

Acarine biodiversity associated with bark beetles in Mexico

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ABSTRACT: The phloem of dying trees provides habitat for a large number of bark beetles and their associated mites. These mites depend on the scolytids for moving from one place to another, and directly or indirectly for their nutrition. In Mexico, there have been very few works on this topic. The first three studies in Mexico included isolated records of these associations, while the last three refer to new records for several states in the country. A total of 62 mites species were recorded in the present study. The most diverse order was Mesostigmata with 66% of the recorded species, followed by the suborder Prostigmata with 24% and the cohort Astigmatina with 10%. *Trichouropoda polytricha* (Vitzthum, 1923), *Proctolaelaps subcorticalis* (Lindquist, 1971), *Proctolaelaps dendroctoni* Lindquist and Hunter, 1965, *Schizosthetus lyriformis* (McGraw and Farrier, 1969) and *Dendrolaelaps neodisetus* (Hurlbutt, 1967) were the most common species associated with bark beetles in this study. *Dendroctonus frontalis* Lindquist and Hunter, 1965 is the bark beetle with the highest reported number of associated mites in Mexico and worldwide. Among the species mentioned in this study, there was an interesting range of feeding habitats and habits. The different associations among beetles and mites provide an interesting topic for future research.

Keywords: Coleoptera, *Dendroctonus*, logs, natural forest, phoretic, symbiosis

INTRODUCTION

Among the bark beetles species, there are symbiotic interactions, many of which are maintained through multiple factors, such as climate, predation and the use of resources. Mites are important symbiotic organisms associated with bark beetles. More than one hundred species of mites have been reported from bark beetles worldwide; some phoretic species are associated with adult beetles and other invertebrates on infested trees (Hofstetter et al., 2013; Lindquist, 1969). Many of these mites depend on bark beetles or other insects to be transported inside the trees (Moser, 1985, Moser et al., 2010). Other studies report other microorganisms such as protozoa and nematodes in these associations (Perotti and Braig, 2011). The galleries of bark beetles (Coleoptera: Curculionidae: Scolytinae) are located under the bark of trees, and all developmental stages live there but other arthropods and microorganisms live and feed there (Lindquist, 1975).

The bark beetles are host species for a diverse community of arthropods and microorganisms that are found subcortically, mainly mites. Lindquist (1975) stated that the associations between mites and other arthropods can be based on a number of factors, namely: 1) the presence of a stable habitat that guarantees the supply of food resources and the protection of both organisms; 2) specificity for the habitat, in which the mite shows preference for the habitat and not for the host; 3) the mites specificity on the host; 4) specificity of the mites for a site on the host; and 5) synchrony of the life cycle of the mite with the insect, the cycle of the first one being shorter than that of

the host, and which represents an adapted state in which it remains until its biological cycle is synchronized with the host.

Several groups of mites are associated with these insects, forming dynamic, interspecific relationships. The relationships of mites and their hosts are defined by distinctive patterns, which have been shaped by long evolutionary processes, involving a succession of interactive responses, which resulted in different biorelationships (Hoffmann, 1988; Krantz and Walter, 2009). The importance of these relationships is that energy flows are created within the trophic networks and they contribute to the structuring of the ecosystem.

Mite communities that live in the galleries of bark beetles are not only associated with these insects but there are species that feed on fungi, leaf litter and other insects (Kaliszewski, 1993; Walter and Proctor, 1999). There is an extensive body of literature, especially related to *Dendroctonus frontalis* Zimmerman, 1868 (Kinn and Witcosky, 1978; Hofstetter, 2011; Hofstetter et al., 2013, Hofstetter et al., 2015), *D. rufipennis* Kirby, 1837 (Cardoza et al., 2008), *Ips typographus* (Linnaeus, 1758) (Takov et al., 2009), *Pityokteines* spp. (Pernek et al., 2008, 2012), and *Scolytus* spp. (Moser et al., 2010, but species associated with ambrosia beetles are just beginning to be studied. Mites are good examples of phoretic organisms; mites associated with insects are transported to new habitats, in which they each play different ecological roles.

