Journal of Chemical Ecology, Vol. 26, No. 5, 2000

CUTICULAR HYDROCARBONS OF TERMITES OF THE HAWAIIAN ISLANDS

MICHAEL I. HAVERTY,[1,*] R. JOSEPH WOODROW,[2] LORI J. NELSON,[1] and J. KENNETH GRACE[2]

[1]*Pacific Southwest Research Station, Forest Service*
US Department of Agriculture
P.O. Box 245, Berkeley, California 94701
[2]*Department of Entomology, University of Hawaii*
Honolulu, Hawaii 96822

(Received June 14, 1999; accepted January 1, 2000)

Abstract—Seven species of termites (Isoptera) belonging to three families are found in the Hawaiian Islands. The Kalotermitidae include *Neotermes connexus* Snyder, *Cryptotermes brevis* (Walker), *Cryptotermes cynocephalus* Light, *Incisitermes immigrans* Snyder, and the recently introduced *Incisitermes minor* (Hagen). *Zootermopsis angusticollis* (Hagen), a native of the Pacific Coastal region of North America has become established on Maui and is the sole representative of the Termopsidae. The only rhinotermitid known to be established in the Hawaiian Islands is *Coptotermes formosanus* Shiraki. A closely related species, *Coptotermes vastator* Light, has been reported from the Hawaiian Islands, but not recently documented. Cuticular hydrocarbon mixtures were characterized for each of the established and introduced species, as well as for *C. vastator* from Guam. The diversity of the hydrocarbon mixtures was extreme. At least half the hydrocarbons of *C. brevis*, *C. cynocephalus*, *I. immigrans*, and *N. connexus* are olefins. *C. formosanus* and *C. vastator* make no olefins, but methyl-branched alkanes comprise ca. 95% and 85% of their hydrocarbon mixtures, respectively. Blends of abundant hydrocarbons are species-specific and can be used to identify a given taxon without the diagnostic castes, soldiers, or imagoes. Cuticular hydrocarbon mixtures appear to correlate with habitat requirements.

Key Words—Cuticular hydrocarbons, chemotaxonomy, Isoptera, tropical termites, gas chromatography, mass spectrometry, Hawaiian Islands, Pacific termites, olefins, methylalkanes.

*To whom correspondence should be addressed.

INTRODUCTION

Ehrhorn (1934) and Zimmerman (1948) wrote the first comprehensive reports of the termite fauna of the Hawaiian Islands. Bess (1970) wrote the most recent report on the termites of Hawaii; he concentrated his description on the biology of the four established species, *Neotermes connexus* Snyder, *Incisitermes immigrans* (Snyder), *Cryptotermes brevis* (Walker), and *Coptotermes formosanus* Shiraki. Since the publication of Bess' chapter, two additional species have become established, and another has been introduced, but is not yet known to be established. Woodrow et al. (1999a) and Scheffrahn et al. (1999) confirm the establishment of *Cryptotermes cynocephalus* Light in the vicinity of Waiahole Valley on the eastern shore of Oahu. *Zootermopsis angusticollis* (Hagen) is now established in the vicinity of Kula on Maui at an elevation of ca. 1500 m. *Incisitermes minor* (Hagen) has recently been introduced in hardwood doors in two disparate locations on Oahu, but it is not clear whether or not it is established. Bess (1970) also considered *C. vastator* to be established on Oahu, but confirmation of these established colonies has not been made.

In this paper we expand the descriptive work of Bess (1970) and Woodrow et al. (1999a) to include documentation of the cuticular hydrocarbon mixtures of all termite species collected from the Hawaiian Islands. Characterization of the cuticular hydrocarbons of each species supports the species specificity of hydrocarbon mixtures for this region and provides another method of identifying species when the diagnostic castes are lacking. Patterns of cuticular hydrocarbon mixtures are correlated with habitat type.

METHODS AND MATERIALS

Collection of Termites. Termites used to document the cuticular hydrocarbons of each termite species in Hawaii were obtained during random collections, primarily on the islands of Oahu and Maui. Collections of *C. formosanus* were made from permanent monitoring stations on the University of Hawaii campus (Haverty et al., 1996b). The colony of *C. vastator* used in this study came from an infested wooden cable spool shipped from Guam to the Alameda Naval Air Station in California.

With the exception of the sample from Guam, termite samples were bagged and brought to the Termite Project laboratory on the University of Hawaii campus, where the termites were separated from wood and other debris. Samples of workers, pseudergates, or nymphs were placed in separate vials, frozen, and then dried (Haverty et al., 1996a,b; Woodrow et al., 1999b). The number of termites in a sample varied by species; 15–20 nymphs or pseudergates of termopsids or kalotermitids, or up to 200 *Coptotermes* workers were dried. Once the termites were completely dry, specimens were placed in a vial that was tightly capped.

Dried samples were mailed to the Forest Service laboratory in Albany, California, for extraction and characterization of cuticular hydrocarbons. Concurrently, fresh (i.e. not dried) voucher samples from each collection were preserved in 70% ethanol and deposited in the University of Hawaii collection.

Extraction Procedure and Characterization of Cuticular Hydrocarbons. In this study cuticular hydrocarbons were extracted, characterized, and quantified in the same manner as reported in Haverty et al. (1997). We have standardized our technique for analyzing cuticular hydrocarbon mixtures from termites (Haverty 1996c). We dry the termites before extraction. Dried specimens make shipping and storage of termites much easier, especially tropical termites. They pose no quarantine problems and require no transportation of flammable solvents in land vehicles or aircraft.

The results of this method are not equivalent to extracting live or freshly frozen termites; differences in the composition of cuticular hydrocarbons extracted from dried or live specimens of a species may be quantitatively different, but qualitative differences would not be expected. "Drying termites prior to the extraction greatly increases the chance of consistently detecting hydrocarbons of low abundance, especially the olefin fraction. . . . There is the possibility that these differences are due to the extraction of hydrocarbons from the internal tissues" (Haverty et al., 1996c).

GC-MS peak areas were converted to percentages of the total hydrocarbon fraction. A summary of the relative amounts of each hydrocarbon for each species were presented to facilitate comparisons. Relative amounts of each hydrocarbon were coded as follows: +++, >3.0%; ++, 1.0–3.0%; +, 0.3–0.99%; and tr, trace amounts of the total hydrocarbon mixture. Representative chromatograms were evaluated to present percentages of the different classes of hydrocarbons and the predominant hydrocarbons in each class for each species.

In the text and tables, we use shorthand nomenclature to identify individual hydrocarbons or mixtures of hydrocarbons. This shorthand uses a descriptor for the location of methyl groups (X-me), the total number of carbons (CXX) in the hydrocarbon component excluding the methyl branch(es), and the number of double bonds following a colon CXX:Y). Thus, pentacosane becomes *n*-C25; 2-methylpentacosane becomes 2-meC25; 13,15-dimethylnonacosane becomes 13,15-dimeC29; and heptacosadiene becomes C27:2. Hydrocarbons are presented in the tables for each species in the order of elution on our GC-MS system within each hydrocarbon class.

RESULTS AND DISCUSSION

In his discussion of the termites of the Hawaiian Islands, Bess (1970) listed a total of four species in four genera and two families. We characterized cuticular hydrocarbons for all of these species, as well as those of the three newly

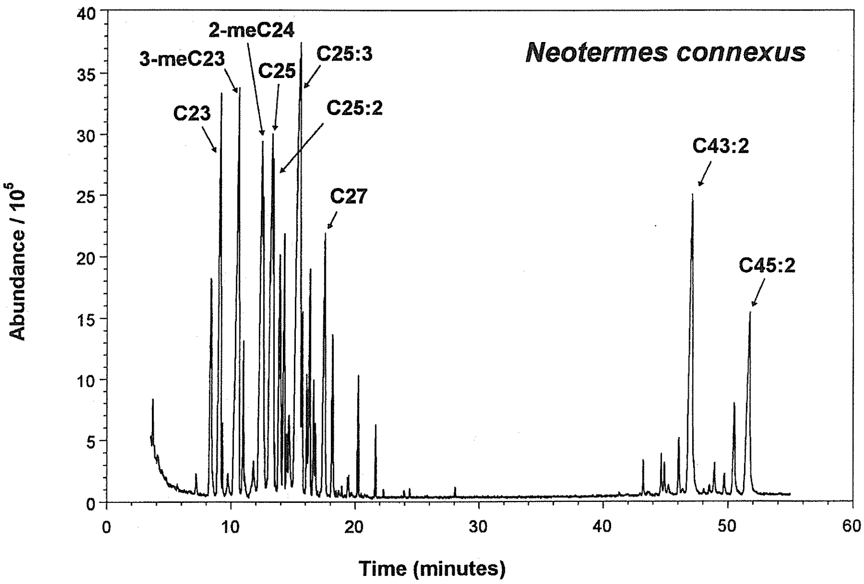

FIG. 1. Total ion chromatogram of the cuticular hydrocarbons from nymphs of *Neotermes connexus* Snyder from Iao Valley Lookout, Maui, Hawaii.

introduced species and *C. vastator*, which is potentially present in Hawaii. Most of the specimens used for these analyses were collected on either Oahu or Maui. Whenever possible, we used collections from multiple locations to include intraspecific variation.

