers. These include *Ac. calcicola*, *Ac. carneorum*, *Ac. aff. cuthbertsonii*, *Ac. melanoxylon*, *Ac. orites*, *Ac. oswaldii*, *Ac. pickardii*, and *Ac. xiphophylla*. As described above, the gall-inducers presumably host-shifted onto these plants. For the present, the roles of geographic opportunity, plant physiology or chemistry, or other factors in determining why these plants, but not others, were colonised remain unclear.

(2) Some opportunistic species in several genera, notably *Akainothrips*, *Brakothrips*, and *Corroboreethrips*, inhabit a set of host plants that are clearly unrelated (e.g. Juliflorae, Plurinerves and Phyllodinae), such that their host plant ranges appear highly variable and hard to predict based on aspects of the plant species.

(3) The general, though not complete, absence of *Koptothrips* attacking galls of *Kladothrips* species on *Acacia* in the Juliflorae is inexplicable, especially given that the phyllode-glueing species on these plants are invaded by diverse exploitative thrips. Moreover, exploiters of another genus, *Turmathrips*, attack gall-inducing *Kladothrips schwarzi*, thus suggesting that the thrips galls on *Acacia* in Section Juliflorae are not immune to invasion.

(4) The species diversity within some opportunistic genera, such as *Akainothrips*, *Dactylothrips*, and *Katothrips*, is remarkably high relative to the other opportunists and other thrips on *Acacia*, and is likely to increase considerably with collecting focused on such genera. As these species are usually collected by beating foliage, the habitats and ecology of those that do not inhabit old phyllode glues or galls are little known. But even so, at present we see relatively few predictable patterns in the diversity and host plant relations of such groups, though more may emerge after more-complete sampling of host plants, followed by combined phylogenetic and behavioural-ecological analysis.

The thrips on Australian *Acacia* are probably not unusual among insects in exhibiting a mix of ecological determinism and apparent historical contingency in their patterns of diversification in host-plant use. However, the striking phylogenetic conservatism of the behavioural-ecological suites, and their parallel patterns of diversity across *Acacia* species, use of sets of related host plants, and predictable associations between thrips hosts and exploiters, indicate that many aspects of their biodiversity will ultimately be explicable, and predictable, from ecological processes. Exploring the limits of such predictability, through expansion of our model clades approach to this entire group, should tell us much about the origin and evolution of species and the nature of evolutionary processes.

CONCLUSIONS

Our analysis of the evolution of host-plant use in Australian *Acacia* thrips has revealed several striking patterns that provide insight into the generation and maintenance of diversity in phytophagous insects. First, the gall-inducing thrips show strong evidence for either cospeciation with their host plants, shifts restricted primarily to closely related *Acacia*, or both processes. Under both hypotheses, only a small subset of extant *Acacia* species are amenable to habitation by gall-inducers or phyllode-gluers. These restrictions in ecological range may be related to aspects of plant physiology, phyllode morphology, geographic range and the presence of large monospecific stands, historical constraints on ability or opportunity to host plant shift, or other factors. Notably, the evidence for cospeciation or restricted shifts is less in the phyllode-glueing thrips, and virtually nonexistent in opportunists and exploiters. This pattern suggests that, as in some other insects (e.g. Farrell & Mitter 1990, 1998; Itino *et al.* 2001; Weiblen & Bush 2002), intimacy of the plant-insect interaction may foster macroevolutionary conservatism in resource use (Crespi *et al.* 1998).

Second, the parallel patterns in host-plant use between gall-inducers and phyllode-gluers suggest that the evolution of plant-insect relationships in domicile-creating *Acacia* thrips may be predictable from ecology to a considerable degree. Understanding when and why such interactions can be considered to be ecologically deterministic, rather than being driven by vagaries of history and geography, is a fundamental question that bears directly on our ability to explain and predict evolutionary-ecological processes (Gould 1989; Ricklefs & Schluter 1993; Losos *et al.* 1998).

Third, the generally high degree of host plant conservatism in this group creates conditions where host-plant shifts to divergent *Acacia* can be identified with relative ease. In each of these cases, the gall-inducers or phyllode-gluers involved are the only species in their behavioural-ecological suite that live on this host plant, and they are relatively divergent in morphology, behaviour, and life history from their relatives that have not shifted hosts, or have not shifted to such a degree. This result is important because the vast majority of speciation events in phytophagous insects appear to involve host-plant shifts (Futuyma & Moreno 1988; Abrahamson *et al.* 1994; Brown *et al.* 1995; Berlocher & Feder 2002), and the ability to partition large-scale host-plant shifts from small-scale shifts or cospeciation in *Acacia* thrips will allow comparative assessment of how host-plant shifting drives speciation and phenotypic change.

Finally, as in other insects, species diversity in *Acacia* thrips appears to be favoured by large host-plant geographic ranges. The numerous cases of closely related thrips species on the same *Acacia* species, and the presence of vicariant sibling-species pairs on some plants, suggest that the geographic-range effect is mediated in part by allopatric speciation. By contrast, a diversity-amplifying effect in opportunists and exploiters of domicile creation is likely to be a simple matter of more ecological niches becoming available. Ecological specialisation *per se* in *Acacia* thrips appears to also be fostered by large host-plant geographic ranges, perhaps because a larger resource base helps in maintaining specialists (Bernays & Chapman 1994) as well as generating them.

Acacia clearly plays a pivotal role in all aspects of the biology of these insects. Further studies of the diversity in host plant use among Australian *Acacia* thrips must center on analysis of why related insect species inhabit related plant species, how host-plant shifting drives phenotypic divergence and reproductive isolation, and how larger plant geographic ranges foster increased insect diversity. Answering each of these questions will be useful for analyses of the evolution of phytophagous insects in general, since comparisons of *Acacia* thrips with other plant-insect systems demonstrate such clear similarities.

EVOLUTION OF SOCIAL BEHAVIOUR

The central tenet of behavioural ecology is that variation among and within species in aspects of ecology selects for variation in behaviour (e.g. Emlen & Oring 1977). One of the most complex and unusual types of behaviour among animals is sociality, which involves cooperative interactions among individuals for mutual gain, tempered by selection to exploit joint benefits for individual gain (Choe & Crespi 1997). In this section, we analyse the behavioural and evolutionary ecology of social behaviour in the Australian *Acacia* thrips, with emphasis on the ecological interactions of social thrips with their host plants, and with the exploitative thrips that utilise their domiciles.

Analysis of the evolution of social behaviour involves determining the necessary and sufficient conditions for the origin and maintenance of alternative forms of sociality. Most generally, we seek to infer why, when, how, and in what lineages the various social systems and behaviours engendering cooperation and altruism have been favoured by natural selection (Hamilton 1964; Lin & Michener 1972; Alexander 1974; Andersson 1984; Alexander *et al.* 1991; Bourke & Franks 1995; Crespi 1996; Crespi & Choe 1997). This topic is of considerable interest to biologists because altruistic behaviour reduces one's own reproduction and thus appears paradoxical to evolutionary theory. Moreover, cooperation, to the extent that it generates joint benefits, is vulnerable to infiltration by cheaters who reap advantages without paying cooperation's costs (Connor 1995; Ward & Kukuk 1998; Avilés 2002).

Social systems have been delineated in many ways. Here, we define 'eusocial' colonies as comprising two or more types of individual that are irreversibly different in traits related to sociality (behaviour, morphology, and reproductivity) (Crespi & Yanega 1995; Choe & Crespi 1997). Such differences normally involve a reproductive division of labour, such that individuals of one type reproduce more and help others in the colony less, while individuals of the other type (or types) reproduce less and help more. By contrast, 'cooperative breeding' colonies exhibit two such types of individual whose differences are facultative, and 'communal' colonies contain individuals who cooperate in some way but are not discretely different in social phenotype. Each of these three categories also manifests considerable variability among and within species in the details of social traits, such as behaviour, morphology, life-history, sex allocation, relatedness, inbreeding, and reproductive skew, and one of the major tasks in the study of social evolution is elucidating the causes of this social biodiversity.

The causes of social diversity between and within lineages are ecological, genetic, and phenotypic. Ecological traits, such as types of nest site, food, natural enemies, or demographics, can favour particular forms of sociality by tipping the balance of fitness payoffs between staying in the natal nest vs dispersing to attempt independent reproduction (e.g. Andersson 1984; Koenig *et al.* 1992). Fitness payoffs from helping are, in turn, critically dependent on the genetic relatedness of helpers to the helped individuals, as higher relatedness will usually facilitate the evolution of cooperation and altruism. Finally, the presence of phenotypic traits, such as weaponry, defensive and building behaviour, wing polymorphism, and foraging ability, that can be modified by selection to serve as social adaptations, is crucial to whether sociality can evolve and the form that it takes in different taxa.

Three main questions are to be addressed in the study of social systems.

(1) How do different aspects of ecology influence the evolution of different social systems and behaviours? Can eusocial species usefully be divided into two ecological modes: 'life-insurers', where helpers mainly forage and nurse, and larvae have long life spans relative to those of adults; and 'fortress defenders', where food-rich, defensible nurseries favour helpers who mainly defend the nest site (Alexander *et al.* 1991; Crespi 1994; Queller & Strassmann 1998)?

(2) How does variation in genetic relatedness, inbreeding, and sex allocation ratios affect social behaviour and evolution, within and among species? Is haplodiploidy important, and if so how?

(3) What factors determine the strength of reproductive division of labour, and the observed levels of reproductive 'skew' (Johnstone 2000; Magrath & Heinsohn 2000)?

Australian *Acacia* thrips are useful in the study of sociality for several reasons. First, these thrips exhibit a wide range of social behaviours, including multiple eusocial and communal species, pleometrosis, and diverse defensive and building behaviours (Crespi & Mound 1997). This variation provides for multiple points of comparison with other social taxa. Second, they share their genetic system of haplodiploidy with the Hymenoptera, but they differ profoundly from this order in ecology. As a result, comparison of Thysanoptera with Hymenoptera allows isolation of the hypothesised effects of haplodiploidy on social evolution, which include high female relatedness, relatedness asymmetries, male production by virgins, and adaptive sex ratio modification. Third, gall-inducing thrips are quite similar ecologically to gall-inducing aphids, many of which also exhibit sociality in the form of defensive soldier castes (Stern & Foster 1996, 1997). Comparison of these two taxa thus helps us to identify convergent causes of the evolution of soldiers, as well as causes of the differences between these two lineages. Finally, the more or less complete species-level phylogeny that we have inferred for the gall-inducers allows for the inference of ancestral social traits, and the conduct of phylogenetically based statistical tests. Indeed, our model clades approach has thus far focused primarily on understanding social evolution in gall-inducing thrips, as this is that topic that motivated much of the recent work on these creatures.

