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STRUCTURAL CORRELATION BETWEEN CUTICULAR HYDROCARBONS AND FEMALE CONTACT SEX PHEROMONE OF GERMAN COCKROACH *Blattella germanica* (L.)

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Abstract—The structural relationships between the cuticular hydrocarbons and the contact sex pheromone of the female German cockroach, *Blattella germanica*, were investigated. Cuticular hexane extracts were separated into hydrocarbon and ketone fractions by TLC or silicic acid column chromatography. The ketone fraction (which contains the major contact sex pheromone component) was analyzed by GC-MS before and after reduction to hydrocarbon. In addition to 3,11-dimethyl-2-nonacosanone, 3,11-dimethyl-2-heptacosanone was also identified. Females have the 3,11- and 3,9-dimethyl C_{27} and C_{29} alkanes, but only the 3,11- isomer of the dimethylketones. In addition to the hydrocarbon components previously reported, a number of new components were characterized. Although the ratios of cuticular hydrocarbons differ among nymphs, adult males, and adult females, they have qualitatively identical hydrocarbon profiles, suggesting that the production of the contact sex pheromone results from the sex-specific oxidation of 3,11-dimethylalkanes to pheromone components by the female.

Key Words—Contact sex pheromone, cuticular hydrocarbons, 3,11-dimethyl-2-nonacosanone, 3,11-dimethyl-2-heptacosanone, German cockroach, *Blattella germanica*, Orthoptera, Blattellidae.

INTRODUCTION

The cuticular lipids of insects play a major role in protecting against desiccation and, in some cases, are involved in inter- and intraspecies chemical communication (Howard and Blomquist, 1982; Blomquist et al., 1987). Many components that function in chemical communication serve as short-range or contact pheromones because of their relatively high molecular weights and low vapor pressures.

The contact sex pheromone of the German cockroach, *Blattella germanica*, is present in cuticular extracts of adult females. This pheromone elicits in males a wing-raising courtship behavior that precedes copulation (Roth and Willis, 1952). The major component of the pheromone is 3,11-dimethyl-2-nonacosanone, with lesser amounts of 29-hydroxy-3,11-dimethyl-2-nonacosanone and 29-oxo-3,11-dimethyl-2-nonacosanone also reported (Nishida and Fukami, 1983). All three compounds independently stimulate males, resulting in a complete courtship response.

The major cuticular hydrocarbons of the German cockroach have been identified as homologous series of straight chain and methyl branched heptacosanes and nonacosanes (Augustynowicz et al., 1987). Since isomers of dimethylheptacosane and dimethylnonacosane were present in the cuticular hydrocarbons, we examined the methyl ketone pheromone fraction to determine if similar isomers and homologs were also present in this fraction. We report that in addition to 3,11-dimethyl-2-nonacosanone, 3,11-dimethyl-2-heptacosanone is also present. In addition to the hydrocarbon components previously reported (Augustynowicz et al., 1987), we report the structure of a number of other hydrocarbons on the surface of the German cockroach.

METHODS AND MATERIALS

Insects. Cockroaches were reared in 2-liter glass jars and fed Purina dog chow and water ad libitum. They were kept at 27°C with a 12:12 light–dark cycle. Males and females were separated on the day of adult emergence and 15-day-old insects were utilized.

Separation of Hydrocarbons and Pheromone. Insects were extracted by immersion in hexane for 10 min followed by two 1-ml hexane washes or were extracted by two 5-min hexane washes. The hexane extracts were combined and the solvent removed under a stream of nitrogen. Internal standards, hexacosane and 14-heptacosanone, were included during extraction to allow quantitation of hydrocarbons and ketones, respectively. Hydrocarbons and pheromone were separated by thin-layer chromatography (TLC) on silica gel type H, developed in hexane–diethyl ether (90:10 v/v) and the bands corresponding to hydrocarbons and the methyl ketone fraction scraped into test tubes

and extracted with diethyl ether. Alternatively, hexane extracts from individual insects were separated on Biosil A mini-columns (Howard et al., 1978).