Neotermes connexus *Snyder*. The cuticular hydrocarbon mixture of *N. connexus* reflected a general pattern seen in most of the drywood termite species examined thus far in the West Indies (Haverty et al., 1997). Cuticular hydrocarbons occurred in two distinct groups: early eluting compounds (23–29 carbons in the parent chain) and late-eluting compounds (41–45 carbons in the parent chain). Early eluting compounds predominate, representing over 80% of the total hydrocarbons (Figure 1).

n-Alkanes present were *n*-C22, *n*-C23, *n*-C24, *n*-C25, *n*-C27, *n*-C28, and *n*-C29 (Table 1). *n*-C23, *n*-C25, and *n*-C27 were most abundant, comprising ca. 7.3%, 8.5%, and 4.1% of the total hydrocarbons, respectively. The other *n*-alkanes accounted for ca. 2.2% of the total hydrocarbons.

Olefins were, by far, the most predominant hydrocarbons, representing over 52% of the total hydrocarbons (Tables 2–4). Monoenes were not abundant (3.1% of the total hydrocarbons); two isomers each of C25:1 and C27:1 accounted for all of these hydrocarbons (Table 2). The dienes and the trienes comprised 26.7% and 22.6% of the total hydrocarbons, respectively. Four isomers of C25:2 and two

TABLE 1. RELATIVE AMOUNTS OF NORMAL ALKANES IN CUTICULAR HYDROCARBONS OF WORKERS OR PSEUDERGATES OF TERMITES FROM HAWAIIAN ISLANDS[a]

	Species[c]							
Hydrocarbon[b]	Neo con	Inc imm	Cry bre	Cop for	Cry cyn	Zoo ang	Inc min	Cop vas
n-C20	o	o	o	o	o	+	o	o
n-C21	o	o	o	o	o	+++	o	o
n-C22	tr	o	o	o	o	+	o	o
n-C23	+++	+++	tr	o	+	+++	++	o
n-C24	++	++	tr	o	tr	o	+	+
n-C25	+++	+++	+++	+	+++	++	+++	+++
n-C26	o	++	++	+	+	tr	++	+++
n-C27	+++	+++	+++	++	+++	++	+++	+++
n-C28	tr	tr	+	+	o	tr	tr	+
n-C29	+	+	+++	tr	+	++	++	tr
n-C31	o	o	tr	o	o	o	o	o

[a]+++, >3.0%; ++, 1.0–3.0%; +, 0.3–0.99% of total hydrocarbon; tr, trace.
[b]Presented in order of elution.
[c]Neo con = *Neotermes connexus*, Inc imm = *Incisitermes immigrans*, Cry bre = *Cryptotermes brevis*, Cop for = *Coptotermes formosanus*, Cry cyn = *Cryptotermes cynocephalus*, Zoo ang = *Zootermopsis angusticollis*, Inc min = *Incisitermes minor*, Cop vas = *Coptotermes vastator*.

isomers of C25:3 accounted for 9.8% and 17.6% of the total hydrocarbons, respectively (Tables 2–4). The late-eluting dienes C43:2 and C45:2 accounted for 12.6% of the total hydrocarbons. Small amounts of the tetraene C45:4 were also seen (Table 4).

Terminally branched monomethylalkanes were identified for C22 to C26 (Table 5). 3-MeC23 and 2-meC24 accounted for 7.0% and 8.1% of the total hydrocarbons, respectively. The remainder of these terminally branched monomethylalkanes comprised ca. 8.6% of the total hydrocarbons (Table 5). Internally branched monomethylalkanes were rare and amounted to only 1.8% of the total hydrocarbons (Table 6). Neither dimethylalkanes nor trimethylalkanes were detected (Table 7).

Incisitermes immigrans *Snyder.* Members of the genus *Incisitermes* are the most common kalotermitids, if not termites, found in the Hawaiian Islands (Bess, 1970; Woodrow et al., 1999a), as well as in the islands of the West Indies. (Collins et al., 1997; Scheffrahn et al., 1994). They live in sound, dead wood of trees of many species, as well as occasionally in structural timber, throughout much of their range (Bess, 1970; Woodrow et al., 1999a). The general pattern of the chromatograms of *I. immigrans* (Figure 2) was similar to that of *N. connexus* (Figure 1) where ca. 70% of the hydrocarbons have 23–29 carbons.

n-Alkanes present were *n*-C23, *n*-C24, *n*-C25, *n*-C26, *n*-C27, *n*-C28, and *n*-C29 (Table 1). *n*-C25 and *n*-C27 were the most abundant, comprising 12.0%

TABLE 2. RELATIVE AMOUNTS OF MONOENES IN CUTICULAR HYDROCARBONS OF WORKERS OR PSEUDERGATES OF TERMITES FROM HAWAIIAN ISLANDS[a]

		Species[d]							
Hydrocarbon[b]	ECL[c]	Neo con	Inc imm	Cry bre	Cop for	Cry cyn	Zoo ang	Inc min	Cop vas
C25:1	24.70	++	+	o	o	o	o	o	o
C25:1	24.80	+	o	o	o	o	o	o	o
C26:1	25.70	o	tr	o	o	+	o	o	o
C27:1	26.30	o	o	o	o	tr	o	o	o
C27:1	26.70	+	+	o	o	+++	o	o	o
C27:1	26.85	+	o	o	o	o	o	o	o
C28:1	27.30	o	o	o	o	tr	o	o	o
C28:1	27.70	o	o	o	o	+	o	o	o
C29:1	28.30	o	o	o	o	tr	o	o	o
C29:1	28.70	o	o	tr	o	+	o	o	o
C31:1	30.70	o	o	tr	o	tr	+	o	o
C33:1	32.70	o	o	tr	o	o	o	o	o
C35:1	34.70	o	o	tr	o	o	o	o	o
C37:1	36.70	o	o	++	o	+	o	+	o
C38:1	37.70	o	o	tr	o	o	o	o	o
C39:1	38.70	o	o	++	o	+	o	++	o
C40:1		o	o	tr	o	o	o	o	o
C41:1		o	o	++	o	+++	o	++	o
C42:1		o	tr	tr	o	o	o	o	o
C43:1		o	+++	++	o	++	o	++	o

[a]See Table 1.
[b]See Table 1.
[c]ECL: equivalent chain length (approximate).
[d]See footnote c, Table 1.

and 7.2% of the total hydrocarbons (Figure 2). The remaining *n*-alkanes totaled ca. 9.3% of the total hydrocarbons.

The unsaturated components constituted ca. 60% of the total hydrocarbons. Olefins with 25 or 43 carbons predominated. C25:2, C43:1, and C43:2 accounted for 14.1%, 4.8%, and 9.0% of the total hydrocarbons, respectively. Two isomers of C27:2 and C45:3 were 10.4% and 8.6% of the total hydrocarbons (Figure 2, Tables 2–4). The remaining unsaturated components totaled to only 13.4% of all hydrocarbons. This species makes the tetraene C45:4 in significant amounts (Table 4).

2- and 3-Methylalkanes were identified for C22–C27, with a 2-meC23 representing 5.5% of the total hydrocarbons, the most abundant (Table 5). Of the 3-methylalkanes, 3-meC23 was the most abundant. These terminally branched monomethylalkanes comprised ca. 10.4% of the total hydrocarbons.

Small amounts of internally branched monomethylalkanes were present in

TABLE 3. RELATIVE AMOUNTS OF DIENES IN CUTICULAR HYDROCARBONS OF WORKERS OR PSEUDERGATES OF TERMITES FROM HAWAIIAN ISLANDS[a]

		Species							
Hydrocarbon	ECL	Neo con	Inc imm	Cry bre	Cop for	Cry cyn	Zoo ang	Inc min	Cop vas
C23:2	23.01	+	o	o	o	o	o	o	o
C25:2	24.75	+	+++	o	o	o	o	o	o
C25:2	25.01	++	o	o	o	o	o	o	o
C25:2	25.35	+++	o	o	o	o	o	o	o
C25:2	25.50	++	o	o	o	o	o	o	o
C26:2	25.60	o	+	o	o	o	o	o	o
C26:2	26.30	+	o	o	o	o	o	o	o
C27:2	26.30	+	+++	o	o	o	o	o	o
C27:2	26.75	o	++	o	o	o	o	o	o
C27:2	27.01	tr	o	o	o	o	o	o	o
C27:2	27.35	++	o	o	o	o	o	o	o
C28:2	27.30	o	tr	o	o	o	o	o	o
C29:2	28.50	+	o	o	o	+	o	o	o
C31:2	30.50	o	o	o	o	+	o	o	o
C33:2	32.40	o	o	tr	o	o	o	o	o
C35:2	34.40	o	o	++	o	o	o	++	o
C36:2	35.40	o	o	+	o	o	o	o	o
C37:2	36.40	o	o	+++	o	+++	++	++	o
C38:2	37.40	o	o	++	o	+	o	o	o
C39:2	38.50	o	o	+++	o	+++	++	o	o
C40:2	39.40	o	o	++	o	+	o	o	o
C41:2		tr	tr	+++	o	+++	++	o	o
C42:2		tr	tr	+	o	tr	o	o	o
C43:2		+++	+++	++	o	+++	+	o	o
C44:2		+	+	o	o	o	o	o	o
C45:2		+++	++	++	o	o	o	o	o

[a]See Tables 1 and 2 for explanation of terms and abbreviations.

a few samples and only at C26 and C27 (Table 6). These compounds occurred in isomeric mixtures. Di- and trimethylalkanes were absent (Table 7).

