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Ralph W. Howard

Southern Forest Experiment Station, USDA, Forest Service, Gulfport, Mississippi

Barbara L. Thorne

Southern Forest Experiment Station, USDA, Forest Service, Gulfport, Mississippi

Sally C. Levings

Southern Forest Experiment Station, USDA, Forest Service, Gulfport, Mississippi

C. A. Mcdaniel

Southern Forest Experiment Station, USDA, Forest Service, Gulfport, Mississippi

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Cuticular Hydrocarbons as Chemotaxonomic Characters for *Nasutitermes corniger* (Motschulsky) and *N. ephratae* (Holmgren) (Isoptera: Termitidae)¹

RALPH W. HOWARD,² BARBARA L. THORNE,³ SALLY C. LEVINGS,⁴
AND C. A. MCDANIEL⁵

Southern Forest Experiment Station, USDA, Forest Service,
Gulfport, Mississippi 39505

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ABSTRACT Forty-four cuticular hydrocarbon components from workers of the termites *Nasutitermes corniger* (Motschulsky) and *N. ephratae* (Holmgren) from three localities in Panama were characterized by capillary gas chromatography-electron impact mass spectrometry. Both species contain qualitatively identical homologous series of n-alkanes; 2-, 3-, 11-, 13-, 14-, and 15-methylalkanes; 11,15-, 12,16-, and 13,17-dimethylalkanes; and 11,15,19- and 13,17,21-trimethylalkanes. Both species also contain a single alkene, 9-hentriacontene. The two species, however, are readily distinguished chemically by differences among the relative abundances of 11 of their major hydrocarbon components.

KEY WORDS Insecta, chemosystematics, taxonomy, gas chromatography

TERMITE SPECIES are taxonomically characterized primarily by examination of imagoes and soldiers. These forms may represent only a small proportion of the population at any given time, and it is not uncommon for these forms either not to be collected or to be collected in very low numbers. Species-specific phenotypic characters from the worker caste would be a very useful addition to termite systematics.

One promising approach has used biochemical characters such as cuticular hydrocarbons (Howard & Blomquist 1982). Two sympatric North American rhinotermitids, *Reticulitermes flavipes* (Kollar) and *R. virginicus* (Banks), possess qualitatively different cuticular hydrocarbon profiles (Howard et al. 1978, 1982). Six other North American *Reticulitermes* species (unpublished data) also possess cuticular hydrocarbon profiles that are different from each other and from those of *R. flavipes* and *R. virginicus*. Clement et al. (1985) have reported similar findings for European species of *Reticulitermes*.

To be of taxonomic use it is not necessary that every species in a taxon have qualitatively different

cuticular hydrocarbons. Rather, some members might have quantitative differences among one or more hydrocarbon components. Such has proven to be the case in two sympatric species of neotropical termitids, *Nasutitermes corniger* (Motschulsky) and *N. ephratae* (Holmgren). We report here the identification of 44 shared cuticular hydrocarbon components from the worker forms of these two neotropical termites, the relative abundances of 30 of the 44 components, and a species-specific characterization of each species in terms of the relative abundances of 11 of the 44 major hydrocarbon components.

Materials and Methods

Source of Insects. Colonies were sampled intermittently between 1980 and 1983 from three locations at least 50 km apart in the Republic of Panama. Nests were haphazardly selected, removed from their locations, bagged, and taken to the laboratory. Workers were taken from the nest debris and hydrocarbons extracted as described below. Voucher specimens of all caste forms were collected and notes made on nest architecture. All colonies were collected in second-growth forest at one of three locations: Frijoles ($n = 17$), Colon ($n = 16$), and Bocas del Toro ($n = 7$). Twenty-two of the colonies were *N. corniger* and 18 were *N. ephratae*. A laboratory accident involving 22 of the samples resulted in obvious paraffin contamination (high abundances of even-carbon-number n-alkanes). The remaining 18 colonies—9 *N. corniger*: Bocas ($n = 1$), Colon ($n = 3$), Frijoles ($n = 5$); *N. ephratae*: Bocas ($n = 1$), Colon ($n = 4$), Frijoles ($n = 4$)—appeared to have, at most, only slight

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² USDA-ARS, Grain Marketing Research Laboratory, 1515 College Avenue, Manhattan, Kans. 66502, and Department of Entomology, Kansas State University, Manhattan, Kans. 66506. Formerly with USDA, Forest Service Forestry Sciences Laboratory, Gulfport, Miss. 39505.

³ Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138.

⁴ Department of Zoology, University of Rhode Island, Kingston, R.I. 02881.

⁵ USDA, Forest Service Forestry Sciences Laboratory, Gulfport, Miss. 39505. Formerly with USDA-APHIS, National Monitoring and Residue Analysis Laboratory, Gulfport, Miss. 39505.

amounts of the paraffin contamination as evidenced by much lower proportions of even-carbon-number n-alkanes.

Taxonomy. *Nasutitermes corniger* and *N. ephratae* can be diagnosed accurately on the basis of several external morphological characters of the alates and soldiers, and by their distinctive nest architectures. Soldiers of both species have a single row of four long setae on the posterior margin of the abdominal tergites; but, in addition, *N. corniger* soldiers have many shorter hairs on the abdominal tergites (Emerson 1925, Snyder 1959). Other characters suggested to distinguish soldiers such as head color or nasus length (Banks 1918) are not useful because of intraspecific variation. The imago body of *N. ephratae* is reddish brown, and the wings are light brown (Emerson 1925, Matthews 1977); imagoes of *Nasutitermes corniger* are dark brown and have charcoal-colored wings (Banks 1918, Dietz & Snyder 1923, Snyder 1959). Also, species are clearly distinguished by the distance between the compound eye and ocellus of the imago. In *N. ephratae*, the ocelli are less than their diameter from the margin of the compound eyes (Banks 1918, Emerson 1925); the ocelli of *Nasutitermes corniger* are positioned about twice their diameter from the compound eye (Banks 1918). Determination of species of several samples was made by Kumar Krishna, American Museum of Natural History. The remainder of the identifications were made by B. L. Thorne. Type material of both species was closely examined.

Both *N. corniger* and *N. ephratae* build carton nests on tree branches, trunks, or stumps. Nests of each species have distinctive external and internal architectural structures (described in detail in Thorne [1980]). Notes on nest architecture were made for each sampled colony. Morphological characters of voucher specimens from all colonies (including soldiers, workers, alates when present, and reproductives when found) were examined in the laboratory. Specimens of each caste from each colony were coded with numerical labels, enabling double-blind examination of each taxonomic character. Specific determinations based on all morphological characters and on nest architecture were consistent for all sampled colonies. Voucher specimens from all colonies will be deposited in the Harvard Museum of Comparative Zoology, Cambridge, Mass.

Chemical Analysis. Cuticular lipids were extracted by immersing 300 to 1,000 workers from each colony in three successive portions of pesticide-grade methylene chloride for 30 to 45 s each. Combined CH_2Cl_2 extracts from each colony were concentrated under nitrogen, and the hydrocarbons were isolated by chromatography on 3-cm minicolumns of Biosil A (BioRad Laboratories, Richmond, Calif.) as previously described (Howard et al. 1978). The hydrocarbons were then analyzed by capillary gas chromatography (GC)-electron impact mass spectrometry (EI-MS) on a Hewlett-

Packard 5790A GC (Hewlett-Packard, Palo Alto, Calif.) containing a bonded phase 30 m $\times$ 0.32-mm DB-1 (J&W Scientific, Rancho Cordova, Calif.) capillary column interfaced to a Hewlett-Packard 5970 Mass Selective Detector operated at 70 eV. A 45-s splitless injection was used, and all GC runs utilized temperature programming from 100 to 320°C at 10°/min, with an initial 2-min hold period and a final 12-min hold period. Ultrapure helium was the carrier gas and the flow rate was 1 ml/min. Retention times were compared with n-alkane standards.

Molecular weights of hydrocarbon components were verified by packed column gas chromatography-chemical ionization mass spectrometry (CI-MS) using a Hewlett-Packard 5710A GC-5982A mass spectrometer. Ultrapure methane at a flow rate of 13 ml/min served as both carrier and ionizing gas, generating an internal source pressure of 0.5 Torr. Chemical ionization spectra were obtained at 200 eV. The GC column used was an all-glass (0.91 m by 2 mm inside diameter) 3% OV-101 + 0.2% Carbowax 20 M on Chromosorb W. Analyses involved temperature programming from 180 to 280°C at 4°/min with a 30-min final hold period.