Gas Chromatography and Gas Chromatography–Mass Spectrometry. Hydrocarbons and the ketone fraction were analyzed by gas chromatography (GC) with a flame ionization detector on both packed and capillary columns. Separations on packed columns utilized a 1.8-m × 3.2-mm-ID glass column packed with Dexsil 300 on Supelcoport, temperature programmed from 200°C to 310°C at 5°C/min. Separations on capillary columns utilized a 60-m × 0.32-mm-ID DB-1 column or a 15-m × 0.53-mm-ID SPB-1 column temperature programmed from 80°C to 270°C at 20°C/min and then to 320°C at 3°C/min. Splitless injection was used on both capillary columns.

Gas chromatography–mass spectrometry (GC-MS) was performed on a Finnigan 4123 using an INCOS data system. Material was separated on a 30-m × 0.72-mm capillary column temperature programmed from 200°C to 260°C at 2°C/min. A Finnigan 8200 high-resolution magnetic MS using a SS300 data system was also used. Material was separated on a 60-m × 0.32-mm DB-1 capillary column with on-column injection.

Reduction of Methyl Ketone. The methyl ketone pheromone components were reduced by a modified Wolff-Kishner reaction (Huang-Minlon, 1946). The methyl ketone fraction (approx. 0.8–1.2 mg) was dissolved in 2 ml of diethylene glycol (DEG) to which 840 μg NaOH in aqueous solution, 1.2 μl hydrazine hydrate, and 1.0 mg 2-nonadecanone were added. The C-19 methyl ketone was added because preliminary studies indicated that the amount of pheromone was below the critical mass of the reaction conditions. The system was refluxed with a water-cooled condenser for 2 hr to allow formation of the hydrazone intermediate. The water was disconnected from the condenser and the reaction mixture gradually warmed to approximately 200°C, a temperature sufficient to evaporate the water and reflux DEG. After formation of crystalline material in the condenser, indicative of the presence of hydrocarbon, water was reconnected to the condenser, and the reaction refluxed for 4 hr more to decompose the hydrazone to hydrocarbon. The reaction mixture was then extracted three times with hexane and the reduced pheromone components purified on a 6-cm × 0.5-mm Biosil A column by eluting with hexane. The hexane fraction was analyzed by GLC and found to contain the reduction products of the principal pheromone components. These were analyzed by GC-MS.

RESULTS

A chromatogram of the cuticular hydrocarbons from adult females separated by capillary GC is presented in Figure 1. The 15 principal hydrocarbon components have been identified previously by Augustynowicz et al. (1987) and are homologous series of heptacosanes and nonacosanes. We have now

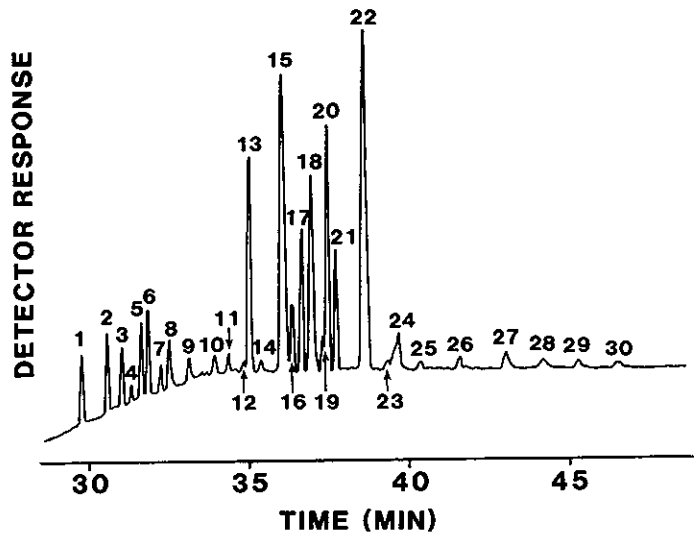

FIG. 1. A capillary column GC trace of the cuticular hydrocarbons from 15-day-old virgin German cockroach females. Peaks are numbered according to the components identified in Table 1.

identified a number of minor components, additional isomers of the major components, and the unknown dimethylalkanes not determined previously (Augustynowicz et al., 1987).

