

PART I

ECOLOGY AND EVOLUTION OF AUSTRALIAN ACACIA THIRPS

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. augonsaxos*, 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 *Caenorhabditis 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 & Nylén 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-constructors’ (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. augonsaxos*, 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, behavioural, 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?
<i>K. acaciae</i>	<i>Ac. harpophylla</i>	large, fat elongate pouch	often	no	in soil	yes
<i>K. antennatus</i>	<i>Ac. aneura, paraneura, ramulosa, adsurgens</i> , related form on <i>aff. citrinoviridis</i>	large, fat elongate cylinder	no	no	in gall	partial
<i>K. atrotrum</i>	<i>Ac. aneura</i>	large and spherical	no	no	in gall	yes
<i>K. augonsaxos</i>	<i>Ac. aprepta, grasbyi, kempeana, resinimarginea, rhodophloia, stowardii</i>	large and spherical	no	no	in gall?	yes
<i>K. ellobus</i>	<i>Ac. cambagei, georginae</i>	medium-sized, flat round disk	often	no	in soil	yes
<i>K. habrus</i>	<i>Ac. melvillei, pendula</i>	small, lens shape	no	yes	in gall	no
<i>K. hamiltoni</i>	<i>Ac. cambagei, georginae</i>	medium-sized, skinny elongate cylinder	very rarely	yes	in gall	no
<i>K. harpophyllae</i>	<i>Ac. harpophylla</i>	medium-sized, skinny elongate cylinder	often	yes (hemi-macropterous)	in gall	no
<i>K. intermedius</i>	<i>Ac. oswaldii</i>	small, lens-shape	no	yes (hemi-macropterous)	in gall	no
<i>K. maslini</i>	<i>Ac. orites</i>	medium-sized conical pouch	unknown	no	in gall?	unknown
<i>K. morrissi</i>	<i>Ac. calcicola</i> , related forms on <i>Ac. carneorum and Ac. aff. culbersoni</i> ('gizzard wattle')	very large, fat elongate cylinder	no	yes	in gall	no
<i>K. pilbara</i>	<i>Ac. citrinoviridis</i>	large, fat elongate cylinder	no	no	in gall	partial
<i>K. rodwayi</i>	<i>Ac. melanoxylon</i>	small, lens-shape	no	no	in gall	no
<i>K. rugosus</i>	<i>Ac. ammophila, cana, enervia, loderi, maranoensis, melvillei, microcephala microsperma, omalophylla, papyrocarpa, pendula, sibilans, tephtrina</i>	large elongate pouch or spherical, sometimes with ribs or spikes on the exterior surface of the gall	often	no	in soil	yes
<i>K. schwarzi</i>	<i>Ac. aprepta, kempeana, resinimarginea, rhodophloia, stowardii</i> , related forms on <i>grasbyi, sibirina</i>	small, skinny elongate cylinder	no	no	in gall	no
<i>K. sterni</i>	<i>Ac. aneura, catenulata, ramulosa</i>	large, spherical, multilocular	no	apterous gall-morph (non-soldier)	in gall	yes
<i>K. tepperi</i>	<i>Ac. aneura, paraneura</i>	large, spherical	no	no	in gall	yes
<i>K. torus</i>	<i>Ac. citrinoviridis</i>	large, spherical	no	no	in gall?	yes
<i>K. waterhousei</i>	<i>Ac. ammophila, ancistrophylla, cana, enervia, inceana, loderi, maranoensis, microcephala, microsperma, omalophylla, papyrocarpa, sibilans, tephtrina</i>	small, skinny elongate cylinder, or lens shape	no	yes	in gall	no
<i>K. yalgoo</i>	<i>Ac. masliniana, mackeyana, nyssophylla</i>	small, elongate cylinder	no	no	in gall	no
<i>K. xiphosus</i>	<i>Ac. xiphosylla</i>	large, fat elongate cylinder	often	no	in gall	unknown
<i>K. zygnus</i>	<i>Ac. pic-kardii</i>	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. morrisoni*, *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, ‘hidiers’ 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. augonsaxos*, *K. pilbara*, *K. tepperi*, *K. schwarzi*, *K. torus*, and *K. zygnus*, 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. morrissi*, 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. morrissi*, 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. Both species inhabit galls that are voluminous but have shapes

