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CORRESPONDENCE OF SOLDIER DEFENSE SECRETION MIXTURES WITH CUTICULAR HYDROCARBON PHENOTYPES FOR CHEMOTAXONOMY OF THE TERMITE GENUS *Reticulitermes* IN NORTH AMERICA

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Abstract—Soldier defense secretions from samples of *Reticulitermes* collected in California, Nevada, Arizona, New Mexico, and Georgia were characterized and correlated with cuticular hydrocarbon phenotypes. Twenty-seven cuticular hydrocarbon phenotypes have been defined, and soldier defense secretion (SDS) phenotypes have been described for 25 of these. Forty-five terpenoid compounds were found, including monoterpenes, sesquiterpenes, and a few diterpenes. The monoterpenes include (−)-α-pinene, (−)-β-pinene, (−)-camphene, myrcene, (*Z*)- and (*E*)-ocimene, and (−)-limonene. The major sesquiterpenes produced are (+)-γ-cadinene, (+)-γ-cadinene aldehyde, (−)-germacrene A, germacrene B, γ-himachalene, and β-bisabolene. Some SDS phenotypes pair with more than one cuticular hydrocarbon phenotype; however, with two exceptions, each hydrocarbon phenotype is associated with only one SDS phenotype. These chemical characterizations lend support to the conclusion that there are numerous undescribed species of *Reticulitermes* in North America.

Key Words—*Reticulitermes*, Isoptera, Rhinotermitidae, subterranean termites, monoterpenes, sesquiterpenes, diterpenes, geranyl linalool, soldier defense secretions, cuticular hydrocarbons.

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INTRODUCTION

We have been studying the foraging ecology of *Reticulitermes* (Isoptera: Rhinotermitidae) from sites in the western and southeastern United States, but have encountered difficulty identifying our collections to species in many locations. According to accepted biogeographical information, only one species, *R. hesperus* Banks, should be present at our California sites; *Reticulitermes* from New Mexico, Arizona, and Nevada should all be *R. tibialis* Banks; and the Georgia sites could be inhabited by the sympatric species *R. flavipes* (Kollar), *R. virginicus* Banks, and/or *R. hageni* Banks (Weesner, 1965, 1970; Haverty and Nelson, 1997; Haverty et al., 1996, 1999b,c, 2000).

The available keys to soldiers were unreliable in identifying many of our samples. For example, all California colonies keyed to *R. tibialis*, not *R. hesperus*, regardless of their geographic origin (Haverty and Nelson, 1997). Soldier samples from Georgia keyed to one of the three extant species that inhabit the southeastern United States (Haverty et al., 1996, 1999b). Alates rarely occur in foraging groups, thus seldom could be used for species determination. When alate specimens were present, however, species determination was often equivocal, especially for colonies determined to be *R. hageni* by soldier morphology. In short, determination of *Reticulitermes* species based on morphology can be uncertain. Because of this, we have routinely examined chemical characters as an aid in determining taxonomic identity.

Chemical characters, such as cuticular hydrocarbons and soldier defense secretions, have proven useful for distinguishing taxa of *Reticulitermes* (Bagnères et al., 1988, 1990, 1991; Baker et al., 1982; Clément and Bagnères, 1998; Clément et al., 1985, 1986; Haverty and Nelson, 1997; Haverty et al., 1996, 1999b; Howard et al., 1978, 1982b; Lange et al., 1989; Parton et al., 1981; Takematsu, 1999; Takematsu and Yamaoka, 1999; Zalkow et al., 1981). Cuticular hydrocarbon biosynthesis is largely genetically determined (Coyne et al., 1994; Kaib et al., 1991; Page et al., 1991), and the resultant mixture of compounds comprises a chemical "signature" enabling recognition at the species, colony, and individual levels, especially important in social insects (Bagnères et al., 1990, 1991; Clément and Bagnères, 1998; Howard, 1993; Howard et al., 1980, 1982a,b; Takahashi and Gassa, 1995). In fact, mimicry of the hydrocarbon signature allows termitophilous beetles to integrate peacefully into *Reticulitermes* colonies (Howard et al., 1980, 1982a). There is also evidence that when two termite species are artificially mixed, there will be some exchange of cuticular hydrocarbons, most likely by passive transfer (Vauchot et al., 1998).

Termite soldier defense secretions are synthesized *de novo* (Prestwich, 1979, 1984, 1988; Prestwich et al., 1981) and are used as weapons against intruders (Mill, 1983; Moore, 1974; Prestwich, 1979, 1983, 1984, 1988; Scheffrahn et al., 1983). Termite soldiers protect the colony against ants and vertebrate

predators, while workers are capable defenders in termite–termite conflicts (Thorne, 1982). Worker termites appear to be devoid of terpenoid compounds, so it is not likely that these chemicals are part of any colony signature (Clément and Bagnères, 1998). Although cuticular hydrocarbons and soldier terpenoid defense secretions probably have very different functions, both are nonetheless useful as taxonomic characters.

We analyzed cuticular hydrocarbons and soldier defense secretions from *Reticulitermes* collected at our experimental sites in California and Georgia, at various other sites in these states, and in Nevada, Arizona, and New Mexico. We report here the results of this chemotaxonomic study, and the complementary nature of these two sets of chemical characters.

METHODS AND MATERIALS

Insects. Termites were collected from monitoring stations at study sites in California and Georgia (Haverty and Nelson, 1997; Haverty et al., 1996, 1999b) or from infested wood in California, Georgia, Nevada, Arizona, and New Mexico (Haverty et al., 1999b) (Table 1). Termite workers were used for hydrocarbon analysis and soldiers from the same collection were used for terpene analysis.

Cuticular Hydrocarbons. Hydrocarbons were extracted from 100–200 dried workers and identified by gas chromatography–mass spectrometry (GC-MS) (Haverty et al., 1996; Page et al., 1997). Termite samples were sorted, separately for each state, on the basis of cuticular hydrocarbon composition and assigned to a hydrocarbon phenotype (Haverty and Nelson, 1997; Haverty et al., 1996, 1999b). Phenotypes are designated by the two-letter state abbreviation, followed by a letter, for example GA-A. Letters were assigned to phenotypes in the order they were discovered. There is no relationship between phenotypes from different states that have the same letter.

Soldier Defense Secretions (SDS). One to 10 soldiers from single collections were covered in *n*-pentane (ca. 200–600 μl) and held below -15°C until analysis. Monoterpenes, sesquiterpenes, and diterpenes extracted from soldiers were identified and quantified by GC-MS. Analysis was by splitless (0.7 min) injection on a 0.25 mm ID $\times$ 30 m 5% phenyl–95% methylpolysiloxane capillary column, helium carrier gas, temperature program 35°C (0.7 min isothermal) to 280°C at 6°C/min, with EI detection at 70 eV. Most compounds were identified by retention time and MS comparison with authentic materials or components of well-characterized essential oils run under identical conditions. In some cases, identification was by comparison with published GC-MS data only and considered tentative (compound name in parentheses). Unknowns were designated by apparent molecular weight and an identifying suffix letter.

Quantities of each terpenoid were calculated as a percentage of the total from integrated peak areas of the total-ion chromatograms without correction by

TABLE 1. COLLECTION LOCALITIES FOR *Reticulitermes* SAMPLES USED TO CHARACTERIZE SOLDIER DEFENSE SECRETIONS

Hydrocarbon phenotype	Localities	County	State	Terpenes (>10%)[a]	Species identification[b]	
					Soldier	Alate
CA-A	Placerville	El Dorado	California	γ-Cadinene	*R. tibialis*	NA
	Kentfield	Marin	California			
CA-A′	Kentfield; Novato	Marin	California	γ-Cadinene	*R. tibialis*	NA
	Cloverdale	Sonoma	California			
CA-B	Placerville	El Dorado	California	γ-Cadinene, Geranyl linalool, γ-Himachalene	*R. tibialis*	NA
CA-C	Placerville	El Dorado	California	Germacrene A	*R. tibialis*	NA
CA-D	Oakland	Alameda	California	Geranyl linalool, Germacrene A, γ-Cadinene	*R. tibialis*	NA
	Kentfield; Novato	Marin	California			
NV-A	Lockwood	Storey	Nevada	Geranyl linalool		NA
	Pyramid Lake; Wadsworth	Washoe	Nevada			
NV-B	Pyramid Lake	Washoe	Nevada	Germacrene A		NA
AZ-A	Hwy 40 ca. 30 mi E of Flagstaff; Intersection of Hwys 277 and 377	Coconino	Arizona	Geranyl linalool, γ-Cadinene		NA
	Second Mesa	Navajo	Arizona			
AZ-B	Second Mesa	Navajo	Arizona	Geranyl linalool, γ-Cadinene		NA
	Prescott NF near: Camp Verde, Jerome, Mingus Mtn., Prescott	Yavapai	Arizona			

