Synonymy of Neotropical Arboreal Termites *Nasutitermes corniger* and *N. costalis* (Isoptera: Termitidae: Nasutitermitinae), with Evidence from Morphology, Genetics, and Biogeography

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ABSTRACT Morphological examination of soldiers and imagos assigned to *Nasutitermes corniger* or *N. costalis* from 13 Neotropical countries and 42 West Indian islands revealed congruent characters and biometric overlap. A portion of the mitochondrial DNA 16S rRNA gene was sequenced from nine *N. costalis* and *N. corniger* samples. Molecular phylogenetic analysis of the *N. costalis*/*corniger* DNA sequences relative to other *Nasutitermes* spp. supported the morphological evidence that these species are conspecific. Complementary biological, behavioral, biochemical, and reproductive ecology further support the presented synonymy. The senior synonym, *N. corniger*, is given nomenclatural precedence. The geographical distribution of *N. corniger* is revised.

KEY WORDS arboreal termite, taxonomy, distribution

TWO OF THE MOST DOMINANT and widely distributed species of the genus *Nasutitermes* Dudley (1890) in the Neotropics are *N. corniger* (Motschulsky 1855) and *N. costalis* (Holmgren 1910). *N. corniger* was originally described from the soldier caste collected in Panama. Banks (1918) slightly modified Motschulsky's soldier description and added the first description of the winged imago, also from Panama. He also compared both winged imagos and soldiers of *N. corniger* with *N. morio* (Latreille 1805) =*N. costalis* in Emerson (1925) and found them to be morphologically similar. In his review of West Indian termite taxonomy, Banks (1919) eluded to a synonymy of the Panamanian *N. corniger* with the West Indian *N. costalis* by stating "*N. morio* =*N. costalis*, ref. Emerson 1925 is common over the entire West Indian area, and a form almost the same (*N. corniger*) occurs in Panama." *N. morio* from Panama was later synonymized with *N. corniger* (Snyder 1949). As it presently stands, the distribution of *N. corniger* is broadly mainland and includes Mesoamerica from southern Mexico to Panama (Snyder 1926, 1949; Holmgren 1910; Maes 1990; Motschulsky 1855; Nickle and Collins 1992) and the South American countries of Colombia, Venezuela, Guiana, Brazil, Ecuador, Bolivia, and Argentina (Snyder 1926, 1949; Araujo 1977; Torales and Armua 1986; Constantino 1998).

The winged imago of *N. costalis* was described from Trinidad by Holmgren (1910) who simultaneously described conspecific soldiers under four different names (as shown below) from French Guyana, Suriname, and the West Indies. The conspecificity of those species with *N. costalis* was recognized by Emerson (1925) who synonymized Holmgren's names and redescribed *N. costalis* based on a series of imagos and soldiers from Guiana, Trinidad, Grenada, St. Lucia, Martinique, Dominica, St. Kitts, Antigua, and the Dominican Republic. Emerson (1925) noted that *N. costalis* is probably conspecific with *N. insularis* (Holmgren 1910) from Costa Rica. *N. insularis* was synonymized under *N. corniger* by Snyder (1949). Emerson (1925) also broadened the geographic range of *N. costalis* to include the Guayanas, Venezuela, the West Indies from Cuba to Trinidad, Guatemala, and Panama. The last two records further suggest either synonymy or sympatry of *N. corniger* and *N. costalis.* The current distribution of *N. costalis* includes the West Indies (excluding Bahamas) and the adjacent part of the South American mainland (Emerson 1925, Snyder 1956, Constantino and Cancello 1992, Scheffrahn et al. 1994).

Studies describing nest morphology (Krecek 1970, Thorne 1980, Scheffrahn et al. 2002), soldier defensive secretion composition (Vrkoc et al. 1973, Vrkoc et al. 1978, Prestwich 1979, Gush et al. 1985), cuticular hydrocarbons composition (Howard et al. 1988, Haverty et al. 1990), and alarm/recruitment behavior (Traniello and Beshers 1985) show congruent data for *N. corniger* and *N. costalis.* Both are considered economically important structural, agricultural, and silvicultural pests (Harris 1971, Edwards and Mill 1986, Constantino 2002a). The morphological similarities and overlapping distribution of *N. corniger* and *N. costalis* (Emerson 1925, Harris 1961, Constantino and Cancello 1992, Constantino 1998, Issa 2000) and in-

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ferences of synonymy by Mathews (1977) and Constantino (2002a) motivated us to reexamine the validity of their unique identities. Recently, we also have been able to conduct long-term field observations of this species in Florida (Scheffrahn et al. 2002). The only molecular genetic analysis of *Nasutitermes* is a study by Miura et al. (2000) that focused on *Nasutitermes* from the Pacific tropics and included only one *N. corniger* and no *N. costalis* samples. Because of the qualitative nature of morphological identification, DNA sequence analysis of a portion of the mitochondrial DNA (mtDNA) 16S rRNA gene has proven useful in genetic analysis of other termites, including *Reticulitermes* (Austin et al. 2004a, b) and *Heterotermes* (Szalanski et al. 2004). In this article, we provide morphological and genetic evidence that these two species be synonymized into a single circum-Caribbean and mainland Neotropical species under the senior synonym *N. corniger.*

Materials and Methods

Morphological examinations are based on ≈1,600 colony samples assigned originally to *N. corniger* or *N. costalis* from 56 geopolitical units, including 42 West Indian islands, 13 Neotropical continental countries, and 787 localities. Measurements were taken with a stereomicroscope fitted with a calibrated micrometric scale. Measurements used include some slight modifications of those suggested by Roonwal (1970). Head capsule photomicrographs were obtained using a digitized three-dimensional imaging system (Auto-Montage, Syncroscopy Inc. Frederick, MD). Names of collectors are coded as follows: Boudanath Maharajh (BM), James A. Chase (JC), Jan Krecek (JK), John R. Mangold (JM), Julian de la Rosa (JR), Paul Ban (PB), Reginaldo Constantino (RC), and Rudolf H. Scheffrahn (RS). Material data followed by inventory code (e.g., FL991) are housed in the University of Florida Termite Collection, Ft. Lauderdale Research and Education Center.

