TARSONEMID MITE ASSOCIATES OF *DENDROCTONUS FRONTALIS* (COLEOPTERA: SCOLYTIDAE): IMPLICATIONS FOR THE HISTORICAL BIOGEOGRAPHY OF *D. FRONTALZS*

JOHN C MOSER[1]

Southern Research Station, USDA Forest Service, 2500 Shreveport Hwy., Pineville, Louisiana. United States 71360

and JORGE E MACÍAS-SÁMANO

Colegio de la Frontera Sur, Carret. Antiguo Aeropuerto Km 2.5, Apartado Postal 36, 30700 Tapachula, Chiapas, Mexico

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Abstract

Seven species of mites (Acari: Tarsenomidae) were associated with two local outbreaks of the southern pine beetle, *Dendroctonus frontalis* Zimmerman, in Chiapas, Mexico; three of these species were new records for Mexico and Central America. The morphology and phoretic behavior of these mites differed little between the western and southern populations from the United States. One major difference was that the hyperphoretic ascospores of the southern pine beetle mycangial fungus, *Ceratocystiopsis* sp. (Ophiostomataceae), were common in sporothecae of *Tarsonemus krantzi* Smiley and Moser (Acari: Tarsonemidae) and *Tarsonemus ips* Lindquist in Chiapas, Mexico, whereas the ascospores of the blue stain fungus, *Ophiostoma minus* (Hedgcock) H. and P. Sydow (Ophiostomataceae), were rare; this situation in the southern United States is reversed. The paucity of behavioral and morphological differences between the two southern pine beetle populations and the relevant historical climatology suggest that the appearance of *D. frontalis* in the southern United States may be a recent event.

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Résumé

Sept especes d'acariens (Acari : Tarsonemidae) ont été observées associées à deux foyers d'infestation du scolyte, *Dendroctonus frontalis* Zimmermann, dans l'état du Chiapas au Mexique. Trois de ces espèces sont nouvelles au Mexique et en Amérique Centrale. La morphologie et le comportement phorétique de ces acariens different peu chez les populations occidentales et méridionales des États-Unis. Cependant, parmi les differences principales, il faut mentionner que les ascospores hyperphorétiques du champignon mycangial du Dendroctone meridional du pin, *Ceratocystiopsis* sp. (Ophiostomataceae), sont frequents dans les sporothèques de *Tarsonemus krantzi* Smiley et Moser (Acari : Tarsonemidae) et de *Tarsonemus ips* Lindquist au Chiapas (Mexique), alors que les ascospores du champignon de la tache bleue, *Ophiostoma minus* (Hedgcock) H. et P. Sydow (Ophiostomataceae), sont rares et que cette situation est inversée dans le sud des États-Unis. La rareté des differences morphologiques et Cthologiques entre les deux populations de même que certains événements climatologiques semblent indiquer que l'apparition de *D. frontalis* dans le sud des États-Unis est vraisemblablement un événement recent.

[1] Author to whom all correspondence should be addressed (E-mail: jmoser@fs.fed.us).

Introduction

One of the most interesting of the 22 families of mites associated with the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), from Mexico and Central America (Moser et al. 1974; Hoffman and Gispert 1980) is the family Tarsonemidae (Acari). This family comprises not only parasitoids of potential interest for the biological control of southern pine beetle in the southern United States, but also important fungivores which consume and transmit ascomycete fungi that may be either detrimental or beneficial to southern pine beetle nutrition (Moser 1985; Moser *et al.* 1995; Lombardaro *et al. 2000).*

The parasitoids (*Iponemus* spp. Lindquist) (Acari: Tarsonemidae) are normally phoretic on the elytral declivities of *Ips* DeGeer (Coleoptera: Scolytidae) spp., but individual mites occasionally phoresitize *D. frontalis* and attack its eggs (Moser and Roton 1971). Although parasitism may reach as high as 90% (Gaebler 1947), our observations indicate that infestations are usually 5% or less. Each species of fungivore [*Tarsonemus* Canestrini and Fanzago (Acari: Tarsonemidae) spp.] has different phoretic preferences as to which species of beetle they ride and where on the beetle they ride (Moser and Roton 1971). They reproduce best on one or more species of subcortical fungi and may introduce negative feedback into *D. frontalis* population dynamics by generating indirect interactions between *D. frontalis* and at least one species of the subcortical fungi (Lombardaro *et al. 2000).*

We list here the tarsonemid species found with the southern pine beetle and its mite associates from two southern pine beetle outbreaks on *Pinus oocarpa* Schiede ex Schlechtendal (Pinaceae) within two localities in Chiapas, Mexico, and discuss the roles these mites may play in the dispersal of the ascospores of fungi important to the development of southern pine beetle larvae. We also compare various behaviors of these Mexican mite species and contrast them to those same species associated with southern pine beetle in the southern United States.