EUSOCIALITY IN GALL-INDUCING THRIPS

Six described species of gall-inducers, and at least 14 sibling species of *Kladothrips waterhousei* on different *Acacia* species, exhibit soldier castes, these comprising wing-reduced, gall-bound, fore leg-enlarged individuals of both sexes that eclose first among the brood of a foundress. These soldiers defend the gall against invaders, mainly species of *Koptothrips*, and females are notably less reproductive than the foundress, with the apparent exception of *K. morrisi* (Kranz *et al.* 2001a). Thus, these species exhibit reproductive division of labour, and permanent caste differences, so soldier-containing colonies can be termed eusocial. Observations and population-genetic data indicate that soldier males also breed, mating with their sister-soldier females to produce inbred females among the dispersers. Despite these similarities among species with soldiers, there is remarkable variability among them in most traits salient to social evolution, including numbers of soldiers, gall size, reproductive skew, sex ratios of soldiers and dispersers, relatedness, inbreeding, and the intensity of defensive behaviour.

Analysis of the social diversity of species with soldiers requires three levels of analysis. First, we must assess what characteristics of thrips in general, and gall-inducing *Acacia* thrips in particular, may have facilitated the evolution of soldier castes. Second, we must assess the differences between species with soldiers and their close relatives without them, in the context of our phylogeny, to infer the particular evolutionary changes that allowed and drove the origin of soldiers, apparently in one lineage but not any others. Finally, we must dissect within a phylogenetic context the selective pressures that have given rise among soldiering species to the remarkable variation in social traits. Throughout these analyses, we draw on parallels and divergences between *Acacia* thrips and other social insects, to uncover and test similarities among taxa that indicate the selective pressures at work.

Commonalities of *Acacia* thrips that allowed soldier evolution

We hypothesise that several characteristics present in all or most gall-inducing *Acacia* thrips represent necessary, though not sufficient, conditions for the evolution of soldiers. Although these traits did not change coincident with the origin of soldiers, their absence would, we believe, have prevented this form of sociality from evolving.

First, the galls of thrips on arid-zone *Acacia* are exceedingly valuable resources that represent food, shelter and reproduction for a lifetime. Since they can only be induced during a narrow time window, they cannot be regenerated or replaced if lost, except perhaps by usurping the preformed gall of another individual. Such high resource value of nest sites has also been implicated in the evolution of eusociality and cooperative breeding across diverse lineages of birds and mammals, Hymenoptera, Isoptera and other insects (Andersson 1984; Hansell 1987; Myles 1988; Alexander *et al.* 1991).

Second, the claustral nature of galls, and the lack of immigration into them, creates strong family structure, and high relatedness among gallmates. Such high relatedness, which can be raised further via within-gall inbreeding, means that the benefits of cooperation and altruism accrue only to close relatives. As a result, the scope of any intraspecific cheating behaviour that might erode cooperative benefits is severely restricted. Similar considerations apply to some mole rats, termites, snapping shrimp, and gall-inducing soldier aphids (Crespi & Choe 1997), although at least in some soldier aphids, immigration of non-relatives can reduce average relatedness without leading to the loss of the soldier caste (Abbot *et al.* 2001; Johnson *et al.* 2002).

Third, the high value of galls makes them tempting targets for both conspecifics and heterospecifics, and foundresses of most *Acacia* gall thrips have evolved enlarged, armed fore legs and defensive behaviour that they use in defending their gall against invaders. These adaptations to pugnacity probably facilitated the origin of soldiers, in that defence by soldiers need only involve the expression of foundress behaviour in a different context, within one's natal gall, rather than requiring the *de novo* evolution of defensive traits. Gall aphids once again provide a useful parallel, in that many of them also exhibit intraspecific fighting during gall induction (Whitham 1979; Aoki & Makino 1982; Akimoto 1989; Ngakan & Yukawa 1996; Inbar 1998).

Finally, haplodiploidy may have facilitated the evolution of soldiers by generating high relatedness among females, relatedness asymmetries, and female-based or split sex ratios (Godfray & Grafen 1988; Kranz *et al.* 2000), by allowing protosoldier females to reproduce without mating, and by giving foundresses the ability to manipulate offspring sex so as to make staying and defending more of a fitness-enhancing option for them than dispersing would be. These hypotheses have a long history in the study of hymenopteran social behaviour (Bourke & Franks 1995), and they are still being tested actively in studies on both groups of haplodiploid insects that exhibit eusociality.

The hypotheses that high resource value, high relatedness, strong pressure from natural enemies, preadaptations to defence, and haplodiploidy are singly or collectively necessary for the origin of thrips soldiers can be evaluated via the accumulation of more data on the genetics, behaviour and ecology of gall-inducers on *Acacia* without soldiers, further study of gall thrips on plants other than *Acacia*, and additional analyses of social evolution in gall aphids. These ideas should also motivate searches for sociality among other taxa, such as haplodiploid mites and burrowing Crustacea.

Differences between species with and without soldiers

Why did gall-inducing thrips with soldiers evolve only along one lineage, and not any others? Given some set of necessary conditions, what additional factors created a situation that was sufficient for the origin of soldiers? There are three main ecological and demographic differences between the species with soldiers and the related species without them.

First, the species with soldiers tend to have much longer-lived galls, persisting for up to one year, in comparison to the galls of the related species *Kladothrips rugosus*, *K. ellobus* and *K. acaciae* in which galls last for only a few months. This relatively high colony longevity, which is also found in aphid species with soldiers as well as in other eusocial insects (Moran 1993; Foster & Northcott 1994; Rhoden & Foster 2002), may favour soldiers because galls are vulnerable for longer periods. High gall longevity may also be a consequence of soldiers, whose presence could allow galls to persist longer in relative safety.

Second, with the exception of the atypical *K. morrisi*, the thrips species with soldiers exhibit relatively small and flat or elongate galls (Crespi & Worobey 1998). The causal connection of gall size and shape to sociality is not clear, but the evolutionary reduction in gall size appears to be related to three factors. Again with the exception of *K. morrisi*, relatively small broods and large eggs relative to body size typify the species with soldiers (Kranz *et al.* 2001a,b; Table 6). This difference is in keeping with their smaller galls and longer life cycle, and it suggests that soldiering species exhibit lower within-gall growth rates, which theoretical models suggest may favour the evolution of soldier defence in gall aphids (Akimoto 1996; Stern & Foster 1996). Next, a high inner surface area to volume ratio typifies small and flat or elongate galls, and is presumably related to the space inside available for feeding, relative to the number of inhabitants. An especially high inner gall surface area to volume ratio is found in galls of two unrelated thrips, *Kladothrips sterni* on *Acacia aneura*, and *Iotatubothrips crozieri* on *Casuarina*, both of which also have multiple generations in the gall. This relationship between life cycle and gall form has thus evolved convergently at least three times (Crespi & Worobey 1998), which suggests that space for feeding is related in some way to gall lifespan. Indeed, these considerations all point to strong causal connections between thrips demographics, gall morphology and physiology, and soldiering. The nature of these connections compels further study, especially as it appears to involve a classically ‘K-selected’ set of life history adaptations. Indeed, as an exception that supports the rule, *K. morrisi*, one of the only gall thrips with soldiers that is the sole gall-inducer on its host plant, exhibits a life history that combines elements of the soldiering species and their close, more ‘r-selected’, solitary relatives (Kranz *et al.* 2001b).

Third, and consistent with their long life cycle, species with soldiers have rates of successful invasion by *Koptothrips* that are as high or higher than those found in the solitary gall-inducer species *K. rugosus*, *K. ellobus* and *K. acaciae* (Crespi & Abbot 1999; Table 6). This apparently paradoxical finding suggests, as observations also demonstrate, that soldiers are often unsuccessful in gall defence, and this may also be due to high rates of invasion before soldiers eclose. A pattern of high parasite pressure favouring the origin and maintenance of sociality has also been proposed for some Hymenoptera (Lin 1964; Lin & Michener 1972; Kukuk *et al.* 1989), and for social taxa (Crespi & Choe 1997).

Differences among species with soldiers

Species with soldiers differ substantially in many traits related to their social evolution, including gall size, the presence and proportion of male founders, relatedness levels, inbreeding levels, reproductive skew, kleptoparasitism rates, number of soldiers and dispersers, soldier morphology, soldier and disperser sex ratios, eclosion order of soldiers by sex, and the propensity of soldiers to defend (Table 6). When these traits are evaluated in a phylogenetic context, three main patterns emerge.

(1) Levels of relatedness and inbreeding can be inferred to have been high (i.e. 0.5 or above) throughout the diversification of soldiers, and apparently notably high near to the origin (Chapman *et al.* 2000). Moreover, the two most-basal species, *K. hamiltoni* and *K. harpophyllae*, are the only two species with soldiers that also have some incidence of male cofounding, which may have served to elevate relatedness, generate relatedness asymmetry, and create split sex ratios among galls. These data implicate high relatedness in the origin of the soldier caste (Chapman *et al.* 2000), although comparisons with the related solitary *Kladothrips* lineage (*K. ellobus* + *K. acaciae* + *K. rugosus* + *K. maslini*) are still required.

(2) We can infer that galls were relatively large during the early evolution of soldiers, and that reproductive skew was relatively low, such that female protosoldiers laid considerable numbers of eggs. Indeed, gall size and skew level are inversely related to one another by independent contrasts analysis, which may be due to relatively small galls constraining the reproduction of soldiers, such that they gain more in inclusive fitness from specialisation for defence (Wills *et al.* 2001). Moreover, recent laboratory experiments have also shown that the propensity of soldiers to fight *Koptothrips* is strongest in the species with the highest reproductive skew (e.g. *K. habrus*), and relatively less in lower-skew species (e.g. *K. morrisi*) (Perry *et al.* 2002). These data suggest that gall size, skew, and motivation to defend have coevolved closely, and that the soldiers evolved specialised morphology before strong reproductive and behavioural division of labour. This scenario contrasts sharply with those proposed for the evolution of workers in Hymenoptera (Wilson, 1971; Bourke & Franks, 1995). A recent theoretical study (Chapman 2003) also demonstrates that soldier reproduction favours the origin of helping; moreover, based on their mating systems, more plesiotypic species with soldiers (e.g. *K. hamiltoni*) exhibit a lower threshold for soldier origin than do more derived species.