Nasutitermes corniger (Motschulsky)

Termes cornigera Motschulsky, 1855: 10 [soldier; briefly described]. Type locality: Panama: Obispo.

Nasutitermes corniger; Snyder (1949): 272 [masculine conversion of name]; Thorne (1980) [nest]; Nickle and Collins (1992) [Figs. 90–91 (soldier)].

Nasutitermes cornigera Banks (1918): 665 [imago, soldier; polygyny and polyandry?; comparisons, generic reassignment]; Banks (1919): 486 [comparisons]; Harris (1961, 1971) [pest status].

Nasutitermes (*Nasutitermes*) *cornigera* Snyder (1926): 31 [Bolivia distribution; polygyny?].

Termes morio Latreille 1805: 69 [St. Domingo]; Hagen (1858a): 27 [imago; Panama only; dubious interpretation by Snyder (1949): 272, because it is cited under both *N. corniger* and *N. costalis* (the latter with question mark)].

Termes (*Eutermes*) *morio*; Desneux (1915): nine [locality]. Synonymized by Emerson (1925) with *Nasutitermes* (*Nasutitermes*) *costalis*: 379.

Eutermes (*Eutermes*) *costaricensis* Holmgren (1910): 210, 237 [soldier, Fig. 24, worker]. Type locality: Costa Rica, Ecuador, Puerto Rico, and Venezuela; Banks in Banks and Snyder (1920): 69, suggested, but did not synomymize with *N. sanchezi*. Material from Costa Rica synonymized by Snyder (1949): 272; material from remaining localities synonymized by Constantino (1998): 180.

Eutermes (*Eutermes*) *insularis* Holmgren (1910): 239 [soldier; Fig. 26]. Type locality: Costa Rica. Synonymized by Snyder (1949): 272.

Eutermes (*Eutermes*) *insularis* form *obscurus* Holmgren (1910): 239–240 [soldier]. Type locality: Costa Rica. Synonymized by Snyder (1949): 272.

Eutermes sp.; Dudley and Beaumont (1889): 56–76, biology.

Nasutitermes sp.; Dudley and Beaumont (1890): 158, 163.

Eutermes (*Eutermes*) *costalis* Holmgren (1910): 293 [imago; Fig. 64]. Type locality: Trinidad. Remains the type species of genus, even if now considered a junior synonym.

Eutermes costalis; Snyder (1949): 272 [incomplete name, no subgenus as used in original citation].

Eutermes morio Banks in Banks and Snyder (1920): 69 [type species of genus, first designation].

Nasutitermes (*Nasutitermes*) *costalis*; Emerson (1925): 379 [imago, soldier; Fig. 55a–d].

Nasutitermes costalis; Snyder (1949): 272–273 [synonymy].

Termes morio Latreille (1805): 69 [imago, St. Domingo]; Burmeister (1839): 767; Hagen (1858b): 200, Hagen (1858a): 27. Synonymized by Banks 1919: 486.

Eutermes (*Eutermes*) *Cayennae* Holmgren (1910): 232 [soldier; Fig. 21]. Type locality: French Guyana: Cayenne. Synonymized by Emerson (1925) with *Nasutitermes* (*Nasutitermes*) *costalis*: 379.

Eutermes (*Eutermes*) *Cayennae* form *atriceps* Holmgren (1910): 234 [soldier]. Type locality: Suriname, Paramaribo. Synonymized by Emerson (1925) with *Nasutitermes* (*Nasutitermes*) *costalis*: 379.

Eutermes (*Eutermes*) *cayennae* form *brevinasus* Holmgren (1910): 234 [soldier, worker]. Type locality: Suriname, Paramaribo. Synonymized by Emerson (1925)with *Nasutitermes* (*Nasutitermes*) *costalis*: 379.

Eutermes (*Eutermes*) *cayennae* form *lividus* Holmgren (1910): 234 [soldier, worker]. Type locality: French Guyana, Cayenne. Synonymized by Emerson (1925) with *Nasutitermes* (*Nasutitermes*) *costalis*: 379.

Eutermes (*Eutermes*) *haitiensis* Holmgren (1910): 227 [soldier, worker; Fig. 18]. Type locality: Haiti. Synonymized by Banks 1919: 487 with *N. morio* and by Snyder 1949: 272.