Cryptotermes brevis (*Walker*). The phragmotic heads of the soldiers, the presence of piles of dry fecal pellets in infested buildings, and the paper-thin outer surface of furniture or wood containing colonies of *C. brevis* are characteristic of this circumtropical species of termite. *C. brevis* is very common in Hawaii, but has never been reported from habitats other than structural timber, furniture, and objects of art, not exposed to moisture (Bess, 1970).

C. brevis clearly reflects the general pattern of hydrocarbon mixtures of drywood termites living in xeric habitats (Haverty et al., 1997). In this species hydrocarbons occurred in two groups; the early eluting compounds consisted

TABLE 4. RELATIVE AMOUNTS OF TRIENES AND A TETRAENE IN CUTICULAR HYDROCARBONS OF WORKERS OR PSEUDERGATES OF TERMITES FROM THE HAWAIIAN ISLANDS[a]

		Species							
Hydrocarbon	ECL	Neo con	Inc imm	Cry bre	Cop for	Cry cyn	Zoo ang	Inc min	Cop vas
Trienes									
C25:3	25.98	+++	o	o	o	o	o	o	o
C25:3	26.07	++	o	o	o	o	o	o	o
C25:3	26.28	o	+	o	o	o	o	o	o
C25:3	26.47	++	o	o	o	o	o	o	o
C27:3	28.03	tr	o	o	o	o	o	o	o
C37:3	36.38	o	o	+	o	o	++	++	o
C38:3	37.30	o	o	tr	o	o	o	o	o
C39:3	38.25	o	o	++	o	+	++	o	o
C40:3		o	o	+	o	o	o	o	o
C41:3		o	o	+++	o	tr	+++	o	o
C42:3		o	o	+	o	o	o	o	o
C43:3		+	++	++	o	++	+++	o	o
C44:3		o	+	o	o	o	o	o	o
C45:3		++	+++	++	o	o	o	o	o
Tetraene									
C45:4		tr	+	o	o	o	o	o	o

[a]See Tables 1 and 2 for explanation of terms and abbreviations.

almost exclusively of *n*-alkanes and terminally branched monomethyl alkanes, and late-eluting compounds were primarily olefins (Figure 3).

n-Alkanes present were *n*-C23, *n*-C24, *n*-C25, *n*-C26, *n*-C27, *n*-C28, *n*-C29, and *n*-C31 (Table 1). *n*-C25 and *n*-C27 were the most abundant, comprising ca. 13% and 11.6%, respectively, of the total hydrocarbons from the samples. All of the other *n*-alkanes combined represented ca. 5.6% of the total hydrocarbons.

Alkenes, alkadienes, and alkatrienes were the predominant class of cuticular hydrocarbons, representing ca. 52% of the total hydrocarbons. The number of carbons ranged from 29 to 45 (Tables 2–4). The late-eluting dienes C37:2, C39:2, C41:2, and C43:2 account for 7.5%, 9.6%, 4.5%, and 2.5% of the total hydrocarbons (Table 3). The trienes C39:3, C41:3, C43:3, and C45:3 add 2.4%, 3.7%, 2.1%, and 2.3% to the total hydrocarbons (Figure 3).

2- and 3-Methylalkanes were identified from C23 to C29. These terminally branched monomethylalkanes comprised ca. 17% of the total hydrocarbons. In *C. brevis* the 2- and 3-methylalkanes almost always occurred in pairs. When the parent chain of these hydrocarbons contained an even number of carbons, the 2-

TABLE 5. RELATIVE AMOUNTS OF TERMINALLY BRANCHED MONOMETHYLALKANES IN CUTICULAR HYDROCARBONS OF WORKERS OR PSEUDERGATES OF TERMITES FROM THE HAWAIIAN ISLANDS[a]

	Species							
Hydrocarbon	Neo con	Inc imm	Cry bre	Cop for	Cry cyn	Zoo ang	Inc min	Cop vas
5-meC21	o	o	o	o	o	++	o	o
3-meC21	o	o	o	o	o	+++	o	o
2-meC22	+++	+	o	o	o	++	o	o
2-meC23	++	+++	+	o	+	o	+++	o
3-meC23	+++	++	++	o	o	+	+++	o
2-meC24	+++	tr	+++	o	+++	o	++	+
3-meC24	o	o	+	o	tr	o	++	o
5-meC25	o	o	o	o	o	tr	o	o
2-meC25	+	+	++	+++	++	o	++	+++
3-meC25	++	+	+++	+++	+++	o	++	+++
2-meC26	+	tr	+	++	o	o	tr	+++
3-meC26	o	o	tr	++	o	o	tr	+
5-meC27	o	o	o	o	o	+	o	o
2-meC27	o	tr	tr	+++	+	o	o	+++
3-meC27	o	tr	+	+++	+	o	o	+++
2-meC28	o	o	o	+	o	++	o	o
3-meC28	o	o	o	+	o	o	o	o
5-meC29	o	o	o	o	o	++	o	o
2-meC29	o	o	tr	+	+	o	o	o
3-meC29	o	o	o	+	o	o	o	tr
2-meC30	o	o	o	o	++	o	o	o
5-meC31	o	o	o	o	o	+	o	o

[a]See Table 1 for explanation of terms and abbreviations.

methylalkane predominated; when the parent chain contained an odd number of carbons, the 3-methylalkane was more abundant (Table 5). The predominant terminally branched monomethylalkanes were 2-meC24 and 3-meC25, with 4.4% and 6.7% of the total hydrocarbons, respectively.

Isomeric mixtures of internally branched monomethylalkanes with parent carbon chains of C25, C27, C37, C39, and C41 occurred in small quantities. The early eluting components (C25 and C27) of this class of hydrocarbons represented <1.0% of the total hydrocarbons (Table 6). The later eluting components (C37, C39, and C41) coeluted with a diene and could not be separately quantified (Table 6).

Dimethylalkanes were not very abundant in *C. brevis* (<0.3% of the total hydrocarbons) and occurred only at C25 and C31 (Table 7). All were found to have the first methyl branch on the 3 carbon. No trimethylalkanes were identified.

Coptotermes formosanus *Shiraki*. Thus far, only this species of rhinotermi-

TABLE 6. RELATIVE AMOUNTS OF INTERNALLY BRANCHED MONOMETHYLALKANES IN CUTICULAR HYDROCARBONS OF WORKERS OR PSEUDERGATES OF TERMITES FROM THE HAWAIIAN ISLANDS[a]

	Species							
Hydrocarbon	Neo con	Inc imm	Cry bre	Cop for	Cry cyn	Zoo ang	Inc min	Cop vas
10-meC20	o	o	o	o	o	+	o	o
7-; 9-; 11-meC21	o	o	o	o	o	+++	o	o
7-; 8-; 9-; 10-; 11-; 12-meC22	o	o	o	o	o	+	o	o
9-; 11-meC23	+	o	o	o	o	++	o	o
7-meC23	o	o	o	o	o	++	o	o
11-; 12-meC24	o	o	o	o	o	o	o	+
9-; 11-; 13-meC25	o	o	+	++	+	+	o	+++
9-; 10-; 11-; 12-; 13-meC26	o	+	o	++	o	o	o	++
7-; 9-; 11-; 13-meC27	+	tr	tr	+++	++	++	o	+++
9-; 10-; 11-; 12-; 13-; 14-meC28	o	o	o	+++	o	o	o	+
9-; 11-; 13-; 15-meC29	o	o	o	+++	tr	++	tr	tr
7-meC29	o	o	o	o	o	+	o	o
14-; 15-meC30	o	o	o	tr	o	o	o	o
11-; 12-; 13-; 14-meC31	o	o	o	o	o	tr	++	o
7-meC31	o	o	o	o	o	+	o	o
9-; 10-; 11-; 12-; 13-; 14-meC32	o	o	o	o	o	o	+	o
11-; 13-; 15-; 17-meC33	o	o	o	tr	o	+	+++	o
9-; 10-; 11-; 12-; 13-; 14-meC34	o	o	o	o	o	o	tr	o
11-; 13-; 15-; 17-meC35	o	o	o	tr	o	+	++	+
11-; 13-; 15-; 17-meC37	o	o	tr	tr	o	+	++	++
12-; 13-; 14-; 15-; 16-meC38	o	o	o	tr	o	o	+	o
11-; 13-; 15-; 17-meC39	o	o	tr	+	o	tr	++	+
11-; 13-; 15-; 17-meC40	o	o	o	tr	o	o	+	o
11-; 13-; 15-; 17-meC41	+	o	tr	+	++	tr	++	o
15-; 16-; 17-meC42	o	o	o	tr	o	o	o	o
11-; 13-; 15-; 17-meC43	o	o	o	+	o	o	+	o

[a] See Table 1 for explanation of terms and abbreviations.

tid has been documented to be established in Hawaii. The cuticular hydrocarbon mixture of *C. formosanus* from Hawaii has been studied in depth (Haverty et al., 1990, 1991, 1996b) Chromatograms of this species showed mostly early eluting compounds with 25–31 carbons in the parent chain; late eluting compounds accounted for a relatively small portion of the total hydrocarbons and have 37–43 carbons in the parent chain. Mono- and dimethylalkanes with 27 or 29 carbons

TABLE 7. RELATIVE AMOUNTS OF DIMETHYLALKANES AND TRIMETHYLALKANES IN CUTICULAR HYDROCARBONS OF WORKERS OR PSEUDERGATES OF TERMITES FROM THE HAWAIIAN ISLANDS[a]