AZ-C(I)	Kaibab NF near Williams	Coconino	Arizona	β-Bisabolene, γ-Cadinene, Geranyl linalool, Myrcene		NA
	Prescott NF near: Camp Verde, Jerome, Mingus Mtn., Prescott	Yavapai	Arizona			
AZ-C(II)	Chiracahua Mts., Coronado, NF	Cochise	Arizona	Geranyl linalool		NA
	Pinoleno Mts., Coronado NF	Graham	Arizona			
NM-A	Albuquerque	Bernalillo	New Mexico	Geranyl linalool		NA
GA-A(I)	Athens	Clarke	Georgia	Geranyl linalool, β-Pinene	*R. flavipes*	*R. flavipes*
	Brasstown Bald; Vogel St. Park	Union	Georgia			
GA-A(II)	Barnesville	Lamar	Georgia	γ-Cadinene, γ-Cadinenal, β-Pinene	*R. flavipes*	*R. flavipes*
	Bledsoe Farm; Westbrook Farm	Spalding	Georgia			
	Plains	Sumter	Georgia			
	Blairsville; Brasstown Bald; Mtn. Branch Expt. Stn.; Vogel St. Park	Union	Georgia			
GA-AB	Bamboo Exp. Stn.	Chatham	Georgia	γ-Cadinenal, γ-Cadinene	*R. flavipes*	*R. flavipes*
	Sapelo Island	McIntosh	Georgia			
GA-C	Bamboo Exp. Stn.	Chatham	Georgia	γ-Cadinenal, γ-Cadinene	*R. virginicus*	*R. virginicus*

CONTINUED

TABLE 1. CONTINUED

Hydrocarbon phenotype	Localities	County	State	Terpenes (>10%)[a]	Species Identification[b]	
					Soldier	Alate
	Athens	Clarke	Georgia			
	Westbrook Farm	Spalding	Georgia			
	Sapelo Island	McIntosh	Georgia			
GA-D	Aldora; Barnesville	Lamar	Georgia	γ-Cadinene	*R. hageni*	*R. hageni*
GA-E	Barnesville	Spalding	Georgia	γ-Cadinene	*R. hageni*	*R. virginicus*
	Brasstown Bald; Mtn. Branch Expt. Stn.	Union	Georgia			
GA-F	Sapelo Island	McIntosh	Georgia	γ-Cadinene	*R. hageni*	*R. virginicus*
GA-G	Sapelo Island	McIntosh	Georgia	γ-Cadinene	*R. hageni*	NA
GA-H	Plains	Sumter	Georgia	γ-Cadinene	*R. hageni*	NA
GA-I	Plains	Sumter	Georgia	γ-Cadinene	*R. hageni*	NA
GA-J	Sapelo Island	McIntosh	Georgia	Germacrene A, Germacrene B	*R. hageni*	NA
GA-K	Bledsoe Farm	Spalding	Georgia	γ-Cadinene	*R. hageni*	NA
	Blairsville; Mtn. Branch Expt. Stn.	Union	Georgia	γ-Cadinene		
GA-L	Sapelo Island	McIntosh	Georgia	γ-Cadinene	*R. hageni*	NA
GA-M	Athens	Clarke	Georgia	γ-Cadinene	*R. hageni*	NA
GA-N	Sapelo Island	McIntosh	Georgia	γ-Cadinene	*R. hageni*	NA

[a] Listed in descending order of abundance (see Tables 3–6 for specific quantities).

[b] Termites used for species identification were of the same hydrocarbon phenotype, but not necessarily from the same collection or locality as the samples used for soldier defense secretion analysis (Haverty and Nelson, 1997, Haverty et al., 1996, 1999b). Keys used for identification are from Weesner (1965) or Nutting (1990). Alate samples were collected along with other castes in wood or monitoring stations, otherwise noted as not available (NA).

response factors. Germacrene A, which gradually rearranges to β-elemene under GC conditions, appeared as a broad hump following the β-elemene peak. Its quantity was determined as the sum of the areas of the β-elemene peak plus the hump, minus the areas of the other peaks superimposed on the hump. Germacrene B behaved similarly (rearranging to γ-elemene) and was quantified by the same technique.

(+)-γ-Cadinene from pooled samples from various collections was purified by silica gel liquid chromatography and preparative GC as described elsewhere (Kim et al., 1994) and positively identified by diffuse-reflectance Fourier-transform infrared spectroscopy of ca. 50 μg of the neat material on powdered KBr in a microcup. Its optical rotation (α_D) was measured in hexane at 20°C.

The enantiomeric identity of a number of the monoterpenes and sesquiterpenes was determined by chiral GC. Conditions were: 10% permethylated β-cyclodextrin–90% OV-1701 capillary column, 0.25 mm ID × 30 m; 1°C/min program (0.5°C/min for β-elemene), 60°C–80°C for monoterpenes, 90°C–140°C for sesquiterpenes; splitless injection (0.7 min); flame-ionization detection; internal retention time reference standard was *n*-undecane for monoterpenes and *n*-tetradecane, *n*-pentadecane, and *n*-hexadecane for sesquiterpenes. Chiral analysis was done on one soldier collection from the hydrocarbon phenotype that was richest in the relevant terpene(s). Before analysis, oxygenated components were removed by passing the pentane solution through activated alumina. Enantiomer identification (indicated by sign of rotation in Tables 2–6 below) was by retention time comparison with authentic materials run under identical GC conditions. In the case of (−)-germacrene A, pooled samples were purified as for γ-cadinene, although under preparative GC conditions only β-elemene was recovered. This was then analyzed by chiral GC and compared to authentic (−)-β-elemene. The Kovats retention indices of the various sesquiterpene enantiomers are presented in Table 2.

RESULTS

Terpenoid Identification. γ-Cadinene and its aldehyde have often been reported from European and American *Reticulitermes* species, but there is some confusion in the literature as to the precise identity of these compounds. The original report (Zalkow et al., 1981) determined them to be the rare (+)-γ_1-cadinene [cadina-4(14),9-diene] and the corresponding C-15 aldehyde, but later literature from these and other authors variously report the hydrocarbon as "γ_1-cadinene" or just "γ-cadinene." We found the GC-MS data and IR spectrum of the hydrocarbon to be identical to that of authentic γ-cadinene [cadina-4,10(15)-diene], and the value of its optical rotation (+100° ± 10°) was the same as that of the common enantiomer found in higher plants. Moreover, its retention time on the chiral GC

TABLE 2. KOVATS RETENTION INDICES OF *Reticulitermes* SESQUITERPENES AND ENANTIOMERS ON PERMETHYLATED β-CYCLODEXTRIN GC COLUMN[a]

Compound and source	Kovats retention index
(−)-β-Elemene, *Abies concolor* cortical oleoresin	1423
(+)-β-Elemene, *Reticulitermes* sp. (GA-J)[b]	1424
(−)-α-Himachalene, *Cedrus deodara* wood	1470
(+)-α-Himachalene, *Reticulitermes* sp. (AZ-B, CA-B) or *Scapania undulata*	1478
(−)-α-Amorphene, *Pinus edulis* oleoresin	1506
(+)-α-Amorphene, *Reticulitermes* sp. (AZ-B) or *Scapania undulata*	1527
(+)-α-Selinene, *Abies concolor* cortical oleoresin	1531
(−)-α-Selinene, *Reticulitermes* sp. (CA-D)	1537
(+)-β-Selinene, *Abies concolor* cortical oleoresin	1532
(−)-β-Selinene, *Reticulitermes* sp. (CA-D)	1540
(+)-γ-Cadinene, *Reticulitermes* sp. (GA, CA, AZ) or *Pinus edulis* oleoresin	1565

[a] 10% permethyl-β-cyclodextrin, 90% OV-1701, 0.25 mm ID × 30 m silica; temperature program 1°/min (β-elemene: 0.5°/min).
[b] Rearrangement product of (−)-germacrene A.

column was identical to that of authentic (+)-γ-cadinene. As for the aldehyde, the NMR data reported by Zalkow et al. (1981) are identical to those given in the literature for cadina-4,10(15)-dien-14-al (Kaiser and Lamparsky, 1983). Thus, these ubiquitous *Reticulitermes* sesquiterpenoids are shown to be (+)-γ-cadinene and its C-14 aldehyde (hereinafter called γ-cadinenal), rather than (+)-γ_1-cadinene and its C-15 aldehyde.

The CA-B collections had a sesquiterpene whose mass spectrum was nearly identical to germacrene A, but which had a slightly different GC retention time. It also did not rearrange to β-elemene as does germacrene A. This compound is tentatively identified as the *cis*-double bond isomer (*Z*,*E*)-germacrene A, also known as helminthogermacrene. It has been reported as the major SDS component in *Amitermes wheeleri* (Scheffrahn et al., 1986). In all examined cases (with the possible exception of β-elemene, the enantiomers of which were poorly resolved), the terpenoids were found to be optically pure (>90%). It is striking that except for (+)-γ-cadinene and its aldehyde, *Reticulitermes* sesquiterpenes are enantiomeric to those found in higher plants (Table 2), many having heretofore been reported only from fungi, liverworts, or marine organisms. This is further evidence that these termites are producing the SDS terpenoids *de novo* rather than sequestering them from ingested terpene-containing plants.

In this study, we identified 20 SDS terpenoids that have not yet been reported from termite soldiers of any family. The names of these compounds appear in bold face in Tables 3–6 below. In addition, we report nine unknowns that may also be

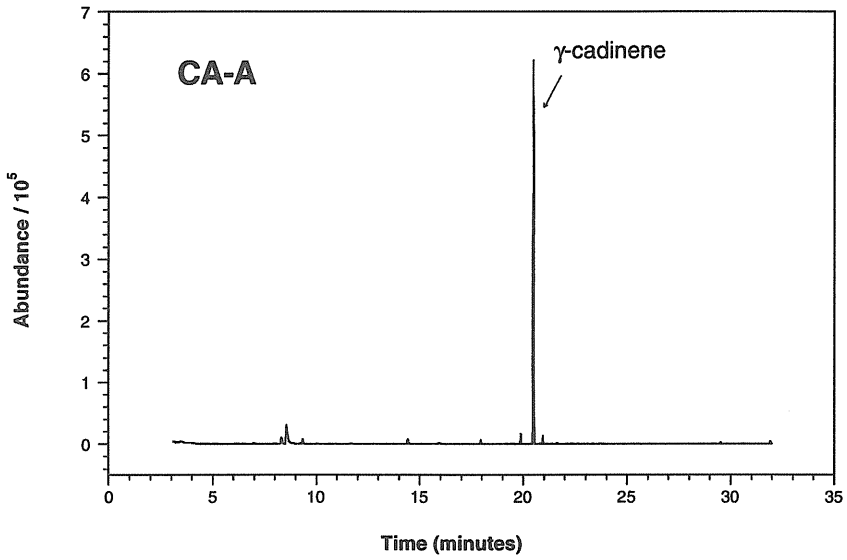

FIG. 1. Total ion chromatogram of defense secretions extracted from soldiers of cuticular hydrocarbon phenotype CA-A.

previously unreported. For brevity in the following discussion, signs of rotation will not be specified, although they are given in Tables 3–6 below.

