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**Chemical Mimicry in the Myrmecophilous
Beetle *Myrmecaphodius excavaticollis***

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Chemical Mimicry in the Myrmecophilous Beetle *Myrmecaphodius excavaticollis*

Abstract. *The myrmecophilous beetle Myrmecaphodius excavaticollis (Blanchard) was found to have species-specific cuticular hydrocarbons acquired from one of its hosts, the ant Solenopsis richteri Forel. Removal from its ant host resulted in loss of the host hydrocarbons, leaving a cuticular pattern innate to the beetle. When beetles were transferred to colonies of three other Solenopsis species, they acquired the specific hydrocarbons associated with each of the new hosts. This passive integration mechanism is coupled with the beetle's armored exterior to enable it to cope with multiple aggressive hosts.*

Myrmecophiles, ant symbionts, have evolved numerous mechanisms for integrating themselves into host colonies. Among these mechanisms are morphological mimicry, defensive and appeasement chemical secretions, and behavioral mimicry (1). We report a novel integration mechanism used by *Myrmecaphodius excavaticollis* (Blanchard) in which passive, nonintegrative, defensive behavior is followed by the integrative acquisition of host-specific hydrocarbons. Individual beetles are able to shed the hydrocarbons of one *Solenopsis* species and acquire the pattern of a different host species. These data partially explain the multiple host capability of this myrmecophilous beetle.

Myrmecaphodius excavaticollis was

probably introduced into the United States from South America with one of its imported hosts, *Solenopsis invicta* Buren or *S. richteri* Forel (2). The beetle has been reported in association with three indigenous species, *S. geminata* (F.), *S. xyloni* McCook (3) and *Iridomyrmex pruinosum* (Roger) (4), as well as with another import, *I. humilis* (Mayr) (3). All developmental stages of the beetles have been found within the mounds of the host ants. Adults move freely among host ants and obtain food directly from workers through trophallaxis, by predation on ant larvae, and by feeding on freshly killed or decomposed workers and ant booty (5). Dispersal flights can occur throughout the year, after which the beetles must find a suitable host

colony, which may not be the same species they originally came from (6, 7).

The integration of *M. excavaticollis* into a host colony in spite of the absence of morphological mimicry and chemical defenses (5) led us to investigate the potential role of host colony odor and species odor in myrmecophile acceptance. Colony odor has both innate and acquired components (8). Ants recognize each other by touching of one's antennae to the other's cuticle, suggesting that the cuticle acts as a source of species-specific (innate) chemicals and provides a large surface for their release. The cuticle can also effectively function to absorb the acquired components of colony odor from the surrounding environment.

Hydrocarbons are cuticular components that are useful chemotaxonomic tools for species complexes in Diptera (9, 10); they have physiological activity as sex attractants in Diptera and Lepidoptera and alarm pheromones in Hymenoptera (11). Cuticular hydrocarbons have been postulated to be semiochemi-

cal cues for caste and species recognition for termites (11), and the termitophilous beetle *Trichopsenius frosti* Seevers synthesizes a cuticular hydrocarbon pattern identical to that of its host, *Reticulitermes flavipes* (Kollar) (12). Hydrocarbons constitute 65 to 75 percent of the cuticular lipids of *S. invicta* and *S. richteri* (13, 14) and are distinctly different for the four *Solenopsis* species hosts of *M. excavaticollis* (15).

The relation between the cuticular hydrocarbons of *M. excavaticollis* and its host was investigated when large numbers of beetles were found in association with *S. richteri* collected from northern Mississippi. The ants and myrmecophiles were isolated from the soil and maintained together in laboratory colony trays (16). Some beetles were separated from their ant hosts and maintained in nest cells where they were fed honey agar.

A group of beetles were removed from *S. richteri* colonies and immediately washed with hexane. Hydrocarbons

were isolated by applying the concentrated wash to a silicic acid column and eluting with hexane. The hydrocarbon fraction was analyzed by gas chromatography (17). A sample of *S. richteri* workers were treated in the same way to obtain a comparative chromatogram of their cuticular hydrocarbons. A comparison of chromatograms of beetle and *S. richteri* hydrocarbons (Fig. 1, A and B) shows that species-specific *S. richteri* hydrocarbons are also present on *M. excavaticollis*. In addition to host hydrocarbons, the beetles show significant amounts of higher molecular weight hydrocarbons. Analysis of cuticular hydrocarbons from beetles isolated from *S. richteri* for about 2 weeks (Fig. 1C) showed a dramatic decrease in host-related hydrocarbons; however, the high molecular weight components remained. The data suggested that *M. excavaticollis* acquired host-specific hydrocarbons and that the components shown in Fig. 1C are innate to the beetle. A less likely explanation is that the beetles are stimu-

