Systematics

Taxonomy, Biogeography, and Notes on Termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of the Bahamas and Turks and Caicos Islands

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ABSTRACT Termite surveys of 33 islands of the Bahamas and Turks and Caicos (BATC) archipelago vielded 3.533 colony samples from 593 sites. Twenty-seven species from three families and 12 genera were recorded as follows: Cryptotermes brevis (Walker), Cr. cavifrons Banks, Cr. cymatofrons Scheffrahn and Křeček, Cr. bracketti n. sp., Incisitermes bequaerti (Snyder), I. incisus (Silvestri), I. milleri (Emerson), I. rhyzophorae Hernández, I. schwarzi (Banks), I. snyderi (Light), Neotermes castaneus (Burmeister), Ne. jouteli (Banks), Ne. luykxi Nickle and Collins, Ne. mona Banks, Procryptotermes corniceps (Snyder), and Pr. hesperus Scheffrahn and Křeček (Kalotermitidae); Coptotermes gestroi Wasmann, Heterotermes cardini (Snyder), H. sp., Prorhinotermes simplex Hagen, and Reticulitermes flavipes Koller (Rhinotermitidae); and Anoplotermes bahamensis n. sp., A. inopinatus n. sp., Nasutitermes corniger (Motschulsky), Na. rippertii Rambur, Parvitermes brooksi (Snyder), and Termes hispaniolae Banks (Termitidae). Of these species, three species are known only from the Bahamas, whereas 22 have larger regional indigenous ranges that include Cuba, Florida, or Hispaniola and beyond. Recent exotic immigrations for two of the regional indigenous species cannot be excluded. Three species are nonindigenous pests of known recent immigration. Identification keys based on the soldier (or soldierless worker) and the winged imago are provided along with species distributions by island. Cr. bracketti, known only from San Salvador Island, Bahamas, is described from the soldier and imago. Two soldierless species, Anoplotermes bahamensis n. sp. and Anoplotermes inopinatus n. sp., from the central Bahamas are described from the imago and worker. The imago of Pa. brooksi is described for the first time. Mutually exclusive distributions were recorded for the following groups: Cr. bracketti/Cr. Cymatofrons + Cr. cavifrons, Ne. mona/Ne. jouteli, Pr. corniceps/Pr. hesperus, R. flavipes/H. cardini + H. sp., and Na. corniger/Na. rippertii. All termites found on the Turks and Caicos also occur in parts of the Bahamas except for the likely exotic H. sp., and the exotic Co. gestroi. Present-day distributions of indigenous termite species are related to two primary factors: dry land connections of the BATC during low sea level stands of the late Pleistocene and the proximity of these emergent lands to the faunal sources of Florida, Cuba, and Hispaniola. Flotsam containing mated reproductives or whole colonies are propagules for overwater dispersal by termites.

KEY WORDS diversity survey, identification keys, West Indies, new species, biogeography

There has been a renewed interest in cataloging the rich diversity of termites (Isoptera) from the West Indies (Darlington 1992; Jones et al. 1995; Collins et al. 1997; Genet et al. 2000; Jones and Nalepa 2002; Scheffrahn et al. 1990, 2003); but to date, detailed deliberate surveys have been inclusive of only relatively small geographic areas with the exception of Puerto Rico and Virgin Islands (Scheffrahn et al. 2003). Our in-

Extending nearly 1,000 km (Fig. 1), the BATC form the longest geologically related archipelago in the New World. Much of the BATC landmass is only a few meters above sea level with a maximum elevation of 62 m on Cat Island. Many of these carbonate islands were continuous on much larger land shelves (Fig. 1) during the late Pleistocene (18,000 years before present [ybp]) (Lambeck et al. 2002) before the rising

terest in the termites of the Bahamas and the Turks and Caicos Islands (BATC) began in 1990 with a survey of Providenciales and Grand Turk (Scheffrahn et al. 1990) and intensified in 1995 when we discovered two new kalotermitid species (Scheffrahn and Křeček 1999, 2001) and two soldierless termitids, described herein, on a survey expedition to Cat and North Andros Islands.

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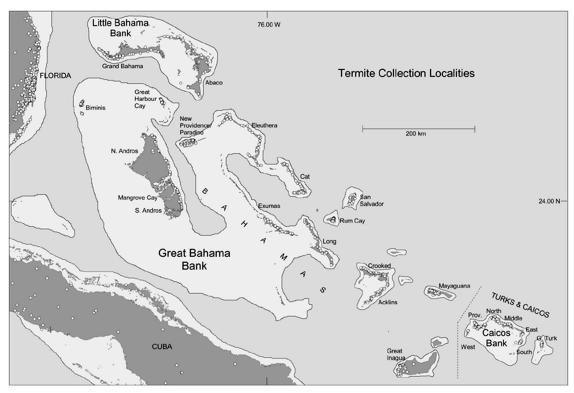


Fig. 1. Termite collection localities (small open circles) of the Bahamas and Turks and Caicos (1990–2005). Submergent shallow water banks shown based on map of West Indies and Central America (1968, National Geographic Society, Washington, DC).

sea level reduced them to their current shorelines. Most or nearly all of the BATC land mass was submerged during high sea levels of the middle Pliocene (3,000,000 ybp; Dowsett et al. 1999) followed by partial submergence 126,000 ybp (Chen et al. 1991).

Banks (1919), who was the first to report on Bahamian termites, listed Neotermes jouteli Banks from Andros, Heterotermes tenuis (Hagen) from "various places", and Nasutitermes rippertii (Rambur) from New Providence and Andros. Snyder (1956) recorded nine species from seven Bahamian islands and Scheffrahn et al. (1990) recorded 12 species from two islands of the Turks and Caicos group. The most recent records for the BATC are included in Scheffrahn et al. (1994). Faunistic additions are listed in Scheffrahn and Křeček (1999, 2001), Křeček et al. 2000, and Scheffrahn et al. 2000, including Cryptotermes cymatofrons Scheffrahn & Křeček and Procryptotermes hesperus Scheffrahn & Křeček as well as many new records for other kalotermitid species. Recently, Reticulitermes flavipes (Kollar) was discovered on Grand Bahama (Scheffrahn et al. 1999) and a second undescribed species of Heterotermes was recognized from Grand Turk after a genetic evaluation of circum-Caribbean Heterotermes spp. (Szalanski et al. 2004). In the present article, we substantially revise the diversity, distribution, and biogeography of termites from the BATC archipelago.

Materials and Methods

We collected and examined 3,006 colony samples from 25 Bahamian islands and 527 samples from eight islands of the Turks and Caicos. Samples from 593 sites (Fig. 1) were collected between February 1990 and September 2005. Collection sites were selected based on geography, habitat type, and accessibility from roadside, trail, or seashore. Termites were manually exposed and aspirated from standing dry, damp, decayed, living, and structural wood; nests; foraging tubes; and under objects on soil, including wood, rocks, and aged livestock dung. Some of our unpublished records of species from the neighboring faunal sources of Cuba, Florida, and Hispaniola are included for biogeographical reference (Table 1).

Morphometric data from specimens preserved in 85% ethanol were obtained using a stereomicroscope fitted with an ocular micrometer. Measurements were adopted from Roonwal (1970), and the color scheme of Sands (1965) was used. The convention of characters important in the description of soldierless termite workers, especially dentition and gut morphology, are taken from Sands (1972). The terms "small" and "large" soldiers (Krishna 1961) are equal to the terms "shortheaded" and "long-headed" soldiers (Banks and Snyder 1920), respectively, to discriminate the two general size morphs of soldiers occurring within many

Table 1. Termites of the BATC or island groups based on current survey

	So	urce	es ^a	Bah	ttle ama ınk		G	Freat	Bah	nama	Bar	ık		Б		Vater : (DWI	Isolati)	on		Caic	eos E	Bank		D	WI
Species	Florida	Cuba	Hispaniola	Grand Bahama	Abaco	Biminis/N. Cat Cay	Great Harbour Cay^b	Andros^c	New Providence d	Eleuthera	$\mathbf{E}_{\mathbf{x}}$ umas e	Cat	Long	Rum Cay	San Salvador	Crooked/Acklins	Great Inagua	Mayaguana	West Caicos	Providenciales	North $Caicos^f$	Middle Caicos	East Caicos	South Caicos	Grand Turk
Cr. brevis ^a	X	X	X	X	X	X	X	X	X	X	X				X	X	X	X		X				X	X
Cr. cavifrons	X	X		X	X	X	X	X	X	X	X	X				X	X							X	
Cr. cymatofrons		X		X	X			X	X	X	X	X	X	X	**		X								
Cr. bracketti n. sp. ^h		X	X	X	v	v	X	X	X	X	X	X	X	X	X X	X	X	X	v	v	v		v	v	v
I. bequaerti I. incisus		Λ	X	Λ	X	X	Λ	Λ	Λ	Λ	Λ	Λ	Λ	Λ	Λ	Λ	Λ	X	X	X	X	X	X X	X X	X
I. milleri	X	X	X	X	X		X	X		X	X		X					X	Λ	21	X		1	2	Λ
I. rhyzophorae	21	X	21	21	21		21	21		X	21		21					21			21	21			
I. schwarzi	X	X	X	X	X			X	X	X		X		X		X		X			X				
I. snyderi	X			X	X	X		X	X					X	X	X	X	X							
Ne. castaneus	X	X	X	X	X	X	X	X	X	X	X		X		X			X		X	X	X			
Ne. jouteli	X	X		X	X	X	X	X			X	X	X	X											
Ne. luykxi	X			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X		
Ne. mona			X															X		X	X		X	X	X
Pr. corniceps			X												X	X		X	X	X	X	X	X	X	X
Pr. hesperus	**	X		X	X	X	X	X	X	X	X	X	X							**					**
Co. gestroi ^g H. cardini	X	X X				X	X	X	X	X	X	X	X	X	X	X	X			X					X
H. sp. ⁱ	X	Λ				Λ	Λ	Λ	Λ	Λ	Λ	Λ	Λ	Λ	Λ	Λ	Λ			X					X
Pror. simplex ⁱ	X	X							X											21					1
R. flavipes	X	21		X	X				21																
A. bahamensis n. sp. ^h					X			X		X	X	X	X	X											
A. inopinatus n. sp. h							X	X		X	X		X		X										
Na. corniger	\mathbf{X}^{g}	X	X		$\mathbf{X}^{\mathbf{g}}$														X	X	X	X	X	X	
Na. rippertii		X				X	X	X	X	X	X	X	X	X											
Pa. brooksi		\mathbf{X}				X	X	X	X	X	X		\mathbf{X}												
T. hispaniolae		X	X					X	X																
Total	13	17	10	12	14	11	12	17	14	15	14	10	12	9	9	8	7	10	5	10	8	5	6	7	7

Columns for Florida, Cuba, and Hispaniola list only those species occurring on the BATC.

Incisitermes and Neotermes spp. Structures useful to identify soldiers of Cryptotermes and Procryptotermes spp. include two pairs of protuberances: one dorsal pair in front of the antennal fossae and one ventral pair projecting forward from the genae. These are called the frontal and genal horns, respectively (Scheffrahn and Křeček 1999). The frontal flange is a ridgelike structure that separates the vertex and the frons in soldiers of the former two genera (Gay and Watson 1982). Formulae are given for relative lengths of antennal articles 2–5. For example, the formula 2>3=4=5 indicates that the second article is longer than the third and the third through fifth are subequal in length.

Photomicrographs were obtained using a digitized three-dimensional imaging system (Auto-Montage, Syncroscopy Inc., Frederick, MD). Termite bodies were photographed after dehydration in absolute ethanol and 1,1,1,3,3,3-hexamethyldisilazane (Nation 1983). Wings in ethanol were mounted between glass slides and air-dried. For Anoplotermes spp., camera lucida outline drawings of digestive tubes were made after removal of fat body and other hemocoel tissues. The enteric valve was cut longitudinally and armature exposed in physiological saline. Worker mandibles and the enteric valve were mounted on microscope slides and photographed using a Nikon Coolpix 4500 digital camera attached to a compound microscope. Survey localities were mapped from geographic coordinates using ArcView ArcMap 9.0 software (Figs. 1 and 5; Environmental Systems Research Institute [ESRI], Inc., Redlands, CA). Locality waypoints were obtained from either global positioning system receiver readings at collection sites, or if before 1998, by

^a Unpublished survey data.

^b Including Anderson Cay.

^c North, South, Mangrove Cay.

^d Including Paradise Island.

^e Little, Great, Barreterre.

f Including Parrot Cay.

g Recent nonendemic past.

^h BATC endemic.

