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Mutualists and Phoronts of the Southern Pine Beetle

Richard W. Hofstetter

Assistant Professor, School of Forestry, Northern Arizona University,
Flagstaff, AZ 86011

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Abstract

The large numbers of invertebrates and microbes that exist only within dying and decayed pines killed by the southern pine beetle (SPB) make this system ideal for the study of species interactions, including mutualism and phorecy. The associated organisms comprise an entire functioning community that includes fungivores, herbivores, detritovores, scavengers, parasitoids, and predators. Because the SPB causes physical state changes in biotic materials and creates a stable supply of resources for an extensive assemblage of species, it can be considered a keystone species, ecosystem engineer, or foundation species. Within the SPB community, species interactions range from mutualistic to commensalistic to antagonistic, depending on the species composition, environmental conditions, and quality of available resources. These species often use SPB adults to access and disperse among trees and can affect the population dynamics, behavior, and evolution of the SPB. In addition, interactions among the community can impact bark beetle-fungal associations and thus, beetle fitness. In this chapter, I provide an overview of the known associations with the SPB, both mutualistic and phoretic, and discuss how these associations impact the SPB and the evolution and ecology within this community.

11.1. INTRODUCTION

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) can be considered a keystone species (Holling 1992), ecosystem engineer (Jones and others 1994), or foundation species (Dayton 1972) in that it causes physical state changes in biotic materials and creates a stable supply of resources for an extensive assemblage of species. Large numbers of invertebrates exist only within dying and decayed pines killed by the SPB, such as nematodes (as high as 90 percent of beetles infested; Atkinson and Wilkinson 1979), bacteria (> 21 species; Vasanthakumar and others 2006), fungi (Whitney 1982), and mites (> 96 species; Moser and Roton 1971). This collection of organisms comprises an entire functioning community that includes fungivores, herbivores, detritivores, scavengers, parasitoids, and predators.

11.1.1. Mutualistic Associations

Among these SPB associates, there are several species that benefit the beetle and receive benefits in return. The benefit of this reciprocal gain to both species, termed mutualism, can be of one or more types, namely, energetic, nutritional, protective, and transport (Morin 1999), and associations have the potential to be obligate or facultative, tight or diffuse, and direct or indirect (Addicott 1995, Morin 1999). In many cases, these associations may be facilitative interactions (i.e., commensalism) in that one of the participants benefits but neither is harmed. The impact and comprehensiveness of positive interactions on the evolution, behavior, and ecology of the SPB is difficult to assess given all the possible combinations of species, interaction types and strengths, and outcomes of trophic organizations within the SPB community. However, some of the best known and best understood positive interactions among the SPB community are described in this chapter. For instance, some benefits to the SPB include the production or enhancement of aggregating pheromones (Brand and others 1976, 1977), alteration and improvement of phloem by altering plant defenses (Paine and others 1997), direct nutritional services (Goldammer and others 1990), and enhanced defense in the form of protection from disease, predators, and parasites.

11.1.2. Phoretic Associations

Dispersal and migration pose major challenges for many organisms living in a discontinuous, ephemeral habitat such as that of SPB-infested

trees. These microorganisms are wind-dispersed, travel under their own power, or attach to another organism for dispersal to trees. Those species that attach to other organisms, called phoronts, are highly adapted for phorecy and often have highly modified phoretic stages, morphs, appendages, or parts. Phoronts often go through behavioral changes 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 and Morand 1993).

Phorecy could be considered an exploitation of the carrier and therefore, parasitic. However, species interactions should be defined in terms of their ultimate effects on the fitness of the participants if they are to make ecological and evolutionary sense (Walter and Proctor 1999). Under most conditions, phoretic organisms can be classified as commensal or facilitative, in that they do not harm the carrier but the phoront benefits (Houck 1994). However, when phoronts are abundant they may interfere with carrier movement, reduce travel distances, and be energetically costly (Kinn 1971, Kinn and Witcosky 1978). Alternatively, phoronts may provide direct or indirect benefits to their carrier. Thus, phoretic relationships may be mutually beneficial to the phoront and the phoretic host, neutral (e.g., commensal – benefiting the phoront), or antagonistic, resulting in a loss of fitness to the carrier.

11.2. ASSOCIATED TAXA

Standing deadwood and trees attacked by SPB are home to a large variety of microorganisms that invade beetle-infested trees by associating with SPB or other colonizing arthropods. Many of these microorganisms, such as bacteria and nematodes that travel on the body of SPB, are covered in other chapters of this book and will only be briefly discussed here. This chapter will primarily focus on the robust diversity of fungi and mites phoretic on SPB that live around and within SPB galleries.

11.2.1. Nematodes

Nematodes are common associates of the SPB (Atkinson and Wilkinson 1979, Joye and Perry 1976, Massey 1974) and interact as parasites (antagonists), commensals, and mutualists of SPB adults, larvae, or eggs. Most nematodes are endoparasitic and travel between trees within adult beetle bodies. However, several

species are ectoparasitic and form cocoon-like structures usually under the elytra of beetles (Figure 11.1). Several nematode species may prey upon parasitic nematodes of beetles and thus have a mutualistic relationship with the SPB. However, we know very little about these species. Nematodes may be important factors regulating populations of the SPB (Moore 1971, Sikorowski and others 1979) and have been reported to reduce fertility and fecundity of SPB (Kinn 1980). Studies by MacGuidwin (1979) showed that SPB females infected with the endoparasitic nematode *Contortylenchus brevicomi* (Massey) Ruhm produced fewer eggs and constructed shorter galleries than healthy females during the 3-week period after attack. Parasitism of either male or female SPB by *C. brevicomi* did not affect survival of progeny, even though the number of eggs was reduced.

11.2.2. Fungi and Bacteria

There are several fungi that are obligate mutualists with the SPB. Female SPBs possess a prothoracic mycangia that consists of paired

female maintains a pure culture of either *Ceratocystiopsis ranaculosus* Bridges & Perry (Barras and Taylor 1973) or *Entomocorticium* sp. A Hsiao & Harrington (Barras and Perry 1972, Happ and others 1976, Hsiao 1996) (Figure 11.2). Each female carries either one of the two fungi or no fungi in each of the mycangial pouches (Bridges 1985). The relative abundance of each mycangial fungus within SPB populations varies with geographic location and time of year (Harrington 2005, Hofstetter and others 2006b). Interestingly, 5-20 percent of females within a population carry both mycangial fungi, one within each mycangial pouch. As the female oviposits within the tree, she may inoculate the area immediately surrounding the eggs with the contents of her mycangium. Early instar larvae feed within short galleries that quickly enlarge into ovate feeding chambers (Payne 1983), within which can be found abundant growth of either of the two mycangial fungi. The larvae likely then feed on fungal hyphae and reproductive structures, receiving the

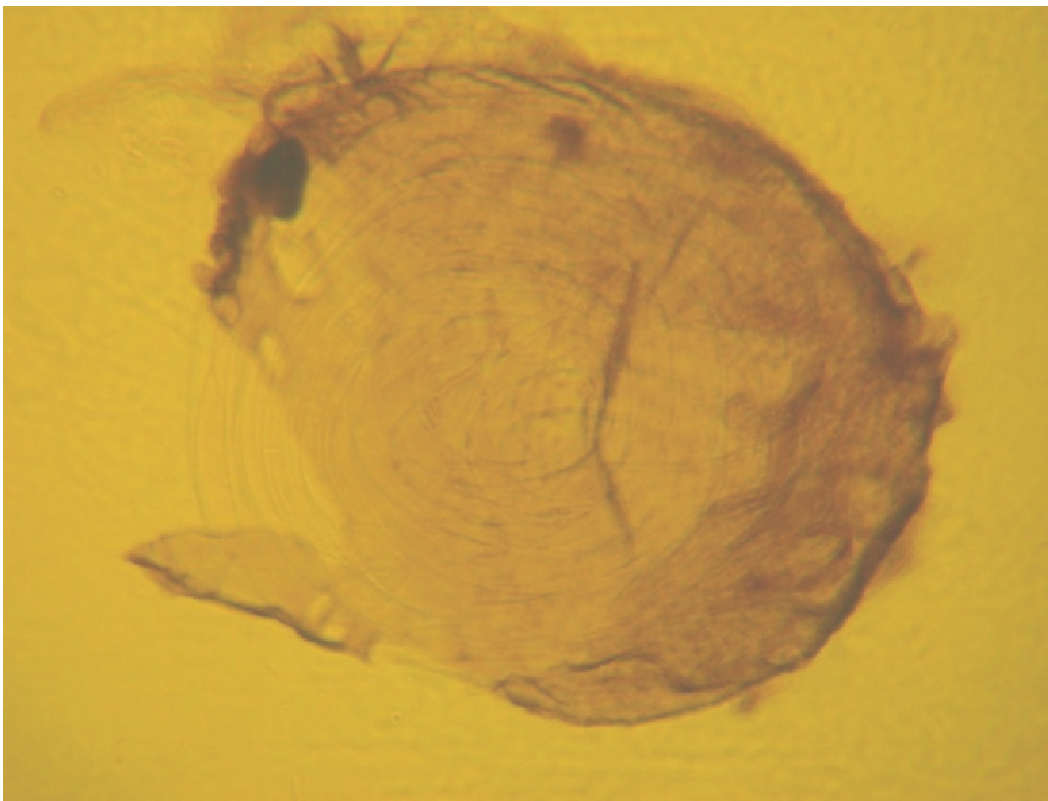
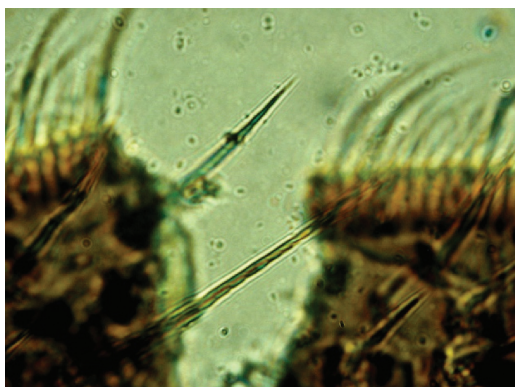
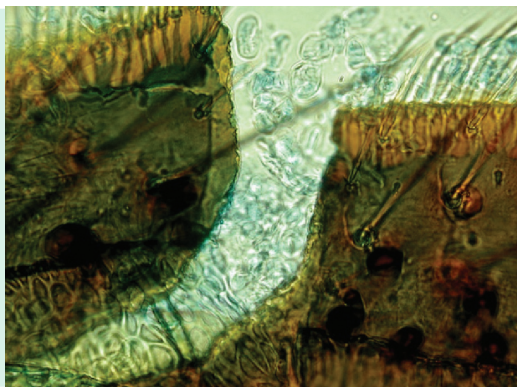


Figure 11.1—Cocoon-like structure (< 1 mm in diameter) created by phoretic nematode. Structure was removed from under the elytra of an SPB caught in a flight trap. Note that the nematode is still within structure. (photograph by R.W. Hofstetter)

invaginations of the exoskeleton, each of which has one pore-like ventral opening and contains two types of secretory cells (Barras and Perry 1972, Happ and others 1971). Within each side of the mycangium, each individual

majority of their nutrition (especially nitrogen and lipids) from the fungi and substantially benefit from the presence of these fungi (Ayres and others 2000, Bridges 1985, Coppedge and others 1995, Goldhammer and others 1990).

