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CURRENT DISTRIBUTION OF THE FORMOSAN SUBTERRANEAN TERMITE AND OTHER TERMITE SPECIES (ISOPTERA: RHINOTERMITIDAE, KALOTERMITIDAE) IN LOUISIANA

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ABSTRACT

A statewide survey in Louisiana on the current distribution of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, and other termite species was conducted with 91 pest control companies, city and state agencies, and the New Orleans Mosquito and Termite Control Board from January 1999 to August 2002. A total of 812 samples were used in the survey constituting all eight known termite species from Louisiana. The subterranean termite species identified were *Reticulitermes flavipes* (Kollar), *R. virginicus* (Banks), *R. hageni* Banks, and *C. formosanus*. The drywood termite species identified were *Incisitermes snyderi* (Light), *I. minor* (Hagen), *Cryptotermes brevis* (Walker), and *Kalotermites approximatus* (Snyder). *Incisitermes minor* was also collected in Mississippi and is a new record in that state. The collective data on the flight season of each species was also recorded.

Key Words: *Coptotermes formosanus*, Rhinotermitidae, Kalotermitidae

RESUMEN

Un reconocimiento de la distribución actual de la termita subterránea formosana, *Coptotermes formosanus* Shiraki y de otras especies de termitas fue llevado a cabo en Louisiana, EE.UU. con la colaboración de 91 compañías de control de plagas, las agencias estatales y municipales, y el Buró de Control de Mosquitos y Termitas de Nueva Orleans desde enero de 1999 hasta agosto de 2002. Un total de 812 muestras fueron usadas en el reconocimiento constituyendo las ocho especies de termitas conocidas de Louisiana. Las termitas subterráneas identificadas fueron *Reticulitermes flavipes* (Kollar), *R. virginicus* (Banks), *R. hageni* Banks, y *C. formosanus*. Las termitas de madera seca identificadas fueron *Incisitermes snyderi* (Light), *I. minor* (Hagen), *Cryptotermes brevis* (Walker), y *Kalotermites approximatus* (Snyder). *Incisitermes minor* fue también colectada en Mississippi y es un nuevo registro en aquel estado. Los datos colectivos sobre la temporada de vuelos para cada especie también fueron registrados.

Translation provided by author.

The Formosan subterranean termite (FST), *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae), was first identified in Lake Charles, Louisiana, in 1966 and in New Orleans in 1967 (Spink 1967). It is widely believed that this exotic species was introduced into the continental U.S. after infested material was brought over from Asia after World War II (Su and Tamashiro 1987). For the past 30 years, FST infestations have been found in other cities and various small communities throughout Louisiana. The main source of introduction to these other areas is caused, in part, by the transportation of infested building materials, utility poles, and railroad ties used in landscaping (La Fage 1987). Then, natural spread has occurred via alate dispersal flights.

The last statewide survey involving the pest control community for all termite species was conducted around the time of the first confirmed re-

port of the FST (Weesner 1965). During the last survey, species and flight data were only recorded from Rapides Parish, which includes the city of Alexandria. *Reticulitermes flavipes* (Kollar), *R. virginicus* (Banks), *R. hageni* Banks (Isoptera: Rhinotermitidae), and *Incisitermes snyderi* (Light) (Isoptera: Kalotermitidae) were collected from this region of the state. Previously, Light (1934) and Snyder (1954) listed five species in Louisiana. They included *R. flavipes*, *R. virginicus* (Isoptera: Rhinotermitidae), *Kalotermites (=Incisitermes) snyderi*, *Kalotermites approximatus* (Snyder), and *Cryptotermes brevis* (Walker) (Isoptera: Kalotermitidae). Recently, Messenger et al. (2000) discovered established populations of *Incisitermes minor* (Hagen) (Isoptera: Kalotermitidae) in New Orleans.

Since the last national survey in 1965, individual statewide termite surveys have been con-

ducted in Georgia (Scheffrahn et al. 2001), Florida (Scheffrahn et al. 1988), Texas (Howell et al. 1987), and South Carolina (Hathorne et al. 2000). These surveys significantly contributed to our understanding of the current distribution of the economically important FST.

