

Review article

Symbiosis and Competition: Complex Interactions Among Beetles, Fungi and Mites

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Abstract

Symbioses among bark beetles and their fungal and mite associates involve complex, multi-level interactions. *Dendroctonus frontalis* attacks and kills southern pines, introducing fungi into the tree. *Ophiostoma minus*, may initially aid beetles in killing trees, but later this "bluestain" fungus becomes an antagonist, competing with larvae for host phloem. Two additional fungi, *Entomocorticium* sp. A and *Ceratocystiopsis ranaculosus* are carried within a specialized mycangium and inoculated into phloem where they are fed upon by beetle larvae. The beetle also vectors several species of phoretic mites which transport spores of *O. minus* and *C. ranaculosus* and can complete their life cycle upon these two fungi. A similar interaction occurs between *Ips avulsus* and its fungal (*Entomocorticium* spp.) and mite (*Elattoma bennetti*) symbionts. Larval beetles feed on fungus as do the mites.

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Female mites feed on fungus growing within beetle galleries, swelling to many times their normal size. Larval mites develop and mate within the females who burst open, giving birth to reproductively mature females. These relationships may be best understood by considering the manner in which symbioses vary with time and resources, and the degree to which other species may affect interactions among symbionts.

Keywords: Insect, fungus, mite, competition, bark beetle, *Ophiostoma*, symbiosis

1. Introduction

Symbiosis may be defined as the "Acquisition and maintenance of one or more organisms by another that results in novel structures and (or) metabolism" (Zook, 1998) ("or" added by authors). We consider herein two complex illustrations of symbiosis between tree killing bark beetles and the fungi and mites they carry.

While others have reviewed the biology and ecology of bark beetle-fungal interactions (Malloch and Blackwell, 1993; Paine et al., 1997), gaps still remain in our knowledge of the relative benefits accrued by the participants in these symbiotic interactions, and key biological details remain unrevealed. We have focused on interactions between a tree killing bark beetle (*Dendroctonus frontalis*) the fungi it vectors, and the phoretic mites it carries. We will briefly consider the interactions in this system (those seeking a more thorough consideration of the topic are directed to Klepzig and Wilkens, 1997; Lombardero et al., 2000; and Klepzig et al., 2000), and then reveal new information pertaining to another symbiotic interaction, that between a less aggressive bark beetle (*Ips avulsus*), the fungus it vectors and one of the mites it carries.

2. The Southern Pine Beetle

Dendroctonus frontalis Zimmermann (Coleoptera:Scolytidae) (Fig. 1a) is the most damaging forest insect in the southern United States (Thatcher et al., 1980; Drooz, 1985; Price et al., 1992). This beetle mounts mass attacks (initiated by females with the use of aggregation pheromones) and kills healthy trees (Paine et al., 1997). Mated female beetles chew egg galleries within the inner bark and phloem (Thatcher, 1960; Payne, 1983), inoculating several fungi in the process (Bramble and Holst, 1940) including *Ophiostoma minus* (Hedgc.) H. and P. Sydow, *Entomocorticium* sp. A (an undescribed basidiomycete, formerly referred to in the literature as isolate SJB122), and *Ceratocystiopsis*

ranaculosus Perry and Bridges. *O. minus* is an ascomycetous fungus which causes "bluestain" within infected wood and is carried phoretically on the *D. frontalis* exoskeleton (Rumbold, 1931; Bridges and Moser, 1983) and by phoretic mites (Bridges and Moser, 1983; discussed in detail below). While this fungus may aid *D. frontalis* in killing trees (Nelson, 1934; Caird, 1935; Bramble and Holst, 1940; Mathre, 1964; Basham, 1970), it is not required for tree death to occur (Hetrick, 1949; Bridges, 1985; Bridges et al., 1985). 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 et al., 1997). Because of this, and because the fungus benefits by receiving transport to new host tissue (Dowding, 1969), the *D. frontalis* - *O. minus* relationship – at the early stages of attack – may be defined as a mutualistic symbiosis. 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, 1970), and higher levels of *O. minus* thus correlate with lowered *D. frontalis* reproductive success (Lombardero et al., 2000). This antagonism between *O. minus* and *D. frontalis* larvae is due to interference by the fungus with interactions between the beetle and its two mutualistic fungi (Klepzig et al., 2000).

