

Phylogenetic analyses of mtDNA sequences corroborate taxonomic designations based on cuticular hydrocarbons in subterranean termites

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Abstract

Cuticular hydrocarbons (CHCs) are valuable characters for the analysis of cryptic insect species with few discernible morphological characters. Yet, their use in insect systematics, specifically in subterranean termites in the genus *Reticulitermes* (Isoptera: Rhinotermitidae), remains controversial. In this paper, we show that taxonomic designations in *Reticulitermes* from California (USA) suggested in light of differences among CHC phenotypes are corroborated by phylogenetic analyses using mtDNA sequences. Analyses based on CHC phenotypes and supported, in part, by behavioral and ecological differences have suggested the presence of more species than the two currently recognized: *R. hesperus* Banks and *R. tibialis* Banks. We analyze a 680 base pair fragment of the mitochondrial DNA cytochrome oxidase (COII) gene from 45 new (21 collection localities) and two previously recorded samples of *Reticulitermes* from California using parsimony and maximum likelihood methods. Both methods result in trees with highly similar topologies. Bootstrapping indicates support for six clades of *Reticulitermes*, and corroborates groupings based on cuticular hydrocarbons. One of the clades, *R. hesperus*, is already recognized in California, while four clades appear to be previously undescribed taxa. Although identification of the final clade is inconclusive, it includes a sample putatively identified as *R. tibialis*. Therefore, using phylogenetic analyses we corroborate chemical characters used to identify taxa, associate a chemical phenotype with a previously described species, and provide additional support for undescribed taxa of *Reticulitermes*.

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1. Introduction

Reticulitermes is a genus of economically important subterranean termites found in temperate climates of the Holarctic (Weesner, 1970). In forest ecosystems they are important decomposers of woody materials, and are the

dominant termites in North America. Proper identification of species is imperative for proper control of these insects in urban settings and for understanding their role in forest ecosystems. However, the taxonomy of North American *Reticulitermes* is problematic and in need of revision (Nutting, 1990; Scheffrahn and Su, 1994; Weesner, 1970). Much of the taxonomic and biogeographical information on *Reticulitermes* spp. was developed in the first half of the last century and needs revision using modern phylogenetic and taxonomic methods (Banks, 1946; Banks and Snyder, 1920; Light, 1934; Miller, 1949; Pickens, 1934a,b; Snyder, 1954).

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The present state of taxonomy using morphological keys on western *Reticulitermes* is not adequate for proper identification of species. Samples of subterranean termite colonies collected in the field typically consist of a few to dozens of workers, a small percentage of soldiers, and, rarely, alates (winged reproductives). The available keys to species, based on the morphology of soldiers and alates (Banks and Snyder, 1920; Snyder, 1954; Weesner, 1965), are difficult to use and unreliable. If only workers are found, the keys are not useful. Even when soldiers and alates are found together in the same sample, the keys can be equivocal. For example, some collections of termites in Georgia (USA) have soldiers within the size range for *R. hageni* Banks, yet alates from the same sample key to *R. virginicus* Banks (Haverty et al., 1996). For *Reticulitermes* spp. from the Pacific Coastal states, Weesner (1965) did not even attempt a key to the soldiers. Nutting (1990) did include a key to soldiers of *Reticulitermes*, but it is based on the original descriptions of Banks and Snyder (1920) and subsequent synonymies by Snyder (1949), and therefore does not add new, easily useable information. According to the most recently published biogeographical information, only two species of *Reticulitermes*, *R. hesperus* Banks and *R. tibialis* Banks, occur in California (Nutting, 1990; Weesner, 1970). However, morphological keys used on samples throughout northern California keyed all soldiers to *R. tibialis* (Haverty and Nelson, 1997).

