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TOWN ANTS

The Beginning of John Moser's Remarkable Search for Knowledge

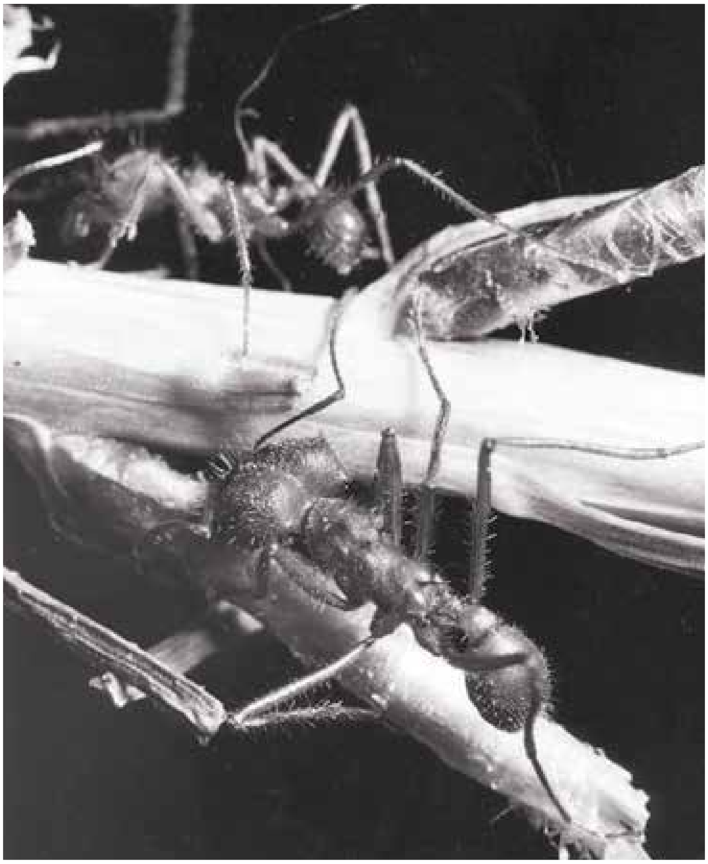

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PHOTO CREDITS

Cover: Town ants (Texas leaf-cutting ants), *Atta texana* (Buckley), clipping needles from a loblolly pine (*Pinus taeda*) seedling.

Unless otherwise noted, the photos are from the collections of John Moser and the U.S. Forest Service.

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CONVERSIONS

1 ha = 2.47 acres and 1 cm = 0.4 inches

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ABSTRACT

John C. Moser's career spans over 50 years, and his research has focused on understanding the biology of town ants (*Atta texana*) and phoretic mites and other associates of ants and pine bark beetles. His approach to developing methods for the control of these pests has been to understand more completely the biology of these organisms. This research approach has established Moser as an internationally recognized expert in leaf-cutting ant biology and as a premier authority on phoretic mites and other associates of pine bark beetles. John's efforts have led to the largest collection (over 30,000 specimens) of mites associated with forest insects in the world. This knowledge is leading entomologists, ecologists, and pathologists to consider the possible role of mites in insect-fungal symbioses and disease transmission in trees.

Keywords: *Atta texana, Dendroctonus frontalis*, Dutch elm disease, fungal ascospores, mites and other pine bark beetle associates, southern pine beetles, southern pines, Texas leaf-cutting ants.

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PREFACE

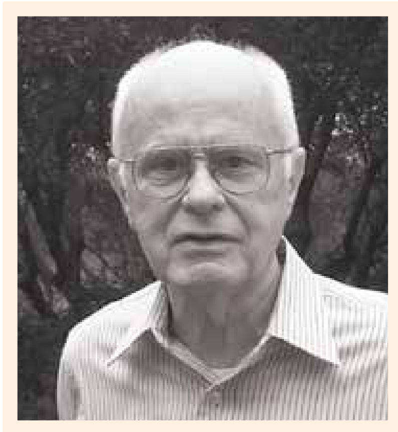

Photo of **JOHN C. MOSER** taken late in his career.

John C. Moser is a long-term scientist who has conducted research for the Forest Service, U.S. Department of Agriculture, Southern Research Station at the Alexandria Forestry Center in Pineville, LA for over 50 years. Retired for over 20 years, he continues to work daily and on most weekends as an emeritus scientist. He is noted for being somewhat eccentric, mainly because he studies mites carried on forest insects, an area that is generally considered out of the mainstream of forest entomological research. Few employees at the Forestry Center, or even the Southern Research Station's scientific staff, understand and appreciate the work that Moser is conducting in entomological research and its significance to the international entomological community.

Although Moser's research assignment related to the control of the town ant (*Atta texana*) was officially terminated in 1962, 4 years after he was hired by the Forest Service, by determination he nevertheless continued studies on the biology and ecology of the ants for decades and became an international authority on leaf-cutting ants. His work with mites associated with bark beetles has also gained him international recognition and respect and made a huge impact on this field of study.

Many aspects of his research published in the most prestigious international scientific journals (*Science* in the United States, *Nature* in the United Kingdom, and *Naturwissenschaften* in Germany) have enhanced his international recognition. His research, too, is becoming critical to understanding the biology of how major tree diseases and tree-killing beetles are transmitted.

Moser's accomplishments are even more significant in light of the administrative difficulties he has faced in pursuing his scientific interests—as they were usually outside the typical research emphasis of the research work units to which he was assigned.

John Moser's long career, his accomplishments, and their significance need to be understood and appreciated. The objective of this publication is to document these research contributions.

— *James P. Barnett*

INTRODUCTION

Scientific breakthroughs can occur through a number of approaches, such as by teams of scientists working together with common goals, by serendipity or happenstance, or sometimes by the dogged determination of a scientist working outside the mainstream of conventional science. The latter approach best fits the accomplishments of John C. Moser, research entomologist with the Forest Service, U.S. Department of Agriculture Southern Research Station.

John Conrad Moser, born in 1929, grew up near Columbus, OH, and was by his own admission a poor student, most likely because he found little that challenged him. Even as a child, John, also called "Bobby" by his parents, demonstrated his willingness to take a different path. At age four, he became distracted while waiting for his mother while she shopped, and left her to walk the 4 miles to their home. Fortunately, he met a stranger and asked, "My mother is lost. Can you show me how to cross High Street without getting hit by the machines?" He was escorted to the police station, and they soon located his mother. To this day, he states, "I could have made it home without any problem."[1]

[1]Barnett, J.P.; Streett, D.A.; Blomquist, S.R. 2012. Oral history interview of March 7, 2012, with John C. Moser. Cassette tape. Pineville, LA: U.S. Department of Agriculture, Forest Service, Southern Research Station, Insects, Diseases, and Invasive Plants Research.

A B-25 Mitchell bomber such as this was used to fly Moser and his high school classmate to Patuxent Naval Air Station in Maryland. (Photo from www.vg-photo.com)

Another example of Moser's independent thinking was during his junior year in high school when he and a friend, who both had joined the Civil Air Patrol during World War II to have something to do, decided that it would be fun to fly to the East Coast. Since his parents were out of town, he obtained permission from the high school principal for he and his friend, Eddy Cooper, to be absent from school for a couple of days and went to Columbus' Lockbourne Field. There they convinced a pilot of the renowned Tuskegee Air Men's squadron of the merit of their visit to the East Coast. The 477th Bombardment Squadron was assigned to Lockbourne Field to be deactivated following the end of World War II, and the pilot from the squadron agreed to fly them to Patuxent Naval Air Station in Maryland in a B-25 bomber. After an overnight stay—and many efforts to answer the repeated question of "What are you guys doing here?"—they were flown back to Columbus the next day (see footnote 1).

Moser graduated from high school in 1947 with a less than spectacular scholastic record, and he had no desire to go to college (Moser 2000). There were no jobs, however, because of the number of veterans coming home from World War II who were seeking employment. So Moser entered Ohio State University (OSU), which was only three miles from his home. Since tuition was only $45.00 per quarter, he could make his tuition by mowing lawns in the summer, even when making only 40 cents per hour (see footnote 1). Thus began the education of one of the most distinguished and internationally recognized forest entomologists of our time.

The objective of this publication is to document the scientific accomplishments of John C. Moser. Equally important is to understand the vision, determination, and commitment required to accomplish this status in light of the administrative and scientific obstacles he faced.

Moser became one of the most distinguished and internationally recognized forest entomologists of our time.

THE NATURE OF JOHN MOSER'S EDUCATION

It was not until his sophomore year at OSU that Moser found an area of science that captured his interest—when he took his first course in entomology. Not only was it interesting, but he began to see a career that had job potential. In addition to the interaction with several OSU professors who began to shape his career, Moser discovered that the leaves of a hackberry tree *(Celtis occidentalis*) in his front yard had many kinds of interesting insect galls. He discussed this with Professor Ralph Davidson, his undergraduate advisor, who encouraged him to observe and take notes regarding the different species of insects.

Moser was particularly intrigued by a tiny, metallic green wasp that was flitting around and inserting its ovipositor into certain galls. He collected some of these wasps and sent them to a scientist at the U.S. Department of Agriculture, Agricultural Research Service Systematic Entomology Laboratory at Beltsville, MD, who identified the wasp as a new species of *Torymus*. This was really exciting to John because it meant that as a lowly sophomore student, "I had observed something that no one else in the world had ever seen" (Moser 2000). This was a pivotal event that launched Moser's career as a research entomologist, as well as a motivation throughout his scientific endeavors.

LEFT: Two types of insect galls that were found on the hackberry tree in Moser's yard. The wasp that Moser first identified as a new species was associated with the inverted cone-shaped gall.

RIGHT: This is the tiny green-metallic colored wasp that Moser found and was identified as a new species of *Torymus*.

During the summers of 1949 and 1950, Moser worked driving and assisting OSU Professor C.H. Kennedy on his insect collecting trips to Upper Michigan and the north coast of Lake Superior in Canada, where they "chased ants" (Kennedy's term) (Moser 2000). Moser states that he was far from the first choice for this job, but he was selected because Professor Kennedy was neurotic and other graduate students were afraid to work for him. Kennedy was difficult to work for, but he was a great teacher and Moser learned the basics of ant behavior and systematics that were to play an important role in his future job selection in the Forest Service. Kennedy told Moser, "If you ever get a chance to work on *Atta*, take it because this is where the real opportunities lie in myrmecology research" (Moser 2000).

Moser commented that in 1951, "much to the surprise of myself and everyone else, I received my B.S. in entomology from OSU. The year 1951 was the apex of the Korean War, and I was facing the draft. However, I was informed that my B.S. in entomology was worth a commission, the drawback being that I must enlist for a minimum of 4 years, and that I would be sent to Korea to participate in a pest control unit. The alternative was to be drafted, serve only 2 years, undergo 16 weeks of basic, but then be sent to work as a tech at a Department of Defense (DOD) research facility, and forever remain a private. I chose the latter" (Moser 2000).

After basic training, Moser was assigned to the Army Chemical Center at Edgewood Arsenal near Baltimore, MD, where he served as a technician at the Army Medical Corps, Insect Physiology Laboratory. He was associated with several other early mentors, namely Leigh E. Chadwick, Detrich H.F.A. Bodenstein who was elected to membership in the National Academy of Science in 1958, and Bertram Sacktor, who were three of the more important insect biochemists at that time. Moser was assigned to Dr. Sacktor, who included him as a junior author on one of his papers published in the 1953 *Biological Bulletin* entitled "Dephosphorylation of ATP by tissues of the American cockroach." This was cutting edge science and John Moser's first publication (Sacktor and others 1953).

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While attached to the Army Chemical Center, Dr. Chadwick allowed Moser to attend his first Entomological Society of America (ESA) meeting that was held in Philadelphia, PA. More important, though, were the three-day passes that Moser received each month. Normally he would visit New York City and Washington, DC on alternate months. While in New York City, he would attend

Broadway shows and, as a member of the military, was allowed free admission to show dress rehearsals (see footnote 1).

During the alternate month's visit to Washington, DC, he normally spent time at the Smithsonian National Museum of Natural History, where he would visit with Barnard D. "Barney" Burks, who was the curator of chalcidoid wasps at the Systematic Entomology Laboratory of the U.S. Department of Agriculture, Agricultural Research Service. Burks helped Moser to describe his new species of *Torymus*, in addition to several other new species of parasitoids that Moser had found associated with the hackberry galls in Columbus, OH (Moser 2000). Burks strongly encouraged Moser to apply to Cornell University as a Ph.D. candidate.

In September 1953, Moser was released from the Army and received the G.I. Bill, which financed the remainder of his graduate education. He returned to his home in Columbus and entered OSU, where in 1954 he completed his Master's degree, majoring in biological control under Professor Alvah Peterson, noted author and one-time President of the Entomological Society of America. His thesis on hackberry galls and description of the parasitoid, *Torymus vesiculus,* was summarized in the 1956 *Journal of the Kansas Entomological Society* (Moser 1956).

A year later, in September 1954, Moser entered Cornell University, majoring in insect ecology and studying under Howard Evans, who taught courses in taxonomy of Hymenoptera and the minor insect classification orders, and who was awarded the Daniel Giraud Elliot Medal from the National Academy of Sciences in 1976. In addition, Moser shared an apartment with John G. "Jack" Franclemont, who taught Lepidoptera systematics and later donated his extensive collection of 350,000 moths and extensive library to Cornell University. These two mentors helped shape Moser's views on the meaning and values of systematic studies to the study of insect interrelationships. At Cornell, he continued his research on the natural enemies of hackberry gall makers. This research was published in 1965 as Bulletin 402 of the New York State Museum and Science Service (Moser 1965). Of Moser's nearly 200 publications, this was his longest, at 95 pages.