Because there have been many unconfirmed reports of the FST throughout the state, the main objective of this survey was to identify and confirm the current distribution of the FST in Louisiana with the help of the pest control industry, the Louisiana Department of Agriculture and Forestry, and mosquito control districts. In addition, the New Orleans Mosquito and Termite Control Board concurrently conducted a separate statewide survey for all subterranean and drywood termite species.

MATERIALS AND METHODS

Pest Management Professional (PMP) Survey

Beginning in January 1999, letters asking for participation in the survey were mailed to 589 PMPs and mosquito control districts throughout Louisiana, including a few pest control companies operating near the state line in Mississippi and Texas. Termite collecting packets were then prepared and sent to each company who returned the postcard with a response of willingness to participate. Each packet included individually numbered collection vials (13 ml polypropylene Snap-Seal®, Corning Brand) containing 85% ethanol, corresponding vial data sheets, return padded envelopes, and a hand-held aspirator. Each participant was encouraged to collect termite alates and soldiers during routine inspections and treatments of residential and commercial structures. They were also encouraged to include any relevant information from each collection on the data sheet, which included date and location of collection, flight date (if applicable), and any additional comments and requests for more collection vials.

N. O. Mosquito and Termite Control Board (NOMTCB) Survey

The senior author and other coworkers conducted a deliberate survey throughout Louisiana from 1999 to 2001. Termites were collected from live and dead trees, state parks, railroad ties, highway rest areas, private and public buildings, and any other type of wood found along highways and parish roads. We also traveled to addresses throughout the state to verify FST infestations and conduct further surveys in the surrounding areas. In addition, samples and FST locations were received from J. McPherson, Program Coordinator, Pesticide and Environmental Programs, Louisiana Department of Agriculture and Forestry, Baton Rouge, LA.

For both surveys, termite alates and soldiers were identified to species using termite keys de-

veloped by Banks & Snyder (1920), Miller (1949), Snyder (1954), Weesner (1965), Scheffrahn & Su (1994), and Hostettler et al. (1995). Samples containing only workers (*Reticulitermes* spp.) or pseudergates were identified to the family and/or genus level. Data from both surveys was entered into a computer database (FileMaker® Pro 3.0, Claris® Corporation). Longitude and latitude coordinates from the NOMTCB survey were recorded at each sample site using a Garmin GPS model 12 CX (Garmin International, Inc., Olathe, KS) hand-held global positioning receiver. Locations of each collection were plotted using Arc-View GIS version 3.1 software (Environmental Systems Research Institute, Inc., Redlands, CA).

RESULTS

PMP Survey

Out of the original 589 survey letter mailings, 91 (15%) companies and individuals agreed to participate by collecting any type of termite they encountered during routine inspections and treatments of urban structures and trees. There was no response from 453 (77%) companies and 45 (8%) responded, but declined to participate. The majority of the companies who declined indicated that they do not conduct termite treatments.

As a result, 52 of the 91 participants returned collection vials for a total of 426 samples. All eight known termite species were collected (Table 1). The majority of these samples were collected from separate addresses. *Reticulitermes flavipes* was the most commonly collected species throughout the state (Table 1). The FST was the second most commonly collected species; however, the majority of the FST samples were collected from the New Orleans and Lake Charles areas (Table 1).

Each participant also included an exact or approximate date of dispersal flight whenever they collected alates. For the subterranean species,

TABLE 1. TOTAL NUMBER OF IDENTIFIED TERMITE SPECIES FROM VIALS COLLECTED DURING THE PMP SURVEY.

Termite species	Number of vials
<i>Reticulitermes flavipes</i>	204
<i>Coptotermes formosanus</i>	118
<i>Reticulitermes virginicus</i>	40
<i>Incisitermes snyderi</i>	9
<i>Cryptotermes brevis</i>	7
<i>Incisitermes minor</i>	3
<i>Kaloterms approximatus</i>	3
<i>Reticulitermes hageni</i>	3
Workers/pseudergates only	39
TOTAL	426

TABLE 2. TOTAL NUMBER OF TERMITE SPECIES AND SAMPLES COLLECTED DURING THE NOMTCB SURVEY.