(3) Several mechanisms appear to link sex allocation with the diversification of thrips sociality. First, strongly split sex ratios occur in a non-social sister-taxon to the clade with soldiers, *Kladothrips rugosus*, due to virginity of a substantial proportion of foundresses (Kranz *et al.* 2000). This finding suggests that sociality arose in the context of split sex ratios, such that soldiers may have evolved first in the female-biased colonies. Second, among the social species studied in detail thus far, there are striking associations between soldier sex ratios, offspring sex ratios, the order of eclosion by sex in soldiers, and the extent of reproductive skew between female soldiers and foundresses (Kranz *et al.* 1999, 2000, 2001b; Chapman *et al.* 2002). Thus, *K. habrus* and *K. waterhousei* exhibit strongly female-biased soldier sex ratios, protogynous (females first) soldier production, an unbiased sex ratio of reproductive dispersers, and relatively high skew. By contrast, *K. hamiltoni* exhibits the opposite pattern: unbiased soldier sex ratio, protandrous soldier production, a very strong female bias in dispersers, and relatively

low skew. Moreover, *K. morrisi* and *K. intermedius* exhibit sex ratio patterns intermediate between these two extremes. These patterns suggest that sex allocation and sociality have coevolved, and we hypothesise that they have done so in the context of sex ratio manipulation by foundresses constraining the reproductive strategies of soldiers. Thus, protogyny forces soldier females to produce male reproductives because they are unmated. The foundress is favoured by frequency-dependence to produce most or all of the female reproductives, resulting in higher skew; the foundress also produces some (late) male soldiers as 'insurance' for production of female reproductives should she die before completing her breeding. By contrast, protandry (males first) may be favoured to ensure that female soldiers can sib-mate soon after eclosion, under a breeding system with especially strong inbreeding (as in *K. hamiltoni*); under such a breeding system, a foundress can be more closely related to her granddaughters than her daughters (Kranz *et al.* 1999), which should also favour the evolution of relatively low reproductive skew.

Protandrous soldier-production may also engender higher motivation (and perhaps more highly developed defensive morphology) in male soldiers than female soldiers, since after male soldiers have mated, their reproductive opportunities diminish and their main option for further maximising inclusive fitness relies on alloparental defence. This is not true for female soldiers, who can continue to oviposit for as long as their offspring will have time to develop. Because production of dispersers is limited by gall size, and not by the number of female soldiers, foundresses may be able to encourage defensive behaviour in their sons by overproducing males. By contrast, protogynous soldier production should instead involve relatively high levels of investment in defence by female soldiers, in part because higher reproductive skew means that female soldiers gain relatively more in fitness from alloparental behaviour. Preliminary data from *Kladothrips habrus* supports such a tendency for female soldiers to defend the gall more readily (Crespi & Mound 1997).

Elucidation of the dynamics of sex ratio-sociality coevolution in social thrips requires further data on soldier and disperser sex ratios, reproductive skew, sex differences in soldier defensiveness, non-linear effectiveness of defence of galls for different numbers of male and female soldiers, relatedness, and inbreeding, from a sufficient number of additional species to enable robust comparative tests. Such data will come predominantly from the *Kladothrips waterhousei* sibling species complex.

Scenario for the origin and diversification of soldiers

Taken together, our phylogeny, data on differences between species with and without soldiers, and data on variation within the lineage with soldiers, can be used to develop an hypothesis for how and why soldiers arose and diversified (Fig. 36). According to our scenario, soldiers originated not long after a host shift from Juliflorae onto Plurinerves, as two lineages diversified onto the ancestors of *Ac. harpophylla*, *Ac. cambagei*, and the other microneurous Plurinerves species. In the lineage that developed soldiers, we infer that males commonly cofounded galls with females, relatedness and inbreeding levels were substantial within galls, and pressure from *Koptothrips* kleptoparasites was high. For some reason, the galls made by this lineage were much more persistent on the plants than those made by the lineages leading to *Kladothrips ellobus*, *K. acaciae*, and *K. rugosus*. This persistence may have been related to a lower rate of nutrient input into the galls, leading to smaller broods, larger eggs relative to body size (such that less nutrient is needed after hatching), and galls

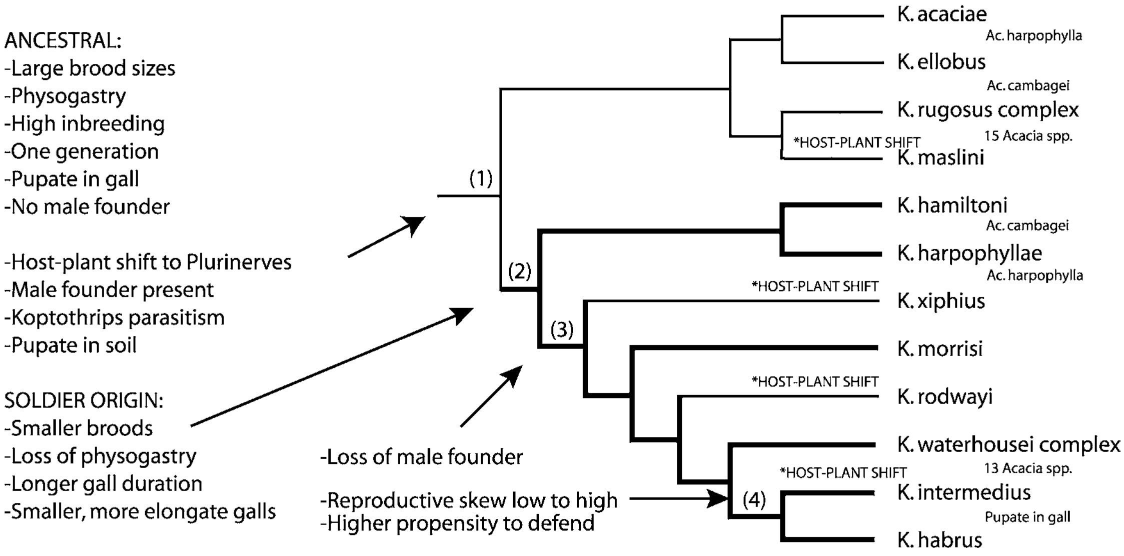

Fig. 36. Results of the 'model clades' approach to the origin, diversification and losses of soldier castes in Australian *Acacia* thrips. The evolution of soldiers is associated with a sequence of macroevolutionary changes in a suite of interacting ecological, morphological, behavioural, life history, and population-genetic traits.

that are generally smaller than those in related lineages. An extension of gall lifespan would not only have made galls vulnerable to invasion for a longer period, but would also have made possible the evolution of two within-gall generations. At some point, the first-eclosing brood of the foundress would have had enough time to produce some offspring of their own.

With the possibility of two generations arrives the nexus of soldier origin: an evolutionary tradeoff between dispersal and staying, and for those who stay, options to reproduce, defend, or both (Fig. 36). Staying within one's natal gall after eclosion would be favoured due to several factors: (1) high costs of dispersal and attempting to found one's own gall, or mate with females after dispersal; (2) the ability to lay one's own eggs or (for male protosoldiers) mate with females in the gall; (3) the ability to benefit from enhanced defence of the gall against *Koptothrips*; and (4) to the extent that altruistic defence is favoured, higher relatedness to sibling gall-mates than to one's own progeny that would be produced after dispersal. In the lineage that evolved soldiers, some or all of these factors presumably tipped the balance towards morphological and behavioural specialisation of the first of the eclosing brood of a foundress to forego dispersal and specialise in within-gall reproduction and defence.

Dispersal costs, which are akin to the ‘ecological constraints’ posited as central to the evolution of alloparental care (Brown 1987; Emlen 1992), are expected to be high in such arid-zone inhabiting insects. We have no evidence as yet, however, that they were higher in the lineage leading to soldiering species than in their *Kladothrips* sister-lineage that did not develop soldiers. This hypothesis could be tested, however, by evaluating the ease of gall induction among lineages, and perhaps by testing for intraspecific covariation between ecological harshness and number of soldiers produced in species like *K. intermedius* that have wide geographic ranges.

We have used genetic and dissection data to infer the ability of female protosoldiers to reproduce, and we have observed male soldiers mating with sisters on numerous occasions. Indeed, our finding that soldier lineages that are more basal exhibit lower skew indicates that high reproduction by protosoldiers may have been critical to the early evolution of the soldier caste.

How much would colonies with protosoldiers have gained in enhanced defence of the gall against *Koptothrips*? At first, individuals eclosing in their natal gall would have been morphologically and behaviourally similar to foundresses, which our observations and collections show are capable of defending against *Koptothrips*. Once protosoldiers became committed to remaining in the gall, there should have been strong selection for reallocation of resources from dispersal adaptations to adaptations for reproduction, defence, or both. In other wing-polymorphic insects, female wing-reduction engenders higher reproduction, earlier reproduction, or both (Harrison 1980; Roff 1986; Roff & Fairbairn 1991; Roff & Bradford 1996; Roff *et al.* 1999), and male wing-reduction can involve earlier reproduction or higher allocation to weaponry used in male-male competition (Crespi 1988). Each of these effects could have facilitated the evolution of wing-reduction in *Kladothrips* protosoldiers.

Enlarged fore legs would presumably have been favoured by selection for more effective defence against *Koptothrips*, which would benefit both offspring and all other gall-mates. Recent behavioural experiments have shown that soldier propensity to defend is lower in more-basal species with soldiers than in *Kladothrips habrus* and *K. intermedius*, such that defensive motivation and ability appear inversely related to levels of soldier reproduction. This pattern is not unexpected given that relatedness among soldiers is not high enough to remove all between-soldier conflict over reproduction and defence, such that given high levels of personal reproduction, each soldier would prefer that a gall-mate took on the dangerous task of fighting off a *Koptothrips*. Moreover, there are higher numbers of soldiers in the more plesiotypic species, such that being less altruistic may incur lower cost in terms of defending the gall as a whole.

Our genetic data provide no evidence that higher relatedness to gall-mates than to one’s own offspring favoured the origin of soldiers, at least in part because high levels of inbreeding tend to reduce such relatedness asymmetries. However, we have inferred that relatedness between gallmates was high at the origin of soldiers (Chapman *et al.* 2002), and that inbreeding levels F_{IS} of foundresses were high, in the order of 0.4–0.6. Such high inbreeding would not only reduce haplodiploidy-induced relatedness asymmetries, it would also tend to make dispersing a more attractive option for incipient (still winged) protosoldiers, due to their higher relatedness to their own offspring under inbreeding. Presumably, this tendency of high inbreeding to retard the evolution of self-sacrificial soldiering was mitigated by the high personal reproduction of protosoldiers.

