Proliferation of the Invasive Termite Coptotermes gestroi (Isoptera: Rhinotermitidae) on Grand Cayman and Overall Termite Diversity on the Cayman Islands

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Abstract

The Asian subterranean termite, *Coptotermes gestroi* (Wasmann) (Isoptera: Rhinotermitidae), was discovered on Grand Cayman Island in 2000 and, by 2014, had been recorded from 102 land-based localities. These data were used in a hierarchical cluster analysis to identify homogeneous clusters of sites to estimate separate introduction points on the island. Results suggest 4 separate introductions of *C. gestroi* to Grand Cayman by boat and 1 by land transport from other previously infested parts of the island. The infestations by boat could be either primary introductions (originating from another island) or secondary introductions (originating from other previously infested parts of Grand Cayman). An individual-based model was used to simulate non-anthropogenic spread of *C. gestroi* over Grand Cayman from 2014 to 2050. The model predicts that by 2050, most of the western part of Grand Cayman will likely be heavily infested by *C. gestroi*, whereas patches of unsuitable habitat restrict the expansion of the species over the central and eastern parts of the island. In the absence of further human introductions, it will likely take a century for *C. gestroi* to saturate the island by natural dispersal only. Based on detailed termite diversity surveys, we provide updated records for 14 termite species, collectively, on Grand Cayman, Little Cayman, and Cayman Brac.

Key Words: cluster analysis; individual based spread model; Little Cayman; Cayman Brac

Resumen

La termita subterránea de Asia, *Coptotermes gestroi* (Wasmann) (Isoptera: Rhinotermitidae), fue descubierta en la Isla de Gran Caimán en el 2000 y por el 2014, había sido registrada en 102 localidades con base en tierra. Se utilizaron estos datos en un análisis de agrupamiento jerárquico para identificar grupos homogéneos de sitios para estimar puntos de introducción separados en la isla. Los resultados sugieren 4 introducciones separadas de *C. gestroi* a Grand Cayman por barco y 1 por transporte terrestre desde otras partes previamente infestadas de la isla. Las infestaciones por barco podría ser la introducción primaria (procedente de otra isla) o introducciones secundarias (originarios de otras partes previamente infestadas de Grand Cayman). Un modelo basado en el individuo fue utilizado para simular la propagación no antropogénica de *C. gestroi* dentro Gran Caimán desde el 2014 hasta el 2050. El modelo predice que para el año 2050, es probable que la mayor parte de la parte occidental de Gran Caimán sea fuertemente atacada por *C. gestroi,* mientras que los parches de hábitat inadecuado restringen la expansión de la especie más en las partes central y oriental de la isla. En ausencia de nuevas introducciones por humanos, es probable que tome un siglo para que *C. gestroi* pueda saturar la isla sólo por dispersión natural. Sobre la base de sondeos detallados de diversidad de termitas, provemos registros actualizados para 14 especies de termitas, de manera colectiva, en las islas de Gran Caimán, Pequeña Caimán y Caimán Brac.

Palabras Clave: análisis de conglomerados; modelo de propagación de base individual; Pequeña Caimán y Caimán Brac

The diversity and distribution of termites (Isoptera) on the Caribbean mainland and West Indian islands have received renewed attention during the past 20 yr (e.g., Scheffrahn & Křeček 1999; Scheffrahn et al. 1994, 2003, 2005a,b, 2006). The great majority of these termite species are non-pestiferous endemics that support ecosystem stability by contributing to cellulose decomposition, soil enrichment, and diet for other animals (Jouquet et al. 2011). Species of the Caribbean genera *Het-* *erotermes* (Rhinotermitidae) and *Nasutitermes* (Termitidae), however, cause significant damage to wood in service, and *Neotermes* (Kalotermitidae) species are known to occasionally damage tree crops (Constantino 2002). Two exotic species pose the greatest threat of structural damage in the West Indies (Scheffrahn et al. 2006) and beyond (Constantino 2002). The West Indian drywood termite, *Cryptotermes brevis* (Walker) (Kalotermitidae), is a long-established and broadly distributed pest in

the New World owing to 5 centuries of anthropogenic spread from its endemic Chilean/Peruvian origin (Scheffrahn et al. 2009). The Asian subterranean termite, *Coptotermes gestroi* (Wasmann) (Rhinotermitidae), on the other hand, is a more recent Caribbean invader first reported on Barbados in 1937 (Adamson 1938). Since then, boat infestations (Scheffrahn & Crowe 2011) have facilitated the spread of *C. gestroi* along the coasts of tropical Florida (Hochmair & Scheffrahn 2010) and numerous West Indian islands (Fig. 1).

Grand Cayman Island, along with Cayman Brac and Little Cayman, are British Overseas Territories. Grand Cayman is best known as a tourist destination and banking center with a high standard of living. The island has a commercial seaport in George Town, and in line with its strong local economy and resort destination status, the island is a noteworthy Caribbean yachting center with ample dockage and boat servicing facilities. Several waterfront neighborhoods have their own private marine dockage. As part of a prosperous resort-driven economy, pest control services on Grand Cayman are available for treatment of household and structural pests including termites. Until 2000, no *C. gestroi* populations were known on Grand Cayman (data herein). Therefore, the first land-based infestation on the island provided a unique opportunity to track the establishment and proliferation of *C. gestroi* on a single island.

The Cayman Islands also have a unique natural ecology that invites ongoing studies in biodiversity and conservation (Oldfield & Sheppard 1997). The first records of termites from the Cayman Islands were offered only recently by the late Smithsonian taxonomist, Margaret S. Collins (Scheffrahn et al. 1994), who, on occasion, visited the islands. Dr. Collins' encouragement to investigate the Caymanian termite fauna prompted the first West Indian study of *C. gestroi* on Little Cayman (Su et al. 2000) and the taxonomy of the genera *Cryptotermes* (Scheffrahn

& Křeček 1999) and *Procryptotermes* (Kalotermitidae) (Scheffrahn & Křeček 2001) occurring on these islands.

In this paper, we analyzed 14 yr of spatial occurrences of *C. gestroi* on Grand Cayman to estimate marine and overland introduction sites and predict the future distribution range of this pest. We also provide new termite records from field surveys of all 3 islands.

