MITOCHONDRIAL DNA GENETIC DIVERSITY OF THE DRYWOOD TERMITES *INCISITERMES MINOR* AND *I. SNYDERI* (ISOPTERA: KALOTERMITIDAE)

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Abstract

The western drywood termite, *Incisitermes minor* (Hagen) and the light southern drywood termite *I. snyderi* (Light) are common drywood termites in southwestern and the southern United States, respectively. Despite the economic importance of these 2 species, no information exists on the mitochondrial genetic diversity of *I. minor* and *I. snyderi*. A molecular genetics study involving DNA sequencing of a portion of the mitochondrial DNA 16S rRNA gene was undertaken to determine the extent of genetic variation in *I. minor* and *I. snyderi*. A total of 12 haplotypes were observed for *I. minor* collected from Florida, Oregon, Arizona, Texas, Utah, and California. For *I. snyderi*, a total of 10 haplotypes were observed from the Bahamas, Florida, Georgia, and Texas. Genetic variation among *I. minor* haplotypes ranged from 0.7 to 3.7% and variation for *I. snyderi* ranged from 0.7 to 2.4%. Maximum parsimony and maximum likelihood analysis revealed 3 distinct clades for *I. snyderi*, whereas, *I. minor* had 2 distinct clades. This is the first study on mitochondrial genetic variation of the drywood termites *I. minor* and *I. snyderi*. There appears to be enough genetic variation within these 2 species for a molecular phylogeographic study, which may provide insight into dispersal and introductions of these species.

Key Words: clades, 16S rRNA, *Incisitermes*, drywood termite, DNA sequence.

Resumen

La termita de madera seca del oeste, *Incisitermes menor* (Hagen) y la termita clara de madera seca del sur, *I. snyderi* (Clara) son termitas comunes de madera seca el suroeste y el sur de los Estados Unidos, respectivamente. A pesar de la importancia económica de estas dos especies, no existe información sobre la diversidad genética mitocondrial de *I. minor* e *I. snyderi*. Se realizó un estudio de genética molecular que incluyó la secuenciación de una porción del ADN mitocondrial del gen 16S rARN para determinar el grado de variación genética en *I. minor* e *I. snyderi*. Un total de 12 haplotipos fueron observados en especimenes de *I. minor* colectados en la Florida, Oregon, Arizona, Texas, Utah y California. Para *I. snyderi*, un total de 10 haplotipos fueron observados en especimenes de las Bahamas, Florida, Georgia y Texas. La variación genética entre los haplotipos de *I. minor* fue entre 0.7 y 3.7% y la variación de *I. snyderi* fue entre 0.7 y 2.4%. El análisis de la parsimonia máxima y probabilidad máxima reveló tres clados (grupos) diferentes de *I. snyderi*, mientras que, *I. minor* tenía dos clados. Este es el primer estudio sobre la variación genética mitocondrial de las termitas de madera seca *I. minor* e *I. snyderi*. Parece que hay suficiente variación genética dentro de estas dos especies para un estudio molecular filogeográfico, lo que puede dar una idea de la dispersión y la introducción de estas especies.

The 2 most widespread species of drywood termites (Kalotermitidae) in the United States are the southeastern drywood termite, *Incisitermes snyderi* (Light) and the western drywood termite, *I. minor* (Hagen). Both species are endemic to the southern Nearctic region. *Incisitermes snyderi* is the only endemic drywood termite in southeastern United States that commonly infests structures (Scheffrahn et al. 1988). The natural range of *I. snyderi* extends from Monterrey, Mexico (RHS, unpublished) north and east to coastal North Carolina (Ebeling 1978) and southeast into the Bahamas archipelago (Scheffrahn et al. 2006). *Incisitermes minor* is the most common structure-infesting drywood termite in the western United States (Su & Scheffrahn 1990). The natural range of *I. minor* extends along the California coast from Mendocino County inland to the Sierra Nevada foothills and south into Baja California and Guaymas, Sonora, Mexico (Light 1934). The natural latitudinal distribution of *I. minor* roughly follows the U.S.-Mexico

border from its epicenter in southern California east to Brewster County, Texas (new easternmost record). Riparian communities in the canyons formed by the Colorado and Virgin Rivers and their tributaries allow *I. minor*'s natural range to reach into northern Arizona and southern Utah, an observation noted by others (Jones 2004). The many records outside this range, including some localities studied herein, should be considered anthropogenic introductions.