Once soldiers originated, their diversification involved two divergent patterns: (1) evolution of enhanced reproductive division of labour in the lineage leading to the sister-species *Kladothrips habrus* and *K. intermedius*; and (2) independent evolutionary losses of the soldier caste in *K. rodwayi* and *K. xiphius*. Enhanced division of labour, represented by high skew and strong defensive propensity, evolved in conjunction with relatively small gall size, low numbers of soldiers, and relatively low levels of the inbreeding coefficient F_{IS} of dispersers. A reduced number of soldiers should be favoured when this results in a higher number of dispersers, given the limited capacity of a gall, and more strongly motivated soldiers should be favoured when soldiers reproduce less and thus specialise more strongly in altruistic defence. The lower F_{IS} levels (on the order of 0.3) in *K. habrus* and *K. intermedius* may also have favoured more highly developed altruism, since under lower inbreeding levels, soldiers are less related to their own offspring, and so may be more inclined to alloparental behaviour.

The diversification of species with soldiers and their relatives also appears to be closely related to patterns of diversification in host-plant use. Thus, the sister group to the lineage with soldiers, ((*K. acaciae* + *K. ellobus*) + (*K. rugosus* + *K. maslini*)), exhibits the same overall pattern in host-plant relationships as the clade with soldiers: (1) a pair of sister species on *Ac. cambagei* (*K. hamiltoni*) and *Ac. harpophylla* (*K. harpophyllae*), which are either basal or sister-group to other taxa in the clade; (2) use of the same large number of closely related microneurous Plurinerves *Acacia* species (by the *K. rugosus* and *K. waterhousei* species complexes); and (3) additional species being found on *Acacia* species (e.g. *orites*, *oswaldii, xiphius*, *melanoxylon*, *calcicola*) that are relatively distant from these. Indeed, evolutionary losses of soldiers appear in both cases to have occurred in association with shifts to phylogenetically divergent *Acacia* hosts (Fig. 36). In *K. rodwayi*, this shift led to habitation of mesic areas, which may have led to reduced kleptoparasite pressure, reduced the level of ecological constraint by making dispersal and independent reproduction less costly, or both (Kranz *et al.* 2002). In *K. xiphius*, the host-plant shift apparently led to habitation of a highly arid region in northern Western Australia, which may have engendered life cycle changes (e.g. shorter-lived galls) favouring a shift to solitary life.

A final dimension of diversity in species with soldiers is found in *K. intermedius*, whose progenitor also appears to have undergone a major host-plant shift, to *Ac. oswaldii*. Possibly as a consequence of this shift, this species is highly unusual among those with soldiers in several respects: (1) dispersers eclose within their natal gall, rather than leaving as second-instar larvae; (2) soldiers are partially winged rather than showing a near absence of wings, and wings are longer in soldiers that are smaller and have smaller fore legs (Crespi 1992a,b); (3) in some populations, galls without any soldiers are not uncommon, which is never the case in other species; and (4) sex ratios are strongly female biased both in soldiers and in dispersers, which is a unique pattern among species with soldiers. Notably, eclosion in the gall, wingedness of foundress offspring, absence of soldiers, and a strong female bias in dispersers are also found in the solitary species *K. rodwayi* (which also exhibits a gall very similar to that of *K. intermedius*) and these traits have apparently evolved in parallel, since these two species are not sister taxa. Have *K. intermedius* and *K. rodwayi* been subject to similar selective pressures, leading to reduction in soldier numbers and, in *K. rodwayi*, their loss altogether? Has *K. intermedius* partially lost the soldier caste? Studies tapping the intraspecific variation found in *K. intermedius* sociality should help to answer these questions, which are rendered especially curious by the strong propensity to defend found in the soldiers of this remarkable species.

Implications for evolution of eusociality in thrips and other animals

Our studies thus far on the soldiers of *Acacia* thrips have several broad implications for the analysis of eusociality. First, the *Acacia* thrips with soldiers fit the pattern found in other insect groups of few, ancient origins of eusociality followed by multiple independent losses (Wcislo & Danforth 1997; Danforth 2002). Such a pattern makes inferences regarding conditions and events at the origins more difficult, but it encourages the search for convergent causes of losses of eusociality, which may be just as useful as origins for testing theory (Crespi & Choe 1997).

Second, our data demonstrate that gall-inducing thrips fit closely the ‘factory-fortress’ model for the evolution of eusociality in groups with soldiers as the main form of alloparental care (Alexander *et al.* 1991; Crespi 1994; Queller & Strassmann 1998). Thus, they exhibit high relatedness, strong pressure from natural enemies, and extremely high value of the nest site resource, which combines food and shelter for adults and offspring. These findings support the hypothesis that there are two more or less discrete ‘modes’ of eusociality, that have been favoured by considerably different selective pressures.

Third, our findings suggest that the three main components of eusociality, namely behavioural, reproductive, and morphological divergence between more-reproductive and more-helpful individuals, evolve in a different sequence for factory-fortress social forms than for eusocial taxa with foraging workers (Chapman *et al.* 2002; Thorne *et al.* 2003). In gall-inducing *Acacia* thrips, morphological and behavioural differences between soldiers and dispersers apparently evolved before strong reproductive differentiation; by contrast, the standard evolutionary scenario for Hymenoptera is that behavioural divergence evolves in concert with substantial skew, and that morphological divergence only follows once these two conditions have been met (Wilson 1971; Bourke & Franks 1995). The factory-fortress route to sociality may differ because defence trades off less strongly with reproduction than does energetically demanding foraging, and because defensive morphology makes reproductive domination by foundresses less likely (Chapman *et al.* 2002).

Fourth, we have described extreme diversity in sex allocation ratio patterns in gall-inducing thrips species with and without soldiers, which is indicative of strong selection, parent-offspring conflict, and rapid evolution. We have suggested that foundresses use the timing and level of soldier and disperser sex ratio as a means to manipulate soldier alloparental and parental strategies towards their own interests. Coupled with our data on lack of relatedness asymmetry, these sex ratio data imply that the main role of haplodiploidy in social evolution may relate more to sex ratio manipulation and capacity for son-production by virgins than to direct effects of relatedness and its asymmetries.

Finally, our findings show that the selective pressures responsible for the origin and diversification of thysanopteran soldiers engender complex coevolutionary trait dynamics that span three levels: (1) relations to host plants; (2) interactions between gall morphology, reproductive skew, brood size and egg size, sex allocation, defensive behaviour, morphology, relatedness, and inbreeding; and (3) pressure from natural enemies.

Elucidating and strengthening the links between and within these levels remains a challenge for future work, one that should repay study with insights into how eusociality, cooperation and altruism evolve among all animals.

BEHAVIOURAL AND SOCIAL DIVERSITY AMONG PHYLLODE-GLUERS

The other form of domicile created by *Acacia* thrips, aside from gall induction, is the glueing of phyllodes, or more generally the use of anal secretions to create a more or less enclosed space within which the thrips can live and reproduce. Like galls, this form of domicile represents a highly valuable resource, and the generation, use, and defence of the domicile has engendered the evolution of various social adaptations. For these species, our main questions focus, as for the gall-inducers, on how aspects of the domicile, levels of genetic relatedness, and other factors have selected for particular forms of social behaviour and social system. Analysing these questions involves comparisons between the different phyllode-glueing species, between phyllode-gluers and gall-inducers, and between phyllode-gluers and other animals that exhibit convergent adaptations.

The habit of glueing phyllodes, like gall-induction, apparently has evolved once and been lost several times. There are three main lineages of gluers, *Dunatothrips*, (*Sartrithrips* + *Panoplothrips* + *Carcinothrips* + *Truncatothrips*), and (*Lichanothrips* + *Paracholeothrips*), the first two of which comprise a monophyletic group. Each of these three groups produces a subtly different form of secretion that is used in different ways.

Lichanothrips and *Paracholeothrips* produce a secretion resembling rubber cement. They use this to glue together the faces of crossed pairs of flat phyllodes, forming a flattened shallow space surrounded by a ring of glue. Alternatively, parallel sets of multiple phyllodes are glued together forming a tent-like or tube-like structure. The glue is secreted in elongate lines along linear phyllodes or phyllode edges (in the *Paracholeothrips* on *Acacia* Section Plurinerves), or crossed phyllodes are held together using patches of glue, with each egg immersed in a pillar of glue around the perimeter of a domicile thus helping to hold it together (in *Lichanothrips*, and in the *Paracholeothrips* on *Acacia* Section Juliflorae). The domiciles of Plurinerves-inhabiting *Paracholeothrips* are often initiated at the sites of former lepidopteran leaf-ties, and they appear to be open to the outside at one or more points, such that the thrips can come and go to feed. As in species studied thus far in the related genera *Lichanothrips* and *Grypothrips*, phyllode glues of *P. clavisetae* are normally initiated by either a single female or a male-female pair (Morris *et al.* 2002b). Some colonies contain up to 16 adults and no brood, and thus may appear pleometrotic (Crespi & Mound 1997), but we believe that these actually represent groups of offspring that have eclosed together. Domiciles of *Paracholeothrips clavisetae* can apparently persist for two generations that are at least partially overlapping, as unhatched eggs are commonly found in domiciles where adult brood has eclosed.

The domiciles of *Paracholeothrips clavisetae* are open to the outside at one or both ends, and loose groups of adults with their bright-red larvae leave the domicile, especially during early morning and late evening, to feed on nearby phyllodes. This habit of feeding in the open is extremely unusual for *Acacia* thrips, and in *P. clavisetae* it may be related to their relatively large colony sizes and the unsuitability of old lepidopteran ties for feeding inside, due to the damage that these phyllode surfaces incurred from feeding by the caterpillars.

When near the domicile entrance, adults of this species will wave their abdomen and rush towards threats such as a slowly approaching paintbrush, which is suggestive of parental defence of the domicile.