Termite species	Number of collections
<i>Reticulitermes flavipes</i>	177
<i>Reticulitermes hageni</i>	65
<i>Reticulitermes virginicus</i>	64
<i>Coptotermes formosanus</i>	40
<i>Incisitermes snyderi</i>	21
<i>Incisitermes minor</i>	9
<i>Cryptotermes brevis</i>	8
<i>Kaloterms approximatus</i>	2
TOTAL	386

R. flavipes alates were recovered from Jan. 17 to April 19, *R. virginicus* alates from March 1 to May 17, *R. hageni* on Dec. 17, 2001 (single record), and the FST from April 12 to May 9. For the kaloter-

mid species, *I. snyderi* alates were recovered from May 10 to July 22, *C. brevis* from May 9 to July 25, and *K. approximatus* from Oct. 10 to Nov. 1. Alate samples of *I. minor* were collected from Sept. 10 to Dec. 4 in Rayne, Cameron, and Le Moyeu, LA; however, monitoring of dispersal flights by the senior author in the New Orleans metro area occurred each year from late April to early June.

NOMTCB Survey

Reticulitermes flavipes was by far the most commonly collected termite species throughout Louisiana (Table 2). *Reticulitermes hageni* and *R. virginicus* were the two second most commonly collected species (Table 2). The number of FST collections only represents a few selected, confirmed sites throughout the state and does not include any samples taken from New Orleans. The distribution of FST infestations in Louisiana has significantly increased since 1966 (Table 3).

TABLE 3. LOCATION OF *COPTOTERMES FORMOSANUS* INFESTATIONS IN LOUISIANA, 1966-2001.

Year	Parish	City
1966*	Orleans	New Orleans, Algiers
	Calcasieu	Lake Charles
1968*	Orleans	New Orleans, Algiers
	Calcasieu	Lake Charles
	Jefferson	Grand Isle
	La Fourche	Raceland
1986*	Orleans	New Orleans, Algiers
	Calcasieu	Lake Charles, Westlake
	Jefferson	Metairie, Gretna, Grand Isle
	La Fourche	Raceland
	St. Tammany	Slidell, Covington
	Lafayette	Lafayette
	East Baton Rouge	Baton Rouge
2001	Orleans	New Orleans, Algiers
	Calcasieu	Lake Charles, Westlake, Moss Bluff, Sulphur
	Jefferson	Metairie, Gretna, Grand Isle, Kenner, Harahan, Westwego, Marrero
	La Fourche	Raceland, Thibodaux, Larose, Cut Off, Galliano
	St. Tammany	Slidell, Covington
	Lafayette	Lafayette
	East Baton Rouge	Baton Rouge
	Ascension	Prairieville
	St. Charles	Norco
	Assumption	Pierre Part
	Terrebonne	Houma, Montegut
	St. Bernard	Chalmette
	Plaquemines	Belle Chase
	Iberia	New Iberia
	Vermilion	Abbeville
	St. Landry	Sunset
2002	Sabine	Noble
	Ouachita	Monroe, West Monroe
	Acadia	Rayne
	St. Mary	Amelia

*La Fage 1987.

In New Orleans, FST flight activity was monitored by the senior author using glue traps (TRAPPER® LTD, Bell Laboratories, Inc., Madison, WI) installed under lights near the French Quarter. Nightly observations and the number of FST alates recovered from glue traps reveal peak flight activity usually occurs from mid-May to early June, with some activity through mid-July (Table 4).

The majority of the *I. minor* and *C. brevis* samples were received from J. McPherson and local residents of New Orleans.

Location data from both surveys for the FST (Fig. 1), *Reticulitermes* species (Fig. 2), and kaloterimid species (Fig. 3) are presented on ArcView-generated maps.