Figure 11.2—Close-up of stained mycangial fungi coming out of the mycangia of a female adult SPB. Left: *Entomocorticium* sp. A; Right: *Ceratocystiopsis ranaculosus*. Note that *C. ranaculosus* cells are much smaller than *Entomocorticium* sp. A. (images taken by R.W. Hofstetter)



Bridges and Perry (1985) found that in the laboratory, SPBs without mycangial fungi produce much shorter galleries and fewer progeny than beetles with mycangial fungi. The same pattern continued through a second generation, suggesting that populations of SPB without mycangial fungi cannot survive for long. Brand and others (1975, 1976) isolated a mycangial fungal culture that was able to convert α -pinene to *cis*- and *trans*-verbenol, and *trans*-verbenol to verbenone. Verbenone is believed to terminate beetle attack (Brand and others 1976) and thus reduce intraspecific competition among beetles (Byers 1989a). The mycangial fungi receive protected, selective transport to the next available resource (Happ and others 1971). The symbiosis between these organisms is clearly mutualistic (Klepzig and others 2001a, 2001b).

Spores of *Ophiostoma* species (*O. minus* Hedge and *O. nigrocarpum* (Davidson) De Hoog (Harrington 2005)) are commonly found on the exoskeleton of SPB (Bridges and Moser 1983, Rumbold 1931), associated insects (Hofstetter 2004), and on phoretic mites (Moser 1985). *Ophiostoma minus* is the most abundant non-mycangial fungal associate, but its abundance varies greatly among beetle populations and across regions (Harrington 2005; Hofstetter and others 2006a, 2006b). *Ophiostoma minus* is an ascomycetous fungus which causes “blue stain” within infected wood. While this fungus may aid the SPB in killing trees (Mathre 1964, Nelson 1934, however see Klepzig and others 2005), it is not required for tree death to occur (Bridges 1985, Bridges and Perry 1985, Bridges and others 1985, Hetrick 1949). Colonization by *O. minus* may, however, cause tree death to occur more quickly or at least differently than it would in the absence of the fungus (Paine and others 1997). Because of this and because the fungus benefits by receiving transport to new host tissue (Dowding 1969), the SPB-*O. minus*

relationship at the early stages of attack may be defined as a mutualistic association. However, as beetle eggs hatch, the introduced fungi grow and colonize the phloem. When colonization by *O. minus* overlaps areas of larval feeding, reduced developmental success—inhibited egg production, slower larval growth and development, and increased mortality—may occur (Barras 1970, Franklin 1970a), and higher levels of *O. minus* thus correlate with lowered SPB reproductive success (Hofstetter and others 2006a, Lombardero and others 2000c). This antagonism between *O. minus* and SPB larvae is due to interference by the fungus with interactions between the beetle and its two mutualistic mycangial fungi (Klepzig and others 2001a, 2001b).

Most bacteria associated with the SPB are found within the guts and alimentary canal of adults and larvae (Moore 1972, Vasanthakumar and others 2006), and within the mycangia of adult females (observations by R.W. Hofstetter; Scott and others 2008). In addition, a suite of bacteria is likely passively picked up on the exoskeleton of beetles and transferred into new host trees. Bacteria and yeasts associated with other bark beetles (e.g., *D. rufipennis* Kirby) are known to inhibit the growth of antagonistic fungi (Cardoza and others 2006) and may influence interactions among beetles and mycangial fungi (Scott and others 2008). Scott and others (2008) identified actinomycete bacteria from the mycangia and the galleries in the presence of mycangia fungus *Entomocorticium* sp. A. Interestingly, the bacteria produces an antibiotic that selectively suppresses the antagonistic fungus, *O. minus*. This indicates that the SPB engages in additional mutualisms with bacteria to regulate fungus-fungus interactions. The functions that most bacteria play in SPB development, host exploitation, reproduction, and interactions with associated organisms remain largely unknown.

11.2.3. Mites

Mites (Chelicerata: Acariformes) are commonly associated with bark beetles (Kinn 1971, Moser and Roton 1971). Approximately 111 species of mites are phoretic on SPB or found within trees killed by the SPB (Figure 11.3). Although mites are often believed to be passive inhabitants of bark beetle communities, we now know that they can have strong interactions with nonmite species, are major components of biological diversity, and can impact bark beetle population dynamics and fungal interactions (Hofstetter and others 2006a, 2006b). Details of the biology and ecology of this important group of organisms are discussed later in this chapter.

11.2.4. Other Phoretic Organisms

Species of pseudoscorpions (Figure 11.4) and other small arthropods, such as fungivorous dipterans and coleopterans, are periodically phoretic on the SPB. Many of these species are also found on predators and competitors associated with the SPB.

11.3. INTERACTIONS WITH SPB

Many of the phoronts associated with SPB have little direct effects on SPB adults, larvae, and eggs. Furthermore, it is likely that many of the phoronts affect the SPB only indirectly by interacting with other species within trees. However, several of the species are direct predators, parasitoids, or pathogens of the SPB. In laboratory tests, Moser (1975) found that 32 of 51 species of mites were predaceous on one or more SPB life stages. Currently, of the 111 known mite species associated with the SPB, 35 percent are likely predaceous on SPB eggs or larvae as well as on other mites or nematodes. Of the remaining 70 mite species, 15 percent are believed to feed on fungi and other microbes, while the remaining 50 percent have unknown feeding preferences and behaviors.

11.3.1. Impacts on Health and Vigor of Beetle Larvae

As stated previously, phoronts can affect beetles in a variety of ways that range from beneficial to antagonistic (Table 11.1). These effects are often context-dependent, in that the interaction can change depending on time of year, host tree condition, local species community within the tree, and so on. Here are several examples of mutualistic interactions among SPB and phoronts. Nematophagous

mites (e.g., *Dendrolaelaps neodisetus* (Hurlbutt)) may benefit SPB larvae by preying on nematodes which are endoparasitic on bark beetles (e.g., nematode *Contorylenchus brevicomi*) (Kinn 1980). Many nematophagous mites and generalist predatory mites attack and kill other mites (Kinn 1983). Some examples include: the eggs and larvae of *Dendrolaelaps quadristus* (Berlese) are preyed upon by *Cercoleipus coelonotus* Kinn; *Histiogaster arborignis* Woodring is fed on by *Mexechesles* spp., *Proctolaelaps dendroctoni* Lindquist and Hunter, and *Hypoapsis* spp.; *Macrocheles boudreauxi* Krantz and *Eugamasus lyriformis* McGraw and Farrier nymphs and adults eat *Dendrolaelaps* spp., cheyletids (Prostigmata) and uropodid mites. Fungivorous mites increase fungal inoculation loads and thus could benefit the SPB if the fungi are mycangial fungi, or harm beetle larvae by introducing antagonistic fungi (discussed below) during colonization and gallery production. For additional information, see chapter 9 of this book.

11.3.2. Impacts on Fungal-Beetle Associations

Trophic interactions among mites, fungi, and the SPB are covered in chapter 9 and are well documented for particular mite-fungal interactions (Bridges and Moser 1983, 1986; Hofstetter and others 2006a, 2006b; Klepzig and others 2001a, 2001b; Lombardero and others 2000c, 2003). *Tarsonemus* mites significantly affect the abundance of and interactions between mycangial and *Ophiostoma* fungi associated with the SPB. *Tarsonemus* possess specialized, flap-like structures of the integument, called C-flaps or sporothecae, which frequently contain *O. minus* and *C. ranaculosus* ascospores (Bridges and Moser 1983, Moser 1985, Moser and others 1995) (Figure 11.5). The collection and inoculation of *C. ranaculosus* ascospores by *Tarsonemus* spp. within SPB-infested trees provide the primary mechanism for which sexual spores of *C. ranaculosus* are transported. This may be one of many cases of pseudopollination between fungi and mites found within bark beetle communities. The transports of fungal spores likely have important consequences for this beetle-mycangial fungal relationship and the maintenance of high genetic variation and cross-fertilization of fungi.