ⁱ Regional endemic of possible recent introduction.

transposing coordinates from hardcopy maps to Digital Map of the World version 1.0 (ESRI).

The names of collectors are abbreviated in the text as follows: Paul Ban (PB), James A. Chase (JC), Jan Křeček (JK), Boudanath Maharajh (BM), John R. Mangold (JM), Tom Nishimura (TN), Julian de la Rosa (JR), and Rudolf H. Scheffrahn (RS). Type and voucher material will be deposited at the Fort Lauderdale Research and Extension Center termite collection and at the following: American Museum of Natural History, New York, NY; National Museum of Natural History (Smithsonian Institution), Washington, DC.; and the Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, FL.

Keys to Isoptera of the Bahamas and Turks and Caicos Islands based on Soldiers or Winged Imagos

Soldiers

1.	Soldierless; worker fore tibiae inflated and greater in median cross-sectional circumference than middle or hind tibiae; postclypeus inflated or not (Fig. 2A and B); soil-dwelling with no foraging tubes built above ground 25 - Soldiers present in widely varying proportions; workers with all tibiae about equal in circumference; postclypeus not inflated; soil-dwelling or nonsubterranean, the former often
2.	constructing foraging tubes above ground 2 Nasutiform, i.e., head distinctly modified by long frontal projection with terminal exocrine orifice; mandibles reduced to nonfunctional
	stubs (Fig. 2C–E)
3.	Head capsule with slight constriction beyond antennal insertion, maximum head width <0.73 mm (Fig. 2C) Parvitermes brooksi - Head capsule without constriction beyond an-
	tennal insertion, maximum head width >0.90
4.	Head covered with dozens of erect setae; red- dish coloration; central Bahamas (Fig. 2D) Nasutitermes rippertii
	- Head with five or six evenly-spaced long setae; blackish coloration; Caicos Islands (Fig. 2E) Nasutitermes corniger
5.	Left mandible with marginal teeth in distal half (Figs. 2M and 3D); wood-dwelling 6
	- Left mandible without marginal teeth in distal half (Fig. 3E–I); subterranean or aboveground nests
6.	Head blackish, strongly phragmotic, truncate; mandibles not projecting far beyond labrum (Fig. 2F-I)

- Head ferruginous orange, elongate; mandibles

projecting well beyond labrum 10

7. Rugosity of head capsule conspicuous; structural wood and furniture only (Fig. 2F) Cryptotermes brevis - Rugosity of head capsule faint or absent (Fig. 8. Frons deep and evenly concave, frontal horns distinct and larger than genal horns 9 - Frons rather flat, slight bilateral concavity along median vertical ridge; frontal and genal horns small, congruent (San Salvador Is.) (Fig. 2G) Cryptotermes bracketti n. sp. 9. Frontal flange, in lateral view, abruptly elevated, cresting over vertex (Fig. 2H) . Cryptotermes cymatofrons - Frontal flange, in lateral view, slightly elevated but not cresting over vertex (Fig. 2I) Cryptotermes cavifrons 10. Head capsule quadrate in dorsal view with distinct frontal flange (Fig. 2J and K), genal - Head capsule elongate in dorsal view, without frontal flange; genal horns inconspicuous 11. Frontal flange broad (Fig. 2J); shallow concavities present behind lateral reaches of flange: frontal horns present; basal mandibular humps inconspicuous . Procryptotermes hesperus - Frontal flange narrow (Fig. 2K); concavities absent behind lateral reaches of flange; frontal horns absent; basal mandibular humps conspicuous, sinuate . Procryptotermes corniceps 12. Third antennal article not clavate (Fig. 2L), similar to second and fourth; pronotum $>2\times$ as wide as long; head pale orange-yellow. Neotermes castaneus - Third antennal article clavate, $\geq 2 \times$ as long as fourth (e.g., Figs. 2M-O and 3B-D); pronotum <2× wider than long; head pigmenta-13. Eye spots pigmented in live or alcohol specimens; anterior margin of pronotum shal-- Eyes spots unpigmented in live or alcohol specimens; anterior margin of pronotum incised or deeply concave (Fig. 3B) 16 14. Very large species, maximum head width of large soldiers ≥2.87 mm, left mandible length ≥2.54 mm; frons and anterior vertex with dense pilosity (Fig. 2M) 15 Neotermes mona - Smaller species, maximum head width of large soldiers ≤2.70 mm, left mandible length ≤2.42 mm; pilosity of head capsule sparse 15 15. Antennal carinae rugose and protrude markedly (Fig. 2N); eyes elongate, without dark satellite facets in live or alcohol specimens; setae on basal mandibular humps distinct; head width of large soldiers 2.4-2.7 mm . .

. Neotermes jouteli

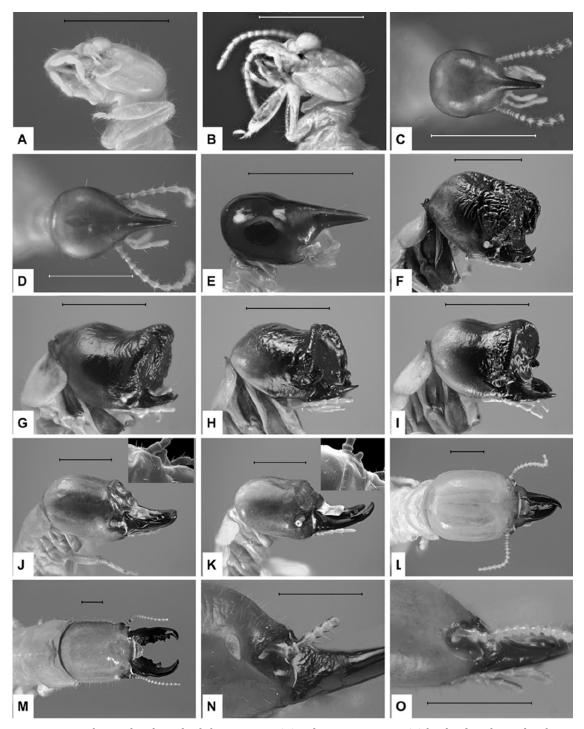


Fig. 2. Lateral view of workers of A. bahamensis n. sp. (A) and A. inopinatus n. sp. (B) head and prothorax; dorsal view of soldier heads of Pa. brooksi (C), Na. rippertii (D), and lateral view of Na. corniger (E); oblique view of soldier heads of Cr. brevis (F), Cr. bracketti n. sp. (G), Cr. cymatofrons, (H), Cr. cavifrons (I), Pr. hesperus (J, inset: left genal horn), Pr. corniceps (K, inset: left genal horn); dorsal view of soldier heads of Ne. castaneus (L), and Ne. mona (M); and lateral view of soldier gena of Ne. jouteli (N) and Ne. luykxi (O). Scale bar = 1 mm.

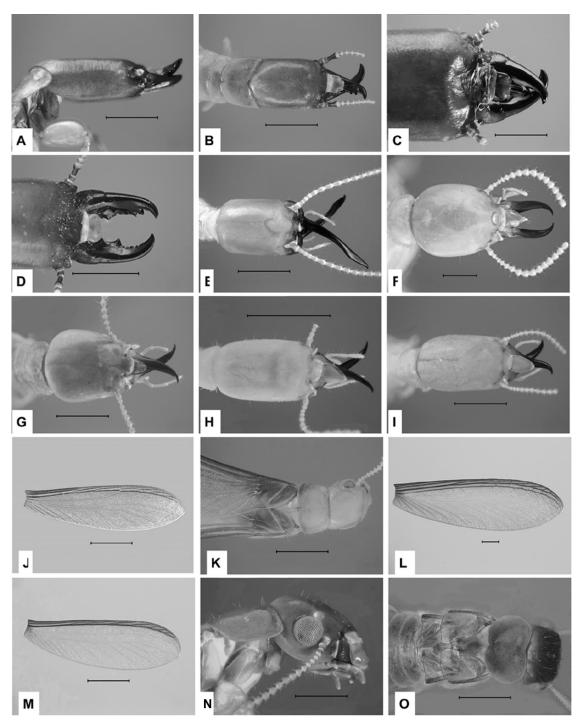


Fig. 3. Lateral view of soldier head of I. bequaerti (A); dorsal view of soldier heads of I. rhyzophorae (B), I. schwarzi (C), I. incisus (D), I. hispaniolae (E), I. co. gestroi (F), I. simplex (G), I. He. cardini (H), and I. flavipes (I); right fore wing of I. bracketti (J); dorsal anterior view of imago of I. hesperus (K); right fore wing of I. scatterius (L) and I. bequaerti (M); lateral view of imago head of I. mona (N); and dorsal view of dealate of I. scale bar = 1 mm.

 Antennal carinae smooth and protrude modestly (Fig. 2O); eyes subcircular, with dark satellite facets in live or alcohol specimens; setae on basal mandibular humps vestigial or absent; head width of large soldiers 1.9-2.4 mm Neotermes luykxi 16. Head capsule markedly compressed dorsoventrally (Fig. 3A) Incisitermes bequaerti Head capsule ovoid in cross section, not markedly compressed dorsoventrally 17 	 25. Postclypeus almost flat, not protruding (Fig. 2A); first proctodeal segment uniformly tubular along its length (Fig. 4L)
17. Smaller species, maximum head width ≤1.1 mm	Winged Imagos (Wings Should Be Flattened between Glass Slides to View Veins in Costal Margin)
 18. Third antennal segment at least 3x longer than fourth; pronotum deeply concave (rare sp., Fig. 3B) Incisitermes rhyzophorae Third antennal segment ≈2× longer than fourth; pronotum deeply concave (uncommon sp.) Incisitermes milleri 	 Three or four pigmented and sclerotized veins in proximal costal margin of fore wing (Fig. 3J, L, M; family Kalotermitidae)
 19. Mandibles massive (Fig. 3C), particularly in large soldiers; basal pilosity on mandibular humps	Median vein of anterior wing curved toward and intersecting radial sector at about half to two-thirds of wing length (Fig. 3J) (median recurvature variable or absent in <i>Cr. brevis</i> ; note couplet 3)
20. Blade of right apical tooth with rather irregular serrations (Fig. 3D); Mayaguana Is. East	tip of wing, not intersecting radial sector unless branched (Fig. 3L and M) 8 3. Arolia between tarsal claws absent, dispersal flights associated with structures only
21. Mandibles stick-like (Fig. 3E); head capsule with conical frontal projection; exposed black carton nests in tree crotches Termes hispaniolae - Head capsule without frontal projection; mandibles sickle-shaped (Fig. 3F-I); nest subterranean or hidden in wood in contact with soil	 4. Setae on middle vertex ≤0.05 mm long 5 - Setae on middle vertex ≥0.1 mm long 6 5. Head capsule with brownish band between eyes, V-shaped mark on frons prominent, chevron pattern on pterothorax indistinct; San Salvador, Crooked Is., and eastward
22. Head capsule ovoid in dorsal view (Fig. 3F and G); fontanelle distinct, opening to anterior or dorsum	absent, chevron pattern on pterothorax distinct (Fig. 3K); Long Is. and westward
23. Fontanelle large and ovoid, opening to anterior (Fig. 3F), and emitting white mucosic secretion when soldier alarmed	 Head capsule, thorax, abdomen, and sclerotized wing veins yellowish, T-shaped mark on pronotum faint or absent
- Fontanelle small and circular, opening to dorsum on vertex (Fig. 3G), secretion not apparent; rare species . Prorhinotermes simplex 24. Mandibles with narrow bases, linear except for ≈30° curvature in distal one-fourth (Fig. 3H) Heterotermes cardini (or H. sp., Grand Turk) - Mandibles with stout bases, 60−90° curvature in distal one-third (Fig. 3I)	with aureate fringe

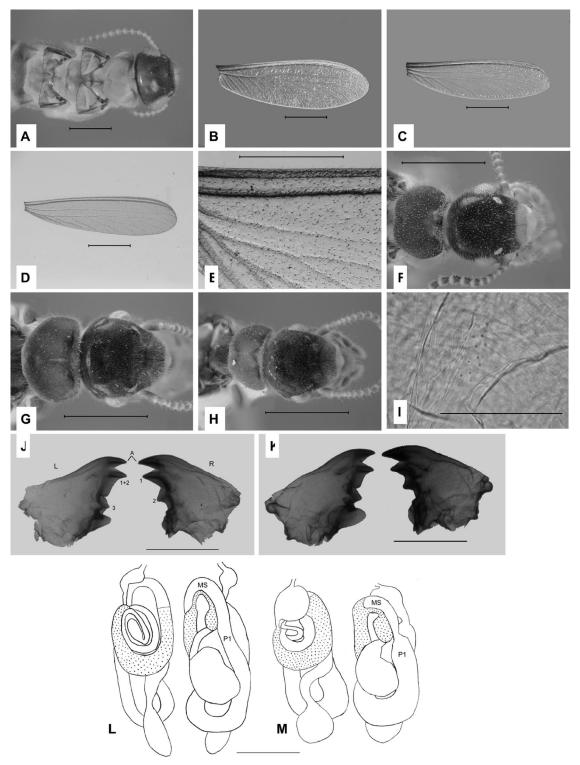


Fig. 4. Dorsal view of dealate of *Na. rippertii* (A); right fore wing of *Pr. simplex* (B), *R. flavipes* (C), *He. cardini* (D); and *Co. gestroi* (E, proximal membrane); dorsal view of imago head and pronotum of *Pa. brooksi* (F), *A. bahamensis* n. sp. (G), and *A. inopinatus* n. sp. (H); longitudinal section of enteric valve and exposed armature of *A. bahamensis* (I); dorsal view of left and right worker mandibles of *A. bahamensis* (J, dentition labeled) and *A. inopinatus* (K); and dorsal (left) and ventral (right) line drawings of digestive tube (mesenteron stippled; MS, mixed segment; P1, first proctodeal segment) of *A. bahamensis* (L) and *A. inopinatus* (M). Scale bar = 1 mm (A–H, L and M), 0.05 mm (I), and 0.5 mm (J and K).