Table 1. Measurements of *N. corniger* soldiers

Measurement (mm)	Range	Mean ± SD
Head length with nasus	1.37–1.77	1.55 ± 0.10
Head length without nasus	0.88–1.18	1.00 ± 0.074
Head width, max	0.82–1.31	1.00 ± 0.11
Nasus width at base	0.26–0.36	0.31 ± 0.027
Nasus width at middle	0.15–0.21	0.17 ± 0.017
Head ht, without postmentum	0.54–0.80	0.67 ± 0.064
Pronotum, max width	0.44–0.65	0.50 ± 0.043
Pronotum, max length	0.16–0.26	0.18 ± 0.022
Hind tibia length	1.01–1.52	1.18 ± 0.10
Total length	2.85–5.23	3.68 ± 0.50

Soldiers ($n = 29$ from 29 colonies) measured originated from one specimen from each colony series; for details, consult "Material Examined and Measured"): USA (Florida), Mexico (2 colonies), Belize, Honduras, Costa Rica, Nicaragua, Panama (2 colonies), Cuba, Jamaica, Turks and Caicos, Dominican Republic, Puerto Rico, Vieques, St. Croix (USVI), Tortola (BVI), Guadeloupe (Basse-Terre), Dominica, Martinique, St. Lucia, St. Vincent, Grenada, Trinidad and Tobago (both islands), Venezuela, Guyana, Suriname, Brazil, Bolivia, Peru, and Ecuador.

Eutermes (*Eutermes*) *haitiensis* form *albus* Holmgren (1910): 228 [soldier]. Type locality: Haiti. Synonymized by Snyder 1949: 273.

Eutermes (*Eutermes*) *martiniquensis* Holmgren (1910): 238 [soldier, worker; Fig. 25]. Type locality: Lesser Antilles: Martinique. Synonymized by Banks 1919: 486 with *N. morio* and by Emerson (1925) with *Nasutitermes* (*Nasutitermes*) *costalis*: 379.

Eutermes (*Eutermes*) *sanchezi* Holmgren (1910): 236 [soldier; Fig. 23]. Type locality: Haiti. Synonymized by Emerson 1925: 379.

Eutermes (*Eutermes*) *sanctae-luciae* Holmgren (1910): 226 [soldier, worker; Fig. 17]. Type locality: Lesser Antilles: St. Lucia. Synonymized by Banks (1919): 486 with *N. morio* and by Emerson (1925) with *Nasutitermes* (*Nasutitermes*) *costalis*: 379.

Nasutitermes morio; Banks (1918): 665; 1919: 482, 486; in Banks and Snyder (1920) [comparisons of imago, soldier; i.e., generic reassignment of *Termes morio* Latreille, 1805]. Synonymized by Emerson (1925) with *Nasutitermes* (*Nasutitermes*) *costalis*: 379.

Nasutitermes sanchezi; Banks (1919): 487 [imago, soldier; i.e., generic reassignment of *Eutermes* (*Eutermes*) *sanchezi* Holmgren (1910)]. Synonymized by Emerson (1925): 379.

The Emerson (1925) redescription of *N. costalis*, now assigned to *N. corniger*, is adequate for both soldier and imago castes and needs no revision. Measurements of the following material are in Tables 1 and 2 for soldiers and imagos, respectively.

Material Examined and Measured. HOLOTYPE of *N. costalis*, TRINIDAD: 10.66° N, 61.40° W; C. Gagzo; 13-VII-1906; N. Holmgren (Holmgren 1906); 1 alate. FLORIDA: Fort Lauderdale; 26.067° N, 80.171° W; RS; 13-V-2002; 1 alate, 1 soldier (FL991). MEXICO: Chiapas, Palenque ruins; 17.449° N, 92.104° W; T. G. Myles and D. A. Muruvanda; 14-I-1997; 1 soldier (MX20). Coba; 20.489° N, 87.735° W; JC and JM; 17-I-1993; 1 soldier (MX 488). BELIZE: Rio Bravo conservation area; 17.837° N, 89.019° W; L. R. Davis Jr.; 3-IV-1997; 1 soldier (BZ 48). HONDURAS: San Pedro Sula, 3,000-ft elevation; 15.50° N, 88.05° W; J. Chapman; 23-I-2002; 1

Table 2. Measurements of *N. corniger* alates

Measurement (mm)	Male ($n = 19$ from 16 colonies)		Female ($n = 19$ from 13 colonies)		Holotype
	Range	Mean ± SD	Range	Mean ± SD	
Head length with labrum	1.42–1.64	1.55 ± 0.045	1.49–1.81	1.62 ± 0.065	1.64
Head length to postclypeus	0.88–1.03	0.96 ± 0.038	0.93–1.06	1.01 ± 0.037	1.05
Maximum head width at eyes	1.34–1.47	1.39 ± 0.040	1.35–1.57	1.42 ± 0.060	1.37
Head ht, excluding postmentum	0.57–0.65	0.62 ± 0.022	0.59–0.72	0.65 ± 0.029	0.65
Maximum eye diam	0.32–0.41	0.35 ± 0.022	0.33–0.41	0.36 ± 0.025	0.34
Minimum distance, eye to head base	0.11–0.14	0.13 ± 0.010	0.11–0.16	0.13 ± 0.013	0.14
Maximum ocellus diam	0.09–0.17	0.12 ± 0.024	0.09–0.17	0.12 ± 0.022	0.12
Eye to ocellus distance	0.11–0.19	0.15 ± 0.020	0.11–0.19	0.16 ± 0.020	0.16
Maximum pronotum length	0.62–0.72	0.68 ± 0.027	0.65–0.78	0.73 ± 0.035	0.74
Pronotum width	1.05–1.19	1.12 ± 0.040	1.10–1.36	1.20 ± 0.061	1.18
Total length with wings	12.10–13.43	12.66 ± 0.46	12.37–15.83	13.74 ± 0.90	13.03
Total length without wings	5.85–7.45	6.81 ± 0.45	6.92–8.65	7.49 ± 0.47	6.92
Fore wing length to suture	9.44–11.04	10.23 ± 0.46	9.98–12.77	11.19 ± 0.81	10.91
Fore wing max width	2.77–3.23	2.98 ± 0.15	2.77–3.53	3.12 ± 0.19	3.10
Hind tibia length	1.49–1.67	1.58 ± 0.048	1.44–1.68	1.56 ± 0.067	1.55