John Moser's education was strengthened and his career focused by the entomologists who served as his mentors—these were the outstanding entomologists of the 20th century. They included individuals from OSU, the Army Chemical Center, Smithsonian's Natural History Museum, and Cornell University. Moser freely admits that his acceptance into Cornell University's

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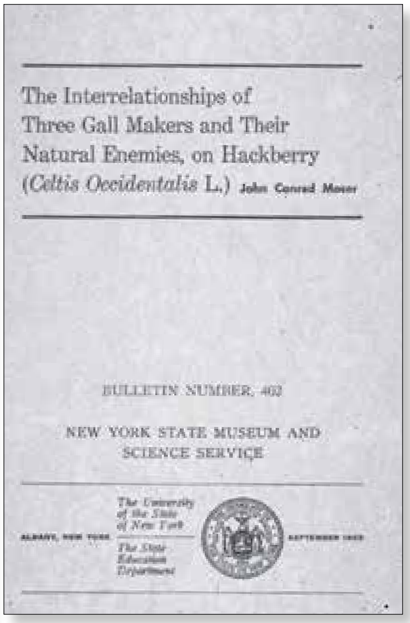

The Interrelationships of
Three Gall Makers and Their
Natural Enemies, on Hackberry
(*Celtis Occidentalis* L.) John Conrad Moser

BULLETIN NUMBER 402

NEW YORK STATE MUSEUM AND
SCIENCE SERVICE

The University
of the State
of New York

The State
Education
Department

ABOVE: Publication documenting Moser's Ph.D. research on gall-making insects.

LEFT: Another gall form found on the hackberry tree that was associated with a different parasitoid wasp.

Graduate School would have been difficult based solely on his academic achievement, but the recommendations from his mentors based on his research capability overcame any such weakness (see footnote 1).

Several months before Moser received his Ph.D. in 1958, the Forest Service's Southern Forest Experiment Station sent Jack Coyne to Cornell University to earn a Master's degree. Today, Coyne is known by his pioneering work of saving and planting scions of loblolly pines that had survived southern pine beetle attack. Coyne informed Moser of a GS-4 position in the Station's Timber Management Research unit at Alexandria, LA. This position had been created for a person to solve pine regeneration problems caused by the town ant, *Atta texana*.

John also had an offer of a GS-9 position (then the going rate for an entry level Ph.D.) from the Forest Service's Northeastern Forest Experiment Station to study predators and parasitoids of the Gypsy moth (*Lymantria dispar*). Moser says, "Professor Kennedy's words rang in my ears, and I took the GS-4 position. I arrived in Alexandria, LA on July 1, 1958, and was the first Ph.D. entomologist hired by the Southern Forest Experiment Station" (Moser 2000).

THE FIRST JOB—UNDERSTANDING TOWN ANT BIOLOGY

When John Moser arrived in Alexandria, LA and reported to work for the Southern Forest Experiment Station's Timber Management Research unit, he was given the assignment to "eradicate" the town ant, a project that "should last a couple of years." Native of western Louisiana and eastern Texas, the town ant can be a significant problem in reforestation by causing pine seedling mortality that results from the clipping of the needles and terminal buds of seedlings. This material is carried into underground chambers, where it forms the fungal substrate each colony cultures for food.

William F. "Bill" Mann, Jr. was the supervisor of the research unit and was noted for his authoritarian management style that often resulted in personal conflicts. Soon there was disagreement on the approach of the proposed research. Mann wanted Moser to perfect methods of killing the ants—the state-of-the-art treatment at the time was to gas the colony with methyl bromide (Johnson 1944). Moser convinced Mann that real control could not be accomplished without knowing something about the biology of the insect.

In September 1958, Moser gave a seminar at the Louisiana Entomological Society meeting at Louisiana State University (LSU). There he met Murray S. Blum, an expert in insect chemical ecology, of the university's entomology faculty and they collaborated for several years on the chemical ecology of town ant pheromones and the ants' mating flights.

Mann's insistence on a short-term effort to control the ant colonies conflicted with Moser's long-term goal to develop a better understanding of the ant's biology, and led to personal conflicts. Despite this, Moser soldiered on, collaborating with elite scientists, often in defiance of his project leader. One such collaboration involved Edward O. Wilson, a renowned ant biologist and winner of many international awards, including two Pulitzer Prizes. Wilson was interested in the chemical ecology and biology studies that Moser and Blum were conducting. During the 4 years that Moser was assigned to the Timber Management

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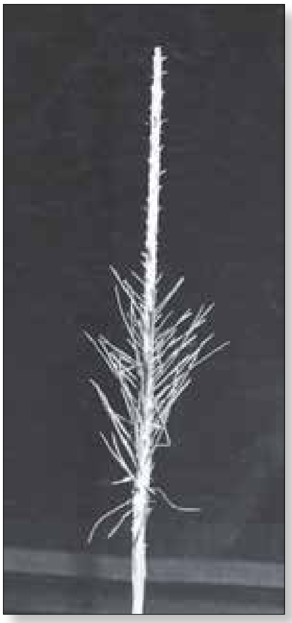
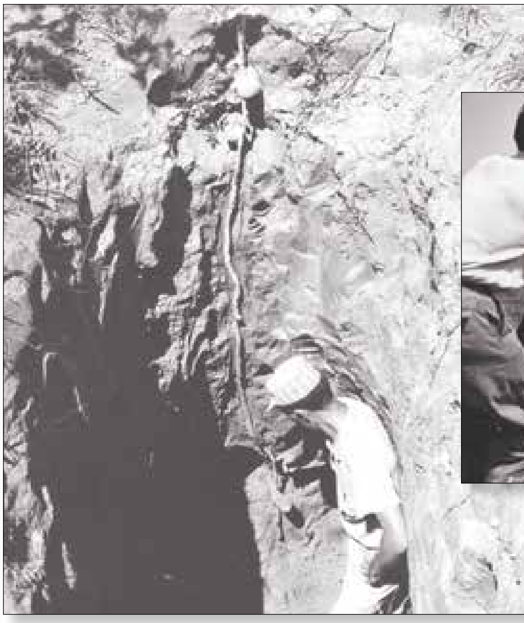




ABOVE: Continental Can Company provided men and equipment to help excavate and map the colony.

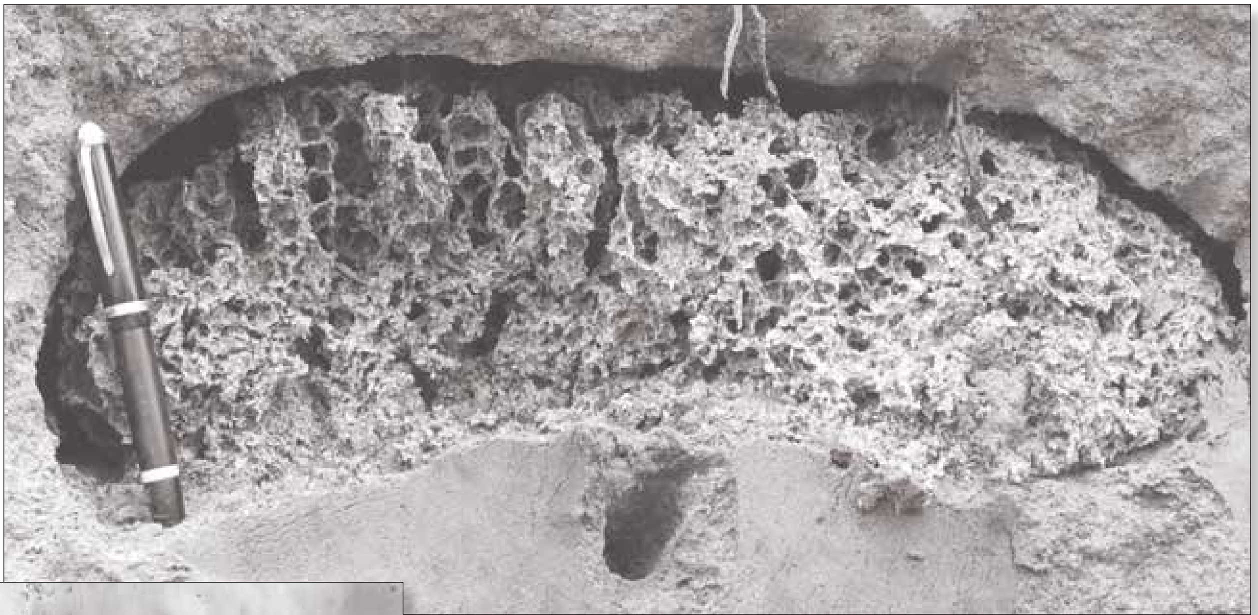
FAR LEFT: Loblolly pine (*Pinus taeda*) seedling defoliated by town ants.

LEFT: Structures of small, new nests were studied by filling them with watery cement and digging around the cast. In this photograph John Moser is observing the cemented nest which had a single gallery extending 12 feet into the ground and three small cavities.

Research unit, Wilson visited Alexandria twice. Both times Moser brought his esteemed guest in through the back door to avoid paying a "verbal tribute" to the project leader (Moser 2000).

Town ants vary in size, ranging from ⅛ to ¾ inch long. The queens, the largest, are rarely seen because they spend their entire lives underground, except for one short mating flight. Medium-sized worker ants do most of the foraging.

The worker ants cut and bring green leaf material into the nests for the "garden" on which a fungus grows—the only known food of the ant. Many smaller workers constantly care for the gardens, keeping them free of contaminating organisms. The need to understand what all went on belowground led to one of the most notable, and logistically and visually impressive, aspects of Moser's town ant research, the excavation and mapping of a large colony. A colony was excavated in 1960 using a bulldozer that cut a swath through it 25-feet wide, 100-feet long, and 12-feet deep (Moser 1963). Fungus-garden cavities were the heart of the nest and averaged a foot in diameter. Occasionally, they are much larger and a person can actually stand within the cavity. They may be as much as 8 feet below the surface and are connected by a series of tunnels used for movement to the surface. Material depleted of nutrients is deposited into dump or detritus cavities. Other cavities are packed with material such as ants, eggs, larvae, pupae, and sometimes green leaves or sand (Moser 1962). The function of these "dormancy" cavities is not clear.



TOP: Fungus garden cavity within a town ant nest.

BOTTOM: This small beetle (*Oosternum attacomis*) (1.3 mm by 0.8 mm) discovered by Moser lives in town ant detritus cavities.

This project, accomplished with significant support from forest industry, provided significant data on the functioning of the ants within the colony and resulted in a number of important publications. One of the first of these was "Probing the secrets of the town ant" (Moser 1962).

Moser (1960) was also quick to defend other similar native ants, such as the harvester ant (*Pogonomyrmex comanche)* that does little damage to agricultural crops.

Discovery of New Inquiline Species

In the ant colonies, several undescribed specimens of inquiline insects (those who live in the nests of others without harm to them) were discovered by Moser. One of these insects described by Spangler (1962) was a minute scavenger beetle (1.3 mm long and 0.8 mm wide) that he named *Oosternum attacomis*. It is found in the detritus cavities of town ant nests.

Another species found underground in the nests of the town ant is a fly in the lesser housefly genera (*Fannia*). Fly larvae scavenge in the detritus cavities of the ant colony. This species appears to move freely as adults through the nests of the ant below the ground surface (Chillcott 1965). Once the adults fully develop, they walk with wings unexpanded through tunnels to the surface where they rest until their wings expand. They then fly off to swarm, mate, and forage for food. Mature females return to the colony's detritus cavities to lay eggs for another generation. This species was named *Fannia moseri*, in honor of John Moser (Chillcott 1965).

Another beetle found in the nests is of the *Euparixia* genera—these are scarab beetles that live as inquilines in detritus cavities. It was named *Euparixia moseri* by Woodruff and Cartwright (1967), also in honor of Moser.

Town Ant Control Treatments

Moser worked to refine and improve the methyl bromide treatments, but the excavation demonstrated that it is difficult to kill the entire colony by methyl bromide (Neelands 1959). The effort to control the ant was expanded by the introduction and evaluation of a new chemical, Mirex® (Bennett 1958). However, the application of Mirex® as a control agent was not finalized until after Moser was transferred from the Timber Management Research unit to a newly established Forest Insect Research unit.

With the transfer of Moser to the Forest Insect Research unit, Bill Mann recruited another entomologist to continue the work on the control of town ants. This scientist, William Echols, evaluated formulations of Mirex® designed especially for town ant control (Echols 1966). However, the development and widespread aerial application of a fire ant (*Solenopsis invicta*) formulation across the rural South by the U.S. Department of Agriculture significantly reduced the number of town ant colonies, and that line of research was terminated.

Because of environmental problems, aerial applications of Mirex® were ended in 1975. Since Mixex® was more effective in eliminating native ant species than the nonnative fire ants, populations of fire ants quickly recovered, but it has taken decades for the town ants to begin reestablishing their earlier niche in the forest ecosystem (Barnett and others 2011).

Moser's research over a 4-year period with the Timber Management Research unit established his credentials as an expert in town ant biology and led to a career-long interest in its ecology and that of its interrelated species.

Injecting methyl bromide gas into a town ant colony was a long-established treatment.

ASSIGNMENT TO SOUTHERN PINE BEETLE RESEARCH

In 1962, an insect research project was established at Pineville under the leadership of William H. "Bill" Bennett, giving Moser an opportunity to transfer to a project much more to his liking. Southern Station Assistant Director L.W. "Les" Orr, who knew that Moser had a penchant for working with "small stuff", asked if he wanted to work on the mites associated with bark beetles. This was an opportunity that Moser quickly embraced. Orr had a reason for suggesting the research on mites because he co-authored a paper with Leach and Christensen (Leach and others 1934) establishing that mites riding on *Ips pini* fed on and disseminated the blue stain fungus in red pine (*Pinus resinosa)* (Moser 2000).

Again, Moser encountered the short-term research attitude that conflicted with his long-term view requiring more thorough research to fully understand insect ecology.