The term phoresy (from the Greek *phora*: carry, have) defines one of the many kinds of association among animals (Trägårdh, 1943). Mites are the main examples. Farish and Axtell (1971) proposed a new definition: "Phoresy is a phenomenon in which an animal actively looks for and lives on the outer surface of another animal for a limited time, during which the linked animal (called a phoretic) stops feeding and development, presumably as a result of dispersal. This process is undoubtedly important in mites' evolution, which has followed different pathways in the Mesostigmata, Prostigmata and Astigmatina (Cross and Bohart, 1969). The families in which phoresy occurs are Macrochelidae, Parasitidae, Laelapidae, Ascidae, Eviphididae and some Uropodines, and some families from other groups, such as the Scutacaridae and Anoetidae (Athias-Binche, 1994; Reynolds et al., 2014)

The bark beetles galleries provide habitat for a large number of boring insects, mainly beetles and their associated mites. The best known mites are those associated with the genera *Dendroctonus*, *Ips*, *Tomicus*, *Hylesinus*, *Hylastes*, *Dryocoetes* and *Scolytus*, each having 15 to 20 species of associated mites, of which 10 or 12 can be common in scolytid habitat (Hofstetter and Moser, 2014). The relationship between the food webs in the galleries and on the bark beetles can be complicated. The feeding habits represented in galleries include fungivory, saprophagy (*Tarsonemus* spp., *Pygmephorus* spp., *Histiogaster* spp., *Histiostoma* spp., among others), polyphagy and nematophagy, as well as specialized predation in the early stages of bark beetles (*Digamasellus* spp., *Lasioseius* spp.) or as monophagous or oligophagous parasites of bark beetles larvae (*Pyemotes* spp., *Paracarophenax* spp. and *Iponemus* spp.) (Lindquist, 1970; Cross and Moser, 1971).

These groups have different degrees of morphological and physiological adaptations. They are usually associated with the insect nymphal stage. However, little is known about the biology of phoretic mite and the host. The discovery of a phoretic relationship guides us to a better understanding of the ecological role of both species (Binns, 1972).

There are records of mites associated with scolytids from 15 countries. Of the total of 178 species of mites, 96 are included in the order Mesostigmata (52%), 55 in the suborder Prostigmata (32%), 14 in the suborder Oribatida (8%) and 13 in the cohort Astigmatina (8%) (Chaires-Grijalva et al., 2012). In Mexico, some studies have been carried out on mites associated with scolytid beetles, especially on conifers (Table 1) (Gispert, 1983; Hoffmann and López-Campos, 2000; Chaires-Grijalva, 2013, 2015; Quiroz-Ibáñez, 2016; Quiroz-Ibáñez et al., 2017). However, due to the difficulty in observing subcortical mites, very little is known about their biology and behaviour. A common characteristic observed in the communities of scolytids is the diversity and the number of organisms present in the subcortical galleries. The main objective of the current study was to document the diversity of mites associated with different species of bark beetles, from 2000 to the present.

MATERIAL AND METHODS

Review of bark beetles collection. Visits were made to different collections of bark beetles and associated mites in Mexico and the USA, namely the Universidad Nacional Autónoma de México (UNAM) (National Collection of Mites), Escuela de Ciencias Biológicas of Instituto Politécnico Nacional (ENCB-IPN) (Mites collection ENCB-IPN), Universidad Autónoma Metropolitana (UAM), Universidad Autónoma Chapingo (UACH) (Acarology Collection), Colegio de Postgraduados (CP) Campus Montecillo (Acarology Collection), Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP) Campus Experimental Pabellón (Entomology and Acarology Collection), and Entomology collection of Centro Nacional de Investigación Disciplinaria en Conservación y Mejoramiento de Ecosistemas Forestales (CENID-COMEF). The United States Forest Service, Southern Research Station in Pineville, Louisiana (USDA - SF) (USDA - FS Forest Mite Collection) collection was also visited. In all of these collections, an exhaustive review of mite species associated with bark beetles.

