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Chemotaxonomy Applied to Fire Ant Systematics in the United States and South America

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INTRODUCTION

Systematics

The genus, *Solenopsis* has undergone many changes over the last 60 years. It has been traditionally divided into several subgenera (Creighton 1930), which were synonymized by Ettershank (1966). In 1968, Baroni-Urbani separated *Diplorhoptrum*, small monomorphic species commonly known as thief ants, from *Solenopsis*. Within the genus *Solenopsis* there are several species complexes, based on morphology. The largest complex is *saevissima*. The *Solenopsis saevissima* complex has undergone many revisions, and is currently undergoing yet another (James Trager, personal communication). Creighton (1930) lumped 16 species into 8 subspecies or varieties. Wilson (1952) believed that most of the subspecies represented unstable hybrid variants and consolidated the complex into two species, *S. interrupta* and *S. saevissima*, and one subspecies, *S. saevissima* var. *richteri*. Ettershank (1966) preserved only *S. saevissima* and *S. interrupta*. Most recently Buren (1972) recognized Ettershank's two species, raised *S. richteri* (the black imported fire ant) and *S. quinquecuspis* to species rank and described two new species, *S. invicta* (the red imported fire ant) and *S. blumi*. There are probably many undescribed *saevissima* complex species in South America (Buren 1972; MacConnell et al. 1976); thus researchers anxiously await Trager's taxonomic revision.

Introduction into the United States

Black fire ants were accidentally imported into the Mobile, Alabama area around 1918. Creighton (1930) identified them as *S. saevissima* var. *richteri*. Then, in the 1940's a red form of imported fire ant was also discovered around Mobile, Alabama; probably introduced in the 1930's (Lofgren 1986). The red and the black form were subsequently named *S. invicta* and *S. richteri*, respectively (Buren 1972). Little is known of the population dynamics that occurred between 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 Buren et al. reported that *S. richteri* occupied 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 thought to occupy all other infested areas.

Biochemical Characters

Venom Alkaloids. The poison gland of *S. saevissima* complex workers contain *trans* 2-methyl-6-alkyl or alkenyl piperidines (MacConnell et al. 1971; MacConnell et al. 1976). The length of the alkyl or alkenyl group varies from C₁₁ to C₁₇ and may contain a single double bond. These compounds are easily referred to by stating their sidechain length and whether or not they have a double bond; e.g. *trans*-2-methyl-6-(*cis*-6-n-pentadecenyl)-piperidine can be simplified to *trans*-C_{15:1}. The venom alkaloid profiles of *S. invicta*, *S. richteri*, *S. geminata* and *S. xyloni* female sexuals are non-specific and consist primarily of *cis* and *trans* C_{11:0} alkaloids (Brand et al. 1973). However, worker alkaloid patterns are species-specific (Brand et al. 1972; MacConnell et al. 1971) and have provided a useful tool for the study of a variety of fire ant problems (Vander Meer 1986a). MacConnell et al. (1976) analyzed the alkaloid profiles of 13 New World fire ant species (most undescribed) and concluded that they have taxonomic value.

Cuticular Hydrocarbons. Insect cuticular hydrocarbons are established taxonomic tools (Carlson 1988; Vander Meer 1986a). The cuticular hydrocarbons of *S. invicta* and *S. richteri* are species-specific (Lok et al. 1975) and composed of normal, methyl, and dimethyl branched compounds. The five major hydrocarbons of *S. invicta* are ubiquitous to the species, even being found in nest soil (Vander Meer et al. 1982; Vander Meer unpublished). *S. geminata* and *S. xyloni* (not members of the *saevissima* complex) also have species-specific cuticular hydrocarbon patterns, composed of normal and mono- and di-unsaturated compounds (Vander Meer unpublished). At the colony level, hydrocarbon patterns change quantitatively with time; however, they are qualitatively invariant (Vander Meer et al. 1989).

We will discuss the use of fire ant biochemical characters and associated behaviors to better understand the present distribution of *S. invicta* and *S. richteri* in the United States and to pinpoint the most probable South American source populations for these two invaders. In addition, we will identify and discuss some interesting taxonomic problems.