Materials and Methods

ESTABLISHMENT OF *C. GESTROI* ON GRAND CAYMAN

In Jul 2000, one of us (P. F.) collected the first sample of *C. gestroi* at Rum Point on Grand Cayman. From then on, P. F. and K. H., working at Pestkil Ltd., a principle Caymanian termite inspection and pest control service provider, amassed *C. gestroi* samples or records from customer inspection calls and termite treatments. Samples were sent to R. H. S. to confirm identification. Although 2 other pest control companies operate on Grand Cayman, Pestkil has approximately 85% of the termite inspection and control market (P. F., pers. comm.). The spatial distribution of the *C. gestroi* localities was used to estimate the number of both boat and overland introduction sites. Termite collection dates, however, could not be used to determine colonization dates because termite discovery dates may lag actual colonization by several years.

Grand Cayman Island is divided into 5 districts. The 1999 annual average household income ranged between 58,635 Cayman Island dollars (CID) (Bodden Town in central south) and CID 47,673 (at East End), indicating a lower income toward the east. This discrepancy could cause some sampling bias because residents in the east may be less likely to call a pest control company than those in other parts of the
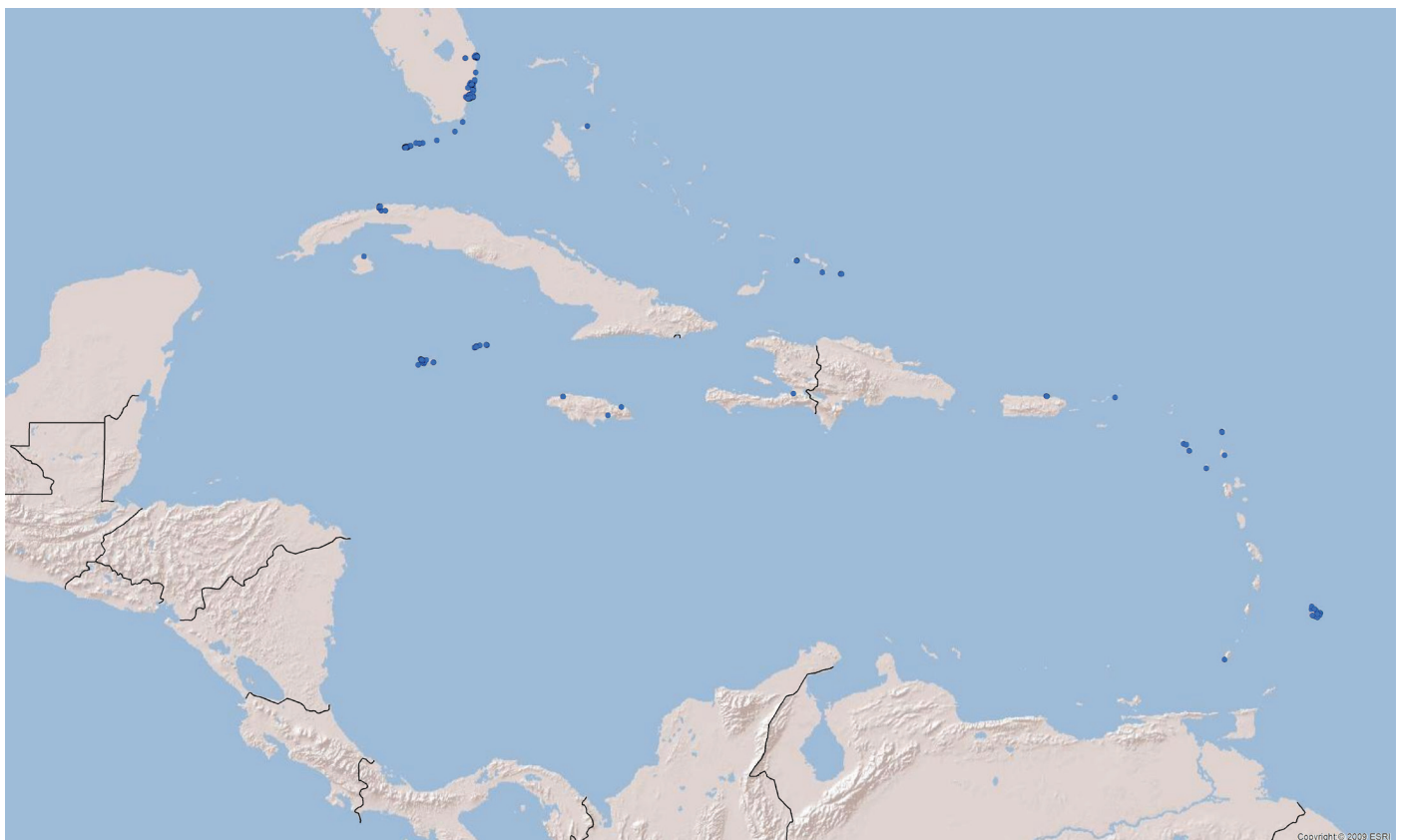

Fig. 1. *Coptotermes gestroi* localities in the greater Caribbean Basin (Source: UF Termite Collection).

island. However, it must be noted that in the wealthier district (Bodden Town), not a single termite incident was reported, and that the remaining districts have more comparable average annual household incomes, ranging between CID 47,673 and CID 54,430.

To determine the likelihood of boat versus overland introduction modes for *C. gestroi*, we followed the procedure of Hochmair & Scheffrahn (2010), who assessed the spatial association of marine dockage with land-borne infestations of *Coptotermes* species in southeastern Florida. We applied hierarchical cluster analysis to identify homogeneous clusters of Grand Cayman termite localities based on their easting and northing coordinates, and then assessed whether these clusters were located near marine dockage. If so, these clusters could indicate separate points of introduction by boat. Clusters can indicate both primary and secondary introductions. A primary introduction describes an infestation from other islands or the mainland and subsequent establishment of a base population. A secondary introduction is established by local dispersal flights of termites from a base population. For an island, the suspected source of a primary introduction is boat traffic, whereas a secondary introduction can be established by boat (most likely if an infestation occurs close to dockage) or by land transport (most likely if an infestation is distant from nearest dockage). Different clusters near boat dockage can either stem from different primary introductions to the island or be the result of fewer primary introductions (possibly even 1) and subsequent distribution by local boat traffic (Scheffrahn 2013). The question of primary, secondary, or multiple same-site introductions can be determined through genetic analysis of termite samples. This analysis was not possible in this study because samples were not available from all the observed locations where locality data were reported.

Hierarchical cluster analysis starts with each termite collection point as a separate cluster and then combines clusters sequentially, reducing the number of clusters with each step, until only 1 cluster is left. The method applies measures of dissimilarities between cases (i.e., points) when forming the clusters. In our approach, dissimilarity was expressed as the squared Euclidean distance between observed points to give greater weight on points that are further apart compared with the simple Euclidean distance. One can choose from a variety of hierarchical clustering analysis methods. Each of them includes rules that govern between which points distances are measured to determine cluster membership. Five cluster analysis methods were tested, i.e., Ward's method, Average Linkage between groups, Average Linkage within groups, Centroid Linkage, and Single Linkage.

