

Taxonomy and Biogeography of *Nasutitermes acajutlae* and *N. nigriceps* (Isoptera: Termitidae) in the Caribbean and Central America

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ABSTRACT The Neotropical termites *Nasutitermes acajutlae* (Holmgren) and *N. nigriceps* (Haldeman) are resurrected as discrete morphological species based on three diagnostic characters of the soldier caste. No consistent differences in alate morphology or in nest architecture have been identified. Based on current sampling, separation of the two species on the basis of cuticular hydrocarbon profiles of workers is equivocal. The known distributions of *N. acajutlae* and *N. nigriceps* are allopatric and consistent with current understandings of the biogeography of the Caribbean islands and Central America.

KEY WORDS *Nasutitermes*, nest architecture, cuticular hydrocarbons

THE *Nasutitermes nigriceps* complex comprises one of the most conspicuous groups of termites in Central America and much of the Caribbean, reportedly ranging into northern South America and Brazil (Emerson 1925, Snyder 1949, Araujo 1977, Mathews 1977). These termites build arboreal nests that are among the largest built by *Nasutitermes* in the Neotropics (maximal recorded measurements close to 2 m in height and >1 m in girth [B.L.T., personal observation]). The termites inhabit lowland and montane forests, mangroves, and occur commonly, but not exclusively, in relatively drier or exposed areas. In their habitats, colonies of these species are numerically and ecologically conspicuous. Their ability to withstand dry conditions coupled with facultative food storage (in the form of nest nodules) may explain the success of these termites even in exposed or marginal habitats.

Morphological variation within this group has long been a source of confusion, but it has been difficult to resolve whether the variation reflected a geographic cline or true species differences. Examination of museum specimens and new collections from the Caribbean and Central America has enabled us to expose a biogeographical pattern within the *N. nigriceps* complex and to divide the group into two species, *N. nigriceps* (Haldeman) and *N. acajutlae* (Holmgren), based on consistent morphological characters.

Taxonomic History. Haldeman's (1853) original description of *Termes nigriceps* from western

Mexico is brief and vague. He expressed uncertainty about whether or not he examined a soldier within the sample. The species description was elaborated extensively by Light (1933) based on specimens from three localities in Mexico. The type material for this species has not been located. Light did not refer to seeing the type specimens. Snyder (1949) does not give the location of the type material. Araujo (1977) states that the type is in the collection of Franklin & Marshall College (presumably the North Museum), Lancaster, PA, but, if so, the curators cannot locate it.

Nasutitermes acajutlae was originally described (as *Eutermes*) by Holmgren (1910) based on specimens from Acajutla, San Salvador; Bahamas (alate); and from St. Thomas, U.S. Virgin Islands (one soldier, one worker, and one alate). Both groups of specimens are labeled as COTYPES; both are in the American Museum of Natural History (AMNH) collection.

Holmgren's assignments regarding *N. acajutlae* have been questioned, and much material from the Caribbean has been grouped with *N. nigriceps*. Banks (1919) commented that the *N. acajutlae* alate, which Holmgren described from San Salvador, is probably *N. rippertii* (Rambur) (originally described by Rambur ([1842]; redescribed by Silvestri [1903]). Banks (1919) described a new species, *N. creolina*, based on alates from the island of Montserrat, now in the Museum of Comparative Zoology (MCZ TYPE 10078) that he considered to represent the adult of *N. creolina*, and soldiers from Trinidad (labeled "paratype", but also containing an MCZ TYPE 10078 label). Emerson (1925) notes that Banks' Montserrat alate does not belong with the

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List 1. Collection locations of material examined for this study

Type material
<i>Eutermes acajutlae</i> COTYPE Acajutla, San Salvador (AMNH)
<i>Eutermes acajutlae</i> COTYPE St. Thomas, U.S. Virgin Islands (AMNH)
<i>Eutermes guatemalae</i> COTYPE San Jose, Guatemala (AMNH)
<i>Eutermes pacificus</i> COTYPE W. coast of South or Central America (AMNH)
<i>Eutermes pilifrons</i> COTYPE Bogota, Colombia (AMNH)
<i>Eutermes pilifrons</i> COTYPE Curacao, Dutch West Indies (AMNH)
<i>Nasutitermes creolina</i> TYPE Montserrat, West Indies (MCZ TYPE 10078)
<i>Nasutitermes creolina</i> PARATYPE Trinidad (MCZ TYPE 10078)
Other specimens ^a
Belize: Boca del Rio on Ambergris Caye
Brazil: Recife, Pernambuco
British Virgin Islands: Anegada, Beef Island (2), Cooper, Eustatia, George Dog (3), Great Camino, Great Thatch, Great Tobago, Guana Island (17), Jost van Dyke (2), Little Camino, Necker, Peter, Scrub, Thatch, Tortola (6), Virgin Gorda
Costa Rica: Guanacaste (6)
Grand Cayman Island: Boddentown, Booby Cay, Canaan Land (2)
Jamaica: Dromilly (4), nr. Constant Springs, Kingston, Priory (9), St. Amis
Mexico: Acapulco (3), Campache, Colima, Guerro, Jalisco (3)
Nicaragua: Leon (4)
Panama: Barro Colorado Island (4), Frijoles, Galeta (7)
Puerto Rico: Isla Maguëyes (2), Guanica, La Parguera (3)
Trinidad: Valencia
Turks and Caicos Islands: Providenciales Island (2)
United States Virgin Islands: St. Croix (5), St. Johns (14), St. Thomas