Reticulitermes *from California.* So far we have characterized five cuticular hydrocarbon phenotypes of *Reticulitermes* in northern California: CA-A, CA-A′, CA-B, CA-C, and CA-D (Haverty and Nelson, 1997). CA-A′ is nearly identical to CA-A, distinguished only by the presence of two fairly abundant pentacosatrienes not found in CA-A, and it appears to be the most common phenotype (Haverty and Nelson, 1997).

Termite collections with cuticular hydrocarbon phenotypes CA-A or CA-A′ produce very similar SDS profiles: γ-cadinene predominates ($\geq$90.0%) (Table 3; Figure 1). A few compounds appear in small amounts ($\leq$2.0%) in some samples of CA-A that were not seen in CA-A′: myrcene, unknown (unk.) 204c, δ-cadinene, (*E*)-γ-bisabolene, and unk. 238a. CA-B samples produced α-himachalene (5.0%), γ-himachalene (13.4%), γ-humulene (1.2%), β-himachalene (4.9%), (*Z*,*E*)-germacrene A (6.8%), δ-amorphene (8.5%), γ-cadinene (39.6%), unk. 204e (1.4%), geranyl linalool (16.7%), and a few other minor components. The SDS mixtures of hydrocarbon phenotype CA-C contain predominantly germacrene A (92.8%), and small amounts of γ-cadinene (3.7%) and α-selinene (2.0%). α-Selinene (9.1%) was a larger component in CA-D, along with germacrene A (33.0%), γ-cadinene (17.4%), and geranyl linalool (38.0%) (Table 3).

TABLE 3. TERPENOID PERCENT COMPOSITION OF SOLDIER DEFENSE SECRETIONS FROM 5 CUTICULAR HYDROCARBON PHENOTYPES OF *Reticulitermes* FROM NORTHERN CALIFORNIA

	CA-A (N = 16)					CA-A′ (N = 10)					CA-B (N = 6)					CA-C (N = 6)					CA-D (N = 10)				
Terpenoid[a]	Mean[b]	SD (%)	Min[c]	Max[b]	Prop ≤ 0.1%	Mean[b]	SD (%)	Min[c]	Max[b]	Prop ≤ 0.1%	Mean[b]	SD (%)	Min[c]	Max[b]	Prop ≤ 0.1%	Mean[b]	SD (%)	Min[c]	Max[b]	Prop ≤ 0.1%	Mean[b]	SD (%)	Min[c]	Max[b]	Prop ≤ 0.1%
(−)-α-Pinene	0.1	0.19	0.0	0.6	0.63	0.0	0.08	0.0	0.2	0.80	0.0	0.01	0.0	0.0	1.00						0.0	0.01	0.0	0.0	1.00
(−)-Camphene																									
(−)-β-Pinene	0.1	0.56	0.0	2.2	0.94	0.1	0.21	0.0	0.7	0.90	0.0	0.02	0.0	0.1	1.00	0.0	0.03	0.0	0.1	1.00	0.0	0.03	0.0	0.1	0.90
Myrcene	0.1	0.25	0.0	1.0	0.94						0.0	0.02	0.0	0.0	1.00	0.0	0.02	0.0	0.0	1.00	0.0	0.02	0.0	0.1	1.00
3-Carene																									
(−)-Limonene	0.1	0.12	0.0	0.4	0.69	0.0	0.08	0.0	0.2	0.80						0.0	0.00	0.0	0.0	1.00	0.0	0.00	0.0	0.0	1.00
Terpinolene																									
(*Z*)-Ocimene																									
(*E*)-Ocimene																									
δ-Elemene																									
Unk. 204a																									
Longifolene																									
Unk. 204b											0.7	0.23	0.3	1.0	0.00										
(+)-α-Himachalene											5.0	1.02	4.1	6.5	0.00										
(*E*)-β-Farnesene																0.2	0.22	0.0	0.6	0.33	0.2	0.19	0.0	0.7	0.20
α-Humulene											0.4	0.12	0.2	0.5	0.00										
***cis*-Muurola-4(14), 5-diene**	0.0	0.10	0.0	0.3	0.81	0.1	0.13	0.0	0.4	0.80	0.0	0.03	0.0	0.1	1.00						0.0	0.03	0.0	0.1	0.90
Unk. 204c	0.0	0.10	0.0	0.3	0.88																0.0	0.03	0.0	0.1	1.00
γ-Himachalene											13.4	3.19	9.7	19.0	0.00										
γ-Humulene	1.6	1.02	0.0	2.7	0.19	1.8	0.97	0.0	2.9	0.10	1.2	0.07	1.1	1.3	0.00	0.0	0.11	0.0	0.3	0.83	0.7	0.79	0.0	2.5	0.40
(+)-α-Amorphene																									

(γ-Curcumene)																					
(−)-β-Selinene															0.2	0.40	0.0	1.0	0.67	0.9	0.85	0.0	2.1	0.40
(−)-α-Selinene															2.0	3.38	0.0	8.6	0.50	9.1	7.43	0.0	21.5	0.10
Unk. 204d																								
β-Himachalene										4.9	1.58	2.8	6.7	0.00										
(Zingiberene)																								
β-Bisabolene	1.1	2.15	0.0	7.9	0.69	0.9	1.62	0.0	4.8	0.70														
(*Z*,*E*-Germacrene A)	0.1	0.39	0.0	1.2	0.88	0.2	0.64	0.0	2.0	0.90	6.8	2.05	4.8	10.5	0.00									
(−)-Germacrene A	1.3	0.02	0.0	5.1	0.38	1.0	1.71	0.0	4.4	0.70						92.8	4.54	87.0	98.4	0.00	33.0	14.68	1.8	53.0	0.00
δ-Amorphene										8.5	1.87	6.2	10.9	0.00										
(+)-γ-Cadinene	90.0	7.37	71.3	100.0	0.00	94.3	3.84	87.1	100.0	0.00	39.6	6.74	31.1	50.6	0.00	3.7	3.54	0.5	9.4	0.00	17.4	9.87	8.2	40.1	0.00
δ-Cadinene	0.2	0.36	0.0	1.2	0.81						0.7	0.15	0.5	0.9	0.00									
10-Epicubebol																								
Unk. 204e										1.4	0.33	0.9	1.9	0.00										
α-Cadinene	1.6	1.23	0.0	5.0	0.19	0.8	1.06	0.0	2.5	0.60	0.8	0.14	0.7	1.0	0.00	0.0	0.06	0.0	0.2	0.83	0.3	0.20	0.1	0.7	0.00
Germacrene B																								
[(*E*)-γ-Bisabolene)]	0.3	0.72	0.0	2.0	0.81																			
(*E*)-α-Bisabolene																								
(+)-γ-Cadinenal																								
Unk. 218a																								
Unk. 272a										0.0	0.02	0.0	0.0	1.00										
Unk. 238a	0.2	0.36	0.0	1.3	0.69						0.0	0.03	0.0	0.1	1.00	0.1	0.11	0.0	0.3	0.83				
Unk. 290a																					0.3	0.33	0.0	1.1	0.40
Geranyl linalool	3.1	3.30	0.0	10.0	0.31	0.8	1.62	0.0	4.7	0.70	16.7	12.67	1.4	34.0	0.00	0.7	1.19	0.0	3.1	0.17	38.0	18.28	10.4	72.1	0.00

[a] Terpenoids are listed in GC elution order. Terpenoids in bold type are newly reported for termite soldiers. Compound name in parentheses or brackets indicates identification is considered tentative. Unknowns are designated by apparent molecular weight and an identifying suffix letter.

[b] Values of 0.0 indicate the compound was detected, but at a level <0.05% of the total SDS.

[c] Values of 0.0 may indicate the compound was not detected, or detected at a level <0.05% of the total SDS.