HYBRID FIRE ANTS IN THE UNITED STATES

Biochemical Evidence

Vander Meer et al. (1985) discovered hybridization between *S. invicta* and *S. richteri* when intermediate Dufour's gland chromatographic profiles were found from colonies identified morphologically as *S. richteri*. The two species are readily distinguished by their venom alkaloids (*S. richteri* does not produce the C₁₅ alkaloids (Fig. 1) that dominate the *S. invicta* pattern), cuticular hydrocarbons (Fig. 1) and Dufour's gland profiles (Vander Meer and Lofgren 1989). Hybrids had alkaloid and hydrocarbon patterns intermediate to those of the parental species (see Vander Meer et al. 1985; Ross et al. 1987). The hybrids had escaped detection for several decades because

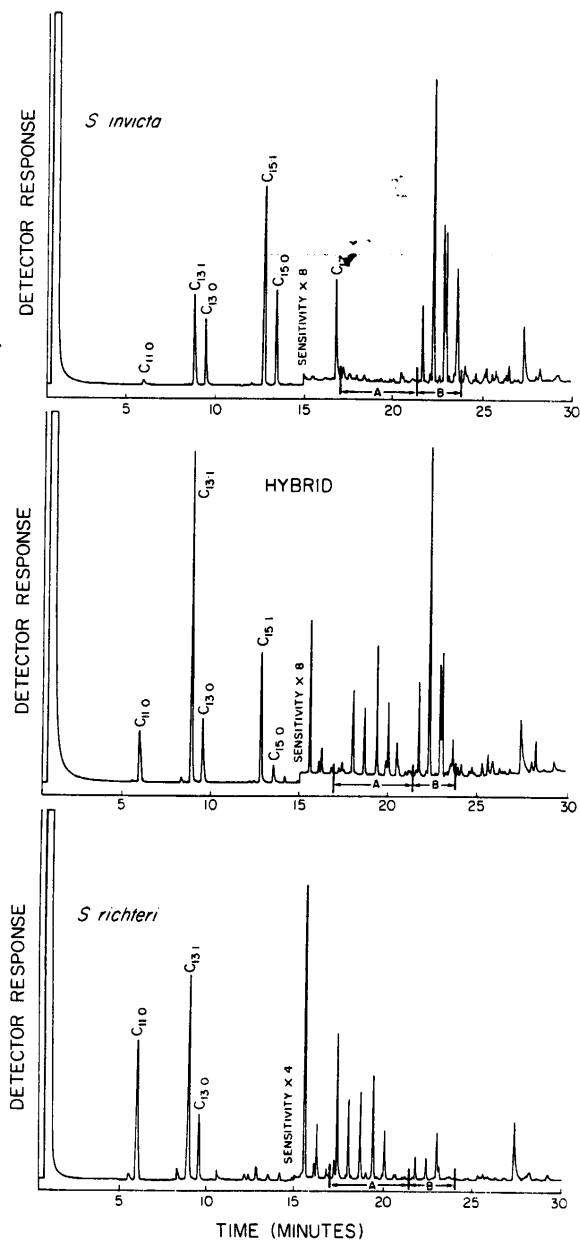


FIGURE 1. Gas chromatograph profiles of *Solenopsis invicta*, *Solenopsis richteri* and their hybrid. Characteristic *S. invicta* hydrocarbons = B; characteristic *S. richteri* hydrocarbons = A.

morphologically they look like *S. richteri*. Field observations were unlikely to detect hybridization (Vander Meer et al. 1985).

Genetic Evidence

Genetic evidence for hybridization based on gene frequency data was obtained by enzyme electrophoresis (Ross et al. 1987) of female sexuals. Four loci differentiated 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). This methodology confirmed the occurrence of hybridization and found that recombinant genotypes predominated in the hybrid zone, indicating that F₁ hybrids are reproductively viable. Isozyme analyses of hybrid and parental workers were also diagnostic. *S. invicta* and *S. richteri* populations were fixed for specific electromorphs of *Glucose phosphate isomerase* (Pgi), whereas the hybrid showed segregation of both electromorph types (S. Narang, personal communication).

Biochemical and genetic methods were highly concordant in differentiating hybrid colonies from the two parental forms. Both methods revealed extensive gene introgression in a north-south study zone of about 120 Km in northeastern Mississippi (Ross et al. 1987).

Behavioral Evidence

Recruitment Pheromone. The fire ant's complex recruitment strategy (Wilson 1962) is governed by a hierarchy of behaviors (Vander Meer 1987; Vander Meer 1986b). The Dufour's gland produces the recruitment pheromone (Wilson 1959). *S. invicta* workers are initially attracted to a trail (attractant pheromone; Vander Meer et al. 1988), then motivated to followed the trail (inducer pheromone; Vander Meer et al. in press), and finally follow it (orientation pheromone; Vander Meer et al. 1981). A bioassay that measured worker response to a point source of Dufour's gland extracts clearly differentiated between the two parental types (Vander Meer and Lofgren 1989). Bioassays using parental and hybrid worker Dufour's gland extracts demonstrated that hybrids could respond to either parental type. Similarly, parental workers responded well to hybrid Dufour's gland extracts (Vander Meer and Lofgren 1989). This provides definitive behavioral evidence for hybridization. As in the chromatographs of venom alkaloids and cuticular hydrocarbons, gas chromatographic examination of hybrid and parental Dufour's gland extracts clearly distinguished between the parents, with an intermediate hybrid pattern (Vander Meer and Lofgren 1989).

