GUANA for 2000

The giant amblypygid whipscorpion
appeared docile and quite harmless
perched on Dr. Lazell's hand
prior to his death.

The Conservation Agency

Exploration, Education, and Research

President
James D. Lazell, Ph.D.
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6 Swinburne Street
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3/29/01

Dr. Henry Jarecki
10 Timber Trail
Rye NY 10580

Dear Henry:

It was a lovely month, October 2000. Small population. Low stress. The few of us got lots done. Razi, Ofra, and I continued collecting data for our three species, multi-island physiological comparison of Anolis lizards: crested, saddled, and grass. Gad and two assistants worked on energetics, locomotion, and combat in male crested anoles.

Stephen Durand finally got here to join the bird banding crew with the Sibleys, and was a great help. We have invited him to come back and run the program in 2001, so Fred can work on clearing trails -- which he has been longing to do for years. The avian highlight of the year was the capture of an adult Swainson's thrush, Catharus ustulatus swainsoni, by the book: "A rare migrant on Cuba, Jamaica, and the Cayman Islands and very rare in the northern Bahamas" (Raffaele et. al., 1998. A Guide to the Birds of the West Indies, Princeton Univ Press).

Our Swainson's thrush, as a full adult, has to have made a complete migration before, and there was no El Nino to make 2000 unusual. We conclude he was on his regular route to South America and we have a discovery of major importance for the study of neotropical migrant birds. Stephen and Fred promise to get this record published.

Barry and Buena Valentine, Phet Souphanya, and Wenhua continued building the insect collection. Barry has applied to you for a tiny grant to finalize and publish a comprehensive list of Guana's beetles. He has about 240 species. Chao's index of species richness (see Bartlett's paper below) predicts 282. We expect a lot of these are going to turn up in Mike Ivie's collection at Montana State. Mike has been working on Virgin Islands beetles for about 20 years, but has gotten very little published. He will not take on a single island project like Guana, but will enthusiastically assist Barry by providing a place to live while doing the work.

Eric and Adam, the marine crustacean team, came through briefly on their way to Anegada. They are planning a website for B.V.I. crustacea. Eric introduced the group from Los Angeles County Museum (LACM), led by Leslie Harris and Todd Zimmerman, to Guana. They were close friends and colleagues at first, but have fallen out. My view is that a little competition is not a bad thing in view of the enormous amount of work to be done in this field. However, I must say I do not much like the attitude of the LACM group, who seem to believe the "Guana Island Project" is their thing and the rest of us do not exist.

Here's a description of what follows:

Jean Lodge's paper describing the mushroom Amanita arenicola, type locality Guana, is out. For some reason, she thought Anguilla was in the B.V.I., and thus does not understand the biogeographic significance of A. arenicola occurring east of the Anegada Passage in the Lesser Antilles (lots of people are like that!). I will get her straightened out. Amanitas are famous mushrooms. Caesar's, A. caesarea, is esteemed as the world's most delicious; the fly amanita, A. muscaria is extremely poisonous and death's angel, A. phalloides, is perhaps the world's most deadly. No one has tried to eat a Guana A. arenicola.

In the lizard world, Greg finally got in gear and finished up our 15 year long project of naming the Carrot Rock skink, a tribute to our fate friend and colleague Bill MacLean. Guana does not own Carrot Rock (I checked: it is Crown Land), but it is our intellectual property -- one of the most amazing bits of land on Earth. And another anole physiology paper is out.

Next Barry's illustrated beetle list leads entomology. Then Charles's planthopper paper is one of my all time favorites. Instead of waiting to get every species identified, and the new ones described, he has produced a superb summary. Especially useful is his use of Chao's index of species richness, which I now will exhort everyone to apply to their collections (as Barry has done for beetles). The team of Bob, Barbara, and Dave have their first paper out resulting from their ongoing molecular and morphological studies of grass-associated insects. This paper expands on one of Charles's planthoppers.

Then an oldie I only just discovered. One of Roy Snelling's discoveries got described and named (for him) from Guana. It is a weird wasp that parasitizes planthoppers. I have added some general, explanatory text to Olmi's technical paper (see copyright concerns, below). Vitor and Scott have at long last got a moth manuscript completed. This is the first of three, and only features the big, showy species. Gloria and I each have a new species named for us! And, there is a big, "coffee table" book out on hawk moths -- or sphinx moths -- that features a Guana Island specimen. The whole story is nostalgia land for me because Margaret Cary (late of Bryn Mawr College), was a great mentor of mine and financed my first trip to the West Indies when I was 17.

We might consider buying this book because, as Vitor and Scott point out, Guana has 22 of the Antilles' known 85 species of hawk moths: 25% of all the species in the West Indies! On Guana! Cuba has 25% of the land area; it is bigger than Guana, not better.

Then I put in a copy of a letter I wrote in response to an inquiry by a butterfly man highly recommended by Gad. I guess my letter scared him off: never heard from him again. Wonder why?

Fred Sibley adds to our dragonfly lore, Roy and colleague add to our known ant fauna, and the termite Neotermes mona, which when discovered on Guana by Margaret back in the 80's caused quite a stir, comes into its own. Barbara reappears in her original role as a termite expert with Mike -- who hasn't been able to come back for years -- with a dandy paper on our termites.

I just got a last minute letter from Eric at Yale on the crustacean work. I have popped it in after insects.

And finally, Clive's piece almost slipped by me unnoticed (I found a stack of reprints in his office one day while waiting for him). At least he neither forgot nor ignored us.

The book is progressing well. I'll send a chunk of text out for review to several critics -- you included -- later this spring. The phone is constantly ringing as all the gang want to line up plans for next October, anticipating a full month full of biologists. Higher stress, but I am looking forward to it too....

The beetle list, parasitic wasp piece, moth paper, hawk moth cover, and carpenter ant bit all exemplify one of my worst copyright concerns: I am forever "illuminating" these reports with text and illustrations out of books. I do it because I believe that without pictures and some generalized, explanatory text, many of these technical papers would be meaningless gibberish. They would be even to me if I didn't go to the bookshelf and pull out an entomology text and look up, for example, Dryinid wasps. I have been doing this for 20 years. No problem as long as it is in the context of "Dear Henry" -- part of an extended letter to you. Put it on the web and there will be dozens of major publishing houses screaming copyright violations.

It would be a long hard job just to go back over all those 20 reports and figure out which books I xeroxed all that good stuff out of. So, clearing copyright is a much bigger job than just getting permissions from the journals that have published Guana papers.... A word to the wise....

All the best,

Skip

P.S: How about Little St. James this year?

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Lizards

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Cover Story

Prior to his death? Whose death, the giant amblypygid? Well, he is safely pickled and tagged, bottled and shelved, at the American Museum of Natural History (AMNH), where he has been tentatively identified as a member of genus Heterophrynus, but not yet known to species. As for Dr. Lazell, well, it is still prior to his death, but as he always says "Everyone who eats bananas dies." You cannot be careful enough.

Actually amblypygids -- name means "short rump" -- are perfectly harmless. Guana has a very common small one, genus Phrynus. In all my years of collecting weird animals all over the world, only once did I ever see a giant like this before. That was on Sage Mountain, Tortola, about 20 years ago. And that was just a shed exoskeleton, not the whole animal. This one, spotted by Birgit in the evening of 8 October 2000, is an absolute first for me.

I made tissue preparations for DNA sequencing from this specimen, the little common one, and all of our scorpions. Dr. Lorenzo Prendini from South Africa has come to AMNH, New York, to work there with Dr. Ward Wheeler on a molecular phylogeny of the scorpion-like arachnoids. Arachnoids are spider relatives. Birgit described her find as a cross between a spider and a beetle. It is certainly one more example of remarkable survival on Guana, and very likely a new species. Guana will be a major blip on the radar screen of arachnoid biology. The photo is by Gad Perry.

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New and interesting ectomycorrhizal fungi from Puerto Rico, Mona, and Guana Islands

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Abstract: A report of putative ectomycorrhizal fungi from Puerto Rico, Mona, and Guana Island in the Greater Antilles includes four species of *Amanita,* three of which are new species; two *Lactarius,* one is new, and two species of *Boletus,* one new. In addition, new distribution records of *Phlebopus beniensis, Russula littoralis, Lactarius ferrugineus,* a new small spored *Phylloporus,* and *Suillus brevipes* with *Pinus caribaea* are reported. Ectomycorrhizal hosts for all but the *Suillus* include *Coccoloba uvifera* (Polygonaceae) and putative hosts *Hymenea courbaril* (Caesalpiniaceae) and *Andira inermis* (Papilionaceae).

Key Words: *Amanita,* Basidiomycetes, *Boletus,* Greater Antilles, *Lactarius, Phlebopus, Phylloporus, Russula, Suillus,* systematics

INTRODUCTION

Guana Island (British Virgin Islands) and Puerto Rico are part of the Puerto Rican Bank in the eastern Greater Antilles. The areas surveyed range from sea level to 1000 m, but the collections reported here were from 1–500 m. The forest types have tropical to subtropical climates and include coastal sand dune communities and subtropical dry, subtropical moist, and subtropical wet forests according to the Holdridge Lifezone system (Ewel and Whitmore 1973).

The most intensively sampled area was the tabonuco forest type, from 100–500 m elev in the Luquillo Mountains of NE Puerto Rico. This forest type has a mean annual rainfall of 250–400 cm/yr and mean monthly temperatures from 22–26 C. Although there are 152 tree species reported for the tabonuco forest type (Brown et al 1983), almost all of them are associated with arbuscular mycorrhizal fungi, although about 5% are also associated with basidiomycetes (Lodge 1996). The presence of the agarics reported here, which are only known to be ectomycorrhizal associates of tree hosts, leaves little doubt about the presence of ectomycorrhizal symbioses. Lodge (1996) reported the presence of thick mantles of basidiomycete hyphae with clamp connections on the roots of *Pisonia subcordata* Awhguly (Nyctaginaceae), *Coccoloba swartzii* Moisn., and *C. pyrifola* Desf. (Polygonaceae), and ectendomycorrhizae in *Andira inermis* (W. Wright) DC (Papilionaceae). Kreisel (1971) demonstrated the presence of ectomycorrhizae in the sea grape, *Coccoloba uvifera* (L.) L., which occurs extensively along the coast of Puerto Rico, often in pure stands. The fungi reported in this paper are most likely associated with these hosts, *Coccoloba rugosa* Desf. (a rare and endangered species), and possibly also with *Hymenea courbaril* L. in the Caesalpiniaceae. Although there are undoubtedly other ectomycorrhizal hosts in these forests the species reported in this paper occur near or under the putative host described above. However, some of the putative hosts reported by Pegler (1983) for the Lesser Antilles are dubious and need to be confirmed.

MATERIAL AND METHODS

Color comparisons were made using Kornerup and Wanscher (1967) and designated Met 6E-4 which indicates the plate, row, and color block. In some cases the pileus color was recorded using Cailleux (1948), noted as Caill. T73 which indicates row T, color block 73. A few others were recorded as Ridgway color names as reproduced by Smithe (1975) and are given in capitalized form, e.g., Drab Gray (0.1Y 6.8/2.1) and accompanied by Munsel color notations in parentheses. Collection numbers preceeded by PR- or GUA- refer to a unique number in the database for the Basidiomycetes of the Greater Antilles project; ledger

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[2] The Forest Products Laboratory in Madison, Wisconsin is maintained in cooperation with the University of Wisconsin and the one in Puerto Rico is maintained in cooperation with the USDA Forest Service, International Institute of Tropical Forestry. This article was written and prepared by a U.S. government employee on official time and is therefore, in the public domain and not subject to copyright.

numbers are also presented, if assigned. Chemical reagents including Melzer's solution, gum-guaiac, 2% phenol, and $FeSO_4$ were used for spot testing tissue samples when appropriate and the reactions recorded. Drawings of the illustrated taxa were made from mounts in Melzer's solution. Smell and taste were recorded when possible from fresh material. E value is length/width ratio of the basidiospore and E_m is the mean E of n = 31 spores. For color images of several of the taxa described here see http://www.cortland.edu/NSF/ga.html.

RESULTS

Eleven putative ectomycorrhizal taxa are described, five of which are new species. The other six species represent new range extensions. The genus *Amanita* has most of these new taxa, therefore, we present a dichotomous key to those species. These are the only species now known in the area covered in this study and are all in the subgenus *Amanita.* The descriptions are presented in three groups corresponding to their taxonomic relatedness.

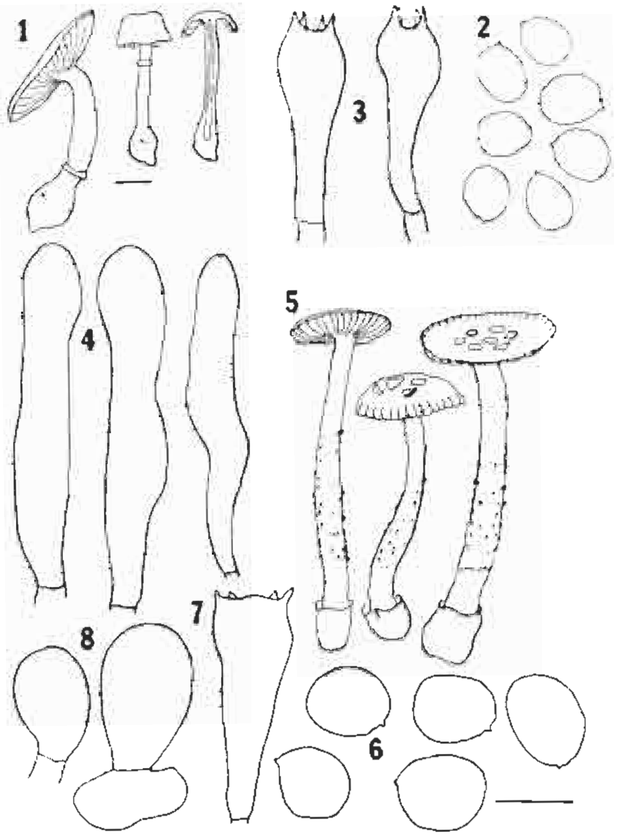
KEY TO THE SPECIES OF *AMANITA* OF PUERTO RICO, AND THE US AND BRITISH VIRGIN ISLANDS

Subgenus *Amanita*; nonamyloid spores, and only associated with species of *Coccoloba.*

1. Annulus cothurnate, persistent; pileus yellow with a white universal veil; cheilocystida clavate to subfusiform; spores 7–10.5 × 4.8–6.0 µm . . . . . . *A. cystidiosa*
1. Not annulate or partial veil evanescent and other characters not as above 2
    2. Pileus pale drab-gray; stipe with a small white, fragile volval cup; spores 9–12.5 × 7–10 µm, subglobose; cheilocystidia pyriform to subglobose . . . . *A. arenicola*
    2. Pileus orange or yellow, spores smaller or <7 µm wide 3
3. Pileus orange-yellow in center, paler over margin; spores 5–7 × 4.5–6.7 µm, subglobose E_m = 1.12 . . . . *A. microspora*
3. Pileus chrome yellow; spores 7–10.5 × 5–7 µm, broadly elliptical E_m = 1.31 . . . . *A. chrysoleuca*

Amanita cystidiosa O. K. Miller et D. J. Lodge, sp. nov. FIGS. 1–4, 9

Pileus 2.0–4.7 cm latus, primo convexus sub vetustate planus, in statu madido subviscidus, in superficie reliquias volvae universalis tenui-farinosas retinens, pallide stramineus, in margine tenuiter sulcato-striatus. Lamellae liberae, subdistantes, ventricosae, 2-seriebus lamellularum praeditae, sub vetustate pallide flavae vel flavae. Stipes 1.9–5.2 cm longus, 0.4–0.7 cm latus, aequus bulbo basali abrupte rotundato praeditus, siccus, albus praeter flavescentem in bulbo per reliquias volvae universalis. Volva partialis persistens, annulum cothurnatum formans. Contextus solidus, albus. Odor non distinctus. Pileipellis e hyphis intertextis latis tenuitunicatis 4.2–20 µm in diametro composita. Volva partialis e hyphis filamentosis tenuitunicatis 5–9 µm in diametro composita. Volva universalis e hyphis intertextis tenuitunicatis 4.0–13.0 µm in diametro cellulas clavatas distinctas 15–27 µm in diametro habentibus composita. Fibulae absentes. Cheilocystidia 45–55 × 7–11 µm, clavata vel subfusiformia, tenuitunicata, ½ vel ⅓ longitudinis eorum protrudentia. Basidia 25–30 × 8–9.5 µm, clavata, tenuitunicata, 4-sterigmatiphora. Basidiosporae 7–9(–10.5) × (4.8–)5.5–6.0 µm (E_m = 1.34: E = 1.15–1.53) brevi-ellipticae, tenues vel leniter crassitunicatae, in solutione Melzeri inamyloideae. Holotypus in thiniis arenarum sub *Coccoloba uvifera,* silva Piñones, prope Loiza, Puerto Rico, 14 Jan 1998 lectus. Leg. Lodge & Miller (NY, OKM 27232).



FIGS. 1–8. *Amanita cystidiosa* and *A. arenicola.* 1–4. *A. cystidiosa.* 1. Fruiting bodies. 2. Basidiospores. 3. Basidia. 4. Cheilocystidia. 5–8. *A. arenicola.* 5. Fruiting bodies. 6. Basidiospores. 7. Basidium. 8. Cheilocystidia. Bars: 1, 5 = 1 cm (upper bar); 2–4, 6–8 = 10 µm (lower bar).

Pileus 2.0–4.7 cm broad, convex, becoming nearly plane in age, subviscid when wet, covered with a very fine mealy, white remains of the universal veil, pale straw yellow (Met 2A2, Met 1A2) ground color, margin finely sulcate-striate. Lamellae free, ventricose, 2 tiers of lamellulae (L = 2), subdistant, yellow (Met 4A3-4), young light yellow (Met 4A2). Stipe 1.9–5.2 cm long, 0.4–0.7 cm wide equal with an abrupt round basal bulb, white except for the bulb which is covered with the appressed remains of the universal veil and plicatis praeditus. Lamellae liberae, angustae, approximatae, albae, lamellulis inserie unica dispositis praeditae. Stipes 9.5–10 cm longus, 0.5–1.0 cm latus, subaequalis basi anguste clavatus, laevis, madidus, obscure albus, cupula volvali fragili alba praeditus. Volva universalis e hyphis filamentosis hyalinis, in partibus subaequis inter cellulas globosas, subglobosas vel pyriformes hyalinas tenuitunicatas mixtis composita. Pileipellis ex serie unica repenti hypharum hyalinarum, cylindracearum 2.5–5.0 µm diametro composita. Fibulae absentes. Cheilocystidia sparsa hyalina pyriformia subglobosa vel globosa 18–30 × 13–17 µm. Basidia 35–55 × 12–14 µm clavata tenuitunicata hyalina, 4-sterigmatophora. Basidiosporae 9–12.5 × 7–10 µm (E_m = 1.25; E = 1.11–1.43), subglobosae vel late ellipticae tenuitunicatae hyalinae, in 3% KOH guttula oleosa ampla flava praeditae, in solutione Melzeri inamyloideae. Holotypes in solo arenoso sub *Coccoloba uvifera* in White Bay Rd., Guana Island, British Virgin Islands, 27 Oct 1997 lectus. Leg. Lodge (NY, GUA 109).

Pileus 3.5–5.5 cm broad, strongly depressed to infundibuliform, moist to sticky, sand covered, smooth, Drab Gray, with flat pale buff (124) (0.9Y 7.77/5.5) detersile patches of universal veil in the center, margin evenly pale Drab Gray (5.64,6.82,2.4) and plicate-striate. Lamellae free, narrow (5 mm broad), close, white, one tier of lamellulae, edges even. Stipe 9.5–10 cm long, 0.5–1.0 cm wide, nearly equal with a narrowly clavate base, smooth, moist, dull white with a small, fragile, white, volval cup, often appressed but one half or more free, often with the ragged remains of the veil in the sand or adhering to the lower stipe. Context soft, fragile, white. Pileipellis of hyphae 2.5–5.0 µm diam, thin-walled, filamentous, hyaline in 3% KOH, yellowish in Melzer's solution. Pileitrama of interwoven, broad, thin-walled, hyaline hyphae (3.4–) 6–25 µm diam, mostly filamentous, sometimes swollen. Lamellar trama of filamentous to broad and swollen, thin-walled hyphae 4.2–21 µm diam. Subhymenium of short, isodiametric cells, thin-walled, hyaline. Universal veil of filamentous, hyaline hyphae intermixed with a nearly equal proportion of globose, subglobose to pyriform, hyaline, thin-walled cells. Clamp connections absent. Cheilocystidia infrequent to frequent, of pyriform to subglobose or globose cells 18–30 × 13–17 µm thin-walled, hyaline. Basidia 35–55 × 12–14 µm clavate, thin-walled, 4-spored, hyaline. Basidiospores 9–12.5 × 7–10 µm (E_m = 1.25: E = 1.11–1.43) subglobose to broadly elliptic, thin-walled, hyaline with a large yellow oil body in 3% KOH, nonamyloid in Melzer's solution.

Habit, habitat, and distribution. In sandy soil under *Coccoloba uvifera* usually on beaches in Puerto Rico, and the Islands of Anguila and Guana in the Virgin Islands, fruiting in wet cool weather from July to December.

Etymology. arena = sand; cola = dweller.

Material examined. BRITISH VIRGIN ISLANDS. ANGUILLA: The Mariners Hotel, 8 Jul 1993, ANG-2, Coll. *D. J. Lodge* (CFMR). GUANA ISLAND: White Bay, beach road, 1 m elev, 180° 28' 39" N, 640° 34' 41" W (all of the following collections), 19 Oct 1997, GUA-38, Coll. *D. J. Lodge* (VPI); 27 Oct 1997, GUA-109, Coll. *D. J. Lodge* (HOLOTYPE, NY; ISOTYPE, CFMR); 2 Oct 1998, GUA-179, Coll. *D. J. Lodge & N. Clum* (CFMR; NY); 2 Oct 1998, GUA-180, Coll. *D. J. Lodge & N. Clum* (CFMR, NY); 2 Oct 1998, GUA-181, Coll. *D. J. Lodge & N. Clum* (NY); 2 Oct 1998, GUA-190, Coll. *D. J. Lodge & N. Clum* (CFMR); 2 Oct 1998, GUA-191, Coll. *D. J. Lodge & N. Clum* (NY); 2 Oct 1998, GUA-192, Coll. *D. J. Lodge & N. Clum* (CFMR, NY); 2 Oct 1998, GUA-193, Coll. *D. J. Lodge & N. Clum* (NY); 2 Oct 1998, GUA-196, Coll. *D. J. Lodge & N. Clum* (CFMR); 2 Oct 1998, GUA-195, Coll. *D. J. Lodge & N. Clum* (CFMR); 2 Oct 1998, GUA-196, Coll. *D. J. Lodge & N. Clum* (CFMR); 2 Oct 1998, GUA-197, Coll. *D. J. Lodge & N. Clum* (CFMR); 5 Oct 1998, GUA-198, Coll. *D. J. Lodge & N. Clum* (PARATYPE, NY; ISOPARATYPE, CFMR); 5 Oct 1998, GUA-199, Coll. *D. J. Lodge & N. Clum* (CFMR, NY); 6 Oct 1998, North Bay Woods near beach, GUA-215, Coll. *D. J. Lodge* (K). USA. PUERTO RICO: Municipio Fajardo, near Luquillo, La Selva (Governor's) beach, 1 m. elev, 21 Dec 1997, PR-4716, Coll. *L. Barley & E. Garcia* (VPI); 21 Jul 1998, same location, PR-4908, Coll. *D. J. Lodge & N. Perez* (CFMR); 21 Jul 1998, PR-4909, Coll. *D. J. Lodge & N. Perez*; Municipio Rio Grande, Piñones Commonwealth Forest, beach near Loiza, 1 m elev, 23 Dec 1997, PR-4717, Coll. *J. Trappe, D. J. Lodge & M. Castellano* (UPRRP).

Observations. The nonamyloid spores, type of volva, lack of a partial veil, and the plicate-striate pileus margin are all characters of the subgenus *Amanita* sect. *Vaginatae*. The characteristic drab gray cap coloration; very small, fragile, white, saccate volva; buff volval patches at the cap center and the distinctive type of universal veil tissue are characteristics of the species. The growth in beach sand, often in foredunes, associated with *Coccoloba uvifera* is a distinctive habitat. *Amanita sinicoflava* Tulloss is similar (Tulloss 1988) but has some obvious differences. In *A. sinicoflava* the volva is deeply saccate and the stipe has characteristic chevron-like rows of fibrils, often grayish in color, and a saccate volva with the "interior pale orangish or pinkish becoming gray" which are all phenotypic characters not present in *A. arenicola*. The pileus coloration and anatomical details of the universal veil combined with differences in spore size are different from the two taxa in sect. *Vaginatae* with a membranous universal veil described by Tulloss et al (1992). Pegler (1983) described *A. antillana* Dennis from the Lesser Antillies. This taxon is found in forests associated with *Coccoloba diversifolia* Jacq. and is in the sect. *Vaginatae* but differs in some respects. The pileus is brown to olive-brown, but the nonamyloid spores, measuring 10–13.5 × 7.5–11.5 µm with E_m = 1.26, are somewhat similar. Dennis (1952)

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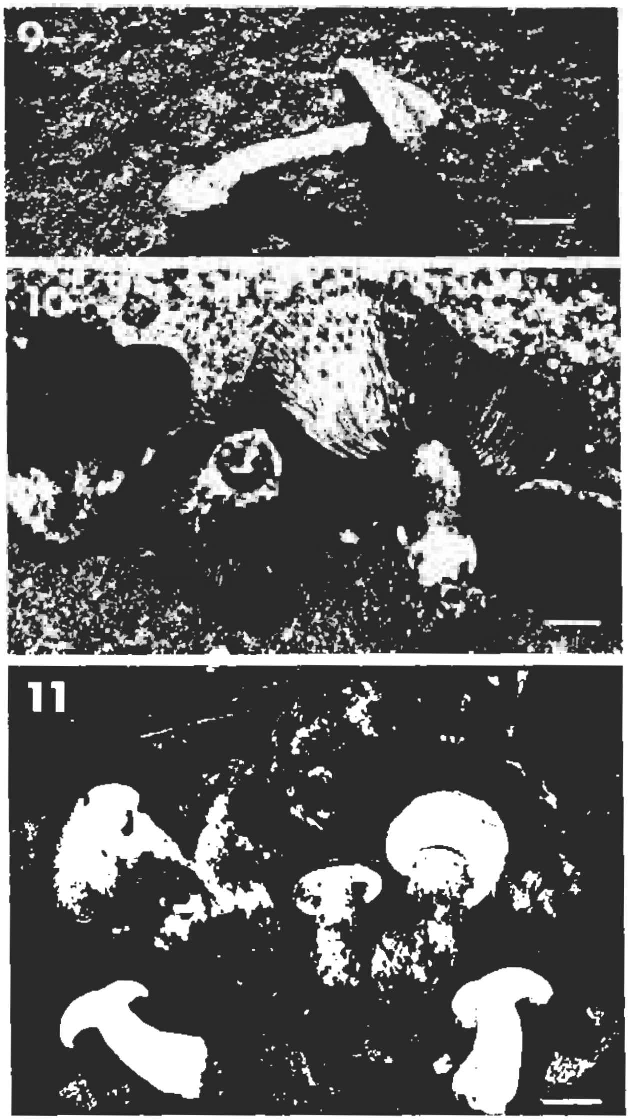


FIGS. 9–11. 9. *Amanita cystidiosa*. 10. *Lactarius coccolobae*. 11. *Phlebopus beniensis*. Bar = 1 cm.

is yellowish (near Met 4A2), fine white rhizomorphs emanate from the base. Partial veil leaves a persistent cothurnate, white annulus which flares upwards but may vary from inferior to superior. Context firm, white, unchanging in cap, stipe white and solid outside with a soft center. Smell not distinctive. Pileipellis of interwoven, broad, thin-walled hyphae 4.2–20 µm diam, hyaline in 3% KOH, yellowish in Melzer's solution. Pileitrama of interwoven broad hyphae 4.2–24 µm diam, hyaline in 3% KOH, yellowish in upper trama to dextrinoid in the lower trama in Melzer's solution. Lamellar trama of thin-walled, hyaline hyphae, yellowish with a hue of deep reddish color [dextrinoid] in Melzer's solution. Partial veil of filamentous, thin-walled hyphae 5–9 µm diam, mostly of short, frequently branched cells. Universal veil of tightly interwoven cells 4.2–13 µm diam, thin-walled, hyaline with frequent, enlarged, distinctive clavate cells 15–27 µm diam, thin-walled, and hyaline. No clamps seen on any tissue. Cheilocystidia 45–55 × 7–11 µm clavate, narrowly clavate to subfusiform, thin-walled, protruding one-third to one-half, numerous. Basidia 25–30 × 8–9.5 µm clavate, thin-walled, 4-spored hyaline in 3% KOH and Melzer's solution. Basidiospores 7–9(–10.5) × (4.8–)5.5–6 µm (E_m = 1.34: E = 1.15–1.53), short ellipsoidal, thin to slightly thick-walled, nonamyloid in Melzer's solution. Spore print pure white.

Habit, habitat, and distribution. Solitary to scattered in sand in the dunes or fore dunes among or close to *Coccoloba uvifera* and a wide spread decumbant shrub, coco plum, *Chrysobalanus icaco* L. (Rosaceae); fruiting in Jan.

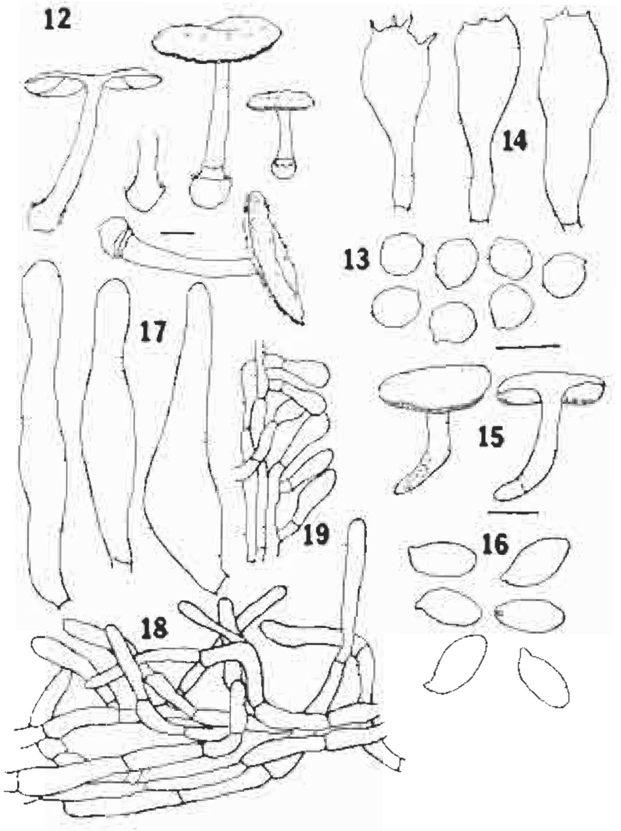
Etymology. *cystidiosa* refers to the cheilocystidia.

Material examined. USA. PUERTO RICO: Piñones Commonwealth Forest, beach near Loiza, 14 Jan 1998, Coll. *D. J. Lodge, O. K. & H. Miller* OKM 27232 (PR-5462) (HOLOTYPE, NY; ISOTYPE, CFMR); OKM 27234 (PR-5463) (PARATYPE, VPI; ISOPARATYPE, UPRRP).

Observations. A taxon meeting this description has not been collected before on Puerto Rico. The species is in the subgenus *Amanita* sect. *Amanita.* In the area where the holotype (OKM 27232) was found, a second collection, (OKM 27234) was made and both were in sand close to *Coccoloba uvifera* on the open beach. The persistent, membranous white annulus that flares; subviscid straw yellow pileus; clavate to subfusiform, thin-walled, protruding, cheilocystidia; filamentous partial veil and filamentous universal veil with clavate end-cells are a combination of unique characters in the genus *Amanita.* The spores are nonamyloid, short elliptic with a thickened wall. The presence of clavate to subfusiform cheilocystidia is the first demonstration of true cystidia for *Amanita* section *Amanita.* Jenkins' (1977) study of the North American taxa in the section *Amanita* reports that the gill edge is "frequently covered with inflated cells or hyphae being remnants of tissue between gills and partial veil." The cystidia in *A. cystidiosa* are derived from the lamellar trama and not remnants of a tissue differentiated during primordial development. Recently described species of *Amanita,* including reports from the Caribbean region by Tulloss (1989, 1990, 1995), Tulloss et al (1992), and Pegler (1983), do not include a taxon phenotypically similar to *A. cystidiosa*.

Amanita arenicola O. K. Miller et D. J. Lodgé, sp. nov. FIGS. 5–8

Pileus 3.5–5.5 cm latus, depressus vel infundibuliformis, madidus, laevis, sublutescenti-canus sed in centro maculis volvae universalis pallide bubalinis ornatus, in margine striis



FIGS. 12–19. *Amanita microspora* and *Boletus ruborculus*. 12–14. *A. microspora*. 12. Fruiting bodies. 13. Basidiospores. 14. Basidia. 15–19. *B. ruborculus*. 15. Fruiting bodies. 16. Basidiospores. 17. Pleurocystidia. 18. Pileipellis. 19. Stipitipellis. Bars: 12, 15 = 1 cm (upper bar); 13–14, 16–19 = 10 µm (lower bar).

stated that the volva was missing on the type collection from Trinidad, even though the fruiting body was carefully excavated. Pegler (1983) states that subsequent collections of *A. antillana* from Guadeloupe and Martinique in the Lesser Antilles have an ochraceous brown volva, unlike the white volva in *A. arenicola*. Examination of the holotype was carried out and the spores are larger than those of our taxon along with the differences in the volva noted above.

Amanita microspora O.K. Miller, sp. nov. FIGS. 12–14

Pileus 3–5 cm latus convexus, vetustate subdepressus primo immaculate albus dein cito super discum flavidus vel ochraceus, margine lata alba striata ornatus, madido viscidus, in superficie areis parvis agglutinatis detersilibus albis atque reliquiis floccosis volvae universalis irregulariter dispersis instructus. Lamellae liberae subdistantes ventricosae, lamellulis curtis infrequentibusque praeditae, primo albae vetustate pallide ochraceae. Stipes 3.5–6 cm longus, 0.3–0.5 cm latus, usque ad bulbum ovalem album abruptum in base usque ad 1.5 cm latum aequalis, albus, siccus, in omni superficie subtiliter granularis, super medium annulis concentricis pallide flavidis atque proxime super et super bulbum basalem squamulis grossis albis ornatus. Contextus firmus albus. Volva partialis nulla. Et odor et sapor non distinctus. Pileipellis cutem e hyphis cylindricis 4.2–13 µm diametro compositam formans. Trama lamellaris e hyphis divergentibus 4–13 µm diam composita.Volva universalis e hyphis filamentosis 2–10 µm diametro inter cellulas pyriformes vel clavatas mixtis composita. Fibulae absentes. Cheilocystidia absentia. Basidia 18–29 × 6–9.5 µm clavata, tenuitunicata, 4-sterigmatophora. Basidiosporae 5–7 × 4.5–6.7 µm [E_m = 1.12; E = 1.0–1.34], globosae vel subglobosae, tenuitunicatae, in solutio Melzeri inamyloideae. Holotypus in solo arenaceo inter thinia littoralia, *Coccolobae uviferae* consociata, prope Piñones, Loiza, Puerto Rico, 19 Nov 1996 lectus. Leg *E. Horak* (ZT 6125).

Pileus 3–5 cm broad, convex becoming slightly depressed in age, pure white at first, soon pale yellow to ochre over the disc with a broad, white, striate margin, viscid when moist with detersile, agglutinated, white patches and the floccose remains of the universal veil unevenly scattered over the surface. Lamellae free, subdistant, ventricose, lamellulae short and infrequent, white at first soon becoming pale ochre in age. Stipe 3.5–6 cm long, 3–5 mm wide, equal with an abrupt oval bulb to 15 mm wide at the base, white, dry, with a fine granular surface and light yellowish tinted belts over the mid surface, coarse white squamules just above and over the basal bulb. Context firm, white. Partial veil absent. Odor and taste not distinctive. Pileipellis of loosely arranged hyphae 4.2–13 µm diam, thin-walled, hyaline to light yellowish in 3% KOH. Pileitrama interwoven, thin-walled hyaline, hyphae 4.2–13 µm diam. Lamellar trama of divergent hyphae 4–13 µm diam, thin-walled, hyaline to light yellowish in 3% KOH and Melzer's reagent, clamp connections absent on all tissues. Universal veil of filamentous hyphae 2–10 µm diam with about 30% ovoid, pyriform to clavate cells 15–32 µm wide and 30–71 µm long, thin-walled, hyaline, clamp connections absent. Cheilocystidia not seen. Basidia 18–29 × 6–9.5 µm diam, clavate, thin-walled, 4 spored. Spores 5–7 × 4.5–6.7 µm, [E_m = 1.12; E = 1.0–1.34] ovoid globose to subglobose, thin-walled, hyaline in 3% KOH, nonamyloid in Melzer's solution.

Habit, habitat, and distribution. On sandy soil in coastal sand dunes with *Coccoloba uvifera*; fruiting in Nov.

Etymology. microspora = small spores.

Material examined. USA. PUERTO RICO: Municipio Rio Grande, Piñones Commonwealth Forest, beach near Loiza, 1 m elev, 19 Nov 1996, ZT-6125. Coll. *E. Horak* (HOLOTYPE, CFMR; ISOTYPE, UPRRP).

Observations. This taxon resembles *Amanita gemmata* (Fr.) Bertillon, which is a nonannulate species that has nonamyloid spores 8.5–11 × 5.5–8.5 µm diam with E_m = 1.38. Our taxon has much smaller, nonamyloid spores (5–7 × 4.5–6.7 µm) with E_m = 1.12. *Amanita cystidiosa* and *A. chrysoleuca* have larger nonamyloid spores.

Amanita chrysoleuca Pegler, Kew Bull. Addit. Ser. IX: 285. 1983.

Pileus 11–62 mm broad, broadly convex, becoming plane to slightly depressed or umbonate, smooth, shiny, moist, deep chrome yellow to orange-yellow, sulcate and translucent striate at the margin, occasionally with pale pinkish buff veil remnants. Lamellae free or narrowly adnexed, 1–6 mm wide, edge even, wavy or slightly serrated, white to cream color. Stipe 50–80 mm long, 4–8 mm wide, equal or tapering somewhat toward apex, dry, base with a small oval marginate bulb. Pileipellis of thin-walled, hyaline hyphae 7–8 µm diam. Pileitrama a textura angularis of thin-walled, hyaline cells 7.6–22 µm diam, lower trama a mixture of filamentous, hyaline hyphae 4.5–6.8 µm diam and ovoid, elliptical to irregular, swollen cells up to 30 µm diam. Lamellar trama narrowly divergent, broad, thin-walled hyphae 9–19 µm diam, hyaline in 3% KOH and Melzer's solution. Cheilocystidia 17–39 × 11–25 µm ovoid, clavate, sphaeropedunclate, thin-walled, hyaline, scarce to absent at times. Basidia 30–40 × 7–11 µm broadly clavate to clavate, thin-walled, hyaline, 4-spored. Basidiospores 7–10(–10.5) × 5–7 µm (E_m = 1.31; E = 1.0–1.7) subglobose, ellipsoidal, occasionally globose, thin-walled, nonamyloid in Melzer's solution, hyaline in 3% KOH with oil bodies in some.

Habit, habitat, and distribution. Gregarious in a subtropical moist forest, on ground; fruiting in Nov.

Material examined. US VIRGIN ISLANDS. ST JOHN: Bordeaux Mtn., 350–400 m elev, 15 Nov 1996, St. J. 280, coll. *E. Horak* (NY); same loc. and date, St. J. 318, coll. *S. A. Cantrell and B. Ortiz* (NY); near Bordeau Mtn. Peak, 17 Nov 1996, St. J. 276, coll. *E. Horak* (NY).

Observations. The chrome yellow pileus, stature, lack of a membraneous volva, and the nonamyloid spores fit the species as described by Pegler (1983). The spores are globose and differ somewhat from the shape described by Pegler. Our spores have E_m = 1.31 while those described by Pegler are 1.56.

Boletus ruborculus Baroni, sp. nov. FIGS. 15–19

Pileus 2.2 cm latus convexus tomentosus rubellus, super discum brunneo-tinctus. Contextus albus vel juxta tubos subcitrinus, in areis flavis immutans vel inordinate caerulescens. Tubi aurei, dente curto decurrenti adnati, 2 mm profundi. Pori concolores angulares 1 mm, ubi contusi immutati vel interdum tarde subcaeruleofusci. Stipes super basem atrovinosus, alibi pallide cremeus vel pallide lutescens, 2.5 cm longus, in apice 0.4 cm latus, aequus laevis sed velamine dense fibrilloso obtectus, solidus, contextu sordide olivaceo-luteo in basi atrovinoso praeditus. Pileipellis trichodermium pallide lutescenti-brunneum e hyphis cylindricis laevibus 4–7 µm diametro compositum formans. Et pleurocystidia et cheilocystidia conformia, hyalina, tenuitunicata, fusoidea vel ventricosa, aliquot cylindrica 40–60 × 6.5–12 µm. Basidia clavata, 4–sterigmatophora, 26–35 × 11–12 µm. Fibulae nullae. Basidiosporae 9–12.4 × 4.8–6.4 µm (E_m = 1.97; E = 1.77–2.27), brevi-subfusiformes. Holotypus in basi arboris viventis in summo collis calcarei. Saeptis Privatis Mata de Platano, Barrio Dominguito, Arecibo, Puerto Rico, 8 Nov 1996 lectus. Leg. *Baroni, Cantrell* et *Bird* (NY, Baroni 8253).

Pileus 2.2 cm broad, convex, matted tomentose, dull brick red (Met 7B4 grayish red, or Met 8C4 dull red), with more brownish hues over the disc (Met 6E4 brown). Context lemon yellow over tubes, sordid whitish elsewhere, unchanging or erratically bluing in yellow areas adjacent to the tubes when exposed. Tubes adnate with short decurrent tooth, 2 mm deep, chancelleries with pores. Pores sordid golden yellow (Met 4C5 chamois), angular, approx. 1/mm, some compound, unchanging when bruised or after a long period becoming slightly bluish fuscous. Stipe 2.5 cm long, 0.4 cm wide at apex, equal, terete, not reticulate, smooth, rhubarb red over the lower ⅓ (Met 10E5-6 violet brown), pallid elsewhere with a cream to yellowish appressed dense fibrillose covering, solid, context rhubarb red in base, dingy olivaceous yellow to apex, not changing color when exposed. Smell and taste not distinctive. Pileipellis a loosely entangled lax trichodermium of cylindric, nonencrusted hyphae in 3% KOH, 4–7 µm diam; in H_2O the end cells possess brownish olivaceous globular intracellular pigments which dissolve in 3% KOH producing a diffuse pale yellowish brown color. Pileitrama a hyaline layer of intricately interwoven, cylindrical hyphae, 5–12 µm diam. Tube trama divergent, with a distinct mediostratum of cylindric to mostly inflated hyphae, 6–16 µm diam, and a diverging laterostratum of cylindric hyphae, 4–6 µm diam. Pleuro- and cheilocystidia similar, hyaline, thin-walled, mostly rounded fusoid, ventricose or some cylindric, 40–60 × 6.5–12 µm. Stipitipellis over the apex a hyaline layer of repent, loosely interwoven, cylindric hyphae, 6–8 µm diam, producing scattered clusters of hyaline, thin-walled, clavate or cylindric caulocystidia, 14–26 × 6–8 µm. Basidia clavate, 4-sterigmate, 26–35 × 11–12 µm. Clamp connections absent. Basidiospores 9–12.4 × 4.8–6.4 µm (= 10.6 × 5.4 µm; E_m = 1.97; E = 1.77–2.27), short subfusiform with pronounced suprahilar depression, smooth, slightly thick-walled, olive brown in 3% KOH. Spore deposit color not known.

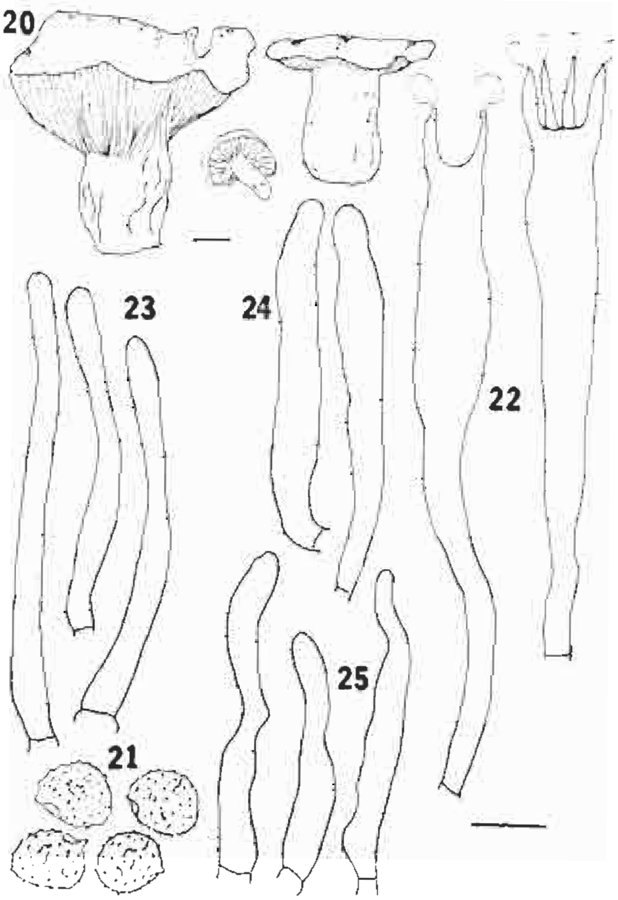
Habit, habitat, and distribution. On the side of a living tree, near *Coccoloba* sp., Nov.

Etymology. rubor = redness; culus = little.

Material examined. USA. PUERTO RICO: Arecibo, Barrio Dominguito, Mata de Platano Private Reserve, N 18° 24′ 49.6″, W 66° 43′ 33.1″, approx. 940 m elev. on top of a limestone hill (a mogote) above bat-inhabited caves, on the side of a living tree. 8 Nov 1996. Coll. *T. J. Baroni, S. A. Cantrell & F. Bird*, PR-4926, ledger 8253 T. J. Baroni (NY, HOLOTYPE).

Observations. Boletus ruborculus is somewhat reminiscent of *B. rubellus* Kromb. and related taxa such as *B. campestris* Smith & Thiers; however, several features may be used to clearly distinguish these taxa. Most importantly both *B. rubellus* and *B. campestris* have distinctly yellowish flesh in the pileus and stipe that becomes obviously blue or bluish green when exposed (Both 1993, Breitenbach and Kränzlin 1991, Smith and Thiers 1971). In the case of *B. rubellus* the surface of the stipe also turns bluish green after bruising. *Boletus ruborculus* has a whitish pileus context that does not turn blue or does so only erratically at the junction with the tubes. The stipe context remains completely unchanged in *B. ruborculus* when exposed, and the stipe surface does not change color when handled or bruised intentionally. The size of the basidiospores also distinguishes *B. campestris* from *B. ruborculus* because they are clearly shorter in *B. ruborculus*, i.e., basidiospores of *B. campestris* measure 11–14(–15) × 4.5–6(–7) µm (Smith and Thiers 1971) whereas those of *B. ruborculus* measure 9–12.5 × 4.8–6.4 µm.

Corner (1972) and Singer (1947) discuss several tropical and subtropical taxa that are superficially similar to *B. ruborculus*, but these taxa are clearly different when compared to *B. ruborculus*. For instance Corner (1972) describes *B. rubellus* subsp. *borneensis* Corner, which has yellow flesh that becomes rapidly and intensely cyanescent on exposure. *Boletus monsfraseri* Corner is similar to *B. ruborculus* by its white unchanging context, but differs markedly by the inflated cells in the pileipellis. *Boletus phoeniculus* Corner has a pileipellis composed of cylindric septate hyphae, but the context is yellow and not cyanescent. *Boletus rubellus* ssp. *consobrinus* Singer is a taxon from limestone soils like *B. ruborculus*, but the context of *B. rubellus* ssp. *consobrinus* is yellow with erratic bluing when exposed, there is a striking pale greenish yellow mycelium at the base of the stipe, and the fresh basidiomata have a disagreeable odor "of old, dirty clothing" (Singer 1947). This group of small red capped boletes, centered around *B. rubellus*, is obviously quite diverse in their combinations of morphological characters.



FIGS. 20–25. *Lactarius coccolobae*. 20. Fruiting bodies. 21. Basidiospores. 22. Basidia. 23. Dermatocystidia. 24. Caulocystidia. 25. Cheilocystidia. Bars: 20 = 1 cm (upper bar); 21–25 = 10 µm (lower bar).

Lactarius coccolobae O. K. Miller et D. J. Lodge, sp. nov. FIGS. 10, 20–25

Pileus (1.8–)5–11 cm latus, robustus planus, sub vetustate elevatus, siccus, primo obscure cremeus deinde mox per discolorationes variegatas brunneas vel atro-brunneas tinctus. Lamellae adnatae, congestae, primo albae sub vetustate brunneae, laticem album producentes, areis superficies ubi contusis vel sectis tarde atrobrunnescentibus reagentibus praeditae. Stipes 2–4 cm longus, 1.2–2.2 cm latus, siccus, apice laevis, in parte inferiore minute hirsutus, obscure albus, brunnescens vel atrobrunnescens ubicumque contusus. Contextus solidus vel tenax, primo albus, ubi sectus vel contusus per colorem obscure brunneum tinctus. Pileipellis velamen e pileocystidiis cylindricis vel fusiformibus 24–65(–122) × 3.6–5.4 µm compositum formans. Subpellis e hyphis implextis gelatinosis 2.7–4.5 µm diametro composita. Basidia 60–79(–85) × 8.1–9.5 µm, clavata, tenuitunicata, 2–vel 4–sterigmatophora. Basidiosporae 7.2–9(–10) × 5.8–8.4 µm, (E_m = 1.26: E = 1.13–1.55) subglobosae, in parte subapicali et verrucis humilibus (<0.3 um altis) amyloideis et reticulis infirmis partialibus praeditae. Holotypus in thiniis arenarum sub *Coccoloba uvifera*, silva Piñones, prope Loiza, Puerto Rico, 14 Jan 1998 lectus. Leg. Lodge and Miller (CFMR, OKM 27240).

Pileus (1.8–)5–11 cm broad, robust, plane, repand or upturned in age, dry, dull cream but soon staining a mottled brown, light brown (Met 6E-F 4-6) to dingy blackish brown, inrolled margin in buttons becoming plane in age. Lamellae adnate, crowded, white at first, with a white whey-like latex that stains the gill tissue dark brown where cut or bruised, in age generally mottled brown and subdistant (Met 5E-F 4-7). Stipe 2–4 cm long, 1.2–2.2 cm wide, equal, with dingy mottled light brown (Met 5D4) to dark brown (Met 5F 5-6), minutely hairy (use lens), smooth just at the apex. Context very firm to tough, white at first but soon staining on exposure to air a dull mottled brown (Met 5E5), when bruised with the knife darkening to dingy brown to black-brown at the base. Taste sweet and mild. Smell strongly of fish or herring, like *L. volemus* (Fr.) Fr., and is a room-filling odor persisting in dried material. Pileipellis an irregular turf of pileocystidia 24–65(–122) × 3.6–5.4 μm cylindrical or tapering toward apex, thin-walled, hyaline or with light brown slightly thick-walled, arising from a narrow layer of interwoven, gelatinized hyphae 2.7–4.5 μm diam, with deep yellow-brown incrusted material in Melzer's solution and 3% KOH. Pileitrama of broader, filamentous, rectangular to irregular thin-walled, interwoven hyphae 4.5–10.5 μm diam, hyaline in Melzer's solution and 3% KOH, with frequent dark yellow brown lactiferous hyphae 7.2–9 μm diam, especially in the lower trama. Lamellar trama of tightly packed, interwoven, thin-walled, hyaline hyphae 3.6–9 μm diam with frequent deep yellow-brown, laticiferous hyphae. Caulocystidia 39–45 × 3.6–5.4 μm cylindrical to narrowly fusiform, occasionally subcapitate, thin-walled, hyaline or with a light brownish hue in 3% KOH, numerous. Cheilocystidia 35–65 × 2.5–5 μm, hyphalike, fusiform with an apical projection to narrowly clavate, thin-walled, hyaline, protruding only slightly if at all, scattered not frequent. Basidia 60–79(–85) × 8.1–9.5 μm clavate, thin-walled, 2 to mostly 4-spored, sterigmata 5.5–7 μm long. Basidiospores 7.2–9(–10.8) × 5.8–8.4 μm, (E_m = 1.26; E = 1.13–1.55) subglobose with a subapical plage, and a short hyaline apiculus, fine very low (<0.3 μm) amyloid often irregular warts and few to frequent weak amyloid partial reticulations.

Habit, habitat, and distribution. Scattered in sand on dunes under *Coccoloba uvifera*; fruiting in November on Guana Island but in January at the Piñones Commonwealth Forest in Puerto Rico.

Material examined. BRITISH VIRGIN ISLANDS. GUANA ISLAND: North Bay Beach, 2 m elev. N 18° 29' 42", W 64° 33' 40", 21 Oct 1998, GUA-186, coll. *N. Clum* (PARATYPE, NY; ISOPARATYPE, VPI). USA. PUERTO RICO: Municipio Loiza, Piñones Commonwealth Forest, beach near Loiza, 2 m elev, 14 Jan 1998, OKM-27240, coll. *D. J. Lodge and O. K. & H. Miller* (HOLOTYPE,CFMR; ISOTYPE, UPRRP).

Observations. The fruiting bodies of this species are very robust, with adnate, close to crowded lamellae and a short stipe and sporophores which are very close to or buried in the sand. The flesh of the fruiting bodies stain brown when bruised, immediately yielding a whey-like white latex in buttons but often the latex can only be observed in age by cutting the specimens in half and observing the latex at the margin of the gills and tramal tissue. The pungent fishy odor persists in the dried specimens, which are very tough. Material soaked in 95% ethanol and water yields a wine colored extract and softens very slowly. In addition, the pileipellis has a turf of pileocystidia best seen in the young specimens arising from a layer of interwoven gelatinized hyphae, the spores have very low ornamentation (mostly >0.2 μm high) and the cheilocystidia are hyphalike to narrowly clavate. It also has numerous caulocystidia. It is a member of the subgen. *Lactifluus* sect. *Lactifluus* (Hesler and Smith 1979). It does appear to be closely related to *L. caribaeus* Pegler (Pegler 1983). Both have similar microscopic anatomy, especially the low individual warts that form the spore ornamentation, and spore size. However, the basidia of *L. coccolobae* are distinctly shorter and the pileipellis is gelatinized. There are distinctive macroscopic differences. The lamellae of *L. caribaeus* are deeply decurrent, subdistant with numerous lamellulae of two lengths, as illustrated by Pegler (1983, Fig. 123A and color Plate 20C), and are not adnate and crowded. In addition, the odor is reminiscent of urine rather than rotting fish. The stipe surface of *L. caribaeus* is described as pure white at first and glabrous. It is found associated with *Coccoloba pubescens* L. and *C. diversifolia* in degraded xerophytic forests and not in a dune habitat. Both of these taxa are distinctly different from any taxon now placed in the section but they have several characters in common with *L. luteolus* Peck. Fruiting bodies of *Lactarius luteolus* are not robust, have a different but similar pileipellis, smaller basidia and higher ornamentation on the spores. In addition, the cystidia are thin-walled in our material and the taste is mild. The holotype of *L. luteolus* was studied and also does not have the extractable wine colored pigment, which is so obvious when sections of *L. coccolobae* are soaked in 95% ethanol.

Lactarius ferrugineus Pegler, Kew Bull. 33: 626. 1979.

This species is widespread in the mountain ranges of Puerto Rico. It has been collected on various soil types under *Coccoloba* spp. and *Pisonia* spp. In the Central Mountain Range, it was found on serpentine soil in the Maricao Municipio Recreation area and on nonserpentine soils in the Municipio of Orocovis in the Toro Negro Commonwealth Forest. In the Luquillo Mts. Caribbean National Forest. *L. ferrugineus* has been collected under *Coccoloba swartzii* in the Municipio of Río Grande, Palo Hueco area.

Material examined. USA. PUERTO RICO: Maricao Municipio, Maricao Recreation area, 25 Jun 1996, 7950 *T. J. Baroni* (NY), and PR-3295, coll. *D. J. Lodge* (CFMR); Municipio of Orocovis, Toro Negro Commonwealth Forest, El Bolo Trail, 10 November 1996, PR-3722, leger *Cantrell* PR-96150, coll. *S. A. Cantrell & C. Betancourt* (UPRRP); Luquillo Mts., Caribbean National Forest, Municipio of Río Grande, Palo Hueco area off Rt. 186, 600 m elev, N 18° 18′ 15′, W 65° 49′ 21″, elev 500–600 m, 7 Oct 1996, PR-3443, ledger Cantrell PR-96111 coll. *S. A. Cantrell* (CFMR); 13 Apr 1998, PR-4860, ledger *Cantrell* PR-9848, *S. A. Cantrell & C. Laboy* (CFMR); 9 Oct 1998, PR-5241, ledger *Cantrell* PR-9889, coll. *S. A. Cantrell & N. Clum* (CFMR); 12 Jan, 1999, PR-5511, ledger Clum NCC-992, coll. *S. A. Cantrell & D. J. Lodge* (CFMR); under *C. rugosa* in the Represa Icaco & Represa Prieto, by waterfall near dam, Caribbean National Forest, Municipio Naguabo, 450 m elev, N 18° 15′ 24″, W 66° 46′ 45″, 7 Jul 1999, PR-5512, ledger *Clum* NCC-9958, coll. *S. A. Cantrell & N. Clum* (CFMR); Aguas Buenas Municipio, near Bayamoncito, on Cerro La Tiza, N 18° 14′ 32.4″, W 66° 10′ 53.9″, 23 Jun 1996, PR-3618, ledger *T.J. Baroni* 7930 (CORT).

Observations. Our specimens fit exactly the description provided by Pegler (1983) for *L. ferrugineus* described from the island of Martinique. This report serves as the first documentation of this taxon from the Greater Antilles. *Lactarius ferrugineus* is easily recognized in the field by its orange brown pileus and stipe with pinkish or buffy tan adnate lamellae. The small to medium sized pileus has a low mamillate or papillate umbo, a subtly rugulose surface, and a short striate or plicate-sulcate margin. The latex is white, unchanging and the taste is bitterish and then peppery hot. The strongly reticulate ornamented spores are also diagnostic.

Lactarius nebulosus Pegler, Kew Bull. 33: 610. 1979.

Material examined. BRITISH VIRGIN ISLANDS. GUANA ISLAND: North Bay woods, in sandy soil under *Coccoloba uvifera*; N 18° 28′ 42″ W 64° 34′ 40″, 24 Oct 1997, *D. J. Lodge* GUA-104 (CFMR).

Observations. The pale to dark grayish pileus, the white lamellae that stain cinnamon-brown, the white or creamy white latex that turns cinnamon-brown, the odor of fish or rotting flesh, and the acrid or peppery taste are characters that help to identify *L. nebulosus* in the field. The distinctive and abundant sphaerocysts in the lamellar trama, the dense turf of narrowly cylindrical hyphae making up the trichodermium of the pileipellis, and the ellipsoid basidiospores with isolated conical amyloid verrucae are distinctive microscopic features of this species. *Lactarius nebulosus* was previously only known from the island of Martinique. This report extends its range to the Virgin Islands in the Puerto Rican Bank. We expect other collections will eventually be found on Puerto Rico and other large islands in the Greater Antilles.

Russula littoralis Pegler, Mycotaxon 12: 93. 1980.

Pileus 3.8–11.0 cm broad, broadly convex, becoming plane with a shallow, broadly depressed disc, surface glabrous, moist or very slightly tacky over the margin, dull yellowish to cream color over the disc (3.4Y 8.4/4.2) (Met 3A4), the margin is olive-gray (Met 3C2-3), to Drab Gray (0.64 6.82/2.4) or brownish gray Glaucus 80 (6.5Y 5.90/1.2) tinted lilac over the outer one-half of the surface. Lamellae adnate, close to crowded, narrow, white, in age yellowish, Pale Horn Color (2.5Y 8.08/3.5) paler than (Met 4A3-4), 4–5 mm broad, 1 mm at margin, with occasional long lamellulae that fork just at the stipe. Stipe 1.5–4.0(–5) cm long, 0.8–1.6(–2.8) cm broad, nearly equal or bulbous, clavate in one specimen, glabrous, dry, dull white. Context soft and pure white, unchanging when bruised. Taste sweet or not distinctive. Odor not distinctive. Pileipellis a turf of erect dermatocystida, hyaline, thin-walled, hyphal-like 1.7–2.5 μm diam, often decumbent in age. Subpellis a dense, thick layer of interwoven, thin-walled hyphae 2–5 μm diam embedded in a hyaline, gelatinous layer in 3% KOH to yellowish in Melzers reagent. Pileitrama a heteromerous tissue of thin-walled, hyaline sphaerocysts 10–29 × 7.5–20 μm diam with filamentous hyphae 3–7 μm diam, hyaline in 3% KOH, light yellow in Melzer's reagent. Lamellar trama of filamentous, inflated, to ovoid cells 3–13 μm diam, thin-walled, hyaline in 3% KOH, yellowish in Melzer's solution. No clamp connections seen. Cheilocystidia and pleurocystidia 50–78 × 8–9 μm diam, numerous, narrowly clavate with subcapitate to mucronate apices, thin-walled, yellowish contents. Basidia 36–41 × 10–12 μm diam, clavate, thin-walled, hyaline, 4-spored. Basidiospores 6.7–10 × 6–8 μm (E_m = 1.15; E = 1.0–1.33) globose, subglobose or broadly ellipsoidal, thin-walled, with a small apiculus and small oval plage, small amyloid warts <0.3 μm high, solitary or partially connected by amyloid, weak low ridges. Spore deposit cream (Met 3A2) to dark cream or pale ochre buff (Romagnesi 1967: IId "crème foncé" to IIIa "ocre pâle"). Reagents: $FeSO_4$ negative; gum-guaiac faint bluish; 2% phenol negative.

Habit, habitat, and distribution. Puerto Rico, Mona and Virgin Islands; fruiting in coastal sand foredunes and dune slack near or under *Coccoloba uvifera* during the rainy season (Sep through Nov) often following several days of torrential rains.

Material examined. BRITISH VIRGIN ISLANDS GUANA ISLAND: North Bay Woods, in sand under *C. uvifera*, 2 m elev. N 18° 29′ 32″ W 64° 33′ 40″, 2 Oct 1997, GUA-103, Coll. *D. J. Lodge* (CORT); 3 Oct 1998, GUA-183, Coll. *D. J. Lodge & N. Chun* (CFMR); 6 Oct 1998, GUA-185, Coll. *D. J. Lodge* (CFMR). White Bay Beach, 2 m elev. N 18° 28′ 39″, W 64° 34′ 41″, 2 Oct 1998, GUA-178, Coll. *D. J. Lodge & N. Chun* (NY); 3 Oct 1998, GUA-184, Coll. *D. J. Lodge & N. Chun* (NY); 1 m elev 5 Oct 1998, GUA-182, Coll. *D. J. Lodge & N. Chun* (NY). USA. PUERTO RICO: Mona Island, Playa de Pajaros, near new ranch and entrance to Cueva del Caballo, 1.5 m elev. N 18° 18′ 15″, W 67° 43′15″, 25 Sep 1995, PR-3792 and PR-3897, Coll. *A. M. Nieves-Rivera* (UPRRP); Puerto Rico Island, Loiza Municipio, Piñones Commonwealth Forest, beach near Loiza, in sand behind foredunes, 2 m elev. near *C. uvifera*, 19 Nov 1996, PR-4985, ledger *T. J. Baroni* 8347, Coll. *T. J. Baroni* (CORT); same location and date, PR-3987, Coll. *D. J. Lodge & T. J. Baroni* (CFMR); same location and date, PR-3988, Coll. *D. J. Lodge* (NY); same location, 14 Jan 1998, OKM-27242, Coll. *D. J. Lodge, O. K. & H. Miller* (VPI).

Observations. The species was described by Pegler (1980) from Grand Macabou, Martinique in sand under the "Seagrape," *Coccoloba uvifera.* This is the identical habitat in which we have found our fungus on Puerto Rico as well as Guana and Mona Islands. The description of *R. littoralis* by Pegler from Martinique in the Lesser Antilles (Pegler 1983) is very close to the material from the same habitats in Puerto Rico, Mona Island and Guana Island. However, the spore size is somewhat larger than that which we have recorded (6.5–8.0 × 5.5–6.5 µm vs 6.7–10 × 6–8 µm, respectively).

Russula puiggari (Speg.) Singer, Lilloa 23: 239. 1950.

= *Clitocybe puiggari* Speg., Bol Acad. Cienc. Cordoba 9: 389. 1889.

= *Russula brasiliensis* Singer, Pap. Mich. Acad. Sci. Arts & Letters 32:108. 1948.

As pointed out by Pegler (1983), *Russula puiggarii* is relatively common in tropical regions of the Lesser Antilles and South America. Our report of this species in Puerto Rico serves as the first for the Greater Antilles. The single collection was found on humus and soil near *Pisonia* aff. *subcordata* Sw. in the El Verde Research area of Puerto Rico; N 18° 19′ 30″, W 65° 49′ 5″, 2 Feb 1998, Coll. *T. Bruns, D. J. Lodge* and *P. Bayman*, PR-4719 (CFMR).

The brown pileus with its distinctly striate or sulcate-striate margin and exposed white context in radial lines due to radial splitting of the surface layers are distinctive field characters of this taxon. The complex, three-layered pileipellis and the strongly reticulate globose basidiospores are also characteristic for this species. Our collection displays all of the morphological features reported for *R. puiggarii* by Pegler (1983) and Singer (1948) except for one minor difference. In our collection the pleurocystidia, which are pseudocystidia, frequently have strangulated or torulose apices. The pleurocystidia of *R. puiggarii* from the Lesser Antilles and South America have been described as simply ventricose. It will be interesting to see if this minor morphological difference is consistent with the northernmost collections of this taxon when further material becomes available.

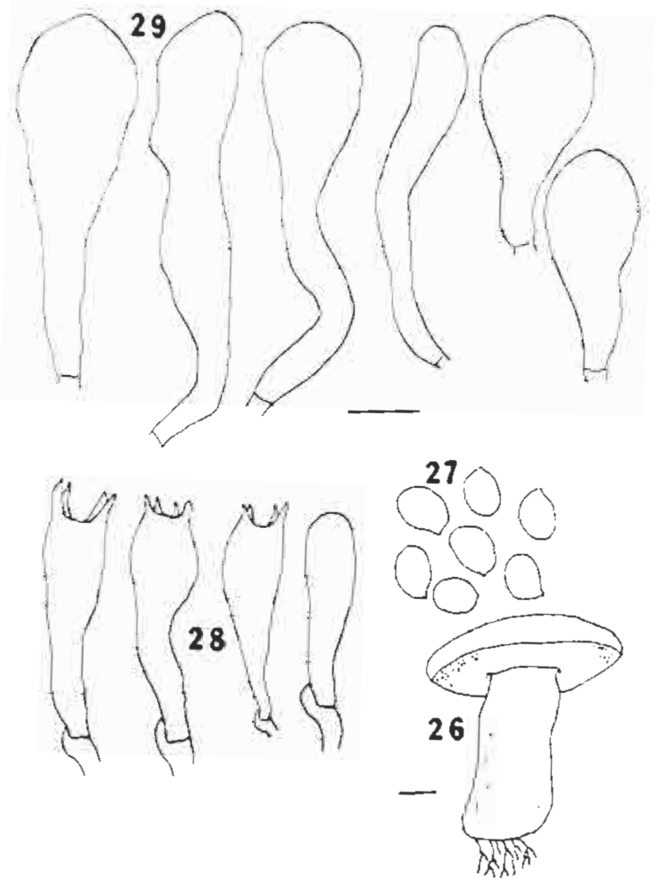
Phylloporus Quél. sp.

