

Comparative Analysis of Cuticular Hydrocarbons from the Ectoparasitoids *Cephalonomia waterstoni* and *Laelius utilis* (Hymenoptera: Bethyridae) and Their Respective Hosts, *Cryptolestes ferrugineus* (Coleoptera: Cucujidae) and *Trogoderma variabile* (Coleoptera: Dermestidae)

RALPH W. HOWARD

U.S. Grain Marketing Research Laboratory, USDA-ARS, 1515 College Avenue, Manhattan, Kansas 66502

Ann. Entomol. Soc. Am. 85(3): 317-325 (1992)

ABSTRACT Cuticular hydrocarbons have been identified from the immatures and adults of two bethylid wasps and their larval beetle hosts. *Cephalonomia waterstoni* Gahan is host specific on *Cryptolestes ferrugineus* (Stephens), whereas *Laelius utilis* Cockerell is commonly associated with a variety of dermestid larvae, including *Trogoderma variabile* Ballion. The cuticular hydrocarbons of *C. waterstoni* larvae consist of n-alkanes (C₂₁-C₃₃), 2-, 3-, 5-, 7-, 11-, and 13-methyl alkanes, one dimethyl alkane (11,15-dimethyl C₂₇), and a C₃₁ monoene and diene. The cuticular hydrocarbon composition of their beetle host differs somewhat, consisting of n-alkanes (C₂₅-C₃₂), 3-, 5-, 11-, and 13-methyl alkanes, a series of Z-8/Z-9-monoenes, and a series of dienes with the double bonds separated by 12 methylene units. No dimethyl alkanes are present in the *C. ferrugineus* larvae. Considerable ontogenetic changes in cuticular hydrocarbon composition occur when *C. waterstoni* eclose to adults. Although both sexes contain the same major cuticular hydrocarbons, their relative abundances vary. In addition to n-alkanes (C₂₃-C₂₇), 2-, 3-, and 5-methyl alkanes, 5,15-, 5,17-, and 5,19-dimethyl alkanes, and a series of Z-11-monoenes are present in both sexes. In addition, the males possess small quantities of Z-7-monoenes. The males have the monoenes as their major components, whereas the females have the 5-methyl alkanes and the dimethyl alkanes as their major components. The cuticular hydrocarbon composition of *L. utilis* and its host *T. variabile* differs considerably from the *Cephalonomia-Cryptolestes* pairing. The major components of the *Laelius* larvae consist of n-alkanes (C₂₃-C₃₃), 3-, 5-, 13-, and 15-methyl alkanes, and a series of Z-9-monoenes. The *T. variabile* larval hydrocarbons consist only of n-alkanes (C₂₂-C₃₅) and 3-, 5-, and 13-methyl alkanes. No unsaturated components were detected. As with *C. waterstoni*, considerable ontogenetic changes in hydrocarbon composition occur for *L. utilis* upon adult eclosion. Unlike *C. waterstoni*, however, only slight differences in composition occur between the sexes. The adult *Laelius* hydrocarbons consist of n-alkanes (C₂₁-C₂₉), 2-, 3-, 7-, 9-, and 13-methyl alkanes, and a series of Z-9-monoenes.

KEY WORDS Insecta, Bethyridae, Cucujidae, semiochemicals

CUTICULAR HYDROCARBONS are major semiochemical agents in a diversity of taxa and ecological systems, serving in roles such as species, gender, and colony recognition cues and as sex pheromones, kairomones, or allomones (Howard & Blomquist 1982, Lockey 1988, Stowe 1988). Although much of the earlier literature on cuticular hydrocarbons was focused on chemically surveying species in a wide range of higher order taxa for the presence of novel compounds (Jackson & Blomquist 1976, Lockey 1988), recent efforts have dealt more with the biological roles of these chemicals, with special attention being

given to social insects and theirinquilines (Howard et al. [1990a] and references therein). In social insect systems, cuticular hydrocarbon profiles tend to be species-specific and are thought to function as important recognition cues for colony members. In a substantial number of cases, it has now been demonstrated that the inquilines associated with social insects possess cuticular hydrocarbon profiles identical or closely similar to that of their hosts; it is thought that this is primarily the means by which these inquilines are able to survive in the colony (Howard et al. 1980, 1990a). In some cases, it has also been shown that the inquilines biosynthesize these cuticular hydrocarbons (Howard et al. 1990b), strongly suggesting a coevolutionary relationship between the inquiline and its host in terms

This article reports the result of research only. Mention of a proprietary product does not constitute an endorsement or recommendation for its use by USDA.

of biochemical processes and adaptive functions such as water conservation, protection from microorganisms, and semiochemical communication.

The primitive aculeate family Bethylidae seems to hold promise for extending these concepts. Its members have evolved to use small larvae as hosts (primarily Coleoptera and Lepidoptera), and these hosts live in cryptic situations such as in the soil, plant stems, wood, seeds, cases, or rolled leaves (Evans 1964). Furthermore, some bethylids are gregarious, have complex polymorphisms, and exhibit subsocial behavior (Evans 1964, Casale 1991). Bethylids subdue their hosts by multiple stinging and lay one to several eggs externally. The resulting bethylid larvae develop as ectoparasitoids, dropping off the exhausted remains of their host to pupate gregariously in silk cocoons nearby. Males normally emerge before females and inseminate their sisters or even their mothers in some cases (Evans 1964).

Virtually nothing is known of the biochemistry or chemical ecology of the Bethylidae. Because of their important position in phylogenetic studies of the Aculeata and because they share some life history traits with social insects, it seemed that a comparative study of some representative bethylid taxa and their hosts might offer insights into our general understanding of the evolution of cuticular hydrocarbons as physiological mediators of water conservation, barriers to environmental stresses, and as semiochemicals. I have selected two bethylids, one of which is nearly host specific (*Cephalonomia waterstoni* Gahan) and one of which is somewhat more catholic in its host range (*Laelius utilis* Cockerell), and I have characterized the cuticular hydrocarbons of their immature stages and adults. I have also characterized the cuticular hydrocarbons of their larval beetle hosts, *Cryptolestes ferrugineus* (Stephens) and *Trogoderma variabile* Ballion, respectively. Particular attention was given to intra- and interspecific comparative analyses of ontogenetic changes, gender-based differences, and possible physiological and semiochemical roles. Basic life history data on these taxa may be found in publications by Rilett (1949a,b), Finlayson (1950), Mertins (1985), Howard & Flinn (1990), and Partida & Strong (1975).

