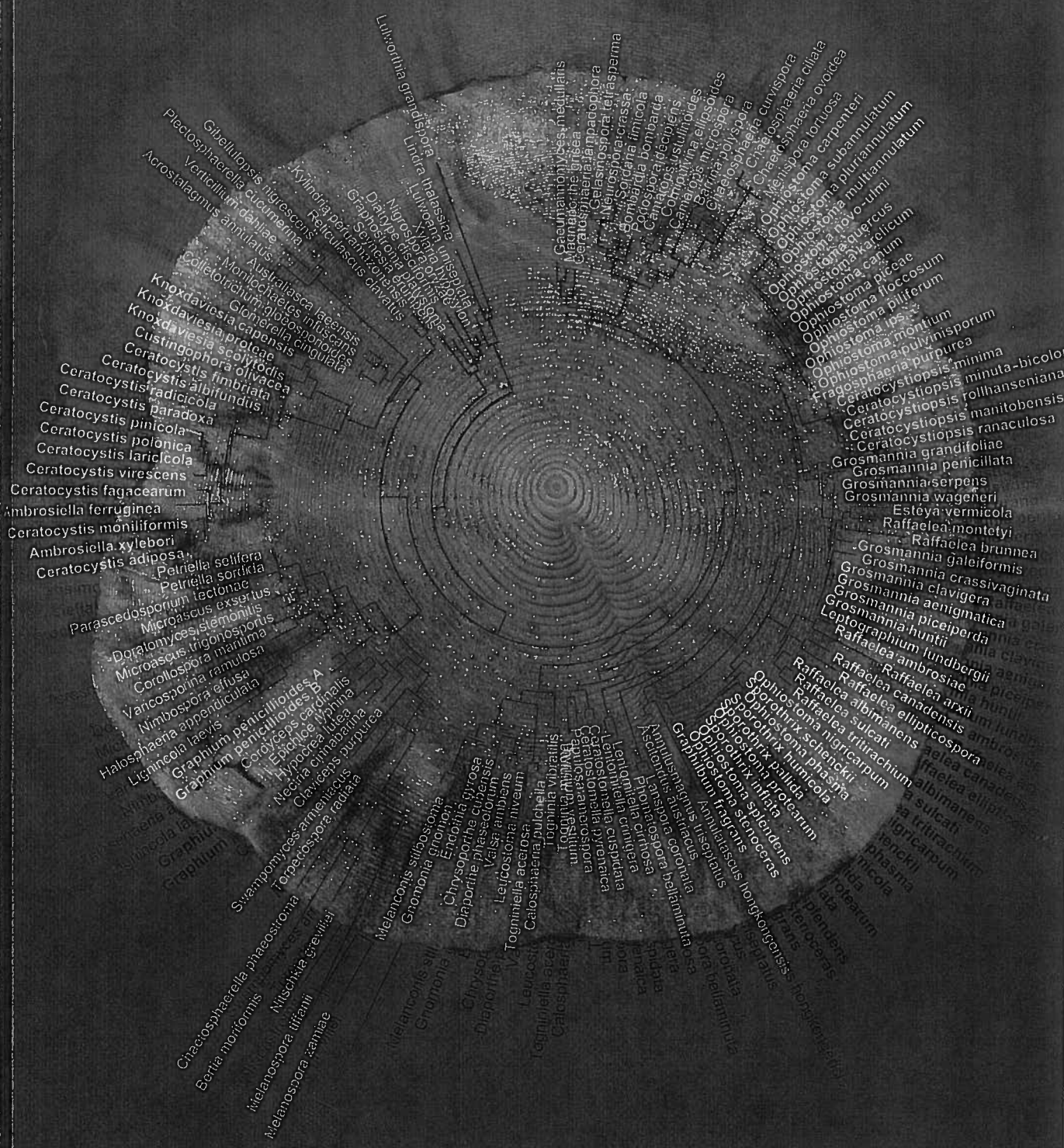


OPHIOSTOMATOID FUNGI

Expanding Frontiers



Edited by Keith A. Seifert, Z. Wilhelm de Beer & Michael J. Wingfield

CBS Biodiversity Series 12

The Ophiostomatoid Fungi: Expanding Frontiers

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Mites associated with bark beetles and their hyperphoretic ophiostomatoid fungi

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Abstract: The role that mites play in many ecosystems is often overlooked or ignored. Within bark beetle habitats, more than 100 mite species exist and they have important impacts on community dynamics, ecosystem processes, and biodiversity of bark beetle systems. Mites use bark beetles to access and disperse among beetle-infested trees and the associations may range from mutualistic to antagonistic, and from facultative to obligate. Many of these mites are mycetophagous, feeding on ophiostomatoid fungi found in beetle-infested trees and carried by bark beetles. Mycetophagous mites can affect the evolution and ecology of ophiostomatoid fungi and thus impact bark beetle-fungal associations and beetle population dynamics. In this chapter, we provide an overview of the known associations of bark beetles and mites and discuss how these associations may impact the interaction between beetles and fungi, and the evolution and ecology of ophiostomatoid fungi.

Key words: *Ceratocystiopsis ranunculosa*, *Dendroctonus frontalis*, *Dryocoetes*, *Ips typographus*, *Entomocorticium*, *Ophiostoma minus*, phoresis, *Scolytus*, symbiosis, *Tarsonemus*.

INTRODUCTION

Mites exist in every environment on Earth in aquatic, terrestrial, arboreal and parasitic habitats. Estimates suggest that 500,000–1,000,000 species of mites exist, but only 45,000 species are named. A large majority of mites are mycetophagous, *i.e.* they feed on fungi. Because of their small size, mites are often phoretic, meaning that they use other organisms to disperse or migrate between habitats. Symbiotic associations between mites and their phoretic hosts may be temporary or permanent, and vary from mutualistic to commensalistic to antagonistic (Walter & Proctor 1999).

Standing dead wood and trees attacked by insects and pathogens are home to a variety of mites that invade alone or in association with wood-inhabiting insects. Beetle galleries within living and dead wood harbour a robust diversity of mite fauna, for example, the more than 96 mite species associated with *Dendroctonus frontalis* (Moser & Roton 1971). These mite communities consist of fungivores, herbivores, scavengers, and predators, and can have important effects on the evolution and ecology of bark beetles and their associated fungi. For instance, some species of mites alter the frequency of beetle-mutualistic fungi or the abundance of antagonistic fungi, which can drastically affect bark beetle behavior and population growth (Hofstetter *et al.* 2006a).

In this chapter, our goal is to provide information that can help with the identification of mites associated with bark beetles and ophiostomatoid fungi, and advance the understanding of mite/beetle/fungal ecology. Towards that end, we briefly describe the natural history of mites and their interactions with beetles. We also list species of mites associated with several bark beetle genera, including *Dendroctonus*, *Scolytus*, *Ips* and *Dryocoetes*. More information on general mite biology, morphology and behavior can be found in Evans (1992), Lindquist (1986), Krantz & Walter (2009), and Walter & Proctor (1999).

WHAT ARE MITES?