Pileus 22 mm broad, moist, somewhat felt-like, orange-brown. Lamellae broadly adnate, lamellate near the stipe to poroid over the margin, 2–3 mm thick, uneven and intervenose, yellow-orange, no blue staining observed when bruised. Stipe 14 × 4 mm equal, moist, smooth, yellowish. Context light buff, firm, bruising pinkish. Pileipellis a trichoderm composed of narrow, nearly cylindrical to narrowly fusiform thin-walled, hyaline cells 34–93 × 3.5–5.0 µm diam arising from a subpellis of interwoven hyphae 3.4–6.5 µm diam, thin-walled, hyaline in 3% KOH and Melzer's solution. Pileitrama of interwoven, thin-walled hyphae 2.5–10.5 µm diam, thin-walled filamentous, hyaline, hyphae on average somewhat larger than the cells of the pileipellis. Lamellar trama of large, hyaline, thin-walled cells 7.6–19 µm diam interwoven but extending almost to the hymenium giving rise to branching subhymenial cells and basidioles, no clamps seen on any tissue. Cheilocystidia long, narrowly fusiform, thin-walled cells 55–64 × 7.5–9.5 µm, hyaline in 3% KOH and Melzer's solution, protruding one-third to one-half beyond the basidia. Basidia 28–43 × 8–9 µm narrowly clavate, thin-walled, hyaline, 4-spored, no clamp connections. Basidiospores 6.5–8.0(–9) × 2.5–3.5(–4) µm diam (E_m = 2.41; E = 1.62–3.00) oblong to oblong-ellipsoidal, thin-walled, light brown in Melzer's solution and 3% KOH.

Habit, habitat, and distribution. One very small cap was found among the *Phlebopus beniensis* collection, OKM 27200, on ground in a subtropical moist forest, on a well drained site, at 70′ elev; fruiting in Jan.

Material examined. USA. PUERTO RICO: Between Luquillo and Sabana Field Station, off of Rt. 991 near Rio Sabana, 300 m elev. above a private chicken farm in subtropical moist forest, N 18° 21′ 3.4″, W 65° 42′ 50″, 10 Jan 1998, Coll. *H. Miller*, OKM 27205 (VPI).

Observations. The single small specimen has spores that are distinctly smaller than found in any known species of *Phylloporus*. The spores of *P. rhodoxanthus* (Schw.) Bres. are 11–15 × 4.5–6 µm (Miller 1973). In addition, the specimen has a very loculate hymen-



FIGS. 26–29. *Phlebopus beniensis*. 26. Fruiting body. 27. Basidiospores. 28. Basidia. 29. Cheilocystidia. Bars: 26 = 1 cm (lower bar); 27–29 = 10 µm (upper bar).

ophore and lacks blue staining when bruised. More material needs to be collected to provide a complete description of this new taxon. The species of *Phylloporus* are mycorrhizal fungi and this species is almost certainly ectomycorrhizal with the same host as that of *Phlebopus beniensis* (Sing & Digilio) Sing., which was fruiting all around this specimen. Additional information about the ecology is given in observations following the description of *Phlebopus beniensis*.

Phlebopus beniensis (Sing. & Digilio) Sing., Beih. Nova Hedw. 77:46. 1983. FIGS. 11, 26–29

= *Paeogyroporus beniensis* Sing. & Digilio, Lilloa 30:150. 1960.

Pileus 2.6–7.1 cm broad, broadly convex, felt-like, dry, smooth, black-brown to deep red-brown [Caill.T73; Met 7F4-6,9F3-4], margin incurved until maturity. Tubes adnate, 2–4 mm deep. Pores 3–4 per mm, stuffed and appearing pustulate at first, opening in age, uneven at maturity, yellow (Met 4A4-6) gradually staining light blue when bruised. Stipe 2.5–5 cm long, 0.9–2.1 cm wide at apex enlarging somewhat toward base to 17–28 mm wide forming a narrowly clavate base, sometimes yellowish just at the apex, black-brown (Met 8E-F4-5) overall with a fine, sparse, evanescent network of yellow fibrils (mycelium, use lens) over the surface, copious light brown rhizomorphs at the base. Context firm, orange-yellow (Met 3A4) when first cut, darkening somewhat when bruised, on standing fading to light straw yellow. Smell stale farinaceous that persists in the dried collections. Taste mild. Pileipellis a narrow layer (40–65 µm thick) of hyaline, gelatinized hyphae 2.5–6.0 µm diam; subpellis of interwoven, yellow-brown, thin-walled hyphae with scattered clamp connections, wine red in 3% KOH and Melzer's solution. Pileitrama of interwoven, thin-walled to slightly thick-walled hyphae, scattered clamp connections, hyaline in 3% KOH and Melzer's solution. Tube trama of slightly divergent, hyaline, thin-walled, hyphae 3.4–5.5(–8.5) µm diam, with scattered yellow-brown oleiferous hyphae, scattered clamp connections. Cheilocystidia abundant, 28–55 × 6–15 µm clavate, broadly clavate, thin-walled, hyaline in 3% KOH and Melzer's solution. Basidia clavate, thin-walled, with a basal clamp connection, hyaline in 3% KOH and Melzer's solution. Basidiospores 5.0–6.8 × 3.8–5.5 µm (E_m = 1.29; E = 1.09–1.52) elliptic, smooth, thin-walled to slightly thick-walled, olivaceous brown. Spore print olive-brown (Met 3E4-5).

Habit, habitat and distribution. On the ground on or near a dirt road at 300′ elev in a dry subtropical forest, on a well drained site; fruiting in Jun.

Material examined. BOLIVIA. Vaca Diez, Guayaramerin, 6 Mar 1956, Singer B1613 (LIL, HOLOTYPE). USA. PUERTO RICO: Municipio Luquillo, between Luquillo and Sabana, off of Rt. 991, above Río Sabana and a private chicken farm, 70 m elev, N 18° 21′ 3.4″, W 65° 42′ 50″, 7 Jun 1997, PR-5034, ledger *T. J. Baroni* 8495, Coll. *T. J. Baroni* (NY); same location, 6 Jun 1998, PR-5452, Coll. *O. Isikhuemen* (DK, CFMR); same location, 10 Jun 1998, PR-5467 ledger OKM 27200, Coll. *D. J. Lodge, O. K. & H. Miller* (CFMR); same location, 15 Jan 1998, PR-5468, ledger OKM 27252 and OKM 27254, Coll. *H. & O. K. Miller* (VPI).

Observations. *Phlebopus* species were first placed in *Phaeogyroporus* Sing. (Singer and Digilio 1960). Species now assigned to *Phlebopus* were segregated from other boletes (Singer 1936, Singer et al 1983) because of their short spores and because of the abundant clamp connections found on the hyphae of the basidiomata. *Phlebopus* is apparently allied to *Gyrodon* Opat. and is placed in the Gyrodontiae (Singer 1986). There are currently seven species known from Africa and or Australasia and three species known from the neotropics. Only one of these three species has previously been reported from the Lesser Antilles (Pegler 1983). This description serves as the first report of a *Phlebopus* for the Greater Antillian island chain. The Puerto Rican collection comes from a dry subtropical forest of approximately 100 m elev. Although no known ectomycorrhizal symbiont was identified as an associate with this bolete, because of the existence of a *Phylloporus* species nearby, we suspect *Phlebopus* may actually form ectomycorrhizae with *Hymenaea courbaril* L. This large leguminous caesalpinoid tree, not presently known as a mycorrhizal former, was a suspect and the dominant tree near to which these two boletes were found. Another possible legume host in the vicinity was *Andira inermis*, which forms ectendomycorrhizae (Lodge 1996).

The black-brown to red-brown smooth cap and distinctive black-brown stipe with a yellow apex, fine yellow pores, and very slow blue staining even when bruised vigorously, are distinctive characters. In addition, the yellow, sparse, evanescent fine fibrils (use lens) over the surface of the stipe is most unusual for a bolete. Young specimens tend to be in the red-brown color range while older caps are black-brown fading to orange-brown. All specimens are evenly or nearly evenly colored with a conspicuously incurved margin. Note that in the same location several additional collections were found. The cap of OKM 27252 was 9.5 cm broad, the cap had faded to red-brown in the center (Met 6F5-6) the rest orange-brown (Met 5C5-6) but the rest of the fresh characteristics were the same as in the specimens described above. The additional collection, OKM 27254, was some distance from the two mentioned above but the two fruiting bodies were old and overmature.

Suillus brevipes (Peck) Kuntze, Rev. Gen. Pl. 3:535. 1898.

We have three collections of this ectomycorrhizal bolete from red clay soil on a bank under planted *Pinus caribaea* Morelet in the Adjuntas Municipio, Guilarte Forest Reserve, on the slopes of Silla de Calderón in Puerto Rico, N 18° E 09′ 17.7″ W 66° E 48′ 34.9″. *Suillus brevipes* is now documented from the Caribbean region. This is a plantation and the *Suillus* is not native. It was most likely introduced to Puerto Rico in pine soil/duff from North Carolina by the USDA Forest Service in 1955 in order to stimulate pine growth (see Vozzo 1971). The chocolate or vinaceous-brown, viscid pileus, lack of a thin white partial veil, and short whitish stipe that lacks prominent glandulae make this species easy to identify in the field. The subfusiform basidiospores that measure 8–9 × 2.4–3.2 μm diam are also typical for this species.

Material examined. USA. PUERTO RICO: Morelet, Adjuntas Municipio, Guilarte Commonwealth Forest, N 18° 9′ 17.7″ W 66° 48′ 34.9″, 7 Nov 1996, PR-1913, ledger *T. J. Baroni* 8241, Coll. *T. J. Baroni* (NY); same location, 24 Jan 1997, PR-4128, Coll. *S. A. Cantrell & D. J. Lodge* (CFMR); same location, 22 Jan 1998, PR-4904, ledger *S. A. Cantrell* PR-9824, coll. *S. A. Cantrell, J. Trappe & M. Castellano* (CFMR).

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A new species of *Mabuya* (Sauria: Scincidae) from the British Virgin Islands

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Abstract.—*Mabuya macleani*, new species, is a pallid, drab, almost patternless skink which is abundant on Carrot Rock, British Virgin Islands. *Mabuya sloanii* shows character divergence in pattern from the new species concordant with geographic approach to within 400 m. On Puerto Rico, *M. sloanii* has a broad middorsal bronzy area on the anterior dorsum. On most of the smaller islands of the Puerto Rico Bank, as well as the Mona and Desecheo Banks to the west, this middorsal area is much narrowed by the presence of well-developed dark dorsolateral stripes stretching from the head to behind the forelimbs. These two pattern types, which apparently intergrade in the vicinity of northeasternmost Puerto Rico, are recognized as *M. s. nitida* Garman and *M. s. sloanii* Daudin, respectively. The specific name "mabouya" Lacépède, formerly applied to Antillean skinks, is shown to be unavailable. The presence of *M. macleani* and another endemic lizard (*Anolis ernestwilliamsi*) on such a small (1.3 ha), poorly isolated, and young (<3000 y) island as Carrot Rock may be a striking case of rapid divergence of insular populations.

> "The coloration is highly interesting . . . several insular forms may be distinguishable when adequate series become available." Karl P. Schmidt (1928)

The scincid lizards of the genus *Mabuya* are nearly tropicopolitan in distribution. We have collected or examined them in numbers from the Antilles, South America, tropical Asia, and Africa. Throughout this vast range, most species are brown with near-black stripes extending the length of the body. A striking exception is on Carrot Rock, a very small (1.3 ha), steep-sided island off the southeast end of Peter Island in the British Virgin Islands (Fig. 1).

On 13 July 1985, while one of us (GCM) climbed the biggest tree on the island in search of anoles, the other (JL) toiled in the dust in the little gully on the windward side of Carrot Rock in which the tree grew, looking for *Sphaerodactylus* geckos. A far larger, drab, pale lizard was turned out, and ran up his sleeve. Although this initial specimen was distinctive, we at first referred to it as *Mabuya mabouya sloanii* (Mayer & Lazell 1988), the common skink of the Virgin Islands (MacLean 1982, Lazell 1983), pending collection of further specimens. Over the next several years JL returned to Carrot Rock occasionally, and found an area where these peculiar pallid lizards were abundant, and succeeded in capturing five more individuals (of dozens seen). These specimens, as well as comparison with *Mabuya* from throughout the islands of the Puerto Rican Bank, have abundantly confirmed the distinctiveness of this population, and also brought into sharp focus a most intriguing evolutionary phenomenon. We here describe this distinctive *Mabuya* as:

Mabuya macleani, new species

Mabuya mabouya sloanii.—Mayer & Lazell, 1988:23 (in part).

Fig. 1. Carrot Rock, British Virgin Islands, viewed from the north, 17 July 1988. Windward is to the left, leeward to the right. The highest elevation is ca. 25 m. From a Kodachrome transparency by GCM.

Holotype.—Museum of Comparative Zoology (MCZ) 170884, collected on Carrot Rock, south of Peter Island, British Virgin Islands, 18°19′45″N, 64°34′18′W, by J. Lazell, 13 Jul 1985 (Fig. 2D).

Paratypes.—All from the type locality: MCZ 182270–72, 17 Jul 1988; MCZ 176728 and University of Michigan Museum of Zoology (UMMZ) 197261, both 26 Oct 1991.

Diagnosis.—A pallid tan to brownish-gray New World *Mabuya* (Dunn 1936, Greer 1970) with one or two pairs of enlarged nuchals (their combined widths more than 75 percent of the width of the parietals); two frontoparietals; parietal overlapping upper anterior temporal (Greer & Nussbaum 2000); midbody scales in 32–34 rows; 16–18 subdigital lamellae under fourth toe of pes; limbs moderately long; dark dorsal markings fragmented or absent on head and separated from dark dorsolateral stripes on nape; nape stripes reduced, separated by all or most of two dorsal scales and not extending more than 21 dorsal scales posterior to parietals; lateral dark stripes poorly developed. *Mabuya macleani* is distinguished from the geographically nearest populations of *M. sloanii* by the much reduced dorsolateral dark stripe, the continuous stripe beginning behind the head in *M. macleani* (on the head in *M. sloanii*), and extending only to the level of the forelimbs (behind the forelimbs in *M. sloanii*).

Description of the type.—Rostral wider than high, bordered dorsoposteriorly by the nasals and paired supranasals, which are in narrow contact. The frontonasal is broader than long and in contact with the frontal. The paired prefrontals are separated medially by the contact of the frontonasal with the frontal. The frontal is about three quarters as long as its distance from the posterior parietal edge. There are four supraoculars, the second the largest. There are three supraciliaries, the first by far the longest. The two frontoparietals are in contact with the second, third, and fourth supraoculars, bordered posterolaterally by the parietals, and posteriorly by the interparietal, in which the parietal foramen is posteriorly situated. The large, paired parietals are in contact posterior to the interparietal, that on

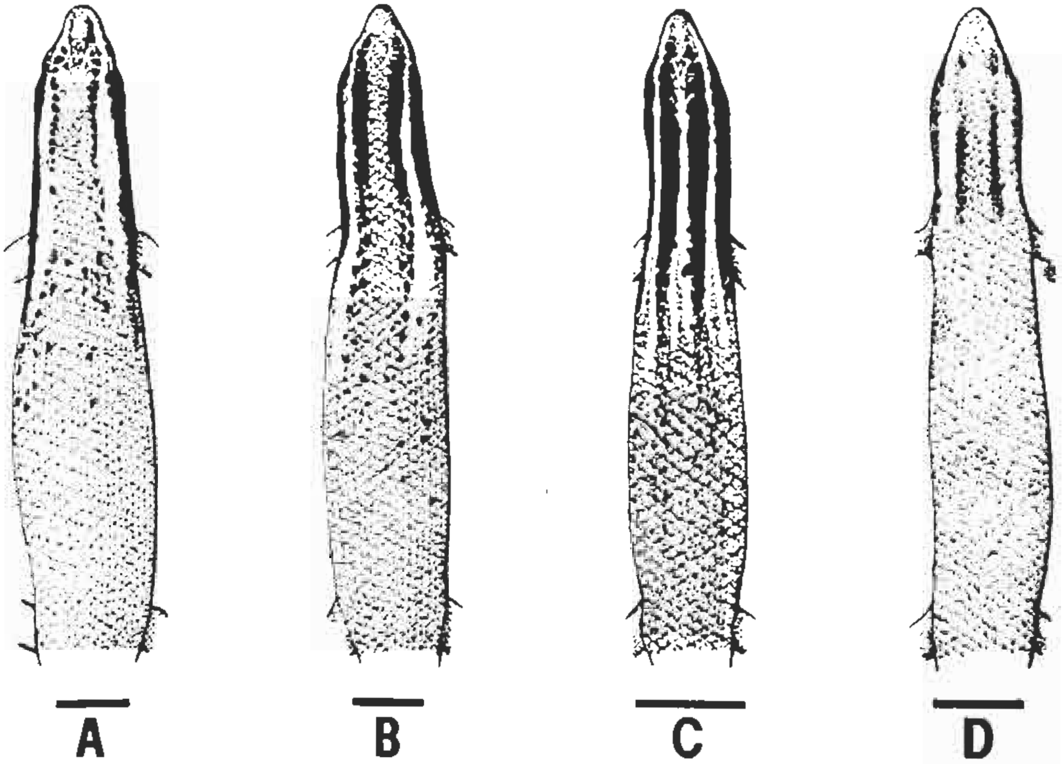

Fig. 2. Dorsal patterns of skinks from the Puerto Rican Bank. A–C, geographically approaching Carrot Rock: A) MCZ 6050, lectotype of *Mabuya sloanii nitida*, San Juan, Puerto Rico, ca 164 km WNW of Carrot Rock. B) MCZ 36624, intergrade, *M. s. nitida* × *sloanii*, Cayo Icacos, ca. 102 km WNW of Carrot Rock. C) MCZ 182273, *M. s. sloanii*, Stoney Bay, Peter Island, British Virgin Islands, 400 m N of Carrot Rock. D) MCZ 170884, type of *Mabuya macleani*, Carrot Rock, British Virgin Islands. Bars below lizards indicate 1 cm in each case.

the right extending further posteriorly. The parietals overlap the upper anterior temporal. There is one pair of transversely enlarged nuchals, but the second and third nuchals are enlarged on the left side.

The nasal is subrectangular in side view, with the large nostril posteriorly located, followed by the postnasal and two loreals; the anterior one on the left is much larger than the posterior, but the two are subequal on the right. The anterior loreal is in contact with the prefrontal, but the posterior loreal is separated from the latter scale by a presupraciliary. The sixth supralabial on the left, and the fifth on the right, are about twice as long as the others, the enlarged supralabial on each side forming a long subocular. There is a clear disk in the lower eyelid about as wide as the ear opening. The temporals are larger than the trunk scales. There are no auricular denticles. There are two pairs of chin shields in contact posterior to the mental.

Scales of body and limbs imbricating, subcycloid, regularly arranged in rows. Thirty-four longitudinal rows at midbody, 57 transverse rows dorsally from parietals to anterior edge of hind limb, 61 ventrally from mental to vent. The vent is bordered anteriorly by eight subequal scales. Scales of soles and palms tubercular, transition from imbricate scales of limb to tubercular scales abrupt. Thirteen lamellae under fourth toe of manus, 17 under fourth toe of pes. Adpressed limbs do not meet.

In life, the type was pallid beige-gray

Table 1.—Some characteristics of *Mabuya macleani.* "Scales" are number of rows around trunk at midbody. "Stripe" is the length of the dorsolateral dark stripe in dorsal scales posterior to the parietals (left/right).

	SVL	Scales	Supra-nasals	Stripe	Nuchal Pairs	Appressed limbs
MCZ 170884	69.5	34	Contact	15/16	1	Fail to meet
MCZ 176728	71.0	32	Contact	18/18	1	Toes barely touch
MCZ 182270	80.5	32	Contact	17/18	2	Fail to meet
MCZ 182271	76.0	32	Contact	18/15	1	Fail to meet
MCZ 182272	63.0	32	Separated	17/18	2	Meet
UMMZ 197261	44.5	32	Fused	21/21	1	Toes overlap

with a faint trace of a lateral stripe extending to just above the axilla. There are two dark dots on the frontonasal and a little dark gray flecking on the supraoculars. The plain lead-gray dark dorsolateral stripes end 15 (left) or 16 (right) dorsal scales posterior to the parietals.

Variation.—Some characteristics of *Mabuya macleani* are given in Table 1, and measurements in Table 2. The holotype is fairly typical of the type series in its squamation, and the paratypes do not present a great deal of variability. Dorsal and ventral head scales of MCZ 182270 are shown in Fig. 3. This specimen shows two unusual conditions: the presence of an intercalary scale separating the first supraocular from contact with the frontal on the left side of the head, and the partial fusion of the fourth supraocular with the parietal, also on the left side. Contact of the supranasals is variable, being separated in one specimen, touching in four, and even fused medially into a single scale in another. The prefrontals are never in contact medially. In lateral view, the head squamation of *M. macleani* is essentially similar to that of *M. sloanii* shown by Schmidt (1928:122).

The following summary of meristic variation gives for each character the range, followed by the mean and sample size in parentheses. For some bilateral characters the sample size has been reckoned by the number of sides rather than specimens, and this is noted after the sample size. Supraoculars: 4 (4.0, 12 sides); supraciliaries: 2–4 (3.0, 6 sides); supralabial subtending the eye (subocular): 5–6 (5.3, 11 sides); mid-

Table 2.—Measurements (mm) of holotype and three paratypes of *Mabuya macleani.*

	MCZ 170884 Holotype	MCZ 182270 Paratype	MCZ 182271 Paratype	MCZ 182272 Paratype
Snout-vent length	69.5	80.5	76.0	63.0
Tail length	52+	67+	56+	75.5
Axilla-groin length	38.0	45.0	40.5	34.5
Snout length	5.4	5.7	5.7	5.0
Snout width	5.5	5.5	5.4	4.9
Head length	11.9	13.0	12.8	11.4
Head width	8.2	10.2	10.2	8.0
Upper arm length	5.5	6.5	6.0	5.0
Lower arm length	4.9	5.5	6.5	4.7
Palm length	1.9	2.8	2.6	2.9
Fourth finger length	4.5	4.5	4.5	4.0
Upper leg length	8.0	8.0	8.0	7.0
Lower leg length	6.6	7.5	7.3	6.6
Sole length	3.4	3.8	4.3	3.1
Fourth toe length	6.5	7.0	7.0	7.5

+ Tail broken or regenerated.

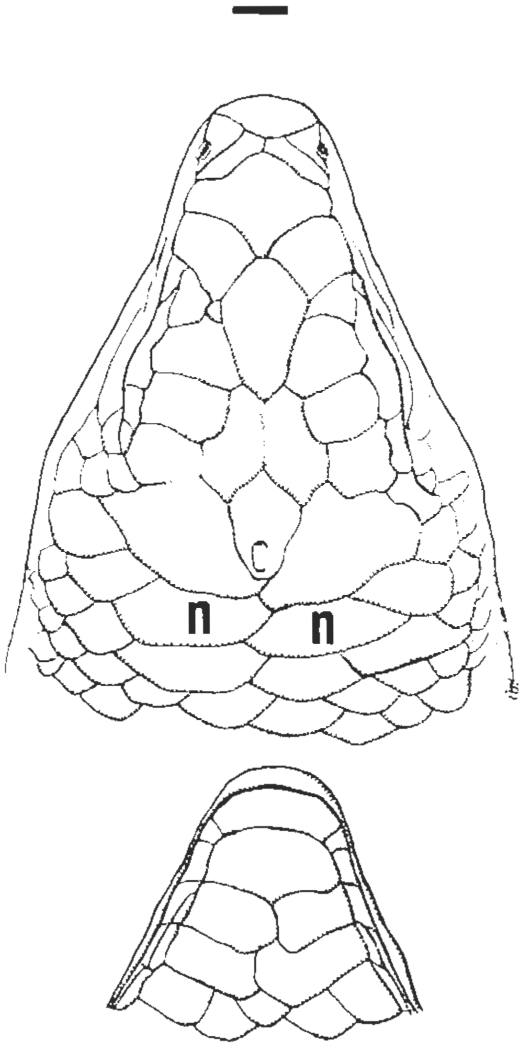

Fig. 3. Aspects of head squamation in MCZ 182770, *Mabuya macleani* paratype. The first pair of enlarged nuchals are marked "n." Bar is 1 mm.

body scale rows: 32–34 (32.3, 6); transverse dorsal rows: 54–58 (56.0, 4); transverse ventral rows: 58–66 (61.2, 6); fourth toe of manus lamellae: 13 (13.0, 4); fourth toe of pes lamellae: 16–18 (17.2, 5).

All *Mabuya macleani* have a much reduced pattern of striping compared to the near-black striping typical of Antillean *Mabuya* (Fig. 2), but the extent of reduction varies, and seems to be size related, with smaller specimens having less reduced markings. All specimens of *M. macleani* have paired blotches on the frontonasal, but they are scarcely evident on the largest specimen (MCZ 182270), in which, were it not for their presence in the other specimens, they might be taken to be merely two of several scattered dark mottlings on the head, rather than reduced pattern elements. In all specimens the dorsolateral stripe is short and starts on the neck, beginning 3–5 (4.6, 12 sides) scales behind the parietals, and extending to the 15th to 21st (17.7, 12 sides) transverse dorsal scale row behind the parietals; the posterior end is thus at about the level of the forelimbs. There is also size related variation in the intensity of the striping, the dorsolateral dark and light stripes being relatively darker and lighter, respectively, in the second smallest specimen (MCZ 182272) than in the larger ones. The most distinctive pattern variation is in the smallest specimen (UMMZ 197261), which, in addition to the frontonasal blotches and dorsolateral dark stripe (which is longest in this specimen, extending from the 5th to 21st scale row), also has two short stripes on the head, extending from the second supraoculars to the parietals.

There appears to be allometric growth of the limbs. The smallest individual, UMMZ 197261, 44.5 mm SVL, has proportionately by far the longest limbs, and MCZ 187220, 80.5 mm SVL, the largest, has the shortest. The other four are intermediate. The type, at 69.5 mm SVL, has slightly shorter limbs proportionately than MCZ 176728, 71 mm SVL, but the overall impression is that limb length fails to keep pace with body growth. In studies of other New World *Mabuya*, based on larger series than available of *M. macleani*, a similar decline in relative limb length has been demonstrated: Rebouças-Spieker (1974) found this to be the case for most samples in her study of *M. agilis*, *M. caissara*, and *M. macrorhyncha*; Rebouças-Spieker & Vanzolini (1990) found it in *M. carvalhoi*; and Avila-Pires (1995) found it in *M. bistriata* (=*ficta* sensu Rebouças-Spieker) and *M. nigropunctata* (=*bistriata* sensu Rebouças-Spieker).

The sexes are similar. Based on broad head, thick tail base, and enlargement of the medial pair of scales bordering the vent, MCZ 182271 was judged to be a male, and dissection confirmed that. Based on narrow head, abruptly tapering tail, and subequal scales bordering the vent, MCZ 187220, the largest available specimen, was judged to be a female, and dissection confirmed that.

Comparisons.—*Mabuya macleani* is morphologically and geographically closest to *M. sloanii*. The latter species is widespread, but nowhere abundant, in the Passage and Virgin Islands, and is also found on Mona and Desecheo (Heatwole et al. 1981, Lazell 1983, 1991, 1995; Mayer 1989). This skink is deep copper to chocolate brown with prominent lateral stripes of near-black and very bold jet black dorsolateral stripes, beginning on the head, and extending continuously down the nape onto the anterior trunk, well past 20 dorsal scales posterior to the parietals (Figs. 2C, 4). The dark dorsolateral stripes are black and separated by silvery-white on the median portions of the two middorsal scale rows. On Puerto Rico, skinks also have near-black lateral stripes extending onto the trunk, but the dark dorsolateral stripes are reduced to heavy blackish blotching on the head, fragmenting and dwindling to speckles on the nape (Fig. 2A). This pattern form was named *M. nitida* by Garman (1887) on the basis of one specimen from Hispaniola and three from Puerto Rico. Stejneger (1904) described this form accurately, mistakenly under the name *M. sloanii*, based on one of two specimens numbered MCZ 6052 from San Juan, Puerto Rico. He also noted the existence of the other pattern type (the actual *sloanii*) under the name *semitaeniata* Wiegmann (1837). Schmidt (1928) also noted the two patterns, and restricted Garman's *nitida* to Puerto Rico. Grant (1931) recognized the distinction in pattern between the Puerto Rican and small island forms as well, using the same erroneous names as did Stejneger. Six Puerto Rican specimens available to us, from San Juan (MCZ 6050, MCZ 6052 [2 specimens]), Ensenada (American Museum of Natural History [AMNH] 6462), and Bayamon (AMNH 14007, UMMZ 73828) agree with Schmidt and Stejneger's descriptions, as did the Puerto Rican specimens available to Grant (1931).

A seventh specimen, from easternmost Puerto Rico (UMMZ 73829, Cape San Juan), shows some approach toward the *sloanii* pattern. A specimen from Icacos (MCZ 36624), an island just east of Puerto Rico, is intermediate between *nitida* and *sloanii* of the smaller islands to the east (Fig. 2B). Based on these specimens and the literature, we recognize *M. s. nitida* as a valid taxon, and confirm Schmidt's restriction of type locality by selecting MCZ 6050 as the lectotype. A similar pattern of geographic variation, with a Puerto Rican mainland form and a Passage/Virgin Islands form showing signs of intergradation in easternmost Puerto Rico and the adjoining cays is found in *Anolis cristatellus* (Heatwole 1976). It is interesting that *s. sloanii* occupies the islands to the east and west of the Puerto Rican main, with *s. nitida* occupying the main in between; a similar peri-Puerto Rican distribution is shown by *Hemidactylus mabouia* (Kluge 1969) and *Epicrates monensis* (Schwartz & Henderson 1991), with related species on the Puerto Rican main (*H. brookii* and *E. inornatus*).

The overall picture is of Puerto Rico Bank *Mabuya sloanii* showing greater character divergence from *M. macleani* as the latter's geographic distribution is approached (Figs. 2, 5). *Mabuya s. nitida* has less dark anterodorsal pigment than does *M. s. sloanii*; however, *M. s. sloanii* occurs to within 400 m of *M. macleani*, but the latter has the least dark pigment of all.

The Caicos Islands, although geologically part of the Bahamas, share a number of herpetofaunal elements with the Puerto Rico Bank (*Anolis*, *Typhlops*–Thomas 1999). The skinks of these islands appear distinct from Puerto Rico Bank ones based on the specimens we have seen. We have

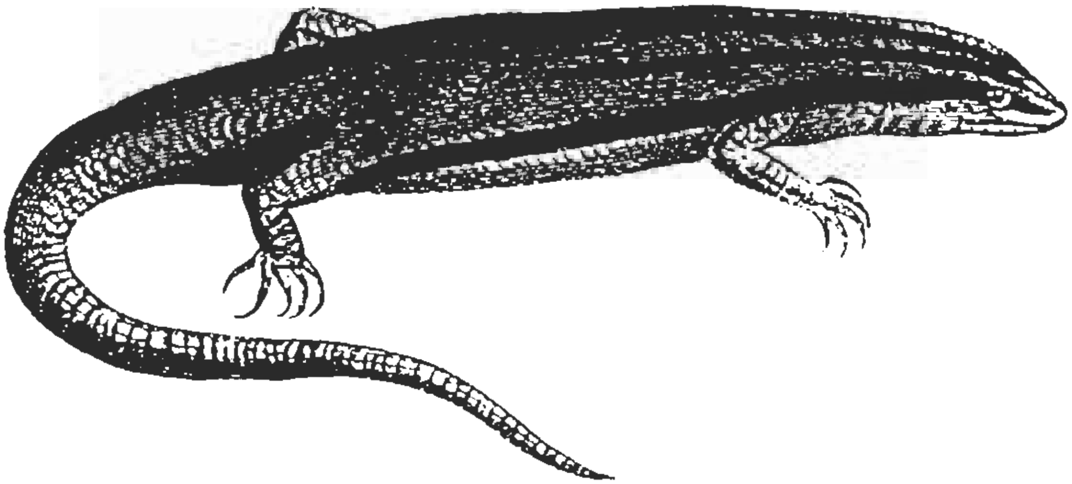

Fig. 4. Daudin's (1802) illustration of his *Scincus sloanii*, the widespread form of the Virgin Islands, showing pattern in side view.

color notes in life for MCZ 182881 from Long Cay, Caicos Bank: dark bronze-brown dorsally, with two very bold cream-white stripes that begin at the snout and extend dorsolaterally onto the costal region, about one-third of the distance from axilla to groin; these light stripes are bordered ventrally by a near-black field, six scale

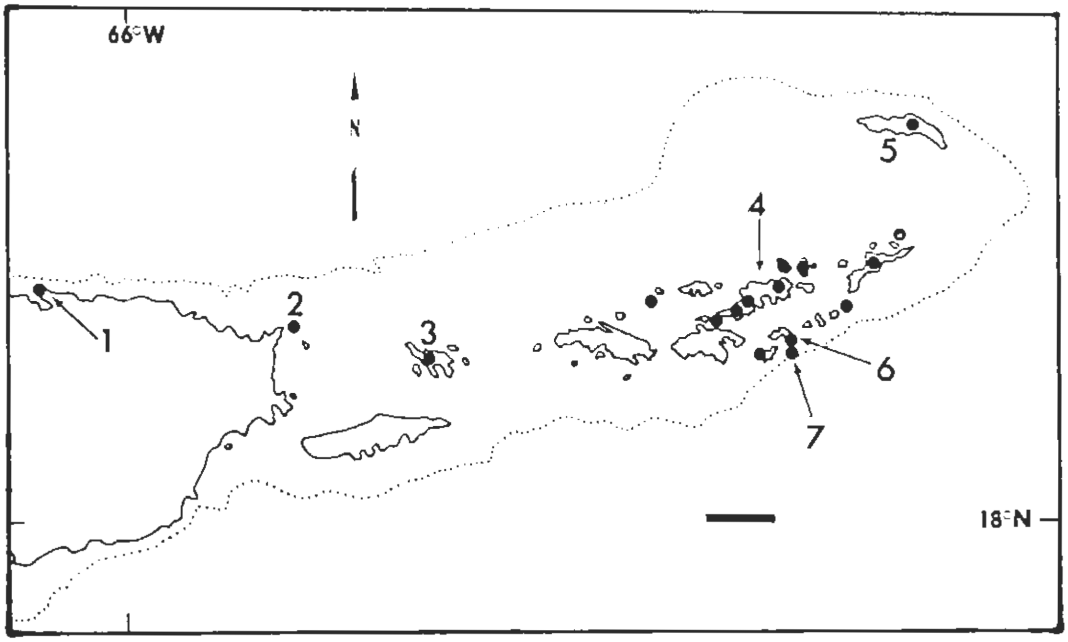

Fig. 5. The eastern portion of the Puerto Rico Bank showing localities from which specimens have been examined. 1, San Juan, Puerto Rico, type locality for *Mabuya sloanii nitida*. 2, Cayo Icacos, represented by an apparent *M. s. sloanii* × *nitida* intergrade. 3, Isla Culebra, 4, Tortola, 5, Anegada, 6, Peter Island, all nominate *M. s. sloanii*. 7, Carrot Rock, type locality for *Mabuya macleani*. Bar indicates 10 km. The dotted line is the edge of the Puerto Rican Bank, ca. 100 m below sea level.

rows wide at the forelimb insertion, and flecked with white speckles. The light dorsolateral stripes are bordered dorsally by near-black stripes one scale wide at the forelimb insertion and separated by four scales across the dorsum at that level. The posterior body is heavily speckled with black dots aligned in longitudinal rows. A preserved series from the same island (AMNH 80125–30) agrees well in pattern with the live specimen described above. The striping pattern most resembles that of the Icacos intergrade (Fig. 2B), except that the middorsal brown area is about twice as wide, thus being more like *nitida*, but differing from the latter in having a broader dorsolateral dark stripe, and in that the Icacos specimen lacks the heavy, aligned body spotting of the Caicos specimens. Such spotting is variable in *M. s. sloanii*, and may be fairly heavy (Grant 1931; UMMZ 80585 [Buck Island off St. Thomas]). White speckling in the lateral dark stripe, which is also seen in specimens from West Caicos (UMMZ 117392–4) and Six Hill Cays (UMMZ 117394–6), is not found in Puerto Rican region specimens. Further study, beyond the scope of the present work, may reveal that the Caicos *Mabuya* should be recognized as a valid taxon.

Dunn's (1936) description of *Mabuya pergravis* of the western Caribbean, "striping very indistinct; pale with dark dots above," may sound superficially similar to *M. macleani*, but the two forms are amply distinct. *Mabuya pergravis* is much more slender, and has fewer midbody scale rows (28–30–Dunn 1936, Dunn & Saxe 1950). Striping is not indistinct in a single specimen from San Andrés, and in those from Providencia the dark dots are numerous (unlike *macleani*, in which there are few or no dark dots dorsally).

In meristic and measurable characters, all New World *Mabuya*, and most from the rest of the world, are slightly, and often only modally, differentiated; as Greer & Nussbaum (2000) noted, "Few unequivocal characters of scalation are available." *Mabuya macleani* differs from *M. sloanii* somewhat in having smaller scales, reflected in higher midbody row counts: 32–34, as opposed to 30–32 in other Puerto Rico Bank *Mabuya* ($n = 20$). It would take larger sample sizes to even demonstrate statistical significance. There may be selection pressure for smaller scales in *M. macleani*. Carrot Rock's other endemic lizard, *Anolis ernestwilliamsi*, has very small scales and is absolutely distinct from its closest relative in this character (Lazell 1983). Interpreting the adaptive significance of scale size in lizards is, however, fraught with difficulties and apparent contradictions (Lazell 1994, Dmi'el et al. 1997).

Etymology.—The species is named in honor of our late friend and colleague Dr. William P. MacLean, III, of the University of the Virgin Islands, who contributed so much to knowledge of the Virgin Island herpetofauna (MacLean 1982), and who aided and assisted our work, and that of many others, on numerous occasions (Lazell & Mayer 1992). He was one of the first, and still few, professional biologists ever to have set foot upon Carrot Rock, and recognize its biotic uniqueness.

Discussion

Ecology.—Carrot Rock has undergone major ecological changes since it was first visited by JL in 1980 (Lazell 1983). Then, most of the windward (eastern) and northern portion of the top of the island was covered with a sprawling growth of sea grape, *Coccoloba uvifera* (Polygonaceae), which had to be either climbed over or crawled under. There were three thickets of sea grape on the edges of the scarp tall enough to stand in the shade of: one on the leeward coast, one on the northern windward coast, and the biggest in the gully–locally called "ghut"–where the first *Mabuya macleani* was collected.

Severe drought characterized the climate of the Virgin Islands during the eighties. It seemed that more precipitation fell in the form of dust—said to have blown all the way from the Sahara—than as water. JL's field notes of 13 July 1985 record:

> "The Rock is in terrible shape! The sea grape looks 90% dead; places I could crawl under before are now just scattered dry sticks. Trying to dig out leaf litter was a nightmare of dust."

Despite the drought, *Anolis* remained common, the first *Mabuya* was secured, and *Sphaerodactylus macrolepis* (MCZ 170890) was also collected–all in the one remaining sea grape thicket in the ghut–in 1985 (Mayer & Lazell 1988). This brought Carrot Rock into compliance with the "rule of three" for Caribbean islands, as predicted (Lazell 1983). On 17 July 1988 conditions were no better, but more *M. macleani* were seen and collected than ever before. Over most of the boulder-jumbled surface of Carrot Rock, skinks have the advantage over would-be captors. In one small area near the top, however, there are few rocks, little vegetation, and a soil substrate. Here a group of us simultaneously sighted eight skinks in a 10 × 20 m (200 m^2) plot (and caught three of the eight). Excluding the bare rock faces and wave-washed talus of the edges, we estimate the top of the island habitable for skinks at ca. 1.3 ha. Using our crude estimate, the total population of Mabuya macleani might be something like 520 individuals. In any case, a density of 12 in 200 m^2 (400 per ha) far exceeds that of skinks or other comparable ground lizards (e.g., *Ameiva*) anywhere in the Antilles.

On 27 October 1994, three *Mabuya macleani* were seen in about two hours on the Rock. JL's field notes mention "the incredible drought," and the appearance of the island as "dead gray still" and "really bleak." Hurricanes Luis and Marilyn struck the Virgin Islands in September 1995. Low-lying areas like Carrot Rock were inundated with sea water, but there was relatively little mitigating rainfall. On this day the Rock was visited with a group of 6 people, but in two hours ashore we saw but two skinks and not a single *Anolis*. Approximately half the sea grapes in the ghut thicket were dead. The large candelabra cactus, *Pilosocereus royenii*, that had crowned the top of the islet (and housed the largest, uncatchable *Anolis*) was "rotting pulp and stark skeleton."

Rainfall in the region began to increase in 1996. On 24 October 1996 a group of us checked the Rock briefly. We did not attempt to collect specimens, but we quickly located three *Anolis ernestwilliamsi* and two *Mabuya macleani*, one of the latter perched on a vine ca. 3 cm above the ground (Schwartz & Henderson [1991] note climbing in *Mabuya mabouya*). Again, from JL's field notes: "Seagrapes are regenerating well; the place generally looks much better than last year."

A brief vegetation survey of Carrot Rock, by Dr. Fred Kraus on 26 October 1991, included, in addition to seagrape and candelabra cactus, *Mammillaria nivosa*, *Melocactus intortus*, and *Opuntia dillenii* (all Cactaceae), and the vines *Capparis flexuosa* (Capparidaceae), *Stigmophyllon periplocifolium* (Malpighiaceae), and *Cavanalia maritima* (Leguminosae). There are "various graminoids including the rare silky foxtail grass *Pappophorum pappiferum*."

Differentiation on small islands.—The distinctiveness of populations inhabiting small islands, and the apparently rapid evolutionary rates involved in achieving this differentiation, have long been known to students of the zoology of archipelagos (Mayr 1963, Lazell 1972). *Mabuya macleani* appears to be an example of this phenomenon. Two aspects of Carrot Rock's geographic situation, in particular, argue for rapid evolution (Fig. 6). First is its short distance, approximately 400 m, from Peter Island. Given this short distance, and the predominant direction of the currents from the northeast, there seems a considerable probability of waif dispersal of skinks from adjacent parts of Peter Island (where typical *M. sloanii* does occur: MCZ 182273) or other islands to windward. Divergence of the Carrot Rock population, especially by

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genetic drift, would have to proceed at a high rate to offset the genetically homogenizing effects of immigration events.

The second aspect is the short time during which Carrot Rock has existed as a separate island. Lowered sea levels during the last glacial period united all of the islands of the Puerto Rico Bank into a single large island (Heatwole & MacKenzie 1967). The age of separation of two islands on the bank can be inferred from the maximum depth of the water now separating them, and the time course of the Holocene sea level rise. We cannot say with certainty what the maximum depth of the channel between Carrot Rock and Peter Island is, because the channel is so shallow and strewn with rocks that only the smallest of boats attempt to pass through the strait, so that accurate soundings are not possible; it cannot be more than a few meters. Based on the time course of Caribbean sea level rise (Fairbanks 1989), a depth of 5 m would correspond to a separation of 3000 years; as the actual depth is almost certainly less than this, this is an upper limit on the time of isolation of Carrot Rock.

The causes of rapid divergence in island populations have long been a matter of contention (Williamson 1981, Berry 1986, Grant 1998), with some arguing for the importance of stochastic factors (e.g., Mayr 1954), while others have stressed the adaptive nature of island differentiation (e.g., Grant 1968, Malhotra & Thorpe 2000). Carrot Rock's proximity to Peter Island argues for a non-stochastic cause, since even a low rate of migration is sufficient to counteract divergence due to founder effect or drift (Crow and Kimura 1970); gene flow is much less effective in counteracting selection (Lande 1980). There is another, in our opinion much stronger, argument for non-stochastic causes: the occurrence on Carrot Rock of another endemic lizard, *Anolis ernestwilliamsi*, which, like *Mabuya macleani*, has a close relative, *A. cristatellus*, widespread on other islands on the Puerto Rican Bank (Lazell 1983; the third species on the island, *Sphaerodactylus macrolepis* is not distinct). As Mayr (1963) noted, production of evolutionary novelties or new species in small, isolated populations is a rare event; if the initiating genetic events are stochastic in nature, it is highly unlikely that, of all the many islands on the Bank inhabited by *Mabuya* (Fig. 5) and *A. cristatellus* (MacLean 1982, Mayer 1989), these events should occur in both taxa on the same island. We infer that there is something about Carrot Rock itself which is conducive to divergence, rather than that there have been two independent occurrences of a rare stochastic event. We can only suggest that it is the unusual environmental conditions of the island (see above under *Ecology*) that are the common factor in divergence of the two species, but could only speculate about the exact conditions influencing one or the other species. Although it is often argued that evolution proceeds faster in smaller populations, adaptive divergence in fact is faster and greater in larger populations (Weber & Diggins 1990, Coyne et al. 1997), making the situation of two endemic lizards on Carrot Rock even more remarkable.

An alternative explanation for the endemicity exhibited by the Carrot Rock saurofauna is that they are relicts, stranded there by post-glacial sea level rise. While we cannot definitively rule out this possibility, the close proximity and very recent separation of Carrot Rock from the main body of the Virgins, and its small size, make it an unlikely refuge for species which have elsewhere gone extinct. Three distributional patterns in the Virgin Islands herpetofauna suggest a relictual distribution, but none match that of the Carrot Rock endemics. *Sphaerodactylus townsendi*, an otherwise Puerto Rican species, occurs in the Virgins only on Frenchcap Cay (Heatwole et al. 1981), but this cay, separated by depths of 22 m, was the earliest of the Virgins to be isolated, about 8000 yr ago when Puerto Rican forms apparently ranged further east on the then exposed bank. Sev-

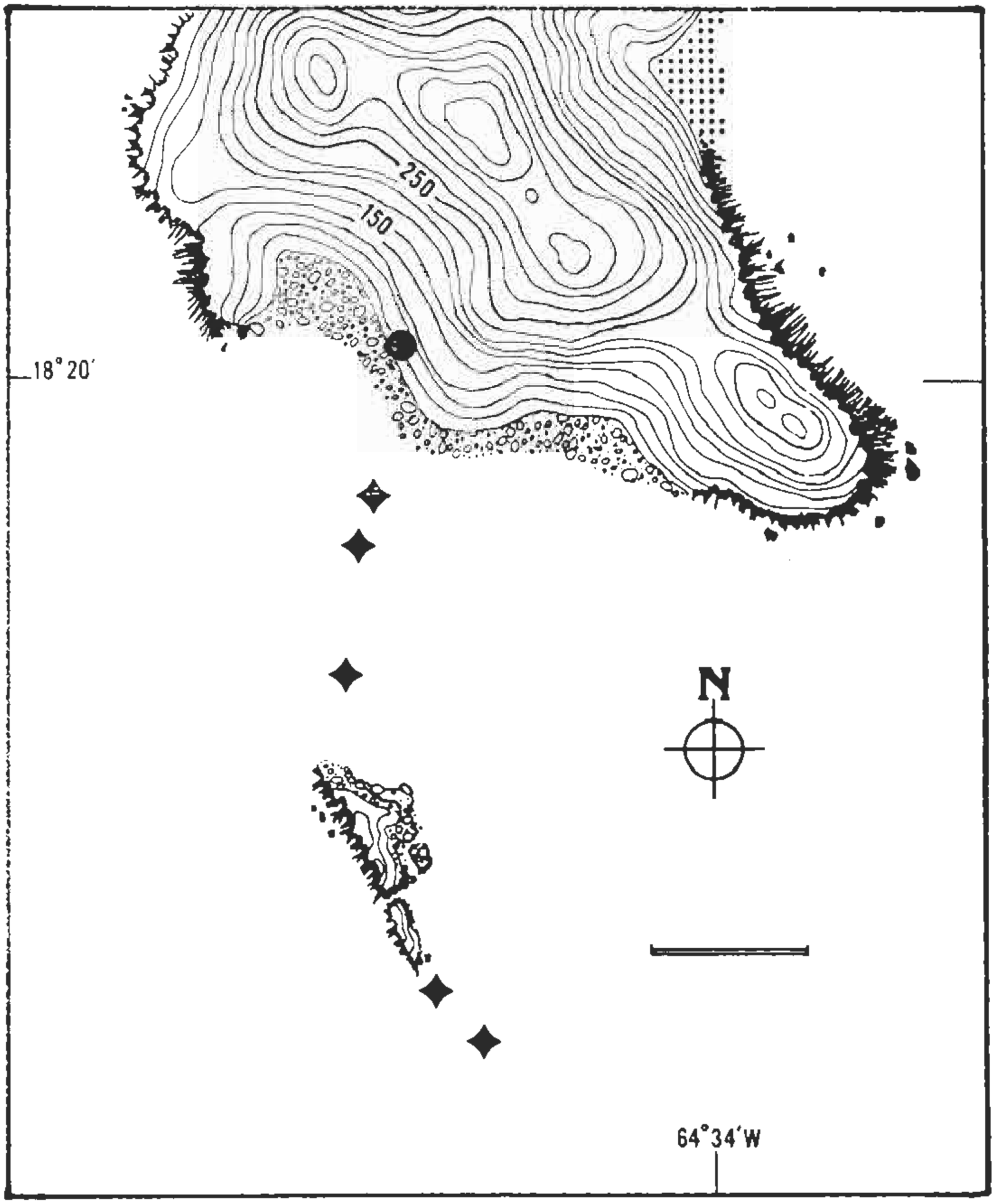

Fig. 6. The south end of Peter Island and Carrot Rock, British Virgin Islands. Dot indicates collection site of *Mabuya s. sloanii*, MCZ 182273, at Stoney Bay. Sand (dots), cobble and scree, and cliffed shorelines are indicated. Black diamonds indicate rocks that break at low water (from U.S. NOAA chart 25641, 1984). Contours are at ca 7.62 m or 25 ft. (from British Directorate of Overseas Surveys 346, Series E 837, 1959). Bar, lower right, indicates 200m.

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eral species (e.g. *Anolis roosevelti*) which occur today on only one or a few islands, although they must have once occurred more widely when sea levels were low, have persisted on the largest islands (Mayer 1989). Finally, several species have disappeared from some larger islands while persisting on some smaller islands (e.g., *Alsophis portoricensis*), but such distributions have resulted from anthropogenic extirpations (Barbour 1930, Mayer & Lazell 1988). The Carrot Rock endemics fit none of these patterns. Furthermore, since close relatives of each are present on Peter Island and throughout the archipelago, supposing that they are pre-sea level rise relicts makes their divergence even more remarkable, or merely pushes the time, but not the mode, of their origin to an earlier glacial cycle. For these reasons, we favor the hypothesis of in situ post-glacial divergence (Lazell 1999).

Nomenclature.—Dunn (1936) referred all Antillean skinks (except *lineolata* of Hispaniola) to the species *Mabuya mabouya* Lacépède (1788), which species he also considered to be widely distributed on the mainland, from Mexico through much of South America. Since then, various authors have studied components of this widespread species or species-group, naming or reviving species as needed, and leaving behind an unstudied residue, to which the name *Mabuya mabouya* might continue to be attached (e.g., Rebouças-Spieker 1974, 1981a, 1981b, Avila-Pires 1995). Lacépède's work, however, is not binominal in its nomenclature, and the name, "mabouya" is thus not available.

Throughout the text of his work, Lacépède uses vernacular names, mostly in French, but some, like "Le Mabouya," deriving from other languages. Some Latin names appear in his "Synopsis methodica," but this is not a table of Linnaean-style binomina, but rather a partial translation into Latin of vernacular names given in the text: French vernacular names are translated, but non-French vernacular names appear unchanged in the "Synopsis". Thus, the French "Le Sourcilleux" of the text appears as "L[acertus]. superciliosus" in the "Synopsis," while "Le Mabouya" of the text appears simply as "Mabouya," as do other non-French vernaculars such as "Jackie" and "Sheltopusik". Names in the table may be uninominal, binominal, or trinominal. Thus "Le Gecko" of the text appears as "Gecko" in the "Synopsis," "La Salamandre terrestre" as "Salamandra terrestris," and "Tortue marin comun" as "T[estudo]. marinus vulgaris".

Although the word "Lacertus" appears as the name of a "genus" in the heading of the "Synopsis," it cannot be read into the remainder of the table so as to turn uninomina into binomina. (Doing so would also turn some binomina in the table into trinomina.) Those names in the table to which Lacépède attached "Lacertus" are specifically listed as such in the table, most often by prefacing the name with "L.". The rule he generally followed is that when the French name is translated as a Latin adjective, it receives the "Lacertus" appellation (e.g., "Le Silloné" of the text becomes "L[acertus]. sulcatus" in the table), whereas names translated as Latin nouns do not (e.g., "Le Dragon" becomes "Draco"); the latter are thus truly uninominal.

In his genus "Lacertus," Lacépède had 26 uninominal and 30 binominal species names; in his genus "Testudo," he had four uninominal, 19 binominal and one trinominal; and similarly for his other genera. Lacépède's work is thus clearly non-binominal, and must be rejected for the purposes of zoological nomenclature. Brongersma (1972), Vanzolini (1977), Savage (1981), Melville (1986), and Smith (1986) also argued that Lacépède was non-binominal, and should be rejected for nomenclatural purposes, and the Commission agreed (International Commission on Zoological Nomenclature 1987). Unfortunately, all these authors but Vanzolini restricted their attention to Lacépède's second volume, on serpents, so that his quadrupeds have not been

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formally rejected. Fortunately, rejection of non-binominal works is automatic under the Code, so action by the Commission is not required.

Lacépède's concept of "Le Mabouya" was composite and confused, with no specific locality. Although largely based on Antillean lizards, he also included Sardinia in its range, and the accompanying figure (pl. XXIV) is not even a *Mabuya*; it appears to be, as surmized by Duméril & Bibron (1839), *Chalcides ocellatus*, which occurs on Sardinia. Losing Lacépède's non-binominal name of dubious application will be no loss.

Recently, some authors (Powell et al. 1996, Hedges 1996, Murphy 1996, Powell et al. 1999, Crother 1999), perhaps aware of the difficulties with Lacépède, have begun using the specific name *bistriata* Spix, 1825 (type locality Belém, Brazil) for Antillean skinks previously (e.g., Schwartz & Henderson 1991) referred to *mabouya*. However, even if the Antillean and Brazilian forms are conspecific, which we consider unlikely, *sloanii* predates *bistriata* by 23 years, and the latter name should not be used.

We thus have not used "mabouya" here for Antillean skinks, but rather use Daudin's (1802; Fig. 4) *sloanii* as the first available name, the type of which still exists (Muséum National d'Histoire Naturelle, Paris 554), has good locality data (St. Thomas), and has been examined for us by G. R. Zug. The Antillean skinks formerly included in the *Mabuya* "mabouya" complex not dealt with in this paper (Lesser Antilles, Jamaica, Hispaniola) are best referred to as the *Mabuya sloanii* complex until their systematics can be resolved.

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Appendix I

Material Examined

Islands in the Puerto Rican area are listed in a roughly west to east sequence, and may be located through reference to the maps in Heatwole et al. (1981) and Lazell (1983), and the gazetteer in Mayer (1989). Numbers in parentheses indicate the number of specimens catalogued as a lot. University of Kansas Museum of Natural History (KU) numbers preceded by a letter are from the Albert Schwartz Field Series.

Mabuya sloanii nitida.—Puerto Rico: AMNH 6462, 14007; MCZ 6050, 6052 (2); UMMZ 73828.

M. s. nitida × *sloanii*.—Puerto Rico: UMMZ 73829. Cayo Icacos: MCZ 36624.

Mabuya sloanii sloanii. –Mona: AMNH 13703, 31896, 31908, 115437; Carnegie Museum (CM) 23774-6; Field Museum of Natural History 215, 134332; UMMZ 73817 (3), 73818 (3), 73824 (15), 73825 (2), 124819; National Museum of Natural History (USNM) 133683. Desecheo: USNM 220995. Culebra: AMNH 14005–6, 32910; UMMZ 73819 (13), 73820 (7), 73822 (16), 73823 (10), 73826 (3); USNM 49586. Cayo Luis Peña: UMMZ 73827. Cayo Norte: University of Puerto Rico Rio Piedras. Culebrita: UMMZ 80786. St. Thomas: MNHN 554, 1088 (by G. R. Zug). Saba Island (off St. Thomas): UMMZ 80580; USNM 304553. Water Island: KU V7409. Buck Island (off St. Thomas): UMMZ 73821 (2), 80585. South Capella Island (adjacent to Buck Island off St. Thomas): UMMZ 80586. Little Tobago: MCZ 158940. Tortola: AMNH 99522. Guana Island: MCZ 166975, 170883; UMMZ 200131; USNM 306182. Great Camanoe: KU V3982. Peter Island: MCZ 182273. Norman Island: USNM 304551. Virgin Gorda: UMMZ 80581, 80582 (3), 80584. Salt Island: UMMZ 74427. Ginger Island: USNM 304550. Prickly Pear Island: USNM 304552. Necker Island: MCZ 176331. Anegada: AMNH 99523–4; CM 17357–8; UMMZ 80583 (28).

Mabuya sloanii complex from Caicos Bank.—Long Cay AMNH 80125–30; MCZ 182881. Six Hill Cays: 117394–6. West Caicos: UMMZ 117392–3.

Mabuya pergravis.—Providencia: Academy of Natural Sciences, Philadelphia 25791-95. San Andrés: UMMZ 127884.

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Evaporative Water Loss in Insular Populations of *Anolis cristatellus* (Reptilia: Sauria) in the British Virgin Islands. III. Response to the End of Drought and a Common Garden Experiment[1]

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ABSTRACT

Evaporative water loss in *Anolis cristatellus* from the British Virgin Islands was negatively correlated with the aridity of their habitats. Phenotypic plasticity and/or differential mortality of less well-adapted individuals allowed rapid changes within populations. Here we report the results of two studies intended to differentiate between the two processes. We took advantage of the end of a major drought to study the rapidity with which populations recovered from unusually dry conditions. Population values changed rapidly from those measured in the past. There was no correlation between long-term habitat aridity and measured water-loss rate, but the multiyear correlation between aridity and skin resistance to water loss persisted. We also conducted a common garden experiment in which animals from the wettest and driest habitats were housed under intermediate conditions for one month. We detected no change in skin resistance to water loss in any of the three populations we studied; however, the mass of lizards from Sage Mountain increased significantly during the experiment, and their water loss per unit mass decreased significantly. These results support the existence of both phenotypic plasticity and genetic differences resulting from rapid selection within populations. The magnitude and relative importance of the two, however, remain to be determined.

Key words: Anolis cristatellus; *British Virgin Islands; evaporative water loss; habitat aridity; phenotypic plasticity; rapid evolution.*

THE MANY ISLANDS OF THE BRITISH VIRGIN ISLANDS (BVI) were part of a single landmass until *ca* 10,000 years ago (Heatwole & MacKenzie 1967). Today the islands experience divergent conditions; some enjoy wet environments and abundant rainfall, whereas others are unexpectedly arid, given their tropical latitude (Dmi'el *et al.* 1997). The coupling of recent origin with divergent abiotic regimes poses an unusually acute evolutionary problem for the BVI fauna and flora. Terrestrial organisms, especially those inhabiting dry environments, risk excessive evaporative water loss (EWL). Mechanisms for preventing this can be behavioral (*e.g.*, choice of activity time or microhabitat), morphological (*e.g.*, elaborate nasal structures that capture water vapor from exhaled air), or physiological (*e.g.*, improved ability of the kidney to concentrate urine). In terrestrial reptiles, reducing cutaneous water loss (CWL) in response to dry conditions is a common physiological mechanism (Bentley & Schmidt-Nielsen 1966, Mautz 1982, Dmi'el 1985, Dmi'el *et al.* 1997, Perry *et al.* 1999).

Previously, we showed that populations of *Anolis cristatellus wileyae* from dry islands had lower CWL rates and higher skin resistance (R) to water vapor than those from wet islands (Dmi'el *et al.* 1997, Perry *et al.* 1999). This pattern could be the result of three mechanisms: phyletic divergence, phenotypic plasticity, and selective divergence. The first explanation is a historical one. Under it, differences between populations could be a result of nonadaptive divergence caused after the islands separated from one another. In this scenario, the correlation with island aridity is a spurious result; however, the physiological variation we found was not related to island nearness (Dmi'el *et al.* 1997, Perry *et al.* 1999). Since nearby islands presumably separated more recently and have a higher

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likelihood of overwater gene exchange, this suggests that phylogenetic divergence was not the cause of physiological differences.

Both remaining explanations are adaptive. Under phenotypic plasticity, individuals modify their R according to current conditions. Hillman *et al.* (1979) and Kobayashi *et al.* (1983) found evidence of such rapid acclimation in water-loss rates for some *Anolis*. The last explanation invokes natural selection. The benefit of reducing water loss during dry years is obvious. Since this presumably carries a cost, selection toward relaxation of water conservation is expected when conditions improve. At the population level, the effects of selection can appear nearly as rapid as phenotypic plasticity (Malhotra & Thorpe 1993). Perry *et al.* (1999) predicted that under a scenario of phenotypic plasticity, a drought or its cessation should cause rapid physiological changes, but no effects would be seen on population size, mean body size within it, or intrapopulation variability in R. Under a selection regime, they predicted that differential mortality would occur during a drought, causing reduced population size and variability in R and an increase in mean body size. Both these changes, and the recovery from drought as reproduction occurs, should be slower than under the phenotypic plasticity scenario.

Of course, the two mechanisms are not necessarily mutually exclusive. A selected difference between populations can be further modified within individuals by phenotypic processes. In that case, individuals from different populations placed together will show some coalescing of their water retention abilities, but some differences will nonetheless remain when the process is completed. Unfortunately, previous results could not be used to distinguish between the two as the causative factor(s) (Perry *et al.* 1999). In this paper, we report new work designed to identify the causative mechanism(s) based on the predictions of Perry *et al.* (1999). First, we took advantage of the end of a prolonged drought in 1995 to investigate the rapidity of response in all previously studied populations to environmental change; additional data were collected in 1997. Second, in 1996, we used a common garden experiment involving individuals from two extreme habitats (one wet and one dry) and the one native to Guana Island (intermediate conditions) to measure water loss of animals in a controlled environment.

MATERIALS AND METHODS

Study populations, collection, and housing.— In 1995, we used the end of a major drought (Perry *et al.* 1999) to observe again all eight populations reported on previously. Although we revisited Carrot Rock and searched for *Anolis ernestwilliamsi*, this tiny islet was recovering from the effects of a major hurricane and no lizard could be found. Additional data on the Guana population were collected in 1997. In 1996, we conducted a common garden experiment. We collected lizards from Sage Mountain on Tortola (the wettest location), Necker Island (a dry location), and Guana Island. All lizards were housed on Guana and treated similarly. As in previous work, we only utilized adult males. In both years, we noosed study lizards in the field during late September and all of October. Collection sites and conditions on them are described in Dmi'el *et al.* (1997), who also developed an aridity index used here to describe, in the absence of rainfall data for these islands, conditions on them. Lizards were transported to the laboratory on the day of capture but not studied until the next day at the earliest. For the work conducted in 1995 and 1997, animals were housed individually and studied the following day. To reduce defecation during testing, lizards were kept without food for 8 to12 hours before experiments began, but were provided with moistened paper during this period to allow them to regain water lost in transit.

For the 1996 common garden experiment, animals were individually marked and housed separately in large, commercial mesh bags (cage dimensions: *ca* 30 × 30 × 60 cm). Cages were placed in a small patch of woods (*ca* 5 × 5 m) near the laboratory. Each animal initially was put in a randomly chosen bag to which it was always returned following measurements. Animals were fed mealworms *ad libitum* daily, except on days when they were used in experiments. During the first week, all animals were watered once a day, in addition to any water they received from normal precipitation. Ambient temperature and relative humidity in the cage area were recorded daily using a minimum–maximum thermometer and electric psychrometer. This allowed us to verify that ambient conditions were similar to those experienced in the lab.

Initial measurements taken from specimens studied in 1995 and 1996 were comparable to those reported in previous work (Table 1). In 1997, we sampled an additional 21 Guana Island individuals. Mass was 8.13 ± 1.39 g ($\bar{x}$ ± SD), surface area was 53.11 ± 7.58 cm^2, and R was 101.63 ± 23.96 s/cm (see below for measurement methods). We also used data on body mass collected during all studies between 1993 and 1996 to look for differences in body size. Sage Mountain, Guana, and

TABLE 1. *Location, sample size (N), and body dimensions of A. cristatellus studied in 1995 and 1996. Data are $\bar{x}$ and SD*

Location	*N*		Mass (g)		Body surface (cm^2)	
	1995	1996	1995	1996	1995	1996
Sage Mt., Tortola	6	8	7.8 (1.0)	7.0 (1.1)	53.8 (3.9)	43.6 (3.4)
Virgin Gorda	6		5.8 (1.0)		44.5 (6.1)	
Bridge, Beef Isl.	6		8.5 (0.9)		53.7 (5.8)	
Bridge, Tortola	6		8.5 (1.5)		47.9 (8.5)	
Guana Island	6	7	7.4 (0.7)	9.0 (1.8)	50.8 (3.6)	56.3 (5.5)
Norman Island	6		6.3 (0.8)		46.1 (8.5)	
Necker Island	6	7	8.8 (1.1)	10.0 (1.0)	58.2 (8.0)	58.7 (5.6)
Anegada	6		7.6 (1.8)		40.1 (11.1)	

Necker Islands were sampled during all four years. Guana and Necker are relatively dry. To balance the design we added the data for Gorda Peak, the second wettest site studied by Dmi'el *et al.* (1997) and Perry *et al.* (1999).

Both collection and laboratory work were conducted during normal times of activity. Whenever logistically possible, lizards were released at the site of capture at the end of the study. Those retained were euthanized and deposited in the Texas Memorial Museum, University of Texas at Austin.

Laboratory procedures.—We closely followed the methodology of Dmi'el *et al.* (1997), ensuring data were comparable among all study years. Briefly, we moved each lizard to a dry plastic box (inner dimensions: 20 × 9 × 7 cm) immediately before starting laboratory work. Boxes were covered with small-mesh wire netting that permitted free exchange of air. Ceiling fans continuously circulated room air, homogenizing temperature and humidity. *Anolis cristatellus* are roughly triangular in cross-shape (Dmi'el *et al.* 1997). Surface area of each lizard was calculated by pressing it against graph paper and tracing the outline of its side and venter. Tracings then were cut out and weighed to the nearest milligram. Lizard surface area was calculated, based on the mass of a known area of the same paper, as the summation of two sides and the bottom area. This method has proved superior to available alternatives (Dmi'el *et al.* 1997).

Water-loss measurements also followed methodology described in detail elsewhere (Dmi'el *et al.* 1997). Briefly, we measured lizard mass change over a period of six to eight hours to obtain rates of total EWL. We used a Precisa balance (model 800M) to weigh lizards to the nearest milligram, a Psychro-Dyne psychrometer (Environmental Tectonics Corporation, Southampton, Pennsylvania) to measure room relative humidity, and a 36-gauge copper-constantan thermocouple connected to a TH-65 electronic thermometer (Wescor Inc., Logan, Utah) to measure skin and room temperature. These differed due to water evaporation from the skin. These data were used to calculate the driving force for water vapor loss. Readings were taken at 60-minute intervals. Animals that defecated during the experiment were immediately reweighed and the study restarted. The integumentary resistance to water loss is less sensitive to changes in immediate environment and therefore a better measure of actual impedance to water loss (Eynan & Dmi'el 1993). It combines the resistance of the skin and that of the boundary layer surrounding it. We calculated integumentary resistance using the equation: $CWL = (eT_s - eT_a)/R$ (Lillywhite & Sanmartino 1993), where CWL is the cutaneous evaporative water loss per cm^2, and eT_s and eT_a are the saturated water vapor density at skin temperature and the actual water vapor density in the air, respectively. CWL values were obtained from the ratios of CWL/EWL measured for each population by Dmi'el *et al.* (1997) and verified by Perry *et al.* (1999). Obtaining these ratios requires procedures that are stressful to the animals, and previously obtained values were consistent among populations and within populations among years.

During the first study, each animal was studied only once. For the common garden experiment, however, all animals were sampled repeatedly. Each day six animals, two from each of the three islands, were tested. Thus, all animals were tested in each three-day period. Animals were not examined during the fourth day, and the cycle was restarted on the fifth day. Extra animals, collected in case of mortality to ensure a large enough sample size of animals from identical environments, were tested every second cycle.