Reported hydrocarbon percent abundance data were based on branched and olefinic hydrocarbon components only. This was done to eliminate any possible bias resulting from unknown levels of possible paraffin contamination. Peak areas were obtained from electronic integration of the mass spectrometric total ion trace (EI-MS). Data were expressed as proportions and then transformed to the arcsine of the square root of proportions for *t* tests (SAS Institute 1982). Reported means are on untransformed data.

Results

Workers of *N. corniger* and *N. ephratae* contain the same cuticular hydrocarbon components (Table 1; Fig. 1). Six classes of hydrocarbons are present: (1) n-alkanes; (2) 2- and 3-methylalkanes; (3) 11-, 13-, 14-, 15-, and 17-methylalkanes; (4) 11,15-, 12,16-, and 13,17-dimethylalkanes; (5) 11,15,19- and 13,17,21-trimethylalkanes; and (6) a single alkene, 9-hentriacontene.

The n-alkanes had retention times identical to those of standard n-alkanes and were completely removed by molecular sieve treatment (Howard et al. 1978). They also gave EI and CI mass spectra identical to those of standard n-alkanes. Branched alkanes were readily identified from their CI-MS determined carbon numbers (Howard et al. 1980b), their equivalent chain lengths (Jackson & Blomquist 1976), and their characteristic EI-MS fragmentation patterns (Jackson & Blomquist 1976, Nelson 1978). The single alkene present was characterized as its dithiomethyl ether derivative (Francis & Veland 1981).

Table 1. Cuticular hydrocarbons of workers of *N. corniger* and *N. ephratae*

GC peak ^a	Hydrocarbon	E.C.L. ^b	C.N. ^c	Diagnostic EI-MS ions (m/z)
1	n-heneicosane	21.00	21	296
2	n-docosane	22.00	22	310
3	n-tricosane	23.00	23	324
4	2-methyltricosane	23.58	24	295, 323, 338
5	3-methyltricosane	23.68	24	281, 309, 338
6	n-tetracosane	24.00	24	338
7	2-methyltetracosane	24.57	25	309, 337, 352
8	3-methyltetracosane	24.68	25	295, 323, 352
9	n-pentacosane	25.00	25	352
10	2-methylpentacosane	25.59	26	323, 351, 366
11	3-methylpentacosane	25.67	26	309, 337, 366
12	n-hexacosane	26.00	26	366
13	2-methylhexacosane	26.63	27	337, 365, 380
14	3-methylhexacosane	26.68	27	323, 351, 380
15	n-heptacosane	27.00	27	380
16	13-methylheptacosane	27.33	28	197, 225, 394
17	2-methylheptacosane	27.65	28	351, 379, 394
18	3-methylheptacosane	27.74	28	337, 365, 394
19	n-octacosane	28.00	28	394
20	14-methyloctacosane	28.31	29	211, 225, 408
21	2-methyloctacosane	28.64	29	365, 393, 408
22	3-methyloctacosane	28.76	29	351, 379, 408
23	n-nonacosane	29.00	29	408
24	11-, 13-, and 15-methylnonacosane	29.35	30	169, 281; 197, 253; 225
25	11,15- and 13,17-dimethylnonacosane	29.65	31	169, 225, 239, 295; 197, 267
26	3-methylnonacosane	29.77	30	365, 393, 422
27	11,15,19-trimethylnonacosane	29.92	32	169, 239, 309, 435
28	n-triacontane	30.00	30	422
29	14- and 15-methyltriacontane	30.31	31	211, 253; 225, 239, 436
30	12,16-dimethyltriacontane	30.60	32	183, 225, 253, 295, 435
31	9-hentriacontene	30.76	31	434
32	n-hentriacontane	31.00	31	436
33	13- and 15-methylhentriacontane	31.33	32	197, 281; 225, 253
34	13,17-dimethylhentriacontane	31.60	33	197, 225, 267, 295
35	13,17,21-trimethylhentriacontane	31.86	34	169, 197, 239, 267, 309, 337, 463
36	n-dotriacontane	32.00	32	450
37	14- and 16-methyldotriacontane	32.31	33	211, 281; 239, 253
38	14,18-dimethyldotriacontane	32.55	34	211, 225, 281, 295
39	12,16-dimethyldotriacontane	32.63	34	183, 253, 323
40	n-tritriacontane	33.00	33	464
41	13-, 15-, and 17-methyltritriacontane	33.29	34	197, 309; 225, 281; 253
42	15,19-dimethyltritriacontane	33.54	35	225, 295
43	13,17-dimethyltritriacontane	33.63	35	197, 253, 267, 323
44	n-tetratriacontane	34.00	34	478

