LITTLE HOUSES IN *Big Trees*

AN AESOP'S FABLE WITH PLANTS

Some of the forest's tiniest creatures render a mighty service to trees. Mite researcher **David Walter** invites you to peer closely at the underside of leaves.

Every part of the woody structure of a tree is colonised by mites, including tree holes. This member of the Cheyletidae was collected from a tree hole, and probably preys on small arthropods associated with nests. Other cheyletid mites live on leaves and some have become parasites of birds and small mammals. *Photo: David Walter*

Mites were among the earliest animals to colonise land.

Although most mites go about their business to our benefit – or at least not to our loss – we mostly only notice the few that cause us detriment. Ticks are unusually large mites with blood-thirsty habits, and the red wheals of scrub itch are caused by the larvae of velvet mites, also called chiggers. This chigger (right) is the larva of an undescribed *Guntheria* species. At left is a spider mite, *Neonidulus teretosus*. Spider mites are plant parasites, named for the webbing produced by some species. They stab plant cells with their mouthparts and suck out the contents. A few dozen species (not this one) are major agricultural pests. This species weaves a tent-like web on the underside of weeping lillypilly (*Waterhousea floribunda*) leaves. Its discovery by the author necessitated the description of a new genus (with Jenny Beard). *Photos: David Walter*

A wander through a cathedral-like tropical rainforest can be inspirational, but where is the much vaunted biodiversity? Why is it so quiet and reserved among the towering trunks and fluted buttresses? One reason is that most of the action takes place far above, in the canopy, and below our feet. And most of the diversity consists of tiny organisms. One group exceedingly abundant in the canopy and the soil, yet almost invisible to us, is the Acari, a fittingly short name for the relatives of spiders and scorpions that we call mites.

In good light a person with keen eyesight can resolve down to about 0.1 millimetres. The average fully grown mite is about 0.5 millimetres long – about the size of a fullstop – and I have measured larval mites as short as 0.05 millimetres. We don't spend much time looking for things this small, but if we did we would see mites everywhere.

As an acarologist, I've spent most of my long career seeing mites everywhere. That is not delusional – with the exception of open ocean, mites are literally almost everywhere, from the tops of mountains to beaches to seamounts to deep marine trenches.

Rainforest mites

When I first became interested in mites living on plants, the canopies of rainforest were considered 'the last biotic frontier', but mites were rarely reported in canopy studies. To paraphrase what one entomological colleague explained to me: 'Yes, we knew there were mites in the canopy, but there were too many, so we ignored them.' Put a tree leaf, branch or piece of epiphyte under a microscope and you usually find more mites than anything else. The average densities in Australian rainforests are typically thousands per square metre of foliage.

It is in soil, though, that mites are most impressively diverse and abundant. Hundreds of thousands of individuals and typically hundreds of species reside in a square metre of forest leaf litter and soil, often at least as deep as roots penetrate, where they graze on detritus, microbes or each other, releasing nutrients for plants to use again. Mites were among the earliest animals to colonise land, and soil mite fossils are known from at least 410 million years ago.

Some mites are plant parasites, sucking up the contents of plant cells with their stylet-like mouthparts. Spider mites, flat mites, rust mites, gall mites, broad mites and the like can cause great damage to crops and often require chemical or biological control. This wasn't always the case. Before synthetic pesticides were widely used mid last century, mites attacking crops were more a curiosity than a problem. As pesticide use increased, mites and other so-called secondary pests boomed as their natural enemies (particularly predatory mites) became collateral damage in the battle to provide food and fibre at minimal cost.