RESULTS

Study 1.—As in previous years, *A. cristatellus* on Guana had higher R values than any other popu-

TABLE 2. *Integument resistance (R) of* Anolis cristatellus *from the BVI measured in 1995 and 1996. Numbers are* $\bar{x}$ *and SD. The aridity index was developed by Dmi'el et al. (1997) and ranges from 1 (wet) to 10 (dry). Data for 1993 are from Dmi'el et al. (1997); those from 1994 are from Perry et al. (1999).*

Location	Aridity index	R (sec/cm)			
		1993	1994	1995	1996
Sage Mt., Tortola	1.0	59 (14)	100 (49)	83 (17)	59 (14)
Virgin Gorda	2.3	29 (15)	100 (34)	81 (11)	
Beef Isl.	5.0	54 (11)	148 (22)	113 (37)	
Bridge, Tortola	5.0	55 (23)	156 (42)	89 (15)	
Guana Isl.	5.0	199 (73)	229 (62)	128 (29)	173 (121)
Norman Isl.	6.3	114 (15)	114 (22)	112 (16)	
Necker Isl.	6.9	155 (25)	186 (40)	78 (10)	121 (32)
Anegada	8.3	128 (27)	150 (61)	84 (8)	

lation measured (Table 2). Given the intermediate environment of Guana, this indicated unexpectedly low water-loss rates in that population. Unlike previous years, there was no significant correlation between R and habitat aridity in 1995 (Spearman's $r_s = 0.08$, one-tailed $P = 0.5$; Fig. 1a). To assess the uniqueness of the 1995 values, we compared island means from that year to those from all other years (Fig. 1b; data from Dmi'el *et al.* 1997 and Perry *et al.* 1999). Whereas no difference was apparent for wetter islands, 1995 values for dry islands were well below normal (paired-sample t-test for islands of average aridity or drier, $N = 6$, $t = 2.002$, df $= 5$, one-tailed $P = 0.05$). The multiyear correlation between habitat aridity and average R at each site was significant whether 1995 data were included or excluded (for both, Spearman's $r_s = 0.71$, one-tailed $P = 0.025$).

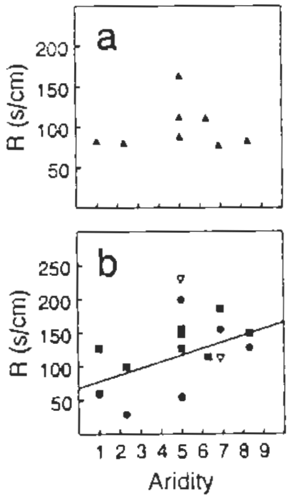

FIGURE 1. The relationship between habitat aridity and mean integumentary resistance (R) in eight populations of *Anolis cristatellus*. The aridity index ranges from 1 (wet) to 10 (dry). (a) 1995 data. (b) data for all other years. Full circles represent 1993 data; full squares are 1994 values; and empty triangles show 1996 rates. The diagonal line represents the linear regression of the average values at each site for 1993, 1994, and 1996.

Intrapopulation variability in R, as measured by SD within years, decreased significantly from 1994 (data in Perry *et al.* 1999) to 1995 (Table 2; $t = 3.315$, df $= 2$, $P = 0.013$; two-tailed t-test for repeated measures). In 1995, it returned to values not significantly different from those measured in 1993 ($t = 1.057$, df $= 7$, $P = 0.41$; two-tailed t-test for repeated measures).

In the absence of precise rainfall data for all years, we ranked rainfall based on available rain-gauge data (G. Perry, pers. obs.) and subjective impressions of authors and of island staff located there year-round. Although imprecise, all these data concurred on the relative amount of rainfall during these years, producing an unambiguous ranking. The relationship between recent rainfall and R values measured in the Guana Island population from 1993 to 1997 demonstrated that skin resistance changed from year to year in accordance with rainfall patterns (Fig. 2). This relationship was more closely related to conditions over the last month than over longer periods (Spearman's rank correlations: for the past ten months, $r_s = -0.70$, df $= 4$; 2-tailed $P = 0.188$; for the past five months $r_s = -0.90$, df $= 4$; two-tailed $P = 0.037$; for the past month, $r_s = -0.975$, df $= 4$; two-tailed $P = 0.005$).

Adult males from wet locations (Sage Mountain and Gorda Peak) were normally smaller than those from dry locations (Guana and Necker; Table 3). Differences between locations ($N = 4$) and years ($N = 4$) were statistically significant (two-way ANOVA; locations: $F = 19.53$, $P < 0.001$; years: $F = 10.06$, $P < 0.001$). A significant interaction

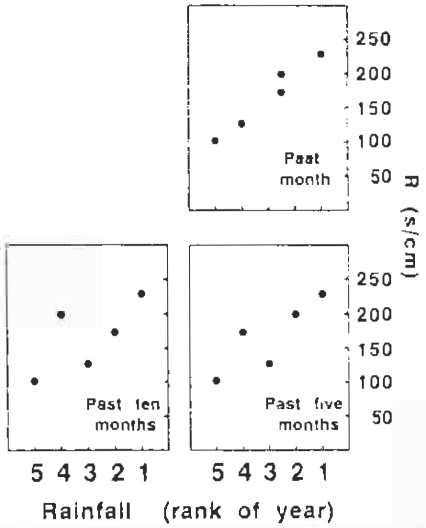

FIGURE 2. Relationship between integumentary resistance to water loss (R) and ranked rainfall during the months before our recurring October studies. The driest year was ranked "1," the wettest "5."

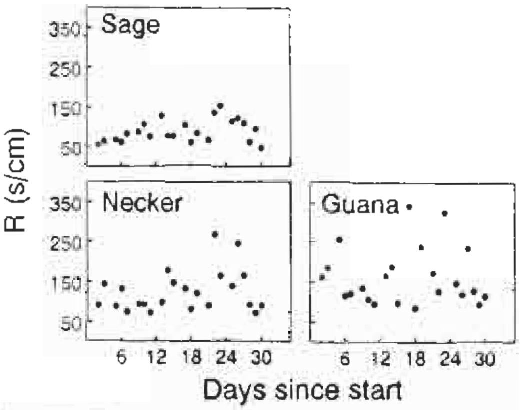

FIGURE 3. Changes in integumentary resistance to water loss (R) in three populations of *Anolis cristatellus* kept on Guana Island during a 30-day common garden experiment. No correlations between R and days since start were significant.

term (location × year: $F = 3.27$, $P = 0.003$) indicated different populations reacted to large-scale changes in abiotic conditions in different ways. A *post hoc* least-significant-difference test ignoring the effect of year indicated the Sage Mountain and Gorda Peak populations were significantly different from each other and from both other populations ($P < 0.015$ in all cases). Those from Guana and Necker Islands, however, were not different ($P > 0.25$).

STUDY 2.—Initial water-loss rates exhibited by the three populations measured in 1996 conformed to past patterns. Measured by their R values at the beginning of the study, Necker Island lizards were better at conserving water than lizards from the wetter Sage Mountain. Guana Island lizards were significantly better at conserving water than both (Table 2; one-way ANOVA: $F_{2,17} = 5.78$, two-tailed $P = 0.012$). None of the three populations showed a significant correlation between R and the number of days since the study started (Fig. 3; for Sage Mt., Spearman's $r_s = 0.28$ and two-tailed $P = 0.19$; for Necker Island, $r_s = 0.16$, $P = 0.46$; and for Guana, $r_s = 0.11$, $P = 0.60$). Similarly, the difference between initial and final individual R values within each population was never statis-

TABLE 3. *Changes in mass (g) of* A. cristatellus *from two wet (Sage Mountain and Virgin Gorda) and two dry (Guana and Necker) populations studied between 1993 and 1996.*

Location		1993	1994	1995	1996	Total
Sage Mountain	$\bar{x}$	5.9	7.0	7.8	7.0	6.9
	SD	0.46	0.52	0.97	1.09	1.00
	N	6	6	5	8	25
Virgin Gorda	$\bar{x}$	4.1	5.3	5.8	—	5.1
	SD	0.30	0.97	1.00	—	1.06
	N	5	6	5	—	16
Guana Island	$\bar{x}$	7.6	6.9	7.4	9.4	7.9
	SD	1.98	1.32	0.72	2.00	1.88
	N	12	5	6	8	31
Necker Island	$\bar{x}$	8.6	6.2	8.8	9.9	8.4
	SD	1.48	0.88	1.08	1.00	1.74
	N	6	6	6	6	24
Total	$\bar{x}$	6.9	6.3	7.5	8.7	7.3
	SD	2.10	1.11	1.39	1.91	1.89
	N	29	23	22	22	96

tically significant (paired t-tests, P always >0.1). The total EWL of Necker and Guana Island lizards did not change significantly during the experiment (Necker: before, 1.7 ± 1.05 mg/g/h; after, 1.5 ± 0.39 mg/g/h; $t = 0.588$, df = 5, one-tailed $P > 0.25$; Guana: before, 1.2 ± 0.88 mg/g/h; after, 1.3 ± 0.82 mg/g/h; $t = 0.152$, df = 5, one-tailed $P > 0.4$). In contrast, Sage Mountain lizards showed a significant improvement in their overall ability to conserve water (before, 2.6 ± 0.50 mg/g/h; after, 1.9 ± 0.60 mg/g/h; $t = 2.102$, df = 5, one-tailed $P = 0.035$).

Body masses of lizards from Necker and Guana Islands decreased slightly during the experiment, but not significantly so (paired t-tests of repeated measures, $P > 0.1$ for both). In contrast, those of Sage Mountain lizards increased significantly from a mean of 7.0 (SD = 1.06) to 7.8 g (SD = 1.12; paired t-test: df = 7, $t = 3.03$, $P = 0.019$).

DISCUSSION

Rogowitz (1996) showed that *A. cristatellus* did not adjust their metabolism to differing thermal regimes. This constrained view of *A. cristatellus* contrasts with the more labile view of *Anolis* water physiology shown by Kobayashi *et al.* (1983). Our previous findings (Dmi'el *et al.* 1997, Perry *et al.* 1999) suggested water-loss rates in *A. cristatellus* can change within a few weeks or months. As expected from this, we found that *A. cristatellus* had a decrease in R following the end of the drought. In one important way, however, these results obtained in 1995, were markedly different than expected. The strong correlation between habitat aridity and R we previously observed (Dmi'el *et al.* 1997, Perry *et al.* 1999) was not discernible during this year. We conducted our study as the extreme 1994 drought (Perry *et al.* 1999) was breaking, and different islands started receiving rains at different points. We suspect that all populations had already reacted to the increased availability of water by the time our study began, but not all had reached a new equilibrium; however, absence of reliable weather stations precluded testing this hypothesis further. Interestingly, the decrease in water conservation ability may indicate a cost to water conservation and selection for greater water loss when conditions allow.

Can our results be used to distinguish the mechanism(s) underlying the physiological differences we saw among years? Perry *et al.* (1999) identified six ways in which phenotypic plasticity and genotypic divergence should differ in this context, and our data allow all of them to be addressed. The first predicted difference involves the speed at which a physiological response occurs. Study 1 and the data of Dmi'el *et al.* (1997) and Perry *et al.* (1999) indicate that changes in R can be rapid, both when the weather changes from wet to dry and when it returns from dry to wet as expected, if the change resulted primarily from phenotypic plasticity. In contrast, a single month was not enough to allow statistically discernible physiological change in R to occur in our common garden experiment. This appears to contradict our finding that the best correlation between R and rainfall occurs over a one-month period (Fig. 2); however, our experiment involved a sharp change in environment, not a relatively continuous one as in natural change, and this may account for the difference.

A second dichotomy listed by Perry *et al.* (1999) involves changes in population size. Population rebound during the shift to wetter conditions should take a relatively long time under the selection scenario, but phenotypic plasticity should allow population size to remain nearly constant from drought to wetter conditions. No obvious change in population size occurred from 1993 to 1995 (J. Lazell, pers. obs.), suggesting phenotypic plasticity may have been involved during the drought. Population size, however, clearly depends on many other factors, and population data are available only for a single site (Guana Island). Perry *et al.* (1999) also predicted that variability in R would remain unchanged if phenotypic processes were occurring, but should be reduced if genotypic change was involved, since mortality should first affect those animals most different from the best-suited phenotype. We found that variability in R significantly decreased from 1994 to 1995, as predicted by the selection scenario.

Smaller individuals have relatively higher surface-to-volume ratios, and should therefore be affected by drought to a greater extent. In support of this, we found that populations from wet habitats tended to be smaller than those from dry ones; however, body size is a complex trait affected by many parameters, as indicated by the differences in how body size changed with alternating hydric conditions on different islands. In our common garden study, captive Sage Mountain lizards were much better feeders and demonstrated a rapid and clearly phenotypic increase in body mass. This demonstrates that change in body size does not allow the two mechanisms to be distinguished. Thus, although large body size is clearly important in overall resistance to water loss, the mechanism by which differences in body size are established and maintained remains unclear. *Anolis ernestwilliamsi*, found on tiny and arid Carrot Rock, is interestingly considerably larger than *A. cristatellus* from which it is recently derived (Lazell 1983).

Our studies support both differential mortality and phenotypic plasticity as causes of year-to-year variation in R. Unfortunately, the results of our short-term common garden experiment were inconclusive. Superficially, they seem to contradict the phenotypic plasticity hypothesis by not showing significant shifts in R. The greatest amount of change, however, was seen, as would be expected, in the Sage Mountain population, which was moved from wet to drier conditions. This was also the only population showing significant changes in body mass or CWL, demonstrating a rapid phenotypic response resulting in an improved ability to conserve water even if the main mechanism was not a change in R. One would expect CWL to be the trait under the highest selective pressure, as it is the amount of water lost that affects physiological, and thus ecological, function.

Overall, our studies appear to demonstrate that both selection-driven evolutionary changes and phenotypically plastic traits were involved at different levels. Under this scenario, much of the observed change probably was due to phenotypic plasticity within each population, but longer-term evolutionary processes have likely set the limits for such changes. A longer-term common garden experiment will be required to fully test this hypothesis.

ACKNOWLEDGMENTS

This project was funded by the Conservation Agency through a grant from the Falconwood Foundation. We thank C. Guyer, S. Hillman, and H. Pough for helpful comments on the manuscript, H. Jarecki for access to Guana Island, R. Branson for permission to work on Necker Island, and O. Dmi'el, G. Friesen, and K. R. LeVering, as well as the entire Guana Island staff, for technical assistance.

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7 March 2001

Dr. James Lazell
Conservation Agency
Six Swinburne Street
Jamestown RI 02835-1414

Dear Skip,

This past October we added 11 families, 50 genera, and 80 species to the 1999 list of Guana beetles. Buena and I had important contributions from Wenhua, Phat Souphanya, the Malaise trap serviced by W. P. Lieu, and Lianna. In addition, we have about 50 species (from eight other Virgin Islands) that we have not yet found on Guana. This latter group provides important clues for future work on Guana, and helps considerably as we identify the new material. The Guana beetle count is now 231, which contrasts nicely with the 163 species mentioned in the 1992 report by Ivie. As a result, Guana will soon be the best known of the Virgin Islands, and will provide a base line for biogeographic and systematic studies of the other Antilles. Several features make the Guana work unique.

1. Although other islands are larger or more diverse, they are also more degraded. The protected ecosystem on Guana is a biological treasure.

2. The protection, plus year-to-year sampling, increases the accuracy of the survey. Our two samples were made under moderately dry conditions (1999) and quite wet (2000). This helps explain the addition of 80 species in 2000; but it is only part of the results; equally interesting are those species present in 1999 but not seen in 2000. These population fluctuations need to be examined more carefully and correlated with varying climate.

3. Discovery and descriptions of new species on Guana and its designation as the type locality (and sometimes the only known locality) bestows scientific importance in perpetuity on the island. Once a Guana locality is published it becomes part of a permanent record that is recognized worldwide.

4. Specimens from the Guana collections have been sent to specialists and museums worldwide, so they may contribute to studies beyond the breadth of our own program.

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5. The excellent physical and financial support from Henry and Gloria provides opportunities not available in one-time studies. This, plus the ideal living conditions, permits maximum effectiveness for all. Especially for participants our age, this frees us to concentrate our efforts on the project, work hard, and still eat and sleep well. That really increases our efficiency.

6. Less obvious but equally important, the scientific diversity of the program is synergistic. The exchange of ideas, specimens, and information benefits all, and combined with the excellent food, make meal times very special. We have received specimens and/or information from everyone in the program, and this, plus the continued help and encouragement from you and Wenhua, has made this very, very special.

The small samples from other Virgin Islands are increasingly useful. The largest lot is from St. John, made by Buena and me in 1996. Anegada and Tortola are tied for second. Anegada because four of us collected for several hours at three sites last year; Tortola because Sage Mountain may be the single richest site in the B.V.I. Our short visit in pouring rain provided many novelties; we need to return. However, counts of species and specimens from all eight Virgin Islands sampled do not come close to our totals from Guana. We are fortunate to be working with a surprisingly rich fauna, under ideal conditions.

In summary, the 2000 session was excellent. The revised checklist and comments (enclosed with this letter) combine data from 1999 and 2000 and all other sources except the Ivie collection in Montana. Ivie's collection is important because it is large and he has had time to get species identifications from specialists in groups where our identifications are incomplete. It makes sense to get the Ivie records, but he is too busy to compile them. A one-week trip to Montana is suggested. If this can be arranged, Ivie has agreed to give us free access to the collection and to set aside time in April to work with us. The planned result of such a visit would be publication of a detailed checklist of Guana Coleoptera. Can the project help with airfare and publications costs?

Best wishes to you and Wenhua.

Sincerely,

Barry

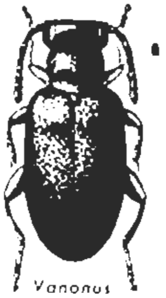
Barry D. Valentine
Professor of Zoology, Emeritus

Preliminary Checklist of Guana Island Coleoptera

genera : species

4 : 4 ADERIDAE (ant-like leaf beetles)
A small family of small beetles with no recent work on the West Indies. Only one identification is firm. Our species were swept from bushes and attracted to ultra-violet light.

Aderus?
Ariotus?
Ganascus?
Gymnoganascus n. sp.



Aderidae

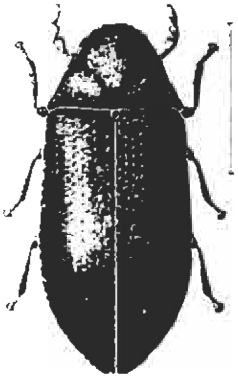
3 : 3 ALLECULIDAE (comb-clawed bark beetles)
Now combined with the Tenebrionidae by many workers. Campbell's (1971) study has 70 Antillean species, with only two from the Virgin Islands, and none from Guana. They occur under dead bark and at ultra-violet light.

Allecula n.sp.
Hymenorus wolcotti Campbell
Lobopoda (L.) thomasensis Campbell

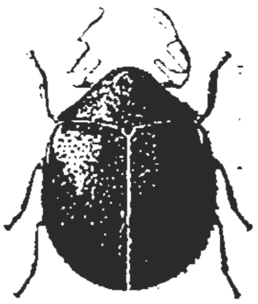
Hymenorus sp.

7 : 13 ANOBIIDAE (drug-store and death-watch beetles)
This family takes a surprising fifth place in the numbers of species on Guana. Many bore in dead wood with varying amounts of damage, others are pests in stored plant materials like grains, coffee beans, tobacco, etc. Ours were taken by beating dead branches and at ultra-violet light.

Caenocara sp.
Cryptorama carinatum White
Cryptorama impunctatum White
Cryptorama megalops White
Cryptorama sp.
Petalium puertoricense Fisher
Petalium sp.
Protheca sp.
Protheca sp.
Tricorynus insulicola (Fisher)
Tricorynus ?pierrei (Lepesme)
Genus?
Genus?



Petalium sp.



Caenocara sp.

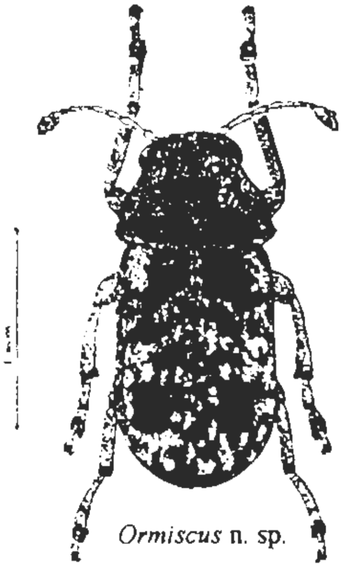
1 : 1 ANTHICIDAE (ant-like flower beetles)
Another small family of small beetles. Adults supposedly eat pollen and small insects, an odd combination. Our single species was taken by beating dead branches over a canvas sheet.

Anthicus sp.

Anthicidae

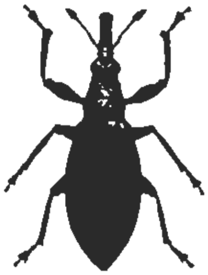
4 : 5 ANTHRIBIDAE (fungus weevils)
These primitive weevils bore into hard, charcoal-like fungi or diseased or dead branches. The Guana species (and one of the genera) are all new to science. We have found them on other Virgin Islands too, but Guana will be the type locality for at least three of them. All were found by beating dead branches and vines, and one also comes to ultra-violet light.

Acaromimus n. sp.
Ormiscus n. sp.
Ormiscus n. sp.
Toxonotus n. sp.
New genus, n. sp.


Ormiscus n. sp.

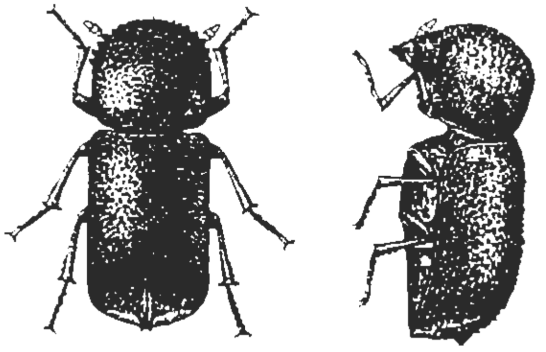
1 : 1 APIONIDAE (apionid weevils)
A family of small weevils whose larvae bore in plant seeds and stems. Small size and hundreds of species make most identifications difficult, we were lucky to find a species with distinctive features. A series was taken sweeping mixed live vegetation.

Apion metum Kissinger


Apion sp.

5 : 5 BOSTRICHIDAE (powder-post beetles)
These are woodborers with many economically important pests distributed worldwide by commerce. *Melalgus femoralis* may be our only native species, and even it may have arrived from another West Indian island. Our individuals occurred in Lindgren funnels, Malaise traps, at ultra-violet light, and beating dead branches.

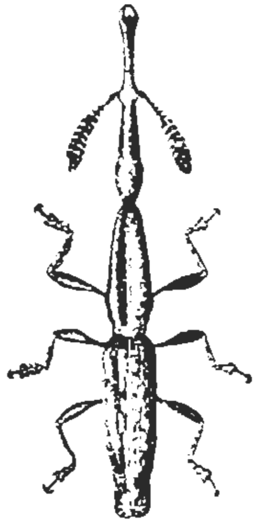
Amphicerus cornutus (Pallas)
Melalgus femoralis (Fabricius)
Tetrapriocera longicornis (Olivier)
Xylomeira tridens (Fabricius)
sp.


Bostrichidae

1 : 1 BOTHRIDERIDAE (no common name)
Recent authors have split this group from the Colydiidae. They occur under dry, dead bark, and in the burrows of other beetles. Larvae are predators of wood-boring beetles, especially buprestids, cerambycids, and platypodids, but are incapable of making their own tunnels.
Bothrideres sp.


Bothrideres

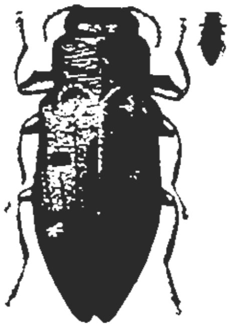
1 : 1 BRENTIDAE (straight-snouted weevils)
The distinctive elongate body makes these primitive weevils easy to recognize. The larvae bore in wood. Although numerous in the tropics, only one species occurs in the Virgin Islands. Our specimens came to ultra-violet light.
Exopleura monilis (Fabricius)


Exopleura monilis (F.)

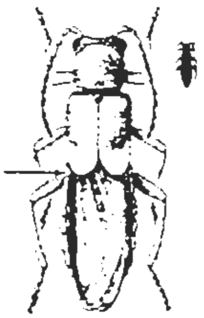
2 : 3 BRUCHIDAE (seed beetles, pea and bean "weevils")
Bruchid larvae are major destroyers of plant seeds. We took specimens beating and sweeping vegetation, and a few at ultra-violet light. We should have more precise identifications soon.
Acanthocelides johnique Johnson
Acanthocelides sp.
?

Acanthoscelides sp.

3 : 3 BUPRESTIDAE (metallic wood-boring beetles)
This is a large family of mostly beautiful metallic beetles. The Virgin Island species are small and rare; we found one specimen last year and only three this year; all were beaten from dead branches. Larvae are wood borers.
Chrysobothris thoracica (Fabricius)
Micrasta ?ornata Fisher
Trigonogya sp.


Chrysobothris

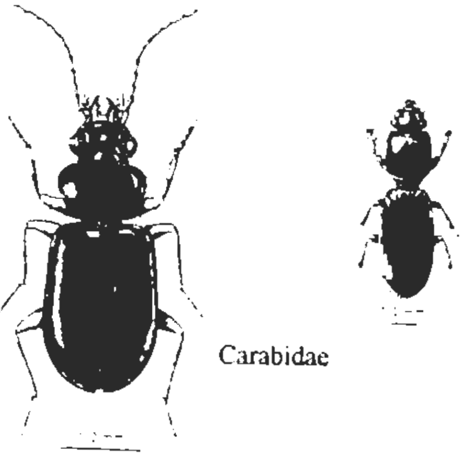
2 : 4 CANTHARIDAE (soldier beetles)
Virgin Island species are minute beetles with soft bodies and short elytra, which we caught in Malaise traps. Larvae are in leaf litter and are occasionally taken in Berlese funnels. Habits of ours are unknown, but related species are predators.
Caccodes sp.
Caccodes sp.
Tytthonyx discolor Leng & Mutchler
Tytthonyx guanaensis Wittmer


Cantharidae

3 : 5 CARABIDAE (ground beetles)

Although a very large family, we have collected only five species. The smallest was chewed up by the largest so we have no specimen to identify. Most are predators; a few eat seeds. Some species live along streams, others in the high forest canopy; their absence on Guana helps explain the unexpectedly low numbers.

Pentagonica sp.
Selenophorus sp.
Selenophorus sp.
Selenophorus sp.
?

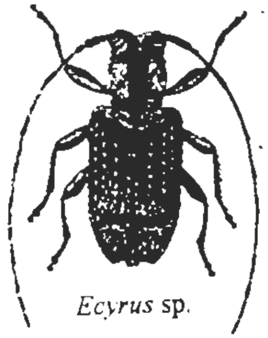

Carabidae

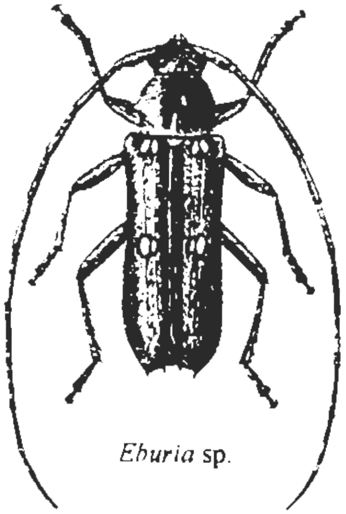
15 : 20 CERAMBYCIDAE (longhorned beetles)

This is the second largest family on Guana. Most are gracefully proportioned, often with long antennae, and are favorites of many collectors. Larvae of our species bore in living or dead wood. Some adults are common at ultra-violet light, but the more rare species require beating dead branches or hand picking at night with the help of a headlamp.

Anelaphus nanus (Fabricius)
Ataxia alboscutellata Fisher
Curtomerus flavus (Fabricius)
Eburia quadrimaculata (Linnaeus)
Ecyrus hirtipes Gahan
Elaphidion irroratum (Linnaeus)
Elaphidion pseudonomon Ivie
Lagocheirus araneiformis (Linnaeus)
Leptostyloides similis (Gahan)
Leptostylopsis sp.
Merostenus attenuatus Chevrolat
Methia necydalia (Fabricius)
Neocompsa cylindricollis (Fabricius)
Neostizocera vanzwalenburgi Fisher
Styloleptus sp.
Urgleptes sp.
Urgleptes sp.
Urgleptes sp.
Urgleptes sp.
Urgleptes sp.


Methia necydalia (F.)

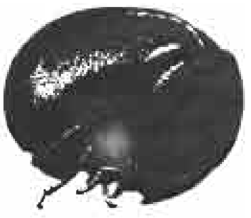

Ecyrus sp.


Eburia sp.


Elaphidion pseudonomon Ivie

1 : 1 CERATOCANTHIDAE (roll-up scarab beetles)
These odd beetles, recently removed from the scarab family, roll into a compact ball when disturbed. Ours were in a Berlese funnel sample and one was beaten from a tangle of vines on a small tree.

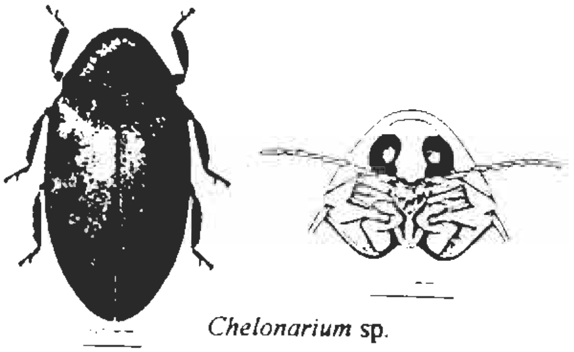
Nesopalla iviei Paulien & Howden



Ceratocanthidae

1 : 1 CHELONARIIDAE (turtle beetles)
These compact, shiny, blackish beetles look like inflated watermelon seeds. The head is invisible from above, and legs and antennae fold precisely into ventral grooves. We know nothing about their life history except larvae of one Australian species occur in rotten wood. Our series was taken by beating, sweeping, and at ultra-violet light.

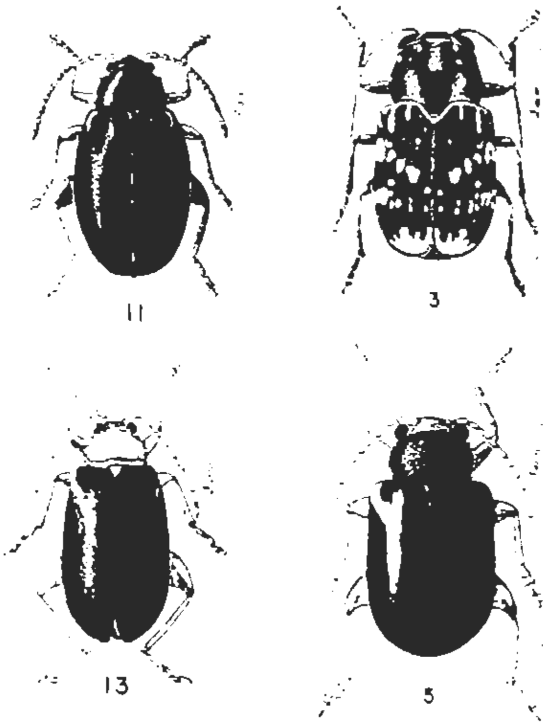
Chelonarium sp.



Chelonarium sp.

13 : 18 CHRYSOMELIDAE (leaf beetles)
This family ranks third in diversity on Guana. We suspect the wet summer contributed to the count because these beetles are leaf eaters. We have added Guana species from the Clark and Ivie manuscript; both authors are former students of Valentine at Ohio State, and Clark has our Virgin Island collection for further study.

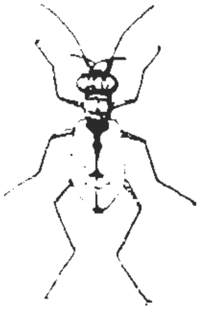
Chalamisus straminea (Suffrian)
Chalcosicya crotonis (Fabricius)
Chalepus sanguinicollis (Linnaeus)
Cryptocephalus krugi Weise
Cryptocephalus perspicax Weise
Cryptocephalus stolidus Weise
Cyrsylus volkameriae (Fabricius)
Diachus nothus (Weise)
Homoschema nigriventre Blake
Homoschema obesum Blake
Lema sp.
Longitarsis chlanidotus Blake
Longitarsis oakleyi Blake
Lysathia occidentalis (Suffrian)
Megistops bryanti Blake
Pachybrachis n. sp. [guana Clark & Ivie]
Pachybrachis sp.
Syphrea sanctaecrucis (Fabricius)



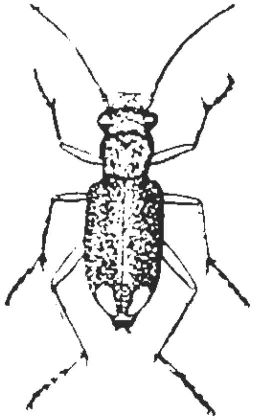
Chrysomelidae

2 : 3 CICINDELIDAE (tiger beetles)
These gorgeous, iridescent, fast, big-jawed predators are favorites for many collectors. Our three species were all on open, sandy areas near water: south beach, edge of the flamingo pond, and by temporary pools at the trash dump. A fourth species occurs in the Virgin Islands (we found it on Anegada), but we do not yet have it from Guana.

Cicindela suturalis Fabricius
Cicindela trifasciata Fabricius
Megacephala sobrina Dejean



Cicindela suturalis F.



Megacephala sobrina Dej.

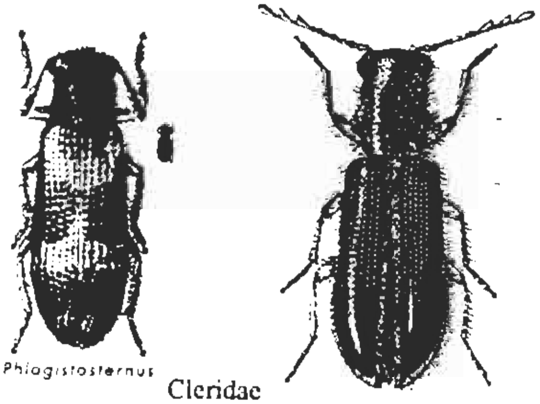
1 : 2 CIIDAE (minute tree fungus beetles)
Most bracket or shelf fungi (polypores) are infested with these tiny brown beetles. Males of some have two tubercles or short horns on their heads. Larvae occur with the adults.

?
?

Ceracis thoracicornis

4 : 4 CLERIDAE (checkered beetles)
Bright patterns, slender form, and high levels of activity make these small predators attractive and a challenge to collect. One of our four species is known only from Guana. It is the cover illustration on Skip's 1992 report, and is one of the few without a color pattern.

Neorthopleura murina (Klug)
Phlogistosternus guana Barr & Ivie
?
?



Phlogistosternus

Cleridae

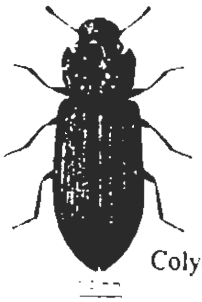
6 : 9 COCCINELLIDAE (ladybird beetles)
All Guana species are probably predators on soft-bodied insects, especially aphids. Unfortunately, the recent major study of the North American species omits the West Indies, and the author tells us he is too busy to examine our specimens. We are looking for another specialist; until we find one, the genera listed below are tentative.

Cryptognatha sp.
Cycloneda sanguinea (Linnaeus)
Pseudoazya trinitatis (Marshall)
Psyllobora sp.
Scymnus sp.
Scymnus sp.
Scymnus sp.
Scymnus sp.
?

Coccinellidae

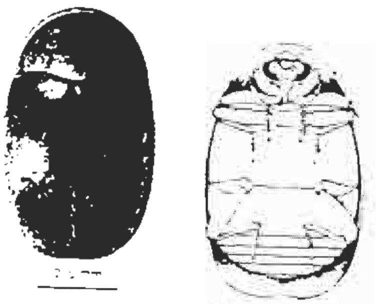
1 : 1 COLYDIIDAE (cylindrical bark beetles)
The usual adult habitat is under dead bark that is damp enough for fermentation and/or fungi and molds. Larvae may be predators. As in the previous family, a recent major study omits the West Indies.

?


Colydiidae

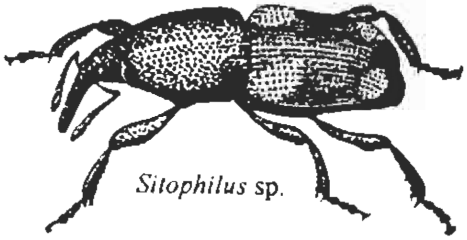
1 : 1 CORYLOPHIDAE (minute fungus beetles)
Since these minute beetles average 1 mm long, and there is no good West Indies literature, we have no identification.

?

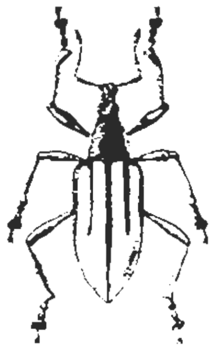

Corylophidae

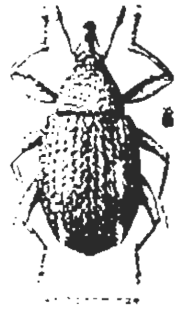
±18:29 CURCULIONIDAE (true weevils)
These weevils constitute the largest family of organisms in the world, with many thousands of species. Identification is difficult because the West Indies fauna is poorly known, and most of the species probably are new and unnamed. Every collecting technique reveals species.

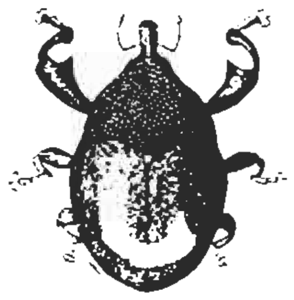
Anthonomus sp.
Anthonomus sp.
Anthonomus sp.
Anthonomus sp.
Anthonomus sp.
"*Cryptorhynchus*" sp.
Decuanellus gladiatus Howden
Decuanellus sp., near *buclavatus* Howden
Diaprepes abbreviatus (Linneaus)
Huaca ayacho Clark
Lembodes sp.
Menoetius curvipes (Fabricius)
Menoetius sp.
Neoulosomus sp.
Pseudomopsis cucubano Wolcott
Rhyssomatus sp.
Sitophilus linearis (Herbst)
Sternechus sp.
Tyloderma sp.
Unknown *cryptorhynchs*: seven species
unknown *tychiine*
?
?


Sitophilus sp.


Menoetius curvipes (F.)


Diaprepes abbreviatus (L.)

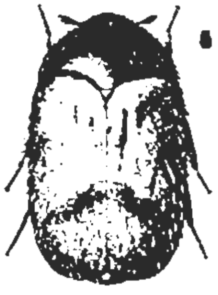



Pseudomopsis cucubano Wolcott

2 : 3 DERMESTIDAE (skin and larder beetles)
These scavengers can destroy an insect collection, herbarium, stuffed animal skin, or a wool sweater with equal gusto. Many are world-wide pests of dry plant or animal products; a few also eat pollen, or rotten animal carcasses. The Guana species can probably be destructive, but we have no data on biology.

Cryptorhopalum sp.
Cryptorhopalum sp.
Trogoderma sp.


Cryptorhopalum sp.


Trogoderma sp.

1 : 1 DYTISCIDAE (predaceous diving beetles)
One of two aquatic beetles from Guana reported by Lianna. We did not find it. As far as known, all species are streamlined predators on other aquatic insects, or those that fall into the water.

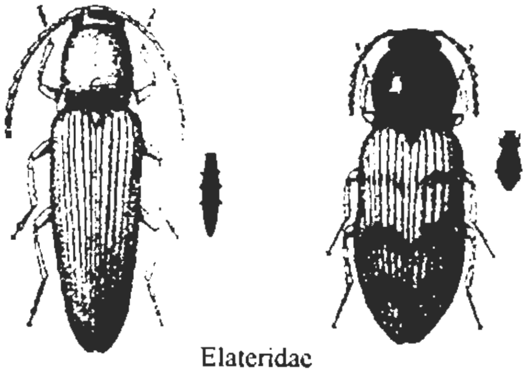
Eretes sticticus (Linnaeus)


Dysticidae

5 : 14 ELATERIDAE (click beetles)
This is the fourth most diverse family on Guana. Click beetles can make a clicking sound by suddenly snapping a spine on the prothorax into a cavity on the mesothorax. The sudden impact can flip the beetle into the air, or eject it from a predator's grasp; it is a unique system. Unfortunately, the many species are very similar, and the West Indies fauna poorly studied.

Aeolus sp.
Aeolus sp.
Conoderus rufidens (Fabricius)
Conoderus bifoveatus (Palisot de Beauvois)
Conoderus sp.
Conoderus sp.
Conoderus sp.
Conoderus sp.
Conoderus sp.
?*Conoderus* sp.
Ischiodontus sp.
Lepidelater misticius Mignot
?*Paradonus* or *Conoderus* sp.
?*Paradonus* or *Conoderus* sp.


Elateridae (ventral view of click apparatus)


Elateridae

1 : 1 ENDOMYCHIDAE (handsome fungus beetles)
We have one small pale brown species, which is totally unexciting. On the mainland, many are larger and attractively patterned. They occur on, and eat bracket fungi and mushrooms.

Eidoreus sp.


Endomychidae

1 : 2 HISTERIDAE (clown and hister beetles)
These are small, compact, heavily armored predators that occur under bark or on dead animal carcasses. We expect more to turn up.
Omalodes sp.
Omalodes sp.

2 : 2 HYDROPHILIDAE (water scavenger beetles)
Lianna reports one species and we found fragments of another at the flamingo pond. All are scavengers or vegetarians.
Berosus metalliceps Sharp
Hydrophilus sp.

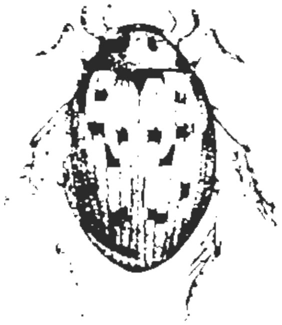
3 : 5 LANGURIIDAE (lizard beetles)
We can identify only one small, common species at lights and in Malaise traps, but have no information on its life history, nor on the identity of the others.
Loberus testaceus Reitter
?
?
?
?

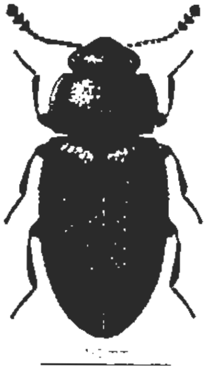
1 : 1 LAEMOPHLOEIDAE (no common name)
This is the flattest beetle on Guana, occurring under bark and at light. Some are major pests in stored plant products, but ours is not one of the pest species.
?

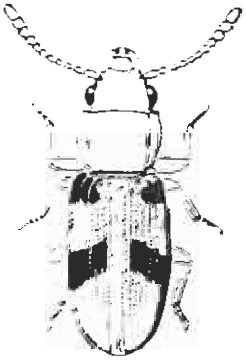
1 : 1 LATHRIDIIDAE (minute brown scavenger beetles)
Four minute specimens of a distinct new species were taken at ultra violet light and in a Berlese funnel. We suspect it is either a predator or eats fungus spores.
Metophthalmus n. sp.

1 : 1 LYCIDAE (net-winged beetles)
The small, elongate new species from Guana is metallic blue and orange with white antennal tips. This is probably warning color as most lyciids are protected by unpleasant chemicals. Adults and larvae are predators.
Leptolycus, n.sp, near *heterocornis* Leng & Mutchler

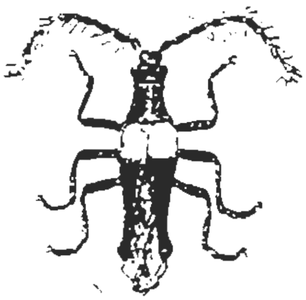

Hister sp.


Berosus sp.


Languriidae


Laemophloeidae


Latridiidae


Leptolycus heterocornis L. & M.

2 : 2 MONOMMATIDAE (opposum beetles)
These are oval, streamlined, weakly inflated like chelonariids, but the head is visible from above. Biology is unknown to us.

Aspathines aenea (Thomson)
Hyporrhagus marginatus (Fabricius)

5 : 7 MORDELLIDAE (tumbling flower beetles)
The Lu and Ivie (1999) paper discusses seven species from Guana that are listed here. Individuals are recognizable by their wedge-shape, humped back, and large conical spine at the end of the abdomen. Adults occur on flowers and come to light; some larvae bore in plant stems.

Falsomordellistena danforthi (Ray)
Glipostenoda guana Lu & Ivie
Mordella atrata Melsheimer
Mordella summermanae Ray
Mordellistena lineata Ray
Tolidomordella basifulva (Quedenfeldt)
Tolidomordella leucocephala (Quedenfeldt)

1 : 1 MYCTERIDAE (no common name)
A small, obscure family that turns up in Malaise trap samples. Biology is unknown to us.

Physcius fasciatus Pic

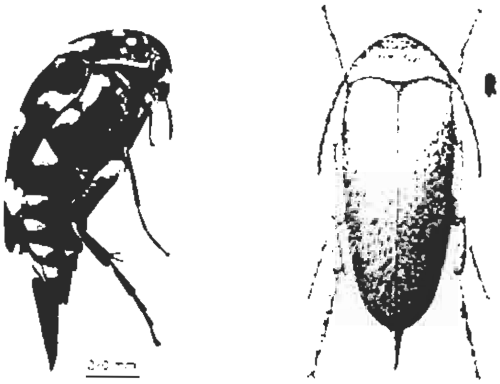
2 : 7 NITIDULIDAE (sap-feeding beetles)
Sap flows, exposed or rotting fruit, fungi, beer, etc. especially if fermented, may attract these small flat beetles by the hundreds. In the U.S., some species, with ants and wasps, are notorious pests at picnics.

Carpophilus (4 sp.)
Stelidota sp.
Stelidota sp.
Stelidota sp.

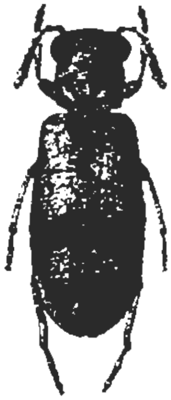
4 : 5 OEDEMERIDAE (false blister beetles)
Beware! The tissues of these slender, soft-bodied beetles contain powerful chemicals that cause painful blisters on human skin. Thick skin, as on finger tips, may not be affected, but don't rub eyes, etc. if you have handled specimens. The several species can be common at lights, or found on flowers or foliage during the day. Adults eat pollen; larvae are stem-borers.

Hypasclera sp.
Hypasclera sp.

Hyporrhagus sp.



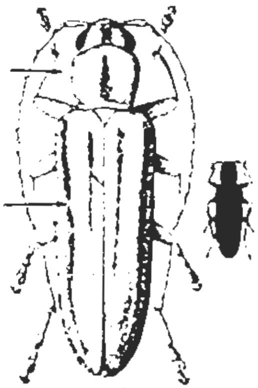
Mordellidae



Physcius fasciatus Pic

Nitidulidae

Oxacis laeta



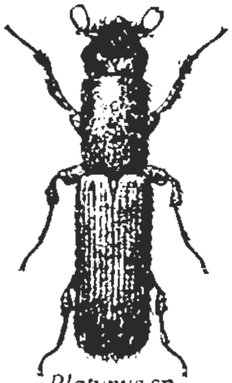
Hypasclera

Oxacis sp.
?
?

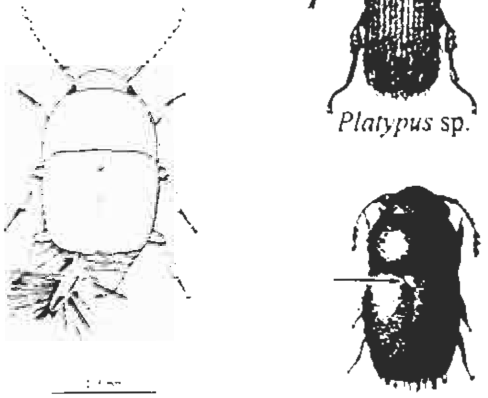
2 : 2 PHALACRIDAE (shining flower beetles)
These small, smooth, shiny, convex beetles fly from flower to flower. Most of ours were collected *en route* in Malaise traps.
Acylomus sp.
sp.


Phalacridae

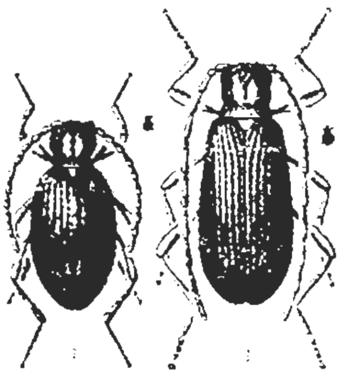
1 : 1 PLATYPODIDAE (ambrosia beetles)
Adults bore into dead or dying wood and infest the burrow walls with fungus spores carried in special depressions. Larvae extend the burrows and eat only this fungus. This is the most elongate of our cylindrical woodborers.
Platypus sp.


Platypus sp.

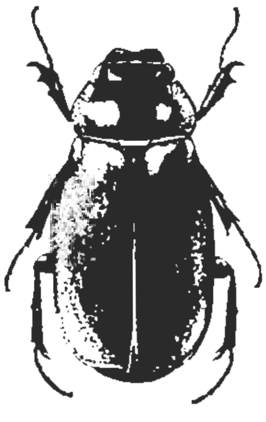
2 : 2 PTILIIDAE (feather-winged beetles)
The smallest beetles in the world are in this family. Ours are one third of a millimeter long and are almost invisible mounted on the tips of human hairs. Each has narrow wings fringed with long setae that increase the surface area. The name *ptilon* is Greek for feather. Our specimens were extracted from leaf litter in a Berlese funnel sample collected by the big water tank.
?
?


Ptiliidae (with exposed wing tip)

1 : 1 PTINIDAE (spider beetles)
A spectacular discovery by Keith Philips was a wingless new genus, new species, still known only from Guana. It was taken in pitfall traps baited with feces.
Lachnoniptus lindae Philips

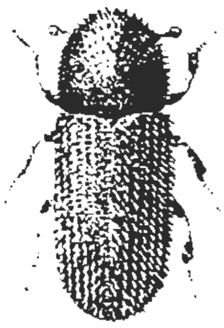

Ptinidae

3 : 5 SCARABAEIDAE (lamellicorn and scarab beetles)
Dung-feeding scarabs (common in the larger Virgin Islands) appear absent on Guana. Larvae of our species are root feeders; adults eat leaves or dead vegetation. The name *lamellicorn* refers to the last 3 (or more) antennal articles which are produced on one side into flat plates which fit closely together and can be spread like a fan.
Ligyrus cuniculus (Fabricius)
Phyllophaga sp.
Phyllophaga sp.
Phyllophaga sp.
Strategus talpa (Fabricius)


Phyllophaga sp.

3 : 6 SCOLYTIDAE (bark beetles)
These are small, cylindrical woodborers closely related to platypodids. Some even transmit fungi from burrow to burrow which is used as larval food.
Hypothenemus sp.
Hypothenemus sp.
Xyleborus ferrugineus (Fabricius)
Xyleborus sp.
Xyleborus sp.
Xylosandrus sp.

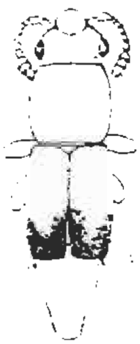

Xyleborus sp.


Hypothenemus sp.

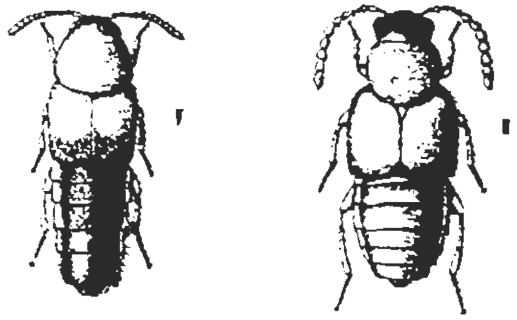
2 : 2 SILVANIDAE (grain beetles)
Some species are worldwide pests of dried foods; others occur under loose bark. They are small, elongate, flattened, brown, and difficult to identify.
Cathartus quadricollis (Guérin-Méneville)
sp.


Cathartus sp.

1 : 1 SMICRIPIDAE (no common name)
This is an obscure family, recently separated from the Nitidulidae. The few species are minute, flattened, and elongate, and the enlarged last abdominal segment projects beyond the elytra. Our small series was taken in a Lindgren funnel baited with ethyl alcohol, suggesting an association with fermented fruit or sap. Comparison with Florida specimens shows that Guana and Florida have different species.
Smicrips sp.

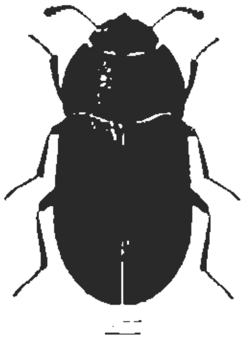

Smicrips sp.

? : 10 STAPHYLINIDAE (rove beetles)
This is a huge family of mostly minute, elongate, flexible beetles, with short elytra that leave several abdominal segments exposed. They are predators, scavengers, and a few eat fungus spores. A partial monograph of the West Indies species (658 pages!) was published in 1943, but it has defied our attempts to identify the Guana species. Over 70 species occur in the Virgin Islands, but none have been recorded from Guana.
Several genera and 10 species, all unidentified


Staphlinidae

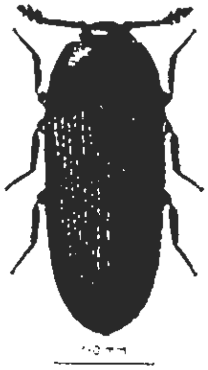
7 : 7 TENEBRIONIDAE (darkling beetles)
A large, widespread family often characteristic of dryer habitats. Our seven species probably constitute a very incomplete list. Larvae are the "wire-worms" sold in pet stores as bird and lizard food.

Adelina sp.
Diastolinus hummelincki Marcussi
Nautes sp.
Platydema micans Zimmerman
Rhipidandrus sp
Strongylium paddai Ivie & Triplehorn
Ulomoides ocularis (Casey)


Tenebrionidae

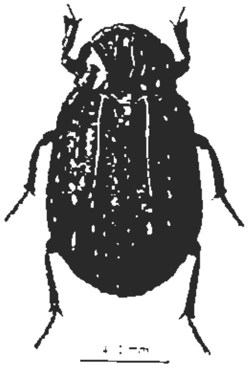
1 : 1 THROSCIDAE (false metallic wood-boring beetles)
This is a small, rare, poorly known group that occasionally comes to ultra-violet light. The same genus occurs in our back yard in Columbus, Ohio, but we have not been able to work out the life history.

Aulonothroscus sp.


Aulonothroscus sp.

1 : 1 TROGIDAE (hide beetles)
Trogids are scavengers on dry animal carcasses. In two visits we have seen only six specimens; all came to ultra-violet light.

Omorgus suberosus (Fabricius)


Omorgus sp.

2 : 3 TROGOSITIDAE (bark gnawing beetles)
Some species are pests of dry plant products. Others live under dead bark. Ours were taken by beating dead branches, or at ultra-violet light; none appear to be pest species.

Airora sp.
Tenebroides sp.
Tenebroides sp.


Tenebroides sp.

1 : 1 Family unknown
1 : 1 Family unknown
1 : 1 Family unknown
1 : 1 Family unknown
1 : 1 Family unknown

57 families
±170 genera
±237 species

Barry D. Valentine
Columbus, Ohio
April, 2001

AN ANNOTATED LIST OF PLANTHOPPERS (HEMIPTERA: FULGOROIDEA) OF GUANA ISLAND (BRITISH WEST INDIES)[1]

Charles R. Bartlett[2]

ABSTRACT: Twenty-seven species of planthoppers (Hemiptera: Fulgoroidea) are reported from Guana Island (British Virgin Islands), 26 for the first time. The full geographic range of each species is summarized. Local biogeography and *alpha* taxonomy needs for Guana species are discussed. Most planthoppers found on Guana (63%) are also known from Puerto Rico, but many species (59%) have never been reported from outside the Puerto Rican Bank.

Guana is a small privately owned island of 299 hectares situated north of Tortola in the Virgin Islands of the British West Indies. Guana Island is in unusually good ecological condition (Heatwole et al. 1981, Mayer and Chipley 1992), and consists principally of steeply hilly terrain, reaching an elevation of 246 m, covered principally by dry scrub woodland. The flora consists of over 300 species (Mayer and Chipley 1992). There is a small area of flat land with principally grassy vegetation plus a salt pond fringed with mangroves and *Sporobolus* grasses. Guana Island has been subject to a wide array of biological investigations (e.g., Mayer and Chipley 1992, Becker and Miller 1992, Evenhuis and Miller 1994, Roth 1994), although there are no previous studies on the auchenorrhynchous Homoptera. Geologically, Guana is a portion of the Puerto Rican Bank, which was connected to Puerto Rico by dry land during the Pleistocene glacial maxima (Heatwole and MacKenzie 1967, Lazell 1996). Puerto Rico became separated from the Virgin Islands approximately 8,000-10,000 years ago (Heatwole and MacKenzie 1967). The vegetation, climate and geology of the Puerto Rican Bank has been recently described by Heatwole et al. (1981). The planthoppers (Fulgoroidea) of Guana, therefore, are expected to be a relictual subset of the Puerto Rican fauna. The objective of this work is to document the planthoppers of Guana Island in a zoogeographic context.

The insects of Puerto Rico are relatively well known (reviewed by Maldonado Capriles 1996). Caldwell and Martorell (1951) provide keys to the fulgoroid fauna except Kinnaridae provided by Ramos (1957). Wolcott (1950), with additions summarized by Maldonado Capriles and Navarro (1967), lists the species of Puerto Rico, including some not treated by Caldwell and Martorell (1951) or Ramos (1957). The only fulgoroid species previously reported from Guana was the flatid *Melormenis basalis* (Walker, 1851) by Medler (1990).

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All other fulgoroids are reported from Guana for the first time.

MATERIALS AND METHODS

Fulgoroids were surveyed during three collecting expeditions by the author (1993, with J. Cryan, 1994 and 1997) in cooperation with The Conservation Agency (Jamestown, Rhode Island). All surveys were conducted during October at times when The Conservation Agency was granted general access to the island for scientific research. Additional specimens from the Virgin Islands were obtained on loan from the Bernice P. Bishop Museum (BPBM, Honolulu, Hawaii) and M. Ivie (Montana State University). Collecting methods included sweeping or beating vegetation, visual inspection of plants, and malaise trapping.

For each species recorded, all specimens examined are reported and a summary of the entire geographic range is provided. The reported range of each species within the Caribbean islands is arranged geographically from west to east, with the Lesser Antilles divided into the Virgin Islands (VI), Leeward Islands (LI), and Windward Islands (WI) following Bent (1977). Synonymy is reported only for species with changes in nomenclature since Metcalf's Catalog of the Homoptera (Metcalf 1936, 1943, 1945, 1948, 1954a, 1954b, 1957, 1958), or for species reported under a different name by Caldwell and Martorell (1951). Junior synonyms are followed by the citation that resulted in the nomenclatural change. Voucher specimens of all species have been deposited primarily in the collection of North Carolina State University, Raleigh; with representative collections at the BPBM and the University of Delaware (Newark, Delaware).

A discovery curve (species accumulation curve) was calculated to evaluate the completeness of the survey and estimate the number of undetected planthopper species on Guana Island. The discovery curve was created by treating each specimen collected as an observation, and randomizing the sequence of observations with a SAS (SAS Institute 1989) program, and plotting observations by cumulative species. Total planthopper species richness was predicted using Chao's (1984) abundance based estimator of species richness, $S_{chao} = S_{obs} + \frac{F_1^2}{2F_2}$, where S_{obs} = number of observed species, F_1 = number of species observed by exactly one specimen, F_2 = number of species observed by exactly two specimens. The variance was computed using the Chao (1987) estimator of standard deviation.

RESULTS

A total of 27 fulgoroid species (or subspecies) among nine fulgoroid families was found on Guana Island. All taxa are listed in Table 1; the five new species will be described elsewhere. Chao's (1984) estimator of species richness (± standard deviation) calculates as 27.1 ± 0.142, and the discovery curve (Figure 1) exhibits a clear leveling-off, suggesting that a high percentage of Guana Island planthopper species were detected.

Of the 27 species, 17 (63%) are also known from Puerto Rico. The species that have **not** been recorded from Puerto Rico are *Bothriocera eborea* Fennah, 1943, *Colpoptera maculifrons flavifrons* Osborn, 1935, *Acanalonia depressa* Melichar, 1901, *Sayiana viequensis* Caldwell, 1951, *Flatoidinus spinosus* Caldwell, 1951, and five new species. *Colpoptera maculifrons*, however, is represented on Puerto Rico by the nominate form (*C. m. maculifrons* Muir, 1924) and two other subspecies (*C. m. maculata* Dozier, 1931, and *C. m. carinata* Dozier, 1936). Also, the Puerto Rican acanaloniid *Acanalonia brevifrons* Muir, 1924, is closely related to *A. depressa* (see **Discussion**). Of Guana Island's 27 species, 16 (59%, excluding *Neomegamelanus elongatus reductus*, see **Discussion**), have not been reported from outside the Puerto Rican Bank (Puerto Rico and the Virgin Islands).

Other than the aforementioned fulgoroid, no other Auchenorrhyncha has been previously reported from Guana Island. Among non-fulgoroid Auchenorrhyncha, a single treehopper species (*Deiroderes inermis* Ramos, 1957), and a single cicada species (*Proarna hilaris* (Germar, 1834)) was found on Guana Island. There were no cercopids found during the present study on Guana Island.

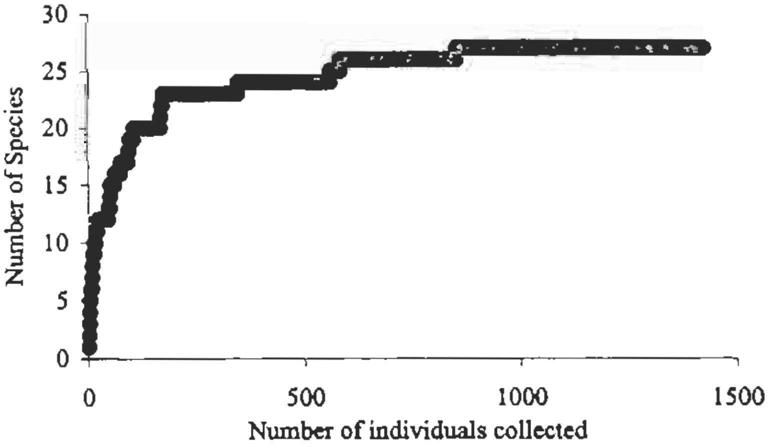

Fig. 1. Discovery curve for Guana Island planthopper species.

Table 1: Fulgoroids of Guana Island, British Virgin Islands.

Species	Island: Specimens examined	Previously reported range (West to East; type locality in **Bold**) (VI = Virgin Is.; LI = Leeward Is.; WI = Windward Is.	References:
Cixiidae			
Bothriocera eborea Fennah, 1943	Guana: 18 Tortola: 52	VI: Tortola, Jost Van Dyke; LI: **St. Kitts**, Nevis, Montserrat; WI: Dominica, Martinique, St. Lucia, St. Vincent	Fennah 1943, 1945, 1949; Caldwell and Martorell 1951
Oliarus slossonae Van Duzee, 1912 = *Oliarus borinquensis* Caldwell, 1951: Mead and Kramer: 1982: 424–426.	Guana: 86 Little Thatch: 1 Tortola: 2 Great Camanoe: 1 St. John: 2	Cuba, Puerto Rico; VI: St. Thomas; USA: **Florida** (but not Mississippi or Texas, Mead and Kramer 1982)	Caldwell and Martorell 1951, Mead and Kramer 1982
Oliarus viequensis Caldwell, 1951	Guana: 2 (♀) Anegada: 3	Hispaniola, Puerto Rico, **Vieques**; VI: St. John; LI: Antigua; USA: FL	Caldwell and Martorell 1951, Mead and Kramer 1982
Pintalia alta Osborn, 1935	Guana: 83 Tortola: 258 Beef: 1	**Puerto Rico**; VI: St. Thomas	Caldwell and Martorell 1951
Delphacidae			
Neopunana caribbensis (Caldwell, 1951) = *Punana caribbensis* Caldwell, 1951: Asche, 1983: 128	Guana: 168 Tortola: 10 St. John: 5 Great Camanoe: 2 Frenchman's Cay: 2 Gt. St. James: 1	Puerto Rico, Vieques; VI: **St. Thomas**	Caldwell and Martorell 1951
Neopunana n. sp.1	Guana: 2		
Neopunana n. sp.2	Guana: 3		
Neopunana n. sp.3	Guana: 3		
Saccharosydne saccharivora (Westwood, 1833)	Guana: 5	Cuba, Jamaica, Hispaniola, Puerto Rico, Vieques; LI: Antigua, Guadeloupe; WI: St. Lucia, Barbados, **Grenada**, Trinidad; Venezuela, USA: Florida, Georgia, Hawaii; British Honduras, Venezuela	Anonymous 1833, Westwood 1833, Crawford 1914, Van Duzee 1917, Spooner 1920, Wolcott 1927, 1936, 1950; Caldwell and Martorell 1951, Box 1953, CIE 1956, Fennah 1959, Metcalfe 1969, Bruner et al. 1975

Species	Island: Specimens examined	Previously reported range (West to East; type locality in **Bold**) (VI = Virgin Is.; LI = Leeward Is.; WI = Windward Is.	References:
Archidelphax havanensis (Crawford, 1914) = *Delphacodes havanensis* (Crawford, 1914): Fennah, 1965: 97	Guana ♂ macropter: 4 ♀ brachypter: 8 ♀ macropter: 1	**Cuba**, Jamaica, Puerto Rico:, Caja de Muertos, Vieques; VI: St. Thomas, St. Croix; WI: Martinique, St. Lucia, Barbados	Crawford 1914, Muir 1918, Osborn 1929, 1935; Wolcott 1936, 1950; Muir and Giffard 1924, Caldwell and Martorell 1951, Fennah 1959, 1965; Miskimen and Bond 1970
Neomegamelanus elongatus reductus (Caldwell, 1951) = *Megamelanus elongatus reductus* (Caldwell, 1951): McDermott 1952: 50-52.	Guana: 13	Puerto Rico, **Vieques.**	Caldwell and Martorell 1951
Toya venilia (Fennah, 1959) = *Delphacodes venilia* Fennah, 1959: Fennah, 1965: 96	Guana: 28 Necker: 14	?Puerto Rico, ?Vieques; LI: **Montserrat**	Fennah 1959, 1965
Derbidae			
Sayiana viequensis Caldwell, 1951	Guana: 24 Anegada: 1	**Vieques**	Caldwell and Martorell 1951
Achilidae			
Catonia arida Caldwell, 1951	Guana: 139 Tortola: 1 Virgin Gorda: 1 Necker: 1 St. John: 1	**Puerto Rico**, Caja de Muertos	Caldwell and Martorell 1951
Catonia cinerea Osborn, 1935	Guana: 64 Tortola: 6 Virgin Gorda: 1	**Puerto Rico**, Caja de Muertos, Vieques; VI: St. Croix	Osborn 1935, Wolcott 1936, 1941, 1950; Caldwell and Martorell 1951
Catonia sp. near *major* Fennah, 1950	Guana: 27 Tortola: 2	LI: **Antigua**	Fennah 1950
Tropiduchidae			
Tangella schaumi (Stål, 1859)	Guana: 1 St. John: 1	Puerto Rico, Caja de Muertos, Vieques; VI: St. Thomas, **St. John**, Jost Van Dyke	Stål 1859, Fennah 1949. Caldwell and Martorell 1951

Species	Island: Specimens examined	Previously reported range (West to East; type locality in **Bold**) (VI = Virgin Is.; LI = Leeward Is.; WI = Windward Is.	References:
Tangia viridis (Walker, 1851) = *Neurotmeta viridis* (Walker, 1851): Fennah, 1965: 100-101	Guana: 97 St. Thomas: 1 St. John: 1	Mona, Puerto Rico, Caja de Muertos, Vieques; VI: **St. Thomas**, Tortola, Virgin Gorda, St. Croix	Osborn 1935, Wolcott 1936, 1941, 1950, Fennah 1949, Caldwell and Martorell 1951, Miskimen and Bond 1970
Flatidae			
Flatoidinus spinosus Caldwell, 1951	Guana: 2	VI: **St. John**, St. Thomas, Tortola	Caldwell and Martorell 1951
Melormenis basalis (Walker, 1851) [nec. Caldwell, 1951] = *Melormenis antillarum* (Kirkaldy, 1909): Fennah, 1965: 107	Guana: 55 Tortola: 8 Virgin Gorda: 2 Great Camanoe: 1 St. John: 2	Mona, Puerto Rico, Caja de Muertos, Vieques; VI: St. Thomas, Jost Van Dyke, Tortola, Virgin Gorda, St. Croix; LI: Anguilla, St. Bartholomew, St. Kitts, Nevis, Montserrat, Antigua; Hawaii (type locality "West Indies" (Walker 1851), but stated as unknown by Fennah (1965))	Melichar 1902, 1923; Beatty 1947, Wolcott 1923, 1941, 1950, Caldwell and Martorell 1951, Fennah 1949, 1965; Miskimen and Bond 1970; Asche 1997.
Petrusa epilepsis (Kirkaldy, 1906) = *Petrusa marginata* (Linne, 1767): Metcalf, 1957: 337-342.	Guana: 268 Tortola: 28 Anegada: 1 St. John: 6 St. Thomas: 1 Scrub: 5	Cuba, Hispaniola, Mona, Puerto Rico, Caja de Muertos, Vieques; VI: St. Thomas, Jost Van Dyke, Tortola, Virgin Gorda, St. Croix; LI: St. Bartholomew, St. Kitts, Nevis, Montserrat, Antigua; WI: Grenada; Brazil, Columbia (type locality unknown)	Melichar 1902, 1923; Myers 1928; Wolcott 1923, 1936, 1941, 1950; Fennah 1941, 1949; Beatty 1947, Caldwell 1950, Caldwell and Martorell 1951, Miskimen and Bond 1970
Pseudoflatoides albus Caldwell, 1951	Guana: 17 Tortola: 6 Frenchman's Cay: 1	**Puerto Rico**	Caldwell and Martorell 1951
Issidae			
Thionia argo Fennah, 1949	Guana: 92 Virgin Gorda: 4 St. John: 1 Scrub: 1	Puerto Rico, Vieques Is., Culebrita; VI: St. Thomas, **Jost Van Dyke**, St. Croix	Fennah 1949, Caldwell and Martorell 1951

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Species	Island: Specimens examined	Previously reported range (West to East, type locality in Bold) (VI = Virgin Is.; LI = Leeward Is.; WI = Windward Is.	References:
Colpoptera maculifrons flavifrons Osborn, 1935	Guana: 3 Tortola: 3	Mona, VI: St. Thomas, **St. Croix**; LI: Antigua	Osborn 1935, Beatty 1947, Wolcott 1950, Miskimen and Bond 1970
Acanaloniidae			
Acanalonia depressa Melichar, 1901	Guana: 79 Tortola 2 Virgin Gorda: 1 Great Camanoe: 2 St. John: 1 Beef: 1	VI: St. Thomas, **St. John**, Anegada, St. Croix	Melichar 1901, Caldwell and Martorell 1951
Kinnaridae			
Prosotropis ♀♀ (poss. *marmorata* Fennah, 1942)	Guana: 2 St. John: 1		
Quilessa fasciata Fennah, 1945	Guana: 131 Tortola: 1 Little Thatch: 1 Virgin Gorda: 3 Cas Cay (St. Thomas): 1 Anegada 10	**Puerto Rico**	Ramos 1957

DISCUSSION

Although it is satisfying that Chao's (1984) estimator of species richness was only slightly higher than the observed species richness, it would be optimistic to claim that all species were detected. It should be noted that these data were not collected for the express purpose of estimating planthopper species richness, and that abundant species were not consistently collected at every encounter. Although additional planthopper species almost certainly occur, these data clearly suggest that a high percentage of species have been detected.