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

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

that lead to an increased ratio of inner surface area to volume, elongate in *K. morrissi* 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
<i>Akainothrips</i>	Botrycephalae, Juliflorae, Phyllodinae, Plurinerves	empty galls, glues or lepidopteran cocoons	
<i>Brakothrips</i>	Juliflorae, Plurinerves		
<i>Corroboreethrips</i>	Juliflorae, Plurinerves	empty galls, glues or lepidopteran cocoons, splits and cracks in stems and bark	
<i>Csirothrips</i>	Juliflorae	empty galls	block open lips with exuviae
<i>Dactylothrips</i>	Botrycephalae, Juliflorae, Phyllodinae, Plurinerves	empty galls, glues or lepidopteran cocoons, splits and cracks in stems and bark	some defend domicile with abdominal pincers
<i>Domeothrips</i>	Juliflorae	empty galls, glues or lepidopteran cocoons	
<i>Grypothrips</i>	Plurinerves	empty galls, glues or lepidopteran cocoons	some apparently defend their domiciles
<i>Heptadikothrips</i>	Plurinerves		
<i>Hexadikothrips</i>	Plurinerves		
<i>Katothrips</i>	Juliflorae, Phyllodinae, Plurinerves	empty galls, glues or lepidopteran cocoons, splits and cracks in stems and bark	some defend domicile chemically
<i>Kellyia</i>	Botrycephala, Juliflorae, Phyllodinae, Plurinerves	empty galls, glues or lepidopteran cocoons	
<i>Ostlingothrips</i>	Juliflorae, Phyllodinae, Plurinerves		
<i>Rhopalothripoides</i>	Botrycephalae, Juliflorae, Phyllodinae, Plurinerves	empty galls, glues or lepidopteran cocoons, splits and cracks in stems and bark	
<i>Warithrips</i>	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
<i>Advenathrips</i>	<i>inquilinus</i>	<i>Dunatothrips vestitor</i> (maybe <i>aneurae</i> but not confirmed)	<i>Ac. aneura</i>
<i>Crespithrips</i>	<i>enigmaticus</i>	<i>Sartrithrips luctator</i> , <i>popinator</i> , <i>mars</i>	<i>Ac. kempeana</i> , <i>stowardii</i> , <i>rhodophloia</i>
	<i>hesperus</i>	<i>Sartrithrips pyctus</i>	<i>Ac. grasbyii</i>
<i>Glaridothrips</i>	<i>koptus</i>	<i>Panoplothrips australiensis</i> , on <i>aneura</i> and <i>catenulata</i> not certain, maybe <i>Paracholeothrips</i> and/or <i>Domeothrips</i>	<i>Ac. aneura</i> , <i>catenulata</i> , <i>shirleyi</i>
<i>Koptothrips</i>	<i>dyskritus</i>	gall inducers on Plurinerves, especially <i>K. rugosus</i> , also <i>K. antennatus</i>	<i>Ac. aneura</i> , <i>maranoensis</i> , <i>melvillei</i> , <i>omalophylla</i> , <i>papyrocarpa</i> , <i>pendula</i> , <i>ramulosa</i> , <i>rhodophloia</i> , <i>sibilans</i> , <i>tephrina</i>
	<i>flavicornis</i>	gall inducers on Plurinerves, especially <i>K. habrus</i> , <i>intermedius</i> , <i>morrissi</i> , <i>rodwayi</i> , <i>rugosus</i> , <i>waterhousei</i>	<i>Ac. calcicola</i> , <i>maranoensis</i> , <i>melanoxyton</i> , <i>melvillei</i> , <i>omalophylla</i> , <i>oswaldii</i> , <i>papyrocarpa</i> , <i>pendula</i> , <i>sessiliceps</i>
	<i>xenus</i>	<i>K. ellobus</i> and <i>hamiltoni</i>	<i>Ac. cambagei</i>
	<i>zenus</i>	<i>K. acaciae</i> and <i>harpophyllae</i>	<i>Ac. harpophylla</i>
<i>Schwarzithrips</i>	<i>glyphis</i>	<i>Dunatothrips skene</i>	<i>Ac. catenulata</i> (Qld)
	<i>zammit</i>	<i>Dunatothrips aulidis</i>	<i>Ac. catenulata</i> (WA)
<i>Triadothrips</i>	<i>arckaringa</i>	<i>Paracholeothrips calcicolae</i>	<i>Ac. calcicola</i>
	<i>briga</i>	<i>Lichanothrips</i> spp.	<i>Ac. harpophylla</i>
	<i>hesmus</i>	<i>Paracholeothrips clavisetae</i>	<i>Ac. ammophila</i> , <i>cana</i> , <i>melvillei</i> , <i>microcephala</i> , <i>pendula</i> , <i>papyrocarpa</i> , <i>sibilans</i> , <i>tephrina</i>
<i>Turmathrips</i>	<i>apistus</i>	<i>Kladothrips schwarzi</i>	<i>Ac. grasbyi</i>
	<i>dyspistus</i>	<i>Kladothrips schwarzi</i>	<i>Ac. kempeana</i> , <i>stowardii</i>
<i>Viciniothrips</i>	<i>bullatus</i>	<i>Dunatothrips skene</i>	<i>Ac. catenulata</i>
<i>Xaniothrips</i>	<i>eremus</i>	<i>Sartrithrips popinator</i>	<i>Ac. kempeana</i> , <i>stowardii</i> , <i>aprepta</i>
	<i>foederatus</i>	<i>Paracholeothrips mulgae</i>	<i>Ac. aneura</i>
	<i>leukandrus</i>	<i>Lichanothrips</i> spp.	<i>Ac. harpophylla</i>
	<i>mulga</i>	<i>Dunatothrips</i> spp. (<i>aneurae</i> and <i>vestitor</i>)	<i>Ac. aneura</i>
	<i>rhodopus</i>	<i>Sartrithrips mars</i>	<i>Ac. rhodophloia</i>
	<i>xantes</i>	<i>Lichanothrips</i> spp.	<i>Ac. harpophylla</i> , <i>argyrodendron</i> , <i>cambagei</i>
	<i>zophus</i>	<i>Dunatothrips</i> spp. (<i>aneurae</i> , <i>armatus</i>)	<i>Ac. aneura</i> , <i>ramulosa</i>