9. Head and pronotum sparsely covered with short	18. V
(≈0.05 mm in length) setae 10	
- Head and pronotum variably covered with long (0.2–0.4 mm in length) setae 11	-
10. Larger species; head width at eyes ≥1.59 mm,	19. C
fore wing maximum width ≥3.13 mm. Max-	
imum diameter of eyes 0.45–0.54 mm. Frons	
rugose; mandibular bases striate; frons sur- rounded by slightly elevated ridge	-
Neotermes jouteli	
- Smaller species; head width at eyes ≤1.52 mm,	20. E
fore wing maximum width ≤3.10 mm. Max-	
imum diameter of eyes 0.38 – 0.42 mm. Frons	
and mandibular bases smooth; frons without ridge Neotermes luykxi	- I
11. Compound eyes very large (Fig. 3N), diameter	- 1
≥0.57 mm; Mayaguana Is. and eastward	
Neotermes mona	21. I
- Compound eyes smaller, diameter ≤0.45 mm Neotermes castaneus	
12. General coloration sepia brown to black 13	_
- General coloration orange to medium	
brown	
13. Head capsule and labrum concolorous or	22. C
nearly so, wing nodulation faint and nodules without darkened apices; larger species, >9	23. (
mm total length with wings; wing membrane	20.
hyaline (common species)	
Incisitermes bequaerti	-
 Labrum contrastingly less pigmented than head capsule, wing nodulation distinct, api- 	
ces of nodules dark; smaller species, ≤7 mm	24. F
total length with wings; wing membrane	
dark	
14. Femora whitish; tibiae pale yellowish (uncommon sp.) Incisitermes milleri	
- Femora sepia brown; tibiae subhyaline, more	-
brownish distally (rare sp.)	
head and pronotum ≈0.2 mm; fore wing	
length from suture ≈12 mm	25. I
Incisitermes schwarzi	
- Head width at eyes ≈1.2 mm or less; longest	
setae on head and pronotum ≈0.1 mm; fore wing length from suture ≈8 mm 16	-
16. General coloration ferruginous; head width with	
eyes ≈1.2 mm, sclerotized wing venation dis-	
tinctly more pigmented proximally versus dis- tally; west of and including Mayaguana and	
Great Inagua Incisitermes snyderi	
- General coloration brownish; head width	C
with eyes ≈1.0 mm, sclerotized wing vena-	Ci
tion uniformly unpigmented along entire wing length; Mayaguana Is. east	Ima
Incisitermes incisus	colora
17. Fore wing scales overlapping hind wing scale	dian p
(Fig. 3O), venation and membrane hyaline	tex oc
to light brown	eyes :
scale (Fig. 4A), venation and membrane au-	erally
reate to blackish 21	sclero

18.	Wing membrane reticulate, hyaline, and de-
	void of interior setae 19
	- Wing membrane smooth with sparse to dense
10	interior setae
19.	Costal margin arched in middle, median vein
	absent (Fig. 4B, Paradise Is. only)
	Prorhinotermes simplex - Costal margin straight in middle, median vein
	present (Fig. 4C, Little Bahama Bank)
	Reticulitermes flavipes
20.	Body light brown, few setae on wing mem-
	brane, membrane opaque (Fig. 4D)
	Heterotermes cardini (widespread) or
-	Body dark brown; dense setae on wing mem-
	brane (Fig. 4E), membrane translucent
	Coptotermes gestroi
21.	Large species (Fig. 4A), length with wings ≈17
	mm, eye maximum diameter ≈0.55 mm;
	wings aureate Nasutitermes rippertii - Moderately large to smaller species, length
	with wings ≤13.5 mm, maximum eye diam-
	eter ≤ 0.35 mm, wings dark 22
22.	General body coloration blackish 23
	- General body coloration brownish 24
23.	
	fontanelle forms forked slit; total length with
	wings ≈12.0 mm Nasutitermes corniger
	- Clypeus concolorous with head capsule, fon-
	tanelle forms simple slit; total length with
0.4	wings ≈8.0 mm Termes hispaniolae Fontanelle distinct, third antennal article is
24.	subequal to second and fourth (Fig. 4F);
	chevron pattern on pterothorax distinct as
	mesonotum is paler than wing scales and
	pronotum Parvitermes brooksi
	- Fontanelle faint or small, third antennal ar-
	ticle noticeably shorter than second and
	fourth, chevron pattern indistinct as me-
	sonotum is concolorous with wing scales and
~~	pronotum
25.	
	(diameter ≈ 0.025 mm, Fig. 4G)
	- Head width at eyes ≈1.0 mm; fontanelle
	small (diameter ≈ 0.05 mm, Fig. 4H)
	sman (diameter ~0.00 mm, Fig. 411)

Kalotermitidae

. Anoplotermes inopinatus n. sp.

Cryptotermes bracketti Scheffrahn & Křeček, New Species

Imago (Fig. 3J; Table 2). In dorsal view, general coloration pale ochraceous; frons, pronotum, and median portion of mesonotum very pale ochraceous; vertex ochraceous, with slight lateral darkening between eyes and occiput; eyes nearly black, ocelli whitish. Chevron pattern on pterothorax pale and weak, laterally ochraceous. Wings with pale ferruginous orange sclerotized venation in costal margin; wing membrane

Table 2. Measurements of Cr. bracketti n. sp. imago

Measurement (mm) $(n = 5 \text{ males}, 5 \text{ females from } 3 \text{ colonies})$	Range	Mean ± SD
Head length with labrum	1.18-1.29	1.24 ± 0.038
Head length to postclypeus	0.88 - 0.98	0.94 ± 0.032
Head width, maximum at eyes	0.93 - 1.01	0.98 ± 0.035
Eye diam, max	0.33 - 0.36	0.34 ± 0.011
Eye to head base, min	0.11-0.16	0.13 ± 0.015
Ocellus diam, max	0.11 - 0.15	0.13 ± 0.010
Pronotum, max length	0.74 - 0.80	0.78 ± 0.025
Pronotum, max width	0.92 - 1.06	0.99 ± 0.045
Total length with wings	9.51 - 11.22	10.48 ± 0.62
Total length without wings	5.25 - 7.38	5.92 ± 0.72
Fore wing length from suture	7.53-8.66	8.15 ± 0.37
Fore wing, max width	2.08-2.44	2.28 ± 0.12

faintly ochraceous to subhyaline. Abdominal tergites, tibiae, and tarsi pale ochraceous to pale ferruginous orange; sternites slightly paler; femora whitish.

In dorsal view, head ovoid; epicranial ("Y") suture distinct, especially its posterior branch and fork; Vshaped mark on frons very faint. Eyes large, unprotruding. Pronotum and head width at eyes equal; anterior margin of pronotum moderately and evenly concave, lateral margins slightly convex, and posterior margin slightly emarginate. Pronotum with moderately dense and longer setae along margins and shorter setae dispersed medially; pilosity on head capsule sparse and short. T-shaped mark on pronotum absent or very faint in majority of specimens. Antennae with 16-18 articles, usually 16; relative length formula variable as basal articles subequal in length, but usually 2 > 3 = 4 = 5. Compound eyes elongate and subovate, rectate along antennal fossae. Ocelli ovoid, widely abutted to eyes. Radius of anterior wings extending approximately two-fifths of wing length, from suture to beyond first branch of five- to six-branched radial sector. Media unsclerotized except for slight sclerotization at fusion with radial sector at approximately two-thirds of wing length from suture. Beyond fusion of media, two to three very faint cross veins between radial sector and cubitus; wing membrane faintly papillose. Arolia distinct.

Comparisons. The imago of Cr. bracketti is generally larger than the Mexican Cr. abruptus Scheffrahn & Křeček (Scheffrahn et al. 1998a). The following measurements do not overlap for Cr. bracketti and Cr.

abruptus, respectively: eye maximum diameter 0.33–0.36 versus 0.28–0.31 mm, total length with wings 9.51–11.22 versus 8.09–8.80 mm, and fore wing length to the suture 7.53–8.66 versus 6.25–6.96 mm. Imagos of its single sympatric congener, *Cr. brevis*, do not have arolia that are present in *Cr. bracketti*. Although *Cr. cymatofrons* measurements are very close to *Cr. bracketti*, the former is slightly darker, including a darker band between the eyes and as well as an aureate fringing of the pronotum that are absent in *Cr. bracketti*.

Soldier (Fig. 2G; Table 3). In dorsal view, anterior half of head capsule black, shading to dark chestnut brown in posterior one-fourth. Antennae white-yellowish to yellowish; articles 3–5 pale brownish. Anteclypeus subhyaline. Mandibles opaque, very dark chestnut brown. Eye spots pale. Pronotum anterior margin and two oblique anterior perimarginal marks chestnut brown. Anterior fourth of pronotum ferruginous, grading posteriorly to pale ferruginous orange or yellowish. Remainder of body, including legs, pale yellowish.

In dorsal view, general shape of head capsule almost subcircular to slightly elongate; head capsule distinctly constricted behind massive frontal flange. Eye spots large, oval, and slightly raised behind constriction. In dorsal view (when frontally elevated in some specimens), anterior of head capsule distinctly bilobed medially; laterally obliquely truncate. Rugosity, particularly on frontal flange, distinct, fine, and shortly sinuous; rugosity on frons fine and sinuosity elongate. Frons with two shallow bilateral concavities along median rise. Central vertex faintly concave and glabrous; surrounded by faint and rather concentric rugosity. Frontal flange not delineated but continuous with vertex. Frontal and genal horns congruent in size and shape, forming short rounded knobs. Labrum with lateral sides parallel, anteriorly widely triangular, and apex slightly rounded. Mandibles short, stout, humped at bases, and moderately recurvate apically; dentition moderately distinct. Antennae with 12-15 articles, usually 12 or 13; relative length formula usually 2 > 3 < 4 = 5. Pronotum large and shieldlike with shallow biconvex anterior indentation; anterior margin crenate; posterior corners subtruncate and posterior margin subrectate.

Table 3. Measurements of Cr. bracketti n. sp. soldier

Measurement (mm) $(n = 12 \text{ from } 7 \text{ colonies})$	Range	Mean ± SD	Holotype
Head length with frontal flange	1.19-1.41	1.34 ± 0.066	1.37
Head length to tip of mandibles	1.37-1.59	1.48 ± 0.070	1.42
Head length to frontal horns	1.19-1.32	1.27 ± 0.040	1.26
Frontal flange width	1.10-1.21	1.16 ± 0.028	1.16
Frontal horns, outside span	0.80 - 0.85	0.83 ± 0.016	0.83
Head width, max	1.18-1.29	1.24 ± 0.034	1.24
Head height, excluding postmentum	0.80-0.90	0.87 ± 0.030	0.85
Pronotum, max width	1.11-1.28	1.22 ± 0.051	1.23
Pronotum, max length	0.90-1.00	0.95 ± 0.034	0.92
Left manible length, tip to ventral condyle	0.62 - 0.67	0.64 ± 0.019	0.64
Total length	4.17-5.30	4.63 ± 0.37	4.30

In lateral view, head capsule usually noticeably overhanging frons. Angle between plane of vertex and frons ≈75–85°; frontal flange without crestlike process. In some specimens, angle between frons and vertex almost perpendicular and in such phenotypes frontal flange slightly crested.