Les Orr wanted to know the identities of these mites and if the same thing was going on with southern pine beetles (SPB) (*Dendroctonus frontalis*), and he thought that Moser could find out all the information needed in about six months. Again, Moser encountered the short-term research attitude that conflicted with his long-term view requiring more thorough research to fully understand insect ecology.

Continuation of Town Ant Research

Fortunately, Moser was able to continue publishing earlier research related to the ecology of the town ant because he had collected significant data related to trail marking and mating flights that needed publication.

TRAIL-MARKING SUBSTANCES—The work of Moser with Murray S. Blum of LSU's Department of Entomology on trail-marking substances of the town ant created a lot of interest. An article published in *Science* established that potent chemicals produced in the ant's poison gland are distributed by the stinger, which is not used for stinging (Moser and Blum 1963). Instead, this ant's stinging defense mechanism has been adapted for the purpose of communication, and its powerful mandibles provide defense by biting (Hermann and others 1970).

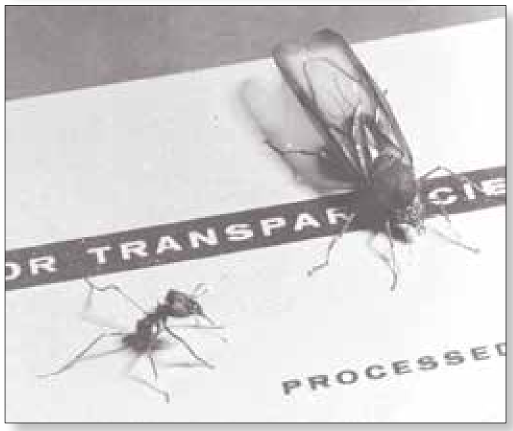
The adapted stinging mechanism provided a chance for Moser to pull a prank on Bill Mann, his supervisor. One day when Mann and Moser were in the field observing town ants, they happened upon a huge population of harvester ants (*Pogonomyrmex comanche*) actively scurrying all around. Mann asked Moser, "Do they bite?" remembering how vicious a bite a town ant can inflict. Moser replied "no" and placed a few harvester ants in Mann's hand. The harvester ants proceeded to sting Mann resulting in substantial pain. Mann responded, "You told me they wouldn't bite!" Moser's response was, "They don't bite. They sting." This did little to improve their strained relationship (see footnote 1).

Studies were undertaken to determine if the trail substances of similar species were also produced in the poison gland. The results demonstrated that sting-associated glands were similar in closely related genera and species (Blum and others 1964). Related research showed that the inquiline roach (*Attaphila fungicola*), which inhabits fungus gardens of the town ant, also follows the ant's odor trails (Moser 1964) and has been observed outside the nest, traveling along the trail used by foraging ant workers. Since this roach is wingless, it may use the odor trail to move from one nest to another (Moser 1967a).

NEST ASSOCIATES AND ENEMIES—In addition to the roach mentioned above, there are many species of insects associated with the town ant. Most of these are found in detritus cavities. Walter and others (1938) listed 44 species of arthropods found in the nests located in Texas, and Moser has found at least that many in Louisiana. He has identified and described many of these species associated with the town ant (Krantz and Moser 2012; Moser 1962, 1963, 1967b; Waller and Moser 1990).

Moser and Neff (1971) described a small fly (*Pholeomyia comans*) that is an associate of the town ant and lays eggs in the detritus cavities of nests. Three species of mites that are carried (phoretic) on the flies were identified and discussed.

Many genera of insects can be found associated with the ant nests. These include silverfish (Thysanura), small cockroaches (Blattodea), crickets (Orthoptera), cydnid bugs (Hemiptera), beetles (Coleoptera), flies (Diptera), and wasps (Hymenoptera) (Waller and Moser 1990).



TOP: Town ant biting the end of Moser's finger.

BOTTOM: Worker town ant (left) with a winged queen ant showing the differences in size.

In addition, at least 75 species of mites are associated with the town ant. The mites are phoretic and depend upon dispersal by riding on the winged ants during their mating flights (Moser 1983).

Although birds and bats consume large quantities of the thousands of winged reproductive ants (alates) that take off from the nests (Warter and others 1962), the number of predators are limited. Minute flies (*Myrmosicarius texana*) (about 1 to 2 mm body length) hover over the ants at nest entrances and along trails and dart down to land on the ants' heads, suggesting parasitism (Waller and Moser 1990). There is, however, little documentation of any significant adverse effects from any of the many associated species.

MATING ACTIVITIES—Moser spent many years studying the mating flights of town ants and has documented many aspects of the environmental and physiological conditions when the flights occur (Moser 1967b). Winged ants develop in early February and March, but swarming generally does not occur until late April or May. The sex ratio is about 1:1. Before swarming will occur, nest surfaces must be soaked from rain, and flights will continue as long as the nests remain wet and temperatures exceed 16 °C. A circadian rhythm seems to trigger swarming at about 3:55 a.m., and most leave the nest surface within 2 minutes (Moser 1967b).

A soil chimney created by new workers about 2 months after the mating flight.

The flights take place in darkness, and little is known of the fate of the alates once they leave the nest. After mating, surviving females land, lose their wings, begin digging tunnels to establish new nests, and become the queens of new colonies (Moser 1983). Moser and Lewis (1981) found that some new colonies expand quickly because more than one queen is involved in its establishment.

PHEROMONE STUDIES—In 1966, David L. Wood of the University of California, Berkeley, an authority on western pine beetle (*Dendroctonus ponderosae*) ecology, visited Pineville to explain advances in chemical ecology of that species. He was fascinated by Moser's chemical ecology studies of the town ant and suggested that he contact Robert M. "Milt" Silverstein of the State University of New York, for possible help in identifying the ant trail pheromone. Silverstein, an expert on the chemistry of insect communication and later in his career a member of the National Academy of Sciences, was eager to work on the town ant pheromone, but financial support was needed for the project (Moser 2000).

ABOVE: Enlarged harvester ant showing the abdomen with the poison sac and stinger.

LEFT: Town ant mound with several entrances into tunnels that lead to underground cavities.

The Forest Service was reluctant to continue research on the town ant because Mirex® had adequately controlled this and other leaf-cutting ants. Silverstein applied to the National Institute of Health and obtained a grant for $60,000 to conduct the research, but he had to visit the Southern Station in New Orleans, LA to convince them that Moser's research should continue. They reluctantly agreed to the project.

In general, pheromones trigger a number of functions such as mating, alarm, attraction, repulsion, and trail following (Moser 1970). The challenges are to identify chemicals eliciting response and determine their function.

Moser's initial task for this project was to collect 8 pounds of town ants. He paid locals to collect the ants in coffee cans, paying them by the pound. Once collected, Silverstein and James H. Tumlinson (Silverstein's post-doctorate graduate student now Ralph O. Mumma Professsor of Entomology, Penn State University) ground up and extracted 150 µg of pure trail substance. This and about 100 other allied compounds extracted from the ant poison sacs were sent to Moser.

His task then was to prepare artificial trails from these compounds and let worker ants indicate which substance was the most active. This turned out to be a pyrrole (a heterocyclic aromatic organic compound) that was named "Attalure." Attalure was the first pheromone demonstrated to elicit trail following for any ant (Tumlinson and others 1971). Unlike most pheromones, Additional tests demonstrated that 24 species of leaf-cutting ants followed the trail pheromone of the town ant. However, when ants of other species were given a choice of following one of two separate trails, they chose the trail of the most closely related species.

which are highly volatile, this compound was a solid of low volatility. Low volatility is needed because the ant requires long-term sources of food that necessitate repeated use of trails. This substance is very powerful; only 330 µg is required to draw a detectable trail around the world (Moser 2000). These results were published in two papers in *Nature* (Moser and Silverstein 1967, Tumlinson and others 1971).

In a follow-up study, the major component of the volatile trail-marking pheromone was identified as methyl 4-methylpyrrole-2-carboxylate. Another component also establishes a trail-following response. The purpose of this second substance was unknown, but it was proposed to allow insects of closely related species the capability to communicate (Tumlinson and others 1972). Sonnet and Moser (1972, 1973) prepared and bioassayed a number of synthetic analogs of the pheromones and determined their sensitivity by ant responsiveness.

Additional tests demonstrated that 24 species of leaf-cutting ants followed the trail pheromone of the town ant. However, when ants of other species were given a choice of following one of two separate trails, they chose the trail of the most closely related species (Robinson and others 1974).

After the initial research on the trail pheromone, Moser suggested that efforts should begin to understand the volatile alarm-causing components of the head, specifically of the mandibular glands of the worker ants. Two components were identified that alarmed and repelled worker ants: 4-methyl-3-heptanone and 2-heptanone (Moser and others 1968).

The capability to split the 4-methyl-3-heptanone pheromone into two volatile components allowed Moser to bioassay which of these alarmed the ant. Although this procedure is now routine, it never had been accomplished for any bioactive substance, such as a pheromone. The bioassay was a breakthrough because it was the first procedure to allow concentrations of volatiles to be determined within minutes (Moser 1983). Silverstein's graduate student, Robert G. Riley, isolated the two substances and sent them to Moser. The bioassay established that only the (+) enantiomer of the mirror-imaged compound was active. In 1974, these findings were published in both *Science* (Riley and others 1974a) and the *Journal of Insect Physiology* (Riley and others 1974b).

Andryszak and others (1990) determined antennal olfactory response of town ants to the trail and alarm pheromones. The results established the queen and male ants responded to lower levels of pheromones, while minor workers in the nest required higher levels to show response.

TIMBER LOSSES FROM A TOWN ANT COLONY—Although biologists and foresters have frequently documented the adverse effects of town ants on agricultural crops and small trees, the economic impact of this defoliation has seldom been determined. Moser (1986) used aerial photographs to locate and determine the size of a colony active in 1955 and made on-ground measurements 30 years later to estimate loss in tree stumpage value.

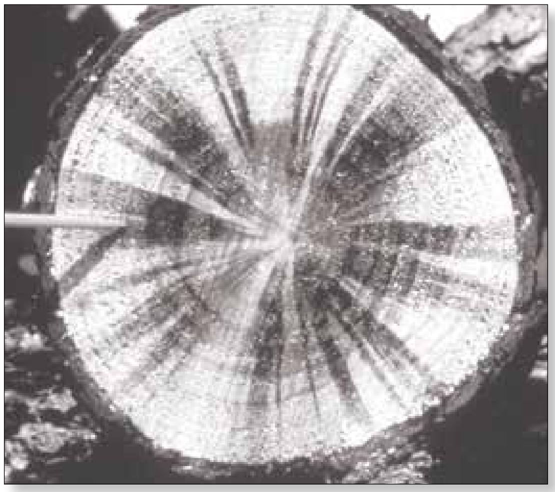
The colony occupied about ¾ acre, and based on 1955 dollars the stumpage value loss was $653. Cost of controlling the ants would have yielded a 15 percent rate of return during the 30-year period (Moser 1986).

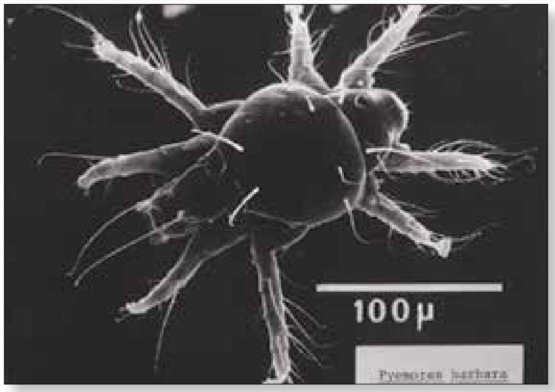
The U.S. Department of Agriculture's aerial application of Mirex® during the 1960s and early 1970s for fire ant control greatly reduced the number of town ant colonies, and it was not until the early 1980s that populations of ants again began to present a problem to reforestation (Weatherby cited in Moser 1983).

As the publication of much of the town ant research neared completion, Moser began to focus his research efforts on issues related to SPB.

Initiation of Research on Mites Related to Southern Pine Beetles

Moser was aided in his research on the mites associated with southern pine beetles (SPB) by the assistance of very talented technical support personnel. His early and long-term assistant, Lawrence M. "Lary" Roton, not only supported Moser's work on the town ant, but led the effort to find and process the different species of mites on SPB. While Moser remained heavily involved in town ant studies, he directed Roton "to learn all you can about mites" (see footnote 1). Roton led the effort to process many of over 20,000 slides of mites in support of Moser's assignment in 1963 to study mites. This effort provided answers to the questions of Assistant Director Les Orr about the array of mite species associated with SPB and the possible transmittal of the blue stain fungus (*Ophiostoma minus*). The identification of these mites was the issue that resulted in Moser beginning mite research.





TOP: The blue stain fungus (*Ophiostoma minus*) is transmitted to southern pines by southern pine beetles and the mites they carry.

BOTTOM: *Pyemotes barbara* was found to be parasitic on the Douglas fir cone moth. Moser and Roton experimented with *Pyemotes* species on SPB to see if they would provide good biological control.

Early in SPB studies, more than 90 species of insects were identified from bolts taken from loblolly pines (*Pinus taeda*) infested by SPB and *Ips* engraver beetles (Moser and others 1971). Many of these species were mites and became the object of Moser's research.

The number of new species found was so great that many of the slides processed by Roton and Moser were often sent to mite taxonomists active in the United States and Europe for identification. Included were specialists Bob Smiley and Ed Baker, U.S. Department of Agriculture Agricultural Research Service, Beltsville, MD; Jay Woodring and Bruce Boudreaux, Louisiana State University, Baton Rouge, LA; Evert Lindquist, Agriculture and Agri-food Canada, Ontario, Canada; Preston Hunter, University of Georgia, Athens, GA; Earle Cross, University of Alabama, Tuscaloosa, AL; Sandor Mahunka, Hungarian Natural History Museum, Budapest, Hungary; Jerry Krantz, Oregon State University, Corvallis, OR; and Jerzy Wiśniewski, Academy of Agriculture, Poznań, Poland. These identifications resulted in a flood of descriptive papers, many of which Moser co-authored with comments on the biology of the various new species. Many of these cooperators have since retired or deceased, leaving no one to replace their taxonomic expertise (Moser 2000).