DISCUSSION

The distribution of the FST in Louisiana has increased dramatically since the first confirmed reports in the mid-60s. However, many of these newer, confirmed infestations have remained relatively localized, and state officials have begun to target these areas for immediate treatment. Most of these localized introductions have occurred around structures, such as churches, or parks and campsites where FST-infested railroad ties were used as landscaping and/or building material. Future monitoring and confirmation of any new FST reports throughout the state is the first step to controlling human-aided spread.

TABLE 4. COMBINED ALATE FLIGHT DATES FOR *COPTOTERMES FORMOSANUS* IN NEW ORLEANS, LOUISIANA, FROM 1998 TO 2001.

Date	Year	Date	Year	Date	Year
May 4	1998	2nd week of Jan.	2000	April 8	2001
May 11		2nd week of Feb.		April 13	
May 16		March 26		April 14	
May 18*		April 18		April 15	
May 19		April 25		April 16	
May 22		April 29		April 24	
May 26		May 3		May 1	
May 29*		May 4		May 4	
June 6		May 5		May 5	
June 8		May 8		May 7	
June 18		May 10		May 9	
June 21		May 14		May 12	
June 23		May 15 *		May 13	
June 28		May 21		May 14	
2nd week of Feb.	1999	May 22		May 15*	
April 6		May 26		May 17	
April 26		May 29		May 20	
April 27		June 4		May 21	
April 28		June 15		May 22	
May 6		June 16		May 23	
May 7		June 17		May 24	
May 12*				May 25	
May 14				May 26	
May 17				May 31	
May 18				June 1*	
May 19				June 4	
May 25				June 7	
May 27				June 11	
May 29*				June 14	
June 6				June 18	
June 9				June 21	
June 10				June 24	
June 22				June 28	
June 27					
1st week of July					
July 7					
July 13					
3rd week of July					

*Largest dispersal flight (s) each year.