Alates males (m) and females (f) measured originated from same colony each unless noted otherwise: Trinidad (holotype f), USA, Florida (m), Costa Rica (f), Panama (m and f from two colonies), Cuba (m and f), Jamaica (m and f), Turks and Caicos (f), Dominican Republic (m and f), Puerto Rico (f), Vieques (m), St. Croix (USVI) (f), Tortola (BVI) (m), Antigua (two m and two f), Guadeloupe (Basse-Terre) (m and f), Dominica (m and f), Martinique (m), St. Lucia (f), St. Vincent (m), Grenada (two m and two f), Trinidad (m and f), Tobago (m), Venezuela (m), Surinam (m and f from two colonies), and Brazil (f).

soldier (CTA62). COSTA RICA: Palo Verde; 10.44° N, 85.30° W; RC; 5-VI-1993; 1 alate, 1 soldier (RC collection #129). NICARAGUA: Managua, Casa Grande; 12.132° N, 86.309° W; J. Nixon; 7-V-2003; 1 soldier (CTA 77). PANAMA: La Jagua Hunting club, 6 mi. SE Pacora; 9.13° N, 79.22° W; A. Emerson; 26-V-1935; 1 alate, 1 soldier (Emerson collection #87). Bocas del Toro Changuinola; 9.32° N, 82.26° W; G. B. Edwards; 29-VI-1981; 1 alate (CTA21). CUBA: La Habana, Marianao; 23.07° N, 82.41° W; JK; 30-V-1972; 2 alates, 1 soldier (CU431). JAMAICA: 0.7 mi. N. Whitehall; 18.307° N, 76.884° W; BM, JC, JK, JM, PB, and Y. Roisin; 26-V-1997; 2 alates, 1 soldier (JA267). TURKS and CAICOS: Providenciales, Doc Withie Apts., Leeward Hwy and Susie Turn; 21.79° N, 72.17° W; B. Diehl; 20-VIII-1990; 1 alate, 1 soldier (TC61). DOMINICAN REPUBLIC: Samana Prov., Las Garitas; 19.221° N, 69.529° W; JC, JK; 9-XI-1996; 2 alates, 1 soldier (DR1509). PUERTO RICO: Hwy 115 and 2; 18.283° N, 67.167° W; JC, JM, RS, JR; 3-VI-1993; 1 alate, 1 soldier (PR253). Vieques, NW coast; 18.125° N, 65.531° W; BM, JC, RS; 20-VII-1999; 1 alate, 1 soldier (PR584). U.S. VIRGIN ISLANDS: St. Croix, Creque Damn; 17.76° N, 64.88° W; PB; 29-VI-1994; 1 alate, 1 soldier (VI25). BRITISH VIRGIN ISLANDS: Tortola, Sage Mountains; 18.25° N, 64.39° W; JK; 23-X-1992; 1 alate, 1 soldier (VI504). ANTIGUA: Seatons; 17.079° N, 61.765° W; BM, JC; 27-VIII-1998; 4 alates, 1 soldier (ANB137). GUADELOUPE: Basse-Terre, Trace Merwart above Vernou; 16.167° N, 61.664° W; BM, JC, JK, JM, RS; 29-V-1999; 2 alates, 1 soldier (GU789). DOMINICA: St. Andrew, Crompton Point; 15.58° N, 61.32° W; JC, JK, JM, RS; 29-V-1994; 2 alates, 1 soldier (DM69). MARTINIQUE: Sud Atlantique, Grde. Anse des Salines; 14.41° N, 69.53° W; JC, JK, JM, RS; 2-VI-1994; 1 alate, 1 soldier (MA98). ST. LUCIA: Vigie Airport; 14.021° N, 60.996° W; BM, JC, JK, JM, RS; 27-V-1998; 1 alate, 1 soldier (STL41). ST. VINCENT: Fancy (end of the road); 13.380° N, 61.171° W; BM, JK, JM; 24-V-1998; 1 alate, 1 soldier (STV52). GRENADA: St. George's at lights; 12.050° N, 61.750° W; C. Starr; 8-VI-1996; 4 alates, 1 soldier (GR135). TRINIDAD and TOBAGO: Tobago: Granby Point at coast; 11.188° N, 60.658° W; JC, JK, JM, RS; 31-V-1996; 1 alate, 1 soldier (TT658). Trinidad: Mt. St. Benedict foothills, forest trail; 10.664° N, 61.399° W; BM, JC, JK, JM, RS; 26-V-1996; 2 alates, 1 soldier (TT99). VENEZUELA: Aragua State, Maracay, Zona Industrial de Santa Cruz; 10.30° N, 67.89° W; O. Cardenas; 26-IV-2001; 1 alate, 1 soldier (SA221). GUYANA: Interior; 6.47° N, 58.28° W; E. Maharajh; 4-X-1997; 1 soldier (SA78). SURINAME: Paramaribo; 5.86° N, 55.15° W; C. deHaas; 13-VI-1992; 1 alate, 1 soldier (SA14). Ibid; 1 alate (SA23). BRAZIL: Indiaporã; 19.98° S, 50.14° W; C. Dietrich; 20-X-1998; 1 alate, 1 soldier (RCc #920). BOLIVIA: Santa Cruz; 17.80° S, 63.17° W; Helm; III-1997; 1 soldier (SA87). PERU: Loreto Prov., Iquitos, Quistococha; 3.65° S, 73.27° W; JK; 8-VI-1981; 1 soldier (SA249). ECUADOR: Archdonia; 1.90° S, 77.83° W; D. Holsappel; 1-IV-1999; 1 soldier (SA168).

