Thrips as architects: modes of domicile construction on Acacia trees in arid Australia

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In Australia, the plant genus *Acacia* includes more than 1000 species, of which over 850 do not bear leaves when mature, but instead have the leaf petioles expanded into leaf-like structures called phyllodes (Maslin 2001). Within the genus *Acacia* in Australia, three major Sections are currently recognized: Section Phyllodineae with 390 species, Section Plurinerves with 210 species, and Section Juliflorae with 240 species. Although from time to time, various Thripidae and Aeolothripidae can be found in the flowers of *Acacia* species, leaf-feeding Phlaeothripinae occur almost exclusively on members of the Plurinerves and Juliforae, with very few on the Phyllodineae. The suite of phlaeothripines on these plants is remarkably extensive, and is now known to exceed 250 species and 30 genera, most of which are currently being described. Moreover, the phlaeothripine genera involved are associated only with the plant genus *Acacia*. This association between thrips and *Acacia* species is particularly curious, because many other extensive plant genera in Australia, such as *Eucalyptus*, do not provide hosts to any phytophagous species of Phlaeothripinae (Mound 1996).

The environment of inland Australia is harsh, with intense insolation, high temperatures, and low humidities. Exposure to these conditions is lethal to many organisms, and individual thrips that are exposed to these extreme conditions can die from dessication within a few minutes. In addition to the difficult environment, the arid parts of Australia are remarkable for their high level of predatory ant activity, both by day and by night. As a result, competition can be intense for potential breeding sites that offer some level of protection from the sun and wind, and the ubiquitous ants. It is thus not surprising that Phlaeothripine species have adapted to life in protective niches, such as in cracks in bark, within leaves mined by beetles or caterpillars, within old galls, and even within abandoned spiders nests. One group of phlaeothripines has developed the ability to induce *Acacia* phyllodes to produce galls, and a second group has developed the unique ability to construct an individual domicile within which to rear their young brood.

Gall induction involves changing the pattern of growth and expansion of the plant cells (Mound & Kranz 1997). On *Acacia*, this is brought about

Fig. 1. Bipinnate leaves and developing phyllodes in young *Acacia melanoxylon*.

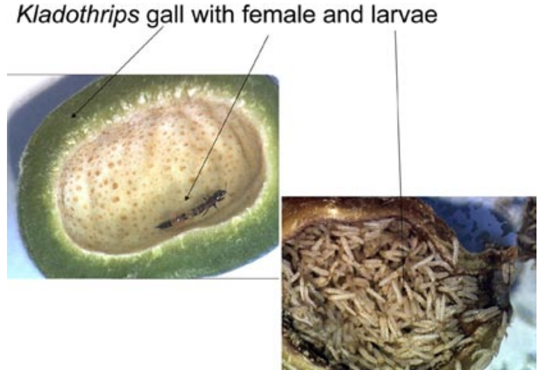

Fig. 2. *Kladothrips* gall on *Acacia pendula* with physogastric female.

by a thrips feeding on a very young phyllode, although the mechanism by which the plant is induced to change its pattern of growth is not understood. The galls vary in size and shape, but are essentially hollow spheres or cylinders, with the thrips feeding on the inner walls. More than 24 species of gall-inducing Phlaeothripinae are known on *Acacia* species in Australia, and these show an interesting range of biologies. Some species lay little more than 10 eggs initially, and this is then followed by a second much larger generation. Other species lay up to 1000 eggs within a few days, and have only this single large generation within that gall. The galls of species employing the former strategy are usually smaller than those employing the second strategy. Moreover, the adults of the first generation in the small galls frequently differ in structure from their gall foundress. They usually have reduced wings, and the fore legs and pronotum are commonly enlarged, and these adults are known to function as soldiers to defend their gall from invading organisms (Mound & Crespi 1995).

Gall-inducing thrips are known from many parts of the world. In contrast, the ability to construct a domicile, by actively manipulating a plant rather than by inducing a plant to change its pattern of growth, is known only amongst the *Acacia* Phlaeothripinae of Australia (Mound & Morris 2001). The process essentially involves gluing together, or sewing together, two or more phyllodes. Thrips that are associated with *Acacia* species with broad phyllodes, such as *Ac. harpophylla*, usually select a pair of phyllodes that are hanging with their faces close together and crossing each other. With phyllodes in this close proximity, a thrips female then pulls them closer together and secretes a ring of glue from the anus to hold them in position. The domicile thus consists of that area of the surfaces of the two phyllodes that is within the ring, and the thrips lays its eggs and rears its young within this circle. The glue, in some species, is laid down as an almost continuous ring, whereas in others an opening in the ring is left at one side. In other species the glue appears to be arranged as an irregular ring of pillars, the basis of each pillar being a thrips egg. Most of these domicile creating thrips species feed only within their domicile, but at least one species

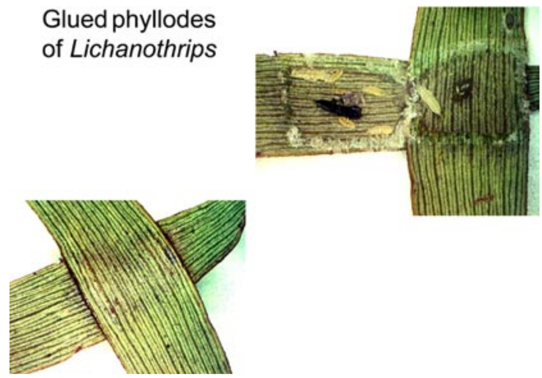

Fig. 3. *Lichanothrips* domicile of glued phyllodes.