Although infestation points can be grouped into clusters, not every cluster might originate from a boat infestation. To determine the potential association of each cluster with a boat dockage, we first identified dockage locations on Grand Cayman that allow inter-island boat traffic. To do so, the island outline polygon was overlaid with 100 m grid cells. Using the background satellite imagery provided in ESRI's ArcGIS 10.3, cells that contained a boat dockage suitable for boats of 10 m length or more (boats large enough to reach out-island destinations) were visually identified and marked (shown as blue squares in Figs. 2 and 3). Furthermore, a set of 102 points were randomly placed in built areas suitable for termite habitat (Fig. 3), which is where termites are typically collected by pest control companies, as opposed to undeveloped areas where no damage is caused by termite infestation.

The generation of the suitability layer based on several source files is described in more detail in the spread model section below. For the generation of the random point layer, which reflects typical termite collection locations of pest treatment companies under assumed randomness, buildings were identified from the ArcGIS imagery background layer, followed by clipping suitable habitat areas to the vicinity of identified buildings. Next, distances were measured between
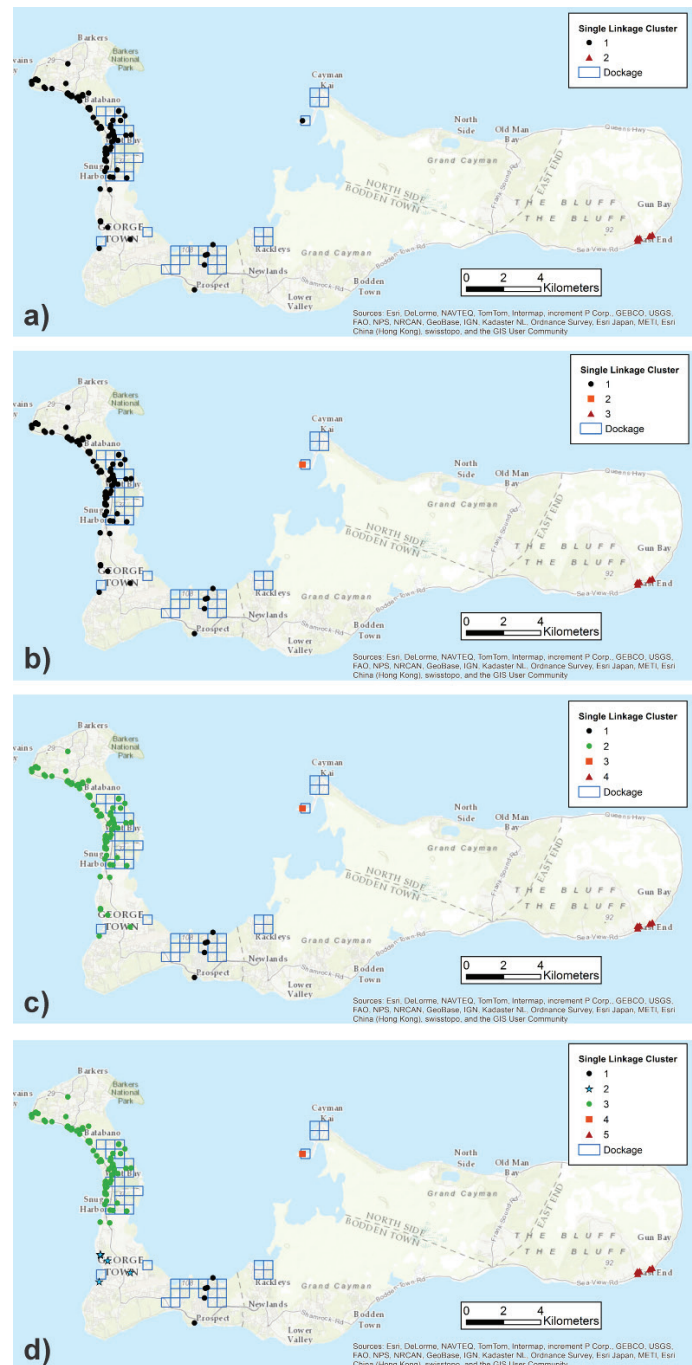
Fig. 2. Hierarchical cluster analysis with 2 (a), 3 (b), 4 (c), and 5 (d) clusters for *Coptotermes gestroi* over Grand Cayman Island.

termite localities in all clusters and the nearest marine docks (using the Spatial Join function in ArcGIS) and compared with distances obtained between random points (located in developed areas) and nearest dockages. Before this, dockage grid cells were substituted by their cell center points, to which the distances were measured. Statistical comparison of distances to dockages between the termite location clusters and the random point set was then used to assess which cluster could originate from infestation by inter-island boat traffic, and which from infestation by land transport or local boat traffic.

In addition, a Monte Carlo simulation was run that repeatedly generated sets of 102 random points and computed the mean nearest