Carcinothrips and *Sartrithrips* foundresses use a type of adhesive that resembles a fine, glue-like webbing to create an oval-shaped domicile 2–3 mm deep and usually several times their body in length, between pairs of flatly opposed phyllodes. The weave of the webbing is usually very tight and the strands short, so it is often difficult to distinguish this secretion as webbing rather than glue. Domiciles of the related genera *Carcinothrips*, *Panoplothrips* and *Sartrithrips* are always founded by single females, and in *Carcinothrips* and *Sartrithrips* they appear to be fully enclosed, preventing movement in or out at least during most of the life cycle, although the exploitative thrips that invade *Sartrithrips* glues presumably have means of overcoming the barricades. By contrast, *Panoplothrips* domiciles, which are formed in the much narrower phyllodes of *Ac. shirleyi* (a plant somewhat phylogenetically removed from the *Acacia* species utilised by other phyllode-glueing species) are open at one end, allowing egress. At least in *S. popinator* and *S. luctator*, domiciles can persist for more than one generation (Mound & Morris 2001).

The phyllode glues of *Carcinothrips*, *Lichanothrips*, *Panoplothrips*, *Paracholeothrips*, *Truncatothrips* and *Sartrithrips* are mostly produced on *Acacia* species with moderate to large phyllodes that provide enough space for brood production even for these relatively large thrips. By contrast, *Dunatothrips* species create domiciles on the smaller phyllodes of *Ac. aneura*, *Ac. catenulata*, *Ac. ramulosa*, and *Ac. lysiphloia*, and they differ from these other genera in a number of important respects. First, *Dunatothrips* secrete a silken webbing to produce their domiciles, and the strands are considerably longer and more obvious than those of other phyllode-gluers. Phyllode glues are constructed by drawing out anal secretions into fine threads, these being stretched across phyllode edges or surfaces to gradually become a sheet of interwoven material.

Second, possibly as a consequence of the more versatile, silken and sheet-like form of these secretions, *Dunatothrips* species exhibit considerable interspecific diversity in domicile form. Two species, *D. aulidis* and *D. skene*, form tent-like structures on phyllode surfaces, with phyllode or a thin webbing at the bottom, flat webbing above, and the thrips living in between. By contrast, *D. vestitor* and *D. gloius* produce loose, sheet-like webbing around apical phyllodes, such that the several phyllodes are not bound together but are simply enclosed by a structure resembling spider silk.

Third, two species, *D. armatus* and *D. aneurae*, use webbing to bind together the edges of several apical phyllodes of the more slender-phyllode forms of *Ac. aneura*. In all of these species, the domicile appears closed to the outside. The thrips apparently remain within to feed and reproduce, although the domicile can be expanded over multiple generations, which must require some exposure to the hazardous world outside.

The social behaviour of the phyllode-gluers is considerably less well known than that of the gall-inducers (Crespi & Mound 1997; Mound & Morris 2001; Morris *et al.* 2002b). The main form of sociality in this group, pleometrosis coupled with multiple generations, can be linked, at least tentatively, to the form and duration of the domicile.

Pleometrosis and multiple generations in *Dunatothrips*

Most of the phyllode-glueing species exhibit colony foundation by a single female, although in *Paracholeothrips clavisetae* a male is often present as well. However, five of the seven *Dunatothrips* species are known to exhibit facultatively pleometrotic domicile formation, whereby in a substantial proportion of incipient colonies, two or more females are found together in a young enclosure, and have apparently worked together to create it. Soon after forming a domicile, foundresses become dealate and produce a brood, in a small distinct cohort of 2–8 offspring, that develop and eclose inside. At least some, if not all, of the brood remain within the domicile, apparently breeding and helping to expand it, and this expansion is either along the phyllode surface (in *D. aulidis* and *D. skene*), or by the incorporation of more phyllodes (in *D. armatus*, *D. aneura*e, and *D. vestitor*). Female offspring that stay in the domicile also become dealate, but males remain winged and presumably mate with sisters and other females. In this way, colonies can eventually comprise over 50 adults. Only haplometrosis has been documented in *D. gloius* (Morris *et al.* 2002b), which forms domiciles on *Ac. lysiphloia*. This plant also exhibits curiously sticky phyllodes, which may in some manner influence the nature of *D. gloius* colony initiation and perhaps favour haplometrosis.

Pleometrosis is an important form of social adaptation because among other insects, such as Hymenoptera, it commonly involves forms of cooperation among the females that jointly start a colony (Keller 1993; Choe & Crespi 1997). Cooperative benefits of joint founding have yet to be documented in *Dunatothrips*. However, recent work has demonstrated that both domicile size and per capita fecundity scale linearly with foundress number, which suggests that benefits do not arise from causes related to enhanced fecundity (Morris *et al.* 2002b). We suspect that the main advantage of pleometrosis relates to two factors: (1) the speed of domicile formation, as unprotected females loose on phyllodes are likely to be easy prey for ants and birds; and (2) ability to repair damaged domiciles, as the presence of multiple females provides 'survivorship insurance' against the loss of all foundresses, which would leave no one to maintain the domicile and thereby protect the brood. Both of these hypotheses are supported from work on social Hymenoptera, and they would be simple to test with field experiments and observations of *Dunatothrips*. The benefits of pleometrosis are presumably balanced by costs, which may include: (1) significant search costs involved in finding cofoundresses, since *Dunatothrips* are seldom found at high densities; and (2) increased density and higher levels of competition between developing brood for food and space in the domicile.

Why do *Dunatothrips*, but apparently few or no other phyllode-gluers, exhibit facultative pleometrosis and long-lived multiple-generation colonies? We believe that one of the main causal factors is that the phyllodes of their host-plants are small relative to those of phyllode-glueing species on other genera, such that it becomes physically possible to enclose several phyllodes, and a relatively large amount of the sheet-like glue is required to make them into an enclosed domicile. Moreover, *Dunatothrips* domiciles appear to be relatively large in comparison to the size of the thrips, and thus require production of relatively more glue for their establishment. *Dunatothrips* domiciles also form much more complex three-dimensional structures than the simple crossed-phyllode structures of the other genera. This irregular structure may also enable expansion of the domicile, thus allowing for multiple generations of breeding—indeed, the coincidence of pleometrosis with multiple within-domicile generations is striking and suggestive of common causes.

Hypotheses on the evolution of *Dunatothrips* pleometrosis can be tested via quantification of the size, structure and duration of phyllodes and domiciles, in relation to the size of the thrips and their colonies, and in the context of a complete species-level phylogeny for the genus. Our current phylogeny suggests that, as one might expect, pleometrosis is derived from haplometrotic lineages. Moreover, the habit of building unusual, especially secretion-rich, tent-like domiciles, found in *D. skene* and its apparently close relative *D. aulidis*, appears to be derived within the genus. More-complete taxon sampling is required to test these hypotheses, and to analyse the social evolution of phyllode-gluers in a comparative context.

Causes of behavioural and social diversity among phyllode-gluers

Just as we distinguished between several life-history modes of gall-inducers, the 'fliers' (with short life cycles), 'fighters' (with soldiers), and 'hiders' (with tightly closed galls), so also can the phyllode-gluers usefully be divided into several categories. First, all *Carcinothrips*, *Sartrithrips* and *Truncatothrips*, and some species of *Lichanothrips* and *Paracholeothrips*, sequester themselves within closed domiciles, within which they produce a brood that disperses after eclosion (Crespi 1992a; Mound & Morris 1999; Mound & Morris 2001; Morris *et al.* 2002b). This life-history strategy may entail relatively low rates of predation, but at a cost of small brood sizes since space for development and feeding are likely to be limiting. Moreover, most of these phyllode-glueing species with closed domiciles inhabit the highly arid zone of Australia, a zone also inhabited by the gall-inducing species with tightly sealed galls.

Second, some species of *Paracholeothrips*, *Panoplothrips*, and *Lichanothrips* have open domiciles and forage outside, at least locally (Crespi & Mound 1997; Crespi, pers. obs.). These species presumably benefit from access to more or better feeding sites, but at a cost of higher vulnerability to predators and parasites. This cost may have increased selection for morphological, behavioural or chemical defences, such as the defensive behaviour seen in adults of *Paracholeothrips clavisetae*, or as can be hypothesised from the unusual bright red colour of their group-foraging larvae.

Third, pleometrotic *Dunatothrips* expand their more or less closed domiciles over multiple generations. This life-history is made possible, apparently, by the larger-scale glue production of cofoundresses, coupled with the relatively close arrangement of small phyllodes on *Ac. aneura* and *Ac. catenulata*, which make expansion feasible physically. A lack of dispersal by eclosing brood may also be favoured by the hardships involved in independent reproduction, as these species also inhabit some of the most arid regions of Australia, and domicile initiation is probably more difficult than in the species of phyllode-gluers exhibiting haplometrosis.

Why do the phyllode-gluers exhibit such different social systems from the gall-inducers? The main differences between these groups lie in the nature of their domicile and their natural enemies. Thus, we hypothesise that pleometrosis is not found among gall-inducers (in thrips or apparently any other insects) because a single foundress can both induce a gall readily and produce sufficient brood to fill it to capacity. A potential benefit of pleometrosis in gall-inducers might be enhanced defence against *Koptothrips*, but it is not clear how individual foundresses would benefit unless success in defence increased non-linearly with foundress number, or unless foundresses were related and gained inclusive fitness benefits from mutualistic or altruistic help.

Conversely, we hypothesise that a soldier caste is not found in the phyllode-gluers because although the large, long-lived domiciles of *Dunatothrips* are subject to occupation by members of more genera of exploiters than any of the other gluers (*Advenathrips*, *Schwarzithrips*, *Vicinothrips*, and *Xaniothrips*; Table 4), species in the former three genera apparently do not kill or evict their hosts. Thus, these three genera of exploiters may impose relatively minor costs upon *Dunatothrips* (from feeding within the domicile) that are not expected to select for the evolution of specialised defenders. Moreover, *Xaniothrips* may normally only evict its hosts, and since domicile creation in gluers is seasonally asynchronous, not being restricted to a short temporal window during phyllode flushes (as it is in gall-inducers), evicted phyllode-gluers should have another chance to breed. The only other potential context for division of labour in pleometrotic *Dunatothrips* would be glue production. This behaviour, however, is employed only for relatively short periods of time, and may not involve high costs; these factors should favour the retention of totipotency by all individuals, as found in other arthropods with similar secretions (spiders, embiids, psocids, mites, and caterpillars; Crespi & Choe 1997).

The upshot of these hypothesised differences between gall-inducers and phyllode-gluers is that phyllode-gluers appear to be subject to weaker ecological constraints on domicile creation and retention, and weaker selection for division of labour. In addition, within-colony relatedness is likely to be lower in pleometrotic *Dunatothrips* than in gall-inducers. Even if cofoundresses are closely related, which we consider unlikely, their brood will be substantially less related among themselves than is the brood of eusocial *Kladothrips*. All of these factors will militate against the evolution of castes, although they by no means suggest that other forms of cooperation are unexpected.