Taxonomy

Mites are classified in the phylum Arthropoda, which encompasses the insects, myriapods, spiders, scorpions, crustaceans, and ticks,

and is characterised by jointed legs and a chitinous exoskeleton. Mites comprise the subphylum Chelicerata, characterised by pincer-like mouthparts called chelicerae, and the absence of antennae, mandibles, and maxillae, which are common in other arthropods such as scorpions, spiders, and harvestmen. Mites also differ from insects because adults have four pairs of legs and lack wings. The mite subclass, Acari, includes organisms in which segmentation is generally inconspicuous or absent, unlike the Araneae (the spiders).

Mites (Acari) are subdivided into two superorders, the Parasitiformes and Acariformes (Krantz & Walter 2009). The Parasitiformes consist of four orders: Ixodida (ticks), Holothyrida (a rare group called holothyrids), Opilioacaridae (a primitive group with only 20 species), and the Mesostigmata (a group with diverse feeding habits). About 12,500 species are described in the Parasitiformes, with the majority occurring in the Mesostigmata. Species of Mesostigmata, including many of the genera found in decaying fungi, are phoretic on beetles (Kinn 1971, Lindquist 1975, McGraw & Farrier 1973), and are prominent predators of nematodes and mites or mycetophagous on ophiostomatoid fungi. The Opilioacarids are omnivores and opportunistic predators, and live in forest litter and under rocks; they feed on fungi, small arthropods and pollen (Walter & Proctor 1998). They generally live in warm, dry temperate or tropical habitats. Opilioacarids have not been found in bark beetle killed trees, but it is possible that they feed on ophiostomatoid fungi.

The Acariformes are divided into the Trombidiformes and Sarcoptiformes, and are the most diverse and abundant of the two superorders, with over 30,000 described species. Acariformes mites occur in most terrestrial habitats. Mites in the Trombidiformes are the most frequent residents of ophiostomatoid and bark beetle habitats (Kinn 1971, Moser & Roton 1971, Moser 1985, Bridges & Moser 1986, Moser *et al.* 1989a, b, Lombardero *et al.* 2000).

Morphology

Although most mites are minute, adult body lengths can vary greatly from 80 μm (some plant parasites) to 3 cm (engorged ticks). In general, mites associated with bark beetles range from 90 μm (*Iponemus* sp.) to 0.5 mm (*Mexecheltes* sp.) long.

Mites have an anterior section resembling a tiny head. This region, the gnathosoma (Fig. 1), is comprised of the chelicera, subcapitulum, and palps. The chelicerae, which are primarily used for capturing and ingesting food, may be highly modified with various structures, such as the Trägårdh's organ, spermatodactyl, and stylophores. Chelicerae may also be used for nonfeeding purposes, such as holding on to the host during phoretic migration (Walter & Proctor 1999).

As mentioned previously, mites have four pairs of legs. Often, the first pair is slender, elongated, lacks well-developed claws and is used like antennae. A cluster of sensory setae may be located near the tips of leg pair I, and are used for assessing a potential sexual partner or prey, by using tentative tapping movements (Walter & Proctor 1999). Sometimes the first two pairs of legs are used in conjunction with the palps and chelicerae to capture prey. Leg pairs II, III, and IV are the primary organs of locomotion.

The remainder of the body is fused into a sac-like idiosoma (Fig. 1) that contains organs for digestion, excretion and reproduction. Digestion in mites is very primitive. The parasitiform (excluding the opilioacariformes) and trombidiform mites only ingest fluids, sucking liquids through filtering structures. However, the sarcoptiform and opilioacariform mites use a different feeding method, cutting off pieces of food that they then move into their mouths. Food fragments form into a food bolus at the base of the esophagus. Entire spores of *Ophiostoma* species sometimes can be seen in the hindgut of mycetophagous mites (Fig. 2). The food bolus is expelled as a fecal pellet through a relatively large anal opening covered by a pair of trapdoor-like valves (Walter & Proctor 1999).

Reproduction in mites can be very creative and varied. Direct transfer of sperm via genitalia is relatively uncommon. In males, appendages are often modified for sperm transfer. Spermatodactyls on chelicerae are sometimes used to channel sperm into the female's genital opening. In some parasitiform species, the male picks up a spermatophore (sperm packet) and places it into the female copulatory passage. Mating rituals and behaviors are further discussed in the next section.

LIFE HISTORY

Reproduction and sex allocation

Mites have extremely diverse mating habits and reproduction; variation in reproductive mode can occur within families, genera and species (Norton *et al.* 1993). Although there is an extensive body of literature on sex ratio biology of mites (e.g., Wrensch & Ebbert 1993, Proctor 1996), knowledge of sex determination and behavior of mites associated with bark beetles is sparse. For most species, the mode of reproduction (haploid or diploid) and the genetic system (e.g., arrhenotoky, parahaploidy, thelytoky, amphitoky) is unknown. Several species of Tarsonemidae are arrhenotokous, thelytokous or amphitokous (Schaarschmidt 1959, Karl 1965). In general, mite species that are haplodiploid (i.e. the union of a sperm and an egg develops as a female, and an unfertilised egg develops as a male) and dependent on beetles for dispersal, have relatively high sex ratios in favor of females (Lindquist 1969, Mitchell 1970). The patchiness and discrete time periodicity of bark beetle habitat allow for tests of evolutionary stable sex allocation strategies (e.g., local mate competition, Hamilton 1967), founder effects (e.g., haystack model, Nagelkerke & Sabelis 1996), exploitation and competition, and island biogeography theory (Terborgh *et al.* 2001, Sanchez & Parmenter 2002).

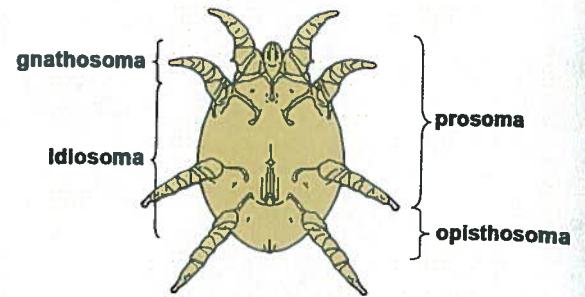


Fig. 1. Diagram of mite morphology, showing major body parts.

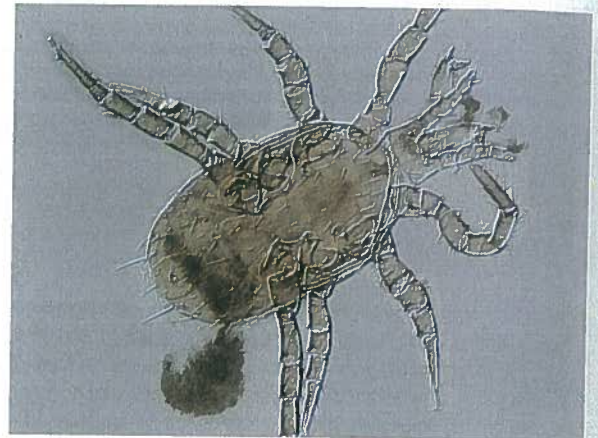


Fig. 2. *Ophiostoma novo-ulmi* in the hindgut of *Proctolaelaps scolyti*.