Materials and Methods

Insects. Cultures of *C. ferrugineus*, *C. waterstoni*, and *T. variabile* were collected from farm-stored wheat in Kansas and have been maintained in my laboratory for at least 1 yr. *L. utilis* was collected from feral populations in the Department of Entomology, University of Wisconsin, Madison, and had been in culture in my laboratory for 3 mo when these experiments began. *C. ferrugineus* was maintained on whole-

wheat flour with 5% brewer's yeast; *T. variabile* was maintained on a 1:1 mixture of whole wheat flour and a diet developed for Indian meal moth (McGaughey & Beeman 1988). Parasites were cultured on last instars (visually estimated to be of the same size) of their respective hosts; newly emerged adults were provided streaks of dilute clover honey as food. Insects were held in an incubator at 30°C, 60% RH, and 16:8 (L:D) photoperiod. Parasitoid immatures to be extracted were gently removed with a fine camel's-hair brush from their larval host shortly before they would have dropped off the host to pupate. Non-parasitized host larvae used were visually estimated to be of the same size as parasitized larvae. Adult parasitoids were at least 24 h old before they were killed for chemical analysis. To obtain enough male *L. utilis* for analysis, female pupae were removed from their cocoons and allowed to emerge as adults in the absence of males. These virgin females were then given *T. variabile* larvae on which to oviposit; accordingly, all their progeny were males.

Chemical Analyses. Insects were killed by freezing at -40°C, and cuticular lipids were extracted by immersing the insects in three successive 1-ml portions of hexane for 1 min each time. The combined portions from each sample were concentrated under a gentle stream of N₂, and hydrocarbons were isolated by chromatography on a 3-cm "minicolumn" of Biosil A (Bio-Rad Laboratories, Richmond, Calif.) as described earlier (Howard et al. 1978).

Mass spectral analyses were conducted using a Hewlett-Packard 5790A GC containing a DB-5 bonded phase capillary column (10 m long, 0.19 mm inside diameter) (J and W Scientific, Folsom, Calif.) connected to a Hewlett-Packard 5970 mass selective detector (MSD) and a Hewlett-Packard 9133 data system. Ultrapure helium was the carrier gas, with a column head pressure of 3.5 kg/cm². Electron impact mass spectra were obtained at 70 eV. Analyses were done using temperature programming, with an initial temperature of 150°C, a final temperature of 320°C, and a program rate of 5°C/min. Signals from the MSD were stored, and peak areas from the total ion trace were used for percentage composition analyses. Retention times of each hydrocarbon component and equivalent chain length (ECL) values were obtained by comparison with known n-alkane standards (Howard et al. 1978). Individual components were identified from their characteristic EI-MS fragmentation patterns (Jackson & Blomquist 1976, Nelson 1978).

Double-bond locations in alkenes were obtained by preparing dithiomethyl (DMS) ethers (Francis & Veland 1981) and examining their electron impact mass spectra. Stereochemistry of the parent alkene was inferred by comparison with the retention time of the DMS ethers of known standards.

Table 1. Cuticular hydrocarbons of larval and adult *C. waterstoni*

| Compound | Equivalent chain length | Mean % composition (SD) | | |
|---------------------------|-------------------------|-------------------------|---------------------|-------------------|
| | | Larvae ^b | Female ^c | Male ^b |
| n-C ₂₁ | 21.00 | 0.3 | ND ^a | ND |
| n-C ₂₃ | 23.00 | 0.4 | 11.4 (5.7) | 7.4 |
| 5-MeC ₂₃ | 23.52 | 0.2 | 10.2 (2.0) | 6.2 |
| 3-MeC ₂₃ | 23.72 | ND | 0.8 (0.1) | ND |
| 5,17-DiMeC ₂₃ | 23.89 | ND | 0.7 (0.3) | 1.1 |
| 5,19-DiMeC ₂₃ | 23.93 | ND | 2.7 (1.0) | 0.7 |
| n-C ₂₄ | 24.00 | 0.1 | 1.3 (0.9) | ND |
| 5-MeC ₂₄ | 24.50 | ND | 1.2 (0.4) | ND |
| 2-MeC ₂₄ | 24.59 | ND | 0.2 (0.1) | ND |
| Z-11-C ₂₅ :1 | 24.69 | ND | 6.0 (1.6) | 15.8 |
| Z-7-C ₂₅ :1 | 24.80 | ND | ND | 3.5 |
| n-C ₂₅ | 25.00 | 1.2 | 12.9 (0.4) | 11.3 |
| 5-MeC ₂₅ | 25.52 | 1.2 | 24.0 (4.4) | 12.0 |
| 3-MeC ₂₅ | 25.74 | 0.8 | 1.8 (0.8) | 1.3 |
| 5,15-DiMeC ₂₅ | 25.85 | ND | 2.5 (0.5) | 1.0 |
| 5,17-DiMeC ₂₅ | 25.91 | ND | 5.2 (0.9) | 6.4 |
| 5,19-DiMeC ₂₅ | 25.95 | ND | 8.9 (0.6) | 8.2 |
| n-C ₂₆ | 26.00 | 1.0 | 1.2 (0.2) | ND |
| Z-11-C ₂₇ :1 | 26.70 | ND | 3.0 (0.5) | 16.9 |
| Z-7-C ₂₇ :1 | 26.81 | ND | ND | 1.0 |
| n-C ₂₇ | 27.00 | 25.8 | 5.0 (1.2) | 4.7 |
| 11/13-MeC ₂₇ | 27.29 | 6.2 | ND | ND |
| 7-MeC ₂₇ | 27.38 | 0.8 | ND | ND |
| 5-MeC ₂₇ | 27.52 | 0.2 | 1.2 (0.2) | 1.0 |
| 11,15-DiMeC ₂₇ | 27.59 | 1.5 | ND | ND |
| 3-MeC ₂₇ | 27.72 | 5.8 | ND | ND |
| n-C ₂₈ | 28.00 | 7.8 | ND | ND |
| Z-11-C ₂₉ :1 | 28.70 | ND | ND | 0.8 |
| n-C ₂₉ | 29.00 | 31.6 | ND | 0.7 |
| 11/13-MeC ₂₉ | 29.31 | 2.0 | ND | ND |
| 3-MeC ₂₉ | 29.73 | 2.7 | ND | ND |
| n-C ₃₀ | 30.00 | 1.8 | ND | ND |
| C ₃₁ :2 | 30.59 | 1.6 | ND | ND |
| C ₃₁ :1 | 30.78 | 2.0 | ND | ND |
| n-C ₃₁ | 31.00 | 3.6 | ND | ND |
| n-C ₃₂ | 32.00 | 0.6 | ND | ND |
| n-C ₃₃ | 33.00 | 0.8 | ND | ND |

^a None detected.^b One replicate of 10 pooled insects.^c Three replicates of 10 insects each.

Statistical Methods. All data were subjected to summary statistics only.

Voucher Specimens. Voucher specimens have been deposited in the Insect Museum of Kansas State University (Manhattan) and the Insect Museum of the University of California (Riverside).

Results

A variety of cuticular hydrocarbons was identified from *C. waterstoni* (Table 1), and there were substantial qualitative and quantitative differences among larvae and male and female adults. Larvae were characterized by n-alkanes (C₂₁-C₃₃), a homologous series of 2-, 3-, 5-, 7-, 11-, and 13-methylalkanes, one dimethylalkane (11,15-dimethylheptacosane), and a C₃₁ monoene and diene. Diagnostic mass spectral ion fragments for these compounds are listed in Table 2.