Genetic Analysis. DNA was extracted from four *N. ephratae* (Holmgren), one *N. guayanae* (Holmgren), one *N. nigriceps* (Haldeman), one *N. rippertii* (Rambur), and nine *N. costalis/corniger* samples from the Dominican Republic, Dominica, Nevis, Guadeloupe, Puerto Rico, Mexico, Ecuador, Suriname, and Jamaica per Szalanski et al. (2004). Polymerase chain reaction (PCR) was applied using the primers LR-J-13007 (5′-TTACGCTGTTATCCCTAA-3′) (Kambhampati and Smith 1995) and LR-N-13398 (5′-CGCCTGTTTATCAAAAACAT-3′) (Simon et al. 1994). These PCR primers amplify an ≈428-bp region of the mtDNA 16S rRNA gene. PCR reactions were conducted using 1 μl of the extracted DNA per (Szalanski et al. 2000), with a profile consisting of 35 cycles of 94°C for 45 s, 46°C for 45 s, and 72°c for 45 s. Amplified DNA from individual termites was purified and concentrated using Microcon-PCR Filter Units (Millipore, Bedford, MA). Samples were sent to University of Arkansas Medical Sciences DNA Sequencing Core Facility (Little Rock, AR) for direct sequencing in both directions using an ABI Prism 377 DNA sequencer (Applied Biosystems Inc., Foster City, CA). GenBank accession numbers for the *Nasutitermes* termites subjected to DNA sequencing in this study are AY623085 to AY623100. Consensus sequences for each sample were obtained using BioEdit 5.09 (Hall 1999). The position of variable nucleotide sites among the DNA sequences was obtained using MacClade version 4 (Sinauer Associates, Sunderland, MA).

The distance matrix option of PAUP* 4.0b10 (Swofford 2001) was used to calculate genetic distances according to the Kimura two-parameter model (Kimura 1980) of sequence evolution. Mitochondrial DNA sequence of *N. acajutlae* (Holmgren) (Kambhampati et al. 1996) was included for phylogenetic analysis, along with mtDNA 16S sequences for *N. triodiae* (Froggatt), *N. magnus* (Froggatt), *N. walkeri* (Hill), *N. exitiosus* (Hill), *N. princeps* (Desneux), *N. bikpelanus* Roisin & Pasteels, and *N. pinocchio* Roisin & Pasteels from Miura et al. (2000). *Longipeditermes longipes* (Haviland) and *Hospitalitermes medioflavus* (Holmgren) (Termitidae: Nasutitermitinae) sequences from Miura et al. (2000) were used as the outgroup taxa for the *Nasutitermes* data set. DNA sequences were aligned using ClustalW (Thompson et al. 1994) and adjusted manually. Unweighted parsimony analysis on the alignments were conducted using PAUP* 4.0b10 (Swofford 2001). Gaps were treated as a fifth character state. The reliability of trees was tested with a bootstrap test (Felsenstein 1985). Parsimony bootstrap analysis included 1,000 resamplings by using the Branch and Bound algorithm of PAUP*.

Results and Discussion

Morphology. As might be expected from such a broadly distributed species, *N. corniger* shows some variability in coloration, dimensions, and morphology of the soldier and imago (Figs. 2 and 3). Variability among *N. costalis* samples from the West Indies and northeastern South America was originally addressed by (Banks 1919) and (Emerson 1925). Additional variability in coloration may be attributed to sample age and storage conditions. *N. corniger* soldiers (Table 1)