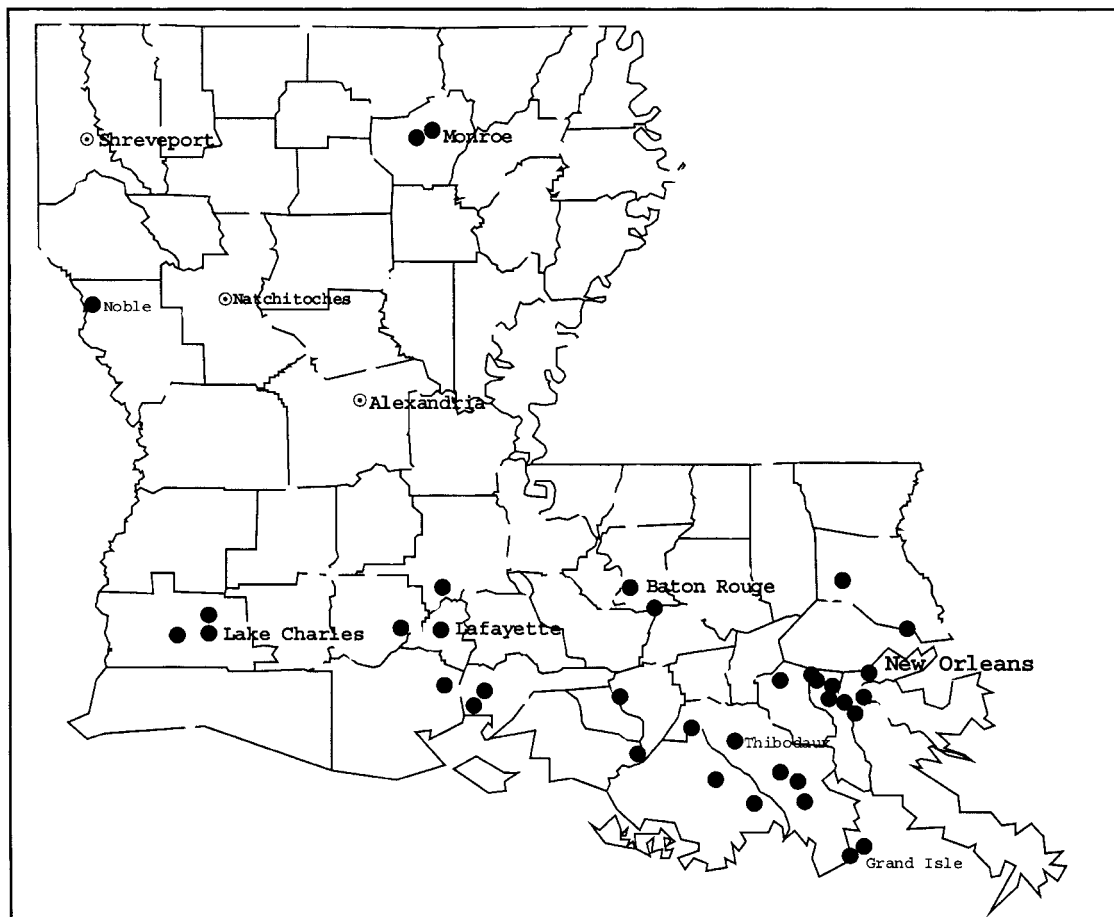


Fig. 1. Current distribution of *Coptotermes formosanus* in Louisiana.

Outside the New Orleans and Lake Charles areas, *R. flavipes* and *R. virginicus* are the two most economically important subterranean termite species, with *R. flavipes* being the most common. The spatial distribution of all three *Reticulitermes* species is consistent statewide; however, *R. flavipes* seems to be more common in the extreme southern portions of the state. For example, samples of *R. flavipes* were collected from house pilings directly in the sand at Holly Beach on the Gulf of Mexico and from fishing camps around the Mississippi River delta basin.

During the PMP survey, *R. hageni* was rarely encountered in structures. In addition, *K. approximatus* was only collected from dead portions of trees and from alates flying into the vehicles of participants on two separate occasions. For both species, this confirms their general status as very limited structural pests (Weesner 1970, Scheffrahn et al. 1988).

Incisitermes snyderi and *C. brevis* are the two most economically important kalotermitid species in Louisiana, with *I. snyderi* being the most com-

mon. *Cryptotermes brevis* is a non-endemic species and has only been recovered from structural lumber and furniture. *Incisitermes snyderi* is an endemic species commonly found in structural lumber and in dead portions of live trees throughout the southern half of the state.

The overall number of *I. minor* collections throughout the state was unexpected. Another interesting discovery was the number of public schools throughout the state with very active *I. minor* infestations, particularly in window framework. *Incisitermes minor* is endemic to CA, AZ, and Mexico, but has been introduced to many areas in the state, and in most cases, inside furniture. For example, a sample was taken from an infested pool table in Natchez, MS. In New Orleans, *I. minor* alates are usually collected from mid-April to mid-June during midday flights. However, alates were recovered after swarming from a window frame in an elementary school in Rayne, LA, during the second week of September 2001. In addition, *I. minor* alates were collected after swarming in a high school in Cameron, LA,