	Species							
Hydrocarbon	Neo con	Inc imm	Cry bre	Cop for	Cry cyn	Zoo ang	Inc min	Cop vas
Dimethylalkanes								
3,11-dimeC21	o	o	o	o	o	+++	o	o
3,11-dimeC22	o	o	o	o	o	tr	o	o
3,11-dimeC23	o	o	o	o	o	+++	o	o
3,7-dimeC25	o	o	tr	o	o	o	o	o
11,15-dimeC27	o	o	o	o	o	o	o	tr
9,13-dimeC27	o	o	o	+++	o	o	o	o
3,15-; 3,17-dimeC27	o	o	o	+	o	o	o	o
12,14-dimeC28	o	o	o	++	o	o	o	o
9,13-dimeC28	o	o	o	+	o	o	o	o
13,15-dimeC29	o	o	o	+++	o	o	o	o
13,17-dimeC29	o	o	o	o	o	o	o	tr
9,13-dimeC29	o	o	o	+	o	o	+	o
5,17-dimeC29	o	o	o	o	o	+++	o	o
3,9-; 3,11-; 3,15-; 3,17-dimeC29	o	o	o	tr	o	++	o	o
3,7-dimeC29	o	o	o	tr	o	+	o	o
13,15-dimeC30	o	o	o	tr	o	o	o	o
10,14-dimeC30	o	o	o	o	o	o	+	o
4,18-dimeC30	o	o	o	o	o	+	o	o
13,15-; 15,17-dimeC31	o	o	o	+	o	o	o	o
9,13-; 11,15-dimeC31	o	o	o	o	o	o	+++	o
5,17-dimeC31	o	o	o	o	o	++	o	o
3,X-; 3,11-; 3,13-dimeC31	o	o	tr	o	o	++	o	o
12,16-dimeC32	o	o	o	o	o	o	+++	o
7,13-; 7,15-dimeC33	o	o	o	o	o	tr	o	o
5,9-; 5,11-; 5,15-dimeC33	o	o	o	o	o	++	o	o
9,13-; 11,15-; 13,17-dimeC33	o	o	o	o	o	o	+++	o
12,16-dimeC34	o	o	o	o	o	o	++	o
9,13-; 11,15-; 13,17-dimeC35	o	o	o	o	o	o	+++	tr
5,17-dimeC35	o	o	o	o	o	++	o	o
12,16-dimeC36	o	o	o	o	o	o	+	o
15,17-dimeC37	o	o	o	+	o	o	o	o
11,15-; 13,17; 15,19-dimeC37	o	o	o	tr	o	o	++	++
5,15-; 5,17-dimeC37	o	o	o	o	o	++	o	o
14,18-dimeC38	o	o	o	tr	o	o	o	o

TABLE 7. CONTINUED

Hydrocarbon	Neo con	Inc imm	Cry bre	Cop for	Cry cyn	Zoo ang	Inc min	Cop vas
11,15-; 13,17-; 15,19-dimeC39	o	o	o	++	o	o	+	+
5,17-dimeC39	o	o	o	o	o	+++	o	o
14,18-; 16,20-dimeC40	o	o	o	tr	o	o	o	o
15,17-dimeC41	o	o	o	++	o	o	o	o
11,15-; 13,17-; 15,19-dimeC41	o	o	o	++	o	o	++	o
5,17-dimeC41	o	o	o	o	o	++	o	o
14,18-dimeC42	o	o	o	tr	o	o	o	o
15,17-dimeC43	o	o	o	+	o	o	o	o
11,15-; 13,17-; 15,19-dimeC43	o	o	o	tr	o	o	+	o
Trimethylalkanes								
13,15,17-trimeC29	o	o	o	++	o	o	o	o
9,13,17-trimeC31	o	o	o	o	o	o	+	o
7,11,15-trimeC31	o	o	o	o	o	o	+	o
9,13,17-trimeC33	o	o	o	o	o	o	+	o
9,13,17-trimeC35	o	o	o	o	o	o	+	o

[a] See Table 1 for explanation of terms and abbreviations.

in the parent chain accounted for ca. 56% of the total hydrocarbons (Figure 4). No unsaturated components were detected (Tables 2–4).

n-Alkanes present were *n*-C25, *n*-C26, *n*-C27, *n*-C28, and *n*-C29. *n*-C27 was the most abundant normal alkane, comprising ca. 2.4% of the total hydrocarbons. The others combined represented <2.4% of the total hydrocarbons (Table 2).

2- and 3-Methylalkanes were identified for C25–C29. In many cases the two peaks were not completely resolved on our system. These terminally branched monomethylalkanes comprise approximately 27% of the total hydrocarbons (Table 5, Figure 4). The coeluting peaks of 2- and 3-meC25 and 2- and 3-meC27 accounted for 21.7% of the total hydrocarbons.

We identified isomeric mixtures of internally branched monomethylalkanes with parent carbon chains ranging from C25 to C43, except for C31, C32, C34, and C36 (Table 6). This class of compounds was very abundant, representing ca. 47% of the total hydrocarbons. One isomeric mixture, 9-, 11-, and 13-meC27 was predominant and accounted for >30% of the total hydrocarbons (Figure 4).

Dimethylalkanes accounted for over 21% of the total hydrocarbon fraction of *C. formosanus*. The most abundant dimethylalkane was 13,15-dimeC29 (Figure 4). This is an unusual compound, with only one methylene group separating

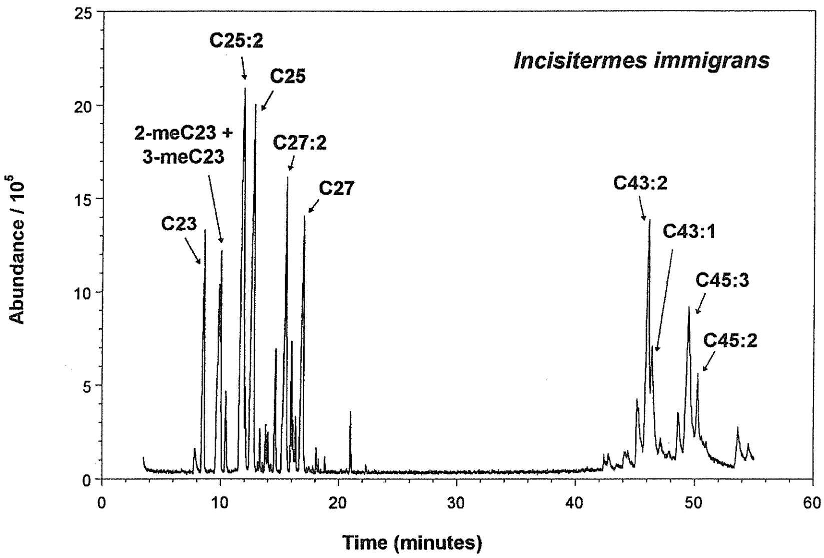

FIG. 2. Total ion chromatogram of cuticular hydrocarbons from pseudergates of *Incisitermes immigrans* Snyder from Coco Crater, Oahu, Hawaii.

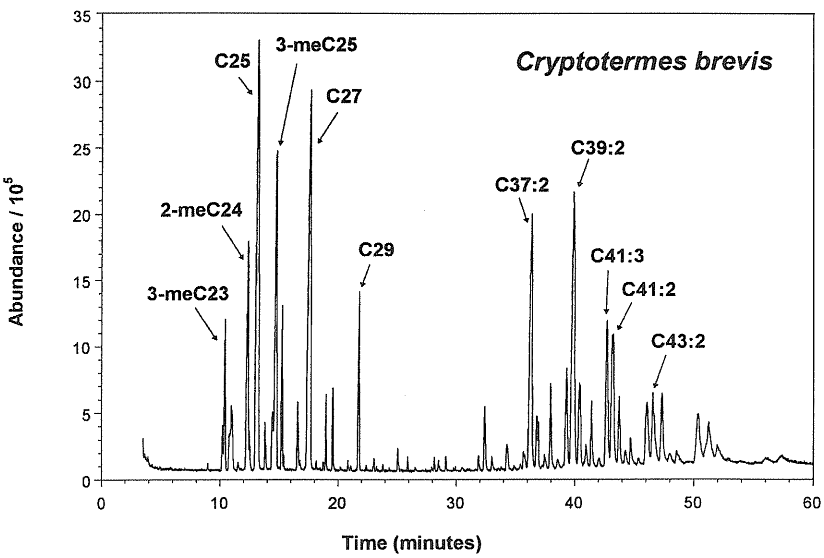

FIG. 3. Total ion chromatogram of the cuticular hydrocarbons from pseudergates of *Cryptotermes brevis* (Walker) from Honolulu, Oahu, Hawaii.

