

Establishment of the African termite, *Coptotermes sjostedti* (Isoptera: Rhinotermitidae), on the Island of Guadeloupe, French West Indies

RUDOLF H. SCHEFFRAHN,^{1, 2} JAN KRECEK,¹ BOUDANATH MAHARAJH,¹ NAN-YAO SU,¹
 JAMES A. CHASE,³ JOHN R. MANGOLD,⁴ ALLEN L. SZALANSKI,⁵ JAMES W. AUSTIN,⁵
 AND JAY NIXON⁶

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ABSTRACT Based on morphological and genetic comparisons, an established population of the African termite, *Coptotermes sjostedti* Holmgren, was identified on the island of Guadeloupe. This is the sixth recorded species of an endemic Old World termite becoming established in the New World. We hypothesize that this species arrived from tropical West Africa by maritime transport.

KEY WORDS survey, introduced species, DNA sequence, genetic variation

SPECIES RECORDS FOR OLD WORLD termites that are established in the New World are rare. Of the nearly 600 species that occur in the Nearctic and Neotropical regions (Constantino 1998), only 5 are not endemic to these regions. All five share the following characteristics common to most invasive termites: (1) colonies reach maturity (i.e., produce dispersal flights) aboard ships or boats, shipping containers, and/or wood products; (2) distributions are disjunct and sympatric with human habitation; and (3) infestations are associated with human structures. Two Old World drywood (kalotermitid) species that have confirmed establishments in the Neotropics include *Cryptotermes dudleyi* Banks, an Indomalayan endemic occurring in Panama, Costa Rica, Colombia, Brazil, and the West Indies, and *Cr. havilandi* (Sjöstedt), a species described from tropical Africa that is now established in Surinam, Guyana, Brazil, and the West Indies (Scheffrahn and Krecek 1999). The New World report of the Indomalayan endemic *Cr. domesticus* (Haviland) by Araujo (1977) remains doubtful (Scheffrahn and Krecek 1999). Three invasive species from the subterranean termite family Rhinotermitidae are established in the New World and include the European *Reticulitermes lucifugus* (Rossi) in Uruguay (Aber and Fontes 1993); the Southeast Asian *Coptotermes gestroi* (Wasmann) (*Co. havilandi* Holmgren per; Kirton and Brown 2003)

in Brazil, Florida, and the West Indies (Scheffrahn et al. 2003); and *Co. formosanus* Shiraki, a Sinopacific endemic now widespread in the southern United States (Su 2003).

During a survey expedition to Guadeloupe in 1999, a large and mature *Coptotermes* colony was discovered in a fallen tree in a submontane rain forest. At the time, it was erroneously assumed to be a curious sample of *Co. gestroi*, a species typically collected around inhabited coastal localities throughout the West Indies. More recent genetic data suggested otherwise. We herein report the discovery of an established population of the African endemic, *Co. sjostedti* Holmgren, on Guadeloupe.

Materials and Methods

Morphometric data from specimens preserved in 85% ethanol were obtained using a stereomicroscope fitted with an ocular micrometer. Measurements were taken from only soldiers and included head length to tips of mandibles, maximum head width, and maximum pronotum width. The number of antennal articles and relative size of basal articles were also determined (Table 1). All specimens are housed by inventory numbers (listed below) at the University of Florida Termite Collection, Ft. Lauderdale Research and Education Center.

Material Examined for Morphology

Coptotermes sjostedti. Guadeloupe; Basse-Terre, Maison de la Foret; 16.17525° N, 61.69403° W; 29 MAY 1999; coll. B. Maharajh, J. Chase, J. Krecek, J. Mangold, and R. Scheffrahn; soldiers, workers, nymphs (GU-756); Ex: fallen tree and stump, submontane rain forest ca. 500-m elevation. Guinea; Conakry, Nongo 156; 9.62198° N, 13.62563° W; 21 SEPT 2000; coll. J. Nixon;

¹ Fort Lauderdale Research and Education Center, University of Florida, Institute of Food and Agricultural Sciences, 3205 College Ave., Fort Lauderdale, FL 33314.

² E-mail: rhsc@ufl.edu.

³ Terminix International, 212 West Campground Rd., McDonough, GA 30253.

⁴ Terminix International, 9051 Florida Mining Blvd., Suite 105, Tampa, FL 33634.

⁵ Department of Entomology, 319 Agriculture Building, University of Arkansas, Fayetteville, AR 72701.