Substantial ontogenetic changes in cuticular hydrocarbon composition occur when *C. waterstoni* eclose to adults. Both sexes contain the

Table 2. Diagnostic EI-MS ion fragments of the cuticular hydrocarbons of *C. waterstoni*

| Compound | Carbon no. | Ion fragment (m/z) ^a |
|---------------------------|------------|---------------------------------|
| n-C ₂₁ | 21 | 296 |
| n-C ₂₃ | 23 | 324 |
| 5-MeC ₂₃ | 24 | 85, 281, 338 |
| 3-MeC ₂₃ | 24 | 281, 309, 338 |
| 5,17-DiMeC ₂₃ | 25 | 85, 113, 267, 295, 337 |
| 5,19-DiMeC ₂₃ | 25 | 85, 295, 337 |
| n-C ₂₄ | 24 | 338 |
| 5-MeC ₂₄ | 25 | 85, 295, 352 |
| 2-MeC ₂₄ | 25 | 309, 337, 352 |
| Z-11-C ₂₅ :1 | 25 | 350 [201, 243, 444] |
| Z-7-C ₂₅ :1 | 25 | 350 [145, 299, 444] |
| n-C ₂₅ | 25 | 352 |
| 5-MeC ₂₅ | 26 | 85, 309, 366 |
| 3-MeC ₂₅ | 26 | 309, 337, 366 |
| 5,15-DiMeC ₂₅ | 27 | 85, 169, 239, 323, 365 |
| 5,17-DiMeC ₂₅ | 27 | 85, 141, 267, 323, 365 |
| 5,19-DiMeC ₂₅ | 27 | 85, 113, 295, 323, 365 |
| n-C ₂₆ | 26 | 366 |
| Z-11-C ₂₇ :1 | 27 | 378 [201, 271, 472] |
| Z-7-C ₂₇ :1 | 27 | 378 [145, 327, 472] |
| n-C ₂₇ | 27 | 380 |
| 11/13-MeC ₂₇ | 28 | 169, 183, 225, 253, 379 |
| 7-MeC ₂₇ | 28 | 113, 309, 394 |
| 5-MeC ₂₇ | 28 | 85, 337, 394 |
| 11,15-DiMeC ₂₇ | 29 | 169, 197, 239, 267, 393 |
| 3-MeC ₂₇ | 28 | 337, 365, 394 |
| n-C ₂₈ | 28 | 394 |
| Z-11-C ₂₉ :1 | 29 | 406 [201, 299, 500] |
| n-C ₂₉ | 29 | 408 |
| 11/13-MeC ₂₉ | 30 | 169, 197, 253, 281, 407 |
| 3-MeC ₂₉ | 30 | 365, 393, 422 |
| n-C ₃₀ | 30 | 422 |
| C ₃₁ :2 | 31 | 432 |
| C ₃₁ :1 | 31 | 434 |
| n-C ₃₁ | 31 | 436 |
| n-C ₃₂ | 32 | 450 |
| n-C ₃₃ | 33 | 464 |

^a Ion fragment values in brackets are for the DMS derivatives. Alkenes without indicated DMS fragments were too low in abundance to give useful DMS mass spectra.

same major components, but their relative abundances vary somewhat (Table 1), and there are apparent sex-specific qualitative differences in some of the minor components. In addition to n-alkanes (C₂₃-C₂₇), 2-, 3-, and 5-methylalkanes and a homologous series of 5,15-, 5,17-, and 5,19-dimethylalkanes is present in both sexes. Males have a homologous series of Z-11- and Z-7-monoenes, whereas the females appear to contain only the Z-11-monoenes. Furthermore, the monoenes are the major components in the males, whereas the 5-methylalkanes and the 5,X-dimethylalkanes are the major cuticular hydrocarbon components of the females (Table 1). Diagnostic mass spectral ion fragments for all of these compounds are shown in Table 2.

The cuticular hydrocarbons of larval *C. ferrugineus*, the host of *C. waterstoni*, differ in several important ways from those of the parasites. They contain a somewhat more restricted series of n-alkanes (C₂₅-C₃₂), a restricted range of 3-, 5-, 11-, and 13-methylalkanes, no dimethylalkanes,

Table 3. Cuticular hydrocarbons of larval *C. ferrugineus*

| Compound | Equivalent chain length | Mean % composition (SD) ^a |
|------------------------------|-------------------------|--------------------------------------|
| n-C ₂₅ | 25.00 | 1.8 (0.2) |
| n-C ₂₆ | 26.00 | 0.8 (0.2) |
| n-C ₂₇ | 27.00 | 23.6 (1.8) |
| 11-MeC ₂₇ | 27.29 | 0.5 (0.2) |
| 5-MeC ₂₇ | 27.52 | 0.3 (0.1) |
| 3-MeC ₂₇ | 27.72 | 0.3 (0.1) |
| n-C ₂₈ | 28.00 | 2.2 (0.4) |
| Z-9-C ₂₉ :1 | 28.70 | 2.3 (0.5) |
| n-C ₂₉ | 29.00 | 15.6 (1.5) |
| 11/13-MeC ₂₉ | 29.31 | 1.0 (0.2) |
| 5-MeC ₂₉ | 29.50 | 0.4 (0.3) |
| 3-MeC ₂₉ | 29.72 | 0.8 (0.3) |
| Z-8/Z-9-C ₃₀ :1 | 29.78 | 0.3 (0.1) |
| n-C ₃₀ | 30.00 | 0.3 (0.1) |
| C ₃₁ :2 | 30.44 | 0.5 (0.2) |
| Z,Z-8, 22-C ₃₁ :2 | 30.52 | 10.9 (0.8) |
| Z-9-C ₃₁ :1 | 30.78 | 23.7 (1.2) |
| n-C ₃₁ | 31.00 | 3.4 (1.0) |
| 11/13-MeC ₃₁ | 31.30 | 1.9 (0.4) |
| 5-MeC ₃₁ | 31.52 | 0.4 (0.1) |
| 3-MeC ₃₁ | 31.72 | 0.5 (0.2) |
| Z-9-C ₃₂ :1 | 31.77 | 0.3 (0.1) |
| n-C ₃₂ | 32.00 | 0.3 (0.1) |
| C ₃₃ :2 | 32.45 | 0.7 (0.5) |
| Z,Z-9,23-C ₃₃ :2 | 32.55 | 2.9 (1.5) |
| Z-9-C ₃₃ :1 | 32.78 | 3.6 (1.6) |
| Z,Z-9,25-C ₃₅ :2 | 34.55 | 0.5 (0.1) |
| Z-9-C ₃₅ :1 | 34.80 | 0.6 (0.2) |

^a Three replicates of 10 insects each.

a homologous series of Z-8- or Z-9-monoenes (C₂₉:1-C₃₅:1), and a homologous series of dienes whose double bonds are separated by 12 methylene units (C₃₁:2-C₃₅:2) (Table 3, compare with Table 1). Diagnostic mass spectral ion fragments for the *C. ferrugineus* compounds are listed in Table 4.