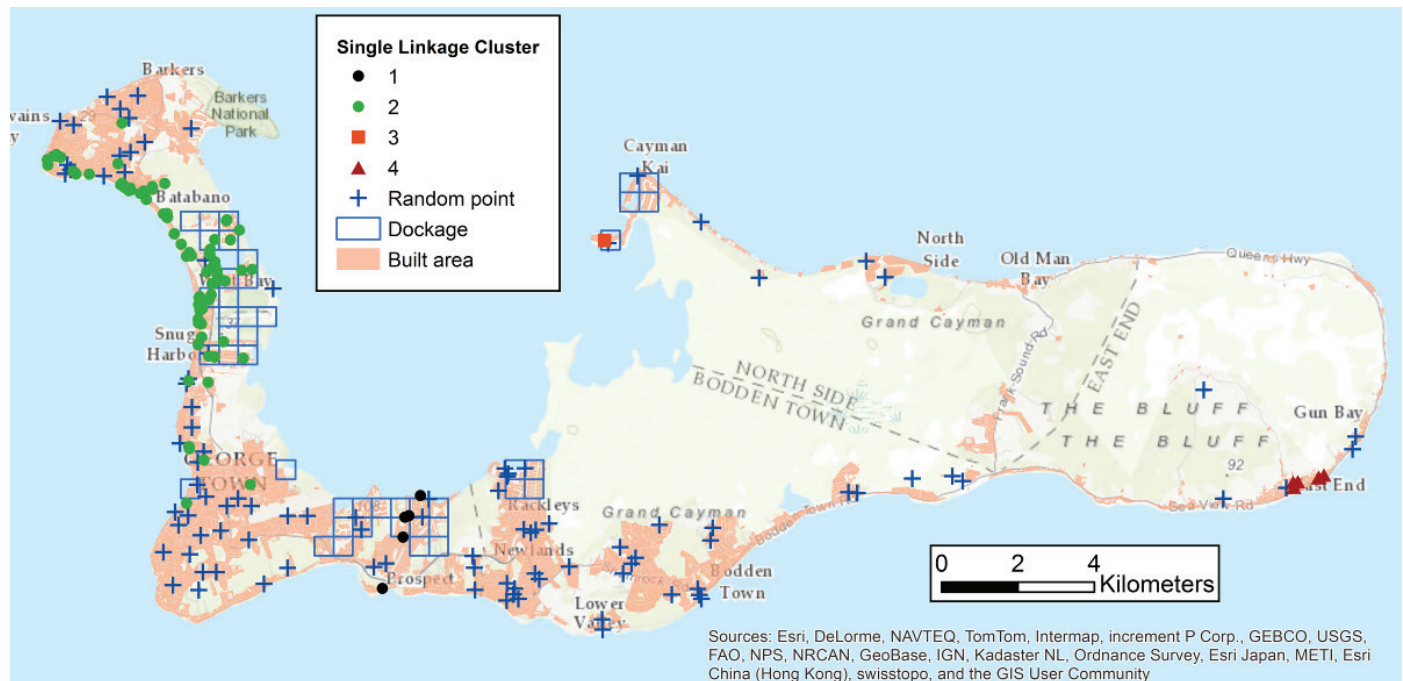**Fig. 3.** Collection localities for *Coptotermes gestroi* over Grand Cayman Island and 102 random points.

neighbor (nn) distances for each of the generated point patterns. This distribution of mean nn distances was then compared with the mean nn distance obtained for observed termite sites. This was done to determine whether observed collection sites are spatially clustered differently than potential termite collection sites (i.e., built areas within suitable habitats), illustrating the effect of boat dockage on the spatial distribution of identified termite locations.

SPREAD MODEL FOR *C. GESTROI* ON GRAND CAYMAN

To account for the local landscape within the simulation model and identify areas unsuitable for the establishment of colonies of *C. gestroi*, a combination of the following vector-type spatial layers was created using ArcMap. A 2006 land cover classification, developed by the Department of Environment, was obtained. The classification was broken down into 4 classes: dry forest, dry shrub land, wetlands, and man-modified. The latter type includes land that has been modified in any way at any time in the past. It includes pasture, agricultural land, secondary forest, built areas, and road allowances. The wetland class comprises various wetland types, such as permanently flooded grasslands, tidally flooded mangrove shrub land/forest, seasonally flooded mangrove shrub land/forest, and seasonally flooded forest.

For the purpose of this study, we considered all non-forested wetland areas as unsuitable for the establishment of *C. gestroi* colonies, regardless of the aforementioned subdivision. Dry shrub land was also considered unsuitable for *C. gestroi*, which nests in larger trees and building voids (Kirton & Brown 2003). We used OpenStreetMap street data (http://www.openstreetmap.org/) for the street network layer, integrated with some manual additions to include segments that were missing, and created a 10 m buffer around each line segment to model the approximate coverage of roads. Furthermore, we manually digitized bare land areas and airport grounds to combine them with the other unsuitable layers. Fig. 4 shows all the individual vector-type layers combined to obtain a single unsuitable habitat polygon layer to use in the simulation model.
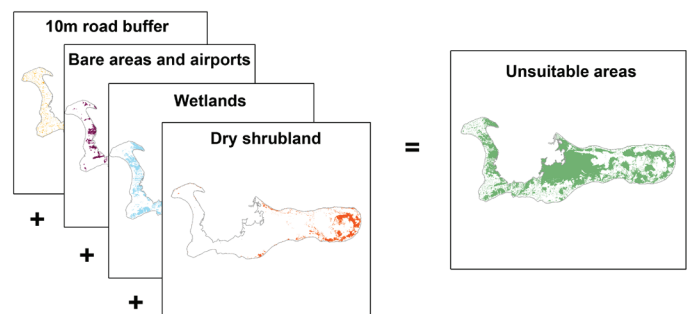

Fig. 4. Vector-type layers used to obtain a surface of unsuitable habitat for *Coptotermes gestroi* on Grand Cayman Island.

The individual-based model by Tonini et al. (2013) was used to simulate the spread of *C. gestroi* over Grand Cayman from 2014 to 2050. The values used in the model for the main ecological parameters (Tonini et al. 2013) are shown in Table 1. Because of the stochastic nature of the model used, 100 replications were run to account for the uncertainty associated with the outcome of a stochastic simulation. A spatial grid with resolution of 100 × 100 m was created to be overlaid at the end of the simulation with all other replications for a given year. The set of *C. gestroi* localities were grouped in each grid cell according to the chosen value for the DEN (maximum density of colonies per ha) parameter, and the centers of the cells infested by at least 1 colony were used as a starting point for the simulation.

TERMITE DIVERSITY STUDIES ON THE CAYMAN ISLANDS

In 1996, J. K. surveyed termites on Grand Cayman (83 colony samples) and Little Cayman Islands (73 samples), followed by a further survey of Grand Cayman in 1999 by J. C. and J. M. (223 samples) and a survey of Cayman Brac in 1999 by J. C., J. M., and R. H. S. (200 samples). A few additional samples, including *Cr. brevis*, were collected on Grand

Table 1. Definition of all parameters used for the spread simulation model of *Coptotermes gestroi* over Grand Cayman Island and their values.

Parameter	Definition	Values
AFP	Colony age at first production of alates	4 yr
PHR	Maximum pheromone attraction distance	3 m
DEN	Maximum density of colonies per ha	1
SURV	Overall survival rate of alates[a]	0.01 (1%)[a]
MAR	Prevalence of male alates in the colony	0.5 (50%)
SCR	Scenario of amount of alates generated by a colony	1,000 for colony age 4 ≤ yr < 9 10,000 for colony age 9 ≤ yr < 14 100,000 for colony age ≥14 yr
DIST	Mean dispersal flight distance	200 m

[a]Overall percentage of alates surviving all phases of a dispersal flight.

