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and Leaf-Cutting Ants
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Diseases of Fire Ants:
Problems and Opportunities

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During a 1973 taxonomic study of fire ants from South America, William F. Buren noticed subspherical, cyst-like bodies in the gasters of alcohol-preserved workers of Solenopsis invicta (Fig. 1). These "cysts" proved to be membrane-bound masses of spores of a microsporidium—the first specific pathogen known from fire ants[1] (Allen and Buren 1974). Buren's observation revitalized interest in biological control research on fire ants. Earlier, Broome (1974) and Federici (personal communication, B. F. Federici, Div. Biol. Control, Dept. Entomol., Univ. Cal., Riverside) had detected only non-specific, facultative pathogens in imported fire ants (IFA) in the United States. The virtual absence of specific pathogens of IFA in this country was later confirmed in an extensive survey by Jouvenaz et al. (1977).

The literature on the pathobiology and microbial control of fire ants consists of just 22 titles, of which 3 are non-primary articles and 4 concern non-specific microbial insecticides. Six of the remaining papers are notes or short papers that merely document observations of pathogens or report negative data. Thus, the study of the diseases of fire ants is largely in an exploratory stage.

SUMMARY OF FIRE ANT PATHOBIOLOGY

Pathogens and other natural enemies of IFA and the tropical fire ant, S. geminata (a nearctic species we have studied as a model) have been reviewed by Jouvenaz (1983). For the convenience of the

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[1]Holldobler (1929) observed the haplosporidium Myrmecinosporidium durum infecting Solenopsis (Diplorhoptrum) fugax. This host is a thief ant; fire ants sens. str. are members of the subgenus Solenopsis.

reader, a summary of fire ant pathobiology is given here. The known pathogens are listed by type in Table 1.

FIGURE 1. Alcohol-preserved worker of S. invicta infected with Thelohania solenopsae. Note the white, spherical cyst-like mass in the partially cleared gaster.

TABLE 1. Specific pathogens of fire ants, Solenopsis spp.

Type of Pathogen	S. invicta[a]	S. geminata	Total
Virus	1	1	1 or 2
Bacterium	1?	-	1?
Fungus	1	-	1
Protozoa			
Microsporidia	2	4	6
Neogregarinida	2	1	2
Nematodes	1	1	2

[a]S. invicta and other members of the S. saevissima complex in South America.

Microsporidia

Only two of the six microsporidia, Thelohania solenopsae (Knell et al. 1977) and Burenella dimorpha (Jouvenaz and Hazard 1978), have been described. The description of a third species is in manuscript.

Thelohania solenopsae. Our knowledge of this species is essentially limited to the description by Knell et al. (1977). Other papers (Allen and Buren 1974; Allen and Silviera-Guido 1974; Jouvenaz et al. 1980) merely document its occurrence or incidence in host populations.

T. solenopsae infects the fat body of workers and sexuals, and the ovaries of queens. Infected cells hypertrophy, forming the cysts observed by Buren in alcohol-preserved specimens. These spore masses typically number 4 to 6 per gaster, although Knell et al. (1977) observed as many as 22 in single workers.

T. solenopsae is dimorphic, producing two morphologically distinct types of spores which develop simultaneously in the same tissues. The numerically predominant spore type is uninucleate and occurs in octets bound by a membrane (a sporophorous vesicle, previously called a "pansporoblast"). These "octospores" arise from plasmodia by endogenous budding. Spores of the secondary type are binucleate, are not bound by a membrane ("free spores"), and arise from disporous sporonts.

Ants infected with T. solenopsae exhibit no gross pathological signs or changes in behavior. Knell et al. (1977) state that "infected colonies may be as large as healthy ones in the field, but cannot be maintained in the laboratory as long as non-infected colonies. Thus, the effect of this microsporidium appears to be one of debilitation caused by destruction of the adult fat body."