^a See Fig. 1.^b E.C.L., equivalent chain length.^c C.N., carbon number, determined by CI-MS.

The identity of each hydrocarbon component represented by each GC peak in Fig. 1 is listed in Table 1, along with equivalent chain length, carbon number, and diagnostic EI-MS ion fragments of each component. Components ranged in carbon number from 21 to 35 and contained only hydrocarbon structures previously known from other insects. The particular mixture of identified components was substantially different from those reported from other species of termites (Moore 1969, Howard et al. 1978, 1980a, 1982, Blomquist et al. 1979, Clement et al. 1985).

Table 2 lists the mean percent composition of all components (excluding the n-alkanes) for both species of *Nasutitermes*, along with the results of the *t* test of the null hypothesis—i.e., that there were no relative abundance differences for each shared hydrocarbon component of the two species. Eleven components were significantly different be-

tween the two species at the *P* = 0.05 level or lower (components 16, 17, 20, 24, 27, 29, 30, 33, 34, 35, 42 [Fig. 1; Table 2]). In general, *N. corniger* has a lower proportion of internally branched monomethyl alkanes and possesses a higher proportion of the dimethylalkanes than *N. ephratae*.

Discussion

When we first began this study and realized that these two species of *Nasutitermes* have the same cuticular hydrocarbons, we reexamined all the morphological characters and nest architecture data for each of our samples, using double-blind analyses. We are certain that every sample was correctly assigned as to species. Our finding of two quantitatively distinct hydrocarbon profiles for workers of the two species is consistent with the morphological criteria for diagnosis of the species.

Fig. 1. Reconstructed total GC-MS traces indicating typical capillary GC patterns for the cuticular hydrocarbons isolated from *Nasutitermes corniger* (A) and *N. ephratae* (B). Numbered peaks are those which differ significantly in relative abundance between the two species (Table 2).

To our knowledge, this is the first report of two social insect species possessing qualitatively identical but quantitatively unique hydrocarbon profiles. All the nearctic species of *Reticulitermes* (Rhinotermitidae) have qualitatively unique hydrocarbon profiles (Howard et al. 1978, 1980a, 1982, Clement et al. 1985), as do four species of fire ants (*Solenopsis*) (Nelson et al. 1980, Vander Meer & Wojcik 1982) and all four species of *Apis* (honey bees) (Francis et al. 1985). Many of these species are sympatric (within a given taxon); thus it does not seem likely that the two observed hydrocarbon patterns (qualitative versus quantitative variation) are related to environmental parameters. Until more taxa are examined, it is premature to speculate further on the origin and phylogenetic significance of these hydrocarbon phenotypes.

To date, all available evidence suggests that cuticular hydrocarbons are promising characters for taxonomic investigations within the Isoptera. Each unique hydrocarbon component may be considered to be a separate character. Like morphological characters, the hydrocarbons can exist in either a present-absent state or have a range of quantitatively variable states. Cuticular hydrocarbons are present on all caste forms, including workers; they consist of multicomponent mixtures often containing well over 40 components. No studies have yet investigated an entire higher taxon (such as a ge-

Table 2. Mean percentage composition ($\bar{x}$) and standard deviations (SD) of cuticular hydrocarbons (excluding n-alkanes) of *N. corniger* and *N. ephratae* workers