Methods and Materials

We selected two southern pine beetle infestations in Chiapas, Mexico. We collected tarsonemid mites by inspecting the inner bark of southern pine beetle infested *P. oocarpa* from bolts cut at a height of about 5 m and from flying southern pine beetle adults near Motozintla (15°15′N, 92°15′W, elevation 1480 m) in southwestern Chiapas. Collections from inner bark were made on 21-27 April 1998 at Motozintla from trees from which southern pine beetle were emerging, and on 13-17 April 1999 at Teopisca (16°57′N, 92°30′W, elevation 2230 m) in eastern Chiapas, from which southern pine beetle adults were callow and just emerging. The inner bark at Motozintla was moist (favoring mite diversity and abundance) and thick, allowing the southern pine beetle to normally pupate in outer bark pupal chambers, whereas at Teopisca the bark was semidry, reducing mite diversity and abundance (Moser and Bridges 1983), and thin, which resulted with many, if not most, of the southern pine beetle pupal chambers being abnormally exposed to the air when the bark was removed. The inner bark from both locations contained numerous patches of bluestain, *Ophiostoma minus* and (or) *Ophiostoma* sp. [= *?nigrocarpum* (Davidson)] (Ophiostomataceae). Surrounding some of these patches were sporophores of the nonstaining mycangial fungus, *Ceratocystiopsis* sp., and those of another bluestain species, *Ophiostoma ips* (Rumbold) (Ophiostomataceae), which were in the beetle galleries.

Most flying adults were trapped on 6 July 1999, although a few were trapped on 21-27 April 1998. Those flying were captured by 12-funnel Lindgren traps baited with two dispensers purchased from Phero Tech Inc., Delta, British Columbia, Canada. One dispenser contained 170 g polybag, 70% (–)α-pinene, >99% purity, with a maximum release rate of 3.5 g/d at 23°C. The other dispenser contained two Eppendorf tubes, each containing 300 μL (+)-frontalin (1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane), 99.3% purity, with a release rate of 2.6 mg/d at 23°C. Temperatures at both Motozintla and Teopisca were approximately 27°C. The traps were placed in the field at 1000 h and removed at 1800 h. The pheromone baits were placed near the tops of the traps.

All beetles, whether collected from southern pine beetle infested wood or from pheromone traps, were immediately placed in vials of 70% alcohol. When we sampled the beetles to collect their associated mites, we examined the beetles and the sediment within the vial (where many of the mites died after abandoning their beetle hosts). Mites picked from the inner bark and from the southern pine beetle were placed in hot lactophenol for several hours and mounted on slides in Berlese's medium (Krantz 1978). We checked the sporothecae of each female tarsonemid mite for the presence of ascospores of the above fungi (Moser *et al.* 1989).

The identity of collected beetles was verified by the seminal rods of each male ***Dendroctonus*** Erichson sp. which were permanently mounted in Berlese's solution on individual slides for comparison with other closely related members of the southern pine beetle complex such as ***Dendroctonus mexicanus*** Hopkins or ***Dendroctonus vitei*** Wood. Identities of the species of Tarsonemidae were determined by EE Lindquist and W Magowski.

Results and Discussion

All of the seminal rods extracted from the 137 ***Dendroctonus*** sp. males trapped or removed from pupal chambers from both locations matched those in the southern pine beetle descriptions by Lanier *et al.* (1988). Of the 156 southern pine beetles trapped, 129 were males. Females of seven tarsonemid species were riding on teneral southern pine beetle and beetle associates picked from infested inner bark (Table 1).

Adults of all known species of the genus ***Iponemus*** are egg parasitoids of pine bark beetles (Lindquist 1969a). Two species were collected here. At least one species, ***Iponemus truncatus eurus*** Lindquist, attacks eggs of southern pine beetle when its galleries intermingle with those of its host, *Ips* sp. (Moser and Roton 1971).