A variety of taxonomic problems were revealed in this study. One particular difficulty was with the forms related to *Acanalonia depressa*: *A. brevifrons* (type locality: Puerto Rico) and *A. impressa* Metcalf and Bruner, 1930 (type locality: Cuba). *Acanalonia impressa* appears to be an endemic Cuban form. Caldwell and Martorell (1951) and Fennah (1949) make conflicting statements as to the geographical limits of *A. brevifrons*. Caldwell and Martorell (1951) report *A. brevifrons* from St. Croix, St. Thomas, and tentatively Anegada, but curiously do not report Puerto Rico (*A. brevifrons* was described from a single Puerto Rican male; Muir 1924) and do not report *A. depressa* in the Virgin Islands. Fennah (1949), however, reports *A. depressa* from Jost Van Dyke, St. Thomas and St. Croix, but limits *A. brevifrons* to Puerto Rico. The published morphological distinctions between *A. depressa* and *A. brevifrons* concern their relative size and subtle differences in the shape of the head and tegmina (Fennah 1949), but genitalic comparisons have never been made. Fennah (1949) suggested that *A. impressa* and *A. brevifrons* should be subspecies of *A. depressa*. The status of these species clearly requires reexamination.

The delphacid *Neomegamelanus elongatus reductus* was described from Puerto Rico and Vieques Island by Caldwell (in Caldwell and Martorell 1951) as a Caribbean subspecies of the otherwise mainland *N. elongatus* (Ball, 1905) (found on the coastal eastern United States, Connecticut to Florida, McDermott 1952, Cummins et al. 1983). Other than geography, no useful morphological distinctions between these subspecies were presented. Comparison of chrotic and phallic features of *Neomegamelanus elongatus elongatus* and *N. elongatus reductus* suggests that there are not sufficient differences to justify subspecific status, although a detailed examination was beyond the scope of the present work. For the purposes of this study *Neomegamelanus elongatus reductus* was not considered a form unique to the Puerto Rican Bank.

Two species found on Guana had some notable differences from described forms. The kinnarid *Quilessa fasciata* lacked the diagnostic markings on the forewings noted by Ramos (1957), and had additional processes on the aedeagal complex. These differences are probably insufficient to consider this form a separate species, but may merit subspecific status. The achilid *Catonia* nr. *major* (from Antigua) showed color and genitalic differences compared to Fennah's (1950) description (this species is only recorded from the holotype), and probably represents a new species.

Zoogeographically, more than half of the species encountered on Guana Island are apparently endemic to the Puerto Rican Bank. Of the remaining species, three others are found also in the Leeward Islands (*Toya venilia*, *Catonia* nr. *major*, and *Colpoptera maculifrons flavifrons*), three were distributed widely within the Caribbean (*Bothriocera eborea*, *Melormenis basalis* and *Anchidelphax havanensis*; the former two largely restricted to the Lesser Antilles), one ranges to northern South America (*Petrusa epilepsis*), three range to the continental United States (*Oliarus slossonae*, *O. viequensis*, and *Neomegamelanus elongatus*), and one is found in both Central America and southeastern United States (*Saccharosydne saccharivora*). It appears odd that more species have an affiliation to North America than to Central America. Modern ideas concerning the origin of the Caribbean fauna (e.g., Rosen 1985, Liebherr 1988) suggest that biological affinities should be strongest with Central America. Ramos (1988: 68) also suggested that the Caribbean Auchenorrhyncha has "little or no affinity to North or South America." The eastern position of the Puerto Rican Bank (relative to the other Greater Antilles and Central America) and long period of time required for vicariance, however, would most certainly obscure biogeographic affinities at the species level.

The issid *Colpoptera maculifrons* Muir, 1924 has five subspecies (including the nominate form) that collectively occur throughout the Caribbean islands. The nominate form along with *C. m. carinata* Dozier and *C. m. maculata* Dozier are recorded from Puerto Rico, with the latter form also recorded from Mona Island (Dozier 1931, Caldwell and Martorell 1951). *Colpoptera maculifrons dominicana* Fennah, 1955, is known only from Hispaniola; *C. m. angustior* Fennah from the Leeward Islands (Antigua, Nevis, St. Kitts, Montserrat) and St. Croix; and *C. m. grenada* Fennah from Grenada (Windward Islands) (Fennah 1955).

The cixiid *Oliarus slossonae* was abundant on agave (*Agave missionum*, Agavaceae) on Guana, a host plant also reported for it on St. Thomas (Mead and Kramer 1982). Perhaps significantly, agave is not reported as a host elsewhere in its range (Mead and Kramer 1982), suggesting that *Oliarus slossonae* may represent a species complex.

The delphacid *Toya venilia* was common on Guana (and nearby islands, R. Denno, pers. comm.) in the grass *Sporobolus virginicus* (Poaceae) near a salt pond. Individuals of this species are commonly brachypterous, with an 85.7% (24 of 28) brachyptery rate among the Guana specimens examined in this study. *Toya venilia* was described from Montserrat (Leeward Islands), the only locality where this species has been unquestionably recorded in the past. Puerto Rican and Vieques Island records are based on Fennah's (1959: 262) assertion that "It appears to be this species which Caldwell and Martorell [1951: 183] have reported from Puerto Rico under the name *Delphacodes nigra*".

A total of 27 species and subspecies of planthoppers (including five new species) were recorded from Guana Island. Most planthoppers found on Guana also occur on Puerto Rico (17 of 27 species, 63%), mostly endemic to the Puerto Rican Bank (16 of 27 species, 59%). The relatively high degree of endemism observed is consistent with the high degree of endemism observed among Auchenorrhyncha in the Greater Antilles by Ramos (1988). It should be noted, however, that this observation is based on substantially incomplete information because many smaller Caribbean islands have no published reports of fulgoroids, and our knowledge of the planthoppers of Jamaica and Hispaniola is quite poor (Ramos 1988). Further surveys of Caribbean Fulgoroidea are needed to more confidently assess planthopper zoogeography.

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Reduced flight capability in British Virgin Island populations of a wing-dimorphic insect: the role of habitat isolation, persistence, and structure

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Abstract. 1. The effects of habitat isolation, persistence, and host-plant structure on the incidence of dispersal capability (per cent macroptery) in populations of the delphacid planthopper *Toya venilia* were examined throughout the British Virgin Islands. The host plant of this delphacid is salt grass *Sporobolus virginicus*, which grows either in undisturbed habitats (large expanses on intertidal salt flats and around the margins of salt ponds, or small patches of sparse vegetation on sand dunes along the shore), or in less persistent, disturbed habitats (managed lawns).

2. Both sexes of *T. venilia* were significantly more macropterous in disturbed habitats (77.1% in males, 12.5% in females) than in more persistent, undisturbed habitats (19.2% in males, < 1% in females).

3. Males exhibited significantly higher levels of macroptery (26.9 ± 7.6%) than did females (2.0 ± 1.7%), and per cent macroptery was positively density dependent for both sexes in field populations.

4. There was no evidence that the low incidence of female macroptery in a subset of island populations inhabiting natural habitats (1.7 ± 1.2%) was attributable to the effects of isolation on oceanic islands. The incidence of macroptery in British Virgin Island populations of *T. venilia* was not different from that observed in mainland delphacid species existing in habitats of similar duration.

5. Rather, the persistence of most salt grass habitats throughout the British Virgin Islands best explains the evolution of flight reduction in females of this island-inhabiting delphacid.

6. Males were significantly more macropterous in populations occupying dune vegetation (37.6 ± 9.8%) than in populations occupying salt flat–pond margin habitats (7.6 ± 5.6%). By contrast, females exhibited low levels of macroptery in both dune (0%) and salt flat–pond margin (< 1%) habitats. Variation in salt-grass structure probably underlies this habitat-related difference in macroptery because flight-capable males of planthoppers are better able to locate females in the sparse-structured grass growing on dunes. This habitat-related difference in male macroptery accounted for the generally higher level of macroptery observed in males than in females throughout the islands.

7. The importance of habitat persistence and structure in explaining the incidence of dispersal capability in *T. venilia* is probably indicative of the key role these two factors play in shaping the dispersal strategies of many insects.

Key words. Delphacid planthopper, dispersal, flightlessness, habitat isolation, habitat persistence, habitat structure, host plant architecture, life history evolution, *Sporobolus virginicus*, *Toya venilia*, wing polymorphism.

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Introduction

With the evolution of flight in insects came an increased ability to track changing resources, negotiate structurally complex habitats, locate mates, and escape predators (Southwood, 1962; Roff & Fairbairn, 1991; Wagner & Liebherr, 1992; Denno, 1994a; Denno *et al.* 1996, in press). Moreover, associated with the appearance of flight capability was the tremendous diversification of the class Insecta (Wagner & Liebherr, 1992). As a consequence of the association between flight capability and the increased radiation and success of the insects, reasons underlying the secondary loss of wings or flight capability, which has occurred repeatedly throughout the Insecta (Roff, 1990; Wagner & Liebherr, 1992), are not immediately apparent.

One of the keys to understanding the evolution of flight reduction in insects lies in elucidating the costs associated with building and maintaining wings and flight muscles, and in demonstrating how such costs are levelled against other life-history traits (Roff, 1986; Denno *et al.*, 1989; Zera & Denno, 1997). Most often, the diversity of costs associated with flight capability are imposed on reproduction (Roff, 1984; Srygley & Chai, 1990; Marden & Chai, 1991; Roff & Fairbairn, 1991; Zera & Denno, 1997). Such reproductive penalties are revealed most easily by comparing the reproductive success of the volant and flightless wing forms of wing-dimorphic insects (Roff, 1986; Denno *et al.*, 1989, in press; Roff & Fairbairn, 1991; Langellotto *et al.*, 2000). In general, flightless females have higher fecundity, reproduce at an earlier age, and produce larger progeny than their flight-capable counterparts (Solbreck, 1986; Roff & Fairbairn, 1991; Denno, 1994b; Zera & Denno, 1997). Similarly, flightless males can acquire matings more successfully and sire more offspring than macropterous males (Novotný, 1995; Langellotto *et al.*, 2000). Indeed, such wing-form comparisons provide widespread evidence for an antagonistic trade-off between flight capability and reproductive success across a wide variety of insect taxa including crickets, planthoppers, aphids, thrips, true bugs, and beetles (Utida, 1972; Roff, 1984; Zera, 1984; Solbreck, 1986; Crespi, 1988; Denno *et al.*, 1989; Dixon, 1998; Langellotto *et al.*, 2000).

Although flightless forms clearly have an inherent reproductive advantage, they are extremely sedentary and are unable to effectively exploit ephemeral habitats, track spatial changes in food availability, manoeuvre efficiently in heterogeneous habitats, or locate widely scattered mates (Waloff, 1983; Roff, 1990; Denno *et al.*, 1991, 1996, in press; Langellotto, 1997; Langellotto *et al.*, 2000). Thus, the dispersal strategy that evolves in a particular species will reflect a balance between the advantage of increased reproductive success resulting from flight loss and the need for wings to track resources (Roff, 1990; Zera & Denno, 1997).

Among the selective forces considered central in shaping the evolution of insect dispersal strategies are habitat isolation, persistence, and structure (Southwood, 1962, 1977; Roff, 1990; Denno *et al.*, 1991, in press; Wagner & Liebherr, 1992; Travis & Dytham, 1999). In general, theory predicts reductions in flight capability for species exploiting habitats that are very isolated, persistent, or dense and low-profile in structure (Southwood, 1962; Roff, 1990; Langellotto, 1997; Denno *et al.*, in press). In particular, habitat isolation has been a longstanding but controversial explanation for the evolution of flightlessness in insect taxa inhabiting oceanic islands (Darwin, 1876; Roff, 1990). The argument asserts that the constant loss of emigrants from oceanic islands should select against flight capability (see Roff, 1990), however the spatial scale at which habitat isolation selects against dispersal has been a subject of considerable debate (Roff, 1990; Wagner & Liebherr, 1992; Denno *et al.*, in press). Notably, recent modelling efforts have shown that the propensity to disperse generally declines with increased habitat fragmentation, but that the predicted outcome depends on patterns of habitat availability and persistence (Travis & Dytham, 1999).

Isolation, and other habitat-related hypotheses for the evolution of flightlessness in insects, have proved difficult to test empirically, however, primarily because of the difficulty of assessing the dispersal ability of the inhabitants (Denno *et al.*, 1991, 1996, in press). Wing-dimorphic insects such as delphacid planthoppers (Hemiptera: Delphacidae) are ideal for investigating the effects of habitat factors on dispersal because migratory adults (macropters with fully developed wings) and flightless adults (brachypters with reduced wings) are so easily recognised (Denno *et al.*, 1991). Moreover, the proportion of macropters in a population can be used as a reliable index of the incidence of potential dispersal (Denno *et al.* 1991, in press). Testing the habitat isolation—flightlessness hypothesis has been challenging as well because comparisons of the incidence of dispersal between island and mainland populations are frequently confounded by other factors such as habitat persistence and structure (Roff, 1990; Denno *et al.*, in press).

Using British Virgin Island populations of the wing-dimorphic delphacid *Toya venilia* (Fennah), the objectives of the work reported here were threefold. First, the incidence of dispersal (per cent macroptery) was compared between populations of *T. venilia* inhabiting undisturbed (relatively persistent) and disturbed habitats throughout the British Virgin Islands, with the expectation of higher levels of macroptery in disturbed habitats. Second, to test the hypothesis that flight reduction is more prevalent on oceanic islands, the incidence of macroptery in island populations of *T. venilia* was compared with known levels of macroptery in mainland populations of other grass-inhabiting delphacid species. For this analysis, possible differences in habitat persistence were controlled by comparing the incidence of dispersal capability between taxa inhabiting habitats of similar age. Last, the incidence of macroptery was compared between populations of *T. venilia* inhabiting two structurally different and habitat-associated growth forms of its host grass *Sporobolus virginicus* (L.) (dense stands on salt flats and sparse stands on beach dunes). Because vegetation structure (dense vs. sparse) is known to influence the ability of male planthoppers to locate mates (Denno, 1994b; Langellotto, 1997; Denno *et al.*, in press), its contribution to habitat-related variation in the incidence of dispersal capability in *T. venilia* populations was examined. Ultimately, this information was used to assess the relative contribution of habitat isolation, persistence, and vegetation structure to the dispersal strategy of this oceanic island-inhabiting planthopper.

Methods

Study organisms

Toya venilia is Caribbean in distribution, having been recorded from the British Virgin Islands, Puerto Rico, and Montserrat (Fennah, 1959). This delphacid is multivoltine and monophagous on the perennial salt grass *Sporobolus virginicus*. Like most delphacids, *T. venilia* is wing dimorphic with both macropters and brachypters occurring in most populations. Wing form in planthoppers is determined by a developmental switch that responds to environmental cues (Denno, 1994b). The sensitivity of the switch, however, is heritable and under polygenic control (Iwanaga & Tojo, 1986; Denno, 1994b; Zera & Denno, 1997). Of all the proximate cues known to affect wing form in planthoppers, population density is by far the most influential (Denno & Roderick, 1990). For most delphacids, the production of the macropterous wing form is density-dependent (Denno *et al.*, 1985; Denno, 1994b), however the threshold density that triggers the production of macropterous forms can differ among species, among populations of the same species, and even between the sexes of the same species (Kisimoto, 1965; Denno *et al.*, 1991). Thus, macroptery may or may not be correlated between the sexes of a species (Denno *et al.*, 1991; Denno, 1994a). Moreover, patterns of density-dependent macroptery in the sexes, be they the same or different, can be maintained under common environmental conditions, suggesting an underlying genetic basis (Denno *et al.*, 1991).

Besides allowing for habitat escape and the colonisation of new habitats (Southwood, 1962, 1977), wings also function in mate location (Ichikawa, 1977; Hunt & Nault, 1991; Langellotto, 1997). In planthoppers, only males search actively for stationary females (Ichikawa, 1977; Claridge & de Vrijer, 1994; Langellotto *et al.*, 2000) and acoustic communication is essential for locating mates (Claridge, 1985; Denno *et al.*, 1991; Heady & Denno, 1991; Heady, 1993). Both males and females communicate through substrate-transmitted vibrations, whereby calls are produced by vibrating their abdomens (Claridge, 1985). Vibrations are transferred to the host plant through the legs or mouth parts (Claridge, 1985). Planthoppers sitting on the same host plant or on adjacent plants in physical contact can sense each other's calls from as far away as 1 m (Ichikawa & Ishii, 1974), however planthoppers resting on neighbouring but slightly separated plants do not detect each other's presence (Ichikawa & Ishii, 1974). Sexually mature males and virgin females call spontaneously on their food plants. After sensing each other, they begin to alternate calls in a duetting fashion (Ichikawa & Ishii, 1974; Claridge, 1985; Heady & Denno, 1991). During duetting, males move toward stationary females and, after locating a female, courtship ensues, followed by mating (Ichikawa & Ishii, 1974; Heady & Denno, 1991).

Given their substrate-borne system of mate location, it is not surprising that vegetation structure has a major impact on the ability of the male wing forms of planthoppers to locate mates. When host plants are isolated and do not come into contact, flight is essential for mate location because only macropterous males can fly among plants, locate females effectively, and acquire matings (Langellotto, 1997). Macropterous males also locate females much more effectively than brachypters under low female-density conditions (Langellotto, 1997). In contrast, in contiguous vegetation, brachypterous males obtain most matings, apparently due in part to their inherent ability to displace rival macropters aggressively during courtship (Langellotto *et al.*, 2000).

The host plant of *T. venilia* is salt grass *S. virginicus*, a perennial that grows in several different habitat types throughout the Caribbean, including most of the vegetated British Virgin Islands (Chase, 1971; Acevedo-Rodriguez, 1996; Table 1). Salt grass grows on intertidal salt flats and around the margins of salt ponds, where it often occurs in dense, expansive, pure stands, frequently in association with mangroves. It also occurs as small patches on the dunes of sandy beaches and the bases of cliffs along the shore. In this beach-dune habitat, the structure of the grass stand is sparse, with culms growing further apart than those occurring on tidal flats. *Sporobolus virginicus* is also grown in managed, suburban habitats where it is encouraged by home owners as a lawn grass in low-lying areas. Although frequently disturbed by mowing, the dense structure of the grass in lawns is more like that of grass growing on salt flats than dunes. Such structural variation in grass form may influence the dispersal strategy of the resident *T. venilia*, particularly the males.

Study sites

The British Virgin Islands lie 100 km east of Puerto Rico and comprise more than 50 small islands and islets between 18°18′ and 18°46′N, and 64°15′ and 64°52′W (Fig. 1). Among the largest islands are Tortola (64 km^2), Anegada (34 km^2), Virgin Gorda (21.5 km^2), and Jost van Dyke (9 km^2). Other islands (e.g. Guana, Beef, Great Camanoe) measure < 5 km^2, and others yet (e.g. Necker, Great Dog, and Salt) are very small (< 1 km^2).

All 11 islands visited supported at least one population of salt grass (Table 1). Although vast expanses of salt grass occurred on the intertidal flats of some islands (e.g. Anegada, Beef, and Virgin Gorda), and wide swaths (5–20 m) surrounded salt ponds on others (e.g. Guana, Great Camanoe, and Tortola), only single small patches occurred on the upper beach and dunes of other islands (e.g. Great Dog and Great Thatch). On some islands such as Guana, salt-pond and dune populations of salt grass co-occurred, but in this case they grew on either side of a central ridge (266 m) and were separated by 500 m. Moreover, these were the only two stands of salt grass on Guana. With the exception of the expansive salt flats on Beef Island (Airport and Trellis Bay area) and Anegada (Flamingo Pond area), salt grass populations were generally small and isolated.

Table 1. Habitats, density, and macroptery of populations of the planthopper *Tova venilia* on salt grass *Sporobolis virginicus* throughout the British Virgin Islands. The location (island and sample site) and date of samples are shown as is the sample size (total number of planthoppers taken at each site) and number of samples (sweeps or D-vac placements) per site. Populations are sorted by habitat, either salt flat/salt pond, beach/dune, or disturbed.

		Density (number per)		Macroptery (%)				
Island, sample site, date	Habitat (area, m^2)	20 sweeps	m^2	Males	Females	Overall	Sample size total (male, female)	Sample no. and type
Salt-flat and salt-pond populations								
Anegada, Flamingo Pond, 19/10/97	Salt flat (5000+)	–	–	75	0	50	6 (4, 2)	D-vac
Beef, Bridge, 16/10/96	Salt flat (500)	3.0	2.8	0	0	0	15 (3, 12)	2, 50 sweep
Beef, Airport, 16/10/96	Salt flat (3000)	3.6	3.4	0	0	0	27 (6, 21)	3, 50 sweep
Beef, Airport, 22/10/98	Salt flat (3000)	28.7	26.7	0	0	0	86 (42, 44)	3, 20 sweep
Beef, E Trellis Bay, 17/10/98	Salt flat (3000)	59.7	55.5	2	0	1	179 (93, 86)	3, 20 sweep
Great Camanoe, Lee Bay, 17/10/96	Pond edge (800)	74.0	68.8	14	7	7	185 (35, 150)	1, 50 sweep
Great Camanoe, Lee Bay, 14/10/98	Pond edge (800)	55.3	51.5	3	0	1	166 (38, 128)	3, 20 sweep
Guana, Salt Pond, 15/10/96	Pond edge (2000)	40.4	37.6	8	1	2	202 (38, 164)	5, 20 sweep
Guana, Salt Pond, 14/10/98	Pond edge (2000)	22.2	20.7	4	0	1	111 (24, 87)	5, 20 sweep
Guana, Salt Pond, 23/10/98	Pond edge (2000)	-	17.5	0	0	0	66 (32, 34)	3, 40 D-vac
Guana, Salt Pond, 23/10/98	Pond edge (2000)	18.8	17.5	3	0	1	94 (26, 68)	5, 20 sweep
Jost Van Dyke, S side 18/10/98	Pond edge (600)	11.0	10.2	0	0	0	22 (9, 13)	2, 20 sweep
Salt, N Side, 15/10/98	Pond edge (200)	-	–	–	–	–	2 (nymphs)	D-vac
Tortola, Belmont Pond, 23/10/98	Pond edge (150)	–	5.8	0	0	0	22 (9, 13)	3, 40 D-vac
Tortola, Josiah Bay, 16/10/98	Salt flat (300)	–	–	0	0	0	40 (9, 31)	D-vac
Virgin Gorda, Biras, 23/10/97	Salt flat (2000)	–	–	46	0	40	15 (13, 8)	D-vac
Beach and dune populations								
Beef, W Trellis Bay, 17/10/98	Beach/dune (60)	19.7	18.3	27	0	8	59 (18, 41)	3, 20 sweep
Great Dog, S Side, 15/10/98	Beach/dune (50)	–	14.2	10	0	7	15 (10, 5)	1, 40 D-vac
Great Thatch, N Side, 18/10/98	Beach/dune (30)	–	30.2	46	0	32	19 (13, 6)	1, 20 D-vac
Guana, North Beach, 21/10/98	Beach/bank (25)	–	32.5	69	0	44	57 (36, 21)	2, 40 D-vac
Necker, N Side, 24/10/97	Beach/dune (75)	–	–	48	0	30	43 (25, 18)	D-vac
Necker, N Side, 19/10/98	Beach/dune (75)	12.6	11.8	9	0	3	38 (11, 27)	3, 20 sweep
Disturbed habitat populations								
Anegada, Settlement, 20/10/97	Lawn (300)	–	–	78	25	62	13 (9, 4)	D-vac
Virgin Gorda, Pond Bay, 22/10/97	Cattle pond (300)	–	–	76	0	49	39 (25, 14)	D-vac

Incidence of dispersal capability in planthopper populations inhabiting undisturbed and disturbed habitats throughout the British Virgin Islands

The incidence of dispersal capability in populations of *T. venilia* (per cent macroptery in both sexes) was compared between undisturbed (relatively persistent) and disturbed (relatively temporary) habitats throughout the British Virgin Islands over the course of a 3-year period (1996–1998). For this comparison, stands of salt grass growing on salt flats, along the margins of salt ponds, and on the upper reaches of beaches and dunes showed no signs of disturbance and were considered relatively persistent habitats for *T. venilia* (Table 1). By contrast, managed lawns and cattle-trampled and browsed stands of salt grass surrounding some salt ponds were regarded as disturbed habitats (Table 1). Using a combination of D-vac and sweep-net sampling, 18 populations (16 undisturbed and two disturbed) were assessed in disjunct stands of salt grass on 11 islands: Anegada (The Settlement and Flamingo Pond), Beef (Bridge, Airport, West Trellis Bay, and East Trellis Bay), Great Camanoe (Lee Bay), Great Dog (South Side), Great Thatch (North Side), Guana (Salt Pond and North Beach), Jost van Dyke (Great Harbor), Necker (North Side), Salt (North Side), Tortola (Belmont Pond and Josiah Bay), and Virgin Gorda (Biras Creek and Pond Bay).

For this assessment, planthoppers were sampled in 1996 using a sweep-net (38 cm diameter) and in 1997 and 1998 using a portable D-vac (1 HP Echo, model PB210E, Gempler's, Mount Horeb, Wisconsin). Extraction of most planthoppers from the dense stands of salt grass required a prolonged period of vacuuming with this portable D-vac in 1997. To achieve more time-efficient extraction of planthoppers in 1998, the conventional sampling head of this D-vac (0.093 m^2) was constricted to 0.031 m^2 by fitting the sampler with a smaller cylindrical plastic head (40 cm long, 20 cm diameter). One sample with this modified D-vac consisted of either 20 or 40 placements of the D-vac head on the vegetation, depending on the size of the grass stand. Each sample with the sweep net consisted of 20 or 50 sweeps to and fro while walking through the stand. The number and size of samples at each site and the date on which they were taken are shown in Table 1. Given the slow extraction of planthoppers in 1997, a consistent number of samples was not taken. Rather, the vegetation was vacuumed at each location for ≈30 min.

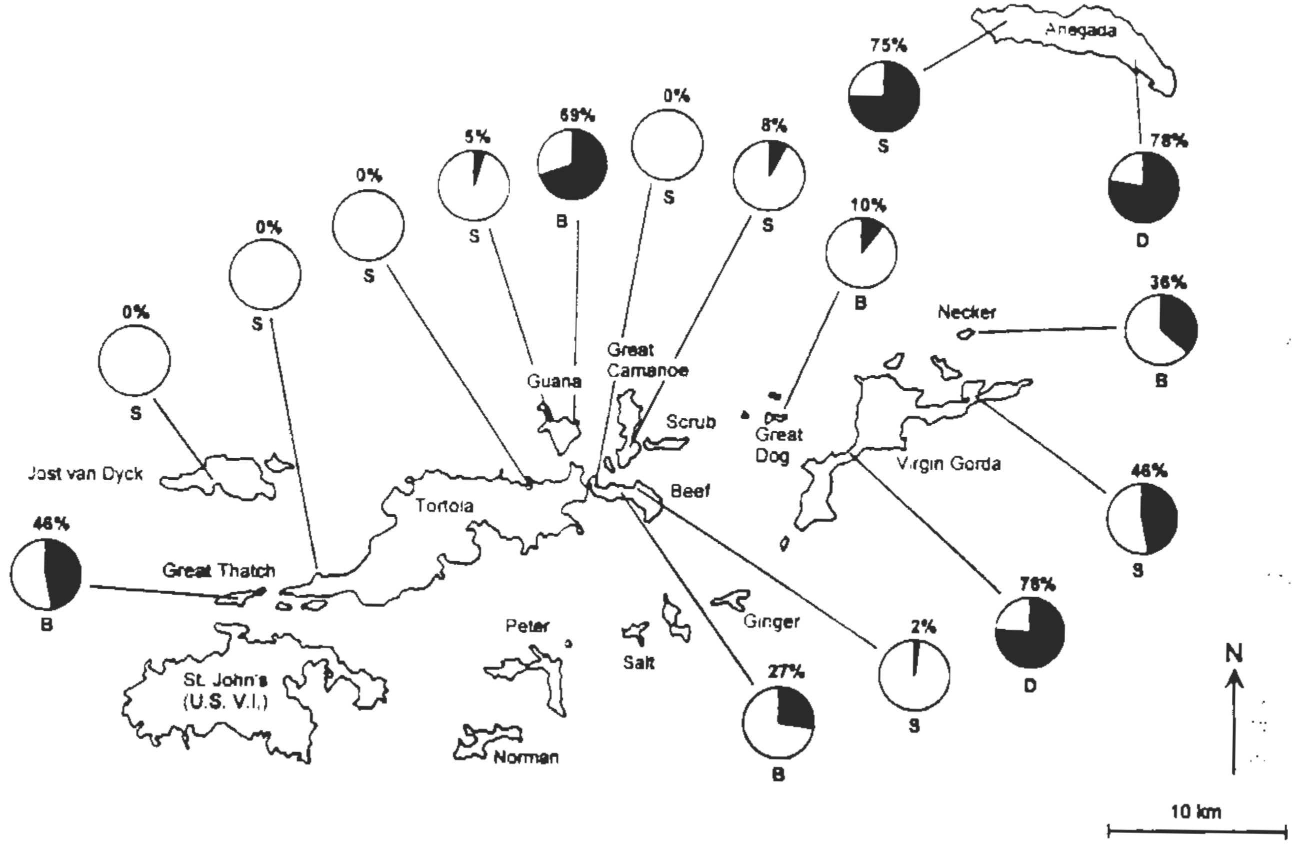

Fig. 1. Incidence of dispersal (% macroptery in males) in populations of the planthopper *Tova venilia* inhabiting salt flat–pond edge habitats (S), beach-dune habitats (B), and disturbed habitats (D) throughout the British Virgin Islands. The black portion of each pie diagram reflects the percentage of macropters in each population.

Planthopper samples were bottled in 95% ethanol and returned to the laboratory where the incidence of macroptery (%) in both sexes of *T. venilia* was determined for each population.

The incidence of macroptery (%) in males and females of *T. venilia* was compared between persistent and disturbed habitats using *t*-tests on angular-transformed data (SAS, 1990). For these analyses, only one value of macroptery (%) was used for each population, and if a population was sampled several times, macroptery was averaged across dates to generate this value. Populations from which fewer than five individuals of either sex were sampled were not included in the analysis.

Incidence of dispersal capability in island and mainland taxa: habitat isolation vs. persistence

To test whether flightlessness was more prevalent on oceanic islands, the incidence of macroptery in British Virgin Island populations of *T. venilia* was compared with published levels of macroptery for mainland-inhabiting delphacids (extracted from Denno *et al.*, 1991). Because habitat persistence has a strong influence on the dispersal strategies of planthoppers (Denno, 1994a; Denno *et al.*, 1991, 1996, in press), it was essential to make the island and mainland comparison between taxa occupying similarly persistent habitats. Thus, it was necessary to quantify habitat persistence roughly for several *T. venilia* populations.

Habitat persistence for a particular species depends on the relationship between the generation time of the organism (τ) and the length of time the habitat remains favourable for development (H) (Southwood, 1962; Southwood *et al.*, 1974). Persistent habitats are characterised by $H/\tau \approx 1$ and temporary habitats by $H/\tau \approx 1$ (Southwood, 1962). Habitat persistence was quantified for three populations of *T. venilia* (Guana, Salt Pond; Beef, East Trellis Bay; Great Camanoe, Lee Bay) by multiplying habitat age (years) by the maximum number of generations/habitat/year; thus, habitat persistence was expressed as the maximum number of generations attainable during the existence of the habitat (see Denno *et al.*, 1991).

Minimum estimates of habitat age were obtained by questioning senior residents of the islands, in particular Oscar Chalwell from Guana/Tortola, who placed minimum estimates of the salt grass habitats sampled on Guana, Beef, and Great Camanoe at 64, 60, and 60 years respectively. Estimates of the annual number of generations for these populations of *T. venilia* were predicted from an existing model established explicitly for planthoppers: *number of*

$\textit{annual generations} = 10.12 - 0.157(^\circ N)$ (from Denno, 1994b). By substituting the latitudes of Guana (18°29′N), Beef (18°26′N), and Great Camanoe (18°28′N) into this equation, the number of annual generations for the three populations of *T. ventilia* was estimated at 7.2. Thus, habitat persistence (maximum number of generations attainable) was estimated at 460, 432, and 432 generations respectively for the Guana, Beef, and Great Camanoe populations.

The mean incidence of macroptery (%) in these three populations of *T. venilia* was then compared with the mean level of macroptery in mainland taxa of delphacids in three ways. First, the observed incidence of macroptery in these three British Virgin Island populations was compared with expected levels of macroptery predicted by a model describing the relationship between habitat persistence and macroptery for mainland delphacid species: $\textit{macroptery}\ (\%) = -5.450 + 1/(\textit{habitat persistence}^{0.045} - 0.095)$ (from Denno *et al.*, 1991). Expected macroptery for the British Virgin Island populations was obtained by substituting habitat persistence values for the three British Virgin Island populations into the mainland-derived model. Observed and expected levels of macroptery were compared using a paired t-test on angular-transformed data (SAS, 1990). Due to small sample size ($n = 3$), a power analysis was performed where power $= 1 - \beta$, the probability of committing a Type II error (Zar, 1996).

Second, the observed level of macroptery in the three British Virgin Island populations of *T. venilia* was compared with that for six species of mainland delphacids [*Laodelphax elegantulus* (Boheman), *Muirodelphax exiguus* (Boheman), *Paraliburnia dalei* (Scott), *Pissonotus piceus* (Van Duzee), *Prokelisia dolus* Wilson, and *Ribautodelphax angulosis* (Ribaut)] existing in similarly persistent grassland habitats (150–350 generations) (extracted from Denno *et al.*, 1991). For this and the following analysis, the incidence of macroptery (%) in British Virgin Island and mainland taxa was compared using a t-test on angular-transformed data.

Third, macroptery in British Virgin Island populations of *T. venilia* was compared with that observed in populations of seven mainland species [*Delphacodes detecta* (Van Duzee), *D. penedetecta* Beamer, *Neomegamelanus dorsalis* (Metcalf), *N. penelautus* (McDermott), *Prokelisia dolus* Wilson, *P. marginata* Van Duzee, and *Toya propinqua* (Fieber)] occupying the same low-profile habitat type (grasses growing on marshes and dunes) along the Gulf of Mexico shore (extracted from Denno, 1978; Denno *et al.*, 1991). For this analysis, no estimates of habitat persistence were required, although the habitats of all the delphacids were generally very persistent (> 500 years; see Denno *et al.*, 1991).

For these three analyses, the incidence of macroptery in British Virgin Island populations should be less than that for mainland taxa if oceanic isolation was an important contributor to the evolution of flightlessness in delphacids. Thus, one-tailed tests were used to assess significance (SAS, 1990). Moreover, for all three analyses, the assessment of macroptery was limited to the female sex because the dispersal strategies of female planthoppers are not compromised by possible flight constraints associated with mate location, as is the case for males (Denno, 1994a; Denno *et al.*, 1991, in press).

Habitat structure and the incidence of macroptery in planthopper populations

The stand area (m^2) of salt grass growing on salt flats, around pond margins, and on beach dunes was estimated visually or by pacing at each of the 18 locations visited (Table 1). Stand area was compared between the salt flat–pond edge habitat and the beach-dune habitat using a t-test. The structure of salt grass (culm density, culm length, and above-ground biomass) was determined by clip-quadrat sampling for stands growing in the two major habitat types (salt flats–pond edges vs. dunes) on three islands (Beef, Guana, and Necker) (Denno *et al.*, 1985). Five samples were taken in each habitat type on the three islands during 19–23 October 1998. Each sample consisted of the removal of all above-ground grass within a 0.047-m^2 wire frame. Subsequently, culm density (number per m^2), culm length (cm), and wet weight biomass (g per m^2) were determined. Because island effects were minimal (ANOVA), t-tests were used to compare culm density, culm length, and grass biomass between the two habitat types. For these analyses, the five habitat samples were averaged within each island resulting in a sample size of three for each habitat type.

The influence of habitat structure on the dispersal capability of both sexes of *T. venilia* was examined by comparing the incidence of macroptery between populations occurring in the two habitat types (sparse stands of salt grass occurring on dunes and dense stands growing on salt flats or around salt pond margins). For each sex, the incidence of macroptery (%) in the two habitat types was compared using a t-test on angular-transformed data. Similarly, a t-test on angular-transformed data was used to compare macroptery (%) between the sexes within each habitat. Sites at which < 10 individuals were collected were excluded from the analysis. The expectation was that higher levels of macroptery would be found in males inhabiting the dunes than in males inhabiting the salt flats because flight is likely to be essential for mate location in the sparsely structured habitat. Habitat-related variation in salt grass structure was not envisioned to influence macroptery in females because they do not search actively for mates. Because macroptery is density dependent in most planthoppers (Denno *et al.*, 1994), the slopes of the relationship between macroptery in both sexes (angular-transformed) and population density in the two habitats (dune and salt flat) were tested to see whether they differed from zero (t-test on the regression coefficients). To test further for habitat effects on the incidence of macroptery, the slopes of the relationship between macroptery (%) and population density (number per m^2) were compared between the two habitat types using ANCOVA with density as the covariate (SAS, 1990). This analysis was run separately for each sex.

Estimates of population density were necessary for the above approaches. D-vac sampling during 1998 allowed for the association of variation in the incidence of macroptery (%) in *T. venilia* with absolute population size (number per m^2). Sweep-net sampling, however, provided only a relative density estimate. To convert sweep-net counts to absolute density data, side-by-side, replicated D-vac (3, 40 placement) and sweep-net

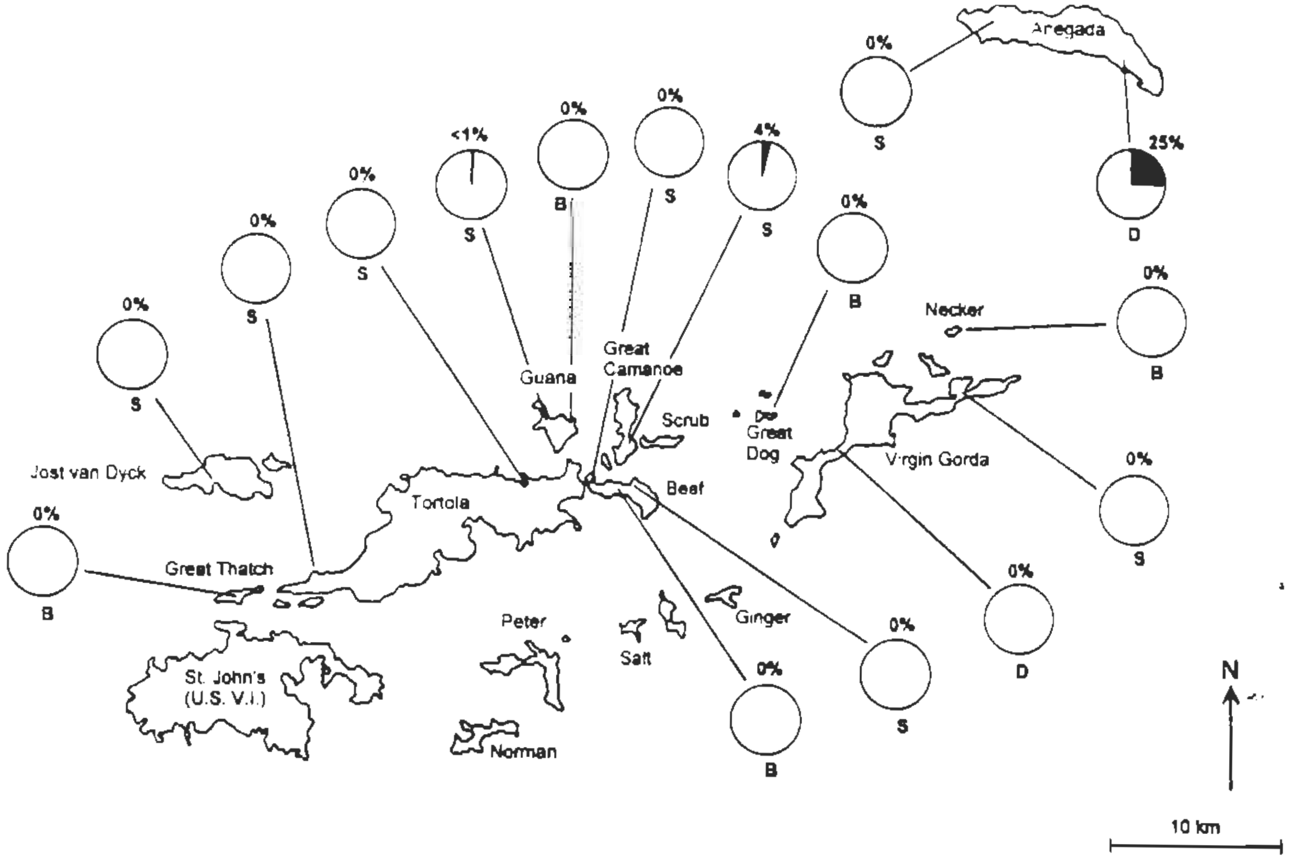

Fig. 2. Incidence of dispersal (% macroptery in females) in populations of the planthopper *Toya venilia* inhabiting salt flat–pond edge habitats (S), beach-dune habitats (B), and disturbed habitats (D) throughout the British Virgin Islands. The black portion of each pie diagram reflects the percentage of macropters in each population

(5, 20 sweep) samples were taken on 23 October 1998 in an expansive stand of salt grass located at the margin of Salt Pond on Guana Island. The resulting planthopper counts from D-vac ($17.5 \pm 7.6\,m^{-2}$, mean ± SEM) and sweep-netting (18.8 ± 7.8 per 20 sweeps) provided a conversion factor (number of planthoppers per m^2 = number of planthoppers per 20 sweeps/1.07), which allowed for the transformation of sweep-net data taken from other sampling locations to absolute densities. All absolute densities (number per m^2) for sweep-sampled populations were estimated using this conversion factor (see Table 1). It was not possible to establish a separate conversion factor in dune vegetation because all dune habitat patches were very small ($< 80\,m^2$) and not easily swept. Regardless, absolute estimates of planthopper density were obtained by D-vac sampling in most dune-grass populations (Table 1).

Results

Incidence of dispersal capability in planthopper populations inhabiting undisturbed and disturbed habitats throughout the British Virgin Islands

Males of *T. venilia* were significantly more macropterous in disturbed stands of salt grass growing in lawns or cattle-trampled habitats (77.0 ± 1.0%, mean ± SEM) than they were in undisturbed stands of salt grass growing on salt flats or dunes (19.2 ± 6.4; $t = 2.88$, $P < 0.05$; Fig. 1). Female planthoppers were also more macropterous in disturbed habitats (12.5 ± 12.5%) than in undisturbed stands of salt grass (0.4 ± 0.3%; $t = 2.66$, $P < 0.05$; Fig. 2). The pattern of elevated macroptery in disturbed habitats prevailed in both sexes even though males were significantly more macropterous (26.9 ± 7.6%) than females (2.0 ± 1.7%) in all habitats sampled ($t = 3.60$, $P < 0.01$) (compare Figs 1 and 2).

Incidence of dispersal capability in island and mainland taxa: habitat isolation vs. persistence

Together, three lines of evidence suggest that the incidence of macroptery in British Virgin Island populations of *T. venilia* is not significantly lower than that exhibited by mainland delphacids. First, the observed levels of macroptery in British Virgin Island populations of *T. venilia* (1.7 ± 1.2%, mean ± SEM) were not significantly lower than predicted values (5.5 ± 0.03%) obtained by substituting habitat persistence values for the British Virgin Island populations into a model based entirely on mainland delphacid species (paired

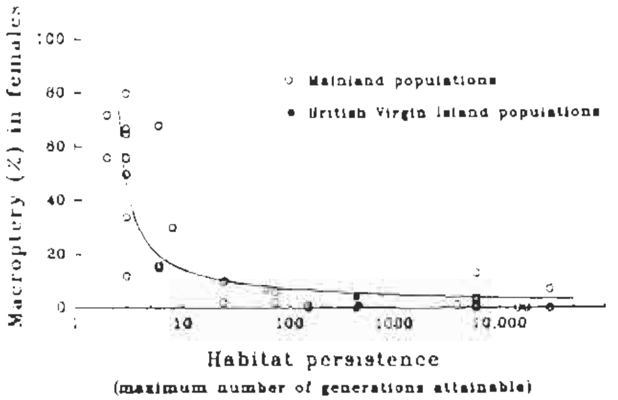

Fig. 3. Relationship between macroptery (%) and habitat persistence (the maximum number of generations attainable) for the females of 41 field populations (35 species) of mainland-inhabiting species of delphacid planthoppers (○) (data from Denno *et al.*, 1991) and three British Virgin Islands populations (Beef, Guana, and Great Camanoe) of the delphacid *Toya venilia* (●). The observed levels of macroptery in island populations of *T. venilia* were not significantly different from those expected using the mainland model [*macroptery* (%) = –5.450 + 1/(*habitat persistence*$^{0.45}$ – 0.095); paired *t*-test, NS] (model adapted from Denno *et al.*, 1991). Thus, with habitat persistence controlled, the incidence of dispersal in field populations was the same for British Virgin Island and mainland taxa of planthoppers.

$t = -2.35$, NS; Fig. 3). Had the error associated with the full regression model been taken into account in the analysis (Fig. 3), however, the one-tailed *P*-value (0.072) would most certainly have been larger. Moreover, given an average difference of 3.85% macroptery between expected (mainland) and observed (island) data, a power analysis on arcsin-transformed data revealed that the likelihood of detecting a difference between the two samples, if indeed it existed, was 43%. Thus, the hint of a difference in macroptery between British Virgin Island and mainland populations does not even verge on significance.

Second, the average incidence of macroptery in British Virgin Island populations of *T. venilia* (1.7 ± 1.2%) did not differ from that for six species of mainland delphacids (1.4 ± 1.1%) existing in similarly persistent grassland habitats ($t = 0.16$, NS). Third, macroptery in British Virgin Island populations of *T. venilia* (1.7 ± 1.2%) did not differ from that observed in populations of seven mainland species of delphacids occupying the same type of low-profile grassland habitats (marshes and dunes) along the shore of the Gulf of Mexico (3.4 ± 1.8%) ($t = -0.59$, NS).

Together, these data suggest that with habitat persistence controlled, habitat isolation at the scale of oceanic islands contributes little to explaining the dispersal strategy of *T. venilia* in the British Virgin Islands. Be it an island or mainland population, habitat persistence appears to be the most crucial factor shaping the dispersal strategy of female delphacid planthoppers (Fig. 3).

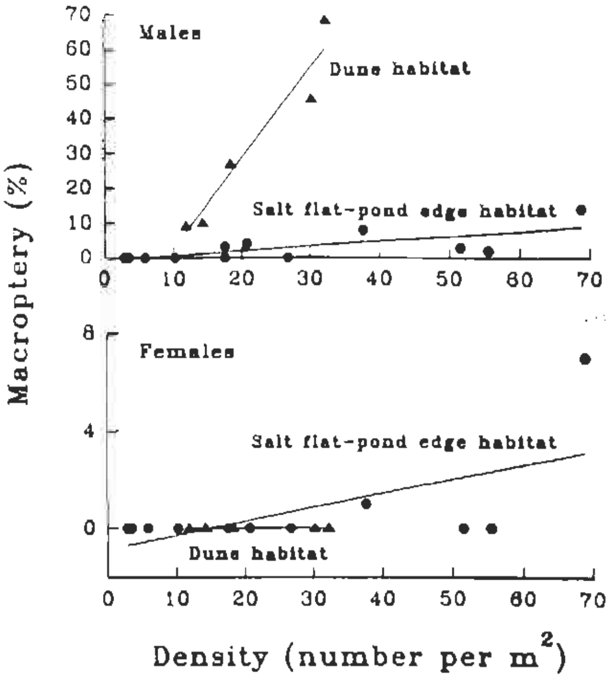

Fig. 4. Relationship between the incidence of macroptery (%) in males and females of the planthopper *Toya venilia* and population density (number per m^2) in two salt-grass habitats (dense stands of *Sporobolus virginicus* growing on salt flats or along edges of salt ponds and sparse stands inhabiting beach dunes) in the British Virgin Islands. For males, macroptery was significantly density dependent in both habitats, but the slopes of the relationship differed (ANCOVA, $F = 96.5$, $P < 0.001$). Macroptery was significantly density dependent for females inhabiting the salt flat–pond edge habitat [macroptery = –0.85 + 0.57(density), $R^2 = 0.39$, $P < 0.05$], but density-dependent macroptery was not detected for females occurring in the dune habitat.

Habitat structure and the incidence of macroptery in planthopper populations

On average, stands of salt grass were significantly smaller on dunes (48 ± 9 m^2, mean ± SEM, $n = 5$) than on salt flats and around the margin of salt ponds (1595 ± 471 m^2, $n = 11$) ($t = 2.52$, $P < 0.05$). Moreover, culms of salt grass grew significantly denser (3753 ± 352 culms m^{-2} vs. 2232 ± 364) and longer (49 ± 2 cm vs. 33 ± 3) on salt flats than on dunes ($t_{\text{culm density}} = 3.0$, $P < 0.01$; $t_{\text{culm length}} = 4.77$, $P < 0.001$). Also, the above-ground biomass (wet weight) of salt grass was significantly greater for salt flat (2755 ± 221 g m^{-2}) than for dune (761 ± 228 g m^{-2}) vegetation ($t = 6.28$, $P < 0.001$).

Males of *T. venilia* were significantly more macropterous in populations occupying dune vegetation (37.6 ± 9.8%) than in populations occurring in stands of salt grass growing on intertidal flats and around salt ponds (7.6 ± 5.6%) ($t = 3.28$, $P < 0.01$). This habitat-related difference in male macroptery accounted for most of the disparity in macroptery between the sexes of *T. venilia* throughout the British Virgin Islands (compare Figs 1 and 2). Moreover, there was a significant positive relationship between macroptery in males (%) and population density in both dune [macroptery = –24.12 + 2.64(density), $R^2 = 0.93$, $P < 0.01$] and salt-flat [macroptery = –0.94 + 0.14(density), $R^2 = 0.54$, $P < 0.01$] habitats (Fig. 4). The slope of the relationship between macroptery and density was significantly steeper for males in dune-inhabiting populations than for males occupying salt flats (ANCOVA, $F = 96.5$, $P < 0.001$), however, further indicating a habitat effect on dispersal capability.

In contrast, there was no difference between the incidence of macroptery in female planthoppers in dune (0%) and salt-flat (0.6 ± 0.5%) populations ($t = 1.11$, NS) (Fig. 2). Also, the incidence of macroptery in female (0.6 ± 0.5%) and male (7.6 ± 5.6%) planthoppers did not differ in the salt-flat habitat ($t = 1.45$, NS). In the dune habitat, however, males were significantly more macropterous (37.6 ± 9.8%) than females (0% ± 0) ($t = 5.95$, $P < 0.01$). Thus, habitat structure appears to have a selective influence on the dispersal strategy only of male planthoppers. Macroptery was significantly density dependent for females inhabiting the salt flat–pond edge habitat [macroptery = –0.85 + 0.57(density), $R^2 = 0.39$, $P < 0.05$; Fig. 4], a slope that did not differ from that for males in this habitat (ANCOVA, $F = 3.24$, NS). Density-dependent macroptery was not detected for females occurring in the dune habitat (0% macroptery at all densities), probably because the high densities that occurred occasionally in salt flat habitats (> 35 planthoppers per m^2) were never observed in dune vegetation (Fig. 4).

Discussion

Both sexes of *T. venilia* exhibit elevated macroptery in disturbed habitats (managed lawns) and reduced flight capability in natural, more persistent habitats (salt flats, salt ponds, and dunes) throughout the British Virgin Islands, a pattern that has been reported for many insects including other delphacid species (Roff, 1990; Denno *et al.*, 1991; Novotný, 1994). Dispersal capability is apparently retained to track the frequent changes in resource quality and abundance that occur in disturbed and temporary habitats (Southwood, 1977; Denno *et al.*, 1991, 1996). Although the incidence of macroptery in populations of *T. venilia* is generally low in undisturbed habitats (< 30% on average), the dispersal strategies of males and females are clearly different (Figs 1 and 2). Males exhibit higher levels of macroptery (26.9 ± 7.6%) than do females (2.0 ± 1.7%) but this difference in dispersal ability is habitat dependent, with males significantly more macropterous than females in dune habitats (37.6 vs. 0%) but not in salt flat–pond edge habitats (7.6 vs. 0.6%). For both sexes, the occurrence of the macropterous form in field populations is positively density dependent (Fig. 4). Thus, fluctuations in population density in the field, coupled with density-dependent macroptery, probably explain much of the within-habitat variation in the incidence of dispersal (Figs 1 and 2). The mechanism underlying the disparity in macroptery between the sexes of *T. venilia* is probably a genetically based difference in the induction of macropters under crowded conditions, a well documented occurrence for other species of delphacids (Kisimoto, 1965; Denno *et al.*, 1991, 1994).

The selective forces underlying the discrepant dispersal strategies of the sexes of this planthopper probably involve several habitat-related factors. Of the major habitat-associated factors thought to influence the dispersal strategies of insects, namely persistence, structure, and isolation (Roff, 1990; Denno *et al.*, 1991, 1996, in press), only habitat persistence and structure showed an effect on island populations of *T. venilia*. There was little evidence that the low incidence of dispersal in several island populations (1.7 ± 1.2% in females) was attributable to the effects of isolation on oceanic islands (Fig. 2). Three analyses revealed that the low level of macroptery in several British Virgin Island populations of *T. venilia* was no different from that observed in mainland delphacid species existing in habitats of similar duration. Rather, the persistence of the natural salt grass habitats throughout the British Virgin Islands probably best explains the evolution of flight reduction in this island-inhabiting delphacid (Fig. 3). That flight capability is retained under certain conditions on oceanic islands is evidenced by the high incidence of macroptery (25%) in females of *T. venilia* exploiting the disturbed lawn habitats on Anegada (Fig. 2).

It might be argued that the assessments of habitat age, and thus persistence for salt grass habitats in the British Virgin Islands (~ 450 possible planthopper generations), are underestimates. This is probably the case. Nonetheless, two lines of evidence suggest that brachyptery increases very rapidly in populations of wing-dimorphic planthoppers given the appropriate circumstances. First, with an increase in habitat persistence, dispersal capability (% macroptery) in field populations declines sharply, suggesting that when the demand for flight is relaxed, flight capability diminishes rapidly (Denno *et al.*, 1991; Fig. 3). Planthoppers existing in habitats lasting only 30 generations are nearly as brachypterous (> 90%) as species occupying habitats a thousand times more persistent. Second, macropterous and brachypterous lines of the planthopper *Nilaparvata lugens* Stål can be established after only 30 generations of selection in the laboratory on an initial population consisting of an equal mix of both wing forms (Marooka & Tojo, 1992). Thus, both field data on habitat persistence (Denno *et al.*, 1991, 1996) and selection experiments in the laboratory (Marooka *et al.*, 1988; Marooka & Tojo, 1992) suggest that dispersal characters respond very rapidly to selection over the course of ecological time. Therefore, the habitats of *T. venilia*, even though possibly underestimated in age, have probably persisted long enough for the dispersal strategy of this planthopper to stabilise. The reduction in dispersal capability of planthoppers in persistent habitats is probably attributable to the reproductive advantage of brachypterous adults (Denno *et al.*, 1989; Zera & Denno, 1997; Langellotto *et al.*, 2000).

Other studies have also shown that habitat persistence rather than oceanic isolation underlies the dispersal strategy of other planthopper species and insects. For example, the incidence of macroptery in Hawaiian island delphacids is low (1.26 ± 0.25%), not different from the mainland average

(1.50 ± 1.15%) (Denno *et al.*, in press), and very similar to the level observed in British Virgin Island populations of *T. venilia* (1.7 ± 1.2%). Notably, habitat persistence and dimensionality were controlled in the Hawaiian island–mainland comparison, whereby the incidence of macroptery was compared only between taxa inhabiting persistent, low-profile vegetation. Similarly, in an extensive analysis of the effects of habitat isolation on the dispersal strategies of a wide diversity of insect taxa (Orthoptera, Hemiptera, Thysanoptera, Psocoptera, Neuroptera, Coleoptera, and Diptera), Roff (1990) showed that oceanic islands do not have higher-than-expected incidences of flightlessness than mainland faunas.

Habitat isolation may contribute to reduced dispersal capability via migrant loss only in the very smallest of habitat patches (Roff, 1990). The highly fragmented yet persistent salt marshes in southern California may provide an example where isolation contributes to the evolution of flightlessness in delphacids. In these habitats, dispersal is virtually absent in populations of *Prokelisia dolus* (0.16 ± 0.36% macroptery; Denno *et al.*, 1996), a level below that (5–8%) predicted by habitat persistence alone (see Denno *et al.*, 1991). By contrast, males of *T. venilia* were much more macropterous (32.2 ± 11.4%) in the small, isolated patches of salt grass on dunes than they were in the large expanses of salt grass associated with salt flats (5.7 ± 3.3%). Although this pattern is attributed here to the constraints associated with mate finding, it illustrates that flight capability can be retained when necessary even in the smallest and most isolated habitats. Therefore, it is argued that at the scale of oceanic islands, and perhaps also at much smaller spatial scales, isolation *per se* plays little role in the dispersal strategies of planthoppers.

Habitat type (dune vs. salt flat–pond edge vegetation) influenced the incidence of macroptery in *T. venilia*, but only in the male sex (Fig. 4). Macroptery in males was almost five times higher in dune habitats (38%) than in salt flat and salt pond vegetation (8%). Higher levels of macroptery in male planthoppers than in females are symptomatic of the difficulties associated with mate location, because only the male sex searches actively for mates (Denno *et al.*, 1991, in press; Claridge & de Vrijer, 1994; Denno, 1994a; Langellotto, 1997). Variation in salt-grass structure, coupled with a generally low population density (25 ± 5 adults per m^2; Table 1), probably underlies this habitat-related difference in macroptery in males of *T. venilia*. The sparse structure of dune vegetation apparently favours the retention of wings because macropters are better able to negotiate such habitats and locate calling females, an effect that has been shown for other delphacid species (Langellotto, 1997). Brachypterous males neither sense nor locate calling females efficiently in heterogeneous vegetation. The situation is reversed in contiguous vegetation, such as the dense stands of salt grass on intertidal flats, a situation where brachypterous males of other planthopper species have been shown to be more successful in locating males and outcompeting macropters for access to them (Langellotto, 1997).

Macroptery was density dependent in the males of *T. venilia*, but the slope of the relationship was significantly steeper in populations occupying dune vegetation than in salt-flat/pond-margin vegetation, further corroborating the effect of habitat type on the incidence of dispersal capability (Fig. 4). A difference in the slope of this relationship is consistent with the view that there is a genetic difference between dune and salt flat-inhabiting populations of *T. venilia*, whereby the density that triggers the production of macropters in males differs between the two populations (Denno *et al.*, 1991, 1996). An independent assessment using amplified fragment-length polymorphism markers also found a significant genetic difference between the dune and salt-pond populations of *T. venilia* on Guana Island (D. J. Hawthorne, unpublished). This is a remarkable finding considering that these two disjunct populations are separated by only 500 m, albeit by an upland ridge. Other marsh-inhabiting planthopper species with similarly low incidences of macroptery (< 20%) show no evidence for the genetic subdivision of populations at such a small spatial scale, although their habitats are relatively contiguous (Peterson & Denno, 1997, 1998). Apparently, the homogenising effects of gene flow between these two populations on Guana Island are offset by the strength of habitat-related differences in selection for the enhancement of flight capability in one habitat and its reduction in the other. The strength of the opposing forces, however, may be less than it appears because gene flow between populations of *T. venilia* depends not only on the fraction of macropters in the population but also on the flight capability of the individuals. One study with gerrids suggests that the flight capability of the macropterous morph decreases as the proportion of macropters declines in the population (Fairbairn & Desranleau, 1987). Thus, for a planthopper species that averages < 30% macroptery, males may be relatively weak flyers, simply flitting around within the habitat in search of females, a behaviour that may diminish frequent gene flow between disjunct populations.

It has been argued that isolation may promote macroptery because only winged adults can colonise small, isolated, and extinction-prone patches (see Travis & Dytham, 1999). If this were the case for the dune-inhabiting populations of *T. venilia*, elevated levels of macroptery would be expected in both sexes in such habitats because planthoppers mate only after they have dispersed to new habitats (reviewed by Denno & Roderick, 1990). In the 3 years of sampling dune vegetation, not one macropterous female was found, even though macropterous males were relatively abundant (Table 1). Moreover, on Guana Island, the extensive Salt Pond population would be the closest source of colonists for the dune-inhabiting population on North Beach. Yet, it is these two populations that show evidence for genetic divergence. Macropterous males in the dune population are more genetically related to their brachypterous counterparts in the dune population than they are to brachypters in the salt-pond population (D. J. Hawthorne, unpublished). Together, these data do not suggest that macroptery in dune populations results from selective colonisation by macropters. Rather, within-habitat selective pressures associated with mate finding appear to be a more parsimonious explanation for elevated macroptery in males.

The lability of dispersal characters in delphacid planthoppers, coupled with their wing-dimorphism, allows the teasing apart of the selective effects of habitat persistence and structure that interact to shape the dispersal strategies of insects. For planthoppers exploiting low-profile host plants, there is an inverse relationship between habitat persistence and dispersal capability (% macroptery), with volant species predominating in temporary habitats and flightless taxa occurring primarily in long-lived habitats (Denno *et al.*, 1991). Habitat dimensionality and macroptery are related positively, with flight reduction evident in species exploiting low-profile vegetation, and wing retention characteristic of arboreal species (Denno, 1994b). Habitat persistence and dimensionality interact such that flight is retained in species exploiting arboreal habitats, even though habitats are persistent (Denno *et al.*, in press). Thus, the effect of habitat persistence on the incidence of flight capability is realised only for species occupying low-profile habitats such as *T. venilia*.

In addition to the three-dimensional nature of the habitat, finer-scale differences in habitat structure also affect the dispersal strategies of planthoppers, particularly for males. It is argued here that the difference in the structure of salt grass between dune and salt-flat habitats influences the searching efficiency of the male wing forms of *T. venilia*, and hence their mating success. Macropterous males of other delphacids are far more effective at locating females in sparse vegetation and under low-density conditions than are brachypters (Langellotto, 1997). The enhanced incidence of macroptery in males of *T. venilia* occupying sparsely vegetated dune habitats probably also reflects the advantage of flight in mate location.

Historically, coastal strand, marsh, and dune communities have been targeted as habitats where isolation may promote the evolution of flightlessness in insects (see Roff, 1990; Wagner & Liebherr, 1992). Recent studies in these same habitats have played a pivotal role in both challenging the significance of isolation and in demonstrating the importance of habitat persistence and structure in the evolution of insect dispersal strategies (Denno *et al.*, 1991, 1996, in press).

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A new generic classification for Thaumatodryininae, Dryininae and Gonatopodinae, with descriptions of new species (Hymenoptera Dryinidae)

Abstract - A new generic classification is proposed for Thaumatodryininae, Dryininae and Gonatopodinae. In the subfamily Dryininae the following new names are proposed in the genus *Dryinus: hansonianus, harpax, arimensis, kovariki, parkerianus, ater, australiae, gibbosoides, pseudoafer* and *dayianus*. The following new species of Dryininae are described: *Dryinus madagascolus*, from Madagascar; *Dryinus lini* and *choui*, from Taiwan; *Megadryinus pulawskii*, from Peru; *Dryinus cruciatus*, from U.S. Virgin Islands; *Dryinus wasbaueri*, from Papua. In the subfamily Gonatopodinae the following new names are proposed in the genus *Gonatopus: aegypti, fortunatus, tussacensis, owaini, pilosoides, ceballosi, operosus, rufoniger, asiae, insulae, variabilis, americae, cobbenianus, flavoides, stephani, boucekianus*. In the same subfamily the following new combinations are proposed: *Gonatopus helleni* (Raatikainen) and *Gonatopus nearcticus* (Fenton). The following new species of Gonatopodinae is described: *Gonatopus sensitivus*, from Madagascar. In the subfamily Anteoninae the following new names are proposed in the genus *Anteon: hirashimai, paraflaccum, gauldense*. The male of *Anteon minimum* (Fenton), from the U.S.A., is described. In the subfamily Bocchinae the new species *Bocchus rossi*, from Western Australia, is described. In the subfamily Apodryininae the male of *Apodryinus masneri* Olmi, from Chile, is described and the genus *Bocchopsis* Olmi is considered senior synonym of *Australodryinus* Olmi. The new name *Bocchopsis australis* is proposed.