Sampling. In addition, samples of bark and logs showing signs of damage by bark beetles (Scolytinae) were obtained from 24 states of Mexico from April 2007 to November 2017. The samples were from the following states: Aguascalientes, Baja California, Ciudad de México, Chiapas, Chihuahua, Coahuila, Colima, Durango, Guanajuato, Hidalgo, Jalisco, México, Michoacán, Morelos, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Sonora, Tlaxcala, Veracruz and Zacatecas (Figure 1). The samples were transported in plastic bags and transferred to Forest Entomology Laboratory at Colegio de Postgraduados, for mite revision under a stereoscopic microscope. The logs were placed in emergence chambers to collect insect adults and then the mites were separated from them.



Figure 1. Sampling states for scolytins and associated mites in Mexico.

Bark beetle identifications. Bark beetles and associated arthropods were collected from bark and log samples with forceps and then placed in separate vials with ethanol. Mites attached to the collected bark beetles were removed and placed in a solution of lactic acid to clear. The specimens collected from the bark beetles were identified by using the keys of Cibrian et al. (1995) and Wood

(2007). The bark beetle identifications were corroborated by Dr. Armando Equihua-Martínez, a scolytin specialist in Mexico.

Mite identifications. Mites attached to the collected bark beetles were removed from each individual, placed in a solution of lactic acid to clear them, mounted on glass slides using Hoyer's medium and identified. In addition to the phoretic associates collected on bark beetles, mites and other organisms found in the bark beetle galleries were also collected and observed. During a visit to the laboratory of the Forest Service of the USA, the first author reviewed the world's largest collection of mites associated with bark beetles. The diagnostic characteristics of the species collected in this work were compared by means of two optical microscopes with phase contrast. The mites were identified by using the keys of Lindquist and Evans (1965), Lindquist and Hunter (1965), McGraw and Farrier (1969), Cross and Moser (1971), Lindquist (1971) and Karg (1993). The species were corroborated by Dr. John C. Moser. The mites were deposited in the personal collection of Dr. Edith G. Estrada-Venegas.

RESULTS

A total of 13,859 mites were collected, including 62 species of mites belonging to three orders, namely: Mesostigmata (41), Trombidiformes (suborder Prostigmata) (15) and Sarcoptiformes (suborder Oribatida, cohort Astigmatina) (6) (Figure 2). The number of species recorded until 1983 was 29; they were included in two orders (Mesostigmata, and Trombidiformes) (in Table 1). It should be noted that from 1983 to 2007 no new results were reported for Mexico.

From the samplings made since 2007, 37 are new records for Mexico (Table 2). Twenty four species (65%) belong to the order Mesostigmata of the species, 10 species (27%) to Trombidiformes (suborder Prostigmata) and three species (8%) to Sarcoptiformes (suborder Oribatida, cohort Astigmatina).

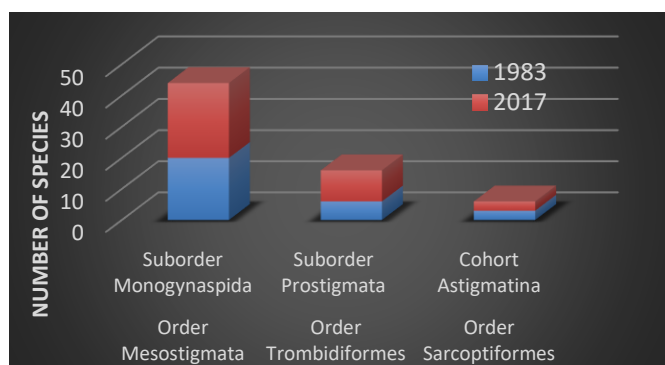


Figure 2. Mite orders associated with bark beetles.

The mesostigmatid mites were the most diverse, with 66% above of the recorded species. In this order are included nine families, as shown in Table 2 and Figure 3. The suborder Prostigmata contributed 24% above of species in three families and the cohort Astigmatina with two families contributed 10% of species. Within the populations collected, the females were most abundant (8415), followed by nymphs (5172).

Ereynetidae and Acaridae were the most abundant families but the most diverse families were Tarsonemidae with eight species and Trematuridae with seven species. The most common species are *Trichouropoda polytricha*, *Proctolaelaps subcorticalis*, *Elattoma* sp. and *Histiogaster* sp. The best represented states of Mexico were Chihuahua, Jalisco and Veracruz.