Due to the problems with the available keys, Haverty et al. (1996, 1999b, 2000) and Haverty and Nelson (1997) examined the suitability of chemical characters, cuticular hydrocarbons, to distinguish taxa (CHCs). CHCs have aided in the identification of cryptic species in a number of arthropod species including ticks, bark beetles, mosquitoes, and grasshoppers (Buckley et al., 2003; Estrada-Peña et al., 1994; Horne and Priestman, 2002; Page et al., 1997). Typically, qualitative differences in many hydrocarbons coupled with large quantitative differences in a few are argued to be species level variation, whereas quantitative variation in the same hydrocarbons is considered population level variation (Estrada-Peña et al., 1994; Haverty and Nelson, 1997; Page et al., 2002).

Variation in CHC profiles has been shown to be polygenically inherited and important for reproductive isolation in *Drosophila* spp. (Coyne et al., 1994; Dallerac et al., 2000; Takahashi et al., 2001). However, CHCs may also show environmental variation, especially in social insects where CHC profiles can vary depending on nesting materials, food, and diet (Liang and Silverman, 2000; Page et al., 1991). Because of the possible environmental variation of CHCs, their use in taxonomy has been controversial. However, we argue that few studies have systematically attempted to quantify the levels (qualitative versus quantitative) of variation to test the use of cuticular hydrocarbons as taxonomic characters. Previous studies in *Reticulitermes* have shown that qualitative

differences in large numbers of cuticular hydrocarbons coupled with large quantitative differences in other hydrocarbons likely represent species level differences and, therefore, can be useful for taxonomic purposes.

The evidence suggesting species-specific mixtures of cuticular hydrocarbons in termites is extensive (Page et al., 2002 and references cited within). In *Reticulitermes* in the western United States repeatable qualitative (presence/absence) and quantitative differences, collectively grouped into CHC phenotypes have been found suggesting the presence of more taxa than currently recognized. Thus far eight CHC phenotypes have been identified in California. Five have been found west of the Sierra Nevada, two in coastal southern California, and one east of the Sierra Nevada (Haverty and Nelson, 1997, unpublished results). If all phenotypes indicate separate species, then there may be at least eight species of *Reticulitermes* in California.

Ecological, behavioral, and additional chemical differences among samples of the CHC phenotypes have supported the suggestion that they represent distinct taxa. Haverty et al. (2003) reported alate flight times differing between two hydrocarbon phenotypes, supporting reproductive isolation between these two phenotypes. Dramatic and unambiguous, interphenotype aggression has been shown among several of the phenotypes studied (Delphia et al., 2003; Haverty et al., 1999a). Workers from colonies possessing different hydrocarbon phenotypes always fight, and the aggression is rapidly expressed. In contrast, when colonies of the same phenotype are paired, aggression is neither consistently rapid nor apparent (Copren, 2004; Delphia et al., 2003; Haverty et al., 1999a). Aggression has been used as a correlate for reproductive isolation under the argument that strong aggression among colonies would prevent mating. In European *Reticulitermes* species the reproductive isolation proposed based on aggression was later supported by chemical and genetic analyses (Clément et al., 2001). Furthermore, separate chemical characters, soldier defensive secretions, have also been found to correlate with CHC phenotypes in western *Reticulitermes* (Nelson et al., 2001). The only information lacking in western North American *Reticulitermes* is phylogenetic confirmation that CHC phenotypes represent monophyletic taxa, which we address in this paper.

We chose to use the cytochrome oxidase II (COII) region of mitochondrial DNA (mtDNA) to examine the putative species complex of *Reticulitermes* in California, previously proposed in the light of the differentiation revealed by CHC phenotypes. This marker has been the most successful and widely used in identifying *Reticulitermes* species (Austin et al., 2002; Jenkins et al., 1999, 2000, 2001; Miura et al., 1998). Other markers such as the nuclear ITS2 were phylogenetically uninformative in *Reticulitermes* (Jenkins et al., 2001; Uva et al., 2004). Phylogenetic analysis of the COII gene supported

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