Riassunto - *Una nuova classificazione per i generi di Thaumatodryininae, Dryininae e Gonatopodinae, con descrizione di nuove specie (Hymenoptera Dryinidae).*

Viene proposta una nuova classificazione per i generi di Thaumatodryininae, Dryininae e Gonatopodinae. Nella sottofamiglia Dryininae sono proposti, nel genere *Dryinus*, i seguenti nuovi nomi: ***hansonianus, harpax, arimensis, kovariki, parkerianus, ater, australiae, gibbosoides, pseudoafer*** e *dayianus*. Sono inoltre descritte le seguenti nuove specie di Dryininae: *Dryi-*

nus madagascolus, del Madagascar; *Dryinus lini* e *choui*, di Taiwan; *Megadryinus pulawskii*, del Peru; *Dryinus cruciatus*, delle Isole Vergini statunitensi; *Dryinus wasbaueri*, di Papua. Nella sottofamiglia Gonatopodinae e nel genere *Gonatopus* sono proposti i seguenti nuovi nomi: *aegypti, fortunatus, tussacensis, owaini, pilosoides, ceballosi, operosus, rufoniger, asiae, insulae, variabilis, americae, cobbenianus, flavoides, stephani, boucekianus*. Nella stessa sottofamiglia sono proposte le seguenti nuove combinazioni: *Gonatopus helleni* (Raatikainen) e *Gonatopus nearcticus* (Fenton). Fra i Gonatopodinae è poi descritta la nuova specie *Gonatopus sensitivus*, del Madagascar. Nella sottofamiglia Anteoninae e nel genere *Anteon* sono proposti i seguenti nuovi nomi: *hirashimai, paraflaccum, gauldense*. Viene anche descritto il maschio di *Anteon minimum* (Fenton), degli U.S.A.. Nella sottofamiglia Bocchinae è descritta la nuova specie *Bocchus rossi*, dell'Australia Occidentale. Nella sottofamiglia Apodryininae viene descritto il maschio di *Apodryinus masneri* Olmi, del Cile, ed il genere *Australodryinus* Olmi viene posto in sinonimia di *Bocchopsis* Olmi. Viene proposto il nuovo nome *Bocchopsis australis*.

Key words: taxonomy, Dryinidae.

The main taxonomic problem of Dryininae and Gonatopodinae was the generic classification of the males. The taxonomy of these two subfamilies in fact was based on females. They showed apparently good generic characters, whereas the males showed only specific differences. In his revisions in fact Olmi (1984, 1989) proposed keys to the genera only for females. The males were treated only in specific keys. Among the Gonatopodinae only genera as *Neodryinus* Perkins, *Echthrodelphax* Perkins, *Haplogonatopus* Perkins and *Esagonatopus* Olmi were easily recognizable in the male sex too.

The above situation was unacceptable of course. It was not possible to admit that almost all the genera of two subfamilies were distinct only in the female sex. This classification was considered however provisionally valid, awaiting to know a bigger number of males. The number of known males in fact was so small that conclusions were impossible.

The number of known males was increased in the last years. It's possible so now to propose a different generic classification for Dryininae and Gonatopodinae, as follows.

MATERIAL AND METHODS

The examined material is kept in the following collections:

BM: Natural History Museum, London, England

CA: California Academy of Sciences, S. Francisco, California
LA: Natural History Museum of Los Angeles County, Los Angeles, California
OL: Department of Plant Protection, Viterbo, Italy
OT: Biosystematics Research Centre, Ottawa, Canada
TM: Taiwan Agriculture Research Institute, Wufeng, Taiwan
WA: National Museum of Natural History, Washington, D.C.

The terminology is that of Olmi (1984).

I have much indebted to the following persons who helped with the collections, either by sending dryinids on loan, or acting as host, when their institutions were visited: Liang-yih Chou (Taiwan), Michael Day (London), Tom Huddleston (London), Karl V. Krombein (Washington), Lubomir Masner (Ottawa), Wojciech J. Pulawski (San Francisco), Roy Snelling (Los Angeles).

Subfamily *Dryininae*

In the past the main taxonomic problem of the Dryininae was the generic classification of the males. Whereas in fact it was possible to propose a satisfactory distinction among the genera on the basis of females, the males seemed all alike, so that only specific classifications were proposable (Olmi, 1984, 1989).

On the basis of females the following genera were recognizable, according to the Olmi system:

Dryinus Latreille 1804
Mesodryinus Kieffer 1906
Perodryinus R.C.L. Perkins 1907
Tridryinus Kieffer 1913
Megadryinus Richards 1953
Alphadryinus Olmi 1984
Gonadryinus Olmi 1989
Cretodryinus N. Ponomarenko 1975 (fossil)

On the basis of studies of the last years now it's possible to add to the above list the following two genera:

Thaumatodryinus R.C.L. Perkins 1905
Pseudodryinus Olmi 1989

For the genus *Thaumatodryinus* in the past (Olmi, 1984) the subfamily Thaumatodryininae was proposed, whereas the genus *Pseudodryinus* was considered belonging to Gonatopodinae (Olmi, 1989). This last attribution however was caused by a mistake in the observation of the spurs of the mid tibiae. According to the original description in mid tibiae of females the spurs were absent (1,0,2 formula). Recently another study of the species of

Pseudodryinus permitted to see a mid tibial spur, not seen in the few previous observed specimens, mostly for the bad conditions of the legs. The formula so was 1, 1, 2, so that this genus could be considered belonging to Dryininae, and not to Gonatopodinae. These observations of course were based all on female specimens, because the males of *Pseudodryinus* were unknown.

The attribution of females of *Pseudodryinus* to Dryininae seemed solve numerous problems. In the meantime however males of *Pseudodryinus* were found in Taiwan (*Pseudodryinus sinensis* n. sp., see later on). They have quadridentate mandibles, whereas the males of Dryininae have tridentate mandibles. This character so leads to think that these males are belonging to Thaumatodryininae. It's obvious that males and females of the same genus cannot belong to different subfamilies. I think so that the subfamily status of Thaumatodryininae is not proposable. The genus *Thaumatodryinus* so (together with *Pseudodryinus*) must be considered belonging to Dryininae, as old Authors thought in the past.

During recent studies on the genera *Bocchoides* Benoit and *Chelothelius* Reinhard, both considered in the past (Olmi, 1984) belonging to Bocchinae, the few known specimens were again examined (one female specimen of *Bocchoides bekilyensis* Benoit; three female specimens of *Chelothelius gryps* Reinhard; one female specimen of *Chelothelius berlandi* Bernard). Recently in fact a new important morphologic character was identified (Olmi, 1992b) to distinguish the subfamilies Bocchinae and Dryininae: the presence or the absence of epicnemia. The lateral regions of the prothorax in fact in Bocchinae are continuous with the mesopleura, so that the epicnemium (or prepectus) is invisible (fig. 30 in Olmi, 1992b). In Dryininae on the contrary the lateral regions of the prothorax are not continuous with the mesopleura, so that the epicnemium is distinctly visible (fig. 31 in Olmi, 1992b). This character is visible both in females and in males. *Bocchoides* and *Chelothelius* have visible epicnemia, so that they are belonging to Dryininae and not to Bocchinae. In the past on the contrary the main difference between Bocchinae and Dryininae was based on the different number and shape of mandible teeth (Olmi, 1984).

After the attribution of *Bocchoides* and *Chelothelius* to Dryininae a comparation with *Mesodryinus* Kieffer and *Alphadryinus* Olmi was tried (Olmi, 1992b).

In the past *Mesodryinus* and *Alphadryinus* were considered different mostly on the basis of the presence or the absence of notaulices in the females (Olmi, 1984). The recent study however of a population of female specimens of *Mesodryinus solaris* Olmi, from the U.S.A., demonstrated that the notaulices can be visible or invisible in the same species. Some specimens of the above species in fact showed distinctly visible notaulices, whereas in other specimens the notaulices were invisible. The synonymy of the two genera can be so proposed (*Mesodryinus* is senior synonym).

The comparison among *Bocchoides*, *Chelothelius* and *Mesodryinus* in the new taxonomic status showed that it was impossible to propose generic differences. The three genera so are considered synonyms and *Chelothelius* is the valid oldest name, as follows:

Chelothelius Reinhard 1863
  (= *Mesodryinus* Kieffer 1906, syn. proposed by Olmi 1992b)
  (= *Bocchoides* Benoit 1953, syn. proposed by Olmi 1992b)
  (= *Alphadryinus* Olmi 1984, syn. proposed by Olmi 1992b)

After the above reflections the following genera can be considered belonging to Dryininae:

Dryinus Latreille 1804
Chelothelius Reinhard 1863
Thaumatodryinus R.C.L. Perkins 1905
Perodryinus R.C.L. Perkins 1907
Tridryinus Kieffer 1913
Megadryinus Richards 1953
Cretodryinus N. Ponomarenko 1975 (fossil)
Gonadryinus Olmi 1989
Pseudodryinus Olmi 1989

The above nine genera however are recognizable mostly on the basis of female specimens. A recent study of almost all the known males demonstrated that the males of *Dryinus*, *Tridryinus*, *Perodryinus* and *Chelothelius* don't show generic differences, whereas the males of *Thaumatodryinus* and *Pseudodryinus* are well distinct. The males of *Gonadryinus*, *Cretodryinus* and *Megadryinus* are unknown.

If the males of *Dryinus*, *Tridryinus*, *Perodryinus* and *Chelothelius* don't show generic differences the four genera can be considered synonyms and *Dryinus* Latreille 1804 is the oldest valid name.

On the basis of the above considerations the following new list of genera of Dryininae can be proposed:

*Dryinus*Latreille 1804
  (= *Chelothelius* Reinhard 1863, n. syn.)
  (= *Mesodryinus* Kieffer 1906, n. syn.)
  (= *Perodryinus* Perkins 1907, n. syn.)
  (= *Tridryinus* Kieffer 1913, n. syn.)
  (= *Bocchoides* Benoit 1953, n. syn.)
  (= *Alphadryinus* Olmi 1984, n. syn.)
Thaumatodryinus R.C.L. Perkins 1905
Megadryinus Richards 1953

Females

1 Enlarged claw very reduced; approximately as long or slightly longer than arolium (fig. 709 in Olmi, 1984) .... 4. *Dryinus autumnalis* (Olmi) group (formerly *Perodryinus*)
— Enlarged claw not reduced, much longer than arolium (fig. 567 in Olmi, 1984) ... 2
2 Enlarged claw without subapical tooth (fig. 669 in Olmi, 1984) or with at least 2 subapical teeth (fig. 702 in Olmi, 1984); rarely with one only subapical tooth, but in this case with a very broad apical lamella (fig. 41 E in Olmi, 1989) .... 3. *Dryinus lamellatus* (Olmi) group (formerly *Alphadryinus, Mesodryinus, Chelothelius, Bocchoides*)
— Enlarged claw with one subapical tooth, never with a broad apical lamella (fig. 567 in Olmi, 1984) 3
3 Notaulices at least partly visible .... 1. *Dryinus constans* Olmi group (formerly *Dryinus, Richardsidryinus*)
— Notaulices invisible .. 2. *Dryinus ruficauda* (Richards) group (formerly *Tridryinus*)

The new species *Dryinus cruciatus* is belonging to the group 1, where it's near *Dryinus citricolus* Olmi and *Dryinus flavoniger* Olmi. In the key to the females of the Neotropic *Dryinus* proposed by Olmi (1989) *D. cruciatus* can be inserted at number 3, as follows:

1 Occipital carina invisible .... 1.*constans* Olmi
— Occipital carina complete or incomplete 2
2 Thorax and propodeum fully or almost fully testaceous 3
— Thorax and propodeum mostly or fully black 4
3 Enlarged claw without lamellae (fig. 563 in Olmi, 1984) .... 2. *citricolus* Olmi
— Enlarged claw with a row of lamellae (fig. 7) .... 3'
3' Occipital carina incomplete; head with POL almost 0,5 as long as OL .... 3. *flavoniger* Olmi
— Occipital carina complete; head with POL longer than OL. ..... 24. *cruciatus* n. sp.

Thaumatodryinus snellingi n. sp.

Description of the female: fully winged; length 3,75 mm; testaceous, with scutellum brown and petiole black; antennae short, approximately as long as head + mesosoma, with tufts of long hairs on segments 5-10; antennal segments in following proportions: 12:5,5:13:12:13:14:11:9,5:8:9,5; antennal segment 5 less than ten times as long as broad (13:2); head swollen, granulated, dull; frontal line absent; occipital carina complete; POL = 5; OL = 2,5; OOL = 8,5; OPL = 2; TL = 3; breadth of the anterior ocellus slightly longer than OL (3:2,5); pronotum hairy, crossed by a strong transversal impression, dull, granulated, with tracks of numerous transversal striae; pronotal tubercles reaching the tegulae; scutum dull, granulated; notaulices little visible, incomplete, reaching approximately 0,8-0,9 length of scutum; scutellum dull, granulated; metanotum shiny, smooth, without sculpture; propodeum dull, reticulate rugose, without transversal or longitudinal keels; fore wing with a dark spot beneath the pterostigma; distal part of radial vein longer than proximal part (32:12); radial cell almost closed; fore tarsal segments in following proportions: 17:4:6:14:22; enlarged claw (fig. 8) with two subapical teeth and a row of 25 lamellae; segment 5 of front tarsus (fig. 8) with 24 lamellae without interruption to the apex; apex with a group of 9 lamellae; tibial spurs 1, 1, 2.

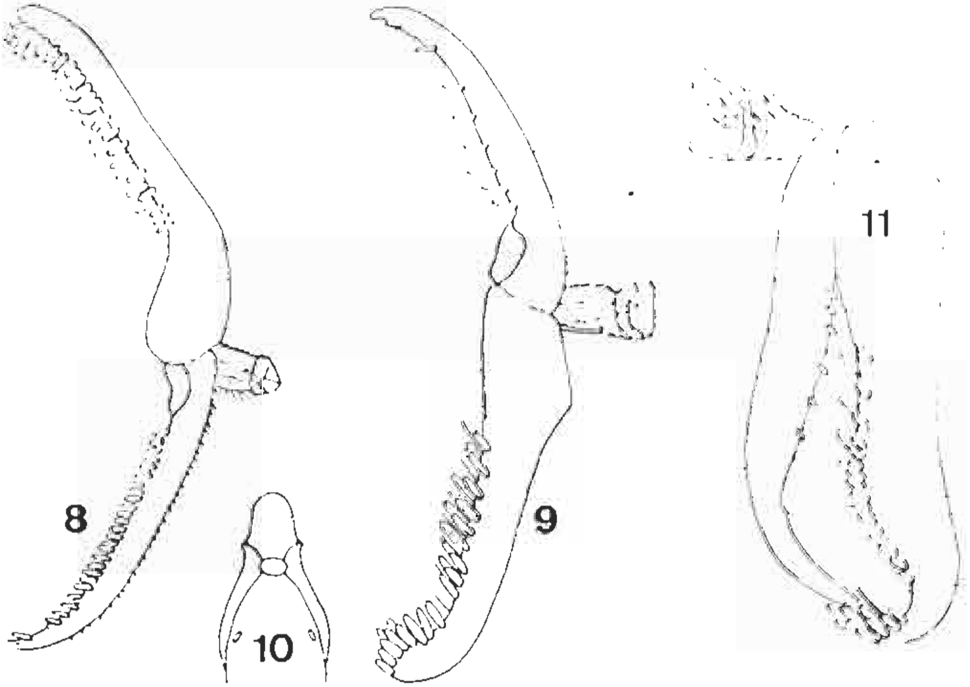
Male: unknown

Locus typicus: Long Man's Pt. trail (Guana I., British Virgin Islands)

Typical material: holotype ♀ in LA

Distribution: only known of the typical locality.

Notes: the species is named in honor of the collector of the holotype, Mr. Roy



Figs. 8-11 - Chelae of holotypes of *Thaumatodryinus snellingi* n. sp. (fig. 8); *Dryinus wasbaueri* n. sp. (fig. 9); *Gonatopus sensitivus* n. sp. (fig. 11); scutum and part of metathorax + propodeum of holotype of *Gonatopus sensitivus* n. sp. (fig. 10) (in dorsal view).

R. Snelling; the holotype was collected by a Malaise trap in a dry evergreen forest on October 21-24, 1992. For the very short antenna *Th. snellingi* is an anomalous species of *Thaumatodryinus*. Usually in fact in this genus the female antennae are much longer.

In the key to the females of Neotropic *Thaumatodryinus* proposed by Olmi (1984) *Th. snellingi* can be inserted at number 4, as follows:

4 Antennae very short and less slender, approximately as long as head + mesosoma .... 7. *snellingi* n. sp.
— Antennae very long and slender, at least 1,5 times as long as head + mesosoma . 5
5 Segment 1 of front tarsus approximately as long as segment 4; head black or brown-black .... 3. *macilentus* De Santis & Vidal Sarm.
— Segment 1 of front tarsus longer than segment 4; head fully reddish or reddish-testaceous or testaceous 6
6 Ocellar triangle very swollen; breadth of the anterior ocellus more than twice as long as OL .... 5. *bruchi* De Santis & Vidal Sarm.
— Ocellar triangle slightly swollen; breadth of the anterior ocellus as long as, or shorter, or less than twice as long as OL .... 4. *rufus* Richards

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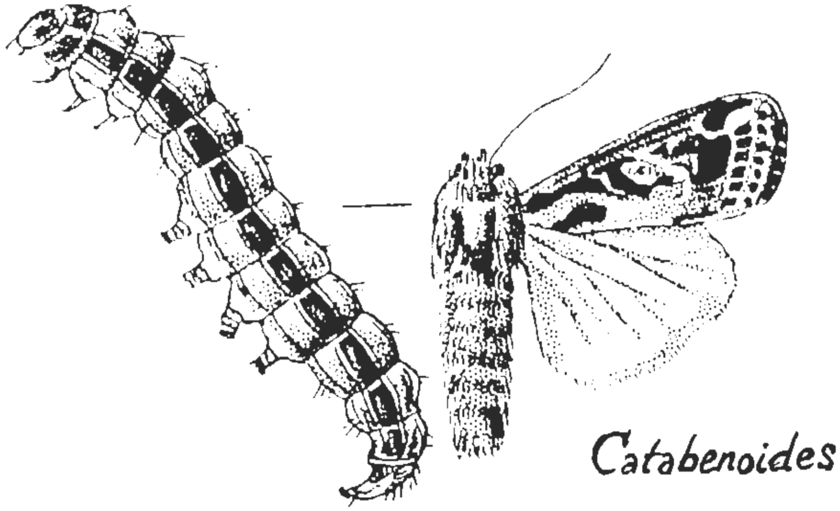
Family Dryinidæ. Dryinid Wasps.—Those who collect and observe leafhoppers and related Homoptera, often find specimens which look as though the abdomen had been ruptured, a hernia-like swelling projecting from between certain segments. This is the habitat of the larva of a Dryinid wasp that forms and lives within the cyst, which is composed of its own shed skins. When full grown the larva leaves the mortally wounded host and spins a cocoon, usually attached to a convenient plant. The females of the wasps, which finally emerge from the cocoons, are remarkable in the possession of a pincher at the end of each front leg, which is formed by the elaboration of the fifth tarsal segment. With these pinchers the wasps catch and hold the small hoppers while they thrust their eggs into the latter's body. The front wings have a well-developed stigma and are often pigmented, but most of the veins are faint or obsolescent. The hind wings are almost veinless. In some species all trace of wings has been lost. The head is broad, the body slender, the prothorax remarkably elongate and drooping. These wasps are very important to man, since the adults, as well as the larvæ, may destroy leafhoppers.



THE LARGE MOTHS OF GUANA ISLAND, BRITISH VIRGIN ISLANDS. A SURVEY OF EFFICIENT COLONIZERS

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"Good boys go to heaven, but the bad boys go everywhere"*
Meatloaf, 1993

ABSTRACT. An illustrated and annotated list of large moths of Guana, a 297 ha island located on the north side of the Caribbean island of Tortola, British Virgin Islands, is presented for the first time. Of the 148 species listed, 98 are distributed throughout the neotropics, 41 throughout the Antilles, with some ranging into Florida, and 9 endemic to the Puerto Rican Bank, two of them described here: Catabenoides lazelli sp. n., and Perigea gloria sp. n. The following new synonyms and combinations were also recognized in this study: Leucania solita Walker, syn. n. [=L. humidicola Guenée], L. dorsalis Walker, sp. rev., L. extenuata Guenée, sp. rev., Kakopoda cincta Smith, syn. n. [=K. progenies (Guenée)], Drepanopalpia polycyma Hampson, syn. n. [=D. lunifera (Butler), comb. n.], Sphacelodes fusilineatus Walker, stat. rev., Ptychopoda monata Forbes, syn. n. and Sterrha insulensis Rindge, syn. n. [=Lobocleta nataria (Walker)], Ptychopoda curtaria Warren, syn. n. [=Idaea minuta (Schaus)]. Pterocypha defensata Walker, stat. rev., is recognized as the senior synonym of P. floridata (Walker), syn. n., reversing a recently published synonymy. A new genus, Catabenoides Poole, gen. n., type-species: Laphygma vitrina Walker, is also described in an appendix, including C. divisa (Herrich-Schaffer), comb. n., C. seorsa (Todd), comb. n., and C. terens (Walker), comb. n., all by Robert W. Poole. The palatability to birds of two species, Diphthera festiva and Calidota strigosa, was tested and the species were shown to be distasteful.

KEY WORDS. Antilles, West Indies, biogeography, Guana Island, Lepidoptera, taxonomy, palatability.

FOOTNOTE TO FIRST PAGE

*We often pejoratively regard widespread species as "weed species" or "pests". Parodying the citation above: "Bad" species go everywhere, "good" species [may] go to Heaven [extinct]. But is it fair to consider them bad simply because they are able to get everywhere? Perhaps "efficient colonizers" is a better term?

Guana is a small island on the north side of Tortola in the British Virgin Islands (18°28'N, 64°35'W) (Fig. 1). While it is small, only 297 ha, and the maximum elevation is 266 m, it bears a relatively rich vegetation and has sustained less damage by feral animals and humans than have many adjacent islands (Lazell, 1996). It has most of the floristic associations of the larger Virgin Islands, with the notable exception of the "aridulate rain forest" of Tortola (D'Arcy, 1967). Despite its small size, Guana has a diverse insect fauna. For example, Guana has 31 species of butterflies (Becker & Miller, 1992), compared to the larger islands of Anegada (3872 ha) (Smith et al., 1991) with 24 species and Tortola (5444 ha) with 31 species (Riley, 1975).

This is the first survey of the moth fauna of this island. J.F.G. Clarke was on Guana briefly in 1956 and 1958 (see Schmitt, 1959), but was not able to collect at lights there. Most of the species here are previously known from Puerto Rico (e.g., Forbes, 1930, 1931, Schaus, 1940, Wolcott, 1951), but most have not been recorded from the British Virgin Islands due to lack of previous sampling. The faunal similarity to Puerto Rico is expected, given that the principal islands of the Virgin Islands (except Saint Croix) lost their connection with each other and with Puerto Rico only about 8,000 to 10,000 years ago, due to eustatic rise in sea level (Heatwole et al., 1981).

We are treating the Lepidoptera of Guana Island in parts. Becker and Miller (1992) reported 31 species of butterflies. The present paper reports 148 species of large moths (Macrolepidoptera, including the unrelated Cossidae and Hyblaeidae for convenience), represented by 1390 specimens. The manuscript was prepared using the classification of Noctuidae of Poole (1989), before the extensive changes in higher classification presented in Kristensen (1998). Future papers will treat Pyraloidea and Microlepidoptera.

The moth fauna of Guana is composed primarily of species with wide distributions in the New World tropics (Table 1). Of the 148 species listed, 50 are endemic to the Caribbean Islands, many of them reaching the Florida Peninsula, and only 9 are apparently restricted to the Puerto Rican Bank. These proportions, however, are not the same for the different families. The highest degree of endemism occurs in the Geometridae and Arctiidae, whereas the lowest occurs in the Sphingidae. This is presumably because of the powerful flying capacity of sphingids, while geometrids and arctiids are clumsy flyers.

Holloway and Nielsen (1998, following Ferguson et al., 1991) presented a chart of 12 moth genera that are widely recorded from remote islands worldwide. Of these 12 genera, 9 genera (including 20 species) are present on Guana (counting Leucania as Mythimna). It is likely that the remaining three genera, especially Agrotis, may be found on Guana in the future.

The material upon which this list is based was collected in July 1984 and 1985 (by S. E. Miller & P. M. Miller), July 1986 (S. E. Miller & M. G. Pogue), July 1987 (S. E. Miller & V. O. Becker), July 1988 (S. E. Miller & C. O'Connell), October 1989 (V. O. Becker) and October-November 1990 (S. E. Miller & T. M. Kuklenski). Collections from 1984-1986 are deposited at the National Museum of Natural History (USNM), Washington, those of 1987-1990 are split between first author (VOB), Bishop Museum, Hawaii (BPBM), and USNM. The largest collections were made by both authors 9-23 July 1987, with over 2200 specimens representing about 300 morphospecies, and by the first author in October 1989, with over 2000 specimens representing over 350 morphospecies.

The list of species by family collected in the 1989 trip (Table 2) gives an impression of the overall fauna, especially the diversity of Microlepidoptera, still under study. Of these 359 species, 243 species (2/3) are Microlepidoptera and pyraloids, and 163 (nearly ½) belong to pyraloids and gelechioids.

The number of specimens listed in this work under each species does not reflect relative abundance, as our objective was only to list the species occurring on the island. Therefore, in the case of species that are common in other parts of the neotropics only one or a few specimens were collected to voucher the record, independent of their abundance. In contrast, in the case of endemic or rare species, usually all specimens were caught.

The excellent results obtained by the first author during the 1989 trip was a surprise, as it was made between 20-40 days after Hurricane Hugo had devastated the island on 18 September. The damage was still evident: all buildings without roofs and without most of their doors and windows, and fallen trees and torn branches scattered all over the island. According to people who were on the island the day Hugo hit, not a single leaf remained on the trees. At the time of his arrival (9 October) the island was completely green again. That same night the collecting was fantastic, as were also most nights during the next 20 days spent there. Not only the quantity, but also the quality of the material was impressive. It seemed that all specimens had emerged that day. Certainly all caterpillars that had reached development had to pupate immediately after the hurricane, and now they were all emerging together. Leaf mines were also abundant. As these tiny species usually have shorter life cycles, they had time to emerge and lay eggs in the 20 days that preceded the arrival. Torres (1992) documented the impact of Hurricane Hugo on Lepidoptera populations on Puerto Rico.

A synoptic collection, containing at least one specimen representing each form was taken to the Smithsonian Institution (USNM), Cornell University (CU), and most importantly, to the Natural History Museum (BMNH), London, by the first author. The list below is a result of the identifications made by comparing this synoptic collection with identified material, especially type specimens (including important voucher specimens and types from Forbes 1930, 1931, Schaus, 1940). The first author has compiled a synonymic list of Antillean Lepidoptera (Becker, in prep.), which has provided further taxonomic background.

This report is addressed not only to lepidopterists, but also to biologists and others interested in the observation and study of the fauna of the Virgin Islands. For this reason we give a brief synopsis of each species to provide a context and to suggest what kind of observations should be undertaken.

Acknowledgements

Sampling on Guana Island was supported by The Conservation Agency, through a grant from the Falconwood Corporation. We thank James D. Lazell for providing arrangements to work on the island. George Proctor, formerly of the Puerto Rico Department of Natural Resources, provided information on plants. Research facilities were provided by the National Museum of Natural History, Smithsonian Institution (USNM) and Natural History Museum, London (BMNH). Most of the work on this paper was done while Becker worked for EMBRAPA-CPAC, Planaltina, and Miller for Bishop Museum, Honolulu. We thank Robert W. Poole and Douglas C. Ferguson (both formerly U.S. Dept. Agriculture Systematic Entomology Laboratory), Martin R. Honey (BMNH), Charles Covell (University of Louisville, Kentucky), Jean-Marie Cadiou and Morton S. Adams for assistance with moth identifications. Poole also allowed us to include his generic description in the appendix. Roy Snelling (Los Angeles County Museum) provided identifications for wasps. Liao Wei-Ping identified the birds. The plates were photographed by Chip Clark (Smithsonian), with assistance from Ronald W. Hodges (USDA). Michael Pogue reviewed the manuscript. The line drawings were prepared by W. Cavalcanti, EMBRAPA-CPAC.

SPHINGIDAE

Eighty five species of sphingids have been recorded from the Antilles (Becker, in prep.), 22 (25%) of them were collected by us in Guana. Nearly all occur in the United States too, so Hodges (1971) illustrated them in color. They are also illustrated in color in D'Abrera (1986). Most of their larvae were illustrated, also in color, by Moss (1912, 1920).

Sphinginae
1. Agrius cingulatus (Fabricius, 1775)
(Sweetpotato hornworm, Pink spotted hawk moth)

ID: Easily separated from other hawk moths by the pink dots on its abdomen.
DIST: United States south to Argentina, including Galapagos.
GUANA: 1 specimen, 1989.
HOST: Its variable larvae (green to dark brown) feed on various plants belonging to Convolvulaceae, including sweet potato.

2. Cocytius antaeus (Drury, 1773)
(Giant sphinx)

ID: Easily distinguished from other sphingids on the island by its dark green wings and the three pairs of yellow dots on the abdomen.
DIST: Southern United States to Argentina; not in Galapagos.
GUANA: 1 specimen, 1989
HOST: Green larvae feed on various Annona species (Annonaceae) such as custard apple.

3. Manduca sexta (Linnaeus, 1763)
(Tobacco hornworm, Carolina sphinx)

ID: Easily distinguished from the other sphingids on the island by its gray wings and six pairs of yellow dots on the abdomen.
DIST: Widespread in the New World, including Galapagos.
GUANA: 5 specimens, 1984, 1988, 1989.
HOST: Pest of cultivated solanaceous plants, such as tobacco, tomato, potato, etc.
COM: Mature larvae are green-yellow with seven pairs of white lateral bands, and red anal horn.

4. Manduca rustica (Fabricius, 1775)
(Rustic sphinx)

ID: Easily distinguished from other sphinx moths on the island by its dark grayish-brown fore wings with transverse grayish-white waiving bands, and three pairs of yellow dots on the abdomen.
DIST: Widespread New World species, present in Galapagos.
GUANA: 2 specimens, 1984, 1989.
HOST: Larva is greenish-gray easily distinguished by its small white nodules on the thoracic segments, mainly on dorsum. They feed on various species of Bignoniaceae, Verbenaceae and Boraginaceae (Hodges, 1971).

5. Manduca brontes (Drury, 1773)

ID: Distinguished from other species in the genus occurring on the island by the absence of yellow dots on the abdomen.
DIST: Antillean species occurring northward to Central Florida.
GUANA: 1 specimen, 1989.
HOST: The larva is similar to that of the tobacco hornworm but feeds on Tecoma (Bignoniaceae) (Hodges, 1971).

Macroglossinae
6. Pseudosphinx tetrio (Linnaeus, 1771)
(Frangipani hornworm)

ID: The largest sphinx on the island; pale gray with irregular darker markings.

DIST: United States throughout the Antilles to Argentina.
GUANA: 7 specimens, 1988, 1990.
HOST: Its conspicuous bright caterpillars - banded black and yellow with reddish brown head and orange legs - are frequently seen defoliating frangipani, Plumeria spp. (Apocynaceae) on the island.

7. Erinnyis alope (Drury, 1773)
(Papaya hornworm)

ID: Easily distinguished from other sphingids on the island by the combination of yellow basal half of hind wings and alternate pairs of light gray and black dots on the abdomen.
DIST: Widespread in the New World, including the Galapagos.
GUANA: 1 specimen, 1989.
HOST: A variety of milk plants, such as papaya (Carica papaya L.) (Caricaceae), Jatropha (Euphorbiaceae) and Alamanda (Apocynaceae).

8. Erinnyis ello (Linnaeus, 1758)
(Cassava hornworm)

ID: Sexually dichromatic. Males have fore wings dark gray with a blackish irregular band along the wing from near base to apex. Females have fore wings light gray with almost no markings. The abdomen has pairs of alternate light gray and black dots dorsally.
GUANA: 5 specimens, 1984, 1990.
DIST: The most common species of the genus in tropical America; also in Galapagos.
HOST: Larvae varying in color from yellowish to green and to brownish have been serious pests of cassava (Manihot) in tropical America; feeds on various Euphorbiaceae.

9. Erinnyis crameri (Schaus, 1898)

ID: Fore wings more brownish than those of former; basal area reddish brown and abdomen with indistinct markings.
DIST: Southern United States, through the Caribbean south to Brazil.
GUANA: 1 specimen, 1989.
HOST: Grayish brown larva, figured by Moss (1920: pl. 7, figs. 3a, b), has been reared on various members of the Apocynaceae (Hodges, 1971).

Erinnyis domingonis (Butler, 1875)

ID: Same size as obscura (see below) but fore wings mostly dark gray.
DIST: Same as obscura, except for Galapagos.
GUANA: 2 specimens, 1987.
HOST: Unknown.
COM: It is very likely that obscura and domingonis are only forms of a same species (Hodges, 1971: 102; Kitching and Cadiou, 2000: note 162). This could be verified by rearing.

11. Erinnyis obscura (Fabricius, 1775)

ID: Similar to E. ello, which is also dichromatic, but easily distinguished by its smaller size and absence of dots on abdomen.
DIST: Southern United States throughout the Caribbean south to Brazil, including Galapagos.
GUANA: 4 specimens, 1984, 1987.
HOST: Its pale yellowish or pale green larvae have been reared on various milk plants such as Philibertia and Cynanchum (Asclepiadaceae).

12. Pachylia ficus (Linnaeus, 1758)
(Large fig hornworm)

ID: Large, dull brown with stout body, quite distinct from other sphingids on the island. Easily recognized by the pale, inverted trapezoidal mark on costa near apex.
DIST: Widespread throughout the New World, but absent from Galapagos.
GUANA: 1 specimen, 1987.
HOST: Moss (1912) figured in color the several forms of its caterpillars, which feed on various species of Ficus (Moraceae). Some are green banded yellow dorsally, while the others are gray brown ventrally and orange, banded black, dorsally.

13. Callionima falcifera (Gehlen, 1943)

ID: Easily recognized by its orange brown color and the metallic silvery mark near center of fore wings.
DIST: Southern United States to Argentina.
HOST: Early stages and food plants are unknown. Other species in the genus have been reared on some apocynaceous plants (Hodges, 1971).
GUANA: 4 specimens, 1987, 1990.
COM: Very similar to, and for a long time confused with, C. parce (Fabricius) (Kitching and Cadiou, 2000: note 91). The specimen illustrated as parce in Hodges (1971, pl. 10, fig. 8) represents this species.

14. Perigonia lusca (Fabricius, 1777)

ID: Medium size dull brown sphinx easily recognized by the bright orange area along the middle of hind wings.
DIST: Southern Florida to Argentina.
GUANA: 27 specimens, 1987, 1988, 1989, 1990.
HOST: Bluish green larva, figured in color by Moss (1912), was reared by him on coffee (Rubiaceae). Recorded from Gonzalagunia spicata (Lam.) Maza and other Rubiaceae in Puerto Rico by Torres (1992).
COM: Kitching and Cadiou (2000: note 448) review names associated with P. lusca.

15. Enyo lugubris (Linnaeus, 1771)

ID: Medium size, dark brown; easily distinguished from other hawk moths in the island by the dentate external borders of both wings.
DIST: Southern United States, throughout the Antilles, south to Uruguay and Argentina, including Galapagos.
GUANA: 3 specimens, 1987, 1989.
HOST: Ampelopsis spp., Cissus spp. and Vitis spp. (Vitaceae) (Hodges, 1971).

16. Aellopos tantalus (Linnaeus, 1758)

ID: Small, dark gray, diurnal, sphinx moth distinguished by the conspicuous white bar across base of abdomen.
DIST: New York south to Argentina.
GUANA: One specimen captured in a Malaise trap, 1990.
HOST: Ixora venulosa Benth. (Rubiaceae) (Biezanko et al., 1949).

17. Eumorpha vitis (Linnaeus, 1758)
(Vine sphinx)

ID: Dark green with fore wings crossed with grayish bands and dashes, and hind wings with anal margins pink. A beautiful and showy species.
DIST: United States throughout the Caribbean to Argentina (not in Galapagos).
GUANA: 2 specimens, 1987, 1990.
HOST: The larvae vary in color; some are dark pink others are pale green or yellow green (Moss, 1912). They feed on grape leaves (Vitis spp.).

18. Cauthetia noctuiformis (Walker, 1856)

ID: The smallest sphingid in the New World, with a wing span slightly over one inch. Gray with basal half of hind wings orange yellow.
DIST: Caribbean.
GUANA: 166 specimens, 1984, 1986, 1987, 1988, 1989, 1990.
HOST: Early stages are unknown but the larvae of C. grotei has been reared on Chiococca alba (L.) Hitch. (Rubiaceae) (Hodges, 1971).
COM: Kitching and Cadiou (2000: note 96) discuss the taxonomy and place the Guana population in the subspecies C. noctuiformis bredini Cary, 1970.

19. Xylophanes chiron (Drury, 1770)

ID: Green with an oblique grayish brown irregular band on the fore wings looking as a leaf with dead areas.
DIST: Mexico, throughout the Antilles to Argentina.
GUANA: 1 specimen, 1987.
HOST: Its showy caterpillar, illustrated in color by Moss (1920: pl. 8, figs. 6a-f), was reared by him on Palicourea, Psychotria and Spermacoce (Rubiaceae). They are glossy green bearing pairs of red, or white red-ringed eye spots on the first two abdominal segments.

20. Xylophanes pluto (Fabricius, 1777)

ID: Green with irregular transverse light and dark bands. Easily recognizable by the wide orange band on the hind wings.
DIST: Southern United States to Brazil.
GUANA: 8 specimens, 1987, 1988, 1989, 1990.
HOST: Torres (2000) described larvae from Puerto Rico, reared from Hamelia patens Jacq. (Rubiaceae). Gundlach (1881), mentioned by Hodges (1971), also described the larvae, which are of two color forms: one is basically green, the other is black, dark violet and red. Gundlach recorded the hosts as Chiococca (Rubiaceae) and Erythroxylum (Erythroxylaceae).

21. Xylophanes tersa (Linnaeus, 1771)

ID: Easily recognizable from the others on the island by its pale greenish gray fore wings which show several ill defined longitudinal lines, almost parallel to each other, running from base to apex; hind wings black with pale yellow marks in the vein interspaces parallel to the external margin.
DIST: Ontario, across the Antilles down to Argentina, including Galapagos.
GUANA: 4 specimens, 1986, 1987, 1989.
HOST: The larvae, beautifully illustrated by Moss (1912: pl. 14, figs. n-q), are yellowish brown with a pair of eye spots laterally on each 1-7 abdominal segments. The larvae feed on Psychotria berteriana DC, Borreria verticillata (L.) Meyer and Diodia sarmentosa Sw. (Rubiaceae) in Puerto Rico (Torres, 1992).

22. Hyles lineata (Fabricius, 1775)
(White-lined sphinx)

ID: Resembles E. vitis, but is readily distinguished by its smaller size, shorter, clubbed antennae and single wide fascia running from near base of dorsum to apex of fore wings, crossed by whitish lines following the veins.
DIST: This powerful flyer, almost diurnal, has reached all continents, as well as remote islands such as Galapagos and Hawaii.
GUANA: 1 specimen, 1988
HOST: Polyphagous. Most common plants are species of Portulaca (Portulacaceae), but includes others such as Fuchsia (Onagraceae), Boerhavia and Mirabilis (Nyctaginaceae), Xantium (Asteraceae), etc.
COM: Larvae are highly variable in coloration and somewhat in maculation. Some specimens basically are black with a pattern of yellow; others are mainly yellow with some black pattern (Hodges, 1971).

NOTODONTIDAE
23. Nystalea nyseus (Cramer, 1775)
(Fig. 15)

ID: Light gray, narrow winged, mottled with dark brown and black scales, easily recognized by the long scales on the base of antennae that forms a crest on the top of the head when resting.
DIST: Mexico, throughout the Caribbean south to Brazil.
HOST: Larvae feed on various Myrtaceae especially on species of the genus Psidium (Todd, 1973: 271).
GUANA: 3 specimens, 1989.
COM: This is the only member of the family present on the island, which is not surprising as the Notodontidae typically occur in moister forests and less than 30 species have been recorded from the Antilles (Becker, in prep.).

NOCTUIDAE
Heliothinae
24. Heliothis subflexa (Guenée, 1852)
(Fig. 16)

ID: Medium sized, pale olive green; fore wings crossed with three olive bands, edged pale basad.
DIST: North America, throughout the Antilles, south to Argentina.
HOST: Solanum nigrum L., Physalis spp. (Solanaceae) (Poole et al., 1993).
GUANA: 2 males, 1989.
COM: Easily confused with the tobacco budworm, H. virescens (Fabricius), not collected but certainly occurring on the island. Male H. subflexa present plain white hind wings, while in H. virescens they are bordered olive-gray. More details on both species can be found in Poole et al. (1993). Haile et al. (1975) discuss movement of Heliothis spp. among the Virgin Islands.

Noctuinae
25. Anicla infecta (Ochsenheimer, 1816)
(Fig. 17)

ID: Gray, with fore wings reddish brown along external margin and hyaline hind wings. Easily recognized by blackish anterior border (patagia) of thorax.
DIST: Cosmopolitan.
GUANA: 6 specimens, 1986, 1989, 1990.
HOST: General feeder, cut worm. The larvae reach nearly 3 cm when fully grown, very variable in color; from gray to yellowish ferrugineous, olivaceous yellow and bright green, to a sordid brown usually flecked with black.

COM: It is very likely that at least three other cut worms should be present in the island. Agrotis ipsilon (Hufnagel), A. subterranea (Fabricius) and Peridroma saucia (Hubner).

Hadeninae
26. Leucania humidicola Guenée, 1852
(Fig. 19)

ID: Medium sized, pale moth. Easily distinguished from other noctuids in the island by its forewing pattern: a long dark dash delimited above by a white line, running from base to middle.
DIST: Antilles to Brazil and to Galapagos (as solita, see below).
GUANA: 2 specimens, 1989
HOST: Hayes (1975) [as solita, see below] gives Sporobolus virginicus (L.) Kunth. (Poaceae) as food-plant.
COM: The Guana specimens were kindly identified as humidicola by Mr. Morton S. Adams. The name humidicola (type-locality: FRENCH GUIANA) has been wrongly applied to a different species by most authors (see dorsalis below), following the misidentification by Hampson (1905). The first author compared a specimen collected by him in COSTA RICA: Guanacaste, El Coco (VOB 33636), identical to those from Guana, with the BMNH collection. It matches the type of solita (type-locality: HONDURAS), and certainly the specimen figured by Hayes (1975), from Galapagos. Therefore L. solita Walker, 1856, syn. n., is a junior synonym of humidicola, not of multilinea Walker (sensu Hampson, 1905, Poole, 1989). We regard multilinea Walker, 1856 as a valid species because we believe that Hayes (1975), who had the types of both multilinea and solita at hand, had good reasons to treat the latter as a valid species.

27. Leucania dorsalis Walker, 1856
(Fig. 18)

ID: Easily confused with the former; dash along middle of fore wings not as conspicuous.
DIST.: Antilles, Florida (Dickel, 1991).
GUANA: 1 specimen, 1988.
HOST: Unknown; presumably on grasses as do its closest relatives L. infatuans Franclemont and L. extenuata Guenée.
COM: This species belongs to a complex previously treated by the authors as humidicola, following a misidentification by Hampson (1905). This complex includes at least the following species: L. extenuata Guenée, 1852 (type-locality: BRAZIL [no further data] (BMNH) [examined]), tayaudi Guenée, 1852 (type-locality: [URUGUAY]: Montevideo, MNHN, Paris [not examined], dorsalis Walker, 1856 (type-locality: DOMINICAN REPUBLIC (BMNH) [examined]), adjuta (Grote, 1874) (type-locality: USA: Alabama (BMNH) [not examined]) and infatuans Franclemont, 1972 (type-locality: USA: Florida (CU) [not examined]). The first author compared a specimen collected by him in BRAZIL: PR, Ponta Grossa (VOB 3301) with the BMNH collection. Externally it matches the types of both extenuata and dorsalis. The only specimen from Guana unfortunately is a female, however a male from St. Thomas, that matches it, was dissected, as well as male specimens from Cuba, Mexico and Brazil. The specimens from St. Thomas and Cuba have genitalia different from those of males from Brazil. Therefore dorsalis Walker, sp. rev. and extenuata Guenée, sp. rev., are hereby removed from the synonymy with humidicola Guenée. The male genitalia of dorsalis specimens from St. Thomas and Cuba closely resemble the illustrations of those of infatuans (Franclemont, 1972: 145, figs. 7-8), and after a revision of this complex it might be revealed that both belong to the same species. Those of male extenuata specimens from Brazil match the illustration of "humidicola" sensu Hampson, presented by Franclemont (1972: 146, figs. 11-12). It is also very likely that tayaudi is a synonym of extenuata.

Amphipyrinae
28. Neogalea sunia (Guenée, 1852)
(Fig. 20)

ID: Another medium sized inconspicuous gray moth resembling S. albula, but darker. Usually distinguished from the latter by the dark marked veins and, for males, by the abdomen thickly clothed with long scales.
DIST: Florida to Brazil, including Galapagos.
GUANA: 6 specimens, 1987, 1989, 1990.
HOST: Lantana (Verbenaceae) (Comstock and Dammers, 1935). Introduced to Hawaii to control Lantana (Riotte, 1991).
COM: Immature stages described by Comstock and Dammers (1935, as Catabene esula). Although this genus was placed in Cuculliinae by Poole (1989), we place it here following the comments by Poole in the appendix to this paper.

29. Catabenoides terminellus (Grote, 1883), comb. n.
(Figs. 2, 3, 22)

ID: This and the following are very closely related species, almost impossible to be distinguished from each other on external characters (see lazelli below). They resemble a small S. albulum but are easily recognized from it by the gray, irregular dot on tornus of fore wings. Females usually have a black line along middle, covering the whole extension of fore wings.
DIST: Southern USA, Antilles.
GUANA: 4 specimens, 1984.
HOST: Unknown.
COM: In order to correctly place this and the following species, we include a description of the new genus Catabenoides by Robert Poole as an appendix to this paper.

30. Catabenoides lazelli sp. n.
(Figs. 4-6, 21)

ID: Light gray, 2.2-2.6 cm. This and the former are very closely related species, almost impossible to be distinguished from each other on external characters (see terminellus above). They resemble a small S. albulum but easily recognized from it by the gray, irregular dot on tornus of fore wings. Females usually have a black line along middle, covering the whole extension of fore wings. The only reliably external feature to distinguish this from terminellus, is the color of patagia. In terminellus there is a transversal line of blackish scales, dividing the patagia along the middle, while in lazelli this line is ochreous.
Their genitalia are also distinct. In the male genitalia of terminellus the distal processes of sacculus are simple, nearly straight rods (Fig. 2), while those in lazelli are complex, branched (Fig. 4).
DIST: Guana, Anegada, St. Croix.
GUANA: 35 specimens, 1984, 1985, 1989, 1990.
MATERIAL EXAMINED: Holotype male: BVI: Guana Id., 1-14.vii.1984 (S. E. & P. M. Miller) (USNM). Paratypes: 13 males, 12 females: Same data as holotype (USNM, BMNH, BPBM, MCZ, VOB); 1 female: Same locality and collector, 5-23.vii.1985 (USNM); 2 males, 1 female: Same locality, x.1989 (V. O. Becker, 70710) (VOB); 2 males, 3 females: Same locality, 24.x-5.xi.1990 (S. E. Miller & T. M. Kuklenski) (BPBM). ANEGADA: 2 males, 1 female: 17-19.vii.1985 (S. E. & P. M. Miller) (USNM). ST. CROIX: 2 males, 2 females, Kingshill, x, xi.1944, v, vi.1945 (H. A. Beatty) (CU); 1 female, same locality, 6-16.vii.1967 (E. L. Todd) (USNM); 1 female, Christiansted, 19. xi.1941 (H. A. Beatty) (USNM); 1 male, 2 females, Mt. Eagle, 6-16.vii.1967 (E. L. Todd) (USNM); 4 males, 1 female, 1 mi W Airport, 6-16.vii.1967 (E. L. Todd) (USNM); 2 males, 1 female, Orangegrove, W End, 6-16.vii.1967 (E. L. Todd) (USNM); 1 male, Blue Mtn., 6-16.vii.1967 (E. L. Todd) (USNM); 2 males, Rust Up Twist, 6-16.vii.1967 (E. L. Todd) (USNM); 1 male, 1 mi N Great Pond, 6-16.vii.1967 ((E. L. Todd) (USNM).
HOST: Unknown.
COM: This species belongs to a complex formerly considered as one species, C. vitrinus (Walker), a species not found in the Lesser Antilles, being closely related to it. Its genitalia (Fig. 4, 5) are

very similar, but shows consistent differences, the most evident is the vesica armed with a single, strong cornutus, whereas in vitrina the vesica bears a series of smaller cornuti. The complex will be treated in a forthcoming revision (Becker, in prep.). This species is dedicated to our friend Dr James "Skip" Lazell, who gave us the opportunity to study this interesting fauna.

31. Spodoptera albulum (Walker, 1857)
(Fig. 23)

ID: Another plain, pale gray, medium sized species, readily distinguished by the presence, on the fore wings, of a very fine black line running along the middle from base to one-fourth. Hind wings almost totally translucent whitish.
DIST: United States, throughout the Antilles, south to Argentina, but not including Galapagos and Bermuda.
GUANA: 5 specimens, 1989, 1990.
HOST: Amaranthus sp. (Amaranthaceae) (Kimball, 1965), cotton (Bruner et al., 1975).
COM: "This is the species previously identified as 'Spodoptera sunia Guenée'. The real Xylopmyges sunia Guenée, 1852 is actually the species currently known as Neogalea esula Druce" (Poole, 1989) (see N. sunia above). Very similar and easily confused with S. eridania, not collected, but very likely to occur on the island. S. eridania is dusted brownish, and lacks the line as mentioned above. Distributions of Spodoptera species in the Caribbean are reviewed in Cock (1985: 92).

32. Spodoptera frugiperda (J. E. Smith, 1797)
(Fall armyworm)
(Figs. 24, 25)

ID: Medium sized, sexually dimorphic, gray species. Males have an oblique whitish dash from middle of costa across the cell. Females have indistinctive pattern, looking almost plain gray.
DIST: Widespread in New World, including Galapagos and Bermuda.
GUANA: 8 specimens, 1986, 1990.
HOST: Polyphagous on herbaceous plants and regarded as a serious pest of maize and other crops (Andrews, 1980).
COM: Todd & Poole (1980) give an illustrated key to the New World species of Spodoptera.

33. Spodoptera latifascia (Walker, 1856)
(Figs. 26, 27)

ID: Another medium sized sexually dimorphic species. Male fore wings show a diffuse pattern of reddish brown and gray on a whitish gray background. Females are darker, easily confused with S. dolichos and bear, on the fore wings, an oblique elongate whitish mark from middle costa to end of cell, followed by three short whitish lines along veins.
DIST: Gulf States of the United States, throughout the Antilles, south to Costa Rica. The population from Costa Rica south to Argentina, previously included under S. latifascia belongs to S. cosmioides (Walker), a closely related but distinct species (Silvain and Lalanne-Cassou, 1997; M. Pogue, pers. comm.).
GUANA: 1 specimen, 1989.
HOST: Polyphagous on herbaceous plants, sometimes becoming a pest of vegetables and nursery seedlings.

34. Spodoptera pulchellum (Herrich-Schäffer, 1868)
(Fig. 28)

ID: Wing pattern similar in both sexes; easily confused with the females of the former. It can be separated from other similar species by the curved whitish line along dorsum, below the anal vein, from basal fourth to just before tornus.
DIST: Florida, Greater Antilles.
GUANA: 1 specimen, 1989.
HOST: Unknown.
COM: This seems to be the first record of this species to the Puerto Rican Bank. Probably overlooked due to its rarity and for been mistaken for its similarity to latifascia, a more common species.

35. Spodoptera dolichos (Fabricius, 1794)
(Fig. 29)

ID: Almost the size of latifascia; both sexes showing similar patter to that of female latifascia. Easily distinguished from the last two species by the two conspicuous, parallel, dark gray bands along thorax.
DIST: Sympatric with latifascia, including in Galapagos.
GUANA: 1 specimen, 1989.
HOST: The larvae feed on a wide variety of plants, both crops and weeds (Ferguson et al., 1991).

36. Magusa orbifera (Walker, 1857)
(Fig. 30)

ID: An extremely polymorphic medium sized (3-4 cm), gray to brown species. In the Guana population, some males have a wide pale area along dorsum of fore wings, others have a very complex and contrasting maculation, while the females tend to be less marked and more brownish. One constant feature is the conspicuous round pale dot near the apex of fore wings and the very broad dark fuscous hind wings. A. affabilis and E. agrotina also have the pale mark at end of apex of fore wings but are at most half its size.
DIST: Widespread throughout the New World, from Canada to Argentina (not reported from Galapagos, but erema Hayes (1975) may be another local variety of this species).
GUANA: 57 specimens, 1989, 1990.
HOST: Various legumes, including Karwinskia and Condalia (Fabaceae) (Kimball, 1965).

37. Condica albigera (Guenée, 1852)
(Figs. 31, 32)

ID: Medium sized, 2.5-3 cm wing span, dark fuscous; fore wings with an irregular small white dot at end of cell, followed by a paler, almost straight transverse line.
DIST: Mexico, throughout Antilles, south to Paraguay.
GUANA: 3 specimens, 1989, 1990
HOST: Unknown.
COM: Easily confused with C. circuita (Guenée), not collected but likely to occur on the island. In circuita the white dot on forewing is round and has a white lunule just under it.

38. Condica mobilis (Walker, [1857])
(Fig. 33)

ID: About same size as preceding, but more reddish brown and orange; white dot on cell usually larger than previous.
DIST: Southern United States, throughout Antilles, south to Argentina.
GUANA: 1 specimen, 1989.
HOST: Unknown.

COM: Commonly referred to in the literature as Perigea apameoides Guenée. The latter is a synonym of C. sutor (Guenée) (Hayes, 1975).

39. Condica sutor (Guenée, 1852)
(Fig. 34)

ID: Same size as the preceding species in the genus; fuscous with fore wings showing little contrasting pattern. Distinguished from albigera and mobilis by the absence of the whitish mark on cell.
DIST: Southern United States, throughout the Antilles, south to Argentina, including Galapagos.
GUANA: 1 specimen, 1990.
HOST: Several species of herbaceous plants including Wedellia, Tagetis (Asteraceae), and celery (Kimball, 1965).

40. Perigea gloria sp. n.
(Figs. 7-9, 35)

ID: Medium sized, 3 cm wing span, pale moth; fore wings shaded dark fuscous, with a series of small dark marks along costa and small black dots along termen, on the spaces between veins. Similar to the former species but with more contrasting pattern and, readily separated by the series of black dots along termen.
DIST: Guana, Tortola.
GUANA: 2 specimens, 1989.
MATERIAL EXAMINED: Holotype male: BVI: Guana Id., x.1989 (V. O. Becker, 70722) (USNM); Paratypes, 1 female, same data as holotype (VOB); 1 male Tortola, Mt. Sage National Park, 460m, 13-15.vii.1987 (V. O. Becker & S. E. Miller, 66865) (VOB).
HOST: Unknown.
COM: Very similar in appearance to P. berinda (Druce), a species from the Greater Antilles and Central America, but with genitalia (Figs. 7-9) very different from those of berinda, being very similar to those of P. glaucoptera (Guenée). This species is dedicated to Ms Gloria Jarecki, for her and her family's support of The Conservation Agency's biodiversity research on Guana Island over the years.

41. Elaphria agrotina (Guenée, 1852)
(Fig. 36)

ID: Small, 2-2.5 cm wing span; fore wings dark fuscous with a paler area along costa and a conspicuous pale dash near apex. Similar to A. affabilis (see below), but larger and with hind wings bordered whitish.
DIST: Florida, throughout the Antilles, south to Argentina.
GUANA: 5 specimens, 1987, 1989, 1990.
HOST: Cotton and beans (Phaseolus) (Fabaceae) (Silva et al., 1968).

42. Elaphria nucicolora (Guenée, 1852)
(Figs. 37, 38)

ID: Same size as former; fore wings dark fuscous, with a broad, ill contrasting, darker triangular mark with base on middle of dorsum and vertex at end of cell. Hind wings whitish.
DIST: Throughout New World tropics including Bermuda. Immigrant to Hawaii.
GUANA: 1 specimen, 1989.
HOST: Various herbaceous plants (Ferguson et al., 1991).

43. Anateinoma affabilis Möschler, 1890
(Figs. 10, 11, 151, 152)

ID: Small, 15 mm wing span; fore wings reddish brown with transverse sinuate lines alternating pale and dark, and with a conspicuous whitish dash on apex. Similar to E. agrotina (see above) but smaller, and fore wings lacking pale area along costa. M. orbifera also has a pale mark on apex, but is almost three times the size of affabilis.
DIST: Puerto Rico and Virgin Islands.
GUANA: 22 specimens, 1987, 1989, 1990.
HOST: Unknown.
COM: Despite the good color illustration presented by Möschler (1890), who described it from Puerto Rico, Hampson (1910) treated this species as an unrecognized taxon in the Erastriinae [=Acontiinae], where it has remained. One of the reasons for this situation is because no material except for the types, which are supposed to be in MNHU, Berlin, has been available to subsequent authors who studied the New World noctuid fauna. No material of this species was found in the BMNH and USNM; for this reason vouchers from the series studied here have been deposited there.

This species does not belong in Acontiinae, but is related to some species currently placed in Elaphria Hübner. However, we prefer not to synonymize Anateinoma under Elaphria as the group needs revision. The male genitalia are illustrated in Figs. 10, 11.

44. Micrathetis triplex (Walker, 1857)
(Figs. 39, 40)

ID: Small, 1.5-2.2 cm wing span, slightly dimorphic, variable in color. Males have pale fore wings speckled with darker small dots, termen dark brown and with a conspicuous dark brown dot at end of cell. Females are darker. Hind wings whitish slightly bordered with dark gray. Easily recognized by the dot on cell and by the two rows of small blackish dots forming two arches, almost parallel to each other, from costa to dorsum.
DIST: Throughout the New World.
GUANA: 14 specimens, 1987, 1989, 1990.
HOST: No foodplant has been reported.

Agaristinae
45. Caularis undulans Walker, [1858]
(Fig. 47)

ID: Undoubtedly the most attractive noctuid on the island. Forewings white bordered and marked olive; hind wings golden yellow bordered reddish-brown with a lunular blackish mark on tornus.
DIST: Hispaniola, Jamaica, Puerto Rican Bank (Kiriakoff, 1976).
GUANA: 9 specimens, 1989.
HOST: No hosts are known for any of the four species in this genus.
COM: Male genitalia illustrated by Kiriakoff (1976).

Bagisarinae
46. Bagisara repanda (Fabricius, 1793)
(Fig. 41)

ID: Small, 2-2.5 cm wing span, pale yellow, dusted gray. Easily identified by the three pale lines crossing the fore wings, more or less equidistant and parallel to each other. These lines are bent basad near costa.
DIST: Widespread from Southeast United States to Paraguay, including Galapagos (Hayes, 1975; Ferguson, 1997).
GUANA: 4 specimens, 1987, 1989.
HOST: Sida glomerata Cav. (Malvaceae) (Hayes, 1975).
COM: Very common on disturbed areas where malvaceous weeds often occur.

Acontiinae
47. Amyna axis (Guenée, 1852)
(Fig. 42)

ID: Small, obscure, fuscous species, easily confused with some small Condica species. Males are easily distinguished from those by the presence of a round, semitranslucent area near base of fore wings.
DIST: Pantropical, including Tahiti and Hawaii.
GUANA: 2 specimens, 1989.
HOST: Chenopodium (Chenopodiaceae), Cardiospermum (Sapindaceae), Parasponia (Ulmaceae), and Amaranthus (Amaranthaceae) (Ferguson, 1991).
COM: The large distribution and obscure pattern have contributed to long synonymy: it was described 18 times (Poole, 1989). Frequently referred to in the literature as A. octo (Guenée), a synonym based on the priority of names established by Nielsen et al. (1996: note 690).

48. Ponometia exigua (Fabricius, 1793)
(Figs. 43-45)

ID: Small, variable, sexually dichromatic species; males are pale yellow with fore wings crossed with diffuse, sinuate olivaceous bands. Females fore wings dark fuscous with a wide, contrasting, pale fascia along costa. In some females this pattern is less contrasting.
DIST: Southern United States, throughout the Antilles, south to Brazil, including Galapagos.
GUANA: 9 specimens, 1989, 1990.
HOST: Waltheria ovata Cav. (Sterculiaceae) (Hayes, 1975).
COM: Commonly referred to in the literature by its junior synonym P. indubitans (Walker).

49. Cydosia nobilitella (Cramer, 1779)
(Fig. 46)

ID: Small showy moth; one of the most attractive noctuids on the island. Forewings present a reticulated pattern with white areas enclosed by dark bluish metallic gray and red lines. Hind wings semitranslucent white in males, dark gray in females.
DIST: Southern United States, throughout Antilles, south to Argentina.
GUANA: 1 specimen, 1984.
HOST: Hampson (1910) mentioned "?Spigelia anthelmia L." (Loganiaceae), following Cockerell (1897). No species of this plant family known from the island (G. Proctor, pers. comm.), although the species occurs on other Virgin Islands (Acevedo-Rodriguez, 1996).
COM: Pattern resembles some species of Atteva (Yponomeutidae) and specimens are often found mixed in collections. Cockerell (1897) and Dyar (1897) described the larvae.

50. Tripudia quadrifera (Zeller, 1874)
(Figs. 153, 154)

ID: The smallest noctuid on the island, 0.7-1.2 cm wing span; resembling a small Olethreutinae (Tortricidae), and C. metaspilaris (see below). Dark gray; fore wings with conspicuous quadrate mark on middle of dorsum.
DIST: Southern United States, throughout the Antilles, south to Brazil.
GUANA: 22 specimens, 1989, 1990.
HOST: Unknown.

51. Tripudia balteata Smith, 1900
(Fig. 155)

ID: Small, on average slightly larger than T. quadrifera. Dark gray. Easily identified by the broad, oblique, yellowish band on fore wings.
DIST: Southern United States, Antilles, south to Brazil.
GUANA: 16 specimens, 1987, 1989, 1990.
HOST. Unknown.

52. Ommatochila mundula (Zeller, 1872)
(Fig. 156)

ID: Small, 1.5-2 cm wing span, dark gray, resembling some Olethreutinae species (Tortricidae). Fore wings are divided across the middle by a pale, almost straight line, the basal half much darker than outer half.
DIST: Southern United States, Antilles, south to Argentina.
GUANA: 14 specimens, 1986, 1989, 1990.
HOST: Unknown.

53. Cobubatha metaspilaris Walker, 1863
(Fig. 157)

ID: Small, 1.5 cm wing span, gray; similar to, but larger than T. quadrifera. In the latter the mark on dorsum is quadrate whereas in metaspilaris it is trapezoidal.
DIST: Antilles.
GUANA: 3 specimens, 1990.
HOST: Unknown.

54. Eumicremma minima (Guenée, 1852)
(Fig. 158)

ID: Very small, 1.2-1.5 cm wing span; fore wings pale crossed with olive and dark olive waiving bands, and with some very small, black dots along termen, the most conspicuous the one near apex and the other near tornus. In resting posture looks like some of the cochylid species (Tortricidae).
DIST: Southern United States, Antilles, south to Argentina.
GUANA: 3 specimens, 1987.
HOST: Gnaphalium (Asteraceae).

54. Eublemma rectum (Guenée, 1852)
(Fig. 161)

ID: Small, 1.5 cm wing span, pale yellow; fore wings clouded with red brown with oblique pale fascia from middle of dorsum to near apex.
DIST: Southern United States, throughout the Antilles, south to Argentina, including Galapagos and Bermuda.
GUANA: 3 specimens, 1989.
HOST: Ipomoea and Convolvulus (Convolvulaceae) (Forbes, 1954) [as E. obliqualis (Fabricius), a homonym].

55. Spragueia margana (Fabricius, 1794)
(Figs. 159, 160)

ID: The smallest of the two Spragueia species on the island; also dimorphic. Similar to S. perstructana (see below). Males easily distinguished from the latter by the absence of orange, by the pale costa, and by the olivaceous shades and marks on fore wings; females by the olivaceous thorax, which is edged pale yellow in S. perstructana.

DIST: Southern United States, throughout the New World tropics, including Galapagos.
GUANA: 1 specimen, 1987.
HOST: Abutilon and Sida (Malvaceae) (Hayes, 1975).

56. Spragueia perstructana (Walker, 1865)

ID: Very similar and slightly larger than former (see above), and also dimorphic.
DIST: Southern United States, Antilles, south to Costa Rica.
GUANA: 1 specimen, 1989.
HOST: Unknown.
COM: Illustrated in color in Kimball (1965: Pl. IV, figs. 31, 37).

57. Thioptera auriferum (Walker, [1858])
(Fig. 162)

ID: Small, 1.5-1.8 cm wing span, yellow; fore wings usually with two very small black dots, and ill defined reddish line beyond the cell, from costa to dorsum, termen edged with laden gray.
DIST: Southern United States, throughout Antilles, south to Brazil.
GUANA: 4 specimens, 1989, 1990.
HOST: Unknown, however Kimball (1965) gives Digitaria ischaemum [Syntherisma impomoea] (Poaceae), as the food plant for T. nigrofimbria, a closely related species.

Sarrothripinae
58. Characoma nilotica (Rogenhofer, 1882)
(Figs. 163-165)

ID: Small, 1-1.2 cm wing span, highly variable, gray species.
DIST: Described from Egypt, hence its name, now Pantropical, including Galapagos, Bermuda, and the Pacific Islands.
HOST: White mangrove, Laguncularia racemosa (L.) C.F. Gaertn. (Combretaceae) (Hayes, 1975); willow, almond, azalea, and "black olive" (Ferguson, 1991).
GUANA: 25 specimens, 1985, 1986, 1990.
COM: Rests flat, looking like some tortricids.

59. Collomena filifera (Walker, 1857)
(Figs. 49, 50)

ID: Medium sized gray species, similar to female S. frugiperda. Distinguished by the whitish diffused band across the subterminal area of fore wings and by the entirely whitish, semitransluscent hind wings (narrowly bordered gray in females).
DIST: Florida throughout the Antilles, south to Brazil.
GUANA: 4 specimens, 1989, 1990.
HOST: Unknown.

60. Motya abseuzalis Walker, 1859
(Fig. 48)

ID: Slightly smaller than C. filifera; whitish gray. Easily recognized by the two, almost parallel, rows of small, black dots along termen, with the one near tornus conspicuously larger. The abdomen of males show two paired black dots dorsally, near apex. Hind wings semitransluscent white, bordered gray.
DIST: Florida, throughout the Antilles, south to Brazil.
GUANA: 1 specimen, 1989.
HOST: Unknown.

Euteliinae

61. Paectes obrotunda (Guenée, 1852)

(Figs. 51, 52)

ID: Medium sized, gray, irrorated brown; males have basal half of antennae strongly pectinate, and long slim abdomen; females have filiform antennae and short stout abdomen. Fore wings with a conspicuous pale lunular mark near base, delimited externally by a narrow, double line.
DIST: Southern United States, throughout Antilles, south to Paraguay.
GUANA: 64 specimens, 1984, 1987, 1988, 1989, 1990.
HOST: Unknown, however, its larvae should be searched on Bursera simaruba (L.) Sarg. (Simarubaceae), as a related species, P. arcigera (Guenée), was reared on B. graveolens (Kunth) Triana & Planch. in Galapagos (Hayes, 1975).

Plusiinae

62. Pseudoplusia includens (Walker, [1858])

(Fig. 53)

ID: Medium sized, grayish brown with bronze luster. Recognized by the small silver markings near center of fore wings.
DIST: United States to northern Chile and Argentina, including Galapagos and Bermuda (Lafontaine & Poole, 1991: 50).
GUANA: 2 specimens, 1989.
HOST: Polyphagous; Ferguson et al. (1991) lists plants belonging to 14 families as foodplants. Can be a minor pest of beans, soy beans, and other leguminous crops.
COM: Generally referred to in the literature as P. oo (Cramer), an homonym. Other species belonging to this subfamily, such as Trichoplusia ni (Hübner) and Argyrogramma verruca (Fabricius) are likely to be collected on the island in the future. These also bear silver marks on the fore wings.