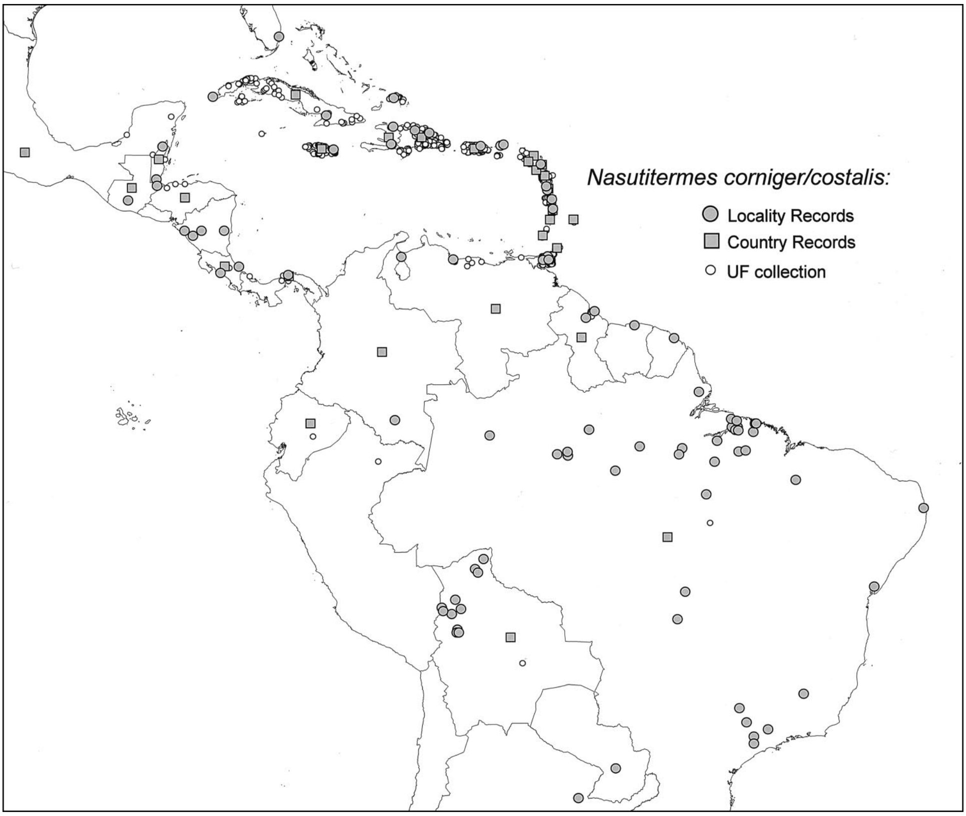

Fig. 1. New World collection sites of *N. corniger* from current study (UF collection), and previously published locality and country records cited in text. Country records do not mark a specific locality.

yielded a distinct continuous range of measurements, particularly in maximum of head width (60% difference between maximum and minimum), nasus width at base (40%), pronotum maximum width and length (48 and 63%), hind tibia length (50%), and in total length (84%). Consistent characters included pilosity of head capsule and abdominal tergites.

The winged imagos (Table 2), including both genders, showed the largest variation range in measurements of the eyes and ocelli, where the greatest variability occurred in the ratio for the distance between the eye and ocellus and the ocellus diameter. Except for the expected variability in total body length, all remaining characters had relatively congruent measurements. Banks (1918, 1919) considered the eye and ocelli measurements and the distance between them as species-specific characters but did not discuss intraspecific or intergender variability.

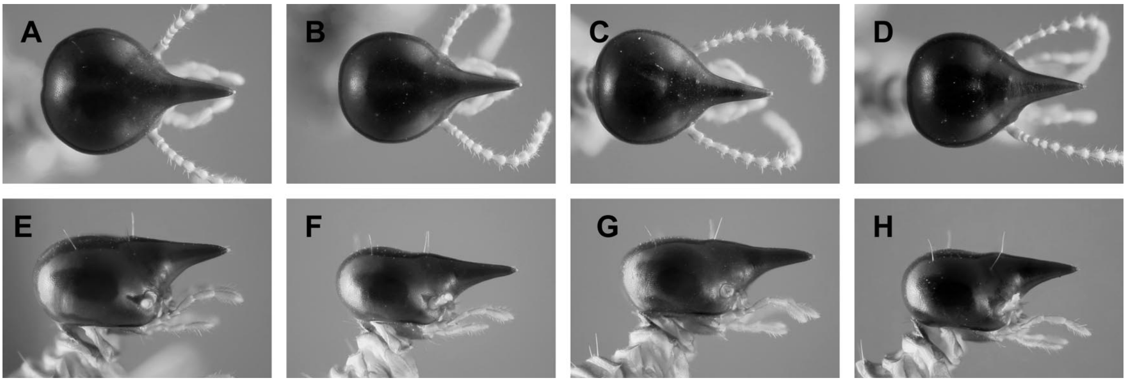

Fig. 2. Photomicrographs of dorsal (A–D) and lateral (E–H) views of *N. corniger* soldier head capsules from Dominican Republic, Mexico, Venezuela, and Trinidad, respectively.