Introductions of *I. minor* from movement of infested wooden timbers and other wooden products have been documented in Iowa, Maryland, New Jersey, New York, Oklahoma, Ohio, Texas, and Washington State (Krishna & Weesner 1969; Snyder 1954); a heavily infested structure was reported in Toronto, Canada (Grace et al. 1991). *Incisitermes minor* has been found in Georgia (Scheffrahn et al. 2001), South Carolina (Hathorne et al. 2000) and Louisiana (Messenger et al. 2000). The latter is significant because *I. minor* was taken from a park tree in New Orleans indicating that it can survive outdoors in non-arid, subtropical climates. In southern California yachts, sailboats, and small pleasure craft harboring mature colonies may serve as floating sources of introduction outside *I. minor's* native range as they set sail for ports of call around the world. Twelve shipborne infestations of *I. minor* were recorded in Florida and Australia onboard yachts, some of which were known to have spent time in California (Scheffrahn & Crowe 2011). This has been the theme for many termite species over the past few years, including *Heterotermes* (Szalanski et al. 2004), *Coptotermes* (Austin et al. 2006, Scheffrahn et al. 2004), *Reticulitermes* (Austin et al. 2005), *Nasutitermes* (Scheffrahan et al. 2005a, 2005b), *Cryptotermes* (Scheffrahn et al. 2008), and others (Scheffrahn & Crowe 2011).

There is more restricted information existing on *Incisitermes* species occupation outside its known range, because in most instances, it appears that infestations did not lead to successful colonization flights with the exception of *I. minor* populations in Japan (Yoshimura et al. 2004). This fact may be associated with the difficulties in general for establishment from social insects such as termites, and because of the time required to establish colony maturity (Harvey 1942). Many infestations are more quickly identified and often eliminated due to the fact that some termites such as *I. minor* frequently try to establish colonies from easily accessed cracks, taking advantage of the shelter to establish copulariums and possessing relatively slow egg-laying rates (Harvey 1934). These access points may likewise be located and inspected by Pest Management Professionals (PMPs) that may attempt control measures or simply destroy the infested materials.

Introductions of *I. snyderi* are less well documented, indicating that this species is not as subject to transport and survival in new localities as is *I. minor* (Krishna & Weesner 1970, Scheffrahn & 12010). These subtle differences in establishment capability might infer that somehow *I. minor* could possibly possess greater reproductive and/or physiologically distinct capabilities to afford broader geographic distributions when compared to *I. synderi* (e.g. improved desiccation protection or water relations, etc.). As behavioral and physiological distinctiveness can be associated with unique phenotypes for each species, a genetic perspective might be useful to understand if the variability would be greater among *I. minor* populations than *I. snyderi* populations. One would generally anticipate greater genetic plasticity among populations that can occupy more variable geographic locations beyond their respective indigenous zones of habitation (Matsuura et al. 2009).

Genetic diversity studies can provide information on the dispersal of a species, enhance molecular diagnostics, and may help with identifying locally adapted populations. Previous studies on genetic diversity of these 2 species are limited to a microsatellite study by Booth et al. (2008) on six populations of *I. minor* from California and another study by Indrayani et al. (2006) on *I. minor* microsatellite diversity in Japan. No studies have even been conducted on genetic diversity of *I. snyderi,* and *I. minor* evaluations are limited to only California and Japan. The objective of this study was to determine the extent of genetic diversity of a mitochondrial DNA (mtDNA) 16S rRNA marker for populations of *I. minor* and *I. snyderi* in the US and the Bahamas.

Materials and Methods

Collected termites were preserved in 100% ethanol. Collected *Incisitermes* samples were identified using morphological characters described in the keys of Scheffrahn & Su (1994). Voucher specimens preserved in 100% ethanol are maintained at the Arthropod Museum, Department of Entomology, University of Arkansas, Fayetteville, Arkansas.