The cuticular hydrocarbon compositions of the parasitoid *L. utilis* and its dermestid host *T. variabile* differ substantially from those of the *Cephalonomia-Cryptolestes* system. The major hydrocarbons found on *L. utilis* larvae are n-alkanes (C₂₃-C₃₃), 3-, 5-, 13-, and 15-methyl alkanes, and a homologous series of Z-9-monoenes (C₂₃:1-C₂₇:1). No dimethyl alkanes or dienes were present (Table 5). Upon eclosion to pupae, the hydrocarbon profile of *L. utilis* changes somewhat. Although n-alkanes are still prominent (C₂₃-C₃₅), the relative abundance of the monoenes is somewhat greater in pupae than in larvae, and the relative abundance of branched alkanes is somewhat less (Table 5).

Adult *L. utilis* differ even more in their cuticular hydrocarbon profiles from those of immature stages. As with *Cephalonomia* adults, there are both qualitative and quantitative differences between male and female *L. utilis*. The major components in both sexes are a series of n-alkanes (C₂₁-C₃₁), and a homologous series of Z-9-monoenes (C₂₂:1-C₂₇:1). In much lower concentrations is a series of 2-, 3-, 7-, 9-, 11-, and 13-methylalkanes. No dimethylalkanes or dienes

Table 4. Diagnostic EI-MS ion fragments of the cuticular hydrocarbons of *C. ferrugineus*

| Compound | Carbon no. | Ion fragment (m/z) ^a |
|------------------------------|------------|---------------------------------|
| n-C ₂₅ | 25 | 352 |
| n-C ₂₆ | 26 | 366 |
| n-C ₂₇ | 27 | 380 |
| 11-MeC ₂₇ | 28 | 169, 253, 394 |
| 5-MeC ₂₇ | 28 | 85, 337, 394 |
| 3-MeC ₂₇ | 28 | 337, 365, 394 |
| n-C ₂₈ | 28 | 394 |
| Z-9-C ₂₉ :1 | 29 | 406 [173, 327, 500] |
| n-C ₂₉ | 29 | 408 |
| 11/13-MeC ₂₉ | 30 | 169, 197, 253, 281, 407 |
| 5-MeC ₂₉ | 30 | 85, 365, 422 |
| 3-MeC ₂₉ | 30 | 365, 393, 422 |
| Z-8/Z-9-C ₃₀ :1 | 30 | 420 [159, 173, 341, 355, 514] |
| n-C ₃₀ | 30 | 422 |
| C ₃₁ :2 | 31 | 432 |
| Z,Z-8, 22-C ₃₁ :2 | 31 | 432 [159, 173, 353, 413, 620] |
| Z-9-C ₃₁ :1 | 31 | 434 [173, 355, 528] |
| n-C ₃₁ | 31 | 436 |
| 11/13-MeC ₃₁ | 32 | 169, 197, 281, 309, 435 |
| 5-MeC ₃₁ | 32 | 85, 393, 450 |
| 3-MeC ₃₁ | 32 | 393, 421, 450 |
| Z-9-C ₃₂ :1 | 32 | 448 [173, 369, 542] |
| n-C ₃₂ | 32 | 450 |
| C ₃₃ :2 | 33 | 460 |
| Z,Z-9,23-C ₃₃ :2 | 33 | 460 [173, 187, 413, 427, 648] |
| Z-9-C ₃₃ :1 | 33 | 462 [173, 383, 556] |
| Z,Z-9,25-C ₃₅ :2 | 35 | 488 [173, 201, 441, 455, 676] |
| Z-9-C ₃₅ :1 | 35 | 490 [173, 411, 584] |

^a Ion fragment values in brackets are for the DMS derivatives. Dienes without indicated DMS fragments were too low in abundance to give useful DMS mass spectra.

were detected. The most striking difference between the sexes is the relative abundance of the Z-9-C₂₅:1, males having a greater relative proportion of this compound (Table 5). Diagnostic mass spectral ion fragments for all hydrocarbons identified from *L. utilis* immatures and adults are shown in Table 6.

The cuticular hydrocarbon composition of larval *T. variabile* is presented in Table 7. The vast majority of the components present is n-alkanes (C₂₁-C₃₅), the remainder of components being a homologous series of 3-, 5-, and 13-methylalkanes. No dimethylalkanes or any alkenes were detected. Diagnostic mass spectral ion fragments are presented in Table 8.

Table 9 presents a comparison of all taxa and stages according to the classes of hydrocarbons present. For the parasitoids, striking ontogenetic changes in the relative abundance of the different hydrocarbon classes occur from the immature to adult stage, and marked male-female dichotomies exist for adults. Clearly, larval *C. ferrugineus* and *T. variabile* possess markedly different distributions of hydrocarbon classes despite living in similar habitats. Finally, neither immature nor adult parasitoids have hydrocarbon compositions that closely reflect those of their larval hosts.

Table 5. Cuticular hydrocarbons of larval, pupal, and adult *L. utilis*

| Compound | Equivalent chain length | Mean % composition (SD) | | | |
|-------------------------|-------------------------|-------------------------|--------------------|---------------------|-------------------|
| | | Larvae ^b | Pupae ^c | Female ^b | Male ^d |
| n-C ₂₁ | 21.00 | ND ^a | ND | 4.7 (3.7) | 1.7 (1.2) |
| Z-9-C ₂₂ :1 | 21.70 | ND | ND | 0.5 (0.1) | ND |
| n-C ₂₂ | 22.00 | ND | ND | 0.6 (0.1) | 0.3 (0.1) |
| Z-9-C ₂₃ :1 | 22.70 | 1.1 (0.6) | 7.3 | 16.4 (5.2) | 16.8 (5.9) |
| n-C ₂₃ | 23.00 | 4.1 (2.4) | 9.7 | 24.4 (4.3) | 18.8 (3.7) |
| 9/11-MeC ₂₃ | 23.37 | ND | ND | 1.0 (0.1) | 1.3 (1.1) |
| 7-MeC ₂₃ | 23.40 | ND | ND | 0.4 (0.1) | 0.8 (0.7) |
| Z-9-C ₂₄ :1 | 23.73 | ND | ND | 4.4 (1.8) | 4.8 (1.8) |
| 2-MeC ₂₃ | 23.88 | ND | ND | 1.0 (0.5) | ND |
| n-C ₂₄ | 24.00 | 0.9 (0.3) | ND | 1.0 (0.3) | 0.8 (0.3) |
| Z-9-C ₂₅ :1 | 24.75 | 4.6 (0.7) | 18.5 | 29.7 (0.2) | 40.9 (14.3) |
| n-C ₂₅ | 25.00 | 15.2 (1.8) | 11.2 | 11.4 (0.3) | 8.3 (2.9) |
| 13-MeC ₂₅ | 25.25 | 8.9 (2.7) | ND | 0.4 (0.1) | 1.6 (1.2) |
| 5-MeC ₂₅ | 25.53 | 0.7 (0.1) | ND | ND | ND |
| 3-MeC ₂₅ | 25.75 | ND | ND | 0.4 (0.1) | ND |
| n-C ₂₆ | 26.00 | 0.7 (0.2) | 1.5 | 0.3 (0.1) | ND |
| Z-9-C ₂₇ :1 | 26.68 | 0.1 (0.1) | ND | 0.8 (0.2) | 1.0 (0.9) |
| n-C ₂₇ | 27.00 | 17.6 (2.1) | 18.9 | 1.5 (0.5) | 2.1 (0.8) |
| 13-MeC ₂₇ | 27.31 | 4.4 (0.1) | ND | 0.3 (0.1) | 0.1 (0.1) |
| 5-MeC ₂₇ | 27.49 | 1.4 (0.1) | ND | ND | ND |
| 3-MeC ₂₇ | 27.73 | 3.8 (0.1) | ND | ND | ND |
| n-C ₂₈ | 28.00 | 0.7 (0.1) | 1.0 | 0.3 (0.1) | 0.1 (0.1) |
| n-C ₂₉ | 29.00 | 10.9 (3.5) | 17.5 | 0.8 (0.2) | 0.6 (0.4) |
| 13-MeC ₂₉ | 29.31 | 10.9 (1.3) | 1.0 | ND | ND |
| 5-MeC ₂₉ | 29.50 | 2.0 (0.3) | ND | ND | ND |
| 3-MeC ₂₉ | 29.72 | ND | ND | ND | ND |
| n-C ₃₀ | 30.00 | 0.7 (0.1) | ND | ND | ND |
| 13-MeC ₃₀ | 30.29 | ND | ND | ND | ND |
| n-C ₃₁ | 31.00 | 3.3 (0.7) | 6.3 | ND | 0.1 (0.1) |
| 13/15-MeC ₃₁ | 31.28 | 5.1 (0.6) | ND | ND | ND |
| n-C ₃₃ | 33.00 | 1.1 (0.3) | 4.9 | ND | ND |
| 15-MeC ₃₃ | 33.34 | 1.7 (0.1) | ND | ND | ND |
| n-C ₃₅ | 35.00 | ND | 2.4 | ND | ND |