Moser developed the broad perspective that research on mites was an opportunity to understand their role in the transmittal of the blue stain and other fungal diseases, and to determine if mite species could provide a biological control of SPB.

To assist in technical training as well as provide quality control in slide processing, Moser established a rating system to evaluate the quality of mite slide development. After mites are mounted on slides by supporting technicians, the quality of the processing is evaluated and a ranking is noted on the slide. The ranking criteria are: very good (vg), good (g), fair (f), and poor (p). Soon any technician who assisted Moser worked diligently to achieve and maintain the highest ranking possible (see footnote 1).

Moser developed the broad perspective that research on mites was an opportunity to understand their role in the transmittal of the blue stain and other fungal diseases, and to determine if mite species could provide a biological control of SPB. He found certain species that fed on the brood (i.e., pupae, larvae, and eggs) of SPB and suggested that they might be reared in sufficient quantities to slow the expansion of SPB populations.

MITES ON SPB RELATED TO THE BLUE STAIN FUNGUS—The first paper that listed the array of mite species associated with the transfer of blue stain fungus by pine bark beetles was published in 1971 (Moser and Roton 1971). There were, however, a number of earlier publications that documented some species of mites associated with

LEFT: *Tarsonemus* mite slide showing fungal spores being carried in the mite's sporotheca.

ABOVE: Bucket trap for SPB with a synthetic pheromone bait.

the bark beetles (Hunter and Moser 1968, Smiley and Moser 1968, Smiley and Moser 1970, Woodring and Moser 1970).

Moser (1976a) documented that SPB can carry a large number of phoretic mites. Based on the 20,000 slides Roton and Moser had processed since 1963, it appeared the tarsonemid mites were the primary players associated with blue stain (Moser 2000). In a related effort, Kinn (1976) then developed a key that helped identify the mites associated with SPB.

Ophiostoma minus is the blue stain fungus associated with SPB, and is introduced into trees by the attacking beetles (Bridges and Moser 1983). This fungus is a major factor causing mortality and/or degradation of wood quality. Colonization of the tree by the fungus is thought to aid development of the beetle in the tree by reducing the moisture content of the wood (Nelson 1934). The fungus can be isolated from the body of the bark beetle, but is not transported in the mycangium (cup-shaped pits in the thorax) as are some other symbiotic fungi (Barras and Perry 1972).

Although the fungus was known to be transmitted by the beetle, there was no understanding of how the beetle becomes inoculated with fungal spores. The work by Bridges and Moser (1983) established that a possible source of inoculum was phoretic mites. Tarsonemid mites feed on the fungus and move from areas of fungus-colonized bark to the cracks in the outer bark where they attach to emerging mature adult beetles (Roton 1978). The association of mites carried by beetles and infestation of pines by the blue stain fungus provides an example of a three-way mutualism among insects, mites, and fungi (Bridges and Moser 1983).

Although beetles were known to carry mites, no specific information was available on where the mites were attached to the beetles. Research by Moser and Bridges (1986) determined that two species of *Tarsonemus* mites attach to different locations on the adult beetle, for one the location is beneath the thorax and for the other beneath the outer wings, but both species are capable of infesting trees with the fungus.

Moser (1985) determined that certain female *Tarsonemus* mites, like their host beetles, carry a specific fungus on which the mites feed inside special morphological, spore-carrying, sac-like structures called sporothecae. The sporothecae is similar to the mycangium described for bark beetles, but differs in that no gland cells are present. In one study, it was determined that over 85 percent of mites carried blue stain fungal spores, and each mite carried an average of 15 spores (Moser and Bridges 1986).

Bridges and Moser (1983) and Moser and Bridges (1983) found that beetles transporting tarsonemid mites carried *O. minus* disease more often than mite-free beetles. That study did not, however, compare mite population levels with the occurrence of blue stain in SPB infestations. Another study showed a significant relationship between the occurrence of phoretic tarsonemid mites and blue stain in SPB populations; the lowest incidences of mites and blue stain were associated with outbreak populations of SPB (Bridges and Moser 1986). Therefore, changes in mite populations could cause changes in blue stain abundance.

IMPROVEMENTS IN METHODOLOGY—As late as the mid-1970s, there was no efficient way to trap live SPB for population studies. Sticky traps were still in common use (Moser 1976b), but they were messy and trapped many nontarget organisms. Moreover, beetles became mired in the sticky material and were of little use for chemical investigations.

Moser and Browne (1978) devised a bucket trap baited with a synthetic pheromone which attracted large numbers of male beetles. When infected bolts were used as bait, roughly equal numbers of males and females were captured.

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Another improvement in methodology was in the tagging of mites with paint for studies of *Pyemotes* females in life-span determinations. Moser and Roton (1970) found that aerosol paint sprayed at a distance of three feet satisfactorily marked the hairs on the mites' bodies without overwhelming the mites with paint and made identification of live stages possible under a microscope.

The study of mite biology was difficult due to the small size of the mites. Lary Roton, Moser's technician who was very creative, was asked to make a movie of the life of a mite; but Kodak®, the premier maker of camera equipment at the time, said that the technology did not exist to make such a movie. Roton located an old 16-mm movie camera, developed a connecting ring to a microscope, and filmed the life cycle of mites.[2] Roton's ingenuity underscores how Moser instilled into his technicians a desire to meet the scientific needs of the program regardless of the difficulty.

Obtaining a continuous supply of beetles for research purposes was difficult. So, Bridges and Moser (1984) developed a continuous mass-rearing technique for SPB. Such a colony was obtained from a natural infestation, and bolts from trees were cut and placed in a screened corner of a laboratory. New bolts were added periodically and the beetles moved into the uninfested bolts. Such a colony was maintained for over a year.

To observe the behavior and development of beetles in the pine's phloem layer, phloem sandwiches were developed, in which a piece of bark and phloem is removed from a live tree and pressed between glass plates. Previous designs required that the insects be placed into this sandwich. Taylor and others (1992) modified the sandwich to allow insects to freely and naturally colonize the phloem sandwich by adding a piece of plywood with holes drilled through it to the bark side. This modification allowed natural infestations by SPB and associates.

Moser instilled into his technicians a desire to meet the scientific needs of the program regardless of the difficulty.

BEGINNING OF RESEARCH ON MEXICAN BEETLES—In the early 1970s, Jack Coyne, Bill Rose, Ed Clark, and Robert Wilkinson sent Moser mite material collected from bark beetles in Mexico, Honduras, and Guatemala. In 1974, the results from these evaluations were published in *Turrialba* as the first list of mites associated with pine bark beetles in Central America (Moser and others 1974). This information would provide rationale for preparing and submitting, in 1997, a grant proposal with Jorge Macías to the Forest Service to conduct a survey of mites and insect associates of SPB in Mexico and Central America.

[2]Barnett, J.P.; Streett, D.A.; Blomquist, S.R. 2012. Oral history interview of March 22, 2012, with Lawrence M. Roton. Cassette tape. Pineville, LA: U.S. Department of Agriculture Forest Service, Southern Research Station, Insects, Diseases, and Invasive Plants Research.

Collecting adult SPB under the bark of *Pinus oocarpa* in Chiapas, Mexico.

Unlike its western cousins, SPB is active all winter and often flies at low temperatures. Flight temperature data are basic to the understanding of bark beetle dispersal, and this understanding is necessary for predicting and managing SPB epidemics.

TEMPERATURE THRESHOLDS FOR SPB FLIGHT—An ongoing need in forestry is to be able to predict SPB activity. The primary approach to anticipate populations is the use of aerial detection. This survey method is good to quantify beetle population changes over large areas, but methods for determining beetle population changes over short periods and small areas are needed. Moser and Dell (1979) found that when SPB brood emerges, the populations of beetles that reach their destination and infect other trees increase as temperature increases and decrease with heavy rain during their period of flight.

Moser and Thompson (1986) plotted the range of flight temperatures for SPB and found the optimum flight temperature was about 27 °C. Observed minimum and maximum flight temperatures were 6.7 °C and 36.7 °C, respectively. The minimum temperature was a surprise because it is the lowest ever recorded for any flying beetle. Unlike its western cousins, SPB is active all winter and often flies at low temperatures. Flight temperature data are basic to the understanding of bark beetle dispersal, and this understanding is necessary for predicting and managing SPB epidemics.

Weather factors were also evaluated in relation to predicting flying populations of the SPB predator clerid beetle (*Thanasimus dubius)* (Moser and Dell 1980). Population trends of the flying clerid beetles were similar to those of SPB. Variations in ratios of predator to prey suggest that in endemic situations, *T. dubius* may suppress SPB populations.

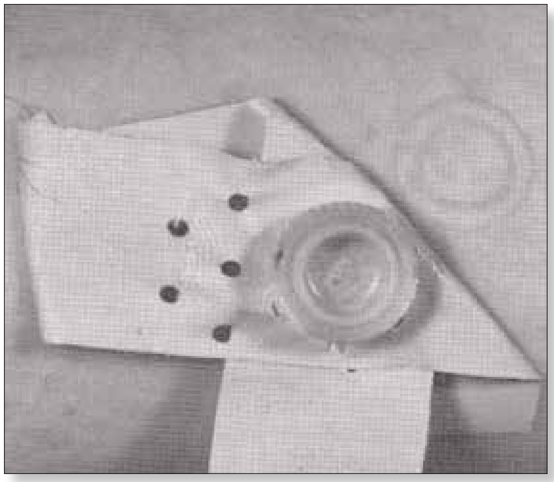
PYEMOTID MITES ASSOCIATED WITH BARK BEETLES—Moser, with Earl Cross of Northwestern State University at Natchitoches, LA and later of the Department of Entomology at the University of Alabama, published a number of studies on the systematics and biology of the pyemotid mites associated with bark beetles (Cross and Moser 1971, Moser and others 1971, Moser and Roton 1972). This group of mites is important because some of the species are parasitoids, while other related species consume and may transmit the mycangial fungi of bark beetles (Moser 2000).

Among the numerous mite species found in galleries of North American bark beetles are those of the genus *Pyemotes*. These mites are insect parasites that exhibit a wide variety of trophic diversity (i.e., they feed on a variety of things) as well as dispersal polymorphisms (i.e., they assume different forms). The genus naturally divides into two different subgroups. In the *scolyti* subgroup, all five species are phoretic on one or more species of bark beetles. In nature, all feed only on immature bark beetle broods (eggs, larvae, and pupae), but not on adults (Moser and others 1987). At least one female morph of each of the five species is a phoretomorph—a mite specialized with claws or suckers for clinging to insects (Moser and Cross 1975)—and one expresses an extreme form of polymorphism known for mites (Cross and Moser 1975, Cross and others 1981, Smiley and Moser 1984a).

In the *ventricosus* subgroup, its ten species are not known to be phoretic, but at least two species possess venom. This subgroup includes the straw itch mites, *Pyemotes tritici*, which produce a toxic rash on human skin, whereas *P. scolyti* and *P. parviscolyti* caused no observable symptoms (Moser 1975a). To bioassay toxicity to humans, Lary Roton volunteered to have female mites that had been feeding on SPB placed under a plastic cap taped to his arm. After four days the cap was removed and the arm appraised for itching, redness, and blisters. The tests were repeated for several species and replications.

Eight species of *Pyemotes* are natural enemies of one or more forest insects. Six of these attack bark beetles, four attack beetles infesting stored timber, one attacks a needle sheath midge, and one attacks the pupae of the Douglas-fir (*Pseudotsuga menziesii*) cone moth (Moser and others 1987).

The pyemotid mites are unique because the females of many of the species have discrete forms that look so different that sometimes they have been placed in different classification families.



TOP: To bioassay the dermatology of *Pyemotes* species, mites were held in the caps (9-mm inside diameter) against the skin for four days.

BOTTOM: Female *Pyemotes giganticus* displaying an extreme form of polymorphism—note enlarged frontal legs.

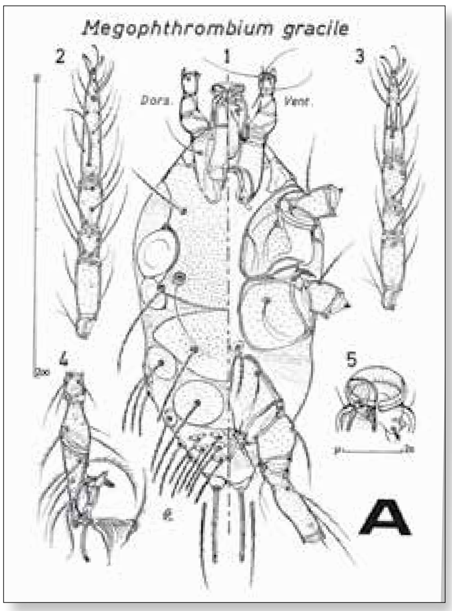
POTENTIAL FOR BIOLOGICAL CONTROL—In 1975, Moser evaluated 51 species of mites that were collected from SPB galleries for their potential as natural control agents for reducing SPB populations. Although 32 of the species showed predation on one or more of the brood stages, four were primary candidates for use as biological control in reducing SPB infestations: *Histiogaster arborsignis, Proctolaelaps dendroctoni, Macrocheles boudreauxi,* and *Dendrolaelaps neodisetus*. Four other species that showed good potential were: *Eugamasus lyriformis, Dendrolaelaps neocornutus, D. isodentatus,* and *Proctolaelaps fiseri* (Moser 1975b). Interestingly, adult beetles were never attacked, a fact that may be explained by the phoretic habits of the mites. Most mites depend upon riding on the adult beetles for dispersal to host material. These mites were evaluated in a controlled laboratory situation and are not known to be predatory to SPB under natural conditions.