⁶ American Pest Management, 6460 New Hampshire Ave., Takoma Park, MD 20912.

Table 1. *Coptotermes* spp. soldier mean (range) measurements

Species	Locality	n	Head length with mandibles (mm)	Head width (mm)	Pronotum width (mm)	No. antennal articles	Antennal formulae
<i>sjostedti</i>	Guadeloupe	10	1.73 (1.68–1.78)	0.95 (0.94–0.99)	0.69 (0.67–0.72)	13	2 > 3 < 4 < 5
<i>sjostedti</i>	Guinea	2	1.69 (1.68–1.70)	0.95 (0.94–0.96)	0.68 (0.67–0.69)	13	2 > 3 < 4 < 5
<i>sjostedti</i> ^a	Cameroon		(1.63–1.77)	(0.97–1.00)	0.70	13	2 > 3 < 4
<i>sjostedti</i> ^b	West Africa		(1.46–1.59)	(0.82–0.93)	(0.54–0.68)	13	
<i>sjostedti</i> ^b	Uganda		(1.57–1.77)	(0.86–1.00)	(0.71–0.82)	13	
<i>intermedius</i>	Togo	10	1.89 (1.78–1.93)	0.99 (0.89–1.01)	0.70 (0.64–0.74)	14	2 > 3 < 4 < 5
<i>intermedius</i> ^b	West Africa		(1.72–1.96)	(0.95–1.04)	(0.64–0.73)	14–15	
<i>gestroi</i>	Nevis	10	2.19 (2.12–2.27)	1.11 (1.06–1.14)	0.85 (0.84–0.86)	15	2 > 3 < 4 < 5

^a From Emerson (1928).

^b From Harris (1966).

four soldiers, one worker (AFR-20); Ex: house. Conakry; Nongo Compound, FBO 153; 9.55173° N, 13.67604° W; coll. J. Nixon; OCT 1999; two soldiers (AFR-14); Ex: building.

Coptotermes intermedius Silvestri. Togo; Lome; 6.12865° N, 1.21812° E; coll. J. Nixon; 3 JUNE 2002; soldiers and workers (AFR-32); Ex: urban tree trunk adjacent to building.

Coptotermes gestroi. Nevis; Bath; 17.13415° N, 62.62958° W; 13 NOV 1997; coll. J. Chase and B. Maharajh; soldiers, workers, nymphs (SKN-191); Ex: coastal mangrove/manchineel forest adjacent to city.

Genetic Analysis

DNA was extracted from the samples following the procedures of Szalanski et al. (2004). Polymerase chain reaction (PCR) was conducted using the primers LR-J-13007 (5'-TTACGCTGTTATCCCCTAA-3') (Kambhampati and Smith 1995) and LR-N-13398 (5'-CGCCTGTTTATCAAAAACAT-3') (Simon et al. 1994). These PCR primers amplify an ≈428-bp region of the mtDNA 16S rRNA gene. PCR reactions were conducted using 1 μl of the extracted DNA per Szalanski et al. (2000), with a profile consisting of 35 cycles of 94°C for 45 s, 46°C for 45 s, and 72°C for 45 s. Amplified DNA from individual termites was purified and concentrated using Microcon-PCR Filter Units (Millipore, Bedford, MA). Samples were sent to the University of Arkansas for Medical Sciences DNA Sequencing Core Facility (Little Rock, AR) for direct sequencing in both directions using an ABI Prism 377 DNA sequencer (Foster City, CA). GenBank accession numbers for the *Coptotermes* termites subjected to DNA sequencing in this study are AY453588–AY453588. Consensus sequences for each sample were obtained using Bioedit 5.09 (Hall 1999), and sequences were aligned using CLUSTAL W (Thompson et al. 1994).

The distance matrix option of PAUP* 4.0b10 (Swofford 2001) was used to calculate genetic distances according to the Kimura 2-parameter model (Kimura 1980) of sequence evolution. Mitochondrial DNA sequences of *Reticulitermes tibialis* Banks (Isoptera: Rhinotermitidae) (GenBank AY538744) and *Heterotermes cardini* (Snyder) (Isoptera: Rhinotermitidae) (GenBank AY453590) were used as the outgroup taxa

for the *Coptotermes* dataset. These two taxa were selected based on their molecular phylogenetic relationship to *Coptotermes* (Austin et al. 2004). DNA sequences were aligned using the PILEUP program in GCG (Genetics Computer Group, Madison, WI) and adjusted manually. Maximum likelihood and unweighted parsimony analysis on the alignments were conducted using PAUP* 4.0b10 (Swofford 2001). Gaps were treated as missing data. 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 maximum likelihood analysis, the default likelihood parameter settings were used (HKY85 6-parameter model of nucleotide substitution, empirical base frequencies) with the exception of the transition/transversion ratio, which was set to 1.357845:1. These parameters were used to carry out a heuristic search using PAUP*, using either the single most parsimonious tree as the starting tree, or step-wise addition.