The previously unidentified dimethylheptacosane (peak 4, Figure 1) has the methyl groups in the 11,15- positions with diagnostic ion fragments at *m/z* 168/169, 196/197, 239, and 267. The fragments containing a single methyl branch have an odd-to-even ratio of about 1 and the fragments that contain a second methyl branch have a higher ratio of odd-to-even mass units. In each spectrum referred to here, if the odd-to-even ratio were near 1, both fragments are listed, whereas if the odd-numbered fragments clearly dominate, only one mass number is listed. The previously unidentified dimethylnonacosane (peak 21, Figure 1) is a mixture of 5,9- and 5,11- isomers with diagnostic ion fragments at *m/z* 84/85, 155, 308/309, 183, 280/281, and 379. In addition to 13,17-dimethylnonacosane, this GC peak (peak 18, Figure 1) also has an isomer with methyl groups in the 11,15- positions (*m/z* 168/169, 224/225, 239, and 295). We have also identified additional isomers in the dimethylheptacosane series. In addition to 5,11-dimethylheptacosane, the 5,9- isomer is also present [*m/z* 351 $(M-57)^+$, 155, 280/281] (peak 6, Figure 1) and in addition to 3,11-dimethylheptacosane, the 3,9- isomer is also present [*m/z* 379 $(M-29)^+$, 155, 280/

TABLE 1. PERCENT COMPOSITIONS OF CUTICULAR HYDROCARBONS FROM LAST INSTAR NYMPHS AND ADULT MALE AND FEMALE *Blattella germanica*