^a If material was available from more than one colony per location, the number of colony samples examined is shown in parentheses.

soldier; Snyder (1949) and Araujo (1977) identify the Montserrat alate as *N. ephratae* (Holmgren). Emerson (1925) synonymized *N. creolina* Banks (1919) with *N. acajutlae* based on identity of soldier morphology. *N. creolina* Banks (Trinidad soldiers only) was synonymized with *N. nigriceps* by Snyder (1949).

Emerson (1925) expanded Holmgren's description of *E. (Nasutitermes) acajutlae* based on specimens from three locations in British Guiana (now Guyana) (one queen, no alates, many soldiers) and from St. Croix and St. Thomas, U.S. Virgin Islands (three queens, no alates, many soldiers). Emerson (1925) does not address Banks' (1919) note that Holmgren's *N. acajutlae* alate from San Salvador may be *N. rippertii*. In his listing of the termites of the world, Snyder (1949) synonymized *N. acajutlae* (Holmgren) with *N. nigriceps* (Haldeman).

In this article, we present evidence that Snyder's synonymy of *N. acajutlae* as *N. nigriceps* was not justified. We resurrect the name *N. acajutlae* (Holmgren) for the species occurring in the Lesser Antilles from Puerto Rico east and south to Trinidad (not recorded from all intervening islands), into Guyana and possibly other locations in South America. *N. nigriceps sens. str.* occurs on Jamaica and the Cayman Islands, as well as Mexico south to at least Panama. A discussion of Caribbean biogeography renders this pattern of distribution consistent with the historical geography of the region.

Materials and Methods

Morphological Separation of *N. acajutlae* and *N. nigriceps*. Collection locations of material ex-

amined for this report are listed in List 1. All or most of the nontype material from each country was relatively fresh (collected by ourselves or colleagues within the past 6 yr), except for the material from Brazil and Mexico (collected >20 yr ago). All specimens were examined with a light microscope. Structures on a series of freeze-dried specimens from Panama, Mexico, Jamaica, St. Croix, St. Johns, Puerto Rico, and Guana Island were examined using scanning electron microscopy.

Voucher specimens are deposited at the United States National Museum, Smithsonian Institution, Washington, DC.

Nest Architecture. Arboreal carton nests of both *N. acajutlae* and *N. nigriceps* were examined externally when collections of termites were taken. In Panama, eight *N. nigriceps* nests were completely or substantially dissected by B.L.T. In large nests of both species the central region can be extremely hard, preventing complete dissection of those galleries and the royal cell. Nests on Jamaica, the Cayman Islands, Puerto Rico, the U.S. Virgin Islands, and the British Virgin Islands were examined externally, and often the outer layers of carton were shaved with a saw or a machete to expose a portion of the gallery system. Three *N. acajutlae* nests on Guana Island were completely dissected.

Cuticular Hydrocarbon Phenotypes of *N. acajutlae* and *N. nigriceps*. Samples of *N. acajutlae* and *N. nigriceps* were gathered along with collections of many other species of termites during an ongoing study of the chemotaxonomy of tropical termites. Occasionally, samples were collected by associates who encountered one of

these two species while conducting field work for other projects.

All collections reported in this article were taken from arboreal nests. The usual method was to make a tangential slice in the nest, then return the nest material and termites to a laboratory to remove the termites. Termites were separated from carton and other debris either directly with forceps or indirectly by placing wet paper towels over the carton to attract the termites. Samples of at least 100 workers were placed in vials and dried over an incandescent light. Termites were dried while alive and for an additional 8–10 h after they died. Voucher specimens from each colony, consisting of each caste present, were preserved in 85% ethanol; samples are kept at the University of Maryland, the Smithsonian Institution, or the Pacific Southwest Research Station in Albany, CA. Dried samples were shipped to the Pacific Southwest Research Station in Albany for characterization of the cuticular hydrocarbons. Dried samples were held at ambient temperature until they were extracted.

Detailed descriptions of extraction procedures for specific termite species have been published elsewhere (Haverty et al. 1988, 1990a, b). Dried termite samples were transferred to clean 20-ml vials and immersed in 10 ml of *n*-hexane for 10 min. The resulting extract of cuticular lipids was pipetted through 4 cm of activated Biosil A in a Pasteur pipet minicolumn to isolate the hydrocarbon components. The hydrocarbon extract was then evaporated to dryness under nitrogen and redissolved in 60 μ l of hexane.