Each female *D. frontalis* possesses a prothoracic mycangium consisting of paired 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 et al., 1971). Within each side of the mycangium, the female maintains a pure culture of either *C. ranaculosus* (Barras and Taylor, 1973) or *Entomocorticium* sp. A (Barras and Perry, 1972; Happ et al., 1976; Hsiau, 1996). Each female may carry either one (rarely both) of the two fungi, or no fungi, in either of the two mycangial pouches (Bridges, 1985). 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 which quickly enlarge into obovate feeding chambers (Fig. 1b) (Payne, 1983) within which can be found abundant growth and sporulation of either of the two mycangial fungi. The larvae likely then feed on fungal hyphae and spores, receiving the majority of their nutrition (especially N) from the fungi and substantially benefit from the presence of these fungi (Bridges, 1985; Goldhammer et al., 1990; Coppedge et al., 1995; Ayres et al., 2000). The mycangial fungi receive protected, selective transport to the next available resource (Happ et al., 1971). The symbiosis between these organisms is clearly mutualistic (Klepzig et al., 2000).

In addition, over 96 species of mites are associated with *D. frontalis* (Moser and Roton, 1971). Among these associates are parasites, predators, fungivores

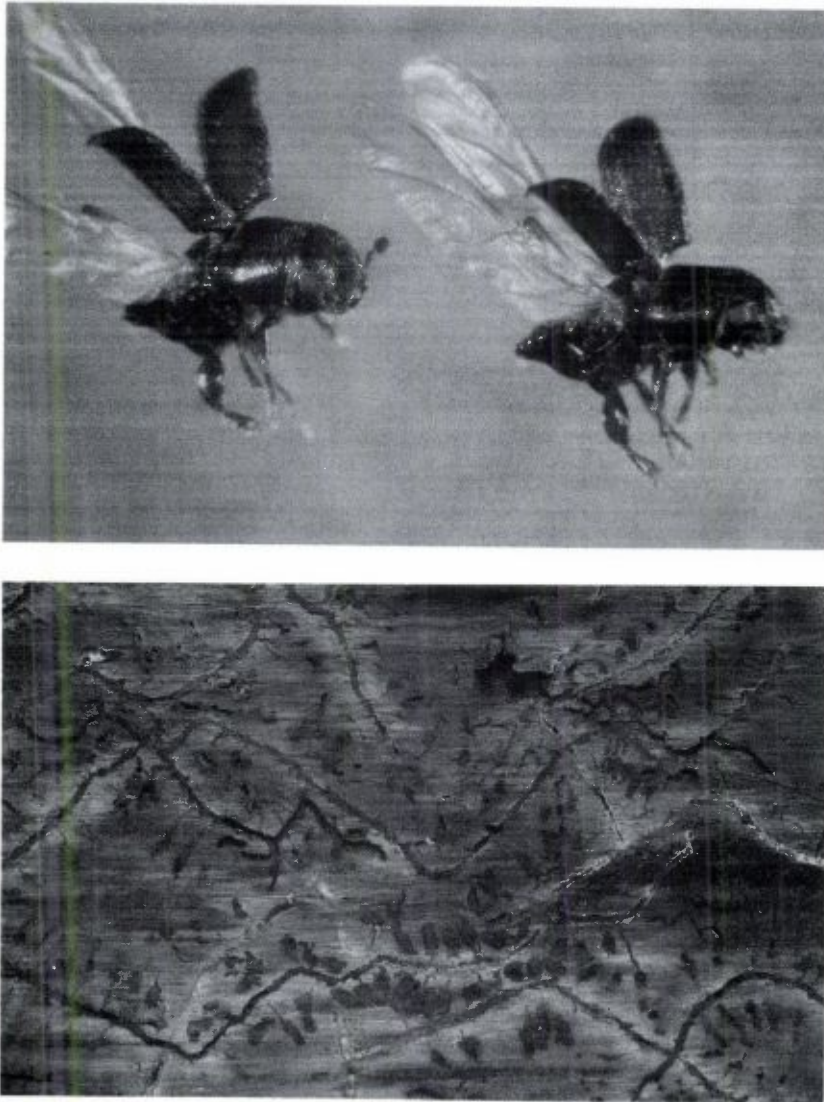


Figure 1. Southern pine beetle, *Dendroctonus frontalis*. A) Flying adult beetles, B) feeding galleries of larvae.

and omnivores (Moser and Roton, 1971; Moser et al., 1971, 1974). Of these, at least 14 species may be phoretic (Moser and Roton, 1971) in which the mite is transported on the external surface of the beetle and does not undergo feeding or ontogenesis during this period of transport (Lindquist, 1969; Smiley and Moser,



Figure 2. *Tarsonemus* sp. mite with flap like sporothecae (located on both sides of mite) containing ascospores of *Ceratocystiopsis ranaculosus*.