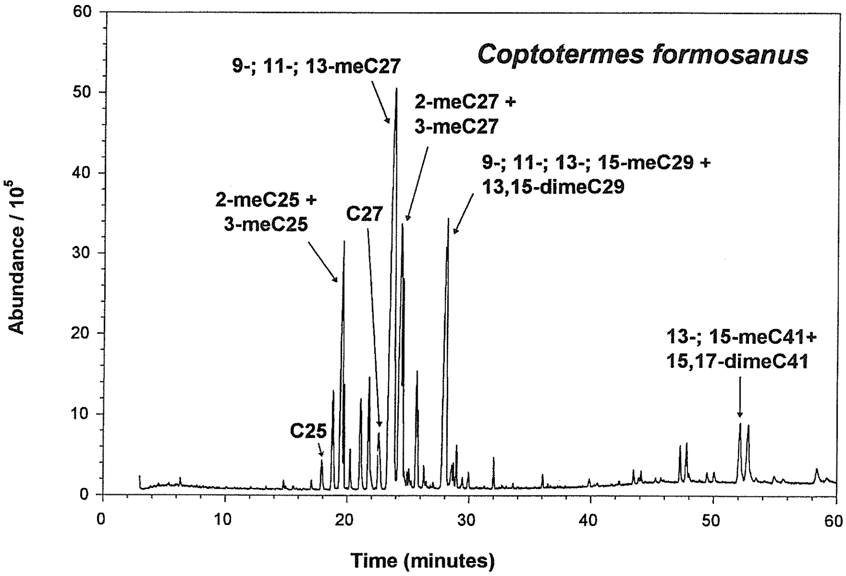

FIG. 4. Total ion chromatogram of cuticular hydrocarbons from workers of *Coptotermes formosanus* Shiraki from Honolulu, Oahu, Hawaii.

the methyl groups (Haverty et al., 1990, 1996b). Dimethylalkanes with similar spacing between the methyl groups occurred at C37, C41, C43, and one trimethylalkane with one methylene group separating the methyl groups was detected in significant quantities at C29 (Table 7).

Cryptotermes cynocephalus *Light*. This species has only recently been discovered to be established in Hawaii, appears to be very restricted in distribution, and has never been reported from structural timber. *C. cynocephalus* also reflects the general pattern of hydrocarbon mixtures of drywood termites living in xeric or tropical habitats (Haverty et al., 1997) and is remarkably similar to *C. brevis*. In this species hydrocarbons occurred in two groups: the early eluting compounds are dominated by one olefin, C27 : 1, and late-eluting compounds were primarily olefins (Figure 5).

n-Alkanes present were *n*-C23, *n*-C24, *n*-C25, *n*-C26, *n*-C27, and *n*-C29 (Table 2). *n*-C25 and *n*-C27 were the most abundant, comprising ca. 8.9% and 4.9%, respectively, of the total hydrocarbons from the samples. All of the other *n*-alkanes combined represented <2% of the total hydrocarbons.

Alkenes, alkadienes, and alkatrienes were the predominant class of cuticular hydrocarbons, representing approximately 69% of the total hydrocarbons. The number of carbons ranged from 26 to 45 (Table 2-4). The early eluting C27:1 accounted for ca. 27.0% of the total hydrocarbons and was the predominant

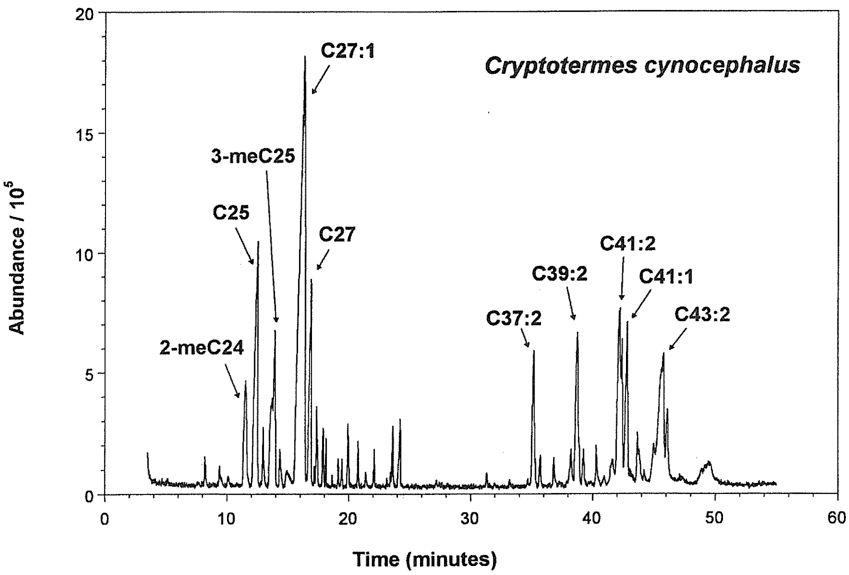

FIG. 5. Total ion chromatogram of the cuticular hydrocarbons from pseudergates of *Cryptotermes cynocephalus* Light from Waiahole Valley Road, Kamehameha Highway, Oahu, Hawaii.

hydrocarbon in the mixture (Figure 5). The late-eluting dienes C37:2, C39:2, C41:2, and C43:2 accounted for 3.8%, 5.2%, 7.5%, and 8.3% of the total hydrocarbons (Figure 5), while the remainder of the dienes accounted for 3.8% of the total hydrocarbons. The trienes added only ca. 2.0% to the total hydrocarbons (Table 4).

2- and 3-Methylalkanes were identified from C23 to C30 (Table 5). These terminally branched monomethylalkanes comprised ca. 11.2% of the total hydrocarbons. As in *C. brevis*, the predominant terminally branched monomethylalkanes were 2-meC24 and 3-meC25, with 3.6% and 3.0% of the total hydrocarbons. Only isomeric mixtures of internally branched monomethylalkanes with parent carbon chains of C25, C27, C29, and C41 were found (Table 6). The early eluting components (C25 and C27) of this class of hydrocarbons represented ca. 2.3% of the total hydrocarbons. The later eluting 11-, 13-, 15-, and 17-meC41 contributed 1.4% to the total hydrocarbons. No di- or trimethylalkanes were identified (Table 7).

Zootermopsis angusticollis (*Hagen*). This is the largest termite established in the Hawaiian Islands. Thus far, this species only has been found in the relatively cool, moist area near Kula, Maui (Woodrow et al., 1999a). It occurs naturally in moist areas along the Pacific Coast of North America (Thorne et al.,

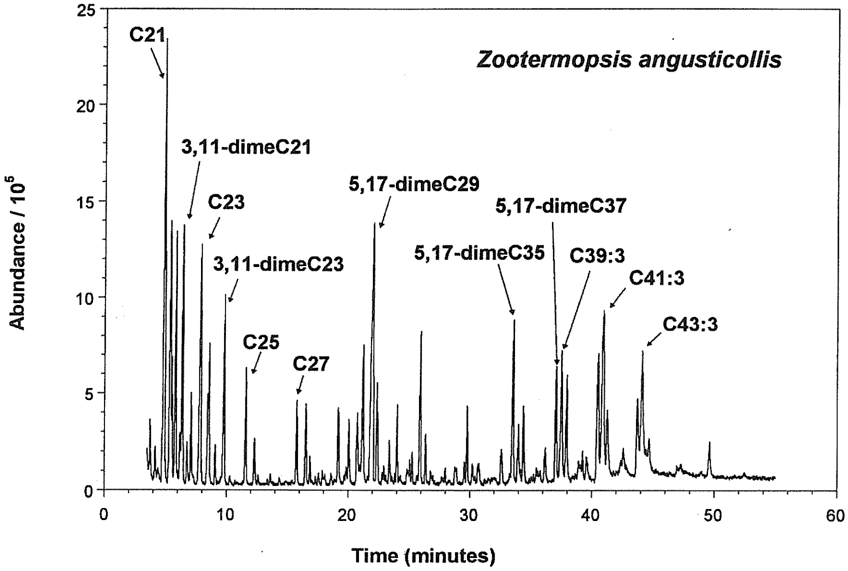

FIG. 6. Total ion chromatogram of the cuticular hydrocarbons from pseudergates of *Zootermopsis angusticollis* (Hagen) from Waiakoa Road, Kula, Maui, Hawaii.

1993). It has been introduced or intercepted in numerous exotic locations, but has not been reported established outside its natural distribution (Gay, 1969). Alates of this species are commonly found in stacks of recently sawn Douglas-fir or redwood lumber and survive transportation over great distances.

The cuticular hydrocarbon mixture of *Z. angusticollis* has been characterized previously (Haverty et al., 1988) and reflects a general pattern seen in termites that inhabit relatively moist, cool habitats (Figure 6). Cuticular hydrocarbons range from 21 to 43 carbons, with relative abundances spread evenly over the range. This is quite different from the pattern of two distinct groups (early eluting compounds with 24–29 carbons in the parent chain and late-eluting compounds with 37–43 carbons in the parent chain) we have seen with drywood termites from the British Virgin Islands (Haverty et al., 1997) or *Reticulitermes* from North America (Haverty and Nelson, 1997; Haverty et al., 1991, 1996a, 1999; Howard et al., 1978, 1982). The mixture of compounds is not dominated by any particular class of compounds, but there is a significant proportion of dimethylalkanes.

n-Alkanes present were *n*-C20, *n*-C21, *n*-C22, *n*-C23, *n*-C25, *n*-C26, *n*-C27, *n*-C28, and *n*-C29 (Table 1). *n*-C21 and *n*-C23 were the most abundant, comprising ca. 8.7% and 4.6% of the total hydrocarbons, respectively. The other *n*-alkanes accounted for about 5.8% of the total hydrocarbons.

Olefins comprise about 20.0% of the total hydrocarbon component. Only one monoene, C31:1, was found (Table 2). Four dienes occur—C37:2, C39:2, C42:2, and C43:2—and comprise only 6.0% of the total hydrocarbon component (Table 3). Trienes predominate the olefin component, with C39:3, C41:3, and C43:3 representing 2.9%, 5.4%, and 4.0% of the total hydrocarbons (Table 4).