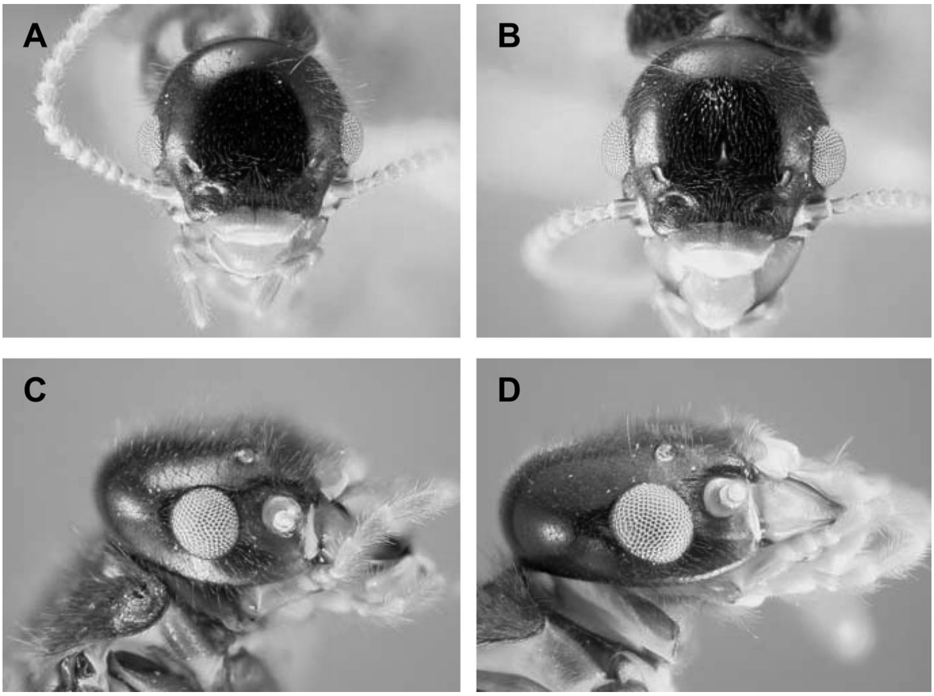

Fig. 3. Photomicrographs of dorsal (A and B) and lateral (C and D) views of *N. corniger* imagos from Guadeloupe and Costa Rica, respectively.

Female measurements are typically larger than males. The fore wing of females is ≈35% longer than that of the males. Although minimum intergender measurements are nearly equivalent or very slightly larger in females, the maximum values are considerably greater in females. The hind tibia length seems to be congruent in both genders with ranges of 1.49–1.67 and 1.44–1.68 mm, respectively, for males and females. Soldiers and imagos from Florida are consistently smaller than conspecifics from other geographies.

Genetic Analysis. The 428-bp region of the mtDNA 16S rRNA gene was subjected to DNA sequencing from nine *N. costalis/corniger* and 12 other *Nasutitermes* taxa (Fig. 4). Among the nine *N. costalis/corniger* DNA sequences, 13 nucleotides were variable and genetic diversity ranged from 0.0% between the Guadeloupe and Nevis samples to 1.8% between the Jamaica and Nevis samples. To facilitate analysis with the DNA sequences from Miura et al. (2000), 17 bp at the 5′ end of our DNA sequences were excluded for phylogenetic analysis. The aligned DNA data matrix, which included 14 *Nasutitermes* taxa as well as the two outgroup taxa, resulted in a total of 421 characters. Of these characters, 111 (26%) were variable and 63 (15%) were phylogenetically informative. This data set had only one most parsimonious tree (Fig. 4) (length = 266, CI = 0.594), as documented using the Branch and Bound search algorithm of PAUP*. Bootstrap analysis of the aligned *Nasutitermes* taxa revealed that *N. costalis/corniger* was monophyletic. Within the *N. costalis/corniger* clade, *N. costalis* from Nevis and Guadeloupe formed a common clade. Relative to *N. costalis/corniger, N. ephratae* was the most similar taxon genetically as well as morphologically.

Geographical Distribution. *N. corniger* occurs over a north-south distance of >6,000 km; from southern Mexico to southern Brazil and northern Argentina, including the West Indies, and much of the region except Chile, Uruguay, and the Bahamas (Fig. 1). There is one introduced population in southeastern Florida (Scheffrahn et al. 2002) currently under an eradication effort. The geographical list includes: Antigua, Argentina, Barbados, Belize, Bolivia, Brazil, Chacachacare Island (Trinidad and Tobago), Costa Rica, Cuba, Dominica, Dominican Republic, East Caicos, Ecuador, FL (USA), French Guyana, Grand Cayman, Grenada, Guadeloupe (Basse-, Grande-Terre), Guana (BVI), Guatemala, Guyana, Haiti, Honduras, Huevos (Trinidad and Tobago), Isla de la Juventud (Cuba), Jamaica, La Desirade (Guadeloupe), Little Tobago (Trinidad and Tobago), Marie Galant (Guadeloupe), Martinique, Mexico, Middle Caicos, Monos Is. (Trinidad and Tobago), Montserrat, Nevis, Nicaragua, North Caicos, Panama, Papua New Guinea, Peru, Providenciales (Turks and Caicos), Puerto Rico, Saba, Saona (Dominican Republic), South Caicos, St. Barthelemy, St. Croix, St. Eustatius, St. Kitts, St. Lucia, St. Martin, St. Vincent, Surinam, Tobago, Tortola (BVI), Trinidad, West Caicos, Union Is. (St. Vincent), Venezuela, and Vieques (Puerto Rico), respectively. Voucher material is housed in the University of Florida of Florida Termite Collection at the Ft. Lauderdale Research and Education Center.