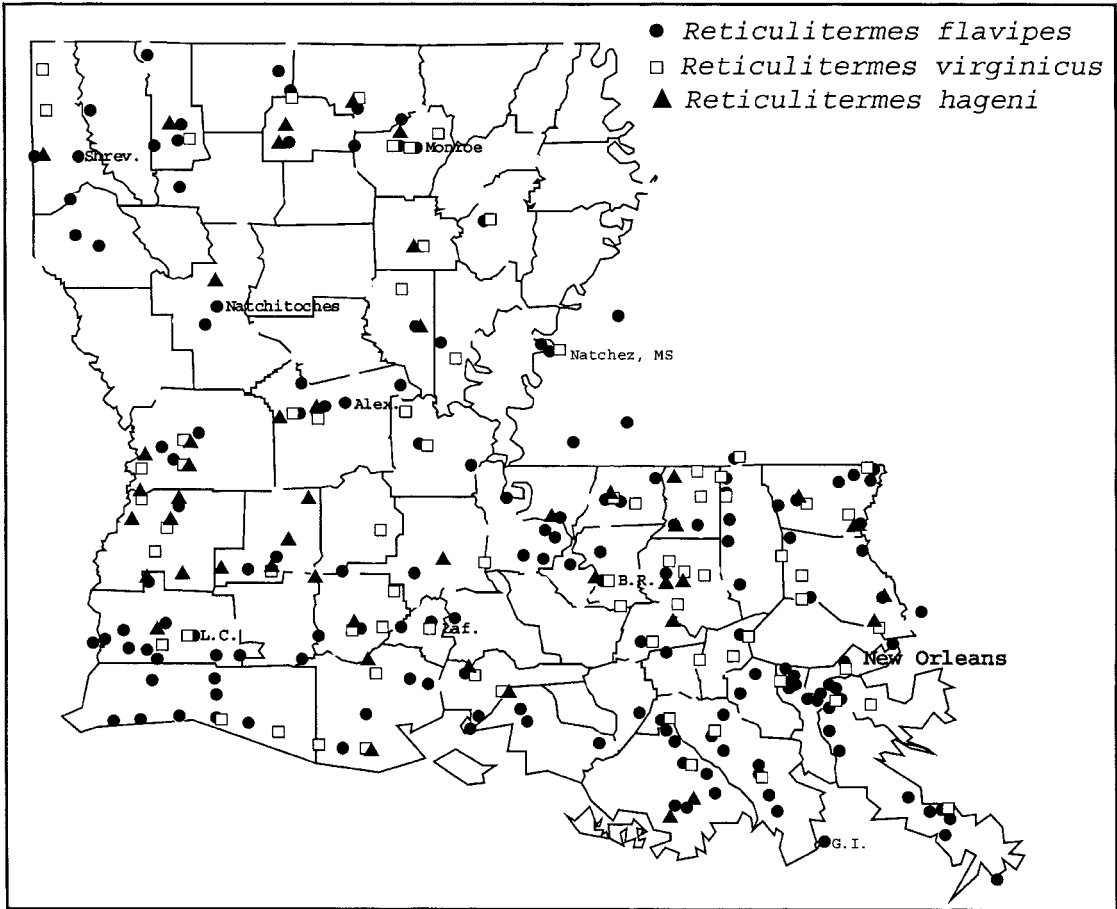


Fig. 2. Combined distribution data of *Reticulitermes* spp. in Louisiana from PMP and NOMTCB surveys.

in late September 2001. Historical records reveal the flight season of *I. minor* usually occurs from July to December, and as early as May in the laboratory (Harvey 1934). In addition, *I. minor* flight records in California (Snyder 1954), Florida (Scheffrahn et al. 1988), and Georgia (Scheffrahn et al. 2001) revealed swarming usually occurs from September to November. An alarming discovery revealed *I. minor* alates swarming in a lumberyard near Le Moyeu, LA, in December 2001. This could lead to future introductions throughout the state.

In addition to the overall survey, a pictorial termite identification key was developed in 2001 to help PMPs, state officials, and termite researchers identify the FST and other economically important subterranean and drywood termite species currently present in Louisiana (Messenger 2002).