2-, 3-, and 5-Methylalkanes were identified in *Z. angusticollis*. These terminally branched monomethylalkanes comprised approximately 11.8% of the total hydrocarbons (Table 5). We identified isomeric mixtures of internally branched monomethylalkanes with parent chains ranging from C20 to C41 (Table 6), which represented about 15.9% of the total hydrocarbons. With the exception of C20 and C22, all of the internally branched monomethylalkanes have an odd number of carbons in the parent chain. Positions of methyl branches ranged from carbon 10 to 15.

Dimethylalkanes constituted ca. 32.9% of the total cuticular hydrocarbon fraction of *Z. angusticollis* and are the most abundant class of hydrocarbons (Table 7). The most abundant dimethylalkane was 5,17-dimeC29 (7.4% of the total hydrocarbons). 5,17-dimeC31–5,17-dimeC41 formed a homologous series, with an odd number of carbons in the parent chain (Table 7, Figure 6). There were no dimethylalkanes with the first methyl branch on carbons 11–15 and the three methylene groups separating the methyl branches. No trimethylalkanes were found (Table 7).

Incisitermes minor (*Hagen*). This species was recently introduced to Oahu, but is not yet considered to be established (Woodrow et al., 1999a). *I. minor* is the predominant drywood termite on the southern West Coast of North America. It is ubiquitous in the Los Angeles, California, area and will likely continue to infest wood products shipped from southern California to Hawaii. For this reason, we chose to include *I. minor* in our discussions. *I. minor* lives in sound, dead wood in trees of many species, but contrary to *I. immigrans*, *I. minor* commonly infests structural timber throughout much of its range (Ebeling, 1975).

The general pattern of the chromatograms of *I. minor* (Figure 7) is more similar to that of *Z. angusticollis* (Figure 6) than that of *I. immigrans* (Figure 2), or other drywood termites from Hawaii or the tropics (Haverty et al., 1997). Hydrocarbons occur in a continuous series from *n*-C23 to dimeC43 without the unoccupied region from C29 to C33.

n-Alkanes present were *n*-C23, *n*-C24, *n*-C25, *n*-C26, *n*-C27, *n*-C28, and *n*-C29 (Table 1). *n*-C25 and *n*-C27 were the most abundant, comprising 10.7% and 8.1% of the total hydrocarbons (Figure 7). The remaining *n*-alkanes totaled ca. 5.0% of the total hydrocarbons. The unsaturated components constituted only about ca. 13.0% of the total hydrocarbons, a proportion much lower than that of tropical kalotermitids. Late-eluting olefins dominated in this component (Tables 2–4).

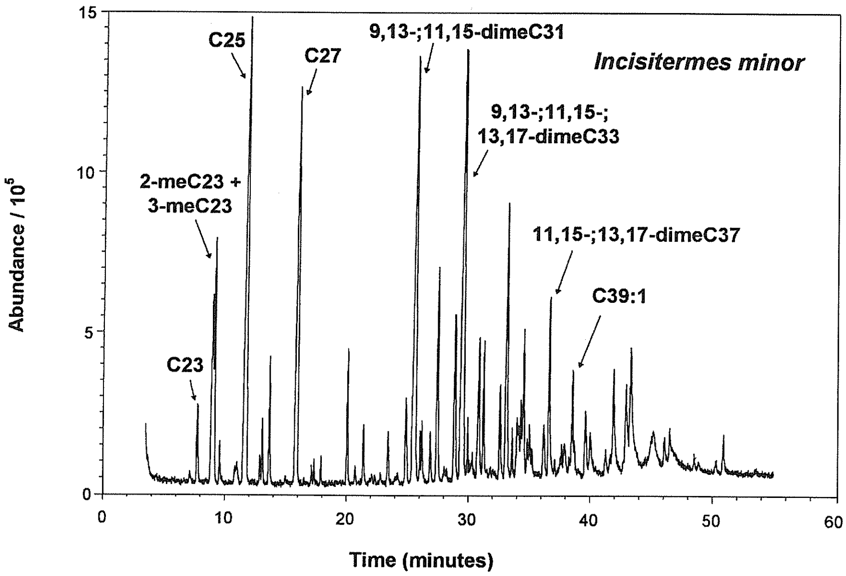

FIG. 7. Total ion chromatogram of cuticular hydrocarbons from pseudergates of *Incisitermes minor* (Hagen) from Waialua, Oahu, Hawaii.

2- and 3-Methylalkanes were identified for C22–C26; 2-meC23, representing 5.6% of the total hydrocarbons, was the most abundant. Of the 3-methylalkanes, 3-meC23 was the most abundant. These terminally branched monomethylalkanes comprised ca. 8.3% of the total hydrocarbons.

Internally branched monomethylalkanes comprised the third most abundant class of hydrocarbons in *I. minor*. Most of them were among the later eluting compounds with carbon numbers in the parent chain ranging from 29 through 43 (Table 6). The isomeric mixture of 11-, 13-, 15-, and 17-meC33 was the most abundant member of this class of hydrocarbons accounting for 3.2% of the total hydrocarbons (Figure 7).

In *I. minor*, dimethylalkanes appear to be the predominant class of compounds constituting ca. 39.9% of the total hydrocarbons. The most abundant dimethylalkanes are 9,13- and 11,15-dimeC31 and 9,13-, 11,15-, and 13,17-dimeC33, accounting for 10.0% and 11.5% of the total hydrocarbons (Figure 7; Table 7). *I. minor* also makes a homologous series of trimethylalkanes with 31, 33, and 35 carbons in the parent chain comprising 2.3% of the total hydrocarbons (Table 7).

Coptotermes vastator *Light*. Because *C. vastator* has been reported, although not confirmed, from Oahu, we included this potential resident in our study. Superficially the cuticular hydrocarbon mixture of *C. vastator* from Guam

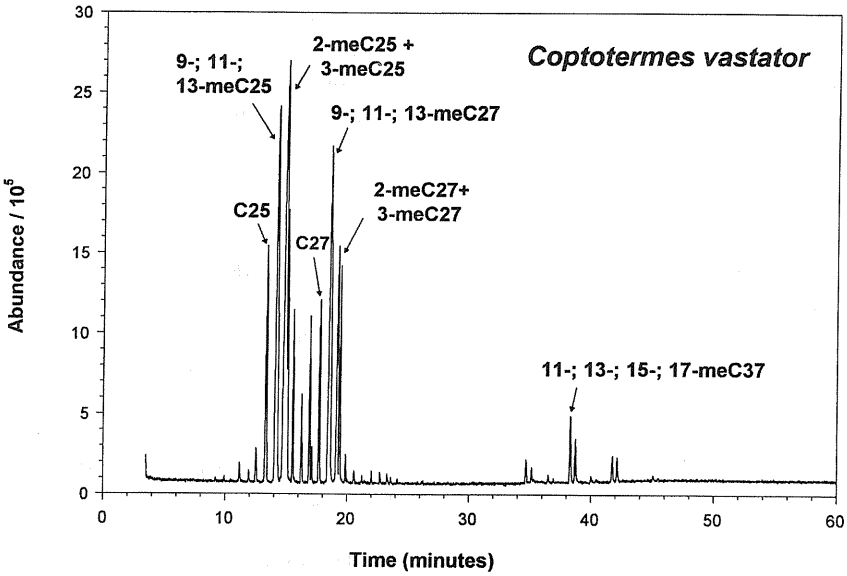

FIG. 8. Total ion chromatogram of cuticular hydrocarbons from workers of *Coptotermes vastator* Light from Guam.

resembles that of *C. formosanus* (Figures 4 and 8). However, in *C. vastator* the predominant early eluting compounds have 25–27 carbons in the parent chain, and C28 and C29 compounds are virtually absent. Late-eluting compounds accounted for a relatively small portion of the total hydrocarbon and have 35–39 carbons in the parent chain. Mono- and dimethylalkanes with 25 or 27 carbons in the parent chain accounted for ca. 75% of the total hydrocarbons (Figure 8). No unsaturated components were detected (Tables 2–4).

n-Alkanes present were *n*-C24, *n*-C25, *n*-C26, *n*-C27, *n*-C28, and *n*-C29. *n*-C25 and *n*-C27 were the most abundant normal alkanes comprising ca. 7.0% and 4.1% of the total hydrocarbons. The others combined represented ca. 4.3% of the total hydrocarbons (Table 1).

2- and 3-Methylalkanes were identified for C25 to C27, with trace amounts of 3-meC29 also found. These terminally branched monomethylalkanes comprise approximately 44.8% of the total hydrocarbons. The coeluting peaks of 2- and 3-meC25 and 2- and 3-meC27 accounted for 39.5% of the total hydrocarbons (Table 5, Figure 8).

We identified isomeric mixtures of internally branched monomethylalkanes with parent carbon chains ranging from 24 to 39, except for 29–34, 36, and 38 (Table 6). This class of compounds was very abundant, representing ca. 37.4% of the total hydrocarbons. Two isomeric mixtures, 9-, 11-, and 13-meC25 and 9-, 11-, and 13-meC27, were dominant and accounted for nearly 31.8% of the total hydrocarbons (Figure 8). Dimethylalkanes were uncommon in *C. vastator* (Table 7) and accounted for only 2.5% of the total hydrocarbons. None of the unusual dimethylalkanes with one methylene group separating the methyl groups, such as 13,15-dimeC29 seen in *C. formosanus* (Figure 4), were detected in *C. vastator* (Table 7). No trimethylalkanes were detected (Table 7).