Comparisons. In lateral view, the Cr. bracketti soldier superficially resembles that of Cr. abruptus Scheffrahn et al. (1998a), because the head capsules of both project anterodorsally. The frontal overhang in Cr. bracketti is bilobate, whereas in Cr. abruptus, the frontal overhang is bluntly peaked. The frons of both species are carinate, but in Cr. bracketti the frons is only carinate along the dorsal two-thirds of the vertical axis, whereas in Cr. abruptus the entire length is carinate. In lateral view, the rugosity on the Cr. abruptus head dorsum is homogenous from the frontal flange to the occiput, whereas in Cr. bracketti, the frontal flange and anterior vertex are finely rugose grading to glabrous at the occiput. In dorsal view, the Cr. abruptus soldier head capsule is distinctly elongate with a median constriction, whereas in Cr. bracketti it is subcircular and its constriction is anterior. In dorsal view, the Cr. abruptus frontal overhang completely eclipses the view of its very short mandibles, whereas in Cr. bracketti the overhang is less pronounced, and its larger mandibles are visible.

Among sympatric congeners, only *Cr. brevis* occurs on San Salvador Island. Soldiers of *Cr. brevis* are generally larger, have robust head capsule rugosity, and are found only in structural wood compared with the smaller, less rugose, and woodland-inhabiting *Cr. bracketti*.

Etymology. This species is named in honor of Thomas Brackett, chief operating officer of Terminix International Inc., in recognition of his and Terminix International's commitment toward the understanding of termite diversity, biology, and control.

Type Material Measured. Holotype Colony. BAHA-MAS. San Salvador Island. Dixon Settlement; 24.103° N, 74.451° W; 25-V-2002; JC, JM, TN, and RS; one holotype soldier, five paratype soldiers, two paratype imagos (BA 1838). Additional specimens from this colony were used for photography (Figs. 2G and 3J).

Paratype Colonies. BAHAMAS. San Salvador Island. White Estates; 24.114° N, 74.453° W; 25-V-2002; 1 paratype soldier (BA 1826). West of lighthouse cemetery, S. Dixon Settlement; 24.101° N, 74.447° W; 25-V-2002; 1 paratype soldier (BA 1848). Near South Point; 23.948° N, 74.497° W; 25-V-2002; 1 paratype soldier, five paratype alates (BA 1863). S. of Baker's Point; 24.113° N, 74.502° W; 26-V-2002; 1 paratype soldier (BA 1870). S. Cockburn Town; 24.044° N, 74.527° W; 26-V-2002; 1 paratype soldier (BA 1896). Sugar Loaf Cemetery on coast; 24.001° N, 74.537° W; 26-V-2002; 1 paratype soldier (BA 1900), and three paratype alates (BA 1902).

Remarks. Cr. bracketti, like Cr. cavifrons and Cr. cymatofrons, is a woodland and coastal species, typically colonizing dead limbs, branches, and larger twigs of trees and shrubs.

Distribution. *C. bracketti* is an exclusive indigenous of San Salvador Island, Bahamas (formerly Watling Island). At \approx 65-km² total area, the enigmatic and isolated range of this species on San Salvador may be one of the smallest of any termite on earth.

Cryptotermes brevis (Walker) (Fig. 2F)

Termes brevis Walker 1853: 524 [imago; type loc.: Jamaica]

Cryptotermes brevis: Banks 1919: 476 [generic reassignment, distribution]; Banks and Snyder 1920: 36, 78, 144 [soldier, soldier fig., distribution, biology]; Scheffrahn and Křeček 1999: 114–127 [alate, soldier, soldier key and figs., distribution]; Scheffrahn et al. 1994 [West Indian distribution], Scheffrahn et al. 2003 [Puerto Rico, Virgin Islands, keys, soldier fig.]

For extended synonymy see Araujo 1977: 11, Bacchus 1987: 40, Snyder 1949: 39, and Chhotani 1970: 9.

Remarks. *Cr. brevis* is the most destructive drywood termite species in the region as well as worldwide (Scheffrahn 2005). It is exclusively synanthropic and infests only wood in service that is not exposed to free water or rainfall. Dispersal flights of *Cr. brevis* are primarily crepuscular or nocturnal. In the northern hemisphere, the major flight season peaks in late May with minor flights in late November.

Distribution. This common pest is almost certainly established on every inhabited island in the West Indies. The strict association of *Cr. brevis* with structural wood and furniture hampered our sampling ability. Still, we collected *Cr. brevis* from 16 BATC islands.

Cryptotermes cavifrons Banks (Fig. 2I)

Cryptotermes cavifrons Banks: Banks 1906: 336–337 [soldier, alate, figs.; type loc.: Kissimmee, Osceola Co., Florida, USA; type species of genus]; Banks and Snyder 1920: 35–38 [alate, soldier, figs., distribution]; Bacchus 1987: 8–9, 43–45 [keys, alate, soldier, figs., distribution]; Scheffrahn and Křeček 1999: 114–120, 126–130, alate, soldier, soldier key and figs., distribution]

Remarks. *Cr. cavifrons* is a common woodland inhabitant of the northern and central Bahamas, living in dead trees or branches or in dead tissues of living trees in variable habitats. It is rare in the southeastern Bahamas and Turks and Caicos islands.

Distribution. Beyond the BATC, *C. cavifrons* is widely distributed throughout peninsular Florida, Cuba, Jamaica, and the Cayman Islands. Among indigenous congeners in the New World, *Cr. cavifrons* is second only to *Cr. longicollis* (Banks) from Central America with respect to expanse of distribution.

Cryptotermes cymatofrons Scheffrahn and Křeček (Fig. 2H)

Cryptotermes cymatofrons Scheffrahn and Křeček 1999: 136–139 [soldier, alate, soldier figs., soldier key, Cuba, Bahamas; type loc.: Bahamas: Cat Island]

Remarks. Although described only recently, *Cr. cy-matofrons* is a common species in inland and littoral woodlands. This species seems ecologically equivalent to and occurs sympatrically with *Cr. cavifrons* throughout much of their respective ranges.

Distribution. Widespread throughout the Bahamas (Table 1), *Cr. cymatofrons* also occurs on Cuba, including Isle of Youth, but is absent from the Turks and Caicos Islands.

Incisitermes bequaerti (Snyder) (Fig. 3A and M)

Kalotermes (Kalotermes) bequaerti Snyder 1929: 81–83 [imago, soldier; type loc.: Cuba: Banos (Oriente) = Banes?]

Incisitermes incisus: Krishna 1961: 356 [new genus, new generic combination]

Remarks. *Incisitermes bequaerti* typically inhabits dry littoral forests and shrub lands. Alates have been taken from colonies throughout the year suggesting no distinct flight season.

Distribution. The species is common and wide-spread from Cuba and the BATC to the Dominican Republic, Puerto Rico east to Culebra, but absent in Florida (original records from the Keys by Miller and Miller 1943 are now attributed to *I. milleri*). This species is reported from Bermuda (Snyder 1956). In the BATC, *I. bequaerti* had been collected on all surveyed islands except Middle Caicos (Table 1).

Incisitermes incisus (Silvestri) (Fig. 3D)

Calotermes incisus: Silvestri 1901: 2 [imago]; Silvestri 1903: 27–28 [imago, soldier, figs.; type loc.: S. Jean, Venezuela]

Kalotermes incisus: Snyder 1949: 16 [catal.]

Incisitermes incisus: Krishna 1961: 356 [new genus, new generic combination]; Scheffrahn et al. 2003 [redescription of alate and small and large soldier, figs.]

Remarks. *I. incisus* is the most common and widespread drywood termite species in the West Indies (R.H.S., unpublished data). It can colonize structural lumber throughout its range.

Distribution. Found throughout the West Indies with the exception of Cuba, Jamaica, and the Bahamas save its northwestern limit of Mayaguana. Like *Pr. corniceps*, this species has been collected on all eight surveyed Turks and Caicos Islands (Table 1), but it was not originally recorded as such (Scheffrahn et al. 1990) owing to its misidentification as *I. snyderi*.

Incisitermes milleri (Emerson)

Kalotermes bequaerti Miller and Miller 1943: 101 [USA, Florida Keys, misidentification with *Incisitermes* milleri (Emerson)]

Kalotermes milleri: Emerson 1943: 18–22 [imago, soldier; figs; type loc.: Elliot Key, Dade Co., Biscayne Nat. Park, Florida, USA]

Incisitermes milleri: Krishna 1961: 356 [new genus, new generic combination];

Remarks. The purplish iridescence of the imago wings in sunlight is a remarkable trait of this species. Together with *I. rhyzophorae*, *I. milleri* is the smallest kalotermitid in the BATC and inhabits tall and shaded hardwood forests, including mangroves. Both species are locality sympatric on Eleuthera.

Distribution. *I. milleri* was described from the two upper Florida Keys (Elliott and Key Largo) and from Jamaica. It is now recorded on ten island groups of the BATC (Table 1), Cuba and Isle of Youth (new records, Křeček, unpubl.), Hispaniola (Scheffrahn et al. 1994), and the Cayman Islands (new records; J.A.C., J.K., J.R.M., R.H.S., unpublished data).

Incisitermes rhyzophorae Hernández (Fig. 3B)

Incisitermes rhyzophorae Hernández 1994: 88–93 [imago, soldier, keys, Figs. 1–3; type loc.: Cayo Sevilla, Province Las Tunas, Cuba]

Remarks. *I. rhyzophorae*, described originally from a single Cuban Cayo, is one of two congeners described recently from the West Indies; the other being *I. furvus* Scheffrahn (1994) from Puerto Rico. In the field, *I. rhyzophorae* resembles *I. milleri*, but the imagos of the former move even more frenetically when extracted from host wood.

Distribution. Collected only on Eleuthera in the BATC (Table 1), it was described from Cayo Sevilla, Cuba, and also occurs at the U.S. Naval Base in Guantánamo (R.H.S., J.A.C., and J.R.M., unpublished data).

Incisitermes schwarzi (Banks) (Fig. 3C)

Kalotermes schwarzi Banks: Banks and Snyder 1920: 22–25 [imago, soldier; figs; type loc.: Paradise Key (near Royal Palm Ranger Station), Everglades Natl. Park, Dade Co. Florida]

Kalotermes schwarzi: Banks 1919: 478 [nomen nudum; occurrence in Florida, Cuba, and Jamaica, records precede description]

Incisitermes schwarzi: Krishna 1961: 354–356 [new genus, new generic combination; figs. imago, minor and major soldier; type species of genus]

Remarks. I. schwarzi can be a locally abundant species that typically inhabits coastal forests, especially mangroves. This species seems to have a higher moisture requirement than I. snyderi. The disproportionately long wings relative to the body length of the

imago make this species easy to distinguish from sympatric congeners.

Distribution. *I. schwarzi* occurs in extreme southern Florida, Cuba (except for Isle of Youth), Hispaniola, and Jamaica. Its distribution in the BATC is widespread, but sporadic.

Incisitermes snyderi (Light)

Kalotermes snyderi Light 1933: 97 [new name; no description; type loc.: Texas, USA]

Kalotermes marginipennis: Banks and Snyder 1920: 20 [imago, soldier; figs., misidentification]

Incisitermes snyderi: Krishna 1961: 357 [new genus, new generic combination]

Remarks. *I. snyderi* typically inhabits drier littoral forests and shrubs. It also infests structural lumber, especially wood members exposed to rain, occasional free water, or on shaded exteriors.

Distribution. This species is much less widespread than previously recorded because of confusion with *I. incisus*. *I. snyderi* occurs in the southeastern United States and across the Bahamas (Table 1). Mayaguana is only known locality where *I. incisus* and *I. snyderi* are sympatric. In correction of published records (Snyder 1956, Scheffrahn et al. 1994), *I. snyderi* is absent from Cuba, the Turks and Caicos Islands, Hispaniola, Virgin Islands, and Mona Island.

Neotermes castaneus (Burmeister) (Figs. 2L and 3L)

Termes castaneus Burmeister 1839: 764 [imago; type loc.: Puerto Rico, California, USA; type species of genus]

Termes castanens: Burmeister 1839: 764 [original spelling]

Neotermes castaneus: Banks and Snyder 1920: 32–35 [imago, soldier, fig., spelling correction]; Krishna 1961 [322–325, figs.]

Remarks. Ne. castaneus has a high moisture requirement and often colonizes xylem tissue within live cambium of trees and larger shrubs. Populated galleries have a characteristic mild fecal odor. This species frequently infests living dooryard and forest trees such as avocado, mango, sea grape, and teak grown in plantations.