Alcohol-preserved specimens were allowed to dry on filter paper, and DNA was extracted according to Liu & Beckenbach (1992) on individual worker termites with the Puregene DNA isolation kit D-5000A (Gentra, Minneapolis, Minnesota). Extracted DNA was resuspended in 50 mL of Tris:EDTA and stored at -20 °C. Polymerase chain reaction (PCR) of a 428bp fragment of the 16S rRNA gene was conducted using the primers LR-J-13007 forward: 5'-TTA CGC TGT TAT CCC TAA-3' (Kambhampati & Smith 1995) and LR-N-13398 reverse: 5'-CGC CTG TTT ATC AAA AAC AT-3' (Simon et al. 1994).

The PCR reactions were conducted with 1 mL of the extracted DNA (Szalanski et al. 2000), having a profile consisting of 35 cycles of 94 °C for 45

s, 46 °C for 45 s and 72 °C for 60 s. Amplified DNA from individual termites was purified and concentrated with Microcon PCR centrifugal filter devices (Millipore, Billerica, Massachusetts) according to the manufacturer's instructions. Samples were sent to the DNA core sequencing facility at The University of Arkansas Medical, Little Rock for direct sequencing in both directions. GenBank accession numbers are HM542448 to HM542468 for the new haplotypes found in this study. DNA sequences were aligned using BioEdit v5.89 (Hall 1999) and adjusted manually. Mitochondrial DNA haplotypes were aligned using MacClade v4 (Sinauer Associates, Sunderland, Massachusetts). Genealogical relationships among haplotypes were constructed using TCS (Clement et al. 2000).

The distance matrix option of PAUP* 4.0b10 (Swofford 2001) was used to calculate genetic distances according to the Kimura 2-parameter model of sequence evolution (Kimura 1980). Additional mitochondrial 16S GenBank sequences from *I. schwarzi* Banks, and *I. banksi* (Snyder) were added to the dataset along with DNA sequences from *Glyptotermes nakajimai* Morimoto (GenBank AB036689), *Calcaritermes temnocephalus* (Silvestri) (GenBank EU253743), and *Kalotermes flavicollis* (Fabr.) (GenBank AY486437) which were added to act as outgroup taxa. DNA sequences were aligned using CLUSTAL W (Thompson et al. 1994). Maximum parsimony analysis on the alignments was conducted using PAUP* 4.0b10 (Swofford 2001). Gaps were treated as missing characters for all analysis. The reliability of trees was tested with a bootstrap test (Felsenstein 1985). Parsimony bootstrap analysis included 1,000 resamplings using the Branch and Bound algorithm of PAUP*.

For Bayesian analysis, the best-fitting nucleotide substitution model was chosen according to the general time reversible + gamma (GTR+G) model among 64 different models using the ModelTest v 3.7 (Posada & Crandall 1998) and PAUP* 4.0b10 (Swofford 2001) programs. Phylogenetic trees were obtained using Bayesian inference with the GTR+G model using Bayesian Evolutionary Analysis Sampling Trees (BEAST) v1.4.2 software (Drummond & Rambaut 2003). For Bayesian inference, 4 Markov chains run for 106 generations with a burn-in of 2 × 104 were used to reconstruct the consensus tree.

Results and Discussion

A total of 12 haplotypes were observed for *I. minor* and 10 for *I. snyderi* (Tables 1 and 2). For

Table 1. Collection data, haplotypes and number of samples for *Incisitermes minor* and *Incisitermes snyderi*.