Taxonomic and Habitat Relationships of Cuticular Hydrocarbon Profiles. One of the objectives of our studies of the termite fauna of the Hawaiian Islands was to begin to build a library of cuticular hydrocarbon profiles correlated with species determinations based on morphological characters. Although termite species occurring in Hawaii are readily identifiable on the basis of morphological characters of the soldiers or alates, they also have diagnostic cuticular hydrocarbon mixtures. Using only the consistently abundant hydrocarbons, one could unambiguously identify species based on the characterization of hydrocarbons of workers, larvae, pseudergates, or nymphs without the sometimes rare soldiers and alates needed for morphological diagnoses (Table 8). Furthermore, characterization of the cuticular hydrocarbons of termites introduced or imported to Hawaii could be used to unequivocally determine whether the species of the intruder was the same as one already established. Separation of closely related taxa has been demonstrated for species of *Zootermopsis* from western North America, *Nasutitermes* from the Caribbean Basin, and *Reticulitermes* from southeastern and southwestern North America based on the consistently abundant hydrocarbons (Haverty and Nelson, 1997; Haverty et al., 1988, 1992, 1996a, 1999).

TABLE 8. KEY TO THE TERMITES OF THE HAWAIIAN ISLANDS WITH CUTICULAR HYDROCARBONS AS CHARACTERS

n-C21 present	*Zootermopsis angusticollis*
n-C21 absent	2
olefins absent	3
olefins present	4
9-; 11-; 13-meC29 + 13,15-dimeC29 present	*Coptotermes formosanus*
9-; 11-; 13-meC29 + 13,15-dimeC29 absent	*Coptotermes vastator*
9,13-; 11.15-dimeC31 present	*Incisitermes minor*
9,13-; 11.15-dimeC31 absent	5
C37 : 2 present	6
C37 : 2 absent	7
C27 : 1 present	*Cryptotermes cynocephalus*
C27 : 1 absent	*Cryptotermes brevis*
C25 : 3 present	*Neotermes connexus*
C25 : 3 absent	*Incisitermes immigrans*

All classes of hydrocarbons are seen among the eight termite species characterized from the Hawaiian Islands. All species have normal alkanes present in their cuticular hydrocarbon mixture: *n*-C25 and *n*-C27 are usually the most abundant; *n*-C21 was only present in *Z. angusticollis*. In general, olefins are the most common of the hydrocarbons found in the termites of Hawaii. The two *Coptotermes* species, however, are completely lacking olefins. Early eluting alkenes are abundant in *N. connexus*, *I. immigrans*, and *C. cynocephalus* and are absent or rare in all other species. Late-eluting olefins, especially those with 41 or 43 carbons, are quite abundant in all olefin-producing species. These late-eluting olefins have one to four double bonds. The positions of these double bonds were not determined, but for the purposes of this study, we feel it is not essential to know their location. Terminally branched monomethylalkanes are common in most of the species. Internally branched monomethylalkanes are not commonly seen or are present in very small amounts relative to all other hydrocarbons; only *C. formosanus* and *C. vastator* incorporate these components in relatively large quantities. Dimethylalkanes are present in relatively large quantities only in *Z. angusticollis*, *I. minor*, *C. formosanus*, and *C. vastator*, species with rather high moisture requirements, and are absent or present in only trace amounts in the other species. Trimethylalkanes are quite rare; they are completely absent in six of the species and are present in small amounts (2.3% of the total hydrocarbons) in *I. minor* and in minor amounts (1.02% of the total hydrocarbons) in *C. formosanus*.

We can use cuticular hydrocarbons to distinguish species by using the worker caste, which does not have many useful morphological characters. The two morphologically similar species of *Coptotermes*, *C. formosanus*, and *C. vastator*, can be easily distinguished by the hydrocarbons of workers. *C. formosanus* contains compounds that do not occur in *C. vastator*. *C. formosanus* contains both 9-, 11-, 13-, and 15-meC29 and 13,15-dimeC29; this is also the case with several other dimethylalkanes of this type (15,17-dimeC41). These compounds are essentially absent in *C. vastator*.

C. brevis and *C. cynocephalus* are distinguishable by the morphology of the soldier caste: size and shape of the head. Cuticular hydrocarbons of the nymphs and pseudergates or workers also contain diagnostic characters. *C. brevis* contains C41 : 3, which appears only in trace amounts in *C. cynocephalus*. *C. cynocephalus* contains C27 : 1 in great abundance; this compound is missing in *C. brevis*.

Distinguishing the two species of *Incisitermes* on the basis of hydrocarbon mixtures is not difficult. The general patterns are so radically different that one does not need to look for diagnostic hydrocarbons. The morphology of the soldiers presents the same story. Clearly the most significant difference between these two species is the abundance of unsaturated components in *I. immigrans*. In contrast, *I. minor* has an abundance of mono- and dimethylalkanes; these are nearly absent in *I. immigrans*.

There are three types of habitats occupied by termites in the continental United States, as well as Hawaii: subterranean, drywood, and dampwood. Some species are difficult to assign and could theoretically occupy two habitats. The only subterranean termite species known to be established in Hawaii is *C. formosanus*. Subterranean termites generally need contact with the soil because of their high moisture requirements. Most of the termites in Hawaii are drywood termites, that is, they live entirely within wood without soil contact. Dampwood termites are much like drywood termites in that they live entirely within wood, but they generally have a much higher moisture requirement. The wood they occupy must either be in contact with soil or still attached to a live tree to provide moisture. *N. connexus* and *I. minor* are members of the drywood termite family, Kalotermitidae, but seem to live in situations with higher moisture availability. *N. connexus* lives in moist habitats, but can withstand periods of drying. Some entomologists in Hawaii consider *Neotermes* to be a dampwood termite. *I. minor* essentially lives in dry wood, but occurs naturally in the relatively mild coastal areas of southern California, up to the San Francisco Bay Area. It also occurs in riparian areas in Arizona. It is difficult to know exactly to which habitat to assign these termites. It might be clearer after examination of the cuticular hydrocarbon mixtures.

The composition of the hydrocarbon mixture is genetically controlled (Toolson and Kuper-Simbrón, 1989; Kaib et al., 1991; Page et al., 1991; Coyne et al., 1994). This composition is only slightly affected by diet and environmental conditions (Hadley, 1977; Espelie et al., 1994; Chapman et al., 1995; Howard, 1998). The primary function of cuticular hydrocarbons is retention of water inside the insect (Blomquist and Dillwith, 1985; Hadley, 1980, 1981, 1985). The cuticular hydrocarbon mixture of subterranean termites is exemplified by the chromatogram of *C. formosanus* (Figure 4). The cuticular hydrocarbons of drywood termites are exemplified by *I. immigrans* (Figure 2). The chromatogram from *Z. angusticollis* is an example of a dampwood termite (Figure 6). It has a hydrocarbon mixture very different from subterranean or drywood termites.

The two subterranean species, *C. formosanus* and *C. vastator*, appear similar with early eluting compounds predominating (Figures 4 and 8). The predominant hydrocarbons are normal alkanes and monomethylalkanes with carbon chain lengths of 25–29. Late-eluting compounds, when present, constitute a small percentage of the total hydrocarbon component. There are no olefins. The cuticular hydrocarbon mixtures of other species of subterranean termites do, however, often contain a significant olefin fraction (Haverty and Nelson, 1997; Haverty et al., 1992, 1996a, 1997, 1999).

The fauna of the Hawaiian Islands includes species of drywood termites at both ends of the moisture-dependence spectrum. We feel that *N. connexus* is dependent upon a high constant environmental moisture supply, usually obtained by inhabiting living trees, whereas *C. brevis*, the furniture termite, is capable of living without access to free water and is unable to thrive when exposed to sustained presence of free water (Collins, 1969; Williams, 1977). The cuticular hydrocarbon patterns of the four drywood species that are established in Hawaii all have the same overall appearance. Hydrocarbons occur in two groups. The first group is comprised of normal alkanes, monomethylalkanes, and olefins in the range of 23–27 carbons. The other group is comprised of higher-molecular-weight olefins or methyl-branched compounds with carbon numbers in the range of 37–45. *n*-Alkanes probably contribute the largest degree of water-proofing of all the cuticular hydrocarbons due to their close-packed nature. Alkenes with low molecular weight probably are used to moderate lipid viscosity. Because insects cannot synthesize *n*-alkanes longer than 34 carbons (Hadley, 1985), long-chain alkenes might have a dual role of regulating viscosity and retaining water at higher temperatures, given the lack of superior, high-molecular-weight alkanes (Hadley, 1980, 1985; Lockey, 1988; Woodrow et al., 1999b).

The two dampwood termites, or termites that live in relatively cool, moist habitats—the established *Z. angusticollis* and the recently introduced *I. minor*—have similar patterns. *I. minor* is taxonomically a drywood termite, but does not have a mixture of cuticular hydrocarbons characteristic of kalotermitids reported in the literature (Haverty et al., 1997). These two species do not possess the two distinct groups of hydrocarbons. The cuticular hydrocarbons range from 21 carbons to 43, with relative abundances spread evenly over the range, and the mixture of compounds is not dominated by any particular class of compounds.

Because cuticular hydrocarbon mixtures are generally species specific and vary little, in the short term, due to environmental influences, we plan to investigate the variation in these mixtures throughout the Hawaiian Islands. Our primary focus will be the abundant *I. immigrans* and *N. connexus* and secondarily *C. formosanus*. This might give us a better understanding of the inherent variability within each group and help us understand how long these termites have been established on the islands.