A single female of ***Iponemus plastographus*** subsp. ?*subalpinus* Lindquist was phoretic on the dorsal elytral surface of a male southern pine beetle from a Lindgren pheromone trap deployed on 28 April 1998. This parasitoid probably feeds on eggs of one of the *Ips* species attacking ***P. oocarpa,*** its phoretic association with southern pine beetle may have been accidental, and it normally parasitizes eggs of ***Ips plastographus*** (LeConte) (Lindquist 1969a). Furthermore, even though this species keyed out to ***I. p. subalpinus,*** there is some doubt about this identification, because this species is known only as an associate of one species of *Ips* from restricted high-elevation areas in northem California and Oregon (EE Lindquist, personal communication).

Ten specimens of ***Zponemus nahua*** Lindquist were present on the elytral declivities of two specimens of ***Ips grandicollis*** (Eichhoff) that were crawling on the inner bark of an infested southern pine beetle bolt. Previously, ***I. nahua*** has been recorded only from ***Ips cribricollis*** (Eichhoff) from Tegucigalpa, Honduras, Durango, Mexico, and New Mexico, United States (Lindquist 1969a; Moser *et al.* 1974). Wood (1982) treats ***I. cribricollis*** as a synonym of ***I. grandicollis,*** but Lanier (1987) regards ***I. cribricollis*** as a distinct species. In the southeastern United States southern pine beetle population and in other areas of the eastern United States, the phoretic egg parasitoid for ***I. grandicollis*** is ***Zponemus confusus oriens*** Lindquist (Lindquist 1969a; Moser and Roton 1971).

TABLE 1. Tarsonemid (Acari) species collected from *Dendroctonus frontalis* and its associates in exposed inner bark and from flying *D. frontalis* caught in Lindgren traps at two localities in Chiapas, Mexico.

Mite species	Location*	Association†	Relative abundance‡
Heterotarsonemus lindquisti	M, T	B, Rs, Cr	I
Iponemus nahua	T	Ig	I
Iponemus plastographus subsp. ?*subalpinus*	M	P	R§
Tarsonemus fuseri	M	B, P	R§
Tarsonemus ips	M, T	B, Rs, P	C
Tarsonemus krantzi	M, T	B, Rs, P	A
Tarsonemus subcorticalis	M, T	B, Pa, P	I

* M, Motozintla; T, Teopisca.

† B, walking on southern pine beetle infested inner bark; Cr, phoretic under elytra of *Corticeus rosei* walking on inner bark; Ig, phoretic elytral declivity *Ips grandicollis* walking on inner bark; P, phoretic on the southern pine beetle; Pa, phoretic elytral declivities of *Pityophthorus annectans* tunnelling and walking on inner bark; Rs, riding on callow southern pine beetles picked from inner bark.

‡ R, I, C, and A, rare, infrequent, common, and abundant as defined by Moser and Roton (1971).

§ New record for the western allopatric population of the southern pine beetle.

We frequently collected females of *Heterotarsonemus lindquisti* Smiley (Acari: Tarsonemidae) on the semidry inner bark at Teopisca, but saw only one on the moist inner bark from Motozintla. No females were phoretic on flying southern pine beetles caught in traps, but at Teopisca they were commonly seen adhering "phoretically" on bodies of *Corticeus rosei* Triplehorn (Coleoptera: Tenebrionidae) that were crawling on the inner bark and under the elytra of brown-black callow southern pine beetles extracted from exposed pupal chambers. We found no individuals of this species on the 156 flying southern pine beetles from Lindgren traps. In Texas, larvae, males, and females are commonly collected from the inner bark of bluestain-free bolts of *Pinus taeda* Linnaeus, as well as phoretic females on southern pine beetles, laboratory reared from these bolts (Bridges and Moser 1986). In the United States, no phoretic females of *H. lindquisti* have ever been seen on southern pine beetles flying into traps, but they were collected from flying *Dendroctonus terebrans* Olivier and *I. grandicollis* from pheromone traps, and also from the southern pine beetle associates *Corticeus glaber* LeConte, *Ips avulsus* (Eichhoff), *Cystlix attenuata* LeConte (Coleoptera: Histeridae), and *Alonium ferruginium* Zimmermann (Coleoptera: Colydiidae) taken from infested inner bark (Moser and Roton 1971). No ascospores were seen on the 21 females mounted on slides from Mexico, or any of 100 specimens collected in Louisiana and Texas. In summary, if this mite is fungivorous, it may not feed on 0. *minus,* and it may be associated with semidry inner bark.