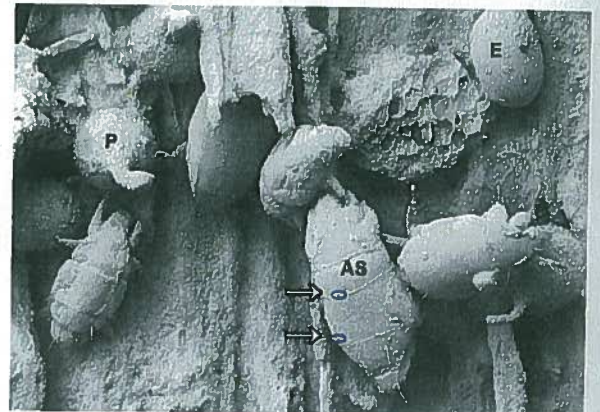
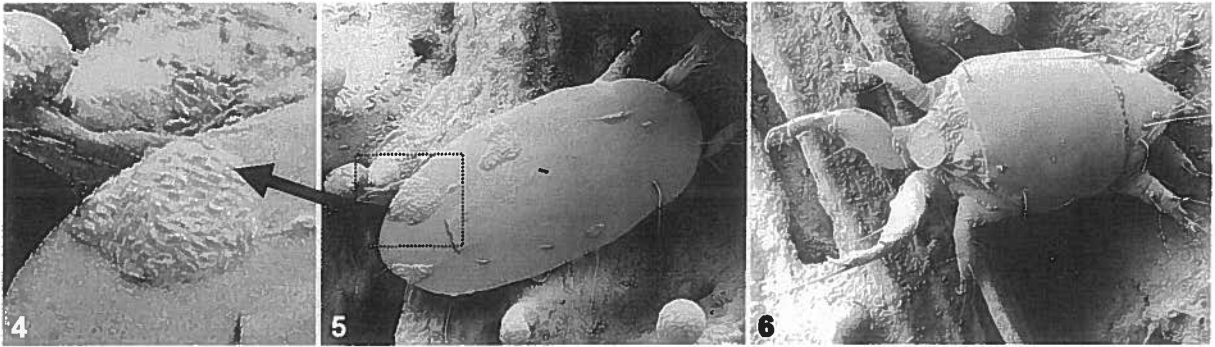


Fig. 3. Scanning electron micrograph of adult and immature *Tarsonemus* mites that feed on *Ophiostoma minus*. Perithecia of *O. minus* (P) and *Tarsonemus* eggs (E) are covered with minute ascospores (AS). (Eric Erbe, Ronald Ochoa, Kier Klepzig).

Growth and development

The basic acarine development sequence is egg, prelarva, larva, (pupa), protonymph, deutonymph, tritonymph, and adult (Krantz 1978). However, suppression of one or more nymphal instars and accelerated development are common in many species. Several lineages are characterised by terminal truncation of nymphal instars and rapid developmental rates (e.g., some Parasitiformes and Acariformes). Some species of Heterostigmata give birth to fully formed, mated adult offspring. Eggs are usually laid individually on the substrate and are not protected by the parent, although some eggs may be carried by adults. Eggs are also quite large, almost



Figs 4–6. Scanning electron micrographs of *Tarsonemus ips* in bark with ascospores of *Ophiostoma minus*. 4. Ascospores of *O. minus* on mite cuticles. 5. Female. 6. Male; note modified IV legs of the male for grasping pharate females (Eric Erbe, Ronald Ochoa, Kier Klepzig).

½ the size of an adult mite in some species (Fig. 3). The typical acarine larva is hexapod and completes its development with little or no change in initial form other than slight increases in girth. Larvae of some species lapse into an inactive, turgid state before becoming a nymph or adult (e.g. *Tarsonemidae*, Lindquist 1986). Males (Figs 4–6) of several species carry virgin females while they are in this quiescent state. Two or three nymph states usually appear between the larval and adult stage (Fig. 3). These nymphs usually have four pairs of legs, although the fourth pair may not be complete (i.e. lack claws). The first nymph or protonymph is free-living and does not always feed. The second nymphal stage or deutonymph assumes the general nonsexual characteristics of the adult, differing from it only in size and in sclerotisation pattern. In many species, phoresy occurs in the deutonymph stage rather than as adult females.

Mites associated with bark beetles generally have one or more generations per season (uni- or multivoltine), unless beetle tenure within trees exceeds one year, in which case generation time may be longer. Development rates vary greatly across taxa and are strongly affected by temperature, humidity and food quality (Lombardero *et al.* 2000). The most rapidly developing acariforms are in some of the tarsonemids, which can complete development in three to five days at moderate temperatures. Mite longevity also is highly variable across species, with some adults living only weeks while others live for several months or years.

Food and host specificity

The eating habits and food preference of bark beetle associated mites are little investigated, although feeding habits for several species associated with the southern pine beetle are known (Tables 1, 3). Mycetophagous species vary from highly specific, feeding on and carrying spores of one fungus (e.g., *Tarsonemus krantzi* on *Ophiostoma minus*, see section on *Dendroctonus* below), to generalists feeding on several fungi (e.g., *Histiogaster* spp.). Mites that are egg parasites are generally highly host specific on a bark beetle species (Lindquist 1986). Many mites associated with bark beetles are predators on nematodes and other small arthropods, and tend to be found in galleries of several bark beetles species.

Movement and dispersal

Dispersal and migration pose major challenges for mites living in discontinuous, ephemeral habitats like beetle-infested trees. Some mites are wind-dispersed, but the primary mode of travel from one resource patch to another is phoresy, or attachment to another

organism for dispersal. Mites are especially adept at phoresy and often have highly modified phoretic stages (e.g., the astigmatan deutonymph) or phase morphs (e.g., phoretomorphs in the Heterostigmata) (Moser & Cross 1975). Phoretic individuals often go through a sequence of behaviors, such as cessation of feeding, or morphological changes that are quite different from nonphoretic individuals of the same species. Many of these behaviors are analogous to those used by parasites to find their hosts (Athias-Binche & Morand 1993). The phoretic relationship may be mutually beneficial to the mite and the phoretic host, commensal (benefiting the mite only), or antagonistic, resulting in a loss of fitness to the phoretic host.

In the case of tarsonemids and some other families, mite species are phoretic on particular species, genera, or families of invertebrates that live in precise habitats in which the mite lives throughout its life cycle. The attachment pattern of phoretic species is reminiscent of the niche partitioning that reduces interspecific competition and predation. Phoretic mite species in non-bark beetle systems sometimes disperse as groups rather than as individual mites, which ensures that unmated mites find mates at their new location. This behavior probably occurs in species that lack parthenogenesis or if the likelihood of mating prior to dispersal is small.

Typically only one life-history stage is phoretic in a given species. In the *Orbatida*, the phoretic stage is the deutonymph, while in the *Trombidiformes* it may be the fertilised adult female (Zhang & Sanderson 1993). Heteromorphic deutonymphs in the *Uropodina* (Fig. 7) attach to their arthropod hosts with a stalk called a pedicel secreted from the anus, although other mites use caudal suckers, claws or chelicerae. Phoretic morphs in many different taxa share similar morphologies: dorsoventral flattening, oval or circular bodies and flanges covering all or some appendages (Binns 1982, Athias-Binche 1991, Norton *et al.* 1993). This convergent morphology may reduce moisture loss when on the host and present a smooth dorsal surface, making it difficult for the host to remove mites by grooming or rubbing.