Distribution. This species is the most widespread among its congeners in the West Indies and occurs throughout much of the BATC as well as Florida, Cuba, Hispaniola, Jamaica, Cayman Islands, Guatemala (Becker 1953), and Nicaragua (Maes 1990). In Florida, *Ne. castaneus* extends north into the Orlando area where oaks are a favored host.

Neotermes jouteli (Banks) (Fig. 2N)

Kalotermes jouteli Snyder: Banks and Snyder 1920: 25 [dealate imago; type loc.: Adams Key (south of Elliot Key), Dade Co., Florida, USA]

Kalotermes jouteli Banks: Banks 1919: 478 [nomen nudum; Bahamian and Cuban occurrence, records preceding description]

Neotermes jouteli: Krishna 1961: 322, 325 [new generic combination]; Scheffrahn et al. 2000 [imago, and small and large soldier redescription, figs., keys; distribution]

Remarks. Ne. jouteli is a large, common woodland and coastal species where it prefers to colonize damp dead wood.

Distribution. Ne. jouteli occurs in the northern and central Bahamas, but is less widespread than Ne. luykxi, and is absent in the southeastern BATC. This species is also common in Cuba including Isle of Youth (Scheffrahn et al. 1994) and in southern Florida (Scheffrahn et al. 2000). Its records from Mexico require confirmation. According to Cancello and Myles (2000), specimens from Morelos, Mexico are similar but not conspecific with Ne. jouteli. A previous record from Hispaniola is now attributed to Ne. platyfrons Křeček and Scheffrahn (2001).

Neotermes luykxi Nickle & Collins (Fig. 2O)

Neotermes luykxi Nickle and Collins 1989: 270 [imago, soldier, figs.; type loc.: Dania, Broward Co., Florida, USA]; Scheffrahn et al. 2000 [imago, small, and large soldier redescription, figs., keys; distribution]; Scheffrahn et al. 1990 [Turks and Caicos]

Remarks. Ne. luykxi, a more diminutive sibling species of Ne. jouteli, also occurs in frequently dampened wood. Both species are very common on some islands, but local populations are typically allopatric.

Distribution. *Ne. luykxi* was collected from most of the surveyed islands of the BATC (Table 1), and it also occurs in southeastern Florida with the exception of the Keys. Unlike *Ne. jouteli*, *Ne luykxi* is apparently absent from Cuba and elsewhere, suggesting an evolutionary origin in Florida or the BATC.

Neotermes mona (Banks) (Figs. 2M and 3N)

Kalotermes mona Banks 1919: 478 [soldier, fig., key; type loc.: Mona Island, Puerto Rico]

Neotermes mona: Krishna 1961: 322, 325 [new generic combination]; Křeček et al. 2000 [imago description, small and large soldier redescription, figs., keys; distribution]; Scheffrahn et al. 1990 [Turks and Caicos Isl.]

Remarks. *Ne. mona* is the largest termite in the BATC. It is an uncommon inhabitant of substantially-sized wood in littoral forests and mangrove swamps. To a lesser extent than *Ne. castaneus*, the colonies sometimes invade the xylem of living trees and large shrubs.

Distribution. In the BATC, *Ne. mona* is confined to Mayaguana and the Turks and Caicos Islands. Other records include Hispaniola (Dominican Republic),

Puerto Rico, Mona, Vieques, and the Virgin Islands (Scheffrahn et al. 1990, Křeček et al. 2000, Scheffrahn et al. 2003). The range of *Ne. mona* is mutually exclusive with that of *Ne. jouteli*, but the former overlaps in range with *Ne. luykxi* on Mayaguana and the Caicos Bank.

Procryptotermes corniceps (Snyder) (Fig. 2K)

Glyptotermes corniceps Snyder 1923: 92 [dealate imago, soldier, fig.; type loc.: Boqueron-Salinas, Puerto Rico]

Procryptotermes corniceps Emerson: Ramos 1946: 13 [Mona Island, Puerto Rico]; Krishna 1961: 378; Scheffrahn et al. 1990 [Turks and Caicos Isl.]; Scheffrahn and Křeček 2001 [alate and soldier redescription, distribution]

Remarks. A common and widespread species occurring more often in coastal rather than inland habitats, and tending to occupy xeric, even windswept, littoral shrubs and tree branches (Scheffrahn and Křeček 2001). Infestations are often marked by large and open galleries that create hollows in the infested wood member. *Pr. corniceps* is a dominant drywood termite on Mayaguana, Acklins, and the Turks and Caicos except for Grand Turk. In the northern and central Bahamas, its dominance is replaced by its mutually exclusive congener, *Pr. hesperus* (Scheffrahn and Křeček 2001).

Distribution. In the BATC *Pr. corniceps* was collected on all islands of Turks and Caicos Islands and on four eastern Bahamian islands with deep sea isolation (Table 1). This species is common in the Dominican Republic, Jamaica, Puerto Rico (Scheffrahn and Křeček 2001), and the Virgin Islands.

Procryptotermes hesperus Scheffrahn & Křeček (Figs. 2J and 3K)

Procryptotermes hesperus Scheffrahn and Křeček 2001: 535–536 [alate imago, soldier, figs., keys, distribution; type loc.: North Andros Island, Bahamas]

Remarks. Like *Pr. corniceps, Pr. hesperus* is a common and widespread species occurring more often in coastal rather than inland habitats, and occupying some of the most xeric littoral shrub lands in a given area (Scheffrahn and Křeček 2001).

Distribution. In the BATC, this species is found only on islands of the Little and Great Bahama Banks (Table 1). In the eastern Bahamas and Turks and Caicos Islands it is replaced by *Pr. corniceps*. Outside the BATC, *Pr. hesperus* occurs on western Cuba, including Isle of Youth and has been collected once on the Yucatan Peninsula (Scheffrahn and Křeček 2001).

Rhinotermitidae

Coptotermes gestroi Wasmann (Figs. 3F and 4A and E)

Coptotermes gestroi Wasmann 1896: 628 [soldier; type loc.: Bhamò, Burma; type species of genus]

Coptotermes havilandi: Holmgren 1911: 192 [imago]; new synonymy; Kirton and Brown 2003: 47; Gay 1967: 77 [imago, soldier, fig.]; Scheffrahn et al. 1990: 624–626 [Turks and Caicos Is., soldier fig.], Scheffrahn et al. 1994 [distribution in the West Indies, Scheffrahn et al. 2003: 182–188, 193–194 [Puerto Rico, Virgin Islands, keys, soldier fig.]

Remarks. This nonindigenous pest species is usually associated with structural infestations and heavy damage. Co. gestroi constructs large carton nests usually above ground in structural voids and within tree trunks. It also has a tendency to infest boats and ships and usually establishes itself near seaports or marinas (Scheffrahn and Su 2005). Crepuscular dispersal flights occur from February through April in the northern hemisphere.

Distribution. Within the BATC, it has been collected only on Providenciales and Grand Turk. A record of *Coptotermes testaceus* (L.) on the Bahamas by Araujo 1977 may either be an error or a misidentified boat interception of *Co. gestroi. Co. gestroi* is a Southeast Asian species that has been introduced to parts of the West Indies, Brazil (Constantino 2002), and Florida (Su et al. 1997, Scheffrahn 2001, Scheffrahn and Su 2005). At the time of this writing, *Co. gestroi* has not been collected from the Bahamas, but it is expected to become established there in the future.

Heterotermes cardini (Snyder) (Figs. 3H and 4D)

Leucotermes cardini Snyder 1924b: 17 [alate imago, soldier; type loc.: Andros Island, Bahamas]

Heterotermes cardini: Snyder 1949: 67 [catalog, new generic assignation]; Snyder 1956: [distribution]; Scheffrahn et al. 1994: 232 [distribution]; Szalanski et al. 2004: 558.

Remarks. Recent genetic analysis (Szalanski et al. 2004) has clarified the identities of numerous West Indian *Heterotermes* populations, including the confirmation that *He. cardini* is the only species of this genus in the Bahamas. *He. cardini* is mutually exclusive to *R. flavipes* in the Bahamas and together, both are the only economically important subterranean termites in the Bahamas.

Distribution. Szalanski et al. (2004) report that *H. cardini* is confined to Cuba, including Isle of Youth and Cayo Conuco (new records), and the Bahamas. All other previous records (i.e., Haiti and Dominican Republic) of *H. cardini* are reassigned to *He. convexinotatus* Snyder. In addition to two previous island records (Andros and New Providence; Snyder 1924b, 1956), 10 new island group records are added (Table 1). All previous records of *H. tenuis* (Hagen) for the BATC are probably *H. cardini*. A previous record of a *Heterotermes* sp. on Grand Bahama (Scheffrahn et al. 1994) is apparently an error.

Heterotermes sp.

Heterotermes sp.: Szalanski et al. 2004: 558–560, 564 [distinct haplotype]

Remarks. Based on genetic analysis (Szalanski et al. 2004), a distinct *Heterotermes* haplotype, and possibly a new species, occurs on Grand Turk and Providenciales, Turks and Caicos. *Heterotermes* sp. tolerates dry habitats and forages on cellulosic debris in contact with the ground. Like other *Heterotermes*, this species builds narrow foraging tubes to span feeding sites above ground, including structures, with nests in the soil.

Distribution. Outside of the Turks and Caicos, Heterotermes sp. occurs in Florida, Jamaica, Cayman Islands, a few northern Lesser Antilles, and the Dutch Antilles. Florida's population was brought by humans as may be the case with other localities excepting Jamaica (Scheffrahn and Su 1995, Szalanski et al. 2004).

Prorhinotermes simplex Hagen (Figs. 3G and 4B)

Termes (Rhinotermes) simplex Hagen 1858: 238 [imago, T. III: Fig. 23]. Holotype (imago); type-loc.: Cuba.

Arrhinotermes simplex: Holmgren 1911: 72

Prorhinotermes simplex: Banks and Snyder 1920: 39

[imago, soldier, Figs. 26–27]

Remarks. Pror. simplex is an estuarine or circumcoastal species. Colonies usually nest inside logs plastered with fecal paste which forms a nest carton. In December and January, workers build flight tubes on upright surfaces from which alates emerge at night. Workers are capable of foraging in soil, but colonies tend to stay centered in and under the logs they infest, sometimes barely above the maximum tidal water line.

Distribution. This species is common in Cuba and presumed to have evolved there. It is somewhat common in southeastern Florida from the Keys to Palm Beach County. This species is rare in Puerto Rico (Scheffrahn et al. 2003) and Jamaica (Araujo 1977). The two nearby location records from Paradise Island suggest the possibility that *Pror. simplex* is not indigenous to BATC, but that this population was introduced with landscaping material from southeast Florida.

Reticulitermes flavipes (Kollar) (Fig. 3I)

Termes flavipes Kollar 1837: 411 [imago; type loc.: greenhouse in Schönbrunn, near Vienna, Austria, introduction]

Leucotermes flavipes: Holmgren 1911: 69 [without description]

Reticulitermes flavipes: Banks and Snyder 1920: 45 [imago, soldier, keys, distribution; type species of genus designated here]; Scheffrahn et al. 1999: 480–482 [Bahamas, first record, distribution]

Remarks. Originally thought to be introduced to Grand Bahama (Scheffrahn et al. 1999), it seems very likely now that *R. flavipes* is indigenous to the northern Bahamas as suggested by its wide occurrence and mutual exclusion with *Heterotermes* on these islands.

Distribution. In the Bahamas, *R. flavipes* is known only from the Little Bahama Bank islands of Abaco and Grand Bahama. Elsewhere, this termite is widely distributed in the eastern United States and has been introduced to Europe, South America, Canada, and the western United States (Austin et al. 2005).