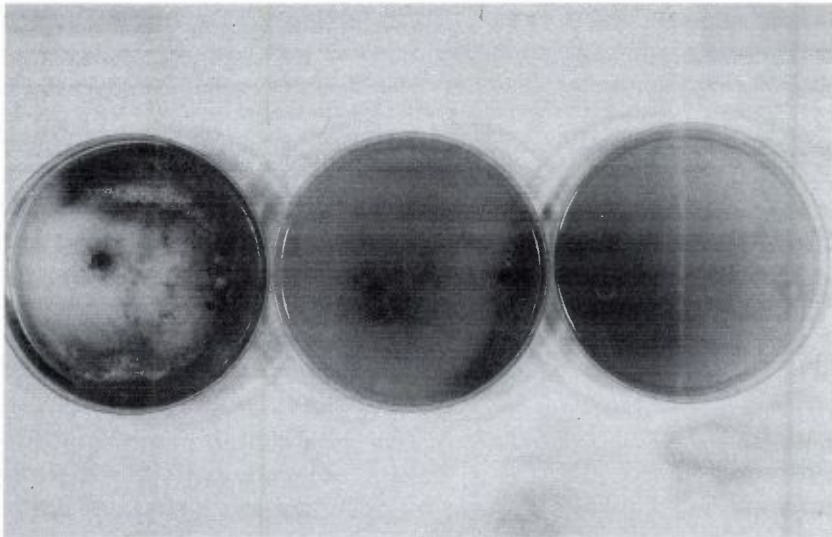


Figure 3. Primary resource capture competitive interactions between A) *Ophiostoma minus* and *Ceratocystiopsis ranaculosus*, B) *Ophiostoma minus* and *Entomocorticium* sp. A., and, C) *Ceratocystiopsis ranaculosus* and *Entomocorticium* sp. A.

1974). In particular, three *Tarsonemus* spp. – *T. ips* Lindquist, *T. krantzii* Smiley and Moser, and *T. fusarii* Cooreman (Moser and Roton, 1971; Smiley and Moser, 1974; Moser, 1976; Bridges and Moser, 1983; Moser and Bridges, 1986) are phoretic on *D. frontalis*, obtaining transport to host material with no directly deleterious effects on the beetle. However, the mites do appear to indirectly impact the *D. frontalis*-fungus-tree interaction (Lombardero et al., 2000; Klepzig et al., 2000). All three mites possess specialized, flap-like structures of the integument (Fig. 2). In *T. ips* and *T. krantzii*, these sporothecae frequently contain *O. minus* and *C. ranaculosus* ascospores (Bridges and Moser, 1983; Moser, 1985; Moser et al., 1995). Contributing to the complexity of this interaction, are the differential competitive capabilities of the *D. frontalis* associated fungi within host tree tissue.

O. minus, *Entomocorticium* sp. A, and *C. ranaculosus*, compete for uncolonized pine phloem. In competition experiments on uncolonized natural and artificial substrates the superior competitor is always *O. minus*, whose rapid growth rate and aggressive resource capture tactics overwhelm the mycangial fungi in primary resource capture (Klepzig and Wilkens, 1997). *Entomocorticium* sp. A. and *C. ranaculosus* are similar in their relative competitive abilities, suggesting a lack of differential competition. When direct confrontations occur between the fungi, the two mycangial fungi noticeably differ in their competitive abilities. *O. minus* quickly grows over *C. ranaculosus* colonies and captures the resource already held by this fungus. In contrast, direct interaction with *Entomocorticium* sp. A slows *O. minus* drastically. If *O. minus* grows after coming into contact with this fungus, it grows around the colony, never growing over the basidiomycete and never capturing the resource it holds (Fig. 3). This limitation on the growth and further spread of *O. minus* suggests either close range antibiotic production or localized nutrient depletion by *Entomocorticium* sp. A. It is important to consider, though, that these interactions are likely not static and that they may change in trees as environmental (abiotic) factors change (Callaway and Walker, 1997).