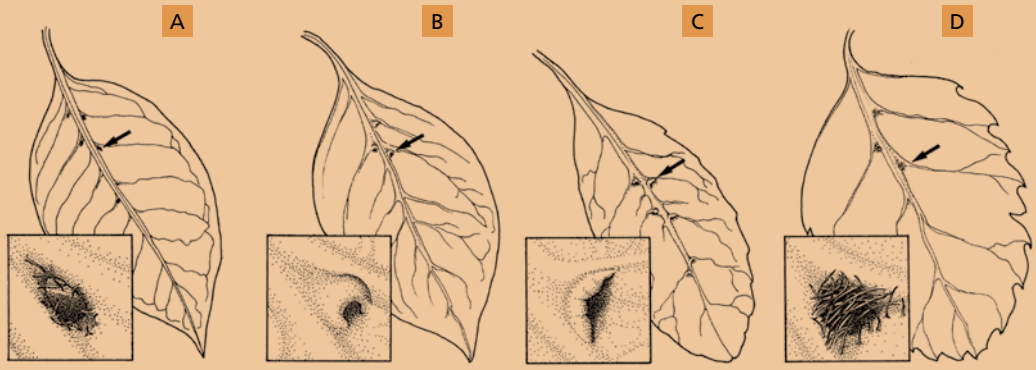
Although plant-parasitic mites sometimes severely damage or kill trees, they are usually hard to find in rainforests, probably because there are hordes of predatory mites eating them. Typically no more than half a millimetre long, these predators are voracious. The best known are members of the Phytoseiidae family (from the Greek for running to and fro on a leaf), which are much better studied than other mites because they are useful biological control agents in agriculture. Although the family is only one of 109 in the mite order Mesostigmata, they make up about 20% of the described species. With high reproductive rates, short generation times, female-biased sex ratios (often 80% or more of the offspring are female), and an active hunting strategy, these tiny eating-machines make short work of a prey population. Many other predatory mites are ambush (sit-and-wait) hunters. They are probably most useful to a plant when they take up residence near the base of a leaf and pick off plant parasites as they try to colonise a leaf.

The vast majority of mites in rainforest canopies feed not on plants or each other, but on fungal hyphae and spores

WHAT ARE MITES?

Mites are not a natural group. DNA studies have shown they are comprised of two lineages of arachnids that are not very closely related and require two superorders to accommodate them: Parasitiformes and Acariformes. Parasitiform mites include ticks, flower mites, bird mites and other parasites, and numerous predatory mites including the leaf-inhabiting Phytoseiidae. All the major plant-parasitic mites belong to the Acariformes as do most of the fungivores and many types of leaf-inhabiting predators.

All mites are small with an unsegmented body and four pairs of legs in the adult (three pairs in the larval stage or only two pairs in gall mites), and a head-like front end that bears chelicerae (claw-like pincers used for feeding) and a pair of sensory palps. This rather simple body plan has been wildly successful – over 50,000 species of mites have been described and hundreds of thousands remain unnamed and waiting for industrious scientists to add them to the Linnaean hierarchy.



Here are some examples of domatia types. A: a 'pit' domatium in coffee (*Coffea arabica*). B: a 'pouch' domatium in northern rose walnut (*Endiandra cowleyana*), a rainforest tree from northeast Australia. C: a 'pocket' domatium in brown quandong (*Elaeocarpus coorangooloo*), a rainforest tree from northeast Australia. D: a 'tuft/pocket' domatium in southern beech (*Nothofagus fusca*), from the South Island, New Zealand. *Illustrations: Anne Prowse*