Termitidae

Apicotermitinae

Anoplotermes bahamensis Scheffrahn and Křeček, New Species

Imago (Fig. 4G; Table 4). In dorsal view, head capsule, antennae, and radial sector of wings dark sepia brown. Anterolateral corners of head capsule paler, brown to pale brown, and concolorous with postclypeus, pronotum, wing scales, costal margin, abdomen, and legs. Fontanelle very faint, circular, and very small (diameter ≈0.025 mm). Very faint dark strip arises from fontanelle; strip extends more anteriorly than posteriorly. Head capsule, postclypeus, pronotum, pteronotum, and wing scales densely covered with minute, pale setal punctations. Slightly larger setal punctations more sparse. Mandibles pale yellow-brown, save darker dentition. Median third of pronotum length with longitudinal midline. One spot near middle of each side on posterior margin of pronotum. Wing membrane opaque sepia brown and with slightly blue-violet iridescence; pilosity conspicuous, with setae of variable length. Head in dorsal view subcircular with exception of projecting mandibles. Head capsule and postclypeus together noticeably wider than long. Postclypeus short, weakly convex, twice as wide as long, and very faintly bilobed along midline. Vertex very slightly and evenly concave; concavity centered just beyond fontanelle. Epicranial suture absent. Mandibles, particularly left, elongate and with few inconspicuous setae near lateral condyle. Antennae with 15 articles, relative length formula 2 >3 < 4 = 5. Compound eyes projecting, medium-sized, and subcircular in lateral view. Ocelli white, oval, and protruding; separated from eyes by slightly less than their maximum diameters. Anterior margin of pronotum very shallowly concave; lateral margins narrowing gradually to small notch in middle of posterior margin. Anterior area of pronotum with faintly sinuous, darkened, and shallowly incised groove. Posterior margin of meso- and metanotum with V-shaped projection along deep median perpendicular emargination.

Worker (Figs. 2A, 4I, 4J, 4L; Table 5). In dorsal view, head capsule yellow-white, pilosity pale yellowish, antennae opaque whitish proximally, pale orange-yellow distally; remaining exoskeleton subhyaline. Pilosity generally moderately dense and of intermediate

Table 4. Measurements of A. bahamensis n. sp. imago

Measurement (mm) $(n = 12 \text{ from } 7 \text{ colonies})$	Range	Mean ± SD	Holotype
Head width at eyes, max	1.16–1.21	1.19 ± 0.019	1.19
Pronotum length, max	0.62-0.69	0.66 ± 0.024	0.65
Pronotum width, max	0.98-1.10	1.04 ± 0.035	1.05
Eye diam, max	0.28-0.30	0.29 ± 0.078	0.29
Eye to head base, min	0.07-0.10	0.09 ± 0.0070	0.07
Ocellus diam, max	0.11-0.14	0.12 ± 0.0059	0.11
Eye sclerite to ocellus, min	0.08-0.10	0.09 ± 0.0052	0.09
Total length with wings	12.90-14.76	13.99 ± 0.70	13.57
Total length without wings	6.78-8.38	7.72 ± 0.50	7.58
Fore wing length from suture	10.51-12.37	11.37 ± 0.67	10.77
Fore wing width, max	2.67-3.03	2.87 ± 0.15	2.74
Hind tibia length	1.19-1.24	1.21 ± 0.015	1.19
Left mandible length	0.69-0.78	0.73 ± 0.031	0.72
Left apical to first + second marginal tooth ^a	0.08	0.08	
Left first + second to third marginal tooth ^a	0.18-0.19	0.19 ± 0.0058	
Left third marginal to molar tooth ^a	0.09	0.09	
Right apical to first marginal tooth ^a	0.09-0.010	0.10 ± 0.0029	
Right first to second marginal tooth ^a	0.16-0.17	0.17 ± 0.0058	
Right second marginal to molar tooth ^a	0.106-0.110	0.108 ± 0.0029	

a n = 2

length. Postclypeus inflation weak with angle between its posterior and anterior of vertex >90° in lateral view; height of postclypeus ≈0.07 mm; postclypeus apex almost congruent with that of vertex. Anterior tibia inflation index ≈ 5.4 (length \div maximum width). Left mandible index (distance from apical tooth to first + second marginal tooth ÷ distance from first + second marginal tooth to third marginal tooth, measured at apex of each tooth) 0.42-0.47 (n=3), right mandible index (distance from apical tooth to first marginal tooth ÷ distance from first marginal tooth to second marginal tooth) 0.61-0.69 (n=3). Anterior edge of third marginal tooth of left mandible sinuous; anterior edge subequal in length with posterior edge; apical teeth on both mandibles retracted relative to underlying teeth (Fig. 4J). Fourteen antennal articles. Crop subcircular, rather small. Mesenteron faintly pimpled,

Table 5. Measurements of A. bahamensis n. sp. worker

Measurement (mm) $(n = 8 \text{ from 5 colonies})$	Range	Mean ± SD
Head width, max	0.85-0.90	0.87 ± 0.015
Head length to postelypeus apex	0.75 - 0.85	0.80 ± 0.029
Pronotum width, max	0.49 - 0.52	0.52 ± 0.012
Postclypeus width	0.41 - 0.43	0.42 ± 0.0097
Postclypeus length	0.20 - 0.23	0.21 ± 0.012
Fore tibia width	0.14 - 0.15	0.14 ± 0.0044
Fore tibia length	0.62 - 0.65	0.64 ± 0.010
Hind tibia length	0.77 - 0.80	0.79 ± 0.010
Left mandible length	0.51 - 0.54	0.52 ± 0.010
Left apical to first + second	0.065 - 0.074	0.069 ± 0.0041
marginal tooth ^a		
Left first + second to third	0.15 - 0.16	0.16 ± 0.0082
marginal tooth ^a		
Left third marginal to molar tooth ^a	0.065 - 0.074	0.071 ± 0.0047
Right apical to first marginal tooth ^a	0.069 - 0.082	0.75 ± 0.0062
Right first to second marginal tooth ^a	0.11 - 0.12	0.11 ± 0.0082
Right second marginal to molar	0.074 - 0.082	0.76 ± 0.0047
$tooth^a$		
Total length of body	4.26 - 4.66	4.44 ± 0.12

a n = 3

short, $\approx 5 \times$ as long as wide; in dorsal view of undissected worker forming about one-half loop. Mixed segment long, $\approx 10 \times$ as long as wide, mesenteric strip of mixed segment narrow, partly obscured under coiled gut and with conspicuous, ovoid termination; first proctodeal segment narrow, long, and sinuous in course, and of continuous diameter (Fig. 4L); enteric valve insertion short, collarlike, faintly inflated and slightly bilobed. Armature of the enteric valve consists of a regularly spaced field of ≈ 20 small spiculi on each cushion (Fig. 4I).

Comparisons. Anoplotermes and the New World Apicotermitinae as a whole are in dire need of revision; a task that is well beyond the scope of this study. Our placement of the two soldierless species into Anoplotermes is done to anchor their specific descriptions. Anoplotermes bahamensis almost certainly falls into a new genus as it does not fit either Anoplotermes or the other four soldierless apicotermitine genera of the Neotropics as described by Mathews (1977) and Fontes (1986). A. inopinatus mirrors the characters of Anoplotermes as reported by Fontes (1986) and therefore should retain its generic assignment after revision of the soldierless taxa.

The imagos of Bahamian Anoplotermes are separable by size with A. bahamensis being the larger of the two. Measurements that separate A. bahamensis and A. inopinatus, respectively, include head width across eyes (1.16–1.21 versus 0.98–1.03 mm), pronotum width (0.98–1.10 versus 0.83–0.92 mm), hind tibia length (1.19–1.24 versus 1.05–1.08 mm), and left mandible length (0.69–0.78 versus 0.59–0.64 mm). The shallow vertex concavity beyond the fontanelle is cordiform in A. inopinatus, whereas in A. bahamensis it is evenly rounded.

Workers of the Bahamian *Anoplotermes* differ in hind tibia length (0.77–0.80 versus 0.72–0.75 mm) and in left mandible length (0.51–0.54 versus 0.44–0.49 mm) for *A. bahamensis* and *A. inopinatus*, respectively.

Table 6. Measurements of A. inopinatus n. sp. imago

Measurement (mm) $(n = 12 \text{ from } 7 \text{ colonies})$	Range	Mean \pm SD	Holotype
Head width at eyes, max	0.98-1.03	1.01 ± 0.022	1.00
Pronotum length, max	0.51-0.56	0.53 ± 0.019	0.51
Pronotum width, max	0.83-0.92	0.87 ± 0.031	0.87
Eye diam, max	0.24-0.28	0.26 ± 0.013	0.25
Eve to head base, min.	0.07-0.10	0.08 ± 0.0090	0.10
Ocellus diam, max	0.10-0.11	0.11 ± 0.0075	0.11
Eve sclerite to ocellus, min.	0.065 - 0.082	0.072 ± 0.0052	0.074
Total length with wings	10.91-12.50	11.72 ± 0.65	11.84
Total length without wings	5.85-7.18	6.46 ± 0.39	6.52
Fore wing length from suture	8.65-10.51	9.60 ± 0.64	9.71
Fore wing width, max	2.14-2.60	2.37 ± 0.15	2.34
Hind tibia length	1.05-1.08	1.06 ± 0.015	1.08
Left mandible length	0.59-0.64	0.61 ± 0.017	0.60
Left apical to first + second marginal tooth ^a	0.082-0.090	0.086 ± 0.0041	
Left first + second to third marginal tooth ^a	0.14-0.15	0.14 ± 0.0024	
Left third marginal to molar tooth ^a	0.090 - 0.094	0.091 ± 0.0024	
Right apical to first marginal tooth ^a	0.086-0.090	0.089 ± 0.0024	
Right first to second marginal tooth ^a	0.106-0.110	0.108 ± 0.0024	
Right second marginal to molar tooth ^a	0.127-0.131	0.129 ± 0.0024	

a n = 3.

The apical teeth of both mandibles of A. bahamensis do not overhang the first marginal teeth to the degree they do in A. inopinatus. The postclypeus elevation of A. bahamensis is shallow (height $0.07 \, \mathrm{mm}$), while in A. inopinatus the postclypeus is strongly inflated to a height of $\approx 0.14 \, \mathrm{mm}$. The anterior tibia inflation index of A. inopinatus is $\approx 4.4 \, \mathrm{versus} \approx 5.4 \, \mathrm{for} \, A$. bahamensis. In A. inopinatus, the crop is voluminous and the first proctodeal segment is abruptly inflated at its anterior while, in A. bahamensis, the crop is smaller and the first proctodeal segment is attenuate throughout. The enteric valve lacks armature in A. inopinatus, whereas A. bahamamensis has groups of small spiculi on each cushion of the enteric valve.

Type Material Measured. *Holotype Colony*. BAHA-MAS. Eleuthera Island. N. Bluff; 25.498° N, 76.722° W; 27-V-2000; JC, JK, BM, JM, and RS; one holotype male alate, four paratype male alates, five paratype female alates, four paratype workers (BA 1293).

Paratype Colonies. BAHAMAS. Eleuthera Island. N. Bluff; same data except for: one paratype female and one male imagos each (BA 1291, 1300). Abaco Island. Hole in the Wall; 25.860° N, 77.190° W; 21-V-2000; JC, JK, BM, JM, and RS; one paratype worker (BA 788). North Andros Island. Mastic Point Cemetery; 25.060° N, 77.970° W; 31-V-1995; JC, JK, JM, JR, and RS; 1 paratype worker (BA 349). Cat Island. 3km ESE Old Bight; 24.217° N, 75.350° W; 27-V-1995; JC, JK, JM, JR, and RS; 1 paratype worker (BA 69). Long Island. N. Seymour's Settlement; 23.664° N, 75.312° W; 28-V-2001; JC and RS; 1 paratype worker (BA 1586).

Etymology. The species name reflects its only known distribution, the Bahamas.

Remarks. A. bahamensis is ecologically similar, and, at some localities, sympatric with A. inopinatus. Both species occur in rich organic soil where nest and flight staging galleries are centered beneath rocks and stones. Based on phenology of alates in colonies and observations of Cuban congeners (J.K., unpublished

data), dispersal flights of both species are likely diurnal and coincide with spring rains. See also A. inopinatus.

Distribution. A. bahamensis is sympatric with A. inopinatus on six islands: North Andros, Eleuthera, Long, Barreterre, Great Exuma, and Little Exuma. Abaco is the lone locality on the Little Bahama Bank and Rum Cay is the only deep water island where A. bahamensis occurs. See also A. inopinatus.

Anoplotermes inopinatus Scheffrahn & Křeček, New Species

Imago (Fig. 4H; Table 6). In dorsal view, head capsule and antennae dark sepia brown; wing scales, costal margins, abdomen, and legs slightly lighter. Anterolateral corners of head capsule pale brown; postclypeus and pronotum slightly darker. First three antennal articles lighter than remainder. Fontanelle small (maximum diameter ≈0.05 mm), oval. Head capsule, postclypeus, all thoracic nota, antennae, wing scales, tergites, and sternites densely and finely dotted by pale setal punctations. Minority of punctations faintly larger. Mandibles, except for darker dentition, pale yellow-brown, similar to proximal part of labrum. Distal part of labrum and anteclypeus subhyaline. Middle of anteclypeus with narrow white, shortly cylindrical, and longitudinal projection with darkened and sclerotized tip. Compound eyes black. Pronotum midline distinct, even, and without dual spots in posterior middle. Wing membranes translucent sepia brown with slight blue-violet iridescence.