Gas chromatography-mass spectrometry (GC-MS) analyses of the hydrocarbons were performed on a Hewlett-Packard 5890 gas chromatograph equipped with a capillary column (25 m by 0.2 mm i.d., HP-1) and a Hewlett-Packard 5970B mass selective detector. The system was interfaced with HP Chemstation software for data acquisition and analysis. Helium was the carrier gas, column flow was 2 ml/min, and the GC-MS was operated in the split mode with a ratio of 7:1 and a temperature program from 200 to 320°C at 3°C/min with a final isothermal hold of 16 min. Electron impact mass spectra were obtained at 70 eV, and scanning was done from 55 to 640 atomic mass units every 1.0 s. *n*-Alkanes, alkenes, and methyl-branched alkanes were identified by their mass spectral fragmentation patterns (Pomonis et al. 1980, Blomquist et al. 1987) and corroborated by calculating equivalent chain lengths (Jackson & Blomquist 1976).

For this study, comparisons between colonies of the same species, between localities of the same species, or between species was empirical and based on qualitative differences in hydrocarbon components. A more detailed assessment of intra- and interspecific variability of the cuticular hydrocarbons of the *Nasutitermes* from the Caribbean Basin is in progress.

Results and Discussion

Morphological Separation of *N. acajutlae* and *N. nigriceps*. The following are three key morphological characters that distinguish soldiers of *N. acajutlae* from *N. nigriceps*: (1) Pilosity on the soldier head capsule is much denser in *N. acajutlae* (Fig. 1A) than in *N. nigriceps* (Fig. 1B). Bristles are present on the head capsule and nasus of *N. acajutlae* soldiers, whereas they are normally absent from the nasus of *N. nigriceps* soldiers except at the tip. Ventrally, bristles can be seen cresting from the posterior margin in *N. acajutlae*, whereas that margin appears nearly or totally glabrous on *N. nigriceps* soldiers. (2) The anterior margin of the pronotum has a distinct medial indentation in *N. acajutlae* (Fig. 1C) but is more evenly convex with only a minor medial indentation in *N. nigriceps* (Fig. 1D). In some *N. acajutlae* specimens, the pronotum has a more gradually convex anterior margin with a rather weaker median incision but still with a more distinct medial indentation than in *N. nigriceps*. R. Scheffrahn (personal communication) has noted that the pronotum shape of *N. acajutlae* soldier specimens he has examined from Puerto Rico are more variable and often intermediate between the two examples illustrated in Fig. 1 C and D. Pilosity of the pronotum is more conspicuous in both bristle size and number on both the anterior and posterior margins of the pronotum in *N. acajutlae* than in *N. nigriceps*. (3) Bristles are present on the ventral portion of the head capsule of *N. acajutlae* on the regions flanking each side of the postmentum (Fig. 2). These areas are glabrous on *N. nigriceps* soldiers.

Measurements of *N. acajutlae* and *N. nigriceps* soldiers are given in Table 1. Although representative, morphometric ranges should not be considered definitive because *Nasutitermes* soldier size is known to vary within and among colonies and locations. For that reason, no statistical comparisons of morphometric figures are made between the two species based on this small sample size. We consider it risky to use morphometrics as diagnostic characters for soldiers of these two species of *Nasutitermes*.

We have not yet discovered characters that unambiguously separate alates of *N. acajutlae* from *N. nigriceps*, although relatively few specimens were available. Alate measurements (Table 2) should be interpreted with the same caveat as above regarding measurements on soldiers.

Nest Architecture. Nests of *N. acajutlae* and *N. nigriceps* are indistinguishable based on sampling to date. The arboreal nests are usually spherical to ellipsoidal, with the long axis occasionally >2.0 m. The outer envelope is irregularly textured with bumps and drip formations. A thin carton layer covers interior galleries, whose walls gradually increase in thickness from the periphery to the center. The center portion of a