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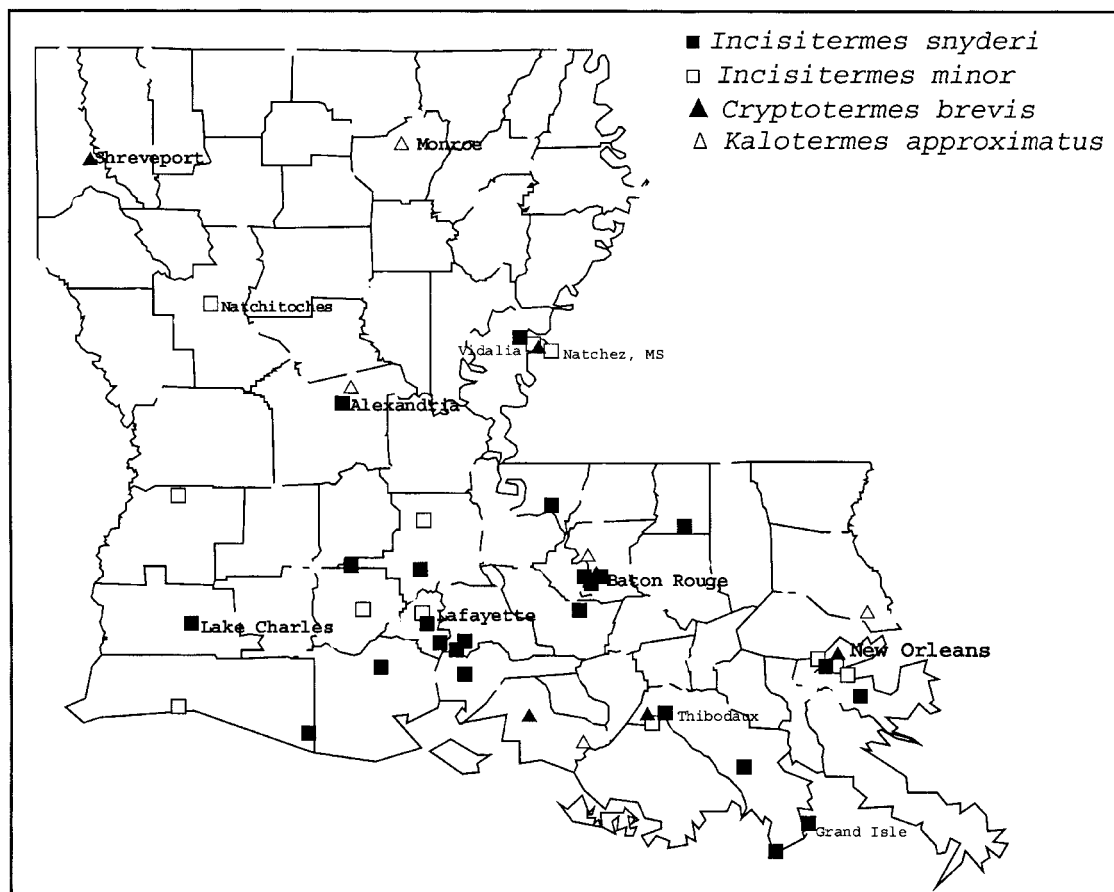


Fig. 3. Combined distribution data of kaloterimid species in Louisiana from PMP and NOMTCB surveys.

Richard L. Robards Termite Services; Hookfin Pest Control Co., Inc.; Sugarland Exterminating Co., Inc.; Couhig Southern Environmental; Terminix—Slidell; Anti-Pest & Veitch, Inc.; Kevin's Pest Control, Inc.; Slug-A-Bug Exterminating Co.; E & G Pest Control, Inc.; Jerome Williams Pest Control Co.; Woods Pest Control; Sears Termite & Pest Control Inc.; Billiot Industries, Inc.; Vexcon Inc.; Stetler Pest Control; A Plus Exterminators, Inc.; Brent's Pest Control Services; Guardian Pest Control; Arceneaux Consulting; Calcasieu Parish Mosquito Control; East Baton Rouge Mosquito and Rodent Control; Mosquito Control, Inc.; St. Bernard Parish Mosquito Control; Louisiana Department of Agriculture and Forestry; and USDA-ARS SRRC. Partial funding for this project was provided by USDA-ARS under the grant agreement No. 58-6435-8-108. This article is Florida Agricultural Experiment Station Journal Series No. R-08828.