GC peak ^a	Hydrocarbon	$\bar{x}$ (SD)		$P > t^d$
		<i>N. corniger</i> ^b	<i>N. ephratae</i> ^c	
4	2-MeC ₂₃	0.06 (0.10)	0.18 (0.38)	NS
5	3-MeC ₂₃	0.02 (0.05)	0.16 (0.38)	NS
7	2-MeC ₂₄	0.16 (0.35)	0.10 (0.17)	NS
8	3-MeC ₂₄	0.05 (0.10)	0.21 (0.39)	NS
10	2-MeC ₂₅	0.32 (0.63)	0.59 (0.80)	NS
11	3-MeC ₂₅	0.13 (0.11)	0.33 (0.39)	NS
13	2-MeC ₂₆	0.35 (0.68)	0.82 (0.75)	NS
14	3-MeC ₂₆	0.10 (0.12)	0.35 (0.43)	NS
16	13-MeC ₂₇	0.09 (0.10)	0.33 (0.28)	*
17	2-MeC ₂₇	0.70 (0.80)	1.85 (0.77)	***
18	3-MeC ₂₇	0.44 (0.41)	0.87 (0.70)	NS
20	14-MeC ₂₈	0.15 (0.22)	0.75 (0.39)	***
21	2-MeC ₂₈	0.66 (0.52)	1.35 (0.96)	NS
22	3-MeC ₂₈	0.18 (0.29)	0.65 (0.66)	NS
24	11-, 13-, and 15-MeC ₂₉	1.11 (0.49)	9.45 (2.80)	***
25	11,15- and 13,17-diMeC ₂₉	8.90 (1.62)	10.32 (3.45)	NS
26	3-MeC ₂₉	0.18 (0.17)	0.40 (0.33)	NS
27	11,15,19-triMeC ₂₉	0.21 (0.14)	0.62 (0.40)	***
29	14- and 15-MeC ₃₀	0.74 (0.48)	3.42 (0.58)	***
30	12,16-diMeC ₃₀	14.16 (2.45)	7.44 (1.29)	***
31	C31:1	0.96 (0.88)	1.00 (0.50)	NS
33	13- and 15-MeC ₃₁	7.47 (1.91)	14.58 (2.94)	***
34	13,17-diMeC ₃₁	55.93 (8.56)	35.19 (4.70)	***
35	13,17,21-triMeC ₃₁	0.11 (0.11)	0.44 (0.32)	**
37	14- and 16-MeC ₃₂	1.02 (0.57)	1.46 (0.45)	NS
38	14,18-diMeC ₃₂	2.25 (0.75)	1.76 (0.71)	NS
39	12,16-diMeC ₃₂	0.08 (0.09)	0.21 (0.23)	NS
41	13-, 15-, and 17-MeC ₃₃	1.49 (1.21)	2.07 (1.11)	NS
42	15,19-diMeC ₃₃	1.49 (1.14)	2.62 (0.58)	**
43	13,17-diMeC ₃₃	0.47 (1.25)	0.46 (0.37)	NS

^a See Fig. 1.

^b $n = 9$ colonies.

^c $n = 9$ colonies.

^d NS, $P > 0.05$; *, P 0.05 to 0.01; **, P 0.01 to 0.001; ***, $P < 0.001$.

nus), but 10 species of the genus *Reticulitermes* can be distinguished using hydrocarbon characters solely from the worker caste (unpublished data).

There are many neotropical *Nasutitermes* species of uncertain affinity (unpublished data) that are prime candidates for examination of cuticular hydrocarbon composition. From a chemosystematic point of view, it will be of considerable interest to see whether these species contain clusters of taxa that resemble *N. corniger* and *N. ephratae* in having quantitatively variable patterns. Other clusters might have the pattern typical of other social insects examined to date (qualitatively variable hydrocarbon profiles).

Despite the promise that cuticular hydrocarbons have as taxonomic characters for termites, they also possess a few drawbacks. Chief among these is that, for many species of termites, the workers are small and possess low absolute quantities of hydrocarbons on their cuticles. Samples must consist of many individuals (typically at least 100 or more). Furthermore, analysis of cuticular hydrocarbons, as with other chemical character analyses, requires

access to chemical equipment. Fortunately, hydrocarbons are relatively stable molecules. They store well, they can be readily extracted under field conditions, and they can be saved for analysis at a later date. Given the difficulties of obtaining complete caste series for termite identification, the minor drawbacks of cuticular hydrocarbons as characters are offset by the ability to identify species solely on the basis of workers. More research will be required before the generality of this method will be known for the Isoptera as a whole. Such studies are now in progress in several laboratories.