Phoretic interactions among mites and beetles have not been studied extensively and many questions remain unanswered: What are the mortality rates of phoretics during beetle flight? What effects do desiccation, predation, and abrasion have on phoretic mite behavior, morphology and survival? Are there trophic interactions among phoretics while on the host? Are interactions between the beetle and its phoretic load passive and accidental, or do beetles actively attempt to remove the phoretics, especially if they are abundant enough to encumber its movements? Do phoretics transfer onto predators of the beetle?

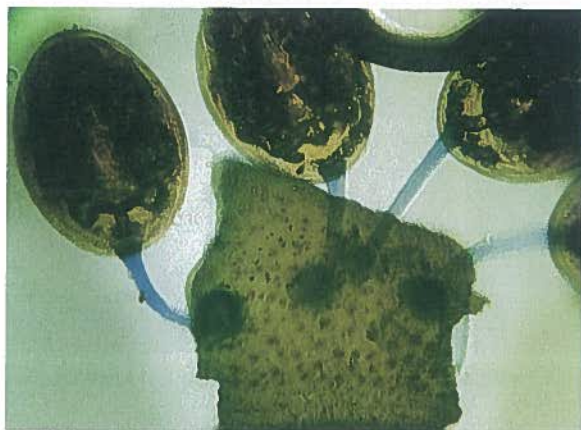


Fig. 7. Trichouropodid mites attached to the exoskeleton of *D. frontalis*. Note the anal glue stalks, termed pedicels (stained blue).

Mortality factors

Few observations are reported on predators and natural enemies of mites associated with bark beetles. Many mite species are subject to predation by small insects and predatory mites, or accidental feeding by large wood boring larvae. Mortality rates suffered during phoresy are undocumented but may be high. Mites appear to be susceptible to entomopathogenic fungi (Schabel 1982, Gerson *et al.* 2009). The greatest mortality is suffered by mites that remain within habitats after phoretic hosts have left.

CASE STUDIES OF MITE/FUNGI/BARK BEETLE RELATIONSHIPS

Mites associated with *Dendroctonus* bark beetles

Much of our general understanding of bark beetle mites comes from research on the community associated with the southern pine beetle, *Dendroctonus frontalis*. More than 96 species of mites live within *D. frontalis*-infested trees (Moser & Roton 1971), perhaps half phoretic on *D. frontalis* adults (Lindquist 1969, Moser & Roton 1971, Smiley & Moser 1974) (Figs 8–24). Trophic interactions among mites, fungi and *D. frontalis* were reviewed by Klepzig & Hoffstetter (2011) and are well documented elsewhere (Bridges & Moser 1983, 1986, Lombardero *et al.* 2000, 2003, Klepzig *et al.* 2001a,b, Hofstetter *et al.* 2006a,b). *Tarsonemus* mites significantly affect the abundance and interactions between mycangial and ophiostomatoid fungi associated with *D. frontalis* (Figs 4, 5). *Tarsonemus* species possess specialised, flap-like structures of the integument called C-flaps or sporothecae, which frequently contain *O. minus* and *Ceratocystiopsis ranaculosa* ascospores (Bridges & Moser 1983, Moser 1985, Moser *et al.* 1995). The presence of *O. minus* in phloem negatively affects *D. frontalis* larvae (Bridges 1983, Bridges & Perry 1985, Goldhammer *et al.* 1990, Lombardero *et al.* 2000) and variance in abundance of *Tarsonemus* appears to be a meaningful driver in *D. frontalis* population dynamics and *O. minus* abundance in infested trees (Lombardero *et al.* 2003, Hofstetter *et al.* 2006a, b).

Most mites associated with *D. frontalis* are in the Acariformes (Kinn 1971, Moser & Roton 1971). Whether this is a common pattern among all bark beetles systems is unknown. Table 1 shows the mites known to travel on adult *D. frontalis* in the southeastern

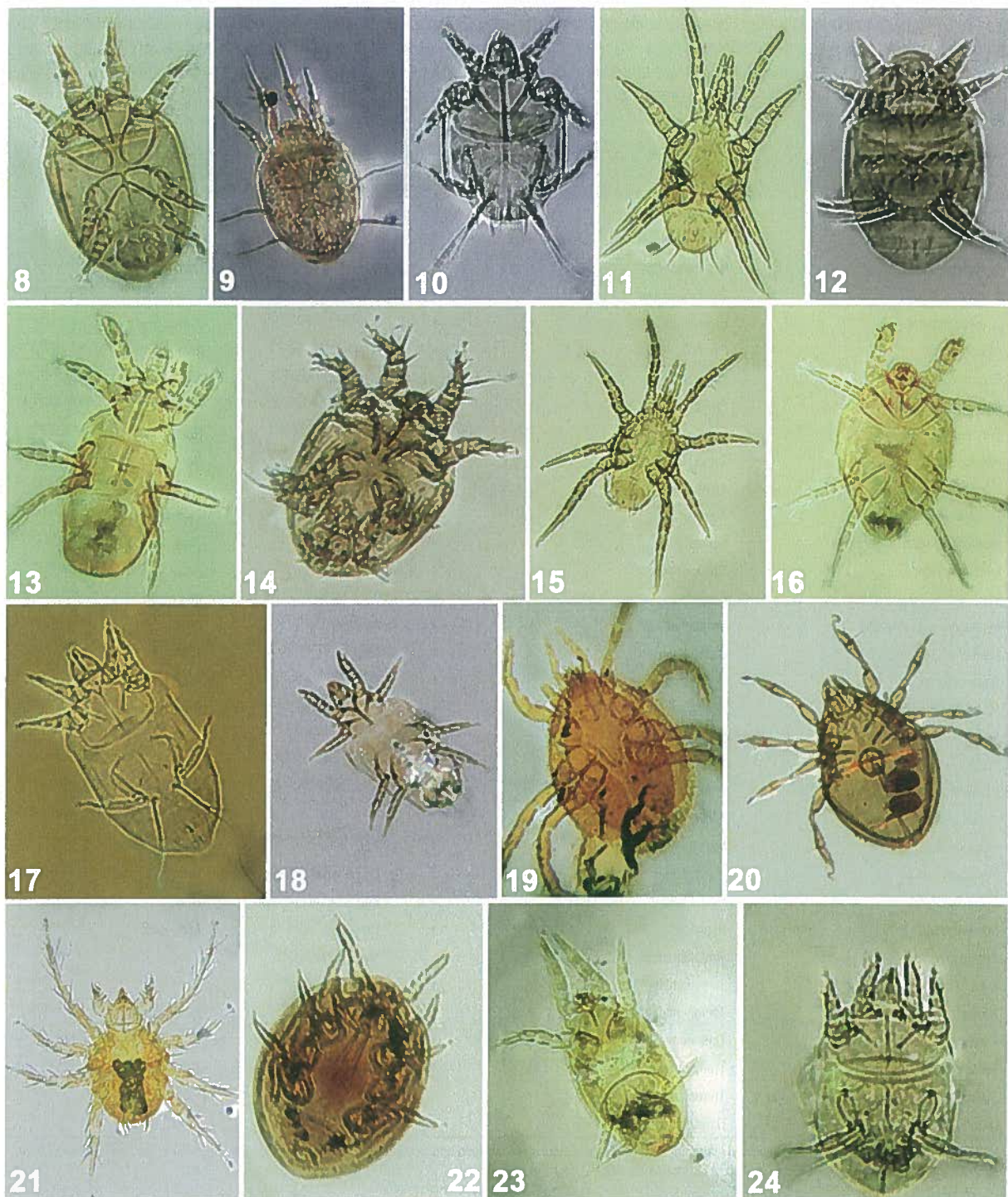
and southwestern United States. Many of the mite species are unique to either the eastern or western United States, but genera are often found in both geographic areas. Tarsonemid mites in the Trombidiformes are often numerous and include parasites of beetles' eggs (Lindquist 1986) and fungivores that often have intricate relationships with beetle-fungi (Moser 1985, Bridges & Moser 1986, Moser *et al.* 1989a, b). Mesostigmata, including many of the genera found in decaying fungi, are especially prominent as predators of nematodes and other mites, and as phoretics on adult *D. frontalis* (Kinn 1971, Moser & Roton 1971, Lindquist 1975, Lindquist & Wu 1991). Oribatid mites, which often associate with bees and wasps, are also common on bark beetles and may act as commensals, mutualists or predators (Kinn 1971). In addition to *D. frontalis*, several species of *Dendroctonus* co-occur in the forests of Arizona. Phoretic mite surveys show that mite species may be host species specific or found on multiple beetle hosts (Table 2). Several mite genera, other than *Tarsonemus*, that are associated with *Dendroctonus* may be partially or wholly mycetophagous; these include, *Elattoma*, *Heterotarsonemus*, *Histiogaster*, *Parawinterschmidia*, *Schwiebia*, and *Tyrophagous* (Moser & Roton 1971).