TABLE 4. TERPENOID PERCENT COMPOSITION OF SOLDIER DEFENSE SECRETIONS FROM 8 CUTICULAR HYDROCARBON PHENOTYPES OF *Reticulitermes* FROM NEVADA, ARIZONA, NEW MEXICO

	NV-A (N=3)					NV-B	AZ-A (N = 4)					AZ-B (N = 16)					AZ-C(I) (N=18)					AZ-C(II) (N = 1)					NM-A (A = 2)				
Terpenoid[a]	Mean[b]	SD (%)	Min.[c]	Max.[b]	Prop. ≤ 0.1%	(N=1)[b]	Mean[b]	SD (%)	Min.[c]	Max.[b]	Prop. ≤ 0.1%	Mean[b]	SD (%)	Min.[c]	Max.[b]	Prop. ≤ 0.1%	Mean[b]	SD (%)	Min.[c]	Max.[b]	Prop. ≤ 0.1%	Mean[b]	SD (%)	Min.[c]	Max.[b]	Prop. ≤ 0.1%	Mean[b]	SD (%)	Min.[c]	Max.[b]	Prop. ≤ 0.1%
(−)-α-Pinene	0.0	0.01	0.0	0.0	1.00	0.0	0.0	0.03	0.0	0.1	1.00	0.0	0.04	0.0	0.2	0.94	0.1	0.22	0.0	0.8	0.89										
(−)-Camphene																															
(−)-β-Pinene	0.0	0.01	0.0	0.0	1.00		0.0	0.01	0.0	0.0	1.00	0.0	0.01	0.0	0.0	1.00	0.0	0.07	0.0	0.3	0.94										
Myrcene						0.1						0.1	0.21	0.0	0.8	0.81	10.2	5.94	1.3	20.3	0.00	0.2	0.23	0.0	0.6	0.55					
3-Carene																	0.0	0.12	0.0	0.5	0.94										
(−)-Limonene	0.0	0.03	0.0	0.1	1.00	0.0						0.0	0.09	0.0	0.3	0.88	1.6	1.04	0.0	3.8	0.11	0.0	0.04	0.0	0.1	0.91					
Terpinoline												0.0	0.10	0.0	0.4	0.94	0.0	0.06	0.0	0.3	0.94										
(Z)-Ocimene												0.0	0.7	0.0	0.2	0.88	3.3	2.56	0.0	7.6	0.06	0.2	0.20	0.0	0.7	0.57					
(*E*)-Ocimene												0.0	0.12	0.0	0.4	0.88	5.3	3.66	0.0	12.8	0.11	0.0	0.10	0.0	0.2	0.71					
δ-Elemene																															
Unk. 204a												0.0	0.5	0.0	0.1	0.88															
Longifolene																	1.1	4.28	0.0	18.2	0.83	0.0	0.03	0.0	0.1	1.00					
Unk. 204b																															
(+)-α-Himachalene												2.1	2.38	0.0	6.6	0.25															
(*E*)-β-Farnesene												0.1	0.11	0.0	0.3	0.75	3.4	1.17	1.8	5.9	0.00	1.2	0.76	0.3	3.1	0.00					
α-Humulene																															
***cis*-Muurola-4(14), 5-diene**												0.1	0.07	0.0	0.2	0.38															
Unk. 204c												0.0	0.05	0.0	0.1	0.88	0.1	0.09	0.0	0.3	0.72										
γ-Himachalene												0.5	0.73	0.0	1.8	0.50															
γ-Humulene							0.3	0.11	0.2	0.4	0.00	0.9	0.60	0.5	2.7	0.00	0.2	0.34	0.0	1.0	0.61										
(+)-α-Amorphene												0.1	0.46	0.0	1.8	0.88															
(γ-Curcumene)												0.0	0.01	0.0	0.1	1.00	3.8	1.37	2.1	7.0	0.00	0.0	0.07	0.0	0.2	0.82					

(−)-β-Selinene						1.0																										
(−)-α-Selinene						0.7																										
Unk. 204d																																
β-Himachalene											0.1	0.13	0.0	0.4	0.81																
(Zingiberene)																0.2	0.25	0.0	0.7	0.67											
β-Bisabolene											0.2	0.26	0.0	0.7	0.56	37.6	10.35	17.8	57.3	0.00	0.8	0.46	0.3	1.8	0.00	0.1	0.13	0.0	0.2	0.50	
[(*Z*,*E*)-Germacrene A]																																
(−)-Germacrene A						97.0					0.0	0.03	0.0	0.1	0.94																
δ-Amorphene											0.6	0.83	0.0	2.5	0.44																
(+)-γ-Cadinene							16.8	2.82	13.4	19.8	0.00	23.1	15.36	9.7	66.7	0.00	17.0	10.63	1.8	40.5	0.00										
δ-Cadinene											0.1	0.12	0.0	0.4	0.81																
10-Epicubebol											0.1	0.06	0.0	0.2	0.75																
Unk. 204e																																
α-Cadinene							0.3	0.08	0.2	0.4	0.00	0.8	0.55	0.0	1.8	0.06															
Germacrene B						1.2																										
[(*E*)-γ-Bisabolene]											0.0	0.03	0.0	0.1	0.94	0.9	0.59	0.0	2.0	0.22											
(*E*)-α-Bisabolene											0.3	0.53	0.0	1.9	0.69	3.3	1.24	1.5	7.2	0.00	0.1	0.10	0.0	0.3	0.64						
(+)-γ-Cadinenal							0.3	0.64	0.0	1.3	0.75	6.1	4.20	0.5	13.2	0.00	0.5	1.08	0.0	3.4	0.75										
Unk. 218a																																
Unk. 272a											0.1	0.44	0.0	1.7	0.94																
Unk. 238a																																
Unk. 290a																																
Geranyl linalool	99.7	0.08	99.6	99.8	0.00	0.0	82.4	2.52	79.5	84.9	0.00	64.4	13.99	26.4	78.3	0.00	11.4	14.08	0.0	50.4	0.28	97.3	1.54	94.7	99.1	0.00	99.8	0.05	99.8	99.8	0.00	

[a] Terpenoids are listed in GC elution order. Terpenoids in bold characters are newly reported for termite soldiers. Compound name in parentheses or brackets indicates identification is considered tentative. Unknowns are designated by apparent molecular weight and an identifying suffix letter.

[b] Values of 0.0 indicate the compound was detected, but at a level <0.05% of the total SDS.

[c] Values of 0.0 may indicate the compound was not detected, or detected at a level <0.05% of the total SDS.

TABLE 5. TERPENOID PERCENT COMPOSITION OF SOLDIER DEFENSE SECRETIONS FROM 14 CUTICULAR HYDROCARBON PHENOTYPES OF *Reticulitermes* FROM GEORGIA

	GA-A(I) (N = 4)					GA-A(II) (N = 28)					GA-AB (N = 25)					GA-C (N = 18)					GA-D-I,K-N (N = 59)					GA-J (N = 5)				
Terpenoid[a]	Mean[b]	SD (%)	Min[c]	Max[b]	Prop ≤ 0.1%	Mean[b]	SD (%)	Min[c]	Max[b]	Prop ≤ 0.1%	Mean[b]	SD (%)	Min[c]	Max[b]	Prop ≤ 0.1%	Mean[b]	SD (%)	Min[c]	Max[b]	Prop ≤ 0.1%	Mean[b]	SD (%)	Min[c]	Max[b]	Prop ≤ 0.1%	Mean[b]	SD (%)	Min[c]	Max[b]	Prop ≤ (%)
(−)-α-Pinene	4.2	1.19	2.5	5.3	0.00	3.7	3.62	0.0	14.1	0.18	0.5	0.22	0.1	0.9	0.00						0.1	0.35	0.0	2.7	0.95					
(−)-Camphene	0.9	0.34	0.5	1.4	0.00	0.7	0.77	0.0	3.2	0.29	0.1	0.05	0.0	0.2	0.52						0.0	0.08	0.0	0.6	0.97					
(−)-β-Pinene	11.5	1.56	9.9	13.6	0.00	10.6	10.54	0.1	36.6	0.11	2.0	0.70	0.5	3.5	0.00						0.0	0.16	0.0	1.2	0.97					
Myrcene	0.0	0.05	0.0	0.1	1.00						0.0	0.02	0.0	0.1	1.00						0.0	0.07	0.0	0.6	0.98					
3-Carene																														
(−)-Limonene	2.6	0.88	2.0	3.9	0.00	2.6	2.82	0.0	10.3	0.18	0.5	0.30	0.0	1.6	0.04						0.0	0.08	0.0	0.6	0.98					
Terpinolene	0.0	0.06	0.0	0.1	0.75	0.1	0.10	0.0	0.3	0.75																				
(*Z*)-Ocimene																														
(*E*)-Ocimene																														
δ-Elemene																										3.5	0.84	2.8	4.9	0.00
Unk. 204a																														
Longifolene																														
Unk. 204b	0.0	0.01	0.0	0.0	1.00	0.0	0.10	0.0	0.5	0.96	0.0	0.02	0.0	0.1	1.00															
(+)-α-Himachalene	0.3	0.48	0.0	1.0	0.75	1.6	2.92	0.0	15.2	0.11	0.1	0.42	0.0	2.1	0.80															
(*E*)-β-Farnesene											0.0	0.05	0.0	0.3	0.96											0.5	0.27	0.0	0.7	0.20
α-Humulene	0.0	0.01	0.0	0.0	1.00	0.0	0.10	0.0	0.5	0.93	0.0	0.02	0.0	0.1	1.00															
***cis*-Muurola-4(14), 5-diene**	0.0	0.01	0.0	0.0	1.00	0.2	0.10	0.0	0.5	0.32	0.3	0.07	0.1	0.4	0.00	0.3	0.10	0.1	0.5	0.00	0.0	0.02	0.0	0.1	0.98					
Unk. 204c	0.0	0.01	0.0	0.0	1.00	0.0	0.04	0.0	0.1	0.93	0.1	0.04	0.0	0.1	0.96	0.0	0.03	0.0	0.1	1.00	0.1	0.25	0.0	1.4	0.93					
γ-Himachalene	0.1	0.10	0.0	0.2	0.75	0.2	0.46	0.0	2.3	0.64	0.0	0.03	0.0	0.2	0.96															
γ-Humulene	0.3	0.34	0.0	0.7	0.50	2.2	0.57	1.0	3.2	0.00	2.6	0.31	2.0	3.3	0.00	1.6	0.51	0.9	2.8	0.00	0.3	0.39	0.0	1.4	0.46					
(+)-α-Amorphene (γ-Curcumene)																														