Head capsule, postclypeus, labrum, and pronotum conspicuous, pigmented, and with pilosity of variable length. Head, in dorsal view, subcircular with exception of projecting mandibles. Head capsule with postclypeus noticeably wider than long. Postclypeus short, weakly convex, about twice as wide as long, and very faintly bilobed along midline. Vertex very shallowly concave in lightly cordiform pattern; concavity cen-

Table 7. Measurements of A. inopinatus n. sp. worker

Measurement (mm) $(n = 12 \text{ from 7 colonies})$	Range	Mean ± SD
Head width, max	0.78-0.85	0.81 ± 0.030
Head length to postclypeus apex	0.72 - 0.78	0.76 ± 0.025
Pronotum width, max	0.46 - 0.49	0.48 ± 0.011
Postclypeus width	0.42 - 0.47	0.44 ± 0.015
Postcylpeus length	0.23 - 0.27	0.25 ± 0.012
Fore tibia width	0.13 - 0.15	0.14 ± 0.0076
Fore tibia length	0.59 - 0.64	0.64 ± 0.020
Hind tibia length	0.72 - 0.75	0.74 ± 0.014
Left mandible length	0.44 - 0.49	0.52 ± 0.018
Left apical to first + second marginal tooth ^a	0.061-0.069	0.065 ± 0.0041
Left first + second to third marginal tooth ^a	0.11-0.12	0.12 ± 0.0047
Left third marginal to molar tooth ^a	0.065 - 0.078	0.069 ± 0.0071
Right apical to first marginal tooth ^a	0.065 - 0.069	0.067 ± 0.0024
Right first to second marginal tooth ^a	0.078 - 0.090	0.083 ± 0.0062
Right second marginal to molar tooth ^a	0.057-0.065	0.061 ± 0.0041
Total length of body	3.72 - 4.52	4.11 ± 0.29

a n = 3.

tered just posterior to fontanelle. Epicranial suture absent. Mandibles, particularly left, elongate and with about 10 variably sized and relatively obvious setae along mandibular bases. Antennae with 15 articles, rarely with 14; relative length formula 2 > 3 < 4 = 5. Compound eyes medium-sized and subcircular in lateral view. Ocelli white, shortly suboval, and protruding; ocellus remote from eye by distance less than maximum diameter of ocellus. In dorsal view, pronotum with anterior margin almost rectate in middle, anterolateral corners slightly raised, general shape of pronotum subtrapezoidal, and posterior margin lightly emarginate. Pronotum anterior margin with bilateral, faintly sinuous, and shallow groove. Posterior margin of meso- and metanotum obtusely and bilaterally pointed along deep median incision.

Worker (Figs. 2B, 4K, 4M; Table 7). In dorsal view, head capsule yellow-white, pilosity pale yellowish; antennae, sternites, tergites, and legs subhyaline. Pilosity generally moderately dense and long. Postclypeus inflation conspicuously bulbous, semiglobate, with angle between postclypeus posterior and vertex anterior <90° in lateral view; height of postclypeus ≈0.14 mm; postclypeus apex distinctly elevated above plane of vertex. Anterior tibia inflation index (see A. bahamensis) ≈ 4.4 . Left mandible index 0.54-0.57, right mandible index 0.73-0.85 (n=3). Anterior edge of third marginal tooth of left mandible straight and longer than posterior edge (Fig. 4K). Apical and marginal teeth of right mandible extremities approximately in line; apical tooth of left mandible weakly receding. Fourteen antennal articles. Crop subcircular, voluminous. Mesenteron conspicuously pimpled, long, $\approx 10 \times$ as long as wide, in dorsal view (on undissected worker) forming one loop. Mixed segment short, adjacent to inner side of intestinal arch, mixed segment $\approx 4 \times$ as long as wide; first proctodeal segment broadens abruptly beyond mixed segment (Fig. 4M); mesenteric part of mixed segment surrounded by malpighian tubules, particularly on reniform termination. First proctodeal segment robust, and looping to enteric valve insertion to form moderately elongate intersegment. Enteric valve insertion ≈2× longer than wide and rather amorphous. Enteric valve armature absent. Additional valve structures consist of irregular and not very well defined axially elongated reticulation, apparently not or only slightly sclerotized.

Comparison. See A. bahamensis.

Type Material Measured. Holotype Colony. BAHA-MAS. Eleuthera Island. N. *Bluff*; 25.498° N, 76.722° W; 27-V-2000; JC, JK, BM, JM, and RS; one holotype male alate, one paratype male alate, two paratype female alates, four paratype workers (BA 1289).

Paratype Colonies. BAHAMAS. Eleuthera Island. N. Bluff; same data as holotype colony except for one female and one male imagos (BA 1290), S. Rainbow W. Coast; 25.333° N, 76.418° W; 25-V-2000; 1 worker (BA 1107), and Alabaster Point; 25.220° N, 76.226° W; 25-V-2000; 1 worker (BA 1133). North Andros Island. Mastic Point Cemetery; 25.060° N, 77.970° W; 31-V-1995; JC, JK, JM, JR, and RS; 1 worker (BA 350). Long Island. Deadman's Cay Area; 23.191° N, 75.113° W; 27-V-2001; JC and RS; 1 worker (BA 1547).

Etymology. Named after the Latin word "inopinatus" meaning "unexpected."

Remarks. Neither Bahamian soldierless species is rare. A. inopinatus was collected at 22 localities on eight islands, whereas A. bahamensis was found at 23 localities on nine islands.

Distribution. Like *A. bahamensis*, *A. inopinatus* is primarily confined to the islands in the Great Bahama Bank, but both spp. were not collected on the Bimini islands and on New Providence. *A. inopinatus* was not collected on Cat Island. Among islands isolated by deep water (Table 1; Fig. 5), *A. inopinatus* occurs only on San Salvador, whereas *A. bahamensis* was collected only on Rum Cay. See also *A. bahamensis*.

Nasutitermitinae

Nasutitermes corniger (Motschulsky) (Fig. 2E)

Termes cornigera Motschulsky 1855: 10 [soldier, laconic description; type loc.: Obispo, Panama; type species of genus by subsequent designation]

Nasutitermes corniger: Scheffrahn et al. 2005a [complete synonymy, distribution]

Nasutitermes costalis: Holmgren 1910: 293 [imago, key, fig.; Trinidad]; Scheffrahn et al. 2005a [new synonymy]

Nasutitermes polygynus: Scheffrahn et al. 2005b [new synonymy]

Remarks. Nearly 4.5 yr after its discovery in Dania Beach, FL (Scheffrahn et al. 2002), *Na. corniger* is now recorded from the Bahamas. A widespread (\approx 300-m-wide) infestation of this arboreal termite was discovered on the Treasure Cay peninsula, Abaco Island, by a Marsh Harbor pest control operator. In August 2005,

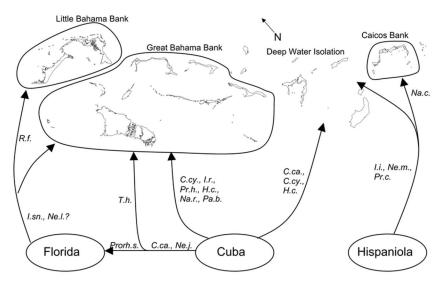


Fig. 5. Hypothesized late Pleistocene termite dispersal routes from Florida, Cuba, and Hispaniola to the BATC based on present-day distributions. Not included are nonindigenous species (*Cr. brevis*, *Co. gestroi*, and *He.* sp.), BATC endemics (*Cr. bracketti*, *A. bahamensis*, and *A. inopinatus*), and species with broader distributions in the West Indies for which an origin is indiscernible including *I. bequaerti* (to Puerto Rico), *I. milleri* (to Cayman Islands and Jamaica), *I. schwarzi* (to Jamaica), and *Ne. castaneus* (to Cayman Is., Jamaica, and mainland Central America). *R.f.*, *R. flavipes*, *I.sn.*, *I. snyderi*; *T.h.*, *Termes hispaniolae*; *Prorh.s.*, *Pror. simplex*; *C.ca.*, *Cr. cavifrons*; *C.cy.*, *Cr. cymatofrons*; *Ne.j.*, *Neotermes jouteli*; *Ne.l.*, *Ne. luykxi*; *I.r.*, *I. rhyzophorae*; *Pr.h. Procryptotermes hesperus*; *H.c.*, *H. cardini*; *Na.r.*, *Nasutitermes rippertii*; *Pa.b.*, *Parvitermes brooksi*; *Na.c.*, *Na. corniger*; *I.i.*, *I. incisus*; *Ne.m.*, *Ne. mona*; and *Pr.c.*, *Pro. corniceps*.

the pest control operator noted a nest on a tree stump and treated two houses that were infested. Soldiers, large and small workers, and shelter tubes that incorporated exterior house paint was collected on 20 September 2005 from a third house that had not yet been treated. In May 2000, the Treasure Cay area had been surveyed for termites without yielding *Na. corniger*. Treasure Cay has a large marina on its grounds and is close to the Bahamas ferry dock. This remarkable find further suggests that this invasive pest has been accidentally introduced by humans to other islands in the West Indies where it was presumed to be indigenous. No doubt other nonindigenous localities around the world are, or will become, the home of *Na. corniger*.

This species constructs characteristic, rather fragile arboreal or epigeal nests of brownish fecal matter. Nests are usually polycalic and polygynous. On the Caicos Bank, Abaco, and Florida, nests are constructed at the base of trees or palms. Dark brown foraging tubes radiating from nests are commonly seen on structural walls, trees, soil and road surfaces, and other substrata. *Na. corniger* feeds on sound wood at or above soil level. Crepuscular dispersal flights commence at the beginning of the spring rainy season.

Distribution. In the BATC, the distribution of *Na. corniger* is mutually exclusive to that of *Na. rippertii*. Except for Grand Turk, *Na. corniger* occurs throughout the Caicos Bank (Table 1). Curiously for a species that should thrive there, *Na. corniger* is absent from Mona Island, most of the Virgin Islands, and Culebra (Scheffrahn et al. 2003). It is widespread and usually common in the remainder of the West Indies and has been reported on mainland America from southern

Mexico to northern Argentina (Scheffrahn et al. 2005a). Aside from recent Florida and Abaco establishments, *Na. corniger* (=*Na. polygynus*) also has a nonindigenous distribution on Papua New Guinea dating to 1944 (Roisin and Pasteels 1996).

Nasutitermes rippertii (Rambur) (Figs. 2D and 4A)

Termes rippertii Rambur 1842: 308, 323 [imago; type loc.: Havana, Cuba]

Eutermes (Eutermes) rippertii: Holmgren 1910: 208 [without description]

Nasutitermes rippertii: Banks 1919: 483–484 [imago, soldier, fig., distribution]; Snyder 1956: 191–192 [distribution]; Scheffrahn et al. 1994: 214–215, 233 [distribution]

Eutermes (Eutermes) bahamensis: Holmgren 1910: 290 [soldier, fig.]; synonymized by Banks 1919: 483–484. Eutermes (Eutermes) cubanus: Holmgren 1910: 291 [soldier, worker, fig.]; synonymized by Banks 1919: 483–484.

Remarks. Na. rippertii is characterized by large, dark brown, arboreal, and epigeal nests. Free-standing epigeal nests are somewhat bullet-shaped and can grow to a height of 2 m. Arboreal nests are elongate, large, and less common than epigeal nests. Na. rippertii feeds on sound, dry wood and may locate nests in structural voids, but is of lesser pest status than N. corniger. Colonies are monogynous and crepuscular nuptial flights commence from May to July.

Table 8. Measurements of Pa. brooksi alate imago

Measurement (mm) $(n = 9 \text{ and } 8 \text{ females from } 10 \text{ localities and } 4 \text{ islands})$	Range	Mean ± SD
Head length with labrum	1.28-1.39	1.34 ± 0.039
Head length to postcylpeus	0.69 - 0.77	0.73 ± 0.024
Head width at eyes, max	1.01-1.11	1.06 ± 0.032
Head height without postmentum	0.49-0.56	0.52 ± 0.016
Eye diam, max	0.29 - 0.33	0.30 ± 0.010
Eye to head base, min.	0.08 - 0.10	0.09 ± 0.0059
Ocellus diam, max	0.13 - 0.16	0.14 ± 0.0072
Eye sclerite to ocellus, min.	0.049 - 0.09	0.067 ± 0.010
Pronotum, max length	0.59 - 0.72	0.65 ± 0.034
Pronotum, max width	0.88 - 1.08	0.99 ± 0.059
Total length with wings	12.24-14.10	13.25 ± 0.63
Total length without wings	6.52 - 7.98	7.20 ± 0.41
Forewing length from suture	10.24 - 11.57	10.95 ± 0.45
Forewing, max width	2.67 - 3.03	2.85 ± 0.15
Hind tibiae length	1.28 - 1.47	1.36 ± 0.053

Distribution. *Na. rippertii* occurs on all islands of the Great Bahama Bank and also on Rum Cay (Table 1). It is absent from the remainder of the BATC. The species also occurs on Cuba, including Isle of Youth (Scheffrahn et al. 1994). Jamaican records (Araujo 1977) are apparently based on misidentification with *Na. nigriceps* (Haldeman).