It is uncertain whether T. solenopsae is one species or a complex of sibling species of microsporidia. It has been detected in a dozen or more described and undescribed Solenopsis spp. in Brazil, Argentina, Uruguay, and Paraguay. Of the 865 colonies (primarily S. invicta) that I have examined from Mato Grosso, Brazil, 67 (7.8%) were infected with this parasite. Attempts to transmit the infection perorally and by placing brood from heavily infected colonies in healthy colonies have not been successful (conspecific brood is adopted).

Burenella dimorpha. By far the best known pathogen of fire ants, B. dimorpha, has served as a model for my basic studies of pathobiology and for the development of protocols. This host-specific pathogen of S. geminata is locally available near Gainesville, Florida, can be transmitted perorally, and infected pupae exhibit pathognomonic signs.

As the specific name indicates, B. dimorpha also produces two morphologically distinct spores: binucleate free spores develop from

disporous sporonts in the hypodermal tissues; uninucleate octospores develop in sporophorous vesicles from plasmodia in the fat body. The free spores develop before the octospores and (in contrast to T. solenopsae) predominate numerically. The development of octospores is temperature-dependent; at optimum temperature (28°C) they constitute ca 35% of the total spore population (Jouvenaz and Lofgren 1984).

Pupae infected with B. dimorpha develop clear, blister-like areas in the vertex of the head and in the petiole (Fig. 2). In sexual pupae, clearing may also develop in the dorsal thorax. The eyes appear sunken and irregular in outline, with deranged facets. These signs are pathognomonic for B. dimorpha infections and are the direct result of destruction of the developing cuticle. The blisters result from tissue fluids seeping between denuded hypodermal tissues and the pupal sheath. The brain and fat body atrophy and recede from the hydraulically distended pupal sheath. In areas where blisters do not occur, cuticle development is slowed or arrested, but the cuticle is not destroyed. The malformation of the eyes is due to destruction of the cuticular lenses, which leaves the ommatidia unanchored distally to become tangled, amorphous masses. The lamina ganglionaris is also destroyed, as is much other neural tissue (Jouvenaz et al. 1984). Infected pupae have never been observed to mature.
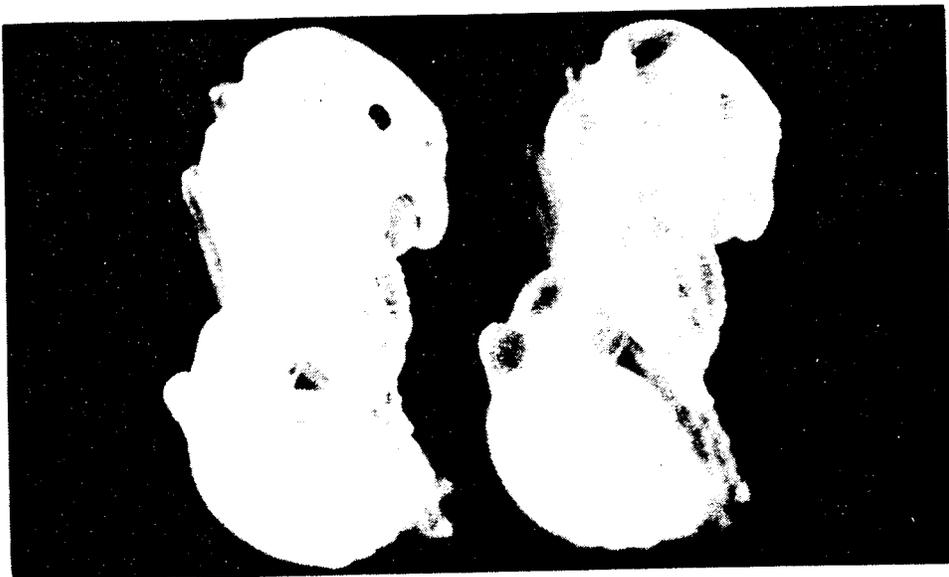

FIGURE 2. Pathognomonic signs of B. dimorpha infection in a pupa of S. geminata (right). Note clear areas in the vertex of the head and in the petiole, and compare the eye to the normal pupa at left (X25).