^a None detected.^b Three replicates of 10 insects each.^c One replicate of 10 pooled insects.^d Two replicates of 10 insects each.

Discussion

Although the cuticular hydrocarbons of well over 100 insect species have now been documented (Lockey 1988), including a small number of Hymenoptera (mostly ants), only three parasitoids have been examined. These three are the codling moth parasitoid *Ascogaster quadridentata* Wesmael (Braconidae), its hyperparasitoid *Perilampus fulvicornis* Ashmead (Perilampidae) (both described by Espelie & Brown [1990]), and an *Orasema* sp. (Eucharitidae) inquiline associated with the red imported fire ant, *Solenopsis invicta* Buren, in Brazil (Vander Meer et al. 1989). The *A. quadridentata* hydrocarbon profiles are dominated by n-alkanes ($\approx 40\%$) and monoenes ($\approx 60\%$) of undetermined double-bond location and stereochemistry. No methylbranched alkanes or dienes are found. In contrast, the cuticular hydrocarbons of the hyperparasitoid *P. fulvicornis* are dominated by mono- and dimethylalkanes (≈ 55 and 35% , respectively), very low proportions of n-alkanes ($\approx 6\%$), and female-only monoenes (6%) of unspecified double bond location and stereochemistry. In both

species, only adults were examined. Cuticular hydrocarbons from pupae and adults of the *Orasema* sp. were partially characterized (Vander Meer et al. 1989). As long as the wasps were inside the ant nest, they were found to contain predominately the five major cuticular hydrocarbons characteristic of *S. invicta* (Nelson et al. 1980). However, adults captured outside the ant nest contained a complex mixture of hydrocarbons of both lower and higher carbon number than those of the ants and only low quantities of the ant hydrocarbons. The chemistry of these free wasps was not reported.

Neither the qualitative nor quantitative hydrocarbon chemistry of the two bethylids examined in this study (Tables 1, 5, and 9) match closely the results reported for the parasites above. This is not unexpected, given that the taxa involved cover three superfamilies and distinctly different ecological niches. Some commonalities do exist, however. Most striking is the distinct ontogenetic changes in hydrocarbon composition from the immature to adult stages and the marked differences in hydrocarbon compositions be-

Table 6. Diagnostic EI-MS ion fragments of the cuticular hydrocarbons of *L. utilis*

| Compound | Carbon no. | Ion fragment (m/z) ^a |
|-------------------------|------------|---------------------------------|
| n-C ₂₁ | 21 | 296 |
| Z-9-C ₂₂ :1 | 22 | 308 [173, 229, 402] |
| n-C ₂₂ | 22 | 310 |
| Z-9-C ₂₃ :1 | 23 | 322 [173, 243, 416] |
| n-C ₂₃ | 23 | 324 |
| 9/11-MeC ₂₃ | 24 | 141, 169, 197, 225, 338 |
| 7-MeC ₂₃ | 24 | 127, 253, 338 |
| Z-9-C ₂₄ :1 | 24 | 336, [173, 257, 430] |
| 2-MeC ₂₃ | 24 | 295, 323, 338 |
| n-C ₂₄ | 24 | 338 |
| Z-9-C ₂₅ | 25 | 350 [173, 271, 444] |
| n-C ₂₅ | 25 | 352 |
| 13-MeC ₂₅ | 26 | 197, 366 |
| 5-MeC ₂₅ | 26 | 85, 309, 366 |
| 3-MeC ₂₅ | 26 | 309, 337, 366 |
| n-C ₂₆ | 26 | 366 |
| Z-9-C ₂₇ :1 | 27 | 378 [173, 299, 472] |
| n-C ₂₇ | 27 | 380 |
| 13-MeC ₂₇ | 28 | 183, 225, 394 |
| 5-MeC ₂₇ | 28 | 85, 337, 394 |
| 3-MeC ₂₇ | 28 | 337, 365, 394 |
| n-C ₂₈ | 28 | 394 |
| n-C ₂₉ | 29 | 408 |
| 13-MeC ₂₉ | 30 | 197, 253, 422 |
| 5-MeC ₂₉ | 30 | 85, 365, 422 |
| 3-MeC ₂₉ | 30 | 365, 393, 422 |
| n-C ₃₀ | 30 | 422 |
| 13-MeC ₃₀ | 31 | 197, 267, 436 |
| n-C ₃₁ | 31 | 436 |
| 13/15-MeC ₃₁ | 32 | 197, 225, 253, 281, 450 |
| n-C ₃₃ | 33 | 464 |
| 15-MeC ₃₃ | 34 | 225, 281, 478 |
| n-C ₃₅ | 35 | 492 |

^a Ion fragment values in brackets are for the DMS derivatives.

tween adult males and females. In *C. waterstoni*, the larval phenotype is dominated by n-alkanes, whereas the adult phenotype is dominated by mono- and dimethylalkanes and monoenes. Furthermore, the larval and adult stages have completely different dimethylalkanes. In *L. utilis*, the larval phenotype is dominated by n- and monomethylalkanes, with only a low proportion of alkenes. The pupal phenotype is dominated by n-alkanes and alkenes, with an almost complete shutoff of monomethylalkanes, whereas the adult *L. utilis* phenotype is heavily dominated by alkenes, a low proportion of monomethylalkanes, and a moderate proportion of n-alkanes (Table 9). Unlike *C. waterstoni*, however, ontogenetic changes in *L. utilis* did not involve production of new compounds, but rather the shutdown of some components and maintenance of others. Inasmuch as no detailed chemistry was reported for adult *Oreasema* sp. (Vander Meer et al. 1989), it is not directly possible to compare the ontogenetic changes in that species with the two bethylids. It is clear from the gas chromatographic traces presented by Vander Meer et al. (1989) that major changes did indeed occur from the pupal to adult transformation and that they

