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Robert K. Vander Meer

USDA

Clifford S. Lofgren

USDA

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USE OF CHEMICAL CHARACTERS IN DEFINING
POPULATIONS OF FIRE ANTS, *SOLENOPSIS SAEVISSIMA*
COMPLEX, (HYMENOPTERA: FORMICIDAE)

ROBERT K. VANDER MEER AND CLIFFORD S. LOFGREN
U.S. Department of Agriculture, Agricultural Research Service
Insects Affecting Man and Animals Research Laboratory
P.O. Box 14565
Gainesville, Florida 32604

ABSTRACT

The fire ants, *Solenopsis invicta* and *S. richteri*, were accidentally imported into the United States in the first half of this century from South America. In their adopted habitat the imported fire ants have thrived causing considerable medical and agricultural problems in the nine widely infested states of the south and southeast. The red imported fire ant, *S. invicta* was considered the dominant ant in the infested areas, having displaced the black imported fire ant, *S. richteri*, into a small enclave in northeastern Mississippi. However, a large reproductively viable *S. invicta*/*S. richteri* hybrid population was recently discovered across northern Alabama and into Mississippi and Georgia by chemical analysis. This paper reports on the use of three species-specific chemical characters (venom alkaloids, cuticular hydrocarbons, and trail pheromones) to define *S. invicta*, *S. richteri*, and hybrid populations in the United States. In addition, these characters have been applied to fire ant taxonomy in South America. We also discuss fire ant population dynamics in the United States and its implications on several models of hybridization. These results have important consequences regarding the species status of the two imported fire ants and the taxonomy of fire ant populations in South America.

RESUMEN

Las hormigas *Solenopsis invicta* y *S. richteri* fueron accidentalmente importadas de Sur America a los Estados Unidos en la primera parte de este siglo. En su medio

adoptado las hormigas han prosperado causando considerables problemas médicos y agrícolas en los nueve estados del sur y del sudeste. La hormiga roja importada *S. invicta*, fue considerada la hormiga dominante en las áreas infestadas, habiendo desplazado a la hormiga negra importada, *S. richteri*, hacia un pequeño enclave en el noreste de Mississippi. Sin embargo, se descubrió por medio de análisis químicos, una población híbrida reproductivamente viable de *S. invicta/S. richteri* en el norte de Alabama y dentro de Mississippi y Georgia. Este papel reporta sobre el uso de caracteres químicos que son específicos de ciertas especies (veneno, alcaloides, hidrocarburos cuticulares, y feromonas de rastro) para definir poblaciones de *S. invicta*, *S. richteri*, e híbridos en los Estados Unidos. Además, estos caracteres han sido aplicados a la taxonomía de las hormigas en Sur America. Nosotros también discutimos el dinamismo de poblaciones de las hormigas en los Estados Unidos y sus implicaciones en varios modelos de hibridación. Estos resultados tienen consecuencias importantes en cuanto al estado de las especies de las dos hormigas y la taxonomía de la población en Sur America.

The taxonomy of the *Solenopsis saevissima* complex has had a tumultuous history, and is currently undergoing another revision (James Trager, University of Florida). Creighton (1930) reviewed the early history, and lumped 16 extant forms into 8 subspecies or varieties. One of these was *S. saevissima* var. *richteri*, a fire ant originally from Argentina that was collected near Mobile, Alabama in the late 1920's. Wilson (1952) considered most of these subspecies as unstable hybrid variants and consolidated the complex into two species, *S. interrupta* and *S. saevissima*, and one subspecies, *S. saevissima* var. *richteri*. Ettershank (1966) went even further and preserved only *S. saevissima* and *S. interrupta*. The most recent taxonomic study (Buren 1972) recognized *S. saevissima* and *S. interrupta* as valid species and raised two subspecies, *S. richteri* (the black imported fire ant) and *S. quinquecupis* to species rank and described two new species, *S. invicta* (the red imported fire ant) and *S. blumi*. Buren (1972) and MacConnell et al. (1976) state that there are a large number of undescribed forms in the *saevissima* complex.