A study by Cardoza *et al.* (2008) found ten species of mites on *Dendroctonus rufipennis* collected in Alaska, including five genera, *Tarsonemus*, *Histiogaster*, *Dendrolaelaps*, *Proctolaelaps* and *Trichouropoda*, that are very similar to the mites found on *Dendroctonus* in the southern United States. *Histiogaster arborsignis* showed a strong feeding preference for the ophiostomatoid fungus *Leptographium abietinum* over other fungi such as species of *Aspergillus* and *Trichoderma*. The *Tarsonemus*, *Trichouropoda* and *Histiogaster* species were all observed to carry ophiostomatoid fungal spores.

Mites associated with *Ips* bark beetles

The spruce bark beetle, *Ips typographus*, is a significant vector of several pathogenic fungi of spruce and causes significant mortality to trees in Europe and Asia (Furniss *et al.* 1990, Solheim 1992, Moser *et al.* 1997). Ascospores or conidia of *Ceratocystis polonica*, *Ophiostoma bicolor*, *Grosmannia piceiperda*, *Pyxidiphora* sp., *Ceratocystiopsis minuta* and *G. europhioides*, all fungi associated with *I. typographus*, have been found on several mites species in Germany, Sweden, and Japan (Moser & Bogenschultz 1984, Levieux *et al.* 1989, Moser *et al.* 1989a, b, Moser *et al.* 1997). More than 85 % of individual mites associated with a population of *I. typographus* carry ophiostomatoid fungi (Moser *et al.* 1989a). The number of spores on individual mites varies from none to hundreds, but is usually less than thirty spores. Large mites, such as *Dendrolaelaps quadrisetus*, tend to have more spores than smaller species. In some cases, smaller mites such as *Histiostoma piceae* transport hundreds of ascospores. *Histiostoma piceae* lives in habitats with lush fungal growth, where spores are abundant. Even parasitoid mites found on *I. typographus*, such as *Iponemus gaebleri*, *Pyemotes dryas*, and *Paracarophenax ipidarius*, can carry moderate numbers of spores (Moser *et al.* 1989a).

Pine engravers (*Ips* spp.) carry one or more ophiostomatoid fungi. However, most *Ips* species are considered non-mycangial and have only casual associations with fungi (Harrington 2005). Mites are frequently found on *Ips* species (Lieutier 1978, Kinn & Roton 1989, Langor 1991, Stone & Simpson 1991, Michalaski *et al.* 1992, Kaczmarek & Michalaski 1995, Takov *et al.* 2009) and appear to be important vectors of many fungi (Malloch & Blackwell 1993).



Figs 8–24. Photomicrographs of common mites associated with bark beetles. 8. *Schwiebia* sp. 9. *Bonomia* sp. 10. *Iponemus truncatus*. 11. *Lasioseius safroi*. 12. *Heterotarsonemus* sp. 13. *Elattoma* sp. 14. *Histiogaster anops*. 15. *Dendrolaelaps quadrisetus*. 16. *Paracarophenax* sp. 17. *Tarsonemus ips*. 18. *Pyemotes* sp. 19. *Cerocoleius* sp. 20. *Paraleius* sp. 21. *Mexecheles virginiensis*. 22. *Uroobovella orti*. 23. *Parawinterschmidtia* sp. 24. *Tarsonemus krantzi*. (Elisabeth Alden, Richard Hofstetter, J. Khai Tran).

For example, mycetophagous specialists such as *Tarsonemus* spp., *Elattoma* spp., and *Histiogaster* spp., which commonly vector fungi associated with *Dendroctonus* beetles, are common on *Ips pini* (Table 3), *I. calligraphus*, and *I. grandicollis* (Moser & Roton 1971, Hodgkin *et al.* 2010), and *I. typographus* (Takov *et al.* 2009). *Ips avulsus*, a small pine engraver in the eastern United States (Wood 1982), has a mutualistic relationship with an *Entomocorticium* sp., although no mycangium has been found (Yearian 1966, Gouger

1971, Yearian *et al.* 1972). The blue-stain fungus *O. ips* is commonly associated with *I. avulsus*, but competes with *Entomocorticium* sp., and negatively affects larval development (Klepzig *et al.* 2001a). The mite *Elattoma bennetti* feeds on the *Entomocorticium* sp. that grows in the galleries and is phoretic on *I. avulsus*. The degree to which *E. bennetti* affects the beetle-fungus relationship is unclear, although it is possible that the mite is a primary vector of the fungus (Klepzig *et al.* 2001a).

Table 1. The distribution and feeding behavior of mite species phoretic on *Dendroctonus frontalis* (SPB) in the USA. Generalist = feeds on multiple fungi, nematodes, and dead invertebrates. Mycetophagous = feeds on specific fungi, often transports and disperses reproductive structures of fungi. We categorise phoretic mites abundance on beetles as rare (< 1 % of beetles have this species), infrequent (1–5 %), common (5–20 %), and frequent (> 20 %). Mites identified by JC Moser and stored as voucher specimens by RW Hofstetter at Northern Arizona University.