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-glucers 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 behavioural-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 glucers	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 haplo-metrotic 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*, *Carcinotrips*). 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 *Csirothrips* 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 PHLAEOTHIRIPIDAE 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.

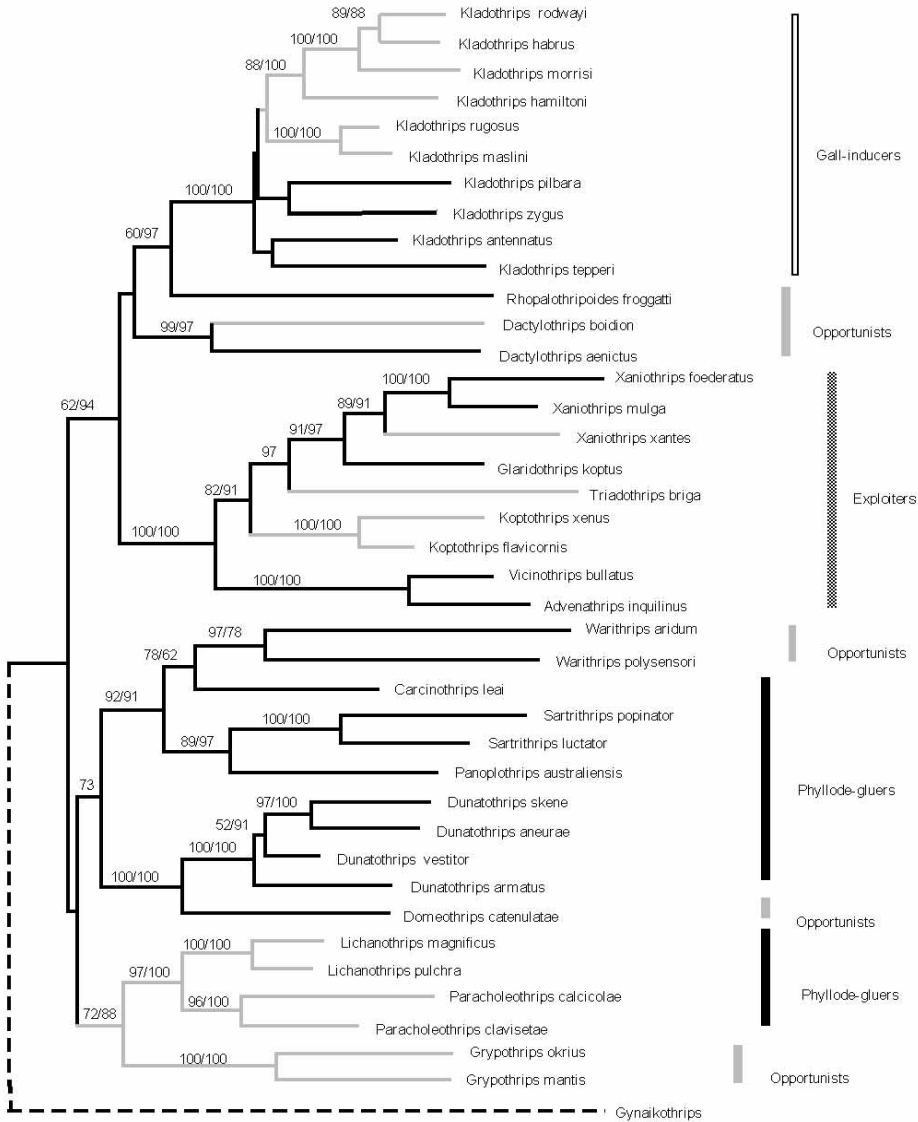


Fig. 28. A phylogeny for *Acacia* thrips based on maximum likelihood analysis of *elongation factor-1a* and *wingless* gene regions, with behavioural/ecological suite indicated (see text). Black branches indicate thrips from *Acacia* section Juliflorae; grey bars indicate thrips from *Acacia* section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