The following scenario for the introduction of fire ants into the United States has been developed based on the earliest records of fire ant infestations (see Lofgren 1986). Black fire ants were accidentally imported into the Mobile, Alabama area around 1918. They were subsequently identified as *S. saevissima* var. *richteri* (Creighton 1930). In the 1940's a red form of imported fire ant was observed around Mobile, Alabama. Based on the population size at that time, it was estimated that this form was probably introduced in the 1930's. The natural spread of both imported fire ants occurred naturally by mating flights (estimated at a 5-6 miles per year) and most importantly, through transportation in infested sod and/or nursery stock by man. The latter led to the disjunct distribution of the ants reported by Bruce et al. (1949) and Culpepper (1953). Initial reports on the interaction of the two forms around Mobile, Alabama, indicated that the red form competitively dominated the black form (Wilson & Eads 1949). Most surveys of imported fire ant populations did not distinguish between the red and the black form, which were named *S. invicta* and *S. richteri*, respectively (Buren 1972). As a result, we know little about the population dynamics of the two species during their rapid expansion over the last three to four decades (see Lofgren 1986 for fire ant distribution maps). However, in 1974 *S. richteri* was reported to occupy only a small triangular area in northeastern Mississippi and northwestern Alabama with an acute apex at Meridian, Mississippi (Buren et al. 1974). *S. invicta* was purported to occupy all other infested areas of the South.

CHEMICAL CHARACTERS AND FIRE ANT TAXONOMY

Venom Alkaloids. The poison sac of fire ants of the *S. saevissima* complex contains primarily *cis* or *trans* 2-methyl-6-alkyl or alkenyl piperidines (MacConnell et al. 1970, MacConnell et al. 1976). The length of the alkyl or alkenyl group varies from C₁₁ to C₁₇ and may contain one double bond. To simplify the nomenclature of these compounds in this paper we will specify different alkaloids by their sidechain length and whether or not they have a double bond. For example, *trans*-2-methyl-6-(*cis*-6-n-pentadecenyl)-piperidine will be designated as *trans*-C_{15,1} (see Fig. 1). The venom alkaloid profiles of female sexuals of the two imported fire ants found in the United States, *S. invicta* and *S. richteri*, and the two native species, *S. geminata* and *S. xyloni*, are very similar, and consist primarily of *cis* and *trans* C_{11,0} alkaloids (Brand et al. 1973). However, worker alkaloid patterns for these species are species-specific (Brand et al. 1972; MacConnell et al. 1971). MacConnell et al. (1976) addressed the chemotaxonomic potential of the venom alkaloids by analysis of 13 New World fire ant species (most undescribed) and concluded that they do have taxonomic value, especially when used in conjunction with classical taxonomy. The species-specificity of the alkaloids has provided a useful tool for the study of a variety of research problems on fire ants (Vander Meer 1986a).

Cuticular Hydrocarbons. There is ample precedence for the use of cuticular hydrocarbons as taxonomic tools (Carlson & Service 1980, Carlson & Bolton 1984). In fire ant research, they have served as useful markers in investigations on a variety of problems not directly related to taxonomy, such as myrmecophile integration (Vander Meer & Wojcik 1982) and nestmate recognition (Vander Meer in press).

The chemical compositions of the cuticular hydrocarbons of *S. invicta* and *S. richteri* are species-specific (Lok et al. 1975; see Fig. 2). They are composed of normal, methyl, and dimethyl branched compounds. Analyses of various *S. invicta* life stages (Vander Meer et al. 1982; Vander Meer unpublished) have shown that the five major hydrocarbons of *S. invicta* are ubiquitous to the species, even being found in nest soil. Preliminary investigation of the cuticular hydrocarbon patterns from pinned specimens of 10 members of the *S. saevissima* complex, including the two imported fire ant species, indicate that although qualitatively they have the same components (at least 30 compounds), there are ample quantitative differences so that all are readily distinguished (Vander Meer unpublished). The cuticular hydrocarbons of *S. geminata* and *S. xyloni* (not members of the *saevissima* complex) are normal and monounsaturated compounds, also with species-specific patterns (Vander Meer 1988).