The presence of *O. minus* in phloem negatively affects SPB larvae (Bridges 1983, Bridges and Perry 1985, Goldhammer and others 1990,

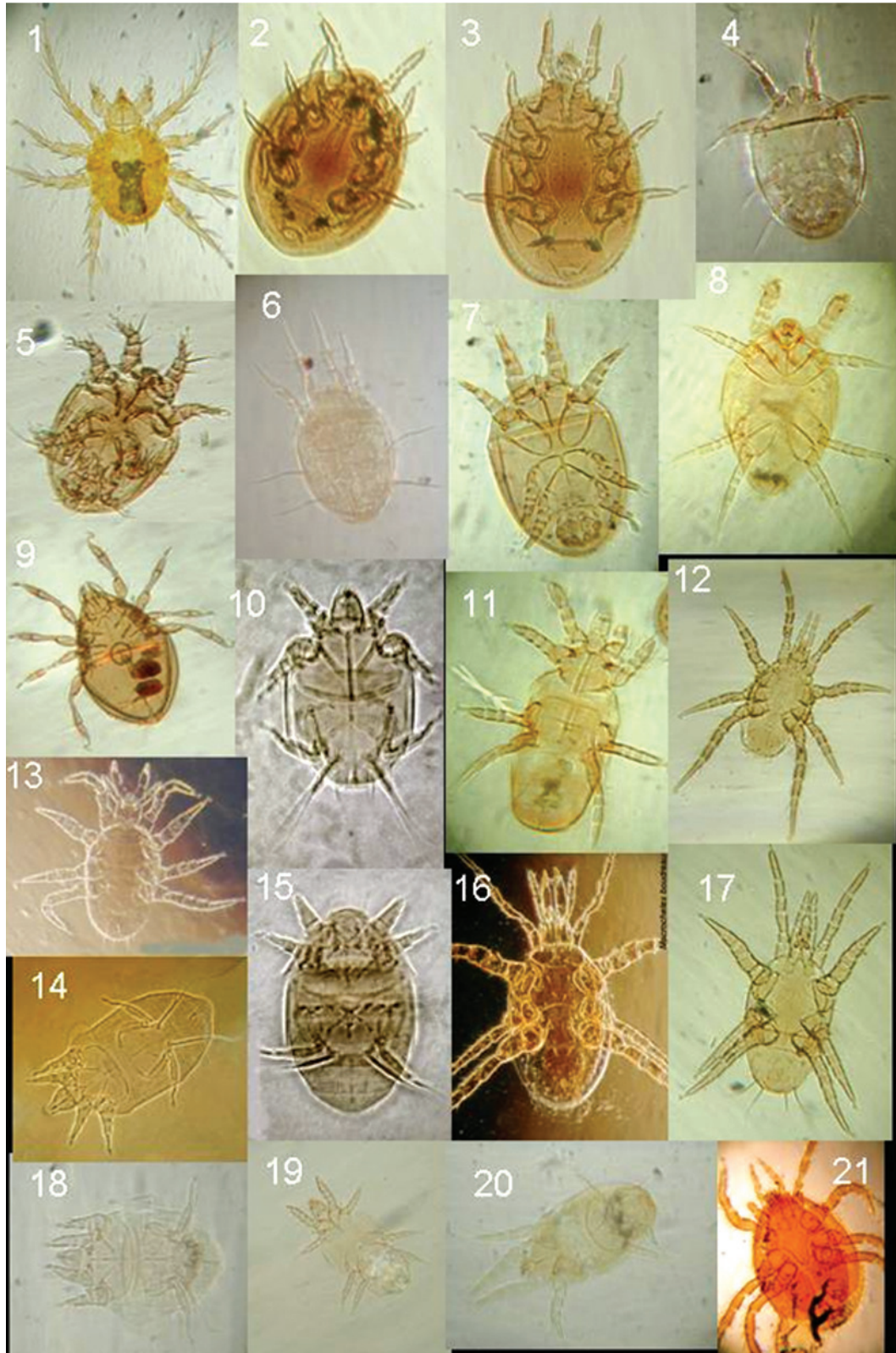


Figure 11.3—Images of common mites associated with bark beetles. Not all mites pictured here are phoretic on the SPB. (1) *Mexecheles virginiensis* Baker, (2) *Uroobovella orri* Hirschmann, (3) *Trichouropoda* sp., (4) *Histiostoma* sp., (5) *Histiogaster anops* Woodring, (6) *Bonomia* sp., (7) *Schwiebia* sp., (8) *Paracarophaenax* sp., (9) *Paraleius* sp., (10) *Iponemus truncatus* Lindquist, (11) *Elattoma* sp., (12) *Lasioseius safroi* Ewing, (13) *Proctolaelaps* sp., (14) *Tarsonemus ips* Lindquist, (15) *Heterotarsonemus* sp., (16) *Macrocheles* sp., (17) *Dendrolaelaps quadrisetus* (Berlese), (18) *Tarsonemus krantzi* Smiley and Moser, (19) *Pyemotes* sp., (20) *Parawinterschmidtia* sp., and (21) *Cerocolieus* sp. (images by Elisabeth Alden, R.W. Hofstetter, and J. Khai Tran)



Figure 11.4 — Pseudoscorpion removed from SPB in Arizona. (photograph by R.W. Hofstetter)

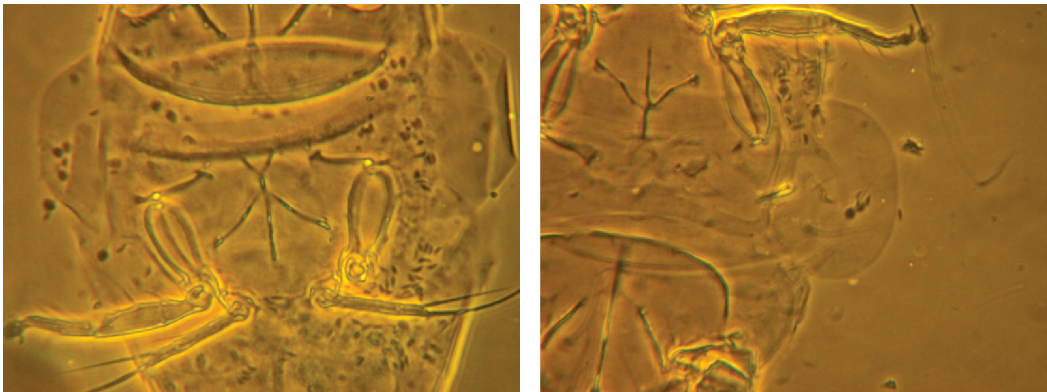


Figure 11.5 — *Tarsonemus krantzi* with fungal spores within sporothecae, also called C-flaps. Mites removed from SPB collected in flight traps in Alabama 2001. (images by R.W. Hofstetter)

Table 11.1—Description of phoretic interactions between SPB and phoront(s)

Impact on SPB	Impact on Phoront	Interaction type	Examples
+	+	Mutualism	Mycangial fungi, <i>Tarsonemus ips</i> carrying mycangial fungi; mite predators (eg., <i>Dendrolaelaps</i> spp.) of parasitic nematodes
-	+	Antagonism	<i>Ophiostoma minus</i> , mite predators/ parasitoids of SPB; pathogenic fungi
0	+	Commensalism, Facilitative	Most fungi and phoretic mites

Combinations in which the impacts on the phoront is – or 0 are unlikely, in that the phoront should benefit (+) from transportation by SPB, thus having an overall positive effect on fitness. However, theoretically the phoront can be harmed or depredated by SPB, in which case the SPB benefits and the phoront is harmed. Situations in which the impact is negative (-) or there is no impact (0) on the phoront would not likely persist over time.

Hofstetter and others 2006a, Lombardero and others 2000c). Variance in abundance of *Tarsonemus* spp. appears to be a meaningful driver in SPB population dynamics and *O. minus* abundance in infested trees (Goldhammer and others 1990; Hofstetter and others 2006a, 2006b; Lombardero and others 2003). Several mite genera other than *Tarsonemus* may be partially or wholly mycetophagous and affect beetle-fungal associations; these include *Elattoma*, *Heterotarsonemus*, *Histiogaster*, *Histiostoma*, *Parawinterschmidia*, *Schwiebia*, and *Tyrophagous* (Moser and Roton 1971).

11.3.3. Impacts on Beetle Population Dynamics

Because the fungus *Ceratocystiopsis ranaculosus* represents an inferior nutritional resource for the SPB (Bridges 1983; Coppedge and others 1995; Goldhammer and others 1990; Klepzig and others 2001a, 2001b) but a superior nutritional resource for *Tarsonemus* mites (Lombardero and others 2000c), seasonal changes in the ratio of the beetle-mutualistic fungi (due to temperature; Hofstetter and others 2007) could influence beetle and mite population dynamics in opposite directions. Field studies by Miller and Parresol (1992) and Bridges (1983) demonstrated increased reproduction in beetle populations when *Entomocorticium* sp. A was the dominant mycangial fungus. Likewise, Hofstetter and others (2006a, 2006b) recorded increased mite reproduction and decreased beetle reproduction during periods when *O. minus* and *C. ranaculosus* were particularly abundant within bark. Hofstetter and others (2007) predicted that the abundance of *C. ranaculosus* relative to *Entomocorticium* sp. A would tend to be highest in the warmest climates where the SPB occurs (for example, Florida and Mexico). Surveys of the SPB mycangia in Mexico and Arizona reveal that *Entomocorticium* sp. A is very uncommon but present (Hofstetter and others, unpublished; Davis and Hofstetter 2009).

Variation in *O. minus* (i.e., blue stain within trees) abundance among and across SPB infestations appears to be driven by the association between *O. minus* and phoretic mites, while the association between *O. minus* and the SPB has little affect on total blue stain within infested trees (Hofstetter and others 2006a, 2006b). Even with large experimental additions of *O. minus* spores to beetles, *O. minus* in the absence of *Tarsonemus* spp. do not reach levels observed in natural infestations (Hofstetter and others 2006a). Field surveys, in

combination with experimental manipulation of *Tarsonemus* on beetles, suggest that *Tarsonemus* is a key factor for *O. minus* abundance and may be necessary for *O. minus* to reach levels high enough (> 45 percent of phloem) to curtail beetle population growth (Hofstetter and others 2006a, Lombardero and others 2003). Apparently, *Tarsonemus* spp. propagate *O. minus* both by transporting ascospores into newly attacked trees (69 percent of phoretic mites carried an average of 18 ascospores per mite in natural infestations; Hofstetter and others 2006b) and by dispersing existing *O. minus* within the phloem of attacked trees (Lombardero and others 2003). *Tarsonemus* spp. presumably propagates *O. minus* because it feeds on it (Lombardero and others 2000c). Because *Tarsonemus* spp. feeds on *O. minus*, it is logical that the addition of *O. minus* leads to an increase in mites, and those infestations with high *O. minus* abundances have high mite densities within phloem. In any case, *Tarsonemus* spp., *O. minus* and beetle reproduction covary in a manner consistent with a system of strong direct and indirect interactions (Figure 11.6). Consequently, while environmental factors can cause short-term fluctuations in SPB abundances, species interactions act as a filter through which short-term environmental effects are translated into long-term population variability (Ives and Gross 1999).