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References Cited

- Banks, N. 1918. The termites of Panama and British Guiana. *Bull. Am. Mus. Nat. Hist.* 38: 659-667.
- Blomquist, G. J., R. W. Howard & C. A. McDaniel. 1979. Structures of the cuticular hydrocarbons of the termite *Zootermopsis angusticollis* (Hagen). *Insect Biochem.* 9: 365-370.
- Clement, J.-L., C. Lange, M. Blum, R. Howard & H. Lloyd. 1985. Chimosystematique du genre *Reticulitermes* (Isoptères) aux U.S.A. et en Europe. *Actes Colloq. Insects Soc.* 2: 123-131.
- Dietz, H. F. & T. E. Snyder. 1923. Biological notes on the termites of the Canal Zone and adjoining parts of the Republic of Panama. *J. Agric. Res.* 26: 279-302.
- Emerson, A. E. 1925. The termites from Kartabo, Bartica District, British Guiana. *Zoologica (N.Y.)* 6: 291-459.
- Francis, G. W. & K. Veland. 1981. Alkylthiolation for the determination of double-bond positions in linear alkenes. *J. Chromatogr.* 219: 379-384.
- Francis, B. K., W. E. Blanton & K. A. Nunamaker. 1985. Extractable surface hydrocarbons of workers and drones of the genus *Apis*. *J. Apic. Res.* 24: 13-26.
- Howard, R. W. & G. J. Blomquist. 1982. Chemical ecology and biochemistry of insect hydrocarbons. *Annu. Rev. Entomol.* 27: 149-172.
- Howard, R. W., C. A. McDaniel & G. J. Blomquist. 1978. Cuticular hydrocarbons of the eastern subterranean termite, *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae). *J. Chem. Ecol.* 4: 233-245.
- 1980a. Chemical mimicry as an integrating mechanism: cuticular hydrocarbons of a termitophile and its host. *Science* 210: 431-433.
- Howard, R. W., C. A. McDaniel, D. R. Nelson & G. J. Blomquist. 1980b. Chemical ionization mass spectrometry: application to insect-derived cuticular alkanes. *J. Chem. Ecol.* 6: 609-623.
- Howard, R. W., C. A. McDaniel, D. R. Nelson, G. J. Blomquist, L. T. Gelbaum & L. H. Zalkow. 1982. Cuticular hydrocarbons of *Reticulitermes virginicus* (Banks) and their role as potential species- and caste-recognition cues. *J. Chem. Ecol.* 8: 1227-1239.
- Jackson, L. L. & G. J. Blomquist. 1976. Insect waxes, pp. 201-233. *In* P. E. Kolattukudy [ed.], *Chemistry and biochemistry of natural waxes*. Elsevier, Amsterdam.
- Mathews, A. G. A. 1977. Studies on termites from the Mato Grosso State, Brazil. *Academia Brasileira de Ciencias*, Rio de Janeiro, Brazil.
- Moore, B. P. 1969. Biochemical studies in termites, pp. 407-432. *In* K. Krishna & F. M. Weesner [eds.], *Biology of termites*, vol. 1. Academic, New York.
- Nelson, D. R. 1978. Long-chain methyl-branched hydrocarbons: occurrence, biosynthesis, and function. *Adv. Insect Physiol.* 13: 1-33.
- Nelson, D. R., C. L. Fatland, R. W. Howard, C. A. McDaniel & G. J. Blomquist. 1980. Re-analysis of the cuticular methylalkanes of *Solenopsis invicta* and *S. richteri*. *Insect Biochem.* 10: 409-418.
- SAS Institute. 1982. SAS user's guide: statistics. SAS Institute, Cary, N.C.
- Snyder, T. E. 1959. New termites from Venezuela, with keys and a list of the described Venezuelan species. *Am. Midl. Nat.* 61: 313-321.
- Thorne, B. L. 1980. Differences in nest architecture between the Neotropical arboreal termites *Nasutitermes corniger* and *Nasutitermes ephratae* (Isoptera: Termitidae). *Psyche* 87: 235-243.
- Vander Meer, R. K. & D. P. Wojcik. 1982. Chemical mimicry in the Myrmecophilous beetle *Myrmecaphodius excavaticollis*. *Science* 218: 806-808.

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