The hypotheses described above regarding social evolution in phyllode-gluers are just that: educated guesses, based on collections of scarce data and scanty behavioural observations. Indeed, we remain ignorant of the adaptive significance of one of the most distinctive morphological features of this group: the strikingly enlarged and modified fore legs found in females of most of these species. Behavioural observations and estimates of genetic relatedness are needed, and they will further transform these creatures into useful systems for the study of social evolution.

BEHAVIOURAL AND SOCIAL DIVERSITY AMONG OPPORTUNISTS

As opportunist thrips on *Acacia* constitute a polyphyletic assemblage utilising a great range of domiciles and habitats, so their behaviour varies tremendously across genera. Moreover, their behaviour has been little studied compared to that of species in the other three behavioural-ecological modes, so for the greater part we have only tantalising hints of complex and unique adaptations.

The most common form of behaviour in opportunists appears to be defence of the domicile, which can be either for personal safety, for parental care, or for defence of a social group as a whole. Thus, in *Katothrips flindersi*, colonies in abandoned weevil leaf mines are started pleometrotically, and one to several adult females defend the leaf-mine exit hole, via release of a defensive chemical (Crespi & Mound 1997). *Dactylothrips aenictus* females defend breeding cavities in old dry fungus or hymenopteran galls, using pincer-like processes on their abdomen; small hymenopteran-gall cavities contain a single female plus brood, whereas large fungus galls may contain dozens of adults that may be engaging in communal defence (Crespi & Mound 1997). Other species of *Dactylothrips* exhibit projections on the distal ends of their abdomens, resembling in microscopic scale the diversity of ceratopsid or beetle horns, and we expect, as in *Dactylothrips kosmos* (Crespi & Mound 1997), that these structures are also used in defence of self and brood. *Grypothrips cambagei* also defends its brood and domicile in old dry *Kladothrips ellobus* galls or gall fragments, dashing madly about and twirling its abdomen when disturbed by curious collectors (Crespi, pers. obs.). *Csirothrips watsoni* practices a different form of defence, packing the open lips of dry *Kladothrips arotrum* galls with the cast exuviae of the gall-inducers to create a plug that barricades them inside (Crespi 1992a). In all of these cases, we hypothesise that the main natural enemy selecting for defence is ants, which are common on *Acacia*, but this thesis requires observational and experimental tests.

Csirothrips-like packing of exuviae into a corner of a glued-phyllode domicile has also been observed in some *Sartrithrips*, where it may function to conserve space. Analogous forms of 'housekeeping' have been observed in aphids (Benton & Foster 1992) and spider mites (Saito 1997), in which they apparently also serve to maintain space and hygiene in a small, enclosed area.

Finally, *Warithrips aridum* exhibits several traits indicative of sophisticated behaviour. It lives in large colonies of several dozen adults plus brood in old, open, yellowish thrips galls on *Ac. adsurgens* and *Ac. rhodophloia*; adults are wing-polymorphic, with multiple generations breeding in the galls; they sport large, armed fore legs especially pronounced in wing-reduced forms; and adults, as well as the bright red larvae, forage on phyllodes short distances away from the domicile (Crespi, pers. obs.). Such bright larvae are highly unusual in Australian *Acacia* thrips, being found also in another species, *Paracholeothrips clavisetae*, which also forages on phyllodes in the open away from its domicile. Might *W. aridum* exhibit altruistic defence of the domicile by wing-reduced adults? On this question we have only scraps of information, as with several other opportunist species such as some *Katothrips* that exhibit male polymorphism, dealation, and abdomen modifications similar to those of *Dactylothrips*. In other, as yet unstudied species, behaviour may be yet more varied and complex.

EVOLUTION OF EXPLOITATIVE BEHAVIOUR

The benefits of personal industry or social co-operation, be they a domicile, a labour force, or a persistent nursery of helpless young, are always counterbalanced in part by costs. One such cost is that enhanced, concentrated resources generated by solitary or social work make especially tempting targets for exploitation by other species. But the adoption of exploitative life histories requires a major evolutionary transition. Among phytophagous insects, such transitions into a new life-history zone are likely to take place rarely, but are expected to have profound macro-evolutionary consequences because adaptive radiation often ensues (Mitter *et al.* 1988; Price & Roininen 1993; Schluter 2000). The main questions involved in analyses of the evolution of host-parasite (or host-exploiter) relationships include the following.

(1) What is the phylogenetic relationship between the hosts and the parasites, and did the parasites originate from their hosts?

(2) What selective pressures and other factors may have favoured the transition to parasitism?

(3) How and why have parasites diversified, in relation to their host insects, and their host plants?

The origin of parasitic life-histories is usually considered with regard to monophyly vs. polyphyly of the parasites, other aspects of the phylogenetic relationship between hosts and parasites, whether the relevant speciation was sympatric or allopatric, and what social, demographic or ecological conditions allowed or favoured the transition (Buschinger 1986; Bourke & Franks 1991; Carpenter *et al.* 1993; Choudhary *et al.* 1994; Ronquist 1994; Ward 1996; Lowe *et al.* 2002). Hypotheses for the origin of parasitism can be divided into four phylogenetic scenarios.

(1) Polyphyly of the parasites, with each parasite species as sister-taxon to its host ('Emery's rule'; Carpenter *et al.* 1993; Parker & Rissing 2002)

(2) Monophyly of the parasites:

  (a) Parasites as sister-taxon to their monophyletic hosts;

  (b) Hosts paraphyletic with regard to their parasites;

  (c) Parasites and hosts do not jointly form a monophyletic group, but are more or less closely related.

Among other insects, there is evidence for scenario (1) in a few ants (Buschinger 1990; Bourke & Franks 1991; Baur *et al.* 1995, 1996) and in globeflower flies (Desprès & Jaeger 1999). Scenario (2a) is found in some allodapine bees (Lowe & Crozier 1997), *Lasius* ants (Hasegawa 1998) and vespine wasps (Pamilo *et al.* 1981; Varvio-Aho *et al.* 1984). Scenarios (2a) or (2b) fit cynipid wasps (Ronquist 1994) and *Eriosoma* aphids (Akimoto 1989); (2b) is found in *Bombus* bumblebees (Michener 1974, 2000; Pedersen 1996) and polistine wasps (Choudhary *et al.* 1994); and (2c) is found in some ants (Ward 1996), *Yucca* moths (Pellmyr *et al.* 1996), and fig wasps (Lopez-Vaamonde *et al.* 2001), although in each of these latter four cases the parasites and hosts are still quite closely related.

The most striking convergent patterns across these diverse taxa are threefold. First, most of the host species exhibit social preconditions for the evolution of parasitism that involve multiple conspecifics, intraspecific usurpation, or both (Michener 1974; Eickwort 1975; Alloway 1980; Pamilo *et al.* 1981; Akimoto 1988a, b; Buschinger 1986, 1990; Hölldobler & Wilson 1990; Field 1992; Batra *et al.* 1993; Carpenter *et al.* 1993; Choudhary *et al.* 1994; Ronquist 1994; Yang & Mitter 1994; Pedersen 1996; Ward 1996; Ngakan & Yukawa 1996; Akimoto & Yamaguchi 1997; Bekkevold & Boomsma 2000; Yang *et al.* 2001; Ronquist & Liljeblad 2001; Stone *et al.* 2002; Miller & Crespi 2003), The presence of multiple conspecifics creates conditions in which individuals tolerate others within their domicile, and intraspecific usurpation provides a behavioural template for the origin of usurpation among species. Multiple conspecific reproductives may also foster parasitism or inquilinism due to relaxation of selection for intercolony discrimination, or a tendency for intraspecific 'cheating' to evolve in such circumstances (e.g. Ward & Kukuk 1998), which could later be expressed in a between-species context (West-Eberhard 1986).

Second, hosts and parasites are closely related even if not paraphyletic or sister taxa. Such close relationships between hosts and incipient parasites may facilitate the origin of parasitism because more closely related species will tend to exhibit more-similar resource requirements with regard to the domicile and habitat (Eickwort, 1975), and they will tend to inhabit similar geographic areas and exhibit similar life-cycle phenology.

Third, the parasites attacking a given host clade are usually monophyletic. This pattern implies that parasites radiate to fill the available 'host niche space' after gaining a foothold in a given host clade, which may prevent the subsequent evolution of additional, ecologically similar parasites within a given assemblage.

In this section we analyse the diversity of parasitic and inquiline thrips in this suite of Thysanoptera on Australian *Acacia*, and present hypotheses for their origin and diversification. We also compare patterns in the evolution of exploitative behaviour in these *Acacia* thrips to those described thus far in other insects, to uncover convergences that may be indicative of common selective pressures and other causes.

BEHAVIOURAL DIVERSITY OF EXPLOITERS AND INQUILINES

Exploitative and inquiline thrips on Australian *Acacia* can be categorised into three main types, based on the nature of their interaction with their thrips hosts. First, some, such as *Koptothrips*, normally engage in lethal fighting with their host thrips, attempting to usurp the domicile. The virulence of this interaction probably follows from the fact that the gall-inducer hosts would almost certainly die if they abandoned their gall, as gall induction can occur only during a time of new phyllode production. Second, some taxa, such as *Xaniothrips*, appear to just evict the host thrips. Finally, some taxa, including *Advenathrips* and *Schwarzithrips*, and possibly *Crespithrips*, cohabit with their hosts. Of these, *Advenathrips* and *Crespithrips* do not exhibit any morphological features indicative of interspecific fighting, and although *Schwarzithrips* has enlarged fore legs, these may be used for intraspecific competition. These inquilines exclusively inhabit the glued phyllodes of pleometrotic, multi-generation *Dunatothrips* colonies.

How did inquilines and parasites originate in Australian *Acacia* thrips? Phylogenetic work by Morris *et al.* (2002a) shows that all of the tremendously diverse *Acacia* thrips exhibiting forms of among-species exploitative behaviour constitute a monophyletic group, with no losses of this life-history mode (Fig. 28). This group appears to be sister-taxon to a clade that includes several opportunist species basally, and all of the gall-inducers as derived. In accordance with this pattern, inference of ancestral states suggests that the exploitative species evolved from an opportunistic lineage, although this hypothesis requires a more complete species-level phylogeny for further testing.

