The Termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of the British Virgin Islands: Distribution, Moisture Relations, and Cuticular Hydrocarbons

by

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ABSTRACT

A survey of the termites (Isoptera) of 19 islands of the British Virgin Islands (BVI) yielded at least eight species belonging to three families. The Kalotermitidae occurring in the BVI are *Neotermes mona* (Banks), *Incisitermes* species (appear close to *I. snyderi* (Light) and *I. incisus* (Silvestri)), *Procryptotermes corniceps* (Snyder), and *Cryptotermes brevis* (Walker). The only representative of the Rhinotermitidae we collected in the BVI is one or more undetermined species of *Heterotermes* (Froggatt). The three species of Termitidae found on Guana Island are *Nasutitermes acajutlae* (Holmgren), *N. costalis* (Holmgren) and *Parvitermes wolcotti* (Snyder). This report presents brief descriptions of the biology of these termites, along with summaries of the collection sites. Cuticular hydrocarbon composition is correlated with apparent moisture requirements of the termites and availability on the various islands.

INTRODUCTION

The British Virgin Islands (BVI) are a complex of more than 50 land masses of various sizes, elevations, and soil types. They are part of the Puerto Rico Bank geological unit, which comprises a broad plateau of land that has been dry or submerged during geological history. The rocks underlying these islands date back to the Cretaceous. Several islands are large enough and possess soils that support Beard's "Evergreen Bushland" (Beard 1945, 1948), as well as littoral and other vegetation associations.

The geographic location and relative size of the several islands of the British Virgin Islands are shown on the map (Fig. 1). All are of volcanic origin except Anegada, a coral and limestone atoll. Tortola, the largest island, has an area of 5444 ha. It supports a protected remnant of

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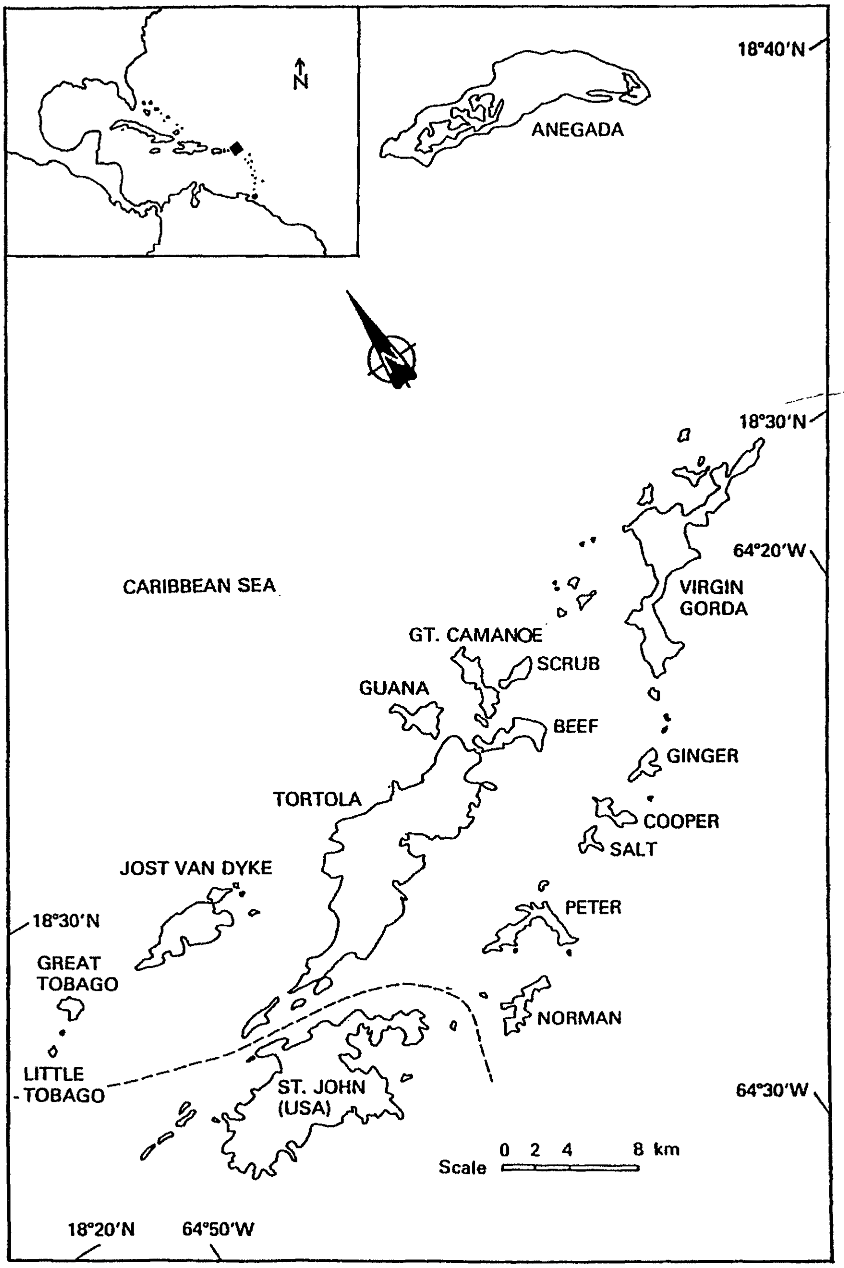