Acknowledgments—The authors are grateful for the sample of *Coptotermes vastator* supplied by V. R. Lewis. We thank C. H. M. Tome, R. J. Oshiro, S. Y. Uchima, and T. K. Brown for their technical assistance. This research was made possible by a cooperative agreement between the University of Hawaii and the Pacific Southwest Research Station. This paper is Journal Series No. 4455 of the Hawaii Institute of Tropical Agriculture and Human Resources.

REFERENCES

BESS, H. A. 1970. Termites of Hawaii and the Oceanic Islands, pp. 449–476, *in* K. Krishna and F. M. Weesner (eds.). Biology of Termites, Vol. II. Academic Press, New York.

BLOMQUIST, G. J. and DILLWITH, J. W. 1985. Cuticular lipids, pp. 117–154, *in* G. A. Kerkut and L. I. Gilbert (eds.). Comprehensive Insect Physiology, Biochemistry, and Pharmacology. Pergamon Press, Oxford.

CHAPMAN, R. F., ESPELIE, K. E., SWORD, G. A. 1995. Use of cuticular lipids in grasshopper taxonomy: A study of variation in *Schistocerca shoshone* (Thomas). *Biochem. Syst. Ecol.* 23:383–398.

COLLINS, M. S. 1969. Water relations in termites, pp. 433–458, *in* K. Krishna and F. M. Weesner (eds.). Biology of Termites, Vol. I. Academic Press, New York.

COLLINS, M. S., HAVERTY, M. I., and THORNE, B. L. 1997. The termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of the British Virgin Islands: Distribution, moisture relations, and cuticular hydrocarbons. *Sociobiology* 30:63–76.

COYNE, J. A., CRITTENDEN, A. P., and MAH, K. 1994. Genetics of a pheromonal difference contributing to reproductive isolation in *Drosophila. Science* 265:1461–1464.

EBELING, W. 1975. Urban Entomology. University of California Press, Los Angeles.

EHRHORN, E. M. 1934. The termites of Hawaii, their economic significance and control and the distribution of termites by commerce., pp. 321–333, *in* C. A. Kofoid (ed.). Termites and Termite Control. University of California Press, Berkeley, California.

ESPELIE, K. E., CHAPMAN, R. F., and SWORD, G. A. 1994. Variation in the surface lipids of the grasshopper, *Schistocerca americana* (Drury). *Biochem. Syst. Ecol.* 22:563–575.

GAY, F. J. 1969. Species introduced by man, pp. 459–494, *in* K. Krishna and F. M. Weesner (eds.). Biology of Termites, Vol. I. Academic Press, New York.

HADLEY, N. F. 1977. Epicuticular lipids of the desert tenebrionid beetle, *Eleodes armata*: Seasonal and acclimatory effects on composition. *Insect Biochem.* 7:277–283.

HADLEY, N. F. 1980. Surface waxes and integumentary permeability. *Am. Sci.* 68:546–553.

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.

HADLEY, N. F. 1985. The Adaptive Role of Lipids in Biological Systems. John Wiley & Sons, New York.

HAVERTY, M. I. and NELSON, L. J. 1997. Cuticular hydrocarbons of *Reticulitermes* (Isoptera: Rhinotermitidae) from northern California indicate undescribed species. *Comp. Biochem. Physiol.* 118B:869–880.

HAVERTY, M. I., PAGE, M., NELSON, L. J., and BLOMQUIST, G. J. 1988. Cuticular hydrocarbons of dampwood termites, *Zootermopsis*: Intra- and intercolony variation and potential as taxonomic characters. *J. Chem. Ecol.* 14:1035–1058.

HAVERTY, M. I., NELSON, L. J., and PAGE, M. 1990. Cuticular hydrocarbons of four populations of *Coptotermes formosanus* Shiraki in the United States: Similarities and origins of introductions. *J. Chem. Ecol.* 16:1635–1647.

HAVERTY, M. I., NELSON, L. J., and PAGE, M. 1991. Preliminary investigations of the cuticular hydrocarbons from North American *Reticulitermes* and tropical and subtropical *Coptotermes* (Isoptera: Rhinotermitidae). *Sociobiology* 19:51–76.

HAVERTY, M. I., NELSON, L. J., THORNE, B. L., COLLINS, M. S., DARLINGTON, J. P. E. C., and PAGE, M. 1992. Cuticular hydrocarbons for species determination of tropical termites, pp. 58–66, *in* C. E. Conrad and L. A. Newell (tech. coords.). Proceedings of the Session on Tropical Forestry for People of the Pacific. Pacific Science Congress, Honolulu, Hawaii, May 22–28, 1991. USDA Forest Service General Technical Report PSW-129.

HAVERTY, M. I., FORSCHLER, B. T., and NELSON, L. J. 1996a. An assessment of the taxonomy of *Reticulitermes* (Isoptera: Rhinotermitidae) from the southeastern United States based on cuticular hydrocarbons. *Sociobiology* 28:287–318.

HAVERTY, M. I., GRACE, J. K., NELSON, L. J., and YAMAMOTO, R. T. 1996b. Intercaste, intercolony, and temporal variation in cuticular hydrocarbons of *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae). *J. Chem. Ecol.* 22:1813–1834.

HAVERTY, M. I., THORNE, B. L., and NELSON, L. J. 1996c. Hydrocarbons of *Nasutitermes acajutlae* and comparison of methodologies for sampling cuticular hydrocarbons of Caribbean termites for taxonomic and ecological studies. *J. Chem. Ecol.* 22:2081–2109.

HAVERTY, M. I., COLLINS, M. S., NELSON, L. J., and THORNE, B. L. 1997. Cuticular hydrocarbons of termites of the British Virgin Islands. *J. Chem. Ecol.* 23:927–964.

HAVERTY, M. I., NELSON, L. J., and FORSCHLER, B. T. 1999. New cuticular hydrocarbon phenotypes of *Reticulitermes* (Isoptera: Rhinotermitidae) from the United States. *Sociobiology* 34:1–21.

HOWARD R. W. 1998. Ontogenetic, reproductive, and nutritional effects on the cuticular hydrocarbons of the host-specific ectoparasitoid. *Cephalonomia tarsalis* (Hymenoptera: Bethylidae). *Ann. Entomol. Soc. Am.* 91:101–112.

HOWARD, R. W., MCDANIEL, C. A., and BLOMQUIST, G. J. 1978. Cuticular hydrocarbons of the eastern subterranean termite, *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae). *J. Chem. Ecol.* 4:233–245.

HOWARD, R. W., MCDANIEL, C. A., NELSON, D. R., BLOMQUIST, G. J., GELBAUM, L. T., and ZALKOW, L. H. 1982. Cuticular hydrocarbons of *Reticulitermes virginicus* (Banks) and their role as potential species- and caste-recognition cues. *J. Chem. Ecol.* 8:1227–1239.

KAIB, M., BRANDL, R., and BAGINE, R. K. N. 1991. Cuticular hydrocarbon profiles: a valuable tool in termite taxonomy. *Naturwissenschaften* 78:176–179.

LOCKEY, K. H. 1988. Lipids of the insect cuticle: origin, composition and function. *Comp. Biochem. Physiol.* 89B:595–645.

PAGE, R. E., METCALF, R. A., METCALF, R. L., ERICKSON, E. H., JR., and LAMPMAN, R. L. 1991. Extractable hydrocarbons and kin recognition in honeybee (*Apis mellifera* L.) *J. Chem. Ecol.* 17:745–756.

SCHEFFRAHN, R. H., DARLINGTON, J. P. E. C., COLLINS, M. S., KRECEK, J., and SU, N.-Y. 1994. Termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of the West Indies. *Sociobiology* 24:213–238.

SCHEFFRAHN, R. H., SU, N.-Y., CHASE, J. A., MANGOLD, J. R., GRACE, J. K., and YATES, J. R., III. 1999. First record of *Cryptotermes cynocephalus* Light (Isoptera: Kalotermitidae). *Proc. Hawaii. Entomol. Soc.* In press.

THORNE, B. L., HAVERTY, M. I., PAGE, M., and NUTTING, W. L. 1993. Distribution and biogeography of the North American termite genus *Zootermopsis* (Isoptera: Termopsidae). *Ann. Entomol. Soc. Am.* 86:532–544.

TOOLSON, E. C. and KUPER-SIMBRÓN, R. 1989. Laboratory evolution of epicuticular hydrocarbon composition and cuticular permeability in *Drosophila pseudoobscura*: Effects on sexual dimorphism and thermal-acclimation ability. *Evolution* 43:468–473.

WILLIAMS, R. M. C. 1977. The ecology and physiology of structural wood destroying Isoptera. *Mater. Org.* 12:112–140.

WOODROW, R. J., GRACE, J. K., and YATES, J. R., III. 1999a. Hawaii's termites—an identification guide. Cooperative Extension Service, College of Tropical Agriculture and Human Resources, University of Hawaii at Manoa, HSP-1, 6 pp.

WOODROW, R. J., GRACE, J. K., NELSON, L. J., and HAVERTY, M. I. 1999b. Modification of cuticular hydrocarbons of *Cryptotermes brevis* (Isoptera; Kalotermitidae) in response to temperature and relative humidity. *Environ. Entomol.* In press.

ZIMMERMAN, E. C. 1948. Insects of Hawaii, Vol. 2. University of Hawaii Press, Honolulu, 475 pp.