Four lines of evidence suggest that the origin of exploitative behaviour in *Acacia* thrips involved inquilinism in the phyllode glues of ancestral pleometrotic *Dunatothrips*. First, the two genera in the basal-most lineage in this clade, *Advenathrips* and *Vicinothrips*, are found in phyllode glues of pleometrotic *Dunatothrips*, and *Advenathrips* are known to cohabit with their hosts. Second, studies of other taxa cited above show that pleometrosis facilitates the evolution of exploitation, apparently by making domiciles more easily infiltrated by heterospecifics. Third, *Dunatothrips* is unusual among *Acacia* thrips that create domiciles because it is associated with four genera of exploitative species (Table 4), whereas other genera have at most two. This pattern suggests that *Dunatothrips* species are more vulnerable to various forms of exploitation, presumably as a result of their pleometrotic colony-founding and long-lived colonies and domiciles. Finally, considerations from evolutionary theory suggest that a transition from opportunistic use of unoccupied glued phyllodes, to use of occupied ones with the hosts still present, is a smaller and thus more likely transition than from opportunism to eviction or killing of the host (Morris *et al.* 2002a). Indeed, cohabiting inquilines in multi-generational phyllode glues should benefit from maintenance and expansion of the domicile, and thus are not necessarily expected to evolve more hostile forms of exploitation.

We suggest that the main selective pressure driving the transitions from opportunism to inquilinism, and from inquilinism to parasitism, is expansion and improvement of the resource base: inhabited phyllode glues and galls are apparently much more common, and comprise higher-quality plant material for feeding, than abandoned or aged ones. This hypothesis could be tested by quantifying the availability of inhabited and uninhabited domiciles, and by measuring the reproductive success (e.g. brood size) of exploiters that take over domiciles of varying ages, or damaged, abandoned ones (in some *Koptothrips*). Inhabited domiciles will also be more predictable in time: in other animal taxa, the prevalence of kleptoparasites is higher for hosts whose life cycles are more synchronous (Wcislo 1987), which allows closer adaptation of parasite life history to that of their enemies. This synchrony hypothesis appears to fit well with the differences between the highly synchronised gall-inducers, which are heavily beset by *Koptothrips* (Crespi & Abbot 1999), and the much less synchronised phyllode-gluers, that more rarely support parasites.

EXPLOITER DIVERSIFICATION

Most of the genera of thrips exploiters comprise only a few species, on a small number of host plants (Table 4). As described above, the number of species per genus of exploitative *Acacia* thrips is notably lower than that of gall-inducers, phyllode-gluers, or opportunists, which suggests that selection in the context of antagonistic interactions with various hosts has led to pronounced morphological diversification across the group as a whole.

Two genera of exploiters, *Koptothrips* and *Xaniothrips*, stand out in that they comprise relatively many species, and attack a wide range of host thrips on many different host plants. These genera are also unusual in being the most 'virulent' of thrips exploiters, either killing or evicting the hosts. We believe that behaviour and diversification are causally related for these two genera, in that each has evolved especially hostile and effective 'key innovations'—morphological and behavioural traits, unique to the group, that have allowed them to radiate extensively.

The genus *Koptothrips* originated relatively early in the diversification of thrips exploiters, apparently as the first group to exploit healthy galls. The transition from opportunism or use of glued phyllodes, to gall usurpation, would appear to be saltatory and evolutionarily difficult. However, for *Koptothrips* this transition was probably eased by their ability to utilise fresh galls that were abandoned due to having holes chewed in them by birds or other predators. Thus, in galls induced by *Kladothrips rugosus* on *Ac. papyrocarpa*, *K. antennatus* on *Ac. aneura*, and *K. morrisi* on *Ac. calcicola*, we have found such breached galls invaded by *Koptothrips dyskritus* or *Ko. flavicornis*, with the hole in the gall having been closed off by production of a cellophane-like partition, which observations show was secreted by the *Koptothrips*. Similarly, *Ko. xenus* can create a partitioned domicile on chewed-open *K. ellobus* galls, and multiple *Ko. zelus* foundresses can invade galls of *K. acaciae*, each living within a partitioned chamber (Crespi & Mound 1997). Such behaviour is lacking in the morphologically more derived species, *Ko. flavicornis*, that attacks *K. habrus*, *K. intermedius*, *K. rodwayi*, *K. rugosus*, and *K. waterhousei* (Crespi & Abbott 1999).

These observations of facultative habitation of fresh but damaged galls, in the relatively basal *Koptothrips*, suggest that this behaviour served as an evolutionary bridge to usurpation via the killing of gall inhabitants. We hypothesise that such usurpation acted as a key innovation in allowing *Koptothrips* to radiate across the *Acacia* section Plurinerves, onto a few *Acacia* species in Section Juliflorae, and into the galls of at least 12 of 22 gall-inducers. The morphological and behavioural basis for interspecific fighting may, as in the gall-inducing species with soldiers, have originated with intraspecific fighting among foundresses. *Koptothrips* foundresses, like those of *Kladothrips*, are lethally intolerant of other foundresses in their galls, using their enlarged fore legs to grasp, pierce, and kill. Within the genus, *Ko. flavicornis* is remarkable in being considerably smaller, with much less-developed fore legs. Morphological and behavioural evidence suggests that this small species uses a different means, a venom, to kill its hosts (Crespi & Mound 1997).

The diversification of *Koptothrips* has apparently been directed by both their host plants and the nature of their host thrips. Thus, *Ko. zelus* and *Ko. xenus* are host-plant specific on *Ac. harpophyllae* and *Ac. cambagei* respectively; this is a notable association because these plants also support a high diversity of other morphologically divergent *Acacia* thrips. By contrast, *Ko. dyskritus* has been found on various *Acacia* species in Section Plurinerves, predominantly attacking *K. rugosus,* with sporadic and rare collections on several Juliflorae. *Ko. flavicornis* is restricted to *Acacia* species in the Plurinerves, but it invades galls not just of *K. rugosus*, but also those of the monophyletic group that includes *K. morrisi, K. habrus*, *K. xiphius*, *K. intermedius*, *K. rodwayi*, and *K. waterhousei*.

We hypothesise that the diversification in host thrips and host plant use in *Koptothrips* can be explained via a combination of cospeciation (or shifting between closely related host plants and host thrips), and host-plant-directed shifts to parasitism of novel host thrips. *Koptothrips* probably originated on *Acacia* in the Plurinerves. They are almost entirely restricted to this group of *Acacia*, and thrips galls on these plants are more open to the outside than those on *Acacia* in the Juliflorae, perhaps because second-instar larvae of these thrips must leave the galls to eclose. Thus, we propose that the ancestor of *Koptothrips* invaded galls of the ancestor of the gall thrips on Plurinerves, and underwent an initial split that led to *Ko. zelus* + *Ko. xenus* + *Ko. dyskritus* (attacking the ancestors of *K. rugosus*, *K. acaciae*, and *K. ellobus*), with *Ko. flavicornis* as its sister-lineage (which attack the other, more-derived thrips in this clade) (Crespi & Abbot 1999: fig.1b). A subsequent split between the progenitors of *Ko. zelus* + *Ko. xenus* and *Ko. dyskritus* mirrors the inferred divergence between *K. acaciae* + *K. ellobus* and *K. rugosus*. *Ko. flavicornis* evolved in association with the monophyletic lineage of gall-inducers (*K. morrisi* + *K. xiphius* + *K. rodwayi* + *K. waterhousei* + *K. habrus* + *K. intermedius*), then apparently shifted to parasitise *K. rugosus* on the large set of *Acacia* host plant species that it shares with *K. waterhousei*. Similarly, *Ko. zelus* and *Ko. xenus* probably added *K. hamiltoni* and *K. harpophyllae* to their victims, as these species inhabit the same plant species as *K. ellobus* and *K. acaciae*.

The scenario outlined here for *Koptothrips* diversification is consistent with the available phylogenies (Crespi & Abbot 1999), although better resolution and support are required for the base of the *Koptothrips* clade. Moreover, it remains to be demonstrated whether the *Ko. flavicornis* and *Ko. dyskritus* that each attack different thrips species on different host plants represent sets of closely related sibling species, or, alternatively, host races or single polyphagous forms. The remarkable levels of morphological variation within the forms that key to *Ko. flavicornis* and *Ko. dyskritus* tend to support the former two hypotheses. However, such variability could also represent among-population differentiation (perhaps driven by spatially varying parasite-host coevolution) (Thompson 1994), rather than differentiation among forms attacking different species of host thrips.

The impetus for the initial diversification of *Koptothrips* was probably the behavioural innovation of invading inhabited galls, rather than damaged, abandoned ones. This trait, coupled with weaponry that presumably evolved in response to intraspecific competition for the valuable, limiting gall resource, opened up a new life-history opportunity for exploitative *Acacia* thrips. In turn, we hypothesise that the invasion of galls led to diversification in the hosts of life-history traits of the gall-inducers that are related to avoidance and defence.

The origin and radiation of *Xaniothrips* appears to represent an analogue to *Koptothrips*, with phyllode-gluers rather than gall-inducers as the hosts. In this genus, the ability to usurp the domiciles of the host thrips derives from the presence of a different innovation, abdominal spikes coupled with invasive behaviour. *Koptothrips* diversified mainly across the Plurinerves, whereas *Xaniothrips* radiated to successfully parasitise four genera of phyllode-gluers on both Plurinerves and Juliflorae, with notable exceptions including only the *Paracholeothrips* on microneurous Plurinerves (whose domiciles are invaded by *Triadothrips*), and *Panoplothrips* on *Ac. shirleyi* (which are invaded by *Glaridothrips*). Indeed, *Triadothrips* and *Glaridothrips* are immediately basal to *Xaniothrips* on our phylogeny of exploiters, and they both attack species whose glued-phyllode domiciles are open to the outside. This phylogenetic pattern suggests that just as *Koptothrips* may have used abandoned galls as an evolutionary bridge to usurpation, *Xaniothrips* may have originated in the context of relatively easy invasion of glued-phyllode domiciles, via selection for more effective means to exploit this highly valuable resource.

Robust analysis of the diversification of *Xaniothrips* requires a complete species-level phylogeny for this genus. However, we note that in two cases, pairs of morphologically similar *Xaniothrips* utilise related host thrips and host plants: *X. eremus* and *X. rhodopus* attack *Sartrithrips* on closely related Juliflorae, and *X. mulga* and *X. xophus* attack *Dunatothrips* on the closely related plants, *Ac. aneura* and *Ac. ramulosa*. This pattern suggests that, as in *Koptothrips*, diversification of the exploiters is directed in part by the relationships among the host thrips and the host plants, despite the host-plant shifting whereby *Xaniothrips* came to colonise so many thrips genera. Similar patterns of exploiters being restricted to related host-thrips and host-plant are also evident in *Crespithrips*, *Triadothrips*, and *Turmathrips* (Table 4).