The community of fungi and mites associated with the SPB likely transforms with seasonal temperatures as well as large scale changes in climate. Changes in the relative abundances of these organisms result from direct effects on reproduction, growth, behavior, and mortality, and from indirect effects through symbiotic species. Such variability in species responses suggests that there is flexibility within this community but species loss will likely occur. Increases in average temperature (as predicted with global climate change) will likely lead to a shift or reduction in community richness and a predominance of a few species. However, increased variability in temperatures could further promote multiple symbionts and associations within this community.

11.4. NATURAL HISTORY OF PHORETIC MITES

Mites are common phoronts of the SPB and impact the ecology and behavior of the SPB. There are many unanswered questions related

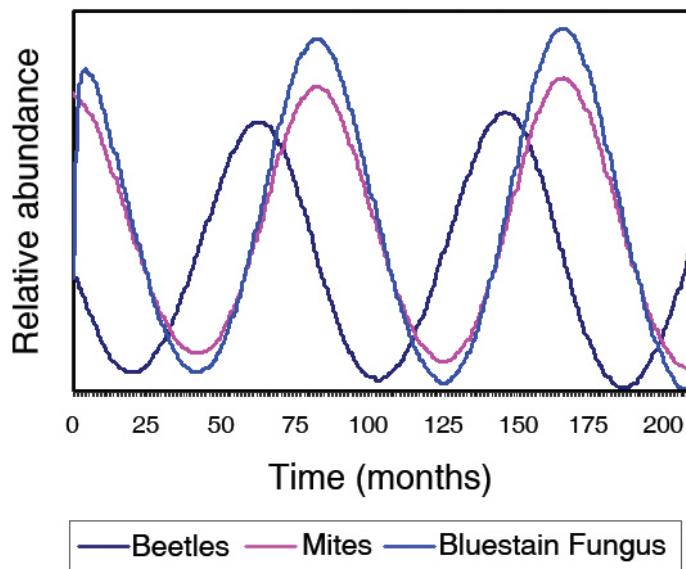


Figure 11.6—Model of SPB, mites, and blue stain fungi abundances through time. The pattern is similar to predator-prey dynamics proposed in other systems. (created by R.W. Hofstetter)

to phoretic mite abundance and behavior. For instance, does the frequency of a mite species on SPB adults indicate preference for the SPB? How do phoretic mite abundances correlate with mite populations within trees? What is the relationship between frequency of phoretic mites on beetles and the numbers of mites per beetle, and how do these two measurements vary? Do beetles actively remove phoronts or discourage mites from attaching to them? What cues do mites use to locate beetle hosts? What effects do environmental factors have on phoretic mite patterns? How have mites affected the evolution of beetle-microbial associations?

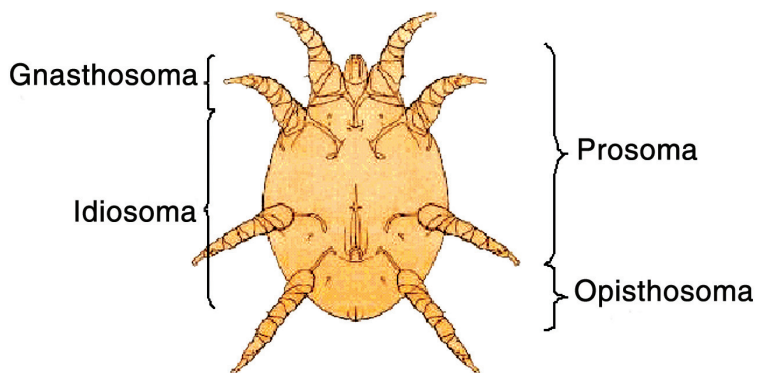
11.4.1. Taxonomy

Mites are in the phylum Arthropoda, which encompasses the insects, myriapods, spiders, scorpions, crustaceans, and ticks. Arthropods are characterized by jointed legs and a chitinous exoskeleton. Mites are in the Subphylum Chelicerata, which is characterized by having two body regions, the prosoma (front body) and the opisthosoma (hind body), which excludes the insects (Figure 11.7). Antennae, mandibles, and maxillae, which are common on other arthropods, are absent in the Chelicerata. Instead, the prosoma contains a head region which has two pairs of pincer-like mouthparts called the chelicerae and the subcapitulum, and a region with four pairs of legs. The posterior body region, the opisthosoma, contains organs for digestion, gas exchange, and reproduction. Mites are in the Class Arachnida, which is comprised of Chelicerata that may possess simple eyes and are primarily terrestrial,

including such groups as the scorpions, spiders, harvestmen, ticks, and mites. The mite Subclass, Acari, contains organisms in which segmentation is generally inconspicuous or absent, unlike the Araneae (the spiders).

Most mites associated with the SPB are in the Orders Astigmata and Prostigmata within the Superorder Acariformes and the Order Mesostigmata within Superorder Parasitiformes (Kinn 1971, Moser and Roton 1971). The Acariformes are the most diverse and abundant of the three mite Superorders (Opilioacariformes, Parasitiformes and Acariformes; Krantz 1978), with more than 30,000 described species. Acariformes mites occur in most habitats and regions of the world and are common phoronts of the SPB. Opilioacarans have not been found in bark beetle-killed trees, but it is possible that they live in decayed wood. About 11,000 species have been described within

Figure 11.7—Morphological regions of a mite.



the Parasitiformes, which includes the Orders Ixodida (ticks) and the Mesostigmata. Many Mesostigmata, including several of the genera associated with decaying fungi, are phoretic on beetles (Kinn 1971, Lindquist 1975, McGraw and Farrier 1973), and are prominent predators of nematodes and mites or mycetophagous on bark beetle fungi (Kinn 1971, Lindquist 1975, Lindquist and Wu 1991, Moser and Roton 1971). Table 11.2 shows the mite species known to travel on adult SPBs 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.

11.4.2. Morphology

Although the majority of mites are minute, adult body lengths can vary greatly from 50 μm (plant parasites) to 3 cm (engorged ticks). In general, mites associated with the SPB range from 60 μm (*Iponemus* sp.) to 0.5 mm (*Mexecheles* sp.).

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

Adult mites have four pairs of legs, with the first pair of legs often being slender, elongated, and lacking well-developed claws. This first pair (Leg I) is used like antennae. A cluster of sensory setae may be located near the tips of Leg I, and are used for sizing up a potential sexual partner or prey by using tentative tapping movements (Walter and 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 that contains organs for digestion, excretion, and reproduction. Digestion in mites is very primitive. The parasitiform 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 fungi can be seen within the hindgut of some mycetophagous mites. The food bolus is expelled as a fecal pellet through a relatively large anal opening covered by a pair of trapdoor-like valves (Walter and Proctor 1999).

11.4.3. Reproduction

Mites have extremely diverse mating habits and reproductive biology/strategies. Variation in reproductive mode can occur within families, genera, and species (Norton and others 1993). Direct transfer of sperm via genitalia is relatively uncommon. In males, appendages are modified for sperm transfer. Spermatodactyls on chelicerae of males 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's genitalia.

Although there is an extensive body of literature on the sex ratio biology of mites (Proctor 1996, Wrensch and Ebbert 1993), knowledge of sex determination of offspring and oviposition 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, and amphitoky) remain unknown. Several species of Tarsonemidae are arrhenotokous, theyletokous, or amphitokous (Karl 1965, Schaarschmidt 1959). In general, mite species that are haplodiploid 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 (for example, local mate competition; Hamilton 1967), founder effects (e.g., haystack model; Nagelkerke and Sabelis 1996), exploitation and competition, and island biogeography theory (Sanchez and Parmenter 2002, Terborgh and others 2001).

11.4.4. Growth and Development

Mites associated with the SPB generally have many generations within each host tree. Development rates vary greatly across mite taxa and are strongly affected by temperature, humidity, and food quality. The most rapidly developing acariforms are in the Tarsonemidae, which can complete development in 3-10 days at moderate temperatures. Mite longevity also is highly variable across species, with some

Table 11.2—The distribution and feeding behavior of mite species phoretic on the SPB in the United States. Generalist = feeds on multiple fungi, nematodes, and dead invertebrates. Mycetophagous = feeds on specific fungi, often transports and disperses reproductive structures of fungi. I categorize phoretic mites abundance on beetles as rare (< 1 percent of beetles have this species), infrequent (1-5 percent), common (5-20 percent), and frequent (>20 percent). Surveys of SPB populations by R.W. Hofstetter in Arizona, Mississippi, and Alabama, and by J.C. Moser throughout Southeast United States. Mites identified by J.C. Moser and stored as voucher specimens by R.W. Hofstetter at Northern Arizona University and J. Moser at Southern Research Station.