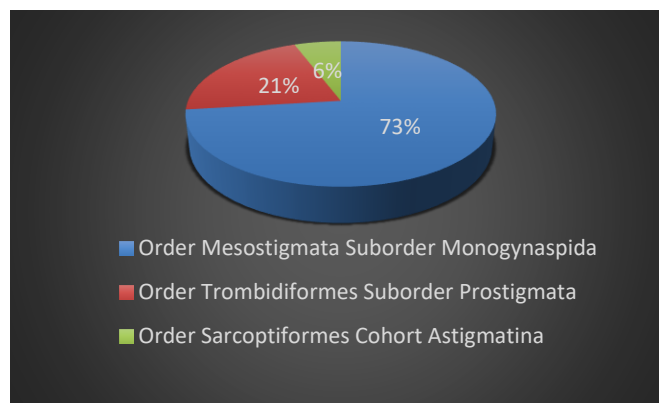


Figure 3. Percentage of species per suborder found in current samplings in Mexico.

DISCUSSION

A great diversity of mesostigmatid mites is associated with bark beetles, although there is no clear distinction between truly cortical species and those that exist on the forest floor (Beaulieu et al., 2006). However, many species of mites live exclusively in decaying wood and subcortically, environments in which they have complex relationships with bark beetles. These mites rely on subcortical insects for their dispersal and introduction into suitable habitats for survival (Szymkowiak et al., 2007)

Mite communities can be large and complex, with multiple food guilds and trophic levels (Lindquist, 1969, McGraw and Farrier, 1969). However, due to the difficulty in observing subcortical mites, very little is known about their biology and behaviour. A common characteristic observed in communities of scolytins are the diversity and the number of organisms present in the subcortical galleries.

There are four dominant groups in the galleries; bark beetles, mites, nematodes and fungi. Barras (1979) has described the subcortical ecosystem of the scolytins as a "supra-organism" due to the co-evolutionary relationships existing in it.

The greatest diversity of mite associations with other arthropods occurs in the Mesostigmata. These associations include occasional, facultative or obligatory phoresy for dispersal. The complexity of these associations suggests a long history of evolution between these mites and their hosts. These range from the synchronization of the life cycle of both species, morphological adaptations, special mechanisms of fixation, physiological adaptations such as resistance to dehydration, cessation of development and metabolic reduction and the absence of response to normal stimuli, such as food, mating behaviour, humidity and temperature (Szymkowiak et al., 2007; Walter and Proctor, 2013).