Phoretic mite species	Mite Family	Occurrence on SPB		Feeding guild	Relative abundance
		SE USA ¹	SW USA ²		
<i>Dendrolaelaps (Longoseius) cuniculus</i>	Digamasellidae ^p	+	+	?	Infrequent
<i>D. neocornutus</i>	Digamasellidae ^p	+		?	Infrequent
<i>D. neodisetus</i>	Digamasellidae ^p	+	+	Nematode predator	Common
<i>D. quadrisetus</i>	Digamasellidae ^p		+	Nematode predator	Infrequent
<i>D. varipunctatus</i>	Digamasellidae ^p	+	+	?	Rare
<i>Elattoma</i> spp.	Pyemotidae ^a	+	+	Mycetophagous ³	Infrequent
<i>E. bennetti</i>	Pyemotidae ^a	+		Mycetophagous ³	Common
<i>Ereynetes scutulalis</i>	Ereynetidae ^a	+	+	?	Rare
<i>Ereynetes</i> spp.	Ereynetidae ^a	+	+	?	Rare
<i>Heterotarsonemus lindquisti</i>	Tarsonemidae ^a	+	+	Mycetophagous	Rare
<i>Histiogaster anops</i>	Acaridae ^a		+	Omnivore ⁴	Common
<i>H. arborsignis</i>	Acaridae ^a	+		Egg & larval predator	Common
<i>Histiostoma varia</i>	Histiostomatidae ^a	+	+	Filter feeder	Common
<i>Iponemus truncatus</i>	Tarsonemidae ^a	+	+	Egg parasitoid	Rare
<i>Licnocephus reticulatus</i>	Eremellidae ^a		+	?	Infrequent
<i>Macrocheles boudreauxi</i>	Macrochelidae ^p	+	+	Predator	Rare
<i>Mexcheles virginiensis</i>	Cheyletidae ^a	+	+	Predator	Rare
<i>Nanacar</i> sp.	Hemisarcoptidae ^a		+	?	Rare
<i>Peracarophenax</i> sp.	Acarophenacidae ^a		+	Egg parasitoid	Rare
<i>Paraleius leontonychus</i>	Oribatulidae ^a	+		?	Rare
<i>Paraleius</i> sp.	Oribatulidae ^a		+	?	Rare
<i>Parawinterschmidtia fumissi</i>	Winterschmidtiidae ^a		+	?	Infrequent
<i>Proctogastrolaelaps libris</i>	Ascidae ^p	+		?	Rare
<i>Proctolaelaps hystrix</i>	Melicharidae ^p	+	+	?	Rare
<i>Pyemotes parviscolyti</i>	Pyemotidae ^a	+		Egg & larval predator	Rare
<i>Pyemotes</i> n. sp.	Pyemotidae ^a		+	Egg & larval predator	Rare
<i>Schwiebia</i> sp.	Acaridae ^a		+	Omnivore	Infrequent
<i>Tarsonemus fuseri</i>	Tarsonemidae ^a	+		Mycetophagous ⁴	Rare
<i>T. ips</i>	Tarsonemidae ^a	+	+	Mycetophagous ⁴	Common
<i>T. krantzi</i>	Tarsonemidae ^a	+	+	Mycetophagous ⁴	Frequent
<i>T. subcorticalis</i>	Tarsonemidae ^a	+	+	Mycetophagous	Rare
<i>Trichouropoda australis</i>	Trematuridae ^p	+	+	Omnivore	Common
<i>T. hirsuta</i>	Trematuridae ^p	+	+	?	Common
<i>Uroobovella orri</i>	Dinychidae ^p	+	+	?	Infrequent

¹ SPB populations in Louisiana, Mississippi, and Alabama, USA; ² SPB populations in Coronado and Coconino N.F., Arizona, USA; ³ Mite believed to feed on *Entomocorticium* sp.; ⁴ Mite is believed to feed on *Ophiostoma* sp.; ^a Order Acariformes; ^p Order Parasitiformes

Mites associated with *Dryocoetes* bark beetles

Although *Dryocoetes* spp. are important agents of mortality in conifers, little is known about their biology and or associated mite community. Table 4 lists the species of phoretic mites collected from *D. confusus* near Flagstaff, Arizona in 2005 and 2006. The most common phoretic mites were *Dendrolaelaps quadrisetus*, which is probably a nematode predator, the omnivore *Histiostoma varia*, and *Uroobovella orri*, whose feeding behavior remains unknown. Other mycetophagous mites present include species of *Elattoma*,

Heterotarsonemus, *Histiogaster*, *Schwiebia*, and *Tarsonemus*, which may influence beetle-ophiostomatoid fungal interactions.

Mites associated with *Scolytus* bark beetles

A great deal of attention has been devoted to mites associated with the *Scolytus* bark beetles that transmit Dutch Elm Disease (DED) (Smiley & Moser 1974, Brasier 1978, Doberski 1980, Hajek & Dahlsten 1985, Moser *et al.* 2005). Many *Scolytus* species infest elm (Pfeffer 1985), but the most economically important are *S.*

Table 2. Survey of phoretic mites on *Dendroctonus* species collected from pheromone baited flight traps in Coconino National Forest and Coronado National Forest in Arizona, USA in summer 2006. Mites of *D. frontalis* are listed in Table 1. Mites identified by JC Moser and stored as voucher specimens by RW Hofstetter at Northern Arizona University. (N = number of individual beetles surveyed).

Mite species	Mite Family	<i>D. approximatus</i> (N = 45)	<i>D. brevicornis</i> (N = 336)	<i>D. valens</i> (N = 82)	<i>D. mexicanus</i> (N = 200)	<i>D. adjunctus</i> (N = 19)
<i>Bonomia</i> sp.	Histiostomatidae ^A	+	+	+		
<i>Dendrolaelaps (Longoseius) cuniculus</i>	Digamasellidae ^P	+				
<i>D. neodisetus</i>	Digamasellidae ^P		+	+		
<i>D. quadrisetus</i>	Digamasellidae ^P			+		+
<i>D. terebrans</i>	Digamasellidae ^P			+		
<i>D. sp.</i>	Digamasellidae ^P		+		+	+
<i>Elattoma</i> sp.	Pyemotidae ^A		+	+		
<i>Heterotarsonemus</i> sp.	Tarsonemidae ^A				+	
<i>Histiostoma</i> sp.	Histiostomatidae ^A	+		+	+	
<i>Histiostoma media</i>	Histiostomatidae ^A		+	+		
<i>Histiogaster anops</i>	Acaridae ^A		+	+		
<i>H. arborsignus</i>	Acaridae ^A			+		
<i>H. rotundus</i>	Acaridae ^A		+			
<i>Iponemus truncatus</i>	Tarsonemidae ^A	+				
<i>Mexcheles virginatus</i>	Cheyletidae ^P	+	+		+	
<i>Nentaria</i> sp.	Trematuridae ^P			+		
<i>Paracarophenax</i> sp.	Acrophenacidae ^A		+			
<i>Parawinterschmidtia furnissi</i>	Winterschmidtiidae ^A		+	+	+	+
<i>P. michiganeosis</i>	Winterschmidtiidae ^A			+		
<i>Proctolaelaps</i> sp.	Melicharidae ^P			+		
<i>P. fiseri</i>	Melicharidae ^P			+		
<i>P. hystrix</i>	Melicharidae ^P			+	+	
<i>P. subcorticalis</i>	Melicharidae ^P		+		+	
<i>Pyemotes</i> n. sp.	Pyemotidae ^A	+				
<i>Saproglyphus</i> sp.	Winterschmidtiidae ^P	+				
<i>Schizostethus lyriformis</i>	Parasitidae ^P			+		
<i>Schwiebia</i> sp.	Acaridae ^A			+	+	
<i>Tarsonemus ips</i>	Tarsonemidae ^A		+		+	+
<i>T. krantzi</i>	Tarsonemidae ^A	+	+		+	+
<i>T. terebrans</i>	Tarsonemidae ^A	+		+		
<i>T. subcorticalis</i>	Tarsonemidae ^A	+				
<i>Trichouropoda</i> sp.	Trematuridae ^P			+	+	
<i>T. australis</i>	Trematuridae ^P		+			
<i>T. hirsuta</i>	Trematuridae ^P	+	+	+		
<i>T. fallax</i>	Trematuridae ^P					+
<i>Uroobovella neoamericana</i>	Dinychidae ^P			+		
<i>U. orri</i>	Dinychidae ^P		+	+		