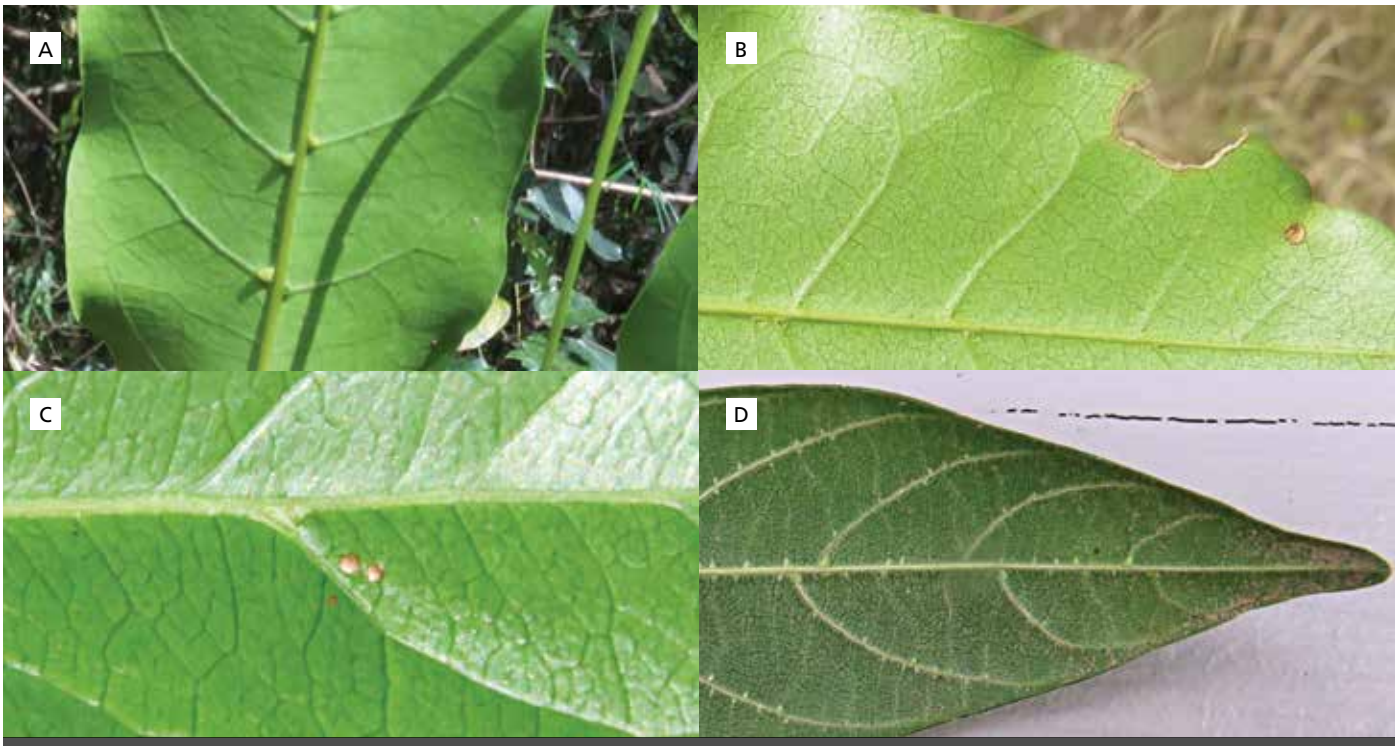
ACARODOMATIA

Domatia are small structures on the underside of leaves in the triangular area where the primary veins branch off the midrib and sometimes in the junctures of secondary leaf veins. The word comes from the Latin for house (domus). These 'little houses' vary in structure from shallow pits protected by tufts of hairs, to cave-like invaginations in the leaf blade, to roofed 'huts'. If you look carefully into them, you are likely to find a mite or evidence of one (cast skins for example). More than a hundred years ago, this observation gave rise to the term 'acarodomatia'.

Acarodomatia are not like galls in being induced by the feeding of mites, but are under the genetic control of the plant. Some plants may be able to regulate the number of domatia produced. Species such as the hard quandong (*Elaeocarpus obovatus*) vary in the number of domatia produced per leaf, possibly in response to nutritional levels. The mites found in leaf domatia are almost always 'good' mites, those likely to be helpful to their host by feeding on leaf pathogens or plant parasites.

Trees, shrubs and lianas in more than 80 families of plants (about 28% of all woody plant families) are known to produce acarodomatia. Temperate deciduous forests in the Northern Hemisphere appear to be the best places to find domatia, with at least half the tree species featuring them. Like other leaf inhabitants, mites must seek shelter in the bark or soil to overwinter and recolonise the tender new leaves each spring. But any reasonably warm, moist forest is a good place to look, including in eastern Australia. Leaf fungi thrive in humid climates, which may be why plants with leaf domatia are most common in wetter habitats. The proportion of species with domatia increases as you head north, peaking in the Wet Tropics. Sclerophyll plants in dry lands such as wattles and eucalypts rarely have leaf domatia.

To look for domatia, try a trail, forest edge or tree fall opening where lianas such as kangaroo vine (*Cissus antarcticus*), native jasmine (*Morinda jasminoides*), and some of the native raspberries like *Rubus moorei* cascade down towards the ground and the leaves of the canopy trees are more accessible. A hand lens helps.