Table 1. Mite species reported associated with bark beetles in Mexico until 1983

Species	Animal host	Plant host	Reference
ORDER MESOSTIGMATA			
TREMATURIDAE			
<i>Trichouropoda australis</i> (Hirschmann, 1972)	<i>D. frontalis</i> <i>I. bonanseai</i>	<i>P. hartwegii</i>	Moser et al., 1974
<i>Trichouropoda hirsuta</i> (Hirschmann, 1972)	<i>D. frontalis</i>	Not recorded	Moser and Roton, 1971
<i>Trichouropoda polytricha</i> (Vitzthum, 1923)	<i>I. bonanseai</i> <i>I. typographus</i>	<i>P. hartwegii</i>	Moser et al., 1989
PARASITIDAE			
<i>Schizosthetus lyriformis</i> (McGraw and Farrier, 1969)	<i>D. frontalis</i>	<i>P. echinata</i> <i>P. taeda</i> <i>P. oocarpa</i> <i>P. contorta</i>	McGraw and Farrier, 1969; Moser et al., 1974; Gispert, 1983
DIGAMASELLIDAE			
<i>Dendrolaelaps neodisetus</i> (Hurlbutt, 1967)	<i>D. frontalis</i> <i>I. bonanseai</i>	<i>P. hartwegii</i>	Moser and Roton, 1971; Gispert, 1983; McGraw and Farrier, 1969
<i>Dendrolaelaps quadrisetus</i> (Berlese, 1920)	<i>D. frontalis</i> <i>I. calligraphus</i>	<i>P. virginiana</i> <i>P. echinata</i> <i>P. taeda</i>	Gispert, 1983
<i>Dendrolaelaps</i> sp.	<i>Ips bonanseai</i>	<i>P. hartwegii</i>	Gispert, 1983
MACROCHELIDAE			
<i>Macrocheles boudreauxi</i> (Krantz, 1965)	<i>D. frontalis</i>	<i>P. echinata</i> <i>P. taeda</i> <i>P. arizonica</i>	Moser and Roton, 1971
ASCIDAE			
<i>Arctoseius cetratus</i> (Sellnick, 1940)	<i>I. bonanseai</i>	<i>P. hartwegii</i>	Gispert, 1983
<i>Arctoseius semicissus</i> (Berlese, 1892)	<i>I. cribicollis</i>	<i>P. montezumae</i>	Gispert, 1983
<i>Asca pini</i> (Hurlbutt, 1963)	<i>I. bonanseai</i>	<i>P. hartwegii</i>	Gispert, 1983
<i>Lasioseius corticeius</i> (Lindquist, 1971)	<i>I. bonanseai</i>	<i>P. hartwegii</i>	Gispert, 1983
<i>Lasioseius safroi</i> (Ewing, 1920)	<i>D. frontalis</i>	<i>P. hartwegii</i>	Gispert, 1983
<i>Proctogastrolaelaps libris</i> (McGraw and Farrier, 1969)	<i>D. frontalis</i> <i>S. multistriatus</i>	<i>P. echinata</i>	McGraw and Farrier, 1969
<i>Proctoalelaps dendroctoni</i> (Lindquist and Hunter 1965)	<i>D. frontalis</i>	<i>P. contorta</i>	Lindquist, 1971; Moser et al., 1974; Gispert, 1983
<i>Proctolaelaps hystricoides</i> (Lindquist and Hunter, 1965)	<i>D. frontalis</i>	<i>P. montezumae</i>	Moser et al., 1974
<i>Proctolaelaps hystrix</i> (Vitzthum, 1923)	<i>D. frontalis</i> <i>D. rhizophagus</i>	<i>P. taeda</i> <i>P. arizonica</i> <i>P. montezumae</i>	Moser et al., 1974
<i>Proctolaelaps subcorticalis</i> (Lindquist, 1971)	<i>D. frontalis</i> <i>I. bonanseai</i>	<i>P. leiophylla</i>	McGraw and Farrier, 1969; Moser et al., 1974; Gispert, 1983
<i>Gamasolaelaps subcorticalis</i> (McGraw and Farrier, 1969)	<i>D. frontalis</i> <i>I. avulsus</i> <i>I. calligraphus</i> <i>I. lecontei</i>	<i>P. taeda</i> <i>P. oocarpa</i>	McGraw and Farrier, 1969
ORDER TROMBIDIFORMES			
SUBORDER PROSTIGMATA			
TARSONEMIDAE			
<i>Tarsonemus endophloeus</i> (Lindquist, 1969)	<i>D. frontalis</i>	<i>P. hartwegii</i>	Moser et al., 1974
<i>Tarsonemus ips</i> (Lindquist, 1969)	<i>D. frontalis</i>		Moser et al., 1974
<i>Tarsonemus triarcus</i> (Lindquist, 1969)	<i>I. bonanseai</i>	<i>P. hartwegii</i>	Gispert and Atkinson, 1982
<i>Ereynetes scutulalis</i> (Hunter, 1964)	<i>D. frontalis</i>		Moser et al., 1974
<i>Heterotarsonemus lindquisti</i> (Smiley, 1969)	<i>D. frontalis</i>		Moser et al., 1974; Lindquist, 1969
<i>Pyemotes</i> sp.	<i>D. frontalis</i>		Moser et al., 1974
ORDER SARCOPTIFORMES			
COHORT ASTIGMATINA			
ACARIDAE			
<i>Histiogaster arborsignis</i> (Woodring, 1963)	<i>D. frontalis</i>		Moser et al., 1974
<i>Histiogaster rotundus</i> (Woodring, 1966)	<i>D. frontalis</i>		Moser et al., 1974
<i>Tyrophagus putrescentiae</i> (Schrank, 1781)	<i>D. frontalis</i>		Gispert and Atkinson, 1982