The intracolonial cycle of transmission of B. dimorpha is from pupae to fourth instar larvae. As the disease progresses, the blisters become more extensive, the cuticle becomes very fragile, and eventually it ruptures. The adult nurses cannibalize the ruptured pupae but do not ingest the spores into their crops. Instead, the spores and all other particulate matter are filtered, diverted to the infrabuccal cavity, and molded into a pellet. The infrabuccal pellet is expelled and placed on the praecipium of a fourth-instar larva, which consumes it ad lib. This larval instar is the only stage in the life cycle of S. geminata that is vulnerable to infection by B. dimorpha. The intracolonial transmission of infection is thus vectored mechanically by adult workers and is facilitated by the destruction of the cuticle (Jouvenaz et al. 1981a).

Only the free spores of B. dimorpha are infectious per os; the octospores are expelled unextruded in the meconium upon pupation. The function of the octospore is unknown, as is the mode of intercolonial transmission of infection. Intracolonial infection rates in field colonies are usually less than 5%, but may approach 100%.

Other microsporidia. One other microsporidium, a dimorphic species, is known to infect S. invicta in Brazil (Jouvenaz and Ellis, in press). Three undescribed species of microsporidia infect S. geminata in Florida, but they have not been studied.

Neogregarines

Mattesia geminata (Apicomplexa: Neogregarinida) infects S. geminata in Florida and Solenopsis spp. in Brazil (Jouvenaz and Anthony 1979). This genus is characterized by cycles of micronuclear and macronuclear merogony, and by gametogeny resulting in the development of two octonucleate spores within a membrane (a gametocyst). In M. geminata, the gametocyst membrane is transient, and the lemon-shaped spores are confined to the hypodermal tissues.

The signs of M. geminata infection occur in pupae and are pathognomonic. The developing eyes become blurred and irregular (much like those of pupae infected with the microsporidium B. dimorpha). The cuticle then melanizes abnormally, beginning in the legs and posterior margins of the sclerites of the gaster. The pupa progresses from a "sooty" appearance to almost solid black (Fig. 3). As in the case of B. dimorpha, infected pupae have never been observed to mature.

The mode of transmission of M. geminata is unknown; our attempts to transmit infection perorally and by placing diseased pupae in healthy colonies have failed. The intracolonial infection rates are usually less than 5% but may exceed 90%.

A second (undescribed) neogregarine infects S. invicta in Brazil. The spores of this species are morphologically distinct from

those of M. geminata and develop in fat body rather than hypodermal tissues. There are neither physical nor behavioral signs of infection, and infected ants survive into adulthood (Jouvenaz, unpublished).
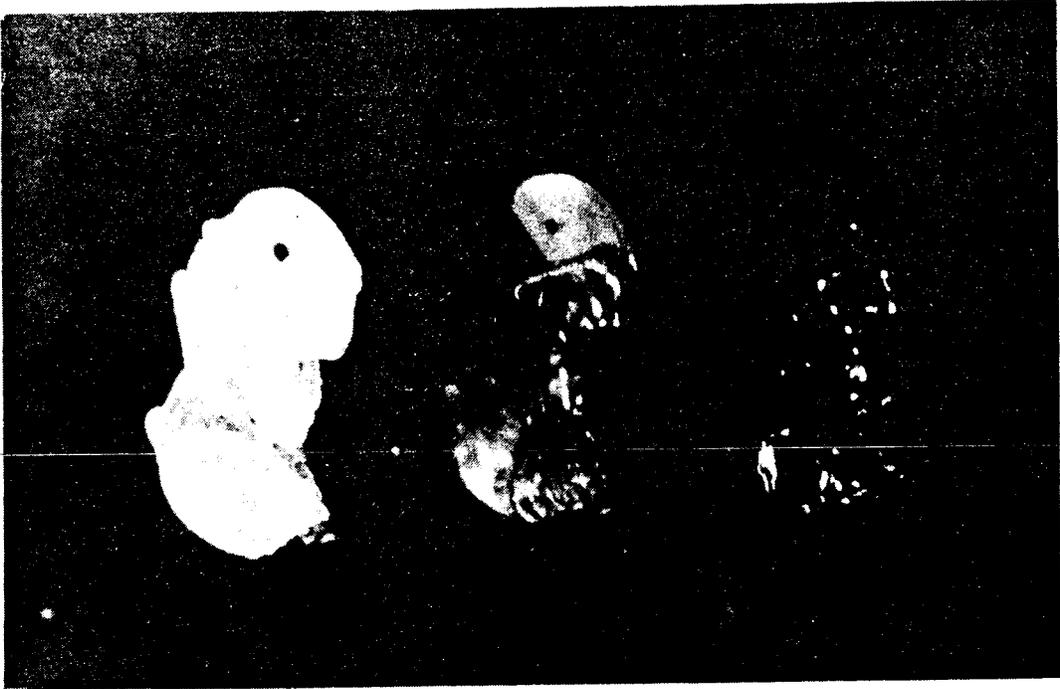