Here are some examples of leaf domatia from rainforest near Mudlo National Park, Queensland. A: kangaroo vine (*Cissus antarcticus*) has large, raised pocket domatia. B: native olive (*Olea paniculata*) has pit domatia with hairs. C: blueberry ash (*Elaeocarpus obovatus*) varies in the number of pocket domatia per leaf from none to about nine. This leaf has a single domatium in the vein axil to the left and above the two brown leaf spots. D: black huskheart (*Alangium villosum tomentosum*) has an unusually high density of pit domatia in both the primary and secondary vein axils. *Photos: David Walter*

This is a leaf oribatid mite, a species in the genus *Scapheremaeus*, found in Queensland rainforest. Its ancestors lived in the soil and lost their eyes, but *Scapheremaeus* mites evolved an eye spot that helps them climb towards the sun. The genus has more than 100 described species from many parts of the world. *Photo: David Walter*

(they are fungivores). Some are opportunists that clean up decaying messes (such as windblown debris and the cast skins or droppings of insects), while others eat virulent plant pathogens. Because fungus-eating mites are not agricultural pests, we know little about them, and what little we do know is because they have sometimes been mistaken for pests. When a crop has leaves with spots or blotches and mites are found there, they are often assumed to be causing the damage. But if the mites are fungivores, they are eating the problem rather than causing it. This reversal of cause and effect provides insight into both the benefits of mite fungivores and a strange and obscure leaf structure.

In search of shelter

While the forest floor seems still and solemn, the rainforest canopy is baked in the sun, washed by floods of rain, and whipped by winds. The larger inhabitants such as birds and mammals can generally shelter from a storm in hollows or crevices or beneath branches. But imagine if you were smaller than a pinhead and living on a leaf when a storm hit. Where would you hide?

The vast green plains of many leaves (like those of citrus trees) offer nowhere for a mite to shelter. The leaf surface, good for shedding rain, is too smooth and flat. But the surface of other leaves (grape vines, for example) is more complex, with valleys and hills (veins), and forests of hairs or small copses barely a millimetre across that might offer safe harbour for a mite.

In the late 1800s a curious Swedish naturalist, Axel Lundström, noticed that tufts of hairs in the vein axils on the underside of linden tree leaves form small enclosures that often contain mites. He called them acarodomatia (Latin for 'little mite houses') and proposed that the mites help protect leaves from pathogenic fungi. Although acarodomatia (often called foveoles) were well known to botanists and considered useful characters for identifying plants, the idea that trees would want to harbour mites was considered eccentric, and Lundström's observations were ignored for almost a century. It was only about 30 years ago that scientists around the world reawakened to the existence of acarodomatia. Although several research groups, more or less simultaneously, began noting the association between mites and leaf domatia, as they are now generally called, the studies of Dennis O'Dowd and Mary Willson in Australia, New Guinea and New Zealand put domatia into the scientific limelight. They demonstrated that foveoles of various shapes – from hairy pits to pockets to hut-like domes – from a variety of unrelated woody plant families have two things in common: they are found in vein axils on the underside of leaves and they typically contain mites considered innocuous or beneficial to plants.

Going beyond correlation to experimentally prove the association has been challenging, however, for domatia can't be removed without damaging leaves and even a small tree may have hundreds of thousands of them. Dennis O'Dowd developed an ingenious technique using a bitumen paint to block access to leaf domatia. Then Dennis and I spent many hours in leech-infested forests, swatting march flies, fielding questions from curious hikers, and using small paint brushes to close hundreds of leaf domatia on a dozen species of rainforest trees, shrubs and lianas. To account for any effect of the paint, we also dabbed it below the domatia on a second set of leaves. The effects were dramatic and consistent: blocking access to leaf domatia reduced the numbers of predatory mites by about 90% and fungus-eating mites by about 80%.

TRAVELLING MITES

One key to the high diversity of mites is their colonisation of larger animals multiple times during their evolutionary history. Beetles, bees, birds, and even butterflies are habitats for a diverse array of mites. Most land vertebrates have mite associates (even we have our scabies, follicle and dust mites), and many invertebrates have symbiotic mite associates. Even slugs have mites that live on them and in their lungs.