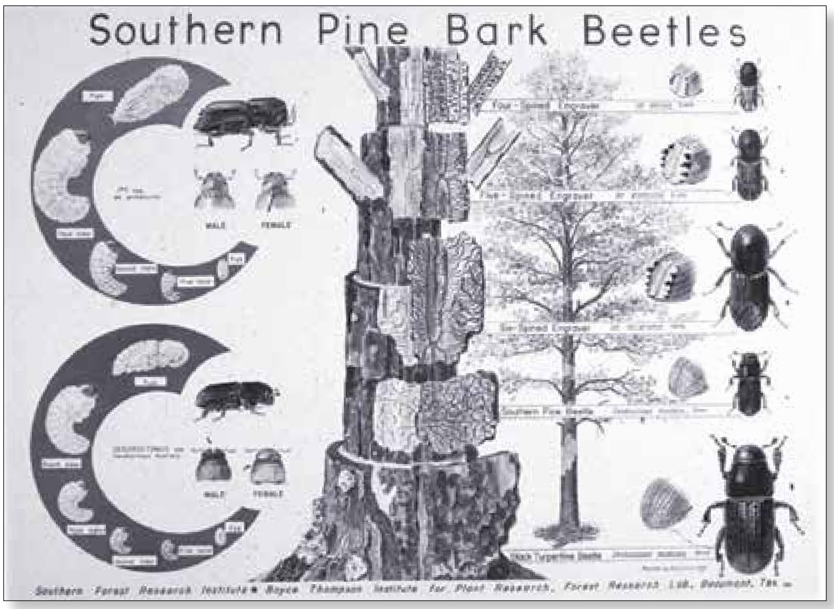
Although many mite species are associated with SPB, only the genus *Pyemotes* is typically predatory to bark beetles. One reason for the success of SPB may be the lack of *Pyemotes* mites associated with it (Moser and others 1978). Only *P. parviscolyti* is associated with SPB and only in a minor way. Under the sponsorship of a PL-480 grant,[3] populations of *Pyemotes* species

[3]Public Law 480 (PL-480) grants resulted from a portion of the repayment from loans made to a developing country for agricultural food commodities. Some of the funds for repayment could be held in the receiving country and used to fund cooperative research between it and U.S. Department of Agriculture scientists.

LEFT: This drawing provides the descriptive information for *Megophthrombium gracile*, a newly documented parasitic mite species.

RIGHT: This drawing illustrates the five bark beetles that attack southern pines and shows the differences in size among the *Ips* beetles (top three), the southern pine beetle, and the black turpentine beetle. Also shown are the locations within the tree bole where the different beetles attack. (Drawing from the Southern Forest Research Institute, Boyce Thompson Institute for Plant Research, Forest Research Laboratory, Beaumont, TX.)





in Poland were bioassayed for potential use in the biological control of SPB in the United States (Moser and others 1978).

Of the pyemotid mites located in Poland, *Pyemotes dryas* was found to offer the greatest potential as a biological control agent because it is a natural enemy of bark beetles (the female of this mite species is morphologically identical to that of the North American native *P. parviscolyti*). Although the mite was predatory to SPB larvae and pupae, the species was precluded from being released in the United States for the control of SPB because there was no phoretic host for the mite. If it could be reprogrammed to ride SPB or one of its associates, it could become a major factor in biological control of SPB (Moser and others 1978).

In a continuing search for predatory mites, Moser discovered a new genus and two new species of mites that were discovered as parasites of flying SPB adults (Moser and Vercammen-Grandjean 1979). These mites, as well as parasitic mites of the Parasitengona family, are found on the outer bark and presumably attach to beetles during or shortly after emergence (Moser 1979). They are found infrequently and have little impact on beetle populations. Other efforts to develop biological controls included evaluations of the transfer of an egg parasite (*Pyemotes giganticus*) that rides on Douglas-fir pole beetles (*Pseudohylesinus nebulosus*) to SPB. Since these mites are phoretic on a wide range of bark beetles, potential exists for their transfer to SPB. Tests showed, however, that although they readily ride on SPB, they are reluctant to attack immature stages of any other bark beetle (Moser 1981).

Although SPB has been the primary focus of efforts to find possible biological control agents, opportunities developed to evaluate control agents for other insects. Moser and others (1986) were first to report a species of *Pyemotes* parasitic on pupae of the Douglas-fir cone moth (*Barbara colfaxiana*) native to the Western United States and Canada. This mite seems capable of explosive population buildups (Moser and others 1987) and has the potential to join the straw itch mite (*Pyemotes tritici*) as a commercial biological control agent (Bruce 1983), but seems to lack the amount of venom needed to be highly effective.

Black turpentine beetles (*Dendroctonus terebrans*), another significant pest of southern pine forests, attack the lower boles of pines damaged by lightning, logging, or other management practices. Currently, control strategies to reduce bark beetle populations are chemical treatments, infested tree salvage, and preventative management of silvicultural practices (Moser 1989). Of potential biological controls, the exotic insect predator, a

Large resin deposits on a southern pine resulting from black turpentine beetle attack. (Photo from Ronald F. Billings, Texas Forest Service)

Moser collaborated with several mite specialists to evaluate and categorize species associated with bark beetles in Germany.

small beetle (*Rhizophagus grandis*), appears to have potential as a control agent (Miller and others 1987). *R. grandis* has been introduced and released for evaluations of potential beetle control in England, France, Belgium, and Canada.

During 1986 and 1987, three shipments of *R. grandis*, reared in Belgium, were shipped to the Alexandria Research Center to test methods of rearing the predators on both black turpentine and southern pine beetles. The rearing attempts failed due to a pathogen problem. They did, however, demonstrate that the predator could be reared on black turpentine beetles using semi-artificial methods. Additional *R. grandis* insects were obtained for field release trials (Moser 1989, Moser and Branham 1988).

Miller and others (1987) summarized the potential of various approaches for developing biological control agents for native North American bark beetles. A number of studies provided evidence that at least two predatory species possess some of the necessary ecological and behavioral characteristics to be considered as potential biological control agents. One involves a North American clerid beetle, *Thanasimus undulatus*, a predator of the Douglas-fir beetle, *Dendroctonus pseudotsugae*, and the other is *Rhizophagus grandis*, a beetle that is a specific predator of *Dendroctonus micans*, the Great spruce bark beetle. Much work remains, however, to finalize the development of such control agents.

COOPERATIVE RESEARCH ON EUROPEAN SPECIES—With a PL-480 grant with Poland obtained in 1974, Moser and his collaborators, Bohdan Kiełczewski and Jerzy Wiśniewski, began research to study the mites associated with Polish bark beetles. Moser was able to travel to Poland in 1975 where he worked with his collaborators to write articles on the potential of *Pyemotes dryas* as a biological control agent (Moser and others 1978). They also reported on surveys of mite associates of bark beetles in Poland (Kiełczewski and others 1983). This latter article reported that 181 mite species were associated with 45 bark beetle species throughout Poland.

Moser collaborated with several mite specialists to evaluate and categorize species associated with bark beetles in Germany. Moser and cooperator Hermann Bogenschütz of the Forest District of Freiburg sampled 800 beetles from a population of 4,725 adult *Ips typographus* collected from pheromone traps in the Black Forest region. From this sample, a new species, *Scutacarus scolyti*, was found (Mahunka and Moser 1980).

The mites attached to the beetles using a large claw located at the end of the mite's first leg. Another new species of mite, *Pseudopygmephorus bogenschutzi*, was described in Mahunka and Moser (1981-1982).

Moser and Bogenschütz (1984) identified 32 species of mites associated with flying *I. typographus* captured in traps in South Germany. Fifteen of these were judged phoretic because they were attached to the beetles. The biology of most of the species was unknown, but three were thought to be potential predators.

From the mite species that Moser and Bogenschütz (1984) evaluated that were captured with *I. typographus*, a new mite subfamily, genus, and species were identified (OConnor and Moser 1985).

The Norway spruce forest of Scandinavia also had widespread outbreaks of *I. typographus*, particularly in Sweden. Moser and others (1989) identified 24 species of phoretic mites associated with *I. typographus*, bringing the total number of phoretic mites identified for this beetle species to 38.

IDENTIFICATION OF OTHER NEW SPECIES—Moser has become the internationally recognized authority on the mites related to bark beetles and other forest insects. Because of this recognition, he has collaborated with numerous scientists interested in identifying species and understanding the role of mites in the biology of host insects. Due to the number of these new genera and species of mites examined, it has been impossible to study the biology and role of all of these insects. Much of this identification effort was carried out with collaboration of Robert L. Smiley of the U.S. Department of Agriculture Agricultural Research Service's Systematic Entomology Laboratory in Beltsville, MD.

A summation of some of these efforts is documented in the publication of *Histiostoma* species associated with various pine bark beetles from Honduras, Guatemala, and Louisiana (Woodring and Moser 1975), two new species of *Ereynetes* of the Southern United States (Hunter and others 1989), a new species of *Microdispodides* associated with a western bark beetle (Smiley and Moser 1984b), and two new phoretomorphic *Siteroptes* from galleries of the SPB (Smiley and Moser 1976). Weatherby and others (1989) documented the biology of a pine needle sheath midge, *Contarinia acuta,* on a new host in Louisiana.

The mite *Pyemotes johnmoseri* was first located and described by Khaustov (1998) in Asia. In 2007, it was found to be a predator of the bark beetle *Hypoborus ficus* which attacks

ROBERT L. SMILEY of the U.S. Department of Agriculture Agricultural Research Service's Systematic Laboratory in Beltsville, MD, led the effort to identify many mite species.

Turkish fig (*Ficus carica*) trees and causes tree decline and mortality (Aksit and others 2007). *Pyemotes johnmoseri* was determined to be a predator of the beetle, has potential to reduce populations of *H. ficus*, and should be further evaluated.

A major reevaluation of the nomenclature of the tarsonemid mites was published by Smiley and Moser (1974) where descriptions of new species of these mites are presented with additional taxonomical information for some taxa. Included are descriptions for one new species of *Ununguitarsonemus*, two new species of *Heterotarsonemus*, four new species of *Tarsonemus*, and the male of *T. ips*, as well as a redescription of the genus *Pseudotarsonemoides*. A special subgroup (lectoype) within the genus *Pseudotarsonemoides* was designated for *P. eccoptogasteris* and included three new species.

Smiley and Moser (1985) also summarized the existing information of the identification and biology of the mite genus *Heterotarsonemus*, as well as describing a new species thought to have a relationship to the Dutch elm disease, *Ceratocystis ulmi* (recently renamed *Ophiostoma ulmi*).

With Meredith Blackwell, Bob Bridges, and Thelma Perry, Moser documented the first case of a fungus with an attachment mechanism for phoresy on arthropods.

ADAPTATION OF A FUNGUS FOR ATTACHMENT TO MITES—With Meredith Blackwell of the Department of Biological Sciences at Louisiana State University and Bob Bridges and Thelma Perry of the Forest Insect Research Unit, Moser documented the first case of a fungus with an attachment mechanism for phoresy on arthropods. Described in *Science* (Blackwell and others 1986a), the previously unknown method of fungal development with extreme specialization for dispersal was discovered. The minute ascomycete, *Pyxidiophora kimbroughii*, is a long, slender, two-celled ascospore found associated with the mites on SPB (Blackwell and others 1986b).

Robert Bridges, John Moser, Meredith Blackwell, and Thelma Perry. Blackwell is a professor of Mycology at LSU and Bridges, Moser, and Perry were with the Station's Forest Insect Research Unit. Blackwell is now a member of the prestigious American Academy of Arts and Sciences.

A darkened region of the ascospores develops into a holdfast for attachment to mites where the spores develop into a *Thaxteriola* anamorph (sexual form). Studies have found *Pyxidiophora* ascospores attached to 116 collections of 35 species of mites that are associated with beetle habitats in trees and wood (Blackwell and others 1989).

Majewski and Wiśniewski (1978) identified a new species of this fungus on mites in Poland and named it *Thaxteriola moseri* in honor of John Moser.

While the effect of the fungus *Pyxidiophera kimbroughii* on bark beetle-infested trees and the beetles themselves is unknown, it is possible that mites associated with the beetle and its habitat are necessary for the spread of such fungi and may be important in the biological complex of insects and fungi that drive tree infestations (Bridges 1983).

Initiation of Research With Chinese Scientists

In 1984, Yang Zhongqi, of Northwest College of Forestry in Beijing, China, arrived in Pineville, LA, to spend a year with Moser researching the biological control of the black turpentine beetle (*Dendroctonus terebrans*). With the aid of Jean-Claude Gregoire of the Laboratoire de Biologie Animale et Cellulaire, Bruxelles, Belgium, they imported *Rhizophagus grandis*, a predator beetle of the European turpentine beetle, *Dendroctonus micans*, to rear, and possibly introduce for control of the black turpentine beetle (Moser 2000).

Although the initial evaluations were positive, the research direction was changed, and this area of research was closed. But the experience gained by Yang Zhongqi has been put to good use. Yang, who is currently Deputy Director of the Institute of Forest Protection, Chinese Academy of Forestry, Beijing, has used the training to develop a program in China to import *R. grandis* in an effort to establish a biological control of the red turpentine beetle, *Dendroctonus valens*, which caused large losses of pines in China (Moser 2000).

Yang Zhongqi and John Moser observing the *Dendroctonus armandi* bark beetle in Central China.

In 1990, Yang Zhongqi arranged for Moser to travel to China to see the bark beetle problems in Central, West, and Northeast China. Of particular interest to Moser was the observation of *Dendroctonus armandi*, which attacks only the species *Pinus* *armandii* in the Qinling Mountains of Central China. This interesting bark beetle is an object of study by Zhongqi and his students, and they are collecting flying beetles so that Moser can study the mites associated with the beetle.