Nestmate Recognition. Nestmate recognition in *S. invicta* has been well studied (see Vander Meer this volume) and it is clear that both environmental and heritable cue sources are involved (Obin and Vander Meer 1988). However, the effect of environmental sources can be limited by rearing colonies in the laboratory under identical conditions (Obin 1986). The residual nestmate recognition response, measured in an aggression bioassay, is primarily due to heritable cues. Aggression bioassays showed no difference in the ability of *S. invicta*, *S. richteri*, or hybrid to recognize the other two populations. However, in intra-population bioassays, *S. invicta* and *S. richteri*

both showed significantly reduced aggression responses, whereas the hybrid responded to other hybrid colonies as intensely as it did to its parents (Obin and Vander Meer 1989). This suggests greater genetic variability for heritable cues in the hybrid than in either parent. This goes along with the observed variability of genetically controlled cuticular hydrocarbons and venom alkaloids. Although these chemical classes have not been implicated as nestmate recognition cues, they represent a model for possible heritable cues. We found distinct and very consistent qualitative patterns for alkaloids and hydrocarbons of the two parent species (Vander Meer et al. 1985; Diffie et al. 1988; Vander Meer unpublished). However, for the hybrid there are patterns representing all possibilities between the two parents. Therefore, the expected high hybrid genetic variability, compared to its parents, is supported by alkaloid and hydrocarbon analyses and the results of nestmate recognition studies.

Extent of the Hybrid Population

Originally thought to be a localized phenomenon (Vander Meer et al. 1985; Ross et al. 1987), hybridization between *S. invicta* and *S. richteri* is now known to be extensive, with large reproductively viable hybrid populations throughout northeast Mississippi, northern Alabama and northwest Georgia (Vander Meer et al. 1985, Diffie et al. 1988). Hybrid populations in Alabama and Georgia have *S. invicta* at their southern border but do not have *S. richteri* at their northern border. The hybrid population is too extensive to have occurred by natural mating flights. Therefore, people may be largely responsible for the hybrids movement, just as in the case of the imported fire ant from the Mobile, Alabama area (Lofgren 1986).

A Look Back in Time

Is imported fire ant hybridization a recent event? Analysis of venom alkaloids from alcohol preserved specimens collected from Meridian to Starkville, Mississippi in 1964 (samples collected for E. O. Wilson) showed alkaloid patterns characteristic of both parental types and their hybrid (Vander Meer unpublished). The results demonstrated that hybridization occurred in and north of Meridian, Mississippi. In addition, analyses of samples collected from Mobile, Alabama in 1949 (E.O. Wilson) showed evidence of hybridization. Therefore, hybridization between *S. invicta* and *S. richteri* has been occurring wherever and whenever the two forms met.

A THEORETICAL MODEL

Initial introduction of both imported species occurred around the Mobile, Alabama area. However, their distributions are now disjunct, with *S. richteri* occupying only a small enclave in northeastern Mississippi, while *S. invicta* occurs in the southern half of the affected states, except for all of Florida. This corresponds to their distribution in South America, where *S. invicta* is in a tropical/sub-tropical area and *S. richteri* is in a temperate zone.

Initial reports (Wilson and Eads 1949; Wilson and Brown 1958) on the interaction of the two forms around Mobile, Alabama, indicate that the red form (*S. invicta*) competitively dominated the black form (*S. richteri*).

Competitiveness in ant populations is mediated to a large extent by their ability to discriminate the chemical cues associated with territory, recruitment and nestmate recognition (Hölldobler and Carlin 1987). In two of three recruitment pheromone behavioral sub-categories, attraction and orientation induction, there is asymmetric species-specificity favoring *S. invicta* over *S. richteri*. *S. richteri* does not respond to *S. invicta* Dufour's gland extracts in an olfactometer or orientation induction bioassay; however, *S. invicta* responds to *S. richteri* Dufour's gland extracts. Thus at least in this aspect of competition for territory and resources it appears that *S. invicta* has an advantage. Since we do not find hybrids south of an approximate East/West line at Meridian, Mississippi it must be concluded that the hybrid is competitively inferior to *S. invicta* in habitats south of this line. Chromatographic evidence indicates that the interface area around Meridian, Mississippi has been stable for at least 25 years, thus the hybrid and *S. invicta* have reached a standoff regarding competitiveness and environmental adaptability. On the northern end of the distribution, chromatographic evidence indicates that the hybrid is displacing a competitively inferior parent, *S. richteri*.