Phoretic mite species	Mite family ^a	Dist. on SPB		Phoretic abundance
		S.E. U.S. ^b	S.W. U.S. ^c	
<i>Dendrolaelaps (Longoseius) cuniculus</i>	Digamasellidae ^P	X	X	Infrequent
<i>D. neocornutus</i>	Digamasellidae ^P	X		Infrequent
<i>D. neodisetus</i>	Digamasellidae ^P	X	X	Common
<i>D. quadrasetus</i>	Digamasellidae ^P		X	Infrequent
<i>D. varipunctatus</i>	Digamasellidae ^P	X	X	Rare
<i>Elattoma</i> spp.	Pyemotidae ^A	X	X	Infrequent
<i>E. bennetti</i>	Pyemotidae ^A	X		Common
<i>Ereynetes scutulis</i>	Ereynetidae ^A	X	X	Rare
<i>Ereynetes</i> spp.	Ereynetidae ^A	X	X	Rare
<i>Eugamasus lyriformis</i>		X		Rare
<i>Heterotarsonemus lindquisti</i>	Tarsonemidae ^A	X	X	Rare
<i>Histiogaster anops</i>	Acaridae ^A		X	Common
<i>H. arborsignus</i>	Acaridae ^A	X		Common
<i>Histiostoma varia</i>	Histiostomatidae ^A	X	X	Common
<i>Iponemus truncatus</i>	Tarsonemidae ^A	X	X	Rare
<i>Licnocephalus reticulatus</i>	Oribatidae ^A		X	Infrequent
<i>Macrocheles boudreauxi</i>	Macrochelidae ^P	X	X	Rare
<i>Mexechesles virginiensis</i>	Cheyletidae ^A	X	X	Rare
<i>Nanacarus</i> sp.	Hemisarcoptidae ^A		X	Rare
<i>Nentaria</i> sp.	Uropodidae ^P		X	Rare
<i>Paracarophanax</i> sp.	Pyemotidae ^A		X	Rare
<i>Paraleius leontonychus</i>	Oribatidae ^A	X		Rare
<i>Paraleius</i> sp.	Oribatidae ^A		X	Rare
<i>Parawinterschmidtia furnissi</i>	Wintershmidtidae ^A		X	Infrequent
<i>Proctogastrolaelaps libris</i>	Ascidae ^P	X		Rare
<i>Proctolaelaps dendroctoni</i>	Ascidae ^P	X	X	Rare
<i>P. hystrix</i>	Ascidae ^P	X		Common
<i>Pyemotes parviscolyti</i>	Pyemotidae ^A	X		Rare
<i>Pyemotes n.</i> sp.	Pyemotidae ^A		X	Rare
<i>Schwiebia</i> sp.	Acaridae ^A		X	Infrequent
<i>Tarsonemus fuseri</i>	Tarsonemidae ^A	X		Rare
<i>T. ips</i>	Tarsonemidae ^A	X	X	Common
<i>T. krantzii</i>	Tarsonemidae ^A	X	X	Frequent
<i>T. subcorticallis</i>	Tarsonemidae ^A	X	X	Rare
<i>Trichouropoda australis</i>	Uropodidae ^P	X	X	Common
<i>T. hirsuta</i>	Uropodidae ^P	X	X	Common
<i>Urobovella orri</i>	Uropodidae ^P	X	X	Infrequent

^a Mite family: ^A Order Acariformes; ^P Order Parasitiformes.

^b SPB populations in Louisiana, Mississippi, and Alabama, U.S.

^c SPB populations in Coronado and Coconino National Forests, Arizona, U.S.

adults living only weeks while others live for several months or possibly a year.

The basic acarine development sequence is egg, prelarva, larva, protonymph, deutonymph, tritonymph, and adult (Krantz 1978). Suppression of one or more nymphal instars and accelerated development are common in many species. Several lineages are characterized 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 not protected by the parent, although some eggs may be carried by adults. Eggs are also quite large, almost half the size of an adult mite in some species. 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 pass into an inactive, turgid state before becoming a nymph or adult (e.g., Tarsonemidae; Lindquist 1986). Males (Figure 11.8B) of several species carry virgin females while they are in this quiescent state. Two or three nymph stages usually appear between the larval and adult stage. These nymphs usually have four pairs of legs, although the fourth pair may not be complete and may lack claws (Figure 11.8A). 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 sclerotization pattern. In many species, phorecy occurs in the deutonymph stage rather than as mature adults.

11.4.5. Food and Host Specificity

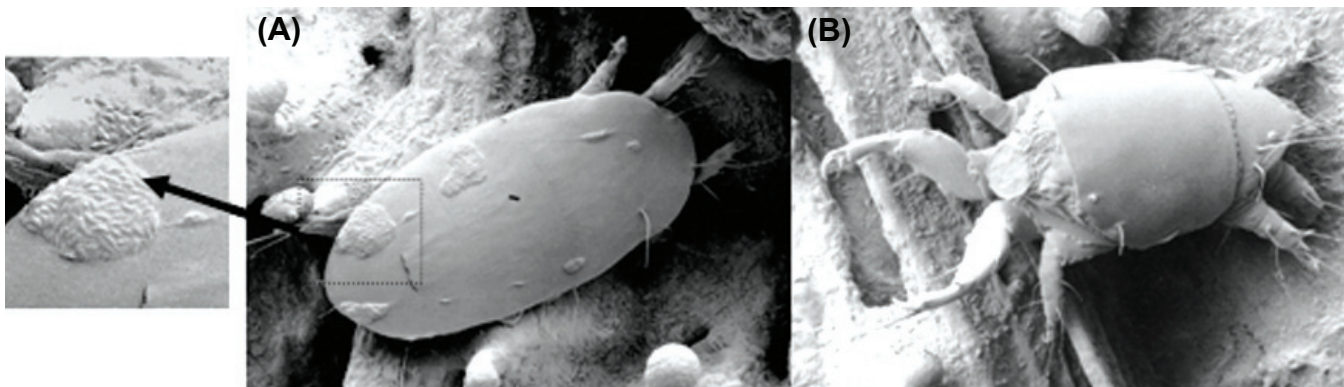
The eating habits and food preference of mites associated with the SPB are well understood compared to other bark beetle communities (Tables 11.2 and 11.3). Most mites associated with bark beetles are predators on nematodes and other small arthropods including SPB larvae and eggs (Table 11.3). Mycetophagous species vary from highly specific, feeding on and carrying spores of one fungus (e.g., *Tarsonemus krantz* on *Ophiostoma minus*; Figures 11.8 and 11.9) to generalists, feeding on several fungi (e.g., *Histiogaster* spp.).

11.4.6. Movement and Dispersal

Typically, only one life history stage is phoretic in a given species. In the Astigmata the phoretic stage is the deutonymph, while in the Prostigmata it may be the fertilized adult female (Zhang and Sanderson 1993). Heteromorphic deutonymphs in the Uropodina attach to their arthropod hosts with a stalk secreted from the anus called a pedicel (Figure 11.10), 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 glances covering all or some appendages (Athias-Binche 1991, Binns 1982, Norton and others 1993). This convergent morphology may serve to reduce loss of moisture when on the host and to present a smooth dorsal surface, making it difficult for the host to remove mites by grooming or rubbing.

In the case of Tarsonemidae and some other families, mite species are phoretic on specific insect species (such as the SPB), genera, or families associated with SPB-killed trees. Some phoretic mite species may disperse as groups rather than individual mites, which ensures that

Figure 11.8—SEM photograph of (A) female and (B) male *Tarsonemus ips* in bark. Ascospores of *O. minus* can be seen on their cuticle. Note the modified IV legs of the male for grasping pharate females. (photographs by Eric Erbe, Ronald Ochoa, and K.D. Klepzig)



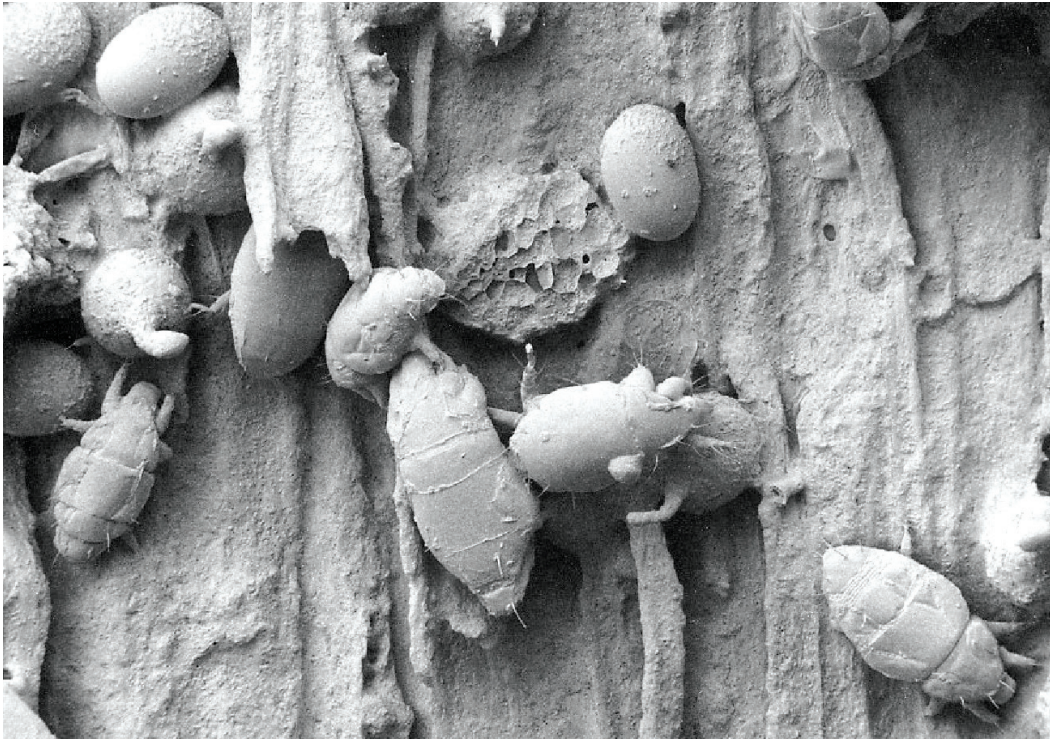


Figure 11.9—SEM photograph of adult and immature *Tarsonemus* mites that feed on *Ophiostoma minus*. Perithecia of *O. minus* and *Tarsonemus* eggs are covered with minute ascospores. (photograph by Eric Erbe, Ronald Ochoa, and K.D. Klepzig)