A single male *Tarsonemus fusarii* Cooreman was taken from the inner bark at Motozintla. This mite is apparently a fungivorous species ubiquitous in many areas and habitats of North America and Europe (Moser and Roton 1971; Suski 1972; Sell and Kaliszewski 1985; Kaliszewski and Sell 1990). Lombardaro *et al.* (2000) documented that *T. fusarii* fed and reproduced on *0. minus, Ceratocystiopsis* sp., and *Leptographium terebrantis* Barras and Perry (Demataceae), but not on *0. ips* or *Entomocorticium* sp. A (Corticiaceae), both of which are associated with the southern pine beetle or its *Ips* spp. associates. *Tarsonemus fusarii* females have been recorded as phoretic only twice: on *Scolytus dimidiatus* Chapuis (Coleoptera: Scolytidae) from Veracruz, Mexico (EE Lindquist, personal communication), and by us in the sediments of an alcohol vial containing 510 males and 105 females of southern pine beetles, reared from infested *P. oocarpa* in May 1999 at Teopisca, Mexico.

We saw large numbers of females and males of
Lindquist on the inner bark of the Motozintla populations, but not at Teopisca. Although the presence of males indicates that a breeding population was present, this could not be determined for certain because the tarsonemid larvae and eggs found could not be determined to this species. Also present were large numbers of adults and brood of the tiny bark beetle, ***Pityophthorus annectans*** LeConte (Coleoptera: Scolytidae), which actively tunnelled the inner bark. As many as 20 females of *T. **subcorticalis*** clustered around the elytral declivities of the adults sitting in galleries, indicating that this beetle was probably the phoretic source of this mite. Both this beetle and mite were absent at Teopisca. In Louisiana, we have recorded this mite phoretic on elytral declivities of flying *Ips **calligraphus*** (Germar) and *I. **grandicollis,*** but not the southern pine beetle. Lindquist (1969b) recorded it phoretic on elytral declivities of *Ips **emarginatus*** (LeConte), ***Zps latidens*** (LeConte), *Ips pini* (Say), and ***Zps plastographus*** LeConte.

Many males and females of ***Tarsonemus ips*** Lindquist and ***Tarsonemus krantzi*** Smiley and Moser were present on the inner bark, often concentrated with their eggs and larvae of both species in many of the patches of bluestain and ***Ceratocystiopsis*** sp. at both localities. In addition, many phoretic females were taken from flying southern pine beetles. Both of these mites transport the hyperphoretic ascospores of, and have positive growth rates on, these fungi (Lombardaro ***et al.*** 2000). These ascospores have never been recorded as hyperphoretic on females of the other species of ***Tarsonemus*** discussed earlier in the paper.

At Motozintla, both male and female southern pine beetles collected from Lindgren traps were examined for species and numbers of phoretic tarsonemids. ***Tarsonemus ips*** and ***T. krantzi*** were the only tarsonemids that we recovered. Of the 156 southern pine beetles sampled, only 44 possessed at least one mite, but male and female southern pine beetles carried similar numbers; 26 and 30% were carried by males and females, respectively. The phoretic numbers were much higher, as 85 of the 176 mites were in the sediments. Of these, 31 of the 101 ***T. krantzi*** were in the vial sediments; in contrast, 54 of the 72 ***T. ips*** were recovered from the alcohol sediments. Of the 91 mites attached to the southern pine beetle bodies, 89 were found under the elytra, a subelytral number for ***T. ips*** which is much higher than that found in Louisiana; only two were attached to the external surface, and these were both ***T. ips.*** Fifteen of the 89 mites seen under the elytra were ***T. ips.*** This reinforces the conclusion by Moser and Bridges (1986) that ***T. krantzi*** normally rides under the elytra, whereas ***T. ips*** normally prefers the ventral thorax. Both species of ***Tarsonemus*** rode both male and female southern pine beetles, and five of the southern pine beetle shared their subelytral space with both species of mites. Of those southern pine beetles possessing mites, the average number of ***T. krantzi*** riding under the elytra was two, with a minimum of one and maximum of 10. The subelytral average for *T. **ips*** was one, with a maximum of two.

Four of the *T. **krantzi*** under the elytra carried the tadpole-shaped ascospores of the southern pine beetles mycangial fungus ***Ceratocystiopsis*** sp. These four mites came from three male and one female southern pine beetle. But only one *T. **ips*** carried these mycangial spores, and this mite was located in the vial sediments. Two mites, both ***T. ips,*** carried the crescent-shaped ascospores of the bluestain fungus, 0. ***minus.*** One mite was under the elytra of a male southern pine beetle, and the other was in the vial sediments. These small numbers of mites harboring ascospores of this bluestain fungus differ dramatically from those in an earlier study (Moser and Bridges 1986) which reported that 85.4% of *T. **krantzi*** and 88.4% of ***T. ips*** carried sporothecal ascospores.