Country	State	County	Haplotype (n) (IM – *I. minor*, IS – *I. snyderi)*
US	Arizona	Cochise	IM5(1)
		Santa Cruz	IM4(1)
	California	Orange	IM1(1)
		Riverside	IM1(1)
		San Diego	IM1(1)
		Tulare	IM3(1)
	Florida	Broward	IM11(1), IS4(1)
		Charlotte	IS3(1)
		Duval	IM1(1)
		Escambia	IM13(1), IS7(1)
		Monroe	IS2(1)
		Volusia	IM10(1)
	Georgia	Camden	IS10(1)
		Fulton	IM1(1)
		Glynn	IS6(1), IS8(1)
	Hawaii	Honolulu	IM1(1)
	Louisiana	Orleans	IM12(1)
	Oregon	Multnomah	IM1(1)
	Texas	Bexar	IM2(1)
		Brewster	IM7(1)
		Harris	IM4(1), IS4(2), IS5(1)
		Hildalgo	IS5(2)
		Jeff Davis	IM9(1)
		Kern	IM8(1)
		Lubbock	IM2(1)
		Matagorda	IS1(1)
	Utah	Washington	IM3(1)
Bahamas			IS1(1), IS7(1), IS9(1)

TABLE 2. *INCISITERMES MINOR* AND *INCISITERMES SNYDERI* HAPLOTYPES.

Species	Haplotype	GenBank	*n*
I. minor	IM1	EF543146	8
	IM2	HM542448	2
	IM3	HM542449	2
	IM4	HM542450	2
	IM5	HM542451	1
	IM7	HM542452	1
	IM8	HM542453	1
	IM9	HM542454	1
	IM10	HM542455	1
	IM11	HM542456	1
	IM12	HM542457	1
	IM13	HM542458	1
I. snyderi	IS1	HM542459	1
	IS2	HM542460	
	IS3	HM542461	1
	IS4	HM542462	3
	IS5	HM542463	1
	IS6	HM542464	1
	IS7	HM542465	2
	IS8	HM542466	1
	IS9	HM542467	1
	IS10	HM542468	1

I. minor, haplotype IM1 was the most common haplotype and also had the widest distribution (California, Georgia, Hawaii, Oregon and Utah); Haplotypes IM2, IM3 and IM4 occurred 2 times each and the remainder of the *I. minor* haplotypes were singletons. With *I. snyderi*, haplotype IS4 was the most common (n = 3), followed by IS7 (n = 2), and the remaining 8 haplotypes were singletons. Of the 3 *I. snyderi* haplotypes observed in the Bahamas, 2 haplotypes were not found in the United States (haplotypes IS1 and IS9), while haplotype IS7 was also observed in Florida. Genetic variation for *I. minor* ranged from 0.7 to 3.7% and from 0.7 to 2.4% for *I. snyderi*. Because of the limited number of locations to consider for genetic evaluation, it is difficult to ascertain if there is any statistical difference in the degree of genetic variation observed for respective species in the present study. How do these differences account for geographical dissemination potential of respective species? As hypothesized, *I. minor* possessed slightly greater genetic variability than *I. snyderi*, but additional sampling from more disparate locations may afford greater clarification of this point. An equally plausible explanation for the dispersal capability of *I. minor vs. I. snyderi*, which doesn't constitute a need or rationale for greater genetic variability, lies in the endemic origin of the species. Examples from other termite species mentioned earlier in this paper present ample evidence to this point. Future genetic studies which include broader sampling will likely assist with this question. The greatest number of *I. minor* structural infestations occur in Southern California