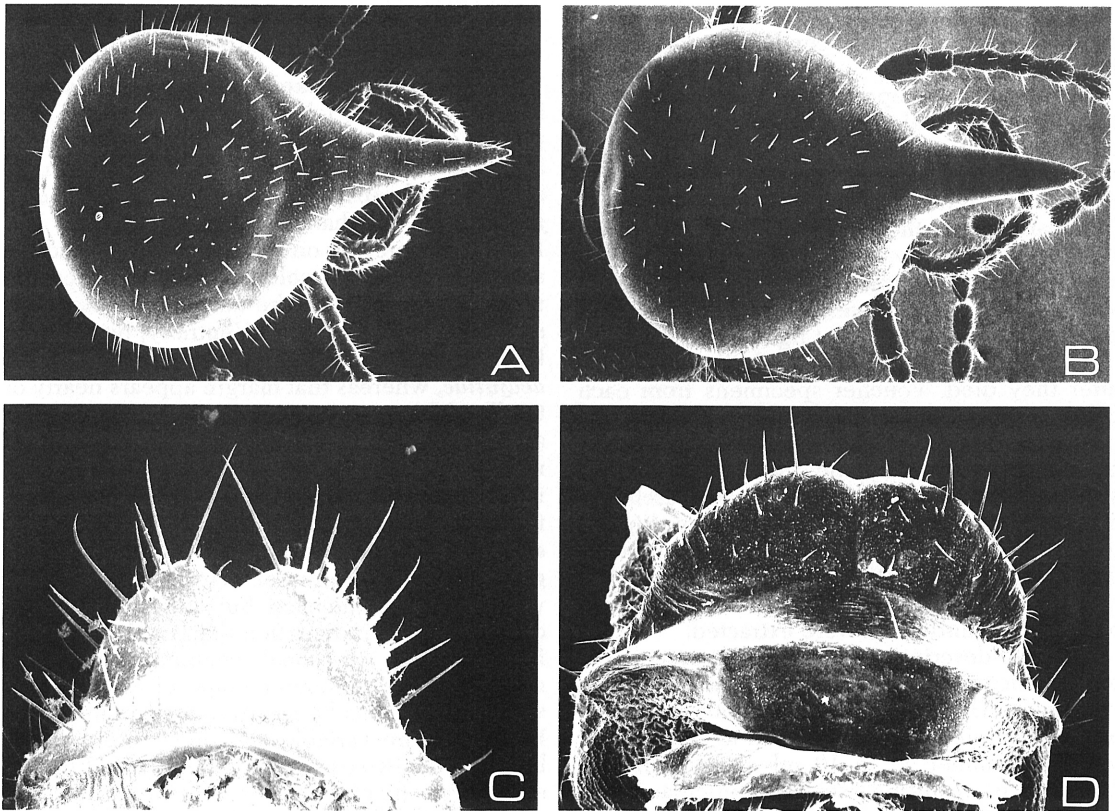


Fig. 1. (A) Soldier head capsule, *N. acajutlae*. (57 $\times$; coll. S. C. Briscoe, St. Johns, U.S. Virgin Islands). (B) Soldier head capsule, *N. nigriceps* (61 $\times$; Acapulco, Mexico, collection of C. H. Seevers, det. A. E. Emerson, AMNH collection). (C) Soldier pronotum, *N. acajutlae*. (166 $\times$, coll. B.L.T., St. Croix, U.S. Virgin Islands). (D) Soldier pronotum, *N. nigriceps*. (168 $\times$, coll. B.L.T., Priory, Jamaica).

mature nest is typically built of very dense carton, with walls of 1–2 cm between galleries. The royal chamber is positioned in this hard central nest core, often adjacent to the origin of forking branches on the host tree.

On Virgin Gorda, British Virgin Islands, *N. acajutlae* has been observed nesting under large rocks in areas where real estate development has reduced available trees and where aggressive control measures are directed at exposed nests.

A unique and distinctive feature of some *N. acajutlae* and *N. nigriceps* nests is the inclusion of spherical *nodules*, first described from nests of *N. nigriceps* in Jamaica by Hubbard (1877). The nodules differ in color and composition from the other nest carton and are embedded in the normal carton matrix within the nest. They apparently function as food reserves, and frequently house clusters of immature termites (Hubbard 1877, Andrews 1911). These nodules will be considered in further detail in a subsequent article.

In general, nests of *N. acajutlae* and *N. nigriceps* resemble each other closely and are readily distinguished from mature nests of other common arboreal *Nasutitermes* species inhabiting the same locality. Mature *N. acajutlae* and *N.*

nigriceps nests are larger than any sympatric congeners and also differ in external appearance. *N. rippertii* builds very large nests (>2 m in height) in the Bahamas (R. Scheffrahn, personal communication), but this species is not known to be sympatric with either *N. acajutlae* or *N. nigriceps*. *N. ephratae* builds regularly spherical or ellipsoidal nests with a smooth shell covering a hard outer gallery layer (Thorne 1980). *N. costalis* and *N. corniger* nest exteriors have a regular texture of small bumps (Thorne 1980), contrasted with the frequently irregular or more exaggerated bumps of an *N. acajutlae* or *N. nigriceps* nest shell.

Cuticular Hydrocarbon Phenotypes of *N. acajutlae* and *N. nigriceps*. We characterized the cuticular hydrocarbons of collections of *N. acajutlae* and *N. nigriceps* (Fig. 3) to see if chemotaxonomic characters, which have proved useful in resolving taxonomic problems of other termite groups, might be helpful in this case. Cuticular hydrocarbons effectively separate at least some other species of *Nasutitermes* from the Caribbean Basin (*N. costalis* and *N. ephratae* [Haverty et al. 1990b, 1992]), as well as subspecies (or sibling species) of the Pacific dampwood ter-