^A = Order Acariformes and ^P = Order Parasitiformes.

multistriatus and *S. scolytus*, known vectors of the DED fungus *O. novo-ulmi*. The *Scolytus* beetles initially infest healthy trees with *O. novo-ulmi* during maturation feeding on the bark of twigs and in twig crotches within the canopy (Lanier & Peacock 1981, Webber & Brasier 1984). Interestingly, larvae of *Scolytus* spp. may not develop in the presence of *O. novo-ulmi* if the fungus and larvae contact each other (Webber & Gibbs 1989), whereas this fungus may be an essential food for several mite species (Moser *et al.* 2005). Four mites, *Elattoma fraxini*, *Proctolaelaps scolyti*,

Pseudotarsonemoides eccoptogasteri, and *Tarsonemus crassus* carry *O. novo-ulmi* spores externally on their body (Moser *et al.* 2010). However, *T. crassus* and *P. scolyti* (Fig. 2) are the most efficient carriers of *O. novo-ulmi* spores. *Tarsonemus crassus* transports spores in their sporothecae, whereas individuals of *P. scolyti* carry spores on their cuticular surface or in their guts. Once ingested, however, it is uncertain if the spores remain viable. Only *S. scolytus*, which is the most efficient vector of *O. novo-ulmi* in Europe (Webber 1990), carried a high number of the mites *T.*

Table 3. The abundance and feeding behavior of phoretic mites collected from *Ips pini* during summer 2005 in the Coconino National Forest, Arizona, USA. Generalist = feeds on multiple fungi, nematodes, and dead invertebrates. Mycetophagous = feeds on fungi, often transports and disperses reproductive structures of fungi. We categorize phoretic mites abundance on beetles as rare (< 1 % of beetles have this species), infrequent (1–5 %), common (5–20 %), and frequent (> 20 %). Mites identified by JC Moser and stored as voucher specimens by RW Hofstetter at Northern Arizona University.

Phoretic mite species	Mite Family	Feeding guild	Relative abundance
<i>Bonomia</i> sp.	Histiostomatidae ^A	?	Rare
<i>Brevipalpus</i> sp. nr. <i>pini</i>	Tenuipalpidae ^A	Phytophagous	Rare
<i>Dendrolaelaps neodisetus</i>	Digamasellidae ^P	Nematode predator	Infrequent
<i>D. quadrisetus</i>	Digamasellidae ^P	Nematode predator	Common
<i>Elatoma</i> sp.	Pyemotidae ^A	Mycetophagous	Frequent
<i>Heterotarsonemus lindquisti</i>	Tarsonemidae ^A	Mycetophagous	Rare
<i>Histiogaster anops</i>	Acaridae ^A	Omnivore	Common
<i>Histiostoma varia</i>	Histiostomatidae ^A	Filter feeder	Common
<i>Iponemus truncatus</i>	Tarsonemidae ^A	Egg parasitoid	Frequent
<i>Mexechesles virginensis</i>	Cheyletidae ^P	Predator	Rare
<i>Paracarophenax</i> sp.	Acrophenacidae ^A	Egg parasitoid	Rare
<i>Parawinterschmidtia</i> sp.	Winterschmidtiidae ^A	?	Infrequent
<i>Proctolaelaps hystrix</i>	Melicharidae ^P	?	Infrequent
<i>Proctolaelaps subcorticalis</i>	Melicharidae ^P	?	Rare
<i>Schwiebia</i> sp.	Acaridae ^A	Omnivore	Infrequent
<i>Tarsonemus ips</i>	Tarsonemidae ^A	Mycetophagous	Frequent
<i>Trichouropoda australis</i>	Trematuridae ^P	Omnivore	Common
<i>T. hirsuta</i>	Trematuridae ^P	?	Common
<i>Uroobovella orri</i>	Dinychidae ^P	?	Infrequent
<i>Vulgarogamasus lyriformis</i>	Parasitidae ^P	Predator	Rare

^A = Order Acariformes and ^P = Order Parasitiformes.

Table 4. Mites associated with *Dryocoetes confusus* near Flagstaff, Arizona, USA. Mites removed from adult beetles (N = 144) collected in baited flight traps during July 2005 and 2006. We categorize phoretic mite abundance on beetles as rare (< 1 % of beetles have this species), infrequent (1–5 %), common (6–20 %), and frequent (> 20 %). Mites identified by JC Moser and stored as voucher specimens by RW Hofstetter at Northern Arizona University.

Phoretic mite species	Mite Family	Relative abundance
<i>Dendrolaelaps quadrisetus</i>	Digamasellidae ^P	Common
<i>Dendrolaelaps</i> sp.	Digamasellidae ^P	Infrequent
<i>Diseius</i> sp.	Ascidae ^P	Rare
<i>Elatoma</i> sp.	Pyemotidae ^A	Rare
<i>Heterotarsonemus lindquisti</i>	Tarsonemidae ^A	Rare
<i>Histiogaster</i> sp.	Acaridae ^A	Infrequent
<i>Histiostoma varia</i>	Histiostomatidae ^A	Common
<i>Lasioseius saftoi</i>	Ascidae ^P	Frequent
<i>Mexechesles virginensis</i>	Cheyletidae	Rare
<i>Paracarophenax</i> sp.	Pyemotidae ^A	Infrequent
<i>Paraleius leontonychus</i>	Oribatulidae ^A	Infrequent
<i>Parawinterschmidtia</i> sp.	Winterschmidtiidae ^A	Infrequent
<i>Proctolaelaps</i> sp.	Melicharidae ^P	Rare
<i>Saproglyphus</i> sp.	Winterschmidtiidae ^A	Rare
<i>Schwiebia</i> sp.	Acaridae ^A	Frequent
<i>Schizostethus lyriformis</i>	Parasitidae ^P	Infrequent
<i>Tarsonemus subcorticalis</i>	Tarsonemidae ^A	Infrequent
<i>Trichouropoda lamellosa</i>	Trematuridae ^P	Infrequent
<i>Trichouropoda</i> sp.	Trematuridae ^P	Infrequent
<i>Uroobovella orri</i>	Urodinychidae ^P	Common

^A = Order Acariformes and ^P = Order Parasitiformes.