Fig. 1. Diagram showing positions of the British Virgin Islands (from Lazell 1995).

aridulate rain forest (D'arcy 1967) on its highest point, Sage Mountain (522 m). Guana Island is smaller (297 ha.), with a maximum elevation of about 260 m, but has a relatively rich, less-disturbed vegetation cover. A partial listing of typical non-littoral trees and shrubs of Guana Island includes 23 trees, 30 shrubs and 2 palms (G. Proctor, Dept. Botany, University of Puerto Rico, personal communication). The floral and faunal richness of Guana Island may be a result of its origin, size, and history of minimal disturbance (Lazell 1989).

The termite fauna of the West Indies, which included preliminary, unpublished data in an early version of this report, was reviewed by Scheffrahn *et al.* (1994). In this paper we present a brief report on the biology of each species and revise and update the distribution records of the termite species found in the BVI. A hypothesis is presented regarding the correlation between species distribution, apparent moisture demands, and cuticular hydrocarbon composition of the termites.

METHODS

Collecting periods of 2 to 4 weeks each were spent on Guana Island, with short trips to other islands of the British Virgin Island complex, from 1986 to 1994, most often during the month of October. An attempt was made to sample termite colonies from every suitable habitat that could be reached. Data on flight times were obtained through census of insects attracted to lights in living quarters and trap lights, but such records are limited seasonally. Trees housing carton nests of *Nasutitermes acajutlae* (Holmgren) were sampled in designated areas on Guana Island. Termite samples were transported to the laboratory on Guana Island, where termites were removed and specimens of all available castes were preserved in 85% ethanol. Species diagnoses were made using keys and descriptions, and by comparisons with type and previously identified material. Much work needs to be done to develop usable keys for the Caribbean fauna, and new descriptions are needed for some species. Whenever possible, samples from these same colonies were collected for hydrocarbon analyses (see Haverty *et al.* 1997). Voucher specimens were deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C.

RESULTS AND DISCUSSION

Collections from 19 islands in the BVI totaled at least eight species in seven genera in three families. The species of termites recorded and the islands on which they were collected, ranked on the basis of moisture availability as determined by vegetation type and density

(Dmi'el *et al.* 1997), are presented in Table 1. These will be considered individually by family.