Cayman by R. H. S. in 2013. Termites were collected along roadsides and trails in as many geographically and ecologically diverse habitats as time and accessibility permitted. Termites were collected from all possible microhabitats from which colonies with brood or foragers were accessible including sound dry or decomposing wood, arboreal and epigeal nests (*Nasutitermes* and *Microcerotermes* [Termitidae], respectively), and in soil underneath stones and logs.

Each locality (Fig. 5) is defined as map-deduced latitude/longitude position from which we searched for termites on foot, typically only 100 m in any direction. Specimens were aspirated and immediately transferred to vials containing 85% ethanol. Upon completion of expeditions, samples were cleaned, identified, labeled, and deposited in the University of Florida Termite Collection, Davie, Florida.

Results and Discussion

ESTABLISHMENT OF *C. GESTROI* ON GRAND CAYMAN

Between 2000 and Jul 2014, Pestkil recorded 102 ground-based *C. gestroi* infestations on Grand Cayman. In Jul 2012, a single water-based *C. gestroi* colony was discovered on a yacht docked at a waterfront house in the Governor's Harbor neighborhood. The Single Linkage, Average Linkage between groups, and Centroid Linkage clustering methods identified the isolated termite sighting at Rum Point (located at the center north of the island, Fig. 2) as its own cluster using the smallest number of total clusters in the solution (3), whereas the 2 other methods (Ward's method and Average Linkage within groups) required a

larger cluster number to classify this point as a separate cluster. Retaining the location at Rum Point as a separate cluster of introduction due to its far distance to the remaining termite collection points seemed to be a desirable solution. Hence, the first 3 clustering methods would be viable options. Point assignments to clusters were identical between these 3 methods for the 2-, 3-, and 5-cluster solutions but slightly different for the 4-cluster solution. For the illustration of the steps of the clustering process and further exploratory analysis, the results of the Single Linkage method are used.

Starting with the set of 102 observed points, the hierarchical cluster process undergoes 101 cluster fusion stages. The last 8 fusion steps in the agglomeration schedule with their characteristics are listed in Table 2. The dissimilarity measure describes the squared Euclidean distance between points or centers of clusters being joined in a fusion step. A sudden increase in the dissimilarity value suggests natural cutting points to determine the best number of clusters before 2 very dissimilar clusters are combined. Table 3 shows that, based on this criterion, the 2-cluster solution is best due to the sudden increase in dissimilarity in the last stage. This can also be observed in Fig. 6, where a natural break at the 2-cluster solution is clearly discernible.

Figure 2a shows the 2 spatial regions resulting from the 2-cluster solution. It separates termite collection points in the western half of the island from those in the east. Large boat dockages are only present in the western half of the island. Considering the large gaps between observed termite points in the western half of the island and the availability of boat dockage in various portions of that cluster makes it, however, unlikely that the termite infestation started from only 1 single point within this cluster and then dispersed from there. If that was the case, one could expect a more even coverage of infestation points in the affected areas without the large observed gaps in-between (Tonini et al. 2013).

A more realistic scenario provides the 4-cluster solution, which reflects another natural cutting point shown in Fig. 6. In this 4-cluster solution, the different point clusters follow generally the clustered pat-
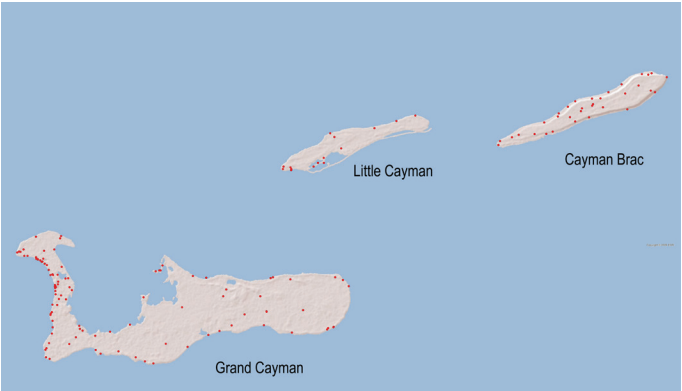
Fig. 5. Termite sampling localities from UF Termite Collection (for purposes of space, the geographic positions of Little Cayman and Cayman Brac are not related to that of Grand Cayman).

Table 2. Agglomeration schedule for the last 8 stages of hierarchical clustering for *Coptotermes gestroi* over Grand Cayman Island using the Single Linkage method.

Stage	Clusters	Dissimilarity
94	8	1.142
95	7	1.482
96	6	1.896
97	5	2.088
98	4	2.949
99	3	17.083
100	2	67.783
101	1	364.919

Table 3. Descriptive statistics of shortest distance sets to nearest marine docks (in meters) for locations of *Coptotermes gestroi* over Grand Cayman Island and random points.

	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Random
n	5	90	1	6	102
Mean	528	1,048	151	18,729	3,228
Standard deviation	527	1,030	—	301	4,023
Median	302	627	151	18,733	2,210

tern of marine dockage locations (Fig. 2c) at least for the western half of the island. Therefore, this solution gives 3 point clusters near boat dockages, 1 of which is the isolated spot at Rum Point. It suggests 3 separate points of infestation through boat traffic and the subsequent spread of termites to the other points of each cluster.

The 5-cluster solution (Fig. 2d) splits the cluster along the Seven Mile Beach to the west into 2 clusters. Each of these 2 new clusters (the larger one to the north and the smaller one to the south) has nearby marine docks, which makes separate introductions in those 2 clusters plausible. The 5-cluster solution would therefore suggest 4 introductions of *C. gestroi* to the island by boat, with at least 1 of them being a primary introduction.