FIGURE 3. Pathognomonic signs of Mattesia geminata infection in pupae of Solenopsis geminata. The pupae are (left to right) normal, diseased, and moribund or dead (X18).

Fungus

The only microorganism that appears to be specifically associated with IFA in the United States is an unidentified, unicellular fungus that occurs in the haemolymph of S. invicta. The cells are club-shaped and multiply by budding. A mycelial form develops in vitro and in the haemolymph of lepidopterous larvae (which are susceptible to infection by injection only). The fungus can be transmitted perorally to healthy S. invicta colonies. Although the cells may become very numerous in the haemolymph, there are usually no physical or behavioral signs of infection. On occasion, however, high mortality with death preceded by tremors has occurred in infected laboratory colonies. It was not unequivocally established that the mortality was due to the fungus. Field populations of S. invicta are not reduced obviously even in areas where the infection rates approach 50%. Jouvenaz et al. (1977) found this organism in 93 (9.23%) of 1,007 colonies of S. invicta from six states.

Bacterium

A possible bacterial infection was observed in one colony of S. invicta in Brazil by Jouvenaz et al. (1980). The bacterium was motile, with a subterminal spore and a parasporal body that remained attached to the spore after disintegration of the sporangium. Unfortunately, it was not possible under field conditions at that time to isolate and culture this organism.

Virus

Virus-like particles (VLP) were found by Avery et al. (1977) in an unidentified species of fire ant of the S. saevissima complex from Brazil. The host colony was infected with an undescribed microsporidium and some individuals had dual infections. The colony was, in fact, collected because of the protozoan infection, and the VLP were discovered in the course of electron microscope studies of the protozoan. Similar VLP were subsequently detected in S. geminata. The VLP were rod-shaped and slightly tapered at both ends, and enclosed by double membranes. There was no evidence of occlusion of the VLP in a protein matrix.

The VLP occurred in both nuclei and cytoplasm of cells in the adipose tissue. The nuclei of infected cells greatly hypertrophied, and contained considerably less condensed nucleoprotein than normal cells. In a specimen in which ca 75% of the fat body cells were infected, both cytoplasm and nuclei were completely disrupted. The mortality rate in this colony was elevated; however, because of the dual infection, the cytopathology and mortality could not be attributed exclusively to either infection. There were no signs of infection in living ants, and the infection rate could not be estimated.

Nematodes

An unidentified nematode was found in the gasters of several alcohol-preserved workers of S. geminata by Mitchell and Jouvenaz (1985). The hosts had been collected months earlier as part of an ecological study and attempts to collect fresh material in the same area were unsuccessful. Jouvenaz and Wojcik (unpublished) subsequently found nematodes, apparently of the family Tetradonematidae (Mermithoidea), in Solenopsis spp. in Brazil. Studies on the latter nematode have just been initiated.