Kalotermitidae

***Neotermes mona* (Banks).** This is the largest termite in the BVI. This species was once thought to be endemic to Mona Island, but recent collections extended the known range to the Dominican Republic and the Turks and Caicos archipelago, in both natural and structural timber (Scheffrahn *et al.* 1990, 1994). Guana Island was the only island where *N. mona* was collected (Table 1). The two colonies of *N. mona* were collected in dead wood on live trees (one colony from *Morisonia americana* [family Caparaceae]); galleries extended into the live portions of the trees. Mature alates were found on Guana Island during the month of October; flights occurred at night and extended over a period of at least several days. The very large size, clear wings, and large eyes makes this species easy to differentiate from other termites of the area.

***Incisitermes* species.** Members of the genus *Incisitermes* are the most common kalotermitids found in the BVI and were collected on every island except for Carrot Rock (Table 1). Soldiers and alates appear to be close to descriptions and identified specimens of *I. snyderi* (Light) and *I. incisus* (Silvestri). Because of the morphological variation and the uncertainty of the taxonomy of *Incisitermes* in the BVI, we were unable to unambiguously assign specimens to a specific taxon within *Incisitermes* (Haverty *et al.* 1997). Previous species identifications of *Incisitermes* in the BVI (Scheffrahn et. al 1994) should be interpreted with caution because of the uncertainties in diagnosing species within this group (R.H. Scheffrahn, Dept. Entomology, University of Florida, personal communication).

Incisitermes soldiers have head shapes of two distinct types, the "long-headed" and the "short-headed," which develop from different instars of the immature stages. The long-headed soldiers tend to be more deeply pigmented than the short-headed morphs. Small, young colonies have only the short-headed form; older colonies have both morphs. The differences in appearance are so pronounced that they might be regarded as different species if collected separately. Alates are pale yellow or yellow-brown, relatively small night-flyers. Alates were collected during the months of July through November in the BVI.

Incisitermes species live in sound, dead trees of many species, as well as in structural timber in the BVI (see Table 1). *Incisitermes* samples were collected in the mangrove association fringing Beef Island and in trees on the wetter side of Guana Island. *Incisitermes snyderi* is a major pest attacking structures in North and Central America and in the

Table 1. Distribution of termite species in the British Virgin Islands ranked by apparent moisture requirements (termites) and availability (islands).
Termite species [1,2]

Island [3]	N mon	P wol	Het sp	N cos	N aca	P cor	I spp
Tortola			X	X	X		X
Virgin Gorda		X	X		X		X
Greater Jost Van Dyke					X		X
Beef			X		X		X
Guana	X	X	X	X	X	X	X
Peter			X		X	X	X
Great Camanoe		X			X	X	X
Eustatia		X			X		X
Cooper					X		X
Lesser Jost Van Dyke			X		X		X
Great Tobago					X		X
Scrub					X	X	X
Ginger					X		X
George Dog					X		X
Great Thatch			X		X	X	X
Anegada					X	X	X
Necker			X		X	X	X
Little Tobago					X		X
Carrot Rock					X		

[1]N mon = *Neotermes mona*; P cor = *Procryptotermes corniceps*; I spp = *Incisitermes* species; H sp = *Heterotermes* species; P wol = *Parvitermes wolcotti*; N cos = *Nasutitermes costalis*; N aca = *Nasutitermes acajutlae*. *Cryptotermes brevis* is circumtropical. It is only associated with structures; records of attack from most inhabited Caribbean islands (see Scheffrahn *et al.* 1994).
[2]Decreasing moisture requirements from left to right.
[3]Decreasing moisture availability from top to bottom (Dmi'el *et al.* 1997).

Caribbean, including the Bahamas, Cuba and Puerto Rico (Harris 1961). This species tolerates wide variations in moisture availability in the field, as well as under experimental challenge (Collins 1969).