In the present study, mesostigmatid mites, contributed the highest number of species associated with bark beetles, mainly in 8 families. Ascidae and Digamasellidae contributed the most species, with the genera *Lasioseius*, *Proctolaelaps*, *Dendrolaelaps* and *Trichouropoda* frequently found in association with 11 bark beetle species, with *Dendroctonus frontalis* (Zimmerman, 1868) being the species with the highest number of mites species.

Moser (1975) reported that *Proctolaelaps dendroctoni*, *P. hystricoides*, *P. hystrix*, *Dendrolaelaps neocornutus*, *D. neodisetus*, *Macrocheles boudreauxi* and *Schizosthetus lyriformis* are natural enemies of *D. frontalis* in Louisiana in the United States of America, while the *Dendrolaelaps quadrisetus*, *Arctoseius cetratus*, *Asca pini*, *Lasioseius cortiseius*, *L. safroii*, *Proctolaelaps subcorticalis* and *Androlaelaps casalis* are only possible candidates as biological control agents (Chaires-Grijalva et al., 2013) However, the impact of these mites on bark beetles in Central America has never been evaluated.

The deutonymphs of the family Trematuridae in the genus *Trichouropoda* were the most abundant; this is the main stage for their dispersion (Bajerlein, 2013), trematurids mites grouped in the elytral decline and ventral surface. In other mesostigmatid families, females have been recorded as the main stages for dispersal and establishment on different hosts (Lindquist, 1969; Moser and Roton, 1971; Krantz and Walter, 2009), which is supported by the results obtained in this work. The phoretic relationships that mites have developed with the scolytins have facilitated specializations.

CONCLUSIONS

In this study, the Mesostigmata contributed 66% of the species, followed by the suborder Prostigmata with 24% and the cohort Astigmatina with 10%. *Trichouropoda polytricha*, *Proctolaelaps subcorticalis*, *Proctolaelaps dendroctoni*, *Schizosthetus lyriformis* and *Dendrolaelaps neodisetus* are the most commonly reported species associated with bark beetles and were reported in all the studies that have been carried out in Mexico. The great diversity is mainly due to the variety of food resources, as well as the great adaptability of the mites present. Among the species mentioned in this study there is an interesting range of feeding habits, as well as habitats and associations with different organisms.

Dendroctonus frontalis is the bark beetle with the highest number of associated mites in Mexico and worldwide (Chaires-Grijalva, 2013). As demonstrated in this study, there is a great diversity of mites associated with bark beetles; this is mainly due to the variety of food resources that bark beetle galleries provide, as well as the wide range of adaptations they have for the different environments in which they occur. Among the species mentioned in this study there is an interesting range of trophic habits, as well as habitats, and different associations that make these groups worthy of more study.

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Table 2. Species reported associated with bark beetles in Mexico from 2007 to 2017