Results

Of the four species of *Coptotermes* known from Africa, only two species occur in tropical West Africa: *Co. intermedius* and *Co. sjostedti* (Harris 1966). The former can be distinguished from the latter by its larger overall measurements (Table 1), its proportionally smaller fontanelle, and its longer head (Harris 1966). Also, *Co. intermedius* typically has 14 antennal articles compared with 13 for *Co. sjostedti*.

The head and pronotum measurements (Table 1) overlap for *Co. sjostedti* soldiers from Guadeloupe and soldiers from Guinea, Cameroon (Emerson 1928), and Uganda (Harris 1966). Although the Guadeloupe soldiers overlap in pronotum and head width measurements with *Co. intermedius* soldiers from Togo and West Africa (Harris 1966), the head lengths of the Guadeloupe soldiers were shorter than *Co. intermedius*. All *Co. sjostedti* soldiers measured had 13 antennal articles, whereas *Co. intermedius* had 14 (Table 1). Fontanelle characters of the soldier were diagnostic for each species as previously reported (Harris 1966). Soldiers of *Co. sjostedti* are much smaller in all measurements than those of the nearest West Indian congener, *Co. gestroi*, from the island of Nevis (Table 1).

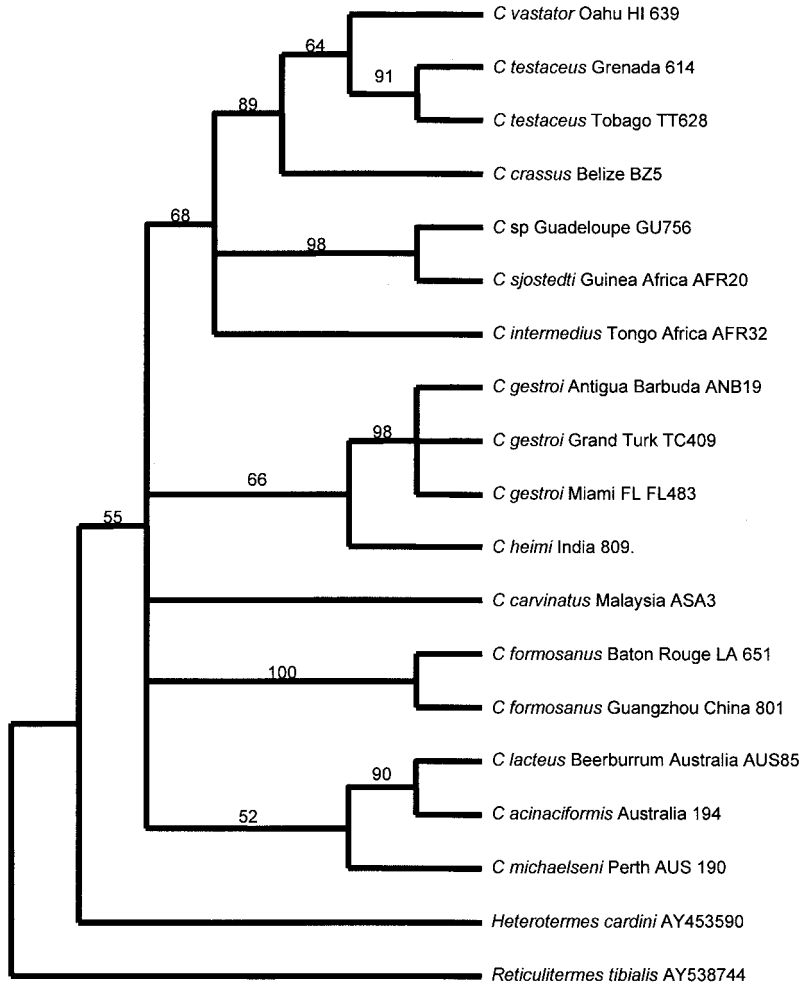


Fig. 1. 16S single most parsimonious tree during a branch and bound search using PAUP*. Bootstrap values for 1,000 replicates are listed above the branches supported at $\geq 50\%$.