FIRE ANT HYBRIDIZATION IN THE UNITED STATES

Biochemical Evidence. Vander Meer et al (1985) presented chemical evidence for the natural occurrence of hybridization between *S. invicta* and *S. richteri*. The two species are readily distinguished by both their venom alkaloids, in which *S. richteri* produces only a little of the C₁₅ alkaloids that dominate the *S. invicta* pattern (Fig. 1), and cuticular hydrocarbon profiles (Fig. 2). We serendipitously discovered intermediate chromatographic patterns while investigating the chemistry and specificity of the trail pheromone. Further studies showed patterns of alkaloids and hydrocarbons intermediate to those of the parental species (see Vander Meer et al. 1985, Ross et al. 1987). The colonies that produced workers with these intermediate patterns were designated as natural hybrids. A mathematical index of similarity was developed using the quantity of alkaloids or hydrocarbons, or both. The index placed a quantitative value on the direction of hybridization (0.00 to 1.00 where 0.00 = *S. invicta* and 1.00 = *S. richteri*).

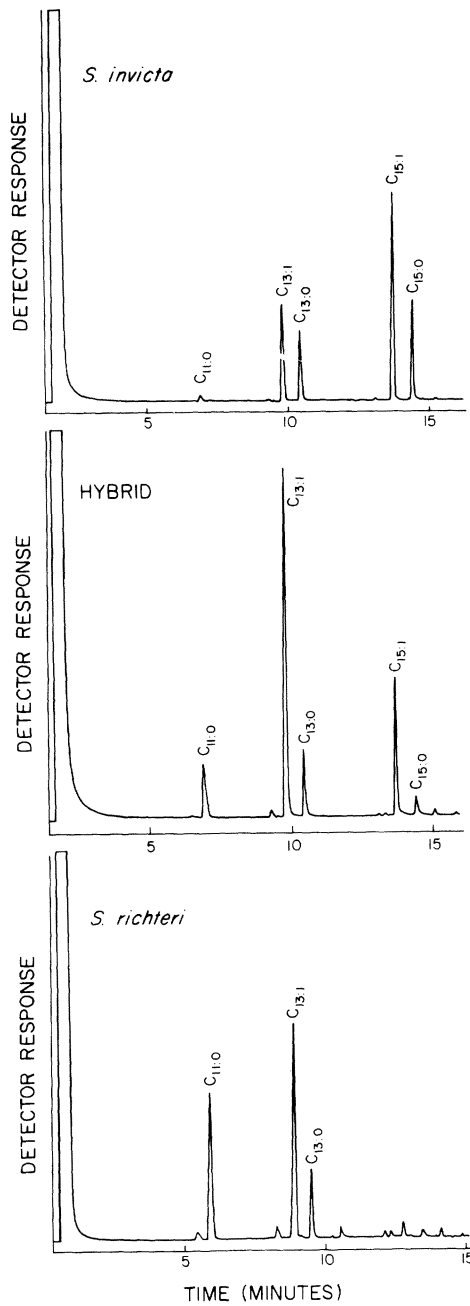


Fig. 1. Gas chromatograph (GC) trace of *S. invicta*, *S. richteri*, and hybrid venom alkaloids. All indicated alkaloids are *trans*. See Ross et al. (1987) for the GC conditions.