Mites lack wings, but many of those that live on plants can float on the wind. Other plant mites hitch rides on larger animals (a behaviour called phoresy, from the Greek 'to carry'). Flower mites in the Neotropics, which feed on pollen and nectar, are carried from flower to flower in the nares of hummingbirds (these mites are the equivalent of a venereal disease for plants). In Australia an unrelated group of mites that live in flowers hitch a ride on spinebills and other honeyeaters. Orange mangroves, correas, mistletoes and other brightly coloured tubular flowers are good places to look for these mites.

The next time you roll a log and see a beetle, millipede or centipede, take a closer look and you are likely to see it is carrying mites. Flies and beetles that breed in dung or live in treeholes are often covered with phoretic mites, many of which have special adaptations for holding on. The same is true of many bee mites. Some bees even have domatia-like 'acarinaria' – pits and pockets in their cuticle in which phoretic mites cluster. It is likely these mites benefit their carriers by protecting larvae within bee nests from fungi and parasites.

AUSTRALIA'S MITES

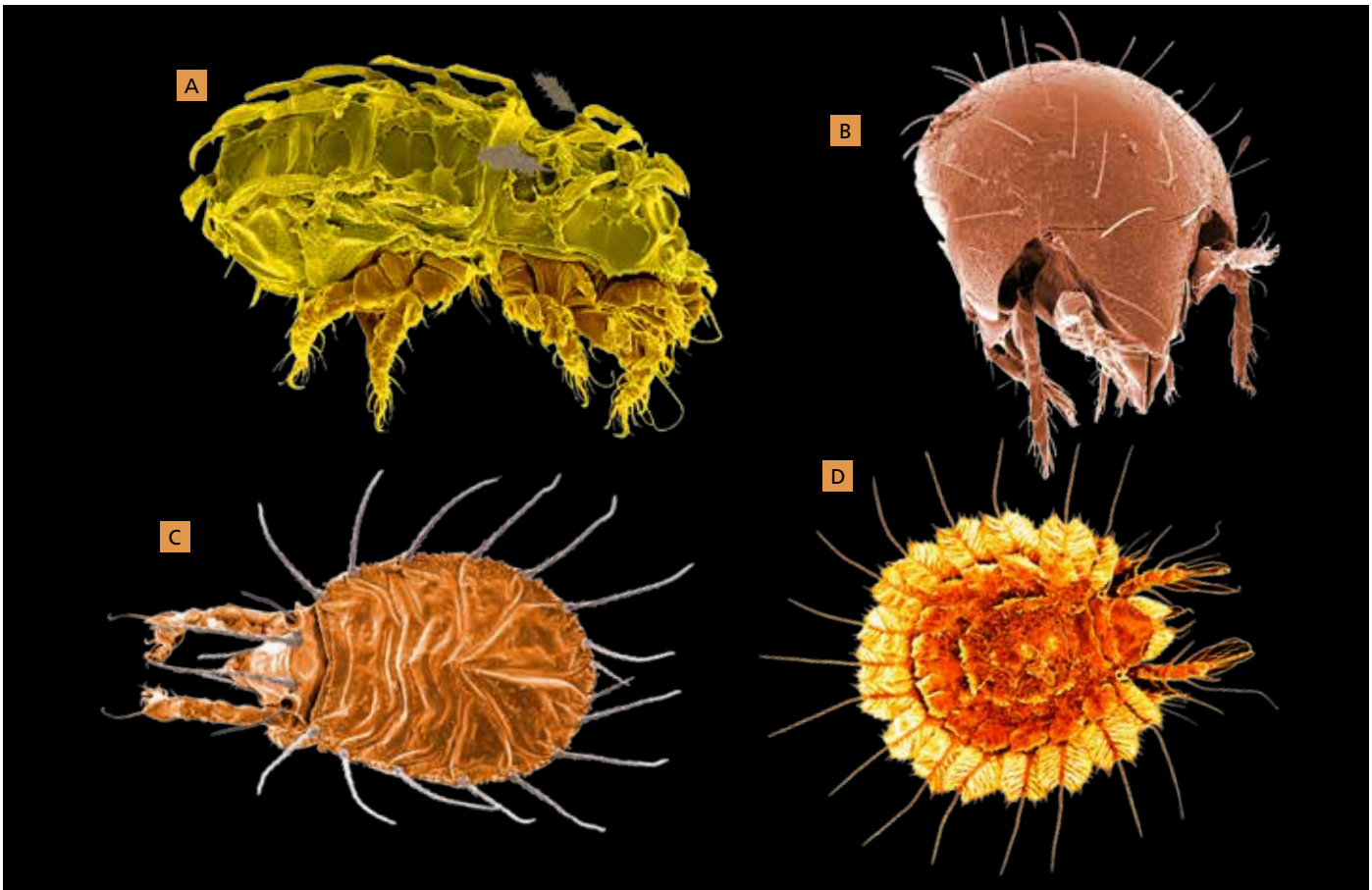
Australia has only about 3000 named species of mites, but this small number is due to a lack of acarologists rather than any deficit in mites. My colleagues and I have estimated there are at least 2000 species, 80% undescribed, living in the rainforest canopy in the Green Mountains region of Lamington National Park in Queensland. It would be surprising if fewer than 30,000 species inhabit Australia. Mites are not well studied on any of the southern continents except Antarctica (where there are over 50 species on the mainland). What little we know of the descendants of the mites of the ancient supercontinent Gondwana indicates that they are often very different from the better known mite groups of the northern continents. For example, my research in eastern Australia has resulted in the description of five new families of mites and a dozen new genera.