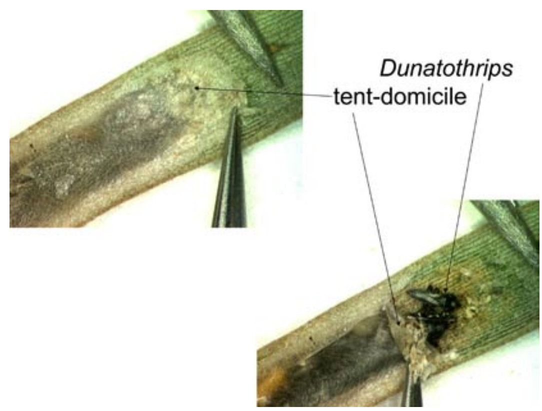

Fig. 4. *Dunatothrips* domicile of silken tent.

is known to forage on the phyllodes outside, both as adults and larvae (Crespi & Mound, 1997).

On *Acacia* species with more slender, even terete, phyllodes, the associated thrips secrete a more silk-like product, rather than a glue. This "silk" has the appearance of "candy-floss", but currently there is no knowledge of the mechanisms involved in its production, nor of the chemical relationships between the different adhesives. Some thrips use this webbing to draw together two or more phyllodes, and thus enclose a small space within which to breed (*Carcinothrips tania*). In one species, *Dunatothrips vestitor*, a group of apical phyllodes is drawn together tightly within which to breed, but then further phyllodes near the apex are drawn in more loosely by a series of threads (Mound & Morris, 2001). The domiciles of this species appear to be longer lasting than in most species, with multiple generations of thrips developing. Moreover, this species exhibits the interesting behaviour known as pleometrosis, the founding of a colony, and creation of a domicile, by a group of females (Morris et al. 2002).

Domicile production through the use of silk threads has led, in two species, to the construction of domiciles entirely from silk. These two species, *Dunatothrips aulidis* and D. *skene*, although congeneric are not particularly closely related within their genus. Yet both of them have the ability to weave a shallow silken tent, beneath which the adult then lays eggs and rears her brood. When completed, each of these tent-like domiciles looks very like a lepidopterous mine on a phyllode, but closer inspection reveals the web of threads, including the marginal threads that stretch out like guy-ropes from the tent margins.

Many problems remain to be investigated concerning these domiciles and the thrips that create them, including the other associated organisms, the chemical relationship between glues and silks, the details of domicile construction and phyllode manipulation by an individual thrips, and the evolutionary origin of these phenomena. Morphotaxonomy provides little evidence concerning evolutionary relationships. Molecular tools have therefore been applied, using two nuclear genes (*wingless & elongation factor-1alpha*) (Morris et al. 2003). The resultant cladogram gives some interesting indications, of which one is particularly remarkable. The two genera of kleptoparasitic species, *Koptothrips* and *Xaniothrips*, would appear to be unrelated judging from their structure, but the molecular data suggests that they are sister-groups. That is, the behaviour involved in kleptoparasitism evolved only once, but the methods of achieving this, whether by attacking with sharp fore tarsal teeth, as in *Koptothrips*, or with the spiny abdomen, as in *Xaniothrips*, has selected for very different body forms. Gall-inducing thrips form a single clade, as might be expected, but all of the domicile creating thrips are also grouped within a single clade. This suggests that the behavioural ability to create a domicile may have evolved once, but has then been lost twice, with species in the genera *Grypothrips* and *Warithrips* living as invaders of domiciles that have been abandoned by their original owners.

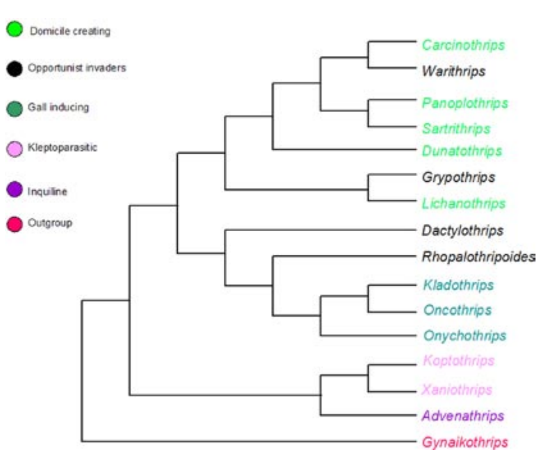

Fig. 5. Relationships between Phlaeothripinae genera from Australian *Acacia* species.

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