PROBLEMS AND OPPORTUNITIES

In their native land in South America, IFA are beset by a complex of natural enemies, including specific diseases, parasites, social parasites, live-in predators, and competitors. I have listed all

of the known diseases in the first part of this paper, and undoubtedly, many more remain to be discovered. Information on the other types of organisms can be found in papers by Jouvenaz et al. (1981b), Jouvenaz (1983), Williams (1980), and Wojcik (Chapter 8). Almost all of these enemies were left behind when IFA were introduced into the United States. The obvious possibility of biological control presented by this situation demands investigation. The primary question raised by the current status of our knowledge is whether or not there is a future for the use of diseases of fire ants for biological control. While some of these may be very pathogenic, their incidence in natural populations is generally low. Essentially, nothing is known about intercolonial transmission of ant diseases. The potential for augmentative releases does not appear bright since none of the known organisms appear easily adaptable to mass propagation techniques. However, the existence of as many agents of disease as have been reported indicates opportunities do exist and their utilization for control of IFA populations in the United States depends upon our ability to unlock complex biological, pathological, and epizootiological relationships between the pathogens and their host. In the remainder of my paper, I will outline the biological and technical problems that lie ahead; however, the adage that problems are only opportunities awaiting discovery is appropos also for biocontrol of IFA.

BIOLOGICAL PROBLEMS

In Brazil, as in the United States, fire ants are most abundant in environments which have been disturbed by man (see Wojcik, Chapter 8). The fact that fire ants are common in many disturbed areas in Brazil may lead one to conclude that prospects for biological control in the United States are poor. This is not necessarily true. Environmental factors that limit natural enemies may exist in Brazil, but not in the United States. For example, if the extended dry season in the State of Mato Grosso (the homeland of S. invicta) is indeed a period of stress, the mortality differential between healthy and diseased colonies at that time may be accentuated, reducing the intercolonial incidence of disease. The dry season may also suppress putative vectors of disease. The wet season, with its lush vegetation, abundant food and water, and mating flights, would logically be a period in which fire ant populations increase. It would also—after a lag period—be a time in which density-dependent natural enemies increase. The return of the dry season, however, would reverse these population trends. The antithesis of this hypothesis is also possible; i.e., stress of dry season makes IFA more susceptible to disease. These hypothetical oscillations of populations of fire ants and diseases may actually prevent disease from reaching epizootic levels in South America. In the infested area of

the United States, however, extended dry seasons do not occur; instead, there are relatively mild and short winters. Could this difference in the environment allow natural enemies to become more abundant in the United States than in Mato Grosso? Such seasonal effects, it must be emphasized, are purely hypothetical at present.

Also of concern for biological control is the tremendous reproductive potential of IFA which tends to mitigate the effects of biological control agents. In the absence of other enemies, pathogens may only serve to increase the rate of colony turnover without significantly affecting population density. Perhaps the primary value of pathogens in IFA management may be as stressors; colonies debilitated by disease may be less able to compete with native ants or deliberately introduced competitive exotic species (Jouvenaz et al. 1981b). Our goal should be to establish and encourage a complex of natural enemies of all types, and to develop pest management techniques that are compatible with these enemies.

The development of a microbial insecticide[2] is not a primary goal of our research. To effectively control an ant colony, a formicide must kill the queen(s) or stop reproduction. This requirement eliminates currently known microorganisms from candidacy as microbial formicides since they appear to affect only larvae or adult workers. Adult insects are typically refractory to infection by protozoa, viruses, and bacteria (bacteremia may result from injury). Certain fungi are able to infect adult insects; however, fire ants apparently fumigate their nests with venom (Obin and Vander Meer 1985), which has antimicrobial—including antifungal—properties (Jouvenaz et al. 1972; Cole 1975). Fire ant queens are also groomed meticulously and fed only regurgitated, filtered liquids. Thus, they appear to be invulnerable to most pathogens. The non-specific nematode, Steinernema feltiae (=Neoaplectana carpocapsae), and perhaps the recently discovered and as yet unidentified nematode from fire ants in Brazil may prove useful for single-mound, biological insecticide treatments. It must be noted, however, that effective and inexpensive chemical toxicants are readily available for this purpose.