Catocalinae

63. Ptichodis immunis (Guenée, 1852)

(Figs. 54, 55)
ID: Medium sized, 2.5-3 cm wing span, pale species. Fore wings crossed with ill defined olivaceous lines, two of them highly contrasting: the antemedial and the postmedial, both bordered internally with lemon yellow.
DIST: Mexico, throughout the Antilles to Brazil.
GUANA: 6 specimens, 1987, 1989, 1990.
HOST: Unknown.

64. Mocis latipes (Guenée, 1852)

(Fig. 58)
ID: Medium sized, 3.5-4 cm wing span, broad winged, dark species. Highly variable in color and pattern. Ground color varies from pale brownish through fuscous to reddish brown. Females tend to have pattern less contrasting than males, and the paler forms could be easily confused with the darker forms of female M. disseverans, a neotropical species recorded from the Greater Antilles. Smaller than M. repanda (see below).
DIST: Southern United States, throughout the Antilles, south to Argentina, including Galapagos and Bermuda.
GUANA: 1 specimen, 1989.
HOST: Several species of grasses, sometimes a pest of grazing land.
COM: The males of the species belonging to this genus can be easily distinguished from other noctuids by the thickly hairy hind legs. Generally referred to in the literature as M. repanda, a different species (see below).

65. Mocis antillesia Hampson, 1913
(Figs. 56, 57)

ID: Same size and easily confused with the former. Ground color pale to pale yellow. Clothing of hind legs usually yellowish in this whereas grayish in M. latipes. Smaller than M. repanda (see below).
DIST: Lesser Antilles, Bahamas.
GUANA: 4 specimens, 1989, 1990.
HOST: Unknown.

66. Mocis repanda (Fabricius, 1794)
(Figs. 59, 60)

ID: Larger than the former two species in the genus, 4.5-5.5 cm wing span. Smaller specimen larger than larger specimens of both M. latipes and M. antillesia. Easily distinguished from the others by shape of postmedial lines in both wings: in the fore wings it is bent inwards after the angle near costa, and fades away before tornus whereas in the former two it is straight and reaches tornus; in the hind wings it is strongly angled outwards before tornus whereas in the others it is straight.
DIST: Antilles and Guatemala.
GUANA: 2 specimens, 1987, 1990.
HOST: Mucuna deeringiana (Bort) Merr. (Fabaceae) [as M. megas] (Martorell, 1976).
COM: Generally known in the literature as M. megas (Guenée), a junior synonym (Poole, 1989). Berio (1953) clarified the status of M. repanda and illustrated the male genitalia.

67. Ophisma tropicalis Guenée, 1852
(Fig. 61)

ID: Same size as M. repanda, but with stouter body. Extremely variable in pattern and color. Easily recognized by the small, conspicuous white dot on base of fore wings close to thorax.
DIST: Southern United States, throughout the Antilles, south to Argentina.
GUANA: 2 specimens, 1987.
HOST: Cupania americana L. (Sapindaceae) (Martorell, 1976).

Ophiderinae
68. Azeta versicolor (Fabricius, 1794)
(Figs. 62, 63)

ID: Medium sized polymorphic species; groundcolor varies from ferrugineous to dark grayish brown. Easily recognized by the pointed fore wings and by the transverse pale dash at middle of fore wings costa.
DIST: Throughout the New world tropics from Florida to Argentina.
GUANA: 23 specimens, 1987, 1989, 1990.
HOST: Canavalia (Fabaceae) (Kimball, 1965).
COM: Commonly referred to in the literature by its junior synonym A. repugnalis (Hübner).

69. Metallata absumens (Walker, 1862)
(Figs. 64-66)

ID: Medium sized, highly variable species. Ground color from reddish brown to gray. Similar to E. cacata but readily separated by the dark brown head and anterior border of thorax, by the nearly rounded border of hind wings, and by the filiform antennae in both sexes. Some specimens bear a black reniform mark at the end of fore wings cell.

DIST: Southern United States, throughout the Antilles, south to Brazil, including Galapagos.
GUANA: 12 specimens, 1987, 1989, 1990.
HOST: Unknown.

70. Plusiodonta thomae (Guenée, 1852)
(Fig. 67)

ID: Medium sized dark brown species with some shinning golden areas on fore wings. Recognized by the single dentate expansion on middle of dorsum of fore wings.
DIST: Described from St. Thomas, considered endemic to the Antilles.
GUANA: 4 specimens, 1987, 1989.
HOST: Unknown.
COM: It is very likely that the continental population, P. clavifera (Walker), belongs to the same species. There is some degree of variation in both the Antillean and the continental populations, and specimens from both regions intergrade into each other. The latter has been reported to Galapagos (Hayes, 1975).

71. Syllectra erycata (Cramer, 1780)
(Fig. 68)

ID: Medium sized reddish ferrugineous species. Fore wings with three transverse lines, angled basad near costa, and with one or two small, round pale dots on outer side of postmedial line. Males also easily distinguished by unique shape of antennae, which are uncommonly thick throughout its length except tip.
DIST: Florida, throughout the Antilles, south to Brazil.
GUANA: 3 specimens, 1986, 1987.
HOST: Unknown.

72. Litoprosopus puncticosta Hampson, 1926
(Fig. 69)

ID: Large, velvet fuscous species. Its narrow wings and stout body resemble a small sphingid. Readily distinguished from other noctuids of same size on the island by the orbicular black mark at lower edge of hind wings.
DIST: Haiti, Virgin Islands.
GUANA: 1 specimen, 1989.
HOST: Unknown, however, a close relative, L. futilis (Grote & Robinson), has been found boring into the flower stalks of Sabal and Serenoa (Arecaceae) (Ferguson et al., 1991).

73. Diphthera festiva (Fabricius, 1775)
(Fig. 70)

ID: Medium sized, bright yellow, with an elaborate pattern of bluish gray lines and three parallel rows of dots parallel to external margin. Hind wings dark gray with pale cilia.
DIST: Widespread throughout the New World tropics, from Florida to Argentina.
GUANA: 2 specimens, 1987, 1989.
HOST: Casuarina equisetifolia L. (Casuarinaceae), Corchorus hirsutus L. (Tiliaceae), Schrankia portoricensis Urb. (Fabaceae), and Waltheria indica L. (Sterculiaceae) (Martorell, 1976). Bright colored larvae reared in Brazil on Sida sp. (Malvaceae) (VOB), a common weed in disturbed areas on the island.
COM: Commonly found in the literature under the synonym Noropsis hieroglyphica (Cramer). Its pattern may be aposematic. One male was tossed towards a gray kingbird, Tyrannus dominicensis (Gmelin), who caught it in the air, returned to its perch, tried to swallow the moth, then spit it out and cleaned its beak against the branch (Becker, personal observation).

74. Gonodonta bidens Geyer, 1832
(Fig. 71)

ID: Showy medium sized moth, cannot be confused with any other in the island. Fore wings velvet dark brown; basal and postmedial areas paler, crossed with waving dark and reddish brown lines. Hind wings dark gray with a bright elongate yellow area at middle. Head conspicuously white.
DIST: Florida, throughout the Antilles, south to Argentina.
GUANA: 1 specimen, 1990.
HOST: Guarea trichilioides L. (Meliaceae), Cupania (Sapindaceae) and Diospyrus (Ebenaceae) (Todd, 1972). Adults have been reported causing damage to oranges in northern Mexico by piercing ripening fruits (Todd, 1959).

75. Melipotis acontioides (Guenée)
(Fig. 72)

ID: Medium to large sized, 3.5-5 cm wing span, light gray species. Hind wings semitransluscent white with a broad gray band along external margin not reaching lower angle; just before lower angle there is, often, a small gray dot.
DIST: Florida, Antilles, south to Brazil, including Galapagos.
GUANA: 4 specimens, 1989.
HOST: Delonix regia (Bojer ex Hook.) Raf. (royal poinciana) and Parkinsonia aculeata L. (Fabaceae) (Martorell, 1976).
COM: Except for M. acontioides, the other species of the genus are very difficult to identify as they look very similar to each other and complicated by the high degree of variation among specimens of one same species. Most Melipotis species recorded for Guana also occur in Southern United States and were reviewed by Richards (1939), and illustrated in color by Bordelon and Knudsen (1999).
The species of this genus are often the most abundant moths coming to light in dry areas of the New World tropics. One of the reasons is that they feed on various leguminous plants such as Acacia, Cassia, Prosopis, and other species that are abundant in such habitats. During certain collecting trips, especially immediately after the beginning of rain season, they came to light in such great numbers that the entire sheet were covered, making it impossible to collect any other moths. In some occasions the lights had to be disconnected and collecting discontinued (Becker, personal observation).

76. Melipotis fasciolaris (Hübner, [1831])
(Figs. 73, 74)

ID: Medium to large sized, 3-4.5 cm wing span, variable species. The most variable species of the genus occurring on the island. In some specimens the pattern is little contrasting while in others the contrast is strong. Most specimens can be easily distinguished from those of other species on the island by the antemedial oblique, pale fascia of fore wings. In this the fascia is straight and with the same width throughout. In some specimens the area basad to this fascia is pale olivaceous.
DIST: Southern United States, Antilles, south to Uruguay.
GUANA: 7 specimens, 1989.
HOST: Unknown, however, "Numerous caterpillars hiding under loose bark of trees of Guaiacum officinale L. (Zygophyllaceae), presumably after feeding at night on the foliage" (Wolcott, 1951). This observation should be checked as this tree generally grows together with many leguminous species, known as food plants to other species of Melipotis.

77. Melipotis contorta (Guenée, 1852)
(Fig. 75)

ID: Same size as larger specimens of former two, but not as variable. Very similar to the following with which it shares the white basal area of hind wings, and pale head and dorsal area of thorax. Easily separated from M. famelica by the pale irregular area at the end of cell. In the latter this is nearly rounded whereas in contorta its lower end extends widely towards the external margin.
DIST: Florida, Antilles.
GUANA: 4 specimens, 1989, 1990.
HOST: Unknown.

78. Melipotis famelica (Guenée, 1852)
(Fig. 76)

ID: Very similar to the former either in size and pattern. Color pattern not highly variable but sexually dimorphic. Females have pattern less contrasting than males. Some males have antemedial fascia tinged reddish brown.
DIST: Southern United States, Antilles, south to Venezuela, including Bermuda (Ferguson et al., 1991).
GUANA: 9 specimens, 1987, 1989, 1990.
HOST: Leucaena latisiliqua (L.) Gillis & Stearn (Fabaceae) (Martorell, 1976).

79. Melipotis ochrodes (Guenée, 1852)
(Fig. 77, 78)

ID: Easily confused with M. indomita, a neotropical species also recorded from the Greater Antilles, but not collected on Guana. Highly variable. Basal area of hind wings semitransluscent gray, not whitish as in contorta or famelica, or almost dark gray as in januaris.
DIST: Antilles, Mexico, south to Brazil.
GUANA: 1 specimen, 1989.
HOST: Prosopis juliflora (Sw.) DC. and Schrankia portoricensis Urb. (Fabaceae) (Martorell, 1976).
COM: The specimen illustrated here, identical to the one collected on Guana, matches the series at BMNH identified as M. ochrodes (type specimen in MNHN, Paris, not examined). It could represent only a smaller form of M. indomita.

80. Melipotis januaris (Guenée, 1852)
(Figs. 79, 80)

ID: On average slightly smaller than all other Melipotis species on the island; sexually dimorphic. Males have fore wings with very contrasting, dark brown pattern; females little contrasting, reddish brown. Easily distinguished from all other species in the island by almost entirely dark gray hind wings.
DIST: Southern United States, throughout Antilles, south to the Guianas and Colombia.
GUANA: 1 specimen, 1987.
HOST: Inga laurina (Sw.) Willd. [as I. fagifolia] (Fabaceae) (Martorell, 1976).

81. Ascalapha odorata (Linnaeus, 1758)
(Witch moth, black witch)

ID: Readily distinguished by very large size and broad wings showing bluish hue. Sexually dimorphic: males blackish gray, females lighter in color, with more contrasting pattern, and with three close, parallel, zig-zag, white lines crossing the wings.
DIST: Originally South American, now Pantropical.
GUANA: 3 specimens, 1982 (J. Lazell), 1988, 1989.
HOST: Various leguminous threes, including Acacia, Cassia and Piptadenia (Hayward, 1969, Hayes, 1975). Comstock (1936), Schreiter (1936) and Bourquin (1947) describe its life history and immature stages.

COM: Illustrated in several works, including Covell (1984), Ferguson et al. (1991), Hayes (1975), and Kimball (1965).

82. Epidromia lienaris (Hubner, 1823)
(Fig. 81)

ID: Large, 5 cm wing span, highly variable gray fuscous species: fore wings with conspicuous reniform black mark at middle and a postmedial, almost straight, pale line.
DIST: New World tropics.
GUANA: 1 specimen, 1990.
HOST: The larvae (as E. pannosa Guenée) were found on Psidium longipes (O. Berg) McVaugh (Myrtaceae), and were fed in the laboratory on P. guayava L., Eugenia axillaris (Sw.) Willd. (Myrtaceae) and on Metopium toxiferum (L.) Krug & Urb. and Rhus copallina L. (Anacardiaceae) (Dickel, 1991).
COM: This is a widespread and highly polymorphic species, described more than 10 times (Becker, 2001), and is commonly known in the literature as E. zetophora Guenée (Hayes, 1975) and E. pannosa (Solis, 1986, Dickel, 1991).

83. Manbuta pyraliformis (Walker, 1858)
(Fig. 86)

ID: Medium sized gray species. Fore wings speckled with small black dots and with an oblique postmedial yellowish fascia; basad area of this fascia light gray, distal area dark gray. Males have pectinate antennae.
DIST: Florida and Antilles.
GUANA: 1 specimen, 1986.
HOST: Unknown.
COM: Poole (1989) listed this species under Epidromia Guenée, however, its genitalia and pectinate antennae are similar to those species currently in Manbuta Walker (Becker, 2001).

84. Ephyrodes cacata Guenée, 1852
(Figs. 82, 83)

ID: Same size and resembling M. absumens (see below). Variable in color, from reddish brown to gray, mottled with black scales. Easily identified by the strongly angled termen of both wings, especially on the hind wing forming a small tail. Male antennae strongly pectinate, female filiform.
DIST: Southern United States, throughout the Antilles, south to Colombia.
GUANA: 5 specimens, 1989.
HOST: Sesbania grandiflora (L.) Pers. (Fabaceae) (Brunner et al., 1975).

85. Concana mundissima Walker, [1858]
(Fig. 84)

ID: Medium sized silky shining gray species; fore wings have fine, broken, transverse lines and a dark dot near middle, closer to dorsum. Hind wings semitransluscent white, edged gray.
DIST: Florida, throughout the Antilles, south to Brazil.
GUANA: 7 specimens, 1989, 1990.
HOST: Unknown.

86. Massala asema Hampson, 1926
(Fig. 85)

ID: Medium sized, 3.5 cm wing span, stout bodied, pale brownish species. Wings shaded brown with ill defined, irregular brownish lines, nearly parallel to each other, from costa to dorsum.
DIST: Antilles.
GUANA: 2 specimens, 1989.
HOST: Unknown.

87. Lesmone formularis (Geyer, 1837)
(Figs. 90, 91)

ID: Medium sized gray, sexually dimorphic species; males have two wide ill-defined dark gray bands across the wings; in spread specimens the bands are continuous, crossing both fore and hind wings. Females do not show these bands, however, the edge of the postmedial band in the hind wings is replaced by a straight yellow fascia running from apex to tornus.
DIST: Southern United States, throughout the New World tropics, including Galapagos.
GUANA: 3 specimens, 1987, 1989.
HOST: Cassia and Mimosa (Fabaceae).

88. Lesmone hinna (Geyer, 1837)
(Figs. 87-89)

ID: Same size and similar to the former. Easily distinguished by the conspicuous round, pale dot on the cell of fore wings.
DIST: Southern United States, throughout the Antilles, south to Brazil.
GUANA: 5 specimens, 1989.
HOST: Unknown.

89. Baniana relapsa (Walker, 1858)
(Figs. 92, 93)

ID: Small to medium sized pale ochreous, sexually dichromatic species. Male fore wings have a conspicuous triangular black patch near base, close to dorsum; postmedial area black, fading gradually towards termen. Females lack the triangular patch and have the distal area lighter gray, resembling P. immunis, but readily distinguished by the dark brown anterior edge of thorax.
DIST: Restricted to the Antilles.
GUANA: 18 specimens, 1986, 1987, 1989, 1990.
HOST: Unknown.

90. Eulepidotis addens (Walker, 1858)
(Fig. 95)

ID: Small, grayish brown; fore wings with three straight lines across, the medial and postmedial double, enclosing a conspicuous ochreus band. Hind wings with diffuse orbicular mark followed by a short tail on the lower part of external margin.
DIST: Antilles.
GUANA: 12 specimens, 1987, 1989, 1990.
HOST: Inga vera Willd. (Fabaceae) (Martorell, 1976).

91. Eulepidotis modestula (Herrich-Schäffer, 1869)
(Fig. 94)

ID: Small, white tinged yellow species. It also has lines crossing the fore wings and a short tail on the hind wings similar to those of former species.
DIST: Antilles.
GUANA: 1 specimen, 1989.

HOST: Ceiba pentandra (L.) Gaertn. (Bombacaceae) (Martorell, 1976).

92. Toxonprucha diffundens (Walker, 1858)
(Fig. 96)

ID: Small sized, 1.8-2.2 cm wing span, gray species. Highly variable; most specimens have pattern as in K. progenies (see above).
DIST: Antilles, south to Brazil.
GUANA: 1 specimen, 1990.
HOST: Unknown, however, other species in the genus have been reared on Acacia (Fabaceae) (Crumb, 1956).

93. Kakopoda progenies (Guenée, 1852)
(Fig. 97)

ID: Medium sized, 2.5-3 cm wing span, broad winged, dark gray moth. Wings crossed with many fine waving lines alternating black and pale. Very similar to and easily confused with T. diffundens (see below), but readily separated by size. The smaller specimens of this species are always larger than the largest of the latter. Males are also easily separated from T. diffundens by the pale brush at the tip of abdomen.
DIST: Florida, throughout the Antilles to Brazil.
GUANA: 4 specimens, 1987, 1989.
HOST: Unknown.
COM: There is no reason to regard K. cincta Smith, 1900, syn. n., described from Florida, as distinct.

94. Parachabora abydas (Herrich-Schäffer, [1869])
(Fig. 98)

ID: Small to medium sized, cupreous brown species; hind wings semitransluscent white, bordered with a wide, diffuse gray area, and veins contrastingly gray.
DIST: Mexico, throughout the Antilles, south to Brazil.
GUANA: 3 specimens, 1988, 1989.
HOST: Unknown.

95. Cecharismena abarusalis (Walker, 1859)
(Fig. 99)

ID: Small brown species with fore wings tinged copper and ferrugineous; apex of fore wings pointed. Very similar to the following, but easily separated by the oblique straight medial line.
DIST: Florida throughout Antilles south to Brazil.
GUANA: 9 specimens, 1987, 1989.
HOST: Unknown, however C. nectarea Möschler has been reared in Puerto Rico on Caperonia palustris (L.) A. St.-Hil. (Euphorbiaceae) (Schaus, 1940).

96. Cecharismena cara Möschler, 1890
(Fig. 100)

ID: Same size and easily confused with the former. Fore wings with violet hue. Readily distinguished from the former by the medial oblique line curved in this and straight in the former.
DIST: Antilles.
GUANA: 2 specimens, 1989.
HOST: Unknown (see C. abarusalis).

97. Glympis eubolialis (Walker, [1866])
(Fig. 101)

ID: Small gray species with fore wings crossed, in the middle, with ill defined, straight dark brown band; area distad to this band usually darker than basal area. Shape, size and color makes it easily confused with Bleptina species (below). Easily distinguished from Bleptina by the porrect labial palpi, which are long, upturned in those species (see below).
DIST: Antilles.
GUANA: 22 specimens, 1989, 1990
HOST: Unknown, however, the larvae of G. concors were found feeding on Sesbania grandiflora (L.) Pers. (Fabaceae) in Puerto Rico (Martorell, 1976).

Herminiinae
98. Drepanopalpia lunifera (Butler, 1878), comb. n.
(Figs. 102, 103)

ID: Small to medium sized, 1.5-2 cm wing span, dimorphic dark fuscous species. Males have very long labial palpi thickly covered with long scales, reflexed over the head back to the posterior margin of thorax. Females have long, porrect palpi. Forewings in males with a reniform, pale mark at end of cell; in females this mark is reduced to small dot.
DIST: Antilles.
GUANA: 9 specimens, 1987, 1989.
HOST: Unknown.
COM: The series in VOB, including specimens from Guana Island, Tortola, Puerto Rico and Cuba, was compared with material in BMNH. The males match the type of D. polycyma Hampson, 1898, syn. n., and the females match the type of Hypena lunifera Butler, 1878. D. polycyma is also curated in BMNH as a synonym of Mastigophorus latipennis Herrich-Schäffer. There is no specimen of latipennis in Coll. Gundlach (IES, Havana) where the type material of the Cuban species described by Herrich-Schäffer is supposed to be deposited. It might be possible that some material is in MNHU, Berlin. After examination of the type(s) it could be possible that both lunifera and polycyma become junior synonyms of latipennis.

99. Lascoria orneodalis (Guenée, 1854)
(Figs. 104, 105)

ID: Small to medium sized, 1.5-2 cm wing span, dark fuscous species, resembling the former. Males also have labial palpi as the former species, but the fore wings have a strong indentation at middle of external margin. Females have long upcurved palpi as in Bleptina.
DIST: Florida, Antilles.
GUANA: 3 specimens, 1987.
HOST: Tomato leaves (Solanaceae) (Martorell, 1976).

100. Bleptina hydrillalis Guenée, 1854
(Fig. 108)

ID: Dark brown, 1.8-2.0 cm. Fore wings crossed by three, well defined, pale lines: a straight line near base, and two sinuate lines, one after the reniform mark on cell, the other before external margin. Reniform mark also pale, but black in some specimens.
DIST: Southern United States, Central America, Antilles.
GUANA: 34 specimens, 1986, 1989.
HOST: Unknown.

101. Bleptina caradrinalis Guenée, 1854
(Figs. 106, 107)

ID: About same size as the former, pale, variable. Dark band across fore wings, in those specimens which bears it, closer to the middle
DIST: Southern United States, throughout the Antilles, South to Brazil
GUANA: 6 specimens, 1989.
HOST: Dead leaves (Kimball, 1965).

102. Bleptina menalcasalis Walker, [1859]
(Figs. 109, 110)
ID: Medium sized, 2.2-2.7 cm wing span, pale species. Forewings diffusely crossed with ill defined, irregular lines. Easily distinguished from other noctuids of same size by the long, upcurved labial palpi.
DIST: Antilles, south to Venezuela.
GUANA: 27 specimens, 1986, 1987, 1989, 1990.
HOST: Unknown, but likely dead leaves (see B. caradrinalis).

103. Bleptina aracalis (Hampson, 1901)
(Figs. 167, 168)

ID: Very small, 1-1.3 cm wing span, variable, fuscous to dark fuscous species. Fore wings often with a dark gray fascia on basal fourth; area basad to this band paler than rest of wings. Easily distinguished from other small species on the island by the very long upcurved labial palpi and by three very small, round, pale dots on fore wings, the first just outside the basal band and the two others close together at end of cell.
DIST: Antilles. The first author collected one male and one female in Mexico: Tamaulipas, El Encino. Recently discovered in Florida (Dickel, 1991).
GUANA: 12 specimens, 1987, 1990.
HOST: Unknown (see previous species).

Hypeninae
104. Hypena lividalis (Hübner, 1790)
(Fig. 111)

ID: Small, gray; fore wings with postmedial line straight, white; area basad to this line olive, distad gray.
DIST: South Palearctic, Pantropical.
GUANA: 2 specimens, 1989, 1990.
HOST: Urtica and Parietaria spp. (Lödl, 1994: 502).
COM: In a revision of the genus, Lödl (1994) listed six synonyms under lividalis, two of them originally described from material collected in the Antilles.

105. Hypena minualis (Guenée, 1854)
(Fig. 166)

ID: Small dark gray species with little contrasting markings. Forewings show a slightly paler basal area, separated from the external dark area by an ill defined oblique, dark gray line from near base of costa to middle of dorsum; they also have a fainted dash near apex. The palpi resemble those of female D. polycyma, but readily separated by the absence of the pale dot on cell.
DIST: Antilles, south to Brazil.
GUANA: 3 specimens, 1989.
HOST: Sida rhombifolia L. (Malvaceae) (Ferguson et al., 1991).

ARCTIIDAE

Arctiinae
106. Hypercompe simplex (Walker, 1855)
(Figs. 112, 114)

ID: Large, white; fore wings with outer half translucent, basal half with a series of annulate black edged spots. Abdomen orange with subdorsal pairs of dark bluish dots. Females much larger than males; spots on the abdomen white.
GUANA: 6 specimens, 1987, 1989.
DIST: Puerto Rico, Virgin Islands and Lesser Antilles.
HOST: Martorell (1976) lists over a dozen hostplants, including Cedrela (Meliaceae), Cissus (Vitaceae), Erechtotes (Compositae), Erythrina (Fabaceae), Ipomaea (Convolvulaceae), tomato, banana, beans, guava, eggplant and Solanum torvum Sw. (Solanaceae).
COM: Commonly found in the literature, including in Martorell (1976), as Ecpantheria icasia (Cramer), a similar species from continental South America.

107. Calidota strigosa (Walker, 1855)
(Fig. 115)

ID: Large gray moth with pink abdomen. Forewings with veins darker than ground color, shortly interrupted with pale. Cannot be confused with any other moth from the island.
DIST: Antilles and Southern United States.
GUANA: 28 specimens, 1984, 1987, 1989, 1990.
HOST: Dyar (1901: 270) reared it on Guettarda elliptica Sw. (Rubiaceae) and described its larvae; Martorell (1976) lists the same plant as its host in Puerto Rico.
COM: Franclemont (1983) and Watson & Goodger (1986) resurrected, respectively, laqueata (Edwards, 1887) (type-locality: USA) and cubensis (Grote, [1866]) (type-locality: Cuba) from the synonymy of strigosa. We believe they are only geographical forms of the same species.

In the resting position, the moth looks cryptic but when touched it opens the wings exposing the bright pink abdomen that seems to be aposematic. A specimen was picked from the collecting sheet by a pearly-eyed thrasher, Margarops fuscatus (Vieillot), and rejected. The same specimen was picked from the ground and placed back on the wall where the bird often perched. The same bird picked up the moth again and then dropped it (Becker, personal observation).

108. Eupseudosoma involutum (Sepp, [1855])
(Fig. 116)

ID: Medium sized white moth, with red abdomen. Cannot be confused with any other species in the island.
DIST: Southern United States, throughout Antilles, south to Argentina.
GUANA: 4 specimens, 1987.
HOST: Guava (Psidium guineense Sw.), Eugenia, Eucalyptus and other Myrtaceae.

109. Utetheisa ornatrix (Linnaeus, 1758)
(Fig. 117)

ID: Medium sized, variable white moth. Most specimens have fore wings white tinged pink; pink costa interrupted regularly with dark gray dots. In other specimens most of the white is replaced by pink and the wing is crossed with transverse rows of dark gray dots. The proportion of gray in the hind wings also varies; in some specimens it is restricted to the borders, while in others it covers most of the area.
DIST: Southern United States, throughout the Antilles, south to Argentina.
GUANA: 5 specimens, 1984, 1988, 1989, 1990.
HOST: Various species of Crotalaria (Fabaceae).

COM: Commonly found flying during the day in open, disturbed areas where its host plants often grow. Pease (1973) discussed the variation of this moth in the Virgin Islands.

110. Utetheisa pulchella (Linnaeus, 1758)
(Fig. 118)

ID: Easily confused with the doted form of U. ornatrix (see above): easily separated by the dots on dorsum of thorax. U. ornatrix has three pairs; pulchella has only three dots.
DIST: African and Oriental species now established in the New World tropics, but very rare in collections. The first author collected two other specimens in Brazil, one at Pipa Beach, south of Natal, Rio Grande do Norte, and the other in Planaltina, DF, near Brasilia, which is the southern most record for the species in the New World.
GUANA: 1 specimen, 1990.
HOST: Myosotis (Boraginaceae) and grasses (Hampson, 1901).

Pericopinae
111. Composia credula (Fabricius, 1775)
(Fig. 113)

ID: Large black, with body and wings dotted white; fore wings with deep red markings on basal half below costa.
DIST: Endemic to the Antilles, this is the only species of the genus found in the Puerto Rican Bank.
GUANA: 10 specimens, 1984, 1986, 1987, 1989.
HOST: Unknown. Its closest relative, C. fidelissima Herrich-Schäffer, from Cuba and Florida, has been reared on Canavalia (Fabaceae), oleander (Nerium) and Echites (Apocynaceae) (Kimball, 1965).
COM: Commonly referred to in the literature by its junior synonym C. sybaris (Cramer). Crepuscular moths commonly found flying along the trails before dark. Todd (1982) states it "occurs throughout the Greater Antilles, and south to Brazil" but that the "continental distribution needs to be studied." Previous authors (Forbes, 1930; Bates, 1933) have considered it to be endemic to the Antilles. In the series in USNM there is only one non-Antillean specimen, an old specimen labeled only "Brazil," which we believe to be mislabeled. We are not aware of any other continental records for this large and colorful species, which would not be missed by collectors.

Ctenuchinae
112. Empyreuma pugione (Linnaeus, 1767)
(Fig. 119)

ID: Large sized wasp like moth with conspicuous red wings and black body. Wings bordered dark gray and body tinged iridescent green.
DIST: Apparently restricted to the Puerto Rican Bank.
GUANA: 9 specimens, 1984, 1987, 1989, 1990.
HOST: Oleander, Nerium oleander L. (Apocynaceae) (Gundlach, 1881).
COM: Day flying; very likely a Müllerian mimic of Pepsis rubra (Drury) (Hymenoptera: Pompilidae) (R. Snelling det.), as its larvae feed on a toxic plant. Similarly to other arctiids, the larvae presumably sequester poison alkaloids from the host plant. Referred to in the older literature as E. lichas (Cramer).

113. Horama pretus (Cramer, 1777)
(Fig. 121)
ID: Large sized wasp like, ochreous brown species, easily distinguished by the broad white band across base of abdomen.
DIST: Antilles.

GUANA: 36 specimens, 1984, 1985, 1987, 1989, 1990.
HOST: Cassine xylocarpa Vent. [as Elaeodendron xylocarpum] (Celastraceae) (Wolcott, 1951).
COM: Day flying, commonly seen visiting flowers. Presumably a Müllerian mimic of Polistes major Palisot de Beavois (Hymenoptera: Vespidae) (R. Snelling det.).

114. Horama panthalon (Fabricius, 1793)
(Fig. 120)

ID: Similar but smaller than former. Easily distinguished by pattern on abdomen: only a small white dash across base, followed by alternated ochreous and black bands.
DIST: Southern United States throughout the Antilles, south to southern Brazil.
GUANA: 13 specimens, 1986, 1989, 1990.
HOST: Unknown.
COM: Dietz & Duckworth (1976) divided the species into three subspecies, regarding the Antillean population belonging to the nominal form. Very likely a Müllerian mimic of Polistes crinitus (Felton) (Hymenoptera: Vespidae)(R. Snelling det.).

115. Cosmosoma achemon (Fabricius, 1781)
(Fig. 122)

ID: Small wasp like moth with unique combination of colors for the island. Mostly orange with vertex of head and subdorsal sides of abdomen metallic bluish green; fore wings with translucent areas.
DIST: Antilles south to Brazil.
GUANA: 10 specimens, 1989, 1990.
HOST: Unknown.

116. Eunomia colombina (Fabricius, 1793)
(Fig. 123)

ID: Medium sized wasp like moth with black body and translucent wings. Fore wings bordered black with a dark, centered red mark at end of cell connected with costa. Thorax striped white; abdomen with a carmine red band across the base, expanding laterally, followed by a white band, partially interrupted dorsally; the rest banded with alternating, narrow, red and white lines.
DIST: Antilles. Hampson (1898) gives also Honduras and Brazil, but the material studied by him should be checked.
GUANA: 1 specimen, 1989.
HOST: "Oruga en las convolvulaceas" (Gundlach, 1881).
COM: Listed as columbina, a misspelling, by Wolcott (1951).

117. Nyridela chalciope (Hübner, [1831])
(Fig. 124)

ID: Medium sized, wasp like, black moth with transparent wings. Head, thorax dorsally, base of wings, legs, and abdomen dorsally and laterally with iridescent blue. Antennae yellow. Forewings bordered black with an oblique transverse band from middle of costa to tornus.
DIST: Described from Havana, known from throughout the West Indies and Central America south to Panama.
GUANA: 1 specimen, 1990.
HOST: Cupania americana L. (Sapindaceae) (Möschler, 1890).
COM: Some authors regard the Central American population as belonging to a separate species, N. xanthocera (Walker).

Lithosiinae

118. Afrida charientisma Dyar, 1913
(Fig. 169)

ID: Very Small, 8-12 mm wing span, slightly variable species. Forewings mostly grayish, slightly tinged with green, crossed by alternating, ill defined whitish and dark gray bands. Easily recognized by the antemedial whitish band across fore wings, starting from costa and running obliquely outwards to middle then bent to base towards dorsum.
DIST: Antilles.
GUANA: 27 specimens, 1985, 1986, 1990.
HOST: Unknown, however, most of the species of this subfamily are lichen-feeders (Hampson, 1900).

119. Progona pallida (Möschler, 1890)
(Fig. 170)

ID: Small pale species, with no markings at all. Forewings slightly dusted gray.
DIST: Previously known only from Puerto Rico.
GUANA: 6 specimens, 1986, 1990.
HOST: Unknown.

120. Lomuna nigripuncta (Hampson, 1900)
(Fig. 171)

ID: Small, 1.3-1.7 cm wing span, whitish moth. Forewings dusted gray, conspicuously spotted with small, dark gray dots.
DIST: Previously known only from Puerto Rico (Field, 1952).
GUANA: 29 specimens, 1984, 1985, 1986, 1990, 1991.
HOST: Unknown (see former species).

GEOMETRIDAE
Oenochrominae
121. Almodes terraria Guenée, [1858]
(Fig. 134)

ID: Medium sized gray species. Wings densely dusted with dark gray scales and crossed with pale and dark ill defined, irregular bands. Males easily recognized by the strongly pectinate antennae nearly the length of fore wings. Females have a slight olivaceous tinge and external margins of both wings more strongly dentate.
DIST: Southern United States, throughout the Antilles to Colombia.
GUANA: 2 specimens, 1990.
HOST. Unknown.

Ennominae
122. Pero rectisectaria (Herrich-Schäffer, [1855])
(Figs. 125, 126)

ID: Medium sized, sexually dimorphic, variable species. Males with ground color varying from pale to dark brown; fore wings with antemedial band, when visible, strongly bent to the base near costa, postmedial band nearly straight, with area distad to it much paler than rest of wing. Females more reddish brown. Easily distinguished from other species of same size by the conspicuous indentations on external margin near apex.
DIST: Puerto Rico, throughout the Lesser Antilles.
GUANA: 42 specimens, 1986, 1987, 1988, 1989, 1990.
HOST: Unknown.

COM: Poole (1987), who revised this large genus, stated that "Either it is rare, or it occurs in areas not commonly collected". Judging from the long series collected by us, it is not rare. It was quite common in October 1989, just after hurricane "Hugo", when the first author had dozens of specimens on the light and selected 10 males and 4 females.

123. Oxydia vesulia (Cramer, [1779])
(Fig. 127)
ID: Large, extremely variable species. Almost impossible to collect two identical specimens. Ground color of both wings varying from pale yellow, through pale gray to brown, clouded and irrorated in various degrees by gray. Fore wings have an oblique post medial band from apex to near middle of dorsum. Easily recognized by the white vertex of head.
DIST: Southern United States, Antilles, south to Argentina.
GUANA: 4 specimens, 1987.
HOST: Acalypha (Euphorbiaceae), Cinchona (Rubiaceae), Cissampelos (Menispermaceae), Citrus (Rutaceae), Persea (Lauraceae), Rosa (Rosaceae), and Securidaca (Polygalaceae) (Martorell, 1976; Torres, 1992).

124. Erastria decrepitaria (Hübner, [1823])
(Figs. 128, 129)

ID: Medium sized yellow moth. Sexually dichromatic: males suffused olive, especially forming a wide bar along external margin; females more yellowish with the external olive area reduced to a fainted irregular band, with a conspicuous dark spot on this band close to tornus.
DIST: Southern United States, throughout Antilles, south to Brazil.
GUANA: 4 specimens, 1987, 1989.
HOST: Unknown.

125. Sphacelodes fusilineatus (Walker, 1860), stat. rev.
(Figs. 130, 131)

ID: Medium sized dichromatic species. Males dark olive brown; fore wings crossed with three equidistant, nearly parallel lines and with a subtriangular gray mark on costa between medial and postmedial line. Females brown with lines same as males, but mark on costa absent.
DIST: Antilles.
GUANA: 25 specimens, 1986, 1988, 1989, 1990.
HOST: Unknown.
COM: This species has been confused in the literature with S. vulnerarius (Hübner). They differ in many features, the most obvious the color of antenna and costal mark of fore wings. In fusilineatus they are light gray, whereas in vulnerarius the antenna is ochreous and the costal mark reddish brown. S. fusilineatus was described from material with no locality label. There is a series in VOB collected in Guana, Tortola, St. Thomas and Cuba. One of these was compared with and matches the type of fusilineatus. It is very likely that this is the species referred to by Kimball (1965: 192) as "5221, 1 S. SP.", and listed by Ferguson (1983: 95) as S. haitiaria Oberthür. The series of vulnerarius in VOB was collected in Cuba, Mexico, and Brazil. In Cuba, fusilineatus was captured at Pinares de Mayari, Holguin, while those of vulnerarius at Viñales, Pinar del Rio. The first locality is dry, similar to the conditions in St. Thomas and Guana, while the second is humid, similar to those areas on the American continent from where the series of vulnerarius came.

126. Macaria paleolata (Guenée, [1858])
(Fig. 132)

ID: Small, slightly variable, pale species. Wings crossed with two ill defined, nearly straight bands; distal area, external to postmedial band, darker than rest of the wing. Distinguished by head and anterior margin of thorax ochreous.

DIST: Antilles
GUANA: 24 specimens, 1989, 1990
HOST: Unknown, however, other species of this large genus have been found feeding on several leguminous species (Fabaceae).
COM: It is very likely that other, similar species occur on the island. Transferred from Semiothisa to Macaria by Scoble (1999).

127. Patalene ephyrata (Guenée, [1858])
(Fig. 133)

ID: Small, variable, pale yellow to pale brown species. Forewings with antemedial band nearly evenly rounded, postmedial band straight to near apex then strongly angled basad to costa. Hind wings with a single, straight band across near middle. Easily recognized by pointed apex and the sinuate external margin of fore wings.
DIST: Antilles (Herbulot, 1984).
GUANA: 41 specimens, 1986, 1987, 1988, 1989, 1990.
HOST: Ficus (Moraceae) and Ricinus (Euphorbiaceae) (Brunner et al., 1975).

128. Cyclomia mopsaria Guenée, [1858]
(Figs. 182, 183)

ID: Small, extremely variable species. Ground color often pale tinged reddish brown, to dark reddish brown. Fore wings varying from unmarked to marked with transverse, ill defined, irregular lines. Hind wings pale to orange, often bordered with reddish brown. If it were not for the bipectinate antennae in the males it could easily be confused with a small noctuid such as Eublemma spp. Easily distinguished from other small geometrids by sharply pointed, porrect labial palpi, unusually long for a geometrid.
DIST: Antilles, south to Brazil.
GUANA: 11 specimens, 1987, 1989, 1990.
HOST: Unknown, however, Erythroxylum havanense Jacq. (Erythroxylaceae) has been listed as food plant of a "Cyllomia sp. [presumably a misspelling] Un gusano medidor", in Cuba (Brunner et al., 1975).
COM: Its extreme variation led to its description several times. It is likely that after revision more names will be added to the six junior synonyms currently listed (Becker, in prep.).

Geometrinae
129. Eucana simplaria Herbulot, 1986
(Figs. 12-14, 141, 142)

ID: Small to medium sized bluish green species. Lines on wings almost indistinct. Vertex of head white; abdomen with traces of a whitish line dorsally. Genitalia (Figs. 12-14) very similar to those of E. niveociliaria (Herrich-Schäffer), illustrated in Ferguson (1985: fig. 25a-e).
DIST: Guadaloupe.
GUANA: 17 specimens, 1986, 1989.
HOST: Unknown, but Scoble (1999) records E. niveociliaria from Rhamnaceae.
COM: Of all greens from the island this is the only bluish species, and slightly larger than the other species. The subfamily was revised for North America by Ferguson (1985) and for the neotropics by Pitkin (1996).

130. Phrudocentra centrifugarium (Herrich Schäffer, 1870)
(Figs. 143-146)

ID: Medium sized, extremely variable, bright green species. Some specimens, usually males, have only small, dark brown dots on wings, one on cell and the others along what would be the

antemedial and postmedial lines, others have larger marks, of various sizes and shapes, whitish or brownish, above tornus. Abdomen has a series of minute, white dots dorsally, one on each segment.
DIST: Florida, throughout Greater Antilles to Puerto Rico (Ferguson, 1985).
GUANA: 4 specimens, 1990.
HOST: Myrica cerifera L. (Myricaceae) (Scoble, 1999).

131. Chloropteryx paularia (Möschler, 1886)
(Fig. 186)

ID: Small olivaceous species. Wings with antemedial and postmedial rows of minute whitish dots forming irregular lines.
DIST: Florida, throughout the Antilles.
HOST: Unknown.
GUANA: 11 specimens, 1987, 1989, 1990.
COM: This is the only species of the greens with this color.
HOST: Myrica cerifera L. (Myricaceae) in Florida (Ferguson, 1985).

132. Synchlora frondaria (Guenée, [1858])
(Fig. 187)

ID: Small, bright green species. Easily distinguished from next species by the concolorous fringes.
DIST: United States, throughout the Antilles, south to Argentina.
GUANA: 29 specimens, 1986, 1988, 1989, 1990.
HOST: Stilingia (Euphorbiaceae), Pluchea, Bidens, Chrysanthemum, Helianthus (Asteraceae), Rubus (Rosaceae), Glycine max (L.) Merr. and Prosopis (Fabaceae) (Ferguson, 1985).

133. Synchlora cupedinaria (Grote, 1880)
(Fig. 188)

ID: Small, bright green species. Wings thickly bordered with brown. Thorax and abdomen brown dorsally; abdomen usually with white dots dorsally. Easily distinguished from the other greens by the brown thorax and abdomen.
DIST: Florida, throughout Greater Antilles to Virgin Islands, to Nevis (Herbulot, 1984).
GUANA: 41 specimens, 1985, 1986, 1988, 1989, 1990.
HOST: Lantana camara L. (Verbenaceae) (Scoble, 1999).

Sterrhinae
134. Semaeopus malefidarius (Möschler, 1890)
(Fig. 135)

ID: Medium sized pale moths densely irrorated with reddish brown scales. Wings crossed with ill defined, hardly contrasting, irregular bands, slightly darker than ground color.
DIST: Puerto Rico, Virgin Islands.
GUANA: 14 specimens, 1989, 1990.
HOST: Unknown.
COM: Closely related to S. castarium (Guenée), from the Greater Antilles.

135. Leptostales noctuata (Guenée, [1858])
(Figs. 136, 137)

ID: Small to medium sized pale species, densely irrorated with olive scales. Fore wings with antemedial and postmedial bands darker than ground color, termen sinuate, apex pointed. Males show a dark mark on cell, in females this mark is reduced and faint.
DIST: Antilles.

GUANA: 19 specimens, 1986, 1987, 1988, 1989, 1990.
HOST: Unknown.

136. Acratodes suavata (Hulst, 1900)
(Fig. 185)

ID: Small white species: wings crossed with three ill defined, little contrasting, grayish bands; medial and postmedial closer together. The only white geometrid on the island with no contrasting marks on wings.
DIST: Southern United States, Antilles.
GUANA: 31 specimens, 1985, 1986, 1987, 1988, 1989, 1990.
HOST: Randia aculeata L. (Rubiaceae) (Kimball, 1965).
COM: It is very likely that A. virgotus (Schaus), described from Jamaica, is another synonym of this. Our series matches the type of this in USNM very well.

137. Lobocleta nataria (Walker, 1866)
(Figs. 172, 173)

ID: Very small gray species; antemedial and postmedial lines dark gray, strongly contrasting, especially in the males; in some males the area between these two lines are dusted dark gray, forming a wide band across the wings.
DIST: Antilles.
GUANA: 29 specimens, 1985, 1986, 1989, 1988, 1990.
HOST: Unknown.
COM: Females from our series match the type of L. nataria, whereas the males match that of Ptychopoda monata Forbes, 1947, syn. n., and a specimen in the BMNH, identified by C. Covell as Sterrha insulensis Rindge, 1958, syn. n.

138. Lobocleta nymphidiata (Guenée, [1858])

ID: Small, white species with wings crossed with 4-5 narrow, irregular dark brown lines, more or less interrupted, looking like rows of dark dots.
DIST: Antilles.
GUANA: 1 specimen, 1985.
HOST: Unknown.

139. Scopula laresaria Schaus, 1940
(Fig. 178)

ID: Small, pale whitish, irrorated with scattered gray scales; fore wings crossed with ill defined, irregular, narrow pale yellowish lines. Same size and similar to the former, but readily distinguished by the blackish vertex of head, white in L. nymphidiata.
DIST: Puerto Rican bank.
GUANA: 9 specimens, 1985, 1988, 1989.

140. Idaea amnesta (Prout, 1922)
(Figs. 179, 180)

ID: Small light gray, densely irrorated with dark gray scales; wings crossed with three, ill defined, irregular, narrow, dark gray lines more or less interrupted, giving the impression that they are densely dotted; both wings with black dot on cell. Females slightly lighter than males.
DIST: Antilles.
GUANA: 27 specimens, 1985, 1986, 1988, 1987, 1989.
HOST: Unknown.

141. Idaea minuta (Schaus, 1901)
(Figs. 176, 177)

ID: Very small, 8-10 mm wing span, pale species. Wings crossed with several, narrow, ill defined, irregular, light brown lines. One of the smallest geometrid species on the island.
DIST: Antilles, USA.
GUANA: 19 specimens, 1985, 1987, 1988, 1989.
HOST: Unknown.
COM: Specimens belonging to this series were identified as minuta by C. Covell, as well as matched the type of Ptychopoda curtaria Warren, 1904, syn. n., from Jamaica, in BMNH.

142. Idaea eupitheciata (Guenée, [1858])
(Figs. 174, 175)

ID: Very small, sexually dimorphic, pale species with wings crossed with irregular reddish brown bands. Males paler than females; fore wings with small tuft of dark scales near dorsum; hind wings with a small tail near tornus. Females darker than males and without the tufts and tails as in males.
DIST: Antilles.
GUANA: 16 specimens, 1985, 1988, 1989, 1990.
HOST: Unknown.

143. Leptostales phorcaria (Guenée, [1858])
(Fig. 181)

ID: Small reddish brown; wings crossed with narrow, ill defined, irregular, yellowish lines; thorax dorsally and fore wing costa yellow. Cannot be confused with any other on the island.
GUANA: 2 specimens, 1989.
DIST: Antilles.

144. Leptostales oblinataria Möschler, 1890
(Fig. 184)

ID: Small olivaceous species with a broad reddish brown band across fore wings, delimited by medial and postmedial bands. Some specimens with this band faded. Cannot be confused with any other species on the island.
DIST: Southern United States, Antilles, to Guyana.
GUANA: 15 specimens, 1988, 1989, 1990.
HOST: Unknown.

Larentiinae
145. Obila praecurraria (Möschler, 1890)
(Fig. 138)

ID: Large species with velvet moss green fore wings and orange ochreous hind wings. Forewings crossed with numerous alternating pale and dark gray waving bands. Hind wings with a wide gray band that extends inwards, along internal margin, to the base. Females have middle of fore wings crossed with a wide, irregular whitish band.
DIST: Antilles.
GUANA: 1 specimen, 1989.
HOST: Unknown.
COM: The specimens of our series match the type of Pterocypha xantholiva Warren, 1895, synonymized with this by Schaus (1940: 326).

146. Pterocypha defensata Walker, 1862, stat. rev.
(Figs. 139, 140)

ID: Medium sized, variable, moss gray. Slightly smaller and similar to the previous species, but lacking the orange ochreous on hind wings.
DIST: Southern United States, Antilles.
HOST: Unknown.
GUANA: 20 specimens, 1986, 1987, 1989, 1990.
COM: Commonly referred to in the literature, including Scoble (1999), by its synonym P. floridata (Walker), but defensata was described in 1862 and floridata in 1863, so defensata is the older name.

HYBLAEIDAE
147. Hyblaea puera (Cramer, 1777)
(Fig. 150)

ID: Medium sized fuscous species with hind wings beautifully decorated with yellow to orange patches. Abdomen, dorsally, crossed with narrow lines behind each segment.
DIST: Pantropical.
GUANA: 2 specimens, 1989, 1990.
HOST: Crescentia cujete L., Spatodea campanulata P. Beauv., Tabebuia heterophylla (DC.) Britton (Bignoniaceae), Petitia domingensis Jacq. (Verbenaceae) (Martorell, 1976).
COM: Immature stages described by Singh (1995) and taxonomy of the related species discussed by Berio (1967). However, H. puera may represent a species complex (Shaffer and Nielsen, 1996).

COSSIDAE
148. Psychonoctua personalis Grote, 1865
(Figs. 147-149)

ID: Medium sized to large, 2-4.5 cm wing span, narrow winged, gray species. Its short strongly pectinate antennae, and abdomen thickly clothed with long scales makes it easily recognized from any other large moths on the island.
DIST: Antilles and Mexico.
GUANA: 5 specimens, 1990.
HOST: The larvae are wood borers into many trees, sometimes causing severe damage to orange, coffee, white mangle, sea grape, etc. (Wolcott, 1951).

Appendix

Catabenoides Poole, gen. n.

[The following new generic description was intended to appear in a fascicle of the series Moths of America North of Mexico. Because this fascicle will not be published in the foreseeable future, the author has permitted us include the new generic name here, in order to allow us to describe Catabenoides lazelli in the proper place.]

Type-species: Adipsophanes terminellus Grote

Catabenoides contains the majority of the species previously placed in Catabena. The genus appears to be an outlier of a large group in southern South America, primarily Paraguay and Argentina. The genus is postulated to be closest phylogentically to Catabena and Neogalea, but it has a number of curious synapomorphies making its affinities somewhat problematical. The principle identifying characters are in the male and female genitalia. In the male valve the bottom margin of the sacculus in both the right and left valves is produced into a long process separate from the clasper. The ventral margins of the valve have strong elongate setae. The sacculus is lightly chitinized proximal to the clasper separating off a much more heavily sclerotized plate.

In addition to the three species known from North America (the type species, C. vitrina (Walker), comb. n., and C. divisa (Herrich-Schäffer), comb. n.), there is one previously described species: Catabenoides scorsa (Todd) (Catabena scorsa Todd) comb. n., from the Galapagos Islands. There are two undescribed species in the West Indies [one of these is described herein as C. lazelli], one undescribed species from central Mexico, and at least two unnamed species from Paraguay. The exact affinities of Catabenoides, Catabena, and Neogalea with the Argentina and Chilean faunas remain to be determined. The single remaining described species in "Catabena" of Poole (1989), Laphygma terens Walker, was described from "Venezuela". The type is hopelessly rubbed and its abdomen is missing. I have not been able to match it with any specimens from the extensive Venezuela material in the USNM. It appears superficially to be a Catabenoides. Therefore for book-keeping purposes, Catabenoides terens (Walker), comb. n. The technical description follows.

Head: Lashes absent; eyes large, naked; frons slightly swollen, very closely scaled; antenna simple, faintly ciliate; palpi unremarkable for the tribe; proboscis normal; two thin ridges of flattened scales between the bases of the antennae. Thorax: Patagia capable of being raised in a hood; vestiture of dorsum of thorax of flattened scales without hairs; slight metathoracic tuft; vestiture of wings of flattened scales; no sign of sexually modified scales in male. Prothoracic leg: Tibia with later ridge of hair giving it a flattened look; no tibial claw; tibia approximately as long as first three tarsal segments; first four tarsal segments with three rows of spines; tarsal claw without a tooth. Mesothoracic and metathoracic legs: Proximal third of tibia with tuft of long hairs and scales; tibia approximately as long as first three tarsal segments. External tympanic region: Approximately as in Supralathosea Barnes & Benjamin, however first tergum much shorter than in Catabena and Supralathosea and with a strong definite proximal lip as in Apharetra Grote; hood strong. Internal tympanic region: Not examined. Abdomen: Very weak tuft on first tergite; male with basal hair pencils and accessory hair pencils in known species. Eighth sternum with strong row of hairs in middle of U-shaped pleurite. Male genitalia: Figs. 2, 3: Valve characterized by production of ventral margin of sacculus into a process of various shapes; ventral margin of valve with strong modified setae; a weak unsclerotized area before origin of clasper; uncus swollen with an apical tooth; juxta and single pointed plate; vesica in type species elongate-ovate, connected by a short neck to body of aedoeagus; type species with a group of elongate, fused spines at apex of vesica and with groups of short, stubby spines near the middle and ventral margin of the vesica; vesica variable in other species. Female genitalia: ovipositor lobes square unmodified; ductus bursae well sclerotized, elongate, mushroom shaped in type species, separated by a distinct junction from the heavily sclerotized upper part of bursa; bursa bilobed, but lobes not distinctly separate; corpus bursae with stellate ridges, but no signum. Larva and foodplants: Unknown for North American species but recorded as Lantana peduncularis Andersson (Verbenaceae) in Catabenoides scorsa from the Galapagos.

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LEGENDS TO FIGURES

Fig. 1. Map of Guana Island. Contours are 20 m. Bar, bottom right, is 400 m. Inset shows the position of the Virgin Islands in the Antilles.

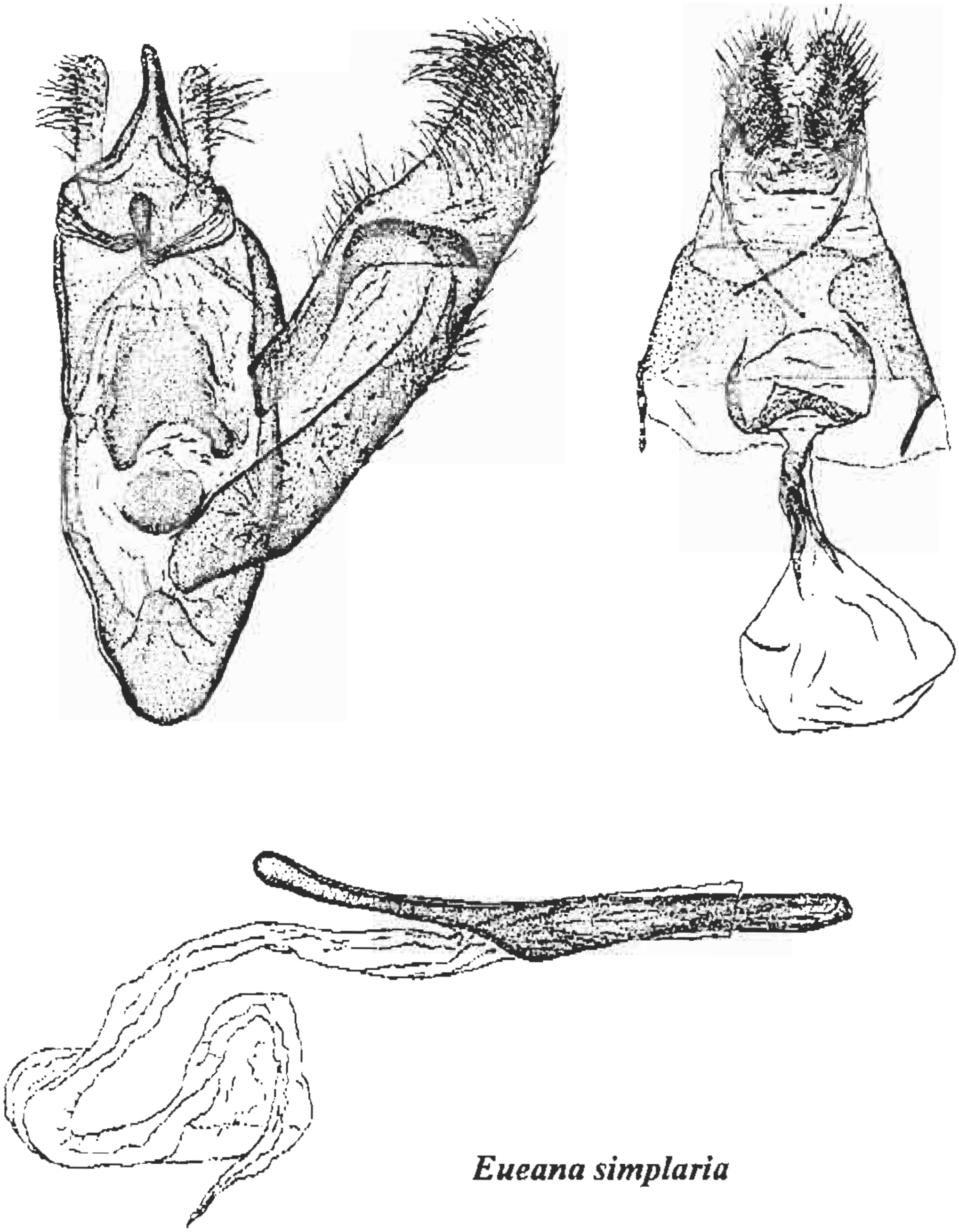
Figs. 2-6. Genitalia of Catabenoides species. 2, 3, terminellus (Grote): 2, male, ventral view, aedeagus removed. 3, aedeagus, lateral view; 4-6, lazelli sp. n.: 4, male, ventral view, aedeagus removed. 5, aedeagus, lateral view; 6, female, ventral view.

Figs 7-9. Genitalia of Perigea gloria sp. n. 7, male genitalia, ventral view, aedeagus removed; 8, aedeagus, lateral view; 9, female genitalia, ventral view.

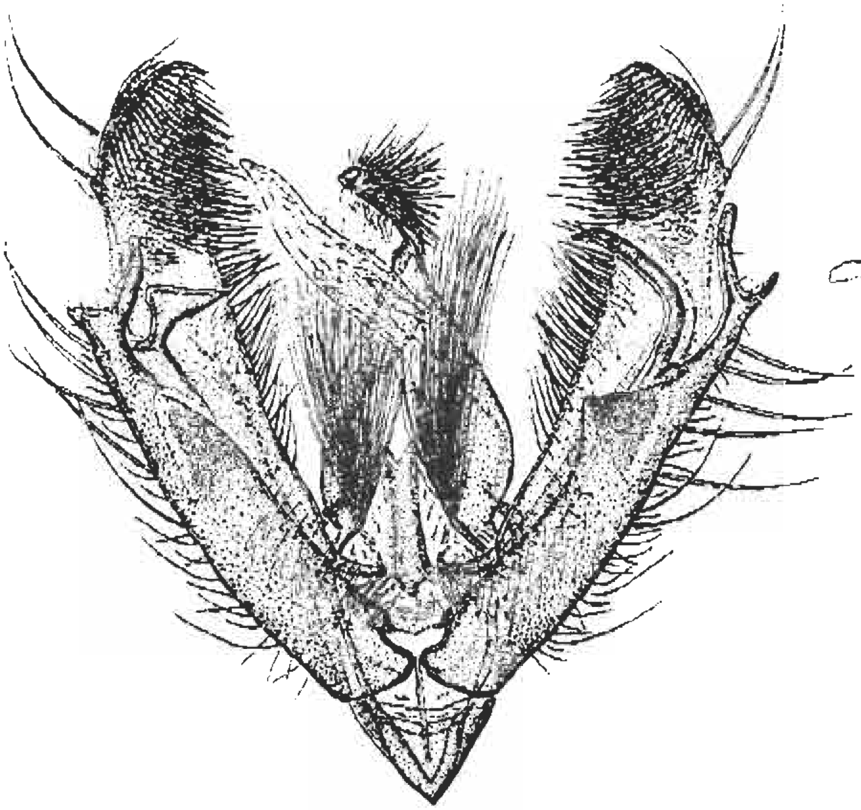
Figs 10, 11. Male genitalia of Anateinoma affabilis Möschler. 10, ventral view, left valva end aedeagus removed; 11, aedeagus, lateral view.

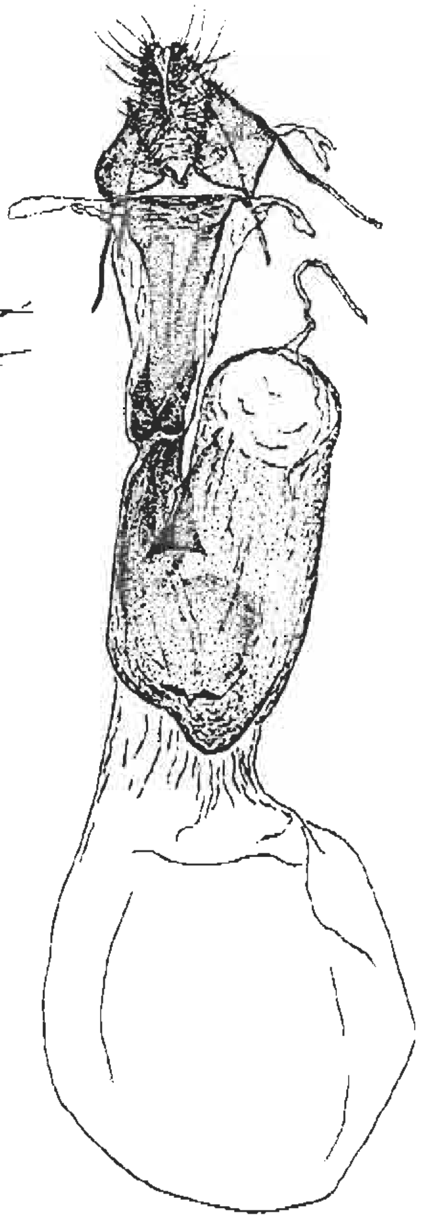
Figs 12-14. Genitalia of Eueana simplaria Herbulot. 12, male, ventral view, left valva and aedeagus removed; 13, aedeagus, lateral view; 14, female, ventral view.

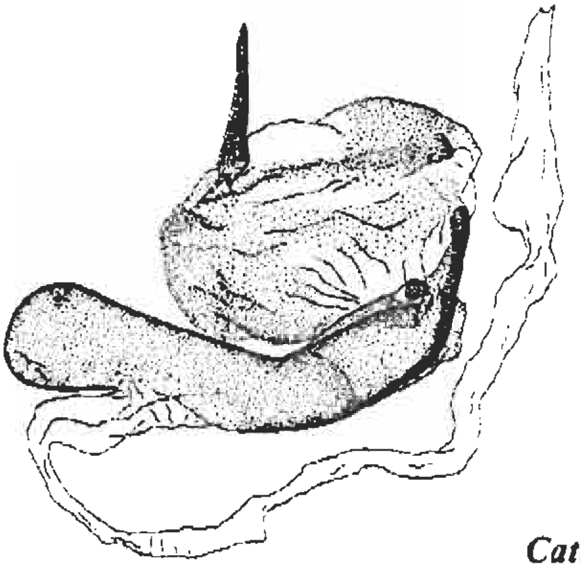
Following are five pages of sample illustrations of moth genetalia. There will also be color plates of all the species: photographs of whole moths.