(−)-β-Selinene																											
(−)-α-Selinene																											
Unk. 204d						0.0	0.08	0.0	0.2	0.75	0.1	0.06	0.0	0.2	0.32	0.1	0.05	0.0	0.1	0.72	0.1	0.40	0.0	2.5	0.95		
β-Himachalene	0.1	0.12	0.0	0.3	0.75	0.3	0.43	0.0	1.8	0.57	0.0	0.02	0.0	0.1	1.00	0.0	0.02	0.0	0.1	1.00	0.0	0.08	0.0	0.7	0.98		
(Zingiberene)																											
β-Bisabolene	0.0	0.01	0.0	0.0	1.00																						
[(*Z*,*E*)-Germacrene A]						0.3	0.33	0.0	1.8	0.14	0.2	0.05	0.1	0.3	0.08	0.0	0.01	0.0	0.0	1.00	0.0	0.02	0.0	0.2	0.98		
(−)-Germacrene A																										50.8	8.09	39.9	59.8	0.00
δ-Amorphene						0.1	0.39	0.0	2.0	0.86																	
(+)-γ-Cadinene	7.9	9.70	0.1	20.4	0.00	56.3	15.38	25.0	80.9	0.00	30.7	6.59	17.1	45.6	0.00	20.1	8.40	11.4	39.9	0.00	95.0	4.13	79.1	100.0	0.00		
δ-Cadinene																					0.4	0.39	0.0	1.2	0.46		
10-Epicubebol	0.0	0.04	0.0	0.1	1.00	0.1	0.08	0.0	0.2	0.64	0.2	0.10	0.1	0.4	0.36	0.0	0.01	0.0	0.0	1.00							
Unk. 204e	0.0	0.03	0.0	0.1	1.00	0.1	0.17	0.0	0.8	0.75																	
α-Cadinene	0.1	0.07	0.0	0.2	0.75	0.2	0.18	0.0	0.8	0.29	0.1	0.06	0.0	0.2	0.76	0.2	0.16	0.0	0.5	0.33							
Germacrene B																										39.9	4.39	34.7	46.6	0.00
[(*E*)-γ-Bisabolene]																											
(*E*)-α-Bisabolene																											
(+)-γ-Cadinenal	2.5	4.15	0.0	8.7	0.50	17.2	10.51	3.4	49.4	0.00	60.3	6.87	45.2	76.3	0.00	76.7	9.00	55.2	86.2	0.00	0.1	0.44	0.0	2.6	0.90		
Unk. 218a						0.2	0.48	0.0	2.1	0.79	1.2	0.29	0.6	1.9	0.00	0.9	0.41	0.0	1.9	0.06							
Unk. 272a	0.0	0.03	0.0	0.1	1.00	0.3	0.61	0.0	2.8	0.54	0.8	0.63	0.3	3.3	0.00	0.1	0.11	0.0	0.3	0.72	3.8	3.40	0.0	12.4	0.24		
Unk. 238a	1.2	0.57	0.4	1.7	0.00	1.4	1.03	0.0	3.4	0.18																	
Unk. 290a	0.0	0.05	0.0	0.1	1.00																						
Geranyl linalool	68.1	14.86	47.0	80.9	0.00	1.0	0.59	0.0	2.3	0.07	0.0	0.04	0.0	0.2	0.96						0.1	0.70	0.0	5.3	0.95	5.3	4.87	2.2	13.9	0.00

[a] Terpenoids are listed in GC elution order. Terpenoids in bold type are newly reported for termite soldiers. Compound name in parentheses or brackets indicates identification is considered tentative. Unknowns are designated by apparent molecular weight and an identifying suffix letter.

[b] Values of 0.0 indicate the compound was detected, but at a level <0.05% of the total SDS.

[c] Values of 0.0 may indicate the compound was not detected, or detected at a level <0.05% of the total SDS.

TABLE 6. COMPARISON OF PERCENT COMPOSITION OF SOLDIER DEFENSE SECRETIONS FOR ALL CUTICULAR HYDROCARBON PHENOTYPES ANALYZED[a]

Terpenoid[b]	CA-A (N = 16)	CA-A′ (N = 10)	CA-B (N = 6)	CA-C (N = 6)	CA-D (N = 10)	NV-A (N = 3)	NV-B (N = 1)	AZ-A (N = 4)	AZ-B (N = 16)	AZ-C(I) (N = 18)	AZ-C(II) (N = 11)	NM-A (N = 2)	GA-A(I) (N = 4)	GA-A(II) (N = 28)	GA-AB (N = 25)	GA-C (N = 18)	GA-D-I,K-N (N = 59)	GA-J (N = 5)
(−)-α-Pinene	tr	tr	tr		tr	tr	tr	tr	tr	tr			4.2	3.7	0.5		tr	
(−)-Camphene													0.9	0.7	tr		tr	
(−)-β-Pinene	tr	tr	tr	tr	tr	tr		tr	tr	tr			11.5	10.6	2.0		tr	
Myrcene	tr		tr	tr	tr		tr		tr	10.2	tr		tr		tr		tr	
3-Carene										tr								
(−)-Limonene	tr	tr		tr	tr	tr	tr		tr	1.6	tr		2.6	2.6	0.5		tr	
Terpinolene									tr	tr			tr	tr				
(Z)-Ocimene									tr	3.3	tr							
(*E*)-Ocimene									tr	5.3	tr							
δ-Elemene																		3.5
Unk. 204a									tr									
Longifolene										1.1	tr							
Unk. 204b			0.7										tr	tr	tr			
(+)-α-Himachalene			5.0						2.1				0.3	1.6	tr			
(*E*)-β-Farnesene				tr	tr				tr	3.4	1.2				tr			0.5
α-Humulene			0.4										tr	tr	tr			
***cis*-Muurola-4(14),5-diene**	tr	tr	tr		tr				tr				tr	tr	0.3	0.3	tr	
Unk. 204c	tr				tr				tr	tr			tr	tr	tr	tr	tr	
γ-Himachalene			13.4						0.5				tr	tr	tr			
γ-Humulene	1.6	1.8	1.2	tr	0.7			0.3	0.9	tr			0.3	2.2	2.6	1.6	0.3	
(+)-α-Amorphene									tr									
(γ-Curcumene)									tr	3.8	tr							
(−)-β-Selinene				tr	0.9		1.0											

(−)-α-Selinene				2.0	9.1		0.7											
Unk. 204d													tr	tr	tr	tr		
β-Himachalene			4.9						tr				tr	0.3	tr	tr	tr	
(Zingiberene)										tr								
β-Bisabolene	1.1	0.9							tr	37.6	0.8	tr	tr					
[(Z,E)-Germacrene A]	tr	tr	6.8											0.3	tr	tr	tr	
(−)-Germacrene A	1.3	1.0		92.8	33.0		97.0		tr									50.8
δ-Amorphene			8.5						0.6					tr				
(+)-γ-Cadinene	90.0	94.3	39.6	3.7	17.4			16.8	23.1	17.0			7.9	56.3	30.7	20.1	95.0	
δ-Cadinene	tr		0.7						tr								0.4	
10-Epicubebol									tr				tr	tr	tr	tr		
Unk. 204e			1.4										tr	tr				
α-Cadinene	1.6	0.8	0.8	tr	0.3			0.3	0.8				tr	tr	tr	tr		
Germacrene B							1.2											39.9
[(E)-γ-Bisabolene]	0.3								tr	0.9								
(E)-α-Bisabolene									0.3	3.3	tr							
(+)-γ-Cadinenal								0.3	6.1	0.5			2.5	17.2	60.3	76.7	tr	
Unk. 218a														tr	1.2	0.9		
Unk. 272a			tr						tr				tr	0.3	0.8	tr	3.8	
Unk. 238a	tr		tr	tr									1.2	1.4				
Unk. 290a					0.3								tr					
Geranyl linalool	3.1	0.8	16.7	0.7	38.0	99.7	tr	82.4	64.4	11.4	97.3	99.8	68.1	1.0	tr		tr	5.3

[a] tr indicates a value <0.3%. All values except those for NV-B are means.

[b] Terpenoids are listed in GC elution order. Terpenoids in bold characters are newly reported for termite soldiers. Compound name in parentheses indicates identification is considered tentative. Unknowns are designated by apparent molecular weight and an identifying suffix letter.

Reticulitermes *from Nevada, New Mexico, and Arizona.* Collections in western Nevada provided us with another cuticular hydrocarbon phenotype, NV-A (Haverty et al., 1999b). The soldiers from these samples produced defense secretions consisting almost exclusively of geranyl linalool (99.7%) (Table 4). One sample with a cuticular hydrocarbon mixture qualitatively and quantitatively nearly identical to phenotype CA-B was also collected in Nevada near Pyramid Lake. However, the soldiers from this colony had a defense secretion comprised of 97.0% germacrene A, 1.2% germacrene B, and 1.0% β-selinene along with traces of myrcene, a composition more similar to soldiers of CA-C than of CA-B (Tables 3 and 4). This sample is referred to here as phenotype NV-B.