***Procryptotermes corniceps* (Snyder).** *P. corniceps* is a relatively xerophilic species. Soldiers of *P. corniceps* are distinctive with proportionally long, strongly curved, sharply pointed mandibles. The heads of the soldiers slope steeply in front and have short hornlike projections on the anterolateral region (Krishna 1961). Alates were present in colonies or appeared at lights at night during the months of July through October on Guana Island. *P. corniceps* alates should be redescribed, as the species was named from dealated imagoes and soldiers. In size, alates of *P. corniceps* are very near those of *I.* nr *snyderi*, *C. brevis*, and *I. incisus*, and are somewhat larger than alates of *Heterotermes*; all are of a yellow-brown color, and all fly at night.

P. corniceps was collected on less than half of the islands we visited in the BVI, including some of the driest (Table 1). It is common in old fence posts made from Gumbo Limbo, *Bursera semaruba*, a soft resinous wood not often attacked by other species of termites. Colonies of *P. corniceps* are also frequently found in dead branches on the ground. There are no records of attack of structural timber by this species.

***Cryptotermes brevis* (Walker).** The pragmatic heads of the soldiers, the presence of piles of dry fecal pellets in infested buildings, and the paper-thin outer surface of furniture or structural wood containing colonies of *C. brevis* are diagnostic of this termite. This circumtropical, widely introduced species has been reported only from wood inside buildings. It is not a native termite of the BVI.

C. brevis has been observed in furniture in the lounge of the Guana Island Club. Since dwellings were usually not included in our survey efforts (unless infestations were brought to our attention), we did not encounter this species in any of our collections. Flights occur at night over a long season.

Rhinotermitidae

***Heterotermes* (Froggatt).** Samples of species of this genus from the Caribbean Basin are so variable that Snyder's (1924) query regarding whether the genus comprises a single, highly variable species, a complex of closely related species, or a cluster of evolving species still needs to be addressed. Emerson began re-working the group and left a series of careful, detailed measurements of known species, but had not finished the task at the close of his work. Until useful species limits are diagnosed, members of this group collected in the BVI are referred to as *Heterotermes* sp. (possibly *H. tenuis* (Hagen), *H. convexinotatus* (Snyder), or *H. cardini* (Snyder) or a new species).

Heterotermes sp. was found on eight islands, ranging from the wettest to one of the driest, Little Tobago. Soldiers of this genus are small, with yellow to yellow-brown heads and dark, slender, smooth, sharply pointed mandibles curved only near the tips. The pronotum is narrower than the width of the head capsule, unlike in soldiers of the family Kalotermitidae. Alates are small, light-brown night swarmers; they were observed flying during the month of July on Guana Island.

Termitidae

***Nasutitermes acajutlae* (Holmgren).** *N. acajutlae* is the most obvious and appears to be the most abundant species of termite in the BVI complex, and was collected on every island sampled in this survey (Table 1). This species constructs enormous nests (up to 1.5 m in diameter, up to 3.0 m in height) composed of dark to silvery-brown, delicate and friable parchment-like outer walls enclosing the variously sized, heavier-walled cells of the carton matrix. Nests are usually spindle-shaped or irregularly rounded. The nests and the nodular food storage bodies contained within are described in more detail by Thorne *et al.* (1996a). *N. acajutlae* was recently resurrected as a species morphologically distinguishable from *N. nigriceps* (Thorne *et al.* 1994, 1996b).

Near White Bay Beach on Guana Island, the most heavily exploited tree species, *Coccoloba uvifera*, had nests, trails, and extensive feeding activity on 79% of 153 trees. *Tabebuia lepidota* had termites on 49.6% of 355 trees. Of the 43 *Pisonia subcordata* 54% had termite galleries, but only three of the trees had nests. In a survey further inland termites were found on 90% of the *C. uvifera* trees, and on 53% of *T. lepidota*. *Bursera semaruba* (Gumbo Limbo or "Terpentine Tree") showed no feeding tunnels and rarely had either nests or runways leading to foraging sites on stems or branches. This may be related to the similarity between some components of the sap of the living tree and the defense secretion of the nasute soldiers (as suggested in other species by Moore (1956); Vrkoc et al. (1978); Valterova et al. (1984)).