New species, genera and even families of mites await discovery in Australia. This pincushion mite (*Xanthodasythyreus toohey*) required a new genus. It was described from specimens collected by the author at the base of a grasstree in Toohey Forest in the middle of greater Brisbane. This mite moves slowly, fortified by 39 long barbed bristles (setae). *Photo: David Walter*

Mutual benefits

Why do rainforest trees and lianas make tiny, mite-sized houses on their leaves? This would make no sense if they provided shelter for plant pests. Plants that helped their parasites would soon have no leaves, as anyone who has watched spider mites destroy a plant can attest. However, after dissecting many thousands of domatia from dozens of plant species, I can attest that spider mites and other plant parasites rarely inhabit domatia.

One reason, which I call the 'cave bear effect', is that a plant parasite hiding in a domatium is more likely to encounter a predator there than on the much larger expanse of the leaf surface. The veins on the underside of a leaf are a natural highway for roaming predators. Hanging out in a domatium would also constrain its feeding options, for domatia rarely cover more than 1% of a leaf's lower surface, and plants would be able to concentrate their chemical defences in that small area. Plant-



Oribatid mites, also called beetle mites, are often the most abundant arthropod in temperate and subtropical forests. They live mostly in soils, leaf litter, lichens, mosses or forest canopies, feeding on microbes, fungi, algae or detritus. Most are tiny. The adult oribatid mite (family Brachychthoniidae) (A), which lives in rainforest soil is less than 0.15 millimetres long – about as small as an unaided human eye can resolve in good light. (B) is an undescribed species from genus *Rostrozetes*. This adult is heavily armoured and safe from most mite predators, except some specialists with mouthparts like bayonet can openers. Almost all mites begin their lives as eggs. Like other arthropods, after hatching they regularly shed their external skeletons and often change their appearance as they develop through various larval and nymph stages before becoming adults. (C) is a soil-living nymph of an undescribed species from genus *Nesopelops*. (D) is a nymph of an undescribed species (family Cepheidae), which lives on the branches and trunks of rainforest trees where it grazes on microbes. *Photos: David Walter*

parasitic mites tend to shelter at their preferred feeding sites, either making their own homes (webs, galls or curled leaf margins), clinging tightly to the surface (as many false spider mites do), or inhabiting crevices on stems (as peacock mites do).

The only plant parasites that seem to occupy leaf domatia with any regularity are the scale insects that sometimes encrust leaf veins and domatia with apparent impunity. Now and then, I have found thrips in domatia. But overwhelmingly the inhabitants are fungus-eating or predatory mites. None of these are known to harm plants and many are likely to benefit them.