Currently, only one species of *Reticulitermes*, *R. tibialis,* is recognized from Arizona and New Mexico (Weesner, 1970). So far, five cuticular hydrocarbon phenotypes have been identified from this region: AZ-A, AZ-B, AZ-C, AZ-D, and NM-A (Haverty et al., 1999b). The terpene profiles for southwestern *Reticulitermes* sorted into four main SDS phenotypes. Hydrocarbon phenotypes AZ-A and AZ-B had similar terpene profiles, primarily comprised of γ-cadinene and geranyl linalool, although quantities were variable (Table 4). AZ-B generally had more γ-cadinenal (0.5–13.2%), than AZ-A (0–1.3%). Soldier defense secretions from hydrocarbon phenotype AZ-C showed evidence of geographic differences (Table 4; Figure 2). Phenotype AZ-C has only been collected from the Petran Montane Coniferous Forests biotic community zone in southcentral Arizona (Brown and Lowe, 1980; Haverty and Nelson, unpublished observations). Samples from the Mogollon (Interior) biogeographic province (Brown et al., 1979), from Prescott to Springerville, Arizona, had soldier defense secretions consisting mainly of myrcene (1.3–20.3%), (*Z*)- and (*E*)-ocimene (0–19.8%), β-bisabolene (17.8–57.3%), γ-cadinene (1.8–40.5%), and geranyl linalool (0–50.4%). These samples were summarized as one group, AZ-C(I), although they were quite variable. There was much less variability in SDS profiles from samples collected in the higher elevations of the Santa Catalina, Santa Rita, Chiricahua, and Pinaleno mountains of the Sonoran biogeographic province (Brown et al., 1979). Samples of this SDS phenotype, AZ-C(II), all produced $\geq$94.7% geranyl linalool. We have not yet collected live soldiers of AZ-D, thus, the defense secretion profile of this phenotype is unknown. Soldiers of hydrocarbon phenotype NM-A yielded almost exclusively geranyl linalool (99.8%) (Table 4).

Reticulitermes *from Georgia.* Fifteen different cuticular hydrocarbon phenotypes have been reported from Georgia: GA-A, GA-AB, GA-B, GA-C, GA-D, GA-E, GA-F, GA-G, GA-H, GA-I, GA-J, GA-K, GA-L, GA-M, and GA-N (Haverty et al., 1996, 1999b). Soldier defense secretions were characterized for all hydrocarbon phenotypes except for GA-B. Two SDS phenotypes were associated with GA-A. Phenotype GA-A(I) was distinguished by a large quantity of geranyl linalool (47.0–80.9%), while in the second phenotype, GA-A(II), this diterpene alcohol never exceeded 2.3% of the total (Table 5; Figure 3). Within

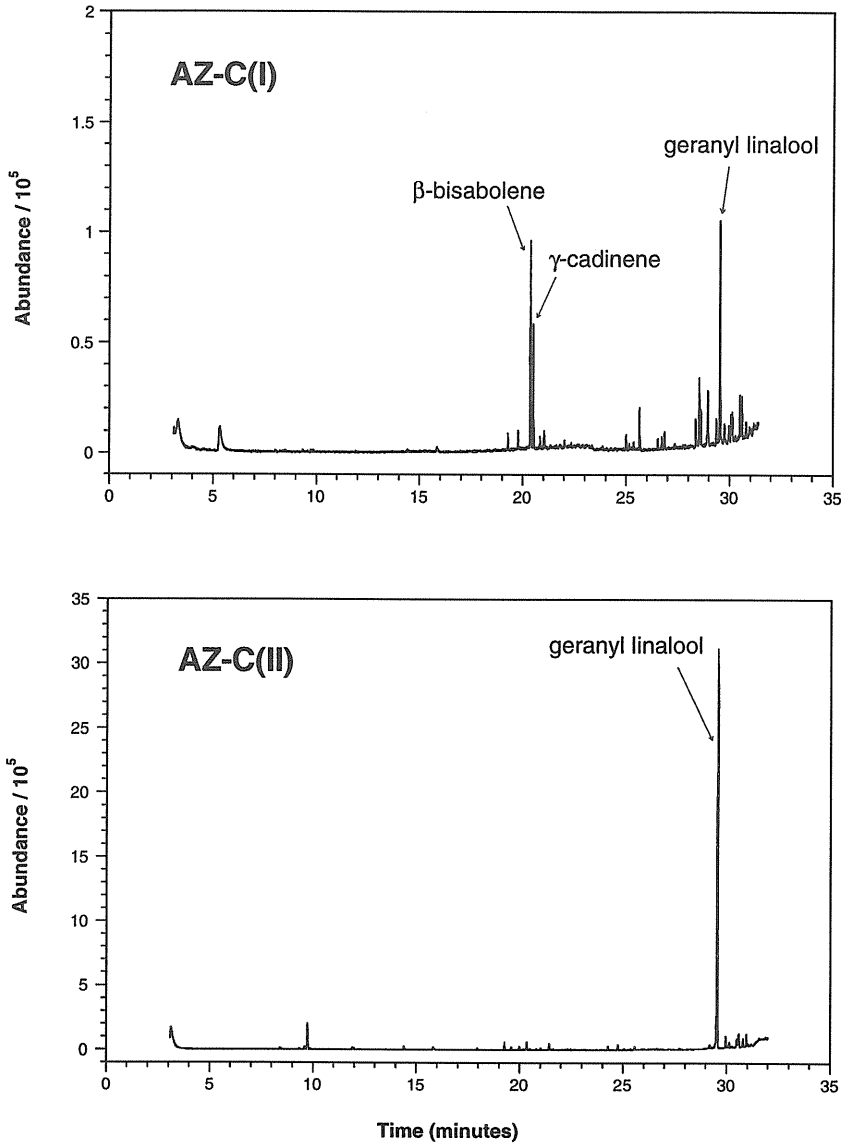

FIG. 2. Total ion chromatograms of defense secretions extracted from soldiers of cuticular hydrocarbon phenotype AZ-C.

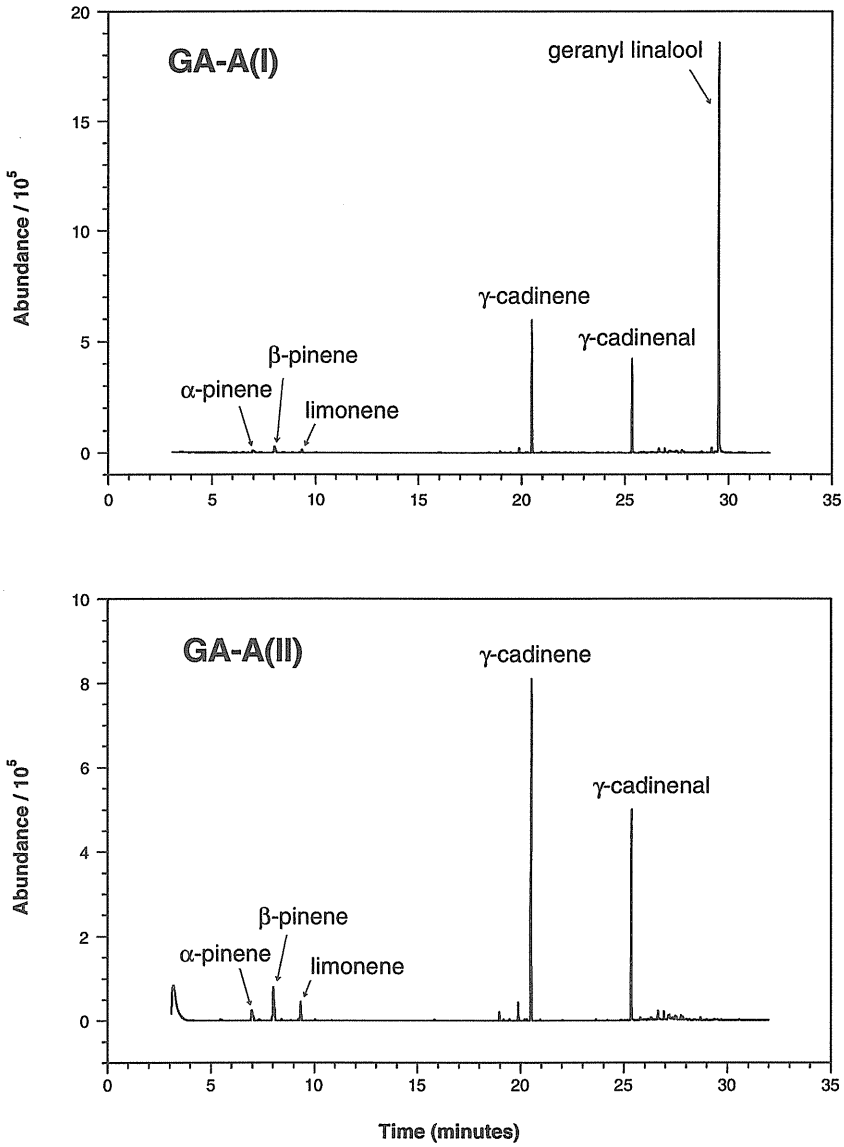

FIG. 3. Total ion chromatograms of defense secretions extracted from soldiers of cuticular hydrocarbon phenotype GA-A.