Mature nests and individuals of *N. acajutlae* are larger than those of the other carton-nest building nasute of the Guana Island, *N. costalis*. Soldiers of *N. acajutlae* have reddish to dark brown heads; alates are quite large, and chestnut brown in color (Thorne *et al.* 1994). Flights were observed to occur during evening hours in October.

***Nasutitermes costalis* (Holmgren).** *N. costalis* is a carton nest-building nasute that is far less common than *N. acajutlae* and is found primarily in the wetter areas of the BVI. Tortola and Guana Island are the only islands where we collected colonies of this arboreal species (Table 1). Mature nests of this species are smaller, often darker in color, and more friable internally than those of *N. acajutlae*.

Soldiers of *N. costalis* are smaller and have reduced pilosity on the head capsule when compared to *N. acajutlae*. The alates are also smaller and darker, with dark brown to black bodies and charcoal wings. Flights occur during the day and were observed during the month of October on Tortola.

***Parvitermes wolcotti* (Snyder).** *P. wolcotti* is a small nasute that lives on dead wood in or on the ground in areas with fairly dense tree cover. Main nests so far observed in the BVI were under stones in the comparatively moist Pinguin Ghut area of Guana Island. Foraging groups have been taken on three other islands in zones of fairly high moisture. *P. wolcotti* alates have very large, protruding compound eyes, and large ocelli mounted on raised projections.

Moisture Relationships and Termite Distributions

The distribution pattern shown by termite species collected in the BVI during this study (Table 1) reflects the importance of moisture which, with temperature, directly affects termite distribution (Collins 1991). However, factors such as deforestation; agricultural, residential, and industrial development; reduction of mangroves; overgrazing by sheep and goats; and restrictions of access by collectors all determine whether or not a termite species is collected on a given island. Therefore, the history of disturbance on an island, along with accidents of sampling, may influence diversity records.

All of the species of termites collected from the British Virgin Islands can be found on Guana Island (Table 1). Despite its small size, Guana Island hosts a diversity of habitats that comprise the range of habitats of the BVI (mangroves, dry lowland shrub and cactus, dry forest, and mesic ravine forests) found within the rest of the island complex, except for an aridulate rain forest. The great majority of our time in the field was spent on Guana Island. This perspective has helped to shape our views on specific termite habitats and is, without doubt, the rea son we have collected all species on Guana Island.

Species of termites are known to differ in their moisture requirements (Collins 1969). The BVI fauna includes species at both ends of the moisture-dependence spectrum, *N. mona* and *C. brevis*. On Guana Island *N. mona* appears to require a high and constant moisture supply; our one colony was found in wet wood in a live tree. In contrast, *C. brevis*, the "furniture termite," is capable of living without access to free water and is intolerant of exposure to high moisture (Collins 1969; Williams 1977; Steward 1982). The ability to tolerate extremely dry conditions appears to have evolved independently in several groups of Kalotermitidae, and depends on rectal water retention and on restriction of water loss by cuticular lipids (Collins 1991).

Of the species present on this island complex, *Nasutitermes acajutlae* seems to be the least moisture sensitive of the Termitidae (Table 1); this is reflected in collections of this species on even the most arid of the islands (Dmi'el *et al.* 1997). A similar pattern is shown by the closely related species, *N. nigriceps*, found elsewhere in the Caribbean, Central, and South America (Thorne *et al.* 1994). *N. costalis* occurs on many of the islands in the Greater and Lesser Antilles, from Cuba south to Trinidad and Tobago (Snyder 1949; Araujo 1977). The relative scarcity of *N. costalis* in the BVI may be related to the lower moisture availability on most of the islands of the complex. Krecek (1970) found that *N.*

costalis distribution patterns and nest composition on Cuba indicated a higher moisture demand than that shown by the other common nasute, *N. rippertii* (Rambur).