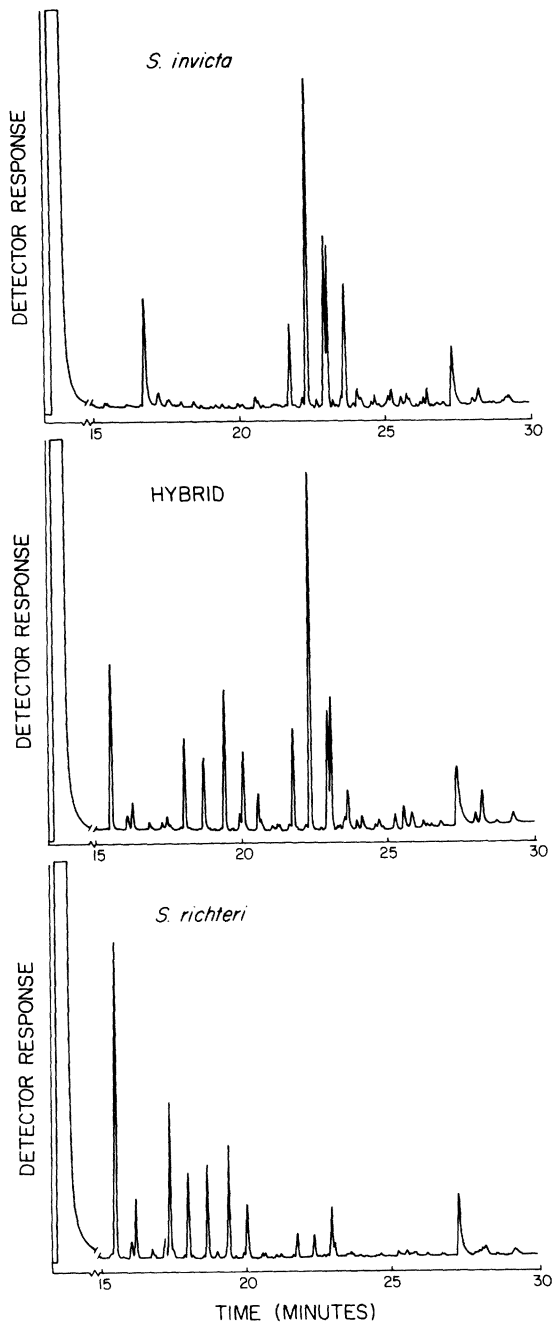


Fig. 2. Gas chromatograph (GC) traces of *S. invicta*, *S. richteri* and hybrid hydrocarbons. See Ross et al. (1987) for the GC conditions.

Values obtained for alkaloids did not necessarily correspond to those for hydrocarbons (Ross et al. 1987, Vander Meer unpublished), indicating the independence of the two biochemical characters.

Genetic Evidence. Genetic data in support of hybridization between the two species were obtained from enzyme electrophoresis (Ross et al. 1987). Four loci were found to differentiate the two parental forms: *alpha-glycerophosphate dehydrogenase-1* (*Agp-1*, EC 1.1.1.8); *Octanol dehydrogenase* (*Odh*, EC 1.1.1.73); *Esterase-2* and *Esterase-4* (*Est-2,4*; EC 3.1.1.1). These enzyme profiles confirmed that hybridization occurred in nature and that hybrid genotypes predominated in the hybrid zone indicating that F₁ hybrids are viable.

The biochemical and genetic methods were highly concordant in distinguishing between the two parental forms and in identifying hybrid colonies. Both methods showed that extensive gene introgression is occurring over a distance of at least 120 km within the limits of the study zone in northeastern Mississippi (Ross et al. 1987).

Behavioral Evidence. The recruitment strategy of the fire ant is complicated (Wilson 1962) and governed by a hierarchy of behaviors (Vander Meer 1987). The source of the recruitment pheromone is the Dufour's gland (Wilson 1959). In *S. invicta*, workers are initially attracted to a trail (attractant pheromone), followed by incitement to trail (inducer pheromone), and finally the actual following of the trail (orientation pheromone). A bioassay that measured the response of workers to a point source of Dufour's gland extracts clearly differentiated the two parental types (Vander Meer 1986b, Vander Meer in press). Bioassays using Dufour's gland extracts of each parent species and hybrid workers, demonstrated that hybrids were capable of responding to either parental type. Similarly, parental workers responded well to extracts of hybrid Dufour's glands. This behavioral evidence supports hybridization between the two species. Gas chromatographic examination of Dufour's gland extracts of the parental forms and their hybrid showed clear separation between the parents and an intermediate pattern for the hybrid (Vander Meer et al. in press).

Hybrid Morphology. The fact that hybrids of *S. invicta* and *S. richteri* have gone undetected for such a long time is related to the morphological similarity of the hybrid to that of *S. richteri*. Consequently, morphological traits or cursory observations in the field made detection of hybrids very unlikely (Vander Meer et al. 1985, James Trager, University of Florida, unpublished).