Table 7. Cuticular hydrocarbons of larval *T. variabilis*

| Compound | Equivalent chain length | Mean % composition (SD) ^a |
|----------------------|-------------------------|--------------------------------------|
| n-C ₂₁ | 21.00 | 0.1 (0.1) |
| n-C ₂₂ | 22.00 | 0.2 (0.1) |
| n-C ₂₃ | 23.00 | 0.3 (0.1) |
| n-C ₂₄ | 24.00 | 0.2 (0.1) |
| n-C ₂₅ | 25.00 | 2.8 (0.5) |
| 13-MeC ₂₅ | 25.33 | 1.3 (0.1) |
| n-C ₂₆ | 26.00 | 1.0 (0.1) |
| 13Me-C ₂₆ | 26.33 | 0.1 (0.1) |
| n-C ₂₇ | 27.00 | 24.2 (3.0) |
| 13-MeC ₂₇ | 27.33 | 0.7 (0.1) |
| 5-MeC ₂₇ | 27.52 | 0.2 (0.1) |
| 3-MeC ₂₇ | 27.73 | 0.8 (0.2) |
| n-C ₂₈ | 28.00 | 2.2 (0.3) |
| n-C ₂₉ | 29.00 | 26.7 (1.8) |
| 13-MeC ₂₉ | 29.30 | 1.9 (0.3) |
| 5-MeC ₂₉ | 29.55 | 0.4 (0.1) |
| 3-MeC ₂₉ | 29.74 | 0.4 (0.1) |
| n-C ₃₀ | 30.00 | 3.3 (0.5) |
| n-C ₃₁ | 31.00 | 24.2 (1.6) |
| 13-MeC ₃₁ | 31.40 | 0.9 (0.2) |
| 5-MeC ₃₁ | 31.53 | 0.1 (0.1) |
| 3-MeC ₃₁ | 31.74 | 0.2 (0.1) |
| n-C ₃₂ | 32.00 | 1.4 (0.2) |
| n-C ₃₃ | 33.00 | 6.0 (1.6) |
| 15-MeC ₃₃ | 33.35 | 0.2 (0.1) |
| n-C ₃₄ | 34.00 | 0.1 (0.1) |
| n-C ₃₅ | 35.00 | 0.2 (0.1) |

^a Three replicates of 10 insects each.

probably involved both qualitative and quantitative aspects.

A comparison of both the qualitative and quantitative compositions of the hydrocarbons from adult males and females of both bethylids and

Table 8. Diagnostic EI-MS ion fragments of the cuticular hydrocarbons of *T. variabilis*

| Compound | Carbon no. | Ion fragment (m/z) |
|-------------------------|------------|-------------------------|
| n-C ₂₁ | 21 | 296 |
| n-C ₂₂ | 22 | 310 |
| n-C ₂₃ | 23 | 324 |
| n-C ₂₄ | 24 | 338 |
| n-C ₂₅ | 25 | 352 |
| 13-MeC ₂₅ | 26 | 197, 366 |
| n-C ₂₆ | 26 | 366 |
| 13Me-C ₂₆ | 27 | 197, 211, 380 |
| n-C ₂₇ | 27 | 380 |
| 13-MeC ₂₇ | 28 | 183, 225, 394 |
| 5-MeC ₂₇ | 28 | 85, 337, 394 |
| 3-MeC ₂₇ | 28 | 337, 365, 394 |
| n-C ₂₈ | 28 | 394 |
| n-C ₂₉ | 29 | 408 |
| 13-MeC ₂₉ | 30 | 197, 253, 422 |
| 5-MeC ₂₉ | 30 | 85, 365, 422 |
| 3-MeC ₂₉ | 30 | 365, 393, 422 |
| n-C ₃₀ | 30 | 422 |
| n-C ₃₁ | 31 | 436 |
| 13/15-MeC ₃₁ | 32 | 197, 225, 253, 281, 450 |
| 5-MeC ₃₁ | 32 | 85, 393, 450 |
| 3-MeC ₃₁ | 32 | 393, 421, 450 |
| n-C ₃₂ | 32 | 450 |
| n-C ₃₃ | 33 | 464 |
| 15-MeC ₃₃ | 34 | 225, 281, 478 |
| n-C ₃₄ | 34 | 478 |
| n-C ₃₅ | 35 | 492 |

Table 9. Comparison of percentage hydrocarbon composition by hydrocarbon class for *C. waterstoni*, *L. utilis*, *C. ferrugineus*, and *T. variabile*

| Stage | % Composition | | | | |
|--------|-----------------------|--------------------|------------------|----------|--------|
| | n-Alkanes | Monomethyl-alkanes | Dimethyl-alkanes | Monoenes | Dienes |
| | <i>C. waterstoni</i> | | | | |
| Larva | 75.0 | 19.9 | 1.5 | 2.0 | 1.6 |
| Female | 31.8 | 39.4 | 20.0 | 8.8 | 0 |
| Males | 24.1 | 20.5 | 17.4 | 38.0 | 0 |
| | <i>L. utilis</i> | | | | |
| Larva | 55.2 | 38.9 | 0 | 5.9 | 0 |
| Pupa | 73.4 | 1.0 | 0 | 25.6 | 0 |
| Female | 45.0 | 3.5 | 0 | 51.5 | 0 |
| Male | 32.8 | 3.8 | 0 | 63.4 | 0 |
| | <i>C. ferrugineus</i> | | | | |
| Larva | 48.0 | 6.1 | 0 | 30.8 | 15.1 |
| | <i>T. variabile</i> | | | | |
| Larva | 92.9 | 7.1 | 0 | 0 | 0 |

A. quadridentata, *P. fulvicornis*, and the *Oraesema* sp. suggests that there are sex-specific hydrocarbon profiles in these species. Such differences are most striking in *C. waterstoni* and *P. fulvicornis* but are also present in the other two species. Although there are no behavioral data for any of these species to assert unequivocally that these differences reflect the usage of some of these hydrocarbons as sex pheromones or cues for gender recognition, it is not an unreasonable hypothesis. At least in the bethylids, males usually emerge from their adjacent cocoons shortly before females and often chew holes through the silk cocoons of females to assist in their emergence, then immediately copulate with their sisters (Evans 1964, Gordh & Móczár 1990). Two questions immediately come to mind. How does the male know which cocoons have females in them, and, under the circumstances, why would a female need a sex pheromone? Although cuticular hydrocarbons are not highly volatile, they would have enough vapor pressure either to contaminate the silk of cocoons or to be perceived through the cocoon. Indeed, extraction of the *C. waterstoni* cocoon silk with hexane and examination by GC-mass spectrometry reveals the presence of low but measurable quantities of the wasp hydrocarbons (unpublished data). Certainly, adequate precedent exists for cuticular hydrocarbons serving as close-range sex pheromones or gender recognition cues (or both) in the Diptera (Howard & Blomquist 1982). Alternatively, where the gender-based difference in hydrocarbon composition is such that the male seems to have the unique compounds (such as in *L. utilis*), one might postulate that the hydrocarbon cues are being used by the female to assess that a male of the correct species rather than some hyperparasite or predator is opening her cocoon. Although bethylids in general are associated with sib mating (Clausen 1940), the females are long-lived, have limited sperm storage

capacity, and may mate with males other than their brothers or sons. Therefore, a convincing argument could be made for cuticular hydrocarbons serving as either sex pheromones or as cues for sex and species recognition. The possibility that other chemical or aural cues are important is of course recognized. A test of this hypothesis has yet to be carried out.