Incisitermes snyderi has been shown to have great flexibility in tolerance of different moisture availability, surviving well in both moist and arid environments (Collins 1969). The apparent scarcity of the dry-adapted *Procryptotermes corniceps* on islands where *Incisitermes* has been collected may reflect sampling accident. *Heterotermes* sp. is common in buildings through the Caribbean, and in natural habitats with suitable soil types. The subterranean habit probably permits access to more constant water sources and thereby increases the diversity of habitats occupied by the species. *P. wolcotti* and *N. costalis* appear to have low tolerance to desiccation; these two species are found either on the "wettest" islands or the more mesic portions of other islands of the BVI.

Epicuticular lipids provide a primary barrier to water loss in terrestrial arthropods (Edney 1967; Hadley 1980, 1985). The physical properties of these lipids are involved in determining rates of water loss from the organism. Studies of water loss rates show that specific temperatures, characteristic of the taxon under study, determine the point at which transpiration rate increases rapidly (Collins 1991). Such "critical temperature" responses have been postulated to result from lipid phase transition in the surface layer (Beament 1961, 1964; Wigglesworth 1972). When extracts of cuticular hydrocarbons from the BVI termite species were analyzed and the percentage of components determined (Haverty *et al.* 1997), the desiccation-tolerant species (*C. brevis, Incisitermes, P. corniceps*, and *N. acajutlae*) all showed a preponderance of high-melting point (late-eluting) components that were absent from profiles of species found in wetter areas or in living trees (Table 2). The presence of large amounts of late-eluting components in a cuticular hydrocarbon mixture suggest a waterproofing layer of higher stability at normal environmental temperatures than would be characteristic of a mixture of lower-melting point hydrocarbons. It is of interest that, for the BVI termite species, the presence of very late-eluting components in the hydrocarbon mixture is generally correlated with habitat (Haverty *et al.* 1997).

Parvitermes wolcotti is the one exception to this pattern. This species is comprised of very small, fast-moving individuals. The cuticular hydrocarbons of this species consists of two groupings: early-eluting components and late-eluting components much like *N. acajutlae* (Haverty et al. 1997). More must be learned about the ecology and evolutionary biology of this species before these patterns can be interpreted.

Table 2. Predominant cuticular hydrocarbons from pseudergates (larvae and nymphs, too) or workers of 8 termite taxa from the British Virgin Islands.[1]

	Termite species[2]							
Hydrocarbon	N mon	P wol	Het sp	N cos	N aca	P cor	I spp	C bre
2-MeC24	++					+++	+++	+++
C25:1					+	++	+++	
C25	+++			++	+++	+++	+++	+++
13-; 11-; 9-MeC25	+++				tr		+	+
2-MeC25	+++					+++	+++	++
3-MeC25	+++					+++	+++	+++
C26	+++		tr		tr	++	++	++
13-; 12-MeC26	+++							
2-MeC26	++		+			+++	++	+
C27:1				tr	+		+++	
C27	+++	+++	+++	++	++	+++	+++	+++
13-; 11-; 9-; 7-MeC27	+++		+++	+	tr	tr	tr	tr
11,15-DimeC27	++		+++	++				
9,17-DimeC27			+++					
14-; 13-; 12-; 9-; 7-MeC28	+	+++	+			tr		
2-MeC28			+++	+			tr	
15-; 13-; 11-; 9-; 7-; 5-MeC29	tr	+	+++	+++			+	
9,X-DimeC28			+++					
13,17-; 11,15-DimeC29				+++				
9,19-; 9,17-DimeC29			+++				+	
7,21-DimeC29			+++					
2-MeC29		++						tr