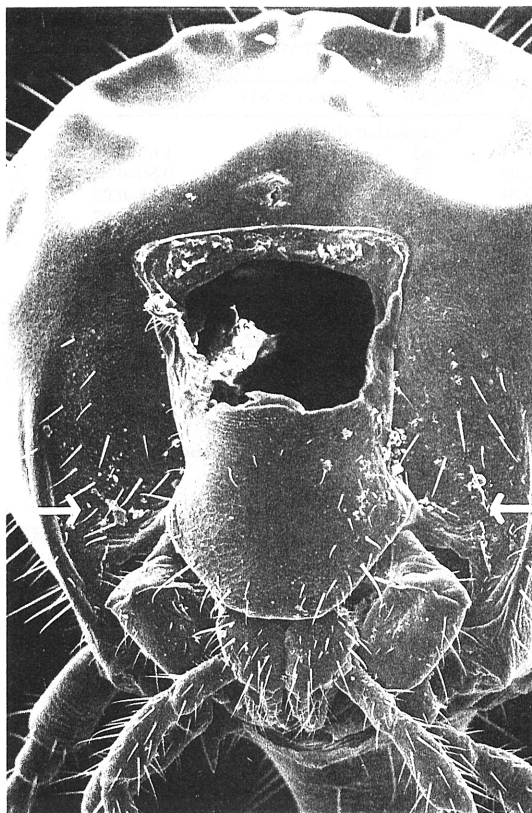


Fig. 2. Ventral view of soldier head capsule, *N. acajutlae* (100 $\times$; coll. by S. C. Briscoe, St. John, U.S. Virgin Islands). Note bristles on each side of the postmentum (arrows). These are absent in *N. nigriceps*.

mites, *Zootermopsis* (Haverty et al. 1988, Thorne & Haverty 1989, Thorne et al. 1993).

Our preliminary data suggest that species determinations on the basis of cuticular hydrocarbons would be equivocal within the *N. nigriceps* complex. The intraspecific variation in cuticular hydrocarbon mixtures within *N. acajutlae*, even among adjacent colonies on Guana Island, British Virgin Islands, is difficult to explain at this

time (Fig. 3 A and B). We have examined specimens of *N. acajutlae* from many islands in the British Virgin Islands (Fig. 3 C and D), Puerto Rico, and Vieques, and *N. nigriceps* from Panama, Belize, and the Cayman Islands (Fig. 3 E and F). The predominant or abundant hydrocarbons from both species are long-chain alkenes (C39:1, C41:1, and C43:1) (Figs. 3 A–F). Other hydrocarbons, especially those with 23 to 29 carbons, occur sporadically in both species, as do occasional long-chained alkenes (C38:1, C40:1, C42:1, C44:1, C45:1, and C47:1), alkadienes (C39:2, C41:2, C43:2, and C45:2), alkatetraenes (C41:4 and C43:4), and alkapentaenes (C41:5). We found little qualitative variation. Most of the variation between colonies on Guana Island and between colonies from different islands lies in the relative proportions of the predominant peaks. We do not yet know how to interpret this variation.

The cuticular hydrocarbon profile of *N. costalis* (Holmgren), which occurs on many Caribbean islands with either *N. acajutlae* or *N. nigriceps*, is quite different from these latter two species (morphological differences between *N. costalis* and *N. acajutlae*/*N. nigriceps* are distinct as well). Comparison of the hydrocarbon profiles of *N. costalis* (Fig. 3 G and H) with those of *N. acajutlae* and *N. nigriceps* (Fig. 3 A–F) demonstrate a species specificity of these chemotaxonomic characters.

Cuticular lipids affect water conservation in termites (Collins 1969). Both *N. acajutlae* and *N. nigriceps* can live in dry, exposed habitats that are largely inhospitable to other arboreal nasutes. The similarity in the hydrocarbon profiles of *N. acajutlae* and *N. nigriceps* may, at least in part, represent a common adaptation to water retention. Clearly, additional research on the factors affecting cuticular hydrocarbon variation in *N. acajutlae* and *N. nigriceps* is warranted.

Geographic Distribution of *N. acajutlae* and *N. nigriceps*. When soldier morphology is used as the basis for species diagnosis, known records of *N. acajutlae* and *N. nigriceps* show distinct allo-

Table 1. Measurements of *N. acajutlae* and *N. nigriceps* soldiers

Measurement	<i>N. acajutlae</i> soldiers ^a		<i>N. nigriceps</i> soldiers ^b	
	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range
Length of head capsule including nasus, mm	1.74 $\pm$ 0.05	1.66–1.89	1.65 $\pm$ 0.05	1.48–1.74
Length from tip of nasus to anterior margin of postclypeus, mm	0.59 $\pm$ 0.07	0.52–0.67	0.60 $\pm$ 0.04	0.50–0.67
Width of head capsule, mm	1.19 $\pm$ 0.07	1.02–1.42	1.07 $\pm$ 0.05	0.97–1.16
Length of foretibia, mm	1.06 $\pm$ 0.02	0.93–1.14	0.96 $\pm$ 0.04	0.87–1.08
Length of hindtibia, mm	1.47 $\pm$ 0.06	1.33–1.64	1.37 $\pm$ 0.05	1.27–1.48

^a Specimens were from the following localities and 10 individuals were measured from each colony (number of colonies from each location given in parentheses): Guana Island, British Virgin Islands (6); Guanica, Puerto Rico (1); Isla Migueyes, Puerto Rico (1); La Parguera, Puerto Rico (1); St. Croix, U.S. Virgin Islands (3); St. John, U.S. Virgin Islands (3). In total, 150 soldier termites were measured.

^b Specimens were from the following localities and 10 individuals were measured from each colony (number of colonies from each location given in parentheses): Acapulco, Mexico (1); Barro Colorado Island, Panama (2); Canaan Land, Grand Cayman (1); Colima, Mexico (1); Galeta, Panama (3); Jalisco, Mexico (2); Leon, Nicaragua (2); Priory, Jamaica (2); Woodstock, Jamaica (1). In total, 150 soldier termites were measured.