Retirement

Moser retired on December 31, 1989 and immediately signed on as a volunteer with the Forest Service. This status meant that he could retain his mite and ant studies and maintain complete control of his research.

Moser's research assignment was under scrutiny in mid-1989, and he was being pressured to terminate his town ant and mite studies. Since he was not interested in the Station's proposed alternative projects, Moser began to consider retirement; with his military service, he had 32 years of Federal service and therefore could retire with an annuity of about one half of his salary. By retiring before December 31, 1989, Moser could withdraw all the funds he had paid into his retirement system and invest it. John and his wife, Martha, had invested aggressively, and his yearly annuities from investments totaled twice his salary, so they could live comfortably without his Forest Service salary (Moser 2000).

Moser retired on December 31, 1989 and immediately signed on as a volunteer with the Forest Service. This status meant that he could retain his mite and ant studies and maintain complete control of his research. He comments that "the arrangement was a bit rocky for 7 years, but with the ascension of Kier Klepzig as project leader, the environment vastly improved" (Moser 2000).

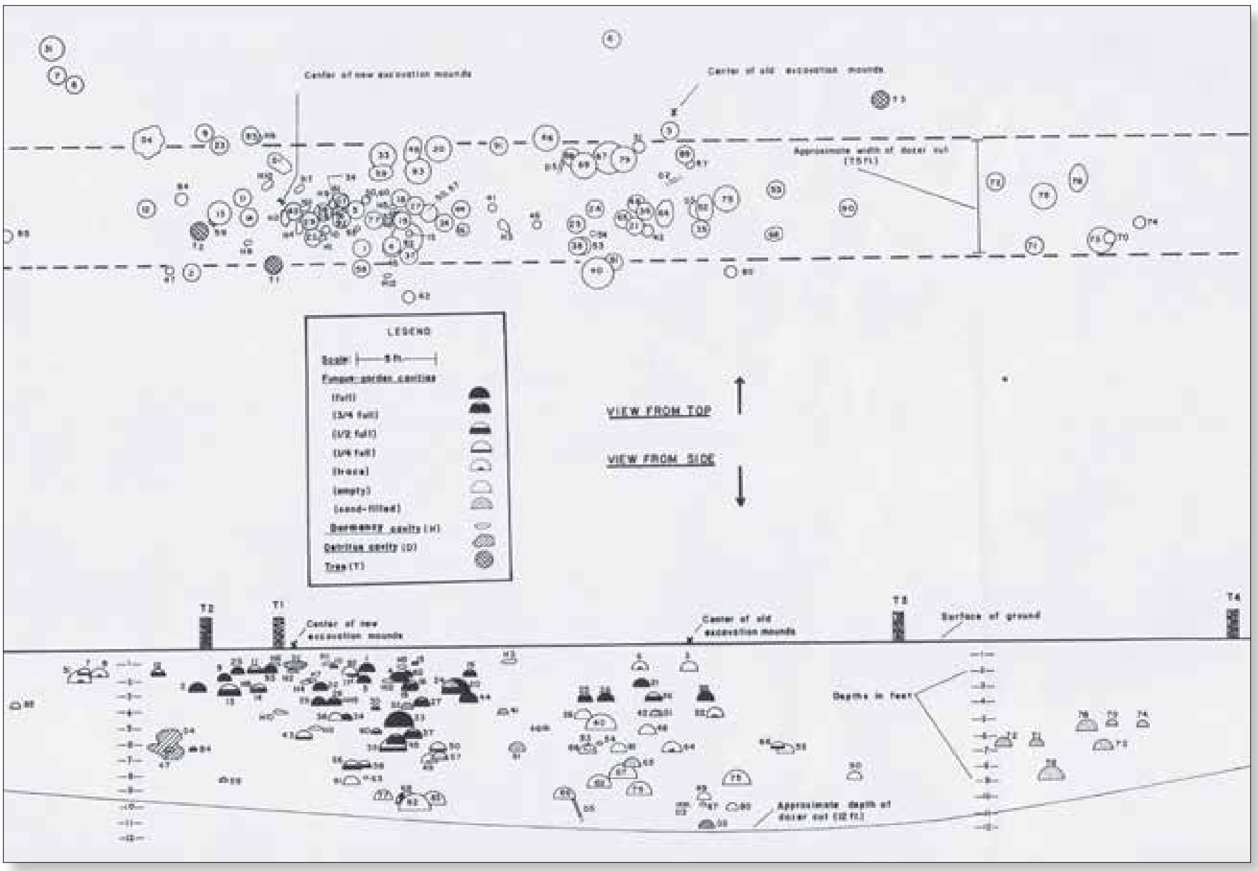
Since his retirement, Moser's primary focus has been on the relationship of the tarsonemid mites to SPB mycangial fungi; he also maintains an interest in the leaf-cutting ants and has renewed his first encounter with entomology with his study of gall wasps.

RESEARCH AFTER RETIREMENT

Excavation and Mapping of a Town Ant Colony

Although the excavation and mapping of the medium-sized town ant colony shown below was done many years earlier, specific information on the effort was not published until 2006. The ant colony located in northern Louisiana was excavated completely, and a three-dimensional model of its external and subterranean features was constructed. In total, 97 fungus gardens, 27 dormancy cavities, and 45 detritus cavities were located (Moser

Map of the excavated town ant colony with views from the top and side. The nest was excavated to a depth of 12 feet and a width of 25 feet.



Documentation of this colony excavation is the last major effort in Moser's long interest in understanding town ants, but he continues to be an international resource for those interested in the biology of leaf-cutting ants.

2006). The complete excavation of such a large colony is rare due to its size and the immense resources and manpower required.

At the center of this nest was a large central cavity (about 3 feet in diameter and height), which in the winter functioned as a protective site for the colony and where the flying ants were reared. Vertical tunnels, possibly as deep as 100 feet, served as wells leading to the water table (Moser 2006). A number of insects associated with the ants lived in the nest; many of these have been described earlier in this document.

Documentation of this colony excavation is the last major effort in Moser's long interest in understanding town ants, but he continues to be an international resource for those interested in the biology of leaf-cutting ants. For example, Moser collaborated with a group of specialists interested in eye size and behavior of day- and night-flying leaf-cutting ant alates (Moser and others 1998, Moser and others 2004). He, too, worked with a German colleague to study the interaction of mites and leaf-cutting ants (Wirth and Moser 2008). However, research on mites associated with bark beetles continues to be his primary interest.

Interrelationships Among Bark Beetles, Mites, Fungi, and Nematodes

An extensive collection of organisms, primarily arthropods and fungi, can rapidly colonize trees that are attacked and killed by bark beetles and pathogenic fungi. The composition and arrival sequence of this community are predictable. Interactions among the key elements in this complex of arthropod natural enemies and associated fungi can affect significantly the reproduction and survival of bark beetles and the pathogenic fungi. These interrelations have not been studied in sufficient detail to assess their role in regulating bark beetle infestations and tree mortality (Stephen and others 1993). Thus began a collaborative effort to clarify these interactions.

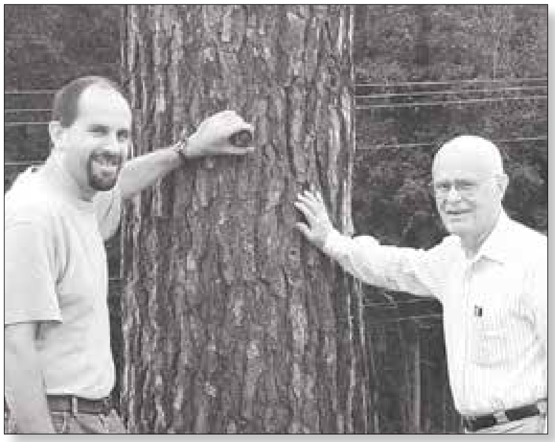
Early in the effort, Moser and others (1995) documented that two species of *Tarsonemus* phoretic mites on SPB not only carried the crescent-shaped ascospores of *Ophiostoma minus* blue stain fungus in their sporothecae, but these mites also carried tadpole-shaped ascospores of one of the two SPB mycangial fungi, *Ceratocystiopsis ranaculosus*, a species described by Thelma Perry (Moser 2000). This discovery of a new means of ascospore dispersal provides an additional pathway for fungal infection in conifers and may result in another agent of mortality of beetle-infested trees.

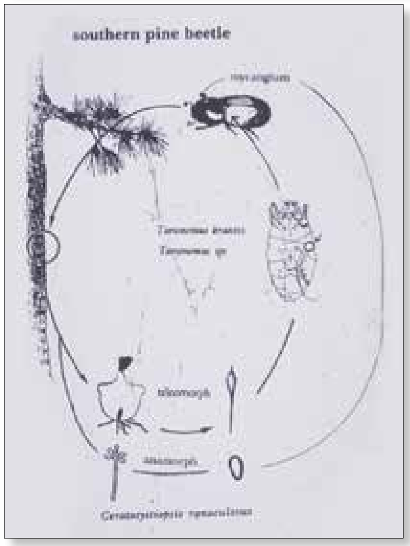
> A note about **THELMA J. PERRY** is due here. She was trained as a medical technician in New Orleans and joined the Forest Insect Research Unit in Pineville in the late 1960s. She worked primarily to support entomologists interested in the fungi in the mycangia of SPB, but also collaborated with Moser on several projects. Perry was one of the earliest female African-American technicians in the Southern Station and is described by Moser as an "excellent technician."[4] Tragically, she died of cancer in 1998.

Klepzig and others (2001a) began a significant effort studying insect-fungal complexes with a focus on bark beetles and their associated organisms, particularly the relationship between the southern pine beetle and its associates in coniferous trees in the Southern United States.

In a review article, Klepzig and others (2001b) summarized the complex, multi-level interactions among bark beetles and their fungal and mite associates. They reported that SPB attacks and kills southern pines, which, in turn, introduces fungi into the tree. *Ophiostoma minus* may initially aid beetles in killing trees, but later this blue stain fungus becomes an antagonist, competing with the beetle larvae for host phloem. Two additional fungi, *Entomocorticium* sp. and *Ceratocystiopsis ranaculosus*, are carried within specialized mycangium in the beetle and inoculate the phloem, where they are fed upon by the beetle larvae. The beetle also carries several species of mites which transport spores of *Ophiostoma minus* and *Ceratocystiopsis ranaculosus*; the mites complete their life cycle on these fungi.

These strong indirect interactions of mites and SPB were studied by Lombardero and others (2003). Studies were conducted to evaluate the effects of phoretic mites on SPB. *Tarsonemus* mites carry ascospores of *Ophiostoma minus*, which tend to out compete mutualistic fungi carried by SPB. Experimental additions and removals of mites from beetles demonstrated that *Tarsonemus* propagate *O. minus* in beetle galleries. The





TOP: Pineville forest insect research scientists Kier Klepzig and John Moser.

BOTTOM: Diagram of the life cycle of *Ceratocystiopsis ranaculosus*. Ascospores are released from the fungus on the inner bark where they enter the sporothecae of adult female mites. Some mites are phoretic on emerging SPB, which disperse not only the mite, but also the fungus (from Magowski and Moser 2003.)

[4]Blomquist, S.R. 2012. Oral history interview of June 12, 2012, with John C. Moser. Unpublished document. Pineville, LA: U.S. Department of Agriculture, Forest Service, Southern Research Station, Insects, Diseases, and Invasive Plants Research.

results indicate that the *O. minus* fungus is an antagonist of SPB: beetle larvae seldom survive in the presence of *O. minus*. Apparently, this is a result of *O. minus* being more aggressive than the two species of mycangial fungi carried by the beetle for nutrition (Hofstetter and others 2006, Lombardero and others 2000). Thus, the population of *Tarsonemus* mites and the fungi they carry may contribute to the population dynamics of SPB. Noted, too, was that the reproduction rate of the mites was more temperature sensitive than for beetles (Lombardero and others 2003). Consequently, seasonal variations in temperature can be anticipated to produce variations in SPB populations.

Leptographium abietinum was the fungus which cultured the nematodes most successfully, and it plays an important role in the bark beetle, mite, and nematode interactions.

Research on the spruce bark beetle, *Dendroctonus rufipennis*, of the Western United States and Canada documented symbiotic associations with a number of microorganisms, especially the fungus *Leptographium abietinum* (Cardoza and others 2008). Eight mite species were associated with the beetle, but the most prevalent was *Histiogaster arborsignis*. Seventy-five percent of the beetles examined carried nematodes, with six species represented. *Histiostoma arborsignis* mites showed strong feeding and oviposition preferences for *Leptographium abietinum* among the fungal species evaluated. *Leptographium abietinum* was the fungus which cultured the nematodes most successfully, and it plays an important role in the bark beetle, mite, and nematode interactions (Cardoza and others 2008).

Mite species associated with tree-feeding insects seldom affect humans; however, high incidences of itching and red, painful welts on people in the Midwestern United States during the summer of 2004 led to the discovery of an imported European species of mite, *Pyemotes herfsi*, preying on gall-making midge larvae on oak leaves (Broce and others 2006). This study also revealed these mites were capable of being dispersed by wind, which made them difficult to control or avoid.

International Collaboration on Species Identification

A major aspect of Moser's collaboration with international specialists is in developing knowledge of species important in understanding biological diversity, and this knowledge may facilitate developing potential control of insect pests. Little progress can be made in biodiversity unless there is information of the species involved in biological complexes. Moser is involved in numerous international collaborations to identify mites and other bark beetle associates.