SDS phenotype GA-A(I), there was marked geographic variation in the amounts of the sesquiterpenes γ-cadinene and γ-cadinenal. Of the four samples making up this phenotype, the two from northern Georgia produced moderate amounts of γ-cadinene (10.7% and 20.4%) and γ-cadinenal (1.3% and 8.7%), while the two from Athens had trace amounts of γ-cadinene ($\leq$0.2%) and no detectable γ-cadinenal. These two sesquiterpenes were the major components for SDS phenotype GA-A(II); γ-cadinene averaged 56.3% of the total, and γ-cadinenal 17.2%. In both GA-A SDS phenotypes, with the exception of the two Athens samples, the ratio of γ-cadinene to its aldehyde was approximately 3:1 (Table 5). These phenotypes both contained monoterpenes (α-pinene, camphene, β-pinene, and limonene) in varying amounts (<0.1–15.9%) (Table 5). All of these GA-A samples keyed to *R. flavipes.*

Hydrocarbon phenotype GA-AB had only one SDS phenotype. This terpene type appeared to be intermediate between those produced by GA-A and GA-C in that it contained a significant monoterpene component, trace amounts of geranyl linalool, and roughly twice as much γ-cadinenal as γ-cadinene (Table 5; Figure 4). All GA-AB samples keyed to *R. flavipes.*

The SDS phenotype produced by GA-C soldiers contained no monoterpenes or geranyl linalool. The predominant components were γ-cadinene (averaging 20.1%) and γ-cadinenal (76.7%); the proportion of the latter was about three

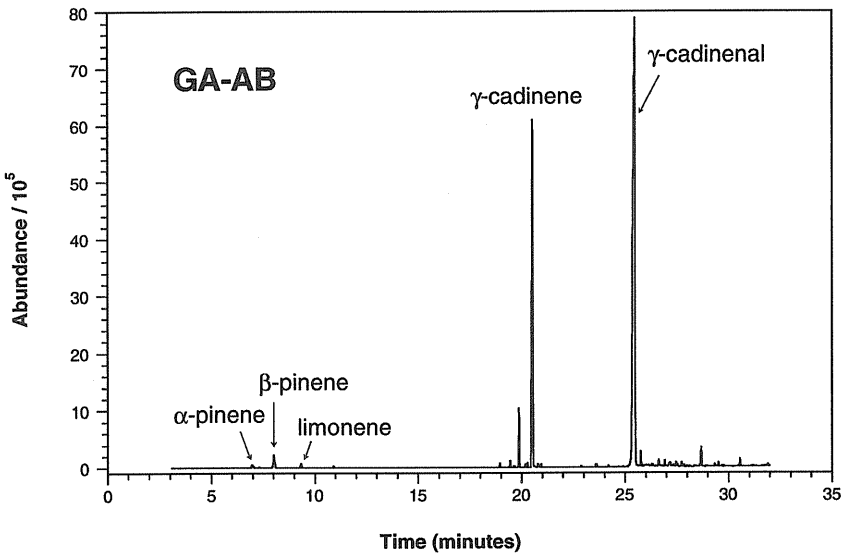

FIG. 4. Total ion chromatogram of defense secretions extracted from soldiers of cuticular hydrocarbon phenotype GA-AB.

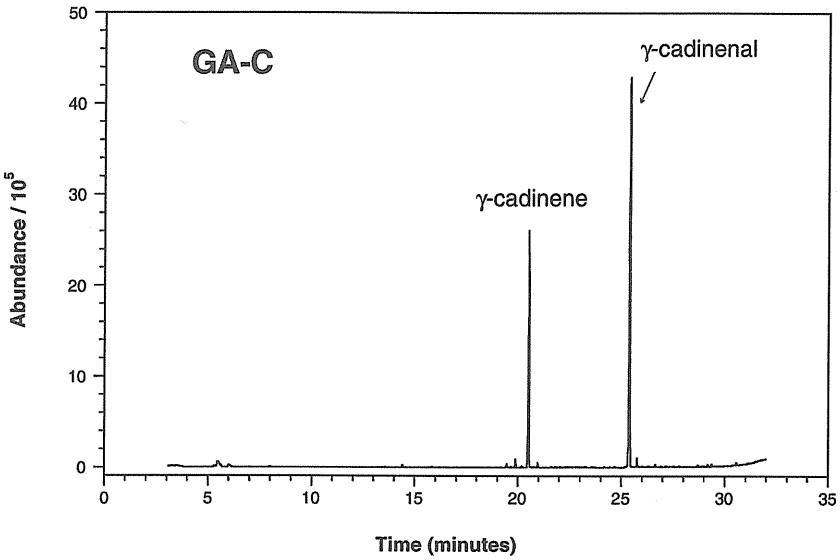

FIG. 5. Total ion chromatogram of defense secretions extracted from soldiers of cuticular hydrocarbon phenotype GA-C.

times that of the former, the opposite of SDS phenotypes produced by GA-A (Table 5; Figure 5). All GA-C samples keyed to *R. virginicus.*

Numerous hydrocarbon phenotypes, specifically those with a predominance of unsaturated hydrocarbon components (GA-D-I, -K to -N) produced nearly identical soldier defense secretions. This terpene mixture consisted primarily of γ-cadinene (79.1–100%) with only a trace of γ-cadinenal (Table 5; Figure 6). An unknown diterpene (M_r = 272, with a base peak of 257) was present in amounts ranging from <0.1% to 12.4%. All these samples keyed to *R. hageni* based on soldier morphology, although GA-D was the only phenotype that keyed to *R. hageni* based on alate morphology. Two of the cuticular hydrocarbon phenotypes, GA-E and GA-F, had alates that keyed to *R. virginicus* (Haverty et al., 1996). Alates were not available for the other phenotypes.

A single, distinct SDS phenotype was associated with hydrocarbon phenotype GA-J and was comprised primarily of germacrene A (50.8%) and germacrene B (39.9%) with lesser amounts of δ-elemene, farnesene, and geranyl linalool (Table 5). These samples all keyed to *R. hageni* based on soldiers.

DISCUSSION

Four SDS phenotypes paired with multiple hydrocarbon phenotypes: CA-C and NV-B produce nearly identical mixtures of soldier defense secretions; as do

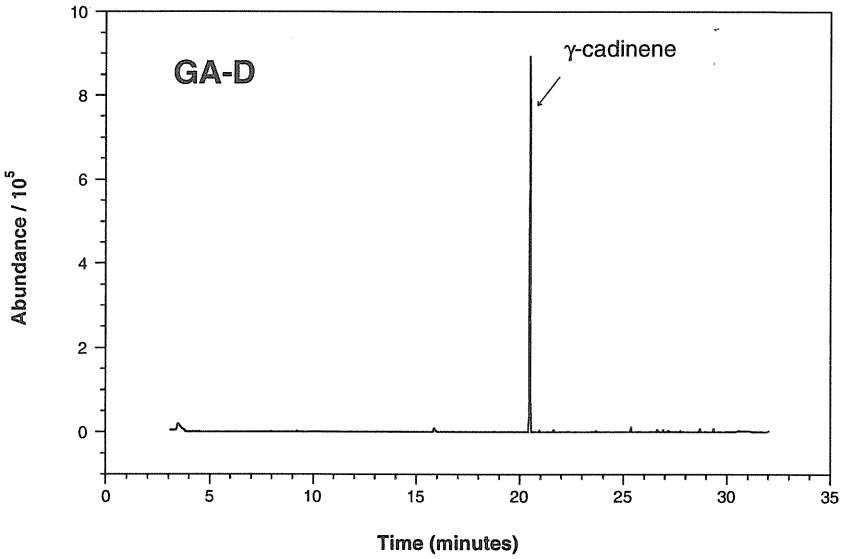

FIG. 6. Total ion chromatogram of defense secretions extracted from soldiers of cuticular hydrocarbon phenotype GA-D.

NV-A, NM-A, and some AZ-C samples; AZ-A and AZ-B; and GA-D-I, -K to -N (Table 6). Conversely, with the exception of AZ-C and GA-A, each hydrocarbon phenotype is correlated with only one SDS phenotype (Table 6).

The results from northern California consistently and repeatedly associate one hydrocarbon phenotype with one distinct soldier defense secretion phenotype (Table 3). We now consider CA-A and CA-A′ to be variations of one hydrocarbon phenotype, as we have recently seen samples from other locations in California that appear to be intermediate between the two (L. J. Nelson, unpublished observations). We believe there are at least four species of *Reticulitermes* represented by hydrocarbon phenotypes CA-A/CA-A′, CA-B, CA-C, and CA-D (Haverty and Nelson, 1997).

The cuticular hydrocarbon composition of the single sample of NV-B is nearly identical to that of CA-B, but we will designate it as a separate phenotype pending further sampling. There was virtually no overlap in terpene composition for these two hydrocarbon phenotypes (Tables 3, 4, and 6).

There are many similarities between NV-A and NM-A in both sets of chemical characters. They could quite possibly represent a single species that occurs in the Great Basin biogeographic province (Brown et al., 1979). AZ-A and AZ-B also likely represent a single taxon, based on their chemical phenotypes. These four phenotypes (NV-A, NM-A, AZ-A, and AZ-B) form a clade when subjected to

phylogenetic (PAUP) analysis based on cuticular hydrocarbons (Page et al., 2001), which may indicate a close taxonomic relationship. AZ-C is a distinct cuticular hydrocarbon phenotype, but exhibits some variability in SDS profiles (Tables 5 and 6; Figure 2). We feel confident that this is a separate species.

Sampling from Georgia has produced 15 cuticular hydrocarbon phenotypes and 6 SDS phenotypes. We consider GA-C (=*R. virginicus*) and GA-J (=undescribed species of *Reticulitermes*) to be distinct species, and we suggest GA-A, GA-AB, and GA-B are either separate taxa or represent intraspecific variation in *R. flavipes*. GA-AB has been found only on Sapelo Island off the Atlantic coast of Georgia, and nearby on the mainland (Chatham County). GA-B has been rarely found in Georgia, despite directed efforts to locate additional samples (Haverty et al., 1996, 1999b).