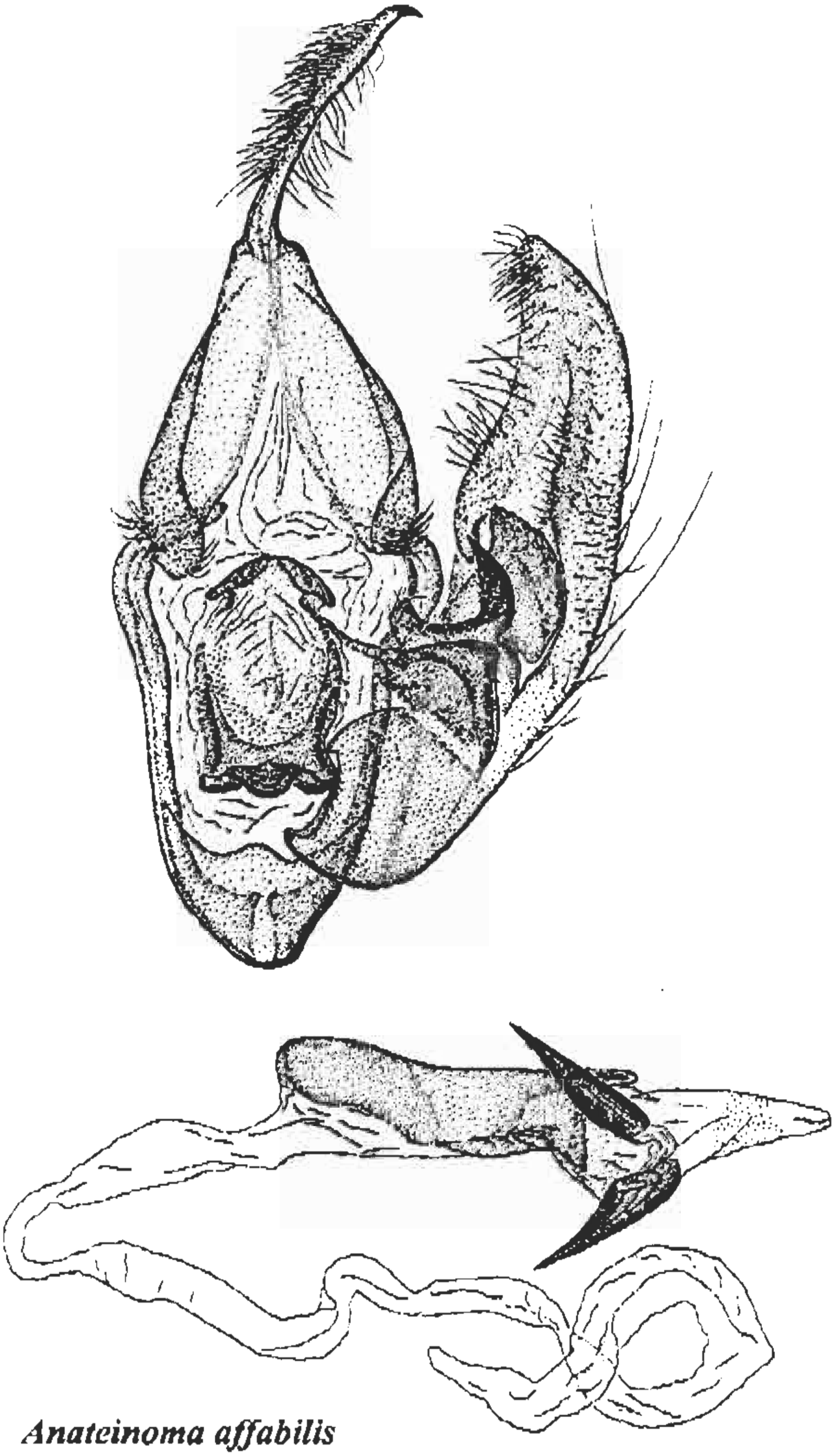
Eueana simplaria



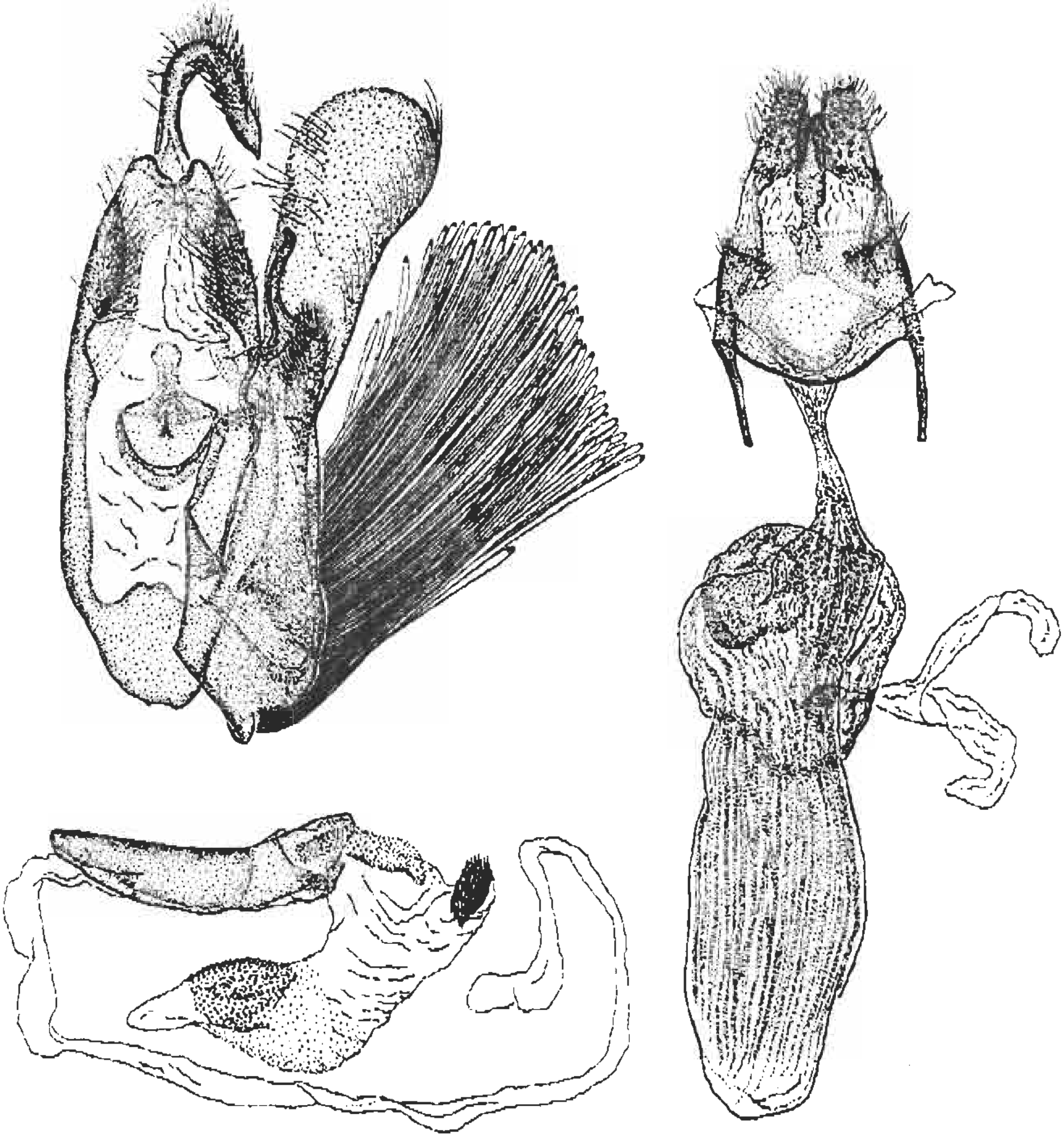




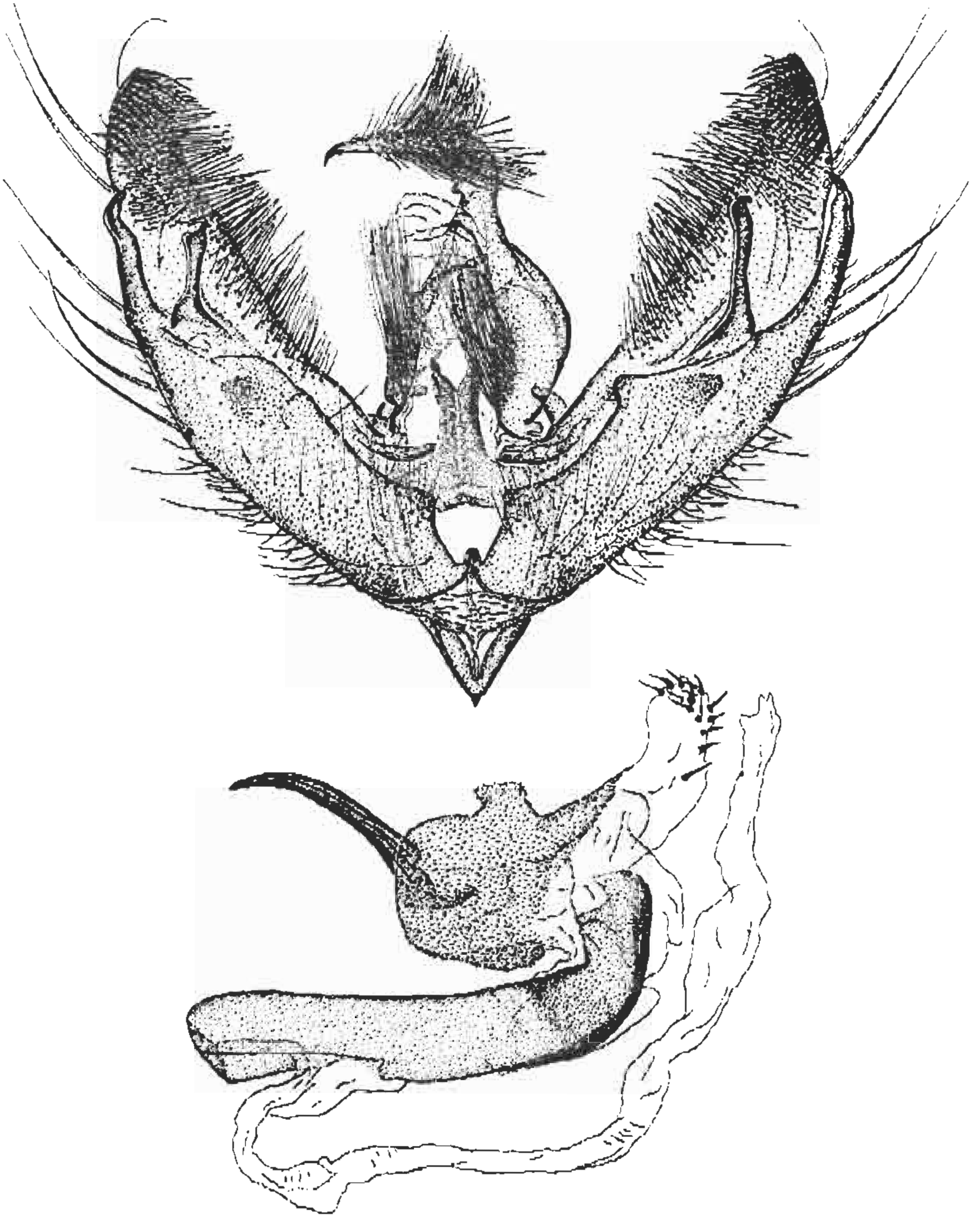
Catabenoides lazelli



Anateinoma affabilis



Perigea gloria



Catabenoides terminellus

→ Lage!

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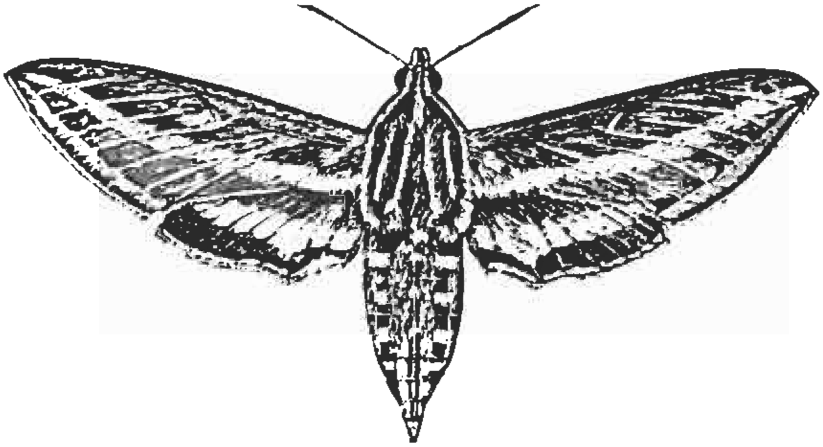
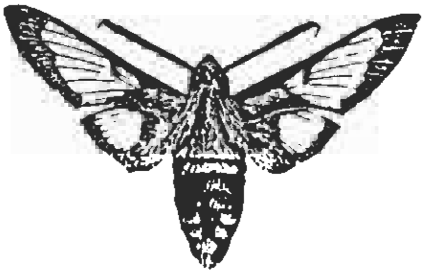
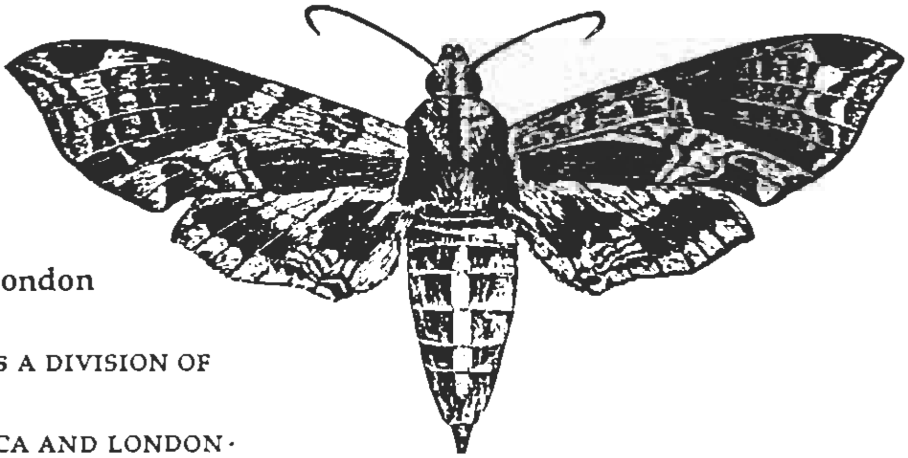
HAWKMOTHS OF THE WORLD

AN ANNOTATED AND ILLUSTRATED REVISIONARY CHECKLIST
(Lepidoptera: Sphingidae)

by **Ian J. Kitching**
and
Jean-Marie Cadiou







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96. *Cautethia noctuiformis* (Walker 1856: 232) was based on a single male from "St. Domingo," that is, Santo Domingo, Dominican Republic. For quite some period subsequently, virtually all further Greater Antillean specimens of *Cautethia* came from Cuba. Many of these were identified as *noctuiformis* but are actually *Cautethia grotei*, including the specimen illustrated by d'Abrera ([1987]) as *noctuiformis*. It is very difficult to distinguish *grotei* from *noctuiformis* on features of the color and pattern. Certainly, the "black dash at the basal end of the dorsum, and triangular black dash on the tornus of the f.w.r. [forewing upperside]" that were said by d'Abrera ([1987]) to be characteristic of *noctuiformis* are not. Both species have both these features, which are individually variable in their degree of development. D'Abrera was misled by the fact that the collection in the BMNH was curated such that those specimens of *grotei* that had the black dashes were placed under *noctuiformis* and those that did not were placed under *grotei*. Fortunately, there are good characters in the male genitalia to separate the two species. It now appears that *grotei* is found in Cuba, the Cayman Islands, the Bahamas, and Florida, while *noctuiformis* is found in the Turks and Caicos islands (T. L. McCabe, personal communication 1988), Hispaniola, Puerto Rico, and the Leeward Islands.

Cary (1970: 267) described the *noctuiformis* from Antigua and Barbuda as a subspecies, *Cautethia noctuiformis bredini*. (As an aside, it should be noted that Margaret M. Cary and Mrs. C. Reed Cary are one and the same person. The *Cautethia* paper was published posthumously under her married name.) Cary characterized *n. bredini* as having pale gray forewings with very fine, sharply defined transverse lines. In contrast, the nominotypical subspecies had forewings in which the areas basal to the antemedian line and between the postmedian line and submarginal line were almost entirely black and the transverse lines were thick with somewhat indistinct edges. However, it would appear that Cary compared *n. bredini* not with nominotypical *noctuiformis* but with a female *g. grotei* (her Figure 1), and the habitus features she described are actually characteristic of the female of this sexually dimorphic species. The darkened coloration is particularly evident in the specimen of *g. grotei* illustrated by d'Abrera ([1987]), although he mislabeled it as a male.

We examined the male genitalia of the holotype of *n. noctuiformis* and of a second specimen from the Dominican Republic, and compared them with those of the holotype of *n. bredini* (as illustrated by Cary (1970) and McCabe (1984)) and a specimen from the British Virgin Islands (Guana Island). We found a number of small differences between Hispaniolan and Lesser Antillean *noctuiformis* that justify maintaining *n. bredini* as a subspecies. This conclusion is further supported by the observation that in all *n. noctuiformis* that we examined, including the holotype, the hindwing yellow band is divided by a thin black line along vein 1A−2A. This line is absent in *n. bredini* (and, indeed, in all other

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The Conservation Agency

Exploration, Education, and Research

President
James D. Lazell, Ph.D.
401-423-2652

6 Swinburne Street
Conanicut Island
R.I. 02835 U.S.A.

November 4, 2000

Dr. P.J. DeVries
Milwaukee Public Museum
800 West Wells St.
Milwaukee, WI 53233

Dear Phil,

Gad Perry sent your vita and publs. list. Obviously you are a terrific candidate to investigate the butterflies of Guana Island. We are really deeply disgruntled at coming in behind Lignum Vitae Key and want our log species number to get up around 2. If MacA-W are right, this will ipso facto increase the log area of Guana to over 4.5 and the owner will be exuberant. This is the only way we can envision to beat sea level rise.

Bob Denno, U. MD (rd 12 @umail.umd.edu, 301-405-3955) has additional records, so we are on the way.

Scott Miller (miller.scott@nmnh.si.edu, 202-357-1355) directs our entomology program, so please be in contact with him. It is high time he and Vitor Becker came back because Guana has undergone a spectacular metamorphosis since the severe drought years, pre-1997. Today, the Island is lush and green beyond the imaginings of those who only knew it in the bad old days.

Miller and Becker work preferentially on moths, I believe, and do not yet have Avagadro's Number of species from the Island - surely a modest goal to strive for.

I hope we will all meet on Guana in October 2001, so you can give these vicious defoliators the thrashing they deserve for endangering vegetarians and the other weak and defenceless creatures of the world.

Best,

Skip Lazell

James Lazell, Ph. D.

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ARGIA

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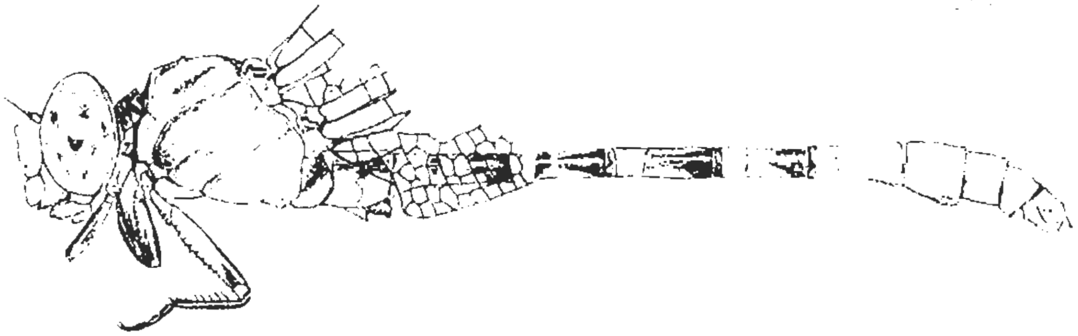

PUBLISHED BY THE DRAGONFLY SOCIETY OF THE AMERICAS

ADDITIONAL COMMENTS ON THE DRAGONFLIES OF THE BRITISH VIRGIN ISLANDS

Fred C. Sibley, 203-729-3582 25 Shirley Street, Naugatuck, CT 06770

In an **ARGIA** note of a year ago I discoursed on an odonate invasion of The British Virgin Islands (BVI) during a strong storm in October 1997. The present note adds to and expands on the BVI list presented there and describes an invasion of *Pantala flavescens* following Hurricane Jose.

LIST ADDITIONS -- The previous note proposed the naive view there were no really permanent water sources on Tortola (the largest and tallest island in the BVI). Fortunately publishing this view resulted in several people suggesting the purchase of a map and what to do with it. Not all of the recommended sites have been visited.

The botanical garden in Roadtown, Tortola, has a small permanent pond and this supports a variety of dragonflies. During two visits in mid-October eight species were found at the pond. The three widespread and common temporary pool species (***Ischnura ramburii, Erythrodiplax umbrata,*** and ***Orthemis ferruginea***) were present but uncommon. ***Brachymesia furcata*** and ***Brachymesia herbida*** (both new species for the BVI) were the most conspicuous species. Two individuals of ***Perithemis domitia*** (new as a resident species) were present on both visits. ***Tramea abdominalis*** and ***Pantala flavescens*** were only represented by 1-2 individuals, but the 17 exuviae recovered represented 13 ***Pantala flavescens***, 3 ***Tramea abdominalis*** and 1 ***Brachymesia herbida***. Only one ***Pantala flavescens*** was circling the pond, but when it was collected another appeared in less than a minute.

1999 was an unusual year with rain showers at regular intervals for months rather than the usual few intense showers followed by long periods with no rain. As a result the temporary roadside puddles and ditches had contained water for months rather than the few days or week of a normal year. Dragonflies were exceptionally numerous, conspicuous and widespread. In addition to the normal three species of temporary pools three species normally rare to non-existent; ***Erythemis vesiculosa, Pantala flavescens*** and ***Tramea abdominalis***, were encountered in several places.

At Brewer's Bay, Tortola a small, normally seasonal, stream contained a narrow pool some 100 feet long. In August Lianna Jarecki, biology professor at Tortola Community College, had found larval dragonflies here, so we revisited in mid-October. ***Ischnura ramburii*** were abundant (commoner than I have seen them at any site) and ***Erythrodiplax umbrata*** common. The third of the ubiquitous species, ***Orthemis ferruginea***, was absent. One pair of ***Tramea abdominalis***, several ***Pantala flavescens*** and several ***Erythemis simplicicollis*** completed the list. Four of the five species were laying eggs but there were no larvae found despite extensive searching.

On Guana Island there are several steep gullies (ghuts) which have small pools after heavy rains. A check of all the major ghuts revealed only one pool still in existence a few days after the last rain. This was a tiny, but deep, rock pool with lots of algae. Sweeping this produced large larvae of ***Tramea abdominalis***. However only ***Erythrodiplax umbrata*** and ***Orthemis ferruginea*** adults were present at the pool. ***Orthemis ferruginea*** larvae (2) were found in a tiny, heavily shaded, semi-permanent, garden pool. Thus in what may have been the best year ever for dragonflies on Guana Island there were fewer than a dozen larvae developing and all in pools that were not present in other years. As in other years the small freshwater seep where the vast majority of the dragonflies congregated and lay eggs was oil coated and didn't have larvae. Only one ***Ischnura ramburii*** was seen this year on Guana Island. This and the scarcity of larvae would support my previous position that the adults seen on the island are all immigrants from other breeding sites.

The BVI list now contains one damselfly and ten dragonfly species. Larvae or exuviae have been found of only 4 species but all except ***Pantala hymenaea*** and ***Tramea calverti*** are now considered to be resident or regular transient breeders. A sight record of ***Anax*** sp? (***junius***) in 1997 and a sighting after Hurricane Jose of an ***Aeshna*** sp? (Oct. 21, 99 on Guana Island) indicate the list is still very incomplete.

RESPONSE OF *PANTALA FLAVESCENS* TO STORMS -- The small size of Guana Island and limited water habitat provides an opportunity to document the sudden appearance of dragonflies after a hurricane. In the predawn of October 21 the minimal hurricane Jose passed directly over the island and for most of the day there were sw winds of 30-50 mph but very little rain.

Pantala flavescens suddenly appeared in numbers within hours after the passing of the hurricane. There were 15 in one spot and the species was widespread on the island. In the afternoon a single female was laying eggs at the seep. Prior to the hurricane there had been sightings or possible sightings on only 5 of 14 days and never more than 2 individuals. The only egg laying was a female at the recently painted dining room floor.

On the morning of the 22nd (24 hours after the eye of the hurricane had passed) it was sunny and calm and there were at least 6 pairs at the seep and several unattached males patrolling. Four of the females laid in tandem, one with male guarding and one separately.

It appears that the storm conditions stimulated the individuals to move, congregate and breed. The species was certainly uncommon on Guana prior to the storm and although more common on Tortola there were no concentrations or egg laying observed. Unfortunately we left the island at 10AM the 22nd and were not able to watch the conclusion of this buildup.

ACKNOWLEDGEMENTS
We want to thank the Jarecki family, the Falconwood Foundation and Skip Lazell of The Conservation Agency who in different ways combined to make our trip to the British Virgin Islands possible. Thanks to Nancy Woodfield of the National Parks Trust for information on the botanical gardens, and to Lianna Jarecki for information about Brewers Bay.

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Camponotus ustus Forel and Two Similar New Species from Puerto Rico (Hymenoptera: Formicidae)

Roy R. Snelling[1] and Juan A. Torres[2]

ABSTRACT. Although *Camponotus ustus* Forel, originally described from St. Thomas, now a part of the American Virgin Islands, has been long considered common in Puerto Rico, we found that such specimens are misidentified and actually represent two distinct species, both previously undescribed. These are described herein as *C. kaura* and *C. taino*. Based on the types and additional material from Mona Island, we have redescribed *C. ustus*. The following new synonymy is proposed: *C. ustus* = *C. ulysses* Forel = *C. furnissi* Wheeler and Mann = *C. sublautus* Wheeler and Mann = *C. depolitus* Wheeler = *C. larvigerus* Wheeler and Mann = *C. larvigerus maculifrons* Menozzi. One purported Colombian variety, *arhuacus* Forel, is tentatively elevated to species. All three species are illustrated, and a key is provided, in English and Spanish, for the separation of the *Camponotus* of Puerto Rico and the Virgin Islands.

RESUMEN. Aunque *Camponotus ustus* Forel, originalmente descrita de la Isla de St. Thomas, se ha considerado común en Puerto Rico, hemos encontrado que estos especímenes had sido identificados incorrectamente y actualmente representan dos especies diferentes y sin describir. Estas nuevas especies son descritas aquí como *C. kaura* y *C. taino*. Basado en los tipos de *C. ustus* y material adicional de la Isla de Mona, hemos redescrito esta especie; las subespecies de *C. ustus* de La Española (*ulysses* Forel, *furnissi* Wheeler y Mann, *sublautus* Wheeler y Mann, y *depolitus* Wheeler) son tratadas como sinónimos. Una variedad presumiblemente Colombiana, *arhuacus* Forel es tentivamente elevada a especie. Las tres especies son illustradas y una clave es presentada, en inglès y español, para identificar las especies de *Camponotus* de Puerto Rico y las Isla Virgenes.

INTRODUCTION

Wheeler (1908) recorded specimens from several Puerto Rican localities as *Camponotus ustus,* and subsequent researchers (e.g., Smith 1937) have been content to accept that identification. We examined many of the specimens seen by Wheeler, Smith, and others; it quickly became apparent that we were dealing with a mixed lot that actually consisted of two species. In order to determine which was the true *C. ustus,* described from St. Thomas, Virgin Islands, RRS examined the syntypic series in the Museum d'Histoire Naturelle, Geneva (MHNG). Despite the unusually poor condition of the few specimens available, it became clear that neither of the Puerto species was conspecific with those syntypes. We were further able to determine, after examining type material of similar-appearing taxa described from other Greater Antillean islands, that neither had been previously described from elsewhere and that both appear to be Puerto Rico Bank endemics.

In order that the names might be available for use by other researchers, in advance of our general treatment of the Puerto Rican ants, we here recharacterize *C. ustus* and describe as new the two Puerto Rican species.

SPECIMENS EXAMINED

In addition to the abundant Puerto Rican material deposited in the Los Angeles County Museum of Natural History (LACM), we have studied important syntypic and other specimens in the collections of the Museum of Comparative Zoology (MCZ), the Museum d'Histoire Naturelle, Geneva (MHNG), and the National Museum of Natural History (USNM).

TERMINOLOGY

The morphological terminology used below is consistent with most recent literature on ant systematics (e.g., Bolton 1994). We differ from Bolton in some respects. For example, we consider the ant head to be hypognathous; therefore, the vertex ("occiput" of some authors) is dorsal, rather than "posterior" and the mandibles are ventral, rather than "anterior." It follows, then, that the antennal sockets and frontal lobes are on the front of the head, not on the "dorsum." The following acronyms and special terms are used in the descriptions:

Cephalix Index (CI)—The ratio of head length

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[2] Departamento de Biologia, Universidad de Puerto Rico, P.O. Box 23360, San Juan, PR 00931-3360, and Instituto Internacional de Dasonomia Tropical, USDA Forest Service, P.O. Box 25000, Rio Piedras, PR 00928-2500.

Contributions in Science, Number 469, pp. 1–10
Natural History Museum of Los Angeles County, 1998

wide as long and almost 4× as wide as propodeum at summit of "declivity." Profemur about 3.5× as long as deep.

Pronotum with 4–6 long erect setae on each side that are weakly inclined forward, longest about 0.9 × MOD; mesonotum with (usually) 3 seta pairs, middle pair longest; summit of propodeal "declivity" with 4 or 5 long setae. Profemur with 1–3 long setae on posterior face and about 6 well-spaced, short setae along ventral margin, longest about 0.20 × depth of femur; meso- and metafemora each with variable number of ventral setae on basal one-fourth to one-third; tibiae without erect or suberect setae; meso- and metatibiae without row of graduated bristles along flexor surface.

Petiole scale thin-cuneate in profile, summit acute; summit, in posterior view, broadly and evenly convex; summit with 3–4 long setae on each side, longest at least subequal to longest pronotal setae.

Gaster moderately shiny, weakly transversely lineolate. T1 with 2 or 3 weakly defined rows of long discal setae in addition to marginal row; longest setae at summit of basal declivity longer than MOD; each following tergum with 1–3 ill-defined transverse rows of long setae.

Color yellowish to brownish or reddish yellow, usually with lower face and frons conspicuously darker; mesosoma with varying degrees of infuscation; terga more or less brown banded.

Media and minor workers, measurements (mm) (*n* = 45): HW 1.07–1.41; HL 1.49–1.80; SL 1.79–1.96; WL 2.3–2.7; TL 6.2–7.7. *Ratios and indices:* CI 127–141; SI 109–122; OI 27–28; OMR 65–71. Generally similar to major workers, but more slender and with more elongate and parallel-sided heads that lack defined dorsolateral lobes (Fig. 2).

Female, measurements (mm) (*n* = 6): HW 1.58–1.86; HL 1.84–2.12; SL 1.68–1.90; WL 3.4–3.8; TL 10.1–10.7. *Ratios and indices:* CI 114–119; SI 87–90; OI 29–32; OMR 83–91.

Head (Fig. 3) margins less convergent below than in major worker, LHW about 0.74 × HW; vertex weakly convex and without defined dorsolateral lobes. Eyes large and extending slightly beyond head margins in frontal view; ocelli small, IOD about 3 × OD; OVD (frontal view) about 2.5 × OD. Scape surpassing vertex margin by about 0.3 × SL. Sculpture and pilosity about as described above for major.

Mesosoma (Fig. 5) normal-shaped for alate female. Propodeum with short dorsal face, broadly rounded into declivity and with several (4–6) long setae slightly above middle of declivity. Legs as described above.

Petiole and *gaster* about as described above.

Male: see Discussion below.

DISCUSSION. Males of the 3 species treated here are similar: all are yellowish to brownish yellow, often with limited darker brownish areas on the head and mesosoma. They are similar in size, about 4.5–5.5 mm long. The smallest of the 3 species is *C. taino,* in which males are seldom over 4.6 mm long, but some individuals up to 4.9 mm long have been seen; HW usually falls between 0.69–0.73 mm and occasionally reaches 0.76 mm. Males of the 2 remaining species, *C. kaura* and *C. ustus,* are usually about 5.4–5.6 mm long, but with some individuals above and below that range. In *C. ustus,* HW ranges between 0.88 and 0.95 mm; too few are available for a trend to be clear, but HW is usually over 0.90 mm. Males of *C. kaura* are a little smaller, with a HW ranging between 0.78 and 0.91 mm, and in over 90% of the 54 males measured it exceeded 0.80 mm, with over 70% falling between 0.82 and 0.91 mm.

The ocelli of *C. kaura* males are generally larger, and the IOD ranges between 1.5–2.5 × OD; in most examples, it is 2.2 or less. In both *C. ustus* and *C. taino,* the ocelli are smaller, and the IOD is 2.3–2.6 × OD, usually about 2.5 × OD.

Pilosity of the antennal scape is consistently different between the 3 species. In *C. kaura,* it consists exclusively of fine, fully appressed pubescence, except for several long, suberect distal setae. The scapal pubescence of *C. taino,* in contrast, is abundant, coarse, and subdecumbent to suberect; the setae are quite short, less than 0.025 mm long. *Camponotus ustus* is also provided with an abundance of similar short setae, but in addition there are scattered fine suberect setae that are about 0.08 mm long.

The metatibiae reflect similar differences: setae are fine and fully appressed in *C. kaura,* relatively coarse and subdecumbent to suberect and uniformly short in *C. taino,* and, finally, similar to *C. taino,* but with additional scattered longer setae in *C. ustus.*

Camponotus kaura

Snelling and Torres, new species

Figures 7–12

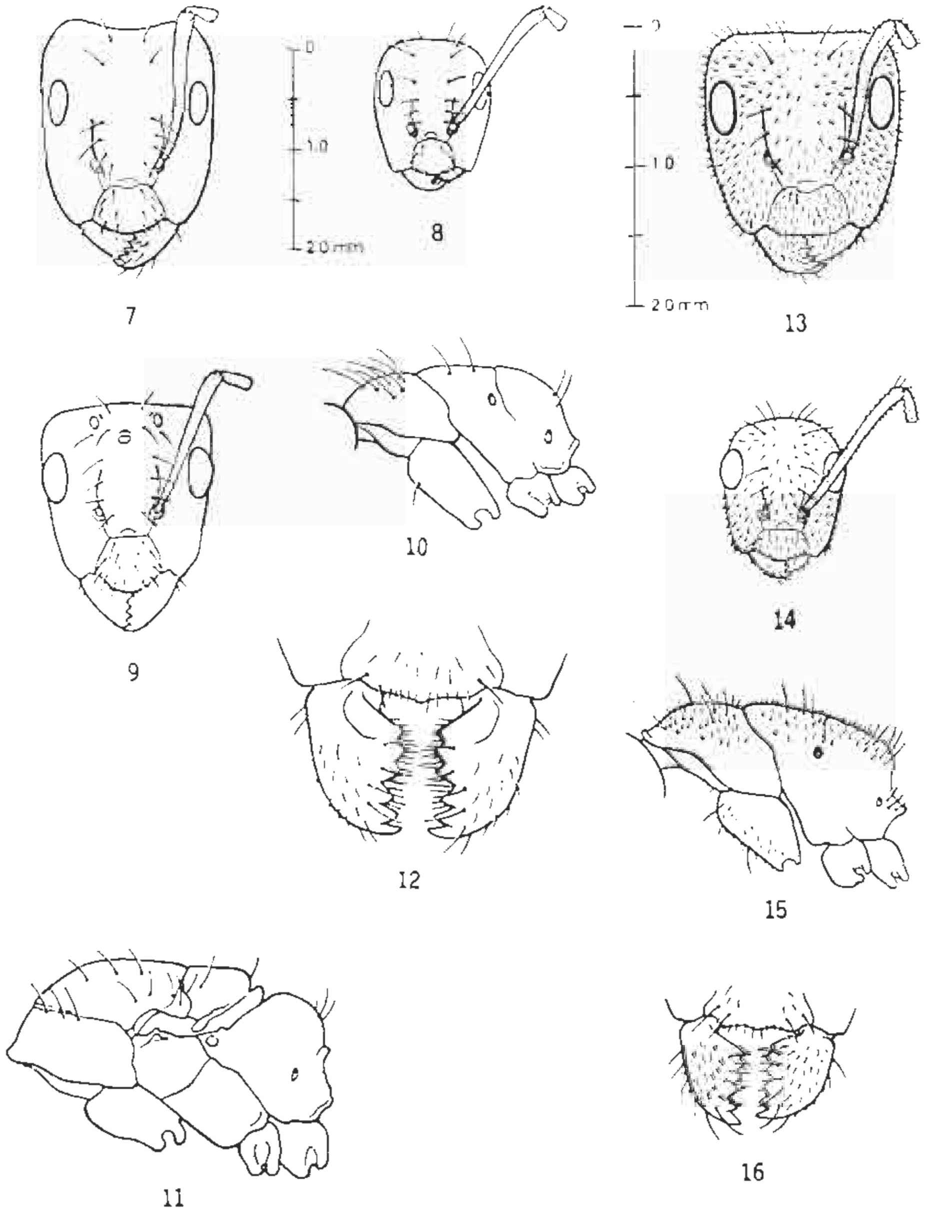
Camponotus ustus: Wheeler, 1908:156. M. Smith, 1937:871–872. In part, misidentification.

Camponotus (Pseudocolobopsis) ustus: Wheeler and Wheeler, 1974:61. Misidentification.

DIAGNOSIS. *Female castes.* Head margins, in frontal view, subparallel and without standing setae between mandible base and dorsolateral angle; antennal scape without standing setae along shaft; free clypeal margin transverse, thin, and without median beveled area above margin; mandible with 6 teeth. *Male:* See Discussion under *C. ustus.*

DESCRIPTION. *Major worker, measurements* (mm) (*n* = 53): HW 1.88–2.16 (2.16); HL 2.10–2.48 (2.44); SL 1.45–1.66 (1.66); WL 2.5–2.9 (2.9); TL 7.5–10.5 (10.5). *Ratios and indices:* CI 105–123 (113); SI 67–72 (68); OI 20–22 (20); OMR 45–50 (50).

Head (Fig. 7) longer than wide in frontal view, sides straight or nearly so, weakly converging below, HW about 0.8 × UHW; dorsolateral lobes distinct and margin between them deeply concave. Eyes large and flat, their outer margins failing to attain lateral head margins by less than minimum



Figures 7–12. *Camponotus kaura.* 7. Major worker, frontal view of head. 8. Minor worker, same. 9. Gyne, same. 10. Major worker, lateral view of mesosoma. 11. Gyne, same. 12. Major worker, mandibles and lower clypeus, enlarged ca. 2×, slightly oblique view. Figures 13–16. *C. taino.* 13. Major worker, frontal view of head. 14. Minor worker, same. 15. Major worker, lateral view of mesosoma. 16. Major worker, mandibles and lower clypeus, enlarged ca. 1.2×, slightly oblique view. Figures 7–11 to same scale; Figures 13–15 to same scale.

diameter of antennal scape. Frontal lobes broad, greatest intercarinal distance about 0.4 × HW; upper intercarinal distance about 0.9 × greatest intercarinal distance. Clypeal midline subangular for most of its length; disc slightly depressed on either side above lower margin; free margin shallowly concave and with blunt median tooth (Fig. 12); in profile, evenly sloping to ventral margin.

Antennal scape distinctly widened distad, extending to, or nearly to, level of dorsolateral lobe. Mandible with 6 teeth.

Front of head slightly to moderately shiny, surfaces finely tessellate; entire front of head sparsely and minutely punctate, clypeus least obviously punctate; mandible moderately shiny between sparse fine punctures that become finer, closer, and more elongate basad and along lower margin; short costae present distad at base of dentate margin. Posterior surface of head shinier, with sparse to scattered minute punctures and coarser, piligerous punctures.

Side of head (including malar area) in frontal view without erect setae; eyes bare; vertex and upper frons with several long setae on each side, outermost longest; frontal lobes with 3 long erect setae widely spaced along carinae. Clypeus with usual basal seta pair and 2 or 3 similar setae along each lateral margin; 4–8 short, erect submedian setae present; 4–6 long, slightly curled, flattened bristles present along ventral margin, extending over closed mandibles. Scape shaft without erect setae. Hypostomal area with 0–4 short erect setae.

Mesosoma (Fig. 10) robust, dorsum moderately convex in profile, metanotal depression weak; posterior declivity weakly concave. Pronotal dorsum about 1.2× as wide as long and about 2.2× as wide as propodeum at summit of declivity. Profemur about 3× as long as deep.

Pronotum with about 10 long suberect to erect setae; longest about 0.4 × minimum eye diameter (MOD); mesonotum with (usually) 4 similar setae; summit of propodeal declivity with 1 pair of long, erect setae. Profemur with 2 or 3 widely spaced erect setae along ventral margin, longest no more than 0.5 × depth of femur; meso- and metafemora without erect setae along either dorsal or ventral margins; all femora with several setae at their apices; all tibiae without erect or suberect setae, but each with several bristles at apex; meso- and metatibiae without row of graduated bristles on flexor surfaces.

Petiole scale thin-cuneate in profile, summit narrowly rounded; summit, in posterior view, varying from weakly concave across middle one-half to weakly convex; summit with 2 or 3 erect setae on each side, longest subequal to longest pronotal setae.

Gaster moderately shiny, weakly transversely lineolate. T1 with 2 long submedian suberect setae at summit and usual marginal row; following segments with transverse median band of wide spaced erect setae in addition to marginal row, setae progressively longer on succeeding segments; appressed pubescence of terga widely scattered and extremely short (<0.03 mm long).

Color basically yellow; areas of varying extent on the head may be darker reddish or even brownish; similarly, metasomal terga may be weakly brown-banded.

Media workers, measurements (mm) (*n* = 6): HW 1.29–1.70; HL 1.38–1.84; SL 1.17–1.35; WL 1.8–2.2; TL 5.8–6.7. *Ratios and indices:* CI 101–108; SI 74–89; OI 23–31; OMR 54–72.

Generally similar to major workers but head more quadrate and without pronounced dorsolateral lobes.

Minor workers, measurements (mm) (*n* = 45): HW 0.85–1.27; HL 1.09–1.56; SL 1.19–1.62; WL 1.6–2.4; TL 4.6–6.6. *Ratios and indices:* CI 117–138; SI 104–113; OI 27–33; OMR 62–90.

Distinctly more slender bodied and with more elongate and parallel-sided heads, vertex evenly convex in frontal view (Fig. 8); antennal scape clearly longer than head; free clypeal margin broadly convex.

Gyne, measurements (mm) (*n* = 11): HW 1.56–1.71; HL 1.78–1.94; SL 1.37–1.49; WL 3.0–3.4; TL 8.8–9.7. *Ratios and indices:* CI 111–117; SI 73–78; OI 28–33; OMR 79–97.

Head (Fig. 9) in frontal view less convergent below than in major worker, LHW about 0.75 × HW; vertex nearly straight across middle. Eyes large and extending slightly beyond head margins; EL about 0.8 × OMD; ocelli small, IOD about 4 × OD; OVD about 3 × OD (frontal view). Scape surpassing vertex by about 0.17 × SL. Sculpture and pilosity about as described above for major.

Mesosoma (Fig. 11) normally shaped for alate female. Dorsal face of propodeum only slightly shorter than declivitous face, abruptly rounded onto it and with 4–6 long setae near summit of declivity. Legs as described above.

Petiole and *gaster* about as described above.

TYPE MATERIAL. Holotype major worker, PUERTO RICO: Caño Gorda, 0–20 m, vic. Guánica, 26 Oct. 1991 (Snelling, Torres, and Canals, RRS #91-14), ex dead wood of black mangrove (*Avicennia germinans*), deposited in LACM. Paratypes: numerous workers, gynes, and males, same data, RRS #'s 91-14 to 91-17; workers, same data except from dead wood of *Coccoloba* (RRS #91-18); paratypes in BMNH, LACM, MCZ, USNM.

ETYMOLOGY. The specific name is a Taino (Arawak) word for a forest dweller; it is to be treated as a noun in apposition.

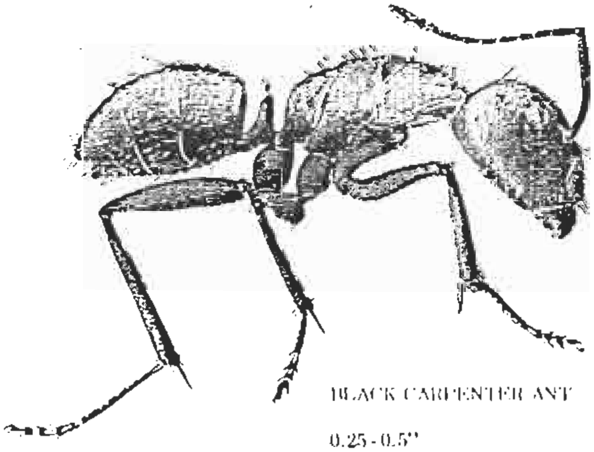
DISCUSSION. In addition to the above paratype material from Puerto Rico, we have seen specimens of all castes from nearly 50 additional sites in Puerto Rico, as well as samples collected by RRS on Tortola and Guana Island, British Virgin Islands.

As noted above in the Discussion under *C. ustus,* we believe that this species is probably a member of the subgenus *Pseudocolobopsis* as that taxon is currently defined.

The material available is generally quite uniform in its features, the most obvious variation being in color. While the color is basically yellow or brownish yellow, the amount and intensity of infuscation of the head of the majors is quite variable. In some individuals, the lower two-thirds of the head may be blackish, but more usually the lower portions of the head are distinctly brown and the remainder is somewhat reddish.

One major worker, from the type nest sample, is unusual in that the head, the longest of any measured, is disproportionately slender for the major subcaste, with a CI of 123. This is the only major examined in which the CI exceeds 113.

This is by far the more common of the two species previously misidentified by Wheeler (1908) and all subsequent authors as C. *ustus*. It is readily separated from C. *taino* by the smooth malar area and lateral margins of the head, since both are devoid of erect setae. This species is separable from true C. *ustus* by the differences in head shape and clypeal structure as noted in the key and figures. In Puerto Rico, C. *ustus* is presently known only from Mona Island.



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REDESCRIPTION OF *NEOTERMES MONA*, A DAMPWOOD TERMITE (ISOPTERA, KALOTERMITIDAE) FROM THE CENTRAL WEST INDIES

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Abstract

The winged imago of *Neotermes mona* (Banks) is described for the first time and the soldier caste is redescribed as two size morphs. The distribution of *N. mona* includes Hispaniola, Turks & Caicos Islands, Puerto Rico, and Virgin Islands. It is the largest kalotermitid in this region.

Key Words: taxonomy, Caribbean, Neotropics, distribution, imago

Resumen

Se describen por primara vez los adultos alados de *Neotermes mona* (Banks) y se redescribe la casta de soldados como formas de dos tamaños. La distribución de *N. mona* incluye Española, las Islas Turcas y Caicos, Puerto Rico y las Islas Virgenes. Este es el mayor kalotermitido de esta región.

For his original description of *Neotermes* (=*Kalotermes*) *mona* from Mona Is., Puerto Rico, Banks (1919) offered little more than a brief soldier comparison with *Incisitermes* (=*Kalotermes*) *schwarzi* (Banks) and *N.* (=*K.*) *jouteli* (Banks) (Banks & Snyder 1920). The description of *N. mona* lacked measurements and was accompanied only by a simple line drawing of a soldier's head and pronotum that resembles Krishna's (1961) definition of the genus *Neotermes*. In light of recent collections of *N. mona* from the Turks and Caicos Is. (Scheffrahn et al. 1990), Mona Is. (Ramos 1946, Jones 1993), Dominican Republic, Puerto Rico, and Guana Is., B.V.I. (Scheffrahn et al. 1994, Collins et al. 1997), and now Vieques Is. (Puerto Rico) and St. John, U.S.V.I., we herein redescribe the soldier as a dimorphic caste and describe the winged reproductive for the first time.

Materials and Methods

Morphometrics of specimens preserved in 85:15 ethanol:water were made with a stereomicroscope fitted with a calibrated ocular micrometer. Specimens for measurement were selected from 81 colony series collected during 1988-1999 from 50 localities on 10 islands in the West Indies (Fig. 1). Measurements of the large and small soldier morphs are presented separately, but other characters do not differ sufficiently to warrant separate descriptions.

Scanning electron micrograph prints were scanned at 600 dpi, and the digital image outline traced using photograph-enhancing software (Photo Magic, Micrografx, Inc., Richardson, TX). The background was converted to black, and the scale bar was digitally redrawn. Latitude and longitude coordinates of collection sites were converted to decimal degrees and mapped (Fig. 1) using ArcView GIS version 3.0a software and relevant map data from Digital Map of the World version 1.0 (Environmental Systems Research Institute, Inc. Redlands, CA).

Neotermes mona (Banks)

Kalotermes mona Banks 1919: 478 [soldier; Fig. 6].
Kalotermes (Neotermes) mona; Snyder *in* Wolcott 1948: 62.
Kalotermes mona; Snyder 1949: 18.
Neotermes mona; Krishna 1961: 322.

Imago (Fig. 2 A-B, Table 1).

In dorsal view, general color almost uniformly ferruginous, except for darker, chestnut brown frons and anterior vertex in majority of specimens, and dark chestnut brown posterior halves of three posterior abdominal tergites. Mandibles dark chestnut brown. Anteclypeus yellowish. Antennae ferruginous orange except for chestnut brown third article. Compound eyes almost black. Chevron pattern on pterothorax faint and wide. Femora yellowish, tibiae ferruginous. Sclerotized wing venation ferruginous, remainder of wings, arolia, and abdominal sternites pale ferruginous orange.

In dorsal view, head capsule suboval with sides rectate and faintly converging to anterior especially in ventral aspect; posterior of head capsule broadly rounded. In oblique view, frons broadly concave, with raised lateral margins, and with delicate striations. In lateral view, frons plane continuous with plane of vertex. Compound eyes large and protruding, subcircular, with long subrectate or slightly concave margins along antennal sockets. Ocelli slightly protruding; comparatively large, oval; broadly contacting eyes. Mandibular bases with striations. Shallow, small, and circular depression centered at intersection of epicranial suture. Head, pronotum, wing scales, abdominal tergites, and sternites with numerous and long setae. Antennae with 19 to 22 articles, usually 21 or 22, relative length formula 2 > 3 > 4 = 5. Pronotum about

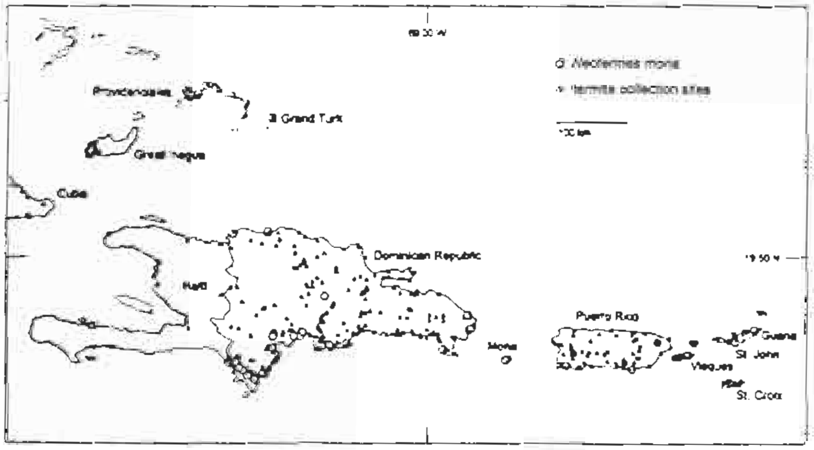

Fig. 1. *Neotermes mona* localities and termite collection sites from 1988-1999.

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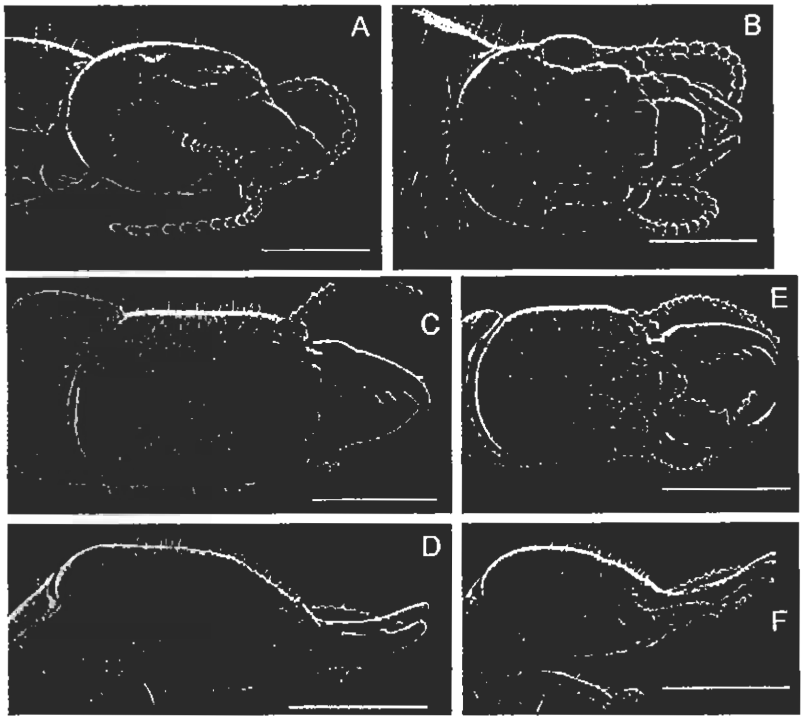

Fig. 2. Scanning electron micrographs of *N. mona*. Oblique (A) and dorsal (B) views of an imago head from Guana Island. Dorsal (C) and lateral (D) views of a large soldier from Guana Island. Dorsal (E) and lateral (F) views of a small soldier from Mona Island. Scale bar equals 1 mm for A-B and 2 mm for C-F.

twice as wide as median length; anterior and lateral margins with raised and rounded rim. Anterior margin of pronotum concave; posterior margin slightly concave. Anterior wings with very long subcosta and radius; subcosta terminating at costal margin near ½ of wing length from suture; radius reaching costal margin at ⅔ of wing length. Radial sector with 4-5 branches along distal half of wing. Sclerotized media with several fine transverse branches to radial sector; posteriorly, few short diagonal and sclerotized branches fade into membrane except for most distal branch that terminates at wing margin. Texture of wing membrane with very faint nodulations. Arolia large.

Comparisons

The alate of *N. mona* resembles that of *N. jouteli*, but the former is larger. Head width at eyes in *N. mona* is ≥2.00 mm, while in *N. jouteli* it is ≤1.81 mm; maximum pronotum width in *N. mona* is ≥2.22 mm versus ≤2.05 mm in *N. jouteli*, and pronotum maximum length is ≥1.49 mm and ≤1.32 mm for *N. mona* and *N. jouteli*, respectively. Total length with wings of the *N. mona* alate is ≥17.89 mm compared to ≤16.05 mm in *N. jouteli*; and wing length from suture is ≥13.35 mm and ≤11.79 mm, respectively. The imago of *N. mona* differs from all other West Indian congeners by its darkened three

TABLE 1. MEASUREMENTS OF *NEOTERMES MONA* IMAGO.

Measurement in mm (n = 5 males, 5 females from 6 colonies)	Range	Mean ± S.D.
Head length with labrum	2.14-2.52	2.38 ± 0.12
Head length to postclypeus	1.63-1.97	1.83 ± 0.10
Head width, maximum at eyes	2.00-2.17	2.10 ± 0.051
Head height without postmentum	1.11-1.21	1.15 ± 0.032
Labrum width, maximum	0.73-0.89	0.82 ± 0.049
Eye diameter with sclerite, maximum	0.57-0.67	0.62 ± 0.033
Eye to head base, minimum from sclerite	0.29-0.38	0.34 ± 0.027
Ocellus diameter, maximum	0.22-0.27	0.24 ± 0.014
Ocellus diameter, minimum	0.16-0.20	0.17 ± 0.011
Eye sclerite to ocellus, minimum	0	0
Pronotum, maximum length	1.49-1.68	1.58 ± 0.068
Pronotum, maximum width	2.22-2.47	2.35 ± 0.095
Total length with wings	17.89-22.01	19.26 ± 1.17
Total length without wings	9.09-11.08	10.08 ± 0.65
Fore wing length from suture	13.35-16.47	14.81 ± 0.80
Fore wing, maximum width	3.56-4.15	3.87 ± 0.17
Hind tibia length	1.77-1.91	1.85 ± 0.041

posterior abdominal tergites. The imago of *N. mona* has a generally darker, ferruginous coloration compared with a lighter ferruginous orange color in *N. jouteli*. The *N. mona* imago has dense pilosity composed of long setae (≤0.3 mm) on the head, pronotum, wing scales, and abdominal sternites and tergites, while the *N. jouteli* imago is adorned with sparse short setae (~0.03 mm long). The setal follicles of *N. mona* are strikingly lighter than the surrounding cuticle, while in *N. jouteli* the follicles are unapparent. The frons of *N. mona* is on an even plane with the anterior vertex, while in *N. jouteli* there is about a 15° slope between the planes of the frons and vertex.

Although alate pilosity characters of *N. mona* are similar to those of *N. castaneus* Burmeister, *N. castaneus* is smaller overall, has much smaller compound eyes than *N. mona*, and its head color is brownish compared to the ferruginous *N. mona* head. The frons of the *N. mona* alate is faintly concave and delicately striate; in *N.castaneus* the frons is faintly convex and striations are absent.

Soldier (Figs. 2 C-F, Tables 2-3).

The soldier caste consists of two distinct morphs, large and small, both usually present in mature colonies. Other than size, there are few distinguishing characters that separate small and large soldiers of *N. mona* compared with some congeners and species in several other kalotermitid genera.

Head capsule generally ferruginous in dorsal view, in some specimens postclypeus, frontal carinae and antennal carinae darker, chestnut brown. Thorax and abdominal dorsum ferruginous orange. Mandibles glossy, almost black, with very dark chestnut brown areas near articulations. Epicranial suture faint or absent. Eyes almost black. Femora yellow-white; remaining sternum pale ferruginous orange. Darker ferruginous postmentum contrasting with ferruginous orange genae.

TABLE 2. MEASUREMENTS OF *NEOTERMES MONA* SMALL SOLDIER.

Measurement in mm (n = 10 from 9 colonies)	Range	Mean ± S.D.
Head length to tip of mandibles	4.37-5.76	4.85 ± 0.52
Head length to postclypeus	2.77-3.42	3.04 ± 0.22
Head width, maximum	2.31-3.13	2.66 ± 0.24
Antennal carinae, outside span	2.18-2.80	2.40 ± 0.19
Head height, excluding postmentum	1.52-1.93	1.83 ± 0.13
Labrum, maximum width	0.64-0.87	0.71 ± 0.069
Postclypeus width, maximum	0.88-1.18	0.98 ± 0.079
Left mandible length, tip to most distant visible point of ventral condyle	2.24-2.84	2.46 ± 0.18
Postmentum, length in middle	1.88-2.34	2.08 ± 0.14
Postmentum, maximum width	0.78-1.06	0.89 ± 0.077
Postmentum, minimum width	0.44-0.64	0.52 ± 0.056
Pronotum, maximum width	2.73-3.28	2.99 ± 0.18
Pronotum, maximum length	1.63-2.02	1.82 ± 0.10
Hind tibia length	1.60-2.15	1.76 ± 0.16
Total length	9.94-13.35	11.39 ± 1.01

In dorsal view, head capsule subsquare, slightly longer than wide, with sides subparallel in large soldiers, faintly convex in small ones; posterior corners of both morphs rounded; median posterior of head capsule rectate. In some individuals of both morphs, sides of head capsule faintly converging anteriorly. Head capsule covered

TABLE 3. MEASUREMENTS OF *NEOTERMES MONA* LARGE SOLDIER.

Measurement in mm (n = 10 from 8 colonies)	Range	Mean ± S.D.
Head length to tip of mandibles	5.69-6.49	6.07 ± 0.30
Head length to postclypeus	3.81-4.31	4.04 ± 0.17
Head width, maximum	2.87-3.43	3.13 ± 0.20
Antennal carinae, outside span	2.57-3.10	2.87 ± 0.17
Head height, excluding postmentum	1.88-2.47	2.27 ± 0.17
Labrum, maximum width	0.72-0.83	0.78 ± 0.044
Postclypeus width, maximum	1.05-1.19	1.13 ± 0.048
Left mandible length, tip to most distant visible point of ventral condyle	2.67-3.07	2.87 ± 0.13
Postmentum, length in middle	2.77-3.10	2.90 ± 0.12
Postmentum, maximum width	0.96-1.14	1.06 ± 0.067
Postmentum, minimum width	0.49-0.54	0.52 ± 0.022
Pronotum, maximum width	3.37-3.96	3.60 ± 0.21
Pronotum, maximum length	2.00-2.37	2.22 ± 0.12
Hind tibia length	1.93-2.20	2.04 ± 0.091
Total length	11.64-15.62	13.48 ± 1.51

with dense mat of setae except on occiput. Body also covered with dense mat of setae. Frons flattened, usually faintly concave. In small soldiers, frons surface smooth; in some of large soldiers frons with very faint reticulate rugosity. Frontal carinae lobed with short pointed tubercle. Labrum linguiform. Mandibles comparatively long and robust; in large soldiers, slightly more robust, with faint, and slightly pilose basal hump; dentition distinct. Antennae with 13 to 19 articles, usually 16 or 17 in both morphs; in small soldiers often only 13 or 14 articles present; third antennal article subclavate, terminal articles usually markedly elongated; antennal formula $2 < 3 > 4 = 5$. Antennal carinae markedly protruding and rugose. Pronotum about twice as wide as long. Anterior margin of pronotum deeply concave; sides of pronotum slightly convex; posterior margin weakly emarginate. All soldiers with short wing pads on meso- and metathorax.

In lateral view, head capsule slightly dorso-ventrally flattened; frons plane sloping 20° from plane of vertex; mandibles moderately curved upward; eyes moderately elongated or less often subcircular, with peripheral satellite facets. Pilosity of frons and anterior vertex much more dense than on occiput. Hind femora moderately broadened in small soldiers and noticeably inflated in large ones. Postmentum narrowed near middle in large soldiers.

Comparisons

Because of size overlap, biometrical separation of small soldiers of *N. mona* from those of *N. jouteli* is possible only on examination of a series of specimens. Both small and large soldiers of *N. mona* tend to be larger than those of *N. jouteli*. In large soldiers, the following measurements do not overlap between these two species. The maximum head width is ≥2.87 mm and in *N. jouteli* ≤2.70 mm, left mandible length is ≥2.67 mm and ≤2.42, maximum width of pronotum is ≥3.37 mm and ≤3.03 mm, and maximum length of pronotum is ≥2.00 mm and ≤1.85 mm, in *N. mona* and *N. jouteli*, respectively. In large soldiers, the mandibles of *N. mona* are more robust but with less developed basal humps and pilosity than those of *N. jouteli*. In small soldiers, the mandibles are more robust in *N. mona* compared to *N. jouteli*, while pilosity and hump proportions are similar. The body of *N. mona* is generally much more pilose than that of *N. jouteli*. The frontal carinae and adjacent frontal area of *N. mona* soldiers exhibit much denser pilosity than in *N. jouteli* in both morphs, especially in large soldiers. The tergum and sternum of *N. mona* soldiers are conspicuously more pilose than in *N. jouteli*.

Material Examined and Measured

USA. Puerto Rico. All samples collected by J. Chase, J. Mangold, J. de la Rosa and R. Scheffrahn. Bosque de Aguirre; 17.93°N, 66.15°W; 1-VI-1993; 1 small soldier (PR-175); 2 large soldiers (PR-176); 1 small, 2 large soldiers, 3 alates (PR-177). Mona Island. All samples collected by S. Jones. Uvero Beach; 18.06°N, 67.90°W; 11-XI-1992; 1 large soldier (PR-409); S. W. airstrip; 18.06°N, 67.91°W; 12-XI-1992; 1 small soldier, 1 alate (PR-416); same data; 1 small soldier (PR-417). British Virgin Islands. Guana Island. North slope near resort; 18.49°N, 64.44°W; 27-X-1992; J. Krecek; 1 small soldier (no. VI-59); same site; X-1991; L. Hernández; 1 large soldier, 1 alate (no. VI-60); same site; 19-X-1992; Krecek, light trap; 1 alate (no. VI-61). British West Indies. Turks & Caicos Islands. Grand Turk Island. 21.46°N, 71.14°W; 6-II-1990; Scheffrahn, and B. Diehl; 1 small soldier, 1 alate (TC-21). Dominican Republic. Barahona Prov., Cabral/Barahona Hwy; 18.23°N, 71.13°W; 20-VI-1991; Chase, Mangold, de la Rosa, and Scheffrahn; 1 small, 1 large soldier (DR-27); La Altagracia Prov., Juanillo; 18.48°N, 68.42°W; 11-VI-1992; Chase, Mangold, de la Rosa, and Scheffrahn; 2 small, 1 large soldier (DR-562); Pedernales Prov., 25 km E. Pedernales; 17.92°N, 71.53°W; 28-X-1993; Chase and de la Rosa; 1 alate (DR-864); Puerto Plata Prov., Punta Rucia; 19.88°N, 71.20°W; 21-VIII-1994; Chase, Krecek, de la Rosa, and Scheffrahn; 1 small, 1 large soldier (DR-946); Peravia Prov., 5 km W. Bani; 18.30°N, 70.12°W; 4-VIII-1995; Chase; 1 alate (DR-1209); Pedernales Prov., Pedernales, beach, forest; 18.03°N, 71.74°W; 3-XI-1996; Chase and Krecek; 1 large soldier (DR-1300); Saona Island (new record). La Romana Prov., Punta Catuano; 18.20°N, 68.78°W; 14-III-1995; Chase and de la Rosa; 1 alate (DR-1130).

Additional Material Examined

Paratype: Puerto Rico. Mona Is. No date or collector given; 1 large soldier, 5 small soldiers, 1 presoldier, and many nymphs (MCZ Type 10076). Vieques Island (new record). Between Red Beach and U.S. Navy observation post installation; 21.90°N, 65.37°W; 24-VII-1999; Scheffrahn, Maharajh, and Chase; 1 nymphoid supplementary, many soldiers and nymphs, 2 larvae (PR-648, 650). U.S. Virgin Islands. St. John (new record). Terminus of paved road, Hwy 107, 18.31°N, 64.71°W; 29-VII-1999; Chase; 1 nymphoid supplementary, many soldiers and nymphs (no. VI-97).

DISCUSSION

Long considered endemic to Mona Is. (Wolcott 1948), *N. mona* is now recorded from a wide geography of the central West Indies (Fig. 1). Within this region, Haiti, the larger Caicos Is., and many of the Virgin Is. have not yet been satisfactorily surveyed for termites (Fig.1) and may support populations of *N. mona*. Surveys of Cuba, Jamaica, the Bahamas, and the Lesser Antilles have not yielded collections of *N. mona* (Scheffrahn & Krecek, unpubl. data). A record of *N. mona* from Barbados by Bennett & Alam (1985) is almost certainly based on misidentification. A *Neotermes* species listed as "nr. *mona*" from Cuba (Scheffrahn et al. 1994) is now recognized to be new species (Krecek & Scheffrahn, unpubl. data).

Neotermes mona is the largest kalotermitid in the West Indies. Snyder (1959) mentions that the alate of *N. araguaensis* Snyder, comparable in size with *N. mona*, is the largest *Neotermes* in the New World. At 22, the maximum number of antennal articles for the *N. mona* imago exceeds Krishna's (1961) diagnoses of ≤21 antennal articles for the *Neotermes* and the Kalotermitidae.

Dispersal flights of *N. mona* are nocturnal. On several occasions, JK observed alates flying around lights between 0100 and 0200 hours in the Dominican Republic and Guana Is. in October and December. Compared with some Kalotermitidae (e.g., *Cryptotermes* and *Incisitermes*), the alates of *N. mona* exhibited robust flight behavior and lacked the tendency to shed wings shortly after alighting.

Neotermes mona is usually a coastal inhabitant where it colonizes substantial woody growth of dry littoral forests, including arboreal cacti and mangroves. This species has also been collected from wood in service (Wolcott 1948, Scheffrahn et al. 1990), however its economic significance appears limited. Galleries of *N. mona* infestations occasionally extend into the xylem elements of living trees or near the tidal zone of dead mangrove trunks; possibly as moisture refugia during drought. Collins et al. (1997) rank *N. mona* as the termite species from the British Virgin Is. having the greatest moisture requirements. Their ranking was based on climatological factors of the 19 islands surveyed and not on experimental data. We contend that, contrary to the rankings of Collins et al. (1997), *N. mona* has a substantially lower moisture requirement than sympatric termite species in the families Rhinotermitidae and Termitidae that have soil access.

In a study of the phylogeny of 10 kalotermitid species, Luykx et al. (1990) selected 13 morphological characters (7 imago and 6 soldier) for cladistic analysis. In their data matrix, the eye pigmentation character for the *N. mona* soldier was erroneously scored as being absent, when it is indeed heavily pigmented. As a result, there are no morphological differences for the selected characters among *N. mona* and its primarily allopatric congeners, *N. jouteli* and *N. luykxi* (Nickle and Collins). Therefore, the morphological cladogram of Luykx et al. (1990) must be revised to show these three *Neotermes* as sister species.

Acknowledgment

The authors thank James A. Chase, John R. Mangold, and Julian de la Rosa for their unyielding efforts to collect termites in the West Indies. We also thank Diann Achor at the University of Florida, Lake Alfred Citrus Research and Education Center, for assisting with scanning electron microscopy; P. D. Perkins, Museum of Comparative Zoology, Harvard University, Cambridge, MA, for the loan of the *N. mona* paratype, and F.W. Howard and T. Weissling for their critical reviewing of this manuscript. Florida Agricultural Experiment Station Journal Series No. R-07236.

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POPULATION ECOLOGY

Nest Growth and Survivorship in Three Species of Neotropical *Nasutitermes* (Isoptera: Termitidae)

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ABSTRACT Long-term growth and survivorship of individual arboreal nests were studied in three species of Neotropical termites in the genus *Nasutitermes*. Of the 29 *N. corniger* (Motschulsky) and seven *N. ephratae* (Holmgren) nests monitored in an area of young second-growth in Panama, 12 (41%) *N. corniger* and four (57%) *N. ephratae* nests remained active throughout the 9- to 11-mo study. There was no significant difference in survivorship between small and large nests of either species. In surviving *N. corniger* nests with a single queen, the net increase in volume was highly correlated ($r = 0.87$, $n = 9$) with queen wet weight. There was a marked seasonality to nest expansion in both *N. corniger* and *N. ephratae*, with growth occurring almost exclusively during the wet season. Seventeen *N. acajutlae* (Holmgren) nests were monitored for 4–9 yr on Guana Island, British Virgin Islands. Four of the 17 (23.5%) *N. acajutlae* nests survived the study period, and two more abandoned their original nest and relocated. Within this limited sample of colonies, *N. acajutlae* nests that were large (>150,000 cm^3) at the beginning of the study had a higher probability of survival than did small (<100,000 cm^3) nests. Nest budding, relocation, and resprouting are mechanisms that *Nasutitermes* may use to create a new nest for all or a portion of an established colony. The ontogeny of incipient *Nasutitermes* colonies is discussed as a sequence in which a young colony remains cryptic within wood, building its population size to a point where the colony can maintain and defend a nest. Early in a wet season, termites then venture from within wood to build and occupy a small arboreal nest.

KEY WORDS *Nasutitermes acajutlae*, *Nasutitermes corniger*, *Nasutitermes ephratae*, termite colony survivorship, termite colony longevity, arboreal nests

THE TROPICOPOLITAN TERMITE genus *Nasutitermes* (Termitidae: Nasutitermitinae) is the most speciose of all isopteran genera, containing 74 described species from the Neotropics alone (Constantino 1998). Unlike most termites, many species of *Nasutitermes* build arboreal carton nests composed of masticated wood and occasionally other materials such as sand cemented together with salivary and fecal fluids (Light 1933, Emerson 1938, Thorne et al. 1996a). The majority of nest-building termites construct mounds on the ground, but nesting in trees has enabled species of *Nasutitermes* and several other genera to colonize and exploit a new habitat (Emerson 1938, Noirot 1970).