At very low production costs for the plant, the domatia provide mites with shelter from storms, a safe place to lay eggs and for young to grow, and a refuge from larger predators. In return, plants gain a resident population of 'bodyguards' that protect them from fungal diseases (as Lundström proposed) and small parasitic arthropods. This mutually beneficial association of tiny mites and giant forest trees reminds me of Aesop's fable *The Lion and the Mouse*, about a mouse that reciprocates the favour of a lion in sparing her life by saving him from a hunter's snare. What's important isn't the size differential – after all, bacteria can kill even the largest mammals – but what the organisms do for each other.

Researchers have experimentally demonstrated some of the benefits inherent in the association. Andy Norton, Greg English-Loeb and colleagues, for example, showed that a tiny tydeid mite (*Orthotydeus lambi*) can reduce damage by powdery mildews in vineyards. These mildews often cause considerable crop losses by coating leaves, shoots and fruits in a whitish miasma of mycelium and spores. The fungus-eating tydeid mites are not common in vineyards because of pesticides and possibly because many grape varieties lack well developed domatia. But when tydeids are abundant, mildews do much less damage, especially on grape leaves with domatia. The more domatia the stronger is the effect.

This may be the third most prevalent mutually beneficial association between animals and plants, after pollination and seed dispersal.

Amber inclusions and fossil leaves indicate that predatory and fungus-eating mites have been living on leaves for tens of millions of years, at least since the Cretaceous. Plant-parasitic mites are even older, known from the Triassic. Hundreds of species across more than 80 woody plant families (more than a quarter of those currently recognised) produce domatia. All are perennials (living several years), so, unlike annuals, they have the luxury of time to accumulate tiny bodyguards. The best explanation for domatia having evolved independently in so many lineages of woody plants is that plants benefit by helping mites. This may be the third most prevalent mutually beneficial association between animals and plants, after pollination and seed dispersal. Understanding this relationship not only makes sense of a mysterious leaf structure, but has resulted in a better understanding of mite pests in agriculture. So, paying attention to one of the smallest groups of organisms in the rainforest has generated interesting and beneficial knowledge. That's something to think about on your next walk in the forest. Try taking a hand lens, turn over some leaves and find a leaf domatium – and if you are lucky, a mite! ■

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The first time **DR DAVE WALTER** saw a mite, in an undergraduate insect morphology class, he declared he'd never work on mites: 'They are too small and have too many legs.' He's spent most of the past 45 years paying for that hubris by investigating the ecology, behaviour and systematics of mites in California, Oregon, Colorado, Florida, Alberta, Victoria, New South Wales, Queensland, the Northern Territory, and Western Australia. During these Sisyphean labours Dave has authored or co-authored far too many peer-reviewed journal papers, annual reviews, book chapters, conference papers, books and interactive keys on mites (about 150 or so). He is currently semi-retired in the Sunshine Coast Hinterlands, but continues his research at the University of the Sunshine Coast and Queensland Museum, and is editor-in-chief of the *International Journal of Acarology.*

PREDATORY MITES

Plant defences against herbivores include those that are always present (constitutive defences like thorns) and those that are induced by herbivore attacks (such as toxins). When domatia house predatory mites that attack plant parasites, they can be considered a constitutive defence. Plant parasitic mites trying to colonise a leaf would have to run a gauntlet of hungry predators and likely be picked off before they could form a colony. Or they might avoid the leaf altogether.

I have found a strikingly close relationship between domatia on rainforest plants and predatory mites. On leaves with domatia it is common to average one or more predatory mites per leaf, but on plants lacking domatia you typically have to search 10 leaves to find a single predator. The more domatia, the more predatory mites one finds.

Fungus-eating mites that inhabit domatia also have to take their chances with the predatory mites, but those that are most common on leaves are either protected by heavy armour (oribatid mites) or are apparently distasteful, for they are rarely eaten (tydeid mites, for example).

This is a member of the Phytoseiidae family, legendary predators of plant-parasitic mites and the most important group of mite biocontrol agents. This species, *Phytoseius oreillyi*, which inhabits hairy leaf surfaces, was described by the author and named in honour of old Pete O'Reilly, in thanks for his research help. *Photo: David Walter*