Table 2. Measurements of *N. acajutlae* and *N. nigriceps* female and male alates

Measurement	Female			Male		
	Mean $\pm$ SD	Range	n	Mean $\pm$ SD	Range	n
<i>N. acajutlae</i> alates ^a						
Head width, including eyes, mm	1.63 $\pm$ 0.06	1.50–1.71	25	1.68 $\pm$ 0.03	1.63–1.72	25
Diameter compound eye, mm	0.63 $\pm$ 0.02	0.60–0.65	25	0.63 $\pm$ 0.04	0.60–0.68	25
Maximum ocellus dimension, mm	0.21 $\pm$ 0.02	0.20–0.24	25	0.21 $\pm$ 0.02	0.18–0.22	25
Length of foretibia, mm	1.10 $\pm$ 0.04	1.10–1.21	25	1.15 $\pm$ 0.16	0.83–1.32	25
Length of hindtibia, mm	1.75 $\pm$ 0.05	1.70–1.86	25	1.72 $\pm$ 0.18	1.30–1.90	25
<i>N. nigriceps</i> alates ^b						
Head width, including eyes, mm	1.68 $\pm$ 0.08	1.56–1.82	9	1.72 $\pm$ 0.10	1.56–1.80	7
Diameter compound eye, mm	0.64 $\pm$ 0.04	0.57–0.72	9	0.65 $\pm$ 0.04	0.60–0.73	7
Maximum ocellus dimension, mm	0.17 $\pm$ 0.02	0.15–0.20	9	0.17 $\pm$ 0.02	0.15–0.20	7
Length of foretibia, mm	1.22 $\pm$ 0.06	1.14–1.30	9	1.23 $\pm$ 0.06	1.14–1.30	6
Length of hindtibia, mm	1.78 $\pm$ 0.13	1.62–1.96	9	1.94 $\pm$ 0.05	1.74–2.00	7

^a Specimens from St. Thomas, U.S. Virgin Islands (COTYPE); Guana Island, British Virgin Islands.

^b Specimens from Barro Colorado Island, Panama; Jalisco and Acapulco, Mexico; and Woodstock, Jamaica.

patric distributions. *N. acajutlae* occurs on Puerto Rico, Vieques Island (near Puerto Rico), all major U.S. Virgin Islands (St. Croix, St. John, and St. Thomas), and on all the major British Virgin Islands (Tortola, Virgin Gorda, Guana, and Anegada). Of the smaller islands in the British Virgin Islands, *N. acajutlae* has been found on George Dog, Scrub, Thatch and such others as have enough soil to support a scrub forest (see List 1). Collections from Trinidad (including soldiers labeled as *N. creolina* Banks, paratype, MCZ Type 10078 collected by W. Beebe in Trinidad [see *Taxonomic History*] and recent collections from Valencia Long Stretch, Trinidad by J.P.E.C. Darlington) also sort as *N. acajutlae*. Collections from the Lesser Antilles islands between the British Virgin Islands and Trinidad are scarce. Surveys of the islands of Guadeloupe, Montserrat, Grenada, and Tobago (J.P.E.C. Darlington 1992, personal communication) revealed no specimens of *N. acajutlae* or *N. nigriceps*. The termite fauna of the Lesser Antilles should be examined further for presence of *N. acajutlae*. Furthermore, material from northern South America should be examined to determine the full southern range of *N. acajutlae*.

N. nigriceps ranges from Panama (and possibly into South America) north through Central America into Mexico. It also occurs on the Cayman Islands and Jamaica. The termite fauna of both Cuba and Hispaniola has been aggressively collected (most recently by J. Křeček in Cuba and R. H. Scheffrahn in the Dominican Republic). Neither *N. acajutlae* nor *N. nigriceps* has been recorded from either of these islands. Specimens from Providenciales Island, Turks and Caicos Islands, British West Indies, seem close, but not identical, to either *N. acajutlae* or *N. nigriceps* (Scheffrahn et al. 1990; R. H. Scheffrahn, personal communication; B.L.T., personal observation). Further sampling and evaluation of material from the British West Indies will be required to substantiate a diagnosis.

The distributions of *N. acajutlae* and *N. nigriceps* thus fit logically with current theories regarding the biogeography of the Caribbean Islands. The geology of the Caribbean land masses is not firmly established, but there is a strong consensus that the Greater Antilles and Lesser Antilles island groups had independent origins (Donnelly 1988). Their present juxtaposition in an apparently regular arc is one of coincidence associated with continental plate movements; it does not reflect historical derivation from a single land mass. The Anegada Passage separating the Greater Antilles, Puerto Rico, and the Virgin Islands from the Lesser Antilles is extremely deep, with a sill depth approaching 2,000 m and basins with ocean depths exceeding 4,000 m (Donnelly 1988).