Nasutitermes nests are built on the trunk or on or around a branch of a host tree. Typically, the termites build a network of trails or "galleries" from the nest to other regions of the tree, down the trunk (sometimes within the trunk), or along the underside of branches to connect the nest with other food sources in the area. *Nasutitermes* nests reach enormous sizes in some species, occasionally exceeding 2 m in height (e.g., *N. acajutlae* Collins et al. 1997; Haverty et al. 1997; *N. rippertii* (Rambur) R. H. Scheffrahn, personal communication). In all species of arboreal *Nasutitermes*, nests are built with reinforced, dense zones of carton that act to protect at least the queen cell from vertebrate predators, damage from a falling branch, or toppling of the nest by a storm or decay of its host tree (e.g., Hubbard 1877, Andrews 1911, Emerson 1938, Thorne 1980, Lubin and Montgomery 1981). These termite nests thus represent the focal reproductive location for the colony, the hub of its foraging network, and a substantial investment of time and energy in construction and maintenance.

In this article we report on long-term studies of arboreal nest growth and survivorship in three species of Neotropical *Nasutitermes*. "Nest growth" refers to the expansion of their carton nest by the termites housed within; "nest survivorship" means survivorship of the termite colony, or portion of the colony, active within the nest. Twenty nine nests of *N. corniger* (Motschulsky) and seven nests of *N. ephratae* (Holmgren) were followed for 9–11 mo in Panama, and 17 nests of *N. acajutlae* (Holmgren) were monitored for 4–9 yr on Guana Island, British Virgin Islands. We tested the null hypothesis that colonies in large and small nests have an equal probability of survival, even though larger nests have a greater volume and physical structure to protect them from injury or disturbance, and they have already survived through the early age classes. The processes of incipient nest formation and relocation of established nests are also discussed.

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Materials and Methods

Study Area. All of the individual *N. corniger* ($n = 29$) and *N. ephratae* ($n = 7$) nests monitored in Panama were located in an area of young second-growth that had been burned 3–6 yr previously, with only small trees left standing, near Frijoles, a settlement on the south shore of the Panama Canal, Panama (9° 09′ N, 79° 51′ W) (Thorne 1983). Every arboreal nest within that region of second-growth was included in the study. All nests were located within a radius of 0.5 km. The *N. acajutlae* nests ($n = 17$) were on or near the flats of White Bay Beach of Guana Island, a small (340 ha; highest peak 246 m), but biologically diverse, reserve in the British Virgin Islands (Lazell 1996). The majority of *N. acajutlae* nests on the White Bay Beach flats were part of the study; however not every nest in the area was included because some were too high in the canopy to measure accurately. In the Panama site by agreement with the landowner, and on Guana Island because it is managed as a conservation area, all nests were left undisturbed by humans during the course of the study.

Nest Measurements. All individual nests included in this study were accessible by standing or climbing. Measurements of the hemiaxes (height, width, and depth) were taken with a measuring tape and recorded on each monitoring date. The position of these measurements was generally at the maximum dimension of height, width, or depth, although if the nest had an exaggerated protrusion that compromised the typically ellipsoidal shape (irregularities most likely to occur in *N. corniger*), account was taken and the recorded measurement was the best fit to a more regular ellipsoid. Nest volumes (cm^3) were estimated as the volume of an ellipsoid ($4/3\ \pi$ a b c, where a, b, and c are lengths of the hemiaxes) (Thorne 1980, 1983, 1984, 1985; Levings and Adams 1984; Leponce et al. 1995). [Note that Weigert (1970) and Weigert and Coleman (1970) used nest length × width × height as an index of arboreal *Nasutitermes* nest volume, and Clarke (1993) used the maximum perimeter of arboreal *Nasutitermes* as a volumetric correlate]. In Panama, portions of all host tree trunks or branches encased by the nest were measured. Their volumes were calculated as cylinders, and subtracted from the total nest volume measurement to yield the volume of the nest carton. On Guana Island the *N. acajutlae* nests were built on substantially larger trees (often on mature sea grape, *Coccoloba uvifera;* Polygonaceae), and were typically perched on the trunk, on a branch, or at the junction of the trunk and a branch. Wood from the host tree did penetrate nests, but for practical reasons the volume of enclosed wood could not be measured precisely. Because these *N. acajutlae* nests were much larger than the Panama series in total and in proportion to wood encased by the nest, host tree wood was not measured or subtracted from the calculation of nest volume.

In Panama, nest measurements were taken during the months of May to July 1979, with additional nests added to the study group throughout that time as different areas of the site were explored (two additional nests were added to the study in October 1979). In total, 29 *N. corniger* nests were included in the study, along with seven *N. ephratae* nests within the same site. Further measurements on the Panama nests were taken from October 1979 to January 1980, with the final measurement of surviving nests made on 1 April 1980.

In total, 17 nests of *N. acajutlae* were measured on Guana Island. One was first measured in July 1989, and 11 additional nests were first measured in October 1992. Subsequent measurements were made in October of 1993, 1994, and 1998. An additional nest was added to the study in 1993 and four more nests were added in 1994.

At the same time that individual nests were measured, photographs of each nest were taken from a specific position and orientation and repeated at each monitoring interval to record the nest profile(s). Scale rulers included in the photos could be used subsequently to check measurements, and photos could be compared with document nest growth.

Nest Dissections. Weights of queens in *N. corniger* colonies were determined following complete dissection of the nest and removal of the queen from the royal cell. Entire carton nests were excised from the host trees (wood encompassed by the nest was included in the sample), placed in thick plastic bags, and transported to the Smithsonian Tropical Research Institute's laboratory on Barro Colorado Island, Republic of Panama. Colonies were refrigerated for 24–48 h to inactivate the termites. Nests were then sequentially shaved and shaken over a collection tray, allowing termites to fall from the exposed galleries. Upon location of the royal cell, the sides were scraped carefully to open the royal chamber and collect the queen(s).

Data Analysis. Nest volumes were calculated for each observation and plotted over the entire length of each study to visualize the variation in growth rate for the nests of all three species of *Nasutitermes.* Initial size of nests of *N. corniger* and *N. acajutlae* were stratified into small ($<3,000\ cm^3$ and $<100,000\ cm^3$, respectively) and large ($>6,000\ cm^3$ and $>150,000\ cm^3$, respectively) size categories. Survivorship of small and large nests was compared with logistical regression (SAS Institute 1998) and contingency table analysis (Steele and Torre 1960). Chi-square values were tested at the $\alpha = 0.05$ level.

Newly Constructed Nests. Observations on incipient nest formation and on nest relocation were made during the course of the study in both sites. Recognition of these events was possible because of long-term familiarity with established nests, making new nests that appeared during the course of the research available for investigation.

Voucher Specimens. Voucher specimens are deposited in the USNM collection of the Smithsonian Institution.

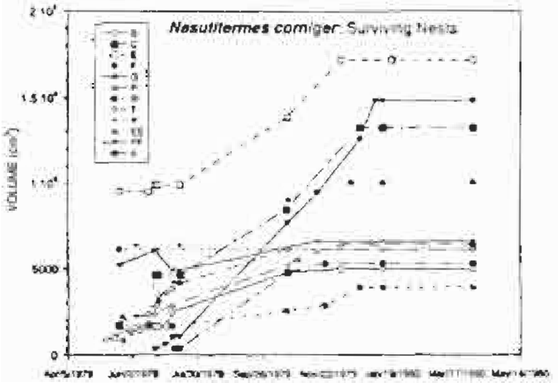

Fig. 1. Growth of *N. corniger* nests that survived throughout the monitoring period. Note consistent lack of growth during the dry season (January through mid-April in 1980). (Figure does not show growth of budded nests.)

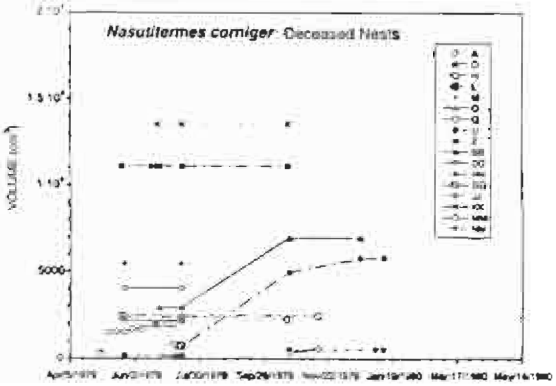

Fig. 3. Growth of *N. corniger* nests that died during the course of the study.

Results

Nest Growth and Survivorship. Of the 29 *N. corniger* nests, 12 (41%) survived the 9–11-mo study period. Of those, only two (17% of the survivors) did not grow at all in external dimensions, but one increased in volume from 296 cm³ on 22 June 1979 to 14,781 cm³ on 5 January 1980, a 4,893% increase in volume in just 6.5 mo (Figs. 1 and 2). Thirteen of the 17 *N. corniger* nests that ultimately died during the study (76%) showed no signs of growth even during the period that they remained active (Fig. 3). There was no relationship between nest volume for *N corniger* at the beginning

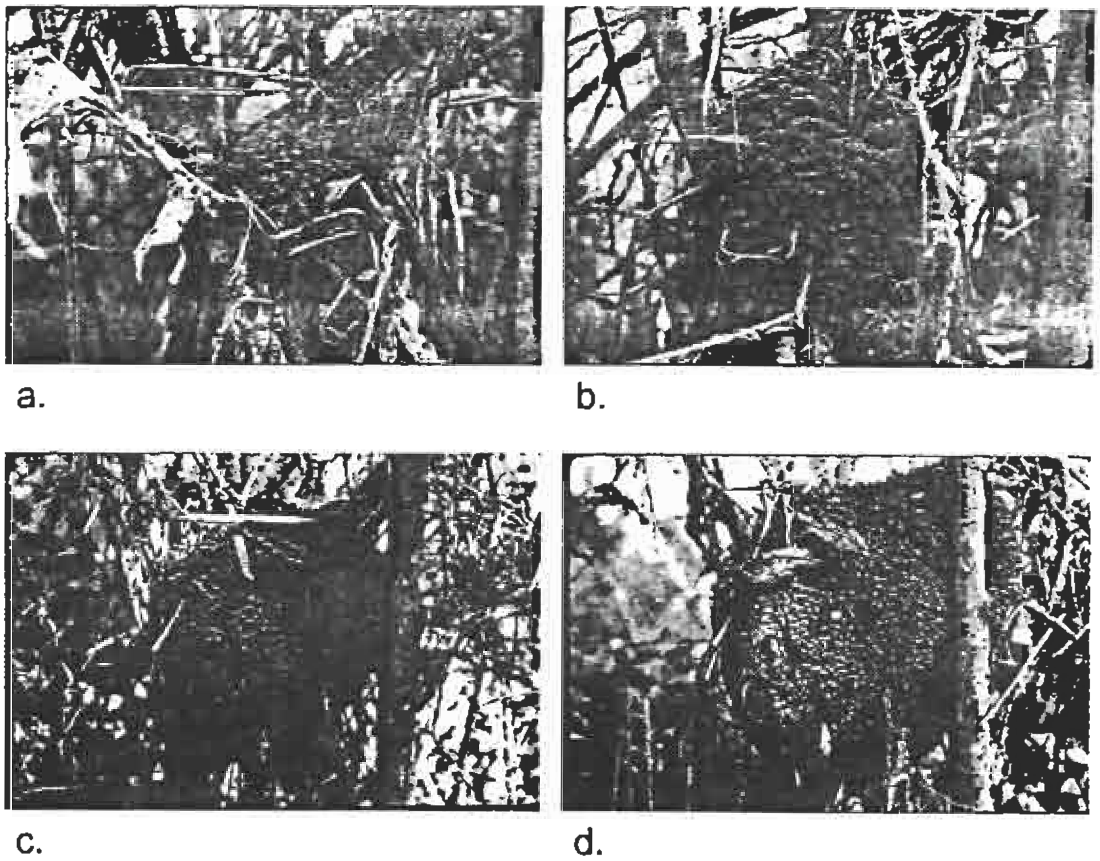

Fig. 2. Growth of *N. corniger* nest FF in Frijoles, Panama, over 5 mo. (a) 22 June 1979. (b) 7 July 1979. (c) 18 October 1979. (d) 14 November 1979.

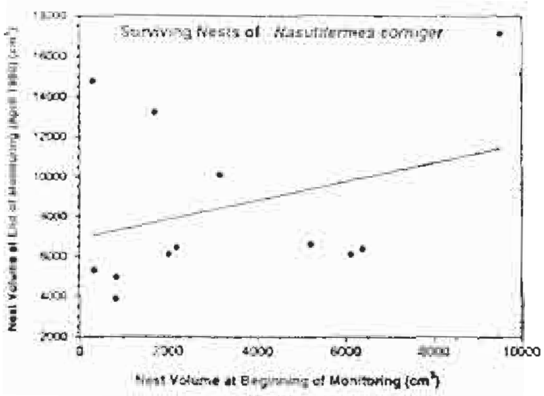

Fig. 4. Relationship between *N. corniger* nest volume at the end of the growth period relative to the initial volume. Data are only from nests that survived the entire study period. The correlation was not significant ($r = 0.32$).

of monitoring and at the end of the monitoring period ($r = 0.32$, $n = 12$) (Fig. 4). Thus, nest size at the beginning of the study was not a good predictor of nest size at the end of the study.

The volume of *N. corniger* nests at the beginning of monitoring (May, June, or July 1979) associated with survivorship to April 1980 is shown in Fig. 5. The two nests for which measurements did not begin until October 1979 (both of which died before April 1980) were not included in this analysis because of a different total monitoring interval. We tried a simple fit using logistical regression and found no significant relationship between initial nest size and survival ($\chi^2 = 0.74$). To test the original hypothesis (Ho: PS = PL, where PS is the probability of survival of small nests, and PL is the probability of survival of large nests), we compared the probability of survival of nests with volumes of <3,000 cm^3 at the beginning of monitoring (PS = 0.375) versus survivorship of nests with a first recorded volume exceeding 6,000 cm^3 (PL = 0.60). There was no significant difference in survivorship over the 9–11-mo period between small and large nests of *N. corniger* ($\chi^2 = 0.86$), leading us to accept the null hypothesis that large and small nests have an equal probability of survival within this population.

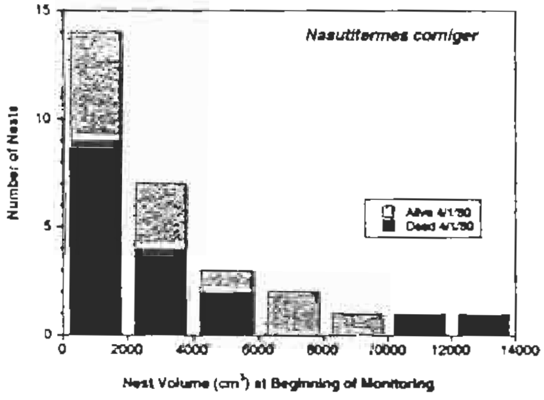

Fig. 5. Survivorship of *N. corniger* nests based on initial size. Monitoring of individual nests began in May, June, or July of 1979.

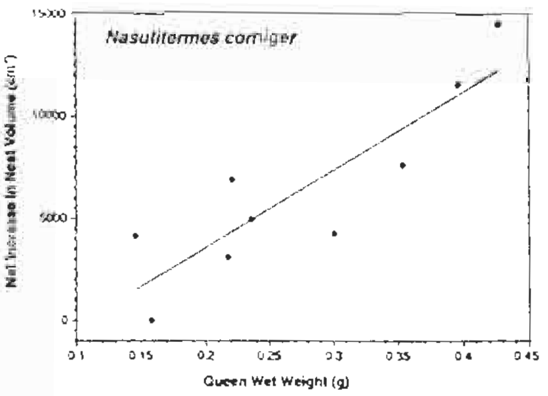

Fig. 6. Relationship between queen wet weight (*N. corniger* colonies with monogynous queens only) and net increase in nest volume during the course of the study. The correlation was highly significant ($r = 0.87$). Monitoring of individual nests began in May, June, or July of 1979. Nests were collected and dissected in April 1980 to expose and measure reproductives.

Another consideration in evaluating growth of *N. corniger* nests is that this species is facultatively polygynous. Because colonies with multiple primary queens grow faster in both population size and nest volume in the early age classes (Thorne 1984, 1985), some of the observed variance in nest growth rates might be explained by queen number. The *N. corniger* nests that survived until April 1980 were collected and all but one (Y) were fully dissected (technique described in Thorne and Noirot 1982). All but two of the nests had a single primary queen; nest G had two queens and nest T contained numerous wingless alates in the queen cell, suggesting that queen replacement was underway. In the monogynous surviving *N. corniger* nests, the net increase in volume from summer 1979 to April 1980 is highly correlated ($r = 0.87$) with queen wet weight at the time of nest dissection (Fig. 6). Notably, several of the nests with the highest growth rates (E, FF, C) also had large queens (>0.35 g). However, nest EE also had a high growth rate, but only a moderately sized monogynous queen (0.22 g) at the time of dissection.

Generalizations about growth rates of *N. ephratae* nests from Frijoles, Panama are risky because of the relatively small number of nests monitored. Four of seven (57%) nests in the study survived the period of the monitoring. The highest growth rate among the survivors was a nest that increased from 1,044 cm^3 on 24 May 1979 to 4,938 cm^3 on 21 November 1979, and then remained at that size through 1 April 1980 (Fig. 7). None of the three nests that ultimately died grew during the study (Fig. 7). One of the four survivors did not increase in size during the monitoring period. The largest *N. ephratae* nest, estimated at 42,272 cm^3 on 24 May 1979, fell to the ground when its host tree, par-

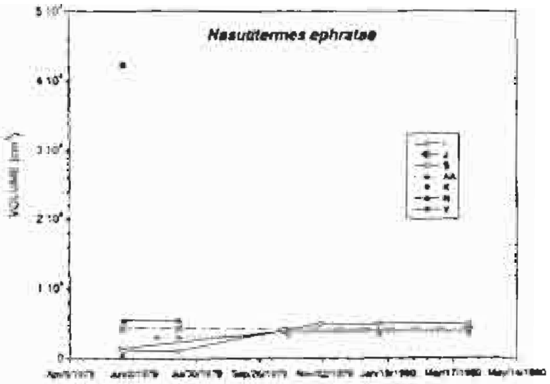

Fig. 7. Growth of *N. ephratae* nests, including survivors (open symbols) and colonies that died (dark symbols) during the course of the study. Note lack of nest expansion during the dry season (January through mid-April in 1980).

Table 1. Volume (cm^3) of nests of *N. acajutlae* on Guana Island, British Virgin Islands, from 1992 to 1998

Colony	Year[b]				
	1992	1993	1994	1996	1998
C1	160,739	186,526	142,424	Relocating	(161,432)[c]
C2[a]	569,185	750,093	902,172		1,251,055
C3	280,730	251,103	288,500		Dead
C4	35,657	Dead			
C5	11,454	23,381	30,192	Dead	
C6	57,738	Dead			
C7	45,629	68,757	87,186	Dead	
C8	9,050	13,205	13,154		Dead
C9	82,491	91,937	Dead		
C10	139,409	208,578	197,072	Dead	
C11	199,444	—	323,421	Relocating	(279,789)[c]
C12	85,790	134,230			287,947
C13		54,629		Dead	
C14			160,896		174,713
C15			66,481		251,983
C16			24,013		Dead
C17			7,830	10,455	Dead

[a] Volume of this colony was 212,171 cm^3 in 1989.

[b] Hurricane Luis damaged buildings on Guana Island in 1995 and limited access to field sites during October, thus no measurements were taken.

[c] These measurements were taken after the colony had relocated.

tially consumed by termites, fell over (event noted and nest dead at 13 July 1979 monitoring). The *N. ephratae* nests that began as the two largest in this study, as well as the smallest nest at the beginning of the project (373 cm^3), died during the course of the research. These trends also suggest acceptance of the original hypothesis (probability of survival is indistinguishable for small and large nests) for *N. ephratae*, although the sample size of seven nests is too small to evaluate with statistical rigor.

There was a marked seasonality to nest expansion in both *N. corniger* and *N. ephratae* (Figs. 1 and 7), with growth usually being limited to the wet season. During the year of the study, the dry season lasted from early January until mid-April 1980. The rare cases in which nest growth did occur over the dry season were in two cases of nest budding in *N. corniger*. Buds had been initiated during the wet season, but there was limited continued growth of the satellite nests during the dry season (budded nests not included in the above data; see below for further discussion of budding).

Nasutitermes acajutlae nests monitored on Guana Island are obviously much larger nests, on average, than for either *N. corniger* or *N. ephratae* at the Panama site (Table 1). *N. acajutlae* characteristically builds larger nests than *N. corniger* or *N. ephratae*, and the habitat for the *N. acajutlae* study was mature vegetation, whereas the Frijoles, Panama, site was young second growth. Of the 17 *N. acajutlae* nests tracked on Guana Island, only four of the 17 (23.5%) survived the duration of monitoring (generally 4–6 yr; 9 yr for a single colony which was a survivor) (Fig. 8). Of the remaining 13 nests, 11 (64.7% of the total) died (Fig. 9), and two (11.8% of the original number) abandoned their original nest and relocated (see below). Including the two relocated but surviving colonies, plus the four nests that remained active during the course of the study, six of the total of 17 colonies (35%), survived the total period of the research. The simple fit using logistical regression revealed no significant linear relationship between initial nest size and survival (χ^2 = 2.47). In contrast with *N. corniger*, *N. acajutlae* nests that were large at the beginning of monitoring (>150,000 cm^3) had a higher probability of survival than small nests (<100,000 cm^3) (χ^2 = 3.84) (Fig. 10), although we caution that the sample size was limited, particularly among large nests.

New Nests from Old. There are three circumstances in which a new *Nasutitermes* nest can arise from an established nest. Nest budding, or active division of a *Nasutitermes* colony, involves construction of a satellite nest that remains, for at least some duration, connected to the healthy original nest by galleries and termite traffic between the two (or more) nests (Thorne 1982a, 1984; Levings and Adams 1984; Atkinson and Adams 1997; for further discussion of budding in termites, which can also be a passive process, see Nutting 1969, Thorne et al. 1999). Nest relocation occurs when a colony abandons its original nest and

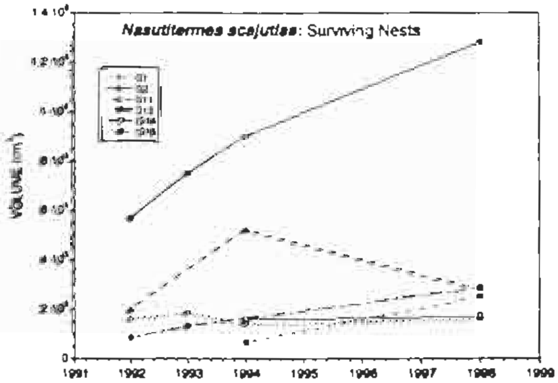

Fig. 8. Growth of *N. acajutlae* nests on Guana Island that survived until October 1998. Growth of relocated nests is not shown.

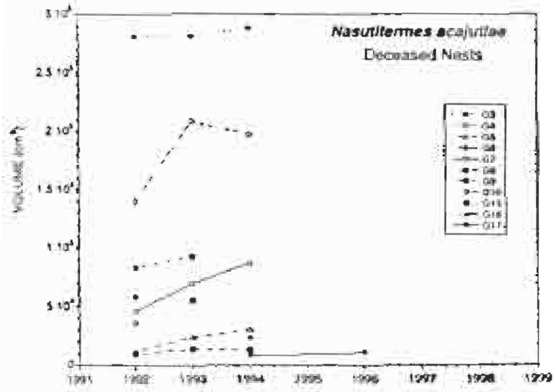

Fig. 9. Growth of *N. acajutlae* nests on Guana Island that died before October 1998.

moves in entirety (including the physogastric queen) into a freshly constructed nest. From our observations, the circumstances initiating such a move always involved dislocation and often substantial injury to the original nest following a fall from its host tree or being tipped over in a mass of fallen branches during a storm. The new nest sites that we observed were all within 10 m of the downed nest, often closer. In one case on Guana Island, an *N. acajutlae* colony (G11) had previously constructed a small, satellite unit of thin carton, apparently used as a foraging hub without reproductives or brood. When the main nest was knocked down, apparently by a storm, the colony relocated into the already established satellite nest, which was rapidly expanded.

Resprouting of a colony occurs when a nest is totally destroyed or removed (as by an armadillo, anteater, or human), and the orphaned termites that remain in the colony's gallery network and foraging locations consolidate and build a new nest. If it is an opportune time of year with alates mature or in development, then alates within the nest may develop into adultoid reproductives and carry on growth of the colony. If nymphs or alates are not present, worker *Nasutitermes* may differentiate into functional ergatoid reproductives under some circumstances (Thorne and Noirot 1982, Noirot and Thorne 1988), or the resprouted nest may remain without reproductives and survive only until its cohort of workers senesce.

B.L.T. observed all three of these rapid nest creation processes in Panamanian *N. corniger*, and documented nest relocation and resprouting in *N. ephratae* in the same habitat. Both authors witnessed relocation of two of the *N. acajutlae* nests in our Guana Island study area, and previously B.L.T. and Margaret Collins observed relocation of a third nest and resprouting of another, also on Guana Island.

Incipient Nests. Long-term observation and familiarity with the sites enabled us to recognize and study newly appearing nests in both the Panama and Guana Island research plots. In Panama, during the course of 2 yr early in the rainy season, B.L.T. observed the appearance, virtually overnight, of four *N. corniger* nests, each 7–10 cm in diameter (nearly spherical, therefore ≈180–524 cm³) and containing ~10,000–16,000 termites (nest only; excludes individuals in foraging galleries and at food sources) (Thorne 1984). On three occasions she found small incipient colonies housed completely within wood, one of which she collected and dissected. That decaying log had no termite carton inside except around a knothole, which was later found to house the tiny royal cell, less than 1 by 1 cm. The primary king and queen inside weighed 0.0063 and 0.0152 g, respectively (wet weights). Approximately 2,000 termites accompanied the royal pair in a 20-cm section of the log.

Arboreal *N. corniger* and *N. ephratae* nests frequently surround a trunk or branch which, when exposed after nest dissection, often contains a hollowed cavity or knothole that served as the original royal cell. In small nests the royal pair may still be lodged in wood; in larger nests the royal cell is generally constructed adjacent to the original copularium. We suggest that the probable ontogeny of arboreal *N. corniger* colonies is that the royal pair remains sequestered in their original copularium embedded in wood for several years as their incipient colony grows. Workers and soldiers in the young colony also remain within the wood, first eating local areas of the host tree and eventually traveling through the tree core, or perhaps building external galleries, to other food sources. Colonies also may be initiated in stumps or logs. When the colony population size approaches 10,000 termites, and when the first rains of the wet season create the right conditions, the colony blossoms into a rapidly constructed arboreal nest, normally adjacent to the royal cell, roughly 10–12 cm in diameter. In this proposed sequence of colony development, arboreal termites remain hidden within their host wood until their colony population size reaches a point that they can repair, maintain, defend, and ultimately expand a visible and exposed nest, although a freshly constructed, small nest remains quite vulnerable. Although some incipient colonies were found within logs, all observed new nests were on trees. This suggests that founding

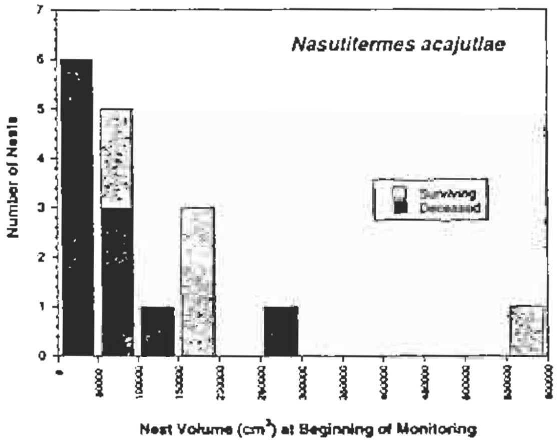

Fig. 10. Survivorship of *N. acajutlae* nests based on size at the beginning of monitoring.

pairs within trees have a higher probability of survival, or that colonies that begin in wood on the ground may move to a tree before or during nest construction. The size of a colony, and its queen, at the time of first nest construction may influence its subsequent rate of growth.

Nasutitermes acajutlae nests on Guana Island were monitored only at yearly intervals so it is impossible to precisely age new recruits or to know their size when they first appeared as carton nests. However, in 1998 we found three new nests that had not been present in 1997. These nests had volumes of 17,981, 7,950, and 7,037 cm^3. We have never seen a *N. acajutlae* nest smaller than 7,000 cm^3 in any habitat, so if they remain cryptic within wood and then "bloom" as does *N. corniger*, a size of ≈7,000 cm^3 may reflect their usual debut size as arboreal nests.

Discussion

There have been very few studies of long-term nest growth and/or survivorship in termites. Banerjee (1975) monitored growth of five incipient colonies of *Odontotermes redemanni* (Wasmann) in India for 2 yr, finding that the annual growth rate of individual mounds was higher for smaller mounds (<75 cm in height) than for larger mounds (>100 cm in height). All five of the mounds that he followed survived the 2-yr study. Roonwal (1977) studied the ratio of height to diameter expansion during growth of mounds of three species of *Odontotermes* in India, determining that the growth pattern was allometric. Korb and Linsenmair (1998) conducted the most detailed demographic study yet completed on termites, measuring a variety of fitness parameters (probability of survival, age of first reproduction, number of alates produced per colony, and lifelong probability of reproduction) on individual *Macrotermes bellicosus* (Smeathman) mounds in an Ivory Coast savanna. This work will be a landmark study when published.

The results of our work on three species of Neotropical, arboreal *Nasutitermes* suggest that a relatively low percentage of individual nests survive for the long term, at least in the sites that we studied. Smaller nests of *N. acajutlae* had lower survivorship than larger nests within this study; the probability of survival of small and large *N. corniger* nests was indistinguishable among nests in this study. Our sample of *N. ephratae* nests was too small to evaluate the association of size and probability of survival. Both the Panama and Guana Island sites were free from human perturbation, but had other risks for termites. In Panama there were anteaters that can climb trees and swipe their sharp claws into *Nasutitermes* nests (Lubin and Montgomery 1981). Once a nest is injured, there are many species of predaceous ants that readily invade *Nasutitermes* colonies. B.L.T. observed *Camponotus* sp. ants clean out an injured *N. corniger* nest in <24 h. Anteaters, ants, or armadillos may attack *Nasutitermes* nests cracked or otherwise damaged after falling from their host tree during a storm. In contrast with Panama, no vertebrate termite predators live in the British Virgin Islands other than lizards that eat termites exploring outside of their nest or galleries. During our 9-yr study, the largest cause of mortality to *N. acajutlae* nests on Guana Island appeared to be hurricanes, with drought stress as another possibly signficant factor. Hurricanes create termite food and habitat by downing trees and branches, but the storms may also dislodge and injure established nests, causing death or inducing the colony to relocate. Inter- and intraspecific competition and territorial interactions among neighboring *Nasutitermes* may also affect growth and survivorship of nests (Thorne 1982a; Levings and Adams 1984; Adams and Levings 1987; Leponce et al. 1995, 1996, 1997). In all three species, the survivorship information presented here does not include the earliest age classes of colonies, which begin sequestered within wood and are therefore invisible to scientists in this type of survey.

In this study we report on the growth and survivorship of individual nests, as opposed to colonies because some *Nasutitermes* are polydomous, meaning that a single intermingling colony may construct and occupy more than one nest (Levings and Adams 1984; Roisin and Pasteels 1986; Adams and Levings 1987; Clarke 1993; Leponce et al. 1995, 1996, 1997; Atkinson and Adams 1997; Thompson and Hebert 1998a, b). Although *N. corniger* colonies are known to form buds and occupy those satellite nests in some habitats (Thorne 1982b, 1984; Levings and Adams 1984; Adams and Levings 1987; Atkinson and Adams 1997), we feel confident that the *N. corniger* nests monitored in this study were each single colonies, not interconnected buds. None of the trails leading from *N. corniger* nests was connected to any other nest. Termites from all nests in the site were evaluated for agonistic behavior in pairwise bioassays, always resulting in aggressive interactions between neighboring nests (Thorne 1982a). The queenright condition of surviving nests, determined upon dissection, suggests that they were independent colonies. Furthermore, the habitat had been cleared of larger trees and burned 3–6 yr previously, so although the *N. corniger* colonies in our study may have been founded before the habitat destruction, they bloomed into arboreal nests within a relatively few years of the beginning of the study. They were thus generally too young to bud, although two of the colonies were observed in the process of budding during the study.

Nasutitermes ephratae colonies are not yet known to bud; the seven in this study were spatially dispersed and almost certainly represented individual colonies. Little is known of colony structure in *N. acajutlae*. Although the monitored nests on Guana appear to represent independent colonies because of a scattered spatial configuration, colonies of the closely related species *N. nigriceps* (Thorne et al. 1994, 1996b) may occasionally occupy more than one nest (Levings and Adams 1984, Clarke and Garraway 1994). Further study of *N. acajutlae* is needed before we can fully interpret the association between nests and colonies.

In both *N. corniger* and *N. ephratae*, nest expansion was confined to the wet season during our study, the only exception being growth of some budded nests. Termites need rain for moisture to open existing walls and effectively masticate materials needed to build additional galleries (Thorne 1984). Colonies may be forced to repair nests during the dry season if that is when an injury occurs, but volume expansion appears to be restricted to the wet season. The occasionally enormous growth rates observed during the course of the wet season may reflect accommodation of a population increase that already occurred, and/or anticipation of growing ranks in the near future. Seasonal patterns of nest growth, particularly following rains, was also noted by Noirot and Noirot-Timothée (1962) in *Cubitermes fungifaber* (Sjöstedt) and by Bodot (1967) in *Amitermes evuncifer* Silvestri, *Cubitermes severus* Silvestri, and *Trinervitermes trinervious* (Rambur) on savannas of the Ivory Coast. Banerjee (1975) reported an inverse relationship between mound building and rainfall in the Indian termite *Odontotermes redemanni* (Wasmann), with reduced construction during heavy rains.

The ability of termite colonies to relocate to a new nest site has been documented in several species. Emerson (1929) witnessed migration of a colony of *Nasutitermes costalis* (Holmgren) including the royal couple, and Emerson (1938) made a persuasive case that every visible arboreal *Constrictitermes cavifrons* (Holmgren) nest is the result of a colony migration because the nests are constructed on living trees with smooth bark, and there is no evidence of excavation of a royal cell into bark beneath the nests. Noirot and Noirot-Timothée (1962) describe nest relocation in *Cubitermes fungifaber* in the Ivory Coast. In the cases of nest relocation that we observed in *N. acajutlae*, *N. corniger*, and *N. ephratae*, colonies abandoned their original nest and moved to a newly built replacement following major disturbance, such as the nest falling to the ground or becoming angled at a severe tilt following storm damage or decay of the host tree. The original nest sometimes was not visibly injured, but repositioned, often in a more vulnerable site.

Growth rates and survivorship of termite nests of a particular species are almost certainly influenced by habitat, season, inter- and intraspecific competitors, and disturbance from predators, drought, storms, and humans. For example, all *N. corniger* nests monitored in this study were in an area of young second growth, a habitat characterized by high vegetative productivity, an age distribution skewed toward young colonies, rapid succession of the young forest and therefore of nest sites, and moderate predator pressure (Thorne 1984). Nest and colony growth and survival rates in this young habitat may be quite different than in a primary forest.

Species of arboreal *Nasutitermes* appear to be remarkably adaptable and resilient, capable of colony budding, relocating, and resprouting to expand and/or adjust to changing circumstances or destruction of the original nest. Despite this flexibility, long-term survivorship of arboreal *Nasutitermes* nests and their associated colonies is low, even though these conspicuous nests appear to be abundant in many Neotropical habitats. Conservation of social insects has only recently been established as an important issue; colonies are now recognized to be more vulnerable than they appear on the basis of numbers of individuals (Pamilo and Crozier 1997). Because of their ecological importance as decomposers, and because they have a lower survival rate than previously predicted, efforts should be made to preserve active *Nasutitermes* nests in natural communities.

Acknowledgments

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27 March 2001

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Dear Skip,

I am writing to summarize the activities of me and Adam Baldinger (Museum of Comparative Zoology, Harvard University) on Guana Island this past October, and update you on our progress and future plans.

As you will recall, Adam and I spent much of the initial visit arranging and eventually attending meetings with Bertrand Lettsome (Chief Conservation and Fisheries Officer, BVI) and Joseph Smith Abbott (Director, National Parks Trust). The meetings were held at the request of the the Minister of Labor and Resources, Mr. Julian Fraser, so that Mr. Abbott and Mr. Lettsome could review our research program. I am pleased to report that the meetings went well, and we have agreed to provide periodic updates on the progress of our findings.

As to our collecting, we were finally able to adequately survey the patch reef and rocks proximal to Bigelow Beach. Unfortunately, time did not allow us to return to Monkey Point, the site of many interesting discoveries, where we hoped to find some of the rare forms we found before. Terrestrially, we collected minute isopods and some land snails from the soil debris adjacent to the "Bat Cave."

We met with an interesting surprise on the patio of the room this year. We collected several large terrestrial isopods which I have not seen before on the island. These conspicuous (10 mm) isopods are closest to *Venezillo culebrae*, which has been found recently on a few islands other than Culebra. But, as you might be aware, the taxonomy of these terrestrial crustaceans is a nightmare, hampered by the older literature often replete with terribly inadequate descriptions. Eventually, I hope to convince

Dr. Stefano Taiti of Italy, a noted expert on tropical terrestrial isopods, to examine these specimens.

Currently, we are working on several projects. First, Adam and Dr. Michael Gable (Eastern Connecticut State University) are describing a new species of the sponge inhabiting amphipod, *Podocerus*, from Monkey Point. They also will report on another species of this genus, previously known only from Brazil.

Second, Adam and I are evaluating the two most conspicuous genera of shore dwelling amphipods, *Ampithoe* and *Hyale*. This is an enormous task because the only reliable way to determine the identity the relevant species is to wade through approximately 125 original descriptions; no world or regional faunal review exists that would allow us to bypass this "legwork."

Finally, aside from the above mentioned projects, we are planning two new ventures. We hope to visit Guana this year with the express purpose of photographing freshly preserved or live specimens. I now have an excellent setup, which we plan to bring to the island, that will allow us to make digital images rapidly. The resulting color information will be valuable in highlighting species differences. Furthermore, after much delay I am developing a website devoted to the microcrustaceans of the island, and our research in general. I expect to go "live" with the website by fall; the new photographs we take on Guana will make a great addition to the website.

Again, both Adam and I wish to thank you and Dr. Jarecki for the opportunity to study on the island.

Best regards,

Eric A. Lazo-Wasem
Collections Manager

cc: Adam J. Baldinger
Museum of Comparative Zoology
Harvard University

Islander

January 1998

Issue 5

Galapagos

Chatham
Islands

Stewart Island

Lamb Island

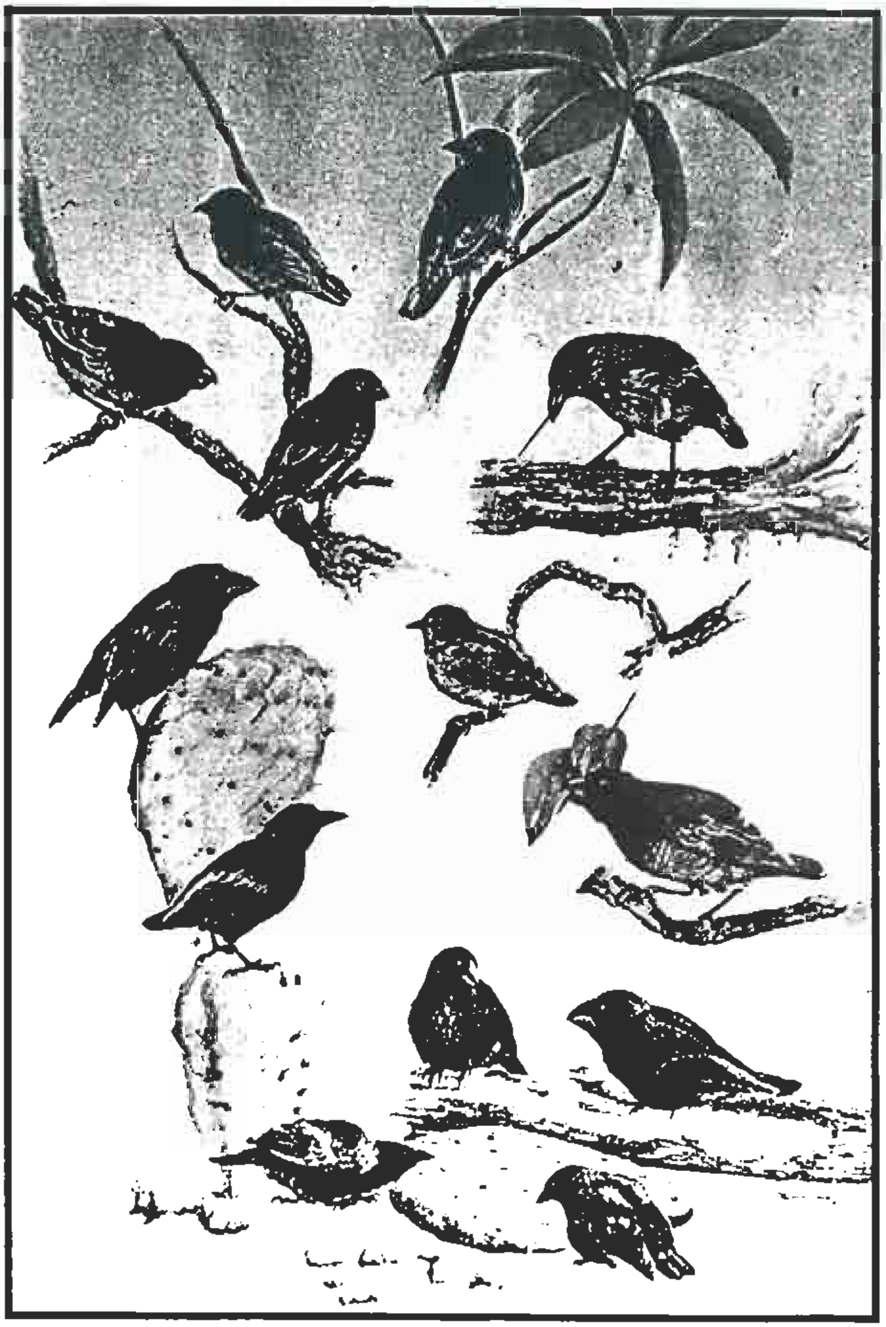
Furneaux Group

British Virgin
Islands

Saba

Bijagos
Archipelago

Welsh
Islands



Environmental Issues in the British Virgin Islands

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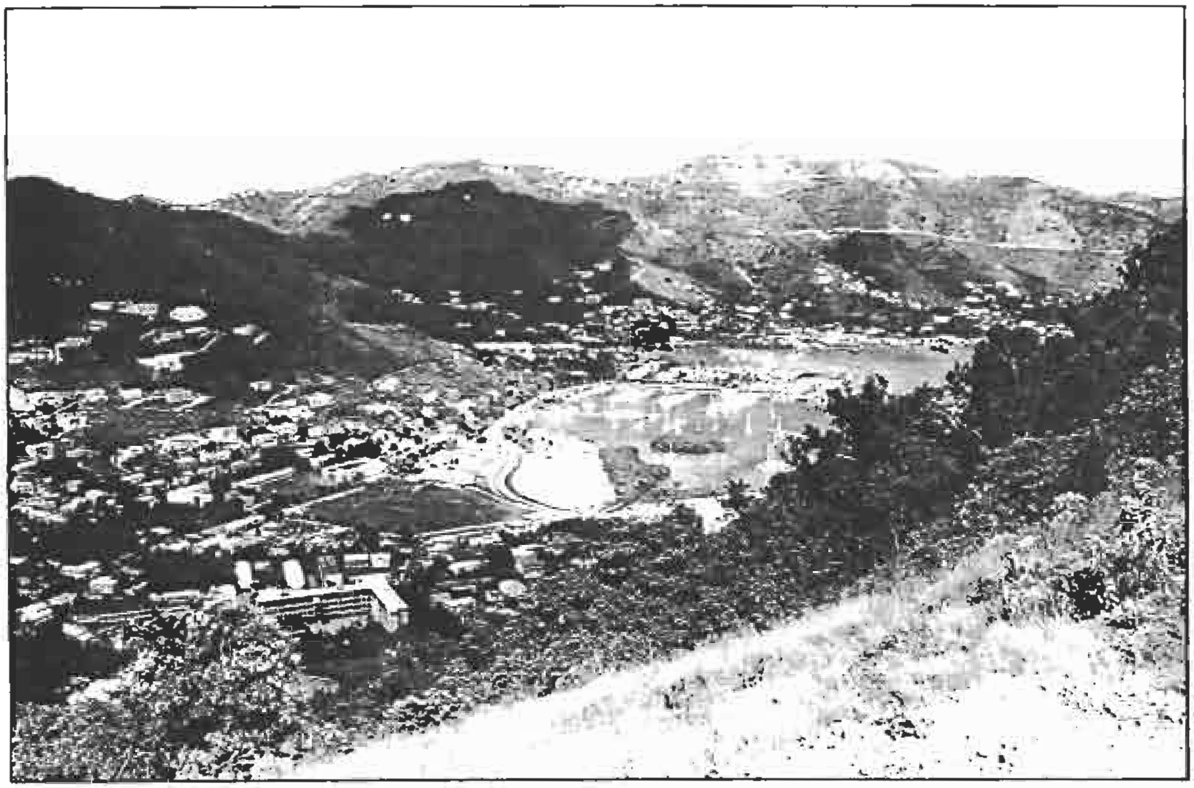


Road Town, Tortola, capital of the British Virgin Islands

The British Virgin Islands lie on the eastern end of the Puerto Rican plateau at approximately 18 N. and 64 W. This island group is comprised of more than sixty islands, cays and offlying rocks with a total land area of just over 150 square km. The eighteen inhabited islands have only 18,000 residents but support over 300,000 tourists annually. To appreciate the environmental problems of the BVI, it is necessary to understand the geological and historical development of the islands.

Volcanic eruptions, earthquakes and other seismic events formed the majority of the British Virgin Islands. Geologic activity stretching back some 70 million years to the late Cretaceous produced the mountainous terrain characteristic of the Eastern Caribbean island arc. These islands remain active as witnessed by recent eruptions on Montserrat, some 300 km to the Southeast. Even today, the Virgin Islands experience numerous earthquakes annually, although most are minor tremors generally going unnoticed. However, earthquakes occuring approximately once each century have altered the topography and caused widespread damage to human habitations. Further changes in topography were associated with sea-level fluctuations during glacial maxima. As recently as 10,000 years ago most of the Puerto Rican plateau was above sea level. Dispersal over land was possible between all the British Virgins and neighbouring islands as well as to Puerto Rico approximately 150 km west. Clearly, the present distribution of flora and fauna was affected by these sea level fluctuations.

Today, the Virgin Island group are pinnacles on the Puerto Rican plateau separated by channels rarely exceeding 50 meters in depth. Both the U.S. and British Virgin Islands extend over a distance of more than 130 km.

The first humans arrived in the eastern Caribbean at least 6,000 years ago, probably island hopping from South America. Evidence of human settlements from the nearby islands of Puerto Rico and Anguilla suggests the British Virgins were inhabited over 4,000 years ago. Recent excavations of a pre-Columbian site on Tortola produced artifacts from the Saladoid and Ostionoid tradition, approximately 600 AD. Pieces of marine shells, sea turtle and other animal bones recovered from middens reveal a dependence upon marine resources for food, tools and other artifacts.

Plantation Era

The recent history of the area begins with the European voyages of discovery. Columbus sailed past the islands in 1493, naming them Las Virgenes after St. Ursula and the 11,000 martyred virgins. Following the initial "discovery," Spaniards briefly inhabited the islands, particularly Virgin Gorda where they started a copper mine. The mine had several periods of activity during it's 400 year history and is currently a national park managed by the BVI National Park Trust. The first permanent European presence was established in the mid-1600's when Dutch colonists settled the western end of Tortola. By the late 1600's, Britain took control of the islands. This ushered in the plantation era with the lucrative sugar, rum and slave trade. Following a brief period of unimaginable wealth for a few and unspeakable miseries for most, the islands entered into a long downward economic spiral. Changes in international politics and economies such as the decline of Spain's influence and the rise of Britain's sea power, the loss of value of sugar production and the abolition of slavery all contributed to the European abandonment of the BVI.

The newly emancipated slaves, lacking education or money, inherited a land stripped of valuable resources and largely depleted of the nutrients necessary for commercial agriculture. For more than a century the Territory languished with a subsistence economy. Small scale peasant agriculture and artisanal fishing provided the economic mainstay for the islands. Trade with nearby islands produced small returns and the area's chief export was labor. It was not until some years after World War II that the BVI began to build the twin pillars of its future economy; tourism and offshore banking. Through the determined efforts of a few farsighted individuals, the Territory's economic outlook gradually began to improve. Tourism, in particular, was embraced for its potential in providing employment opportunities for the local population. Paralleling the worldwide development in tourism, the BVI began to capitalize on its tropical climate and its excellent combination of sun, sea and sand. Within two decades the economy made dramatic improvements and with it, the expectations of the local populace rose.

Road cuts on east end of Tortola

Economic Onslaught

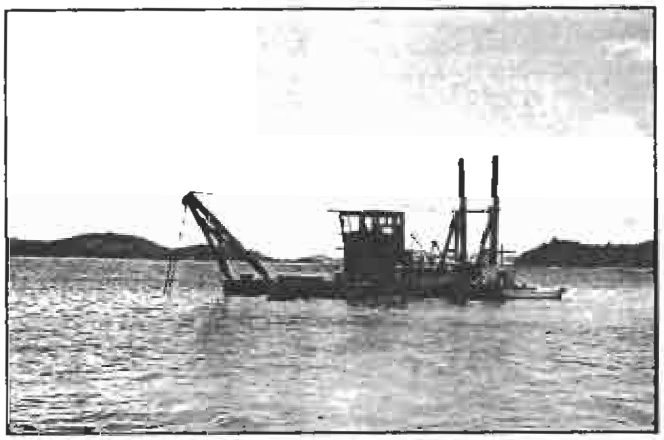
The new found economic success fueled desires to emulate the standards and lifestyle of the developed world. The rush toward growth proceeded without a master plan for development. Construction experienced a boom that has not yet subsided. Pressures for development of coastal areas escalated year by year. Lacking a comprehensive plan, zoning restrictions or development controls, an assault on the environment began on numerous fronts. Coastal wetlands were reclaimed at an alarming rate. New roads began to crisscross the islands. The road cuts, coupled with extensive construction projects forged ahead without proper environmental safeguards. Consequently, torrential rains on the steep slopes caused large-scale erosion. Following heavy rains, much valuable topsoil was washed into the sea contaminating once clear water.

This loss to the land also had catastrophic consequences to the marine environment where coral reefs and seagrass beds suffered repeated and often fatal smothering from land based sediments. Modern technological achievements allow local fishermen to use improved materials in traps, fish new areas farther afield and process, freeze and export their catch. As a result, populations of fish, crustaceans and molluscs were rapidly decimated. Without effective enforced fishing regulations, fishermen continued to overharvest virtually all species of marine life including endangered species of sea turtles.

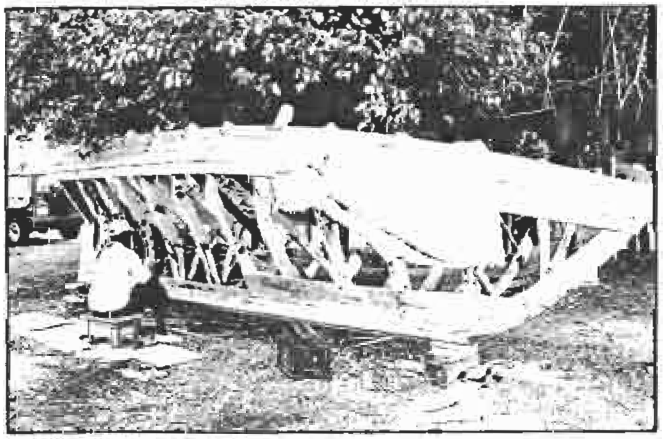
The economic onslaught has placed entire habitats at risk. Endangered species of endemic wildlife are poorly understood, lack protection and may become extinct before their plight is recognized. Already, at least one species of lizard, a bird and the Caribbean Monk Seal have been lost forever. One species of amphibian, a toad, not reported since the 1960's, is almost certainly extinct. Several additional species balance precariously on the brink of extinction. Natural habitats and indigenous species are threatened by the large-scale introduction of exotics, both intentional and accidental. Exotic plants imported for ornamental and agricultural purposes have introduced pest species of insects, mites and snails. Numerous viral, bacterial and fungal diseases are now established on the islands and causing considerable damage. Mongoose, feral goats and cats represent a monumental plague on fragile island ecosystems in the BVI and worldwide.

Coastal Development

The tourist industry, which caters largely to boating, yachting and diving interests needs a healthy, pristine marine environment. It is not surprising that the demands of the tourist industry come into conflict with the results of commercial activities along the coast. What little flat land exists, lies along the coast. Consequently, development pressures are greatest along the shore, especially in wetlands. Mangrove communities, estuaries, shallow water seagrass beds and coral reefs are particularly vulnerable. Since many of these ecosystems are close to the shore, they are easily affected by human activities. Many of the bays and littoral zones of the BVI contain alluvial and salt pond deposits. Thus, they are likely sites for reclamation projects.



Dredging in Fat Hogs Bay, Tortola



Local boatbuilder using an adze to build a Tortola sloop

Well over 75% of the mangrove communities on Tortola have been lost. The remaining few stands are under assault, either by slow piecemeal reclamation projects or by large-scale development plans. A classic example concerns a large healthy Red Mangrove forest that existed at Pockwood Pond on the south coast of Tortola. The mangroves were adjacent to the power station, incinerator, cement plant, rock quarry and various commercial ventures. The commercial interests needed to expand but available land was scarce. An "accidental" fuel spill killed most of the forest. Rather than clean up, replant and restore the mangrove community, permission was granted to reclaim the area as an industrial site. Furthermore, the reclamation efforts extended well out to sea beyond the limits of the mangrove forest. Coral reefs and all near shore marine communities were affected.

The largest stand of mangroves still intact lies on the south coast of Tortola at Paraquita Bay. This large semi-enclosed lagoon supports a healthy thriving mangrove ecosystem. The government has designated the bay an official hurricane shelter for boats and yachts and given mangrove protection a high priority. Nevertheless, trees are cut, presumably for the making of charcoal, and the shoreline is filled for human use. Effective enforcement of local environmental laws is sadly lacking.

Salt ponds have not fared much better. These "wastelands" that do nothing but "stink and breed mosquitoes" have also been filled or dredged for marina development. Few salt ponds remain intact.

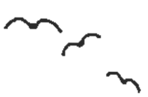
The need for raw materials for the construction industry encouraged the mining of beach sand in several locations. Josiah's Bay on the north coast of Tortola has been heavily mined for years. The result is disastrous for the beach and dune ecosystems in the area. Erosion by the sea, particularly during the winter months caused considerable habitat loss.

Extensive dredging at numerous locations in the islands provide fill for reclamation projects, sand for the construction industry and create channels and basins for shipping interests and the yachting industry. Dredging generally proceeds without the use of turbidity screens or other mitigation efforts. The impact on the surrounding marine communities has been devastating.

Waste Disposal

The problems associated with waste disposal are becoming acute in several areas. Sewage, solid waste disposal, oil, fuel and chemical contamination have become topics of concern and debate in recent years. The developing tourist economy has only exacerbated the problems. In general, per capita energy consumption and waste production is greater in areas dependent on tourism. Tourists require more water, more fuel for transport and activities and tend to prefer foods imported from their home countries. The resulting waste must be disposed by the host community. On small islands like the BVI, solid waste disposal consumes valuable flat land. The incinerator processes a large portion of the waste produced. However, abandoned cars, large appliances, batteries and much debris still litter the landscape. Recycling is of limited value because of the prohibitive costs of shipping recyclable materials to recovery or reprocessing centers.

Sewage treatment facilities are virtually non-existent. Most dwellings still use septic tanks while a few discharge their effluent directly into the environment. Until recently, a drainage channel functioning as an open sewer ran through downtown Roadtown, Tortola and emptied into Road Harbor. The noxious odors emanating from that channel became a potential health hazard and such an embarrassment to government, that it was finally covered. Few yachts or boats sailing in the BVI have or use holding tanks for their waste. In crowded



anchorages or marinas the sewage produced affects water quality. When yacht generated sewage is combined with run off, sewage and pollution from land, the result is often devastating to the marine environment. Two examples in the BVI include Virgin Gorda Yacht Harbor and Wickhams Cay in Road Harbor.

Unfortunately, even if boats were required to use holding tanks, not one pump out facility is currently operating in the BVI. Furthermore, no treatment facilities exist which can handle the effluent produced by the hundreds of charter yachts cruising the BVI waters every day. A few hotels, resorts and commercial enterprises have installed small scale sewage treatment plants. These are commendable efforts and deserve encouragement, but much larger, more comprehensive government mandated and supported projects are desperately needed.

Boatyards and yacht haulout facilities are environmental nightmares. Lacking government controls and exercising little self restraint, these businesses are caught in a catch 22 position where they cannot afford to initiate environmental safeguards while trying to survive in an increasingly competitive world. The result is that toxic anti-fouling paints, hazardous residues from painting, fiberglassing and other yacht work, including oil and fuel, foul the waters near boatyards. The detrimental affects on marine life can be seen by even the most casual observer. In addition, boatyards, and auto service stations have become storage areas for large quantities of used motor oils. This oil waste is often stored in metal containers which eventually corrode and spill their contents on the ground. Much of this oil finds its way into the sea. It is hoped that in the future most of this oil will be burned in the incinerator.

Environmental Management

It is against this backdrop of environmental deterioration that the future of the BVI must be planned. While development is likely to continue long into the foreseeable future, environmental concerns are becoming a high priority issue. Individuals and organizations are advocating new approaches to environmental management. As habitat loss and environmental degradation become more apparent, and occasionally critical, the collective voice of the community is beginning to be heard. Government is responding by providing support for environmental education, initiating monitoring programs, encouraging public cooperation and proposing legislation to protect the remaining natural resources. Nearly everyone recognizes the problems and the dire predictions for the future if no action is taken.

The economy of the BVI is based on tourism that markets a pristine environment. Advertising itself as "Nature's Little Secrets", the BVI is attempting to attract ecotourists. Yachting and diving are among the most popular activities attracting visitors to the islands. Both depend on healthy environments. The loss of these environments, or even the public perception of environmental degradation, would have dire consequences for businesses dependent on tourism. Any stagnation in tourism could reverberate throughout the economy very quickly and government would be hard pressed to remedy the situation.

The primary branch of government mandated to deal with the environment is the Conservation and Fisheries Department that functions under the Ministry of Natural Resources and Labor. With a staff exceeding a dozen individuals and headed by Bertrand Lettsome, the C&FD has wide ranging responsibilities. The Department is subdivided into two divisions, Conservation and Fisheries, each with different activities and responsibilities. Monitoring water quality throughout the Territory, sea turtle nesting studies and marine resource management represent a few ongoing efforts. As the official government representative, the C&FD is often the first agency to respond to an environmental problem. Oil spill response, pollution and wildlife issues are all under the jurisdiction of the Department. In addition, the C&FD patrols the marine environment aboard its own vessels or those of other governmental agencies. Environmental education programs for the public schools are frequently developed and implemented. Within the limitations imposed by finances and staffing the C&FD does a commendable job.

The National Parks Trust is an NGO that receives some government funding. Public education, establishing and maintaining protected areas and a boat mooring system are major activities of the NPT. The most popular parks and protected areas include the wreck of the RMS Rhone, a mass of huge boulders on the shoreline called the Baths at Virgin Gorda, The Copper Mine, the rainforest at Mt. Sage National Park and the J.R. O'Neal Botanical Gardens in Roadtown. Substantial resources are required to manage and maintain a park system that encompasses both terrestrial and marine habitats. The Trust's marine patrol boat, the Rhone Ranger, is used primarily to install and maintain the boat mooring system on popular dive sites throughout the BVI.

This mooring system, originally conceived, funded and implemented by the BVI Dive Operators in the mid-80's, now covers most dive sites in the islands. Well over 100 moorings are in use and plans call for more than twice that number. The value of moorings in reducing anchor damage to marine habitats is well documented. It is encouraging that the BVI has been a world leader in this area. In addition to the efforts by the National Parks Trust, private businesses and individuals have installed and used moorings in the BVI. One private company, Moor Seacure, Ltd. began installing moorings in 1983. With over 100 moorings currently in use, this company is at the forefront in demonstrating how a private enterprise can protect the environment and still make a profit.

In addition to the mooring project, the NPT is involved in reforestation programs, primarily on park lands. School groups, service organizations and private individuals all participate in tree planting activities. Efforts are also underway to establish a new national park on Anegada.

The Guana Island Wildlife Sanctuary is privately funded but works closely with government and NGO's. The Sanctuary's goal is to preserve the island ecosystems of the BVI. Toward this goal, visiting scientists from many countries conduct ecological research on land and in the sea.

Community College
The H. Lavity Stoutt Community College is a center for environmental education and research. This tertiary institution began offering classes in 1990. Since that time student enrollment has increased more than tenfold with new courses and programs introduced every semester. The College is funded primarily by government and enjoys broad community support. As the Territory's highest educational institution, the College is frequently called upon to provide scientific assessment and education in environmental matters.

Community involvement goes well beyond conducting scientific research and the teaching of courses. The College seizes every opportunity to serve the local population through enrichment programmes, technical guidance or collaborative projects. A public lecture series focuses on environmental issues. Whenever possible the College prefers to work with the NPT and C&FD on environmental matters. This cooperation covers both marine and terrestrial related issues.

In its efforts to serve the larger Caribbean region, the College has been designated a Centre of Specialization in Marine Studies by the Organization of Eastern Caribbean States [OECS]. This designation helped secure OECS funding for the pending construction of a Marine Science Center. While the marine studies programme is intended to focus on the yacht tourism industry, environmental issues are also a major consideration. The marine science center is envisioned as a resource for the local community with a sphere of influence that will extend throughout the Caribbean region and beyond. Marine related projects and interests of the science faculty include mangrove reforestation, hypersaline pond ecology, Queen Conch biology, artificial reef construction, reef monitoring and fish population studies to name but a few.

H. Lavity Stoutt Community College, Paraquita Bay Campus

Aquaculture has recently been introduced into the islands to provide additional sources of income for the population and to help reduce fishing pressure on the reef fish communities. This project started with the introduction of hybrid varieties of Tilapia, particularly *Oreochromis mossambicus*. This fish was stocked in small ponds used by farmers to irrigate crops and water livestock. Since the BVI lack significant fresh water ecosystems, the introduction of Tilapia pose little threat to native flora and fauna. Future plans call for the mariculture of marine algae, mollusks, crustaceans and fish. Several projects have been proposed and are under consideration.

Chief livestock officer with local farmers introducing Tilapia into fish ponds

As a project linked to the International Year of the Reef, Reefcheck 97 evaluated the current status of coral reef health throughout the world. The BVI's involvement was first proposed by the Association of Reef Keepers [ARK], and the project gained momentum and considerable public support. Scientific leadership was provided by College faculty and the International Center for Living Aquatic Resource Management [ICLARM] office in Tortola. Reefcheck enlisted dive shops, local SCUBA divers and many enthusiastic individuals. In the future the BVI plans to build on this success by participating in the Global Coral Reef Monitoring Network [GCRMN].

The BVI has long depended on technical expertise from outside sources. Despite intensive educational efforts by the College and other organizations, the needs are too great to be met by such a small population. Consequently, numerous environmental projects are funded and staffed from external sources, most often the UK. One such project currently underway is funded by ICLARM. Under the direction of John Munro and Maggie Watson, this study focuses on larval recruitment of coral reef fish populations. As part of a long term investigation, it seeks to understand the dynamics of population change in important commercial species of fish.

On the terrestrial side, significant steps are being taken to restore natural habitats and prevent the extinction of endangered flora and fauna. College staff are working with the NPT to protect and preserve the Anegada Rock Iguana which faces extinction from habitat loss and competition from feral goats This effort has several facets including the creation of a national park on Anegada. This important project is facing considerable local opposition. Issues related to land ownership and rights of use are of great significance to the native Anegadians. Until the problems surrounding the land ownership issues are resolved, most locals will oppose the creation of any park, protected area or environmental project. They generally insist that their long standing demands be given first priority. Numerous political issues must be solved before a park could have any chance of success.

The reintroduction of Flamingos to the Anegada salt ponds has been hailed as a resounding success. Flamingos, once abundant throughout the islands, were extirpated as a breeding species early in the 20th century. Through the combined efforts of the NPT, Guana Island Wildlife Sanctuary, Bermuda Zoo, Conservation Agency and others, a small flock was reintroduced nearly a decade ago. The birds quickly adapted to their new surroundings and responded to the abundant food supply. Within a few years, courtship and nest building was observed. In 1995, breeding members of the flock successfully fledged five young. With the occasional arrival of transient Flamingos, the flock now exceeds 20 birds and further increase is expected.

The reintroduction of additional extirpated species is underway. White-crowned Pigeons have been released at the Guana Island Wildlife Sanctuary and additional species will be reintroduced in the future. Attempts are underway to build enclosures to protect young iguanas during their most vulnerable period. The idea is to release the headstarted animals in fenced areas where feral competing livestock is excluded.

Members of the student Nature Club have joined with the Department of Agriculture to begin a native plant nursery. The use of native plants, rather than exotics, will be encouraged wherever new landscaping is planned. Such plants can also be used in habitat restoration projects, particularly when re-establishing native animals like the Anegada Rock Iguana.

Preventing the extinction of additional flora and fauna is the goal of an Endangered Species Restoration Project. Ecological research into the life history needs of rare species is used to develop captive breeding programmes. Offspring produced by this effort can be used to rebuild wild populations and restore natural habitats.

Growing Environmental Awareness

Numerous additional environmental initiatives are underway and the Anegada Horseshoe Reef protected area deserves special mention. As the largest coral reef system in the BVI, and one of the largest in the Caribbean, its value cannot be overstated. Several years ago, the government declared the entire reef area off limits to commercial and recreational activities. Patrolled by the Conservation and Fisheries Department, the protection seems to be working. Although some fishermen are still permitted to work the waters, most of the reef remains undisturbed.

Meanwhile, the local government has taken steps to deal with the growing problem of sewage disposal. The first public sewage treatment facility will be constructed at Cane Garden Bay on the north shore of Tortola. This moderately populated bay is lined with houses, hotels, restaurants and bars which service the many pleasure yachts stopping every day. Discharges from the boats combined with run off from the land has significantly reduced the water quality. Periodic algal blooms discolor the water and discourage the visiting tourists. Public opinion is firmly behind efforts to preserve the water quality along Tortola's most popular beach.

Private businesses have also made strides in environmental protection. Some have taken pride in demonstrating how a business can make a profit while preserving the quality of the environment. A case in point may be found at Hodges Creek in Tortola. Two adjacent marinas have adopted vastly differing views on environmental awareness. The marina developed by Tropic Island Yacht Management exercised considerable care in preserving the mangrove fringe along the shoreline. Docks were constructed outside the mangroves with few access points through the trees. Dredging was controlled and at some distance from the mangroves to minimize disturbance. The result permitted the operation of a successful business while saving a valuable mangrove ecosystem. The adjacent marina project has removed all shoreline mangroves in its reclamation and is proceeding with virtually no environmental safeguards.

Hodges Creek, Tortola. Tropic Island Yacht Management on left. Dredging without environmental safeguards in the foreground

The British Virgin Islands was catapulted from a sleepy third world economy to the mainstream of the 20th Century experience within the timespan of a generation. The problems of environmental degradation are more severe when space is limited. With a small land mass and population, the Territory was ill prepared for the hordes of tourists and rampant development of modern times. As the economy boomed, the environment suffered. The seriousness of the problems and the speed with which they arrived caught government and the people by surprise. Yet, despite the problems, hope is on the horizon. Government, supported by NGO's and a concerned citizenry, is taking steps to meet the challenge. While the problems surrounding the environment are complex and often political, everyone recognizes the need for action.

The B. V. Islanders want a clean healthy environment for themselves, and for their children. It is the responsibility of the current generation to hold the environmental future as a sacred trust. Most in the BVI believe that a clean, healthy environment is the way to remain "Nature's Little Secrets".