11,15-; 12,16-; 13,17-DimeC30				+++				
13,17-DimeC31				+++				
15-; 13-; 11-; 9-MeC31	tr		+	+++				
C37:2						++		+++
C39:2					+	+++	+	+++
C39:1			tr		+++	++	tr	++
C40:1					+++			
C41:5					+++			
C41:4					+++			
C41:3		+++				+++	+	+++
C41:2					++	+++	++	+++
C41:1					+++	+++	+	++
C43:4		+++			+++	+		
C43:3		+++				++	+++	++
C43:2					+	++	+++	++
C43:1					+++		++	++
C43:54		+++					+	
C45:3		+++					++	++
C45:1					++		+++	

[1]Relative proprtions of the total hydrocarbon mixture for each species. +++ = > 3.0 %; ++ = 1.0 to 3.0 %; + = 0.3 to 0.99 %; and tr = < 0.3 %; blank = not detected.

[2]N mon = *Neotermes mona*; C bre = *Cryptotermes brevis*; P cr = *Procryptotermes corniceps*; I spp = *Incisitermes* species; H sp = *Heterotermes* species; P wl = *Parvitermes wootti*; N cs = *Nasutitermes costalis*; N aca = *Nasutitermes acajutlae*.

Our survey of the termite fauna of the British Virgin Islands has provided baseline information on the biodiversity of the region and the data to evaluate the association between cuticular hydrocarbons and the arid and mesic termite habitats.

ACKNOWLEDGMENTS

We extend sincere thanks to Dr. Henry and Gloria Jarecki and the staff of the Guana Island Club for their support and hospitality during the course of this project. We thank R.H. Scheffrahn for constructive comments on an earlier draft of this manuscript, and J. Lazell for support and discussion throughout the project. L.M. Hernandez and J. Krecek assisted in the collection of several species. L.J. Nelson characterized the cuticular hydrocarbons for each species. This research was funded, in part, by a series of grants to the authors by The Conservation Agency through grants from the Falconwood Foundation and a cooperative agreement between the Pacific Southwest Research Station and the University of Maryland.

TRIBUTE

Dr. Margaret S. Collins (1922-1996) passed away while on a Caribbean island, studying the termites that captured her interest so completely. Well known as an adventurous tropical field biologist, Dr. Collins energetically devoted her career to work on termites in a variety of locations in the Neotropics and North America. It was our privilege to have this exceptional person as our friend and collaborator. She lived her life with enthusiasm, integrity, and a rich sense of humor, and she made many substantive contributions to the field of termite biology.

- MIH and BLT

REFERENCES

Araujo, R.L. 1977. Catalogo dos Isoptera do Novo Mundo. Acad. Brasileira de Ciencias, Rio de Janiero. 92 pp.

Beament, J.W.L. 1945. The water relations of the insect cuticle. Biol. Rev. 36: 281-320.

Beament, J.W.L. 1964. The active transport and passive movement of water in insects. Advan. Insect Physiol. 2: 67-129.

Beard, J.S. 1945. Foresty in the Leeward Islands. The British Virgin Islands report. Development and Welfare in the West Indies Bulletin. 7A: 1-6.

Beard, J.S. 1949. Natural Vegetation of the Windward and Leeward Islands. Oxford Forestry Memoirs 21, Oxford University Press, U.K.

Collins, M.S. 1969. Water relations in termites. *In* Biology of Termites, Vol. I, K. Krishna and F.M. Weesner [eds.], Academic Press, New York, pp. 433-458.

Collins, M.S. 1991. Physical factors affecting termite distribution. Sociobiology 19: 283-286.

D'Arcy, W.G. 1967. Annotated checklist of the dicotyledons of Tortola, Virgin Islands. Rhodora 69(780): 385-450.

Dmi'el, R., G. Perry, & J. Lazell. 1997. Evaporative water loss in nine insular lizard populations of *Anolis cristatellus* group in the British Virgin Islands. Biotropica (In press).

Edney, E.B. 1977. Water balance in desert arthropods. Science 156: 1059-1066.