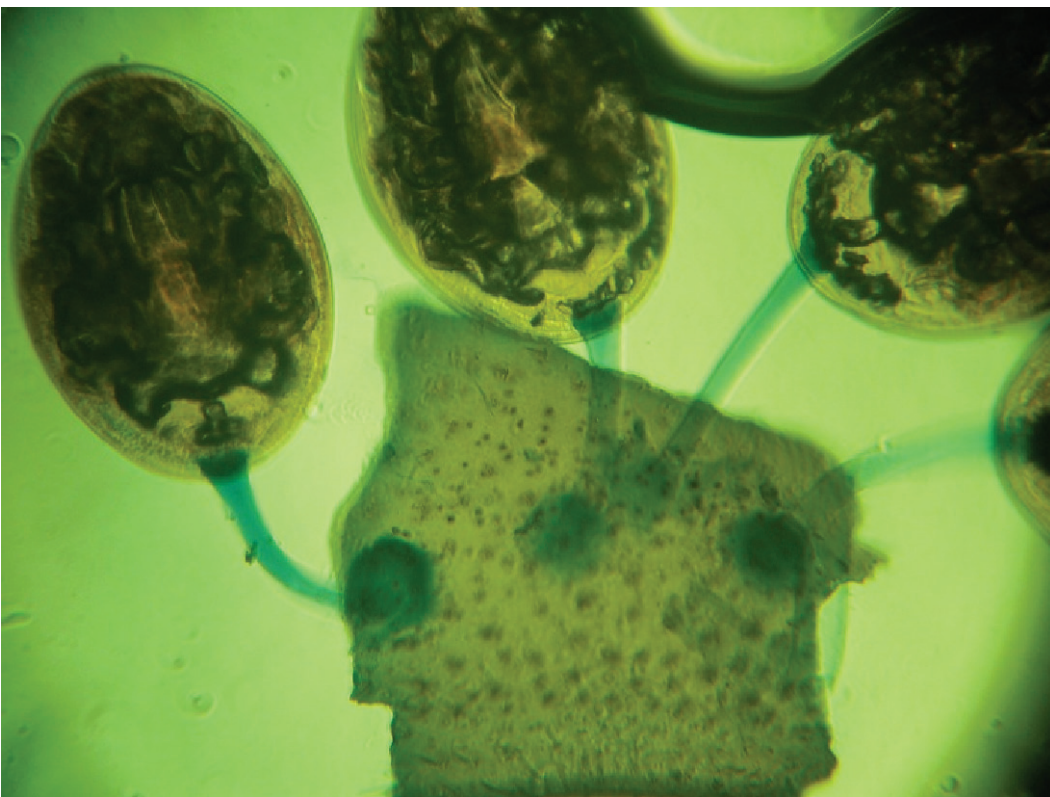


Figure 11.10—Uropodina mites attached to the exoskeleton of SPB. Note the anal glue stalks, termed pedicels (stained blue). (photograph by R.W. Hofstetter)

unmated mites find mates at their new location. This behavior likely occurs in species that do not exhibit parthenogenesis, or if the likelihood of mating prior to dispersal is small.

The attachment pattern of phoretic species on the SPB is reminiscent of niche partitioning that reduces interspecific competition and predation. Several species appear to attach to specific locations on beetle hosts (Figure 11.11),

Table 11.3—Mites found within the bark of SPB-infested trees. Additional information on feeding behavior and relative abundance of each species within bark is included. It is important to note that some of the bark-inhabiting mite species were likely introduced by beetle species other than SPB, such as *Ips pini*, and are not directly associated with SPB. Relative abundance scale: Rare = < 1.0 mites/m² bark; low = 1-5 mites/m² bark; Moderate = 6-50 mites/m² bark; high = > 50 mites/m² bark (continued)

#	Mite species found in SPB-infested bark	Feeding guild	Relative abundance	Frequency in samples	References
1	<i>Acrocheyla impolita</i> Smiley and Moser	Mite predator	Low	61%	Moser and Roton 1971
2	<i>A. virginiensis</i> (Baker)	Generalist predator	Rare	10%	Moser and Roton 1971
3	<i>Amblyseius guatemalensis</i> (Chant)	?	Rare	13%	Moser and Roton 1971
4	<i>Ameroseius longitrichus</i> Hirschmann	?	Low	6%	Moser and Roton 1971, Moser 1975
5	<i>Androlaelaps casalis</i> (Berlese)	Egg, mite predator	Rare	3%	Moser and Roton 1971, Moser 1975
6	<i>Histiostoma (Anoetus) conjuncta</i> Woodring and Moser	?	Rare	6%	Moser and Roton 1971
7	<i>H. insolita</i> Woodring and Moser	?	Rare	10%	Moser and Roton 1971, Moser 1975
8	<i>H. media</i> Woodring and Moser	?	Rare	10%	Moser and Roton 1971
9	<i>H. sordida</i> Woodring and Moser	?	Low	29%	Moser and Roton 1971, Moser 1975
10	<i>Bakerdania sellnicki</i> (Krczal)	?	Low	3%	Moser and Roton 1971
11	<i>Blattisocius keegani</i> Fox	Egg/mite predator	Rare	6%	Moser and Roton 1971
12	<i>Bryobia</i> sp. (<i>praetiosa</i> complex)	Phytophagus	Rare	2%	Moser and Roton 1971
13	<i>Cercoleipus coelonotus</i> Kinn	Nematode, mite, egg/larval predator	Rare	19%	Moser and Roton 1971, Moser 1975, Kinn 1971
14	<i>Cryptograthus barrasi</i> Smiley and Moser	?	Rare	1%	Moser and Roton 1971
15	<i>C. capreolus</i> (Berlese)	?	Rare	2%	Moser and Roton 1971
16	<i>C. taurus</i> (Kramer)	?	Rare	6%	Moser and Roton 1971
17	<i>Cunaxoides andrei</i> Baker and Hoffmann	?	Rare	4%	Moser and Roton 1971
18	<i>Cyta latirostris</i> (Hermann)	?	Rare	1%	Moser and Roton 1971
19	<i>Dendrolaelaps brachypoda</i> (Hurlbutt)	?	Rare	3%	Moser and Roton 1971
20	<i>D. (Longoseius) cuniculus</i> (Chant)	?	Low	2-60%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
21	<i>D. isodentatus</i> (Hurlbutt)	Egg/larval predator	Moderate	0-35%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
22	<i>D. neocornutus</i> (Hurlbutt)	Egg/larval predator	Moderate	5-35%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
23	<i>D. neodisetus</i> (Hurlbutt)	Larval/Nematode predator	High	74-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
24	<i>D. quadrisetus</i> (Berlese)	Nematode predator	Low-Moderate	25-100%	Moser and Roton 1971, Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished

continued

Table 11.3 (continued)—Mites found within the bark of SPB-infested trees. Additional information on feeding behavior and relative abundance of each species within bark is included. It is important to note that some of the bark-inhabiting mite species were likely introduced by beetle species other than SPB, such as *Ips pini*, and are not directly associated with SPB. Relative abundance scale: Rare = < 1.0 mites/m² bark; low = 1-5 mites/m² bark; Moderate = 6-50 mites/m² bark; high = > 50 mites/m² bark (continued)

#	Mite species found in SPB-infested bark	Feeding guild	Relative abundance	Frequency in samples	References
25	<i>D. quadrisetosimilis</i> (Hirschmann)	?	Rare	1%	Moser and Roton 1971
26	<i>D. quadritorus</i> Robillard	?	Rare	1%	Moser and Roton 1971
27	<i>D. rotoni</i> (Hurlbutt)	Egg/larval predator	Rare	6%	Moser and Roton 1971, Moser 1975
28	<i>D. varipunctatus</i> (Hurlbutt)	Larval predator	Low	13%	Moser and Roton 1971
29	<i>Elattoma (Pygmephorrellus) bennetti</i> (Cross and Moser)	Mycetophagous ³	Low	17-42%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
30	<i>Ereynetoides scutulalis</i> Hunter	?	Moderate	11-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
31	<i>Eugamasus (Vulgarogamsus) lyriformis</i> McGraw and Farrier	Larval/pupal predator	Moderate	1-80%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
32	<i>Eupelops</i> sp.	?	Rare	3%	Moser and Roton 1971
33	<i>Eupodes</i> sp.	?	Rare	3%	Moser and Roton 1971
34	<i>Eutogenes vicinus</i> Summers and Price	Mite predator	Rare	1%	Moser and Roton 1971
35	<i>Gamasellodes reactiventris</i> Lindquist	?	Rare	6%	Moser and Roton 1971
36	<i>Gamasiphis</i> sp.	?	Rare	3%	Moser and Roton 1971
37	<i>Gamasolaelaps subcorticalis</i> McGraw and Farrier	Larval predator	Rare	0-13%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
38	<i>Glycyphagus</i> n. sp.	?	Rare	3%	Moser and Roton 1971
39	<i>Gymnolaelaps</i> sp.	?	Rare	1%	Moser 1975
40	<i>Heterotarsonemus lindquisti</i> Smiley	Mycetophagous	Low	0-48%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
41	<i>Histiogaster anops</i> Woodring	Generalist ⁴	Low	1-25%	Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished
42	<i>H. arborsignis</i> Woodring	Generalist predator; mycetophagus	Moderate	23-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
43	<i>H. rotundus</i> Woodring	Generalist predator; mycetophagus	Low	29%	Moser and Roton 1971, Moser 1975
44	<i>Histiostoma (Anoetus) varia</i> Woodring	Filter feeder	Low-Moderate	13-70%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
45	<i>Hoplocheylus pickardi</i> Smiley and Moser	?	Rare	1%	Moser and Roton 1971
46	<i>Hypoaspis disjuncta</i> Hunter and Yeh	Mycetophagus	Rare	3%	Moser and Roton 1971, Moser 1975
47	<i>H. krantzi</i> Hunter	?	Rare	0-3%	Stephen and Kinn 1980, Moser and Roton 1971

continued

Table 11.3 (continued)—Mites found within the bark of SPB-infested trees. Additional information on feeding behavior and relative abundance of each species within bark is included. It is important to note that some of the bark-inhabiting mite species were likely introduced by beetle species other than SPB, such as *Ips pini*, and are not directly associated with SPB. Relative abundance scale: Rare = < 1.0 mites/m² bark; low = 1-5 mites/m² bark; Moderate = 6-50 mites/m² bark; high = > 50 mites/m² bark (continued)