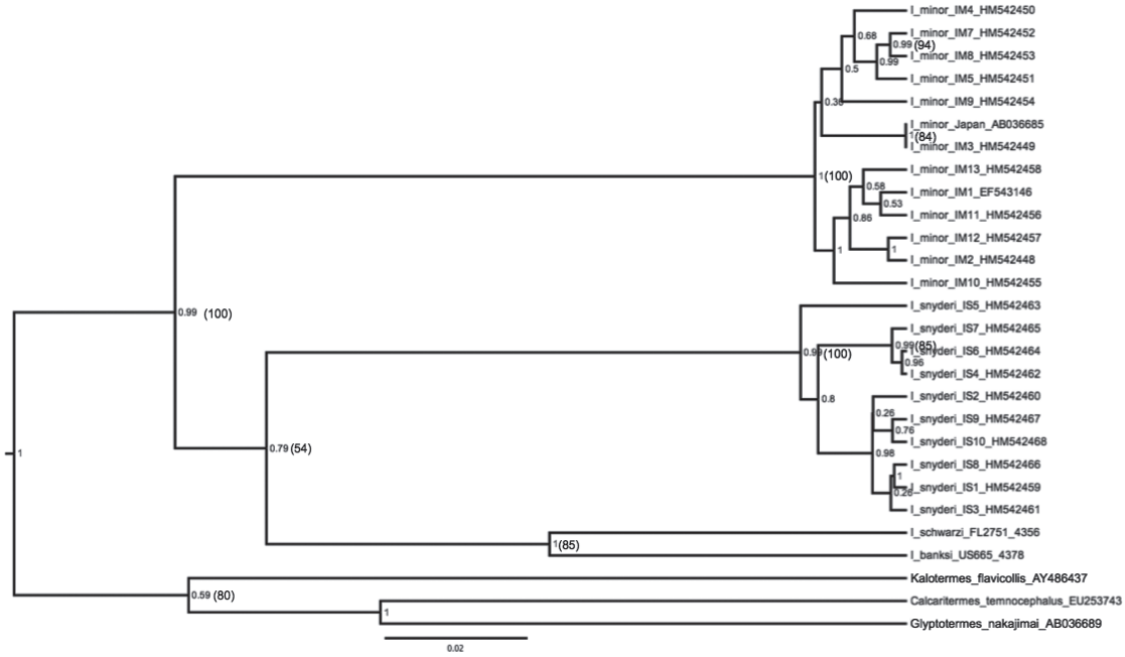

Fig. 1. Bayesian phylogenetic relationships of *Incisitermes* mtDNA 16S sequences. Posterior bootstrap values are provided at each node, and maximum parsimony (MP) bootstrap values (> 75) are provided in parenthesis.

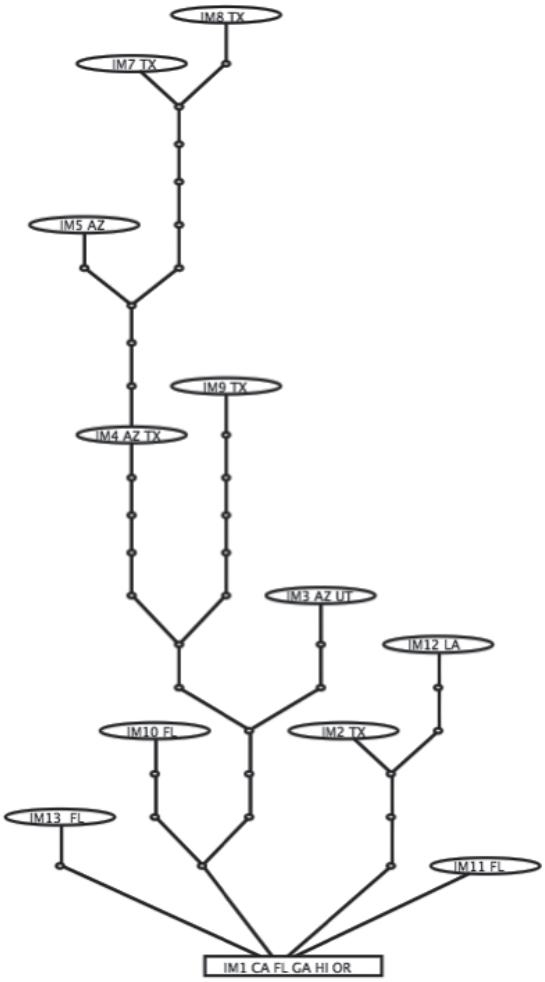

Fig. 2. Genealogical relationships among *Incisitermes minor* 16S haplotypes estimated by TCS (Clement et al. 2000). State or country (Bahamas) locations are provided for each haplotype. A unit branch represents one mutation and small ovals indicate genotypes that were not observed.