Hybrid Population Dynamics. Initially, hybridization between *S. invicta* and *S. richteri* was thought to be a localized phenomenon, occurring between Meridian and Starkville, Mississippi. However, further analyses of collections made throughout Alabama and Georgia now indicate that the range of the hybrid is extensive throughout northern Alabama and northwest Georgia (Fig. 3). Populations of the hybrid in Alabama and Georgia do not have the parental *S. richteri* at their northern border. Since it is not likely that migration of the magnitude required by their current distribution could occur by natural mating flights, we postulate that man has been largely responsible for movement of the hybrid just as in the early spread of the imported fire ant from the Mobile, Alabama area. In addition to rapid dissemination, the hybrid had to be highly competitive with its *S. invicta* parent to the South in order to maintain its territory.

Hybridization in the Past. We developed methods for the analysis of venom alkaloids from alcohol preserved specimens (Vander Meer & Lofgren in preparation). Using these techniques we analyzed samples collected from Meridian to Starkville, Mississippi in 1964. Alkaloid patterns characteristic of both parental types and their hybrid were

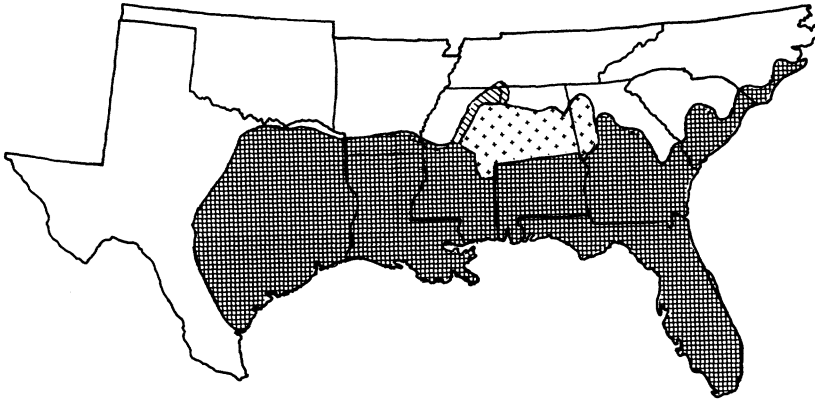


Fig. 3. Map of the Southern United States showing the current population range of *S. invicta* (squares); *S. richteri* (diagonal line) and the hybrid (plus marks).

found (Fig. 1). The results demonstrated that hybridization was occurring around and north of Meridian, Mississippi. In addition, analyses of samples collected around Mobile, Alabama in 1949 show evidence of hybridization. We conclude that hybridization has been occurring for a long time wherever the two forms met.

Hybridization Models. Based on the above results, we can account for the current zone of hybridization. Several models are available for consideration.

A) The dispersal-dependent model of neutral introgression (see Moore 1977) is based on the lack of a barrier to gene flow without any competition between parental forms. This model can be discarded based on known fire ant characteristics: 1) a high reproductive rate for both species, and 2) they are very competitive, consequently, under this model, secondary contacts and introgression would result in the appearance of rapidly decaying clines at the site of first contact.

B) In a dynamic equilibrium model there is selection against the hybrid, which is balanced by gene flow from between the parental populations. Mitigating against this model is the large population of hybrids located in Alabama and Georgia (Fig. 3), where there is no parental species on its northern boundary. Based on this model these hybrid populations should collapse.

C) A third model invokes the advance of a competitively superior genotype (*S. invicta*), with the hybrid zone moving in the direction of the inferior competitor (Barton & Hewitt 1985), which in this case would be *S. richteri*. This model cannot explain the hybrid populations in Alabama and Georgia (Fig. 3) where the inferior competitor is absent. However, in Mississippi we are observing a northward movement of hybrid, with subsequent displacement of *S. richteri*.

D) The bounded hybrid superiority model dictates that there is an advantage to recombinant genotypes in habitats intermediate to those favored by the parental forms. This model is consistent with hybridization occurring wherever the two parental types meet, with subsequent population equilibrium based on habitat suitability; i.e. the hybrid could not maintain itself in the southern half of the infested area, where the subtropical *S. invicta* has an environmental advantage. Further north, for instance Meridian, Mississippi, the hybrid is capable of maintaining its territory against *S. invicta*. This model also explains the persistence of the hybrid populations in northern Alabama and Georgia (see Fig. 3). It does not deal with the apparent advance of the hybrid in northern Mississippi, displacing *S. richteri*.