Two of the more intriguing problems in the area of basic pathobiology may be related. These are (1) the mode of intercolonial transmission of infection and (2) the function of the octo-

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[2]Microbial insecticides are applied in lieu of, or in conjunction with, toxicants to achieve rapid pest control in the treated area. The pathogen is not expected to become permanently established in the target pest population. Thus, microbial insecticides are pathogens that are employed in the manner of chemical toxicants.

spores of dimorphic microsporidia. Summerlin et al. (1975) demonstrated extensive food and possibly worker exchange between colonies of S. invicta. Such exchanges alone may affect transmission of those infections that occur in adult workers. Ants infected with B. dimorpha and M. geminata, however, do not mature. These infections are confined to the brood chambers; and, in the case of B. dimorpha, the ruptured pupae are cannibalized by nurses who feed the solids, including the spores, to fourth-instar larvae. In view of this behavior, one wonders how spores are transferred to brood in conspecific colonies frequently enough to sustain the pathogen.

Only the free spores of B. dimorpha are infective perorally for fire ant larvae. What then is the function of the octospore? Surely these morphologically very distinct spores have a function. And the raison d'etre of spores is to infect something. Since B. dimorpha octospores do not infect fire ants, they evidently infect something else—an intercolonial vector, perhaps. Or perhaps the vector is only mechanical, but "primes" the spore for extrusion by passage through the gut. In any event, this putative vector is proving elusive.

TECHNICAL PROBLEMS

The first technical problem encountered in microbial control of IFA research was the efficient screening of colonies for pathogens. This problem is still not completely solved. The phase-microscopic examination of aqueous mass extracts of samples of ants described by Jouvenaz et al. (1977) is quite sensitive for the detection of fungi, spore-forming protozoa, and nematodes. Pathogenic bacteria are difficult, though not impossible, to detect by this procedure. Viruses (with the possible exception of occluded viruses) are undetectable.

The first virus known from fire ants was seen during the electron microscopic study of protozoan-infected specimens from Brazil, as mentioned earlier (Avery et al. 1977). Avery et al. subsequently detected virus-like particles in phosphotungstic acid negative stains of ultracentrifuge pellets of extracts of S. geminata. Since electron microscope facilities are not available to us in Brazil, we must develop protocols for preserving partially processed extracts to send to the United States. Care must be taken to eliminate bacteria from these samples, or confusion of bacteriophage with ant viruses could result. Even if satisfactory procedures for preparing such samples are developed, the time lapse between collection of the colonies in Brazil and their examination in the United States presents obvious difficulties. Tissue culture techniques have not yet been developed for IFA.

Other technical problems that will be encountered before diseases may be established in the United States include: (1) the development of more rigorous laboratory and field evaluations of the

potential of candidates for introduction; (2) the safety of the proposed introductions must be ascertained; (3) methods of mass production and dissemination (including inoculum size, formulation, mechanics of dispersal, schedule of dissemination) will have to be developed; and (4) procedures for monitoring the establishment, spread, and impact of introduced pathogens must be developed.

I have attempted to introduce the known diseases of fire ants and to point out some of the problems and opportunities they present for basic research in ecology and pathobiology, as well as the possibility of using them in biological control. It is evident that this research is in its infancy. We are not yet acquainted with all of the diseases of fire ants; we understand little or nothing of the role they play in IFA population dynamics. Much work remains before we may even estimate the probability of using pathogens to help manage IFA populations.

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