Parvitermes brooksi (Snyder) (Figs. 2C and 4F)

Nasutitermes (Tenuirostritermes) brooksi Snyder 1925: 105–106 [soldier, figs.; type loc.: Soledad near Cienfuegos, Cuba]

Parvitermes brooksi Emerson: Snyder 1949: 305, 376 [type species of new genus, new generic assignation, catalog, distribution]; Scheffrahn and Křeček 1993: 595 [soldier key to West Indies spp.]; Scheffrahn et al. 1994: 214, 217, 221, 234 [distrib.]; Roisin et al. 1996: 775 [taxonomy, worker, figs.]

Imago (Fig. 4F; Table 8). Previously undescribed. In dorsal view, head capsule chestnut brown to dark sepia brown; slightly paler anterior periantennal areas and with remarkable punctation from pale insertions of dense setae; contrasting pale ochraceous fontanelle slit; front of fontanelle with two pairs of paler elongate spots; occiput with faint V-shaped mark with paler center. In lateral view, ventral occiput with pair of longitudinal pale marks. Epicranial suture consists only of remnants of posterior branch. Postclypeus ochraceous; part of anteclypeus opaque whitish and part subhyaline. Antennae sepia brown to dark sepia brown, darker distally. Mandibles pale ochraceous to ochraceous, except for darker dentition. Compound eyes dark grayish, ocelli opaque white. Pronotum ochraceous to sepia brown; pterothorax distinctly paler, pale ochraceous to brown. Abdominal tergites brown, sternites ochraceous. Wing membranes smoky ochraceous, venation brown, except for sepia brown fringe along posterior edge of radial sector.

In lateral view, head capsule moderately flattened dorsoventrally at occiput; vertex moderately elevated; in dorsal view, head capsule with mandibles ovoid; eyes and ocelli large, both oval, and separated by maximum diameter of ocelli; ocelli moderately protruding, opaque white. Head capsule, postclypeus, and labrum densely pilous; pronotum, legs, and all abdominal tergites and sternites covered with long setae. Antennae with 15 articles; formula 2=3>4=5. Pronotum somewhat saddle-shaped; anterior elevation delineated laterally by dark line; anterior middle of elevation slightly emarginate; pronotum without median longitudinal line, but with pair of pale central perimarginal spots.

Comparisons. The Pa. brooksi imago differs from three other described allopatric congeners, i.e., Pa. dominicanae Scheffrahn et al. (1998b), Pa. toussainti (Banks 1919), and Pa. wolcotti (Snyder 1924a), as follows: the epicranial suture of *Pa. toussainti* is slight. but complete, whereas in Pa. brooksi only remnants of its posterior branch are visible; the fontanelle slit of Pa. brooksi is a linear bar, whereas in Pa. toussainti it is wider anteriorly. The postclypeus of *Pa. toussainti* is brown, whereas in Pa. brooksi it is ochraceous. The pronotum of *Pa. brooksi* is without a median longitudinal line, but with a pair of light spots near the middle of the posterior margin; in *Pa. toussainti* this pattern is reversed. The image of *Pa. wolcotti* possesses distinctly larger compound eyes (0.38-0.43 versus 0.28-0.33 mm in *Pa. brooksi*), and it is also distinctly larger in most measurements, except for head height, total length with and without wings, and hind tibiae length. The Pa. dominicanae imago has ferruginous coloration in contrast to the chestnut brown coloration of Pa. brooksi. Pa. dominicanae has an indistinct fontanelle without a slit, whereas the Pa. brooksi fontanelle is distinct and has a contrasting slit. A slight concavity surrounds the fontanelle of *Pa. dominicanae*, whereas in Pa. brooksi this area is flat.

Soldier (Fig. 2C; Table 9). The original description and diagnosis by Snyder (1925) of the *Pa. brooksi* soldier is adequate, although it is based on a single series of soldiers from the type locality. We provide more complete measurements from eight Cuban and eight Bahamian localities (Table 9). Both sets of measurements are congruent with the exception of hind tibia length (possible error in Snyder 1925). We observed no obvious geographic variability within the range of this species.

Remarks. Pa. brooksi is primarily a forest species where the soil has a richer organic and clay content. This species nests in the soil but on rare occasions, Pa. brooksi builds small earthen epigeal nests at the base of trees. Galleries, coated with black fecal lining, are most typically found beneath rocks and stones. Pa. brooksi feeds on cellulosic surface debris; mainly small branches and sticks. Earthen-colored foraging tubes run on the outside of food items and through leaf litter but are seldom seen much above soil level. Based on alate appearance in nests and direct observations on Cuba (Jan Křeček, unpublished), Pa. brooksi flies in late spring (May and June) in association with rain. Alates in Cuba have been collected both nocturnally

Table 9. Measurements of P. brooksi soldier

	Range	Mean ± SD	Snyder (1925)
Head length with nasus	1.08-1.23	1.14 ± 0.041	1.10
Head length without nasus	0.69-0.77	0.72 ± 0.022	0.70
Head width, max	0.64-0.72	0.67 ± 0.026	0.65
Nasus width at base	0.14-0.18	0.16 ± 0.011	
Nasus width at middle	0.074-0.09	0.08 ± 0.0068	
Nasus length	0.37-0.46	0.42 ± 0.023	0.40
Head height, without postmentum	0.39-0.44	0.42 ± 0.016	
Pronotum, max width	0.33-0.38	0.35 ± 0.015	0.35
Pronotum, max length	0.11-0.16	0.13 ± 0.010	0.20
Hind tibia length	0.65-0.74	0.70 ± 0.026	0.90
Total length	2.45-3.51	2.96 ± 0.30	2.20

and diurnally, (J.K., unpublished data), but only during rain.

Distribution. *Pa. brooksi* is a widespread and a surprisingly locally abundant species, occurring on practically all islands of the Great Bahama Bank with the exception of Cat Island (Table 1.) It is absent from the remainder of the BATC. Otherwise, *Pa. brooksi* occurs only on Cuba, including Isle of Youth (Banks 1919, Barreto 1923).

Termitinae

Termes hispaniolae (Banks) (Fig. 3E)

Mirotermes hispaniolae Banks 1918: 662 [winged imago, type loc.: Panama; with original author declaration: "species based on soldiers from Hayti", original description of imago not assigned as n. sp.], Banks 1919: 481–482 [soldier, original description assigned as n. sp., soldier figs., Haiti, Cuba]

Mirotermes (Mirotermes) hispaniolae: Emerson 1925: 437–439 [alate, soldier redescription, soldier fig.] Termes hispaniolae Emerson: Adamson 1937: 141, 145 [generic reassignment]; Snyder 1949: 181 [catalog], Snyder 1956: 190, 195–201 [distribution, keys]; Constantino 1991: 203, 206, 208 [distribution, soldier fig.]; Scheffrahn et al. 1994: 234 [West Indian distribution], Scheffrahn et al. 2003: 182–188, 195, 197 [Puerto Rico, Virgin Islands, soldier fig., keys]

Remarks. *T. hispaniolae* constructs diffuse carton nests in the crotches and hollows of dead trees or limbs, particularly in sea grape (*Cocoloba uvifera* (L.) along coastlines. Nests are made of characteristic thick, blackish, and hard carton.

Distribution. *T. hispaniolae* is widespread and often common in the West Indies and on the surrounding mainland of Central America. In the BATC this species is rare and has only been collected from a few locations on S. Andros and New Providence (Table 1).

Discussion

Although the geologic history of the West Indies is complex (Hedges 2001), the composition of the BATC is more clearly understood to be a tectonically stable carbonate platform (Chen et al. 1991). As a consequence of its stability and low elevation, most or all of the BATC land mass was submerged 3,000,000 ybp when sea levels of the middle Pliocene rose to some 25-40 m above present level (Dowsett et al. 1999). The most recent high water stand of 6 m above present occurred 126,000–123,000 ybp during the last (Sangamon) interglacial stage when substantial land areas of the BATC were again submerged (Chen et al. 1991). As sea levels receded during the onset of the Wisconsinan glaciation, the BATC coalesced into several large islands approximating the limits of contemporary shallow water banks (Fig. 1). Beginning ≈18,000 ybp, the oceans of the late Pleistocene again rose until presentday shorelines were attained ≈6,000 ybp (Lambeck et al. 2002). It is thus hypothesized that most termite species dispersed to the BATC from their original indigenous sources between the Sangamon interglacial high water mark (126,000-123,000 ybp) and present time with the greatest number of dispersal events occurring around the time of the last low water period (18,000 ybp). But, it is also entirely possible that some termite species existed on the few small emergent land areas of the BATC as early as the middle Pliocene sea level maximum of 3,000,000 ybp.

Overwater dispersal is a primary mechanism for radiation of nonvolant land animals between islands of the West Indies and circum-Caribbean mainland (Hedges 2001), including its herpitofauna (Glor et al. 2005). Termites are poorly adapted for long-distance aerial dispersal because they are weak fliers and mating occurs only after dispersal flights (Scheffrahn et al. 2003). Overwater dispersal of termites would be favored for species that nest in or on wood. In such a scenario, a reproductively fit colony within a piece of wood or within a nest clinging to a tree or branch could be set adrift during storms, landslides, hurricanes (Censky et al. 1998), or tsunamis (Scheffers and Kelletat 2004) and could remain a viable raft for weeks or months. The smaller ocean gaps (Fig. 1) of the late Pleistocene must have favored the success of such flotsam to make new landfall with viable colonies. Overwater dispersal of obligate soil-nesting termites (e.g., Anoplotermes and other soldierless genera, Parvitermes, Amitermes, Caribitermes, and Antillitermes) would be difficult to envision, and the presence of the three soil nesting species (two Anoplotermes spp. and Pa. brooksi) in the Bahamas remains problematic. Nevertheless, soil nesting species account for 33 and 50% of the termite fauna of Cuba and Hispaniola, respectively, whereas only 13% of indigenous BATC species are soil nesters. Even with only three soil-nesting species, the Bahamas are an exception with respect to the remainder of the West Indies where soil-nesting termites occur only on the large islands of Cuba, Hispaniola, Puerto Rico, Trinidad, and their respective shallow water islands.

Based on distributions of indigenous termite species, the BATC archipelago can be divided into four faunal zones (Table 1; Fig. 5): Little Bahama Bank (Grand Bahama and Abaco), Great Bahama Bank (Bimini to Long), southeastern islands in deep water (Rum Cay and San Salvador to Great Inagua), and the Caicos Bank. Mayaguana seems to be transitional between the latter two zones. Termite dispersal routes from centers of diversity in Florida, Cuba, and Hispaniola to the BATC also can be established based on current distributions (Fig. 5). Not included in dispersal route estimates (Fig. 5) are nonindigenous species (Na. corniger in Florida and Abaco, Cr. brevis, Co. gestroi, and H. sp.), BATC endemics (Cr. bracketti, A. bahamensis, and A. inopinatus), and indigenous species with a broader distribution in the West Indies for which an origin is indiscernible including I. bequaerti (to Puerto Rico), I. milleri (to Cayman Islands and Jamaica), I. schwarzi (to Jamaica), and Ne. castaneus (to Cayman Is., Jamaica, and mainland Central Amer-

The possibility of allopatric speciation of the two Anoplotermes species and Cr. bracketti from overwater dispersal events is difficult to reconcile given that the soil-nesting termites of the Bahamas probably originated from mainland sources during recent times. Cuba has only been modestly surveyed for termites and both Bahamian Anoplotermes species may ultimately be discovered on Cuba. Also, the occurrence of Anoplotermes on Abaco, Rum Cay, and San Salvador cannot be accounted for by either Pleistocene land connections or overwater dispersal. The origin of Cr. bracketti on isolated San Salvador island may be the result of a more distant overwater source or speciation of a congener that endured on the island during the high water stand of the middle Pliocene (maximum elevation on present-day San Salvador is 37 m).

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