Ascospores of other common species of fungi, such as the rectangular 0. ***ips,*** "small hat" yeasts (Moser ***et al.*** 1989), and the large, black "heads" of ***Pyxidiophora*** spp. (Pyxidiophoraceae) (Blackwell ***et al.*** 1986) (which often attach to tarsonemid mites associated with the southern pine beetle in Louisiana), were conspicuously absent on all of the approximately 600 tarsonemids examined in this study. Round, unidentified conidia were seen on the occasional mite, but usually only numbering one or two spores per mite.

These tarsonemid mites, and their southern pine beetle host, differed little morphologically and behaviorally from the mites and southern pine beetle in the southern United States. Two allopatric populations of the southern pine beetle (and their associated arthropods) exist, one in the southeastern United States from east Texas to Virginia, and one that extends from the mountains of Arizona and Nuevo Leon to northern Nicaragua (Lanier *et al.* 1988). At one point, this gap is presently only about 650 km between Monterrey in Nuevo Leon and Bastrop and Waller counties in southeastern Texas. Although this and other studies (Lanier *et al.* 1988) show minor ecological differences between these two populations, no one has suggested that these differences are large enough to warrant even subspecific rank between the two populations. A major reason for this may be that the populations were separated only recently, and thus have had little time to differentiate.

The forest and woodland communities grew as much as 600 m lower in elevation during the last Wisconsin glacial period than they do today (Van Devender 1990). This event may have been a major factor in bridging the gap between the forests in Nuevo Leon and east Texas, because in west Texas the glacial period allowed the growth of pinyon pines, which could be exploited by the southern pine beetle. Indeed, evidence from packrat middens has documented the presence of Ice Age woodlands in the Big Bend area of the Rio Grande in Texas at 11 470 years BP, when pinyon pine, *Pinus remota* (Little) D.K. Bailey and Hawksworth, was dominant (Lanner and Van Devender 1998). Although there are no records of the southern pine beetle attacking pinyon pine, the latter is presently infested by *D. mexicanus* (Cibrian *et al.* 1995), a species so closely related to the southern pine beetle that we conclude that the southern pine beetle would probably also attack pinyon pine. Thus it appears that the pinyon pine populations in west Texas may have provided the avenue from which the southern pine beetle invaded the pine populations of the southern United States. This leap may have happened 4000-5000 years BP when the southern pines moved westward from their very small refugia in southern Florida and finally reached east Texas (Webb 1986). This avenue may now be absent, since pinyon pines are now in low numbers except for two counties in Texas south of New Mexico (Ronco 1990). Thus the appearance of the southern pine beetle in the southern United States seems to be a relatively recent event.

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References

Blackwell M, Bridges JR, Moser JC, Perry TJ. 1986. Hyperphoretic dispersal of a *Pyxidiophora* anamorph. *Science (Washington, DC) 232: 993-5*

Bridges JR, Moser JC. 1986. Relationship of phoretic mites (Acari: Tarsonemidae) to the bluestaining fungus, *Ceratocystis minor*, in trees infested by southern pine beetle (Coleoptera: Scolytidae). *Environmental Entomology* 15: 951-3

Cibrian D, Mendez JT, Campos R, Yates HO III, Flores JE. 1995. Forest insects of Mexico. *North American Forestry Commission FAO Publication 6*

Gäbler H. 1947. Milble als Eiparasit des Buchdruckers (*Ips typographus* L.). *Nuchrichtenblatt für den Deutschen Pflanzenschutzdienst* **1:** 113-5

Hoffman A, Gispert C. 1980. Los acaros como agentes de control-biolbgico de algunas plagas forestales. pp. 187-92 *in* A Saenz-Colin, R Salinas-Quinard, D Cibrian Tovar (Eds), *Primer Simposio Nacional Sobre Parasitologia Forestal 18 e 19 de febrero de 1980.* Urupan, Michoacán: Memoria Sociedad Mexicana de Entomologia

Kaliszewski M, Sell D. 1990. *Tarsonemus fusarii* Cooreman i *Tarsonemus parafusarii* Kaliszewski (Acari: Tarsonemidae) w Polsce, ze szczegolnym uwzglednieniem ekologii. *Zeszyty Problemowe Postepow Nauk Rolniczych 373:* 195-215

Krantz *G. 1978. A manual of acarology.* Corvallis: Oregan State University Book Stores, Inc.