Table 5. Phoretic mites of predators and competitors of bark beetles collected in baited flight traps. Predators and competitors of bark beetles were collected during summer 2005 in Coconino National Forest, Arizona. Mites identified by JC Moser stored as voucher specimens by RW Hofstetter at Northern Arizona University.

Mite species	Mite Family	<i>Enoclerus sphegus</i> (N = 176)	<i>Temnochilla chloridia</i> (N = 201)	<i>Platysoma</i> sp. (N = 35)	<i>Cortecius</i> sp. (N = 23)	<i>Elacatis</i> sp. (N = 25)	Cerambycidae & Buprestidae (N = 16)
<i>Anoetidae</i> sp.	Histiostomatidae ^A	+					
<i>Bonomia</i> sp.	Histiostomatidae ^A	+	+	+		+	
<i>Dendrolaelaps cuniculus</i>	Digamasellidae ^P		+				+
<i>D. neodisetus</i>	Digamasellidae ^P	+	+	+	+		+
<i>D. varipunctatus</i>	Digamasellidae ^P			+			
<i>D.</i> sp.	Digamasellidae ^P			+			
<i>Eiattoma</i> sp.	Pyemotidae ^A	+	+		+		
<i>Gamasina</i> sp. ^P			+				
<i>Heterotarsonemus lindquisti</i>	Tarsonemidae ^A				+		+
<i>Histiostoma</i> sp.	Histiostomatidae ^A	+	+	+			
<i>H. media</i>	Histiostomatidae ^A			+	+		
<i>H. varia</i>	Histiostomatidae ^A			+	+		
<i>H. sordida</i>	Histiostomatidae ^A		+	+			
<i>Histiogaster anops</i>	Acaridae ^A	+					
<i>H. arborsignis</i>	Acaridae ^A	+	+				+
<i>H.</i> sp.	Acaridae ^A			+			
<i>Nanacar</i> sp.	Hemisarcoptidae ^A	+	+				
<i>Pachylaelapidae</i> sp.	Pachylaelapidae ^P		+				
<i>Parawinterschmidtia</i> sp.	Winterschmidtidae ^A	+	+			+	+
<i>Proctolaelaps dendroctoni</i>	Melicharidae ^P				+		
<i>P. fiseri</i>	Melicharidae ^P		+				
<i>P. hystrix</i>	Melicharidae ^P	+					
<i>P. subcorticalis</i>	Melicharidae ^P		+		+		
<i>Pyemotes</i> sp.	Pyemotidae ^A				+		
<i>Saproglyphus</i> sp.	Winterschmidtidae ^A	+	+			+	+
<i>Schwiebia</i> sp.	Acaridae ^A	+	+	+			+
<i>Schizostethus lyriformis</i>	Parasitidae ^P				+		
<i>Tarsonemus ips</i>	Tarsonemidae ^A	+					+
<i>T. krantzi</i>	Tarsonemidae ^A		+				
<i>Trichouropoda</i> sp.	Trematuridae ^P		+		+		+
<i>T. denticulata</i>	Trematuridae ^P						+
<i>T. hirsuta</i>	Trematuridae ^P		+				+
<i>T. lamellosa</i>	Trematuridae ^P						+
<i>Uroobovella neoamericana</i>	Dinychidae ^P		+				
<i>U. orri</i>	Dinychidae ^P		+	+	+		+

^A = Order Acariformes and ^P = Order Parasitiformes.

crassus and *P. scolyti* (Moser *et al.* 2010). The high efficiency of *S. scolytus* in spreading DED may be a result of its association with these mites.

Mites on the predators and competitors of bark beetles

Predators and competitors of bark beetles are potential phoretic hosts for many mite species within beetle-infested trees and ophiostomatoid habitats (Table 5). Predators and competitors

are often large, mobile, and excellent fliers, and thus make good phoretic hosts. Predators may provide a way for mite species to switch habitats, even between coniferous- and hardwood-beetle communities. Mycetophagous mites on predators and competitors probably feed on late-successional fungi. Surveys of predators of bark beetles in the southern United States reveal that the most frequent phoretic mites are in the genera *Histiostoma*, *Parawinterschmidtia*, *Dendrolaelaps*, *Trichouropoda* and *Saproglyphus*, most of which are believed to be omnivores or predators.

The mycetophagous habits of mites associated with large wood boring beetles (i.e. Cerambycidae, Buprestidae) remain largely unknown. Wood borers create extensive habitat within trees and are phoretic hosts for many mite species. Mite populations can be extremely high on wood borers, for example, 1816 *Dendrolaelaps fukikoe* individuals were found on a single sawyer beetle (Enda & Tamura 1980). Most mite associates are not monospecific and may be common on other non-bark beetle hosts (e.g., Tenebrionidae, Cleridae, Histeridae, Elateridae) (Kinn 1983).

CONCLUSIONS

Tiny organisms such as mites, which are often hidden or considered irrelevant, interact in a more complex and significant way than previously acknowledged. Studies of beetle communities reveal that mites, bark beetles and associated fungi represent networks of species interactions that can influence ophiostomatoid abundance, characteristics, and evolution (Lombardero *et al.* 2000, Hofstetter *et al.* 2006a, Roets *et al.* 2009, 2013). Nonlinear relationships between linked species (e.g. threshold effects of *Ophiostoma minus* on beetles; Hofstetter *et al.* 2006a), imbedded feedback structures (e.g., mite-*O. minus* mutualism) and dependencies (e.g., mites phoretic on beetles) within the community, contribute to the dynamics of beetle and fungal populations. Understanding the dynamics of tree-killing bark beetles (e.g., *Ips typographus*, *Dendroctonus frontalis*, *Scolytus multistriatus*) and fungi, and the mechanisms that lead to their fluctuations has an applied economic value. Such knowledge could lead to effective new ways to control these pernicious pests.

Many mites species phoretic on bark beetles involve complex symbiotic interactions with ophiostomatoid fungi belonging to *Ceratocystis*, *Ceratocystiopsis*, *Ophiostoma*, *Leptographium*, *Grosmannia* and related genera (Kirisits 2004, Cardoza *et al.* 2008, Moser *et al.* 2010) and their host trees and beetles (Klepzig *et al.* 2001b, Hofstetter *et al.* 2006a). The occurrence of hyperphoretic fungal spores, both conidia and ascospores, on phoretic mites suggests that they can transport fungi, many of which are ophiostomatoid fungi, to their host trees (Moser 1985, Moser *et al.* 1989b, 1995) and tree pathogens (Moser *et al.* 2010). Several mite species such as *Tarsonemus* species possess specialised structures called sporothecae that improve spore transport (Moser 1985, Bridges & Moser 1986) and epitomise the tight association between some mite and fungal species.

Earlier concepts of the regulation of bark beetle populations focused primarily on trophic interactions or climate. Although these factors play an important role in beetle demographics and population growth, it is unlikely that any one factor is responsible for the dynamics exhibited by beetle and fungal populations. A more comprehensive approach that recognises the multiplicity of environmental factors, interacting organisms, and interdependencies among all species in the community will better explain patterns in species populations. Focusing solely on one species, such as the bark beetle, may hinder our understanding of complex communities and population dynamics, since "nature may not feel herself limited by our lack of imagination" (Wolda & Dennis 1993).

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