Strictly interpreted, no one model adequately explains all of the data and observations made on the fire ant populations in the United States. However, an asymmetric bounded hybrid superiority model would satisfy all the known observations. The hybrid is bounded to the south by *S. invicta*, which is being held in check by the hybrid at a geographic point where an equilibrium has been reached balancing differences in competitiveness and environmental conditions. To the north, in Alabama and Georgia, the hybrid only has to compete with environmental conditions; therefore the hybrid is asymmetrically bounded. However, in northern Mississippi, the hybrid is competing with both the environment and *S. richteri*. The observed northward displacement of *S. richteri* by the hybrid indicates that the hybrid may successfully outcompete *S. richteri* through its entire range, ultimately eliminating this parental form from the United States.

The Question of Species. Buren (1972), reinstated *S. richteri* as a species and classified *S. invicta* as a new species based primarily on the observation that in the United States, where both forms had ample opportunity to hybridize, no hybridization was found and there was little phenetic variability. Our discovery of hybridization through chemical characters, coupled with hybrid morphology that is almost identical to *S. richteri*, negates the criteria used to specify *S. invicta*. Obviously, where the two forms have the opportunity to mate they are successful at producing viable hybrids (Vander Meer et al. 1985, Ross et al. 1987). Therefore, if hybrids are not found in their native South America there must be pre-mating isolation mechanisms that prevent gene flow. Our laboratory is currently surveying likely areas of Brazil and Argentina for *S. invicta*/*S. richteri* hybridization. Although there are good reasons to question the validity of *S. invicta* as a separate species, it will remain in good standing until definitively proven otherwise.

THE FIRE ANT IN SOUTH AMERICA

S. invicta and *S. richteri*. The same biochemical characters (venom alkaloids and cuticular hydrocarbons) developed for the study of fire ant hybridization in the United States are currently being applied to specimens collected by our laboratory in South America. The holotype for *S. invicta* was collected in Cuiaba, Mato Grosso, Brazil. Chemical analysis of samples from Cuiaba did not show the typical chromatogram pattern (chromatotype) that is associated with *S. invicta* found in the United States. However, chromatotypes identical to United States' types were found in samples from Caceres, Mato Grosso, Brazil about 200 km west of Cuiaba. Perhaps, the great agricultural related changes made by man in that area of Brazil, coupled with the weedy nature of the fire ant (Tschinkel 1986) has altered the fire ant species distribution from what it was in 1972. *S. invicta* chromatotypes have also been found in northern Argentina, although we cannot be certain of the exact origin of *S. invicta* populations in the United States, Argentina may be the most likely source.

The type locality for *S. richteri* is Buenos Aires, Argentina (Buren 1972). Chromatotypes near Buenos Aires were discovered, which were identical to those of *S. richteri* found in the United States (collections by D. P. Wojcik & D. P. Jouvenaz, USDA). The Buenos Aires area is a likely source for *S. richteri* in the United States, although other areas have not yet been extensively investigated.

Studies are planned to survey additional areas in Argentina to determine whether *S. invicta* and *S. richteri* meet to form hybrids.

Other *S. saevissima* Complex Members. Based on hundreds of chromatographic analyses of samples collected in Brazil and Argentina, we can conclude that at the present time, there are several distinct chromatotypes. Additional samples are being collected in order to determine the variation within populations. In the future we expect

to combine the biochemical tools with morphological and genetic characters to further investigate this important but difficult area of fire ant taxonomy and population dynamics.

CONCLUSION

The difficulty of the *S. saevissima* complex taxonomy has been recognized for a long time. For example Creighton (1930) wrote, "In approaching the subject of *S. saevissima* one has the unpleasant feeling that he is entering a battle-field strewn with unexploded missiles and that there is a strong possibility that one of these taxonomic duds may, through tampering, bring the investigator to grief". Wilson (1952) also commented that the *S. saevissima* complex "has consistently presented some of the more knotty problems of ant taxonomy". We hope that the chemical characters we have developed will aid in sorting out this very complex taxonomic problem.

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