	Percent composition			
	Adult		Last instar	
	Male	Female	Male	Female
1. *n*-Heptacosane	1.8 ± 0.2	2.1 ± 0.3	1.7 ± 0.2	3.7 ± 0.4
2. 11- and 13-Methylheptacosane	4.6 ± 0.3	2.6 ± 0.3	3.1 ± 0.3	4.4 ± 0.3
3. 5-Methylheptacosane	2.5 ± 0.2	1.8 ± 0.1	3.4 ± 0.3	3.9 ± 0.3
4. 11,15-Dimethylheptacosane	0.6 ± 0.1	0.8 ± 0.2	0.7 ± 0.2	1.0 ± 0.2
5. 3-Methylheptacosane	2.9 ± 0.1	2.7 ± 0.2	3.2 ± 0.5	3.7 ± 0.3
6. 5,9- and 5,11-Dimethylheptacosane	1.4 ± 0.3	1.7 ± 0.2	3.7 ± 0.4	4.3 ± 0.1
7. *n*-Octacosane	0.8 ± 0.1	1.4 ± 0.2	1.3 ± 0.4	1.5 ± 0.4
8. 3,11- and 3,9-Dimethylheptacosane	1.4 ± 0.3	1.9 ± 0.2	4.9 ± 0.5	5.4 ± 0.2
9. 12- and 14-Methyloctacosane	2.0 ± 0.2	2.0 ± 0.3	2.7 ± 0.7	1.9 ± 0.4
10. 2-Methyloctacosane	1.2 ± 0.2	1.3 ± 0.2	1.6 ± 0.5	1.5 ± 0.3
11. 4-Methyloctacosane	1.2 ± 0.2	1.0 ± 0.2	1.5 ± 0.7	1.5 ± 0.5
12. Unknown	0.5 ± 0.1	0.4 ± 0.1	1.1 ± 0.4	1.1 ± 0.2
13. *n*-Nonacosane	6.0 ± 0.3	7.4 ± 0.2	5.8 ± 0.5	8.0 ± 0.6
14. Unknown	1.0 ± 0.2	0.5 ± 0.1	1.5 ± 0.5	1.2 ± 0.5
15. 9-, 11-, 13-, and 15-Methylnonacosane	22.7 ± 0.6	14.5 ± 0.2	16.3 ± 3.3	11.2 ± 0.3
16. 7-Methylnonacosane	3.3 ± 0.1	2.5 ± 0.1	2.9 ± 0.3	3.0 ± 0.1
17. 5-Methylnonacosane	6.2 ± 0.2	5.5 ± 0.2	6.8 ± 0.5	6.4 ± 0.4
18. 13,17- and 11,15-Dimethylnonacosane	5.9 ± 0.2	8.6 ± 0.5	3.1 ± 0.4	3.8 ± 0.2
19. Unknown	0.9 ± 0.04	1.0 ± 0.1	0.8 ± 0.2	1.2 ± 0.1
20. 3-Methylnonacosane	8.6 ± 0.5	10.3 ± 0.4	6.0 ± 0.6	6.3 ± 0.2
21. 5,9- and 5,11-Dimethylnonacosane	4.8 ± 0.2	5.8 ± 0.3	4.0 ± 0.6	4.5 ± 0.2
22. 3,7-, 3,9-, and 3,11-Dimethylnonacosane	14.0 ± 0.4	18.6 ± 0.7	19.6 ± 2.5	16.1 ± 1.3
23. Unknown	0.9 ± 0.1	0.5 ± 0.02	0.8 ± 0.3	0.6 ± 0.1
24. 11-, 13-, and 15-Methyltriacontane	1.1 ± 0.1	2.2 ± 0.1	1.4 ± 0.2	1.7 ± 0.2
25. Unknown	0.2 ± 0.02	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.1
26. 4,8- and 4,10-Dimethyltriacontane	0.5 ± 0.03	0.8 ± 0.1	0.3 ± 0.1	0.5 ± 0.1
27. 11-, 13-, and 15-Dimethylhentriacontane	2.2 ± 0.2	1.0 ± 0.1	1.0 ± 0.2	0.9 ± 0.1
28. 13,17- and 11,15-Dimethylhentriacontane	0.4 ± 0.04	0.6 ± 0.1	0.4 ± 0.2	0.2 ± 0.1
29. 5,9- and 5,11-Dimethylhentriacontane	0.4 ± 0.1	0.5 ± 0.03	0.2 ± 0.1	0.4 ± 0.1
30. 10,12-Dimethyldotriacontane	0.2 ± 0.04	0.1 ± 0.05	0.0	0.2 ± 0.1
Total (μg/insect)	180.6 ± 7.0	174.2 ± 5.6	33.8 ± 2.8	37.3 ± 0.7

ion fragments at 183, 252/253, and 379 in Figure 4A indicate that only the 3,11- positional isomer of dimethylheptacosane is present. The same is true for the 31-carbon component with the ion fragments at 183, 280/281, and 407, indicating that only the 3,11- isomer is present (Figure 4B). These data indicate

281] (peak 8, Figure 1). In addition to the 11-, 13-, and 15-methylnonacosane the 9- isomer is also present (*m/z* 140/141 and 308/309) (peak 15, Figure 1).

Minor components not identified in the paper by Augustynowicz et al. (1987) consist of 2-methyloctacosane [*m/z* 365 $(M-43)^+$] (peak 10, Figure 1) and 4-methyloctacosane [*m/z* 365 $(M-43)^+$, 337/336 $(M-71/72)^+$] (peak 11, Figure 1). Both 2- and 4-methylalkanes give strong ion fragments at *m/z* $(M-43)^+$, whereas 4-methylalkanes also show ion fragments at $(M-71)^+$ and $(M-72)^+$ (Blomquist et al., 1987). Other minor components present are 4,8- and 4,10-dimethyltriacontane [*m/z* 407 $(M-43)^+$, 141, 169, 308/309 and 336/337), 11-, 13-, and 15-methylhentriacontane (*m/z* 168/169, 206/207, 224/225, 252/253, 280/281 and 308/309), 13,17- and 11,15-dimethylhentriacontane (*m/z* 168/169, 196/197, 224/225, 239, 267, 252/253, 295 and 323), 5,9- and 5,11-dimethylhentriacontane [*m/z* 407 $(M-57)^+$, 84/85, 155, 183, 308/309 and 336/337], and 10- and 12-methyldotriacontane (*m/z* 154/155, 182/183, 308/309 and 336/337).