One isolated cluster of termite sites, located to the south-east of the island, visually stands out because it is far from marine dockages on the island. Due to a lack of dockage in the south-east of the island, this introduction occurred most likely overland, e.g., by transportation of infested timber, originating from an established population on the western half of the island. There is, however, the possibility that infestations even in this cluster stem from introduction by boat, e.g., when an infested boat anchored in close proximity to land and termite alates were flying out that day towards land. Given that termites are weak flyers that avoid dispersal flights in windy conditions (which are often found on the open sea), this scenario is very unlikely. The termite discovery dates of this isolated cluster (years 2011 and 2014) are later than termite discovery dates of clusters in the western part of the island, which are, when using the 4-cluster solution from Fig. 2c, 2001 to 2014 (cluster 1), 2003 to 2014 (cluster 2), and 2001 (cluster 4). This suggests that the south-eastern cluster was established (probably by land transport) after the other clusters and thus originated from one of the other termite populations on the island.
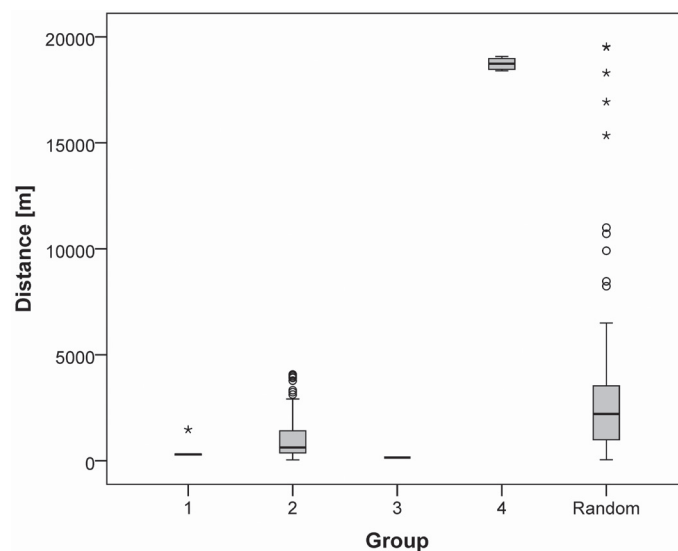
The clusters in the western portion of the island, due to their close proximity to marine dockages, can be assumed to originate from boat traffic between Grand Cayman Island and other Caribbean islands (primary introduction) or from already infested areas on Grand Cayman Island (secondary introduction). To verify the potential of infestation of the 3 westernmost clusters by inter-island boat traffic statistically,
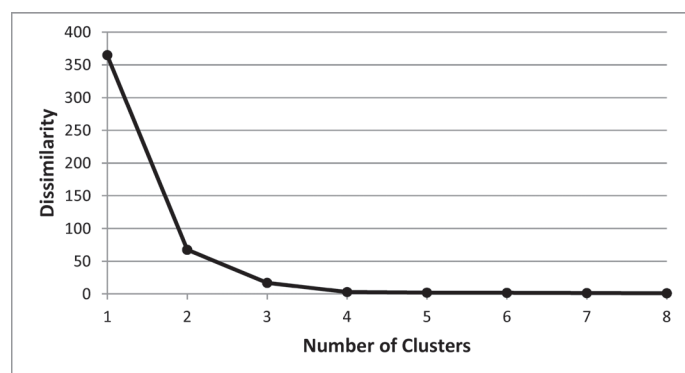
distances between termite sightings in all clusters and the nearest marine dock were measured. The point pattern from the 4-cluster solution was used for this task (Fig. 2c) instead of the 5-cluster solution to retain larger cluster sizes for statistical testing. Together with a set of 102 random points placed around built areas, this resulted in 5 sets of distances to the nearest marine dockage, i.e., 1 for each of the 4 clusters and 1 for the random point set (Fig. 3).

Figure 7 visualizes how the distances to the nearest marine dockage are distributed for the previously described point sets. The horizontal line in the middle of each box indicates the median of distances for clusters 1 through 4 and the random point set. Visual inspection suggests shortest distances to marine dockage for clusters 1 (South Bay), 2 (Seven Mile Beach), and 3 (Rum Point), and largest distances for cluster 4 (south-east of island). Distances for the random point set are mostly found in-between. Descriptive statistics for distances associated with the 5 point sets are provided in Table 3. Sizes of the 4 cluster point sets vary between 90 (cluster 2), and 1 (single observation at Rum Point in cluster 3).

Because sample sizes are small, a nonparametric test was used to check for significant differences between distances to the nearest marine dockage. Results show that the distances to nearest docks associated with clusters 1 and 2 are significantly shorter than the distance for the random point set (Mann–Whitney, $n_1 = 5$, $n_R = 102$, $Z = -2.568$, $P < 0.02$, 2-tailed; and Mann–Whitney, $n_2 = 90$, $n_R = 102$, $Z = -5.934$, $P < 0.0001$, 2-tailed). For cluster 3, which consists of only 1 point with a distance to the nearest marine dockage of 151 m, the difference to the median distance for the random point set is not significant at a 5% level of significance (Mann–Whitney, $n_3 = 1$, $n_R = 102$, $Z = -1.614$, $P = 0.078$), which is due to the low power of the test given the small sample size.

Fig. 6. Plot for the Single Linkage clustering method for *Coptotermes gestroi* over Grand Cayman Island.

Fig. 7. Plot for the Single Linkage clustering method for distances to the nearest marine dockage of *Coptotermes gestroi* over Grand Cayman Island.
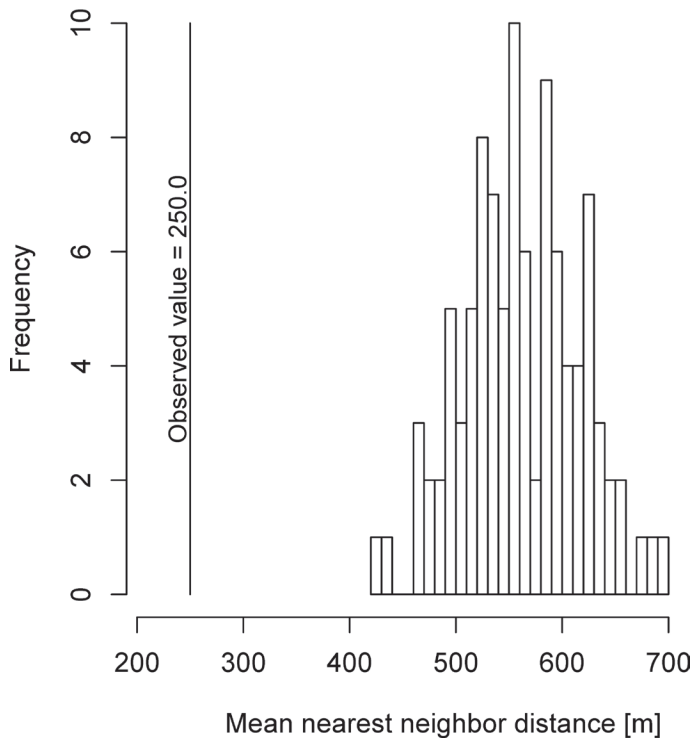
Fig. 8. Distribution of mean nearest neighbor distance obtained from Monte-Carlo simulation with 102 randomized points placed in built areas within suitable habitats.