Many models have been developed to explain hybrid zones (see Vander Meer and Lofgren 1988). Moore's (1977) "bounded hybrid superiority" model is most useful. In this model an advantage exists for 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 and subsequent population equilibrium based on habitat suitability. This model also explains the persistence of hybrid populations in northern Alabama and Georgia. However, it does not deal with the apparent advance of the hybrid in northern Mississippi, displacing *S. richteri*. An asymmetric bounded hybrid superiority model would satisfy all 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 does not compete with either parent, and thus is asymmetrically bounded. However, in northern Mississippi the hybrid competes with both the environment and *S. richteri*. The observed northward displacement of *S. richteri* by the hybrid indicates that the hybrid may successfully out compete *S. richteri* through its entire range, eventually eliminating this parental form from the United States.

Buren (1972) reinstated *S. richteri* as a species and classified *S. invicta* as a new species based largely on the observation that no hybridization was found and there was little phenetic variability in the United States. The discovery of hybridization through chemical characters, coupled with the observation that hybrid morphology is almost identical to *S. richteri*, neutralizes the criteria used to specify *S. invicta*. Where the two forms have the opportunity to mate they are successful. Therefore, if they are "good" species, pre-mating isolation mechanisms must exist in their native South America.

THE FIRE ANT IN SOUTH AMERICA

The species-specific cuticular hydrocarbon and venom alkaloid patterns are largely invariant within the United States *S. invicta* and *S. richteri*

populations. Thousands of samples from Brazil and Argentina were collected and analyzed by gas chromatography. One objective was to search for the specific chromatotypes that correspond to those found for *S. invicta* and *S. richteri* in the United States.

An exact match for *S. invicta* was found for specimens collected around Caceras, Brazil and south along the Paraguay River. No collections were made in Paraguay; however, the chromatotype resumed at the Paraguay/Argentina border and continued south along the Paraguay/Parana River to Sante Fe, Argentina. Different *Solenopsis* chromatotypes were found south of Sante Fe and to the east in a parallel direction along the Uruguay River. Therefore, the *S. invicta* chromatotype is found only along a narrow but very long corridor from Brazil to Argentina. This distribution approximates that given by Buren et al. (1974); although we extended its range further south in Argentina.

The United States *S. richteri* chromatotype was found only in a small lowland area of Argentina, approximately 100 km north of Buenos Aires, across the Parana River and close to the Uruguay border. These samples were identified morphologically as *S. richteri* (James Trager personal communication). Based on extensive surveys, the closest *S. invicta* and *S. richteri* come to each other is about 200 km. Other *Solenopsis* species exist between the two. No evidence for *S. invicta*/*S. richteri* hybrids was found. This data offers the simplest explanation for hybridization in the United States: in Argentina a geographic isolation barrier exists. Thus pre-mating isolation mechanisms were not selected for and when the geographic barrier was removed; i.e. accidental importation into the same area of the United States, hybridization occurred. Whether or not geographic isolation is enough to consider two populations different species is a good question, but one left to the taxonomists.

Other samples (identified morphologically as *S. richteri*; James Trager personal communication), collected from many areas of the Province of Buenos Aires, Argentina, including near the *S. richteri* type location, Buenos Aires (Buren 1972), had similar hydrocarbon profiles but differed dramatically in the alkaloid patterns. The alkaloid patterns were consistent and were composed primarily of *cis* and *trans* C₁₁ alkaloids. This pattern characterizes *geminata* or *xyloni* complex species more than a *Saevissima* complex species. There was no evidence for mixing of the two *S. richteri* chromatotypes, even though in one instance colonies were sympatric. The two chromatotypes probably represent two cryptic species. Since the United States *S. richteri* do not match the *S. richteri* from the type location, the United States *S. richteri* need another name. In another scenario, if the two fire ant forms imported into the United States are ultimately considered a single species, then United States *S. richteri* and its corresponding chromatotype in Argentina can be synonymized to *S. invicta*.

CONCLUSION

Creighton (1930) recognized the difficulty of studying the *saevissima* complex by likening it to "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." These studies

hoped to add another techniques to the taxonomic arsenal so that the battlefield may be a little less dangerous.

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