The relatively young Lesser Antilles developed as a volcanic chain along the Caribbean plate. There is little probability that land connections existed between these volcanos from the Miocene period onward (Donnelly 1988). The origin of the Greater Antilles was earlier and is subject to greater debate. These islands probably arose as volcanoes as well, although the island of Cuba remains a geologic enigma because of the complexity of its structural fragments, which may reflect a continental origin (Donnelly 1988).

For the purposes of this article, the precise geological origin of the Greater Antilles is of less interest than the recent dynamics of sea level and, thus, land bridges associated with the islands. A clear and concise review of this phenomenon, and its relevance to Caribbean biogeography, is presented in Lazell (1989) and summarized below.

During the Sangamon interglacial period (100,000 yr ago, preceding the last great ice age), all of southern Florida, nearly all of the Bahamas, and much of the current land area of the Caribbean islands was underwater (Fig. 4). Sea level was $\approx$ 21 m above present level. The Würm glaciation period began $\approx$ 80,000 yr ago, ice accu-

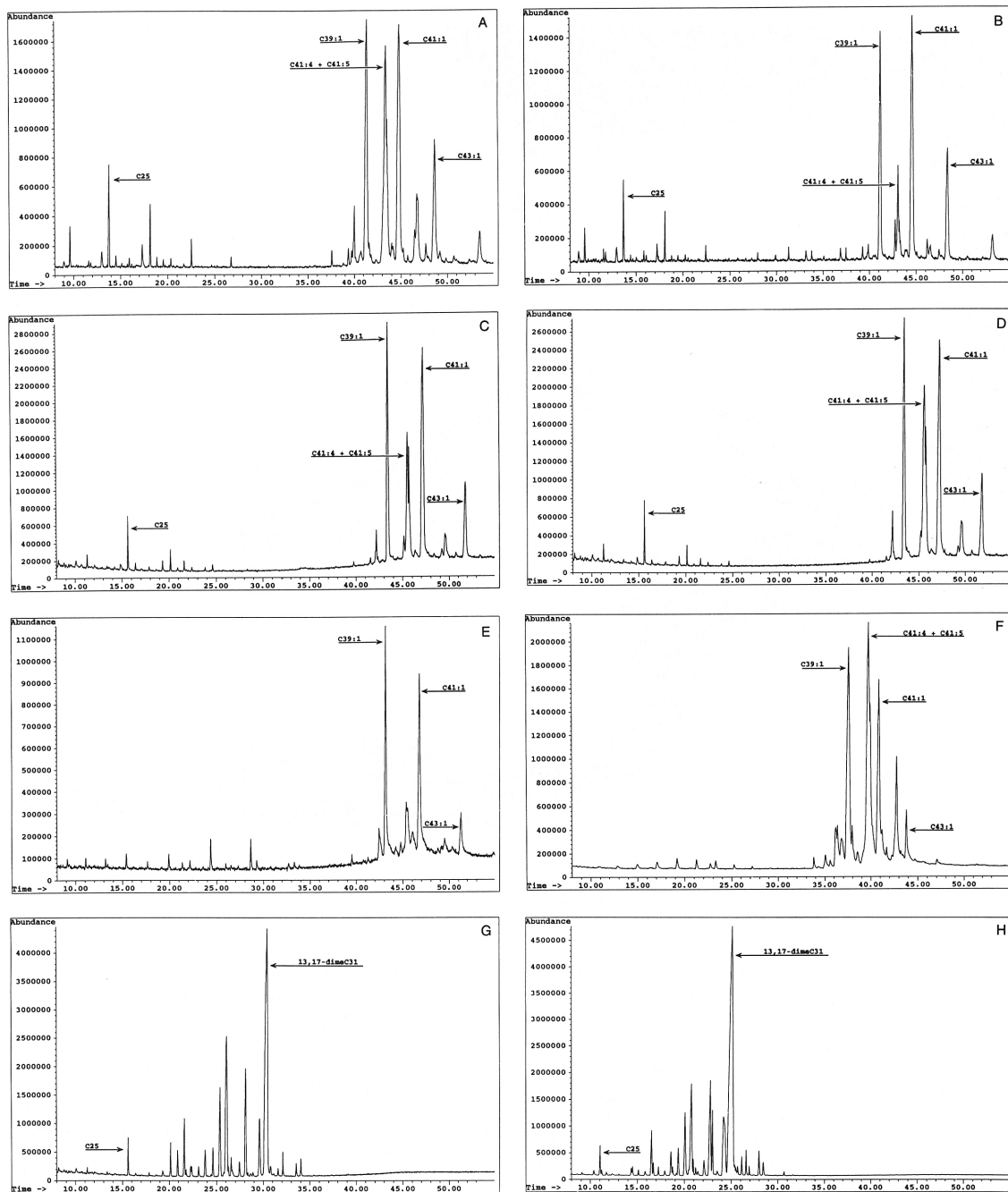


Fig. 3. Gas chromatograms of the surface hydrocarbons of three species of *Nasutitermes*. (A) *N. acajutlae* (colony 3) from Guana Island, British Virgin Islands; (B) *N. acajutlae* (colony 17) from Guana Island, British Virgin Islands; (C) *N. acajutlae* from Necker Island, British Virgin Islands; (D) *N. acajutlae* from Virgin Gorda, British Virgin Islands; (E) *N. nigriceps* from Grand Cayman, Cayman Islands; (F) *N. nigriceps* from Galeta, Panama; (G) *N. costalis* from Tortola, British Virgin Islands; (H) *N. costalis* from Trinidad.

mutating around the poles and slowly lowering sea levels until the glacial maximum 17,000 yr ago. At that time, land exposure was greatest and sea level fell to ≈ 120 m below modern level. During the interval of the Würm Glacial Maximum, the Nicaraguan area of Central America

extended broadly to the east, forming a stepping stone land bridge to Jamaica.