As noted, bethylids are gregarious ectoparasitoids and, by definition, complete their larval development using the resources of a single host (Clausen 1940). In fact, however, their trophic ecology is not so different from some obligate predators such as syrphid flies in the genus *Microdon* whose larvae use a single food resource, the ant brood of their host (Stanley-Samuelson et al. 1990). In two *Microdon*-ant associations, the larval flies have cuticular hydrocarbon compositions identical to those of the larval ants, and the flies biosynthesize these hydrocarbons themselves rather than procuring them from the ants via either ingestion or mechanical transfer (Howard et al. 1990a, b). Other workers have shown that, to a limited extent, dietary hydrocarbons can be directly used as cuticular hydrocarbons (Howard & Blomquist 1982), but these are generally only the n-alkanes. However, Thompson & Barlow (1974, 1983) have shown that a variety of parasitic Hymenoptera, including ectoparasitoids, have whole-body fatty acid compositions that exactly mimic the host on which they are reared; successive generations of parasites reared on different hosts always adopt the fatty acid profile of the current host. Inasmuch as cuticular hydrocarbons are biosynthesized from fatty acids (albeit from different enzyme complexes from those which metabolize most of the energy reserve and membrane structural fatty acids) (Howard & Blomquist 1982, Lockey 1988), and inasmuch as at least one ectoparasitoid (*Oraesema* sp.) (Vander Meer et al. 1989) has been reported to have identical cuticular hydrocar-

bons as its host, I thought it important to compare the cuticular hydrocarbons of *C. waterstoni* and *L. utilis* with those of their hosts.

As even a cursory examination will show, hydrocarbon profiles of the larval bethylid parasitoids show little resemblance to those of the hosts on which they are reared (Tables 1, 3, 5, 7, and 9). The hydrocarbons of larval *C. ferrugineus* are dominated by n-alkanes, Z-8- and Z-9-monoenes, and an extensive series of dienes with the double bonds widely separated. The n-alkanes and monoenes are common to most insects (Lockey 1988), but the dienes are somewhat more unusual. However, similar dienes have been reported from *Drosophila* spp. (Diptera) (Jackson & Bartelt 1986), a sawfly (Hymenoptera) (Bartelt et al. 1984), and *Sitophilus* spp. (Coleoptera) (Nelson et al. 1984). As Table 1 indicates, larval *C. waterstoni* have no olefins, with the exception of low quantities of a C₃₁:1 and C₃₁:2, to which I was unable to assign double-bond locations. The ECL values of these two compounds, however, are identical to those of corresponding compounds in larval *C. ferrugineus*. It is possible that these compounds in the parasite sample arose as surface contamination from the beetle host in the course of my transferring wasp larvae from the host.

The cuticular hydrocarbon profile of larval *T. variabile* is even more strikingly different from its parasitoid *L. utilis* than is the case for the *Cephalonomia-Cryptolestes* system. This beetle has mostly n-alkanes (93%), with a small proportion (7%) of 3-, 5-, and 13-methylalkanes, and no other hydrocarbons. This may be contrasted with the larvae of two other dermestids, *Trogoderma granarium* Everts, which has n-alkanes, n-alkenes, and 2- and 3-methylalkanes (Malinski et al. 1986); and *Attagenus megatoma* (F.), which has n-alkanes, n-alkenes, 2-, 3-, and internal methyl-branched alkanes (Baker 1978).

The striking disparity between the cuticular hydrocarbons of the two bethylids and their two hosts clearly argues against the wasps simply transferring ingested host hydrocarbons onto their own cuticle. These findings, especially for host-specific *Cephalonomia*, also add to the circumstantial evidence suggesting that chemical mimicry of cuticular hydrocarbon composition in inquiline-host relationships is the result of co-evolution rather than simply happenstance (Howard et al. 1980, Stowe 1988, Howard et al. 1990a).

To the extent that cuticular hydrocarbons are a phenotypic response to needs for water conservation and protection from abrasion and invasion by microorganisms (Jackson & Blomquist 1976, Hadley 1981, Howard & Blomquist 1982), one might anticipate that, because the two bethylids and their hosts examined in this study all live in similar habitats, these parasites and their hosts might have fairly similar distributions of hydro-

carbon classes. Clearly this is not so (Table 9). These differences do not appear to be readily explainable by, for example, body size (volume), because the two insects with the greatest proportion of n-alkanes, larvae of *C. waterstoni* and *T. variabile* (75 and 92.9%, respectively), differ in bulk by at least 100-fold. One might argue that the parasitoid can use such a high proportion of n-alkanes (which are normally associated with relatively humid environments) because it is in essence feeding on a nearly liquid diet, but *T. variabile* larvae are feeding on an extremely dry diet that requires them to satisfy much of their water requirements from metabolism. Nor do the hydrocarbon compositions appear to be governed by life stage, because the two larval parasites differ from each other as well as from their host larvae. Similarly, adults of the two parasite species show striking differences in class composition (Table 9). Adults of neither species of parasitoid are known to seek out free water. They do engage in blood feeding from the wounds produced by their stings, but this is more likely for protein than for water. Given the disparities among these four taxa in proportions of n-alkanes to monomethyl- and dimethylalkanes, and to monoenes and dienes, the data strongly suggest that, for them, factors other than cuticular hydrocarbon composition are the primary mediators of cuticular permeability to water (Hadley 1981, 1984; Toolson et al. 1990).

Acknowledgment

I thank C. A. McDaniel (USDA-Forest Service, Gulfport, Miss.), E. Toolson (University of New Mexico, Albuquerque), and L. Seitz (USDA-ARS, Manhattan, Kans.) for their constructive comments on an earlier draft of this manuscript. I also thank S. Krauth (University of Wisconsin, Madison) and G. Gordh (University of California, Riverside) for confirming the identifications of *C. waterstoni* and *L. utilis*, respectively.

References Cited

- Baker, J. E. 1978. Cuticular lipids of larvae of *Attagenus megatoma*. *Insect Biochem.* 8: 287-292.
- Bartelt, R. J., T. P. Krick & R. L. Jones. 1984. Cuticular hydrocarbons of the yellowheaded spruce sawfly, *Pikonema alaskensis*. *Insect Biochem.* 14: 209-213.
- Casale, A. 1991. Some notes on the parental and parasocial behaviour of *Sclerodermus domesticus* Latreille (Hymenoptera Bethylidae). *Ethol. Ecol. Evol.* (special issue) 1: 35-38.
- Clausen, C. P. 1940. *Entomophagous insects*, McGraw-Hill, New York.
- Espelie, K. E. & J. J. Brown. 1990. Cuticular hydrocarbons of species which interact on four trophic levels: apple, *Malus pumila* Mill.; codling moth, *Cydia pomonella* L.; a hymenopteran parasitoid, *Ascogaster quadridentata* Wesmæel; and a hyperparasite, *Perilampus fulvicornis* Ashmead. *Comp. Biochem. Physiol. B Comp. Biochem.* 95: 131-136.