O. minus is clearly best able to colonize the phloem available in the early stages of *D. frontalis* attack, due especially to its rapid growth and relatively high tolerance of pine allelochemicals (Bridges, 1987). If *O. minus* does assist in killing trees, this is advantageous to the beetle and disadvantageous to the tree. As female beetles begin inoculating the mycangial fungi into the phloem of the attacked tree, the aggressively saprophytic characteristics of *O. minus* may become a disadvantage for *D. frontalis*. At this point, the female needs to establish colonies of the mycangial fungi to serve as a larval food source. *C. ranaculosus*, grows faster than *Entomocorticium* sp. A. but is not capable of excluding growth of *O. minus* enough to allow larval development (Klepzig and Wilkens, 1997). Given this and its apparent relative inferiority as a larval nutritional substrate (Bridges, 1983; Goldhammer et al., 1990; Coppedge et al.,

1995), *C. ranaculosus* appears to be of less value as a symbiont than *Entomocorticium* sp. A. *Entomocorticium* sp. A, grows more slowly than *C. ranaculosus*, but can grow and provide nutrition for *D. frontalis* larvae, even when surrounded by *O. minus*. Establishing a viable culture of *Entomocorticium* sp. A (apparently the most beneficial of the two mycangial fungi) may be a key to larval *D. frontalis* success. It is within this complex of competitive interactions that the phoretic mites appear to play their most significant role.

Despite their nebulous benefits as symbionts, both *O. minus* and *C. ranaculosus* are maintained within the *D. frontalis* system. This may be largely due to the role of *Tarsonemus ips* and *T. krantzi* as vectors of these two fungi. Tellingly, neither of these mites have ever been found to transport *Entomocorticium* sp. A. This dichotomy may be due to the different benefits accrued by the mite in exchange for vectoring these fungi. Both of these mites can successfully reproduce, and their offspring thrive (larval survival to first reproduction approximately equal to 90%), on colonies of *O. minus*. Both mites have positive growth rates when feeding upon new hyphal growth of the *O. minus* and *C. ranaculosus*. However, neither of these mites have significant population growth when feeding on the fungus they do not transport, *Entomocorticium* sp. A. In addition, field observations show that over ten times the number of *Tarsonemus* sp. mites are found within patches of *O. minus* infested phloem vs. other areas (Lombardero et al., 2000).

Thus, in this interaction, the mites play the role of facilitators of a symbiotic relationship by virtue of maintaining their own symbiotic relationship. By transporting certain fungi to serve as substrate for their own reproduction and development, the *Tarsonemus* mites indirectly influence the dynamics of the interactions between their beetle hosts, the fungi they interact with, and the tree host which contains them all. A similarly complex, though perhaps less highly evolved, relationship is found between a less aggressive beetle and the fungi and mites it carries.

3. The small southern pine engraver

Ips avulsus (Eichoff) (Fig. 4) is often considered along with its frequently co-occurring pine engraver species – *Ips calligraphus* (Germar) and *Ips grandicollis* (Eichoff). Together, these three bark beetles cause losses of millions of board feet of pine timber, although they usually only attack weakened or dying trees (Connor and Wilkins, 1983). Of the three, *I. avulsus* is one of the less aggressive and does not frequently kill trees (Mason, 1970). In this bark beetle species, the male initiates the attack, creating a nuptial chamber where he is joined by one to several females. The females create egg galleries and niches within the inner bark, sealing their eggs in place with bits of inner bark formed into plugs