REFERENCES CITED

- BANKS, N., AND T. E. SNYDER. 1920. A revision of Nearctic termites with notes on biology and geographic distribution. *Bull. Smithsonian Mus.* 108: 1-228.
- HARVEY, P. A. 1934. Life history of *Kalotermes minor*, pp. 217-233. *In* C. A. Kofoid, S. F. Light, A. C. Horner, M. Randall, W. B. Herms, and E. E. Bowe [eds.] *Termites and termite control*. 2nd ed. University of California Press, Berkeley. 795 pp.
- HATHORNE, K. T., P. A. ZUNGOLI, E. P. BENSON, AND W. C. BRIDGES. 2000. The termite (Isoptera) fauna of South Carolina. *J. Agric. Urban Entomol.* 17: 219-229.
- HOSTETTLER, N. C., D. W. HALL, AND R. H. SCHEFFRAHN. 1995. Intacolonny morphometric variation and labral shape in Florida *Reticulitermes* (Isoptera: Rhinotermitidae) soldiers: significance for identification. *Florida Entomol.* 78: 119-129.
- HOWELL, H. N., P. J. HAMAN, AND T. A. GRANOVSKY. 1987. The geographical distribution of the termite genera *Reticulitermes*, *Coptotermes*, and *Incisitermes* in Texas. *Southwest. Entomol.* 12: 119-125.
- LA FAGE, J. P. 1987. Practical considerations of the Formosan subterranean termite in Louisiana: a 30-year problem, pp. 37-42. *In* M. Tamashiro and N.-Y. Su [eds.], *Biology and control of the Formosan subterranean termite*. College of Trop. Agr. Human Resources, Univ. of Hawaii, Honolulu, HI.
- LIGHT, S. F. 1934. The termite fauna of North America with special reference to the United States, pp. 127-135. *In* C. A. Kofoid, S. F. Light, A. C. Horner, M. Randall, W. B. Herms, and E. E. Bowe [eds.] *Termites and termite control*. 2nd ed. Univ. of California Press, Berkeley. 795 pp.
- MESENGER, M. T. 2002. The termite species of Louisiana: an identification guide. *New Orleans Mosquito*

- and Termite Control Board. Bull. No. 01-01. 2nd ed. 12 pp.
- MESSENGER, M. T., R. H. SCHEFFRAHN, AND N.-Y. SU. 2000. First report of *Incisitermes minor* (Isoptera: Kalotermitidae) in Louisiana. *Florida Entomol.* 83: 92-93.
- MILLER, E. M. 1949. A handbook on Florida termites. Tech. Ser., Univ. Miami Press, Coral Gables, Florida. 30 pp.
- SCHEFFRAHN, R. H., AND N.-Y. SU. 1994. Keys to soldier and winged adult termites (Isoptera) of Florida. *Florida Entomol.* 77: 460-474.
- SCHEFFRAHN, R. H., J. R. MANGOLD, AND N.-Y. SU. 1988. A survey of structure-infesting termites of peninsular Florida. *Florida Entomol.* 71: 615-630.
- SCHEFFRAHN, R. H., N.-Y. SU, J. A. CHASE, AND B. T. FORSCHLER. 2001. New termite (Isoptera: Kalotermitidae, Rhinotermitidae) records from Georgia. *J. Entomol. Sci.* 36: 109-113.
- SNYDER, T. E. 1954. Order Isoptera. The termites of the United States and Canada. National Pest Control Assn., New York. 64 pp.
- SPINK, W. T. 1967. The Formosan subterranean termite in Louisiana. Circular No. 89, Louisiana Agricultural Experiment Station, Baton Rouge. 12 pp.
- SU, N.-Y., AND M. TAMASHIRO. 1987. An overview of the Formosan subterranean termite in the world; pp. 3-15 in M. Tamashiro and N.-Y. Su [eds.], *Biology and control of the Formosan subterranean termite*. College of Trop. Agr. Human Resources, Univ. of Hawaii, Honolulu, HI.
- WEESNER, F. M. 1965. Termites of the United States, a handbook. Natl. Pest Contr. Assn., Elizabeth, NJ. 70 pp.
- WEESNER, F. M. 1970. Termites of the Nearctic region, pp. 477-525. In K. Krishna and F. M. Weesner [eds.], *Biology of termites*. Vol. 2. Academic Press, New York. 643 pp.