Species	Mites collected			Animal host	Plant host
	♀	♂	Nymph		
ORDER MESOSTIGMATA					
SEJIDAE					
<i>Sejus boliviensis</i> Hirschmann and Kaczmarek, 1991	5	2	1	<i>D. frontalis</i>	<i>P. hartwegii</i>
NENTERIDAE					
<i>Nenteria ca. breviunguiculata</i> Willmann, 1949			9	<i>D. frontalis</i>	<i>P. hartwegii</i>
<i>Nenteria</i> sp.	1			<i>D. frontalis</i>	<i>P. teocote</i>
TRICHOUROPODIDAE					
<i>Trichouropoda adjuncti</i> Wisniewski and Hirschmann, 1988			54	<i>D. frontalis</i>	<i>P. hartwegii</i>
<i>Trichouropoda australis</i> Wisniewski and Hirschmann, 1988	9			<i>D. frontalis</i>	<i>P. hartwegii</i>
<i>Trichouropoda hondurasae</i> Hirschmann and Wisniewski, 1986			38	<i>D. frontalis</i>	<i>P. teocote</i>
<i>Trichouropoda fallax</i> Vitzthum, 1926	2		11	<i>D. frontalis</i>	<i>P. teocote</i>
<i>Trichouropoda ovalis</i> (C.L. Koch, 1839)			62	<i>D. rhizophagus</i>	<i>P. arizonica</i>
<i>Trichouropoda polytricha</i> (Vitzthum, 1923)	4	1	135	<i>I. bonanseai</i> <i>I. typographus</i>	<i>P. hartwegii</i>
<i>Trichouropoda</i> sp. 1			6	<i>D. frontalis</i>	<i>P. teocote</i> <i>P. hartwegii</i>
<i>Trichouropoda</i> sp. 2			18	<i>D. frontalis</i>	<i>P. teocote</i> <i>P. hartwegii</i>
<i>Trichouropoda</i> sp. 3			17	<i>D. frontalis</i>	<i>P. teocote</i> <i>P. hartwegii</i>
<i>Trichouropoda</i> sp. 4			31	<i>D. frontalis</i>	<i>P. teocote</i> <i>P. hartwegii</i>
<i>Trichouropoda</i> sp. 5			4	<i>D. frontalis</i>	<i>P. teocote</i> <i>P. hartwegii</i>
<i>Trichouropoda</i> sp. 6			1	<i>D. frontalis</i>	<i>P. teocote</i> <i>P. hartwegii</i>
<i>Trichouropoda</i> sp. 7			4	<i>D. frontalis</i>	<i>P. teocote</i> <i>P. hartwegii</i>
PARASITIDAE					
<i>Schizosthetus lyriformis</i> (McGraw and Farrier, 1969)	10	1	30	<i>D. frontalis</i> <i>D. valens</i> <i>I. bonanseai</i> <i>I. calligraphus</i> <i>I. confusus</i> <i>I. grandicollis</i> <i>P. mexicanus</i>	<i>P. echinata</i> <i>P. taeda</i> <i>P. oocarpa</i> <i>P. contorta</i>
DIGAMASELLIDAE					
<i>Dendrolaelaps neocornutus</i> (Hurlbutt, 1967)	17	3	5	<i>D. frontalis</i> <i>D. rhizophagus</i>	<i>P. echinata</i> <i>P. arizonica</i>
<i>Dendrolaelaps neodisetus</i> (Hurlbutt, 1967)	17		9	<i>D. frontalis</i> <i>I. bonanseai</i>	<i>P. hartwegii</i>
<i>Dendrolaelaps quadrisetus</i> (Berlese, 1920)	8			<i>D. frontalis</i>	<i>P. hartwegii</i>
<i>Dendrolaelaps</i> sp.	2			<i>D. frontalis</i>	<i>P. oocarpa</i>
MACROCHELIDAE					
<i>Macrocheles boudreauxi</i> (Krantz, 1965)	6	1	1	<i>D. frontalis</i>	<i>P. arizonica</i> <i>P. echinata</i> <i>P. taeda</i>
<i>Macrocheles</i> sp.			11	<i>D. frontalis</i>	<i>P. arizonica</i>
ASCIDAE					
<i>Arctoseius cetratus</i> (Sellnick, 1940)	2			<i>I. bonanseai</i>	<i>P. hartwegii</i>
<i>Arctoseius semicissus</i> (Berlese, 1892)	5			<i>I. cribicollis</i>	<i>P. montezumae</i>
<i>Asca pini</i> (Hurlbutt, 1963)	8		2	<i>I. bonanseai</i>	<i>P. hartwegii</i>
<i>Lasioseius corticeius</i>	1		1	<i>I. bonanseai</i>	<i>P. hartwegii</i>
<i>Lasioseius dentatus</i> Fox, 1946	1			<i>D. frontalis</i>	<i>P. hartwegii</i>
<i>Lasioseius imitans</i> Berlese, 1910	10		4	<i>D. adjunctus</i>	<i>P. hartwegii</i>
<i>Lasioseius safroi</i> (Ewing, 1920)	29		8	<i>D. adjunctus</i> <i>D. frontalis</i> <i>I. bonanseai</i>	<i>P. hartwegii</i>
<i>Lasioseius</i> sp.	26		3	<i>D. frontalis</i>	<i>P. teocote</i>