The remaining 10 hydrocarbon phenotypes from Georgia all possess the same terpene phenotype. Cuticular hydrocarbon phenotypes GA-D, GA-E, GA-F, GA-G, GA-H, GA-I, GA-K, GA-L, GA-M, and GA-N also have a common theme in their abundant production of certain olefins (Haverty et al., 1996, 1999b). Although some phenotypes appear to be restricted to certain geographic localities, they have all been seen from multiple collections. Variation in cuticular hydrocarbon composition due to the influence of seasonal or environmental effects has not been ruled out. However, when mitochondrial DNA genotypes of several colonies of *Reticulitermes* in Georgia were examined, samples with hydrocarbon phenotypes GA-I and GA-L (which were identified as *R. hageni* based on soldier morphology) formed a separate clade from phenotypes GA-D (identified as *R. hageni* by soldiers and alates) (Jenkins et al., 2000). Resolution of this taxonomic conundrum will require additional biological, chemical and genetic information.

The use of state designations for hydrocarbon phenotypes will undoubtedly be revised when we have sampled more widely and the phenotype distributions can be delineated more clearly. There are a few parallels in chemical characters when comparing collections from distant locations. For example, the hydrocarbon profiles of GA-A and GA-AB are qualitatively and quantitatively similar to CA-A/A′ (Haverty and Nelson, 1997; Haverty et al., 1996; Page et al., 2001), the main difference being the quantities of C_{33} methylalkanes present. Their terpene secretions are less similar, although the percent ranges of γ-cadinene and geranyl linalool overlap in some cases (Tables 3, 5, and 6). The hydrocarbon profile of the single sample of AZ-D appeared to be nearly identical to CA-A′. We were unable to collect soldiers from this colony, so the terpene profile remains unknown until more collections can be made in northwestern Arizona as well as other localities in the Great Basin Desert.

Termite collections that keyed to *R. hageni* by soldier morphology presented us with a wide array of hydrocarbon phenotypes (11), but with the exception of GA-J, all had the same SDS phenotype. This terpene phenotype is characterized by the abundance of γ-cadinene (averaging 95% of the total), as is the terpene

phenotype found in CA-A/A′ (Tables 3, 5, and 6; Figures 1 and 6). However, these 10 hydrocarbon phenotypes from Georgia are, as a group, qualitatively quite dissimilar in hydrocarbon components from phenotype CA-A/A′. The former have an abundance of olefins (>50% of total hydrocarbon) and the latter are characterized by a predominance of normal and methylbranched alkanes (Haverty and Nelson, 1997; Haverty et al., 1996, 1999b; Page et al., 2001).

No terpene compound was seen in every sample, although γ-cadinene and geranyl linalool were present in some amount in most phenotypes. The only phenotype with no detectable geranyl linalool was GA-C (Tables 5 and 6). γ-Cadinene was not detected in hydrocarbon phenotypes NV-A, NV-B, NM-A, or GA-J (Tables 4–6). Monoterpenes were seen in most phenotypes, in trace amounts, but were consistently present in cuticular hydrocarbon phenotypes GA-A and GA-AB (Tables 5 and 6).

Our results add to the body of knowledge already accumulated regarding the utility of these chemical characters for distinguishing taxa of North American *Reticulitermes*. Howard et al. (1978, 1982b) first reported the cuticular hydrocarbons of *R. flavipes* and *R. virginicus* collected near Gulfport, Mississippi. "γ_1-Cadinene" and "γ_1-cadinenal" were reported by Zalkow et al. (1981) as the major soldier cephalic secretion components of both *R. flavipes* and *R. virginicus* from Mississippi. Quantities were reported only for *R. flavipes*, and the two sesquiterpenes were present in nearly equal amounts. The identity of these sesquiterpenes is here revised to (+)-γ-cadinene and (+)-γ-cadinen-14-al. A few of our *R. flavipes* samples within groups GA-A(II) and GA-AB had comparable proportions to those reported by Zalkow et al. (1981), however, we found considerable variation in terpene composition within the three *R. flavipes* groups (Tables 5 and 6).

Clément et al. (1985) also examined frontal gland secretions and described four phenotypes of *Reticulitermes* in the southeastern United States: *R. flavipes* 1 and 2, *R. virginicus*, and *R. malletei*. Both *R. flavipes* phenotypes, Rf1 and Rf2, had γ-cadinene, geranyl linalool and small amounts of monoterpenes, but Rf1 also had γ-cadinenal. They also reported γ-cadinene and γ-cadinenal from *R. virginicus* and γ-cadinene alone in what is referred to as the species *R. malletei*. These would correspond to the SDS from our cuticular hydrocarbon phenotypes GA-C and GA-D-I, -K to -N, respectively (Haverty et al., 1996, 1999b). The hydrocarbon phenotype of *R. malletei* as reported in Bagnères (1989) is equivalent to our cuticular hydrocarbon phenotype GA-M (Haverty et al., 1999b).

Bagnères et al. (1990) documented the cuticular hydrocarbons and soldier cephalic secretions of *R. flavipes* in the southeastern United States and *R. santonensis* in France. The hydrocarbons of these two species were found to be qualitatively, but not quantitatively, identical. *R. flavipes* exhibited polymorphism in both sets of chemical characters, while *R. santonensis* did not. Three hydrocarbon phenotypes of *R. flavipes* were defined by multivariate analysis, two of which had unique

defensive secretion phenotypes (A and B), while the third was further divided into four defensive secretion phenotypes (C–F). Terpenes identified were α-pinene, β-pinene, limonene, γ-cadinene, cadinene aldehyde, and geranyl linalool. Phenotype A was defined as having the three monoterpenes and two sesquiterpenes, while B had only the two sesquiterpenes. Phenotype C exhibited all six compounds, D the two sesquiterpenes and geranyl linalool, while E and F had no γ-cadinene, only its aldehyde. Phenotype E also produced geranyl linalool, as did F, and F also had the three monoterpenes.

All but two of our samples identified as *R. flavipes* had γ-cadinene in quantities of at least 10.0% of the total. Those two samples, from Athens, Georgia, showed only traces of γ-cadinene and no γ-cadinenal, their profiles consisting mostly of geranyl linalool (>75.0%) and monoterpenes. As for *R. santonensis*, its terpene profile included the monoterpenes, geranyl linalool, and an unidentified sesquiterpene (Bagnères et al., 1990). γ-Cadinene and its aldehyde were absent. These authors suggest that *R. santonensis* and *R. flavipes* are the same species and that the lack of chemical variation in *R. santonensis* results from a founder event of a single colony of *R. flavipes* being successfully introduced to Europe from the United States (Bagnères et al., 1990).

The primary function of the various termite-produced terpenoid compounds has been attributed to their effectiveness in deterring predation by ants, either by toxicity or repellency (Zalkow et al., 1981; Baker et al., 1982; Mill, 1983; Scheffrahn et al., 1983; Clément et al., 1988; Lemaire et al., 1990). There is a strong indication of coevolution between termites and ants: where they are sympatric, the ants are less sensitive to the specific terpenoid compounds and where they are allopatric the ants are more sensitive (Zalkow, et al., 1981; Lemaire et al., 1990). Further behavioral studies are needed involving *Reticulitermes* species' defensive compounds and their effects on predators. Although an untested hypothesis, variation in SDS may reflect adaptation to the local ant fauna and could explain the presence of multiple SDS phenotypes of GA-A and AZ-C.

Howse and Bradshaw (1980) discussed the use of chemical data in ant and termite systematics and felt that the behavioral or ecological roles of the various chemicals should be known in order to be useful in this context. However, Prestwich (1983) suggested that the necessity of understanding the biological or ecological functions of the chemical characters is perhaps less important than knowing their biosynthetic relationships and that the phylogeny of the biosynthetic pathways reflects genetic drift or founder effects, rather than selective pressure. Brand (1978) stated that all available evidence, including chemical data, should be taken into account in describing a taxon and suggested that the biosynthetic homology of chemical characters provides a closer look at genetic relationships than does the similarity of morphological characters. Chemical variation certainly seems as likely to affect behavior as would variation in morphology. This suggests that chemical characters such as cuticular hydrocarbons and soldier defense

secretions are ideal tools for understanding the evolutionary relationships of the taxa in question, particularly so once the full elucidation of their biosynthesis has been achieved.

We believe, and have so stated, that existing keys to species of *Reticulitermes* are grossly inadequate and give a false sense of confidence in identifying species (Haverty and Nelson, 1997; Haverty et al., 1996, 1999b). Taxonomic assessments based on chemical characters and those based on morphological characters are not always in agreement. Takematsu and Yamaoka (1999) recently examined the cuticular hydrocarbons of six species of *Reticulitermes*, including three undescribed species, in Japan, Korea, and Taiwan. They observed nine different hydrocarbon phenotypes and recommended that four subspecies be elevated to species status. Takematsu (1999) then published a revision of *Reticulitermes* species in Japan, which included cuticular hydrocarbon data to supplement the more conventional characters used in taxonomy.

We agree that chemical characters have a place in the description of species. The more differences that exist to distinguish two groups of organisms, the greater the likelihood of their being separate species (Futuyma, 1998). Genetic studies of this genus will provide additional clarification. In studies of European *Reticulitermes*, variation in the composition of soldier frontal gland secretons has been correlated with differences in frequencies of esterase alleles (Clément, 1981; Parton et al., 1981). In future research we will attempt to match chemical characters with DNA sequences for all cuticular hydrocarbon phenotypes, building on previous work in this area (Jenkins et al., 1998, 1999, 2000). Agonistic behavior bioassays using *Reticulitermes* from northern California demonstrated a high degree of correlation between aggression and hydrocarbon phenotype (Haverty et al., 1999a). These chemotaxonomic studies have served to benefit our studies of ecology, behavior, and control of *Reticulitermes* (Getty et al., 1999a,b, 2000a,b; Haverty et al., 1999a,c, 2000). We hope further study will allow us to fully characterize these taxa.

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