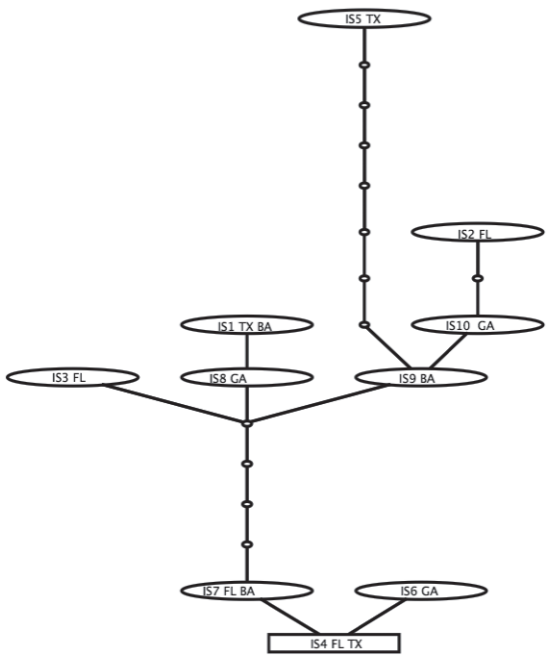

Fig. 3. Genealogical relationships among *Incisitermes snyderi* 16S haplotypes estimated by TCS (Clement et al. 2000). State or country (Bahamas) locations are provided for each haplotype. A unit branch represents one mutation and small ovals indicate genotypes that were not observed.

(RHS unpubl. obs.), with occasional surprises such as populations recently recovered in Southern New Mexico (JWA unpubl.). Therefore, the southern California haplotype, IM1, may posit the greatest capability to undergo anthropogenic dispersal, from the populations evaluated in the present study.

Of the 477 characters used for the phylogenetic analysis, a total of 99 characters (21%) were parsimony informative. The maximum parsimony analysis resulted in a tree of a length of 293 and a confidence index value of 0.741. *Incisitermes minor* and *I. snyderi* were both monophyletic (Fig. 1). Both phylogenetic and TCS analysis revealed several distinct clades within *I. minor*: haplotypes IM1 and IM2 from California and Texas; *I. minor* AB036685 from Japan with IM3 from Utah and IM5, IM7-9 from Arizona and Texas (Figs. 2 and 3). For *I. snyderi* haplotype IS5 (Texas) was the most distal and formed a distinct clade. Haplotypes IS4 (Texas, Florida), IS6 (Georgia) and IS7 (Florida, Bahamas) formed a distinct clade relative to the other *I. snyderi* haplotypes. If you divide the *I. minor* samples into those collected within their endemic range (defined earlier) with those collected outside this range, you will see that many outside the range fall within the IM1 haplotype. The clade (from Fig. 1) in our phylogenetic tree containing IM1 also contains most of the samples collected outside the natural endemic range including Georgia Hawaii, Louisiana, Oregon, and Florida. The relative ease of intra-continental travel and commerce, coupled with the fact that infested wood can be easily transported, has resulted in isolated occurrences of *I. minor* infestations throughout the United States (Cabrera & Scheffrahn 2005), and the occurrences of specimens evaluated in the current study are no exception. The second clade (also Fig. 1) which includes *I. minor* from Arizona and Texas specimens, im-

plies native geographical affinities. There is no clear explanation for the position of the Japan and Tulare haplotype except to say that Tulare County, California has native *I. minor*, and a large forest products industry from which Japan imports large quantities of products. It is speculation at best to assume infested materials were brought to Japan, but at least this is 1 plausible explanation for this occurrence in the present study.

Incisitermes snyderi haplotypes show no apparent geographic patterns. Most specimens of *I. snyderi* samples taken from collections used in the present study were obtained in dead tree branches; in some instances, specimens (particularly those from Texas) were taken from infested fences and in 2 instances structures adjacent to infested fencing (JWA, pers. comm.). All *I. snyderi* samples in this study came from coastal localities suggesting that haplotypes could represent populations that established between locations via overwater dispersal during and after the last Pleistocene low sea levels (Scheffrahn et al. 2006).

This is the first study on mitochondrial genetic variation of the drywood termites *I. minor* and *I. snyderi*. There appears to be enough genetic variation within these 2 species for a molecular phylogeographic study which may provide insight into the evolution, dispersal and introduction history and establishment of these species.

Acknowledgments

Research was supported in part by the University of Arkansas, Arkansas Agricultural Experiment Station.

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