Table 2. Species reported associated with bark beetles in Mexico from 2007 to 2017 (Continued)

Species	Mites collected			Animal host	Plant host
	♀	♂	Nymph		
ORDER MESOSTIGMATA					
MELICHARIDAE					
<i>Proctolaelaps dendroctoni</i> (Lindquist and Hunter, 1965)	28	1	7	<i>D. frontalis</i> <i>D. ponderosae</i>	<i>P. contorta</i>
<i>Proctolaelaps hystricoides</i> (Lindquist and Hunter, 1965)	14		4	<i>D. frontalis</i>	<i>P. echinata</i> <i>P. montezumae</i> <i>P. taeda</i>
<i>Proctolaelaps hystrix</i> (Vitzthum, 1923)	17	3	5	<i>D. frontalis</i> <i>D. rhizophagus</i>	<i>P. arizonica</i> <i>P. montezumae</i> <i>P. taeda</i>
<i>Proctolaelaps subcorticalis</i> (Lindquist, 1971)	93	3	41	<i>D. frontalis</i> <i>D. mexicanus</i> <i>I. bonanseai</i> <i>I. cribicollis</i>	<i>P. leiophylla</i> <i>P. montezumae</i>
<i>Proctolaelaps</i> sp.	57			<i>S. schevyrewi</i>	<i>U. pumila</i>
LAELAPIDAE					
<i>Androlaelaps casalis</i> Berlese, 1887	1			<i>D. frontalis</i>	<i>P. teocote</i>
<i>Hypoaspis</i> (<i>Cosmolaelaps</i>) ca. <i>Vacua</i> Michael, 1891	26	2	8	<i>D. frontalis</i>	<i>P. teocote</i> <i>P. hartwegii</i>
ORDER TROMBIDIFORMES					
SUBORDER PROSTIGMATA					
PYGMEPHORIDAE					
<i>Elattoma</i> sp.	7200			<i>I. calligraphus</i>	<i>P. chiapensis</i>
TARSONEMIDAE					
<i>Tarsonemus ips</i> (Lindquist, 1969)	6			<i>D. frontalis</i>	<i>P. teocote</i>
<i>Tarsonemus krantzi</i> (Smiley and Moser, 1974)	17			<i>D. frontalis</i>	<i>P. teocote</i>
<i>Tarsonemus</i> sp.1	2			<i>D. frontalis</i>	<i>P. teocote</i>
<i>Tarsonemus</i> sp.2	40	6		<i>D. frontalis</i>	<i>P. teocote</i>
<i>Tarsonemus</i> sp.3	26			<i>D. frontalis</i>	<i>P. teocote</i>
<i>Tarsonemus</i> sp.4	5	2		<i>D. frontalis</i>	<i>P. teocote</i>
<i>Tarsonemus</i> sp.5	2			<i>D. frontalis</i>	<i>P. teocote</i>
<i>Tarsonemus</i> sp.6	2			<i>D. frontalis</i>	<i>P. teocote</i>
<i>Tarsonemus</i> sp.7	2			<i>D. frontalis</i>	<i>P. teocote</i>
<i>Tarsonemus</i> sp.8	2			<i>D. frontalis</i>	<i>P. teocote</i>
EREYNETIDAE					
<i>Ereynetes scutulis</i> (Hunter, 1964)	10			<i>D. frontalis</i>	<i>P. teocote</i>
ORDER SARCOPTIFORMES					
COHORT ASTIGMATINA					
ACARIDAE					
<i>Histiogaster</i> sp.	700	243	2374	<i>S. schevyrewi</i>	<i>U. pumila</i>
<i>Cosmoglyphus</i> sp.			1279	<i>S. schevyrewi</i>	<i>U. pumila</i>
HISTIOSTOMATIDAE					
<i>Histiostoma varia</i> (Woodring and Moser, 1970)			980	<i>I. calligraphus</i>	<i>P.chiapensis</i>

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