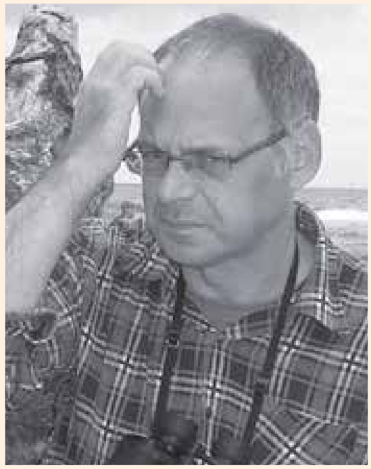
Moser is one of only a few forest insect taxonomists in the United States; therefore, identification of the many new species associated with bark beetles now being discovered requires the involvement of international specialists. Such collaboration began with Polish scientists Bohdan Kiełczewski and Jerzy Wiśniewski in 1974. Later, Wojciech L. Magowski worked with Moser to describe three new species of the genus *Acanthomastix* (Magowski and Moser 1993), describe a new genus and species of mite associated with the bark beetle *Pseudopityophthorus* (Magowski, and others 2005), and redescribe the species-group *Tarsonemus minimax* with a description of two new species (Magowski and Moser 2003).

Ips typographus, the European bark beetle pest that ranges across much of Europe, parts of Asia, and even in Japan, carries numerous species of mites that also carry fungal ascospores. Ten morphologically distinct types of ascospores were found on bodies of 17 species of mites associated with *I. typographus* collected in Sweden (Moser and others 1989). *Ophiostoma polonicum*, the pathogenic blue stain fungus, was noted on nine mite species.

Studies of *I. typographus* European bark beetles in Germany and Georgia (country) were investigated for protozoa, fungi, mites, and nematodes. Of all these possible antagonists, none were capable of reducing beetle populations (Burjanadze and others 2008). In addition, Levieux and others (1989) identified a number of mites associated with *I. sexdentatus* in Germany. In Bulgaria, 818 specimens of *I. typographus* were tested for the presence of phoretic mites; five genera of mites were collected, making this the first report of phoretic mites on *I. typographus* in Bulgaria (Takov and others 2009).

Investigation of flying *I. typographus japonicus* from Japan found 12 species of phoretic mites, three of which were not previously recorded in Europe (Moser and others 1997). On the mites were found seven distinct species of fungal spores; *Ophiostoma bicolor* was the most common species, with the pathogenic *Ceratocystis polonicum* present in small numbers.

A mite, *Schizosthetus simulatrix*, common on bark beetles ranging throughout Europe and Asia, was studied to understand its morphology and ecology (Kaluz and others 2003), and the genera of commonly encountered associate species were



WOJCIECH L. MAGOWSKI of A. Mickiewicz University in Poznań, Poland, was a collaborator studying tarsonemid mites.

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redescribed (Al-Atawi and others 2002). Hofstetter, Moser, and McGuire (2009) observed *S. lyriformis* preying on eggs and larvae of *I. pini*, verifying that it is a predator of bark beetles in the Western United States.

The species composition and abundance of phoretic mites of bark beetles *(Pityokteines* spp.) on Silver fir (*Abies alba*) were investigated in Croatia. Ten mite species were documented for the first time (Pernek and others 2008). None of the species appeared to have the potential to be used for biological control of the beetles. In a later study, new associates of the beetles were recovered (Pernek and others 2012).

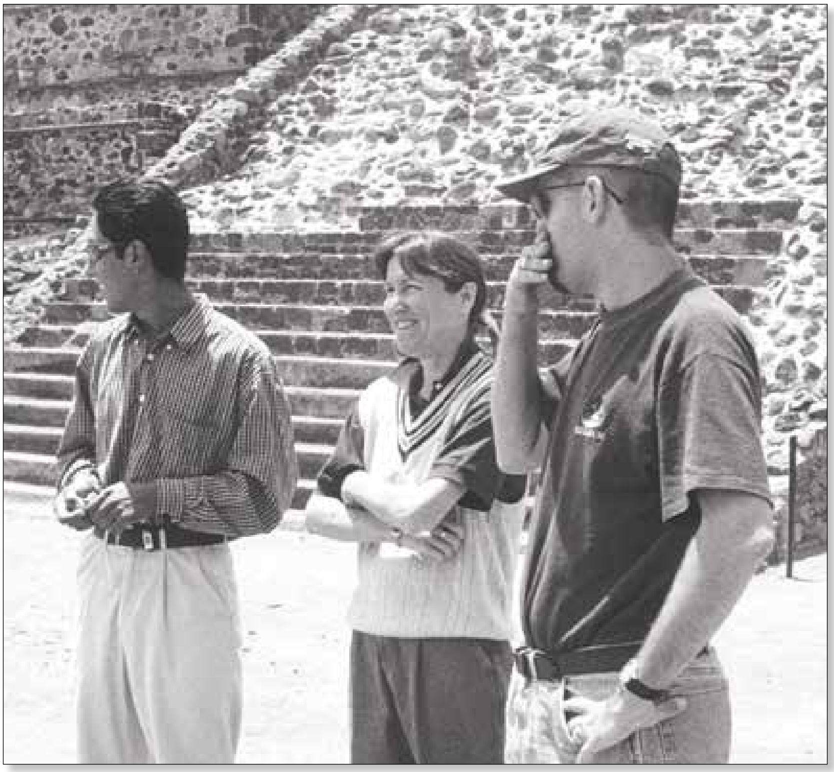
Collaboration with Mexican Scientists

At the 2000 Entomological Society of America meeting in Montreal, Macías and Moser presented their initial findings. In the paper, they stated reasons why they believe SPB invaded the United States from Mexico only about 5,000 years ago—a fact that has important implications for SPB control and future research directions.

The international effort with scientists in Mexico has a broader context. Although cooperation began in the 1970s when Triplehorn and Moser (1970) identified two new species of the bark beetle *Corticeus* from Mexico and Honduras, it was not until Moser met Jorge Macías of Chiapas, Mexico, while attending the Western Forest Insect Work Conference in the 1990s that collaboration began in earnest. Macías was pursuing a Ph.D. under John Borden at Simon Fraser University and planned to return to Chiapas to study population ecology of SPB. Moser mentioned that he had a draft proposal to study the arthropod natural enemies of SPB; the proposal had been previously rejected as "pie in the sky" by the Forest Service.

Conditions changed, however, following a visit in 1996 by President W.J. "Bill" Clinton to the President of Mexico. One of the results of this visit was the release of some research money for cooperative forest research in Mexico. Moser added Jorge Macías' name and resubmitted the proposal to the Forest Service staff at the Washington Office (Moser 2000).

The proposal was judged as second in all the proposals submitted, and as a result the Forest Insect Research Work Unit in Pineville, LA, received $15,000 in "seed money." The timing was great: it arrived late in 1997, at the time when Macías received his Ph.D. and was returning to Tapachula, Chiapas, Mexico, to join El Colegio de la Frontera Sur (ECOSUR). Macías immediately began his studies on the SPB problem in Southern Mexico and neighboring countries. Since his initial budget for research was nearly zero, the grant money and the subsequent visit by Moser and the Pineville research unit staff provided a real boost for him.



TOP: **JORGE MACÍAS** of Colegio de la Frontera Sur in Tapachula, Chiapas, Mexico. (Photo courtesy of Brian Sullivan)

LEFT: Jane Hayes (center) and Kier Klepzig (right) with host at Teotihuacan, Mexico.

Since, there have been frequent communications, as well as trips by the Pineville staff to Chiapas, and at least one trip to Pineville by Macías to coordinate the joint research on mite and insect associates, mycangial fungi, and the impact of clerid predators (Moser 2000).

At the 2000 Entomological Society of America meeting in Montreal, Macías and Moser presented their initial findings. In the paper, they stated reasons why they believe SPB invaded the United States from Mexico only about 5,000 years ago—a fact that has important implications for SPB control and future research directions (Moser and Macías-Sámano 2000). For example, John Reeve and others have shown in the United States that natural enemies have an impact on SPB populations, with the most predominate candidate being the clerid, *Thanasimus dubius* (Turchin and others 1999). But in Mexico, *T. dubius* is absent and another clerid, *Enoclerus ablusus*, fills this ecological niche and seems to be regulating SPB in Mexico and Central America.

Although the *Tarsonemus* mites associated with SPB mycangial fungi in Chiapas seem to be the same as those in the Southern United States, the relative number of ascospores of different species that they carry are not. Preliminary indications are that in Chiapas, these mites carry lots of *Ceratocystiopsis* ascospores, but few of the *Ophiostoma* ascospores—a situation that is reversed in the Southern United States. One possible explanation for this difference is that the species of these two SPB-associated fungi may differ in the Southern United States and Mexico (Moser 2000).

Supplementing this research is the recent discovery of the Mexican bark beetle, *Dendroctonus mexicanus*, in the Southwestern United States. Both the Mexican bark beetle and SPB were found infesting the logs of Chihuahua pine (*Pinus leiophylla* var. chihuahuana) in the Chiricahua Mountains of southeastern Arizona (Moser and others 2005a). It is not known whether this is a recent introduction or if the two similar species have been co-occurring in this area for some time.

A beetle species new to science was captured in the same trapping surveys for bark beetles in Arizona that discovered the presence of the Mexican bark beetle in the United States. This beetle (*Lascontus fitzgibbonae)* seems to be an associate of one or more of the bark beetle species as a predator (Kingsolver and others 2006).

Role of Mites in Disease Transmission

Since the appearance of Dutch elm disease (DED) in the early 20th century, elm (*Ulmus* spp.) trees in Europe, North America, and parts of Asia have been seriously affected by this destructive vascular wilt disease that is carried by two related species of *Ophiostoma*. The well-known tree pathogens, *O. ulmi* (Buism.) Nannf. and *O. novo-ulmi* Braiser, are vectored by insects, in this case the elm bark beetles in the genus *Scolytus* and also in North America by *Hylurgopinus rufipes* (Lanier and Peacock 1981).

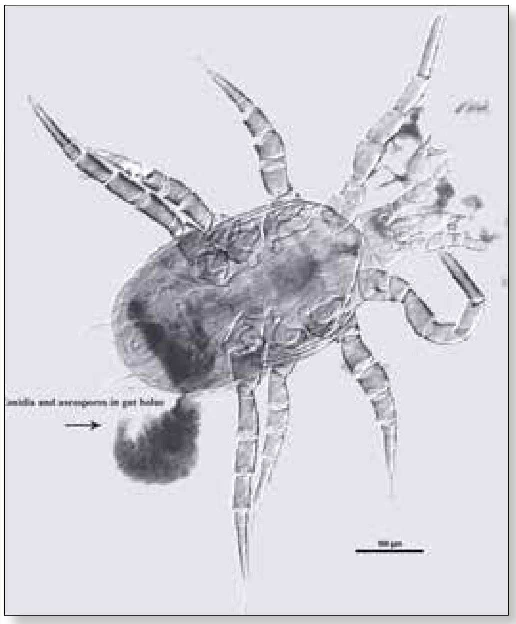
Scolytus multistriatus and *S. pygmaeus* are primary beetle species infesting elm trees in Europe and in the 20th century have been introduced and established in North America, Australia, and New Zealand. Although both species are regarded as secondary bark beetles that breed in stressed elm trees, logs, and branches, they serve as vectors of DED pathogens from diseased to healthy trees. These beetle species do not possess a mycangium, so ascospores are carried on their body surface (Moser and others 2005b). Considering the importance of *Scolytus* species in the transmittal of the DED pathogens, control measures against the insects form an essential part of the integrated management strategies against DED.

Although a great deal of research has been devoted to the bark beetles attacking elm species and the pathogenic fungi that the beetles carry, there has been little emphasis on the mites known to be carried on the beetles. An intriguing role the mites play on conifers is the relation to the transmission of the pathogens, mycangial symbionts, and fungal antagonists of bark beetles (Bridges and Moser 1983; Moser and others 1989; Moser and others 1995; Moser and others 1997; Klepzig and others 2001a, b). Mite taxa associated with bark beetles attacking elm trees may differ, but their roles should be similar to the mite associates of conifer bark beetles.

An investigation was conducted to record and quantify the fungal ascospores of *Ophiostoma novo-ulmi* on phoretic mites of three elm bark beetles species common in central Europe. Spores were found on 4 of the 10 mite species phoretic on *Scolytus* spp., and all 4 had spores attached externally to their body surfaces (Moser and others 2010). However, the mite *Tarsonemus crassus* carried many spores within its sporothecae, which are two paired pocket-like structures adapted for fungal transmission. Numerous spores were also found in the gut of *Proctolaelaps scolyti*. The beetle *Scolytus scolytus*, which is the most efficient vector of *O. novo-ulmi* in Europe, carried high numbers of *T. crassus* and *P. scolyti*. Therefore, the high efficiency of *S. scolytus* in spreading Dutch elm disease may be partly due to its association with these two mites and the spores of *O. novo-ulmi* they carry (Moser and others 2010). The fact remains, however, that these two mites alone are capable of transmitting Dutch elm disease.

RIGHT: ***Proctolaelaps scolyti*** **showing Dutch elm disease spores in the gut. These spores may remain viable even after digested, which reinforces the conclusion that mites significantly aid in transmission of the disease.**

LEFT: The southern pine beetle (left) and the Mexican pine beetle (right) are closely related species and are difficult to distinguish.



John Moser collecting fire ants from a nest in his yard.

Fire Ants and Associated Mites

The red imported fire ant, *Solenopsis invicta*, accidently introduced into the United States between 1933 and 1945, is an invasive species that has caused great negative economic and societal effects across the entire South. This small insect, originally from Brazil, has sparked much consternation and research. The biology, ecology, and control measures of fire ants have been extensively studied, but few studies have been conducted on the mites associated with the red imported fire ant, specifically on the monogyne (i.e., single queen) colonies found in Louisiana (Moser and Blomquist 2011).