The percent composition of the hydrocarbon fraction from males, females, and nymphs is presented in Table 1. No qualitative differences were observed between the different life stages or sexes, and the 3,*x*-dimethylalkanes were present in all groups. However, consistent quantitative differences were observed between 15-day-old adult males and virgin females (Table 1). The most prominent components extracted from cuticles of females were isomers of 3,*x*-dimethylnonacosane (18.6 $\pm$ 0.7%, 32.4 $\pm$ 1.4 μg), while isomers of internally branched monomethylnonacosanes (9-, 11-, 13-, and 15-) were the most abundant components of males (22.7 $\pm$ 0.6%, 41.0 $\pm$ 2.2 μg). Last nymphal instar males also have more 9-, 11-, 13-, and 15-methylnonacosanes than last instar females.

A chromatogram of the methylketone fraction after isolation by TLC and analysis by packed column GC is presented in Figure 2. The major components are 3,*x*-dimethyl-2-nonacosanone (79.2%) and 3,*x*-dimethyl-2-heptacosanone (8.1%). Since the cuticular hydrocarbons had isomers of dimethylnonacosane in the 3,11-, 3,9-, and 3,7- positions and dimethylheptacosane in the 3,11- and 3,9- positions, we determined whether these same positional isomers are present in the methyl ketone pheromone fraction. Mass spectra of dimethyl-2-nonacosanone and dimethyl-2-heptacosanone are shown in Figure 3 with the M^+ ion fragments at *m/z* 450 and 422, respectively. The ion fragments at *m/z* 127, 141, 155, 169, and 197 are indicative of a 2-keto group with an adjacent methyl branch in the hydrocarbon chain. The position of the methyl groups could not be determined from these data.

The methyl branch positions of dimethyl-2-nonacosanone and dimethyl-2-heptacosanone were determined by reducing the ketone to the hydrocarbon followed by GC-MS analysis. The mass spectra are presented in Figure 4. The

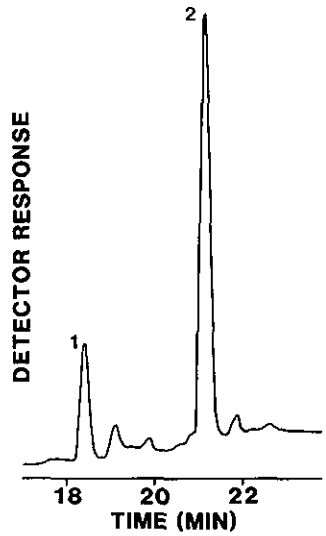

FIG. 2. A packed column GC trace of the methyl ketone fraction from 15-day-old virgin German cockroach females. 1 = 3,11-dimethyl-2-heptacosanone, 2 = 3,11-dimethyl-2-nonacosanone.

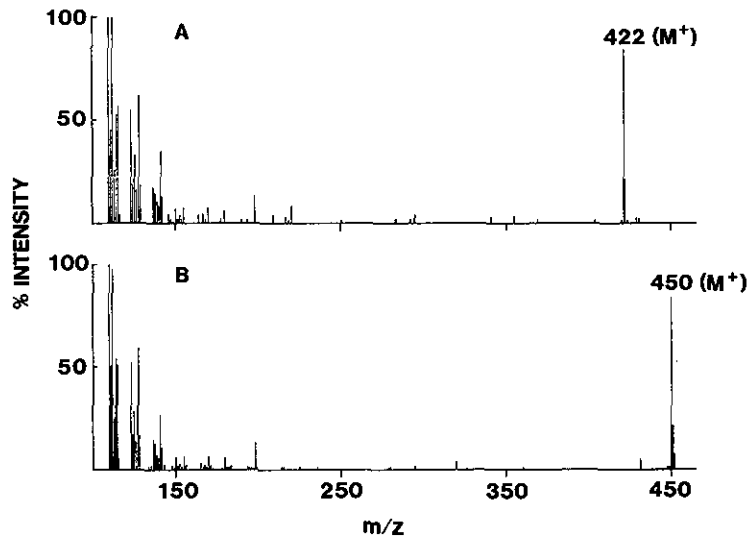

FIG. 3. Mass spectra from the methyl ketone fraction: (A) 3,11-dimethyl-2-heptacosanone; (B) 3,11-dimethyl-2-nonacosanone.