The neotropical endemic, *Co. testaceus* L., occurring as far north as Grenada (Scheffrahn et al. 1994), is very distinct from *Co. sjostedti* and *Co. gestroi* and larger than both in all measurements (Mathews 1977).

Harris (1966) noted that *Co. sjostedti* is an inhabitant of West African rain forests and is responsible for much damage to buildings and timbers along the West African coast. Harris (1966) reported a crepuscular dispersal flight for *Co. sjostedti* in July in Garamba Park (Congo), agreeing with the late May appearance of nymphs in the Guadeloupe population.

The 428-bp region of the mtDNA 16S rRNA gene was subjected to DNA sequencing from 11 described species of *Coptotermes* and 2 *Coptotermes* spp. Within the genus, genetic diversity ranged from 0.6% between the *Coptotermes* sp. from Guadeloupe and *Co. sjostedti* from Conakry, Guinea to 6.6% between *Co. vastator* Light and *Co. lacteus* (Froggatt). The aligned DNA data matrix resulted in 440 characters. Of these characters, 83 (19%) were variable and 51 (12%) were

phylogenetically informative. This dataset had only one most parsimonious tree (Fig. 1; length = 173, CI = 0.642), as documented using the Branch and Bound search algorithm of PAUP*. Bootstrap analysis of the aligned *Coptotermes* taxa revealed that *Coptotermes* sp. Guadeloupe and the African *Co. sjostedti* formed a common clade that resulted in a sister group with *Co. vastator* + *Co. testaceus* + *Co. crassus* Snyder and *Co. intermedius* from Lome, Tongo. The relationship of *Coptotermes* sp. Guadeloupe and *Co. sjostedti* relative to the other *Coptotermes* taxa was the same for the maximum likelihood analysis ($-\ln L = 1492.91272$).

Discussion

In the first survey dedicated to cataloging the termite fauna of Guadeloupe, Darlington (1992) recorded 12 species (75 colony samples) from 25 sites, encompassing mountainous volcanic Basse-Terre and the limestone hills of Grande Terre. Our more exhaus-

tive 1999 survey recorded an additional five species, including *Co. sjostedti*, from 78 sites (718 samples) on Basse-Terre, Grande Terre, and the neighboring limestone islands of Marie Galant and La Desirade (Scheffrahn and Kreczek 1999, 2001, Szalanski et al. 2004, R. H. S., unpublished data). Based on these surveys, we postulate that if other populations of *Co. sjostedti* occur on Guadeloupe, they are rather localized or may exist in urban habitats that we did not collect.

The habitus of the single *Co. sjostedti* population known on Guadeloupe contrasts with those of other Old World exotics in that *Co. sjostedti* was found in an undeveloped mountainous riverbed several kilometers from the nearest human settlement. The only structure within the vicinity was a recently constructed footbridge crossing the Bras David River. The rate of dispersal or extent of distribution of *Co. sjostedti* cannot be verified at present, but one can compare the condition of *Co. sjostedti* on Guadeloupe with its New World congeners. The localized distribution of *Co. sjostedti* on Guadeloupe suggests more limited dispersal ability compared with *Co. gestroi*. *Co. gestroi* has become widespread on Barbados since their discovery >60 yr ago. However, *Co. testaceus* remains very localized on Grenada since they were discovered there in 1936 (Adamson 1938, 1948), and they may be endemic to that island (R.H.S., unpublished data).

Much as *Co. gestroi* and other species have been introduced to new locations in Florida and the West Indies by dispersal flights from shipboard infestations (Su et al. 1997), *Co. sjostedti* might have followed the same scenario by infesting ships visiting African ports-of-call. Although the endemic source of *Co. sjostedti* is rather certain, the timing and mechanism of its establishment on Guadeloupe is open to considerable speculation. The earliest introduction of *Co. sjostedti* might have resulted from a shipboard infestation during European colonial development. Thomas (1997) reported thousands of slave voyages between Guadeloupe and equatorial West Africa from the mid-1600s to the mid-1800s. A more recent introduction could be attributed to private, commercial, governmental, or military maritime transport of infested goods or containers. Woods from West Africa have been imported into Guadeloupe in recent times, but more precise information is unavailable (C. Bordereau, personal communication).

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