Lanier GN. 1987. The validity of *Ips cribricollis* (Eich.) (Coleoptera: Scolytidae) as distinct from *I. grandicollis* (Eich.) and the occurrence of both species in Central America. *The Canadian Entomologist* **119: 179-87**

Lanier GN, Hendrichs JP, Flores JE. 1988. Biosystematics of the *Dendroctonus frontalis* (Coleoptera: Scolytidae) complex. *Annals of the Entomological Society of America* **81: 403-18**

Lanner RM, Van Devender T. 1998. The recent history of pinyon pines in the American Southwest. pp. 177-82 *in* RM Richardson (Ed), *Ecology and biogeography of Pinus.* Cambridge: Cambridge University Press

Lindquist EE. 1969*a*. Review of the Holarctic tarsonemid mites (Acarina: Prostigmata) parasitizing eggs of pine bark beetles. *Memoirs of the Entomological Society of Canada 60*

19696. New species of *Tarsonemus* (Acarina: Tarsonemidae) associated àwith bark beetles. *The Canadian Entomologist* **101:** 1291-314

Lombardaro MJ, Klepzig KD, Moser JC, Ayres MP. 2000. Biology, demography and community interactions of *Tarsonemus* (Acarina: Tarsonemidae) mites phoretic on *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Agricultural and Forestry Entomology 2:* 1–10

Moser JC. 1985. Use of sporothecae by phoretic *Tarsonemus* mites to transport ascospores of coniferous bluestain fungi. *Transactions of the British Mycological Society 84: 750-3*

Moser JC, Bridges JR. 1983. Technique for rearing mite-free southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae) adults. *Annals of the Entomological Society of America 76: 942-5*

—— 1986. *Tarsonemus* (Acarina: Tarsonemidae) mites phoretic on the southern pine beetle (Coleoptera: Scolytidae): attachment sites and numbers of bluestain (Ascomycetes: Ophiostomataceae) ascospores carried. *Proceedings of the Entomological Society of Washington 88: 297-9*

Moser JC, Roton LM. 1971. Mites associated with the southern pine bark beetles in Allen Parish, Louisiana. *The Canadian Entomologist* **103: 1775-98**

Moser JC, Wilkinson RC, Clark EW. 1974. Mites associated with *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae) in Central America and Mexico. *Turrialba 24:* 379-81

Moser JC, Perry TJ, Solheim H. 1989. Ascospores hyperphoretic on mites associated with *Ips typographus*. *Mycological Research 93: 513-l*

Moser JC, Perry TJ, Bridges JR, Yin H-F. 1995. Ascospore dispersal of *Ceratocystiopsis ranaculosus*, a mycangial fungus of the southern pine beetle. *Mycologia 87: 84-6*

Ronco FP Jr. 1990. *Pinus edulis* Englem., Pinyon. pp. 327-37 *in* RM Bums, BH Honkala (Eds), Silvics of North America. *US Department of Agriculture Agriculture Handbook 654*

Sell D, Kaliszewski M. 1985. *Tarsonemus fusarii* Cooreman 1941 and *Tarsonemus parafusarii* Kaliszewski 1983 (Acari: Heterostigmanta) in Poland. pp. 589-92 *in* BR Striganova (Ed), *Soil Fauna and Soil Fertility, Proceedings of the 9th International Colloquium on* Soil *Zoology.* Moscow: Nauka

Suski ZW. 1972. Tarsonemid mites on apple tress in Poland X. Laboratory studies on the biology of certain mites species of the family Tarsonemidae (Acarina, Heterostigmata). *Zeszyty Problemowe Postepow Nauk Rolniczych* **129: 11 l-37**

Van Devender TR. 1990. Late Quatemary vegetation and climate of the Sonoran Desert, United States and Mexico. pp. 134-64 *in* JL Betancourt, TR Van Devender, PS Martin (Eds), *Packrat middens, the last 40,000 years of biotic change.* Tuscon: The University of Arizona Press

Webb T III. 1986. Vegetational change in eastern North America from 18,000 to 500 yr B.P. pp. 63-9 *in* C Rosenzweig, R Dickenson (Eds), *Climate-vegetation interactions.* Boulder: Office for Interdisciplinary Earth Studies, University Corporation for Atmospheric Research

Wood SL. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs 6*

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