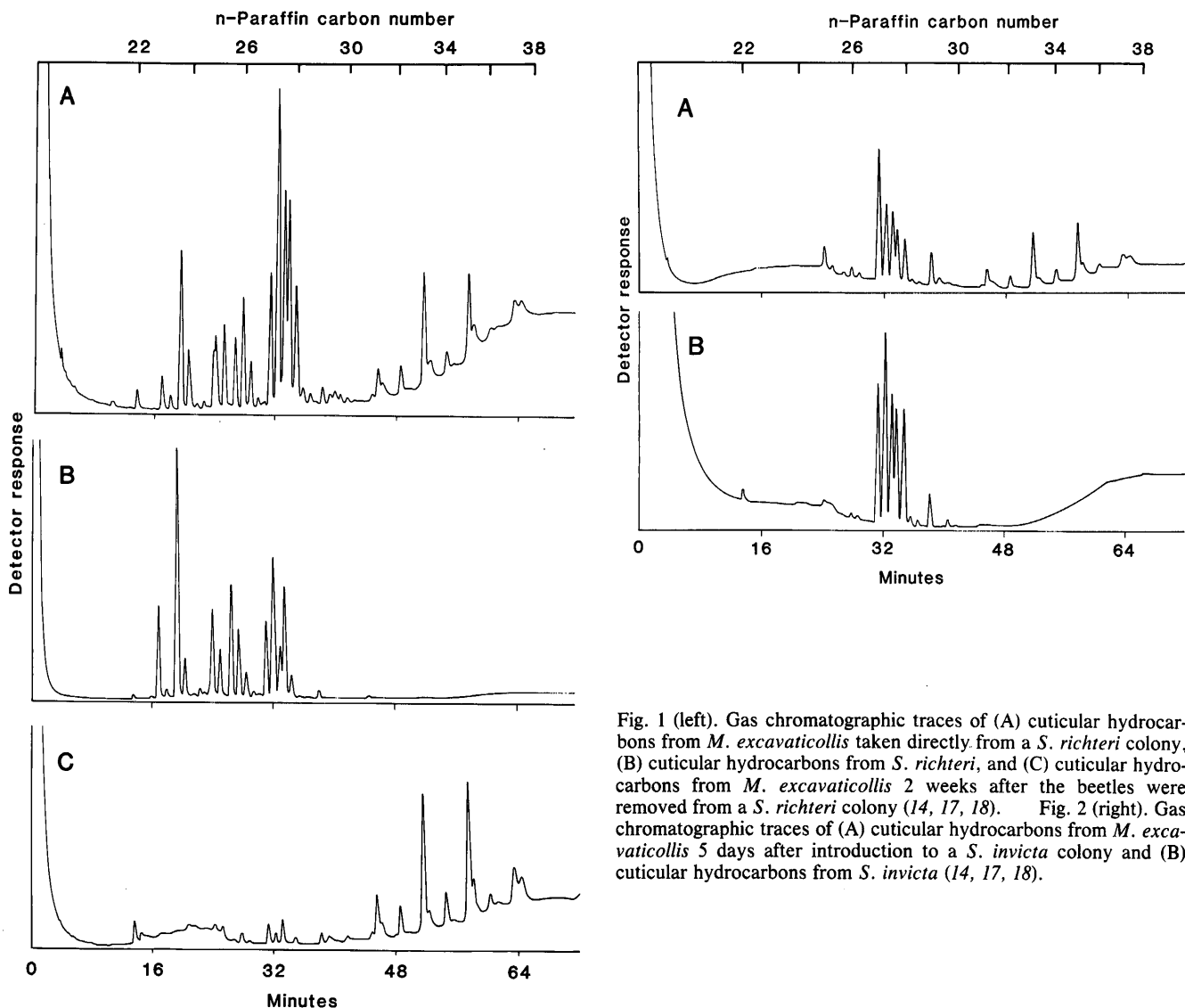


Fig. 1 (left). Gas chromatographic traces of (A) cuticular hydrocarbons from *M. excavaticollis* taken directly from a *S. richteri* colony, (B) cuticular hydrocarbons from *S. richteri*, and (C) cuticular hydrocarbons from *M. excavaticollis* 2 weeks after the beetles were removed from a *S. richteri* colony (14, 17, 18). Fig. 2 (right). Gas chromatographic traces of (A) cuticular hydrocarbons from *M. excavaticollis* 5 days after introduction to a *S. invicta* colony and (B) cuticular hydrocarbons from *S. invicta* (14, 17, 18).

lated to produce *S. richteri* hydrocarbons when in contact with the host. It is also evident that cuticular components are in a continuous state of flux.

If the host hydrocarbons are acquired, then this multiple-host myrmecophile should be able to change its hydrocarbon pattern to match that of the host species. To test this hypothesis, we collected beetles from *S. richteri* colonies, isolated them for 2 weeks, and then introduced them into laboratory colonies of *S. invicta*. After 5 days, the beetles were removed and analyzed for cuticular hydrocarbons as described. The data (Fig. 2, A and B) show that the *M. excavaticollis* taken from *S. richteri* colonies acquired the cuticular hydrocarbons of its new host, *S. invicta*. The same phenomenon occurred when previously isolated beetles were introduced into *S. geminata* and *S. xyloni* colonies. Although the switching of hydrocarbon patterns from one host to another weakens the likelihood that they are synthesized by the beetle, we also found that freshly killed isolated beetles had acquired *S. invicta* hydrocarbons within 2 days after exposure to the ant colony. These data eliminate biosynthesis as a possibility and support a passive mechanism of hydrocarbon acquisition. When initially introduced into a host colony, the *M. excavaticollis* were immediately attacked. The response of the beetles was to play dead and wait for the attacks to cease, or they moved to an area less accessible to the ants. Within 2 hours after introduction into a host colony, the beetles' cuticle contained 15 percent of host hydrocarbons. The accumulation of hydrocarbon continued up to 4 days until the beetles' cuticle contained about 50 percent host hydrocarbons. Beetles surviving this long were generally no longer attacked.

The beetles can acquire the host cuticular hydrocarbons by ant-beetle contact, grooming behavior, regurgitation of ant postpharyngeal gland contents (which contain large amounts of species-specific hydrocarbons), and by ingestion. However, the overall mechanism used for integration of *M. excavaticollis* into its host colonies involves the initial passive defensive behavior that must enable it to survive long enough to acquire the species odor of its host as well as the environmental part of the host's colony odor.

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