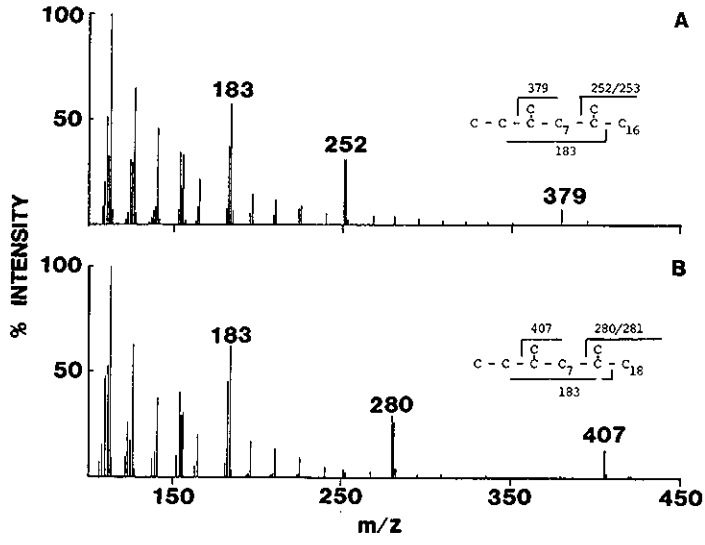

FIG. 4. Mass spectra of the reduced methyl ketone fraction from female German cockroaches: (A) reduced 3,11-dimethyl-2-heptacosanone; (B) reduced 3,11-dimethyl-2-nonacosanone.

that the principal dimethylketone component is 3,11-dimethyl-2-nonacosanone with lesser amounts of 3,11-dimethyl-2-heptacosanone also present.

DISCUSSION

The principal cuticular hydrocarbons of the German cockroach are composed of homologous series of straight chain, mono-, and dimethyl heptacosanes and nonacosanes (Augustynowicz et al., 1987). Also present as minor components are homologous series of hentriacontane except that components with the 3,*x*- branching patterns are absent.

In female German cockroaches, the 3,*x*-dimethylalkanes comprise the major type of hydrocarbon. Hydrocarbons with 3,*x*-dimethyl branching patterns were first reported in the fire ants, *Solenopsis invicta* and *S. richteri* (Nelson et al., 1980), where they were present in trace amounts. This type of hydrocarbon has also been reported in the housefly, *Musca domestica* (Nelson et al., 1981) and more recently in several other species (Blomquist et al., 1987). However, in all the previous species examined that contain 3,*x*-dimethylalkanes, they are present in trace amounts. The relatively large amounts of the 3,*x*-dimethylalkanes in the female German cockroach may reflect their use as the biosynthetic precursor to the dimethylketone contact pheromone components.

pattern but apparently are not as specific as to chain length. Only the 3,11-isomers were found in the methyl ketone fraction, but both heptacosanone and nonacosanone homologs were present. The absence of 3,11-dimethylhentriacosane in the hydrocarbon profile and absence of the corresponding methyl ketone also suggests specificity of the enzyme for a 3,11- isomer. Indeed, the ratio of 3,11-dimethylheptacosanone to its hydrocarbon analog (4.4) is similar to the ratio of 3,11-dimethyl-2-nonacosanone to its hydrocarbon analog (4.3), suggesting equal efficiency in conversion of both hydrocarbons to their respective methyl ketones.