In light of geological dynamics and recent glacial history, the most logical explanation to account for the current distribution of the closely related species *N. acajutlae* and *N. nigriceps* as-

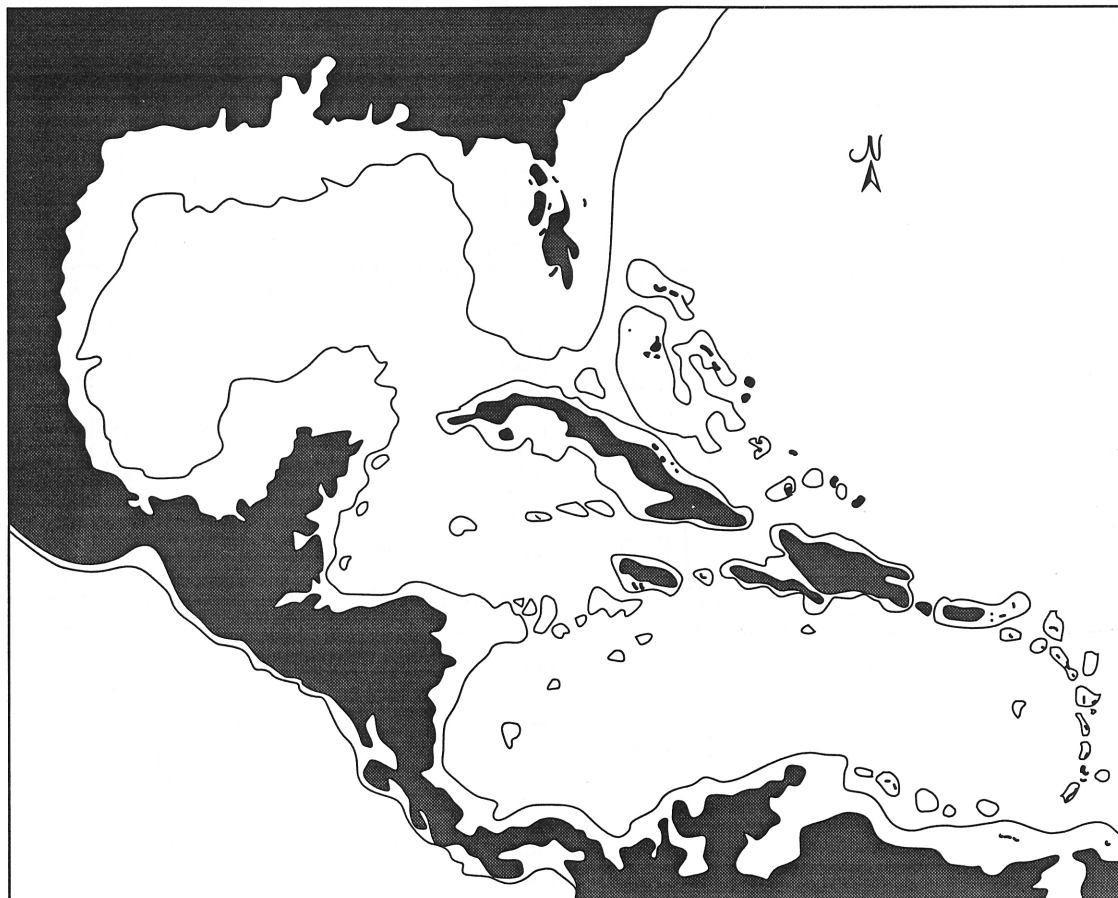


Fig. 4. Approximate land areas and distance relationships within the Caribbean Basin over the past 100,000 yr. Sea level during the Würm (or Wisconsinan) Glacial Maximum (17,000 yr ago; solid line) compared with land masses during the Sangamon Interglacial period (100,000 yr ago; stippled). Redrawn from Lazell (1989).

sumes an ancestral population of one or the other species inhabiting, most probably, a lowland region of northern South America, and perhaps ranging into either Central America or the Caribbean. Speciation occurred in a manner that is impossible to detail until more is known about discrete species boundaries or clinal variation of the fauna in northern South America. The modern range of *N. acajutlae* resulted from migration along the Caribbean arc from Trinidad to Puerto Rico. Once established in Central America, *N. nigriceps* probably dispersed over the Nicaraguan land bridge to the Cayman Islands and Jamaica during the Würm Glacial Maximum. Further sampling of termites from the British West Indies and from Colombia, Venezuela, and Guyana will help in understanding the historical biogeography and radiation of the group.

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