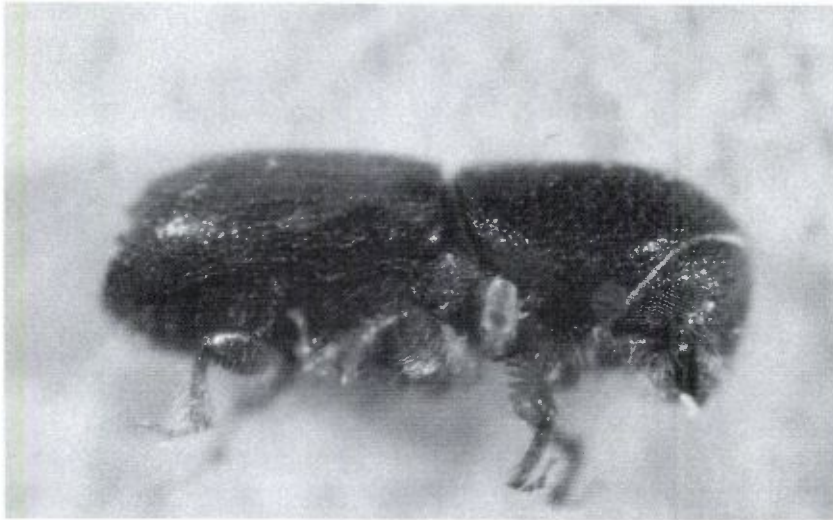


Figure 4. Smaller southern pine engraver, *Ips avulsus*, adult.

(Gouger et al., 1975; Moser and Roton, 1971). Once the larvae hatch, they feed in short, broad galleries, greatly enlarged at the distal end (similar to the types of galleries created by *D. frontalis* larvae and markedly dissimilar to those typically created by other *Ips* species).

As the larvae develop and eventually pupate, growth of a white, heavily sporulating fungus becomes obvious. This fungus [previously identified as a *Tuberculariella* sp. (Yearian, 1966), and an *Ambrosiella* sp. (Gouger, 1971)] is considered to be in the same genus - *Entomocorticium* - as the *D. frontalis* mycangial fungus (Sullivan, BT, personal communication). The fungal growth is so abundant that newly formed pupae are covered with spores (Gouger, 1971). In addition, newly emergent beetles graze on the fungal growth (Yearian, 1966).

Despite the similarities here to the gallery system, behavior and biology of *D. frontalis*, no mycangium has been discovered in *I. avulsus* (Gouger, 1971; Gouger et al., 1975). Instead, it has been hypothesized that the mutualistic *Entomocorticium* sp. is transmitted phoretically (by propagules adhering to the beetle exoskeleton) or via endozoic transfer (passage of propagules through the intestinal tract) (Gouger, 1971). Evidence does at least provide an indication that the mouthparts and digestive system are involved in the transmission of this fungus, whether or not a specialized structure exists to carry the spores. *Ips avulsus* guts contain a mixture of spores, starch, and fine grained tree tissues. Adult males and females both deposit gelatinous feces on the roof of the nuptial chamber. While entering trees, adult males pass frass between their



Figure 5. *Ips avulsus* phoretically carrying the mite *Elattoma bennetti* on legs.

mouthparts and front legs, compressing the moist phloem with their mouths before expelling it back into the gallery. While ovipositing, adult females use their mouthparts to close the end of each egg niche with a phloem plug (Gouger, 1971).

Regardless of this apparent dissimilarity in the mode of fungal transmission, there are some striking similarities in the manner in which both *D. frontalis* and *I. avulsus* interact with their fungal (and mite) symbionts. As in the *D. frontalis* system, *I. avulsus* carries a bluestain fungus – *Ophiostoma ips* (Rumbold) Nannf. – and there are apparently competitive interactions between this fungus and the nutritional mutualist of *I. avulsus* larvae (Yearian, 1966; Yearian et al., 1972). The interaction here seems to involve interference with larval mycophagy by the *Ophiostoma* sp. Wild populations (with their full mycoflora complement) are significantly more fecund and successful than are fungus free or *O. ips* infested populations (Yearian et al., 1972). Much as in the *O. minus*/*D. frontalis* interaction, *O. ips* renders pine logs unsuitable as breeding material for *I. avulsus* (Yearian, 1966). Areas fully colonized by the bluestain fungus become essentially unsuitable for beetle reproduction (although a few larvae may feed and survive). The dependence of *I. avulsus* larvae on their fungal mutualist is not obligatory, however. It is possible to successfully (although at a much reduced level of success) rear *I. avulsus* minus their fungal mutualist. These two beetles are also similar in the manner in which they interact with phoretic mites.