Hadley, N.F. 1980. Surface waxes and integumentary permeability. Amer. Sci. 68: 546-553.

Hadley, N.F. 1985. The adaptive role of lipids in biological systems. John Wiley and Sons, Inc. New York, 319 pp.

Harris, W.V. 1961. Termites; their recognition and control. John Wiley and Sons. New York, 187 pp.

Haverty, M.I., M.S. Collins, L.J. Nelson, & B.L. Thorne. 1997. Cuticular hydrocarbons of the termites of the British Virgin Islands (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae). J. Chem. Ecol. (In press).

Kreéek, J. 1970. Nest structure, humidity and colony composition in two species of *Nasutitermes* in Cuba (Isoptera). Acta Entomol. Bohemoslov. 67: 310-317.

Krishna, K. 1961. A generic and phylogenetic study of the family Kalotermitedae (Isoptera). Bull. Amer. Nus. Hat. Hist. 122: 303-408.

Lazell, J. 1989. Guana: A natural history guide. The Conservation Agency, Jamestown, Rhode Island.

Lazell, J. 1995. Natural Necker. The Conservation Agency, Jamestown, Rhode Island.

Light, S.F. 1933. Termites of western Mexico. Univ. California Publ. Entomol. 6: 79-164.

Moore, B.P. 1956. Volatile terpenes from *Nasutitermes* soldiers (Isoptera, Termitidae). J. Insect Physiol. 10: 371-375.

Scheffrahn, R.H., J.P.E.C. Darlington, M.S. Collins, J. Krecek, & N-Y. Su. 1994. Termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of the West Indies. Sociobiology 24: 213-238.

Scheffrahn, R.H., N-Y. Su, & B. Diehl. 1990. Native, introduced, and structure-infesting termites of the Turks and Caicos Islands, B.W.I. (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae). Florida Entomol. 73: 622-627.

Snyder, T.E. 1924. Descriptions of new species and hitherto unknown castes of termites from America and Hawaii. Proc. U.S. Nat. Mus. 64(6): 1-40, plates 1-5.

Snyder, T.E. 1949. Catalog of the termites (Isoptera) of the world. Smithsonian Miscellaneous Collections 112: 1-490.

Steward, R.C. 1982. Comparison of the behavioral and physiological responses to humidity of five species of dry-wood termites, *Cryptotermes* species. Physiol. Entomol. 7: 71-82.

Thorne, B.L., Haverty, M.I., & M.S. Collins. 1994. Taxonomy and biogeography of *Nasutitermes acajutlae* and *N. nigriceps* (Isoptera: Termitidae) in the Caribbean and Central America. Ann. Entomol. Soc. Amer. 87:762-770.

Thorne, B.L., M.S. Collins, & K.A. Bjorndal. 1996a. Architecture and nutrient analysis of arboreal carton nests of two Neotropical *Nasutitermes* species (Isoptera: Termitidae), with notes on embedded nodules. Florida Entomol. 79: 27-37.

Thorne, B.L., M.I. Haverty, & M.S. Collins. 1996b. Antillean termite named for a locality in Central America: taxonomic memorial to a perpetual error. Ann. Entomol. Soc. Amer. 89: 346-347.

Valterova, I., J. Krecek, & J. Vrkoc. 1984. Frontal gland secretion and ecology of the Greater Antillean termite *Nasutitermes hubbardi* (Isoptera, Termitidae). Acta Entomol. Bohemoslov. 81: 416-425.

Vrkoc, J., J. Krecek, & I. Hrdy. 1978. Monoterpenic alarm pheromones in two *Nasutitermes* species. Acta Entomol. Bohemoslov. 75: 1-8.

Wigglesworth, V.B. 1972. The Principles of insect physiology, 7th edition. John Wiley and Sons, Inc., New York, 827 pp.

Williams, R.M.C. 1977. The ecology and physiology of structural wood destroying Isoptera. Mater. und Organismen 12: 111-140.