CONCLUSIONS

The evolution of exploitative behaviour in *Acacia* thrips exhibits several patterns remarkably similar to those in other insects: the inquilines and parasites are monophyletic and related to their hosts but not as their sister-group; pleometrosis of the hosts may have fostered the transition from opportunism to inquilinism; and key innovations apparently drove the evolution of the inquiline and parasite forms, with more virulent forms of exploitation (i.e. in *Koptothrips* and *Xaniothrips*) apparently evolving from more benign ones. These patterns provide evidence of convergence across disparate insect groups in the dynamics of host-parasite evolution.

Exploitative *Acacia* thrips also reveal patterns that may provide novel insights into how parasitism evolves. Thus, in two apparent cases, the transition to invasion of galls with living hosts (the origin of *Koptothrips*), and the transition to invasion of diverse phyllode-glueing species (the origin of *Xaniothrips*), we hypothesise that the adoption of these new life history types was eased by transitional stages: use of damaged galls as a bridge to use of intact ones, and use of continually open phyllode glues as a bridge to exploitation of closed ones. Moreover, in both of these cases, adoption of a more virulent life history apparently led to more rapid speciation and exploitation of a large diversity of host thrips and host plants—might such key innovations foster radiation and diversification in other types of parasite?

A second factor generating and directing *Acacia* thrips exploiter diversity is the tritrophic nature of their associations, with both host plants and host thrips. In multiple exploiter genera, thrips exploiter-host relationships are apparently directed in part by relationships between the thrips hosts (gall-inducers and phyllode-gluers) and their *Acacia* hosts. These associations across three ecological levels will only be revealed with species-level phylogenies for the plants and both groups of insects, coupled with experiments to uncover the genetic and environmental determinants of host-range evolution.

Exploiter diversity must be ultimately and intimately related to the diversity of hosts, and in *Acacia* thrips this linkage is mediated via the domiciles created by the gall-inducers and phyllode-gluers. But we suspect that this diversity cascade can flow both ways, such that exploiters, acting as strong selective pressures on their hosts, can lead to host adaptations that facilitate the evolution of both increased species diversity and increased morphological and behavioural diversity (e.g. soldier castes, novel forms of glued-phyllode domiciles). Natural enemies may favour host speciation though host-plant shifts that engender escape from such natural enemies (Abrahamson *et al.* 1994; Brown *et al.* 1995; but see Keese 1997), or by diversifying selection in subdivided populations with pleiotropic effects on reproductive isolation (Nosil *et al.* 2002). Analysis of the dynamics of host-parasite relationships across populations, ecological levels, and evolutionary time will demonstrate the role of parasites in the genesis of biodiversity, in *Acacia* thrips and other animals.

EVOLUTION OF DIVERSITY

As Darwin saw the fauna of the Galapagos Islands as a microcosm of evolutionary change worldwide, we envision Australian *Acacia* thrips as a model for evolutionary diversification in phytophagous insects. This diversification has taken place in multiple dimensions across time and space, with increases in species numbers, behavioural-ecological suite (gall-inducer, phyllode-gluer, opportunist, and exploiter), life-history, social behaviour, host-plant use, and morphology. Our main goal in this monograph has been to describe and begin to explain this diversity, in terms of natural selection and other processes, and in the context of phylogeny.

The impetus for the radiation of *Acacia* thrips was the domination of the Australian interior by this plant genus, beginning some 20–30 million years ago as this flat continent drifted north into a lower latitude and transformed from rain forest to desert. *Acacia* species that were adapted to dry habitats in the rain forest came to dominate the landscape, forming vast, often monospecific mosaics as they radiated and adapted to various regimes of rainfall and soil type. The *Acacia* species that pioneered this increasingly arid landscape harboured thrips, probably living in some tight space on stems or phyllodes. The diversification of *Acacia* thrips was presumably driven by three main processes: host-plant effects including ecological interactions and plant phylogenesis, ecological and behavioural interactions among thrips species, and vicariance involving geographic separation of plants, thrips, or both.

Host-plant effects on *Acacia* thrips diversification involve a general pattern, repeated across multiple genera, of more closely related thrips species inhabiting more closely related plants, but with occasional shifts to more distant hosts. We have presented evidence that the evolution of gall-inducing thrips and *Acacia* has involved extensive cospeciation or restriction of host-plant shifts to closely related *Acacia*. In the former case, speciation is driven passively by the plants, whereas in the latter, aspects of plant geography, chemistry, or phenology, coupled with the selective pressures involved in the ability of the thrips to establish on a new host, determine whether or not a new species will arise. But whether the cospeciation or the restricted-shifts hypothesis is correct, the effect on diversity is the same: more species, but species with low levels of phenotypic divergence from their progenitors.

In contrast to the scenarios above, shifts to more divergent host plants appear to drive both speciation and major changes in morphology, behaviour, and life history. Such effects are most noteworthy in the evolution of *Kladothrips intermedius*, *K. maslini*, *K. rodwayi*, *K. xiphius* and *Dunatothrips gloius*, but they may also have occurred in *K. morrisi*, *K. pilbara*, *K. torus*, and *K. zygus*, as well as in the diversification of the many genera of exploitative thrips. Parallel patterns across genera also provide strong evidence for phenotypic effects of large-scale host-plant shifts: for example, four new, divergent species have evolved on *Ac. calcicola*: *K. morrisi*, *Lichanothrips calcis*, *Paracholeothrips calcicola*e, and *Triadothrips arckaringa*.

The most far-reaching diversity-generating effects apparently arose from the largest-scale host plant shifts, those between the Juliflorae and Plurinerves. Thus, the shift of gall-inducers to Plurinerves coincided with the evolution of both eclosion out of the gall and participation of males in gall founding, and two important clades, the genus *Koptothrips* and (*Lichanothrips* + *Paracholeothrips* + *Grypothrips*), apparently evolved in concert with a shift to this *Acacia* section. These shifts to Plurinerves are also reminiscent of an escape-and-radiation scenario (Ehrlich & Raven 1964), whereby host-shifting to a new taxonomic group of plants leads to diversification across unoccupied niche space, which amplifies both species numbers and phenotypic diversity among species.

Ecological and behavioural interactions among thrips species generate diversity in several ways. First, as described in detail above, the creation of domiciles by gall-inducers and phyllode-gluers has created new niches for exploiters invading inhabited sites, and opportunists living in old or abandoned ones. This pattern recalls the ‘nest-webs’ of hole-nesting birds, whereby the industry of woodpeckers creates the cavities used by owls, chickadees, and others (Martin & Eadie 1999). The diversity-amplification hypothesis is supported by correlations in species numbers across behavioural-ecological modes, and by the observations that the inferred time of origin of exploiter clades does not precede that of their hosts, nor can the origin of opportunists in phyllode glues be inferred as earlier than the evolution of the phyllode-gluers themselves (Fig. 28). Second, antagonistic interactions between exploiters and hosts apparently led to the remarkable morphological and behavioural diversity among exploiter genera, and various life-history, morphological, and behavioural adaptations among gall-inducers and phyllode-gluers. For example, the gall-inducers on *Acacia* in the section Plurinerves exhibit two life-histories, one involving a very short life cycle, and the other involving a long life cycle and soldier castes. These life histories appear to have been strongly shaped by *Koptothrips* parasites, and indeed soldiers would be highly unlikely to have evolved without the strong selective pressures that they impose. These hypotheses can be tested further via intraspecific, among-population analyses of the nature of selective forces exerted by exploiters on life history, morphology and behaviour.

Diversity has also been generated by the more typical processes, via allopatric separation of thrips populations, followed by divergent effects of selection, drift, or both. These processes are implicated by the presence of geographically separated sister-taxa (e.g. *Sartrithrips bapto* and *S. mars*; *Sartrithrips luctator* and *S. pyctus*; *Xaniothrips mulga* and *X. zophus*; *Dunatothrips skene* and *D. aulidis*), and by strong genetic differentiation between populations (e.g. *K. intermedius* in Western Australia being over 5% different in mtDNA from those in the east; Crespi, unpubl. data). Allopatry may also have led to thrips speciation on the same host plant, followed by sympatry. Thus, we observe *Kladothrips* sister-lineages on *Ac. aneura* (*K. sterni*, *K. arotrum*, and *K. tepperi*), apparently related *Dunatothrips* on *Ac. aneura* (*D. aneura*e, *D. vestitor*, and *D. armatus*), and closely related *Lichanothrips* (*L. albus*, *L. curvatus*, *L. magnificus*, *L. metopus*, *L. pulchra*, *L. semifuscipennis*, and *L. triquetus)* on *Ac. harpophylla*. We hypothesise that these patterns have arisen from past fragmentation and allopatry of widespread plant populations, which led to species-level divergence of their thrips inhabitants, perhaps driven by small population sizes. This hypothesis can be tested using phylogeographic data to assess whether related species exhibit well-separated ‘centers of origin’ (Avise 2000).

Finally, we note that many of the *Acacia* species inhabited by thrips exhibit distributions in parapatric, more or less monospecific, mosaics that are determined by local soil types. Such a host-plant geographic template may promote parapatric or peripatric speciation, which might help to explain the diversification patterns of *K. rugosus*, *K. waterhousei*, *K. schwarzi* and *K. augonsaxxos*, if they occurred via shifts to host plant species that were both closely related and adjacent. Certainly, for the *Kladothrips* on Plurinerves, species inhabiting the widespread plants *Ac. cambagei* and *Ac. harpophyllae* are more basal on the phylogeny, and have given rise to thrips species on much more localised *Acacia* species that are distributed across the eastern periphery of their ranges (Pedley 1987; Maslin 2001).

A more-complete understanding of the causes of diversity in Australian *Acacia* thrips must await targeted sampling and description of under-represented groups such as the opportunists, and species-level phylogenies for the entire clade. Moreover, collection of further data on behaviour, ecology, life-history, and phylogeography will allow inference of the processes of diversification across all levels, from genotype to geographic distribution. This world of Australian *Acacia* thrips may still be rife with demons, but it is also rich with promise to help answer the outstanding evolutionary and ecological questions of our generation. Such studies take on an unexpected degree of urgency, since rabbit and sheep herbivory of seedlings is preventing many species of arid-zone *Acacia* from regenerating (Lange & Purdie 1976; Lange & Graham 1983; Auld 1993), and the remaining, aging stands date back to the fencing of the Australian landscape.

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