#	Mite species found in SPB-infested bark	Feeding guild	Relative abundance	Frequency in samples	References
48	<i>H. sp. nr. praesternalis</i> Willman	Egg predator	Rare	1%	Moser 1975
49	<i>H. vitzthumi</i> (Womersley)	Larval predator	Rare	1%	Moser 1975
50	<i>Iponemus calligraphi calligraphi</i> Lindquist	Egg parasitoid	Rare	3%	Moser and Roton 1971, Moser 1975
51	<i>I. confusus oriens</i> Lindquist	Egg parasitoid	Rare	10%	Moser and Roton 1971, Moser 1975
52	<i>I. truncatus</i> Lindquist	Egg parasitoid	Rare	1%	Moser and Roton 1971, Moser 1975
53	<i>Kleemannia sp.</i>	?	Rare	1%	Moser 1975
54	<i>Lasioseius corticeus</i> Lindquist	Egg/larval predator	Low	32%	Moser and Roton 1971
55	<i>L. dentatus</i> (Fox)	Egg predator	Rare	3%	Moser and Roton 1971, Moser 1975
56	<i>L. epicriodopsis</i> DeLeon	Larval predator	Rare	1%	Moser and Roton 1971, Moser 1975
57	<i>L. neometes</i> McGraw and Farrier	?	Rare	3%	Moser and Roton 1971
58	<i>L. tubiculiger</i> (Berlese)	Egg predator	Rare	1%	Moser 1975
59	<i>Ledermulleria segnis</i> Koch	?	Rare	3%	Moser and Roton 1971
60	<i>Leptus n. sp.</i>	Predator	Rare	9%	Moser and Roton 1971
61	<i>Licnocephelus reticulatus</i>	?	Rare	1%	Moser, pers. comm.
62	<i>Liodes sp.</i>	?	Rare	2%	Moser and Roton 1971
63	<i>Macrocheles boudreauxi</i> Krantz	Predator	Low	11-80%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
64	<i>M. mammifer</i> Berlese	Predator	Rare	1%	Moser 1975
65	<i>Melichares monocharmi</i> (Lindquist)	?	Rare	2%	Moser and Roton 1971
66	<i>Mesotritia sp.</i>	?	Rare	2%	Moser and Roton 1971, Moser 1975
67	<i>Mexechesles virginiensis</i> Baker	Predator	Low	1-10%	Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished
68	<i>Microtydeus n. sp.</i>	?	Rare	1%	Moser and Roton 1971
69	<i>Nanacarus sp.</i>	?	Rare		Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished
70	<i>Nenteria sp.</i>	?	Rare	1%	Moser and Roton 1971
71	<i>Neophyllobius lorioi</i> Smiley and Moser	?	Rare	3%	Moser and Roton 1971
72	<i>Neoraphignathus howei</i> Smiley and Moser	?	Rare	1%	Moser and Roton 1971
73	<i>Neotrombidium n. sp.</i>	?	Rare	2%	Moser and Roton 1971
74	<i>Oodinychus sp.</i>	?	Rare	1%	Moser and Roton 1971

continued

Table 11.3 (continued)—Mites found within the bark of SPB-infested trees. Additional information on feeding behavior and relative abundance of each species within bark is included. It is important to note that some of the bark-inhabiting mite species were likely introduced by beetle species other than SPB, such as *Ips pini*, and are not directly associated with SPB. Relative abundance scale: Rare = < 1.0 mites/m² bark; low = 1-5 mites/m² bark; Moderate = 6-50 mites/m² bark; high = > 50 mites/m² bark (continued)

#	Mite species found in SPB-infested bark	Feeding guild	Relative abundance	Frequency in samples	References
75	<i>Paracarophenax</i> sp.	Egg parasitoid	Rare	1%	Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished
76	<i>Paracheyletia wellsi</i> (Baker)	Mite predator	Rare	4%	Moser and Roton 1971
77	<i>Paraleius leontonychus</i> Berlese	?	Rare	1-5%	Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished
78	<i>Paraleius</i> sp.	?	Rare	3%	Moser and Roton 1971
79	<i>Paraupalopis hodgesi</i> Smiley and Moser	?	Rare	1%	Moser and Roton 1971
80	<i>Parawinterschmidtia furnissi</i>	?	Low-Moderate	5-20%	Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished
81	<i>Peloribates</i> sp.	?	Rare	5%	Moser and Roton 1971
82	<i>Pleuronectocelaeno drymoecetes</i> Kinn	Egg/larval predator	Rare	0-32%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
83	<i>Podocinum pacificum</i> Berlese	?	Rare	3%	Moser and Roton 1971
84	<i>Proctogastrolaelaps libris</i> McGraw and Farrier	?	Low	6-80%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
85	<i>Proctolaelaps bickleyi</i> (Bram)	Larval/nematode predator	Low	1-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
86	<i>P. dendroctoni</i> Lindquist and Hunter	Larval/pupa/mite predator	Moderate	87%	Moser and Roton 1971, Moser 1975
87	<i>P. fiseri</i> Samsinak	Larval predator	Low	13%	Moser and Roton 1971, Moser 1975
88	<i>P. hystricoides</i> Lindquist and Hunter	Larval predator	Low	39%	Moser and Roton 1971, Moser 1975
89	<i>P. hystrix</i> (Vitzthum)	Larval predator	Low	10%	Moser and Roton 1971, Moser 1975
90	<i>P. xyloteri</i> Samsinak	?	Rare	2%	Moser and Roton 1971
91	<i>Prosocheyla acanthus</i> Smiley and Moser	?	Rare	4%	Moser and Roton 1971
92	<i>Pseudoparasitus thatcheri</i> Hunter and Moser	Egg/larval predator	Low	19%	Moser and Roton 1971, Moser 1975
93	<i>Pyemotes parviscolyti</i> Cross and Moser	Egg/larval predator	Low	30%	Moser and Roton 1971, Moser 1975
94	<i>Scapheremaeus palustris</i> (Sellnick)	?	Rare	9%	Moser and Roton 1971
95	<i>Scheloribates</i> sp.	?	Rare	3%	Moser and Roton 1971
96	<i>Schwiebia</i> sp.	Generalist	Moderate-High	0-80%	Stephen and Kinn 1980
97	<i>Spinibdella depressa</i> (Ewing)	?	Rare	1%	Moser and Roton 1971
98	<i>Tarsonemus fuseri</i>	Mycetophagous ⁴	Rare	1%	Moser and Roton 1971

continued

Table 11.3 (continued)—Mites found within the bark of SPB-infested trees. Additional information on feeding behavior and relative abundance of each species within bark is included. It is important to note that some of the bark-inhabiting mite species were likely introduced by beetle species other than SPB, such as *Ips pini*, and are not directly associated with SPB. Relative abundance scale: Rare = < 1.0 mites/m² bark; low = 1-5 mites/m² bark; Moderate = 6-50 mites/m² bark; high = > 50 mites/m² bark

#	Mite species found in SPB-infested bark	Feeding guild	Relative abundance	Frequency in samples	References
99	<i>T. ips</i> Lindquist	Mycetophagous ⁴	Moderate	26-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
100	<i>T. krantzi</i> Smiley and Moser	Mycetophagous ⁴	High	54-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
101	<i>T. subcorticalis</i> Lindquist	Mycetophagous	Low	77%	Moser and Roton 1971
102	<i>Trichogalumna</i> sp.	?	Rare	1%	Moser and Roton 1971
103	<i>Trichoribates</i> sp.	?	Rare	1%	Moser and Roton 1971
104	<i>Trichouropoda australis</i> Hirschmann	Generalist	High	77-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
105	<i>T. hirsuta</i> Hirschmann	Generalist	Low-High	8-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
106	<i>T. lamellosa</i> Hirschmann	Nematode/ larval predator	Low-High	58%	Moser and Roton 1971, Moser 1975, Kinn 1987
107	<i>Tydeus</i> n. sp.	?	Rare	1%	Moser and Roton 1971
108	<i>Tyrophagus putrescentiae</i> (Schrank)	Mycetophagus	Low	58%	Moser and Roton 1971, Moser 1975
109	<i>Uroobovella americana</i> Hirschmann	Larval predator	Rare	23%	Moser and Roton 1971, Moser 1975
110	<i>U. laciniata</i> Berlese	?	Rare	3%	Moser and Roton 1971
111	<i>U. orri</i> Hirschmann	?	Low	32%	Moser and Roton 1971, Moser 1975

while others may attach anywhere on the body. Whether species compete or exclude other individuals or species from particular locations is not known. Species may have adaptations

that allow them to hold on to specific structures and locations on the beetle body. Why some species select particular locations on the beetle body is unknown. Presumably, attachment sites vary in their exposure and difficulty to hold fast. How do attachment location patterns on SPB compare to other phoretic systems?

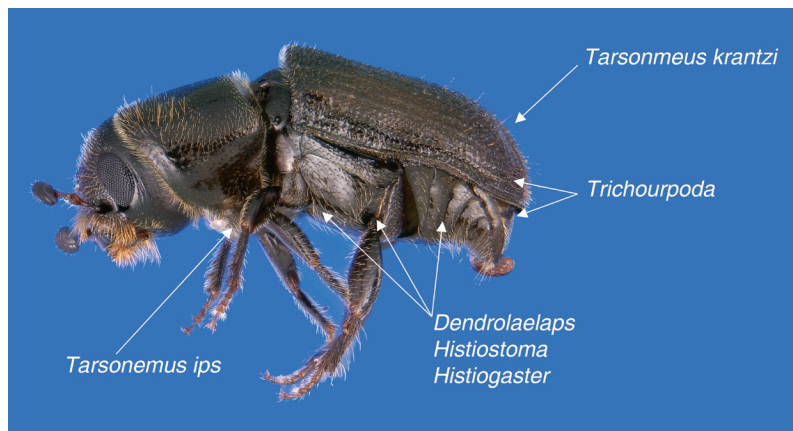


Figure 11.11—General locations of some phoretic mite species and genera on SPB during flight. (photograph by Erich G. Vallery, USDA Forest Service, SRS-4552, www.forestryimages.org).

Anywhere from 10 to 90 percent of flying SPB within a population carry phoretic mites (Hofstetter and others 2006a, 2006b; Moser 1976b), but this number can vary seasonally. For example, *Proctolaelaps dendroctoni*, *Longoseius cuniculus*, and *Macrocheles boudreauxi* are most common in early summer. During midsummer, *Dendrolaelaps neodisetus*, *Eugamasus lyriformis*, and *Trichouropoda australis* are most abundant, and *Tarsonemus krantz* and *T. ips* increase in numbers from spring through early fall (Hofstetter and others 2007). Hofstetter and others (2006b) and Evans and others (in review) exposed sections of SPB-infested trees from Mississippi and Alabama and observed significant effects of temperature on

phoretic mite species abundances on emerging beetle progeny. In general, *Trichouropoda* spp. and *Dendrolaelaps* spp. abundances increased with temperature (up to 32 °C), while *Tarsonemus* spp. were most abundant at cooler temperatures (between 22 and 26 °C).