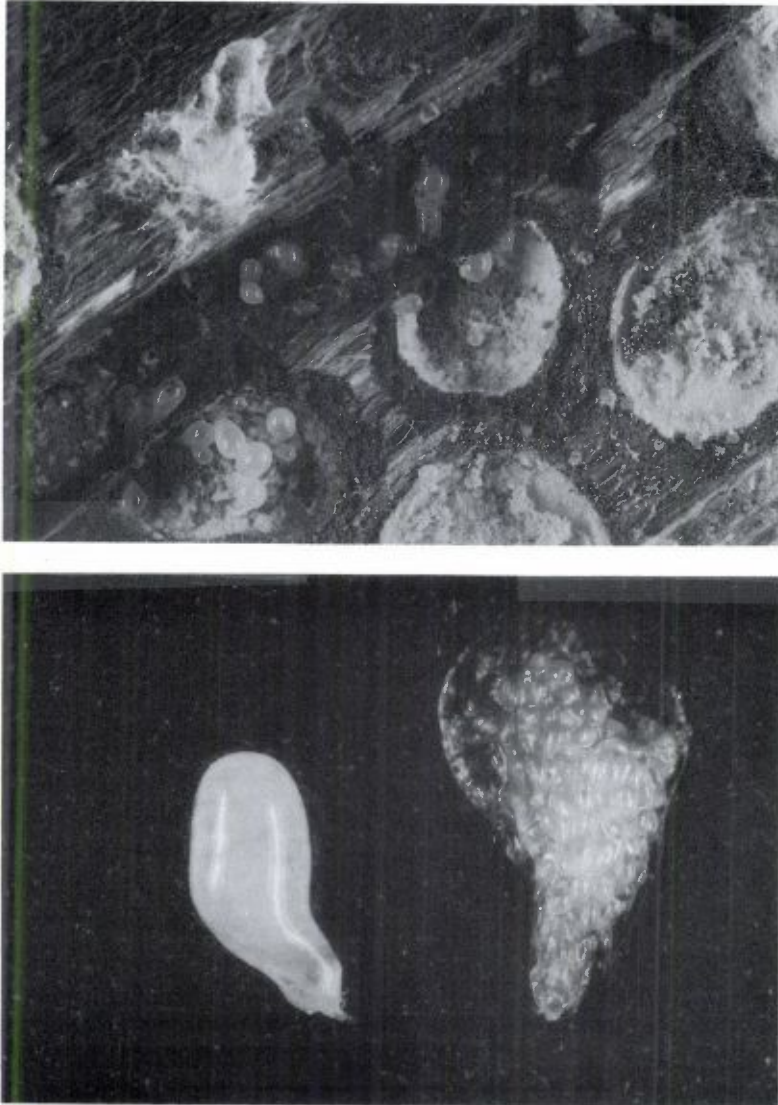


Figure 6. *Elattoma bennetti*. A) Feeding on symbiotic fungus of *Ips avulsus*, and B) physogastric female (left), ruptured female with newly emerged brood (right).

Ips avulsus is associated with a number of mite species (approximately) equal to that found associated with *D. frontalis*. Of these species, at least 13 are phoretic (Moser and Roton, 1971). One of the more noteworthy and biologically interesting mites associated with *I. avulsus* is *Elattoma bennetti*

(Fig. 5). We have observed this mite feeding within the *Entomocorticium* sp. lined galleries of *I. avulsus* (Fig. 6a). As the females feed they become physogastric (massively swollen) and thus more noticeable within the galleries (Fig. 6b). The female *E. bennetti* continue to feed and swell, nourishing developing larval mites within their abdomens. These developing mites mate while still inside the parent female who, after prolonged feeding and swelling, ruptures to give birth to reproductively mature adult mites (Fig. 6b). These mites are then ready to be carried phoretically to the next tree (and next source of *Entomocorticium* sp.) by emerging *I. avulsus*. As in the *D. frontalis* system, there is a high degree of dependence by a phoretic mite on the symbiotic fungus of its bark beetle host. The degree to which the mite affects the beetle-fungus relationship is unclear, although the possibility certainly exists for the mite to vector the fungus. At the very least, the life cycles of all three organisms are tightly interwoven, even interdependent.

4. Discussion

The interactions we have discussed here share several commonalities. Both interactions involve three very taxonomically distinct groups in tightly linked relationships. Both interactions involve intricate specializations on the part of the symbionts, whether morphological, physiological or behavioral, to maintain these interactions. Both interactions occur within the context of ecologically and economically important forest pest systems. And both interactions require novel research approaches to unravel the complexities within. These relationships may be best understood by considering, in a multidisciplinary fashion, the manner in which symbioses vary with time and resources, and the degree to which other species may affect interactions among symbionts. The similarities and differences between, and details of, these interactions may have implications to other arthropod-fungus symbioses as well.

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