It appears that only adult females have the enzymes necessary to synthesize the methyl ketone pheromone. Both 3,11-dimethyl C_{27} and C_{29} hydrocarbons are present in males, but apparently the enzyme system is not. We report different hydrocarbon composition profiles from that previously reported (Augustynowicz et al., 1987). Augustynowicz et al. (1987) found that the 11-, 13-, and 15-methylnonacosane isomers were most abundant (16.5%), followed by 3- (14.7%) and 5-methylnonacosane (10.4%). The 3,7-, 3,9-, and 3,11-dimethylnonacosane isomers made up 11.3% of the cuticular hydrocarbons. We report that in adult females the 3,7-, 3,9-, and 3,11-dimethylnonacosane isomers make up the largest group by percent composition (18.6%) followed by the 9-, 11-, 13-, and 15-methylnonacosane isomers (14.5%). In adult males the most abundant hydrocarbons were the 9-, 11-, 13-, and 15-methylnonacosanes (22.7%), whereas the 3,*x*-dimethylnonacosane isomers make up only 14.0% of the hydrocarbon fraction (Table 1). These differences between our results and those of Augustynowicz et al. (1987) are clearly due to the combining of male and female cockroaches in their analysis.

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The 3,*x*-dimethylheptacosanes and nonacosanes both contain 3,11- and 3,9-dimethyl isomers with the nonacosane series also containing the 3,7- isomer. The methylketone component of the pheromone has been identified as only one isomer, the 3,11-dimethyl-2-nonacosanone (Nishida et al., 1974). Since the cuticular hydrocarbons contain at least two positional isomers of 3,*x*-dimethylnonacosane and dimethylheptacosane, we performed experiments to determine if female cockroaches also had the same homologs and positional isomers of methyl ketones as they have for the hydrocarbons. Unlike the hydrocarbons, the C_{31} methyl ketone component of the pheromone contains only the 3,11-isomer, as was also shown by Nishida et al. (1974). We have found, however, that the heptacosanone homolog is also present, but again, only as the 3,11-isomer.

The structural similarities between the cuticular hydrocarbons and the contact pheromone suggests a similar biosynthetic origin. Malonyl-CoA serves as the two-carbon donor for chain elongation during hydrocarbon synthesis. In insects methyl branches in cuticular hydrocarbons arise from the substitution of methylmalonyl-CoA for malonyl-CoA at specific biosynthetic steps during this elongation (Blomquist et al., 1987). Various substrates have been shown to serve as precursors to methylmalonyl-CoA. In the housefly, *Musca domestica*, studies with [1-^{13}C] propionate showed that 3,*x*-dimethylalkanes were formed by the insertion of propionates, as methylmalonyl-CoA derivatives, during the early stages of chain elongation (Dillwith et al., 1982). The source of the propionyl-CoA and methylmalonyl-CoA used in branched alkane biosynthesis has been shown to be the amino acids valine and isoleucine in the housefly and American cockroach (Dillwith et al., 1982; Halarnkar et al., 1985). In termites, succinate is converted to the methylmalonyl unit that forms the methyl branch group (Chu et al., 1980; Blomquist et al., 1980).

Two possible explanations exist to account for the presence of the carbonyl group at the 2-position of the pheromone component. The female cockroach could oxidize the preformed hydrocarbon at this position or fail to reduce the carbonyl group that is present at this position during the condensation reaction by which the hydrocarbon is synthesized. The epoxides in the sex pheromone of the housefly (Blomquist et al., 1984) and the gypsy moth (Prestwich, 1987; Kasang, 1974) arise from the insertion of an oxygen into a preformed alkene. Similarly, the carbonyl group in the (Z)-14-tricosene-10-one pheromone component of the female housefly arises from the insertion of an oxygen into a preformed chain. A cytochrome P-450 polysubstrate mixed function oxidase hydroxylates the carbon chain, and the secondary alcohol is then apparently oxidized to the ketone (Ahmad et al., 1987).

Assuming that the methyl ketone pheromone components arise from a preformed hydrocarbon, the enzyme(s) involved in synthesis of the pheromone would require a high degree of specificity for a 3,11-dimethylalkane branching

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