Why would John Moser become interested in studying fire ants, an insect outside the usual range of interest for a forest entomologist? For a number of years, Moser's wife, Martha, had a serious medical condition, and John went home each day at noon to assist her during lunch. During these trips, he observed fire ant mounds in his lawn and as an ant expert, he began studying them instead of applying ant bait to them. Of special interest was the presence of mites and their role in the biology of the ants.

For a number of years, Moser's wife, Martha, had a serious medical condition, and John went home each day at noon to assist her during lunch. During these trips, he observed fire ant mounds in his lawn and as an ant expert, he began studying them instead of applying ant bait to them.

Twenty-two nests were marked and checked daily for a 16-month period. Some nests died during the 2 years and others moved. So, not all 22 nests were sampled on each date. The winged reproductive ants or alates were found to fly between the hours of 11:30 a.m. and 3:00 p.m.; daily flights were triggered only after a suitable amount of rain and with acceptable minimum flight temperatures (Moser and Blomquist 2011). Duration of flight was about 2.5 hours, and once alates from a single nest began to fly, the period of flight for that nest was 15-30 minutes. Alates were plucked from nest surfaces using forceps as the winged females and males prepared to fly, usually from the tips of grass leaves.

The first efforts dealt with identifying phoretic mites associated with the fire ant workers and alates. Four species of *Scutacarus* and one of *Imparipes* were documented as phoretic, and of these, three were new species: *Imparipes louisiana*, *Scutacarus nanus*, and *S. tertius* (Ebermann and Moser 2008). Khaustov and Moser (2008) identified two additional new species of mites associated with the fire ant: *Petalomium hofstetteri* and *Caesarodispus klepzigi*.

Walter and Moser (2010) described another new mite species phoretic on fire ants. Named *Gaeolaelaps invictianus*, this and other species of this genus are generally predators, and it is assumed that this species may act as a generalist predator in the ant colony.

Wirth and Moser (2010) documented a new species, *Histiostoma blomquisti,* associated with the fire ant. It was dedicated to Stacy Blomquist who has contributed significantly to the mite research effort. A deutonymph (a mite larva stage) was attached to ant queens in large numbers, some with more than 200 deutonymphs of *H. blomquisti*. The presence of these on the flying ants' bodies stimulates the cleaning behavior of worker ants, but the deutonymphs were not removed in this process. It was speculated that the deutonymphs may produce chemical components that repel cleaning workers, and they remain strongly adhered to the carrier.

In central Louisiana, large numbers of phoretic mite species seem to be an important component of *S. invicta* nests. They occupy many ecological niches in the nests, such as regulating the nest soil fungi and acting as predators, parasitoids, or both of each other and the ants. Also, the many microorganism species phoretic on the mites may be essential to nest biology, as well as possibly affecting the vigor of both the ants and the mites (Moser and Blomquist 2011).

TOP: Fire ant alate preparing to fly from a grass.

BOTTOM: This mite, ***Caesarodispus klepzigi***, is named in honor of Kier Klepzig.

Hackberry Gall Makers

Moser has had a long-term interest in hackberry tree (*Celtis* spp.) galls; his earliest research had as its focus understanding the insects responsible for the galls on a hackberry tree in his front yard (Moser 1956, 1965). In 1997, Moser obtained galled leaves of *Celtis tournefortii* from Kornik, Poland, and found the galls resulted from a new species of the midge genus *Celticecis* (Gagné and Moser 1997).

Moser and Gagné (in press) have currently completed a comprehensive document of the North American gall midges of hackberries. Before this publication, *The North American gall midges (Diptera: Cecidomyiidae) of hackberries (Cannabaceae: Celtis* spp.), little was known about hackberry gall midges, and only 11 North American species had been named and only sketchily described. The extensive monograph details 23 species of gall midges found in North America north of Mexico and provides keys to the galls and larvae (second and third instars) of these Nearctic gall midges.

IMPLICATIONS FOR FUTURE RESEARCH

John Moser continues his efforts to understand the relationships among insects and their associates for major entomological pests such as the southern pine beetle. His research on the mites and other associates of these primary insects has opened a new opportunity for increasing our understanding of the transmission of tree diseases within forest ecosystems. He, too, has put together one of the world's largest collection of slides of mites that are associated with major insect pests.

John Moser continues his efforts to understand the relationships among insects and their associates for major entomological pests. His research … has opened a new opportunity for increasing our understanding of the transmission of tree diseases within forest ecosystems.

One aspect of Moser's legacy is provision in the wills of John and his wife, Martha, to fund the establishment of two chairs in entomological systematics—one at Cornell University and another at Ohio State University. John has been an aggressive stock investor and has the capability to fund the two professorships that will require about 2 million dollars each. He may well have additional funding to provide support for several graduate students that would study under each of the professors (Moser 2000).

Moser also plans to will the contents of his office in the Alexandria Research Center to the Southern Research Station with the provision that the contents remain attached to the Forest Insect Research Work Unit at Pineville and not be dispersed to other research units or universities.[5] This would preserve the major collection of mite slides that will be key to the identification of new mite species.

Although these plans are in place, Moser has no intention of fading away. He "has files stuffed with unpublished material" and has a lot of things that he still wants to do. For instance, he has cooperative agreements with a number of scientists dealing with leaf-cutting ants and bark beetle mites. Several of these collaborations will result in descriptions of new mites associated with bark beetles in North and Central America, with keys to these species (Moser 2000). Others will focus on increasing the understanding of how mites interact with their bark beetle hosts and with each other.

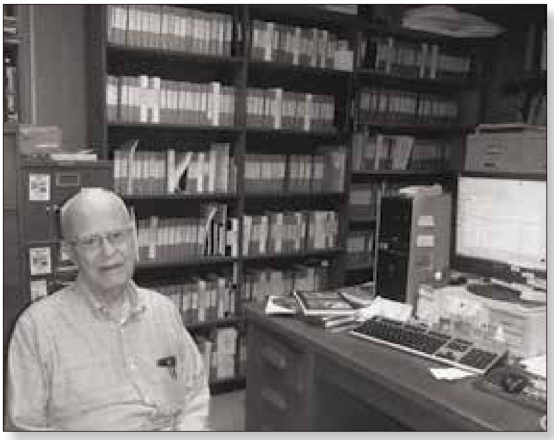
[5]Barnett, J.P.; Streett, D.A.; Blomquist, S.R. 2012. Oral history interview of March 7, 2012, with John C. Moser. Cassette tape. Pineville, LA: U.S. Department of Agriculture Forest Service, Southern Research Station, Insects, Diseases, and Invasive Plants Research.

Charles Triplehorn (left); long-time friend and college roommate, Susan Fisher; Chair of Entomology Department, Moser; and John Wenzel, curator of Ohio Museum of Biodiversity, at the event of Moser's bequest to Ohio State University for an endowed chair for insect systematics.

Opportunities exist as well to document an interesting case of biological control in Chile, where the tip moth, *Rhycionia bouliana*, is being attacked by a parasitoid pyemotid mite. Another instance relates to describing a new species of *Bakerdania,* a phoretic pyemotid mite found in association with the SPB mycangial fungus, *Ceratocystiopsis*, found in SPB galleries in Guatemala (Moser 2000).

The role of mites in the biological control of insect pests and transmittal of tree diseases are areas of research that must be pursued and may offer opportunities to manage both major insect pests and plant diseases in a more innovative and productive way.

SIGNIFICANCE OF MOSER'S CONTRIBUTIONS



John Moser in his office with shelves holding about half of his mite collection. Each box on the shelves contains 100 slides, and each slide is numbered—the current number is 53,097. That is a lot of mite slides!

John Moser has worked for the Southern Research Station as a dedicated and productive research scientist and a volunteer for over 50 years, and he continues to work in his office daily and on most weekends. However, when we examine John's research in greater detail, we find a cutting-edge research program with publications in several of the world's top scientific journals, including four *Science* articles and two articles in *Nature*. Early in his career, John's work with Murray Blum was some of the earliest behavioral studies showing that ant foraging trails were marked by secretions (Blum and others 1964). Later, John was the first to report that the roach inquiline, *A. fungicola,* responded to the pheromone trail emitted by a different species, the town ant. John's work with R.M. (Milt) Silverstein established the volatile nature of the town ant alarm pheromone and the presence of at least two compounds of the town ant trail-marking pheromone consisting of volatile and nonvolatile components. John's later collaboration with Silverstein led to the isolation and chemical identification of the first ant trail pheromone by Tumlinson and others (1971, 1972) that was the major volatile component of the trail-marking substance produced by the town ant. John and Silverstein later investigated the biological responses of enantiomers of the principal alarm pheromone of *Atta texana*. Enantiomers are nonsuperimposable mirror images of the same molecule which have identical physical and chemical properties. This was the first report of insects being able to differentiate between enantiomers of the alarm pheromone. John was also one of the first to report on the complete excavation and mappings of a leaf-cutting ant nest (Moser 2006). When John's research focused more on SPB, he (and Bridges) were one of the first to demonstrate that the ophiostomatoid fungus, *O. minus* (formerly *Ceratocystis minor*) was transmitted phoretically by two phoretic mites on southern pine beetles (Bridges and Moser 1983, 1984).

Throughout John's career he has untaken research problems that have interested him, and this initiative led to his significant scientific career as a Forest Service scientist.

John Moser's efforts have brought international recognition to the Forest Service, Southern Research Station for its excellence in scientific research. His expertise in the biology of leaf-cutting ants continues to be sought world-wide where those ants are present. The effort on mites brings new understanding of the biology of major forest insect pests and their insect associates. Increased knowledge of these relationships now provides an opportunity to understand the role of mites in the transmission of some of our major plant diseases and potential biological control of insect pests.

Moser's efforts, especially as a volunteer over the last 20 years, have brought recognition and respect to the Insects, Diseases, and Invasive Plants Research Work Unit to which he is attached. Seldom has a volunteer research scientist contributed so much to a research program and gained international respect in the process. In recognition of his contributions to the taxonomy of forest insects, 20 species of the associates of town ants, SPB, and other forest beetles have been named in his honor (see appendix).

It is important to recognize that during most of the period that Moser has volunteered his time and expertise, the Insects, Diseases, and Invasive Plants Research Work Unit in Pineville, LA, has provided technical support for his efforts. Since 2001, Stacy R. Blomquist, who has a master's degree in entomology, has assisted Moser on a part-time basis. Her talents have done much to increase the scientific productivity and recognition of the program.

The effort of Moser to focus on research that has been generally unappreciated has shown what such dedication can accomplish. Not only has his research been internationally accepted, but it now offers prospects for a greater understanding of disease movement in forest trees. This commitment continues thanks to his funding of major university professorships that will support study and training in insect systematics. These chairs will assure that scientists with appropriate taxonomic skills will be available to continue his program on understanding the role of mites and associated species in forest entomology.

The effort of Moser to focus on research that has been generally unappreciated has shown what such dedication can accomplish. Not only has his research been internationally accepted, but it now offers prospects for a greater understanding of disease movement in forest trees.

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APPENDIX

Species of arthropods and a fungus named in recognition of John C. Moser's contributions to the taxonomy of forest insects.

Species name and describer	Year designated	Description of species
Fannia moseri Chillcott	1965	Fly (Diptera) found in nests of leaf-cutting ants feeding on fresh detritus.
Histiogaster moseri Woodring	1966	Mite found in boring dust of the southern pine beetle (*D. frontalis*) from *Pinus oocarpa* in Teguciqualpa, Honduras.
Dendrolaelaps moseri (Hurlbutt)	1967	Predatory mite found associated in galleries of elm bark beetles (*Scolytus multistriatus*) in Delaware, OH.
Euparixia moseri Woodruff & Cartwright	1967	Beetle found associated with leaf-cutting ant (*Atta texana*) nests near Flatwoods, LA.
Tarsonemus moseri Smiley	1967	Fungivore mite collected from the inner galleries of loblolly pine with southern pine beetle (*Dendroctonus frontalis*) in Elizabeth, LA.
Laelaspis moseri (Hunter & Glover)	1968	Mite found associated with ants; role in the ant colony is unknown.
Neivamyrmex moseri Watkins	1968	Ant collected from excavated surface subsoil of leaf-cutting ants (*Atta texana*) seven miles west of Alexandria, LA.
Nenteria moseri Hirschmann	1972	Mite found in inner bark of Endlicher pine (*Pinus rudis*) and in southern pine beetle (*Dendroctonus frontalis*) galleries of Guatemala.
Oplitis moseri Hirschmann	1972	Mite found phoretic on fire ants (*Solenopsis invicta*).
Trichouropoda moseri Hirschmann	1972	Mite found associated with bark beetle (Scolytidae) galleries in Canada.
Uroobovella moseri Hirschmann	1972	Mite collected from bark beetle (Scolytidae) galleries in Honduras.
Metagynella moseri Hirschmann	1975	Mite found associated with the Bess beetle (*Odontotaenius disjunctus*).
Thaxteriola moseri Majewsky & Wiśniewski	1978	Fungus found associated with mites from Poland.
Proctolaelaps moseri Wiśniewski	1980	Mite found living in the galleries of bark beetles in Poland.
Metagynella moserisimilis Hiramatsu	1981	Mite found associated with a stag beetle (Lucanidae) in Taiwan.
Dendrolaelaps moserisimilis Shcherbak	1984	Predatory mite found under the bark of a poplar tree in Poltava, Ukraine.
Julolaelaps moseri Hunter & Rosario	1986	Mite found on large millipede (family Spirostreptidae) in the Insect Zoo, Smithsonian Institute, Washington, DC.
Neobonzia moseri Smiley	1992	Predatory mite of small arthropods that was found on the outside bark of a loblolly pine in Elizabeth, LA.
Pyemotes moseri Yu & Liang	1996	Parasitic mite found on bark beetles (*Cryphalus* sp.) infesting Chinese hickory trees from Hebei, China.
Pyemotes johnmoseri (Khaustov)	2004	Mite which preys on fig tree bark beetles (*Hypoborus ficus*) in Turkey.