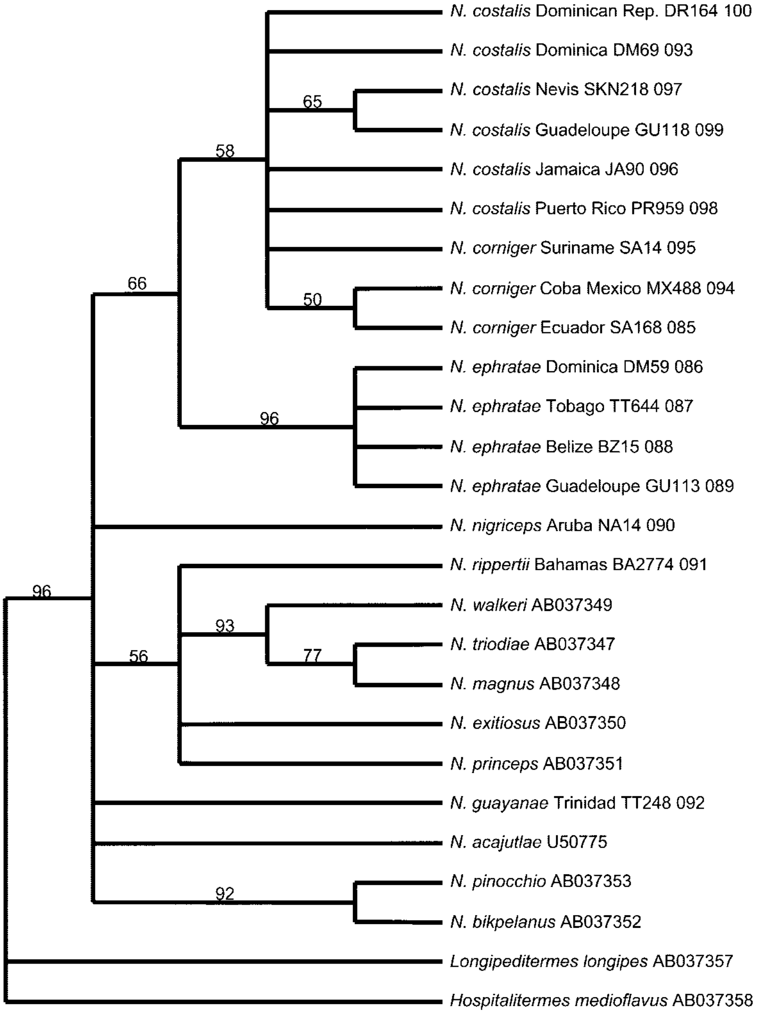

Fig. 4. Single most parsimonious tree during a branch and bound search using PAUP* (Swofford 2001). Bootstrap values for 1000 replicates are listed above the branches supported at ≥50%. University of Florida code and last three digits of GenBank accession numbers given for samples sequenced in this study. Full GenBank accession numbers provided for all others.

The merger of *N. costalis* with *N. corniger* resolves a conundrum that has perpetuated over nearly a century of provincial taxonomic conclusions. These practices lead to a common habit of assigning names based primarily on geography. If a specimen fitting (Emerson's 1925) description of *N. costalis* originated from the West Indies, then *N. costalis* was the favored name; if from the mainland, typically *N. corniger* was used. In fact Haverty et al. (1990) conceded that identification between these two species was "impossible without locality information." Because both names, *N. corniger* and *N. costalis,* have been used extensively over the last century, the "Principle of Priority" (Article 23, International Commission on Zoological Nomenclature 1999 is invoked. In doing so, the senior synonym, *N. corniger,* becomes the valid name of this species.

N. corniger is arguably the most common, least cryptic, and widespread species in the Neotropics, and further synonymy into this species could elevate its dominance even more. Constantino (2002a) and Mathews (1977) together list three additional *Nasutitermes* spp. that may be candidates for synonymy with *N. corniger,* including *N. tatarendae* (Holmgren 1910) from Bolivia and Brazil, *N. araujoi* (Roonwal and Rathore 1976) from Brazil, and *N. globiceps* (Holmgren 1910) from Paraguay. Ultimately, a generic revision of New World *Nasutitermes* is needed to elucidate the composition of this difficult genus, but it also represents a daunting and complex task.

Because the identity of the original type species for *Nasutitermes, N. morio* (Latreille), was in doubt, Emerson (1925) designated *N. costalis* as type species. Of the many synonyms of Holmgren (1910), Emerson 1925) selected *N. costalis* because he had the greatest confidence in its identity. Constantino (2002b) concluded that criteria of Emerson (1925)*N. costalis* as type species were incorrect but that he coincidentally chose a valid name from the first group of original names given by Banks (1918). As it turns out, *N. corniger* was likely the species that Dudley and Beaumont (1890) had studied in Panama as the basis for describing the genus *Nasutitermes* (Constantino 2002b).

N. corniger is highly adaptable to colonization of contrasting habitats in urban, agricultural, and natural environments. In the Greater Antilles, for example, this termite can be found in very dry and exposed coastal localities as well as in rain forests at elevations of up to 1000 m (R.H.S., unpublished observation). In Florida, we have observed *N. corniger* populations engulfing foraging territories occupied by *Reticulitermes* spp. and effectively warding off predation by ants, including dense populations of *Pheidole megacephala* (F.). *N. corniger* consumes wood of almost any form, including hardwoods and softwoods that are dry, wet, or partially decayed. It attacks dead twigs and branches in trees; tree stumps; wood debris on the ground; and structural wood, including framing, plywood, pressboard, hardwood handles, bamboo, wooden artwork, and fences. Nests are highly visible wherever this species occurs and, as they age, nests grow in volume and in number of connected carton satellites. Nests, composed mostly of friable feces, are generally ovoid and grow by sprouting new lobes. Thorne (1980) reported a nest of *N. corniger* in Panama being 68 cm in length and weighing 28 kg. Nests may be constructed high in trees or structures, bases of tree trunks, or occasionally on the open soil. In urban areas, nests also are built in building voids such as attics. According to Krecek (1969), nest sites may be dictated by moisture requirements. Nest structures are usually polycalic (Thorne 1982a, b; Levings and Adams 1984) and may contain either single reproductive pairs or multiple queens and/or kings (Krecek 1970, Thorne 1984). Mobility among queens and kings within the original nest and adjoining nest structures is remarkably agile for a higher termite (J.K., unpublished observation). Colonies of *N. corniger* produce multiple, crepuscular dispersal flights over the rainy season (May–November) that usually commence after precipitation (J.K. and R.H.S., unpublished observations).

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