The fact that the observed distances for these 3 clusters are shorter than distances for random points gives statistical evidence that infestations in these clusters are associated with (intra- or inter-island) boat traffic. Further, results show that the median distance to the nearest marine dock associated with cluster 4 is significantly larger than the distances for the random points (Mann–Whitney, n_4 = 6, n_R = 102, Z = −3.943, P < 0.0001), suggesting that these termite infestations were not introduced by inter-island boat traffic but either by local boat traffic originating from another locality on Grand Cayman Island, or, more

likely, by land transport, given the newly constructed condominiums in that cluster region.

One might argue that observed clusters are not solely based on boat and overland introduction sites but caused by the patchiness of potential collection areas, i.e., built areas. To analyze whether the pattern of observed infestation points differs from built areas, we first computed the mean nn distance for the 102 observed termite locations, which was 250.0 m. This was followed by a Monte Carlo procedure with 100 realizations of generating 102 points that were randomly placed inside the built area polygons, followed by a mean nn computation for each generated point pattern. This resulted in the distribution of mean nn distances under the null hypothesis of termite locations being randomly distributed within built areas. Figure 8 plots the distribution of mean nn distances based on the Monte Carlo simulation (mean = 561.7 m, SD = 54.83 m) and the mean nn distance of the observed termite distribution pattern (250.0 m). The result indicates significant clustering of termite locations when controlling for patchiness of built areas (P < 0.01) and therefore a different cluster pattern between observation sites and built areas.

SPREAD MODEL FOR *C. GESTROI* ON GRAND CAYMAN

The outcomes of all model replications are grouped and visualized by 3 color-coded occupancy envelopes as described in Tonini et al. (2013). The ">0%" (yellow) occupancy envelope shows all areas predicted to be infested in one or more model replications. The "50%" (orange) occupancy shows all areas predicted to be infested by at least half of all simulation runs. Finally, the "100%" (red) occupancy envelope shows areas that are predicted as infested by all model replications. Figure 9 shows the results of the simulation in 2050.

A visual inspection of the results suggests that the termite spread will proceed fairly slowly over the suitable areas in the island if no additional anthropogenic transport occurs. By 2050, most of the western part of Grand Cayman will likely be infested by *C. gestroi*, whereas patches of unsuitable habitat restrict the expansion of the species over the central and eastern parts. In the absence of human movement, it will likely take a century for *C. gestroi* to saturate the island by natural means.
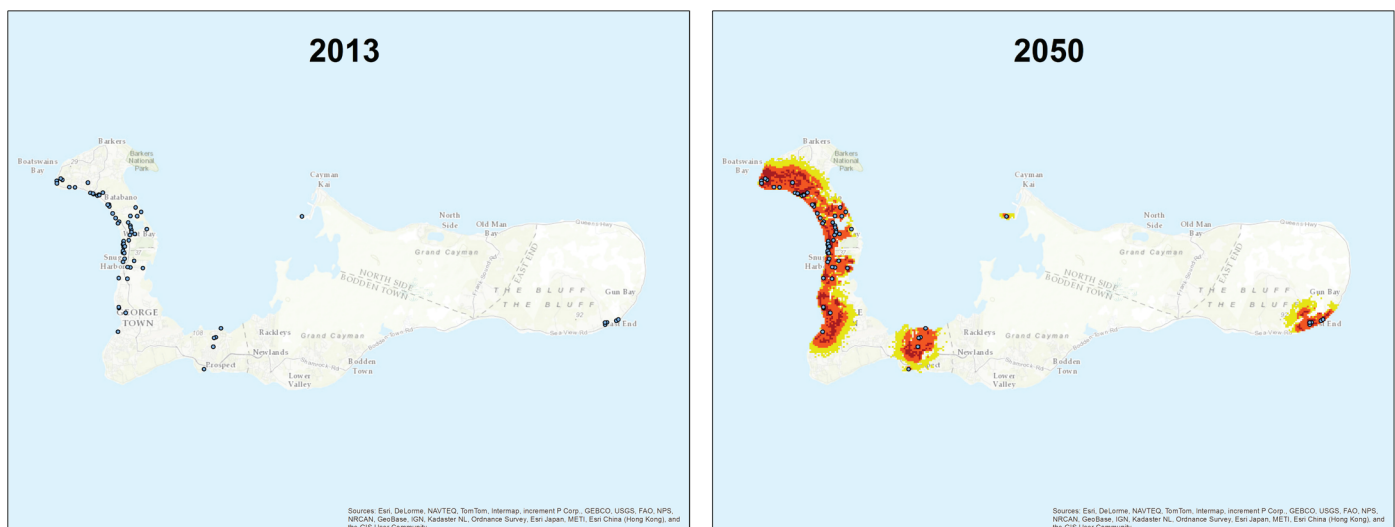

Fig. 9. Areas predicted as infested by the simulation model for *Coptotermes gestroi* over Grand Cayman Island. Sampled termite locations in 2014 are mapped (points). Yellow, orange, and red cells indicate the >0%, ≥50%, and 100% occupancy envelopes, respectively.

Table 4. Localities for termites from the Cayman Islands and surrounding areas.

FAMILY, Species	Localities*						
	CAB	GCA	LCA	CUB	JAM	MLC	FLA
KALOTERMITIDAE							
Cryptotermes brevis Walker	X	X	X[h]	X	X	X	X
Cryptotermes cavifrons Banks	X	X	X	X	X	X	X
Cryptotermes nitens Scheffrahn & Křeček	X[g]	X[g]	X[g]		X		
Cryptotermes spathifrons Schjeffrahn & Křeček			X[g]	X			
Incisitermes milleri Emmerson[a]	X[g]	X[g]	X[g]	X	X	X	X
Incisitermes schwarzi Banks[b]	X	X	X	X	X	X	X
Neotermes castaneus Burmeister	X[g]	X	X[g]	X	X	X	X
Procryptotermes edwardsi Scheffrahn[c]	X[g]		X[g]	X	X		
RHINOTERMITIDAE							
Coptotermes gestroi Wasmann[d]	X[g]	X[g]	X	X	X	X	X
Heterotermes **sp. nov.**		X			X		
TERMITIDAE							
Microcerotermes c.f. *arboreus* Emerson	X	X	X			X	
Nasutitermes corniger Motschulsky[e]		X		X	X	X	X
Nasutitermes nigriceps Haldeman		X			X	X	
Termes hispaniolae Banks[f]	X[g]	X	X[g]	X	X	X	

*Locality abbreviations as follows: Cayman Brac (CAB), Grand Cayman (GCA), Little Cayman (LCA), Cuba (CUB), Jamaica (JAM), Mainland Caribbean (MLC), Florida (FLA).
[a-f]Corrected species designations from Scheffrahn et al. (1994).
[g]Island species records from this study.
[h]Not recorded but presence highly likely.