- Evans, H. E. 1964. A synopsis of the American Bethyridae (Hymenoptera, Aculeata). Bulletin 132, Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
- Finlayson, L. H. 1950. The biology of *Cephalonomia waterstoni* Gahan (Hym., Bethyridae), a parasite of *Laemophloeus* (Col., Cucujidae). Bull. Entomol. Res. 41: 79-97.
- Francis, G. W. & K. Veland. 1981. Alkylthiolation for the determination of double-bond positions in linear alkenes. J. Chromatogr. 219: 379-384.
- Gordh, G. & L. Móczár. 1990. A catalogue of the world Bethyridae (Hymenoptera: Aculeata), Memoirs of the American Entomological Institute 46, American Entomological Institute, Gainesville, Fla.
- Hadley, N. F. 1981. Cuticular lipids of terrestrial plants and arthropods: a comparison of their structure, composition, and waterproofing function. Biol. Rev. 56: 23-47.
1984. Cuticle: ecological significance, pp. 685-693. In J. Bereiter-Haha, A. G. Matoltsy & K. S. Richards [eds.], Biology of the integument. Vol. 1, Invertebrates. Springer, Heidelberg.
- Howard, R. W. & G. J. Blomquist. 1982. Chemical ecology and biochemistry of insect hydrocarbons. Annu. Rev. Entomol. 27: 149-172.
- Howard, R. W. & P. W. Flinn. 1990. Larval trails of *Cryptolestes ferrugineus* (Coleoptera: Cucujidae) as kairomonal host-finding cues for the parasitoid *Cephalonomia waterstoni* (Hymenoptera: Bethyridae). Ann. Entomol. Soc. Am. 83: 239-245.
- Howard, R. W., C. A. McDaniel & G. J. Blomquist. 1978. Cuticular hydrocarbons of the eastern subterranean termite, *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae). J. Chem. Ecol. 4: 233-245.
1980. Chemical mimicry as an integrating mechanism: cuticular hydrocarbons of a termitophile and its host. Science 210: 431-433.
- Howard, R. W., R. D. Akre & W. B. Garnett. 1990a. Chemical mimicry in an obligate predator of carpenter ants (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am. 83: 607-617.
- Howard, R. W., D. W. Stanley-Samuels & R. D. Akre. 1990b. Biosynthesis and chemical mimicry of cuticular hydrocarbons from the obligate predator, *Microdon albicomatus* Novak (Diptera: Syrphidae) and its ant prey, *Myrmica incompleta* Provancher (Hymenoptera: Formicidae). J. Kans. Entomol. Soc. 63: 437-443.
- Jackson, L. L. & R. J. Bartelt. 1986. Cuticular hydrocarbons of *Drosophila virilis*: comparison by age and sex. Insect Biochem. 16: 433-439.
- Jackson, L. L. & G. J. Blomquist. 1976. Insect waxes, pp. 201-233. In P. E. Kolattukudy [ed.], Chemistry and biochemistry of natural waxes. Elsevier, Amsterdam.
- Lockey, K. H. 1988. Lipids of the insect cuticle: origin, composition and function. Comp. Biochem. Physiol. B. Comp. Biochem. 89: 595-645.
- Malinski, E., E. Hebanowska, J. Szafranek & J. Nawrott. 1986. The composition of the hydrocarbons of the larvae of the Khapra beetles, *Trogoderma granarium*. Comp. Biochem. Physiol. B. Comp. Biochem. 84: 211-215.
- McGaughey, W. H. & R. W. Beeman. 1988. Resistance to *Bacillus thuringiensis* in colonies of Indian meal moth and almond moth (Lepidoptera: Pyralidae). J. Econ. Entomol. 81: 28-33.
- Mertins, J. W. 1985. *Laelius utilis* [Hym.: Bethyridae], a parasitoid of *Anthrenus fuscus* [Col.: Dermestidae]. Entomophaga 30: 65-68.
- Nelson, D. R. 1978. Long-chain methyl-branched hydrocarbons: occurrence, biosynthesis and function. Adv. Insect Physiol. 13: 1-33.
- Nelson, D. R., C. L. Fatland, R. W. Howard, C. A. McDaniel & G. J. Blomquist. 1980. Re-analysis of the cuticular methylalkanes of *Solenopsis invicta* and *S. richteri*. Insect Biochem. 10: 409-418.
- Nelson, D. R., C. L. Fatland & J. E. Baker. 1984. Mass spectral analysis of epicuticular n-alkadienes in three *Sitophilus* weevils. Insect Biochem. 14: 435-444.
- Partida, G. J. & R. G. Strong. 1975. Comparative studies on the biologies of six species of *Trogoderma*: *T. variabile*. Ann. Entomol. Soc. Am. 68: 115-125.
- Rilett, R. O. 1949a. The biology of *Cephalonomia waterstoni* Gahan. Can. J. Res. Sect. D Zool. Sci. 27: 93-111.
- 1949b. The biology of *Laemophloeus ferrugineus* (Steph.). Can. J. Res. 27D: 112-148.
- Stanley-Samuels, D. W., R. W. Howard & R. D. Akre. 1990. Nutritional interactions revealed by tissue fatty acid profiles of an obligate myrmecophilous predator, *Microdon albicomatus*, and its prey, *Myrmica incompleta* (Diptera: Syrphidae) (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am. 83: 1108-1115.
- Stowe, M. K. 1988. Chemical mimicry, pp. 513-580. In K. C. Spencer [ed.], Chemical mediation of evolution. Academic, New York.
- Thompson, S. N. & J. S. Barlow. 1974. The fatty acid composition of parasitic Hymenoptera and its possible biological significance. Ann. Entomol. Soc. Am. 67: 627-632.
1983. Metabolic determination and regulation of fatty acid composition of parasitic Hymenoptera and other animals, pp. 73-106. In T. E. Mittler & R. H. Dadd [eds.], Metabolic aspects of lipid nutrition in insects. Westview, Boulder, Colo.
- Toolson, E. C., T. A. Markow, L. L. Jackson & R. W. Howard. 1990. Epicuticular hydrocarbon composition of wild and laboratory-reared *Drosophila mojavensis* Patterson and Crow (Diptera: Drosophilidae). Ann. Entomol. Soc. Am. 83: 1165-1176.
- Vander Meer, R. K., D. P. Jouvenaz & D. P. Wojcik. 1989. Chemical mimicry in a parasitoid (Hymenoptera: Eucharitidae) of fire ants (Hymenoptera: Formicidae). J. Chem. Ecol. 15: 2247-2261.

Received for publication 9 October 1991; accepted 9 December 1991.