Mite abundances and distributions within trees can vary with height of the tree and season. Stephen and Kinn (1980) found more mite species in the upper boles of SPB-infested trees than in the lower boles. More mites in the upper bole are likely due to higher numbers of attacking bark beetles and beetle species in that portion of the bole. *Trichouropoda australis* and *Dendrolaelaps neodisetus* were more abundant in the lower bole, while *Pygmephorus bennetti* and *Tarsonemus ips* were most abundant in the upper bole. The distribution of *Tarsonemus krantz* was somewhat uniform over the entire bole. *Trichouropoda* spp. and *Dendrolaelaps* spp. mites are much larger than *Tarsonemus* spp. and *Pygmephorus* spp., giving support to the hypothesis that the flight ability of beetles can be impacted by mite loads. Flying SPB can carry at least 20 percent of their weight in mites (Moser 1976a, 1976b).

Predators and competitors of the SPB are potential phoretic hosts for many species (Table 11.4) (Kinn 1983). Predators and competitors are often large in size, mobile, and excellent fliers, and thus make good phoretic hosts. The disadvantages of using these hosts are that they may not be common or predictable within trees. Interestingly, these phoretic hosts may provide a way for phoronts to switch habitats, even between coniferous- and hardwood-beetle communities. 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*, many of which are believed to be generalist feeders or predators and are common associates in other bark beetle communities. The mycetophagous mites that are phoretic on predators and competitors of the SPB probably feed on late-successional fungi. However, the feeding habits of many mites associated with large woodboring beetles (i.e., Cerambycidae, Buprestidae) and predators remain largely unknown. Woodborers create extensive habitat within trees and are phoretic hosts for many mite species. For example, a single sawyer beetle was found to have 1,816 phoretic *Dendrolaelaps fukikoe* on its body (Enda and Tamura 1980).

11.4.7. Mortality Factors

Few observations have been reported on the predators and natural enemies of mites associated with the SPB. Many mite species are likely subject to predation by small insects and predatory mites or accidental feeding by invertebrate larvae. Mortality rates suffered during phorecy have not been documented but may be high. Phoretic mites quickly climb off the beetles that are attacked by predators. Whether these mites climb onto the attacker likely varies with the length of the attack and the species attacking. Mites appear to be susceptible to entomopathogenic fungi (Schabel 1982). However, the greatest mortality is suffered by mites that remain within habitats after phoretic hosts have left (Hofstetter 2004).

11.5. EVOLUTION OF MUTUALISMS AND ITS IMPLICATIONS ON SPB

Although mutualisms occur in virtually all ecosystems (Boza and Scheuring 2004), there is great variation in the way positive species interactions likely evolve. It is commonly thought that environmental heterogeneity and harsh conditions facilitate mutualistic tendencies (Bertness and Callaway 1994, Boza and Scheuring 2004, Morin 1999, Tewksbury and Lloyd 2001). For instance, mutualisms may allow for the exploitation of resources in marginal environments (Addicott 1995, Davidson and Morton 1981). Habitat amelioration is a common mutualist process that promotes the exploitation of harsh environments (Morin 1999). In this way, mutualism(s) between tree-killing bark beetles and microbes may allow beetles and their associates to utilize resources within a habitat that would be inaccessible without each other. To put another way, the mutualism(s) between SPB and their symbiotic fungi enable SPB to persist across a broad host range, host condition, and physical environment that would not be possible in the absence of these mutualists. In fact, in most mutualisms, the niche or physical space occupied by a species in the presence of interspecific interactions is actually greater than that occupied when the species lives alone (Bruno and others 2003). In addition, many mutualisms begin to evolve between beetles and phoronts under more benign conditions (i.e., within a colonized tree) that entail benefits of protection, defense, and nutrition, and eventually dispersal for the phoront.

Table 11.4—Phoretic mites of predators and competitors of bark beetles collected in baited flight traps during summer 2005 in Coconino National Forest, Arizona. Mites identified by J.C. Moser and stored as voucher specimens by R.W. Hofstetter at Northern Arizona University

Mite species	Mite family ^a	<i>Enoclerus spegus</i> (N=176)	<i>Temnochilla chloridia</i> (N=201)	<i>Platysoma</i> species (N=35)	<i>Cortecius</i> species (N=23)	<i>Elacatis</i> species (N=25)	Cerambycidae & Buprestidae (N=16)
<i>Anoetidae</i> sp.	Anoetidae ^A	X					
<i>Bonomia</i> sp.	Histiostomatidae ^A	X	X	X		X	
<i>Dendrolaelaps cuniculus</i>	Digamasellidae ^P		X				X
<i>Dendrolaelaps neodisetus</i>	Digamasellidae ^P	X	X	X	X		X
<i>Dendrol. varipunctatus</i>	Digamasellidae ^P			X			
<i>Dendrolaelaps</i> sp.	Digamasellidae ^P			X			
<i>Elattoma</i> sp.	Pyemotidae ^A	X	X		X		
<i>Gamasina</i> sp.	Ascidae ^P		X				
<i>Heterotarsonemus lindquisti</i>	Tarsonemidae ^A				X		X
<i>Histiostoma</i> sp.	Histiostomatidae ^A	X	X	X			
<i>Histiostoma medea</i>	Histiostomatidae ^A			X	X		
<i>Histiostoma varia</i>	Histiostomatidae ^A			X	X		
<i>Histiostoma sordida</i>	Histiostomatidae ^A		X	X			
<i>Histiogaster anops</i>	Acaridae ^A	X					
<i>Histiogaster arborsignis</i>	Acaridae ^A	X	X				X
<i>Histiogaster</i> sp.	Acaridae ^A			X			
<i>Nanacarus</i> sp.	Hemisarcoptidae ^A	X	X				
<i>Pachylaelapidae</i> sp.	Pachylaelapidae ^P		X				
<i>Parawinterschmidtia</i> sp.	Winterschmidita ^A	X	X			X	X
<i>Proctolaelaps dendroctoni</i>	Ascidae ^P				X		
<i>Proctolaelaps fiseri</i>	Ascidae ^P		X				
<i>Proctolaelaps hystrix</i>	Ascidae ^P	X					
<i>Proctolaelaps subcorticalis</i>	Ascidae ^P		X		X		
<i>Pyemotes</i> sp.	Pyemotidae ^A				X		
<i>Saproglyphus</i> sp.	Saproglyphidae ^P	X	X			X	X
<i>Schwiebia</i> sp.	Acaridae ^A	X	X	X			X
<i>Schizostethus lyriformis</i>	Parasitidae ^P				X		
<i>Tarsonemus ips</i>	Tarsonemidae ^A	X					X
<i>Tarsonemus krantzi</i>	Tarsonemidae ^A		X				
<i>Trichouropoda</i> sp.	Uropodidae ^P		X		X		X
<i>Trichouropoda denticulata</i>	Uropodidae ^P						X
<i>Trichouropoda hirsuta</i>	Uropodidae ^P		X				X
<i>Trichouropoda lamellosa</i>	Uropodidae ^P						X
<i>Uroobovella neoamericana</i>	Uropodidae ^P		X				
<i>Uroobovella orri</i>	Uropodidae ^P		X	X	X		X

^a Mite family; ^A Order Acariformes; ^P Order Parasitiformes

The strength and reliability of mutualisms greatly influence SPB dynamics. Palmer and others (2003) outlined three general factors that influence mutualism strength or specificity: 1. variability in the quality of alternative partner species, 2. the reliability/dependence of mutualist species, and 3. the effectiveness of partner selections. Thus, consistency is a key element of long-term mutualist associations, and mycangial fungi and the SPB is a good example (Klepzig and Six 2004). It is thought that the relative strength and importance of most mutualisms vary temporally and spatially with respect to the extent that they confer reciprocal benefit (Bronstein 2001). This implies that some level of context dependency is inherent in many mutualisms (Bronstein 1994), and in fact many species interactions in the SPB community range from mutualistic to commensalic to antagonistic, given varying sets of environmental conditions, resource quality, and presence of particular species (Klepzig and Six 2004). The relationship between the SPB and phoretic *Tarsonemus* provides an example: Tarsonemids phoretic on bark beetles carry weakly pathogenic fungi (*Ophiostoma* sp.) that are introduced to host trees during colonization by beetles. Fungi may aid beetles in overcoming tree defenses; however, they are generally antagonistic to beetle larvae and are actively avoided by the larvae and adults (Lombardero and others 2000c). In addition, context dependency is relevant to interactions between sympatric bark beetle species with a shared resource (e.g., *Ips avulsus* and SPB; Klepzig and others 2001a, 2001b), as interactions between species can also shift from mutualistic to antagonistic under varying conditions.

The classical view that mutualisms exist independently of other species and are bound by tightly evolved species interactions is being overturned in favor of the idea that many mutualist pairs act indirectly upon one another (Stanton 2003) and are influenced exogenously (e.g., temperature). Positive-species interactions are not always equally reciprocal (Bronstein 1994), and consequently, localized variations in fitness and fecundity for individual species potentially alter mutualism effects and ecological functionality. The relative ubiquity of mutualisms has consequences on SPB dynamics and resource capture, and speculation has arisen that mutualistic interactions play an equal role in shaping community structures, as do predation and competition (Berlow and others 2004, Hofstetter and others 2006a). The diversity and abundance of positive species interactions in the SPB community can facilitate complex interactions due to multiple mutualistic associations. Phoretic species and mutualists competing for access to the SPB is likely a very dynamic process that changes over both ecological and evolutionary time and at multiple spatial scales (Hofstetter and others 2006a, 2006b; Palmer and others 2003).

11.6. ACKNOWLEDGMENTS

This chapter is dedicated with gratitude to Dr. John C. Moser, whose extraordinary work with mites and other associates of bark beetles over his entire career has both driven and enriched the field of phoretic biology and bark beetle ecology.