TERMITE DIVERSITY STUDIES ON THE CAYMAN ISLANDS

Fourteen termite species are now collectively known from the Cayman Islands (Table 4). As a result of our surveys, 3 new species of drywood termites were added to the Caymanian fauna, *Cryptotermes nitens* Scheffrahn & Křeček (Scheffrahn & Křeček 1999), *Cr. spathifrons* Scheffrahn & Křeček (Scheffrahn & Křeček 1999), and *Procryptotermes edwardsi* Scheffrahn (Scheffrahn & Křeček 2001). We now also report
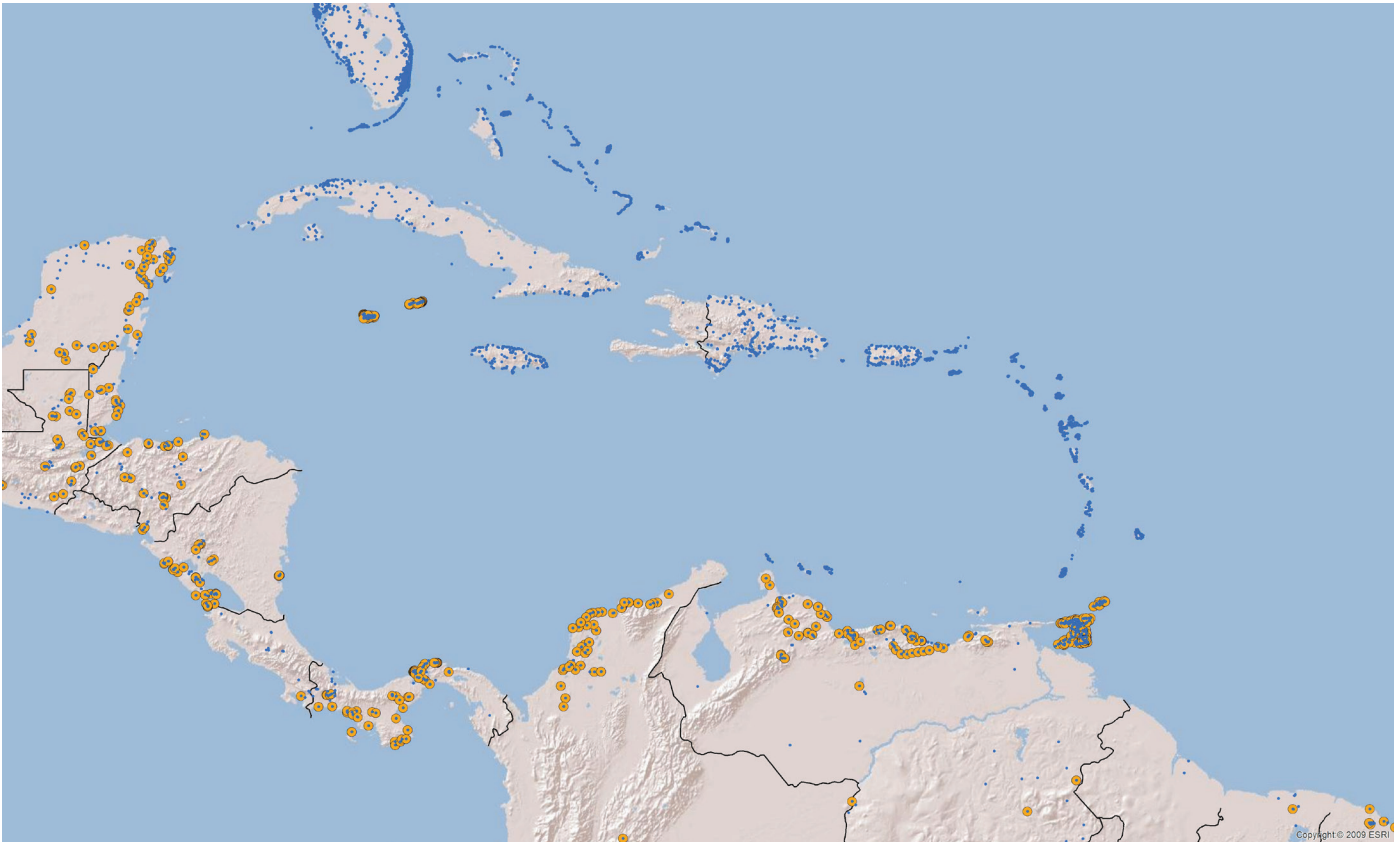

Fig. 10. Caribbean basin survey localities for all termites (blue dots) and for *Microcerotermes* species only (orange dots) (Source: UF Termite Collection).

15 new island records and revise their nomenclature (Table 4). Nomenclatural changes since Scheffrahn et al. (1994) are from the following subsequent synonymies: *Nasutitermes costalis* = *Na. corniger* (Scheffrahn et al. 2006), *C. havilandi* = *C. gestroi* (Kirton & Brown 2003), *Incisitermes tabogae* = *I. schwarzi* (Kalotermitidae) (James et al., 2013), and *Termes melindae* = *T. hispaniolae* (Termitidae) (Scheffrahn, unpublished data). *Incisitermes milleri* was listed as *Incisitermes* sp., and *P. edwardsi* was incorrectly recorded as *P. corniceps* in Scheffrahn et al. (1994).

The Cayman Islands termite fauna has a close affinity with Cuba and Central America but with some exceptions. The endemic drywood species *Cr. nitens* is known only from the Cayman Islands and Jamaica (Scheffrahn & Křeček 1999). An undescribed species of *Heterotermes* on Grand Cayman has a disjunctive range of populations in Jamaica, Grand Turk, Bonaire, and Florida suggesting it has recently been introduced to some of these localities (Szalanski et al. 2004). *Nasutitermes nigriceps* occurs also in Jamaica and Central America, but it is replaced on Cuba by *Na. rippertii*. As on most small West Indian islands, no soil-feeding species occur on the Caymans Islands.

The occurrence of *Microcerotermes* c.f. *arboreus* is the most interesting biogeographical anomaly of the Cayman Island termite fauna. Although *Microcerotermes* species are widespread throughout the Caribbean mainland, the Caymanian records for this genus are unique among all other West Indian islands with the exception of the continental islands of Trinidad and Tobago (Fig. 10). This genus is in dire need of revision, and we cannot be certain that the species from the Caymans is conspecific with *M. arboreus* as described by Emerson (1925).

Acknowledgments

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